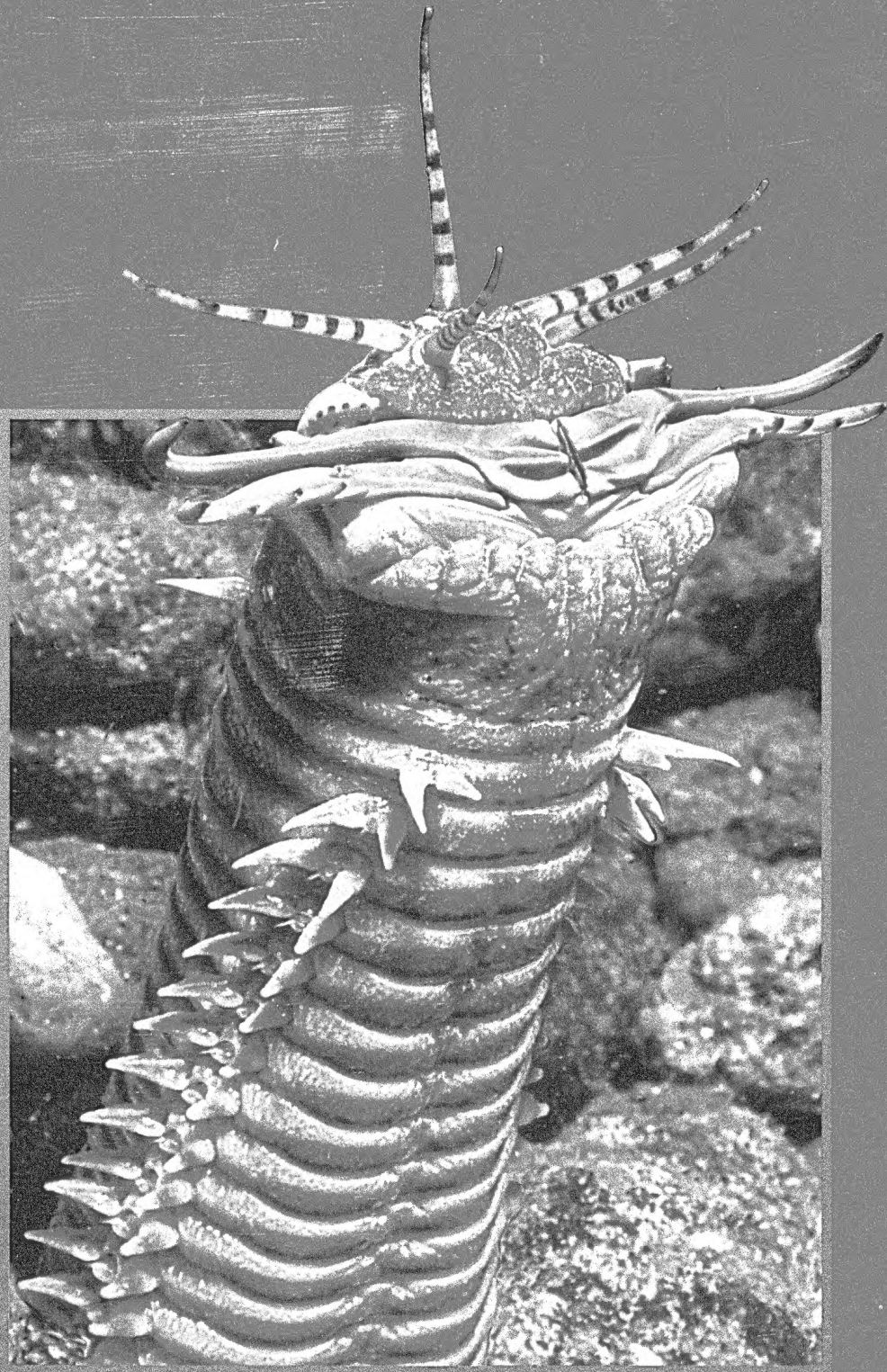




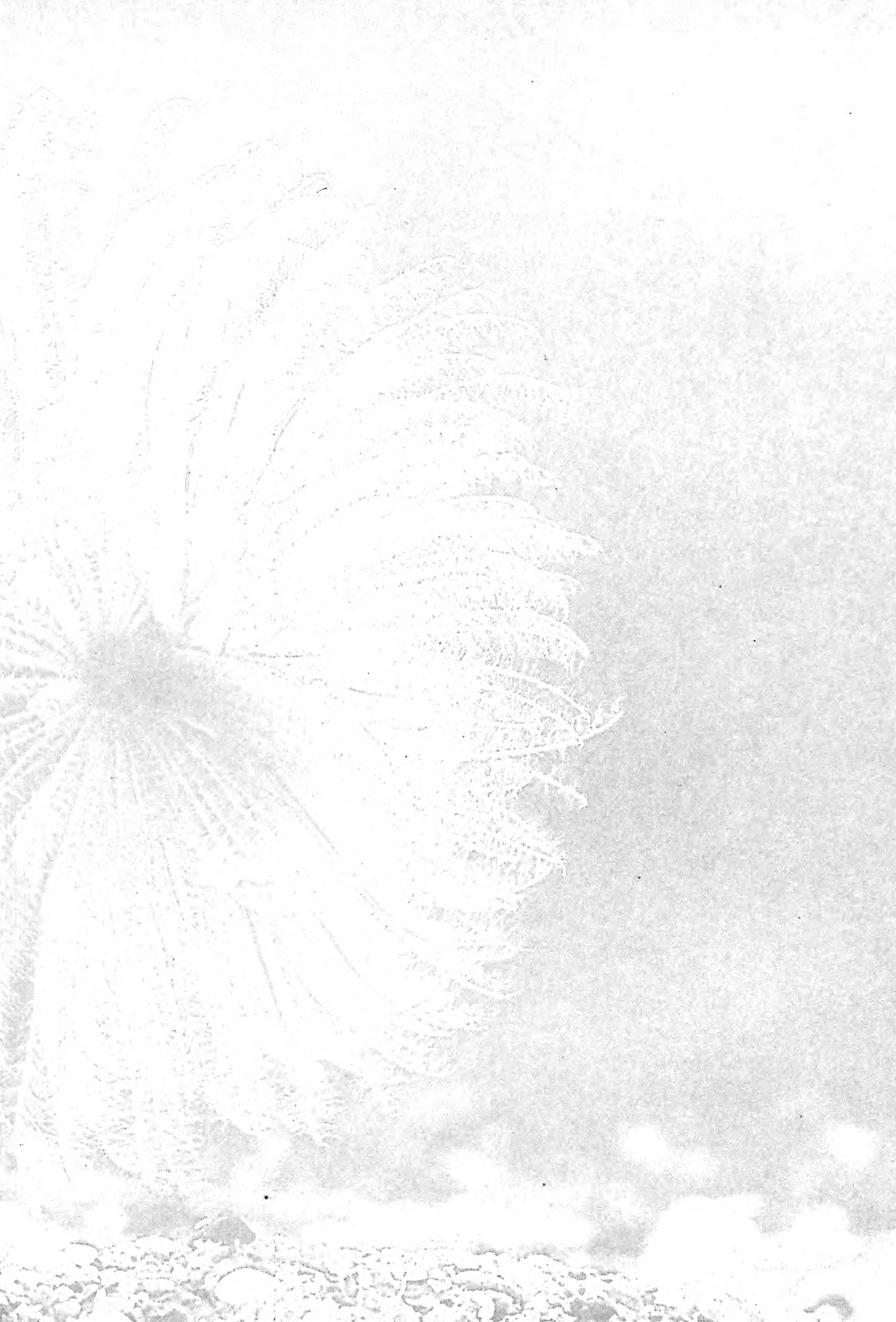
POLYCHAETES & ALLIES

The Southern Synthesis



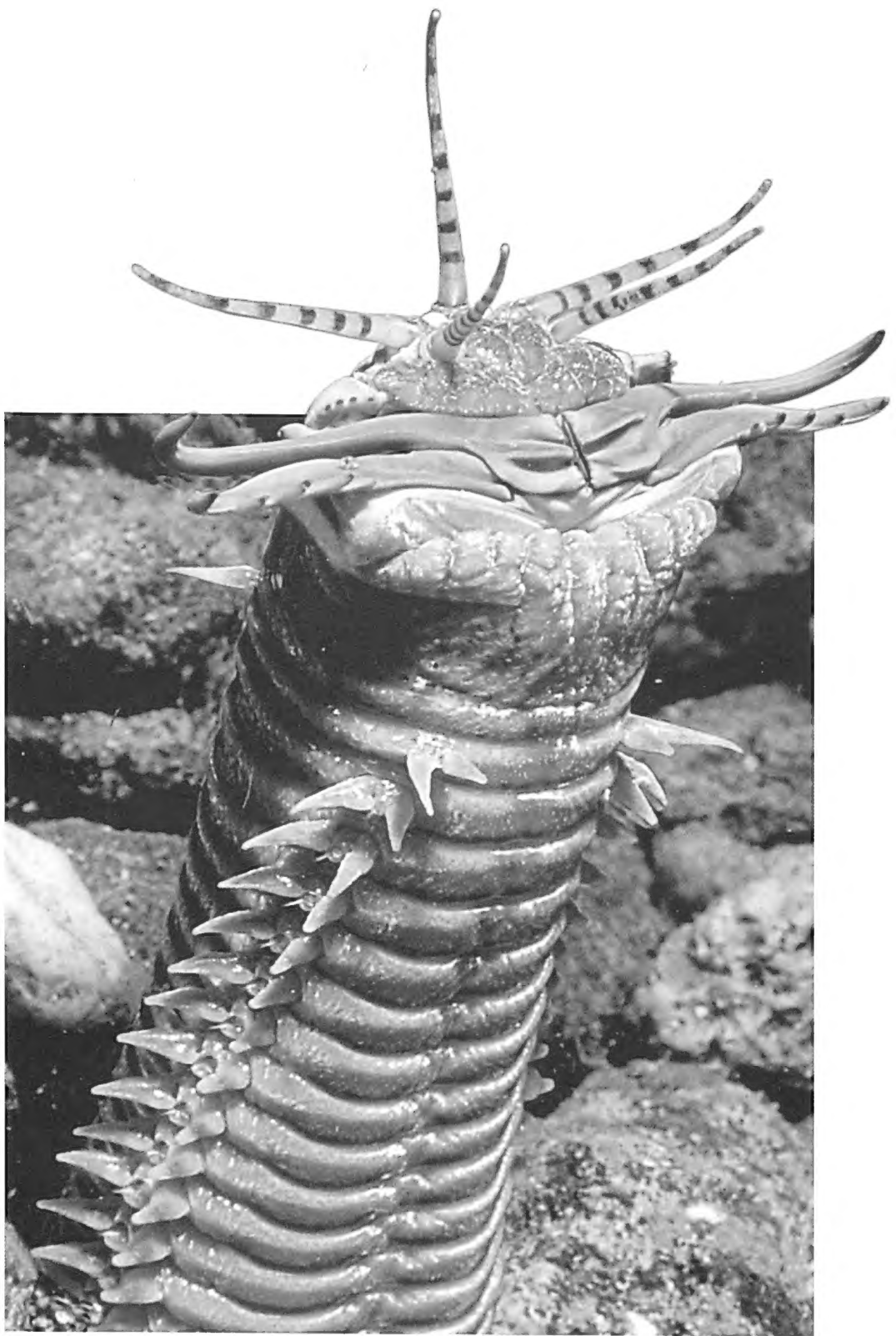
FAUNA OF AUSTRALIA
VOLUME 4A POLYCHAETA, MYZOSTOMIDA,
POGONOPHORA, PHTHURA, SIPUNCULA





POLYCHAETES & ALLIES

The Southern Synthesis



At night, *Eunice aphroditois* (Eunicidae) emerges from its burrow to feed and awaits, with open jaws, for prey. Once it has been detected and is within range, the jaws will snap shut, and the prey is then drawn into the buccal cavity. These worms feed on a variety of invertebrates including crustaceans and also algae. When they detect vibration they withdraw rapidly into their burrow. They are found on shallow coral reefs and may reach lengths of 1–2 metres. [Roger Steene]

Back cover: Yangarriny Dalwangu (1932-) Northeast Arnhem Land, Northern Territory. **Ancestors of the Yirritja moiety** circa 1979. Ochres on *Eucalyptus bark* (155.0 x 56.0 cm). Collection: Australian National Gallery, Canberra.

Australian Biological Resources Study, Canberra



POLYCHAETES & ALLIES

The Southern Synthesis

FAUNA *of* AUSTRALIA

Volume 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula



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Endpapers. *Sabellastarte australis* (Sabellidae), shown with its tentacular crown extended, is one of the most common feather-duster worms along the east coast of Australia. It occurs in lower intertidal and shallow subtidal areas and is a frequent inhabitant of rock pools. The crown is 20–50 mm in diameter. [K. Atkinson]

Background to colour Plates. *Protula* species (Serpulidae), showing its tentacular crown extended from its calcareous tube. The crown functions as a feeding organ and is also involved in respiration; it reaches 5–10 mm in diameter. A well-developed blood vessel carrying erythrocrurin is present along each radiole of the tentacular crown. [K. Atkinson]

PREFACE

The *Polychaetes & Allies*, the second volume on Australian invertebrates in the *Fauna of Australia* series, is notable in a number of ways. The largest taxon, Polychaeta, provides the primary focus for the volume. It is referred to the traditional Linnaean rank of Class in the Contents for the volume, although there is debate over whether this rank, or indeed whether a Linnaean ranking system *per se* can be applied usefully to the annelids. In keeping with this trend, such ranks are generally avoided in the polychaete treatment.

Polychaetes are strongly represented in the Australian region (within Australia's Exclusive Economic Zone, its islands and the Australian Antarctic Territory) where 67 of 81 families known worldwide are recorded (see Appendix 1). Several of the unrecorded families are pelagic, and are included because they occur in New Zealand; however, these 14 families have little import globally, representing in all less than 0.7% of all polychaete species. In this context, the present treatment of Polychaeta is the most comprehensive account ever published. Its focus is Australian, but the volume has strong international relevance through inclusion of 83% of polychaete families and liberal use of appropriate extralimital examples.

Below family level, regional diversity is considerable. Some 420 genera and 1139 species have been recorded, 11% of which await description in Australian museum collections; undoubtedly far more new species await collection, particularly from the continental shelf and beyond.

Polychaetes are most important ecologically. They occur in a wide range of habitats, from inland salt and fresh waters to the ocean floor, where our knowledge of diversity is most limited. They dominate marine and estuarine soft bottom benthic communities in terms of numbers of species and individuals, and are abundant in all other benthic communities. They exhibit a range of feeding strategies and are critical in marine food chains, as important prey for many crustaceans, molluscs, fish, wading birds and other organisms, and as predators in their own right. Polychaetes play a major role in the breakdown, subduction and incorporation of organic matter into sediments and their aeration. Because of their ubiquitous distribution, the species composition of polychaetes in a benthic community can indicate the 'health' of that community; increasingly, polychaetes are useful pollution indicators. Some species are economically important as bait for amateur fishers, as serious fouling organisms or as pests of commercial shellfish.

Treatment of the Myzostomida and Pogonophora as separate entities may seem anomalous, as current views on their taxonomic status range from Phylum or Class level to simply single families within the Polychaeta. This range of views is represented here. The arrangement of taxa reflects primarily the initial request to authors for texts on Myzostomida and Pogonophora as classes; the editors were influenced also by the value of publishing in full the first complete review of myzostomes in English. In the Polychaeta, family level treatments of myzostomes and pogonophores are cross-referenced to the separate treatments.

Myzostomida are diverse, with over 100 species in northern Australia. Pogonophora are recorded in Australian waters for the first time. Only a few unnamed species of perviate pogonophores have been made; Monilifera or Vestimentifera have yet to be recorded. The diversity and biology of Australian sipunculans are comparatively well-known, largely through the efforts of the late Stan Edmonds. Some 39 Australian species, representing all six families, have been described; their affinities are largely Indo-West Pacific. Echiurans are poorly known in comparison, Edmonds recording 13 species in three families for the group.

This volume accords with the primary role of the *Fauna of Australia* series, providing authoritative syntheses of the primary zoological literature across the fauna to family level, for the benefit of a broad, non-specialist clientele. The text, sourced from 2370 such papers, of which 80% are on polychaetes, provides overviews at phylum or class and family level on Morphology & Physiology, Natural History and Biogeography & Phylogeny. The glossary minimises the need for reference to specialist literature. The numerous illustrations, almost all commissioned for this volume, are based primarily on Australian material.

The Australian Biological Resources Study thanks all who contributed to the development of the volume. The entire team of authors contributed well beyond their initial brief, with consistent advice and enthusiasm for the project. Pat Hutchings provided invaluable technical advice throughout from planning to completion; Chris Glasby contributed enormously in terms of text, the glossary, written jointly with Kristian Fauchald and Pat Hutchings, and as an editor. These contributions were balanced by the equally enthusiastic and exacting reviewers who ensure the quality of the volume's content: David George (Polychaeta, The Natural History Museum, London); Igor Eeckhaut (Myzostomida, Université de Mons, Belgium); Verena Tunnicliffe (Pogonophora, University of Victoria, Canada); Teruaki Nishikawa (Echiura, Nagoya University, Japan) and Edward Cutler (Sipuncula, Harvard University, USA). The illustrators' skills are reflected in the beautiful line art throughout the volume, contributed by Anna Murray (Australian Museum, Sydney), Kate Nolan (Museum Victoria, Melbourne) and Ian Grant (Norwood, South Australia); Anna also checked the polychaete figures and their captions. Photographers Kathie Atkinson, Gary Bell, Karen Gowllett-Holmes, Nigel Holmes, Michael Marmach, Leslie Newman & Andrew Flowers, Greg Rouse, Roger Steene and Bill Wood clearly reveal the hidden beauty of these animals. Pat Hutchings and Kate Attwood (Australian Museum), with help from Alex Muir (The Natural History Museum, London) and Linda Ward (National Museum of Natural History, Washington), thoroughly checked the polychaete references. Linda Ward and Kristian Fauchald arranged for the loan of Kinberg (1857, 1910) for preparation of plates of his Australian types. Rick Johnson (Australian Museum) extracted polychaete distributional data from the Museum's database. Jose Saiz Salinas (Univ País Vasco, Bilbao) identified the sipunculan genera in the colour photographs, and Edward Cutler, Peter Gibbs (Marine Biological Association, Plymouth) and Rudi Scheltema (Marine Biological Laboratory, Woods Hole) checked sources of artwork for the Sipuncula.

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Authors' contributions are listed here with page numbers as a ready source of reference for purposes of citation. Its primary purpose is to ensure that authors receive due recognition for their contribution. Examples of citations are provided on page iv.

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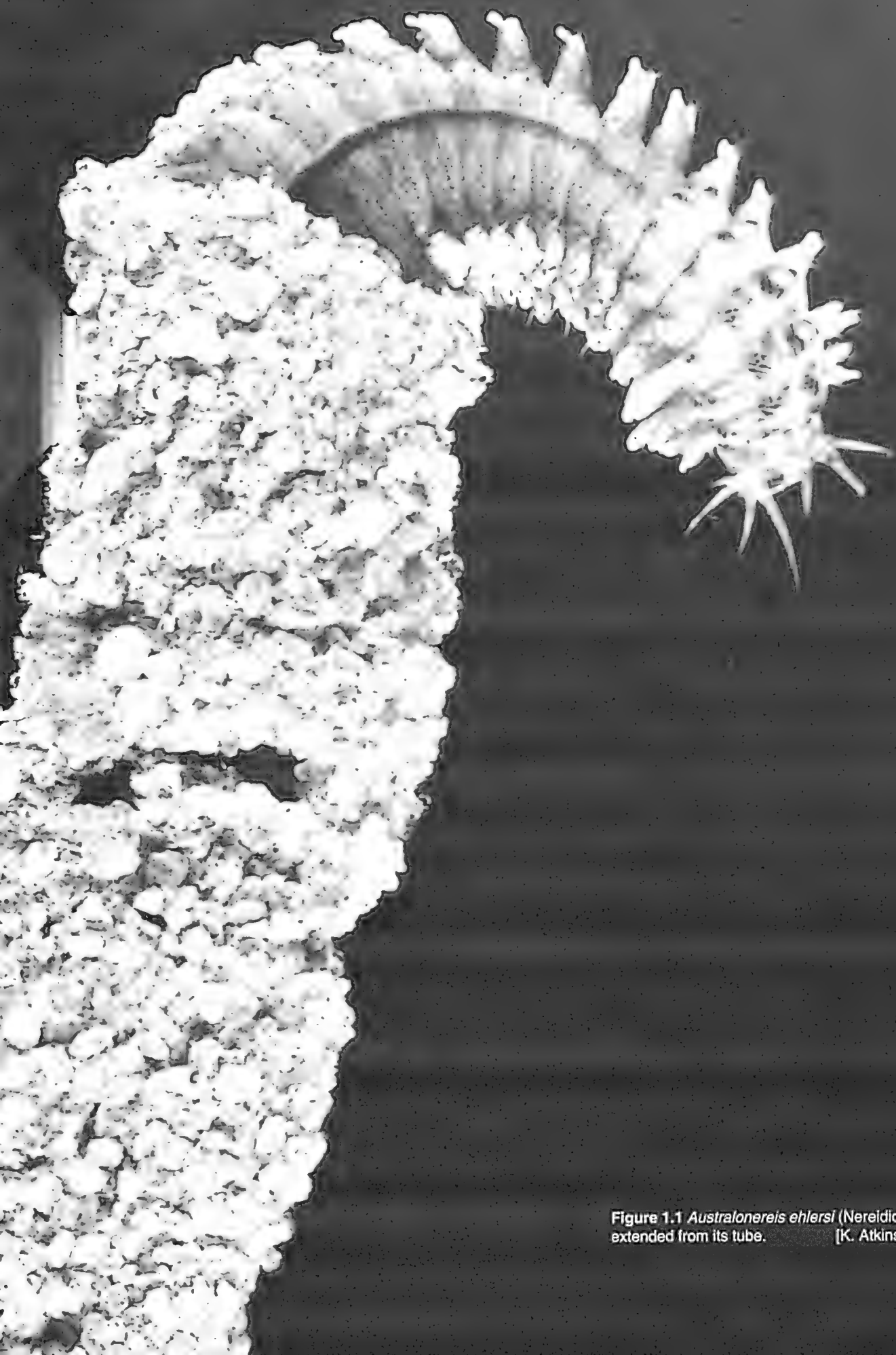


Figure 1.1 *Australonereis ehlersi* (Nereididae)
extended from its tube. [K. Atkinson]

1. CLASS POLYCHAETA

Christopher J. Glasby, Patricia A. Hutchings, Kristian Fauchald, Hannelore Paxton,
Gregory W. Rouse, Charlotte Watson Russell & Robin S. Wilson

DEFINITION AND GENERAL DESCRIPTION

Polychaetes, like other members of the phylum Annelida, consist of two presegmental regions, the prostomium and peristomium, a segmented trunk (metastomium) and a postsegmental pygidium (Figs 1.1, 1.8; Pls 1.1–9.4). The nuchal organs, a pair of chemosensory structures on the postero-lateral margin of the prostomium, are apparently the only synapomorphy of the Polychaeta which distinguishes them from other Annelida (Rouse & Fauchald 1995). Nuchal organs vary from well-developed posteriorly projecting loops to inconspicuous pits or grooves (Fig. 1.2). The largest nuchal organs are found in the Amphinomidae and the Euphrosinidae, where the ciliated folds on the caruncle represent the nuchal organs (Fig. 1.2A; Purschke 1997). Rouse & Fauchald (1995) suggested that Annelida can be a monophyletic taxon only by assuming that chaetae arose independently on the Echiura and the 'Annelida'. Subsequently, Rouse & Fauchald (1997) found that the Annelida was monophyletic, though weakly supported, and consists of the Clitellata and Polychaeta.

Polychaetes usually have a well-defined head with sensory and/or feeding appendages, followed by numerous body segments which may be differentiated into thoracic and abdominal regions. Typically, each segment bears a pair of parapodia and associated chaetae. However, considerable morphological variation is found amongst polychaetes, often reflecting the diversity of life styles of these animals. For example, capitellids that burrow through sediments tend to have few, if any, sensory or feeding appendages and reduced parapodia, whereas nereidids that crawl actively over the substratum have well-developed sensory appendages and parapodia (Fig. 1.3). Also, species of the terebellid genus *Hauchiella* have a distinctly terebelliform body (enlarged thorax, tapering abdomen), but differ from most other tube-dwelling terebellids (and other polychaetes) in lacking chaetae; they live naked in fine sediments associated with coralline algae of New Zealand's rocky shores; this genus occurs in Australia, but precise habitat data is not available. Members of pelagic families are often very different structurally from closely related benthic groups, in having large well-developed eyes, expanded foliaceous parapodial lobes and almost transparent bodies. Many of the features characteristic of polychaetes are lacking or reduced in interstitial, small-bodied forms making their familial affinities obscure; anterior appendages, parapodia, chaetae and internal features such as circulatory systems and nephridia may be lost or modified compared to larger relatives.

Numerous other 'characteristic' traits are present in members of the Polychaeta. In many taxa, especially active ('errant') predators, antennae and palps are present on the prostomium. The sensory antennae are innervated by single tracts from the forebrain, whereas the paired palps are innervated by double tracts either from the posterior part of the brain or from the nerve ring passing around the foregut. Palps and antennae may appear externally similar, but the former usually emerge from a more ventral position on the prostomium and are often more robust. Palps range in form from paired grooved ciliated feeding appendages in spioniforms to paired sparsely ciliated, ovate or circular (in cross section) sensory appendages in the Phyllodocida, to forming the numerous appendages of the tentacular crown in the Sabellida (Fig. 1.10). The peristomium may bear tentacular palps (paired or multiple) or fleshy cirri (cirri may be absent). Many of the prostomial and peristomial (head) appendages present in 'errant' species are lacking in tube dwelling or burrowing 'sedentary' species.

The anterior region of the digestive tract, the buccal organ, contains the buccal cavity which leads anteriorly to the mouth. In many polychaetes, an eversible non-muscular proboscis forms the anterior part of the buccal organ. In many groups, the buccal organ is in a ventral position and may be either heavily (Fig. 1.14D) or poorly muscularised. Other groups such as nereidids, nephtyids and glycerids have an axial buccal organ and a well-developed associated musculature (pharynx; Fig. 1.14A, B), whereas in others the buccal organ may be soft and sac-like (Fig. 1.14C, H; Dales 1962a). The buccal cavity may have a sclerotinised lining and hardened teeth-like structures or jaws (Fig. 1.14B, F, G). In other taxa lacking a buccal organ, the anterior gut is a simple tube without any obvious modifications (Fig. 1.14E).

Most species have paired, segmentally arranged, fleshy parapodia which differ greatly in size and structure, reflecting their various functions of anchorage, gas exchange, locomotion and protection. Parapodia are usually biramous, consisting of a dorsal ramus (branch), the notopodium, and a ventral one, the neuropodium, each of which may carry bundles of chaetae (Fig. 1.11); the notopodial ramus is often reduced in size. The chaetae are highly specific and greatly diversified. Several different types of chaetae may be present in each species, but in nearly all taxa unjointed, tapering chaetae (capillaries) are present. One stout internal chaeta (acicula) may be present in each ramus; they are used to support the parapodia, especially in taxa where the parapodia are well developed. Anteriormost segments may be cephalised during ontogeny and usually involves the modification of associated parapodia and the loss of chaetae; often the parapodial cirrus remains and becomes elongated, forming a tentacular cirrus.

1. CLASS POLYCHAETA

The circulatory system is closed in most taxa, but may be reduced or missing. Branchiae may be present or absent; in species lacking branchiae it is thought that respiration occurs across the body wall. Nephridia are most often metanephridia, but protonephridia occur, especially in species with reduced circulatory systems.

Polychaetes exhibit a wide range of reproductive strategies and even within a family several may be found. They are typically dioecious, but many species are hermaphroditic. Both sexual and asexual reproduction occurs within the group. Gametes are proliferated from the germinal epithelium which is typically attached to the septa of the anterior segments. In most cases, the gametes are released into the coelom where they develop; occasionally all development occurs on the germinal epithelium. At the time of spawning the gametes are usually released to the exterior via gonoducts, although in some species the body wall ruptures releasing all the gametes; in these species, the animal does not survive spawning. Polychaetes exhibit a wide range of spawning periodicity, from every few weeks, to breeding annually either once (monotelic) or for several years (polytelic) After fertilisation, a free-swimming larval trochophore stage may be produced or a brooded larval stage which develops directly into a juvenile. Asexual reproduction is also variable. In some species, the animal splits into individual segments each of which develops into a new individual, or the body may split into a number of fragments each of which develops into a new individual.

Most polychaetes live in the marine environment and are well represented in every benthic habitat from estuarine muds and sands to coral and rocky reefs to the muds of the deep sea. They also occur in the pelagic environment as meroplankton and holoplankton. Several families are represented in freshwater, but only the aeolosomatids and the morphologically similar potamodrilids appear to be better represented in freshwater than in the marine environment. A few species, including some nereidids and the very small-bodied *Stygocapitella*, live in rotting vegetation on the seashore and beside rivers. In these cases, the environment is usually very wet, often completely water-logged, so the terrestrial nature of these taxa is more apparent than real. Parasitic polychaetes are also known and are found in a number of families including Eunicidae, Oeonidae and Sabellidae (*Caobangia* species). Recently, a parasitic species of the pelagic family Typhloscolecidae was found living on a chaetognath (Øresland & Pleijel 1991).

The definition of the Polychaeta has been expanded recently to reflect the recent advances in our understanding of the phylogeny of the group (see Fauchald & Rouse 1997; Rouse & Fauchald 1997). Apart from those families traditionally included in the group (see for example, Fauchald 1977), Fauchald & Rouse have suggested that the aeolosomatids and potamodrilids (until recently considered clitellates), the myzostomids, and the pogonophorans (including the vestimentiferans) should also be included (see Phylogeny for further discussion). The recent classification of Rouse & Fauchald (1997), with a few exceptions, is followed here (see Table 1.3). The Myzostomida and Pogonophora are treated separately (see Chapters 2 and 3 respectively).

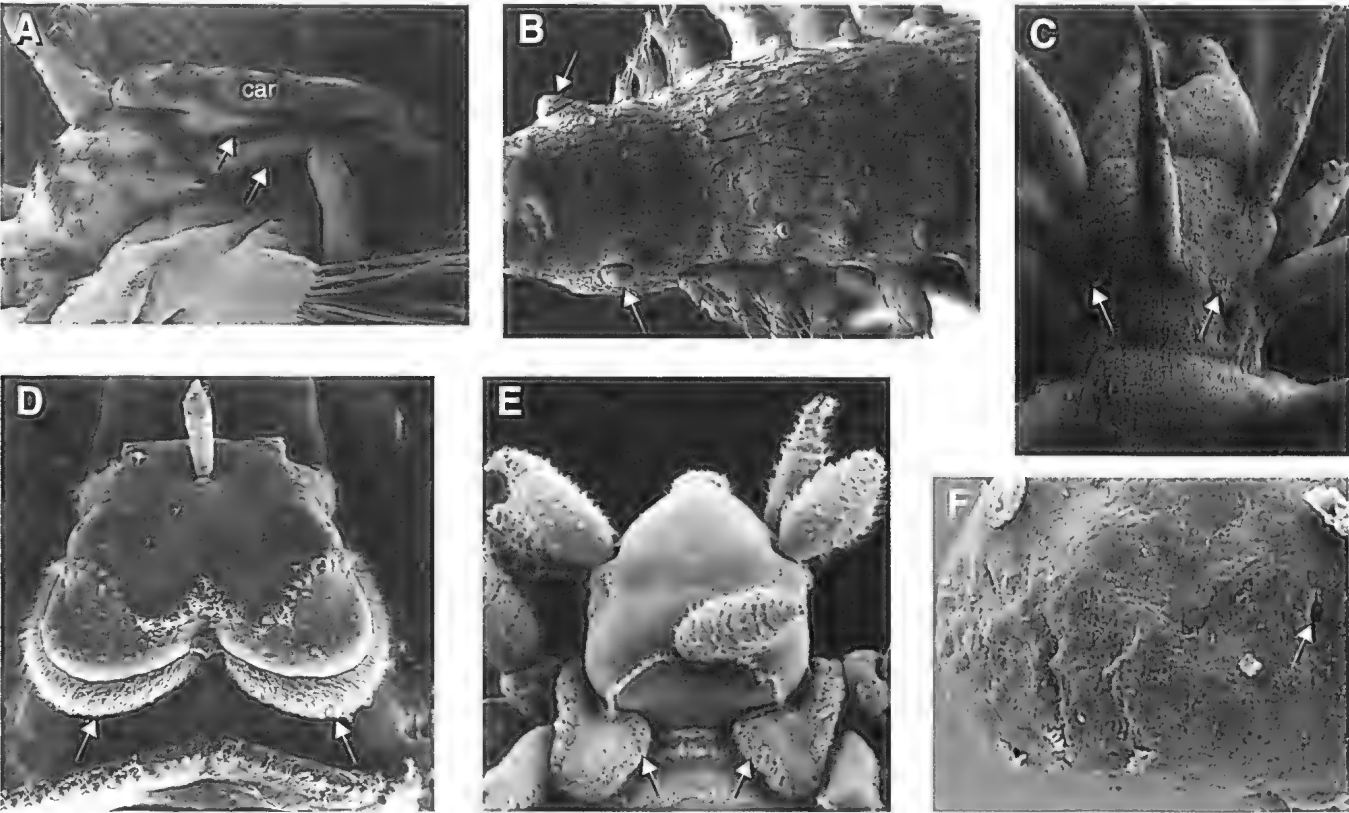


Figure 1.2 Polychaete anterior ends showing nuchal organs. **A**, well-developed nuchal organs comprising a continuous ciliary band adjacent to the caruncle, dorso-lateral view of *Eurythoe complanata* (Amphinomidae); note only one loop of the nuchal organ is shown. **B**, everted cone-shaped nuchal organs, dorsal view of *Glycera convoluta* (Glyceridae). **C**, small inconspicuous dorso-lateral nuchal organs, dorsal view *Brania subterranea* (Syllidae). **D**, postero-lateral crescent-shaped nuchal organs, dorsal view *Gyptis propinqua* (Hesionidae). **E**, nuchal organs on the fringes of nuchal epaulettes, dorsal view of *Notophyllum foliosum* (Phyllodocidae). **F**, nuchal pits, dorso-lateral view *Stygocapitella subterranea* (Parergodrilidae); note only one nuchal pit is shown. Arrows indicate the nuchal organs. car, caruncle. (A–C, F, from Purschke 1997; D, from Pleijel 1998; E, from Pleijel 1993)

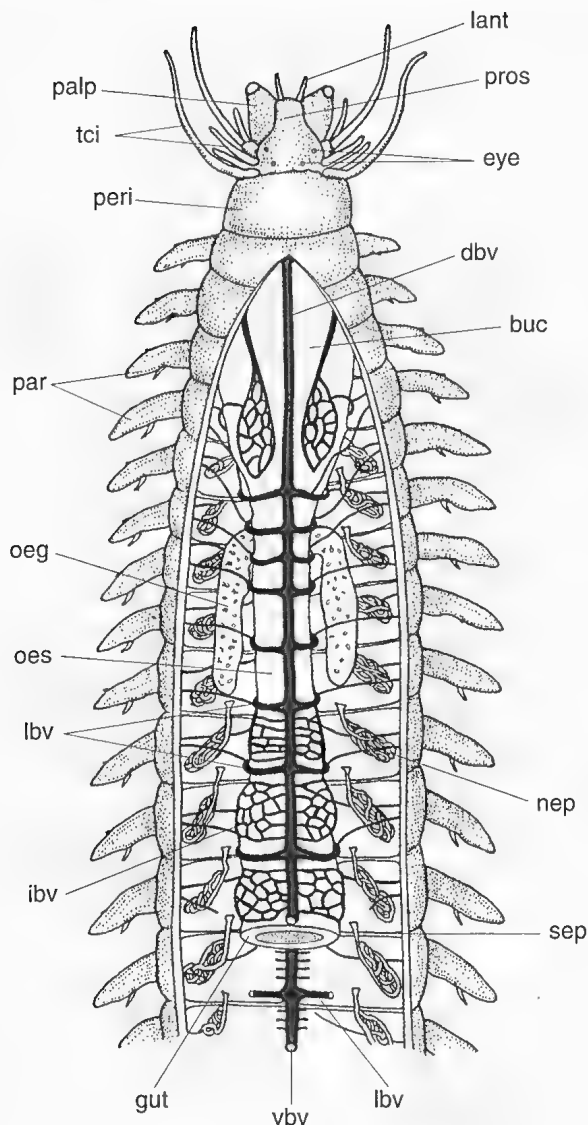


Figure 1.3 An anterior end of a nereidid showing the arrangement of internal and external features. **buc**, buccal organ; **dbv**, dorsal blood vessel; **eye**, eyes; **gut**, gut; **ibv**, intestinal blood vessels; **lant**, lateral antenna; **lbv**, lateral blood vessels; **nep**, nephridium; **oeg**, oesophageal gland; **oes**, oesophagus; **palp**, palp; **par**, parapodia; **peri**, peristomium; **pros**, prostomium; **sep**, septum; **tci**, tentacular cirri; **vlv**, ventral blood vessel. (After Brown 1950)

Worldwide, about 13 000 polychaete species have been described, although only 8000 of these are considered as 'reasonable' (K. Fauchald personal observation). Snelgrove *et al.* (1997), based on the work of Grassle & Maciolek (1992) and Mackie, Parmiter & Tong (1997), suggested that polychaete biodiversity may be as high as 25 000 to 30 000 species. Some of the highest numbers of species of polychaetes in soft sediments, found anywhere in the world, have been recorded from southern Australia (Poore & Wilson 1993). Coleman, Gason & Poore (1997) collected 800 species of macrofauna, of which 24.4% were polychaetes, in just 10 m² of sediment in Bass Strait. Also 700 species, of which 33% were polychaetes, have been recorded from the sediments of nearby Port Phillip Bay (Poore, Rainer, Spies & Ward 1975). Certainly a large number of undescribed taxa remain in Australian waters as nearly every recently published faunal survey and revision demonstrates.

HISTORY OF DISCOVERY

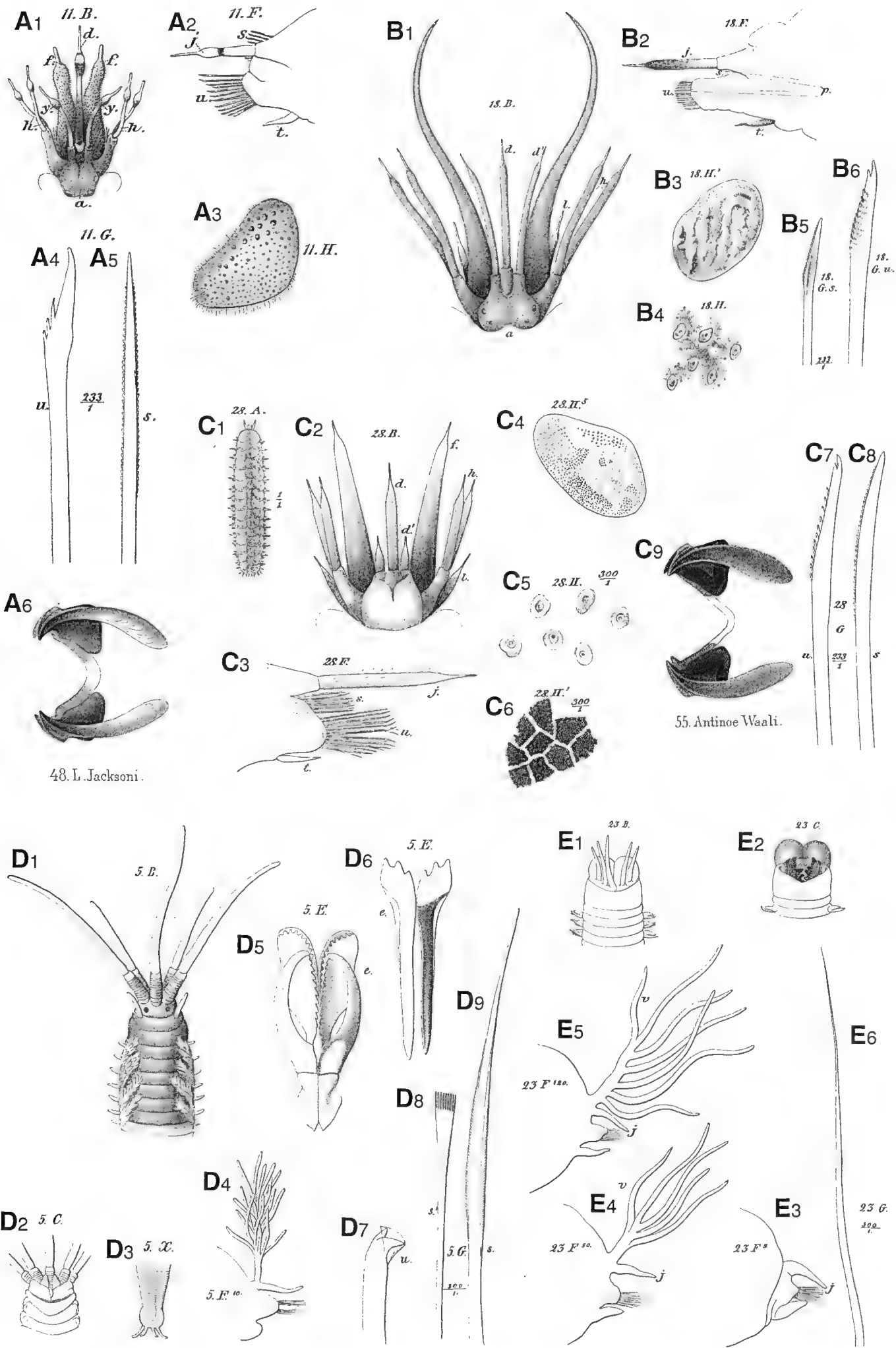
The first description of a polychaete recognised for taxonomic purposes is found in Linné (1758). During the following 100 years or so polychaetes were part of the large, loosely defined group called Vermes which is no longer considered valid. Early descriptive and classificatory work of great importance can be found in the writings of Lamarck (1818) and Cuvier (1817) and in the overview of the French fauna summarising the state of knowledge at about 1830 issued by Audouin & Milne Edwards (1834). Ashworth (1912a) discussed the early history of scientific polychaete exploration elegantly. The pre-scientific history of polychaete description was treated in more detail by Hempelmann (1937).

Grube first formally recognised the polychaetes as a uniform group in 1850. Within the Annelida he defined five orders. The Appendiculata contained all polychaetes known at the time, excluding the genus *Tomopteris* which was placed in a separate order, Gymnocopa. *Peripatus*, considered an annelid at that time, was placed in the order Onychophora, but is now recognised as a separate phylum. Grube's two last orders, Oligochaeta and Discophora, contained the oligochaetes and leeches respectively, which are now united in the class Clitellata. A few, extremely poorly known forms, such as those in the genus *Tibiana*, which was based on eunicid-like tubes, were considered to be coelenterates and excluded from the Appendiculata. Grube subdivided the Appendiculata into two suborders, Rapacia and Limivora, so named to reflect the modes of feeding, but included a variety of structural characters in defining them. Members of the Rapacia included mostly what elsewhere have been called 'errant' polychaetes (Audouin & Milne Edwards 1834); the Limivora included mostly 'sedentary' polychaetes.

Quatrefages (1865) designated a subdivision originally proposed by Blainville (1825) in which the 'sedentary' polychaetes were recognised as having distinctly regionalised bodies and the 'errants' as lacking such regions. Another classification was proposed by Benham (1894, 1896), although it was not subsequently adopted. Benham created the orders Cryptoccephala which contained the families Sabellidae, Serpulidae and Sabellariidae; and Phanerocephala which contained all other polychaetes.

Hatschek (1893) divided the polychaetes into two groups, Cirrifera and Acirra. Among the Cirrifera he listed three major groups, Spiomorpha, Amphinomorpha and Rapacia. Rapacia included the scale-worms, nereidids, phyllodocids and related taxa in addition to the eunicids. Hatschek listed the myzostomids in an appendix to the Rapacia. The Drilomorpha, Terebellomorpha and Serpulimorpha were included in the Acirra. At the same time Hatschek formally recognised the Archiannelida, which included a number of families of small-bodied taxa, as a separate class of annelids. However, the archiannelids are no longer considered as a valid group and all have been assigned to the Polychaeta (see Rouse & Fauchald 1997); some families, for example, Nerillidae, Polygordiidae, Protodrilidae, Protodriloididae and Saccocirridae, can be assigned to specific clades within Polychaeta, but the affinities of other families such as Parergodrilidae and Psammodrilidae are obscure. Although Hatschek's two major groups, Acirra and Cirrifera, have been disregarded by most later authors, the other new names, such as Terebellomorpha and Spiomorpha, have been used by many later authors, with roughly the content Hatschek originally gave them. However, the classification by Rouse & Fauchald (1997) does recognise, in part, the concepts of Acirra and Cirrifera.

1. CLASS POLYCHAETA



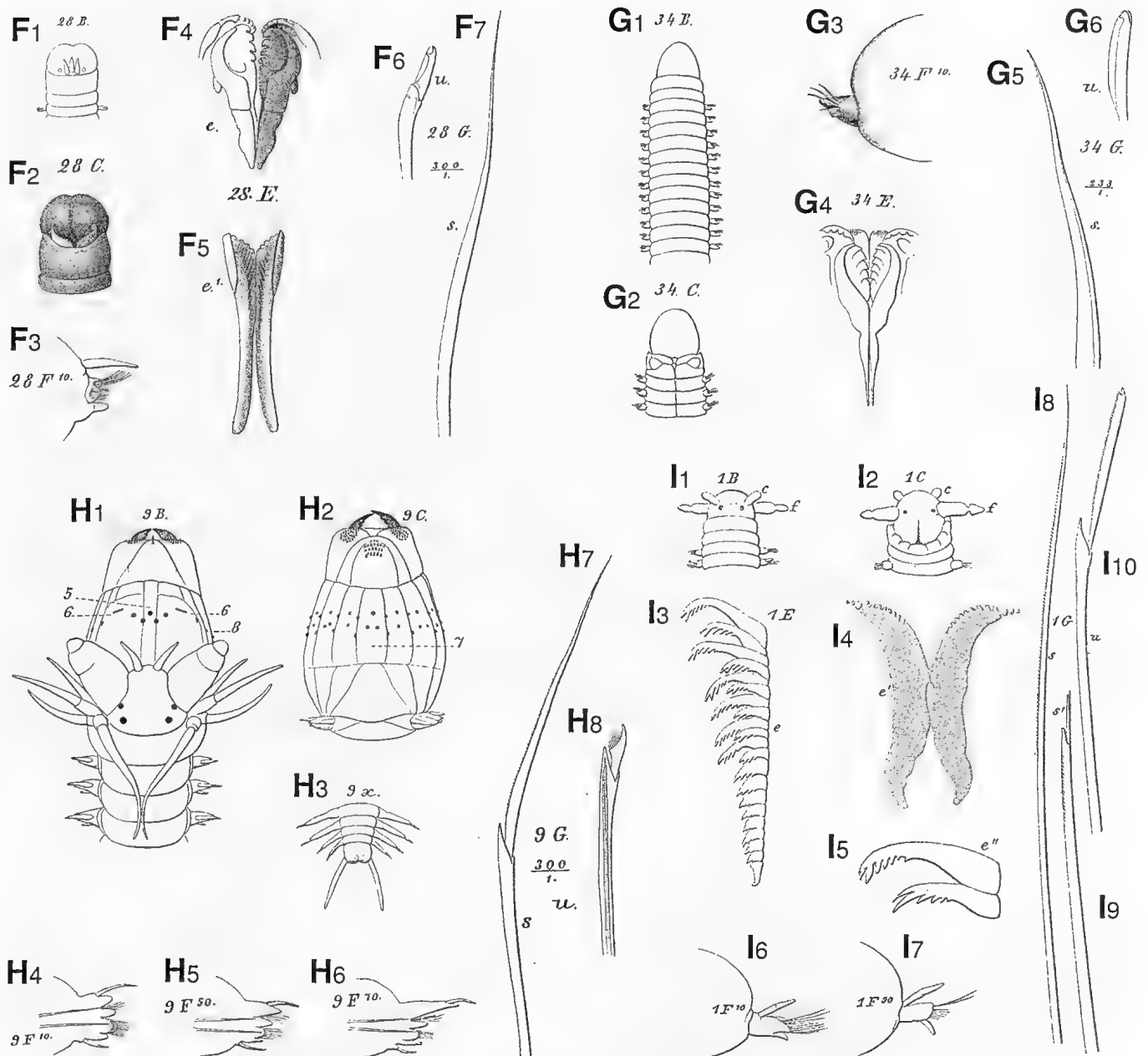


Figure 1.4 Australian polychaete type specimens from Port Jackson (Sydney) described and published in Kinberg (1857, 1910). Nine of the 15 species figured by Kinberg are shown here, the remainder are in Figure 1.5. The figures were published as lithographs. **A**, *Lepidonotus jacksoni* (Polynoidae): 1, anterior end, dorsal view (11B); 2, parapodium (11F); 3, elytron (11H); 4, neurochaeta (11Gu); 5, notochoeta (11Gs); 6, jaws (48). **B**, *Lepidonotus striatus* (now known as *Hyperhalosydna striata*; Polynoidae): 1, anterior end, dorsal view (18B); 2, parapodium (18F); 3, elytron (18H); 4, arrangement of tubercles on an elytron (18H); 5, notochoeta (18Gs); 6, neurochaeta (18Gu). **C**, *Antinoe waahli* (now known as *Harmothoe waahli*; Polynoidae): 1, entire animal, dorsal view (28A); 2, anterior end, dorsal view (28B); 3, parapodium (28F); 4, elytron (28H); 5, arrangement of tubercles on elytron (28H); 6, ?pigmentation of elytron (28H); 7, neurochaeta (28Gu) 8, notochoeta (28Gs); 9, jaws (55). **D**, *Diopatra dentata* (Onuphidae): 1, anterior end, dorsal view (5B); 2, anterior end, ventral view (5C); 3, posterior end (5X); 4, parapodium from chaetiger 10 (5F¹⁰); 5, 6, jaw apparatus (5E); 7, subacicular hook (5Gu); 8, pectinate chaeta (5Gs¹); 9, limbate chaeta (5Gs). **E**, *Nauphanta novaehollandiae* (now *Marphysa*, possibly *M. mossambica*; Eunicidae): 1, anterior end, dorsal view (23B); 2, anterior end, ventral view showing jaws (23C); 3, parapodium from chaetiger 9 (23F⁹); 4, parapodium from chaetiger 50 (23F⁵⁰); 5, parapodium from chaetiger 120 (23F¹²⁰); 6, limbate chaeta (23G). **F**, *Lycidice brevicornis* (now known as *Lysidice ninetta*; Eunicidae): 1, anterior end, dorsal view (28B); 2, anterior end, ventral view showing jaws (28C); 3, parapodium from chaetiger 10 (28F¹⁰); 4, 5, jaw apparatus (28E); 6, compound falciger (28Gu); 7, limbate chaeta (28Gs). **G**, *Lumbriconereis jacksoni* (now known as *Lumbrineris jacksoni*; Lumbrineridae): 1, anterior end, dorsal view (34B); 2, anterior end, ventral view (34C); 3, parapodium from chaetiger 10 (34F¹⁰); 4, jaw apparatus (34E); 5, limbate chaeta (34Gs); 6, simple hook chaeta (34Gu). **H**, *Perinereis novaehollandiae* (now known as *Perinereis amblyodonta*; Nereididae): 1, anterior end, dorsal view, pharynx everted (9B); 2, anterior end, ventral view of everted pharynx (9C); 3, posterior end, dorsal view (9X); 4, parapodium from chaetiger 10 (9F¹⁰); 5, parapodium from chaetiger 50 (9F⁵⁰); 6, parapodium from chaetiger 70 (9F⁷⁰); 7, heterogomph spiniger (9Gs); 8, heterogomph falciger (9Gu). **I**, *Staurocephalus loveni* (now known as *Schistomeringos loveni*; Dorvilleidae): 1, anterior end, dorsal view (1B); 2, anterior end, ventral view (1C); 3, maxillae (1Ee); 4, manibles (1Ee); 5, two free denticles of the maxillae (1Ee"); 6, parapodium from chaetiger 10 (1F¹⁰); 7, parapodium from chaetiger 30 (1F³⁰); 8, simple chaeta (1Gs); 9, furcate chaeta (1Gs'); 10, compound falciger (1Gu). (A1–A5, B, C1–C8, from Kinberg 1857: A1–A5, pl. 3.11; B, pl. 4.18; C1–C8, pl. 6.28. A6, C9, D–I, from Kinberg 1910: A6, pl. 10.48; C9, pl. 10.55; D, pl. 13.5; E, pl. 16.23; F, pl. 17.28; G, pl. 18.34; H, pl. 20.9; I, pl. 21.1)

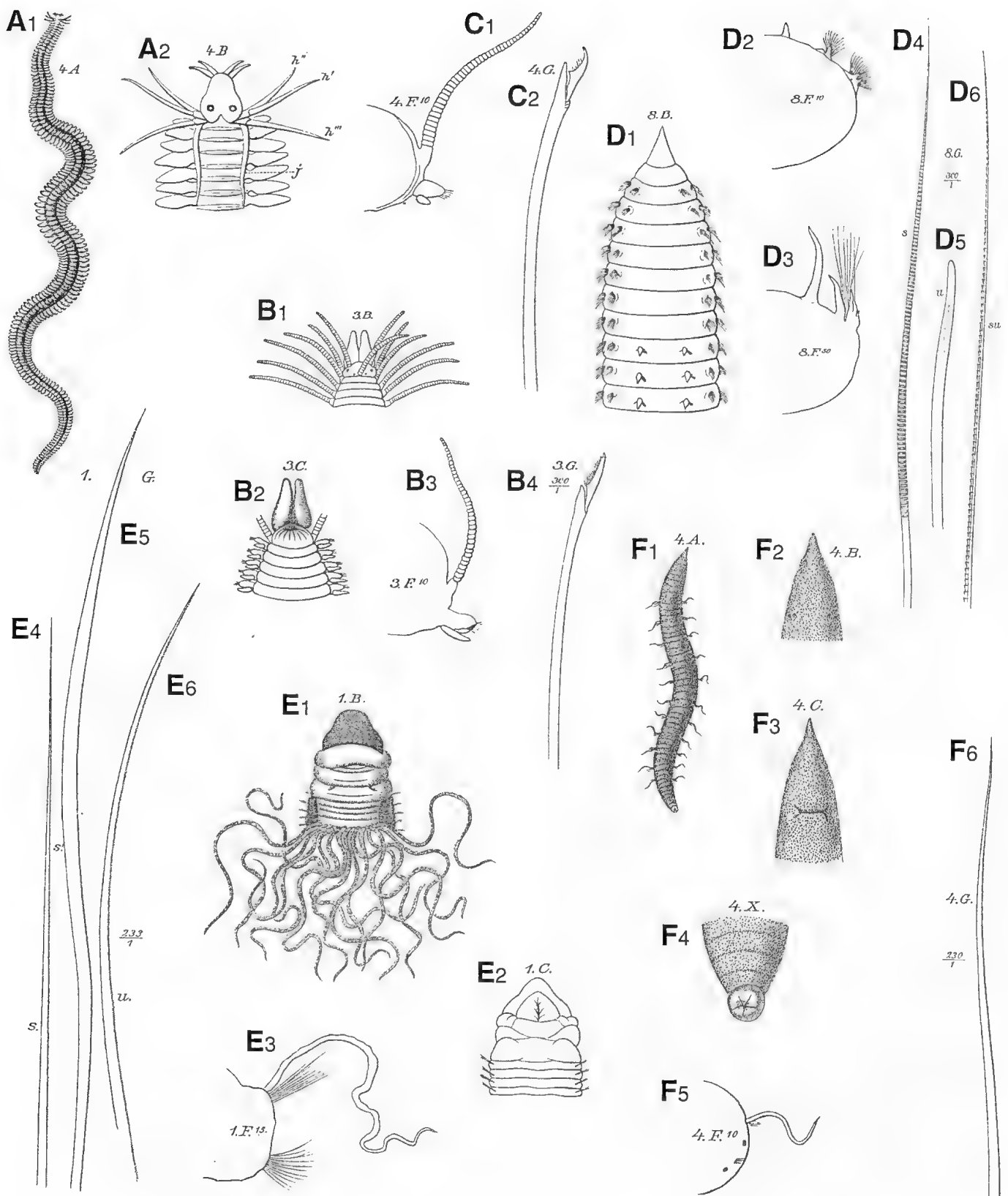


Figure 1.5 Australian polychaete type specimens from Port Jackson (Sydney) described and published in Kinberg (1910). Six of the 15 species figured by Kinberg (1857, 1910) are shown here, the remainder are in Figure 1.4. The figures were published as lithographs. **A**, *Phyllodoce novaehollandiae* (Phyllodocidae): 1, entire animal (4A); 2, anterior end, dorsal view (4B). **B**, *Thoe fusiformis* (now known as *Typosyllis variegata*; Syllidae): 1, anterior end, dorsal view (3B); 2, anterior end, ventral view (3C); 3, parapodium from chaetiger 10 (3F¹⁰); 4, compound falciger (3G). **C**, *Eurymedusa picta* (possibly a junior synonym of *Odontosyllis polycera*; Syllidae): 1, parapodium from chaetiger 10 (4F¹⁰); 2, compound falciger (4G). **D**, *Labotas novaehollandiae* (now known as *Scoloplos novaehollandiae*; Orbiniidae): 1, anterior end, dorsal view (8B); 2, parapodium from chaetiger 10 (8F¹⁰); 3, parapodium from chaetiger 50 (8F⁵⁰); 4, crenulate chaeta (8Gs); 5, spine (8Gu); 6, crenulate capillary (8Gsu). **E**, *Timarete fecunda* (now known as *Timarete anchylochaetus*; Cirratulidae): 1, anterior end, dorsal view (1B); 2, anterior end, ventral view (1C); 3, parapodium from chaetiger 15 (1F¹⁵); 4–6, three types of capillary chaetae (1Gs, s', u). **F**, *Travisia lithophila* (Opheliidae): 1, entire animal, dorsal view (4A); 2, anterior end, dorsal view (4B); 3, anterior end, ventral view (4C); 4, posterior end (4X); 5, parapodium from chaetiger 10 (4F¹⁰); 6, capillary chaeta (4G). (From Kinberg 1910: A, pl. 22.4; B, pl. 24.3; C, pl. 24.4; D, pl. 24.8; E, pl. 25.1; F, pl. 25.4)

During the twentieth century several systems of classification have been used. Quatrefages' (1865) system was adopted in two extensively used handbooks by Fauvel (1923, 1927; see also Fauvel 1953) as well as by Uschakov (1955), Day (1967) and Hartmann-Schröder (1971). The terms 'errants' and 'sedentaries' became well entrenched in the literature, despite complaints about the inadequacies of the definitions (Day 1967; Hartman 1968). A different system proposed by Dales (1962a, 1963a, 1977) used structural similarities of the buccal organ to furnish criteria for a primary breakdown of the polychaetes. Taxa with an axial buccal organ were separated into three orders: Phyllodocida with a strongly muscular pharynx, and Capitellida and Spionida without muscularised pharyngeal walls. Subdivision of the Phyllodocida was based on the distribution of nephridial structures (protonephridia, metanephridia, metanephromixia and mixonephridia) as categorised earlier by Goodrich (1945). Families with ventral buccal organs were grouped into nine orders, partially based on the degree of development of the buccal organ: an eversible ventral buccal organ in three orders (Eunicida, Amphinomida and Magelonida), a non-eversible buccal organ in six orders (Ariciida, Cirratulida, Oweniida, Terebellida, Flabelligerida and Psammodrillida) and finally one in which the buccal organ had been lost (Sabellida only). This system has not been widely adopted.

Fauchald (1977), in his classification, defined 17 orders without emphasis on any single morphological feature, but he had a distinct preference for features of the anterior end for defining the orders. Although defined differently, the orders contained approximately the same taxa as those listed in Dales (1963a). Both Fauchald and Dales listed their orders in such a fashion that a higher classification could be assumed from the scheme, but without identifying supra-ordinal taxa. The new orders added by Dales and Fauchald were mostly for morphologically unusual families such as Spintheridae, Sternaspidae and Oweniidae.

Pettibone (1982) recognised 25 orders, including one for each of the five traditional 'archiannelidan' families in addition to the orders defined by Dales (1963a) and Fauchald (1977). Pettibone, however, often emphasised different morphological structures than those used by Dales and Fauchald.

At the family or superfamily level, several more recent phylogenetic studies (see for example, Blake & Kudenov 1978; Kudenov & Blake 1978; Orensanz 1990; Frame 1992) have used more or less traditional methods of systematic analysis. Cladistic studies are, however, becoming more common and include such works as those by Fitzhugh (1989, 1991a) and Rouse & Fitzhugh (1994) on sabellids and related taxa, and Fitzhugh (1987) and Glasby (1991, 1993, 1999a) on nereidid and nereidoid families. Pleijel (1991, 1998) has studied the phyllodocids and hesionids, and Westheide and his students have published several papers (see Westheide 1977, 1997; Licher & Westheide 1994) on relationships among taxa at various levels.

Studies of the Australian Fauna

The first records and descriptions of Australian polychaetes were made by European specialists (for example, Schmarda 1861; Ehlers 1864–1868; Baird 1865; McIntosh 1885; Augener 1913, 1914, 1922, 1927; Fauvel 1917, 1922) who received material from expeditions to Australia; Kinberg was one specialist who actually accompanied several expeditions to Australia and published (1857, 1865, 1866, 1910) on the material collected (see Figs 1.4, 1.5). Hartman (1948a) reviewed the types of Kinberg and redescribed many of them.

Consequently, most of the type material of the earliest described species from Australian waters is housed in European institutions. Schmarda (1861) also described some Australian (Fig. 1.6) and New Zealand material, but many of his types were lost when the boat capsized on its return voyage. Ernst Ehlers (Fig. 1.7A) made a significant contribution to the taxonomy of polychaetes worldwide. Although he did not describe many species based on Australian mainland material, he did describe them from other Gondwanan areas, including Antarctica, South America, Africa and New Zealand, that also occur here (Ehlers 1864–1868, 1904, 1913). From the 1880s onwards workers based in Australia and New Zealand began to document the Australian fauna (see for example, Haswell 1883, 1884, 1886a and others; Benham 1916, 1921; review by Glasby & Read 1998). During this era many species previously only known from European waters were recorded from Australian waters. Many of these European species names continue to be used even though it is highly unlikely that they in fact occur here. Only when detailed revisions of families are undertaken are these records found to represent new Australian species (see Hutchings & Glasby 1986a, 1986b, 1987; Hutchings & Peart in preparation).

William Aitcheson Haswell (Fig. 1.7B) had a profound influence on the knowledge of Australian polychaetes during the late 1800s and early 1900s. He worked extensively from a small marine zoological station at Watson's Bay, Sydney Harbour. He published numerous papers including many with descriptions of new Australian species. Following his arrival in Australia from Scotland in 1897, he became a valued biologist in the Australian zoological community. At one time he was President of the Linnean Society of New South Wales and an active member of the Royal Zoological Society of New South Wales as well as a trustee of the Australian Museum (1891–1923) and a Fellow of the Royal Society of London (1897). His biological interests were extensive and included other invertebrate groups such as Crustacea and Bryozoa and, the study of invertebrate and vertebrate morphology. After working as the Curator of the Queensland Museum (1880) and acting Curator of the Australian Museum (1883) Haswell was appointed to the teaching staff of Sydney University (1884) and became the first Challis Professor of Biology (1890); he retired from the University in 1918.

After this initial interest in the polychaete fauna few studies were undertaken, until the 1950s and 1960s when notable papers by Hartman (1954, 1963, 1966c), Kott (1954), Dew (1958, 1959) and Straughan (1966, 1967a) were published. Both Dew and Straughan worked on shallow water serpulids. All of these studies were summarised in the catalogue compiled by Day & Hutchings (1979), which lists species recorded from Australian and New Zealand waters together with their locality according to the literature; this catalogue is in the process of being revised and updated by Hutchings & Johnson.

Since the late 1970s taxonomic effort has focussed on family-level revisions, and these include mainly species from shallow coastal waters (see Hutchings 1977, 1997a, 1997b; Rainer & Hutchings 1977; Hutchings & Rainer 1979; Hutchings & Glasby 1982, 1985, 1986a, 1986b, 1987, 1988, 1990; Hutchings & Turvey 1982, 1984; Hutchings & Murray 1984; Hutchings & Reid 1991; Hutchings, Reid & Wilson 1991; Hutchings & McRae 1993; Hutchings & Smith 1997; Hutchings & Peart in preparation). These studies documented many undescribed species and, although they removed many records of so-called 'cosmopolitan' species from Australian waters, many remain including *Lumbrineris latreilli*, *Marphysa sanguinea*, *Chaetopterus variopedatus* and *Cirratulus cirratus*.

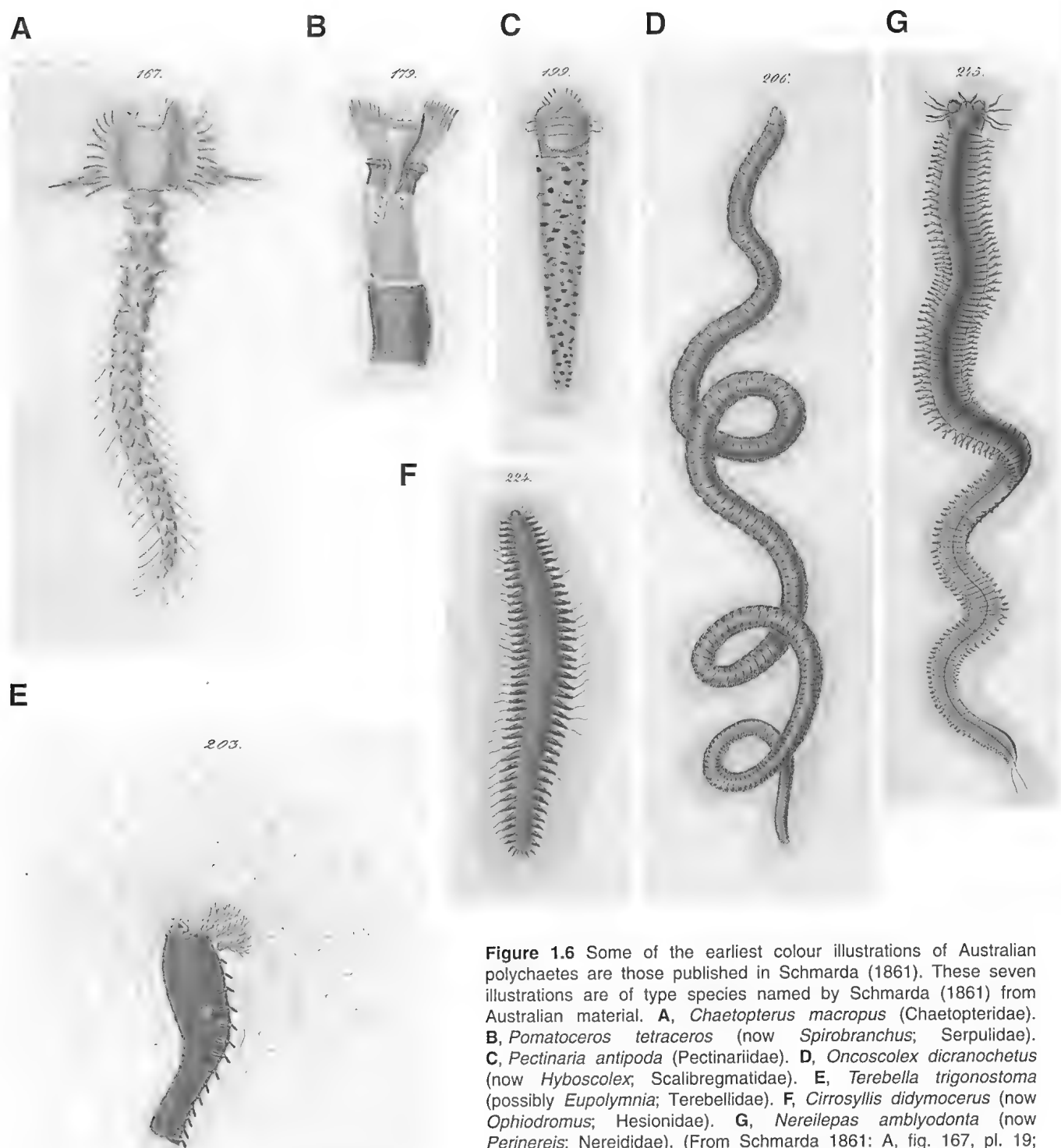


Figure 1.6 Some of the earliest colour illustrations of Australian polychaetes are those published in Schmarda (1861). These seven illustrations are of type species named by Schmarda (1861) from Australian material. **A**, *Chaetopterus macropus* (Chaetopteridae). **B**, *Pomatoceros tetraceros* (now *Spirobranchus*; Serpulidae). **C**, *Pectinaria antipoda* (Pectinariidae). **D**, *Oncoscolex dicranochetus* (now *Hyboscolex*; Scalibregmatidae). **E**, *Terebella trigonostoma* (possibly *Eupolymnia*; Terebellidae). **F**, *Cirrosyllis didymocerus* (now *Ophiodromus*; Hesionidae). **G**, *Nereilepas amblyodonta* (now *Perinereis*; Nereididae). (From Schmarda 1861: A, fig. 167, pl. 19; B, fig. 179, pl. 21; C, fig. 199, pl. 24; D, fig. 206, pl. 26; E, fig. 203, pl. 25; F, fig. 224, pl. 28; G, fig. 245, pl. 31)

Hartmann-Schröder collected extensively around most of the Australian coast and described in a series of papers much of the intertidal fauna from sandy substrata, including many new species (see Hartmann-Schröder 1979, 1980, 1981a, 1983, 1984, 1985a, 1986, 1987; Hartmann-Schröder & Parker 1990, 1995). Additional new taxa have been described by Blake & Kudenov (1978), Paxton (1979, 1986a, 1986b, 1993, 1996), Ben-Eliahu, Hutchings & Glasby (1984), Hutchings & Glasby (1982, 1985), Wilson (1984, 1988, 1990), Watson Russell (1986, 1987, 1989, 1998), Hanley (1989, 1991, 1993), Rainer & Kaly (1988), Hanley & Burke (1989, 1990, 1991a, 1991b), Rouse (1990a, 1990b, 1993a), Glasby (1999a) and Wilson & Glasby (1993).

Despite the recent upsurge in polychaete taxonomic studies, the number of taxa yet to be discovered still appears to be very high. This is a reflection of the present rate of species discovery and the fact that many families have yet to be studied comprehensively. Recent surveys of Jervis Bay on the South coast of New South Wales by Hutchings (1994), and in Botany Bay, New South Wales by Wilson (1998) and Port Phillip Bay by Wilson, Heislars & Poore (1998) have revealed many undescribed taxa. Certainly, sampling offshore or in areas away from the centres of major populations as well as undersampled cryptic habitats in the intertidal zone and the pelagic habitat reveals the highest number of undescribed taxa. Furthermore, virtually nothing is known about the interstitial polychaete fauna. In an encouraging development,

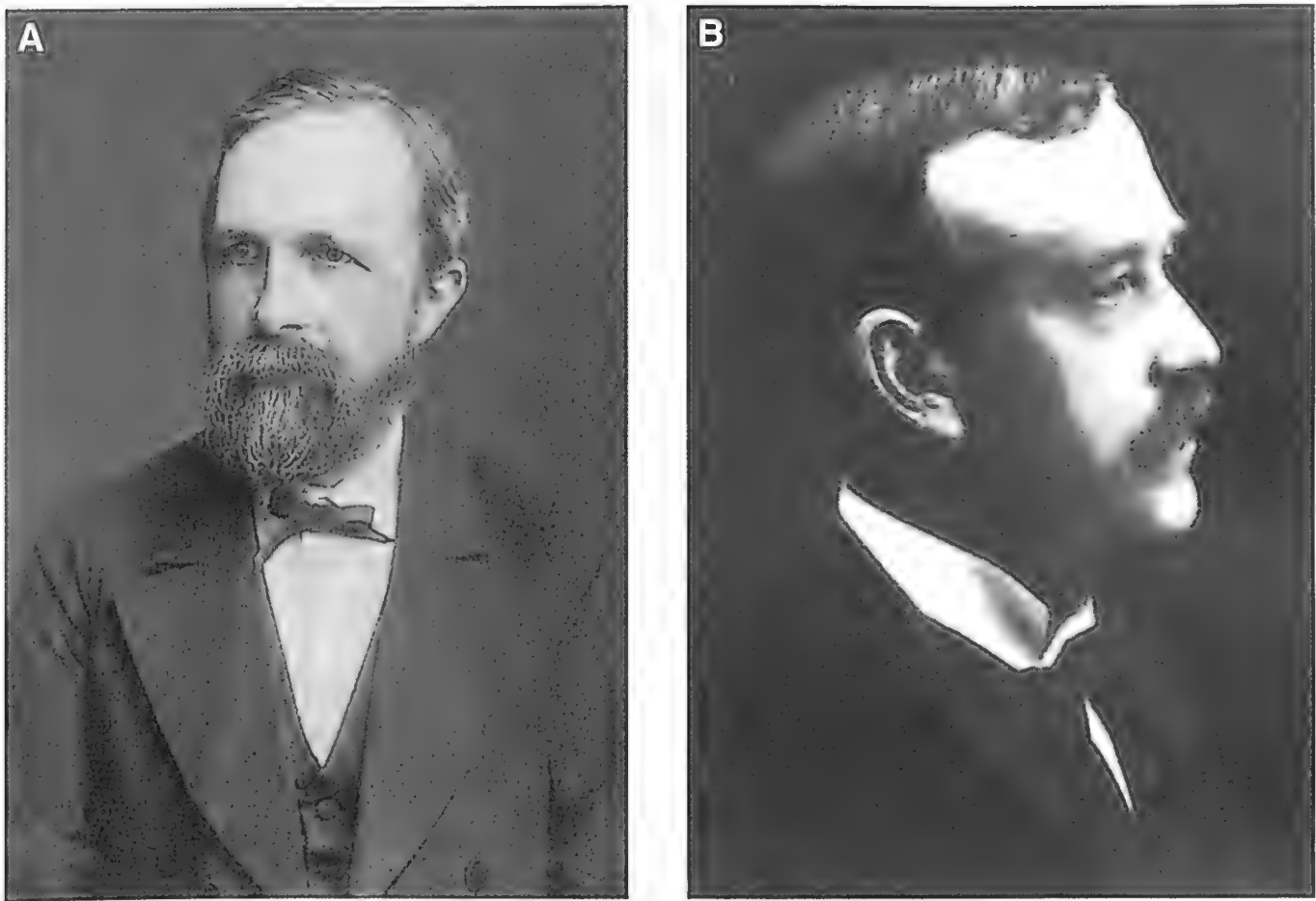


Figure 1.7 Polychaete biologists. **A**, Ernst Ehlers (1835–1925) worked extensively on the taxonomy of polychaetes worldwide. This photograph was taken in 1876. **B**, William Aitcheson Haswell (1854–1925) was appointed the first Challis Professor of Zoology, University of Sydney in 1890. He published numerous papers on Australian polychaetes. His Professor in Edinburgh described him as “an excellent naturalist and a thoroughly reliable gentleman”.

[A, courtesy of the Smithsonian Institution, photo no. 93-7015; B, courtesy of School of Biological Sciences, University of Sydney]

polychaete workers are now employed in two of the State Museums and extensive collections are being established which greatly facilitate major family revisions. The present lack of knowledge of the polychaete fauna often hampers benthic studies and makes faunal comparisons between areas difficult; many species are identified only to the genus level.

Virtually, all known polychaete families have been recorded from Australian waters; of the 81 families (see Appendix 1) recorded worldwide 67 are found in the Australasian region. Currently, about 1140 species are known from Australian waters and perhaps another 20–30% remain to be described, especially from northern Australia and in deeper waters.

MORPHOLOGY AND PHYSIOLOGY

General Features

Though uncommon in freshwater and virtually absent on land, polychaetes are found in every marine habitat – from deep-sea sediments to intertidal interstices, from coral rubble to swimming freely in the water column, preying on plankton. Polychaetes vary greatly in form, and range in size as adults from less than a millimetre, as in some interstitial species, to well over 3 m (for example, in Australian beach worms *Onuphis* and *Australonuphis* species) in length, and may live from a few weeks to several years.

The most commonly seen polychaetes are the mobile forms that live amongst algae, under stones or crawl over the sediment. These forms tend to have well-developed eyes and

other sensory appendages. Many other polychaetes are burrowers in sand or mud. Some dig continuously through the sediment. Others live in permanent burrows or tubes which they secrete or construct from gathered materials. Those that live in permanent tubes are basically sessile and have special extensible appendages to gather food. Such appendages, projected from the tube, either collect food from the surrounding surfaces or filter it directly from the water. Often only the feeding appendages are visible and they tend to be brightly coloured, resembling flowers (such as, in sabellids and serpulids) or spaghetti (such as, in terebellids, Fig. 1.32 and cirratulids Fig. 1.33).

A variety of polychaetes have evolved to live a permanently pelagic existence. These forms, which all appear to be derived from benthic forms, usually have very well-developed eyes and are active predators on other plankton.

The polychaete body consists of three basic regions. The presegmental region is derived from the episphere, prototroch and the area surrounding the mouth in the larvae, and makes up the prostomium and peristomium in the adult worm (Fig. 1.8). The episphere gives rise to the prostomium; the prototroch and buccal region, including the metatroch posterior to the mouth, give rise to the peristomium (Schroeder & Hermans 1975). The bulk of the body is comprised of serially repeated segments derived from the ectotoloblast ring; this form of segmentation is referred to as metamerism (Fig. 1.8).

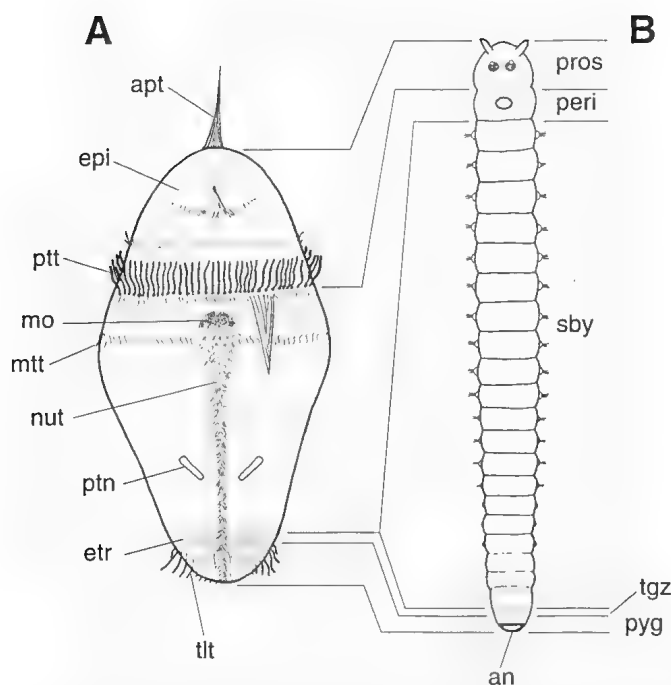


Figure 1.8 The correlation between body regions of a larva and an adult polychaete. Note that much of the adult body is derived from the posterior growth zone of the larva. **A**, larval body. **B**, adult body. **an**, anus; **apt**, apical tuft; **e****pi**, episphere; **etr**, ectoteloblast ring; **mo**, mouth; **mtt**, metatroch; **nut**, neurotroch; **peri**, peristomium; **pros**, prostomium; **ptn**, protonephridium; **ptt**, prototroch; **pyg**, pygidium; **sby**, segmented body; **tgz**, teleoblastic growth zone; **tlt**, telotroch. (**A**, after Rouse 2000; **B**, after Nielson 1995, based on Schroeder & Hermans 1975)

Each segment is, in principle, limited by septa from neighbouring segments (Fig. 1.9). Usually dorsal and ventral mesenteries separate a pair of coelomic compartments. Each segment usually carries parapodia and chaetae, in addition to various segmentally arranged internal organs such as nephridia. However, all segments are basically united by the digestive, vascular, muscular and nervous systems and so have little autonomy. Segments are formed sequentially in polychaetes and are established during development from paired mesodermal growth zones that originate from the 4d micromere (Anderson 1966). Some polychaetes have a fixed number of segments (for example, fabriciine sabellids), but in many others, segments continue to be added throughout life (for example, in some eunicids).

The mesodermal growth zones are part of the third region of the body; the post-segmental pygidium. New segments are derived during growth along the anterior edge of the pygidium (Schroeder & Hermans 1975) and the youngest segment in the body of a polychaete is always the most posterior. The pygidium may be a small structure, essentially just carrying the anus (for example, in species of the opheliid genus *Travisia*) or it may be a larger structure on which the anus is present, centrally or off-centre dorsally or ventrally (for example, in some maldanids). The pygidium may be smooth, or carry one or more pairs of pygidial cirri.

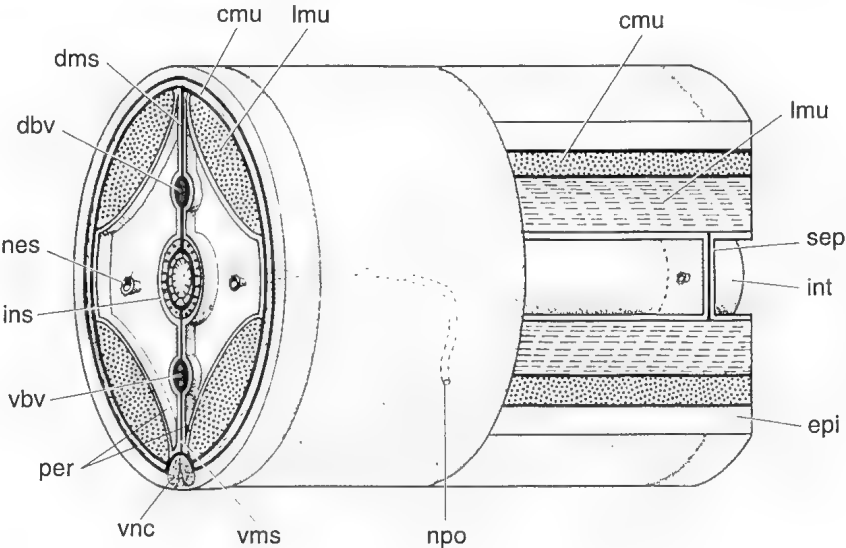
Although the coelom is strictly defined as having a peritoneal lining over all surfaces, in numerous polychaete taxa the coelom is directly in contact with the longitudinal muscle layer (Fransen 1988). The occlusion of the coelom in certain polychaetes is regarded as a secondary phenomenon (Bartolomaeus 1994). Physiological problems associated with the evolution of the coelom are related to the expansion of the body and the distance of the gut from the outer surface. This means that transport of respiratory gases and nutrients cannot be accomplished by diffusion alone. Most polychaetes with a coelom therefore have a circulatory system (see below).

Most polychaetes have chaetae, the exceptions being the Histiobdellidae, Poeobiidae, Protodrilidae, most polygordiids, some small members of Dorvilleidae and the terebellid genus *Hauchiella*. Chaetae (also called setae) are bundles of chitinous, thin-walled cylinders held together by sclerotinised protein. They are produced by a microvillar bed of certain invaginated epidermal cells and so can be defined as cuticular structures that develop within epidermal follicles. Chaetal ultrastructure is similar in all cases, but there is considerable diversity of external form (Specht 1988). Apart from the Polychaeta, chaetae are also found in the Clitellata, Myzostomida, Echiura and Brachiopoda.

External Body Features

In the following description of the major external body features of polychaetes, those associated with the circulatory system (for example, branchiae), nervous system (for example, sensory organs) or reproduction (for example, intromittent organs) are dealt with in those sections rather than here. The body of polychaetes is covered by a flexible external cuticle. Epidermal microvilli secrete a network of fibres that are in part collagenous and also contain scleroprotein. The epidermis is usually a columnar epithelium, ciliated in certain areas of the body.

Figure 1.9 Diagram of one complete segment of a generalised polychaete. **cmu**, circular muscle; **dbv**, dorsal blood vessel; **dms**, dorsal mesentery; **e****pi**, epidermis; **ins**, intestinal sinus; **int**, intestine; **l****mu**, longitudinal muscle; **nes**, nephrostome; **npo**, nephridiopore; **per**, peritoneum; **sep**, septum; **v****b****v**, ventral blood vessel; **v****m****s**, ventral mesentery; **v****n****c**, ventral nerve cord. (After Fransen 1988)



Head and Head Structures

The head is composed of the prostomium, peristomium and, in some instances, fused anterior segments known as cephalised segments. The prostomium contains at least part of the brain, and often carries eyes, antennae and palps (Fig. 1.10). The prostomium varies greatly in shape from a conical structure to a simple T-shape (for example, some spionids and scalibregmatids) and may be fused to the peristomium. In some groups, such as the maldanids and paraonids, the combined structure of the prostomium and peristomium is well separated from the rest of the body as a distinct head. In other taxa, the joint structure comprises a peristomial ring and a tentacular crown; the prostomium proper is no longer identifiable as a separate entity (for example, in sabellids and serpulids). In many polychaetes, the only adult peristomial structure visible is the area immediately surrounding the mouth and, most noticeably, the roof of the mouth (as in terebellids and trichobranchids). However, in some polychaetes, such as eunicids and dorvilleids, the peristomium is seen as one (or two) complete rings separating the prostomium from the first segment.

Head appendages include antennae, palps, peristomial cirri and, associated with one or more cephalised segments, tentacular cirri (see Fig. 1.10). Antennae are always located on the prostomium. Up to three antennae may be present: a pair of lateral antennae and one median antenna. Most common are simple, tapering or digitiform antennae, as found in phyllodocids and nephtyids. Some may be articulated, for example, in eunicids, and others consist of a basal ceratophore and a distal ceratostyle, as seen in onuphids. The lateral antennae may be located at, or near the frontal edge of the prostomium, as found in nereidids. In some taxa, for example, aphroditids, only the single median antenna is present. The outer (or outer lateral) 'antennae' of onuphids and eunicids are paired dorso-lateral palps. In the Dorvilleidae, the paired antennae are more or less frontal. The frontal, tapering antenna-like structures sometimes referred to as frontal palps in the onuphids are dorsal lips (Orrhage 1995).

All palps, whether emerging from the prostomium or the peristomium, are innervated from the middle (or posterior) part of the brain, or partially or wholly from the circum-oesophageal ring (see Orrhage 1990, 1991, 1995, 1996) and are considered homologous structures. Palps can be divided into two structurally different groups: grooved feeding palps and ventral, tapering sensory palps (Orrhage 1980). In all but one family, the feeding palps have ciliated paths, often located in a longitudinal groove giving each palp a U-shaped cross-section (for example, acrocirrids, spionids and terebellids). The exception is the family Magelonidae, in which the palps lack a longitudinal ciliated path, but are studded with papillae (Fig. 1.10D); these palps also emerge ventrally at the corners of the mouth, rather than dorsally, as in the spiomorphs with which they are usually compared. Despite these differences the palps in magelonids are homologous with grooved palps (Orrhage 1966). A single pair of grooved palps is present in many polychaetes (for example, in flabelligerids and spionids). Almost always, grooved palps are attached on the dorsum at or near the junction of the prostomium and peristomium (Fauchald & Rouse 1997).

In terebellids and trichobranchids, numerous grooved palps are attached along the fusion line of the prostomium and peristomium. In the sabellids and serpulids, the grooved palps form a prostomial tentacular crown (Fitzhugh 1989). The prostomial derivation is visible in developing juveniles in which the buds for the crown appear in front of the prototroch (Rouse 1993a). In adults, the crown consists of three or more

pairs of radioles which may carry a large number of pinnules. Groups of multiple peristomial grooved palps are known as buccal tentacles. They are always ciliated (for example, ampharetids and pectinariids). In the ampharetids, they lie on a fold of tissue located dorsally in the buccal cavity and can be flipped out as a group or retracted. However, in alvinellids and pectinariids they are structurally very similar, but permanently exposed.

Ventral sensory palps are morphologically more uniform than grooved palps, although they may vary in relative size considerably. In most instances, they are tapered or digitiform, and relatively short when compared with grooved palps. The sensory palps of amphinomids are slender, tapering structures located ventro-laterally on the prostomium. In eunicids and onuphids, the palps (traditionally called outer, or outer lateral, antennae) are located dorso-laterally and are slender, tapering structures. In eunicids and onuphids, the ventral inflated pads located in front of the mouth represent lips (Orrhage 1995), though they have often been referred to as palps. Ventral palps are most commonly tapered with digitiform or pointed tips (for example, in acoetids and phyllodocids). Peristomial cirri differ from palps and antennae and are attached dorso-laterally near the anterior edge of the first ring in onuphids, or in a similar position on the second ring in eunicids. Peristomial cirri are often referred to erroneously as tentacular cirri (Fauchald & Rouse 1997).

The first segments often differ in size and shape from the following ones and their parapodial structures are often different as well. Dorsal and/or ventral cirri of cephalised segments which differ obviously in length or structure or both from those of other segments are called tentacular cirri (for example, in nereidids and phyllodocids). Differences between cephalic and body segments may be visible only in the presence of cirri; thus tentacular cirri can be present on a segment in which the parapodia otherwise resemble those elsewhere in the body (for example, in some nephtyids). In other taxa, the occurrence of tentacular cirri is the only indication of the presence of cephalised segments. For instance, in hesionids, the four to eight pairs of tentacular cirri present, apparently on a single segment, actually indicate a number of fused segments. In syllids, the first segment is about the same size as the following segments, but the only parapodial structures present are two pairs of tentacular cirri.

The first segment may be fused to the head in a variety of patterns. In polynoids, acoetids and similar taxa the fusion is only present ventrally so that the sensory palps appear to emerge from the first chaetiger. Alternatively, the first segment may be wholly fused to the head (prostomium/peristomium), as in pectinariids, sabellariids and some pisionids. In sabellariids, the notopodia are present in the first segment and the notopodial chaetae form the operculum. In some pisionids, such as *Pisione* species, the first segment bears only neuropodia which have large, acicular chaetae. In amphinomids and euprosinids, the distinct first segment is wrapped around the head, so that the parapodia stretch anteriorly on both sides of the prostomium without being fused to it. In these two families, the first parapodia become located frontally on either side of the prostomium, which is usually strongly tilted ventrally (Fauchald & Rouse 1997).

Musculature, Parapodia and Chaetae

Beneath the epidermis of polychaetes lies a layer of circular muscle (Figs 1.9, 1.11B). This muscle layer forms a nearly continuous sheath around the body, except in those taxa with well-developed parapodia. Thick longitudinal muscles lie

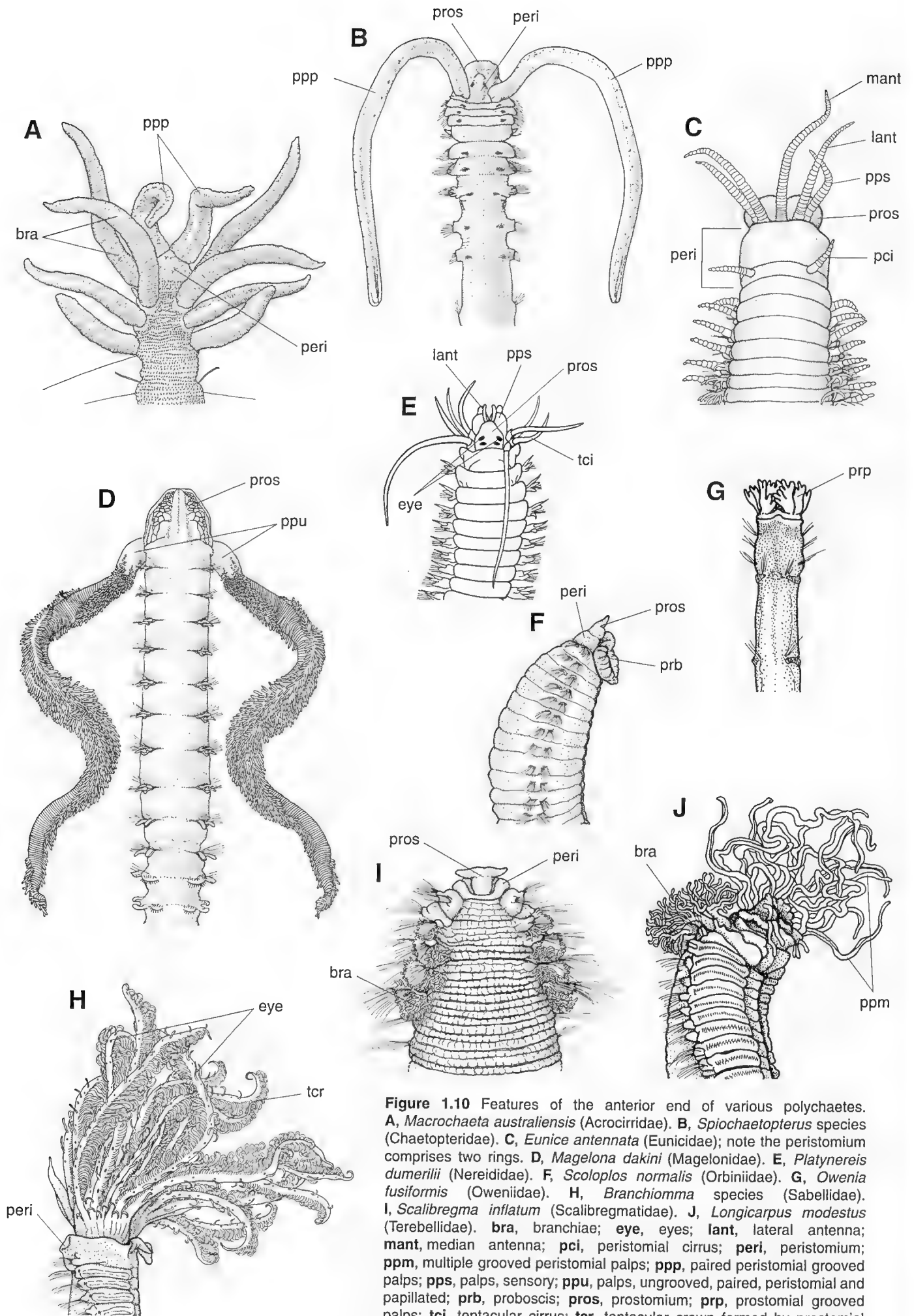


Figure 1.10 Features of the anterior end of various polychaetes. **A**, *Macrochaeta australiensis* (Acrociiridae). **B**, *Spiochaetopterus* species (Chaetopteridae). **C**, *Eunice antennata* (Eunicidae); note the peristomium comprises two rings. **D**, *Magelona dakini* (Magelonidae). **E**, *Platynereis dumerilii* (Nereididae). **F**, *Scoloplos normalis* (Orbiniidae). **G**, *Owenia fusiformis* (Oweniidae). **H**, *Branchiomma* species (Sabellidae). **I**, *Scalibregma inflatum* (Scalibregmatidae). **J**, *Longicarpus modestus* (Terebellidae). **bra**, branchiae; **eye**, eyes; **lant**, lateral antenna; **mant**, median antenna; **pci**, peristomial cirrus; **peri**, peristomium; **ppm**, multiple grooved peristomial palps; **ppp**, paired peristomial grooved palps; **pps**, palps, sensory; **ppu**, palps, ungrooved, paired, peristomial and papillated; **prb**, proboscis; **pros**, prostomium; **prp**, prostomial grooved palps; **tci**, tentacular cirrus; **tcr**, tentacular crown formed by prostomial grooved palps. [A, B, D, E, K. Nolan; C, F–J, A. Murray]

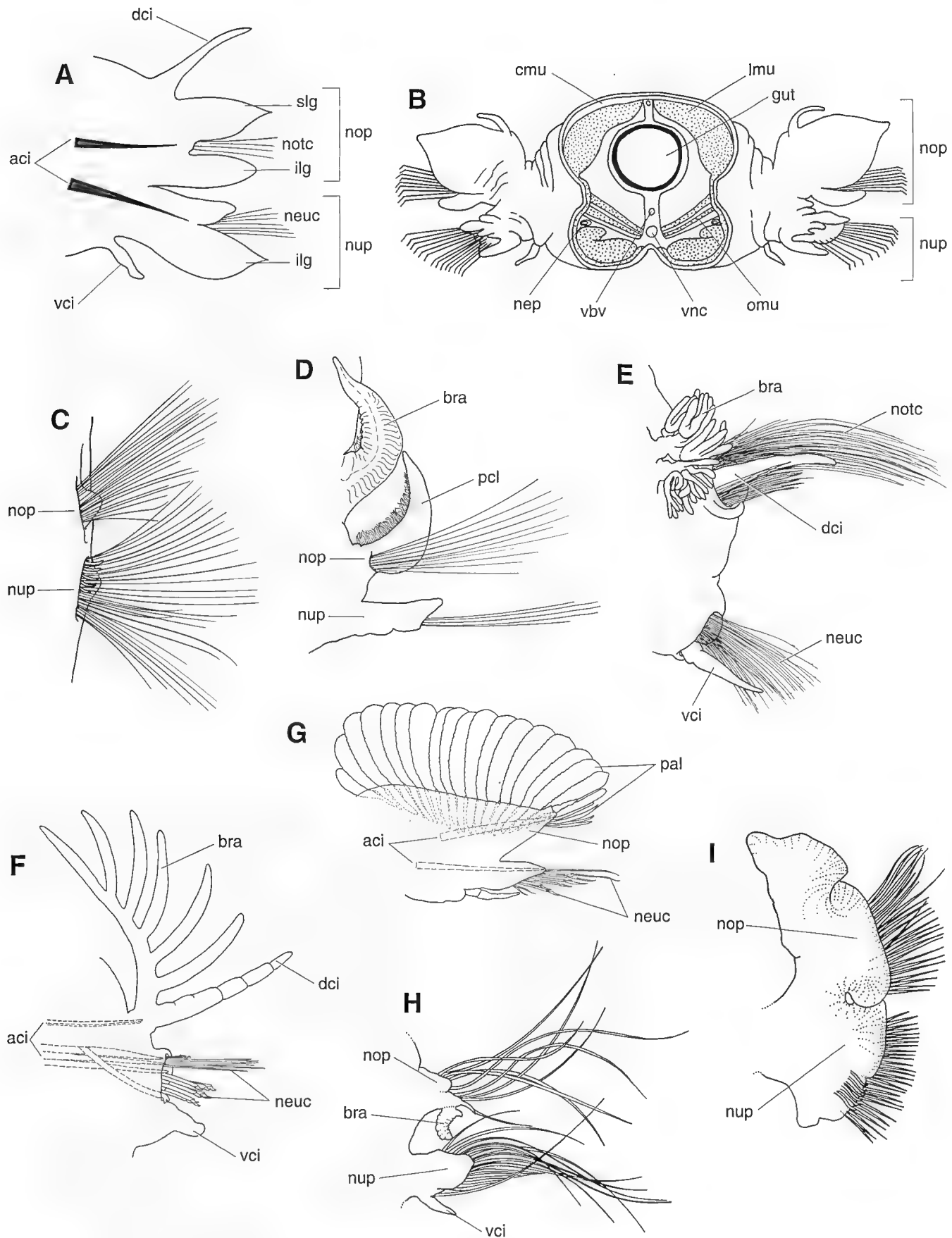


Figure 1.11 Parapodia. **A**, stylised nereidid parapodium. **B**, transverse section of a nereidid showing parapodia, body wall and coelom. **C–I**, parapodia from various polychaetes: **C**, *Scoloplos normalis* (Orbiniidae), anterior thoracic parapodium from chaetiger 4; **D**, *Scoloplos normalis* (Orbiniidae), mid-abdominal parapodium from chaetiger 28; **E**, *Eurythoe* species (Amphinomidae), parapodium of chaetiger 13; **F**, *Eunice antennata* (Eunicidae); **G**, *Paleaquor setula* (Chrysopetalidae); **H**, *Nephtys longipes* (Nephtyidae); **I**, *Scoelepis victoriensis* (Spionidae). **aci**, aciculae; **bra**, branchia, **cmu**, circular muscle; **dci**, dorsal cirrus; **gut**, gut; **ilg**, inferior ligule; **lmu**, longitudinal muscle; **nep**, nephridium; **neuc**, neurochaetae; **nop**, notopodium; **notc**, notochaetae; **nup**, neuropodium; **omu**, oblique muscle; **pai**, paleae; **pcl**, postchaetal lobe; **slg**, superior ligule; **vbv**, ventral blood vessel; **vci**, ventral cirrus; **vnc**, ventral nerve chord. (A, after Meglitsch 1972; B, after Barnes 1974)

[C-G, A. Murray; H, I, K. Nolan]

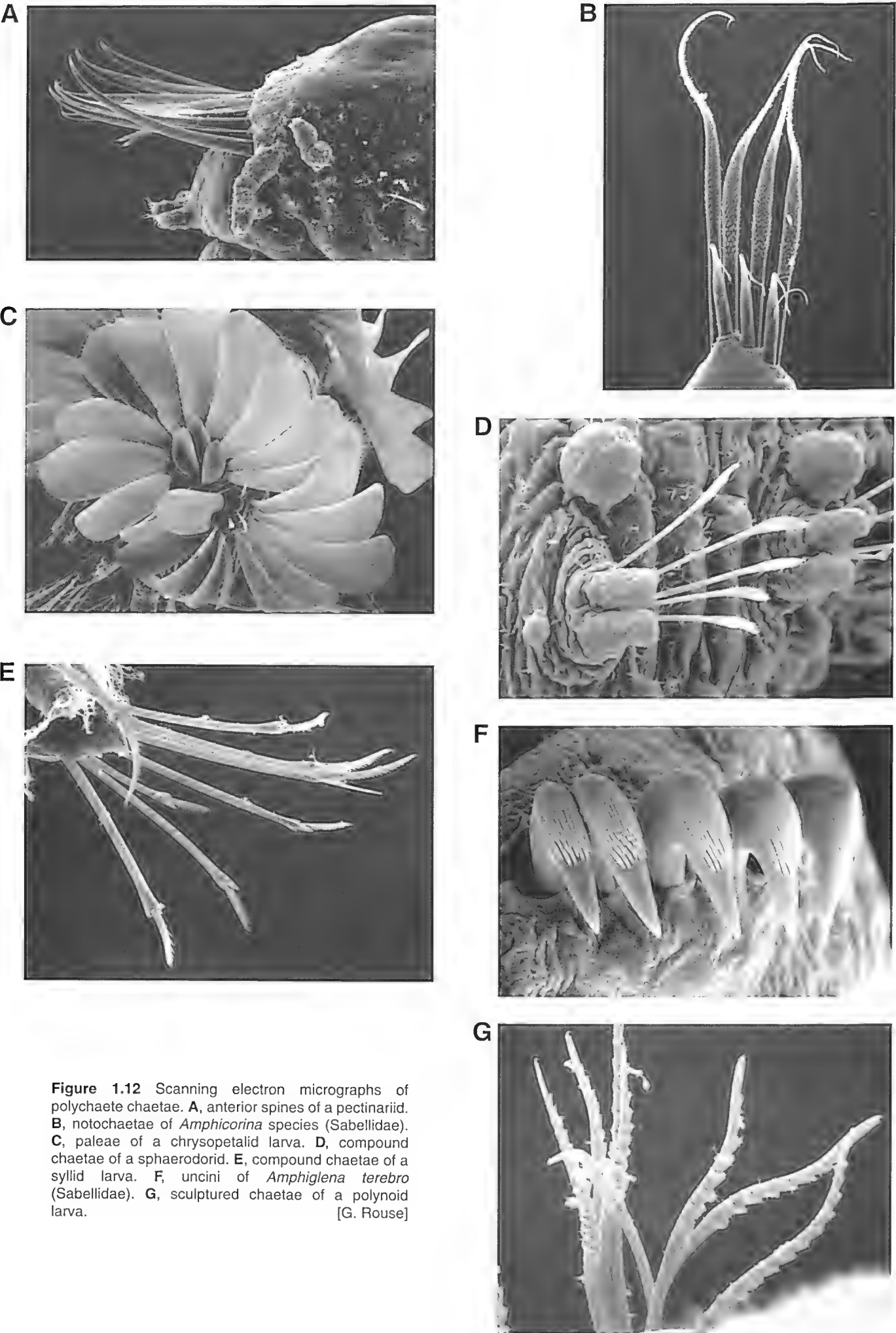


Figure 1.12 Scanning electron micrographs of polychaete chaetae. **A**, anterior spines of a pectinariid. **B**, notochaetae of *Amphicorina* species (Sabellidae). **C**, paleae of a chrysopetalid larva. **D**, compound chaetae of a sphaerodoriid. **E**, compound chaetae of a syllid larva. **F**, uncini of *Amphiglena terebro* (Sabellidae). **G**, sculptured chaetae of a polynoid larva. [G. Rouse]

beneath the circular muscle layer. In almost all polychaetes, the longitudinal muscles are present as four distinct bands (Rouse & Fauchald 1997). In addition to the circular and longitudinal muscle layers, series of 'oblique' muscle fibres that join the ventral area of the body with the mid-lateral region may be present. The innermost body wall component in most, but not all polychaetes, is a thin peritoneal layer lining the coelom (Gardiner 1992).

Parapodia are unjointed appendages on the segments of many polychaetes (Fig. 1.11). They are equipped with musculature derived mainly from the circular muscles and carry chaetae in most taxa. Parapodial structures vary, but in principle consist of two rami, a dorsal notopodium and a ventral neuropodium, on each side of the segment. Each ramus may have prechaetal and postchaetal ligules (for example, in nephtyids and nereidids). Ligules and conical lobes may be distinct throughout most of the body or limited to only part of the body (for example, in onuphiids). Especially within the Phyllodocida the number and shape of parapodial ligules and lobes vary greatly, both within and among families. Many terms are used to characterise these structures and their usage varies among the families.

In many polychaetes, the two parapodial rami differ in size or structure or orientation. For example, sometimes the neuropodia are larger than the notopodia, and point laterally or ventro-laterally with the notopodia pointing dorso-laterally or dorsally. The neuropodia are often supported by aciculae and may be distally conical or truncate. In some groups with projecting neuropodia, the notopodia are expanded into transverse ridges which more or less cover the dorsum. Neuropodia may be low, thick, sometimes glandular, transverse structures referred to as tori. These bear chaetae, either hooks or uncini, most frequently in one or a few rows, as present in sabellids and terebellids, or as dense fields, as seen in oweniids. Notopodia in taxa with tori are often short, truncate cylinders (for example, in maldanids) or they are muscular flaps (as in chaetopterids). In some taxa, such as terebellids, notopodia may be missing from posterior segments of the body. In sabellids, sabellariids and serpulids, the position of the torus is inverted on a part of the body so that they become notopodial in position. Although a torus is usually present on one ramus, in capitellids they are present in both rami at the posterior end of the body (Fauchald & Rouse 1997).

The dorsal and ventral cirri are distinctive parapodial features. Dorsal cirri are usually located at or on the upper edge of the notopodium (for example, in nereidids), but may also be found on the body-wall above the notopodia, as seen in eunicids. Ventral cirri are carried on the lower edge of the neuropodia or on the adjacent body-wall, as in syllids and nereidids. In many taxa, such as eunicids and hesionids, the dorsal cirri are slender, tapering or cirriform, but in the scale-worms some of the dorsal cirri are present as elytra (scales) which are held horizontally above the dorsal surface.

Chaetae may be extended or retracted by muscles which are usually attached to the inner, convex side of the epidermal invaginations. Commonly, chaetae in a fascicle have a joint investment of musculature, but if more than one type of chaetae are present in a fascicle, each may have separate musculature. Chaetal ultrastructure is similar in all cases, but there is considerable diversity of form. In all but two families of polychaetes, chaetae are bundles of thin-walled cylinders comprising a chitin-sclerotinised protein complex (Specht 1988). In the Amphinomidae and Euphrosinidae, the chaetae are also impregnated with calcium carbonate, which makes

them brittle and easily broken; this may have a possible defensive function. Examples of various chaetae are shown in Figures 1.12 and 1.44.

Many polychaetes, for example, amphinomids, eunicids, phyllodocids, polynoids, have internal chaetae, known as aciculae (singular = acicula), which form internal 'skeletal' or supporting rods for the parapodia. They are formed in the same manner as the projecting chaetae, but are attached to musculature in such a fashion that they are not everted, although they may protrude slightly. Numbers of aciculae vary from one in some parapodia, as in nephtyids, to two or more, sometimes forming a vertical series, for example, in eunicids, or forming bundles, as found in amphinomids. Supporting rods in the notopodia of apistobranchiids and in both rami of posterior segments of orbiniids are also aciculae.

Notochaetae and neurochaetae may resemble each other, or each ramus may have different chaetae. In sabellids and serpulids, anterior notochaetae are capillaries and the neurochaetae are uncini. On the posterior end, the position of the chaetae is switched so that the posterior notopodia carry uncini and the posterior neuropodia carry capillary chaetae. This shift in chaetal position and concomitant shift in parapodial shape, is referred to as chaetal inversion. Sabellariids also have chaetal inversion. In all other polychaete families, uncini are present in neuropodial positions along the body (for example, chaetopterids, pectinariids and terebellids).

In compound chaetae (Figs 1.12D, E, 1.44M-P), a joint or a hinge links a shaft to an appendage. The base of the appendage may fit into a socket at the distal end of the shaft, and is held in place by either a single basal ligament (for example, in glycerids and syllids), or an additional marginal ligament is present, as in eunicids. In a third arrangement, the whole outer layer of chaetal fibres forms a hinge (for example, flabelligerids). The socket at the end of the shaft may be symmetrical (homogomph, for example, certain nereidids), or one edge may be cut away in relation to the other edge (heterogomph, for example, many families of Phyllodocida). The appendages may be blunt or tapering to slender tips. When they are blunt, they may be dentate (for example, in eunicids, lumbrinerids, onuphiids, sigalionids, syllids; Fig. 1.12D, E) or falcate (for example, acrocirrids, flabelligerids, pisionids). Appendages tapering to slender, often filiform tips are present in such taxa as glycerids, goniadids, hesionids, nereidids and phyllodocids.

Spines (Fig. 1.44Q-Y) are thicker than capillary chaetae, may be curved or straight, and have simple, bluntly tapering tips. Spines may be present in a single anterior chaetiger, such as the palaeae of ampharetids and pectinariids (Fig. 1.12A), or the opercular chaetae of sabellariids. In chaetopterids, a pair of spines is present in chaetiger 4. In other taxa, such as amphinomids, cirratulids and orbiniids, spines may be present in many segments.

Hooks are thick, distally curved chaetae (Fig. 1.44Z-AE). They are often distally dentate and have various forms of guards or hoods. Distally dentate hooks are present in numerous families, such as capitellids, magelonids, maldanids, oweniids, sabellids and spionids. The cladistic analysis by Rouse & Fauchald (1997) suggested that dentate hooks evolved independently several times. Uncini are distally dentate chaetae in which the end piece is very much larger than the shaft (Fig. 1.44AF, AG). The shaft may be replaced by one or two thin, flattened ligaments attached to each end of the uncinus (as in chaetopterids). Uncini are present in chaetopterids, pectinariids, sabellariids, sabellids (Fig. 1.12F), serpulids, terebellids and other families.

Compound chaetae and some simple hooks may be covered with a hood (for example, in capitellids and lumbrinerids), or a pair of guards (as in eunicids and spionids). As the term implies, a hood has an opening on one side. The opening may be rounded, or form a slit in some taxa, such as capitellids. Guards are paired delicate chitinous sheaths protecting the tip of some chaetae.

Locomotion

Polychaetes use various forms of locomotion, as reviewed by Trueman (1978). In more mobile groups, such as nereidids, the circular muscle layer tends to be limited, but frequently special locomotor muscles are associated with the parapodia. The septation in these groups tends to be complete, such that segments have a constant volume and are basically independent units that have to be co-ordinated. These groups can display several patterns of locomotion from slow crawling to rapid swimming (Fig. 1.13A, B). For example, in *Nereis diversicolor*, the longitudinal muscles on each side of a given segment act out of phase with each other; when a parapodium moves forward the one on the other side moves backwards and when the longitudinal muscles on one side contract those on the other relax (and are stretched) (Fig. 1.13C). Sequential contraction and relaxation in adjacent segments results in waves of motion which pass

forward along the body. The parapodia are maximally extended and come into contact with the substratum when they are at the crest of each wave (Fig. 1.13D). The aciculae and other chaetae protrude and grip the substratum; as the crest of the wave passes the chaetae are retracted and the parapodium contracts and lifts off the substratum. When the worm crawls slowly, the wavelength of the undulations along the body is relatively short (four to eight segments) with a small amplitude. To crawl faster, the worm increases both the wavelength and amplitude of the undulations, which allows more power to be applied by the parapodia as they contact the substratum.

In burrowing and tube-dwelling polychaetes, both the circular and longitudinal muscles bands tend to be well developed; these act in concert to produce peristaltic contractions. Tubiculous polychaetes tend to have complete septa and reduced parapodia, resulting in a movement that is essentially peristaltic. The parapodia often carry chaetal types known as uncini which can dig into the side of the tubes. These can then act as anchors, allowing the worm to withdraw rapidly into the tube by contraction of the longitudinal muscle bundles.

Many burrowing polychaetes have little septation between segments and the coelomic contents are thus free to move from one part of the body to another. For example, many arenicolids burrow by embedding and anchoring the anterior

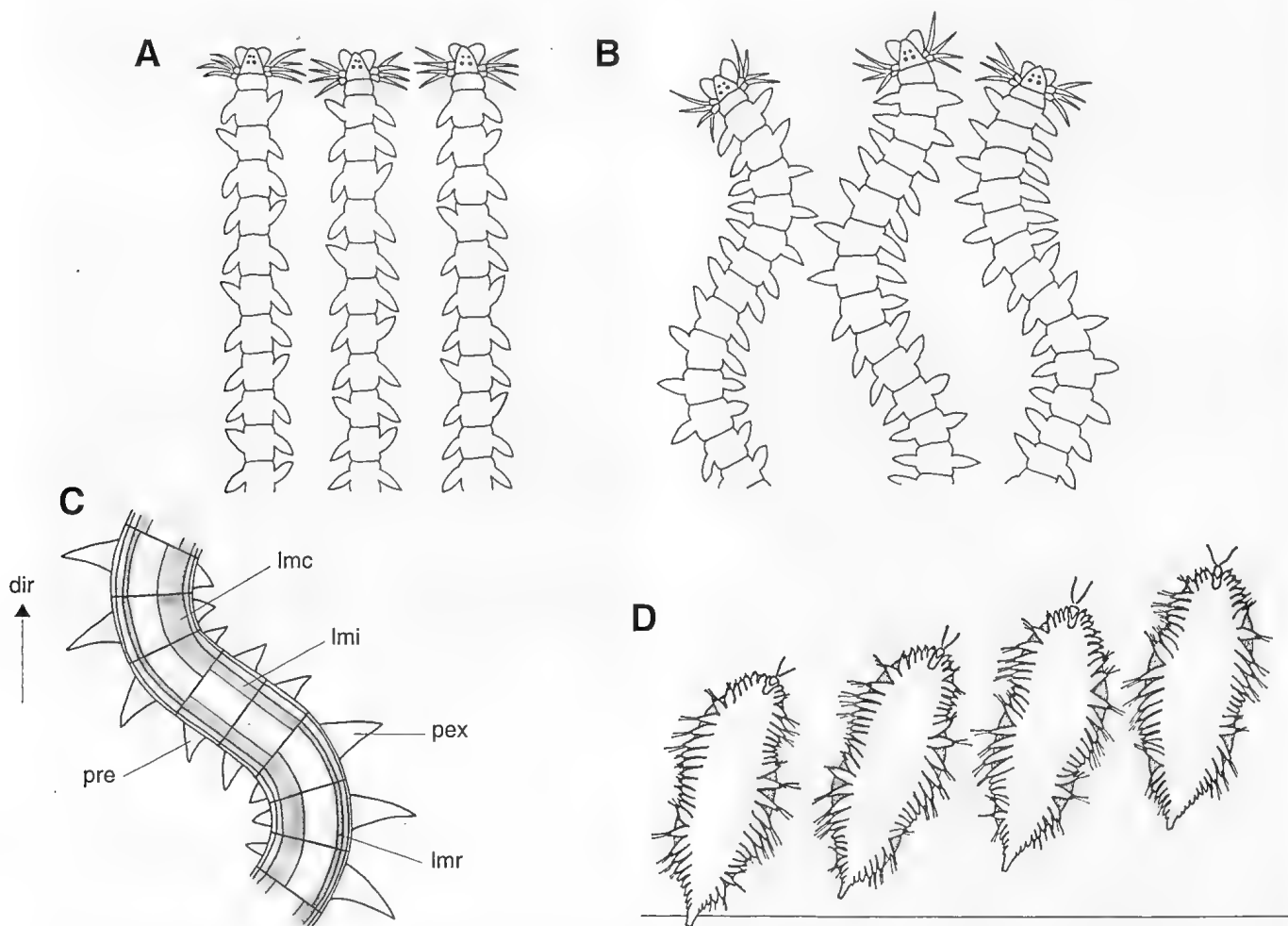


Figure 1.13 Locomotion in polychaetes. **A, B**, diagrammatic representation of locomotion in *Nereis*; chaetae not shown: **A**, slow crawling; **B**, rapid crawling. **C**, dorsal view of several segments of *Nereis* species during crawling. Note the states of contraction of longitudinal muscles (stippled), the body curvature, and the retraction and extension of parapodia. **D**, about half a complete parapodial cycle of *Aphrodita aculeata* (Aphroditidae), viewed from below; time interval between successive drawings is one second. **dir**, direction of locomotion; **lmc**, longitudinal muscles fully contracted; **lmi**, longitudinal muscles relaxed and incompletely stretched; **lmr**, longitudinal muscles relaxed and fully stretched; **pex**, parapodium extended and in contact with substratum; **pre**, parapodium retracted and lifted. (**A, B**, after Barnes, Calow & Olive 1993; **C**, after Russell-Hunter 1979; **D**, after Mettam 1971)

[**A, B**, K. Nolan]

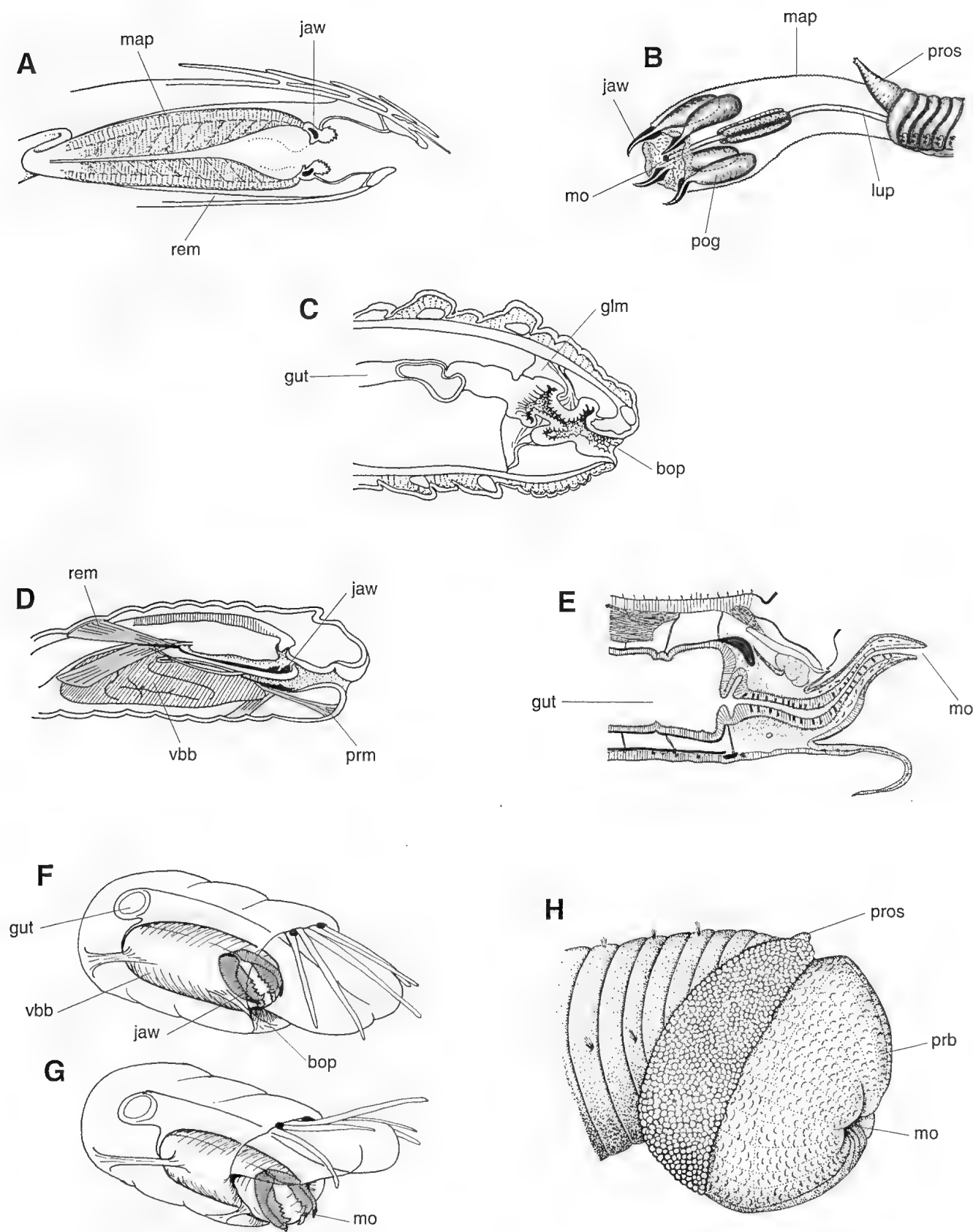


Figure 1.14 Anterior ends of polychaetes showing different buccal organs. **A**, muscularised axial buccal organ of *Aphrodita aculeata* (Aphroditidae) with pharynx and jaws retracted. **B**, muscular axial pharynx everted (proboscis) and four jaws of *Glycera americana* (Glyceridae). **C**, simple axial buccal organ of *Abarenicola vagabunda* (Arenicolidae). **D**, muscularised ventral buccal organ showing muscle bulbus and jaws of *Marphysa sanguinea* (Eunicidae). **E**, longitudinal section through the anterior end of *Pomatoceros triqueter* (Serpulidae), buccal organ absent. **F**, **G**, anterior end of an euniceid with muscularised ventral buccal organ with muscle bulbus and jaws retracted (**F**) and everted (**G**). **H**, anterior end of *Notomastus latericeus* (Capitellidae) with the simple axial buccal organ and eversible proboscis. **bop**, buccal opening; **glm**, gular membrane; **gut**, gut; **jaw**, jaw; **lup**, lumen of pharynx; **map**, muscularised axial pharynx; **mo**, mouth; **pog**, poison gland; **prb**, proboscis; **prm**, protractor muscle; **pros**, prostomium; **rem**, retractor muscle; **vbb**, ventral buccal bulb. (**A**, **C**, **D**, after Dales 1962a; **B**, after Barnes 1974; **E**, after Thomas 1940; **F**, **G**, after Barnes, Calow & Olive 1993; **H**, after Barnes 1980)

end in muddy or sandy substratum. This is accomplished by contracting the circular muscles of the posterior region, forcing the coelomic fluid into the anterior region of the body and causing it to swell. The more posterior segments are then contracted using the longitudinal muscles and are drawn forward towards the anchored anterior segments. With contraction of the circular muscles in the anterior segments, the posterior end of each segment is protruded as it elongates, enabling it to anchor in the sediment. The head is then pushed forward and the proboscis everted to allow the animal to deepen the burrow. The cycle then begins again. However, an arenicolid is only capable of maintaining such activity for a short time and is largely sedentary in its burrow. Annelids with complete septation that burrow or crawl can sustain their activity for much longer (Trueman 1978).

Feeding and Digestion

The initial mouth region in larval annelids (the stomadeum) may give rise to a variety of adult structures collectively called buccal organs. The structure of the buccal organs was used by Dales (1962a) as a basic criterion in an influential study on grouping polychaete families. His system has been modified for use here. It includes four groups distinguished by their buccal organ: muscular axial buccal organ; simple axial buccal organ; ventral buccal organ which may be simple or have well-developed musculature, and; buccal organ absent or occluded. The muscular region of the buccal organ is called the pharynx; the eversible non-muscular region is often referred to as the proboscis.

Families with a muscular axial buccal organ. In many polychaetes, the pharynx is eversible and surrounded by thickened, strongly muscular walls (Fig. 1.14A, B). It may be retracted into a sheath, especially in taxa which have large jaws, such as nereidids, or very heavy musculature, for example, hesionids and nephtyids. In other taxa, such as glycerids, goniadids and phyllodocids, the pharynx is partially retracted and inverted. The mouth proper is located at the tip of the fully everted pharynx. In some families, such as the Phyllodocidae, the muscular eversible pharynx lacks jaws; in others, jaws are present, as in the Glyceridae, Hesionidae, Nereididae, Pisionidae and Polynoidae.

Jaws may be present as a bilaterally arranged pair (as in nereidids), as one or two dorso-ventrally arranged pairs (as in polynoids), as two pairs forming a cross (as in glycerids) or as a circlet of smaller or larger pieces (as in goniadids). In some Syllidae, the pharynx is tipped with papillae which may be sclerotinised; behind the mouth opening, but usually projecting forward sufficiently to reach the mouth when fully everted, may be a single dorsal, pointed tooth. In syllids, the eversible structure leads into a strongly muscularised proventricle in which the muscle fibres are arranged radially.

Families with a simple axial buccal organ. The sac-like eversible proboscis present in certain taxa (for example, arenicolids, capitellids, some maldanids and opheliids; Fig. 1.14C, H) relies on fluid pressure from the coelom for eversion. Musculature or glands are not especially developed. The worms with this structure tend to have reduced septa in the anterior part of the body. This arrangement allows the contraction of the posterior part of the body to exert considerable force on the buccal apparatus through the free movement of the coelomic contents. Muscles associated with a thickened first septum retract the proboscis.

Families with a simple ventral buccal organ. A variable, often complex set of folds, musculature and glands present on the ventral side of many polychaetes is usually referred to as a ventral buccal organ. This is the most common form of buccal

organ in polychaetes. Ventral buccal organs may be simple eversible muscular pads, as in sand/mud-eating groups such as the Orbiniidae and Opheliidae. The outer end of these pharynges may be frilled and densely ciliated. The lateral walls of the eversible proboscis of paraonids is folded and broadly connected ventrally to a deep buccal organ.

Ventral buccal organs may be eversible or non-eversible. Purschke (1988a) has argued that they have evolved many times in polychaetes. Rouse & Fauchald (1997) showed that either this could be the case or that ventral buccal organs were a primitive state for polychaetes.

Families with a ventral buccal organ with well-developed musculature. In many of the Eunicida, the ventral and lateral walls of the buccal organ are muscular and the lining is sclerotinised into a varying number of jaw pieces (Fig. 1.14D, F, G). The jaws are separated into a pair of ventral mandibles and two or more pairs of lateral maxillae.

The maxillae are arranged in various ways (see Fig. 1.45; Kielan-Jaworowska 1966). In labidognath polychaetes, the jaws are highly differentiated (Fig. 1.45E–G), and situated such that when the jaw apparatus is withdrawn, the larger pieces are located in a pocket with the smaller pieces arranged in semi-circles at the anterior end of the pocket. Families with this arrangement include Onuphidae, Eunicidae and Lumbrineridae. In prionognath polychaetes (Fig. 1.45B–D), more or less similar jaw-pieces are located in two rows on longitudinal ridges. Such families include Oeonidae and Histriobdellidae and probably Hartmaniellidae. Two additional terms for maxillary assemblages are used, placognaths and ctenognaths. The former have exclusively been reported from fossils. Ctenognath jaws (Fig. 1.45A) comprise relatively large basal maxillae and symmetrically arranged rows of numerous anterior denticles in longitudinal series without carriers. They occur in dorvilleids and various extinct taxa. Maxillae of juvenile onuphids and eunicids have a ctenognath arrangement, but are far less differentiated than the denticles present in dorvilleids.

In amphinomids and euprosinids, the ventral wall of the buccal organ is also muscularised and eversible and the cuticular lining is sclerotinised. The sclerotinisation is less obvious than in euniceans; instead of forming distinct jaws, the whole ventral lining forms reinforced ridges and papillae in a file-like structure.

Families with buccal organ absent. The buccal cavity in many polychaetes lacks obvious differentiation of the wall as large glands or additional muscular layers and it is not eversible (Fig. 1.14E). This condition is found in filter-feeding groups such as Sabellidae and Serpulidae.

Accessory Feeding Structures

Associated with the simple forms of buccal organs (ventral or simple axial), or where a buccal organ is absent, other structures facilitate feeding. These include palps, tentacles, or a tentacular crown. As discussed above, all of these structures can be regarded as homologous and referred to as grooved palps. A single pair of grooved palps is present in many polychaetes (for example, in flabelligerids and spionids). These palps are nearly always attached dorsally at or near the junction of the prostomium and peristomium. In terebellids, trichobranchids, ampharetids and pectinariids, numerous grooved palps are present. In the sabellids and serpulids, the grooved palps form a prostomial tentacular crown. The crown has a complex ciliary pattern basically similar to the ciliated grooved structures present in, for example, the paired palps of spionids (Gardiner 1988; Fauchald & Rouse 1997).

Feeding Methods

The diverse, feeding structures in annelids can be grouped into several functional categories. A given functional category can contain taxa that have different buccal organs; thus feeding categories are not indicative of phylogenetic relationships, but are useful for ecological purposes. The categories used here are derived from Fauchald & Jumars (1979).

Raptorial Feeding

Raptorial feeders use their buccal apparatus, usually an eversible muscular ventral or muscular axial pharynx, to seize food items. Members of the Eunicida and Phyllodocida, the two groups in which jaws have evolved, use them to either seize live animals (carnivores), tear off pieces of algae (herbivores) or to grasp dead and decaying matter (scavengers). Some of the raptorial groups, such as the Phyllodocidae, lack jaws and use their eversible pharynx to capture prey. Members of the eunicidan family Onuphidae, such as *Australonuphis* species, are well known from Australian beaches (Paxton 1979). These burrowing polychaetes emerge to seek their prey where waves break. They have powerful jaws and feed on small to medium-sized invertebrates as well as drift algae. *Australonereis ehlersi* (Fig. 1.1), a nereidid that builds a temporary tube predominantly in sheltered sandy habitats on the Australian east coast, is probably omnivorous, using its powerful jaws attached to the eversible pharynx to grasp food that comes near the tube; however, other feeding modes have been postulated for their species (see family Nereididae).

Non-Selective Deposit-Feeders

Many polychaetes ingest mud, or sand and show little discrimination in the size or type of particles eaten. Any digestible organic material in the ingested sediment is assimilated as it passes through the alimentary canal. This form of feeding is called non-selective deposit-feeding. The majority of groups using this method have a simple ventral or axial buccal organ. Some non-selective deposit-feeders, such as arenicolids and maldanids, live in relatively permanent burrows or tubes and feed on the continuous rain of sand or mud falling around the burrow (Fig. 1.15A). Others, such as orbinids, which do not have permanent burrows or tubes, move about the sediment, eating it as they tunnel. The amount of nutritional value in sediment varies; shallow-water mud deposits tend to contain high densities of non-selective deposit-feeders. The total organic matter in such areas can be as low as 1–2% and most deposit-feeders have to eat continually. The processing time for sediment, from ingestion to ejection through the rectum, can be as little as 15 minutes in taxa such as *Arenicola marina* (Kermack 1955).

Selective Deposit-Feeders

Some deposit-feeders do not ingest sediment haphazardly, but use their palps or buccal organs to sort organic material from the sediment prior to ingestion. Others select sediment particles of a particular size range, usually the smaller particles. As smaller particles have a greater surface area to volume ratio than large particles, they carry more food proportionately per weight ingested. Hence, it is more efficient to eat smaller particles than a random selection of various-sized particles.

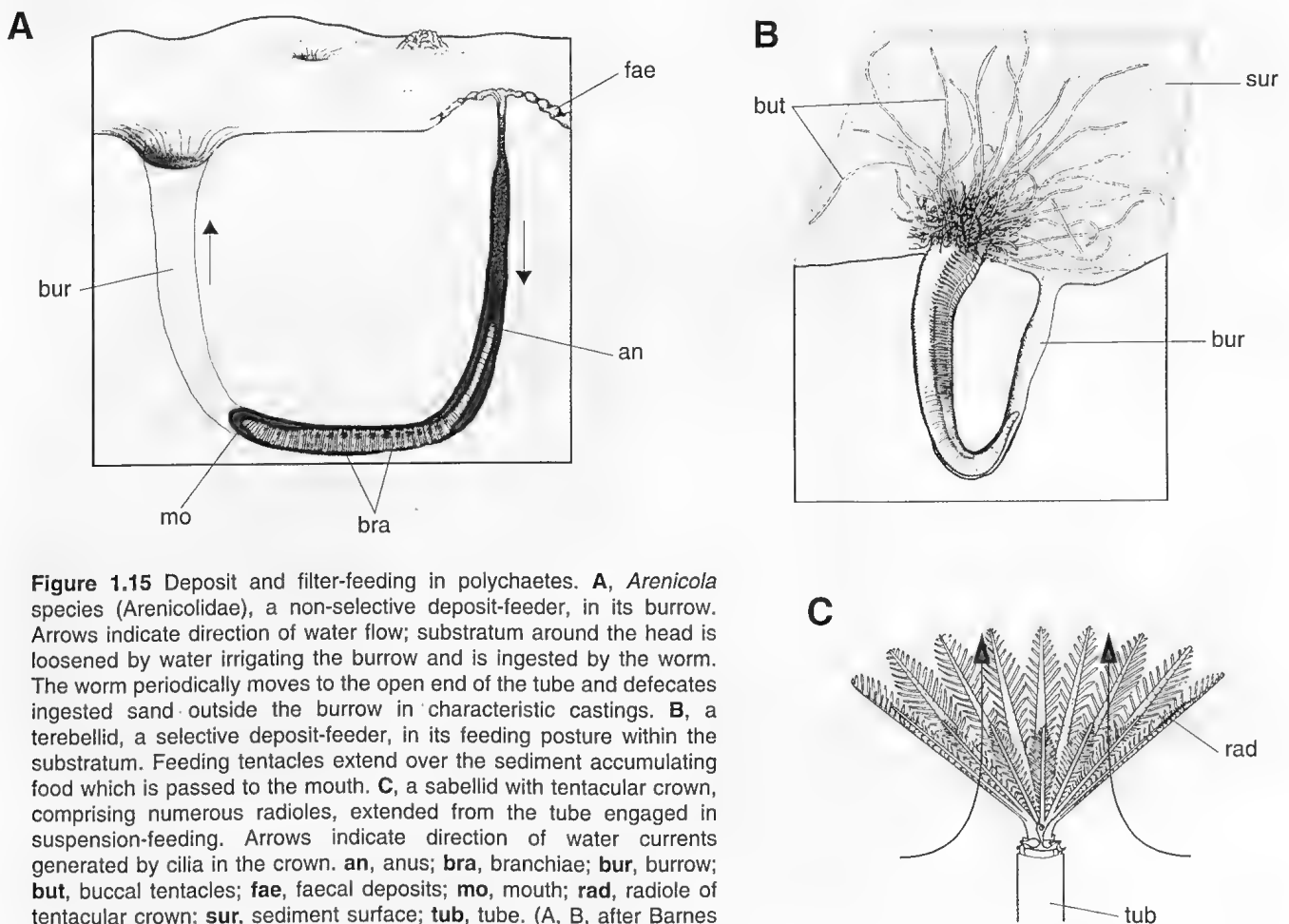


Figure 1.15 Deposit and filter-feeding in polychaetes. **A**, *Arenicola* species (Arenicolidae), a non-selective deposit-feeder, in its burrow. Arrows indicate direction of water flow; substratum around the head is loosened by water irrigating the burrow and is ingested by the worm. The worm periodically moves to the open end of the tube and defecates ingested sand outside the burrow in characteristic castings. **B**, a terebellid, a selective deposit-feeder, in its feeding posture within the substratum. Feeding tentacles extend over the sediment accumulating food which is passed to the mouth. **C**, a sabellid with tentacular crown, comprising numerous radioles, extended from the tube engaged in suspension-feeding. Arrows indicate direction of water currents generated by cilia in the crown. **an**, anus; **bra**, branchiae; **bur**, burrow; **but**, buccal tentacles; **fae**, faecal deposits; **mo**, mouth; **rad**, radiole of tentacular crown; **sur**, sediment surface; **tub**, tube. (A, B, after Barnes 1974; C, after Newell 1970)

Selective deposit-feeders usually live in tubes. The method of sorting varies according to the types of palps present. Terebellids may lay out their numerous buccal tentacles, each with a longitudinal mucus-filled ciliated groove, over the sediment surface (Figs 1.15B, 1.32). Detritus is selected or rejected. The selected particles stick to the mucus and are carried along the groove by ciliary action to the base of the buccal tentacle. Each buccal tentacle is wiped periodically on the lower lip where cilia carry the mucus plus detritus into the mouth. Those polychaetes, such as spionids, which have only a single pair of grooved palps use a similar method of feeding; they sweep the palps over the sediment surface or wave them in the water column to gather food. Lumbrinerids are usually reported to be herbivorous or carnivorous, though some have been reported as deposit-feeders. Petch (1986) studied the burrowing and feeding behaviour of an Australian lumbrinerid in Westernport Bay, and found that they were selective deposit-feeders, ingesting sediment of a smaller particle size. Other selective deposit-feeders include pectinariids, oweniids and possibly opheliids (Fauchald & Jumars 1979).

Filter-Feeders

Polychaetes in a number of groups filter suspended particles from the water column. These filter-feeders all live in some sort of tube. The best-known are sabellids (see Fig. 1.15C), serpulids and some chaetopterids. Sabellids and serpulids have elaborate palps in the form of tentacular crowns. A funnel is formed as the crown is expanded out of the tube. On each radiole cilia beat and create a current in the surrounding water. This current passes through the radioles into the funnel, swirls around its base and then passes upwards and outwards. Food particles are trapped on small branches of the radioles, termed pinnules, and carried into the groove by cilia. The ciliary current transports the particles towards the base of the

radioles where the material is sorted. Small particles are swallowed, but large ones are diverted from the mouth and dropped into the water. Some species sort the particles into three sizes; mid-sized particles are used in construction of the tube (Nicol 1930; Mayer 1994).

Digestive Tract

The digestive tract may be differentiated in certain families (for example, flabelligerids, terebellids), but this has been described for very few families. In most polychaetes, the gut is essentially a simple tube (Fig. 1.16A), supported, at least, by a dorsal mesentery and by partial to complete septa between the segments. In many polychaetes, the gut is distended in each segment and reduced in diameter where it passes through each septum. The gut may be longer than the body. For example, in cirratulids it zigzags through the body cavity, passing through the septa at the mid-line, but forming alternating loops at the side of the segments. In ampharetids and pectinariids, the gut may form one or two loops in the anterior part of the body (Fig. 1.16B). Such loops in the gut are associated with incomplete septa, at least in the anterior end, so that the gut lies more or less free in the body-cavity. In some polychaetes, such as aphroditids and polynoids, distinct branches of the gut extend laterally and sometimes dorsally into the bases of the dorsal cirri and other appendages (Fig. 1.16C). Dales & Pell (1971) demonstrated that these side branches show physiological differentiation in scale-worms. The ultrastructure of the various gut regions found in polychaetes have been reviewed by Michel (1988). Jeuniaux (1969) and Michel & DeVillez (1978) reviewed the nutritional physiology found in polychaetes using a range of feeding mechanisms. Penry & Jumars (1990) assessed the gut architecture of deposit-feeding and carnivorous polychaetes and have inferred possible constraints on digestion and foraging.

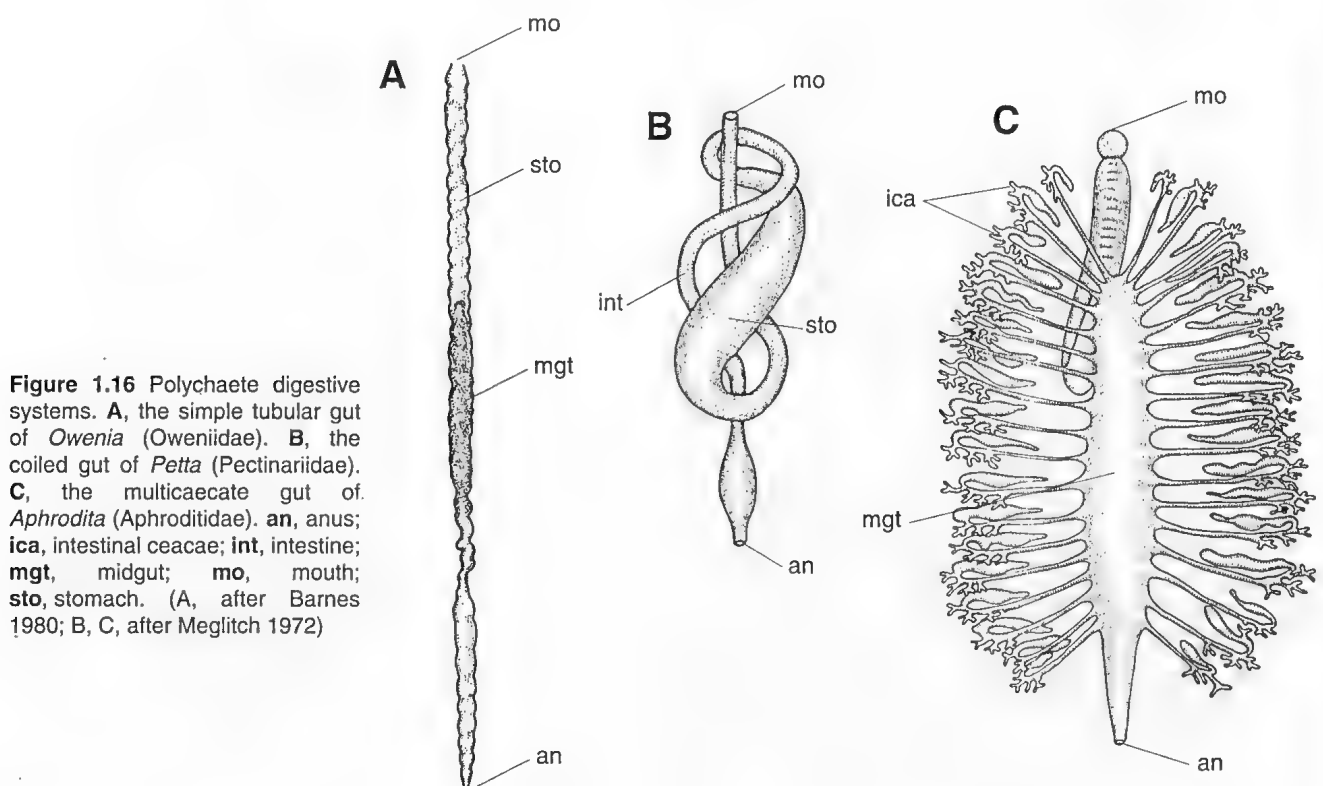


Figure 1.16 Polychaete digestive systems. **A**, the simple tubular gut of *Owenia* (Oweniidae). **B**, the coiled gut of *Petta* (Pectinariidae). **C**, the multicacate gut of *Aphrodita* (Aphroditidae). an, anus; ica, intestinal caecae; int, intestine; mgt, midgut; mo, mouth; sto, stomach. (A, after Barnes 1980; B, C, after Meglitch 1972)

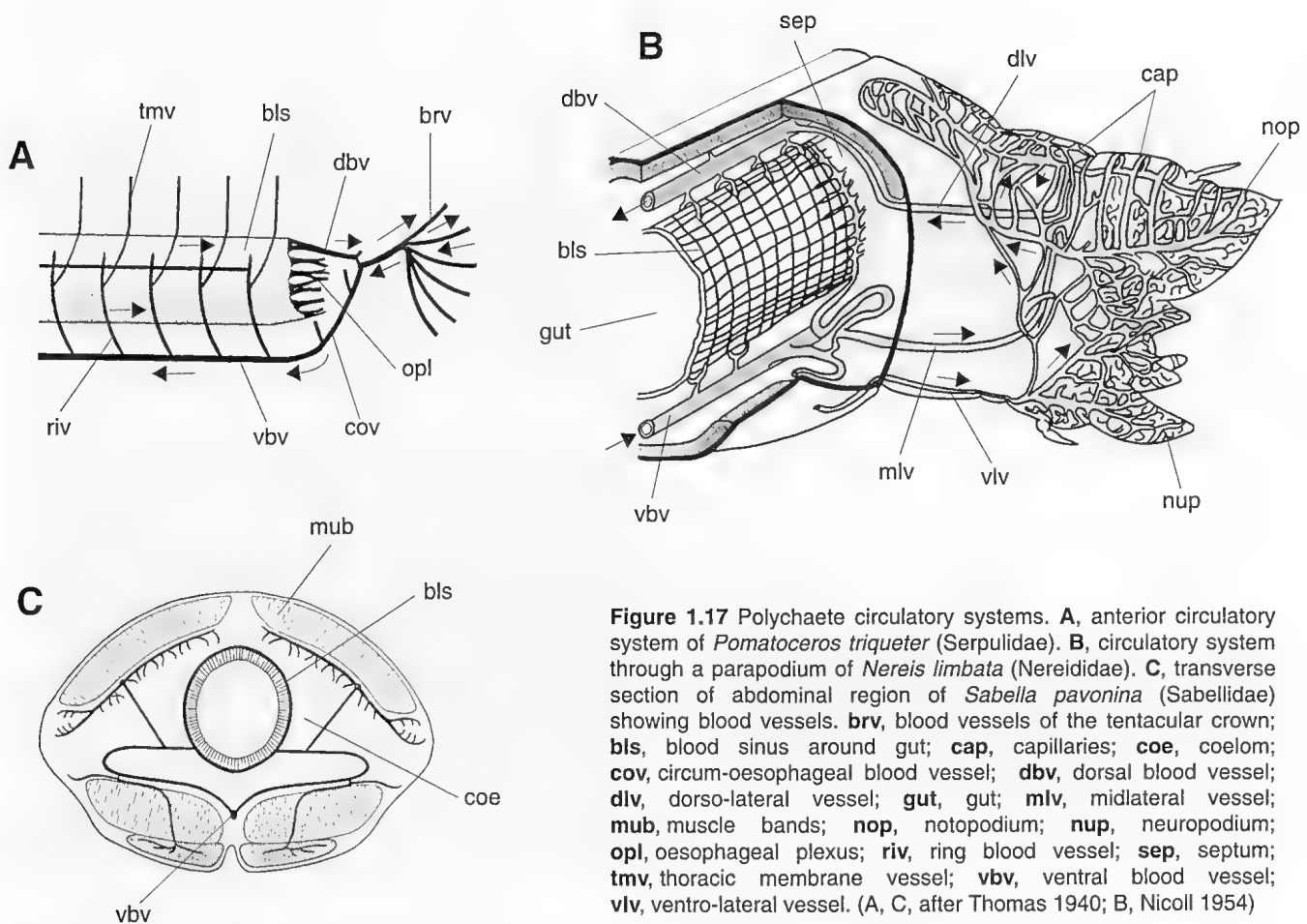


Figure 1.17 Polychaete circulatory systems. **A**, anterior circulatory system of *Pomatoceros triquetrum* (Serpulidae). **B**, circulatory system through a parapodium of *Nereis limbata* (Nereididae). **C**, transverse section of abdominal region of *Sabella pavonina* (Sabellidae) showing blood vessels. **brv**, blood vessels of the tentacular crown; **bls**, blood sinus around gut; **cap**, capillaries; **coe**, coelom; **cov**, circum-oesophageal blood vessel; **dbv**, dorsal blood vessel; **dlv**, dorso-lateral vessel; **gut**, gut; **mlv**, midlateral vessel; **mub**, muscle bands; **nop**, notopodium; **nup**, neuropodium; **opl**, oesophageal plexus; **riv**, ring blood vessel; **sep**, septum; **tmv**, thoracic membrane vessel; **vbv**, ventral blood vessel; **viv**, ventro-lateral vessel. (A, C, after Thomas 1940; B, Nicoll 1954)

Circulation and Respiratory Structures

The closed circulatory system of most polychaetes comprises medial, dorsal and ventral longitudinal vessels, linked by smaller vessels, capillary beds and gut lacunae (Hanson 1949a); some examples are shown in Figure 1.17. The blood flows anteriorly in the dorsal vessel and towards the pygidium in the ventral vessel. The latter lies directly beneath the gut and has branches that supply the body wall muscles, the epidermis and, if present, the branchiae. The flow from these areas returns blood to the dorsal vessel via lateral vessels situated in each segment, and thence around the gut to the ventral vessel. As in all annelids, blood flow in polychaetes depends on movements of the body wall and muscles surrounding the dorsal blood vessel. Some taxa, usually tube-dwelling forms, have specialised pumping organs or 'hearts'. Many branchiae are also contractile. Although a complete, closed circulatory system is present in most polychaetes, it is limited in a number of families, such as Phyllodocidae. In these groups major blood-vessels are present, but the distal capillary vessels are lacking. A circulatory system is absent in many small polychaetes (for example, histriobdellids), and also in larger-bodied families such as capitellids, glycerids and goniatids (Smith & Ruppert 1988).

Many polychaetes have elaborate branchiae (gills), developed as extensions of the body wall and containing a loop of the vascular system and epidermal capillaries. The branchiae serve to increase vastly the surface area available for gas exchange.

In many families (for example, some Eunicidae, Opheliidae and Scalibregmatidae), the branchiae are associated directly with dorsal cirri or the notopodial lobes. These parapodial branchiae may consist of single filaments (as in opheliids), be tufted (as in amphinomid) or pectinate (as in eunicids). In

other taxa, such as spionids, branchiae may emerge from the dorsum between the notopodia and the dorsal mid-line of the body; they are usually separate from the notopodia. Dorsal branchiae take a variety of shapes. The simple kinds may have a circular cross-section or be flattened and may be digitiform or tapering and are often heavily ciliated along the narrow edges. They may be present on many segments (as in cirratulids) or be limited to a few segments anteriorly (as in ampharetids and terebellids). Dorsal branched branchiae often have a stalk and a distal group of filaments. Each filament may be branched dichotomously, as in certain terebellids, or flattened and foliose as are those of pectinariids. Inter-ramal branchiae are unique to the nephtyids; tapering, curved and usually ciliated along both edges, these branchiae are suspended from the notopodial ramus between the parapodial rami (Fauchald & Rouse 1997).

In tube-dwellers or burrowers, the branchiae tend to be regionalised at the anterior or posterior end, usually where there is maximum water flow. The paired branchiae of terebellids are situated on the dorsal part of the anterior segments and have a surface area equivalent to one third of the body wall of those segments (Mangum *et al.* 1975). The tentacular crown is the primary site of respiration in the tubicolous Sabellidae and Serpulidae, though there is some evidence for auxiliary respiration across the body wall by generating water currents through the tube (Hanson 1950b). The notopodial ligules of the nereidids and the dorsal cirri of the phyllodocids may have obvious vascularisation, but they lack characteristic capillary loops; they are not considered branchiae.

The blood of most annelids does not contain cells, although they have been recorded in a number of polychaete families (for example, magelonids). Groups lacking a circulatory system may have special cells in the coelom that contain a

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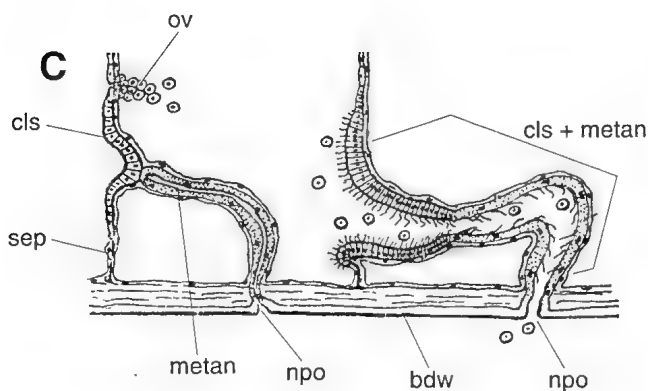
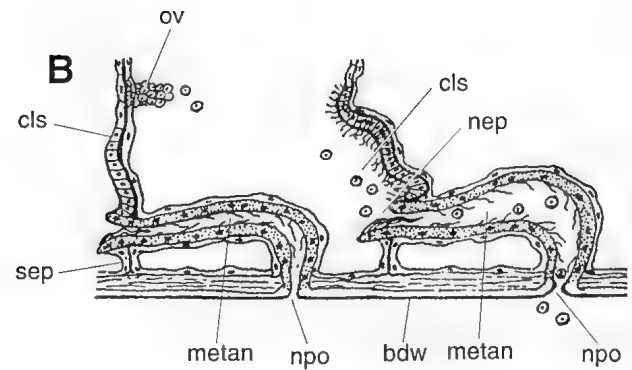
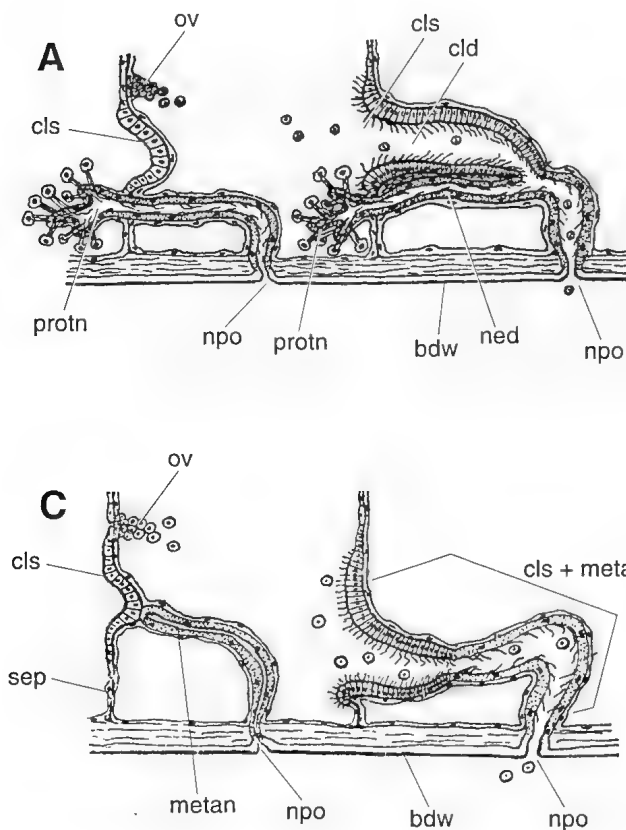


Figure 1.18 Development of three different types of nephridia found in polychaetes. **A**, development of protonephromixia. Early stage (left) with protonephridium formed and coelomostome beginning. Mature stage (right) with coelomostome fused with nephridioduct. **B**, development of metanephromixia. Early stage (left) with metanephridium formed and coelomostome beginning. Mature stage (right) with coelomostome grafted onto the nephrostome. **C**, development of mixonephridium. Early stage (left) with metanephridium and coelomostome forming. Mature stage (right) with coelomostome fused completely with a metanephridial nephrostome. **bdw**, body wall; **cld**, coelomoduct; **cls**, coelomostome; **metan**, metanephridia; **ned**, nephridioduct; **nep**, nephrostome; **npo**, nephridiopore; **ov**, ovary; **protn**, protonephridium; **sep**, septum. (Modified after Goodrich 1945)

form of haemoglobin. Most other annelids have respiratory pigments dissolved in the blood, although many small species completely lack pigments. The respiratory pigments of polychaetes may be grouped as haemoglobins or chlorocruorins. The former gives the blood a red colour and the latter green. The pigments serve to transport oxygen to the tissues, and polychaetes can draw about 50–60% of the oxygen from the water that comes into contact with the body or branchiae (Weber 1978a). The heart body is a plug of tissue which almost occludes the lumen in the dorsal (supraoesophageal) vessel of many polychaetes such as acrocirrids, ampharetids, flabelligerids, cirratulids, pectinariids and terebellids. The role of these ‘heart’ tissues, in general, appears to be the formation of blood, but in certain taxa it may also have a mechanical function which maintains blood flow (Kennedy & Dales 1958).

Nephridia and Excretion

In most polychaetes, there are usually two fluid systems, the coelom and the circulatory system, and both (if present) are involved in the excretion of waste products. To achieve this excretion there must be ducts to the exterior. There has been considerable debate over the structure, function and evolution of the excretory system in polychaetes (see Rouse & Fauchald 1997). Monumental studies by Goodrich (1895, 1945) on excretory systems in invertebrates published more than 50 years ago are still influential. Because of the diversity of their excretory organs, Goodrich focussed much of his efforts on polychaetes. He showed that annelids have connections to the exterior from the coelom via nephridia and by gonoducts, also called coelomoducts. Both types of ducts tend to be arranged segmentally.

The theoretical basis of Goodrich’s interpretation rests on the observation that, in polychaetes in particular, mesodermal coelomoducts and ectodermal (or ectomesodermal) nephridia can fuse to form single structures. Nephridia can lie closed off in the coelom (= protonephridia; Figs 1.18A, 1.19A) or have an open funnel (= metanephridia; Fig. 1.18B) termed a nephrostome. All nephridia open externally by nephridiopores. In polychaetes, the inner end of a nephridium projects or opens into the coelom of the segment in front of the one in which the nephridiopore is located. Filtration units (podocytes) lie between the circulatory system and the coelom, and increased pressure in the blood vessels results in filtered vascular fluid containing waste products entering the coelom. These waste products are then selected and excreted via the open ducts of the metanephridia. In many instances in which a protonephridial system is present, a circulatory system is absent or reduced. Protonephridia have specialised terminal cells between the duct to the exterior and the coelom. These terminal cells are responsible for directly filtering the waste products from the coelomic fluid.

Coelomoducts may have a funnel (coelomostome) and gonoducts to the exterior, but they are often combined with nephridia. Goodrich defined such structures as nephromixia and classified them into three groups: protonephromixia, metanephromixia and mixonephridia (Fig. 1.18). In protonephromixia, mesodermal components are grafted onto a canal of the protonephridium. The term metanephromixia was used when there was clear morphological evidence that mesodermal funnels have been added to open nephrostomes, and mixonephridia for when the coelomic ends of the nephridia were completely fused with coelomostomes. Metanephromixia do not appear until sexual maturity, whereas mixonephridia form much earlier. However, the line between metanephromixia and mixonephridia is difficult to draw. Lately, Goodrich’s work has been subject to some

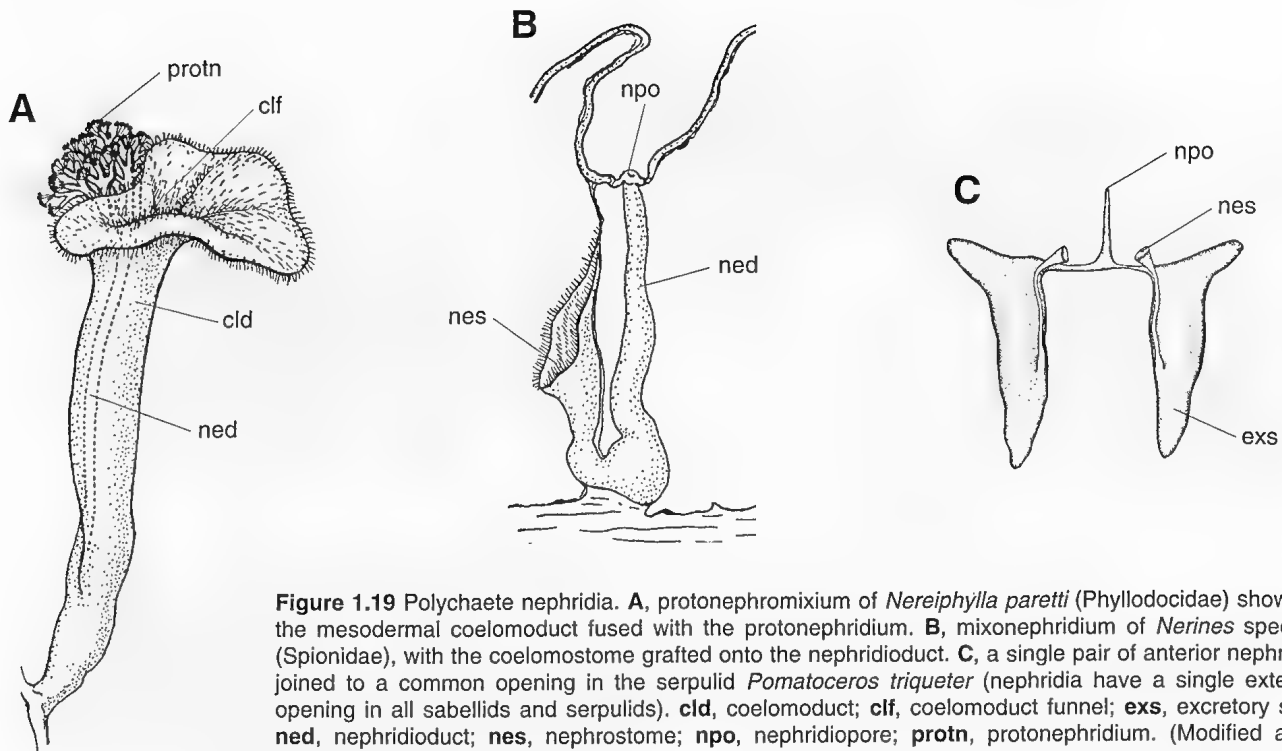


Figure 1.19 Polychaete nephridia. **A**, protonephromixium of *Nereiphylla paretii* (Phyllodocidae) showing the mesodermal coelomoduct fused with the protonephridium. **B**, mixonephridium of *Nerines* species (Spionidae), with the coelomostome grafted onto the nephridioduct. **C**, a single pair of anterior nephridia joined to a common opening in the serpulid *Pomatoceros triqueter* (nephridia have a single exterior opening in all sabellids and serpulids). **cld**, coelomoduct; **clf**, coelomoduct funnel; **exs**, excretory sac; **ned**, nephridioduct; **nes**, nephrostome; **npo**, nephridiopore; **protn**, protonephridium. (Modified after Goodich 1945)

criticism (Bartolomaeus 1989; Bartolomaeus & Ax 1992) and further study of polychaete excretory systems is needed (see Rouse & Fauchald 1997).

In capitellids and some small-bodied polychaetes such as histriobdellids, the nephridial ducts and gonoducts are wholly separate. Metanephromixia and protonephromixia are present only in members of the Phyllodocida. Mixonephridia are present in nearly all other polychaetes including amphinomids, ampharetids, eunicids, flabelligerids, opheliids, sabellids and spionids (Fig. 1.19B).

The distribution of nephridia in polychaetes varies, but most commonly nephridia are present along most of the body (for example, amphinomids, euphosinids, eunicids, glycerids, hesionids, nereidids, orbiniids; Fig. 1.3) with no differentiation between fertile and non-fertile segments. In other groups, there is a single anterior pair of exclusively excretory nephridia (Fig. 1.19C) and numerous posterior ducts that apparently function exclusively as gonoducts (for example, in cirratulids, flabelligerids, sabellids, serpulids). In a third group of families, about five to seven pairs of nephridia are present in the anterior part of the body (for example, in arenicolids, scalibregmatids, terebellids), but in these families the anterior nephridia are excretory and the posterior ones act as gonoducts (Rouse & Fauchald 1997).

Osmoregulation

Most polychaetes are osmoconformers, which may explain why very few groups live in freshwater. When exposed to low salinities, most polychaetes swell up in an uncontrolled manner. Certain intertidal and estuarine species are able to withstand short periods of stress caused by changing salinities. The few polychaetes that have been able to penetrate and live in freshwater mostly belong to the families Nereididae and Sabellidae. These are almost certainly osmoregulators, although how they accomplish this is unknown. The very few terrestrial polychaete genera (for example, *Parergodrilus* and *Hrabiella*) are found only in very damp environments. Ogelsby (1978) has reviewed

osmoregulation in polychaetes. The nereidid, *Simplisetia limnetica*, is a freshwater polychaete found in the upper reaches of the Hawkesbury River (Glasby 1986). Another unusual Australian polychaete, with tolerance to osmotic stress, is the small sabellid, *Manayunkia athalassia*, from ephemeral saline lakes near the Coorong, South Australia (Hutchings *et al.* 1981). Polychaetes are reported as being virtually incapable of resisting desiccation, but *M. athalassia* is capable of surviving in dry salt-lake beds over several months during summer and can tolerate salinities of up to three times that of normal seawater.

Nervous System and Sensory Structures

The brain, or cerebral ganglion, in polychaetes originates, and is usually situated in the prostomium. The brain varies morphologically, from most complex in active, mobile forms such as species of *Australonereis* (Nereididae) and *Eunice* (Eunicidae) to simple and modestly differentiated in deposit-feeders such as *Ctenodrilus* species (Ctenodrilidae). This variation in brain morphology is correlated with the degree of sensory input the brain receives, since burrowing, sedentary forms tend to have few sensory appendages. In all taxa, the brain is dorsal and is connected to the ventral nerve cord by two circum-oesophageal connectives (commissures). In polychaetes with simple brains, there are no obvious subdivisions (Fig. 1.20A, B). In polychaetes with a complex brain, there are three distinct divisions: a forebrain, mid-brain and hind brain (Fig. 1.20C, D).

The forebrain has palpal and buccal centres and the anterior roots of the circum-oesophageal connectives. The mid-brain has antennal and optical centres and the posterior roots of the circum-oesophageal connectives. The hindbrain has centres for the nuchal organs. The ventral nerve cord, which is usually made up of a coupled pair of cords, runs the length of the body. It varies in thickness and dilates into a ganglion in each segment, from which pairs of segmental nerves pass out to the body wall, muscles and gut (Bullock 1965). Various aspects of polychaete neurophysiology were reviewed by Mill (1978).

1. CLASS POLYCHAETA

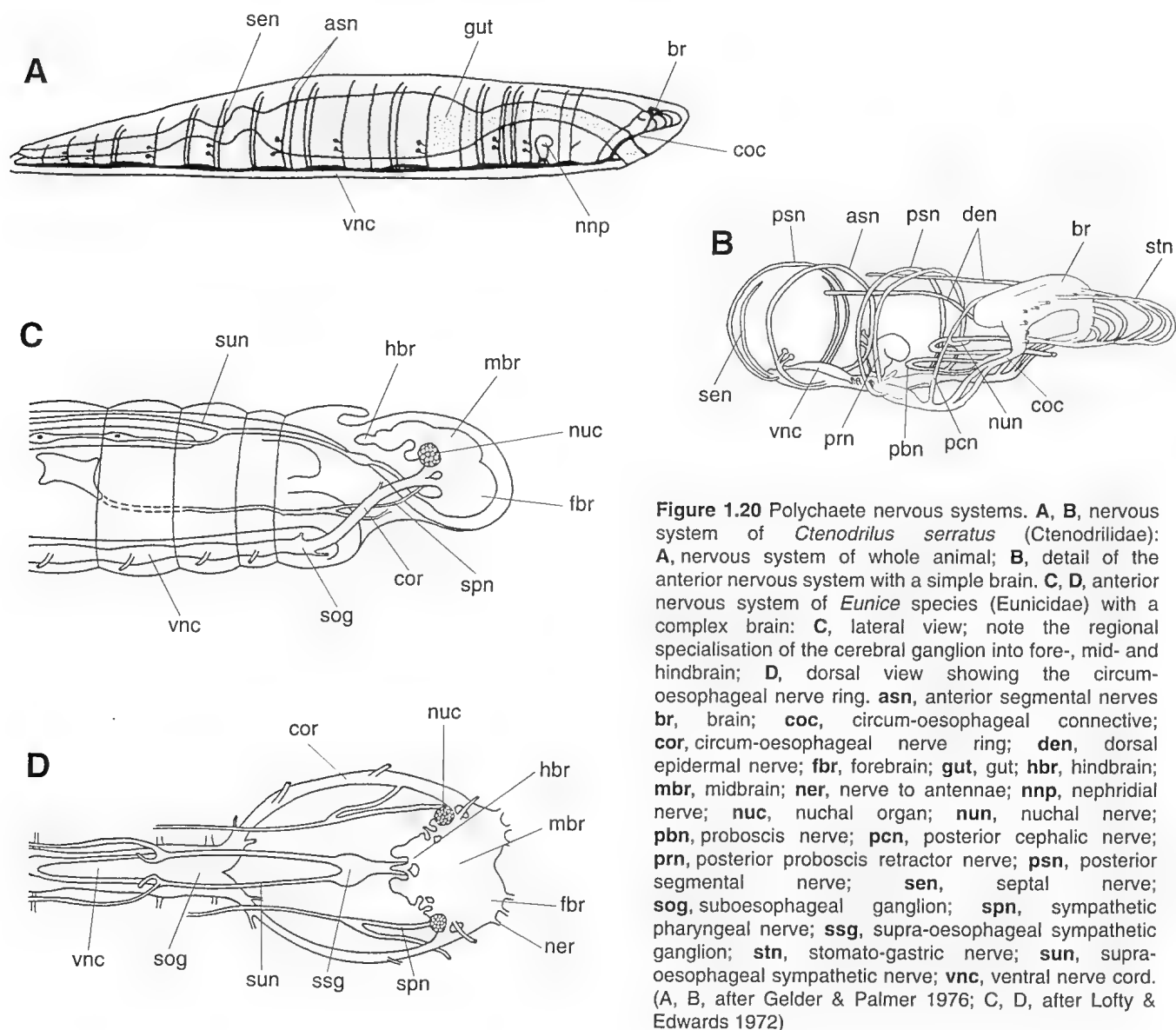


Figure 1.20 Polychaete nervous systems. **A, B**, nervous system of *Ctenodrilus serratus* (Ctenodrilidae): **A**, nervous system of whole animal; **B**, detail of the anterior nervous system with a simple brain. **C, D**, anterior nervous system of *Eunice* species (Eunicidae) with a complex brain: **C**, lateral view; note the regional specialisation of the cerebral ganglion into fore-, mid- and hindbrain; **D**, dorsal view showing the circum-oesophageal nerve ring. **asn**, anterior segmental nerves; **br**, brain; **coc**, circum-oesophageal connective; **cor**, circum-oesophageal nerve ring; **den**, dorsal epidermal nerve; **fbr**, forebrain; **gut**, gut; **hbr**, hindbrain; **mbr**, midbrain; **ner**, nerve to antennae; **nnp**, nephridial nerve; **nuc**, nuchal organ; **nun**, nuchal nerve; **pbn**, proboscis nerve; **pcn**, posterior cephalic nerve; **prn**, posterior proboscis retractor nerve; **psn**, posterior segmental nerve; **sen**, septal nerve; **sog**, suboesophageal ganglion; **spn**, sympathetic pharyngeal nerve; **ssg**, supra-oesophageal sympathetic ganglion; **stn**, stomato-gastric nerve; **sun**, supra-oesophageal sympathetic nerve; **vnc**, ventral nerve cord. (A, B, after Gelder & Palmer 1976; C, D, after Lofty & Edwards 1972)

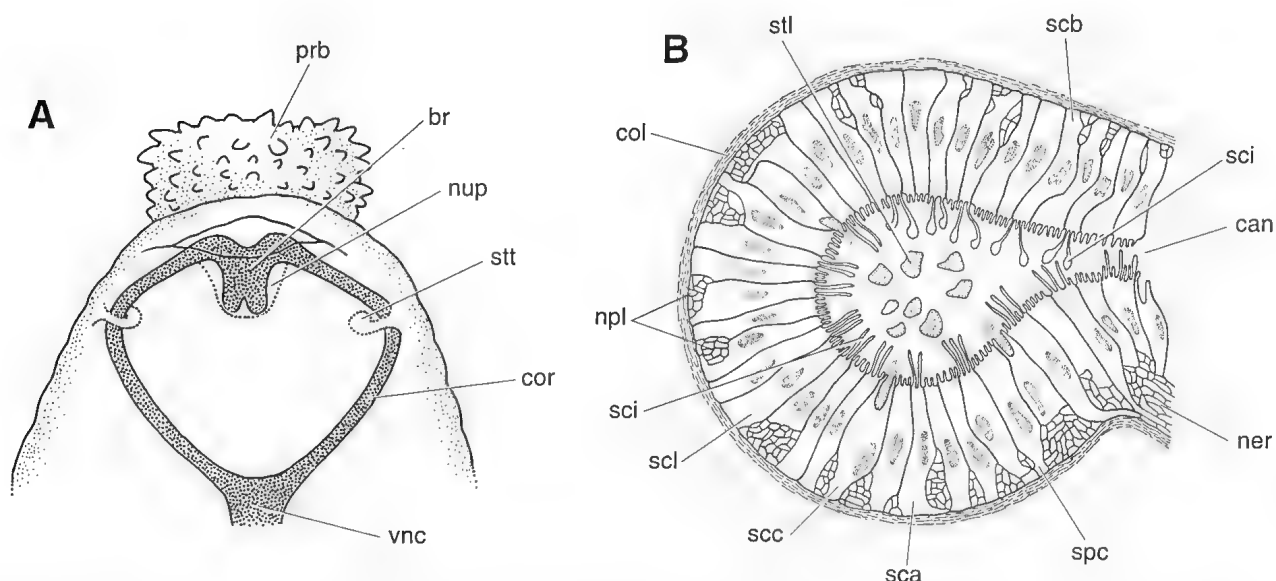


Figure 1.21 Statocysts. **A**, position of the statocysts and anterior nervous system of *Arenicola* species. **B**, a section through a statocyst of *Arenicola marina* (Arenicolidae) showing the statoliths that fall against sensory cilia, allowing the worm to orient itself with respect to gravity. **br**, brain; **can**, canal; **col**, collagen envelope; **cor**, circum-oesophageal nerve ring; **ner**, nerve; **npl**, nerve plexus; **nup**, nuchal pouch; **prb**, proboscis; **sca**, sensory cell type A; **scb**, sensory cell type B; **scc**, secretory cell; **sci**, sensory cilium; **spc**, supporting cell; **stl**, statolith; **stt**, statocyst; **vnc**, ventral nerve cord. (A, after Wells 1951a; B, after Nowak 1978)

[K. Nolan]

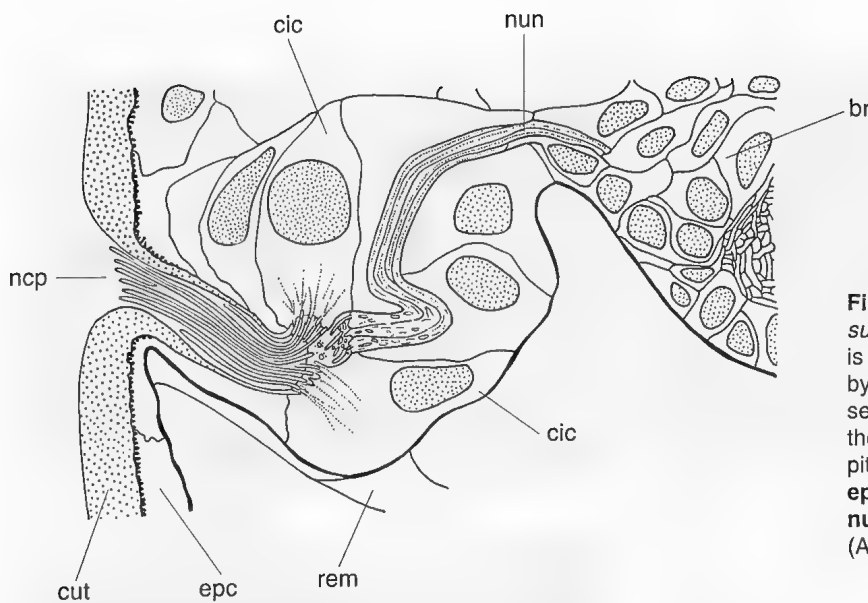


Figure 1.22 Nuchal organ of *Stygocapitella subterranea* (Parergodrilidae). The nuchal pit is lined by unciliated cells at the opening and by ciliated supporting cells at the base; sensory perikarya are located in the brain, and their dendrites terminate at the bottom of the pit. **br**, brain; **cic**, ciliated cell; **cut**, cuticle; **epc**, epidermal cell; **nucp**, nuchal pit; **nun**, nuchal nerve; **rem**, retractor muscle. (After Purchke 1986) [K. Nolan]

Sensory Organs

Polychaetes have several major kinds of sensory structures. They include palps, antennae, eyes, statocysts, nuchal organs and lateral organs. Polychaetes also may have a variety of epidermal sensory cells responsive to light and touch scattered over the body.

As discussed in the section on head structures, palps are of two basic forms, both innervated from the forebrain. Ventral sensory palps are found in members of the Phyllodocida and Eunicida. In most cases, they are tapered or digitiform and relatively short compared with grooved palps. Grooved palps are found in a large number of polychaetes and generally have a feeding function, but presumably also serve a tactile role. Antennae are found only in the Phyllodocida and Eunicida; they are always located on the prostomium, and probably have a largely tactile role. They are innervated by the midbrain. Three antennae may be present, a lateral pair and a single median one (Bullock 1965).

Statocysts are found in a range of polychaetes, usually burrowing or tubicolous forms. They act as gravity receptors, and range in number from the one pair found in many sabellids to more than 20 pairs, as observed in orbinids. They are always located dorsally in the anterior part of the body and are usually innervated from the circum-oesophageal connective (Fig. 1.21A). Statocysts may be simple open pits in the epidermis or deep invaginations that connect to the outside via ciliated canals. In some taxa, the statocysts are subepidermal and have no outside connection. The space within the statocyst contains either sand grains or special hard secretions called statoliths (Fig. 1.21B). These fall against receptor cells that line the lumen of the statocyst, providing stimuli that allow the worm to orient itself (Storch & Schlötzer-Schrehardt 1988).

Nuchal organs are paired ciliated structures which are generally innervated directly from the posterior part of the brain (Figs 1.2, 1.22). Nuchal organs are present only in polychaetes and are thought to be a synapomorphy for the members of the group (Rouse & Fauchald 1997). The assumption that these have a chemosensory role has not been demonstrated. They may be simply ciliated patches or grooves as in syllids, folds as in flabelligerids, or pits, sometimes with eversible folded or finger-shaped structures as in glycerids, nephtyids and opheliids. Some nuchal organs are paired, ciliated folds on each side of a posterior

prolongation of the head (for example, in some spionids). The caruncles of amphinomids and euprosinids carry the nuchal organs (Fig. 1.2A; Storch & Schlötzer-Schrehardt 1988; Purschke 1997).

Lateral organs are internally ciliated pits or ciliated papillae present segmentally between the notopodia and neuropodia (or dorsal to the neuropodia when notopodia are missing). Lateral organs are found in groups such as capitellids, opheliids, orbinids, paraonids, pectinariids, scalibregmatids and spionids (Rullier 1951). Recently, Hayashi & Yamane (1994) described a probable sensory structure which they called the dorsal cirrus organ. It is a ciliated structure on the lower side of the notopodia in eunicid (and related) polychaetes. Dorsal cirrus organs or similar organs may be more widespread among the polychaetes, but as yet most families have not been examined for their presence.

With the exception of a few burrowing forms, most polychaetes have some type of photoreceptor or eyes (Fig. 1.23). In general, eyes are located on the prostomium. Their complexity varies from simple pigmented cups or ocelli, and well-developed eyes with lenses, to compound eyes analogous to those found in arthropods (Eakin & Hermans 1988). Ocelli occur in a wide range of polychaete families. They can be as simple as two cells, a sensory cell and a pigmented support cell (Fig. 1.23A). Other forms of ocelli are more complex, but still may be composed of only a few dozen cells. They probably perceive information about light direction and intensity. In certain families of the Phyllodocida, particularly the swimming predatory alciopids, the eyes are probably capable of forming an image. The eyes of alciopids can be up to a millimetre across and so large that they protrude laterally from the head and press into the brain. They comprise a primary retina containing thousands of cells, a secondary retina overlain by a lens and other accessory structures (Fig. 1.23D, E; Hermans & Eakin 1974).

Compound eyes evolved independently from those of arthropods. They are also found on the tentacular crowns of some sabellids and serpulids and have been documented in the Australian serpulid *Spirobranchus giganteus* by Smith (1984a). The compound eyes are arranged along the radioles (Fig. 1.23B) or at their extreme tips and may be numerous. Up to 50 separate units called ommatidia comprise each compound eye. Each ommatidium is composed of three cells: a receptor cell forming a ciliary receptive segment, and two pigment cells surrounding an extracellular lens (crystalline

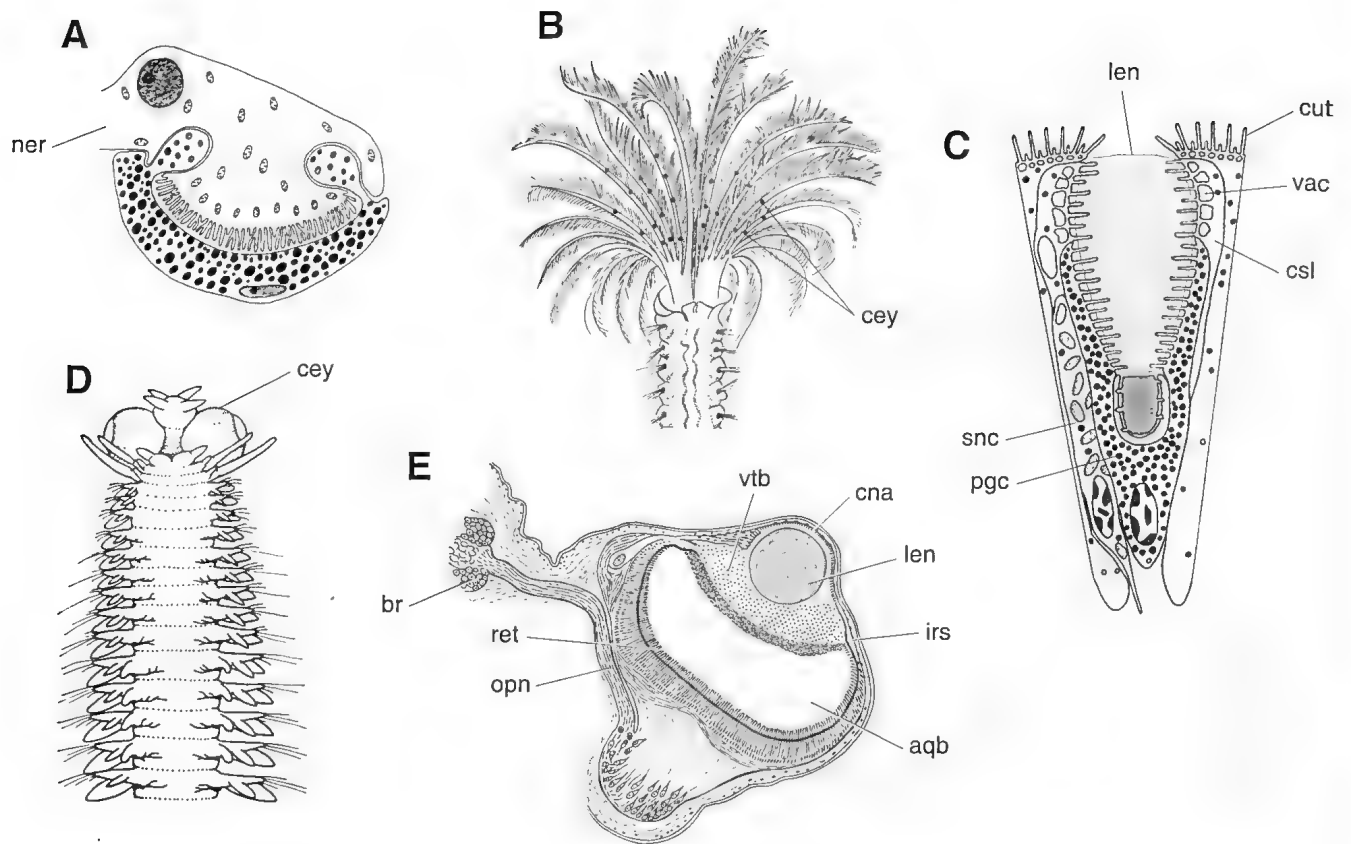


Figure 1.23 Photoreceptors. **A**, simple ocellus of *Armandia brevis* (Opheliidae). **B**, dorsal view of anterior end of the sabellid *Pseudopotamilla reniformis*, showing tentacular crown with compound eyes. **C**, an ommatidium from a compound eye of *Sabella melanostigmata* (Sabellidae); up to 50 ommatidia make up a single compound eye. **D**, dorsal view of the alciopid *Plotohelmis capitata*, showing the large eyes. **E**, longitudinal section through the compound eye of the alciopid *Vanadis tagensis*. **aqb**, aqueous body; **br**, brain; **cey**, compound eye; **cna**, cornea; **csl**, cell surrounding lens; **cut**, cuticle; **irs**, iris; **len**, lens; **ner**, nerve; **opn**, optic nerve; **pgc**, pigment cells; **ret**, retina; **snc**, sensory cell; **vac**, vacuole; **vtb**, vitreous body. (A, after Mill 1978; B, after Eakin & Hermans 1988; C, after Nilsson 1994; D, after Day 1967; E, after Hermans & Eakin 1974) [E. K. Nolan]

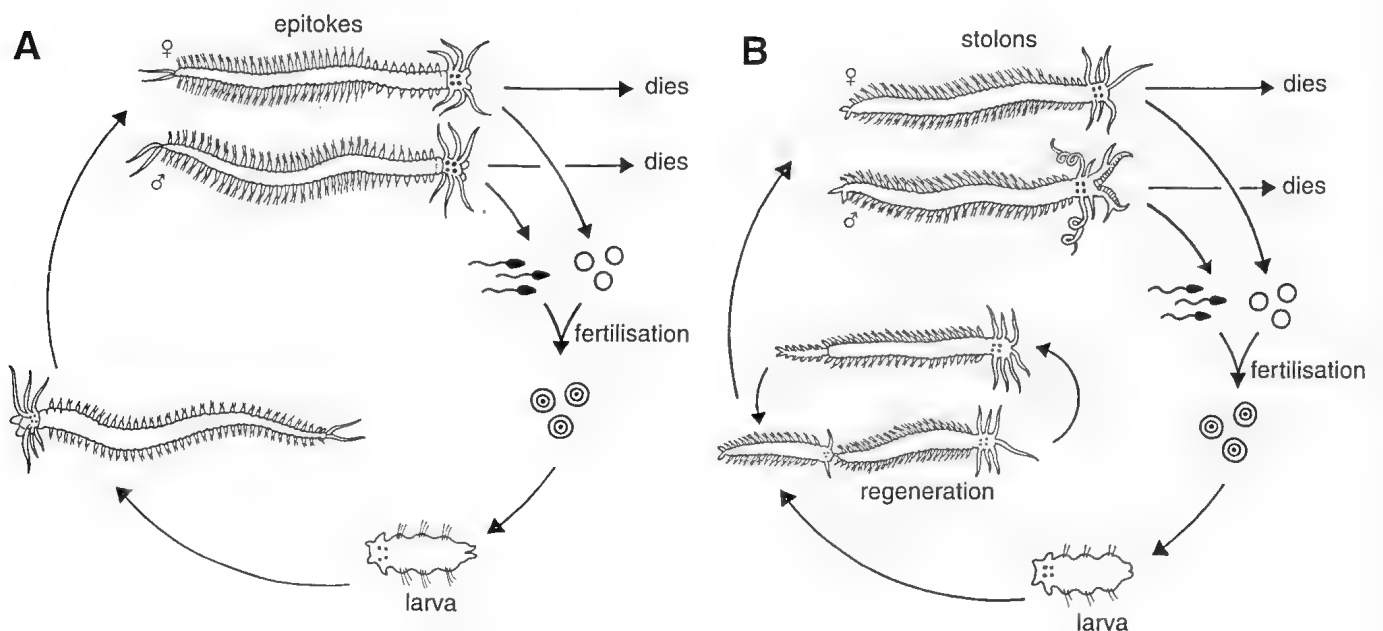


Figure 1.24 Life cycles showing the two processes whereby pelagic metamorphosed sexually mature worms are produced. **A**, epigamy in Nereididae in which the whole worm is transformed into a swarming epitoke, and once the gametes are released the epitokes die. **B**, schizogamy in Syllidae in which posterior segments of sexually mature worms become detached as migratory gamete-bearing stolons; the anterior end of the worm continues to live and the stolon dies after the release of gametes. (After Barnes, Calow & Olive 1993) [K. Nolan]

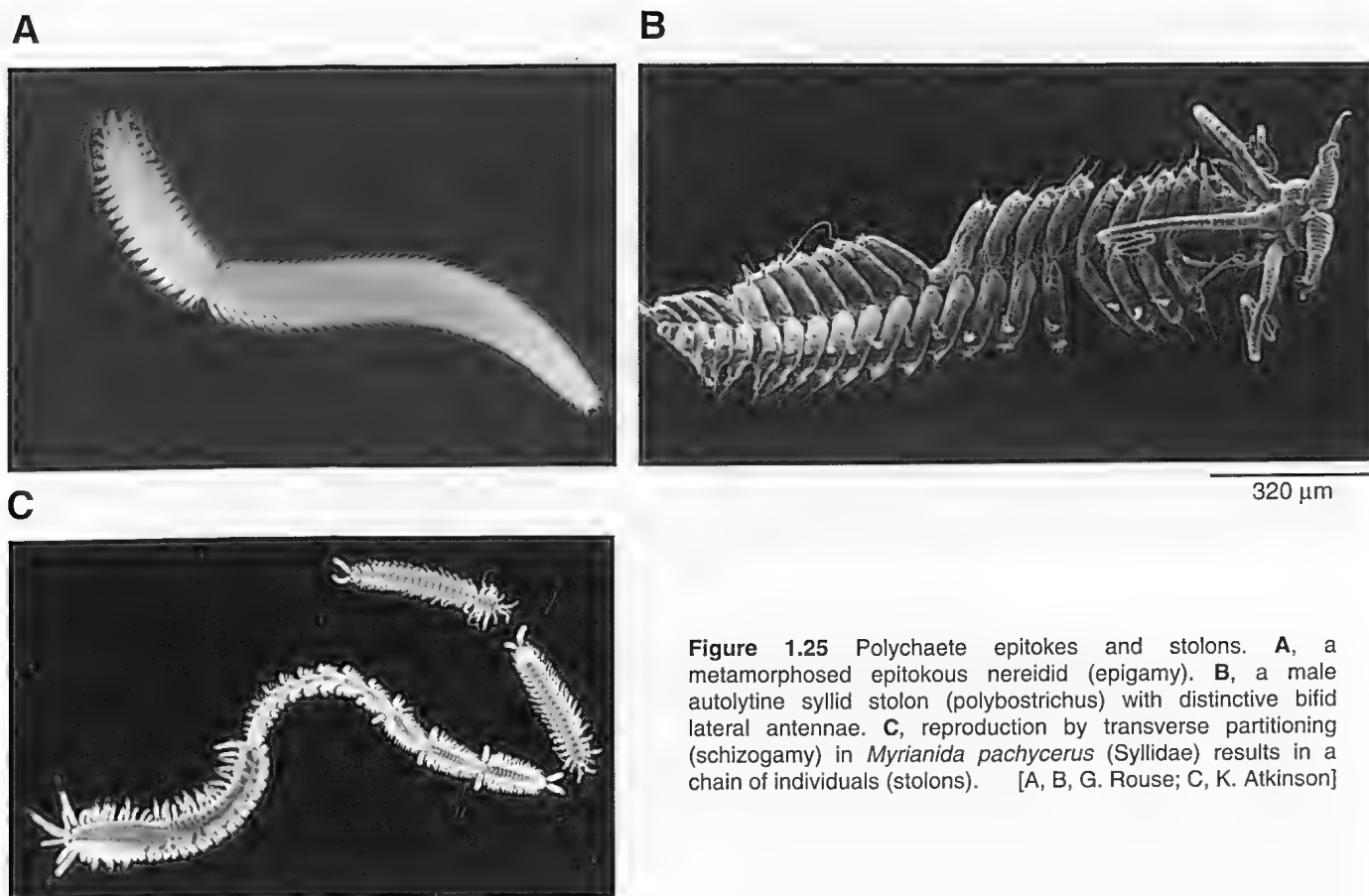


Figure 1.25 Polychaete epitokes and stolons. **A**, a metamorphosed epitokous nereidid (epigamy). **B**, a male autolytine syllid stolon (polybostrichus) with distinctive bifid lateral antennae. **C**, reproduction by transverse partitioning (schizogamy) in *Myrianida pachycerus* (Syllidae) results in a chain of individuals (stolons). [A, B, G. Rouse; C, K. Atkinson]

cone). The eyes cannot form images, but they are extremely sensitive to visual motion because, in concert, they cover such a wide area. Any motion will trigger a retraction of the worm into the tube (Nilsson 1994).

REPRODUCTION

Polychaetes exhibit an amazing diversity of reproductive strategies including both asexual and sexual, and can be used to illustrate all types of reproduction found within the invertebrates.

Sexual Reproduction

Within the Polychaeta there is an enormous diversity of reproductive and developmental modes. In a single family of polychaetes, some species may brood a few large, yolky eggs and develop directly into juveniles, and still others may be ovoviviparous and give birth to young worms. Other species may spawn many small eggs which are fertilised in the water column. These develop into planktotrophic larvae that can remain in the plankton for weeks or months before settling and metamorphosing into a juvenile.

At least a quarter of the polychaete families are known to have more than one mode of fertilisation and larval development (Wilson 1991). For example, the Capitellidae, Dorvilleidae, Maldanidae, Nereididae, Sabellidae, Serpulidae, Spionidae, and Syllidae all have species with external fertilisation and swimming larvae. Other species within each of these families have sperm transfer of one type or another, associated with some form of larval protection and direct development (Schroeder & Hermans 1975; Jamieson & Rouse 1989).

Wilson (1991) reviewed sexual reproduction in the Polychaeta and identified 17 modes based on the type of larvae and the site of development. He categorised species as: free-spawning (external fertilisation) with no care of larvae; brooding of larvae (four types), or; using gelatinous encapsulation of larvae. Offspring were either released as lecithotrophic larvae, planktotrophic larvae or larvae that underwent 'direct development'. Although traditionally polychaete reproduction is thought of in terms of external fertilisation and planktotrophic larvae (see Rouse & Fitzhugh 1994), only 79 of 306 species studied exhibit this form of sexual reproduction (Wilson 1991). A further 44 species showed external fertilisation and lecithotrophic or direct developing larvae. The remaining polychaetes exhibited some form of brooding. Of course, this is by no means an indication of the real proportions of the various reproductive modes among polychaetes; it only reflects our sampling.

Polychaete reproduction has been reviewed comprehensively by Schroeder & Hermans (1975), and Fischer & Pfannenstiel (1984) edited a volume dedicated to reviews and studies of various aspects of polychaete reproduction. Other reviews are available on aspects such as oogenesis (Eckelbarger 1983, 1988; Olive 1983b); spermiogenesis and sperm structure (Olive 1983a; Franzén & Rice 1988; Jamieson & Rouse 1989; Rice 1992); fertilisation and development (Schroeder 1989) and physiology of reproduction (Olive & Clark 1978; Olive 1984).

Gametogenesis, Gametes and Gonoducts

Most polychaetes that have been studied lack permanent gonads. The origin and proliferation of germ cells is poorly understood, as is the early stages of gamete development. The process of gamete proliferation most commonly attributed to polychaetes concerns liberation of gametogonia or gametocytes into the coelom from germ cells lining the peritoneum. The patches of germ cells can be found in body segments, or

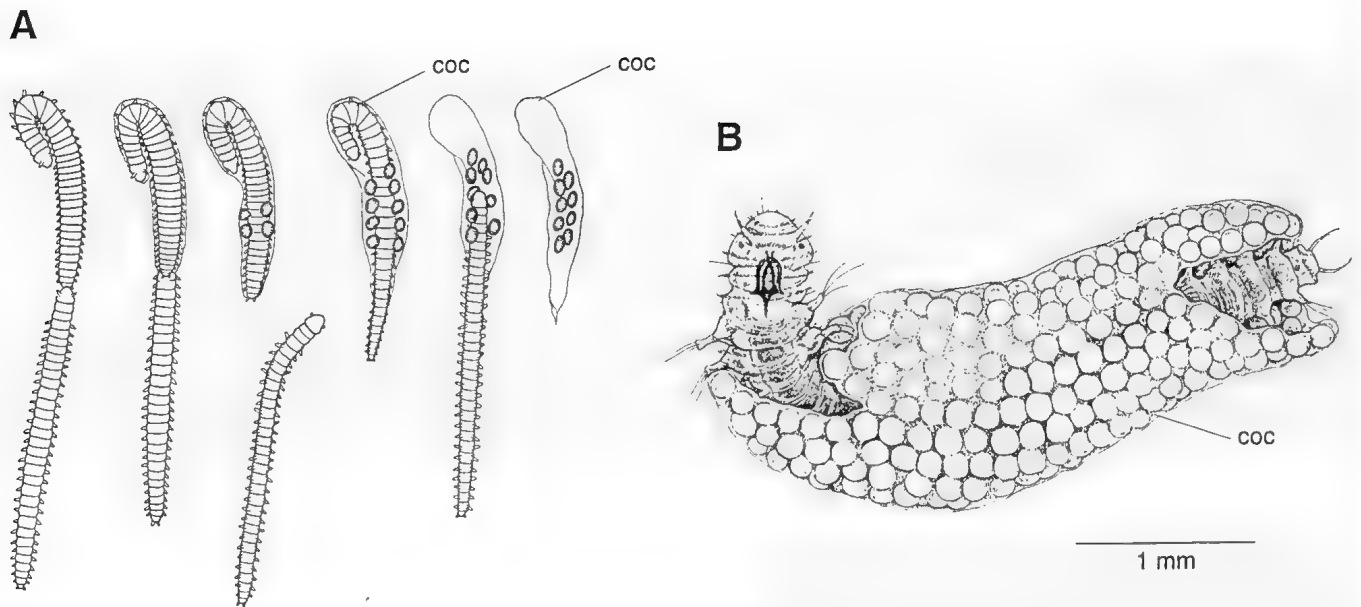


Figure 1.26 A, Pseudocopulation and cocoon production by the dorvilleid polychaete *Ophryotrocha* species. The male approaches the back end of the female who begins to secrete a sheath of mucus around her body. The male releases sperm into the mucus and the female releases eggs and then crawls out leaving the eggs to be fertilised and develop. B, female of *Ophryotrocha labronica* in cocoon filled with embryos. coc, cocoon. (A, after Westheide 1988a; B, after Åkesson 1967)

restricted to a relatively small region of the body. Gamete maturation thereafter occurs while they are floating freely in the coelomic fluid (Schroeder & Hermans 1975). Although it appears that this process may be true of males, Eckelbarger (1988 and references therein) has determined that of the 30 polychaete families where oogenesis has been studied, half utilise some form of intra-ovarian vitellogenesis before ovulation. The form of intra-ovarian oogenesis varies, though most ovaries are retroperitoneal. Cells of the peritoneum, termed follicle cells, can maintain close contact with the developing oocytes. Additionally, the ovaries may be associated with blood vessels and/or nurse cells. Where the oocytes are released into the coelom (that is, extra-ovarian) for vitellogenesis they may be solitary, or associated with nurse cells. Amoebocytes may also be associated with vitellogenesis. Eckelbarger (1983) reviewed the various forms of vitellogenesis and gives numerous examples. It should be noted that various types of oogenesis can occur within a given polychaete group. For example, in some Australian species of *Micromaldane* (Maldanidae) solitary oogenesis occurs whereas in *M. nutricula* oocytes develop in association with clusters of nurse cells (Rouse 1992a).

The testes of most polychaetes usually contain only spermatogonia and stem cells. The presence of later stages within the testes occurs in families such as the Polynoidae and Flabelligeridae. No observation of fully differentiated sperm in testes has been documented (Olive 1983a). In nearly all polychaetes, the sperm develop in syncytial masses which have been referred to as rosettes, morulae or platelets; these terms are often used inter-changeably for bundles of spermatids or spermatocytes (Schroeder & Hermans 1975). The number of cells in a syncytium can vary from four to hundreds. Polychaetes show a great range of sperm morphologies, traditionally grouped as either as 'primitive' or 'modified' based on the terminology of Franzén (1956). He argued that sperm with a 'primitive' morphology were associated with external fertilisation and have a head comprising a simple acrosome, spherical nuclei and a small number of mitochondria, and a free flagellum. Modified sperm were any that deviated from this pattern and were not associated with external fertilisation. Rouse & Jamieson (1987) examined the sperm and reproduction of a number of

Australian polychaetes and proposed a new system of classifying sperm based on function, rather than an *ad hoc* judgement of phylogenetic pattern.

In most polychaetes, gametes are usually expelled from the body through gonoducts associated with the nephridial system. However, in many forms, especially those with epitokes, gametes (particularly eggs) are shed by rupture of the body wall (Clark 1961).

Fertilisation Mechanisms

Many of the polychaetes that utilise broadcast spawning have methods that increase fertilisation success; one such method is synchronous spawning. Environmental cues for synchronous spawning were reviewed by Olive (1984). In addition to temporal synchrony, many benthic species swarm to the surface regions of the water column and spawn. This widespread method is accomplished by morphological changes termed epitoky. An epitoke, as defined by Schroeder & Hermans (1975), is a polychaete individual that is morphologically modified to leave the bottom for the purposes of reproduction.

Epitokes can arise by two different processes (Fig. 1.24). Epigamous epitokes are the result of the transformation of the pre-existing individual from an atoke into the epitoke. Examples occur in the Amphinomidae, Cirratulidae, Dorvilleidae, Glyceridae, Nephtyidae, Nereididae, Opheliidae, Phyllodocidae, Scalibregmatidae and Syllidae, amongst others (Durchon 1984). The most well-known are the epigamous epitokes of the Nereididae (Figs 1.24A, 1.25A; Clark 1961). Schizogamous epitokes arise by modification and separation from the posterior end of the worm (Fig. 1.24B). Such epitokes occur in the Eunicidae, the most famous of which is the Palolo worm, *Eunice viridis*, from Samoa (Caspers 1984), which has also been recorded from waters just north-east of Australia (Bartlett 1946). Schizogamous epitokes are also found in the Syllidae where the term stolonisation is often used (Fig. 1.25C; Schroeder & Hermans 1975).

On the Great Barrier Reef the simultaneous swarming and spawning of many species of polychaetes has been documented by Hutchings & Howitt (1988). They found that 33 species from seven families (Amphinomidae, Dorvilleidae, Eunicidae, Hesionidae, Nereididae, Phyllodoceidae and Syllidae) swarm at various times during the period October–January. All of these represent species that are usually found in sediment or coral substratum. The species vary considerably in the types of morphological change they undergo, but most are epitokous forms.

As indicated in Wilson (1991), the majority of polychaetes utilise some form of brooding of larvae. This is usually coincident with transfer of sperm between individuals. Sperm are often packaged for transfer as either spermatophores or spermatozuogmata.

Spermatophores are bundles of sperm that are enclosed by a sheath or capsule that isolates them from the surrounding environment. Spermatophores may be transferred during copulation or pseudocopulation, or are released into the water column to be gathered by the female. They may be stored in sperm receptacles (spermathecae) or attached to the epidermis. In the latter case, this comprises a form of hypodermic insemination (see below) and occurs in the Hesionidae. Hsieh & Simon (1990) reviewed the presence of spermathecae and spermatophores in a variety of polychaete groups. Spermatozuogmata differ from spermatophores in that the sperm are not surrounded by an external covering (see Rouse 1992b). Often spermatozuogmata resemble bundles of late spermatids. These structures are found in members of the Arenicolidae, Syllidae, and Terebellidae and have been described in several Australian species of the Maldanidae (Rouse 1992b, 1994).

Sperm transfer mechanisms are diverse amongst polychaetes and different aspects have been reviewed by Olive (1983a), Westheide (1988a), Jamieson & Rouse (1989) and Schroeder (1989). The structure of male copulatory organs and female sperm receptacles has been reviewed by Westheide (1988a). Sperm, whether packaged or not, reaches the female in various ways.

Direct interaction with an intromittent organ. Many polychaetes have organs that can be termed a ‘penis’ or intromittent organ, although the structure and use of such structures varies considerably. In some taxa, the penis, or penes, are inserted into a female receptacle/s and the term copulation is appropriate, as has been described for various Australian *Saccocirrus* species by Brown (1981). In other taxa, females may have no sperm receptacle, and sperm is transferred by a process known as hypodermic insemination. For example, the Australian histriobdellid, *Stratiodrilus novaehollandiae*, has a chitinised penis that is inserted, seemingly at random, into the female’s body (Haswell 1913). The Hesionidae and Dorvilleidae also include species with penes (intromittent organs) (Westheide 1984, 1988a; Eibye-Jacobsen & Kristensen 1994).

Pseudocopulation. This form of sperm transfer occurs in a number of polychaetes and may involve transfer of spermatophores, spermatozuogmata, or free sperm. In the terebellid *Nicolea zostericola*, males shed spermatozuogmata via their elongate nephridial papillae; females collect them via their feeding tentacles and spawn shortly afterwards (Herpin 1925). Species of the dorvilleid genus *Ophryotrocha* are well known for their pseudocopulation, during which eggs and sperm are deposited into a cocoon (Fig. 1.26; Westheide 1984). Some other polychaete groups, such as nerillids, polynoids, and protodrilids, display pseudocopulation (Schroeder & Hermans 1975; Westheide 1984).



Figure 1.27 Lateral view of a female exogonine syllid with late stage larvae glued to the ventral surface by glandular secretions. Once the larvae have developed a requisite number of segments and chaetae they detach and live as free individuals. [G. Rouse]

Non-contact. Sperm or spermatophores released freely into the water column are gathered by, or swim to the female. Males of several spionid species release spermatophores that are detected by females and manipulated into spermathecae (Rice 1978). Free sperm are released in mucus during nuptial ‘dances’ by males of the syllid *Autolytus prolifera* and may then stick to the body of the female (Gidholm 1965). In many sessile polychaetes, such as sabellids and serpulids, the sperm released into the water is detected, collected by females and stored in spermathecae (Rouse 1992c).

Life Cycles

The various forms of polychaete life cycles have been reviewed by Olive & Clark (1978) and Olive (1984), who demonstrated the difficulties in developing a system for classifying life cycles as diverse as those of polychaetes. The more generally used classification of life cycles, discussed by Olive (1984), is the division of life cycles into two broad divisions: semelparous and iteroparous. Semelparity refers to breeding only occurring once per lifetime (Fig. 1.24). Iteroparity, where breeding occurs several times in a lifetime, can be divided into annual iteroparity (breeding yearly) and continuous iteroparity with breeding taking place over an extended breeding season. The latter condition can in some cases be such that breeding occurs throughout the lifetime of the worm after maturity. Olive & Clark (1978) also reviewed the physiology of reproduction in polychaetes. Most of our knowledge about reproductive endocrinology is confined to the Arenicolidae, Nephtyidae and Nereididae, and no work has been done on endocrine systems of Australian polychaetes.

Gonochorism and Hermaphroditism

Gonochorism is the most common sexual condition found in polychaetes; however, hermaphroditism is widespread (Schroeder & Hermans 1975). This has led to a conclusion that gonochorism is the plesiomorphic condition of the

1. CLASS POLYCHAETA

Polychaeta. However, little has been done to test this idea empirically. In a study of the evolution of reproduction in the Sabellidae, Rouse & Fitzhugh (1994) found that various forms of hermaphroditism have evolved independently several times from gonochorism. Similar studies on the Polychaeta as a whole would be of value.

Hermaphroditism, although occurring in various forms, can be divided into two basic types: simultaneous and sequential (Schroeder & Hermans 1975). Simultaneous hermaphroditism refers to individuals having viable eggs and sperm at the same time. It has been recorded for members of the Capitellidae, Hesionidae, Nereididae, Maldanidae, Sabellidae, Serpulidae, and Syllidae. A speciose polychaete group in which all members are simultaneous hermaphrodites is the spirorbine serpulids. Various forms of simultaneous hermaphroditism can be defined in terms of the location of gametes. In some taxa, the eggs and sperm can be found in the same segments. In others, they are isolated in different body regions. Sequential hermaphroditism can take several forms: protandrous sequential, protogynous sequential, or bi-directional (for examples, see Schroeder & Hermans 1975). A complication arises with the above classification when, as commonly occurs, protandry or protogyny leads to simultaneous hermaphroditism.

Embryology, Development and Larvae

In terms of development, the early embryology of all polychaetes is essentially similar. Although polychaete eggs can range in size from less 50 µm in diameter to more than 1 mm, they all show a sequence of holoblastic (complete) spiral cleavage to the 64-cell stage. The division may be equal or unequal, depending on how yolky the eggs are. The germ layers are formed from a few well-defined cells in the blastula. For example, all future mesoderm is formed from descendants of the 4d micromere. Eggs that were provided with small amounts of yolk tend to develop into larval forms that have to feed in order to complete development (Anderson 1966). These are termed 'planktotrophic larvae'. Embryos that are provided with enough yolk to complete a large part of their development without feeding are called 'lecithotrophic larvae' and those that can develop completely into young worms are called 'direct developers' (Fig. 1.27).

Some of the most obvious features of polychaete larvae are the ciliary bands that are used for locomotion and feeding (Figs 1.8, 1.28). The prototroch is the anterior-most transverse ring and lies anterior to the mouth. A second transverse ring, the metatroch, lies posterior to the mouth. The telotroch is the posterior-most ring and encircles the pygidium. A longitudinal ventral band, called the neurotroch, is also common. Many polychaetes also have an apical tuft of cilia at the anterior tip of the larva. These bands are not always present depending on the larval form and some larvae may only show the prototroch. Larvae that are direct developers and brooded by the parent may lack all ciliary bands (Rouse 1999).

The embryology and/or larval development of a wide range of Australian polychaetes has been studied. These include species in the Histiobdellidae (Haswell 1900, 1916), Maldanidae (Rouse 1992a), Onuphidae (Paxton 1993), Orbiniidae (Anderson 1961), Sabellidae (Rouse 1993a; Rouse & Fitzhugh 1994), Saccocirridae (Sasaki & Brown 1983), Serpulidae (Haswell 1887; Wisely 1958; Andrews &

Anderson 1962; Marsden & Anderson 1981), Spionidae (Blake & Kudenov 1981) and Syllidae (Haswell 1920a); larvae are illustrated in Figures 1.29 and 1.30.

Asexual Reproduction

Asexual reproduction in polychaetes is widespread and occurs in several different forms. In polychaetes, and other annelids, it involves subdivision of the body and regeneration of the missing parts. This process, termed schizotomy, was divided further into paratomy and architomy by Schroeder & Hermans (1975). Paratomy refers to the formation of a recognisable complete individual that then separates from the 'parent' stock, whereas architomy is simple fission or fragmentation of the body with no prior cephalisation. There is, however, a grade between these two extremes.

Paratomy occurs in polychaete taxa such as the ctenodrilids and some spionids, but is best-known in the Serpulidae and Sabellidae. In serpulids of the genera *Salmacina* and *Filograna*, paratomy has been well studied by Faulkner (1930) and Vanini (1950). Schroeder & Hermans (1975) listed various sabellids as being architomic. However, this is not the case and, as has been shown by Knight-Jones & Bowden (1984), paratomy is common in this group. All the species involved also appear to have sexual reproductive phases.

Architomy is far more widespread in polychaetes and has been documented in many groups (Schroeder & Hermans 1975). The most extreme case of architomy is found in the cirratulid genus *Dodecaceria*. These worms may continue to fragment into sections until single segments result. Fragments originating from middle body segments are then capable of regenerating a new individual (Gibson & Clark 1976). Other polychaete families listed by Schroeder & Hermans (1975) as showing architomy include the Chaetopteridae, Dorvilleidae (as Dinophilidae), Syllidae, Spionidae and Tomopteridae.

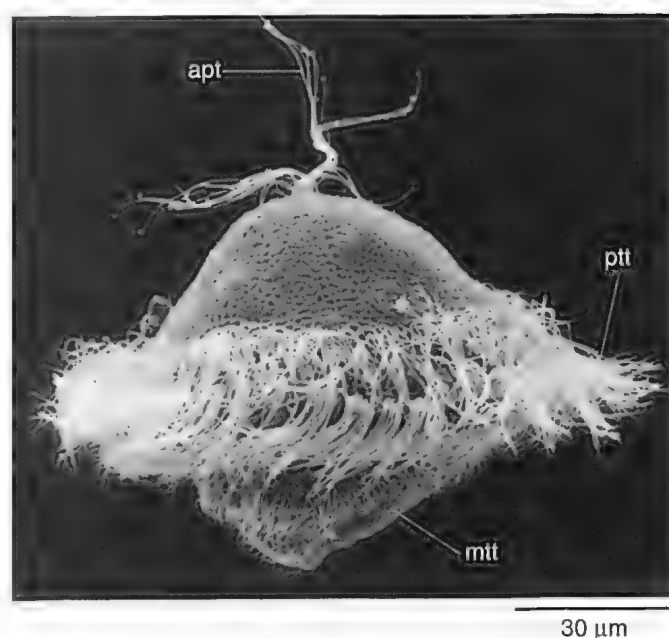


Figure 1.28 Trochophore of *Spirobranchus giganteus* (Serpulidae). apt, apical tuft; mtt, metatroch; ptt, prototroch. [G. Rouse]

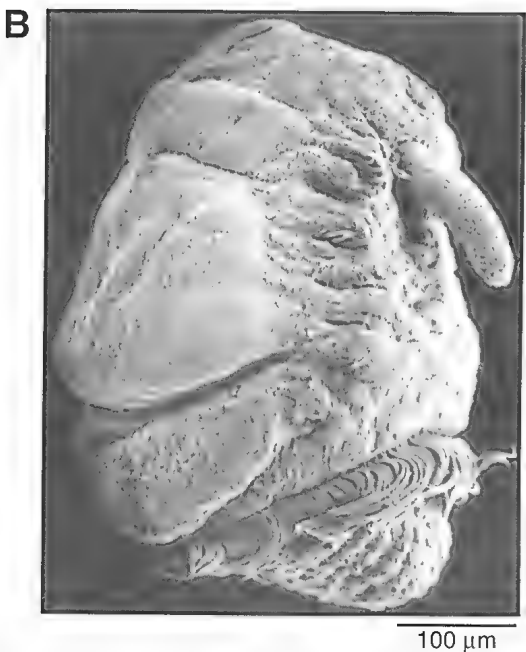
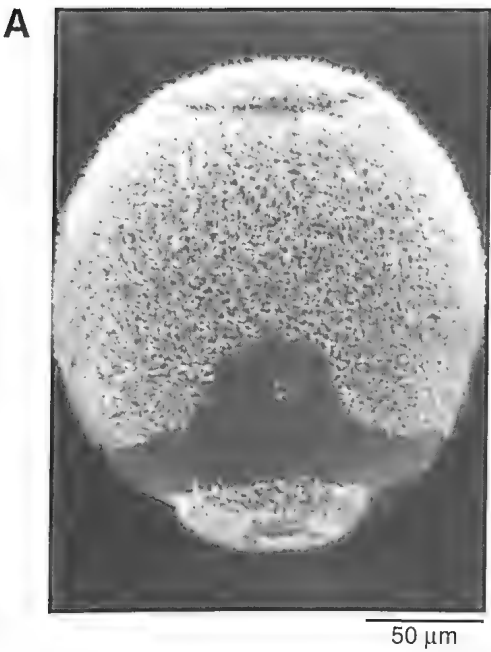


Figure 1.29
Polychaete larvae from the plankton.
A, eunicid.
B, chaetopterid.
C, glycerid.
D, terebellid.
E, phyllodocid.
F, spionid.
[G. Rouse]

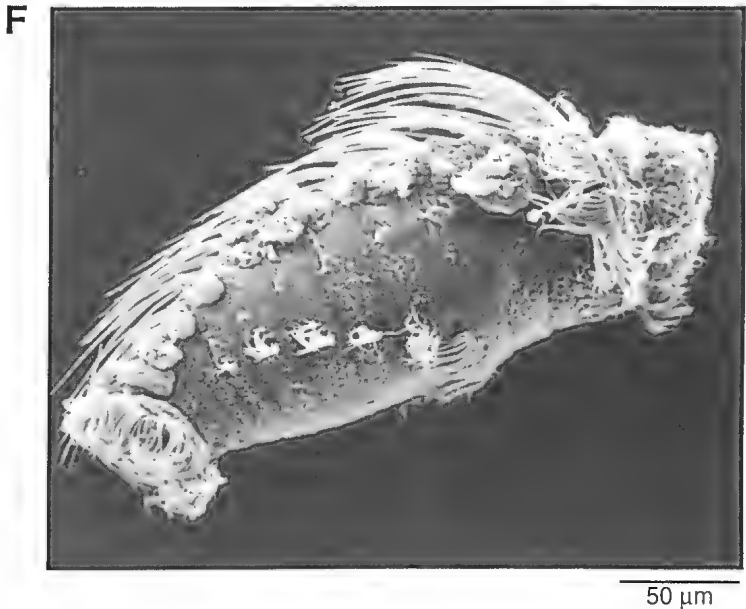
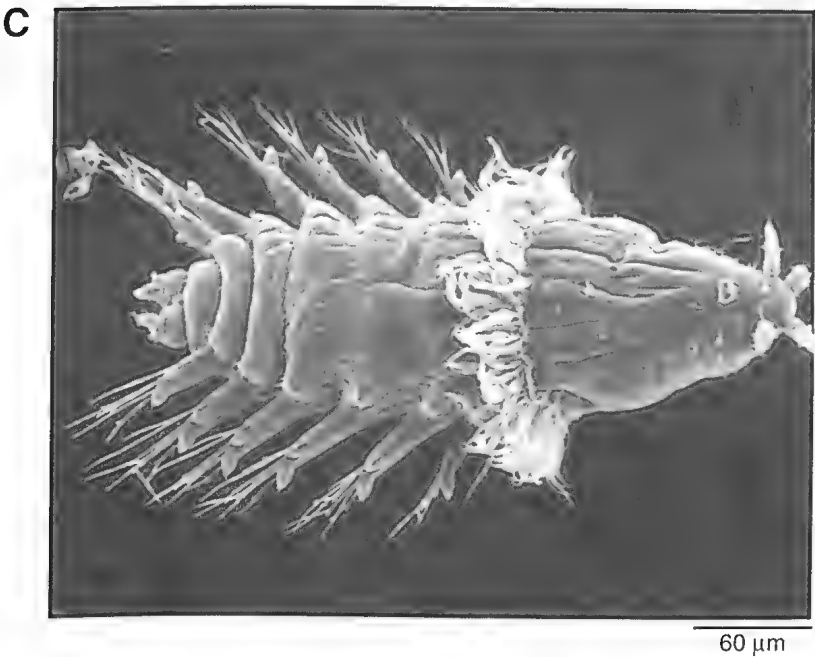




Figure 1.30 Lateral view of a larva of the maldanid *Micromaldane pamalae* removed from the female tube.
[G. Rouse]

NATURAL HISTORY

Ecology

As a group, polychaetes are predominantly marine. They live in a wide range of habitats from the intertidal to the deepest depths of the ocean, and at all latitudes. Some species occur in the more saline sections of estuaries, and others tolerate the lower, fluctuating salinities found further upstream, for example, several species of *Ceratonereis* (now all placed in the genus *Simplisetia*) in south-eastern Australia (Hutchings & Glasby 1982; Glasby 1986).

Some notable exceptions occupy non-marine habitats which are often challenging from an osmotic perspective. A few species of spionids live in freshwater lakes in South Australia (Blake & Woodwick 1976). The nereidid *Nereis limnicola* is found in a range of salinities in California and physiological studies have been carried out to determine how these soft-bodied worms cope with reduced salinities (Jones 1967). The Australian sabellid *Manayunkia athalassia* has been recorded from hypersaline ephemeral lakes adjacent to the Coorong Lagoon in South Australia (Hutchings, Decker & Geddes 1981) and recently an undescribed species of *Manayunkia* has been found in hypersaline ephemeral lakes in the wheat belt of Western Australia (P. Hutchings personal observation). *Manayunkia athalassia* lives in gelatinous tubes and can survive within a dessicated, ball-like structure when the lakes dry up during the summer months when air temperatures may exceed 40°C. Experiments have shown that after distilled water was added to the dried mud, active worms were seen after 24 hours in salinities ranging from 27–95‰.

A few species occur in semi-terrestrial environments in the supralittoral zone. These are primarily nereidids and include species groups such as *Namalycastis abiuma* and *Namanereis littoralis* (Glasby 1999a). Specimens of *N. abiuma* are found under *Enteromorpha* mats in the leaf litter along the landward margin of the mangroves on Lizard Island, Great Barrier Reef, where they would be covered by freshwater during the wet season and tidal inundations are infrequent. Members of *Caobangia* (Sabellidae) burrow exclusively into freshwater molluscs in South-East Asia (Jones 1974; Fitzhugh 1989).

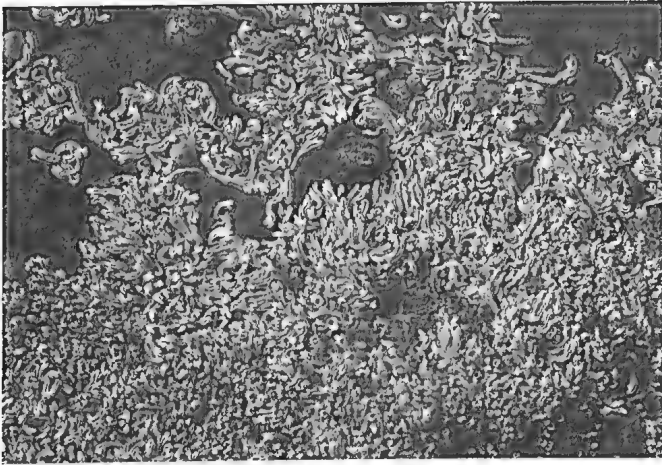
Polychaetes of several families (Ampharetidae, Eunicidae, Polynoidae, Serpulidae and Spionidae) have been collected from deep-sea vents. Although these species are usually described as new, typically they belong to genera which appear not to be especially adapted for this type of habitat, just a short distance from the 'smoke' plumes. In contrast, vestimentiferan Pogonophora (Jones 1988), which are regarded as polychaetes by some authors (see Rouse & Fauchald 1997) are greatly modified and occur very close to the vents, immersed in the sulphur plumes (see Chapter 3).

In the marine environment, polychaetes may burrow into the surface layers of a range of sediments from fine muds to coarse gravel, in both intertidal and subtidal environments. Some live naked in the sediments, burrowing freely through them. Others live in tubes, which range from semi-permanent mucus types, as those in the terebellid *Polycirrus* and the onuphid *Australonuphis*, to well-constructed firm tubes of fine sediment (Sabellidae – *Myxicola* species) or sand grains (Pectinariidae – *Pectinaria* species); *Chaetopterus* species (Chaetopteridae) live in parchment-like tubes (Pls 7.4–7.6). Some form dense aggregations, as seen in many spionids, and some species of the onuphid *Diopatra*, whereas others are well separated (Eunicidae – *Marphysa* species) so that the feeding activity of one individual does not impinge upon its neighbours.

Although competition between Australian species has not been studied, a considerable amount of work has been undertaken on extra-limital species. Wilson (1990) provided a summary of competition and predation in marine soft-sediment communities which are often dominated by polychaetes. Soft-sediments are three-dimensional structures, so vertical and horizontal partitioning of space can occur, which may reduce direct interactions between potential competitors. However, interactions do occur, typically between conspecifics or closely-related species. Roe (1975) has shown that species of nereidids exhibit territoriality and can be aggressive towards each other. Opheliids also exhibit behavioural patterns which influence population density (Woodin 1974; Tamaki 1985b). Wilson (1983) manipulated the population densities of two species of co-occurring spionids and found that the migration in and out of the experimental containers was strongly density dependent, suggesting that each individual requires a certain amount of space in which to forage and obtain sufficient nutrients. High rates of sediment disturbance by burrowing organisms can have significant deleterious effects on suspension-feeders and tube builders (Wilson 1981; Posey 1987).

Recent studies by Naylor & McShane (1997) have shown how adult polychaetes can modify recruitment of other species to hard substrata. The spionid *Boccardia chilensis* and the cirratulid *Dodecaceria berkleyi*, which inhabit coralline encrusted boulders, have been shown to capture and consume larvae of the abalone *Haliotis iris* in New Zealand. Thus the refugia from water currents and fish predation offered by coralline surfaces are offset by the biological hazards associated with resident infaunal polychaete predators. Such interactions may well occur in Australian waters. Similarly, infaunal predators have a major influence on the survivorship of invertebrates recruiting to soft sediments. For example, deposit-feeding polychaete species are responsible for a significant mortality of larval and post-settlement invertebrates (see Woodin 1976). However, Wilson (1991) has suggested that while adult-larval interactions are detectable both in the field and in the laboratory, the operative mechanisms are difficult to determine. It is difficult to distinguish between larvae avoiding high densities of adults

A



B



Figure 1.31 *Galeolaria caespitosa* (Serpulidae), often called Sydney coral, forms dense aggregations on the rocky shores of eastern Australia. The tentacular crowns of the worms are only expanded and visible at the mouth of the tube, when the animals are covered by sea water and the worms are filter-feeding. **A**, massed tubes of *G. caespitosa* on a rocky substratum. **B**, *G. caespitosa* will inhabit many structures, as shown living on the pylons of a jetty in Coffs Harbour. The white bands on the pylons are the encrustations formed by the living worms.

[A, K. Atkinson; B, K. Gowlett-Holmes]

or high densities of adults causing an increase in mortality of settling larvae by ingestion or suffocation. Some work has also been done on infaunal predators modifying community structure. *Glycera dibranchiata* preys upon *Neanthes virens*; exclusion of the glycerid results in enhanced survivorship of the nereidid (Ambrose 1984a, 1984b).

Tubicolous species are fairly immobile within the sediments, although video footage has shown that deep-sea terebellids can 'pick-up' their tubes and move. Continuous tube building may represent a form of locomotion in some tube building worms (Fauchald & Jumars 1979). If disturbed, some species will leave their tubes and settle elsewhere and others seem to leave their tubes even when not disturbed and can actively swim (Fauchald & Jumars 1979). Tubicolous species continually maintain their tubes and extend them as they grow, but with the exception of those secreted by serpulids, tubes break down rapidly once the animal dies. The serpulids secrete calcareous tubes on firm substrata; even fragments of dead shell or tests of echinoderms may be sufficient for a large colony of *Salmacina* to develop. Typically, serpulids

occur either as isolated individuals on rocky outcrops or in dense colonies. The lower levels of exposed rocky shores along eastern Australia are dominated by the serpulid *Galeolaria caespitosa*, commonly called 'Sydney coral' (Fig. 1.31 Pls 7.1–7.3). In more brackish water, members of the genus *Ficopomatus* can form dense colonies, which may block cooling intake pipes of power stations (ten Hove 1979). Sabellariids also build solid sand tubes firmly cemented onto rocks forming small reefs, some of which occur in northern New South Wales. Off the Florida coast extensive sabellariid reefs composed entirely of *Phragmatopoma lapidosa* are found. These reefs are up to 500 m long, with an average width of 20 m and occur about 100 m from shore (Eckelbarger 1976a).

Some polychaetes, such as species of the cirratulid *Dodecaceria*, actively bore into calcareous substrata (Knox 1971; Gibson 1977; Hutchings 1986). Species of *Boccardia* and *Polydora* (Spionidae) are important pests of oysters and other bivalves, causing blisters to develop in the shells where the worms have bored. Boring occurs by acid dissolution of the substratum; this chemical dissolution may be assisted by the large modified chaetae on segment 5 in spionids (Blake & Evans 1973; Zottoli & Carricker 1974). Polychaetes are among the first colonisers of recently dead coral and play a major role in the bioerosion of coral substrata (Hutchings 1986).

Polychaetes are also found in live coral. For example, the Christmas tree worm '*Spirobranchus giganteus*', which exhibits a wide range of colour morphs even on a single coral head, is one of the most conspicuous polychaetes on the Great Barrier Reef (Smith 1985; Pls 6.1, 6.2). This species complex prefers to settle on live, rather than dead, coral (Marsden 1987). It is more of an associate of the coral than a borer. After the larva has settled on the coral, having avoided being ingested by a coral polyp, it secretes a fine calcareous tube and stimulates the coral to grow around it. As the coral grows, the worm continually secretes its tube to ensure the tube opening is kept clear of the coral skeleton. The worm must maintain an open tube in order to survive. The result is that the tube of the worm may extend several millimetres down into the coral skeleton in a large coral colony, providing protection for the worm from predation. Coral polyps are voracious planktivores, so settling *Spirobranchus* larvae must avoid the localised water feeding currents generated by the ciliated polyps. Rates of successful settlement for this species are likely to be low. Typically, when the coral colony dies so does the commensal polychaete (P. Hutchings personal observation), and the dead coral is then bored by a wide

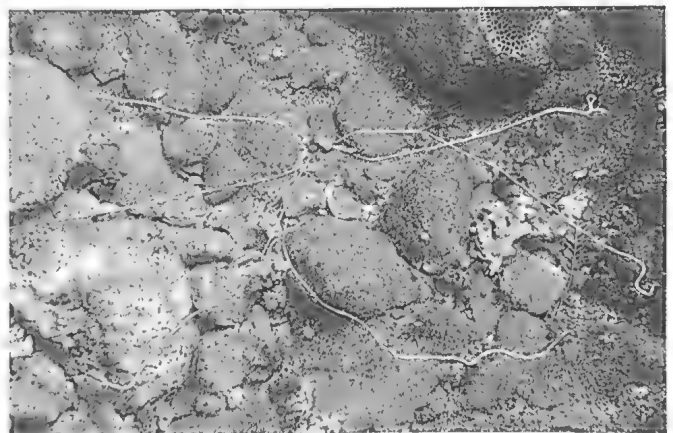


Figure 1.32 Long white feeding tentacles of the terebellid *Reteterebella queenslandia* spreading over the substratum in search of food.

[R. Steene]

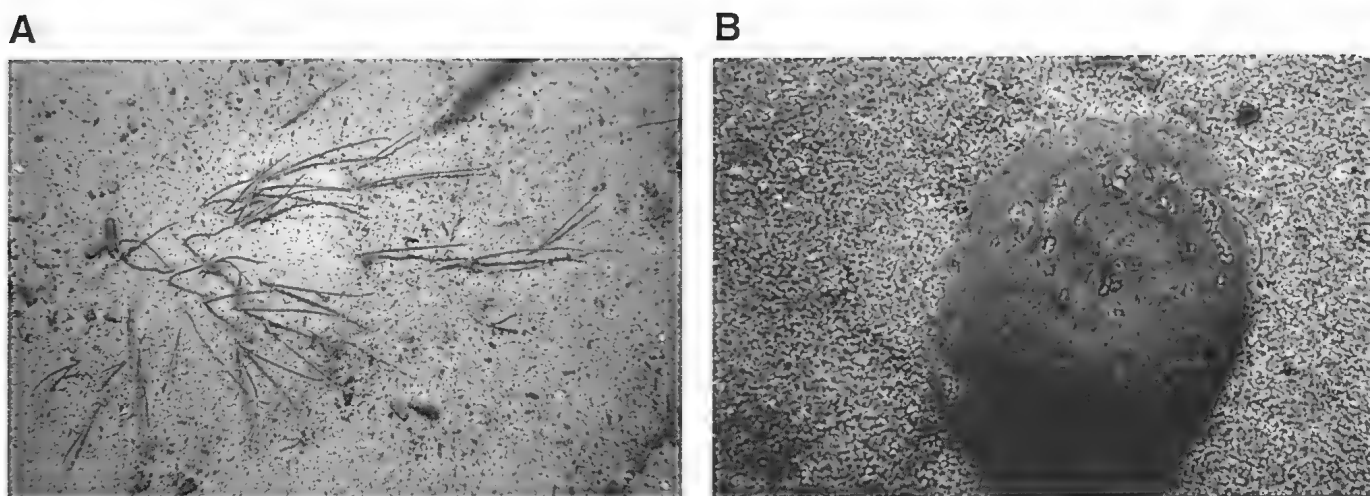


Figure 1.33 A cirratulid living buried in muddy-sand in the protected waters of Norfolk Bay, Tasmania. **A**, tentacles extended for feeding and branchiae for respiration. **B**, the entire worm coiled into a ball after removal from the substratum. [K. Gowlett-Holmes]

variety of organisms including a diverse group of boring polychaete species (including representatives of sabellids such as *Hypsicomus*, the cirratulid *Dodecaceria* and various eunicids; Hutchings 1986). Comparison of macro-infaunal boring polychaete assemblages across the Indo-Pacific shows that some species are widespread occurring in Madagascar, Great Barrier Reef and French Polynesia, but others occur at only one of these sites (Hutchings & Peyrot-Clausade 1988). Once burrows are vacated due to the death of the borers, non-boring, opportunistic polychaete species move in.

The terebellid *Reteterebella queenslandia* is common on the Great Barrier Reef. The body of the animal is never visible, but its long white feeding tentacles are frequently seen spread out for several metres over the reef substratum (Fig. 1.32; Pl. 9.4). Touching the tentacles evokes a rapid withdrawal and it seems likely that chemical compounds in the tentacles prevents them from being eaten by fish and other predators. Such compounds have been found in the tentacles of *Melinna palmata*, a species occurring in Northern Europe and a member of the closely related Ampharetidae (Gibbs, Bryan & Ryan 1981). The body of *R. queenslandia* remains deep in crevices at the base of the coral, such that once the larva has settled and metamorphosed the animal becomes effectively trapped by the coral substratum as it grows. Like *R. queenslandia* the body of cirratulids is never visible; the feeding tentacles and branchiae extend above the sandy substratum (Fig. 1.33).

Many species live under rocks or in crevices, either free-living (nereidids and polynoids; Pls 3.5, 3.6) or with their tubes cemented to the undersurfaces of rocks. For example, the terebellid *Thelepus robustus* lives in dense colonies with their gravelly shell tubes cemented to the undersides of boulders in the shallow subtidal areas of tropical Australia. Many of the polychaete species that live in seagrass beds also occur in nearby non-vegetated sediments (Collett, Hutchings, Gibbs & Collins 1984; Hutchings & Jacoby 1994), although species such as *Nereis posidonea* and some spirorbines which live on the seagrass blades are restricted to this habitat. Holdfasts of kelp and most smaller algal species provide habitats for polychaete species. Several species of capitellids, nereidids and even some terebellids can be found inside logs rotting on the floor of mangrove forests. In addition, oyster colonies growing on the trees on the seaward margin of the mangroves provide another habitat for polychaetes. Other species, such as the large aphroditids, live on the surface of the sediment and are regularly collected during commercial benthic trawling.

Polychaetes thrive in both clean and polluted environments. Species of *Capitella* and some cirratulids are often regarded as indicators of organic pollution. Dense populations of *Capitella* build up rapidly in oil-contaminated sediments (Grassle & Grassle 1974). Some intertidal species are able to tolerate periods of low oxygen levels or reduced salinities during low tide by building up oxygen debts which are repaid on the incoming tide (Warren 1981). Such physiology may allow some species to live in highly anaerobic sediments. Sediments with extremely high levels of heavy metals, such as those at Port Pirie in South Australia where an iron ore smelter has been in operation since the beginning of the 1900s, are almost exclusively colonised by polychaetes. Ward & Hutchings (1996) found 42 species of invertebrates at the most contaminated sites adjacent to the outflow pipes; three of the four most abundant species were polychaetes. One of these, a species of *Capitella*, occurred almost exclusively at the most contaminated site at a density of 322 worms per m², indicating that the species is self-sustaining and can tolerate very high concentrations of metals.

Members of some polychaete families, for example, Tomopteridae, Alciopidae and Iospilidae, are holopelagic and holoplanktonic. Species in these families appear to be widespread, although no studies have been undertaken on Australian members. In addition, many other species have a pelagic stage. This may be a modified swimming stage of a mature individual (referred to as an epitoke or heteronereid in the case of nereidids) which releases gametes into the water, or a larval stage lasting a few hours to several weeks.

Several polychaete species are commensal. Large tubiculous terebellids often have a commensal polynoid living in their burrow, and some polynoid genera are found on the undersurface of holothurians. (Fig. 1.34A) and in the ambulacral grooves of asteroids and on the disc of ophiuroids (Fig. 1.34B) as well as on antipatharian corals. Hanley & Burke (1991a) studied such commensal species occurring in northern Australia, and found a close relationship between species of polynoid and species of holothurian. Large sponges provide another habitat favoured by many species of syllids and some spionids, where worms can be found in the skeletal matrix or attached to the outside of the sponge. The exact nature of these relationships, the manner in which these polychaetes find their specific hosts or whether they employ specialised reproductive methods is poorly known (Martin & Britayev 1998).

Members of a few families of polychaetes are parasitic. Histriobdellids all occur in the branchial chambers of marine and freshwater crustaceans, and the single species included in the family Ichthyotomidae is parasitic on the fins of eels. Parasitic species have also been recorded in the families Iphitimidae (now in the Dorvilleidae) (Rossi 1984), Arabellidae (now Oeonidae) (Emerson 1974; Uebelacker 1978) and Nautiliniellidae (Miura & Laubier 1989).

Polychaetes are themselves hosts to a variety of parasites, both internal and external. The latter appear to be mainly copepods and entoprocts (= kamptozoans). Copepods, as yet unidentified to species, have been found attached to an Australian species of *Amaeana* (Terebellidae) and tropical species of *Marphysa* (Eunicidae). Many of the larger New Zealand terebellid species have entoprocts attached to the body surface, usually the abdomen (C. Glasby personal communication). Ectoprocts (Bryozoa) have also been seen attached to polychaetes. Gregarines (protozoans) are commonly seen within the coelomic fluid of many species of polychaetes; a few species of *Coccidiasoma* (gregarine protozoans) have been described from polychaetes. About 200 species of archigregarines, have been recorded from polychaetes. They appear to be species-specific. The potential impact of these parasites appears not to have been studied, but presumably under normal conditions the polychaetes and the parasites co-exist.

Life History

As discussed in the Reproduction section, polychaetes exhibit a wide range of reproductive strategies (Bentley & Pacey 1992; Giangrande 1997) and the control of reproduction has been extensively studied for several species within several families. They have an extremely well-developed endocrine system which can allow for synchronous spawning (Olive 1984). They also exhibit a variety of recruitment strategies (Keough 1983; Marcus & Schmidt-Gengenbach 1986; Blake 1993; Woodin, Lindsay & Wetthey 1995). The majority of work on settlement behaviour has been carried out on intertidal gregarious species (Keough & Raimondi 1995). O'Donnell (1984) showed how the larvae of the serpulid *Galeolaria caespitosa* are attracted to settle by the presence of adults of the species. This has also been shown to be true for spirorbine serpulids (Knight-Jones 1951). Juveniles of species that exhibit brood protection, such as many small sabellids and spionids, are released and settle next to the adults.

However, the presence of adults in many species that produce pelagic larvae is not necessary for settlement, and factors such as sediment type appear to be critical, or in some cases the degree of wave exposure. For example, beachworms (Onuphidae) are only found on surf beaches and some species of *Marphysa* only occur in sheltered situations like Moreton Bay, southern Queensland. But at this stage we can only surmise the factors critical for settlement and survival for most Australian species. Some species occur widely within Australian waters in a range of habitats, such as the terebellid *Nicolea amnis*, whereas others occur very locally in a specific habitat, for example, the terebellid *Hadrachaeta aspera* which is known only from the seaward margins of mangroves in the Sydney region.

Sex ratios vary widely in polychaetes. Some species have sex ratios of 1:1; in others, females predominate and in the nereidid *Nereis limnicola* no males have ever been found (Smith 1950; Baskin & Golding 1970). Many are hermaphrodites and others change sex during their lives (Pfannensteil 1984). Polychaetes have a life span ranging from a few weeks to months (spirorbines and fabriciines) to several years (nephtyids). Based on annual growth rings on the jaws, Estcourt (1975) suggested that members of a New Zealand population of the nephtyid *Aglaophamus verrilli* could live for at least 5 years. The life histories of few Australian species have been studied. They include the orbinid *Scoloplos (S.) simplex* (Anderson 1961) (incorrectly identified as *Haploscoloplos fragilis*) and three species of nereidid: *Australonereis ehlersi*, *Simplisetia erythraeensis* (Dorsey 1981; see Hutchings & Turvey 1982 and Hutchings & Glasby 1985 for name changes) and the freshwater species *Simplisetia limnetica* (Glasby 1986). Schroeder & Hermans (1975) listed all species for which information on life histories is known; this was updated by Wilson (1991).

Feeding Strategies

Polychaetes exhibit a wide range of feeding strategies. These strategies include carnivory, herbivory and scavenging (collectively referred to as raptorial), as well as filter-feeding, and selective or non-selective deposit-feeding (Fig. 1.15; Fauchald & Jumars 1979). Although often the feeding strategy of a polychaete species can be inferred from the morphology of its anterior end, not all species with well-developed sets of jaws are carnivores. In fact, the beach worms (onuphids), which have extremely well-developed

A



B

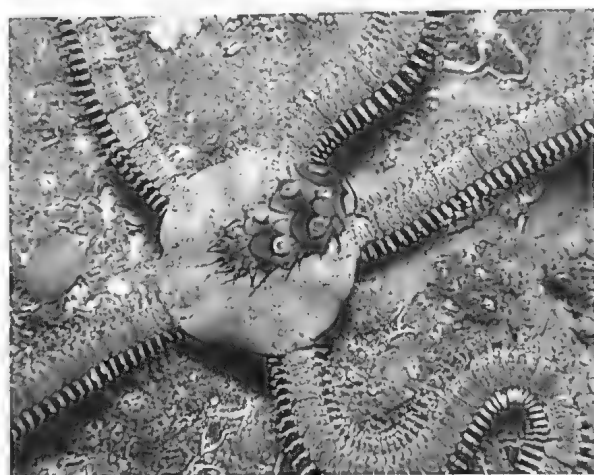


Figure 1.34 Commensal relationships. **A**, a scale-worm living on a holothurian. **B**, a scale-worm, *Lepidonotus melanogrammus* (Polynoidae), living on the ophiuroid *Ophionereis schayeri*. [A, B. Wood; B. K. Gowlett-Holmes]

1. CLASS POLYCHAETA

jaws, feed on drift algae as do many nereidids, such as *Neanthes virens*. *Perinereis vallata*, a common intertidal species in Victoria, has also been observed feeding on drift algae (R. Wilson personal communication). One species of nereidid having well-developed jaws and a muscular pharynx has been shown to filter feed in the laboratory (Harley 1950, 1953; Goerke 1966). Variations in feeding strategies may occur even within a genus. Many species are probably highly opportunistic and can feed on a wide range of food. The efficiency with which they can utilise food has not been studied for any Australian species. Certainly faecal pellets often contain algal remains, suggesting limited ability to break down plant matter, perhaps indicating a lack of the enzyme cellulase.

Many selective deposit-feeders not only collect particles for ingestion but also for tube construction, and any unsuitable particles collected can be rapidly rejected and deposited some distance from the animal (Dales 1955a). Similarly, faecal pellets can also be ejected some distance away to ensure the animal does not re-ingest them, at least in the short term.

Members of some families, such as the Capitellidae, swallow the sediment and play a major role in bioturbation and aeration of the sediment (Kristensen 1988). Recent work by Levin *et al.* (1997) has shown how mud-swallowing malidanids can rapidly subduct packets of organic matter deep into the sediment.

Behaviour

Polychaetes have a small brain and appear to exhibit few behavioural patterns. Sabellids and serpulids respond to shadows passing over them and retreat rapidly back into their tubes. Their tubes are usually considerably longer than the worm, providing a deep retreat away from danger, although observations of individuals with regenerating heads indicate that sometimes the predator is quicker than the worm. Large sabellids and serpulids often have well-developed compound eyes on the tentacular crown; Smith (1985) has undertaken detailed studies on their structure in species of *Spirobranchus*. Sabellids can become habituated to passing shadows. Nereidids have been 'trained' to turn left or right in a maze by using mild electric shocks (Clark 1960a).

Beachworms have a well-developed sense of smell, used to advantage by collectors, who drag berley, for example, rotten fish heads, over the sand in front of the worm burrows, causing the worms to emerge slightly out of their tubes and allowing them to be caught (Fig. 1.35). Other species also respond to food in the water column or on the surface of the sediment. Many species can shed posterior segments, and the anterior end of the worm will swim or crawl away to safety. Presumably this behaviour pattern is utilised when the worms are under threat from predatory birds or fish. Worms regenerating posterior segments are commonly seen, and the process of regeneration has been shown to be controlled by hormones (Golding 1974; Golding & Olive 1978).

Many species exhibit complex reproductive behaviour. Some polynoid species pair during the breeding season, despite being so highly aggressive to one another outside of the breeding season that two individuals cannot be left together in a small container overnight, as one will eat the other. During mating the male polynoid mounts the female. The eggs are fertilised as they are laid and are attached to the dorsum underneath the elytra (Daly, Evans & Morley 1972). The intricate behavioural patterns of those species that undergo mass spawning are controlled by hormones to ensure that all mature individuals spawn in synchrony. The males enter the

water column first and secrete pheromones which stimulate the females to leave their burrows and swim up into the water column. The mature worms may then undertake nuptial dances which are presumed to ensure high rates of fertilisation (Schroeder & Hermans 1975; Olive 1984; Fischer & Pfannensteil 1984). In Australia, various species of nereidids, phyllodocids and amphinomidids have been reported as undergoing such nuptial dances at Lizard Island, Great Barrier Reef (Hutchings & Howitt 1988). In addition to the response of the worms to pheromones in the water column, several species on the Great Barrier Reef are luminescent during spawning, suggesting that they are responsive to light (Hutchings & Howitt 1988).

Worms respond to changes in temperature, day length and phases of the moon, which they use to co-ordinate spawning and development of the gametes to ensure that all individuals within a population are ready to spawn simultaneously. The anterior ends of some species are covered with sensory structures (for a review see Storch & Schötzer-Schrehardt 1988), which apparently respond to environmental cues and stimulate the endocrine system to produce hormones that target specific organs (Olive 1984).

Polychaetes play a critical role in the marine benthic food chain, not only in recycling organic matter within the sediments and helping in the breakdown of plant material, but as prey items for a wide variety of other organisms. One of the major food items of the cod in the North Sea is *Melinna cristata* (now referred to as *M. elisabethae*; P. Hutchings personal observation) and Dou (1995) has shown that flatfish also feed on polychaetes. Edgar & Shaw (1995a, 1995b) analysed the gut contents of 91 species of fish from Western Port Bay, Victoria and found that many species fed on polychaetes (>25% at two sites), although the majority fed on crustaceans at most sites. They further suggested that most small fish species do not have specialised diets. Their results mirrored those from other seagrass habitats elsewhere in southern Australia (Burchmore, Pollard & Bell 1984; Robertson 1984).

Polychaetes on intertidal mudflats are preyed upon by wading birds at low tide and fish and crustaceans at high tide. They are an important component of the diet of the migratory Bar-tailed Godwit in the Sydney region (The Australian Museum 1994). Kent & Day (1983) showed that *Simplisetia pseudoerythraeensis* (now *S. aequisetis*) is preyed upon by a number of wading shore birds including red necked stints, sharp tailed sandpipers and curlew sandpipers during summer, and red necked stints and curlew sandpipers during winter; the same species is preyed upon by flounders at high tide throughout the year. Many species of the marine gastropod genus *Conus* selectively feed on polychaetes. Kohn (1978) described how these gastropods insert their proboscis deep into the coral in search of boring species of polychaetes.

Introduced species

Some species of polychaetes have been accidentally introduced into Australian waters. During the late 1940s and early 1950s, Pacific Oysters, *Crassostrea gigas*, were imported into Tasmania from Japan and, with them apparently, several species of mud worms of the spionid genus *Polydora*. Some of these species bore into the oyster shell, while others enter the oysters as larvae via the mantle cavity (Handley & Bergquist 1997), affecting its appearance and hence the market value of the oysters. Some species of *Polydora* also bore into the native commercial oyster *Saccostrea commercialis*. Confusion in the taxonomy of

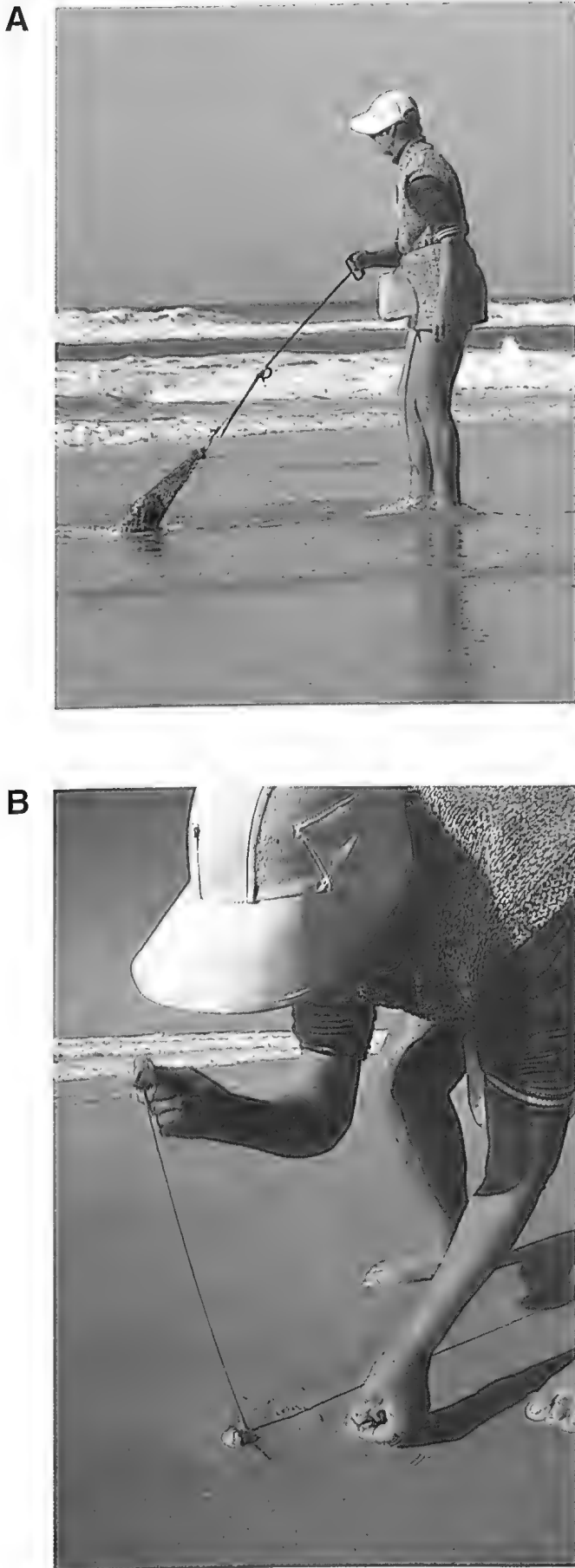


Figure 1.35 Catching giant *beach worms (*Australonuphis parateres*, Onuphidae). The worms are a popular bait for fishing; they may reach up to 2 m in length. **A**, using berley to attract the worms to the surface of the sand. **B**, extracting the worm from its burrow. [K. Atkinson]

Polydora and the widespread transfer of both Pacific Oysters and Sydney Rock Oysters around the eastern Australian coast makes it difficult to differentiate between native and introduced species. All seem to have some negative impact on the two species of oysters. Transfer of the oysters into freshwater or less saline waters for fattening, reduces *Polydora* infestation, although Handley & Bergquist (1997) found that increasing the intertidal exposure of oysters and shifting oysters to deeper harbour channels may also be effective ways of managing polydorid infestations, at least in New Zealand.

Species of serpulids are components of hull-fouling assemblages and several species have been distributed around the world and become well-established in their new environment. The arrival of *Ficopomatus enigmaticus* in Australian waters from India (ten Hove & Weerdenburg 1978) probably occurred early this century. Dense colonies of fouling serpulids are sometimes found in the intake pipes of power stations and require power stations to chlorinate incoming water to prevent these and other encrusting animals from settling. Species of spirorbine serpulids have been translocated around the world on floating seaweed (Knight-Jones, Knight-Jones, Thorp & Gray 1985).

More recently, the large sabellid, *Sabella spallanzanii*, which attains 400 mm in length, has been introduced by shipping from the Mediterranean (Pl. 5.4). Initially, it was thought that the species was introduced as larvae transported in ballast water. However, studies on its reproductive biology in Italy suggest this is unlikely as the larval stage is too short (Giangrande & Petraroli 1994). Rather, it appears that juveniles or adult worms were transported as hull-fouling organisms, most likely in protected areas of the hull such as the chain locker or behind the propeller, where hull cleaning is less effective and water movement is restricted. Large populations have been recorded from Cockburn Sound, Western Australia and Port Phillip Bay, Victoria (Wilson, Heislors & Poore 1998), with other records from southern Australia. It should be noted that this introduced species resembles native species, so that casual underwater identifications should be verified against voucher specimens. Genetic studies have confirmed that the Australian populations resemble most closely those from the Mediterranean (Ward & Andrew 1996). Dense populations of *S. spallanzanii* change local water movement patterns as a result of the feeding currents created by their large tentacular crowns and probably prevent the development of any benthic communities beneath them. Little is known about how the ecology of this part of Port Phillip Bay has been impacted by the replacement of a previously diverse benthic community with effectively a monoculture of a species that is distasteful to a wide range of predators. Recently, the population of *S. spallanzanii* in Port Phillip Bay has crashed, but it appears to be recovering. This will facilitate studies on its reproduction and dispersal ability and the impact that it has on native benthic communities.

Economic Significance

Polychaetes are used for bait by amateur fishers all over the world and traditionally these worms have been collected from the wild (Figs 1.35, 1.36; Olive 1994). Increasingly, the mud flats and seagrass beds in which the bait worms live have been closed for collection, creating a considerable demand for farmed worms. In Britain, *Neanthes virens* is farmed and airfreighted around Northern Europe. This species spawns once a year in the wild, but throughout the year on the farm under the influence of species-specific reproductive

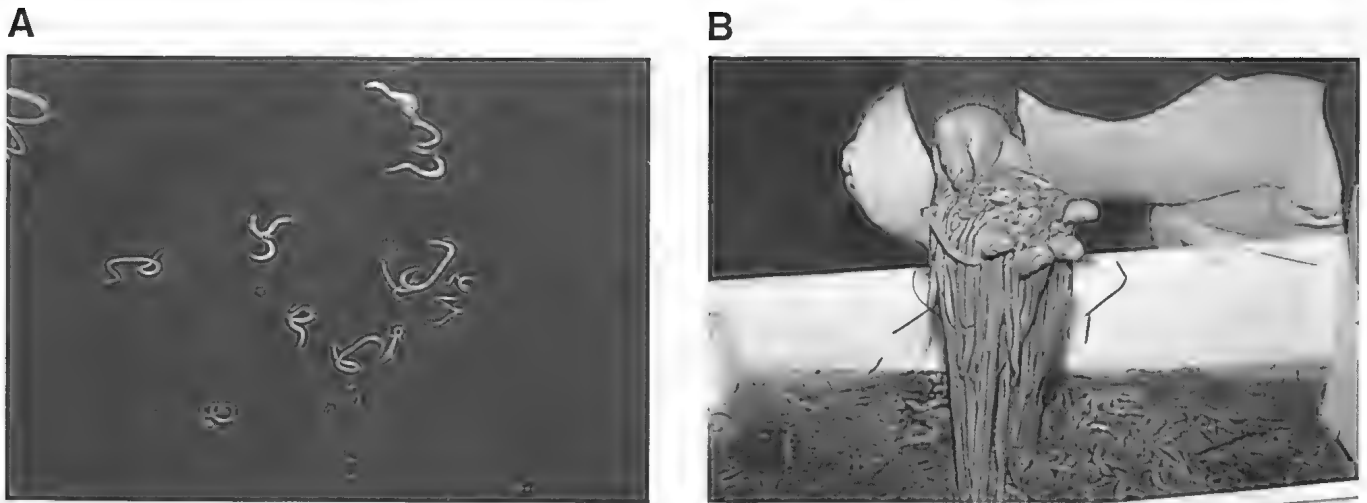


Figure 1.36 The timing of the annual mass swarming of *Glycera* cf. *americana* over the tidal flats of the upper regions of Gulf St Vincent, South Australia, is highly predictable (Huie 1985, personal communication). **A**, on the ebb tide on the second or third night after New Moon in late July, and for up to 3–5 nights thereafter, countless worms leave the sand and writhe towards the surface. **B**, they collect in large numbers in back eddies, where bait collectors may scoop up sufficient for their year's supply.

[J. Huie]

hormones, which have been isolated and commercially synthesised. This technology is now being sold under franchise in Northern Europe.

In Australia, several companies are experimenting with breeding species of *Marphysa* (Pl. 1.3), *Diopatra* and beach worms (*Australonuphis*; Pl. 1.4) for bait, but so far there is no commercial production; currently a small individual of *Marphysa* of about 5 g wet weight fetches A\$0.70 in Sydney. In Australia, especially New South Wales, the mud flats and seagrass beds where these bait worms occur are being closed to all types of bait collecting, primarily to conserve seagrass beds. This will affect both amateurs, who require no license to collect, and licensed professional bait diggers. The New South Wales Fisheries Department is currently looking at limiting licenses to collect beachworms commercially as a precautionary measure in view of the lack of information on the rate of recruitment or life span of these species.

With few exceptions, polychaetes are harmless, but some of the amphinomids will leave broken barbed chaetae with poison glands in the skin when handled. Some people develop local reactions to these worms and hence they are referred to as 'fire worms'. Large species of *Eunice*, *Marphysa* and *Australonuphis* can inflict bites and draw blood from those trying to catch and extract them from their burrows (see frontcover showing *Eunice aphroditois* with jaws open). Blood worms (*Glycera* species) on the east coast of the United States of America can cause bad infection, referred to as 'bait digger's arm'. When handled, aphroditids will shed their notochaetae which can become embedded in the collector's skin and cause local irritations.

The presence of particular species of polychaetes may be used to indicate that the environment is organically enriched (polluted). For example, species of *Capitella* and some cirratulids are indicative of sediments with high organic loads. In such situations, very few other macrobenthic organisms are present (Ward & Hutchings 1996).

METHODS OF STUDY

As the methods used in the study of polychaete biology, taxonomy and ecology are similar to those employed in other groups of marine invertebrates, discussion has been limited here to a brief comment on collection and preservation. Good

accounts of polychaete collection and specimen treatment can be found in Fauchald (1977), George & Hartmann-Schröder (1985) and Mackie (1994). Techniques for dealing with meiofaunal polychaetes can be found in Westheide (1990a) and for pelagic forms Gibbs (1976) may be useful. Information on methods of laboratory culture and rearing of polychaetes is scattered in the literature, but specific references are those of Reish (1953, 1981) and Reish & Richards (1966).

In the intertidal zone or in shallow water, techniques for collecting polychaetes include direct collection by hand, aided by forceps, hand ('yabby') pumps and other vacuum-creating devices, shovels and garden trowels, and even the use of bait bags to lure beach worms within reach. When collecting, take only the material that is needed, and do this with care and consideration for the environment. Simple measures such as returning a log or rock to its original position will assist the survival of attached organisms. The importance of procuring polychaetes from crevices and other inaccessible habitats using levering devices such as crow bars, should be assessed carefully against the environmental damage caused. Where the water depth exceeds about a metre collection is more comfortable by diving using SCUBA. Large quantities of polychaetes can be collected from muddy substrata or seagrass beds using an airlift pump, and the material sorted later. When polychaetes are collected together with sediment it is often necessary to sieve the material through appropriately sized mesh screens in order to reduce the volume of sediment prior to sorting.

In deep water, a variety of remote collecting devices may be used to collect benthic species. They include box corers, dredges, benthic grabs and sledges, trawl and plankton nets, and baited traps. Such equipment is usually deployed from a boat. Samples retrieved may be treated effectively by sieving and sorting under a stereoscopic microscope or a good hand lens. Planktonic species, and pelagic larvae and sexually-modified swimming adults of benthic forms can be collected by towing a plankton net behind a boat; the latter group can also be collected from the shore at night using a dip net and light to attract them into the net.

Polychaetes must be fixed in either formalin or in another high-quality fixative before being transferred to a preservative. A minimum of 24 hours is required in a solution of 3% formaldehyde in sea water (in the case of marine

species), buffered if possible. Prior to fixation, brief relaxation with either a 7% MgCl_2 (or MgSO_4) or alternatively with oil of cloves is recommended, especially for fragile species. Clean the specimens, as far as possible, of mucus and debris; it is far easier to observe details of chaetal structures when the chaetae are clean. The volume of fixative in relation to the volume of tissue should be large, preferably about 10:1 and the vessel in which the fixation is taking place should be inverted gently a few times to ensure good penetration. The best general preservative for polychaetes is 70% ethyl alcohol; relatively large volumes of preservative should be used in relation to the volume of tissue and specimens should be stored in appropriately sized jars so that worms do not become to distorted.

Permits are required before collecting can be undertaken in some locations. In terms of the Constitution, control of the collection of components of the Australian fauna is the responsibility of the six States and two mainland Territories which comprise The Commonwealth of Australia. There are a number of administering authorities in each State or Territory and it is essential to obtain the permission of each relevant authority before collecting begins. Permission to enter any land is a separate issue which collectors should clarify with landowners before collecting. This applies especially to Aboriginal lands and heritage areas.

To assist researchers, a detailed guide to requirements for collecting Australian plants and animals is available (ABRS 1993). The guide provides the contact personnel and addresses of State and Commonwealth authorities responsible for issuing collection permits and licenses. Copies of this guide may be obtained from the Australian Biological Resources Study, GPO Box 787, CANBERRA ACT 2601; telephone (02) 6250 9430 or 6250 9443, facsimile (02) 6250 9448 or 6250 9555. The guide is also available on the Internet at <http://www.anbg.gov.au/abrs/grants/guide/collect.htm>.

Import and export of legally collected material from Australia requires strict observance of international conventions, such as the Convention on International Trade in Endangered Species (CITES). Further information may be obtained from the Chief Executive Officer, Biodiversity Group, Environment Australia, GPO Box 787, CANBERRA ACT 2601; telephone within Australia (06) 2250 0200, or from overseas +61 6 2250 0200.

BIOGEOGRAPHY

Polychaete families and most genera are typically worldwide in their distribution, reflecting the very old age of the group (Fauchald 1984, and see below). Until recently many polychaete species were regarded as being 'cosmopolitan' or having very wide discontinuous distributions. Many species originally described from the Arctic were also reported from the Antarctic and others were reported from both sides of major ocean basins. Probably because of the history of polychaete studies in Australia, a large number of species recorded here were first described from Northern Europe by European workers who late in the last century and early this century received collections from Australia. However, increasingly as the Australian material of these European species is examined in detail it is being shown that they are, in fact, undescribed species and not the European species. For instance, Hutchings & Glasby (1991) showed that of the 32 species of terebellids recorded from Australia up to 1979 (listed in Day & Hutchings 1979), probably only one is a valid record – the rest and many others have been described as new species, and the total fauna for this family in Australia

exceeds 120 species. The trichobranchid *Terebellides stroemii* has been widely reported from all parts of the world including Australia. A recent study by Hutchings & Peart (in preparation) has shown that the species does not occur in Australia and in fact material previously identified as *T. stroemii* consists of four new species.

Our knowledge of the distribution and ecology of the Australian polychaete fauna is patchy: intertidal and shallow subtidal assemblages in southern Australia are reasonably well-known, especially for the larger species, but this cannot be said for northern areas of Australia especially the north-west. Further, throughout Australia our knowledge of polychaetes inhabiting depths greater than about 50 m is extremely limited. The only deep-water area where polychaete assemblages have been studied in detail is Bass Strait. During the past 2–3 decades extensive benthic surveys have been undertaken in various locations such as Port Phillip Bay, Botany Bay, Jervis Bay, Moreton Bay, Halifax Bay and major attempts have been made to identify the polychaetes to species. In addition to these studies, brief surveys at specific locations in New South Wales (Twofold Bay, Hutchings, van der Velde & Keable 1989; Wallis Lake, Hutchings 1974a; Careel Bay, Pittwater, Hutchings & Rainer 1979; Elizabeth and Middleton Reefs, Hutchings 1992) have been undertaken by Museum staff and other polychaete workers. Also, beginning in the 1980s revisions of a few families have been undertaken, however many families have yet to be revised. Certainly among these unrevised families many new species (and genera) await discovery.

Ideally, biogeographic studies should be conducted on monophyletic groups well known in terms of their taxonomy, distribution and phylogeny. Clearly, very few groups of Australian polychaetes are well known from this point of view; exceptions are the Terebellidae, Nereididae and Spionidae for which taxonomic and phylogenetic studies have been done or are in progress (see Hutchings & Turvey 1984; Hutchings & Glasby 1986a, 1986b, 1987, 1988; Glasby 1999a; Wilson 1990) and Onuphidae (Paxton 1986a, 1986b, 1993). However, these better known families have not been subject to analytical-type biogeographic studies. Thus, the following discussion of polychaete biogeography is mainly descriptive, concerning generalised distribution patterns. At present, we can only speculate on why or what caused these biogeographic patterns, in particular large-scale ones.

Large-scale patterns. Historically, polychaetes have contributed relatively little to our understanding of large-scale biogeographic patterns in the sea, compared to other major invertebrate groups. The group does not feature highly in the classic studies of marine zoogeography (Briggs 1974; Ekman 1953). Reasons for this include the perceived wide distribution of polychaete taxa at all levels, the poor state of taxonomic knowledge for many groups, especially over a broad geographic area, and the lack of available robust phylogenies for most groups.

Taxonomic revisions of several families of polychaetes (Aphroditidae, Nephtyidae, Nereididae, Onuphidae, Sigalionidae, Spionidae, Terebellidae, Trichobranchidae) in Australian waters have identified a high degree of endemism, particularly in southern Australia. For example, Rainer & Kaly (1988) identified 12 (possibly 13) endemic species of Nephtyidae out of total of 18 in Australia; Wilson (1990) identified 17 endemic species in the *Prionospio* group (Spionidae) in a total of 20 species from southern Australia; and, Hutchings & McRae (1993) identified 13 endemic species of Aphroditidae out of a total of 18 in Australia. In a study of Austral polychaetes belonging to six taxonomically

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Table 1.1 Number of species in selected polychaete families in each of the distributional categories identified by Wilson & Allen (1987); see Figure 1.37A. The Widespread Australian distributional category encircles Australia; it is additional to those of Wilson & Allen. Distributional data sourced as follows: aphroditids – Watson Russell (1989, 1990), Hutchings & McRae (1993); nephtyids – Rainer & Hutchings (1977); Rainer & Kaly (1988); nereidids – Hutchings & Glasby (1982), Hutchings & Reid (1990, 1991), Hutchings & Turvey (1982), Hutchings *et al.* (1991), Hartmann-Schröder (1985), Wilson (1984, 1985), Wilson & Glasby (1993), Glasby (1999a); terebellids – Hutchings & Glasby (1986a, 1986b, 1987, 1988), Hutchings (1990, 1997a, 1997b); trichobranchids – Hutchings & Peart (in preparation).

Distribution Pattern	Aphroditidae 19 species	Nephtyidae 18 species	Nereididae 68 species	Terebellidae 97 species	Trichobranchidae 10 species	Totals 212 species
Widespread Indo-West Pacific	7	4	22	13	1	47 (22%)
Indian Ocean	0	0	0	0	0	0
Western Pacific	0	0	0	1	0	1
Endemic North-Western Australia	1	5	2	24	0	32 (15%)
Endemic North-Eastern Australia	3	2	1	15	0	21 (10%)
Endemic Western Australia	0	0	1	0	0	1
Endemic Eastern Australia	0	0	2	1	0	3
South-Western Australia	1	1	1	0	0	3
South-Eastern Australia	0	5	5	21	1	32 (15%)
Endemic South Coast	0	0	5	1	2	8
General Southern	5	0	24	8	2	39 (18%)
Widespread Australia	2	1	5	13	4	25 (12%)

well-known families, the polychaete fauna of southern Australia was shown to be highly endemic in comparison to other Austral shores with 67% of species endemic to this region. At the genus level, however endemicity is much lower, with only two (spionids *Australospio* and *Orthoprionospio*) in a total of 67 genera from all major polychaete clades found to be endemic to southern Australia (Glasby & Alvarez 1999). Although these levels of species endemism may appear impressive, they are much less than those for marine species in general, estimated to be over 90% for most groups in southern Australia (Wilson & Allen 1987).

Wilson & Allen (1987) identified 11 common distributional patterns displayed by Australian shallow water benthic species (Fig. 1.37A); Figure 1.37B gives the corresponding water temperatures. In general, these distributional patterns are also applicable to the polychaete fauna, except that an additional distributional type (widespread Australian) is required to adequately describe the full range of distributional types. Further, many polychaete species which have a general southern distribution also occur in New Zealand and in some cases the small islands of the Southern Ocean. Among polychaete species, the most common distributional types are Widespread Indo-west Pacific (22%), General Southern (18%), endemic North-western Australia (15%) and South-eastern Australia (15%) (Table 1.1). The widespread Australian distributional pattern accounts for 12% of all species in this survey; many of these species have also been recorded in other parts of the world and may actually represent species groups, but some are apparently true widespread endemics. Our poor taxonomic knowledge of polychaetes in neighbouring regions means that these estimates of endemism are very approximate. Classic general southern groups include the monospecific nereidid genera *Australonereis* (*A. ehlersi*; Fig. 1.1) and *Olganereis* (*O. edmondsi*), some members of *Simplisetia* and the

terebellid *Thelepus plagiostoma*. Widespread Indo-west Pacific species can be found in the nereidid genus *Perinereis* (*P. helleri*, *P. nigropunctata*, *P. nuntia*); also, many other species widespread in the northern half of Australia (for example, the terebellids *Thelepus robustus*, *Loimia ingens*) are considered in this category, with the assumption that they will be recorded in other Indo-west Pacific areas with further collecting. The Nephtyidae contain a large proportion of South-eastern Australian endemics, including *Nephtys australiensis*, *N. inornata* and *N. longipes*, and many species of terebellid are endemic to North-western Australia.

Among the Terebellidae, three types of distributional patterns were found to occur in coastal species: those occurring all around the coast; those with a widespread distribution but usually restricted to a particular biogeographic region (northern or southern), and those with very restricted distributions (Hutchings & Glasby 1991); however, only two of these distribution patterns were recognised in the Aphroditidae (Hutchings & McRae 1993); the north-south one was not apparent, perhaps because aphroditids are relatively less common in shallow coastal waters, compared to Terebellidae. Among trichobranchids restricted to Australian waters three patterns of distribution occur: five species occur throughout Australia; three species have a southern distribution; and, two species have a very restricted distribution (Hutchings & Peart in preparation).

The observed widespread Australian distributional pattern occurring in all polychaete groups may indicate ancient species which, over time and repeated small episodes of concerted dispersal of populations, have colonised a wide area. This example of 'range expansion' appears to have occurred in several polychaete species now found in southern Australia and New Zealand (Glasby & Alvarez 1999). In contrast, range expansion by long-distance dispersal (via larvae for example), is thought to be less common among the

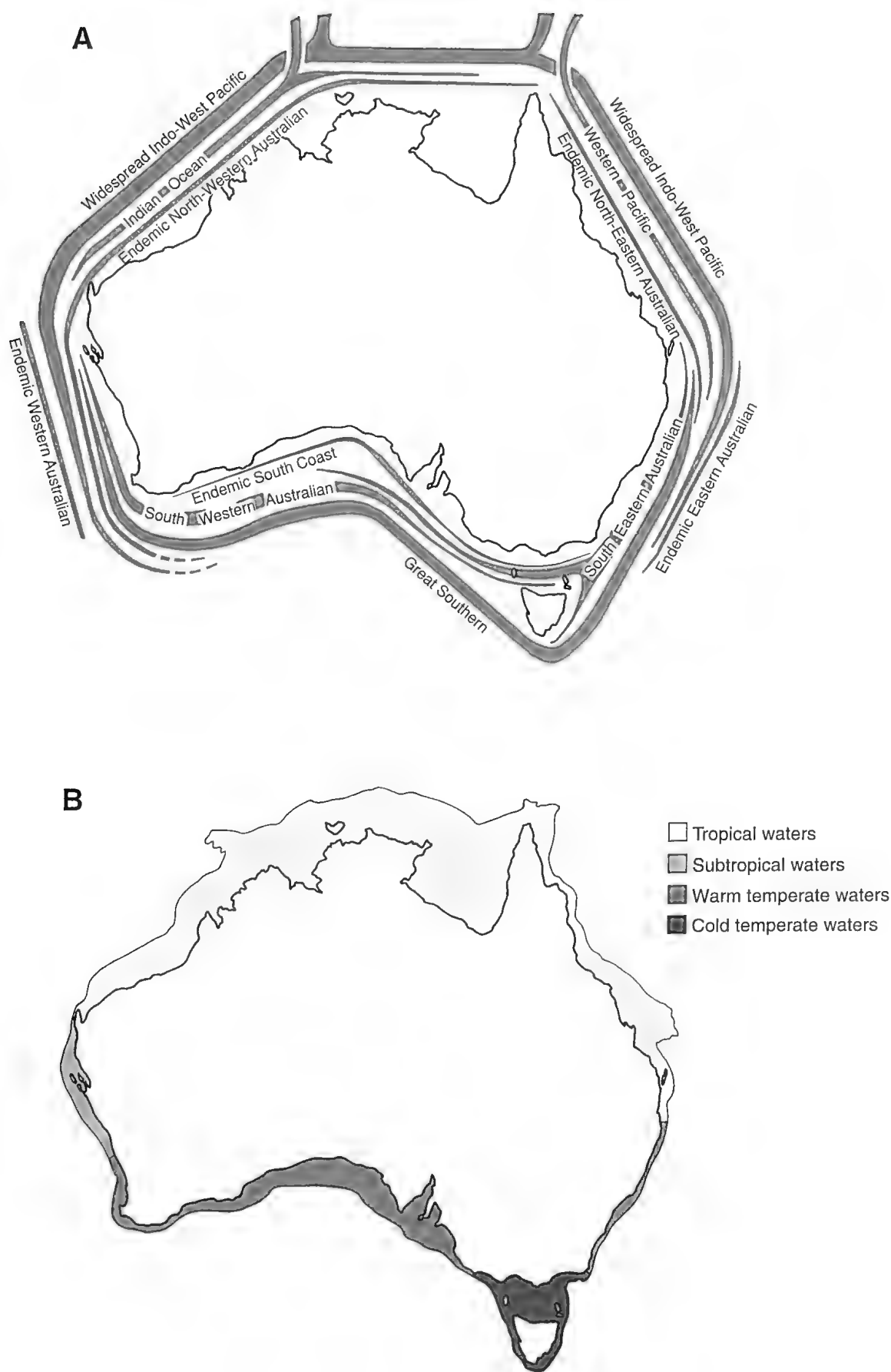


Figure 1.37 **A**, Common distribution patterns of shallow water benthic animals on the Australian coast, showing approximate boundaries of the Indo-West Pacific Region (northern Australian sector) and Southern Australian Region and the wide Eastern and Western Overlap Zones between them. **B**, broad distributional patterns of water temperature over the Australian continental shelf. (A, from Wilson & Allen 1987; B, modified after Thackway & Cresswell 1998).

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groups of polychaetes studied by these authors. Species with localised distributions may be associated with a particular restricted type of habitat, have a peculiar insular biology, or the distribution may be an artefact caused by incomplete sampling.

A north–south pattern of distribution appears to correspond closely to the general pattern of distribution of marine groups; the northern biota being derived from the Indo-West Pacific (that is, Pan-Pacific Tethyan), and the southern biota has a temperate Palaeoaustral origin (Poore 1994, 1995; Wilson & Allen 1987). These two distinct marine biotas are reflected in the classification of marine provinces in Australia: a southern region and a northern region with overlapping zones on the east and west coasts (Ponder 1995; Wilson & Allen 1987). It should be mentioned though that this concept of marine biogeographic regionalisation, developed largely on the basis of non-quantitative analysis of species distributional patterns, may turn out to be an oversimplification; more rigorous studies involving congruence in the distributional patterns of many unrelated taxa with a known phylogeny (= cladistic biogeography) are required to test critically the position of the biogeographic boundaries.

One family of polychaetes, the Onuphidae, is much better represented in the southern hemisphere than in the northern (in terms of generic diversity). This has led to speculation of a southern, or Palaeo-austral, origin for the group (Paxton 1986a). However, maximum diversity of a group in a particular area is not necessarily equated with the group having been there the longest, for there are many other factors involved in speciation and cladogenesis. A similar southern origin was postulated for *Namanereis* (Namanereidinae) on the basis of a cladistic biogeographic study (Glasby 1999b), yet today this genus is most diverse in the tropics with only a single (relict) species occurring in southern Australia.

The biogeographic regions, or areas of endemism, seen today around the coast of Australia may be the result of major tectonic events that occurred in the late Mesozoic and Tertiary. Poore (1994, 1995) identified three tectonic events important to this process, in order:

- the severing of marine faunal links between Australia and Western Antarctica, South America and South Africa;
- the severing of marine faunal links with New Zealand and eastern Antarctica;
- invasion of Laurasian Tethyan biota into northern Australia as Australia collided with South-east Asia.

Associated with these major tectonic events were changes in sea level, water temperature and formation of geographical barriers, which contributed to speciation and extinction, and the shaping of the faunal composition of the biogeographic regions that we see today. A consequence of the first two episodes in this series of events is that Australia's coastal biota should be, in general terms, more similar to that of New Zealand than that of South America and South Africa. This is the same pattern observed in the polychaete fauna, in which southern Australia is 'sister area' to New Zealand regions (Glasby & Alvarez 1999). However, evidence for an invasion of Laurasian Tethyan biota into northern Australia among Polychaeta is not currently available, although the suggestions are there. For example, of the five extralimital species of Aphroditidae occurring in Australia, four occur in Indonesia (Hutchings & McRae 1993) and in the Nereididae a few species (*Dendronereides heteropoda*, *Leonnates jousseaumei* and *Namalycastis abiuma* occurring in northern Australia are also found in Indonesia (Hutchings & Reid 1990, 1991;

Glasby 1999a). However, the polychaete fauna to our north is very poorly known and until a similar taxonomic effort has been devoted to revising groups in this area, we will not be able to estimate the effect and nature of this 'invasion'.

Diversity and small-scale patterns. Polychaetes are often a major component of the benthos in terms of both numbers of individuals and species, regardless of water depth or latitude. They also live in a very diverse range of habitats (Hutchings 1998). Some studies suggest that there are distinct latitudinal gradients, with diversity increasing towards the tropics (Rex, Etter & Stuart 1995); however, if the data from the Norwegian Sea, which has low diversity due to recent glaciation events, is removed, then the trends are less clear (Gray 1997). In the Southern Hemisphere, such a gradient has also been questioned, in part because of the purported high diversity in the Antarctic for many groups, including polychaetes. Hartman (1966a) recorded 457 species of polychaetes from the Antarctic, although she indicated that the best known areas were from the Subantarctic to the Antarctic Convergence; polar regions are less well-known, suggesting that the total polychaete diversity for the entire Antarctic and Subantarctic will be higher. Some of the highest levels of species diversity for soft sediments have been recorded from southern Australia (Poore & Wilson 1993). Coleman, Gason & Poore (1997) found 800 species of macrofauna (of which 24.4% were polychaetes) in 10 m² of sediment in Bass Strait and 700 species (of which 33% were polychaetes) have been recorded from the sediments of nearby Port Phillip Bay, Victoria (Poore, Rainer, Spies & Ward 1975).

Other workers have suggested that benthic macro-invertebrate diversity increases from shallow areas to the deep sea (Grassle & Maciolek 1992), based largely on data from the northern hemisphere (polychaetes represent a very large proportion of this biodiversity). However, data from the Norwegian continental shelf (Gray 1994) and southern Australia (Poore & Wilson 1993) contradicts this hypothesis. In fact, the Australian data reveals that shallow coastal waters may have benthic macroinvertebrate biodiversity as high as that of the deep sea (Poore 1995).

Numerous benthic studies in coastal embayments in Australia have been undertaken over the past 30 years (Port Phillip Bay – Poore *et al.* 1975; Wilson, Heislors & Poore 1998; Western Port – Coleman, Cuff, Drummond & Kudenov 1978; Moreton Bay – Stephenson 1980a, 1980b; Jervis Bay – Hutchings & Jacoby 1994; Upper Spencer Gulf – Hutchings *et al.* 1993). Although mainly in temperate regions, they all show that in soft sediments, including seagrass areas, polychaetes are one of the dominant groups both in terms of number of individuals and species (see Hutchings 1998). Repetitive sampling at the same site over time reveals that recruitment occurs seasonally and variations in the species composition occur annually. Sites in Jervis Bay, New South Wales, sampled quarterly over 3 years revealed polychaete species new to a particular site even since the previous sampling period. The Jervis Bay study also showed that most polychaete species were represented by a few individuals; of the 171 species collected, more than 25% were represented by less than 10 individuals over 3 years. Only seven species were consistently present in large enough numbers over time and space for a detailed analysis of their distribution to be conducted (Hutchings & Jacoby 1994). Studies on polychaete recruitment to coral substrata on the northern Great Barrier Reef also revealed spatial and temporal variations in recruitment, with significant differences between sites and between years (Hutchings & Murray 1982).



Figure 1.38 Fossilised marine worm burrows (*Skolithos*) from Ordovician or Early Silurian Tumblagooda Sandstone, Western Australia. [K. Atkinson]

In contrast, our knowledge of the continental shelf fauna is extremely limited. The only area studied in detail is eastern Bass Strait, where a study of benthic communities (Coleman *et al.* 1997) produced 195 polychaete species representing 40 families from 105 grab samples. When this material was identified in 1992, only 40 species (21%) could be confidently given species names (so-called 'cosmopolitan' species names were not accepted) (R. Wilson unpublished data). Polychaetes from the Australian continental slope and deep sea are almost entirely unknown. Investigations of slope communities have recently commenced, for example, Poore *et al.* (1994) analysed the composition and diversity of isopod crustaceans, but polychaetes collected from these stations of south-eastern Australia remain unstudied.

Because of these sampling biases it is difficult to analyse thoroughly polychaete distributions and assemblages within a major biogeographic region. However, major differences can be expected to occur within regions especially where habitats differ substantially, for example between the Great Barrier Reef and the adjacent coast. Also, in southern Australia there appears to be distinct assemblage differences between shelf, inshore marine embayments, and estuarine environments. For example, Wilson (1990) found that six species of the *Prionospio* complex occur only in marine embayments of south-eastern Australia, particularly the muddy sediments of seagrass communities; two species in the complex are restricted to estuaries in the area; and five species occur on the continental shelf in muddy carbonate sediments. Only two of the total of 13 species found in south-eastern Australia occur widely in both inshore waters and on the shelf. In the Spencer Gulf, major differences in species composition (of which polychaetes were dominant) were found between intertidal unvegetated mudflats of the northern Spencer Gulf and similar habitats (including shallow subtidal seagrass areas) further south near Port Pirie. This result was thought to be the result of differing hydrological regimes between the two

areas, although differences in the scales of sampling and taxonomic discrepancies also may have been influential (Hutchings *et al.* 1993).

More subtle differences in species composition were found between vegetated and unvegetated soft bottom habitats within Jervis Bay, with both areas having a core of common species; differences were mainly attributable to rarer species with very restricted distributions (Hutchings & Jacoby 1994).

FOSSIL RECORD

A thorough treatment of fossil polychaetes is beyond the scope of this review. A brief overview of fossils is presented, with emphasis on Australian forms and establishing an approximate age for clades identified by Rouse & Fauchald (1997). Compilations of fossil polychaete taxa can be found in Howell (1962); however, this work should be viewed cautiously because a review of these taxa belonging to Phyllodocida and Eunicida showed some to be non-polychaetes, and other species are in need of reclassification (Kozur 1970). A brief review of fossil Annelida is provided by Robison (1987), and Szaniawski (1996) has reviewed the available information on scolecodonts, the fossilised jaws of polychaetes. Major regional revisions of fossil invertebrates, including polychaetes, are those of Thompson (1979) for the Pennsylvanian fauna of Northern Illinois (United States of America) and Conway Morris (1979, 1985) for the Middle Cambrian Burgess Shale (Canada). There appears to be no comprehensive list of fossil polychaetes of Australia, although those of New Zealand were summarised by Fleming (1971, 1974).

Polychaetes generally do not fossilise well, apart from their jaws (scolecodonts), chaetae, and tube and burrow structures. Fossilised burrows are referred to as trace fossils. The calcified opercula of serpulids also fossilise well. One of the simplest and widespread of all trace fossils is the ichnogenus *Skolithos*, which is represented by simple vertical or

subvertical burrows (Fig. 1.38). *Skolithos*, also known as piperock, is found from the late Precambrian to the Recent, and is thought to represent past high-energy, shallow marine sedimentary environments (Ekdale & Lewis 1993 and references therein). Some of the examples of ancient piperock are likely to represent sabellariid reefs. However, those from Tumblagooda Hill near Kalbarri (Fig. 1.38) are unlikely to be sabellariid tubes, as the tubes are straight and parallel vertically rather than radiating outward, slightly curved and intertwined as expected of preserved sabellariid reefs (Ekdale & Lewis 1993); in addition, there are no extensive present-day sabellariid reefs known in Australia (see Sabellariidae).

Entire fossilised worms are far less common, but have been found from the Pennsylvanian fauna of Northern Illinois (Thompson 1979), with the oldest dating back to the mid-Cambrian of the Burgess Shale (Conway Morris 1979, 1985). Such a poor fossil record unfortunately provides little insight into the origin and evolutionary history of the Polychaeta or Annelida.

Suggestions that the origin of the polychaetes predates the Cambrian are based on records of trace fossils (Robison 1987) and on arthropod-like fossils from the Ediacara Epoch, but both should be viewed cautiously. Two of the best-known 'polychaetes' from this epoch in South Australia are *Spriggina* and *Dickinsonia*. Glaessner (1976) suggested that Sprigginiidae, represented by *Spriggina* and *Marywadea*, were related to phyllodocimorph polychaetes, specifically in the structure of the pharynx, but also noted that in most respects the family was unlike any living annelid. *Dickinsonia* was thought to be allied to Spintheridae (Wade 1972). However, debate continues over whether these taxa are polychaetes, or even metazoans (Seilacher 1992). The Sprigginiidae for example, may belong to the Arthropoda (Conway Morris 1991; Waggoner 1996) or the Annelida (Jenkins 1992), and *Dickinsonia* has been variously interpreted as an annelid, cnidarian or flatworm (see discussion in Valentine 1992). Trace fossils from the Early Cambrian representing penetrating burrows may have been made by pseudocoelomates such as priapulids or the annelid-like paleoscolecsids, rather than by true polychaetes (Valentine 1994).

Annelid-like fossils dating back to the Early Cambrian from Kangaroo Island, South Australia include *Palaeoscolex* (Palaeoscolecidae), the 'opheliid-like' *Mysocolex* and the possible spiomorph *Vetustovermis* (Glaessner 1979). However, recently Wills (1998) endorsed the view that palaeoscolecsids are not polychaetes, but priapulids, and Briggs & Nedin (1997) suggested that species of *Myoscolex* are probably arthropods. From Yorke Peninsula, a bizarre form allocated a class of its own, Thambetolepidea, may have annelidan or molluscan affinities (Jell 1981).

By the Middle Cambrian true polychaetes had certainly appeared, with the aciculates *Wiwaxia* and *Canadia* having prostomia with appendages, well-developed parapodia and diverse chaetal forms (Table 1.2). In fact, considerable taxonomic diversification among polychaetes had already occurred by this time, with six genera represented in the Burgess Shale at a single locality in Western Canada (Conway Morris 1979, 1985), suggesting that branching events required of annelid diversifications occurred well before the onset of the Cambrian explosion. Together with morphological divergence studies, those utilising molecular clocks also indicate that the major clades of metazoans (including polychaetes) may date back to the Proterozoic,

well before the Cambrian (Conway Morris 1993; Fortey *et al.* 1996; Wray *et al.* 1996; Ayala, Rzhetsky & Ayala 1998). The implication of these studies is that it decouples early metazoan phylogeny from the so-called Cambrian 'explosion', and implies that there is a substantial gap in the fossil record preceding the Precambrian.

Fauchald (1984) suggested that most orders of polychaetes were present before the end of the Palaeozoic. Recent evidence based on body fossils, or parts thereof, suggests that this was probably a conservative estimate. Most of the major clades recognised nowadays appear to have representatives dating back to the Early to Middle Palaeozoic. The Opheliidae (Scolecida) and Flabelligeridae (Canalipalpata: Terebellida) have been recorded from the Devonian (Thompson 1979). Canalipalpata: Spionida is known from polydroid trace fossils dated to the Devonian (Blake & Evans 1973). Serpulidae (Canalipalpata: Sabellida) date back at least to the Devonian, but the minute coiled tubes of possible spirorbines may extend the age of the taxon back to the Ordovician, even early Cambrian (Beus 1980; Robison 1987; Landing 1993). Aciculata: Phyllodocida possibly may have been represented by the now extinct forms *Wiwaxia* and *Canadia*, which occurred in the Middle Cambrian (Butterfield 1990), however, scolecodonts belonging to this group (Glyceridae and Goniadidae) are not known until the Triassic (Szaniawski 1996; Fig. 1.39). Aciculata: Eunicida is represented by various euniceans having diverse forms of maxillae dating back to the Ordovician, including those with ctenognath-types (among Recent Eunicida only found in some Dorvilleidae) and labidognath-types (found in Eunicidae, Onuphidae and Lumbrineridae) (Kielan-Jaworowska 1966); however, the presence of diversified maxillae in this group suggests that their ancestors existed even earlier.

The fossil record of polychaetes through the Palaeozoic and Mesozoic can be traced through the stratigraphic record of scolecodonts (Fig. 1.39); however, the amount of useful information that scolecodonts can yield is limited, partly because of the poor state of scolecodont systematics (Szaniawski 1996). The oldest scolecodonts are early Ordovician, but by the late Ordovician 13 families had appeared. In the Middle Devonian Burdekin Formation in Queensland, two families have been reported: Oenonidae represented by *Arabellites* (1 species) and *Ildraites* (1 species) and possibly Dorvilleidae represented by three species of *Staurocephalites* (Cook & Turner 1994). However, scolecodonts are common from Ordovician and Devonian deposits throughout Australia (see Paxton this volume) and representatives of other families may be expected to be found. By the end of the Devonian, however, scolecodonts of many of these families had disappeared from the fossil record; most of those that persisted this period are thought to have yielded the ancestors of modern-day families. For example, Atraktopronidae or Skalenopronidae are ancestors of Oenonidae; Kielanopronidae are possibly ancestors of Hartmaniellidae; Sciotopronidae are ancestors of Lumbrineridae and Tetrapronidae or Mochtyellidae are ancestors of Dorvilleidae (Szaniawski 1996). A few groups appear to have become extinct by the end of the Carboniferous (for example, Polychaetaspidae) or at least by the end of the Palaeozoic (for example, Kallopronidae). Thus, the fossil record based on scolecodonts indicates that toward the end of the Palaeozoic most polychaete taxa became extinct, but during the Triassic many forms appeared that resembled Recent ones; the reasons for this remain unclear.

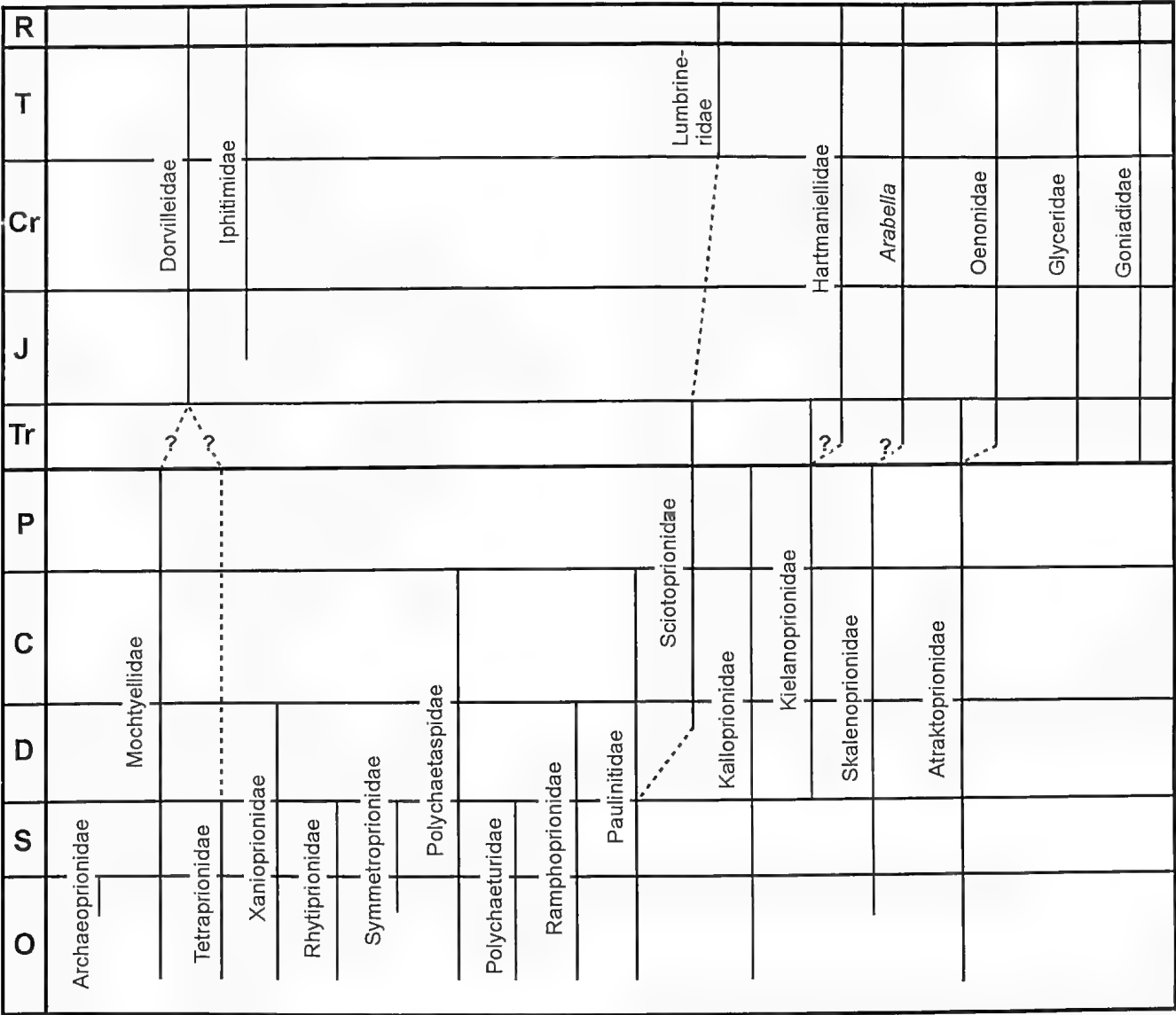


Figure 1.39 Stratigraphic distribution of most of the polychaete families for which fossil jaws are known (after Szaniawski 1996). Note the possibility that *Arabella* (presently placed within Oenonidae) has been derived independently from other members of Oenonidae (*Oenone*, *Tainokia* and *Halla*). C, Carboniferous; Cr, Cretaceous; D, Devonian; J, Jurassic; O, Ordovician; P, Permian; R, Recent; S, Silurian; T, Tertiary; Tr, Triassic.

Table 1.2 Approximate age of the major clades of polychaetes (identified by Rouse & Fauchald 1997) estimated by the oldest known fossil.

Clade	Oldest fossil	Fossilised taxon	Reference
Scolecida	Devonian	Opheliidae	Thompson 1979
Palpata			
Canalipalpata			
Sabellida	Devonian	<i>Serpula helicalis</i> (Serpulidae)	Beus 1980
Spionida	Devonian	polydroids (Spionidae)	Blake & Evans 1973
Terebellida	Devonian	Flabelligeridae	Thompson 1979
Palpata			
Aciculata			
Eunicida	Ordovician	various eunicidans having both ctenognath and labidognath maxillae	Edgar 1984, Fauchald & Rouse 1997
Phyllodocida	Middle Cambrian	<i>Wiwaxia</i> ; <i>Canadia</i> (?Chrysopetalidae)	Butterfield 1990

PHYLOGENY

Phylogenetic studies on polychaetes and their allies may be divided broadly into three types: whole animal morphology-based studies (to date only Rouse & Fauchald 1997); studies of a few characters or organ systems (for example, Bartolomaeus 1995; Purschke 1997; Westheide 1997), and molecular studies (for example, Winnepeninckx *et al.* 1995; McHugh 1997; Kojima 1998), usually from a single gene of ribosomal RNA (18S) or amino acid sequences (EF-1 α). To date, there have been no published studies combining morphological and molecular data, the so-called 'total evidence' approach (Kluge 1989). The results obtained from the latter two approaches need to be viewed cautiously, since both suffer from inadequate sampling: the organ systems approach uses a subsample of potentially available morphological data and taxa, and all molecular studies to date suffer from a strong representational bias regarding the taxa used for study; that is, no molecular studies to date have utilised an adequate sample of polychaete family taxa. However, a recent study by Brown *et al.* (1999) attempts to address this issue. For this reason more emphasis is placed on the results of Rouse & Fauchald (1997), particularly in respect to phylogenetic relationships within Polychaeta. With regard to higher-level phylogenetic relationships, an overview of the main competing hypotheses is given without promoting any in particular because all proposed phylogenies at this level require further corroboration.

Increasingly, polychaetes are becoming the subject of rigorous phylogenetic studies within family groups, families and subfamilies. Polychaete taxa studied in this way include Alciopidae (Wu & Lu 1993, 1994), Dorvilleidae (Eibye-Jacobsen & Kristensen 1994), Hesionidae (Pleijel 1998), Nereididae and nereidiforms (Fitzhugh 1987; Glasby 1993; Pleijel & Dahlgren 1998), Onuphidae (Paxton 1986a), Phyllodocidae (Pleijel 1991; Eibye-Jacobsen 1993), Pilargidae (Fitzhugh & Wolf 1990; Licher & Westheide 1994), Sabellidae (Fitzhugh 1989; Rouse & Fitzhugh 1994), Spionidae (Sigvaldadóttir *et al.* 1997), Syllidae (Nygren 1999) and Amphitritinae: Terebellidae (McHugh 1995).

In contrast, cladistic studies of subfamilies and genera utilising species are less common. Examples are species of *Prionospio* (Spionidae) (Sigvaldadóttir 1998), species within Namanereidinae (Nereididae) (Glasby 1999a, 1999b) and the sabellid genus *Amphiglena* (Rouse & Gambi 1997, 1998). The lack of species-level phylogenies has hindered the study of polychaetes in terms of their historical biogeography, speciation and co-evolution.

Relationships within 'Annelida'

Traditionally, polychaetes have been grouped together with Oligochaeta and Hirudinea (= Clitellata) in the phylum Annelida. However, recent morphological and molecular studies suggest that the beard-worms, Pogonophora (including Vestimentifera), regarded by many as a separate phylum, or phyla, also belong to Annelida (Bartolomaeus 1995; Black *et al.* 1997; Kojima 1998; Kojima *et al.* 1993; McHugh 1997; Rouse & Fauchald 1995, 1997). These recent studies support earlier ones (see for example, George & Southward 1973; van der Land & Nørrevang 1975, 1977; George 1977) suggesting annelid affinities. An exception is the study of Winnepeninckx *et al.* (1995) who placed Pogonophora together with Echiura outside the Annelida. As a clade within the Annelida, or within the Polychaeta, the

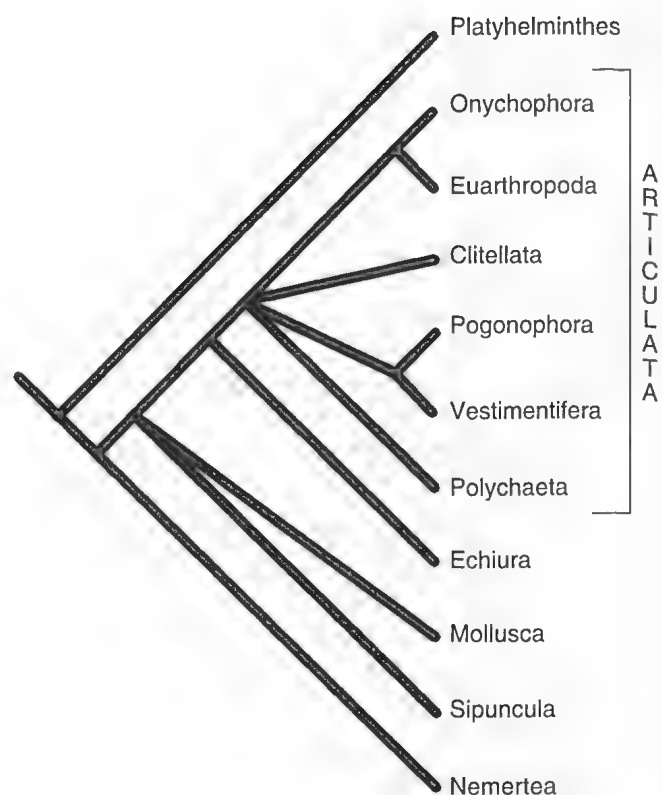


Figure 1.40 Strict consensus (summary) tree from the analysis by Rouse & Fauchald (1995). They argued that a monophyletic Annelida could not be formulated. Their study assumed the monophyly of Polychaeta; an assumption tested in their subsequent study (Rouse & Fauchald 1997).

pogonophores revert to the original family name applied to the group, Siboglinidae (McHugh 1997; Rouse & Fauchald 1997).

Recent consensus of opinion suggests that inclusion of pogonophores within Annelida makes the latter monophyletic. However, the analysis of Rouse & Fauchald (1995) yielded another controversial finding: that Annelida is non-monophyletic and therefore that the taxon be abandoned in favour of a more inclusive one, Articulata, which includes both Annelida and Arthropoda (Fig. 1.40). A major factor contributing to non-monophyly of Annelida in their analysis was the equivocal phylogenetic position of Clitellata – either sister to the Arthropoda or to a combined Polychaeta and Pogonophora. The conclusions and methodology in Rouse & Fauchald (1995) were challenged by Eibye-Jacobsen & Nielsen (1996); this critique, which focused mainly on cladistic methods, was rebutted by Rouse (1997). In their more detailed treatment of the relationships among annelids, Rouse & Fauchald (1997) found evidence for a monophyletic Annelida that was a sister group to Arthropoda. However, they noted that the characters used in their study were selected for resolving relationships amongst polychaete taxa and, given the inadequacies of available coding methods, the possibility of a paraphyletic Annelida with respect to Arthropoda deserves further investigation. Jenner & Schram (1999) discussed how cladistic methodological differences hinder the comparison of studies investigating metazoan phylogeny.

An annelid–arthropod sister-group relationship is supported by nearly all cladistic papers based on morphology (see Eernisse, Albert & Anderson 1992; Rouse & Fauchald 1995, 1997; Nielsen 1996); however, there have been two studies based on morphological data that have suggested that annelids

are closer to molluscs than they are to arthropods (Eernisse *et al.* 1992; Schram & Ellis 1994). Both of these analyses were shown to be flawed by Rouse & Fauchald (1995), particularly involving character construction and scoring. Schram & Ellis (1994) also had a coding inconsistency between the matrix published by Schram (1991) and that used by Schram & Ellis (1994) to rebut criticism by Backeljau, Winnepenninckx & De Bruyn (1993). Correction of this error (involving nephridia in entoprocts) gives the results obtained by Backeljau *et al.* (1993) and provides no support for rejecting the Articulata (G. Rouse personal observation).

In contrast to the morphological cladistic analyses, there is a growing body of evidence from molecular sequence data that Articulata is not a valid taxon. Recent analyses using sequence data from 18s rDNA or 18s rRNA, have suggested that Arthropoda belong to a clade that contains Nematoda and other taxa that moult their cuticle (Aguinaldo *et al.* 1997; Eernisse 1997; Giribet & Ribera 1998). Aguinaldo *et al.* (1997) erected a new taxon, Ecdysozoa, containing the arthropods, nematodes and some other aschelminth taxa. Halanych *et al.* (1995) suggested that the lophophorate taxa Ectoprocta (= Bryozoa), Phoronida and Brachiopoda were part of a clade whose other members were Annelida and Mollusca. They called this clade Lophotrochozoa. Brachiopoda are of interest since they have chaetae that are identical to those seen in annelids (see for example, Gustus & Cloney 1972). Most molecular studies, based on 18S rRNA, however, support the view that annelids, molluscs and several other protostome phyla constitute a monophyletic group, Eutrochozoa (see Eernisse 1997 for a review); however, taxon sampling in all of these studies has been limited. More results showing that Articulata is not monophyletic based on other gene sequences will provide compelling evidence for a re-examination of the morphological basis for the taxon. For example, doubts over the homology of segmentation between arthropods and annelids have been raised previously (see for example, Minelli & Bortoletto 1988) and deserve further investigation.

Although Rouse & Fauchald (1995, 1997) found Echiura to be the sister group to Articulata (Fig. 1.39), the possibility that Echiura should also be placed within Annelida has been revived lately. The placement of Echiura within Annelida is an old idea dating back to Cuvier (1817) and Lamarck (1818). Nielsen (1995), Nielsen *et al.* (1996) and Eiby-Jacobsen & Nielsen (1996) included Echiura within Annelida, *a priori*, on the basis that they have lost segmentation and that chaetae must have evolved once only. McHugh (1997) proposed that Echiura fall inside Annelida based on molecular sequence data. The results in Rouse & Fauchald (1997) suggest that chaetae could have evolved twice, once in Echiura and once in Annelida (Polychaeta, Clitellata and Pogonophora), or that the presence of such structures is plesiomorphic for Articulata and they have been lost in Arthropoda. However, there is no morphological evidence to support the suggestion by Nielsen (1995) and McHugh (1997) that Echiura have lost segmentation, and the nature of any such possible 'loss' has not been fully discussed. Does it mean that the Echiura in fact have many fused 'segments' or only a single 'segment'? Though teloblastic growth was reported for Echiura by Hatschek (1880), three subsequent studies (Torrey 1903; Baltzer 1925; Newby 1940) investigating growth found no such thing. Other features such as the presence of multiple epidermal glandular rings, repeated larval ganglia and multiple nephridia (Nielsen 1995; McHugh 1997) imply that Echiura have multiple fused segments. However, multiple epidermal glandular rings do not indicate mesodermal segmentation. The formation of larval ganglia in echiurans is

by an initial proliferation followed by division of existing ganglia. This is therefore not homologous to the formation of segmental ganglia (Newby 1940) and cannot be used as evidence in favour of Echiura being 'cryptically' multisegmented. The presence of multiple nephridia can be contrasted with the fact that some echiurans have only a single pair of nephridia (Pilger 1993). Since the relationships within Echiura are unknown, the plesiomorphic condition for nephridial number cannot as yet be determined. However, since the cladistic branch support for Articulata (and Annelida) in Rouse & Fauchald (1997) is weak, further investigation into the position of Echiura (and Sipuncula) should be pursued, using both morphological and molecular sequence data.

Phylogenetic relationships within Polychaeta cannot be completely assessed until we first answer the questions: what is a polychaete and is the group monophyletic? Rouse & Fauchald (1997) found that there is no sister group for Clitellata within Polychaeta that can be identified on current morphological evidence. However, the relationships among the Clitellata are still poorly understood. Further study in this area may identify likely plesiomorphic clitellates that can be targeted for detailed morphological study. Rouse & Fauchald (1995, 1997) favour monophyly of a broadly-defined Polychaeta, including Aeolosomatidae, Potamodrilidae, Myzostomida and Pogonophora, based on the presence of parapodia, nuchal organs and mixonephridia; some taxa are hypothesised to have secondarily lost nuchal organs and secondarily developed other types of nephridia (for example, protonephridia).

In contrast, several studies based on morphology, DNA and amino acid sequences, have suggested that polychaetes are a grade of non-clitellate annelids from which clitellates are derived (McHugh 1997; Westheide 1997; Kojima 1998). That is, Polychaeta is a paraphyletic group. Westheide (1997) and Westheide & Purschke (in Westheide *et al.* in press) have adopted a different approach to Rouse & Fauchald (1997) in their assessment of annelid relationships (see also Giangrande & Gambi 1998). This involves the use of a procedure (which they state is Hennigian) in which characters are evaluated on the basis of functional considerations, such as habitat, body size and reproductive biology. The justification is that such consideration allows the construction of scenarios of phylogeny and of ancestral 'species'. This approach results in a phylogenetic hypothesis that considers oligochaetes and leeches as derived polychaetes and that provides for characterisation of the ancestral annelid (Fig. 1.41).

The argument by Westheide (1997) and Westheide & Purschke (in Westheide *et al.* in press) to establish that the plesiomorphic annelid had elaborate parapodia is based on the origin and primary functional significance of septa. They suggested that septa, the fundamental elements in segmentation, are primarily the prerequisite for the existence of blood vessels that run transversely. In order for transversely running vessels to be formed in an elongate organism, the coelom must be subdivided into pairs of spaces in such a way as to produce double layers of epithelia, with the basal matrices facing one another. Westheide (1997) speculated that serially arranged transversely running blood vessels became necessary to supply correspondingly serially arranged external appendages on both sides of the body, which could be the precursors of parapodia. The formation of septa, and hence segmentation, would thus be directly correlated with the development of parapodia, and parapodia with chaetae would be part of the basic body plan of Annelida (or Articulata). Their reasoning also emphasises that clitellate annelids are a highly evolved taxon within Annelida. They

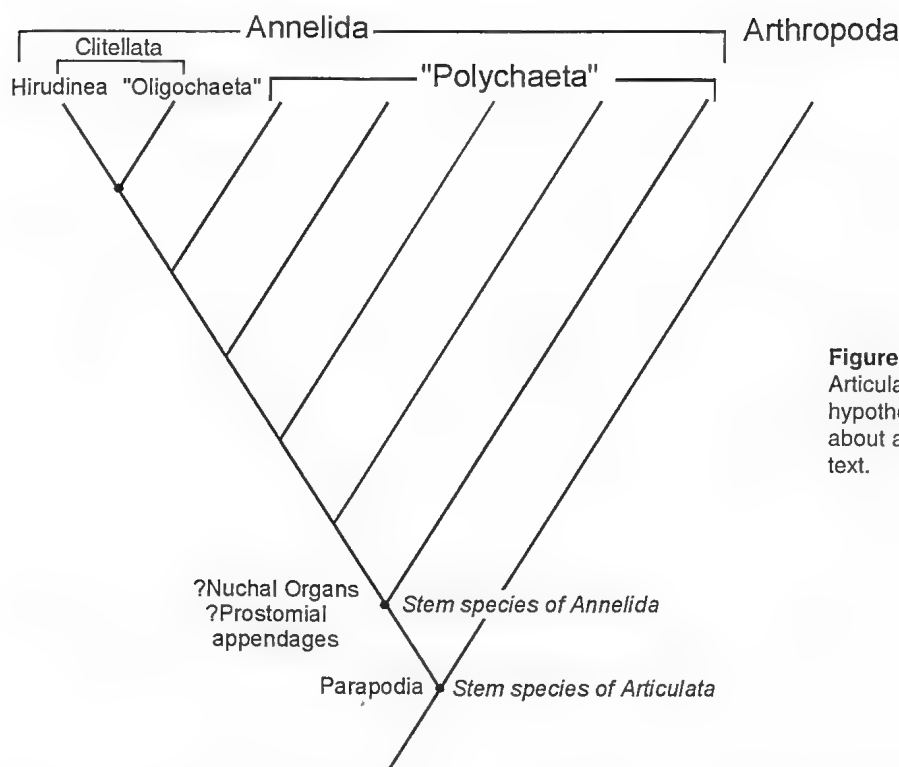


Figure 1.41 Phylogenetic relationships within Articulata according to Westheide (1997). This hypothesis involves an elaborate scenario about annelid evolution which is outlined in the text.

argue that Clitellata must be inferred, on the basis of functional considerations, to have arisen not in the marine, but in the terrestrial environment. Westheide (1997) and Westheide & Purschke (in Westheide *et al.* in press) do not, however, identify the sister group for Clitellata within Polychaeta (Fig. 1.41).

For the 'basic annelid body plan' then Westheide & Purschke (in Westheide *et al.* in press) postulated the following characters: biphasic life cycle with planktonic trochophore larva and benthic adult stage, adult with (1) homonomous segmentation, (2) biramous parapodia with numerous chaetae, (3) dorsal bristles with a protective function, (4) gonads in all segments, (5) metanephridia, (6) prostomium with paired palps and presumably three antennae, (7) nuchal organs, (8) simple ciliated foregut (dorso-lateral folds), at least in the juvenile stages, (9) collagenous cuticle, (10) epibenthic mode of life. This hypothetical organism would currently fall within the clade Phyllodocida.

Relationships within 'Polychaeta'

Most of the currently accepted polychaete families are morphologically distinctive and many are defined by implied or confirmed autapomorphies; exceptions include several less-speciose families that are not defined by any known autapomorphies (Fauchald & Rouse 1997). These are Ctenodrilidae, which may make Cirratulidae paraphyletic – both taxa have paired filiform dorsal branchiae; Poeobiidae, which may make Flabelligeridae paraphyletic with both taxa having similarly-arranged eversible branchiae anteriorly; Pholoidae (including arguably Pholoididae; see Hutchings & McRae in review), which may make Sigalionidae paraphyletic, since they are the only two scale-worms having compound chaetae; Alciopidae, which may make Phyllodocidae paraphyletic with both families having foliose dorsal cirri; Trichobranchidae, which may make Terebellidae paraphyletic – both groups are recognised by their multiple grooved tentacles (palps) apparently arising from the prostomium (unlike the closely related ampharetids whose palps are peristomial in origin); and Uncispionidae; which may make Spionidae paraphyletic though the former is too

poorly known to decide at this point (Sigvaldadóttir *et al.* 1997). Therefore, the number of polychaete families more than likely will decrease with further higher-level systematic studies. Fauchald & Rouse (1997) provided a succinct overview of each of the currently recognised traditional families together with a history of systematic research on Polychaeta.

Relationships between polychaete families are still poorly understood. In the most recent cladistic study of the group, Rouse & Fauchald (1997) identified higher groupings within the Polychaeta that reflect hypothesised evolutionary relationships. In their study, most of the families were allocated to higher (non-Linnean) taxonomic rankings. Of uncertain affinity within Polychaeta were the oligochaete-like families Aeolosomatidae and Potamodrilidae, and Psammodrillidae and Parerogodrilidae. The latter two families together with a few other groups which have a small body size and a simple body structure, were until recently, classified as 'archannelids'. However, Archannelida is now considered to be polyphyletic and most of the archannelidan families have been assigned to existing large-bodied polychaete families (see Rouse & Fauchald 1995).

As mentioned above, the weight of evidence now places pogonophores and vestimentiferans (now collectively Siboglinidae) within a traditionally-formulated Annelida. Morphological evidence places them as sister group of sabellidan polychaetes (Bartolomaeus 1995, 1997; Rouse & Fauchald 1997). Support for this position lies in the fact that both sabellidans and pogonophores have a single pair of nephridia in the first segment (Bartolomaeus 1995), but this character may be homoplastic according to the more exhaustive analysis of Rouse & Fauchald (1997). The sister group of the pogonophore – sabellidan clade is very tenuous, with Terebellida *sensu stricto*, Oweniidae and Chaetopteridae all possibilities (Bartolomaeus 1995; Fitzhugh 1989; Rouse & Fauchald 1997). The terebellid sister grouping has been suggested because all three groups have anteriorly curved uncini with a reduced manubrium and are aligned in transverse rows (Bartolomaeus 1995; Meyer 1996). Alternatively, molecular studies suggest that pogonophores are the sister-group of the polychaetes, Maldanidae (McHugh

1997) and Sternaspidae (Kojima 1998), but both of these studies utilised a limited number of polychaete taxa, and the former did not include members of the Sabellida.

The phylogenetic position of Oweniidae has probably caused more debate than any other polychaete family, particularly as they are not like polychaetes in lacking a cuticle and have a unique type of body wall construction (Gardiner 1978; Gardiner & Rieger 1980). Two divergent views prevail: either they are a basal group within Annelida on the basis of having unspecialised monociliated cells on the tentacles, the similarity of larval nephridia with those of deuterostomes and the myoepithelial lining of the coelom (Gardiner 1978; Smith *et al.* 1987), or they are placed well within Polychaeta, either as sister group of the sabelliforms (Fig. 1.42; Rouse & Fauchald 1997) or sister to a larger group comprising Terebellida – Pogonophora – Sabellida (Meyer & Bartolomaeus 1996). The latter study also proposed that the neuropodial hooks of Oweniidae, terebelliforms, Siboglinidae and sabelliforms, and their proposed sister group (Psammodrillidae, Arenicolidae and Maldanidae) are homologous. In contrast, the phylogeny of Rouse & Fauchald (1997) would suggest the independent acquisition of this type of neuropodial hook in Arenicolidae and Maldanidae, at least. The fact that multiciliated epidermal cells have been found on another oweniid (Westheide 1997) and that the larval morphology also supports the placement of the oweniids as derived polychaetes (Rouse 1999) tends to reject arguments that the oweniids are a plesiomorphic group of annelid.

The following discussion of the phylogeny of polychaete families is based upon the clades identified in the study of Rouse & Fauchald (1997) (Fig. 1.42). However, it should be noted that with the exception of Aciculata, most of the more inclusive clades identified by Rouse & Fauchald are not well supported cladistically as measured by the Bremer support index (Bremer 1994). Further, the authors note that selection of their preferred cladogram, upon which their clade-based classification is based, was essentially arbitrary. Depending on the method of character coding and analysis some families, particularly those at the bases of major clades in Figure 1.42, show very different phylogenetic affinities. Families showing particular lability in this sense include Oweniidae in a basal position within Sabellida; Chaetopteridae as basal within Spionida; Chrysopetalidae as basal to the non-scale-worm Phyllodocida; Amphinomidae and Euphrosinidae as sister group to the remaining Eunicida and the placement of the clade Capitellidae – Arenicolidae – Maldanidae (Fig. 1.42). Chaetopteridae may be the sister group of the Sabellida on the basis of the autapomorphy of nuchal organs in the form of posterior projections (Rouse & Fauchald 1997); Chrysopetalidae may belong to a clade with Hesionidae and Nereididae on the basis of several possible synapomorphies, including chaetal shafts having a distinct medulla and cortex (Glasby 1993; Pleijel & Dahlgren 1998); Amphinomidae and Euphrosinidae may be the sister group to the remaining Aciculata (Rouse & Fauchald 1997); Capitellidae, Arenicolidae and Maldanidae may not be members of the Scolecida and instead fall within the Canalipalpata. The phylogenetic relationships of these families in particular require further study.

Rouse & Fauchald suggested that Polychaeta comprised two major clades, Palpata and Scolecida (Fig. 1.42). Palpata, which include the vast majority of families, are named for the presence of palps, an autapomorphy of this group (palps are secondarily lost in Lumbrineridae). This homology hypothesis was largely based on the series of papers by Orrhage (for example, Orrhage 1996). The palps of Palpata appear to be either prostomial or peristomial in origin

(Orrhage 1996) and may take various forms including feeding types (paired or multiple grooved processes and 'tentacular' crowns) and sensory types, which are often digitiform or pad-like structures, either ventral or ventro-lateral in position on the prostomium. Scolecida, in contrast, are not circumscribed by any unique autapomorphies, although its members tend to have parapodia with similar-sized rami and two or more pairs of pygidial cirri. The Scolecida comprise Arenicolidae, Capitellidae, Cossuridae, Maldanidae, Opheliidae, Orbiniidae, Paraonidae, Questidae, and Scalibregmatidae; none of the clades within Scolecida are particularly well supported, with the possible exception of Questidae – Orbiniidae – Paraonidae, a clade supported by the presence of an muscular ventral buccal bulb, which nevertheless occurs homoplastically in other polychaetes.

Palpata comprise two major clades, Canalipalpata and Aciculata. Aciculata, the best-supported clade in the analysis of Rouse & Fauchald (1997), is named after one of its autapomorphies, the presence of aciculae supporting (often) well-developed parapodia. The presence of ventral cirri is another autapomorphy, and other characteristic features of the group include the presence of a pair of both prostomial antennae and sensory palps, and cirriform dorsal cirri on the parapodia. Families belonging to Aciculata, but having uncertain affinity include, Nerillidae, Spintheridae and Aberrantidae, of which the latter does not occur in Australian waters. Two clades were identified within Aciculata: Eunicida and Phyllodocida. Eunicida contains the traditionally-included families Dorvilleidae, Eunicidae, Lumbrineridae, Oeonidae and Onuphidae, as well as Amphinomidae and Euphrosinidae. They have as an autapomorphy the presence of a ventral hypertrophied pharynx, but also characteristically have ventro-lateral sensory palps on the prostomium and parapodial branchiae. Phyllodocida is a large clade with two autapomorphies, the presence of ventral sensory palps and an axial hypertrophied pharynx (often with jaws), but is also characterised by the presence of tentacular cirri in most taxa. This concept of Phyllodocida is essentially the same as has been recognised in all recent higher classifications of the polychaetes (for example, Fauchald 1977; George & Hartmann-Schröder 1985). Myzostomida were found to fall within Phyllodocida as they have an axial hypertrophied pharynx, although it must be assumed that they lost their ventral sensory palps; their position (as Myzostomatidae) with Phyllodocida therefore requires confirmation as acknowledged by Rouse & Fauchald (1997). However, Myzostomida are treated as a separate group in this work (see Chapter 2).

Canalipalpata have as an autapomorphy the presence of grooved palps, usually peristomial in origin, although in three taxa (Sabellidae, Serpulidae and Oweniidae) the grooved palps are prostomial. Canalipalpata consists of three major clades, Sabellida, Spionida and Terebellida, whose relationship to one another is unresolved. The Sabellida of Rouse & Fauchald (1997) is a more inclusive taxon than accepted in previous classifications and includes Siboglinidae (= pogonophores) and, somewhat controversially, the Oweniidae (see discussion above). Like-wise, the Terebellida, contains in addition to the traditionally-included families, the taxa Acrocirridae, Cirratulidae and Flabelligeridae, Ctenodrilidae, Fauveliopsidae, Poeobiidae and Sternaspidae. The placement of Sternaspidae as a possible sister taxon of Echiura, proposed by earlier zoologists (see review by Dahl 1955), was indicated in a recent molecular study based on elongation factor 1 α (nDNA) (McHugh 1997). This implies that the Echiura may also be members of the Terebellida, although few polychaete taxa were included in this study.

1. CLASS POLYCHAETA

The concept of the Spionida proposed by Rouse & Fauchald (1997) is similar to current usage (Fig. 1.42). Canalipalpata also contain Polygordiidae and several interstitial families having uncertain affinity, including Protodrilidae, Protodriloididae and Saccocirridae. Once part of the informal taxon Archiannelida, members of these families have simplified body forms, which tend to obscure their phylogenetic affinities. The analysis of Rouse & Fauchald (1997) suggests that these interstitial families may form a monophyletic group. Purschke & Jouin (1988) also proposed monophyly of Protodrilidae, Protodriloididae and Saccocirridae on the basis of several purported autapomorphies including the cellular composition of the ventral buccal bulb and the presence of two pygidial lobes

with adhesive glands. However, verification is needed as to whether the group is allied to the spioniform taxa as suggested by Purschke & Jouin (1988). Of the other ‘archiannelidan’ families, Nerillidae is thought to belong to Aciculata *incertae sedis* (Rouse & Fauchald 1997) and Dinophilidae were subsumed into Dorvilleidae by Eibye-Jacobsen & Kristensen (1994). All three clades within Canalipalpata were weakly supported and not specifically defined with reference to apomorphy-based ancestors.

The classification of Polychaeta discussed above represents a considerable advance on previous attempted classifications (see Fauchald & Rouse 1997 for a review) because it is based on a phylogeny estimated using a large number of available morphological characters and a rigorous analysis involving

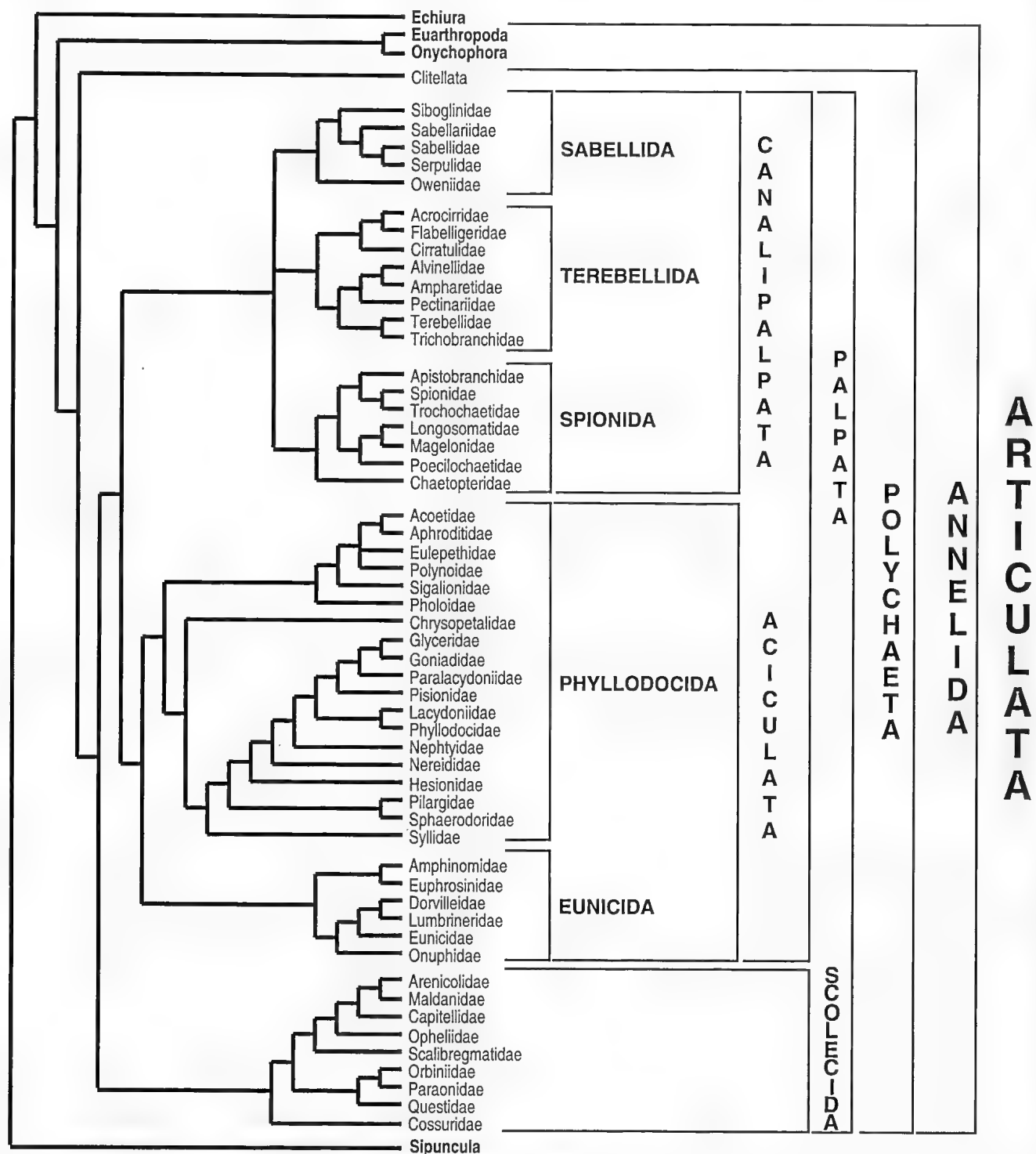


Figure 1.42 Classification of polychaete taxa based on the phylogeny of Rouse & Fauchald (1997). The 29 polychaete taxa excluded from this tree were placed within clade names shown here based on a more inclusive analysis and arguments in the text (see Table 1.3 for the classification of excluded taxa). Note that Pogonophora (and Vestimentifera) are now referred to as the Siboglinidae (Sabellida); however, this group is treated separately in this work (see Chapter 3).

different types of character coding and weighting. The study highlights deficiencies in our knowledge of certain polychaete features, particularly anatomical (resulting in missing character data) and methods of cladistic analysis, such as the appropriateness of the various types of character coding and weighting issues (see also Pleijel 1995). Perhaps as a result of these deficiencies, many of the clades identified in the analysis are weakly supported and their monophyly will need to be confirmed with further cladistic studies, ideally utilising different suites of characters. Rouse & Fauchald (1997) deliberately avoided reference to hypothetical ancestors or hypotheses about the evolution of annelids or polychaetes. The reason for this lies in the argument that evolutionary history of a feature can be inferred only after all homology hypotheses have been rigorously assessed, in both a primary sense, and then in the context of congruence with other data in a parsimony analysis (de Pinna 1991). To introduce any evolutionary scenarios (for example, Westheide 1997, as described above) and ordering of character states is to add additional assumptions that cannot be adequately assessed. The methodology for inferring phylogeny seen in Westheide (1997) and Westheide & Purschke (in Westheide *et al.* in press) involves the development of elaborate scenarios of hypothetical ancestors and so involves many assumptions and lacks elements of repeatability.

CLASSIFICATION OF THE ANNELIDA AND POLYCHAETA

Introduction

Through most of this century the Annelida has been split into two main groups; the Polychaeta and Clitellata, with Myzostomida being given class status by some workers (Jägersten 1940; Prenant 1959), or as members of the Polychaeta (Hartman 1969; Schroeder & Hermans 1975; Pettibone 1982). In addition, several small groups have been regarded as families of uncertain affinities within the Annelida, or 'associated' with the Annelida (Fauchald & Rouse 1997).

Although the monophyly of the Clitellata is not currently contested and the classification within the clade is problematic (Omodeo 1998), the history of the classification within the Polychaeta and the monophyly of the group itself is much more contentious. One of the most influential classifications of polychaetes, originally derived from Quatrefages (1865), divided the Polychaeta into two orders (or subclasses), the 'Errantia' and 'Sedentaria' (Fauvel 1923, 1927; Day 1967; Hartman 1968, 1969). Although these authors tended to just list the various polychaete families in either the 'Errantia' or 'Sedentaria', Hemplemann (1931), Hartmann-Schröder (1971) and Uschakov (1955; see Fig. 1.43) were unusual in dividing each of the two subclasses into a number of orders. Their systems in some ways resembled some of the classifications of the nineteenth century (for further discussion see Fauchald & Rouse 1997). Day (1967) considered the two major polychaete groups as an 'arbitrary grouping' used for 'practical purposes' and did not recognise any taxonomic levels between orders and families. Other authors probably had similar attitudes and probably did not regard this system as providing any phylogenetic perspective on polychaetes. Rather, it conveniently divided the group into two approximately even halves.

A system proposed by Dales (1962a) rejected the concept of 'Errantia' and 'Sedentaria', and used the structure of the buccal organ and nephridia to provide criteria for an analysis of the polychaetes at the family level, and resulted in them being classified into 14 orders (Fig. 1.43). Dales (1977) reviewed developments in phylogeny studies since his earlier

(Dales 1962a) publication, but left his classification unchanged. Dales (1962a, 1977) did draw phylogenetic trees of the Polychaeta, albeit somewhat unresolved, but incorporated little of this information into his classification. For instance he did not group the Capitellida and Spionida into a 'superorder' or subclass though this is clearly implied in figure 17 of Dales (1962a).

The classification of polychaetes by Fauchald (1977) comprised 17 orders (Fig. 1.43). Although delineated differently, the orders contained roughly the same taxa as those listed in Dales (1962a) and they were listed without any interrelationships being specified. Fauchald (1977: 7) did, however, state that 'the sequence of families indicates an increasing morphological distance from the ancestral polychaete'. This implies that the orders he listed last (for example, Terebellida, Sabellida) were presumably more apomorphic than the taxa listed first (for example, Orbiniida, Ctenodrilida). Pettibone (1982) recognised 25 orders, including, in addition to the orders defined by either Dales (1962a) or Fauchald (1977), orders for each of the five 'archiannelidan' families, and new orders for the Myzostomatidae and Poeobiidae. Pettibone gave no reasons for her classification. Many of the new orders created by Dales, Fauchald and Pettibone were for morphologically unusual families (for example, Oweniidae, Psammodrillidae, Spintheridae, Sternaspidae). A recent classification of the Polychaeta by Hartmann-Schröder (1996) includes 22 orders and closely resembles that of Pettibone (1982). A detailed history of the classification of polychaetes is reported in Fauchald & Rouse (1997).

All classifications of polychaetes used by authors recently appear to follow the reasoning expressed by Dales (1977: 526) whereby "*All of the families of the Class Polychaeta are distinct, but some show obvious resemblances while others appear to be isolated. ... The grouping of families into larger groups presents some difficulties, therefore, and while some groups of families or orders emerge, there remains a series of families with no close affinities with any other group. My own view is that it is better to leave such families in isolated orders until their affinities are understood than it is to reduce the value and coherence of natural orders by including such families in one or another group on tenuous evidence.*" This philosophy could equally be applied to the position of the Clitellata, which was treated by all polychaete workers as belonging outside the Polychaeta.

Classification used in this Volume

A new classification was proposed by Rouse & Fauchald (1997) to replace previous schemes, which were clearly unsatisfactory (see Phylogeny). Given the variability in results from the different coding methods in Rouse & Fauchald (1997), the selection of a new polychaete classification was not straightforward. The *A/Pwr* analysis was deemed to be the best solution. The consensus tree derived from this analysis is shown in Figure 1.42 and shows the major clade names. Most of the 29 families that were excluded from Figure 1.42 can be easily placed in the classification. Thus, the classification used in this volume is outlined in Table 1.3. The families that were proposed to be paraphyletic generally have their excluded members placed in close proximity for example, Ctenodrilidae with Cirratulidae; Poeobiidae and Fauveliopsidae with the Flabelligeridae. Note that in this volume the Myzostomida are treated as outside the Polychaeta, as are the Siboglinidae. Since no sister group has been proposed for the Clitellata (see Phylogeny), the finding of Rouse & Fauchald (1997) that the clitellates lie outside the Polychaeta is accepted here.

Figure 1.43 Three major classifications of Polychaeta and related taxa. **A**, Uschakov 1955. **B**, Dales 1962a. **C**, Fauchald 1977.**Uschakov 1955**

Polychaeta

Errantia

Phyllodocemorpha

Phyllodocidae

Alciopidae

Tomopteridae

Typhloscolecidae

Aphroditidae

Chrysopetalidae

Glyceridae

Nereimorpha

Syllidae

Hesionidae

Pilargiidae

Nereidae

Nephthyidae

Sphaerodoridae

Amphinomorpha

Euphrosynidae

Spintheridae

Eunicomorpha

Eunicidae

Sedentaria

Spiomorpha

Ariciidae

Spionidae

Magelonidae

Disomidae

Paraonidae

Chaetopteridae

Cirratulidae

Drilomorpha

Chloraemidae

Scalibregmidae

Opheliidae

Capitellidae

Arenicolidae

Maldanidae

Oweniidae

Sabellariidae

Sternaspidae

Terebellomorpha

Pectinariidae

Ampharetidae

Trichobranchidae

Terebellidae

Serpulimorpha

Sabellidae

Serpulidae

Dales 1962

Annelida

Archannelida

Polychaeta

Phyllodocida

Phyllodocidae

Alciopidae

Tomopteridae

Typhloscolecidae

Aphroditidae (*sensu lato*)

Chrysopetalidae

Glyceridae

Goniadidae

Sphaerodoridae

Pisionidae

Nephthyidae

Syllidae

Hesionidae

Pilargiidae

Nereidae

Capitellida

Capitellidae

Arenicolidae

Scalibregmidae

Maldanidae

Opheliidae

Sternaspida

Sternaspidae

Spionida

Spionidae

Disomidae

Poecilochaetidae

Longosomidae

Paraonidae

Apistobranchidae

Chaetopteridae

Sabellariidae

Eunicida

Onuphidae

Eunicidae

Lumbrineridae

Arabellidae

Lysaretidae

Dorvilleidae

Histriobdellidae

(Ichthyotomidae)

Amphinomida

Amphinomidae (*sensu lato*)

Magelonida

Magelonidae

Ariciida

Ariciidae

Cirratulida

Cirratulidae

Ctenodrilidae

(Stygocapitellidae)

Oweniida

Oweniidae

Terebellida

Pectinariidae

Ampharetidae

Terebellidae

Flabelligerida

Flabelligeridae

Psammodrilida

Psammodrilidae

Sabellida

Sabellidae

Serpulidae

Myzostomaria

Oligochaeta (sub-division not included here)

Hirudinea (sub-division not included here)

Fauchald 1977

Polychaeta

Orbiniida

Orbiniidae

Paraonidae

Questidae

Ctenodrilida

Ctenodrilidae

Parergodrilidae

Psammodrilida

Psammodrilidae

Cossurida

Cossuridae

Spionida

Spioniformia

Apistobranchidae

Spionidae

Magelonidae

Trochochaetidae

Poecilochaetidae

Heterospionidae

Chaetopteriformia

Chaetopteridae

Cirratuliformia

Cirratulidae

Acrocirridae

Capitellida

Capitellidae

Arenicolidae

Maldanidae

Opheliida

Opheliidae

Scalibregmidae

Phyllodocida

Phyllodociformia

Phyllodocidae

Alciopidae

Lopadorhynchidae

Pontodoridae

Aphroditiformia

Aphroditacea

Aphroditidae

Polynoidae

Polyodontidae

Pholoididae

Eulepethidae

Sigalionidae

Chrysopetalecea

Chrysopetalidae

Palmyridae

Pisioniacea

Pisionidae

Nereidiformia

Hesionidae

Pilargiidae

Syllidae

Calamyzidae

Nereidae

Antonbruunidae

Glyceriformia

Glyceridae

Goniadidae

Lacydoniidae

Suborder not recognised

Iospilidae

Nephtyidae

Sphaerodoridae

Tomopteridae

Typhloscolecidae

Amphinomida

Amphinomidae

Euphrosinidae

Spintherida

Spintheridae

Eunicida

Eunicea

Onuphidae

Eunicidae

Lumbrineridae

Iphitimidae

Arabellidae

Lysaretidae

Dorvilleidae

Superfamily not recognised

Histriobdellidae

Ichthyotomidae

Sternaspida

Sternaspidae

Oweniida

Oweniidae

Flabelligerida

Flabelligeridae

Poeobiidae

Fauveliopsida

Fauveliopsidae

Terebellida

Sabellariidae

Pectinariidae

Ampharetidae

Terebellidae

Trichobranchidae

Bogueidae

Sabellida

Sabellidae

Sabellongidae

Caobangidae

Serpulidae

Spirorbidae

Families of uncertain affinities:

Dinophilidae

Nerillidae

Polygordiidae

Protodrilidae

Saccocirridae

Table 1.3 Classification of Polychaeta modified after Rouse & Fauchald (1997) followed in this work. Eighty-one families are listed; Myzostomatidae and Siboglinidae are not included, and Eunicida and Amphinomida are recognised here, both as *sensu stricto*. The Linnean categories for higher taxa are not used and the families are listed in alphabetical order under clade names. Further details about relationships within major clades are available in Rouse & Fauchald (1997). Families not yet recorded from Australia are indicated with an asterisk (*).

POLYCHAETA	Family Eulepethidae	SPIONIDA
SCOLECIDA	Family Glyceridae	Family Apistobranchidae
Family Arenicolidae	Family Goniadidae	Family Chaetopteridae
Family Capitellidae	Family Hesionidae	Family Longosomatidae*
Family Cossuridae	Family Ichthyotomidae*	Family Magelonidae
Family Maldanidae	Family Iospilidae	Family Pöccillochaetidae
Family Opheliidae	Family Lacydoniidae	Family Spionidae
Family Orbiniidae	Family Lopadorhynchidae	Family Trochochaetidae*
Family Paraonidae	Family Nautiliniellidae*	Family Uncispionidae*
Family Questidae	Family Nephtyidae	
Family Scalibregmatidae	Family Nereididae	TEREBELLIDA
PALPATA	Family Paralacydoniidae	Family Acrocirridae
ACICULATA	Family Pholoidae	Family Alvinellidae*
EUNICIDA <i>sensu stricto</i>	Family Phyllodocidae	Family Ampharetidae
Family Dorvilleidae	Family Pilargidae	Family Cirratulidae
Family Eunicidae	Family Pisionidae	Family Ctenodrilidae
Family Hartmaniellidae*	Family Polynoidae	Family Fauveliopsidae
Family Lumbrineridae	Family Pontodoridae*	Family Flabelligeridae
Family Oenonidae	Family Sigalionidae	Family Pectinariidae
Family Onuphidae	Family Sphaerodoridae	Family Poeobiidae*
EUNICIDA <i>incertae sedis</i>	Family Syllidae	Family Sternaspidae
Family Diurodrilidae	Family Tomopteridae	Family Terebellidae
Family Histriobdellidae	Family Typhloscolecidae	Family Trichobranchidae
AMPHINOMIDA <i>sensu stricto</i>	ACICULATA <i>incertae sedis</i>	CANALIPALPATA <i>incertae sedis</i>
Family Amphinomidae	Family Aberrantidae*	Family Polygordiidae*
Family Euphrosinidae	Family Nerillidae	Family Protodrilidae
PHYLLODOCIDA	Family Spintheridae	Family Protodriloididae*
Family Acoetidae	CANALIPALPATA	Family Saccocirridae
Family Alciopidae	SABELLIDA	POLYCHAETA <i>incertae sedis</i>
Family Aphroditidae	Family Oweniidae	Family Aeolosomatidae
Family Chrysopetalidae	Family Sabellariidae	Family Parergodrilidae
	Family Sabellidae	Family Potamodrilidae*
	Family Serpulidae	Family Psammodrilidae*

Key to the families of Polychaeta

Families are the basic taxonomic unit of higher-level classification in the Polychaeta in the sense that they are both easily recognisable and diagnosable, and most are likely to be monophyletic. Further, the family is often the level at which most biologists begin their identification. Recognition of orders or other higher-level taxa and their diagnosis is by contrast more difficult (and monophyly more tenuous), and therefore no attempt has been made to include them in this key; however, they are included in a more readily updatable interactive CD ROM version of this key (see Glasby & Fauchald 2000).

The key was developed largely using the DELTA system (Dallwitz, Paine & Zurcher 1993) and a database of about 100 characters (the same dataset used in the interactive key). It comprises 82 families currently assigned to Polychaeta; these include the newly assigned Aeolosomatidae, Pomatodrilidae and Myzostomatidae (Fauchald & Rouse 1997), but not Siboglinidae (= pogonophores and vestimentiferans). Six families, Ctenodrilidae, Dorvilleidae, Opheliidae, Pilargidae, Psammodrilidae and Spionidae, appear more than once in the key as they are variable (polymorphic) for some key characters. Characters in bold are the defining features of the family (that is, autapomorphies) (after Fauchald & Rouse 1997), however the groupings of families within the key do not necessarily reflect current ideas on phylogeny. Families indicated by an asterisk (*) are those not recorded from the Australian region, including the Australian Antarctic Territory. The key works only with adult specimens in good condition; other keys are available for the identification of polychaete larvae (for example, Bhaud & Cazaux 1982, 1987).

- 1(0) Segmentation present, 15 or more; macrobenthic and pelagic forms (includes most families) 2
- Segments present, 13 or fewer; minute interstitial forms 54
- Segments present, 13 or fewer; slender, elongate interstitial forms 60
- Segments present, 13 or fewer; parasitic or commensal forms 63
- Segmentation absent; pelagic form; body encased in gelatinous sheath with protruding papillae Poeobiidae* (Fig. 1.46A–C)
- 2(1) Prostomium without paired slender antero-lateral antennae (Fig. 1.10A–C; though antennae on mid- or posterior prostomium may be present; the globular antero-lateral projections of onuphids are not antennae) 3
- Prostomium with paired slender antero-lateral antennae (Fig. 1.10E; rarely in addition to a pair of similar antero-lateral palps) 37

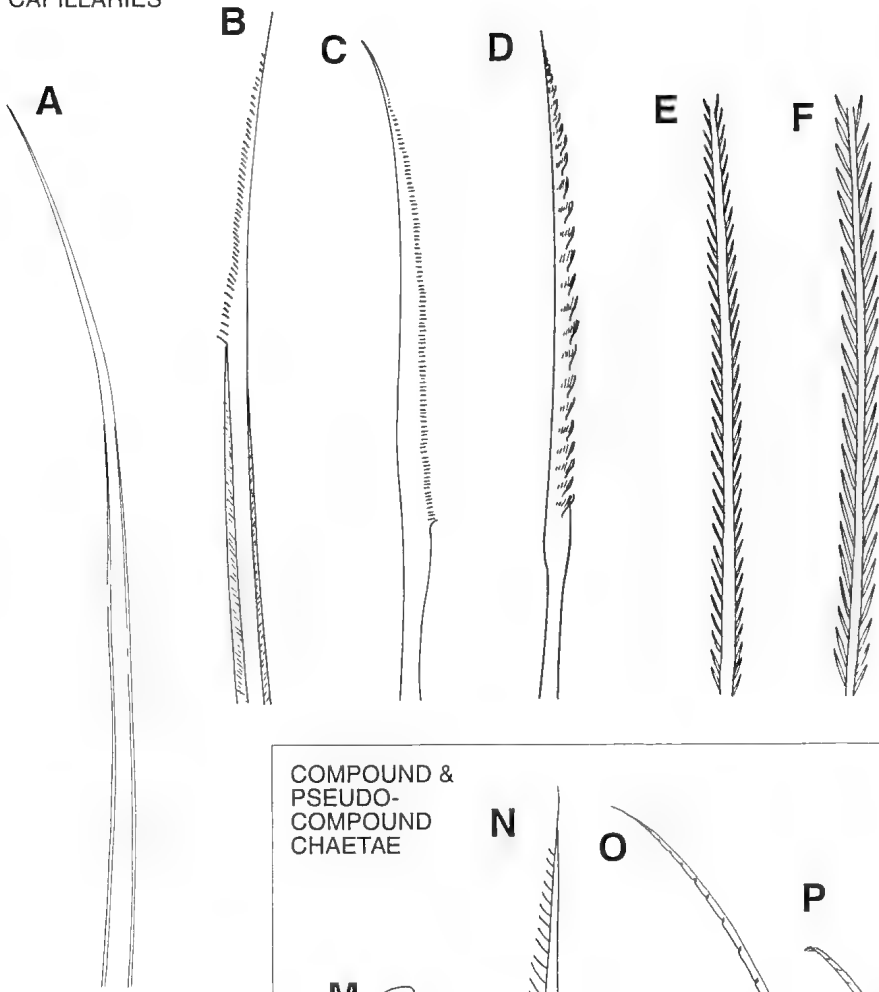
1. CLASS POLYCHAETA

- 3(2) Tentacular cirri present, two pairs; parapodial lobes not foliaceous, some dorsal cirri modified as elytra (= scales); **silk-like chaetae may form felt on dorsum**; mainly benthic forms Aphroditidae
 — Tentacular cirri present, one, two or four pairs; parapodial lobes or dorsal cirri foliaceous; pelagic forms4
 — Tentacular cirri absent; parapodial lobes and dorsal cirri not foliaceous; pelagic or benthic forms. . . .5
- 4(3) Tentacular cirri, one pair, very long with internal aciculae; notopodia similar in size to neuropodia, elongate and ending in foliaceous lappets distally, dorsal cirri and chaetae absent Tomopteridae
 — Tentacular cirri, two pairs; notopodia extremely reduced; dorsal cirri foliaceous; chaetae present.Iospilidae
 — Tentacular cirri, four pairs (**two pairs foliaceous, anteriorly directed**); notopodia present, but smaller than neuropodia, dorsal cirri foliaceous; chaetae present.Typhloscolecidae
- 5(3) **Prostomium shovel-shaped; palps paired, heavily papillated subdistally**; chaetiger 4 or 5 unmodified Magelonidae
 — Prostomium shape otherwise; one pair extremely reduce palps, or palps absent; chaetiger 4 or 5 unmodified Pilargidae (in part)
 — Prostomium shape otherwise; palps paired, grooved; chaetiger 4 or 5 modified, usually enlarged, and carrying specialised chaetae, including spines (Figs 1.10B, 1.44Q–T)6
 — Prostomium shape otherwise; palps absent or present in various arrangements and forms including a tentacular crown (Fig. 1.10A, F–J); chaetiger 4 or 5 unmodified7
- 6(5) **Three distinct body regions**; prostomium not posteriorly prolonged; branchiae absent; uncini present. Chaetopteridae
 — Body regionation absent; **prostomium posteriorly prolonged**; branchiae present; uncini absent.Spionidae (in part)
- 7(5) Body with distinct thorax and abdomen; thoracic uncini in neuropodial position, abdominal ones notopodial (ie. chaetal inversion)8
 — Body regionation present or absent; chaetae, if present, not inverted10
- 8(7) Palps paired, grooved; **chaetae of first two parapodia thickened (paleae), forming an operculum** Sabellariidae
 — Palps in form of tentacular crown; chaetae of first parapodia similar in form to those following (operculum, if present, a modified tentacle).9
- 9(8) Thoracic membrane present; tube calcareous. Serpulidae
 — Thoracic membrane absent; tube otherwise Sabellidae
- 10(7) **Posterior (abdominal) parapodia shifted dorsally**; aciculae present only in posterior notopodia. Orbiniidae
 — Posterior parapodia not shifted dorsally; aciculae absent.11
 — Posterior parapodia not shifted dorsally; aciculae present throughout.31
- 11(10) Parapodia of chaetiger 1 anteriorly directed and wrapping around head; elongate postchaetal lobes present.12
 — Parapodia of chaetiger 1 more or less laterally directed and free from head; postchaetal lobes, if present, not elongate.13
- 12(11) Chaetae of first parapodium elongate, forming a cage around head; parapodia biramous throughout; **postchaetal lobes flask- or spindle shaped** Poecilochaetidae
 — Chaetae of first parapodium similar in form to other chaetae; **parapodia biramous, except for a series of midbody segments which lack notopodia**; postchaetal lobes of various shapes. . Trochochaetidae*
- 13(11) Uncini absent; paleae absent in first parapodia14
 — Uncini present, usually pectinate (Fig. 1.44AF); paleae usually present in first parapodia.28
 — Uncini present, usually crested (Fig. 1.44AG); paleae absent in first parapodia29
- 14(13) **Branchiae present, attached to peristomium, digitiform or tapering, four or more pairs (may be retractable)**; body papillate and/or with gelatinous sheath.Flabelligeridae
 — Branchiae absent (though functionally similar abdominal vascular lamellae may be present); body surface otherwise15
 — Branchiae present, emerging from parapodia; body surface otherwise18
 — Branchiae present, emerging from dorsum (may be restricted to anterior or posterior region; rarely fused basally to notopodia); body surface otherwise20

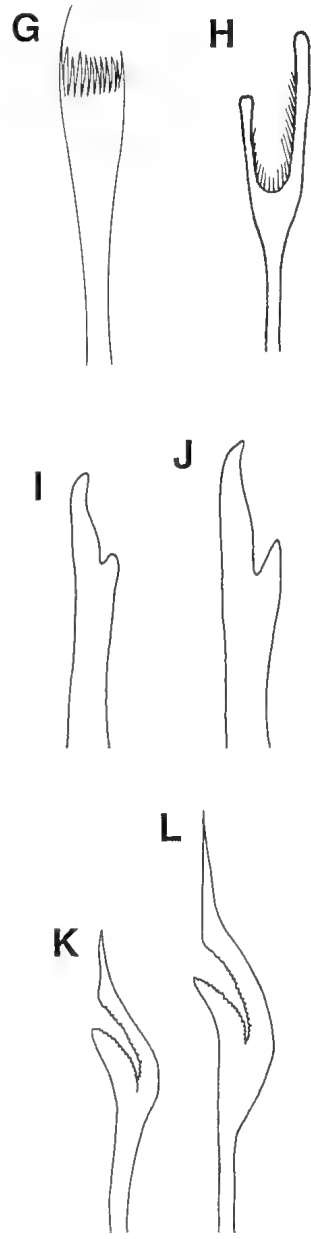
- 15(14) Parapodial lobes absent or papillar; body surface often smooth and shiny16
 — Neuropodia at least represented by low ridges (tori); body surface otherwise.17
- 16(15) **Body fusiform with deep mid-ventral groove**; inter-ramal papilla absent Opheliidae (in part)
 — Body usually more or less cylindrical, without mid-ventral groove; inter-ramal papilla present Fauveliopsidae
- 17(15) Prostomium bluntly conical; median chaetigers not elongate; **multidentate hooded hooks (Fig. 1.44Z, AA) in single rows in posterior neuropodia (and notopodia)** Capitellidae
 — Prostomium part of complex fused unit; median chaetigers not elongate; **small, non-hooded hooks (Fig. 1.44AB) arranged in dense irregular fields in neuropodia** Oweniidae
 — Prostomium narrow, keel- or ridge-shaped; **median chaetigers elongate, with prominent tori encircling body (bamboo-shaped)**; hooks with subdistal beard (non-hooded; Fig. 1.44AC), arranged in single rows in neuropodia. Maldanidae
- 18(14) First trunk segment with both notopodia and neuropodia, though smaller than those following; neuropodia short, more-or-less conical lobes, hooks absent19
 — First trunk segment a smooth ring, lacking parapodia; neuropodia low ridges (tori); dentate hooks present. Arenicolidae
- 19(18) Dorsal and ventral cirri present; short tufted parapodial branchiae; body fusiform or with long tapered abdomen, never grooved mid-ventrally Scalibregmatidae
 — Dorsal and ventral cirri absent; single, tapering parapodial branchiae; **body fusiform, usually with deep mid-ventral groove**. Opheliidae (in part)
- 20(14) Palps present, grooved, usually paired (palps may be lost, in which case palpal scars always present) ..
21
 — Palps absent25
- 21(20) Branchiae flattened slightly, more or less triangular; hook chaetae present.22
 — Branchiae digitiform, slender; hooks absent23
- 22(21) **Prostomium posteriorly prolonged**; capillary chaetae with smooth margins; all hooded hooks slender with shaft more or less straight (Fig. 1.44AD). Spionidae (in part)
 — Prostomium not posteriorly prolonged; capillary chaetae include smooth and/or hirsute types (Fig. 1.46E); **some hooded hooks enlarged and strongly curved (Fig. 1.46F, G)**
 Uncispionidae* (Fig. 1.46D)
- 23(21) Body divided into three regions; **strongly elongate median chaetigers with nearly complete circlets of simple spines** Longosomatidae*
 — Body regionation absent, median chaetigers not elongate, circlets of spines absent24
- 24(23) Body covered with epidermal papillae; compound falcate chaetae present. Acrocirridae
 — Body surface smooth; compound chaetae absent Cirratulidae
- 25(20) Branchiae paired, filiform; capillary chaetae serrated; hooks bidentate, hooded. Questidae
 — Branchiae, if present, paired, filiform; capillary chaetae smooth; hooks distally dentate, unprotected. ...
 Ctenodrilidae (in part)
 — Branchiae present, otherwise; capillary chaetae smooth or serrated; hooks absent26
- 26(25) Body ovoid or dumbbell-shaped; body surface with epidermal papillae; **cuticularised shield covering venter of posterior end** Sternaspidae
 — Body longer than wide, more or less cylindrical; body surface smooth; cuticularised shield absent ..27
- 27(26) Dorsal-branchiae paired, flattened, on anterior segments ; peristomial ring absent (peristomium around mouth only). Paraonidae
 — **Single dorsomedial branchial filament arising from anterior chaetiger**; peristomium a single ring .
 Cossuridae
- 28(13) Tentacles outside buccal cavity; capillary chaetae with finely serrated margins; **tube cone-shaped, made of cemented sand grains**. Pectinariidae
 — **Tentacles within buccal cavity**; capillary chaetae with smooth margins; tube otherwise
 Ampharetidae

1. CLASS POLYCHAETA

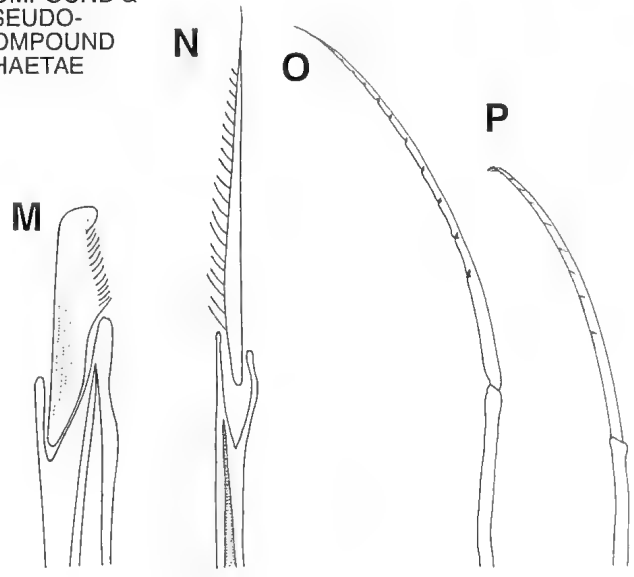
CAPILLARIES



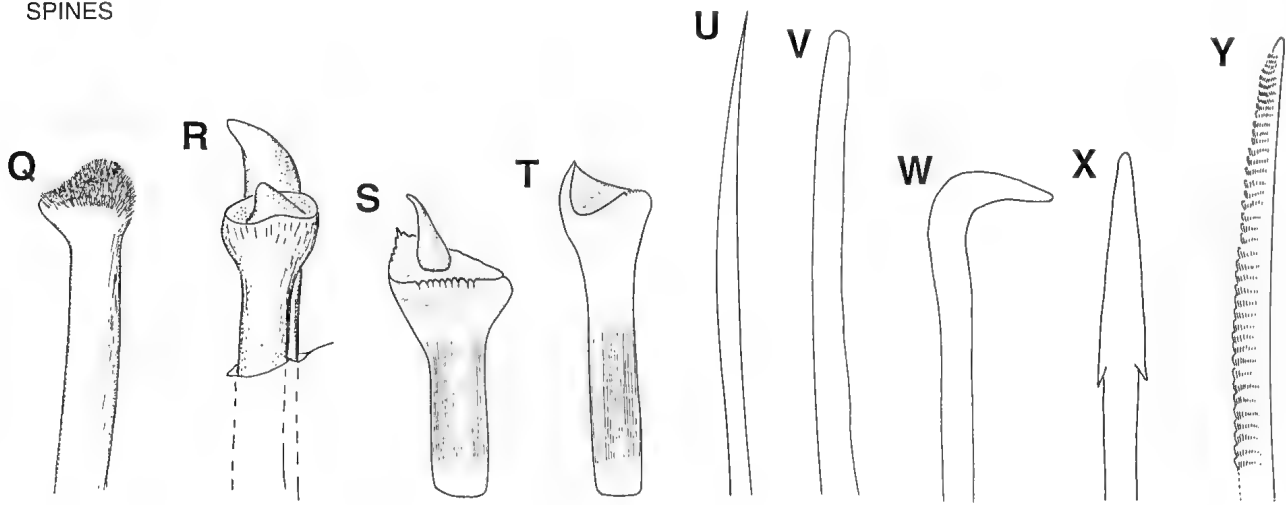
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SPINES



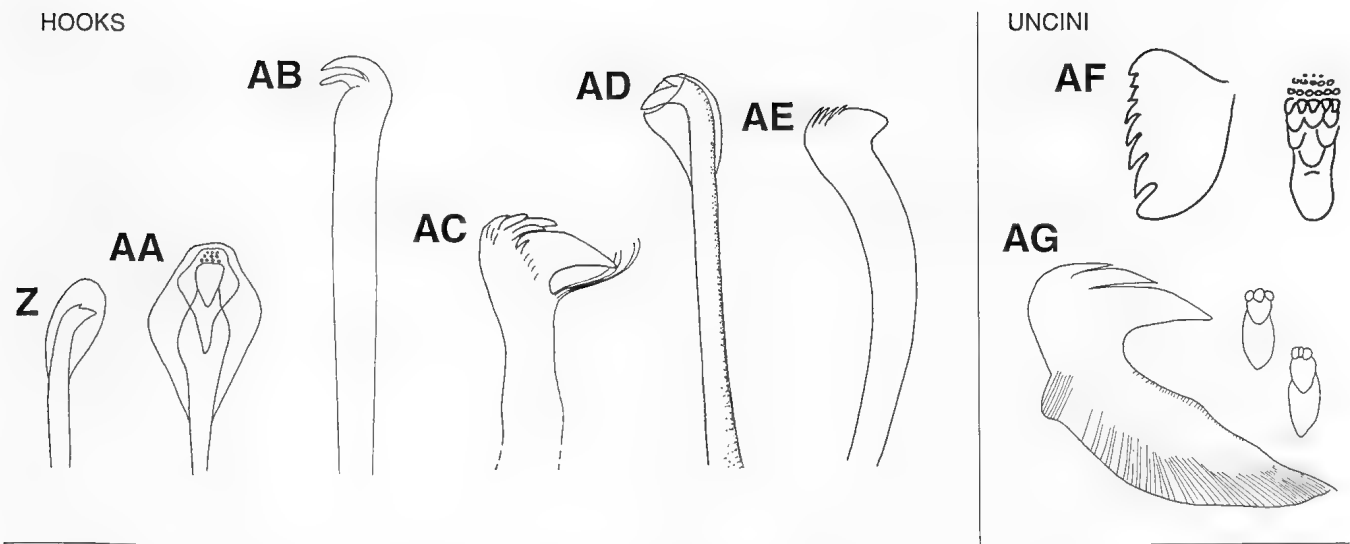


Figure 1.44 Various forms of chaetae. A–F, capillaries: A, smooth capillary; B, C, hirsute capillaries; D, spinose capillary; E, F, pinnate capillaries. G–L, comb and furcate (forked) chaetae: G, comb chaeta; H, lyrate chaeta; I, J, furcate chaetae; K, L, ringent chaetae. M, N, compound chaetae: M, falciger; N, spiniger. O, P, pseudocompound chaetae: O, spiniger; P, falciger. Q–Y, spines: Q, R, spionid-type spines; S, T, chaetopterid-type spines; U, V, weakly curved spines; W, sharply bent or curved spine; X, harpoon-shaped; Y, spine with series of subdistal spinelets. Z–AE, hooks: Z, AA, hooded multidentate hook in lateral (Z) and frontal (AA) view; AB, unprotected bidentate hook; AC, hook with subdistal beard; AD, hooded bidentate hook; AE, unprotected multidentate hook. AF, AG, uncini: AF, pectinate uncinus, lateral and frontal views; AG, crested uncinus, lateral and frontal views. A, AG, *Reteterebella aloba* (Terebellidae); B, C, *Lanassa exelysis* (Terebellidae); D, Y, *Harmothoe charlottae* (Polynoidae); E, F, *Poecilochaetus trachyderma* (Poecilochaetidae); G, *Eunice elseyi* (Eunicidae); H, *Scoloplos normalis* (Orbiniidae); I–L, *Euphrosine armata* (Euphrosinidae); M, N, generalised chaetae (Nereididae); O, P, *Sthenelais pettiboneae* (Sigalionidae); Q, *Boccardia proboscidea* (Spionidae); R, AD, *Boccardia chilensis* (Spionidae); S, T, *Spiochaetopterus costarum* (Chaetopteridae); U, V, *Scolecopides aciculatus* (Spionidae); W, AE, *Terebellides* species (Trichobranchidae); X, *Phylo fimbriatus* (Orbiniidae); Z, AA, *Mediomastus calliopensis* (Capitellidae); AB, *Myriochele scotiae* (Oweniidae); AC, *Maldane californiensis* (Maldanidae); AF, *Amythasides macroglossus* (Ampharetidae). (A–C, AG, after Hutchings & Glasby 1988; D, O, P, Y, after Hutchings & Murray 1984; E, F, after Read 1986; G, after Fauchald 1986; H, X, after Day 1977; I–L, after Kudenov 1993; M, N, after Hutchings & Reid 1990; Q, R, U, V, AD, after Blake & Kudenov 1978; S, T, after Bhaud 1972; W, AE, after Hutchings & Peart in preparation; Z, AA, after Warren, Hutchings & Doyle 1994; AB, after Blake 1984; AC, after Green 1991; AF, after Holthe 1986a)

- 29(13) **Sharply curved spines present in anterior neuropodia** (Fig. 1.44W); capillary chaetae with smooth margins; thoracic uncini long-shafted (acicular; Fig. 1.44AE) Trichobranchidae
- Anterior curved spines if present not neuropodial; capillary chaetae with smooth or serrated margins (Fig. 1.44A–C); thoracic uncini usually without shafts (avicular; Fig. 1.44AG) 30
- 30(29) Body regionation absent, parapodia similar in position and basic structure throughout; spines present in anteriormost notopodia Alvinellidae* (Fig. 1.46H)
- Body usually differentiated into swollen thorax and tapering abdomen; anterior notopodial spines absent Terebellidae
- 31(10) Ventral cirri absent; **ctenognath jaw apparatus with many small dentate maxillae** (Fig. 1.45A; jaws may be reduced to varying degrees) Dorvilleidae (in part)
- Ventral cirri absent; jaws absent 32
- Ventral cirri present, cirriform or tapering; jaws absent or present (but structure otherwise) 33
- Ventral cirri absent (though inflated pads may be present); jaws present, structure otherwise 36
- 32(31) Body disc-shaped, flattened; palps absent; **long transverse notopodial ridges carrying notochaetal spines**; median antenna present Spintheridae
- Body shape otherwise; palps present; notopodial lobes slender lacking chaetae (but with aciculae); median antenna absent Apistobranchidae
- 33(31) Hook chaetae absent; comb chaetae absent; jaws otherwise 34
- Hooks present (in neuropodia), falcate or dentate; comb chaetae present (Fig. 1.44G); labidognath jaw apparatus (Fig. 1.45E, F) 35
- 34(33) Prionognath jaws with four pairs of maxillae; **maxillary carriers paddle-shaped, loosely attached to base of Mx I** (Fig. 1.45B) Hartmaniellidae* (Fig. 1.46I)
- Single pair of lateral scissor-shaped jaws; maxillary carriers slender Ichthyotomidae* (Fig. 1.46J, K)
- **Ctenognath jaw apparatus with many small dentate jaw maxillae** (jaws may be reduced to varying degrees); maxillary carriers absent or if present, short and often fused to base of Mx I as base-plate (Fig. 1.45A) Dorvilleidae (in part)

1. CLASS POLYCHAETA

- 35(33) **Paired ventro-lateral palps comprising short, ringed basal palpophore and distal palpostyle (resemble antennae);** single peristomial ring carrying paired cirri. Onuphidae
 — Paired ventro-lateral sensory palps more-or-less smooth, or beaded (resemble antennae); two peristomial rings, cirri present or absent. Eunicidae
- 36(31) Dorsal cirri present, foliaceous; **prionognath jaw apparatus with variable number of maxillae (may be symmetrical or asymmetrical)** (Fig. 1.45C) Oeonidae
 — Dorsal cirri absent; **labidognath jaw apparatus with 4 pairs of maxillae** (Fig. 1.45G). Lumbrineridae
- 37(2) **Large fusiform postchaetal lobe adorned with sensory hairs;** ventral cirri absent; aciculae absent Aberrantidae* (Fig. 1.46L, M)
 — Postchaetal lobes not enlarged; ventral cirri present; aciculae present. 38
- 38(37) Some dorsal cirri modified as elytra (= scales); benthic forms 39
 — Dorsal cirri foliose throughout; pelagic and benthic forms 42
 — Dorsal cirri otherwise; benthic forms 46
- 39(38) Elytra alternating throughout body; **silky fibre-like notochaetae used to line tube;** facial tubercle present. Acoetidae
 — Elytra alternating anteriorly, present on all chaetigers or absent posteriorly; notopodial silk chaetae absent; facial tubercle absent 40
- 40(39) Compound chaetae with appendages distally falcate Pholoidae
 — Compound chaetae with appendages both falcate and spinigerous (Fig. 1.44O, P). Sigalionidae
 — Compound chaetae absent 41
- 41(40) **Neuropodia distally truncate, with sclerotinised ridges; neuroaciculae elongate, axehead-shaped distally;** capillary chaetae smooth Eulepethidae
 — Neuropodia distally tapered, without sclerotinised ridges; neuroaciculae distally tapered; capillary chaetae spinose (Fig. 1.44D) Polynoidae
- 42(38) Notopodia represented by dorsal cirri only 43
 — Notopodia represented by at least one chaetal lobe and/or chaetae Lacydoniidae
- 43(42) Benthic forms; **all chaetae compound spinigers with shafts distally spinose and inflated** Phyllodocidae
 — Pelagic forms; compound spinigers with shafts not inflated/spinose distally 44
- 44(43) Median antenna present; **eyes with large camera-type lenses;** capillary chaetae present Alciopidae
 — Median antenna absent; eyes otherwise; capillary chaetae absent 45
- 45(44) Pharynx with terminal papillae only; compound chaetae with oar-shaped or slender (spinigerous) appendages Lopadorhynchidae
 — **Pharynx densely covered with very long papillae;** compound chaetae all spinigerous. Pontodoridae*
- 46(38) Caruncle present, conspicuous, bordered by ciliary nuchal band (Fig. 1.2A); chaetae calcified, hollow 47
 — Caruncle absent, nuchal organs usually indistinct ciliated grooves or eversible cones (Fig. 1.2B) (rarely paired posterior loops); chaetae chitinous with core 48
- 47(46) Notopodia short, cylindrical or conical; single tufted notopodial branchiae; furcate chaetae not ringent Amphinomidae
 — Notopodia elongated crests, many small, branching branchiae along notopodial crests; furcate chaetae include ringent (Fig. 1.44K, L) and non-ringent types (Fig. 1.44I, J). Euprosinidae
- 48(46) **Four jaws in a cross, each supported basally by an aileron** Glyceridae
 — Two pairs dorsoventral jaws, not in a cross or supported basally. Pisionidae
 — **One pair lateral jaws (macrognaths), dorsal and ventral arc of accessory jaw pieces (micrognaths) and sometimes also chevrons** Goniadidae
 — Jaws absent, or one pair lateral jaws. 49
- 49(48) Prostomium shape quadrangular to pentagonal; **inter-ramal cirrus (branchiae) present in anterior parapodia (Fig. 1.11H) (rarely cirrus absent)** Nephtyidae
 — Prostomium shape otherwise; inter-ramal cirrus absent. 50

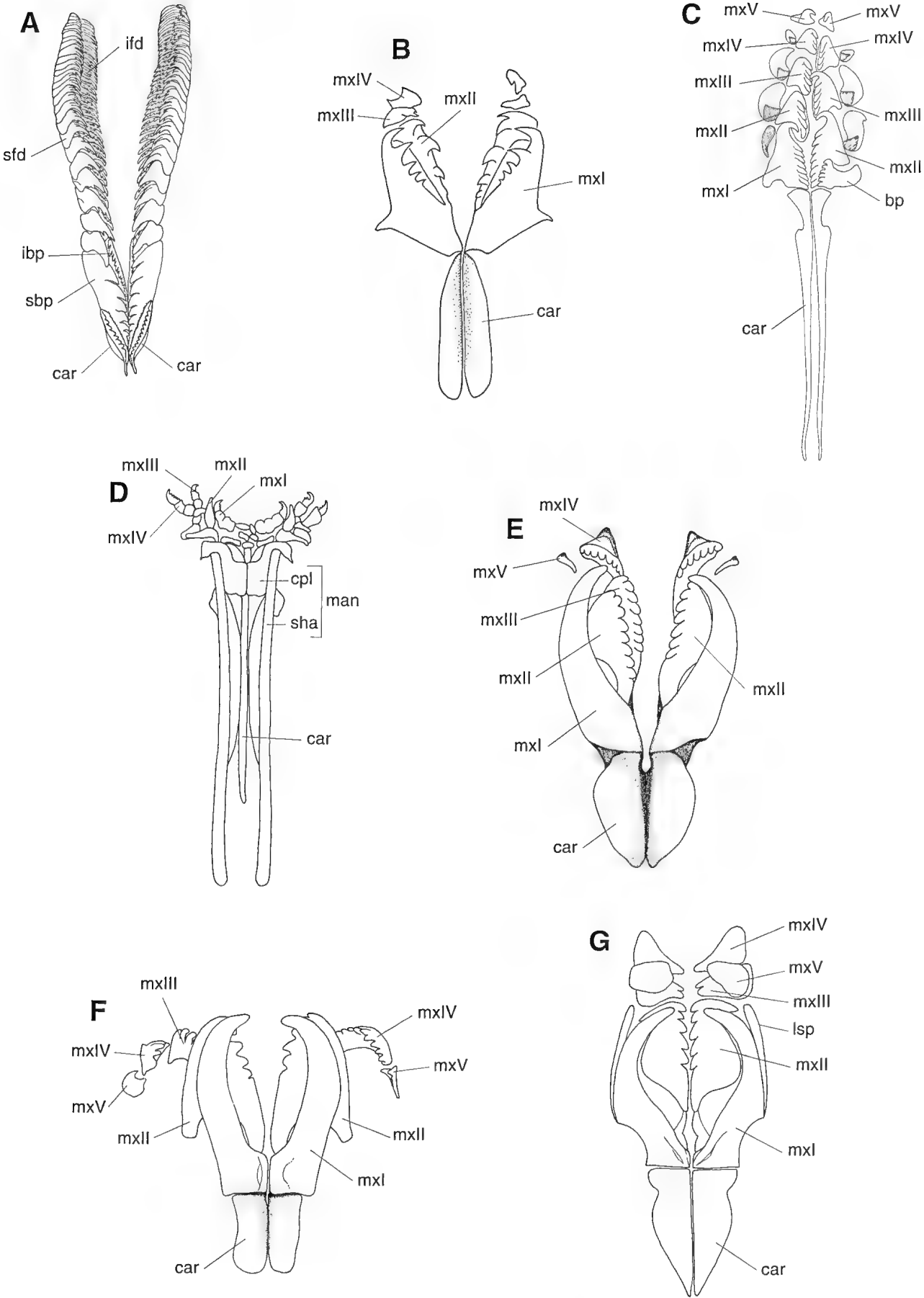


Figure 1.45 Jaws and arrangement of maxillae of *Eunicida sensu stricto*. **A**, Ctenognath type. Dorvilleidae, *Schistomeringos loveni*. **B–D**, Prionognath type: **B**, Hartmaniellidae, *Hartmaniella erecta*; **C**, Oenonidae, *Oenone fulgida*; **D**, Histiobdellidae, *Stratiodrilus tasmanicus*. **E–G**, Labidognath type: **E**, Onuphidae, *Hirsutonuphis mariahirsuta*; **F**, Eunicidae, *Eunice antennata*; **G**, Lumbrineridae, *Lumbrineris* cf. *latreilli*. **bp**, basal plate; **car**, carrier; **cpl**, cutting plate; **ibp**, inferior basal plate; **ifd**, inferior free denticle; **lsp**, lateral support; **mxI–V**, maxillary plates I–V; **man**, mandible; **sbp**, superior basal plate; **sfd**, superior free denticle; **sha**, shaft. (B, after Imajima 1977; D, after Haswell 1900) [A, C–G, A. Murray; B, K. Nolan]

1. CLASS POLYCHAETA

- 50(49) **Notochaetal paleae present, arranged in fans across dorsum (Fig. 1.11G)**Chrysopetalidae
 — Notochaetal paleae absent.51
- 51(50) **Dorsal body surface with large spherical epidermal papillae arranged in two or more rows; proventricle present, but inconspicuous**Sphaerodoridae
 — Body surface usually smooth (rarely papillated, if so, not in rows); **proventricle with radiating muscle fibres present (visible through body wall)**Syllidae
 — Body surface smooth; proventricle absent52
- 52(51) **Four to eight pairs of tentacular cirri on at least two reduced achaetous segments; compound chaetae present**Hesionidae
 — **Three or four pairs of tentacular cirri on collar-like segment; compound chaetae present (Fig. 1.44M, N)**Nereididae
 — Two pairs of tentacular cirri; compound chaetae absent.Pilargidae (in part)
 — Tentacular cirri absent; compound chaetae present or absent.53
- 53(52) Notopodia with lobes and chaetae; chaetae include spinose capillaries and compound spinigers.Paralacydoniidae
 — Notopodia without lobes (only dorsal cirrus, which may be enlarged) or chaetae; all chaetae simple, distally curved spines.Nautiliniellidae* (Fig. 1.46N–P)
- 54(1) Prostomium with paired antero-lateral appendages; parapodia represented only by an ‘**inter-ramal parapodial cirrus**’; hooks absentNerillidae
 — Prostomium without antero-lateral appendages; parapodia represented by notopodial cirri and low ridge-like neuropodia (tori); chaetae include **multidentate, unprotected hooks with slender shafts**Psammodrilidae* (in part)
 — Prostomium without paired antero-lateral appendages; parapodia absent55
- 55(54) Chaetae present.56
 — Chaetae absent59
- 56(55) Peristomial ring absent (peristomium only around mouth)57
 — Peristomial ring presentParergodrilidae
- 57(56) Dentate hooks present.Ctenodrilidae (in part)
 — Hooks absent (capillary chaetae only)58
- 58(57) Epidermal coloured glands absentPotamodrilidae* (Fig. 1.46Q)
 — Epidermal coloured glands present.Aeolosomatidae
- 59(55) Pygidial cirri enlarged, toe-like, adhesive appendages.Diurodrilidae
 — Pygidial cirri, if present not toe-like, adhesive.Dorvilleidae (in part)
- 60(1) Parapodia absent61
 — Parapodia uniramous throughoutSaccocirridae
 — Both notopodia and neuropodia present over part of body; chaetae include **multidentate, unprotected hooks with slender shafts**Psammodrilidae* (in part)
- 61(60) Pygidium bilobed (deeply furcate resembling toes) with adhesive glands, pygidial cirri absent; buccal organ present.62
 — Pygidium not bilobed, inflated, with adhesive glands and sometimes two or three pygidial cirri; buccal organ absentPolygordiidae*
- 62(61) **Paired palps distinct from prostomium, with internal cavities connected behind brain**Protodrilidae
 — Paired palps extensions of prostomium, without internal cavitiesProtodriloididae*
- 63(1) Body disc-shaped; posterior end not cleft; jaws absent; echinoderm symbiont.Myzostomatidae see Chapter 2
 — Body longer than wide; **deeply cleft posterior end forming two large ‘feet’**; jaws present, prionognath type (Fig. 1.45D); symbiont of decapod crustaceans.Histriobdellidae

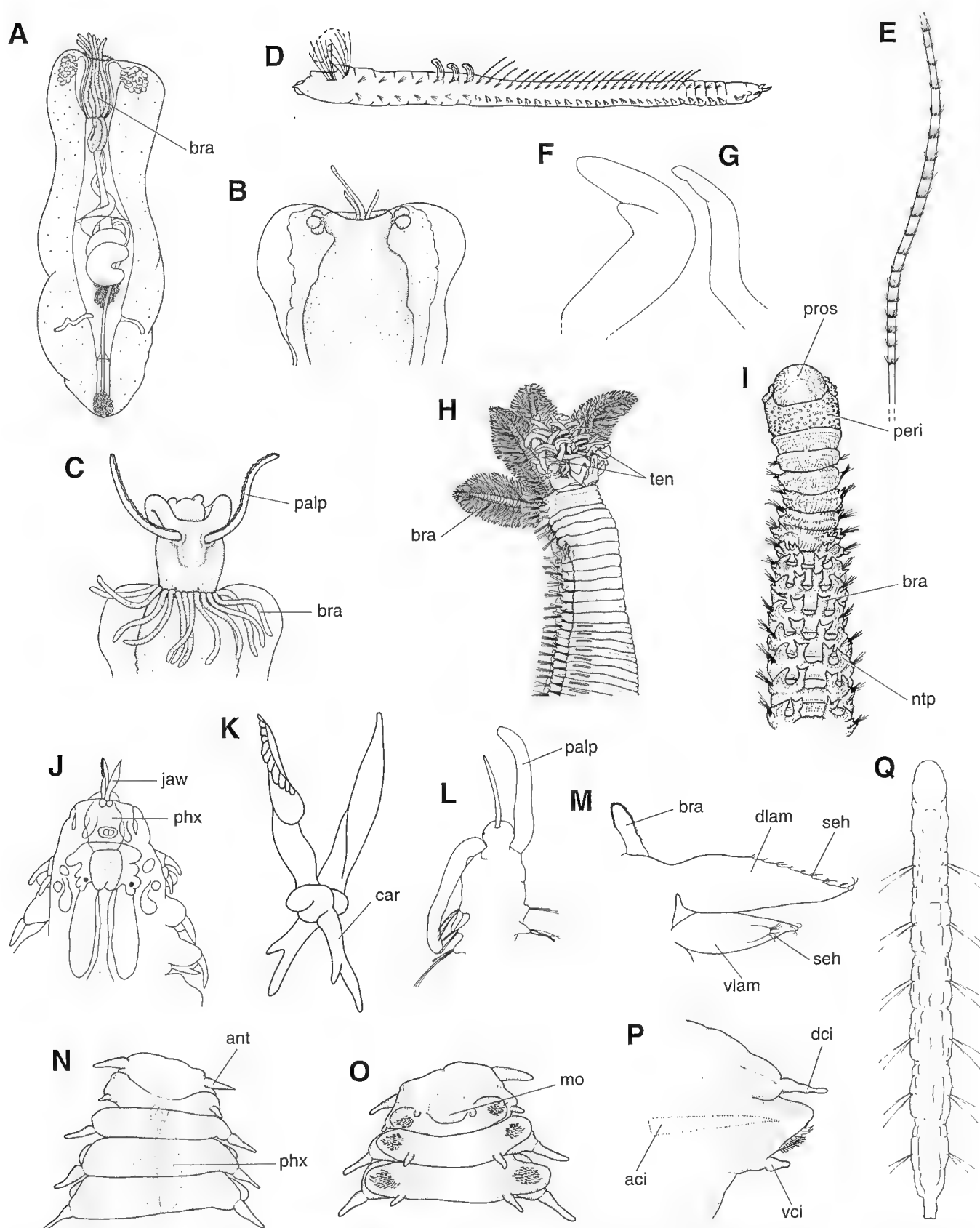


Figure 1.46 Some families not represented in Australian waters. **A–C**, Poeobiidae, *Poebius meseres*: **A**, entire animal, dorso-lateral view; **B**, anterior end with head retracted, lateral view; **C**, anterior end with head everted, dorsal view. **D–G**, Uncispionidae, *Uncispio hartmanae*: **D**, entire animal showing the three body regions, lateral view; **E**, hirsute capillary; **F, G**, enlarged hooded hooks. **H**, Alvinellidae, *Paralvinella grasslei*, anterior end showing four pairs of branchiae, ventro-lateral view. **I**, Hartmaniellidae, *Hartmaniella erecta*, anterior end, dorsal view. **J, K**, Ichthyotomidae, *Ichthyotomus sanguinarius*. **J**, anterior end, dorsal view; **K**, scissor-shaped jaws. **L, M**, Aberrantidae, *Aberranta palpata*: **L**, anterior end with most dorsal and ventral lamellae missing, dorsal view; **M**, middle parapodium with chaetae omitted; posterior view. **N–P**, Nautiliniellidae, *Natsumia bifurcata*: **N**, anterior end, dorsal view; **O**, anterior end, ventral view; **P**, parapodium. **Q**, Potamodrilidae, *Potamodrilus fluvialis*. **aci**, acicula; **ant**, antenna; **bra**, branchia; **car**, maxillary carrier; **dci**, dorsal cirrus; **dlam**, dorsal lamella; **jaw**, jaw; **mo**, mouth; **ntp**, notopodium; **palp**, palp; **peri**, peristomium; **phx**, pharynx; **pros**, prostomium; **seh**, sensory hairs; **ten**, tentacles; **vci**, ventral cirrus; **vlam**, ventral lamella. (A–C, after Robbins; D–G, after Green 1982; H, after Desbruyères & Laubier 1982; I, after Imaijima 1977; J, K, after Fauvel 1923; L, M, after Wolf 1987; N–P, after Miura & Laubier 1990; Q, after Bunke 1988) [A–C, A. Murray]

SCOLECIDA

The name Scolecida, formulated by Rouse & Fauchald (1997) in their reclassification of polychaetes, is derived from Scoleciformia, a name introduced by Benham (1896). Scoleciformia appears to have been last used as a taxon name by Goodrich (1945). The Scolecida includes many of the taxa initially placed in the Scoleciformia by Benham and subsequent workers and is derived from *skolex* (Greek), meaning worm. The families included in Scolecida by Rouse & Fauchald (1997) are listed in Table 1.3 and Figure 1.47. The total number of described species in the clade would appear to be over 800 worldwide, divided into about 130 genera. The Scolecida has some similarities to Benham's (1896) Scoleciformia, which contained the Arenicolidae, Maldanidae, Opheliidae, Scalibregmatidae, as well as the Flabelligeridae and Sternaspidae. Benham (1896), however, placed the Capitellidae in a separate suborder, the Capitelliformia, and the Orbiniidae (as Ariciidae) into the Nereidiformia. The remaining three families had not been erected in Benham's time.

Only two autapomorphies support the clade Scolecida in Rouse & Fauchald (1997), the presence of parapodia with similar rami and the presence of two or more pairs of pygidial cirri (see Fig. 1.47). In many ways, this group represents the simple-bodied forms of polychaetes and it is likely that

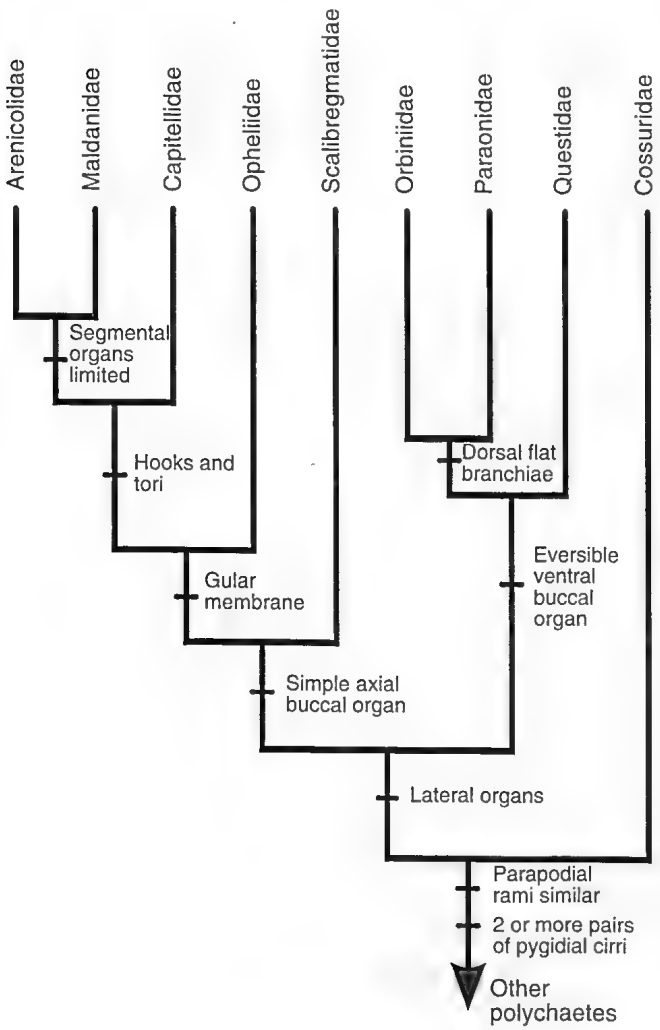
further analysis will show that it is not a monophyletic grouping. Other features that are shared by members of the Scolecida, that are not apomorphic, include a prostomium that is clearly demarcated from the peristomium by a groove, the first segment is similar to those following and bears similar appendages (that is, there are no tentacular cirri), the buccal organ has dorso-lateral folds, and capillary chaetae are always present. Members of the Scolecida typically lack prostomial appendages, the exception being some paraonids which have a single median antenna. Relationships within the Scolecida show the Cossuridae as sister group to the remaining taxa, which all share the presence of sensory 'lateral' organs along the body. Cossurids were once thought to be cirratulids until Day (1963) considered them as a distinct group and placed them into their own family. The clade formed by the Orbiniidae, Paraonidae and Questidae is supported by the presence of an eversible ventral buccal organ, but similar buccal organs are found in other polychaete groups. Further, some orbiniid and paraonid taxa have a non-muscular axial proboscis, but this is thought to be derived from the ventral buccal organ (Purschke & Tzvetlin 1996; Fauchald & Rouse 1997). This grouping was also postulated by Fauchald (1977) who placed the three families in Orbiniida. Questids bear a superficial resemblance to various marine members of clitellate groups such as tubificids. However, they are clearly polychaetes in having nuchal organs and they have none of the apomorphies of the Clitellata. The Paraonidae and Orbiniidae share the apomorphy of dorsal flattened branchiae in the analysis of Rouse & Fauchald (1997), and this grouping has also been postulated by previous workers (for example, George & Hartmann-Schröder 1985).

The other remaining clade of the Scolecida is comprised of five families and all have an eversible simple axial buccal organ (Fig. 1.14H). These five families were grouped as the Capitellida by Dales (1963). The Scalibregmatidae and Opheliidae were found to form a grade with respect to the Arenicolidae, Capitellidae, Maldanidae clade by Rouse & Fauchald (1997). These two families are often grouped together and were placed as the Opheliida by Fauchald (1977). However, the presence of a gular membrane in the anterior body grouped the Opheliidae with the Arenicolidae, Capitellidae and Maldanidae rather than with Scalibregmatidae. Opheliids like *Travisia* and *Euzonus* resemble scalibregmatids like *Neolipobranchius* in body form and having distinct epidermal rugosity. The possible non-monophyly of the Opheliidae or Scalibregmatidae deserves further investigation. The taxa Arenicolidae, Capitellidae, and Maldanidae have been grouped together as a more restricted version of the Capitellida by Fauchald (1977) and all share the presence of long-handled hooks organised as neuropodial tori. Rouse & Fauchald (1997) placed the Maldanidae as the sister group to the Arenicolidae. It is possible the latter taxon is paraphyletic and the relationship of the Maldanidae to arenicolid groups such as *Branchiomaldane* should be investigated.

Family Arenicolidae

Arenicolids, or lugworms, are elongate soft-bodied worms which usually live in a burrow in soft sediments in the intertidal and shallow subtidal zones. They have a small blunt head with no appendages and branched branchiae on their mid-body segments (Fig. 1.48A); their body is often swollen and covered with a thick rugose, annulated epidermis.

The prostomium is small and rounded or conical. The peristomium is typically reduced to lips around the mouth, but some genera such as *Branchiomaldane* appear to have a



complete peristomial ring (Rouse & Pleijel in press). Antennae and palps are absent. Nuchal organs are paired dorso-lateral pits on the prostomium. Longitudinal muscles are in four distinct bands (Storch 1968) and the body segmentation is distinct. The first segment is similar to the other segments and has no parapodial structures in adults; tentacular cirri are absent. Notopodia are short, distally truncate cylinders or cones, and the neuropodia are present as tori (Fig. 1.48A). Dorsal and ventral cirri are absent. Branchiae are present as branching tufts associated with notopodia in the mid-section of the body in most taxa and as simple, tapering structures in *Branchiomaldane*. Epidermal papillae are absent. Pygidial papillae are absent. Lateral organs are absent (Rullier 1951); dorsal cirrus organs have not been observed and are presumably absent. The simple axial pharynx (= proboscis) is sac-like and covered externally with large papillae. A gular membrane is present, and the gut is a straight tube. The segmental organs are mixonephridia (Goodrich 1945); only a few pairs are present anteriorly, the first pair is purely excretory. The circulatory system is closed, and a heart body is absent. Aciculae are absent. Chaetae are present as variously ornamented notopodial capillaries and as distally dentate, unprotected neuropodial hooks (Fig. 1.48B, C). This definition is based on Fauchald & Rouse (1997).

Arenicolids were among the first polychaetes described and are mentioned in pre-Linné publications according to Ashworth (1912b), however, the first species formally described was *Arenicola marina* by Linné (1758). Johnston (1835) subsequently erected a family for the group. They are easily recognised, but surprisingly difficult to diagnose using unique characters (Rouse & Fauchald 1997). Although glandular caeca are characteristically present in all arenicolids, they also occur in some other polychaete families. The characteristic thick, rugose epidermis is also found in some scalibregmatids, although not as well developed

(Ashworth 1901) and capitellids (Eisig 1887). The structure and distribution of the pinnate bushy branchiae are uniform in all arenicolids, except in *Branchiomaldane* species which have sessile branchial filaments (usually no more than three) beginning from chaetiger 18; in the other genera they begin from chaetiger 7. Arenicolids are usually considered to be related to maldanids and capitellids; these three families are grouped together in the order Capitellida in several reviews (Dales 1963a; Fauchald 1977; Pettibone 1982; see Fig. 1.43) and as a clade within Scolecida by Rouse & Fauchald (1997).

No subfamilies are recognised within the Arenicolidae. Worldwide, five genera are recognised and Fauchald (1977) indicated that 28 species have been described as well as several subspecies within the two most speciose genera, *Abarenicola* and *Arenicola*. Since then an additional species of *Branchiomaldane* has been described by Fournier & Barrie (1987). Day & Hutchings (1979) recorded seven species, including species of *Abarenicola* and *Arenicola*, from Australian waters, many of which were described by Wells (1962, 1963). Unpublished records from the Australian Museum database indicate that a species of *Branchiomaldane* is present at Pittwater, New South Wales; if correct this would be a new generic record for Australia. The last revision of the genera was undertaken by Wells (1959).

Arenicolids are particle-feeders, and live in muddy sand in the intertidal and shallow subtidal zones except for members of *Branchiomaldane* which live in muddy rock crevices (Day 1967). The existence of arenicolids in muddy sandy beaches can usually be detected by the presence of funnel-like depressions which mark the head end of the burrows and earthworm-like castings at the tail end (Fig. 1.15A). *Arenicola lovèni*, which is one of the larger species and may reach a length of 1 metre, burrows in estuarine sand banks where the subsurface layers are semi-liquid. In this species the head end

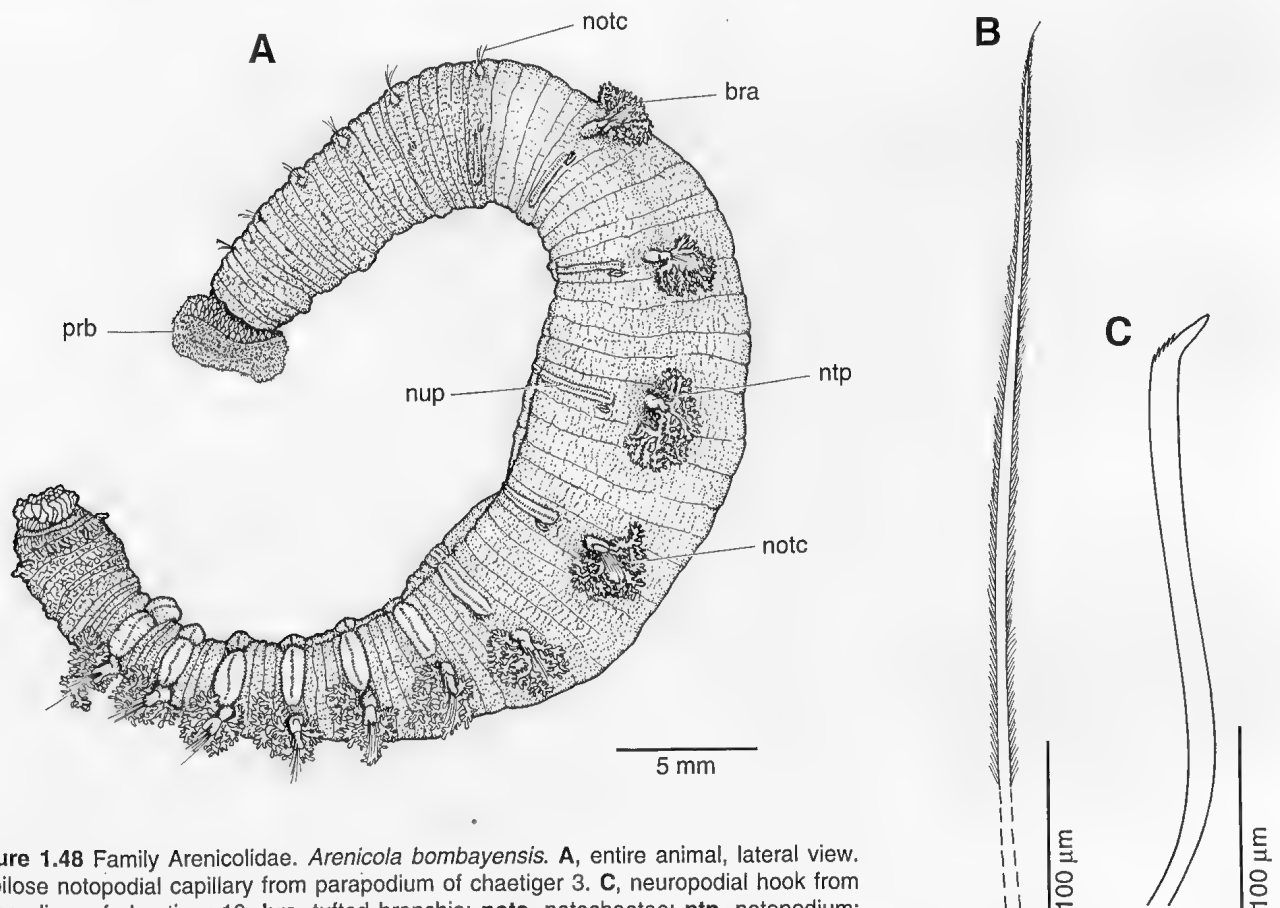


Figure 1.48 Family Arenicolidae. *Arenicola bombayensis*. **A**, entire animal, lateral view. **B**, pilose notopodial capillary from parapodium of chaetiger 3. **C**, neuropodial hook from parapodium of chaetiger 10. **bra**, tufted branchia; **notc**, notochaetae; **ntp**, notopodium; **nup**, neuropodium; **prb**, proboscis everted.

[A. Murray]

1. CLASS POLYCHAETA

of the burrow is marked by the usual depression, but the tail end lacks castings. Faecal material excreted by this species is in a semi liquid state and is squirted out a considerable distance. Most arenicolids live on sheltered beaches, but some species live on more exposed shores and in these cases the worm casts will be carried away by wave action. It appears that arenicolids do not occur in deep waters. In Australia, *Arenicola bombayensis* is occasionally found in seagrass beds as well as intertidal mud flats in southern Australia (Fig. 1.48A; Hutchings 1974a; Hutchings & Murray 1984). No Australian arenicolid species is common.

Arenicolids, in general, are large worms up to 140 mm in length. They have elongate, sometimes regionated, bodies with numerous annulated segments and are typically robust except for species of *Branchiomaldane* which are small (less than 40 mm in length). The first segment is achaetous, and subsequent segments are chaetigerous. The first segment has been shown to have chaetae in the juvenile stages, but these are lost during development (Ashworth 1904). Posterior chaetigerous trunk segments are branchiate. In some genera, a posterior 'tail' region of achaetous segments is also present. The number of segments in the trunk region is constant in some genera and not in others. Apart from the genus *Branchiomaldane*, which has two annuli per segment, the other genera have five annuli per segment on the branchiferous segments, but fewer on the anterior abbranchiate segments.

Much of the work on the hydrostatic skeletons of polychaetes has been performed using *Arenicola marina*. Chapman (1958) has reviewed these studies; basically the animal needs to retain its coelomic fluid in order to burrow effectively. A loss of 0.38 ml, which represents about 25% of the total volume of coelomic fluid of a large *Arenicola*, will double the time taken to burrow. If the posterior end is amputated burrowing time is only increased by about 30% above that of an intact worm as the circular muscles immediately contract in front of the amputation minimising the loss of coelomic fluid (Chapman & Newell 1947). Arenicolids have three anterior septa which separate the proboscis from the posterior coelom and prevents accidental eversion by movements of fluid in the coelomic cavity (Dales 1963a). The coelomic fluid continues to function as a hydrostatic skeleton even when filled with gametes.

The feeding modes of arenicolids have been extensively studied; many species make suitable subjects as they can be maintained in the laboratory over long periods of time. Fauchald & Jumars (1979) provided a table of the various studies on arenicolid species. Early studies on gut contents showed that sand and detritus were present (Rauschenplat 1901; Jordan 1913; Blegvad 1914; Hempelmann 1931) or only detritus (Yonge 1954). The most detailed studies have been on *Arenicola marina*, the common European species. This species occupies a U-shaped burrow consisting of a sediment-filled head-shaft, an open horizontal gallery and an open tail-shaft. It has generally been accepted (Wells 1945; Longbottom 1970a) that the animal feeds by ingesting sediment at the base of the head-shaft; much of this material was originally derived from the surface and, therefore, Thamdrup (1935) characterised them as surface deposit-feeders even if the actual food intake takes place at depth. A modified feeding strategy has been proposed by Krüger (1959) and Hartmann-Schröder (1971) that the maintenance of an irrigation current would tend to lead to the capture of plankton in the irrigation water in the sand immediately in front of the worm. Jacobson (1967) quantified the organic content of the surrounding water and the sediment and showed that the sediment in the head shaft had elevated levels

of organic material compared to the surrounding sediment and the water column. He suggested that the funnel created by irrigation movements would tend to concentrate organic detritus of low specific gravity. Hobson (1967) showed that, although such filtering is possible, essentially they feed on a sinking column of sand in the head shaft. Wells (1966) and Schäfer (1962) have attempted to resolve these apparent conflicting modes of feeding and suggest that the importance of each may be related to the sediment composition. In low nutrient, coarse sand, filtration may be relatively more important than in high-nutrient, fine sand. The pumping effort would be much greater in fine than in coarse sediments. Fauchald & Jumars (1979) concluded that at most of the sites investigated in detail the surface deposit-feeding mode is the most important.

Early studies suggested that arenicolids are non-selective feeders (Kermack 1955; Retière 1967; Wolff 1973). However, Wells (1945, 1966) showed that large particles such as shell fragments are not ingested, rather they are sorted at the base of the head shaft. On beaches where high densities of animals occur, this will lead to the formation of an almost continuous layer of coarse particles 150–200 mm below the surface. MacGinitie & MacGinitie (1968) found that only small particles are consumed and the mucus secreted while feeding differs in quality from the secretions made while burrowing, suggesting a higher level of selectivity than previously thought.

Arenicolids can digest a range of small animals such as ciliates, flagellates and nematodes, but diatoms which have thick cellulose walls pass through undigested (Hylleberg 1974). Sand which has passed through the gut rapidly gains a much larger population of bacteria than the surrounding sand and Hylleberg (1974) refers to this as a sort of 'gardening'. Plante & Mayer (1994) further suggested that macrofaunal activity may not only stimulate microbial biomass production, but also simultaneously increase the microbes susceptibility to digestion within the gut of the animal.

Arenicolids swallow sediment by everting their pharynx which lies in front of the first septa; it is everted solely by fluid pressure, whereas retraction is achieved by the relaxation of body wall muscles accompanied by the contraction of muscles joining the first septum/body wall to the pharynx. The structure of the pharynx of several species of *Arenicola* has been described in detail by Wells (1954) as well as the eversion process. The precise mechanism varies according to the habitat in which the species live.

The anatomy of the gut was described by Kermack (1955). It consists of an oesophagus which leads from the buccal cavity to the stomach and an intestine which lie together in the trunk of the body and then to the rectum in the tail region. The oesophagus can be divided into an anterior part, which is lined with cuticle, and a posterior part, which is divided into two parts histologically. The first of these parts which passes through the septa has thick muscular walls with a simple epithelial lining forming papillae arranged in roughly longitudinal rows. The second part is far more glandular, with thinner muscle layers and with the epithelium partially ciliated. In this region, a pair of oesophageal pouches arise, which are thin-walled, contractile and lined with a simple squamous epithelium. The anterior part of the stomach is thin walled and has a poorly developed musculature. The epithelium contains some phagocytic and some ciliated cells. The density of ciliated cells increases posteriorly and forms in the posterior stomach a ventral ciliated gutter which continues to the anus. The posterior section of the stomach has convoluted walls and numerous mucus- and enzyme-secreting

cells; the secreting cells have been studied by Kaganovskaya (1976, 1978a, 1978b, 1983). From the posterior of the stomach the gut gradually transforms into the intestine which is narrower than the stomach. The intestine leads into the rectum which is attached by septa to the body wall. Kermack (1955) found the stomach to be the main region for digestion, with food particles being taken up phagocytically by epithelial cells then transferred to amoebocytes at the base of these cells, where they are moved into the blood stream or into the peritoneum.

The enzymatic properties of the gut of *Arenicola* were investigated by Longbottom (1970b). Carbohydrases, proteases and esterase/lipases are largely confined to the stomach and the caeca. The caeca appear to be the source of the lytic activity and visually resemble the stomach in terms of the colour of its contents. The stomach may also be an additional source of lytic activity. Plante & Mayer (1994) measured the bacteriolytic activities along the alimentary canal and tested the relative efficiency of the bacteriolysis. The digestive caeca, anterior stomach and posterior stomach exhibited high levels of lytic activities whereas bacteriolytic activities were negligible in all other regions of the gut. Similarly, faecal castings exhibited no lytic capabilities. Ingested sediment is exposed to the lytic portion of the gut for about 20 minutes. As lytic activity cannot be detected posterior to the stomach this may indicate that *Arenicola* species are able to recycle digestive secretions. In *Arenicola* species, which ingest large quantities of low quality food, an ability to recycle such secretions may be an efficient adaptation. They secrete relatively large quantities of digestive fluid and exhibit short gut residence times.

The relative importance of bacteria in the diet of arenicolids is still being debated and perhaps less than 10% of the required carbon of such deposit-feeders is obtained from bacteria (Kemp 1987, 1990; Plante *et al.* 1989 and references therein). The focus on carbon versus nitrogen for energy may have tended to underestimate the relative contributions of bacteria (Tenore *et al.* 1982; Jumars *et al.* 1990). Another factor which needs to be taken into account when attempting to develop a balance sheet is the competition between the worm obtaining nutrients from the bacteria and the bacteria absorbing soluble digestive products (Plante *et al.* 1990). Thus, there may be a dual function for the lytic agents in *Arenicola marina* – competitive removal of bacteria and nutritive gain.

Some data suggest that for species of *Arenicola*, lipids may be stored in the body wall and function as a reserve for the period of reduced food intake during the winter (Mayes & Howie 1985).

The arenicolid heart described by Dales & Cummings (1987) is not homologous with the heart bodies of other polychaetes. They found that the heart body of arenicolids consists of involuted tissue containing myofibrils on a collagenous membrane without an inner endothelium to which haemocytes adhere. They suggested that the heart bodies are mechanical in function rather than functioning to produce haemoglobin and in removing toxic wastes. Arenicolids have instead extravasal or 'chloragogen' tissue which extends along various vessels including blind-ending vessels which project into the coelom. This tissue is responsible for the production of haemoglobin molecules (Braunbeck & Dales 1985). Initially the dark granules of haematin, which appear in the granular endoplasmic reticulum of these tissues, was thought to be a by-product of haemoglobin breakdown, but Kennedy & Dales (1958) and Magnum & Dales (1965)

showed that they are the by-products of haemoglobin synthesis. In addition, these cells also take up unwanted material from the body fluids (Braunbeck & Dales 1984).

Arenicolids typically live intertidally or in shallow waters; they are well-adapted to inhabiting burrows, often in poorly aerated muddy sediments. They irrigate their burrow by pumping water through it. Up to 90 ml of water may be pumped through a burrow in 10 minutes by an average sized species of *Arenicola* (Dales 1963a); oxygen, from the water, is taken up by the branchiae. The rate of pumping appears not to be related to oxygen levels in the water, suggesting it is controlled by an internal pacemaker (Wells 1950). Arenicolids also undertake aerial respiration when water levels falls below burrow openings. Bubbles of air are trapped between the worm body and the burrow walls, and oxygen is absorbed from the bubble, which is subsequently released and the process repeated. Low levels of oxygen can be utilised as the haemoglobin can become highly saturated at low oxygen concentrations, and can release oxygen to the tissues at these levels (Jones 1955), which must occur regularly in these habitats.

It has been suggested that arenicolids can store oxygen during low tides, although Dales (1963a) noted that such a storage capacity may be very limited. So if no oxygen storage occurs, do they develop an oxygen debt during low tide? Studies by Borden (1931) found that after 2 hours of anaerobic conditions, no debt was detectable, and worms would survive for up to 9 days without oxygen (Hecht 1932). This is achieved by the worms utilising glycogen, but without accumulating lactic acid, as happens in warm-bodied animals (Dales 1958). Instead the glycogen is metabolised to a mixture of acids. The worm also reduces its metabolic activity and under normal circumstances intertidal worm burrows are rarely exposed for more than 9 hours. More recently it has been shown that under periods of hypoxia and the onset of anaerobic metabolism, enhanced autoxidation of free haemoglobins occurs and involves the release of hydrogen peroxide into the blood and haemolymph (Abele-Oeschger & Oeschger 1995).

As well as being subjected to low oxygen levels, arenicolids are also subjected to abrupt dilution of the water in their burrows after heavy rain at low tide. *Arenicola marina* responds to this by becoming inactive, compressing itself at the bottom of its burrow and irrigating the overlying water only about once per hour, full activity only being resumed when the salinity rises. Shumway & Davenport (1977) suggested that *Arenicola* is an osmotic and ionic conformer, but controls the concentration of body fluids by remaining inactive at the bottom of its burrow during periods of stress. Cellular levels of sodium, chloride and potassium in *Arenicola* decrease as surrounding salinity decreases (Freeman & Shuttleworth 1985) and this is related to an influx of seawater. At 25% seawater, the mechanisms for regulation of cell volume break down and sodium and water enter the cells. However, on return to full-strength seawater, restoration of cell volume is accompanied by active accumulation of seawater. Worms can survive immersion in 35% seawater and be re-equilibrated with 100%, but not from greater dilutions. This re-equilibration involves a reduction of 50% in the volume of the intracellular water, but also involves a recovery of the 44% of the organic solute lost during the equilibration to 35% seawater (Freeman & Shuttleworth 1977).

Functional gonoducts have been reported in arenicolids by Gamble & Ashworth (1899). They are present in anterior segments, with one pair being purely excretory (Goodrich 1945).

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Arenicolids have three main longitudinal nerve fibres, a lateral pair and a median nerve fibre. All anastomose with one another and are joined by a single pair of large nerve cells.

Statocysts are present and appear to be very important in the orientation of these burrowing species. Three types are present within the family, although it seems that within a species only one type is present. Removal of the statocysts prevents the worm from being able to re-orientate itself. Typically arenicolids lie vertically in the sediment and can right themselves if turned horizontal.

Studies have shown that sediment temperature plays a role in the control of reproduction. On mud flats in Ireland the sediment acts as a heat sink absorbing periodic high inputs at the surface, so that the average temperature at depth exceeds that of the surface during late spring and summer (Mayes & Howie 1985). Proliferation activity in the testis is low during the winter, rises during the spring and reaches maximum levels in early summer (Howie & McClenaghan 1965; Olive 1972). Male and female gametes appear in increasing numbers in the coelom in spring (late March and early April). Thus, both the proliferation and release of gametes into the coelom occurs under conditions of increasing temperature. As no evidence for endocrine control of gamete proliferation has been found (Olive 1972), it seems possible that the initiation of the reproductive activity is a consequence of a general increase in metabolic activity due to increasing temperature and perhaps food (Mayes & Howie 1985). Feeding activity is ten times higher in summer than winter, and Cadée (1976) suggested that the low activity in winter results from a combination of low temperatures and low food availability. Synchronisation of gamete release occurs in late summer and Mayes & Howie (1985) suggested that this is related to declining ambient temperatures. Although temperature is not a direct cue for spawning (Howie 1984), it will not occur if ambient temperatures remain above a certain level, and a limiting temperature of 15°C has been suggested (Howie 1963). The gametes of ripe males and females of *Arenicola* comprise about 25% of total weight. The coelomic fluid appears to be the major source of nutrients available to the developing gametes. As they develop, coelomic fluid levels increase as levels of protein in the gut tissues decline. It appears that the protein (and non-protein nitrogen) requirements of the developing gametes are supplied by the gut tissues, via the coelomic fluid (Mayes & Howie 1985).

Olive (1984) suggested that endogenous mechanisms ensure that there is a co-ordinated production of uniformly mature batches of oocytes and sperm, and that these are likely to involve negative feedback loops in *Arenicola marina*, as suggested by Howie & McClenaghan (1965). Olive (1984) postulated that a drop in air temperature leads to the release of a hormone which stimulates spawning. Such a hormone, produced by the prostomium, and controlling the release of gametes, has been found by Howie (1963, 1966). A short time before spawning, the cerebral ganglia contains a phase-specific hormone which can be extracted from both males and females. If injected into mature animals, spawning occurs. As spawning is well synchronised at the level of local populations, hormone release may be triggered by some environmental stimulus, such as a fall in temperature (Duncan 1960). This hormone has been isolated and studied in detail by Meijer (1979a, 1979b). It appears to act directly on prophase I oocytes (Howie 1961b) and sperm aggregates (Howie 1961a) and it may trigger the release of membrane-bound calcium in the oocyte cortex (Meijer 1980). A diagrammatic scheme of the endocrine controlling mechanisms in *Arenicola marina* is given by Franke & Pfannenstiel (1984) and in more detail by Pfannenstiel & Grothe (1988). It

appears that the sperm maturation factor (SMF) in *Arenicola marina* is probably an arachidonic acid or a derivative, but where SMF is synthesised is unknown and therefore it is not known if SMF should be classified as a neurohormone (Pfannenstiel & Grothe 1988).

Spawning of *Arenicola marina* along the British and Irish coasts occurs over a 3 week period during the autumn. However, Howie (1984) indicated that elsewhere in Europe spawning may occur at other times and may be brief (epidemic) or prolonged. In contrast, another British species, *Arenicola ecaudata*, has been reported as breeding throughout the year (Southward & Southward 1958). Whereas most species of arenicolids mass spawn, *Arenicola clapedii* broods juveniles in the adult burrow (Okuda 1946). Another form of brooding is exhibited by *Arenicola brasiliensis* which extrudes mucous cocoons containing fertilised eggs from the burrows and they remain attached by a stalk for 4–5 days. Pelagic trochophores break free from the cocoons and settle after 4–5 days. The adult complement of chaetigers is acquired after about 6.5 weeks (Bailey-Brock 1984). Other studies on the life history of various species of arenicolids, predominantly *A. marina* and *A. cristata*, are listed by Schroeder & Hermans (1975).

Development of gametes occurs in the coelomic cavity. In *Arenicola marina*, several spermatogonia form a single cluster and leave the gonad at a very early stage. Proliferation occurs within these clusters (Sawada 1984). Detailed ultrastructural studies have been undertaken by Sawada (1975, 1984) on the various stages of spermatogenesis in *Arenicola brasiliensis*; the sperm are classified as a 'primitive' type or aquasperm (*sensu* Jamieson & Rouse 1989).

The oocytes of *Arenicola marina* are produced on the germinal epithelium and then released into the coelom where vitellogenesis occurs (Meijer 1979a, 1979b; Rashan & Howie 1982). A mature worm of about 4 g in weight contains about 316×10^3 oocytes. It seems likely that, as no nurse cells are present, the coelomic fluid is the source of oocyte nutrition during vitellogenesis. A marked increase in the protein content of the fluid coincides with the onset of vitellogenesis.

Hermaphroditism has been reported in *Branchiomaldane vincentia* by Ashworth (1904) and appears to be simultaneous with both eggs and sperm originating in the same segment.

The development of the early fertilised oocyte has been studied by Child (1900), and Lillie (1906a) described the later development of the mesoblast bands. The development of larval nephridia has been studied by Lillie (1906b).

Arenicola marina can reach sexual maturity within a year under experimental conditions, but in the field it normally takes 2 years and under some circumstances may take 3 years. The species can breed more than once, but mortality is high after spawning. Based on rates of recruitment, Howie (1984) estimated that individuals may live for up to 6 years.

Densities of *Arenicola marina* on northern European tidal flats are extremely constant over time; Flach & Beukema (1994) have investigated the mechanisms by which this is achieved. Arenicolids are able to influence distribution patterns of neighbouring individuals and those of other species via bioturbation of surrounding sediments. At normal densities, adult lugworms turn over the top sediment to a depth of up to a few decimeters each year (Cadée 1976). This negative effect also impacts on the densities of other benthic invertebrates in the area. Flach (1993) and Flach & de Bruin (1993) showed that sediment-disturbing animals such as lugworms destroy the tubes of tube-building animals such as

some amphipods, making them vulnerable to predation by epibenthic predators (Flach & de Bruin 1994). Flach (1992) showed that *Arenicola* species had strong negative effects on the densities of various juvenile worms (high densities of juveniles are only found when adults are scarce) and bivalve species. Laboratory studies showed that sediment reworking by lugworms stimulated the amphipod *Corophium* to emigrate.

Juvenile lugworms appear to be more mobile than adult worms and their densities can decline in winter during periods of migration due to tidal currents. However, such currents rarely affect the adults (Beukema & de Vlas 1979). High densities of juveniles are found in 'nursery' areas where conditions are less suitable for adults, such as the higher intertidal zones (Farke, De Wilde & Berghuis 1979). The juveniles tend to recruit to higher intertidal areas than where the adults normally live and migrate in winter to lower and more offshore areas (Chapman & Newell 1949; Flach & Beukema 1994).

Deposit-feeders such as arenicolids are relatively sedentary and are more widely spaced than suspension-feeders (Levinton 1972). Some data suggest that population densities and growth rates of *Arenicola marina* in the Wadden Sea are limited by food availability. Growth rates are inversely related to population levels. Under conditions of eutrophication, when food supply to herbivores increases, densities of lugworms on the mud flats increases significantly (Beukema & Cadée 1986).

Australian species of arenicolids are rarely collected and have never been observed in high densities (P. Hutchings personal observation) so it seems unlikely that similar mechanisms operate for these species.

The activities of *Arenicola* species have been studied in detail. For instance, Wells & Albrecht (1951a) observed, in the laboratory, a regular cycle of activity, including feeding, defaecation and irrigation. None of these activities can be undertaken simultaneously. These activities appear to be controlled by spontaneous internal clocks in the central nerve cord and the oesophageal plexus (Wells & Albrecht 1951a, 1951b). For example, movement of the worm to the surface normally occurs prior to defaecation and continues at regularly spaced intervals when the animal is fasting and the rectum is empty (Wells 1945). Irrigation of the burrow occurs when the animal is surrounded by well-oxygenated water and continues when oxygen levels drop to low levels.

Arenicola marina is sensitive to metal contaminated sediments, with copper being more toxic than either zinc or cadmium. As concentrations of the metals increase the arenicolids leave the sediment and are vulnerable to predation. Metal concentrations were higher in the ambient sediment than in worm casts (Bat & Raffaelli 1998) and this may be due to particle size selection, dissolution or absorption of metals in the gut or a combination of these factors. Contrary results were found by Brown (1986) who noted that metals were concentrated in the worm casts. Bat & Raffaelli (1998) suggested that this common European species may be useful for whole sediment bioassays, although it is important to assess the effects of specific contaminants on their own or in combination.

Arenicola marina is collected throughout Northern Europe for sea angling bait. In a designated part of a northern England estuary, an area was deliberately set aside for bait digging (200 m x 2 km); within 6 weeks no arenicolids were present. Olive (1994) estimated that over 4 million worms were collected during this period. Collecting was mainly by semi-

professional bait diggers for commercial sales. Obviously natural populations cannot withstand these pressures and attempts are currently underway to breed this species commercially in Ireland. Similar rearing projects have been taking place for many decades, but none have proved commercially viable to date.

Family Capitellidae

Capitellids resemble terrestrial earthworms (Pl. 1.1). They have a pointed or rounded head which lacks appendages and a long cylindrical body. Parapodia are poorly developed and chaetae appear to arise directly from the body wall (Fig. 1.49A). They are often reddish in colour and may be tightly coiled on the collecting sieve.

The distinctly grooved prostomium is a short, blunt cone and the peristomium forms a complete ring (Rouse & Pleijel in press; in contrast to Rouse & Fauchald 1997 who suggested that the peristomium was reduced to lips around the mouth). Antennae and palps are absent. The nuchal organs comprise a pair of dorso-lateral pits. The longitudinal muscles form distinct bundles. Segmentation is distinct. The first segment lacks parapodia and chaetae and is longer than the second segment (Fig. 1.49A) which carries the first chaetae. In a variable number of anterior chaetigers, both parapodial rami, bearing short truncate lobes, may be deeply recessed into the body wall; tori replace these lobes in more posterior chaetigers. Dorsal and ventral cirri, and epidermal papillae are absent; 'branchiae' are also considered absent although extensions of the posterior body wall, in some species, may have a respiratory function (Fig. 1.49D). Pygidial cirri may be present or absent; when present their number varies in different taxa. Lateral organs are present, and dorsal cirrus organs have not been observed and are presumed to be absent. A simple axial eversible pharynx (= proboscis) is present. A gular membrane is situated between chaetigers 4 and 5, and the gut is a straight tube. Metanephridia are present; the nephridia and coelomoducts are entirely separated, the latter appearing only at sexual maturity (Eisig 1887; Goodrich 1900, 1945). The number of segmental organs is variable. A circulatory system and heart body are lacking. Aciculae are absent; other chaetae include capillaries and hooded hooks. Capillary chaetae (Fig. 1.49H) and hooded hooks (Fig. 1.49I, J) occur on both rami on a variable number of anterior chaetigers; posteriorly, hooks are present on both rami. The hooks are small and in a single row on each torus (Fauchald 1977). This definition is based upon that of Fauchald & Rouse (1997).

The first capitellids to be described were placed in the clitellate genus *Lumbricus*. The genus *Capitella* was described by de Blainville (1828) and the capitellids were recognised as a distinct family among the polychaetes by Grube (1862). The family has always been considered to be related to the arenicolids and the maldanids, a relationship supported by the recent cladistic analyses by Rouse & Fauchald (1997).

Capitellids are frequently encountered in surveys and are difficult to identify. The counts of segments with differing arrangements of soft structures and chaetae, which are used frequently to identify genera and species (Fauchald 1977), have to be interpreted with care, since the distribution of various features is related to size and may change ontogenetically (Ewing 1982; Fredette 1982). The potential problems this can cause are well demonstrated by Fredette (1982) who undertook a detailed study of a population of *Heteromastus filiformis* in a colonising experiment. At his

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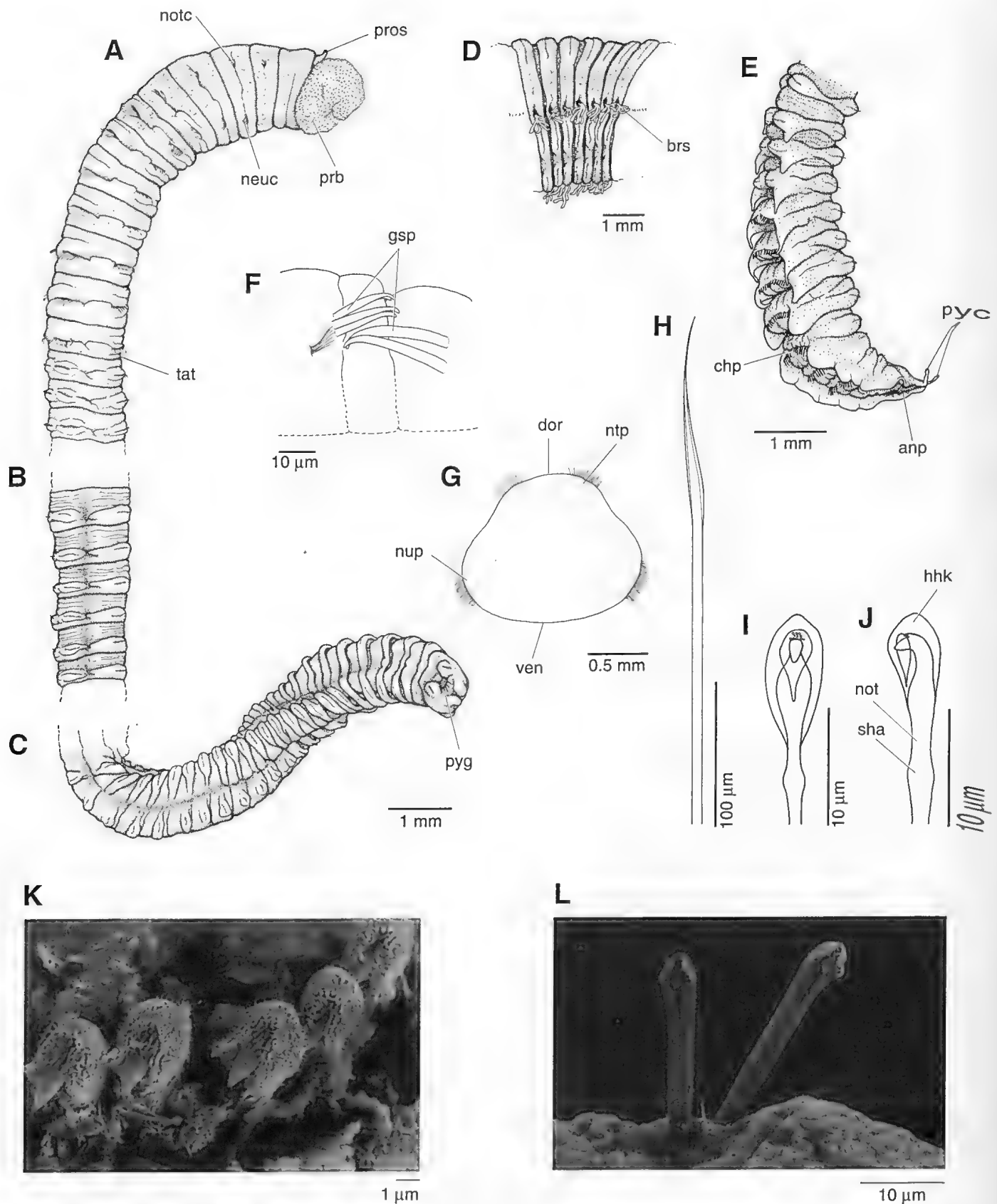


Figure 1.49 Family Capitellidae. **A–C**, *Notomastus torquatus*, parts of the entire animal: **A**, anterior end, lateral view; **B**, several mid-body segments, lateral view; **C**, posterior end, latero-ventral view. **D**, *Dasybranchus* species, mid-body/posterior segments (ca chaetigers 80 to 86) bearing 'branchial'-like structures, latero-ventral view. **E**, *Scyphoproctus towraensis*, posterior end with anal plate, lateral view. **F**, *Capitella 'capitata'*, thoracic segments (7 to 9) showing genital spines, lateral view. **G**, **H**, *Notomastus torquatus*: **G**, transverse section of body at chaetiger 10 (thoracic) showing arrangement of notopodia and neuropodia; **H**, capillary notochaeta from thoracic chaetiger 11. **I**, **J**, notochaeta of *Mediomastus australiensis*: **I**, frontal view of abdominal notopodial hook from chaetiger 23; **J**, lateral view of **I**. **K**, hooded hooks on chaetiger 12, *Mediomastus fragilis*. **L**, hooded hooks on chaetiger 14, *Mediomastus californiensis*. **anp**, anal plate; **brs**, 'branchial'-like structure; **chp**, chaetae of anal plate; **dor**, dorsum; **gsp**, genital spine; **hhk**, hood surrounding hook; **neuc**, neurochaeta; **not**, notch; **notc**, notochaeta; **ntp**, notopodium; **nup**, neuropodium; **prb**, proboscis everted; **pros**, prostomium; **pyc**, pygidial cirri; **pyg**, pygidium; **sha**, shaft; **tat**, thoracic/abdominal transition; **ven**, ventral surface. (K, L, after Warren, Hutchings & Doyle 1994) [A. Murray]

study site, two species of capitellids occurred, *Heteromastus filiformis* and *Mediomastus ambiseta*. Species of *Heteromastus* have 11 thoracic chaetigers, of which the anterior five segments have capillary chaetae and the six posterior ones have hooded hooks; in *M. ambiseta* the first four chaetigers bear capillary chaetae, as do some posterior thoracic chaetae. Juvenile capitellids were found with capillaries on the first three chaetigers and the remaining segments bore hooded hooks. Sampling of *H. filiformis* at weekly intervals confirmed ontogenetic replacement of capillary chaetae with hooded hooks on thoracic chaetigers four and five.

Similar developmental patterns have been observed by George (1984) in *Capitella* and highlight the problem of identifying juvenile capitellids. It is also likely that capitellids in the process of regenerating damaged anterior segments may also exhibit similar patterns of chaetal replacement. These studies highlight the need for a comprehensive revision of the family, a task that will require assessment of the studies by Grassle (1984) and Grassle & Grassle (1976), as discussed under reproduction. The only published comprehensive systematic study is the world revision of the genus *Mediomastus* by Warren *et al.* (1994).

No subfamily groups are recognised, although those genera with genital spines (Fig. 1.49F) are normally grouped together. Warren (1991) discussed some problems in the taxonomy of this group and synonymised *Capitomastus* Eisig 1887 and *Capitellides* Mesnil 1897 with *Capitella* Blainville 1828, although it is unclear as to whether or not these changes have been generally accepted. Fauchald (1977) summarised the major diagnostic features of each genus based largely on the schematic drawings of Hartman (1947a) in which the distribution of the different types of chaetae along the thorax are illustrated; recently-described genera also reflect these features. Characters defining these genera need re-assessment, including the usefulness of the number of thoracic chaetigers, and the distribution of chaetal types along the thorax. Another confounding problem is that several genera have been described in which posterior thoracic chaetigers have mixed fascicles of capillaries and hooded hooks, often making the demarcation between the thorax and the abdomen difficult to discern. In addition, the use of the presence of 'branchiae' as a generic character presents problems since 'branchiae' can be completely retracted in preserved individuals and may only be observed in living material, for example, in some species of *Dasybranchus*. Increasingly, detailed studies of the hooded hooks using scanning electron microscopy are being shown to yield useful specific characters (Thomassin & Picard 1972; Doyle 1991; Warren *et al.* 1994).

Fauchald (1977) listed 133 species in 36 genera, 16 of which are known only from the type species. Since then an additional six genera and 23 species have been described. In 1979, Day & Hutchings recorded 14 species from Australian waters; however *Notomastus hemipodus* has been redescribed as *Notomastus torquatus* by Hutchings & Rainer (1979) and others may have been misidentified. Since then six new species have been described from Australian waters (see Hutchings & Murray 1984; Doyle 1991; Warren *et al.* 1994) and combined with the unpublished records from the Australian Museum, the capitellid fauna may consist of at least 37 species in 18 genera.

Capitellids live in mucus-lined burrows or tubes comprising detritus and mud in fine sand/mud sediments, and are often associated with seagrass beds in Australia (Collett *et al.* 1984). They occur from estuaries to the deep sea. However,

they are often poorly represented in deep sea samples as they are easily damaged or fragment during sampling, making identifications difficult or impossible. Capitellids need to be extracted carefully from sediments to ensure that complete animals are collected, as in some species diagnostic features are only present on posterior abdominal segments. For example, in the Australian species *Notomastus torquatus* characteristic 'branchiae' are not present until abdominal chaetiger 110, and in *Scyphoproctus* the arrangement of chaetae on the terminal plaque is diagnostic (Fig. 1.49E).

Capitellids may be among the most commonly encountered polychaetes (Fauchald 1977), especially in some highly polluted habitats. Species of the *Capitella* 'capitata' complex are considered to be indicators of organic pollution, and are capable of invading areas where significant defaunation has occurred, either through natural causes or anthropogenic effects such as oil spills (Grassle & Grassle 1974).

The body is divided into a thorax and abdomen; in *Scyphoproctus* posterior segments fuse to form a cephalic plate with acicular embedded spines. The demarcation between thorax and abdomen is usually distinctly indicated by a change in the orientation of the notopodia and neuropodia, but in some genera the change appears to occur over several segments. Capitellids may have over 100 segments. In some genera, males have distinctive genital spines on segments 8 and 9. Otherwise the sexes can only be distinguished by the presence of mature gametes in the coelom.

Capitellids have well-developed circular and longitudinal muscles and complete septa which facilitate burrowing through sediments using the pharynx. The thorax is typically stout and muscular and is highly extensible. The numerous rows of abdominal chaetae may be used to grip the substratum as the thorax is extended. Fitzhugh (1991b) refuted the hypothesis of Woodin & Merz (1987) which concerned the mechanical significance of hooded hooks, and their proposal that hook orientation is highly predictive of tube type.

Two main groups of chaetae are present: (1) capillaries which tend to be restricted to anterior thoracic segments (Fig. 1.49H), and; (2) multidentate hooded hooks which may occur on the posterior thorax and on all abdominal segments (Fig. 1.49I-L). Typically, capillaries are slender and smooth winged, although Warren *et al.* (1994) showed that considerable variation in the structure of the capillaries occurs in *Mediomastus* and they are thus of some taxonomic value; similar patterns may be present in other genera. Doyle (1991) and Warren *et al.* (1994) showed that the structure of the hooded hooks may vary along the body and the dental formulae of the hooks may vary within a torus. In addition, genital and acicular spines are present in some genera.

Capitellids are considered non-selective deposit-feeders (Fauchald & Jumars 1979) which feed by everting a papillose sac-like proboscis. The structure of the pharynx of capitellids is shown by Purshke (1988a). Epithelial cells of the proboscis secrete a mucopolysaccharide (Michel 1967, 1970b, 1972) which appears to be used to agglutinate sand grains and possibly to select organic particles of low specific gravity. The ciliated papillae reported from the pharynx of *Notomastus latericeus* (Michel 1970, 1972) are presumed to be related to feeding. The structure of the salivary glands in *Notomastus latericeus* has been described in detail by Michel (1973). Gut contents always include algal fragments, suggesting that some selection may occur (Fauchald & Jumars 1979).

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The digestive system of capitellids is poorly known, although Eisig (1887) elegantly described the morphology of the straight gut. Subsequent studies by Bierdermann (1911) and Jordan (1913) indicated that the gut cells of capitellids are in part secretory.

Extensions of the body found in some species may have a respiratory function. However, since there is no circulation system in capitellids, these extensions contain cavities from the coelomic cavity and cannot therefore be accurately defined as branchiae (Rouse & Fauchald 1997).

The coelomic fluid includes coelomocytes containing haemoglobin (Dales 1963a; Dales & Dixon 1981). These coelomocytes show few organelles or lipid inclusions (Sean & Boilly 1980). Although this may indicate that these cells lack synthetic activity and have a short life span, the periphery is packed with micropinocytotic vesicles and a system of membranous vacuoles occurs just below the surface of the cell. Many species are capable of tolerating very low oxygen levels as they live in deoxygenated, organically rich sediments. Presumably oxygen levels are restored on the incoming tide.

Nuchal organs in capitellids have been studied in detail by Bullock (1965) and Mill (1978). They comprise well-developed, paired epidermal structures located dorsally on the prostomium. Schlötzer-Schrehardt (1986, 1987) suggested that these organs have a chemoreceptive function, based on ultrastructural studies of *Heteromastus filiformis*. Further details of the structure are given by Storch & Schlötzer-Schrehardt (1988).

Small pigmented rhabdomic 'ocelli' were found embedded in the prostomium of *Heteromastus filiformis* by Rhode (1986a, 1986b). He postulated that they are probably chemosensory rather than photoreceptive in nature.

Detailed studies on spermiogenesis, sperm storage and sperm morphology by Eckelbarger & Grassle (1987a) showed that species of *Capitella*, *Capitomastus* and *Capitellides* lack a well-defined testis. However, in young males, germ cells proliferate from a few specialised regions of the peritoneum of chaetiger 8; spermatogonia are released into the coelom where spermiogenesis is completed.

George (1984) photographed clusters of mature long-headed sperm 'encapsulated' in the walls in the central portion of the paired coelomoducts between chaetigers 7 and 8 in a capitellid later described as *Capitella caribaeorum* (Warren *et al.* 1986). Eckelbarger & Grassle (1987b) also observed mature sperm stored in the central portions of the paired genital ducts (coelomoducts) in nine other capitellid species. The epithelial cells lining the genital ducts are well supplied with microvilli and evidence suggests that they secrete glycogen-rich materials into the ducts (Eckelbarger & Grassle 1987b). All nine species studied have modified primitive sperm as defined by Franzén (1956) or 'introsperm' as defined by Jamieson & Rouse (1989), although the sperm do vary significantly from each other in terms of the length of their acrosome, nucleus and middle piece. Although it has been assumed by several workers (Wilson 1933; Hartman 1947a; Reish 1974) that capitellids may copulate or produce spermatophores, this was not apparent in any of the nine species studied by Eckelbarger & Grassle (1987a). Grassle (unpublished data in Eckelbarger & Grassle 1987b) suggested that some morphological 'females' raised in isolation since hatching can produce fertilised eggs and viable larvae. However, these individuals were identified as females only by the presence of hooded hooks and the absence of genital chaetae in the notochaetal bundles of chaetigers 8 and 9.

Females isolated for periods up to 2 weeks sometimes produce viable larvae, so some sort of short-term sperm storage can occur.

In the laboratory, Eckelbarger & Grassle (1987b) found that newly secreted brood tubes containing embryos in early cell division are frequently occupied by two individuals, a male and a female, and they assumed that some sort of pseudocopulation occurs. Successful *in vitro* fertilisation has also been reported for some species (Wilson 1933; Grassle & Grassle 1984) suggesting that copulation and spermatophore production may occur in the family, but not universally. Sperm production was low in all nine species investigated, but all oocytes produced were fertilised, regardless of whether 50 or 10 000 eggs were produced. Eckelbarger & Grassle (1987a) suggested that in some species, sperm are stored in the genital ducts of the female and fertilise the coelomic eggs as they pass through the ducts to the outside. As egg laying occurs within the tube of the female, the need to produce large numbers of sperm is minimised.

Eisig (1878, 1887) stated that spermatophores which are held within the male genital ducts of *Capitella* species are transferred to the female during copulation; once within the female they would disintegrate, releasing sperm into the coelom where fertilisation occurs. This is in contrast to the studies by Eckelbarger & Grassle (1987a) who observed only the presence of mature sperm in the genital ducts of both sexes in *Capitella* species 1. George (1984) reported sperm accumulation in vesicles in the walls of the coelomoducts of a species of *Capitella* in which all individuals are self-fertilising hermaphrodites, although George suggested that they may be protandrous. The encapsulated sperm are from another individual and the surrounding tissue is acting as a seminal receptacle until the sperm are required for inseminating the eggs. For many capitellid genera no information is available on spermatogenesis.

Eckelbarger & Grassle (1983) investigated the development of ovarian follicle cells and mature eggs in four of the sibling species of *Capitella* recognised by Grassle & Grassle (1976). They found distinct and consistent morphological differences which paralleled those found by Grassle & Grassle (1976) in terms of the amounts of lipid and glycogen present, which is uncommon for polychaetes. The relative differences in the amount of lipid and glycogen stored in the ovarian follicle cells presumably reflects the differences in types and quantities of yolk material stored in the eggs. In turn, this will have a significant effect on embryogenesis and larval development, particularly when egg size and larval development vary so widely between these sibling species. The ovaries of these species are all paired, sac-like organs suspended by mesenteries in the ventral coelomic cavity throughout the mid-body segments as they are in *Capitella caribaeorum* (George 1984; Warren *et al.* 1986). Each ovary consists of a sac (follicle) in which the oocytes complete vitellogenesis. Oocytes are then released into the coelom.

Warren *et al.* (1994) recorded that the diameter of mature oocytes is consistent within a species of *Mediomastus*, and the range of oocyte means found within this genus are smaller than those recorded within the genus *Capitella*.

Two populations of *Capitella* studied in detail in British Columbia by Qian & Chia (1991) varied extensively in fecundity, egg size and adult size. The authors suggested that this reflects genetic variation, which allows the population to respond to changes in the environment. For example, 90% of sibling offspring from a single female fed on different diets responded by modifying their growth rate, fecundity, egg size and egg energy content; in the remaining 10%, these variables

remained similar to those of the mother. This seems to indicate that reproductive characteristics are genetically based.

Subsequent work on these populations showed that the average number of spawnings per lifetime varied from 3.2 ± 0.95 (range 2 to 5 times) and the interval between spawnings was about 30 days (Qian & Chia 1992a). Total fecundity ranged from 398 to 3862, with a hatching rate of about 79%. Thus a single female could produce about 1650 juveniles during its lifetime. Fecundity changed with age; later broods were smaller than earlier ones. This is the reverse of that found by George (1984) for *C. caribaeorum* (described by Warren *et al.* 1986). By producing more and larger eggs at a younger age, animals can establish a new population in a new habitat more rapidly than species which breed at a later age. Certainly the studies by Grassle & Grassle (1976) indicated that *Capitella* species can rapidly colonise new habitats. Other studies on *Capitella* have shown that sibling individuals can exhibit either planktotrophic or lecithotrophic development, and that the time taken to reach sexual maturity ranges from 45–120 days (Qian & Chia 1992b).

Juvenile mortality of *Capitella* species on mud flats is high. Qian & Chia (1994) suggested that predation is a major factor affecting the recruitment and population dynamics of this group. They also found that laboratory studies of growth rates, and other parameters were similar to those found *in situ* in the field.

Some capitellids (for example, *Capitella* species) build tubes at or near the surface of the sediment, whereas others (for example, *Heteromastus filiformis*) build horizontal or vertical tubes or burrows extending some 150 mm beneath the surface. These tubes maintain contact with the surface and allow the worms to feed in black anoxic muds, obtaining oxygen from the overlying waters through irrigation of the burrow (Linke 1939; Schafer 1962). Some species, such as *Notomastus latericeus*, are tubicolous as juveniles, but become free-living as adults (Wilson 1937). *Capitella ovincola* lives in the egg masses of squids and is reported as feeding on the jelly in which the eggs are embedded without harming the developing squid embryos (Hartman 1947a; MacGinitie & MacGinitie 1968).

Several species of *Capitella* may be present in a small area (Grassle & Grassle 1974, 1976) and Fauchald & Jumars (1979) suggested that the reported lack of selectivity in the diet of capitellids may be due to sibling species being confused. Some members of the *Capitella* 'capitata' complex can be maintained in the laboratory on a diet of the algae *Enteromorpha* species, or on alfalfa powder (Reish 1957a). *Capitella* species may also be coprophagous and under culture conditions can eat up to 19% of its body weight in faecal pellets within a 48 hour period (Frankenberg & Smith 1967). George (1984) raised a species of *Capitella* to sexual maturity on agar alone. *Capitella* 'capitata' can also take up dissolved primary amines from the surrounding waters (Stephens 1975). All these studies illustrate that the selectivity of species of capitellids may have been underestimated.

Fauchald & Jumars (1979) suggested that despite many capitellids being tubicolous, they are usually motile deposit-feeders. Although some species such as members of the *Capitella* 'capitata' complex may be relatively non-selective, others such as *Notomastus latericeus* and *Dasybranchus caducus* may be more selective. Particle size and composition may be important environmental parameters for these less opportunistic species.

Capitella species have been used extensively to investigate the rates of nutrient uptake and assimilation, as they are easy to raise in the laboratory. In experiments using a variety of food types ranging from commercially available fish flakes to benthic diatoms and summer and winter detritus, Marsh *et al.* (1989) showed that differences in growth rates were related to nitrogen content. Levels of amino acids were also critical. Also, they found that juvenile worms grew on spring detritus, but not on summer detritus, indicating the probable importance of micronutrients (polysaturated fatty acids, amino acids) for the growth of juvenile *Capitella* species in the field; further, worms did not actively select some foods over others. Given the sensitivity of juvenile growth rates to 'food' availability and the importance of these growth rates in determining juvenile recruitment and mortality in laboratory populations (Grémare *et al.* 1988b) and field communities (Marsh 1988), the nutrition of newly settled juveniles may be an important factor controlling the seasonal dynamics of opportunistic deposit-feeders.

Grassle & Grassle (1974, 1976) described the recovery of *Capitella* 'capitata' populations after a major oil spill. Dense populations of *C. 'capitata'* re-established rapidly; at one stage, densities of 400 000 worms per m² were recorded, although these populations subsequently crashed. Grassle & Grassle (1974) considered this species to be opportunistic; it has been found in every part of the world where benthic studies have been undertaken. However, Grassle & Grassle (1976) provided evidence that populations of *Capitella* in Massachusetts are actually a species complex comprising as many as six sibling species, based on differences in life histories, reproductive modes, morphology and enzymes. They characterised the morphology and life histories of each of the species, which are, morphologically, very difficult to distinguish using traditional characters. However, differences are evident in the size of the mature oocytes, the number of eggs within a brood and the time that the larvae spend in the plankton.

Grassle & Grassle (1976) were able to maintain these species over several generations in the laboratory. In the field, up to five species may occur at one time and place. They suggested that the six species of *Capitella* present in this area represent distinct temporal adaptations to disturbed environments, based partly on their dispersal capabilities and partly on the relative length of their breeding seasons. Additional studies on the differences between these species with regards to form and number of genital spines, sperm and larval morphology have been undertaken by Eckelbarger & Grassle (1987b). Numerous subsequent studies have used representatives of these species (see Forbes & Lopez 1987; Grémare *et al.* 1988a, 1988b; Marsh *et al.* 1989); no formal descriptions of any of these species have been published to date.

Grassle (1984) discussed speciation in the genus *Capitella*, in which speciation has occurred without obvious changes in the morphology of the adult, and where hybridisation has not been achieved, despite many laboratory trials. Therefore, it is not possible to determine whether the isolating barriers are pre-mating or post-mating in origin. Study at sites in which two to three sibling species occur seem to indicate that the sibling species show differences in the time of their peak breeding abundances. Grassle suggested that development of these sibling species may be a response to rapid environmental change. Species of *Capitella* are typically found in disturbed or changeable environments such as an estuary or lagoon where salinity is subject to sudden change on a seasonal basis, or under polluted conditions where the normal diverse benthic community is absent. Even species found in deep-sea sediments, generally regarded as stable,

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have been found on relatively ephemeral habitats, such as wood panels (Turner 1977) and as early colonists in defaunated azoic sediments (Grassle & Grassle 1978).

Capitella 'capitata' has been regarded as an excellent indicator of organic pollution or environmental disturbance (Grassle & Grassle 1974, 1976). Coastal areas with restricted water movement where fish farms are located, often create azoic areas immediately below the fish cages. Tsutsumi (1987) found that a species of the *Capitella* 'capitata' complex rapidly colonised these areas, building up large densities as a result of a short life cycle and continual reproduction in the population. Lecithotrophic larvae were produced. Tsutsumi accepted that species in this complex are opportunistic, but suggested that such organically polluted areas represent natural habitats for this species complex, an observation confirmed by Grassle & Grassle (1974, 1976).

Dense concentrations (322 individuals/m²) of *Capitella* 'capitata' have been recorded close to a lead-zinc smelter in Spencer Gulf, South Australia (Ward & Hutchings 1996). Levels of heavy metals in these sediments were amongst the highest metal concentrations recorded in marine sediments; high organic loads were also present. Despite these conditions, *Capitella* was thriving and there was evidence that they were breeding and that they were in a self-sustaining population.

Day (1967) reported that commensals, especially polynoid scale-worms, such as *Harmothoe lunulata* and *Lepidasthenia maculata*, are common in the tubes of *Dasybranchus caducus*, which lives in deep burrows in sandy mud.

Family Cossuridae

Cossurids are small thread-like worms with numerous segments. They have a blunt head without appendages and a single long branchial filament placed dorsally on an anterior segment (Fig. 1.50A). They live in sandy mud in depths ranging from shallow intertidal areas to abyssal depths.

The prostomium is bluntly conical. The peristomium forms a distinct ring; it is sometimes referred to as an achaetous segment (Fig. 1.50A; see Fournier & Petersen 1991) and has been often confused with a segment (Rouse & Pleijel in press). Anterior appendages are lacking (Laubier 1963; Fournier & Petersen 1991). A pair of nuchal organs are present (Laubier 1963) as short dorso-lateral ciliated grooves on the posterior prostomium. The longitudinal muscles are grouped in bundles (Tzetlin 1994), and segmentation is distinct (Fig. 1.50A). The first segment and appendages are similar to subsequent ones; parapodia have similar rami (Laubier 1963) and capillary chaetae. The parapodial rami are often nearly confluent in the first or first few segments. Both notopodia and neuropodia are low, ridge-shaped or papilla-like structures; dorsal and ventral cirri are absent (Fig. 1.50B). A single median branchia (often referred to as a median

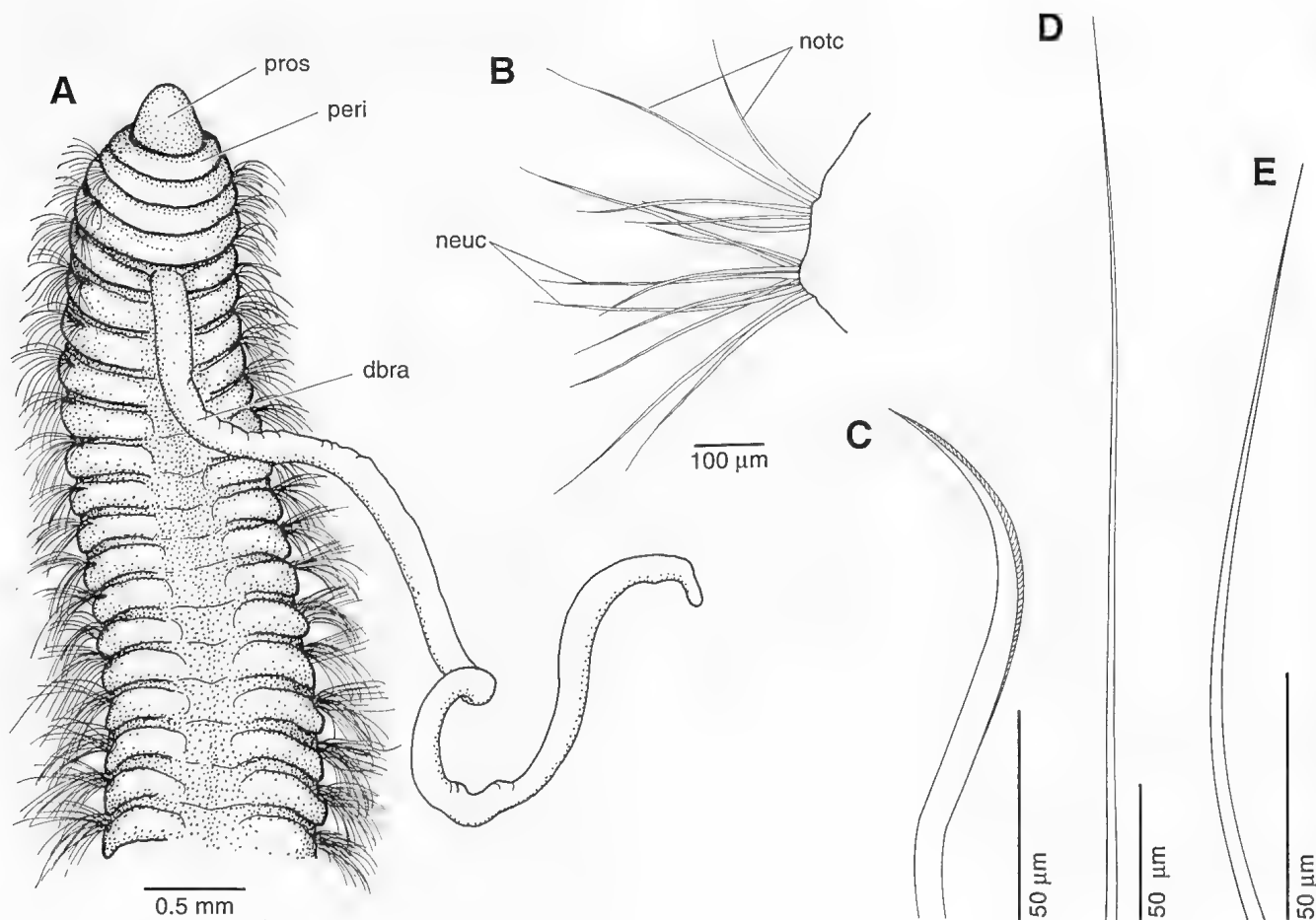


Figure 1.50 Family Cossuridae. *Cossura* species. **A**, anterior end, dorsal view. **B**, parapodium of chaetiger 18, anterior view. **C**, neurochaeta from parapodium of chaetiger 8. **D**, neurochaeta from parapodium of chaetiger 23. **E**, posterior abdominal chaeta. **dbra**, dorsal median branchia; **neuc**, neurochaetae; **notc**, notochaetae; **peri**, peristomium; **pros**, prostomium. [A. Murray]

tentacle) is present dorsally on one anterior chaetiger (Fournier & Petersen 1991). Epidermal papillae are lacking. Three or more pygidial cirri are present in some taxa (Uschakov 1955; Jones 1956). Lateral organs and dorsal cirrus organs have not been observed. Aciculae are lacking; the chaetae are limbate, slender capillaries (Fig. 1.50C–E), and in one genus, *Cossurella*, acicular spines are also present on posterior segments (Ewing 1987). This definition is based upon Fauchald & Rouse (1997).

Day (1963) erected the family to accommodate the genus *Cossura* which had originally been placed within the family Cirratulidae. In his opinion the presence of a single, median 'tentacle' (branchia) distinguished cossurids from cirratulids which have paired tentacles and branchiae. The family was placed in its own order by Fauchald (1977) and in the order Scolecida by Rouse & Fauchald (1997).

Laubier (1963) produced a key to all known species of *Cossura*; Day (1967) suggested that several of these may be synonymous as the genus has few useful taxonomic characters. Fournier & Petersen (1991) summarised the major diagnostic characters of many of the species of *Cossura*, dividing it into those species with a dorsal branchial filament arising on chaetiger 2 or 3 and those with a filament arising from chaetiger 4 or between chaetigers 4 and 5. The genus includes about 20 species. The second genus in the family, *Cossurella*, has been reviewed by Ewing (1987), who provided a key to the five known species, and transferred the single species of *Heterocossura* to this genus.

The family has been recorded in Australia, although no species have been formally described. At least four species are known to occur: one in Port Phillip Bay (Poore *et al.* 1975); at least two species from the Hawkesbury River, New South Wales (Hutchings & Murray 1984), and; one from Botany Bay and Pittwater (Wilson 1998, FAC report).

The characters that have been used to distinguish species in this poorly-known family include: the chaetiger on which the branchial filament arises; the structure and distribution of chaetae; the apparent number of achaetous 'segments' before chaetigerous segments commence, and; the presence and number of uniramous chaetigers. Fournier & Petersen (1991) emphasised that many species are incompletely known or described.

Tzetlin (1994) reported that cossurids do not build tubes; rather, they continuously produce mucus to which sediment particles adhere. Cossurids are very fragile and once extracted from the sediment usually break into fragments and die.

The body wall is thin with a poorly developed muscle layer (Rouse & Tzetlin 1997). Cossurids have an anterior muscular thorax and a posterior weakly muscularised abdomen (Tzetlin 1994). In *Cossura* cf. *longocirrata*, the thorax consists of 20–22 chaetigers and has a diameter of 350–400 μm . Beneath the epidermis and basal lamina of the thoracic region lies a single layer of longitudinally arranged muscle cells. In the anterior thoracic region, the longitudinal muscles are arranged into two ventro-lateral bands and a single dorsal band (Tzetlin 1994), whereas, posteriorly they form four longitudinal, two dorso-lateral and two ventral bands. Circular muscles are poorly developed and have been only observed by Rouse & Tzetlin (1997) in the areas of inter-segmental fissures. In these areas, and where the parapodial muscle complexes are absent, the dorsal and ventral bundles of longitudinal muscles on each side are fused. Oblique muscles are restricted to the regions of the parapodial complexes.

In the thoracic region, the body wall consists of two groups of cells, those attached only to the basal membrane of the epidermis and those attached to the basal lamina of the gut. Coelomocytes and coelenchyme were not observed by Rouse & Tzetlin (1997) in this part of the animal.

The abdominal region of mature females of *Cossura* cf. *longocirrata* comprises 35–43 segments and is 4–5 mm in length. The epidermis in this region is about 4–5 μm thick in addition to the 1 μm thick cuticle and is comprised of squamous cells. The cuticle consists of an amorphous collagenous matrix with no orthogonal layers of collagenous fibres. The coelom is more spacious in the abdominal region (Rouse & Tzetlin 1997) and coelomocytes are common. They are usually located along the lateral and dorso-lateral surfaces of the intestine and have an amoeboid form. Coelomocytes contain numerous granules, but their origin and functional role is unclear.

Day (1967) suggested that cossurids are deposit-feeders. They have an eversible buccal organ bearing 15 heavily ciliated tentacles attached to the roof of the buccal cavity. Tzetlin (1994) found that these tentacles consist of an outer columnar epithelial layer, within which lie two longitudinal muscle cells and two cells without contractile filaments inside a ring of basal membrane. As the buccal tentacles do not contain any coelomic space or any circular muscles they cannot be extended or contracted using hydrostatic pressure of the coelomic cavity. Tzetlin (1994) suggested that when the wide mouth is fully opened the tentacles are pressed onto the substratum, feeding currents are created by the high density of cilia, and food particles are transported along the tentacles into the mouth. In structure and position, cossurid buccal tentacles appear unique and not homologous with the similarly named structures in ampharetids and alvinellids (Tzetlin 1994).

The alimentary canal is a straight tube (Fournier & Petersen 1991) and lacks a gular membrane (Tzetlin 1994). Pygidial cirri are present on the pygidium; these may have additional lobes or processes (Fournier & Petersen 1991).

Cossurids have a weakly developed dorsal blood vessel that connects to the intestinal vascular plexus, and two distinct blood vessels are present in the branchiae. No heart body has been observed. The elongate dorsal branchial filament does not take part in feeding and is always found stretched along the trunk inside the mucous tube; presumably it has only a respiratory function (Tzetlin 1994).

Little is known about the nephridial and reproductive systems, although gametes have been recorded in the posterior part of the body (Rouse & Tzetlin 1997). Mature females usually have oocytes in all abdominal chaetigers except for the last few. Both oocytes and follicle cells are retroperitoneal and early stages of both are found in the ventro-lateral region of the intestine. The follicle cells can be easily distinguished from the germ cells by their size and shape as well as the type of cytoplasm which contains electron-dense granules (Rouse & Tzetlin 1997).

During early vitellogenesis each oocyte is encapsulated by three to four follicle cells. Initially the oocytes lack microvilli on their surface, but later in vitellogenesis, microvilli appear on both oocytes and follicle cells. Cytoplasmic branches between the oocytes and the follicle cells were observed by Rouse & Tzetlin (1997). Mature oocytes are about 100–130 μm in diameter, contain three types of yolk granules, and have a well-developed vitelline membrane. Follicular blood vessels run in the coelomic space lateral and ventral to the intestine; they are most obvious

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where the main body of vitellogenic oocytes are found. Rouse & Tzetlin (1997) did not observe oocytes with a string of nurse cells, unlike Fournier & Petersen (1991). They also found no evidence for hermaphroditism as suggested by Fournier & Petersen (1991), although there is a possibility that species may be protandric hermaphrodites.

Rouse & Tzetlin (1997) observed various stages of spermiogenesis in the abdominal coelom of males. Spermatogonia and spermatocytes were not clearly identified and only stages of spermiogenesis were observed in detail. Sperm have spherical heads 3 µm long, comprising a spherical nucleus, a conical acrosome and a simple mid-piece; the latter consists of four rounded mitochondria and an anchoring apparatus. The sperm is similar to those found in species having external fertilisation (Franzén 1956) and is classified as an ect-aquasperm (Rouse & Jamieson 1987).

Blake (1993) described *Cossura longocirrata* as a dominant member of the silty sediments off the North Atlantic coast of North America and suggested that it breeds all year, but with peaks of activity in the summer months. He found that his specimens were gonochoric. *Cossura pygodactylata*, from the Bay of Biscay, breeds between February and April (Bachelet & Laubier 1994).

The only study of cossurid juvenile development is that by Bachelet & Laubier (1994) of *C. pygodactylata* in Arcachon Bay, France. They described benthic juveniles which closely resemble adult cossurids, although segmentation is somewhat obscure. Juveniles were collected in the upper 20 mm of mud, which had a high organic content. They recorded initial densities of juveniles as high as 32 000 per m², but numbers fell dramatically over the next 1–2 months.

Family Maldanidae

Maldanids are often referred to as bamboo worms because of the similarity of their bodies to bamboo stems (Pl. 1.2). They have a blunt head which lacks appendages, very long body segments and parapodia that are reduced to low ridges which encircle the body. They are bulk-ingestors of sand particles and live on sheltered sand flats, intertidally and subtidally.

Maldanids usually have a fixed, maximum number of body segments. The head is formed from the prostomium, the peristomium and, sometimes, at least one achaetous segment (Fig. 1.51A, B). An eversible pharynx, with a simple axial or ventral buccal organ, is present; gular membrane is also present. Maldanids have paired nuchal slits and there is often a cephalic rim and cephalic keel. An anal plaque may also be present; it may have crenulations (Fig. 1.51A, C) or cirri on the margin. Each small parapodium consists of a low, rounded notopodium, which has capillary chaetae of various kinds and a neuropodium, which forms a long torus with hooks in one or two rows (Fig. 1.51A, D). The hooks have a large main fang surmounted by a series of smaller teeth; a fringe, or 'beard', usually surrounds the basal teeth. The nephridial/coelomoduct system is restricted to a few anterior segments. Maldanids are tubicolous. The tubes usually have a membranous lining and are covered with mud, shell or sand, though some 'tubes' are as simple as consolidated burrows. The tubes often extend slightly above the sediment surface.

The family Maldanidae was erected by Malmgren in 1867 to accommodate several previously described species. The family was subsequently divided into five subfamilies by Arwidsson (1907); the Euclymeninae, Lumbriclymeninae, Maldaninae, Nicomachinae, and Rhodininae. Recently

several new subfamilies have been proposed: the Clymenurinae by Imajima & Shiraki (1982a) and Notoproctinae by Detinova (1985). The family Boguidae, containing several species in two genera (Hartman & Fauchald 1971), has been relegated to a subfamily (Boguinae) of the Maldanidae (Wolf 1983). The relationships within and among the various subfamilies have yet to be rigorously investigated, and some revision is almost certainly required. Significant papers on the taxonomy of the family are those by Arwidsson (1907), Day (1967), Fauchald (1977) and Imajima & Shiraki (1982a, 1982b). Important papers concerning groups within Maldanidae include those of Verrill (1900) on what is now regarded as Lumbriclymeninae, and Light (1991), who revised the Maldaninae and erected several new genera. The subfamilies as diagnosed by Fauchald (1977) are used here.

Worldwide, the family comprises more than 200 described species in over 30 genera (Fauchald 1977; Light 1991), though as a whole it has not been reviewed in detail since Arwidsson (1907). Four of the eight subfamilies have been reported from Australian waters: Euclymeninae, Maldaninae, Lumbriclymeninae and Nicomachinae; this represents 13 species and eight genera (Knox & Cameron 1971; Day & Hutchings 1979; Hutchings & Murray 1984; Rouse 1990a); several others are found in the Australian Antarctic Territory and New Zealand. Maldanids are found in most marine regions, from polar areas to tropical reefs and, although they are regarded as common in continental shelf sediments they also occur in shallow sea-grass beds and mudflats as well as intertidally in algal mats.

Maldanids range in size from 3 mm to more than 200 mm. The prostomium is fused to the peristomium, which is represented by the buccal region only. A cephalic rim and keel as well as caudal plaques are present in members of the Euclymeninae and Maldaninae (Fig. 1.51B, C). A caudal plaque only is present in the Nicomachinae, and the Lumbriclymeninae lacks all of these structures. The posterior segments are collared in some maldanids, but a collar is absent in members of the Lumbriclymeninae. Hooks are arranged in single rows in the Lumbriclymeninae, Nicomachinae and some Maldaninae. The position of the anus varies from terminal in the Euclymeninae to dorsal in the Maldaninae.

A series of papers by Pilgrim (1964, 1965a, 1965b, 1966a, 1966b, 1977, 1978) on the morphology and functional anatomy of members of the Maldaninae and Euclymeninae provide the most detailed knowledge on maldanids. Pilgrim (1977) described the parapodia, chaetae and locomotion in a variety of maldanids.

Both simple axial proboscides and ventral buccal organs occur within the family, but the systematic importance of these structure has yet to be fully investigated (Orrhage 1973). Pilgrim (1965b, 1966a) described the morphology of the buccal apparatus and alimentary system of a number of maldanids. Feeding mechanisms of maldanids have been reviewed by Fauchald & Jumars (1979). More recent anatomical and ecological studies have been provided by Kudenov (1977a, 1978, 1982), Tzetlin (1989) and Green (1994). Hughes (1979) described the feeding modes of three sympatric species of maldanids in Canada. Each species fed at different levels in the sediment; all were non-selective deposit-feeders. Although most maldanids are deposit-feeders, McDaniel & Banse (1979) described a novel way of filter-feeding by *Praxillura maculata*. Mangum (1962) described how populations of two different species can show

either orange or green colouration. It would seem that this is caused by retention of the green pigment mesobiliverdin, from algae the worms are ingesting with the sediment.

The circulatory system of maldanids is closed and has been described in detail for *Clymenella torquata* and *Euclymene oerstedii* by Pilgrim (1966b). In the maldanid genera *Branchioasychis* and *Johnstonia*, the posterior segments may have multiple vascularised digitiform extensions covering the segments (Fauvel 1927). These extensions are unique to these genera and are not considered homologous with branchiae in other polychaetes. These genera have not been recorded from Australian waters.

The nephridial organs of maldanids were classified as mixonephridia by Goodrich (1945) with little apparent evidence. Pilgrim's (1978, fig. 2b) illustration does, however, most resemble a mixonephridium. Four anterior pairs of mixonephridia occur in chaetigers 5 to 9 or 6 to 10 in two species of maldanid studied in detail by Pilgrim (1978). This resembles the situation found in arenicolids, though it appears that in maldanids they all are involved in

reproduction, whereas in arenicolids the anterior pair is excretory only. There have been no physiological studies on maldanid excretion.

Information on reproduction in maldanids is available for representatives of Euclymeninae, Nicomachinae and Boguinae (see reviews by Rouse 1992a, 1992b). Sexual reproduction varies from broadcast spawning and free-swimming lecithotrophic larvae to intratubular brooding of directly-developing larvae. No feeding larvae have been documented to date in the Maldanidae. The four species of Australian Maldanidae where reproduction has been studied in detail are all members of the nicomachine genus *Micromaldane*. Rouse (1992a, 1992b) found that all are brooders, with eggs being fertilised in the tube in batches of two to more than 30 (depending on the species). The directly-developing larvae crawl from the tube as juveniles. Read (1984) studied a New Zealand population of *Axiiothella serrata* and suggested that this species also broods its larvae; it also has sperm of the 'ent-aquasperm' type (Jamieson & Rouse 1989). Asexual reproduction has been reported in the family for one species (Tzetlin & Markelova 1986), but has not been recorded for any Australian species studied to date.

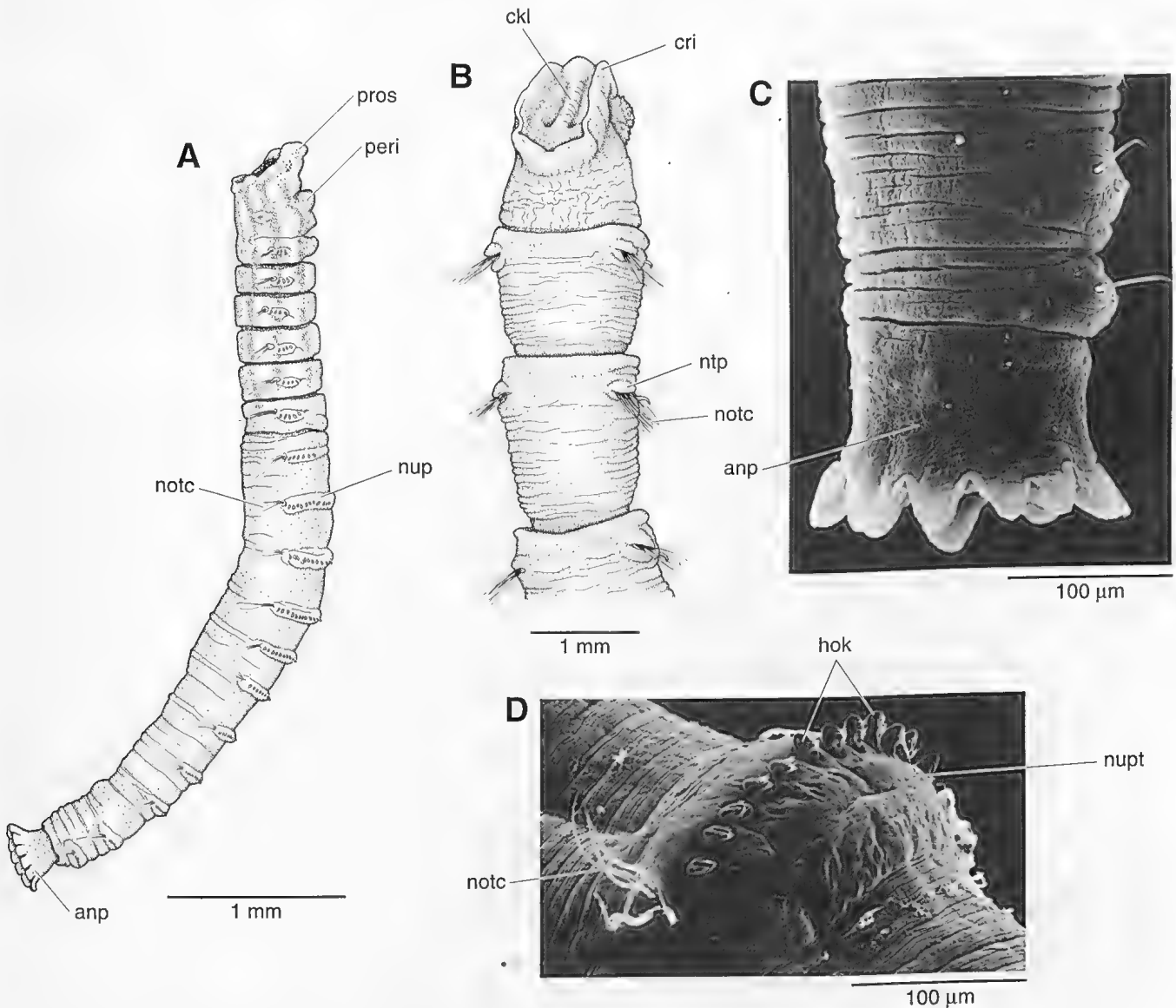


Figure 1.51 Family Maldanidae. **A**, entire animal of *Micromaldane pamela* (subfamily Nicomachinae), lateral view. **B**, anterior end of *Euclymene trinalis* (subfamily Euclymeninae), dorso-lateral view. **C**, anal plaque and several last body segments of *Micromaldane nutricula*, dorso-lateral view. **D**, neuropodial torus with hooks of *Micromaldane pamela*. **anp**, anal plaque; **ckl**, cephalic keel; **cri**, cephalic rim; **hok**, neuropodial hooks; **notc**, notochaetae; **ntp**, notopodium; **nup**, neuropodium; **nupt**, neuropodial torus; **peri**, peristomium; **pros**, prostomium. [A, B, A. Murray; C, D, G. Rouse]

1. CLASS POLYCHAETA

Maldanids usually live in soft sediments and can be major components of the benthos (Hughes 1979). Most species are subtidal and their biology is largely unknown. Some intertidal species such as *Clymenella torquata* have been studied overseas (Newell 1951). Recruitment and population dynamics of *Axiiothella serrata* from New Zealand has been studied in detail by Read (1984) and individuals appear to have a lifespan of 3–4 years. Four species of *Micromaldane* described from Australia can all be found intertidally (Rouse 1990a). These are all relatively small species reaching at most 8 mm long, and live in sandy tubes attached to the bases of turfing algae and ingest sediment. The tubes of maldanids have a membranous lining covered with mud, shell or sand, although some tubes are little more than consolidated burrows. Regeneration has been reported in maldanids (Moment 1951; Clavier 1983). All maldanids have a fixed maximum number of segments and if they lose part of their body to predators they can regenerate the exact number of segments lost. Maldanids can regenerate the anterior or posterior ends of the body (or both simultaneously). However, the mid-region contains critical segments (often 8, 9 and 10) that if lost will result in the death of the worm (Clavier 1983). Maldanids are parasitised by crustacean copepods (Bresciani 1963; Capaccioni *et al.* 1993), as well as gregarine and coccidian protists (Ormieres 1975; Landers & Gunderson 1986; Landers 1991). No parasites have been recorded as yet from Australian maldanids.

Rouse & Fauchald (1997) found the Maldanidae to be the sister group to the Arenicolidae based on the distribution of the nephridial organs and their shared lack of lateral organs with respect to other members of the Scolecida (Fig. 1.47). The monophyly of the Arenicolidae is not well supported and arenicolid taxa such as *Branchiomaldane* show many similarities with both families (Mesnil 1898). Any cladistic analysis of the Maldanidae should probably consider the arenicolids as well. So little is known about Australian maldanids that no biogeographical conclusions can be drawn. The Australian endemics *Micromaldane pamela* and *M. nutricula* have been recorded from Sydney to the southern Queensland coast, but not on the Great Barrier Reef, where other species of *Micromaldane* are found (Rouse 1990a). There is no trace of maldanids in the fossil record.

Family Opheliidae

Opheliids have a fusiform-shaped body with relatively few, indistinct segments and poorly developed parapodia. The head is compact and lacks appendages. Some species are iridescent. They burrow head downwards in sand or mud.

The prostomium is usually conical, and a distal palpode is present in some taxa (Fig. 1.52A). The peristomium is reduced and fused with the prostomium or forms a distinct ring (Rouse & Pleijel *in press*). Antennae and palps are absent. The nuchal organs are paired and eversible. The longitudinal muscles are grouped in bundles, and segmentation is usually not distinct. The first segment is similar to subsequent segments, and all parapodia are similar. Both parapodial rami are small, and in most taxa the notopodium is slightly smaller than the neuropodium (Brown 1938), but in *Travisia*, both rami are well developed and large. The branchiae are single filaments closely associated with the notopodium (Fig. 1.52B). Dorsal and ventral cirri and epidermal papillae are lacking. The pygidium is either hood-shaped without internal and marginal cirri or hoodless with multiple cirri (Fig. 1.52A). Lateral organs are present, but dorsal cirrus organs have not been observed. The buccal organ is axial and simple, and has a sac-like eversible proboscis. A

gular membrane is present and the gut is a straight tube. The circulatory system is closed and a heart body is present. Aciculae are absent, and all the chaetae are variously ornamented capillaries (Fig. 1.52C, D). Both metanephridia and protonephridia are reportedly present in different genera. Goodrich (1945) called the segmental organs mixonephridia. Brown (1938) found that nephridia were limited to three segments in *Ophelia*, but other genera have many pairs of nephridia. This definition is based upon that of Fauchald & Rouse (1997).

Opheliids were first described by Savigny (1822) and grouped among the sedentary forms, despite the lack of tubes and distinct body regions in some (for example, *Ophelina*). The family was recognised by Grube (1850) and its name given the correct form by Malmgren (1867). The opheliids are usually aligned with the scalibregmatids, which the *Travisia*-like taxa resemble in particular in their simple parapodia with capillary chaetae and their distinct epidermal rugosity (Ashworth 1901).

A brief review of the family is found in Fauvel (1927), and Støp-Bowitz (1945) provided a key to Norwegian species including five species of *Ophelina*. Tebble (1953) reviewed the species of *Ophelia*. Subfamilies are not generally recognised; Hartmann-Schröder (1971) recognised a series of subfamilies, but this has not been followed by most subsequent workers, including Fauchald (1977). However, Bellan *et al.* (1990) undertook a phenetic analysis of the 12 described genera and confirmed the subdivision into three subfamilies as originally proposed by Hartmann-Schröder (1971); these are the Ophelininae, Opheliinae and Travisinae. A subsequent paper on the Travisinae by Dauvin & Bellan (1994) suggested that the subfamily contains only the genus *Travisia* and that the genera *Dindymenides* and *Kesun* should be synonymised with *Travisia*. They also provided a key to all 27 species of *Travisia*, as well as a synthesis of the relationship between species and their biogeographical distribution.

In 1977, Fauchald listed 11 genera of opheliids represented by 138 species. Since then, one additional genus, *Lobochesis*, has been described from Australian waters (Hutchings & Murray 1984) and 14 new species, of which four are from Australia: *Lobochesis bibranchiata*, *L. longiseta*, *Ophelia elongata* and *O. multibranchia* (Hutchings & Murray 1984). In addition, nine other species were reported by Day & Hutchings (1979) as having been recorded from Australian waters, although several of these are based upon a single record and require further investigation. Also, many of these species have a supposedly wide distribution which, in reality, may reflect a number of different (undescribed) taxa.

Opheliids have been studied extensively by ecologists working on sandy beaches (see Tamaki 1985a, 1985b), estuarine conditions (Harris 1991), and also in the deep sea (see Jumars 1978). In Australia, Dexter (1984) studied the fauna of exposed sandy beaches in the Sydney region, including several species of opheliids described by Hutchings & Murray (1984). All species are marine, although in Australia they also occur in the marine parts of estuaries such as the Hawkesbury River. Opheliids occur from the intertidal zone to deep water.

Species of opheliids may be present in very large numbers. For example, Dales (1952a) recorded densities of an intertidal species of 10 000–11 000 per m²; at such densities they must have considerable impact on the bioturbation of the sediment.

Opheliids may be one of three basic shapes: short, thick and grub-like (as in species of *Dindymenides* or *Travisia*); very slender, nearly smooth and torpedo-shaped (as in species of

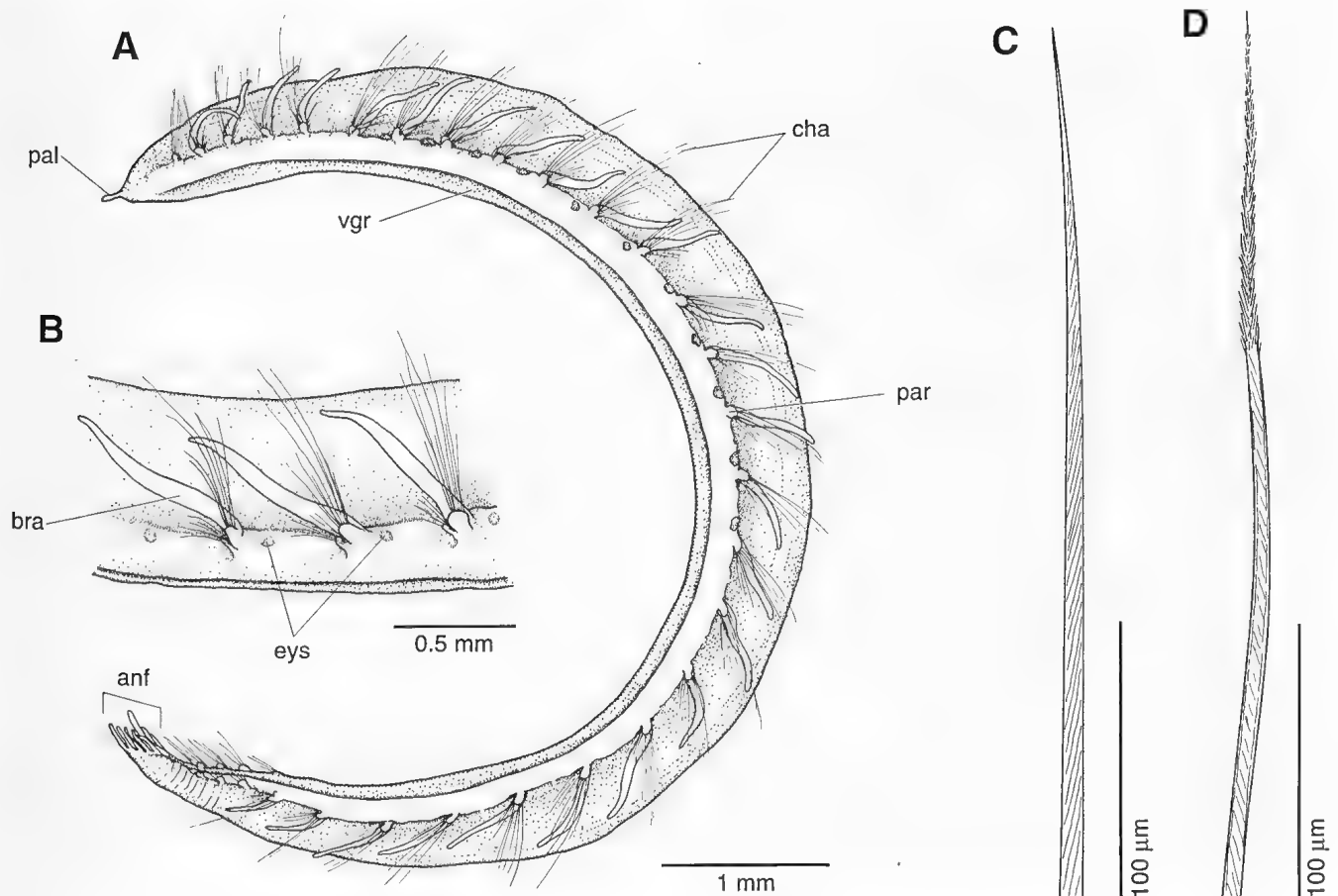


Figure 1.52 Family Opheliidae. **A–C**, *Armandia intermedia*: **A**, entire animal, latero-ventral view; **B**, mid-segments showing branchiae and parapodia, lateral view; **C**, capillary chaeta from parapodium of chaetiger 9. **D**, capillary chaeta from parapodium of chaetiger 18, *Travisia cf. concinna*. **anf**, anal funnel; **bra**, branchia; **cha**, chaetae; **eys**, eye spots; **pal**, palpode; **par**, parapodium; **vgr**, ventral groove. [A. Murray]

Armandia and *Polyophthalmus*), preserved specimens of which are often C-shaped (Fig. 1.52A); or, anteriorly inflated and posteriorly cylindrical or narrow (as in species of *Ophelia*, *Euzonus* and *Lobochesis*). Species range from a few millimetres to about 30 mm in length.

Genera are separated on body shape, the degree of development of the ventral groove, the nature of the pygidium, and the presence or absence of branchiae and lateral eye spots. Specific characters include those above plus the number of segments and the arrangement of the branchiae. The ventral groove is well delineated in all genera except *Travisia*, and is formed from strongly developed longitudinal ventral muscles, which form the ridges of the groove. The groove may extend along the whole length of the body or be restricted to the posterior half. The body is fusiform and segments are poorly differentiated, and therefore the best method for determining the numbers of segments is to count the bundles of chaetae. The number of segments varies between 30 and 60, and for a given species is fairly constant, especially in *Armandia* and *Ophelia*. The parapodia are biramous and the parapodial lobes and their chaetae rarely provide diagnostic characters. Most of the chaetae are very narrow winged capillaries (Fig. 1.52C, D). The branchiae are typically cylindrical projections which arise postero-dorsally to the notopodia and are normally well developed (Fig. 1.52B); they are absent in *Polyophthalmus*, *Tachytrypae* and some species of *Ophelia* and *Ophelina*. Lateral eye spots are restricted to particular segments in the middle of the body and occur at segmental intervals between the parapodia (Fig. 1.52B; Day 1967).

Storch (1988) found the epidermis in *Travisia* to be stratified at the ultrastructural level; this is unusual amongst invertebrates. Below the cuticle, which has an electron dense outer layer and many membrane-limited vacuoles, is a range of cells, some of which have bundles of tonofilaments, others contain vacuoles, Golgi fields and many inclusion bodies. Extensive intercellular spaces occur between these cells, which rest on a well-developed basal nerve cell plexus. Below this is a thick collagen layer which contains many nerves and single fibrocytes.

Few studies have been carried out on polychaete muscular systems (see for example, Lanzavecchia, de Eguileor & Valvassori 1988). However, one opheliid, *Ophelia bicornis*, has been studied by Pilato, D'Urso & Sperlonga (1978). They found in a single segment 59 muscles each with a different function, indicating the complexity of polychaete musculature.

The structure and method of pharyngeal eversion has been partially described by Dales (1962a). Opheliids have one to three intact anterior septa. It appears that species with a single septum have a backwardly extending septal pouch, which can respond to changes in fluid pressure in the anterior part of the coelom; when there are several septa the most anterior ones are more muscular. The entire pharynx lies in front of the most anterior septum, and retractor muscles, which arise from the body wall just in front of the first septum, attach to the pharynx (Dales 1962a). Eversion of the pharynx is presumably effected by pumping coelomic fluid into it.

1. CLASS POLYCHAETA

Opheliids are considered non-selective deposit-feeders (Blegvad 1914; Hunt 1925; Yonge 1928; Retière 1967). Guerin (1971) indicated that *Polyophthalmus pictus* feeds on dead copepods and other organic debris, strongly suggesting selectivity in this species. *Euzonus* species feed primarily on organic matter adsorbed onto sand grains (Fauchald & Jumars 1979), but do not appear to be able to digest diatoms (McConnaughey & Fox 1949). Fauchald & Jumars (1979) suggested that opheliids are more selective in their food sources than implied in the literature.

McConnaughey & Fox (1949) calculated that the turnover rate for *Euzonus* was about 84 gm of sediment per year per worm. Based on the organic content of the sand and the faecal matter they suggested that the worms have about a 96% absorption efficiency, a very high rate considering that the passage time of sediment through the gut was only about 15 minutes.

Some studies concerning the substances absorbed and stored during digestion have been undertaken (see Fox *et al.* 1948). *Thoracophelia mucronata* is able to breakdown extracellular chlorophylls and obtains its nutrition from the colloidal organic matter adsorbed onto sand particles.

In all opheliids studied to date, a heart body is present in the circulatory system (Picton 1899; Brown 1938; Hartmann-Schröder 1958). Presumably, the parapodial branchiae are normally used in the uptake of oxygen, although Dales (1952a) suggested that when worms are uncovered by the tide the rectum may be used as a type of lung. At this time the worm burrows upwards, posterior end first, forming a small hole above themselves, allowing access to air; the head is down in the sand. The elongated chaetae present posteriorly may break the surface and prevent sand grains from falling onto the area around the anus during respiration. Fox *et al.* (1948) showed that opheliids contain haemoglobin free in the blood vessels in a colloidal solution. Dales suggested that the large amounts of haemoglobin present in some intertidal species may allow the worms to survive during heavy storms when they must burrow deep into the sediments to avoid being washed away.

Goodrich (1945) stated that the segmental organs are mixonephridia; however, both metanephridia and protonephridia have been described in the family. McConnaughey & Fox (1949) reported protonephridia in *Euzonus mucronata* (as *Thoracophelia*) and Hartmann-Schröder (1958) described metanephridia in several genera. The distribution of the nephridia appears to vary between genera, for example, in *Ophelia* metanephridia are restricted to three segments (Brown 1938), whereas in *Travisia* and *Ophelina* up to 27 pairs are present (Hartmann-Schröder 1958). Based on the studies by Bellan *et al.* (1990), Rouse & Fauchald (1997) suggested that the protonephridial condition is a secondary feature.

Hermans (1969) investigated the structure of the prostomial photoreceptors and the segmental eye spots, or ocelli, in *Armandia*. The eye spots consist of a single photoreceptor cell with about 15 sensory processes. These processes are composed of a central core of neurofibrils surrounded by a mitochondrial layer and a compact array of microvilli. The sensory processes project and nearly fill the ocellar cavity, which is lined by squamous glial cells. Enclosing the photoreceptor is a pigment cup made up of about 30 cuboidal cells full of brown pigment. These cells form a mesothelium which is in direct contact with the coelom and is separated

from the glial cells by a basal lamina. Slender muscles traverse the coelom and pass between the cells of the pigment cup. The prostomial photoreceptors are composed of microvilli rather than folds containing labyrinthine tubular infoldings of the cell surface as earlier reported by Hermans & Cloney (1966). Such microvilli have been referred to as rhabdomeres (Eakin 1963). No studies appear to have been undertaken on the mechanisms by which opheliids respond to light. Behavioural observations have shown that *Armandia brevis* responds negatively to light during the benthic stage and positively during the epitokous phase of its life history.

Opheliids have lateral organs (Rullier 1951; Hartmann-Schröder 1958) and multiple pygidial cirri which are presumed to have a sensory function (Brown 1938). The ultrastructure of the nuchal organ in one opheliid species, *Ophelia bicornis*, has been studied by Nowak (1978). The dendrites of the primary sensory cells terminate in the olfactory chamber (named by Whittle & Zahid 1974) as enlarged sensory bulbs bearing a few microvilli and one sensory cilium.

In opheliids, the sexes are separate and occur in about equal numbers (Dales 1952a). The reproductive strategies of four species of opheliids have been investigated. Wilson (1991) stated that all four undergo mass spawning, two produce planktotrophic larvae (Dales 1952a) and two produce lecithotrophic larvae (Wilson 1948; Riser 1987). Wilson (1991) incorrectly cited Riser as working on *Ophelia bicornis*, whereas he worked on *O. verrilli* which produces lecithotrophic larvae. An Australian species of *Armandia* has ecto-aquasperm, which appears to be the typical type found in this family (Jamieson & Rouse 1989). However, for most opheliids no information on reproduction is available.

Riser (1987) suggested that *Ophelia verrilli*, at least, can live up to 6 years of age and reported spawning in spring and early summer when they reached 2 years of age. Oocytes and sperm resemble those found by Wilson (1948) for another species of *Ophelia*. After external fertilisation, cleavage occurs and a morula is usually developed within 72 hours, although faster rates are obtained with higher temperatures. After about 12 days, when two fully-formed chaetigers are present, the larva attaches itself to a sand grain; at this stage the gut is full of yolk. Riser (1987) recognised three stages of juvenile development. In the first stage (up to 18 chaetigers), juveniles actively feed on diatoms and foraminiferans. Second stage juveniles are characterised by a slight increase in the number of chaetigers and chaetae per parapodium. During the third stage of development, the blood vascular system is complete, the worms become pinkish in colour like the adults, and lose most of their adhesive capabilities; the nuchal organ develops motile cilia and, branchiae and nephridia develop and become functional. However, Riser (1987) was unable to resolve the relationship between the numerous juvenile nephridia and the adult complement of nephridia.

Ophelia bicornis has a short-lived, free-swimming larval stage (Wilson 1948). Once the larvae are about 6–8 days old and has three chaetigers, larval behaviour changes. The larva no longer swims towards light and when ready to metamorphose it will attach itself to a sand grain using its anal papillae and its parapodial lobes. The apical cilia, prototroch, telotroch and neurotroch disappear and all powers of swimming are lost. The body elongates and the worm crawls amongst the sand grains and gradually develops into an adult over a period of several months.

Dales (1952a) found that a *Thoracophelia* species followed the same pattern of larval development as that of *Ophelia*, but that development was far more rapid. Breeding was prolonged, occurring throughout summer and he suggested that the worms take more than 1 year to mature and that individual worms live for several years, breeding annually.

Although oogenesis has not been studied in opheliids, some work has been done on spermatogenesis (Ochi *et al.* 1977). Several spermatogonia form a dense cluster and are released from the gonad at an early stage; the rest of development occurs in the coelom. Proliferation of spermatogonia occurs in these clusters and cytoplasmic bridges occur between the spermatogonia. As the latter continue to grow and proliferate, the cytoplasmic bridges move into the centre to form a large spherical bulge composed of a central mass of cytoplasm referred to as a cytophore. Meiosis and successive spermiogenesis take place within the cytophore. Sperm disc formation ends in morphological maturation of the spermatozoa. The cytophore is thought to help in synchronising the various stages of development of the sperm (Sawada 1984). The resultant sperm is regarded as being of the primitive type (Franzén 1956), although only one species of opheliid has been investigated.

Riser (1987) found that different life stages of *Ophelia verrilli* occupy different levels on the beach, with large adults at the lowest levels and the majority of small adults and pre-adults living at mid-tide levels. Wilson (1952) suggested that species may spawn on a rising tide and thus, avoid oocytes being washed out to sea.

In Japan, Tamaki (1985a) found that from spring to summer, a discrete settlement of *Armandia* larvae occurred every spring tide to an intertidal sand flat. As the worms became older and larger they migrated seawards. There is also some evidence that populations of other polychaete species may influence the settlement of juvenile *Armandia* (Tamaki 1985b).

Dauvin & Bellan (1994) investigated the biogeographical distribution of the genus *Travisia* (with which they synonymised *Kesun* and *Dindymenides*). They found that of the 27 species, 21 are found on the continental shelf and 14 of these are restricted to the shelf at depths less than 200 m. Eleven taxa occur at depths below 2500 m and three of these occur at abyssal depths. Although the genus occurs worldwide, it is particularly well represented in the Pacific Ocean with 21 species, seven species occurring in the Antarctic Ocean and 10 in the Atlantic Ocean. Sixteen of the 21 species occurring in the Pacific are restricted to this ocean. Eight species that exhibit wide geographical ranges also exhibit a wide bathymetric range.

Bellan & Dauvin (1991) have undertaken similar biogeographic studies of the genus *Ophelia*. Most of the 32 known species live in clean fine or medium sand communities in the infralittoral zone and have restricted distributions. The majority of species are restricted to the Atlantic Ocean.

In Australia, the distribution of opheliids is poorly known. Two species (*Armandia intermedia* and *Polyophthalmus pictus*) appear to be widely distributed in Australia, whereas others have a far more localised distribution; *Lobochesis longiseta*, is known only from a single beach in New South Wales (Hutchings & Murray 1984). However, the two widespread species, once investigated in detail, may include several undescribed taxa. One large undescribed species of *Armandia*, which occurs on sandy spits on the Great Barrier Reef, is an important diet item for some nesting seabirds (P. Hutchings personal observation).

Family Orbiniidae

Orbiniids are elongate, thread-like to robust worms. They have a 'ragged' abdomen, the result of the presence of dorsal branchiae and dorsally-shifted parapodia. They are deposit-feeders found from shallow tidal zones to abyssal depths.

Orbiniids have a regionated body; thoracic segments bear lateral parapodia and abdominal segments have dorsal parapodia. The prostomium lacks appendages and precedes one or two achaetigerous annuli. The ventral pharynx is unarmed and when everted is either sac-like or branched. Chaetae may be capillary, furcate or different types of spines, but rarely hooks. A putative autapomorphy of the family is the dorsal shift in the orientation of the parapodia in the posterior part of the body (Fig. 1.53A; Fauchald & Rouse 1997).

The family has been classified together with the 'errant' families (see Audouin & Milne Edwards 1834; Benham 1896), with spionid-like families under Spiomorpha (Uschakov 1955; Clark 1969), and together with Paraonidae under Orbiniida (Fauchald 1977; George & Hartman-Schröder 1985). Rouse & Fauchald (1997) placed the Orbiniidae in Scolecida, together with Paraonidae and a number of other families (Fig. 1.47).

Orbiniids were for many years classified under Ariciidae. Hartman (1942) noted that the name of the type genus, *Aricia* was invalid and proposed the replacement name *Orbinia*, upon which the new family name was based. Orbiniidae have been the subject of a few major taxonomic revisions including those of Eisig (1914), Hartman (1957), Pettibone (1957a) and Day (1973). Most of the information presented below comes from these works. Day (1977) reviewed the Australian and New Zealand orbiniids, adding seven new species and describing a new genus, *Leitoscoloplos*, to replace *Haploscoloplos*. Later Mackie (1987) reviewed all of the species assigned to *Leitoscoloplos*, adding a new species from Australia, *L. bilobatus*, and transferring *Leitoscoloplos normalis* to *Scoloplos*.

Worldwide, some 150 described species in 18 genera are arranged in two subfamilies, Orbiniinae and Protoariciinae. Both subfamilies have been recorded in Australia – the orbiniines: *Leitoscoloplos*, *Nainereis*, *Orbinia*, *Phylo*, *Scoloplos* and *Uncorbinia*; the protoariciines: *Proscoplos*, *Protoaricia* and *Protoariciella*. New orbiniid species, including the first protoariciines, were described by Hartmann-Schröder & Hartmann (1980, 1981, 1983, 1991). Several species found in Australia (for example, *Nainereis laevigata*, *Scoloplos armiger*) are purported to be cosmopolitan; however, fundamental differences in the type of larval development of various populations of '*S. armiger*' occur, suggesting that several different species are involved (Blake 1980; Plate & Husemann 1991). The monospecific orbiniine genus *Uncorbinia* has only been recorded from Australia. About 25 species have been recorded from Australian waters.

Orbiniids are moderate-sized polychaetes, often ranging from 35–100 mm in length; interstitial species may only be a few millimetres long (Hartman 1957), but some species may reach 400 mm. The body is typically long and slender with the abdomen appearing ragged due to the dorsally directed parapodia and branchiae (Fig. 1.53A, B). The shorter thorax, often dorso-ventrally compressed, has lateral short-lobed parapodia whereas the near-cylindrical abdomen bears dorsal parapodia with longer, more slender, lobes; the transition between thorax and abdomen is generally weak in the protoariciines but abrupt in the orbiniines. The Australian orbiniine genus *Uncorbinia* is atypical in having parapodia

1. CLASS POLYCHAETA

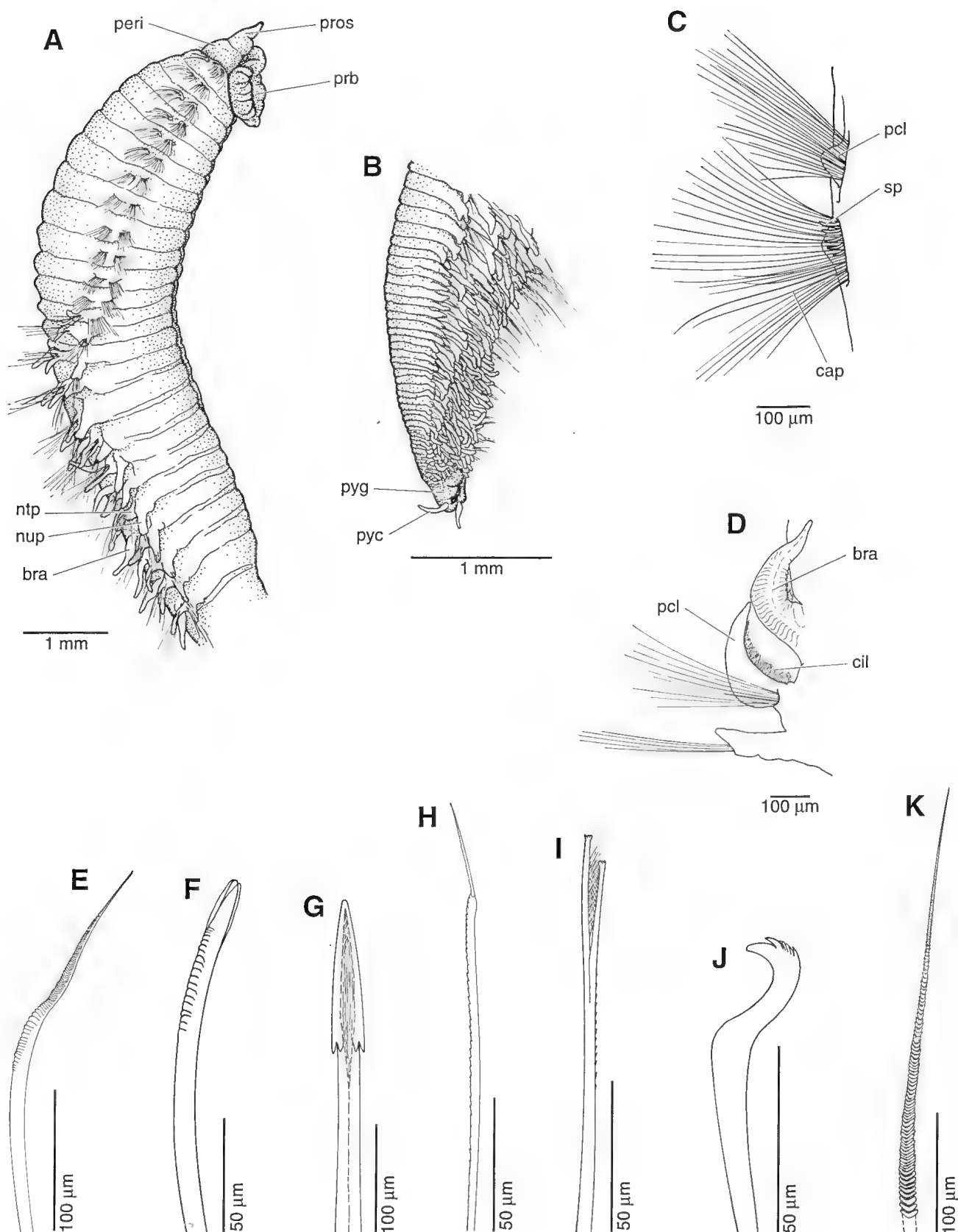


Figure 1.53 Family Orbiniidae. **A**, anterior end of *Scoloplos normalis*, lateral view. **B**, posterior end of *Scoloplos cylindrifer*, dorso-lateral view. **C**, **D**, parapodia of *Scoloplos normalis*: **C**, anterior thoracic parapodium from chaetiger 4, anterior view; **D**, mid-abdominal parapodium from chaetiger 28, anterior view. **E–K**, chaetae: **E**, subuluncini from thoracic neuropodium of chaetiger 9, *Nainereis grubei australis*; **F**, hooded spine from thoracic neuropodium of chaetiger 9, *Nainereis grubei australis*; **G**, arrow-shaped spine from thoracic neuropodium of chaetiger 14, *Phylo felix*; **H**, flail-tipped chaeta from abdominal neuropodium, *Orbinia hartmanae*; **I**, furcate abdominal chaeta, *Phylo felix*; **J**, 'swan-shaped' hook from abdominal neuropodium, *Proscoloplos confusus*; **K**, crenulate capillary from abdominal neuropodium of chaetiger 28, *Scoloplos normalis*. **bra**, branchia; **cap**, capillary chaetae; **cil**, cilia; **ntp**, notopodium; **nup**, neuropodium; **pcl**, postchaetal lobe; **peri**, peristomium; **prb**, proboscis; **pros**, prostomium; **pyc**, pygidial cirrus; **pyg**, pygidium; **sp**, spine. [A. Murray]

that are of similar size and orientation (lateral) along the length of the body (Hartmann-Schröder 1979). The colour of living specimens ranges from orange through yellowish-red and many species have bright red branchiae (Hartman 1957).

The shape of the prostomium varies from pointed (conical) to blunt (distally rounded or square). The first annulus behind the prostomium is thought to represent the peristomium and the second, when present, is an achaetigerous segment (Eisig 1914); they may be smooth or annulated. However, Rouse & Pleijel (in press) have suggested that there are two peristomial rings. Pharynges are variable; they are non-muscular and axial in orbiniines and muscular and ventral in protoariciines. They are typically unarmed and appear either sac-like or branched when eversed (Fig. 1.53A). Anatomical and ultrastructural studies suggest that the larvae of orbiniines have a ventral muscle bulb and a tongue-like organ which is later replaced in adults by a non-muscular axial-type pharynx, whereas the ventral pharynx persists through development in the protoariciines (Dales 1962; Purschke 1988b). Paired chemosensory nuchal organs are located on the prostomium postero-laterally; eyes may be present.

Parapodia are biramous, though anterior ones lack aciculae and do not project far from the body wall (Fig. 1.53C). Each notopodium consists of a single postchaetal lobe which varies in shape from short and triangular through cirriform to foliaceous (Fig. 1.53C, D). Posterior ones are supported by one to several aciculae and carry crenulate capillaries and, sometimes, furcate chaetae (Fig. 1.53I). Neuropodia are more variable along the body of an individual. Thoracic neuropodia are low, ranging in shape from digitate to mammiform, unlike those on the abdomen which are more elongate, may be flanged or notched basally and are supported by one to several acicula. Neuropodia carry crenulate capillaries (Fig. 1.53K) as well as spines, which may be hooded (Fig. 1.53F) and are often arranged in conspicuous fascicles in the thoracic neuropodia; subuluncini (Fig. 1.53E) occur in *Protoaricia* and *Nainereis*. Abdominal neuropodia may carry modified crenulate capillaries or flail-tipped chaetae (as in *Orbinia hartmanae*; Fig. 1.53H) or strongly bent, crested hooks (in *Proscoplos* and *Pettibonella*; Fig. 1.53J). Age-related gain and loss of spines has been reported in members of *Scoloplos* (Curtis 1969; Mackie 1987). In *Phylo* species, stout modified spines (Fig. 1.53G) emerge from epithelial glandular pouches in posterior thoracic segments, and may function in defence (Eisig 1914). Dorsal and ventral cirri are absent.

Podal, subpodal and stomach papillae occur in many species and their distribution is a useful specific character. Also of specific importance is the presence and distribution of inter-ramal cirri (also called lateral organs when reduced in size to a low mound) of posterior thoracic and abdominal chaetigers.

Segmentally paired branchiae are present over most of the body in most orbiniids. Usually they are conspicuous strap-like or triangular processes with fimbriated or ciliated lateral margins (Fig. 1.53D); in some genera (*Nainereis*, *Protoaricia*) cilia continue on dorsal ridges between the bases of the paired branchiae or on the dorsal edge of the notopodial lobe (*Scoloplos*; Fig. 1.53D). According to Storch & Alberti (1978), the branchiae of *Scoloplos armiger* contain blood spaces (rather than distinct vessels) lined by the basement lamina of the epidermis and coelomic epithelium; thus, the 'branchiae' of orbiniids may not be homologous with true branchiae of other polychaetes. The circulatory system of *Phylo foetida* has been described by Timofeev (1930). The segment on which the first branchiae appear is used in combination with other characters to distinguish species.

The pygidium carries one to many pygidial cirri, or cirri may be absent (Fig. 1.53B).

Orbiniids have complete septation. *Leitoscoloplos elongatus* burrows by peristaltic movement using the prostomium, posterior end and parapodia as anchorage points (Parkinson 1978). Adults removed from the substratum roll into a ball or coil, with the branchial side (dorsum) and cephalic structures innermost and can swim by rapid opening and closing of the coil (Hartman 1957).

The nervous system is known only for two European species of *Orbinia* (Orrhage 1966).

Reproduction has been studied in several orbiniid species; only one of these occurs in Australian waters – *Scoloplos* (*S.*) *simplex*, originally identified as *Haploscoloplos fragilis* (Anderson 1961). Most species appear to be gonochoristic and fertilisation is thought to be external (Chapman 1965). Many species lay eggs in gelatinous cocoons, which are thought to prevent excessive dispersal of the larvae (Chapman 1965; Gibbs 1968). Japanese populations of *Nainereis laevigata* deposit eggs in thin ribbon-shaped clusters and may attach them to stems of *Zostera* (Okuda 1946). *Scoloplos* (*S.*) *simplex* produces cylindrical gelatinous cocoons around its eggs (Anderson 1961, originally described as *Haploscoloplos fragilis*). Eggs are 150–250 µm in diameter and colour typically ranges from cream through yellowish-cream-brown to brown-orange (Anderson 1961; Blake 1980).

Hatching occurs 1.5–22 days after fertilisation depending on the species, at which time the embryos of most species become pelagic for 1–20 days (Anderson 1961; Blake 1980). Delayed hatching in a population or species results in resorption of cilia and a reduced or absent pelagic phase; the viscosity of the jelly in the egg mass probably determines when the larvae escape and may change as the larvae develop (Anderson 1961; Blake 1980). Embryos show a ciliary pattern of akrotoch, prototroch, metatroch, telotroch and neurotroch and a series of segmental bands that varies in degree of development between species; larvae do not feed in their planktonic phase (Anderson 1961). Embryos may develop three to 12-segments prior to settlement (Anderson 1961; Blake 1980). The peristomium is fused with the first one (or two) embryonic trunk segments (Anderson 1961).

Orbiniids are deposit-feeders, ingesting sediment particles, detritus, and associated organisms such as diatoms and foraminiferans (Parkinson 1978; Purschke 1988b). Unlike other deposit-feeders, orbiniids do not feed while burrowing (Parkinson 1978; Rice, Bianchi & Roper 1986). The egestion of waste particles at the sediment surface by *Scoloplos* species contributes to the vertical mixing of the surface layers of sediment (Rice *et al.* 1986).

Orbiniids are common infaunal polychaetes of bays and estuaries. Several orbiniine species occur in estuaries of New South Wales, often in sandy-mud sediments associated with seagrass beds; two species, *Scoloplos normalis* and *S. simplex*, live in low saline areas (Hutchings & Murray 1984). The protoariciines of Australia are currently only known from sediment trapped within encrusting algae on rocky shores.

The phylogenetic position of Orbiniidae has varied over the years. Originally considered related to the errant groups, more recently Orbiniidae have been grouped together with spionid-like families under Spiomorpha (Uschakov 1955; Clark 1969). The most recent opinions suggest that they are best grouped together with Paraonidae and with or without Questidae (Fauchald 1977; George & Hartmann-Schröder

1985). A recent cladistic analysis of polychaete families supports the close relationship of Orbiniidae with Paraonidae and Questidae, although whether the group is monophyletic or paraphyletic could not be established unequivocally (Rouse & Fauchald 1997). Rouse & Fauchald (1997) placed all three families together with several others (but not including the spiomorphs) in the monophyletic taxon Scolecida (Fig. 1.47).

The subfamily Orbiniinae is characterised by having a single achaetous annulus (peristomium) following the prostomium, a non-muscular pharynx, well-developed parapodia and accessory lobes, and numerous well-developed branchiae (Fig. 1.53A). Among the more speciose orbiniine genera are *Leitoscoloplos*, *Orbinia*, *Phylo*, *Scoloplos* and *Nainereis*. Subgenera of *Orbinia*, *Scoloplos* and *Nainereis* are commonly used (Pettibone 1957a). The Protoariciinae contain smaller, more slender species that have two achaetous annuli (a peristomium and achaetous trunk segment), and branchiae that are poorly developed or absent; the subfamily includes *Protoaricia*, *Protoariciella*, *Pararicia*, *Proscoloplos*, *Scolopella*, *Schroederella*, *Orbiniella* and *Pettibonella*. The Protoariciinae were assumed to be monophyletic in the cladistic analysis of the subfamily by Solis-Weiss & Fauchald (1989). They found that the genera *Protoariciella*, *Scolopella* and *Schroederella* are the most apomorphic protoariciines and that *Pettibonella* and *Proscoloplos* are sister groups defined by the presence of curved hooks (Fig. 1.53J). Relationships between other genera were found to be equivocal. There are indications, however, that distinction between the two subfamilies may not be warranted with the features of protoariciines merely being juvenile expressions of characters fully developed in orbiniines. Blake & Hilbig (1990) found that the number of achaetous annuli changes from two to one during ontogeny in a species of *Leitoscoloplos*.

Several different distribution patterns are apparent amongst Australian orbiniids. Widespread species that have been reported outside Australian waters are *Leitoscoloplos bifurcatus*, *L. kerguelensis*, *Nainereis laevigata*, *Phylo felix*, *Proscoloplos confusus*, *Scoloplos* (*S.*) *armiger*, *S. simplex*, *S. difficilis*, *S. johnstonei*, and *S. normalis*. Species with a temperate distribution on the west, south and east coasts are *Protoariciella australiensis* and *Scoloplos cylindrifer*. Some species occur only on the east coast (*S. novaehollandiae*), whereas others such as *L. latibranchus*, *Nainereis victoriae* and *Uncorbinia brevibranchiata* appear to have restricted distributions within Australia. Members of *Scoloplos* (*Leodamus*) have a mainly Southern Hemisphere distribution, and a Gondwanan origin for the subgenus is possible.

Family Paraonidae

Paraonids are elongate, thread-like worms. They have a coiled body and a bluntly conical prostomium. They are deposit-feeders and are found from the littoral zone to abyssal depths.

Members of the Paraonidae have a well-defined prostomium often with a single postero-dorsal antenna, branchiae that are usually present on the mid-anterior body, and chaetae that include capillaries, spines and hooks (Fig. 1.54A). The family may be monophyletic on the basis of the presence of paired dorso-lateral nuchal slits (Fauchald & Rouse 1997), although how these differ from nuchal organs of other polychaetes is unclear.

The family has been regarded variously as members of the order Orbiniida (for example, Fauchald 1977), Spiomorpha (for example, Clark 1969), or to belong to the unranked taxon Scolecida (Rouse & Fauchald 1997).

Important revisions of the group include those of Cerruti (1909), who proposed the family name Paraonidae as a replacement for Levinseniidae, and Strelzov (1973), whose work was translated from Russian in 1979 (Strelzov 1979). The earliest described paraonid species were placed in the Spionidae and Orbiniidae. The generic classification is uncertain. For example, Katzmann & Laubier (1975) and Hartley (1981) considered *Aricidea*, *Aedicira*, *Allia* and *Acmira* (= *Acesta*), as subgenera of *Aricidea sensu lato*; *Paradoneis* and *Paraonides* as full genera rather than as junior synonyms of *Cirrophorus*, as proposed by Strelzov (1973), and; *Paraonella* as a junior synonym of *Paraonides*.

Worldwide, about nine genera are represented, three of which have been reported in the literature from Australian waters: *Aricidea sensu lato*, *Levinsenia* (= *Tauberia*) and *Paraonis*. However, species of *Cirrophorus*, *Paradoneis* and *Paraonides* are listed in museum collections and a revision of the Australian members of the family would certainly increase significantly the number of known genera and species. Several paraonid species have been reported in low numbers in bays and estuaries throughout Australia (Poore *et al.* 1975; Hartmann-Schröder & Hartmann 1980, 1990, 1991a; Hutchings & Murray 1984). European and British paraonid species are reasonably well-known, taxonomically (Katzmann & Laubier 1975; Laubier & Ramos 1973; Hartley 1981), but elsewhere the group is poorly-known and still there are many generic-level taxonomic problems.

Paraonids inhabit soft bottoms, sand to mud sediments from the littoral zone to 6000 m, although members of *Paraonis*, *Aricidea* (*Aricidea*), *Aricidea* (*Aedicira*) and *Paraonella* are mainly restricted to coastal and shelf areas (Strelzov 1979).

Paraonids are small, thread-like polychaetes with up to 200 segments. They range in length from 2–3 mm up to 40 mm and are usually uniform yellow to brown in colour in life (Hartman 1957; Strelzov 1979). A cuticle, 2–10 µm thick, covers an epithelium, which is glandular, particularly laterally behind each parapodium and on the venter. The body comprises an abranchiate anterior and posterior regions and a slightly wider branchiate mid-section where parapodia are best developed and which may be flattened dorso-ventrally (Fig. 1.54A). The prostomium is well developed, more-or-less bluntly conical, and carries a single postero-dorsal median antenna (for example, *Aricidea sensu lato*, *Cirrophorus*) or the antenna may be absent (*Levinsenia*, *Paraonis*, *Paraonides*, *Paradoneis*); a pair of eyes is often present (Fig. 1.54B). The peristomium is poorly developed, comprising only the ventral area around the mouth in adults (Strelzov 1979). The anal lobe is slanted obliquely dorsally and usually bears two to three pygidial cirri (Fig. 1.54A).

Paraonids typically have a non-muscular axial eversible buccal organ (Dales 1962a). However, larvae have a muscular ventral pharynx and this usually (but not always) changes to the adult non-muscular axial type during ontogeny (Purschke & Tzetlin 1996). The pharynx opens to a ventral mouth, which is surrounded by lips, of which the lateral ones are ciliated (Strelzov 1979).

Parapodia are biramous, although both rami are poorly developed and have no aciculae (Fig. 1.54C, D). The postchaetal notopodial lobe is long and cirriform to foliose and the postchaetal neuropodial lobe is often smaller, more rounded, but absent in the posterior body. The cirriform to strap-like branchiae emerge from the dorsal surface above the parapodia on the mid-anterior body. Transverse rows of cilia occur on the dorsal surface of branchial segments and on the lateral margins of the branchiae (Fig. 1.54D). Capillary chaetae are present throughout the body together with

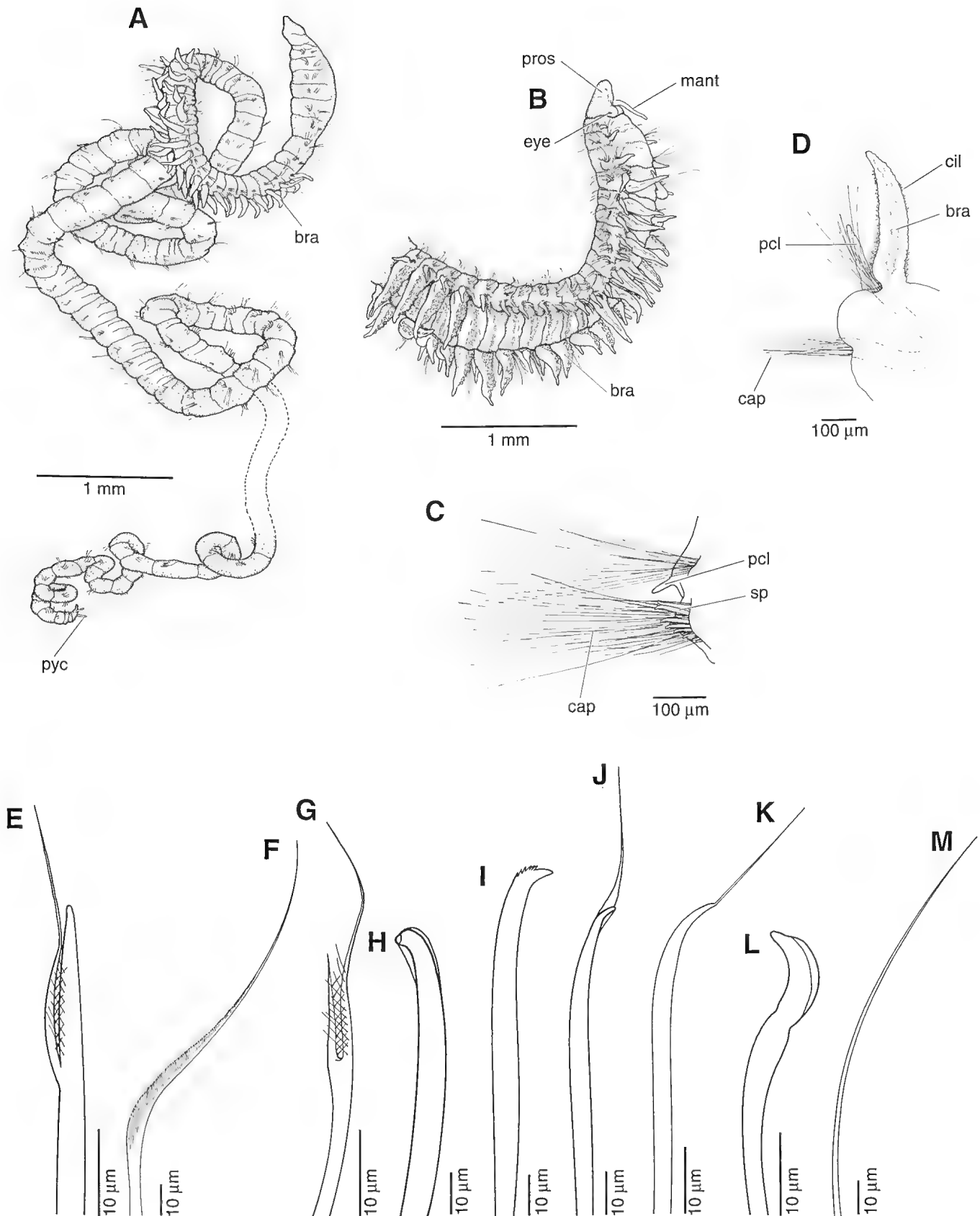


Figure 1.54 Family Paraonidae. **A**, entire animal of *Levinsenia gracilis*; some middle segments are not shown. **B**, anterior end of *Aricidea* cf. *fauveli*, ventro-lateral view. **C**, **D**, parapodia of *Aricidea* (*Acmira*) species: **C**, from chaetiger 12, anterior view; **D**, from posterior chaetiger, anterior view. **E–M**, chaetae: **E**, notopodial bayonet chaeta from anterior postbranchial chaetiger, *Cirrophorus* species; **F**, neuropodial capillary from chaetiger 6, *Aricidea* (*Allia*) species; **G**, notopodial lyrate chaeta from posterior chaetiger, *Cirrophorus* species; **H**, posterior neuropodial hook, *Aricidea* species; **I**, neuropodial spine from posterior chaetiger, *Aricidea* (*Acmira*) species; **J**, neuropodial spine from posterior chaetiger of *Aricidea* cf. *fauveli*; **K**, modified neurochaeta from posterior chaetiger, *Aricidea* (*Allia*) species; **L**, neuropodial hook from posterior chaetiger, *Levinsenia gracilis*; **M**, capillary from posterior chaetiger of *Aricidea* (*Allia*) species. **bra**, branchia; **cap**, capillary chaetae; **cil**, cilia; **eye**, eye; **mant**, median antenna; **pcl**, postchaetal lobe; **pros**, prostomium; **pyc**, pygidial cirrus; **sp**, spine. [A. Murray]

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specialised, mainly, acicular chaetae in posterior parapodia, which purportedly function as anchor points during locomotion. Capillaries in anterior parapodia are flanged and finely serrated (Fig. 1.54F) whereas those of posterior parapodia are thin, straight and rounded in cross-section (Fig. 1.54M). Thicker specialised chaetae include the lyrate (Fig. 1.54G) and bayonet (Fig. 1.54E) types, pseudo-compound chaetae, hooks with a subterminal or terminal spinelet (Fig. 1.54J, K), hooded hooks (Fig. 1.54H, L) and spines with or without distal teeth (Fig. 1.54I; Strelzov 1979). Specialised chaetae may occur either in the notopodia (*Paradoneis* and *Cirrophorus*) or in the neuropodia (*Aricidea*, *Levinsonia*, *Paraonis*).

Limited observations suggest that paraonids can evert the anterior part of the pharynx (proboscis) to form a flat ciliated surface on which food particles are channeled toward the mouth. The widely-reported estuarine species, *Paraonis fulgens*, feeds in tight horizontal spirals below the sediment surface, moving upwards or downwards before the next spiral (Röder 1971; Risk & Tunnicliffe 1978). Fauchald & Jumars (1979) suggested that this pattern of feeding may be common to many species in the group. Likely food items are foraminiferans, diatoms, dinoflagellates and possibly also the bacterial film surrounding sand grains (Risk & Tunnicliffe 1978; Strelzov 1979; Gaston, McLelland & Heard 1992). The digestive tract is a straight tube consisting of a buccal cavity, pharynx, oesophagus and intestine.

The vascular system has been described by Cerruti (1909) and Strelzov (1979). Respiration is facilitated by the beating of branchial and interbranchial cilia. Each branchia is supplied by two, large, deeply-embedded vessels connected by numerous transverse capillaries; oxygenated blood travels along the dorsal blood vessel to the rest of the body without the aid of a heart. Blood is red or reddish-yellow.

Metanephridia are the typical excretory organ in this group, but range from typical metanephridia in the genus *Aricidea* (Cerruti 1909) to intermediate types between protonephridia and metanephridia (Strelzov 1979).

The nervous system has been studied for only a few species, but appears to be similar within the family (Orrhage 1966; Strelzov 1979). Paraonids lack sympathetic nerves emanating from the antero-ventral cerebral commissure, which are typically present in Spionida. The brain, which lacks a hind region, is located in the anterior part of the prostomium.

Sensory organs comprise a pair of retractile, kidney-shaped nuchal organs on the postero-lateral prostomium and a retractile, papilla-like sensory organ on the anterior margin of the prostomium. Strelzov (1979) suggested that the latter is homologous with the cephalic apical antenna of the larvae. The single postero-dorsal median antenna is innervated by two nerves from the postero-dorsal cerebral commissure, and is homologous with the median antenna of Spionidae and Trochochaetidae (Orrhage 1964, 1966). Other sensory organs are the prebuccal ciliated band and the ciliated lateral organs under the dorsal parapodial lobes on each segment; the latter are widespread in other (distantly related) polychaete groups.

Paraonids are dioecious. Gametes develop in discrete gonads of the postbranchial segments and are expelled by rupture of the body wall. Spawning in surface waters apparently occurs in at least some species (Strelzov 1979 and references therein); this is supported by the finding of enlarged eyes and natatory chaetae in mature *Paradoneis armata* (López-Jamar *et al.* 1987), features typically found in epitokous forms. Larvae are poorly-known, but are thought to include both direct and indirect developing types (Bhaud 1983b).

Spawning was reported in early summer in a population of *Paradoneis armata* from north-western Spain; the decrease in the population density prior to recruitment in the following winter indicates that death of adults may have ensued (López-Jamar *et al.* 1987).

Population densities for some species can reach very high levels. López-Jamar *et al.* (1987) reported mean densities of about 5000 worms per m² for *Paradoneis armata* in estuarine sands of north-western Spain, and *Paraonis fulgens* reaches densities of over 10 000 per m² in shallow waters off the mouth of the Mississippi (Gaston *et al.* 1992). Increases in population density have been recorded, outside Australia, for several non-Australian species in response to organic pollution, particularly hydrocarbons (Dauer & Conner 1980; López-Jamar *et al.* 1987).

Based on anatomical similarities, the Paraonidae have generally been considered to be closely related to the other spiomorph families, Apisthobranchidae, Poecilochaetidae, Spionidae and Trochochaetidae (Clark 1969; Dales 1962a; Orrhage 1964). However, their external morphology strongly resembles members of Orbiniidae; this has led others to suggest a phylogenetic affinity between these two families (Mesnil & Caullery 1898; Fauchald 1977). Strelzov (1979) suggested, however, that the shared external resemblances are the result of convergence and favours a spiomorph relationship. In the only cladistic analysis of these families, Paraonidae are placed as sister group of Orbiniidae (Fig. 1.47); both families have flattened dorsal branchiae, although this feature is homoplastic within Polychaeta (Rouse & Fauchald 1997).

Phylogenetic relationships within the family are unknown, but are urgently required, for example, to ascertain monophyly of controversial genera such as *Paraonides* and *Paradoneis* and the validity of the subgenera *Aricidea sensu stricto*, *Aedicira*, *Allia*, and *Acmira*.

Family Questidae

The Questidae are a species-poor oligochaete-like group. They are elongate and slender and have a blunt head without appendages. They feed on the bacterial/diatom film on the surface of sand grains.

Questids have a prostomium lacking appendages, followed by a peristomium and a single achaetous segment. The trunk segments often show secondary annulation, particularly in the mid-body region. They have reduced parapodia and chaetae emerge directly from the body wall in two bundles. Chaetae include serrated capillaries, hooks with a subdental ligament and trifurcate chaetae. A ventral muscular eversible pharynx is present. The anus is surrounded by two lateral lobes. Putative autapomorphies of Questidae include the presence of accessory flagellar microtubules in mature sperm and other unique features (among Annelida) of the sperm, as described below (Jamieson 1983b; Jamieson & Webb 1984).

The family is now considered to belong to Scolecida (Rouse & Fauchald 1997), although earlier classifications put the group within Orbiniida (Fauchald 1977) or in an order by themselves (George & Hartmann-Schröder 1985).

Erected by Hartman (1966), Questidae was known for two formally described genera: *Questa* containing three species, and *Novaquesta* with one species (*N. trifurcata*). However, recently Giere & Erséus (1998) added four new species to the family and relegated *Novaquesta* to a junior synonym of *Questa* on the basis of a cladistic analysis. The morphology

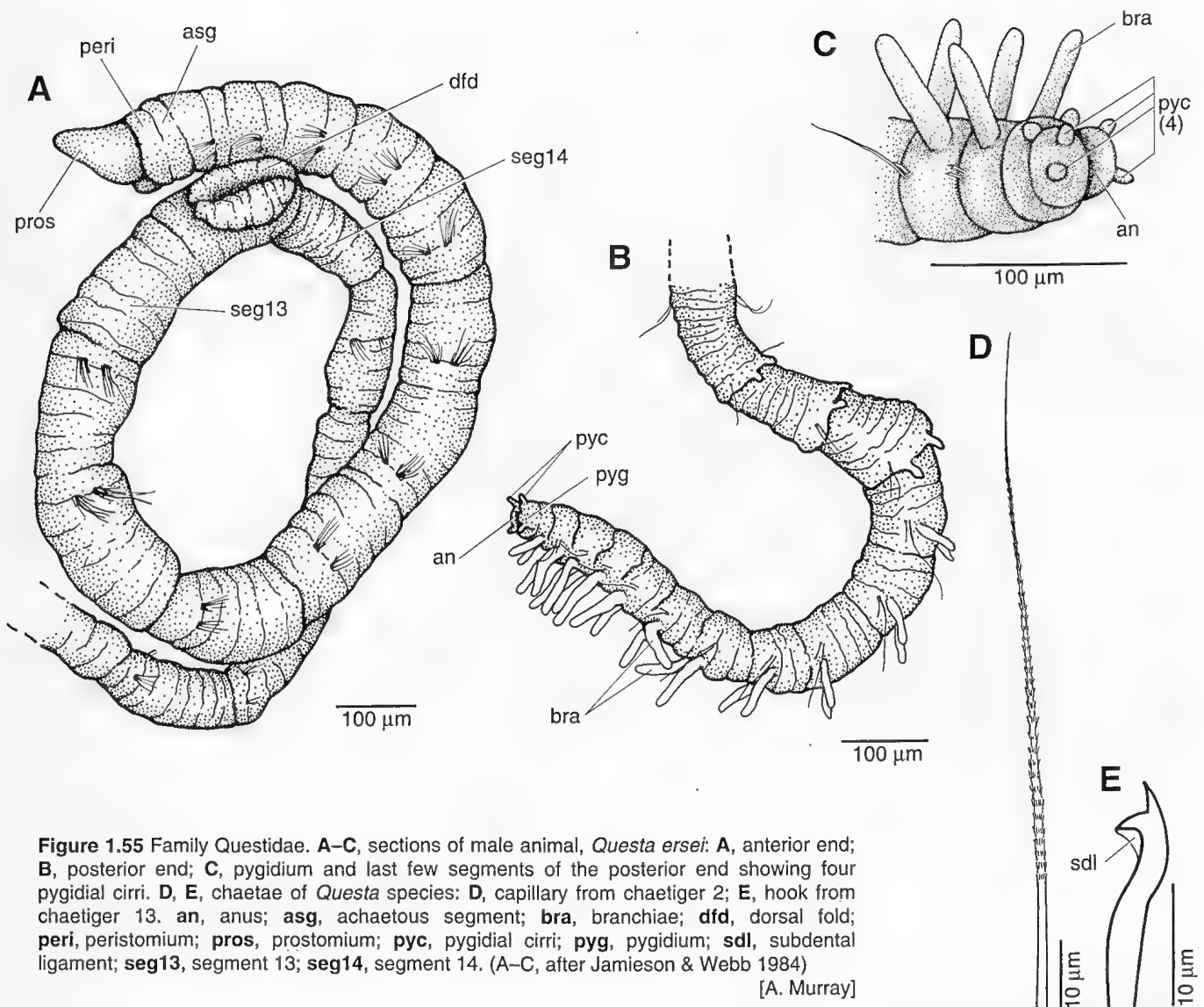


Figure 1.55 Family Questidae. **A–C**, sections of male animal, *Questa ersei*: **A**, anterior end; **B**, posterior end; **C**, pygidium and last few segments of the posterior end showing four pygidial cirri. **D**, **E**, chaetae of *Questa* species: **D**, capillary from chaetiger 2; **E**, hook from chaetiger 13. an, anus; asg, achaetous segment; bra, branchiae; dfd, dorsal fold; peri, peristomium; pros, prostomium; pyc, pygidial cirri; pyg, pygidium; sdl, subdental ligament; seg13, segment 13; seg14, segment 14. (A–C, after Jamieson & Webb 1984)

[A. Murray]

and reproductive biology have been studied for *Questa trifurcata* (Giere & Riser 1981) and for the Australian species, *Questa ersei* (described by Jamieson & Webb 1984).

Questids occur in fine to medium sand rich in organics as well as in carbonate sediments such as coral rubble and shell. They occur in shallow waters to the deep sea, but rarely in dense populations. They move between sand grains by using their long and flexible hair-like chaetae. They ingest sand grains, diatoms and plant material by protrusion and retraction of their tongue-like buccal pad (Giere & Riser 1981).

The family has been recorded from both coasts of North America, the Gulf of Mexico, Caribbean, the Galapagos Islands, Philippines and the Mediterranean Sea (Hobson 1970, 1976; Westheide 1981; Taylor & Gathof 1984; Somaschini & Gravina 1993; Giere & Erséus 1998). One species, *Questa caudicirra*, is thought to have a cosmopolitan distribution (Somaschini & Gravina 1993). The Australian species, *Q. ersei*, occurs on the Great Barrier Reef (Heron Island, Wistari Reef, Lizard Island) and the Houtman Abrolhos Islands; further questid species are likely to be found with more intensive sampling of interstitial, reefal habitats.

Questids attain a length of up to 10 mm and have up to about 60 chaetigers and are usually reddish-orange in colour. The prostomium is subconical to broadly rounded anteriorly and lacks appendages and eyes. Paired slit-like nuchal organs occur on the postero-lateral margin of the prostomium and

anterior segments; in *Questa trifurcata* similar structures also extend ventrally (Giere & Riser 1981). Apart from nuchal organs, the only other apparent sensory organ is a series of lateral organs located between the notopodium and neuropodium on all segments (Giere & Erséus 1998). The peristomium and achaetous first segment are more or less conspicuous annuli (Fig. 1.55A). Parapodia are biramous with short, papilliform chaetal lobes and lack aciculae (Hartman 1966; Hobson 1970). Septa are well developed except in the genital segments. Simple ciliated branchiae may be present on the dorsal surface of middle and/or posterior segments (*Questa ersei*) (Fig. 1.55B) or absent (*Q. trifurcata*). The pygidium is bilobed or rounded (Fig. 1.55C). Dorsal and ventral pairs of pygidial cirri occur in most species of *Questa* (one pair may be absent), but are absent in *Q. trifurcata*. In addition to serrated capillaries (Fig. 1.55D) and bifid hooks (Fig. 1.55E) which are present in all parapodia, *Q. trifurcata* also has trifurcate chaetae and trifid hooks in anterior parapodia.

In *Questa trifurcata* and *Q. ersei* the ventral mouth opens into a small buccal cavity that leads into a narrow, unarmed, ventral pharyngeal organ. The pharyngeal tube is sharply demarcated from the ciliated oesophagus, which in turn leads into an intersegmentally constricted intestine. A pair of ventro-lateral caeca arises from the anterior intestine; their position and length varies within a species (Giere & Erséus 1998).

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The dorsal blood vessel branches in segment 1 and forms an anterior loop which supplies the brain and circum-pharyngeal vessels; these unite in segments 2 and 3 to give rise to the median ventral vessel. Lateral vessels along the intersegmental furrow of the intestine connect the dorsal and ventral longitudinal vessel (Giere & Riser 1981).

Nephridia are mentioned by Giere & Riser (1981) and Giere & Erséus (1998), but there are no details as to distribution or function. Nephridiopores emerge slightly ventral to the notopodium (Giere & Erséus 1998).

The morphology of the brain and nerve cord of *Q. trifurcata* were described by Giere & Riser (1981). The brain is trapezoidal in shape and is contained wholly within the prostomium.

Questids are dioecious. Ovaries on the anterior septa of segments 12 and 13 produce two (usually) yolky eggs up to 200 µm in diameter which are confined to these segments. Two or three oopores open latero-ventrally on segments 12 to 14 (Giere & Riser 1981). One (*Q. ersei*) or two (*Q. trifurcata*) unpaired spermathecae in segments 5 to 7 of females open via pores to the dorsal surface between segments 5 and 6 (*Q. ersei*) or via two unilateral pores (left side) on segments 5 and 6 (*Q. trifurcata*). A glandular and papillated girdle, analogous to an oligochaete clitellum, is present on segments 9 to 11 (Giere & Riser 1981; Jamieson & Webb 1984), although it may not be recognisable externally.

In mature males, sperm develop in segments 11 and 12 within discrete testis sacs. Each sac tapers and leads via a coiled duct into a pair of muscular sperm reservoirs then into narrow efferent ducts which pass to a large, glandular copulatory protruberance (dorsal fold) on the dorsal surface of segments 13 to 15 (Fig. 1.55A; Giere & Riser 1981; Jamieson & Webb 1984).

A modified flagellate-type sperm, 'introsperm' (*sensu* Jamieson & Rouse 1989), has been described for *Q. ersei* by Jamieson & Webb (1984) and for an undescribed species of *Questa* (Jamieson 1983b). Ultra-structural investigation has revealed several unique features of the sperm, which may represent further autapomorphies of the family. They include the six-rayed symmetry of the acrosome vesicle and in the axoneme, the presence of two postcentriolar dense cylinders and accessory flagellar microtubules peripheral to the nine normal doublets (Jamieson 1983b; Jamieson & Webb 1984).

Questids copulate back to back bringing together the dorsal folds of the male (Fig. 1.55A) with the spermathecal segments of the female. Following mating the female secretes a gelatinous belt into which mature eggs are deposited (Giere & Riser 1981; Jamieson & Webb 1984).

Larvae of *Q. trifurcata* develop in oval-shaped cocoons deposited in autumn months (in the Northern Hemisphere), and emerge after 4–6 weeks at the 7-chaetiger stage (Giere & Riser 1981).

Questidae were thought to have affinities with oligochaetes (Hartman 1966b; Fauchald 1977) and Paraonidae (Hartman 1966b). More recently a relationship with the 'archannelid' polychaetes (such as Protodrilidae and Dinophilidae) has been suggested on the basis of similarities in sperm and buccal organ morphology (Jamieson 1983b; Jamieson & Webb 1984). However, resemblance to clitellates is superficial, especially in certain reproductive characteristics. Like many clitellates, the genital organs of questids are concentrated into a few segments and a glandular girdle that secretes cocoons is present. Unlike that of clitellates, however, the questid girdle is anterior to the oopores and they are gonochoristic, unlike

oligochaetes which are hermaphrodites (Giere & Riser 1981). Further, the absence of an acrosome tube in the sperm of questids distinguishes them from clitellates (Jamieson 1983a, 1983b; Jamieson & Webb 1984). On the other hand members of Questidae share with polychaetes the presence of paired nuchal organs (Jamieson 1983b), an autapomorphy of Polychaeta (Rouse & Fauchald 1995, 1997), a ventral pharyngeal organ, lateral organs and the prostomial position of the supra-oesophageal ganglia. Phylogenetic relationships within the family are largely ambiguous (Giere & Erséus 1998). Only *Q. ersei* and *Q. bicirrata* formed an unambiguous clade, suggesting a northern Australia–Philippines sister-area relationship.

Family Scalibregmatidae

Scalibregmatids are maggot-shaped or moderately long worms with a rugose and annulated epidermis. The head is 'horned', but lacks true appendages; branchiae are tufted and branched and are associated with the parapodia. They live in galleries in soft sediments in a wide range of depths.

The prostomium is truncate or T- or V-shaped. The peristomium forms a ring which is partially subdivided into two on the dorsal and lateral surfaces (Ashworth 1901). Antennae are absent, as are external palps, although Orrhage (1966, 1993) found palpal nerves. Nuchal organs comprise short ciliated grooves. The longitudinal muscles are grouped in bundles. Segmentation is distinct, the first segment being similar to the second, with small, fully-developed parapodia. Both rami on the parapodia are short, conical or truncate, and dorsal and ventral cirri are lacking. Branching branchiae are present in most taxa and are associated with the parapodia. Multiple pygidial papillae are present or absent. Lateral organs are present; dorsal cirrus organs have not been observed. The pharynx is an eversible, simple axial sac (= proboscis); there is no gular membrane and the gut forms a simple tube. The chaetae consist of both smooth and ornamented capillaries, furcate chaetae (in many taxa), and spines that are present on the first chaetigers in some taxa; there are no aciculae. This definition is based upon Fauchald & Rouse (1997).

The scalibregmatids were first described from Scandinavia (Rathke 1843; Örsted 1843) and were originally associated with another polychaete family, the Opheliidae. The original family name Scalibregmidae was changed for nomenclatural reasons to Scalibregmatidae (Bertelsen & Weston 1980).

Until recently, the Scalibregmatidae comprised a well-circumscribed group characterised by capillary and furcate chaetae, usually with a strongly wrinkled or areolated epidermis (Fauchald 1977). Kudenov & Blake (1978) reviewed the family and the characters useful to define genera. However, with the addition of more species since the 1970s, a definition of the family has become more difficult. Fauchald (1977) suggested that some genera (*Proscalibregma*, *Scalispinigera*) may not be members of this family although he retained them in his key to worldwide genera. Blake (1981a), however, moved *Proscalibregma* to the opheliids, and suggested that *Scalispinigera*, which contains two species, are related to the hesionids; however, the latter two species lack sensory palps and compound falcigers and so are unlikely to be members of Hesionidae (C. Glasby personal communication).

Kudenov & Blake (1978) recognised 33 species grouped into 13 genera. Subsequently, Blake (1981a) described an additional six species from South America and the Antarctic.

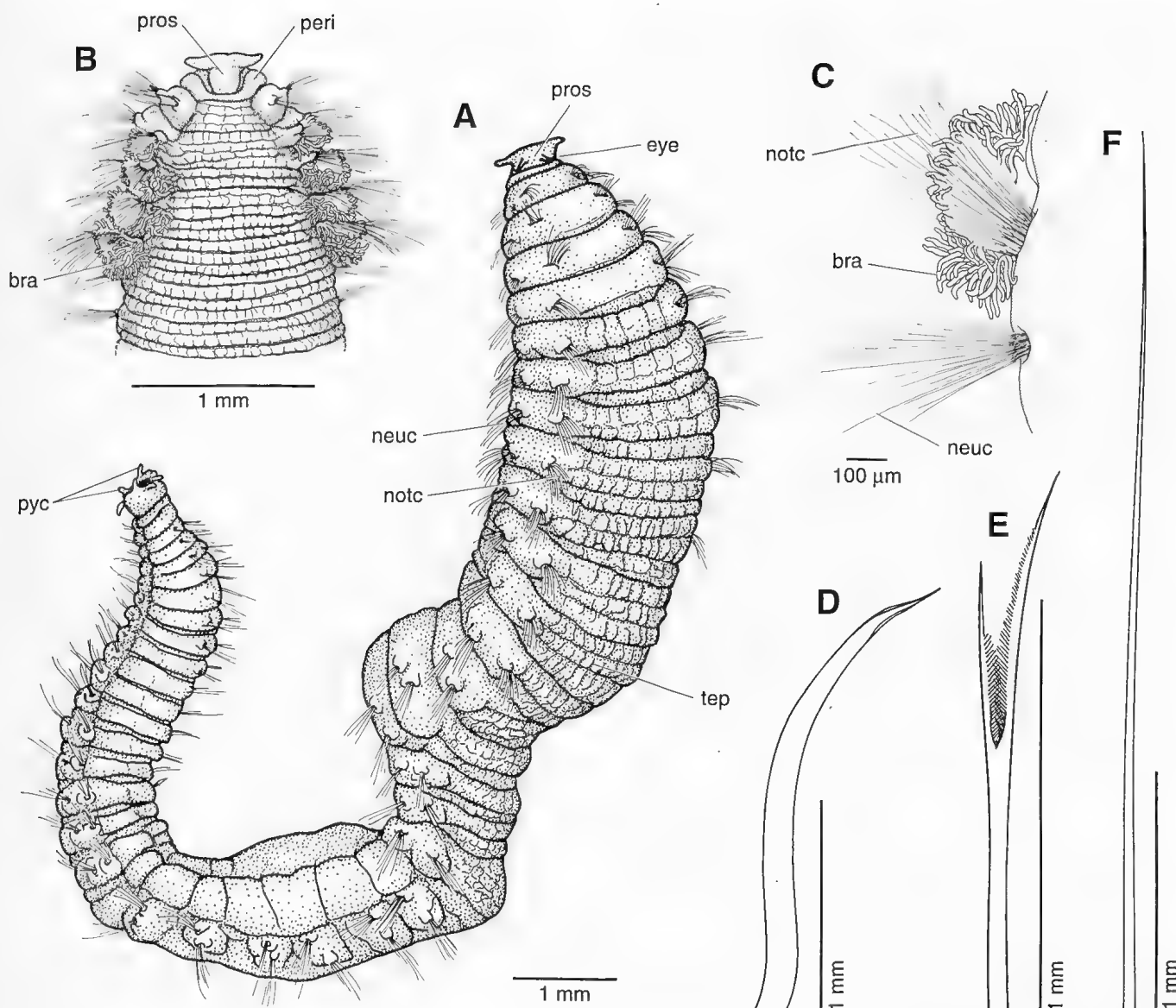


Figure 1.56 Family Scalibregmatidae. **A**, *Hyboscolex dichranochaetus*, entire animal, dorso-lateral view; branchiae absent in this genus. **B**, **C**, *Scalibregma inflatum*: **B**, anterior end, dorsal view; **C**, parapodium of chaetiger 5, anterior view. **D–F**, *Asclerocheilus heterochaetus*: **D**, spine from notopodium of chaetiger 1; **E**, furcate chaeta from parapodium of chaetiger 38; **F**, capillary from parapodium of chaetiger 38. **bra**, branchia; **eye**, eye; **neuc**, neurochaeta; **notc**, notochaeta; **peri**, peristomium; **pros**, prostomium; **pyc**, pygidial cirri; **tep**, tessellated epithelium. [A. Murray]

Since then two additional species and one new genus have been described, so the total known world fauna is about 40+ species belonging to 14 genera.

A single species of *Scalibregma*, *Hyboscolex*, *Asclerocheilus* and two species of *Oligobregma* have been recorded from Australian waters. In addition, unpublished records from Museum Victoria, indicate that a *Hyboscolex* species occurs in eastern Bass Strait, in depths of 27–45 m, and a species of *Scalibregma* occurs in depths of 43–45 m.

Scalibregmatids are mud-dwelling polychaetes, seldom found by casual collecting or during surveys (Kudenov & Bläke 1978). The Australian species generally occur intertidally and in shallow subtidal environments; one is found in deeper water (57 m) south of New Caledonia. In general, the family appears to be far more common in the deep sea and some genera are known only from abyssal depths. Kudenov & Bläke (1978) provided a detailed table of the bathymetric distributions of species showing that of the 33 species they recognised, 17 occur in depths below 1000 m. It is anticipated

that many species remain to be described, especially from deeper waters off the Australian coast. Levin *et al.* (1991) reported the family from eastern Pacific deep seamounts.

These polychaetes do not build tubes, but live in galleries in soft sediments, often buried as much as 0.3–0.6 m below the surface (Ashworth 1901; Hertweck & Reinneck 1966). Day (1967) reported that species of *Hyboscolex* live in muddy rock crevices and often occur in old tubes formed by other invertebrates. *Parasclerocheilus* species live under loose stones in muddy environments and those of *Scalibregma* have been dredged from similar environments.

Ashworth (1901) explored the anatomy of *Scalibregma*; the morphology of other genera has not been studied in detail. Scalibregmatids have a strongly rugose epidermis, and furcate chaetae are present in many taxa. They have two distinct body forms: relatively long-bodied and only moderately swollen anteriorly, as in *Scalibregma*, or; they may be thick and maggot-shaped, as in *Polyphysia*. Scalibregmatids resemble the opheliids in the subdivision of each segment into two or three rings. The ‘tentacular processes’ described by Ashworth

1. CLASS POLYCHAETA

(1901) are slightly extended antero-lateral corners of the prostomium, but they are not considered homologous with the antennae. Similar structures are also present in some spionids (Fauvel 1927). No other information appears to be available on the morphology or physiology of scalibregmatids.

Scalibregmatids have a sac-like eversible pharynx. The feeding strategies of only two species have been investigated (Fauchald & Jumars 1979), *Scalibregma inflatum* and *Polyphysia crassa*. Both are active burrowers and feed on detritus in the sediment (Dales 1963a; Hartmann-Schröder 1971; Elder 1972). *Scalibregma inflatum* may also feed at the surface and has been termed non-selective (Mare 1942); however, Fauchald & Jumars (1979) could find no evidence to support this statement. Day (1967) suggested that *P. crassa* also feeds on foraminiferans, perhaps by repeated eversion and retraction of the pharynx, as proposed by Dales (1963a). The pharynx is everted by increased pressure of the coelomic fluid through contraction of the muscles of the specialised anterior septa which act as diaphragms; the pharynx is retracted by relaxing the muscles of the body wall and contraction of those which arise from the junction of the first septum with the body wall and are directed forward on to the pharynx.

According to Ashworth (1901) scalibregmatids have a closed circulatory system and no heart body; no further information appears to be available.

Metanephridia, as mixonephridia, are present (Ashworth 1901; Goodrich 1945). Ashworth (1901) did not believe that the posterior nephridial ducts were large enough to function as oviducts, and quoted an observation by Danielssen (1859) who reported that eggs were squeezed out intersegmentally through strong muscular contractions, an observation that needs verification. Functional gonoducts have been described for *Scleocheilus minutus* by Dehorne & Dehorne (1913).

Little information is available on the reproduction of scalibregmatids. They have been observed swimming in the plankton in European waters, associated with spawning (Fage & Legendre 1927; Clark 1954) and on the Great Barrier Reef (Hutchings & Howitt 1988). Apparently they undergo relatively minor morphological changes in comparison to many other epitokous species; only the capillary chaetae become enlarged and more numerous, and perhaps the eyes also become enlarged (Schroeder & Hermans 1975).

Mackie (1991) found oocytes in the coelom of *Scalibregma inflatum* from August to March in specimens collected in Scotland. The oocytes were discoid with a maximum diameter of 150 µm between January and March. Juveniles were collected during April, with maximum numbers being recorded in August. Mackie suggested that the species has a maximum life span of about 2 years at this locality, although the animals can become reproductive in their first year.

PALPATA

Palpata is a name established by Rouse & Fauchald (1997) and such a group of polychaetes had never been formulated before. Virtually all polychaete taxa, with the exception of those in the Scolecida and a few *incertae sedis* taxa were placed into the Palpata (see Table 1.3); a total of about 70 families. In this volume, two of these taxa, the Myzostomatidae (Myzostomida) and Siboglinidae (traditionally = Pogonophora) are treated as outside the polychaetes. This means that 68 families are treated as

members of the Palpata, representing the vast bulk of the diversity of polychaetes. Most of the major groups of the Palpata have been recorded from Australian waters.

In several of their restricted cladistic analyses, Rouse & Fauchald (1997) found the clade Palpata as formulated here. However, the fact that taxa that lack palps, such as the Paraonidae and Scalibregmatidae, do appear to have 'palpal' innervation (Fig. 1.10; Orrhage 1966, 1993), indicates that some taxa classified outside the Palpata may have actually lost palps. This supposition is supported by the fact that in some analyses of Rouse & Fauchald (1997) the Palpata would basically be synonymous with the Polychaeta and so taxa belonging to the Scolecida (as used here) would be inferred to have lost palps. This implies that the Palpata as formulated here is in fact a paraphyletic taxon. Given the fact that the presence of palps and a peristomium limited to lips were the only synapomorphies supporting this taxon, the validity of the Palpata as formulated here requires further investigation.

All palps are similarly innervated and are considered homologous structures (Orrhage 1996). Palps can be divided into two structurally different groups, grooved 'feeding' palps and ventral 'sensory' palps (Orrhage 1980). Feeding palps usually have ciliated paths, often located in a longitudinal groove giving each palp a U-shaped cross-section. A great many different morphological features are grouped under the term 'grooved palps'. These structures differ in number, placement (either peristomial or prostomial), and aspects of basic structure and closer investigation of the homology of all these structures is warranted. Ventral sensory palps are morphologically more uniform than grooved palps. In most cases, they are tapering or digitiform and relatively short, compared to grooved palps.

ACICULATA

Aciculata is a name established by Rouse & Fauchald (1997) for a large group of polychaete taxa. This group does, however, include all members of the Errantia (as defined by Uschakov 1955, see Fig. 1.43; see also Fauchald & Rouse 1997). Nearly half of all polychaete families (about 41) have been placed into Aciculata by Rouse & Fauchald (1997) (see Table 1.3). In this volume one of these, Myzostomatidae, is treated as outside the polychaetes (see Chapter 2). The relationships proposed among the major groups of the Aciculata by Rouse & Fauchald (1997) are shown in Figure 1.57.

Aciculata is one of the strongly-supported clades identified by Rouse & Fauchald (1997). The name refers to one of the synapomorphies for the group, the presence of a particular chaetal type called aciculae. Aciculae are stout tapered chaetae that differ in that much or all of the chaeta remains internalised in the parapodium (Fig. 1.11A). They are attached to musculature in such a way that they will not be everted, thus forming internal 'skeletal' rods for the parapodia. Numerous other features, such as the presence of ventral sensory palps, prostomial antennae, dorsal cirri, ventral cirri, one pair of pygidial cirri and segmental organs in most segments, were proposed to be synapomorphies for the taxa included in the Aciculata by Rouse & Fauchald (1997).

Aciculata has two major taxonomic groups: Phyllodocida and Eunicida (Fig. 1.57; Rouse & Fauchald 1997). The former is a stable taxon that has a large membership showing numerous synapomorphies. The Eunicida was reformulated to include the Amphinomidae and Euprosinidae, taxa that were usually placed as a separate order called Amphinomida. In this volume, the name Eunicidans is used to match the traditional

formulation for the group. Rouse & Fauchald (1997) placed three families; Aberrantidae, Nerillidae and Spintheridae as members of the Aciculata, but did not place them within any sub-taxon of the group; they are treated as Aciculata *incertae sedis*. These three taxa have never been related to each other and they almost certainly will be found to have sister groups with different members of the Aciculata.

Members of most of the major groups of the Aciculata have been recorded from Australian waters. The Aciculata is such a vast group that they can be found in virtually any marine environment from deep-sea sediments to coastal intertidal zones; many are also planktonic and some live in freshwater.

EUNICIDA

Rouse & Fauchald (1997), under the name Eunicida, combined Eunicida *sensu* Fauchald (1977) and Amphinomida *sensu* Fauchald (1977) on the basis of the two groups having a well-developed ventral pharynx. However, Eunicida *sensu stricto*, with its complex sclerotised/mineralised jaw apparatus, is presently thought to constitute a monophyletic group (= Eunicidans), and is treated here separately from Amphinomidans (Amphinomidae and Euphrosinidae). Two families, Diurodrilidae and Histiobdellidae, were classified by Rouse & Fauchald (1997) as Eunicida *incertae sedis* and are here considered as Eunicidans *incertae sedis*.

‘EUNICIDANS’

‘Eunicidans’ are distinguished by having a ventral eversible pharynx with a complex jaw apparatus consisting of ventral mandibles and dorsal maxillae composed of a number of different elements (Table 1.4). This apparatus is an autapomorphy for eunicidans. The jaws are reduced or absent only in some meiofaunal species of the Dorvilleidae and the Diurodrilidae, and some parasitic oeononids, presumably lost

as an adaptation to their mode of living. The prostomium is either unadorned or has some or all of the following complex sensory structures: antennae, eyes, palps and buccal lips. The peristomium is either a single ring, or two rings separated by a groove; peristomial cirri may be present or absent. Parapodia and chaetae are usually present; they are both absent in Diurodrilidae and some species of Dorvilleidae. Parapodia are mostly sub-biramous; the notopodia are very reduced, represented only by dorsal cirri with embedded aciculae or other notopodial rudiments. In the Diurodrilidae and some dorvilleids, the notopodia are absent, resulting in uniramous parapodia. Chaetae are generally simple, capillary or limbate in form, and additional compound chaetae are present in most species. Pygidial cirri number two or four.

The eunicidans have been treated as a family (Ehlers 1864–1868; Fauvel 1923; Day 1967), superfamily (Kinberg 1865; Hartman 1944a; Fauchald 1970) or order (Dales 1962a; Kozur 1970; Fauchald 1977; Orensanz 1990). Historical reviews of taxonomic studies are available in McIntosh (1910) and Hartman (1944a).

Orensanz (1990) gave a valuable review of the ‘Eunicomorpha’. He considered extinct and extant forms, grouping them into five superfamilies and 16 families: seven families with extinct members, eight families with extinct and extant representatives, and the extant Histiobdellidae of uncertain affinities. ‘Ichthyotomidae’, comprising a single species known only from the Mediterranean, is an ectoparasite of eels and has been included in Eunicida (Fauvel 1923; Fauchald 1977); however the present account follows Pettibone (1982), Orensanz (1990) and Rouse & Fauchald (1997) in regarding it as a member of the Phyllodocida. The families Iphitimidae and Dinophilidae are here considered as part of the eunicidan family Dorvilleidae following the convincing arguments of Eibye-Jacobsen & Kristensen (1994). Thus, eight families with living representatives are recognised as eunicidans; they comprise 93 genera and over

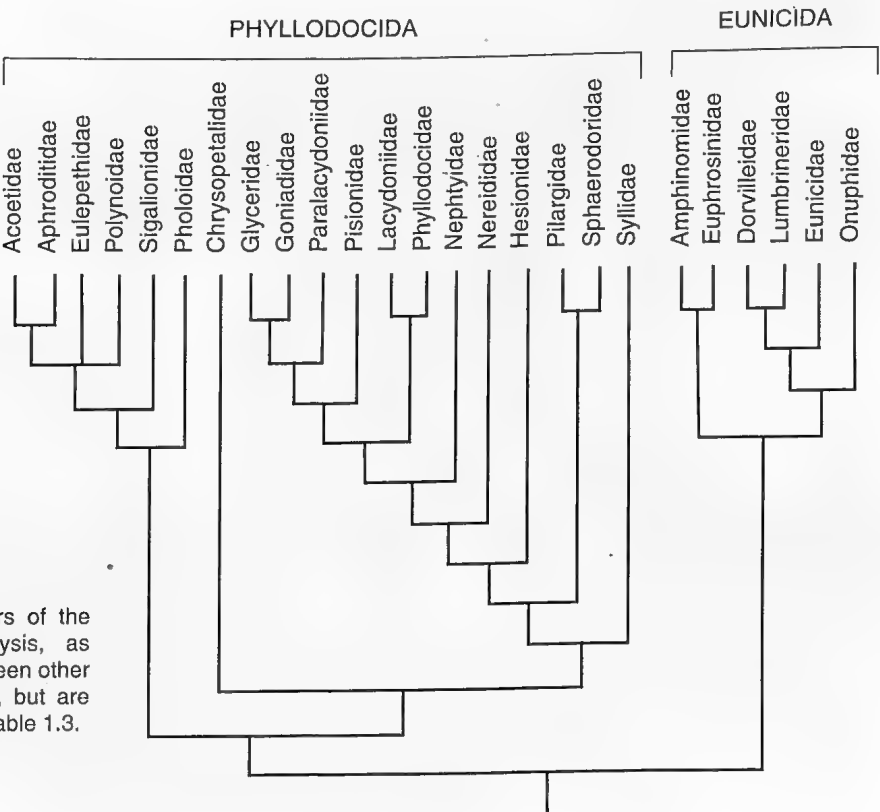


Figure 1.57 Relationships among members of the Aciculata from a restricted taxon analysis, as described by Rouse & Fauchald (1997). Sixteen other families were not included in this analysis, but are proposed to be members of Aciculata; see Table 1.3.

1000 species. The extant Australian fauna is extensive. All of the recognised families, except for Hartmaniellidae, are represented, and comprise 135 reported species in 38 genera. Three extant species of hartmaniellids are known from China, Japan, Madagascar and the Gulf of Mexico; they reach up to 25–50 mm in length. Carboniferous to Cainozoic fossil representatives of the family are known from North America and Europe (Szaniawski & Imaizumi 1996).

Eunicidans include the smallest and largest extant polychaetes ever recorded; they range in size from less than a millimetre to about 6 m. Judging from the size of fossilised jaw elements, extinct worms may also have reached a similar maximum size. Most eunicidans have a typical errant morphology and a very large number of similar segments; over a 1000 segments may be present. The body has no distinct body regions, but the anterior segments may be modified for certain activities, particularly in members of Onuphidae. The characteristic iridescence of the eunicidans is caused by the regular arrangement of the collagenous cuticular fibres (Hilbig 1986).

There has been confusion in the literature concerning the names given to prostomial appendages of eunicidans and their homologues in members of other 'orders'. Orrhage (1995), however, re-investigated the morphology of the eunicidan cephalic nervous system and demonstrated convincingly that the structures previously generally referred to as 'antennae' in onuphids and eunicids represent antennae and palps, and the structures previously referred to as 'palps' represent buccal lips; this terminology is accepted here.

The peristomium comprises one apodous ring in onuphids, some dorvilleids and diurodrilids, and two apodous rings in all other eunicidans. Åkesson (1967a) showed that the two rings in *Eunice kobiensis* represent a subdivided peristomium. This has also been confirmed for dorvilleids (Eibye-Jacobsen 1994), and it has been suggested that the subdivided peristomium may represent an autapomorphy for Eunicida *sensu stricto* (Eibye-Jacobsen & Kristensen 1994).

The jaw apparatus is mineralised with aragonite or calcite and covered with a thin layer of scleroproteins, or consists entirely of scleroproteins and minor trace metals (Colbath 1986a). The ventral mandibles are a pair of flattened shafts, anteriorly widened into cutting plates which are more or less fused along their median line. The mandibles function generally as an area for muscle attachment and support for the dorsal maxillae rather than grasping or biting (Haffner 1959). The maxillae consist of various paired and/or unpaired pieces, connected by thin ligaments; the number of pieces varies between, and to a lesser degree within, families. The maxillary apparatuses, functioning mainly as biting and grasping structures, have been grouped into five evolutionary grades or types (Table 1.4). Ehlers (1864–1868) proposed the first two types, Prionognatha and Labidognatha, to which Kielan-Jaworowska (1966) added Placognatha and Ctenognatha, and Mierzejewski & Mierzejewska (1975) added Xenognatha. Although these types are not clades, but grades of evolution, they are still helpful in considering the phylogeny of extinct and extant eunicidans (Kielan-Jaworowska 1966; Wolf 1980; Edgar 1984; Orensanz 1990).

The mandibles show growth lines, and their gradual growth throughout life in all eunicidans is generally accepted (Paxton 1980; Colbath 1987). Periodical shedding and replacement of maxillae is evident in the ctenognath Dorvilleidae and extinct placognath Mochtyellidae (Kielan-Jaworowska 1966; Mierzejewski 1978). Paxton (1980) suggested that

labidognath and prionognath maxillae grow by expansion resulting from a combination of resorption and deposition through the inner epidermal layer, but this has been rejected by Colbath (1987) and the matter remains unresolved.

Eunicidans are found worldwide from the intertidal zone to great depths. Most species are infaunal burrowers, epifaunal crawlers, or tube builders. Although some are exclusively carnivores or herbivores, most are omnivorous scavengers. However, members of the Histriobdellidae live epizoically in branchial chambers or on surfaces of crustaceans. Most species are broadcast spawners, but some undergo epitoky in association with lunar periodicity. Different forms of broodcare, and rare cases of asexual reproduction and viviparity have been reported.

Because of their durable jaw elements, eunicidans have an excellent fossil record extending back to the Ordovician. Most of these fossils, however, are isolated jaw elements referred to as scolecodonts. Whole jaw assemblages were extremely rare until Kielan-Jaworowska (1966) described material from Poland dissolved out of erratic boulders of Ordovician and Silurian age; many have been described since. Although isolated maxillary plates are common from Ordovician to Devonian deposits in Australia (G. Bischoff personal communication) only one published report is available; Cook & Turner (1994) described six Devonian scolecodont species of placognath and prionognath types from Queensland. Herring (1974) in an unpublished thesis reported Ordovician to Devonian maxillary elements of prionognath and labidognath types from south-eastern Australia.

It is presumed that the primitive jaws of pre-Ordovician times first developed as thickenings of the pharyngeal cuticle, in the form of thin and later, thicker sclerotised plates on which folds and ridges developed becoming later denticulated ridges (Kielan-Jaworowska 1966). The xenognath type (Table 1.4), consisting of one pair of plates with denticulated ridges, resembles this hypothetical structure most closely and may represent the most primitive type (Mierzejewski & Mierzejewska 1975). Placognath and ctenognath types are characterised by having anterior rows of free denticles in addition to the posterior plates; carriers are either absent or insignificant. Xenognath and placognath types are only found in extinct taxa, whereas the ctenognath type is present in extinct taxa and most members of only one extant family, the Dorvilleidae, making it the most ancestral family of eunicidans on fossil evidence.

Prionognath and labidognath types are considered to be more derived (Kielan-Jaworowska 1966); they lack the rows of numerous free denticles, have six or fewer pairs of maxillary plates and a pair of well-developed posterior carriers. The two halves of the prionognath type maxillae are arranged in parallel rows; as interpreted by Orensanz (1990) it only includes one extant family, the Oeonidae. The labidognath type maxillae are so arranged as to form a semicircle in the retracted pharynx, and occur in the extant families Eunicidae, Hartmaniellidae and Onuphidae. The Lumbrineridae may be transitional between prionognath and labidognath, with most species fitting the labidognath type (Orensanz 1990). The affinities of the Histriobdellidae, extremely specialised for its epizoic existence, are uncertain according to Orensanz (1990), but the jaws are considered as prionognath by Rouse & Fauchald (1997). The Diurodrilidae, jawless interstitial forms, may belong in the ctenognath Dorvilleidae (Rouse & Fauchald 1997).

Table 1.4 Evolutionary grades of maxillary apparatuses of extinct and extant eunicidans.

	Xenognatha	Placognatha	Ctenognatha	Prionognatha	Labidognatha
Occurrence	extinct	extinct	extinct & extant	extinct & extant	extinct & extant
Extant families			Dorvilleidae	Oeononidae ?Histriobdellidae	Eunicidae Hartmaniellidae Onuphidae most Lumbrineridae
Maxillary apparatus					
Carriers	present (pseudocarriers)	absent	present (small)	present (long)	present (short)
Plates	1 pair	1–2 pairs	2 pairs	4–5 pairs in parallel rows	4–5 right and 4–6 left plates form a semicircle in the retracted pharynx
Free denticles	absent	2 anterior rows	2–14 anterior rows	absent	absent

Family Dorvilleidae

Dorvilleids may be free-living, symbiotic or parasitic. The family includes some of the smallest polychaetes known. Larger forms have head appendages, well-developed parapodia and are characterised by having a ctenognath jaw apparatus. Smaller forms have lost some, or all, of the head appendages, parapodia and jaws.

The Dorvilleidae is the only extant family of the Eunicida with ctenognath jaws (Fig. 1.58C). It displays a greater diversity in external morphology and jaw structure than any other family in the Eunicida; this may be attributed to the antiquity of the group and the specialisations adopted by most members for a meiofaunal existence. The prostomium is generally rounded and has a pair of ventro-lateral, simple to biarticulated palps and a pair of dorsal, simple or articulated antennae (Fig. 1.58A, B); both palps and antennae may be absent. Eyes are present or absent. The peristomium is a single ring or is subdivided into two rings.

The parapodia are usually sub-biramous (Fig. 1.58E); the notopodium is represented only by a simple to biarticulated dorsal cirrus with or without an embedded acicula. Secondly, the parapodia may be uniramous or absent. Branchiae are occasionally present. Neuropodia bear typically supra-acicular simple (Fig. 1.58F) and furcate chaetae (Fig. 1.58G), and subacicular compound falcigers (Fig. 1.58H) and/or spinigers. However, some or all chaetal types may be absent and the inferiormost chaetae may be simple. Ventral cirri may be present or absent. Pygidial cirri number two or four, may be absent, or may include an

unpaired pygidial stylus. Dorvilleids, particularly the smaller species, are often ciliated in the form of ciliary bands around the prostomium, peristomial rings and trunk segments.

The mandibles (Fig. 1.58D) are unfused and the maxillae are not mineralised; both may be reduced or absent. Typically, maxillae consist of carriers, and paired superior and inferior basal plates with numerous anterior free denticles (Fig. 1.58C). Supplementary rows of spinous denticles may also be present.

Grube (1855) described the first dorvilleid as *Staurocephalus rubrovittatus*, and the family names of Staurocephalidae and Stauronereidae were widely used until Chamberlin (1919) rectified the nomenclatural problems and established Dorvilleidae as the family name (Hilbig 1995). The family was recognised for only the type genus, *Dorvillea*, and *Ophryotrocha* for almost a century until Pettibone (1961) revised the family, describing *Protodorvillea* and *Papilliodorvillea* and resurrecting *Stauronereis*. The great diversity of dorvilleids, however, only became evident with the work by Jumars (1974). He described six new species in three new genera from abyssal depths and provided a phylogeny of the family based on external characters and hard jaw parts. A number of descriptions of new genera and species, by numerous authors followed (for example, Oug 1978; Wainright & Perkins 1982; Westheide 1982; Westheide & Riser 1983; Glasby 1984; Westheide & Nordheim 1985; Wolf 1986a, 1986b; Nordheim 1987; Orensanz 1990; Hilbig & Blake 1991; Eibye-Jacobsen & Kristensen 1994). Many of these were meiofaunal with pedomorphic characteristics.

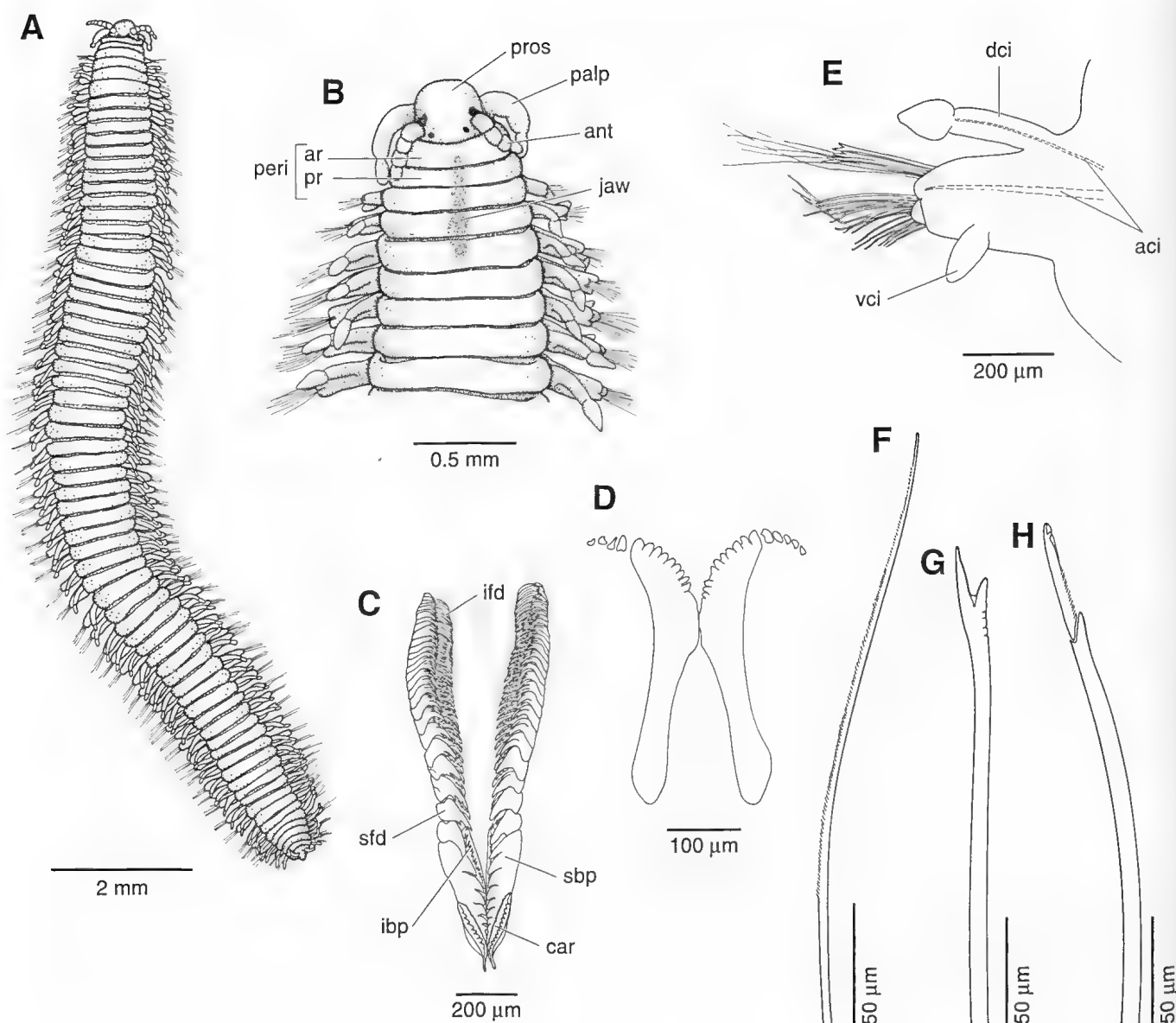


Figure 1.58 Family Dorvilleidae. *Schistomeringos loveni*. **A**, entire animal, dorsal view. **B**, anterior end, dorsal view. **C**, **D**, jaw parts: **C**, maxillae, dorsal view; **D**, mandibles, ventral view. **E**, parapodium from chaetiger 10, anterior view. **F–H**, chaetae from parapodium of chaetiger 10: **F**, simple chaeta; **G**, furcate chaeta; **H**, compound falciger. **aci**, aciculae; **ant**, antenna; **ar**, anterior ring; **car**, carrier; **dci**, dorsal cirrus; **ibp**, inferior basal plate; **ifd**, inferior free denticle; **jaw**, jaw apparatus; **palp**, palp; **peri**, peristomium; **pr**, posterior ring; **pros**, prostomium; **sbp**, superior basal plate; **sfd**, superior free denticle; **vci**, ventral cirrus.

[A. Murray]

The Dorvilleidae as recognised here also includes Dinophilidae *pro parte* and Iphitimidae. Sveshnikov (1958) suggested that the dinophilids could be regarded as secondarily reduced eunicemorph polychaetes. Although earlier considered as unlikely (Hermans 1969), this idea has recently received convincing support (Åkesson 1977; Orensanz 1990; Eibye-Jacobsen & Kristensen 1994). Orensanz (1990) recognised the close relationship among Dorvilleidae, Iphitimidae and Dinophilidae, but treated the three families separately. Eibye-Jacobsen & Kristensen (1994) tested several phylogenetic hypotheses and provided convincing evidence that the three families should be combined. They also recognised and provided a key to the 33 genera in the Dorvilleidae. The Dinophilidae, comprising four genera, were also previously considered as one of the 'archiannelidan' families (Fauchald 1977). Kristensen & Niilonen (1982) studied the genus *Diurodrilus* and removed it from the Dinophilidae, placing it in a new family, the Diurodrilidae; the other three genera are considered to be dorvilleids. All known species of *Iphitime* are symbionts of

crustaceans and were regarded as members of the Lysaretidae (now Oenonidae) until Fauchald (1970) raised the genus to family status. After a free-living iphitimid (Kirkegaard 1977) and dorvilleids with similar jaw structures became known, Armstrong & Jumars (1978) suggested that the two families were synonymous; Gaston & Benner (1981) placed the *Iphitime* among the Dorvilleidae.

The first Australian dorvilleids described were *Schistomeringos loveni* (Figs 1.4I, 1.58A) (Kinberg 1865) and *Dorvillea australiensis* (McIntosh 1885), from Port Jackson where both species still occur; they were originally described in the genus *Staurocephalus*. Glasby (1984) reviewed two genera from southern and eastern Australia and listed three species of *Schistomeringos* and two of *Dorvillea*. Since then, two meiofaunal species, *Coralliotrocha natans* and *Pettiboneia australiensis*, have been described by Westheide & Nordheim (1985) from the Great Barrier Reef, and Hartmann-Schröder (1985a) described *Schistomeringos paraloveni* from South Australia and reported *Ophryotrocha claparedei* from northern New South Wales (Hartmann-

Schröder 1989, 1990). Other species observed from Australian waters are *Dinophilus gyrotilatus* and *Ophryotrocha labronica* (H. Paxton personal observation), an undescribed species of *Protodorrillea* (H. Paxton personal observation), *Coralliotrocha* and *Parapodrilus* (R. Kristensen personal communication). Thus, the total number of Australian dorvilleids is 14 in 8 genera; the worldwide dorvilleid fauna comprises about 110 species in 33 genera.

Most dorvilleids are very small to small in size and include some of the smallest polychaetes; the largest female specimen of *Neotenotrocha sterreri* (the holotype) measures just a quarter of a millimetre in length. Species of *Dorrillea* are among the largest in the family, for example, *D. australiensis* can reach a length of 100 mm and consist of 150 segments. Typically, larger species are vermiform without any body regionalisation and have a full complement of jaw elements, head appendages and parapodial structures. There is an increasing degree of paedomorphic organisation from this 'typical' form to the most reduced meiofaunal taxa that have a larval appearance, lack jaws, parapodia and chaetae, and have ciliary rings and sensoria. The anatomy and ultrastructure of the pharynx of 'dinophilids' and 'dorvilleids' *sensu stricto* has been investigated by Purschke (1985a, 1987); he showed that the two forms are not directly homologous.

Many dorvilleids are carnivores, but they can survive on a herbivorous diet (Fauchald & Jumars 1979). Some of the smaller species, particularly *Ophryotrocha* species, are well known to scrape algae off the walls of aquaria and thrive in culture on a diet of spinach (Åkesson 1975). Glasby (1984) observed detrital material and sediment in the gut of *Schistomeringos loveni* from Sydney and calcareous material in specimens of the same species from the Great Barrier Reef, suggesting that *S. loveni* can feed on detrital matter as well as bore into corals (Hutchings & Peyrot-Clausade 1988). Symbiotic or parasitic dorvilleids are members of the genus *Iphitime* (Paiva & Nonato 1991) and some species of *Ophryotrocha* live in the branchial cavities or on the carapace of decapod crustaceans (Martin, Abelló & Cartes 1991).

The very small 'dinophilids' and *Apodotrocha progenerans* lack a blood vascular system, but have protonephridia. Slightly larger forms, such as *Dorrillea sociabilis* and *Ophryotrocha puerilis*, have a blood vascular system and metanephridia (Smith & Ruppert 1988). These reports support the model of Ruppert & Smith (1988) that animals which have a blood vascular system should have metanephridia and that animals lacking such a system should have protonephridia.

References to dorvilleid reproduction and development are available in Richards (1967), Åkesson (1975) and Westheide (1982). The sexes are usually separate and lack sexual dimorphism, except in the genera *Dinophilus* and *Ophryotrocha*. Species of the former display male dwarfism (Sudzuki & Sekiguchi 1972), whereas many species of the latter show only slight size differences (Åkesson 1984), but have marked differences in jaws structure between the sexes (Pfannenstiel 1975). Epitokal modifications, such as enlarged eyes and more numerous and longer chaetae, have been observed in species of *Dorrillea* (Richards 1967), *Ougia* and *Parougia* (Oug 1978) and *Protodorrillea* (H. Paxton personal observation). Reproduction has been most extensively studied in the genus *Ophryotrocha* which can be easily reared in laboratory cultures. Gonochorists, consecutive hermaphrodites, simultaneous hermaphrodites, and viviparity have been reported in this genus (Åkesson 1975, 1994). Asexual reproduction has been reported in species of *Dorrillea* (Åkesson & Rice 1992).

Primordial germ cells and early stages of oogenesis in *Ophryotrocha puerilis* have been studied by Pfannenstiel & Grünig (1982); each oocyte is attached to a nurse cell. *Dinophilus gyrotilatus* has an aberrant form of oogenesis; dimorphic oocytes are present (Grün 1972). Sperm for several species of *Ophryotrocha* and 'dinophilids' have been described by Jamieson & Rouse (1989) as the 'introsperm' type. Introsperm never enter the water as in the case of internal fertilisation or are introduced very transiently into the water during pseudocopulation (Rouse & Jamieson 1987). Most species of *Ophryotrocha* pseudocopulate after a brief courtship display. During pseudocopulation male and female gametes are shed directly into an egg case or cocoon which is then tended by both parents. The sperm are very modified, lacking a midpiece and most or all of the flagellum, rendering them immotile. In *Dinophilus*, copulation is by hypodermic impregnation and the fertilised eggs are laid in cocoons or capsules (Westheide 1984).

Small dorvilleid species often brood their egg masses, whereas moderately sized species broadcast spawn, sometimes after a brief swarming phase. Free-spawning species, such as *Dorrillea rudolphi*, spend a week as lecithotrophic planktonic larvae before they settle (Richards 1967), whereas the larvae of brooding species undergo direct development and leave the egg case after about a week (Åkesson 1973). The dorvilleid jaw apparatus undergoes a series of moults before the adult condition is reached (Sudzuki & Sekiguchi 1972).

Dorrilleids move freely through the substratum. The smaller species are interstitial, living between sand grains, and larger ones can be found underneath stones or shells. They surround themselves with abundant quantities of mucus, but do not build solid tubes like many other eunicidans.

Species of *Ophryotrocha* can easily be kept in culture (Pfannenstiel 1973a) and have been used for a number of studies including sexual differentiation in consecutive hermaphrodites (Pfannenstiel 1973b; 1975; Kegel & Pfannenstiel 1983); life history studies (Åkesson 1982); induced hermaphroditism (Bacci, Lanfranco, Mantello & Tomba 1979); sex ratio and allocation (Sella 1990; Sella & Bona 1993; Premoli & Sella 1995); crossbreeding to study incipient speciation (Åkesson 1984); assessing the effects of chemicals on reproduction (Åkesson 1970, 1983); and, the effects of temperature and salinity on life cycles (Åkesson & Costlow 1978).

Species of *Ophryotrocha* are often introduced into aquaria with marine animals or plants or even seawater. Such a population from Sydney Harbour has been maintained for several years (H. Paxton personal observation). Morphological and life history studies indicate that it is a species of the *O. labronica* complex. Crossing experiments with several populations of *O. labronica* and closely related species have demonstrated that the Sydney population is closest to a population from Naples, Italy, raising the possibility that they may have been introduced with ballast waters or other means of human intervention (B. Åkesson personal communication).

Dorrilleids are found in all the oceans of the world, at all depths. The Australian dorvilleid fauna is probably much more extensive than present records indicate. *Dorrillea similis* and *Schistomeringos sphairatolobos* are only known from the tropical eastern coast, whereas *S. filiformis* extends to the eastern subtropical zone (Glasby 1984), and *S. paraloveni* lives in the antiboreal zone of South Australia (Hartmann-

Schröder 1985a). *Schistomeringos loveni* is very widespread, occurring from tropical Queensland to Tasmania and South Australia, whereas the large *Dorvillea australiensis* has been reported from New South Wales along the southern coast to Western Australia (Glasby 1984).

The Dorvilleidae represent the most ancient living members of the Eunicida (Kielan-Jaworowska 1966; Orensanz 1990). The affinities within Dorvilleidae have been examined by Eibye-Jacobsen & Kristensen (1994). Their preferred cladogram identifies four clades each with at least three genera and five with two genera each, whereas the remaining genera stand as autapomorphic lines. The plesiomorphic clade includes the more or less 'typical' dorvilleids (with characters such as a full complement of jaw elements, head appendages and parapodial structures) comprising the genera *Schistomeringos*, *Dorvillea*, *Protodorvillea* and *Meiodorvillea*. The other genera are characterised by an increasing loss of the 'typical' dorvilleid characters as an adaptation to a meiofaunal life with *Ikosipodus*, *Neotenotrocha*, *Parapodrilus*, *Apodotrocha* and the three genera of 'dinophilids', *Apharyngtus*, *Trilobodrilus* and *Dinophilus*, placed as the most derived genera. It is interesting to note that all the 'iphitimids' except *Pinniphitime* combine in a clade with *Ophryotrocha* and *Parophryotrocha*.

Fossil dorvilleids from the Jurassic and Cretaceous include species of *Ophryotrocha*, *Schistomeringos*, and perhaps *Dorvillea* (Szaniawski & Gazdzicki 1978; Erve 1981). The related, extinct Tetraprionidae, however, are known from Ordovician and Silurian periods (Fig. 1.39; Kozur 1970). Kozur (1970) formally recognised the relationship between Dorvilleidae and Tetraprionidae by establishing the superfamily Dorvilleacea for the two families. No Australian fossils are known.

Family Eunicidae

Eunicids have many segments and may attain a length of up to 6 m (Pl. 1.3). They may be free-living, tubicolous or burrowers in a wide range of habitats including crevices and under rocks on rocky shores, in sand or mud and dead coral. The head bears sensory appendages. Some species are sometimes referred to as blood worms for their well-developed parapodial branchiae are often blood-red.

Members of the Eunicidae are distinguished from other families in Eunicida by having a prostomium with one to three antennae which lack ringed ceratophores (Fig. 1.59A). Fauchald's (1992a) definition of the family is followed here, but the traditional terminology applied to prostomial appendages is replaced with that proposed by Orrhage (1995). The prostomium is bilobed or entire, with a pair of reduced to well-developed buccal lips. Species of *Eunice* have five prostomial appendages comprising two palps and three antennae (Fig. 1.59A); one to two antennae and/or palps may be absent in other genera. Eyes are usually present. The peristomium consists of two rings; a pair of peristomial cirri is present or absent on the posterior ring. The parapodia are sub-biramous (Fig. 1.59D); the notopodium is represented only by a dorsal cirrus with or without embedded aciculae. Branchiae, when present, consist of single or pectinate filaments. The neuropodia have superior limbate (Fig. 1.59E) and pectinate chaetae (Fig. 1.59F), and inferior compound falcigers (Fig. 1.59G) or spinigers, and subacicular hooks (Fig. 1.59H), and ventral cirri. Pygidial cirri number two or four. The jaws comprise ventral, unfused mandibles (Fig. 1.59C), and dorsal maxillae of the labidognath type (Fig. 1.59B). The maxillae are mineralised with aragonite and comprise a pair of short

carriers and four to five toothed plates on the right and five to six toothed plates on the left. The maxillary plates are asymmetrical with the right maxilla III missing and the right maxilla IV being larger than the corresponding left one.

The family Eunicidae is one of the oldest polychaete families and hence its early history is beset with nomenclatural problems which have been discussed in detail by Fauchald (1992a). Although Savigny (1820) is usually accredited with the family name, Fauchald demonstrated that the first valid mention of the family is by Berthold (1827). Some authors have interpreted the Eunicidae to include other eunicidan families as subfamilies (see Fauvel 1923; Day 1967), a view which has generally been abandoned and is not followed here. Important revisions include those by Hartman (1944a), Fauchald (1970) and Orensanz (1990). Worldwide, Fauchald (1977) recognised 241 species in 7 genera, of which about 150 belong to *Eunice* and about 50 to *Marphysa*.

The earliest descriptions of Australian eunicids are either insufficient (for example, *Lysidice robusta*), beset with nomenclatural problems (for example, *Eunice tentaculata*), or are only based on the original collection, with no further reports since they were first collected (for example, *Eunice aequabilis* and several other species of *Eunice* collected during the *Challenger* expedition and described by McIntosh 1885). Most of the common Australian species have wide Indo-Pacific distributions. The apparent morphological uniformity of eunicids complicates their classification. Fauchald (1986, 1992a) has examined and redescribed type specimens of *Eunice* in preparation for further revision. The present treatment follows Orensanz (1990) who recognised seven eunicid genera; *Paraeuniphysa* (Wu & He 1988) and *Fauchaldius* (Salazar-Vallejo & Carrera-Parra 1997) have been described since. Five of these genera, *Eunice*, *Lysidice*, *Marphysa*, *Nematonereis* and *Palola* occur in Australia and comprise at least 40 species.

Eunicids range from less than 10 mm to 6 m in length, and consist of up to 1500 segments (Fauchald 1992a). There is no regionalisation of the body, but the parapodia gradually change shape along the body. The general morphology is very uniform within the family, differing only in the shape and number of appendages of the prostomium, and the number and distribution of the branchiae.

The respiratory pigments in *Eunice aphroditois* are extra-cellular haemoglobins as they are in most other larger polychaetes (Weber 1978b). The innervation of the cephalic nervous systems of *E. norvegica* and *E. pennata* has been re-examined and compared with that of other polychaete families (Orrhage 1995). Orrhage proved that the previously referred to 'ventro-lateral antennae' [outer lateral antennae (A-I) of Fauchald (1992a)] are homologous with palps, and the 'palps' are part of the alimentary canal and thus represent buccal lips.

Eunicids are dioecious and show no sexual dimorphism. Most reports of reproduction in the Eunicidae comprise observations of swimming reproductive worms or eggs in gelatinous masses (Richards 1967). The spermatozoa of *Marphysa* species are of the ect-aquasperm type (Jamieson & Rouse 1989), typical of broadcast spawners. The best known eunicid reproductive pattern is that of the Pacific Palolo worm, *Palola viridis*. The adults live in rock and coral crevices, and the posterior parts of the worms become modified and filled with gametes. The time of spawning is correlated with lunar phases and occurs once a year at which time the worms leave their burrows and the posterior ends (the epitokes) detach. The epitokes come to the surface, forming large writhing swarms. After spawning the epitokes die, whereas the anterior parts (the atokes) return to their

burrows and regenerate (Hauenschild, Fischer & Hofmann 1968; Fauchald 1992b). The circumtropical *Palola siciliensis* occurs in Australia, but is not known to swarm. The gametes of Palolo worms are shed via the ruptured body wall of the epitokes. Gonoducts, however, have been described for *Marphysa gravelyi* from India (Schroeder & Hermans 1975). Generally, the eunicids have mixonephridia with a simple excretory canal and a large coelomostome that also functions as a genital funnel (Goodrich 1945). The oocytes are relatively large (at least 100 µm in diameter) and provide sufficient nutrition for the planktonic larva to survive without feeding (lecithotrophic) until it settles on the bottom to assume a benthic existence. For several species of eunicids developmental studies report the presence of planktonic atrochal larvae that settle on the bottom after 3–8 days (Richards 1967); direct development is unknown for eunicids (Bhaud & Cazaux 1987).

Juveniles are mostly free-living in cracks and crevices, but some become tubicolous as they become larger (Fauchald & Jumars 1979). *Eunice aphroditois* is a large species growing to more than 1 m in length and can be found under rocks at low tide on the rocky shores along the southern Australian coast. It is a dark purple-brown colour with a brilliant iridescence

(Dakin, Bennett & Pope 1966). Younger *E. aphroditois* are errant, but larger ones make a simple papery tube (Day 1967). Other eunicids, however, construct tougher, more complex tubes. *Eunice impex*, recently reported from Jervis Bay, New South Wales, builds a tree-like structure that comprises up to 20 primary tubes, basally entwined into a stem that is partially embedded in the sediment. Distally the tubes branch with up to 11 terminating branches per primary tube (Jacoby, Wallner, Langtry & Hutchings 1995). Different tree-like tubes are produced by *Eunice metatropos* from Western Australia, in which the primary tubes, after separating from the surrounding tubes, branch alternately, producing a zigzag appearance (Hanley 1986).

Other eunicids burrow in sand and mud or in dead coral. *Palola* species are known to attach themselves with maxillae to the coral while the mandibles are used as a rasp to gouge and scrape the coralline rock (Gathof 1984). On the Great Barrier Reef eunicid tunnels in dead corals show clear signs of the inhabitant's teethmarks (P. Hutchings personal communication). Anteriorly, the worm is very muscular, supporting the large protrusile jaw apparatus, as well as providing strength for burrowing and locomotion. Free-living

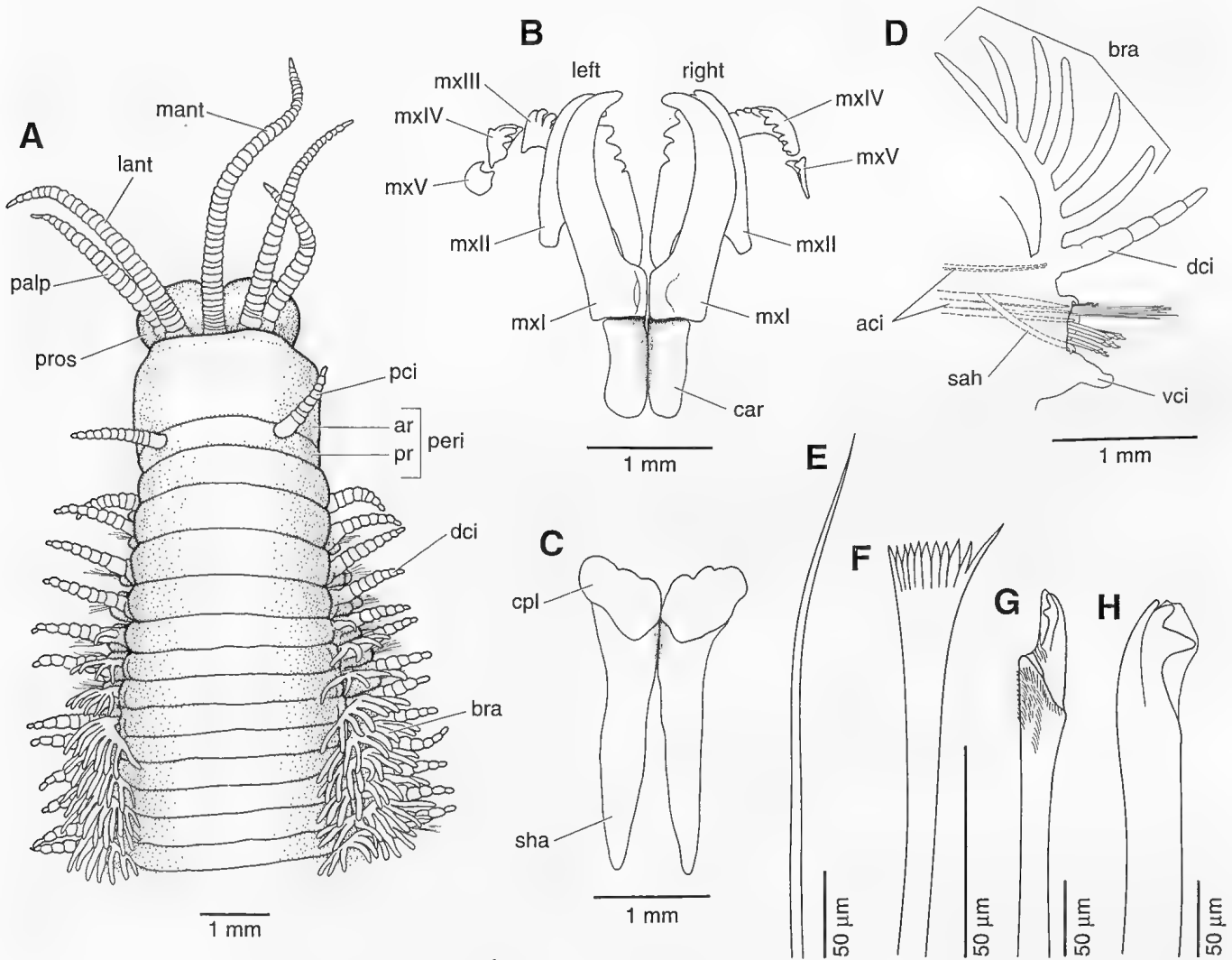


Figure 1.59 Family Eunicidae. *Eunice antennata*. **A**, anterior end, dorsal view. **B**, **C**, jaw parts: **B**, maxillae, dorsal view; **C**, mandibles, ventral view. **D**, parapodium from chaetiger 29, anterior view. **E**–**H**, chaetae: **E**, simple limbate chaeta from parapodium of chaetiger 41 (wings obscured); **F**, pectinate chaeta from parapodium of chaetiger 41; **G**, compound falciger from parapodium of chaetiger 29; **H**, subacicular hook from parapodium of chaetiger 29. **aci**, aciculae; **ar**, anterior ring; **bra**, branchia; **car**, carrier; **cpl**, cutting plate; **dci**, dorsal cirrus; **lant**, lateral antenna; **mant**, median antenna; **mxI**–**V**, maxillary plates I–V; **palp**, palp; **pci**, peristomial cirrus; **peri**, peristomium; **pr**, posterior ring; **pros**, prostomium; **sah**, subacicular hook; **sha**, shaft; **vci**, ventral cirrus. [A. Murray]

1. CLASS POLYCHAETA

and tubicolous species are mainly carnivores, whereas burrowing species are omnivores, feeding on organisms living in the substratum (Fauchald & Jumars 1979).

Eunicids have a lifespan of several years and have been classed by Fauchald (1983) in his second pattern of life diagrams, which show low reproductive efforts, moderately large to large eggs, and non-planktotrophic development. Hutchings & Jacoby (1994) studied the temporal and spatial patterns in the distribution of infaunal polychaetes in Jervis Bay, New South Wales and found that the densities of *Eunice australis* from vegetated sites varied significantly with time. They concluded that the animals probably reach maturity in their second year, are broadcasters and recruit by pelagic larvae.

Many of the larger eunicids are valued as bait worms; particularly the 'bloodworm' or 'mud worm', *Marphysa* species, which occurs in estuaries. It has been reported as *Marphysa sanguinea* from Western Australia, New South Wales and Queensland (Hutchings & Murray 1984), but is now regarded as an undescribed species (P. Hutchings personal communication).

Eunicids are present in all marine benthic environments and are particularly common in tropical shallow seas, in coral reef rubble and in mangrove swamps (Fauchald 1992a). A number of species also live in slope and abyssal depths (Fauchald 1982a). The family is represented in all Australian states (Day & Hutchings 1979). The larger species (for example, *Eunice antennata*, *E. aphroditois*, *E. australis*) have been reported more widely than smaller species, but this may be due to their greater visibility.

The closest relative, or sister group, of Eunicidae is the family Onuphidae. The synapomorphies are a similar jaw apparatus, parapodial structures and the presence of antennae. The affinities within the family are less clear and the generic divisions are still far from satisfactory (Orensanz 1990). Of the extinct families, only the Paulinitidae (records until the end of the Carboniferous period; Fig. 1.39) shows strong similarity to the extant Eunicidae and Onuphidae and can be regarded as their possible ancestor (Kozur 1970). Isolated Palaeozoic eunicid jaw pieces have been reported from Europe and North America, and the oldest completely fossilised specimens of the family are known from the Upper Carboniferous of the Essex fauna in the United States of America (Thompson & Johnson 1977). Australian eunicid fossils are not known.

Family Lumbrineridae

Lumbrinerids are long, slender worms which usually burrow through sediments or crawl over the substratum or in crevices; some are tubicolous. Their cylindrical or globular head lacks any obvious appendages and their smooth body gives them an earthworm-like appearance.

Lumbrinerids are distinguished from other members of Eunicida by the usual absence of antennae and palps, and the presence of symmetrical maxillae with generally short carriers. The prostomium (Fig. 1.60A) is rounded or pointed, and only in species of *Lysarete* and *Kuwaita* does it bear small antennae. Small nuchal papillae are present or absent. The peristomium consists of two rings and lacks peristomial cirri. Parapodia (Fig. 1.60D) are uniramous (neuropodia only) to sub-biramous where the notopodium is reduced and is only represented by conical knobs with internal aciculae, or flattened dorsal cirri. Branchiae are generally absent. The neuropodia have simple limbate chaetae (Fig. 1.60E) and

usually simple and/or compound hooks (Fig. 1.60F, G). Compound spinigers are rarely present (*Lumbricalus*). Pectinate chaetae and subacicular hooks are absent. Ventral cirri are generally absent and pygidial cirri number two or four. The jaws consist of ventral, fused mandibles and dorsal maxillae (Fig. 1.60B, C). In most lumbrinerids the maxillae are of the labidognath type. Some, however, appear to be transitional to the prionognath type and have been referred to as sub-prionognath by Orensanz (1990). The maxillae are mineralised with calcite, and composed of four or five pairs of symmetrical plates (maxilla I with lateral support or bridle) and a pair of usually short carriers.

The family Lumbrineridae was erected by Schmarda (1861) and has been treated as a subfamily of Eunicidae by several authors (see McIntosh 1910; Fauvel 1923; Day 1967). As a result of the extreme external uniformity of these animals, most species were placed in the nominal genus. Although a number of genera had been erected by earlier workers, only three or four genera are generally recognised (Hartman 1944a; Day 1967; Fauchald 1977). A new period of revisionary work, including resurrecting old and describing new genera, with greater emphasis on the jaw apparatus and the recognition of autapomorphic characters was started by Orensanz (1973) and followed by Levenstein (1977), Hartmann-Schröder (1979), Perkins (1979) and Miura (1980). Orensanz (1990) revised the family and provided a key to 11 genera. Frame (1992) resurrected *Scoletoma* and described a new genus, *Lumbricalus*. The works of Orensanz (1990) and Frame (1992) are followed here. Worldwide, Lumbrineridae include more than 200 species in 13 genera.

The earliest records of Australian lumbrinerids are those of *Lumbrineris brevicirra* and *L. jacksoni*, both from Sydney, New South Wales. Although members of the family are very common and have been reported in many papers, no studies have been dedicated to Australian lumbrinerids. Twelve species in four genera have been reported from Australian waters: *Lysarete australiensis*, *Augeneria verdis*, *Arabelloneris broomensis* and nine species of *Lumbrineris sensu lato*. The actual diversity, however, is expected to be much higher.

Lumbrinerids are long and muscular or thread-like, and usually do not exceed 100 mm in length and 2 mm in width. However, some giant worms such as *Lumbrineris impatiens* from the Italian coast can reach 400 mm in length (Gambi *et al.* 1994). There is no regionalisation of the body, but the shape of the parapodial lobes gradually changes along the length of the body.

Lumbrinerids are usually free-living and burrow in sand or mud, or creep between algal holdfasts and in crevices (Pettibone 1982). Some lumbrinerids are tubicolous; *Ninoe nigripes* builds tubes of mucus mixed with mud and sand (Pettibone 1963), and some species have been observed building temporary mucous housings in aquaria (Fauchald & Jumars 1979). One species, *Lumbrineris flabellicola*, is a symbiont of scleractinian corals, attaching their membranous transparent tubes to the side of the host (Martin & Britayev 1998 and references therein). Lumbrinerids have been reported as herbivores, carnivores and deposit-feeders (Fauchald & Jumars 1979).

Lumbrinerids are dioecious and show no sexual dimorphism. Spermatozoa of a species of *Lumbrineris* has been shown to be of the ect-aquasperm type (Jamieson & Rouse 1989). Oocytes range in diameter from 190–500 µm and are often found in gelatinous masses (Richards 1967). In the Japanese population of the presumably cosmopolitan *Lumbrineris latreilli*, the egg masses are attached to algae, where the

embryos undergo direct development; the juveniles leave when they attain four to seven body segments (Okuda 1946). In contrast, a population of *L. impatiens* from the North Atlantic French coast has planktonic lecithotrophic larvae (Cazaux 1972). Nothing is known about the reproduction or development of Australian lumbrinerids.

Lumbrinerids have a lifespan of several years. They have been classed by Fauchald (1983) in his second pattern of life diagrams; this includes features such as low reproductive efforts, moderately large to large eggs, and non-planktonic development.

Lumbrinerids are most common in sandy and muddy bottoms at shelf depths, but can be found anywhere from the intertidal zone to abyssal depths (Fauchald 1977). A number of species

are presumed to have a cosmopolitan distribution. However, members of the family are difficult to identify, and further study may show more restricted distributions.

Traditionally, the Lumbrineridae were considered to be closely related to the Eunicidae and Onuphidae (Hartman 1944a; Kielan-Jaworowska 1966). However, Kozur (1970) recognised that the lumbrinerid genus *Lysarete* can be considered as the sole Recent representative of the extinct Paulinitaceae; other members of the Lumbrineridae are thought to be derived from the extinct Sciotoprionidae (Szaniawski 1996; Fig. 1.39). This new interpretation aligns *Halla* and *Notocirrus* (previously members of Arabellidae, but now in Oeononidae) with the Lumbrineridae. This has been supported by Orensanz (1990) by stating that the Oeononidae is the closest extant relative or sister group of the Lumbrineridae.

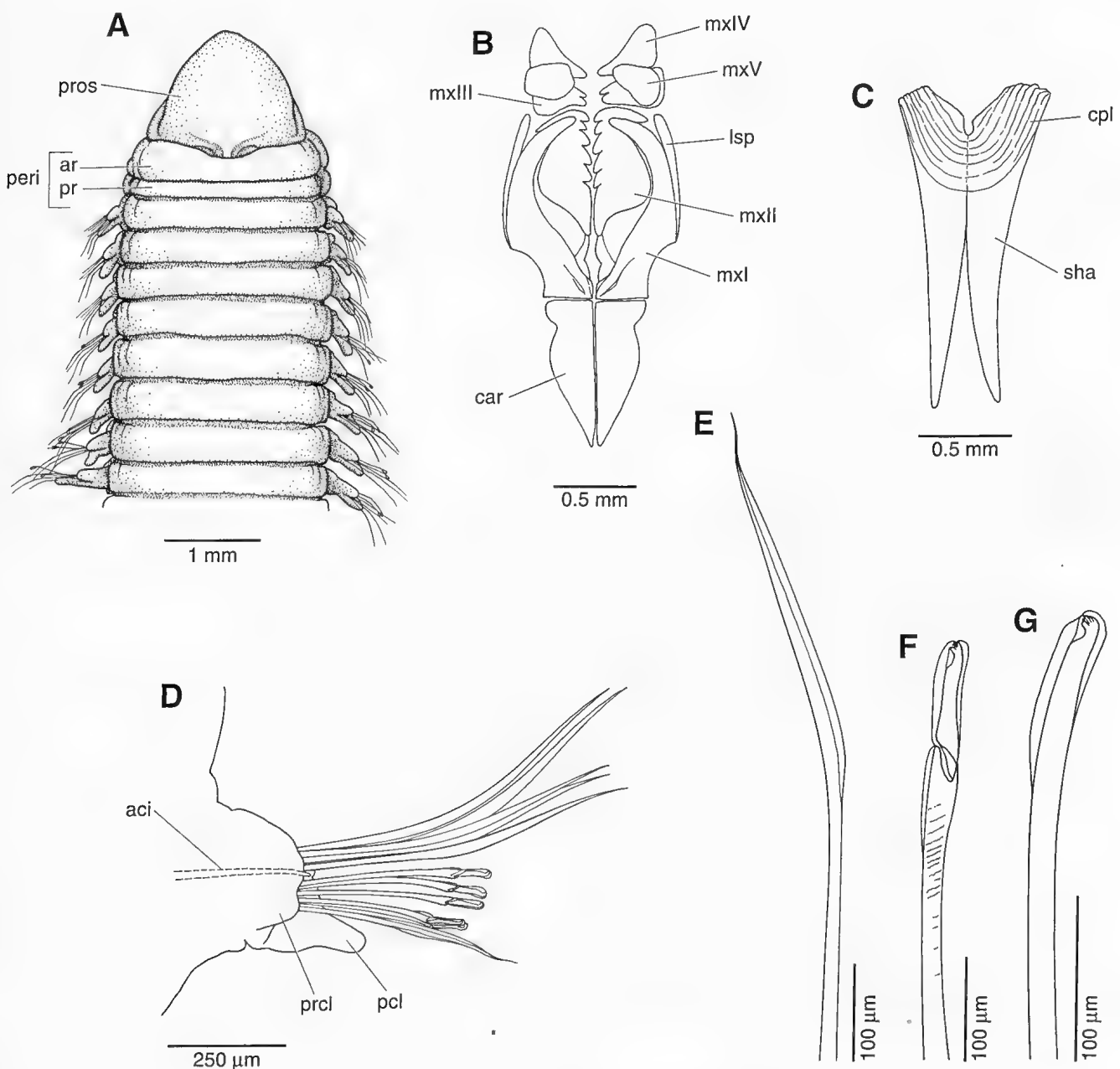


Figure 1.60 Family Lumbrineridae. *Lumbrineris* cf. *latreilli*. **A**, anterior end, dorsal view. **B**, **C**, jaw parts: **B**, maxillae, dorsal view; **C**, mandibles, ventral view. **D**, parapodium from chaetiger 11, anterior view. **E–G**, chaetae: **E**, simple limbate chaeta from parapodium of chaetiger 11; **F**, compound hook from parapodium of chaetiger 11; **G**, simple hook from parapodium of chaetiger 43. **aci**, acicula; **ar**, anterior ring; **car**, carrier; **cpl**, cutting plate; **lsp**, lateral support; **mxI–V**, maxillary plates I–V; **pcl**, postchaetal lobe; **peri**, peristomium; **pr**, posterior ring; **prcl**, prechaetal lobe; **pros**, prostomium; **sha**, shaft. [A. Murray]

Family Oeononidae

Oeononids are mostly large worms which burrow in sand and mud, but a number of species are parasitic. They resemble lumbrinerids in appearing earthworm-like, but can be distinguished from them by the presence of a flattened head.

The Oeononidae are the only extant family of Eunicida with maxillae clearly defined as prionognath. The prostomium is rounded or pointed (Fig. 1.61A), and is generally without appendages, except for one small antenna in *Tainokia* species, and three in species of *Oeonone* and *Halla*; eyespots may be present at the posterior margin. The peristomium may consist of one or two rings. Parapodia are sub-biramous (Fig. 1.61D). The notopodia are represented by button-like to lamellate lobes (dorsal cirri) with internal aciculae. Branchiae are absent. The neuropodial chaetae are simple limbate (Fig. 1.61E); in some genera additional bidentate subacicular hooks (Fig. 1.61F) or large spines are present. Ventral cirri are absent; pygidial cirri number two to four. The mandibles (Fig. 1.61C) are unfused, lack visible growth rings, and may be reduced or absent in some species. The maxillae (Fig. 1.61B) are unmineralised, and are generally composed

of five pairs of plates and long, slender carriers often with a ventral ligament (or 'third carrier'). The maxillary plates are asymmetrical in species of *Oeonone* and *Notocirrus* where the first right maxillary element is a 'basal plate' and the right maxilla III is lacking. This is common in extinct labidognath and prionognath jaws, but is not found in any other extant eunicidan family. The maxillae may be reduced or absent in some parasitic species.

Although the family Oeononidae [as Oeononidea (sic)] was erected by Kinberg (1865), it was not widely used and has only been recently resurrected for the genera *Oeonone*, *Halla* and *Tanaikoia* (which were placed in the Lysaretidae for most of this century) and the genera of Arabellidae. Kinberg (1865) established the families Lysaretea (sic), Oeononidea (sic) and Laidea (sic); he included Lysaretea in his group A (symmetrical maxillae and short carriers), and Oeononidea and Laidea in his group B (asymmetrical maxillae and long carriers). Although Ehlers (1864–1868) grouped *Lysarete* with *Oeonone* and *Arabella*, he acknowledged later (1887) that *Lysarete* is related to the lumbrinerids and *Oeonone* to the arabellids (Ehlers 1887). Hartman (1944a), however, followed

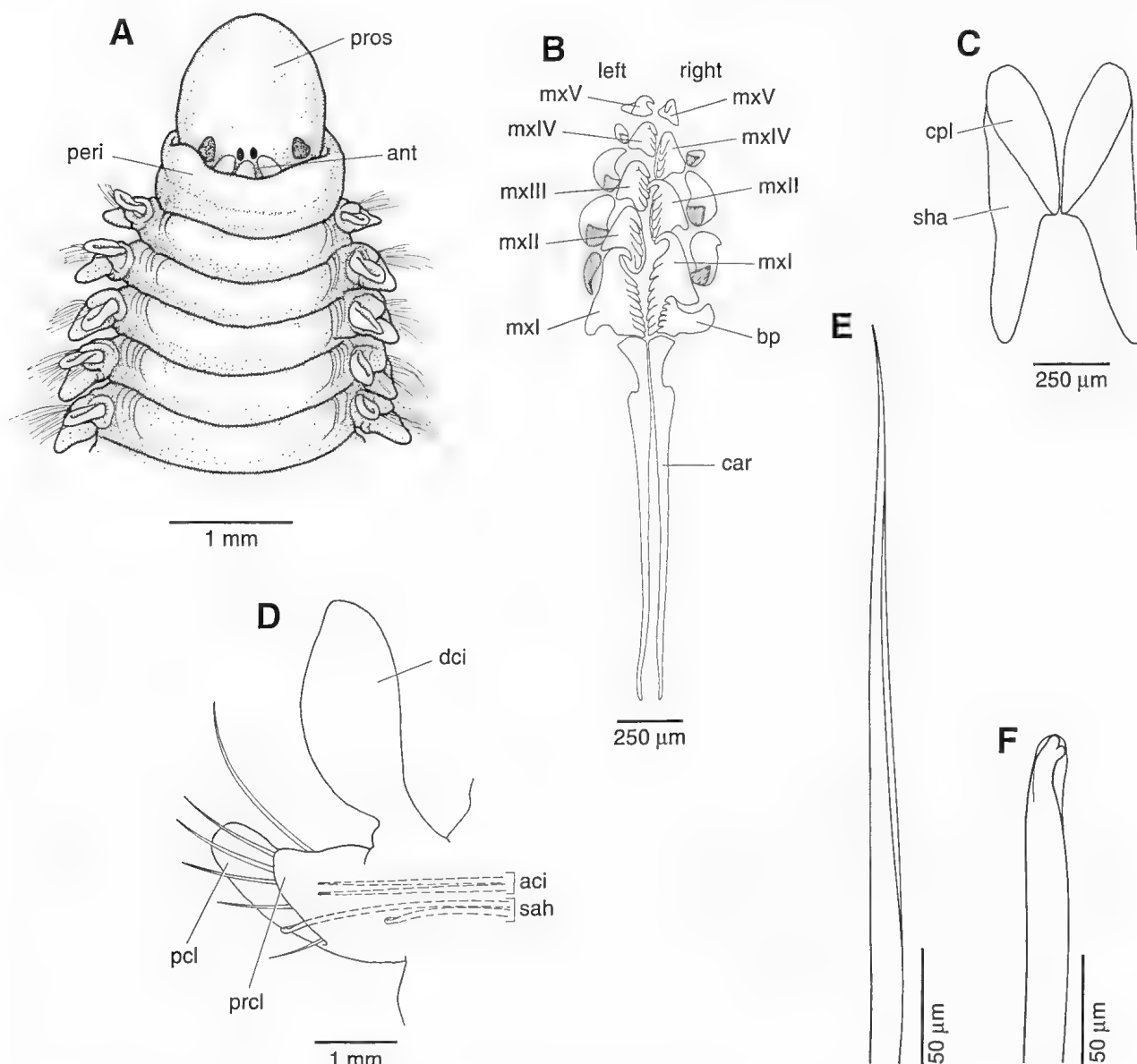


Figure 1.61 Family Oeononidae. *Oeonone fulgida*. **A**, anterior end, dorsal view. **B**, **C**, jaw parts: **B**, maxillae, dorsal view; **C**, mandibles, ventral view. **D**, parapodium from chaetiger 45, anterior view. **E**, **F**, chaetae from parapodium of chaetiger 45: **E**, simple limbate chaeta; **F**, subacicular hook. **aci**, aciculae; **ant**, antenna; **bp**, basal plate; **car**, carrier; **cpl**, cutting plate; **dci**, dorsal cirrus; **mxI–V**, maxillary plates I–V; **pcl**, postchaetal lobe; **peri**, peristomium; **prcl**, prechaetal lobe; **pros**, prostomium; **sah**, subacicular hooks; **sha**, shaft. [A. Murray]

Ehlers' (1864–1868) earlier classification and placed the Oeononidae into synonymy with the Lysaretidae. She also proposed the new name Arabellidae for Kinberg's Laidea since the name of the type genus, *Lais*, was pre-occupied. The greater emphasis on maxillary characters for use in taxonomy was initiated by palaeontologists such as Kielan-Jaworowska (1966) and Kozur (1970). Kozur (1970) discussed the jaw structure of *Lysarete* in the palaeontological literature, noting the polyphyly of Lysaretidae, and limited the family to *Lysarete*. Colbath (1989) revised the Lysaretidae and came to the same conclusion. Colbath (1989) also resurrected the Oeononidae for *Oenone*, *Tainokia* and *Halla*, leaving *Lysarete* as the only genus in Lysaretidae. Orensanz (1990), who moved *Lysarete* to Lumbrineridae, considered the Lysaretidae to be a synonym of Lumbrineridae. Furthermore, he showed that the redefined Oeononidae should include the genera that were considered as Arabellidae, and that the latter is a synonym of the former. The classification of Orensanz (1990) is followed here; he also provided a key to the 11 genera he recognised. An additional genus, *Pholadiphila* described by Dean (1992) is placed in Oeononidae. Thus, at present the family comprises 12 genera and about 100 species.

The first Australian oeononid described was *Halla australis* from Port Jackson (Haswell 1886a); it may be synonymous with *Oenone fulgida* which has been widely reported from Australia (Day & Hutchings 1979). Three species of *Arabella* and two species of *Drilonereis* have also been reported from Australian waters. The number of Australian species (six species in three genera), however, is expected to increase when the family is studied in detail.

Oeononids are long and mostly quite large, up to 900 mm long and more than 10 mm wide for more than 1000 segments. There is no regionalisation of the body. They are mainly free-living, burrowing in sand and mud. Although they are not tubicolous, they secrete copious amounts of mucus which lubricates their burrow (Pettibone 1982). Most are predators, but a number of species are endoparasitic in other polychaetes, bivalves and echiuroids (Pettibone 1957b; Dean 1992). Some species, for example, *Notocirrus spiniferus*, are parasitic only for the early part of their life cycle and leave their host before they reach sexual maturity (Pettibone 1957b), whereas others, such as *Haematocephalus terebellidis*, may spend their entire life cycle as a parasite (Wirén 1886).

Oeononids are dioecious and show no sexual dimorphism. The free-living *Arabella iricolor* from Massachusetts, United States of America, spawn throughout summer; small specimens were found among pile scrapings (Pettibone 1963). However, larvae and juveniles of up to 200 segments of *Notocirrus spiniferus* from the same region were found in the body cavity of an onuphid polychaete (Pettibone 1957b). Nothing is known about the reproduction of Australian oeononids.

Oeononids are found from the intertidal zone to great depths (Pettibone 1982), and have been reported from all Australian states, except for the Northern Territory. The Lumbrineridae is the extant sister group to the Oeononidae (Orensanz 1990). The prionognaths have an extensive fossil record dating from Ordovician to Recent (Fig. 1.39). The maxillae from the extinct *Atraktopirion* and *Skalenoprion* are indistinguishable from those of extant oeononids and should be regarded as such (Orensanz 1990). In his combined classification scheme of Eunicida, Orensanz proposed a superfamily Oeononoidea to include the extinct Polychaetaspidae and Kalloprionidae, and the extant Oeononidae and Lumbrineridae. Middle Devonian scolecodonts of *Arabellites* and *Ildraites* have been reported from Queensland (Cook & Turner 1994).

Family Onuphidae

Onuphids are mostly tubicolous polychaetes; they may be sedentary in their tubes, or epibenthic crawlers pulling their tube around with them (Pls 1.4, 1.5). Some shallow-water species, such as the giant beachworms, which are a sought after fishing bait, are more vagile and do not have permanent tubes. Onuphids have a head with well-developed sensory appendages and the anteriormost parapodia are often enlarged and specialised for a particular mode of life.

Members of the Onuphidae are distinguished from all other eunicidans by having five prostomial sensory appendages with ringed ceratophores (Fig. 1.62A). The family definition used here is that of Paxton (1986a), except that the traditional terminology of prostomial appendages is replaced with that proposed by Paxton (1998) after Orrhage (1995). The rounded prostomium bears a pair of small dorsal frontal lips (rarely absent), three antennae and two palps (Fig. 1.62A). Each of the antennae and palps comprises a basal ringed ceratophore and a distal smooth style. Ventrally, a pair of large bulbous upper lips is present. Eyes may be present or absent. The peristomium is a single apodous ring, with or without a pair of dorsal peristomial cirri.

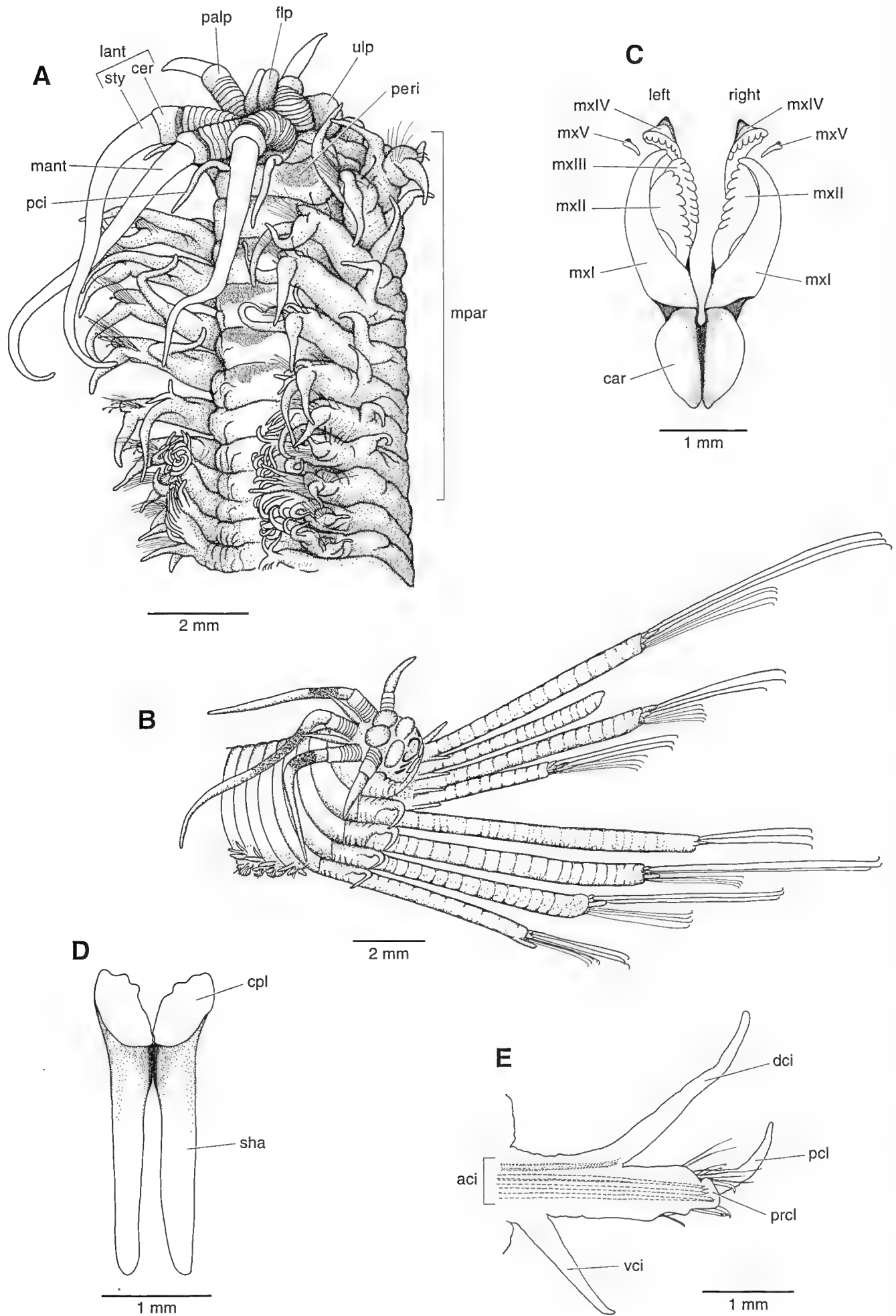
The first two to eight pairs of parapodia are modified (Fig. 1.62A, B). They are often longer, have different parapodial lobes and chaetae than those following, and thus are specialised for digging, locomotion or tube building. The modified parapodia have digitiform ventral cirri (Fig. 1.62E, F), the remaining unmodified ones (Fig. 1.62G, H) have glandular pads. Dorsal cirri (Fig. 1.62E–H) are present throughout or are reduced to absent on posterior chaetigers. Filaments of the branchiae, when present, are simple, pectinately or dichotomously branched, or spirally arranged (Fig. 1.62G). Parapodia are sub-biramous; the notopodium is represented only by a dorsal cirrus with or without embedded aciculae. Modified parapodia have simple or pseudo-compound hooks (Fig. 1.62I); pectinate and/or limbate chaetae are present or absent. Chaetae of unmodified parapodia are pectinate (Fig. 1.62J), simple limbate (Fig. 1.62K) and subacicular hooks (Fig. 1.62L); compound limbate chaetae (spinigers) are sometimes present and falcigers are rare. Pygidial cirri number two or four.

The jaws consist of ventral, unfused mandibles, and dorsal maxillae of the labidognath type (Fig. 1.62C, D). The maxillae are mineralised with aragonite, and comprise a pair of short carriers and 3–5 toothed plates on the right and 4–6 toothed plates on the left. The maxillary plates are asymmetrical with the right maxilla III missing and the right maxilla IV being larger than the corresponding left one.

The Onuphidae comprise two subfamilies: the Onuphinae and Hyalinoeciinae. In members of the Onuphinae the parapodia generally have dorsal cirri with internal aciculae, subacicular hooks in a ventral position, lower limbate chaetae absent posterior to the origin of the former (Fig. 1.62G), and four pygidial cirri. In members of the Hyalinoeciinae, dorsal cirri lack internal aciculae, subacicular hooks are in a median position in the fascicle (Fig. 1.62H), lower limbate chaetae occur to the end of the body, and two pygidial cirri are present.

The family Onuphidae erected by Kinberg (1865) as 'Onuphiidae' has remained unchanged, although it has been treated as a subfamily of Eunicidae by several authors (see McIntosh 1910; Fauvel 1923; Day 1967). Until about 1970, the family comprised only 11 recognised genera and the unsatisfactory state of the generic classification was expressed repeatedly (see for example, Hartman 1944a;

1. CLASS POLYCHAETA



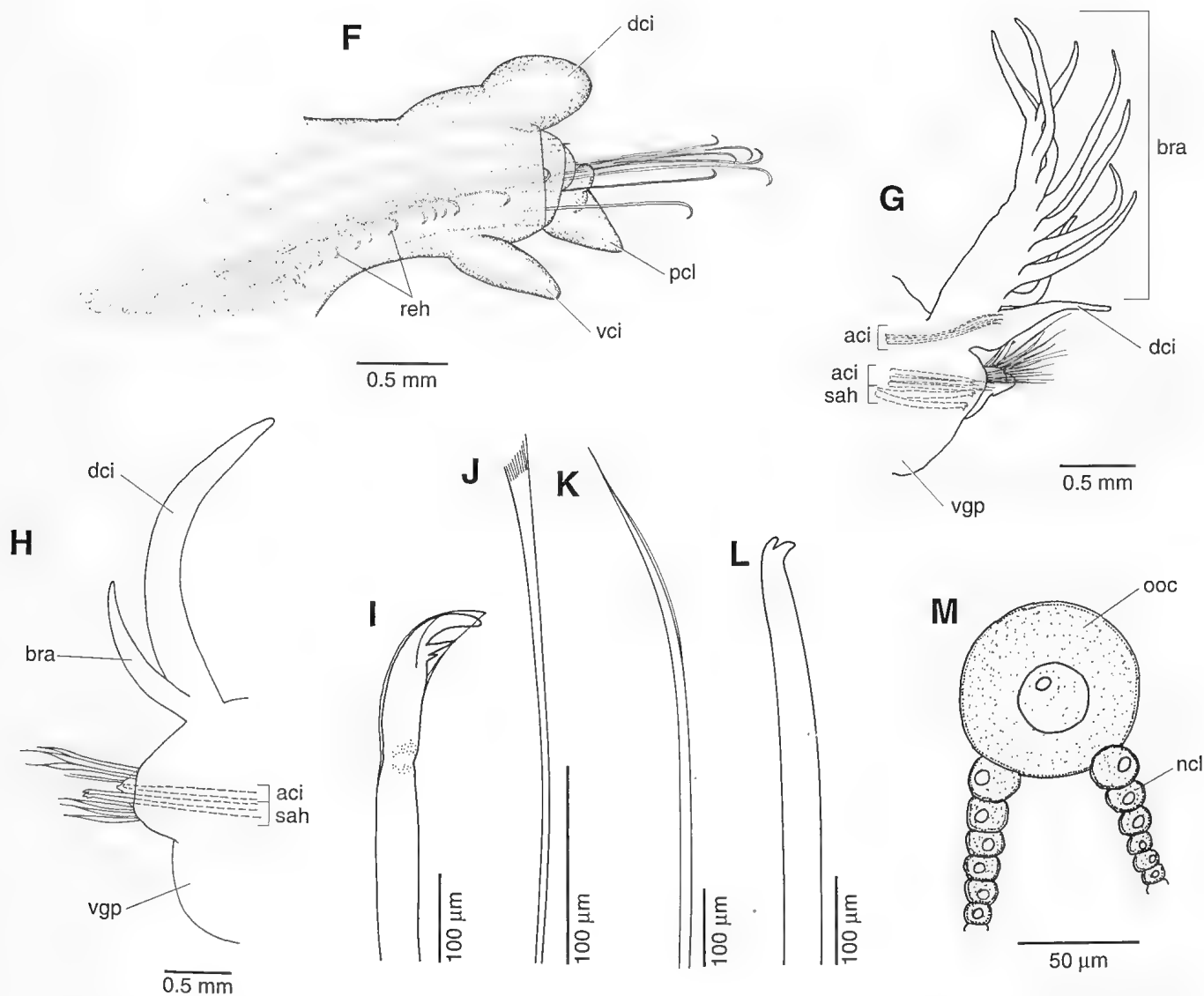


Figure 1.62 Family Onuphidae. **A**, anterior end of *Hirsutonuphis mariahirsuta*, dorso-lateral view. **B**, anterior end of *Longibrachium longipes*, dorso-lateral view. **C**, **D**, jaw parts of *Hirsutonuphis mariahirsuta*: **C**, maxillae, dorsal view; **D**, mandible, ventral view. **E**, parapodium of *Hirsutonuphis mariahirsuta* from chaetiger 3, anterior view. **F**, parapodium of *Brevibrachium maculatum* from chaetiger 1, anterior view. **G**, posterior parapodium of *Hirsutonuphis mariahirsuta* from chaetiger 30, anterior view. **H**, parapodium of *Hyalinoecia tubicola* from chaetiger 29, anterior view. **I**, pseudocompound hook from chaetiger 3 of *Hirsutonuphis mariahirsuta*. **J–L**, chaetae from chaetiger 31 of *Hirsutonuphis mariahirsuta*: **J**, pectinate chaeta; **K**, limbate chaeta; **L**, subacicular hook. **M**, **N**, oocytes: **M**, oocyte of *Australonuphis teres* with strings of nurse eggs; **N**, oocyte of *Hyalinoecia tubicola* with cluster of nurse cells. **aci**, aciculae; **bra**, branchia; **car**, carrier; **cer**, ceratophore; **cpl**, cutting plate; **dci**, dorsal cirrus; **flp**, frontal lip; **lant**, lateral antenna; **mant**, median antenna; **mpar**, modified parapodia; **mxl–V**, maxillary plates I–V; **ncl**, nurse cell; **ooc**, oocyte; **palp**, palp; **pcl**, peristomial cirrus; **pcl**, postchaetal lobe; **peri**, peristomium; **prcl**, prechaetal lobe; **reh**, replacement hook; **sah**, subacicular hook; **sha**, shaft; **sty**, style; **ulp**, upper lip; **vci**, ventral cirrus; **vgp**, ventral glandular pad. (**B**, **F**, after Paxton 1986b; **H**, **M**, **N**, after Paxton 1986a) [A, C–E, G–L, A. Murray; B, F, M, N, H. Paxton]

Pettibone 1970a). Since 1970 taxonomic studies have resulted in the redefinition and erection of new genera (Pettibone 1970a; Kucheruk 1978; Fauchald 1982b) and phylogenetic analyses of the family (Paxton 1986a; Orensanz 1990). Paxton (1986a) recognised 22 genera grouped into two subfamilies: Onuphinae with at least 200 species in 16 genera and Hyalinoeciinae with 70 species in 6 genera. Keys to genera are provided in Paxton (1986a) and Orensanz (1990).

The first Australian species described was *Diopatra dentata* (Kinberg 1865), from collections made in Sydney, New South Wales by the Swedish *Eugenie* expedition. *Australonuphis teres*, also from Sydney, was described soon after by Ehlers

(1864–1868). Both species are still among the most abundant Australian members of the family. Australian studies of Onuphidae include those of beachworms (Paxton 1979), the *Rhamphobrachium* complex (Paxton 1986b), *Diopatra* species (Paxton 1993), and *Hirsutonuphis* species (Paxton 1996). Collections from the eastern Australian shelf and slope by Museum Victoria and environmental surveys in the Sydney area in the last decade have recorded previously unknown genera and species. The currently identified Australian onuphid fauna comprises 60 species (of which 26 are thought to be new to science) in 16 genera (H. Paxton unpublished data).

1. CLASS POLYCHAETA

Onuphids range from a few millimetres to 3 m in length. The hyalinoecines are mostly short-bodied, the onuphines are generally larger and have numerous segments, some more than a thousand. There is no regionalisation of the body, but the most anterior parapodia are modified. They are longer, variously orientated, and bear different lobes and chaetal arrangements than the following unmodified parapodia. Anterior modification ranges from slight, as in *Onuphis* species, to very pronounced, as in species of the *Rhamphobranchium* species complex, in which the first three to four pairs of parapodia and chaetae can be greatly extended. This reaches its most extreme development in *Longibrachium longipes* from Queensland (Fig. 1.62B). Since these long grapple-like hook chaetae are easily broken, they are continuously replaced by newly formed hooks as is illustrated for *Brevibrachium maculatum* (Fig. 1.62F). Onuphids are well cephalised. The prostomium has well-developed nuchal grooves ranging from straight to almost circular in shape, palps and antennae, the latter with complex sensory buds (Paxton 1986a).

The respiratory pigments of *Diopatra cuprea* and *D. neapolitana* are extracellular haemoglobins as seen in most other larger polychaetes (Weber 1978b). Metanephridia are present as mixonephridia (Goodrich 1945). The innervation of the cephalic nervous system of *Hyalinoecia tubicola* and *Nothria conchylega* has been re-examined and compared to that of other polychaete families (see Orrhage 1995). Orrhage proved that the previously referred to 'ventro-lateral antennae' (anterior lateral antennae of Paxton 1986a) are homologous with palps, and the 'palps' (frontal palps and labial palps of Paxton 1986a) are a part of the alimentary canal and thus represent dorsal and ventral buccal lips (labelled 'frontal lip' and 'upper lip' by Paxton 1998).

Most onuphids are tubicolous. The tubes usually comprise an inner mucous to parchment-like lining secreted by its inhabitant, and an outer layer of foreign particles such as mud, sand, small shells and seaweed. Foreign particle selection and tube construction is often species specific. Only rarely is the tube completely secreted, as in the transparent quill-like tubes of *Hyalinoecia*, where the chemical composition is a combination of onuphid acid and a mucoprotein (Defretin 1971; Moermans 1974). *Hyalinoecia tubicola* and *Diopatra cuprea* actively irrigate their tubes to ventilate their branchiae (Dales, Mangum & Tichy 1970). This activity is thought to be governed by an endogenous pacemaker rather than a reflex feedback response to environmental variables (Dales, Mangum & Tichy 1970). Onuphids are primarily omnivorous scavengers (Fauchald & Jumars 1979).

Onuphid reproduction and development has been discussed by Richards (1967), Paxton (1986a, 1993, 1996) and Hsieh & Simon (1987). The sexes are usually separate and show no sexual dimorphism, but instances of hermaphroditism (Lieber 1931) and male dwarfism (Hartman 1967) have been observed. Sperm transfer involving spermatophores, and the presence of seminal receptacles (Hsieh & Simon 1990) as well as viviparity (Orensanz 1990) have been reported. Asexual reproduction has not been recorded. During oogenesis, onuphid oocytes are associated with nurse cells (Schroeder & Hermans 1975), which occur in two different types of arrangement. In the onuphines, the nurse cells are attached to the oocyte as two strings of cells (Fig. 1.62M), whereas in the hyalinoecines they are attached in a cluster (Fig. 1.62N). Onuphids have mixonephridia with a simple excretory canal and a large coelomostome that also functions as a genital funnel (Goodrich 1945). Single eggs have been observed in the nephridial ducts of *Diopatra* species (Lieber 1931). The Australian giant beachworms can produce as many as 100 000 oocytes and are probably broadcast spawners producing lecithotrophic planktonic larvae. However, other species such as *Diopatra gigova* and *D. lilliputiana* produce a few large eggs (maximum size 1.4 mm in diameter) that undergo direct development and brood care in the parental tube. *Diopatra albimandibulata* and *D. maculata* attach their egg masses to the outer surface of the parental tube where the embryos undergo direct development (Paxton 1993). Although onuphids do not undergo metamorphosis and juveniles appear as miniature adults, their morphology differs from the adults in the size of the antennae, the presence of eyes, number of modified parapodia, and distribution and types of chaetae and branchiae. A study of the development of modified parapodia of three species of *Hirsutonuphis* demonstrated that the smallest juveniles had only one pair of modified parapodia. As the juveniles grew, the parapodia became consecutively enlarged and the chaetae were replaced by pseudocompound hooks until the typical adult number of modified parapodia for the species was reached (Paxton 1996). It is probable that this pattern also applies to other genera.

Onuphids can be classed as perennial species (Fauchald 1983). Some of the larger species, such as the beachworms (*Australonuphis* species), can most likely live for more than 5 years. Although they display clear growth rings on their mandibles numbering up to 15 rings, these rings cannot be used for age determination since the periodicity of the rings has not yet been established.



Figure 1.63 Family Onuphidae. *Diopatra aciculata* foraging from the safety of its tube, showing the three long antennae, two palps and the paired lips comprising the prostomial appendages. These worms can occur in great numbers and are often dug up for use as fishing bait. They live in the intertidal zone to a depth of 66 m along the coast of southern Australia. [N. Holmes]

Tubes of onuphids are generally embedded in or attached to the substratum. The best known tubes are those of *Diopatra* species (Fig. 1.63), which are often found in rocky intertidal areas where they are exposed during low tide. The tube of *Diopatra dentata*, which occurs along the New South Wales coast, is distinctive; it is covered predominantly by shell fragments that are attached at right angles in close circles, but it is the section of the tube which protrudes from the substratum like a chimney that makes it conspicuous. These 'shaggy' tubes afford protection from predators and house a host of small invertebrates that provide prey.

The tube of *Diopatra aciculata* is very different in that it is covered by sand and minute pieces of shell (Fig. 1.63), giving it a smooth appearance; however, the occasional larger piece of seaweed or shell is embedded towards the distal end. This species occurs on the southern coast of Australia, and in great numbers in tidal sandflats near Adelaide, where it is dug up as fishing bait. The genus is best represented in warmer waters and the greatest diversity is on the northern coasts of Australia where six species occur. Of the nine Australian species, eight are endemic (Paxton 1993). *Epidiopatra* also has spiralled branchiae, otherwise only found in *Diopatra*, but lacks peristomial cirri. The worms are very small and the genus probably has a progenetic origin. In contrast to *Diopatra*, species of *Epidiopatra* are often found in deep water. Only one species, *E. hupferiana*, has been reported from off New South Wales in a depth of 50 m.

Most onuphines live permanently in tubes and are sedentary once they have settled. Some shallow-water species, however, appear to be more vagile; the best known of these are the giant Australian beachworms of the genus *Australonuphis*. They secrete large amounts of mucus to strengthen their burrows, but no permanent tubes are made. These worms occur in millions on many surf beaches of eastern Australia. Due to their great length and muscular body, the beachworms are highly valued as bait by fishermen and professional bait collectors. They can be collected from sandy beaches in an interesting manner. A piece of fish or meat is dragged over the sand in the shallow back-wash of the waves (see Fig. 1.27A). The worms poke their heads out of the sand in response to the detection of the bait. Once the worm is located, the collector waits for the next wave, and as the worm reappears, lures it out with a smaller hand-held piece of bait, and grabs the worm behind its head using fingers or pliers (see Fig. 1.27B). They have a well-developed olfactory sense which detects food items; they rise very quickly to the surface once stimulated. This allows collectors to attract the worms with bait. Although beachworms normally feed on small invertebrates and seaweeds, they can move some distances toward a larger food source, as for example a washed up whale or sheep (Paxton 1979).

Two species of *Australonuphis* occur in Australia: *A. teres* (the adult is commonly known as Kingworm and the juvenile as Stumpy) and *A. parateres* (commonly known as Slimy). Both species live on surf beaches on the eastern Australian coast where they are sympatric over most of their range. The Slimy occurs from Adelaide, South Australia to Yeppoon, Queensland, and the Kingworm is known from Lakes Entrance, Victoria to Maroochydore, Queensland. Their northern limits are dictated by their different habitat requirements. The Kingworm requires a greater amount of wave action and thus does not occur further north where the sheltering effect of the Great Barrier Reef reduces the wave action. When sympatric, this difference in wave tolerance results in different preferred habitats. The Slimy is found from half-tide to low-tide levels, but in greatest numbers on sand flats or spits. The Kingworm has a zonation with size

(presumably age): the youngest are highest up on the beach and oldest are furthest out. Young Kingworms (Stumpies) live mainly on the slope of the beach, whereas the large adults are so far out that they can be collected only at the lowest tides (Paxton 1979).

Australonuphis teres and *A. parateres* are of some economic significance since they are collected by many professional bait collectors and sold frozen as fishbait; even 'worming pliers', manufactured especially for catching beachworms have been available. Another genus, *Hirsutonuphis*, is represented by two large species that are also referred to as beachworms. *Hirsutonuphis gygis* was discovered at Fraser Island, Queensland, where it is known to bait collectors as a rare beachworm that is difficult to catch. A different colour morph of probably the same species has recently been reported from Sydney, New South Wales (Paxton 1996). *Hirsutonuphis mariahirsuta* (commonly known as Hairy Mary or Wiry) occurs from Camden Haven, New South Wales to Yeppoon, Queensland. Although it is quite common, it is not liked by fishermen as a baitworm. Three other species of *Hirsutonuphis* are found on the eastern coast of Australia in shallow depths (intertidal to 70 m); however, they are small species, reaching less than 100 mm in length.

The genus *Aponuphis* was known previously only from the Mediterranean Sea and eastern North Atlantic where it is often associated with *Posidonia* seagrasses. Three new species of *Aponuphis* are being described, however, from eastern Australia (H. Paxton in preparation). *Kinbergonuphis taeniata* is a small worm occurring in shallow depths from Bass Strait to Mackay, Queensland. Another 10 species of this genus have been collected from eastern Australia, but are still awaiting detailed study; at least half of them are endemic to Australia. They are small, slender worms, and most species are from shallow waters, but two species are from depths of 450–800 m. A closely related genus, *Mooreonuphis*, previously thought to be limited to the New World, is represented by two undescribed species from shallow depths from Sydney, New South Wales. The worms are very small, measuring about 10 mm in length. They build tubes that are covered by sand grains and are usually built up from the opening of an empty snail shell. *Onuphis holobranchiata* is found on most Australian coasts. It lives in shallow water like *O. eremita* from the Northern Territory. Three undescribed species of *Onuphis* from the continental slope of eastern Australia to depths of 2250 m have been collected by members of Museum Victoria. Among the same material are two species of *Notonuphis* and three species of *Paradiopatra*, also as yet undescribed.

The *Rhamphobrachium* complex includes *Brevibrachium* and *Longibrachium* together with *Rhamphobrachium*. The three genera have modified parapodia with long retractile parapodia and chaetae. *Brevibrachium augeneri* is only known from south-east Australia, whereas *B. maculatum* is found in Victoria, Australia, and New Zealand. *Longibrachium longipes*, with the most extremely modified parapodia (Fig. 1.62B), is only known from one collection near Fraser Island, Queensland, from a depth of 73 m. *Rhamphobrachium* is represented in Australia by three endemic species from New South Wales and Queensland. *Rhamphobrachium noeli* is found in depths of less than 10 m, whereas *R. hutchingsae* and *R. pyriforme* are deep-water species as typical for the genus, living in depths of 155–800 m (Paxton 1986b). Probably all species of the complex build a tube, most of which are tough and parchment-like. Presumably they forage from their tube opening by extending their modified parapodia with long spiny, grapple-like hooks, perhaps using the hooks in a sieve-like action.

1. CLASS POLYCHAETA

Most hyalinoecines are epibenthic crawlers. They crawl by using their very large first parapodia that extend from the tube, pulling their tube with them. At least three species of *Hyalinoecia* with their quill-like tube are found on Australian coasts to depths of 1850 m. The tube is slightly curved and open at both ends. The anterior end has a slightly larger diameter and towards the posterior end are three valves which are short flaps across the lumen. These valves may protect the worm, but also allow irrigation of the tube in one direction. The worm lies in the tube with its head towards the larger end, undulates to irrigate the tube, and can extend the anterior part of its body to crawl and forage. The tube is wide enough that the worm can turn around inside it. As the worm grows it extends the tube anteriorly, chews off the narrow posterior end and replaces the valves (Dales, Mangum & Tichy 1970). Species of *Nothria* also have large anterior parapodia, analogous to the legs of caterpillars, which are used for crawling around, pulling the protective tube. *Nothria* species have a flattened body with poorly-developed longitudinal muscles. These animals construct flattened tubes to accommodate their oval shape and seem to offset the poor muscular system by a shortened body. At least two species of *Nothria* occur in Australia, one as deep as 2900 m. Two as yet undescribed species of *Leptoecia* have been recently collected from off the eastern Australian coast from New South Wales to Tasmania in depths of up to 2250 m. These small worms, measuring less than 5 mm, lie in a clear tube, and look similar in appearance to the miniature *Hyalinoecia* species. However, *Leptoecia* differ from *Hyalinoecia*, in that they lack frontal lips and the anteriormost maxillae, and it is possible that the genus is of progenetic origin.

Members of the Onuphidae are found in all the oceans of the world, at all depths. The Australian records are primarily from the eastern coast, a reflection probably due to the more concentrated sampling efforts in that region. Although some genera have a worldwide distribution, and are found from the shallowest to the deepest depths, most have a limited geographic and depth distribution. In terms of genera, the family is much better represented in the Southern Hemisphere than in the Northern. Three genera, *Hartmanonuphis*, *Brevibrachium* and *Notonuphis*, are restricted to the southern oceans, and another three, *Australonuphis*, *Heptaceras* and *Hyalospinifera*, have only been reported south of 25°N. Only *Americanuphis* is restricted to the Northern Hemisphere. This strong southern representation may suggest a southern centre of origin (Paxton 1986a).

The closest relative or sister group of the Onuphidae is the family Eunicidae. However, the Onuphidae is more specialised having features such as distinct frontal lips and palps and antennae with well-developed ceratophores, all of which are apomorphic features that mark it as the most derived family in Eunicida (see Fig. 1.57 and Rouse & Fauchald 1997 for an alternative view). The relationships within the family have been analysed by Paxton (1986a) and although the individual genera within the two subfamilies can be grouped into larger units on morphological and ecological characteristics, it is difficult to define these larger units by unequivocal synapomorphies.

Isolated fossilised jaw pieces that were attributed to the Onuphidae have been reported from North America from Ordovician deposits (Howell 1962). However, Kozur (1970) considered these records as doubtful and gives the earliest occurrence of onuphids as from the Upper Cretaceous. Australian fossils are not known.

EUNICIDANS INCERTAE SEDIS

In their complete cladistic analyses, Rouse & Fauchald (1997) found Diurodrilidae and Histriobdellidae to fall as basal members of Annelida or Polychaeta. However, they classified these two families as members of Eunicida, albeit *incertae sedis* and they are placed in Eunicidans *incertae sedis* here. Rouse & Fauchald (1997) argued that the basal placement of Diurodrilidae and Histriobdellidae in their complete analyses supported the idea that taxa that show extensive loss of features may be placed inaccurately. Diurodrilidae and Histriobdellidae are unusual among polychaetes in lacking chaetae and all parapodial structures, as well as having very simple body forms. However, they also show features that suggest that they are not primitive polychaetes, and instead should be considered as derived taxa. Worldwide, there are three genera and about 18 species.

Histriobdellids have a pair of ventral sensory palps and three antennae, features that suggest they should be included as members of Aciculata. In terms of placing them within Eunicida, Rouse & Fauchald (1997) followed Mesnil & Caullery (1922), who found that the jaws of Histriobdellidae are so similar to those of eunicemorph polychaetes that it is arguably unlikely to have arisen convergently.

The genus *Diurodrilus* was originally placed in Dinophilidae before being placed into its own family, Diurodrilidae (Kristensen & Niilonen 1982). However, the unusual features of the group appear to have been emphasised by Kristensen & Niilonen (1982) and similarities with *Dinophilus* were disregarded. *Dinophilus* is now regarded as a derived member of Dorvilleidae (Eibye-Jacobsen & Kristensen 1994) and *Diurodrilus* may also belong in this family. Molecular sequence data may be required to properly resolve the placement of these taxa within the Eunicidans.

Both Diurodrilidae and Histriobdellidae have representatives in Australian waters.

Family Diurodrilidae

Members of the Diurodrilidae are minute, interstitial polychaetes which inhabit clean medium to coarse intertidal and subtidal sands. They have a short, grub-like body without parapodia or chaetae, and have a pair of short pygidial 'toes' as their only appendages.

Diurodrilids have a prostomium that lacks appendages and bears two transverse restrictions, a peristomium, five indistinct trunk segments and a pygidium (Fig. 1.64A). The prostomium lacks antennae and all other appendages. A ventral pharyngeal muscle bulb is present, as is a prepharyngeal gland anterior and two salivary (oesophageal) glands posterior to the pharynx. Jaws are absent. Parapodia and chaetae are absent; the only appendages are two, typically forked, pygidial 'toes' with adhesive glands and muscles. The body is covered by a cuticle which in some species is regionally thickened, forming clear patterns of plates that are species-specific (Fig. 1.64B). Ciliation is present as sparse patches, transverse rows or sensoria; ciliophores, specialised ciliated areas arranged in species-specific patterns, are also present (Kristensen & Niilonen 1982).

Diurodrilus is the sole genus in the family and was described for *D. minimus* by Remane (1925) for specimens collected from the North Sea. Six species are now known from the Atlantic and Pacific Oceans. Two species have been reported

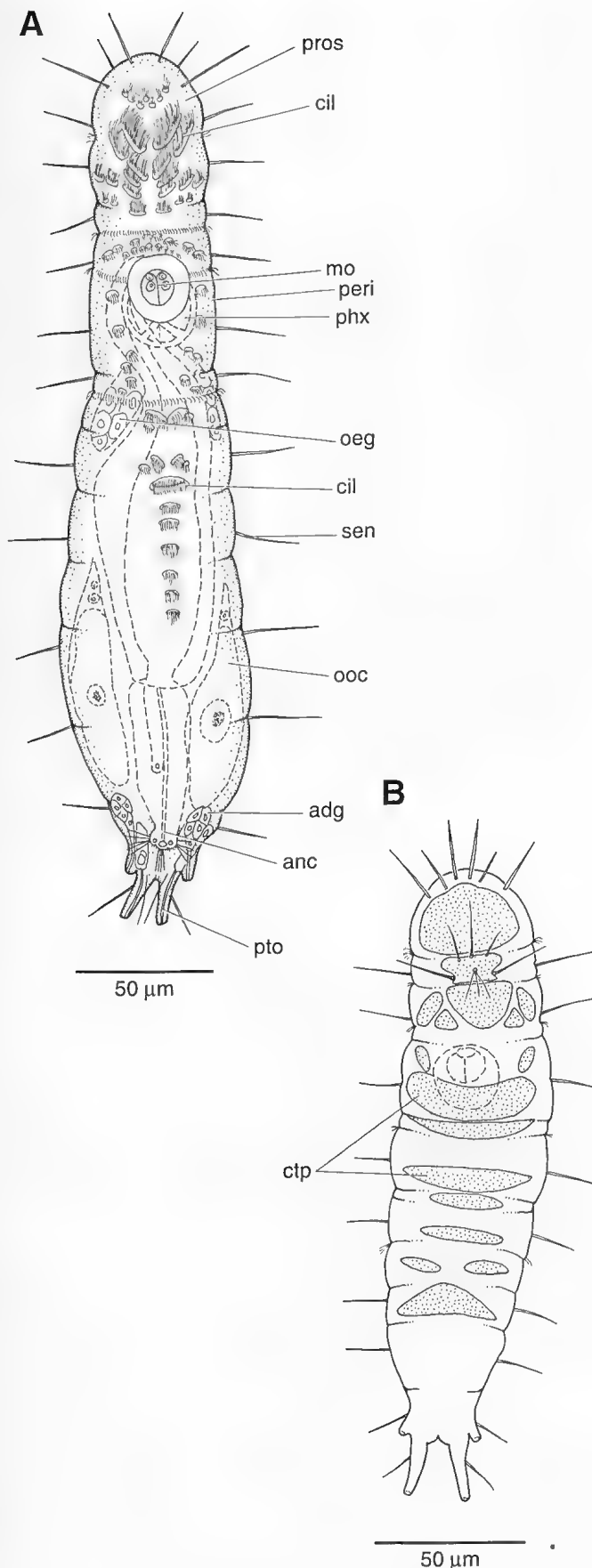


Figure 1.64 Family Diurodrilidae. *Diurodrilus* species. **A**, entire adult female, ventral view. **B**, entire young female, dorsal view showing 'cuticular plates'. **adg**, adhesive gland; **anc**, anal cone; **cil**, ciliophore; **ctp**, cuticular plates; **mo**, mouth; **oeg**, oesophageal gland; **ooc**, oocyte; **peri**, peristomium; **phx**, pharynx; **pros**, prostomium; **pto**, pygidial 'toe'; **sen**, sensorium. (After draft illustrations by R.M. Kristensen) [A. Murray]

from New Zealand (Riser 1984) and a new species was recently collected from Queensland, Australia (R. Kristensen personal communication). The genus *Diurodrilus* was placed in the Dinophilidae (now part of Dorvilleidae) until Kristensen & Niilonen (1982) demonstrated that it deserved familial status and erected the Diurodrilidae, declaring it a family of uncertain affinities. Kristensen & Eibye-Jacobsen (1995) stated that the phylogenetic relationships of the Diurodrilidae to other families still remain unclear.

Diurodrilids measure less than 0.5 mm in length. They can move rapidly by using the ciliophores on the trunk as locomotory organs (Kristensen & Niilonen 1982). The adhesive glands of the prostomium and 'toes' produce an adhesive secretion as well as release granules which are involved in the breaking of adhesive attachment (Gelder & Tyler 1986). A blood vascular system is absent, but segmentally positioned protonephridia are present according to Westheide (1990a).

Little is known about the reproductive biology of diurodrilids. Ovigerous females of *D. westheidei* were found to contain clusters of sperm near the largest oocyte, and Kristensen & Eibye-Jacobsen (1995) speculated that the anal cone may function as a copulatory apparatus. Spermatozoa are highly specialised; they have a giant acrosome, a nucleus located in the 'middle piece' between the mitochondria, and a slightly modified flagellum (Kristensen & Eibye-Jacobsen 1995).

Family Histriobdellidae

Histriobdellids are small highly-modified forms, parasitic on the branchial chambers of crustaceans. The head has palps, tentacles and an internal jaw apparatus linking them to the eunicidans. However, their trunk, bears little resemblance to other eunicids. They lack parapodia and chaetae, but have lateral appendages in the form of cirri and foot-like structures.

Histriobdellids are indistinctly annulated eunicidans without true parapodia or chaetae (Fig. 1.65A). They are secondarily simplified, and are symbionts/parasites of marine and freshwater crustaceans. The prostomium bears five sensory and a pair of locomotory appendages. The sensory appendages have been referred to as 'tentacles' (Haswell 1900) or 'antennae' (Fauchald 1977). However, in view of the recent studies by Orrhage (1995) the ventro-lateral pair should probably be referred to as palps and the dorsal three as antennae. Another pair of locomotory appendages is present at the posterior end of the trunk; several other paired appendages (lateral cirri and claspers) are present in *Stratiadrilus* species, but are absent from *Histriobdella*. The jaws (Fig. 1.65B) comprise ventral mandibles and dorsal maxillae which are considered to be of the prionognath type (Rouse & Fauchald 1997). The mandibles have unfused cutting plates and very long shafts. The maxillae consist of a long median carrier and three to four pairs of distally toothed plates, each articulating with basal pieces.

The first histriobdellid was reported as a doubtful serpulid larva by van Beneden in 1853 and in a later paper assigned by him (1858) to the Hirudinea. Haswell (1900) discussed its affinities with archiannelid families and Rotifera. He mentioned that Hatschek (1891) suggested that *Histriobdella* represented a degenerate eunicid, but did not discuss it. Mesnil & Caullery (1922) described the jaw apparatus in detail and established its homology with eunicidans. Only two genera are known: *Histriobdella* and *Stratiadrilus*. The former is monotypic and the latter has eight species, two of which occur in Australia. An illustrated key to six *Stratiadrilus* species has been compiled by Vila & Bahamonde (1985).

1. CLASS POLYCHAETA

The monotypic *Histriobdella* lives on marine lobsters in the North Atlantic and off the west coast of America. Species of *Stratiodrilus* are found in Australia, the southern region of South America, Madagascar, and South Africa. Except for *S. cirolanae* from Africa, which lives on marine isopods, all other species of *Stratiodrilus* live on freshwater crayfish (Führ 1971). A table giving the geographical distribution and the respective hosts of seven species is given in Amaral & Morgado (1997). Also, crayfish are often hosts to temnocephalid flatworms. Cordero (1927), when describing *S. platensis*, the first species of this genus from South America, noted that the co-existence on the same host of *Stratiodrilus* and *Temnocephala* both in South America and Australia was no coincidence. Harrison (1928) noted that the geographical distribution of *Stratiodrilus* species supports a Gondwanan origin of the group. He further hypothesised that the freshwater species of *Stratiodrilus* must have had a marine origin, and the subsequent discovery of *S. cirolanae* on South African marine isopods by Führ (1971) supports his point. The histriobdellids have undoubted eunicidan affinities, but they cannot be related to any particular extant member of the group (Orensanz 1990).

Histriobdellids are very small, range 0.5–1.5 mm in length, and have five indistinct segments. The Australian species, *Stratiodrilus tasmanicus* (Fig. 1.65A) and *S. novaehollandiae* live in the branchial chambers of freshwater crayfish (Haswell 1900, 1913) and feed on the microflora that grow in the

branchial chambers of their hosts (Cannon & Jennings 1987). The adhesive organs of the sucker-like locomotive appendages produce an adhesive secretion and release granules which are involved in the breaking of the attachment (Gelder & Tyler 1986). Histriobdellids lack a blood vascular system (Haswell 1900), but have protonephridia as is typical for such tiny worms (Goodrich 1945).

The animals are dioecious. Spermatozoa of *Stratiodrilus novaehollandiae* and *Histriobdella homari* are of the 'introsperm' type (Rouse & Jamieson 1987). In the former, the male has a sclerotised spinous copulatory organ and sperm is transferred by transdermal (hypodermic) injection, whereas in the latter, transfer is probably by apposition of genital pores (Jamieson & Rouse 1989).

'AMPHINOMIDANS'

Amphinomidans comprise two families: Amphinomidae and Euphrosinidae. The taxon, Amphinomae, equivalent to Amphinomidans dates back to Lamarck (1818). The Amphinomida was first used as a taxon name by Dales (1962a), but other names such as Amphinomorpha have also been used this century. Rouse & Fauchald (1997) did not provide a name for the clade comprised of Amphinomidae and Euphrosinidae, which was found in all of their analyses, but it seems appropriate to use the name Amphinomidans for

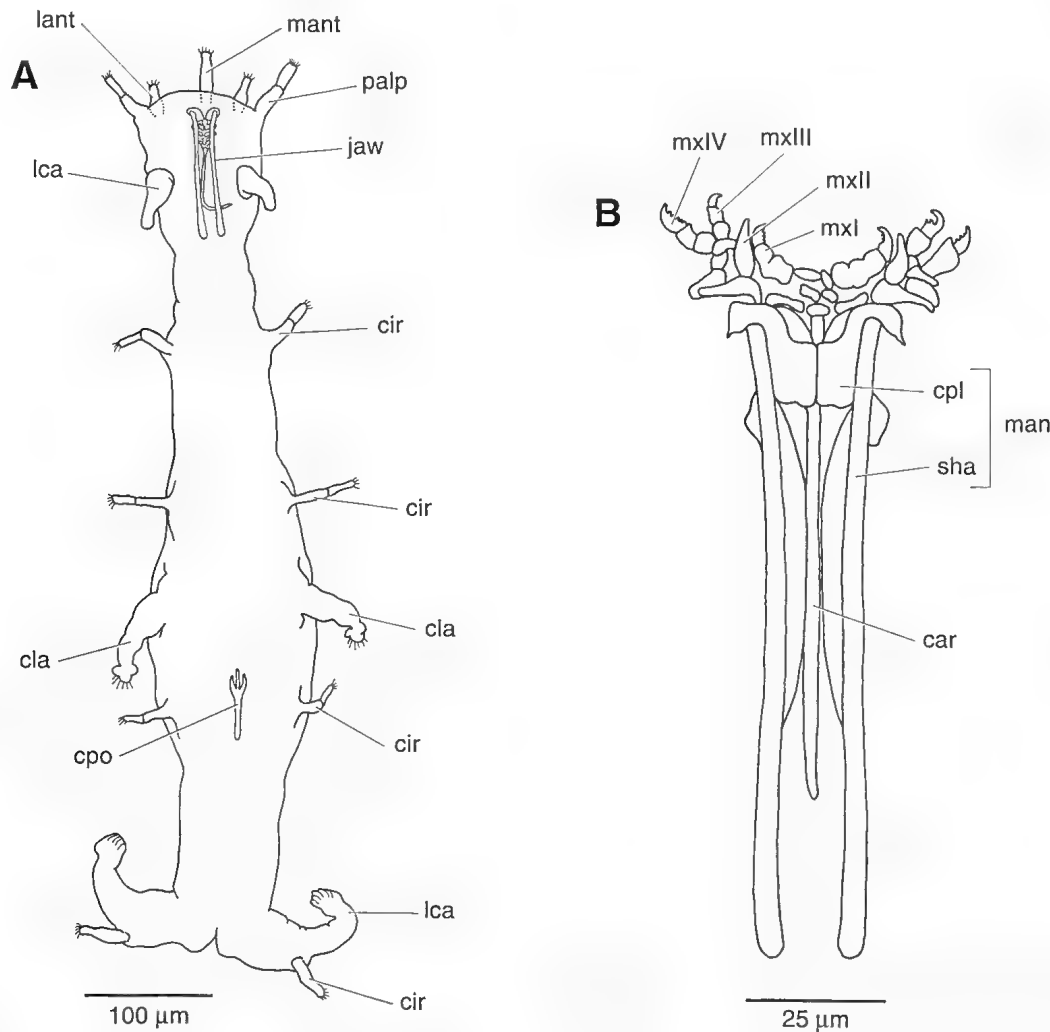


Figure 1.65 Family Histriobdellidae. *Stratiodrilus tasmanicus*. **A**, entire animal, ventral view. **B**, jaws with maxillae everted, ventral view. car, carrier; cir, cirrus; cla, clasper; cpl, cutting plate; cpo, copulatory organ; jaw, jaw apparatus; lant, lateral antenna; lca, locomotory appendage; man, mandible; mant, median antenna; mxI–IV, maxillae plates I–IV; palp, palp; sha, shaft. (B, after Haswell 1900)

[A. Murray]

this group here. They are grouped together on the presence of calcareous chaetae. Rouse & Fauchald (1997) included these two families within the taxon Eunicida, and it is true that the amphinomid/euphrosinid clade was often the sister group to the eunicidan group of polychaetes in their analyses (Fig. 1.57). But in some cases these taxa formed a grade. Further investigation is needed to resolve the placement of the Amphinomidans within the Aciculata and the use of the name Eunicida. Apart from the Amphinomidae and Euphrosinidae there is a possibility that Spintheridae could also belong to Amphinomidans, but further investigation is required. Kudenov (1991) described a new genus, *Archinome*, which seemed to combine features of both euphrosinids and amphinomids, and named a new family Archinomidae (now included in the Amphinomidae) for this genus. A new family was not justified according to Kudenov (1994b) since recognition of the Archinomidae appears to render the Amphinomidae paraphyletic (see below). Recognition of the Euphrosinidae may also make the Amphinomidae paraphyletic, but a detailed cladistic analysis of the whole assemblage is needed.

Amphinomidans occur worldwide from the intertidal zone to abyssal depths, although they are most common in shallow warm waters. At present, the group includes about 180 nominal species in about 24 genera. There have been a number of records of amphinomidans from about seven genera from Australian waters (Day & Hutchings 1979; Australian Museum database). Worldwide, Euphrosinidae comprises five genera and more than 53 described species, most of which belong in *Euphrosine*; several records of this genus have been reported for Australian waters (Day & Hutchings 1979).

Family Amphinomidae

Amphinomids are either elongate or ovate with a flattened solid body, often rectangular in cross-section (Pls 2.1–2.3). The head is often hidden and bears a caruncle. The parapodia bear tufts of stout chaetae and branched branchiae. The chaetae are often fragile and may break when handled, lodging under the skin and causing local irritation and infection; thus they are commonly known as fire worms. They are often highly coloured and common in shallow water and are conspicuous in coral reef areas.

The prostomium comprises two parts, forming overall a triangle, rounded and widest anteriorly. The peristomium is reduced to lips, as illustrated by Hartman (1951a). Paired lateral antennae and a median antenna are present on the anterior and posterior prostomial lobes, respectively (Gustafson 1930). The ventro-lateral palps are slender and located on the anterior prostomium. The nuchal organs are attached to the edge of the caruncle, which extends posteriorly from the prostomium (Fig. 1.2A); these complex structures usually comprise several folds and ciliated tracts (Storch & Welsch 1970). The longitudinal muscles are grouped in four bundles (Storch 1968) and segmentation is present. The first segment curves around the prostomium and bears parapodia similar to those posteriorly. All parapodia are biramous and bear truncate cylindrical notopodia and tapering neuropodia, which project beyond the notopodia (Fig. 1.66C); dorsal and ventral cirri are present. The branchiae are branched structures attached to the notopodial bases. Epidermal papillae and pygidial cirri are absent (Marsden 1963), and lateral organs and dorsal cirrus organs have not been observed. The thickened muscular lower lip of the mouth is eversible, rugose and covered with a thick cuticle (Dales 1962a). A gular membrane is lacking. The gut comprises a

straight tube. Mixonephridia are present, and presumed to be in most segments (Goodrich 1945). A heart body is absent from the closed circulatory system. Aciculae and other chaetae, including variously ornamented capillaries and spines, often dentate, are calcified to some degree (Gustafson 1930) and usually very brittle. This definition is based upon Fauchald & Rouse (1997).

Some confusion exists as to the authority for the family Amphinomidae. Kudenov (1993) suggested that the authority should be Lamarck (1818), whereas Hartman (1959a) credited Savigny. Kudenov (1993) stated that Lamarck, using an unpublished manuscript of Savigny's (1809; illustrations, 1813) wrote the descriptions and published the taxa originally recognised by Savigny. The existence of Savigny's manuscript, quoted by Lamarck, does not constitute publication in the sense of the Nomenclatural Code, so Lamarck is the author of this family.

The systematics of the family are not well understood (Kudenov 1995). Fauchald (1977) placed them within the order Amphinomida, although the recent cladistic study by Rouse & Fauchald (1997) places them within the Eunicida. Prior to 1977, the order Amphinomida included the amphinomids and euphrosinids, either as two subfamilies of the Amphinomidae, or as two separate families, as they are regarded here. Historically, spintherids were also included because of their superficial resemblance to the other taxa (Manton 1967); the analyses of Rouse & Fauchald (1997) indicated the close relationship between these three families, but Spintheridae was classified as Aciculata *incertae sedis*. Kudenov (1991) presented a detailed discussion on whether Amphinomidae comprises one family with several subfamilies, or several families when he described the new family Archinomidae. Subsequently, Kudenov (1994b) changed his view, placing the single genus *Archinome* in the Euphrosinidae, but, in 1995, reiterated that the Archinomidae was in fact a valid family; however, it is treated here as a part of Amphinomidae.

Detailed anatomical studies of amphinomids were made by Gustafson (1930). Amphinomids and euphrosinids are characterised by the presence of a caruncle; this unusual development of the nuchal organ is a synapomorphy shared with the Euphrosinidae, according to Rouse & Fauchald (1997). These two families also include the only polychaetes with calcified chaetae (Gustafson 1930). The pharyngeal structure, with its sclerotinised, rugose eversible lower lip, is another unusual feature shared by the two families. The family may be paraphyletic by recognition of the euphrosinids. One major difference between the families lies in the structure of the notopodia, which are short, truncate cylinders, or cones, in the amphinomids and elongated crests in the euphrosinids. The branchiae are single tufts associated with the notopodia in the amphinomids and are spread out along the crests as smaller, less-branched groups in the euphrosinids. The existence of the family Archinomidae (see Kudenov 1991), based on the genus *Archinome*, complicates the issue further, in that it has the caruncular structure of a euphrosinid and the notopodia of an amphinomid.

Kudenov (1995) stated that 19 genera and around 130 species of amphinomids are generally considered valid, based upon Fauchald (1977) and Hartman (1959a). Only the genus *Eurythoe* has been revised (Bindra 1927) and Fauchald (1977) proposed that *Linophærus* is a senior synonym of *Pseudoeurythoe*; both assessments were based on the literature. One of the most speciose genera, *Eurythoe*, exhibits morphological variation as a result of its reproductive

1. CLASS POLYCHAETA

behaviour (see below); at least, in the widespread species *Eurythoe complanata* (see Kudenov 1974). Thus a major revision of the family is urgently needed.

Day & Hutchings (1979) listed 20 species in seven genera for Australia; since then unpublished records of *Pareurythoe chilensis* and *Linopherus* species have been added to the Australian Museum database. The most commonly reported Australian species are *Eurythoe complanata* and species of *Chloeia* and *Pherecardia*. A detailed study of *E. complanata* is necessary to determine if Australian records constitute a single species and to assess its specific relationship to other populations of this widely distributed species as it may comprise a group of sibling species.

Characters used to identify species of amphinomids include prostomial morphology and the development of prostomial appendages, eyes and the caruncle, as well as the distribution of branchiae, chaetal types and the distribution of notopodial and neuropodial aciculae (Kudenov 1995).

Amphinomids are commonly found in shallow tropical, and subtropical waters; a number have also been reported from abyssal depths and polar regions (Kudenov 1993). Most are small, cryptic species, especially those in intertidal and shallow subtidal habitats, where they occur in crevices between rocks or in dead coral substrata. Other taxa, such as *Amphinome* species, live on driftwood or floating pumice; these have been seen regularly on the beach at Lizard Island, Great Barrier Reef, following submerged volcanic activity in the Pacific. Species of *Hipponoa* are inquilinistic commensals, which live in the mantle cavity of the stalked barnacle, *Lepas* (Kudenov 1977b). Species inhabiting sediments may be strongly reduced (Kudenov & Blake 1985). *Benthoscolex cubanus* parasitises the intestine of the abyssal sea urchin, *Archeopneustes hystrix*; in some populations, 80–100% of the urchins were infected, but typically by a single polychaete (Emson *et al.* 1993). *Benthoscolex cubanus* feeds on foraminiferans and other fragments of organic material in the gut of the sea urchin; this species appears to have few adaptations to this life style, although the cuticle is thicker than in most polychaetes.

When disturbed, most amphinomids assume a defensive posture by arching their body dorsally to display expansive fascicles of notochaetae. Some, such as *Eurythoe complanata*, widely reported from Australia as 'fire worms', can evoke nasty reactions, such as inflammation and swelling, in humans. If this species is picked up, the brittle, calcareous harpoon notochaetae break off and become lodged in the skin, together with the discharge of an acidic neurotoxin present in the chaetae.

Most amphinomids are small, although some species of *Amphinome*, *Eurythoe* and *Hermodice* approach lengths of 500 mm and widths in excess of 15 mm, excluding chaetae.

Some amphinomids are brightly pigmented; some have characteristic colour patterns, especially species of *Chloeia* and *Notopygos*. Two major body forms are represented in the family: some are grub-like and oval in cross-section with a limited number of segments; others are elongate and subrectangular in cross-section and have many segments (Fig. 1.66A). The prostomium consists of anterior and posterior lobes and is usually surrounded by anterior chaetigers and dense fascicles of notochaetae. The anterior lobe carries the palps and lateral pairs of antennae and an anterior pair of eyes. On the posterior lobe is the medial antenna, and an additional pair of eyes and the caruncle, which extends posteriorly. The shape of the caruncle/nuchal organ complex varies from a flat, unadorned plate, as in

Paramphinoe, to a sinuous lobe in *Pareurythoe*, a median keel with a pair of lateral ridges in *Amphinome*, and in the *Chloeia-Notopygos* species complex the medial keel is surrounded by complexly folded margins. A caruncle is absent in *Hipponoa* (Kudenov 1977b, 1994a).

The pharynx is highly muscular, unarmed and bears numerous transverse ridges. Parapodia are biramous with the notopodia (Fig. 1.66C). The latter bear chaetae arranged in radiating circular whorls, with one or two dorsal cirri and one ventral cirrus respectively. Branchiae may be present on some notopodia, or on all notopodia, although they are typically absent from the first few segments. They include dentritic, bipinnate or palmate forms. All chaetae are simple and calcareous (Fig. 1.66D–H); notochaetae include bifurcate and harpoon chaetae, and smooth or spurred spines and capillaries (Fig. 1.66D, E, H). Neurochaetae may include recurved hooks, bifurcate chaetae, smooth or spurred spines and capillaries (Fig. 1.66G). Aciculae are typically blunt, distally club-shaped.

Based on their anatomy, Gustafson (1930) implied that all amphinomids are carnivores, an observation supported by field studies. The mouth has a muscular, eversible lower lip used for rasping and possibly squeezing food material. Most amphinomids are slow-moving carnivores, feeding on sessile sponges (Dales 1963a), anemones (Ebbs 1966), hydroids (Dales 1963a) and ascidians (Day 1967; Kudenov 1995, Fauchald & Jumars 1979). *Hermodice carunculata*, common on Caribbean coral reefs, feeds on living coral. Marsden (1963) reported numerous cases of this species feeding on *Porites porites* and *P. asteroides* by opening its mouth and everting its buccal mass over or onto the coral; the worms could only be dislodged by gentle pulling. Another tropical species of *Pherecardia* preys upon injured crown-of-thorns starfish, *Acanthaster planci* (Glynn 1984).

Species of *Chloeia* and *Notopygos* are active predators whereas others, such as *Eurythoe* and *Pareurythoe*, are omnivorous, and according to Kudenov (1995), have a preference for animal remains. Prey is detected by contact rather than by remote sensing, but experiments in which semi-digested coral matter was put in the water column also attracted these animals (Lizama & Blanquet 1975). The worms attack single coral polyps or anemones by everting their ventral rasping pad onto the prey. Some predigestion takes place before the polyp remnants are swallowed. Amphinomids are least active during the day (Marsden 1962; Kudenov 1974). *Eurythoe complanata* is usually hidden during daylight hours, whereas *Hermodice carunculata* will sit out in the open and feed during late afternoon and early morning.

The digestive tract consists of five main regions. The buccal organ can be everted or folded forward on itself and extruded through the mouth. It is anchored to the body wall by anterior and posterior sets of muscles. The oesophagus is short. The long intestine begins on chaetiger 8 to 10, extending posteriorly and the short rectum opens posteriorly at the anus (Marsden 1963). Each of these structures is described in detail for *Hermodice carunculata* by Marsden (1963). Various secretory cells have been recognised in the buccal cavity; they may secrete enzymes capable of preliminary digestion. Presumably, this species must have some immunity to coral nematocysts, which are taken into the body in large numbers and eliminated in quantity in the faeces. Marsden (1963) investigated the stomatogastric nervous system and this agrees in general with the descriptions by Gustafson (1930) and Storch (1912).

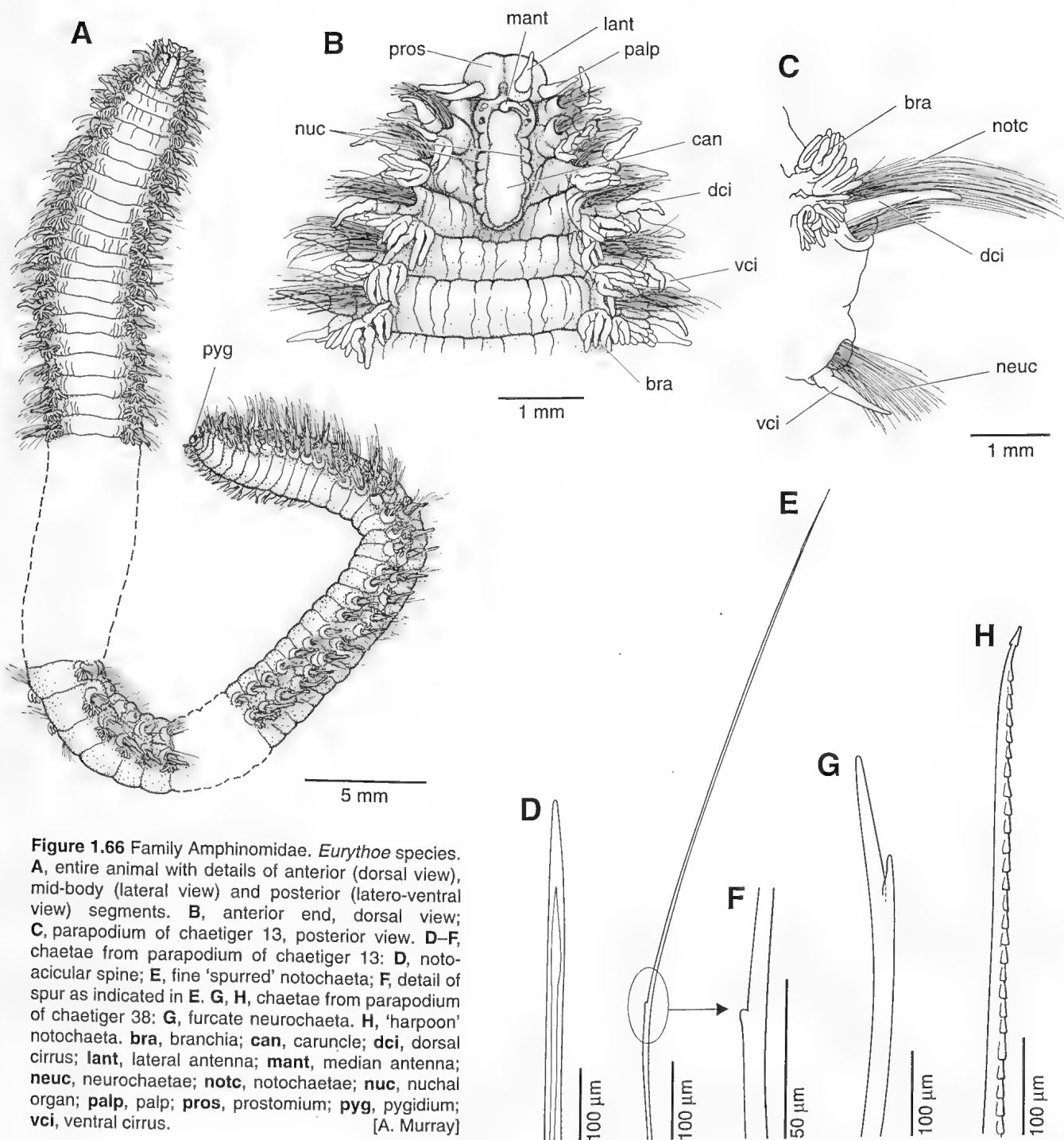


Figure 1.66 Family Amphinomidae. *Eurythoe* species. **A**, entire animal with details of anterior (dorsal view), mid-body (lateral view) and posterior (latero-ventral view) segments. **B**, anterior end, dorsal view; **C**, parapodium of chaetiger 13, posterior view. **D–F**, chaetae from parapodium of chaetiger 13: **D**, notochaeta; **E**, fine 'spurred' notochaeta; **F**, detail of spur as indicated in **E**. **G**, **H**, chaetae from parapodium of chaetiger 38: **G**, furcate neurochaeta. **H**, 'harpoon' notochaeta. **bra**, branchia; **can**, caruncle; **dci**, dorsal cirrus; **lant**, lateral antenna; **mant**, median antenna; **neuc**, neurochaetae; **notc**, notochaetae; **nuc**, nuchal organ; **palp**, palp; **pros**, prostomium; **pyg**, pygidium; **vci**, ventral cirrus. [A. Murray]

The nuchal organs are represented along side the caruncle (Fig. 1.2A; Storch & Welsch 1970). The integument of amphinomids contains many innervated ciliary cells (Storch & Welsch 1970); the functional significance of this is unclear (Marsden & Hassessian 1986).

The microanatomy of the supra-oesophageal ganglion of *Eurythoe complanata* has been studied in detail by Marsden & Galloway (1968). They described three types of ganglion cells, 12 ganglionic nuclei and four commissures. They compared these structures with those in another amphinomid, *Hermodice carunculata*, and found that the nervous connections of the eyes are much better developed in the latter species. *Hermodice* species are diurnal in nature whereas *Eurythoe* species are nocturnal. There is some evidence that migration of retinal pigment and a change in effective pupal size may occur in *Hermodice*. A definite rod layer adjacent to the pigmented retina is present and is distinct from the relatively homogenous lens. The cuticle above the eye forms a

corneal layer, which is completely separate from the underlying lens. In *Eurythoe*, the eye consists of two confluent depressions, a deep ventral cup and a more shallow dorsal cup; its lens has a larger surface area and curves from the dorsal onto the lateral surface of the prostomium (Marsden & Galloway 1968).

Amphinomids typically have separate sexes. The gametes proliferate from the peritoneum of the parapodial muscles in *Hipponoe gaudichaudi*, and from the gut wall in *Eurythoe complanata* and *Pareurythoe californica* (Kudenov 1974; reviewed by Clark & Olive 1973).

The breeding biology of *Eurythoe complanata* has been studied in detail by Kudenov (1974). In the Gulf of California, this species exhibits both asexual and sexual reproduction. In spring, individuals undergo architomic scissiparity by splitting the body into one or more parts; these then regenerate heads, or tails, or both. Kudenov (1974)

1. CLASS POLYCHAETA

documented the rate of segment replacement and the growth processes involved. In the summer, about 12–13% of the population undergoes sexual reproduction. The sex ratio is 1:1 and large numbers of oocytes are produced from the peritoneal linings surrounding the blood vessels and the gut. Gametes are spawned through two pseudopores formed by the lateral rim of the pygidium and the intestine. Gametes are released into the intestine through lesions in the gut wall and transported by muscular contractions and the ciliated lining of the gut to the pygidium. Females release all the oocytes at once, whereas the males do not release all their spermatozoa. Rouse (1986) suggested that the contents of the sperm acrosome may facilitate sperm movement through the egg jelly. A detailed description of the structure of the sperm, an 'ect-aquasperm', is given by Rouse & Jamieson (1987).

Benthoscolex cubanus lives in the intestine of a sea urchin, *Archeopneustes hystrix* and breeds throughout the year. The sex ratio is 1:1. Females produce small non-buoyant oocytes which seem likely to give rise to free-swimming larvae.

Amphinome rostrata, commonly found drifting on wood and associated with stalked barnacles, has been observed brooding. Young have been found attached to the female, wrapped around her parapodia near the branchiae (Pettibone 1963). Augener (1924a) found 20 juveniles, 3–10 mm in length, attached to one large female 90 mm long. Brooding has also been recorded for *Hipponoa gaudichaudi*; the young are found attached to the female during April and May in the North Pacific (Augener 1924a, in Pettibone 1963, although year misquoted). Additional data on this species are given by Kudenov (1977b). The juveniles are brooded in the intersegmental grooves and the juveniles migrate from the ventral side to the dorsum as they increase in size. Kudenov (1977b) suggested that the species is a protandric hermaphrodite, with smaller individuals having higher densities of spermatozoa, which decreases as the number of segments increases as the animal grows. The lower and upper limits for sexually functional males is from 18–22 segments; worms with more than 23 segments are functionally females and generally lack spermatozoa. Like *A. rostrata*, this species also lives on drift wood, so perhaps brooding is an adaptation to this life style.

Family Euphrosinidae

Euphrosinids have a short, compact body, with abundant chaetae (Fig. 1.67A). The head is hidden by the anterior segments, and has eyes and antennae and a well-developed caruncle. Well-developed branchiae are present on the lateral and dorsal sides of the body. Euphrosinids, together with amphinomids, are referred to as fire worms.

The prostomium is reduced to a narrow ridge, and the peristomium is represented only as lips around the mouth (Kudenov 1993). A pair of small lateral antennae is present; a median unpaired antenna is located more posteriorly on the prostomium (Fig. 1.67B, C). Although palps are lacking palpal nerves are present, and run to the ventro-lateral lips (Gustafson 1930); the position of these nerves correspond to those of the palpal nerves in amphinomids, suggesting a loss of palps. The nuchal organ/caruncle process is three-lobed with longitudinal ciliated ridges, attached frontally and projecting as free lobes posteriorly. The longitudinal muscles form bundles and segmentation is distinct. The first segment is distinct and is curved dorso-laterally around the prostomium so that the first parapodia project anteriorly on both sides of the prostomium without being fused to it (Gustafson 1930). The notopodia comprise transverse ridges which nearly meet medially; the neuropodia project laterally,

tapering to blunt tips. Dorsal and ventral cirri are present. The branchiae are divided into small branching bundles behind the notopodia (Fig. 1.67A, D). One pair of inflated pygidial cirri is present. Epidermal papillae are absent and lateral organs and dorsal cirrus organs have not been observed. The buccal organ is a thick, eversible ventral muscle mass covered with thickened cuticle. A gular membrane is absent; the gut is a straight tube (Gustafson 1930). The segmental organs are mixonephridia and are present in most segments. The circulatory system is closed and a heart body is lacking. Aciculae are present and chaetae are calcified. Furcate (Fig. 1.67E–G) and capillary chaetae are present, but most chaetae are spine-like with characteristic 'ringent' ornamentation. This definition follows that of Fauchald & Rouse (1997).

Euphrosinids were for a long time included in the Amphinomidae, although they were placed in a separate family many decades ago. Their family status was recognised only after Gustafson's (1930) study of the anatomy and morphology of both groups. Fauchald & Rouse (1997) accepted that euphrosinids comprise a morphologically well-defined group, but were concerned that their separation as a family would make it difficult to diagnose the Amphinomidae; they placed amphinomids and euphrosinids as sister groups within the Eunicida.

Two genera, *Euphrosine* and *Palmyreuphrosysne*, containing 42 species, were recognised by Fauchald (1977); subsequently an additional genus, *Euphrosinella*, and 11 species have been described by Hartmann-Schröder & Rosenfeldt (1988, 1992), Kudenov (1993) and Blake (1985). At present, five genera are assigned to the family: *Euphrosine*, *Palmyreuphrosysne*, *Euphrosinella*, *Erchinome* and *Archinome*. Possibly six species have been collected from Australian waters. Day & Hutchings (1979) listed only *Euphrosine masterii* from a single record from Queensland; they listed it within the family Amphinomidae. Unpublished data from Museum Victoria and the Australian Museum, include several additional records: two species of euphrosinids from Bass Strait (Museum Victoria collections); *Euphrosine superba* from the Lord Howe Island lagoon and from Shell Harbour, New South Wales; *Euphrosine longesetosa* from Port Jackson, Nelson's Bay and Port Stephens, New South Wales, and; an unnamed species of *Euphrosine* from North Head, Port Jackson, New South Wales (Australian Museum collections).

Euphrosinids are well represented in the Antarctic. Hartmann-Schröder & Rosenfeldt (1988, 1992) and Kudenov (1993) described several species from this region, often from deep water. Kudenov (1993) provided keys to the Antarctic species of *Euphrosine*, based on characters such as the type and numbers of branchiae, and chaetal features (see Kudenov 1987 for discussion). In addition, *Archinome rosacea* has been described and collected from hydrothermal vents and deep water (Blake 1985). Fauchald & Jumars (1979) suggested that the family is better represented in deeper waters than the closely related Amphinomidae. However, Day (1967) recorded some South African species from the intertidal zone.

The body is stout, short and oval in outline (Fig. 1.67A), with relatively few segments; *Euphrosine* has less than 50, and *Euphrosinella* has 15 (Detinova 1985). The head comprises the prostomium and the reduced peristomium. The caruncle/nuchal organ complex has a median keel, three pairs of longitudinal folds, eight ciliated ridges and a small nuchal cirrus. Neurochaetae are arranged in tufts and notochaetae are present in transverse rows on the dorsum, with branchiae inserted at the bases of the notopodia. The well-developed

branchiae are presumably used for oxygen exchange. Studies by Vogt & Kudenov (1994) showed that the relationships of notochaetal prong length to each other and to body size are useful species-specific characters, for although they vary along the body and within chaetal fascicles they are consistent for a species. The chaetae of euphosrinids are calcareous, and sometimes they are heavily calcified.

Euphosrinids have mixonephridia in most segments (Ehlers 1864–1868; Goodrich 1900, 1945; Fage 1906). The nephridia open between the bases of adjacent parapodia. Goodrich (1900) suggested that these organs function as a nephridium and a genital duct as the histology of the large coelomic funnel and the walls of the nephridial canal are very different.

According to Naville (1933), euphosrinids undergo morphological changes associated with spawning to become epitokes. The eyes enlarge, and the notopodial capillaries become much longer and thinner than the unmodified ones. The animals swim by using these modified chaetae.

Virtually nothing is known about reproduction in euphosrinids, although Gustafson (1930) described a fenestrated chorion surrounding the oocytes, the function of which is unknown (Schroeder & Hermans 1975). Reproduction in euphosrinids has not been investigated (Wilson 1991).

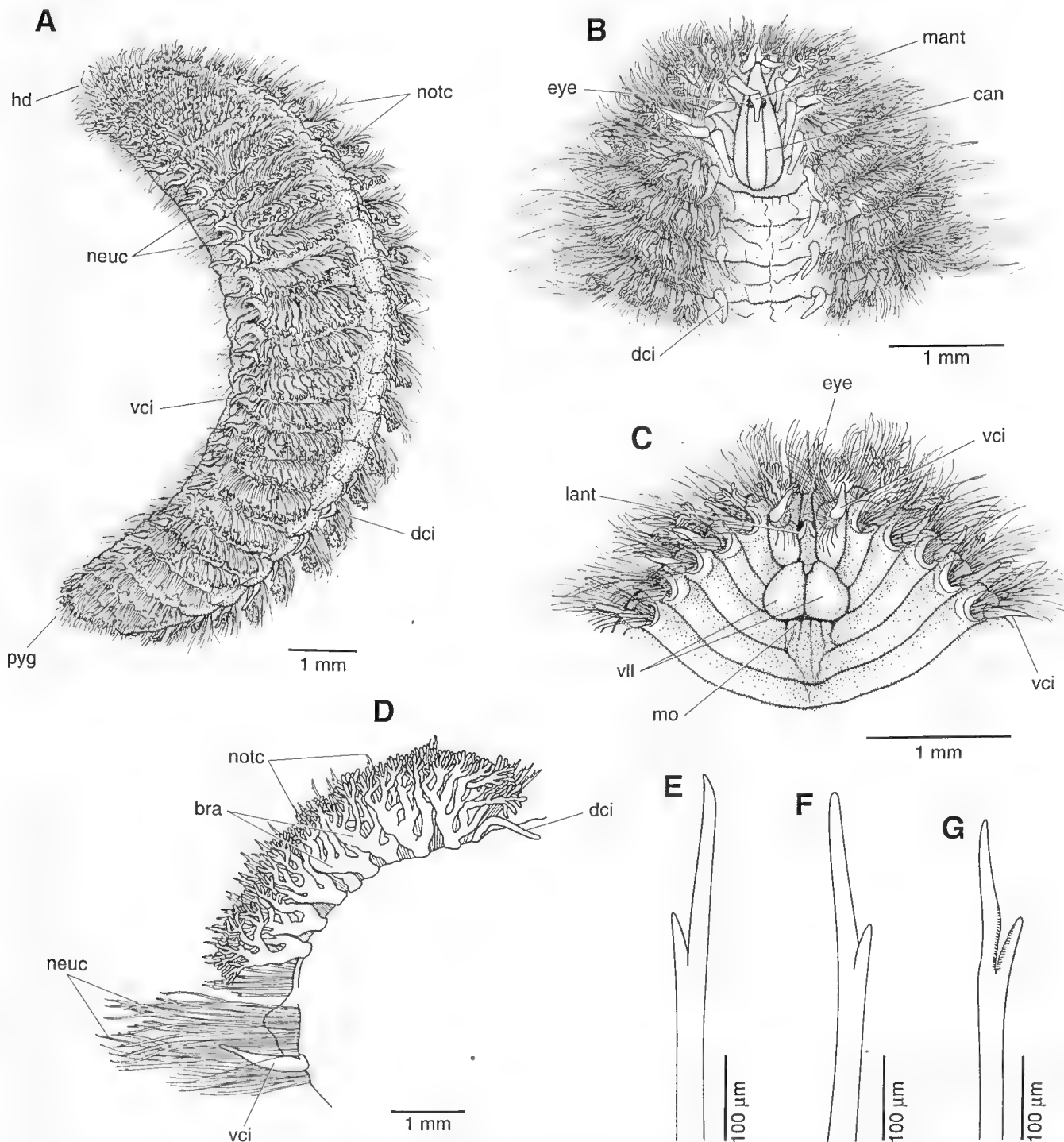


Figure 1.67 Family Euphosrinidae. **A–C**, an unidentified euphosrinid species: **A**, entire animal, dorso-lateral view; **B**, anterior end, dorsal view; **C**, anterior end, ventral view. **D–G**, *Euphosine* cf. *superba*: **D**, parapodium of chaetiger 19, posterior view; **E**, furcate neurochaeta from parapodium of chaetiger 19; **F**, furcate notochaeta from parapodium of chaetiger 32; **G**, ringent notochaeta from parapodium of chaetiger 32. **bra**, branchiae; **can**, caruncle; **dci**, dorsal cirrus; **eye**, eye; **hd**, head; **lant**, lateral antenna; **mant**, median antenna; **mo**, mouth; **neuc**, neurochaetae; **notc**, notochaetae; **pyg**, pygidium; **vci**, ventral cirrus; **vll**, ventro-lateral lips.

[A. Murray]

1. CLASS POLYCHAETA

Euphrosinids are carnivores (Fauchald & Jumars 1997). They feed mainly on sponges, but they will also feed on bryozoans and corals (Gustafson 1930); they use an eversible, ventral hypertrophied pharynx with a thickened ridged cuticle to scrape prey off the substratum (Gustafson 1930). McIntosh (1894) found large quantities of sponge spicules and chitin fragments in the gut of *Euphrosine foliosa* and *E. cirrata*. Day (1967) recorded that a species of the same genus in South Africa feeds only on sponges, and Fauchald & Jumars (1979; unpublished observations of Sanders, Grassle & Hampton) reported that a deep-water species of *Euphrosine* feeds exclusively on foraminiferans.

PHYLLODOCIDA

The name Phyllodocida was coined by Dales (1962a) and was subsequently used by other workers such as Fauchald (1977) and Pettibone (1982) for essentially the same group of polychaetes. Rouse & Fauchald (1997) found strong support for the monophyly of this assemblage, and continued the use of the name Phyllodocida. Prior to Dales (1962a) the group had never been regarded as a monophyletic taxon. In some classifications, for example, Uschakov (1955) Phyllodoce-morpha and Nereimorpha were given equal rank in the Errantia, along with the Eunicimorpha and Amphinomorpha (Fig. 1.43). In other classifications members of the Phyllodocida were placed with eunicids and amphinomids as the Rapacia or Nereimorpha (for example, Benham 1896; Hatschek 1893), thus corresponding to the taxon Aciculata used in this volume.

Rouse & Fauchald (1997) found Phyllodocida, as formulated here, in all of their cladistic analyses (Fig. 1.57). The monophyly of the group was supported by features such as the ventral position of the sensory palps, the presence of tentacular cirri, the loss of dorso-lateral folds, the presence of an axial muscular proboscis, and the presence of compound chaetae with a single ligament. A total of 28 families was placed in Phyllodocida by Rouse & Fauchald (1997) (see Table 1.3). One major difference in the formulation of Phyllodocida by Rouse & Fauchald (1997) and that of previous workers was that they placed Myzostomida (as Myzostomatidae; incorrectly spelt as Myzostomidae) in the group. In this volume, however, the Myzostomida are treated as outside Polychaeta (see Chapter 2). Rouse & Fauchald (1997) did not further subdivide the Phyllodocida, though others, such as Fauchald (1977) and Hartmann-Schröder (1996) have done so. The hypotheses developed by other authors, such as Fauchald (1977) and Hartmann-Schröder (1996), for the relationships among the various Phyllodocida families vary considerably, and also conflict with recent studies (for example, Glasby 1993; Pleijel & Dahlgren 1998) on subgroups of the clade. Further investigations at more restricted levels to determine the monophyly of many of the taxa appears to be required before relationships among the entire Phyllodocida can be assessed accurately.

Members of most families of Phyllodocida have been recorded from Australian waters. Only three families, Ichthyotomidae, Nautiliniellidae and the pelagic Pontodoridae have no recorded representatives from Australian waters; the latter family, however, is described briefly in the following section as it may be found with further collecting. Ichthyotomidae is a monotypic family represented by a single species, *Ichthyotomus sanguinarius*, a parasite of eel fins (see Fig. 1.46J, K); recorded from Naples. Nautiliniellids are deep-sea bivalve commensals or parasites found in hydrothermal vents or cold seeps (see Fig. 1.46N–P); only one genus is known. Like most polychaetes, many members of the

Phyllodocida are associated with marine sediments, rocks, or algal mats from the intertidal zone to extreme depths. There are also many planktonic species, as well as some that live in freshwater.

Family Acoetidae

Acoetids are long scale worms with numerous segments, covered by elytra. They are tubiculous, living in thick pliable tubes. They are widely distributed, but are never common in benthic samples.

The prostomium is distinct, and bears large ommatophores anteriorly in some genera. The peristomium is represented only by lips around the mouth. Lateral and median antennae are present (Fig. 1.68B). The ventral, tapering palps lack articulations; they are fused to the medial side of the first pair of parapodia (Pettibone 1989a). Nuchal organs are present. The longitudinal muscles comprise four bands (Storch 1968). The first segment curves around the prostomium; its parapodia are structurally similar to others but they are fused to the base of the prostomium. Two pairs of tentacular cirri are present. The neuropodia are distinctly longer than the notopodia. Elytra replace some of the dorsal cirri along the body; ventral cirri are present. In some acoetids, finger-like epidermal branchiae extend into the space between the elytra and the body wall (Pettibone 1989a). Lateral organs and dorsal cirrus organs have not been observed, and epidermal papillae are lacking. The pygidium bears one pair of cirri. The eversible, muscular axial pharynx bears two pairs of dorso-ventrally oriented jaws (Fauvel 1923; Pettibone 1989a), and terminal papillae are present around the mouth. There is no gular membrane; the gut has lateral branches (Storch 1968). As in all scale-worms, metanephridia are present (Goodrich 1945). No other information is available on the structure of segmental organs. The circulatory system is unknown, although presumed to be closed; the presence of a heart body has not been confirmed. Aciculae are present, as are variously ornamented capillaries and spines (Fig. 1.68D–F; Pettibone 1989a). Fine silk-like notochaetae are released and woven to form tubes (Fig. 1.68G; Pflugfelder 1934; Pettibone 1989a). The microscopic structure of the acoetid 'branchiae' is unknown; thus, it is unknown whether or not they function as 'true' branchiae in the sense of the term used here. This definition is based on that of Fauchald & Rouse (1997).

As scale-worms, acoetids were initially assigned to the Aphroditidae and Rouse & Fauchald (1997) concluded that the Acoetidae form a sister clade with the Aphroditidae (Fig. 1.57). The presence of spinning glands define the clade as being monophyletic. They share with aphroditids the ability to produce masses of very thin pliable chaetal strands, which in aphroditids form the dorsal felt covering certain genera. In acoetids, these fibres are detached and used to weave the walls of their thick, pliable tube (Fig. 1.68G). Acoetids lack compound chaetae as do the aphroditids and polynoids. Pettibone (1989a) resurrected the generic name *Acoetes*, thereby making available the name Acoetidae as the earliest family-level name proposed for this taxon. Her action removed a problem with the use of *Polyodontes* as the type genus for the family. The family name Polyodontidae is a junior homonym of a family of fishes. Day (1967) regarded the group as a subfamily (Polyodontinae) within the family Aphroditidae, and Muir (1982) placed them as a subfamily of the Polynoidae, but neither classification has been widely accepted. Pettibone's (1989a) detailed chronological synopsis of Acoetidae, and its genera and species revealed a fair degree of complexity and confusion in this family. No subfamilies were recognised.

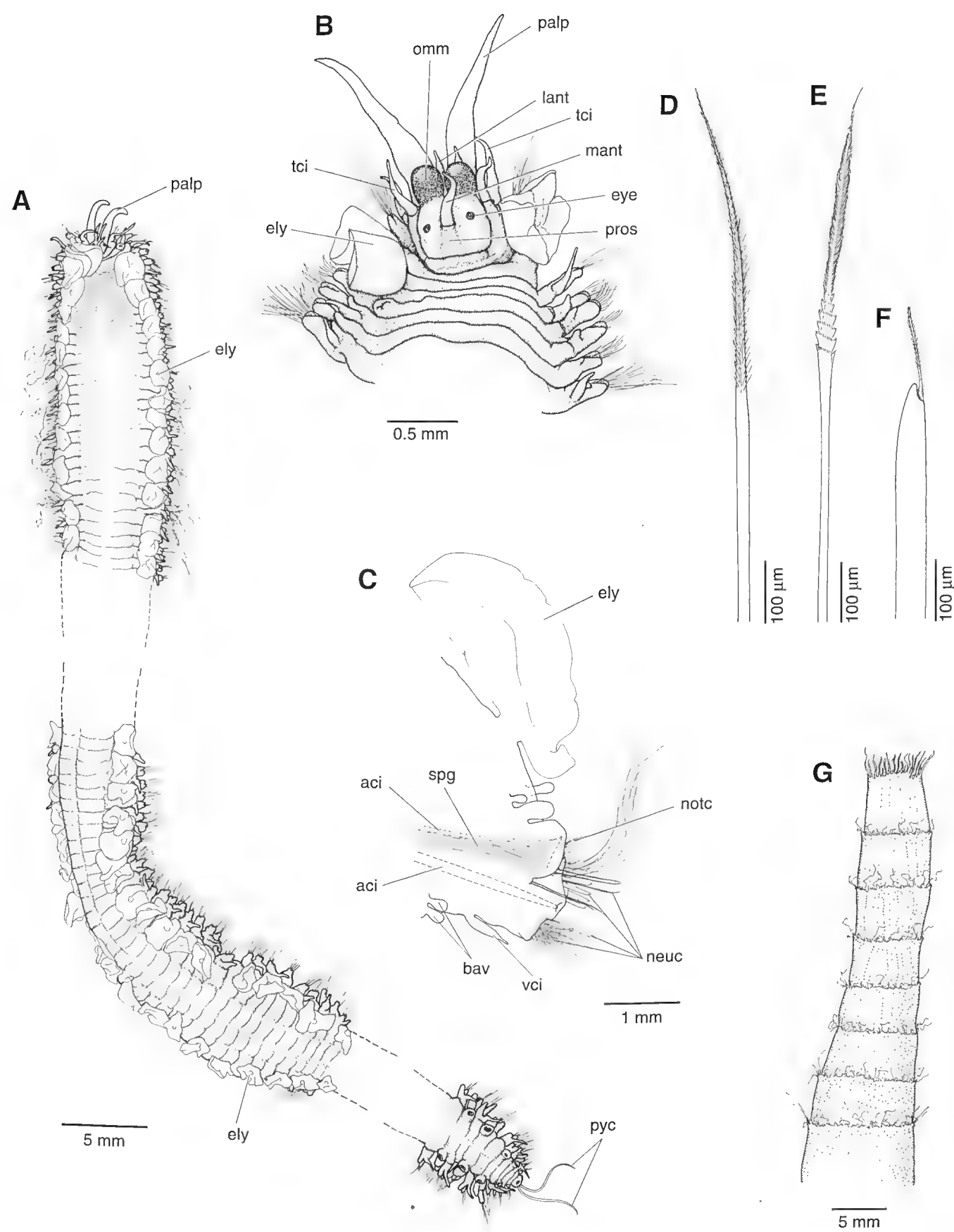


Figure 1.68 Family Acoetidae. **A**, *Eupanthalis* species, animal with details of anterior, middle and posterior segments, dorsal view. **B–F**, *Polyodontes australiensis*: **B**, anterior end, dorsal view; **C**, parapodium of chaetiger 26, anterior view; **D**, superior neurochaetae from parapodium of chaetiger 26; **E**, spinose neurochaeta from parapodium of chaetiger 27; **F**, stout aristate neurochaeta from parapodium of chaetiger 27. **G**, anterior section of tube of ?*Euarche* species 'A', an Australian species collected from Moreton Bay. **aci**, acicula; **bav**, basal vesicles; **ely**, elytron; **eye**, eye; **lant**, lateral antenna; **mant**, median antenna; **neuc**, neurochaetae; **notc**, notochaetae; **omm**, ommatophore; **palp**, palp; **pros**, prostomium; **pyc**, pygidial cirri; **spg**, spinning gland; **tci**, tentacular cirrus; **vci**, ventral cirrus. [A. Murray]

1. CLASS POLYCHAETA

Worldwide, nine genera are recognised (Pettibone 1989a; Shen & Wu 1993) containing 43 species. Pettibone (1989a) in her revision did not accept all of the described species as the type material is damaged, so that this species number may be conservative.

In Australia, three genera, each with one species, have been recorded. *Polyodontes australiensis* (Fig. 1.68B–F) has been recorded from the New South Wales coast and Tasmania by Hartman (1966c), Benham (1916, as *Eupompe australiensis*) and Hutchings & Murray (1984). *Polyodontes melanotus*, described from Queensland by Monro (1931), is now referred to as *Acoetes melanotus* (new combination Pettibone 1989a). *Eupanthalis* species has been recorded from off Cronulla, New South Wales (Australian Museum unpublished records; Fig. 1.68A). Acoetids are never found in large numbers; and perhaps they are territorial, as are some polynoids, which may explain why single individuals are usually collected, and then often only as fragments.

Acoetids are widely distributed from the low intertidal zone to the deep sea (to 1500 m) and have been recorded from most oceans, except apparently the Arctic and Antarctic seas (Pettibone 1989a).

Individuals are long lived and occupy permanent tubes which may harbour various commensal species, such as bryozoans (Nielson 1964; Pettibone 1989a). The strange organisms recorded by Horst (1917) on the parapodia of *Polyodontes atromarginatus* are loxosomatid kamptozoans (Pettibone 1989a). The kamptozoans are anchored by their long peduncles to the deep pockets of the inner layer of the soft mud tubes, where they utilise the food-bearing currents in the respiratory chamber of their host (Franzén 1962). Other cohabitants include gastropod molluscs on the surface of the worm (Moore 1972), bivalve molluscs between the parapodia (Rullier 1965) and a commensal polynoid in the tube (Fox & Ruppert 1985).

Acoetids are long, rounded in section and have numerous segments; they may reach lengths of up to 300 mm and widths of 40 mm. They live in a fibrous tube made of long, silk-like, chitinous threads secreted by the segmental spinning glands (Fig. 1.68C) and woven into a criss-cross spiral. These tubes are unique amongst the polychaetes in their general construction and the lack of any membranous lining. The threads appear to be homologous with the fibres which form the dorsal feltage of *Aphrodita*. They are modified chaetae produced from the notopodium and are contained in a convoluted sac, which intrudes into the body cavity. Pflugfelder (1934) provided a detailed description of these spinning glands, which consist of numerous fine silk-like shiny golden threads tightly packed into a rope-like structure, and excretory cells and loose connective tissue. The silk-like threads are formed like chaetae with trichogenic cells secreting large numbers of fine fibres held together by chaetal coats. Their tubes are tough (Pettibone 1989a) and are sometimes mixed with mud, clay or sand particles, making the resultant tube quite thick. The tube is open at both ends, although, according to Lindroth (1941), only one end is functionally open; it extends above the substratum by 50–100 mm (Pflugfelder 1932) and provides a site for sponges, algae and branched bryozoans to attach themselves. A specimen of *Panthalis oerstedii* in an aquarium was observed forming its tube; it used the parapodia of the second segment to manipulate the spinous fibres (Watson 1895).

Acoetids have a well-developed head. The prostomium and the first tentacular segment are more or less fused and bear long palps, antennae, tentacular cirri and eyes. The eyes may be large and sessile or supported by projecting ommatophores

(Fig. 1.68B). Pettibone (1989a) classified the prostomium of acoetids into four categories based on the development of the ommatophores (stalked eyes) and used these features in her key to the genera of Acoetidae. The distal border of the eversible pharynx is encircled by a row of sensory papillae, of which those mid-dorsally and mid-ventrally placed have expanded bases. The number of papillae ranges from nine to 39 across the different genera. Two pairs of strong, hooked jaws are present, each bearing seven to 17 lateral teeth. Wolf (1986c) reported the presence of venom glands associated with the piercing type jaws in two species. The dorsum is partially covered by elytra, which begin on segment 2 and alternate regularly with the dorsal cirri, except for the second and third pairs which are found on consecutive segments 4 and 5. The elytra are attached to prominent bulbous elytraphores. They are relatively small compared to the size of the animal and do not cover the dorsum. Elytra are round to oval with smooth margins (Fig. 1.68A, C) and the more posterior elytra may have a lateral pouch. Short ventral cirri are present on all chaetigerous segments. The parapodia are biramous, but may appear uniramous as the two rami are very closely aligned; both rami are supported by aciculae (Fig. 1.68C). The chaetae are all simple; capillary notochaetae and stouter neurochaetae, including both acicular and aristate types are present (Fig. 1.68D–F; Pettibone 1989a).

Acoetids are carnivores, and capture their prey by partially leaving their tube, seizing it with their jaws and rapidly withdrawing back into their tube. Watson (1895) observed *Panthalis* lying on its back with the head and the two long palps protruding from the tube, ready to seize passing prey.

The elytra move up and down continuously, creating a water current down the body, and presumably aiding respiration (Watson 1895). Some species have branchiae on the anterior, dorsal and posterior faces of the parapodia and at their base. These non-vascularised branchiae may be papilliform, filamentous or arborescent coelomic extensions, and are covered by a thick cuticle. In some species of *Eupolyodontes*, a large pair of branchiae are present on the prostomium (Pettibone 1989a). Pettibone (1989a) suggested that branchiae are few or lacking in some of the smaller species where the integument is delicate and thin-walled, implying that oxygen exchange occurs across the body wall in these species. Rouse & Fauchald (1997) suggested that the structures referred to as branchiae by Pettibone (1989a) are not homologous with branchiae in other families; this view is supported here.

Nephridial papillae are lacking (Pettibone 1989a). Based on Goodrich's (1945) review, Rouse & Fauchald (1997) assumed that acoetids have metanephridia as have closely related groups, although no acoetids have been examined. Pflugfelder (1934) recorded that the nephridia were positioned close to the lower part of the spinning glands, closed to the coelom and were composed of follicles filled with golden-yellow granules enclosed in a chitin-like membrane. He suggested that these granules were waste products, and their colour highlighted the adjacent spinning glands. He also noted additional excretory granules in small vacuoles in the epithelium of the longitudinal folds of the intestinal caecum, in the connective tissue of the peritoneum, between the parapodial musculature and in the epidermal cells of the body integument.

Åkesson (1963) conducted a detailed study of the anterior end of *Panthalis oerstedii*, including the external morphology of the brain, and nerve connections to the ommatophores, vestigial eyes, antennae and palps. The paired sessile and paired stalked eyes of acoetids were described by Pflugfelder (1932a, 1932b). In *Polyodontes tidemani*, the sessile eyes

comprise an optic vesicle beneath a thick cuticle and epithelium. The proximal retina of the vesicle consists of a row of yellowish-brown sensory cells enclosed by dark brown supporting cells. A row of unpigmented rods is also present. The central cavity contains gelatinous material with connective fibrils and a lens. In the stalked eyes, both the pigmented sensory and supporting cells attain a considerable length; the sensory cells have a large basal nucleus, plasma containing homogenous gelatinous material and parallel nerve fibrils extending distally into the colourless rods and basally to the optic nerve. The support cells are slender, and wider distally due to the nucleus and a thickened concentration of pigment; the support fibres form the walls of the rods and extend into the lens area.

According to Pflugfelder (1932a, 1932b) *Eupolyodontes amboinensis*, which he referred to as *E. sumatranus*, has large stalked eyes. The optic vesicle consists of a thin-walled, curved cornea, which encloses an anterior chamber, and a diaphragm resembling an iris with a pupil-like break in the anterior part of the lens. The large lens almost completely fills the posterior chamber, and is composed of uniform concentric layers and an unstratified area next to the retina. The latter consists of bottle-shaped, pigmented, sensory cells, forming lamellar-like projections on the rod wall. These sensory cells have a gelatinous consistency and are woven together to form a large number of closed chambers, covered with fine grained plasma and containing fine nerve fibrils. The supporting cells, which surround the sensory cells, are wider distally with a nucleus and concentration of pigment, with support fibres extending into the rod area. A basal layer is found above the epidermis and thick cuticle. Eakin & Hermans (1988) suggested that the eyes of acoetids may have some image formation, but this needs to be confirmed.

The sexes in acoetids are separate; sperm and large yolky eggs have been observed in the body cavity by Pettibone (1989a), but no information is available on their reproduction. It is assumed from their large size that they live for several years. Pflugfelder (1934) suggested that the preformed fracture zone near the exit for the spinning fibres facilitated the release of mature gametes. No information is available on development and growth.

Eisig (1887) recorded fishermen collecting individuals of *Polyodontes maxillosus* in the Bay of Naples from depths of 30 m using long lines baited with worms or smaller fishes. These animals have a muscular pharynx and strong jaws and will take the bait, but the fishermen were only bringing up anterior ends. Pettibone (1989a) surmised that the posterior end pulled itself back into the tube and regenerated a new head. Saint-Loup (1889) recorded a similar phenomenon in the Gulf of Marseille at depths of 50 m. The specimen collected had an extensible pharynx of 30 mm with a diameter greater than that of the body and the opening of the pharynx was 30 mm in diameter.

Family Alciopidae

Alciopids are thin, delicate, pelagic polychaetes with large eyes and a transparent or semi-transparent body. They are distinguished from other members of the Phyllodocida primarily by their complex spherical eyes with an internal lens; the eyes are much larger than the remainder of the prostomium (Fig. 1.69A, B).

Throughout most of the literature, both palps and antennae of alciopids have been referred to as antennae, but in this treatment the homologies and terminology used by Fauchald & Rouse (1997) are followed. The anterior margin of the

prostomium carries a pair of antennae and a more ventral pair of palps (Fig. 1.69B). A median antenna is located between the eyes. Nuchal organs are present; they are ciliated and located posterior to the eyes. The peristomium is reduced. The pharynx is muscular and eversible, and bears at least one pair of papillae or grasping fleshy lateral horns placed distally; jaws are absent. The first segment is incomplete dorsally, and has one pair of tentacular cirri; the next two segments have two to four pairs of tentacular cirri (Fig. 1.69B). Biramous parapodia with leaf-like dorsal cirri, which may be reduced on anterior-most segments, commence on segment 4. Chaetae are simple or compound (Fig. 1.69C, D), and aciculae are present. The pygidium has one pair of cirri or a single pygidial cirrus. The structure and form of the parapodia and chaetae provide all the characters necessary to attain a generic identification; a single well-preserved parapodium is sufficient for this purpose (Apstein 1900). This description follows that of Fauchald & Rouse (1997).

The most recent taxonomic treatments of the family Alciopidae include those by Dales & Peter (1972), Uschakov (1972) and Rice (1987). The generic classification, however, of the Alciopidae is little changed from the revision by Støp-Bowitz (1948).

Worldwide, there are 10 genera and 34 species (Rice 1987; Støp-Bowitz 1991). Five species, *Alciopina gazellae*, *Vanadis formosa*, *V. studeri*, and one unidentified species of each *Alciopa* (Augener 1927) and *Torrea* (Fig. 1.69B–D; Museum Victoria unpublished data), are known from Australian mainland waters; none are endemic (Day & Hutchings 1979). Another three species live in the waters of the Australian Antarctic Territory: *Rhynchonerella bongraini*, *R. petersii* and *Vanadis antarctica* (Hartman 1964). Alciopids are generally poorly known worldwide as it is difficult to obtain undamaged specimens of these fragile worms from traditional plankton hauls. In Australia, the scarcity of records can also be attributed to the lack of examination of many Australian collections of pelagic polychaetes.

Alciopids live in tropical and temperate oceans throughout the world from surface waters to a depth of at least 300 m (Rice 1987); many species appear to be pantropical in distribution. As mentioned above, they also live in Antarctic waters, but apparently not in those of the Arctic (Maurer & Reish 1984).

Alciopids may reach body lengths of up to 300 mm, for example in *Vanadis formosa*, which may also have more than 200 segments (Uschakov 1972). Other species, however, may only reach lengths of 30 mm and have 50 segments. Members of most alciopid genera have transparent bodies without significant musculature and swim slowly with a spiralling action (Rice 1987). Species of *Rhynchonerella* and *Alciopa*, however, have muscular bodies and are strong swimmers (Rice 1987).

The eyes of alciopids are vastly more sophisticated than in any other family of the Polychaeta, and are comparable in complexity and function to cephalopod and vertebrate eyes. Alciopid eyes are remarkably convergent with those of deep-sea cephalopods and fishes; structures in common include the cornea, iris, spherical lens, a primary retina in the focal plane of the lens and paired accessory retinas beside the lens (Fig. 1.69E; Wald & Rayport 1977). In the surface-water genus *Torrea*, the wavelengths of maximum sensitivity differ for primary and secondary retinas. The data for the deeper-water genus *Vanadis* are less clear, but in that genus the sensitivity of the retinas closely matches the wavelengths (460–480 nanometres) that penetrate deepest and at which bioluminescence is strongest (Wald & Rayport 1977). The

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orientation of the eyes differs between species, and in some the retina appears totally blind to light from above (Dales 1955b).

Alciopids are regarded as pelagic carnivores (Fauchald & Jumars 1979). Prey items are captured by the eversible pharynx. The papillae or horns present on the end of the pharynx often have mucous glands which produce secretions that probably assist in the capture of prey (Rice 1987). As in the related Phyllodocidae, hard jaws are absent, but some species have hardened papillae on the surface of the pharynx when everted (Rice 1987). Prey items include crustaceans (copepods and euphausiids) and pelagic tunicates (Thaliacea) (Dales 1955b); however there have been no quantitative studies of diet. The gut of *Naiades cantrainii* is simple, thin-walled and greatly inflated within each segment, but narrows to pass through a connecting slit between segments (Dales 1955b).

Alciopid nephridia have been described by Goodrich (1900) and Dales (1955b). Groups of solenocytes occur at the base of each parapodia and cluster around a large, clear, ciliated vacuole (coelomostome), which empties to the exterior of the body via a nephridial duct. The nephridial duct passes posteriorly through the septum and opens just anterior to the parapodium of the following segment. In males, the coelomostomes are converted into seminal vesicles which enclose the testes. For example, in species of *Naiades* seminal vesicles occur only between segments 15 and 29; in other genera they are less regionalised. Dark pigmented segmental glands may also occur at the base of some parapodia, but are apparently not associated with the nephridial system (Dales 1955b); their function is unknown, although they may contain mucus-secreting cells. Distinct ovaries have not, as yet, been detected in any alciopid. In *Rhynchonerella angelini* and *Alciopa reynaudii* oögonia are released into the coelom as packets of cells (Eckelbarger & Rice 1988).

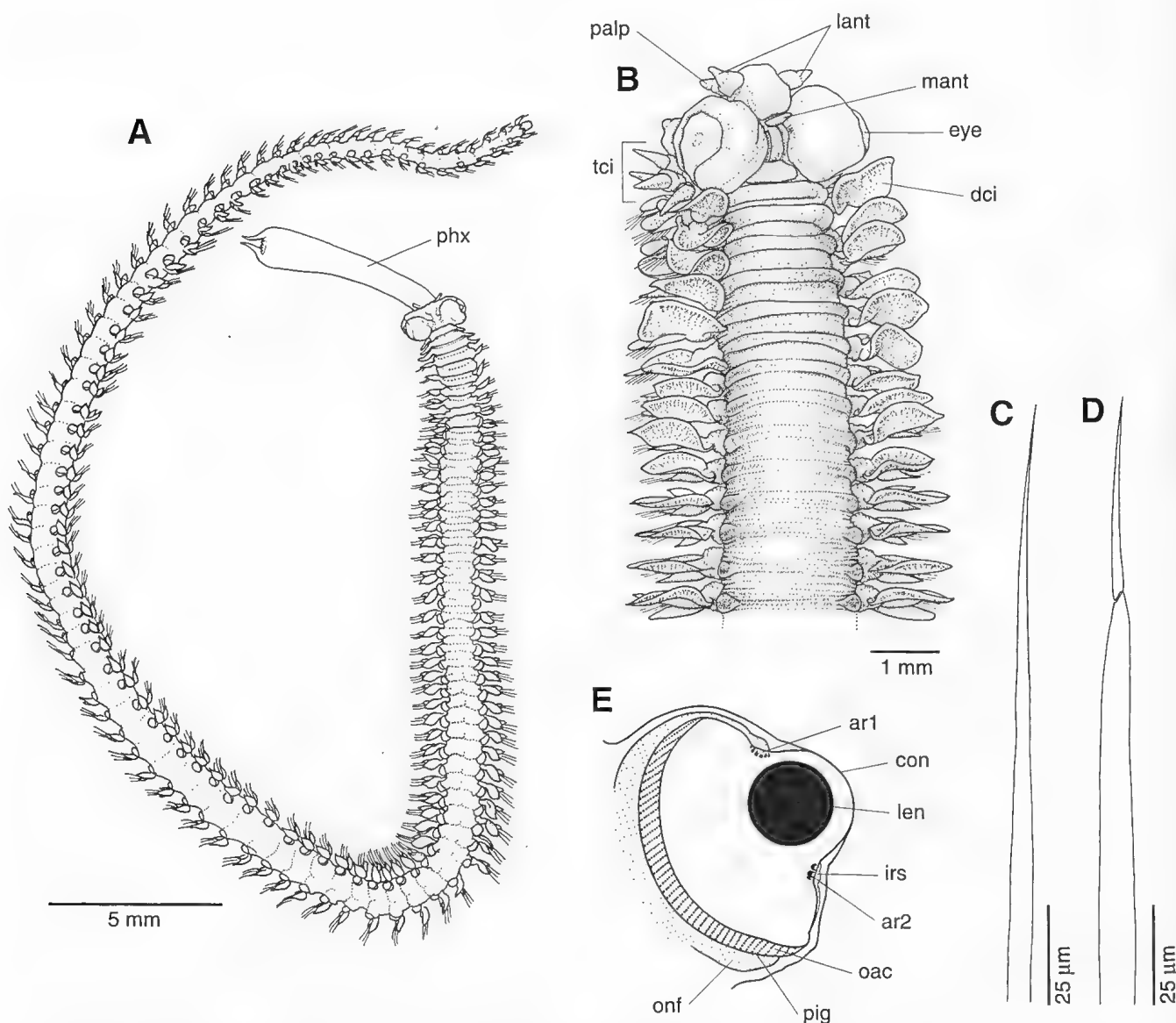


Figure 1.69 Family Alciopidae. **A**, *Torrea candida*, entire animal with pharynx everted, dorsal view; specimen from the Bay of Naples Aquarium, Italy. **B–D**, an undescribed Australian species of *Torrea*: **B**, anterior end, dorsal view; **C**, simple chaeta; **D**, compound chaeta. **E**, cross-section of eye of *Torrea candida*. The cornea is two layered, the outer continuous with the skin and the inner continuous with the iris and retina. Accessory retinas are visible on each side of the lens. The main retina comprises a single layer of photoreceptor and auxillary cells stratified into three layers: a distal layer of receptor elements or outer auxilliary cells, a thin layer of orange-red pigment which continues anteriorly to form the iris and a thick layer of cell bodies ending in optic-nerve fibres. **ar1**, accessory retina 1; **ar2**, accessory retina 2; **con**, ornea; **dci**, dorsal cirrus; **eye**, eye; **irs**, iris; **lant**, lateral antennae; **len**, lens; **mant**, medium antenna; **oac**, outer auxillary cells; **onf**, optic-nerve fibres; **pig**, pigmented layer; **tci**, tentacular cirri (4 pairs). (E, after Wald & Rayport 1977) [K. Nolan]

Judging by the prevalence of sperm storage structures in females, copulation occurs in most, if not all, species. Sperm may be agglutinated into packets by secretions from ventral glands present in males, and are stored by females in receptacles formed by modification of one or two pairs of parapodia on an anterior segment (Dales 1955b). The likely adaptive significance of sperm storage by females in sparsely-distributed planktonic species has been widely noted (Dales 1955b; Rice 1987).

Many alciopids occur at depths below the photic zone. Harvey (1952) and Okada (1925) have reported the presence of luminescence in members of the Alciopidae, but no photogenic organs have been identified. Clark (1970) studied the highly-developed mucous glands present ventrally between the segments in males of *Rhynchonerella angelini*; their function is unknown, but Clark speculated that they may contain bioluminescent products.

Members of the Alciopidae host species of gregarine protozoan parasites; different species occur in the coelom and in the intestine (Corbel *et al.* 1979).

The Alciopidae are recognised widely as being closely related to the benthic Phyllodocidae. Fauchald & Rouse (1997) also indicated that recognition of Alciopidae as a family may render the Phyllodocidae paraphyletic. Dales (1955b) suggested that the alciopids may have been derived from a form similar to that of members of the genus *Eulalia* (Phyllodocidae).

A cladistic analysis of relationships among genera of alciopids has been published by Wu & Lu (1993). Their analysis based on parsimony agrees with the earlier phenetic treatment of Rice (1987) in grouping the genera *Alciopa*, *Vanadis*, *Torrea* and *Naiades* together. This conclusion is also in broad agreement with the earlier scheme of evolutionary relationships in alciopids of Dales (1955). All three studies also agree that the presence of simple capillaries alone in *Naiades* is a derived character state in a family where more diverse chaetal types are otherwise present.

Family Aphroditidae

Aphroditids are commonly referred to as sea mice, and may be found washed up on the beach. They are stout, solid worms with an oval body and a dorsum covered in a 'felt' which is often highly iridescent. They are active carnivores with numerous head appendages which are presumably used to hunt their prey.

The prostomium is a frontally rounded double lobe, and the peristomium is reduced to lips around the mouth. A median antenna is present (Fig. 1.70A, B); lateral antennae are absent. A facial tubercle is prominent in most taxa. Ventral, tapering, unarticulated palps are present; they are fused to the anterior surface of the first pair of parapodia. Nuchal organs are present (Rullier 1951). Longitudinal muscles are present in four bundles (Storch 1968); segmentation is distinct. The first segment is curved around the prostomium and has parapodia which are similar to those of other body segments (Fig. 1.70B). Two pairs of tentacular cirri are present. The notopodia are always shorter than the neuropodia. Either dorsal cirri or elytra are on segments throughout; ventral cirri are present. Elytra are absent in *Palmyra* (Watson Russell 1989). Simple papillae are present on the venter and parapodia in many taxa. Pygidial cirri are present according to Fauvel (1923), but are absent according to Fordham (1925). Lateral organs and dorsal cirrus organs have not been observed. The buccal organ is an eversible muscular axial

pharynx with two pairs of dorso-ventrally arranged jaws which are poorly developed in some species (Day 1967); terminal pharyngeal papillae are present. The gular membrane is absent, and the gut has paired side-branches (caeca) in most segments. The segmental organs, mixonephridia, are present in most segments (Darboux 1899; Goodrich 1945; Hanson 1949a). The circulatory system is closed and the heart body absent. Aciculae are present. Chaetae are variously ornamented capillaries and spines (Fig. 1.70D–O). Notochaetae are spines, capillaries and fine silky fibres, which form a dorsal felt in many taxa. The silky fibres are produced by spinning glands. This definition is based upon Fauchald & Rouse (1997).

Aphroditids were among the first polychaetes described in 1758 by Linné and, the family is sometimes defined to include all scale-worms. Recently, the scale-worms have been split into six families (Acoetidae, Aphroditidae, Eulepethidae, Polynoidae, Pholoidae and Sigalionidae – see Fauchald & Rouse 1997). The aphroditids are most similar to the acoetids; these two families share the presence of fine, silken notochaetae. In acoetids, these are used to form the tube; in aphroditids, of which only some species are capable of producing such chaetae, they form a felt covering the dorsum.

Seven genera containing 63 species were recognised by Fauchald in 1977; since then an additional 12 species have been described; seven of these were newly described from Australian waters, bringing the total for this region to 18 (Hutchings & McRae 1993). Only five of these are known to occur outside Australian waters. Sixteen species are known from the Indonesian Archipelago, and it seems likely that some of these species will be found in northern Australian waters when more sampling takes place in this region.

There has been no comprehensive revision of the family since it was erected by Malmgren (1867). Aphroditids from Scottish waters have been reviewed by Chambers (1985). Hutchings & McRae (1993) examined representatives of all known genera, in their Australian revision, except for the monospecific *Hermionopsis* and *Heteraphrodita*. Watson Russell (1989) placed the monospecific genus *Palmyra* in the Aphroditidae; it was previously regarded as belonging to the Chrysopetalidae. Hutchings & McRae (1993) examined large numbers of individuals of several species and therefore were able to study the variation of a character with respect to increasing size and presumably age. They found that the following characters are useful in characterising species and genera: shape and structure of the median antenna; facial tubercle and any ornamentation, length and ornamentation of the palps, and; the distribution and types of chaetae. However, many species of aphroditids are known only from the type material and so perhaps additional useful characters will be found in the future.

Aphroditids occur worldwide. They are slow-moving worms which live in soft muddy or sandy sediments mostly in the subtidal zone, but are also often found in deep water (Day 1967). The European species *Aphrodita aculeata* may be found at low water mark on sandy beaches, often just below the sediment surface. Species are normally found in low numbers suggesting that they live a solitary life. Aphroditids do not form tubes, although the dorsal felt is often covered in sediment and epizoons such as spirorbine polychaetes and barnacles.

The distributions of Australian species of aphroditids are illustrated by Hutchings & McRae (1993) and consist of three major geographical patterns. Species with an extensive geographical range, such as *Aphrodita australis* and *A. goolmarris*, those with a restricted distribution such as

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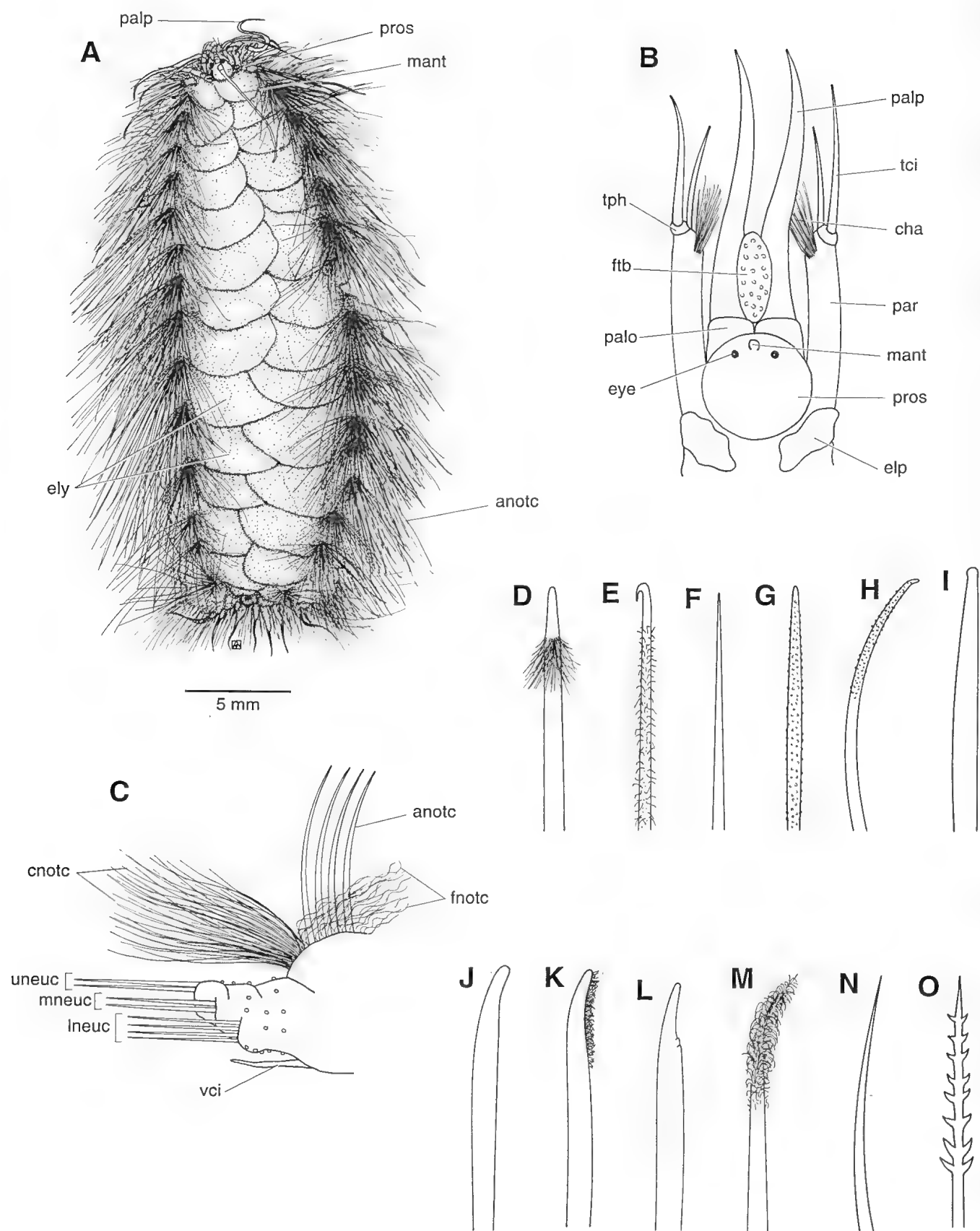


Figure 1.70 Family Aphroditidae. **A**, dorsal view of entire animal, *Laetmonice moluccana*. **B**, **C**, morphological aspects of a generalised aphroditid: **B**, prostomium and first segment, dorsal view; **C**, parapodium, posterior view. **D**–**I**, notochaetal types of a generalised aphroditid: **D**, triangular tip with fine hairs radiating from expansion; **E**, hooked tip with fine hairs and tubercles; **F**, acicular, smooth; **G**, acicular, tuberculated; **H**, bent with distal region densely tuberculated; **I**, paleal-like, smooth. **J**–**O**, neurochaetal types of a generalised aphroditid: **J**, slightly curved tip; **K**, slightly curved tip with plumose margin; **L**, slightly curved tip with two small teeth; **M**, pilose tipped; **N**, extended tip; **O**, bipinnate. **anotc**, acicular notochaeta; **cha**, chaeta; **cnotc**, capillary notochaetae; **elp**, elyrophore; **ely**, elytra; **eye**, eye; **fnotc**, felt notochaetae; **ftb**, facial tubercle; **lneuc**, lower tier of neurochaetae; **mant**, median antenna; **mneuc**, middle tier of neurochaetae; **palo**, palophore; **palp**, palp; **par**, first parapodium; **pros**, prostomium; **tci**, tentacular cirrus; **tph**, tentaculophore; **uneuc**, upper tier of neurochaetae; **vci**, ventral cirrus. (After Hutchings & McRae 1993)

[A. Murray]

Laetmonice dolichoceras and *L. wonda* and a species *A. malkaris* which is known only from a single locality. Similarly, the monospecific genus *Palmyra* represented by *P. aurifera* is known only from Ashmore Reef off the Northern Territory.

Aphroditids are typically large robust polychaetes and mature individuals may be up to 200 mm in length and 80–90 mm in width, although the single species of *Palmyra* is about 15 mm long and 8 mm wide. Hutchings & McRae (1993) suggested that immature specimens 2–3 mm long cannot be reliably identified to species level as they lack particular chaetal structures and there is limited information available on the changes of various structures such as chaetae, palps and tentacles with increasing size (and presumably age). They often have many segments each bearing parapodia. The number of segments is relatively constant for a particular species. Hutchings & McRae (1993) found that within the genus *Aphrodita* there were two groups of species, those with relatively few segments (32–36) and those with more than 40 segments. It seems likely that once a certain number of segments have been attained, growth occurs only by expansion of segments. Most aphroditids tend to be oval in shape; *Aphrodita* has an attenuated caudal region and species of *Laetmonice* vary from elongate through oval to cigar-shaped. All aphroditids are flattened ventrally and arched dorsally. The ventral surface is rugose and papillated.

The prostomium varies from rounded to oval in-shape, and bears a median antenna which may be simple as in many species of *Aphrodita*, or compound, consisting of a basal ceratophore and a terminal style. The ceratophore may be smooth or finely papillated. The development of ocular peduncles or a raised ocular area varies between genera. Nuchal flaps are present in some genera, whereas a facial tubercle is present in all genera (Fig. 1.70B). Palpal length appears to be relatively constant within a species, and they may be with or without ornamentation. In *Palmyra*, the prostomium can be retracted and concealed by the anterior segments. The first (or tentacular) segment projects anterolaterally and is fused to part of the prostomium; it has two pairs of tentacular cirri and uniramous parapodial lobes which may bear paleae and/or capillary chaetae.

The dorsum is covered to a varying extent by elytra and the number of pairs varies between genera and sometimes, as in *Laetmonice*, between species, or may be absent as in *Palmyra*. Observing these elytra may be difficult, as in most genera the capillary notochaeta form a dorsal felt covering the elytra. The elytra, if present, occur on segments 2, 4, 5 and 7 and continue alternately to segments 23 or 25, then on every third segment to the posterior end. Segments without elytra have long dorsal cirri. Mettam (1971) has shown that the elytra and the dorsal cirri are homologous structures. A well-developed felt is present in all species of *Aphrodita* and *Heteraphrodita*, whereas in *Laetmonice* and *Pontogenia* the development varies between species and is absent in *Palmyra* and *Aphrogenia*. Iridescent capillary notochaeta are present in some species of *Aphrodita*. In addition, acicular notochaetal spines are present and these are variously ornamented as illustrated in Figure 1.70D–I. In *Palmyra*, *Pontogenia* and *Aphrogenia*, the notochaeta are flattened paleae, which curve over the dorsum and maybe with or without serrated margins. Several kinds of neurochaetal spines are also present; these range in form from bipinnate to smooth with a variously developed basal spur and additional teeth, to ones which may be frayed or pilose (Fig. 1.70J–O).

Septa are present in the trunk segments behind the pharyngeal region, although they are reduced and transparent. Anteriorly the septa become reduced to fine strands or appear to be lacking, but in these segments a small area of septum connects the interparapodial oblique muscles and the body wall (Mettam 1971).

Species of *Aphrodita* move by a fast stepping action, individual parapodial movements being an extension and retraction of the neuropodium with co-ordinated chaetal movement (Mettam 1971). The downward and backward propulsive stroke raises the animal clear of the substratum and the waves of parapodial activity travel along the body (Mettam 1971).

As the parapodia are used in locomotion, the body wall is a basketwork of longitudinal and diagonal muscles which maintain a constant body shape. Mettam (1971) provided a detailed description and illustrations of the body wall muscles. Similarly, he described the muscles of the parapodial walls and how the movement of the parapodium is effected by the acicular muscle complex and the intrinsic parapodial wall muscles. Mettam's (1971) descriptions supercede those of Fordham (1925) and Storch (1968).

Most authors appear to regard aphroditids as carnivores. Fauchald & Jumars (1979) indicated that information was available for five species. Feeding modes of *Aphrodita aculeata* have been studied by Blegvad (1914), Hunt (1925) and Pearson (1971); for *Aphrodita* species by Yonge (1928); *Hermione hystrix* by Hempelmann (1931); *Laetmonice filicornis* by Hartmann-Schröder (1971); and a unidentified species of *Laetmonice* by Day (1967). Fauchald & Jumars (1979), however, stress that few direct observations have been made and many reports just repeat earlier studies. Gut contents of several specimens of *A. aculeata* have been examined by Blegvad (1914) and Hunt (1925) and found to contain fragments of other polychaetes especially terebellids and sabellids, although many individuals had empty guts. Day (1967) stated aphroditids lack jaws and that species of *Aphrodita* feed on detritus and microscopic animals; *Laetmonice* species are often found with the gut diverticula distended by foraminiferans. However, aphroditids do have jaws, even though they are irregularly shaped and less obviously grasping than those found in other scale-worm families. Fauchald & Jumars (1979) suggested that they specialise in feeding on slow moving animals. They believed that there is insufficient evidence that they could sustain themselves by scavenging. The gut content cited by Day (1967) for *Laetmonice* may indicate that they may be selective in what they prey upon. More recently Mettam (1980) kept *Aphrodita aculeata* in the laboratory where the animals were observed to feed on a range of live prey including molluscs, crustaceans and worms, including a specimen of *Neanthes virens* three times the length of the sea mouse. Such prey items were swallowed head first, swallowing was laboured, but rhythmic accompanied by rapid elytral beating and presumably accomplished by sucking pulsations of the pharynx. The prey was drawn slowly into the gut, not macerated by the pharynx, and passed through the intestine. Undigested remains, including a set of jaws, acicula and chaetal bundles, were ejected as a faecal pellet. Some scale-worms ingested passed through the gut little damaged suggesting digestion and absorption is not efficient. Faecal pellets subsequently produced contained masses of excretory cell blebs derived from the digestive caeca. These contain haem derivatives which a carnivore might be expected to produce (Dales & Pell 1971).

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Mettam (1980) found no evidence to support Day's (1967) statement that they were deposit-feeders. Mettam also found that *Aphrodita* species only feed when buried in the sediment. His observations confirm that they are active carnivores as they captured both large active polychaetes as well as sedentary species.

The structure of the axial muscular pharynx has been studied in detail by Dales (1962a) and Fordham (1925). A thin-walled short buccal tube is inverted on protrusion of the very muscular pharynx. The oesophagus is looped anteriorly to allow for forward movement on protrusion of the pharynx (Dales 1962a, fig. 7). Protrusion occurs, as both Darboux (1899) and Fordham (1925) have described, by increased pressure of the coelomic fluid. Fordham suggested that the muscles attached to the buccal tube play a role in protrusion, but Dales (1962a) suggested that they have a more important role in retraction. When the pharynx is withdrawn their contraction would enlarge the buccal tube and allow the pharynx to pass through the mouth. Around the mouth are a series of circular muscles forming an incomplete ring, which on contraction would squeeze the pharynx back into its original position.

The intestine has numerous paired caeca in which digestion and absorption takes place. In *Aphrodita aculeata*, the entrance to each caecum is surrounded by cells, which effectively forms a sieve through which only small particles of food may pass. The sieves are elaborate ciliated structures and they presumably prevent the caeca from collapsing under high coelomic pressure produced during locomotion (Mettam 1971). The epithelium lining the walls of a caecum is complex and contains several kinds of secretory and absorptive cells (see Dales & Pell 1971). The epithelial cells contain two distinct cell types, one excretory and the other secretory, which are both responsible for the production of the brown fluid found within the caeca. The brown fluid consists of haem, and a non-haem brown pigment, which probably comprises lipofuscin and non-haem iron compounds. They suggested that the haem is derived from the food in the gut, whereas the non-haem brown pigment is excreted into the lumen. This fluid is ejected from the anus when the animal is disturbed and may be used as a defence mechanism. The presence of the gut haems is interesting since haems are absent from the blood of *Aphrodita*, although a small quantity does occur in the ventral nerve cord. Earlier Phear (1955) had identified the haem in the gut fluid as methaemoglobin. However, Dales & Pell (1971) could find no evidence of absorption occurring within the caeca which Fordham (1925) had suggested, although it may occur. A diagrammatic representation of the gut of *Aphrodita aculeata* is given by Michel (1988).

A detailed ultrastructural study of the gut, including the caeca of *Aphrodita aculeata*, was carried out by Welsch & Storch (1970). They found that the glandular cells of the pharynx and the caeca are rich in hydrolytic enzymes and the pharynx, in addition, shows evidence of alkaline phosphatase and aminopeptidase. They suggested that there is little evidence of functional separation of the midgut and the caeca; both areas appear to produce secretory material as well as being involved with absorption, which somewhat contradicts the findings of Dales & Pell (1971).

The rectum is unusual amongst the polychaetes in having a series of strongly ciliated ridges projecting into it (Dales 1963a).

Fordham (1925) described 'heart-bodies' associated with the nephridia, rather than as inserts in the dorsal blood vessels. Fordham's structures are here considered 'glomerulus'-like structures, differing positionally and structurally from heart-bodies present in other polychaetes. Aphroditids have a closed vascular system (Hanson 1949a), and Rouse & Fauchald (1997) suggested on the evidence above that a heart body is absent.

Fordham (1925) suggested that both the elytra and the dorsal body wall function as respiratory surfaces although he did not describe the presence of any distinct respiratory structures. The irrigatory movements in *Aphrodita* have been described by van Damm (1940) who found that the dorsum between the elytophores acts as a respiratory surface and the water lying there is periodically ejected at the caudal end. A fresh current is simultaneously drawn in below the caudal end and passes along the ventral surface in a series of grooves. The ejection of water is by a combination of compression of the elytophores and elevation of the ventral body wall to draw in a fresh supply of water. During inspiration the elytra are elevated and the body wall is depressed, forcing water to the dorsal surface between the parapodia. These observations of van Damm are supported by the studies of the muscles by Mettam (1971).

The morphology and histology of the cerebral ganglion of *Aphrodita aculeata* was described by Fordham (1925) and re-examined by Åkesson (1963). The cerebral ganglion is an almost globular nerve mass present at the anterior extremity of the body, with a small median antenna inserted at the anterior margin and the palps inserted ventrally. The covering epidermis forms the brain capsule from which is secreted a thick cuticle. On the dorsal side, the cuticle is thinner on a pair of inconspicuous rounded elevations and two rudimentary eyes are found on each elevation. They are globular with a diameter of less than 40 µm and the proximal part of each eye has the shape of a pigment cup. Åkesson further described the internal anatomy and he illustrated the prostomial mesoderm. Although he was unable to study juvenile or larval stages, he suggested that the lateral antennae are represented only by the ceratophore mesoderm, which runs to the palpary nerve. He found no major nerves going to the eyes.

No information on reproduction is available on any species. It is presumed that most aphroditids have a pelagic larval stage, although members of *Palmyra* have large yolky eggs (300–400 µm) suggesting direct benthic development with limited ability to disperse (Watson Russell 1989). No developmental studies on the early stages of any species of aphroditids have been undertaken.

Hutchings & McRae (1993) found a considerable size range in some Australian species with one species *Aphrodita kulmaris* ranging from 18–100 mm in length suggesting a long-lived species.

The lower Cambrian fossil record includes forms with possible aphroditid affinities (Conway Morris 1985). The Burgess Shale material of the Middle Cambrian includes forms with flattened, paleae-like scales and erect spines (sclerites of wiwaxiids, Bengtson & Conway Morris 1984) and polychaetes with large notochaetal fascicles of imbricating paleae (Conway Morris 1979). Such structures resemble chaetal structures found in the aphroditids, especially *Palmyra*, and may represent early forms of this family.

Family Chrysopetalidae

Members of the Chrysopetalidae are fragile, flattened worms recognised primarily by the golden/silvery/coppery coloured petal-like hairs, or paleae, that cover their upper surface. They are active scavengers and carnivores living in crevices in rock, coral, dead shell, seaweed holdfasts and among the tubes of sedentary polychaetes on the shores and down to great depths in muddy and sandy sediments with a gravel/shell component.

These small, mobile polychaete worms are distinguished primarily by their biramous parapodia which support golden or silver-coloured, flattened notochaetae (= paleae) and/or spines that form semi-radiate, imbricating fans covering the dorsum (Fig. 1.71A, B). Both notochaetae and the shafts of falcigerous compound neurochaetae are composed internally of longitudinal channels stacked with transverse septa. Chrysopetalids have a well-differentiated prostomium with a posterior nuchal organ, a pharynx with two jaws and a pygidium with two pygidial cirri and/or conical appendage.

The phylogenetic position of chrysopetalids is still problematical. The family displays a unique notochaetal morphology, but also has other characters found within the Aphroditiformia and Nereidoidea classificatory groups, as defined by Fauchald (1977). Day (1967) included the Chrysopetalidae in the Palmyridae. Fauchald (1977) placed the families Chrysopetalidae and Palmyridae within the order Phyllodocida, suborder Aphroditiformia, superfamily Chrysopetalacea. The rosettes of notochaetal paleal fans are the most obvious character shared by palmyrids and chrysopetalids. The larger, robust palmyrids, however, have a distinct aphroditid head and chaetal characters including non-compartmented, simple neurochaetae. Subsequently, *Palmyra* was included as a non-scaled genus within the family Aphroditidae and the Chrysopetalidae retained as the sole family within the superfamily, Chrysopetalacea, suborder Aphroditiformia (Watson Russell 1989).

In a recent cladistic analysis of the Polychaeta, Rouse & Fauchald (1997) continued to include Chrysopetalidae in the Phyllodocida within the clade Aciculata. Evidence of monophyly of the family is: 'Paleal notochaeta of characteristic structure (Butterfield 1990; Westheide & Watson Russell 1992)' (Fauchald & Rouse 1997).

The first chrysopetalid described – *Palmyra* (= *Chrysopetalum*) *debilis* by Grube (1855) from the Mediterranean – was placed within the family Palmyridae. Ehlers (1864–1868) subsequently established the family Chrysopetalidae to include *Chrysopetalum* Ehlers 1864 from the Adriatic Sea; *Paleanotus* Schmarda 1861 from South Africa and *Bhawania* Schmarda 1861 from Sri Lanka. Levinsen (1879) later included his genus, *Dysponetus*, from Greenland. In a review of the chrysopetalid tropical fauna of Florida, Perkins (1985) described two new genera *Hyalopale* and *Treptopale* and San Martín (1986) described *Acanthopale* from Cuba. Watson Russell (1986) described *Paleaequor* from eastern Australia and *Strepternos* (Watson Russell 1987, 1991) from abyssal depths in the western Atlantic. Kisseleva (1992) described *Victoriella* from the Black Sea and Watson Russell (1998), described *Arichlidon* from tropical western and eastern Australia.

Worldwide, a total of 11 genera and 41 species are described. Nine genera (7 described, 2 undescribed) comprising 23 species (5 valid species described, 18 undescribed) have been found along Australian littoral and continental shelves. *Chrysopetalum*, *Paleanotus*, *Bhawania*, *Dysponetus*, *Treptopale*, *Paleaequor* and *Arichlidon* occur in Australian

waters. *Victoriella*, *Strepternos*, *Hyalopale* and *Acanthopale* are not recorded from Australia, although the latter genus has been recorded from New Guinea. Of the described genera found in Australian waters, *Dysponetus* species occur worldwide between 78° N and 70° S; the other genera have temperate/tropical distributions between 60° N and 60° S worldwide, except for *Paleaequor* and the undescribed genera which are known only from Pacific and Atlantic waters.

Augener (1913) first identified *Chrysopetalum occidentale* (type locality California coast) from south-western Australia (Shark Bay to Albany). He also described the same species from Auckland and Campbell Islands (Augener 1924b), New Zealand (Augener 1924b) and from Sydney Harbour and Port Jackson Heads, eastern Australia (Augener 1927).

Reichelt (1979) and Hutchings (1981) recorded the family (as Palmyridae) from Heron Island and Lizard Island, Great Barrier Reef, respectively. *Paleanotus debilis* (= *Chrysopetalum debile*) was recorded by Buzhinskaya, Obut & Potin (1980) from Scott Reef, north-western Australia.

Hartmann-Schröder's pan-Australian collecting trip in the 1970s resulted in many new records of chrysopetalids and the description of two new species. She recorded *Paleanotus debilis* (= *Chrysopetalum debile*) from Port Hedland (1979), Cape Naturaliste (1982) and Walpole (1983), Western Australia, Warrnambool, Victoria (1987), Eden, Batemans Bay, Lake Macquarie, Maclean, New South Wales (1989) and Heron Island, Queensland (1991a).

Paleanotus chrysolepis (type locality, The Cape, South Africa) was recorded from south-western Australia (Augener 1913) and Port Phillip Bay, Victoria (Poore *et al.* 1975). Hartmann-Schröder also listed this species from Port Augusta, South Australia (1985a), from Eden, Batemans Bay, and Lake Macquarie, New South Wales (1989) and from Heron Island, Queensland (1991a). She further noted an unidentified species of *Paleanotus* from Warrnambool, Victoria (1987).

Undescribed species of *Bhawania* have been recorded from Broome and Port Hedland (Western Australia) and Lizard Island (Great Barrier Reef; Hartmann-Schröder 1979; Hutchings & Murray 1982). Hartmann-Schröder (1981a) also described *Bhawania* (= *Chrysopetalum*) *multisetosa* from Kalbarri, Western Australia, and further, recorded its occurrence in Geraldton (1981a), Cape Naturaliste, Exmouth Gulf (1982), and at Dunsborough and Margaret River, Western Australia (1983).

Hartmann-Schröder (1982) described *Dysponetus bulbosus* from Cape Naturaliste, Western Australia, and also listed *Dysponetus* species from Warrnambool, Victoria (1987).

Watson Russell (1986) described a new genus and species, *Paleaequor setula*, from Halifax Bay, Queensland, with a range across northern tropical Australia to southern Papua New Guinea. Hartmann-Schröder (1990) also recorded this species from Brisbane, Queensland. Watson Russell (1998) described the genus, *Arichlidon*, and two new species, *A. hanneloreae* from tropical Australia and *A. acropetalon* from deeper waters off Queensland.

In Australia, species of *Bhawania*, *Chrysopetalum*, *Paleanotus*, *Treptopale* and *Arichlidon* are associated predominantly with offshore coral islands, reefs, atolls and volcanic submerged sea mounts ranging from the North West Shelf, Western Australia to Lord Howe Island, Tasman Sea, Eastern Australia. Several are also widely distributed throughout the Indo-West Pacific for example, *Arichlidon*

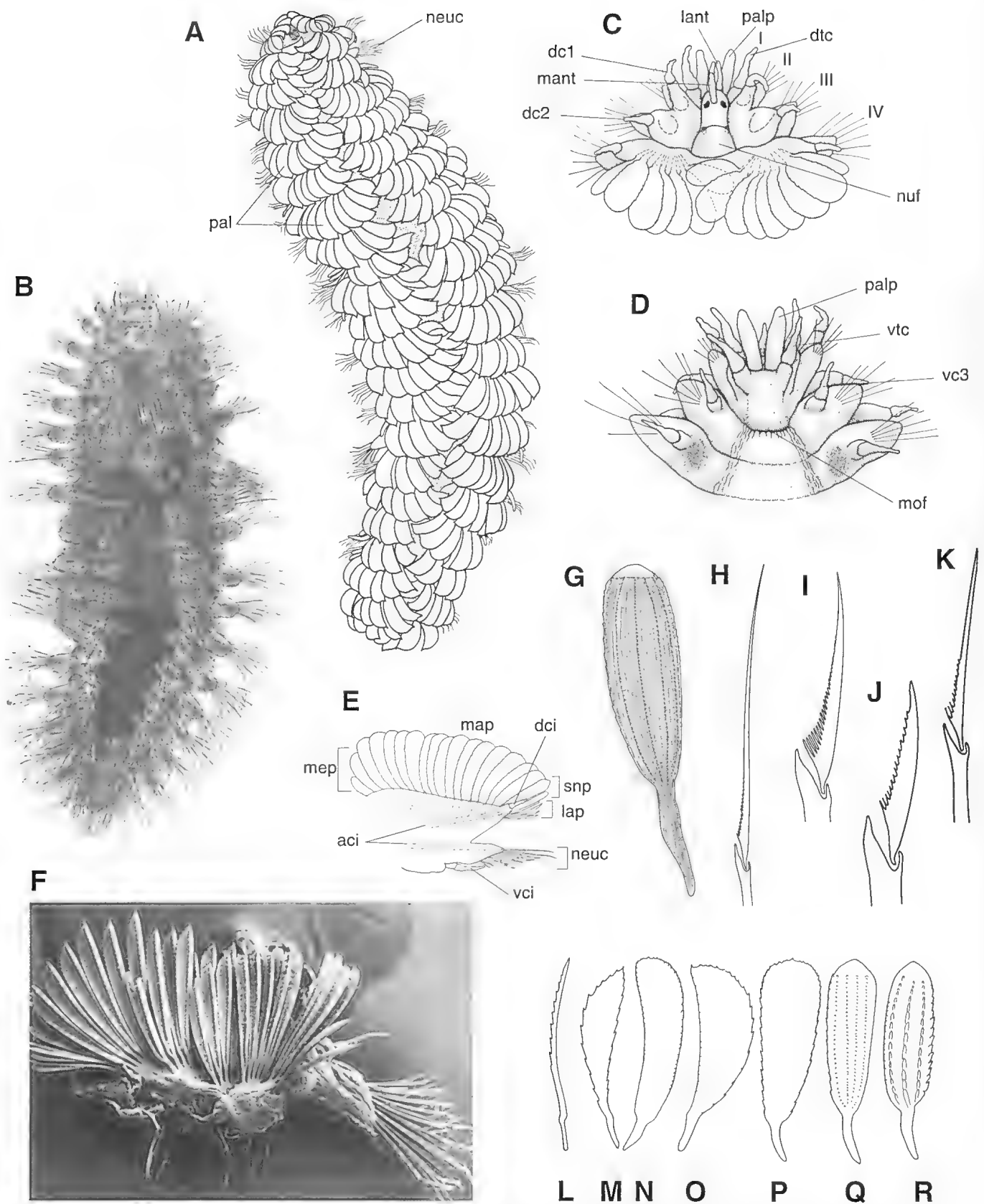


Figure 1.71 Family Chrysopetalidae. **A**, entire animal of *Paleanotus* species, dorsal view. **B**, entire specimen of *Chrysopetalum* species collected from Bondi, New South Wales, dorsal view. **C**, anterior end of *Paleaequor setula*, dorsal view; paleae on chaetigers 1 and 2 removed. **D**, anterior end of *Paleaequor setula*, ventral view. **E**, parapodium from chaetiger 30 of *Paleaequor setula*, ventral view; notochaetal paleal groups shown. **F**, mid-body notopodia and neuropodia with paleae and compound neurochaetal fascicles of *Chrysopetalum* species. **G**, a main palea from the mid-body showing internal and external structure of *Paleaequor setula*. **H–K**, compound neurochaetae from chaetiger 34 of *Paleaequor setula*: **H**, superior spiniger; **I**, mid-superior falciger; **J**, mid-inferior falciger; **K**, inferior spiniger. **L–R**, the main paleal type of the seven genera found in Australian waters: **L**, *Dysponetus*; **M**, *Chrysopetalum*; **N**, *Treptopale*; **O**, *Paleanotus*; **P**, *Arichlidon*; **Q**, *Paleaequor*; **R**, *Bhawania*. **aci**, aciculae; **dci**, dorsal cirrus; **dc1**, dorsal cirrus chaetiger 1; **dc2**, dorsal cirrus chaetiger 2; **dtc**, dorsal tentacular cirrus; **lant**, lateral antenna; **lap**, lateral paleae; **mant**, median antenna; **map**, main paleae; **mep**, median paleae; **mof**, mouth fold; **neuc**, neurochaetae; **nuf**, nuchal fold; **pal**, paleae; **palp**, palp; **snp**, subunit 1 notochaetal paleae; **vci**, ventral cirrus; **vc3**, ventral cirrus chaetiger 3; **vtc**, ventral tentacular cirrus; **I–IV**, segments I–IV. (C, D, E, H–K, after Watson Russell 1986; F, from Westheide & Watson Russell 1986; L–R, from Watson Russell 1987)

hanneloreae. This same species also inhabits coastal coral reefs with one locality record from western Bass Strait. As *Arichlidon* species are known to have pelagic larvae and the East Australian Current provides a mechanism for the dispersal of such larvae south, this record is not surprising.

Paleaequor setula also occurs in northern Australia–New Guinea, in coastal habitats in turbid waters from muddy, sandy sediments in harbours, at the entrance to tidal creeks and calcareous muds at the bases of inshore coral reefs.

A few, mainly undescribed species of *Chrysopetalum* and *Paleanotus* are restricted to southern Australian subtropical and temperate waters: on the east coast between 30° and 45° S and on the west coast between 25° and 35° S. *Chrysopetalum multisetosa*, for example, is found on rocky reefs between Shark Bay, Western Australia and Kangaroo Island, South Australia. A new *Chrysopetalum* species is recorded from Middleton Reef, Tasman Sea, south down the New South Wales coast to Bass Strait and eastern Tasmania. In general, the chrysopetalid faunas of south-eastern and south-western Australia show little affinity with each other or with tropical faunas.

The morphology of congeneric chrysopetalid species, in the main, is very conservative and in the past has led to recognition of cosmopolitan species. From examination of extant chrysopetalid types and material recorded from Australia it is clear, however, that chrysopetalids with older species names have been misidentified, and that they represent new taxa.

The body shape varies from nearly spherical to elongate and slender. Adult body length ranges from 2–3 mm with less than 30 segments (*Dysponetus*) to 50 mm with up to 300 segments (*Bhawania*).

The prostomium has four eyes or no eyes, a median and two lateral antennae and cylindrical or ovoid antero-ventrally inserted palps (Fig. 1.71C, D). The nuchal organ may form a well-defined, raised, oval caruncle (*Chrysopetalum*), a half-moon-shaped nuchal fold (*Paleanotus*, *Treptopale*, *Arichlidon*, *Paleaequor*; Fig. 1.71C), or a thickened ridge (*Bhawania*) situated behind the prostomium. The peristomium is externally invisible in the adult. The first two segments are fused in part and bear tentacular cirri in a number of arrangements. The cephalic lobe in all latter genera, except *Chrysopetalum*, is capable of retraction to a greater or lesser extent within the anterior four segments. Species of *Dysponetus* differ in exhibiting variable features of the prostomium and anterior segments (for example, caruncle absent, mouth papillae present, segment 2 with differing arrangements of cirri and chaetae; Dahlgren & Pleijel 1995), and are currently under review by T. Dahlgren & F. Pleijel (personal communication).

In the genus *Chrysopetalum*, segments 1 and 2 each bear a pair of dorsal and ventral tentacular cirri (that is each segment has eight cirri in total); both segments are uniramous with or without notochaetae and aciculae. In all other paleate genera, including *Paleaequor* (Fig. 1.71C, D), segment 1 supports two pairs of tentacular cirri (that is four cirri in total) and segment 2 is biramous with notochaetae, dorsal cirri and neurochaetae; ventral cirri are absent. Third and subsequent segments are biramous with well-developed parapodia supported by aciculae and neurochaetae and dorsal and ventral cirri (Fig. 1.71C, D).

Dorsal cirri are present on all segments and are retractile in the genera *Bhawania*, *Paleaequor* and *Strepternus*. Neuropodia have ventral cirri and compound neurochaetae

with falcigerous or spinigerous articles and heterogomph joints; small, simple neurochaetal spines are sometimes present. Transitory neurochaetae, observed in some gametogenic individuals of the genus *Arichlidon*, are composed of a long, slender shaft, a homogomph joint and a spinigerous article. The pygidium has two pygidial cirri and, in some genera, a median conical appendage.

Generic differences include the degree of retractability of the prostomium and first segments within the anterior end; number, shape and size of appendages on the prostomium and segments 1 and 2; and morphology of the nuchal organ and pygidium. Chaetal features, especially those of paleal notochaetae, including colour, degree of cover, shape, ornamentation and pattern (see Fig. 1.71L–R), are primary generic characters. Identification to species is based primarily on the number, type and position within parapodia, of the paleal notochaetae and neurochaetae.

Patterns of chrysopetalid chaetal morphology include some chaetal types that are present only at the anterior or posterior end and other chaetal types in the middle body segments that may increase, decrease or be absent at the anterior and posterior ends. Generally, the largest number and full range of adult chaetal types are found on the middle body segments. Changes in shape, number and pattern of chaetae occur with growth, so for identification to species it is necessary to compare both a size range of specimens and the middle body segments from adults of the same size. Similarly, it is essential to have entire specimens to identify larval chrysopetalids.

Notopodia of mid-body segments have a dorsal transverse ridge in which fascicles of foliaceous paleae and spines (paleate species) or only spines (*Dysponetus* species) arise both above and below the dorsal acicula. In paleate species, the notochaetae are divided into different types (see Fig. 1.71E): (1) a small fascicle of subacicular, narrow lateral paleae; (2) a large fascicle of supra-acicular, broad main paleae; (3) a small fascicle of short median paleae that arise at an angle to the main group at the dorsal mid-line; (4) a number of subunit paleae, typically situated between preceding paleae groups, and; (5) a number of small serrate spines anterior to the three mentioned groups. Neuropodia of mid-body segments bear a subacicular fascicle of compound neurochaetae (Fig. 1.71E, F) that may be divided into three or four groups, depending on the article type (spinigers or falcigers) and their position (Watson Russell 1986, 1991). The neurochaetal groups of *Paleaequor setula* are shown in Figure 1.71H–K.

Individual paleae comprise a round basal shaft embedded in the epidermis that broadens distally into a flattened blade and terminates in a sharply pointed or rounded tip (Fig. 1.71G). Each palea has thickened, serrate lateral margins and is smooth and slightly convex on the inner ventral side and slightly concave on the outer dorsal side; the latter may be ornamented with tubercles or raised serrated ribs which commonly gather detrital scale and bacteria (Westheide & Watson Russell 1992).

Internally, paleae are composed of broad medullary channels stacked with a regular series of horizontal fibrous diaphragms (Fig. 1.71G). The medullary part of the palea is surrounded by irregular rows of narrow tubular channels within the chaetal cortex. Westheide & Watson Russell (1992) have published micrographs of sectioned paleae yet to erupt through the surface of the parapodial epidermis which illustrate the continuous process of paleae morphogenesis.

1. CLASS POLYCHAETA

Chrysopetalids have a partially differentiated, highly muscular pharynx with two bilateral, chitinous, stylet-shaped jaws. The brown jaws can often be seen through the ventral body wall within the first five segments or their tips may protrude from the eversible pharynx. The jaws are similar in shape in all genera: distally long, slender and pointed, flaring out mid-way and narrowing proximally with a conspicuous longitudinal groove running the entire length. The inner margins of the jaws are finely or coarsely dentate. The jaw structure suggests a piercing and sucking function; a histological study is needed to corroborate the possibility that a toxin is released to facilitate this mode of feeding.

The nephro-genital system is not fully understood (Glasby 1993). The excretory organs have been described as typical mixonephridia in both sterile and fertile segments of the body (Fage 1906). Goodrich (1945) considered the group to have metanephromixia.

The nervous system of *Chrysopetalum debile* was described by Racovitza (1896). The cephalic lobe is composed of three regions. The sincipital region supports three antennae and four eyes and the middle brain, which has a pair of antennal ganglia, four optical ganglia and a nerve for the median antenna. The palp region supports two palps with distal retractile tissue and an anterior brain with a pair of palp ganglia. The nuchal region of the posterior brain has two nuchal nerves. The nuchal organ is formed from the evagination of the body wall and has mucus-producing glandular cells and an equatorial ridge with long cilia on its dorsal surface.

Cilia are present in the majority of genera. Thick clumps of cilia are located in narrow bands or discrete patches inter-ramally and in a row anterior to the insertion of paleal fascicles; their function is probably sensory, but is not yet fully known.

Chrysopetalids are reported to have separate sexes and external fertilisation (Pettibone 1982). Ehlers (1864–1868) described eggs of *Chrysopetalum fragile* (= *debile*) as reddish-violet and measuring 27–55 µm in diameter. Blake (1975b) described trochophores and unfertilised pink eggs, measuring 70 µm, from *Paleanotus bellis* adults spawning in the laboratory. Dahlgren & Pleijel (1995) reported ripe males of *Dysponetus caecum* and females with whitish eggs about 100 µm in diameter. Watson Russell (1997) described pink eggs ranging in size from 30–75 µm and numbering up to 60 per parapodium in mature female specimens of *Strepternos didymopyton*. Parapodial changes during gametogenesis in *S. didymopyton* include glandular activity and elongation of the cirrophore of dorsal cirri; the presence of longer denser cilia in the inter-ramal areas; swelling of the neuropodial tip and the area posterior, and; evidence of large swollen, golden gonoducts of the type described by Fage (1906) – gonoducts are present inside the parapodia.

Levensen (1879) reported finding spermatozoa in a specimen of *Dysponetus pygmaeus*. Sperm have been observed in the parapodia of a number of different chrysopetalid species and in *Strepternos didymopyton*. These resemble 'tiny rounded spheres with minute swollen poles' (Watson Russell 1997), like the primitive type of sperm described by Franzén (1970) or aquasperm (Jamieson & Rouse 1989).

Gamete-bearing adults belonging to species of the genera *Paleanotus*, *Treptopale* and *Arichlidon* have been collected from the plankton in coastal embayments and lagoons of tropical reefs. Transitory, specialised neurochaetae, observed

in ovigerous females belonging to *Arichlidon* species, are the only secondary sexual characteristics reported (Watson Russell 1998).

Planktonic larvae have been described in developmental studies on chrysopetalids (see Mileikovsky 1962; Cazaux 1968; Blake 1975b; Kisseleva 1992). The internal body of an early trochophore is filled with yolk, and a functional gut is present; evidence of feeding becoming evident only in later trochophores. Metatrochophores and nectochaetes have dense oil globules in the gut and apparently live off these reserves until benthic settlement and full metamorphosis takes place (Cazaux 1968; Blake 1975b; Watson Russell 1987, 1997).

The planktonic larvae have fascicles of serrate, simple, provisional chaetae on the anterior segments. These chaetae make it easier for the larvae to remain suspended in deep water, so enabling them to be transported long distances. As larvae can remain at the six-segment stage for up to 3 weeks (Cazaux 1968), it is apparent that some chrysopetalid species have the potential for long range dispersal and for delaying metamorphosis while seeking a suitable benthic site (Watson Russell 1997).

Folded, primary paleae fans appear at the generation of the sixth segment and are spread out across the dorsum of the six- to seven-segmented larva at the stage of impending metamorphosis and settlement. Development of the anterior end and ontogenetic chaetal development, involving chaetal generation, replacement and loss, has been observed through the post-larval and juvenile to adult growth periods. Adult paleae are initiated in the posterior segments of the individual and in the lateral position of the notochaetal fascicle; a process that is clearly seen where the adult chaetae are different in shape from those of the larva and juvenile (Watson Russell 1997).

Chrysopetalidae were believed formerly to be rare, but ecological surveys in Australia over the past 20 years have shown that they form a diverse and significant part of temperate and tropical polychaete faunas. New collecting techniques (for example, SCUBA-operated dredges, corers and fine-meshed sorting screens) have also contributed to the collection of larger numbers of smaller species as well as larvae and juveniles.

Hutchings & Murray's (1982) study of recruitment of polychaetes onto dead coral at Lizard Island on the Great Barrier Reef showed that chrysopetalid taxa were fourth among the seven most numerically dominant species, with large numbers settling preferentially onto older blocks at the windward side between January to April. This suggests a summer recruitment period by planktonic larvae, preferably at a site exposed to south-east trade winds. Overseas studies have also shown recruitment of chrysopetalid planktonic larvae to living and dead coral substrata (McCloskey 1970; Renaud-Mornant, Salvat & Bossy 1971; Peyrot-Clausade 1974). The first study showed greater recruitment to sites with higher current, surge and clear water.

Chrysopetalids are most frequently found in clear waters ranging from the intertidal to abyssal depths (4000 m). They inhabit cracks and crevices and vacated burrows of boring species in coral reefs (Hutchings 1981) and rocky reefs, a wide range of algal and seagrass habitats, rotting wood and mixed sand/mud substrata often with a shelly gravel component. They also occur among invertebrate tube aggregations including vermetid and dendropomid reefs, inside sponges, living corals and the branchial structures of

molluscs and crustaceans. *Paleanotus* and *Chrysopetalum* species are recorded from fouling faunas in eastern Australia, Japan, southern California and Chile.

Little is known of the feeding biology of free-living chrysopetalids. However, it appears that feeding is largely opportunistic and strongly related to habitat. *Paleaequor* species occur almost exclusively on sandy sediments, sometimes in association with large groups of tube-dwelling polychaetes, and it is probable that they are omnivores feeding on small sand-dwelling invertebrates (Watson Russell 1986). Species in the abyss-dwelling genus *Strepternos* have thick, bluntly serrated, stylet-like jaws (Watson Russell 1991) and have been observed feeding on teredo molluscs (Pholadidae, *Xylophaga*) *in situ* on experimental wooden panels (Turner 1977). Algal material has been noted in the stomachs of *Paleanotus* and *Treptopale* species which have been collected from foliaceous and coralline algae (C. Watson Russell personal observation). Other species of *Paleanotus* have been collected from inside the branchiae of molluscs and the carapace of crustaceans, suggesting a semi-parasitic, scavenging mode of feeding.

Chrysopetalids share with members of the hesionid and nereidid families internally compartmented, falcigerous compound neurochaetae and a partially differentiated pharynx (Glasby 1993). A parsimony analysis on a number of chrysopetalid species by Dahlgren & Pleijel (1995) indicated the hesionids emerging as a subgroup within the chrysopetalids, rather than in outgroup position, suggesting the need for further investigation.

Glasby (1993) included the Chrysopetalidae in the superfamily Nereidoidea, on the basis of three synapomorphies: anterior or, rarely, antero-ventral palps; paired pharyngeal retractor muscles and presence of metanephromixia. However, he noted their position as a member of the Nereidoidea appears tenuous considering the uncertainty in the type of pharyngeal retractor muscles and the nephro-genital system' (Glasby 1993).

Few authors have dealt with relationships of Chrysopetalidae at the generic level. In their study of *Chrysopetalum* (= *Dysponetus*) *caecum*, Dahlgren & Pleijel (1995) provided a detailed comparison of generic characters; Watson Russell (1987) and Perkins (1985) have also discussed generic relationships. Currently, there are no studies on relationships at the specific level.

The Chrysopetalidae are probably very old, with the majority of the eleven nominal genera exhibiting worldwide distributions. Primitive musculature is reported for this group (Storch 1968) and the paleate genera share morphologically similar chaetal arrangements to the paleate fossil polychaete families, Canadiidae and Wiwaxiidae, from the Canadian Burgess shale in the mid-Cambrian period (Butterfield 1990; Westheide & Watson Russell 1992; Conway Morris & Peel 1995; Watson Russell 1997). No chrysopetalid fossils have been reported from Australia.

Family Eulepethidae

Eulepethids are long-bodied scale-worms which burrow in soft sediments. All the chaetae are simple. They are uncommon and the family is represented by only a small number of species.

The prostomium is small and surrounded by anteriorly-directed parapodia. The peristomium is reduced to lips (Pettibone 1986a). A pair of lateral antennae and a median antenna are present (Fig. 1.72B). The bases of the tapering,

ventral palps are fused to the ventro-medial part of the first parapodia. Nuchal organs are present. The first segment carries two pairs of tentacular cirri (dorsal and ventral) and curves around the prostomium. Notopodia are shorter than the neuropodia, which are themselves truncated (Fig. 1.72D). Dorsal cirri are present on segments 3 and 6 only, and are replaced by marginally lobate elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21 and 24. Elytra occur on alternating segments over the first half of the body; more posteriorly pseudoelytra are present or segments lack both elytra and dorsal cirri. Ventral cirri are present over the whole length of the body. True branchiae are lacking (see below). The pygidium bears one pair of cirri. Lateral organs and dorsal cirrus organs have not been recorded. The buccal organ is eversible, muscular and axial, with the two pairs of jaws placed dorso-ventrally; terminal papillae are present. There is no gular membrane; the gut is presumed to have diverticula in each segment (Darboux 1899). The nephridia are probably metanephridia. Their relationship to the coelomoducts is unknown, as is the arrangement of segmental organs and the circulatory system. Aciculae are present (Fig. 1.72D, G) and the chaetae comprise variously ornamented capillaries and spines. This definition is based on that given by Fauchald & Rouse (1997).

Pettibone (1969a) referred to the enlarged digitiform structures above the notopodial lobe on non-elytrigerous segments as branchiae. However, in the absence of information on their internal structure, Rouse & Fauchald (1997) considered that they were more likely homologous with the dorsal cirri.

Pettibone (1969a) revised the Eulepethidae and provided a detailed account of the history of the family. Also, according to Pettibone (1969a) the family is known from relatively few species from widely scattered areas in the Western Indian Ocean, Pacific Ocean, the Gulf of Mexico, Atlantic Ocean and the Adriatic Sea, in depths ranging from the low intertidal to 823 m. Closer examination of currently available specimens and any additional specimens collected may show that some of these widely scattered records represent undescribed species.

Grube (1875, 1878) described the first species, *Eulepis hamifera*, although he placed it in the family Sigalionidae. McIntosh (1885) described two additional species, stating that they should be regarded as a new family; nevertheless, he placed them in the Polynoidae. Additional species were described by Darboux (1900) who created a new tribe, Eulepidinae, within the Aphroditidae. Treadwell (1901), Horst (1913, 1917, 1922) and Fauvel (1918, 1919a, 1919b, 1919c) described additional species within this tribe, which Augener (1918) subsequently raised to family status, as Eulepididae. Chamberlin (1919) replaced the generic name of *Eulepis* with the name *Eulepethus*, substituted Eulepethinae for Eulepidinae, and transferred the subfamily to Sigalionidae. Hartman (1939) referred *Eulepethus* to *Pareulepis* and proposed a new family Pareulepididae. Pettibone (1969a) reviewed this literature and decided that there were good grounds for creating a new family, Eulepethidae, based on the nominal genus *Eulepethus* Chamberlin. Eulepethidae also predates Pareulepididae Hartman, based on *Pareulepis*, which is the oldest available generic name in the family, but with a different type-species.

The eulepethids are a morphologically uniform group of scale-worms. As with all other scale-worms, they have periodically been considered members of the Aphroditidae. They resemble the polynoids, acoetids and aphroditids in lacking compound chaetae. All species are solid-bodied and

1. CLASS POLYCHAETA

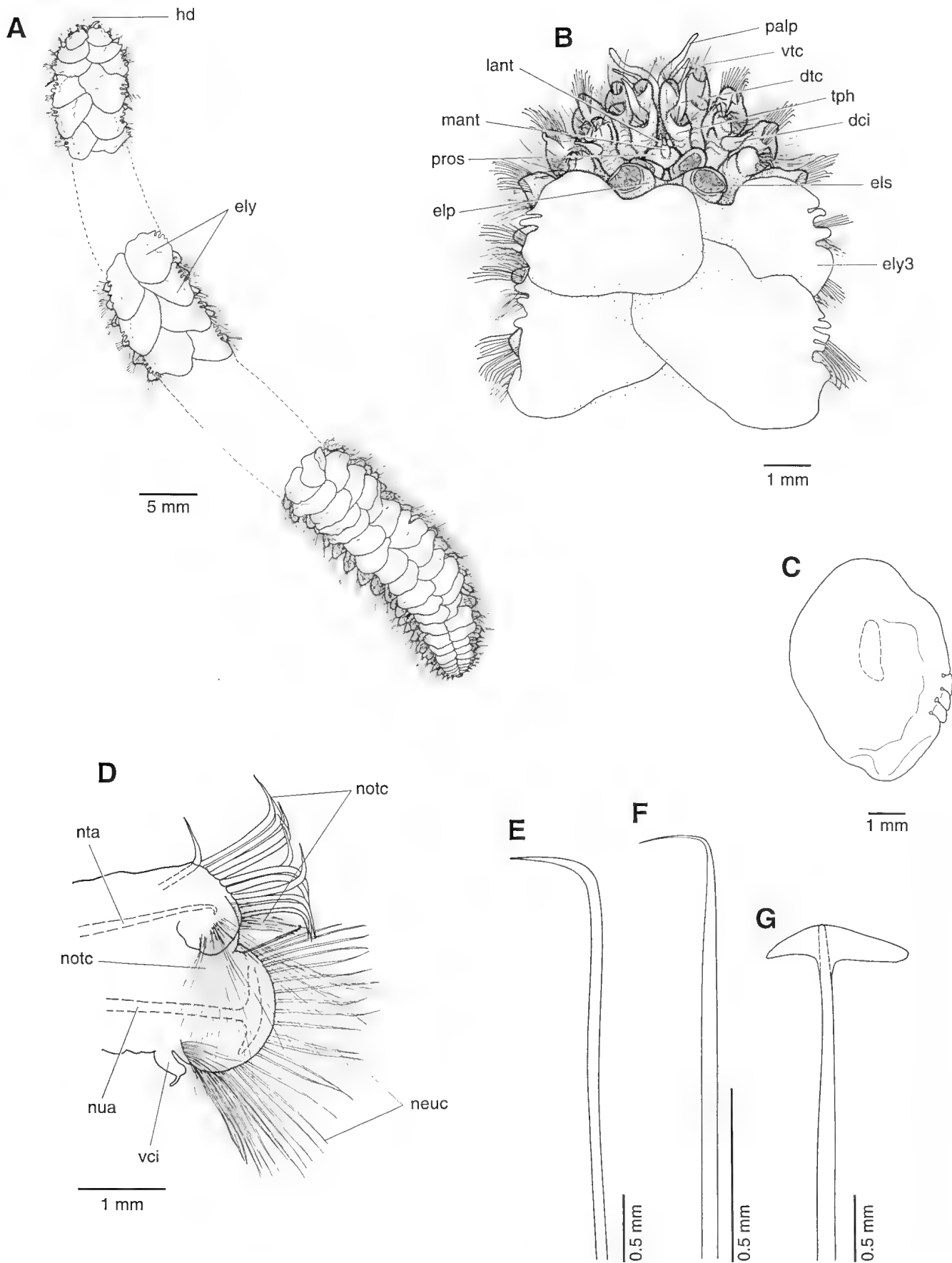


Figure 1.72 Family Eulepethidae. *Mexieulepis* species. **A**, dorsal view of entire animal, anterior, middle and posterior sections shown in detail. **B**, dorsal view of anterior end with first two pairs of elytra removed. **C**, elytron from chaetiger 13. **D**, posterior view of parapodium of chaetiger 21 with elytron removed. **E**, **F**, chaetae from parapodium of chaetiger 27: **E**, superior notochaetal spine; **F**, neurochaetal spine. **G**, neuroacicula from parapodium of chaetiger 27. **dci**, dorsal cirrus; **dte**, dorsal tentacular cirrus; **elp**, elyrophore; **els**, elytral scar; **ely**, elytra; **ely3**, elytron 3; **hd**, head; **lant**, lateral antenna; **mant**, median antenna; **neuc**, neurochaetae; **notc**, notochaetae; **nta**, notoacacula; **nua**, neuroacacula; **palp**, palp; **pros**, prostomium; **tph**, tentaculophore; **vci**, ventral cirrus; **vtc**, ventral tentacular cirrus. [A. Murray]

nearly quadrangular in cross-section. Pettibone (1986a) discussed the relationship of the eulepethids to the Aphroditidae, Polynoidae and the Sigalionidae, and Rouse & Fauchald (1997) provided additional information. The form of the wide neuropodia appears to distinguish this family from other scale-worms. These neuropodia are truncate distally with their distal edges supported by narrow, sclerotinised ridges and the hammer-shaped aciculae terminate in the middle of the neuropodia (Fig. 1.72D).

Six genera and 14 species are recognised worldwide. In Australia, there are no published records of this family. However, one specimen of a species of *Mexieulepis* is recorded from Embley River, Weipa, Gulf of Carpentaria, Queensland (Fig. 1.72; Australian Museum, unpublished records). Also, large numbers of *Grubeulepis* cf. *geayi* and *Mexieulepis* species have been collected from Bass Strait (Museum Victoria unpublished records).

Eulepethids are burrowers in soft sediments (Pettibone 1969a), and one species has been recorded as living as a commensal with a tube-building, acoetid scale-worm.

The head of eulepethids is retracted between the anterior segments of the body (Fig. 1.72B). The prostomium is small and globular and bears three small antennae (median and lateral) and a pair of long smooth palps. The first segment bears a pair of tentaculophores, each with two bundles of chaetae and dorsal and ventral tentacular cirri. Nuchal organs are club-shaped. The muscular pharynx is strong and eversible, with two pairs of plate-like jaws; its opening is encircled with soft papillae.

Eulepethids appear to have a variable number of elytra attached by stout elytraphores. The elytra vary in shape along the body. Often the first 12 pairs increase in length, the last pair of which is longer posteriorly and subrectangular in shape (Fig. 1.72A); subsequent elytra are smaller and sometimes foliaceous. The ornamentation of the elytra varies along the body from entire to notched (Fig. 1.72C) or fimbriated lateral borders; although generally the surfaces of elytra are smooth, occasionally scattered microtubercles are present. Pettibone (1986a) suggested that elytra may elongate during development. If this is so, juvenile eulepethids may not be identifiable to species.

Eulepethids have biramous parapodia, although the notopodium is smaller than the neuropodium (Fig. 1.72D). The notopodium is supported by a hook-tipped notoacicula and has capillaries and distally curved spines (Fig. 1.72E). The neuropodium is supported by a hammer-shaped acicula (Fig. 1.72G; chitinous plates present distally form the hammer shape) and has pectinate, limbate and non-limbate capillaries and distally curved spines (Fig. 1.72F). Pettibone (1986a) also indicated that chaetal types may vary with age and along the body, so descriptions of chaetae should clearly indicate the segment on which they occur. Ventral cirri are present; the anterior ones are short and tapered and more posteriorly become globular with filamentous tips; the dorsal cirri alternate with elytraphores.

Studies of internal anatomy are largely lacking, but structures are presumably similar to those reported for other scale-worm families (Fauchald & Rouse 1997). No detailed information is available on the alimentary system, although the gut has diverticulae, according to Darboux (1899). The nephridia are presumed to be metanephridia, based on Goodrich's (1945) study (Rouse & Fauchald 1997). No information is available on respiration, circulation, reproduction or development of eulepethids.

Family Glyceridae

Glycerids, sometimes called bloodworms, are long-bodied active burrowing predatory worms which live in soft sediments (Pl. 2.4). They are distinguished by having four jaws at the distal end of a long, highly muscular eversible pharynx.

The prostomium is conical and annulated, and bears four small terminal appendages (Orrhage 1999). The conical nuchal organs of *Glycera convoluta* (see Fig. 1.2B) are apparently the only published observations of nuchal organs in glycerids (Purschke 1997). A long muscular eversible pharynx is present, and terminates with four jaws arranged in a cross (Fig. 1.73A). Several types of pharyngeal papillae cover the pharynx, usually with one or two types present on any one species; species may be distinguished by the presence of different types. The peristomium is reduced. Terminal papillae are absent. The first segment with parapodia is similar to subsequent segments. Parapodia are biramous in all genera except *Hemipodus*, in which all are uniramous. In biramous parapodia, the neuropodia are larger than the notopodia, and prechaetal and postchaetal lobes and lappets may be present. Dorsal and ventral cirri are present (Fig. 1.73B). True branchiae are absent, but the structures often termed branchiae are located dorsal to the parapodia and contain no circulatory system (Fauchald & Rouse 1997); these structures are referred to here as coelomic loops (Fig. 1.73B; Fauchald & Rouse did not recommend any new terminology). Coelomic loops are of taxonomic value, but are retractile in some taxa and thus their apparent absence may be difficult to verify. Aciculae are present. Notochaetae, if present, are simple (Fig. 1.73C); neurochaetae are compound (Fig. 1.73D). One pair of pygidial cirri is present. This description is based on that of Fauchald & Rouse (1997).

The family Glyceridae was described by Grube (1850), although the first species now classified as a glycerid was described by Müller (1776) and Savigny (1818). The most recent taxonomic work is that of O'Connor (1987), who provided a review of species from the North Atlantic and Mediterranean, including keys and a discussion of identification procedures and taxonomic characters. The generic classification is stable and has been unchanged since Hartman's (1950) study. Glycerids are very similar to members of the Goniadidae, and inexperienced sorters often confuse members of these families. Goniadids differ, however, in having a single pair of large jaws and numerous smaller jaw articles in a circle; notopodial lobes are lacking on anterior chaetigers, but are well developed and similar in size to neuropodial lobes on posterior chaetigers.

Globally, the family includes three genera and 160 species, although only about a quarter of these species are thought to be valid (M. Böggemann & D. Fiege personal communication). The genus *Glycerella* contains two species. Nine species of the other two genera, *Glycera* and *Hemipodus*, are known from Australian and Australian Antarctic Territory waters (Hartman 1964; Day & Hutchings 1979; Hutchings & Murray 1984). About six species, some apparently undescribed, have been collected during the benthic studies of shelf depths in south-eastern Australia (Museum Victoria database; Australian Museum database).

Glycerids are widely distributed in soft sediments and are active burrowers. If disturbed, they are able to rebury themselves quickly, using rapid thrusting actions of the eversible pharynx. They are found in all oceans from the intertidal to the deep sea.

1. CLASS POLYCHAETA

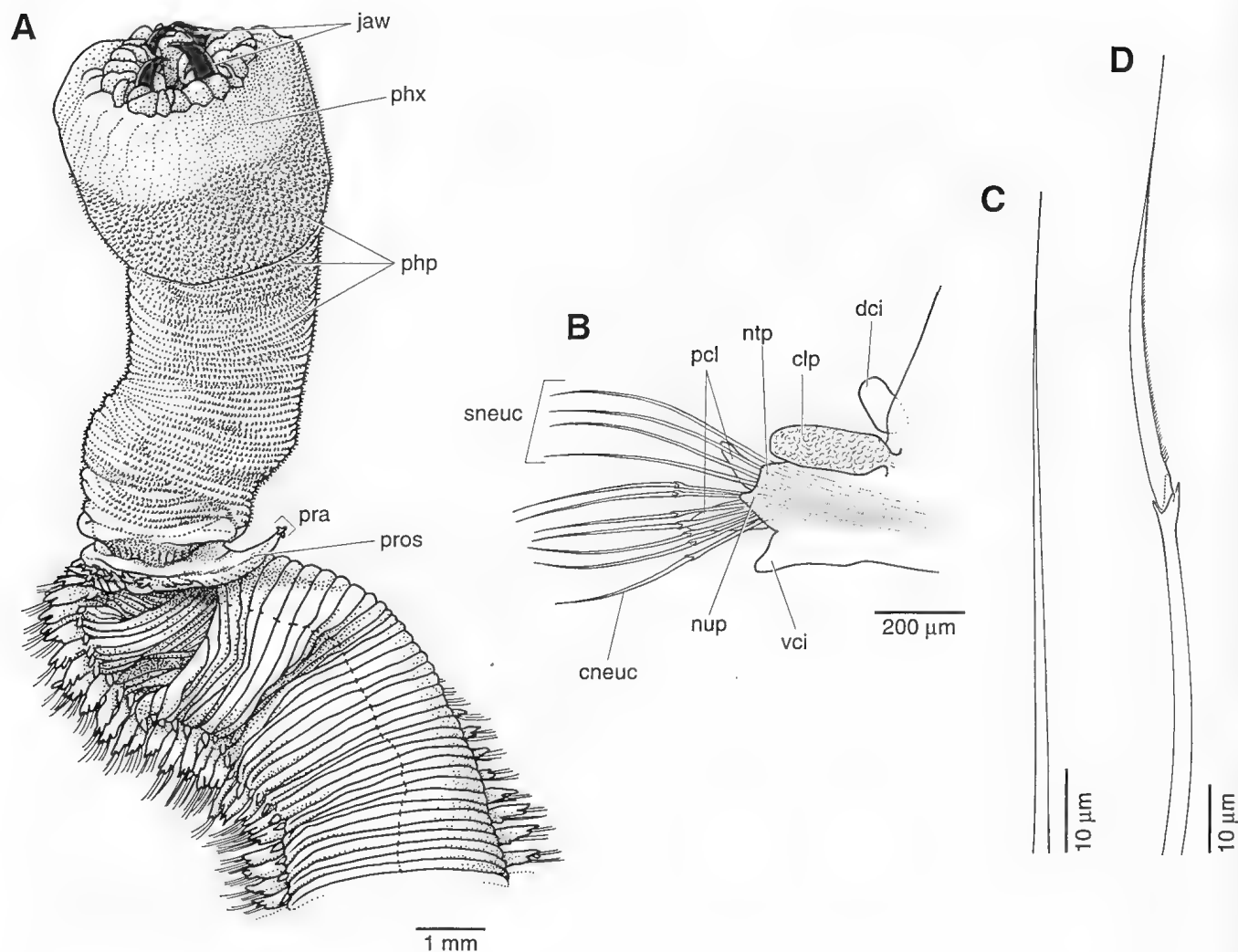


Figure 1.73 Family Glyceridae. **A**, anterior end of *Glycera* species with pharynx everted. **B**, parapodium of chaetiger 33 of *Glycera* species, dorsal view. **C**, **D**, chaetae of *Glycera* species: **C**, simple notochaeta; **D**, compound neurochaeta. **clp**, coelomic loop; **cneuc**, compound neurochaeta; **dci**, dorsal cirrus; **jaw**, jaws; **ntp**, notopodium; **nup**, neuropodium; **pcl**, postchaetal lobes; **php**, pharyngeal papillae; **phx**, pharynx, everted; **pra**, prostomial appendages; **pros**, prostomium; **sneuc**, simple neurochaetae; **vci**, ventral cirrus.

[K. Nolan]

Glycerids may reach almost 400 mm in length and have several hundred segments (Klawe & Dickie 1957), but they fragment easily and complete specimens are uncommon in collections. There is little regionalisation of the body and the segments are all similar. The four pharyngeal jaws are made of scleroprotein and hardened by trace metal components (mostly copper), which reach their highest concentration in the tips of the jaws (Michel *et al.* 1973; Gibbs & Bryan 1980a). Important species-level taxonomic characters are the form of the jaw supports (called ailerons), structure of the pharyngeal papillae, number and shape of parapodial lobes and coelomic loops, and the number of prostomial and segmental annulations (O'Connor 1987).

In *Glycera*, a venom gland is situated at the base of the jaws, and the venom is carried to the tip of the jaws by a duct as first suggested by Ehlers (1864–1868). The venom of *Glycera convoluta* contains a neurotoxin, which has a reversible presynaptic action, as well as several proteinases (Michel & Imhoff 1975; Michel & Keil 1975; Thieffry *et al.* 1982). The venom produced by *Glycera dibranchiata* also has a neurotoxin, and may even cause a localised reaction in humans if bitten and the jaws penetrate the skin sufficiently; this reaction may last for 3 days (Sandrof 1946; Klawe & Dickie 1957).

Unlike most other polychaetes, the circulatory system of glycerids is open. Respiratory pigments are found in the coelomic fluid which is circulated by the action of cilia; there is no heart (Hoffmann & Mangum 1970; Mangum 1970). Weber & Heidemann (1977) reported a striking interspecific variability in glycerid haemoglobins, but there have been no attempts to use these data in taxonomic or phylogenetic studies. Glycerids provide a convenient experimental supply of invertebrate haemoglobin and their respiratory biochemistry is well studied (see, Seamonds *et al.* 1971; Terwilliger *et al.* 1976). The coelomic fluid of *Glycera dibranchiata* contains an antibacterial agent, which represents a class of bactericide distinct from those known in other invertebrates and vertebrates (Anderson & Chain 1982; Chain & Anderson 1983a, 1983b).

Osmoregulation has been studied in the highly euryhaline, estuarine species *Glycera dibranchiata*. It is an osmoconformer which regulates cell volumes by changing cellular concentrations of free amino acids (Machin 1975; Costa *et al.* 1980). It is not known if this mechanism is used by other glycerids.

Simpson (1959) and Manaranche (1966) described the brain morphology of *Glycera dibranchiata* and *G. convoluta*; both species have a saccular structure in the brain, possibly of

secretory or sensory function. Simpson (1959) also described paired anterior nerve tracts terminating at the four prostomial antennae; these antennae are undoubtedly sensory in function. Orrhage (1999) on the other hand considered that the prostomial appendages were neither palps or antennae, and that they were structures unique to glycerids and goniadids. Further, he regarded the prostomium as composed of two fused palps. Stolte (1928, 1932) described the extension of the pharynx in *Glycera unicornis*; it can be accurately directed at a disturbance of the water which is sensed by prostomial receptors. Wells (1937) described the physiology of this response in *G. dibranchiata*.

The sexes are separate, and neither asexual reproduction nor hermaphroditism have been recorded. Paired gonads occur in median segments in *Glycera dibranchiata* (Simpson 1962a). The nephridio-genital system of glycerids has nephromixia, in which the protonephridium and solenocytes never open to the exterior (Goodrich 1945). Release of gonads must thus occur through rupture of the body wall, and most, but perhaps not all, worms die after spawning (Simpson 1962b; Creaser 1973). At least nine species of *Glycera* are known to form breeding swarms in surface waters; these swarms frequently involve epitokal modifications including elongation of parapodia and chaetae, and reduction in body wall thickness (Simpson 1962a). Both endogenous cues (for example, maturity of gametes) and exogenous cues (for example, temperature, tide) appear to determine the timing of spawning, which may occur once or twice per year in *G. dibranchiata* when worms are 3–4 years old (Simpson 1962b; Creaser 1973). Spawning swarms of an unidentified glycerid (or perhaps goniadid) have been recorded in the Gulf St Vincent, South Australia; swarms apparently appear once a year at high tide during the dark phase of the moon (Fig. 1.36; Huie 1985). In north-eastern America, non-breeding adults of *G. dibranchiata* also swim in surface waters in significant numbers (Dean 1978b), but the available genetic evidence suggests that this does not usually result in significant mixing of populations from different estuaries (Bristow & Vadas 1991).

Larval development of glycerids has been described by Åkesson (1968), who recognised four stages: an early undifferentiated trochophore; a metatrochophore with differentiated segments; an older metatrochophore with conical prostomium; and a metatrochophore with well-developed prostomium ready for metamorphosis. Åkesson (1968) and Hanström (1927) described the development of the anterior nervous system in larval glycerids.

The literature summarised by Fauchald & Jumars (1979) indicated that glycerids include both carnivorous and detritivorous species. Apparently only the carnivorous species form complex burrow systems, from which the worms detect and capture prey moving on the sediments above them (Ockelmann & Vahl 1970).

In north-eastern America and South Australia, glycerids are known as blood worms. They are valued commercially by anglers as a bait species and are harvested by digging or netting during spawning (Creaser *et al.* 1983; Huie 1985). Overharvesting of glycerids in north-eastern America is resulting in reduction in size or elimination of worms from some areas (Wilson & Ruff 1988); no comparable data are available in Australia.

The effects of common environmental pollutants, such as mercury and cadmium, on haemoglobin function in glycerids have been investigated by Rice & Chien (1979) and Preston & Chen (1989), but this has not, as yet, resulted in a method for using glycerids as indicators or bioassays of heavy metal

pollution. Gibbs & Bryan (1980a) showed that levels of copper in body tissue of glycerids are elevated in worms from sites with high environmental levels of copper; although the concentration of copper in jaws of glycerids from such sites remains constant.

Uschakov (1972) suggested that the nearest relatives of Glyceridae (and Goniadidae) are the families Nephtyidae and Sphaerodoridae. Åkesson (1968) speculated that Glyceridae (including Goniadidae) are most closely related to the Tomopteridae, on the basis of similar ontogeny and adult morphology of the muscular axial pharynx. Most recently, Rouse & Fauchald (1997) proposed the Glyceridae-Goniadidae as a sister group to the Paralacydoniidae and as a highly derived clade within the Phyllodocida (Fig. 1.57).

The mineralisation of glycerid jaws and their high levels of protein (more than 50% of dry weight, Michel *et al.* 1973) apparently predispose them to fossilisation (Szaniawski 1974; Thompson 1979; Colbath 1986b). Fossil glycerid jaws of very similar form to those of Recent species are known from Triassic, Jurassic and Cretaceous deposits from Europe and North America (Mierzejewska & Mierzejewski 1977).

Family Goniadidae

Goniadids are long-bodied, active, burrowing, predatory worms characterised by having a muscular pharynx bearing one pair of large jaws and a circle of smaller jaw elements (Fig. 1.74A, B).

The prostomium is conical and annulated, and bears four small terminal appendages (Fig. 1.74A; Orrhage 1999). A long, muscular eversible pharynx is present; it bears one pair of large jaws and a dorsal and ventral arc of numerous smaller denticles, which together form a complete circle. Pharyngeal papillae are well developed and are of several types (Fig. 1.74C); they may be differentiated along the pharynx. Terminal pharyngeal papillae are present. The peristomium is reduced to lips. The first segment has parapodia and is similar to subsequent segments. Parapodia are anteriorly uniramous with neuropodia and dorsal cirri only, and posteriorly biramous with notopodia almost as large as neuropodia (Fig. 1.74D, E). Dorsal and ventral cirri are present throughout. Coelomic loops (see Glyceridae) and branchiae are absent. Aciculae are present. Notochaetae, where present, are spines (straight or distally curved); neurochaetae are compound spinigers and falcigers (Fig. 1.74F–I). One pair of pygidial cirri is present. This description is based on that of Fauchald & Rouse (1997).

Goniadids are more diverse morphologically than the Glyceridae, but they are much less well known biologically. The two families can be distinguished by the form of the parapodia; goniadids have larger parapodia which are fully biramous on posterior chaetigers, but their notopodia are reduced to a dorsal cirrus anteriorly, whereas glycerid parapodia from anterior and posterior positions are similar. Globally, goniadids comprise nine genera and 73 species. The classification adopted here follows Fauchald (1977), which is based on Hartman (1950). Day & Hutchings (1979) recorded only three species of *Goniada* from Australian waters (*G. antipoda*, *G. australiensis*, *G. emerita*), but about six, as yet unidentified species, representing the genera *Goniadella*, *Goniadides* and *Glycinde*, are also known from unpublished studies of the shallow-water soft-bottom benthos of south-eastern Australia (Australian Museum and Museum Victoria unpublished databases). Like glycerids, goniadids occur mostly in soft sediments, but goniadids are more common in the deep sea. The greater generic diversity of goniadids and

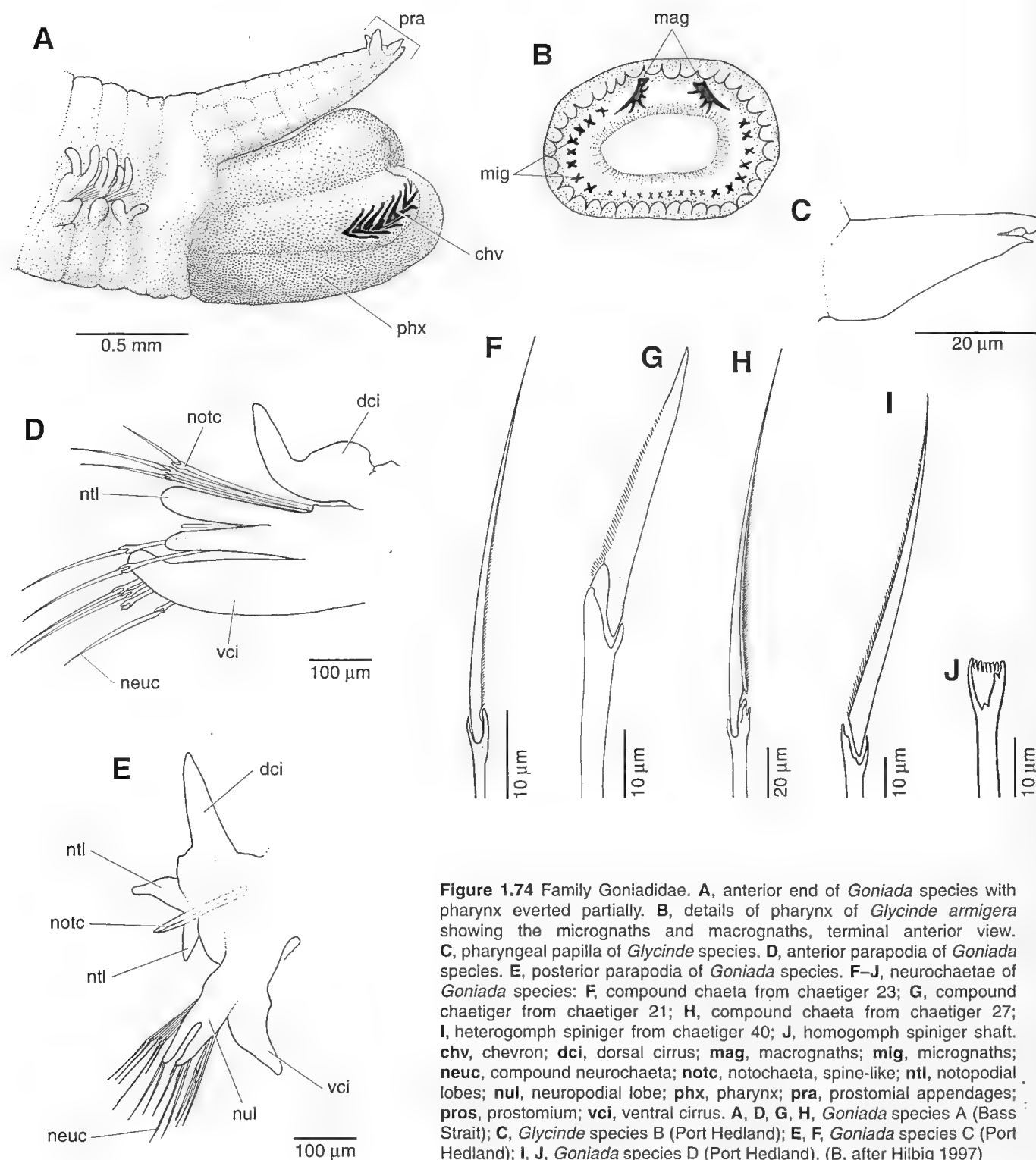


Figure 1.74 Family Goniadidae. **A**, anterior end of *Goniada* species with pharynx everted partially. **B**, details of pharynx of *Glycinde armigera* showing the micrognaths and macrognaths, terminal anterior view. **C**, pharyngeal papilla of *Glycinde* species. **D**, anterior parapodia of *Goniada* species. **E**, posterior parapodia of *Goniada* species. **F–J**, neurochaetae of *Goniada* species: **F**, compound chaeta from chaetiger 23; **G**, compound chaetiger from chaetiger 21; **H**, compound chaeta from chaetiger 27; **I**, heterogomph spiniger from chaetiger 40; **J**, homogomph spiniger shaft. **chv**, chevron; **dci**, dorsal cirrus; **mag**, macrognaths; **mig**, micrognaths; **neuc**, compound neurochaeta; **notc**, notochaeta, spine-like; **ntl**, notopodial lobes; **nul**, neuropodial lobe; **phx**, pharynx; **pra**, prostomial appendages; **pros**, prostomium; **vci**, ventral cirrus. **A, D, G, H**, *Goniada* species A (Bass Strait); **C**, *Glycinde* species B (Port Hedland); **E, F**, *Goniada* species C (Port Hedland); **I, J**, *Goniada* species D (Port Hedland). (B, after Hilbig 1997)

[K. Nolan]

the scarcity of biological studies suggests that it may be unwise to assume that the biology and ecology of goniadids is always similar to that of the morphologically similar glycerids.

Goniadids may reach 760 mm in length (Pettibone 1963). Two distinct body regions can be recognised, characterised by uniramous parapodia anteriorly and biramous parapodia posteriorly; the transition between the two types of parapodia may be abrupt or occur over up to 40 segments or more (Hartman 1950). Important genus- and species-level taxonomic characters are the number of jaw articles, the presence or absence of paired lateral V-shaped sclero-proteinaceous processes called chevrons, the structure of the pharyngeal papillae, the number and shape of parapodial

lobes and the number of prostomial and segmental annulations. The pharyngeal papillae are larger and more diverse in form than those of glycerids, and may be sclerotinised in some genera. The composition of the jaws has been investigated for *Goniada maculata*, and found to have lower copper concentrations than those in glycerids; instead, calcium and magnesium are the most important metals (Gibbs & Bryan 1980b). Hartman (1950) and Hubendick (1952) have made detailed examinations of the morphology of the pharynx and developed a terminology for pharyngeal papillae, which they call organs, and demonstrated their taxonomic value.

Little is known about the feeding habits of goniadids. Mattson (1981) studied the feeding behaviour of *Goniada maculata* and described it as a carnivore which feeds principally on

deposit-feeding polychaetes; *G. maculata* does not make permanent burrows. In contrast, many carnivorous glycerids detect prey on the sediment surface from within permanent burrow systems. Several earlier studies have inferred carnivory in other species of goniadids, but there are no direct observations (Fauchald & Jumars 1979).

Functional gonoducts have been described in *Goniada* (Goodrich 1898; Fage 1906), perhaps indicating that spawning is not associated with rupture of the body and death. However, epitokes with specialised capillary chaetae and histolysis of the body wall have been recorded in goniadids (Støp-Bowitz 1941). Moore (1903) and Hartman (1950) described schizogamy in species of *Ophioglycera*; the posterior end is modified to produce stolons.

Family Hesionidae

Hesionids are benthic polychaetes which typically have long tentacular and dorsal cirri (Fig. 1.75A; Pls 2.5–2.7). The cirri are readily broken during collection and examination.

The prostomium is distinct and usually has one pair of antennae (Fig. 1.75B), rarely two pairs or none; a single median antenna is also present in many taxa. One pair of ventral articulated palps is usually present, rarely absent. The peristomium is reduced to lips. The first two to four segments are fused, and, on the fused segment, four to eight pairs of tentacular cirri (Fig. 1.75B), which may be supported by aciculae, are present. This cephalisation of anterior segments may be an autapomorphy for the family (Glasby 1993; Fauchald & Rouse 1997). The pharynx is differentiated into anterior and posterior regions and may carry jaws, accessory denticles or soft papillae in a terminal ring. Nuchal organs are ciliated patches located on posterior extensions of the prostomium (Fig. 1.2D). Parapodia are biramous; notopodia are always smaller than neuropodia. Dorsal and ventral cirri are present throughout; dorsal ones often very long and may be annulated (Fig. 1.75D, E). Aciculae are present. Notochaetae, if present, are simple (Fig. 1.75E), and neurochaetae are compound falcigers (Fig. 1.75F, G). One pair of pygidial cirri is present. This description is based on those by Glasby (1993) and Fauchald & Rouse (1997).

The first species, now placed in the Hesionidae, was described by Müller (1776); the family Hesionidae was described by Grube (1850). Perhaps because of their small size and fragility, many species of hesionids are poorly described. In his review and cladistic analysis of the hesionids Pleijel (1998), though preferring a rank-free phylogenetic classification, recognised taxa equivalent to three subfamilies and 22 genera, grouped genera into tribes and listed about 150 nominal species from global localities. Day & Hutchings (1979) listed six genera and 10 nominal species from Australia. At least eight species have been recorded in soft bottom benthic studies in south-eastern and north-western Australia, but these collections have yet to be resolved against existing records and the new classification of Pleijel (1998). Two genera previously placed in the Hesionidae, *Hesionides* and *Microphthalmus*, were shown by Pleijel & Dahlgren (1998) to not belong in that family; these taxa may constitute a monophyletic group allied with the Pilargidae, but their placement remains uncertain (Pleijel & Dahlgren 1998). Useful summaries of available biological data on the family are Uebelacker (1984) and Hilbig (1997b).

Hesionids occur widely, from subtidal habitats, including both hard bottoms and soft sediments, to the deep sea, but they are rarely dominant numerically. They are not common intertidally, except as interstitial forms.

Hesionids range in size up to 55 mm and 80 segments in large species (Blake 1985). Behind the anteriormost fused segments, regionalisation of the body is absent; all segments are similar. Pleijel (1998) provided a comprehensive list of taxonomic characters used to differentiate genera, but does not include a key. Most genus-level characters pertain to the prostomium, anterior segments and their appendages. Differences in the ultrastructure of chaetae assists in the separation of closely related species (Specht & Westheide 1988).

Fauchald & Jumars (1979) proposed that all larger hesionids are carnivores, a prediction confirmed thus far by studies which showed that a species of *Podarke* was a carnivore with a penchant for harpacticoid copepods (Shaffer 1979) and that species of *Ophiodromus* and *Nereimyra* were both carnivores and scavengers (Oug 1980). Hesionids may actively seek prey or may wait for passing organisms within reach of their burrows (Oug 1980). Prey are detected by chemoreceptors and, especially, by touch through the long cirri (Shaffer 1979; Oug 1980).

Most large hesionids have metanephridia (Goodrich 1945; Westheide 1986). Paired protonephridia previously reported from interstitial forms (Clausen 1986; Westheide 1986) are no longer known from the Hesionidae following the removal by Pleijel & Dahlgren (1998) of the interstitial taxa *Hesionides* and *Microphthalmus* from the family.

The sexes are separate. Asexual reproduction is unknown in hesionids, but sequential protandrous hermaphroditism is known in *Hesione pantherina* (Schroeder & Hermans 1975). Some hesionids are active swimmers, and these probably spawn in the water column. Reproduction in large hesionid species appears to take place in animals that are about 2 years old; after spawning worms do not die. In animals maintained in laboratory culture, development of more gametes begins again after spawning (Haaland & Schram 1983; Schram & Haaland 1984).

Other reports of simultaneous hermaphroditism, and of copulatory organs of varying complexity for transfer and storage of sperm (Westheide 1967; Zunarelli-Vandini 1968; Schroeder & Hermans 1975) relate to the interstitial taxa *Hesionides* and *Microphthalmus*, removed from the Hesionidae.

Larval development has been studied in three species of hesionids from the polluted Oslofjord, Norway (Haaland & Schram 1982, 1983; Schram & Haaland 1984). In each case, development is planktotrophic, and larvae lack yolk or oil droplets. Larvae remain in the plankton for one to two months, and then a longer period of development as benthic larvae before development of gonads begins in the second year of life.

Olive & Pillai (1983) studied *Kefersteinia cirrata* from the United Kingdom and showed that temperature and especially day length are the important cues for initiation of oogenesis in that species. No studies of the biology of hesionids from Australia are available.

Like many polychaetes in other families, hesionids may be hosts to gregarine parasites (Clausen 1993); hesionids are not known to parasitise other organisms. However, several species of *Gyptis* and *Ophiodromus* are known to be commensal with echinoderms (Martin & Britayev 1998).

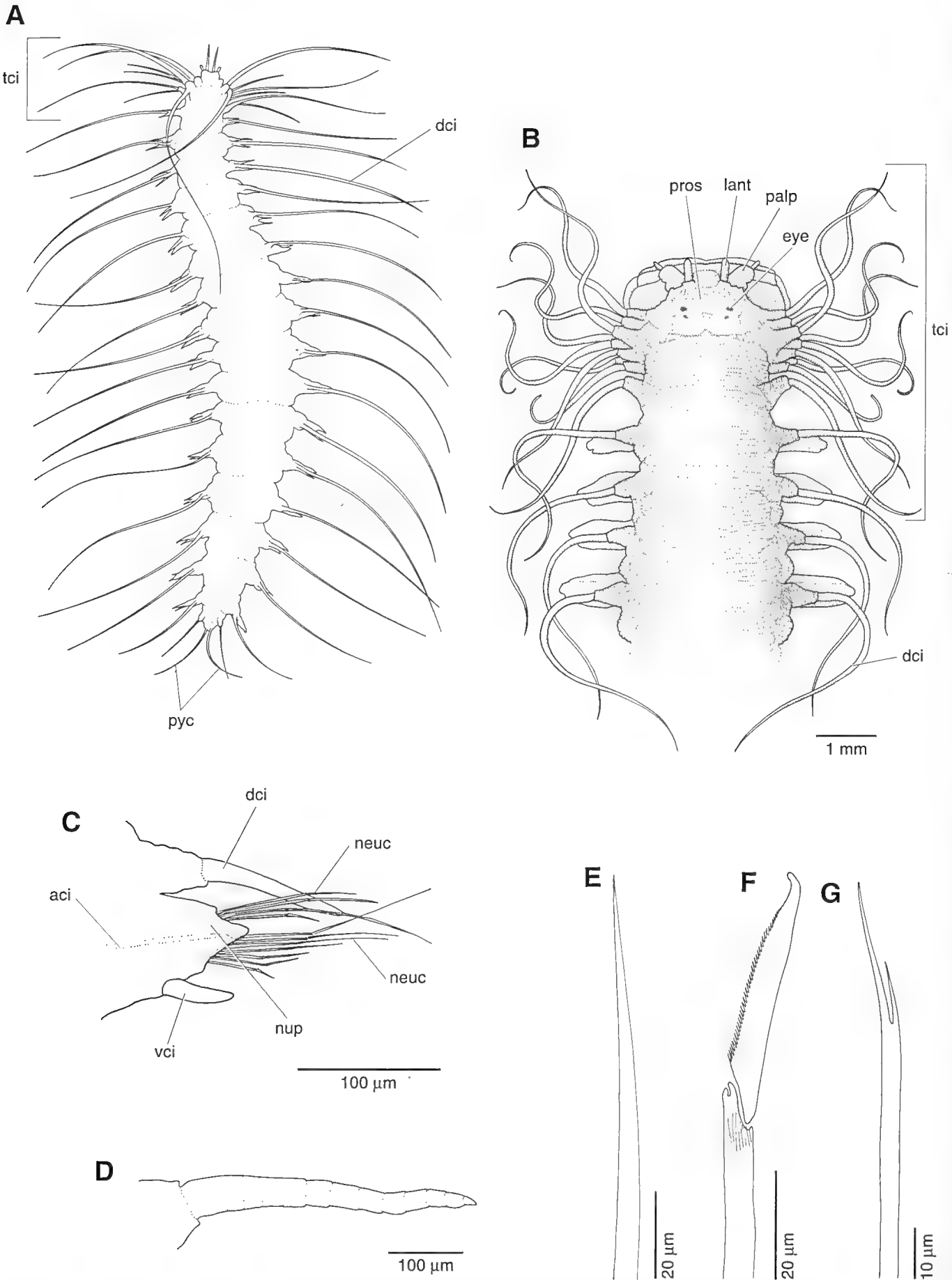


Figure 1.75 Family Hesionidae. **A**, entire animal of an Australian hesionid species, dorsal view. **B**, anterior end of *Leocrates* species, dorsal view. **C**, median parapodium of *Nerimyra* species, anterior view. **D–F**, cirrus and chaetae of *Nerimyra* species: **D**, details of dorsal cirrus; **E**, simple chaeta; **F**, compound chaeta. **G**, forked chaeta of an Australian *Gyptis* species, from chaetiger 14. **aci**, acicula; **dci**, dorsal cirrus; **eye**, eye; **lant**, lateral antenna; **neuc**, neurochaeta, compound; **nup**, neuropodium; **palp**, palp, articulated; **pros**, prostomium; **pyc**, pygidial cirri; **tci**, tentacular cirrus; **vci**, ventral cirrus. (A, after Coleman 1991, scale not available) [K. Nolan]

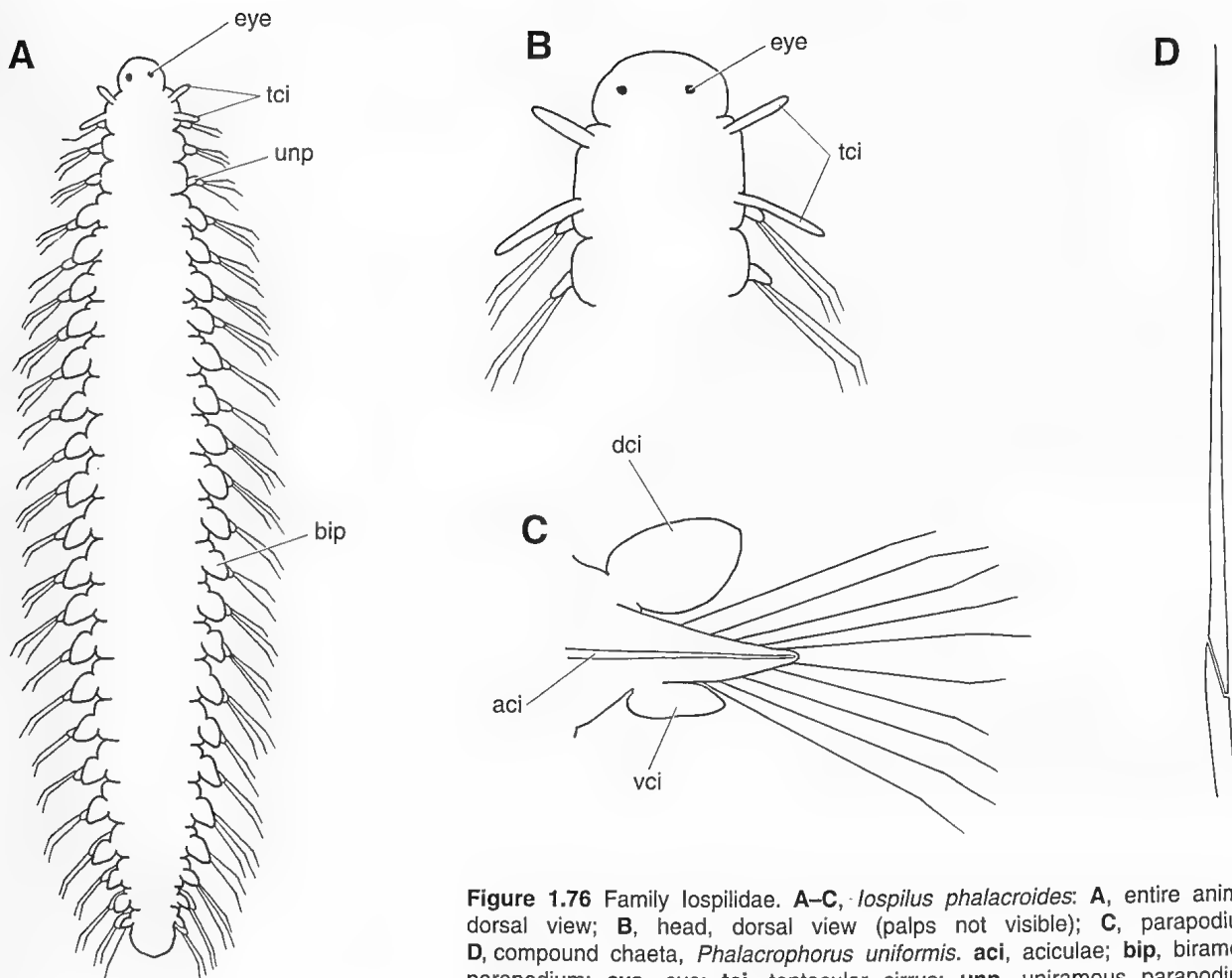


Figure 1.76 Family Iospilidae. **A–C**, *Iospilus phalacroides*: **A**, entire animal, dorsal view; **B**, head, dorsal view (palps not visible); **C**, parapodium. **D**, compound chaeta, *Phalacrophorus uniformis*. **aci**, aciculae; **bip**, biramous parapodium; **eye**, eye; **tci**, tentacular cirrus; **unp**, uniramous parapodium; **vci**, ventral cirrus. (After Day 1967, scales not available) [K. Nolan]

Most polychaete species used as pollution indicators are deposit-feeders, so it is unexpected to find among them several species of (presumably) carnivorous hesionids as pollution indicators, reaching higher numbers and larger size in polluted oxygen deficient environments than in adjacent unpolluted habitats (Zunarelli-Vandini 1971; Haaland & Schram 1982). An unidentified species of a large hesionid is common in Macquarie Harbour, Tasmania, where it lives in anoxic sediments heavily polluted with tailings from a copper mine (R. Wilson unpublished data). Studies of the biology of taxa from such habitats are required and should provide a valuable understanding of hesionids as pollution indicators.

Glasby (1993) analysed the relationships of a group of families then placed in the superfamily Nereidoidea (Hesionidae, Nautiliniellidae, Nereididae, Pilargidae and Syllidae) and found hesionids to be most closely related to the Chrysopetalidae, the two families being linked on the basis of having cylindrical palps. However, Glasby (1993) admitted that the relationship is tenuous and that important data, such as knowledge of the nephridial system in chrysopetalids, are lacking. Pleijel & Dahlgren (1998) confirmed the sister-group relationship between Hesionidae and Chrysopetalidae, but also found support for the inclusion of Hesionidae within the Chrysopetalidae. The more inclusive phylogenetic analysis of Rouse & Fauchald (1997) showed hesionids to be a sister group to the Nereididae and other phyllodociform families, belatedly supporting decisions by Fitzhugh (1987) and Glasby (1991) to use hesionids as outgroups for phylogenetic studies of nereidids.

Family Iospilidae

Iospilids are small, short-bodied, pelagic worms. Their affinities with other families within the Phyllodocida are uncertain, and they are often considered a subfamily of the Phyllodocidae.

The following description is based on that of Fauchald & Rouse (1997). The prostomium is small and apparently fused to the first segment (Fig. 1.76A). The peristomium is reduced to lips. One pair of palps is present, antennae are absent. Nuchal organs are present. One pair of eyes may be present. The pharynx is eversible and carries a pair of hooks in *Phalacrophorus*, but is unarmed in the other genera. The first segment is poorly defined and has two pairs of tentacular cirri. The anterior segments have only neuropodia present; subsequent segments are biramous (Fig. 1.76B). Dorsal and ventral cirri are present throughout. Aciculae are present. All chaetae are compound spinigers (Fig. 1.76C, D). Branchiae and pygidial cirri are absent. The body is short and has fewer than 60 segments.

The most recent and complete review of the family is by Uschakov (1972), who treated iospilids as a subfamily of the Phyllodocidae. Uschakov (1972) recognised four genera: *Iospilus*, *Iospilopsis*, *Pariospilis* and *Phalacrophorus*, which together comprise seven species (Fauchald 1977). None are recorded from mainland Australian waters, although *Phalacrophorus pictus* is recorded from waters of the Australian Antarctic Territory (Hartman 1964). However, it is highly likely, given the wide distribution of many iospilid species (Dales 1957a), that species will be recorded from

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Australian waters; better sampling techniques and sorting regimes of plankton samples will also increase the likelihood of finding isopilids. No studies of the biology or ecology are available for this poorly known family.

Family Lacydoniidae

Lacydoniids are uncommon, though widespread, slender-bodied, benthic worms.

The following description is based on that of Fauchald & Rouse (1997). The prostomium is rounded or trapezoidal, and has a pair of lateral antennae and a pair of short simple ventral palps (Fig. 1.77A, B). The peristomium is reduced to lips. A median dorsal antenna is present in some species. The eversible muscular pharynx lacks jaws; terminal papillae are present. The first segment is distinct and has two pairs of small tentacular cirri. The parapodia are biramous (Fig. 1.77D), but the notopodia are always smaller than the neuropodia. Small papilliform or flattened dorsal and ventral cirri are present. Aciculae are present. Notochaetae are long simple capillaries, and neurochaetae are compound spinigers. The pygidium bears two pairs of pygidial cirri (Fig. 1.77C).

Except for the revision by Uschakov (1972), there is little published information on the family. Worldwide, there are two genera, *Lacydonia* and *Pseudolacydonia*, and eight species. Uschakov (1972) provided a key to genera and species of *Lacydonia*. *Paralacydonia*, treated as a member of this family by Fauchald (1977), is now recognised as belonging in its own family (Pettibone 1963; Fauchald & Rouse 1997). No lacydoniids have been recorded from mainland Australian waters, but *Lacydonia mikrops* has been recorded from the Wilhem II coast in the Australian Antarctic Territory (Ehlers 1913); *Lacydonia oculata* also occurs in Antarctic waters (Pleijel & Fauchald 1993). Lacydoniids are poorly known benthic polychaetes, but they are widespread, having been recorded from polar to tropical seas and from littoral habitats to depths of 5600 m. Their biology and ecology have not been studied.

The classification of Fauchald (1977) allied the Lacydoniidae with the Glyceridae and Goniadidae on the basis of structure of parapodia, chaetae and prostomium. The phylogenetic treatment of Rouse & Fauchald (1997), however, no longer supports this classification and instead shows the Lacydoniidae to be most closely related to the Phyllodocidae (Fig. 1.57).

Family Lopadorhynchidae

Lopadorhynchids are predatory pelagic polychaetes, often grouped as a subfamily of the Phyllodocidae. They have broad, flattened bodies and well-developed parapodia and chaetae.

The Lopadorhynchidae comprises two dissimilar groups (see discussion by Fauchald & Rouse 1997); the following description is based on the group which includes only the type genus *Lopadorhynchus*; variations present in the other group (which includes *Maupasia*, *Pedinosoma* and *Pelagobia*) are given in square brackets. The prostomium has a pair of lateral antennae and a pair of simple ventral palps (Fig. 1.78B). The peristomium is reduced to lips. Nuchal organs are present as ciliated pits. A muscular eversible pharynx is present and has terminal papillae; jaws are absent. The prostomium is partly fused to the first one or two segments, which bear two or three pairs of tentacular cirri. Simple hook chaetae are present on the first segment [or are absent]. The anterior parapodia are similar to subsequent ones [or the anterior parapodia are strongly muscularised and enlarged]. The parapodia are biramous, with notopodia shorter than neuropodia. Dorsal and ventral cirri are present throughout (Fig. 1.78A, C); dorsal cirri are long and slender or foliose. Aciculae are present. After the segments with tentacular cirri, chaetae are all composite. One pair of pygidial cirri is usually present (Fig. 1.78A), but they may be rudimentary or absent. This description is based on the works by Uschakov (1972) and Fauchald & Rouse (1997).

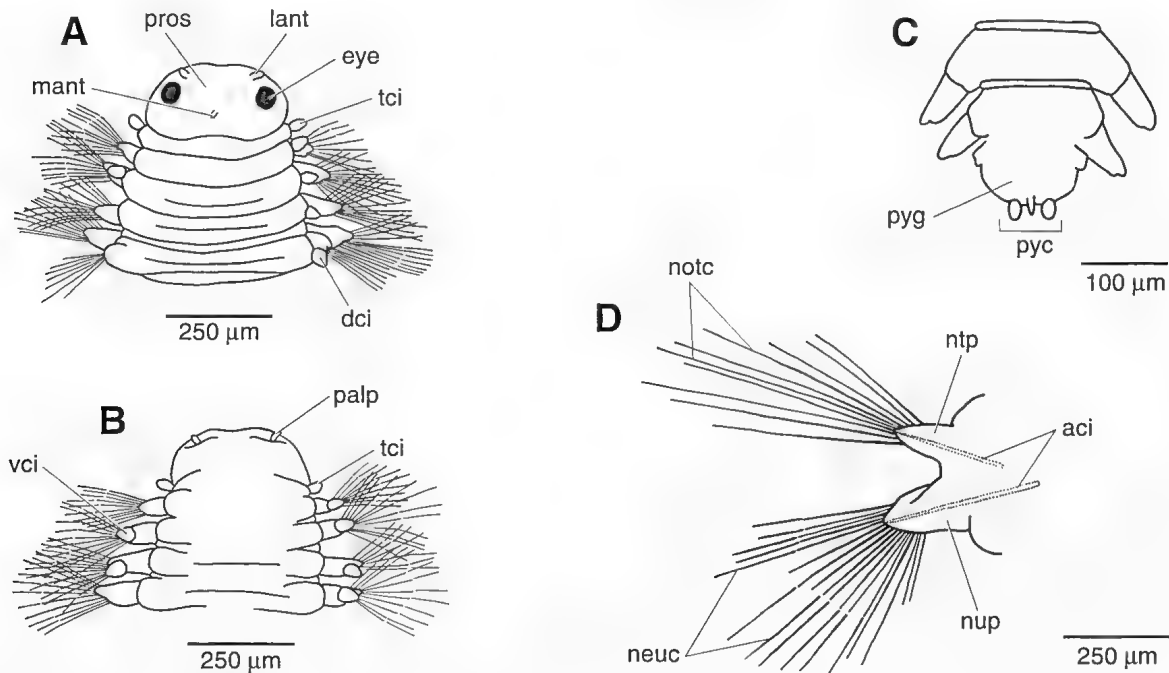


Figure 1.77 Family Lacydoniidae. *Lacydonia oculata*. **A**, anterior end, dorsal view. **B**, anterior end, ventral view; one pygidial cirrus obscured. **C**, posterior end, ventral view; one pygidial cirrus obscured. **D**, parapodium from about chaetiger 20, posterior view; dorsal and ventral cirrus not shown. **aci**, aciculae; **dci**, dorsal cirrus; **eye**, eye; **lant**, lateral antenna; **mant**, median antenna; **neuc**, neurochaetal compound spinigers; **notc**, notochaetal capillaries; **ntp**, notopodium; **nup**, neuropodium; **palp**, palp; **pros**, prostomium; **pyc**, pygidial cirri; **pyg**, pygidium; **tci**, tentacular cirrus; **vci**, ventral cirrus.

[K. Nolan]

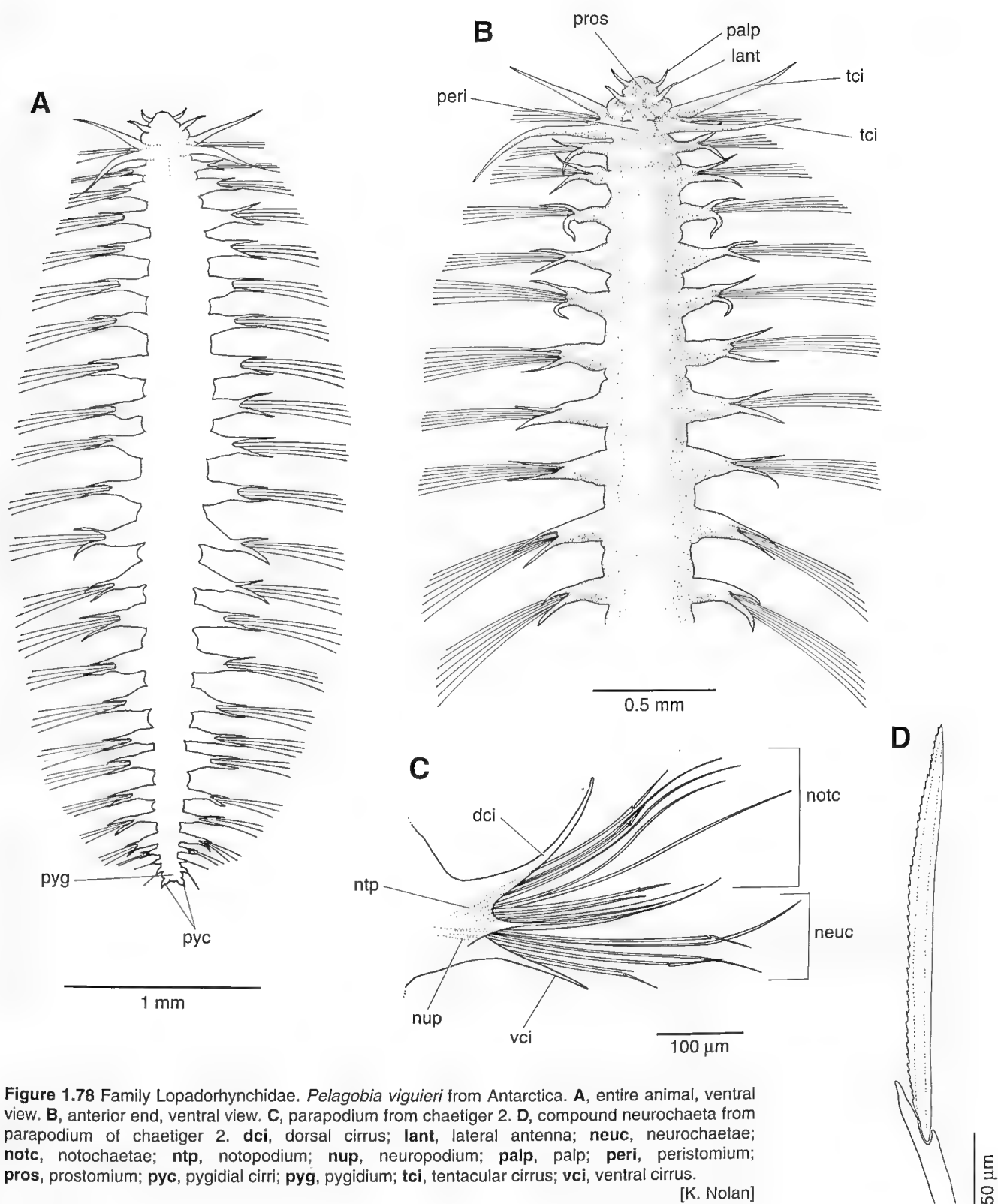


Figure 1.78 Family Lopadorhynchidae. *Pelagobia viguieri* from Antarctica. **A**, entire animal, ventral view. **B**, anterior end, ventral view. **C**, parapodium from chaetiger 2. **D**, compound neurochaeta from parapodium of chaetiger 2. **dci**, dorsal cirrus; **lant**, lateral antenna; **neuc**, neurochaetae; **notc**, notochaetae; **ntp**, notopodium; **nup**, neuropodium; **palp**, palp; **peri**, peristomium; **pros**, prostomium; **pyc**, pygidial cirri; **pyg**, pygidium; **tci**, tentacular cirrus; **vci**, ventral cirrus.

[K. Nolan]

The family was described by Claparède (1868), but the first species was described by Grube in 1855. The most recent revisions of the family are those by Uschakov (1972) and Dales & Peter (1972); Uschakov treated Lopadorhynchidae as a subfamily of the Phyllodocidae. Uschakov (1972) and Dales & Peter (1972) both agreed that the family includes four genera; Uschakov provided keys to the species. The largest genus, *Lopadorhynchus*, was treated by Kim (1967), however, the reviews by Dales (1957a), which included a key to all seven species, and Dales & Peter (1972) viewed the genus more conservatively and recognised additional species.

Globally, the family comprises 16 species belonging to four genera: *Lopadorhynchus*, *Maupasias*, *Pedinosoma* and *Pelagobia*. None, as yet, have been recorded from mainland Australian waters, but the wide distribution of the family, especially in tropical and temperate waters, suggests that this reflects a lack of collecting effort. Hartman (1964) recorded three species, *Maupasias caeca*, *Pelagobia longicirrata* and *P. viguieri* (Fig. 1.78), from the waters of the Australian Antarctic Territory or widespread in Antarctic seas. Lopadorhynchids are exclusively pelagic, and live from surface waters to depths of at least 1000 m (Uschakov 1972). Diurnal vertical migrations from surface waters to greater depths during daylight have also been reported (Dales 1957a).

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Lopadorhynchids have a short, broad and flattened body of up to 35 segments and may reach 35 mm long and 7 mm wide, but many species are much smaller (Uschakov 1972). Species may be transparent or have lightly pigmented bodies. The characters that define the genera are the arrangement of tentacular cirri and chaetae on anterior segments, and the degree of fusion of the anterior segments. Important characters used for species identifications are the size and shape of the tentacular cirri, parapodia and chaetae.

Lopadorhynchids are probably all predators, but their prey are unknown (Fauchald & Jumars 1979). Dales (1955b) discussed the morphological adaptations of lopadorhynchids: they have poorly developed eyes and appear to rely on tactile antennae and tentacular cirri to detect prey; prey may be held by the modified and enlarged anterior parapodia and chaetae. The pharynx is papillose and has mucous glands, the secretions of which may also have a role in handling prey (Dales 1955b). Fat bodies are present in *Pelagobia* species and apparently contribute to buoyancy control (Friedrich 1949).

The sexes are separate, but their reproductive biology is unknown. Uschakov (1972) reported that female *Lopadorhynchus appendiculatus* carry eggs in the parapodia.

Development of the nervous system in *Lopadorhynchus* larvae was described in detail by Åkesson (1967b). He showed that conclusions about phylogeny made by Kleinenberg (1886) and Meyer (1901) were based on inaccurate observations; the well-developed larval protonephridia were mistaken for nerves.

Phylogenetic relationships of lopadorhynchids have not been investigated thoroughly, but Dales (1955b) and Uschakov (1972) noted the similarity of larvae and adults to those of some benthic Phyllodocidae, and speculated that lopadorhynchids may have been derived from a similar ancestral form.

Family Nephtyidae

Nephtyids are benthic polychaetes distinguished by the presence of an inter-ramal branchia attached to the ventral notopodial margin. The oblique musculature and internal morphology of the segments also appears to be unique (Clark & Clark 1960; Fauchald & Rouse 1997).

Nephtyids have a quadrangular prostomium that flattens anteriorly, terminating in a pair of antennae and a more ventrally located pair of simple palps (Fig. 1.79A). Nephtyids are often referred to in the literature as having two pairs of antennae; the present interpretation of the homology of palps and antennae follows Rouse & Fauchald (1997). The peristomium is reduced, and parapodia of anterior chaetigers surround the mouth. The first chaetigerous segment is smaller than the next and is usually anteriorly directed with prolonged dorsal and ventral cirri sometimes termed tentacular cirri. All subsequent segments are similar in form, and all parapodia are biramous; unlike most polychaetes, the body is distinctly squarish in cross section. Posterior segments taper gradually to the pygidium; the anus is terminal and has a single ventral cirrus. An eversible muscular pharynx is present, with a terminal ring of papillae and rows of subdistal papillae (Fig. 1.79B). Proximally the surface of the pharynx is bare or may carry verrucae, forming a granulate appearance. One pair of lateral jaws is present, and in *Dentinephtys* a pair of hard trepans with eight or nine whitish teeth is located internally on the everted pharynx. The biramous parapodia have dorsal and ventral aciculae throughout. Chaetae are capillaries and may be smooth, serrate, or barred; lyrate chaetae are also present in

Aglaophamus, *Inermonephtys* and *Micronephtys*. The description is based on Rouse & Fauchald (1997) and Hilbig (1997c).

The genus *Nephtys* was described by Cuvier (1817) to accommodate species that were originally placed in the genus *Nereis*. The family Nephtyidae was erected by Grube in 1850. In addition to *Nephtys*, four additional genera have been described: *Aglaophamus*, *Micronephtys*, *Inermonephtys* and *Dentinephtys*. However, the genera *Aglaophamus*, *Nephtys* and *Micronephtys* may require reassessment as the correct generic placement for some species is uncertain (Rainer & Kaly 1988; Hilbig 1997c).

Four of the five known genera of Nephtyidae occur in Australian waters; *Dentinephtys* is known from a single species from Japan and California. The Australian fauna comprises 18 species, of which 12 or 13 are endemic (Rainer & Kaly 1988). As elsewhere, the most diverse genera are *Aglaophamus* and *Nephtys*, with seven Australian species each. The characters that are most important for species discrimination include the arrangement of papillae and verrucae on the pharynx and the shape of inter-ramal cirri and the segments on which they occur. The most common species in inshore bays of south-eastern Australia is *Nephtys inornata*, while the most common estuarine species is *Nephtys australiensis* (Museum Victoria unpublished databases; Rainer & Hutchings 1977). Recently, published reviews of Australian Nephtyidae have incorporated material from most shallow water habitats and most geographical regions and excluding the slope and deep sea, the family appears taxonomically well-known in Australia (Rainer & Hutchings 1977; Rainer & Kaly 1988). Nephtyids occur from intertidal sediments to the deep sea, and in shelf and inshore depths; in Australia they are found in both muddy and sandy sediments (Museum Victoria unpublished databases).

The body of nephtyids is very muscular and these worms are able to burrow and swim powerfully. It has been suggested that swimming ability in some nephtyid species is enhanced by the development of forms with long chaetae and that these may be adaptations for dispersal prior to reproduction, although it is notable that long chaetae are only observed prior to the appearance of internal oocytes (Garwood & Olive 1981). Similar development of long chaetae occurs in *Nephtys longipes* in southern Australia (R. Wilson unpublished data; Rainer & Hutchings 1977).

Nephtyids burrow in sediments to a depth of at least 200 mm, but do not form permanent tubes. At least one species, *Nephtys hombergii* from the North Sea, has been investigated and found to remain an active burrower in anaerobic intertidal sediments utilising metabolic pathways that do not produce lactate. In this respect, its anaerobic energy pathway is similar to that of the intertidal arenicolid *Arenicola marina* and unlike intertidal nereidids such as *Neanthes virens* (Schottler 1982). Catastrophic mortality may nevertheless occur in populations of nephtyids under severe hypoxia (Fallesen & Jorgensen 1991), and anaerobic metabolic pathways must convey strong selective advantages in nephtyids (Pedersen 1991).

The ability of nephtyids to burrow and swim swiftly is achieved by rapid lateral sinusoidal movements. This ability is promoted by unique intracellular calcium phosphate granules which convey exceptional rigidity to the longitudinal musculature – a structure which is effectively a flexible internal skeleton (Gibbs & Bryan 1984).

No studies of the biology of nephtyids in Australia have been undertaken, but Estcourt (1975) has studied the population structure of *Aglaophamus verrilli* from Tasman Bay, New

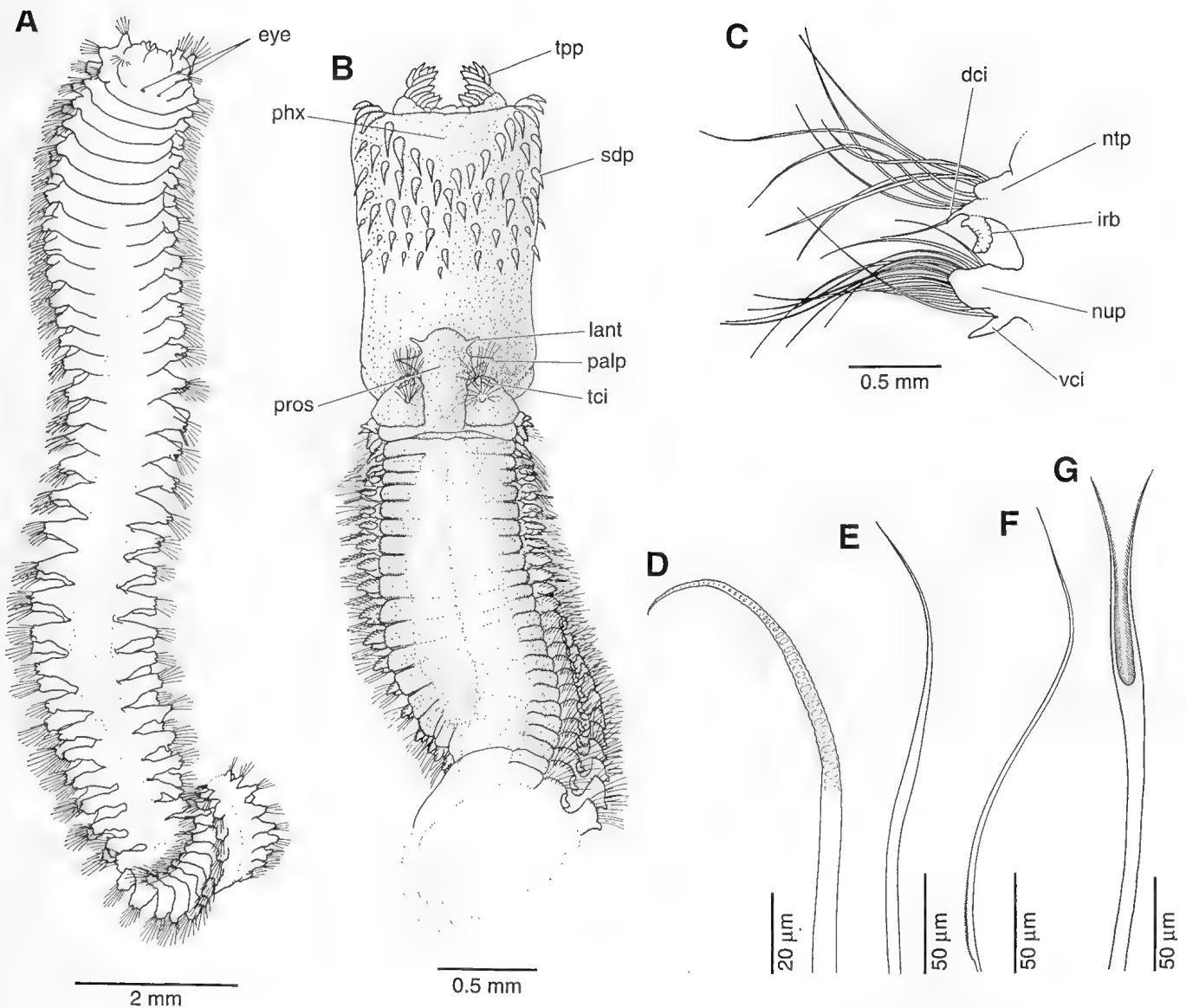


Figure 1.79 Family Nephtyidae. **A**, entire animal of *Nephtys inornata*, dorsal view. **B**, anterior end of *Nephtys longipes* with pharynx everted, dorsal view. **C**, parapodium of *Nephtys longipes* from chaetiger 15. **D**, **E**, chaetae of *Nephtys inornata*: **D**, barred notochaeta from parapodium of chaetiger 10; **E**, notochaeta from parapodium of chaetiger 10. **F**, neurochaeta of *Nephtys longipes* from parapodium of chaetiger 15. **G**, lyrate chaeta from neuropodium of a posterior chaetiger, *Inermonephtys palpata*. **dci**, dorsal cirri; **eye**, eyes; **irb**, inter-ramal branchia; **lant**, lateral antenna; **ntp**, notopodium; **nup**, neuropodium; **palp**, palp; **phx**, pharynx, everted; **pros**, prostomium; **sdg**, subterminal pharyngeal papillae; **tci**, tentacular cirrus; **tpp**, terminal pharyngeal papillae; **vci**, ventral cirri. [K. Nolan]

Zealand. Examination of growth rings in the jaws (Kirkegaard 1970) showed that this species, which also occurs in Queensland, Australia, was found to live for at least 5 years. Elsewhere, it has been suggested that *Nephtys caeca* may exceed 6 years of age, with one exceptionally large individual having jaws with 15 growth rings (Caron *et al.* 1995).

The majority of published studies indicate nephtyids to be predators, seeking other motile invertebrates which are captured by the muscular eversible pharynx. Reviews of the literature on feeding in nephtyids list small molluscs, crustaceans and polychaetes as the primary prey items (Clark 1962; Fauchald & Jumars, 1979); this generalisation is supported by subsequent studies of *Nephtys oligobranchia* from India, which feeds primarily on oligochaetes (Srinivasa-Rao & Rama-Sarma 1978), and of *Nephtys bucera* in New Jersey, United States of America, where spionid polychaetes and juvenile bivalves are the principal prey items in a diet that also includes small crustaceans (McDermott 1987). A few

studies have suggested subsurface deposit-feeding in nephtyids, either on the basis of sand in the gut or because of the seeming dominance of the worms in a habitat with few prey items (Rauschenplat 1901; Sanders 1960). However, there is little direct evidence of deposit-feeding by nephtyids; this would seem to be exceptional behaviour in the family.

Sexes are separate in nephtyids, fertilisation of gametes occurs in the water column, and the larvae are planktonic (Hilbig 1997c). Reproductive success in European species varies according to seasonal conditions and geography (Olive & Morgan 1991), but there are no studies of reproductive biology in nephtyids from Australia.

Nephtyids are not known from the fossil record, and there are no published studies of phylogenetic relationships among nephtyid taxa. Rouse & Fauchald (1997) placed the family as part of a grade of non-scale-worm Phyllodocida (Fig. 1.57).

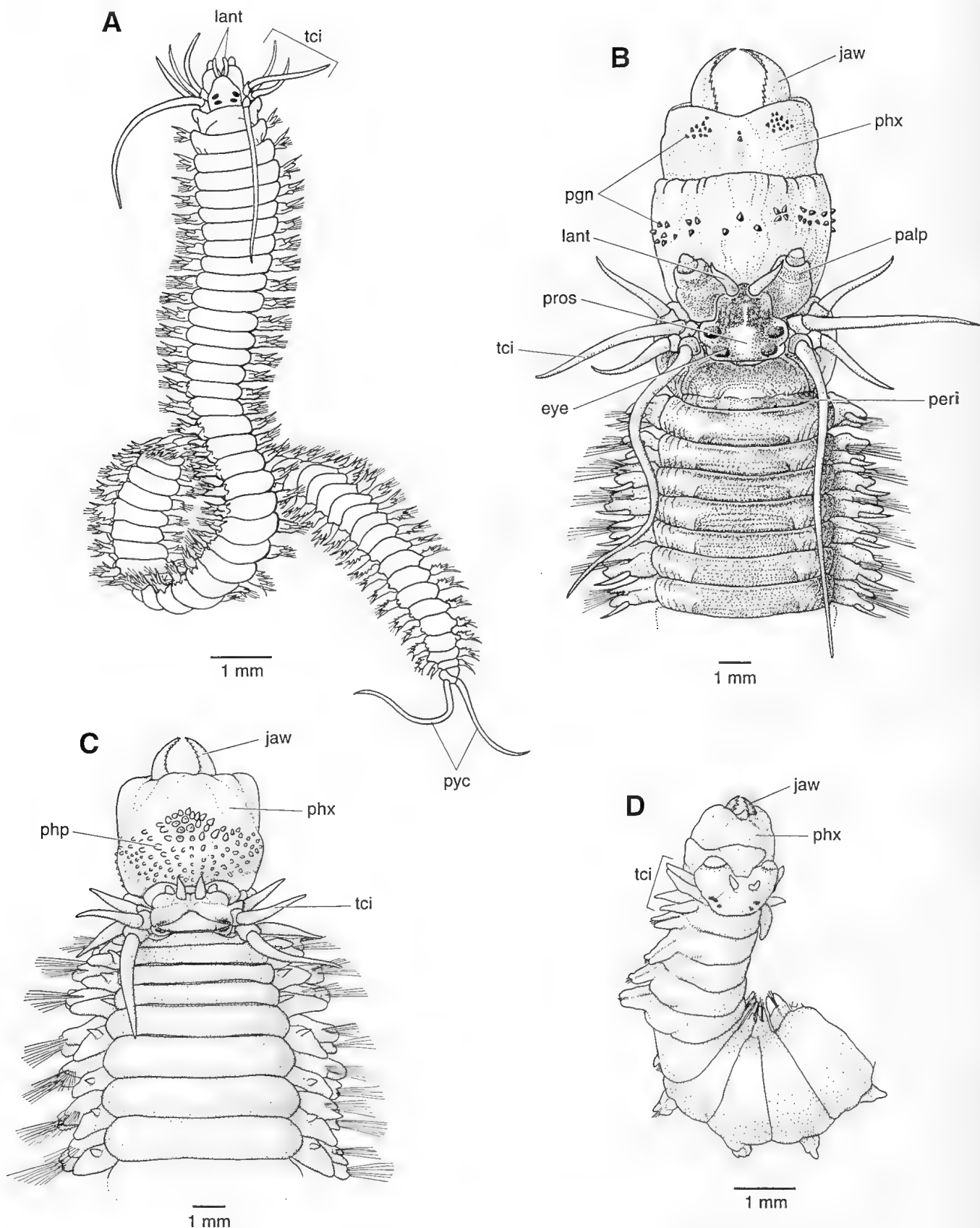


Figure 1.80. Family Nereididae. **A**, entire animal of *Platynereis dumerilii antipoda*. **B–D**, anterior ends with pharynx everted, dorsal views: **B**, *Neanthes vaalii*; **C**, *Australonereis ehlersi*; **D**, *Namanereis littoralis*. **E**, parapodium from chaetiger 20 of *Neanthes cricognatha*, anterior view. **F**, parapodium from chaetiger 74 of *Pseudonereis gallapagensis* from Chile, anterior view. **G, H**, notochaetae: **G**, homogomph falciger from median parapodium, *Nereis maxillodentata*; **H**, homogomph falciger from posterior parapodium, *Nereis onychophora*; **I–K**, neurochaetae from median parapodia: **I**, simple falciger, *Simpliseta* species; **J**, heterogomph falciger, *Nereis maxillodentata*; **K**, heterogomph spiniger from parapodium of chaetiger 13 of *Neanthes kerguelensis*. **dci**, dorsal cirrus; **dnol**, dorsal notopodial ligule; **dnul**, dorsal neuropodial ligule; **eye**, eye; **jaw**, jaw; **lant**, lateral antenna; **neuc**, neurochaetae; **notc**, notochaetae; **nta**, notoacacula; **nua**, neuroacacula; **palp**, palp, articulated; **peri**, peristomium; **pgn**, pharyngeal paragnaths; **php**, pharyngeal papillae; **phx**, pharynx, everted; **pnol**, pre-chaetal notopodial ligule; **pnul**, post-chaetal neuropodial ligule; **pros**, prostomium; **pyc**, pygidial cirri; **tci**, tentacular cirri (4 pairs); **vci**, ventral cirrus; **vnol**, ventral notopodial ligule; **vnul**, ventral neuropodial ligule.

[K. Nolan]

Family Nereididae

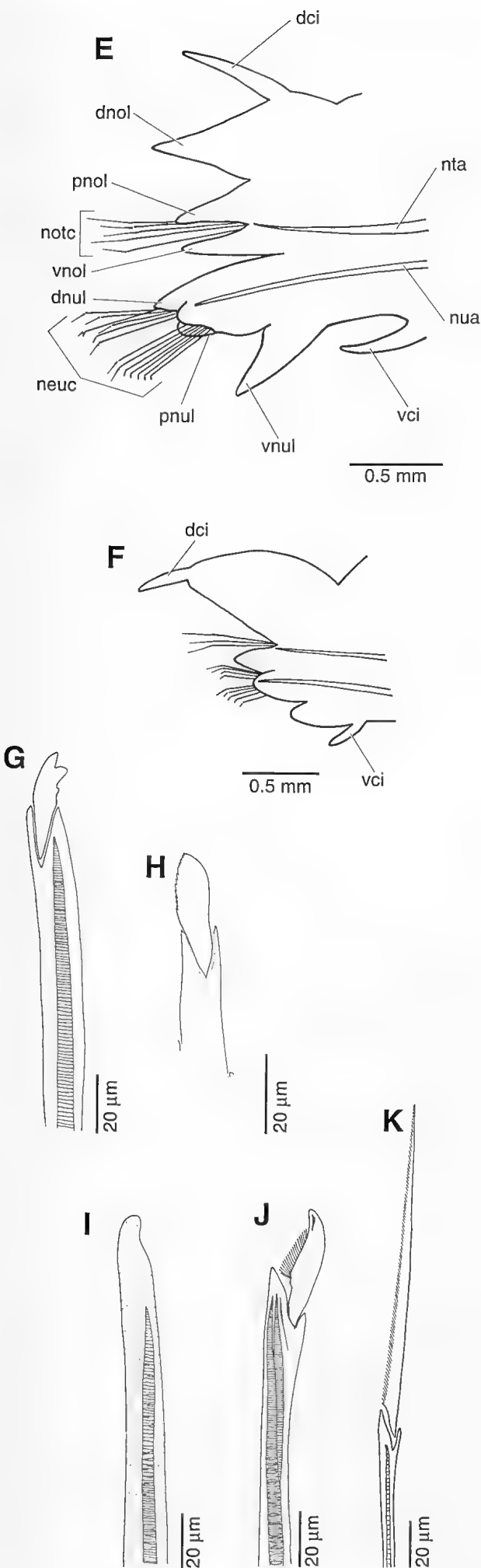
Nereidids are common, widespread benthic polychaetes which have been extensively studied (Pl. 3.1). They are distinguished by having an eversible pharynx with one pair of jaws and, usually, accessory papillae or denticles in a regular pattern.

The following description is based on the studies of Glasby (1993) and Fauchald & Rouse (1997). The prostomium is triangular to T-shaped and is at its widest posteriorly. It has one pair of antennae, rarely a single antenna or none, and one pair of articulated ventral palps (Fig. 1.80B). The peristomium and the first segment are fused and carry two to four pairs of tentacular cirri, four pairs in most genera (Fig. 1.80A–D). The tentacular cirri are derived from peristomial cirri and tentacular cirri from the first segment, but the peristomium and first segment are fused; the distinction is only apparent during development. The muscular eversible pharynx is differentiated into distinct regions; it has a pair of lateral jaws and usually accessory denticles (paragnaths) or papillae (or both) are present in a regular arrangement (Fig. 1.80B–D). Terminal papillae are absent. Nuchal organs are present as short ciliated grooves, barely exposed. Notopodia and neuropodia are present, usually each with at least one flattened lobe (Fig. 1.80E, F). Aciculae are present. Notochaetae may be compound spinigers or falcigers (Fig. 1.80G, H) or both; neurochaetae include compound spinigers (Fig. 1.80K) and falcigers (Fig. 1.80I, J) in two fascicles. All chaetae are compound, but chaetal articulation may be fused in posterior segments in some taxa. One pair of pygidial cirri is present.

The family Nereididae was described (as the Nereidae) by Johnston (1845), but the first nereidid species were described by Linné (1758), Müller (1776) and Fabricius (1780). Much of the recent literature is based on the classifications proposed by Hartman (1959b), Pillai (1961) and Banse (1977a, 1977b), but the only modern and comprehensive review is the phylogenetic revision by Fitzhugh (1987). Fitzhugh (1987) reduced the number of subfamilies from four to three: Gymnonereidinae (18 genera), Namanereidinae (5 genera) and Nereidinae (15 genera). As noted by Glasby (1991), Fitzhugh defined the Gymnonereidinae to include all non-namanereid genera that lack paragnaths; this is probably not a monophyletic taxon. The Fitzhugh subfamily classification is followed here, but further work is required; only the predominantly freshwater Namanereidinae appear well defined, on the basis of several characters: pharynx lacking papillae or paragnaths, spherical palpostyles, and notopodial lobes absent, and neuropodia supported by noto- and neuroaciculae (Glasby 1991).

Globally the Nereididae include at least 39 genera and 535 species; at least 17 genera and 70 species are known from Australia (R. Wilson unpublished data). In Australia, as overseas, the Nereididae have been well studied; useful Australian reviews include those by Hartman (1954), Hutchings & Turvey (1982), Wilson (1984), Hutchings & Reid (1990, 1991), Hutchings *et al.* (1991) and Wilson & Glasby (1993).

Nereidids are among the most widespread and frequently encountered of intertidal polychaetes. They are found not only in a wide range of marine habitats, but have been collected from habitats such as freshwater-filled tree holes and caves (Hartmann-Schröder & Marinov 1977; Glasby *et al.* 1990). Species of *Eumereis* are symbionts of hermit crab shells (Harrington 1897). Nereidids are common inhabitants of the inshore and shelf benthos down to deep-sea and hydrothermal



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vent environments (Fauchald 1972; Blake 1985). Given their otherwise wide geographic and ecological distribution, the absence of nereidids from interstitial habitats is conspicuous. In Australia, estuarine and freshwater species in the genus *Simplisetia* (previously *Ceratonereis sensu lato*) have much more restricted distributions than other taxa, and at least three species each appear to be restricted to the estuaries of a single river system (Hutchings & Glasby 1982; Ben-Eliahu *et al.* 1984; Glasby 1986).

Australian nereidids are typically less than 100 mm long with fewer than 150 segments, but intertidal species such as *Perinereis vallata* may reach almost 200 mm and 300 segments (R. Wilson unpublished data). The body plan of all nereidids is similar, with only the fused peristomium and first segment cephalised (Fig. 1.80A, B). Most body segments are similar and there is little regionalisation of the body. There is some variation in the form of parapodia and chaetae from anterior to posterior segments; elongated dorsal notopodial lobes, homogomph falcigers (Fig. 1.80G) or stout simple chaetae formed by fusion of compound falcigers (Fig. 1.80I) are present in posterior segments in some genera (Hutchings & Glasby 1982; Hutchings *et al.* 1991). Principal taxonomic characters in nereidids are the number and arrangement of pharyngeal papillae and paragnaths, the number and form of parapodial lobes present on anterior and posterior segments, and the type and form of chaetae and the segments in which they occur.

Many nereidids undergo extensive modifications of eyes, parapodia and chaetae into epitokous forms which are adapted for swimming. Typically, epitokes have enlarged eyes, parapodia with large flattened lobes and compound chaetae with flattened paddle-like terminal articles; however, some members of the Namanereidinae develop slender compound spinigers and capillary chaetae upon sexual maturity (Glasby 1999a). Epitokes also show regionalisation; a limited number of anterior segments usually remain almost unmodified whereas the posteriormost segments are often strongly reduced. Sexual dimorphism may also be apparent in epitokes, with distinctive enlargement of anteriormost dorsal and ventral cirri occurring on a different number of segments in males and females. Morphological changes during epitoky have been reviewed by Clark (1961).

Gray (1939) studied locomotion in *Hediste* (= *Nereis*) *diversicolor* from British waters. In this species, fast walking involves sinuous waves of contraction passing from anterior to posterior, whereas slow walking only involves movement of parapodia which form rotation strokes using the chaetae to grasp the substratum. Swimming involves a similar action to fast walking, but is very inefficient, so the adaptive pressure in favour of epitokal modifications in all species that swim to release gametes into the water column must be significant.

Feeding in nereidids has been reviewed by Goerke (1971a) and Fauchald & Jumars (1979). Jaw morphology is a poor guide to feeding strategy, as the large jaws, which are present in all nereidids, are variously used for gathering surface sediments for ingestion (Fong 1987), as well as for scavenging large food items such as plant matter or even other worms (Tsuchiya & Kurihara 1979; Ryan 1980). Two nereidid species commensal with hermit crabs scavenge food remnants and may even eat the eggs of the host crab (MacGinitie & MacGinitie 1949; Goerke 1971b). The studies reviewed by (Goerke 1971a; Fauchald & Jumars 1979) indicated that surface deposit-feeding and herbivory are the most common nereidid feeding habits, although omnivory and carnivory are also known. The great diversity of feeding strategies in

nereidids is also evident within a species, the best documented example being *Hediste diversicolor* in European waters, which may consume sediment, seize larger particles or may lay a mucous net across the burrow as a suspension-feeding apparatus (Goerke 1971a; Esselink & Zwarts 1989). Dorsey (1981) speculated that *Australonereis ehlersi* in Port Phillip Bay, Victoria, may be a deposit-feeder; it may also construct a mucous suspension-feeding net, on the basis that only fine particles were observed in the gut of that species and that the strongly glandular ventral surface is indicative of mucus-secreting capability. *Simplisetia aequisetis* (= *Ceratonereis pseudoerythraeensis*) in the same habitat scavenges dead microcrustaceans and selectively deposit-feeds, although it avoids ingesting the finest mud-silt particles (Dorsey 1981).

The circulatory system in nereidids consists of longitudinal dorsal and ventral blood vessels, from which many smaller vessels branch to pass through the coelom and tissues. All blood vessels are connected, and blood passes from the dorsal to ventral blood vessels through the smaller vessels (Karandikar & Thakur 1946). Nakao (1974) made a histological study of the circulatory system in *Nereis japonica*, and showed that the blood vessels lack a lining of endothelial cells and that the circulatory system is a modified interstitial space. The high oxygen affinity of blood haemoglobins in nereidids, coupled with burrow irrigation, enable these worms to survive in anaerobic intertidal sediments (Economides & Wells 1975), although the capacity to switch to anaerobic metabolic pathways is also important in this habitat (Schottler 1979). Ability to regulate uptake of oxygen over a wide range of oxygen tensions is most evident in species that occur in the most anaerobic sediments (Kristensen 1983).

Nephridia typically occur in all except the anterior- and posteriormost segments (Goodrich 1945). Each nephridium consists of a funnel-like nephridiostome, which projects forward in the coelomic fluid and passes back through the septum into the next segment. The mass of the nephridium is located on the body wall at the base of the parapodia. The importance of the nephridial system in osmoregulation in nereidids is demonstrated by comparative studies which have shown that the development and degree of vascularisation of the nephridia is greatest in species inhabiting brackish or euryhaline waters (Krishnan 1952; Krishnamoorthi 1963; Jones 1967).

Smith (1957) and Orrhage (1993) described the central nervous system of *Neanthes virens* and *Nereis pelagica*; it comprises separate ganglia with no single integrated brain mass as in other polychaete families. Orrhage (1993) also studied the homology of palp nerve roots among nereidids, which, along with the Apistobranchidae, differ from all other polychaete families studied in lacking nerve root 4.

The eyes of adult nereidids begin to develop in the late trochophore larva (light sensitive cells occurring in earlier larval stages are not homologous with adult eyes) (Eakin & Westfall 1964; Rhode 1992). Adult eyes are cup-like structures comprising a retina of light sensitive cells, with a cornea formed by cuticular cells. Between the retina and cornea is a mass of tubular extensions of supportive cells which form a lens-like mass (Eakin & Hermans 1988). The optical properties of the lens structure are unknown (Eakin & Brandenburger 1985). Spectral sensitivity has been studied in *Nereis mediator* from California (Yingst *et al.* 1972). In this species, maximum sensitivity is to light of about 480 nm wavelength, but the range of high sensitivity (400–540 nm) is very broad.

The sexes are almost always separate. Hermaphroditism, which may be simultaneous or protandrous, is known in only five nereidids, mostly freshwater or estuarine species which do not form epitokes (Feuerborn 1932; Schroeder & Hermans 1975). Asexual reproduction has not been reported in the Nereididae. Reproduction is typically monotelic, with adults typically dying after spawning, however, males of a Californian nereidid, *Neanthes caudata*, survive spawning to incubate eggs and reproduce more than once (Reish 1957b). Adults frequently mature in 1 year, but in some species worms may take 2–3 years to mature, possibly even 5–6 years (Wilson & Ruff 1988). The only Australian life history studies are of estuarine species, *Australonereis ehlersi* and *Simplisetia aequisetis* and the freshwater species *S. limnetica*, all of which complete their life cycle in 1–1.5 years (Dorsey 1981; Glasby 1986).

The extensive literature on regulation of reproduction in nereidids has been summarised by Schroeder & Hermans (1975), Franke & Pfannenstiel (1984) Olive (1984) and Bentley & Pacey (1992). These studies show that a combination of environmental factors (principally temperature and lunar cycle, secondarily day length and salinity) and endogenous factors (for example, neurosecretory hormones and release of sexual pheromones into the water) are responsible for the timing and synchrony of reproduction in nereidids. Reproductive patterns in nereidids vary according to habitat as well as between different taxa. Atokous reproduction and brooding of eggs in burrows or specially constructed tubes is most likely to occur in estuarine or freshwater species such as *Australonereis ehlersi*, *Simplisetia aequisetis* and *S. limnetica* in southern Australia (Dorsey 1981; Glasby 1986). *Nicon aestuariensis*, from New Zealand, is an exceptional estuarine species which has a 2 year life cycle and swarming epitokes (Estcourt 1966). Glasby (1986) suggested that *S. limnetica*, which is restricted to the Upper Hawkesbury River in New South Wales, may be derived from the widely-distributed *S. aequisetis*, and that additional species of *Simplisetia* with local distributions and specialised reproductive habit await discovery in other Australian rivers and estuaries. If so, this would provide additional evidence of reproductive adaptation as an important factor in speciation in nereidids (Smith 1958).

Epitoky and swarming in surface waters are typical in marine species, but despite the extensive overseas literature relating to such species there are no similar studies of epitokous nereidids in Australia. However, Hutchings & Howitt (1988) recorded a large number of nereidid species swarming in the water column at Lizard Island, Great Barrier Reef, in November and December, during coral spawning; also Hutchings (personal communication) has observed swarming nereidids in the Sydney region. Nocturnal swarming of nereidids without epitokal modifications has also been recorded in non-reproductive nereidids (Dean 1978a), but this behaviour has not been recorded in species from Australia.

Development of larvae to a demersal juvenile stage of three to six segments may occur in 4–40 days (Reish 1957b). Larvae of estuarine and freshwater species may spend little or no time in the plankton, and in these the trochophore stage may be suppressed. Allozyme studies of estuarine nereidid species have demonstrated considerable genetic variation between populations, but it is not clear whether this is due to restricted gene flow between estuaries or to high selective pressure (Mustaquim 1988; Hateley *et al.* 1992).

The burrows of intertidal and estuarine nereidids are best known; they serve to protect the worms from predators such as fish and wading birds (Esselink & Zwarts 1989). Several

species have been shown to exhibit territorial behaviour in defense of their burrows, and defence may be a principal function of the jaws, which are used to bite intruders and even cannibalise losers in intraspecific encounters (Roe 1975). Fighting is density dependent and fights are usually won by the resident worm (Miron *et al.* 1992).

In Port Phillip Bay, Victoria, a common nereidid, *Simplisetia aequisetis* (previously known as *Ceratonereis pseudoerythraeensis*), is a preferred prey of greenback flounder, which selectively consume larger worms (Kent & Day 1983). *Australonereis ehlersi* and *S. aequisetis* are also the prey of wading birds in Port Phillip Bay (Dorsey 1981), and predation is probably a significant influence on the size structure of populations of these species.

Culture of nereidid worms occurs overseas, where worms are important commercially as fish bait (Okuda 1933; Wilson & Ruff 1988) and are also valued for their ability to treat sewage waste (Inamori *et al.* 1979; Kurihara 1983). Populations of nereidids in southern Australia are also under some pressure from bait collectors, but, although some pilot studies have taken place, as yet no large scale culture projects have succeeded in Australia (R. Wilson unpublished data).

Several nereidids have been studied with regards to their use as bioassay organisms for heavy metals and organic pollutants in marine environments as well as for laboratory toxicity tests (Reish *et al.* 1976; Mason *et al.* 1988). However, nereidids are not effective for assays of all metals, for example, zinc does not accumulate in nereidids in proportion to its concentration in the environment (Bryan & Gibbs 1980). For cadmium and PCBs, nereidids provide highly sensitive bioassays, with tissue concentrations 10 to 1000 times the environmental concentration (Goerke & Ernst 1977; Rice & Chien 1977). No published studies of Australian species as bioassay organisms are available.

Glasby (1993) provided a cladistic analysis of the Nereidoidea *sensu* George & Hartmann-Schröder (1985) and placed the Nereididae as a sister taxon of the clade (Chrysopetalidae–Hesionidae). Synapomorphies for the clade Nereididae–(Chrysopetalidae–Hesionidae) according to Glasby (1993) are a partially differentiated pharynx, which is divided into anterior and posterior sections by a break in the musculature; and differentiated neurochaetae, in which the shaft has a distinct internal medulla with a compartmentalised channel. Autapomorphic states defining the Nereididae in this analysis are fusion of the peristomium and the first segment, the presence of notopodia with at least one flattened lobe, and the presence of compound notochaetae.

Nereidid jaws can be found readily in Recent marine sediments (Brenchley 1979; Colbath 1986b), but they are not readily fossilised (Szaniawski 1974; Colbath 1986b). Nereidid fossils are unknown from Australia.

Family Paralacydoniidae

The Paralacydoniidae are a poorly known family of uncommonly collected benthic polychaetes. They have a blunt head with four small appendages and well-developed parapodia.

The prostomium tapers to a blunt tip and bears a pair of terminal anterior antennae and a pair of ventral palps; the antennae and palps are of a similar size (Fig. 1.81A, B). Irregular scattered brown pigment spots are present on the prostomium and dorsum; eyes are apparently absent. The pharynx has a terminal ring of papillae; jaws are absent

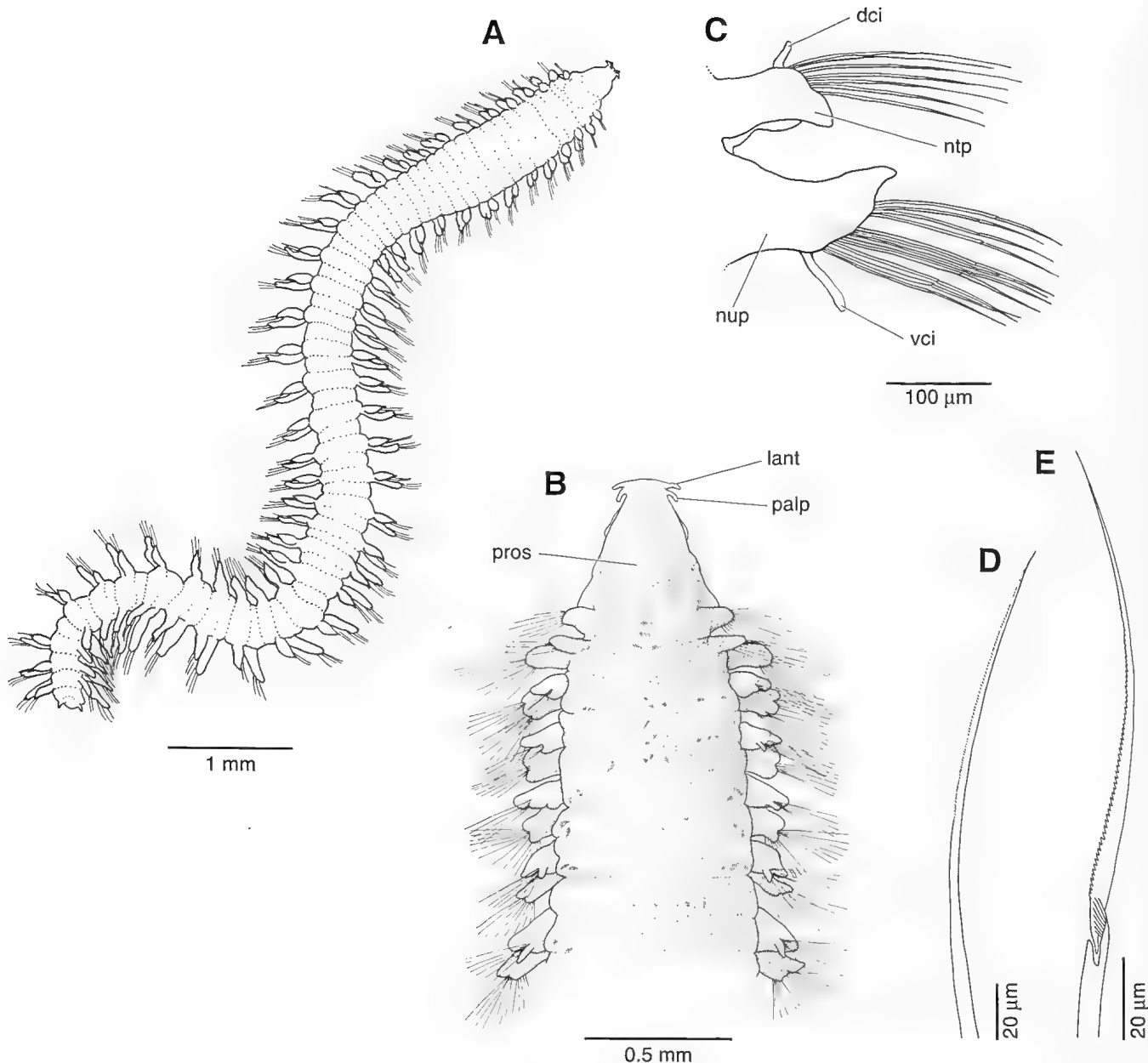


Figure 1.81 Family Paralacydoniidae. *Paralacydonia weberi*. **A**, entire animal, dorsal view. **B**, anterior end, dorsal view. **C**, parapodium from chaetiger 15. **D**, capillary from notopodium of chaetiger 15; **E**, compound spiniger from neuropodium of chaetiger 15. **dci**, dorsal cirrus; **lant**, lateral antenna; **ntp**, notopodium; **nup**, neuropodium; **palp**, palp; **pros**, prostomium; **vci**, ventral cirrus. [K. Nolan]

(Blake 1997). The peristomium, reduced dorsally, is present ventrally as lips around the buccal opening; it lacks cirri or other appendages. The first segment has neuropodia with neurochaetae and reduced ventral cirri; notopodia and notochaetae are lacking [R. Wilson original observation, AM W202391; in agreement with Fauvel (1914); the report by Pettibone (1963) that the first segment lacks parapodia is apparently an error]. All other segments are biramous, with widely separated parapodial lobes. Notopodia and neuropodia have small postchaetal and larger prechaetal lobes, and small dorsal and ventral cirri, respectively. Neuropodia are longer than notopodia. Aciculae are present in both parapodial lobes (Fig. 1.81C). Notochaetae are capillaries, serrated on one margin (Fig. 1.81D), and neurochaetae are compound spinigers similarly serrated (Fig. 1.81E). The pygidium is bulbous and has a pair of long cirri (Blake 1997). Except as noted, the above description is based on Rouse & Fauchald (1997); original observations and the figures are based on the

sole Australian specimen, AM W202391. Other relevant references are Fauvel (1914), Augener (1927), Pettibone (1963) and Blake (1997).

Pettibone (1963) and Blake (1997) treated paralacydoniids as being most similar to the Nephtyidae, whereas Rouse & Fauchald (1997) placed the paralacydoniids as sister taxa to the Glyceridae and Goniadidae, a grouping supported by the absence of tentacular cirri, first segment having neuropodia and neurochaetae, and the presence of spinigerous compound chaetae. A sister group relationship with Glyceridae and Goniadidae would suggest that the four small prostomial appendages are homologous with those of Glyceridae and Goniadidae and do not represent antennae and palps (see Orrhage 1999). Paralacydoniids can be distinguished from nephtyids by the presence of a uniramous first segment and compound neurochaetae, and from glycerids and goniadids by the absence of jaws and the presence of more prominent parapodial lobes.

The family contains a single genus, *Paralacydonia*, which was originally placed in the family Lacydoniidae. Pettibone (1963) gave the genus familial status. Two species of *Paralacydonia* are known: *P. paradoxa*, originally described from the Mediterranean, is now recorded from widespread localities, and; *P. weberi* is known from Indonesia. A third species, *P. mortenseni*, was described from New Zealand by Augener (1924b), who later (1927) synonymised it with *P. weberi*. The type material of these species has not been reviewed (Blake 1997), and Uschakov (1958) treated all species as synonyms of *P. paradoxa*. In the absence of a taxonomic review, the sole Australian record, from Halifax Bay, North Queensland, is referred to *P. weberi* (Australian Museum, unpublished record). Collectively, records of *Paralacydonia* species range over about 25–3000 m. All species are apparently known only from soft sediments (Blake 1997).

There are no studies of internal anatomy, reproduction or other biological aspects of this infrequently collected family.

Family Pholoidae

Pholoids are a morphologically variable group of small scale-worms. Many live interstitially, others live under rocks, in crevices and on muddy bottoms with shells and debris. They are found from the intertidal zone to great depths.

The prostomium is truncated and the peristomium reduced to lips. A pair of lateral antennae and a median antenna are usually present (Fig. 1.82A). The ventral palps are fused to the ventral side of the first segment; they taper and have no articulations. Nuchal organs have not been observed. The arrangement of the longitudinal muscles has not been recorded. Segmentation of the body is distinct. The first segment curves around the prostomium and bears well-developed parapodia, the neuropodia of which are fused to the lower side of the head; chaetae are present in some taxa and two pairs of tentacular cirri may be present. In other segments, the neuropodia are better developed than the notopodia, but both have a well-developed ramus (Fig. 1.82C). The dorsal cirri alternate with elytra in all segments in *Pholoides*; *Pholoe*, however, lacks cirriform dorsal cirri and elytra are present on every second segment anteriorly and on all posterior segments. Ventral cirri and a pair of pygidial cirri are present. Branchiae and epidermal papillae are lacking and lateral organs and dorsal cirrus organs have not been observed. The buccal organ is an axial, muscular, eversible pharynx, bearing terminal papillae anteriorly and two pairs of dorso-ventrally arranged jaws. A gular membrane is lacking; the gut is a straight tube (Heffernan 1988). In juvenile *Pholoe minuta*, nephridia are reported to be metanephridia without any mesodermal involvement (Bartolomaeus & Ax 1992); the condition in mature individuals is unknown. Aciculae are present. Compound falcigerous chaetae (Fig. 1.82E, F) are present and have single ligaments (soft tissue connects the shaft to the blade in compound chaetae); they resemble those present in certain sigalionids (for example, *Sthenelanelia*). Other chaetae are variously ornamented capillaries (Fig. 1.82D). Epidermal papillae similar to those present in the aphroditids may be present. This definition is based on that of Fauchald & Rouse (1997).

Kinberg (1858) based Pholoidae on the genus *Pholoe*. Hartman & Fauchald (1971) recognised a related family, Peisidicidae, based on the genus *Peisidice*. *Peisidice* is a subjective synonym of *Pholoides* (Hartman & Fauchald 1971); accordingly Fauchald (1977) changed the name of the

family Peisidicidae to Pholoididae. Pettibone (1992a) synonymised Pholoididae with Pholoidae, retaining the older name Pholoidae, although the two 'families' differ in some characters currently used to differentiate other scale-worm families, for example, the distribution of elytra on posterior chaetigers. These are present on all posterior chaetigers in *Pholoe* (Pholoidae) and on alternate chaetigers in *Pholoides* (Pholoididae). Recognition of either one or two families with elytra and compound chaetae in addition to the Sigalionidae may make the latter paraphyletic. Pettibone (1992a) also listed the characters that separate Pholoidae from the closely related Sigalionidae.

Pettibone (1992a) recognised six genera, *Pholoe*, *Laubierpholoe*, *Imajimapholoe*, *Taylorpholoe*, *Pholoides* and *Metaxypsamma*, and 12 species in Pholoidae. Members of the family are found worldwide although some species have restricted distributions. In Australia, two species of *Pholoides* are known, *P. dorsipapillata* from the Great Australian Bight, southern Australia (Averincev 1978) and a new species from Bass Strait (Hutchings & McRae in press). Only one species of *Pholoe* is known from Australian waters, an incomplete specimen collected in Bass Strait. None of the other genera that Pettibone (1992a) recognised are known from Australia. It seems likely that with additional collecting, especially of the interstitial fauna, additional species will be found in Australian waters.

Hutchings & McRae (in press) in their study of the Australian representatives of this family, have retained the family name Pholoididae, with the single genus *Pholoides*; the genus *Pholoe* is transferred to the Sigalionidae. Members of the family Pholoididae are characterised by concentric rings on each elytron (Fig. 1.82B). Such rings are absent in *Pholoe* and other genera of Sigalionidae. The genera erected by Pettibone (1992a) were considered invalid by Hutchings & McRae (in press).

Pettibone (1992a) provided a key to all genera, and Hutchings & McRae (in press) have prepared a key to the Australian species of *Pholoides*. The taxonomy of this group is confused, and in many cases species have been described from a single damaged specimen. Pettibone (1992a) briefly discussed the confusion over the type species of the genus *Pholoe*.

The distribution of *Pholoe parva*, an intertidal member of the interstitial fauna in northern Japan, was studied by Yamanishi (1985). The worms were found low on the shore out of the major surf zone, and were sticky to touch because of the substances produced by their adhesive glands. Their 'stickiness' presumably aids them in staying within the coarse sediment. Such a character combined with their small size and flattened body are all adaptations to interstitial life (Swedmark 1964).

Pholoids are small, with a few to moderate number of segments (19 to 90); the body is flattened, the dorsal surface may be covered with scattered tubercles (Fig. 1.82A) and the ventral surface may bear papillae. The elytra are attached to the dorsum by nodular elyrophores on most alternate segments. In the highly modified genus *Metaxypsamma*, elytra and notopodia are lacking. Wolf (1986c) observed that the distribution of the paired nodular lobes with filiform papillae in *Metaxypsamma* is similar to that of the elytra in other species of the family; their presence in adults appears to be a retention of a larval character, that is, they are neotenic. The elytra are soft and delicate with surface and marginal papillae, or stiff and rigid with concentric rings and a fringe of marginal papillae (Fig. 1.82B). The elytra may or may not cover the dorsum.

1. CLASS POLYCHAETA

The prostomium is rounded, fused to the first tentacular segment and withdrawn between the anterior segments (Fig. 1.82A). It usually bears two pairs of eyes and a median antenna. Lateral antennae may also be present. The tentaculophores arise on the first segment antero-laterally to the prostomium. Chaetae may be present or absent, and one or two pairs of tentacular cirri may be present. The paired palps emerge ventrally to the tentaculophores. The pharynx is eversible and has two pairs of hooked jaws. Nine pairs of papillae are present on the dorsal and ventral borders of the pharynx. Parapodia are biramous (Fig. 1.82C), except in *Metaxypsamma*. The notopodia comprise a conical acicular lobe with or without subdistal papillae. The neurochaetae are compound with a smooth or distally spinose shaft and short, unidentate falcate blades (Fig. 1.82E, F); the notochaetae are finely spinose capillaries (Fig. 1.82D).

Pholoids are carnivorous and presumably use their eversible jawed pharynx to catch small prey items. Pleijel (1983) analysed the gut contents of *Pholoe minuta* and found that they feed on sedentary polychaetes, especially spionids, and small crustaceans.

No information is available on the circulatory or nervous systems of pholoids. As branchiae are absent, oxygen uptake probably occurs over the entire surface of these small animals.

The development of metanephridia in *Pholoe minuta* has been studied and illustrated by Bartolomaeus & Ax (1992). They showed that the metanephridium develops from an intermediary protonephridium.

The sexes are separate. The ovigerous segments begin between segments 6 to 11 and continue to between segments 16 to 23 in *Pholoe parva*. According to Yamanishi (1985), between 11 and 24 oocytes are present per worm and ovigerous females were present from May to June; males were never collected.

Some species of *Pholoe* are free-spawners and have a planktotrophic larva (Rasmussen 1956; Cazaux 1968; Blake 1975b; Christie 1982; Heffernan & Keegan 1988; see review by Wilson 1991). *Pholoe swedmarki*, however, broods its eggs within its body, and development is direct (Laubier 1975). Spawning and larval development of *Pholoe minuta* has been studied in detail by Heffernan & Keegan (1988). Populations in Ireland spawn in spring (March–April). Development of an eight-cell stage and a ciliated gastrula occurred within 4 hours and 16 hours of fertilisation, respectively. Trochophore larvae (100–120 µm in length) were observed swimming in the water column within 1–2 days of fertilisation, and within 4 days they were feeding. Notopodia and elytra develop after the 4-chaetiger stage. Reproductive

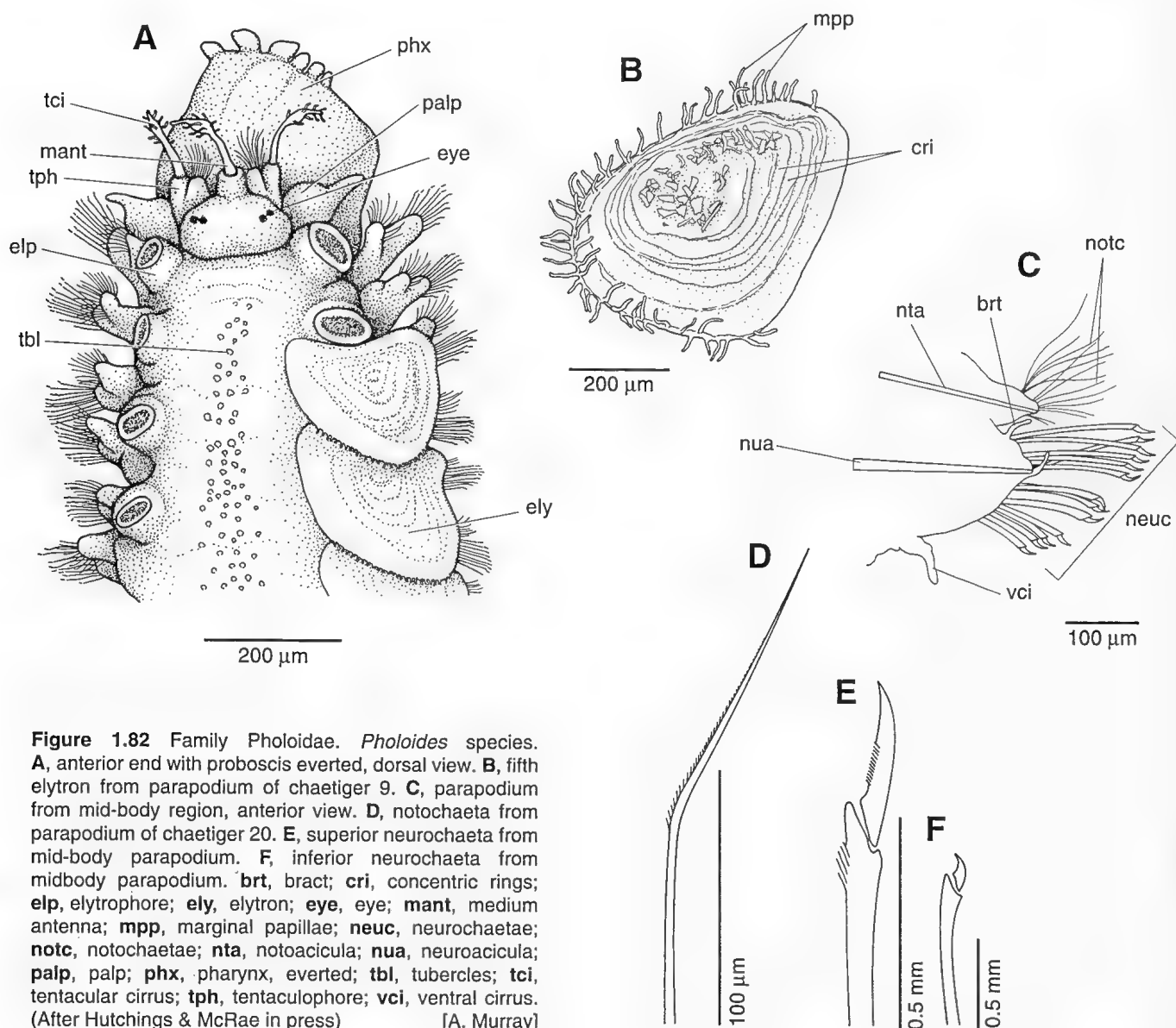


Figure 1.82 Family Pholoidae. *Pholoides* species. **A**, anterior end with proboscis everted, dorsal view. **B**, fifth elytron from parapodium of chaetiger 9. **C**, parapodium from mid-body region, anterior view. **D**, notochaeta from parapodium of chaetiger 20. **E**, superior neurochaeta from mid-body parapodium. **F**, inferior neurochaeta from midbody parapodium. **brt**, bract; **cri**, concentric rings; **elp**, elyrophore; **ely**, elytron; **eye**, eye; **mant**, medium antenna; **mpp**, marginal papillae; **neuc**, neurochaetae; **notc**, notochaetae; **nta**, notoacacula; **nua**, neuroacacula; **palp**, palp; **phx**, pharynx, everted; **tbl**, tubercles; **tci**, tentacular cirrus; **tph**, tentaculophore; **vci**, ventral cirrus. (After Hutchings & McRae in press) [A. Murray]

strategies employed by *Pholoe minuta* range from planktotrophy (Rasmusen 1956, 1973; Blake 1975b; Lacalli 1981) through lecithotrophy (Svesnikov 1960; Blake 1975a; Curtis 1977) to direct development (Thorson 1946). It is possible that the species does exhibit this variation depending on locality; however, it would appear more likely that several species of *Pholoe* have been confused under the name *Pholoe minuta*.

Family Phyllodocidae

Phyllodocids are common benthic polychaetes which are often brightly coloured (Pls 3.2, 3.3). They are distinguished from other families in the Phyllodocida by having an eversible papillated pharynx and leaf-like dorsal cirri.

The prostomium bears a pair of anterior antennae, and a pair of simple ventral palps similar to the paired antennae (Fig. 1.83A–C). A median antenna or nuchal papilla, and one pair of eyes may also be present. A muscular eversible, often papillose, pharynx and terminal papillae are present. Jaws are lacking. One pair of nuchal organs is present. The first segment usually has one pair of tentacular cirri; two pairs are present in *Eteone*. The first two to three segments may be partially fused and bear in total two to four pairs of tentacular cirri. Dorsal and ventral cirri are foliose; dorsal cirri are usually much larger than ventral ones (Fig. 1.83D). Parapodia are uniramous or biramous with weakly developed notopodia. Chaetae are absent from the first segment; thereafter neurochaetae are present as compound capillaries and, rarely, simple chaetae. Notochaetae, if present, are simple capillaries. One pair of pygidial cirri is present. This description follows Pleijel (1991) and Fauchald & Rouse (1997).

The family Phyllodocidae was established by Örsted (1843), although the first species now recognised as phyllodocids were described by Linné (1767). Major taxonomic revisions of the Phyllodocidae include those of Bergström (1914), Uschakov (1972), Pleijel (1991, 1993) and Eibye-Jacobsen (1993). The most comprehensive review of the morphology, ecology and biology of the family is given by Uschakov (1972). The above diagnosis is based on Pleijel (1991), and the classification adopted here follows his phylogenetic revision (1991), which recognises three subfamilies: Notophyllinae, Phyllodocinae and Eteoninae. The Notophyllinae are distinguished by the presence of inflated paired antennae, nuchal organs which are basally fused to the cirrophores of the first pair of tentacular cirri, ventral cirri which have an oblique orientation to the longitudinal axis of the parapodia. The Phyllodocinae are distinguished by the presence of a nuchal papilla (albeit strongly reduced in *Paranaitis*); Eteoninae are distinguished by having nuchal organs present as dorso-lateral ciliated pits or dorsal posterior outgrowths from the prostomium (Pleijel 1991). The pelagic families, Iospilidae, Lopadorrhynchidae (see previous descriptions of families), were treated by Uschakov (1972) as subfamilies of the Phyllodocidae, but are now considered to represent distinct families (Fauchald & Rouse 1997). Keys to genera are more useful and usable than attempts to make subfamily identifications.

Pleijel (1991) recognised 18 genera and globally there are over 350 species; at least 11 genera and 35 species are recorded from Australia (R. Wilson unpublished data). Taxonomic treatments which include Australian species are those of Hutchings & Murray (1984), Wilson (1988), Hartmann-Schröder & Parker (1990) and Eibye-Jacobsen (1991b).

Phyllodocids require careful fixation (preferably after narcotisation) to preserve the pharynx (everted), tentacular cirri and dorsal cirri in a condition that will allow accurate identifications. Small or poorly preserved specimens are often impossible to identify, especially if the taxonomically crucial pharynx is retracted.

Phyllodocids are benthic worms which are almost exclusively marine or estuarine; the only known freshwater phyllodocids are species of *Eteone* from the north-west Pacific (Wu & Chen 1963; Volova 1969). Relatively few phyllodocids live in estuarine waters; these species appear to escape the effects of reduced salinity by secreting a protective mucous sheath (Uschakov 1972). Most phyllodocids show little ecological specialisation at the generic level, except for *Eteone*, species of which only occur on soft sediments (Uschakov 1972). At the species level the few available studies on *Eteone* are contradictory: Kravitz & Jones (1979) reported species of *Eteone* to segregate according to sediment type, but Olivier *et al.* (1992) studied larval settlement in one of the same species, *E. longa*, on a tidal flat and found no evidence of selectivity across sediments ranging from 1 to 20% mud fraction. The possibility that these studies indicate habitat selection occurring after settlement in species of *Eteone* needs to be confirmed by further studies.

Important generic characters in phyllodocids include the degree of fusion of the first two to three segments (which may be entire and distinct or partially fused and reduced), the number of tentacular cirri; the presence or absence of a fifth (median) antenna; and the form of the eversible pharynx and associated papillae. Body segments and parapodia are usually similar after the first few segments. Structure of the chaetae is relatively constant and thus not usually taxonomically useful in the Phyllodocidae, but careful observation of chaetae assists in identification of species of *Eteone* and *Paranaitis* (Eibye-Jacobsen 1991a).

Phyllodocids are typically less than 100 mm in length for 50 to 100 segments, but some species of *Phyllodoce* may reach 300 mm and have 600 segments (Pleijel 1993). In comparison to adults, juveniles may be less pigmented and may have differently shaped dorsal cirri. Juvenile *Eumida ockelmanni* have a terminal ring of proboscideal papillae which becomes reduced during development, forming only micropapillae in sexually mature adults (Eibye-Jacobsen 1987). Ontogenetic and sexual variation, however, have not been investigated in most species.

The eversible pharynx is used to catch prey. Intertidal forms, such as species of *Phyllodoce*, follow mucous trails left on intertidal mud flats by prey species and have been observed hunting on a rising tide (Fauchald & Jumars 1979; R. Wilson personal observation). The pharynx also has sensory functions, and also secretes the digestive enzyme trypsin, as shown by studies of *Eulalia viridis* and *Phyllodoce mucosa* (Michel 1970). The large papillae of the terminal region of the pharynx of *E. viridis* are both sensory and adhesive in function (Michel 1968); both these functions assist in the capture of prey.

According to Uschakov (1972), the vascular system of phyllodocids is poorly developed. There are no branchiae or other organs for gas exchange. Continuous movements of the body and vascular leaf-like dorsal cirri ensure oxygen exchange through the body surface. The lateral branches from the dorsal and ventral blood vessels are open to the coelom, and the direction of blood flow in the dorsal blood vessel is usually anterior to posterior (Gravier 1896), but flow may also occur in the opposite direction (Uschakov 1972). The

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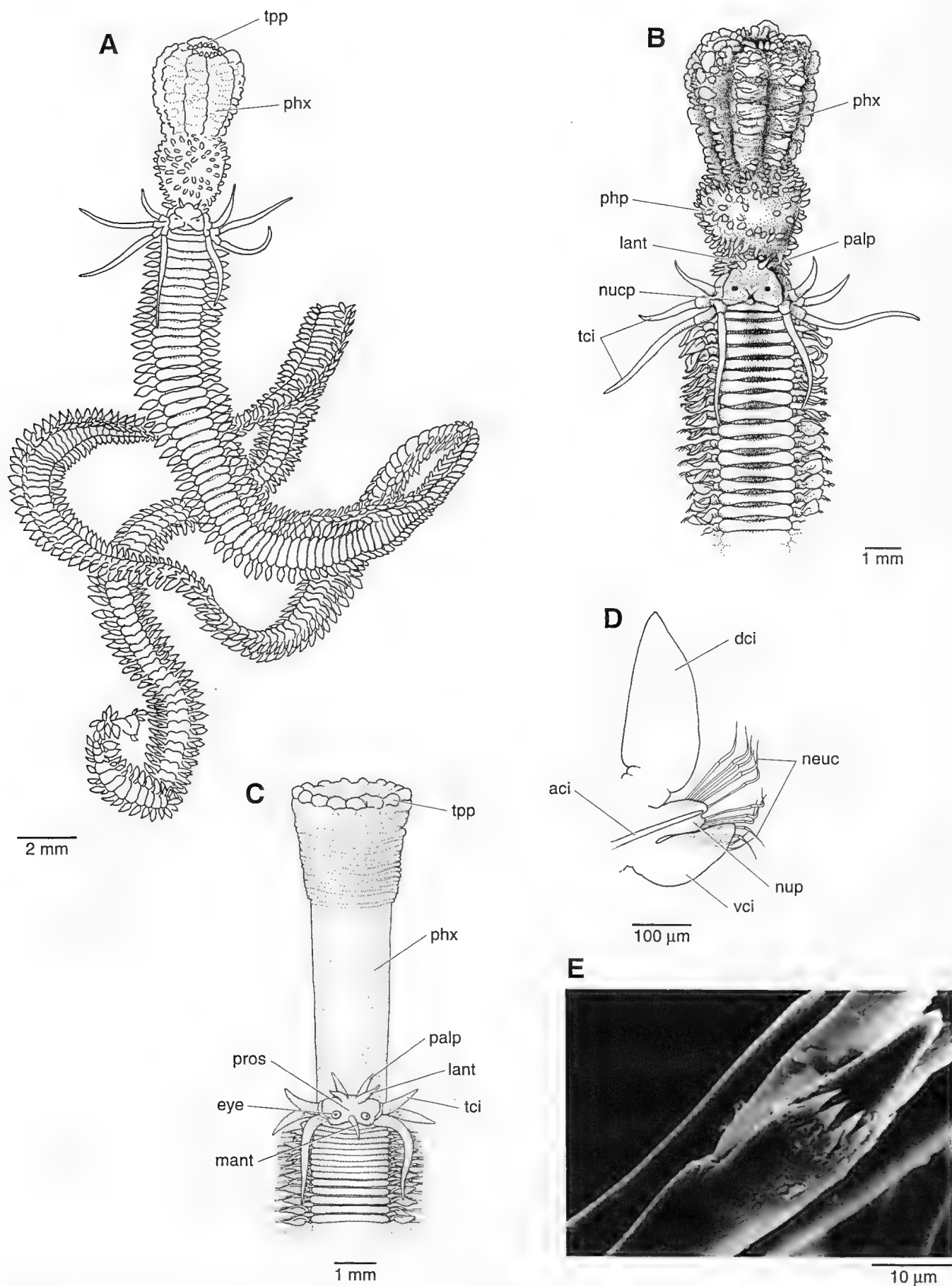


Figure 1.83 Family Phyllodocidae. **A, B**, *Phyllodoce* species A: **A**, entire animal with pharynx everted, dorsal view; **B**, anterior end with pharynx everted, dorsal view. **C**, anterior end of *Eumida fusciculata* with pharynx everted, dorsal view. **D**, median parapodium of *Phyllodoce* species B. **E**, neurochaetae from parapodium of chaetiger 25 of *Eteone palari*; a single large tooth and two or three tiers of smaller teeth are visible on the distal part of the shaft. **aci**, acicula; **dci**, dorsal cirrus; **eye**, eye; **lant**, lateral antenna; **mant**, median antenna; **neuc**, neurochaetae; **nucp**, nuchal papilla; **nup**, neuropodium; **palp**, palp; **php**, pharyngeal papilla; **phx**, pharynx, everted; **pros**, prostomium; **tci**, tentacular cirri; **tpp**, terminal pharyngeal papilla; **vci**, ventral cirrus. (E, after Wilson 1988) [A–D, K. Nolan]

haemoglobin is colourless and it is not involved in oxygen transport, but is used for binding oxygen to sensitive tissues (Uschakov 1972).

Like other families in the Phyllodocida, Phyllodocidae have protonephromixia, (Goodrich 1945). Paired ducts from the protonephromixia open at the ventral base of the parapodia; there is apparently little intergeneric variation in the morphology of this system (Uschakov 1972). At sexual maturity an independent gonoduct develops which funnels gametes to the outside (Uschakov 1972).

All species of Phyllodocidae studied have paired ventral nerve cords, with three to five main nerve rings per segment. Comparative studies of the nervous system have been used by Pruvot (1885), Gravier (1896) and Bergström (1914) to establish the homology of the appendages of the anterior segments, which are subject to fusion to varying degrees in different genera; these results are not all in agreement, but only a few genera have been studied (Uschakov 1972). More recently, Lebskii (1970) and Ushakova & Evdonin (1984) have accurately described the nervous systems of *Eulalia viridis* and *Phyllodoce groenlandica*.

Many phyllodocids form breeding swarms in surface waters, but only the adults of a few species undergo somatic changes at sexual maturity. *Eulalia bilineata*, *Mystides limbata* and two species of *Protomystides* have been reported to have specialised capillary chaetae in breeding adults (Schroeder & Hermans, 1975). Other species, including *Eumida sanguinea*, *Pirakia punctifera*, *Phyllodoce mucosa* and *P. lamelligera*, form breeding swarms of adults which have no somatic modifications at sexual maturity (Fage & Legendre 1927; Gravier & Dantan 1928; Sach 1975). *Eulalia viridis*, from north-eastern United Kingdom, also breeds without somatic sexual modifications of adults and apparently without forming swarms in surface waters (Olive 1975a); they breed when they are at least 2 years old and are polytelic. *Notophyllum foliosum* is apparently unique within the family as it carries its eggs in yellow gelatinous ribbons attached to posterior notopodia (McIntosh 1908; Okada 1930a). *Eulalia viridis*, from British waters, produces gelatinous, green egg masses which are attached to brown algae (McIntosh 1908; Nolte 1938), but at least one population appears not to produce such egg masses (Olive 1975a). Sach (1975) also reported mucous egg masses, each containing more than 10 000 eggs, in *Phyllodoce mucosa*. There are no reproductive studies of phyllodocids from Australia; however, Rouse (1988) described the sperm ultrastructure in *Eulalia*.

Larval development has been described in *Eteone dilatata*, *Eteone picta*, *Eteone longa*, *Eulalia viridis*, *Phyllodoce maculata* and *Phyllodoce mucosa* (Blake 1975b; Olive 1975a; Cazaux 1985; Lacalli 1986; Zavarzina & Tzetlin 1986). In these species, larvae develop through one or two trochophore and two metatrochophore stages before settling as 5- to 9-segmented larvae. Trochophores are strongly phototactic and swim actively by beating the ciliated prototroch; swimming activity has been observed to decrease in the latter stages of larval development (Olive 1975a; Cazaux 1985). Length of larval life before settlement varies, at least, from 8–65 days.

Control of breeding has been studied experimentally in *Eulalia viridis* and *Phyllodoce mucosa* (Olive 1980; Roehrkasten 1984). Both studies found that day length is unimportant, but that temperature influences oogenesis and spawning. In both species, endogenous control of sexual development is important (Sach 1975; Olive 1980); in *E. viridis* one such hormonal regulator of oogenesis is produced by the prostomium (Olive 1975b, 1976). In contrast, somatic growth, such as regeneration of caudal segments,

does not require the prostomium or head to be intact; the endocrinology of phyllodocids is therefore unlike that of the nereidids (Olive & Moore 1975).

Feeding in the Phyllodocidae has been studied in fewer than 10 species (Fauchald 1977), none from Australian waters. Experiments by Emson (1977) showed that *Eulalia viridis*, from the United Kingdom, will only consume damaged or moribund animal tissue, and Sanders *et al.* (1962) reported *Eteone heteropoda* to be a deposit-feeder. However, most studies have shown phyllodocids to be predatory carnivores (Chlebovitsch 1959; Simon 1965; Michaelis 1971). Fauchald & Jumars (1979) summarised these studies; different degrees of prey selectivity in different species is present, and it appears that feeding specialisations may vary significantly between species and even within species between populations.

Eumida sanguinea and the terebellid *Lanice conchilega* may be symbiotic, at least in Dutch estuaries (Wolff 1973) and a species of *Mystides* and *Protomystides* are reported as being commensal with foraminiferans and vestimentiferans respectively (Martin & Britayev 1998). *Eulalia viridis* from the English Channel has been reported to harbour coccidian parasites (Hennere 1966). There are no reports of phyllodocids as parasites.

As carnivores, phyllodocids may be expected to be more sensitive indicators of heavy metal pollution than polychaetes that are lower in the food chain, but this potential has not been investigated. However, McLusky & Phillips (1975) studied the effects of copper being passively absorbed from experimental solutions by *Phyllodoce maculata* and showed that lethal levels of copper in body tissue are not constant (as in the nereidid *Neanthes virens*), but that toxicity appears related to the rate of copper uptake.

The Phyllodocidae have generally been considered to be among the most primitive families of the Phyllodocida, principally due to the reduced cephalisation of anterior segments (Bergström 1914; Uschakov 1972). Uschakov (1972) proposed a phylogeny that relates the Phyllodocidae most closely to the Alciopidae, Typhloscolecidae and Lacydoniidae, and more distantly to glycerids and related families (Glyceridae, Goniadidae, Nephtyidae, Pisionidae and Sphaerodoridae). The classification of Fauchald (1977) instituted a similar system, and placed all of the above families together with nereidiform families in the Order Phyllodocida as did Rouse & Fauchald (1997).

Phylogenetic relationships within the Phyllodocidae have been studied by Bergström (1914), Uschakov (1972), Pleijel (1991) and Eibye-Jacobsen (1993). Bergström (1914) proposed five subfamilies based principally on the numbers, arrangement and innervation of tentacular cirri, but this work was rejected by subsequent authors. Uschakov (1972) presented a phylogeny based solely on the arrangement of tentacular cirri and fusion of anterior segments with *Eteone* as a separate branch at the base of the tree. Uschakov's scheme recognised close relationships between *Phyllodoce*, *Paranaitis* and *Chaetoparia*, a view shared by later authors. The recent cladistic studies of Pleijel (1991) and Eibye-Jacobsen (1993) are more directly comparable. Eibye-Jacobsen differed in regarding the nuchal papilla and medial dorsal antenna as different structures, not homologues as treated by Pleijel. These authors also differed in their interpretation of the homology of the anterior segments and their tentacular cirri. The resulting cladograms differ in a number of interesting respects, notably the placement of *Eteone*, which is a sister-group to the *Paranaitis*–*Chaetoparia*–*Phyllodoce* clade according to Eibye-Jacobsen,

1. CLASS POLYCHAETA

but is terminally located on a clade that includes none of these genera in the cladogram of Pleijel. Another significant dichotomy is the placement of the clade *Eumida*–*Sige-Pterocirrus*, which is close to a clade including *Notophyllum* and *Clavodoce* according to Eibye-Jacobsen, but is more closely allied to *Eulalia* and related genera in the cladogram of Pleijel. More information on morphology, and additional (possibly biochemical) characters, will be required to resolve these questions.

The cosmopolitan distribution of almost all phyllodocid genera, and apparently some species, such as *Phyllodoce longipes*, which is widespread in the Northern and Southern Hemispheres (Pleijel 1988), suggests that the most meaningful biogeographic studies must proceed within genera and alongside cladistic analyses. The only cladistic study of a genus of phyllodocids is the revision of *Eumida* (Eibye-Jacobsen 1991b); this study included no biogeographic analysis, and the cladogram presented places the only two Australian species in a poorly resolved clade that includes both Gondwanan and Tethyan species. This suggests that in *Eumida*, at least, the Australian species are of ancient origin and that no major radiation has occurred in habitats. There are no fossilised remains attributable to the Phyllodocidae.

Family Pilargidae

Members of the Pilargidae are uncommon nereidiforms with reduced parapodia and simple chaetae. They are usually free-living, surface sediment dwellers.

Pilargids have an elongate, cylindrical or dorso-ventrally flattened body that is sometimes inflated anteriorly. The prostomium, which may be incised, bears two or three antennae, or antennae are absent (Fig. 1.84A, B). The palps are usually biarticulate, but they may be fused together or reduced, and two pairs of peristomial (or tentacular) cirri are usually present (rarely absent). The pharynx is usually unarmed and has a circlet of distal papillae. The parapodia are biramous, but with the notopodial ramus reduced (Fig. 1.84B, C). Notochaetae are spines (may be absent), and neurochaetae include capillaries (Fig. 1.84D), furcate chaetae and spines. The purported autapomorphy of the family is the presence of neuropodial capillaries, which distinguishes them from other nereidiforms (Glasby 1993).

Pilargidae are members of the large clade, Phyllodocida (Rouse & Fauchald 1997), considered an order in most recent classifications (for example, Fauchald 1977; George & Hartmann-Schröder 1985). Lower-level classification is less certain; their membership within the superfamily Nereidoidea (George & Hartmann-Schröder 1985; Glasby 1993) has been challenged by the finding that the superfamily may be paraphyletic (Fig. 1.57; Rouse & Fauchald 1997; Pleijel & Dahlgren 1998).

The family was described in 1899 by Saint-Joseph, but many workers in the first half of the twentieth century did not accept the family, instead placing pilargids in either Hesionidae or Syllidae. Revisionary studies by Hartman (1947b) and Pettibone (1966) served to clarify the concept of the family. Two subfamilies were defined by Salazar-Vallejo (1986), *Synelminae* and *Sigambrinae* (= *Pilarginae* of Salazar-Vallejo & Orensanz 1991), but their monophyly is not supported by recent cladistic analyses (Fitzhugh & Wolf 1990; Licher & Westheide 1994). In addition, the monophyly of several genera, including *Ancistargis*, *Litocorsa*, *Parandalia*, *Sigambra* and *Synelmis*, is questionable (Fitzhugh & Wolf 1990; Licher & Westheide 1994), resulting in estimates of the number of valid genera of 10 to 14, depending on the

authority. Further, Pleijel & Dahlgren (1998) suggested that the interstitial hesionids, *Microphthalmus* and *Hesionides*, may fall within the Pilargidae as may *Antonbruunia*, the only taxon within the questionable family Antonbruunidae.

Only three genera, *Ancistrosyllis*, *Synelmis* and *Sigambra*, have been reported from Australian waters (Hartmann-Schröder & Hartmann 1979; Hutchings & Murray 1984), although several others are listed in museum holdings, including *Pilargis* (Australian Museum, Queensland Museum), *Cabira* (Australian Museum, Queensland Museum), *Litocorsa* (Australian Museum), and *Loandalia* and *Parandalia* (Australian Museum, Museum Victoria). *Ancistrosyllis* and *Sigambra* appear to be the most speciose genera in Australian waters, but this needs to be confirmed.

The integument may be smooth, aereolated or, as in species of *Ancistrosyllis*, *Cabira*, *Paracabira* and *Pilargis*, the surface epithelium may be more or less papillated. Papillae are generally more numerous on the dorsum, the head appendages and the cirri. The cuticle is thick and iridescent in *Synelmis* species giving the long body a stiff, wiry appearance. The prostomium is of variable shape. Eyes are usually absent (see below). Palps are usually biarticulate consisting of a large palpophore and small button-like palpostyles, but show considerable variation in shape and the degree of articulation and fusion. A peristomial annulus is present and usually carries two pairs of cirri (Glasby 1993; Licher & Westheide 1994); alternately the peristomium has been interpreted as reduced to an area around the mouth, in which case the first segment carries the two pairs of cirri (Fauchald & Rouse 1997); cirri are absent in some genera such as *Loandalia* (Fig. 1.84B). The axial pharynx is long, cylindrical and muscular in *Ancistrosyllis* and *Synelmis*, but globular and weakly muscular in *Pilargis*; it usually has a circlet of distal papillae. The eversible portion of the pharynx may be smooth or ornamented basally with papillae or spines (= chitinised papillae) as in species of *Sigambra* or *Cabira*. Jaws are present in *Cabira* and the poorly-known monotypic genus *Talehsapia*.

Parapodia are sub-biramous and carry aciculae, but the notopodium is reduced in size with few chaetae (Fig. 1.84C). Neuropodia are approximately conical. Dorsal cirri are present in most species; ventral cirri are present in all species except on the parapodia of chaetiger 1 in species of *Cabira*, *Loandalia*, *Otopsis* and *Talehsapia* (Licher & Westheide 1994). A single straight or distally curved spine occurs in the notopodia of most species; capillary chaetae also may occur. Spines also may be present in the neuropodia, but most often there are capillary chaetae, either smooth, serrated, or sometimes furcate (Fig. 1.84D). The anus is terminal and the pygidial segment normally bears two pairs of anal cirri; in some *Parandalia* and *Loandalia* species the pygidium forms a plaque. Branchiae occur only in *Loandalia* species (Licher & Westheide 1994).

Pilargids have a relatively well-developed brain which may be divided into a forebrain, midbrain and hindbrain, based on gross morphology (Fitzhugh & Wolf 1990). The forebrain is long and bifurcate in species of *Synelmis* and *Parandalia*. The midbrain of *Loandalia* and *Parandalia* species has a pair of pigmented nerve ganglia, which have been called subdermal eyespots (Fig. 1.84B). The hindbrain of pilargids bears two to five posterior lobes which are usually pigmented. On the postero-lateral margin of the prostomium paired nuchal organs (contained within nuchal slits) are visible in most pilargids; as in other polychaetes these probably have a chemosensory function.

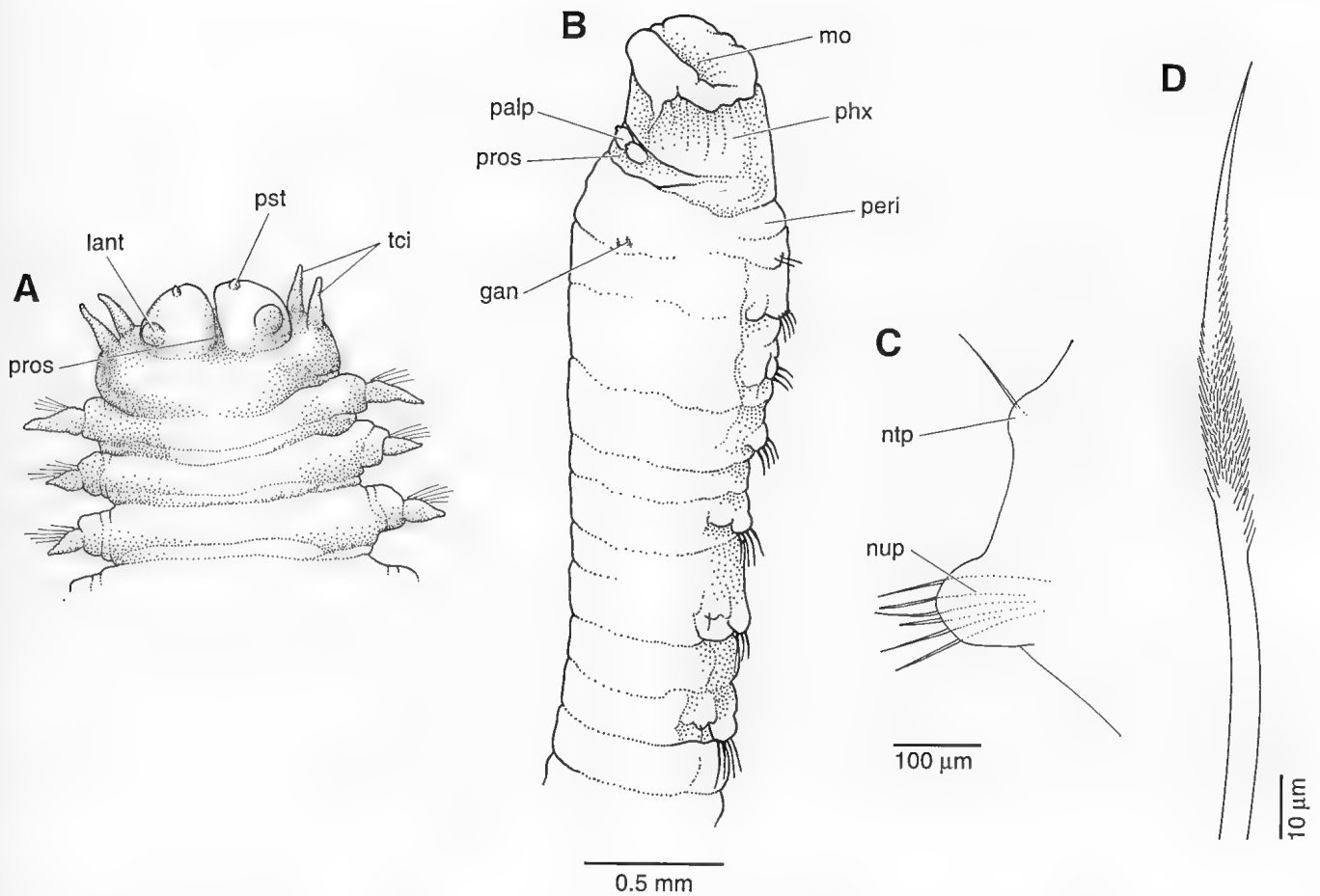


Figure 1.84 Family Pilargidae. **A**, *Pilargis* species, dorsal view of anterior end. **B–D**, *Loandalia* species: **B**, anterior end with pharynx everted, dorso-lateral view; **C**, parapodium, ventral cirrus not shown; **D**, capillary neurochaeta from parapodium of chaetiger 45. **gan**, pigmented nerve ganglion; **lant**, lateral antenna; **mo**, mouth; **ntp**, notopodium; **nup**, neuropodium; **palp**, palp; **peri**, peristomium; **phx**, pharynx, everted; **pros**, prostomium; **pst**, palpostyle; **tci**, tentacular cirrus. (A, after Hartman 1947, scale not available) [K. Nolan]

Reproduction in the Pilargidae is almost unknown. Sexes are apparently separate (Pettibone 1982). Larvae are known only for one species of *Pilargis* (Cazaux 1970), two *Ancistrosyllis* species (Bhaud 1973; Blake 1975b) and a species of *Sigambra* (Kumaraswami-Achary 1975). They are planktonic at least to the 9- to 11-chaetiger stage. Most adult features (antennae, cirri, chaetae) have developed by this stage, although juvenile ciliation may continue until at least the 16-chaetiger stage.

Pilargids are found on soft substrata of the continental shelf, slope and abyssal depths, inshore and in estuaries, in sediment ranging from coarse sand to mud, although many species apparently favour fine sediments. Population densities are generally low, for example, 12–32 worms per m² in the British Isles (Pearson 1970) and pilargids are never the dominant polychaetes. In eastern Australia, *Sigambra parva* occurs intertidally in lower reaches of estuaries in mud to sand, often associated with the seagrasses, *Posidonia* and *Zostera* species (Hutchings & Murray 1984). In north-western Australia, *Sigambra pettiboneae* occurs on the surface of mud flats incorporating some sand and detritus (Hartmann-Schröder & Hartmann 1979).

Most pilargids are probably carnivores or omnivores, but some appear to be active predators or scavengers (Pearson 1970; Fauchald & Jumars 1979). Most species are free-living, surface sediment dwellers, although those with reduced head appendages and parapodia (for example, species of *Loandalia* and *Litocorsa*) may burrow. Two species are known to be commensal with other polychaetes: *Pilargis berkeleyae* lives

in the tubes of chaetopterid polychaetes (Britaev 1993) and *Ancistrosyllis commensalis* in the burrow of a capitellid (Gardiner 1976).

Traditionally, Pilargidae have been considered to be allied closely with other nereidoid families, specially Hesionidae and Syllidae. A sister-group relationship with the Syllidae and Nautiliniellidae suggested by Glasby (1993) was supported by four synapomorphies: presence of a distinct peristomial segment carrying one to two pairs of cirri; an uncephalised first segment (that is, parapodia not modified); absence of pharyngeal jaws, and; notopodia that are either reduced or absent. Fitzhugh & Wolf (1990) speculated that Syllidae was the sister group of Pilargidae, but did not consider Nautiliniellidae. Pleijel & Dahlgren (1998) could not establish precise sister-group relationships for the family: Pilargidae could be the sister group of a group containing Nereididae, Hesionidae and Chrysopetalidae, sister group of a group containing Nautiliniellidae and Antonbruunidae, or a sister group to a large clade containing nereidiforms, aphroditiforms and Pisionidae. By contrast, Rouse & Fauchald (1997) found evidence for a close association with Sphaerodoridae (Fig. 1.57).

Licher & Westheide (1994) favoured a close relationship between Pilargidae and Hesionidae and, somewhat controversially, suggested that the pilargid ancestor evolved progenetically from a hesionid species; hence Hesionidae was paraphyletic without inclusion of Pilargidae. According to these authors and Licher (1994), similarities in head morphology (such as numbers of head appendages and

numbers of pairs of tentacular cirri) of juvenile stages of some of the larger hesionid species and some pilargids indicate a close affinity between the two groups. Licher & Westheide (1994) also identified further autapomorphies of Pilargidae as the presence of stout chaetae in the notopodia and fleshy biarticulated palps. However, as suggested by Glasby (1993), simple, stout notochaetae may be viewed as a symplesiomorphic feature shared with aphroditoids, the purported sister group of the nereidiforms. Further, the nature of the articulation of the pilargid palps is poorly known and may be similar to the biarticulated palps of nereidids, which would possibly make the character homoplastic among nereidiforms.

Recent cladistic analyses do not fully support the subfamilial groupings first established by Salazar-Vallejo (1986). Although the monophyly of the core group of synelmine genera (*Litocorsa*, *Loandalia*, *Parandalia* and *Synelmis*) was supported by studies of Fitzhugh & Wolf (1990) and Licher & Westheide (1994), both studies found that recognition of the Synelminae leaves the Sigambrinae paraphyletic (even if one were to include *Otopsis*, which Salazar-Vallejo placed in the Sigambrinae). Nevertheless, this core group of synelmine genera form a well-circumscribed monophyletic group defined on the basis of their cylindrical body shape, loss of pharyngeal papillae, straight notopodial spines, neuropodia with distally pointed neurochaetae, and gross morphological features of the brain (longer than wide; well demarcated forebrain, midbrain and hindbrain; bifurcated forebrain) (Fitzhugh & Wolf 1990; Licher & Westheide 1994). The more apomorphic synelmine genera (*Talehsapia*, *Parandalia*, *Loandalia*) have a simplified body plan including a reduced prostomium and anal cirri, and lack antennae, peristomial cirri, notopodial aciculae, dorsal cirri, and the ventral cirri on chaetiger 1 (Fitzhugh & Wolf 1990; Licher & Westheide 1994).

Fitzhugh & Wolf (1990) and Licher & Westheide (1994) also found support for a second monophyletic group containing *Ancistrosyllis*, *Cabira*, *Paracabira* and *Pilargis*, defined by papillation of the integument and hindbrain with three or five lobes, which together constitute the bulk (but not all) of the 'Sigambrinae'. The monotypic genus *Antonbruunia* possibly could also be included within the Pilargidae (Salazar-Vallejo 1986; Glasby 1993) although the evidence is weak (Fitzhugh & Wolf 1990; Licher & Westheide 1994).

The synelmine group of Salazar-Vallejo (1986) is distributed from the tropics to high latitudes, but shows greatest diversity in shallow tropical waters (Salazar-Vallejo & Solís-Weiss 1986). The apparent wide geographical and bathymetric ranges of many pilargid species has led some authors to suggest that they represent relict species of a formerly more widespread group (Hartman 1947b; Pearson 1970) or that the group had a former Tethyan distribution (Salazar-Vallejo & Solís-Weiss 1992); however, it may simply reflect our inability to discern taxonomically closely-related species.

Family Pisionidae

The Pisionidae is a poorly studied group of small and slender interstitial worms that often have a thick cuticle. Typically, they are found in sand in shallow waters. Within the family, there is considerable variation in head structures.

The prostomium is small and located between the large, anteriorly-directed first parapodia in *Pisone*; it is conical in *Pisionidens*. The peristomium is reduced to lips. Paired frontal antennae are present (*Pisionidens indica*) or absent (*Pisone remota*); a single median antenna occurs in *Pisionella hancocki*. The palps are fused to the ventral

surfaces of the first parapodia in *Pisone* (Fig. 1.85A), and emerge ventrally on the conical head in *Pisionidens*. Nuchal organs are absent, at least in *Pisone* (G. Rouse personal communication). The longitudinal muscles are grouped in bundles, and segmentation is present. The first segment is folded around the prostomium and bears parapodia in *Pisone*; it is indistinct and bears two pairs of tentacular cirri in *Pisionidens*. The neuropodia are well developed; the notopodia comprise short cirri with an internal acicula. Dorsal and ventral cirri are present. Branchiae and epidermal papillae are absent, and lateral organs and dorsal cirrus organs have not been observed. One pair of pygidial cirri is present. The buccal organ is an axial, muscular eversible pharynx with terminal papillae and may bear two pairs of dorso-ventral jaws. A gular membrane is absent, and the gut is straight. The segmental organs are protonephromixia and occur in numerous segments. Ova may be present in up to 40 segments in *Pisone*, but gonads are restricted to a few segments in *Pisionidens*. A circulatory system and heart body are lacking. Aciculae are present. All chaetae are neuropodial and include compound chaetae with distally falcate appendages attached to shafts by single ligaments. Capillary chaetae are present and some other chaetae are spine-like (Fig. 1.85C), but are no thicker than capillaries. *Pisionidens* has aciculae only. This definition is based on that of Fauchald & Rouse (1997).

Confusion exists in the literature as to the correct authority for this family. The authority accepted here is Levinsen 1887, not Southern (1914) as cited by Fauchald (1977), Fauchald & Rouse (1997) and other workers.

The generic subdivision of the Pisionidae has been reviewed by Siewing (1953), Laubier (1967) and Stecher (1968). *Pisionura* (Hartman & Fauchald 1971) does not belong to this family, according to Hartmann-Schröder (1975). Pisionids appear to be members of the Phyllodocida (*sensu* Fauchald 1977); other relationships have been debated, not least because the family includes taxa with very different head structures. The proposed classification of the Polychaeta by Rouse & Fauchald (1997) placed the Pisionidae within the Phyllodocida as a sister-group of the glyceriforms and Paralacydoniidae (Fig. 1.57). The two pairs of dorso-ventral jaws, if present, resemble those of scale-worms (Åkesson 1961; Stecher 1968).

Fauchald (1977) recognised four genera, *Pisionella*, *Pisionidens*, *Anoplopisone* and *Pisone*, and 14 species of pisionids; since then nine additional species have been described, including one from Australia (Hartmann-Schröder & Parker 1990). Fauchald (1977) provided a key, based on Laubier (1967), which separates genera on the presence or absence of a median antennae, the number of cephalic appendages and whether the pharynx has jaws or is unarmed.

In Australia, two named species are known: *Pisone gopalia* (Alikunhi 1941) and *P. tortuosa* (Hartmann-Schröder & Parker 1990), both recorded from shallow waters of the upper Spencer Gulf, South Australia. An undescribed species of *Pisone* occurs in the Sydney region (Australian Museum database; Fig. 1.85), and a few specimens belonging to the family have been collected from Gladstone and Saunders Beach, north of Townsville, Queensland, all in shallow water (Australian Museum database). Additional species have been described from Papua New Guinea by Wilde & Govaere (1995).

Most pisionids are associated with shallow-water sandy areas and have been studied as part of the interstitial fauna for the last 80 years. They are active burrowers found in the soft sediments of intertidal and shallow subtidal zones (Hartmann-

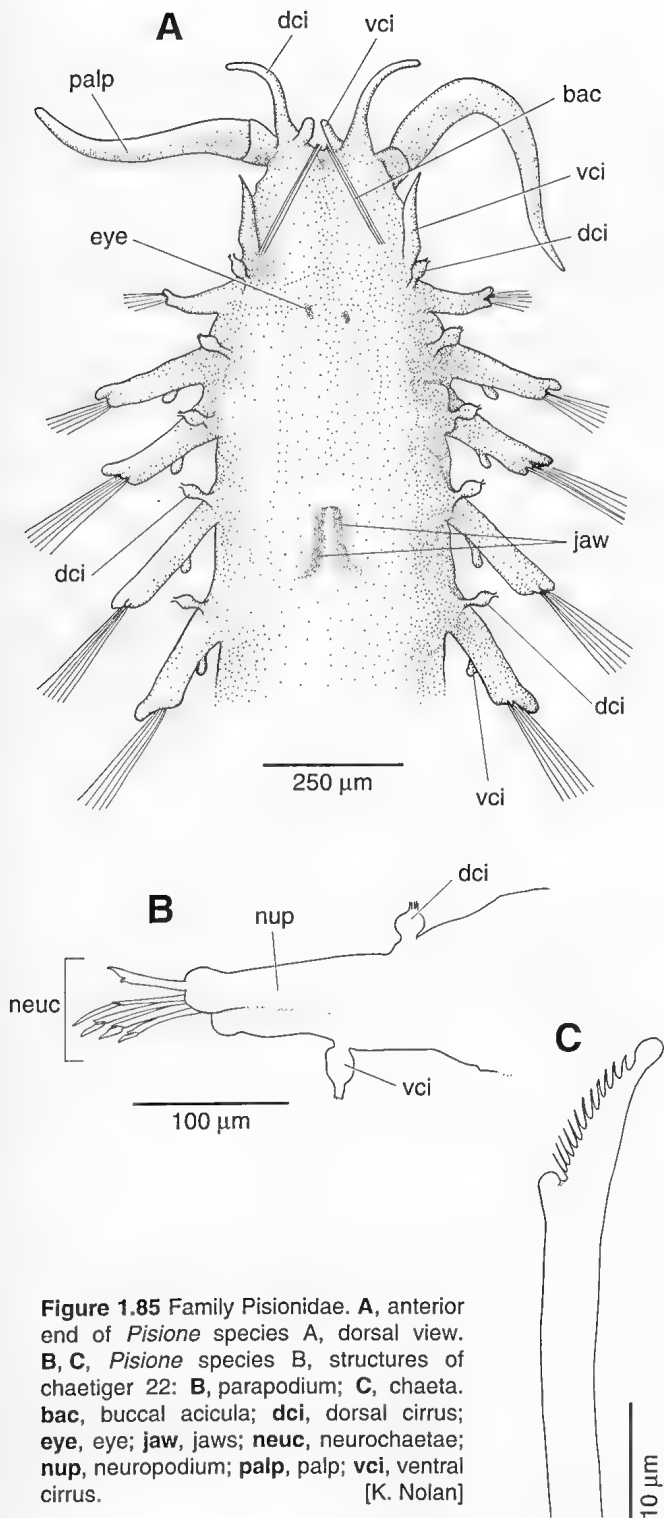


Figure 1.85 Family Pisionidae. **A**, anterior end of *Pisione* species A, dorsal view. **B**, **C**, *Pisione* species B, structures of chaetiger 22: **B**, parapodium; **C**, chaeta. **bac**, buccal acicula; **dci**, dorsal cirrus; **eye**, eye; **jaw**, jaws; **neu**, neurochaetae; **nup**, neuropodium; **palp**, palp; **vci**, ventral cirrus. [K. Nolan]

Schröder & Parker 1990). They have been recorded globally from warm temperate to tropical seas, and are one of the rarer families encountered in benthic studies. This may reflect the relatively few studies of interstitial fauna that have been conducted and/or that they are, in fact, a rare group.

Pisionids are 10–25 mm in length; the cuticle is often relatively thick. Pisionids have either a well-developed prostomium or one which is greatly reduced. If the prostomium is well developed, it has a pair of frontal antennae, a pair of lateral palps and two pairs of subdermal eyes (*Pisionidens*). In pisionids with a reduced prostomium, antennae are either lacking (for example, *Pisione*; Fig. 1.85A) or reduced to a single median one (for example, *Pisionella*);

the palps are fused ventrally to the first chaetigerous segment; in *Pisionidens* the first segment is indistinct and has two pairs of tentacular cirri. A pair of enlarged buccal aciculae are directed forwards in front of the mouth (Fig. 1.85A). The peristomium is reduced to lips around the mouth (Siewing 1953; Stecher 1968). The ventral and dorsal parts of the body wall are covered with cilia and circular pores of glands which are presumed to be sensory (Govaere & de Wilde 1993). The pharynx is eversible and may bear jaws (Hartman 1939; Aiyar & Alikunhi 1940). The parapodia are uniramous, with projecting neuropodia bearing cirri dorsally and ventrally (Fig. 1.85B) as interpreted by Rouse & Fauchald (1997) based on comparisons with *Pisione* and *Pisionella* (Hartman 1939; Stecher 1968), and a chaetigerous lobe with one or two aciculae. In *Pisionidens*, juveniles have compound chaetae and cirri which are lost in adults (Aiyar & Alikunhi 1940). Other genera may have compound (Fig. 1.85C) and simple chaetae. A pair of anal cirri and copulatory organs may be present on the pygidium. The lack of a circulatory system in pisionids (Smith & Ruppert 1988) can be attributed to their small body size.

Aiyar & Alikunhi (1940) described the development of genital funnels from mesodermal tissue in *Pisionidens*. Fauchald & Rouse (1997), however, interpreted these structures as protonephridia. Although nephridia are present along the body, the development of gonads and gonoducts is limited to a few segments.

Australian populations of *Pisione gopalia* include both males and females. Females have one to three ovarian groups, each extending into five to 16 consecutive segments. In addition, one to three pairs of seminal receptacles corresponding to the ovarian groups are present in the segment following each group. The parapodium of the segment containing the seminal receptacle is greatly reduced, with a duct which Hartmann-Schröder & Parker (1990) suggested is a combined nephridium and gonoduct, a view contrary to that of Smith & Ruppert (1988). Males have a pair of sperm sacs, a pair of genital funnels and a pair of copulatory organs. The parapodia of the copulatory organ-bearing segment are greatly modified: each parapodium terminates in a papilla with stiff cuticular projections and a hook-like retractile process where the duct of the sperm sac opens. The position of these copulatory organs varies individually from chaetiger 20 to 22.

Schroeder & Hermans (1975) illustrated schematically the male genital tract and copulatory organ of *Pisione remota*, based on the work of Stecher (1968). There is some disagreement as to the timing of the development of the copulatory organ. Stecher (1968) claimed it develops only with the periodic development of sexual maturity, a view disputed by Hartmann-Schröder (1970). In *Pisione subulata*, male copulatory organs are present in several segments, and the ventral cirrus of each parapodium is elongated and may help in the process of copulation. The copulatory organ of *Pisione crassa* has been described in detail by Yamanishi (1991). The organ arises from the base of the main parapodial lobe and extends laterally as a large paddle-like structure. The structure consists of a spiral structure surrounded by a sheath-like arc and a cuticular membrane. Copulation has not been observed so it is unclear as to the role the copulatory organ plays in reproduction. In some species with reduced parapodia, sucker-like structures, which may help in copulation, appear on the ventral side of both sexes during the reproductive period (Aiyar & Alikunhi 1940). More recently, Yamanishi (1998) reviewed the male copulatory apparatus of 10 species and discussed the evolutionary trends exhibited by these structures.

1. CLASS POLYCHAETA

Spermatogenesis is almost completed in the testis before the sperm pass through the genital funnel, which forms in association with the protonephridium and a heavily ciliated gonoduct, to a muscular, glandular enlargement which functions as a seminal vesicle for sperm storage until mating.

Oogenesis occurs on the germinal epithelium. Some 15 to 20 eggs develop in each segment (Stecher 1968), growing to fill the coelomic cavity completely. The oocytes leave the coelom via the protonephromixium, the opening of which is moderately wide; the separate excretory and genital ducts unite as the funnel base passes through the septum. The ciliated gonoduct thus formed opens on the posterior ventral surface at the base of the parapodium. Immediately before the canal reaches the exterior it is joined to the non-ciliated seminal receptacle, which stores the sperm received during copulation (Schroeder & Hermans 1975).

In individuals of *Pisone remota*, about 600 to 800 oocytes, each about 50 µm in length are produced at one time. Spermatozoa are inserted into the female pores and the fertilised eggs are spawned directly into the sediment where indirect development occurs (Stecher 1968); free-swimming trochophores are produced. These larvae use a mucous net for feeding (Åkesson 1961). The spermatozoa of several species of *Pisone* are immotile and a tail may be present or absent. The spermatozoa are transferred to the seminal receptacles of the female where they may be stored for several months. Within a few days of the spermatozoa being introduced into the receptacles they undergo considerable morphological change. Spermatozoa in the receptacles are smaller than those found in the male coelom and are surrounded by a circlet of cytoplasmic extensions (Alikunhi 1951). This may indicate that spermiogenesis is completed in the female reproductive duct (Schroeder & Hermans 1975).

Family Polynoidae

Polynoids are commonly known as scale-worms because their dorsum is covered by ornamented scales (referred to as elytra; Fig. 1.86A; Pls 3.4–3.6). They have a well-developed head with numerous sensory appendages, few body segments and well-developed parapodia; they are active carnivores.

The prostomium is bilobed or rounded, and the peristomium is reduced to lips around the mouth. Paired lateral antennae are present in most taxa, and a median antenna is present in many taxa. The ventral palps are fused to the first segment and are tapering without articulations. Nuchal organs are present. The longitudinal muscles are grouped into bundles, and segmentation is distinct. The first segment curves around the prostomium, and usually has very small biramous parapodia, with the neuropodia fused to the lower side of the head, and two pairs of tentacular cirri (Fig. 1.86B). The parapodial rami are distinct, and the neuropodia are usually longer than the notopodia in all segments; sometimes the notopodia are very short with few chaetae (Fig. 1.86C). Dorsal cirri and elytra occur on alternate segments, at least anteriorly; the posterior end may or may not be covered by elytra. Ventral cirri are present. Branchiae are absent (see below) as are epidermal papillae. A pair of pygidial cirri is present. Lateral organs and dorsal cirrus organs have not been observed. The buccal organ is an axial, muscular eversible pharynx with terminal papillae and two pairs of dorso-ventral jaws. A gular membrane is absent, and the gut has segmentally arranged side-branches (caeca). Mixonephridia, are present in many segments (Darboux 1899; Goodrich 1945). The circulatory system is closed and a heart body is

absent. Aciculae are present. Chaetae occur as variously ornamented capillaries and spines (Fig. 1.86D–F). This definition is based on that given by Fauchald & Rouse (1997).

The first polynoids were described by Müller in 1776 as species belonging to the genus *Aphrodita*. The genera *Polynoe*, *Harmothoe* and *Lepidonotus* were known by 1830 (Audouin & Milne Edwards 1834). All scale-worms (a common name for any worms bearing dorsal scales or elytra so this includes polynoids as well as the other scaled families) were originally included in the family Aphroditidae. Over the years, one apparently uniform group after another has been segregated into its own family (or subfamily), whereas the remnant taxa were retained in the Polynoidae. The recognition of Acoetidae, Aphroditidae and Eulepethidae has left the Polynoidae without a unique feature uniting the whole family. A major revision of the scale-worms is clearly needed.

Fauchald (1977) recognised four subfamilies in the Polynoidae and these have been widely accepted. Since then several additional subfamilies have been recognised, primarily by Pettibone (1976a, 1989b, 1996) and also by Hanley (1989), but these have not been widely used. Hanley (1989) does, however, provide a list of the 19 subfamilies and their authorities which have been proposed over a number of years. A thorough revision of all the subfamilies is needed and with it the types of characters that are useful at this level, as currently the designation of subfamilies appears to have been on a fairly ad hoc basis; Fauchald (personal communication) is currently undertaking a major revision of the family.

Pettibone, in 1982, recorded a worldwide polynoid fauna of about 120 genera and 600 species. Since then at least another 45 genera and 148 species have been described. With a total of 165 genera and 748 species the Polynoidae is one of the most speciose and, generically, rich polychaete families. Polynoids occur worldwide and are regularly collected in benthic samples. An identification guide to the polynoids present in Scottish waters, many of which occur throughout northern Europe, is given by Tebble & Chambers (1982) together with keys.

In Australia, Day & Hutchings (1979) recognised 22 genera and 57 species. Since then a new subfamily and six new genera have been described (Hanley 1989, 1991, 1993; Hanley & Burke 1989, 1990, 1991a, 1991b) as well as additional new species by Hutchings & Rainer (1979) and Hutchings & Murray (1984). Examination of the unpublished database of the Australian Museum has revealed that an additional 24 species have been catalogued, suggesting that a large part of the polynoid fauna remains to be documented. Some of the names listed by Day & Hutchings (1979) appear to be in the wrong genus, so a major revision of the well-represented Australian polynoid fauna is urgently needed.

Polynoids are found worldwide from the tropics to the Antarctic (Hartman 1978) and the Arctic (Britaev *et al.* 1986). They occur from the intertidal zone (Hanley & Burke 1990) to deep water (Levenstein 1981, 1984; Pettibone 1989c) and may be common on both soft sediments and hard substrata. One species, *Antinoella sarsi*, may be partially pelagic swimming rapidly using its long parapodia (Pettibone 1963).

Species occur in a wide variety of habitats, including seagrass beds and areas of reduced salinity (Hutchings & Murray 1984), coral reefs (Hanley 1993) and ocean vents (Pettibone 1985a, 1985b, 1988, 1989c; Miura & Hashimoto 1991). They typically live amongst algae, under stones or in crevices or in burrows of other animals. Fauchald & Jumars (1979) suggested that they are less common in deeper water, but they have been reported from abyssal and hadal depths (Hartman

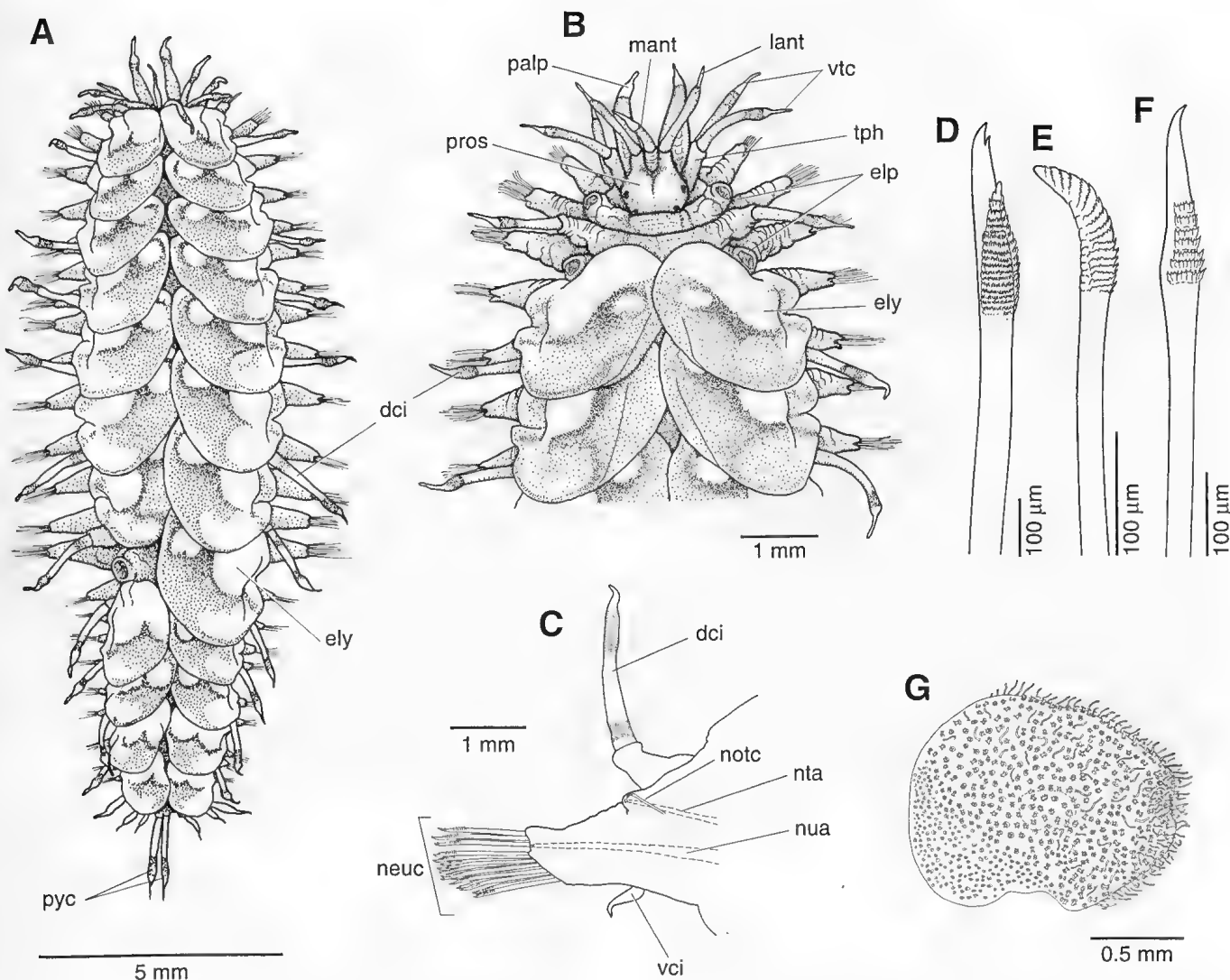


Figure 1.86 Family Polynoidae. **A–E**, *Lepidonotus melanogrammus*: **A**, entire animal, dorsal view; **B**, anterior end, dorsal view, first and second elytral pairs removed; **C**, anterior view parapodium from chaetiger 11; **D**, bidentate neurochaeta from parapodium of chaetiger 11; **E**, notochaeta from parapodium of chaetiger 11. **F**, unidentate neurochaeta from parapodium of chaetiger 13, *Gastrolepidia clavigera*. **G**, elytron from middle parapodium of *Harmothoe charlottae*. **dci**, dorsal cirrus; **elp**, elytophores; **ely**, elytron; **lant**, lateral antenna; **mant**, median antenna; **neuc**, neurochaetae; **notc**, notochaeta; **nta**, notoacacula; **nua**, neuroacacula; **palp**, palp; **pros**, prostomium; **pyc**, pygidial cirri; **tci**, tentacular cirri; **tph**, tentaculophore; **vci**, ventral cirrus. [A. Murray]

1971). Species have been found associated with experimental wood panels and in caves in the deep ocean (Pettibone 1985c). A large number of species have been recorded as living commensally with a wide range of invertebrates. They have been recorded in association with asteroids (Pettibone 1969b; Hartmann-Schröder 1981b; Ruff 1991), ophiuroids (Pettibone 1993), crinoids (Hanley 1984), holothurians, (Britayev & Zamiahlyak 1994), sponges (Pettibone 1993; Martin *et al.* 1992), corals (Hartmann-Schröder 1985b), antipatharians and gorgonians (Pettibone 1991a, 1991b), deep-sea mussels (Pettibone 1984, 1986b) and keyhole limpets (Gerber & Stout 1968). Polynoids are also commonly found living in tubes of other polychaetes, especially terebellids (P. Hutchings personal observation). Some species show morphological adaptations to a commensal lifestyle. For example, in *Gastrolepidia clavigera*, which lives on holothurians, serially arranged scute-like processes are developed laterally on the ventral side of each segment. These processes increase the surface area in contact with the host, making them difficult to dislodge from their hosts (Gibbs 1969). Members of some genera, for example, *Asterophilia*

and *Capitulatinoe*, are all commensal, whereas in other genera, for example, *Lepidasthenia* and *Scalissetosus*, only some species are commensal. Hanley (1989) suggested that most members of the subfamily Arctonoinae were commensal, predominantly with echinoderms. Hartman (personal communication cited in Fauchald & Jumars 1979) espoused a theory that any polynoid species with little or no elytral ornamentation would be found to be commensal, and to date this appears to be valid.

Polynoids that live on echinoderms (Fig. 1.34) are typically found in the feeding grooves of the arms or, on holothurians, firmly attached to the undersurface. Presumably the host provides some protection and perhaps food scraps. Polynoids are found in the branchial chambers of bivalve molluscs; they are thought to utilise some of the food of the host. Some species appear to be host-specific and often only a single individual is present on the host. This raises questions about how these individuals find their host and how they successfully breed, as many scale-worms actually pair just before spawning. These interesting ecological questions, however, remain unanswered. Certainly, on the Great Barrier

1. CLASS POLYCHAETA

Reef several species of holothurians have commensal polynoids, but not every individual has a commensal. Presumably recruitment to the holothurian occurs at the time of settlement of the polynoid; it seems unlikely that adult worms would be able to change their host since the holothurians tend to live as isolated individuals on the reef and adjacent sediment.

Gibbs (1969) summarised the data on polychaetes found living in association with echinoderms in the Solomon Islands. Polynoids, are found on several species of echinoderms and are not specific as previously thought. In a few cases, the same species was found on three groups of echinoderms, for example, *Hololepidella minuta* occurred on a crinoid, asteroid and an ophiuroid.

Polynoids range in body shape from oval to long and slender. Some species, for example, *Eulagisca gigantea* from the Antarctic, may reach 190 mm in length and 100 mm in width, with 40 segments; however, most polynoids are much smaller. The prostomium is oval and slightly bilobed with the anterior borders rounded, projecting as anterior peaks (as in *Harmothoe*) or extending anteriorly to form ceratophores for the lateral antennae (as in *Lepidonotus*; Fig. 1.86A, B). One to three antennae (often referred to as medial and lateral antennae) and a pair of ventral palps are present. Two pairs of eyes are present or eyes are absent. The first segment has tentaculophores inserted laterally to the prostomium, and parapodia each with a single acicula; notochaetae are present or absent, and a pair of ventral and dorsal tentacular cirri are present. In some genera, for example, *Alentia* and *Eulagisca*, the posterior part of the prostomium is covered by a nuchal fold. The eversible pharynx is large, cylindrical and muscular with a pair of strong recurved jaws and a circlet of marginal papillae.

The paired elytra are attached to prominent elytraphores arising from the notopodia of segments 2, 4, 5 and 7 and then on alternate segments on the anterior part of the body, with variable distributions posteriorly. The number of pairs of elytra is constant within a genus and varies from relatively few (7–21) to very numerous. Even though they are easily detached, the number of pairs can be ascertained by counting the number of elytraphores present (Fig. 1.86B). Elytra may be minute, as in *Hermenia*, or large and overlapping, and they may cover the entire dorsum (Fig. 1.86A) or leave the mid-dorsum and posterior end uncovered. Elytra may be smooth, or covered with micro- or macrotubercles, and the margins may be fringed or smooth. In some species, the elytra may be heavily encrusted with sand grains and other inorganic material. Dorsal cirri with basal cirrophores and distal styles are found on the non-elytra-bearing segments. In some genera dorsal tubercles are present on these segments in the position corresponding to the elytraphores. They may be inflated and bulbous, transversely elongated and form pseudo-elytra (as in *Euphionella*) or distally bifurcated (as in *Acholoe*). Elytra may be distinctively pigmented and in *Acholoe* they are luminescent. Branchiae are usually absent, although digitiform 'branchial' filaments may be present on the anterior and posterior edges of the parapodia (as in *Chaetacanthus*).

Parapodia are biramous and supported by aciculae; the notopodia and neuropodia may be equally developed, but more typically the notopodia are smaller with few (Fig. 1.86C) or no notochaetae present. All polynoid chaetae are simple, but vary greatly in number, size and ornamentation (Fig. 1.86D–F). Notochaetae may form large radiating bundles and the neurochaetae may be short or greatly elongated. Ventral cirri are short and tapered and a pair of anal cirri is present (Pettibone 1982).

Characters used to separate genera are the number of pairs of elytra, and their coverage of the dorsum, the point of insertion of the lateral antennae, the relative thickness of the notochaetae compared with the neurochaetae and chaetal ornamentation. For separating species the ornamentation of the chaetae (Fig. 1.86D, F) and the elytra (Fig. 1.86G) are often used. However, the constancy of these characters with increasing size (and presumable age) and the variations occurring along the body have rarely been documented. Many species, even recently described ones, are based on single or few specimens; the variability within a species needs to be better documented. As fresh material is often highly pigmented, the potential of such pigment patterns as taxonomic characters needs to be investigated. For example, many of the common intertidal polynoid species on the New South Wales coast appear to have characteristic elytral and body pigmentation patterns which facilitates rapid identification in the field and from photographs.

The type of chaetae present may be a reflection of the surrounding sea water temperature. Thus it is possible that a species occurring over a wide temperature range may have been described as two species if based solely on their chaetal morphology. For example, Hillger & Reish (1970) amputated parapodia from two polynoid species, *Halosydna brevisetosa* and *H. johnsoni*, and found that bifid chaetae developed in warm temperatures and unidentate chaetae in colder waters. It is this character that is used to separate these two species, and they concluded that *H. johnsoni* is a synonym of *H. brevisetosa*. The importance of this feature within the polynoids is unknown, but perhaps should be considered when two morphologically similar species occur along a temperature gradient.

Elytra can be moved by muscle and tendon cells and they are also richly supplied with a variety of receptor cells (Anton-Erxleben 1981). A detailed study of the elytra of *Iphione muricata* has been undertaken by Storch & Alberti (1995). They found that elytra are flat, pocket extensions of the distal integument of the dorsal cirri. The elytra have a reticulate pattern of polygonal areas and each polygon area is composed of small chambers. Transmission electron microscopy revealed that each polygonal area is lined with a type of cuticle that is widespread in polychaetes. The cuticle is composed of unbanded collagen fibrils which are irregularly arranged and embedded in an electron-lucent matrix. Apically, there is a thin epicuticle of low electron-density which lines the small chambers. The ventral cuticle differs and contains collagen fibrils arranged in criss-crossing layers which are embedded in a matrix that extends beyond the fibre zone to form the epicuticle. When polynoids lose their elytra the elytraphore remains as a stump which is rapidly closed by musculature in the wound healing process. Elytral dehiscence occurs across a distinct line in *Iphione*, and only during strong mechanical stimuli. Regeneration of the elytra then occurs. Uschakov (1973) reported finding very small elytra attached to elytraphores laterally and suggested that these are the regenerating elytra.

Polynoids are considered to be carnivores (Fauchald & Jumars 1979; Pettibone 1982), feeding on small crustaceans, echinoderms, polychaetes, gastropods, sponges and hydroids (Darboux 1899; Blegvad 1914; Korringa 1951; Meunier 1930; Hartmann-Schröder 1971; Rasmussen 1973). A large percentage of algal fragments have been found in the guts of *Harmothoe imbricata* and *Lepidonotus squamatus* (Rauschenplat 1901). Schäfer (1972) found that algal remnants made up 18.2% by weight and occurred in 83% of the animals. In contrast, the most common prey, amphipods, made up 65.6% by weight and occurred in 87% of the

specimens. Algal fragments occurred in the gut almost as frequently as the most important food item and may be of major nutritional importance to the animal, although perhaps they are just accidentally ingested [see Fauchald & Jumars (1979) who quote from Streltsov (1966)]. In order to resolve this matter, studies need to be carried out to investigate if these polynoids have enzymes capable of breaking down algal cell walls.

The gut contents of some of the commensal species have been investigated. *Halosydna brevisetosa* feeds on the faecal matter of its host, the nudibranch *Melibe leonina* (Ajeska & Nybakken 1976). This species is also known to live freely in mussel beds and has also been reported as living commensally with terebellids (Blake 1975a).

The semi-pelagic polynoid *Antinoella sarsi* may be a detritus-feeder according to Hartmann-Schröder (1971). However, based upon its gut contents, Meunier (1930) and Sarvala (1971) both suggested that it is a carnivore.

Juvenile polynoids become carnivores immediately upon metamorphosis (Dean & Blake 1966; Cazaux 1968; Rasmussen 1973) independent of the length of the preceding larval life. Species with planktotrophic larvae feed on various sorts of phytoplankton (Cazaux 1968).

The method of food capture has been studied in the laboratory for *Harmothoe imbricata* by Daly (1973b). This species uses its palps to detect vibration from the prey before attacking it. The worms were fed amphipods and polychaetes, and although they explore vibrating non-food particles, they did not attack.

The commensal species of polynoid may be classified into four feeding categories (MacGinitie & MacGinitie 1968). They may feed on the food of the host. In cases where the host is a carnivore this represents a simple extension of the normal feeding habits for the family. Alternatively, they may feed basically as an ectoparasite on the host, or they may feed on the faecal matter of the host as described by Ajeska & Nybakken (1976). Finally, they may feed on the food or pseudofaeces of a selective deposit-feeding host.

Fauchald & Jumars (1979) noted that, of the 550 polynoid species known at the time, information on feeding biology was only available for 14 species, and this information was of variable reliability.

Dales (1962a) figured an everted pharynx of *Eunoe oerstedii*, which is similar in structure to that of all scale-worms. Extrusion is achieved in this species by increased pressure of the coelomic fluid. Polynoids, like some of the other scale-worms, have guts with numerous paired caeca arising along most of their length (Darboux 1899). The fine structure of the midgut and caecal epithelia has been studied in *Harmothoe imbricata* and *Lepidonotus squamatus* by Zavarin & Punin (1981) and Punin (1981) respectively. The midgut epithelium consists of columnar cells with long apical cilia and short microvilli. By following the incorporation of labelled tritiated thymidine, they showed that young cells are mainly found between folds and old cells with degenerating nuclei are present in the folds. The main part of each caecum is lined with a thin, compact epithelium, which has a short brush border; this is illustrated diagrammatically by Michel (1988). Serous gland cells, which probably secrete proteolytic enzymes, are present (Sellier 1910). The vacuolated cells that are present may be absorptive or excretory, perhaps producing the brown haemic substance found by Dales & Pell (1971). Basal cells, possibly endocrine secreters, were found in the midgut and caecal epithelia by Zavarin *et al.* (1984).

Polynoids have a closed circulatory system and a heart body is absent (Darboux 1899; Hanson 1949a). Blood pigments are lacking and according to Grassé (1959) the blood circulation system is reduced.

The epidermal extensions which may be present on the elytophores and on the body wall under the elytra have been assumed to have a respiratory function, but they do not correspond to branchiae as defined by Rouse & Fauchald (1997). Ciliary tracts on the parapodial lobes (Segrove 1938) and the dorsal body surface create a lateral flow of water between the parapodia and this moves backwards dorso-laterally between each row of elytra. Although the elytra are not ciliated and perform no pumping or fanning action, their shape does direct the flow posteriorly (Lwebuga-Mukasa 1970). Polynoids often retreat into sheltered places during the day, often wedging themselves into crevices. In these situations the elytra are used to direct water. The ciliary currents not only bring a fresh flow of water to the body surfaces, but also carry away fine particulate material which otherwise might accumulate around the body.

Polynoids, although present in Australian estuaries, are typically found in fully saline areas. None are found in regularly fluctuating salinities, suggesting that their osmoregulatory abilities are limited.

Daly (1973a) documented the development of the nephridia of *Harmothoe imbricata* during maturation of the gametes. Only the nephridia in the segments containing gametes change during this period. Basically the walls of the nephridia are progressively elaborated during gamete maturation. The folds that develop in the nephridial walls allow for expansion of the nephridia by gametes accumulating as individuals mature. The extent of the swelling is more marked in females than males where, nephridia filled with oocytes occupy almost the entire coelom. After the breeding season the nephridia of both sexes return to a near-juvenile state, although a few folds in the walls may remain. Nephridia in segments outside the fertile region of the body remain as simple thin-walled tubes throughout the life of the worm. Gametes are spawned via the nephridia of the adjacent posterior segment to that in which they developed. Each nephridium opens to the outside on the tip of a papilla on the posterior, ventro-lateral margin of the segment. During maturation of females these papillae elongate and become directed dorsally between the parapodia. In males, the papillae also become elongated, but are directed ventro-laterally. After the breeding season the papillae of both males and females regress to a near-juvenile state. Just before spawning a sphincter muscle develops just below the tip of the papillae, which probably regulates the release of gametes.

The eyes of *Arctonoe vittata*, which lives between the mantle and the foot of the keyhole limpet, *Diodora aspera*, have been investigated (Singla 1975). This species has two pairs of cup-shaped eyes, with a cornea consisting of a thick epithelium covered by a cuticle. The pupil of the anterior and posterior pairs of eyes open at different angles suggesting that the worm may have a wide field of view. The centre of the cup is filled with a crystalline lens and the cup is lined with two types of cells, photoreceptor cells and pigment supporting cells, both containing dark brown pigment. The photoreceptors are rhabdomeric and are illustrated by Singla (1975). Singla (1975) suggested that the crystalline spherical lens should enable *Arctonoe vittata* to form some sort of image in addition to gathering light. As the lens changes shape it is accompanied by a change in the size of the pupil under different light conditions, suggesting that the eyes are functional photoreceptors and may play a role in host

selection. The eyes of *Lepidonotus* have been studied by Gotow (1976). He recorded electrical responses to light on the prostomial surface and believed that they were derived from the eyes.

The morphology of the brain of two species of *Harmothoe* have been studied by Åkesson (1963) and both are very similar. The brain is bilobed, with the proximal part of the median antenna ceratophore fused to the anterior parts of the brain. The innervation of the palps and the origin of the main nerves is shown diagrammatically by Åkesson (1963). A similar brain structure is also present in *Lepidonotus* except for the innervation associated with the lateral tentacles which form a direct anterior continuation of the frontal peaks.

The antennae, palps, tentacular and parapodial cirri and pharynx are covered in sensory cells. In *Harmothoe*, the dorsal cirrus bears 1000–1200 sensory cells and the ventral cirrus has 500–800 sensory cells (Horridge 1963). Those of *Lepidonotus* are figured by Storch & Schlötzer-Schrehardt (1988).

Polynoids have separate sexes. Few detailed studies on polynoid breeding biology are available. Wilson (1991) reported studies of 11 species belonging to the genera *Acholoe*, *Halosydna*, *Harmothoe*, *Lagisca* and *Lepidonotus* and Daly (1972) studied the reproductive biology of *Harmothoe imbricata*, a common intertidal species from Northern Europe and northern California. Most of these species exhibit free-spawning and planktotrophic larvae (Cazaux 1968; Blake 1975a; Reish 1980; Bhaud & Cazaux

1987). The only species exhibiting a different strategy is *Harmothoe imbricata* which broods its young on the exterior of its body (under the elytra) and releases planktotrophic larvae (Daly 1972; Blake 1975a). *Harmothoe imbricata* breeds in March and April and maturation of oocytes begins the preceding September. In Northern Europe, settlement of larvae occurs in April and May and the animals first breed the following year, survive spawning and continue to spawn during the following subsequent years. Each female spawns twice during the breeding season. In contrast, males contain sperm throughout the breeding season and shed only a small proportion of gametes at each spawning. In females, the whole of vitellogenesis occurs while the oocytes are still attached to the segmental blood vessels. Additional details of oogenesis are given by Garwood (1981). Vitellogenesis is temperature-regulated and the first stage of vitellogenesis will not occur at temperatures above 15°C (Garwood & Olive 1978). Gametes develop in segments 12 to 22 in males and from segment 8 to the pygidium in females.

A mature sperm of *Harmothoe imbricata* has a head which is 28 µm long with an elongated nucleus and a long conical acrosome. This differs from sperm found in some other species of *Harmothoe* which resemble the primitive polychaete type with an ovoid head which have described by Franzén (1956). Rouse (1988) described the sperm of *Lepidonotus* as 'aquasperm'.

Harmothoe imbricata is normally solitary, but during the breeding season pairs of worms are found in crevices along the shore. Each pair consists of a mature male and female with

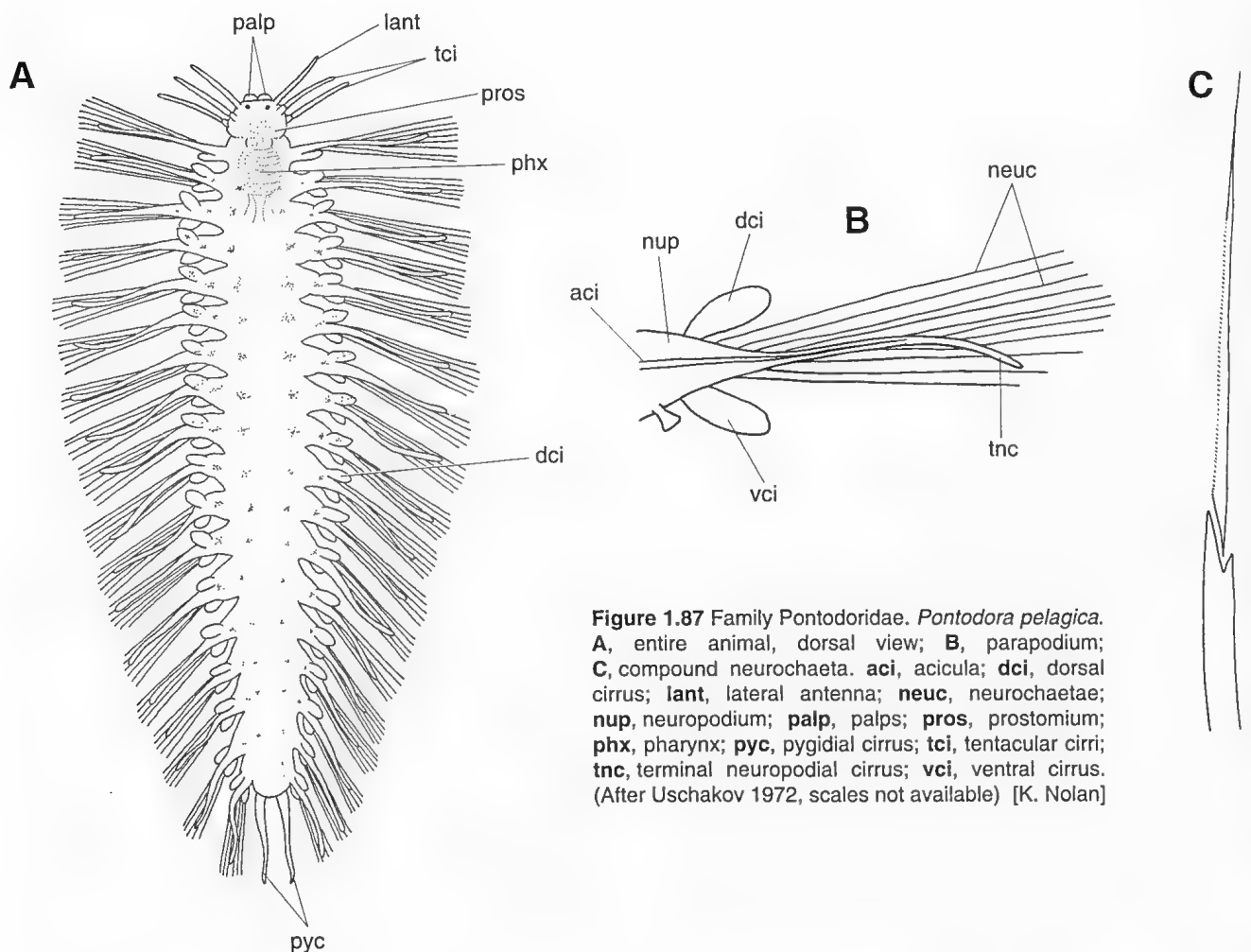


Figure 1.87 Family Pontodoridae. *Pontodora pelagica*. **A**, entire animal, dorsal view; **B**, parapodium; **C**, compound neurochaeta. **aci**, acicula; **dci**, dorsal cirrus; **lant**, lateral antenna; **neuc**, neurochaetae; **nup**, neuropodium; **palp**, palps; **pros**, prostomium; **phx**, pharynx; **pyc**, pygidial cirrus; **tci**, tentacular cirri; **tnc**, terminal neuropodial cirrus; **vci**, ventral cirrus. (After Uschakov 1972, scales not available) [K. Nolan]

the male resting on the dorsal surface of the female. As the eggs are spawned they are directed into the space between the dorsal body surface and the elytra. Males appear to be stimulated to spawn by the presence of spawned oocytes and it seems likely that the sperm are carried in under the elytra by the ciliary tracts on the dorsum and the ventro-lateral orientation of the nephridial papillae also directs the sperm under the elytra. The embryos develop under the female parents elytra for about 16 days. Daly (1973a) provided a timetable of the development. After 6 days short cilia are visible in the apical tuft region and within 10–15 days the prototroch, gut and mouth region develops. By day 16, the swimming larvae are released into the water column where they begin to feed. Cazaux (1968) working on the same species, but in warmer waters, stated that the embryos take only 12 days to develop. A detailed study of the arrangement of the cilia on the trochophore stage has been undertaken by Holborow *et al.* (1969).

Reproduction in *Harmothoe imbricata* appears to be controlled by temperature and day-length. Olive (1984) suggested that this mechanism synchronises development of the gametes. They are normally antagonistic to each other. Immature males that attempt to mount immature females are repulsed and attacked by the female and two females kept together will fight. However, there is a change in behaviour as the females approach maturity (Daly 1973a). As the female matures her level of aggression to the male falls and once she is gravid she will allow the male to mount. Daly (1973a) suggested that the critical turning point in the behaviour of the female may be the release of the oocytes from the external walls of the blood vessel into the coelom which occurs 2–3 days before spawning. Gland cells in the ventral cirri of mature males contain an opaque white secretion which is not present in mature females. This secretion may be involved in the reproductive process as mature males with ventral cirri removed can pair normally, but were unable to fertilise the eggs. No other morphological changes were observed in *Harmothoe* other than the changes in the structure of the nephridia.

Daly (1973a) in his study of the reproduction of *Harmothoe imbricata* noted that many individuals at any one time were regenerating posterior segments suggesting that posterior segments were easily lost, perhaps due to predation and aggression between individuals outside of the breeding season.

Spacing between individuals of *Harmothoe imbricata* has been investigated by Daly (1972). Males tend to occur closer together than females. Encounters between immature worms normally lead to separation, with one worm moving away rapidly from the other, but fighting sometimes occurs. Females show more marked avoidance behaviour than males. Also when a male has mounted a mature female, he will attack intruding males, but not females. Encounters require tactile contact before an action is taken. Similarly, the commensal *Acholoe astericola* shows no response to its asteroid host *Astropecten irregularis* until tactile contact is made (Davenport 1953a, 1953b). In contrast, chemo-reception has been demonstrated for several other commensal polynoids (Davenport 1966; Gerber & Stout 1968).

Ectoparasitic copepods have been recorded on the prostomium and anterior segments of three Antarctic polynoids by Gravier (1912) who also summarises earlier records.

Family Pontodoridae

The Pontodoridae is a monotypic family of small transparent pelagic polychaetes.

The prostomium bears a pair of long antero-lateral antennae and a pair of long tapering ventral palps. Nuchal organs are present. A short muscular eversible barrel-shaped pharynx is present; the surface of the everted pharynx is covered with scattered oblong papillae and terminal papillae. Jaws are absent. The first segment is indistinct, and bears two pairs of long tentacular cirri. The neuropodial lobes of the parapodia are elongate (Fig. 1.87B). Notopodia are represented only by a digitiform dorsal cirri (present from chaetiger 2). Neurochaetae are compound (Fig. 1.87C). Aciculae and one pair of very long pygidial cirri are present. This description follows that of Uschakov (1972) and Fauchald & Rouse (1997). The best description of the only species in the family, *Pontodora pelagica*, is given by Uschakov (1972). Animals are small, usually reaching 2–5 mm with 17 to 18 segments.

The Pontodoridae were treated as a subfamily of the Phyllodocidae by Uschakov (1972), but were given familial status by Fauchald (1977) and Fauchald & Rouse (1997). They are distinguished from phyllodocids by the presence of terminal neuropodial cirri (Fig. 1.87B). *Pontodora pelagica* has not been recorded from Australia, but the lack of systematic study of Australian plankton and the wide distribution of this species elsewhere suggests that it probably will be found in Australian waters. *Pontodora pelagica* is recorded from the north-west, tropical and south-east Pacific Ocean, the tropical Atlantic Ocean, and the Indian Ocean (Uschakov 1972; Day 1975; Shen 1978; Fernandez-Alamo 1993). Nothing is known of the biology of this species, which could easily be overlooked in plankton samples due to its small size and transparent body.

Family Sigalionidae

Sigalionids are also referred to as scale-worms. However, they have much longer bodies than polynoids. The dorsum of sigalionids is covered to a varying extent by elytra; in some species the elytra are covered in sand grains. They have a well-developed head with many appendages, numerous segments and well-developed parapodia and chaetae.

The prostomium is anteriorly blunt or rounded, and the peristomium reduced to lips around the mouth. Paired lateral and a median antennae are present in most taxa (Fig. 1.88B); the latter may be absent (Mackie & Chambers 1990). Although the lateral antenna originates on the prostomium it may be fused to the parapodia of the first segment. The palps are ventral and tapering, and are without articulations; they are fused basally to the parapodia of the first segment. Nuchal organs are present. Longitudinal muscles are grouped in bundles, and segmentation is distinct. The first segment curves around the head; and is fused basally to the prostomium. Parapodia and two pairs of tentacular cirri are present on the first segment. Parapodia are biramous and the neuropodia are longer than the notopodia (Fig. 1.88D). Dorsal and ventral cirri are present. At the anterior end, dorsal cirri alternate with elytra. Some taxa have tapering dorsal cirri on segment 3, whereas others have neither elytra or dorsal cirri on segment 3. Elytra are present on every segment of the posterior end. True branchiae are absent (but see below). The ventral surface may be smooth or papillated. One pair of pygidial cirri is present. Lateral organs and dorsal cirrus organs have not been observed. The buccal organ is an axial muscular eversible pharynx; terminal papillae and two pairs

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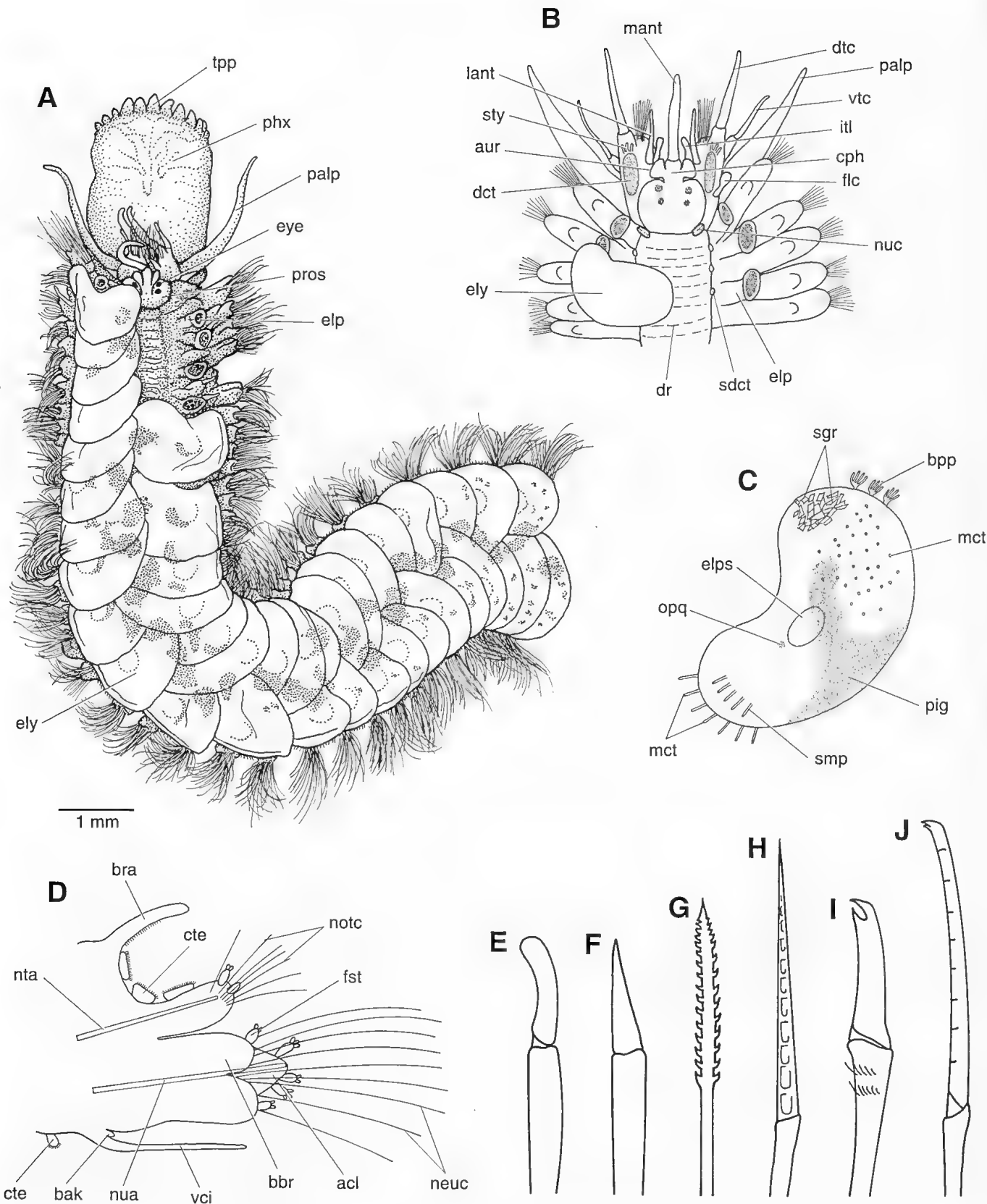


Figure 1.88 Family Sigalionidae. **A**, *Fimbriosthenelais* species, anterior end, dorsal view with pharynx everted; some elytra and parapodia 2 and 7 are removed. **B–J**, diagrammatic figures of a generalised sigalionid: **B**, anterior end, dorsal view. **C**, elytron. **D**, parapodium. **E–J**, types of neurochaetae: **E**, compound chaeta with blunt-tipped blade; **F**, compound chaeta with conical-tipped blade; **G**, bipinnate spine; **H**, canaliculate spiniger; **I**, compound falciger with no articles on blade; **J**, compound falciger with articulated blade. **acf**, acicular lobe; **aur**, auricle; **bak**, basal knob; **bbr**, bilobed bract; **bra**, branchia; **bpp**, branched papilla; **cph**, ceratophore; **cte**, ctenidium; **dcl**, dorsal ctenidium (segment I); **dr**, dorsal ridges on segments II–IV; **dte**, dorsal tentacular cirrus; **elp**, elytron; **elps**, elytron attachment scar; **ely**, elytron; **eye**, eye; **flc**, flap-like modified ctenidium; **fst**, fimbriated stylus; **itl**, inner tentacular lobe; **lant**, lateral antenna; **mant**, median antenna; **mct**, microtubule; **neu**, neurochaetae; **notc**, notochaetae; **nta**, notoacacula; **nua**, neuroacacula; **nuc**, nuchal organ; **opq**, opaque spot; **palp**, palp; **phx**, pharynx, everted; **pig**, pigment; **sdct**, small dorsal ctenidium; **sgr**, sand grains; **smp**, submarginal papilla; **tpp**, terminal papilla; **vci**, ventral cirrus; **vtc**, ventral tentacular cirrus. (After Hutchings & McRae in press) [A. Murray]

of dorso-ventrally oriented jaws are present. The gular membrane is absent, and the gut has segmentally arranged side branches (caeca). Mixonephridia are present in most segments. The circulatory system is closed and lacks a heart body (Darboux 1899). Aciculae are present. The parapodia bear compound chaetae which taper to fine tips or are distally dentate or falcate. The chaetal shafts and appendages are joined by a single ligament. Other chaetae are variously ornamented capillaries. In many taxa, slender, digitiform extensions from the body wall project under the elytra; these presumably have a respiratory function. This definition is based on that of Fauchald & Rouse (1997).

The first sigalionids were described by Audouin & Milne Edwards (1832). Sigalionidae and Pholoidae are the only two families of scale-worms with compound chaetae. Sigalionids have been recognised as a distinct group of scale-worms since they were first described; the family was reviewed in part by Pettibone (1969c, 1970b, 1970c, 1970d, 1971, 1992b, 1997). More recently, Mackie & Chambers (1990) have re-examined the type material of several of the major genera and have synonymised *Thalenessa* and *Eusigalion* with *Sigalion*. Hutchings & McRae (in press) have revised some genera of the Australian sigalionid fauna. Chambers (1985) reviewed the species found in Scottish waters.

Currently, the family is not divided into subfamilies, although Chamberlin (1919) divided the family into two subfamilies. One of these, Eulepethinae, was elevated to a family by Pettibone (1969a). Later Pettibone (1997) used the subfamily name Pelögeniinae and credited this to Chamberlin 1919 and referred species of *Psammolyce* and *Pelogenia* to it. However, Chamberlin (1919) did not use the name Pelogeniinae, and thus the subfamily should be credited to Pettibone (1997).

Keys to the genera are provided by Fauchald (1977) and Hutchings & McRae (in press). Many genera are poorly known, and a comprehensive review of all the genera is urgently needed.

Fauchald (1977) recorded 16 genera and 156 species, although *Pholoe* containing 10 species is now regarded as belonging to the family Pholoidae. Pettibone (1982) indicated that 20 genera with 160 species are known, and since then another 8 genera and 16 species have been described. Hutchings & McRae (in press) following Mackie & Chambers (1990) have accepted 18 genera as valid. Thus, currently about 18 genera are recognised and about 180 species described worldwide.

In Australia, the family Sigalionidae is represented by at least 20 species in 10 genera, of which 13 are new species (Hutchings & McRae in press). Of these genera, seven have not been described from Australia prior to the work of Hutchings & McRae. Additional species of the genera *Psammolyce*, *Sigalion* and *Sthenelais* also occur in Australian waters, but these remain to be described. As most sigalionids are relatively long worms with a large number of segments, they tend to fragment during collection. As the type and distribution of chaetae along the body is one of the main diagnostic features, complete individuals are required for identification; also it appears that characters may change with size and presumably age. Also a full complement of elytra are required as these may change in shape along the body.

Sigalionids occur worldwide and are common in benthic samples, although they are rarely present in large numbers. They occur from the intertidal zone to deep water and also occur in estuarine habitats (Hutchings & Murray 1984). Typically they are found on soft sediments or associated with seagrass beds in shallower water. Fauchald & Jumars (1979)

suggested that they are most abundant at continental shelf depth. Sigalionids have been recorded from the eastern Pacific seamounts at depths ranging from 788–3353 m by Levin *et al.* (1991), although not in large numbers. A few genera are represented by small, interstitial species.

Most sigalionids burrow rapidly in mud and sand. Day (1967) reported that *Thalenessa oculata* has an unusual method of burrowing. Instead of digging in head first, it lies flat on the sand and by rotation of its parapodia scoops out the sand below until its body is covered. This species lives in the shallow subtidal and intertidal areas where wave action may uncover it, so presumably this method of burrowing is an adaptation to this. A few groups such as *Sthenelanelle* are tubiculous. Tubes are long, tough and fibrous and are composed of threads produced by notopodial spinning glands.

Most sigalionids are long and narrow, tapering posteriorly and quadrangular in cross-section, with numerous segments (300+). The elytra may completely or partially cover the dorsum (Fig. 1.88A). In *Psammolyce*, the dorsum and the elytra are encrusted with sand grains. The ventral surface may be smooth or papillated. The oval to rectangular prostomium is fused anteriorly and laterally to the first segment, and has a pair of long tapering ventral tentacular cirri (Fig. 1.88B). Three antennae are usually present. The median antenna may or may not have a ceratophore, and sometimes a pair of auricular lobes or ctenidia is present. When present there are one to two pairs of eyes. Eyes are lacking in some of the deep-sea species of *Leanira* which live in mud. A pair of rounded ciliated nuchal organs is present (Pruvot & Racovitzta 1895).

The tentaculophores of the first segment each have a single acicula, notochaetae and a pair of dorsal and ventral tentacular cirri which are directed forward, dorsal to the palps. The eversible pharynx is large and muscular with two pairs of interlocking jaws and a border of papillae around the mouth.

Numerous pairs of elytra are present on segments 2, 4, 5 and 7, on alternating segments from 8 to 25 or to 27 and then on every segment. The elytra may have smooth or papillated lateral margins and their surfaces may be smooth or covered with microtubercles (Fig. 1.88C). Dorsal tubercles are found on all segments without elytra. Except on a few anterior segments, ciliated digitiform extensions ('branchiae') are attached to the lateral sides of the elytraphores and dorsal tubercles of all segments. Sigalionids can elevate their elytra above the dorsum and the notochaetae arch over their edges so as to form a pair of respiratory channels above the parapodia in which the branchiae are situated (Day 1967). Also, on the dorsal part of the notopodium are three cup-shaped ciliated ctenidia which form ciliated grooves along the latero-dorsal parts of the body.

Parapodia are biramous, with the notopodia smaller than the neuropodia (Fig. 1.88D). Notopodia are club-shaped with digitiform papillae or stylodes and long fan-like bundles of finely spinous capillaries. Neuropodia are subconical and surrounded by basal bracts with fringes of papillae and distal stylodes. Neurochaetae include compound falcigers or spinigers, which are either long and multiarticulate or short and conical (Fig. 1.88E, F, H–J); simple bipinnate spines (Fig. 1.88G) may also be present. Ventral cirri are short and tapered, sometimes with long accessory papillae on the cirrophores. The pygidium has a pair of long anal cirri.

Notopodia and elytra are absent in the interstitial group, *Metaxypsamma* (Wolf 1986c). Wolf (1986c) suggested that these neotenic features are coincident with an adaptation to an interstitial habit.

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Sigalionids are considered predators, as they have a muscular eversible pharynx with four jaws. However, Fauchald & Jumars (1979) commented that there is very little evidence to support this. Fauchald & Jumars (1979), following the work of others listed four species of sigalionids as carnivores; *Pholoe minuta*, which appears in this table, is now regarded as belonging to the Sigalionidae (according to Hutchings & McRae in press). Yonge (1954) found polychaetes and detritus in the gut of *Psammolyce arenosus*.

The jaw structure resembles that found in other scale-worms (Michel *et al.* 1973). Wolf (1986c) examined the jaw structure of several genera; each jaw had an internal canal and a large white spongy mass of glandular tissue adhering to the dorsal side of the large, ventro-lateral plate. This glandular mass leads into the internal canal within the fang of each jaw. This spongy mass is interpreted by Wolf (1986c) as being a venom gland. This structure is also found in the Polynoidae, Pholoididae and Acoetidae. The interstitial species of *Metaxypsamma* also appear to have a venom gland judging by the presence of a small duct in the jaw containing cellular material (Wolf 1986c).

Sigalionids have metanephridia as mixonephridia (Darboux 1899; Goodrich 1945). Functional gonoducts have been described by Fage (1906) for species of *Sigalion* and *Sthenelais*, although the final stages of the development and the opening of the duct to the exterior have not been described.

Little is known about reproduction in sigalionids. *Sthenelais boa* appears to be the only species whose reproduction has been studied (Bhaud & Cazaux 1987); it releases gametes directly into the water column and the larvae are planktotrophic. A study of planktonic larvae of benthic polychaetes in southern Japan by Yokouchi (1991) found that sigalionid larvae predominated from April to July with scattered individuals at other times. Sigalionid trochophores and nectochaetes were amongst the most common polychaete larvae recorded. They were thought to be feeding on the phytoplankton, since they were most numerous during the spring phytoplankton bloom. Individuals of *Sthenolepis* (as *Leanira*) *grubei* have been shown to contain mature gametes throughout the year suggesting that the population may spawn continuously throughout the year (McNulty & Lopez 1969).

Family Sphaerodoridae

Sphaerodorids are small benthic worms distinguished by the presence of a series of macrotubercles arranged in rows on the dorsal and, usually, ventral surfaces of the body (Fig. 1.89C). Other papillate structures are also present.

The prostomium and peristomium are not distinct; they appear fused to the body in most taxa. One pair of antennae and one pair of simple ventral palps are present, as is a median antenna (Fig. 1.89A). Nuchal organs are present. The first segment has one pair of tentacular cirri. The muscular eversible pharynx has terminal papillae; jaws are absent. A muscular proventricle is present. Parapodia have well-developed neuropodia, and ventral cirri are present (Fig. 1.89D); lateral macrotubercles of Fauchald (1974b) may represent dorsal cirri, as called by Ruderman (1911) and Reimers (1933), or else notopodia and dorsal cirri are absent. At least two rows of tubercles are present on the dorsum, often with a retractile nipple-like end; smaller papillae may also be present. Tubercles and papillae also often occur on the ventral surface. Chaetae are composite or simple. Aciculae and a pair of pygidial cirri are present. This description follows that of Fauchald & Rouse (1997).

The principal taxonomic characters of Sphaerodoridae were reviewed in detail by Fauchald (1974b), the most important being the number, form and arrangement of epidermal tubercles. Three types of tubercles occur: macrotubercles, large spherical protuberances (Fig. 1.89B, C); microtubercles, smaller structures with a basal collar, and; papillae, simple cylindrical or conical protuberances. The number of antennae and their length are characteristic at the generic level and the form of the antennae, which are sometimes bifid or branched, at the species level. Chaetae are usually uniform on all chaetigers except for chaetiger 1, which may carry one or two simple curved spines. The distribution and shape of the chaetae, which may be compound falcigers (Fig. 1.89E) or simple with a subdistal enlargement, provide generic and specific characters.

The Sphaerodoridae were first recognised as a distinct family by Malmgren (1867), although the first species now recognised as sphaerodorids were described in 1843 by Rathke & Oersted. Most subsequent authors divided sphaerodorids into only two genera, although the two genera were differently diagnosed and named by different authors. In his revision of the family Fauchald (1974b) recognised nine genera and provided keys to all genera and species known at the time. Many new taxa have been described subsequently, but none from Australian waters. The genus *Levidorum* lacks tubercles and anterior appendages and was treated as an aberrant sphaerodorid by Fauchald (1974b), but the genus was removed to a new family, Levidoridae, by Perkins (1987). However, Glasby (1993) synonymised the Levidoridae with the Syllidae. None of the the described species of *Levidorum* is known from Australia. Borowski (1994) discussed heterogeneity of the genus *Sphaerodoropsis* and suggested a subdivision of that genus. The family Sphaerodoridae now comprises 10 genera and 79 species (Borowski 1994), including three genera and four species known from Australian and Australian Antarctic Territory waters (Hartman 1964; Fauchald 1974b). Four as yet unidentified species are known from shallow water benthic surveys in south-eastern Australia (Museum Victoria and Australian Museum databases, unpublished data).

Most sphaerodorids are known from deep water, or from high latitudes in both the Northern and Southern Hemispheres. They are most common on soft sediments. They were thought by Fauchald (1974b) to occur less commonly in shallow water, but recent collecting has produced 39 species from shelf depths compared with 23 deep water species and a further 17 species that range from shallow to deep waters (Borowski 1994).

Sphaerodorids fall into two broad types: they may have short 'grub-like' bodies, which are typically less than 5 mm long with fewer than 30 segments, or; may be more elongate and reach up to 15 mm with more than 50 segments. However, intermediate types do exist and use of body form as a taxonomic character requires caution, especially if the sample includes juveniles (Fauchald 1974b). *Ephesiella antarctica* from waters of the Australian Antarctic Territory is notable among sphaerodorids in reaching a length of 50 mm (Hartman 1964; Fauchald 1974b).

Fauchald & Jumars (1979) hypothesised that sphaerodorids are mostly surface deposit-feeders, but there is no evidence for this beyond the observation of organic matter and sand in the gut of *Sphaerodoropsis balticum* reported by Reimers (1933). *Commensodorum commensalis* is commensal with another polychaete, *Terebellides stroemii* (Trichobranchidae),

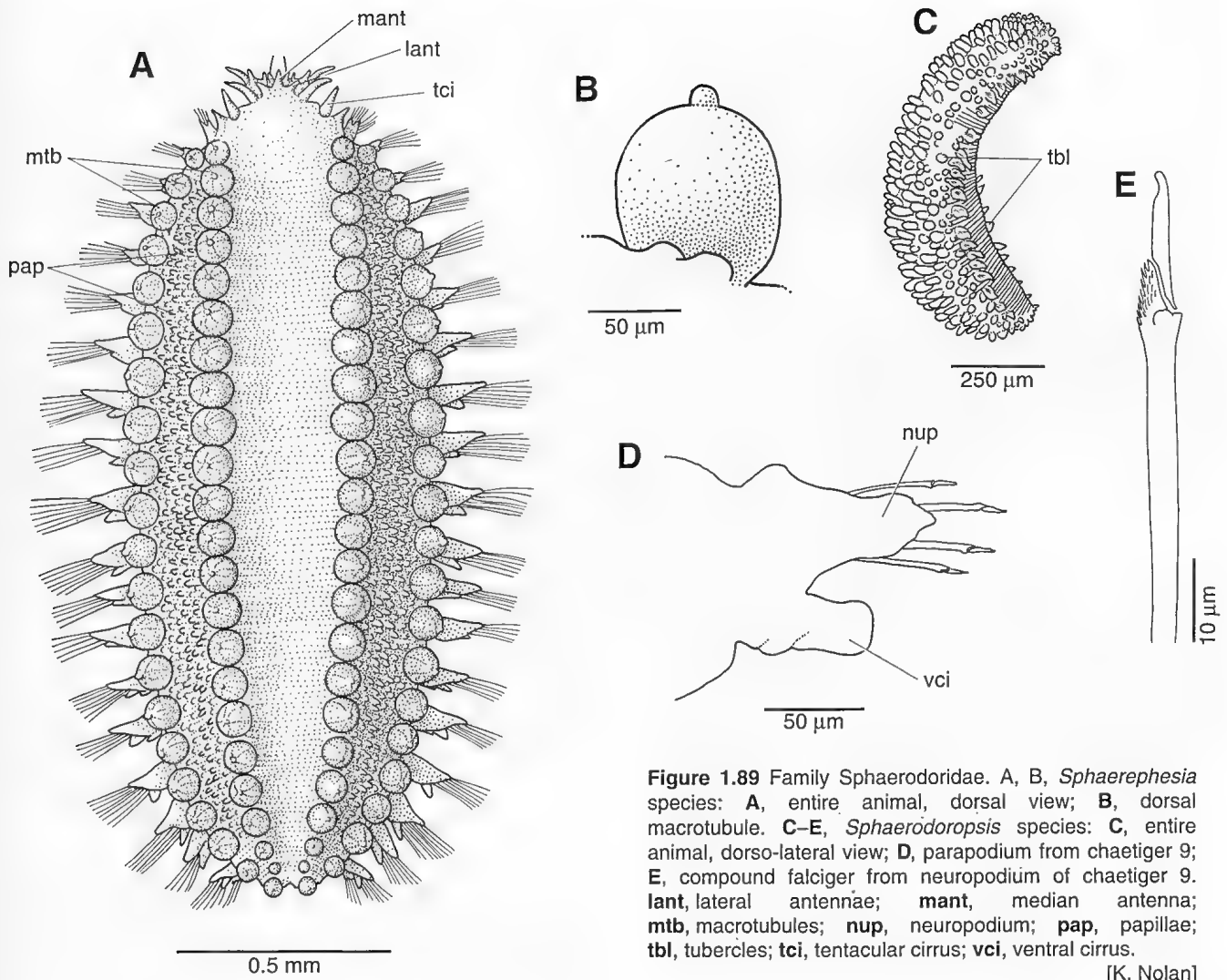


Figure 1.89 Family Sphaerodoridae. **A, B**, *Sphaerephesia* species: **A**, entire animal, dorsal view; **B**, dorsal macrotubule. **C–E**, *Sphaerodoropsis* species: **C**, entire animal, dorso-lateral view; **D**, parapodium from chaetiger 9; **E**, compound falciger from neuropodium of chaetiger 9. **lant**, lateral antennae; **mant**, median antenna; **mtb**, macrotubules; **nup**, neuropodium; **pap**, papillae; **tbl**, tubercles; **tci**, tentacular cirrus; **vci**, ventral cirrus. [K. Nolan]

where it occurs in Sweden (Lutzen 1961), and *Sphaerodorum ophiurophoretos* occurs symbiotically with an ophiuroid (Martin & Alva 1988).

Reproduction of *Sphaerodorum gracilis* has been studied in the United Kingdom by Christie (1984). Sexes of this species are separate and the gonads are dispersed as clusters floating in the coelomic fluid. Oogenesis takes 12 months, whereas spermatozoa were only observed in the month of spawning, October. Mature oocytes are yolky and 200–250 µm in diameter. External fertilisation and direct lecithotrophic larval development are assumed, as this occurs in other sphaerodorids, in which oocyte size may reach 700 µm (Mileikovsky 1967a). *Ephesiella mixta*, a minute deep-water species, appears to be a self-fertilising hermaphrodite in which the embryos are retained in the body cavity (Hartman & Fauchald 1971).

Family Syllidae

Syllids are generally small, slender worms with three antennae and (usually) conspicuous dorsal cirri (Pls 4.1–4.3). They are usually free-living and are very common in shallow coastal waters in soft sediments, on hard substrata and as epibionts.

The Syllidae are a speciose and widely distributed group of polychaetes distinguished by the presence of a uniquely-muscularised region of the anterior digestive tract, the proventricle (Glasby 1993; Fig. 1.90A), which is often visible

through the body wall. Other features setting syllids apart from other nereidiforms include: a pair of lateral and one median antenna (antennae rarely absent); paired, simple palps that may be fused together to varying degrees; one or two pairs of peristomial cirri (also called tentacular cirri; rarely absent); a muscular axial-type pharynx that may be armed or unarmed, and; reduced parapodia (notopodia represented by dorsal cirri only in non-reproductive forms) having simple or compound neurochaetae (Fig. 1.90E–G).

They are members of the large clade, Phyllodocida (Rouse & Fauchald 1997), which is considered an order in many recent classifications (for example, Fauchald 1977; George & Hartmann-Schröder 1985). Lower-level classification is less certain, with the suggestion of membership within the superfamily Nereidoidea (George & Hartmann-Schröder 1985; Glasby 1993) challenged by the finding that the superfamily may be paraphyletic (Rouse & Fauchald 1997). The families Calamyzidae, erected by Fauchald (1977), and Levidoridae (Perkins 1987) are no longer considered valid and are treated here as members of the Syllidae (Glasby 1993; Fauchald & Rouse 1997).

The family was erected by Grube (1850). Important early taxonomic works included those of Quatrefages (1866), Fauvel (1934a, 1934b) and Rioja (1925). Rioja divided the Syllidae into four subfamilies, the Syllinae, Autolytinae, Eusyllinae and Exogoninae, all of which have been recognised by subsequent workers, although it appears more for practical reasons than based on sound phylogenetic studies (Fauchald 1977). The first comprehensive, general work on

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syllid biology was that of Malaquin (1893). Several notable regional taxonomic revisions include those on Scandinavian autolytines (Gidholm 1966b), Japanese syllids (Imajima 1966a, 1966b, 1966c, 1966d, 1966e, 1967), syllids from the Caribbean and Gulf of Mexico (Uebelacker 1984; Russell 1987a, 1989a, 1989b, 1990; San Martín 1990, 1991a, 1991b, 1991c, 1992) and syllids of the western Atlantic (Perkins 1980). By contrast, global revisions at any taxonomic level are lacking and this has severely hampered the study of syllid phylogeny and biogeography.

The first Australian syllid species were collected in Port Jackson by the Swedish *Eugenie* expedition (1851–1853) – *Thoe fusiformis* (possibly as a junior synonym of *Typosyllis variegata*) and *Eurymedusa picta* (possibly a *Trypanosyllis*) and later described by Kinberg (1910; Fig. 1.5B). Haswell (1886a) described a further six species, also from Port Jackson, five under *Syllis* and one under *Gnathosyllis*; the latter is now considered a junior synonym of *Typosyllis*. Augener (1913) described 14 new species and one new genus (*Rhopalosyllis*) from south-western Australia. Haswell (1920a, 1920b) described a further eight new species from Port Jackson, five under the subgenus *Syllis* (*Typosyllis*) (considered here a full genus, *Typosyllis*), one new species of *Pionosyllis*, a new species of *Exogone* and a new species of *Grubea* (now placed under *Brania*). Kinberg's type material and that of Haswell's first described species are thought to be lost; however the types of Haswell's later described species are deposited in the Australian Museum. Thereafter, the number of new syllid species discovered slowed dramatically until the arrival of Hartmann-Schröder whose studies on the polychaete fauna of the Australian coast yielded many new species and genera (Hartmann-Schröder & Hartmann 1979, 1980, 1981a, 1982, 1983, 1984, 1985a, 1986, 1987, 1989, 1990, 1991a). Despite these studies, many more syllid species are likely to be discovered in poorly-collected near shore habitats and on the continental shelf.

The 60 to 70 genera (Garwood 1991; Kudenov & Harris 1995) have been divided traditionally between four subfamilies, the Autolytinae (5 genera), Eusyllinae (~18), Exogoninae (~11) and Syllinae (~16), with some taxa unable to be placed. Whether the subfamilies constitute monophyletic groups or not has been questioned (see Fauchald 1977).

The Autolytinae are recognised by the presence of small fused palps (fused at least partially), nuchal organs forming epaulettes, a long pharyngeal tube, which is coiled or sinuous, the absence of ventral cirri, unarticulated dorsal cirri, and schizogamous reproduction. The Exogoninae are distinguished by their small body, large palps fused for at least half their length, indistinct nuchal organs, pharyngeal tube usually straight, dorsal cirri short and not articulated (absent on chaetiger 2 in some *Sphaerosyllis*), the presence of ventral cirri, the absence of segmental ciliary bands and dorsal cirri on chaetiger 2 in larvae and epigamous reproduction. The Eusyllinae are distinguished by their basally fused palps, usually smooth or irregularly wrinkled antennae, tentacular and dorsal cirri, the presence of ventral cirri, large distinctive nuchal organs, a pharyngeal tube that is usually straight, ciliated larval stages and epigamous reproduction. The Syllinae are recognised by their prominent palps which are usually separate, their usually small and indistinct nuchal organs, a straight pharyngeal tube, dorsal cirri that are usually long and articulated, presence of ventral cirri and segmental ciliary bands in the larvae, and schizogamous reproduction (Fig. 1.24B; Uebelacker 1984; Garwood 1991).

The Australian fauna includes at least 32 genera: *Amblyosyllis*, *Astreptosyllis*, *Autolytus*, *Branchiosyllis*, *Brania*, *Ehlersia*, *Eurysyllis*, *Eusyllis*, *Exogone*, *Haplosyllis*, *Langerhansia*, *Myrianida*, *Odontoautolytus*, *Odontosyllis*, *Opisthodonta*, *Opisthosyllis*, *Parahaplosyllis*, *Paraopisthosyllis*, *Parapionosyllis*, *Parasphaerosyllis*, *Pionosyllis*, *Plakosyllis*, *Proceraea*, *Procerastea*, *Rhopalosyllis*, *Sinpalposyllis*, *Sphaerosyllis*, *Streptosyllis*, *Syllides*, *Syllis*, *Trypanosyllis* and *Typosyllis* (Day & Hutchings 1979; Hartmann-Schröder & Hartmann 1979, 1981a, 1982, 1983, 1987, 1990, 1991a; Kudenov & Dorsey 1982; San Martín & López 1998). Many of these genera have widespread global distributions, but a few are apparently restricted to Australian waters: *Astreptosyllis*, *Odontoautolytus*, *Parahaplosyllis*, *Paraopisthosyllis*, *Rhopalosyllis*, *Sinpalposyllis*. Genera particularly well-represented in Australian waters are the exogonine *Sphaerosyllis* with over 20 described species and subspecies, the syllines, *Typosyllis* (~36) and *Opisthosyllis* (~7), and the autolytines, *Proceraea* (7) and *Procerastea* (3). Strangely, the most speciose autolytine genus, *Autolytus*, which has over 100 species described worldwide, is apparently represented by only a handful of species in Australia (Day & Hutchings 1979).

Syllids are generally small and slender, usually less than 10 mm long and 1 mm wide. Most species have more or less cylindrical bodies, although those of *Trypanosyllis* are strongly dorso-ventrally flattened (Fig. 1.90B). Many species are brightly coloured, the result of pigments in the epidermis, gut, oocytes or, in *Odontosyllis* species from Bermuda, bright green phosphorescence in mucous glands (Kennedy 1969).

The epidermis may be smooth or papillated (Fig. 1.90A). Epidermal papillae cover the body of members of *Sphaerosyllis* and, together with secretions from integumentary glands, facilitate entrapment of fine particles on the body surface (Haswell 1920a; Riser 1991). In the Autolytinae, a ring of cilia is present on the body segments and on prostomium in some genera (for example, *Autolytus*, *Myrianida*), but segmental ciliation is lacking in species of *Proceraea* and *Procerastea* (Gidholm 1966b).

Several types of integumentary glands occur over the dorsal and ventral surfaces and on the cirri in the exogonines, but their nature and function are not well-known (Riser 1991); Haswell (1920a) suggested that those at the base of the parapodia in *Exogone fustifera* and *Sphaerosyllis hystrix* produce a viscous excretion with which the female attaches discharged ova onto her body wall. Autolytines have three types of gland cells on the dorsal body surface: basiphil bacillary glands producing a polysaccharide-rich secretion and two types of sphaerulate glands, one producing a protein-rich secretion; in addition, parapodial glands either project internally into the coelom and exit via a pore ventrally at the base of the parapodia or occur in the epidermis of the parapodia.

A rounded prostomium, usually wider than long, bears a pair of lateral antennae and a median one, all of which may be articulated, smooth or wrinkled; rarely are antennae absent. A pair of antero-ventral conical palps range from being completely fused to free from one another (Fig. 1.90A, B); palps are reduced in size in *Autolytus* and are rarely absent. Typically, there are two pairs of lensed eyes and often a smaller anterior pair of ocelli, though other combinations occur and eyes are rarely absent. The lensed eyes of *Odontosyllis enopla* (and perhaps other species in the genus) act as a fibre optics system directing light upon the underlying photoreceptors. Maximum sensitivity is in the green part of

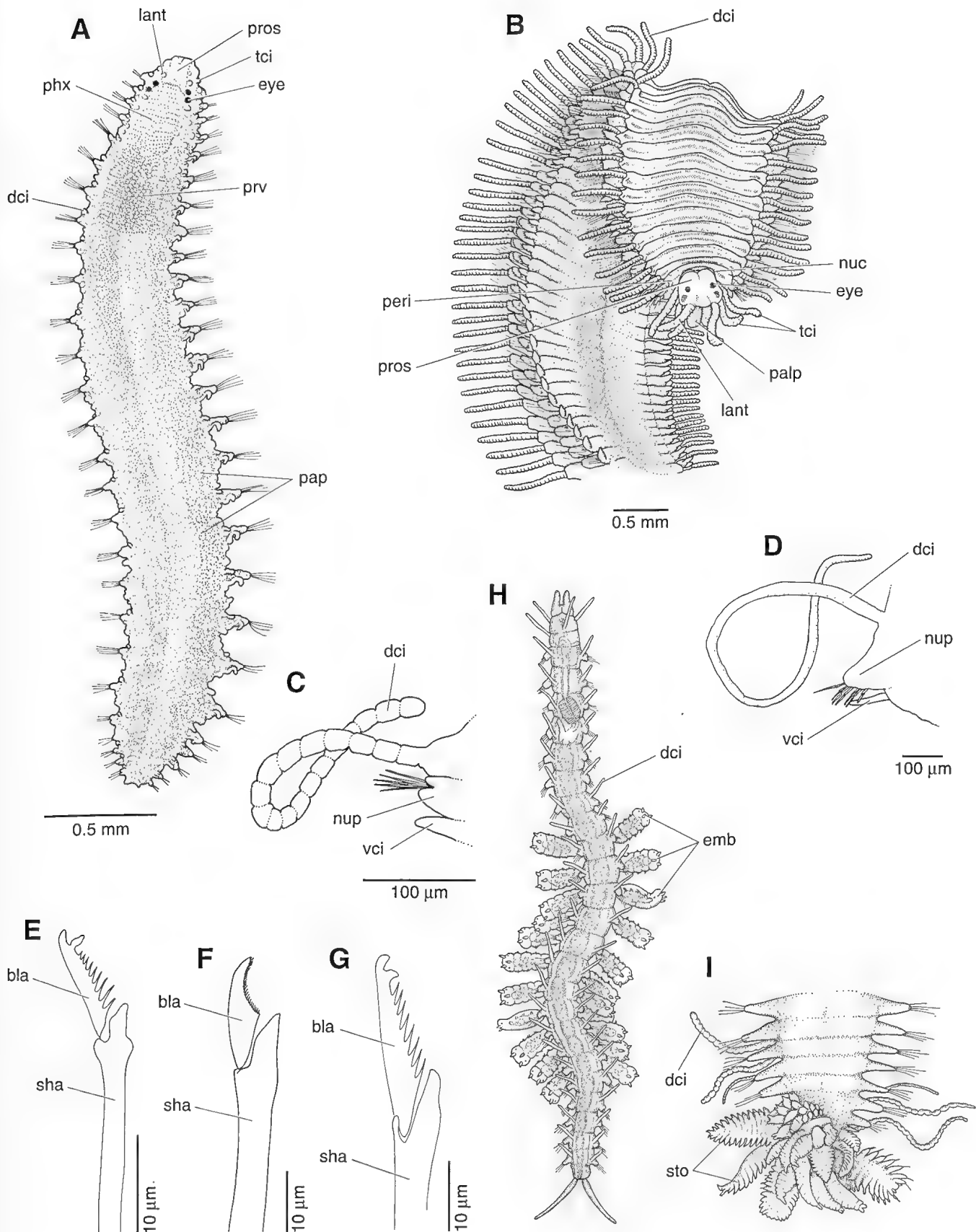


Figure 1.90 Family Syllidae. **A**, entire animal of *Sphaerosyllis* species (Exogoninae), dorsal view. **B**, dorsal view of anterior end and ventral view of mid-body of *Trypanosyllis* species (Syllinae); median antenna absent. **C**, parapodium from mid-body, a sylline species. **D**, parapodium from chaetiger 31, an eusylline species. **E–G**, chaetae: **E**, heterogomph falciger from mid-body chaetiger, a sylline species; **F**, heterogomph falciger from posterior chaetiger, *Trypanosyllis* species; **G**, heterogomph falciger from chaetiger 31, an eusylline species. **H**, externally brooded embryos in *Pionosyllis elegans* are attached to the ventral cirri by glandular secretions. **I**, multiple male stolon production from the venter of posterior segments in *Trypanosyllis crosslandi*. **bla**, blade; **dci**, dorsal cirrus; **emb**, embryos; **eye**, eye; **lant**, lateral antenna; **nuc**, nuchal organ; **nup**, neuropodium; **palp**, palp; **pap**, papillae; **peri**, possible peristomium (see text); **phx**, pharynx; **pros**, prostomium; **prv**, proventricle; **sha**, shaft; **sto**, stolons; **tci**, tentacular cirri; **vci**, ventral cirrus. (H, after Pierantoni 1903; I, after Potts 1911)

[K. Nolan]

1. CLASS POLYCHAETA

the visible spectrum, which corresponds to that of the green bioluminescence emitted by these worms during spawning (Wilkens & Wolken 1981; Wolken & Florida 1984).

Nuchal organs are present as short ciliated grooves (Fig. 1.90B) or paired epaulettes extending posteriorly from the posterior margin of the prostomium (Fig. 1.2C). The well-developed epaulettes of Autolytinae, containing four to eight rows of small ciliated cells, extend posteriorly up to seven chaetigers from the dorso-lateral margin of the posterior prostomium; these organs increase in length over the life of the worm (Gidholm 1966b). A modified three-layered cuticle protects the sensory elements of the nuchal organs (Purschke 1997).

The peristomium (or first segment, see below) usually bears two pairs of cirri, although only one pair are present in the exogonines, *Exogone* and *Sphaerosyllis* and the eusylline, *Parapionosyllis*; rarely are cirri absent. A dorsal occipital flap extends anteriorly covering the posterior prostomium in some species of Syllinae and Eusyllinae.

A complex, eversible, axial-type pharynx consists of a cuticular-lined anterior region and a posterior proventricle (or gizzard) and ventricle (Haswell 1921; Purschke 1988a). The mouth opens into a short pharyngeal sheath (buccal cavity) and leads into a longer pharyngeal tube, which at its anterior end is a circlet of papillae through which open numerous fine ducts of the pharyngeal glands. The pharyngeal tube may be straight, or sinuous/coiled (autolytines and *Amblyosyllis*), unarmed (*Syllides*) or carry a single conical-shaped mid-dorsal tooth (*Sphaerosyllis*, *Syllis*), a series of teeth in a ventral arc (*Odontosyllis*), or a complete ring of teeth (trepán), as in *Trypanosyllis* and most autolytines. The mid-dorsal tooth may be located in the anterior or the posterior part of the pharyngeal tube. The armature of syllids is composed of a typical cuticle or sclerotised cuticle (Purschke 1988a and references therein). The pharyngeal tube leads into a conspicuous muscular proventricle and then into a thin-walled ventricle, which posteriorly has a ciliated epithelium and often, paired, lateral caeca (caeca absent in Autolytinae). The paired water-filled caeca are thought to function in bouyancy control (Jeuniaux 1969). Thereafter is the intestine which also has a ciliated epithelium.

The proventricle probably functions as a pump giving syllids suctorial-feeding capabilities (Fauchald & Jumars 1979), but the paired chitinous plates inside the proventricle at its anterior end may also assist in the mechanical digestion of food (Haswell 1921). Whereas pharyngeal muscle cells of most polychaetes are obliquely striated, those of the syllid proventricle consist of radial muscle fibres that are cross-striated with up to 20 zigzag bands. Under light microscopy the outer ends of the radial muscle fibres appear as rows of dots, often coloured in the living animal (Haswell 1921). Occupying the core of the radial muscle fibres are numerous microcrystalline inclusions that contain calcium and phosphorus and are involved in calcium metabolism – whether these inclusions are storage sites for excess calcium or provide a skeletal framework is unclear (Ponsolle, Wissocq & Galle 1974; Briggs, Chaffee & Anderson 1985; Purschke 1988a).

Notopodia are reduced to dorsal cirri only in non-reproductive individuals, although additional notopodial lobes and notochaetae may be present in reproductive individuals. Dorsal cirri vary greatly in shape and length: long, cirriform types may be articulated (*Typosyllis*, *Trypanosyllis*), wrinkled (*Eusyllis*, *Streptosyllis*) or smooth (*Odontosyllis*, *Pionosyllis*); shorter types may be ovoid (*Exogone*) or pyriform

(*Sphaerosyllis*) (Fig. 1.90C, D). Ventral cirri are digitiform in most taxa, but absent in Autolytinae (Fig. 1.90C, D). The dorsal cirri characteristically show alternation patterns in length and/or shape that are remarkably constant between individuals of the same species (Gidholm 1966b).

Chaetae include compound falcigers in most species (Fig. 1.90E–G), and compound spinigers in some species of *Exogone* and *Pionosyllis*. Simple chaetae, either smooth or ornamented, occur exclusively in a few genera (for example, *Haplosyllis*), but in others accompany compound types, usually only one or two in superior and inferior positions in the parapodia. Chaetae of autolytines consist of a dorsal bayonet-type chaeta and ventrally a series of compound chaetae with bidentate blades; members of the genus *Procerastea* also have a number of additional types derived from the modification of compound chaetae, most commonly fusion of blade and shaft (Gidholm 1966b). Swimming or natatory chaetae (usually hair-like) develop in the notopodia of middle and posterior segments in epitokous members of the Exogoninae and Eusyllinae.

Regeneration of posterior segments missing, either as the result of injury or schizogamous reproduction (see below) is possible (as in many polychaetes), provided the break occurs after the start of the intestine (Okada 1929, 1938). Many syllids are also capable of limited regeneration of missing anterior regions, often only one or two chaetigerous segments in addition to the head (Berrill 1952). Species capable of asexual reproduction can completely regenerate missing anterior ends, including the pharyngeal region (Okada 1929). At least one species, *Procerastea halleziana*, has been observed to undergo rapid multiplication as a result of fragmentation. Fragmentation in this species is induced by strong contraction of the longitudinal segmental muscle causing breakage at many predetermined points along the body (the megasepta), which correspond to deep constrictions of the alimentary canal (Okada 1929). Each fragment then regenerates anterior and posterior ends. Other syllid species are also likely to reproduce in this way.

Diets of most members of Autolytinae and Syllinae are thought to include colonial invertebrates (corals, hydrozoans and bryozoans) and sponges. The autolytines feed mainly on hydroid polyps. Soft-bottom-inhabiting eusyllines feed on diatoms and detritus, and exogonines are selective deposit-feeders (Hamond 1969; Fauchald & Jumars 1979; Hartmann-Schröder 1991b; Sardá & San Martín 1992). Other eusylline species, for example, *Odontosyllis enopla*, are carnivorous, probably predating spionids (Fischer & Fischer 1995). Two syllines, the species complex *Haplosyllis spongicola* and the western Atlantic *Branchiosyllis oculata*, are sponge parasites, grazing on the soft tissue of the sponge surface; by ingesting the sponge pigment, some take on the same colour as their host (Dauer 1973; Fauchald & Jumars 1979; Pawlik 1983). Many other syllid species are known, or thought to be, commensal with especially sponges, hydrozoans and anthozoans; some appear able to enclose themselves by structurally modifying the surface of the host and, like members of *Procerastea*, actually feed on the host (Utinomi 1956; Wright & Woodwick 1977; Hartmann-Schröder 1992; Glasby 1994; Martin & Britayev 1998).

Feeding probably involves piercing the surface of the prey with the pharyngeal tooth and sucking out the contents using the proventricle (Fauchald & Jumars 1979). This accords with the feeding behaviour of *Brania clavata*, individuals of which were observed sucking out the contents of harpacticoids and young amphipods (Kisseleva 1986); however, such direct

observations appear to be rare. The idea that the tooth is equipped with a basal poison gland and is used to stab prey (Haswell 1886b) needs confirmation.

Syllids have metanephridia in all body segments, except for the anterior- and posterior-most. The metanephridium unites with the ciliated coelostome in segments containing mature gametes to function as a genital duct as well an excretory organ (= metanephromixium) (Goodrich 1945, and references therein). The metanephridial duct is simple and straight and opens externally via a ventral pore (nephridiopore) and internally into the coelom of the next anterior segment (through the septum) via an open ciliated funnel, or nephrostome (Goodrich 1945; Smith & Ruppert 1988).

The literature on the reproductive biology of Syllidae is extensive, but very few studies involve Australian species. General information on reproduction in the family has been derived from the reviews of Schroeder & Hermans (1975) and Garwood (1991), but important primary references include those of Malaquin (1893), Potts (1911), Okada (1937), Durchon (1959), Durchon & Wissocq (1964), and Gidholm (1965).

Syllids can reproduce both asexually and sexually and, sexes are typically separate; however, hermaphroditism occurs in several species representing all four subfamilies (Schroeder & Hermans 1975, table 2), including *Typosyllis corruscans* (= *Syllis corruscans*) from the intertidal zone in Port Jackson. When sexually mature this species divides into two regions at about the 100th segment – a long dark female region and a shorter orange-coloured male region; a pair of large eyes develops on the first segment of the male stolon before it detaches from the female, swims away and later develops antennae and a pair of palps (Haswell 1886a). Another species, *Brania pusilloides* (as *Grubea pusilloides*), from the shores of Port Jackson, is a simultaneous hermaphrodite, producing a single ovum in each of segments 11 (or 12) to 16 (or 17) and sperm in segments 9 and 10 (or 10 and 11). Viviparous reproduction, in which unfertilised ova develop within the body cavity of the female, has been reported in a few species in *Typosyllis*, *Ehlersia*, and *Exogone* and is likely to be common to all species of *Dentatisyllis*; developing juveniles may take up coelomic fluid of the parent with their hindgut or dissolved organic matter may be absorbed through the epidermis (Ding, Licher & Westheide 1998).

Syllines and autolytines typically reproduce by schizogamy, although other modes, such as epigamy also occur, especially in Autolytinae (see Gidholm 1966a). Reproductive individuals (stolons), specially adapted for swimming and spawning in the water column, are budded off from the benthic adult (stock) for swarming and spawning, then die. Single or multiple stolons develop either from the pre-pygidial proliferative zone of the stock (scissiparity), from the pre-pygidial zone of the preceding stolon (except the first stolon which is formed by fission) producing a succession of stolons (Fig. 1.25C), or from the venter of one to many posterior segments of the stock in species of *Trypanosyllis* (Fig. 1.90I; Potts 1913; Garwood 1991).

In the Syllinae, stolons may develop head appendages before separation (for example, *Typosyllis hyalina*) or the process may not be completed until after separation (for example, *Haplosyllis spongicola*, *Typosyllis cirropunctata*). Natatory or swimming chaetae may appear in the stolons before or after separation. Malaquin (1893) identified five different types of sylline stolons, based largely on the degree of development of the head appendages and Potts (1911) provided further examples of species with the different types of stolons. These

are, from the simplest to the most complex: acephalic (occurs in *Haplosyllis spongicola*, *Typosyllis cirropunctata*); 'Tetraglène', poorly defined head with two pairs of eyes, but lacking antennae and palps (occurs in *Trypanosyllis* species and *Exogone gemmifera*); 'Chaetosyllis', prostomium well defined, cleft, one or two pairs of eyes and a pair of lateral antennae (occurs in *Typosyllis prolifera* and *Opisthosyllis brunnea*); 'Tetracère', well-defined prostomium with a single pair of eyes, a pair of lateral antennae and a pair of palps (occurs in *Syllis amica*; no species recorded from Australia), and 'Pentacère' (or Ioda), prostomium like that of adult with two pairs of eyes, three antennae and a pair of palps (occurs in *Typosyllis hyalina*, *T. corruscans*). Other anatomical changes to the developing stolon include hypertrophy of nephridia to form gonoducts and the transformation of longitudinal muscles. When mature, syllid stolons are usually filled with gametes throughout their length, and all will die after spawning. There is no sexual dimorphism amongst the stolons.

In Autolytinae, stolons typically are produced singly by scissiparity from an anterior segment (typically 14) or a posterior segment, or in chains, in which the last in the series is the oldest and best developed (gemmiparity), depending on the species (Gidholm 1966b). Gametes are passed from gonads in the stock to a separate gamete cavity within the coelom of the stolons through septal openings which develop in the stock. Autolytine stolons also have capillary chaetae in at least some parapodia, and nephridia modified to function as gonoducts. The head and prostomial appendages are fully developed before separation from the stock, but differ in male ('Polybostrichus') and female ('Sacconereis') stolons: in males (Fig. 1.25B) there is a median antenna, two bifid lateral antennae and two small 'frontal processes' of uncertain homology; in females lateral antennae are simple and the frontal processes are absent; the stolons of both sexes lack palps that are present in the ancestral stock (Gidholm 1966b).

Members of the Eusyllinae and Exogoninae typically reproduce by epigamy in which the whole non-reproductive animal transforms into a breeding individual (epitoke) by the hypertrophy of cephalic appendages, enlargement of eyes, elongation of antennae, addition of swimming (natatory) chaetae between the parapodial lobes and dorsal cirri of some segments, and enlargement of nephridia to serve as gonoducts. Unlike epigamy in the aberrant autolytine, *Autolytus alexandri* and members of the Nereididae, epigamy in the eusyllines and exogonines is often reversible enabling females to return to the bottom after spawning, and feed and reproduce again (Gidholm 1966a; Daly 1975; Fischer & Fischer 1995).

The usual mode of reproduction in the Syllidae appears to be free-spawning of eggs and sperm (as ect-aquasperm) in the water column and external fertilisation. Internal fertilisation in the egg sac (= brood chamber) occurs in members of the Autolytinae (Gidholm 1965; Qian & Chia 1989a) and sperm are modified accordingly (= ent-aquasperm; Jamieson & Rouse 1989). In autolytines, male and female stolons swim in an undulating manner prior to mating. A sex pheromone released by the female induces the male to swim in a small circle around the female, while ejecting sperm which attach to the ventral body surface of the female. Eggs are released into the ventral egg sac a few hours after mating, whereupon fertilisation takes place (Gidholm 1965). Females of *Autolytus* species brood embryos and larvae (up to 5000) in a brood pouch (a common pouch formed by the modification of the egg sac) on the ventral surface of the body (Qian & Chia 1989a).

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External brooding of eggs has also been reported for species in the Eusyllinae and Exogoninae. Exogonine syllids attach eggs directly to the female body until at least three chaetigers have developed (Fig. 1.27). In the exogonine *Sphaerosyllis*, eggs are brooded either on the dorsal or ventral surface (Riser 1991). The nature of brooding in the Eusyllinae is less clear, partly as a consequence of suspect identifications (Garwood 1991); brooding has been reported in at least one Australian species, *Pionosyllis augeneri* (Hartmann-Schröder & Hartmann 1979). Eggs attached ventrally are glued to the body surface by glandular secretions (Fig. 1.90H; Potts 1911; Haswell 1920a), whereas dorsally brooded eggs are attached either by membranous or fibrillar structures, or by delicate epitokous capillary chaetae which touch or penetrate the egg (Kuper & Westheide 1998).

Oocytes are produced from discrete ovaries, and in some exogonines (*Brania*, *Exogone* and *Sphaerosyllis*), their development is facilitated by nurse cells (Cognetti-Varriale 1965). Mature exogonine females typically have one, two or four ova per segment (Haswell 1920a).

Experimental studies suggest that light-temperature effects on reproductive activity are mediated by the endocrine system, as in many other polychaetes. Stolonisation in the Syllidae appears to be controlled by an inhibitory hormone released from the pharyngeal region, specifically the proventricle in Syllinae (Heacox & Schroeder 1982; Franke 1983). Franke (1983) suggested that reproduction in *Typosyllis prolifera* is under the primary influence of cyclic hormonal stimuli from the prostomium which controls the release of 'stolonisation-inhibiting' hormone from the proventricle. Stolonisation is initiated when the level of 'stolonisation-inhibiting' hormone decreases periodically during the summer months. Periodicity in the levels of hormone (and hence stolonisation) in species of *Typosyllis* is likely to correspond to summer lunar cycles (Franke 1986), but the situation is not completely clear (Heacox 1981).

The karyology of only 14 syllid species is known, of which most are Mediterranean species (Curini-Galletti, Lardicci & Regoli 1991). Generally congeneric species show similar karyotypes, and chromosome number is low for members of the subfamilies Exogoninae ($2n = 8-18$) and the Autolytinae ($2n = 8-12$); a low number maybe a plesiomorphic trait.

Studies of embryology and larval development include those of Malaquin (1893) concerning mainly the subfamilies Syllinae, Eusyllinae and Autolytinae; Cazaux (1969, 1984) who published on the Syllinae and Eusyllinae, and; Okada (1930b), Schiedges (1979b) and Qian & Chia (1989a) who published on the Autolytinae. Syllid larvae hatch from the egg capsules either as a trochophore, or after parapodia have begun to develop (nectochaetes); at this stage the larvae generally have three prostomial antennae, two pairs of eyes, lack palps, and has only the dorsal pair of peristomial cirri, or if the ventral pair is present they are poorly developed (Okada 1930b). However, the precise timing of the development of head appendages varies between species, as does the duration of larval stages.

A free-swimming larval stage may be absent (*Autolytus*) or if present (as in the Syllinae and most Eusyllinae) it is relatively short compared to other polychaetes. Larvae of species with a swimming stage develop cilia early in development, prior to the trochophore stage. Brooding exogonine and eusylline species have neither cilia nor a swimming phase, whereas autolytines may or may not have ciliated larvae. Many Syllidae (except the Exogoninae) have spines in addition to cilia in the apical tuft. Metamorphosis is completed within

4-6 weeks of fertilisation in *Syllis variegata*, *Autolytus alexandri* and *Odontosyllis enopla* (Cazaux 1984; Fischer & Fischer 1995; Qian & Chia 1989a, respectively).

Relatively little has been published on syllid life cycles and population dynamics. Life cycles and demography may vary widely, even within a genus. For example, *Streptosyllis websteri*, from the eastern Atlantic, breeds twice in its life time during an extended spawning season at the beginning of its third year. However, *Streptosyllis verrilli* from the western Atlantic breeds only once in the ninth or tenth month of life in a short spawning season, and then dies, although death after only one spawning appears to be atypical for a eusylline (Garwood 1982; Sardá & San Martín 1992). Not surprisingly population densities of the latter species vary considerably over the year, from a minimum over the breeding period in the summer months (a few hundred individual per square metre) to a maximum in autumn of several thousand individuals per square metre (Sardá & San Martín 1992).

Schiedges (1979a) has shown experimentally that diurnal photoperiod is the main external cue for reproduction (namely, stolonisation) in *Autolytus* species. Swarming of stolons is initiated at dusk and dawn with animals swimming towards the light and gathering near the surface, at which point males are attracted to females by a female sex pheromone (Gidholm 1969).

Individuals of several species of *Odontosyllis* become bioluminescent prior to and during the breeding period. A species reported from Australia, *O. polycera*, becomes bioluminescent while simultaneously developing epitokal modifications (including enlargement of eyes and formation of swimming chaetae) about 1 month prior to the breeding period (Daly 1975). Bioluminescent signals also play a role in the visual attraction of the sexes to one another during mating in the Bermuda fireworm, *O. enopla*; such behaviour as a prelude to mating occurs predictably 2-3 days after a full moon (Galloway & Welch 1911; Markert, Markert & Vertrees 1961; Wilkens & Wolken 1981). Post-spawned individuals also emit bioluminescent flashes as a startle response; it may be part of a nocturnal foraging behaviour common to all members of the genus (Fischer & Fischer 1995).

Syllids are normally free-living though members of the Autolytinae associated with hydroids often construct hyaline, mucous tubes over the colonies (Gidholm 1966b; Fauchald & Jumars 1979). They are very common in coastal shallow waters, in soft sediments, on hard substrata, and as epibionts on algae, seagrasses, and on sessile metazoans. A few genera (for example, *Sphaerosyllis*) also occur in deeper waters below the continental shelf. Overseas studies suggest that syllids can be the dominant (most speciose and numerous) polychaete group on rocky bottoms and seagrass beds, though many species have a fairly narrow range of habitat preference, with factors such as depth, seagrass density, sediment type and degree of exposure affecting the micro-distribution of species (Somaschini & Gravina 1994). Exogonines and eusyllines are abundant meiofaunal polychaetes, typical of tidal or shallow subtidal sand-mud sediments, crevices in hard substrata and as epibionts and endobionts of algae and sessile invertebrates. Many species of *Exogone*, for example, live inside the cavities of sponges, especially large Demospongia, although they may not feed on the sponge (unlike some syllines) or be host specific (Pascual, Núñez & San Martín 1996). Species of *Sphaerosyllis* often dominate the meiofauna, living in the interstices of sand-muddy sediments of the intertidal and shallow subtidal zones associated with crevice biota, kelp holdfasts, calcareous polychaete tube mats and coralline algae (Westheide 1990b; Riser 1991). Syllids

are also abundant on coral reefs being the numerically dominant polychaete group on both hard and soft substrata on the Great Barrier Reef (Hutchings 1974b; Reichelt 1979), and in other types of limestone habitats in the Indo-Pacific, including intertidal limestone platforms and amongst rhizophytic *Halimeda incrassata* (Kohn & White 1977; Naim 1988).

Coelomic parasites belonging to the polychaete genus *Labrostratus* (Oeonidae) have been reported from several syllids including two species reported from Australian waters, *Haplosyllis spongicola* complex and *Sphaerosyllis hystrix* (Uebelacker 1978; San Martín & Sardá 1986). Uebelacker (1978) recorded a 0.2% incidence of parasitism (one parasite per host) with the parasitic oeonid almost completely filling the coelomic cavity of the host.

The phylogenetic position of the Syllidae is uncertain. They are thought to form a monophyletic group with Nautiliniellidae and Pilargidae on the basis of the following synapomorphies: an annulus behind the head bearing one or two pairs of peristomial cirri (or tentacular cirri), absence of cephalisation of the first segment and associated parapodia, lack of true pharyngeal jaws and poorly developed (essentially uniramous) parapodia (Glasby 1993). However, despite a recent study of the nervous system of members of the group (Orrhage 1996), the issue of homology of the peristomium and the first segment (and their appendages) among nereidoids has not been clarified. Rouse & Fauchald (1997) suggested that the achaetous annulus bearing cirri in Syllidae and other nereidoids represents a cephalised first segment, and that the peristomium is limited to a small area around the mouth. Partly on the basis of this interpretation of homology, Rouse & Fauchald (1997) found that Syllidae were the sister group of a large clade including nereidiforms, phyllodiciforms and glyceriforms. Pleijel & Dahlgren (1998) were not able to settle the issue of the phylogenetic position of Syllidae, finding evidence for affinities with both nereidoids and the Sphaerodoridae.

Several authors have speculated on phylogenetic relationships within the Syllidae, on whether the subfamilies are monophyletic, and on which of the reproductive strategies (epigamy or schizogamy) is ancestral. Most support appears to be in favour of epigamy being ancestral (Potts 1911; San Martín 1984; Garwood 1991), but the case for schizogamy has also been suggested (Malaquin 1893). When epigamy was viewed as being ancestral, then either schizogamy has arisen twice in the family (Garwood 1991), or just once, with the primitive stem type thought to have been represented by the stolons of the *Haplosyllis spongicola* complex (Potts 1911) or those of *Trypanosyllis* species (San Martín 1984). However, in the only cladistic study of the group Nygren (1999) found that it was equally parsimonious (likely) that schizogamy is the ancestral state with epigamy evolving twice as it was for epigamy being the primitive state with schizogamy arising twice. Further, he found support for the monophyly of Autolytinae, Exogoninae and Syllinae, whereas Eusyllinae was found to be polyphyletic. Garwood (1991) also suggested that the pattern of reproductive modes in Syllidae largely supports the monophyly of the four classical subfamilies.

The Syllidae are represented from the intertidal zone to shelf depths across all continents. In Australia the distribution patterns, as deduced from the works of Hartmann-Schröder (cited above), appear to mirror those of other polychaete groups (for example, Hutchings & Glasby 1991) and reflect those patterns established for marine groups in general (for example, Wilson & Allen 1987). Thus species may have a mainly northern distribution (such as *Brania opisthodentata*,

Odontosyllis langerhansiaesetosa, *Parapionosyllis bifurcata*, *P. bifurcatoides*, *Pionosyllis augeneri*, *Syllides articulatus spinosus*), a mainly southern distribution (such as *Sphaerosyllis magnoculata*, *Streptosyllis aequisetata*, *Eusyllis brevicirrata*, *Typosyllis lincolniensis*, *T. albanyensis*), or occur along the entire coastline (such as *Brania longisetosa*, *Exogone sexoculata*, *Pionosyllis samsonensis*, *Sphaerosyllis horrocksensis*, *Typosyllis gerhardi*). A few Australian species show in their present-day distribution obvious Gondwanan connections (for example, *Odontosyllis polycera*, *Sphaerosyllis nathani*, and *Syllides sexoculata*). Many widespread species supposedly have a cosmopolitan distribution, however, this probably reflects our poor knowledge of the taxonomy of this group in Australia.

Family Tomopteridae

Tomopterids are distinctive planktonic polychaetes with a transparent body. The presence of a long pair of rigid tentacular cirri originating from the second segment immediately distinguishes tomopterids from other members of the Phyllodocida.

The prostomium and peristomium are fused to the first segment. A pair of ventral tentacular cirri (which may be absent in some species or in adults) is located on the second segment (Fig. 1.91). Antennae are absent, and one pair of large tapering unarticulated ventral palps is present. The nuchal organs form a pair of dorsal crests. A short eversible muscular pharynx is present, but terminal papillae and jaws are lacking. Segment 2 is the first visible segment; it bears one pair of posteriorly directed tentacular cirri which may be as long as the entire worm and is supported internally by rigid acicula. External chaetae are lacking. Parapodia are biramous with foliose notopodial and neuropodial lobes; some authors refer to these as dorsal and ventral cirri, but dorsal and ventral cirri are lacking according to Fauchald & Rouse (1997), as are branchiae and pygidial cirri. The posterior region may be modified into an elongate tail. This description follows that of Fauchald & Rouse (1997).

The taxonomic treatments of Tebble (1960) and Dales & Peter (1972) recognised two genera: the monotypic *Enapteris* and *Tomopteris* with about 40 species (Fauchald 1977). Uschakov (1972) further divided *Tomopteris* into two subgenera: *T. (Johnstonella)* distinguished by having rosette organs present, and reduced parapodia in the caudal region, and; *T. (Tomopteris)* distinguished by the lack of rosette organs, and absence of reduced caudal parapodia. Keys to species of *Tomopteris* were provided by Støp-Bowitz (1948) and Dales (1957a). Dales & Peter (1972) reviewed the records of tomopterid species worldwide.

Three species of *Tomopteris* have been recorded from Australian waters; two of these, *T. australiensis* and *T. mortenseni*, have type localities in south-eastern Australia. The third species, *T. huxleyi*, was described from Torres Strait, but is listed as indeterminable by Hartman (1959a). Only *T. mortenseni* has been recorded subsequently, from India (Fauvel 1932). A specimen from Museum Victoria is tentatively identified here as *T. australiensis* although as Dales & Peter (1972) noted, Augener's description does not distinguish that species from others in the genus. Four additional species plus unidentified material of *Tomopteris* are known from Australian Antarctic Territory waters (Hartman 1964; Ikeda & Hing Fay 1981). As for other planktonic polychaetes, Australian records of tomopterids are likely to increase significantly when collections of Australian plankton are studied systematically.

1. CLASS POLYCHAETA

Tomopterids live from surface waters to a depth of at least 3000 m, but most records (and most collections) are from less than 500 m. The family is distributed throughout the world, but most species are known from only one area and only a few are regarded as cosmopolitan or nearly so (for example, *Tomopteris apsteini*, *T. elegans*, *T. planktonis*). Tomopterids are carnivores and consume chaetognaths, tunicates and fish larvae (Lebour 1923; Rakusa-Suszczewski 1968). The report by Lebour of unicellular algae in the gut was disputed by Rakusa-Suszczewski.

Tomopterids usually attain 70 mm in length, exceptionally 135 mm (Uschakov 1972); large specimens are always females (Åkesson 1962). Up to 30 segments with parapodia may be present. Diagnostic characters used to determine species include the form and length of nuchal organs (crests which extend from the tentacles to the eyes and ventrally) and the types of parapodial glands and lobes present. Uschakov (1972) recognised four kinds of parapodial glands: chromophile glands (large glands consisting of ducts with a common opening) which are found on the ventral parapodial lobes from segment 3 or 4; hyaline glands, which have small red to dark brown ducts present on dorsal and ventral lobes of

a single parapodium; rosettes, which are modified hyaline glands present on ventral parapodial lobes of the first two or more segments, and; spur glands, which are present with chromophile glands on ventral parapodial lobes. Greeff (1882) reported bioluminescent parapodia in *Tomopteris*, but it is not clear which of the parapodial glands are bioluminescent (Meyer 1924). Uschakov (1972) stated that the chromophile glands are luminescent organs, but there have been no comparative studies of the structure or function of these glands.

Excretion occurs via protonephromixia (Åkesson 1964). Seminal vesicles in male *Tomopteris onisciformis* store sperm collected from the coelom (Schroeder & Hermans 1975). Meyer (1926) described unique oviducts in *Tomopteris catharina* which appear to be unrelated to typical polychaete coelomoducts (Schroeder & Hermans 1975). Terio (1950a) has suggested that asexual reproduction occurs, but this remains unsubstantiated. Terio (1950b) reported hermaphroditism in *Enapteris euchaeta*.

Innervation of the head and tentacular cirri has been described briefly by Meyer (1924). Åkesson (1962) presented details of the development of the head of *Tomopteris helgolandica* and clarified the homologies of the first segments and its appendages.

The tissue of *Tomopteris* is much higher in protein, lipid and carbohydrate than other so-called gelatinous zooplankton (Clarke *et al.* 1992) and may be a significant planktonic food resource. Åkesson (1962) reported that *Tomopteris helgolandica* may be so abundant in Swedish waters that it fouls prawn trawling nets.

The Tomopteridae are frequently included for convenience in taxonomic treatments of the pelagic families of the Phyllodocida, but only Gravier (1896) and Meyer (1926) considered that tomopterids and phyllodocids are related, because of similarities in the nephridial system and development of the mesoderm. However, Schroeder & Hermans (1975) considered the oviducts of *Tomopteris* to be unique, as are the cephalic appendages (Uschakov 1972). Rouse & Fauchald (1997) placed Tomopteridae in the order Phyllodocida, but their affinities with other families in that order remain unclear.

The only confirmed fossil tomopterid is *Eotomopteris aldridgei*, from the Carboniferous of Scotland (Briggs & Clarkson 1987). *Spriggina*, from the late Precambrian Ediacara Fauna of South Australia, was originally considered to be related to tomopterids (Glaessner 1958), but Glaessner (1984) later retracted his opinion. Conway Morris (1979) has even doubted the placement of *Spriggina* in Polychaeta.

Family Typhloscolecidae

The Typhloscolecidae are small, transparent, pelagic polychaetes of uncertain affinity. They are distinguished by having reduced parapodia with large paddle-like dorsal and ventral cirri; the cirri are readily lost in preserved specimens.

The prostomium tapers to an anterior median antenna and nuchal organs are present as a pair of large occipital crests. Palps and paired antennae are absent. A single median antenna is present in two (*Travisiopsis* and *Typhloscolex*) of the three known genera (Fig. 1.92A, B). A muscular eversible pharynx is present, but terminal papillae have not been observed; jaws are lacking. A glandular organ of unknown function, termed the retort organ, lies in the dorsal wall of the pharynx. Two or three anteriormost segments each carry a

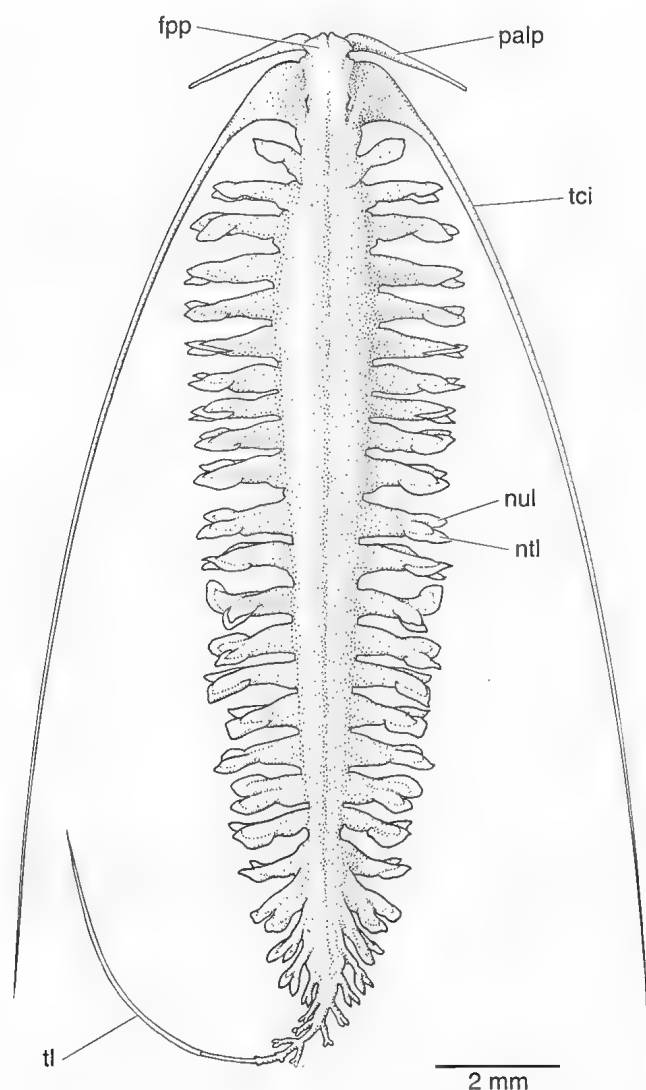


Figure 1.91 Family Tomopteridae. *Tomopteris australiensis*, dorsal view of entire animal. **fpp**, fused prostomium and peristomium; **ntl**, notopodial lobe; **nul**, neuropodial lobe; **palp**, palp; **tci**, tentacular cirrus; **tl**, tail. [K. Nolan]

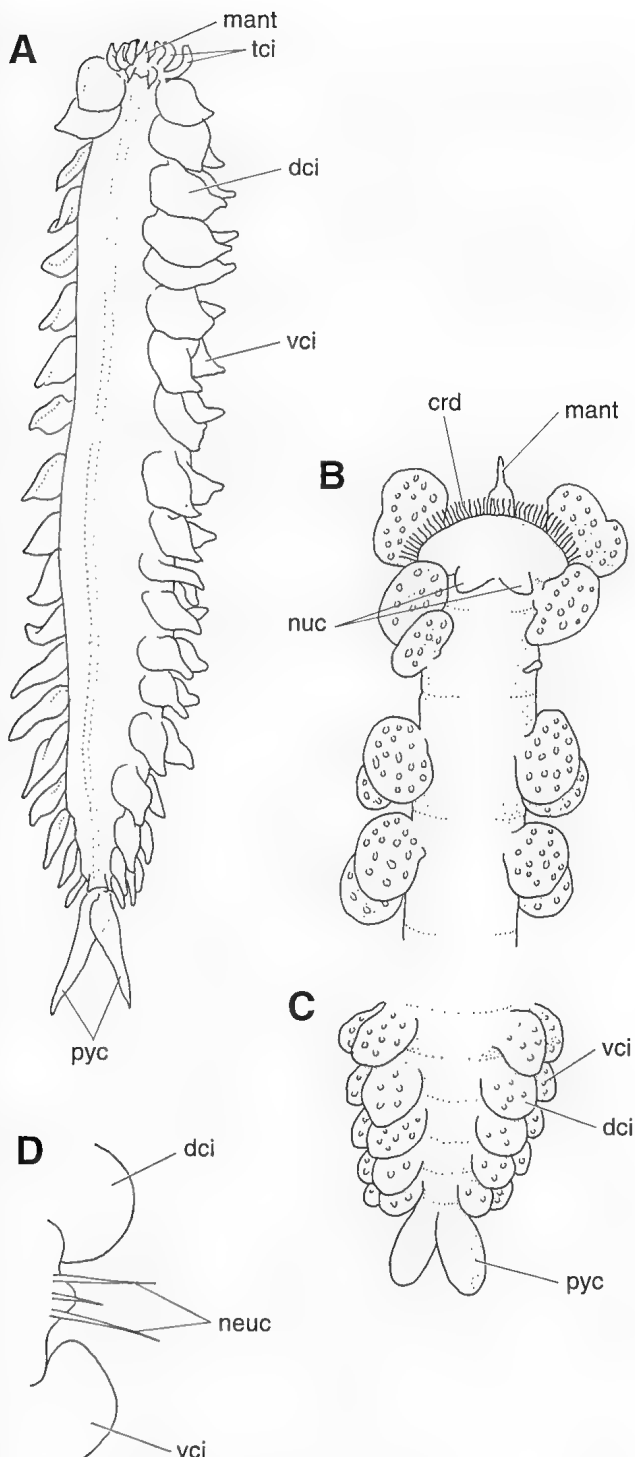


Figure 1.92 Family Typhloscolecidae. **A**, *Traviopsis lanceolata*, dorso-lateral view of entire animal. **B**, anterior end of *Typhloscolex muelleri*, dorsal view. **C**, posterior end of *Typhloscolex muelleri*, dorsal view. **D**, parapodial lobes of *Traviopsis lobifera*. **crd**, ciliated ridge; **dci**, dorsal cirrus; **mant**, median antenna; **neuc**, neurochaeta; **nuc**, nuchal organs; **pyc**, pygidial cirrus; **tci**, tentacular cirri; **vci**, ventral cirrus. (After Uschakov 1972, scales not available) [K. Nolan]

pair of leaf-like cirri which enclose the prostomium laterally. The parapodia are biramous; the neuropodia are larger than the notopodia (Fig. 1.92D). Aciculae and chaetae, as capillaries and spines, are present. There is a pair of pygidial cirri (Fig. 1.92C). This description follows that of Fauchald & Rouse (1997).

Three genera, *Sagitella*, *Traviopsis* and *Typhloscolex* are currently recognised; these are distinguished by the form of the prostomium (presence or absence of a ciliated ridge;

Fig. 1.92B) and presence or absence of a median papilla. Detailed species descriptions are given by Friedrich (1950). Dales & Peter (1972) provided a synopsis of records from worldwide localities, and Uschakov (1972) provided a key to the genera.

Thirteen species of Typhloscolecidae are currently known. None is recorded from Australian waters, but at least five species (from the three genera) have distributions which indicate that they will eventually be found in Australian waters (Dales & Peter 1972). Two species, *Traviopsis levinseni* and *Typhloscolex muelleri* are known from the waters of the Australian Antarctic Territory (Hartman 1964). *Sagitella kowalewskii* is known from New Zealand (Benham 1929). Elsewhere, typhloscolecids range from polar to tropical waters and from the surface to depths exceeding 4000 m (Uschakov 1972).

Worms may reach 40 mm in length and have 50 segments, but are generally less than 15 mm with fewer than 30 segments (Uschakov 1972).

Little is known of the biology of typhloscolecids apart from a study of *Sagitella* species by Uljanin (1878), who reported protogynous sequential hermaphroditism, release of gametes through gonoducts which develop at gametogenesis, and brooding of young which remain attached to the parent.

Chaetognaths appear to be an important food item of typhloscolecids. Øresland & Pleijel (1991) reported an unidentified species of *Typhloscolex* ectoparasitic on the chaetognath *Eukrohnia hamata*. Feigenbaum (1979) reported that species of *Typhloscolex* and *Sagitella* eat the heads of *Sagitta* and other chaetognaths. The chaetognaths are much larger than their predators, but only the head of the chaetognath is eaten, perhaps partly explaining the frequency of headless and damaged chaetognath specimens in plankton samples.

Dales (1955b) speculated that typhloscolecids may have arisen by neotenus extension of the larval phase of a benthic polychaete, but he did not discuss the relationships that they may have with other families. Uschakov (1972) and Fauchald (1977) agreed that the Typhloscolecidae are of uncertain affinity, although Rouse & Fauchald (1997) placed them in the order Phyllodocida.

ACICULATA INCERTAE SEDIS

Rouse & Fauchald (1997) placed three families, Aberrantidae, Nerillidae and Spintheridae, as members of the Aciculata, but did not place them within any other sub-taxon of the group. No-one has suggested that these three taxa are related and they almost certainly will be found to have sister groups with different members of the Aciculata. Members of Nerillidae and Spintheridae have been recorded from Australian waters, but members of Aberrantidae are unknown.

The first member of Aberrantidae was described by Hartman (1965) without being assigned to a family, but was compared to the spionids, based on observations of the palps. The family was named by Wolf (1987) who also described a second species, but made no comments as to their systematic placement. He had, however, indicated that *Aberranta* was a link between the Paraonidae and Spionidae (Wolf 1984a). Mackie *et al.* (in preparation) suggested that the family is more closely related to a euniciform group or the Nerillidae than to any other polychaetes. Currently, only two aberrantid species are known, both from the Atlantic Ocean.

1. CLASS POLYCHAETA

The Nerillidae were placed within the now defunct, Archiannelida (Goodrich 1912). However, their relationship to other polychaetes is still unclear, although the presence of compound chaetae in some members clearly supports their probable placement somewhere within Aciculata. Purschke (1985b) found a high degree of similarity in the pharyngeal organ of nerillids and protodrilids, and Orrhage (1974) presented evidence for a relationship to the Spionida. Westheide (1990) remarked that nerillid morphology was similar to that of juvenile onuphids. Rouse & Fauchald (1997) found the Nerillidae to be consistently a basal group of the Aciculata. Further study of the nerillid palps, chaetae and other structures may help identify a sister group within Aciculata.

Members of the Spintheridae are ectoparasites of sponges. They have been considered to be related either to amphinomids and euprosinids (see Fauvel 1923; Hartmann-Schröder 1971) or treated as a separate order (see Fauchald 1977). Sharov (1966) considered spintherids ancestral to the arthropods, but Manton (1967) reviewed their anatomy and comprehensively rejected Sharov's views. In the analyses of Rouse & Fauchald (1997), the Spintheridae were either a basal polychaete group, a basal group of the Aciculata or the sister group to the Amphinomidae and Euprosinidae within the Aciculata. The latter placement is probably correct, but further study is required.

Family Nerillidae

Nerillids are minute worms which inhabit mainly the interstitial spaces of intertidal and subtidal sands. Small palps and antennae are usually present on the head and characteristic inter-ramal parapodial cirri are usually present along the body.

Nerillids measure about 0.3–2 mm in length; most species have nine segments, but as few as seven may be present (Fig. 1.93A). The prostomium is fused to the peristomium and bears three slender smooth or articulated antennae and a pair of clavate, lateral to ventro-lateral palps; both antennae and palps may be absent. Generally, all segments bear chaetae, but chaetae may be absent from the first segment. Chaetae are compound (Fig. 1.93B) or simple capillaries. Parapodial cirri are usually present, although they may be absent on some or all segments. In some species, for example, *Nerilla australis*, the cirri of the first segment are much longer than the following ones. The pygidium usually bears two anal cirri. The ventral pharynx has intracellular skeletal elements known as 'buccal pieces'.

Nerilla antennata, described by Schmidt (1848), was the only species in the family until Delachaux (1921) described *Troglochaetus beranecki* from a freshwater cave. The number of recognised genera and species has increased since 1921, bringing the present worldwide diversity to about 40 species in 15 genera. Only one, *Nerilla australis* described by Willis (1951), is known from Australia; it lives in salt marshes among mangroves and *Zostera* beds on Phillip Island, Westernport, Victoria. However, considering that *Nerilla antennata*, and species of *Mesonerilla* and *Nerillidium* have been reported from New Zealand (Riser 1984), more species are expected to be found in Australia. A new species of *Nerilla* has recently been discovered from a cave on Christmas Island (R. Wilson personal communication).

Most nerillid species are marine, living in infralittoral sediments where they browse on diatoms and bacteria on grains of sand; some live intertidally, in estuaries, or even in continental subterranean waters (Jouin 1971). They glide over

the substratum using the cilia of the midventral groove to propel themselves. The anatomy and ultrastructure of the pharyngeal organ has been studied by Purschke (1985b) and shown to be composed of a solid muscle bulbus, a tongue-like, rod- or bridge-shaped muscular organ, and a heavily ciliated lower lip. The intracellular skeletal elements ('buccal pieces') of the tongue-like organ are striated and associated with tonofilaments. Nephridia are in the form of metanephridia, protonephridia and enteronephridia (two to six blind-ending ciliated canals opening into the stomach) (Jouin 1967).

Nerillids are dioecious or protandric hermaphrodites. Eggs are produced in small numbers and are fertilised externally during pseudocopulation, or via spermatophores attached to the eggs or deposited in their vicinity (Jouin 1968). Development is direct. Oocytes are attached to the substratum singly or in groups (cocoons), or in a number of species attached to the female's body as in many syllids. The developing embryos are attached to the anterior or posterior end of the female, and leave her when they reach an advanced juvenile stage (Westheide 1990a).

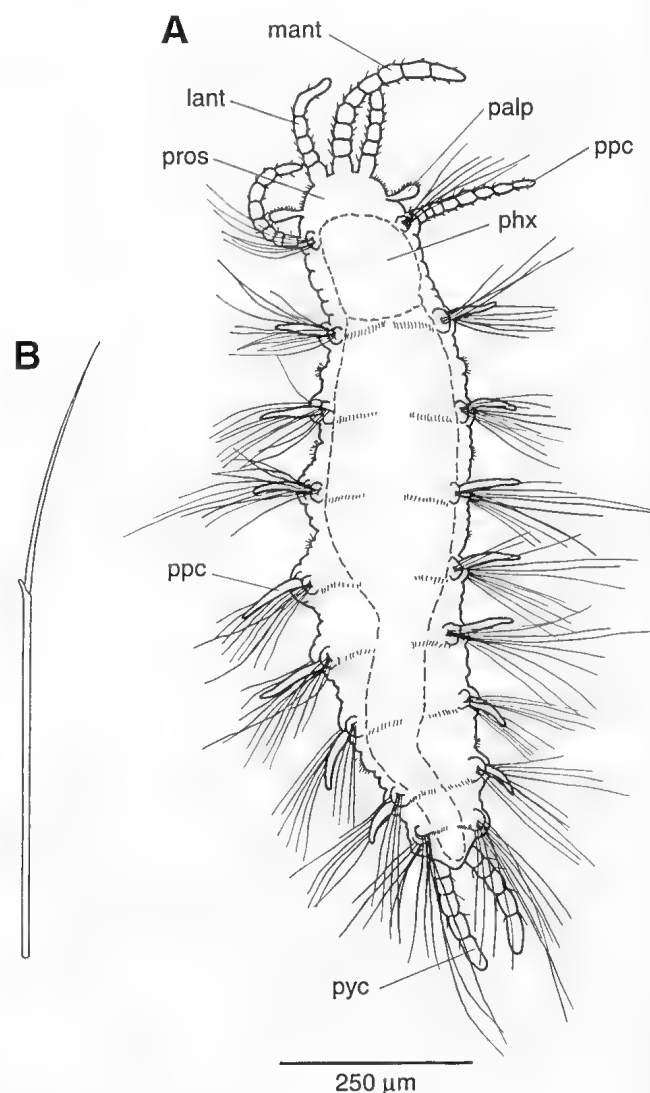


Figure 1.93 Family Nerillidae. **A**, entire animal of *Nerilla australis*, dorsal view. **B**, compound chaeta of *Mesonerilla roscovita*. **lant**, lateral antenna; **mant**, median antenna; **palp**, palp; **phx**, pharynx; **ppc**, parapodial cirrus; **pros**, prostomium; **pyc**, pygidial cirrus. (A, after Willis 1951; B, after Westheide 1990a) [A. Murray]

The Nerillidae were placed with the Archiannelida. However, the traditional view of the 'archiannelids' as primitive ancestors of the annelids (see Hermans 1969 for a review) became increasingly rejected (Fauchald 1977). Their relationship to other polychaetes is still unclear. Purschke (1985b) found a high degree of similarity in the pharyngeal organ of nerillids and protodrilids, and Orrhage (1974) showed some evidence for a relationship to the Spionida (*sensu* Pettibone 1982). However, the present treatment follows Rouse & Fauchald (1997) who treat the Nerillidae as *incertae sedis* in the Aciculata group pending further investigation.

Family Spintheridae

Spintherids are disc-shaped sponge ectoparasites or commensals. They are characterised by having long transverse notopodial ridges which carry spines.

Spintherids are dorso-ventrally flattened, ovoid-shaped polychaetes. The prostomium is minute, carries a single median antenna (Fig. 1.94A) and usually four eyes, and is enveloped by anterior parapodia. A muscular, cylindrical pharynx opens to a ventral mouth (Fig. 1.94B); jaws are absent. The peristomium and first segment are reduced and inconspicuous. The parapodia are biramous and elongate (Fig. 1.94C) with anterior ones directed anteriorly and posterior ones directed posteriorly; dorsal and ventral cirri are usually absent. A purported autapomorphy of the family is the presence of notopodia which form transverse membranous ridges over most of the dorsal surface (Fauchald & Rouse 1997). Notochaetae are spine-like, distally entire or bifid (Fig. 1.94D) and arranged in transverse rows. Neuropodia are cylindrical and carry compound neurochaetae which have a folded joint and a strongly curved blade (Fig. 1.94E). Detailed anatomical and morphological information on the group can be found in Graff (1888) and Manton (1967); Hartman (1948b) reviewed the taxonomy of the group.

The Spintheridae are an enigmatic group with no obvious close relatives among extant families. They have been classified under Amphinomorpha/Amphinomida (see Uschakov 1955; Clark 1969) or they are placed in their own order (Fauchald 1977; George & Hartmann-Schröder 1985). Rouse & Fauchald (1997) considered the family *incertae sedis* within the large clade Aciculata.

The family contains a single genus, *Spinther*, and 12 species (Yamamoto & Imajima 1985). Only one species, *Spinther australiensis* has been described from Australian waters, although another, possibly undescribed, species occurs in Jervis Bay, New South Wales (Fig. 1.94A). The majority of known species occur in cold waters of the Northern Hemisphere, although this may, in part, reflect collecting effort. Apart from *S. australiensis*, the only other known Southern Hemisphere species is *S. usarpia* from the Antarctic Peninsula (Hartman 1967).

Spintherids live in association with sponges. They are either ectoparasites feeding directly on the sponge, or feed commensally on the epibionts associated with the host (Jeuniaux 1969; Fauchald & Jumars 1979). Some species also occur with hydrozoans (George & Hartmann-Schröder 1985). They have a sedentary lifestyle, being incapable of strong locomotory movements because of weak body wall musculature. They attach to the surfaces of sponges using their strongly-curved compound neurochaetae and are inconspicuous as a result of being the same colour as their host (Manton 1967; George & Hartmann-Schröder 1985).

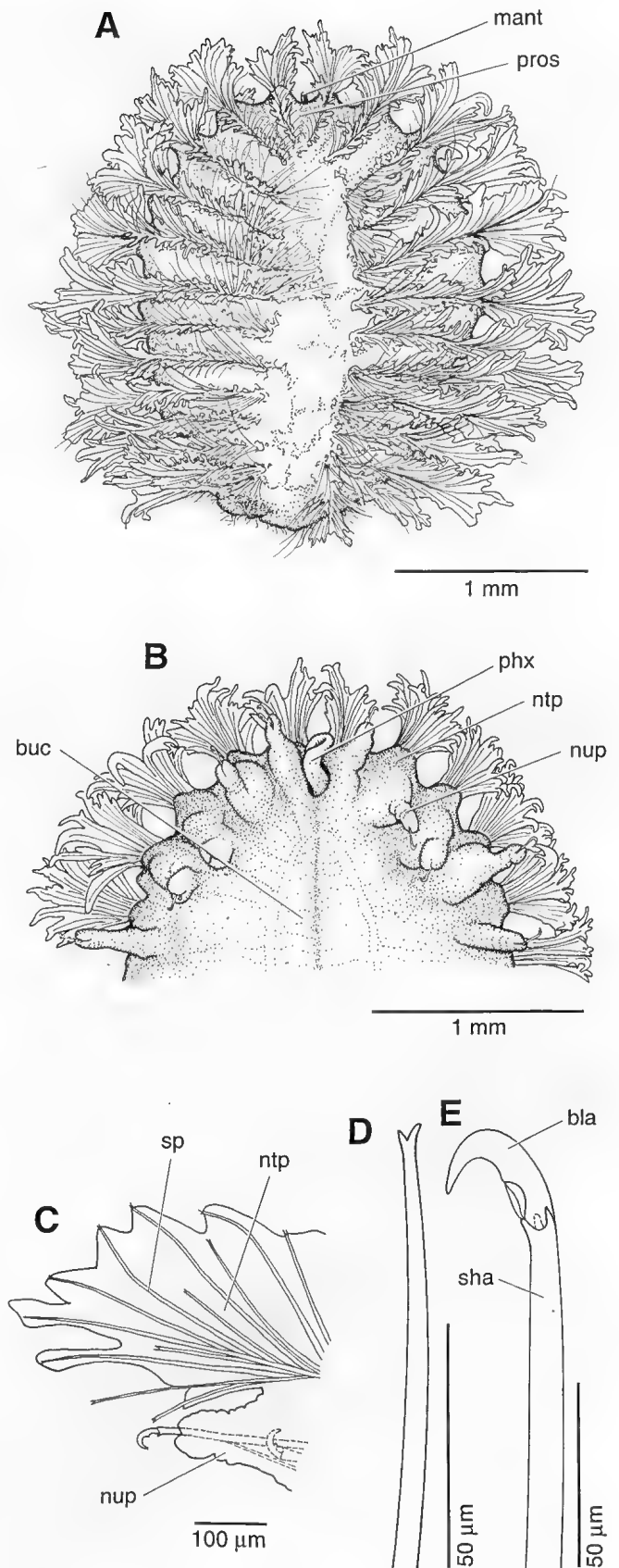


Figure 1.94 Family Spintheridae. *Spinther* species. **A**, entire animal, dorsal view; posteriormost parapodium on left hand side missing. **B**, anterior end, ventral view. **C**, neuropodium and part of notopodium from chaetiger 8, anterior view. **D**, notochaetal spine from chaetiger 8. **E**, compound neurochaeta from chaetiger 8. **bla**, blade; **buc**, buccal organ; **mant**, median antenna; **ntp**, notopodium; **nup**, neuropodium; **phx**, pharynx, partially everted; **pros**, prostomium; **sha**, shaft; **sp**, spine. [A. Murray]

Spintherids range in size up to 50 mm, but are typically less than 30 mm in length with several species less than 10 mm; maximum number of segments is about 50 (Yamamoto & Imajima 1985). The characteristic flattened discoidal bodies (Fig. 1.94A) develop with age, so that in *S. arcticus* body shape is not established until the worm is about 9 mm long (Manton 1967). Morphological characters used to discern species include whether or not the venter is papillated, the presence or absence of a distal cirrus on the neuropodia and the fine structure of the chaetae (Yamamoto & Imajima 1985).

The ventral pharynx is weakly muscular and can be everted completely, tongue-like, without being turned inside out as in other polychaetes, in order to feed on soft tissue of the sponge (Fig. 1.94B; Manton 1967; Dales 1977). The pharynx opens externally through a ventral mouth and connects internally via a short oesophagus into an expansive gut characterised by many pairs of lateral gut diverticula; these extend from the intestinal zone between the septa to the periphery of the animal (Graff 1888; Manton 1967).

CANALIPALPATA

Canalipalpata is a group of polychaetes established and named by Rouse & Fauchald (1997) in their reclassification of Polychaeta; the name refers to the presence of grooved palps. Canalipalpata is a massive group of polychaetes that encompasses about half of the diversity of the group, as indicated in the cladogram (Fig. 1.95). The complete membership of the Canalipalpata is shown in Table 1.3. Together with its sister group, Aciculata, the Canalipalpata comprise the Palpata.

Rouse & Fauchald (1997) included Pogonophora within Canalipalpata as Siboglinidae, but this group is treated separately in this volume as Pogonophora (see Chapter 3). Of the remaining families, members of most have been recorded and described from Australian waters. The synapomorphy for the Canalipalpata is the presence of grooved palps. The groove along each palp is longitudinal and ciliated and these palps, in contrast to those of the Aciculata, are feeding structures. Rouse & Fauchald (1997) identified three major clades within Canalipalpata and a number of taxa that are regarded as *incertae sedis* for the group.

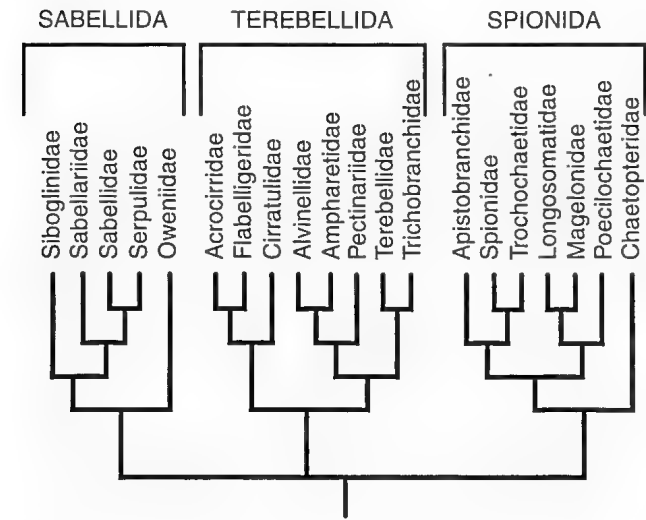
The three major clades of Canalipalpata are Spionida, Sabellida, and Terebellida (Fig. 1.95). These names have quite a long history, and in the case of the latter two taxa the membership has been reformulated significantly by Rouse & Fauchald (1997). The variable nature of the grooved palps, in terms of position and number, was used by Rouse & Fauchald (1997) to subdivide Canalipalpata. In many cases, the palps are peristomial structures (for example, Spionida, Sabellariidae, Acrociiridae, Pectinariidae) and this would appear to be the plesiomorphic condition for the group. However, they may also be prostomial structures, as seen in Sabellidae, Terebellidae and Oweniidae. The number and basic structure of the palps is also variable with members of the Acrociiridae, Flabelligeridae, Sabellariidae, and Spionida, always having a single pair of grooved palps. In the Sabellidae and Serpulidae, the palps have been transformed into a tentacular crown and in many members of the Terebellida there are multiple (sometimes hundreds) grooved palps. Many representatives of each of Sabellida, Spionida and Terebellida have been recorded from Australian waters.

Four *incertae sedis* families have been assigned to Canalipalpata: Polygordiidae, Protodrilidae, Protodriloididae and Saccociridae. These families were formerly grouped within the now defunct, Archiannelida. All have structures that appear to be homologous with a pair of grooved palps, though those of the Polygordiidae and Protodriloididae are solid and further morphological investigation is required to determine their position. Members of Polygordiidae and Protodriloididae have not been reported from Australian waters, although they have been recorded from New Zealand (Riser 1984; von Nordheim 1989); both are likely to also occur in Australia. Several members of Saccociridae have, however, been described and studied from New South Wales waters (Brown 1981), and a few species of Protodrilidae have been recently collected from Queensland.

SABELLIDA

Classifications of polychaete annelids have previously grouped Serpulidae Latreille, 1825 (fan worms) with Sabellidae Latreille, 1825 (feather-duster worms), based on the shared presence of the tentacular crown (Figs 1.99A, 1.101A), under such names as Serpulacea (Grube 1850; Malmgren 1866; Meyer 1888), Sabelliformia (Levinsen 1883; Benham 1896) and Serpulimorpha (Hatschek 1893; Hemplemann 1931; Uschakov 1955). Dales (1962a) proposed that the serpulids and sabellids be grouped at the ordinal level as Sabellida and this name has subsequently been used most commonly (for example, Fauchald 1977; Pettibone 1982), although the membership and lower level classification within the order have been unstable.

The family Sabellariidae (sand-mason worms) was considered by Meyer (1888) and Hatschek (1893) to be the sister group to the sabellid/serpulid clade, but this view was subsequently ignored or rejected in most classifications (for example, Dales 1962a; Fauchald 1977; Pettibone 1982). Dales (1962a) argued that sabellariids are more closely related to spionid taxa than to members of Sabellida. He contended that the morphological features used to ally the sabellariids with Sabellida, such as an anterior pair of nephridia with a single opening and the presence of chaetal inversion were based on inaccurate observations. Orrhage (1980) has shown, however, (see also Krishnan 1950) that sabellariids have separate exits for the anterior pair of nephridia, a situation also found in families such as Cirratulidae and Flabelligeridae. Dales (1952b, 1962a) stated correctly that the chaetal distribution found in sabellariids differs from that in sabellids and



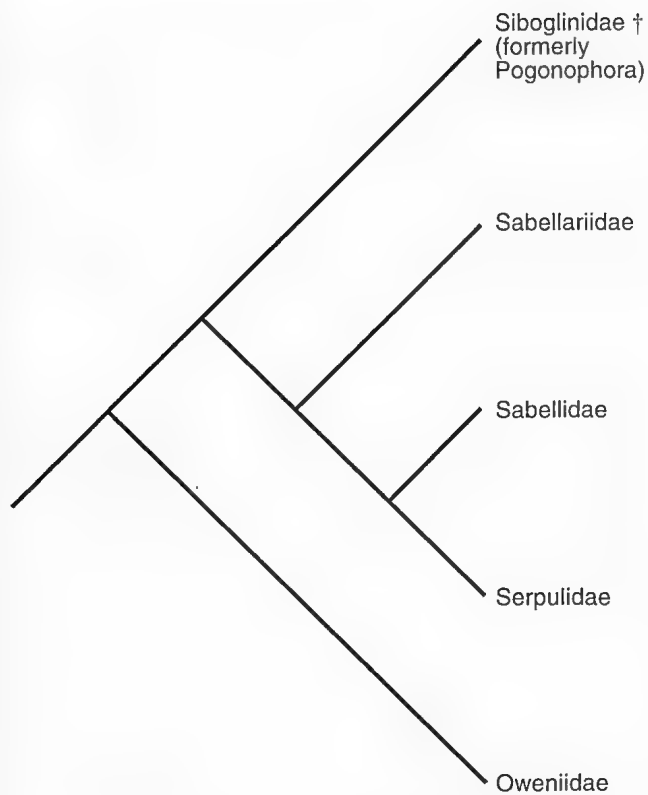


Figure 1.96 Cladogram illustrating the relationships amongst the members of the Sabellida. Based on Fitzhugh (1989) and Rouse & Fauchald (1997). †The family Siboglinidae is treated in this volume as Pogonophora.

serpulids. Members of the latter two taxa have an anterior thoracic region with dorsal (notopodial) capillary or limbate (hooded, *sensu* Fitzhugh 1989) chaetae and ventral (neuropodial) uncini, whereas the abdominal region has the opposite arrangement of chaetae. Sabellariids have an anterior parathoracic region with capillary or limbate chaetae in both notopodia and neuropodia. The abdominal region has notopodial uncini and neuropodial capillary chaetae (Fauchald 1977). However, the occurrence of uncini in a notopodial position in the abdominal region is found only in these three families. This dorsal occurrence of uncini (chaetal inversion) was used by Knight-Jones (1981) to re-align the sabellariids with the sabellids and serpulids; Holthe (1986a) subsequently placed the Sabellariidae Johnston, 1865 in the Sabellida.

Fauchald (1977) included five families in the Sabellida: the Caobangiidae, Sabellongidae, Sabellidae, Serpulidae and Spirorbidae. Fitzhugh (1989) assessed relationships amongst these families, finding that recognition of the monotypic families Caobangiidae and Sabellongidae left Sabellidae paraphyletic and placed the genera *Caobangia* and *Sabellonga* within Sabellidae. Serpulidae were paraphyletic, too, if the Spirorbidae were excluded and hence, he recommended that they be restored to subfamilial status in Serpulidae. Fitzhugh (1989) regarded Sabellariidae as belonging to the Sabellida, based on chaetal inversion. Rouse & Fauchald (1997) found the Sabellariidae to be the sister group to the Sabellidae/Serpulidae clade; the synapomorphy for the group is postulated here as the possession of notopodial uncini and neuropodial capillary or limbate chaetae in the abdominal region. The synapomorphies uniting the Sabellidae and Serpulidae are the presence of a tentacular crown, the single opening for the anterior pair of nephridia, and the inverted faecal groove (Fitzhugh 1989).

Rouse & Fauchald (1997) also found that the Oweniidae and Siboglinidae (formerly the Pogonophora) formed a clade with these taxa. They applied the name Sabellida to the clade that comprised all of these families (Fig. 1.96). The Sabellida is identified by the presence of a limited prostomium fused to the peristomium and the possible loss of peristomial lips. Further investigation is required on the status and delimitation of the Sabellida, but the classification of Rouse & Fauchald (1997) is followed here. The exception is that the Siboglinidae is treated here as the class Pogonophora (see Chapter 3). The position of the Oweniidae within Sabellida, in particular, warrants further investigation. In a cladistic analysis using larval characteristics, in addition to adult morphological ones, Rouse (1999) found that they form a clade with Polygordiidae, Protodrilidae, Protodriloididae and Saccocirridae, but no changes to the higher classification of Rouse & Fauchald (1997) were proposed.

Fitzhugh (1989, 1991a) studied the relationships amongst the genera of Sabellidae in some detail. Comprehensive analyses of the relationships within Oweniidae, Sabellariidae and Serpulidae have yet to be performed. Members of Serpulidae are common on hard substrata in all marine environments from the intertidal to the abyssal though they are more common in shallow waters. They are also found in brackish-water environments. Sabellids and oweniids can be found from intertidal areas to shelf depths and are usually associated with soft sediments. Sabellids can also be found in algal mats or attached to hard substrata. A few sabellids are found in freshwater; some sabellids are capable of boring into limestone and can be a factor in bioerosion of coral reefs. Sabellariids are important reef-builders on hard substrata in shallow marine waters.

Family Oweniidae

Oweniids live in characteristic tubes of cemented sand grains (Fig. 1.97E). They may have a crown (feeding and respiratory in function) or this may be absent. Oweniids have relatively few elongate segments and poorly developed parapodia with capillary chaetae and hooks.

The prostomium is fused to the peristomium. In *Owenia*, the head is a low, lobed terminal structure; in other taxa, it is rounded frontally, sometimes inflated and bilobed (Hartman 1969). The peristomium forms a complete ring behind the prostomium. Antennae are absent. The prostomial palps are lobed in *Owenia*, but may be a pair of grooved palps which emerge dorsally, or are lacking (illustrated in Hartman 1969). Nuchal organs have not been observed (Rullier 1951). The longitudinal muscles are grouped in bundles, and segmentation is present. The first segment is similar to the second segment; in these segments only notopodia are present. Subsequent segments have both notopodia and neuropodia. Notopodia are short, truncated cylinders; the neuropodia are wide with a flattened torus (Fig. 1.97A, B). There are no dorsal or ventral cirri, branchiae or epidermal papillae. Pygidial cirri are usually absent; although some species have multiple pygidial cirri. The buccal organ is eversible and ventral (Wilson 1932; Dales 1957b). Gular membranes are absent, and the gut is a straight tube. Segmental organs, termed mixonephridia by Goodrich (1945), open individually on one or a few anterior segments. The circulatory system is closed, and a heart body is lacking (S. Gardiner personal communication). Aciculae are absent. Various ornamented capillary chaetae (Fig. 1.97C) are present in the notopodia and very small, unhooded dentate hooks in the neuropodia (Fig. 1.97D). This description follows that of Fauchald & Rouse (1997).

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The family has been known as Ammocharidae, a name based on the invalid generic name, *Ammochares*, now regarded as a synonym of *Owenia*. No revisions of the family have been undertaken, although various biological investigations have been undertaken by Wilson (1932), Dales (1957b), Hartman (1969), Gardiner (1978), and Nilsen & Holthe (1985). Several regional faunistic works have treated oweniids, including those by Uschakov (1955), Clark (1960b) and Nilsen & Holthe (1985).

The oweniids lack a cuticle, and the structure of the body wall is different from all other polychaetes (Gardiner 1978; Gardiner & Rieger 1980). Some authors (for example, Bubko 1973) have suggested that oweniids are related to the 'archannelidan' families on the basis of the unusual morphological structure of the body wall. The presence and structure of small hooks (Fig. 1.97D) on the neuropodia has been used to group the oweniids with a variety of families from the Spionida to the Sabellida. Rouse & Fauchald (1997) placed the Oweniidae within the Sabellida.

Worldwide, five genera (*Owenia*, *Galathowenia*, *Myriochele*, *Myrioglobula* and *Myriowenia*) and at least 30 species are recognised; *Owenia* is the most speciose genus (based upon Fauchald 1977; Nilsen & Holthe 1985). Opinions vary as to the status of the other genera; one or two are known only from the type species. Nilsen & Holthe (1985) did not accept *Galathowenia* as a valid genus. No subfamilies have been recognised.

Hartman (1959a) in her catalogue of the world polychaetes suggested that several described species of *Owenia* should be synonymised with *O. fusiformis*, a species that has been reported widely from around the world. Based on a study of specimens of *O. fusiformis* from a range of localities around the world, Dauvin & Thiébaud (1994) found evidence to support Hartman's (1959a) idea that *O. fusiformis* was a 'cosmopolitan species', which lived from the low water mark to depths of 2350 m, except for the Antarctic. Dauvin & Thiébaud (1994) synonymised several other species of *Owenia* with *O. fusiformis*, although the type material of these species was not examined. Furthermore, relatively few characters were examined, namely the development of the thoracic collar, presence or absence of eye spots, thoracic pigmentation and the structure of the tube. In polychaetes, characters such as the structure of the tube and the presence or absence of eye spots are often site specific and not useful to separate species. Nilsen & Holthe (1985), for instance, found that the presence of eye spots in species of *Myriochele* was consistent only within a population, not a species. Use of other characters, such as the detailed structure of the notopodia and neuropodia, would be preferable for the elucidation of species. Thus the studies of uncini using scanning electron micrographs by Thomassin & Picard (1972) have proved very useful in distinguishing species.

In Australia, *Owenia fusiformis* has been widely reported, but the material has not been examined in detail or compared with material from the type locality of Naples. Nilsen & Holthe (1985) stated that no type material is available and may never have been designated. The only other oweniids recorded from Australia are undescribed or unnamed species of *Galathowenia*, *Myriochele*, *Myrioglobula* and *Myriowenia* collected off Sydney (Deep Water Ocean Outfall Monitoring program, unpublished records); voucher specimens have been lodged in the Australian Museum.

The family occurs worldwide from the intertidal zone to deep water in sandy and muddy sediments. However, the distribution of genera and species will remain somewhat confused until the taxonomy of the group is clarified.

Fauchald (1977) suggested that the family is uncommon in abyssal depths; one species has been found in the hadal zone of the Kermadec Trench at 8210–8300 m (Kirkegaard 1956). All species construct a characteristic tube made of fine sediment; *Owenia fusiformis* is encased in a relatively close fitting, tough tube longer than the animal (Fig. 1.97E).

Oweniids are usually small, ranging from a few millimetres to 20–30 mm in length with tubes 40–50 mm in length. However, *Owenia fusiformis* from the United Kingdom can attain 100 mm or more in length. Size differentiation between the sexes has not been recorded.

The structure of the ciliated epidermis on the feeding and respiratory crown of *Owenia* has been investigated in detail by Gardiner (1978). Unspecialised monociliated cells are the dominant cell type; currently *Owenia* is the only polychaete genus known to have such cells, also present in phoronids, brachiopods and the hemichordates. Storch (1988) stated that such cells are also widespread in primitive Metazoa.

The ultrastructure of the muscles found in *Owenia* have been investigated by Fontes *et al.* (1983). They studied the regeneration of muscle tissue following body damage.

Feeding in *Owenia fusiformis* has been studied in detail by Dales (1957b). These worms may feed either by ciliary means or by swallowing sand and detritus. During ciliary-feeding, the prostomial palps, which form the bilaterally symmetrical crown, are extended out through the elastic cone of transparent material extending from the entrance of the tube. This mobile crown has four main units per side, each divided into four to six branches which end in two to four small bifid lobes. Each of these lobes is strongly ciliated on its oral surface; these cilia move particles down the lobe into gutters at their base. Small cilia in the gutters beat inwards towards the axis of the crown. Mucus from cells present on both the oral and aboral surfaces of the crown assists in trapping particles. The crown forms a funnel at the base closed by a single dorsal lip and two ventro-lateral lips, all of which are expansions of the prostomium. The lips are hollow and extremely mobile. They are expanded by an inflow of coelomic fluid and have a complicated musculature with which they can generate a variety of rippling events. The crown also contains an extensive coelomic cavity. Closure of the crown is brought about by the circular crown muscles acting against the hydrostatic pressure of the body fluid; relaxation of the muscles permits the crown to open.

The mobile crown can thus direct mucus-coated strings of particles towards the mouth as well as discarding unwanted material. Ciliary-feeding occurs with the worm almost in a vertical position and may continue for many hours. During ciliary-feeding, the lips are not used very much, but they are important when the animal is manipulating sand grains and detritus. The animal ingests sand grains by bending over, until the crown sweeps the surface of the sediment. The crown then closes, picking up sand grains which are manipulated by the lips. Particles less than 200 µm are ingested; larger ones are either rejected or used for tube building or repairing the tube. The buccal organ lying below the ventro-lateral lips is used for applying the sand grains to the tube (Watson 1901) and is not involved in feeding. The feeding strategies of other oweniids have not been investigated.

The gut has a ciliated buccal region, a short ciliated oesophagus, a stomach region with highly involutioned walls, a mid-gut region with thinner and less convoluted walls, and a hind gut with very thin walls capable of great distension. Dales (1957b) investigated the histochemistry of the gut and suggested that the stomach is the primary, if not the only site

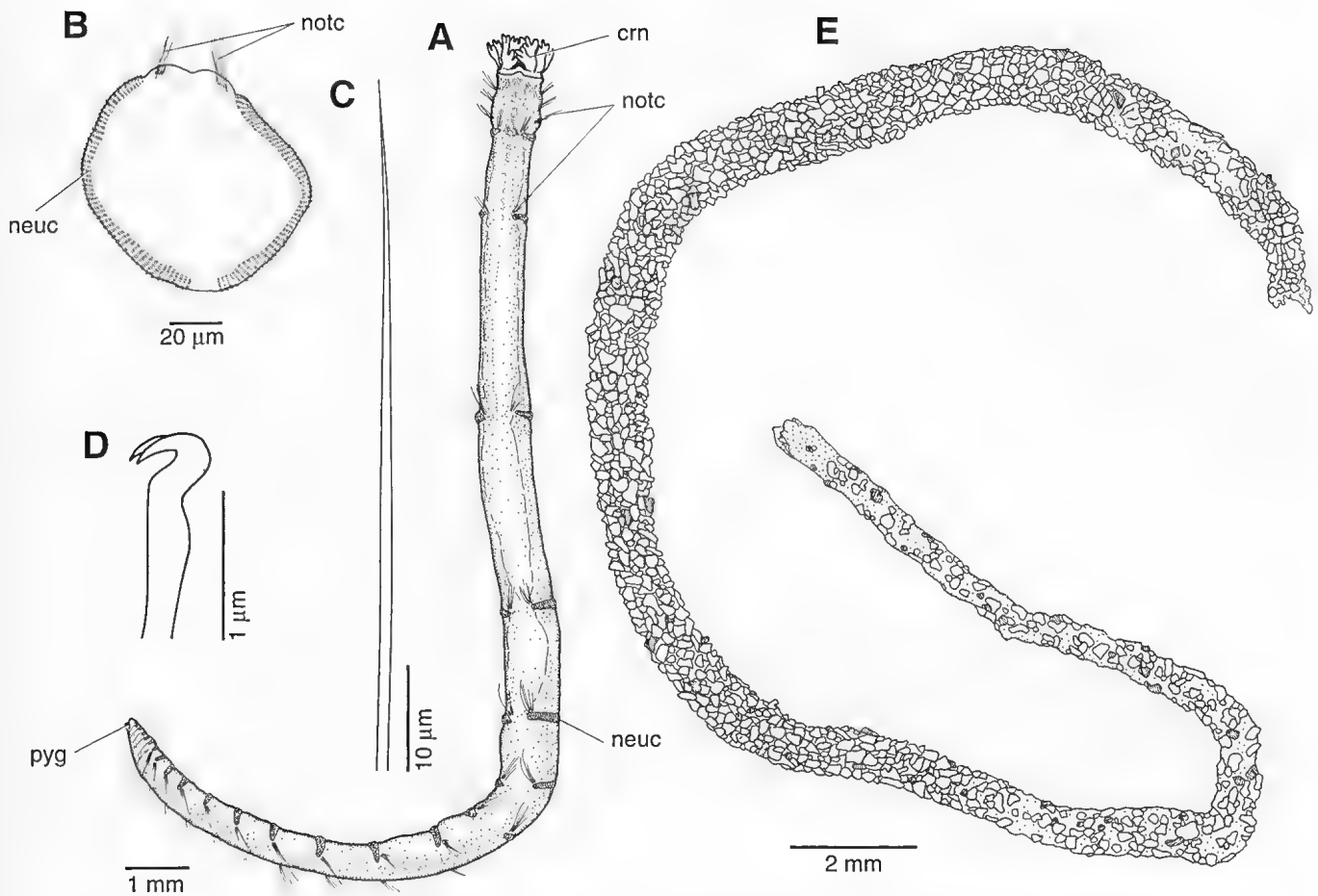


Figure 1.97 Family Oweniidae. *Owenia fusiformis*. **A**, entire animal, dorsal view. **B**, transverse section of body showing chaetal distribution. **C**, capillary notochaeta from parapodium of chaetiger 10. **D**, neurochaetal hook from parapodium of chaetiger 10. **E**, tube. **crn**, crown; **neuc**, neurochaetal 'patch'; **notc**, notochaetae; **pyg**, pygidium. [A. Murray]

for the secretion of enzymes; the mid-gut is the absorptive region and the rectum or hind gut stores and elaborates the faecal pellets. The worm reverses in its tube to defaecate.

The crown of *Owenia* is also used for respiration, its light reddish-brown to greenish colour reflecting its elaborate blood supply (Dales 1957b, 1958). *Owenia* has a well-developed closed vascular system and the respiratory pigment erythrocrucorin is dissolved in the blood (Wells *et al.* 1981); a heart body is lacking (Drasche 1885). Warren & Dales (1980) suggested that these worms have the ability to withstand prolonged anoxia. A study of those living at or just below the spring tide level showed that they are often buried by wave action; under such circumstances they must resort to anaerobic metabolism. The tube is not irrigated, but is two to three times longer than the worm and contains levels of dissolved oxygen similar to those in the surrounding sand (Wells *et al.* 1981). When the crown is expanded it is likely to be bathed in well-oxygenated water.

Wells *et al.* (1981) found the presence of erythrocrucorin surprising given the ability of these worms to live anaerobically. Such a blood pigment would greatly facilitate oxygen transport from the expanded crown where the partial pressure of oxygen is high to tissues where the partial pressure of carbon dioxide may be low. They suggested that erythrocrucorin may buffer tissue pH by binding protons released during anaerobic metabolism when the animal is buried in the sand. Although Warren & Dales (1980) could not measure the internal pH of the worm to confirm this,

because of its small size, they suggested that with appreciable desaturation of the blood pigment, activity could be maintained by anaerobic metabolism.

Metanephridia are present (Gilson 1895). Goodrich (1945) classified these as mixonephridia, although Rouse & Fauchald (1997) suggested that this needs to be confirmed. One or two pairs of nephridia are present; in *Owenia* they occur in the fifth chaetigerous segment. Gilson (1895) argued that they were responsible for gamete release, whereas Wilson (1901) observed spawning from the posterior region of the body through the anal pores. Subsequently, Smith *et al.* (1987) identified the protonephridia in the larvae of *Owenia* and they found that the terminal cells are not typical of polychaete larvae; rather, the paired nephridial sacs are lined by monociliated podocytes which rest on an underlying extracellular matrix. They suggested that this structure is primitive and may be the ground plan for all polychaete protonephridial terminal cells.

Lagutenko-Yu (1985, 1987) investigated the structural organisation of the nerve plexus in *Myriochele oculata* and, subsequently, related the synaptic endings in the basal lamina of this species to locomotion.

In *Owenia*, individuals may live up to 3 years in the English Channel. They are polytelic, although only a few individuals can reproduce at 1 year of age (Ménard, Gentil & Dauvin 1989; Gentil, Dauvin & Ménard 1990). The effective fecundity is correlated with the length of the female and may vary from 6000 eggs for a 40 mm female to 85 000 eggs for a female of 110 mm in length (Thiébaud & Dauvin 1991).

Rouse (1988) investigated the structure of sperm of *Owenia fusiformis* from Cleveland, Queensland. They have a cap-like acrosome, a subspherical nucleus, a small number of cristate mitochondria and two centrioles. Rouse inferred from this morphology that the gametes are released into the water column where fertilisation occurs; Rouse & Jamieson (1987) referred to them as ect-aquasperm rather than primitive sperm (Franzén 1956) to avoid any phylogenetic implications.

Wilson (1932) studied, in detail, the larval development of *Owenia fusiformis* from southern England. Gametes were released from two pores near the anus, and ripe individuals had swollen posterior segments full of gametes. Within 24 hours of external fertilisation, a distinctive planktotrophic mitraria larva was produced. Within 2–3 days the mitraria developed into a trochophore larvae which swam actively and could feed. After a pelagic larval stage of about 4 weeks, the larvae metamorphosed, but delayed settlement until a suitable substratum was available. Metamorphosis occurred rapidly and the juvenile then secreted a mucous tube in which sand grains became embedded.

The development and growth of juveniles of *Owenia fusiformis* from the eastern English Channel has been studied in detail by Thiébaud & Dauvin (1992). Significant growth only occurs after 6 weeks as a benthic larva and considerable variation occurs between individuals. The post-larval stage has a crown with six lobes. Subsequently, seven juvenile stages may be recognised with the number of lobes increased by successive dichotomous divisions and the growth of new branches (Thiébaud & Dauvin 1992).

Dauvin & Thiébaud (1994) summarised the breeding patterns of *Owenia fusiformis*, which range from populations exhibiting a discrete summer spawning (Cazaux 1973; Buchanan *et al.* 1978) to those which breed throughout the year (McNulty & Lopez 1969). Others showed maximum recruitment in the spring with lower levels of recruitment throughout the rest of the year (Fager 1964). Curtis (1977) reported that *Owenia fusiformis* reproduces asexually by fragmentation and regeneration in the absence of favourable conditions for gametogenesis and spawning. The range of variation in breeding patterns that have been reported would suggest that several species have been confused. Little information is available on breeding patterns in representatives of other oweniid genera.

Oweniids are commonly found in benthic surveys of soft sediments from estuaries to deep water. *Owenia fusiformis* was collected regularly, although in low numbers, from both muddy/sandy sites and *Posidonia* seagrass beds during the 3-year benthic study of Jervis Bay, New South Wales (Hutchings & Jacoby 1994). Densities were greater in muddy/sandy sites than in vegetated sites, with the highest numbers in deeper sites. Whereas maximum numbers were recorded in February (in all years) in the vegetated sites, no such pattern was recorded at the unvegetated sites. This may suggest that recruitment occurs over several months each year, although gravid individuals were not observed during the study.

A detailed phylogenetic study of the family has not been undertaken. Nilsen & Holthe (1985) suggested, based upon the development of the uncini, that *Myriochele* could be a paraphyletic taxon, and that *Owenia* and *Myrioglobula* are sister groups. They also considered that *Myriowenia* is the most isolated genus within the family, and contains many endemic species. Rouse & Fauchald (1997) regarded the paired palps found in *Myriowenia* as plesiomorphic and the crown present in *Owenia* to be derived.

Family Sabellariidae

Sabellariids, or sand-mason worms, live in a sandy tube cemented onto rocky substrata; some species form extensive reefs (not known from Australia). Sabellariids have short compact bodies divided into distinct sections. The head end consists of an operculum with numerous golden paleae which surround the mouth and the buccal cirri, and which almost fill the entrance to the tube.

The prostomium is fused to the peristomium and is largely indistinct, but forms, at least, a median keel. The peristomium is visible only as lips around the mouth. Antennae are absent. Paired palps are located lateral to the central ridge of the prostomium, and nuchal organs are present medial to the palpal base. The longitudinal muscles are grouped in bundles. Segmentation is distinctive. The first segment is completely fused to the head, with its notochaetae and those of the next segment forming the operculum, which consists of two lobes or peduncles the fusion of which varies between genera. The neuropodia are short cylinders, and the notopodia are reduced to tori (Fig. 1.98A, B). Dorsal and ventral cirri are absent. The branchiae lie dorsally and are flattened (Fig. 1.98A). Epidermal papillae and pygidial cirri are lacking. A ventral buccal organ and a gular membrane are lacking. The gut is a straight tube. The segmental organs are mixonephridia, comprising a single anterior pair of excretory organs, and posterior gonoducts. The circulatory system is closed and a heart body is present (Meyer 1887; Picton 1899). Aciculae are absent. Chaetal inversion is present: the uncini are notopodial rather than neuropodial, and the chaetae comprise variously decorated capillaries, spines and uncini (Fig. 1.98F–H). This definition is based on that of Fauchald & Rouse (1997).

Sabellariids were first described as sabellids, and moved to the terebellids by Savigny (1822). Grube (1850) placed them in a separate family among the limivores (sedentaries), and Levinsen (1883) gave them status as a separate suborder, using the name Hermelliformia. Dales (1963a) listed them in the order Spionida and Fauchald (1977) assigned them to the Terebellida. More recently, the sabellariids have been considered related to the sabellids and serpulids, based on the shared presence of chaetal inversion (Fitzhugh 1989). In the most recent classification of the polychaetes, Rouse & Fauchald (1997) placed them within the Sabellida (Fig. 1.96).

Sabellariids have also been referred to as the Hermellidae. The systematics of the family were revised by Hartman (1944b).

In 1977, Fauchald recorded seven genera and 61 species. Since then four new genera have been described (Carrasco & Bustos 1981; Lechapt & Gruet 1993; Kirtley 1994) and 46 new species, many by Kirtley (1994).

In Australia, only one species, *Idanthyrus australiensis*, has been recorded according to Day & Hutchings (1979). However, a revision of the family currently underway by Hutchings & Peart (in preparation), has identified four additional genera and about 14 undescribed species. These include unpublished records of *Idanthyrus pennatus* from southern Australia (Pl. 4.4), *Lygdamis giardi* from Botany Bay, New South Wales and *L. indicus* from off the Sydney coast, New South Wales (Australian Museum database).

Sabellariid species are largely distinguished on chaetal characters, especially the shape of the paleae (Fig. 1.98D, E); the family is fairly conservative in terms of gross morphology.

Most sabellariids live in colonies formed by mass settlement (Wilson 1970a, 1970b; Eckelbarger 1978) and often form major reefs (Schäfer 1972). All sabellariids build a tube of

sand grains which is firmly cemented onto a hard substratum (Fig. 1.98I). The majority of species occur in shallow water, including intertidal areas, but members of two genera (*Phalacrostemma*, *Monorchus*) appear to be common at slope depths (Fauchald 1977). At least one species, *Sabellaria cementarium*, forms reefs at some localities and in other areas is not gregarious (Pawlik & Chia 1991).

Sabellariids range from a few millimetres to 50–60 mm in length and have a robust body. Species exhibit no sexual dimorphism except perhaps when gravid and ripe male and female gametes may vary in colour.

Sabellariids are easily recognised by the presence of a well-developed operculum with one to three rows of golden paleae (Fig. 1.98A, D, E) which almost fill the entrance to the tube. The operculum covers the prostomium which may be completely fused dorsally, but is always free ventrally and bears numerous buccal cirri on either side of the mouth. The peristomium is completely fused to the prostomium and is in part covered laterally by the projecting first segment, the chaetae of which form part of the operculum. A cirriform lobe with a pair of grooved palps (peristomial in origin; Meyer 1887; Dales 1952b; Orrhage 1978) is present in front of the mouth.

The body is divided into four regions. The anterior section comprises two short uniramous segments with ventral capillaries only. The parathoracic region consists of three to four biramous segments with dorsal cirriform branchiae, stout oar-shaped notochaetae and capillary neurochaetae (Fig. 1.98G). The abdominal region is formed of numerous biramous segments with dorsal cirriform branchiae, notopodial uncini and neuropodial capillaries (Fig. 1.98B) and the caudal region comprises rudimentary achaetous segments which are bent back under the body (Fig. 1.98A).

The opercular paleae and the nuchal hooks are deciduous (Fig. 1.98C–E). Gruet (1991) provided quantitative information on the rates of production and shedding of these chaetae, which emerge on the surface of each side of the dorsal midline of the crown and then shift progressively from the dorsal to the ventral sides along the row where they are shed periodically (Ebling 1945).

A detailed study of the structure and evolution of the anterior end of several species of sabellariids has been carried out by Orrhage (1978). He provided a useful table listing the terms used by previous workers for the various anterior structures. Early comprehensive reviews of morphological studies on the group include those by Meyer (1888), Johansson (1927), Binard & Jeener (1928) and Gustafson (1930). Biochemical studies have been undertaken by Jorge *et al.* (1969); they found that ionic levels varied between males and females.

The gut of sabellariids is strongly differentiated along its length (Rouse & Fauchald 1997). Michel (1977) found that sabellariids have both absorptive and serous gland cells with a brush border of apical microvilli, but only the absorptive cells contain an apical layer of intracytoplasmic dense bodies; these are figured in Michel (1988). The gland cells contain zymogen granules that are thought to secrete proteolytic enzymes into the intestinal lumen.

Smith (1986) showed that the blood vascular system in *Sabellaria cementarium* begins to develop during the metatrochophore stage; at the same time as the onset of apposing basal extracellular matrices (ECM) of adjacent myoepithelial peritoneal layers and blood sinuses also form by separation of the basal ECM of peritoneal cells from the basal ECM of the gut epithelium. Blood vessels and sinuses

are lined only by the ECM of overlying cell layers. This species, like most polychaetes, has two well-developed fluid transport systems, the blood vascular system and the segmented coelomic cavities. This allows for fluid transport across septal bulkheads between regionally restricted sites; Ruppert & Carle (1983) hypothesised that this is of adaptive significance for animals partitioned by septa. The concurrent development of the coelomic and blood vascular systems in sabellariids provides additional support for this. Extracellular haemoglobins are not synthesised until later. It seems likely that blood vessel formation is coincident with the onset of feeding (Fransen 1988).

The branchiae of sabellariids presumably function as sites for oxygen exchange, but this needs to be confirmed.

Sabellariids have an anterior pair of excretory mixonephridia, and gonoducts posteriorly (Meyer 1887; Goodrich 1945). Smith & Ruppert (1988) suggested that peritoneal podocytes are the site of filtration for these systems. These podocytes overlie the vessels of the peri-oesophageal plexus situated near the nephrostomes of the nephridioducts (Smith & Ruppert 1988). Larval sabellariids at the trochophore stage have protonephridia (Smith & Ruppert 1988). These consist of a protonephridial duct, which opens distally via the nephridiopore at the surface of the animal, and ends proximally in specialised cells which are the sites of filtration.

The functional morphology of the larval tentacles of *Phragmatopoma californica* has been studied by Amieva & Reed (1987).

The brain is surrounded by ganglia cells except on the ventral side (Orrhage 1978). Four commissures are present, situated antero-dorsally, antero-ventrally, postero-dorsally and postero-ventrally. The first two communicate with the ventral roots of the oesophageal connective and last two commissures merge laterally into the dorsal roots of this connective. Orrhage (1978) detailed further the circum-oesophageal connectives and the manner in which the chaetal sacs are innervated. An elegant schematic figure of the cephalic nervous system; palps and the anterior chaetae is given by Orrhage (1978). He compared the general development of the brain with those of other polychaetes and confirmed his (1966) suggestion that the presence of the commissures in the brain of polychaetes is a primitive and generalised feature of the polychaetes. Orrhage (1978) described the innervation of the nuchal organs.

Populations of sabellariids appear to have similar numbers of males and females (Dales 1952b). Individuals may live up to 10 years (Wilson 1971), although Gruet (1986) suggested a life span of 3–5 years. After settlement, initial densities in reef-building species may be 4 million worms per m², but reduce to about 12 000–15 000 mature worms per m² within a few months (Kirtley 1994).

The ovaries of sabellariids are distinct, retroperitoneal, paired structures located on the genital blood vessels which extend from the caudal face of the intersegmental septa of abdominal segments (Fauré-Fremiet 1924; Eckelbarger 1979). Eckelbarger (1984a) suggested that direct uptake of yolk precursors from the circulatory system occurs. Oogenesis is not synchronised and all stages of development can generally be found within the ovary. Vitellogenesis occurs before the oocytes are released into the coelomic cavity. Two morphologically distinct types of yolk are produced during vitellogenesis, one apparently formed autotynthetically and the other heterosynthetically. During early larval development both types of yolk are present within the ectoderm and endoderm; the larvae begin to feed within 25–30 hours and

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utilise all the yolk within 60 hours. The structure of the surface of the mature oocytes has been investigated by Franklin (1966) and the factors determining the activation of oocytes by Peaucellier (1978) and Faure-Fremiet (1924).

The ultrastructure of spermatogenesis has been investigated in the reef-building species, *Phragmatopoma lapidosa*, by Eckelbarger (1984b). Spermatogonia are released into the coelom from the small testes; they are attached to the walls of the intersegmental blood vessels, where they develop into mature sperm. Franzén (1956) referred to the sperm as the 'primitive' type. The structure of the sperm of an Australian species, *Idanthysus pennatus*, has been studied by Rouse (1986). No studies appear to have been carried out on the factors controlling reproduction or spawning.

After external fertilisation, young trochophores are produced within 12 hours. Within 24 hours a recognisable prototroch has developed and the larvae are swimming actively. The larval development of *Phragmatopoma californica* was followed in detail by Dales (1952b). These soon become capable of feeding and within 36 hours the first pair of chaetal sacs are visible. By the time the larvae are ready to settle after about 2 months in the plankton they are clearly recognisable as sabellariids. Dales (1952b) observed the origins and homologies of the paleae, showing that they are derived from segments 1 and 2. He traced also the ontogenesis of the chaetae and observed chaetal inversion along the length of the body, thus explaining why the uncini are notopodial rather than neuropodial.

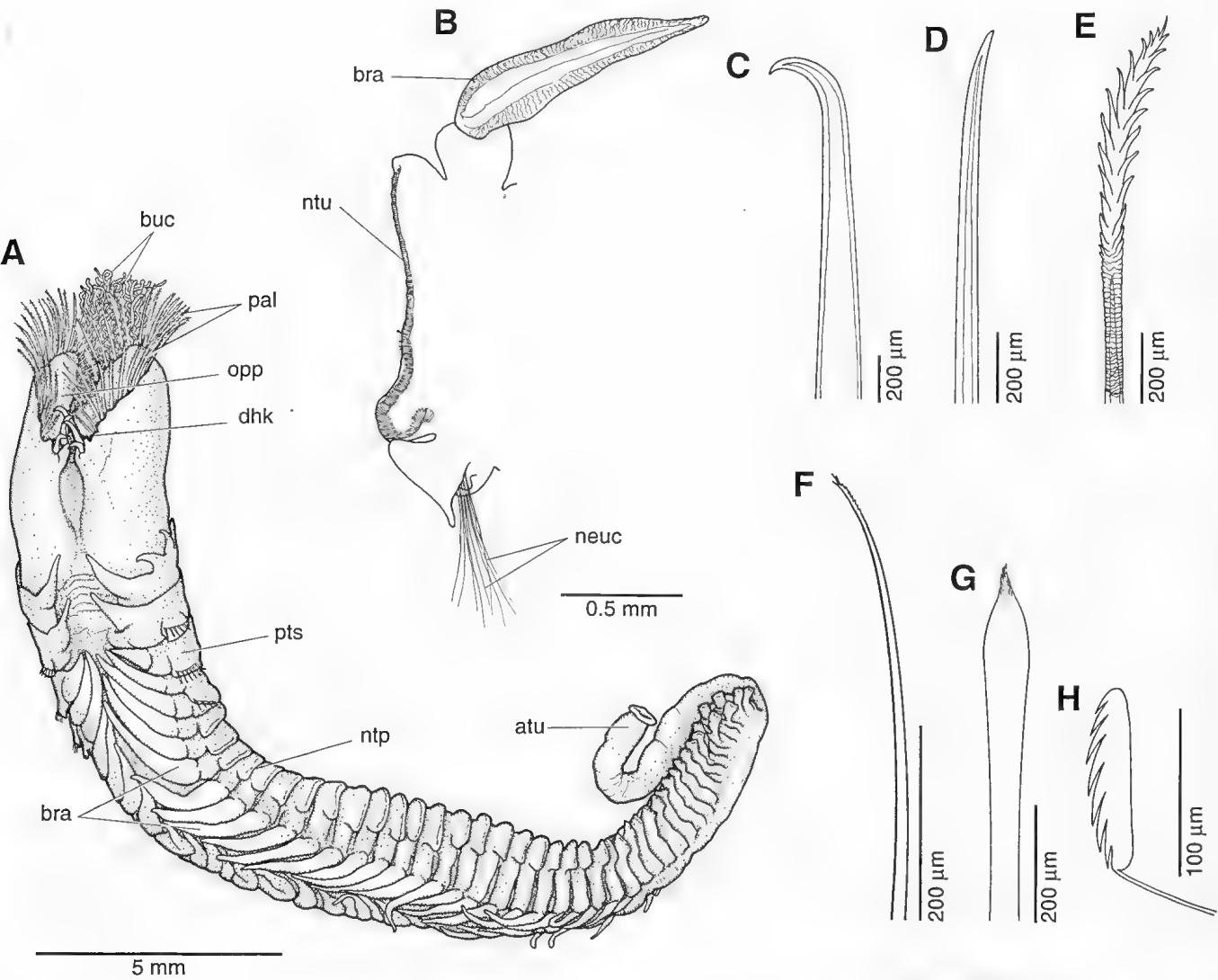
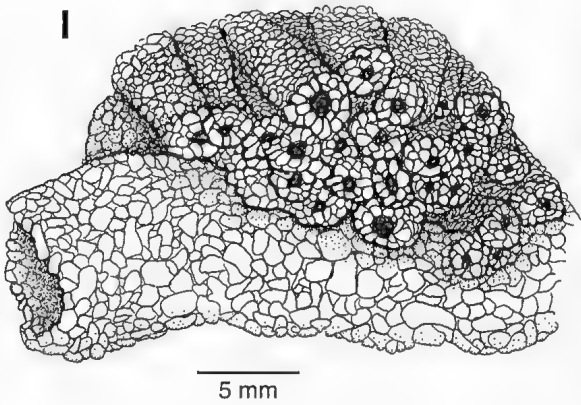


Figure 1.98 Family Sabellariidae. *Idanthysus pennatus*. **A**, entire animal, dorso-lateral view. **B**, parapodium of chaetiger 7, posterior view; **C**, a dorsal hook from the operculum. **D**, inner palea from opercular peduncle. **E**, outer palea from opercular peduncle. **F**, **G**, chaetae from (parathoracic) chaetiger 2: **F**, accessory chaeta; **G**, oar-shaped chaeta. **H**, notopodial uncini from chaetiger 1. **I**, part of tube aggregation. atu, anal tube; bra, branchiae; buc, buccal cirri; dhk, dorsal hook; neuc, neuropodial capillary chaetae; ntp, notopodium; ntu, notopodial uncini; opp, opercular peduncle; pal, paleae; pts, parathoracic segment. [A. Murray]



The metamorphosis of other species of sabellariids has been studied by Eckelbarger (1978), who found that the larvae in general respond positively to a weak light source, although some show no response. Earlier studies by Wilson (1929) clearly established that pre-metamorphosed larvae can detect the adult tube cement or mucoid tubes of other larvae; during the searching phase immediately prior to settlement the larvae contact the substratum with their ventral surface, mouth region and tentacles. He found also that aged tube cement was less effective than fresh cement in inducing settlement, suggesting that microbial growths or other surface films might prevent larvae from detecting these substances. Wilson (1970a, 1970b) also found that settling larvae can distinguish between the natural tubes of their own species and those of sympatric species. Larvae can also delay metamorphosis until a suitable substratum is available (Wilson 1977).

The marked variability in development times for larvae reported within a range of species under laboratory conditions has been reviewed by Pawlik (1986, 1988a, 1988b). Factors such as temperature and nutritional quality of the phytoplankton are important (Pawlik 1990). Similarly, species exhibit varying patterns of spawning, some spawning all their gametes during a restricted breeding season (polytelic reproduction), and others apparently breeding throughout the year. This contradicts Smith & Chia (1985) who suggested that all sabellariids are polytelic. Pawlik & Chia (1991) discussed how two species of sabellariids co-occurring along the west coast of the United States of America maintain their isolation by temporal separation of spawning and hybrid inviability. This may explain why the two species are clearly separated within a subtidal reef, with *Sabellaria cementarium* making up the upper reef and *Idanthyrus ornamentatus* occurring on the lower parts of the reef (Posey *et al.* 1984). Pawlik & Chia (1991) suggested that differences in the location of competent larvae in the water column may serve to separate these species. Larvae may partition themselves as a function of water depth by responding differently to light, temperature or pressure. Also, Pawlik (1988b) showed that free fatty acids (FAA) are responsible for inducing settlement in *Sabellaria* and *Phragmatopoma*. The two genera differed considerably in the amount of FAAs produced; the FAAs are part of a highly specific chemosensory mechanism for larvae to recognise the presence of adult conspecifics, and such differences may be widespread within the family.

Based on a detailed study of eight species, Eckelbarger (1978) suggested that the changes occurring at metamorphosis follow a typical and distinctive pattern characteristic for each species (see tabulated results in Eckelbarger 1978). At metamorphosis the larvae construct mucoid tubes which are attached to a stable substratum; the tentacles start to gather sand grains which are cemented to the mucoid tube by secretions from the building organ. Amieva *et al.* (1987) have identified sensory organs potentially involved in substratum selection.

The planktonic larval stages of sabellariids are generally similar and difficult to identify to species until the paleae develop (Mauro 1975). A summary timetable of the various larval stages for different species is provided by Eckelbarger (1977).

The development of the sabellariid larval cuticle has been studied. Eckelbarger & Chia (1978) showed how the egg envelope is incorporated into the larval cuticle and retained up to the 16-hour trochophore stage when it is gradually replaced by one consisting of branching microvilli.

Most sabellariids are shallow-water; reef-building colonial tube-dwellers which build a tube of sand grains cemented to a hard substratum (Wilson 1970a, 1970b; Schäfer 1972;

Eckelbarger 1978). The structure of the cement, which binds the sediment grains together, has been investigated by Jensen & Morse (1988). The cement is made up of at least one type of protein, similar to a silk protein. This material is secreted by the tube-building organ located just beneath the mouth and other glandular areas on the ventral surface of the parathoracic segments (Vovelle 1965). Reef-building species construct massive aggregations of vertically arranged, honeycomb-like, parallel tubes, primarily composed of sand grains and shell fragments. The amino acid composition of sabellariid tubes has been summarised by Gaill & Hubt (1988).

Extensive reefs are formed by *Phragmatopoma lapidosa* from Brazil to southern Florida (Hartman 1944b). Several studies have investigated the effect these extensive intertidal reefs have on beach sediments (Kirtley 1967; Multer & Milliman 1967; Gram 1968). Gram (1968) showed how the worms select the finer sediments for building their tubes, with a consequent significant effect on the distribution of beach sediments. Caline *et al.* (1988) have shown how the interaction of hydrodynamic and sedimentological factors plays a major role in promoting or restricting the distribution of sabellariids. In areas where sabellariids form major reefs, they change the beach profile, wave patterns and modify sediment sorting regimes on beaches. Removal of these reefs would modify beach profiles and could lead to changes in sediment movement along the coast.

Eckelbarger (1978) noted that not all species of sabellariids form extensive colonies. *Sabellaria floridensis* and *Lygdamis muratus*, from Florida and the English Channel, respectively do not form reefs and the larval behaviour of these species is very different from those of species that do form extensive reefs. Similarly, no Australian species are known to form extensive colonies.

Populations of *Phragmatopoma lapidosa* have been investigated in Florida (Eckelbarger 1976a). Larval development is controlled by temperature with optimal development occurring between 24–26°C; in laboratory studies metamorphosis and settlement took place within 14–30 days of spawning. However, this larval development time could not be verified for populations in the field. It appears that spawning occurs throughout the year although, as Wilson (1970a, 1970b) found, the larvae of *Sabellaria alveolata* and *S. spinulosa* demonstrated widely differing rates of development and individual ability to settle. Adults contained gametes throughout the year and juveniles developed gametes 4 months after settlement. Life history studies on various species of sabellariids (Wilson 1929; Dales 1952b; Cazaux 1964; Curtis 1973, 1975) have shown that larval development is fairly uniform within this group.

Sabellariids are suspension-feeders that use their buccal cirri (= oral tentacles, Rouse & Pleijel in press) and prostomial tentacles (= palps) to create feeding currents and trap suspended particles in mucus. The ciliary currents on these structures cause food particles to be transported to the mouth, as illustrated by Dales (1952b). They may also be detrital feeders (Kirtley 1994). Larvae under culture conditions thrive on phytoplankton (Eckelbarger 1975a).

Until the revision of the Australian sabellariids is completed (Hutchings & Peart in preparation) only some generalised comments concerning the distribution of the family in Australia can be made. The family is primarily marine, occurring from the intertidal zone to deep water; few are found in areas of fluctuating salinity. The Australian intertidal and shallow subtidal species range from widely distributed ones to those with very localised distributions.

1. CLASS POLYCHAETA

The phylogeny of the family has not been investigated and many of the recently described species are known only from the type series. No subfamilies are recognised.

Many fossil forms have been referred to sabellariids (Caline *et al.* 1988) albeit solely based on tubes. Sabellariid tube fossils are known from Mexico, Chile and the United States of America (Kirtley 1994).

Family Sabellidae

Sabellids are most easily recognised by the combination of their tentacular crown and mucous/sediment tube (Fig. 1.99A, H; Pls 5.1–5.4); this clearly distinguishes them from serpulids. In common with serpulids, Sabellidae have a body with distinct thoracic and abdominal regions, indicated by chaetal inversion and a faecal groove. Like serpulids, they have also a pair of anterior excretory nephridia with a single exit. Sabellids are commonly referred to as feather-duster worms because of the organisation of the tentacular crown of many of the larger species.

The first sabellid to be described formally was *Sabella penicillus* by Linné (1767). The family Sabellidae was erected by Latreille (1825). The first significant subdivision of the Sabellidae was made by Rioja (1923) who divided the sabellids into three subfamilies, based largely on chaetal characters: the Fabriciinae contained genera with thoracic uncini with long handles (acicular); the Myxicolinae was erected for the genus *Myxicola*, which has abdominal uncini forming nearly complete rings around the body, and; the Sabellinae which contains members with avicular thoracic uncini, usually with short handles, and companion chaetae which are usually present. Johansson (1927) subsequently modified Rioja's (1923) scheme assigning *Myxicola* to the Fabriciinae. Fauchald (1977) followed the system of Rioja (1923) and retained the Myxicolinae. Fitzhugh's (1989) detailed cladistic analysis of the sabellids and associated taxa showed that recognition of the families Caobangiidae and Sabellongidae resulted in paraphyly of Sabellidae. As a result, he made significant changes to the classification of the group and the latter two families were accorded generic status within the Sabellidae. Monophyly of Sabellidae was supported by three chaetal synapomorphies: (1) thoracic neuropodial uncini with the main fang surmounted by a broad series of smaller teeth; (2) the proximal region of uncini with a handle or shaft, and; (3) limbate abdominal neurochaetae. Fitzhugh was able to confirm monophyly for only two sabellid subfamilies, the Fabriciinae and Sabellinae; he also transferred a number of genera previously included in Fabriciinae to Sabellinae. These included *Chone*, *Desdemona*, *Euchone*, *Jasmineira*, and *Fabrisabella*. The genus *Myxicola* was also referred to Sabellinae. The Fabriciinae is currently diagnosed by a number of synapomorphies, including the presence of branchial hearts, the absence of ventral lips and the presence of abdominal uncini with an elongate proximal manubrium (Fitzhugh 1989). Rouse (1995) also postulated a number of synapomorphies for the Fabriciinae among features of the reproductive system, including sperm structure. The subfamily Sabellinae was emended by Fitzhugh (1989) to include all those sabellids with a radiolar skeleton in two or more rows; the skeleton comprises large supporting cells with thick walls. In the most recent cladistic analysis of the Sabellidae, Rouse & Fitzhugh (1994) suggested that *Caobangia* Giard, 1893 be regarded as *incertae sedis* until further material is examined. Significant publications on the Sabellidae are those by Bush (1905), Rioja (1923), Zenkevitch (1925), Johansson (1927), Hartman (1951b), Banse (1956, 1957, 1970, 1972), Knight-Jones (1981, 1983),

Perkins (1984), Fitzhugh (1989, 1991a), Rouse & Fitzhugh (1994) and Knight-Jones & Perkins (1998). The subfamilies recognised in this treatment are the Sabellinae and Fabriciinae *sensu* Rouse & Fitzhugh (1994).

Sabellids are distributed worldwide and are associated with hard surfaces or soft sediments at all latitudes from intertidal areas to shelf depths. Some species (for example, in the genus *Pseudopotamilla*) are capable of boring into limestone (calcium carbonate) substrata and hence are common in coral reef environments. Members of *Caobangia* are symbionts of molluscs, boring into the shells of both freshwater gastropods and bivalves (Martin & Britayev 1998). The Sabellidae are unusual amongst polychaetes in having a number of freshwater species. These include the genera *Caobangia* (Jones 1974; Fitzhugh 1989, 1991a; Rouse & Fitzhugh 1994), *Brandtika*, *Monroika* and several species of *Manayunkia* (Zenkevitch 1925).

A number of sabellid species have been described from Australia, particularly from the east coast. Haswell (1884) described several species of sabellids from the Sydney area. Two of these species appear to have been incorrectly synonymised by Hartman (1959a) with species described in other countries. After Haswell's early efforts, few sabellid species were recorded from Australian waters until relatively recently. Day & Hutchings (1979) reported 18 species in the subfamily Sabellinae and one species of Fabriciinae from Australian waters, though this includes some incorrect synonyms. Subsequently, Hartmann-Schröder (1981a, 1982, 1986, 1989, 1991a) and Rouse (1990b) described a number of small species in the genus *Amphicorina* (see revision in Rouse 1994) bringing the number of species in this genus recorded in Australian waters to 10. Perkins (1991) and Fitzhugh (1992) erected new sabellid genera for species described from the Great Barrier Reef. Additional descriptions and records of the Sabellidae by Hutchings, Decker & Geddes (1981), Hutchings & Murray (1984), Hartmann-Schröder (1989), Fitzhugh (1990), Rouse (1990b) and Perkins (1991) bring the total number of species recorded in Australian waters to more than 30, most of them in the Sabellinae.

The smallest sabellid so far described is *Fabriciola minuta* which has an adult length of only 0.85 mm (Rouse 1996a). The longest sabellid recorded by Rouse & Fitzhugh (1994) was a specimen of *Schizobranchia insignis* that had a body 260 mm long, though they found specimens of *Eudystilia vancouveri* with a greater total volume. Rouse & Fitzhugh (1994) found that body volume ranged over more than five orders of magnitude across the Sabellidae. The number of thoracic segments present is usually eight, but varies from as few as four in genera such as *Pseudobranchiomma* to 12 as found in the Australian species *Amphiglena terebro*. The number of abdominal chaetigers can vary from two to four as found amongst the Fabriciinae to more than 100 in some of the larger sabellines. The body terminates with the post-segmental pygidium, which is usually semi-circular and may bear a pair of eyes (Fig. 1.100E). All members of the Sabellidae described to date have a tentacular crown, except *Sabellonga disjuncta*, which was probably described from an incomplete specimen (Fitzhugh 1989). All members of the Sabellinae have a radiolar skeleton that has at least two rows of cells in cross section and may have four or more in the median region of a radiole (Fitzhugh 1989). Most members of the Fabriciinae lack a radiolar skeleton, though Rouse (1993b, 1996) described two species of *Fabriciola* with a radiolar skeleton comprising one row of cells. Members of the genus *Caobangia* also have a radiolar skeleton with one row of cells. The sabellid crown comprises a number of radioles and can number from as few as two pairs in *Monroika* to several

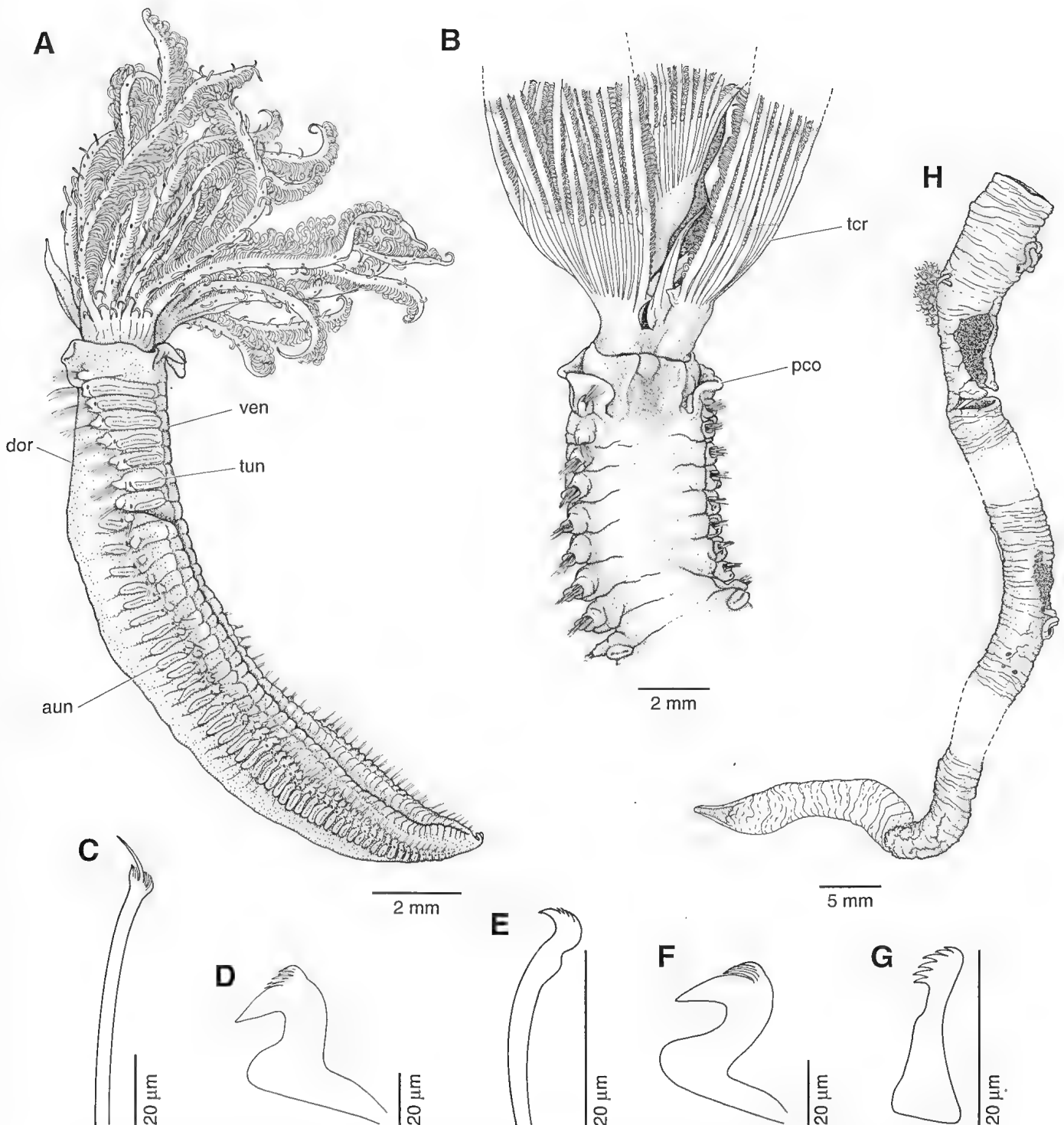


Figure 1.99 Family Sabellidae. **A, B**, *Branchiomma* species: **A**, whole animal, lateral view; **B**, anterior end of *Sabella spallanzanii* showing the proximal half of the tentacular crown, dorsal view. **C–E**, thoracic chaetae: **C**, 'companion' notochaeta of *Demonax* species; **D**, neurochaetal uncinus of *Demonax* species; **E**, neurochaetal uncinus of *Fabriciola* species. **F, G**, abdominal notochaetae: **F**, uncinus of *Demonax* species; **G**, uncinus of *Fabriciola* species. **H**, anterior, middle and posterior sections from a 90 mm long tube of *Branchiomma* species. **A–D, F**, subfamily Sabellinae; **E, G**, subfamily Fabriciinae. **aun**, abdominal uncini (notopodial); **dor**, dorsum; **pco**, peristomial collar; **tcr**, tentacular crown; **tun**, thoracic uncini (neuropodial); **ven**, ventral surface.

[A. Murray]

hundred in species of *Sabella*. Other structures of the crown include dorsal and ventral lips and various additional appendages that appear to be derived from radioles or pinnules. These are discussed by Perkins 1984 and Fitzhugh 1989).

The six types of thoracic notochaetae and six forms of abdominal neurochaetae are essentially similar. These chaetae, and their distributions amongst taxa, are discussed by Fitzhugh (1989). In sabellids, as in several other polychaete

families including serpulids, the first thoracic chaetiger bears notochaetae only. In some sabellines, the neuropodia have a row of companion chaetae in front of the uncini (Figs 1.99C, 1.100C). Every other chaetiger also has uncini, except in a few taxa such as *Caobangia*. The uncini occur in the neuropodia of the thoracic region and the notopodia of the abdomen; variation in forms of uncini are discussed and classified by Fitzhugh (1989). Uncini of various sabellines and fabriciines are illustrated in Figures 1.99D–G and 1.100B–D.

1. CLASS POLYCHAETA

In most sabellid species the tube is constructed by an active process of particle sorting and combination with a complex mixture of organic compounds, usually referred to as mucus (Nicol 1930; Lewis 1968a; Vovelle, Rusaouen-Innocent, Grasset & Truchet 1994). In *Chone mollis*, however, Bonar (1972) reported that the tube is made from a mixture of sediment and mucous sheets secreted by the worm as it burrows into the sediment. In many larger sabellids, the tube is permanently occupied (Nicol 1930), but in some sabellines and many members of the Fabriciinae, the tube may be abandoned and a new one constructed (Lewis 1968a; Bonar 1972). Vovelle *et al.* (1994) have studied in detail the organic components of sabellid tubes. The tube described for *Calcisabella piloseta* has a calcareous matrix with sediment particles incorporated (Perkins 1991; G. Rouse personal observation) and this suggests it is not homologous with the tube of serpulids. Further study of *C. piloseta* would be of interest to determine if a pair of ventral calcareous glands are present, as found in all serpulids.

Several studies on feeding in the Sabellidae have been made (Nicol 1930; Dales 1957c; Fitzsimons 1965; Lewis 1968a; Bonar 1972; Merz 1984). Virtually all sabellids are suspension-feeders with varying abilities in particle sorting. *Manayunkia aestuarina* is unusual in that it is a deposit-feeder (Lewis 1968a). Large species, such as *Sabella pavonina*, can discriminate particles on size; those too large for feeding or tube building are rejected, medium-sized particles are used for tube building and small particles are ingested (Nicol 1930). Dales (1957c) measured feeding rates of two sabellid species and found that *S. pavonina* could filter 73 ml/hour and *Myxicola infundibulum* 286 ml/hour. Sizes of particle ingested by *Chone mollis* are less than 15 µm and about 1–2 µm for small species such as *Fabricia sabella* and *Manayunkia aestuarina* (Lewis 1968a). Bonar (1972) found diatoms and organic detritus in the gut of *Chone mollis*.

As in serpulids, the tentacular crown is also the primary site for respiration in sabellids (Fox 1938). Wells (1951b, 1952) studied respiration in *Sabella pavonina* and *Myxicola infundibulum* and found that the crown is responsible for most of the respiratory requirements for the latter species; in *S. pavonina*, tube irrigation resulted in significant respiration through the body surface and greater ability to survive loss of the crown. Giangrande (1991) found that the crown of the large sabelline *Eudystilia vancouveri* was responsible for 80% of respiratory requirements, a similar result to that found for *M. infundibulum*. The circulatory system in the Sabellidae has been studied and reviewed by Hanson (1950b). In all sabellids, a blood sinus around the gut is connected to a ventral vessel by segmentally arranged ring vessels. Some variation in other components of the circulatory system has been observed (Hanson 1950b). Sabellids, like serpulids, sabellariids, cirratulids, flabelligerids and some other polychaete groups, have a pair of anterior excretory nephridia that are classified as mixonephridia (Goodrich 1945). The single exit for the pair of nephridia is a synapomorphy for serpulids and sabellids (Orrhage 1980). In addition to the anterior pair of nephridia, paired ciliated ducts to the exterior occur in chaetigers involved in gamete production (Zenkevitch 1925). In the Fabriciinae, males have a dorsal sperm duct running along the thoracic region and opening behind the tentacular crown (Rouse 1995).

Orrhage (1980) reviewed the structure of the sense organs and nervous system in sabellids; it is very similar to serpulids. Contrary to earlier opinions, he found that sabellids have a pair of nuchal organs at the base of a dorsal pit above the mouth. Orrhage (1980) suggested, on the basis of the

innervation patterns, that the tentacular crown of sabellids and serpulids is homologous to the palps of spiomorph polychaetes. Sabellids often have a pair of eyes in the peristomium and pygidium. When present in the Sabellinae they are red. In the Fabriciinae, they may be black or red. The ultrastructure of the peristomial and pygidial eyes of the sabelline *Chone ecaudata* have been studied by Ermak & Eakin (1976). Members of the Sabellinae often have eyes on the tentacular crown and the structural details of some of these have been documented by Kerneis (1975). Fitzhugh (1989) divided these into several types, but further study is warranted.

Both asexual and sexual reproduction occur in the Sabellidae. Asexual reproduction takes the form of schizotomy and has been reviewed by Knight-Jones & Bowden (1984). It has been recorded in sabellines such as *Sabella variabilis*. Sexual reproduction in the Sabellidae was reviewed in detail by Rouse & Fitzhugh (1994). Sabellids display a range of sexual reproductive modes, from broadcast spawning to ovoviviparity. All fabriciines thus far studied are gonochoric, continuous brooders of directly-developing larvae, and females are capable of storing sperm. Plesiomorphic sabellines, such as *Amphicorina* have a reproductive mode similar to that of the Fabriciinae, though homologies among reproductive structures, such as spermathecae, are still unclear (Rouse 1992c). Intratubular brooding is uncommon in the more apomorphic sabellines, whereas broadcast spawning or extratubular brooding is the norm, with exceptions including *Potamilla* and *Amphiglena* species. Amongst the most highly derived sabellines *Eudystilia* and *Schizobranchia* species are broadcast spawners (McEuen, Wu & Chia 1983).

Rouse & Fitzhugh (1994) identified three types of gamete distribution in the Sabellidae. Gametes limited to the abdominal chaetigers, or in both thoracic and abdominal segments are states found in the Sabellinae. The condition of gametes being limited to only thoracic segments is only found in the Fabriciinae (Rouse 1995). Sabellids are usually gonochoric, but some species are simultaneous hermaphrodites, or protandric hermaphrodites. Depending on the species, simultaneous hermaphrodites may have eggs and sperm in the same segments or in different segments. Spermatogenesis in sabellids may be in tetrads or clusters of spermatids attached to a cytophore. Mature sperm have a spherical or cylindrical nucleus, and mitochondria may also be spherical or elongate (Rouse 1992d, 1995). Little is known of oogenesis in the Sabellidae. Christensen (1980) determined the chromosome number for three sabellid species, all members of the Sabellinae: *Sabella penicillus*, *Myxicola steenstrupii* and *Chone infundibuliformis* all have a diploid count of 28.

All sabellids have lecithotrophic larvae and may have a planktonic phase lasting up to 2 weeks, though many have no free-swimming phase. Detailed information on larval development within the Sabellidae is available for species of *Amphicorina*, *Amphiglena*, *Chone*, *Demonax*, *Fabricia*, *Fabricinuda*, *Manayunkia*, and *Megalomma*. Some less detailed accounts are available for species of *Branchiomma*, *Caobangia*, *Pseudopotamilla*, *Potamethus*, *Potamilla*, and *Sabella*. McEuen *et al.* (1983), Knight-Jones & Bowden (1984), Rouse (1993a) and Rouse & Fitzhugh (1994) have summarised information on reproduction and development in the Sabellidae. Development in three Australian sabellids has been studied to date, all of them intratubular brooders with directly developing larvae; *Amphicorina bicoloris*, *A. brevicollaris* and *Amphiglena terebro* (see Rouse 1993a; Rouse & Fitzhugh 1994).

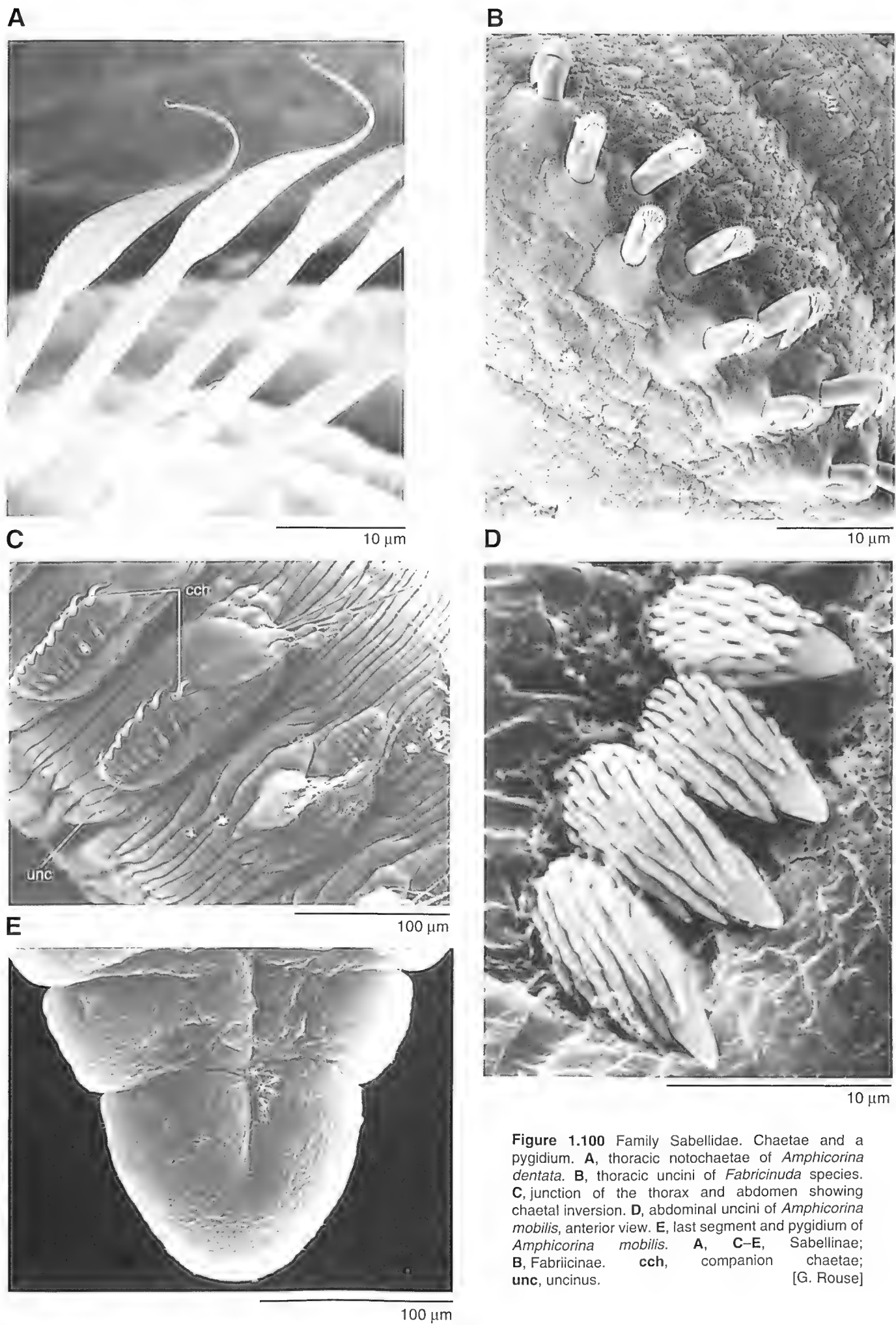


Figure 1.100 Family Sabellidae. Chaetae and a pygidium. **A**, thoracic notochaetae of *Amphicorina dentata*. **B**, thoracic uncini of *Fabriicinae* species. **C**, junction of the thorax and abdomen showing chaetal inversion. **D**, abdominal uncini of *Amphicorina mobilis*, anterior view. **E**, last segment and pygidium of *Amphicorina mobilis*. **A**, **C–E**, Sabellinae; **B**, Fabriicinae. **cch**, companion chaetae; **unc**, uncinus. [G. Rouse]

1. CLASS POLYCHAETA

A number of studies on sabellid life histories and ecology are available, though these have been mainly on smaller species that are intratubular brooders, for example, *Fabricia sabella* (Lewis 1968b) and *Manayunkia aestuarina* (Bell 1982). *Fabricia sabella* can reach population densities of up to $1.5 \times 10^6 \text{ m}^{-2}$ on sheltered rocky shores. Lewis (1968b) found that such high densities were related to the amount of silt suspended in the water column. Members of the genus *Caobangia* all live in fast-flowing freshwater streams where they burrow into the shells of molluscs. Reproductive and developmental features of *Caobangia* species were examined by Jones (1974) who found larvae are brooded in the maternal body before exiting via a larval duct. Giangrande & Petraroli (1994) studied the life cycle of a large sabelline, *Sabella spallanzanii* (see below); it is a protandric hermaphrodite, capable of reaching 400 mm in length. Based on growth rate studies over 1 year this mature size could be reached in around 2 years.

Sabellids have limited direct economic benefit or impact and as yet no ecological studies have been made on Australian sabellids. However, one sabellid, *Sabella spallanzanii*, has recently come to prominence in Australia; see Knight-Jones & Perkins (1998) for a revised description of this species. This large species appears to have come to Australian waters from the Mediterranean, and is found in high numbers in Western Australia, South Australia and Victoria (Corio Bay, Port Philip Bay; Wilson *et al.* 1996, 1998). It has been suggested that *S. spallanzanii* can reach such population densities that it is having adverse effects on native Australian filter-feeders such as scallops. Sabellids are parasitised by a variety of organisms including copepods (Gotto 1960, 1979) and protists such as gregarine apicomplexans (MacKinnon & Roy 1935).

All of the sabellids so far described in Australia are endemic. One of the most commonly seen sabellids is *Sabellastarte australis* (Haswell 1884). This species is found along the east coast of Australia in lower intertidal and shallow subtidal areas and may have a tentacular crown (often white or orange) up to 100 mm in diameter. Usually the crown is seen projecting from a crevice or from under a boulder. *Sabellastarte australis* is commonly referred to in guidebooks as *S. indica* after it was incorrectly synonymised by Hartman (1959a).

Sabellid fossils are unknown and thus, of necessity, ideas about the phylogeny of the group have been based on extant taxa only. Fitzhugh's (1989, 1991a) analyses concentrated on the relationships within the Sabellidae, and for character polarisation he used the Serpulidae. The support for monophyly of the family is based on chaetal characters (Fitzhugh 1989, 1991a) and is not particularly strong. However, there is strong support for monophyly of the subfamilies Sabellinae and Fabriciinae (Fitzhugh 1989; Rouse 1995). Rouse & Fitzhugh (1994) studied the evolution of various reproductive features in the Sabellidae and also assessed the influence of body size on these characters. They suggested that the ancestral sabellid was gonochoric, had sperm with an elongate head and was a brooder of directly-developing larvae. The general covariation of small body size with these reproductive traits suggests that small body size is also plesiomorphic for the family. Within the Sabellinae, sperm with a spherical nucleus and mitochondria, external fertilisation, and swimming larvae are secondarily derived, and brooding has subsequently re-appeared in specialised taxa such as *Amphiglena*, *Perkinsiana* and *Potamilla*.

Smith (1991) considered the Sabellida to comprise the Serpulidae and Sabellidae and the sister group to the sabellariids. In a novel hypothesis, he suggested that the

Sabellidae is paraphyletic, in which the Sabellinae (Banse 1957; Fauchald 1972) is the sister group of the Serpulidae (including the Spirorbinae). However, the synapomorphies proposed by Smith (1991) for a Sabellinae/Serpulidae clade stated here do not withstand close scrutiny, especially given the revision by Fitzhugh (1989). The four synapomorphies listed by Smith (1991) for his Sabellinae/Serpulidae clade are: suspension-feeding only; loss of pygidial eyespots; short-handled uncini on the thorax, and; eyespots on the tentacular crown. Suspension-feeding occurs in most members of the Fabriciinae and deposit-feeding has only been described for one species *Manayunkia aestuarina* (Lewis 1969). Eyespots are found in many members of the Sabellinae, though they often fade after fixation. Many of the taxa presently placed in the Sabellinae have long-handled uncini (see Fitzhugh 1989). The occurrence of eyespots on the tentacular crown of the members of the Sabellinae is restricted to apomorphic members of the clade (Fitzhugh 1989) and thus does not support this feature as being homologous with their occurrence in the Serpulidae. Present evidence suggests that Smith's (1991) hypothesis is incorrect, but further studies into the monophyly of the Sabellidae are warranted.

Very little has been published on the biogeography of sabellids. In one study, Fitzhugh, Giangrande & Simbora (1994) showed that previous hypotheses concerning migration of a fabriciine species from African waters into the Mediterranean had been based on inadequate observations of material. In fact, several new species were described in the genus *Pseudofabriciola*. Considerably more taxonomic studies are required both in Australia and overseas before any robust biogeographic hypotheses concerning sabellids can be proposed.

Family Serpulidae

Serpulids are filter-feeding organisms and can be recognised easily by their characteristic tentacular crown and the presence of a calcareous tube; the latter is the most obvious feature that identifies serpulids (Pls 6.1–6.5, 7.1–7.3). As in the sabellids, the Serpulidae have marked thoracic and abdominal regions, indicated by chaetal inversion and a faecal groove. Also like sabellids, serpulids have a pair of anterior excretory nephridia with a single exit. Serpulids are commonly referred to as fan worms after the fan-like tentacular crown.

The formal taxonomic history of serpulids dates back to Linné who described several serpulids (and a few molluscs) under the name *Serpula* in the group Vermes Testacea (Linné 1758). The first formal recognition of the Serpulidae as a family is traceable to Latreille (1825) and no further subdivisions were made until Chamberlin (1919) established the Spirorbinae for those serpulids with asymmetric bodies and a coiled tube (Fig. 1.101F), thus placing all other serpulids into the Serpulinae. Further subfamilies erected were: Filograninae by Rioja (1923) for those serpulids without an operculum and Ficopomatinae by Pillai (1960) for those serpulids that lived in brackish water and had toothed collar chaetae. Pillai (1970) suggested that the Spirorbinae 'possessed several important characters which are peculiar to themselves and necessitate their inclusion in a separate family', namely the Spirorbidae.

Fauchald (1977) also recognised the Spirorbidae as well as Serpulidae. He acknowledged 331 species of serpulids, divided into three subfamilies; the Serpulinae with 44 genera; the Filograninae with five genera and the Ficopomatinae with five genera. Of these 54 genera, 22 were monotypic and

another 13 had only two species. In the Spirorbidae, he recognised 26 genera; there were no subfamily divisions. The 26 spirorbid genera contained 162 species, though three of the genera contained 91 species and nine of the genera were monotypic.

Uchida (1978) revised the Serpulidae and also supported the integrity of the Spirorbidae. He created 11 subfamilies and numerous new genera, though he recognised only 233 species, compared to the 331 of Fauchald (1977). Of the 61 genera accepted by Uchida (1978), 26 were monotypic, and 15 comprised only two species each. Uchida's (1978) work has been severely criticised by ten Hove (1984) and his subfamilies have not been used.

The Spirorbinae have been the subject of an extensive series of papers by E.W. Knight-Jones and P. Knight-Jones. P. Knight-Jones (1978) accepted the familial status assigned to spirorbids by Pillai (1970) and revised the family. She recognised 14 genera, a number of subgenera, and around 120 species. She also divided the Spirorbidae into six subfamilies, based on states of a single character: the method of larval brooding, with generic divisions made on other features such as chaetae. Bianchi (1979) also accepted the Spirorbidae as a family and proposed a superfamily, Serpuloidea, comprising the Serpulidae and Spirorbidae. Ten Hove (1984) and Fitzhugh (1989) argued for return of Spirorbidae to subfamilial status in the Serpulidae because recognition of the Spirorbidae makes the Serpulidae paraphyletic. This arrangement is accepted here. As a subfamily, the synapomorphies for the spirorbid genera are coiled tube (Fig. 1.101F), body asymmetry and fewer than four thoracic chaetigers. Ten Hove (1984) suggested that the Filigraninae are paraphyletic and recognition of the Spirorbinae may well also make the Serpulinae paraphyletic (ten Hove 1984; Fitzhugh 1989). Recent revisions have reinforced the idea that many of the serpulid genera are also of doubtful validity.

Five species of serpulids had been described by different authors from brackish waters in various localities around the world. Each of these had been the basis for a monotypic genus. Subsequently, ten Hove & Weerdenburg (1978) synonymised these in *Ficopomatus*, and removed the subfamily Ficopomatinae that had been erected by Pillai (1960). Thus, presently the serpulids can be divided reasonably into the Filigraninae (probably paraphyletic), the Serpulinae (probably paraphyletic) and the Spirorbinae, while acknowledging that revision is obviously required. For the purposes of this chapter the Filigraninae are diagnosed as serpulids without an operculum; the Serpulinae as those serpulids with an operculum, but without a coiled tube (Fig. 1.101E) and the Spirorbinae serpulids with an operculum and a coiled tube (Fig. 1.101F). Significant publications on the Serpulidae include those by Bush (1905, 1910), Chamberlin (1919), Rioja (1923), Johansson (1927), Uchida (1978), ten Hove (1984), Bianchi (1981).

A number of serpulid species have been described from Australia, particularly from the eastern coast. Publications describing serpulids in the Filigraninae and Serpulinae include those by Haswell (1884, 1886a), Dew (1959) and Straughan (1966, 1967a, 1967b). A number of new species of Spirorbinae were described by Wisely (1962), Knight-Jones (1973), and Knight-Jones, Knight-Jones & Llewellyn (1974). Many other records of this family exist for these waters (Knox & Cameron 1971; Day & Hutchings 1979; Hutchings & Murray 1984; Knight-Jones & Knight-Jones 1984). Day & Hutchings (1979) reported 57 species in the subfamily Serpulinae, three species in the Filigraninae and 24 species of

Spirorbinae from Australian waters, though they include some incorrect synonyms. The study of the latter group by Knight-Jones & Knight-Jones (1984) included 23 valid species from the east coast of Australia.

Serpulids have a worldwide distribution and are nearly always associated with hard substrata, usually rocks. However, they are often found epizoically on corals (especially members of *Spirobranchus*), crustacean carapaces, the shells of molluscs and brachiopods, the test of ascidians and on various algae and seagrasses. Species of *Ditrupa* (Serpulinae) and *Helicosiphon* (Spirorbinae) do, however, have tubes that are not attached (Knight-Jones 1978; ten Hove & Smith 1990); *Ditrupa* species can be abundant in sediments of continental shelves (ten Hove & Smith 1990). Although the majority of serpulids have been described from shallow or intertidal waters, a number have been described from depths of 6000 m (Zibrowius 1977). Two genera, *Bathymvermilia* and *Laminatubus*, have been erected for species found in abyssal depths (Zibrowius 1977; ten Hove & Zibrowius 1986); *L. alvini* occurs at hydrothermal vents (2600 m depth).

Serpulids range in size from around 2 mm to more than 100 mm in length, housed in a tube several times longer than the worm. The number of thoracic chaetigers varies from as few as three in some spirorbines (Knight-Jones & Fordy 1979) to as many as 12, as reported in *Filigrana* species (Fauchald 1977); seven is the most common. Numbers of abdominal chaetigers are more variable, from as few as 10 in smaller species to more than 100 segments in species of *Laminatubus*, *Spirobranchus* and *Protula*. The first chaetal segment bears notochaetae only (absent in some taxa). Usually, the chaetae are associated with the collar and thoracic membrane and are referred to as collar chaetae. The morphology of collar chaetae can differ from chaetae on other segments, for example, 'fin and blade' chaetae or simple limbate chaetae. In some serpulids, the first chaetiger is not associated with the collar. The remaining thoracic chaetigers have capillary, limbate (Fitzhugh 1989), geniculate, or bayonet notopodial chaetae (see ten Hove 1984) and neuropodial uncini. The abdominal region has the reverse chaetal organization. Abdominal neurochaetae are usually capillaries, particularly in posterior chaetigers, limbate, geniculate, or trumpet-shaped. The uncini of serpulids are usually rasp-shaped (multiple rows of teeth) without a handle (Fig. 1.101C, D). Usually the teeth are the same size, though the basal tooth (or teeth) is larger in some taxa. Uncinal forms in thoracic and abdominal chaetigers are usually similar.

The functional relationship of locomotion within the tube and chaetal distribution have been investigated by Knight-Jones & Fordy (1979) and (Knight-Jones 1981). Serpulids generally lie with the dorsal surface against the substratum and locomotion is limited to emergence from, and withdrawal into the tube. Withdrawal is achieved by contraction of the longitudinal muscles and anchoring of abdominal uncini, in which all teeth face forwards, and backward thrusting by collar chaetae, when present. Emergence is accomplished with the aid of the abdominal neurochaetae and thoracic notochaetae (Knight-Jones & Fordy 1979; Knight-Jones 1981).

The development of the tentacular crown of serpulids has been described in detail for a number of species (see below). Each half has a complement of radioles with pinnules and a dorsal lip. Detailed studies of the innervation and musculature and overall structure of the adult crown of a number of serpulids were made by Hanson (1949b) and Orrhage (1980). According to Hanson, the crown is 'basically similar in all serpulids studied, containing an internal 'skeleton' that is unlike that found in the sabellid subfamily Sabellinae.

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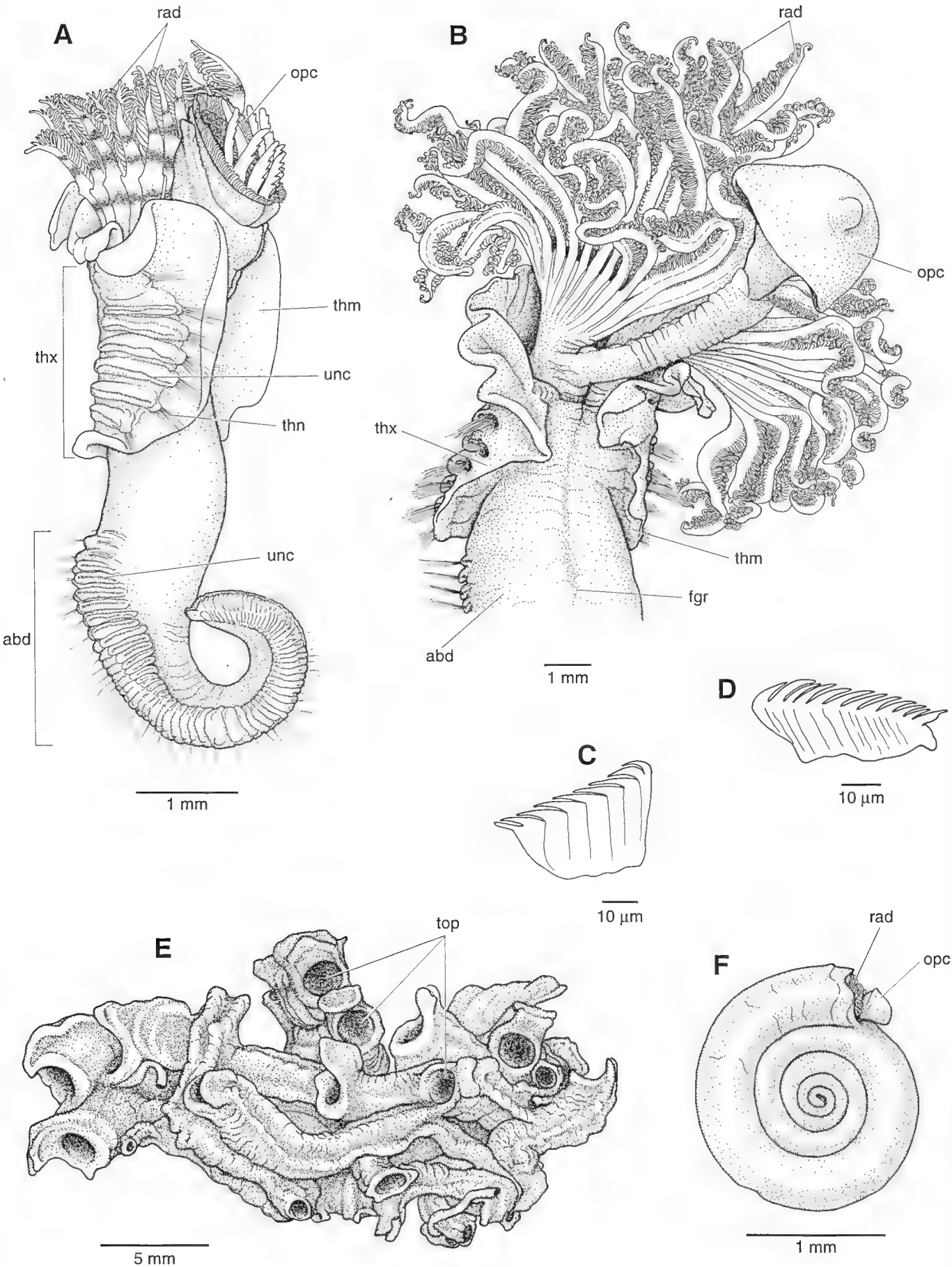


Figure 1.101 Family Serpulidae. **A**, entire animal of *Galeolaria caespitosa*, lateral view. **B**, anterior end of *Neovermilia globula*, dorsal view. **C**, **D**, uncini of *Galeolaria caespitosa*: **C**, thoracic neuropodial uncinus from parapodium of chaetiger 6. **D**, notopodial uncinus from the third abdominal chaetiger. **E**, tube aggregation of *Galeolaria caespitosa*. **F**, tube of the spirorbine *Metalaespira tenuis*, dorsal view. **abd**, abdomen; **fgr**, food groove; **opc**, operculum; **rad**, radioles; **thm**, thoracic membrane; **thn**, thoracic notochaetae; **thx**, thorax; **top**, tube opening; **unc**, uncini. [A. Murray]

Orrhage (1980) found the serpulid and sabellid crowns to be homologous and also to be the specialised homologues of the 'palps' of spiomorphic polychaetes. Serpulids may have from as few as three pairs of radioles to 20 or more. The nature of the often striking pigmentation patterns of the tentacular crowns of serpulids was studied by Dales (1962b). He found that the pigment astaxanthin (or an astaxanthin ester) is responsible for the bright red color of the crown in *Serpula vermicularis* and *Protula intestinum*. A blue pigment found in taxa such as *Pomatoceros triqueter* and the Australian species *Galeolaria caespitosa* could not be identified (Fig. 1.101A).

Many serpulids also have an operculum (Fig. 1.101A, B) as part of the tentacular crown, which serves to plug the tube on withdrawal; it is a transformed radiole (see ten Hove 1984). Pillai (1970) argued that the operculum of spirorbines was different from that of other serpulids, providing his justification for elevation of the former group to family status. Ten Hove (1984) argued that in all serpulids the operculum is derived from the second most dorsal radiole, though its position may alter subsequently. When present, the operculum is often used in serpulid taxonomy. Its structure and development has been described for several species (Thorp 1975; Potswald 1977; ten Hove 1984). A detailed description of the blood circulation system of the operculum was given for *Pomatoceros lamarckii* by Bubel (1983b).

The tube of serpulids (Fig. 1.101E, F) is formed from a mixture of calcium carbonate (calcite or aragonite) interspersed with a mucopolysaccharide matrix. A calcareous tube reported for a member of the Sabellidae, *Calcisabella piloseta*, differs from the serpulid tube for, although it has a calcareous matrix, sediment particles are also incorporated (Perkins 1991). The process of tube formation in serpulids has been investigated by Hedley (1956a, 1956b, 1958), Vovelle (1956), Neff (1971) and Vovelle, Grasset & Truchet (1991). The energetics of tube formation were documented by Dixon (1980); in *Ficopomatus enigmaticus*, energy expenditure in tube formation is twice that for somatic growth and gamete production. A pair of glands in the ventral part of the peristomium, just behind the collar (Hedley 1956b), secrete a mucopolysaccharide matrix which, in the environment in the lumen of the glands, results in precipitation of calcium carbonate from the seawater. The mixture of calcium carbonate and mucopolysaccharide is then applied to the leading edge of the tube by the collar (Clark 1956b, 1958, 1976). The structure of the glands has been studied for a number of serpulid species of *Ficopomatus*, *Hydroides*, *Marifugia*, *Pomatoceros*, *Serpula* and *Spirorbis* (Absolon & Hrabê 1930; Swan 1950; Hedley 1956a, 1958). Other aspects of the nature of the epidermis and cuticle of serpulids have been investigated by Bubel (1983a).

The thoracic membrane is continuous with the peristomial collar and can extend for the length of the thoracic region (Fig. 1.101A, B). In some serpuline taxa, for example, *Crucigera*, *Hydroides*, *Serpula* and *Laminatubus*, the membrane fuses posteriorly to form a ventral apron extending behind the thoracic region. In some spirorbine genera, such as *Neodexiospira* and *Romanchella*, the posterior part of the peristomial collar and anterior thoracic membrane fuse dorsally immediately behind the collar. According to Bush (1910), a thoracic membrane is absent in a few serpulids, notably *Salmacinopsis setosa*. However, in species of *Chitinopoma*, *Chitinipomoides*, *Hyalopomatus*, and *Rhodopsis* the thoracic membrane is very short and may extend only to the first or second chaetiger (Zibrowius 1969; Ben-Eliahu & ten Hove 1989); this may be the case in *S. setosa*.

The tentacular crown is involved in feeding and respiration. All serpulids are reputedly filter-feeders, though few studies have been conducted (Fauchald & Jumars 1979). Dales (1957d) found that small serpulid species such as *Spirorbis spirorbis* and *Salmacina dysteri* filter somewhat less than 0.3 ml/h. Larger species, such as *Pomatoceros triqueter*, filter a volume of 27 ml/h. Davies, Stuart & De Villiers (1989) reported that a substantial population of *Ficopomatus enigmaticus* that had colonised a large marina could completely filter the marina water in 26 hours. No studies are available to date on particle selection by serpulids (as there are for sabellids), though Davies *et al.* (1989) suggested that particles in the size range of 2–16 µm were preferred by *F. enigmaticus*. Serpulids lack a pharynx or buccal organ (Dales 1962a). The oesophagus and much of the gut is ciliated, and Hanson (1949b) attributed movement of food along the alimentary canal to ciliary action, rather than to peristalsis.

Although the tentacular crown is the primary site of respiration in the Serpulidae there is some evidence for auxillary respiration across the body wall via generation of water currents through the tube (Knight-Jones & Fordy 1979). Haswell (1884) described circulation in the Australian species *Hydroides elegans* and *Spirobranchus tetracerus* (as *Pomatoceros elaphus*). Hanson (1949a, 1950a, 1950b) studied the mechanics of circulation in a number of species and reviewed circulation in the family Serpulidae. In all serpulids studied to date, the blood moves from the abdomen forward along a sinus surrounding the alimentary canal. Anteriorly it passes through dorsal, transverse, and circum-oesophageal vessels to a ventral vessel which carries blood posteriorly. Among a series of (blind-ending) peripheral blood vessels is the vessel that supplies the tentacular crown. Contractile myoepithelial cells surround the tentacular crown blood vessel, which rhythmically fills and empties when the crown is extended into the water. Blood returning from the tentacular crown enters the ventral vessel and travels posteriorly (Hanson 1949a, 1950a, 1950b). A heart body is absent and movement of the blood is presumably achieved through peristalsis or contraction of myoepithelial cells. The only blood pigment reported for the family is chlorocruorin (Weber 1978b), but the red colour of the blood in *Protula* species (see colour plate background) indicates that erythrocrucorin is also present in the family.

Haswell (1884) described the anterior excretory nephridia in several Australian serpulids, *Galeolaria caespitosa*, *Hydroides elegans* and *Spirobranchus tetracerus*. The morphology of the serpulid nephridial system was reviewed most recently by Orrhage (1980). As in sabellids, sabellariids, cirratulids, flabelligerids and some other polychaete groups there is a pair of anterior excretory nephridia. The single exit for this pair of nephridia is a synapomorphy for serpulids and sabellids. The nephridia are classified as mixonephridia (Goodrich 1945). Haswell (1884) first noticed that in addition to the anterior pair of nephridia there is a pair of ciliated ducts to the exterior in many abdominal chaetigers, through which gametes are expelled. It seems likely that these are coelomoducts only, though a nephridial component has not been disproved. Potswald (1967a) noted the presence of ducts in male segments of spirorbines and referred to them as reduced coelomostomes.

The structure of the sense organs and nervous system of serpulids has been reviewed in detail by Orrhage (1980). He found, contrary to earlier opinions, that serpulids have a single nuchal organ that lies at the base of a dorsal pit above the mouth. Orrhage (1980) found close similarities between the nervous system of serpulids and that of sabellids and he

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argued that on the basis of the innervation patterns the tentacular crown of serpulids (and sabellids) is homologous with the palps of spiomorph polychaetes. The brain of serpulids, although not as elaborate as those of some of the more mobile predatory polychaetes, is relatively complex compared to that of terebellids and other tubicolous groups. Serpulids often have a pair of red peristomial eyes, but no details of their structure are available. Smith (1984a) discovered eyes on the tentacular crown of a serpulid, *Spirobranchus giganteus*, from the Great Barrier Reef, and described their ultrastructure.

Both asexual and sexual reproduction occur in the Serpulidae; all species that have been reported to reproduce asexually also exhibit sexual reproduction. Asexual reproduction involves budding of the posterior end of the worm, a process termed paratomy (Schroeder & Hermans 1975). This form of reproduction occurs in *Filograna implexa*, *Salmacina* species, *Josephella marenzelleri* and *Rhodopsis pusilla* (Nishi & Yamasu 1992a). At present, studies are available on fertilisation and larval development of 30 species of serpulids, not including the Spirorbinae (Nishi & Yamasu 1992a). Of these, 16 are broadcast spawners with planktotrophic or lecithotrophic larvae. Fourteen species are known to brood larvae, in a variety of ways: free in the tube, in calcareous brooding pouches outside the tube, attached to the branchial crown, or in pouches of the thoracic membrane. Under current classification, these 30 species group into 20 genera. For the spirorbine information is available on reproductive methods for nearly every described species (around 120). All spirorbine species are brooders of lecithotrophic larvae that have a swimming stage; the method of brooding has been the basis of classification of this group for some time (Bailey 1969; Knight-Jones & Fordy 1979). Larvae are brooded either in masses attached to the tube, to the parent, or in opercular chambers. Reproductive strategies vary considerably in the Filograninae. *Protula tubularia*, studied by Salensky (1882) and Meyer (1888), is a broadcast spawner with lecithotrophic larvae. Other filogranines are, however, either intratubular or extratubular brooders of lecithotrophic larvae (Nishi & Yamasu 1992a). Operculate members of the Serpulinae may be broadcast spawners with planktotrophic larvae, or brooders with lecithotrophic larvae (see Nishi & Yamasu 1992a). One unusual species, *Paraprotis dendrova*, broods larvae in a mass attached to a modified radiole (Nishi & Yamasu 1992b; Uchida 1978). In all species, it appears that fertilisation is external, either freely in the water or in the water of the tube. Where fertilisation occurs in the tube then the presence of spermathecae have been documented or are implicated (Daly & Golding 1977; Picard 1980; Rouse 1996b). Sperm appear to be released freely into the water; spermatophores or spermatozuogmata have not been reported in the Serpulidae.

Serpulid gametes are always found in the abdominal region. Species can be gonochoric, simultaneous hermaphrodites with eggs and sperm in different segments, or protandrous hermaphrodites (Segrove 1941; Rullier 1960; Potswald 1967a; Nishi & Yamasu 1992a). All Spirorbinae are simultaneous hermaphrodites, with oocytes in the anterior abdominal chaetigers and sperm in the more posterior segments. Spermatogenesis in serpulids may be in tetrads or clusters of spermatids attached to a cytophore (Franzén 1956, 1982; Potswald 1967b; Picard 1980). Mature sperm have a round head, and mitochondria are spherical or elongate with a complex midpiece (Franzén 1956, 1982; Nishi 1992). Oogenesis has been described for several species including *Filograna implexa*, *Hydroides norvegicus*,

Pomatoceros triqueter and *Spirorbis spirorbis* (Faulkner 1930; Nordback 1956; Jyssum 1957; King, Bailey & Babbage 1969; Potswald 1972).

Karyotype studies on serpulids have been reviewed by Christensen (1980). All members of the Spirorbinae have a diploid chromosome count of 20 (Dasgupta & Austin 1960). Members of the Serpulinae range from $2n = 22$ to $2n = 26$, with some reports of $2n = 14$ and $2n = 28$. In *Filograna implexa*, the only filogranine studied to date, the diploid chromosome count is 20.

A summary of the numerous studies of larval development in the Serpulidae can be found in Schroeder & Hermans (1975) and Nishi & Yamasu (1992a). Development can either be planktotrophic or lecithotrophic. There always appears to be some swimming phase, though in spirorbines and filogranines this may be only for a matter of hours. Species such as *Ficopomatus uschakovi*, *Galeolaria caespitosa*, *Hydroides norvegicus* and *Spirobranchus giganteus* found in Australian waters have planktotrophic larvae, which normally swim for 10–21 days before settling with three chaetigers and the rudiments of the tentacular crown (Wisely 1958; Andrews & Anderson 1962; Straughan 1968; Marsden & Anderson 1981; Smith 1984b). The larvae then secrete a mucoid tube and the remains of the prototroch and metatroch are resorbed or cast off. Rouse & Fitzhugh (1994) have briefly reviewed serpulid larval development. Larval behaviour has been studied for numerous species and a series of classic experimental studies of larval settlement were performed by Knight-Jones on spirorbine larvae (Knight-Jones 1951, 1953). Marsden (1984, 1987, 1990, 1991, 1994) carried out detailed studies on the larval behaviour of *Spirobranchus* species in relation to settling on live coral. De Vantier, Reichelt & Bradbury (1986) hypothesised a novel mutualistic relationship between *Spirobranchus giganteus* and massive coral colonies in the genus *Porites*. They argued that the corals provide protection for the worms and an ideal location for feeding. The neighbouring coral polyps benefited from the protection provided by the worms against predation by the crown-of-thorns starfish *Acanthaster planci*. Other studies on larval behaviour of Australian species include those by Wisely (1960), O'Donnell (1984), Smith (1984b) and Marsden (1988).

A number of studies have been made on the ecology and life histories of serpulids, including several on Australian species (Schroeder & Hermans 1975; Nishi & Yamasu 1992a). In one of the most detailed ecological studies, Straughan (1968, 1972) examined a population of the brackish-water serpulid *Ficopomatus uschakovi* (referred to as *Merceriella enigmatica*) in the Brisbane River (Queensland). She found a mixture of gonochoric individuals and protandric hermaphrodites, with a spawning peak in summer months; most larvae settled during spring tides and preferred to settle on rough, dark and opaque surfaces. O'Donnell (1984) studied *Galeolaria caespitosa*, an inhabitant of the intertidal zone of rocky shores on the Australian coast. She found greatest larval settlement during early summer; gastropod grazing limited recruitment on bare rock, but had no effect on recruitment of young when amongst aggregations of adults.

Serpulids are economically important as one of the most significant groups of marine fouling polychaetes. Wisely (1959) found three serpulids to have potential significance as fouling organisms in Sydney Harbour: *Hydroides elegans* (as *H. norvegicus*) and two species of Spirorbinae. Straughan (1972) considered the same to be true of *Ficopomatus uschakovi* in the Brisbane River (Queensland) and advised that boats be removed from the water during times of peak larval activity in early summer. In a study on marine

organisms introduced into the Australian environment, Hutchings, van der Velde & Keable (1987) found that no foreign serpulids have become established in Australia as yet; reports of European species such as *Hydroides norvegicus* and *Ficopomatus enigmaticus* in Australian waters are erroneous. Serpulids are parasitised by copepods (Gotto 1979) and a variety of unicellular organisms (Théodoridès & Laubier 1962). An unusual copepod parasite, *Octophiophora lacertae*, has been found in association with serpulids on the Great Barrier Reef (Stock 1988).

Spirorbines are extremely common and are often seen on rocks and algae in the intertidal zone. They are easily recognised as small flat tubular spirals (Fig. 1.101F). One of the most common polychaetes found in Australia is the endemic serpulid *Galeolaria caespitosa* (Fig. 1.101A, E). It is found along the entire southern part of the continent (and Tasmania) from Perth (Western Australia) to North Stradbroke Island (Queensland) and has been referred to as 'Sydney Coral' in New South Wales (Pope 1948). *Galeolaria caespitosa* can occur in such dense aggregations (Fig. 1.101E) that the tubes form a distinct band in the rocky intertidal zone. Another commonly seen serpulid is *Filograna implexa* which is very small (3–4 mm long), but forms dense lacy aggregations up to 300 mm in diameter. The white lacy tubes contrast with the red bodies of the worms when they are extended. *Filograna implexa* is found in sheltered lower intertidal areas under rocky overhangs and in similar sheltered areas subtidally.

Several authors have speculated on the phylogeny of the Serpulidae or groups within this taxon. Caullery & Mesnil (1897) discussed the evolution of the Spirorbinae and argued that they are a derived group of serpulids based on a reduction of the number of thoracic chaetigers. In contrast, Knight-Jones (1981) proposed that sabellids and serpulids evolved from spirorbin-like ancestors. She argued that the only value in having an inverted faecal groove and chaetal reversal is for coiled taxa, and that uncoiled taxa must be phylogenetically constrained to have such features; this inversion has been retained in other serpulids even though their bodies are not coiled. Knight-Jones' (1981) contention implies that the recognition of the Sabellidae makes the Serpulidae paraphyletic. Smith (1991) rejected Knight-Jones' (1981) hypothesis and instead argued that Sabellidae are paraphyletic with the Sabellinae the sister group to the Serpulidae rather than the Fabriciinae. Ten Hove (1984) agreed that the Serpulidae are monophyletic and proposed a phylogeny of the group based on the morphology of the tentacular crown. He suggested that the subfamily Filograninae is paraphyletic, forming a grade with respect to Serpulinae. Filograninae taxa such as *Josephella* may be the sister group to Serpulinae. He argued that the most plesiomorphic serpulids are taxa such as *Protula* and *Salmacina*, and suggested a possible sister group relationship between Spirorbinae and serpulid taxa such as *Pomatoceros*. Uchida (1978) proposed a series of complicated hypotheses for the evolution of the Serpulidae which have been criticised by ten Hove (1984).

In a substantial literature, serpulid fossils have been dated as far back as the Palaeozoic. The validity of many of these records are now being questioned. Putative fossil serpulids have, on further investigation, turned out to be cirratulid polychaetes, vermetid gastropods, or coralline algae (ten Hove 1994). In a review of serpulid fossils, ten Hove & van den Hurk (1993) also questioned the validity of many other records and recommended their re-assessment. Unequivocal serpulid fossils date back to the Cretaceous, including representatives of 12 extant genera (Lommerzheim 1979). Few fossil serpulids have been documented in Australia;

among them some relatively recent fossils from the east coast (Flood & Frankel 1979) and South Australia (Bone & Wass 1990).

Little has been published on the biogeography of the Serpulidae. In part, this can be related to the poor quality of most taxonomic work on this group until relatively recently. For example, in revising the genus *Ficopomatus*, the existence of numerous 'cosmopolitan' serpulid species has been shown to be false (ten Hove & Weerdenburg 1978). Further taxonomic study and more systematic collections of serpulids are required for the Australian fauna. Exemplifying the achievements of a rigorous approach, Knight-Jones & Knight-Jones (1984) documented the occurrence of spirorbin species along the east coast of mainland Australia and Tasmania. They found 23 species and noted a decrease in diversity in warmer tropical waters, particularly of tube-brooding species. Opercular-brooding species were found at all latitudes. Similar studies (see Knight-Jones & Knight-Jones 1991; Knight-Jones, Knight-Jones & Buzhinskaya 1991) in other areas have led to suggestions that opercular-brooding species are found mainly at low latitudes. Tube-brooding members of genera such as *Paralaeospira*, *Protolaeospira* and *Romanchella* are found only in southern latitudes and those in the *Spirorbis* and *Circeis* are restricted to northern ones. Further studies are required to determine the historical and ecological factors involved in such distributions. Australia has a number of endemics, including *Galeolaria caespitosa* (Fig. 1.101A) and *Metallaeospira tenuis* (Fig. 1.101F).

SPIONIDA

The name Spionida was first used by Dales (1962) for a group of eight polychaete families and was ranked as an order (see Fig. 1.43). Prior to that the name Spiomorpha was used usually for a taxon that included Spionidae and a varied assortment of other polychaete groups (Mackie 1996). Fauchald (1977) formulated Spionida differently to Dales (1962) by removing Paraonidae and Sabellariidae, and including Magelonidae (see Fig. 1.43). He also divided Spionida into three groups: Spioniformia (with six families), Chaetopteriformia (with Chaetopteridae) and Cirratuliformia (with Acrocirridae and Cirratulidae). The membership of Spionida formulated by Rouse & Fauchald (1997; see Table 1.3) basically matches the grouping of Spioniformia plus Chaetopteriformia from Fauchald (1977), with the addition of the subsequently erected Uncispionidae. Cirratuliformia *sensu* Fauchald (1977) were placed as members of Terebellida by Rouse & Fauchald (1997) and this is accepted for the purposes of this volume. The total number of described species in Spionida would appear to be around 600 worldwide, divided into about 48 genera, most being members of Spionidae. The synapomorphies for Spionida as defined by Rouse & Fauchald (1997) are the presence of a pair of peristomial grooved palps, nuchal organs forming posterior projections, and anterior excretory nephridia and posterior segmental organs for gamete release. The relationships among most of the members of the Spionida are shown in Figure 1.102. However, it should be noted that in their Multistate analyses Rouse & Fauchald (1997) showed the Spionida, as formulated here, was a paraphyletic group with respect to the majority of polychaetes. A detailed cladistic analysis of Spionidae used Trochochaetidae, Poecilochaetidae and Uncispionidae as outgroups (Sigvaldadóttir *et al.* 1997). They did not consider the placement of Chaetopteridae, Longosomatidae, or Magelonidae.

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The relationships shown in Figure 1.102 are supported by relatively few features and further investigation is required. The position of the Chaetopteridae within Spionida, in particular, warrants further investigation. In a cladistic analysis using larval characteristics, in addition, to adult morphological ones, Rouse (1999) found that Chaetopteridae fell within Sabellida, but no changes to the higher classification of Rouse & Fauchald (1997) were proposed.

The Spionidae, the most speciose family within Spionida (with more than 400 described species grouped into about 38 genera) are well represented in Australian waters. They are found, usually living in tubes in sediments, of all oceans and estuaries worldwide and can be significant pests when they infest shellfish. The remaining seven families of Spionida have relatively few described species and it is not surprising that some have yet to be recorded from Australian waters. Although Longosomatidae and Trochochaetidae have not been recorded from Australian waters they have been

collected from New Zealand and will most likely be found in Australia; Apistobranchidae has been collected from Antarctic waters. Chaetopteridae, Magelonidae and Poecilochaetidae are represented in Australian waters by a few species. Members of the Uncispionidae (Fig. 1.46D–G; erected by Green 1982) are not known from Australian waters, although there are unpublished records from New Zealand (G. Read personal communication). The only literature records are from the north-eastern Pacific. The family is not described in the following section, although it is included in the key to the families of Polychaeta. Sigvaldadóttir *et al.* (1997) suggested that recognition of the Uncispionidae may make the Spionidae paraphyletic, but did not synonymise the two families.

Family Apistobranchidae

The Apistobranchidae are long, fragile benthic polychaetes. They are distinguished from other members of the Spionida by the presence of dorsal notopodial lobes supported by aciculae.

The prostomium is rounded anteriorly; antennae are absent. A pair of grooved palps is located posteriorly to the prostomium and nuchal organs are located at their bases (Fig. 1.103A). The peristomium is reduced to lips. The first segment bears only neuropodia. Thereafter all segments are biramous with each parapodia consisting of a broad neuropodial lobe, a serrated subpodal membrane, a dorsal notopodial lobe with an internal aciculum and an inter-ramal lobe (Fig. 1.103B, C). Branchiae and ventral cirri are absent. Numerous pygidial cirri are present. Aciculae are only present in notopodia; neurochaetae are terminally bifid or otherwise modified capillaries (Fig. 1.103D–F). This description follows that of Fauchald & Rouse (1997).

Six species of apistobranchids have been described worldwide, but their taxonomic history is confused and several species are poorly described. A single genus, *Apistobranchus*, contains all species. Blake (1996a) suggested that there may be up to five valid species of *Apistobranchus*, and provided a key. The first apistobranchid was described as belonging to the family Orbiniidae, and another species was initially placed in the Chaetopteridae. Subsequently, the genus *Apistobranchus* was erected within the Orbiniidae before being given family status by Mesnil & Caullery (1898). In erecting the family Apistobranchidae, Mesnil & Caullery (1898) recognised their similarity to the Spionidae, a judgement recently confirmed by the cladistic analysis of Rouse & Fauchald (1997) who placed Apistobranchidae as a sister group to Spionidae and Trochochaetidae (Fig. 1.102).

Apistobranchids are not known from the waters of mainland Australia, but *Apistobranchus glacerae* is known from the Antarctic Peninsula (Hartman 1978). Elsewhere, apistobranchids are known from Europe, the Gulf of Mexico, the north-west Pacific, Japan, the Arctic and from off the coast of California (Blake 1996a). All species occur in muddy sediments on the continental shelf and slope. Taxonomic study of polychaetes from these habitats in Australia has barely begun, and it is likely that the family will eventually be recorded in Australian waters.

There have been no studies of the biology of apistobranchids, although Orrhage (1974) found small eggs and ‘primitive’ sperm in one species of *Apistobranchus*, possibly indicative of external fertilisation and planktonic development (Blake 1996a). However, apistobranchid larvae or reproduction have never been observed.

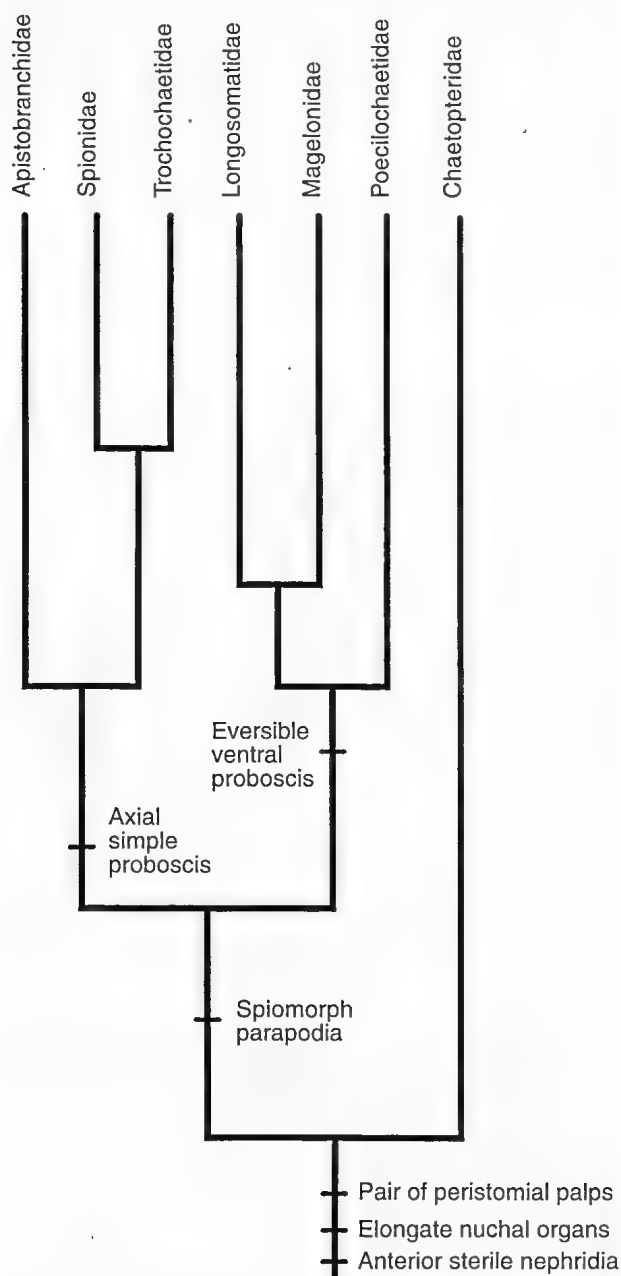


Figure 1.102 Relationships among families in the Spionida from the preferred cladogram of Rouse & Fauchald (1997). The Uncispionidae were not included in this analysis, but are proposed to be members of the Spionida.

Family Chaetopteridae

Chaetopterids are tubicolous benthic polychaetes with a pair of long, grooved palps (Pls 7.4–7.6, 8.1). The fragile body is differentiated into three distinct regions characterised by unusually modified parapodia (Fig. 1.104F).

The prostomium is small and rounded; antennae are absent. One pair of grooved peristomial palps is present (Fig. 1.104A). Nuchal organs are located laterally on the prostomium. Differentiation of parapodia divides the body into three regions (Fig. 1.104B): the first and subsequent anterior segments have notopodia only; the mid-body segments have biramous parapodia with prominent achaetous notopodia and neuropodia, and; posterior segments have less prominent parapodia, with both lobes pointed or with neuropodia present as tori. Dorsal and ventral cirri, branchiae and pygidial cirri are all absent. Aciculae are absent. Chaetae are lancet-shaped capillaries (Fig. 1.104B, C), anteriorly, modified spines on chaetiger 4 (Fig. 1.104D), and uncini in median and posterior neuropodia (Fig. 1.104E). This description follows that of Fauchald & Rouse (1997).

The family Chaetopteridae was erected by Audouin & Edwards (1833), but the first and most widely known species, *Chaetopterus variopedatus*, was described by Renier (1804). The principal recent taxonomic works are those by Gitay (1969), Bhaud (1977), Bhaud *et al.* (1994) & Blake (1996b). Globally, the Chaetopteridae includes four genera, *Chaetopterus*, *Mesochaetopterus*, *Phyllochaetopterus* and *Spiochaetopterus*, and about 30 nominal species (Blake 1996b). In Australia, all known genera are recorded, and at least seven species (Museum Victoria and Australian Museum unpublished databases).

Many species have uncertain taxonomic status, especially widely distributed species including the nominotypical species, *Chaetopterus variopedatus*. Although about 25 nominal species of *Chaetopterus* are described, many authors accept only a single species, *Chaetopterus variopedatus*, which is reportedly cosmopolitan in both tropical and temperate seas (Day 1967; Hartman 1969). Scheltema (1974) recorded the long-lived planktotrophic larvae of *C. variopedatus* and another widely distributed chaetopterid, *Spiochaetopterus costarum*, from surface oceanic waters and took this as indicative of trans-oceanic larval dispersal. However, Bhaud (1978) identified additional taxa from Scheltema's samples. Petersen (1984) interpreted the taxonomic status of *Chaetopterus variopedatus* differently, suggesting that North Atlantic records alone represent about 10 species. However, the necessary taxonomic revision remains to be completed and few species of chaetopterids are adequately described. Until such taxonomic studies have been completed and published, chaetopterids will be unsuitable for biogeographic studies, and studies of the biology of individual species should document source material carefully.

Chaetopterus 'variopedatus' (whether one or many species) constructs a tube at intertidal to shelf depths in soft sediments throughout the world. It is also a fouling organism, forming tubes on pier piles and other hard substrata [according to Petersen (1984), these records represent different taxa]. The tubes of *Chaetopterus* are often U-shaped, whereas those of the other genera are branched and less regular. The other chaetopterid genera are also mostly from soft sediments, ranging from intertidal to shelf depths, although several species occur in slope depths (Blake 1996b).

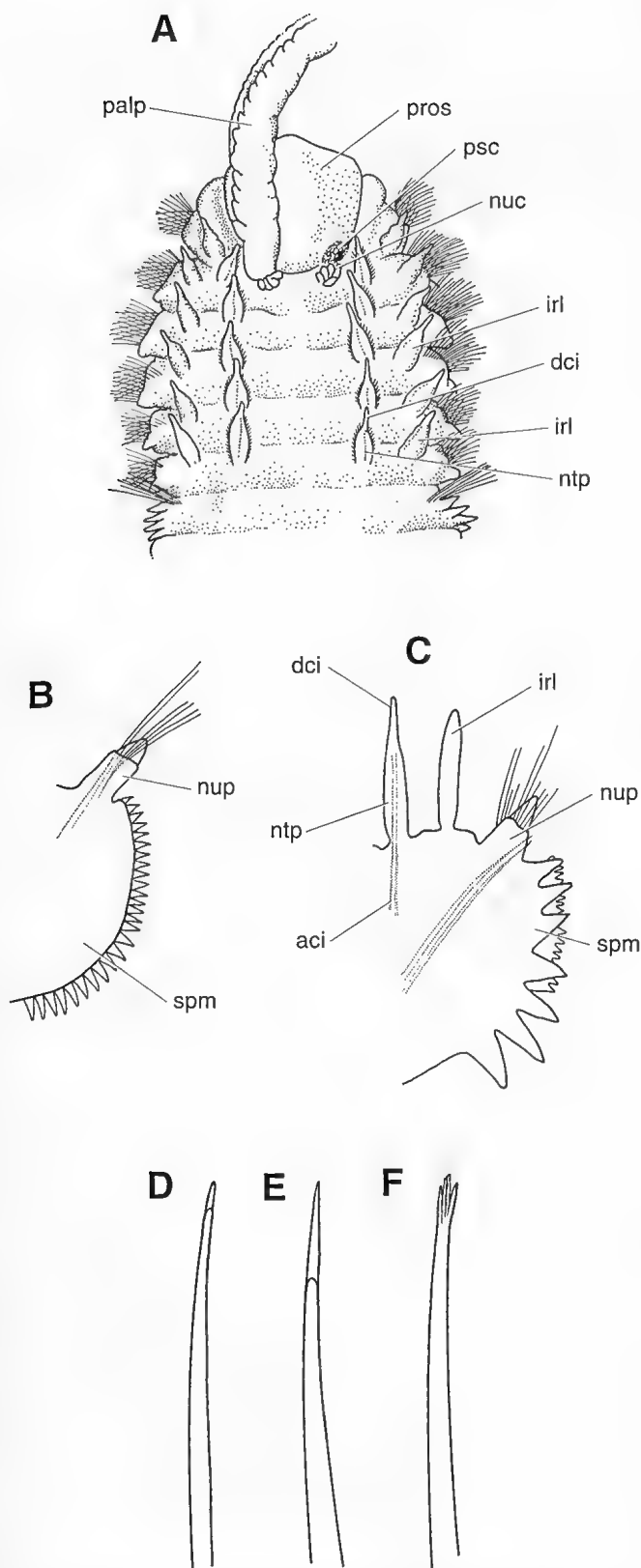


Figure 1.103 Family Apistobranchidae. **A**, anterior end of *Apistobranchus ornatus*, dorsal view; right palp missing. **B, C**, parapodia of *Apistobranchus glaciera* showing marginal serrations of the subpodal membrane: **B**, parapodium of chaetiger 5, posterior view (notopodium and inter-ramal lobe not shown); **C**, parapodium of chaetiger 7, posterior view. **D–F**, neurochaetae, variously worn, *Apistobranchus ornatus*. **aci**, acicula; **dci**, dorsal cirrus; **irl**, inter-ramal lobe; **ntp**, notopodium; **nuc**, nuchal organ; **nup**, neuropodium; **palp**, palp; **pros**, prostomium; **psc**, palpal scar; **spm**, subpodal membrane. (A, D–F, after Blake 1996a; B, C, Hartman 1978; scales not available)

[K. Nolan]

1. CLASS POLYCHAETA

The body of chaetopterids is divided into three regions, with a ciliated groove running the length of the body dorsally. The morphology of the body is best understood in terms of the filter-feeding mechanism employed in the family. All chaetopterids are suspension-feeders, using a mucous bag to collect particles from the water current which is maintained through the tube (Barnes 1965). The anterior body region is dorso-ventrally flattened and includes ventral glands used to secrete the tube. The heavily modified chaetae of chaetiger 4 are used to cut the tube walls, allowing the worm to extend the tube or to insert a new branch (Blake 1996b). The mid-body region is distinguished by the presence of highly modified notopodial lobes which secrete the mucous bag in which

suspended particles are trapped. These enlarged notopodia are held closely against the inside of the tube, and are moved to create a suction pump, maintaining water movement through the tube. Periodically the movement of water is reversed, and cilia pass a bolus of food particles and mucus anteriorly to the mouth along the dorsal groove. Detailed descriptions of the function and energetics of the suspension-feeding mechanism in *Chaetopterus* can be found in MacGinitie (1939), Barnes (1964, 1965), Brown (1975) and Riisgård (1989).

In the widespread species complex of *Spiochaetopterus costarum*, feeding behaviour differs slightly. The notopodia of the midbody are modified as branched foliaceous lobes,

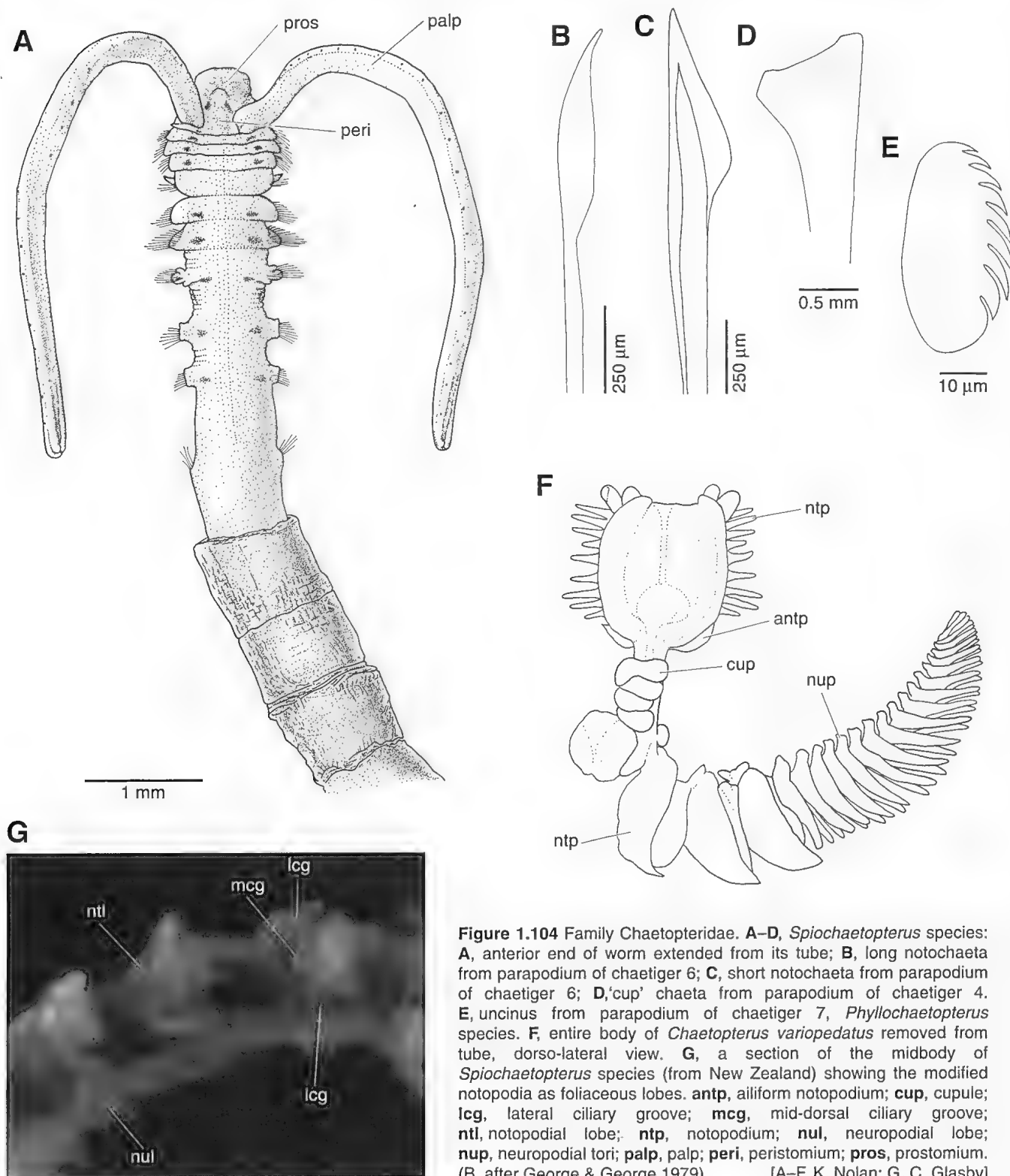


Figure 1.104 Family Chaetopteridae. **A–D**, *Spiochaetopterus* species: **A**, anterior end of worm extended from its tube; **B**, long notochaeta from parapodium of chaetiger 6; **C**, short notochaeta from parapodium of chaetiger 6; **D**, 'cup' chaeta from parapodium of chaetiger 4. **E**, uncinus from parapodium of chaetiger 7, *Phyllochaetopterus* species. **F**, entire body of *Chaetopterus variopedatus* removed from tube, dorso-lateral view. **G**, a section of the midbody of *Spiochaetopterus* species (from New Zealand) showing the modified notopodia as foliaceous lobes. **antp**, alliform notopodium; **cup**, cupule; **lcg**, lateral ciliary groove; **mcdg**, mid-dorsal ciliary groove; **ntl**, notopodial lobe; **ntp**, notopodium; **nul**, neuropodial lobe; **nup**, neuropodial tori; **palp**, palp; **peri**, peristomium; **pros**, prostomium. (B, after George & George 1979) [A–F, K. Nolan; G, C. Glasby]

which form three ciliary rings (Fig. 1.104G; water current is produced by the beating cilia and membranelles of the ciliary rings (C. Glasby personal communication; Nishi & Arai 1996). A mucous bag secreted on the second chaetiger of the midbody region traps suspended food particles entrained in the water current, and a food ball is produced. When the food ball is large enough it is carried forward to the mouth along the mid-dorsal ciliary groove. The whole process of mucous bag secretion and ball production takes between 30 seconds and 2 minutes (Nishi & Arai 1996). This species also uses mucous string feeding when suspended particle concentrations are high. The mucous strings, formed by the mid-dorsal ciliary rings, traps particles and both are rolled up by the foliaceous notopodia and passed forward in the dorsal groove; this process may be facilitated when the worm inverts itself forming a J-shape (Nishi & Arai 1996).

The posterior body region is relatively unmodified and contains the gametes in sexually mature adults; males have white parapodia, whereas yellow coiled ovaries and eggs colour the parapodia of females (Costello *et al.* 1957). The sexes are separate and fertilisation is external, although reproduction has only been described in laboratory studies (Costello *et al.* 1957). A description of chaetopterid larvae is summarised in Blake (1996b). Larvae are spherical, up to 1 mm in diameter and are already divided into three regions. The characteristic modified chaetae of chaetiger 4 in adults are already identifiable in larvae, which may have up to three mesotrochal bands. The larvae are long-lived planktotrophs. Detailed descriptions of larval development are found in Enders (1909), Werner (1953), Cazaux (1965) Bhaud (1966) and Mileikovsky (1967b). Asexual reproduction has been recorded in colonies of *Phyllochaetopterus prolifica*; autotomous fragments regenerated as new individuals (Potts 1914).

Populations of chaetopterids may reach high densities in shallow waters, resulting in stabilisation and sediment trapping in otherwise mobile sediments (Bailey-Brock 1979). The tough, parchment-like tubes are persistent structures, and provide homes for crabs and other polychaetes such as pilargids and polynoids (Baird 1865; Britaev 1993; Ng & Sasekumar 1993). However, no such commensal associations have yet been recorded in Australia. Green bodies in the intestinal walls of species in *Mesochaetopterus*, *Phyllochaetopterus* and *Spiochaetopterus* from a single location in Canada were tentatively identified as a flagellate micro-organism, and *Chaetopterus* apparently also harbours an identical or similar organism (Berkeley 1930). This association has not been studied in detail, but is possibly symbiotic. Bioluminescence has been described in *Chaetopterus* and *Mesochaetopterus*, the luminous organs being unicellular components of the epithelium; the distribution of these luminous organs apparently assists in identification of live specimens, or species identification based on histological preparations (Fujiwara 1935).

Family Longosomatidae

The Longosomatidae (previously Heterospionidae) are poorly known benthic polychaetes. They are characterised by having elongate median body segments, each encircled by a nearly complete ring of chaetae, and by anterior elongate branchial filaments.

The prostomium is subtriangular and carries eversible nuchal organs. The peristomium is reduced and bears a pair of grooved palps. The thoracic region of 7 to 9 (usually 9) chaetigers has segments with low postchaetal lobes; dorsal and ventral cirri are absent. Post-thoracic chaetigers are markedly elongate. Segmental divisions are poorly delimited. Up to eight pairs of filament-like dorsal branchiae are present on thoracic chaetigers from chaetiger 2 (Fig. 1.105A, B). The posterior end (Fig. 1.105C) consists of several short inflated segments carrying falcate spines, pygidial cirri are absent. Aciculae are absent; chaetae occur in dense fascicles of capillaries, including thickened aristate and subuluncini-like capillaries, and spines (Fig. 1.105D–F). This definition is based on Borowski (1995) and Fauchald & Rouse (1997).

The first species described was *Heterospio longissima* by Ehlers (1874), from deep water off Ireland; he did not place this species in a family. Much later Hartman (1944b) erected a new family (Longosomatidae) and genus for a Californian species, *Longosoma catalinensis*. Subsequently realising it should be placed in *Heterospio*, she proposed to change the family name Heterospionidae. However, Longosomatidae (originally spelt Longosomidae) has priority. Borowski (1995) listed and compared the six described species and several unnamed forms; all longosomatid species are referred to the genus *Heterospio*. No species are yet known from Australian waters, although Knox (1960) has recorded an unnamed species from New Zealand.

Longosomatids live in soft sediments, ranging from coastal habitats to abyssal depths, and are recorded from scattered localities in the Pacific and Atlantic Oceans, as well as the Mediterranean Sea, East China Sea and Red Sea. Their rarity in most benthic collections, and certainly their infrequent collection as whole worms, may partly be due to their ability to retreat within deep burrows out of reach of sampling equipment (Borowski 1995). However, in one survey in Marlborough Sounds, New Zealand, they proved relatively common in muds at less than 65 m depth (Estcourt 1967), with up to 16 taken in one 0.25 m² grab sample.

Longosomatids are medium-sized polychaetes about 1 mm wide and 50 mm long. The grooved palps are highly deciduous and have rarely been observed. The degree of fusion of prostomium and peristomium remains uncertain. Either the peristomium is reduced to lips and the first segment is achaetigerous (Fauchald & Rouse 1997; Rouse & Fauchald 1997) or the annulus behind the prostomium is the peristomium (Borowski 1995).

Nothing is known of the reproductive or feeding biology of longosomatids, but their possession of palps suggests they are probably at times surface deposit-feeders (Fauchald & Jumars 1979).

Longosomatids are placed within Spionida by Rouse & Fauchald (1997; Fig. 1.102); their similarities with the Spionidae include grooved peristomial palps and dense fascicles of capillary chaetae in anterior segments. However, longosomatids are also similar to the Cirratulidae (in the Terebellida), with which they share cinctures of chaetae and expanded posterior segments (characters not included in Rouse & Fauchald's analysis), as well as filamentous branchiae, grooved peristomial palps, head and parapodial morphology, and chaetal types. Characters supporting Rouse & Fauchald's Spionida and Terebellida clades in most of their analyses are apparently either homoplastic or reversals, and the affinities of longosomatids deserve further study.

Family Magelonidae

Magelonids are benthic polychaetes which have a distinctive shovel-like prostomium. They are distinguished from other members of the Spionida by the presence of a pair of palps with elongate papillae.

The prostomium is flattened and shovel-shaped with one pair of palps attached ventro-laterally (Fig. 1.106A, B); nuchal organs are absent. The palps are round basally and have an expanded papillated distal region. The pharynx is eversible; jaws are absent. The first segment, in adults, lacks parapodia and chaetae. The parapodia of remaining segments are biramous; each ramus has a low ridge of chaetae and supporting podial lobes. Dorsal and ventral cirri, and branchiae are absent. Aciculae are absent. Chaetae are simple; capillaries and dentate hooded hooks are present (Fig. 1.106D–F). Chaetae of chaetiger 9 are modified spine-

like capillaries (Fig. 1.106C). One pair of pygidial cirri is present. This description follows that of Fauchald & Rouse (1997).

The Magelonidae was erected by Cunningham & Ramage (1888) and contains a single genus, *Magelona*, and over 50 described species (Blake 1996c). Descriptions of new species from the intertidal zone in Brazil (Bolivar & Lana 1986), shelf depths in the Gulf of Mexico (Uebelacker & Jones 1984) and Thailand (Nateewathana & Hylleberg 1991), and at least four apparently undescribed Australian species indicate that both globally and in Australia, many additional species remain to be described. Magelonid species live in soft sediments, mostly from the inshore and shelf depths; they are less common on the continental slope (Blake 1996c; Museum Victoria unpublished databases). The taxonomy of the genus *Magelona* has been discussed in a series of papers by Jones (1963, 1971, 1977, 1978), but there is no recent worldwide review of *Magelona*. A brief taxonomic history of the family is given by Blake (1996c).

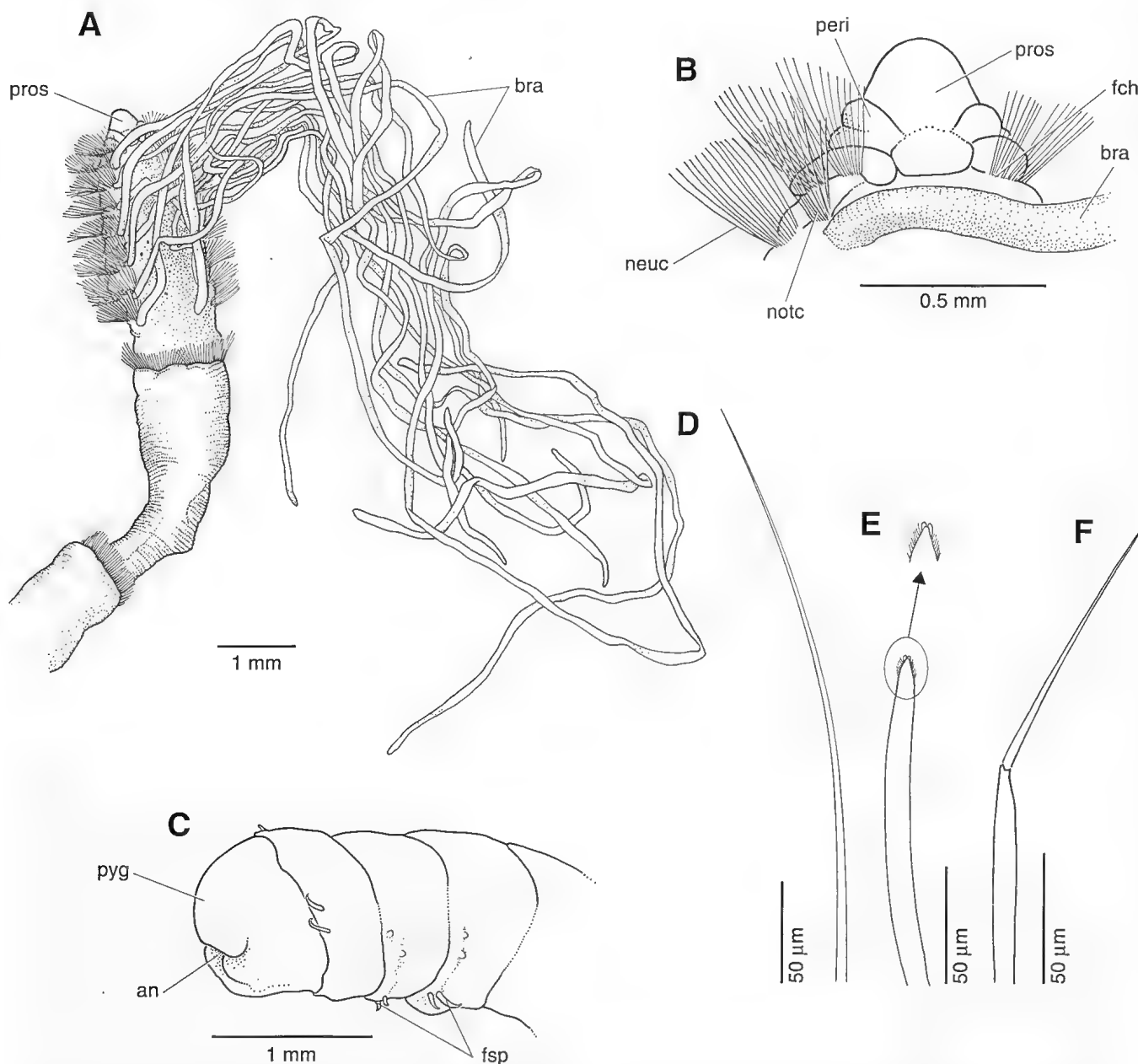


Figure 1.105 Family Longosomatidae. An undescribed *Heterospio* species from New Zealand. **A**, anterior end, dorsal view. **B**, detail of head, dorsal view. **C**, posterior end. **D–F**, chaetae: **D**, notochaetal capillary; **E**, spine of posterior chaetiger with detail of tip; **F**, aristate notochaeta. **an**, anus; **bra**, branchiae; **fch**, first chaetiger; **fsp**, falcate spines; **neuc**, neurochaetae; **notc**, notochaetae; **peri**, peristomium; **pros**, prostomium; **pyg**, pygidium.

[K. Nolan]

The best known species in Australia is *Magelona dakini* (Fig. 1.106B), which is widespread in south-eastern Australia. However, additional species, also occur in Australian waters, including three apparently undescribed species from the continental shelf of south-eastern Australia and another from and inshore waters in north-western Australia (Museum Victoria unpublished databases).

The distinctive prostomium of magelonids is presumed to be used for burrowing through soft sediments. However, only the eversible pharynx has been observed undertaking this activity. Also, magelonids are surface deposit-feeders and apparently do not obtain food from subsurface sediments ingested while burrowing (Jones 1968). The pharynx is everted by the hydrostatic pressure of the blood, and not through direct

muscular action (Jones 1968). The paired papillated tentacular palps, which are held above the sediment, are respiratory as well as involved in collecting descending food particles (Jones 1968).

The blood pigment in magelonids is haemerythrin (Wells & Dales 1974). The sexes are separate, but little is known of reproduction. Fertilisation is apparently external and gametes are present in adults, and planktonic larvae occur in coastal waters during the summer (in three British species) (Wilson 1982). Larval development from fertilised eggs through to settlement was described for the same three British species by Wilson (1982). There have been no studies of magelonids in Australian waters, and very few studies anywhere on their biology.

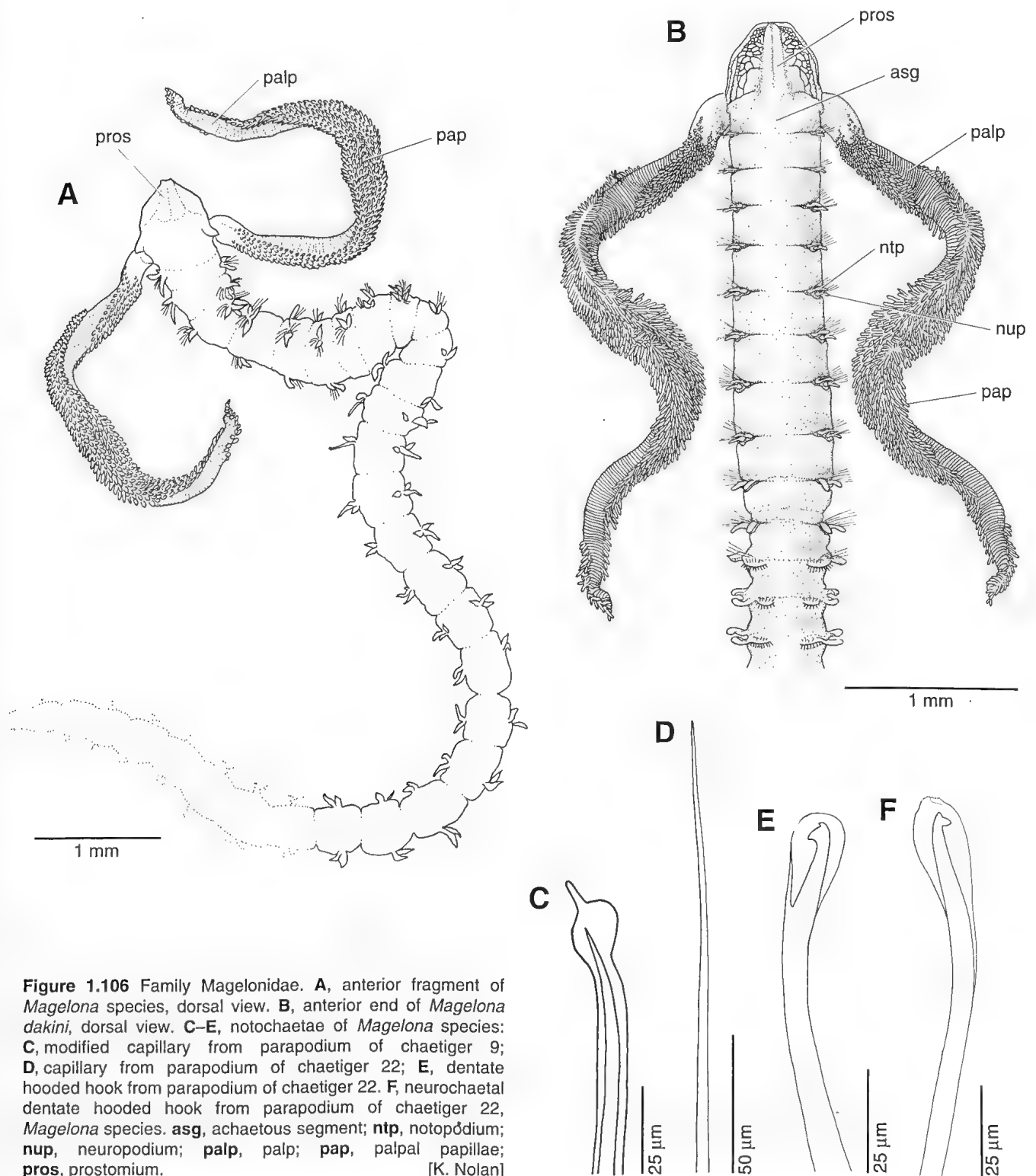


Figure 1.106 Family Magelonidae. **A**, anterior fragment of *Magelona* species, dorsal view. **B**, anterior end of *Magelona dakini*, dorsal view. **C–E**, notochaetae of *Magelona* species: **C**, modified capillary from parapodium of chaetiger 9; **D**, capillary from parapodium of chaetiger 22; **E**, dentate hooded hook from parapodium of chaetiger 22. **F**, neurochaetal dentate hooded hook from parapodium of chaetiger 22, *Magelona* species. **asg**, achaetous segment; **ntp**, notopodium; **nup**, neuropodium; **palp**, palp; **pap**, palpal papillae; **pros**, prostomium. [K. Nolan]

Family Poecilochaetidae

The Poecilochaetidae are benthic polychaetes that live in soft sediments. They have a pair of grooved feeding palps, forward-projecting chaetae which makes a cephalic 'cage' and flask-shaped parapodial lobes (Fig. 1.107A, B, C).

The prostomium is anteriorly truncate. A median ventral papillose antenna is present. Nuchal organs are present as three posteriorly directed digitiform lobes. The peristomium is reduced to lips, and one pair of grooved peristomial palps is present. The first segment is similar to subsequent segments, though it may be slightly enlarged and parapodia and chaetae project anteriorly (Fig. 1.107B). The parapodia are biramous; each lobe is a ridge with a flask-shaped tapering postchaetal lobe (Fig. 1.107C). Dorsal and ventral cirri are absent. Branchiae are present as flattened parapodial structures. Numerous pygidial cirri are present. Aciculae are absent. Chaetae are all simple; feathered or otherwise modified capillaries or thick spines are present (Fig. 1.107D-H). This description follows that of Fauchald & Rouse (1997).

The family Poecilochaetidae was erected by Hannerz (1956), and the sole genus, *Poecilochaetus*, was previously included in the Trochochaetidae. At least 31 species are known globally (Read 1986; Miura 1988, 1989; Imajima 1989b; Mackie 1990; León-González 1992). Most species occur in shallow warm temperate seas, although three species are known from the deep sea; they appear to occur mostly in fine sediments (Read 1986).

Little is known of poecilochaetids in Australia. *Poecilochaetus exmouthensis* was described from north-western Australia by Hartmann-Schröder (1980) and three unidentified species occur in Bass Strait (Museum Victoria unpublished database). Read (1986) described three species of *Poecilochaetus* endemic to New Zealand waters and provided a key to all species known at that time; however, the number of described species has almost doubled since 1986.

Little is known of the biology of poecilochaetids. The tubes are U-shaped and lined with mucus; a water current is maintained through the tube (Allen 1904). Fauchald & Jumars (1979) reported that both suspension- and deposit-feeding occurs in the family; the grooved palps which are normally held above the sediment are used for this activity. The tubes of populations of one species have been found to harbour commensal crabs of the family Pinnotheridae (Taylor 1966).

Sexes are separate, but reproductive behaviour has not been observed directly; it is assumed that fertilisation is external. The larvae apparently live for a long time in the plankton (Hannerz 1956).

Family Spionidae

Members of the Spionidae are benthic polychaetes with a pair of grooved feeding palps (Pl. 8.2). They are common and widespread in soft sediments throughout most marine habitats. They are distinguished from other families in the Spionida by having foliaceous notopodia and neuropodia, and a posterior prolongation of the prostomium. One group of genera, the polydorids, burrow into mollusc shells and other calcareous substrata.

The prostomium is often rounded and truncate, but may be pointed or have a pair of lateral horns. A pair of highly mobile, grooved tentacular feeding palps which arise from the peristomium is always present (Fig. 1.108A, B); they are often lost in preserved specimens. A median antenna may also be present. The prostomium is elongated posteriorly and bears

paired nuchal organs. The parapodia are biramous (Fig. 1.108C, D), except for the first segment which may lack notochaetae in some taxa. Dorsal and ventral cirri are absent. Branchiae are often present, either restricted to a few anterior segments or present on most segments; they are located on the dorsum adjacent to the notopodial lobes to which they may be partially or completely fused. Branchiae are usually somewhat flattened, and may be simple and laterally ciliated, or may carry pinnae or lamellae (Fig. 1.108D). Other structures also referred to as branchiae may occur ventrally (in *Lindaspio*, not known from Australia) or as accessory structures on notopodia (in *Dispio* species). The pygidium may have paired elongate anal cirri, or more numerous and smaller cirri and/or lobes. Aciculae are absent. Notochaetae and neurochaetae include simple capillaries, either smooth or limbate, and simple hooks with apical teeth (Fig. 1.108E, F); compound chaetae are absent. Both hooks and capillaries may be sheathed, the latter in some taxa as stout sabre chaetae in ventral neuropodial positions (Fig. 1.108G). Other chaetal types present include recurved hooks and modified spines. In many spionids, all segments are similar, but in *Polydora* and related genera (commonly known as polydorids, see below), the fifth segment is modified and carries one or several additional types of chaetae including simple spines (Fig. 1.108H), stout brush-tipped and terminally cusped spines (Fig. 1.108I), and more slender accessory chaetae. This description is based on the studies of Blake & Kudenov (1978) and Fauchald & Rouse (1997).

The Spionidae, described by Grube (1850), has been revised by Foster (1971) and Blake & Kudenov (1978). The most recent treatment of the polydorids is that by Blake (1996d). Generic relationships within the family have been explored in a cladistic analysis by Sigvaldadóttir *et al.* (1997), and the position of the spionids within the polychaetes has been treated by Rouse & Fauchald (1997). Here the generic concepts of Sigvaldadóttir *et al.* (1997) are followed, in particular for *Prionospio* and related genera, whereas the generic arrangement of polydorids follows that as defined by Blake (1996d).

Worldwide, about 38 genera are recognised; of these 24 are known from Australian waters. Spionids, with regards to body form, are among the most diverse of polychaete families, and many hundreds of species are known globally. The Australian fauna is at least as diverse as that of any other region, and includes about 96 described species, and a number of undescribed species from shelf habitats (Museum Victoria, unpublished databases). Australian spionids, particularly from the south coast, are well-known taxonomically compared with many of the other Australian polychaete families; Australian studies include Blake & Woodwick (1976), Blake & Kudenov (1978), Hutchings & Rainer (1979), Hartmann-Schröder (1980, 1981a), Hutchings & Turvey (1984) & Wilson (1990).

Spionids are among the most ubiquitous of polychaetes, and occur, often in large numbers, in virtually all marine habitats. The species-rich genus *Prionospio* often dominates benthic communities in coastal and shelf habitats (Wilson 1990), whereas the related monotypic and endemic *Orthoprionospio* with *O. cirriformia* occurs widely in southern Australian estuaries (Blake & Kudenov 1978). Another member of this group of genera is known only from anchialine caves in north-western Australia (R. Wilson in preparation). Spionids also occur in freshwater habitats; for example, *Boccardia limnicola* inhabits coastal freshwater lakes in south-eastern Australia (Blake & Woodwick 1976). A number of species of *Polydora*, *Boccardia* and related genera live in burrows in calcareous habitats such as mollusc shells, coralline algae and

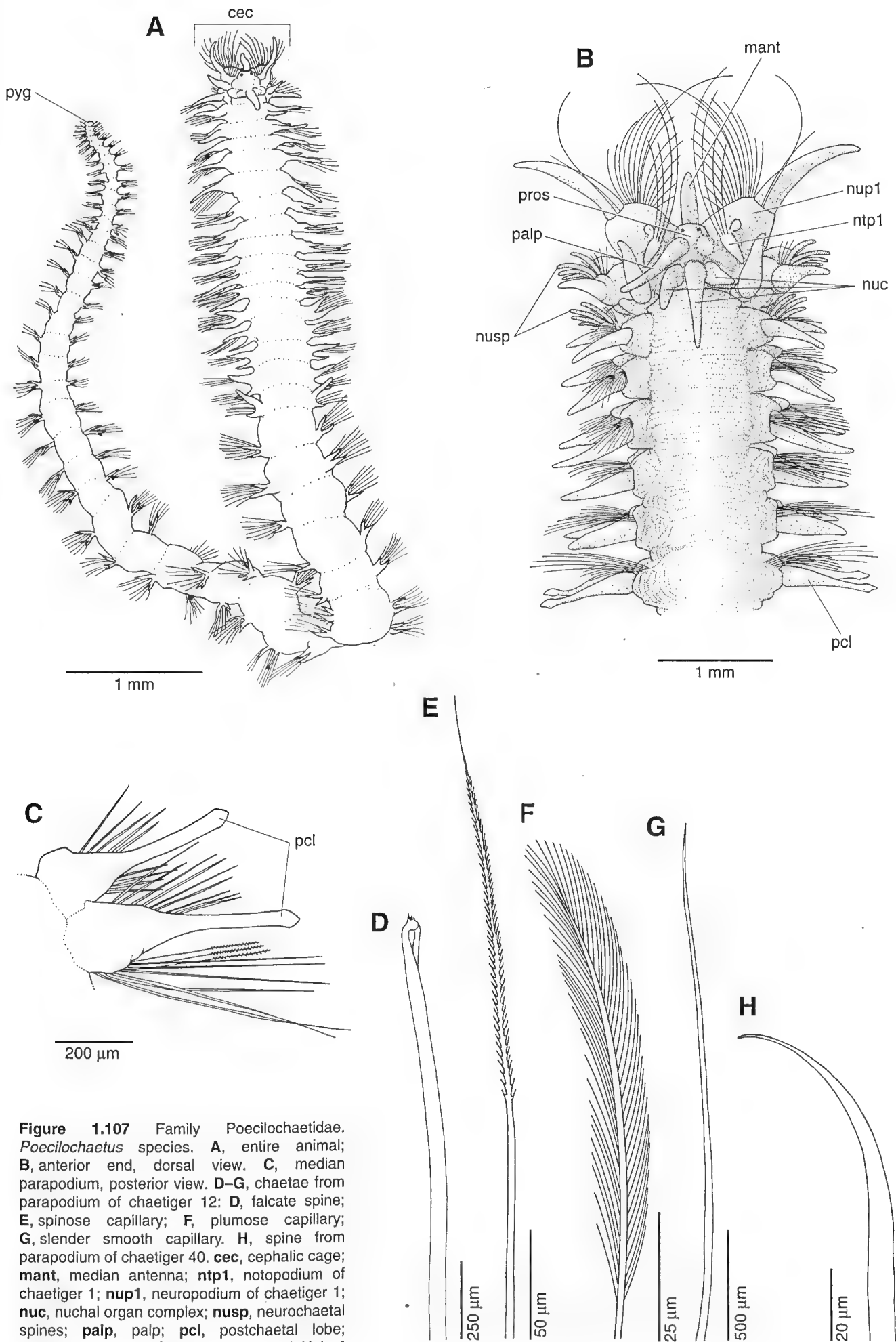


Figure 1.107 Family Poecilochaetidae. *Poecilochaetus* species. **A**, entire animal; **B**, anterior end, dorsal view. **C**, median parapodium, posterior view. **D–G**, chaetae from parapodium of chaetiger 12: **D**, falcate spine; **E**, spinose capillary; **F**, plumose capillary; **G**, slender smooth capillary. **H**, spine from parapodium of chaetiger 40. **cec**, cephalic cage; **mant**, median antenna; **ntp1**, notopodium of chaetiger 1; **nup1**, neuropodium of chaetiger 1; **nuc**, nuchal organ complex; **nusp**, neurochaetal spines; **palp**, palp; **pcl**, postchaetal lobe; **pros**, prostomium; **pyg**, pygidium. [K. Nolan]

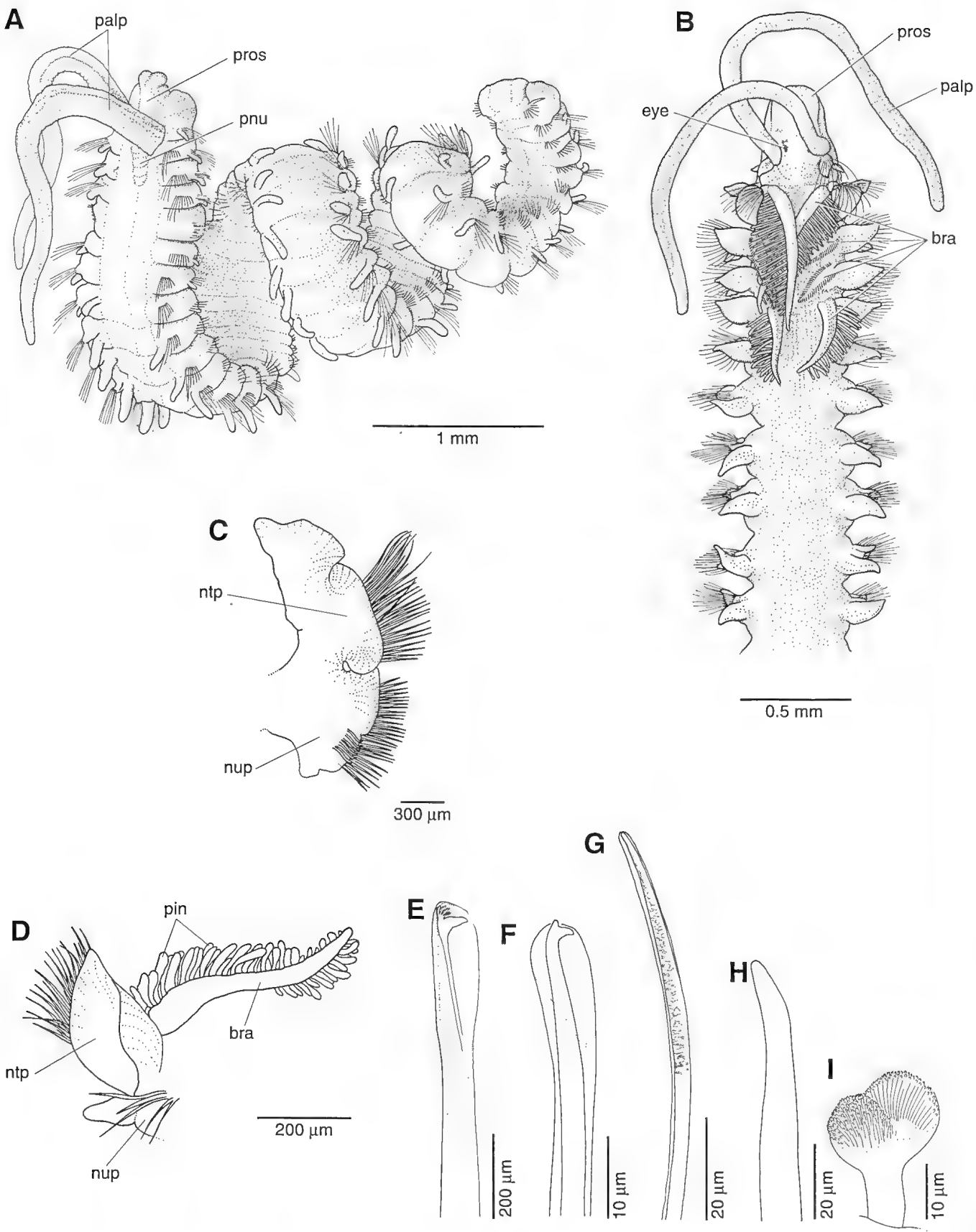


Figure 1.108 Family Spionidae. **A**, entire animal of *Polydora* species. **B**, anterior end of *Prionospio coorilla*, dorsal view. **C**, parapodium from chaetiger 25, *Scolelepis victoriensis*. **D**, parapodium from chaetiger 5, *Prionospio kirrae*. **E–I**, chaetae: **E**, neuropodial hooded hook, *Prionospio nirripa*; **F**, neuropodial hooded hook, *Prionospio kirrae*; **G**, neuropodial sabre chaeta from parapodium of chaetiger 48, *Prionospio kirrae*; **H**, spine from parapodium of chaetiger 5, *Carazziella* species; **I**, brush-tipped spine from parapodium of chaetiger 5, *Carazziella* species. **blv**, blood vessel; **bra**, branchiae; **eye**, eye; **ntp**, notopodium; **nup**, neuropodium; **palp**, palp; **pin**, pinnae; **pnu**, posterior projection of prostomium carrying the nuchal organs; **pros**, prostomium.

[K. Nolan]

corals (Blake & Evans 1973), whereas other polydorids live in sediments, often muds, where they may occur in very high densities.

The Spionidae include a distinctive group of genera (*Boccardia*, *Boccardiella*, *Carazziella*, *Dipolydora*, *Polydora* and *Pseudopolydora*) which are loosely called the polydorids. Polydorids have a moderately to highly modified fifth chaetiger (Fig. 1.108A); the segment is enlarged and bears spine-like chaetae. At least 115 species are known worldwide (Blake 1996). Their small size and great morphological variability means that they present major taxonomic difficulties where accurate species identifications are required. All polydorid genera occur in Australia. The most recent review treats only species from California (Blake 1996) and the best review of Australian species is that given by Blake & Kudenov (1978).

Spionids are positioned to feed at the sediment-water interface, either as deposit- or suspension-feeders; some species may alternate between deposit- and suspension-feeding modes depending on environmental conditions (Taghon *et al.* 1980; Dauer *et al.* 1981). *Malacoceros indicus*, studied at Lizard Island, Queensland, is an obligate surface deposit-feeder and never raises its feeding palps into the water column; it also shows no evidence of particle-size selection (Dauer & Ewing 1991). In most taxa, the feeding palps bear a deep longitudinal groove lined by cilia; six functional types of cilia have been identified (Dauer 1994). Potential food particles are transported to the mouth by ciliary action, or in taxa lacking a palpal groove by muscular contraction of the palp (Dauer 1983, 1985). Direct feeding by capture of particles by the proboscis has also been observed (Daro & Polk 1973), but is probably unusual. Particles rejected by the proboscis are removed by water currents initiated by branchial cilia (Dauer 1985); these processes can result in greatly increased sedimentation rates around high density spionid populations (Frithsen & Doering 1986; Blake 1996d).

Asexual reproduction has been recorded in a number of polydorid taxa and occurs by autotomy (Hobson & Green 1968; Kudenov & Blake 1978; Tzvetlin & Britayev 1985). Blake (1996d) divided spionid genera into two groups based on the mode of sexual reproduction. In one group, including *Aonides*, *Laonice*, *Prionospio*, *Spiophanes*, *Scolecopsis* and *Malacoceros*, gametes are discharged into the water where fertilisation occurs. In the other group, which includes *Spio*, *Microspio* and the polydorid genera, internal fertilisation occurs after copulation; many of these genera maintain larvae in capsules until they are released for a planktonic phase. Some members of this latter group have modified sperm, introsperm (Jamieson & Rouse 1989).

Formation of egg capsules and larval development in spionids comprise a variety of forms and reproductive strategies, perhaps accounting in part for the diversity and wide range of habitats of spionid species. Egg capsules may be cylinders, bead-like strings or spherical capsules; they may be anchored to the interior of the adult tube or may be deposited in the sediment (Okuda 1946; Blake 1969; Day & Blake 1979). Development may involve a single larval type, or, in many species, more than one pattern of development may occur, even within a single egg capsule (Blake 1996). Unfertilised nurse eggs may provide nutrition for developing larvae in the same egg capsule; this process is termed adelphophagy and apparently occurs in more than half of spionid species thus far studied (Simon 1967; Blake & Woodwick 1975). Development may be planktotrophic or lecithotrophic and may be a species-specific character, or both types of development may occur in a single species, depending on

seasonal conditions and nutrient availability (Blake 1996). Numerous studies of intraspecific variability in reproductive strategy and population genetics indicate strongly that this plasticity is a major factor in the radiation of spionid species (Simon 1967; Clark 1977; Rice & Simon 1980; Levin 1984). Evidence of selection processes operating during larval development were revealed by a study of a polydorid, *Boccardia proboscidea*, in Australia, where the fastest-developing larvae not only consumed nurse eggs, but also cannibalised smaller larvae in the same capsule (Petch 1991). A review of variability in reproduction and development in spionids is given by Blake (1996).

Many species in the polydorid group bore into mollusc shells and other calcareous substrata, and thus have attracted the attention of aquaculture and other shellfish industries. Nevertheless, only a few species are recorded commonly as causing significant damage to the host organism; these include *Polydora ciliata*, *P. hoplura* and *P. websteri* (Blake & Evans 1973). The latter two species, both of which have northern hemisphere type localities, are recorded from south-eastern Australia where they may damage both native oysters (*Saccostrea* species) and the introduced Pacific oyster, *Crassostrea gigas* (Whitley 1890; Roughley 1922; Blake & Evans 1973; Blake & Kudenov 1978). However, polydorids are difficult to identify and it is likely that some records attributed to these species are misidentifications (Korringa 1951; Blake & Evans 1973). Polydorids may occur on shells as surface fouling organisms, but shell damage occurs through either formation of U-shaped burrows or mud-blisters (Blake & Evans 1973). Mud-blisters are formed when the worm penetrates the oyster from outside or enters the open valves while the oyster is feeding. Mud deposits then accumulate around the worm inside the mantle cavity of the oyster, which secretes chitinous and nacreous layers over the irritation (Blake & Evans 1973; Bailey-Brock & Ringwood 1982). Mud-blisters impair oyster growth and also reduce the marketability of the oyster; various treatments and farming practices are used to control polydorids in oyster culture (Wisely 1980; Bailey-Brock & Ringwood 1982; Handley & Bergquist 1997). The incidence and effects of polydorids on commercial molluscs and other species in Australia is poorly known. Elsewhere, polydorids also bore holes in scallop (*Pecten* species) and abalone (*Haliotis* species) shells as well as in a large number of mollusc, coral and coralline algal species of no commercial significance; various burrow shapes are known and the morphology appears dependent both on the polydorid and on the host species (Blake & Evans 1973; Blake 1981b; Bergman *et al.* 1982; Kojima & Imajima 1982; Baxter 1984). Recruitment of *Polydora* to coral substrata has been studied by Hutchings *et al.* (1992).

Despite the commercial significance of polydorids to oyster and other mollusc fisheries, surprisingly little is known about the mechanisms by which these worms penetrate calcareous substrata. Zottoli & Carriker (1974) described shell dissolution and tube formation in *Polydora websteri*, which makes a burrow in the shells of the bivalves *Crassostrea virginica* and *Mytilus edulis*. It uses the modified spines of the fifth chaetiger to maintain a constant tube diameter, while the shell matrix is etched and dissolved by an acidic secretion of the worm. Other evidence has suggested a greater role for physical abrasion of the shell by the modified spines (Sato-Okoshi & Okoshi 1993), although the ability of *P. websteri* to construct burrows even if the modified fifth chaetiger spines are removed shows that chemical dissolution of the shell is the crucial factor (Haigler 1969). Recently, Sato-Okoshi (1999) described the burrow structure of various species of boring spionids.

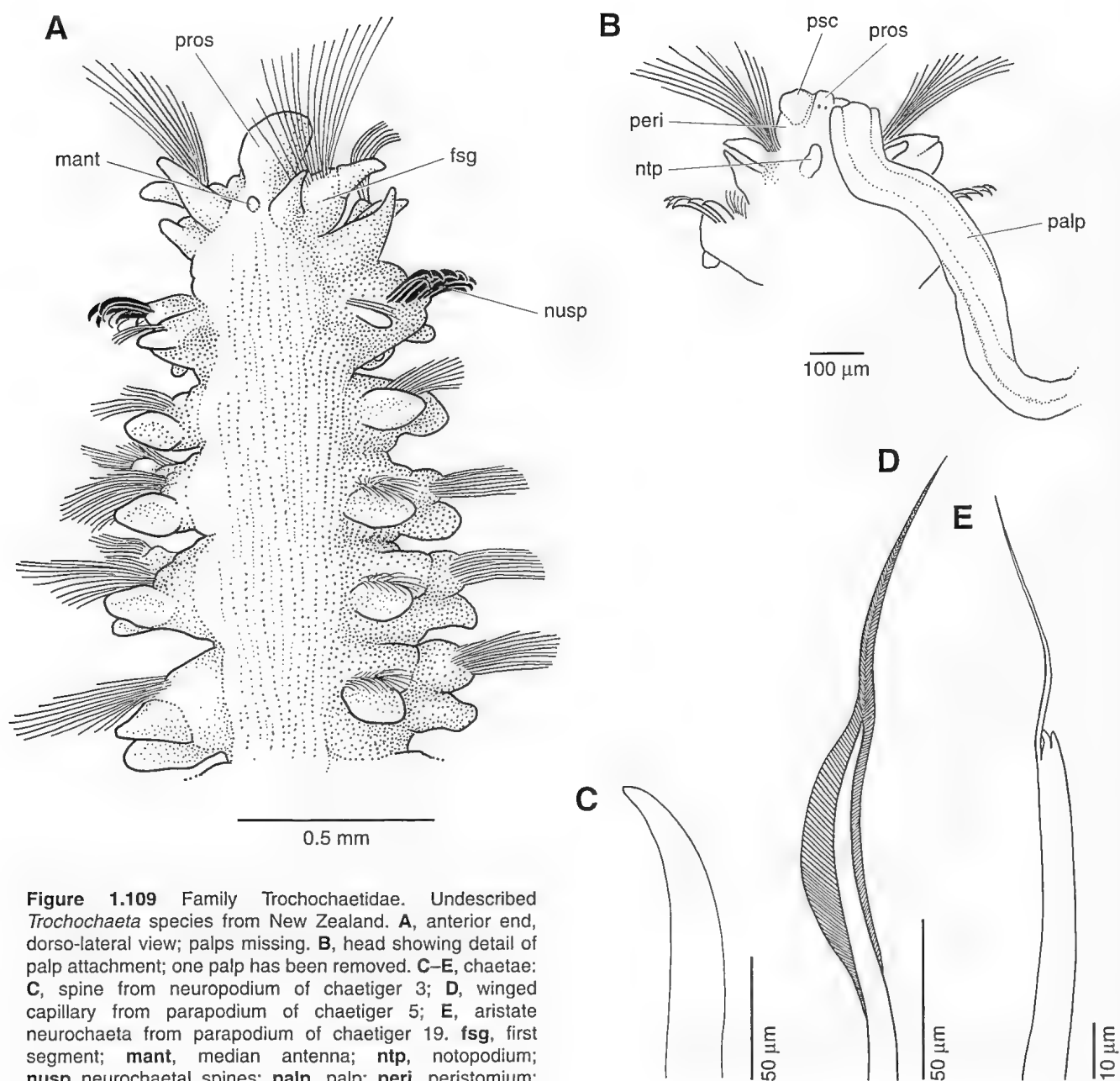


Figure 1.109 Family Trochochaetidae. Undescribed *Trochochaeta* species from New Zealand. **A**, anterior end, dorso-lateral view; palps missing. **B**, head showing detail of palp attachment; one palp has been removed. **C–E**, chaetae: **C**, spine from neuropodium of chaetiger 3; **D**, winged capillary from parapodium of chaetiger 5; **E**, aristate neurochaeta from parapodium of chaetiger 19. **fsg**, first segment; **mant**, median antenna; **ntp**, notopodium; **nusp**, neurochaetal spines; **palp**, palp; **peri**, peristomium; **pros**, prostomium; **psc**, palpal scar. (A, C–E, from one specimen, B from another) [K. Nolan]

The papers cited above describe a spionid fauna that is mostly endemic to southern Australia. Other regions, both tropical and temperate, are also now known to support spionid faunas with significant, often dominant, endemic components (Ward 1981; Blake 1983; Maciolek 1985; Hylleberg & Nateewathana 1991; Sigvaldadóttir 1992).

Spionids, which lack fossilisable hard parts, are unknown in the fossil record except as trace fossils. Polydorid-like burrows, however, are known from fossil shells, mostly of Pleistocene age, but including some from Triassic and even Devonian formations (see review by Blake & Evans 1973); none have been recorded from Australia.

As yet there are no biogeographical studies of spionids; such studies, however, show promise based on the high degree of endemism reported above and the availability of phylogenetic hypotheses about these taxa (Sigvaldadóttir *et al.* 1997). However, distributional anomalies may be caused by accidental dispersal by humans. This may be more of a problem in polydorids due to the widespread traffic in edible shellfish during the past century, which has undoubtedly translocated species around the world.

Family Trochochaetidae

Trochochaetids are benthic polychaetes with paired grooved feeding palps; they live in soft sediments. They have a series of uniramous parapodia on the median body segments, which distinguish them from other Spionida.

The prostomium is anteriorly rounded, and a median antenna may be present. Paired grooved peristomial palps are present (Fig. 1.109B). Nuchal organs are present as ciliated grooves on the posterior prolongation of the prostomium. The first segment has biramous parapodia which project anteriorly (Fig. 1.109A), but is otherwise similar to subsequent chaetigers. Several median chaetigers have only neuropodia and neurochaetae; the notopodial lobe is reduced to a small cirrus. Branchiae, tentacular cirri and dorsal and ventral cirri are absent. Numerous pygidial cirri may be present, as may several ventral retractile cirri (Pettibone 1976b). Aciculae are absent. Chaetae are all simple, variously ornamented capillaries and spines (Fig. 1.109C–E). This description follows that of Fauchald & Rouse (1997).

Following the removal of the genus *Poecilochaetus* from the Trochochaetidae to the Poecilochaetidae, only the genus *Trochochaeta* remains in the Trochochaetidae (Hannerz, 1956). Globally, nine species of *Trochochaeta* are known (Pettibone 1976b; Dean 1987; Imajima 1989a); Pettibone (1976b) provided a key to all species. The main taxonomic studies are those by Pettibone (1976b) and Mackie (1990).

Trochochaetids have not yet been recorded from Australia, despite extensive sampling of the continental shelf of south-eastern Australia. At least one species of *Trochochaeta* occurs on the continental shelf and slope of New Zealand (Fig. 1.109).

Trochochaetids occur in soft sediments from shallow inshore waters to at least 3000 m; two species are attributed to depth ranges of about 10–1500 m (Pettibone 1976b). They construct complex tubes lined with mud which has been consolidated by mucus (Thulin 1921).

Weitbrecht (1984) provided a detailed description of the structure and function of major anatomical features in the three body regions of *Trochochaeta multisetosum* (from California). The thoracic region is locomotory, and the movable neuropodial spines are apparently used to grip the interior of the tube. The anterior abdominal region can be flattened and undulates up and down, generating water movement through the tube. The posterior abdominal region contains gametes and genital ducts and clusters of eversible neuropodial spines.

Sexes are separate. Both planktotrophic and lecithotrophic larval development has been described in two *Trochochaeta* species that have been studied from the North Atlantic (Buzhinskaja & Jørgensen 1987). However, larvae of both species have long swimming chaetae apparently adapted for pelagic dispersal (Buzhinskaja & Jørgensen 1987). No studies of Australian species of *Trochochaeta* have been made.

TEREBELLIDA

The name Terebellida was first used by Dales (1962) with the rank of order, and included Ampharetidae, Pectinariidae, and Terebellidae (see Table 1.3). Dales made no mention of the Trichobranchidae, but this may have been an oversight. Prior to this, the names Terebellomorpha or Terebelliformia had often been used for essentially the same grouping of taxa. Exceptionally, Holthe (1986b) continued with the use of the name Terebellomorpha, with the rank of order, to group Alvinellidae, Ampharetidae, Pectinariidae, Terebellidae, and Trichobranchidae. Fauchald (1977) included Boguidae and Sabellariidae in Terebellida, in addition to the usually included taxa. Boguidae has now been shown to be a member of Maldanidae (Wolf 1983).

Sabellariidae is generally regarded as being a member of Sabellida (see Fitzhugh 1989) and this is where they are classified in this volume. A detailed review of the history of the taxa included in Terebellida can be found in Holthe (1986b). Terebellida was expanded considerably by Rouse & Fauchald (1997) to include a clade in which most members have a single pair of palps (Acrocirridae, Cirratulidae, Flabelligeridae etc.). This clade of polychaetes contains members (for example, Acrocirridae and Cirratulidae) that are referred to as Cirratulida. The formulation by Rouse & Fauchald (1997) has made Terebellida a very diverse taxon with 12 families (see Table 1.3), but they identified several clear synapomorphies for this grouping, namely the presence of a first segment with no chaetae, a gular membrane, and a heart body (Fig. 1.110). These forms all have either a pair, or

multiple, grooved palps. It should be noted that not all of the analyses in Rouse & Fauchald (1997) resulted in the same grouping of taxa listed as Terebellida here. Although Alvinellidae, Ampharetidae, Pectinariidae, Terebellidae, and Trichobranchidae always formed a clade, the remaining taxa often formed a clade with other taxa, such as Spionida. Further investigation is clearly required.

Holthe (1986b) indicated that the worldwide number of valid described species in Terebellida (that is, Alvinellidae, Ampharetidae, Pectinariidae, Terebellidae, and Trichobranchidae) was about 700, grouped into more than 130 valid genera. There have been many further descriptions, particularly in Terebellidae, from Australian waters since that time (for example, Hutchings & Glasby 1988; Hutchings 1993; Hutchings & Smith 1997). With the inclusion here of

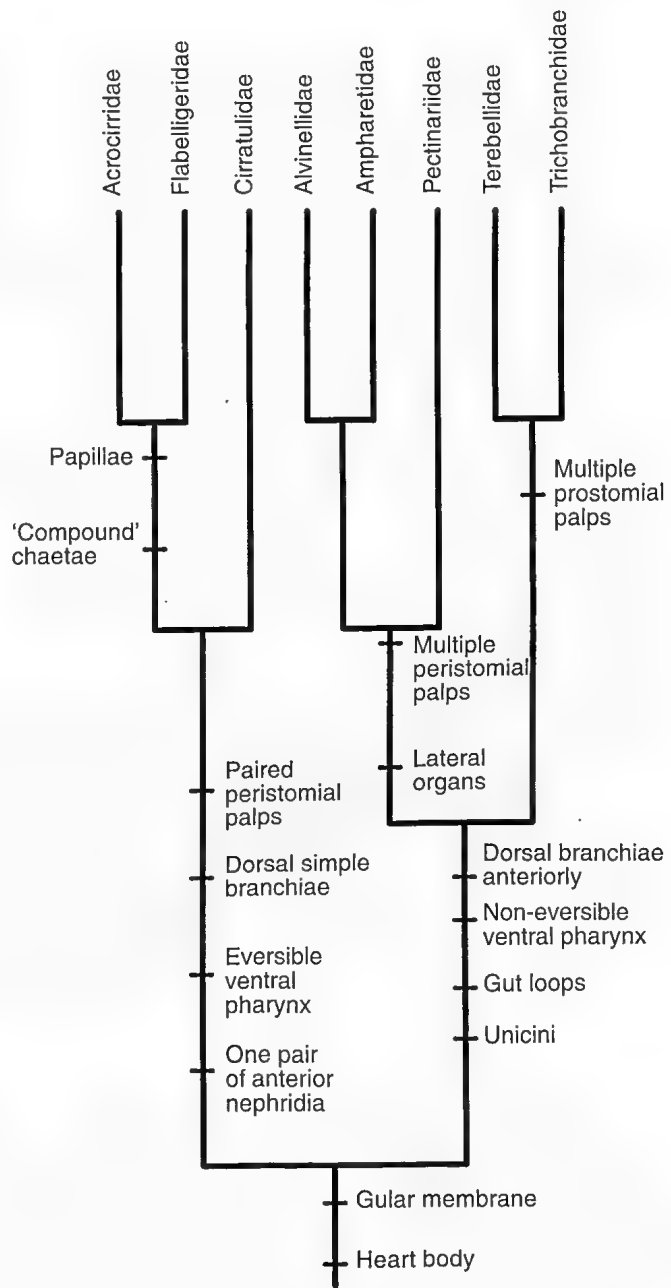


Figure 1.110 Relationships among taxa in the Terebellida from the preferred cladogram of Rouse & Fauchald (1997). Ctenodrilidae, Fauveliopsidae and Sternaspidae were not included in this analysis, but are proposed to be members of the Terebellida.

1. CLASS POLYCHAETA

the Acrocirridae, Cirratulidae, Ctenodrilidae, Fauveliopsidae, Flabelligeridae, Poeobiidae and Sternaspidae the total number of species in the clade is over 1000 in about 200 genera. No members of the Alvinellidae, Fauveliopsidae, or Poeobiidae have been recorded from Australian mainland waters, but the latter two families will probably be found to occur with further collecting.

The Alvinellidae, large tubiculous worms associated with deep-sea hydrothermal vents, are not described in the following section, although they are referred to in the family key. Of the remaining taxa, the Cirratulidae and Terebellidae are the most diverse with numerous species described and recorded in Australia (Day & Hutchings 1979; Hutchings & Glasby 1991).

Family Acrocirridae

Acrocirrids are small thread-like or maggot-shaped worms. The head region usually has a pair of palps and anterior pairs of branchiae. Parapodia are reduced with chaetae arising from the body wall. They live in soft sediments.

The prostomium is either rounded and distinct, as in *Macrochaeta* (Fig. 1.111A), or forms a narrow keel between the compressed anterior segments, as in *Acrocirrus*; eyespots are present. Antennae are absent. Rouse & Fauchald (1997) considered the peristomium to be limited to the buccal region. Although typically the peristomium is referred to as the first segment which forms a narrow ring dorsally and then projects forward under the prostomium, it is in fact the peristomium. The issue was confused by Banse (1969), who was unable to decide whether or not the palps were prostomial or peristomial. According to Rouse & Pleijel (in press) the peristomium is limited to the pair of palps. The palps are readily lost and have not been described in numerous early publications. Nuchal organs are present (Okuda 1934).

No information is available on the organisation of the longitudinal muscles. The thorax and abdomen are poorly differentiated. Segmentation is distinct; the first segment is reduced dorsally and lacks parapodia and chaetae, but bears the first pair of branchiae (Banse 1969). In other segments, the parapodial rami are small, truncated cones, all similar in form. In some taxa, the notopodia are larger than the neuropodia on some segments (Banse 1969). Dorsal and ventral cirri are absent. Usually, four pairs of simple branchiae are present on segments 2 to 5 (Fig. 1.111B; Banse 1969). Lateral organs and dorsal cirrus organs have not been recorded. The epidermal papillae resemble those of flabelligerids (Mesnil 1899).

The ventral buccal organ is unarmed, and is presumed to be eversible. The gut forms a simple straight tube, and there is no gular membrane. Metanephridia are present (Okuda 1934); Fauchald & Rouse (1997) commented that they resemble those of cirratulids. The first pair of segmental organs are excretory (Banse 1969), and subsequent organs are presumed to be gonoducts. Okuda's (1934) observation of numerous segmental organs in the anterior region requires confirmation. A heart body is present in the closed circulatory system (Mesnil 1899; Okuda 1934). The notochaetae are segmented and spinose, and neurochaetae comprise compounded hooded falcigers (Fig. 1.111D–F). The joints in the large compound chaetae comprise superficial grooves or folds. There are no aciculae.

The narrow keel-shaped prostomium in *Acrocirrus* forms a ridge which reaches nearly to the upper lip (Banse 1969); it resembles a short, median antenna in dorsal view. Numerous epidermal papillae cover the body to various degrees (Okuda 1934); some look like dorsal or ventral cirri, but none seems to be differentiated from other body papillae. According to Banse (1969), the first three segments are achaetous. This definition is based on Fauchald & Rouse (1997).

Acrocirrids were originally described as cirratulids with compound chaetae (Fauvel 1927; Day 1967). Okuda (1934) added important information on internal structures and Banse (1969) diagnosed a new family for *Acrocirrus* and *Macrochaeta*. The family shares with the flabelligerids features such as the structure of the epidermal papillae and compound hooks.

Fauchald (1977) recognised three genera and 19 species, whereas Banse (1969) recognised only two genera, *Acrocirrus* and *Macrochaeta*. Fauchald (1977) included the deep-water genus *Flabelligella* following Orensanz (1974); the inclusion of this genus has not been widely accepted. Banse (1978) described an additional two species and Averincev (1980) another. In Australia, two species have been described: *Acrocirrus aciculigerus*, from the Sydney region, and *Macrochaeta australiensis*, from Port Phillip Bay and Westport, Victoria. Banse (1969) provided a key to the family and Kudenov (1976) gives one for the genus *Macrochaeta*.

Acrocirrids occur worldwide in soft sediments, from tropical regions to near the Antarctic continent and from the intertidal zone to depths of 5000 m (Banse 1969); intertidal species may occur under stones.

Acrocirrid species are typically small, ranging in length from less than 10 mm to about 66 mm for the Australian species, *Acrocirrus aciculigerus*. *Macrochaeta* species appear to be considerably smaller than those of *Acrocirrus*.

The gut is a simple tube (Okuda 1934). Acrocirrids are presumed to be selective deposit-feeders which use their buccal organ to swallow sediment. Banse (1969) referred to this structure as a pharynx and Rouse & Fauchald (1997) assumed that it is eversible.

Anterior excretory nephridia have been noted by Marion & Bobretzky (1875), Mesnil (1899) and Banse (1969). Okuda (1934) suggested that several pairs of anterior nephridia are present, prompting Rouse & Fauchald (1997) to suggest further investigation. Okuda also observed gametes in the posterior segments, suggesting that posterior gonoducts are present. Also nuchal organs and epidermal papillae are present according to Okuda (1934).

Kudenov (1976) collected mature individuals of *Macrochaeta australiensis* in January. Males had sperm platelets and morulae, and spermatozoa were present in the coelom. The headpiece of the sperm measured 2 µm in diameter; the acrosome appearing flattened. Polygonal oocytes about 125 µm in diameter were present.

Acrocirrids are a poorly known group that appear to resemble flabelligerids most closely in terms of the structure of epidermal papillae and compound hooks. The Acrocirridae, Flabelligeridae and Cirratulidae form a clade within the Terebellida (Rouse & Fauchald 1997; see Fig. 1.110).

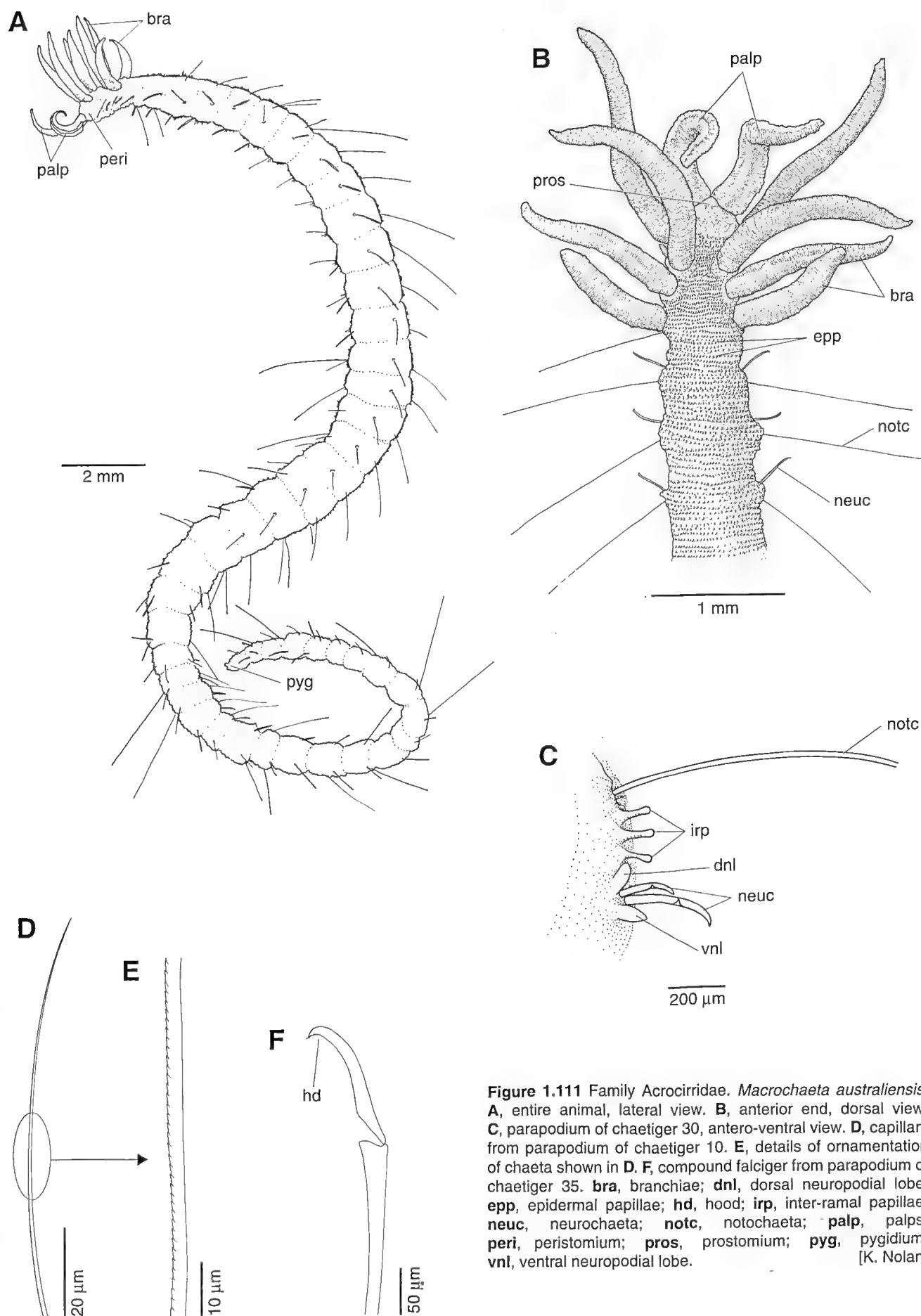


Figure 1.111 Family Acrocirridae. *Macrochaeta australiensis*. **A**, entire animal, lateral view. **B**, anterior end, dorsal view. **C**, parapodium of chaetiger 30, antero-ventral view. **D**, capillary from parapodium of chaetiger 10. **E**, details of ornamentation of chaeta shown in **D**. **F**, compound falciger from parapodium of chaetiger 35. **bra**, branchiae; **dnl**, dorsal neuropodial lobe; **epp**, epidermal papillae; **hd**, hood; **irp**, inter-ramal papillae; **neuc**, neurochaeta; **notc**, notochaeta; **palp**, palps; **peri**, peristomium; **pros**, prostomium; **pyg**, pygidium; **vnl**, ventral neuropodial lobe. [K. Nolan]

Family Ampharetidae

Ampharetids are short and compact, tubiculous worms. Numerous retractile buccal tentacles are present. Branchiae are paired and segmently arranged and may be smooth, lamellate or papillose. The body is divided into a thorax with both noto- and neuropodia and an abdomen with neuropodia only. Notochaetae are capillaries and neurochaetae are uncini.

The prostomium is relatively small, and is elongated, rounded, or pointed. It is situated on top of a larger unit consisting of the fused first and second segments. The peristomium is reduced to lips and the roof of the mouth. Antennae are absent. Palps are short, slender peristomial buccal tentacles attached to a dorsally located curtain within the buccal cavity; occasionally one or two very much larger grooved palps are present (Hartman 1969). Nuchal organs are comma-shaped, and are situated laterally on the prostomium. Longitudinal muscles are in four bands; segmentation is well-defined. Parapodia first occur on segments III to V. Short cylindrical notopodia are present on the thorax and neuropodia are tori throughout. Dorsal and ventral cirri are absent. Up to four pairs of branchiae are present on the anterior segments; branchiae may all be similar or structurally different along the body or between species. Epidermal papillae are absent. The pygidium may be unadorned or may have many cirri (Uschakov 1955; Holthe 1986a). Lateral organs are present (Rullier 1951), but dorsal cirrus organs have not been observed; presumably they are absent. The buccal organ is non-eversible (Fauvel 1897; called a food-sorter by Dales 1963). A gular membrane is present between two anterior segments (Meyer 1887; Hessle 1917). The gut is straight in some taxa, but is mostly looped (Wirén 1885). Segmental organs are mixonephridia (Goodrich 1945); the first pair is excretory, the others act as gonoducts (only a few anterior pairs are present). The circulatory system is closed (Wirén 1885) and a heart body is present (Picton 1899; Kennedy & Dales 1958). Aciculae are absent. Chaetae are present as notopodial thoracic capillaries and neuropodial uncini; in some taxa, slender, peg-like chaetae are present in anterior neuropodia. Anterior notopodial paleae are present in some taxa (Fig. 1.112A); other taxa have paired large hooks (Fig. 1.112E) dorsally in paleal positions, but many taxa are without either paleae or hooks. This definition is based on that given by Fauchald & Rouse (1997).

Ampharetids closely resemble terebellids and were included with them until Malmgren (1866) gave ampharetids familial status. The main feature used to separate the two families is behavioural: ampharetids can withdraw their buccal tentacles completely into their mouth, whereas terebellids cannot. Rouse & Fauchald (1997) placed the Ampharetidae as a sister group to the Terebellidae within the Terebellida (Fig. 1.110).

Hessle (1917) reviewed the earlier taxonomic studies of the family made by Malmgren (1865) and Fauvel (1897), Nilsson (1912) on the nervous system, Wirén (1885) on the alimentary canal and Meyers (1887) on the nephridia. Although Hessle (1917) in general followed Malmgren (1865) he observed that many of the genera were very narrowly defined and consisted of only one or two species. Hessle proposed a classification based upon the number of pairs of nephridia, but admitted that their distribution was not constant, even within a genus. Day (1964) suggested therefore that a generic classification based on this character was not very usable. However, his own classification based on the number of pairs of uncinigerous segments, number and type of branchiae also leads to a large number of genera, many of which are known by one or a few

species. Since then many additional genera have been described based on a single, or a few specimens; a taxonomic revision is urgently needed.

Chamberlin (1919) proposed three subfamilies: Melinninae, Ampharetinae and Samythininae. Using Chamberlin's study and considering the additional genera described since then, Day (1964) proposed two subfamilies, Melinninae and Ampharetinae, which have become widely accepted. Day (1964) suggested that because of the variability in the paleae of the subfamily Samythininae it could not be justified.

Members of the Melinninae are distinguished by having smooth buccal tentacles, the lack of paleae, and one or two pairs of stout notopodial hooks sometimes present behind the branchiae (Fig. 1.112B). Small acicular neurochaetae are embedded in segments III, IV and often on V and VI. Neurochaetae, as uncini, are present from segment VII and always have a single row. Numerous (20–90) abdominal segments are present.

Members of the Ampharetinae are distinguished by having either smooth buccal tentacles with a groove along one side, or are papillose. Paleae are often present (Fig. 1.112A). Notopodial hooks are absent posterior to the branchiae. Neurochaetae are absent from segments III to VI. Neurochaetae (as uncini) are present from segment VII and may often have one, or more than one, series of teeth. Few (8) to many (62) abdominal segments are present.

Holthe (1986b) proposed a series of tribes within each of the subfamilies, but they have not been used by other workers. He also proposed another subfamily, Uschakovinae, which he suggested is probably part of the Ampharetidae, although the buccal tentacles cannot be withdrawn into the mouth. The latter feature is one of the major characteristics separating the family from the terebellids. This group needs to be reassessed.

Prior to Day (1964), 49 genera were recognised as valid; Day recognised 33 genera. Fauchald (1977) recognised 61 genera with 210 species. Of these 61 genera, 40 are known only by a single species and may be known only from type material. An additional 12 genera and 35 species at least have been described since then. Fauchald (1977) noted that, although the review of the family by Day (1964) greatly reduced the number of monotypic genera, it raised the question of whether the characters used by him to distinguish genera were any more appropriate than those which he disregarded.

In Australia, Day & Hutchings (1979) recorded seven species in five genera. Since then two additional species have been described by Hutchings & Rainer (1979), and Hartmann-Schröder (1981). An Australian revision of the family is being undertaken by Hutchings & Peart (in preparation) and to date an additional six genera have been recognised in Australian waters. Another three genera are present according to the records in the database of the Australian Museum. Clearly, the Australian ampharetid fauna is rich and diverse and probably contains many new species. The collections being examined at present by Hutchings & Peart are primarily from shallow coastal locations; as ampharetids tend to be diverse in deeper waters, this revision may be only an interim one.

Williams (1987) undertook a revision of Californian ampharetids, and based on an examination of the type material made several changes. However, since then no revisionary work has been undertaken. Jirkov (1994) outlined a proposal to revise the family, but an expanded version of this abstract does not appear to have been published.

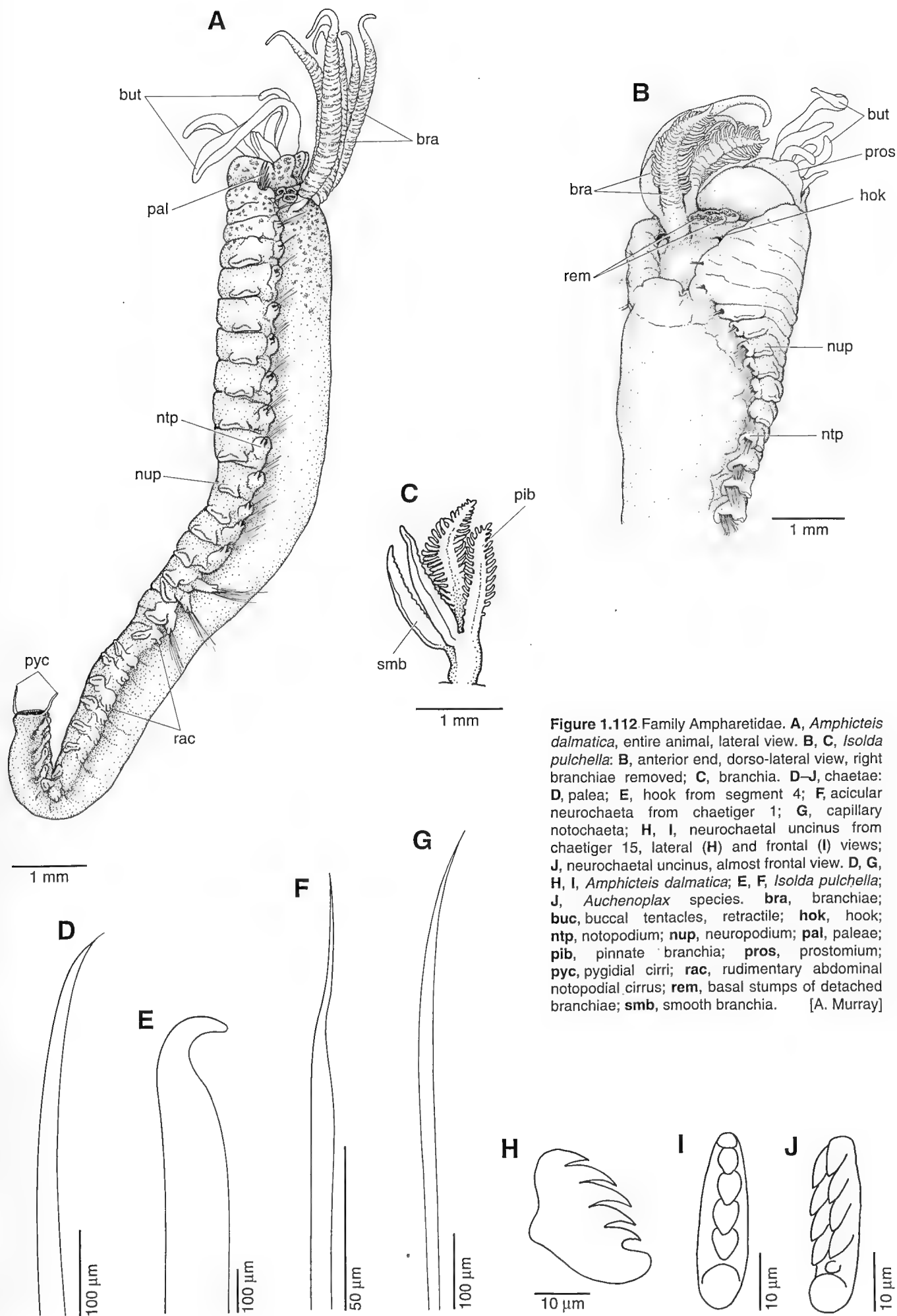


Figure 1.112 Family Ampharetidae. **A**, *Amphicteis dalmatica*, entire animal, lateral view. **B**, *Isolda pulchella*: **B**, anterior end, dorso-lateral view, right branchiae removed; **C**, branchia. **D–J**, chaetae: **D**, palea; **E**, hook from segment 4; **F**, acicular neurochaeta from chaetiger 1; **G**, capillary notochaeta; **H**, **I**, neurochaetal uncinus from chaetiger 15, lateral (**H**) and frontal (**I**) views; **J**, neurochaetal uncinus, almost frontal view. **D**, **G**, **H**, **I**, *Amphicteis dalmatica*; **E**, **F**, *Isolda pulchella*; **J**, *Auchenoplax* species. **bra**, branchiae; **buc**, buccal tentacles, retractile; **hok**, hook; **ntp**, notopodium; **nup**, neuropodium; **pal**, paleae; **pib**, pinnate branchia; **pros**, prostomium; **pyc**, pygidial cirri; **rac**, rudimentary abdominal notopodial cirrus; **rem**, basal stumps of detached branchiae; **smb**, smooth branchia. [A. Murray]

1. CLASS POLYCHAETA

Ampharetids live in fragile tube of sandy mud; sometimes they are attached to sponges, compound ascidians or the shells of living molluscs. Few species live in shallow water and they become common with increasing depth (Day 1967). Some species have been recorded living close to hydrothermal vents (Solís-Weiss 1993; McHugh & Tunnicliffe 1994). They are also well represented on the Eastern Pacific seamounts (Levin *et al.* 1991) and are the second most species-rich family in the deep-sea trenches (Levenstein 1991). Virtually all ampharetids are marine and are rarely found in areas of fluctuating salinity; two species, however, have been recorded from the river Danube (Europe) in freshwater (Gruia & Manoleli 1974). Species may be either solitary or live in dense colonies (Hutchings 1973) in both cold and warm waters (Hernández-Alcántara & Solís-Weiss 1991).

Day (1964) reviewed the morphology of the ampharetid anterior end, concluding that the paleal segment (when paleae are present) is the third segment (see also Fauvel 1927 and Holthe 1986b); consequently, the first and second segments are achaetigerous and completely fused to the head. Holthe (1986b) discussed the buccal tentacles present within the terebellomorphs; the dorsal curtain to which these are attached in the ampharetids is an autapomorphy for the family.

The feeding apparatus, in ampharetids, consists of protrusible buccal tentacles. The usual statement, that the buccal tentacles are retractable into the mouth (compare with Fauvel 1927 and Fauchald 1977) is easily misunderstood: the buccal tentacles, although having considerable individual mobility, are protruded as a group, rather than individually.

Storch (1988) investigated the surface of the tentacles of *Amphicteis gunneri* and found that it is occupied by densely arranged structures. The structure of the feeding tentacles of *Melinna maculata* has been studied by Storch & Gaill (1986) who found that they have a deep median groove that is lined with multiciliated epithelial cells.

The prostomium may bear eyespots and, sometimes, a pair of glandular ridges, which project from the antero-lateral margins as blunt, anteriorly divergent processes. The shape of the prostomium varies according to whether the buccal tentacles are withdrawn into the mouth or extended, so its shape is a limited value character. Day (1961) suggested that there are two achaetous segments preceding the branchiae in all genera. Thus the first branchiferous segment, which bears the paleae in some genera, in his opinion, becomes segment III. In genera such as *Phyllocomus*, *Melinna*, *Isolda*, *Amphicteis* and *Ampharete* four pairs of branchiae are present. Day (1961) found that the four branchiae of *Amphicteis gunneri* are supplied by four blood vessels corresponding to segments III, IV, V and VI. However there is a tendency for the anterior segments to become telescoped during development, so often the branchiae are grouped on the dorsal surfaces of segments III and IV. In *Phyllocomus* the first two pairs are on segment III and the last two pairs are segmentally arranged. Other branchial arrangements present within the family, include 2:2 or 3:1, where the three pairs of branchiae are arranged in a transverse row across segment III with the fourth pair immediately behind. In some genera the number of pairs of branchiae have been reduced to three or two, and may be separated from one another or united by a basal web. Often this basal web unites only the first three pairs of branchiae leaving the fourth pair free. Branchiae may be smooth and cylindrical in shape or may have lateral papillae (= pinnate; Fig. 1.112C) or flanges or even a series of lateral lamellae.

The fusion of anterior segments has led to the loss of chaetae in some genera. In *Isolda* and *Melinna* the neurochaetae of segments III to VI are present, but may be absent in VII in other melinnine genera. Segment III always lacks notochaetae, those of segment IV are stout hooks and those on segment V and VI are either small hooks or absent. In *Melinnopsis*, the large hooks are absent, but notopodial capillaries are present on V and VI.

In the subfamily Ampharetinae, neurochaetae are absent on segments III to VI. In some genera the notochaetae of segment III are enlarged to form paleae whereas those on segments IV to VI are typical capillary notochaetae, although they may be small or absent.

Day (1964) summarised the existing information of the internal anatomy of the group, which is largely based on studies by Hessle (1917) and Annenkova (1930). Ampharetids may have one well-developed septum separating the first few segments from the rest of the body.

The posterior thorax begins at segment VII and is marked in all genera by the commencement of neurochaetal uncini. The number of thoracic uncinigerous segments varies from 9 to 14 and is constant within a genus. Posterior thoracic notopodia are conical projections; some genera have a notopodial cirrus. In most genera, notopodia bear winged capillaries, although in some the notochaetae of one particular segment have minutely spinulose tips. The thoracic neurochaetae are uncini (Fig. 1.112H–J) with one or more rows of teeth above the base; the number of rows seems to be constant within a genus.

The change from thorax to abdomen is marked by the loss of notochaetae and either the complete loss of the notopodium or a reduced notopodium, which may or may not have notopodial cirri; these appear to be *denovo* structures not related to dorsal cirri associated with notopodia (Holthe 1986b). The neuropodia remain and the uncini tend to have more rows of teeth than thoracic ones. The number of abdominal segments varies considerably in ampharetids; according to Day (1964) it is not a useful specific character and is not constant within a genus. The pygidium is terminal and may be encircled by a number of low indistinct papillae or may bear a reduced number of longer anal cirri (Uschakov 1955; Holthe 1986a).

Characters that are used to separate genera are: the number and type of branchiae, and their arrangement; the number of thoracic uncinigerous segments, and; the number of rows of teeth on the uncini. Specific characters, which are less well defined as many genera are monospecific, include the type of branchial ornamentation, the degree of development of the branchial web and the development of abdominal notopodia. Mackie & Pleijel (1995) provided a detailed synopsis of character differences between three species of *Melinna*, which may be helpful for other genera.

A considerable amount of variation within *Paedampharete acutiseris* has been documented by Russell (1987) with characters such as the number of pairs of branchiae varying from two to three, the number of paleae per fascicle ranging from none to 11 and the number of thoracic uncinigerous segments from one to 12. Russell suggested this species may have evolved in response to living in a physically disturbed environment. This species lives in areas where high velocity currents periodically sweep across the abyssal ocean floor in the western North Atlantic. If this sort of variation is more widespread it will certainly require a major rethink of the sorts of characters used to separate genera and species in this family.

The flexibility of capillary chaetae of several polychaete species, including the ampharetid *Amphicteis mucronata*, have been investigated by Merz & Woodin (1991). They found that those of the middle segments are the stiffest, although they did not detect a relationship with size of the chaetae or the worm, and that stiffness is not predictable from the taxonomic relationship of the individuals.

Ampharetids are deposit-feeders. Food particles are collected by mobile tentacles that arise from the roof of the buccal cavity (Yonge 1928; Remane 1933; Dales 1963; Day 1964, 1967). The feeding of *Ampharete grubei* has been described in detail by Fauvel (1897) and more recently for a species of *Amphicteis* by Self & Jumars (1978). They suggested that particle selection may be mediated by winnowing during particle transport along the tentacles. The tubes of *Melinna palmata* and *M. elisabethae* (formerly *M. cristata*; see Mackie & Pleijel 1995) project obliquely above the substratum; at night the animals emerge partially from their tubes to spread their buccal tentacles over the substratum, keeping their branchiae upright. Animals kept in the laboratory will effectively clear in one night a circular patch overnight around the mouth of the tube by collecting all the sediment. They appear to sort the sediment, ingesting some particles, using others for tube construction, and some may be expelled from the immediate feeding area (P. Hutchings personal observation). Tubes are constructed of mud and shell fragments, although Warwick & Davies (1977) showed that this species will also incorporate into their tube any available large items such as large sand grains, coal, foraminiferan tests, leaf debris and polystyrene spherules.

Although ampharetids appear to be tubiculous and non-motile, the family is well represented bathyally where food is sparse (Hartman 1965; Hessler & Jumars 1974), suggesting that some form of locomotion may be necessary. The shallow-water species *Ampharete grubei* will build horizontal tubes in aquaria when the bottom is covered with a thin layer of sediment (Fauvel 1897). *Melinna elisabethae* (described as *Melinna cristata* by Hutchings 1973) reaches population densities of 5000 worms per m², with tubes forming a turf binding up the soft sediments. These tubes are orientated vertically and so densely packed that continuous tube building seems unlikely. Fauchald & Jumars (1979) summarised the available literature on the feeding biology of 14 species; information is unavailable for most ampharetids. However, the anterior morphology of most species is fairly similar, suggesting that they feed in a similar manner.

Oyenekan (1988) has suggested that *Melinna palmata* is carnivorous, perhaps feeding on *Caulleriella caputesocis*, although he does not provide any evidence to support this statement or how the animals actually catch their prey.

Gut contents have been examined in a few ampharetids and the ingested material included detritus, unicellular algae and larval invertebrates (Fauvel 1897; Hessle 1925; Hut 1925; Mare 1942). They start feeding as newly settled juveniles with 2–3 chaetigers (Nyholm 1951; Zottoli 1974), with the first tube being formed immediately after settlement or in the case of *Amphicteis floridus*, within a few days (Zottoli 1974). In this latter species, juveniles feed by a muscular pumping of the lips before the tentacles are developed.

Although Fauchald & Jumars (1979) reported that there is no published evidence of selectivity, they suggest that most marine species are selective, including *Melinna elisabethae*. The freshwater species, *Hypania invalida*, feeds on blue-green algae, in addition to green algae and diatoms, whereas *Hypaniola kowalewskii*, another species in the same habitat, avoids ingesting blue-green algae. Both species appear to be

able to breakdown plant cells; as they live in riverine conditions feeding mainly on pelagic organisms, they must employ different feeding strategies to those of more typical marine ampharetids (Gruia & Manoleli 1974).

Ampharetids that live around the hydrothermal vents appear not to have symbiotic chemoautotrophic bacteria, in contrast to other taxa such as alvinellids found in the same habitat (Desbruyeres & Laubier 1982). *Pavlovinella palmiformis*, is found living around deep-sea hydrothermal vents; individuals living at low temperature (17°C) vent sites have higher levels of phospholipid fatty acids than those at warm temperature (probably about 30–40°C) vent sites. This may be an adaptation to allow optimal membrane function (Taghon 1988).

Fauvel (1897) demonstrated the presence of a non-eversible buccal organ in the family. Dales (1963) referred to the buccal organ as a lip and food sorter. Purschke & Tzetlin (1996) have documented the presence of dorso-lateral ciliary folds in the anterior part of the gut in ampharetids. The gut is a relatively straight tube divided into a pharynx, oesophagus, stomach and intestine (Day 1964), although in *Amphicteis* it is looped (Wirén 1885). In some genera at the junction of the oesophagus and the stomach a pair of lateral pouches project forwards, and in others an internal diverticulum is present in the ventral wall of the stomach.

Two to five pairs of nephridia have been reported (Day 1964). The arrangement of the nephridia does not appear to be constant within the family or within a genus (Hessle 1917). They are found in anterior segments from about segment V to segment XI, although they may be absent from some segments. They are mixonephridia (Goodrich 1945). The first pair is excretory only, as commonly found in the terebellomorphs. In *Melinna elisabethae*, functional gonoducts develop close to the time of spawning and then regress after spawning (Hutchings 1973a).

Reproduction has been investigated in relatively few ampharetids. Wilson (1991) lists four species in four genera and they vary from brooding with indirect development in *Alkamaria romijina* (Wesenberg-Lund 1934) to free-spawning with entirely direct benthonic development in *Ampharete grubei* (Thorson 1946). Another species, *Hobsonia florida*, also broods, but within a tube and with direct development (Zottoli 1974). A further two species, *Amphicteis floridus* and *Melinnexis arctica*, brood young in the parent tube (Annenkova 1931; Zottoli 1967; Schroeder & Hermans 1975). *Melinna elisabethae* is free-spawning and produces lecithotrophic larvae (Nyholm 1950; Hutchings 1973a, 1973b, described as *M. cristata*). *Melinna palmata* breeds in a similar manner to *M. cristata* (Grehan *et al.* 1991). The widespread hydrothermal vent species *Amphisamytha galapagensis* probably mass spawns and produces non-feeding demersal larvae which undergo a short, lecithotrophic benthonic larval development; reproduction in this species is continuous.

The development of oocytes in ampharetids is gonochoric, the oocytes being proliferated from the germinal epithelium and released into the coelom where vitellogenesis occurs. In *Amphisamytha galapagensis*, a full range of oocyte sizes are found throughout the year suggesting that they produce gametes either continuously or semi-continuously. In contrast, in both species of *Melinna* investigated, gametes are proliferated over a few months and ceases some months prior to spawning. In *M. elisabethae* spawning occurs over a short period (Hutchings 1973a, 1973b, described as *M. cristata*), whereas in *M. palmata* spawning occurs over several months, with some variations reported between populations (Guillou

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& Hily 1983; Grehan *et al.* 1991). In Southampton, England, *M. palmata* has a prolonged breeding season with peaks in March and July (Oyenekan 1988).

Spermatogenesis has been reported in detail for *Melinna elisabethae* by Hutchings (1973a, described as *M. cristata*); most of it occurs within the coelom. Sperm ultrastructure has been investigated in *Amphisamytha galapagensis* by McHugh & Tunnicliffe (1994); they described a sperm typical of species that have external fertilisation (Sawada 1984). Only the acrosome shows any complexity, which can be related to egg envelope specialisations rather than fertilisation mode. They suggested that fertilisation either occurs in the water column or in the tube.

Ampharetids produce large numbers of large yolky oocytes and some estimates are given for various species by Hutchings (1973a), McHugh & Tunnicliffe (1994) and Grehan *et al.* (1991).

The proliferation of gametocytes on the germinal epithelium of *Melinna elisabethae* has been studied by Hutchings (1973a, described as *M. cristata*). She showed that the germinal epithelium exists in proliferative and non-proliferative states; the former begins immediately after spawning in late December/early January and is maintained until September. The rate of release of gametocytes into the coelom varies during this period with peaks in January and April. In September, DNA synthesis ceases on the germinal epithelium in both males and females, with no further release of gametocytes into the coelom. Hutchings speculated that there is a feedback system operating from the coelomic gametes which initiates the change from proliferative to the non-proliferative state of the germinal epithelium. Clark & Olive (1973) provided a diagram of how this feedback loop could work.

The larval development of *Melinna palmata* has been studied by Grehan *et al.* (1991). Cleavage is spiral, holoblastic and unequal. Early development is planktonic and lecithotrophic, with settlement occurring within 7 days of fertilisation, at the 3-chaetiger stage. The newly settled benthonic juvenile undergoes metamorphosis in a mucus tube. Shortly after, the rudimentary structures for feeding and respiration appear and gradually segments are added. By the time the animal reaches the 35-chaetiger stage (about 82 days), all the adult species characters are present. The earliest juvenile stage of *Amphisamytha galapagensis* found by McHugh & Tunnicliffe (1994) was a 9-chaetiger stage and they speculated that there is no pelagic stage. *Melinna elisabethae* has been recorded as having a pelagic larval stage of 3–5 days in the plankton (Nyholm 1951, described as *M. cristata*). Larval development has also been partially documented for *Schistocomus sovjeticus* by Okuda (1947).

Melinna elisabethae and *M. palmata* both exhibit incomplete spawning and mature oocytes are resorbed after commencement of new proliferation; this is used as evidence that both species exhibit polytely (Grehan *et al.* 1991; Hutchings 1973b, described as *M. cristata*).

Ampharetids appear to have an almost even male to female sex ratio with values ranging from 1.3:1 to 1:1 (Hutchings 1973b; Retière 1979; Grehan *et al.* 1991). *Melinna* species do not breed until they are at least 2 years old, and Grehan *et al.* (1991) suggested that a few individuals survive to 3 years of age. Van Dover *et al.* (1988) suggested that individuals of *Amphisamytha galapagensis* take 3.3 years to reach maturity. Hutchings (1973b) suggested that *M. elisabethae* (described as *M. cristata*) may reach maturity at 2 years of age and spawn annually for several years.

The branchiae of two species of *Melinna* have been reported to contain high levels of copper, which Gibbs *et al.* (1981) suggested provided a deterrent against predatory fish. However, in their revision of this genus Mackie & Pleijel (1995) found that at least *M. elisabethae* was an important food for several species of bottom-living fish, including haddock and flounder. They noted that many of the specimens of *M. elisabethae* had branchiae with regenerating tips, suggesting that the high concentrations of copper found by Gibbs *et al.* (1981) may afford protection only from some species of fish.

The effects of surface deposit-feeders such as *Hobsonia florida* on the succession of intertidal benthic communities has been studied by Gallagher *et al.* (1983). It is known that deposit-feeders make profound changes to their local environment by producing faecal pellets and building tubes and making the environment hospitable to taxa that otherwise would not settle or could not survive in an area (Fager 1964; Mills 1969). They found that this species facilitated the immigration of the crustacean *Tanais* species and oligochaetes. Settlement of *H. florida* was enhanced by a bivalve mollusc. Gallagher *et al.* (1983) suggested that facilitation rather than inhibition is the dominant process governing succession in this particular intertidal benthic community.

Large number of gregarines have been reported in the coelom of a number of *Melinna* species. Grehan *et al.* (1991) speculated that they reduce reproductive fecundity as low numbers of oocytes were found in *M. elisabethae* (Hutchings 1973a, described as *M. cristata*) and *M. palmata* (Grehan *et al.* 1991).

The syllid species *Calamyas amphictenicola* has been reported as an ectoparasite on a species of *Amphicteis*.

Dense populations of *Melinna palmata* are found in muddy sediments in Southampton waters, in the United Kingdom; this species prefers sediments of <60% silt. In this community, *M. palmata* was one of the most dominant species numerically. Mature breeding females were found throughout the year, with maximum breeding in the March–July period and peaks in March and July. The annual secondary production was estimated at 0.421 g m⁻² year⁻¹, based on population cohorts. The ratio between annual production and mean biomass (P:B ratio) was estimated as 2.19 (Oyenekan 1988). This population is normally monotelic; gametes are released over a period of about 6 months during the second year of growth. Individuals do not survive to breed again during the following year.

Family Cirratulidae

Members of the Cirratulidae are small to medium-sized polychaetes with numerous segments. They mainly live in sediment associated with rock crevices, algal holdfasts or seagrass, but some species live in mud tubes or bore into calcareous structures such as coral and mollusc shells (Fig. 1.33; Pl. 8.3). They have long filamentous branchiae and two, to many, palps behind a smooth conical or slightly rounded head.

Cirratulids have a conical or anteriorly rounded prostomium (Fig. 1.113A, B) that lacks appendages and a peristomium fused with a least two segments. Palps are present either as paired, grooved tentacles arising from the posterior prostomium (Fig. 1.113B) or as multiple filaments arising from the anterior segments (Fig. 1.113A). Parapodia are biramous with papillar lobes and simple chaetae (capillaries,

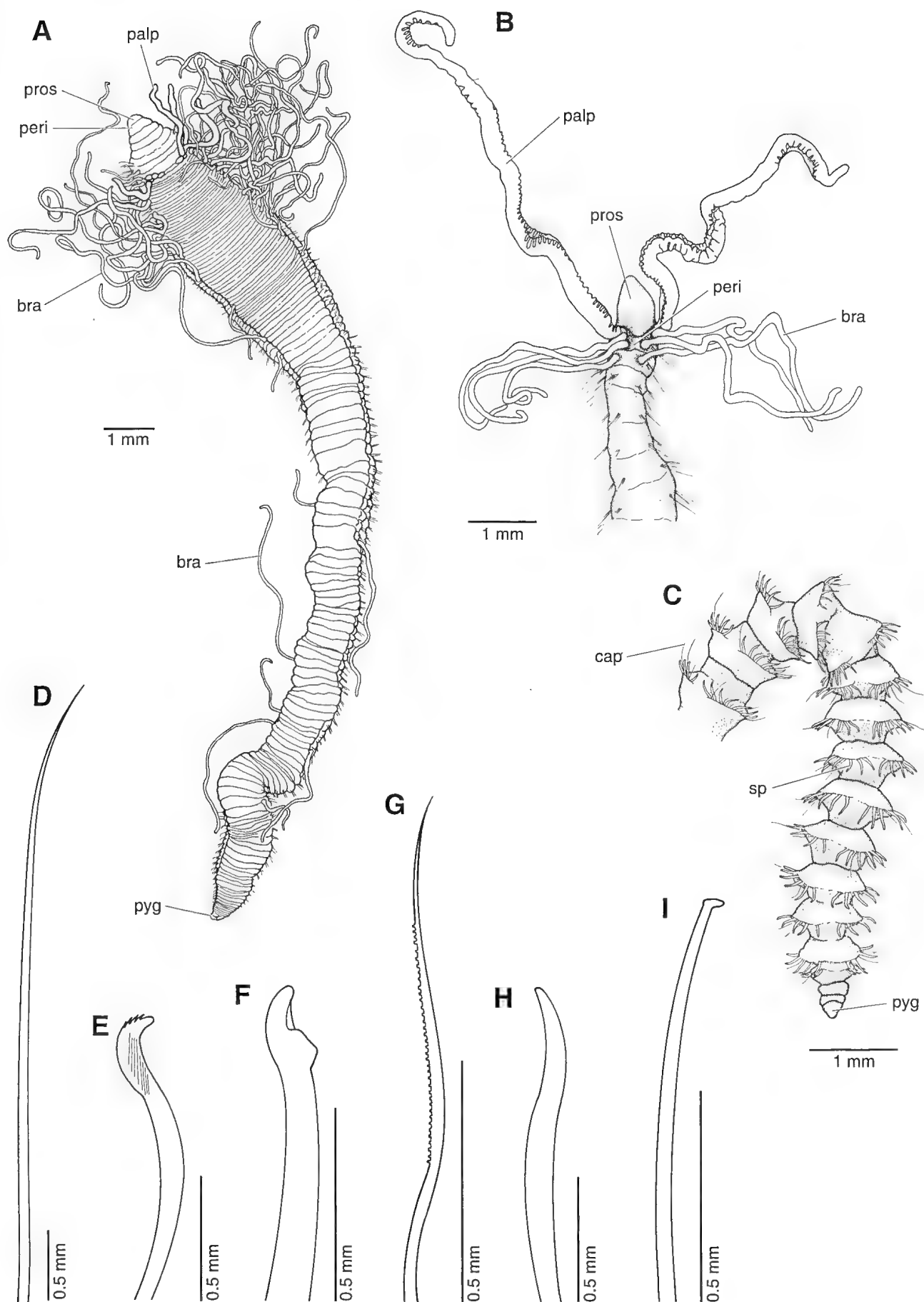


Figure 1.113 Family Cirratulidae. **A**, entire animal of *Cirriformia* cf. *filigera*, dorsal view. **B**, anterior end of *Dodecaceria* species, dorsal view. **C**, posterior end of *Chaetozone setosa*, dorsal view. **D–I**, chaetae: **D**, capillary notochaeta from mid-body chaetiger, *Cirratulus* species; **E**, spine from mid-body neurochaetiger of *Caulleriella dimorphosetosa*; **F**, hook from mid-body neurochaetiger, *Dodecaceria* species; **G**, capillary notochaeta from posterior chaetiger, *Monticellina aphelocephalus*; **H**, spine from posterior chaetiger of *Chaetozone setosa*; **I**, spine from posterior chaetiger of *Tharyx longisetosa*. **bra**, branchia; **cap**, capillary; **palp**, palp; **peri**, peristomium; **pros**, prostomium; **pyg**, pygidium; **sp**, spine. [A. Murray]

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hooks and spines). Paired, slender branchial filaments arise from the dorsal surface of each segment usually, over much of the body (Fig. 1.113A,B).

The Cirratulidae have been classified together with the spiomorphs (see Fauchald 1977; George & Hartmann-Schröder 1985), terebellomorphs (Benham 1896), or placed in their own order together with Ctenodrilidae (Dales 1963a). Rouse & Fauchald (1997) placed them in the clade Terebellida (Fig. 1.110).

Since the family was first described by Carus, Peters & Gerstäcker (1863), notable reviews include those of Grube (1872), Caullery & Mesnil (1898), Hartman (1961) and Blake (1991). Blake (1991) reviewed the bipalpatate cirratulids from the western North Atlantic, redefined the genus *Tharyx* to include some Australian species formerly identified as *Caulleriella*, and divided former members of *Tharyx* between a new genus, *Aphelochaeta*, and the resurrected genus *Monticellina*. Despite these studies, the family is in need of a comprehensive systematic revision, with many potential new species and genera (see, for example, Wolf 1984b), and likely synonymies of existing genera (Day 1991). Further, there is concern over the monophyly of some genera, such as *Cirratulus*. *Cirratulus* is here regarded in its broader sense to include species having wedge-shaped to conical prostomia and parapodia with capillary and sometimes acicular chaetae (see Petersen 1991).

Presently, about 11 genera are recognised worldwide, of which at least eight have been recorded from Australian waters: *Cirratulus*, *Cirriformia*, *Dodecaceria*, *Tharyx*, *Monticellina*, *Aphelochaeta*, *Chaetozone* and *Caulleriella* (Day & Hutchings 1979; Hutchings & Murray 1984). The number of species both worldwide and in Australia cannot be estimated accurately in the absence of a taxonomic revision of the group; records of several species, including *Cirriformia filigera* and *C. tentaculata*, which are widely reported from Australian shores and which purportedly occur worldwide, may turn out to be misidentifications. Australian cirratulids (except *Dodecaceria*) live in bays and estuaries in a range of sediment types, often associated with seagrass beds (Hartmann-Schröder & Hartmann 1981a; Hutchings & Murray 1984). Species of *Cirriformia*, in particular, appear to prefer low oxygen, muddy sediments. *Dodecaceria berkeleyi* has been reported from calcareous substrata, coralline algae and molluscs shells in Australian and New Zealand waters (Knox 1971; Hartmann-Schröder & Hartmann 1981a, 1990, 1991a).

Cirratulids range in length up to 250 mm. Some are a dark green to black in colour in life (*Dodecaceria*), whereas others are orange-red (*Cirriformia*). The anterior end may be tapered or inflated slightly (Fig. 1.113A), and the posterior end may be dorso-ventrally flattened or expanded (for example, in species of *Aphelochaeta*, *Chaetozone*, *Dodecaceria*). Anterior segments are usually very short compared with middle and posterior segments, which may be bead-like (*Aphelochaeta*, *Chaetozone*, *Monticellina*) or more or less cylindrical, like the anterior ones (*Tharyx*, *Cirriformia*) (Fig. 1.113A, C).

The prostomium may have one pair of eyespots. The peristomium may be elongate and appears fused with anterior segments to varying degrees, more so in *Cirriformia* and *Cirratulus*. A pair of thick, grooved feeding tentacles (palps) arises from the posterior region of the peristomium in *Dodecaceria*, *Tharyx*, *Monticellina*, *Aphelochaeta*, *Chaetozone* and *Caulleriella* (Fig. 1.113B). Many palps, arranged in two patches or transverse series, occur over the dorsal surface of one or a few anterior chaetigers in species of *Cirriformia* and *Cirratulus* (Fig. 1.113A). The homology

suggested by Day (1991) between the paired peristomial palps and the multiple palps of anterior segments (which were previously referred to as tentacular cirri) has been confirmed by others: the palps of all cirratulids appear to originate from the peristomium and in some taxa they divide longitudinally and move posteriorly during the course of development (Wilson 1936; George 1962, 1963).

Cirratulids have an unarmed protrusible ventral pharynx (Dales 1962a).

Parapodia are biramous and have papillar lobes and lack aciculae. Simple capillary chaetae usually occur in every chaetiger and may be smooth or have a serrated edge (*Monticellina*) (Fig. 1.113D, G). Gently curving, slender spines may taper to a point (*Chaetozone*, *Cirriformia*), be multidentate or bifid (*Caulleriella*), apically knobbed (*Tharyx*) or aristate and are most common in middle and posterior chaetigers (Fig. 1.113E, H, I). Stout, excavate hooks are present in species of *Dodecaceria* (Fig. 1.113F). *Chaetozone* species have spines arranged in dorso-lateral arcs almost encircling the body posteriorly (Fig. 1.113C). Emphasis has been placed on the type of chaetae present for definition of some genera and on the type and distribution of chaetae along the body to define species (for example, Hartman 1961; Wolf 1984b). However, chaetal succession occurs during development in some species (George & Petersen 1991), so the use of chaetal characters should be used cautiously. For example, in *Cirriformia* species, juvenile bifid hooks are replaced totally by capillary chaetae in adults (Wilson 1936; George 1964a; Blake 1975a).

One pair of dorso-lateral filiform branchiae per segment is usual over most of the body, but branchiae may be restricted to a few segments or be clavate as in some *Dodecaceria* species (Fig. 1.113A, B). Branchiae begin on the first achaetous segment (which is fused to the peristomium) or one of the anterior chaetigers.

The pygidium usually has a small ventral lobe, a terminal anus and lacks pygidial cirri (Fig. 1.113C).

A heart body is present and the circulatory system is closed (Kennedy & Dales 1958). In species of *Cirriformia* and *Cirratulus*, the brown pigments coproporphyrin, coprohaematin and urohaematin are present; species of *Dodecaceria* have a yellow-green fluorescent water-soluble pigment (Dales 1963b; Kennedy 1969).

Cirratulids have a single anterior pair of excretory nephromixia and numerous posterior pairs of gonoducts (Goodrich 1945; Olive 1970). However, gonoducts are absent in some species, including the widespread species *Cirratulus anchylochaeta* and the *Chaetozone setosa* complex of species from British waters. It is possible that gametes can be expelled either through a rupture in the body wall (Krishnan 1950) or via modified anterior nephromixia (Christie 1985).

Asexual reproduction by architomy, has been reported in species of *Cirratulus*, *Timarete*, and some species of *Dodecaceria*. Species of the latter genus can reproduce both asexually by fragmentation and regeneration of missing regions, and sexually as an epitoke (Caullery & Mesnil 1898; Gibson & Clark 1976; Gibson 1979, 1981; Petersen 1991). Parthenogenesis has also been reported in species of *Dodecaceria* (Gibson 1977; Gibson 1981). Knox (1971) reported that *D. berkeleyi* reproduces asexually within its tube by autotomising into two halves, each half regenerating a head end and tail end respectively; he suggested that this may be the usual method of reproduction in the genus.

In *Dodecaceria fimbriatus*, a species that occurs on both sides of the North Atlantic (the European form is often referred to as *D. caulleryi* in the literature), the method of asexual reproduction is slightly different. Fragmentation of the stock worm within its burrow yields an anterior and posterior region as well as a middle region comprising a series of single segments. Both the anterior and posterior region and each of the single segments of the middle region can regenerate its missing parts and form a new individual (Gibson 1979).

Most cirratulids, however, are gonochoristic and have external fertilisation. Epitoky has been reported in a few species, including *Cirratulus cirratus* in British populations, although other studies of the same species have not reported epitokous individuals. Indeed reproductive mode may vary widely between closely related, and even supposedly the same species (George 1967; Blake 1975a; Schroeder & Hermans 1975; Gibson 1981).

Paired gonads consisting of plates of cells are situated on the posterior face of segmental septa, in close association with blood capillaries in mid-posterior body segments (Olive 1971; Gibson 1981; Christie 1985). Early development of oocytes and sperm occurs in the gonads before release and maturation in the coelom; delayed release of oocytes has been reported in *Tharyx marioni*, in which discrete ovaries form (Gibbs 1971). Cirratulids have relatively large (range 110–300 µm) yolky eggs and development is generally thought to be direct (Christie 1985, and references therein). Females may produce as few as 600 eggs (as in *Tharyx marioni*) or as many as 1000–5000 (as in *Caulleriella caputesocis*) (Gibbs 1971).

In externally fertilising species, early development either takes place directly in the sediment, as in *Tharyx marioni*, within a fusiform gelatinous mass deposited in the mud as in *Cirratulus cirratus*, or pelagically, for example, in *Cirriformia tentaculata* and *C. spirabrancha* (Blake 1975a, and references therein). The development of embryos and larvae has been followed for several Northern Hemisphere species (for example, Wilson 1936a; Dales 1951; Blake 1975a; Farke 1979). Larvae of free-spawning species, whether benthic or planktonic, are non-feeding; feeding commences after settlement and metamorphosis.

No information is available on the reproductive strategies and population structure of Australian cirratulids. However, some generalisations can be made from the numerous studies of Northern Hemisphere species. Within the Cirratulidae a distinct breeding season may be absent (Olive 1970), extend over the greater part of the year, excluding the colder months (George 1964a; Öyenekean 1987), restricted to periods over the spring and summer (Farke 1979; Lechapt 1983) or to a few days following a full moon in spring (Dales 1951).

Within a group of closely-related species occupying the same region there may be variation in the onset of gametogenesis, rates of gametocyte development and breeding period (Christie 1985). Polyteley is possible in species of *Dodecaceria* inhabiting dead *Porites* substrata at Lizard Island, Great Barrier Reef. Hutchings *et al.* (1992) reported an overall increase in population numbers of the one or more species over a two year period and suggested that this may be because individuals are capable of breeding several times. However, the population increase may also have been attributable to asexual reproduction.

Populations of *Tharyx marioni* increased to a maximum of about 70 000 individuals per square metre about 6 months after the main breeding activity (Farke 1979). A relatively slow average annual growth rate of 8 mm per year was recorded for *Cirriformia tentaculata* and growth was most rapid at a temperature of 20°C (George 1964a).

Most cirratulids are free-living in sediment, rock crevices, under rocks or associated with algal holdfasts or sea grass. Bipalate species of *Monticellina*, *Aphelochaeta*, and *Tharyx* inhabiting low-oxygen sediments in bathyal depths encase themselves in mudballs, which may provide an effective refuge from predation (Jumars 1975; Levin & Edesa 1997). *Dodecaceria* species construct a calcareous tube cemented together to form a matrix, or they bore into calcareous structures such as molluscs (Hartman 1961; Fauchald & Jumars 1979 and references therein). *Dodecaceria berkeleyi* drills a short, blind-ending tube into the shell of gastropods (*Cominella adspersa* and *Haliotis iris*) or coralline substrata; it lives in the tube, doubled-over with both ends protruding from the opening (Knox 1971). This species is unusual among cirratulids in being able to prey upon the larvae and post-settlement juveniles of the abalone *Haliotis iris* (Naylor & McShane 1997).

Cirratulids are generally considered to be surface deposit-feeders, using their grooved palps to collect and transport food to the mouth. Flatterly (1916) suggested that they actively select both size and composition of particles to be ingested. *Cirriformia tentaculata* living in British mud flats utilises about 8% of the organic material, compared to a theoretical potential rate of utilisation in the species of about 14%, as a result of the rapid rate of passage through the gut (George 1964b).

Overseas studies have shown that species of *Cirriformia*, and to a lesser extent *Cirratulus*, appear to be tolerant to hypoxic conditions in the sediment. They survive by extending their anteriorly-directed branchiae into well-oxygenated water at the sediment-water interface and because of enhanced oxygen binding capabilities due to the activity of erythrocrurins (extracellular haemoglobins) (Blake 1975a; Warren 1981; Warren, Wells & Weber 1981). Waste products are excreted through the tentacles (term used by Hult; most probably branchiae) and the anterior body wall; this is mainly in the form of ammonia in *Cirriformia spirabrancha* from California (Hult 1969).

Cirratulidae are generally considered to be allied to spioniforms (see Clark 1969; Fauchald 1977; Rouse & Fauchald 1997; George & Hartmann-Schröder 1985) and terebellomorphs (Benham 1896). The cladistic analysis of Rouse & Fauchald (1997) confirmed a possible terebellomorph association with the family (together with Flabelligeridae and Acrocirridae) sister group of the more strictly-defined terebellomorphs including Ampharetidae, Pectinariidae, Terebellidae and Trichobranchidae (Fig. 1.110).

The family may be divided into two groups on the basis of palp number and origin: the bipalate *Dodecaceria*, *Tharyx*, *Monticellina*, *Aphelochaeta*, *Chaetozone*, and *Caulleriella* and genera having multiple palps including *Cirratulus* and *Cirriformia* (Blake 1991; Day 1991), although whether they constitute monophyletic groups has not been established. George & Petersen (1991) found that *Dodecaceria* has features that set it apart from the rest of Cirratulidae and that it is more closely related to genera currently assigned to Ctenodrilidae.

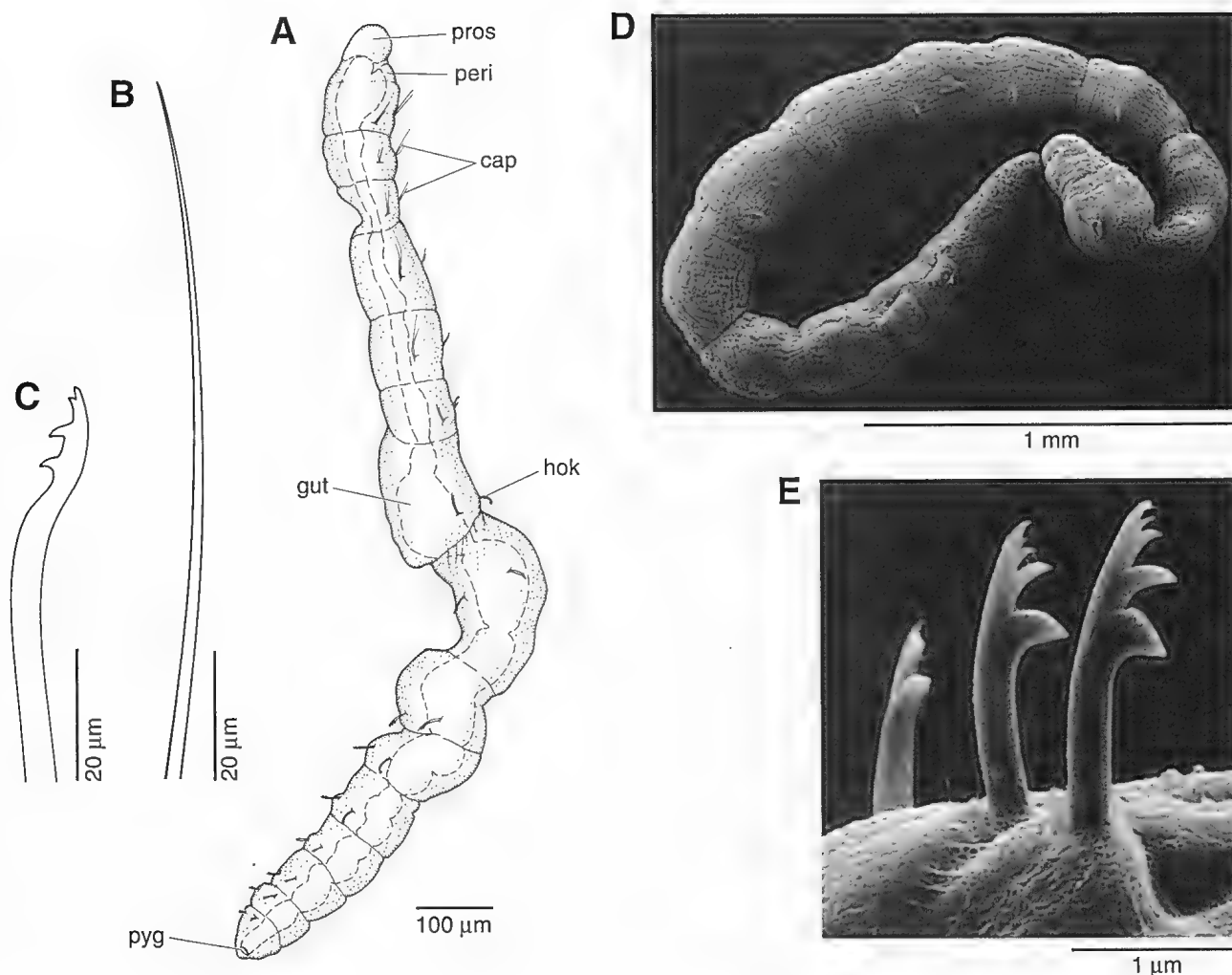


Figure 1.114 Family Ctenodrilidae. **A–C**, *Aphropharynx* species: **A**, lateral view of entire animal; **B**, capillary chaeta from parapodium of chaetiger 12; **C**, multidentate hook from parapodium of chaetiger 12. **D**, **E**, scanning electron micrographs of a non-Australian ctenodrilid, *Ctenodrilus* cf. *serratus*: **D**, entire animal; **E**, chaetal hooks. **cap**, capillary chaetae; **gut**, gut; **hok**, chaetal hook; **peri**, peristomium; **pros**, prostomium; **pyg**, pygidium. [A–C, A. Murray; D, E, G. Rouse]

Family Ctenodrilidae

Ctenodrilids are small, grub-like or slender-bodied polychaetes with little differentiation between the head and tail. The parapodia are not developed and the chaetae are simple. They live on soft sediment.

The short prostomium is truncated anteriorly (Fig. 1.114A, D), and the peristomium is reduced to lips around the mouth (Wilfert 1973; this interpretation is questioned by Rouse & Pleijel in press) or forms a distinct annulus (Fig. 1.114A, D), based on larval developmental studies (Qian & Chia 1989b) and scanning electron micrographs of adults (Peterson & George 1991). Antennae and palps are absent. Paired nuchal pits are present (Petersen & George 1991). The longitudinal muscles are grouped in bundles (Sokolow 1911) and segmentation is present. The first segment is similar to other chaetigers, and tentacular cirri, parapodia and parapodial cirri are lacking. Paired, filiform, dorsal branchiae are present in some taxa. Epidermal papillae, pygidial cirri and lateral organs are not present; dorsal cirrus organs have not been observed and are probably lacking. An eversible ventral buccal organ is present and the gut is a straight tube (Petersen & George 1991). A gular membrane is absent. The segmental organs are mixonephridia; there is only one excretory pair, and gametes exit through the more posterior ducts (Caullery & Mesnil 1898). The circulatory system is closed, and a heart

body is present. Aciculae are absent. Capillary chaetae are present in the Raphidrilinae; other chaetae are distally dentate hooks. The chaetae have been referred to as proteinaceous (Wilfert 1973); if verified, this state would be unique among the polychaetes. This definition is based upon that of Fauchald & Rouse (1997).

The ctenodrilids were described in detail by Caullery & Mesnil (1898). They were considered part of the Cirratulidae by Fauvel (1927) and Day (1967), which they resemble in lacking antennae and the presence of poorly-developed parapodia with simple chaetae. Dales (1963a) considered them a separate family within his order Cirratulida. Hartmann-Schröder (1971) treated them as a separate family within the Drilomorpha. Fauchald (1977) placed them in the order Ctenodrilida (see Fig. 1.43), together with the Parergodrilidae with which they share a small body size, a simple body construction with a limited number of segments and no anterior appendages. Recognition of Ctenodrilidae may make it difficult to characterise the Cirratulidae, as the filiform branchiae present in the Cirratulidae are also present in one subfamily of the Ctenodrilidae. Rouse & Fauchald (1997) suggested that Ctenodrilidae together with Fauveliopsidae, Poebiidae and Sternaspidae all form a clade with the Acrocirridae, Cirratulidae and Flabelligeridae in the Terebellida (Fig. 1.110).



Plate 1.1 Capitellidae. Capitellids, shown removed from their tube of shell and sand fragments, resemble earthworms in appearance; these were collected from lagoonal sediments at Heron Island, Great Barrier Reef. The bright red colour derives from high concentrations of haemoglobin dissolved in their blood. [K. Atkinson]

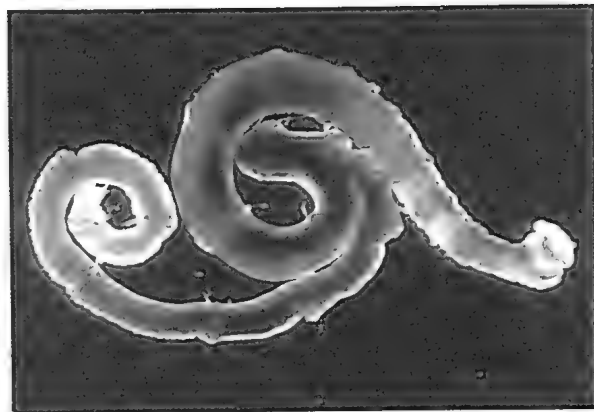


Plate 1.2 Maldanidae. Bamboo worms resemble bamboo stalks, once removed from their tube. These non-selective deposit-feeders live in a variety of sediments where they ingest large quantities of sand particles. This example was collected in lagoonal sediments at Heron Island, Great Barrier Reef. [K. Atkinson]

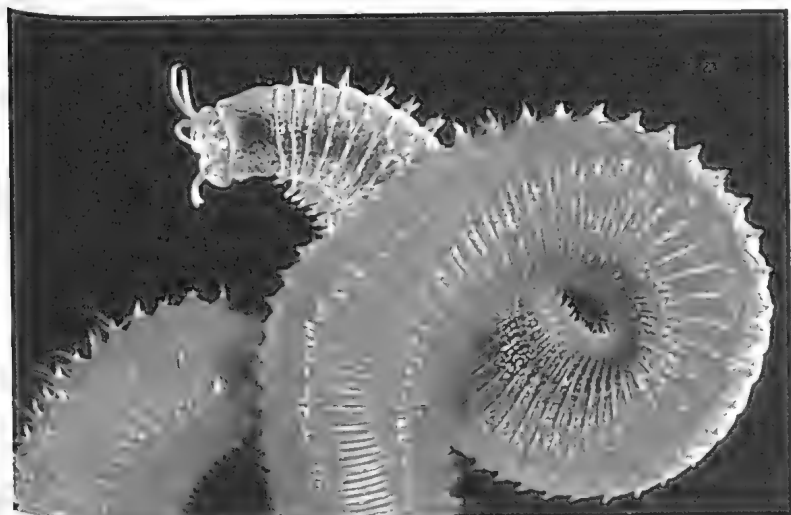


Plate 1.3 Eunicidae. Bloodworms, *Marphysa* species, are large, long lived carnivores or omnivores on mud flats and seagrass beds of the east and west coasts of Australia. Their size makes them valuable as fishing bait. Note the well-developed segmental branchiae and the iridescent sheen that is characteristic of this family. [K. Atkinson]

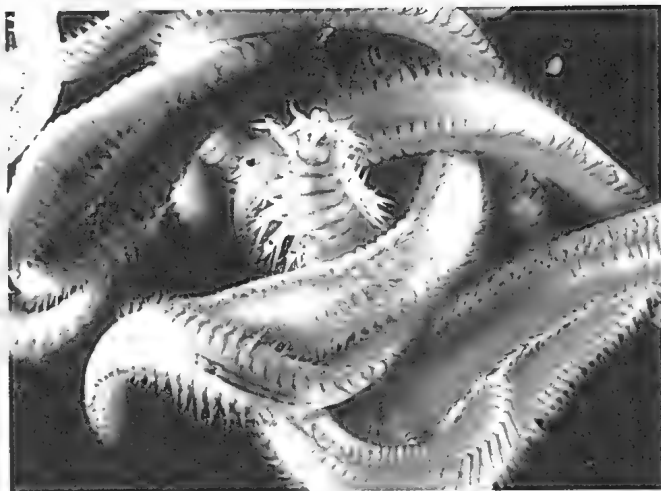


Plate 1.4 Onuphidae. The giant beachworm, *Australonuphis parateres*, extracted from a surf beach, where they occur in great numbers, and attain lengths of 2-3 m. They have well-developed segmental branchiae along the body. Although they have a complex set of jaws they often feed on drift algae. Nevertheless, they can be lured easily from their sandy burrow with fish or meat, and along the eastern coast of Australia they are highly valued as a most effective bait for fishing in the surf zone. [K. Atkinson]

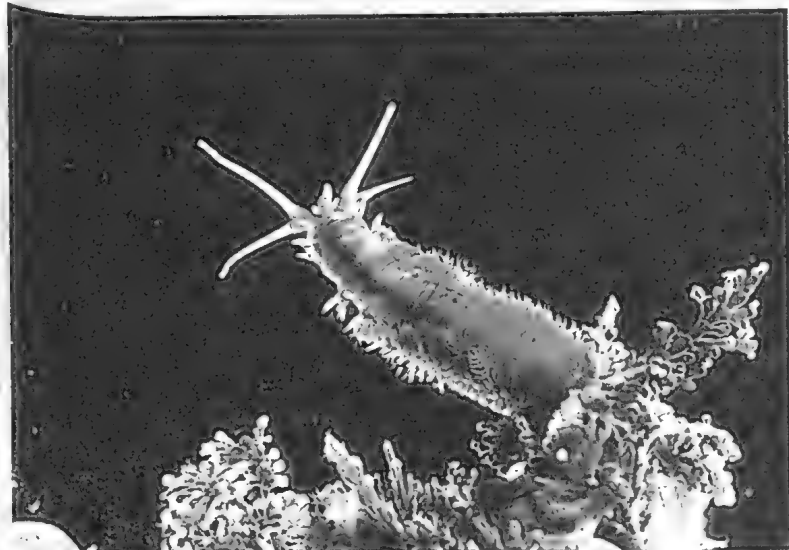


Plate 1.5 Onuphidae. *Diopatra dentata* extended from its tube in search of prey; it builds a distinctive tube with shell fragments and other foreign particles or algae attached at right angles in close circles. It occurs intertidally to 30 m depth in New South Wales; note the 'bottle brush' segmental branchiae visible from chaetiger 5. [K. Atkinson]



Plate 2.1 Amphinomidae. A small group of the amphinomid 'fire worm', *Eurythoe complanata*, illustrates the range of colour morphs in this species. They grow to 30–50 mm in length and are common beneath boulders in the intertidal zone and shallow coastal waters along the east coast of Australia. [K. Atkinson]

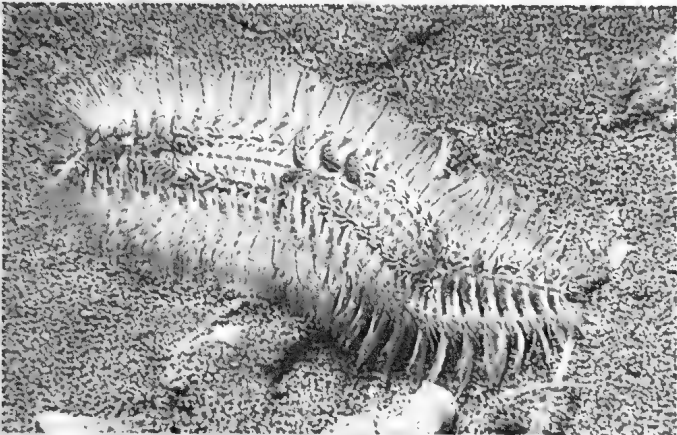


Plate 2.3 Amphinomidae. *Chloeia flava* hunting over sediment in a coral reef area. These worms are known as 'fire worms', for the reaction induced in some people to a neurotoxin in the brittle notochaetae which break off in the skin when the worm is picked up. [R. Steene]

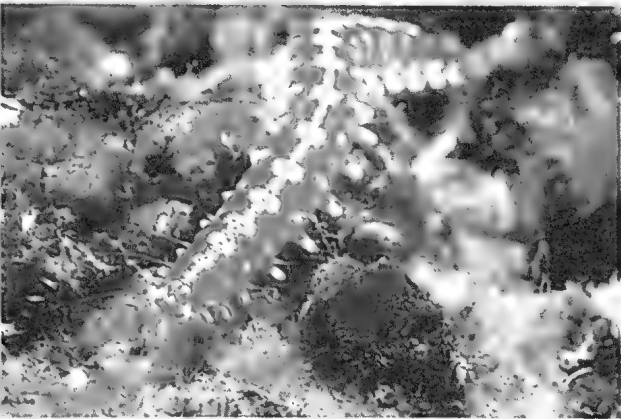


Plate 2.5 Hesionidae. *Hesione* species, a carnivore like other hesionids, seen crawling actively over the reef in search of food, which the worm detects with its long tentacular cirri. [R. Steene]

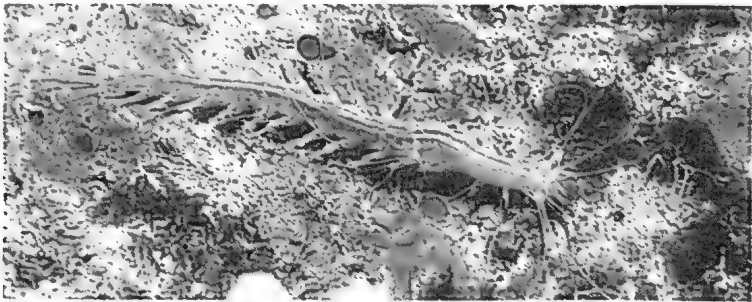


Plate 2.7 Hesionidae. *Leocrates* species, showing how the parapodia move in sinusoidal waves down the body. In this genus, the body is short and stout, there are always 16 chaetigerous segments and the cuticle has a metallic lustre. [R. Steene]

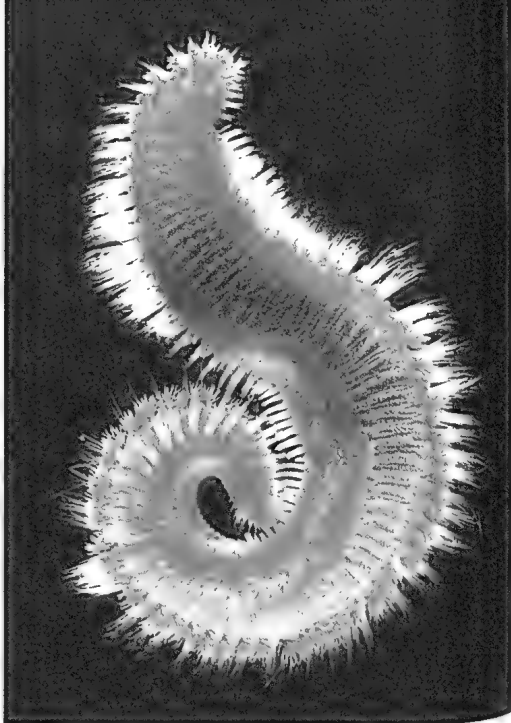


Plate 2.2 Amphinomidae. A single worm, *Eurythoe complanata*, shows its dark red bushy branchiae adjacent to the parapodia. [K. Atkinson]

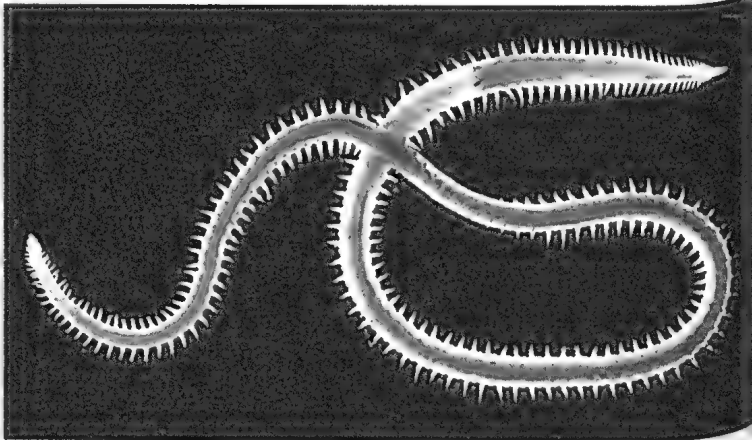


Plate 2.4 Glyceridae. Glycerids are predatory worms which burrow in soft sediment. With the pharynx in a non-everted position, as shown here, the large set of four hardened jaws is clearly visible through the body wall at about chaetiger 28. The pharynx can be rapidly everted to catch unsuspecting prey, such as small crustaceans. [K. Atkinson]

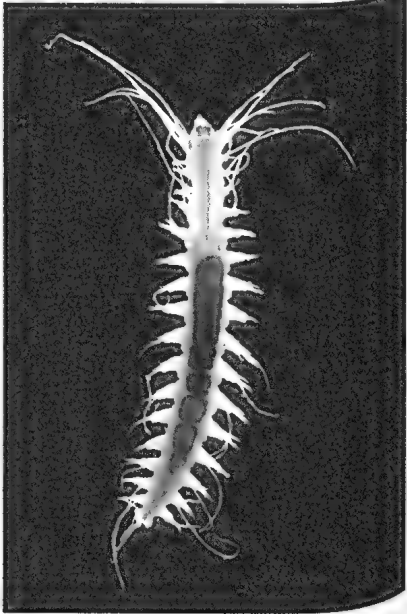


Plate 2.6 Hesionidae. Hesionid with muscular pharynx visible through the body wall; with two pairs of eyes and long tentacular cirri. [K. Atkinson]

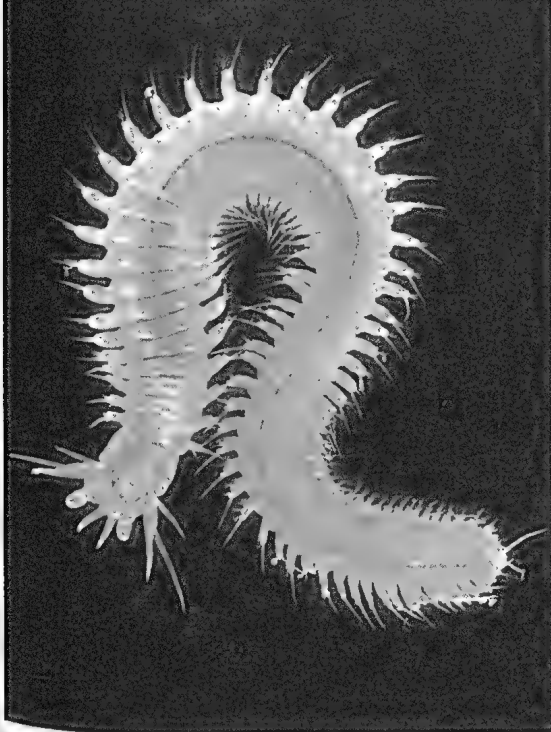


Plate 3.1 Nereididae. *Perinereis amblyodonta*, common on rocky shores of southern Australia and New Zealand. A well-developed dorsal blood vessel shows along the length of the body. [K. Atkinson]



Plate 3.2 Phyllodocidae. *Eumida* species moving from a resting position in a crevice in the reef; most phyllodocids are thought to be carnivorous. [N. Holmes]

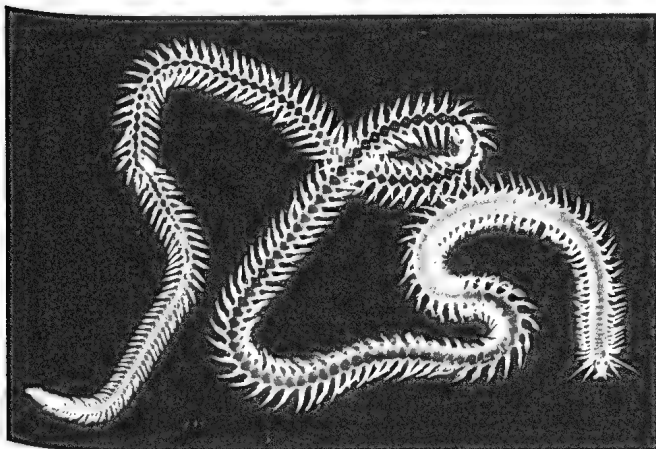


Plate 3.3 Phyllodocidae. Phyllodocid collected in coral reef sediments, with well-developed expanded dorsal cirri all along its body. [K. Atkinson]

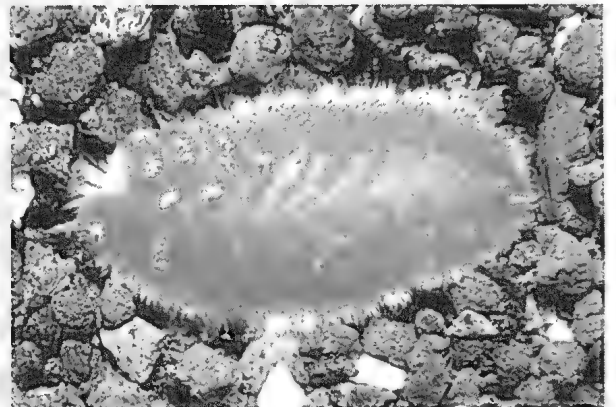


Plate 3.5 Polynoidae. A scale-worm, probably *Iphione* species, crawling over coarse sediment in tropical Australian waters (head at left). This polychaete is an active carnivore. Encrusting barnacles are present on some elytra. [R. Steene]

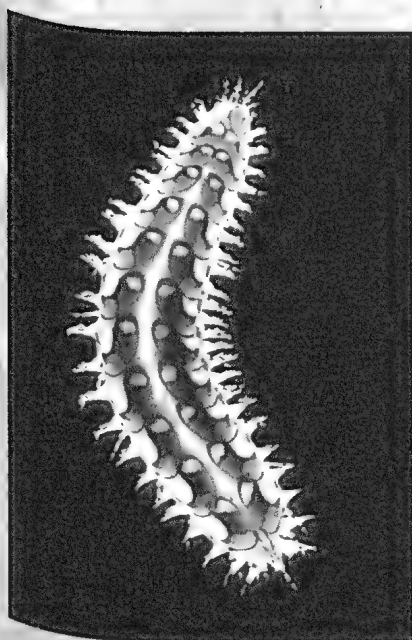


Plate 3.4 Polynoidae. *Lepidonotus melanogrammus* is a common polynoid on the rocky intertidal shore of New South Wales. The elytra (scales) display a distinctive pigment pattern and do not cover the dorsum. This is a solitary species occurring in pairs only during breeding. It is an active carnivore. [K. Atkinson]



Plate 3.6 Polynoidae. A polynoid with distinctively pigmented elytra (scales). [R. Steene]



Plate 4.1 Syllidae. An autolytine syllid, heavily laden with eggs, on coralline algae.
[K. Gowlett-Holmes]

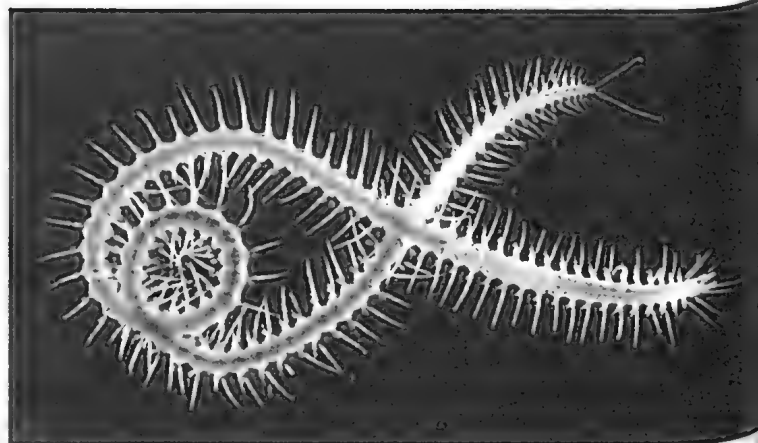


Plate 4.2 Syllidae. A species of Syllinae collected in lagoonal sediments at Lizard Island, showing beaded dorsal cirri.
[K. Atkinson]

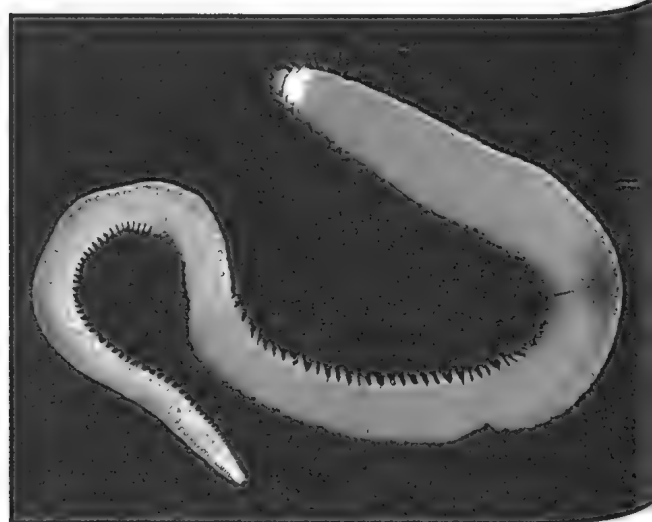
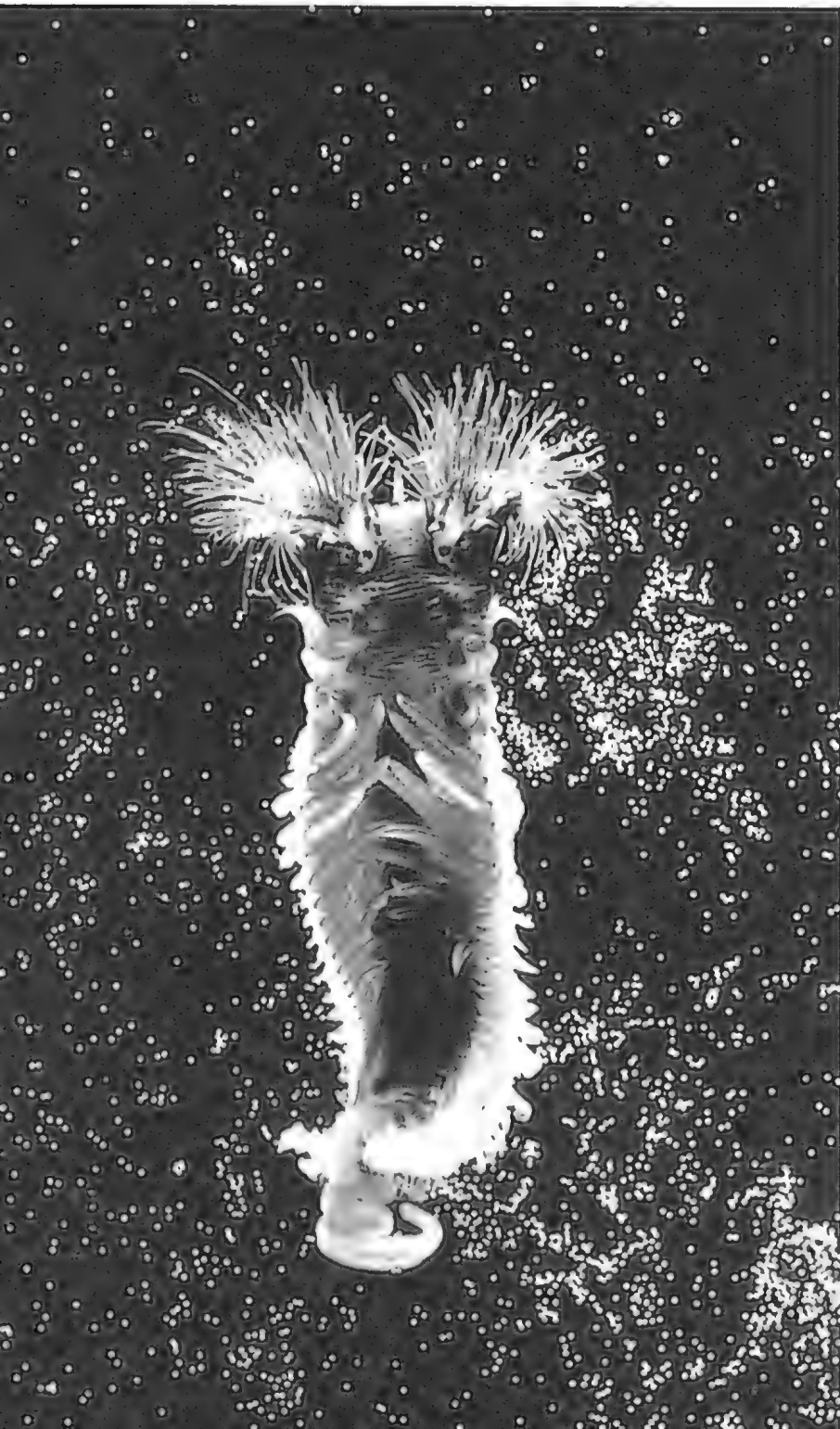


Plate 4.3 Syllidae. *Pionosyllis* species from the shallow subtidal zone in Port Phillip Bay, Victoria. [M. Marmach]

Plate 4.4 Sabellariidae. When removed from its sandy tube, this worm sheds as many as 20 000 oocytes; *Idanthyrus pennatus* commonly encrusts intertidal rocks and shallow subtidal waters along Australia's east coast.
[K. Atkinson]

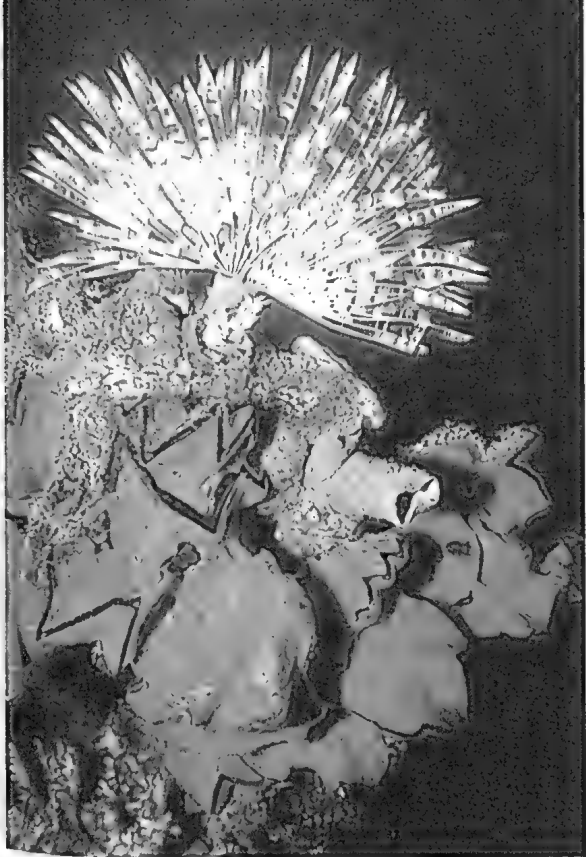


Plate 5.1 Sabellidae. *Sabellastarte* species on the Great Barrier Reef, showing one individual with a fully expanded tentacular crown some 50–100 mm in diameter, and another completely retracted into its muddy tube. [R. Steene]

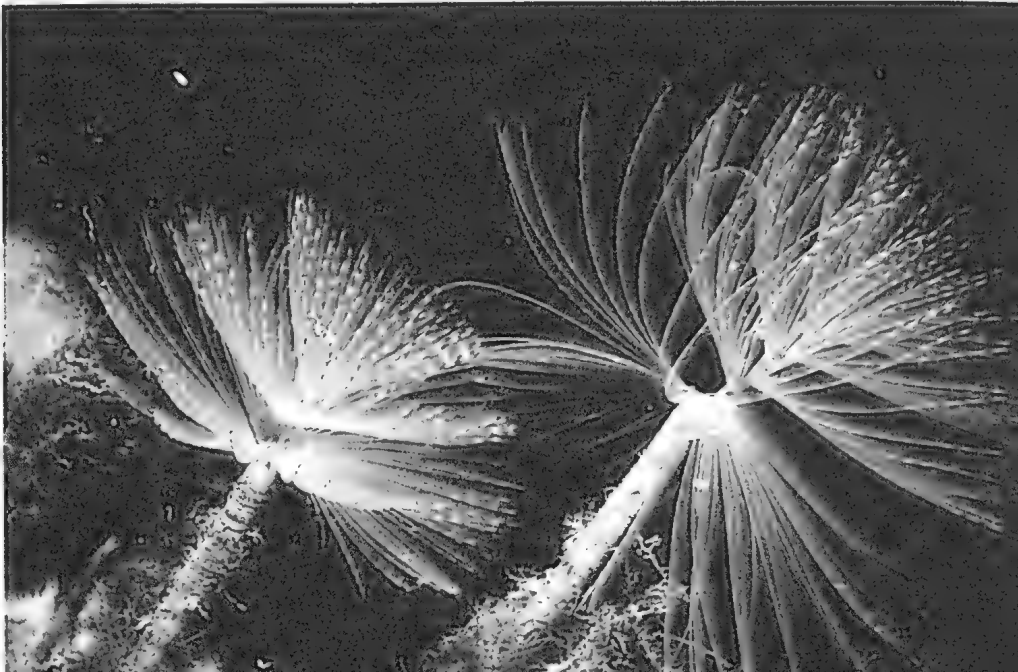


Plate 5.2 Sabellidae. Sabellids in seagrass beds, *Posidonia* species; their extended tentacular crown is about 20–30 mm in diameter. [R. Steene]



Plate 5.3 Sabellidae. A colourful sabellid on the Great Barrier Reef. Each radiole in the crown has numerous fine filaments along its length which sieve food from feeding currents. Passed down the axis of each radiole to the mouth, they may be eaten, used for tube construction or rejected. The crown is 50–100 mm in diameter. [R. Steene]

Plate 5.4 Sabellidae. *Sabella spallanzanii* on a jetty pile, showing the distinctive spiral tentacular crown, 50–100 mm in diameter. This introduced Mediterranean species, perhaps via a ship's hull, has become a serious pest in southern Australian waters. [K. Gowlett-Holmes]



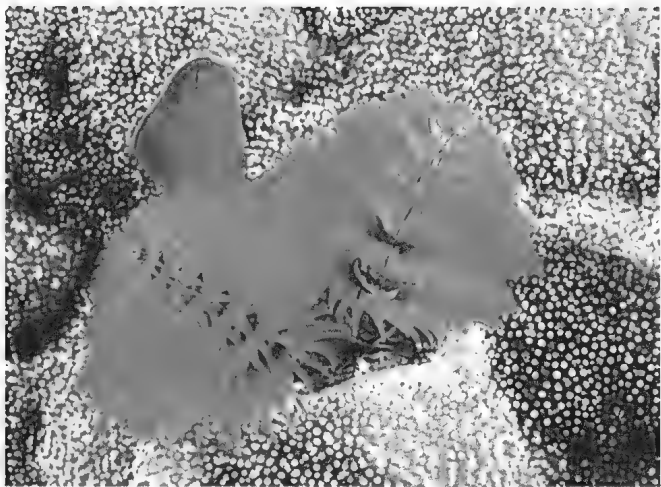


Plate 6.1 Serpulidae. Common on the Great Barrier Reef, the 'Christmas Tree Worm', *Spirobranchus giganteus*, occurs on live coral in a variety of colours. The coral grows around the calcareous tube secreted by the juvenile worm, and is continuously lengthened to ensure an entrance is maintained. The crown may be 10–20 mm in diameter. [B. Wood]

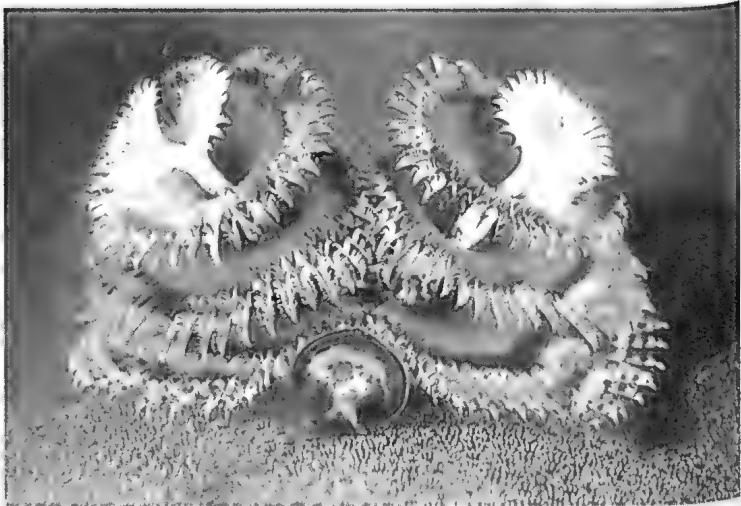


Plate 6.2 Serpulidae. *Spirobranchus giganteus*, showing the operculum (centre) which closes the tube in response to a shadow, such as that of a predatory fish swimming over the tube; crown 10–20 mm in diameter. [G. Bell]

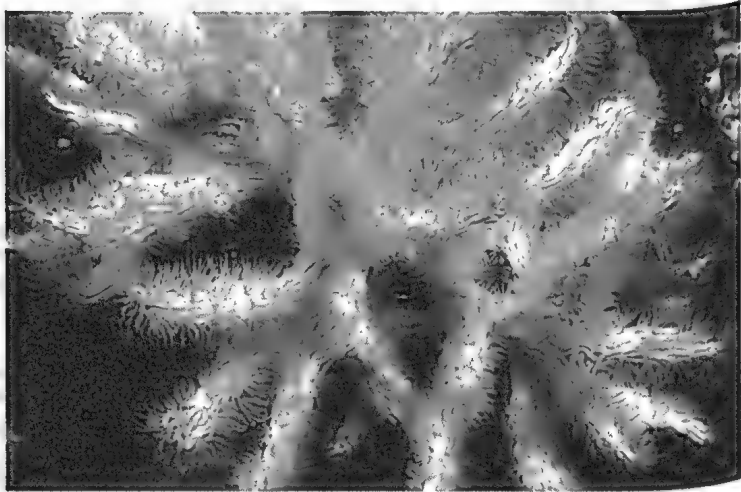


Plate 6.3 Serpulidae. Hundreds of tubes of individual *Filograna implexa* may fuse to form this branching calcareous structure. Individual tubes are 3–5 mm in length. [B. Wood]

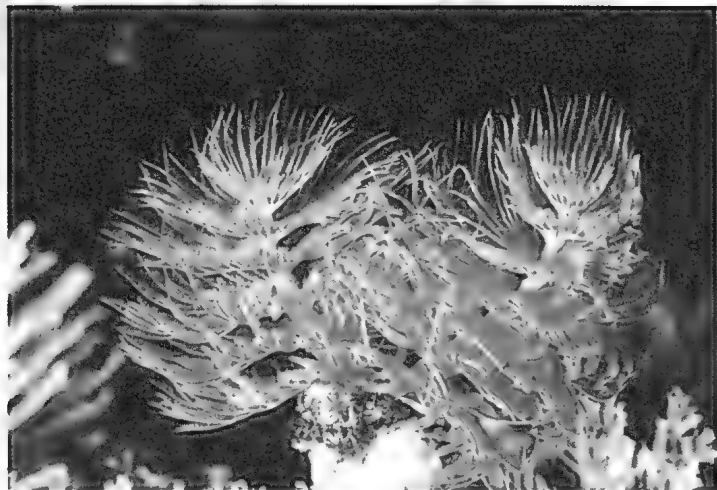


Plate 6.4 Serpulidae. *Protula* species. One of the few serpulid genera which lacks an operculum. Its tube is 5–10 mm in diameter. [G. Bell]

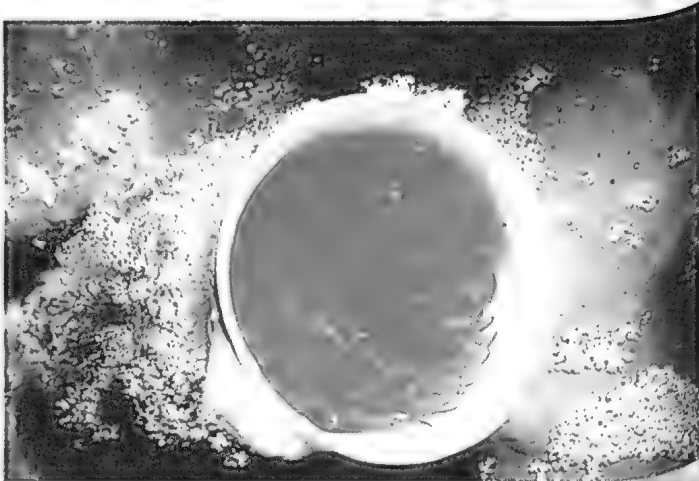


Plate 6.5 Serpulidae. Looking into the calcareous tube of *Protula* species, showing the retracted tentacular crown. Common throughout the Great Barrier Reef. The tube is 5–10 mm in diameter. [B. Wood]

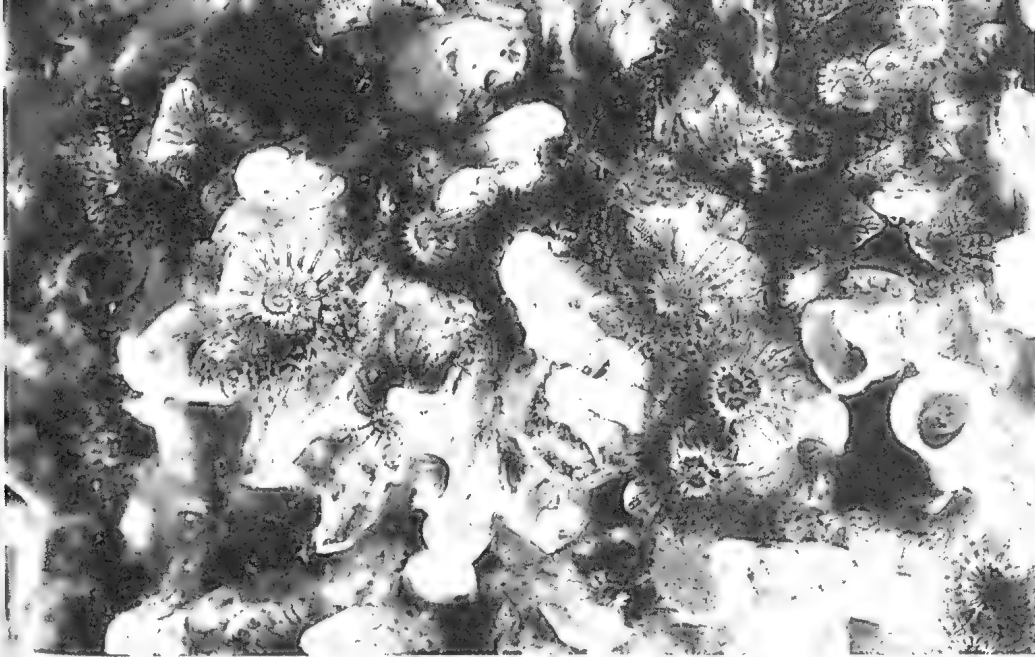


Plate 7.1 Serpulidae. Colony of *Galeolaria caespitosa*, many with tentacular crowns fully expanded, feeding and respiring. This species forms a distinctive intertidal band of 'Sydney Coral' along exposed rocky beaches in south-eastern Australia.

[K. Atkinson]

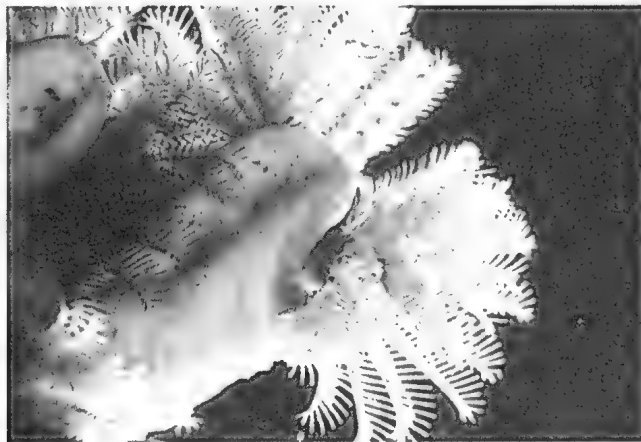


Plate 7.3 Serpulidae. Close-up of the tentacular crown of *Galeolaria caespitosa*.

[K. Atkinson]

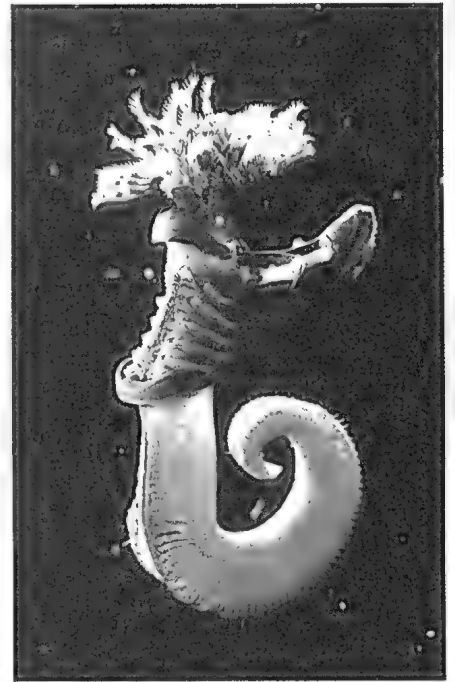


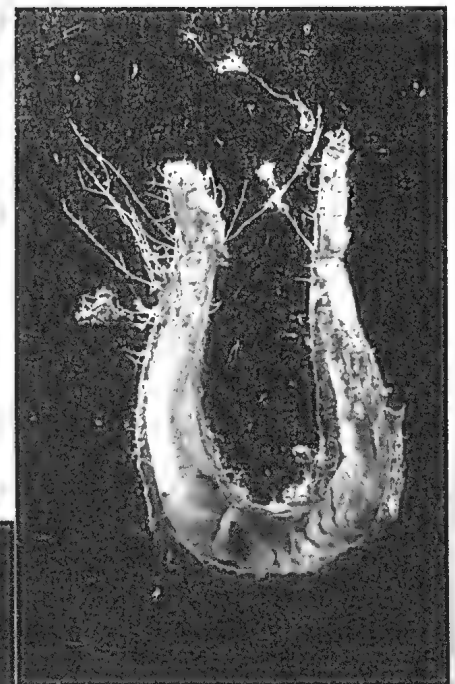
Plate 7.2 Serpulidae. Whole animal of *Galeolaria caespitosa* 'extracted' from its calcareous tube.

[K. Atkinson]



Plate 7.4 Chaetopteridae. At low tide in an estuarine seagrass bed in New South Wales, both ends of the U-shaped tube of *Chaetopterus variopedatus* emerge from the mud.

[K. Atkinson]



Plates 7.5 & 7.6 Chaetopteridae. *Chaetopterus variopedatus*. The worm (Plate 7.5, above), seen through a window cut in the parchment tube, pumps water through the tube, straining and entrapping food particles in a mucous pouch. The body regions (Plate 7.6, left) are described in more detail in Fig. 1.104. Worms attain 50–100 mm in length.

[K. Atkinson]



Plate 8.1 Chaetopteridae. Two worms, *Mesochaetopterus* species, one removed from its sand and shell tube, the other *in situ*. The anterior palps are used for feeding. Enlarged parapodial lobes at midlength draw water currents and food particles into the tube. Worms grow to 10–20 mm in length. [K. Atkinson]

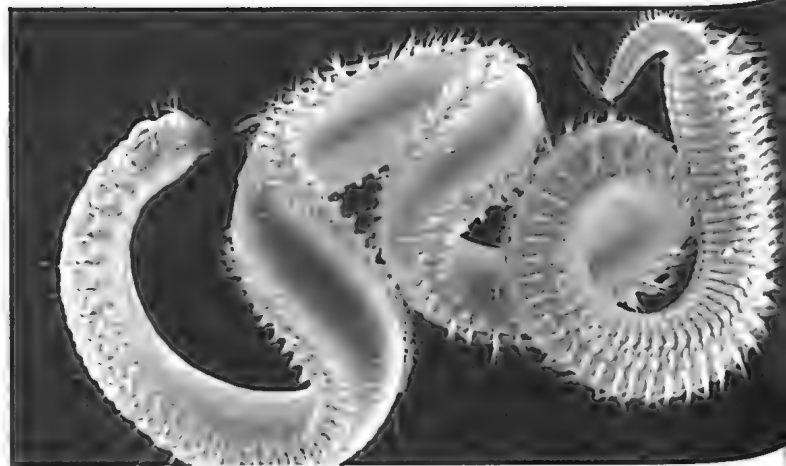


Plate 8.2 Spionidae. *Malacoceros indicus*, Lizard Island, Great Barrier Reef. This species lives in coarse coralline sand and uses its long palps for feeding. The head of this worm is regenerating and segmental branchiae are well-developed. Adult worms attain 20–40 mm in length. [K. Atkinson]

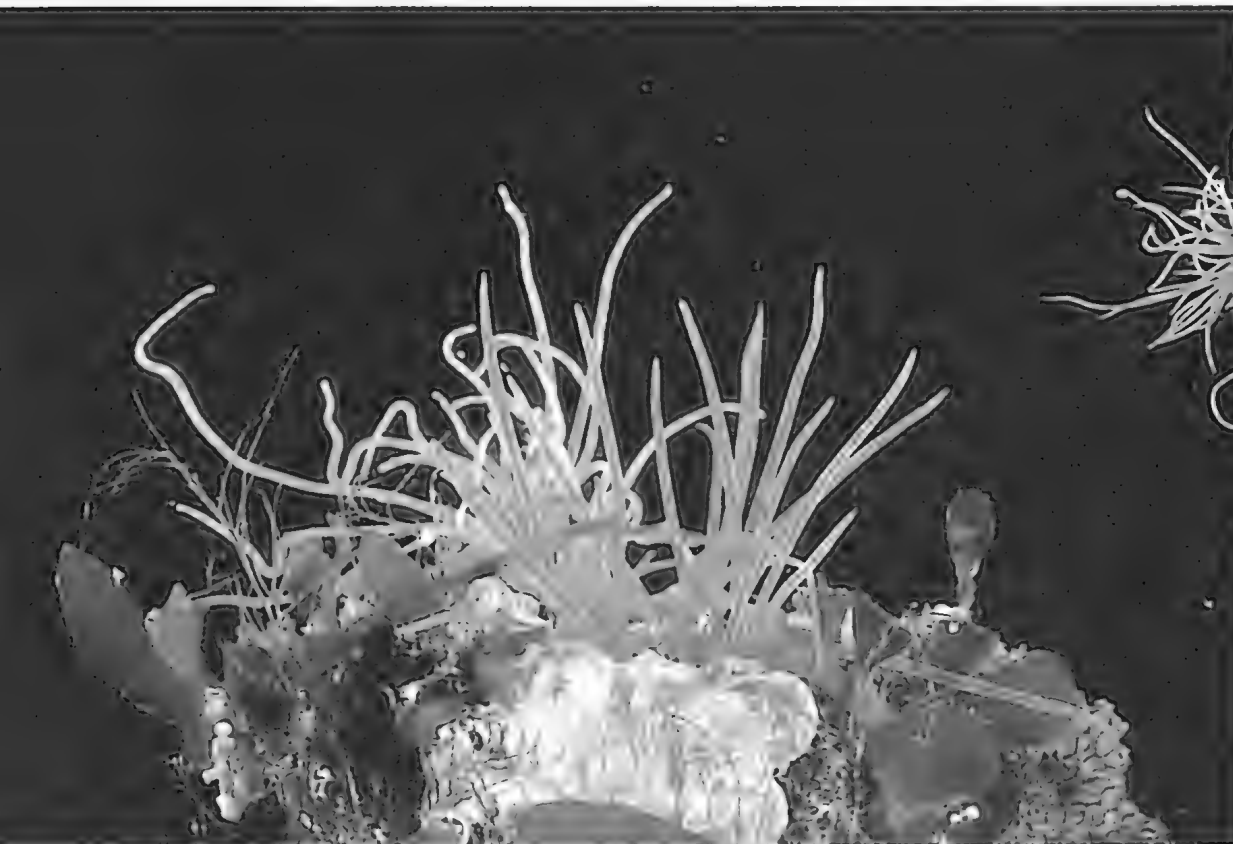


Plate 8.3 Cirratulidae. Partially emergent cirratulid (above) in a rock pool, showing numerous grooved palps used to collect the sediment on which it feeds; bright red haemoglobin distinguishes the segmental filiform branchiae from the yellowish palps (right). The worms reach lengths of 20–50 mm. [K. Atkinson]

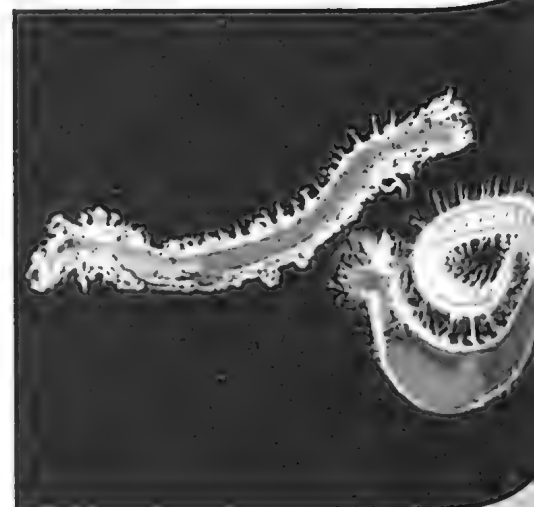


Plate 8.4 Flabelligeridae. *Flabelligera* species, removed from the sediment; note the well-developed cephalic cage and anterior branchiae. Worms attain 20–50 mm in length. [K. Atkinson]

Plate 9.1 Terebellidae. *Eupolymnia koorangia* is common around Australia. This individual inhabited a tube under a rock on the Great Barrier Reef. The numerous banded buccal tentacles are used to 'vacuum' the substratum in search of food. Animal 30–50 mm in length. [R. Steene]

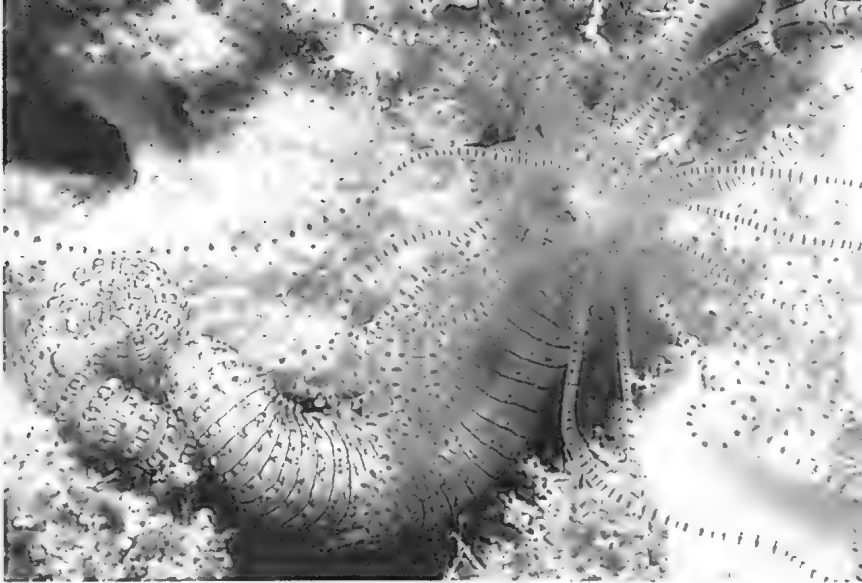


Plate 9.3 Terebellidae. *Loimia ingens* removed from its tube, showing its numerous banded buccal tentacles and three pairs of branched branchiae. When removed from its tube this species can swim actively for a few minutes, using strong sinusoidal contractions of the body. Adults are 100–150 mm in length. [K. Atkinson]

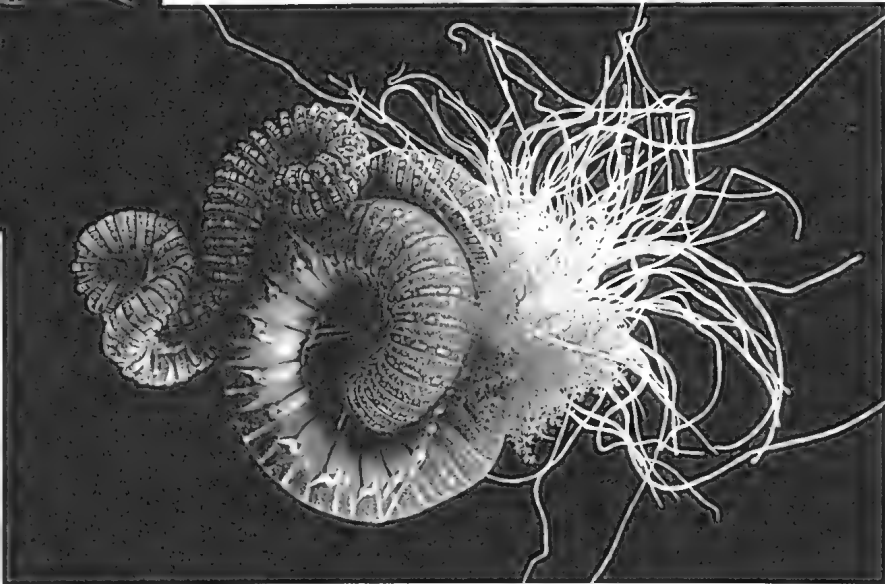


Plate 9.2 Terebellidae. *Loimia ingens*, protruding slightly from its tube of sand and shell fragments; common throughout Australia north of 36°S; this animal was found in seagrass beds of Careel Bay, Pittwater, New South Wales. [K. Atkinson]

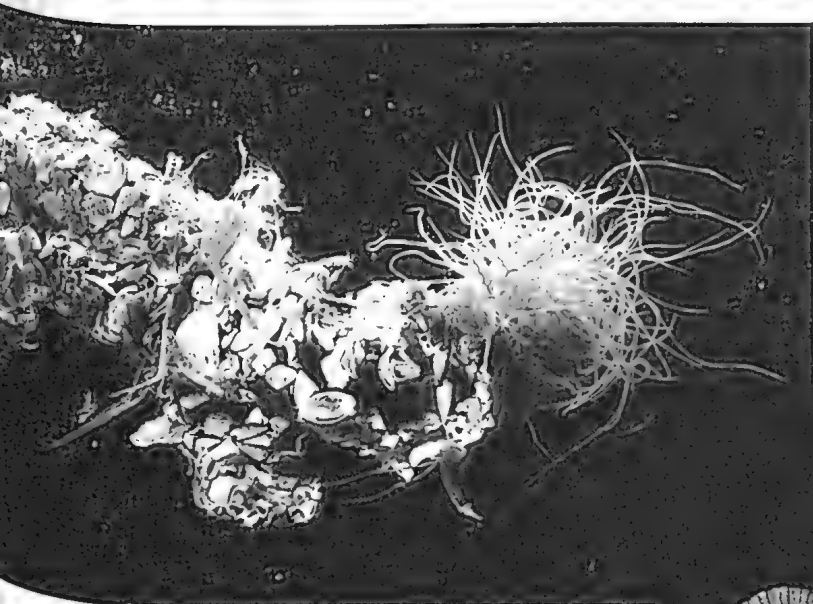


Plate 9.4 Terebellidae. *Reteterebella queenslandia*, extracted from its tube buried deeply in the coral, reveals its soft bloated body, very long tentacles, and bushy branchiae. It reaches 50–100 mm in length. [L. Newman & A. Flowers]





Plates 10.1 & 10.2 Myzostomatidae. The myzostome at the cyst opening, showing its cirri (Plate 10.1, left) and outside the cyst (Plate 10.2, below) is thought to be a juvenile or young protandric male of *Myzostoma polycyclus*, one of the commonest multicirrate Indo-West Pacific species. Such temporary occupation of cysts is known for only three other myzostome species. [G. Rouse]

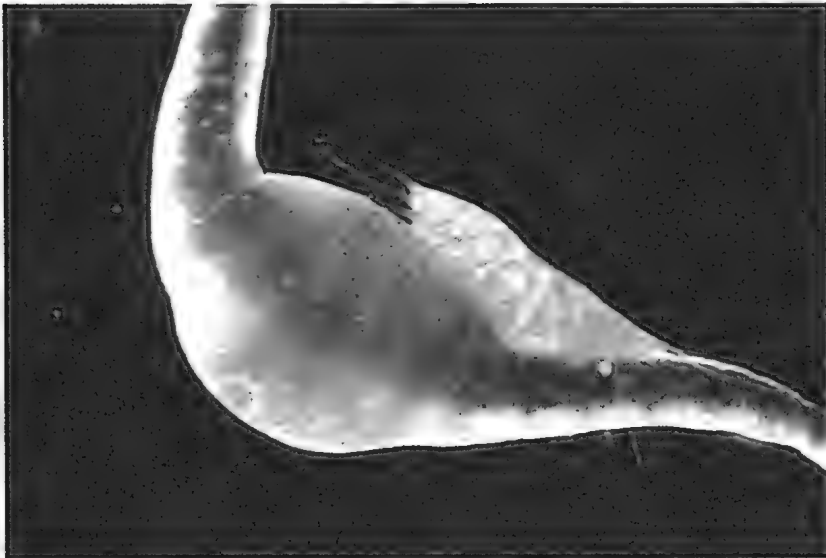


Plate 10.3 Myzostomatidae. Adult *Myzostoma polycyclus* on its crinoid host. Although the image is of a Japanese specimen, this species occurs in Australian waters.

[G. Rouse]

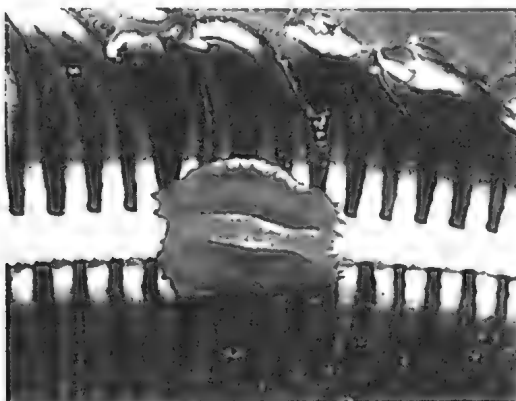


Plate 10.4 Myzostomatidae. *Myzostoma* (possibly) *furcatum*, from Japan, on its host. *Myzostoma furcatum* is found in Australian waters. [G. Rouse]

PLATE 11: ECHIURA

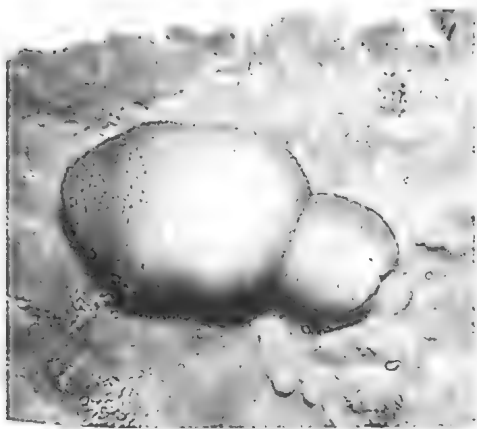


Plate 11.1 Thalassematidae.
Anelassorhynchus porcellus forms a tube in mud and debris under a rock, and extends its proboscis to feed, presumably collecting simultaneously the fragments of coral, shell and sand found in its gut. [N. Holmes]

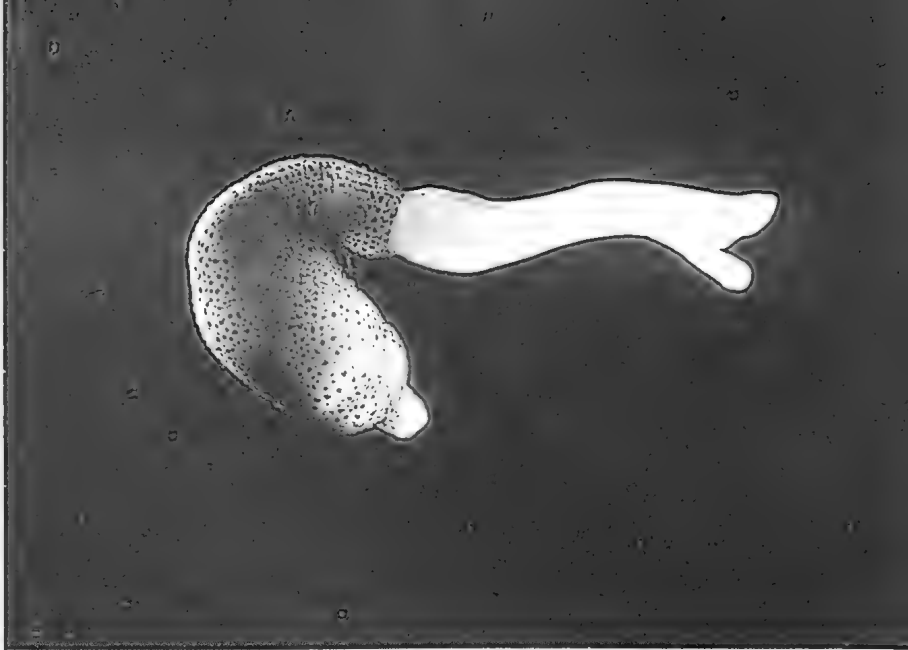


Plate 11.2 Thalassematidae. An unidentified thalassematine echiuran from Lizard Island, Great Barrier Reef, showing a papillate skin and grooved proboscis. [K. Atkinson]

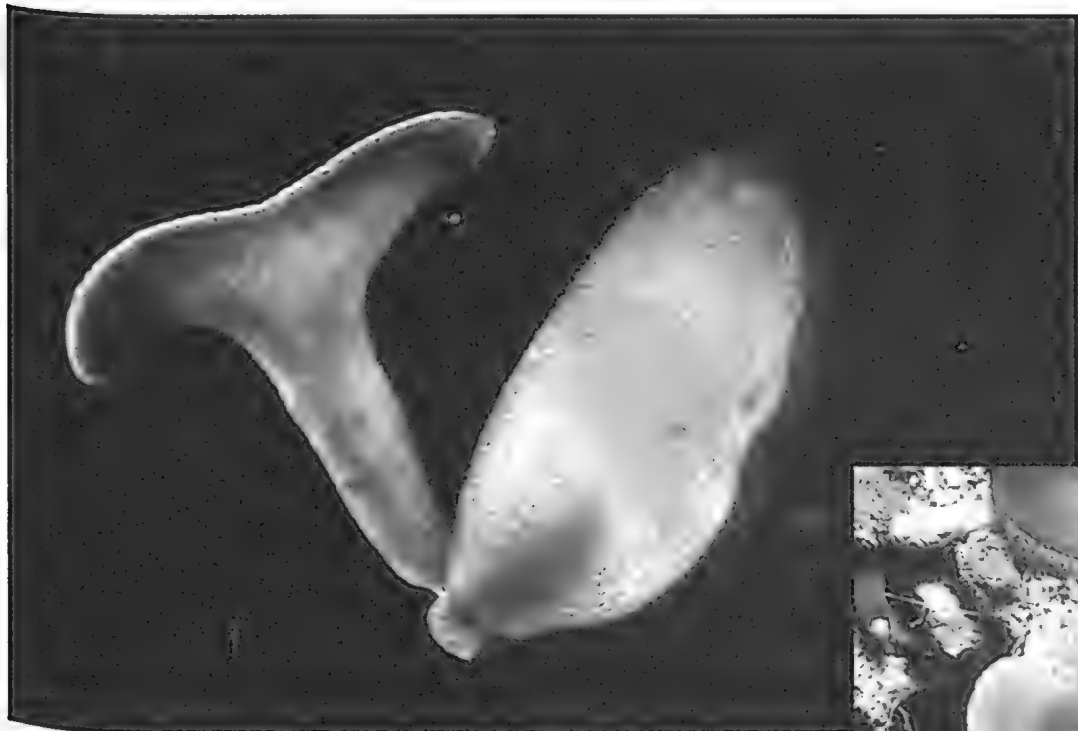
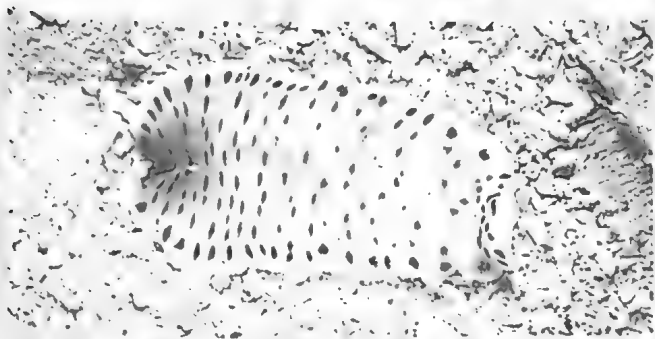
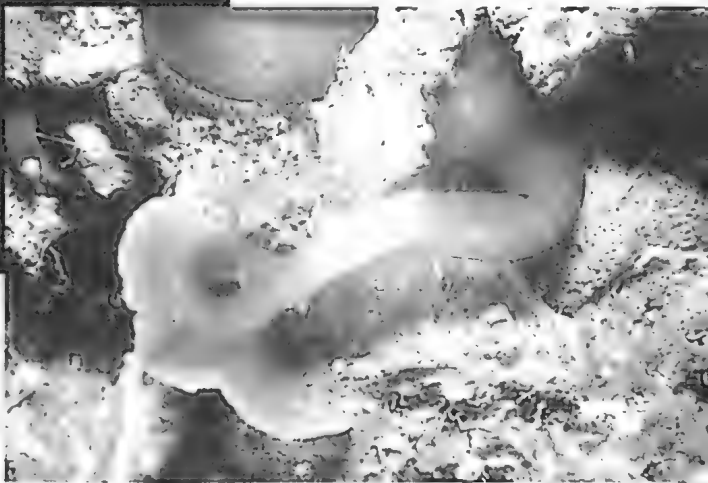


Plate 11.3 Bonelliidae. An unidentified spoon worm collected at One Tree Island, Great Barrier Reef, showing the bifid proboscis typical of most bonelliids. [G. Rouse]

Plate 11.4 Bonelliidae. *Metabonellia haswelli* occurs most often in rubble-reef areas next to seagrass beds; it feeds at night, extending its proboscis from the burrow for up 1 m. [N. Holmes]



Plates 11.5 & 11.6 Ikedidae. Proboscis of an echiuran, tentatively identified as an undescribed species of *Ikeda*; recorded several times from St Vincent Gulf and Coffin Bay, South Australia. It may extend up to 1.5 m during feeding and form a cup-like structure posteriorly, near the mouth (Plate 11.5, above). The neat accumulations of sand and other detritus along the probosceal midline (Plate 11.6, right) suggest that cilia move particles in the mucus, visible laterally, towards the centre of the proboscis, as in other echiurans, and are then withdrawn into the mouth [N. Holmes]





Plate 12.1 Phascolosomatidae. *Phascolosoma annulatum* is a cold water, reef-dwelling species known from southern Australia, New Zealand and Campbell Island.
[N. Holmes]



Plate 12.2 Aspidosiphonidae. *Aspidosiphon steenstrupii*, lying under a rock on the Great Barrier Reef with its introvert extended, showing the caudal and anal shields on the posterior and anterior ends of the trunk, respectively.
[K. Gowlett-Holmes]

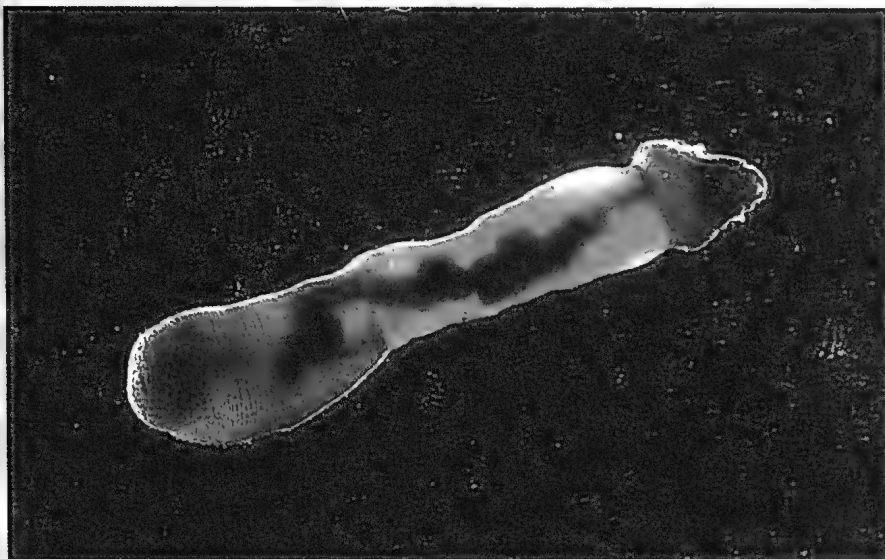


Plate 12.3 Aspidosiphonidae. An unidentified species of *Aspidosiphon* from Lizard Island, Great Barrier Reef.
[K. Atkinson]

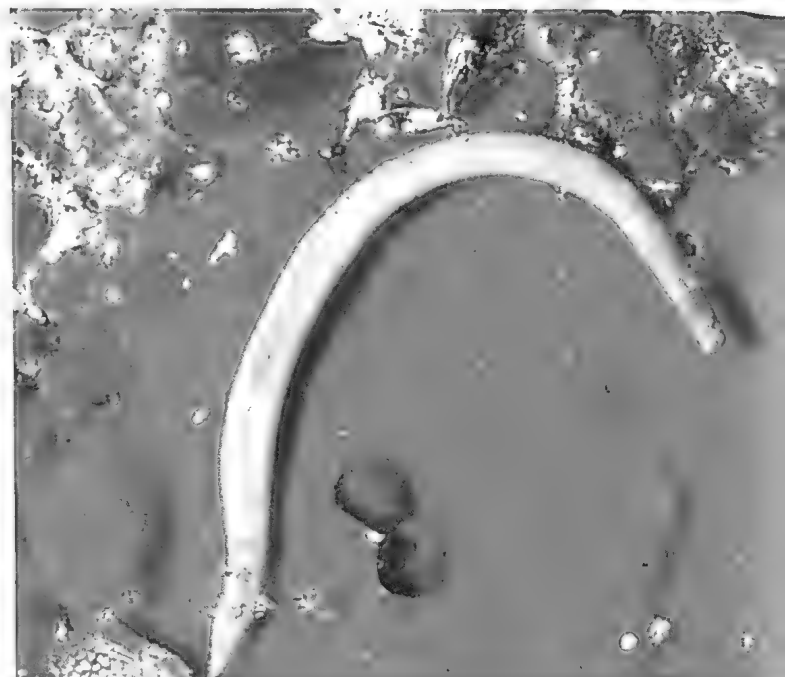


Plate 12.4 Sipunculan, tentatively placed in the Phascolosomatidae, from Heron Island, southern Great Barrier Reef.
[L. Newman & A. Flowers]

Fauchald (1977) recognised two subfamilies (Ctenodrilinae and Raphidrilinae, as redefined by Hartmann-Schröder 1971), which together contain three genera (*Ctenodrilus*, *Raphidrilus* and *Zeppelina*) and eight species. Since then some additional species have been described. George & Petersen (1991) reviewed the genus *Zeppelina*, accepted by Fauchald (1977) as valid. They examined type material of most species and concluded that seven of the eight nominal species were not valid, referring them to existing species within the family Cirratulidae; the remaining species was a synonym. They suggested that formulation of the genus *Zeppelina* was based on an incomplete understanding of the development of stages and life histories of the cirratulids and that there was no valid reason for maintaining the genus. Species assigned to this genus were found to be juveniles or asexual regenerates of *Dodecaceria* (Cirratulidae). Petersen & George (1991) made another change to the classification of the family by including the genus *Raricirrus* in the Ctenodrilidae; it was originally placed in the Cirratulidae.

The genus *Aphropharynx* was omitted by Fauchald (1977), presumably by error. Petersen & George (1991) provided a key to the recognised genera of the family, and accepted the two subfamilies of Hartmann-Schröder (1971) and four genera, *Raphidrilus* in the subfamily Raphidrilinae, and *Raricirrus*, *Ctenodrilus* and *Aphropharynx* within the subfamily Ctenodrilinae. Although Petersen & George (1991) retained the subfamilies, they stated that further study may prove the continued use of these taxa to be unjustified.

There are no published records of the family in Australia (Day & Hutchings 1979). However, the Australian Museum has unpublished records from Lizard Island, Great Barrier Reef, of an *Aphropharynx* species collected from coarse sediments in shallow water. Recently, the family has been found in coral substrata at Lizard Island, Great Barrier Reef and the Coral Sea including Osprey Reef (P. Hutchings personal observation). In addition, Museum Victoria has representatives of the family from various sites near Madang, Papua New Guinea, all from coarse sand in deep water.

Some species of ctenodrilids have been found close to oil platforms, suggesting that they may have a high tolerance to hydrocarbon pollution (Moore 1991). Moore proposed that they may be the first indicator of sediments subjected to hydrocarbon contamination from oil exploitation activity. *Ctenodrilus serratus* has been referred to as a marine pollution indicator by Reish (1974) and Carr & Reish (1977). According to Fauchald (1977), ctenodrilids are commonly found at the bottom of laboratory aquaria, following introduction into the aquaria through the seawater system.

Ctenodrilids are small, sedentary worms (3–20 mm long) which lack parapodia and have few to many distinct segments. The prostomium and peristomium lack any appendages, and the simple pharynx is partially eversible. Tentacles are absent, but simple branchial filaments may be present (Fig. 1.114A). Chaetae arise directly from the body wall. The variety of simple chaetae present includes capillaries (Fig. 1.114B), pectinate to coarsely serrated forms, and distinctive distally dentate hooks (Fig. 1.114C, E).

Ctenodrilines lack branchiae and reproduction is mainly or exclusively asexual, whereas raphidrilines have branchiae and reproduce both asexually and sexually. A pair of excretory segmental organs are situated anteriorly and gonoducts are present more posteriorly (Mesnil & Caullery 1897).

Purschke (1988b) made a detailed study of the anatomy and ultrastructure of the ventral pharyngeal organ of ctenodrilids. The pharyngeal organs comprise a muscular bulbus and a tongue-like organ. The bulbus consists of transverse muscle fibres and interstitial cells with voluminous cell bodies. Although salivary glands are not present, there are numerous gland cells in the bulbus epithelium, which secrete a medium for clumping food particles together, for ciliary transport and for gliding, cleaning and protection of the epithelia (Purschke 1988a). The tongue-like organ is formed by lateral folds, which projects into the large pharyngeal lumen.

The circulatory system is closed and a heart body is present (Monticelli 1910; Wilfert 1973). High concentrations of iron were found in the heart body of *Raricirrus beryli* by Vovelle *et al.* (1994), who suggested that this structure may play a part in the detoxification mechanisms employed by this species, which is abundant in the oilfields of the northern North Sea.

The nuchal organs in *Raricirrus* have been described by Petersen & George (1991) as small flat, narrowly oval areas found on the antero-lateral part of the prostomium. Each is surrounded by a circular field of cilia comprising a medial, comma-shaped field of cilia and a dorso-lateral band of cilia, which continues ventrally to form a broad band in front of the mouth. In contrast, the cilia in *Raphidrilus* are limited to the nuchal depression and are absent from the prostomial surface (Sokolov 1911). Hartmann-Schröder (1971) used the absence of nuchal organs to identify the subfamily Raphidrilinae, however, Petersen & George (1991) pointed out that some species in this group have nuchal organs, and suggested that this character may be distinctive at the genus level rather than at the subfamily level.

The nervous system of ctenodrilids has been studied by Gelder & Palmer (1976).

Ctenodrilids may be hermaphroditic or have separate sexes; both asexual and sexual reproduction occurs.

Raphidrilus nemasoma reproduces sexually and has a free-swimming larval stage (Qian & Chia 1989b). This species produces pear-shaped egg masses made of soft mucoid material, each of which may contain up to 1000 eggs, all fertilised. The brilliant green eggs are attached to the inside of the mass by mucous strings. Development within an egg mass is not synchronous, so that stages from newly fertilised eggs through blastula, gastrula and early trochophore stages may be present simultaneously. Three days after fertilisation the early trochophore stage is reached; by the seventh day, the larval head has begun to differentiate and one pair of nuchal organs appears although the gut is not yet distinct. The first chaetiger develops after 8 days and the gut starts to differentiate, although the larvae are still attached by the mucous strings within the egg mass. After 10 days, the larva has two to three chaetigers, is no longer attached by the mucous strings and moves freely within the egg mass. About 11 days after fertilisation, the larva emerges from the egg mass and crawls on the bottom. Metamorphosis then occurs, a fully functional gut develops and the larva begins to feed on diatoms. Within 5 weeks, the juvenile has developed eight to 11 chaetigers and by 2 months of age, the worm is almost the same length as an adult (about 3 mm). Mature adults of this species can produce egg masses much larger than themselves. This could suggest that more than one worm contributes to an egg mass or, more probably, that individual egg masses are produced by a single female over a period of time (Qian & Chia 1989b), which would account for the variation in development stages within a single egg mass. Spawning occurs during the summer months.

1. CLASS POLYCHAETA

Ctenodrilus serratus reproduces asexually by transverse fission or budding; the sexually reproducing individual is a protandric hermaphrodite and is viviparous (Caullery & Mesnil 1898). The morphological changes associated with asexual reproduction have been described by Kennel (1882) and Peters (1923).

Morphological changes associated with formation of a new prostomium appear sequentially on the dorsal surface of a series of segments, usually commencing with segment 5 or 6. Up to nine such separation zones have been observed. Each new individual in the chain is thus formed from a length of parent worm corresponding to a single segment but includes a septum and portions of the segment on either side. In addition to these segments, the head and tail pieces also survive to produce complete new individuals by regeneration.

Ctenodrilids appear to be detritivores; they stir up detritus using the eversible lower lip and feed on benthic diatoms as well as detritus (Fauchald & Jumars 1979). *Ctenodrilus serratus* has been seen living as a commensal with sea urchins off the coast of California, United States of America (K. Fauchald personal observation), so other modes of feeding may be possible. In laboratory cultures, ctenodrilids have been fed on algae. *Rhaphidrilus nemasoma* lives intertidally either interstitially in shallow marine sands or in rotting holdfasts of seaweeds.

The major part of the ingested material in the gut of *Raricirrus beryli* examined by Moore (1991) was sand. The size range of these grains indicated that the worms were selecting larger grains, avoiding the clay particles present in the surrounding sediment. They appear to collect the sediment using their eversible pharynx. They were able to avoid drill cuttings from the oil platform, which were abundant in the area, and Moore (1991) suggested that this species is a selective subsurface motile feeder, which uses a labial mechanism for feeding, corresponding to the SMX feeding guild system of Fauchald & Jumars (1979).

Family Fauveliopsidae

Fauveliopsids are small, grub-like worms, mainly found in the deep sea, either free-living or inhabiting the dead shells of gastropods, scaphopods and the tests of foraminiferans. They are characterised by the presence of inter-ramal papillae in each parapodium.

Fauveliopsidae are a small, more-or-less discrete, family of flabelligerid-like worms. A possible autapomorphy of the family is the presence of inter-ramal papillae in each parapodium, although similar papillae are also found in the Flabelligeridae (Fauchald & Rouse 1997), and may therefore be an autapomorphy for a more inclusive taxon. Two distinct morphs occur in the family. Some species are short-bodied, cylindrical, indistinctly segmented, truncate at each end, and preserved specimens are usually stiff and arched dorsally (Fig. 1.115A); others are longer, inflated anteriorly and/or posteriorly and have more distinct segmentation. The number of segments varies from about 10 to more than 50, with mature individuals of many species having a fixed number of segments. The first and/or last few segments are often shorter than the middle ones.

The body surface is smooth and shiny, or minutely papillated resulting in a rugose or dull appearance. They have a small frontal prostomium of variable shape (square, subglobular, pyriform), which may be medially invaginated, and is usually retracted between the first chaetiger (Fig. 1.115A); eyespots are rarely present. A pair of large ciliated nuchal organs lie dorso-laterally on the posterior prostomium (Riser 1987). The peristomium is a single annulus and includes ventrally a pair of lateral lips (sometimes also a ventral lip) around the mouth. Fauchald & Rouse (1997) interpreted these as palps, but other studies suggest that palps are absent (Hartman 1978; Riser 1987). Rouse & Pleijel (in press) suggest that there is little evidence to support this and larval studies are needed to establish the true nature of the head. The pharynx is looped dorso-ventrally from the mouth to the septum of chaetiger 2/3 (resembles a ventral buccal organ) and opens to a ventral mouth; the gut is ciliated throughout its length and lacks a sphincter (Riser 1987).

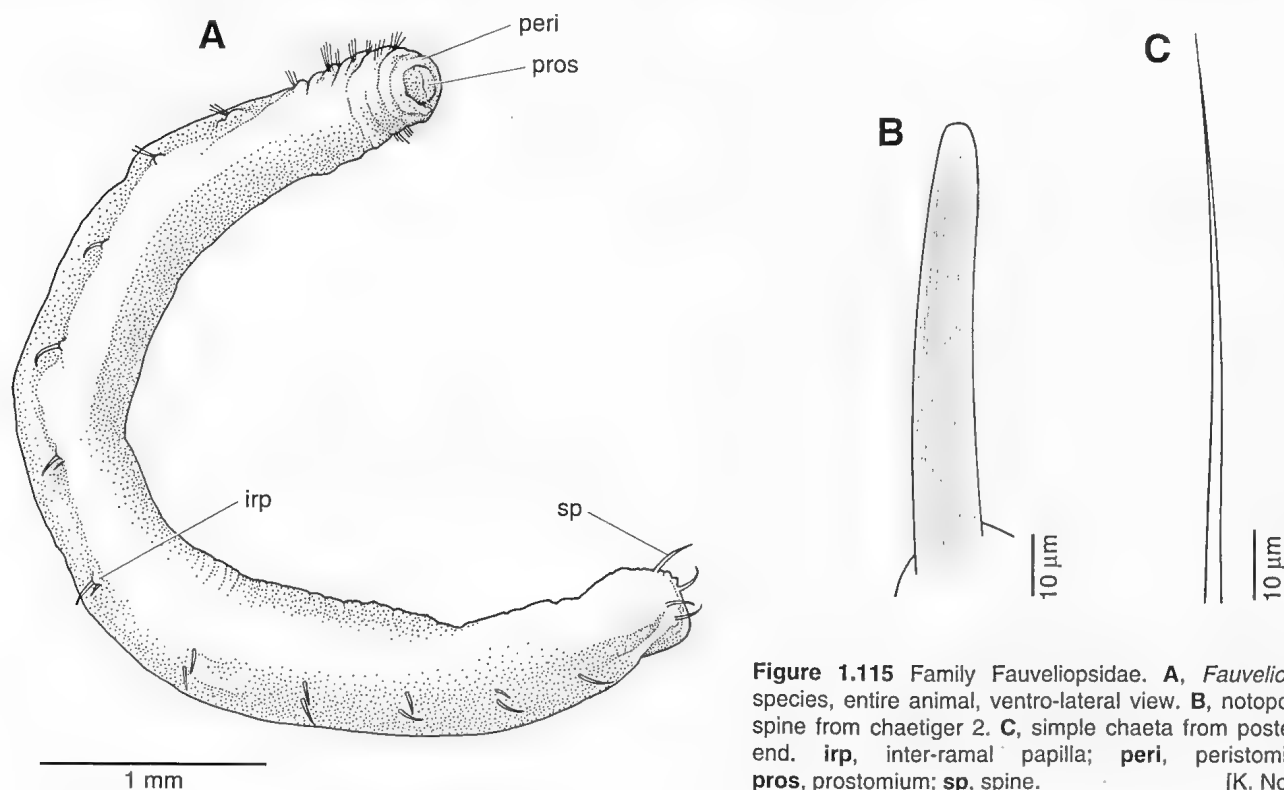


Figure 1.115 Family Fauveliopsidae. **A**, *Fauveliopsis* species, entire animal, ventro-lateral view. **B**, notopodial spine from chaetiger 2. **C**, simple chaeta from posterior end. **irp**, inter-ramal papilla; **peri**, peristomium; **pros**, prostomium; **sp**, spine. [K. Nolan]

Parapodia are biramous, with low papillate rami; the inter-ramal papillae vary in size and shape (conical, subspherical, clavate) between species. Few simple chaetae are present in each rami, including spines (which may be more or less curved; Fig. 1.115B) and longer capillary chaetae (Fig. 1.115C). The thickness of both the spines and capillaries typically varies slightly along the body, and intermediate forms are sometimes present. Chaetal spines of the last parapodium sometimes form a cage around the pygidium (Fig. 1.115A). The pygidium is terminal and may be surrounded by papillate anal cirri and/or may be retracted within the last few segments.

The family was erected by Hartman (1971) for four flabelligerid-like genera, including the type genus, *Fauveliopsis*; however, the concept of the family has since been narrowed to include only the type genus. Fauveliopsids have been classified in the order Flabelligerida together with Flabelligeridae and Acrocirridae (George & Hartmann-Schröder 1985), or in an order by themselves (Fauchald 1977). The cladistic analysis of Rouse & Fauchald (1997) suggests a sister-group relationship with Flabelligeridae, or with both Flabelligeridae and Sternaspidae; they placed all of these families together in Terebellida.

Riser (1987) provided details of the internal anatomy of *Fauveliopsis arenicola*, *F. brevis* and *F. glabra*. Fauveliopsids appear to have separate sexes. Female gonads occur on the posterior wall of the septum between chaetigers 5 and 6 (possibly chaetigers 9/10 in *F. glabra*); they are single in *F. arenicola* and *F. glabra* and paired in *F. brevis*. Vitellogenesis begins in the ovary and continues as ova are shed posteriorly into (paired or single) fluid-filled ovisacs (formed from the septal walls), which extend posteriorly to chaetigers 8 to 12. Mature oocytes vary in size and number, with a few large ones in *F. arenicola* and *F. jameoquensis*, and many smaller ones in *F. glabra* and *F. brevis*; they appear to be restricted to one or a few median segments (Riser 1987; Núñez *et al.* 1997). Spermiogenesis occurs in paired sacs extending back into chaetiger 8 in *F. brevis*; the vas deferens leads from the sacs to a pair of nephridial papillae just anterior to parapodia 7.

The smooth-bodied species appear to be free-living whereas the papillated ones inhabit the dead shells of gastropods, scaphopods and the tests of foraminiferans (Hartman & Fauchald 1971; M. Petersen personal observation). About twenty species are known, although several await formal description; only one has been reported in Australian waters. *Fauveliopsis challengeriae* was collected by the *Challenger* in 3566 m at Station 157, which is part of the Australian Antarctic sector. Most species are bathyl or abyssal; exceptions are *F. adriatica*, which occurs in the Adriatic Sea in depths of 61–66 m (Katzmann & Laubier 1974); *F. arenicola* occurs in nearshore calcareous sands in northern New Zealand, and *F. jameoquensis* occurs in lagoon sediments at 5 m in the Canary Islands.

Family Flabelligeridae

Flabelligerids are relatively short worms with few segments and they usually have a papillose epidermis (Pl. 8.4). They have an indistinct head with buccal tentacles which are normally retracted into a membranous sheath. The anterior segments often bear elongate chaetae directed forward forming a cephalic cage (Fig. 1.116C). The parapodia are indistinct and the chaetae arise directly from the body wall.

The prostomium is a narrow ridge, which Spies (1975) referred to as the prostomial lobe, and the peristomium is reduced. Antennae are absent, and peristomial paired grooved palps are located at the corners of the mouth. Nuchal organs are paired ciliated ridges lateral to the prostomium. The longitudinal muscles are arranged in bundles. The first segments are fused to form the branchial membrane (or cephalic hood; Fig. 1.116A). Parapodia are biramous and poorly developed (Fig. 1.116B). All notopodia and neuropodia are short, and are distally truncate or tapering. Dorsal and ventral cirri are absent. Dorsal segmental branchiae are present and arise from the cephalic hood (see below). Lateral organs and dorsal cirrus organs have not been observed. Papillae of a characteristic structure are present, often especially dense and long around chaetae (Mesnil 1899; Schlieper 1927). An eversible ventral buccal organ is present and the gut is looped. A gular membrane is present. Segmental organs are present as mixonephridia; the anteriormost pair is excretory and the more posterior ones function as gonoducts. The circulatory system is closed, and a heart body is present. Aciculae are absent. Chaetae are present as falcate compound falcigers and variously ornamented capillaries (Fig. 1.116D–F). The relatively thick, distally blunt chaetae present in many species of flabelligerids have been called spines; however, Fauchald & Rouse (1997) referred to them as modified capillaries. This definition follows that of Fauchald & Rouse (1997).

Initially, the flabelligerids were regarded as terebellids [for example, see Audouin & Milne Edwards (1834)], but were recognised as a distinct family by Quatrefages (1849), under the name Chloraemidae. Most flabelligerids are densely covered with papillae, which are irregularly distributed and of characteristic construction similar to the inter-ramal papillae present in the fauveliopsids. Many flabelligerids are heavily invested with sediment granules (for example, *Ilyphagus*, see Hartman 1969: 293) or are covered with a mucous sheath (for example, species of *Flabelligera*).

Rouse & Fauchald (1997) suggested that recognition of the Poeobiidae may make the Flabelligeridae paraphyletic as they both share many features (Heath 1930; Robbins 1965); however, at this stage both families are recognised.

Worldwide, Fauchald (1977) recognised 126 species in 14 genera. Since then, however, two additional genera (Fauchald & Hancock 1981; Buzhinskaya 1994) and one species (Kirkegaard 1996) have been described. Also, the only known species (*Helmetophorus rankini*) belonging to the family Helmetophoridae has been transferred to the Flabelligeridae (Glasby & Fauchald 1991). In Australia, eight species have been recorded (Day & Hutchings 1979) representing six genera; no additional unpublished records are present in the Australian Museum database.

The family has not been revised recently, although Light (1978) has reviewed the species in *Flabelligerina*, and concluded that only one (*F. essenbergae*) belongs in the genus. The other two species within this genus, *F. commensalis* and *F. macrochaeta*, are referred to *Flabelligera* and *Flabelligella* respectively.

The family is found worldwide from the intertidal zone to abyssal depths, although species are rarely abundant. Some genera are tubiculous, whereas others live under stones and some burrow just below the surface of the sediment. A species of *Pherusa* is abundant as a boring organism in living colonies of corals in Hong Kong Harbour (Scott & Cope 1990). Such infestations have not been observed elsewhere in the South Pacific (P. Hutchings personal observation).

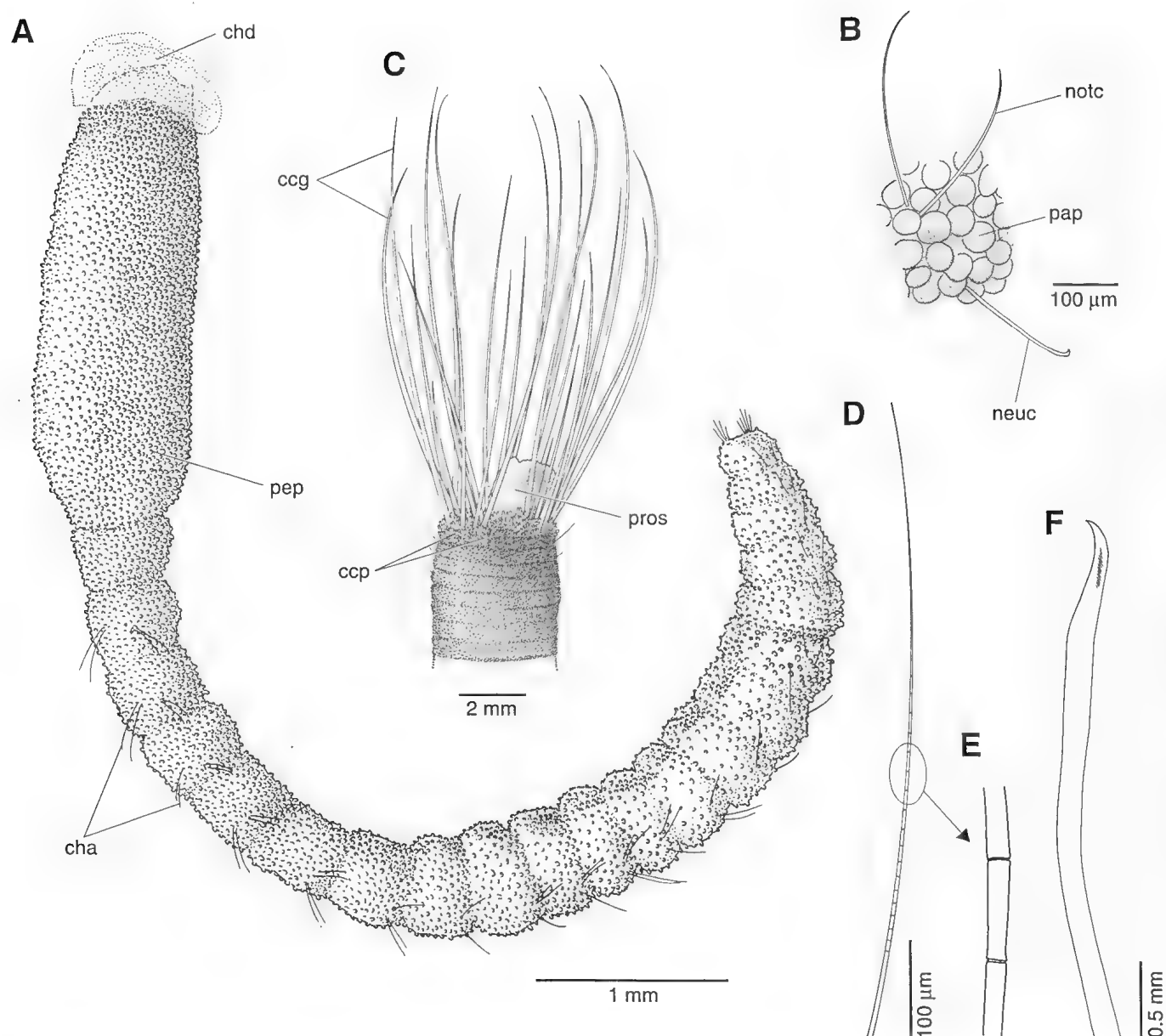


Figure 1.116 Family Flabelligeridae. **A, B**, *Diplocirrus* species: **A**, entire animal, dorso-lateral view; **B**, chaetae and papillae of chaetiger 15. **C**, anterior end of *Therochaeta* species showing the cephalic cage, dorsal view. **D–F**, chaetae from chaetiger 20 of *Pherusa* species: **D**, barred capillary with details of surface shown in **E**; **F**, spine. **bra**, branchiae; **ccg**, capillary chaetae forming cephalic cage; **ccp**, cephalic cage papillae; **cha**, chaetae; **chd**, cephalic hood; **neuc**, neurochaeta; **notc**, notochaeta; **pap**, papilla; **pep**, papillate epidermis; **pros**, prostomium. [K. Nolan]

Flabelligera affinis is found under loose stones on rocky shores and creeps around like a caterpillar using its hooked chaetae, according to Day (1967). *Piromis* species live in sandy pools on intertidal rocky shores and their sand covered cuticle provides protection from small predators as they burrows through the surface layers (Day 1967). Species of *Pherusa* are more sedentary and as well as burrowing into live corals they also occur in the abandoned burrows of rock-boring bivalves; the tail is often folded back against its body so that the faecal pellets can be expelled from the mouth of the tube (Day 1967).

A species of *Pherusa* from Argentina burrows into dense layers of coralline algae found intertidally on exposed beaches (Amor 1994). This species probably bores using a combination of chemical secretions as well as by physical abrasion of the substratum. Anterior glands secrete acid mucopolysaccharides, which may be involved in dissolving the calcareous substratum. The worms produce a blind-ending

tube measuring up to 30 mm in length and when the animal retreats into the tube the dorsal shield of the first three chaetigers effectively closes off the burrow.

The prostomium of flabelligerids is poorly defined and is fused with the peristomium to form the head. Spies (1975) suggested that the prostomium consisted of the prostomial lobe with four eyes, nuchal organs, dorsal lip and palps, whereas Rouse & Fauchald (1997) suggested that the prostomium consists only of the prostomial lobe and that the other organs are either peristomial (upper lip) or emerge from the junction of the prostomium and peristomium. Rouse & Pleijel (in press), however, reject the concept that the nuchal organs are peristomial in origin. In preserved animals, the head is typically retracted and surrounded by a membranous sheath (= cephalic hood; Fig. 1.116A), and it is difficult to distinguish the various structures especially the arrangement of the branchiae. In life, a pair of conspicuous stout, grooved feeding palps extend forwards on either side of the mouth,

often beyond the cephalic cage. They originate from a flanged base at the ventral edge of the prostomial lobe. At the base of the palp, a joint marks internally the septum that separates the palp lumen from the general body coelom. The ventral side of the palp has a large ciliated groove. In *Piromis*, the tip of the palp is expanded to form a pad (Spies 1975). The palps move by the contraction of the circular muscles and two to four longitudinal muscle bands acting against the fluid in the lumen of the palp. The palps also have a longitudinal septum, which presumably enables them to be highly mobile. The tips of the palps are sensitive to changes in light and touch (Spies 1975). A tongue-shaped or semi-circular cephalic hood bears a number of branchial filaments. A complicated series of gutter-like ciliary tracts are found on many species running over the surface of the prostomium. They consist of an outer and inner pair. The outer pair originates on the flank of the prostomial ridge near its tip and extends ventrally around the base of the prostomial lobe to terminate in a hooded pit on the dorsal sides of the dorsal lip. The inner pair are confluent around the bases of the palp and terminate in the nuchal organ (Spies 1975).

In *Flabelliderma commensalis*, the peristomium consists of a dorsal lip, paired median lips (which can be retracted by the pharyngeal retractor muscles) and an unpaired ventral lip. The ventral lip has seven ventral ciliary tracts which converge inside the mouth (Spies 1975).

Elongate capillary chaetae of the first one to six anterior segments form a cephalic cage in most species of *Pherusa*, *Flabelligera*, *Piromis* and *Therochaeta* (Fig. 1.116C), but not in most species of *Brada* and *Diplocirrus*. Interspersed with the chaetae are sensory papillae; when the worm is disturbed the head retracts and the two halves of the fan close over the head (Spies 1975). The chaetae of the following segments consist of annulated notochaetae and neurochaetae which are modified to form distally curved spines. They may be simple as in *Pherusa*, or in *Piromis* they are pseudo-compound falcigers often with bidentate tips and in *Flabelligera* they are stout compound falcigers with simple tips. In *Brada*, *Pycnoderma* and *Diplocirrus*, the neurochaetae resemble the notochaetae and are slightly stouter. The surface of the body is usually glandular and may be covered by debris, a crust of sand grains or by a translucent mucilaginous coat, which may be toughened so as to appear cartilaginous in consistency. Skin papillae project into this body covering. They vary in form from small, wart-like and arranged in annular rings to elongate and club-shaped. The length of the papillae varies across the body. The longest ones occur around the cephalic cage (Fig. 1.116C), and the shortest ones on the venter; those on the dorsum are of intermediate length.

Features used to distinguish species include: the presence of a mucoid or sand grain sheath covering the body; the shape and distribution of epithelial papillae; size and number and arrangement of branchial filaments; the degree of development and the number of chaetigers forming the cephalic shield, and; the shape and structure of the notochaetae and neurochaetae (Milligan 1984).

Flabelligerids are surface deposit-feeders; sediment coated with organic material is usually gathered by the grooved palps, from around the animal and from that accumulated on the chaetae of the first two chaetigers; this is illustrated by Fauchald & Jumars (1979). The water currents created by the branchiae may be involved in the feeding process (Fauchald & Jumars 1979). Fauchald & Rouse (1979) provided a list of feeding studies of flabelligerids. There are very few investigations of feeding and these include studies by Blegvad

(1914) and Hunt (1925). In a more recent feeding study on a species of *Pherusa*, Amor (1994) observed the chaetae of the cephalic cage separating and moving backwards to form a filtering system. The ciliated grooved base of the palps are swept regularly across the cephalic cage and food particles are transported by the rapid ciliary current to the mouth between the dorsal and medial lips. This species feeds during the day on detritus and small planktonic organisms.

According to Spies (1975), *Flabelliderma commensalis* is a ciliary mucoid detritivore which feeds on the faecal material of its sea urchin host (*Centrostephanus coronatus*). Most commonly the worm is found on the aboral surface of the sea urchin with its head near the host's anus. Two methods of feeding have been observed. Detritus is collected from the host in the ciliated gutters of the palps, trapped in mucus and carried to the dorsal lip. The dorsal lip manipulates the resultant strand of mucus and detritus and directs it into the mouth. The regular movements of the median lips, in and out, pull the strand into the mouth. Only the median and ventral lips are retractable. In the other method, suspended detritus is carried to the branchial field by ciliary currents created by the nuchal organ, prostomial ridge and the branchiae. The branchiae are continuously retracted and expanded and this action manipulates the mucus into boluses which are periodically picked up by the palps and carried to the mouth (Spies 1975).

Flabelligerids have a gular membrane (Schlieper 1927). The gut is looped over most of the body length as septa are absent. According to Dales (1963a) the presence of such a coiled gut is common among deposit-feeders, presumably to maximise retention time within the gut to increase absorption.

Externally, branchial filaments are located on a peristomial branchial membrane; however, Spies (1975) demonstrated that blood vessels associated with the branchiae emerge from the heart posterior to the emergence of the vessel covering the brain, suggesting a more posterior origin. In addition, these vessels emerge in a double row further suggesting that the branchiae are segmentally derived. The structure of the branchiae of *Pherusa plumosa* has been investigated by Storch & Alberti (1978) and they found that they contain blood spaces within the surface epithelium, which is irregularly infolded. Although the epidermis and the cuticular layer are reduced compared with epidermis elsewhere on the body, their structure is similar (Storch & Welsh 1972). The structure of the branchial filament is illustrated by Gardiner (1988). Species of *Pherusa* have branchiae with blood spaces extending deep into the epidermis forming intraepidermal capillaries (Gardiner 1988); this is one of four types of genuine branchiae, recognised by Storch & Alberti (1978). Members of *Pherusa* have about 80 to 90 filiform branchiae arranged in two groups as well as a single pair of much larger dorsal branchiae (Amor 1994). The dorsal branchiae are the longest, and are all filiform, contractile and ciliated along their length. The branchiae also produce feeding currents within the cephalic cage which tend to concentrate food particles at the base of the two dorsal branchiae. Spies (1975) has described in detail the branchial structure and their arrangement in several species.

Flabelligerids are one of the few polychaete families to have a green respiratory pigment, probably chlorocruorin (Spies 1973). The pigment is dissolved in the blood. They have a closed circulation with a heart body (Mesnil 1899; Picton 1899; Spies 1973). The blood vascular system has been described by Spies (1973) and includes a ventral and a dorsal blood vessel. The dorsal vessel extends from chaetiger 3 to 17

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through the dorsal septa. It receives lateral vessels segmentally and in the third chaetiger a short thick vessel from the heart. Anteriorly, it terminates in an array of short branched vessels in the first chaetiger near the beginning of the head retractor muscle. The ventral vessel runs the length of the animal; posterior to chaetiger 9 it runs through the ventral septa. It gives rise to segmental vessels in each chaetiger. Spies (1973) also described the perineural vessels and the segmental vessels. A large gut sinus is also present; it originates in the region of the oesophagus as a plexus of vessels derived from the supra-oesophageal vessel and it extends to the anus. The gut sinus varies in thickness and sheaths the oesophagus, gastric caecum, hind stomach and intestine and appears to be a continuous space.

The heart is a large pumping vessel dorsal to the oesophagus, originating as two roots from the gut sinus dorsal to the hind stomach. The heart, which continuously pumps, has an internal skeleton lining and well-developed layers of circular and longitudinal muscles. This description is based on *Flabelliderma commensalis*, one of the few flabelligerids without a mucous coat; it may have a higher respiratory exchange rate through the body wall (Spies 1973). Spies (1973) discussed the fact that the blood system varies between species and that *Pherusa plumosa* has many more branchiae and hence a more complicated blood system.

Spies (1973) speculated that the respiratory pigment chlorocruorin is produced within the heart body as the cells found in flabelligerids resemble those described for terebellids by Dales & Pell (1970), which also appear to synthesise respiratory pigments. Also the elaborate folding of the basal lamina in the heart body cells also suggest that it is an active site for the transfer of material between these and the blood. Dales & Pell (1970) suggested that in the terebellids they operate by reverse pinocytosis.

Metanephridia are present as mixonephridia (Goodrich 1945). In *Pherusa*, two pairs of nephridia are present. The nephridiopores, located on the branchial membrane, discharge both waste products and gametes (Amor 1994). This conflicts with the findings of Schlieper (1927) who reported a single anterior pair of excretory nephridia and posterior gonads and gonoducts.

The structure of the cerebral ocelli in *Flabelliderma commensalis* has been described by Spies (1975). The somata of the receptor cells lie outside the multicellular pigmented cup. Leading from each soma is a narrow cylindrical middle segment of the sensory cell that passes over the lateral rim of the ocellar cup. Before ending in a bundle of inversely directed microvilli (rhabdomeres) the cell forms a clear dilation lacking in cytoplasmic organelles (Eakin & Hermans 1988). These swellings of the receptor cells, are collectively termed, by Spies (1975), a 'lens-corneal' area. Similarly developed lens-like corneal areas are found in *Flabelligera*. All the species studied by Spies (1975) have two pairs of eyes except for *Coppingeria longisetosa* and *Diplocirrus capensis* which lack eyes.

The nuchal organs comprise a pair of hooded pits located on the lateral sides of the prostomium. These pits are confluent with the inner and outer ciliary tracts of the prostomium. The organs are lined with densely ciliated columnar cells (Spies 1975).

The sensory papillae, which occur near the base of the cephalic cage, are elongate club-shaped structures; dense nerve-like tissue is present in the heads of the papillae (Spies 1975). In addition, there are numerous shorter mucus-secreting papillae on the outer surface of the cephalic cage as well as on the general body surface. In *Flabelliderma essenbergae*, the cephalic cage is immobile and is embedded in a mucous coat. In *Flabelligera infundibularis*, the thick mucous coat covers the entire body except where the chaetae emerge anteriorly from the cage (Spies 1975).

Little is known about the reproduction of flabelligerids, except for *Flabelliderma commensalis*. Gravier (1911, 1923) reported that the Antarctic species *Flabelligera mundata* broods its fertilised oocytes on the outside of its body and the eggs undergo direct development. The developing eggs are laid in a thick layer of mucus along the dorsum of the animal. Brief references have been made to the presence of gonads (Cunningham & Ramage 1888; Jourdan 1887; Joyeux-Laffuie 1887). These studies provide conflicting evidence as to the number of pairs of gonads present, ranging from six to eight pairs. Spies (1977) suggested that this may be due to the relatively slow development of the anterior gonads.

Reproduction in a Californian population of *Flabelliderma commensalis* has been studied in detail (Spies 1977). This species is dioecious, with no morphological differences between males and females, except at maturity; the white testes and green ovaries are visible through the body wall respectively in males and females. Eight pairs of gonads are present, each pair is situated in the anterior part of the coelom of chaetigers 2 to 9. The coelom posterior to chaetiger 9 is closed by the sac-like septum between chaetigers 9 and 10. The gonads receive blood from a sub-branch of the segmental vessel and gametes mature within the walls of the blood vessels.

The mature ovary in *Flabelliderma commensalis* is elongate and consists of numerous radial cords, each cord consisting of a central blood vessel covered with oocytes. Vitellogenesis occurs throughout summer and autumn leading to spawning in December. Similarly, all stages of spermatogenesis occur within the gonad. The retention of gametes within the gonad until spawning is relatively unusual within polychaetes, where typically much of the development occurs within the coelom. It appears that this species spawns over a day or so, and a few days later pelagic larvae were collected in the plankton. Larval development from a 7- to 13-chaetiger stage took place in 30 hours. Within a month of spawning, juvenile worms were found on the host sea urchin.

Pherusa species exhibits indirect development from November to February along the Argentinian coast and Amor (1994) was able to collect various larval stages within coralline algae suggesting that the species produces benthonic larvae, although these were not described by Amor.

Little information is available on population densities of flabelligerids; they are typically sparsely represented in quantitative samples. A rock-boring species of *Pherusa* has been found in densities of 14 burrows per 100 cm² with only seven burrows inhabited (Amor 1994).

A species of archigregarine has been described from the body of *Flabelligera affinis* by Simdyanov (1992). It has not been reported from any other species.

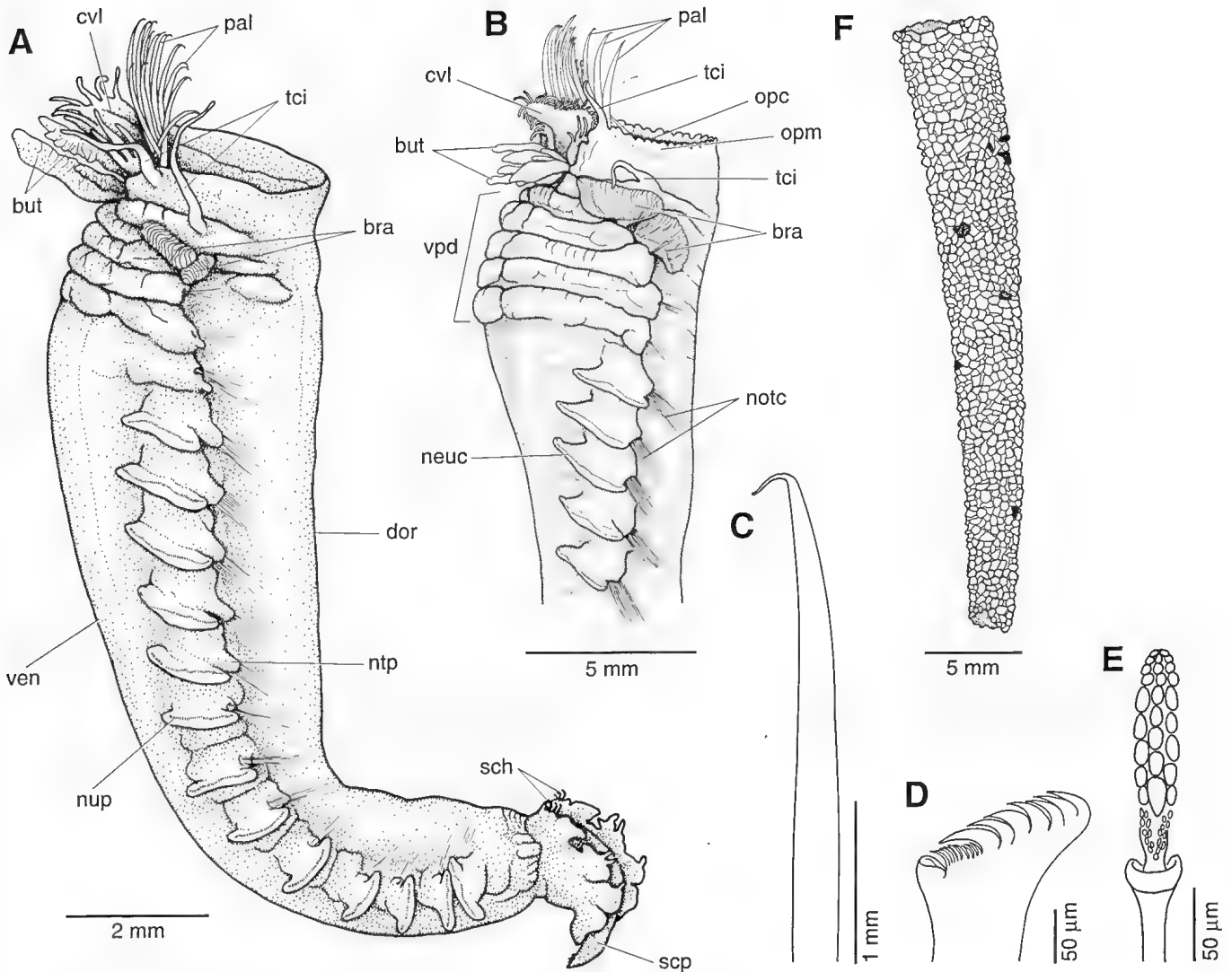


Figure 1.117 Family Pectinariidae. **A**, *Pectinaria antipoda*, entire animal, lateral view. **B–E**, *Amphitene crassa*: **B**, anterior end, ventro-lateral view; **C**, palea; **D**, **E**, uncini from chaetiger 6, lateral (**D**) and frontal (**E**) view. **F**, tube of a pectinariid. **bra**, branchiae; **but**, buccal tentacles; **cvl**, cephalic veil; **dor**, dorsum; **neuc**, neurochaetae; **notc**, notochaetae; **ntp**, notopodium; **nup**, neuropodium; **opc**, operculum; **opm**, opercular margin; **pal**, paleae; **sch**, scaphal spines; **scp**, scaphe; **tci**, tentacular cirrus; **ven**, venter; **vpd**, ventral pads. [A. Murray]

Family Pectinariidae

Pectinariids are easily recognised by their tube of cemented sand grains which resembles an ice-cream cone (Fig. 1.117F). They also have a characteristic set of golden paleae surrounding the mouth which they use for digging in soft sediments.

Pectinariids are characterised by having a reduced prostomium which is completely fused to the peristomium; the latter is reduced to lips around the mouth. Antennae are absent. The peristomial palps (buccal tentacles) are grooved and inserted on or around the lips, and cannot be retracted into the buccal cavity (Fig. 1.117A). A cephalic veil (tentacular membrane) is present, and nuchal organs appear to be represented by dorsal ciliated crests (Nilsson 1912; Söderström 1930). The longitudinal muscles are grouped in bundles. Segmentation is distinct and the first segment is completely fused to the head and bears golden notopodial paleae (Fig. 1.117B). Other notopodia are short, truncate cylinders; the neuropodia are tori. Anteriorly, two pairs of dorsal, branching branchiae are present. Lateral organs are present (Rullier 1951), as internally ciliated pits between the notopodia and neuropodia. There is a ventral buccal organ and the gut is looped. A gular membrane, between two anterior

segments, is present. Nephridia are mixonephridia (Goodrich 1945), comprising a few pairs of anterior nephridia and posterior gonoducts. The circulatory system is closed, and a heart body is present. The posterior end is a flattened scaphe with spine-like chaetae. Aciculae are absent. Chaetae are present as notopodial capillaries, spines (paleae; Fig. 1.117C) and neuropodial uncini (Fig. 1.117D, E). The worms live in a cone-shaped tube of unique shape and construction (Fig. 1.117F).

No major revision of the family has been undertaken, although Fauvel (1927), Nilsson (1928) and Holthe (1986a) discussed the family in some detail. No subfamilies are recognised.

Pectinariids were amongst the first polychaetes to be described. Lucas & Holthuis (1975) discussed the confused state of taxonomy in this family and presented evidence that the generic name, *Pectinaria*, and the specific names, *belgica* and *koreni*, are invalid. *Pectinaria belgica* and *P. koreni* are both well-studied and common European species. These authors showed that the type species of the genus *Pectinaria*, (*Nereis cylindraria belgica*) is a senior synonym of *Lagis koreni* and that *Nereis pectinata* is a senior synonym of *Pectinaria belgica* sensu Malmgren. Nielsen & Kirkegaard

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(1978), however, made an application to the International Commission of Zoological Nomenclature to preserve the names *Pectinaria koreni* and *P. belgica* under the Plenary Powers of the Commission. This was accepted by the Commission (1982), and so *P. belgica* and *P. koreni* remain as valid species.

The pectinariids have always been considered to be related to the terebellids (Savigny 1822; Grube 1850; Levinsen 1883; Fauvel 1927); although they do not closely resemble them externally, except for the presence of tori with uncini; however, they do share many internal morphological features.

Some workers, such as Holthe (1986a), accepted only two genera, *Petta* and *Pectinaria*, whereas Fauchald (1977) recognised three additional genera (*Lagis*, *Amphictene* and *Cistenides*). Holthe regarded the latter three genera as subgenera of *Pectinaria*, however, the rationale for the subgenera seems rather tenuous (Fauchald 1977; Hutchings & Peart in preparation). A major revision of the family is needed, involving better definition of the genera to allow assessment of their status. For example, *Cistenides* may represent a species group within the genus *Pectinaria*.

In Australian waters, Hutchings & Peart (in preparation) have found two genera and six species, of which five are being described as new. Fauchald (1977) recorded 46 described species; since then no additional species have been described, apart from the Australian species, making a total of about 51 described species. Many species are known only from the type locality.

Pectinariids are free-living tubicolous species and have been recorded from a wide variety of sediments in Australian waters, from fully marine habitats to protected waters where salinity drops briefly after heavy rain. Species are rarely found in large numbers, although one undescribed species of *Pectinaria* is widely distributed in the soft-bottom communities in Jervis Bay, New South Wales.

Pectinariids are one of the most characteristic families of polychaetes with their large golden paleal chaetae and their gently tapering, tusk-shaped, very fragile sand tube. The tube is composed of a single layer of sand grains. The paleae can effectively close the entrance to the tube and may protect the worm from being eaten by predators.

Pectinariids are typically about 10–20 mm in length. A very large new species of *Amphictene* dredged from off the reefs in the Abrolhos Islands, West Australia, ranged from 35–97 mm in length and 10–26 mm in width (Hutchings & Peart in preparation).

This family is one of few in which the number of segments is constant, 22 in all species. The body is divided into three regions: a thorax, an abdomen and a posterior scaphe (Fig. 1.117A). The head consists of a reduced prostomium which is fused to the peristomium (Holthe 1986a). The buccal tentacles are non-retractile, grooved and located on or around the lips; they are considered by Rouse & Fauchald (1997) to be peristomial in origin. Early larval stages initially have a pair of these structures which are clearly similar to those seen in sabellariids (Watson 1928). The conspicuous

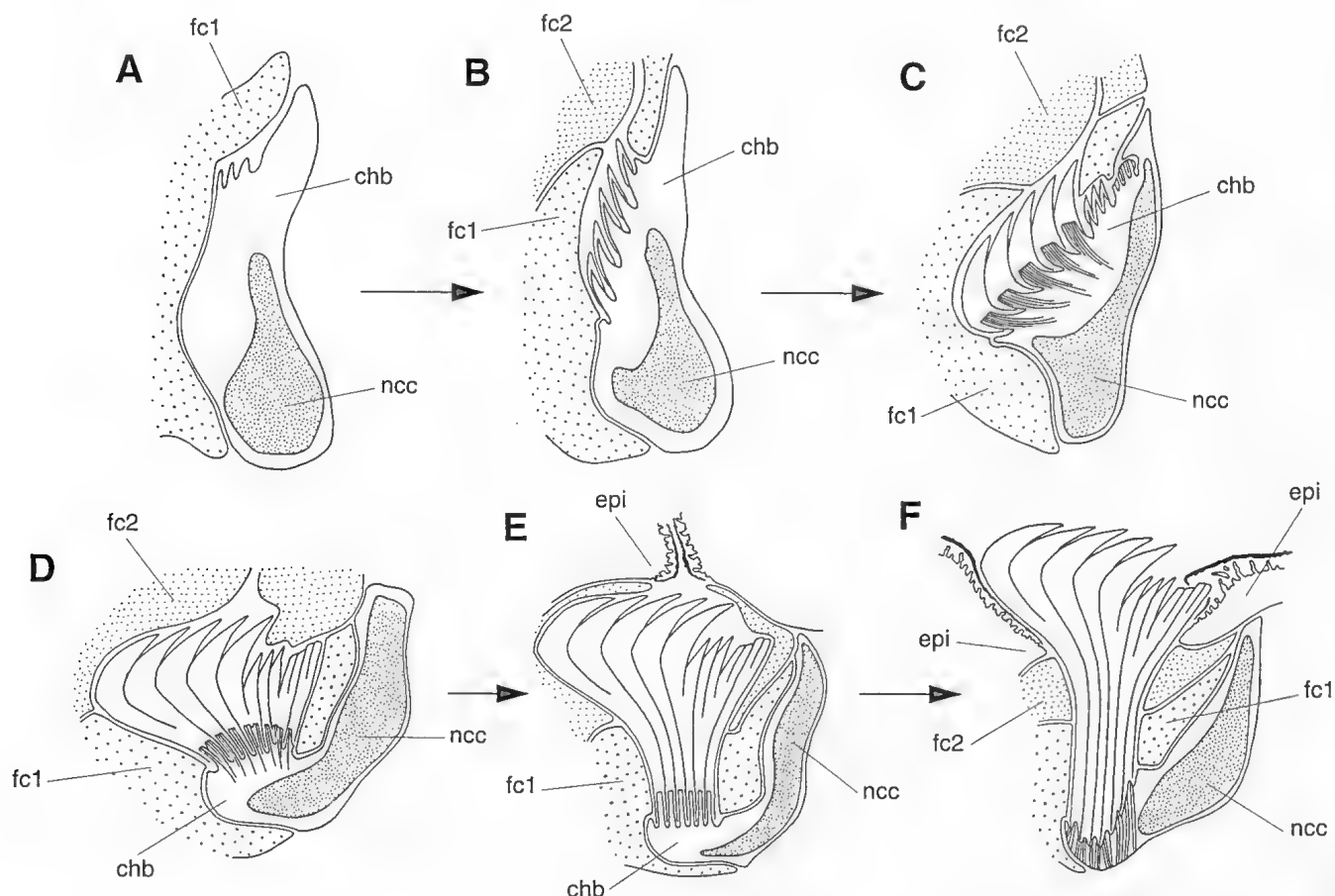


Figure 1.118 Family Pectinariidae. Formation of uncini in *Pectinaria koreni* and *Pectinaria auricoma*. **A**, the chaetoblast generates microvilli along an apicobasal axis. **B**, chaetal material surrounds the stout microvilli. **C**, microvilli are withdrawn by actin filaments and their orientation determines the curving of the spines; additional microvilli are formed where the chaetoblast and the first follicle cell have met. **D**, **E**, tapering of the manubrium is caused by merging of microvilli. **F**, actin filaments are replaced by intermediate filaments which attach the uncinus to the follicle. **chb**, chaetoblast; **epl**, epidermis; **fc1**, first follicle cell; **fc2**, second follicle cell; **ncc**, nucleus of chaetoblast. (After Bartolomeaus 1995) [K. Nolan]

paleae are notopodial and are surrounded by the cephalic veil; they occur on the first segment. The peristomium forms an operculum which may be well or poorly developed. The raised margins of the operculum may be smooth or divided into triangular lappets and cirri may also be present. Dorsal lamellate branchiae are present on segments 4 and 5. The anterior segments have paired ventral glandular areas and a small central shield. The last five segments are fused, forming a flattened plate or scaphe, with lateral pairs of scaphal spines (Fig. 1.117A).

Bartolomeaus (1995) described in detail the structure and formation of the neurochaetal uncini in *Pectinaria*, (Fig. 1.118) based on the development of trochophores and juvenile stages. The special structure of the uncini is the result of a temporal modification of the actin-filament system of the chaetoblast. The chaetoblast develops microvilli along the apicobasal axis of the cell and a surrounding follicle cell secretes chaetal material around the tips of the microvilli. The deposition of the chaetal material creates the spines of the uncini and the microvilli form their core.

Males and females exhibit no external morphological differences, although at the time of spawning, males and females may be distinguished by the colour of their coelomic gametes.

The characters used to separate the genera are: the degree of fusion of the cephalic veil to the operculum; the marginal ornamentation of the cephalic veil and the operculum; the number of uncinigerous segments present, and; the number of rows of vertical teeth on the uncini (Fig. 1.117D, E). Characters used to separate species include the presence or absence of scaphal papillae and their shape.

Pectinariids live head down in the sediment, with the narrower end of the tube protruding just above the sediment surface. The worm can move through the sediment by using its paleae to dig. Glandular cells in the integument are responsible for tube-building (Truchet & Vovelle 1977). The cell secretions produce a matrix to which sand grains adhere as well as a mucous lining, and contain large amounts of magnesium, calcium and phosphorus. In *Petta pusilla*, specific cells produce homogenous granules with sulphhydryl proteins and phosphorus-rich polysaccharides, calcium, magnesium and iron in heterogenous inclusions (Vovelle 1979a, 1979b). The cuticle is composed mainly of unbanded collagen fibres arranged in layers, which criss-cross one another at approximately 55° to the longitudinal axis of the animal (Storch 1988). They have a gular membrane which forms a complete, or near complete, muscularised septum, present between two successive anterior segments. This membrane differs from the following septa in being muscularised.

Pectinariids are selective, subsurface deposit-feeders (Dobbs & Scholly 1986). Two variants of feeding methods have been recorded. In *Pectinaria koreni*, paleae and tentacles are used to dig a loosely constructed cavity which extends from the broad end of the tube and continues as a narrow channel to the sediment surface, thus forming a 'U'-shaped space; the space is irrigated by the respiratory movements of the worm (Hessle 1925). In this position the worm can move horizontally through the sediment. The worm feeds by using its tentacles to collect sediment which is then swallowed. In the second method the same species was observed collecting subsurface sediments with their buccal tentacles which are then transported along the ciliated grooves to the ventral mouth (Dobbs & Scholly 1986). They did not observe the paleae being used to dig through the sediment as Hessle (1925) and Watson (1928) recorded.

Pectinariids eject unconsolidated faeces from the tube onto adjacent sediment surfaces. They also produce unconsolidated pseudofaeces, which is texturally indistinguishable from faeces. These are made up of sediment particles transported from depth, moved upwards between the worm and its tube and ejected (Watson 1928; Schäfer 1972). Taxa with the ability to relocate material from depth to the sediment surface were referred to as 'conveyor-belt species' by Rhoads (1974). In addition, as the worm pumps water through the tube, fine particles in suspension at the sediment-water interface (Watson 1928) are drawn in to the feeding area where the buccal tentacles are moving through the sediment continuously.

Dobbs & Scholly (1986) found that passage through the gut varied from 1–6.5 hours in *Pectinaria koreni* with an anterior diameter of 2–5 mm. Calculated rates of reworking the sediment increased exponentially as a function of increasing anterior tube diameter. This species preferentially ingested large-sized sediment particles. They showed also that these worms only built 'U'-shaped burrows in hypoxic high-nutrient, fine-grained sediments, as postulated by Fauchald & Jumars (1979) and that individuals living in coarse sediments did not live in 'U'-shaped burrows or develop a permanent burrow system.

Dobbs & Scholly (1986) suggested that the ingestion of larger particles by *Pectinaria koreni* confounds the current perception of optimal foraging by deposit-feeders; they should select the smallest particles (Taghorn *et al.* 1978). However, this behaviour may allow them to ingest faecal pellets of the co-occurring bivalve *Abra alba*, which provide the worms with organics and microbes from the pellet surface and/or soluble compounds from within the pellets. This may represent an example of a trophic interaction, and has been reported for other pectinariids (Whitlatch 1974; Ronan 1977).

The structure of the gut is incompletely known in pectinariids. The ventral pharynx has been described by Watson (1928). Dales (1963a) referred to it as a ventral buccal organ in which the lips are used to sort food particles. The alimentary canal is much longer than the worm and forms one or two loops in the anterior part of the body. Such looping is feasible as the septa are poorly developed in pectinariids, so the gut lies more or less free in the body cavity (Fauchald & Rouse 1997). The looped gut is figured by Michel (1988). Ronan (1977) found that most nematodes, crustaceans and foraminiferans passed unharmed through the gut, although 30% of the smallest copepods and polychaetes were killed and partially digested. The intestine of *Pectinaria koreni* secretes amylase, trypsin and probably lipase (Brasil 1904).

Pectinariids have a closed circulation system with dorsal and ventral longitudinal vessels, linked by vessels, capillary beds and gut lacunae. The heart body comprises a plug of tissue almost occluding the lumen in the dorsal vessel (Mesnil 1899). Kennedy & Dales (1958) suggested that heart bodies are responsible for the formation of blood cells.

The two pairs of dorsal lamellate branchiae are presumably important sites for gas exchange, as may be the rest of the body epidermis, but no studies have been done on the physiology of respiration. Storch & Alberti (1978) examined the structure of the parallel lamellae of the branchiae of *Pectinaria koreni* using scanning and transmission electron microscopy. Clusters of cilia are present (figured by Storch & Alberti 1978). The branchial lamellae consist of cuboidal to flattened epithelial cells and subepidermal blood spaces. They lack coelomic epithelium (Storch & Alberti 1978, fig. 2). The nearly homogenous cuticle is thin and penetrated by microvilli. The subepithelial blood vessels release blood into

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a system of spaces immediately below the epidermis of the branchial lamellae. Storch & Alberti (1978) concluded that these spaces may be very important sites for gas exchange.

Goodrich (1945) described in general the segmental organs of terebellomorphs, which have mixonephridia, but he did not actually specify pectinariids; further investigation is required (Rouse & Fauchald 1997). They have a few anterior pairs, the anterior-most of which function as nephridia and the posterior ones as coelomoducts (Meyer 1887; Hesse 1917).

Pectinariids appear to be primarily monoecious although Dehorne (1925) reported in *Lagis koreni* that they are simultaneous hermaphrodites, in which eggs and sperm probably originate on the same germinal epithelium.

In studies on vitellogenesis in *Pectinaria*, Tweedell (1966) showed that RNA synthesis takes place in the immature oocytes and thymidine is incorporated into the cytoplasm in developing oocytes. Oocytes are shed into the water column where prematuration or initial activation of the oocytes occurs (Tweedell 1961). In this instance, the primary oocyte proceeds to first meiotic metaphase before the egg is fertilised and maturation divisions are completed after sperm penetration. The spawned oocyte is lens-shaped, the shorter axis representing the future animal-vegetal axis (Tweedell 1980). Asexual reproduction has not been observed in the family.

Based on observations of two species, pectinariids undertake mass spawning of gametes and have a planktotrophic larvae (Wilson 1991); however more detailed studies are needed. Wilson (1936b) described the very early stages of *Pectinaria koreni* and illustrated 3-day old trochophores. The subsequent metatrochophore stage of a species of *Pectinaria* found in the plankton off Port Erin in the United Kingdom was described by Gravely (1909). Even at this stage the paleae are clearly visible. Other chaetae start to develop during the metatrochophore stage 11, when the worm is about 80 μm in length. Recently metamorphosed worms, complete with their sandy tubes, remain in the plankton for a short time before becoming benthic in habit. Laboratory studies have shown that larvae of *Pectinaria koreni* can actively select a suitable substratum for settlement and that the presence of adults also affects larval settlement (Desroy, Oliver & Retière 1997). The larvae can move hundreds of millimetres over many days to select a suitable substratum. If larvae settle on suitable sediments in the presence of adults they become re-suspended almost immediately, as a consequence of the bioturbation activities of the adults.

Studies of populations of *Pectinaria gouldii* in New Jersey, United States, revealed multiple cohorts throughout the year, with juveniles being collected from early July to October (Busch & Loveland 1975) and a life span of a year or more. They preferred fine sediments to coarse sediments and densities of 804 worms per m^2 were recorded; however, adjacent to the heated cooling waters of a power station densities of 51 160 worms per m^2 were recorded during one sampling period.

Several studies have focussed on the rate of sediment reworking. Gordon (1966) reported rates of 6 gm/day, depending on temperature, amount of organic material and availability of interstitial water in the sediment. However, Dobbs & Scholly (1986) reported far lower rates. Sediment reworking produces an unstable surface which is resuspended easily by tidal currents and may be an important factor in limiting the distribution of many suspension-feeders and sessile epifauna (Rhoads & Young 1970).

Pectinariids construct their tube by cementing individual sand grains together with a proteinaceous glue (Watson 1928). The size of the sand grains used increases as the worm grows and the shape of the tube is similar regardless of the sediment composition (Busch & Loveland 1975). Species recorded from coral reef areas may incorporate foraminiferans into their tubes (Long 1973).

All species are marine, although some have been recorded in shallow protected bays where salinities may fall after heavy rain. The deepest depth to which they have been recorded is over 2000 m. Busch & Loveland (1975) reported that *Pectinaria gouldii* is preyed upon by a variety of fish and may be an important dietary component for some species.

A fossilised pectinariid tube has been recorded from Japan (Katto 1976).

The Australian species exhibit a variety of geographical distributions (Hutchings & Peart in preparation). One species is widely distributed around Australia, several others are restricted to the east coast and one species is found only in West Australia and Queensland. All Australian species appear to be endemic.

Family Poeobiidae

Poeobiids have a sac-like gelatinous body without external segmentation or chaetae (Fig. 1.119A). The head bears a circlet of eversible branchiae. They are pelagic and, to date, only one species has been described.

The prostomium is truncate and retractable (Fig. 1.119B, C). The peristomium is assumed to be reduced, but Rouse & Pleijel (in press) suggest that there is no evidence to support this concept. There are no antennae. The paired, grooved peristomial palps are located dorso-laterally to the mouth. Nuchal organs are present. The arrangement of longitudinal muscles is unknown; segmentation is indistinct, and two septa divide the body into three coelomic pockets (Robbins 1965). All parapodial structures are lacking. Five to seven pairs of eversible branchiae occur at the anterior end (Fig. 1.119); these branchiae appear similar to those present in flabelligerids (Robbins 1965). Epidermal papillae of the flabelligerid type are present. A ventral, eversible buccal organ is present and the gut is folded. A gular membrane is apparently present. Lateral organs and dorsal cirrus organs have not been observed. The excretory organs are metanephridia, and the segmental organs are possibly mixonephridia. A single pair of nephridia is present anteriorly; opening in front of the branchiae (Robbins 1965). A pair of gonoducts is present. The circulatory system is closed and a heart body is present. No chaetae, or aciculae, are present. This definition is based on that of Fauchald & Rouse (1997).

The family was erected by Heath (1930) for the sole species, *Poeobius meseres* collected off Monterey Bay, California in the water column at a depth of 350 m. Since then no additional species have been described, although the type species has been recorded several times. Later, Robbins (1965) indicated that the species has been recorded from depths of 350–1300 m, off the coast of Southern California in cold waters.

Robbins (1965) summarised the history of classification of the family, providing details of the affinities of this group with either the Polychaeta or the Echiura. Heath (1930) considered that the family represented a link between the Annelida and the Echiura, and Newby (1940) and Dawydoff (in Grassé 1959) placed the Poeobiidae within the Echiura. Remane

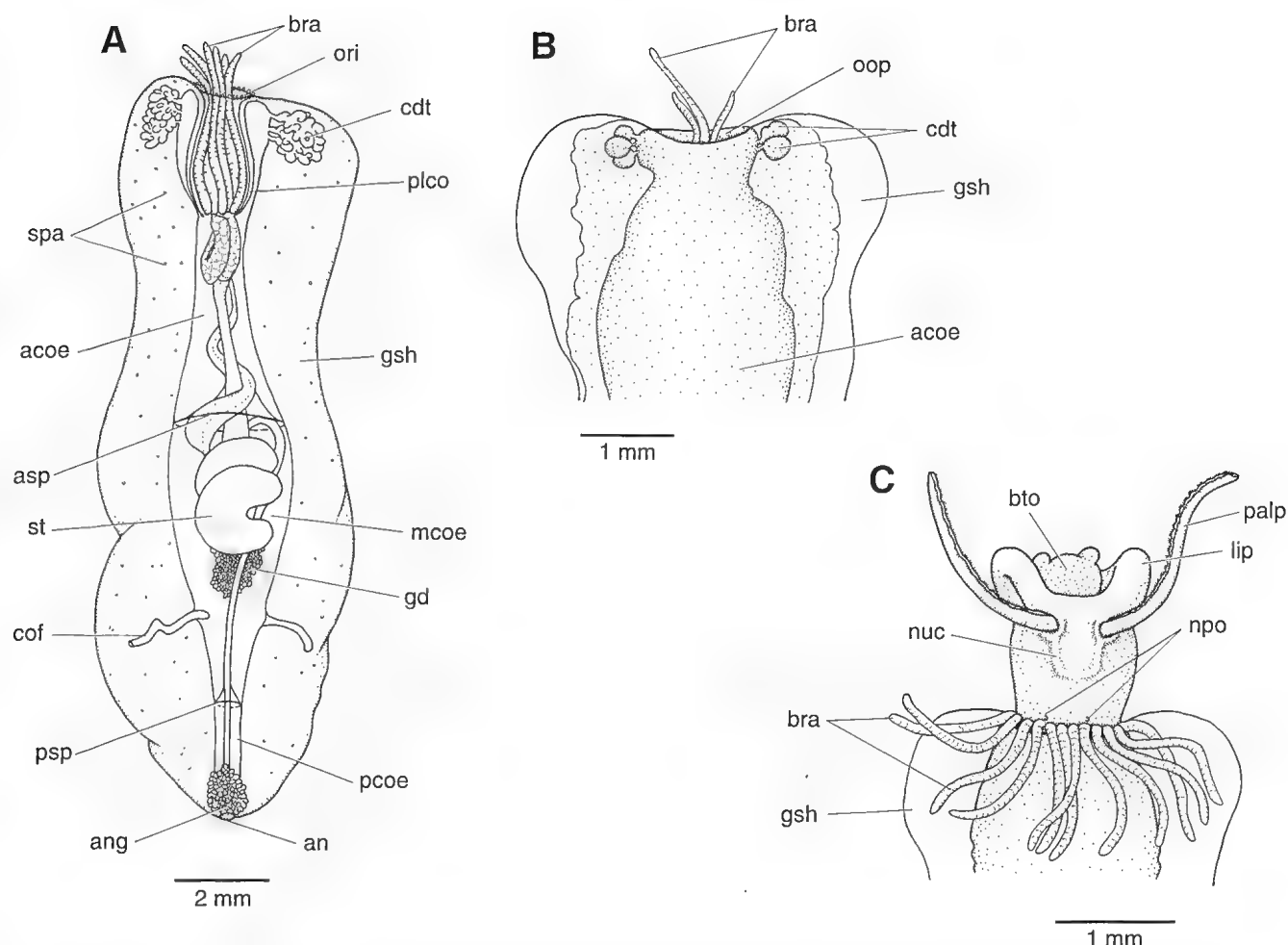


Figure 1.119 Family Poeobiidae. *Poeobius meseres*. **A**, entire animal, dorso-lateral view. **B**, anterior end with head retracted, lateral view. **C**, anterior end with head everted, dorsal view. **an**, anus; **ang**, anal gland; **asp**, anterior septum; **bra**, branchiae; **bto**, buccal 'tongue'; **cdt**, coelomic diverticula; **cof**, coelomic funnel; **gd**, gonad; **gsh**, gelatinous sheath; **lip**, lips; **mcoe**, middle coelom; **npo**, nephridial pores; **nuc**, nuchal organ; **oop**, oral opening; **ori**, oral ring; **palp**, palp; **pcoe**, posterior coelom; **plco**, palpal coelom; **psp**, posterior septum; **spa**, sensory papillae; **st**, stomach. (After Robbins 1965) [A. Murray]

(1933b) and Bock (1942) retained the group in the polychaetes. Pickard (1947) also suggested that they were closer to the polychaetes than echiurans, albeit rather aberrant. Hartman (1955) described the morphology of the head region and decided that they were polychaetes, most closely related to Flabelligeridae. This view is supported by the cladistic analysis of Fauchald & Rouse (1997) which placed them well within the polychaete clade. The difficulty in classifying these animals is well illustrated in Figure 1.119A; superficially at least, these animals do not resemble polychaetes.

Rouse & Fauchald (1997) placed Poeobiidae within the Terebellida, a group that also contains the family Flabelligeridae (Fig. 1.110).

Poeobius meseres has been recorded from the Subarctic water mass, the transitional waters of the California current (McGowan 1960) and from the eastern tropical Pacific and the Gulf of Alaska (Berkeley & Berkeley 1960). Robbins (1965) indicated that the species is common in midwater collections off Southern California. The family has not been recorded from Australian waters, although it should be noted that no work has been undertaken on Australian pelagic polychaete species. The family is probably far more widespread than appears from the literature; it is highly modified morphologically and may have been mis-identified by plankton sorters.

Poeobius meseres can be collected using an Isaacs-Kidd midwater trawl in depths of 350–1300 m. The use of such trawls is to be preferred to using plankton nets where many other organisms tend to become enmeshed in the gelatinous sheath of the poeobiids. The species does not appear to migrate diurnally within the water column (Childress & Thuesen 1993).

The body is sac-like and lacks external segmentation or chaetae. Based on the figures provided by Robbins (1965), the species is about 36 mm in length and 6 mm in width. The head is indistinct. The entire body is encased in a gelatinous sheath, which is covered by a hypodermal or cuticle layer; sensory papillae are scattered throughout the anterior and posterior regions of the sheath. Numerous granular protuberances of the cuticle occur on the rim of the oral ring (Fig. 1.119A). The subterminal mouth bears a pair of grooved palps and a highly mobile, eversible buccal organ. The five to seven pairs of eversible branchiae are sparsely ciliated and contain a vascular loop which arises as a ramification of the bifurcation of the dorsal vessel as it enters the anterior end. It is presumed that the five to seven pairs of branchiae are the main sites for the exchange of oxygen, and the anal region, which is highly muscular and vascularised, may also be important for respiration. The blood pigment appears to be chlorocruorin which changes in colour from green to red with increasing concentration (Robbins 1965).

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The coelomic cavity is divided into an anterior, middle and posterior coelom by two septa. The anterior coelom extends throughout the head region and posteriorly to the first septum, which lies between the ventral nerve ganglia five and six. This coelom communicates with the exterior through nephridia. The middle coelom extends to the second septum situated between ventral nerve ganglia nine and ten, and is connected to the exterior by coelomic funnels. The posterior coelom extends from the second septum to the rectum and does not have a connection to the exterior. Robbins (1965) listed the major organs of each coelom; there is no serial duplication of organs within them. Movement of all organs attached to the septa, including body wall musculature, gut and major blood vessels, distorts the septa and causes circulation of the coelomic fluid. Coelomocytes are found in all three coeloms as well as within muscle layers, in the epidermis of the head, and the coelom of the palps. The cytoplasm of these cells is filled with coarse yellow-brown granules and, as they are often closely associated with the nephridia, it seems likely that they function in excretion.

The anterior coelom has six to eight sac-like extensions located at the anterior-most portion of the gelatinous sheath, in both dorsal and ventral positions. Each diverticulum (Fig. 1.119B) protrudes between the muscle layers into the sheath, where it branches and terminates in a number of closed sacs. The diverticula are most conspicuous in ripe individuals, when they are either filled with masses of sperm or three to five eggs. Robbins (1965) made no suggestion as to the function of these diverticula.

The single pair of nephridia lies dorsally in the anterior coelom just behind the head. Each one communicates to the exterior via an elevated nephridiopore situated just anterior to the branchiae. These appear to function solely for excretion. Gametes are released through a pair of lateral coelomic funnels present in the middle coelom near the gonad. The funnels are lined with non-ciliated coelomic mesothelium. The sexes in poeobiids are separate. Robbins (1965) suggested that the gametes are moved along these funnels by activity of the body wall musculature and the resultant changes in hydrostatic pressure of the coelomic fluid.

Gametes are proliferated from the single gonad and released into the coelom where they complete their development. Mature individuals appear greatly distended with gametes. In southern California breeding appears to take place during the winter months. Ripe oocytes are bright yellow and about 160 µm in diameter at maturity. Mature spermatozoa appear to be of the primitive type as defined by Franzén (1956) and are referred as aquasperm by Jamieson & Rouse (1989). Fertilisation has been achieved in the laboratory, but development was aborted after the first two cleavages (Robbins 1965) and no additional studies have been carried out.

Poeobiids have a brain, circum-oesophageal connectives, suboesophageal ganglia and a fused double ventral nerve cord with nine ganglia, various nerves and epidermal sense organs. The brain is bilobed, comprising two masses of cells which project ventrally and are joined by connectives. Three main nerves arise from the brain, two of which innervate the nuchal organ and the palps; the third extends posteriorly. The nuchal organ is situated dorsally on the head and consists of a pair of ciliated ridges which surround the bases of the palps. Robbins (1965) found that the nuchal organs consisted of supporting cells interspersed with glandular cells and strongly ciliated cells, resembling closely the structure of those in other polychaetes.

Poeobiids are ciliary mucus-feeders, whereby particles are trapped on the palpi by mucus secreted by the glandular cells on the eversible buccal pad. They feed on diatoms, radiolarians, planktonic foraminiferans and algae (Robbins 1965). In life, the eversible buccal pad is held out and appears to undulate, presumably assisting the trapping of food particles on the pad. More recently, Uttal & Buck (1996) studied the diet of *Poeobius meseres*.

The alimentary canal consists of an oesophagus with heavily folded walls and a coiled stomach where digestion occurs (Fig. 1.119A). The intestine has a strongly ciliated groove which appears to facilitate the movement of faecal pellets to the anus. A digenean trematode was found attached to the gut wall in one specimen by Robbins (1965).

Much remains to be investigated concerning the distribution and ecology of poeobiids. Childress & Thuesen (1993) found that increasing pressure did not appear to have an effect on the metabolic rates of poeobiids. This suggests that deeper living gelatinous zooplankton have higher rates than would be expected from studies on fish and crustaceans in the same habitats; therefore this group (including poeobiids) may be more important in the carbon budget at greater depths than previously suspected.

Family Sternaspidae

Sternaspids are easily recognised by their short swollen bodies, consisting of a few segments (Fig. 1.120A). The posterior segments are fused to form a reddish, ventral sclerotinised plate, which is surrounded by chaetae.

The prostomium is distinct and truncate anteriorly, and the peristomium is reduced to lips around the mouth. Antennae and palps are absent; nuchal organs are also lacking (but see Dahl 1955). Longitudinal muscles are grouped in many bands, and segmentation is distinct. The first segment is similar to those behind, and bears similar chaetae. The whole of the anterior part of the body is retractable. Several segments of the posterior venter are covered by a sclerotinised shield. The parapodia are biramous except at the posterior end. Only notopodia are present in the posterior region covered by the shield, and consist of very short, truncate cylinders (Fig. 1.120A). Rami are short, barely raised papillae. Dorsal and ventral cirri are absent. The simple branchiae are situated posteriorly and dorsally. Epidermal papillae similar to flabelligerid papillae are present. Pygidial cirri are absent. There is an eversible axial sac-like pharynx and the gut is folded. A gular membrane is lacking. The segmental organs are mixonephridia, of which the anteriormost pair is excretory, and the posterior pair are gonoducts (Goodrich 1945). The circulatory system is closed, and a heart body is lacking (Vejdovsky 1882). Aciculae are absent. Chaetae consist of capillaries and heavy spines (Fig. 1.120B–D). This definition is based upon that of Fauchald & Rouse (1997).

The sternaspids were initially considered to be related to the echiurans (Blainville 1828) and were included in *Gephyrea armata* (Quatrefages 1866; Appendix B of Fauchald & Rouse 1997). Superficially, sternaspids do not resemble other polychaetes and they have been difficult to relate to other polychaetes; some authors place them as an 'isolated group'. Most often they have been grouped tentatively with other polychaetes which have few anterior appendages and simple, capillary chaetae and spines. Levinsen (1883) considered them a separate order. Hatschek (1893) related them to the drilomorph families, and Benham (1896) treated them as one of the scolecimorph families. More recently, they have been

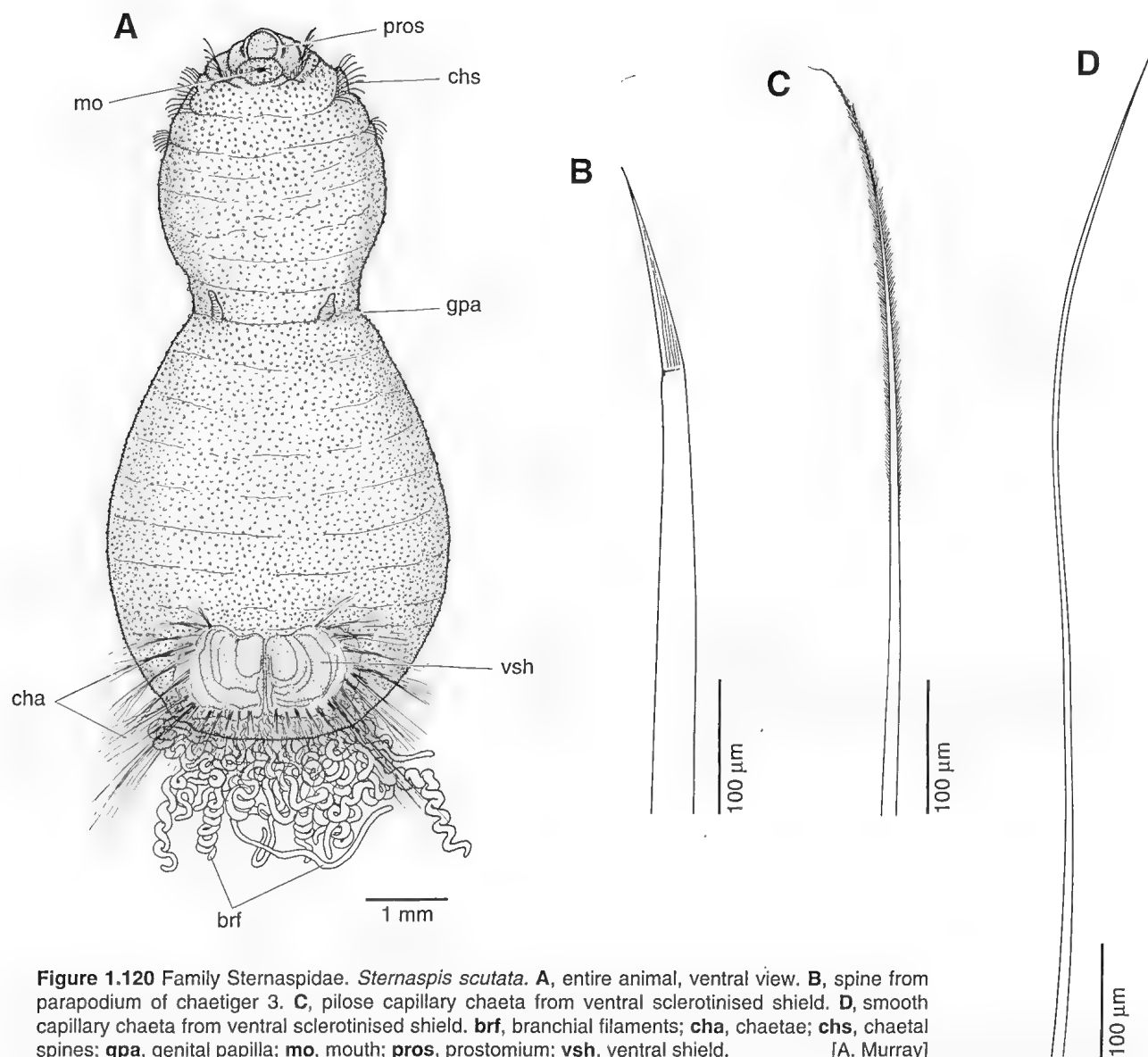


Figure 1.120 Family Sternaspidae. *Sternaspis scutata*. **A**, entire animal, ventral view. **B**, spine from parapodium of chaetiger 3. **C**, pilose capillary chaeta from ventral sclerotinised shield. **D**, smooth capillary chaeta from ventral sclerotinised shield. **brf**, branchial filaments; **cha**, chaetae; **chs**, chaetal spines; **gpa**, genital papilla; **mo**, mouth; **pros**, prostomium; **vsh**, ventral shield. [A. Murray]

considered a member of the Drilomorpha (Uschakov 1955) and as a separate order (Dales 1963a; Fauchald 1977; George in George & Hartmann-Schröder 1985), as summarised by Fauchald & Rouse (1997). The primary references for this group are Vejdovsky (1882) and Goodrich (1898). The family Sternaspidae has recently been placed in the order Terebellida by Rouse & Fauchald (1997).

Sternaspidae comprise a single genus, *Sternaspis*, in which about 12 species are recognised (Fauchald 1977). In Australia, one species, *Sternaspis scutata*, has been recorded off the South Australian coast (Benham 1916); in Moreton Bay, Queensland (Stephenson *et al.* 1974) and; Calliope River and Auckland Creek, near Gladstone, Queensland (Saenger *et al.* 1980). Unpublished records from the Australian Museum database indicate that a species of *Sternaspis* occurs at Sandy Cape, Rottnest Island, Western Australia.

Sternaspids occur in sandy and muddy substrata in all depths, but are usually found in depths of 100–200 m, rarely in large numbers (Fauchald 1977). They are easily recognised in sediment samples by their characteristic dark yellow to reddish chitinated shield. No studies have documented the distribution of species, although the type species, *S. scutata*, (Renier 1807) has been reported as being cosmopolitan from the Arctic to the Antarctic in shallow to great depths (Day 1967); in reality several species may be present.

Sternaspids have a short, swollen body, are often ovoid or dumb-bell shaped and comprise few segments. The anterior end consists of a small prostomium, which can be retracted (Vejdovsky 1882), an eversible pharynx, a peristomium reduced to lips around the mouth (Goodrich 1898) and the first three segments bear rows of acicular chaetae (Fig. 1.120A, B). Two bundles of minute chaetae are embedded in the body wall in each of the following eight segments. The posterior end is covered by a stiff, chitinated and mineral-impregnated shield bearing radiating bundles of capillary chaetae on its margin (Fig. 1.120A). Numerous filiform branchiae arise from two postero-dorsal plaques at the base of the shield and these may be rolled into spirals.

Sternaspids are deposit-feeders. According to Dales (1963a) they lie head-down just under the surface of the mud, with the branchiae on the sediment surface presumably to enhance oxygen exchange. In these animals the septa have mostly broken down and the gut is greatly coiled, presumably to maximise adsorption of nutrients. The gut retains its connection to the body wall *via* the dorsal and ventral mesenteries and by septal muscle fibres (Dales 1963a). The simple, eversible, axial pharynx is presumably used to scoop up the sediment.

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Dahl (1955) was unable to find a nuchal organ in sternaspids. However, Rouse & Fauchald (1997) suggested that the anteriorly located upper lip nerve represents a remnant nuchal organ. Dahl (1955) suggested that the cuticular papillae are sensory, and the only sensory structures present.

Dales (1963a) stated that *Sternaspis* has special copulatory appendages (but gave no further information); these are probably the genital papillae (Fig. 1.120A). Some information on life cycles of sternaspids is given by Childs (1900) and Vejdovsky (1882). Information on reproduction in sternaspids is fragmentary. Studies include the structure of the oocyte immediately after release but prior to fertilisation (Villa 1976) and the structure of the mature oocytes before release (Notarbartalo 1970).

Family Terebellidae

The Terebellidae are an abundant and species-rich family of often large and conspicuous marine worms (Pls 9.1–9.4). Typically, they have a robust body with a large number of buccal tentacles and branched or simple branchiae (Fig. 1.121A). They are generally tubiculous, but some live naked in the sediment; naked species lack branchiae and have an expanded tentacular membrane.

The Terebellidae have a reduced prostomium which is fused along its posterior edge to the peristomium. The peristomium is also fused with the first anterior body segment, and projects forward beneath the prostomium as an extended upper lip. Palps are usually present as numerous (buccal) tentacles, which emerge at the point of fusion between the peristomium and the prostomium (Fig. 1.121A). Nuchal organs are usually present, and the longitudinal muscles form bands. Segmentation is typically distinct. The first segment, fused to the head, has no parapodia or chaetae. Parapodia are typically biramous; they are lacking in some species (for example, *Hauchiella* species). The notopodia are cylindrical, either slender or truncate, and are often restricted to the anterior segments of the body. Neuropodia are present as tori or may be absent. Branchiae, if present, are dorsal and situated only on a few anterior segments. Epidermal papillae and pygidial cirri are absent. There is a non-eversible ventral buccal organ (Sutton 1957). Mixonephridia are present in each segment; anteriorly, these ones function as excretory organs and the posterior ones are used as gonoducts. Chaetae are present as a variety of ornamented capillaries and uncini (Fig. 1.121H–U); they are rarely absent. Aciculae are absent. The diagnosis is based largely on Rouse & Fauchald (1997).

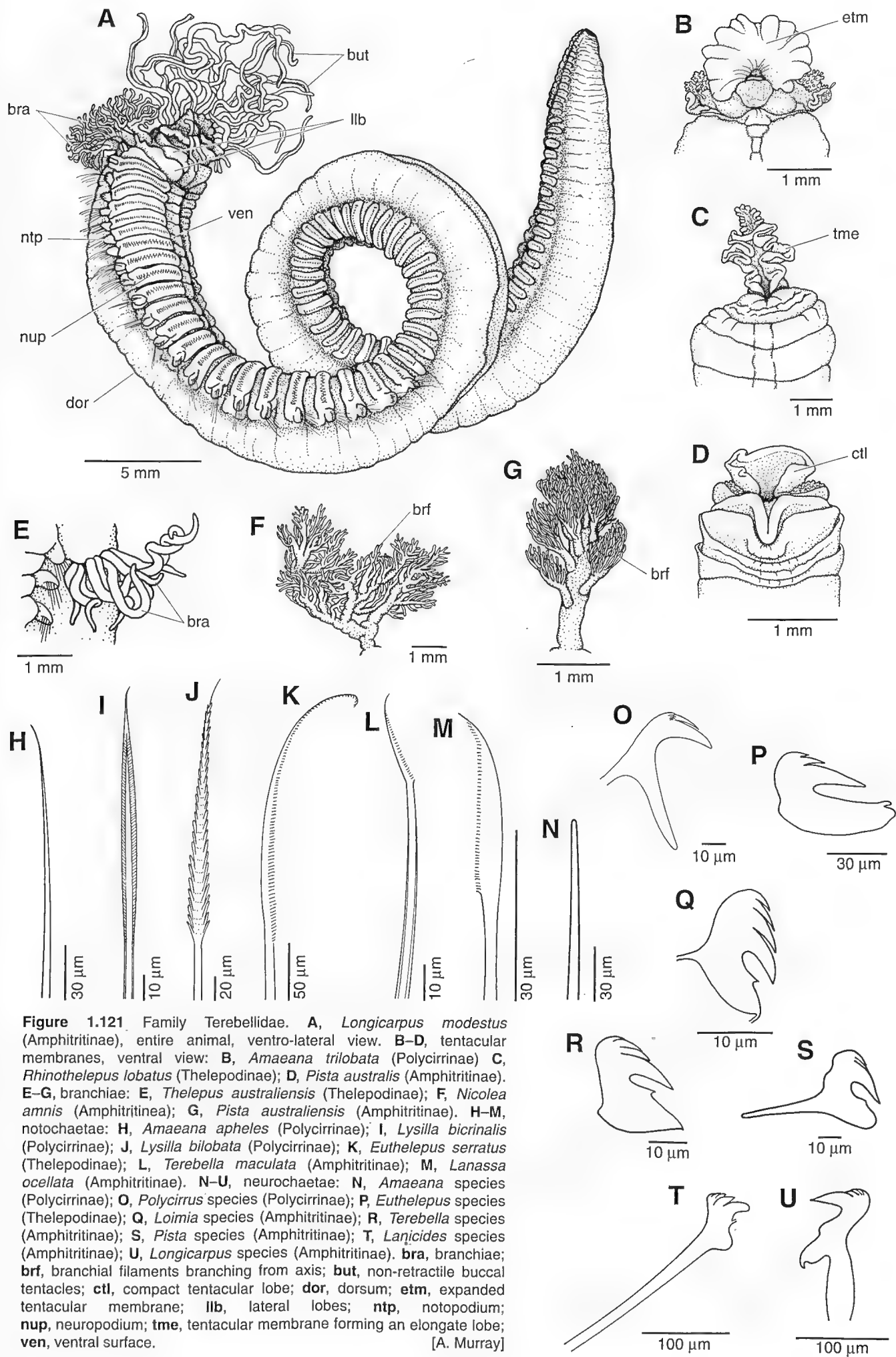
The family Terebellidae was originally defined by Grube (1851) as the Terebellacea and was revised by Malmgren (1867). The first terebellids were described by Müller in 1776; the family was recognised early on, under the name Amphitritae based on the genus *Amphitrite*. The family originally included the ampharetids and pectinariids, but Malmgren (1867) removed them and they are now treated as separate families within the Terebellida. The Terebellidae were divided into four subfamilies, but only three (Polycirrinae, Thelepodinae, Amphitritinae) are recognised here. The two genera of the fourth subfamily, Artacaminae, have been split between Amphitritinae and Trichobranchidae; *Artacamella* was transferred to the Trichobranchidae by Holthe (1977), and Hutchings (1977) and subsequently McHugh (1995) considered that *Artacama* would be better placed in the Amphitritinae. Fauchald & Rouse (1997), however, appear to have inadvertently accepted Artacaminae as a subfamily of the Terebellidae. The Trichobranchidae was recognised by Malmgren (1867) as a subfamily of

Terebellidae, but Hessle (1917), who redefined Terebellidae, elevated the trichobranchids to familial status. Some workers, including Day (1967), however, still regarded trichobranchids as a subfamily of Terebellidae. Hessle (1917) revised and proposed a classification of the family on the basis of the structure and distribution of nephridia; this treatment was not generally adopted. Later significant studies include works on larvae by Heimler (1983), a review of the classification by Holthe (1986b), and a phylogenetic analysis of the Amphitritinae by McHugh (1995).

Members of the subfamily Polycirrinae are often brightly coloured worms that live naked in sediments, or in mucous tubes. They have an expanded, highly mobile/flexible tentacular membrane (actually the expanded dorsal portion of the prostomium fused with the peristomium) with a large number of buccal tentacles, of two types: some of uniform thickness, others with expanded globular tips (Fig. 1.121B). The body is often poorly segmented, and both an inflated thorax and midventral glandular pads are absent; although the anterior latero-ventral surface is glandular and often tessellated. Branchiae are absent. Notopodia are usually present; they are elongate and often have ornamented chaetae (Fig. 1.121J). Neuropodia are either present or absent; if present they have either avicular or acicular chaetae (Fig. 1.121N, O). Chaetae are absent in *Hauchiella* species (as are parapodia), and *Biremis* species have only neurochaetae. *Enoplobranchus* species have elongate notopodial lobes, which are furcate and heavily vascularised. Nephridia often have prominent nephridial papillae and are often visible through the body wall. Hutchings & Glasby (1986b) reviewed the Australian Polycirrinae. Common species are *Amaeana trilobata* and *Lysilla apheles*. The genus *Polycirrus* is currently being revised by Glasby & Hutchings (in preparation) and contains additional Australian species.

Thelepodines are tubiculous species, often with a robust tube. They have an expanded or non-expanded tentacular membrane, with buccal tentacles of one type and of uniform thickness (Fig. 1.121C). The body is robust and has typically well-demarcated segments. The distinction between thorax and abdomen is often unclear externally as notopodia may continue for many segments. Branchiae are present as simple unbranched filaments which arise directly from the body wall, typically on segments 2 to 4 (Fig. 1.121E). Ventral pads may be discrete on anterior segments, but often the entire venter is glandular. Notopodia have either smooth-tipped capillary or serrated-tipped capillary chaetae as in *Euthelepus* species (Fig. 1.121K; Hutchings & Glasby 1986b). Neurochaetae are avicular with elongate bases (Fig. 1.121P). Australian examples are: *Rhinothelepus* species, which are common in seagrass beds along the eastern coast; *Thelepus extensus* and *T. australiensis* which are common in southern waters, and; *T. robustus* which is common in northern waters. All these species occur in shallow subtidal environments often associated with seagrass beds.

Amphitritine species are typically tubiculous, often with robust tubes. The tentacular membrane is compact (Fig. 1.121D) and has buccal tentacles of one type, all of uniform thickness. The body is often robust with well-demarcated segments, but some species, especially those within abbranchiate genera, may be very small and have poorly developed segmentation. The thorax and abdomen are usually well demarcated. Branchiae are either present or absent; if present, they are usually stalked, branched and arranged in pairs on anterior segments (Fig. 1.121F, G). Notochaetae are present as variable numbers of pairs; their structure and ornamentation varies (Fig. 1.121L, M). Neurochaetae typically continue along the body almost to the pygidium, and



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are present as long-handled and/or short-handled uncini (Fig. 1.121Q–U). The structure of both notochaetae and neurochaetae may also vary along the body. Ventral pads are well developed. Lateral lobes and expansion of the peristomium are present in many genera. Nephridial papillae are often conspicuous. Examples of Australian species are: *Loimia ingens*, a large, conspicuous species found widely in Australian waters; *Reteterebella queenslandia*, which is common on the Great Barrier Reef, although all that is visible are its long buccal tentacles spread out over the reef (Fig. 1.32); *Terebella pappus*, which is common throughout southern Australia, but it is replaced by *Terebella tantabiddycreekensis* in northern Australia; *Nicolea amnis*, which seems to occur throughout coastal Australian waters. *Pista australis*, a very distinctive species with bottle brush-like branchiae, is found in southern Australia.

Characters used to distinguish species are the structure and distribution of chaetae, structure of branchiae if present, structure of the head (peristomium and prostomium), and the structure and distribution of lateral lobes if present. Some genera appear more conservative than others and increasingly when a range of material is examined some variation in these characters is apparent. In the Polycirrinae, which lack many terebellid features, defining species may be more difficult. This is certainly true of species of *Hauchiella* which lack branchiae, parapodia and chaetae.

Worldwide, the Terebellidae comprise 61 described genera and 452 species. Of the 61 genera, 26 are known only from the type species. They live in a wide range of habitats, but are not well represented in environments with fluctuating salinities. In Australia, extensive revisions of the family have been undertaken (see Hutchings & Glasby 1986a, 1986b, 1987, 1988; Hutchings 1990, 1997a, 1997b) and currently 32 genera comprising 110 species are known in the three subfamilies: 29 species of Polycirrinae, 55 species of Amphitritinae and 26 species of Thelepodinae. Of the 32 genera, seven are known only from Australia, (five genera of Amphitritinae and two Thelepodinae). Australia and New Zealand have about 20 terebellid genera in common, but at present it is not clear how many species are shared between the regions (C. Glasby personal communication). Similarly, some genera which occur in Australia have also been recorded from South-East Asia, but so far, no Australian species of those genera have been recorded from South-East Asia. Although the diversity of Australian terebellids appears high when compared with that in other regions of the world, it may be a reflection of the numerous studies undertaken on the Australian fauna and the lack of similar studies elsewhere. Other regions may well have a similar diversity, but have, as yet, not been investigated. Certainly, the Antarctic is reported to have a high diversity (Hartman 1966a; P. Hutchings unpublished data).

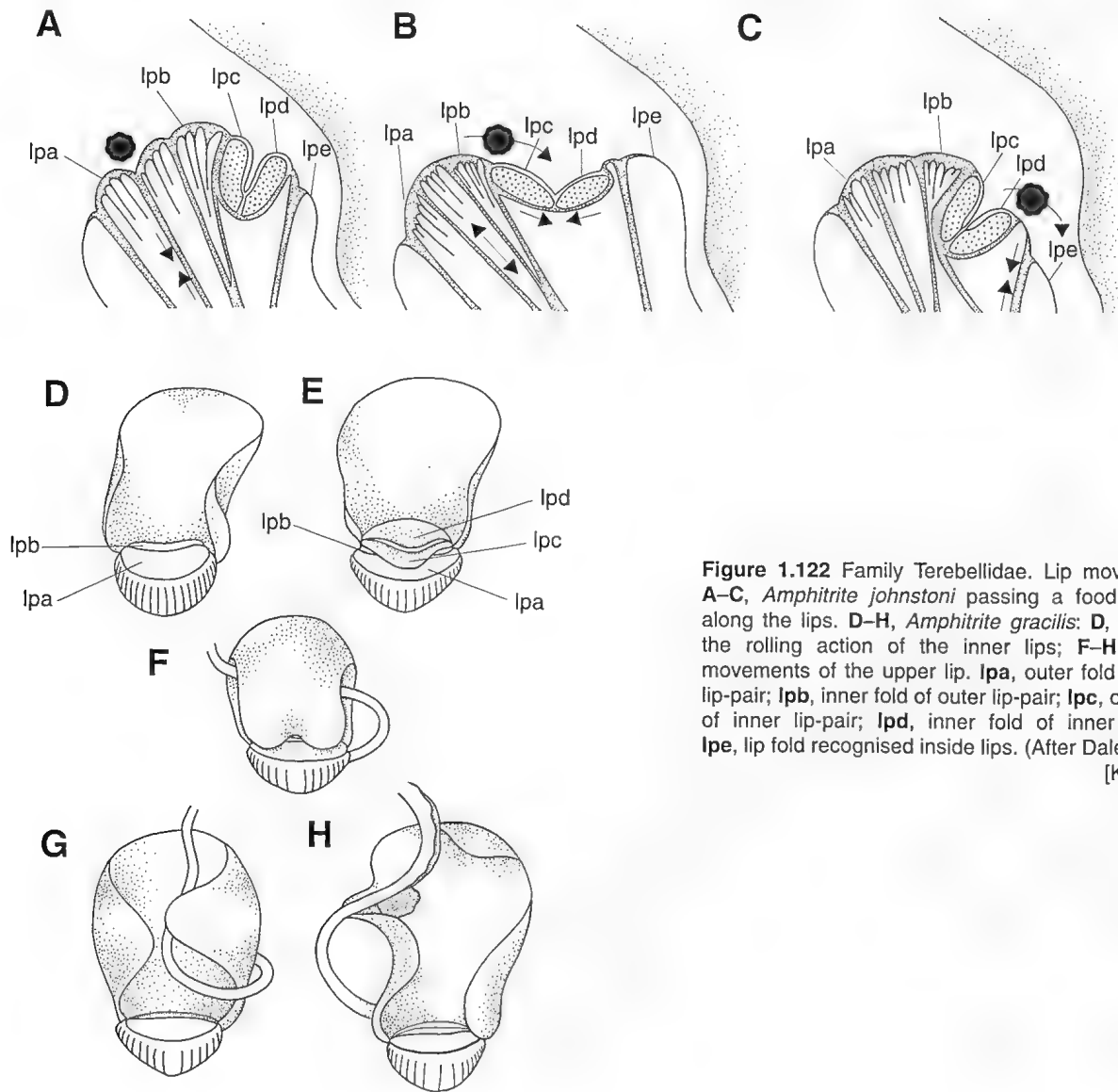


Figure 1.122 Family Terebellidae. Lip movements. A–C, *Amphitrite johnstoni* passing a food particle along the lips. D–H, *Amphitrite gracilis*: D, E, show the rolling action of the inner lips; F–H, typical movements of the upper lip. lpa, outer fold of outer lip-pair; lpb, inner fold of outer lip-pair; lpc, outer fold of inner lip-pair; lpd, inner fold of inner lip-pair; lpe, lip fold recognised inside lips. (After Dales 1955) [K. Nolan]

In Australia, terebellids are found from the intertidal zone to deep water, living in a variety of fine sediments and habitats such as algal holdfasts, deeply embedded within coral reefs, in seagrass beds and amongst pneumatophores of mangroves. Of the tubiculous species, some live upright within the sediment (for example, *Loimia ingens*), but many others, for example, *Thelepus robustus*, cement their tube to the undersurface of rocks or boulders. Others live naked within the sediment, for example, *Polycirrus rosea* and *Amaeana trilobata*. Some species, such as *Hadrachaeta aspeta*, occur as single individuals, whereas others such as *Thelepus robustus* are gregarious with numerous individuals cemented to the underside of a single boulder. Some terebellids, such as *Nicolea amnis*, may occur all around Australia, whereas others, such as *Terebella maculata*, found in the waters of north-western Australia, have a very restricted distribution. *Terebella tantabidycreekensis* and *Thelepus robustus* live in tropical waters, whereas *Terebella pappus* and *Thelepus extensus* are found in southern Australia.

Terebellids have a distinct head and tail region. They usually have a large number of segments which continue to increase in number with increasing size of the animal; over 200 segments can be present in large worms. They range in size from 1–2 mm to 300 mm in length; many of the abbranchiate amphitritines are small. The demarcation between thorax and abdomen varies from well-defined to very indistinct; it is well-defined when notochaetae are restricted to the anterior thoracic segments. Large numbers of non-retractile buccal tentacles are present, and in life the various head structures and lateral lobes are highly mobile.

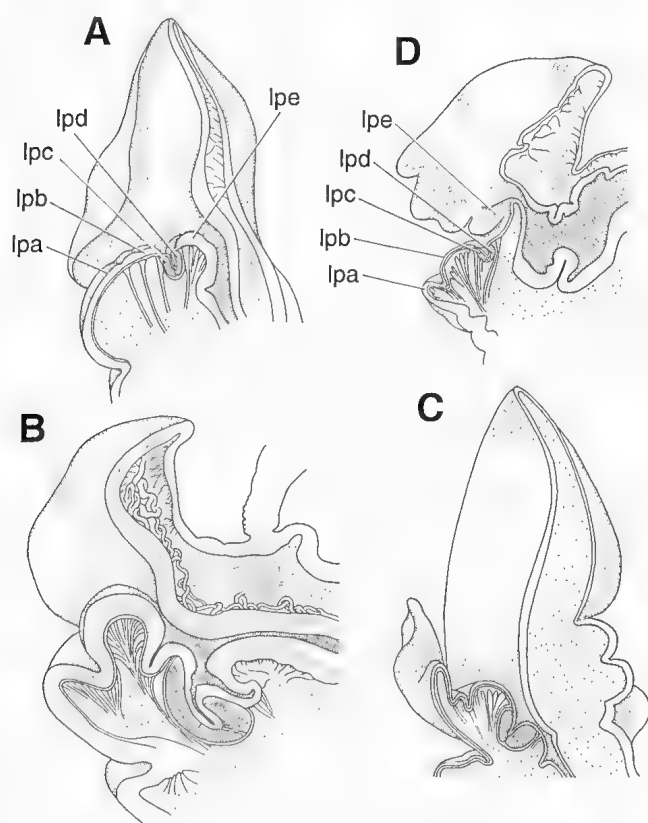


Figure 1.123 Families Terebellidae and Trichobranchidae. Comparison of lip structure. **A–C**, Terebellidae: **A**, *Polycirrus aurantiacus*; **B**, *Amphitrite johnstoni*; **C**, *Lanice conchilega*. **D**, Trichobranchidae, *Terebellides stroemii*. **lpa**, outer fold of outer lip-pair; **lpb**, inner fold of outer lip-pair; **lpc**, outer fold of inner lip-pair; **lpd**, inner fold of inner lip-pair; **lpe**, lip fold recognised inside lpd. (After Dales 1955a)

[K. Nolan]

Parapodia are biramous and are without aciculae. Notopodia are usually cylindrical in shape, inserted dorso-laterally and mobile; a number of capillary chaetae are present. Neuropodia are present as glandular tori which are sessile or form pinnules; if present they typically extend to the pygidium, and are inserted ventro-laterally. The shape and length of neuropodia change along the body. Neurochaetae are usually arranged in single rows, but may be present in double rows in the posterior thorax of some amphitritines. Chaetal form often varies along the body. Also, neurochaetae change in form from juveniles to adults, thus making juvenile specimens often difficult to identify; such changes in the structure of neurochaetae has been shown to occur within species of *Loimia* (Hutchings & Glasby 1988). It also appears that the number and/or size of branchial filaments may increase with age or at least size of the worm; this may also be influenced by habitat. Branchiae are often missing from specimens when collected and it has been suggested that they may be eaten by predators. Certainly branchiae can be regenerated (Hutchings & Glasby 1987).

Terebellids have longitudinal muscle bands (Storch 1968). They may have either a firm muscular body wall, such as in many amphitritines, or a flaccid body such as in species of *Polycirrus*. A gular membrane is present (Hessle 1917; Sutton 1957) between two successive anterior segments and consists of a muscularised septum.

The epidermis, which lies on a thin fibrous extracellular layer, is a monolayered epithelium consisting of supportive, ciliary, secretory and sensory cells covered by a cuticle. Supportive cells vary in shape within the Polychaeta and in the terebellid *Lanice conchilega* they are very long and may reach up to 70 μm in some parts of the body. Storch (1988) provided a schematic representation of the epidermis and investigated the cuticle of *L. conchilega*. In the cuticle, collagen is not laid down regularly as typically found in polychaetes, but is up to 10 μm thick. The secretory cells play an important role in tube building. Bielakoff, Damas & Vovelle (1975) have studied tube construction in *L. conchilega* in terms of the histology and histochemistry of secretions. They found that as many as 14 types of glandular cells in the adult are responsible for providing secretions for tube construction. Some terebellid larvae, for example those of *L. conchilega*, construct tubes, and Tiberi & Vovelle (1975) found that the dorsal gland of *L. conchilega* was the main site responsible for the secretions used in tube building.

The buccal tentacles of several species of *Polycirrus* are luminescent. The luminescence is produced within the mucus secreted by groups of glandular cells which occur along the length of the tentacles (Harant & Grassé 1959). The chemical processes involved have not been investigated. Luminescence can be initiated when the animal is disturbed.

Terebellids are usually either sedentary and tubiculous or live naked in the sediments, but some worms are capable of swimming. For example, the deep-sea species *Biremis blandi*, which has been recorded from depths of 600 m, has been observed, from a submersible, swimming with poorly coordinated 'wriggles' of its body. Also tubiculous species when removed from their tubes often actively swim up into the water column in a sinusoidal fashion; presumably this is not typical behaviour.

Terebellids are selective surface deposit-feeders (Dales 1955a; Fauchald & Jumars 1979). The numerous grooved buccal tentacles (sometimes referred to as feeding tentacles), which are highly extensile, extend over the surface of the sediment. Once extended the epithelium of the tentacles along the groove secretes a fine layer of mucus. Movement of the

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fine cilia along the margins of the tentacles creates water currents which disturb fine surface particles; the particles adhere to the mucus. The cilia beat towards the mouth and small bundles of mucus-coated sediment are moved along the grooves of the tentacles to the mouth by contractions of the tentacular muscles. The sediment packages, including very small particles such as diatoms, are passed to the lips (a highly mobile upper lip and two pairs of smaller lips beneath the mouth). The food particles are rolled across the lips by serial contractions, which causes the lip surface to ripple (Dales 1955a). Once particles reach the lower lips they are either rolled into the mouth or are rolled off onto the outer lip and discarded (Fig. 1.222). Dales (1955a) studied the variation in lip structures of a number of terebellids (Fig. 1.223) and discussed the relationship of the various structures to the species feeding style or habit; he also illustrated the feeding behaviour in terebellids.

Meyer (1887) suggested that the movement of the highly extensile tentacles was controlled by four conical pouches on the gular membrane and that fluid from these sacs was forced into the tentacles. Dales (1955a), however, showed that even if this anterior coelom was opened the tentacles were still highly mobile, and he suggested that most of the extension of the tentacles is due to ciliary creeping. The tentacles roll over and open out the ciliary groove to present a flat ciliated surface to the substratum and then 'crawl' along rather like a planarian. The tentacles have a complicated musculature that consists of transverse and oblique muscles that are responsible for the curling and rolling movements of the tentacles, and individual muscle fibres situated towards the edges of the groove cause the rippling and squeezing movements of the groove edges.

The morphology of the alimentary canal of a number of terebellids was illustrated by Wirén (1885). The mouth leads into a long narrow oesophagus which opens into a wide thin-walled fore-stomach, followed by a hind stomach, which has a well-developed muscle layer (see Dales 1955a for more information). Transport of material along the gut is thought to be mainly by muscular action (Dales 1955a). The pH of the oesophageal contents is distinctly lower than that of seawater, suggesting that some enzymes are secreted in the posterior end of the oesophagus, as well as in the stomach and an acid medium is maintained throughout the gut region, with the pH rising on entering the hind-intestine. Digestion is probably entirely extracellular with absorption taking place in the fore-intestine and in the anterior part of the hind-intestine (Dales 1955a).

Terebellids may play host to several symbiotic polychaetes, particularly the larger species which harbour commensal polynoids; the nature of the relationship between the two groups is unclear. Dales (1955a) also reported that the scale-worm, *Gattyana cirrosa*, lives in the tubes of *Amphitrite johnstoni*; this species moves forward in the burrow to take food from *A. johnstoni* as irrigation movements are reduced and ingestion begins.

Terebellids have a well-developed blood system, often with a conspicuous heart-body. The circulatory system has been studied by: Wirén (1885), who undertook classical morphological studies of several terebellids; Friedman & Weiss (1980), who elucidated cytoplasmic events in the synthesis and secretion of haemoglobin and the metabolism of iron in *Amphitrite ornata*, and; Mangum *et al.* (1975), who investigated the functioning of coelomic and vascular haemoglobin in three species of terebellids.

The heart body, situated within the supra-oesophageal dorsal blood vessel, is cylindrical and has a thin wall which is deeply corrugated by luminal projections (Friedman & Weiss 1980). The heart body assists the pumping of blood around the body, as does general muscular movement. The blood, which lacks blood corpuscles, has high molecular weight respiratory pigments dissolved in the plasma, typically haemoglobin. Sometimes chlorocruorin is present, as in some Australian thelepodines. Haemoglobin has also been found in coelomic cells of a number of terebellids (Mangum *et al.* 1975; Friedman & Weiss 1980). Mangum *et al.* (1975) found large differences in oxygen affinity between vascular haemoglobin and coelomic haemoglobins. The relatively high molecular weight haemoglobins dissolved in blood have a relatively low oxygen affinity and transport oxygen primarily to coelomic fluid rather than deep tissue. In contrast, the haemoglobins present in the coelomic cells have a high oxygen affinity. The coelomic cells are responsible for 30-55% of the total oxygen consumption both at high tide, when oxygen transport is believed to be their major function, and at low tide when oxygen storage predominates. Mangum *et al.* (1975) further suggested that the major target organ of oxygen transported by the vascular system is not muscle, nerve, nephridia or other internal organs (which in fact have no muscular supply), but rather the metabolically active coelomic cells and gametes.

Branchiae, if present, are well supplied with blood as often are the lateral lobes. In the monotypic genus *Enoplobranchus*, the notopodia are elongate and vascularised. Obviously in species that lack branchiae, gas exchange must occur across the body wall, and probably does even in species with branchiae. Although many abbranchiate Amphitritinae genera include relatively small individuals, many of the polycirrine, which are also abbranchiate, are large, but typically live naked in the sediments. Perhaps in these species the expanded tentacular membrane also facilitates oxygen uptake.

According to the study of Goodrich (1945) terebellids have mixonephridia, with anterior ducts excretory and posterior ducts functioning as gonoducts. However, Smith (1988, 1992) rejected this terminology, arguing that the excretory organs are metanephridia on the basis that the ciliated funnels in at least two species of terebellids contain two distinctly different tissues; these correspond to the nephrostomial and coelomostomial components of the nephromixium as defined by Goodrich (1945). Rouse & Fauchald (1997) rejected Smith's interpretation as they are not similar to the metanephromixia of a number of other families including Syllidae and Hesionidae; more work is needed to clarify this situation. Smith (1988, 1992) provided detailed drawings of the nephromixial systems of a range of terebellid genera. He concurred with Hessle's (1917) finding that within the genus *Pista*, several types of nephromixia occur and has suggested removing several species from *Pista*. Although accepting in principle that the structure of nephromixia is a useful generic character, until more species in a wide range of genera are examined it is premature to start reorganising genera and species solely on this character. No studies appear to have been conducted on the osmoregulatory abilities of terebellids.

A number of sensory organs have been recorded for terebellids. A single pair of statocysts is present as subepidermal vesicles, which communicate with the exterior via ciliated canals (Storch & Schlötzer-Schrehardt 1988). The receptor epithelium of the statocysts is composed of supporting cells and sensory cells bearing cilia which lack rootlets; gland cells are absent (Heimler 1983). Statocysts develop, at least in *Lanice conchilega*, from epidermal invaginations of the first segment on the metatrochophore. The chemosensory nuchal organs are usually present, but

sometimes they may be indistinct; if absent, they are presumed to have been lost (Rullier 1951; Heimler 1983; Rouse & Fauchald 1997). However, this contradicts McHugh's (1995) view that they were uniformly absent in Amphitritinae and Polycirrinae. Eyespots, occur on the fused prostomium and peristomium in many terebellids; there have been no studies investigating their structure or function.

Multicellular solitary sensory cells have been recorded in the tentacular epithelium of *Lanice conchilega* (Schulte & Riehl 1976), but the function of these cells is not known; they may be related to feeding. Trochophores of *Lanice conchilega* have primary sensory cells which constitute the apical organ (Heimler 1981). The sensory cells are generally considered to be mechanoreceptor or chemoreceptor organs. These cells have a few long cilia with a 9+2 microtubule pattern and long rootlets; their axons are connected to the neuropile of the brain.

Terebellids are dioecious; asexual reproduction has not been recorded. Sexual dimorphism does not occur except just before spawning when the colour of the gametes distinguishes males from females; gravid females may be pinkish to greenish and males cream-coloured. Gametes are proliferated by patches of germinal epithelium and released into the coelomic cavity where the vitellogenic phase of oogenesis and spermatogenesis occurs (Eckelbarger 1976b).

The coelomic amoebocytes appear to play a role in nutrient storage and Eckelbarger (1976b) suggested that these nutrients provide developing oocytes with raw materials during vitellogenesis. The mechanism by which amoebocytes obtain nutrients is not known, although Dales (1957c, 1961) suggested that fat is synthesised by the cell or taken directly from body fluids. Dales (1964) found that the coelomic amoebocytes make pseudopodial contacts with the gut wall and the outer walls of blood vessels. However, no nutrient transfer from amoebocyte to oocyte has been demonstrated in terebellids.

Ripe gametes are shed from the body cavity through the reproductive nephridia. Smith (1989a, 1989b) showed that in *Lanice*, the surface of the oocytes becomes reticulated at maturity and he postulated that this 'new' surface may allow recognition of mature oocytes, which are the only ones to be shed. Bhaud (cited in Smith 1989b) has reported a similar change in oocyte surface structure in *Eupolyornia nebulosa*. Scott (1911) also suggested that the ciliated funnels of nephridia of *Amphitrite ornata* accepted only mature oocytes. All species studied undergo external fertilisation. There is no evidence of self-fertilisation, although hermaphrodites have been rarely observed (McHugh 1993). The sex ratio is typically 1:1, and terebellids appear to survive spawning. Individuals of some species may live for several years. Spawning periods vary from a discrete period of only a few days annually to a prolonged period of several months (for example, *Thelepus crispus* spawns over 6 months) to spawning throughout the year (for example, *Ramex californiensis* which produces cocoons throughout the year) (McHugh 1993). A detailed investigation of gametogenesis in *Nicolea zostericola* was undertaken by Eckelbarger (1975b); it is monotelic and spawns two to five times over a period of two weeks at the end of its one year span. In contrast, *Neoleprea streptochoeta* is polytelic, and Duchêne (1980a) suggested that it has a life span of just over 5 years, breeding annually. As yet there are no studies on the role and presence of the endocrine system in the control of breeding.

Terebellids exhibit a wide range of reproductive strategies. Species may be free-spawning with a lecithotrophic larvae; or they may brood eggs, which have either direct or

lecithotrophic development, inside their tube; or have embryos which develop within a gelatinous mass and are released as lecithotrophic larvae; or brood encapsulated embryos, which undergo direct development, inside the tube. Wilson (1991) recorded the reproductive modes for seven species of terebellids (six amphitritines and one thelepodine), and McHugh (1995) provided data on two additional species of amphitritines.

McHugh (1993) studied the development of four terebellid species. Development ranged from those that mass spawned and produced a benthonic larva which after about 7 days settled as a 5-chaetiger juvenile, to those which are brooded to the 1-chaetiger stage, which then emerge for 1 day in the plankton before settling as juveniles of 8 chaetigers. Another species has direct development within a cocoon and juveniles are released at the 11-chaetiger stage. Bhaud (1988) found that both temperature and food supply influenced the rate of development of *Eupolyornia nebulosa* and that spawning was correlated with lunar phases (Bhaud 1991); this species has eggs which develop within a mucous sac and a feeding benthonic larval stage of about 15 days.

The juvenile pelagic stages of some species live in the plankton (Bhaud 1988) and feed presumably by filter-feeding. Unidentified juvenile amphitritines have been observed in the plankton at Lizard Island during the summer (P. Hutchings personal observation).

Unencysted metacercariae of digenean trematodes have been found in the metanephridial sacs of *Amphitrite ornata*. The metacercariae feed on the tissues of the metanephridia and they may also ingest host vascular haemoglobin (Vandergon *et al.* 1988). Numerous gregarines are commonly observed within the coelomic fluid of terebellids. Terebellids have also been recorded as intermediate host for trematodes; the final host is a fish (Koie & Petersen 1988). It appears that the trematodes are species specific with regards to their host.

The spatial and temporal effects of terebellid tubes in soft sediments have been investigated by Trueblood (1991). By manipulating the density of terebellids, he showed that terebellids actively avoid each other's feeding tentacles. This was previously shown by Anderson & Kendziorok (1982) working with *Thelepus crispus* and they suggested that the cause was competition for food and or space. Terebellid tubes have a limited role in affecting the short-term succession of animals in a soft bottom community, with regards to temporal patterns (Trueblood 1991). However, they do affect the spatial patterns of recruitment of capitellids and dorvilleids. Trueblood (1991) postulated that it could be due to the hydrodynamic effects of the terebellid tubes or to interactions between recruiting infaunal animals.

Woodin & Merz (1987) investigated the functional aspects of a range of terebellid chaetae in relation to the types of tubes they occupy. The forces necessary to dislodge worms from their tube was measured; the forces applied to the tube mimicked fish feeding on the worms. They found that hooks are orientated to resist removal of worms from their tubes. Using this data they then developed a phylogeny of the various groups of polychaetes examined. Fitzhugh (1991b) reconsidered the data and found that no present systematic data exists to support Woodin & Merz's (1987) phylogenetic hypotheses.

Although terebellids are often extremely abundant in many benthic communities, they are not used for fish bait, and certainly are not regarded as pest species by the aquaculture industry. They tend to occur in non-polluted, fully marine environments.

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According to Rouse & Fauchald (1997) the terebellids are a sister-group to the trichobranchids within the clade Terebellida (Fig. 1.110). McHugh (1995) undertook an analysis of the amphitritines and presented a preliminary classification, but stressed that the large number of homoplasies indicates the need to find and use additional characters; she suggested that the evolution of morphological characters, reproductive modes or biogeographical patterns may be useful. McHugh also discussed the likelihood that not all genera of amphitritines are monophyletic and questioned the validity of some of the many monospecific genera. Many of these genera are known only from a single type specimen and additional material needs to be examined to clarify their status. McHugh's study did not support the various tribes in the classification of Holthe (1986b).

Hutchings & Glasby (1991) examined the distribution patterns of Australian terebellids, and found that over 85% of the species are endemic to Australia. The remaining species are primarily Indo-Pacific species. However, the majority of genera are worldwide, with only seven genera, *Arranooba*, *Hadrachaeta*, *Lanicola*, *Tyira*, *Pseudoproclea*, *Deçathelepus* and *Pseudothelep*, endemic to Australia. It is expected that with more worldwide studies some of the so-called endemic genera will be found in South-East Asia and the Indo-Pacific. Hutchings & Glasby (1991) recognised three major patterns of species distribution within the terebellids: species which occur throughout Australia; those which have a southern or northern distribution, and; those with a very restricted distribution.

Terebellids are soft-bodied worms and thus do not readily fossilise. However, various fossilised tubes found in the Erins Vale Formation (Late Permian), Southern Sydney Basin, New South Wales have been identified by Pickett (1972) as perhaps belonging to Terebellidae. Howell (1953) recorded 16 genera of possible terebellids on the basis of construction in fossil tubes, ranging in age from Cambrian to the Recent.

Family Trichobranchidae

Trichobranchids tend to have a relatively short, compact body with an extended tentacular membrane and numerous buccal tentacles of two types (Fig. 1.124A). Branchiae range from simple filaments to rosettes to a single stout stalk bearing two to five lamellate lobes. Some species live in muddy tubes.

The Trichobranchidae are characterised by the fusion of the prostomium to the peristomium along the anterior margin of the prostomium. The peristomium forms extended lips; the upper lip may be expanded to form lateral lobes and the lower lip may be greatly expanded to form a ridged, conical eversible proboscis which may be completely retracted (Fig. 1.124A, B). The palps are represented by multiple grooved buccal tentacles, which cannot be retracted into the mouth. Nuchal organs are present in *Trichobranchus* species, but not in *Terebellides* species (Rullier 1951); the condition is unknown for other genera (McHugh 1995). Segmentation is distinct. The first segment is fused to the head and lacks parapodia and chaetae. The body is divided into two regions: the thorax, bearing notochaetae and neurochaetae, and the abdomen, with neurochaetae only. Branchiae occur dorsally on segments 2 to 4; the filaments may be filiform (Fig. 1.124B), foliaceous, rosette-like in two or three groups or may form a single large branchia bearing two to five lamellate lobes (Fig. 1.124A, D). Ventral glandular pads are absent. The pygidium is smooth or lobed and small cirri may be present. Lateral organs and dorsal cirrus organs have not been observed. There is a non-eversible ventral buccal organ

and the gut is looped. A gular membrane is present. Nephridia are present as metanephridia; the relation to coelomostomes has not been documented. The anteriormost pair of nephridia are excretory in function; the posterior ones presumably act as gonoducts. The circulatory system is closed and a heart body is present (Wirén 1885). Aciculae are absent; other chaetae are variously ornamented capillaries and uncini which may be acicular, or avicular with short or long shafts (Fig. 1.124F–I).

Trichobranchids have been considered as a subfamily of the Terebellidae by some workers, such as Day (1967). Fauvel (1927) divided the genera within this family between two subfamilies within the Terebellidae (Trichobranchinae – comprising *Trichobranchus* and *Octobranchus*, and Canephorinae, containing *Terebellides* – the name Canephorinae, as Fauchald & Rouse (1997) pointed out, being invalid as it is based upon an invalid generic name). Currently, the trichobranchids are regarded as a separate family, but closely related to the terebellids. The Trichobranchidae has been placed in the Terebellida clade by Fauchald & Rouse (1997; Fig. 1.110). No major revision of the family has been undertaken, although Hessle (1917) and Holthe (1986a) both discussed the family in some detail. No subfamilies are recognised.

Worldwide, trichobranchids occur predominantly in soft sediment in shallow water; they may be locally abundant. Currently, eight genera have been described, of which four are known only by the type species. The type species of *Trichobranchus* and *Terebellides* have been recorded widely as a result of subsequent synonymies; they were originally described from Northern Europe. For example, Hartman (1959a) synonymised virtually all species of *Terebellides* with *T. stroemii* and similarly many species of *Trichobranchus* were synonymised with *T. glacialis*. In her review of *Terebellides*, Williams (1984) suggested that several species had been confused; she described some new species using additional characters, but others were left as morphs. Solis-Weiss, Fauchald & Blankensteyn (1991) and Hutchings & Peart (in preparation) examined these regional morphs and described additional species. This suggests that all described species of *Terebellides* which were synonymised with *T. stroemii* should be re-examined using the additional characters suggested by these later studies. This will probably reveal that most of these species are, in fact, valid and that *T. stroemii* is restricted to northern Europe rather than having a cosmopolitan distribution. Until this is done it is difficult to estimate the number of species present in this family worldwide. However, within Australia, four genera are known (*Artacamella*, *Octobranchus*, *Trichobranchus* and *Terebellides*) represented by 10 species. Currently, all these species are known only from Australia; some have wide distributions within Australia, others have very restricted distributions (Hutchings & Peart in preparation).

Trichobranchids are sedentary, tubiculous worms which live in soft sediments from shallow water to depths of 2700 m (Hutchings & Peart in preparation). Fauchald (1977) suggested that they are more common in cold water and thus may be represented best in deep water. In Australian waters, they are common in moderate depths in Bass Strait, but they are also common in the shallow waters of Botany Bay and Moreton Bay. Far more sampling has been done in temperate than in tropical Australian waters (P. Hutchings & R. Peart personal observations) and no material has been collected in deep water, so it is unclear whether Fauchald's (1977) suggestion is also valid for Australia at this stage. Reports suggest that trichobranchids do not form well-constructed tubes; Dales (1955a) proposed that particles rejected in feeding and those in contact with the body become

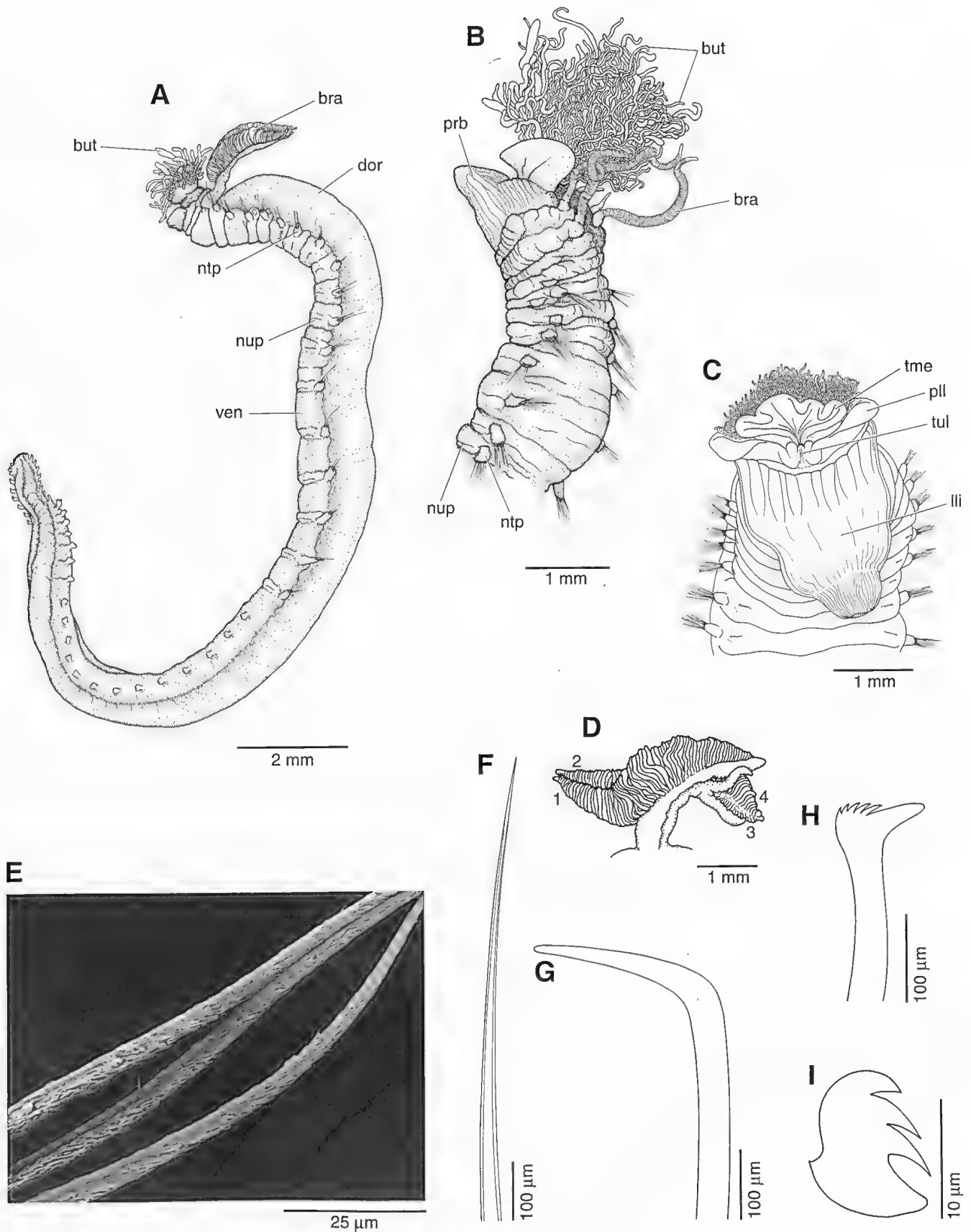


Figure 1.124 Family Trichobranchidae. **A**, *Terebellides* species, dorso-lateral view of entire animal. **B**, **C**, anterior end of *Artacamella* species: **B**, lateral view; **C**, antero-ventral view. **D**, four lobed branchia of *Terebellides stroemii*, lobes numbered. **E**, **F**, notochaetae of *Terebellides* species: **E**, details of the hirsute structure; **F**, thoracic capillary chaeta. **G**–**I**, neurochaetae of *Terebellides* species: **G**, spine from parapodia of chaetiger 1; **H**, anterior, acicular thoracic hook; **I**, anterior abdominal uncinus. **bra**, branchia; **but**, buccal tentacles; **dor**, dorsum; **lli**, lower lip/proboscis; **ntp**, notopodium; **nup**, neuropodium; **pll**, peristomial lateral lobe; **prb**, proboscis; **tme**, tentacular membrane; **tul**, trilobed upper lip; **ven**, ventral surface. (E, from Hutchings & Peart in preparation) [A–D, F–I, A. Murray]

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agglutinated to form a sleeve in which the worm lives. However, some Australian species do make well-constructed tubes of fine mud.

Trichobranchids have a distinct head and tail region, with a fixed number of thoracic segments, which bear both notopodia and neuropodia (Fig. 1.124A). The number of abdominal segments varies; these bear neuropodia only. Numerous non-retractile, relatively short, buccal tentacles are present and the various head structures are highly mobile. The tentacles are considered to be palpal in nature and emerge prostomially, as for the Terebellidae, based on positional relationships in the juveniles (Heimler 1983), although Rouse & Fauchald (1997) suggested that this requires further investigation. Trichobranchids range in size from a few millimetres to up to 100 mm in length.

The parapodia are biramous and lack aciculae. The rectangular notopodia, inserted dorso-laterally, are mobile and bear a bundle of notochaetae. The neuropodia extend to the pygidium and are present as glandular tori which may be sessile or form ventro-lateral pinnules. The shape and length of the neuropodia changes along the body. The neurochaetae are arranged in single or double rows. The thoracic neurochaetae differ from abdominal ones; thoracic ones are long-handled hooks, of which the anteriormost may be simple curved spines (Fig. 1.124G, H); abdominal neurochaetae are short-handled, avicular uncini (Fig. 1.124I). The notochaetae are ornamented capillaries (Fig. 1.124E). Juvenile specimens may be difficult to identify. All species have branchiae; the position of the easily detached branchial filaments is discernible by the readily visible branchial scar. Trichobranchids are not sexually dimorphic, except just before spawning when the colour of the gametes distinguishes males and females. Gravid females may be pinkish to greenish and males cream-coloured.

Species are distinguished basically on the structure, distribution and alignment of the chaetae, including the segment on which they first appear, the structure of the branchiae, and the structure of the head (peristomium and prostomium).

Trichobranchids have longitudinal muscle bands (Storch 1968), although their development and the completeness of the septa varies somewhat between species. They also have a gular membrane (Hessle 1917; Sutton 1957); this muscularised septum occurs between two anterior segments, dividing the coelom into anterior and posterior parts (Smith 1992).

Trichobranchids are non-selective deposit-feeders. They use the numerous grooved buccal tentacles to collect sediment which they either swallow or use to construct their tubes. In *Terebellides*, the lip structure has been profoundly modified (Fig. 1.123D; Dales 1955a). The upper lip is derived from the prostomium, whereas the outer lips are formed from the peristomium. The upper lip is expanded to form an anteriorly projecting funnel. Hessle (1925) reported that *Terebellides stroemii* digs in the sediment using its spade-shaped upper lip, rather than using its relatively short buccal tentacles to collect food as occurs in the terebellids. Dales (1955a) suggests that the rolling movements of the outer lips may help to push food collected in the funnel into the mouth. In *Trichobranchus*, the upper lip is cleft ventrally which allows the lower lips to roll directly into the mouth and to transfer food into the mouth. They obtain their nutrition from the bacterial and algal films covering the sediment particles. Presumably, like terebellids, trichobranchids can use the muscular lips to eject unwanted particles some distance away from the animal. In *Artacamella*, the peristomium is expanded to form a

retractible proboscis (Fig. 1.124B), which may be used to scoop up sediment, as observed in terebellids of the genus *Artacama* (Dales 1955a).

Trichobranchids have a non-eversible, ventral buccal organ (Wirén 1885) and a looped gut (Meyer 1887). The alimentary tract consists of an oesophagus, foregut, midgut and hindgut. In *Terebellides* and *Octobranchus*, a stomach is present in the midgut between the oesophagus and intestine; the epithelial area of the fore-stomach is greatly increased by numerous folds and extends forward as a lateral lobe (Michel *et al.* 1984) which partly envelops the oesophagus. This great increase in the capacity to digest prey and absorb nutrients may be critical for these worms, which are typically only about 20–30 mm in length. The structure and function of glands attached to the stomach of *Terebellides stroemii* have been described in detail by Michel *et al.* (1984) and they suggest that the stomach may have secretory, absorptive and excretory functions. It is also becoming apparent that early work carried out using classical microscopy to investigate 'secretions' (see Michel & de Villez 1978 for references) requires re-investigation with ultrastructural and cytochemical techniques (Michel 1988). Investigations on the intestine of *Terebellides stroemii* showed that the absorptive cells contain spherocrystals rich in calcium and phosphorus that may also have an excretory role (Michel *et al.* 1984). The absorptive cells have a characteristic microvillous brush border, and are involved in pinocytosis and probably intracellular digestion by means of lysosomal enzymes. They also store glycogen and lipids. Mucous and ciliary cells work in the packing and transport of faecal pellets which are discharged via the anus situated at the tip of the pygidium.

Trichobranchids have a well-developed blood system and appear to have a heart body, as illustrated by Wirén (1885). This heart body pumps blood around the body; however general movement will also tend to move blood around the body. The blood lacks blood corpuscles, but a high molecular weight respiratory pigment is dissolved in the plasma. The branchiae are well supplied with blood.

Trichobranchus glacialis has four pairs of coelomoducts in anterior segments (segments 3 to 6) and the ducts open to the exterior in a latero-dorsal position. Christie (1986) observed that the coelomoducts enlarge at maturity, presumably to allow the discharge of gametes to the outside. Hessle (1917) reported that all the nephridia were metanephridia in trichobranchids but gave no details of their structure, distribution or their relationship to the coelomoducts. Meyer (1887) reported that nephridia are restricted to only a few pairs anteriorly, of which the foremost pair are excretory only.

Little is known about the sense organs and nervous system of trichobranchids. Some species have groups of eyespots, but it is not known if they are actually light sensitive. Lateral organs and dorsal cirrus organs have not been observed (Fauchald & Rouse 1997).

Sexes are separate in the Trichobranchidae, and it seems likely that the sex ratio is 1:1. Reproduction has only been studied in the Northern European populations of *Trichobranchus glacialis* and *Terebellides stroemii*. Both species are dioecious, with annual spawnings. In *Trichobranchus glacialis*, there are discrete germinal epithelia just above the ventral nerve cord and surrounding the ventral blood vessel in chaetigers 2 to 4. The ovaries comprise no more than two cell types, oogonia and previtellogenic oocytes (Christie 1985), bound together with follicle cells, similar to those observed by Eckelbarger (1975b) in the terebellid *Nicolea zostericola*. The germinal epithelium of both sexes produces the early gametocytes, which are then released into

the coelom where vitellogenesis and spermatogenesis occur; the process takes about 8–9 months to complete. Spawning in this species occurs in December to January, and Christie (1986) suggested that these worms may be polytelic. Populations of the same species occurring in a higher latitude produced larger eggs at a different time of the year (Curtis 1977). This suggests that either the species exhibits geographical variation in reproduction or that two species have been confused.

Early development has been studied in only two species of trichobranchids. Although fertilisation has not been observed in *Trichobranchus glacialis*, it is presumed to be external, with the sperm having a 'primitive' morphology (Franzén 1956); Jamieson & Rouse (1989) referred to the sperm as aquasperm. As large oocytes are produced, Christie (1986) suggested that they give rise to larvae with a non-pelagic larval stage, that is, direct, lecithotrophic development. *Terebellides stroemii* deposits its eggs in spherical, slimy masses, about 4 mm in diameter. These are attached either to the entrance of the adult tube or on decaying blades of the seagrass *Zostera* (Willemoes-Suhm 1871) where development occurs, and larvae emerge as globular trochophores. The larvae are relatively small and have never been recorded in the plankton, leading Thorson (1946) to suggest that they must have a very reduced pelagic stage or no pelagic stage at all.

Curtis (1977) found that *Terebellides stroemii* spawns for the first time at the age of 2 years and then continues to spawn annually during its 5-year life span. The species has a restricted breeding season from October to November. Although Christie suspected that *Trichobranchus glacialis* survives spawning and may spawn the following year this was based on largely circumstantial evidence. No information is available on the synchrony of breeding in relation to spawning. However, the fact that spawning is synchronised in both species studied suggests that environmental cues operate early in the reproductive cycle to initiate proliferation of cells on the germinal epithelium and subsequently co-ordinate the development of the gametes. This ensures that all gametes are mature within an individual and can be spawned on receipt of the final cue for spawning. Duchêne (1977, 1980b) described the population dynamics of *Terebellides stroemii* in Banyuls, France.

No information is available for any Australian trichobranchid. However, both mature worms and juveniles of an undescribed species of *Terebellides* are present in samples collected in Botany Bay over 2 years, suggesting that this species also survives spawning and lives for more than 1 year. This species has been described by Hutchings & Peart (in preparation).

Trichobranchids are detritivores; they occur mainly in fully marine conditions, although Remane & Schlieper (1958) recorded *T. stroemii* in salinities of 3‰ in the Baltic. In some soft bottom communities, they can be a major component of the macrofaunal assemblage, for example, a new species of *Terebellides* is common at several sites within Botany Bay (Wilson 1998).

Little is known about the ecology of this family, apart from brief anecdotal information given in taxonomic studies.

The sphaerodorid polychaete, *Sphaerodoridium commensalis*, has been found to live as a commensal in the tube of *Terebellides stroemii* by Lützen (1961). The parasitic copepods, *Melinnacheres steenstrupi* and *M. terebellides*, have been found as ectoparasites on *T. stroemii* by Levinsen (1878) and Bresciani & Lützen (1961).

Trichobranchids are not eaten by humans or used as fish bait. They may be preyed upon by fish and other mobile predatory groups, but there are no records of such organisms selectively feeding on members of this family.

No fossil record has been documented, although from tube structure it would be impossible to distinguish between fossil terebellid and trichobranchid tubes. Possibly some of the fossilised worm tubes attributed to terebellids are in fact trichobranchids.

As trichobranchids have not been systematically studied in any major region of the world, and their taxonomy has been confused, little can be said about their biogeography, other than in Australian waters. *Artacamella* is represented by three species, of which one, *A. dibranchiata*, occurs only in Port Phillip Bay, and two new species, which occur around Australia. A single new species of *Octobranchus* is restricted to southern waters. One of two new species of *Trichobranchus* is restricted to Bass Strait, and the other occurs around Australia. *Terebellides* is represented by four new species, one is restricted to Bass Strait; the other three occur all around Australia. So there appear to be two distribution patterns: species with a very restricted distribution and those widespread within Australia. As far as is known all the Australian species of trichobranchids are endemic (Hutchings & Peart in preparation).

CANALIPALPATA INCERTAE SEDIS

Rouse & Fauchald (1997) placed four families, Polygordiidae, Protodrilidae, Protodriloididae and Saccocirridae, as members of the Canalipalpata, but did not place them within any other sub-taxon of the group. In their complete cladistic analyses, these four families formed a clade that was either associated with taxa that belong within the Canalipalpata, Scolecida, or was part of a basal polytomy of the Polychaeta. Historically, the Polygordiidae, Protodrilidae, Protodriloididae and Saccocirridae have been generally considered as members of the so-called Archiannelida (Hatschek 1878). Hatschek (1878) argued that *Polygordius* (which at that time included members of *Protodrilus*) represented the most primitive annelid and that *Saccocirrus* was also primitive, even though it has chaetae. Although this view of these taxa being a primitive group was soon challenged (Goodrich 1901), the prevailing view through most of this century was that the Archiannelida represented a primitive group of polychaetes. However, this view was rejected by Hermans (1969) who argued the Archiannelida was a polyphyletic assemblage of groups that had convergently evolved to live in the interstitial environment. Hermans (1969) did, however, retain the actual taxon name Archiannelida. It was not until Fauchald (1977) placed the various archiannelid families as 'families of uncertain affinity' that the Archiannelida was finally discarded.

The close relationship between *Polygordius*, *Protodrilus* and *Saccocirrus* that was recognised by Hatschek (1878) was supported by Goodrich (1901), though they differed on the phylogenetic placement of the group. However, Westheide (1990a) argued that the similarity of body shape and palps had arisen independently in *Polygordius*. Further investigation on the placement of *Polygordius* is required and anatomical studies of its buccal organ and palps are necessary. Purschke & Jouin (1988) demonstrated that *Protodriloides*, *Protodrilus* and *Astomus* (= *Parenterodrilus*) (Protodrilidae) and *Saccocirrus* (Saccocirridae) formed a monophyletic group.

1. CLASS POLYCHAETA

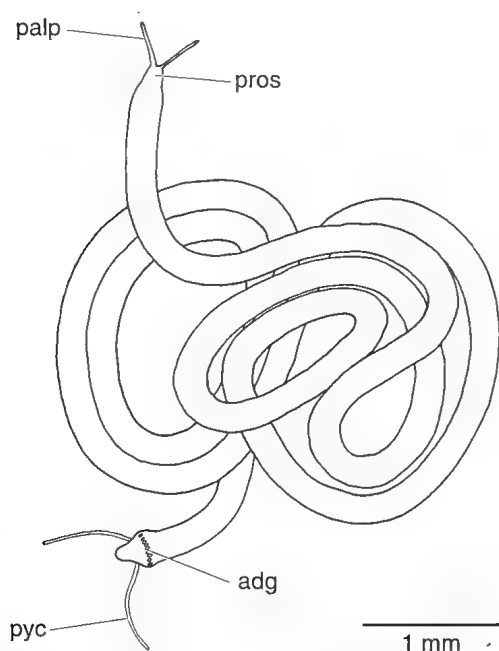


Figure 1.125 Family Polygordiidae. Entire animal of *Polygordius appendiculatus*, dorsal view. **adg**, adhesive glands; **palp**, palp; **pros**, prostomium; **pyc**, pygidial cirrus. (After Westheide 1990a) [A. Murray]

Protodriloides was found to be the sister group to the other three genera, and so they transferred it from Protodrilidae to its own family, the Protodriloididae. Shared derived characters support family status for *Protodrilus* and *Parenterodrilus* as Protodrilidae, as well as apomorphies for *Saccocirrus* as the Saccocirridae. The latest phylogenetic analysis of polychaetes by Rouse & Fauchald (1997) supported Purschke & Jouin (1988), but also included *Polygordius* (Polygordiidae) in the same monophyletic group.

Members of all four families live interstitially in clean coarse sediments from the upper intertidal to shallow subtidal areas. A few members of Protodrilidae and Saccocirridae have been recorded from Australian waters. Although species of Polygordiidae and Protodriloididae have been reported from the Indo-Pacific region and New Zealand respectively (Riser 1985; Nordheim 1989), none is reported from Australian waters.

Family Polygordiidae

Members of the Polygordiidae are minute to small interstitial worms. They are elongate nematode-like forms with weak segmentation (or segmentation absent), without parapodia and with or without chaetae.

Polygordiids are slender and thread-like, reaching up to 100 mm in length and 1 mm in width for 185 segments (Westheide 1990a). The prostomium (Fig. 1.125) has two solid, stiff anterior palps (previously referred to as tentacles) and two pigmented eyes may be present. External segmentation is indistinct or absent and the external surface is smooth and slightly iridescent. External ciliation is present only in nuchal slits, sometimes on tentacles, or rarely as scattered ciliary tufts. Parapodia are absent and chaetae are either absent (*Polygordius*) or present as capillaries in the posterior part of the body (*Chaetogordius*). The bulbous pygidium bears a circle of adhesive glands; anal cirri may be present or absent.

The largest genus, *Polygordius*, comprises about 15 species (Westheide 1988b) and *Chaetogordius* is monotypic. Although some species occur in the Indo-Pacific region (Jouin 1971; Jouin & Rao 1987), none are known from Australia. Species of *Polygordius* live in coarse sediments in infralittoral and intertidal zones.

Polygordiids are gonochoric, except for *Polygordius triestinus*, which may be a hermaphrodite (Fauvel 1927). Sperm are of the 'ect-aquasperm' type (Jamieson & Rouse 1989). Eggs and sperm are released through the ruptured body wall, fertilisation is external and young larvae are of the typical trochophore type. Further development follows two different patterns: those in one group, including *P. neapolitanus* develop into so-called 'exolarvae', and those in the other including *P. appendiculatus* develop into 'endolarvae'. In the exolarva, the developing segments trail behind the presegmental part of the larva, forming the trunk of the young animal, and in the endolarva, the developing segments are folded up inside the larval body. At metamorphosis, large parts of the larval body are cast off and ingested by the juvenile (Westheide 1990a).

Family Protodrilidae

Protodrilids are minute to small interstitial worms. They have a pair of flexible palps distinct from the prostomium, unlike protodriloids in which the palps are extensions of the prostomium.

Protodrilids are slender and filiform, range from 2–15 mm in length and have 21 to 77 segments (Fig. 1.126). The prostomium has two palps (previously referred to as 'tentacles') with internal canals which connect behind the brain, two nuchal organs, so-called statocysts [actually photoreceptors (see Purschke 1990a, 1990b)], and, in some species, simple pigmented eyes. *Protodrilus* species have a ventral pharynx with a tongue-like organ, whereas a digestive system is completely lacking in *Parenterodrilus*. External ciliation includes single and adjoined stiff sensory cilia, which are arranged in various patterns. A continuous ventral band of cilia is always present along the length of the body, and tufts and rings of cilia may be present on the prostomium and trunk. The trunk is segmented, but lacks parapodia and chaetae; usually two pygidial adhesive lobes are present.

The first protodrilid was described as *Polygordius purpureus* by Schneider (1868) from specimens collected in the North Sea; it was later referred to *Protodrilus* in the 'archiannelid' family Protodrilidae. The Protodrilidae comprises the genera *Protodrilus* and the monotypic *Parenterodrilus* (proposed as a new name for *Astomus* by Jouin 1992). The species of *Protodrilus* were reviewed by Nordheim (1989); he described six new species of which five were from New Zealand and presented a detailed table comparing the 30 known species. Although the family has never been formally reported from Australia, three species have recently been collected in Queensland (R. Kristensen personal communication).

Protodrilids live in interstitial spaces of relatively clean, detritus-poor coarse sediments on intertidal or subtidal areas; most species feed on the bacterial films of their substratum. They creep continuously by means of their ventral ciliary band. Substances secreted from the adhesion-producing glands, particularly the pygidial lobes, attach the worms to the substratum (Westheide 1990a). *Parenterodrilus taenioides* from the coral sands of Moorea, French Polynesia, has a residual gut which has lost any digestive function. Its extended lateral lobes increase its epidermal surface through which it absorbs and digests dissolved organic substances (Jouin 1979, 1992).

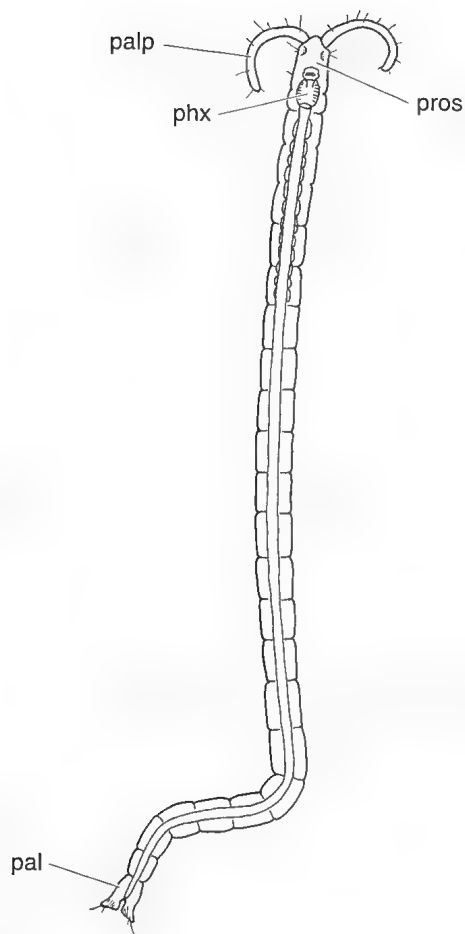


Figure 1.126 Family Protodrilidae. Entire animal of *Protodrilus adhaerens*, dorsal view. **pal**, pygidial adhesive lobe; **palp**, palp; **phx**, pharynx; **pros**, prostomium. (After Westheide 1990; scale not available) [A. Murray]

The animals are dioecious. At sexual maturity males are distinguished by the presence of lateral organs, which form the spermatophores and are associated with the openings of sperm ducts. Two kinds of sperm are produced by males, one structurally more simple and possibly not fertile. Fertilisation is internal; females take up spermatophores (Westheide 1990a) and produce two to more than 150 eggs per fertile segment. The fertilised eggs are released in most species by partial bursting of the epidermis (Nordheim 1989) and in a few species through oviducts that consist of a coelomic funnel connected to a protonephridium (Jouin 1970). Development is indirect and includes a pelagic larval stage (Nordheim 1989).

Family Protodriloididae

Protodriloidids are minute to small interstitial worms. They were formerly included with Protodrilidae, but may be distinguished from them by having paired palps as extensions of the prostomium.

Protodriloidids are slender and flat, measure up to 13 mm in length and have up to 50 segments (Fig. 1.127A). They have a prostomium with two solid anterior palps (previously referred to as tentacles) that are direct extensions of the prostomium rather than implanted as in protodrilids and saccocirrids. The prostomium has two nuchal organs, but lacks the eyes and so-called statocysts of protodrilids; the ventral pharynx lacks a tongue-like organ. The segmented trunk bears a ventral ciliary

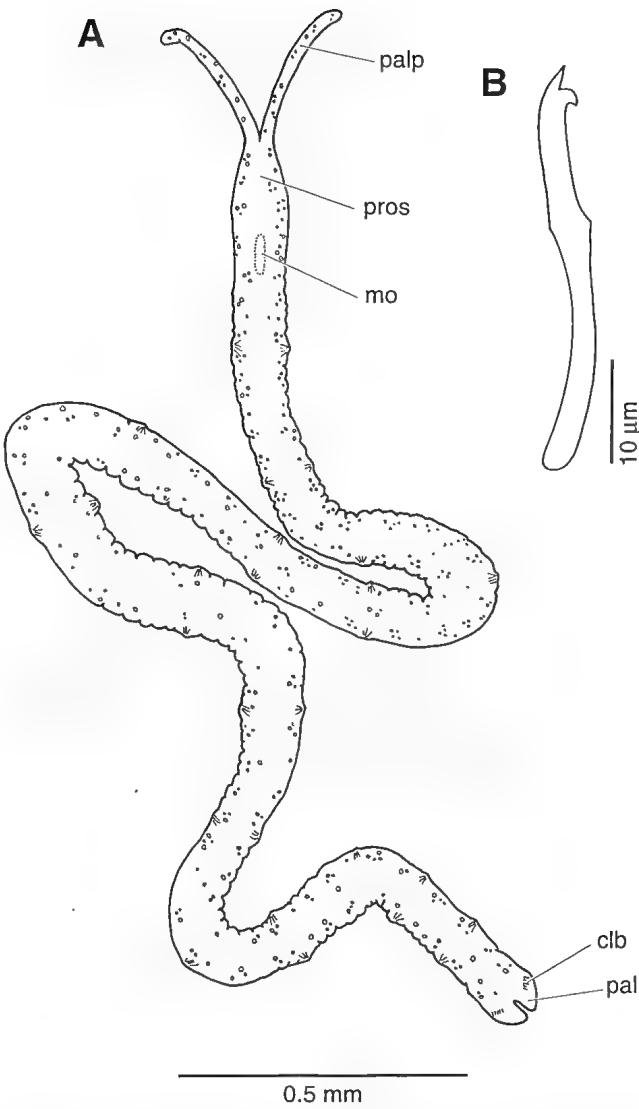


Figure 1.127 Family Protodriloididae. *Protodriloides symbioticus*. **A**, whole animal, dorsal view. **B**, bidentate hook. **clb**, ciliary band; **mo**, mouth; **pal**, pygidial adhesive lobes; **palp**, palp; **pros**, prostomium. (After Westheide 1990a) [A. Murray]

band and two pygidial adhesive lobes. Although parapodia are absent, chaetae may be present in the form of distally dentate hooks (Fig. 1.127B).

Protodriloides symbioticus and *P. chaetifer* are the only known species in the family. They were placed in the genus *Protodrilus* until Jouin (1966) recognised that they differed fundamentally in tentacle structure, reproductive biology and development from the other species and erected the genus *Protodriloides*. As the result of an ultrastructural study of the ventral pharynx and a phylogenetic study of protodrilids and saccocirrids, Purschke & Jouin (1988) erected the new family Protodriloididae. The spelling of the family name has been corrected to Protodriloididae by Fauchald & Rouse (1997). Although the family has not yet been reported from Australia, *Protodriloides* species has been found in New Zealand (Riser 1984), and it is most likely that they will be collected in Australian waters.

Protodriloidids are interstitial dwellers, with habits similar to the protodrilids. They creep by means of their ventral ciliary band and adhere to sand grains by the secretions from the segmentally arranged adhesion-producing glands or hold on with their chaetae (Westheide 1990a).

Protodriloidids are dioecious. Females secrete cocoons into which they lay a small number of large yolky eggs. Sperm are spherical and aflagellate, and eggs are assumed to be fertilised in the cocoon during some kind of pseudocopulation. The fertilised eggs undergo direct development and the juveniles remain in the cocoon for up to 25 days, by which time they have attained most of the adult characters (Westheide 1990a).

Family Saccocirridae

Saccocirrids are minute to small interstitial worms. They have paired anterior palps and segments with reduced parapodia and chaetae.

Saccocirrids are slender, distinctly segmented, and reach about 20 mm in length for up to 200 segments (Fig. 1.128A). The prostomium bears two palps (previously referred to as 'tentacles') with internal canals that connect behind the brain by basal ampullae, two nuchal organs and usually two pigmented eyes (Fig. 1.128B). A ventral pharynx with a muscular tongue-like organ and ventral ciliation may be present. Gonads are present on one or both sides of the body. The uniramous parapodia are retractile and bear different kinds of simple chaetae (Fig. 1.128C–E). The pygidium is bilobed and bears adhesive papillae.

The single genus, *Saccocirrus*, comprises about 20 species (Purschke & Jouin 1988). Brown (1981) reported the first Australian saccocirrids: *Saccocirrus krusadensis*, originally described from India, and two new species, *S. jouinae* and *S. tridentiger*. Two species were recently collected in Queensland (R. Kristensen personal communication). The geographical distribution of 17 species is given by Brown

(1981). Although only one genus is presently recognised, it can be divided into two groups on the basis of a number of characters. One group, with a worldwide distribution, has bilateral gonads, the longest chaetae with expanded tips, and the ventral side unciliated, and the pharyngeal organ may be absent. In the other group, species from the Indo-Pacific region, the position of the gonads is unilateral, the longest chaetae are deeply bifid, the ventral surface is usually ciliated, and a muscular pharynx is present (Brown 1981; Sasaki & Brown 1983; Purschke & Jouin 1988). It has been hypothesised that the first mentioned group of species displays ancestral features and that the second group may comprise specialised species with regressive evolution of gonads and secondary development of ventral ciliation (Brown 1981).

Saccocirrids live in coarse intertidal and shallow subtidal sands. They move actively in a leech-like fashion, attaching to sand grains by secretions from the caudal appendages, body wall and palps (Pettibone 1982). The three reported Australian species were collected from sediments of the lower intertidal zone around rocky outcrops on the central New South Wales coastline. They are herbivorous browsers, sweeping algae into the mouth with the ventral ciliary band, whereas species without ventral ciliation are known to be carnivorous, feeding on copepods (Brown 1981).

The animals are dioecious and they have complicated reproductive systems. The fertile segments are in the middle region of the body and may comprise up to 100 segments. Each fertile segment has its own reproductive system with paired or unpaired genital structures, comprising a gonad and gonadal ducts, and intromittant organs for males and spermathecae for females (Brown 1981). Although sperm

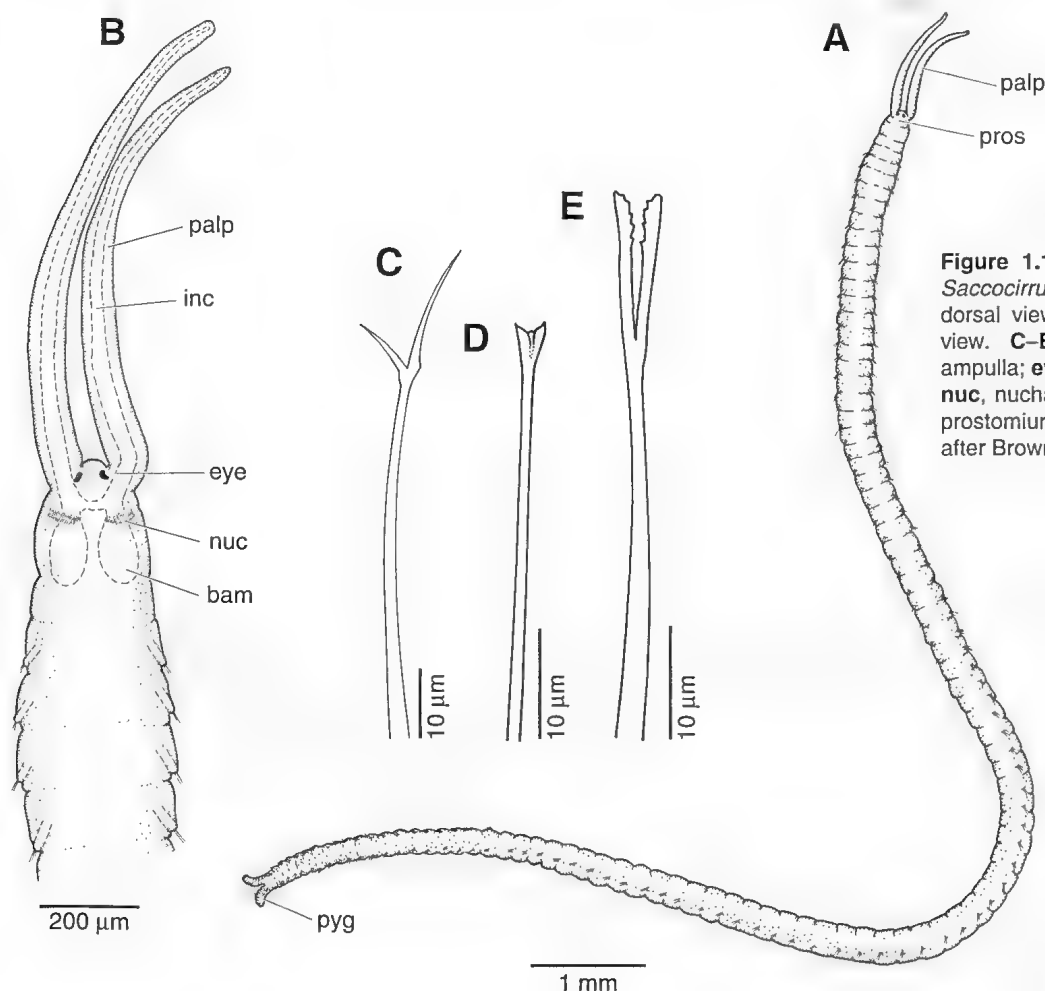


Figure 1.128 Family Saccocirridae. *Saccocirrus jouinae*. **A**, entire animal, dorsal view. **B**, anterior end, dorsal view. **C–E**, chaetae. **bam**, basal ampulla; **eye**, eye; **inc**, internal canal; **nuc**, nuchal organ; **palp**, palp; **pros**, prostomium; **pyg**, pygidium. (C–E, after Brown 1981) [A. Murray]

transfer has not yet been observed, it must be assumed for these species. Synchronous mass spawning for *Saccocirrus uchidai* from Japan and larval development of *S. uchidai* and the Australian *S. krusadensis* have been described (Sasaki & Brown 1983). The fertilised eggs are very small with a diameter of less than 100 µm, develop into a swimming trochophore larva after 18–36 hours, and are planktotrophic when they are 2–3 days old. By 7–11 days, *S. krusadensis* larvae have three chaetigerous segments, whereas *S. uchidai* larvae do not develop chaetae until the 12 to 14 segment stage, when they have already settled and metamorphosed.

POLYCHAETA INCERTAE SEDIS

Rouse & Fauchald (1997) placed four families, Aeolosomatidae, Potamodrilidae, Parergodrilidae and Psammodrillidae, as members of the Polychaeta, but did not place them within any other sub-taxon of the group. Prior to this, Aeolosomatidae and Potamodrilidae were usually considered in relation to the Clitellata, either as a member of the group (Bunke 1967), or more recently as the sister group (Bunke 1985). This placement as sister group (called the Aphanoneura by Timm 1981) to the Clitellata was rejected by Bunke (1986), but he also could not relate them to any group of polychaetes, thus leaving the two families isolated. Recently, Moon *et al.* (1996) presented an analysis of molecular sequence data for a species of *Aeolosoma*, a mollusc, a polychaete, and three clitellates. They inferred that *Aeolosoma* was the sister group to the clitellate clade. However, further sampling of polychaetes across a range of taxa is probably advisable to test whether the Aeolosomatidae and Potamodrilidae are clitellates or polychaetes. Rouse & Fauchald (1997) only included Aeolosomatidae, Potamodrilidae, Parergodrilidae and Psammodrillidae in their complete taxon set analyses. In one analysis (*A/Pec*), these taxa either fell as part of a large basal polytomy of polychaetes or Aeolosomatidae, Potamodrilidae, Parergodrilidae formed a clade with Ctenodrilidae and Psammodrillidae grouped with Capitellidae, Arenicolidae, and Maldanidae. In the *A/Pwc* analysis, Aeolosomatidae, Potamodrilidae and Parergodrilidae either formed a grade with respect to Polygordiidae, Protodrilidae and Protodriloididae or they were a basal clade of polychaetes. The Psammodrillidae either were a basal polychaete group or were a sister group to a large clade that mainly comprised taxa with grooved palps. In the *Mc* analysis, the four taxa under discussion here were part of a large basal polytomy. Thus, at present it is not possible to place these taxa with any confidence within the Polychaeta.

Undescribed representatives of Aeolosomatidae have been recorded (but not published) from Australian waters. Potamodrilidae is unknown from Australia; the group is only known for a single species in the genus *Potamodrilus* which appears to be restricted to European freshwater streams (Bunke 1988) – it is not described further, although the taxon does appear in the family key.

Parergodrilidae, originally containing only *Parergodrilus*, was thought to belong in the Archiannelida by Reisinger (1925). Subsequent detailed work on *Stygocapitella subterranea*, led Karling (1958) to place it in its own family, and led Reisinger (1960) to group the two taxa together under the Parergodrilidae and place it within the Polychaeta; no detailed placement was given. Fauchald (1977) grouped the Parergodrilidae with the Ctenodrilidae as the order Ctenodrilida, but did not justify this decision. A single species, *S. subterranea*, is known from Australia.

Psammodrillidae was erected by Swedmark (1952), and was placed by Fauchald (1977) in its own order, Psammodrillida. Rouse & Fauchald (1997) suggested that a relationship for the psammodrillids with the arenicolids and maldanids should be assessed. This hypothesis was also proposed by Meyer & Bartolomaeus (1996, 1997). Swedmark (1952, 1955, 1958) first found psammodrillids in mesopsammic environments off France. Kristensen & Nørrevang (1982) reported another species from Greenland. They have been recorded from New Zealand (Riser 1984), but not as yet from Australia.

Aeolosomatids (30 described species in three genera) and potamodrilids (one described species; see Fig. 1.46Q) are small, slender flattened worms which mostly reproduce asexually by forming chains. Most species live in freshwater.

Family Aeolosomatidae

Aeolosomatids are minute oligochaete-like worms which inhabit mostly freshwater. Like the similar potamodrilids they lack head appendages and parapodial lobes, but may be distinguished from them by the presence of coloured epidermal glands all over the body surface.

Aeolosomatids are minute, ciliated worms (Fig. 1.129A) with no clear affinity to other polychaetes. The large, lobe-like prostomium is almost completely ciliated ventrally and has lateral ciliated grooves (Fig. 1.129B) that have been interpreted as nuchal organs by Rouse & Fauchald (1997); the muscular pharynx lies in the peristomium. Constrictions along the trunk give the appearance of external segmentation, but they actually represent a chain of zooids produced by paratomy (fragmentation). Parapodia are absent. Chaetae are usually present as four bundles per segment; they are rarely absent. They comprise usually only capillaries, but in some species, some sigmoid hooks may be present, or, rarely, only hooks. The body is often brightly coloured due to the epidermal gland cells. Each gland cell consists of a vacuole, filled with red, green, blue-green, yellow, or sometimes colourless liquid; the function of the gland cells is unknown (Bunke 1988).

Aeolosomatids have been known since the description of *Aeolosoma hemprichi* by Ehrenberg in 1831. They were considered as oligochaetes until Brinkhurst (1971a) noted that the position of the gonads, the structure of the 'clitellum' and gonoducts were not consistent with the pattern of Oligochaeta. The similarity of the ventral pharyngeal bulb with that of *Protodrilus* and *Dinophilus* species led Brinkhurst to consider a connection with some of the so-called 'archiannelids' as had been suggested a long time ago by Sedgwick (1898). However, ultrastructural studies of sperm by Bunke (1986) do not support this or a sister group relationship with any other annelid grouping, thus leaving the Aeolosomatidae as a group with 'uncertain affinities'. A recent analysis of molecular sequence data inferred that the aeolosomatids are a sister group of the oligochaetes (Moon *et al.* 1996), whereas a cladistic analysis of morphological characters of the annelids placed them among the polychaetes (Rouse & Fauchald 1997). The Aeolosomatidae includes the genera *Aeolosoma*, *Rheomorpha* and *Histricosoma* and forms a monophyletic taxon comprising about 30 known species (Bunke 1988). *Aeolosoma niveum* and *A. hemprichi* have been reported from the Southern Hemisphere (Brinkhurst 1971b). Although there have been no published records of aeolosomatids from Australia, members of the group are known to be distributed widely throughout Australia (A. Pinder & R. Kristensen personal communication).

1. CLASS POLYCHAETA

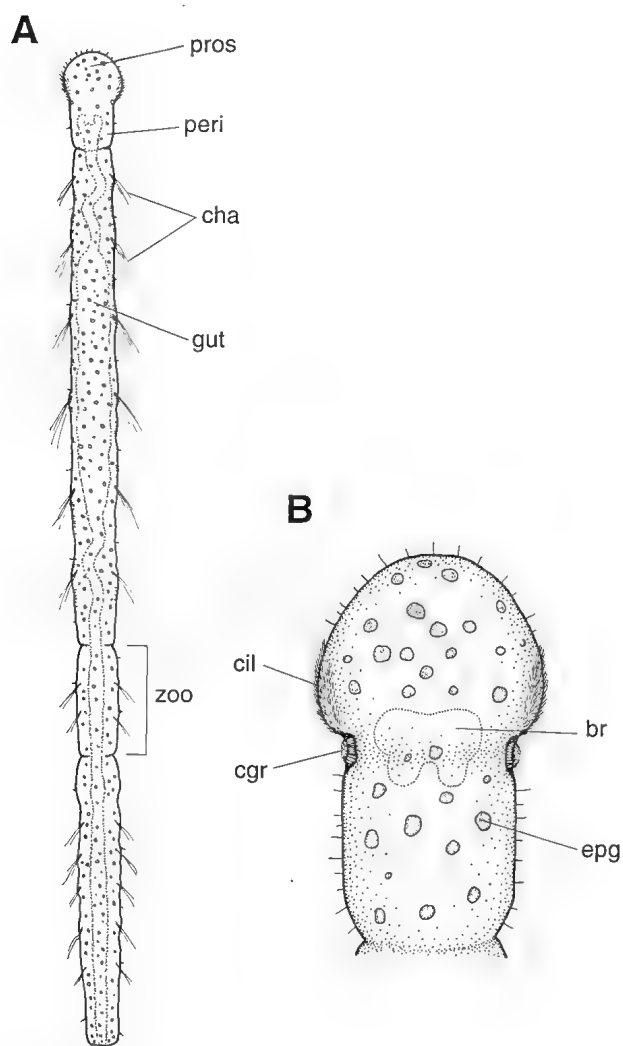


Figure 1.129 Family Aeolosomatidae. *Aeolosoma hemprichi*. A, entire animal with three zooids, dorsal view. B, anterior end, dorsal view. br, brain; cgr, ciliary groove; cha, chaetae; cil, cilia; epg, epidermal gland cell; gut, gut; peri, peristomium; pros, prostomium; zoo, zooid. (After Bunke 1967, scale not available) [A. Murray]

Aeolosomatids are slender and filiform, ranging from 0.3–10 mm in length. They usually live in freshwater habitats, especially ponds and lakes, but a few species are found in brackish water, and one marine species has been recorded (Westheide & Bunke 1970).

Aeolosomatids are hermaphrodites, but sexual reproduction appears to be suppressed and most species reproduce by paratomy. A worm usually consists of two to eight zooids; the first zooid having a species-specific number of segments. Paired female gonads develop in the midregion of the body and paired male gonads in anterior and posterior segments. The glandular epithelium ventral to the ovary forms a gonopore. Sperm are discharged through the metanephridia and appear to be transferred directly into the spermathecae (Bunke 1988).

Family Parergodrilidae

Parergodrilids are very small grub-shaped worms that lack head and pygidial appendages and parapodial lobes (Fig. 1.130A). They are either marine, inhabiting sands of the upper beach slope (*Stygocapitella*) or terrestrial, inhabiting decomposing terrestrial plant debris (*Parergodrilus*).

The family was erected by Reisinger (1925) based on the freshwater genus, *Parergodrilus*, from Austria. Only two species are known: *Parergodrilus heideri* is found throughout Europe in thick, wet layers of decomposing litter and rotten stumps in beechwood forest; less frequently in and beside freshwater streams and pools. *Stygocapitella subterranea* has been reported from the North-east Pacific, North Atlantic, North Sea, Mediterranean, Black Sea, as well as from the Augusta and Margaret River areas in Western Australia (Hartmann-Schröder 1983) and coarse sand beaches in New Zealand (Riser 1984). However, it is likely that *S. subterranea* consists of a complex of morphologically-similar species, especially considering that its reproductive biology is not conducive to wide dispersal of larvae (see below).

A detailed study of the morphology of the two species is provided by Karling (1958). Differences between the two species were emphasised by Karling, and a new family was created for *Stygocapitella* (Stygocapitellidae), which was considered close to Ctenodrilidae and Capitellidae. However, Reisinger (1960) found important similarities between *Parergodrilus* and *Stygocapitella* and moved the latter to the Parergodrilidae. The phylogenetic position of the family within the Polychaeta is unknown (Rouse & Fauchald 1997). A general introduction to the group can be found in Westheide (1990).

Parergodrilids have a rounded prostomium and the peristomium is a complete annulus. Antennae and palps are absent. A pair of retractable nuchal organs are present on the prostomium in *Stygocapitella* (Fig. 1.2F), but absent in *Parergodrilus* (Purschke 1986). Numerous sensory papillae cover the body surface. A muscular gular membrane is absent, but the septum behind the head is better developed than subsequent ones, which are almost lacking (Karling 1958; Reisinger 1960). Segments are few (8 to 13), all similar and lack parapodia. Aciculae are absent, but simple chaetae are present in paired ventro-lateral bundles; capillaries and furcate types in *Stygocapitella* (Fig. 1.130B, C) and spines in *Parergodrilus*. The pygidium lacks anal cirri. The eversible ventral buccal organ leads to an oesophagus, stomach, intestine and hind gut; the intestine is coiled in *Stygocapitella*. Nephridia, as metanephridia, are present along the body (*Stygocapitella*) or restricted in distribution (*Parergodrilus*). The circulatory system of *Parergodrilus* is closed and a heart body is absent; it is presumably present in *Stygocapitella* and lies at the level of the oesophagus (Westheide 1990).

The purported autapomorphy of the group is the unique arrangement of muscle and glandular cells of the ventral pharynx (Rouse & Fauchald 1997); however, the pharynx of the two genera differs slightly in the form of the tongue like-organs and the muscle bulb, present in *Stygocapitella*, is lacking in *Parergodrilus* (Purschke 1987b; Westheide 1990). The tongue-like organ can be everted and is used to browse the substratum for food particles.

A strong cuticle overlies the weak body musculature consisting of a network of circular and longitudinal muscle fibres (Karling 1958; Reisinger 1960). Movement is accomplished in *Stygocapitella* by hooking the anterior end around sand grains and pulling the body forward by muscular contraction and straightening of the posterior body (Riser 1980).

Sexes are separate. In males of *Stygocapitella*, a sperm sac containing two testes leads to a pair of spermioducts that emerge through glandular pores on the ventral side of the tenth segment (Fig. 1.130A). Females of *Stygocapitella* have an ovarial sac containing two ovaries that leads to a pair of

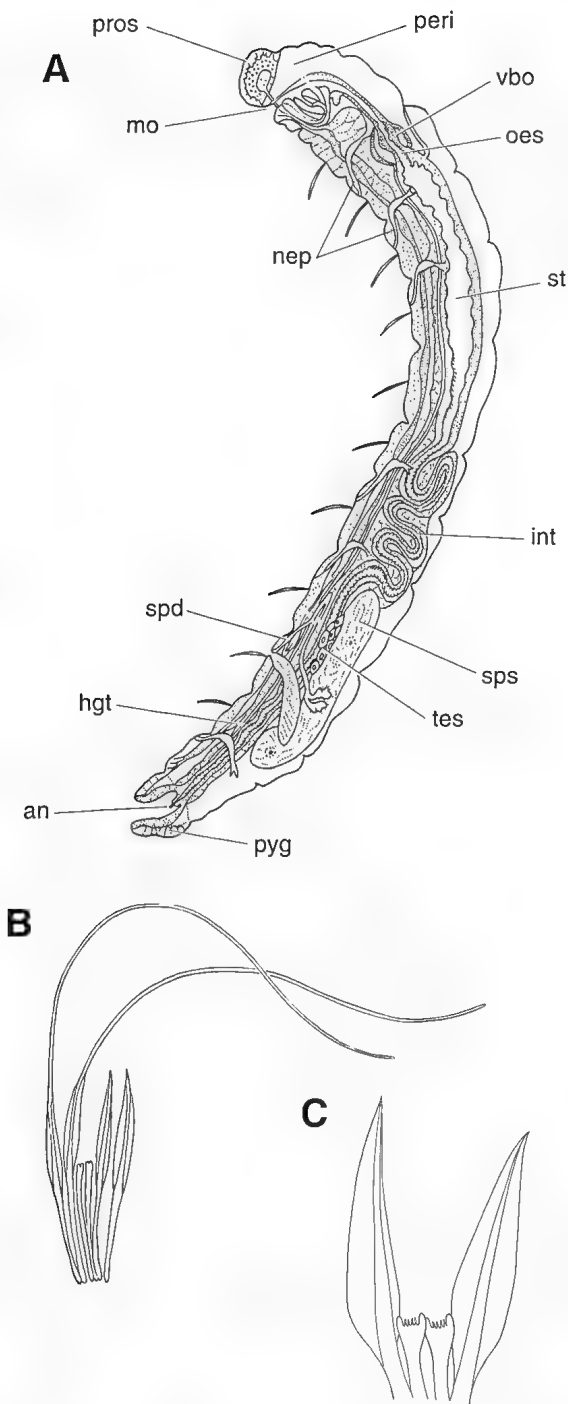


Figure 1.130 Family Parergodrilidae. *Stygocapitella subterranea*. **A**, entire animal, sagittal view of a male. **B**, chaetae from parapodium of chaetiger 1. **C**, chaetae from parapodium of chaetiger 2; specimen from southwestern Australia. **an**, anus; **hgt**, hindgut; **int**, intestine; **mo**, mouth; **oes**, oesophagus; **peri**, peristomium; **pros**, prostomium; **pyg**, pygidium; **spd**, sperm duct; **sps**, sperm sac; **st**, stomach; **tes**, testis **vbo**, ventral buccal organ. (A, C, after Karling 1958; B, after Hartmann-Schröder 1983) [K. Nolan]

oviducts that emerge through pores on the ventral side of the body between segments 10 and 11. Part of the oviduct functions as a seminal receptacle suggesting that copulation and internal fertilisation occur (Westheide 1990). *Stygocapitella* produce large yolky eggs (Riser 1984). The eggs are shed with a jelly cover and fixed between sand grains; development is direct with 4-chaetiger stage juveniles resembling adults (Westheide 1990).

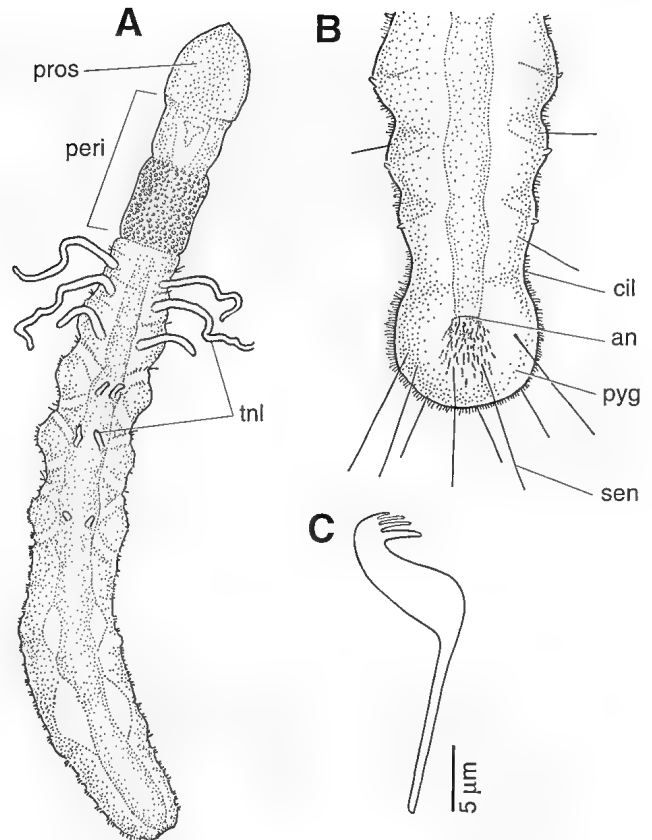


Figure 1.131 Family Psammodrilidae. *Psammodrilus balanoglossoides*. **A**, entire animal, dorsal view. **B**, pygidium, dorsal view. **C**, uncinus. **an**, anus; **cil**, cilia; **peri**, peristomium; **pros**, prostomium; **pyg**, pygidium; **sen**, sensoria; **tnl**, thoracic notopodial lobes. (After Swedmark 1952, scales not available) [K. Nolan]

Family Psammodrilidae

The Psammodrilidae are a family of small, short, grub-like polychaetes which live in interstitial habitats (Fig. 1.131A).

The prostomium is anteriorly rounded, and the peristomium forms two rings. Antennae and palps are absent. Nuchal organs are present or absent. The buccal cavity is simple, and the anterior digestive tract has a muscular ring, a feature apparently unique among polychaetes (Swedmark 1955). The first segment is not differentiated from the next segment. The anterior 'thorax' has slender notopodial lobes with aciculae; posterior 'abdomen' has indistinct neuropodia and uncinial chaetae. Tentacular cirri, dorsal and ventral cirri are absent. branchiae and pygidial cirri are absent. This description follows that of Fauchald & Rouse (1997).

Worldwide, two genera and three species are described, *Psammodrilus* with two species (*P. balanoglossoides* and *P. aedifactor*) and *Psammodriloides* with a single species (*P. fauveli*). There are no Australian records, but a species resembling *Psammodrilus balanoglossoides* was recorded by Riser (1984) from the intertidal zone of Pakiri Beach, New Zealand. Two unique features for the psammodrilids have been reported: the anterior digestive tract forms a strong muscular pump (Swedmark 1955); and aciculae lack the scleroprotein sheath which is common to other polychaetes (Kristensen & Nørrevang 1982). Many phylogenetically informative characters are absent in these small interstitial worms, and the relationship of psammodrilids to other polychaete families is unknown (Rouse & Fauchald 1997). No studies of the biology of psammodrilids have been undertaken.

1. CLASS POLYCHAETA

Appendix 1. Generic and species diversity for polychaete families of the world, arranged alphabetically by clade globally and for the Australian region (defined in Glossary). **First number in each column indicates total for genera or species; numbers of undescribed taxa, in [], are part of that total, as are Antarctic species (Ant).** + indicates an unknown number of additional taxa; Figures are based on Fauchald's (1977) list; plus data drawn from the taxonomic literature and polychaete databases maintained by the authors, the Australian Museum, Sydney and Museum Victoria, Melbourne. Readers are cautioned to note that the status of taxonomy for many families varies greatly from poorly known, unrevised groups to well-researched, recently revised groups (for example, see pp. 39 and 40). Hence numbers of genera and species listed are broad indicators of diversity only, and inappropriate for most statistical comparisons without further details for each family. * family not recorded for Australia; NZ family recorded for New Zealand; † Australian family under revision; †† Australian family recently revised; ††† major revision required; @ includes 'cosmopolitan species' undoubtedly formed of numerous sibling species.

		WORLDWIDE		AUSTRALIA	
	AUTHOR	Genera	Species	Genera	Species
SCOLECIDA					
Family Arenicolidae	Johnston, 1835	5	29[1]	2	8[1]
Family Capitellidae	Grube, 1862	42	156	ca 18	ca 37[17]
Family Cossuridae	Day, 1963	2	ca 26	1	4[4]
Family Maldanidae	Malmgren, 1867	30+	200+	8	13
Family Opheliidae	Malmgren, 1867	12	138+	5	13
Family Orbiniidae	Hartman, 1942	18	ca 150	6	ca 25
Family Paraonidae	Cerruti, 1909	12	86	3	3[+]
Family Questidae	Hartman, 1966	2	9	1	1
Family Scalibregmatidae	Malmgren, 1867	14	40+	4	7[2]
PALPATA					
ACICULATA					
EUNICIDANS					
Family Dorvilleidae	Chamberlin, 1919	33	ca 110	8	14[3]
Family Eunicidae	Berthold, 1827	9	ca 300	5	ca 40
Family Hartmaniellidae *	Imajima, 1977	1	3	–	–
Family Lumbrineridae	Schmarda, 1861	13	ca 250	4	12
Family Oeonidae	Kinberg, 1865	12	ca 100	3	6
Family Onuphidae †	Kinberg, 1865	22	ca 270	16	60[26]
EUNICIDANS incertae sedis					
Family Diurodrilidae	Kristensen & Niilonen, 1982	1	9	1	1[1]
Family Histriobdellidae	Vaillant, 1890	2	9	1	2
AMPHINOMIDANS					
Family Amphinomidae	Savigny in Lamarck, 1818	19	ca 130	ca 7	ca 22[1]
Family Euprosinidae	Williams, 1851	5	53+	1	ca 7[6]
PHYLLODOCIDA					
Family Acoetidae	Kinberg, 1856	9	43	3	3
Family Alciopidae	Ehlers, 1864	10	34	3	7[1](3Ant)
Family Aphroditidae ††	Malmgren, 1867	7	75	5	18
Family Chrysopetalidae †	Ehlers, 1864	11	41	9	23[18]
Family Eulepethidae	Chamberlin, 1919	6	14	2	[3]
Family Glyceridae	Grube, 1850	3	78	2	9
Family Goniadidae	Kinberg, 1866	9	73	4	9(6)
Family Hesionidae	Grube, 1850	22	ca 150	6+	10+
Family Ichthyotomidae *	Eisig, 1906	1	1	–	–
Family Iospilidae	Bergstrom, 1914	4	7	1	1(1 Ant)
Family Lacydoniidae	Bergstrom, 1914	2	8	1	2(2 Ant)
Family Lopadorhynchidae	Claparede, 1868	4	16	2	3(3 Ant)
Family Nautiliellidae *	Miura & Laubier, 1990	1	1	–	–
Family Nephtyidae †	Grube, 1850	5	120	4	18
Family Nereididae †	Johnston, 1865	43	535	21	86
Family Paralacydoniidae	Pettibone, 1963	1	2	1	1
Family Pholoidae ††	Kinberg, 1858	6	12	2	3
Family Phyllodocidae	Orsted, 1843	18	356	11	35
Family Pilargidae	Saint-Joseph, 1899	10	53	8	8[+]

		WORLDWIDE		AUSTRALIA	
	AUTHOR	Genera	Species	Genera	Species
Family Pisionidae	Levinsen, 1887	4	23	1	2
Family Polynoidae †††	Malmgren, 1867	165	748	ca 28	ca 87
Family Pontodoridae *	Bergstrom, 1914	1	1	—	—
Family Sigalionidae †	Malmgren, 1867	18	180	10	20
Family Sphaerodoridae	Malmgren, 1867	10	79	3	8[4+](+Ant)
Family Syllidae	Grube, 1850	66	819	ca 32	77+
Family Tomopteridae	Johnston, 1865	2	41	1	3
Family Typhloscolecidae	Uljanin, 1878	3	13	2	2(2Ant)
ACICULATA incertae sedis					
Family Aberrantidae *	Wolf, 1987	1	2	—	—
Family Nerillidae	Levinsen, 1883	15	ca 40	1	2[1]
Family Spintheridae	Johnston, 1865	1	12	1	1
CANALIPALPATA					
SABELLIDA					
Family Oweniidae @	Rioja, 1917	5	30	5[4]	5[4+]
Family Sabellariidae †	Johnston, 1865	11	107	1	18[14]
Family Sabellidae	Malmgren, 1867	39	344	13	30+
Family Serpulidae	Johnston, 1865	80	402	36	88
SPIONIDA					
Family Apistobranchidae	Mesnil & Caullery, 1898	1	6	1	1(1Ant)
Family Chaetopteridae	Audouin & Milne Edwards, 1833	4	41	4	7
Family Longosomatidae * NZ	Hartman, 1944	1	6	—	—
Family Magelonidae	Cunningham & Ramage, 1888	1	50	1	7[4]
Family Poecilochaetidae	Hannerz, 1956	1	31	1	4[3]
Family Spionidae	Grube, 1850	38	453	24	81
Family Trochochaetidae * NZ	Pettibone, 1963	1	11	—	—
Family Uncispionidae *	Green, 1982	1	1	—	—
TEREBELLIDA					
Family Acrocirridae	Banse, 1969	2+1	24	2	2
Family Alvinellidae *	Desbruyeres & Laubier, 1986	2	ca 14	—	—
Family Ampharetidae †	Malmgren, 1866	76	210+	15	18[11]
Family Cirratulidae	Carus, 1863	11	159	8	14
Family Ctenodrilidae	Kennel, 1882	7	9+	1	[2+]
Family Fauveliopsidae	Hartman, 1971	1	ca 20	1	1(1Ant)
Family Flabelligeridae	Saint-Joseph, 1894	17	ca 130	6	8
Family Pectinariidae †	Quatrefages, 1866	5	ca 51	2	6[5]
Family Pocobiidae *	Heath, 1930	1	1	—	—
Family Sternaspidae	Carus, 1863	1	12	1	1
Family Terebellidae ††	Malmgren, 1867	61	452	32	110
Family Trichobranchidae †† @	Malmgren, 1866	5	30+	4	10
CANALIPALPATA incertae sedis					
Family Polygordiidae *	Czerniavsky, 1881a	2	16	—	—
Family Protodrilidae	Czerniavsky, 1881a	2	31–34	1	[3]
Family Protodriloididae * NZ	Purschke & Jouin, 1988	1	2	—	—
Family Saccocirridae	Czerniavsky, 1881b	1	ca 20	1	5[3]
POLYCHAETA incertae sedis					
Family Aeolosomatidae	Beddard, 1895	3	ca 30	1	[1+]
Family Parergodrilidae	Reisinger, 1925	2	2	1	1
Family Potamodrilidae *	Bunke, 1967	1	1	—	—
Family Psammodrilidae * NZ	Swedmark, 1952	2	3	—	—

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2. CLASS MYZOSTOMIDA

Mark J. Grygier

DEFINITION AND GENERAL DESCRIPTION

Myzostomes are soft-bodied marine worms that are almost all commensal with, or parasites of echinoderms, especially crinoids but also ophiuroids and asteroids (Pls 10.1–10.4). They have diverse body forms (see Fig. 2.1): some are elongate, oval or disc-like; others are irregular. They are superficially unsegmented, but the repetition of certain body parts has usually been considered an indication of metamerism. A coelom is lacking or, interpreted otherwise, is represented only by the internal spaces of the female and male reproductive systems. A proboscis or introvert is often present (Figs 2.2A, 2.13B, 2.15, 2.19A), derived ontogenetically either from the entire anterior end of the body (in the order Proboscidea) or from the rear of the oral cavity (in the order Pharyngidea). Five pairs of unarticulated, unbranched legs or parapodia are present, each containing a protrusible hook, usually some replacement hooks and a support rod (or aciculum) (Fig. 2.4A). The hook apparatus is almost always present even when the parapodia are rudimentary (Figs 2.10B, 2.12, 2.13B, 2.14E). Most species have sucker- or pit-like lateral organs which are usually protrusible; their number and location vary (Figs 2.11A, 2.14B, 2.15, 2.17A, 2.18, 2.19A). The body margin often bears cirri (Figs 2.1A–C, E, F, 2.2B).

The epidermis is overlain by a thin cuticle and is usually a myo-epithelium with a basal membrane (Fig. 2.3A) or a syncytium with sunken nuclei. It may be ciliated. The dermis surrounding the internal organs consists of obliquely striated muscles and parenchyma cells (Fig. 2.3A).

The gut is entire, but the locations of the mouth (or, alternatively, the proboscis pocket opening) and anus are variable: dorsal, marginal or ventral in different taxa. The pharynx is surrounded by a muscle bulb (Figs 2.2A, 2.10A, 2.11A, B; 2.12, 2.14A, E, 2.16B, 2.17B, 2.18, 2.19B); jaws and teeth are absent. One to three (rarely more) pairs of branched or, rarely, anastomosing diverticula extend from the stomach (Figs 2.2C, 2.12, 2.14D, 2.17A, 2.18), except in one species. The intestine usually resembles a cloaca (Figs 2.2A, C, 2.11B, 2.17B, 2.18, 2.19B) in that it receives one pair (rarely more) of ducts, sometimes partly fused, from the anterior part of the uterus; in one genus the common pore of the ducts is external (Fig. 2.14A, E); in a few species the ducts are absent. These ducts have been most commonly called metanephridia, but any role in excretion or gamete release is doubtful. However, five pairs of protonephridia are known from one species. The nervous system (see Figs 2.6, 2.11A, C; 2.16D; 2.18) has a circum-oesophageal ring with poorly developed cerebral ganglia, a peribulbar or a prebulbar nerve ring in the proboscis, and a ventral nerve cord that is, fundamentally, long and ladder-like, but most often is

condensed to a single cord or a compact mass; five pairs of major lateral nerves serve the parapodia, and up to six pairs of intermediate nerves may be present.

Myzostomes are almost all protandric hermaphrodites. In the female system, lateral diverticula branch off the anterior part of the unpaired dorsal uterus (Figs 2.2C, 2.14E); these diverticula lie dorsal (rarely ventral) to the gut diverticula or enclose the latter. The posterior part of the uterus, or oviduct, lies dorsal to the intestine and opens close to the anus (Figs 2.2A, 2.14A, 2.17B, 2.19B).

The ovaries, which may be single or double, paired or unpaired; lie dorsal to the gut on the floor of the anterior part of the uterus (Figs 2.2C, 2.11B) or ventro-lateral to the gut in the uterine diverticula (Figs 2.12, 2.14B, E). Oocytes accompanied by two accessory cells implant and grow in the epithelium of the diverticula and are later released into the lumen.

The male system is paired (Figs 2.2B, 2.11A, 2.12, 2.14D, 2.16C, 2.18). The testes are diffuse or compact and usually lie ventral to the digestive system, but occasionally are dorsal. The seminal ducts empty through one or two pairs of vasa deferentia into a pair of seminal vesicles (sometimes absent) that exit lateral to the third pair of parapodia. A pair of protrusible penes may be present. Spermatozoa develop in vacuoles inside spermiocysts. In the mature spermatozoon (Fig. 2.7A–C), the flagellum passes alongside and outside the main cell body and has a centriolar derivative at its free end; there is no nuclear membrane, and the chromatin is condensed into one or more rows of bead-like bodies.

Hypodermic internal fertilisation takes place by means of a spermathecal syncytium derived from spermiocysts that are transferred in a spermatophore (Fig. 2.7D).

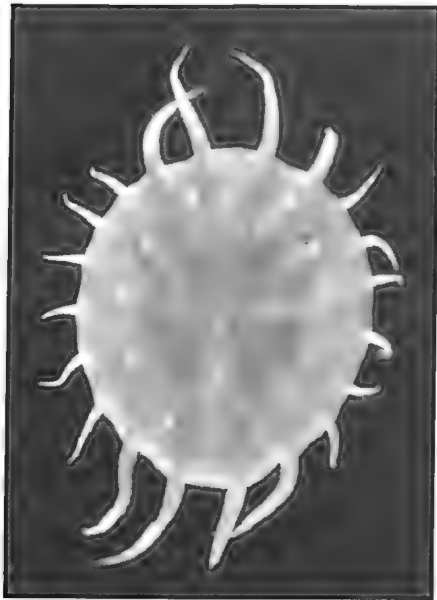
The larva (Fig. 2.8) is a trochophore that temporarily develops two clusters of chaetae and a retractable caudal process.

The Myzostomida comprises two orders and eight families. Two families, Myzostomatidae and Endomyzostomatidae, are known from Australian waters.

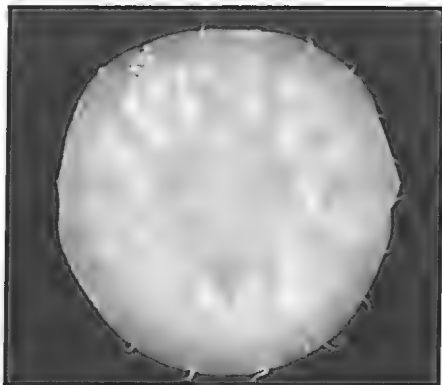
HISTORY OF DISCOVERY

Myzostome worms were first discovered on crinoids (*Antedon* species) in European seas in the 1820s. Pioneering studies on the two common species, *Myzostoma cirriferum* and *M. glabrum*, were published from the 1840s through to the mid-1860s (see citations in Graff 1877 and Nansen 1885). In his worldwide monographic studies, Graff (1877, 1883, 1884a, 1884b, 1884c, 1885a, 1885b, 1887) described more than half of the known species of crinoid-associated

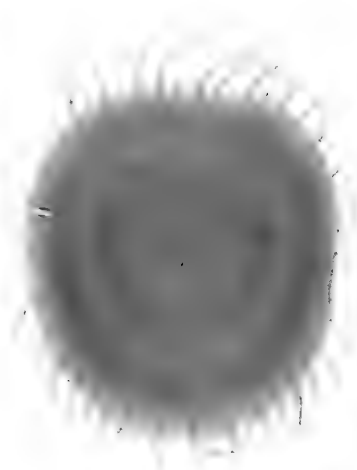
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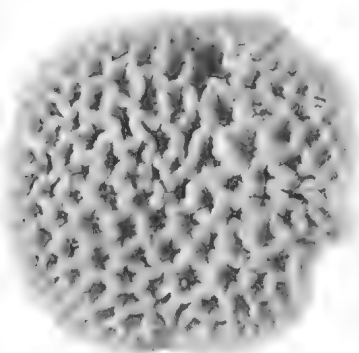
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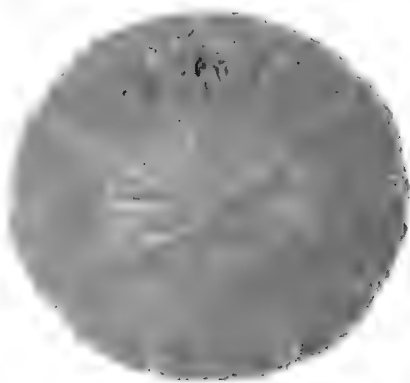
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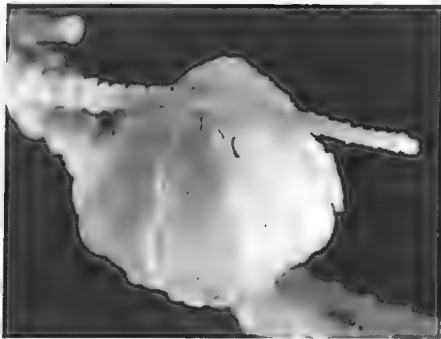
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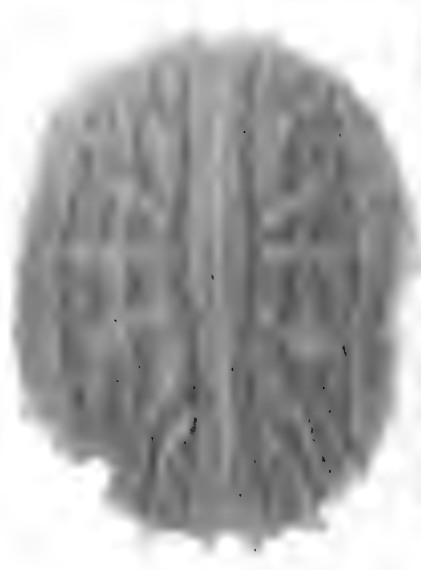
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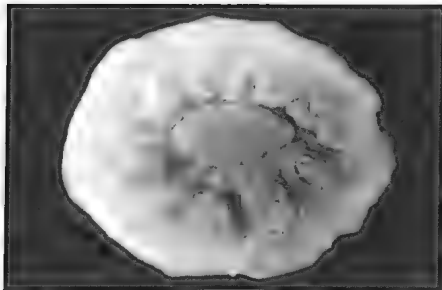
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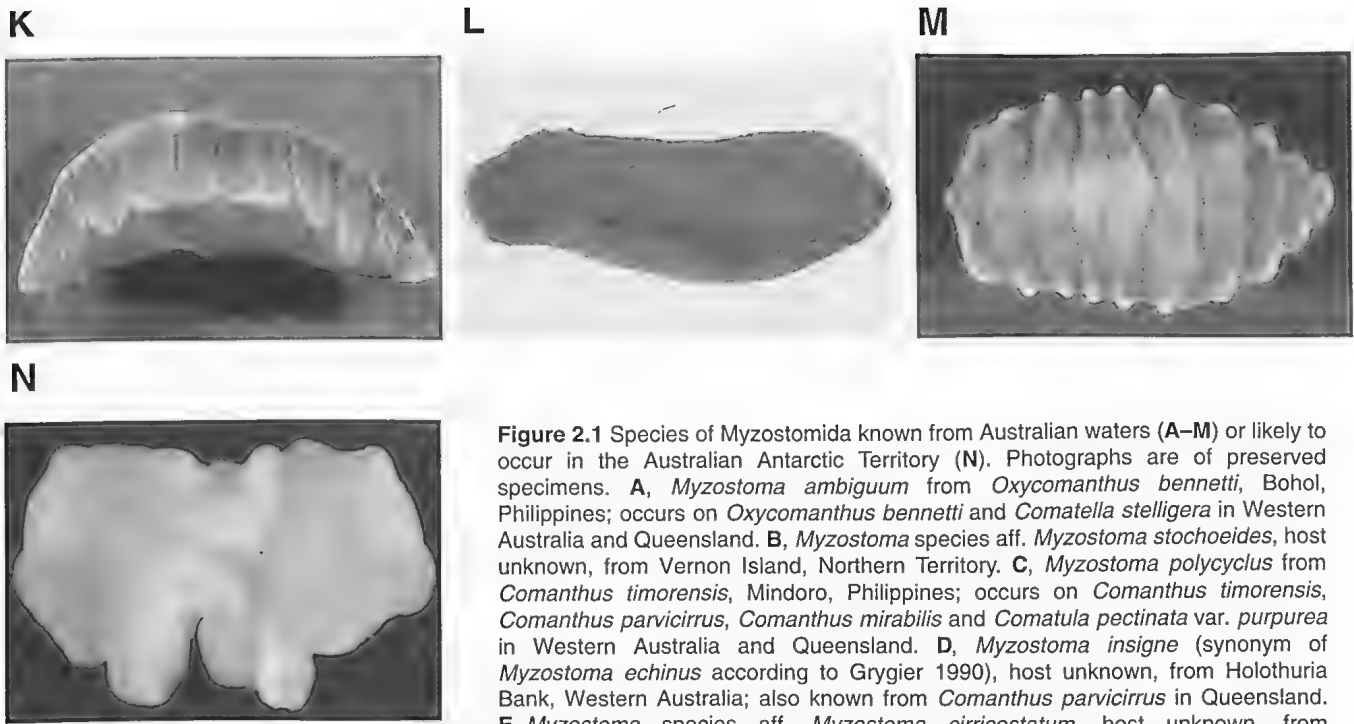


Figure 2.1 Species of Myzostomida known from Australian waters (A–M) or likely to occur in the Australian Antarctic Territory (N). Photographs are of preserved specimens. **A**, *Myzostoma ambiguum* from *Oxycomanthus bennetti*, Bohol, Philippines; occurs on *Oxycomanthus bennetti* and *Comatella stelligera* in Western Australia and Queensland. **B**, *Myzostoma* species aff. *Myzostoma stochoeides*, host unknown, from Vernon Island, Northern Territory. **C**, *Myzostoma polycyclus* from *Comanthus timorensis*, Mindoro, Philippines; occurs on *Comanthus timorensis*, *Comanthus parvicirrus*, *Comanthus mirabilis* and *Comatula pectinata* var. *purpurea* in Western Australia and Queensland. **D**, *Myzostoma insigne* (synonym of *Myzostoma echinus* according to Grygier 1990), host unknown, from Holothuria Bank, Western Australia; also known from *Comanthus parvicirrus* in Queensland. **E**, *Myzostoma* species aff. *Myzostoma cirricostatum*, host unknown, from

Halmahera, Indonesia; occurs on *Lamprometra palmata* and *Comanthus* species in Western Australia. **F**, *Myzostoma mortenseni*, host unknown, from Lizard Island, Queensland (same specimen photographed in life by Stamman *et al.* 1985); also known from *Comanthina schlegeli*, *Comanthus briareus*, *Comaster gracilis* and perhaps *Himerometra* species in Queensland. **G**, *Myzostoma plicatum* from *Lamprometra palmata*, Houtman Abrolhos, Western Australia; also known from *Lamprometra palmata*, *Stephanometra spinipinna* and *Comatella stelligera* in Queensland. **H**, gall of *Myzostoma willemoesii* on *Glyptometra tuberosa*, Negros, Philippines; occurs on *Glyptometra inaequalis* off New South Wales. **I**, *Myzostoma fissum* (synonym: *Myzostoma striatum*; see Eeckhaut *et al.* 1998) from *Lamprometra palmata*, Houtman Abrolhos, Western Australia; widespread in Australia on *Lamprometra palmata*. **J**, *Notopharyngoides aruensis* from *Oxymetra erinacea*, Sunda Strait, Indonesia; occurs in Northern Territory and Queensland, on *Stephanometra oxyacantha* in the latter instance. **K**, *Hypomyzostoma* species (Myzostoma species 4 of Grygier 1988) from *Lamprometra palmata*, Cobourg Peninsula, Northern Territory; also known from *Lamprometra palmata* in Western Australia. **L**, *Hypomyzostoma nanseni* from *Stephanometra spicata*, Cobourg Peninsula, Northern Territory; also known from *Stephanometra oxyacantha* in Queensland and *Lamprometra palmata* in Western Australia. **M**, *Hypomyzostoma sulcatum*, host unknown, Darwin, Northern Territory; also known from *Oligometrides adeonae* in Western Australia. **N**, *Asteromyzostomum* species of Grygier (1988) from sea star *Labidiaster* species, near McMurdo Sound, Antarctica. The specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (A, C, E, L, M, N), the Natural History Museum, London (F, G, H), the Australian Museum, Sydney (D), and the Northern Territory Museum of Arts and Sciences, Darwin (B, I, J, K). [M.J. Grygier]

myzostomes. Works by other authors include: regional taxonomic studies by McClendon (1906), Boulenger (1913), Remscheid (1918) and Atkins (1927); a controversy about the sexual system between Beard (1884, 1898) and Wheeler (1896, 1899), and; anatomical studies of *Myzostoma*, *Asteriomyzostomum* and *Protomyzostomum* by Nansen (1885, 1887), Stummer-Traunfels (1903) and Fedotov (1912, 1914, 1916, 1925, 1929), respectively. Stummer-Traunfels (1926) comprehensively reviewed the earlier literature and Jägersten (1936, 1937, 1939a, 1939b, 1940a, 1940b) studied the histology, reproductive biology and taxonomy of several genera, with particular attention to *M. cirriferum*. Jägersten's (1940a) systematic synthesis largely inspired the review by Prenant (1959) and represented the state of the art in myzostome studies for decades except for a few significant, but isolated works (see for example, Kato 1952; Wagin 1954). In the 1980s, taxonomic studies on the group were revived (for example, Grygier 1989, 1990, 1992; Eeckhaut, VandenSpiegel & Grygier 1994; Eeckhaut & Jangoux 1995; Eeckhaut 1998; Eeckhaut, Grygier & Deheyn 1998) and electron microscopical studies of the reproductive biology, spermatology and general anatomy were initiated (for example, Afzelius 1983, 1984; Pietsch & Westheide 1987; Mattei & Marchand 1988; Eeckhaut & Jangoux 1992, 1993a, 1993b, 1995, 1997; Eeckhaut 1995; Eeckhaut, Dochy & Jangoux 1995).

Very little work has been done on Australian Myzostomida. Graff (1884b, 1887) described a few species collected by the *Challenger* Expedition in the Torres Strait and Arafura Sea; most of his material is housed in The Natural History Museum, London. Potts (1915) studied the coloration of specimens from Murray Island, Torres Strait, in relation to their hosts' coloration, and Atkins (1927) described the species involved; efforts to locate this collection have failed. Day & Hutchings (1979) listed the Australian species based on the earlier papers, and Jangoux (1987, 1990) listed the cysticolous and gallicolous species. Stamman, Phillips, Phillips & Segar (1985) published a colour photograph of a living Australian specimen on its host, and Eeckhaut *et al.* (1998) identified it (Fig. 2.1F herein). Lester & Sewell (1989) reported unidentified myzostomes on five species of comatulid crinoids at Heron Island. Fabricius & Dale (1993) documented the presence and relative abundance of myzostomes on 15 species of comatulids from the central part of the Great Barrier Reef, especially Davies Reef; efforts to locate this large collection have also been unsuccessful. Grygier's (1990) summary of literature records and unpublished museum collections showed the presence of at least 20 species in Queensland, 17 in the Northern Territory and one in South Australia; Grygier (1989, 1992) gave detailed distribution data for two of these species. Eeckhaut *et al.* (1998) described, illustrated and provided

2. CLASS MYZOSTOMIDA

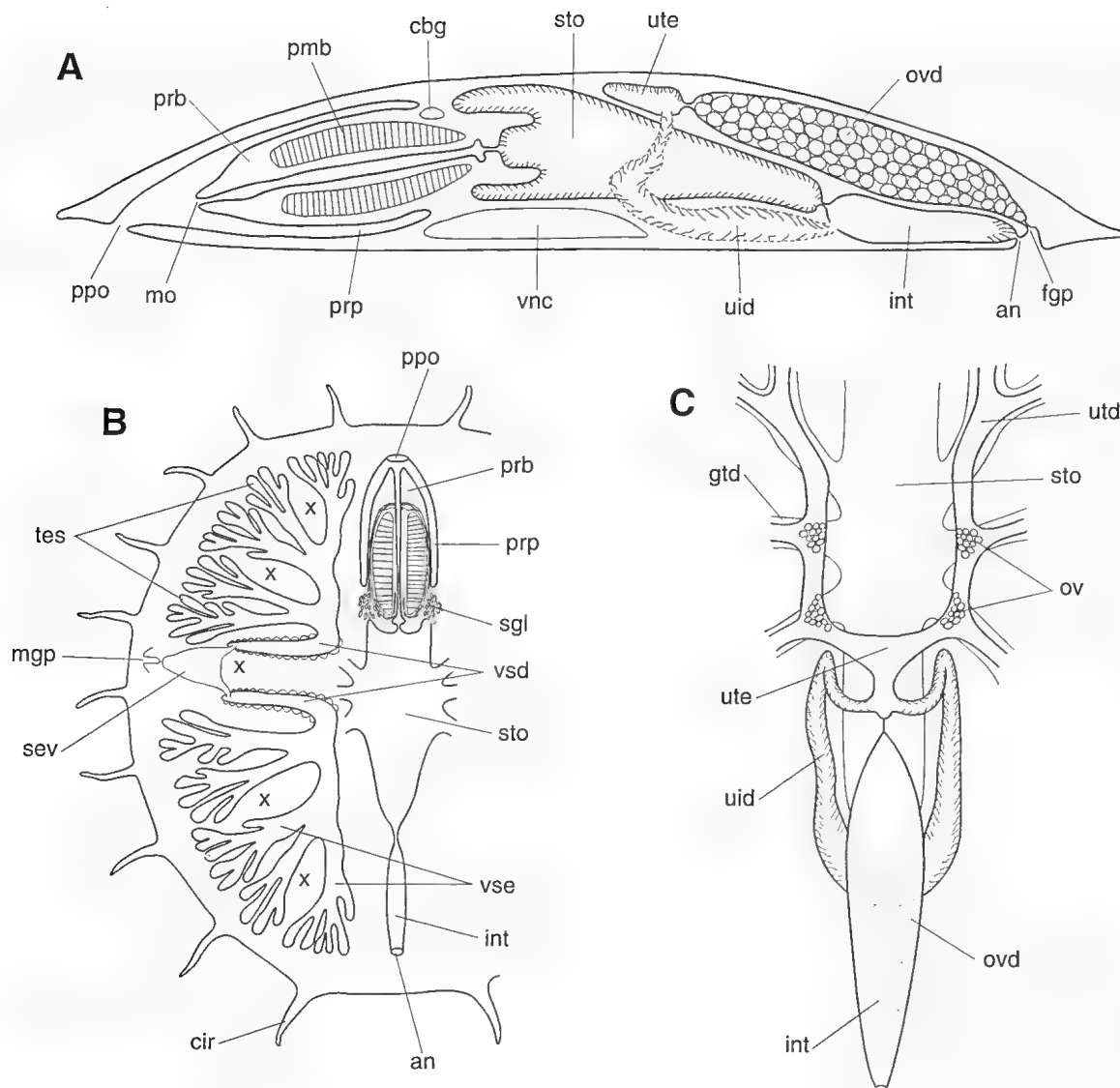


Figure 2.2 Anatomy of *Myzostoma cirriferum* (Myzostomatidae, Proboscidea). **A**, internal organs, sagittal view. **B**, digestive tract and male reproductive system, ventral view. **C**, digestive tract and female reproductive system, dorsal view. an, anus; cbg, cerebral ganglion; cir, marginal cirrus; fgp, female genital pore; gtd, gut diverticula; int, intestine; mo, mouth; mgp, male genital pore; ov, ovaries; ovd, oviduct; pmb, pharyngeal muscle bulb; ppo, proboscis pocket opening; prb, proboscis; prp, proboscis pocket; sev, seminal vesicle; sgl, salivary gland; sto, stomach; tes, testes; uid, utero-intestinal duct; utd, uterine diverticula; ute, uterus; vnc, ventral nerve cord (or mass); vsd, vas deferens; vse, vas efferens; x, sites of parapodia. (After Jägersten 1939b)

[I. Hallam]

distribution maps and new Australian records for eight species of myzostomes, one of them new. Most of these Australian myzostome specimens are in the National Museum of Natural History, Smithsonian Institution, the Museum of Comparative Zoology, the Australian Museum, the Western Australian Museum and the Northern Territory Museum of Arts and Sciences. In order to prepare the present review, the author examined additional unpublished collections housed in some of these museums.

No myzostomes have been reported from the Australian External Territories. Six species of *Myzostoma*, *Proto-myzostomum*, *Endomyzostoma* and *Asteromyzostomum* have been recorded from crinoid, ophiuroid and asteroid hosts in Antarctic waters (Stummer-Traunfels 1908; Boulenger 1916; Fauvel 1936; Grygier 1988, 1989; Bartsch & Faubel 1995), but from the Antarctic Peninsula and the Weddell, Bellinghausen and Ross Seas, not the Australian Antarctic Territory.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Myzostomes are basically bilaterally symmetrical, often with a superficial, superimposed radial symmetry. They are not segmented *per se*, but there is a certain repetition of body parts. The body form varies from elongate and 'worm-shaped', as in *Mesomyzostoma* species (Fig. 2.12), to oval, shield-shaped or circular, as in many species of *Myzostoma* (Fig. 2.1A–F). Species of *Asteriomyzostomum*, and especially those of *Contramyzostoma* (Fig. 2.15) and *Asteromyzostomum* (Figs 2.1N, 2.18), have a body that is broader than it is long. The worms are usually flat and thin, but may also be thick and dome-shaped, semi-cylindrical or even mushroom-shaped. Diverse elaborations of the posterior end of the body are common in species of *Myzostoma* (Fig. 2.1H) and *Asteromyzostomum* (Figs 2.1N, 2.18). Radial or transverse

dorsal ridges are present in many Myzostomatidae (Fig. 2.1G, I, M), and some species of *Myzostoma* have plate-like thickenings, prominent papillae or reticulate ridges on the dorsal side (Fig. 2.1E). The body margin of most myzostomatids and some endomyzostomatids bears cirri; their numbers and lengths are important diagnostic features. Typically 10 pairs (Fig. 2.1A, B), often more (Fig. 2.1C, F), and sometimes fewer or none (Fig. 2.1J) are present. Some myzostomatids, particularly *Hypomyzostoma* species (Fig. 2.1K, L), have numerous large or small marginal scallopings or irregular margins instead of discrete cirri.

Members of the Myzostomatidae have a retractable proboscis that often bears several pairs of buccal papillae (Fig. 2.1D). The proboscis of *Pulvinomyzostomum* and *Endomyzostoma* species is not homologous with this and is never so armed.

Most myzostomes have five pairs of legs or parapodia (examples in Fig. 2.1), all of which have a protrusible, hook-shaped chaeta (Figs 2.2B, 2.4). The parapodia tend to be inconspicuous except in myzostomatids, in which they are well developed, lobiform and often highly extensile. Sometimes they bear a button-like or pointed cirrus on the medial side of their proximal fold.

Most myzostomes also have sucker- or pit-like lateral organs that are often protrusible and sensory in function. Myzostomatids have four pairs of lateral organs, each pair alternating with the parapodia (Fig. 2.1B). However, in other

families they are located in different positions, or in greater or lesser numbers (Figs 2.11A, 2.15, 2.17A, 2.18) or may even be absent.

Body Wall and Musculature

Many histological studies of the integument have been made, but transmission electron microscopical studies are few and concern only *Myzostoma cirriferum* and *Contramyzostoma bialatum* (see Eeckhaut & Jangoux 1993a, 1995; Eeckhaut 1995). The following description is based on the former species.

The epidermis, bounded by a cuticle and basement membrane (Fig. 2.3A), consists of sensory-secretory areas and non-innervated, myo-epithelial areas. Sensory-secretory areas are found on the cirri, body margin, buccal papillae, parapodia and parapodial folds (see nervous system section below). Myo-epithelial areas (Fig. 2.3A) comprise covering cells, ciliated cells and myo-epithelial cells. The covering and ciliated cells are covered densely with microvilli that protrude nearly all the way through the four-layered cuticle, and are joined together by a zonula adhaerens and a septate desmosome. The ciliated cells are dispersed and each has a tuft of simple or paddle-shaped cilia (see Eeckhaut *et al.* 1994) with $9 \times 2 + 2$ axonemes and ciliary rootlets. The myo-epithelial cells lie beneath the other cells, perpendicular to the

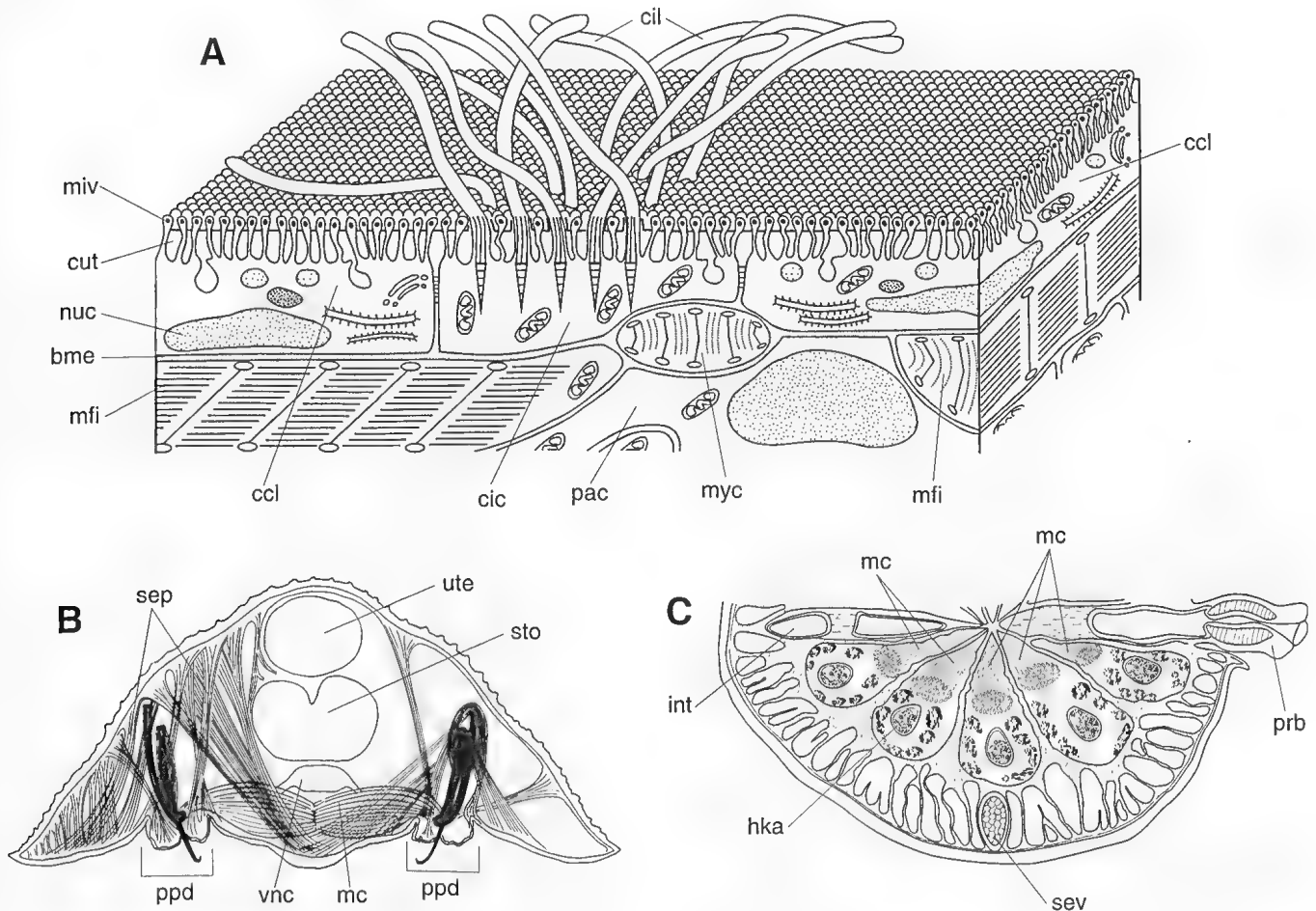


Figure 2.3 A, microanatomy of the non-sensory integument (three cell types underlain by a basal membrane) of *Myzostoma cirriferum*. B, C, musculature of *Myzostoma glabrum*: B, semi-transverse view showing muscular septum on left and parts of parapodial musculature on left and right; C, half a horizontal section showing ventral musculature. bme, basement membrane; ccl, covering cell; cic, ciliated cell; cil, cilia; cut, cuticle; hka, parapodial hook apparatus; int, intestine; mc, muscular centralis; mfi, muscle fibre in dermis; miv, microvilli; myc, myo-epithelial cell; nuc, nucleus; pac, parenchyma cell; ppd, parapodium; prb, proboscis; sep, septa; sev, seminal vesicle; sto, stomach; ute, uterus; vnc, ventral nerve cord (or nerve mass). (A, after Eeckhaut & Jangoux 1993a; B, C, after Graff 1877)

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2. CLASS MYZOSTOMIDA

antero-posterior axis of the body and in contact with the basement membrane; the myofibrils within them, although parallel, show no regular arrangement in cross section. Species of *Contramyzostoma* also have covering cells, myo-epithelial cells and patches of cilia.

The integument is unciliated in most pharyngidean genera, but is ciliated in patches in *Endomyzostoma* species and uniformly ciliated in *Pulvinomyzostomum* and male *Mycomyzostoma*. The cuticle of *Asteriomyzostomum asteriae* is uniquely formed from the individual caps on each epidermal cell. The integumental musculature in all myzostomes comprises circular and longitudinal fibres. These lie below the uninterrupted basement membrane of the epidermis in *Myzostoma* (Fig. 2.3A). In contrast, in *Proto-myzostomum* and *Stelechopus*, in which the epidermal cells reportedly form a syncytium and, at least in the former genus, there is no basement membrane, the epidermis nuclei are sunken below the integumental muscles (Fedotov 1914; Jägersten 1940a; Nigmatullin 1970; Bartsch & Faubel 1995). In species of *Asteriomyzostomum*, the epidermal cell nuclei are sunken through *holes* in the basal membrane (Wagin 1954).

Beneath the epidermis and filling the spaces around the gonads and digestive system is a dermis consisting of double obliquely striated muscle fibres and parenchyma cells that are variable in form (Fig. 2.3A). In some species, the dorsal part of the dermis includes a thick collagenous layer (Rao & Sowbhagyavathi 1974).

The musculature of motile forms like *Myzostoma* species (Fig. 2.3B, C; see Graff 1877) includes, in addition to the integumental muscles, dorso-ventral muscles that form the septa, the muscles of the parapodia and lateral organs, the longitudinal retractor muscles of the proboscis, sheaths of circular and longitudinal muscle fibres around the internal organs and muscle sheets above and below the nervous system. In *Myzostoma*, a ventral muscle mass composed of radially directed fibres is especially well developed (Fig. 2.3C). The mass includes: the five pairs of muscoli centrales of the parapodia; the anterior proboscis retractor; the posterior muscles that surround the intestine, and; twelve primary septa. These septa alternate with the parapodia and divide distally to encompass the lateral organs and then form a connected web of secondary radial septa near the margin.

The ten lateral body chambers defined by the primary septa are open to the main longitudinal chamber in which the uterus, gut and nervous system lie (Fig. 2.3B). The more central dorso-ventral muscles that make up the septal walls converge on the ventral muscle mass, whereas those nearer the margin converge ventrally outward (Fig. 2.3B); the muscles that make up the secondary septa run straight up and down. In a very robust species, such as *M. glabrum* (Fig. 2.3B), the gaps between the component muscles of the septa are small, whereas in others, such as *M. cirriferum*, the gaps are great, there are no real body chambers, and most of the muscles run directly dorso-ventrally.

There is no mineralised skeleton nor any evidence of a hydrostatic skeleton. The only hard parts are the parapodial hook apparatus described below.

Locomotion

Some species are more motile than others. Cysticolous, gallicolous and endoparasitic forms are immotile. In motile members of the Myzostomatidae, the parapodia are capable of great extension and have a powerful, complex musculature. They consist of two parts (Fig. 2.4A): the parapodial fold,

which is a low, obliquely conical continuation of the ventral body wall that may have a cirrus on its medial face, and the parapodium itself. The support rod (aciculum) within provides support for the limb, and the rod's distal manubrium guides the hook that provides traction; the hook can be withdrawn inside the parapodium. The support rod is permanent, but one or more replacement hooks are constantly being secreted.

Stummer-Traunfels (1903, 1910) described in great detail the internal structure of the parapodia of *Asteriomyzostomum asteriae* and *Myzostoma gigas* (for the latter, see Fig. 2.4A). The external integument, minus most muscles except for

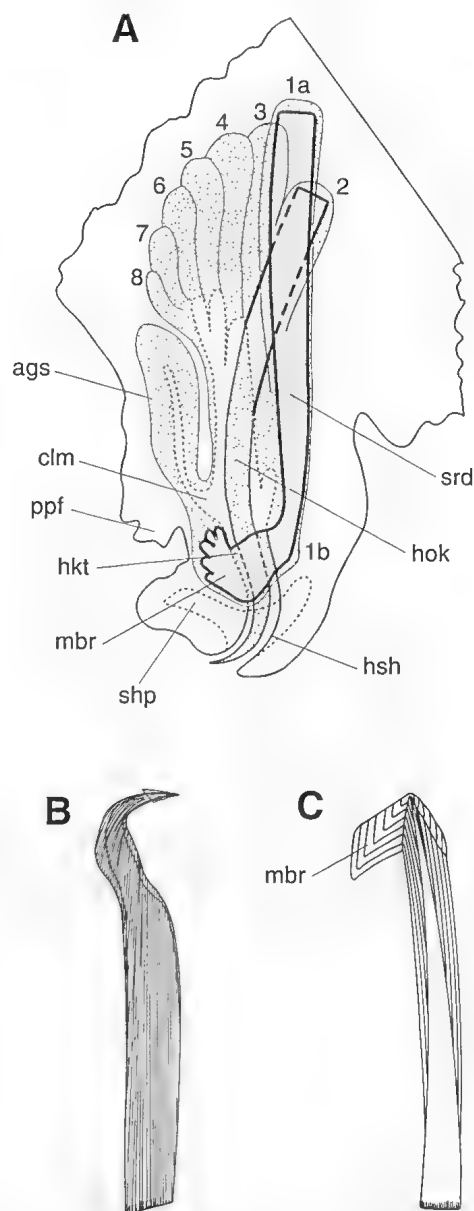


Figure 2.4 Parapodium, hook and support rod structure in *Myzostoma*. **A**, chaetal gland of parapodium of *Myzostoma gigas*. **B**, a hook of *Myzostoma* species (reported as *Myzostomum ambiguum*) with artificially loosened sheath at tip and internal tubes shown as striae. **C**, support rod of *Myzostoma gigas* showing central core of shaft (structurally equivalent to hook), concentric layers of mantle around core and growth lines of distal manubrium. **ags**, accessory gland sac; **clm**, central lumen; **hkt**, hook tube; **hok**, hook; **hsh**, hook sheath; **mbr**, manubrium; **ppf**, parapodial fold; **shp**, sheath pocket; **srd**, support rod; **1a**, **1b**, support rod follicles; **2–8**, hook and replacement hook follicles. (A, after Stummer-Traunfels 1926; B, C, after Jägersten 1936)

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sphincters, continues inside the parapodium as the hook sheath. Parapodial glands presumably empty a lubricating fluid into the sheath pocket, a diverticulum of the hook sheath. More proximally is the chaetal gland or chaetal sac, consisting of several follicles that secrete the support rod, the hook in use, and a varying number of replacement hooks. The support rod's core and manubrium are secreted by the proximal and distal parts, respectively, of one follicle (two distinct follicles in *M. gigas*; Fig. 2.4A); the intervening part of the rod passes through parenchyma, which presumably secretes the mantle layer (see below). A row of replacement hook follicles in sequential stages of development leads up to the follicle of the hook in use. The hook's shaft passes first through a lumen into which accessory gland cells empty; in *M. gigas* there is a distinct accessory gland sac (Fig. 2.4A). The shaft then passes through a tube defined by the manubrium into the hook sheath, from which its tip can be protruded or retracted by muscular action. The smallest replacement hook follicles are completely enclosed, but those with more fully developed replacement hooks open into the accessory gland lumen.

Jägersten (1936) provided the most detailed light microscopical study of the microstructure of the hooks and support rods; they have generally been supposed to be chitinous structures. Both appear superficially to consist of a tapered, fibrillar core surrounded by a homogeneous mantle except near the base. In addition, the support rod has a curved manubrium attached at the tip (Fig. 2.4B, C). However, only the support rod truly has a mantle; the core of the support rod corresponds structurally to an entire hook, except that the tip of the hook has a thin protective sheath. The hooks and the support rod cores have a substructure of tightly packed, parallel tubes. At the base, processes of the basal secretory cell of the follicle penetrate into the tubes. The tubes are uniform in the support rods, but in the hooks their lumen becomes narrower nearer the sides and the material itself becomes harder; nonetheless, there is no precise boundary between the inner and outer regions. In the curved, distal part of the hook, the tubes are generally oriented obliquely relative to the long axis (Fig. 2.4B). The mantle layer of the support rod, which is secreted by cells other than the basal cell, has no tubes, but is made of several concentric, cylindrical (not conical) layers of homogeneous material (Fig. 2.4C). The manubrium consists of inner and outer secreted layers, both of which show growth lines; the irregular distal end apparently grows by the addition of small clumps of material.

The musculature of the hook apparatus is not attached directly to the hook and support rod, but to a membrane bordering the chaetal sac that is derived from the integumental basal membrane. This musculature has been described in detail for some species of *Myzostoma* (Fig. 2.3B; Graff 1877; Stummer-Traunfels 1910) and *Asteriomyzostomum* (Stummer-Traunfels 1903). The principal difference between the Myzostomatidae and the other families is the lack of a strong *musculus centralis* in the latter, whereas in the former it generally contributes to the formation of a powerful ventral muscle mass (Fig. 2.3B, C).

Feeding and Digestive System

Myzostomes associated with crinoids (except the endoparasitic *Mesomyzostoma* and stalk-dwelling *Mycomyzostoma*) all feed by means of their proboscis on particles entrained in the ambulacral grooves of their host's pinnules, arms, or disc, or, for *Pulvinomyzostomum*, in the host's gut. However, it is exceedingly uncommon to find identifiable gut contents in these worms.

The digestive system consists of a mouth, pharynx, stomach with usually two or three pairs of branching diverticula, and an intestine and anus. Jägersten (1940c), Platel (1962), Eeckhaut (1995), and Eeckhaut, Dochy & Jangoux (1995) have studied in detail the digestive system of *M. cirriferum* (Fig. 2.2A, B). In this species and other Myzostomatidae, the mouth, at the tip of a retractable proboscis that represents the anterior portion of the body, is encircled by a lip that in different species often bears several pairs, or a corona, of ciliated, sensory, buccal papillae (Fig. 2.1D). In members of the Pharyngidea, the proboscis is a protrusion of the rear of the oral cavity and lacks buccal papillae, or it is absent and the mouth is terminal (see Figs 2.10A, 2.11A, B, 2.12, 2.13B, 2.14A, D, 2.15, 2.16B, 2.17B, 2.18, 2.19). The circum-oral tentacles of *Asteromyzostomum* species are much longer than buccal papillae (Fig. 2.18); they are probably not their homologues, and serve primarily to anchor the myzostome to its host sea star's integument.

In *Myzostoma*, the pharynx traverses the proboscis and is unciliated (Fig. 2.2A). It is lined with glandular cells and is surrounded in part by a basement membrane-bounded muscle bulb with alternating radial and circular muscles. Such a muscle bulb is present in all myzostomes and serves for ingestion; the mechanism is described by Eeckhaut *et al.* (1995). Processes from salivary gland cells, deeply sunken into the parenchyma at the base of the proboscis (Fig. 2.2B), pass both inside and outside the muscle bulb to open into the pharynx at the bulb's anterior end (according to Platel 1962) or onto the lip (according to Eeckhaut *et al.* 1995); they secrete acid mucopolysaccharides (Platel 1962). Salivary glands open into the homologous region, the mouth cavity, in *Mesomyzostoma*, *Protomyzostomum* (Fig. 2.11B) and *Asteriomyzostomum* (Fig. 2.17B); no such glands occur in *Pulvinomyzostomum* and *Mycomyzostoma*.

The midgut, comprising the stomach and its diverticula (Figs 2.2A, 2.11B, 2.17B, 2.19B), is separated from the pharynx and intestine by sphincters. Diverticula are absent from female *Mycomyzostoma*; males lack a gut. In *Myzostoma*, the epithelium of the stomach, diverticula and intestine each consists of a different kind of cell; none is glandular. The stomach epithelium is ciliated (Fig. 2.2A); these cilia have a 9x2+2 axoneme and no rootlets. Such cilia are also present in *Endomyzostoma*, but are absent in *Protomyzostomum* and *Asteriomyzostomum*. Platel (1962) implied that the presence of ciliated low epithelium or unciliated high epithelium, or a mixture of the two, in the stomach of *M. cirriferum* depends on the recency of feeding. In this species, the cells of the diverticula and intestine bear microvilli, but cilia are absent except for those around the anus (Fig. 2.2A); in contrast, the entire intestine is ciliated in *Protomyzostomum* (Fig. 2.11B) and *Asteriomyzostomum*. The cells of the diverticula are vacuolated and serve both for intracellular digestion of food particles and the excretion of digestive wastes (see excretion section below).

Circulatory System and Respiration

There is no special circulatory system. The midgut diverticula, however, ramify throughout the body (Figs 2.1B, 2.12, 2.14D, 2.17A, 2.18) and serve to distribute nutriment, at least. Gills are absent, and respiration apparently takes place through the entire body surface. Some myzostomes, however, have been observed to pump sea water in and out through the anus (Nansen 1885); this may indicate an additional site of oxygen uptake. Most cysticolous and gallicolous forms maintain two openings to their domicile, which might allow for a respiratory current.

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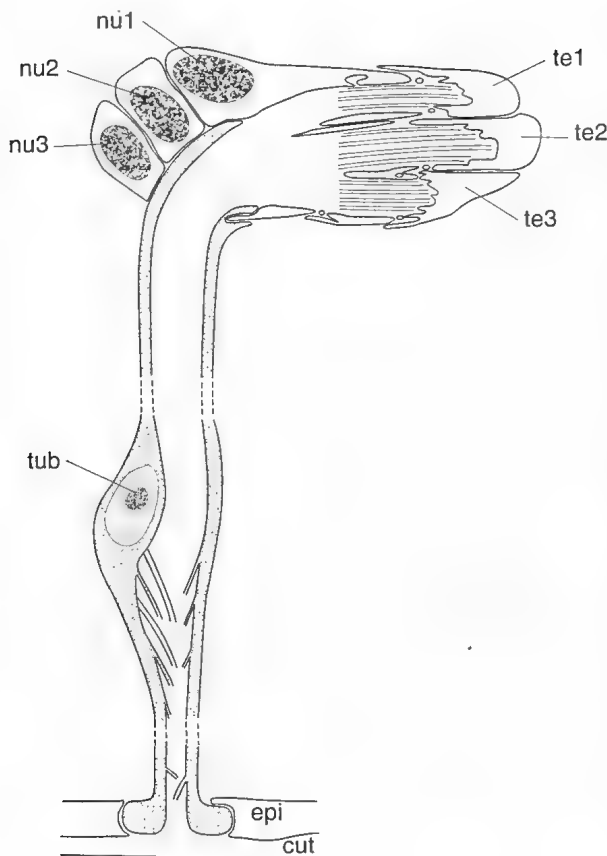


Figure 2.5 A single protonephridium of *Myzostoma cirriferum* (Myzostomatidae, Proboscidea); five pairs have been observed. **cut**, cuticle; **epi**, epidermal cell; **nu1–nu3**, nuclei of terminal cells; **te1–te3**, terminal cells; **tub**, tubule cell. (After Pietsch & Westheide 1987) [I. Hallam]

Excretion

The gut diverticula of *Myzostoma cirriferum* are the principal site of excretion of waste derived from the intracellular digestion of food (Jägersten 1940c; Platel 1962; Eeckhaut 1995; Eeckhaut *et al.* 1995). Each epithelial cell develops a large vacuole that fills with yellow-green concretions of excreta contributed by smaller endocytotic digestive vacuoles. The apical part of the cell with the vacuole buds off into the lumen as an excretory vesicle. Vesicles then accumulate in the rear of the stomach, becoming cemented together by a mucopolysaccharide into a mass that is eventually transferred into the intestine and expelled. In *Protomyzostomum*, the excreta simply fills the inside of the cell, not a special vacuole, and is released into the lumen when the cell disintegrates (Jägersten 1940a).

Five pairs of protonephridia have been found in *M. cirriferum* (Pietsch & Westheide 1987); they are located anterior to each pair of parapodia and spaced equidistantly across the midline. Each protonephridium comprises three terminal cells and a tubule cell (Fig. 2.5). Each terminal cell has six to nine flagella, each of which is encircled by 10 cytoplasmic rods, and the tubule cell is ciliated. Fenestrated regions of the terminal cells connect the lumen to the surrounding parenchyma and presumably serve for filtration. The presence of protonephridia has not yet been confirmed for any other species.

The single pair of ciliated utero-intestinal ducts (multiple sets in *Protomyzostomum polynephris*, absent in *Mycomyzostoma* and *Stelechopus*), termed nephridia by many authors, usually connect the uterus to the anterior part of the intestine; in *Endomyzostoma* these ducts pass directly to the exterior. These ducts are discussed below in connection with reproduction; they are probably not filtratory organs, but may serve to expel waste material from the uterus.

Nervous System and Sense Organs

The nervous system has been described most thoroughly for several species of *Myzostoma* (Fig. 2.6), in which it consists of a circum-oesophageal ring, proboscis nerves, a ventral nerve mass and peripheral nerves (Nansen 1885, 1887; see also Boulenger 1913). Three pairs of nerves connect a prebulbar ring, located distally in the proboscis, with the circum-oesophageal ring posteriorly; in the latter, the cerebral ganglia are very poorly developed. Nerves pass anteriorly from the prebulbar ring into each buccal papilla and two pairs of nerves travel posteriorly along the pharynx towards the base of the proboscis. The ventral nerve mass is compact and consists of ganglion cells that are located between and dorso-lateral to two longitudinal commissures. An intermediary longitudinal nerve and five major and six minor pairs of lateral nerves are also present. The longitudinal commissures are connected by a major transverse commissure at the anterior and posterior ends, four thick transverse commissures alternating with the major lateral nerves, and five minor commissures at the levels of the major lateral nerves.

Each of the five main lateral nerves on each side splits into two outer, one intermediate and two inner nerves. The two outer nerves branch extensively near the body margin and each also innervates a marginal cirrus. The two inner nerves serve the muscles and glands of the respective parapodium. The intermediate nerve bifurcates, one branch going to the musculus centralis of the respective parapodium, and the other to the body margin.

The six pairs of minor lateral nerves innervate muscles and the gonads. The first pair innervates the anterior body margin, and the sixth pair the posterior part of the body; the others each split into an upper and lower main branch and several ventrally directed branches.

Nervous connections to the lateral organs have been followed in *Protomyzostomum*, where the main lateral nerves serve these organs and the parapodia (Fedotov 1914); in *Asteriomyzostomum* branches of the intermediate nerves probably serve the lateral organs (Stummer-Traunfels 1903).

Similar compact nervous systems are found in some pharyngidean genera (Figs 2.17B, 2.18). However, elongate ones have been described in *Mesomyzostoma* and *Stelechopus*, both with a single nerve cord, and in *Protomyzostomum* species and males of *Mycomyzostoma calcidicola*, with either a single or a double nerve cord (Figs 2.11A, 2.16D); details for each genus are given in the family sections below. All have five pairs of major lateral nerves, but there are fewer minor pairs in species of *Stelechopus* and *Protomyzostomum* than in *Myzostoma*.

Sense organs are principally tactile and/or olfactory; eyes are absent. The marginal cirri and buccal papillae are evidently sensory, but in *Myzostoma cirriferum* and some other species the cirri may also have an additional function. A ventral groove lined with supposed adhesive cells runs along each

marginal cirrus. Two similar grooves run along the edges of the triangular marginal processes in species such as *M. furcatum*.

Except in some pharyngidean genera, the body is ornamented with patches of cilia. Cilia over the general body surface are evidently non-sensory (Fig. 2.3A; Eeckhaut & Jangoux 1993b), but in *M. cirriferum*, at least, those on the marginal cirri, buccal papillae, lateral organ domes, parapodia and parapodial folds, and in dorsal and ventral bands near the body margin have a sensory function. In these regions of sensory/secretory epithelium, branched nerve endings project through the basal membrane and between the basal parts of the epidermal cells. Each nerve process ends in a single cilium, presumably a mechanoreceptor.

The lateral organs, sucker-like processes found near the body margin, are now interpreted as mechano- and chemosensory structures rather than as attachment devices. Their ultrastructure has been investigated only in *M. cirriferum*

(Eeckhaut & Jangoux 1993a). In this species and other myzostomatids, there are almost always four pairs ventrally, outside of, and alternating with, the parapodia (see Fig. 2.1B). Such a lateral organ consists of a ciliated, villose dome surrounded by, and either retracted within or protruding from, an integumental fold. The inner surface of the fold is entirely secretory; its gland cells resemble those of the parapodial integument. The epidermis of the dome comprises vacuolated cells together with an admixture of ciliated sensory cells and a distinct kind of secretory cell. The microvilli of the vacuolated cells project well beyond the cuticle. Each process from the sensory cells ends in a cilium. The cell body of the secretory cells, similar to those in the cirri, lies below the general epidermis.

In other families, lateral organs may be absent (most species of *Endomyzostoma* and *Mycomyzostoma*) or present, as: two ventral pairs (*Stelechopus*); four ventral pairs alternating with the parapodia (other *Endomyzostoma* and *Asteriomyzostomum* species – in the latter sometimes with a posterior medial one present; Fig. 2.17A); five dorsal pairs directly opposite the parapodia (*Protomyzostomum*; Fig. 2.11A); 10 ventral pairs alternating with the parapodia (*Pulvinomyzostomum*; Fig. 2.19A); or up to 40 lateral organs scattered mostly along the lobed posterior body margin (*Asteromyzostomum*; Fig. 2.18). Further details are given in the family sections.

Endocrine and Exocrine Systems

Nothing is known about possible endocrine function in myzostomes and reports on exocrine glands are entirely anatomical, with a little histochemistry; they principally concern arrays of secretory cells. The parapodial glands, accessory glands and chaetal glands of the parapodia are described under Locomotion. Salivary glands are described in the Feeding and Digestive System section. The secretory cells of the integument and lateral organs are described in the Body Wall and Musculature and Nervous System and Sense Organs sections above, respectively.

Reproduction

Most, if not all, myzostomes are protandric hermaphrodites, passing through a functional male stage to a hermaphroditic stage and, in some species, on to a functional female stage (Wheeler 1896). Only *Mycomyzostoma calcidicola* is considered to be dioecious (Eeckhaut 1998), although there is some question regarding *Endomyzostoma* species.

According to the prevailing histological interpretation, the ovaries are usually located on or are sunken into the floor of the uterus above the stomach in the vicinity of the origin of the midgut diverticula, either as one or two unpaired organs or as one or two pairs (Figs 2.2C, 2.11B, 2.12). The ovaries are found ventral to the gut in uterine diverticula in a few Myzostomatidae, for example, in *Myzostoma adhaerens* (synonym of *M. furcatum* according to Grygier 1990) and *Notopharyngoides platypus*, and perhaps all species of *Endomyzostoma* (Fig. 2.14B, C, E; Wheeler 1896; Stummer-Traunfels 1908; Remscheid 1918). The ovaries produce triplet cells consisting of an oocyte together with two accessory cells. These are given off into the lumen, travel out into the diverticula (uterus lumen and diverticular spaces being considered the coelom); they attach to or possibly penetrate the epithelium, which in *Myzostoma* is ciliated dorsally. According to Wheeler (1896), the accessory cells are then absorbed by the oocyte, but their nuclei remain distinct until yolk begins to develop. However, according to Jägersten

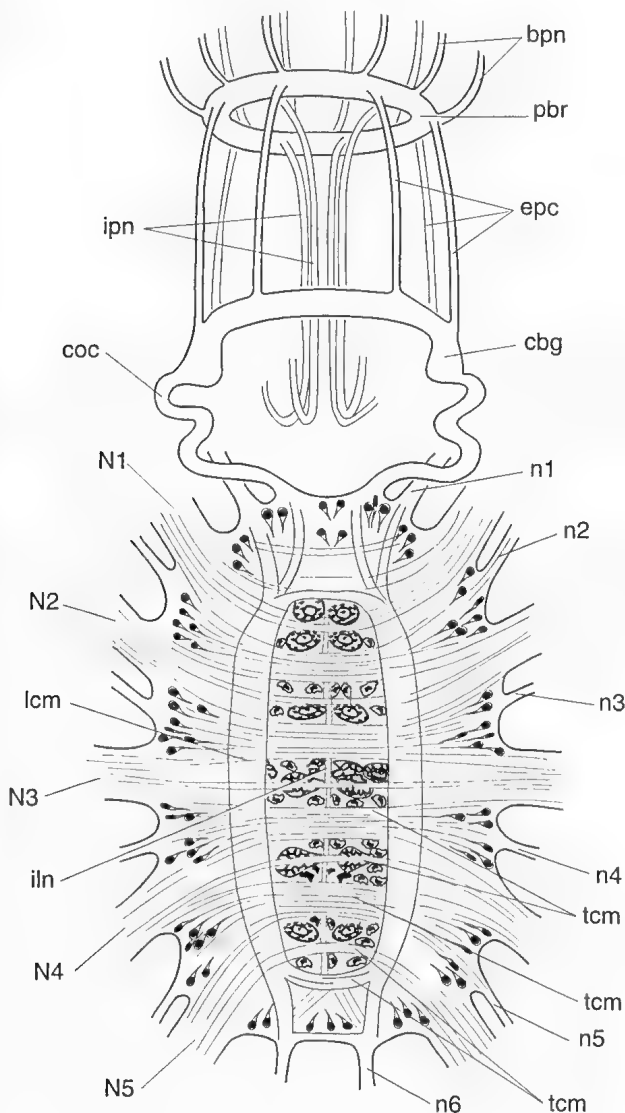


Figure 2.6 Central nervous system of *Myzostoma giganteum* (Myzostomatidae). **bpn**, buccal papillae nerves; **cbg**, cerebral ganglion; **coc**, circum-oesophageal connective; **epc**, external proboscideal connectives; **iln**, intermediary longitudinal nerve; **ipn**, internal proboscideal nerves (pharyngeal nerves); **lcm**, longitudinal commissure; **n1–n6**, minor lateral nerves; **N1–N5**, major lateral nerves; **pbr**, prebulbar nerve ring; **tcm**, transverse commissure. (After Nansen 1887) [I. Hallam]

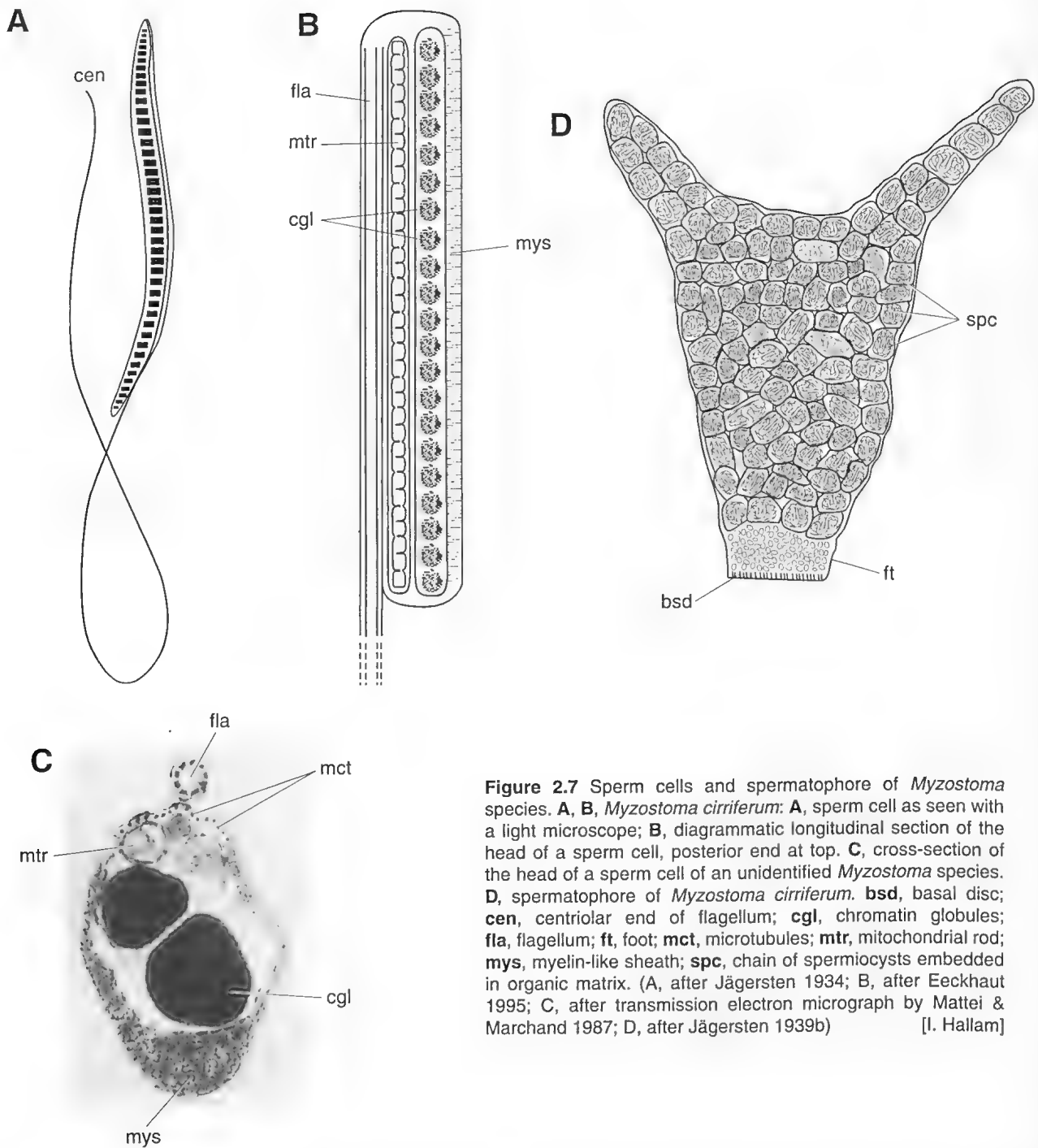


Figure 2.7 Sperm cells and spermatophore of *Myzostoma* species. **A, B**, *Myzostoma cirriferum*: **A**, sperm cell as seen with a light microscope; **B**, diagrammatic longitudinal section of the head of a sperm cell, posterior end at top. **C**, cross-section of the head of a sperm cell of an unidentified *Myzostoma* species. **D**, spermatophore of *Myzostoma cirriferum*. **bsd**, basal disc; **cen**, centriolar end of flagellum; **cgl**, chromatin globules; **fla**, flagellum; **ft**, foot; **mct**, microtubules; **mtr**, mitochondrial rod; **mys**, myelin-like sheath; **spc**, chain of spermiocysts embedded in organic matrix. (A, after Jägersten 1934; B, after Eeckhaut 1995; C, after transmission electron micrograph by Mattei & Marchand 1987; D, after Jägersten 1939b) [I. Hallam]

(1939b), the accessory cells transform into follicle cells and eventually several layers of follicles become attached to each side of the dorsal ciliary band, displacing and obscuring the original epithelial cell lining. In either case, the oocytes enlarge, detach from the epithelium and accumulate in the uterus; the posterior portion of the latter, lying dorsal to the intestine, is often referred to as the oviduct (Fig. 2.2A). The female gonopore is located just behind the anus and may be very closely associated with it.

Eeckhaut (1995) presented a different interpretation of the female reproductive system, based on ultrastructure. Like Wheeler (1896) and Jägersten (1939b), he studied *Myzostoma cirriferum*. A single diffuse ovary containing oogonia and previtellogenic and vitellogenic oocytes overlies all the uterine diverticula; this area is not merely a zone for maturing cells. The diverticula have an epithelium with a basement membrane, and the latter separates the developing ova and their surrounding parenchyma cells from the lumen, which is considered a branched oviduct rather than a coelom.

The anatomy and histology of the male reproductive system have been most closely studied in *Myzostoma cirriferum* (see Jägersten 1934, 1939b), including by transmission electron microscopy (Eeckhaut 1995). Less detailed observations have been made on many other species. In typical species of *Myzostoma*, the male system consists of testes, two pairs of vasa deferentia (anterior and posterior on each side), and a pair each of seminal vesicles and penes that open lateral to the third pair of parapodia (Fig. 2.2B). The testes occur as two pairs, comprising many follicles scattered diffusely in the parenchyma at the ends of dendritic vasa efferentia, mostly below the gut diverticula though some extend dorsally (most are dorsal in *M. 'ambiguum'* and *M. longimanum*: Jägersten 1939b) and with their outer border falling far short of the body margin. A basal membrane, or tunica propria, bounds the follicles, at least in *M. cirriferum*, and also the vasa efferentia, which have no cellular lining. The basal membrane bounds the vasa deferentia and seminal vesicles, too, both of which have an epithelium. In *M. cirriferum*, this epithelium consists of vesicular gland cells in the vasa deferentia,

spumous gland cells in most of the seminal vesicle and vacuolated gland cells near the exit of the latter. The epithelium-lined spaces have often been considered a coelom, but Wheeler (1896) disagreed with that interpretation and Jägersten (1939b) noted that the relevant embryological information is lacking. A short canal leads from the seminal vesicle to the gonopore at the end of the penis. The penis, which varies greatly in length among species, is ordinarily retracted into the body as an ectoderm-lined penial tract, which is ciliated around the gonopore. The aperture seen at the body surface or on a distinct papilla when the penis is retracted is the outer end of this temporary penial tract. The tract disappears when the penis is fully extended; it has often been misnamed the ejaculatory duct (see discussion in Jägersten 1939b). In some species, such as *M. cirriferum*, the extended penis may reach well beyond the body margin.

According to Jägersten (1939b), the innermost end of a follicle is lined with stem cells that give rise to spermatogonia and spermiocyst cells. The latter engulf the former to form spermiocysts, and spermatogenesis proceeds in intracellular vacuoles (see below). Eeckhaut (1995) did not observe stem cells; his records began with formed spermiocysts. The spermiocysts are aligned in single file in the distal parts of the follicles and in the vasa efferentia, which thus are solid cell-strings with no lumen. When the spermiocysts enter the vasa deferentia, the spermatids mature into spermatozoa. Other small cells are present in the ducts and seminal vesicles. They have been regarded by various authors as, for example, abortive spermiocysts (Nansen 1885; Stummer-Traunfels 1903; Eeckhaut 1995), nurse cells (Fedotov 1914) or lymphocytes (Jägersten 1934). The vasa deferentia have rings of muscle fibrils that give them a segmented appearance and cause peristalsis. The entrance to the seminal vesicle is closed by a muscular sphincter, and spasmodic contractions of the distal end of the duct force quantities of spermiocysts into the vesicle, where formation of the spermatophore takes place (see below).

The seminal vesicle is covered by a layer of circular muscles; external to them a discontinuity in the parenchyma, which extends proximally to include the vasa deferentia, allows the vesicle to slide outward into the penis when the latter is extended. A ventral sheet of vesicle retractor muscles bends around the distal end of the discontinuity. The penis retractor muscles originate dorsally and pass beneath the seminal vesicle to a point near the inverted end of the penis.

Structural differences in the male system among the Myzostomatidae most often involve the length of the penes, whether or not they form distinct papillae when retracted, and the location of the aperture of the penial tract. *Myzostoma 'ambiguum'* of Jägersten (1939b) and *M. longimanum* additionally have the seminal vesicle divided into a proximal narrow duct and a distal sac-like portion, unlike in *M. cirriferum*. In most members of this family, the penis on each side protrudes from the angle at the outer base of the third parapodium, but in *M. cirriferum* and a few other species (for example, *M. glabrum*, *M. fissum* and *M. plicatum*) the penial tract opens close to the body margin, with a fixed integumental tube extending from near the third parapodium to the aperture. Jägersten (1939b) stated that *M. cirriferum* is unusual in displaying a well-defined boundary between the vasa efferentia and vasa deferentia. In other species, the epithelium (or possibly connective tissue) continues to varying degrees into the former ducts (for example, lining the whole system except the follicles in *M. 'ambiguum'*); or else no epithelial lining is found at all (for example, in *M. cuniculus* and *M. longitergum*; Eeckhaut *et al.* 1998).

Details of the male system in pharyngidean myzostomes are given individually in the family sections below. In the Pharyngidea, protrusible penes are absent and sometimes (for example, *Mycomyzostoma calcidicola*) seminal vesicles are also lacking. Compact, rather than diffuse, testes occur in many Endomyzostomatidae and also in *Stelechopus hyocrini*.

Literature on the ultrastructure of myzostomidan spermatozoa and their spermatogenesis is extensive (see Bargalló 1977; Afzelius 1983, 1984; Mattei & Marchand 1988; Eeckhaut 1995). In *Myzostoma cirriferum*, the cell body is 30 µm long and the free part of the flagellum is 70 µm long (Fig. 2.7A). The sperm cell has a flagellum, but the flagellar centriole is at the free end, which is therefore anterior. The nucleus is not bounded with a nuclear membrane, but sits within an open, myelin-like sheath (Fig. 2.7C); it contains a string of darkly staining, bead-like chromatin bodies, varying from 40 to 60 in different populations of *M. cirriferum* (Fig. 2.7A, B). Usually two rod-shaped mitochondria lie parallel to each other by the open side of the nucleus. The mitochondria (Fig. 2.7C) are surrounded on the outside by 22 to 24 microtubules (fewer in the species studied by Mattei & Marchand 1988), two of which (the 'dorsal rods') are attached to the plasma membrane and thus to the flagellum alongside. The flagellum has a 9x2+0 axoneme structure and, except for its most posterior end, lies outside the main body of the cell (Fig. 2.7C); it freely extends anteriorly beyond the cell body to a sharp spine derived from a pre-centriolar vesicle. The spermatozoon can swim flagellum foremost by flagellar undulations, or, more efficiently, flagellum hindmost by undulations of the cell body.

The spermatids develop within vacuoles inside host cells called spermiocysts. All sperm in the same spermiocyst are at the same stage of development. Originally the spermatid nucleus has a typical nuclear membrane, but this later opens and allows the nucleoplasm and cytoplasm to mix. The chromatin has already begun condensing into small spheres at the earliest stages; the spheres get larger and more numerous and later form a row. The multilayered, myelin-like sheath is presumably derived from the Golgi apparatus. Typical small mitochondria fuse to form the rod-shaped mitochondria of the mature sperm (Fig. 2.7B). The two 'dorsal rods' appear against the plasma membrane before being joined by the remainder of the intracellular microtubules, which had earlier formed a manchette around the nucleus. The development of the flagellum is very peculiar. According to Mattei & Marchand (1988), the centriole and a vesicle atop it first migrate up a cytoplasmic canal away from the original posterior end of the sperm, then the canal ruptures for most of its length, leaving most of the flagellum outside the cell body, but in contact with it. The centriole continues to migrate until the anterior end of the axoneme, tipped with a vesicle-derived spine, extends well beyond the originally anterior end of the cell body (Fig. 2.7B), and the posterior end of the axoneme has been drawn up within the originally posterior end of the cell body. This explanation differs from earlier descriptions (Jägersten 1939b; Afzelius 1984), which assumed that the free part of the flagellum is always the original posterior end.

Copulation is effected hypodermically by the transfer of a spermatophore from one individual to another, a process that has been studied most thoroughly in *Myzostoma cirriferum* (Jägersten 1939b; Eeckhaut & Jangoux 1991; Eeckhaut 1995). A specimen of any size can receive a spermatophore, but only larger individuals can deposit one. Spermatophores of *M. cirriferum* are up to 0.5 mm long and each have two short arms (Fig. 2.7D); arms are absent from the spermatophores of '*M. ambiguum*' (Kato 1952) and *M. alatum* (Eeckhaut & Jangoux 1992). A spermatophore is

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formed within one of the seminal vesicles and is expelled through the gonopore at the end of the everted penis, thus becoming attached to the surface of the recipient worm. The body and arms of the spermatophore contain chains of spermio cysts coated by or enclosed in an extracellular matrix (Eeckhaut & Jangoux 1992); each spermio cyst consists of a large cyst cell and one to three coiled clumps of spermatozoa in vacuoles inside. The foot of the spermatophore contains chains of smaller spermio cysts with abortive germ cells; the contents of vesicles in the basal disc probably act in penetrating the recipient worm's integument. The spermio cysts enter the worm as a large, digitate, motile syncytium, which delivers the sperm to the oocytes in the uterus, presumably by breaking through the wall of the latter. The entire copulatory process lasts at most a few hours.

The pair of ciliated ducts connecting the uterus to the intestine in most species (Figs 2.2A, C, 2.17B, 2.18, 2.19B) probably serves to expel the spent syncytium and excess gametes after fertilisation. These ducts may be completely separate or be fused at either the proximal or distal end. *Protomyzostomum polynephris* has supernumerary ducts on each side (Fig. 2.11B). In species of *Endomyzostoma*, the ducts' common pore is external near the anus, not inside the intestine (Fig. 2.14A, E). Although these ducts do not serve for excretion in the same sense as nephridia (see excretion section above), their superficial resemblance to metanephridia of many polychaetes is one factor in the prevailing interpretation of the internal spaces of the female reproductive system as a coelom (disputed by Eeckhaut 1995).

Embryology and Development

Embryological studies have been conducted on four species of European and Japanese myzostomes. Newly spawned, fertilised eggs are no more than 50 µm in diameter; the maximum number obtained from a single female of *M. cirriferum* kept in the laboratory was close to 500 eggs (Eeckhaut & Jangoux 1993b). The egg membrane becomes the larval cuticle, so no hatching occurs. Brooding of the eggs and early larvae occurs only in some species of *Endomyzostoma*, in which the upturned lateral edges of the body form a dorsal brood chamber.

The following sequence of events follows spawning in a species of *Myzostoma* (misidentified as *M. ambiguum*) (Kato 1952) and in *M. cirriferum* (Eeckhaut & Jangoux 1993b; Eeckhaut 1995). The maturation divisions produce two polar bodies. A polar lobe forms at the vegetal pole and fuses with the CD blastomere after the first cleavage. A second polar lobe forms and fuses with the D blastomere after the second cleavage. A third polar lobe forms, blastomere D divides, blastomeres A–C divide (a spiral division) and the polar lobe fuses with blastomere 1D (the last two stages are reversed in '*M. ambiguum*').

From this point on, four larval stages are distinguishable in *M. cirriferum*: (1) the spherical protochophore with a prototroch and an apical tuft; (2) the pyriform trochophore; (3) the pyriform metatrochophore (Fig. 2.8) with two tufts of four denticulate chaetae, a ventral mouth just anterior to the prototroch, the prototroch divided into tufts, and an eventually retractile post-anal pygidium with a ciliary band and terminal cilia, and; (4) the metamorphic larva that loses the cilia and chaetae. The larvae reach a final length of 100–120 µm, excluding the chaetae. This entire process takes about 5 days in the plankton. Basically, the same series of larval stages occurs in *M. glabrum*, but with usually six chaetae per tuft in the metatrochophore (Jägersten 1939a, as *M. parasiticum*),

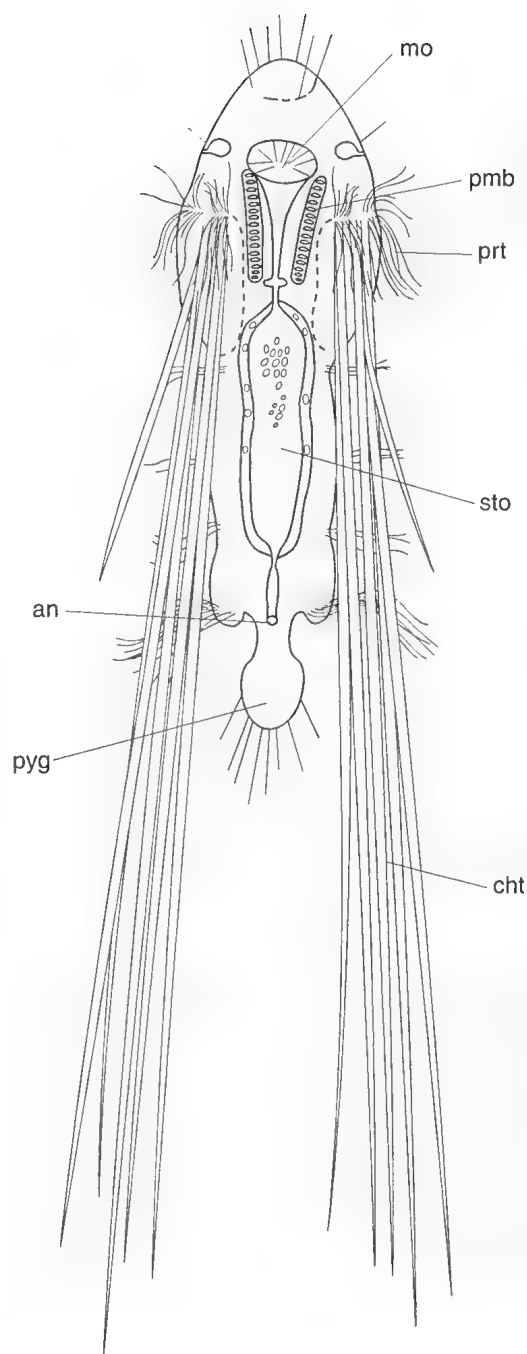


Figure 2.8 Planktonic larva (late metatrochophore) of *Myzostoma glabrum*. **an**, anus; **cht**, chaetae; **mo**, mouth; **pmb**, pharyngeal muscle bulb; **prt**, prototroch; **pyg**, pygidium; **sto**, stomach. (After Jägersten 1939a)

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and also in *M. alatum* (Eeckhaut & Jangoux 1992). '*Myzostoma ambiguum*' differs primarily in having several additional ciliary bands, and it takes at least 8 days to reach the late metatrochophore stage.

The metatrochophores of *M. cirriferum* are captured by the tube feet of their eventual host crinoid as potential food particles, and the denticulate chaetae catch onto the host. If too young, the larva is rejected or occasionally swallowed. The metamorphosing worms become embedded in temporary cysts in the walls of the ambulacral grooves of the host's pinnules, where they remain through the young male stage. The cysts are formed from fused tube feet and ambulacral lappets.

Following metamorphosis (Eeckhaut & Jangoux 1993b), the smallest, barrel-shaped juveniles of *M. cirriferum* have a non-retractile proboscis and only the third pair of parapodia. The remaining four pairs of parapodia, the lateral organs and the anus appear later. The proboscis gradually retracts into a pocket in the anterior end of the trunk and the buccal papillae appear. At the same time, the animal becomes wider and flatter, and has developed marginal cirri and penes by the time it reaches the male stage. Previously, similar observations were made on this species (Jägersten 1940a) and on the larvae of '*M. ambiguum*' (Kato 1952; including a description of the elaboration of the gut diverticula) and the post-metamorphic stages of *M. divisor* (Grygier 1989).

NATURAL HISTORY

Life History

Aside from descriptions of early ontogeny, detailed studies of life history have been made only for *Myzostoma cirriferum* infesting the crinoid *Antedon bifida* in Europe. In Loch Creran, Scotland (Woodham 1992), juveniles begin to appear on the host in October, are numerically dominant from November to April and are mostly replaced by adults from June. In the summer, 100% of the hosts are infested with up to 3200 adult myzostomes each. Infestation rates and abundance drop off sharply in the late autumn, to about 50% and less than 10 per host. The life span is inferred to be less than a year, limited by post-spawning mortality, and only the latest spawned individuals overwinter as adults. At Roscoff, France (Eeckhaut 1995; Eeckhaut & Jangoux 1997), the newly settled juveniles and young males remain encysted in the host's ambulacral integument for no more than 2 months; the older males and hermaphrodites then live freely as ectocommensals for 4–5 months. Reproductive activity is constant through the year. The total life span is about 190 days. The population increases by additional recruitment from mid-January to March, to a maximum of about 71 worms per host. Then the numbers decline, possibly due to predation by facultatively commensal amphipods, but remain steady at a lower level through the summer to the beginning of winter.

Ecology

Myzostomes are usually regarded as obligate commensals, semiparasites or parasites of echinoderms, especially of crinoids. They have, however, also been isolated from a Japanese hexactinellid sponge (Okada 1920) and found as endoparasites of a Puerto Rican antipatharian coral (Goenaga 1977); the identity of the latter worms as myzostomes has been verified (M.J. Grygier personal observation).

Most species of Myzostomatidae are associated with crinoids and belong to at least three ecological types: (1) vagile forms, which move rapidly and freely over the host (see for example, Fig. 2.1A–C); (2) external sessile species, which include round forms that usually sit on the disc (see for example, Fig. 2.1F) and elongate forms that are usually attached to the arms or pinnules (see for example, Fig. 2.1K, L); and (3) a few species that live in skeletal crypts, soft tissue cysts, pinnule galls (see for example, Fig. 2.1H) or the mouth (see for example, Fig. 2.1J). In addition to these, about six species of *Myzostoma* are ectocommensals of various kinds of ophiuroids.

Species of *Endomyzostoma* and *Contramyzostoma* all inhabit cysts or galls on the disc or arms of their host crinoids (Fig. 2.13A, C). *Mycomyzostoma calcidicola* lives in a spherical cyst of the stalk of a crinoid. *Asteriomyzostomum* species are endoparasites of asteroids, whereas species of *Asteromyzostomum* are ectoparasites of other asteroids. *Pulvinomyzostomum pulvinar* lives in the oesophagus and stomach of its host crinoid. Species of *Mesomyzostoma* and *Protomyzostomum* are also endoparasites, the former in the gonads of crinoids, the latter in the gonads or in external cysts of basket stars or in the coelom of other ophiuroids. Forms, as yet undescribed, inhabit the dorsal coelom of the Antarctic ophiuroid *Ophionotus victoriae* (Bartsch & Faubel 1995) and the connective tissue of the calyx of a comatulid crinoid (Heinzeller, Aschauer, Lange & Welsch 1995).

Woodham (1992) summarised the infestation rates and degrees of infestation for some European species. Eeckhaut & Jangoux (1993b), comparing their own data with those of Platel (1962), noted that the morphology and behaviour of the larvae and juveniles of *Myzostoma cirriferum* favour the maintenance of very high or universal infestation rates and high numbers of myzostomes per host in environments where the host crinoid occurs more densely. The very high values obtained by Woodham (1992), also in a dense crinoid population, support this idea.

In their population study of crinoid symbionts on the Great Barrier Reef, Fabricius & Dale (1993) grouped all species of myzostomes together; about 20% of the symbionts were myzostomes, found on 15 of the 43 crinoid species examined. Stout and nocturnal crinoids, and members of the Comasteridae, were more likely to have symbionts of all kinds than other comatulids. Previously, Grygier (1990) had noted that comasterids were a dominant host family for Indo-Pacific myzostomes and that one species could host a diverse assortment of worms (for example, 10 species of myzostomes on *Comanthus parvicirrus*). Based on the author's present study, the proportion of comasterid host crinoids in a given region of Australia is about 40–60% of the total hosts, and higher in tropical Queensland than elsewhere (Table 2.1).

Fabricius & Dale (1993) noted that comasterids cannot cover their ambulacral grooves and, since myzostomes feed upon particles carried along these grooves, easy food accessibility in this family may favour myzostome infestation. In their study, the greatest numbers of individual myzostomes were found on *Comatula purpurea* (but on not more than 20% of the specimens), *Himerometra crassipinna* and *H. magnipinna*. The highest density followed the crinoids' own density pattern: highest on mid-shelf reefs, lower near the edge of the continental shelf and in the lagoon. Regarding co-occurrence with other non-host-specific crinoid associates, there were more frequent associations of myzostomes with polynoid polychaetes and three species of the pontonine shrimp *Periclimenes* than would be expected by chance, and less frequent associations with the isopod *Cartetolana integra* and the alpheid shrimp *Synalpheus stimpsoni*.

Data on host crinoids of Australian myzostomes are summarised in Table 2.1. In all, 54 species have been implicated as hosts. Host species are more diverse in the tropical regions of Queensland and Western Australia than elsewhere. These two regions have 15 host species in common (of 44 total), four of which are also hosts in the Northern Territory: *Comanthus briareus*, *C. wahlbergi*, *Comatella stelligera*, *Lamprometra palmata*. Together, these four species host 19 or 20 species of myzostomes, just three or four of which are common to all three regions, at most seven being shared by at least two regions.

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Table 2.1 Geographic distribution and host apportionment of Australian Myzostomida, based on literature and on the author's data from museum surveys (Grygier 1990, and subsequent surveys of additional collections). All values are given as numbers of purported species.

Regions ¹	SE	QLD	NT	NW	H-A	SW	TS
All Myzostomida	≈10	≈54	≈15	≈35	≈6	3	≈3
Endomyzostomatidae							
<i>Endomyzostoma</i>	1	1	—	3–4	—	—	—
Myzostomatidae							
<i>Notopharyngoides</i> ²	—	1	1	—	—	—	—
<i>Hypomyzostoma</i> ³	1?	≈8	4	≈7	—	—	—
<i>Myzostoma</i>	≈8	≈43	≈10	≈24	≈6	3	≈3
Body typical, thin ⁴	4	13	3	7	3	3	2
Body typical, thick ⁵	—	9	1	4	—	—	—
With supernumerary cirri ⁶	1	4	1	2	1	—	—
With caudal process(es) ⁷	1	9	3	5	—	—	—
Other ⁸	2	8	2	5	2	—	1
Identified species	≈4	≈24	≈6	≈16	3	1	1
Total host crinoid species	≥10	≥35	≥10	≥27	5	3	3–4
Comasterid species	4	21	4	13	3	2	2
Myzostome species per host species	1–2	1–6	1–2	1–4	1–2	1	1
Myzostome species with 3 or more hosts	—	7 ⁹	—	1 ¹⁰	—	—	—
Hosts with 3 or more myzostome species	—	7 ¹¹	—	—	—	—	—

1. SE, Fraser Island, Queensland, to Spencer Gulf, South Australia, and Tasmania; QLD, Great Barrier Reef and Torres Straits Islands; NT, Northern Territory; NW, Western Australia north of Shark Bay, including Indian Ocean banks; H-A, Houtman Abrolhos and nearby coast; SW, Perth to Recherche Archipelago; TS, Lord Howe Island and Elizabeth and Middleton Reefs, Tasman Sea.
2. = *Myzostoma platypus* species-group (Grygier 1990); type: *M. ijimai* (see Fig. 2.1J).
3. = *Myzostoma crosslandi* species-group (Grygier 1990); type: *M. folium* (see Fig. 2.1K, L).
4. round or oval, disc- or shield-shaped, thin-bodied species with 10 pairs of marginal cirri; for example, *M. ambiguum*, *M. stochoeides* (see Fig. 2.1A, B).
5. dome- or puck-shaped bodies with rudimentary or no marginal cirri; for example, *M. echinus*, *M. horologium* (see Fig. 2.1D).
6. species with more than 20 marginal cirri that are clearly differentiated from the body proper; for example, *M. polycyclus* (see Fig. 2.1C, F).
7. species with one or more posterior lobes of the body, bearing cirri or not, into which the internal organs penetrate; for example, *M. fissum*, *M. intermedium* (see Fig. 2.1I).
8. species with other unusual forms or ornamentation (for example, *M. attenuatum*, *M. plicatum*, *M. chelonoideum*) (see Fig. 2.1G).
9. *M. mortenseni*, *M. coriaceum*, *M. plicatum*, *M. polycyclus*, *Hypomyzostoma* species (= *M.* species 4 of Grygier 1988), two unidentified or undescribed species.
10. *Hypomyzostoma nanseni*.
11. *Comanthus parvicirrus*, *C. timorensis* (probably synonymous with the former; if so, Australian *C. parvicirrus* hosts nine myzostome species in all, the highest on any single host species), *C. wahlbergi*, *Comanthina schlegelii*, *Comatella stelligera*, *Stephanometra oxyacantha*, *Lamprometra palmata*.

Host specificity for Indo-West Pacific myzostomes, including Australian species, may be species-specific, family-specific, or non-specific (Grygier 1990). In the Australian fauna, few species of myzostomes infest as many as three or four host species in a given geographic region; conversely, few host species are infested by three or more myzostome species (see Table 2.1). The usual number of host or symbiont species for a myzostome or crinoid, respectively, is one or two.

Several endoparasites of myzostomes have been described in the older literature (see review by Jägersten 1941). These include: encysted larvae of a cestode, *Taenia myzostoma*, from *Myzostoma graffi*, and a trematode, *Distoma myzostomatis*, from *Notopharyngoides platypus* (several authors have mentioned undescribed trematode larvae from other myzostome hosts); a supposed amoeba, *Amoeba myzostomatis*, from *M. glabrum* (true nature unclear), and; a fecampiid turbellarian, *Glanduloderma myzostomatis*, from *M. brevilobatum* and, presumably, *M. longimanum*. More

recently, Grygier (1989, 1992) reported other unidentified endoparasitic helminths from *M. attenuatum*, *M. lobatum* and *M. bocki*, and so did Eeckhaut *et al.* (1998), from *M. longitergum*, *M. capitocutis* and *M. stochoeides*. Such parasites are not uncommon in museum collections examined by the author. Indications of predator-induced injury, such as asymmetries in body outline and in the number of parapodia or lateral organs, are also common.

Behaviour

Some species of Myzostomatidae move freely upon their host crinoids. Their marginal cirri are contractile, the lateral organs and proboscis are protrusible, and the parapodia are used for locomotion in any direction. Feeding is accomplished by protruding the proboscis into the host's ambulacral groove and ingesting entrained food particles. Studies on sexual behaviour have been conducted only on *Myzostoma*

cirriferum (Eeckhaut 1995), as recounted in the reproduction section above. No ethological studies are available concerning transfer of myzostomes between crinoids, or territoriality upon hosts. Although the larvae of *M. cirriferum* are captured passively and do not seek out their hosts, they do show a preference for grabbing with their parapodia at long, thin substrata, such as crinoid arms or (even) spaghetti of similar dimensions (Eeckhaut 1995). In sessile species, such as *M. glabrum* and *M. alatum*, which are permanently attached to the host's disc, it is common for a protandric male individual to sit on the dorsum of a larger hermaphrodite (Graff 1877; Eeckhaut & Jangoux 1992).

Economic Significance

Myzostomes have no commercial value, and none is known to infest any pest sea star.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Myzostomes occur almost worldwide in marine environments, from the intertidal to depths of over 3000 m. Their greatest diversity naturally corresponds to regions of greatest crinoid diversity, namely the tropical Indo-West Pacific and, to a considerably lesser degree, the tropical Western Atlantic. In temperate waters, they are probably most diverse in Japan, perhaps because of the influence of the warm Kuroshio Current in supporting a high diversity of crinoids. In deeper waters of the western Pacific, the fauna of myzostomes on stalked crinoids is relatively rich. Regions of low crinoid diversity may nonetheless be home to a relatively diverse assortment of myzostomes (north-western Europe) or to only a few species (California). None is yet known from the eastern tropical and south-eastern Pacific.

Grygier, in 1990, indicated that the myzostome fauna of Queensland seemed to be part of a widespread Tropical Indo-West Pacific fauna, whereas that of the Northern Territory seemed to be different. At the time, the Western Australian fauna was almost unknown, and only one species was noted from the south-eastern coast. Since then, additional collections (principally those of the Australian Museum, the Western Australian Museum and the Museum of Comparative Zoology) have been examined and an up-to-date summary of the distribution of Myzostomatidae and Endomyzostomatidae around Australia is presented in Table 2.1. About two thirds of the species are of uncertain identity or new. Of the 10 species of *Myzostoma* from the Northern Territory, six are known within Australia only from the Territory; the other four also occur in both Queensland and Western Australia. The latter two regions alone, with a total count of 54 species of *Myzostoma*, share an additional nine species; thus having about 13 in common. Given such a degree of faunistic overlap, it appears that all myzostomes of tropical Australia belong, after all, to the Indo-West Pacific biogeographical province.

In comparison with the tropical regions, relatively few species are recorded for the temperate coasts of Australia (Table 2.1). Some of these are tropical outliers and one is amphitropical (*M. bocki* is known from Perth and Japan: Grygier 1992), but the south-east in particular has a different and as yet undescribed fauna.

A few myzostome records from islands and reefs in the Tasman Sea constitute the first positive records from any Australian External Territory (Table 2.1).

Affinities with Other Groups

Early assignments of myzostomes to the Trematoda, Crustacea or Stelehopoda (with Tardigrada and Pentastomida) are no longer considered seriously. Fedotov (1929, 1938) regarded the Myzostomida as true annelids with affinities to polychaetes and archiannelids, whereas placement as a class in Annelida was adopted by Kato (1952), on the basis of ontogenetic evidence. Consequently, authors of textbooks and encyclopedias typically have placed the group as an order of Polychaeta or class of Annelida, citing as evidence the parapodia with support rods and hooks (similar to polychaete parapodia with acicula and chaetae), the trochophore-type larva and the supposed metamerism. A position within the Polychaeta among the phyllodocidan families is also favoured in a cladistic analysis of polychaetes by Rouse & Fauchald (1997). However, several alternative hypotheses are still current and being debated, and no biochemical systematic studies of nucleic acid sequences have been published.

Jägersten (1940a) combined the Myzostomida and Annelida as two classes within a coelomate, protostome group called Chaetophora; the putative defining characters, most of which are not exclusive, include parapodial chaetae, a ventral nerve cord, a hindgut and anus, metanephridia and trochophore larvae.

Wagin (1976, 1979) recognised three superphyla within the Spiralia, of which one, the Trochozoa Oligomera, included molluscs, myzostomes and dinophilids; these all lack so-called primary heteronomy of the metamerites in ontogeny. Myzostomes were regarded as more primitive than molluscs. This is probably a paraphyletic classification, because one of the other superphyla, the Trochozoa Polymera, may have originated from among the Trochozoa Oligomera, according to Wagin.

Mattei & Marchand (1987) noted numerous ultrastructural similarities between the spermatozoa of Myzostomida and Acanthocephala (spiny-headed worms). They regarded these two taxa as sister groups linked by synapomorphic sperm and placed them in a single phylum, the Procoelomata.

Eeckhaut (1995) compared myzostomes to turbellarians and polychaetes. The only synapomorphy shared by myzostomes and polychaetes could be the cirri; the dorsal and ventral parapodial cirri of polychaetes might correspond to the marginal cirri and medial parapodial cirri of myzostomes, but homologies of these various structures have yet to be proven. Eeckhaut denied the presence of both metamerites and a coelom in myzostomes. He thus considered the Myzostomida as an acoelomate phylum, not closely related to polychaetes, but with advanced features (such as the trochophore larva and a myo-epidermis) that set them apart from flatworms.

Haszprunar (1996), in a cladistic study aimed at establishing the relations of the Mollusca, estimated that the Myzostomida arose between the molluscan lineage and a eucoelomate group including sipunculans, echiurans and ordinary annelids, but he cautioned that this result was probably not very stable. A similar result, but with the sipunculans removed to the molluscan lineage, was obtained in a cladistic study of the entire Metazoa (Zrzavý *et al.* 1998).

Affinities Within the Taxon

Jägersten (1940a) published a phylogenetic tree for the genera of Myzostomida (modified here as Fig. 2.9). It shows the purportedly advanced, or at least characteristic, features distal to each branch point or node. Homoplasy is evident, and the order Pharyngidea is paraphyletic with respect to the Proboscidea. *Protomyzostomum* and *Stelechopus* are separated from the remaining genera on the basis of having several, rather than three, pairs of midgut diverticula (both conditions being apomorphic compared to an unbranched gut in a hypothetical ancestor), and the presence of sunken epidermal nuclei.

Mesomyzostoma branches off separately in Jägersten's (1940a) tree, but no synapomorphy links it to the remaining genera; thus, Figure 2.9 shows it as part of a basal polytomy. The habitat within the host's reproductive system can serve as an autapomorphy for this genus; no particular unique and advanced morphological character was noted by Jägersten. The remaining group of genera is characterised by having a shortened ventral nerve cord. *Asteriomyzostomum* branched off next in Jägersten's (1940a) tree, also without supporting autapomorphies (though again, habitat, namely ectoparasitism

on sea-stars, may serve). *Asteromyzostomum* can be accommodated in the vicinity, and perhaps as the sister group of *Asteriomyzostomum* (Fig. 2.9), on the basis of the reduced number of midgut diverticula (one or two pairs), the laterally broadened body and the common host class.

Pulvinomyzostomum and *Endomyzostoma* (synonym: *Cystimyazostomum*) are related, according to Jägersten (1940a), by both having a pharynx-derived proboscis. We can add that the branches of the uterus surround the gut diverticula in these two genera (also true, convergently, in *Protomyzostomum polynebris*). The same is true for *Contramyzostoma*, which formally remains *incertae sedis* because of the nature of its proboscis is not known. However, if it does belong to the clade here under discussion, the U-shaped gut with dorsal mouth and anus suggests a close relationship to *Pulvinomyzostomum* (Fig. 2.9). This potential three-genus clade is joined to the final branch, the order Proboscidea (that is, *Myzostoma* and allies), by the presence of marginal cirri, which are presumed to have been lost secondarily in *Pulvinomyzostomum* and some species of *Endomyzostoma*. The protrusible penis of the Proboscidea is

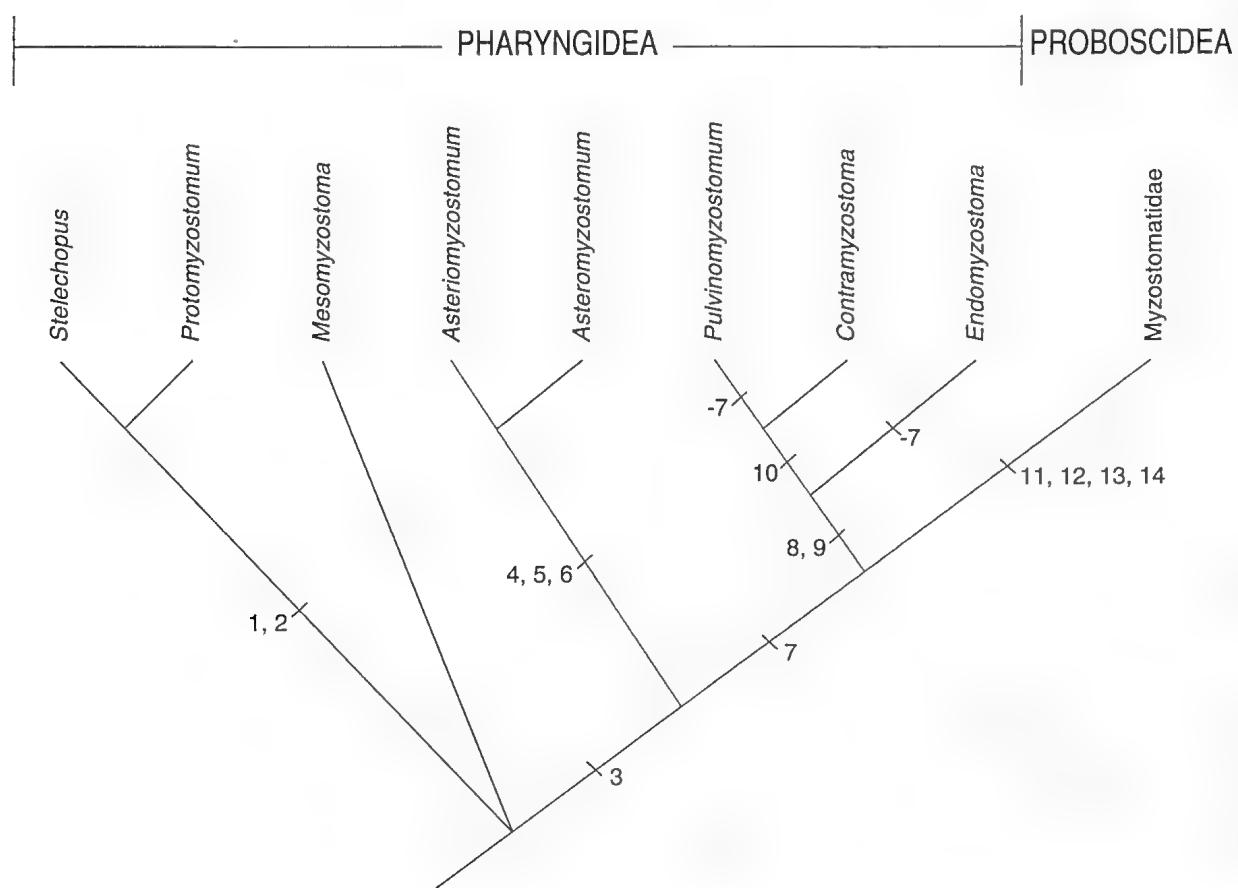


Figure 2.9 An estimate of phylogenetic relationships among the genera of Myzostomida, based in part upon characters discussed by Jägersten (1940a). The order Pharyngidea is paraphyletic. Putative apomorphies supporting this tree morphology are: 1, more than three pairs of gut diverticula; 2, epidermis a syncytium with its nuclei sunken below the muscle layer; 3, ventral nerve cord shortened antero-posteriorly; 4, gut diverticula reduced to one or two pairs; 5, body expanded laterally (but by different means in the two genera); 6, parasites of Asteroidea; 7, marginal cirri present (-7, represents sporadic independent losses); 8, large proboscis derived as protruded pharynx (homology not confirmed for *Contramyzostoma*); 9, uterine branches enclosing gut diverticula (convergently so in one species of *Protomyzostomum*); 10, mouth and anus both dorsal and gut U-shaped; 11, pair of protrusible penes; 12, well-developed lobiform parapodia with muscoli centrales forming mid-ventral muscle mass; 13, large proboscis derived ontogenetically from entire anterior end of juvenile's body, and; 14, prebulbar nerve ring. [M. Grygiel]

interpreted here as an apomorphy, not a plesiomorphy lost independently four times in all the other genera, as in Jägersten's (1940a) scheme.

Fossil Record

Deformities on fossil crinoids and occasionally other fossil echinoderms have been attributed to myzostomes by many authors since the first observations by Graff (1885a); a heterogeneous form genus, *Myzostomites*, has been proposed for some of them. The great majority of supposed myzostome traces from fossil crinoids involve the columns of stalked crinoids; they are most often seen as barrel-shaped swellings that sometimes have slits, apertures or internal hollows. Franzén (1974) noted that almost none of these fossils resembles the impressions left by activity of extant myzostomes.

All myzostome-induced deformities in Recent crinoids concern the arms, pinnules or disc, except for the cysts of *Mycomyzostoma calcidicola*, which involve the column and cirri of *Saracrinus nobilis* (Eeckhaut 1998). Several authors (see Meyer & Ausich 1983) have, therefore, recognised only certain arm deformities, none older than Pennsylvanian, as fossil traces of cysticolous or gallicolous myzostomes (see for example, Welch 1976, text-fig. 2). However, Eeckhaut (1998) believes that the discovery of *M. calcidicola* ought to revive the debate about older Palaeozoic column deformities.

Classification

The classification outlined in Table 2.2 and adopted here is based on that of Jägersten (1940a) with modifications to reflect the current state of knowledge. Six of the eight families, marked with an asterisk, are not known from Australian waters. However, members of the Protomyzostomatidae, Asteromyzostomatidae and Pulvinomyzostomatidae have been recorded from Antarctic waters and are likely to occur in the Australian Antarctic Territory.

For the group as a whole, Graff's (1877) name Myzostomida has precedence over Perrier's (1897) name Philocrinida. Jägersten (1940a) proposed a division into two orders: Proboscidea and Pharyngidea. Proboscidea includes one family, Myzostomatidae, with a single genus *Myzostoma*. The Pharyngidea comprise six families, each with one genus: Stelechopodidae (*Stelechopus*), Protomyzostomatidae (*Protomyzostomum*), Mesomyzostomatidae (*Mesomyzostoma*), Cystimyzostomatidae (*Cystimyzostomum*; see nomenclatural remarks below), Asteriomyzostomatidae (*Asteriomyzostomum*) and Pulvinomyzostomatidae (*Pulvinomyzostomum*). Of these seven families, only the Myzostomatidae and Cystimyzostomatidae (as Endomyzostomatidae here, see below) are known to occur in Australian waters.

Wagin (1954) proposed a new genus, *Asteromyzostomum*, in a new subfamily, outside the context of Jägersten's classification. He considered it to be derived from a *Myzostoma*-like ancestor. However, it lacks the characteristic *Myzostoma* proboscis, which is the defining character of the order Proboscidea. Accordingly, Wagin's subfamily is elevated here provisionally to family Asteromyzostomatidae

in the Pharyngidea. Eeckhaut (1995) placed the genus in the Asteriomyzostomatidae with no explanation; Figure 2.9 shows that there might be some justification. *Asteromyzostomum* is not known from Australia.

Species-groups like those diagnosed by Grygier (1990) within the heterogeneous genus *Myzostoma* were implicit already in Graff's (1884b) *Challenger* Expedition monograph. Several available genera have been proposed by Perrier (1897) and Uchida (1992) for subsets of *Myzostoma sensu lato*: *Cercomyzostoma*, *Polymyzostoma*, *Hypomyzostoma* (= *M. crosslandi*-group; type: *M. folium*), *Notopharyngoides* (= *M. platypus*-group; type: *M. ijimai*); the last two have been accepted by Eeckhaut *et al.* (1998) and Grygier & Nomura (1998), and are thus adopted here.

Perrier (1897) proposed two additional genera, *Endomyzostoma* and *Heteromyzostoma*, for species subsequently included by Jägersten (1940a) in *Cystimyzostomum*, a junior synonym and thus invalid. Grygier in Eeckhaut (1998) recognised *Endomyzostoma* (type: *M. pentacrini*) as the valid name of this genus; elevated to family level, Perrier's (1897) subfamily, now as Endomyzostomatidae, thus has priority over Cystimyzostomatidae and is to be used instead.

Eeckhaut & Jangoux (1995) placed their new genus *Contramyzostoma* in the Cystimyzostomatidae (that is, Endomyzostomatidae), but this assignment was based on the relation with the host, not on morphology, and may not withstand closer scrutiny. Another new genus, *Mycomyzostoma*, was described in the same family by Eeckhaut (1998), and possibly yet another (family assignment uncertain) has been discovered by Heinzeller *et al.* (1995). None of these new forms is known from Australia, although *Saracrinus nobilis*, the host of *Mycomyzostoma calcidicola*, occurs off the north-western coast.

Table 2.2 Classification of the extant Myzostomida. Families marked with an asterisk (*) have not been recorded from Australian waters. †See Affinities with Other Groups for discussion concerning the position and rank of Myzostomida.

Class MYZOSTOMIDA†
Order PROBOSCIDEA
Family Myzostomatidae
Order PHARYNGIDEA
Family Stelechopodidae*
Family Protomyzostomatidae*
Family Mesomyzostomatidae*
Family Endomyzostomatidae
Family Asteriomyzostomatidae*
Family Asteromyzostomatidae*
Family Pulvinomyzostomatidae*

Key to the orders and families of Myzostomida

- 1(a) Marginal cirri usually present in ten or more pairs (Figs 2.1A–C, E, F, 2.2B), but sometimes body margin even, irregular or scalloped (Fig. 2.1G, I–L). Parapodia usually well developed (Fig. 2.3B; 2.4A). Proboscis present, movable and retractable (Figs 2.1D, 2.2A, B). Prebulbar nerve ring present anterior to pharyngeal muscle bulb; connected to, but not incorporating cerebral ganglia (Fig. 2.6). Diverticula of female reproductive system generally located dorsal to and following the midgut diverticula (Fig. 2.2C). Protrusible penis on each side lateral to third parapodium (Fig. 2.1B). Mostly living externally on crinoids or ophiuroids as adults. Order Proboscidea, Myzostomatidae
- 1(b) Marginal cirri absent or fewer than 10 pairs. Parapodia small to vestigial. Proboscis present or absent. Prebulbar nerve ring absent or represented by plexus. Cavities of female reproductive system usually broadened, sometimes enclosing midgut diverticula (Fig. 2.14B). Penes absent or rudimentary. Adults mostly encysted (Fig. 2.13A, C), gallicolous, inquiline or endoparasitic Order Pharyngidea, 2
- 2(a) Body margins upturned dorsally in functional female or hermaphrodite stage (Figs 2.14B, C, 2.19A). Proboscis present (Figs 2.13B, 2.19). Marginal cirri present in some. Midgut diverticula at least in part passing through or contained within uterine diverticula (Fig. 2.14B). Testes almost always compact (Fig. 2.14D) 3
- 2(b) Body margins not upturned (Figs 2.10; 2.11A, 2.12), or, if so, also thrown into complex folds (Figs 2.1N, 2.18). Proboscis absent. Marginal cirri absent. Stomach and midgut diverticula ventral to uterus and its diverticula [except *Protomyzostomum polynephris* as in 2(a)]. Testes diffuse (Fig. 2.11A) or as large, open sacs 4
- 3(a) Mouth and anus both dorsal (Fig. 2.19). Lateral organs present, 10 pairs (Fig. 2.19). Ovaries found dorsal to gut. Living within oesophagus and stomach of crinoids. Pulvinomyzostomatidae†
- 3(b) Mouth and anus both terminal (Fig. 2.14A). Lateral organs absent, or four pairs. Ovaries found ventral to gut (Fig. 2.14B, C). Living in cysts or galls on crinoids (Fig. 2.13A, C) Endomyzostomatidae†† (synonym: Cystimyzostomatidae)
- 4(a) Body longer than wide. Parapodia positioned more or less along body margins (Figs 2.11A, 2.12). Mostly endoparasites of crinoids or ophiuroids. 5
- 4(b) Body wider than long (Figs 2.1N, 2.17A, 2.18). Parapodia found ventrally, close to but not along margins. Parasites of asteroids 7
- 5(a) Lateral organs absent. Epidermis of discrete cells. Two pairs of uniseriably branched midgut diverticula. Ventral nerve cord running whole length of body. Endoparasites of crinoid reproductive system (Fig. 2.12) Mesomyzostomatidae
- 5(b) Lateral organs present. Epidermis a syncytium with nuclei sunken below integumental muscle layer. Stomach with three or more pairs of diverticula (Fig. 2.11A) or as large, open sac (Fig. 2.10A). Ventral nerve cord not longer than one-half body length (Fig. 2.11A) 6
- 6(a) Anus not protruded. Parapodia slightly protruding with ring-like cuticular thickenings. Two pairs of lateral organs far anteriorly and far posteriorly. Midgut and uterus as large, open sacs; oviduct and utero-intestinal ducts absent. Associates of deep-sea stalked crinoids. (Fig. 2.10A, B) Stelechopodidae
- 6(b) Anus protruded on conical process. Parapodia not protruding, sometimes found in indentations of body margin. Five pairs of lateral organs found dorsally, more or less opposite parapodia. Midgut with numerous lateral diverticula which sometimes anastomose. Oviduct and at least one pair of utero-intestinal ducts present. Endoparasites or cysticoles of basket stars and brittle stars (Ophiuroidea) (Fig. 2.11A, B) Protomyzostomatidae
- 7(a) Body flat and oval with simple margin. Mouth ventral and anus dorsal. Parapodia arranged in oval. Four pairs of lateral organs alternating with parapodia; one extra medial posterior lateral organ sometimes present. Male genital openings lateral. Endoparasites. (Fig. 2.17A, B) Astერიomyzostomatidae
- 7(b) Body fungus-like, posterior margin thrown into complicated lobular folds that bear many supernumerary lateral organs. Mouth and anus terminal, former surrounded by circum-oral tentacles. Parapodia located along anterior margin. Male genital openings on anterior margin. Ectoparasites. (Figs 2.1N, Fig. 2.18) Asteromyzostomatidae

† *Contramyzostoma* (Fig. 2.15), assigned to the Cystimyzostomatidae by Eeckhaut & Jangoux (1995), probably has affinities to both Pulvinomyzostomatidae and Endomyzostomatidae (see Fig. 2.9) and is considered *incertae sedis* herein.

†† *Mycomyzostoma* (Fig. 2.16), assigned to the Endomyzostomatidae by Eeckhaut (1998), is morphologically so simplified as to defy family assignment; it is considered *incertae sedis* herein.

Order PROBOSCIDEA

Members of the Proboscidea are distinguished by the presence of a movable and protrusible proboscis in which a prebulbar nerve ring is present; the peribulbar nerve ring, when present, is incomplete. The proboscis is derived ontogenetically from the anterior part of the juvenile's body; thus, the salivary glands empty into the anterior end of the pharynx or onto the tip of the proboscis. The parapodia are usually well developed, sometimes each with a medial cirrus. Ten or more pairs of marginal cirri are usually present, but by no means universal. The uterine diverticula follow dorsally along the midgut diverticula. A protrusible penis is present on each side of the body.

The Proboscidea comprises the single family Myzostomatidae.

Family Myzostomatidae

The Myzostomatidae are a large family of commensal or semi-parasitic marine worms (Pls. 10.1–10.4). They mostly live externally on crinoids, but a few live in galls on crinoids or externally on ophiuroids. The distinguishing features of the family are those of the order.

The family name was originally proposed as Myzostomidae, an 'incorrect' spelling that has been widely used. However, from 1989 the nomenclaturally correct spelling Myzostomatidae has been used consistently by the author. The grammatical root for the formation of the family name based on *Myzostoma* is 'Myzostomat-', not 'Myzostom-', for it is derived from 'stomatos', the genitive form of the Greek word 'stoma'. The other family names used in this chapter similarly represent corrections of original misspellings.

The family comprises several nominal genera: *Myzostoma*, *Hypomyzostoma* and *Notopharyngoides* are recognised here. The principal genus, *Myzostoma* (junior synonyms *Myzostomum* and *Cyclocirra*), includes about 100 validly described species; its type, *M. cirriferum*, is the best known and studied of all myzostome species. *Myzostoma* comprises a heterogeneous collection of species and will probably become more restricted as well-defined subsets are removed as distinct genera; Grygier (1990) has briefly defined unnamed species-groups. Recognition seems premature for some of the genera proposed by Perrier (1897), for example *Cercomyzostoma* for species with caudal processes and *Polymyzostoma* for those with more than 20 marginal cirri. Fishelson (1974) used a *nomen nudum*, *Eumyzostomum*, for specimens identified by V.L. Wagin (L. Fishelson personal communication); no published work by Wagin defining the genus has been found.

The Australian myzostomatid fauna is very diverse and includes representatives of all three genera (see Table 2.1). About 71 species of *Myzostoma* are recognised from Australia by the author, although only about 24 can be identified with certainty. Most live in the tropical regions of Australia; 14 have been found in two or more of the six tabulated geographic regions (Table 2.1). These 71 purported species can be grouped by body form: typical and thin-bodied (23 species), typical and thick-bodied (18), multi-cirrate (5), having one or more caudal processes (12), and other (13). In addition, three or four species of *Myzostoma* occur on a similar number of comatulids at Lord Howe Island and the Elizabeth and Middleton Reefs in the Tasman Sea (Table 2.1). Three Antarctic species, *M. antarcticum* and *M. divisor*, from comatulid crinoids, and *M. gerlachei* from an ophiuroid, have not yet been reported from the Australian Antarctic Territory,

but are likely to occur there. Only one species of *Notopharyngoides*, *N. aruensis*, has been reported from Australian waters; it lives on an unidentified host in the Northern Territory and on *Stephanometra oxyacantha* in Queensland. Some 15 species of *Hypomyzostoma* have been noted by the author, possibly an over-estimate due to the abundance of transversely banded or ridged forms similar to *H. fasciatum* and *H. dodecaphalcis*; almost all are tropical.

The morphology of *Myzostoma* species (as represented mostly by *M. cirriferum*) is covered extensively above in the general introduction to the Myzostomida; this section briefly characterises the other two genera and describes the range of morphological variation within *Myzostoma*.

The genus *Notopharyngoides* has three described species from the Indo-West Pacific: *N. platypus*, *N. aruensis* (Fig. 2.1J) and *N. ijimai*. They live singly or in pairs in soft cysts on the host's arms or disc, or freely on the host, or in the host's mouth (Grygier & Nomura 1998; Eeckhaut *et al.* 1998). The body is round or oval, but the margins may be upturned; cirri may be present or absent. The proboscis pocket opens either ventrally (*N. platypus*) or dorsally. Two to four low, steep-sided protuberances are present along the ventral midline; the anus is at the rear of the posterior one. The parapodial folds are wide, flat, kidney-shaped lobes; the lateral organs are in the centre of similar round lobes. A ventral submarginal shelf (*N. ijimai*) or ring of lappets (the other species) may coalesce with some of the lateral organ lobes. Aspects of the internal morphology were described by Wheeler (1896) for *N. platypus* and Remscheid (1918) for *N. aruensis*.

The genus *Hypomyzostoma* (Fig. 2.1K–M) comprises at least 11 described species, including representative species such as *H. folium*, *H. crosslandi*, *H. elongatum*, *H. dodecaphalcis* and *H. nanseni*. They live extended lengthwise along the arms or pinnules of crinoids. The body form is elongate with a convex dorsum and, generally, a concave ventral side. The parapodia lie at equal intervals in two parallel rows; the first pair is much closer to the anterior end than the fifth is to the rear. The lateral organs lie very near the margin; the first two pairs tend to be displaced anteriorly and the last two posteriorly with respect to the nearby parapodia. Cirri are absent; however, the margin may have numerous large, rounded projections or scallopings, or may bear denticle-like processes, or be nearly smooth. Transverse dorsal colour stripes or ridges may be present. The parapodial fold usually bears a button-like medial cirrus, and the parapodium itself typically bears a villose pad and a longitudinal groove. The proboscis pocket and the anus both open ventrally; buccal papillae are absent. Aspects of the internal morphology were described by Graff (1877) for *H. elongatum*, Boulenger (1913) for *H. crosslandi* and Remscheid (1918) for *H. taeniatum* and *H. sulcatum*. Encysted juveniles have been noted for two species (Remscheid 1918; Grygier 1988).

As a 'catch-all' genus including about 100 described species, *Myzostoma* shows an enormous range of morphological variation. Commonly the body shape, ignoring any caudal processes, is round, shield-shaped or oval (Fig. 2.1A–G); oval-elongate or bullet-shaped bodies are uncommon. Caudal processes may comprise a single upturned or furled lobe, several finger-like lobes (Fig. 2.1I), pairs of small, triangular lobes, or two or four or more grossly enlarged cirral bases with or without apical cirri. The body varies in thickness from membranous (Fig. 2.1B) to robust (Fig. 2.1E); hemispherical (Fig. 2.1D) or hemicylindrical body forms occur. A thin, translucent marginal zone not penetrated by the internal organs may be present (Fig. 2.1B). Colour patterns vary and

2. CLASS MYZOSTOMIDA

can include contrasting circles or stripes (Fig. 2.1C). Many species have a dorsal longitudinal ridge and numerous radiating ridges (Fig. 2.1G, I); less commonly, dorsal tubercles or other kinds of sculpturing are present (Fig. 2.1E). The margin usually bears cirri, which may be long or short or of variable lengths (if the latter, usually the anterior and posterior several pairs are longer than the lateral ones; Fig. 2.1A). The cirri may taper or be even in diameter, or they may be minute nubs. The number of cirri is usually 20 (10 pairs; Figs 2.1A, B, E, 2.2B), but some species have up to 100 or more (Fig. 2.1C). The 10 pairs are usually spaced evenly, but in several species they are distributed in pairs flanking each lateral organ. A considerable number of species lack cirri, but may have numerous rounded projections (Fig. 2.1G), or a lobed, membranous fringe; in others the margin is simple. The parapodia vary in relative size, extensibility, shapes and relative sizes of the hooks and support rods, presence or absence of medial cirri, distance of the array from the centre or the midline and extent of anterior displacement of the array. The size, shape and relative position of the lateral organs vary; a few species have more than the usual four pairs (five or six). The proboscis usually has buccal papillae that vary in number from four to at least 30 (Fig. 2.1D), but some species have none. The proboscis pocket usually opens ventrally, but may open marginally. The anus is ventral, marginal or, rarely, dorsal. When everted, the penes usually protrude directly from the lateral bases of the third parapodia; however, in certain species the apertures from which they protrude are displaced close to the body margin (Fig. 2.2B). Internally, the pattern of midgut diverticula, and thus also of uterine diverticula, varies greatly: There may be either two or three pairs of main gut diverticula (Fig. 2.2C), and their subsequent branching may be very limited or very extensive (Fig. 2.1B). The ovaries are located either in the uterus dorsal to the stomach or in a pair of uterine diverticula at different levels lateral or ventro-lateral to the stomach (Fig. 2.2C). The pair of utero-intestinal ducts may be separate or they may be fused at either the uterine end or the intestinal end.

Order PHARYNGIDEA

Members of Pharyngidea are distinguished by the absence of a myzostomatid-type proboscis. If present, the proboscis is formed as a protrusion of the posterior wall of the oral cavity; thus the salivary glands, when present, empty into the oral cavity. A peribulbar nerve ring, incorporating the cerebral ganglia, is sometimes present. Compared to proboscideans, marginal cirri are fewer or absent, the parapodia are poorly developed, penes are generally absent, and the female reproductive system usually consists of broad spaces rather than narrow diverticula; gut diverticula often penetrate these spaces. Most pharyngideans are enclosed or otherwise permanently fixed to their host; they do not live freely upon their hosts.

The Pharyngidea comprises seven families. Only species of one family, Endomyzostomatidae, are found in Australian waters. Descriptions of the other six families are provided as several may yet be found in Australia or its external territories.

Family Stelechopodidae

The family Stelechopodidae is represented by the single species *Stelechopus hyocrini*. It was first collected during the *Challenger* Expedition off the Crozet Islands in the Indian Ocean (Graff 1884b); animals were found on stalked crinoids, *Hyocrinus* and *Bathycrinus* species, at depths of 750–875 m.

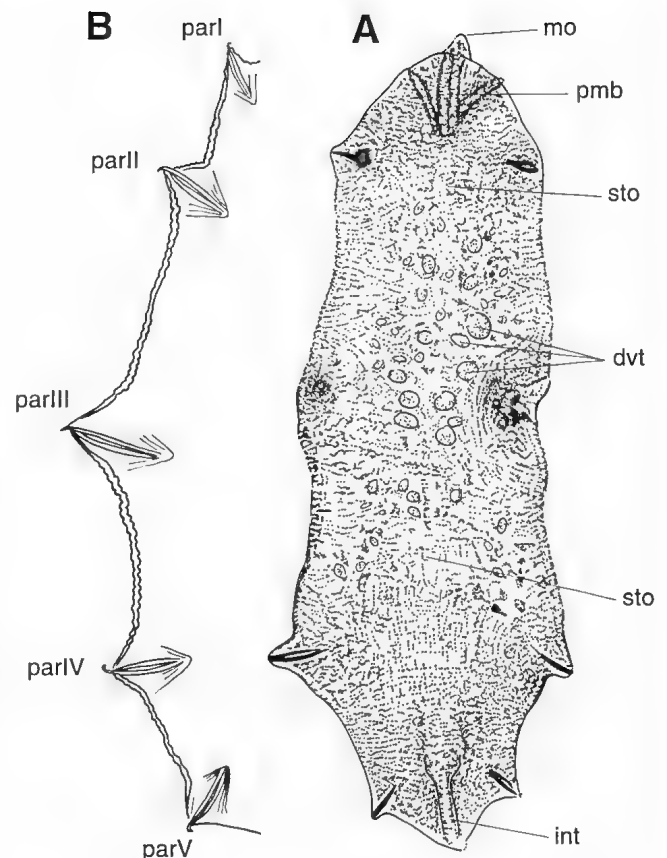


Figure 2.10 Family Stelechopodidae. *Stelechopus hyocrini*. A, entire animal flattened on slide. B, body margin showing parapodia. dvt, dorso-ventral trabeculae; int, intestine; mo, mouth; parI–parV, parapodia I–V or their hook apparatus; pmb, pharyngeal muscle bulb; sto, stomach. (A, after photomicrograph by Jägersten 1940a; B, after Graff 1884b) [I. Hallam]

The precise relationship between *S. hyocrini* and its hosts is unknown. Jägersten (1940a) redescribed the species, giving details of its histology.

The following summary of the morphology of *Stelechopus hyocrini* is primarily based on Jägersten's (1940a) study. The body is flat and elongate, reaching a size of 3.5 x 0.9 mm (Fig. 2.10A). The unusually thick (60 µm) cuticle is papillose. The nuclei of the epidermal syncytium are sunken beneath the longitudinal and circular integumental muscle strands. There is very little parenchyma. The small parapodia are usually positioned ventro-laterally along the length of the body (Fig. 2.10B), or sometimes marginally or dorso-laterally; their integument has circular folds. The third pair of parapodia is the largest, and the first and fifth pairs the smallest; the first pair or one of its members is occasionally absent. Although parapodial musculature is present, but there is no musculus centralis, nor a ventral muscle mass. Marginal cirri are absent. Only two pairs of lateral organs have been observed: simple, deep invaginations in front of the first pair of parapodia and behind the fifth pair.

The mouth is at the end of a very small, apparently non-retractile, anterior process (Fig. 2.10A), behind which the pharynx passes through a small muscle bulb. The midgut is a large, open space interrupted by trabeculae that enclose dorso-ventral muscles; it may represent the combined stomach and gut diverticula of other myzostomes (Jägersten 1940a). The short intestine leads to the anus beneath the posterior end of the body.

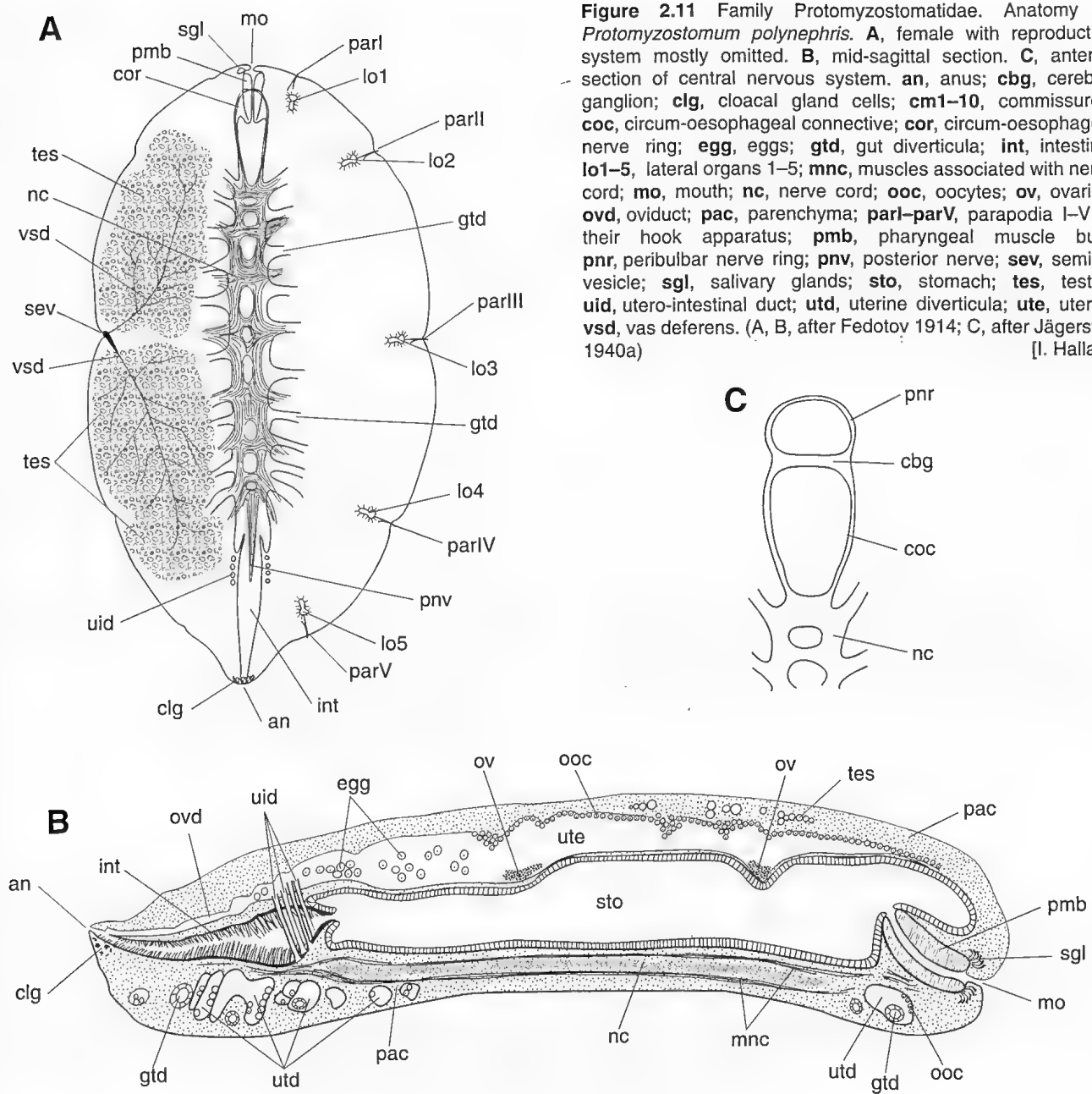


Figure 2.11 Family Protomyzostomatidae. Anatomy of *Protomyzostomum polynephris*. **A**, female with reproductive system mostly omitted. **B**, mid-sagittal section. **C**, anterior section of central nervous system. **an**, anus; **cbg**, cerebral ganglion; **clg**, cloacal gland cells; **cm1–10**, commissures; **coc**, circum-oesophageal connective; **cor**, circum-oesophageal nerve ring; **egg**, eggs; **gtd**, gut diverticula; **int**, intestine; **lo1–5**, lateral organs 1–5; **mnc**, muscles associated with nerve cord; **mo**, mouth; **nc**, nerve cord; **ooc**, oocytes; **ov**, ovaries; **ovd**, oviduct; **pac**, parenchyma; **parI–parV**, parapodia I–V or their hook apparatus; **pmb**, pharyngeal muscle bulb; **pnr**, peribulbar nerve ring; **pnv**, posterior nerve; **sev**, seminal vesicle; **sgl**, salivary glands; **sto**, stomach; **tes**, testes; **uid**, utero-intestinal duct; **utd**, uterine diverticula; **ute**, uterus; **vsd**, vas deferens. (A, B, after Fedotov 1914; C, after Jägersten 1940a) [I. Hallam]

The female reproductive system comprises a uterus with anastomosing diverticula. It is dorsal to, and co-extensive with the midgut and, like the latter, is interrupted by dorso-ventral trabeculae (Fig. 2.10A). Ovaries were not found, but young oocytes were present on the dorsal wall, and rather small, ripe oocytes (60–100 µm) were free in the lumen. Histological examination has shown that the thin wall separating this cavity from the midgut breaks down, thus allowing ripe oocytes to enter the midgut. Neither a lateral pair of ducts from the uterus nor a medial oviduct was found; the eggs may be expelled via the gut.

The male reproductive organs are paired and lie ventral to the midgut; on each side is a long, folded, generally open sac that shows very little differentiation into follicles and ducts. It has a few trabeculae like those of the midgut and a laterally directed exit duct that opens through a weak sphincter on the body margin just above the third parapodium. There appear to be no protrusible penes and no certain evidence of spermiocysts.

The ventral nerve cord is elongate and single-stranded, reaching nearly the length of the body. It gives rise to about eight pairs of lateral nerves, one opposite each of the five parapodia, and the third, fifth and seventh between the parapodia. An anterior nerve ring was not observed.

Family Protomyzostomatidae

Protomyzostomatids are endoparasites or cyst dwellers of ophiuroids and usually live in temperate to cold seas. The single genus *Protomyzostomum* includes five described species, of which four are found in the Russian Arctic, Bering Sea, Sakhalin and Japan; they are endoparasites of the gonads or cyst-dwellers on the arms or discs of basket stars (Ophiuroidea) (Fedotov 1912, 1914, 1916, 1925; Okada 1922; Jägersten 1940a; Nigmatullin 1970). The fifth species, *P. glanduliferum*, occurs in the Antarctic. It inhabits the ventral coelom (rarely the dorsal) of the brittle star *Ophiacantha disjuncta*. An undescribed myzostome that may belong to this family is an endoparasite of the large antarctic

2. CLASS MYZOSTOMIDA

brittle star *Ophionotus victoriae* (Bartsch & Faubel 1995). Both species have been found only in the Weddell Sea, but they may also live in the Australian Antarctic Territory.

The following account is based primarily on *Protomyzostomum polynephris* (see Fedotov 1912, 1914), an endoparasite that consumes the genital sacs in the affected gonad lobes of *Gorgonocephalus eucnemis*. Such feeding leads to partial or full castration of the host, depending on the intensity of the infestation. Up to five adult individuals of *P. polynephris* live together in capsule-like cysts that eventually become calcified. Young worms occur in the bursal cavities or beneath the bursal epithelium. Infestations of up to half the population of the host species occur, with from one to at least 119 parasites per host. The Antarctic *P. glanduliferum* also shows a host prevalence of about 50% (Bartsch & Faubel 1995).

Adult *Protomyzostomum polynephris* (Fig. 2.11A, B) are the largest of all myzostomes and may reach a size of 32 mm long by 15 mm wide and a thickness of 2–3 mm. The body is oval and flat, but in life is either rolled up or irregularly folded within its capsule. There is a thin cuticle, but no external cilia. The epidermal cells are sunk beneath a muscular layer, with no basal membrane; their distal portions form a syncytium through which criss-crossing circular and longitudinal muscles pass. Integumental gland cells occur only near the anus and sometimes the mouth. The body musculature is weak and includes dorso-ventral muscles, muscles above and below the nerve cord, and muscles sheathing the gut and female reproductive system.

The poorly-developed parapodia are present on the body margin in the young, but close to the ventral margin in older individuals; they often occupy indentations of the margin (Fig. 2.11A). Only those of mid-sized individuals have replacement hooks. The musculature of each parapodium is independent. Marginal cirri are absent in all species. The five pairs of lateral organs are small and inconspicuous except in *P. cystobium*, and they are located dorsally, more or less directly opposite the parapodia (Fig. 2.11A). Each lateral organ has a ciliated floor and a central part surrounded by gland cells; in *P. polynephris* a canal leads inward from the floor. The musculature of the lateral organs includes sphincters, retractors, dilators and protractors, but there is no surrounding capsule formed from dorso-ventral muscles. The mouth and anus are terminal, the mouth opening on a distinct, small or large, conical papilla (Fig. 2.11A, B). A proboscis and buccal papillae are absent, but the pharynx can be protracted and retracted to some extent. A sphincter and dilator muscles surround the mouth. The small pharyngeal muscle bulb (Fig. 2.11B) has two layers of circular fibres and irregularly arranged radial fibres. Salivary gland cells empty into the posterior part of the mouth cavity. Eight to 13 (most often 10) more or less ramifying diverticula branch irregularly off the long stomach on each side in *P. polynephris* (Fig. 2.11A). *Protomyzostomum sagamiense* has 16 to 25 such diverticula on each side; only three or four are present on each side in *P. cystobium* and *P. glanduliferum*. Posterior to the stomach there is a shorter, ciliated intestine.

Protomyzostomatids are hermaphrodites, the smaller ones being more actively male, the larger ones more female. Two diffuse ovaries are usually present, one behind the other, on the ventral side of the uterus over the gut (Fig. 2.11B); *P. glanduliferum* has one ovary. The uterus has to eight to 18 diverticula per side irregularly along its anterior two-thirds, often parallel to and, in *P. polynephris*, sometimes enclosing the midgut diverticula; some enter the ventral part of the body

(Fig. 2.11B). In *P. cystobium* they all pass ventrally between the gut diverticula and can anastomose. The oviduct empties into the intestine internally just before the anus. Ciliated ducts run dorso-ventrally between the lower part of the uterus and the lower or middle part of the anterior portion of the intestine; they number three to seven per side in *P. polynephris* (Fig. 2.11B); *P. cystobium* has only one pair. The diffuse testicular follicles (Fig. 2.11A) are dorsal to the female organs in *P. polynephris* and *P. glanduliferum* and dorsal to the gut diverticula in *P. cystobium*, but mostly lie ventral to the gut diverticula in *P. sagamiense*. The testes lead into an anterior and posterior pair of vasa deferentia. These empty, via small seminal vesicles and non-protrusible, nipple-like penes, through a pair of marginal slits between the third parapodia and third lateral organs.

The nervous system in *P. polynephris* and *P. cystobium* is ladder-like with a circum-oesophageal ring and peribulbar ring (Fig. 2.11C) and a widely separated pair of ventral nerve cords (Fig. 2.11A). The cords are joined by 10 commissures and give off eight main pairs of lateral nerves and an unpaired posterior nerve. Pairs 3, 5 and 7 are thinner than the others and innervate the sex organs, whereas the other pairs each split into two branches that serve the respective parapodium and lateral organ (and penis). The nervous system is quite different in *P. astrocladi* (Jägersten 1940a). The ventral nerve cord is unpaired, although two fibrous tracts are present within it. Besides the main lateral nerves, innumerable other interconnected nerve tracts forming a plexus are present. They are more developed ventrally than dorsally, and supposedly Fedotov (1925) mistook these for muscles.

Family Mesomyzostomatidae

The two known mesomyzostomatid species are endoparasites of the reproductive organs of comatulid crinoids. The better known species, *Mesomyzostoma reichenspergi*, was collected from *Amphimetra discoidea* in the Aru Islands, Indonesia (Remscheid 1918). It can be assumed to occur in northern Australia. It lives in the sterile longitudinal canals of the crinoid arm, and not in the gonads themselves. *Mesomyzostoma katoi* is found in the gonads of *Oxycomanthus japonicus* in Japan (Okada 1933).

The body of *M. reichenspergi* (Fig. 2.12) is vermiform, up to 1.91 mm long and 3 to 6.5 times longer than wide; *M. katoi* reaches a size of 4.5 x 0.45 mm. A cuticle is present, but external cilia are absent. The integumental musculature includes outer circular and inner longitudinal muscles. Other longitudinal muscles encompass the pharynx, stomach and gut diverticula, and circular muscles ensheath the cloaca and uterus. Muscles also surround the ventral nerve cord.

Parapodia are represented only by slight lateral protrusions. Five pairs of independent hook apparatus are present in *M. reichenspergi* and three to four pairs in *M. katoi* (Fig. 2.12). Each consists of one or two hooks and a support rod. Marginal cirri and lateral organs are absent.

A proboscis and proboscis pocket are absent. From the terminal mouth the pharynx passes through a small pharyngeal muscle bulb and a sphincter into the long, narrow stomach. At about mid-body in *M. reichenspergi* and three-quarter body length in *M. katoi*, two pairs of diverticula branch off to the anterior and posterior ends of the body (Fig. 2.12); each diverticulum gives rise to a single row of closely spaced, laterally directed side branches. The long, narrow intestine extends to the terminal anus.

Family Endomyzostomatidae

Members of the Endomyzostomatidae live in cysts or galls on crinoids. Galls are formed from enlarged and deformed crinoid ossicles, whereas cysts are fleshy or incorporate many supernumerary ossicles.

Until recently, this family supported one genus concept with three available names, each with a different type species: *Endomyzostoma* (*Myzostoma pentacrini*), *Heteromyzostoma* (*M. tenuispinum*), and *Cystimyza* (*M. cysticum*). The name *Endomyzostoma* only is recognised as valid here (see discussion under Classification). Eeckhaut & Jangoux (1995) assigned the new genus *Contramyzostoma* to this family, as did Eeckhaut (1998) for *Mycomyzostoma*, but these are treated here separately because the true affinities of these genera are uncertain. The family is also known as *Cystimyza*.

The boundaries of the Endomyzostomatidae are not firmly established. Jägersten (1940a) included at least 10 nominal species in *Cystimyza*, comprising the majority of gallicolous and cysticolous myzostomes from crinoids. Jangoux (1987, 1990), however, returned the gallicoles, including *M. pentacrini* and *M. tenuispinum*, to *Myzostoma* and restricted *Cystimyza* to cysticoles. He also transferred into *Cystimyza* some species from the Myzostomatidae that are otherwise referable to *Notopharyngoides* (*N. platypus*, *N. ijimai*), *Hypomyzostoma* (*H. taeniatum*) and *Myzostoma* (*M. willemoesii*; see Fig. 2.1H). Jangoux's classification is not supported by comparative morphology and is here considered artificial. The species-level taxonomy also appears to be artificial. *Endomyzostoma cysticum* has been reported to form different types of cysts on different parts of the body of an assortment of crinoid species from the Caribbean, Red Sea, Japan, Indonesia and Antarctica, and it almost certainly comprises several distinct species, despite opinions to the contrary by Stummer-Traunfels (1908). Histological study of this genus has not been as thorough as for most of the other myzostome genera (see works by Graff 1884b; Wheeler 1896; McClendon 1906; Stummer-Traunfels 1908).

The domicile of endomyzostomatids takes several forms (see Graff 1884b; Boulenger 1916; Remscheid 1918; Eeckhaut & Améziane-Cominardi 1994): a crypt hollowed out between and within enlarged arm ossicles; a cavity within swollen pinnules; a relatively soft cyst with some calcified elements along the ambulacrum of a pinnule, arm or disc (Fig. 2.13A); a hard, bean-shaped gall involving one or two arm ossicles; a hard, sac-like or liver-shaped, multi-plated cyst of the arms, pinnules or disc (Fig. 2.13C). Cysts may have a single opening, as in *Endomyzostoma deformatum*, but usually two are present, one of which faces into the ambulacral groove and the other is near the posterior end of the body.

The Australian fauna investigated by the author includes at least three species of *Endomyzostoma*. A form referable to *E. clarki* lives in galls on the arms of at least two species, including *Metacrinus cyaneus* and unidentified specimens, of metacrinine stalked crinoids off north-western and south-eastern Australia. Another, which might be referred to *E. cysticum* of Remscheid (1918) (Fig. 2.13C) or may be polytypic, lives in a liver-shaped, multi-plated cyst on the arms or pinnules of several species of comatulids in tropical Australia, including *Himerometra robustipinna*, *Heterometra crenulata* and *Pontometra andersoni*. An undescribed species that resembles *E. deformatum* lives in a small, soft cyst along the arm ambulacra of *Comatella stelligera* at Barrow Island, Western Australia. In addition, *E. cysticum* of Stummer-

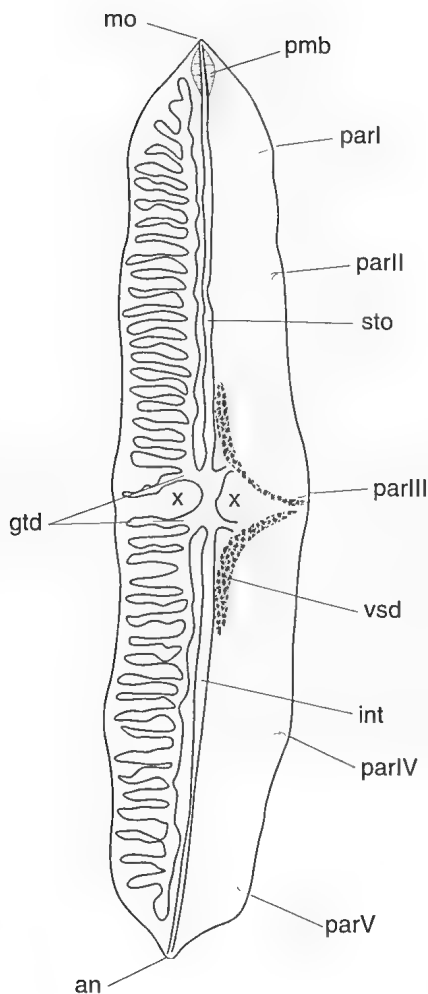


Figure 2.12 Family Mesomyzostomatidae. Morphology of *Mesomyzostoma reichenspergi*; ovary sites indicated by x. an, anus; gtd, gut diverticula; int, intestine; mo, mouth; parI–parV, parapodia I–V or their hook apparatus; pmb, pharyngeal muscle bulb; sto, stomach; vsd, vas deferens. (After Remscheid 1918) [I. Hallam]

The female reproductive organs overlie the digestive organs. A pair of short utero-intestinal ducts branch off the uterus and enter the intestine through a common ventral pore. Also branching from the uterus are two pairs of diverticula that overlie the gut branches; they often bulge with ova released from their dorsal wall. The two ovaries lie in ventral pouches of the uterus between the two pairs of diverticula. The oviduct overlies the intestine and empties terminally. The testes generally lie beneath the gut diverticula. In *M. reichenspergi*, the anterior and posterior vas deferens on each side (Fig. 2.12) join at a small, well-muscled seminal vesicle that exits through a sphinctered ejaculatory duct dorsal to the third pair of parapodial hooks. Supposedly, male gonopores are absent in *M. katoi*.

The circum-oesophageal nerve ring encircles the end of the mouth tube in front of the pharyngeal muscle bulb. The single ventral nerve cord runs the length of the body and gives rise to five pairs of large nerves to the parapodia, an undetermined number of finer nerves between these, and some terminal nerves.

2. CLASS MYZOSTOMIDA

Traunfels (1908) and Boulenger (1916), an Antarctic species that forms a soft cyst on the arms and discs of *Promachocrinus kerguelensis* and *Antedon adriani* (Figs 2.13A, B, 2.14A, D, E), undoubtedly occurs in the Australian Antarctic Territory; such cysts have been seen on crinoids from off Adélie Land (M.J. Grygier personal observation).

The female body is 2–11 mm long and round in outline when flattened, but in life it is typically trough-shaped or folded in two with the lateral margins upturned and even meeting or overlapping (Fig. 2.14A–C). In *E. deformatore*, all margins are upturned, so the true dorsum is obscured. The dorsal cavity so formed serves in some species as a brood chamber for the fertilised eggs and early larvae. The proboscis (a protruded pharynx) and the anal papilla are both terminal (Figs 2.13B, 2.14A). The five pairs of small parapodia form an arc on the upturned surface on each side (Fig. 2.13B) and may protrude slightly, be discoidal, or be reduced to the hook apparatus alone, depressed into grooves. *Endomyzostoma inflator* supposedly has no parapodia at all. Most species reportedly have no lateral organs, except for *E. clarki* (McClendon 1906) and *E. tenuispinum* (Eeckhaut & Améziane-Cominardi 1994), both of which have four pairs alternating with the parapodia. Marginal cirri are absent or reduced in number; at most five to seven pairs, in *E. tenuispinum*. The body surface bears tufts of cilia (Jägersten 1940a; Eeckhaut & Améziane-Cominardi

1994). The dorso-ventral musculature is well developed (Fig. 2.14C), but the parapodial musculature is feeble and there is no mid-ventral muscle mass.

The mouth cavity extends as a shallow proboscis pocket to about midlength of the pharyngeal muscle bulb (Fig. 2.14A). The stomach is ciliated and surrounded by a sheath of longitudinal and circular muscles, and the gut diverticula are highly branched. *Endomyzostoma tenuispinum* has 20 to 30 branched gut diverticula on each side, but far fewer are present in *E. deformatore*. There is no anal sphincter in the female stage; a flap is present.

Sexuality may be variable, and there is some question about whether supposed testes have been correctly identified in some species (Jägersten 1939b). In *Endomyzostoma pentacrini* and *E. deformatore*, two or three hermaphrodites usually occur together in separate cavities in a gall; the male system is developed only unilaterally, with the testicular follicles in a compact mass. Pairs occur in other species: a large functional female and a dwarf, protandric male. Both sexual systems supposedly occur in all individuals, but only one system is active (Wheeler 1896; McClendon 1906; Stummer-Traunfels 1908).

Male-stage individuals are round and flat, and about 1 mm in diameter; they lack marginal cirri and have stubby parapodia, and most (all?) lack lateral organs (Fig. 2.14D, E). They have three pairs of weakly branched midgut diverticula. The testes

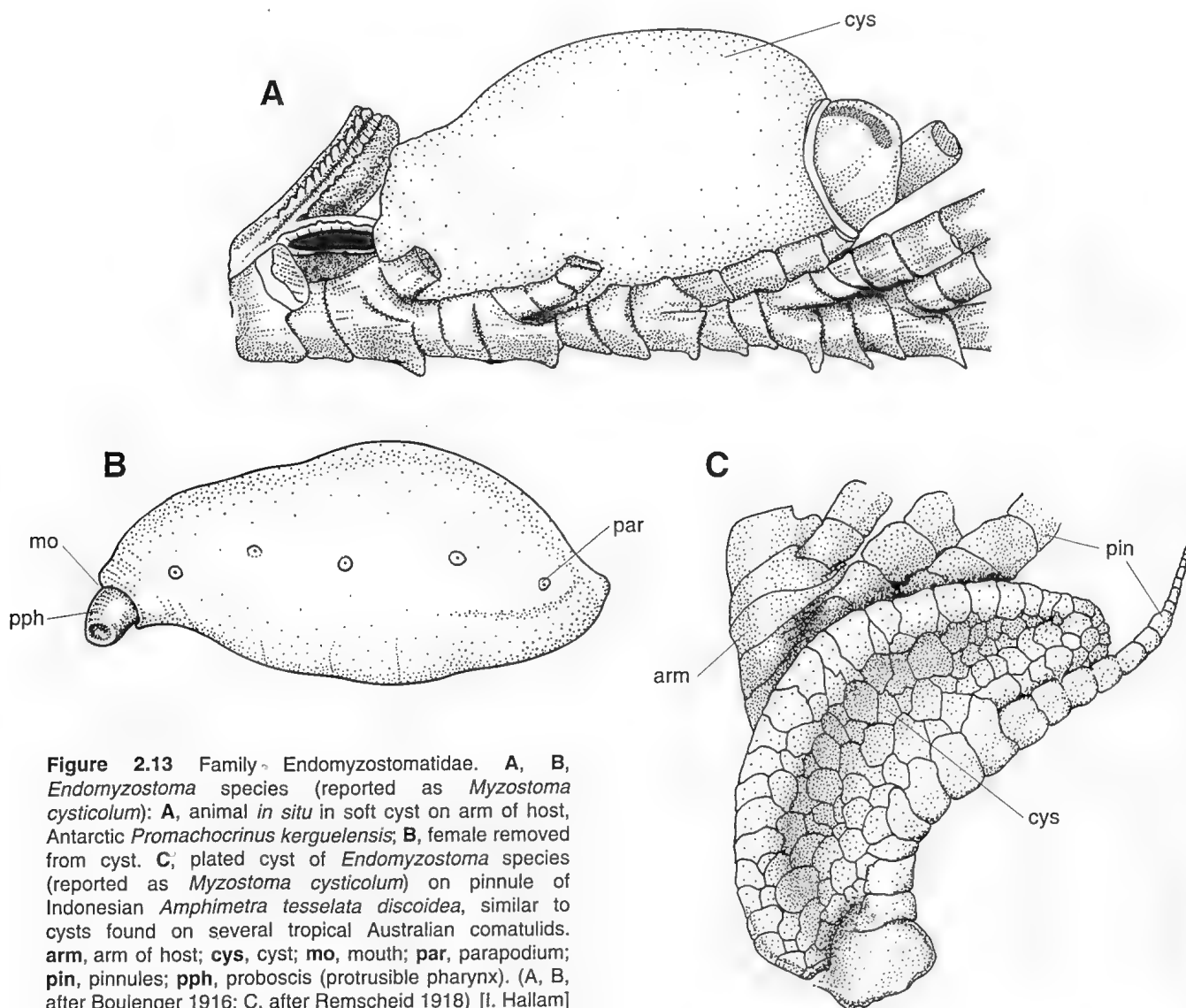


Figure 2.13 Family Endomyzostomatidae. **A**, **B**, *Endomyzostoma* species (reported as *Myzostoma cysticolum*): **A**, animal in situ in soft cyst on arm of host, Antarctic *Promachocrinus kerguelensis*; **B**, female removed from cyst. **C**, plated cyst of *Endomyzostoma* species (reported as *Myzostoma cysticolum*) on pinnule of Indonesian *Amphimetra tessellata discoidea*, similar to cysts found on several tropical Australian comatulids. **arm**, arm of host; **cys**, cyst; **mo**, mouth; **par**, parapodium; **pin**, pinnules; **pph**, proboscis (protrusible pharynx). (**A**, **B**, after Boulenger 1916; **C**, after Remscheid 1918) [I. Hallam]

are compact (Fig. 2.14D) and located between the second and third pairs of gut diverticula (except for the diffuse testes in *E. inflator*). Each testis has a central collecting space that is directly connected to the male genital aperture on each side of the body; the aperture is usually marginal, but occasionally ventral or dorsal near the margin. The penis is not protrusible. The female reproductive system develops in the males (Fig. 2.14D, E) as an epithelium-lined organ with a dorsal cavity, a pair of ventrally directed passages that surround the bases of the second and third pairs of gut diverticula, and a pair of ventral cavities connected across the midline, from each of which three lateral diverticula arise and follow beneath the gut branches (Stummer-Traunfels 1908). Two pairs of undeveloped ovaries are located at the bases of these diverticula. Precursors of the female gonopore and common utero-intestinal duct pore are also present.

In the female stage, the usual relative positions of the ovaries and testes are inverted (Fig. 2.14C); the ovaries are located ventral to the gut, whereas the testes are dorsal and protrude into the uterus and its diverticula (Wheeler 1896; McClendon 1906; Stummer-Traunfels 1908). According to Jägersten

(1939b), though, the dorsal testes of *E. belli* (Fig. 2.14C) are more likely spermatic syncytia invading the female after mating (see reproduction section above). The cavities of the female system are only partly lined by an epithelium, the remainder by a pseudoepithelium of reticular connective tissue. The lateral passages have become greatly expanded and fused with the ventral cavities and their diverticula so as to suspend the gut diverticula within capacious lateral sacs (Fig. 2.14B; see also Wheeler 1896). The ventral cavities are connected across the midline between the stomach and ventral nerve mass by several irregular passages. In this stage, the two pairs of ventral ovaries (Fig. 2.14B, C) are much bigger than in the male stage. In females of *E. cysticum*, the male genital openings are found dorsally near the margin, outside the third pair of parapodia (Stummer-Traunfels 1908). The testes no longer produce sperm, and Stummer-Traunfels thus suggested that earlier reports of females lacking testes were mistaken.

A pair of utero-intestinal ducts (Fig. 2.14A, E) begin at the posterior end of the uterus as ciliated canals and then broaden into a pair of contorted, glandular, unciliated end-sacs, the exit

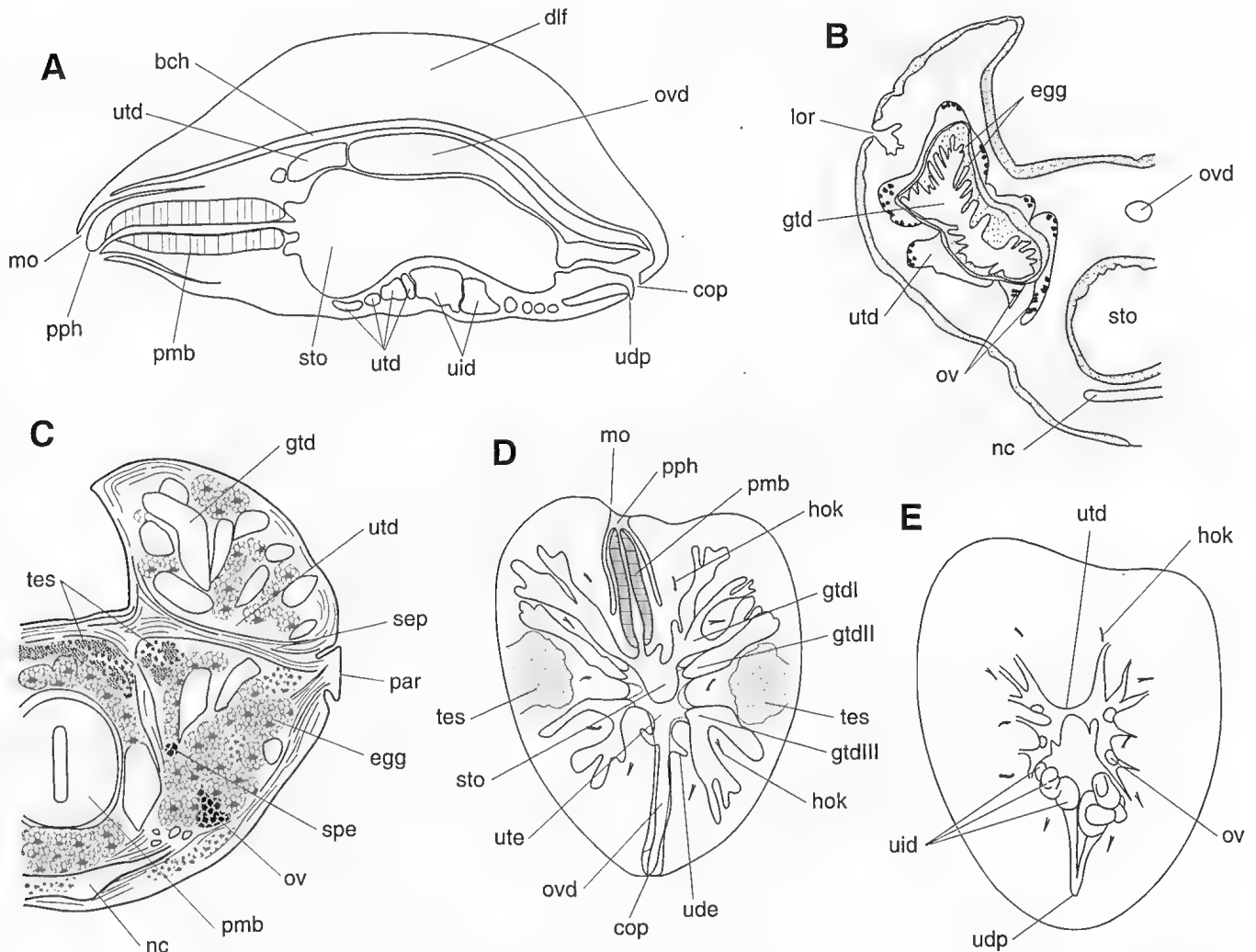


Figure 2.14 Family Endomyzostomatidae. **A**, female of Antarctic *Endomyzostoma* species (reported as *Myzostoma cysticola*), sagittal section just off midline. **B**, one half of a cross-section, dorsal side up, of a female *Endomyzostoma clarki*, a gallicolous species from Japan, and, evidently, also from Australia. **C**, one half of a cross-section of a female *Endomyzostoma belli*, sectioned more anteriorly than in **B**. **D**, **E**, morphology of a male Antarctic *Endomyzostoma* species (reported as *Myzostoma cysticola*), **E** more ventral than **D**. **bch**, mid-dorsal brood chamber; **cop**, common anal and female genital opening; **dlf**, dorso-lateral fold; **egg**, eggs; **gtd**, gut diverticula; **gtdI-III**, main gut diverticula I-III in **D**; **hok**, parapodial hooks; **lor**, lateral organ; **mo**, mouth; **nc**, nerve cord; **ov**, ovaries; **ovd**, oviduct; **par**, parapodium; **pmb**, pharyngeal muscle bulb; **pph**, proboscis (protrusible pharynx); **sep**, muscular septum; **spe**, sperm; **sto**, stomach; **tes**, testes; **ude**, entrance to utero-intestinal duct; **udp**, common external exit pore of utero-intestinal ducts; **uid**, utero-intestinal duct; **utd**, uterine diverticula; **ute**, uterus. (**A**, **D**, **E**, after Stummer-Traunfels 1908; **B**, after McClendon 1906; **C**, after Wheeler 1896)

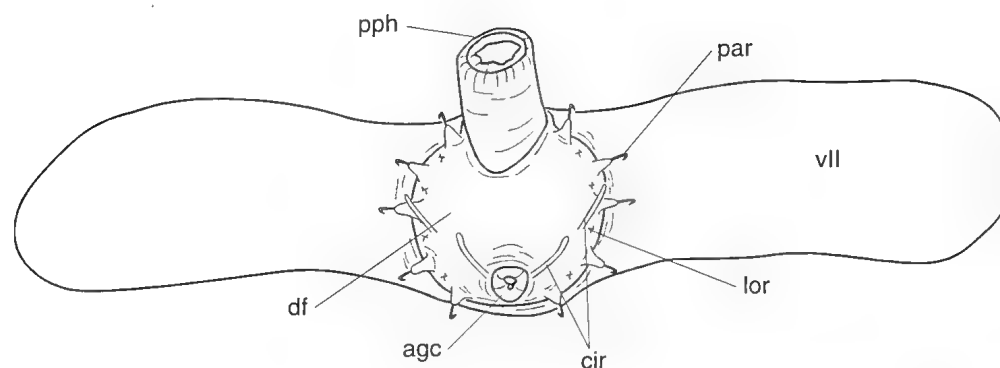


Figure 2.15 Family Endomyzostomatidae. *Contramyzostoma bialatum* (*incertae sedis*), dorsal view. **agc**, anogenital cone; **cir**, cirri; **df**, dorsal field; **lor**, lateral organ; **par**, parapodium; **pph**, proboscis (protrusible pharynx); **vll**, ventro-lateral lobe. (After Eeckhaut & Jangoux 1995) [I. Hallam]

ducts of which fuse. The common duct so formed is also glandular and unciliated and opens at a pore just anterior to the anus, not inside the intestine as usual (Wheeler 1896; Stummer-Traunfels 1908).

The ventral nerve cord or mass has not been described in detail.

Contramyzostoma. Only a brief mention of this genus will be given here, because its assignment to the Cystimyzostomatidae (that is, Endomyzostomatidae) by Eeckhaut & Jangoux (1995) is not based on morphology and may be erroneous. The type-species, *C. bialatum*, lives in cysts on the arms and disc of *Comaster gracilis* off Singapore; it is about 2 mm wide. The central part of the anatomically ventral side is produced into two large lateral lobes (Fig. 2.15), such that the outer parts of the ventral side have come to be situated on the small, functionally dorsal side. This 'dorsal field' is round and bears five pairs of parapodia, four pairs of lateral organs and two pairs of posterior cirri; the parapodia are outermost, with their hooks directed outward, and the cirri are innermost. The 'dorsal field', but not the ventral surface, is ciliated. A relatively large proboscis and an anogenital cone arise from the 'dorsal field', connected by a U-shaped gut. Salivary gland cells situated at the pharynx-stomach boundary empty distally on the proboscis. Two diverticula extend from the stomach into each lateral lobe, where they meet to form a loop on each side. The two supposed ovaries are diffuse and lie in the parenchyma of the lateral lobes (as mentioned in the reproduction section above, Eeckhaut's concept of the myzostome ovary differs from that of earlier authors). The mid-dorsal uterus has looped diverticula that enclose the gut diverticula. The nervous system consists of a circumoesophageal nerve ring and condensed ventral nerve mass.

The lateral protrusions of the mid-ventral surface and the looped diverticula of the stomach and uterus are unique features. The location of the gut diverticula within the cavities of the female system agrees with the structure in *Endomyzostoma* and *Pulvinomyzostomum*. The dorsal positions of the mouth and anus conform with the latter, and most or all parapodia being visible in dorsal view is also a feature shared with *P. pulvinar*. *Contramyzostoma* could be considered an extremely modified *Pulvinomyzostomum*, but differs in having only four pairs of lateral organs and in its location in the host. Unfortunately, the nature of the proboscis remains unknown; the *Myzostoma*-like arrangement of the salivary gland cells suggests, however, that *C. bialatum* belongs to the Proboscidea, not the Pharyngidea.

A second species was described from *Comatella stelligera* in Papua New Guinea by Eeckhaut *et al.* (1998), but it was only tentatively assigned to this genus on the basis of its hypertrophied ventral surface. In many respects it differs considerably from the type-species, and its features were not taken into account in the present treatment of the systematic position of the genus (Fig. 2.9).

Mycomyzostoma. Eeckhaut (1998) included this genus in the Endomyzostomatidae because of its cysticolous life style, lack of cirri and lateral organs, and its separate sexes as some species of *Endomyzostoma* supposedly have (although as noted above, so far as is known *Endomyzostoma* species are hermaphrodites). The regression of many characters is extreme. The parapodial hook apparatus and testicular spermioyysts of the male and the presence of spermiatic syncytia in the female are all that identify this parasite as a myzostome. Assignment to the Endomyzostomatidae is not supported by the diffuse (instead of compact) testes and by the absence of gut diverticula passing through uterine diverticula. Therefore, *Mycomyzostoma* is treated as *incertae sedis* herein.

The sole species, *Mycomyzostoma calcidicola*, was originally described from specimens collected off New Caledonia, but its host, *Saracrinus nobilis*, also occurs off north-western Australia. A female or a male-female pair lives in a multiplicated, rounded cyst of the stalk of the pedunculate crinoid host (Fig. 2.16A). The cysts are closed or have a single minute opening. Each cyst contacts the base of a cirrus and three or four columnar ossicles, including a nodal ossicle, and the female's proboscis fits a cavity in the side of the stalk. The female has a small proboscis and a large, spherical trunk up to 7 mm across (Fig. 2.16B); the trunk surface is heavily wrinkled except for a flat ano-genital plate, and there are no traces of parapodia, lateral organs or cirri. The pharynx, with a muscle bulb, but no salivary glands, leads into a large, longitudinally pleated digestive sac with no diverticula. The ventral nervous system is condensed. The ovary (*sensu* Eeckhaut 1995) is diffuse, with oocytes developing in the parenchyma. The ciliated diverticula of the reproductive system run between the gut pleats, and they have a common exit with the anus. A uterus and oviduct in the usual sense are evidently absent, and no utero-intestinal ducts were described. The male is much smaller (<1 mm), and is flat and rectangular in outline, with external ciliation and four pairs of lateral indentations (Fig. 2.16C, D). A proboscis, gut, lateral organs and cirri are absent. Five pairs of parapodia are represented by hooks and support rods; the former extending from ventral apertures halfway between the midline and the body margin.

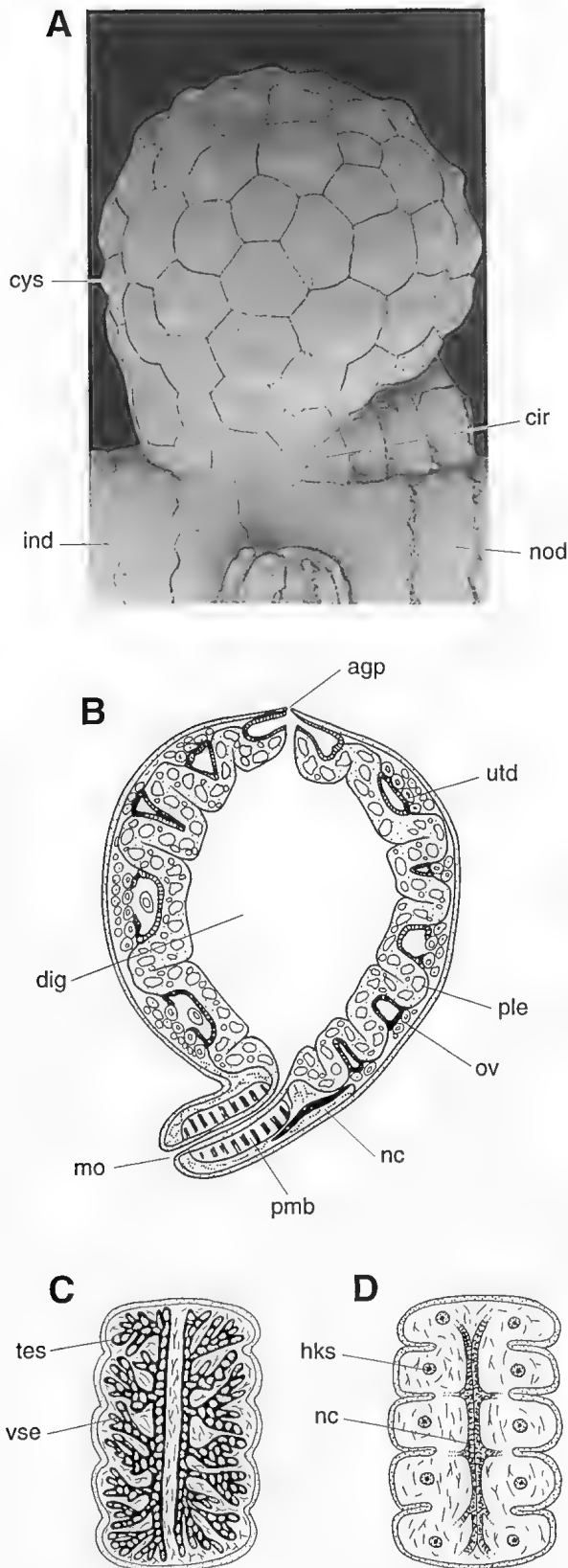


Figure 2.16 Family Endomyzostomatidae. *Mycomyzostoma calcidicola* (incertae sedis). **A**, cyst in situ on host crinoid, *Saracrinus nobilis*. **B**, mid-sagittal section of female; **C**, horizontal dorsal section of male showing reproductive system; **D**, horizontal ventral section of male showing ventral nerve chain and hook sites. **agp**, anogenital pore; **cir**, cirrus (extending to right); **cys**, cyst comprising supernumerary ossicles; **dig**, digestive sac; **hks**, site of hook; **ind**, internodal ossicle; **mo**, mouth or entrance to pharynx; **nc**, nerve cord; **nod**, nodal ossicle; **ov**, ovary; **ple**, pleat of digestive sac; **pmb**, pharyngeal muscle bulb; **tes**, testes; **utd**, uterine diverticula; **vse**, vas efferens. (After Eeckhaut 1998) [B–D, I. Hallam]

The nervous system includes a pair of conjoined ventral longitudinal cords and five pairs of lateral nerves (Fig. 2.16D). The testis is diffuse and marginal (Fig. 2.16C); many ducts join a pair of longitudinal efferent ducts that are assumed to exit near the third pair of parapodia. Vasa deferentia, seminal vesicles and penes are absent.

Family Asteriomyzostomatidae

The Asteriomyzostomatidae are represented by two species that are endoparasitic in sea stars. The better known species, *Asteriomyzostomum asteriae*, lives in the pyloric caeca of two species of *Sclerasterias* in the Mediterranean (Stummer-Traunfels 1903). *Asteriomyzostomum fisheri* inhabits the body cavity of *Tosia* (*Pentagonaster*) *leptoceramus* off southern California (Wheeler 1905). Australian representatives are unknown.

The body is flat, oval and wider than long; up to 5–6 mm long and 8.5 mm wide (Fig. 2.17A). The five pairs of reduced parapodia are close to the margin ventrally. Marginal and parapodial cirri are absent. The mouth is located ventrally at varying distances from the anterior end; a proboscis and proboscis pocket are absent. The anus and, just before it, the female genital opening, are located dorsally at two-thirds the body length (Fig. 2.17B). Four pairs of lateral organs alternate with the parapodia (Fig. 2.17A); an unpaired ninth, postero-medial one is present in *A. asteriae*.

The body wall consists of cuticle, epidermis, basement membrane and muscular sheath. The epidermis consists of cylinder cells and gland cells, the latter being much more abundant ventrally. The cuticle is formed from the 2–3 μ m thick caps on each cylinder cell; these caps remain distinct. Except where disturbed by dorso-ventral or parapodial muscles, the integumental musculature consists of an outer layer of radial muscle fibres and an inner layer of concentric ones. The body musculature resembles that of *Myzostoma cirriferum*: two thin layers of mostly transverse muscles above and below the ventral nerve mass, and dorso-ventral muscles, many near the margin and others forming perforated radial septa, especially laterally.

The lateral organs are papilliform, with a sphincter-closed passage leading to an internal cavity (Fig. 2.17B); the integument of the cavity can be protruded as a mushroom-like structure. Beneath the glandular-appearing epithelium of the lateral organ is a thick layer of highly vacuolated connective tissue; surrounding this is a capsule of integumental muscles that is instrumental in the protrusion of the organ and is penetrated by the lateral organ's dorso-ventral retractor muscles and nerves.

The gut is short and its posterior section is bent dorsally (Fig. 2.17B). The mouth cavity is divided into anterior and posterior parts; many salivary gland cells surround and empty into the posterior part. Two principal pairs of gut diverticula are present, and each diverticulum subdivides into five main branches; further subdivision occurs near the body margin (Fig. 2.17A). The intestine is ciliated, but the stomach and its diverticula are not.

All specimens examined were functional hermaphrodites. The uterus and its two pairs of branching diverticula are lined with a ciliated epithelium except for the terminal branches of the diverticula. In *A. asteriae*, each of the paired ovaries lies in a ventral pit at the base of one of the first pair of main diverticula, whereas in *A. fisheri* the ovary is unpaired and lies over the stomach. The uterine diverticula are dorsal to those of the stomach. The ciliated utero-intestinal ducts have an

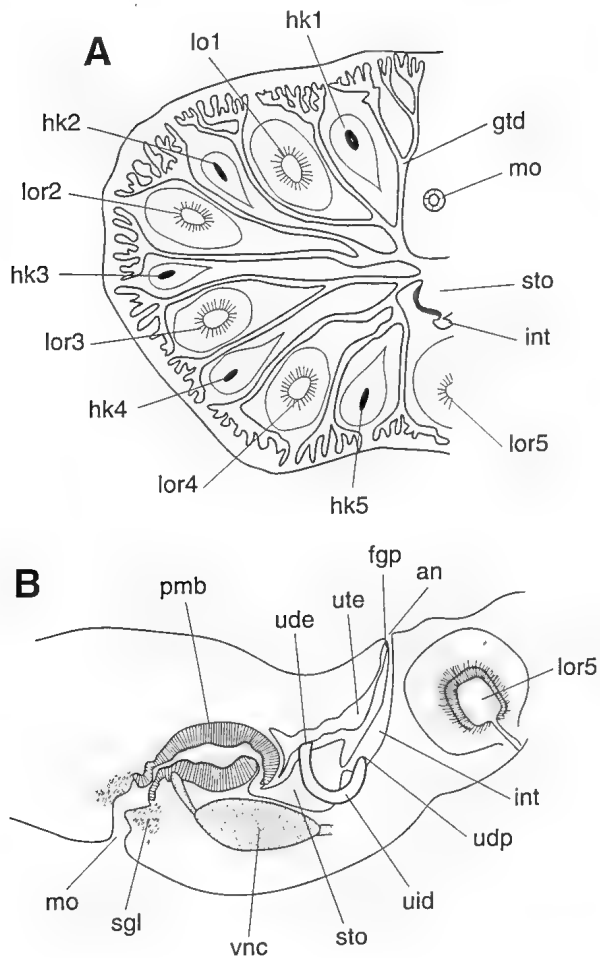


Figure 2.17 Family Asteriomyzostomatidae. Morphology of *Asteriomyzostomasteria*. **A**, ventral view of one side of animal, showing digestive system. **B**, mid-sagittal view, anterior and posterior ends of body omitted. **an**, anus; **fgp**, female genital pore; **hk1–5**, hook apparatus of parapodia 1–5; **int**, intestine; **lor1–5**, lateral organs (**lor5** unpaired); **mo**, mouth; **pmb**, pharyngeal muscle bulb; **sgl**, salivary glands; **sto**, stomach; **ude**, entrance to utero-intestinal duct; **udp**, exit pore of utero-intestinal duct; **uid**, utero-intestinal duct; **ute**, uterus; **vnc**, ventral nerve cord. (After Stummer-Traunfels 1903) [I. Hallam]

expanded middle section, are separate for their whole length and enter the intestine close behind the stomach (Fig. 2.17B). The male organs are ventral to the gut and its diverticula. They occur mostly in the posterior half of the body in *A. fisheri*. The testes are diffuse. In *A. asteriae*, only one pair of vasa deferentia is present, seminal vesicles are lacking, and the penes are poorly developed. In contrast, *A. fisheri* has an anterior and posterior vas deferens and an ejaculatory duct on each side.

The nervous system consists of a circum-pharyngeal ring around the anterior part of the muscle bulb, with no associated peribulbar or prebulbar ring, and a ventral nerve mass below the stomach, constructed like that of *Myzostoma* (Fig. 2.17B). The peripheral nerves remain undescribed in detail, but the paired lateral organs in *A. asteriae* are quite possibly innervated by branches of the four pairs of intermediate nerves from the ventral mass, and the unpaired one by the most distal pair of nerves, which also serve the intestine and the pair of uterine ducts.

Family Asteromyzostomatidae

The family Asteromyzostomatidae is represented by the single genus *Asteromyzostomum*. Three described species from the Russian Arctic and two unnamed species from the Antarctic and Atlantic have been recorded; four of the species were found ectoparasitic on sea stars, whereas the Atlantic one was disassociated from its host (Wagin 1954; Grygier 1988). The three Russian species, *A. witjasi* (the best known; Fig. 2.18), *A. arcticum* and *A. multiplicatum*, live in the ambulacral grooves of their hosts, *Psilaster pectinatus*, *Urasterias lincki* and *Crossaster papposus*, respectively. *Asteromyzostomum witjasi* is one of the deepest living myzostomes, having been collected from 2260 m in the Bering Sea. The undescribed Antarctic species (Fig. 2.1N), found attached to the sides of the arms of a *Labidiaster* species outside McMurdo Sound, will most likely occur in the Australian Antarctic Territory. In all species, the mouth is inserted through the integument of the host and held in place by numerous circum-oral tentacles (Figs 2.1N, 2.18).

In *Asteromyzostomum*, the body is wider than long through hypertrophy and lateral spreading of the equivalent of the post-parapodial sector of the body of a typical, disc-shaped species of *Myzostoma* (Wagin 1954). Females of *A. witjasi* are up to 4.2 mm long and 14.5 mm wide, and *A. multiplicatum* reaches 15.2 mm wide. The posterior margin has a great number (up to three orders) of convoluted, lobular folds that resemble a fungus and make up two-thirds to nearly all the body volume (Figs 2.1N, 2.18). The degree of folding is much more pronounced in older females than in young protandric males.

The four (in one species) or five pairs of vestigial, button-like parapodia are all found ventrally along the straight or concave anterior margin on either side of the mouth, with the third pair lying somewhat farther from the edge than the others (Fig. 2.18). The parapodial musculature was not described in detail, but is supposedly well developed and complete when compared to that of *Myzostoma*. Marginal and parapodial cirri are absent. The edges of the posterior folds bear 40 or more oval lateral organs ventrally, each with an opening and inner cavity (Fig. 2.18). A single pair of larger lateral organs lies between parapodia four and five in *A. witjasi*, but none between other parapodia; however, some have been illustrated between the parapodia in *A. arcticum*.

The epithelium consists of cuboidal cells, which overlap like scales on folds of the body and pharynx and on the bases of the circum-oral tentacles. The basal membrane has perforations through which the sunken epithelial cells extend. Within the body, the space between the internal organs and the muscles is filled with stellate and amoeboid parenchyma cells. The musculature has no radial character, but a bilateral one. The many dorso-ventral muscles do not form septa. All the fibres in the well-developed muscle sheets above and below the nervous system are parallel to the front margin of the body, and the very strongly developed postero-ventral regions of these sheets serve to contract the posterior folds.

The mouth leads into the pharynx, which traverses a strong muscle bulb and opens shortly beyond into the broad, sac-like stomach. The single pair of lateral gut diverticula immediately branch into major anterior and posterior diverticula (Fig. 2.18). Side branches of the anterior one bifurcate between the parapodia, whereas the posterior one branches more extensively by bifurcating into the posterior lobes. The stomach protrudes far into the intestine, and the anus opens just ventral to the posterior end of the body.

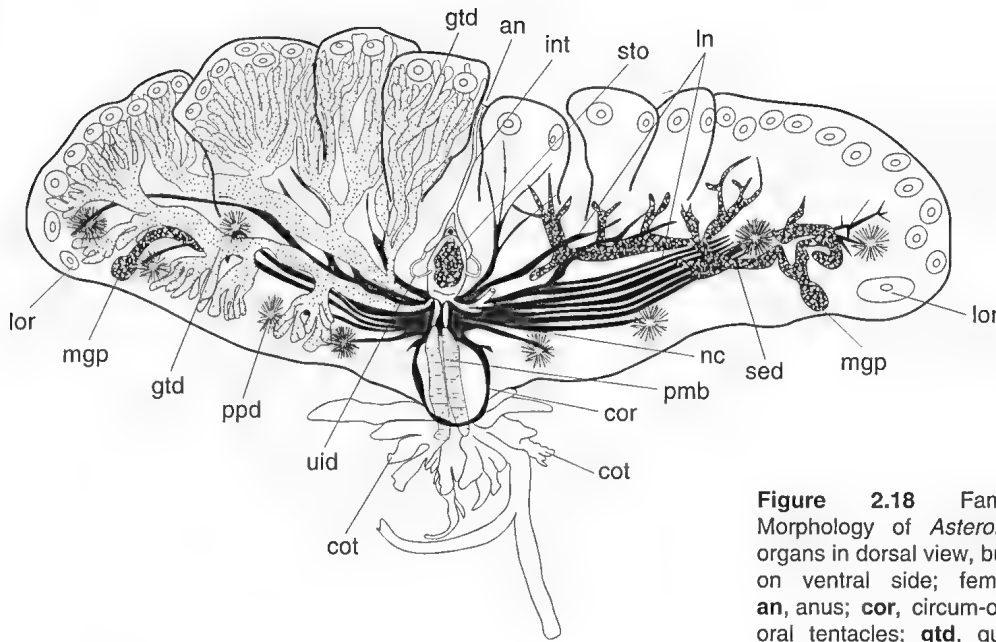


Figure 2.18 Family Asteromyzostomatidae. Morphology of *Asteromyzostomum witjasi*, internal organs in dorsal view, but parapodia and lateral organs on ventral side; female genital organs omitted. **an**, anus; **cor**, circum-oesophageal ring; **cot**, circum-oral tentacles; **gtd**, gut diverticulum; **int**, intestine; **ln**, lateral nerves; **lor**, lateral organs; **mgp**, male genital pore; **nc**, nerve cord; **pmb**, pharyngeal muscle bulb; **ppd**, parapodium; **sed**, seminal duct; **sto**, stomach; **uid**, utero-intestinal duct. (After Wagin 1954) [I. Hallam]

Wagin's (1954) description provides no clear distinction between uterus and oviduct. The uterus, lying dorsal to the gut, opens just behind the anus; its diverticula lie dorsally parallel to those of the stomach. Two utero-intestinal ducts exit the uterus, abruptly broaden, and merge to form the anterior part of the intestine (Fig. 2.18). The testes are diffusely distributed in the parenchyma ventral to the gut. Fine seminal canals join into seminal ducts; these empty into the vasa deferentia, which open into a much expanded, deeply situated pair of penes along the anterior margin of the body between the third and fourth parapodia (Fig. 2.18). The description does not say whether the supposed penes are protrusible; perhaps they are merely seminal vesicles.

The nervous system consists of a circum-oesophageal ring connected to a laterally extended ventral ganglion or plexus. This plexus is shorter and more concentrated than the ventral nerve mass of *Myzostoma* and gives rise to 10 parallel pairs of lateral nerves (Fig. 2.18).

Family Pulvinomyzostomatidae

The Pulvinomyzostomatidae includes one described species, *Pulvinomyzostomum pulvinar* from Europe; it has been extensively studied by Jägersten (1940a). The adult female stage occupies the oesophagus and stomach of its host crinoid of the genus *Leptometra*, often with its posterior end protruding from the mouth. Because of the bowed shape body (Fig. 2.19B), the host's gut is not blocked. Small male-stage individuals are found on the body of the female (Fig. 2.19A), or around the host's mouth if there is no female. A female of an unidentified species of *Pulvinomyzostomum* has been isolated from the Antarctic crinoid *Promachocrinus kerguelensis* collected off South Georgia (M.J. Grygier personal observation); this species may also occur in the Australian Antarctic Territory.

In the female, the anterior and lateral body margins are folded up and inward so the dorsal surface is partly depressed (Fig. 2.19A). The integument is completely ciliated. Both the

mouth and anus are dorsal. A retractile, ciliated proboscis arises from a shallow pocket that reaches back only to the anterior end of the pharyngeal muscle bulb (Fig. 2.19B). Marginal parapodial cirri and buccal papillae are lacking. The second and third pairs of the very small parapodia are the most dorsal and are directed laterally; the first pair is more widely separated across the midline than the fifth (Fig. 2.19A). Usually, 10 pairs of non-protrusible lateral organs are present, one pair each in front of, and behind the first and fifth parapodia and two pairs in each space between the parapodia (Fig. 2.19A). Their inner surface consists of reticulate connective tissue underlying a layer of sensory cells.

The 'male' is oval, its length one and a half times its width. The mouth, in the form of a shallow proboscis pocket, opens terminally, and the anus is subterminal and dorsal. Five pairs of papilliform parapodia are present, the third flanked by the male genital openings. Six to 10 pairs of lateral organs are present before sex changes begin (Eeckhaut & Jangoux 1992). Marginal cirri are lacking, but the smallest males have clumps of long cilia at sites that may correspond to reduced cirri; the remainder of the body surface is ciliated, except mid-ventrally in very small specimens. The cilia on the dorsal side beat back to front (that is, opposite to those of *Myzostoma cirriferum*).

The transition from the male stage to the female stage occurs in the absence of a female. It involves a broadening and upward bending of the ventral and anterior parts of the body, and downward bending of the posterior end. The mouth is moved to the dorsal side. The proboscis is formed as the rear wall of the original mouth cavity becomes produced like a papilla. The mouth itself widens and its cavity becomes the proboscis pocket as the proboscis grows.

At most, the cuticle is extremely thin. The epidermis consists of one type of cell, the inner ends of which are at different levels. The parenchyma is unusually thick and, although there are many muscles in it, especially near the margin, defined muscle layers are lacking.

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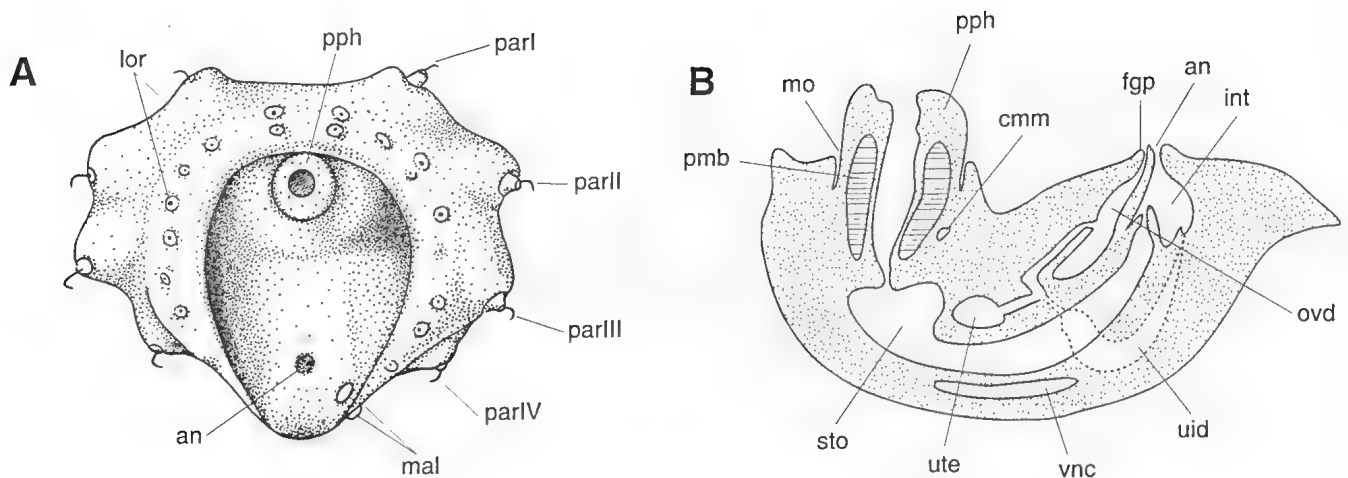


Figure 2.19 Family Pulvinomyzostomatidae. *Pulvinomyzostomum pulvinar*. **A**, female with two males, dorsal view; fifth pair of parapodia present ventrally, but not visible. **B**, female, mid-sagittal view. **an**, anus; **cmm**, commissures; **fgp**, female gonopore; **int**, intestine; **lor**, lateral organs; **mal**, males; **mo**, mouth; **ovd**, oviduct; **parl-parlV**, parapodia I-IV; **pmb**, pharyngeal muscle bulb; **pph**, proboscis (protrusible pharynx); **sto**, stomach; **uid**, utero-intestinal duct; **ute**, uterus; **vnc**, ventral nerve cord. (After Jägersten 1940a)

The pharynx passes through the muscle bulb into the stomach; salivary glands are absent. The elongate stomach empties into the intestine and also gives rise to three pairs of branching diverticula. For the most part these lie inside (rather than ventral to) the branches of the female reproductive system, either freely inside the lumen or anchored to the wall, and covered with an epithelium.

The uterus bears three pairs of side branches, the distal one of which bifurcates. Subsequent branching gives rise to several large sacs. A pair of ovaries is located at the base of the middle pair of side branches. Developing eggs are attached in follicles to all walls of the side branches. A posterior duct from the uterus bends twice before opening into the dorsal side of the oviduct, and the latter opens dorsally just in front of the anus (Fig. 2.19B). A pair of utero-intestinal ducts exit the uterus just before the posterior duct and occasionally fuse to each other before opening into the ventral side of the intestine (Fig. 2.19B).

The male reproductive system is compact. The testicular follicles lie in a cluster outside the third parapodia and over the genital aperture, with a cavity in between. There is no penis. The female system, including the paired utero-intestinal ducts, develops very shortly before the transition to the female stage.

The nervous system of the female consists of a dorsal cerebral ganglion behind the pharyngeal muscle bulb, linked by a pair of circum-oesophageal connectives to a condensed ventral ganglion about one third as long as the body (Fig. 2.19B). Five pairs of main lateral nerves and six pairs of intermediate nerves are present; three of the latter pairs arise from main nerves and the connectives. The cerebral ganglion and the attached peribulbar nerve ring encircling the muscle bulb branch off about six pairs of nerves anteriorly that merge into a plexus. In the male, the ventral ganglion is narrower and nearly cylindrical. The intermediate nerves arise separately from all the respective main lateral nerves.

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3. CLASS POGONOPHORA

Eve C. Southward

DEFINITION AND GENERAL DESCRIPTION

Pogonophores are marine tube-dwelling worms (Fig. 3.1) in which the midgut has become a trophosome filled with symbiotic chemosynthetic bacteria; the mouth and other parts of the alimentary canal are absent in adults. These animals depend on the bacteria in the trophosome for their nutrition; the bacteria require reduced sulphur compounds (or methane) for growth and the host animals live in places where these are available. Zoologically, pogonophores are triploblastic, multi-compartmented coelomates, with from one to many tentacles on a small head region. The long body is variously subdivided in the different subgroups, but the short hind region, termed the opisthosoma, is always divided by septa into many chaetigerous segments. The animals secrete a chitin-protein complex to form the tubes in which they live. The tubes are unbranched and may be simple or segmented, patterned with rings or uniform in colour.

The Pogonophora, including the three subclasses Perviata, Monilifera and Vestimentifera, are here treated as a class of the Annelida. The Vestimentifera is regarded as a separate phylum by some authors (see Jones 1985b; Gardiner & Jones 1993). Recently, Rouse & Fauchald (1997) reclassified the Pogonophora as members of the clade Sabellida within Polychaeta, grouping all taxa under the family Siboglinidae (for further discussion, see Phylogeny and Classification and Figure 1.35 under Class Polychaeta). The name Pogonophora is derived from *pogon* (Greek) meaning 'beard' and *phor* (Greek) meaning 'to bear', hence 'beard-bearer', referring to the numerous tentacles of the first species, *Lamellisabella zachsi*, placed in this group by Johansson (1937). Pogonophores are commonly called 'beard worms'.

Members of the Perviata live partly buried in sea-floor sediments. The slender tubes (0.1–3 mm in diameter) are set vertically in the sediment with the upper end of the tube projecting above the substratum. The opisthosoma is used for burrowing into the sediment. They are typically found on continental slopes and in deep trenches. Jones (1981) established the name Perviata; derived from *pervius* (Latin) meaning 'open', the name refers to the open tube, that is, it lacks an obturaculum, a structure that closes the tube in members of the Vestimentifera (or Obturata).

Moniliferans are small worms which have two anterior tentacles and no obturaculum. Most of them live in narrow, contorted, non-ringed tubes in decaying wood or other plant debris, on the sea floor. This group was included in the Perviata until Ivanov, in 1991, transferred it to this new subclass. The name Monilifera is derived from *monile* ('necklace' in Latin) and refers to the form of the bridle which resembles a string of beads.



Figure 3.1 Giant tube worms, *Riftia pachyptila* (Riftiidae), flourish in warm water emerging at a hydrothermal site more than 1500 m down in the Pacific Ocean on the East Pacific Rise. Dark red plumes extend from live animals (centre, top right). Brachyuran crabs are seen scrambling over the many dead tubes of these animals. This species is unlikely to occur in Australian waters, as suitable habitats are lacking. [T. Shank]

Vestimentiferans are distinguished by the presence of an obturaculum and a vestimentum. The obturaculum is a thick, funnel-shaped structure with equal right and left halves, closely adhering together, but developed from separate bases. It is placed in the centre of the anterior plume of tentacles, and seals the aperture of the tube once the animal has withdrawn. The vestimentum is a body region with lateral vestimental flaps that enfold the anterior part of the body, behind the plume. The tubes are attached to hard substrata, including adjacent tubes, and grow upwards into the water, often in clumps or clusters. They live close to hydrothermal vents on mid-ocean ridges and around cold sulphidic or hydrocarbon seeps on continental slopes. The group is also referred to as Obturata. The name Vestimentifera is derived from *vestimentum* and *ferre* ('garment' and 'to bear', respectively, in Latin) and refers to the waistcoat-like vestimental folds of these animals (Webb 1969). Obturata, the counterpart of

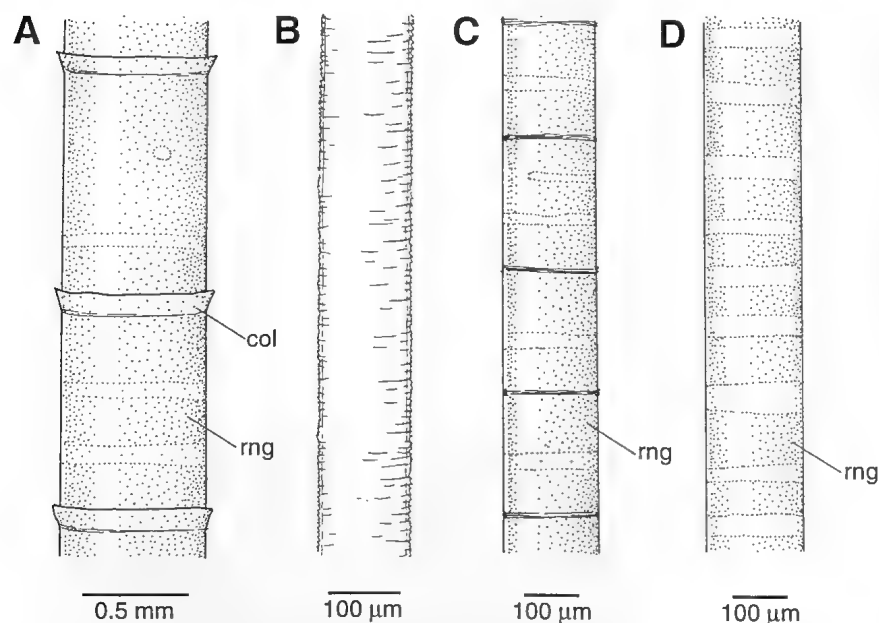


Figure 3.2 Sections of tubes of perviate pogonophores. **A**, anterior part of tube showing the collars of overlapping segments of *Polybrachia canadensis* (Polybrachiidae). **B**, a generalised non-ringed 'type' tube of various *Siboglinum* species (Siboglinidae) and juveniles of other species in different families. **C, D**, *Diplobrachia floridana* (Polybrachiidae): **C**, anterior part of tube showing segmentation; **D**, middle part of tube. col, collar; rng, ring. [E.C. Southward]

Perviate, is derived from *obturo* (Latin) meaning to 'close up' and refers to the cork-like obturaculum which closes the tube of vestimentiferans.

Pogonophores occur in all oceans and, worldwide, there are 146 species and 27 genera grouped in 13 families (Table 3.1). They are not well known from Australian waters; only a few collections of unnamed species of perviate pogonophores have been made, and as yet no members of Monilifera or Vestimentifera have been recorded.

Reviews of the Pogonophora include a brief account of New Zealand species by Ivanov (1962), an extensive monograph by Ivanov (1963), and short reviews by Cutler (1982), A.J. Southward & Southward (1988) and E.C. Southward (1989). Vestimentiferans from hydrothermal vent habitats are detailed in a popular account by Jones (1984), described extensively by Jones (1988) and are well illustrated in National Geographic by Lutz & Haymon (1994).

HISTORY OF DISCOVERY

The first perviate Pogonophora were collected in 1900 during the *Siboga* expedition through the Indonesian islands, 500–1000 km north of Australia. The specimens from this expedition were given to the French zoologist Maurice Caullery, who studied the material for many years. Caullery (1914, 1944) described the gutless worms, in their hair-like tubes, as a new type of invertebrate of uncertain affinities, for which he established the genus *Siboglinum* and the family Siboglinidae. The next pogonophore to be discovered was *Lamellisabella zachsi*, from the North Pacific. Uschakow (1933) described this as a new sabellid polychaete. Johansson (1937, 1939), however, did not agree with the polychaete identification and nor could he easily attribute it to any other phylum, so he placed it in a new class, Pogonophora (of the group known then as Vermes Oligomera).

In 1949, the Russian specialist, A.V. Ivanov described a second species, *L. gorbunovi* from the Arctic Ocean. Several years later, Ivanov (1951) decided that the genus *Siboglinum* described by Caullery should also be included in the Pogonophora. Later, Russian explorations collected many new pogonophores. Ivanov worked and extensively published on pogonophores and in his monograph of 1963 listed 70 species, 14 genera and 5 families; he also provided a

compilation, in English, of his work which had been previously published in Russian, along with additional material. In 1991, Ivanov transferred the Sclerolinidae from Perviate to a new subclass, Monilifera. Since then, new genera and species of perviates and moniliferans have been described by Ivanov and others, bringing the total in 1995 to 127 species, 18 genera and five families in Perviate and six species, one genus and one family in Monilifera (Table 3.1).

Table 3.1 Families, genera and number of species of Pogonophora.

Subclass PERVIATA
Family Oligobrachiidae
<i>Oligobrachia</i> (10), <i>Crassibrachia</i> (2), <i>Birsteinia</i> (1), <i>Nereilinum</i> (2), <i>Unibrachium</i> (2)
Family Siboglinidae
<i>Siboglinum</i> (67), <i>Siboglinoides</i> (3)
Family Polybrachiidae
<i>Polybrachia</i> (7), <i>Heptabrachia</i> (6), <i>Diplobrachia</i> (8), <i>Cyclobrachia</i> (1), <i>Galathealinum</i> (4), <i>Zenkevitchiana</i> (1), <i>Choanophorus</i> (1), <i>Krampolinum</i> (1)
Family Lamellisabellidae
<i>Lamellisabella</i> (7), <i>Siphonobrachia</i> (2)
Family Spirobrachiidae*
<i>Spirobrachia</i> (3)
Subclass MONILIFERA
Family Sclerolinidae
<i>Sclerolinum</i> (6)
Subclass VESTIMENTIFERA
Family Lamellibrachiidae
<i>Lamellibrachia</i> (5)
Family Escarpiidae
<i>Escarpia</i> (2)
Family Tevniidae
<i>Tevnia</i> (1), <i>Oasisia</i> (1)
Family Ridgeiidae
<i>Ridgeia</i> (1)
Family Alaysiidae
<i>Alaysia</i> (1)
Family Arcovestiidae
<i>Arcovestia</i> (1)
Family Riftiidae
<i>Riftia</i> (1)

The seas in the Indonesian region are rich in perviate pogonophoran species (Kirkegaard 1956; Southward, E.C. 1961, 1975c; Ivanov 1963). The Timor Trench is the closest published locality of perviates to Australia, but there are also specimens from the Coral Sea in the Museum of Tropical Queensland, and from New South Wales and Victoria in the Museum of Victoria. Thirteen species, all probably new, have been found in these samples. Much more collecting and research is needed to establish the distribution and taxonomy of Pogonophora in Australian seas. They probably occur all round the continent in soft sediments in depths of more than 200 m.

The vestimentiferans were unknown until 1969, when Webb described *Lamellibrachia barhami* from the continental slope off southern California, north-eastern Pacific, now presumed to be a cold seep environment. He assigned this new pogonophore to a new family, Lamellibrachiidae, in a new order, Vestimentifera, and new class, Afrenulata. In 1970, another species of *Lamellibrachia* was collected in the Atlantic, off Guyana, and described as *L. hymesii* by van der Land & Nørrevang (1975). They regarded Vestimentifera and Pogonophora as separate classes within the phylum Annelida. A few years later, hydrothermal vents (hot springs) on the Galapagos Rift, eastern Pacific, were found to harbour amazing oases of invertebrate life close to hot, sulphidic effluent, at depths of more than 2000 m (Lonsdale 1977). Tube-worms more than a metre long and 20–30 mm in diameter were abundant. These were named *Riftia pachyptila* by Jones (1981; see Fig. 3.1) and placed in a new family, Riftiidae, and subphylum Obturata, separated from the newly named subphylum Perviatea (for the original pogonophores), both in the phylum Pogonophora; the name Vestimentifera was not used. Exploration of more hydrothermal sites in the deep Pacific has revealed three further genera of vestimentiferan worms (*Ridgeia*, *Tevnia*, *Oasisia*; Jones 1985b; Tunnicliffe 1991), whereas species of the genera *Lamellibrachia* and *Escarpia* are known from cold seep habitats, in the Pacific and Atlantic Oceans. *Lamellibrachia* species have since been found at two hydrothermal sites, but in apparently cool conditions: one in the Lau Basin, south-west Pacific (Southward, E.C. 1991) and the other at Middle Valley in the north-east Pacific (Southward, E.C. *et al.* 1996). Additional inhabited hydrothermal sites have been found in the Back-Arc Basins of the western Pacific. The nearest of these to Australia is the Manus Basin, north of Papua New Guinea, where a new genus of vestimentiferan has been recently found (Galkin 1992; Southward, E.C. & Galkin 1997). In 1985, the names Vestimentifera and Pogonophora were used again by Jones, for separate phyla, in place of the names Obturata and Perviatea. Ivanov (1988, 1989) and E.C. Southward (1988, 1993) have continued to regard the two groups as classes of one phylum. The Vestimentifera, presently, includes 13 species, eight genera and seven families (Table 3.1).

MORPHOLOGY AND PHYSIOLOGY

A detailed description of perviate pogonophoran morphology is available in Ivanov (1963). Comprehensive reviews include those of E.C. Southward (1993) and Gardiner & Jones (1993). The morphology of moniliferans is given by Webb (1964c) and E.C. Southward (1972).

Ivanov (1963 and earlier) viewed the Pogonophora as deuterostomian, and considered the main nerve trunk to be dorsal, and the tentacular side to be ventral. A dorsal ciliated band and ventral papillae are also present. The body was

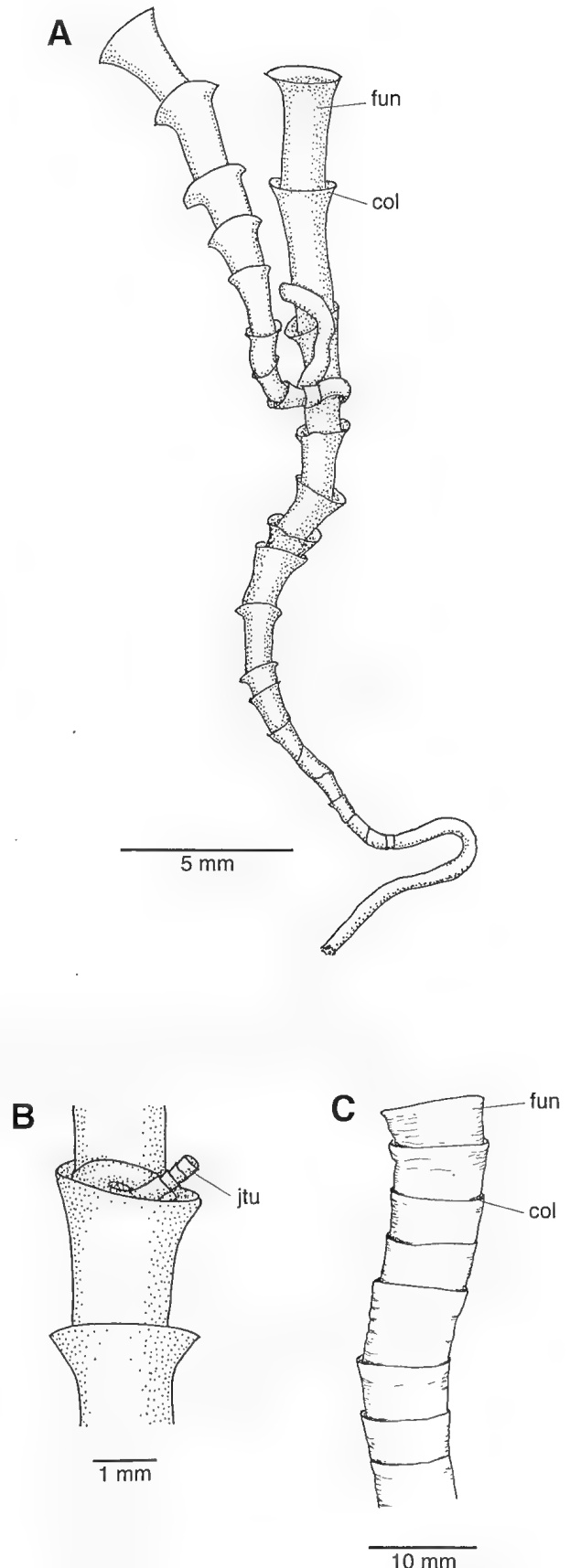


Figure 3.3 Tubes of vestimentiferan pogonophores. **A, B**, *Ridgeia piscesae* (Ridgeiidae): **A**, two entire tubes, one entwined around the other; **B**, tube of a juvenile which had settled on the collar of older tube. **C**, anterior section of tube of *Lamellibrachia barhami* (Lamellibrachiidae). **col**, collar or flange; **fun**, funnel; **jtu**, juvenile tube.

[E.C. Southward]

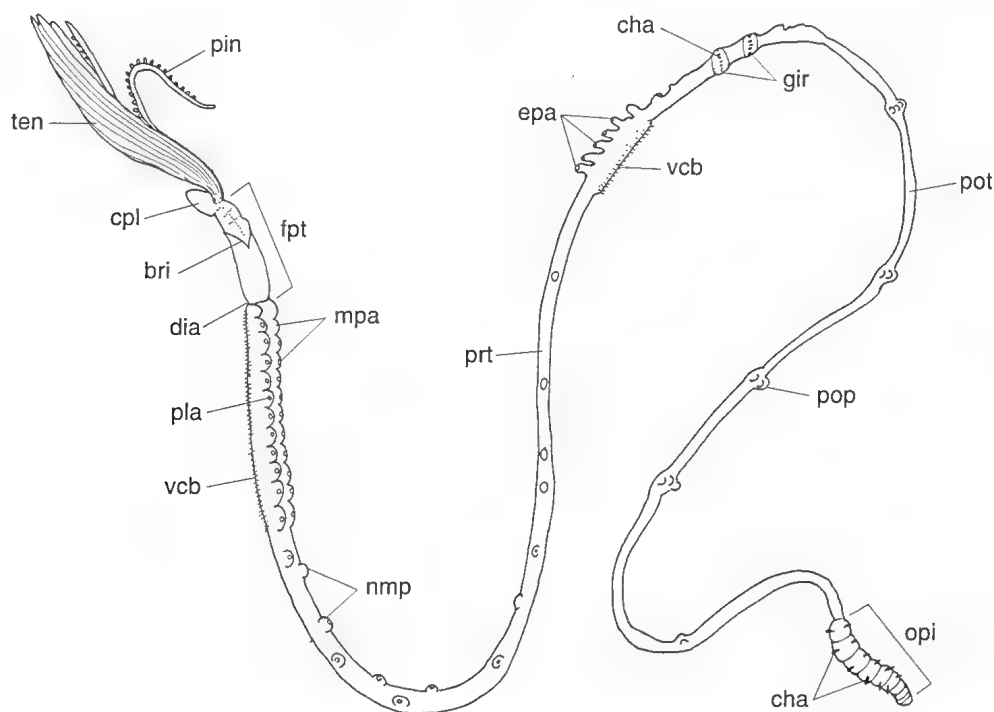


Figure 3.4 External features of a generalised perviate pogonophore. **bri**, bridle; **cha**, chaetae; **cpl**, cephalic lobe; **dia**, diaphragm; **epa**, enlarged papillae; **fpt**, forepart; **gir**, girdles; **mpa**, metameric papillae; **nmp**, non-metameric papillae; **opi**, opisthosoma; **pin**, pinnules; **pla**, plaque; **pop**, postannular papilla; **pot**, postannular region of trunk; **prt**, pre-annular region of trunk; **ten**, tentacles; **vcb**, ventral ciliated band. (After Southward 1984) [E.C. Southward]

considered to be three-segmented (the opisthosoma was unknown). This view of orientation and segmentation was generally accepted at the time. With the discovery of the segmented opisthosoma (Webb 1964a; Ivanov 1965) zoologists began to alter their opinions. Pogonophora are now generally regarded as protostomian. The position of the larval mouth has been determined for both perviates and vestimentiferans (Southward, E.C. 1988; Jones & Gardiner 1988; Callsen-Cencic & Flügel 1993), and now, the mouth and main nerve tract are regarded as ventral, the tentacular side as dorsal. The reader will therefore notice some differences in terminology between this account and the older literature.

External Characteristics

The tubes of perviates are narrow and linear, and look like hairs, brown algal filaments or thick fibres (see Fig. 3.17); they are sometimes discarded as non-animal during sorting of samples. Sclerolinid (*Monilifera*) tubes are also hair-like, but less linear than perviate tubes. Vestimentiferan tubes are generally stiff and upstanding, attached to rocks or to one another at their bases (see Figs 3.1, 3.13). Perviate tubes are variously coloured; although they may be transparent or white through grey to brown, or even black, in different species, they are usually yellowish to reddish brown, often with a pattern of dark and light rings. Vestimentiferan tubes are usually whitish or grey-brown. The anterior part of the tube may be segmented, sometimes forming a series of collars or funnels in perviates and vestimentiferans (Figs 3.2, 3.3). Perviate tubes range from 0.1–3 mm in diameter, varying little within a species and usually uniform in any one tube. Increments are added to both ends as the animal grows, especially the posterior end, which is lengthened as the animal burrows backwards into the sediment; the length ranges from a few centimetres to more than 1 m. Vestimentiferan tubes are more tapered, increasing from a juvenile diameter of less than

1 mm to attain 2–30 mm, depending on the species; the posterior end is at first a sealed bulb. Length varies considerably, the largest vestimentiferans have tubes which may grow to over 2 m.

When alive, the animal occupies most of its tube. Perviates are frequently transparent, and thus red blood is often visible in the large blood vessels. In some species, patches of brown or yellow epidermal pigment are visible in living animals. Preserved specimens are usually colourless and partly contracted into a spiral, due to the ventral position of the strongest muscle fibres. Tentacles number from one to over 200 and are attached dorsally to the anterior end of the animal, just behind a small cephalic lobe (Fig. 3.4). In most species, each tentacle has a longitudinal row of pinnules. The forepart of the body, between the cephalic lobe and the diaphragm (Fig. 3.4), is cylindrical, often with shallow mid-dorsal and mid-ventral grooves, and has a variable number of transverse grooves behind the tentacle base. The bridle (frenulum), consists of a pair of thickened and tanned cuticular ridges which run diagonally around the forepart, and is sometimes fused or sometimes separated dorsally and ventrally. The muscular diaphragm region between forepart and trunk is usually narrowed externally. Perviates have a long trunk with a number of distinct regions. The anterior metameric region has two rows of tube-forming glands inside papillae or continuous ridges separated by a mid-dorsal furrow; the papillae are paired fairly regularly in many species. A band of cilia lies opposite the metameric region on the ventral side (Fig. 3.4). Circular or oval adhesive plaques, which are thickened areas of cuticle with a raised margin (Fig. 3.5B–D), are sometimes present on the metameric papillae and usually present on the more posterior papillae. Further along the trunk anterior to the girdles is a dorsal region of enlarged papillae, present in many species; opposite this region is a ventral ciliated patch or band. The girdles (annuli) comprise two pairs of epidermal ridges carrying bristles (chaetae) which encircle the middle region of the trunk (Fig. 3.4). Variations in the

girdle arrangement may produce the appearance of three rings or even long spirals. Behind the girdle region, the post-annular trunk is thinner and papillae are spaced at wider intervals. This region is fragile and usually broken, but the complete post-annular region may be twice as long as the pre-annular region. The short posterior region of the body, termed the opisthosoma (Fig. 3.4), is divided into numerous segments by internal septa. Each segment has four peg-like chaetae with round heads, aligned in two rows each side of the opisthosoma.

Moniliferans have a more uniform body than perviates. The forepart bears two tentacles close to the anterior end and the cephalic lobe is very small. There is no frenulum (bridle), just a patch or row of plaques on papillae, and there is little external differentiation between forepart and trunk. A ventral ciliated band extends along the posterior forepart and anterior trunk. The trunk has a short region of paired ventral papillae anteriorly, with scattered papillae with plaques on the remainder. The girdles, if detectable, are at the posterior end of the trunk. A row of chaetae is present on each segment of the opisthosoma.

Live vestimentiferans have a red branchial plume, surrounding a white obturaculum. The body is brown or greenish in colour, and red blood vessels are visible. The plume consists of numerous pinnulated tentacles, termed branchiae, grouped on concentric lamellae (Fig. 3.6A, B). The funnel-shaped obturaculum is a paired structure, with closely adhering right and left halves. The branchial lamellae arise within the anterior margin of the vestimental region, their bases covered by a collar-like fold. There is no cephalic lobe and no bridle. The sides of the vestimental region are expanded into muscular flaps, which curl over the dorsal side of the body (Fig. 3.6A, B). A ventral ciliated band runs from behind the collar to the posterior end of the relatively short vestimental region. Many low papillae tipped with cuticular plaques (Fig. 3.5A) are present on both the vestimental region and the trunk. The long trunk is not divided into regions as it is in perviates and girdles of chaetae are absent. The opisthosoma consists of many short segments, each bearing rows of numerous chaetae (Fig. 3.6C).

Pogonophoran chaetae have a slender shaft and an oval, serrated head (Fig. 3.7). They are reminiscent of polychaete uncini, except that the teeth are arranged in anterior and posterior groups, pointing towards one another. The shape and size of the chaetal head and arrangement of the teeth are species-specific.

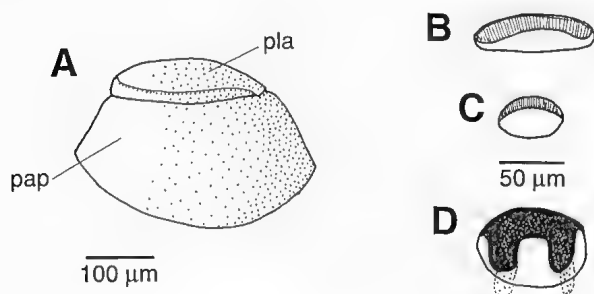


Figure 3.5 Cuticular plaques of pogonophores. **A**, plaque on a papilla, as in *Lamellibrachia* (Vestimentifera, Lamellibrachiidae). **B–D**, shapes of plaques in *Perviatea*; thickened regions hatched or dotted: **B**, elongate; **C**, oval; **D**, horseshoe-shaped. **pla**, plaque; **pap**, papilla.

[E.C. Southward]

Body Wall, Musculature and Coelom

The single-layered epidermis is covered by a cuticle of collagen fibres (Gaill *et al.* 1991), laid down extracellularly in criss-cross layers among the microvilli of the epidermal cells. Two muscle layers, the outer circular and the inner longitudinal, complete the body wall. The coelom is not lined by a separate epithelium. The cuticle is thickened and tanned in places to form the adhesive plaques characteristic of all groups (Fig. 3.5) and also the bridle of perviates. Chaetae are present as chitinous rods, formed in pockets of the epidermis and controlled by special muscle fibres. The oval, toothed heads of chaetae (Fig. 3.7) can grasp the interior of the tube. Epidermal secretory cells, most abundant on the anterior parts of the body, produce chitin and protein for use in tube building.

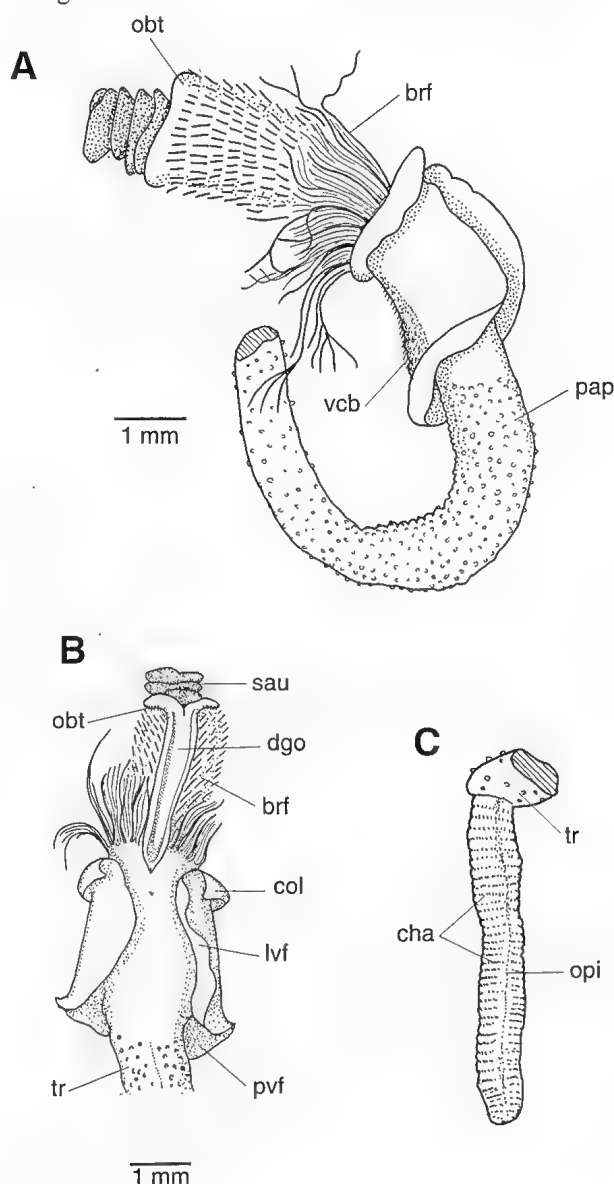


Figure 3.6 External features of *Ridgeia piscesae* (Vestimentifera, Ridgeiidae): **A**, lateral view of anterior end and part of trunk; **B**, dorsal view of anterior end; **C**, lateral view of opisthosoma. Cut surfaces are shown by cross hatching. **cha**, rows of chaetae; **col**, collar; **brf**, branchial filaments; **dgo**, dorsal groove of obturaculum; **lvf**, lateral vestimental fold; **obt**, obturaculum; **opi**, opisthosoma; **pap**, papillae; **pvf**, posterior vestimental fold; **sau**, saucer of brown cuticular material; **tr**, trunk; **vcb**, ventral ciliated band.

[E.C. Southward]

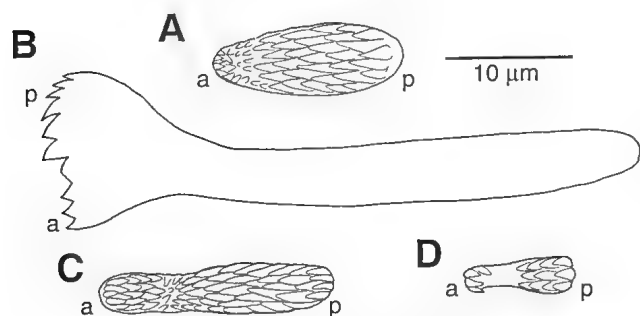


Figure 3.7 Chaetae of Pogonophora. **A–C**, girdle chaetae of perviates: **A**, *Siboglinum atlanticum* (Siboglinidae); **B**, *Siboglinum fiordicum*; **C**, *Lamellisabella coronata* (Lamellisabellidae). **D**, a opisthosomal chaeta of the vestimentiferan, *Lamellibrachia columna* (Lamellibrachiidae). **A, C, D**, oval toothed heads; **B**, head and shaft in lateral view. a, anterior; p, posterior. [E.C. Southward]

The coelomic compartments of perviates and moniliferans are: (1) the unpaired 'protocoel', designated by Ivanov (1963) and is located in the cephalic lobe with tentacle coeloms arising from it; (2) a pair of coeloms in the forepart, separated by a median mesentery (the 'mesocoel' of Ivanov 1963); (3) a pair of coeloms in the trunk, separated by mesentery and trophosome (the 'metacoel' of Ivanov 1963); and followed by (4) a series of coeloms in the opisthosoma, which form as pairs of splits in the mesoderm of the posterior segments, but lose the median mesentery as they develop (Southward, E.C. 1975a). The vestimentiferan anterior coelom is greatly reduced in the adult, where it may be the link between the tentacle coeloms. The vestimental region has much reduced paired coeloms, to which the slender paired obturacular coeloms are probably linked (Southward, E.C. 1988). The paired coeloms in the trunk are obscured by development of the large trophosome, whereas the opisthosoma has paired segmental coeloms separated by a muscular median mesentery (Jones 1985a, 1985b; Gardiner & Jones 1993).

Locomotion

Pogonophores move little more than to extend their tentacles from the tube into the water; a rapid retraction of the anterior end has been observed, notably in vestimentiferans. Perviates are thought to stay mainly inside their tubes, and use the opisthosoma to burrow down into the sediment. The tube is lengthened as the burrow extends.

Feeding and Digestive System

Early in life, pogonophores develop a mouth and gut, but they soon come to depend for their energy requirements on the symbiotic chemoautotrophic bacteria which multiply in the endoderm of the trunk segment during the post-settlement phase. Perviates absorb, through the epidermis, dissolved organic compounds (such as glucose and amino acids) from the sediment pore water, and so supplement the bacterial contribution (Southward, A.J. & Southward 1981; Southward, A.J. *et al.* 1986).

The trophosome is a cylindrical organ lying between the dorsal and ventral blood vessels. It occupies the last two-thirds of the trunk in perviates and moniliferans, and the whole trunk in vestimentiferans. It is formed of two epithelia, an outer peritoneum and an inner bacteriocyte layer, separated

by a system of blood sinuses (Fig. 3.8). The bacteria are contained in vacuoles in the bacteriocytes (Southward, E.C. 1982). The bacteria obtain energy by oxidising reduced sulphur compounds, and use it for the fixation of carbon dioxide and production of organic compounds. The pogonophore *Siboglinum poseidoni* is known to harbour methanotrophic bacteria which use methane as both energy and carbon sources (Schmaljohann & Flügel 1987). In the vestimentiferan genus *Riftia*, both sulphide and oxygen are transported bound to haemoglobin in the blood (Arp, Childress & Vetter 1987; Fisher 1990). Carbon dioxide is carried in high concentrations by blood and coelomic fluid (Toulmond *et al.* 1994). The oxygen-binding function of haemoglobin has also been shown in perviates (Terwilliger *et al.* 1987), but sulphide binding and carbon dioxide transport have not yet been demonstrated. Blood circulates through the trophosomal sinuses, in close contact with the bacteriocytes. The animals make use of the carbon fixed by their symbionts, either by absorbing organic compounds excreted by the living bacteria, or by digestion of some of the bacteria in intracellular vacuoles. The relative importance of these routes probably varies with species and circumstances.

Circulatory System

Pogonophores have a well-developed, closed circulatory system. Dorsal and ventral longitudinal vessels are present, linked at either end by pinnule vessels in the tentacles and by septal vessels in the opisthosoma. Connecting vessels in the trunk include those for trophosome circulation. The longitudinal vessels have muscular walls and a thin, non-cellular lining. There is no endothelium. Most of the minor vessels are sinuses between epithelia, with little or no muscle development. The heart region, present as a thickening of the dorsal vessel, has strongly developed muscle fibres, and is located near the tentacle bases; it pumps blood into afferent tentacular vessels, from which the blood traverses the pinnules and returns by efferent tentacular vessels to the thin walled ventral vessel. Circulation through the body is slow, forward in the dorsal vessel and posteriorly in the ventral vessel, impelled mainly by peristalsis of the vessel walls. The bright red blood contains a high concentration of haemoglobin in solution, and very few circulating blood cells. The haemoglobin binds and transports both oxygen and sulphide, the latter in a non-toxic form that can be released to the chemoautotrophic bacteria.

Respiration

The tentacles, with their pinnules, are the main site of oxygen uptake. In perviates, the pinnules are single epidermal cells, whereas in vestimentiferans they are multicellular; moniliferans have no pinnules on their tentacles. Looped sinuses run close to the surface of the pinnules, joining afferent to efferent tentacular vessels. The haemoglobin dissolved in the blood has a high affinity for oxygen and will carry it to both the animal tissues and the trophosomal bacteria. Bacterial fixation of carbon dioxide requires a net intake of carbon dioxide to supply the needs of the total symbiosis (Toulmond *et al.* 1994).

Excretion

A pair of ciliated, tubular excretory organs is situated anteriorly in both perviates and vestimentiferans; they open through pores on the dorsal side just behind the bases of the tentacles. They have not been investigated in moniliferans.

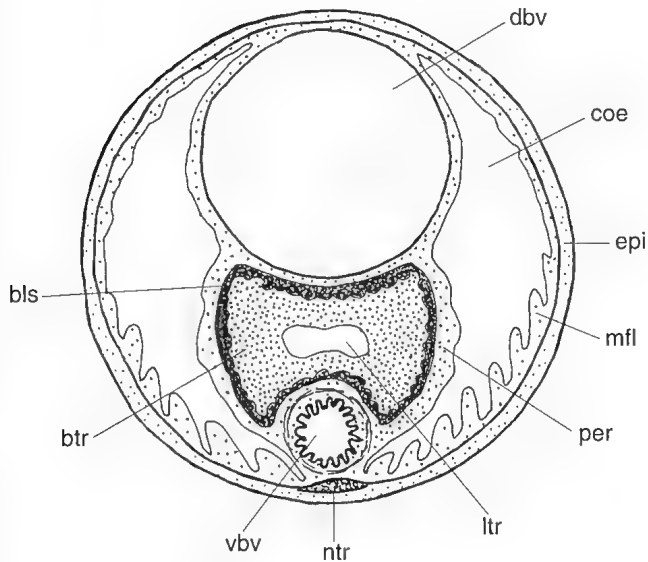


Figure 3.8 Transverse section of postannular region of the trunk of *Siboglinum fiordicum* (Perviate, Siboglinidae), showing the trophosome between the longitudinal blood vessels. **bls**, blood sinus; **btr**, bacteriocyte layer of trophosome; **coe**, coelom; **dbv**, dorsal blood vessel; **epi**, epidermis; **ltr**, lumen of trophosome; **mfl**, muscle fibre layer; **ntr**, nerve trunk; **per**, peritoneal layer covering trophosome; **vbv**, ventral blood vessel. [E.C. Southward]

The inner loops of the excretory organs are closely adherent to an enlarged and thin-walled part of the ventral blood vessel. In some of the larger perviate species, there is a connection between the excretory ducts and the anterior coelomic cavity which may allow some exchange of fluids. The removal of nitrogenous wastes from the blood is probably accomplished mainly by the trophosome bacteria, to satisfy their nitrogen requirement. Mineral wastes occur as insoluble granules in some trophosomal cells; they may be stored there for the life of the animal.

Nervous System

The nervous system lies entirely within the epidermis; an anterior brain extends to a mid-ventral nerve tract running along the body (Fig. 3.8). The brain of perviates is a concentration of nerve cell bodies and fibres, situated largely on the ventral side of the cephalic region, but extending to the dorsal side to give off tentacular nerves. The brain of vestimentiferans lies at the junction of the obturaculum with the vestimental region, supplying nerves to the branchial filaments and the two halves of the obturaculum. A giant axon extends from the posterior part of the brain, accompanying the nerve trunk as far as the girdles in perviates and to the rear end of the trunk in vestimentiferans. The opisthosoma of the perviate *Siboglinum fiordicum* has a well-differentiated ladder-like nervous system. The median nerve tract is accompanied by two lateral tracts of nerve fibres. The three are linked by transverse bands of nerve fibres in each segment. Each segment also contains two 'ganglia', small masses of nerve cell bodies from which the transverse fibres originate. This arrangement appears to be linked to the coordination of chaetal movement and muscular activity in burrowing (Southward, E.C. 1975a). In each segment of the opisthosoma, there are lateral groups of sensory cells (four types) which probably include mechanoreceptors and chemo-

receptors. Vestimentiferan opisthosomes have a median nerve trunk, but details of the innervation of the multiple chaetae and the sensory system are not known.

Single sensory cells, which may be photoreceptors, have been found in the cephalic region of *Siboglinum fiordicum* (Nørrevang 1974), and bands of sensory cells occur in sensory filaments in the branchial plumes of vestimentiferans (Gardiner & Jones 1993).

Exocrine Glands

Several types of epidermal secretory cell have been described. The most abundant and active are those involved in providing secretions for tube construction. Multicellular pyriform glands secrete chitin and mucopolysaccharides for use in building the tube. Their ducts open on the surface of the epidermis, often on papillae and carry the secretions from several cells. Such glands are abundant in the forepart of perviates, the vestimental region of vestimentiferans, more scattered in the trunk in both and present in the opisthosomal segments. Single-celled epidermal glands produce the proteinaceous component used in tube construction; also there are a few unicellular mucus-producing glands among the ciliated cells of the ventral ciliated band and in the ciliated tracts found on the tentacles of some perviates.

Reproduction

Most pogonophores reproduce sexually, but asexual reproduction is not uncommon in the Monilifera; in this process the body fragments into two or more fragments and regenerates anterior and posterior ends. The sexes are separate, except in one known hermaphrodite. The gonads lie in the trunk segment.

Perviate pogonophores have paired female gonads in the anterior part of the trunk; oocytes are formed at the front ends of the ovaries, posterior to the diaphragm, mature, and pass into oviducts which open to the exterior a little in front of the girdle region. Males have paired testes in the postannular region. Spermatogonia in the testes divide to produce groups of spermatids. They develop into spermatozoa with long narrow heads, consisting of a small helical acrosome and a long nucleus surrounded by three spirally wound mitochondria (Franzén 1973). The spermatozoa are carried forward in a pair of sperm ducts from in front of the girdles to the anterior end of the trunk, where they open through a pair of gonopores (occasionally one). While in the sperm ducts, bundles of spermatozoa are combined with fibrous material and moulded into spermatophores. The spermatophores are elongate bodies with a very long tail of fibrous material at one end; the size and shape vary greatly between species (Fig. 3.9). They are stored in the anterior part of the sperm duct, where the coiled 'tail' or filament adheres to one side of the spermatophore; when released into sea water, the tail uncoils to form a long and sticky filament which assists the spermatophore to become entangled with another pogonophore. After some hours in sea water the covering of the spermatophore fragments and the spermatozoa are free to swim. Fertilisation takes place in the oviduct; it is not known how the spermatozoa locate the female gonopore. The fertilised eggs are released and moved up the tube to lie in the front of the female, where, if they are large, they stay and develop in the tube (Webb 1964b; Southward, E.C. 1975b; Bakke 1976, 1983). Species with small eggs (*ca* 150 µm)

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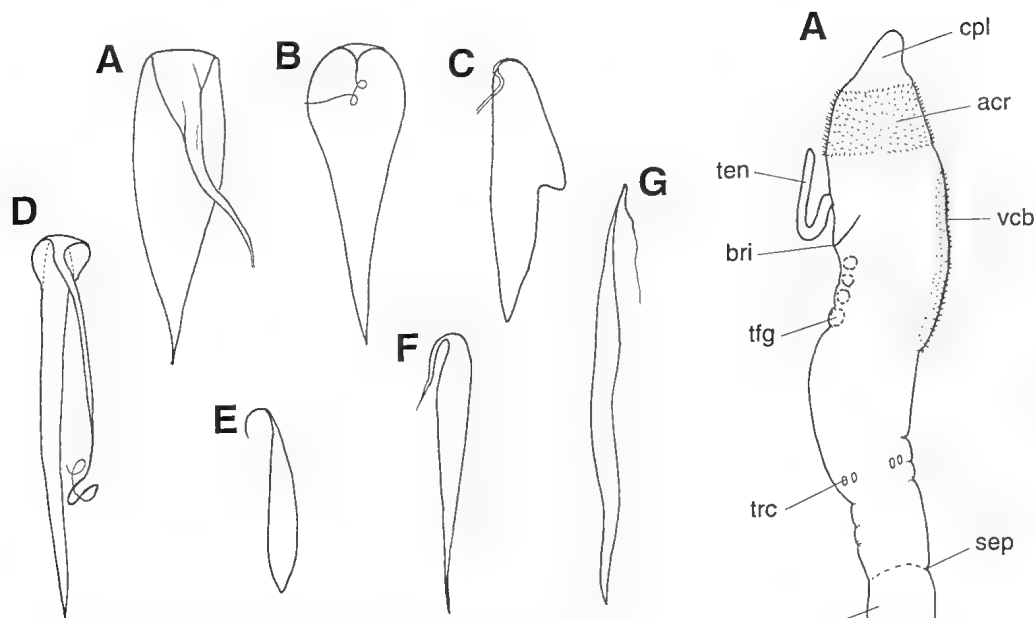


Figure 3.9 Spermatophores of perviate pogonophores. Most of the filament is omitted. **A**, *Lamellisabella coronata* (Lamellisabellidae), length 650 μm ; **B**, *Spirobrachia belajevi* (Spirobrachiidae), length 1500 μm ; **C**, *Galathaealinum arcticum* (Polybrachiidae), length 1800 μm ; **D**, *Oligobrachia hawaiiensis* (Oligobrachiidae), length 300 μm ; **E**, *Siboglinum bayeri* (Siboglinidae), length 120 μm ; **F**, *Zenkevitchiana longissima* (Polybrachiidae), length 1500 μm ; **G**, *Siboglinum candidum*, 350 μm . **A, B, C & F**, leaf-shaped; **D, E & G**, spindle-shaped. (Adapted from Southward 1975b) [E.C. Southward]

apparently do not incubate them in the tube; the eggs must be released into the sea and presumably have a pelagic development, yet to be discovered.

Moniliferans produce large eggs, and do not, apparently, produce spermatophores. Their reproduction has not been studied in any detail.

Vestimentiferans produce large numbers of small eggs (80–100 μm in diameter). The elongate female gonads lie in the anterior part of the trunk and the oviducts open through gonopores at the anterior limit of the trunk segment, well inside the vestimental space. Fertilisation is internal and the eggs are shed to develop pelagically. The male has numerous testicular tubules, embedded among the lobes of the trophosome, which join paired sperm ducts as they run along the trunk. The spermatozoon develops an elongate head, with a helically grooved acrosome and a corkscrew-shaped nucleus spirally encircled by two slender mitochondria in series. Spermatozoa accumulate in bundles in the sperm ducts. The two male gonopores lie a little farther back than those of the female, each one opening into a ciliated groove in the epidermis of the vestimental region. The two ciliated grooves run forward to the collar region. *Riftia* species apparently shed sperm freely, whereas *Ridgeia* species produce small sticky sperm masses which can be passed to neighbouring females (Southward, E.C. & Coates 1989).

Embryology and Development

Development in Perviatea and Vestimentifera has been recently reviewed by E.C. Southward (in press). The development of the perviate *Siboglinum fiordicum*, a Norwegian species, has been studied extensively from egg to near adult; this and other

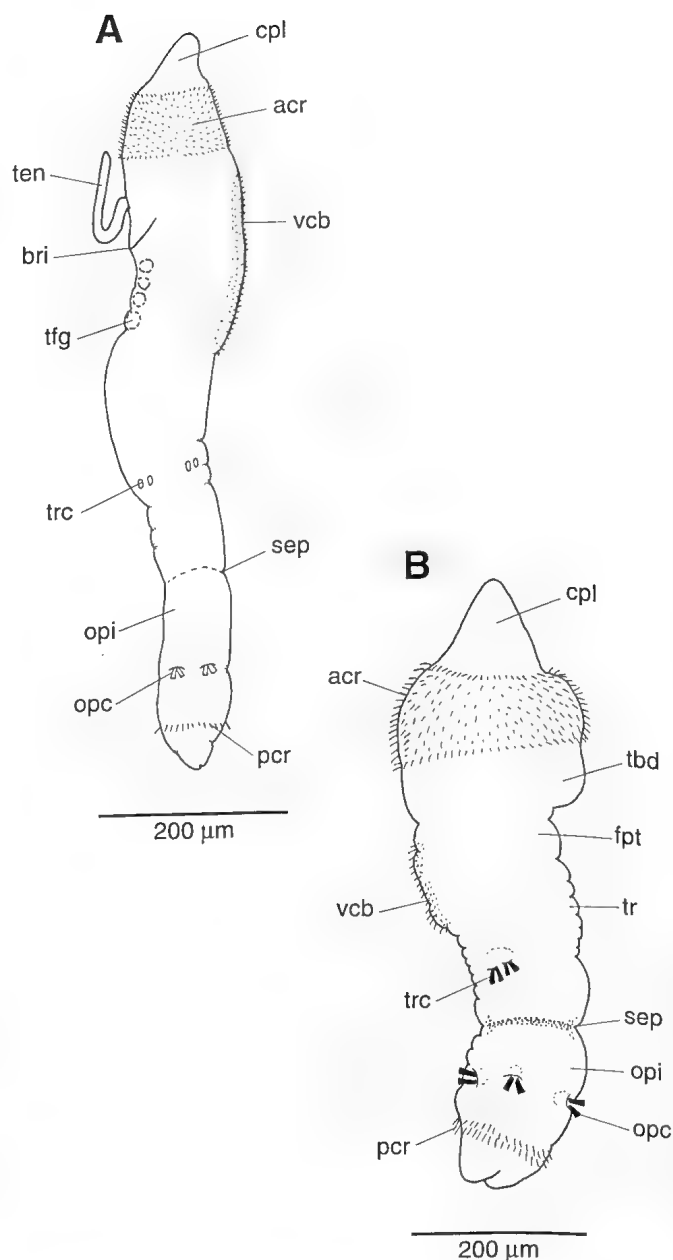


Figure 3.10 Settlement stage embryos of perviate pogonophores. **A**, *Siboglinum gosnoldae* (Siboglinidae). **B**, *Siboglinum fiordicum*. **acr**, anterior ciliated ring; **bri**, bridle; **cpl**, cephalic lobe; **fpt**, forepart; **opo**, opisthosomal chaeta; **opi**, opisthosoma; **pcr**, posterior ciliated ring; **sep**, septum; **tbd**, tentacle bud; **ten**, tentacle; **tfg**, tube-forming gland; **tr**, trunk; **trc**, trunk chaeta; **vcb**, ventral ciliated band. (A, adapted from Southward 1988; B, adapted from Southward 1975b) [E.C. Southward]

incubating species have provided the most detailed information on stages in embryology. In all the incubated species studied, the eggs are about 500 μm in diameter, often elongated to fit in the narrow tube, and rich in yolk. Several are laid simultaneously and develop more or less synchronously within the female's tube. Cleavage follows a modified spiral pattern (Bakke 1976; Gureeva 1988). Gastrulation occurs by overgrowth of smaller cells over larger yolk containing cells (Ivanov 1963, 1988), among which a ciliated gut cavity develops. Anterior and posterior rings of ciliated cells are formed, and a longitudinal band is present on the ventral side. At this stage the embryo is pear-shaped; subsequently it elongates and forms a posterior septum,

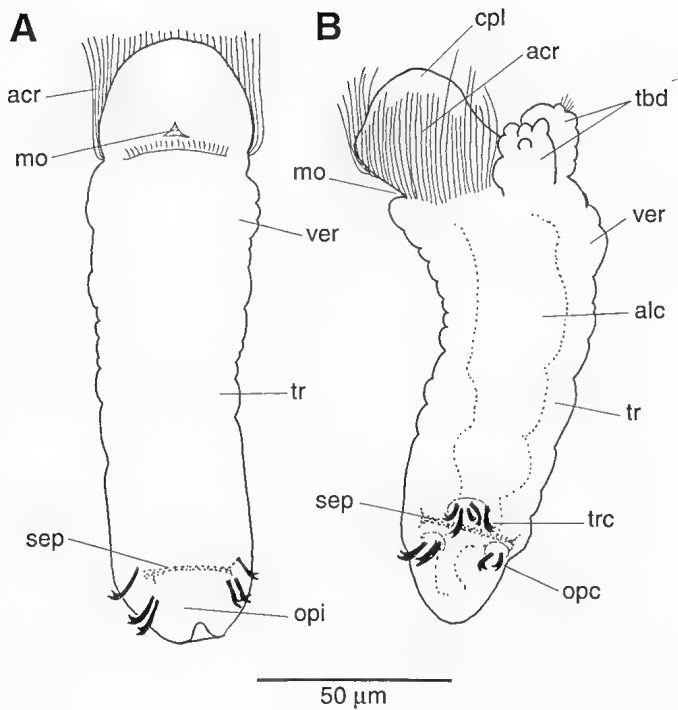


Figure 3.11 Recently settled post-larvae of *Ridgeia piscesae* (Vestimentifera, Ridgeiidae): **A**, ventral view; **B**, lateral view. **acr**, anterior ciliated ring; **alc**, alimentary canal; **cpl**, cephalic lobe; **mo**, mouth; **opi**, opisthosoma; **opc**, opisthosomal chaeta; **sep**, septum; **tbd**, tentacle buds; **tr**, trunk; **trc**, trunk chaeta; **ver**, vestimental region. (Adapted from Southward 1988) [E.C. Southward]

defining the opisthosoma (Webb 1964b). When the worm-shaped larva emerges from the maternal tube, it has no functional gut and is still dependent on yolk in the endodermal cells. The larva (Fig. 3.10) is longer than the original egg, and is able to swim, crawl and burrow using its ciliated rings and ventral ciliated band. It has the rudiment of its first tentacle and two chaetigerous segments, equivalent to the trunk and first opisthosomal segment of the adult. It is this larva that searches for a suitable sediment for settlement and once found begins to burrow, head-down at first and then in reverse (using the opisthosoma). It lines its burrow with tube material and is capable of burrowing down several centimetres almost immediately (Bakke 1977). It is not known how the symbiotic bacteria are transferred to the larvae; they have not been seen in the embryo, but phagocytic uptake of bacteria into the trophosome cells of juvenile *Siboglinum poseidoni* has been described by Callsen-Cencic & Flügel (1995).

The development of eggs in vestimentiferan species of *Lamellibrachia* and *Escarpia* from the Gulf of Mexico has been studied by Young *et al.* (1996). These eggs are slightly more than 100 µm in diameter, and cleavage is spiral and unequal, resulting in a large D-macromere at the 4-cell stage. The larva is similar to the trochophore of a typical oviparous polychaete, having two parallel equatorial bands of cilia. It differs in not having an apical tuft, and in lacking compound cilia. No mouth or gut was visible after 3 weeks of development. It is suggested that the larvae can disperse without feeding, relying on yolk, for several weeks.

Newly settled juveniles of *Ridgeia* species (Vestimentifera) are not much larger than their eggs. In their own gelatinous tubes, they have been found on the tubes of older specimens (Southward, E.C. 1988). The youngest juvenile found is similar to an annelid trochophore larva (Jones & Gardiner 1988). It has capillary and hooked chaetae on the trunk segment, which are later lost. The first opisthosomal segment has both larval and adult type chaetae; posterior to this, the segments have adult type chaetae only. The larva has a mouth, gut and anus, which remain open for some time in the developing juvenile (Fig. 3.11); the mouth region elongates to form a ventral ciliated funnel as tentacles begin to develop dorsal to it (Jones & Gardiner 1988, 1989; Southward, E.C. 1988; Gardiner & Jones 1993). Small bacteria are present in the lumen of the gut, presumably the food of the free-swimming and newly settled stages. At a slightly later stage, intracellular symbiotic bacteria colonise the midgut, which develops into the trophosome.

NATURAL HISTORY

Life History

In the perviate pogonophore, *Siboglinum fiordicum*, which develops directly, the dispersal phase lasts a few hours, and the only metamorphosis is the change from dependence on yolk to dependence on symbiotic bacteria in the trophosome. *Siboglinum fiordicum* probably takes more than 2 years to reach sexual maturity. Vestimentiferans, which develop pelagically, have a more marked metamorphosis. The juveniles develop the adult body form of branchial plume, vestimental region, trunk and opisthosoma by the time they are 3 mm long. Vestimentiferans colonising hydrothermal vents often seem to settle 'en masse', since large numbers of young can be found growing on older tubes. Vent animals are confined to small areas, often geographically isolated, and are relatively short-lived, and so need adaptable dispersal strategies. They need to be able to repopulate their original or neighbouring sites, within perhaps a kilometre, and they also need to be able to colonise more distant sites. Vestimentiferans have a non-feeding planktonic larval life of 2 weeks or more. Their dispersal depends on near-bottom currents. Hydrothermal plumes have also been suggested as a means for carrying deep-sea vent animals long and short distances to other vent sites (see review discussions by Copley 1998 and Speer 1998). Where mass colonisation by vestimentiferans of new sites has been found, growth to adult size can be completed in 2 years (Lutz & Haymon 1994; Southward, E.C. *et al.* 1996).

Ecology and Behaviour

Perviate pogonophores live in sediments, moniliferans (Sclerolinidae) in decaying wood, and vestimentiferans live close to hot or cold sulphidic springs. They are all dependent on chemosynthesis, carried out by symbiotic chemoautotrophic bacteria in their trophosome. The bacteria use reduced sulphur compounds, such as sulphides or thiosulphates, and require oxygen to oxidise these to provide the energy to produce ATP (adenosinetriphosphate). They can then fix carbon dioxide, with the help of the enzyme ribulose biphosphate carboxylase, and synthesise organic compounds.

Dissolved sulphide is limited in distribution because of its rapid chemical oxidation in ordinary sea water. Perviate pogonophores live in sediments (Fig. 3.12) where the deeper layers are reduced (grey or black in colour) and the surface

3. CLASS POGONOPHORA

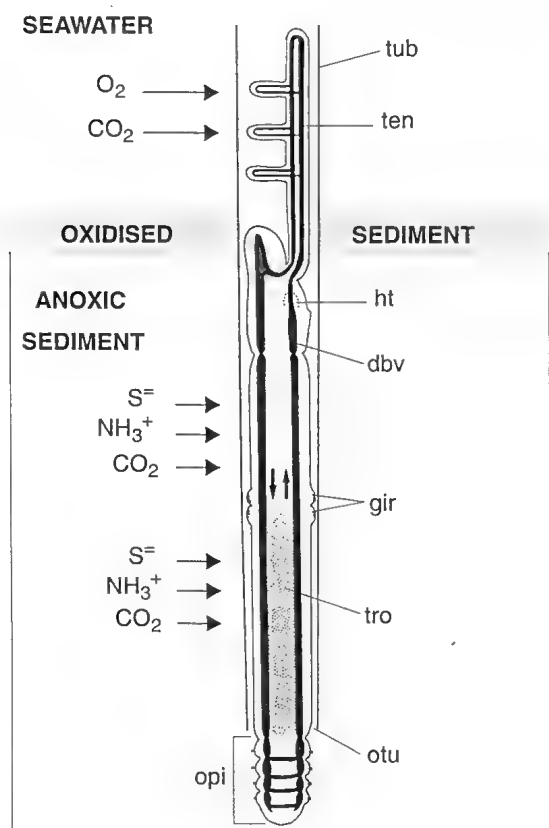


Figure 3.12 Diagram showing a perviate pogonophore living in its environment. The tube is vertical in the sediment, the surface of which is oxidised. The deeper sediment is anoxic. The overlying seawater contains dissolved oxygen (O_2) and carbon dioxide (CO_2). The animal's blood (shown black) carries oxygen from the tentacle and pinnules to the trophosome in the buried trunk. Bacteria in the trophosome receive reduced sulphur and inorganic nitrogen from the sediment pore water by diffusion. dbv, dorsal blood vessel; gir, girdles; ht, heart; opi, opisthosoma; otu, open tube; ten, tentacle; tro, trophosome; tub, tube. [E.C. Southward]

layer is oxidised (brown in colour). The water above the sediment contains oxygen. The pogonophoran tubes are permeable to gases and small molecules in solution. The animal's length allows it to bridge the redox discontinuity, so that oxygen can be carried by its blood, bound to haemoglobin, to the bacteria in the lower part of its trunk where sulphide or thiosulphate diffuse in from the sediment. Sediment pore water (that is, water between the sediment particles) and overlying sea water provide dissolved carbon dioxide. Organic nitrogen may be obtained as dissolved organic compounds or ammonia from the pore water. One species, *Siboglinum poseidoni*, lives in methane seeps, where there are high concentrations (mM) of methane and has methane-oxidising bacterial symbionts (Dando *et al.* 1994).

Sediments inhabited by pogonophores include soft mud and muddy sand. The best known species, *Siboglinum fiordicum*, lives in muddy sand at 25–330 m depth in Norwegian fjords, but this shallow occurrence is somewhat unusual. Most pogonophores live between about 200–3000 m on continental slopes. There is evidence of depth zonation of species on both sides of the Atlantic Ocean, where sampling has been extensive (Southward, E.C. 1979). In the Pacific, in addition to living on continental slopes, perviate pogonophores have been found in several of the deep trenches, the deepest having been recorded at 9735 m in the Kuril-Kamchatka Trench.

Moniliferans, *Sclerolinum* species, live in plant remains, partly buried in mud, and often black with decay. In the fjords near Bergen in Norway, *Sclerolinum brattstromi* has been found in submerged tree branches, especially under the bark, and in discarded paper, rope and clothing. The posterior parts of the tubes penetrate among the plant fibres, but the anterior ends are open to the overlying water, where the tentacles can absorb oxygen.

Vestimentiferans live at hydrothermal vents and cold seeps, both habitats where there is effluent rich in sulphides. Hydrothermal regions occur at spreading ridges in the deep-sea floor, where sea water circulates through new crustal rocks and emerges as hot as 360°C; the seawater sulphate is reduced to sulphide during its passage through the hot rocks. Minerals accumulated during this passage precipitate to form chimneys around the outflows as the vent water mixes with cold sea water. Vestimentiferans settle and grow on some of these chimneys, where vent and normal bottom water mix and the surface is comparatively cool (ca 20°C). They may also settle on lava around sites of diffuse venting. Typically, the tubes are in groups, clusters or large bushes, the young frequently settling on older tubes. The animals extend their red branchial crown and white obturaculum into the water, leaving the rest of the body, from the collar backwards, inside the tube.

Vestimentiferan tubes are often covered by growths of filamentous bacteria, small limpets and snails, and the tubes of polychaetes, and galatheid crabs have been found among them. Larger crabs and fish may feed and polynoid polychaetes may nibble on the branchial plumes. Species differences between geographically separate vent populations are large (Tunnicliffe 1991; Desbruyères & Segonzac 1997), and vestimentiferans are absent from some hydrothermal regions, such as the Mid-Atlantic Ridge.

Cold seeps occur where sedimentary rocks are under pressure, causing fluids to be squeezed out. This happens near the edges of continents where the sea floor is being subducted, as at the Pacific coasts of North America and Japan. Sulphidic and hydrocarbon seeps (including methane) may emerge at almost any depth, from nearshore to deep in the side of a trench. Vestimentiferans, different from the hydrothermal species, have been found at cold seeps at depths from a few hundred metres to 4000 m. They are found in clusters or bushes, apparently growing outward from a common source, rather than on one another, and form a substratum and shelter for other animals, such as hydroids and anemones (MacDonald *et al.* 1989). Possible predators include large buccinid snails.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Perviate pogonophores have been found from the Arctic and Antarctic to the tropics, in all the oceans and at most depths, apart from the intertidal and immediate subtidal zones. However, most records and the majority of species have been collected from continental slope depths of about 200–3000 m. The Japan, Kuril, Aleutian and Peru-Chile Trenches in the Pacific have a diverse and abundant pogonophoran fauna, down to more than 9000 m. The shallowest records are: *Siboglinum fiordicum* from 25 m, Norway; *Galathealinum arcticum* from 36 m, Canadian Arctic, and; a species of *Siboglinum* from 24 m, Gulf of Mexico. The latter is the warmest habitat known (17°–26°C), and is an exception to the

apparent upper temperature limit of about 15°C for the group. Knowledge of geographical distribution is very incomplete, but some generalisations can be made: species have restricted distributions whereas genera and families are widespread; coastal seas and regions off the coasts of continents and large islands are far richer in Pogonophora than are the abyssal plains of the oceans; each of the inshore seas of the Pacific has a different assemblage of pogonophores; trenches near continents have a large proportion of endemic species (Ivanov 1963). Recent discoveries of pogonophoran populations have been made at a hydrothermal site (Lau Basin) and two cold seep sites (Gulf of Mexico and Oregon).

The Australian Region, where pogonophores are not well known, is bordered on the north by the Indo-Malay Region, where there are many pogonophoran species (Southward, E.C. 1961, 1975c); to the north-east by the Bougainville Trench which has endemic species (Ivanov 1963); to the east by the New Zealand area with five species (Ivanov 1962; Batham 1973); and to the far south by records from the Antarctic, mostly of unnamed species (Ivanov 1963). Samples in the Australian Museum and Museum Victoria show that perviate pogonophores of the genera *Siboglinum*, *Siboglinoides* and *Diplobrachia*, and possibly *Oligobrachia* and *Polybrachia*, have been collected in Australian seas (off Queensland, New South Wales and Victoria, at depths of 400–3000 m). Several more genera, perhaps including moniliferans (*Sclerolinum* species) may occur, and pogonophores will probably be found all around the continental slopes of Australia, a much larger area than their present recorded occurrence. Families to be expected are included in the descriptions below.

It is less likely that vestimentiferans will be found on the continental slope of Australia but, if cool saline or hydrocarbon seeps are discovered in future, the genus *Lamellibrachia* might be expected, at normal seafloor temperatures. The biogeography of vestimentiferans is not very well understood, but any Australian species may well be related to the western Pacific fauna of back-arc basins and continental slopes. One hydrothermal vent vestimentiferan (*Arcovestia ivanovi*; Southward, E.C. & Galkin 1997) is known from a seafloor spreading centre in the Manus Basin, north of Papua New Guinea, and there are other back-arc spreading centres such as the Woodlark Basin where hydrothermalism and associated vestimentiferans may be found in future.

Affinities with other Groups

The relationship of pogonophores to other invertebrate groups has been discussed ever since the first description of *Siboglinum*, which could not be assigned to a known phylum (Caullery 1914, 1944). The absence of a mouth and alimentary canal in pogonophores made it difficult to determine which side was dorsal, and for a considerable time the side of the body with the nerve trunk was considered to be dorsal; there appeared to be three coelomate segments in the embryo and the adult, so a deuterostomian affinity was presumed (Ivanov 1963). A relationship to hemichordates was suggested. However, it was not known then that the hind end had been lost in all the adult specimens examined up to that time. When the opisthosoma was found and described in 1964 (Webb 1964a; Ivanov 1965), it became obvious that it was divided by septa into numerous coelomate compartments forming serial segments with metamerically repeated organs

and lateral bristles (chaetae) (Southward, E.C. 1975a). A close relationship to annelids was then suggested, and authors began to reverse their ideas of the dorso-ventral orientation of pogonophores. Protostomian affinity was confirmed by developmental studies of vestimentiferans and perviates, which have shown that the larval mouth and the main nerve trunk are both ventral.

Debate on relationships has continued, and current opinions vary. Some zoologists favour the inclusion of Pogonophora in the phylum Annelida; others would separate Pogonophora and Annelida at phylum level, while Ivanov maintained that pogonophores are not closely related to annelids, and their similar anatomical features are the result of convergence, not descent (Ivanov 1988; Malakhov, Popelyaev & Galkin 1996). Molecular biological studies are in progress in various laboratories; results have linked vestimentiferans with Annelida (Kojima *et al.* 1993; Suzuki, Takagi & Ohta 1993; Yuasa *et al.* 1992; McHugh 1997), supporting conclusions from comparisons of chaetal structure and arrangement (George & Southward 1973; Bartolomaeus 1995; see also Rouse & Fauchald 1995, 1997).

Affinities within the Taxon

There is some disagreement about whether Vestimentifera should be included within the Pogonophora, or be classified as a separate phylum. Jones (1985b) and Gardiner & Jones (1993) have followed the latter course. The difference of opinion hinges more on the definition of the term phylum than on the distinctions between the two groups. Here the Vestimentifera is considered a subclass within the class Pogonophora. Their affinities are demonstrated by their juvenile segmentation, the arrangement of chaetae, the development of trophosome and adoption of internal symbiotic bacteria. Body wall structure, surface plaques, the pattern of teeth on the chaetae, structure of the pyriform tube-forming glands and the chitinous tube are characters in common, not shared with other groups in the Annelida. The differences in morphology quoted by Jones become apparent during juvenile development (Southward, E.C. 1988).

The phylogeny of the Pogonophora (Perviate), according to Ivanov (1963), places the order Athecanephria as the more primitive of the two orders designated; they have simpler excretory ducts and fewer, freer tentacles. Members of the order Thecanephria, however, have more elaborate excretory ducts, and they generally have more tentacles bearing more pinnules and, in some cases, adhesion of adjacent tentacles. Ivanov suggested that in both orders a modest number of tentacles (six to eight) is the primitive state, and that increase in tentacle number has been accompanied by an increasing development of pinnules. He considered that reduction of tentacle number to two or one has occurred more than once in Athecanephria (*Nereilinum*, *Siboglinum*, *Siboglinoides* and *Crassibrachia*), and separately in the Thecanephria (*Diplobrachia*).

Since the publication of Ivanov's monograph (1963), many new species of perviate pogonophores have been described, and several new genera, but the only new family proposed has been the Sclerolinidae (Webb 1964c). Subsequently, the Sclerolinidae have been placed in a new subclass, Monilifera (Ivanov 1991; Ivanov & Selivanova 1993), equal in rank to Perviate and Vestimentifera.

3. CLASS POGONOPHORA

In the classification of the phylum Vestimentifera of Jones (1985b), the nine species were divided into two classes, Basibranchia and Axonobranchia (here treated as orders), according to the anatomy of the branchial crown and its blood system. The Axonobranchia includes the one family, Riftiidae, with one genus, *Riftia*. Basibranchia was divided into two orders and four families. Since then two more families have been added to the Basibranchia (Southward, E.C. 1991; Southward, E.C. & Galkin 1997).

Symbiont Affinities

All symbionts in pogonophores are Gram-negative bacteria. Almost all are sulphur-oxidising chemoautotrophs. One pogonophore, *Siboglinum poseidoni*, has methane-oxidising symbionts, which must have been acquired separately and not have evolved from a sulphur-oxidiser. Similar forms of symbiotic bacteria occur within each subclass of Pogonophora. Those in Perviata are slender and rod-shaped. In Monilifera, they are larger, and oval or rounded, and those in Vestimentifera are large and spherical. Study of the symbionts of vestimentiferans using molecular methods (16S rRNA; see review by Nelson & Fisher 1995) have shown that all the sulphur-oxidising symbionts belong to the class Proteobacteria, gamma subdivision, and that only one species of symbiont is present in *Riftia pachyptila*. This is probably the same symbiont species found in the sympatric vestimentiferan, *Tevnia jerichonana*. At present there is no evidence that symbionts are transferred via the eggs in vestimentiferans; it is suggested that they may be acquired from the environment by each individual.

Fossil Record

Fossil tubes of *Hyolithellus micans* from Middle Cambrian clay in Denmark, also known from European and North American Lower Cambrian formations, are attributed convincingly to Pogonophora by Poulsen (1963). One of these fossil tubes is illustrated alongside a very similar tube of a modern pogonophore, *Lamellisabella* species, by E.C. Southward & Southward (1967). Other reported pogonophore fossils are from North America, China and Poland (Adegoke 1967; Wang 1983; Mierzejewski 1986). Descriptions of fossil hydrothermal and cold seep systems refer to tubular fossils, which may be vestimentiferans; they are recorded from as far back as the Silurian period (see review by Tunnicliffe 1991; Kuznetsov, Zaikov & Maslennikov 1991; Kuznetsov, Maslennikov & Zaikov 1993).

COLLECTION AND PRESERVATION

Anchor dredges and box corers have been used successfully to collect Pogonophora. Fine-meshed trawls may also be used to drag pogonophoran tubes out of mud. Manned submersibles, such as *Alvin*, can collect vestimentiferans and other large tubes 'by hand', using a remotely operated manipulator. Figure 3.13 shows tubes of *Lamellibrachia barhami* collected by *Alvin* which is seen in the background. Slow washing and sieving usually damages the animals; hand picking can speed sorting, as the tubes are easy to detect in the mud samples because they are strong, flexible and slightly elastic. Animals for taxonomic study may be fixed in buffered formalin and stored in ethanol or isopropanol. Rose Bengal staining is not recommended; it obscures the anatomy of the animals and the colour of the tube. Large vestimentiferans may be partly dissected or eased from their tubes before fixation (the most useful characters are at the anterior end) and the tube should then



Figure 3.13 The tubes of a number of individuals of *Lamellibrachia barhami* (Lamellibrachiidae) in the hands of James Childress; the animals themselves have withdrawn into the tubes. The animals were collected from a sedimented hydrothermal site in Middle Valley, north-east Pacific at a depth of 2420 m. The submersible, *Alvin*, from which the collection was made, is in the background.

[E.C. Southward]

be kept with the animal. Small pogonophores are best examined first under a dissecting microscope, then mounted temporarily in 50% glycerine under a large coverslip on a slide, for study at higher magnification. Only then should the tube be slit or otherwise removed to study the animal. If a male contains spermatophores a few can be dissected out for measurement. Scanning electron micrograph techniques, if available, can be used to record the shape of separated spermatophores (Fig. 3.9), surface plaques (Fig. 3.5) and heads of chaetae (Fig. 3.7).

Description and identification of pogonophores require: measurements of the tube and the animal; examination of colour and size of rings and presence or absence of segmentation in the tube; the counting of tentacles and examination of pinnules; detailed records of the papillae and their arrangement, and; whether and where cuticular plaques are present. The shape and size of the chaetae and the spermatophores are important and must be recorded if present.

CLASSIFICATION

The extant families of the Pogonophora are outlined in Table 3.2. The families Lamellisabellidae, Sclerolinidae and Lamellibrachiidae are not yet known from the Australian region, but have been found in neighbouring waters and are likely to be found there.

Table 3.2 Classification of the extant families of Pogonophora. Families marked with an asterisk (*) have not been recorded from Australian waters. †Jones (1985b) placed *Oasisia* in Tevniidae, thus Oasisiidae is here considered under Tevniidae, although recent molecular studies do not support this. The Vestimentifera is sometimes referred to as Obturata.

Class POGONOPHORA

Subclass PERVIATA

- Order Athecanephria
 - Family Oligobrachiidae
 - Family Siboglinidae
- Order Thecanephria
 - Family Polybrachiidae
 - Family Lamellisabellidae*
 - Family Spirobrachiidae*

Subclass MONILIFERA

- Family Sclerolinidae*

Subclass VESTIMENTIFERA

- Order Basibranchia
 - Family Lamellibrachiidae*
 - Family Escarpiidae*
 - Family Tevniidae*†
 - Family Ridgeiidae*
 - Family Alaysiidae*
 - Family Arcovestiidae*
- Order Axonobranchia
 - Family Riftiidae*

Key to families of the Pogonophora, subclasses Perviata and Monilifera, found or likely to be found on the Australian continental shelf and slope.

- 1(a) Tubes regular, variously coloured; cephalic lobe distinct, one to >200 tentacles; forepart with obvious bridle; trunk demarcated from forepart PERVIATA 2
- 1(b) Tubes narrow and curled or sinuous, walls transparent yellow or brown, of irregular thickness; cephalic lobe indistinct, two tentacles, no pinnules; forepart and trunk not clearly separated; usually in decaying wood or plant debris MONILIFERA Sclerolinidae
- 2(a) Anterior part of the trunk with two rows of papillae or two ridges, each containing a single row of internal glands. 3
- 2(b) Anterior part of trunk with two wide ridges, each containing two or more rows of pyriform glands Oligobrachiidae
- 3(a) Tentacles not firmly joined together 4
- 3(b) Tentacles firmly joined together in parallel. 5
- 4(a) Tentacles one or two; spermatophores narrow; plaques usually absent from anterior trunk papillae. Siboglinidae
- 4(b) Tentacles two to many; spermatophores leaf-shaped; plaques usually present on anterior trunk papillae Polybrachiidae
- 5(a) Tentacles joined, forming a cylinder Lamellisabellidae
- 5(b) Tentacles joined, forming a spiral plate. Spirobrachiidae

Subclass PERVIATA

Members of this subclass have slender unbranched tubes and are usually buried vertically in sediment; the tubes may be ringed and/or segmented. The cephalic lobe is small, with one to over 200 tentacles and the short, cylindrical forepart has an oblique bridle. The trunk is long with variously organised papillae and, near its middle, two girdles of numerous chaetae. The short opisthosoma is divided into many segments, each with four chaetae. Spermatophores are present in males. The subclass comprises two orders, Athecanephria and Thecanephria. All families are likely to be found in Australian waters.

Order ATHECANEPHRIA

Members of the Athecanephria are characterised by having short excretory ducts associated with the lateral cephalic blood vessels (only observable by sectioning), and from one to 18 tentacles. The forepart has a distinct bridle, and often has patches of white or coloured epidermal glands. The anterior part of the trunk has two rows of dorsal papillae or two longitudinal ridges each with one or more rows of internal glands. The postannular part of the trunk has widely spaced ventral glandular shields and opposite each, one to three dorsal papillae. The spermatophores are spindle-shaped, rarely flattened. Members of this group are sediment dwellers, found worldwide. There are seven genera, and 87 species, referred to two families, Oligobrachiidae and Siboglinidae.

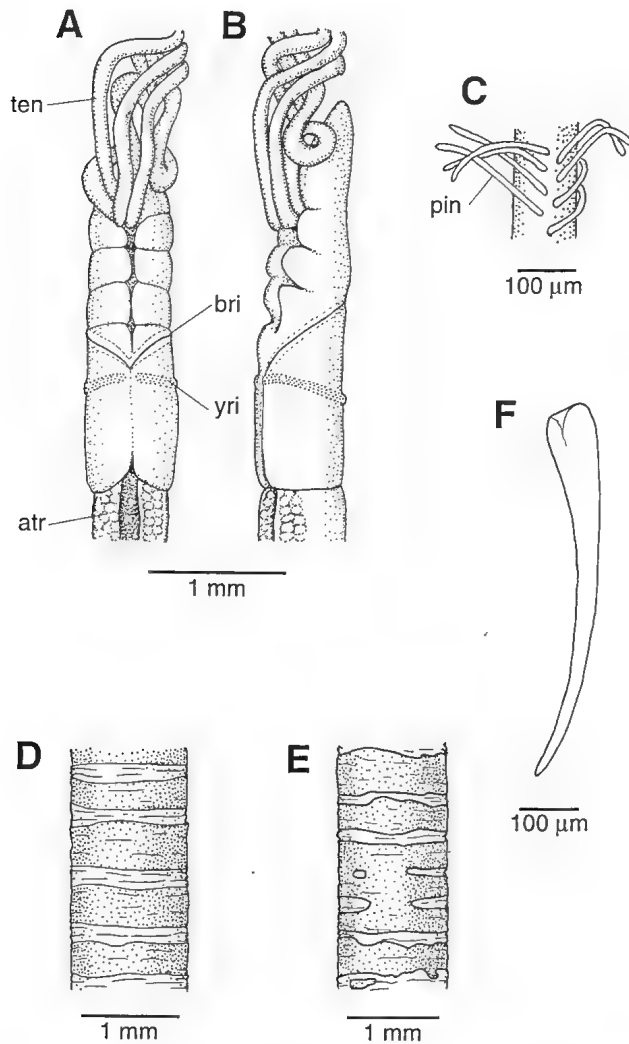


Figure 3.14 Family Oligobranchiidae. *Oligobranchia kernohanae*, from New Zealand. **A**, **B**, anterior end of animal: **A**, dorsal view; **B**, lateral view. **C**, part of tentacle showing pinnules. **D**, **E**, brown ringed tube showing regular (**D**) and irregular (**E**) rings. **F**, spermatophore. **atr**, anterior region of trunk; **bri**, bridle; **pin**, pinnule; **ten**, tentacle; **yri**, yellow ring. (Adapted from Batham 1973)

[E.C. Southward]

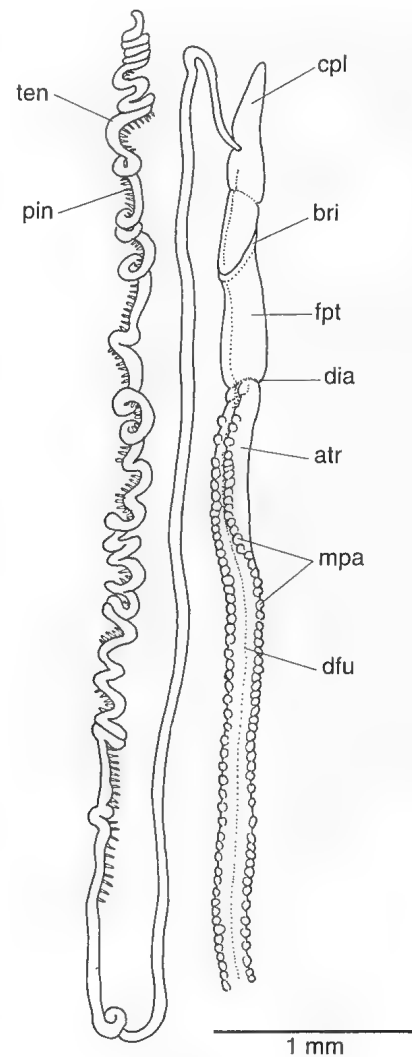


Figure 3.15 Family Siboglinidae. *Siboglinum caulleryi*, from the North Pacific, showing the long tentacle (partly pinnulated), short forepart and anterior part of trunk with many metameric papillae. **atr**, anterior region of trunk; **bri**, bridle; **cpl**, cephalic lobe; **dia**, diaphragm; **dfu**, dorsal furrow; **fpt**, forepart; **mpa**, metameric papillae; **pin**, pinnule; **ten**, tentacle. (After Ivanov 1963)

[E.C. Southward]

Family Oligobranchiidae

Most oligobranchiids are distinguished by having two longitudinal ridges on the anterior part of the trunk, containing multiple rows of pyriform glands (Fig. 3.14A, B); species of *Birsteinia* have two rows of large papillae with multiple glands. The tubes are unsegmented, colourless, white, brown or black, and are usually ringed. The largest tubes are about 1 mm in diameter. Tentacle number varies from one (*Unibrachium* species), or two (*Nereilinum* and *Crassibrachia* species), to three to 18 tentacles (*Oligobranchia* and *Birsteinia* species); they usually have pinnules (Fig. 3.14C). The base of the tentacular crown is horseshoe-shaped. Orange, brown or red markings occur frequently on the forepart and tentacles of *Oligobranchia* and *Nereilinum* species. The spermatophores are spindle-shaped (Figs 3.9D, 3.14F), sometimes slightly flattened close to the base of the filament, where small wing-like projections may be present

(Fig. 3.12D). Developing eggs may be found in the tubes of females (see Southward, A.J. & Southward 1963; Gureeva 1988; Ivanov 1988).

The family Oligobranchiidae was established by Ivanov (1957) and revised by Ivanov (1963) and E.C. Southward (1978a). Genera (and number of species) included are *Oligobranchia* (10), *Nereilinum* (2), *Unibrachium* (2), *Birsteinia* (1), and *Crassibrachia* (2). The family is widely distributed north of the equator, mainly on continental slopes in the Atlantic and Pacific. *Nereilinum murmanicum* is found in waters as shallow as 170 m in the Arctic Ocean near Murmansk (Ivanov 1961) and *C. sandersi* lives at 2000–5000 m in the western Atlantic (Southward, E.C. 1968). In the Southern Hemisphere, *O. kernohanae* (Fig. 3.14) has been found at depths of 420–750 m in four continental slope canyons off Otago, New Zealand, and near the west coast of North Island at 230 m (Batham 1973). A possible new species of *Oligobranchia* is among undescribed Australian material.

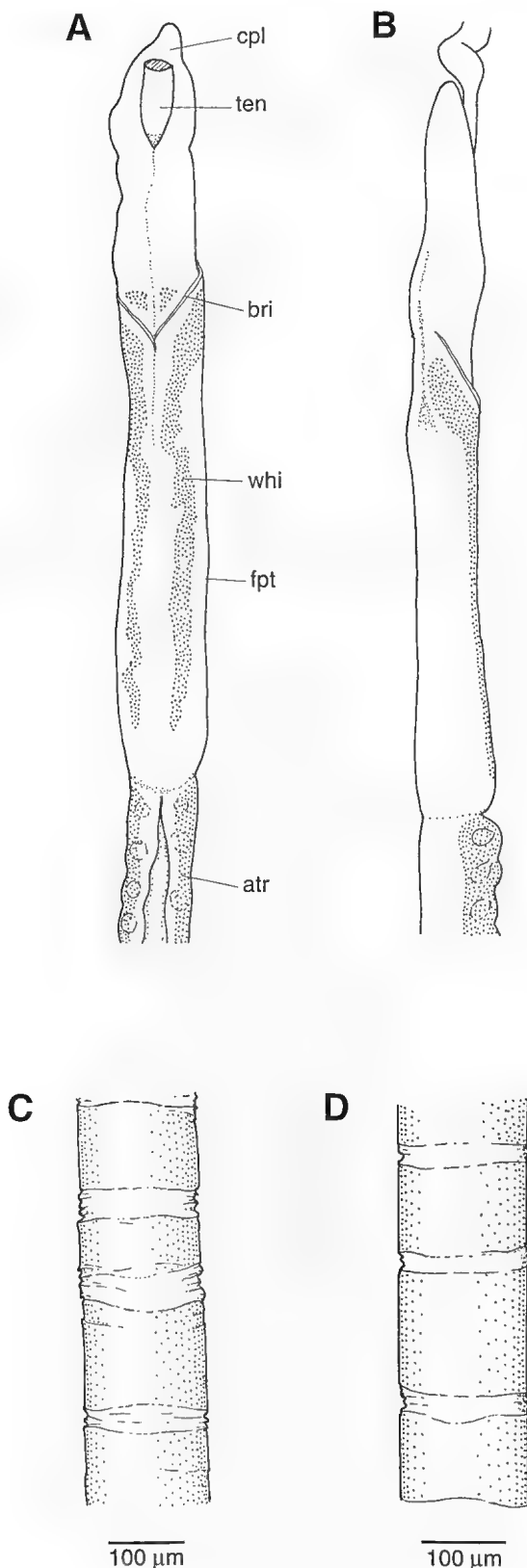


Figure 3.16 Australian Siboglinidae. A *Siboglinum* species from the Coral Sea, probably new. **A, B**, forepart of animal; patches and ribbons of whitish cells, indicated by stipple, are characteristic of 'ribbon-bearing' species, such as *Siboglinum taeniophorum*: **A**, dorsal view, most of the tentacle has been removed; **B**, lateral view. **C, D**, sections of tube: **C**, wrinkled part of tube; **D**, smooth part of tube. **atr**, anterior region of trunk; **bri**, bridle; **cpl**, cephalic lobe; **fpt**, forepart; **ten**, tentacle; **whi**, patches of white cells.

[E.C. Southward]

Family Siboglinidae

Members of this family are distinguished from oligobrachiids by having two rows of papillae on the anterior trunk region (Fig. 3.15) each containing single glands and usually without cuticular plaques. A few of the anterior papillae may merge into short ridges. The tubes of some are unsegmented, with a flexible anterior end, whereas others have a stiffer, segmented, anterior region. Rings are often present (Fig. 3.16C, D) and may be reddish brown, yellow, grey or colourless. The largest tubes are about 0.5 mm in diameter. The cephalic lobe is distinct and bears one (*Siboglinum*) or a pair of tentacles (*Siboglinoides*); pinnules may be present in some species (Fig. 3.15). Spermatophores are spindle-shaped (Fig. 3.9 E, G). Large eggs develop in the tube of the female in some species of *Siboglinum* (see Caullery 1944; Ivanov 1957; Bakke 1976). Others have smaller eggs which may develop pelagically.

The family Siboglinidae was established by Caullery (1914) who described *Siboglinum* in more detail much later (Caullery 1944), but he was still unable to attribute the animals to any known phylum. Ivanov (1951) placed Siboglinidae among the Pogonophora, and described many new species (Ivanov 1957, 1963). The two genera, *Siboglinum* and *Siboglinoides*, include 67 and 3 species, respectively. The genus *Siboglinum* has a wide bathymetric range, from about 25 m in Norway and the Gulf of Mexico to 8000 m in the Kuril-Kamchatka Trench. It is known from all oceans. Several new species of *Siboglinum* are among undescribed pogonophores from Australian waters (for example, see Fig. 3.16). Species of *Siboglinoides* are known from the Indian and Atlantic Oceans and an apparently new species is present in undescribed material from Australian waters.

Order THECANEPHRIA

Members of this order have long excretory ducts associated with the dorsal wall of the median ventral blood vessel (only detectable by sectioning). The tube may be segmented and/or ringed, the anterior end flexible or stiff, sometimes with a hard anterior funnel, and its wall colourless, brown or black. Two to over 200 tentacles are present, sometimes joined together in parallel; pinnules are present on the tentacles. The anterior trunk bears two rows of papillae, each containing several pyriform glands; one or more cuticular plaques is present on each papilla. The postannular part of the trunk has dorsal transverse rows of papillae at intervals, with little or no glandular epidermis on the ventral side. The spermatophores are leaf-shaped. Members of the order are sediment dwellers. The group occurs worldwide and includes 11 genera and 41 species, in three families: Polybrachiidae, Lamellisabellidae and Spirobrachiidae.

Family Polybrachiidae

Polybrachiids usually have segmented tubes, at least in the anterior part, with segments often overlapping one another, forming collars (Figs 3.2A, 3.17B); tubes of young animals may be entirely unsegmented. The small tubes of *Diplobranchia* species (Fig. 3.2C, D) resemble those of the segmented type of certain *Siboglinum* species. Larger brown-ringed tubes are found in species of *Heptabrachia* and *Polybrachia*; the tubes of *P. canadensis* are shown in Figure 3.17. *Galathealinum* species have uniformly brown tubes and those of *Zenkevitchiana* species are translucent white. The largest tubes are greater than 2 mm in diameter. The number of tentacles ranges from two to four in

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Diplobranchia species to 100 to 260 in *Galathealinum* species; the tentacles are not joined. The base of the tentacular crown is horseshoe-shaped or circular. The anterior part of the trunk has two rows of metamerically arranged papillae, each topped with small cuticular plaques; the latter are absent in *Zenkevitchiana* species. The spermatophores are flat and leaf-shaped (Fig. 3.9C, F). Eggs are small and probably develop pelagically. The development of settled juveniles has been studied in large samples of *P. canadensis*, where the smallest juveniles (less than 0.1 mm tube diameter) have only one tentacle and resemble *Siboglinum* species; the number of tentacles increases with increasing tube diameter, to the adult condition of 0.6 mm tube diameter and 30 to 40 tentacles (Southward, E.C. 1969).

The family was named and later revised by Ivanov (1952, 1963). Eight genera (and their species numbers) are included: *Polybrachia* (7), *Heptabrachia* (6), *Cyclobrachia* (1), *Diplobrachia* (8), *Zenkevitchiana* (1), *Galathealinum* (4), *Choanophorus* (1) and *Krampolinum* (1). Members of the family have been found in all oceans except the Southern Ocean (Antarctic). Their depth range is extensive, from 36 m in the Arctic (*G. arcticum*) to more than 9000 m in the Japan and Kuril Trenches (*H. subtilis* and *Z. longissima*). *Galathealinum brachiosum* has been found at cold seeps off Oregon. Material from Australia includes an undescribed species of *Diplobrachia* and possibly a *Polybrachia* species.

Family Lamellisabellidae

The Lamellisabellidae are characterised by the cylindrical arrangement of the tentacles. The tentacles number from 10 to 30, with their bases arranged in a circle and joined side by side; the pinnules point inwards. Cuticular thickenings may be present on the outer surfaces of the tentacles. The tubes are stiff and straight, and are more strongly tapered than in members of other families; they are sometimes segmented anteriorly, and are light or dark brown in colour, but not ringed. The anterior diameter of the tube ranges from 0.3–2 mm. The cephalic lobe is usually flattened, and its forepart bears well-defined bridle ridges, with dark keels. The anterior part of the trunk has two rows of metamerically arranged papillae, each topped by a strong cuticular plaque; the plaques have dark, horseshoe-shaped (Fig. 3.4D) or kidney-shaped anterior thickenings and are placed on small cushions of epidermis. The spermatophores are flat and leaf-shaped (Fig. 3.9A).

The family was named by Uschakow (1933) as a subfamily of Sabellidae (Polychaeta) to include a new genus and species, *Lamellisabella zachsi*, found in the Sea of Okhotsk. Johansson's (1937) study of the same material led him to establish a new class, the Pogonophora, separate from Annelida. Ivanov (1952) described *Lamellisabella zachsi* in more detail in a new treatment of Pogonophora. The family name has been retained, and another genus, *Siphonobrachia*, was added by Nielsen (1965). Plaques are kidney-shaped in both species of *Siphonobrachia*. Those in the seven species of *Lamellisabella* are horseshoe-shaped (Ivanov 1963; Southward, E.C. 1978b). The family occurs on continental slopes in the Pacific, Indian and Atlantic Oceans; the shallowest species, *Siphonobrachia ilyophora* has been collected at 200 m off Miami (Nielsen 1965), and the deepest, *Lamellisabella johannsoni*, at 6000 m in the Japan Trench (Ivanov 1963).

The nearest collections of lamellisabellids to Australia are those of *Lamellisabella pallida* near the Molucca Islands, and *Siphonobrachia lauensis* at a hydrothermal site in the Lau Back-arc Basin, near Fiji (Southward, E.C. 1975c, 1991). It is quite likely that lamellisabellids will be found on the Australian continental slope.

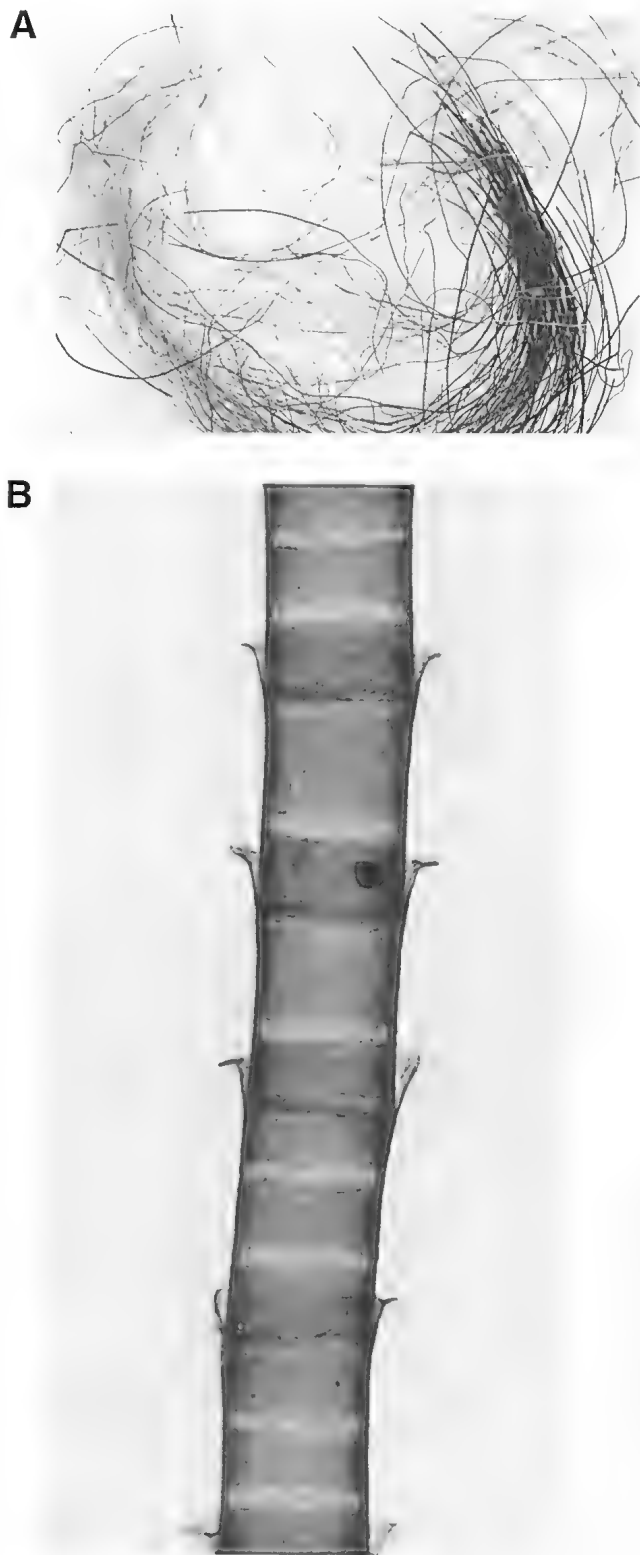


Figure 3.17 Family Polybrachiidae. Tubes of *Polybrachia canadensis*. **A**, mass of tubes. **B**, section of a tube showing the collars formed by the overlapping segments; tube diameter is ca 0.5 mm. These specimens were collected from muddy sediments on the continental slope from a depth of 1830 m near Queen Charlotte Islands in the north-east Pacific. [A.J. Southward]

Family Spirobrachiidae

Members of the family Spirobrachiidae are characterised by the spiral arrangement of the numerous tentacles which are fused into a tentacular plate, the bases borne on a spiral lophophore; the pinnules all point into the space enclosed by the spiral. The tubes are brown or black, without rings, and up to 3 mm in diameter; they may have an anterior funnel and slight segmentation. The cephalic lobe is flattened; the forepart has well-defined bridle ridges with dark keels. The anterior part of the trunk has two rows of metamerically arranged papillae, on which are small cushions carrying cuticular plaques with hoop-shaped thickenings. The spermatophores are leaf-shaped (Fig. 3.9B).

The family was established by Ivanov (1952) and comprises three species of one genus, *Spirobrachia*. *Spirobrachia grandis* is found in the deep part of the Bering Sea (3260 m), *S. beklemishevi* in the Kuril Trench (9000 m) in the North Pacific, and *S. leospira* in the South Sandwich Trench (8000 m), South Atlantic (Gureeva 1975). Occurrence of members of this deep-water family in the Australian region seems unlikely, but not impossible.

Subclass MONILIFERA

Members of this subclass have small, non-ringed, brown or yellow tubes; these are often serpentine or curled, and have walls of irregular thickness (Fig. 3.18D). It is difficult to extract more than short sections of the animal from the tube at any one time, and thus it is best, at first, to study the animal through the semi-transparent wall. The two tentacles lack pinnules, and the cephalic lobe is extremely small (Fig. 3.18A, B). The forepart has rows or groups of cuticular plaques instead of continuous bridle keels. As in Perviata, the transition from forepart to trunk is smooth. There are two lines of pyriform glands, under slightly raised ridges, along the sides of the anterior trunk; plaques are absent. The remaining section of the long trunk is not divided into regions; a few scattered papillae with plaques may be present. Chaetae are restricted to the extreme posterior end of the trunk, and the opisthosoma (Fig. 3.18C) which is divided into several short segments, each with lines of small chaetae. Usually the spermatozoa are free in the male ducts; flat spermatophores were reported in *Sclerolinum sibogae* (Southward, E.C. 1961), but this may have been a mistaken observation.

Ivanov (1991) transferred the family Sclerolinidae to a new subclass, the Monilifera, a decision reinforced by the studies of Ivanov & Selivanova (1993) on the wood-living species *Sclerolinum javanicum* from the Java Trench with reference to pogonophoran classification. The class comprises only the one family, Sclerolinidae, and six species in the genus *Sclerolinum*.

Family Sclerolinidae

The family, Sclerolinidae, was established by Webb (1964c) to include *Sclerolinum sibogae*, originally placed in the family Polybrachiidae (Southward, E.C. 1961), and a new species from Norway, *S. brattstromi*. The availability of living material from Norwegian fjords allowed Webb to make new observations on the anatomy. *Sclerolinum brattstromi* lives in rotting wood and also has been found in discarded rope, cardboard, paper and clothing at the bottom of fjords near Bergen, exploiting the sulphides produced by the decay of

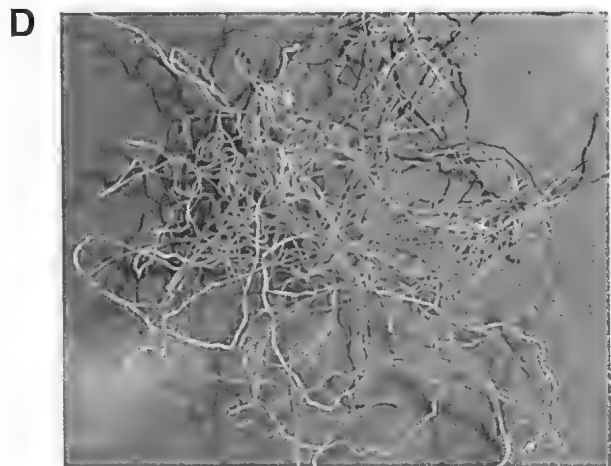
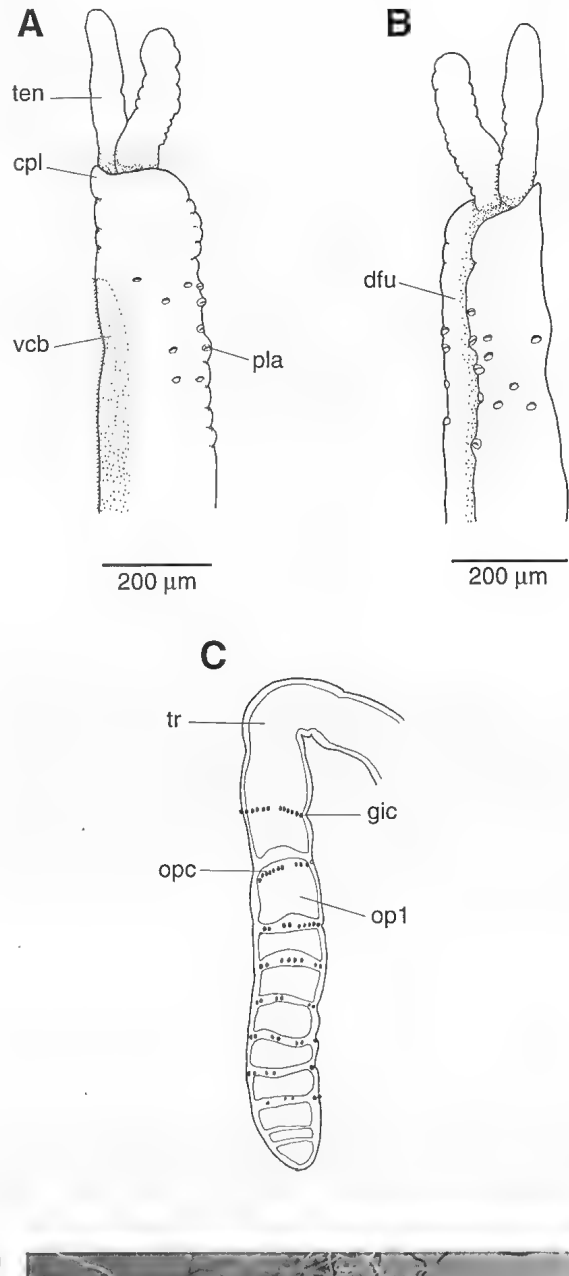


Figure 3.18 Family Sclerolinidae. **A–C**, *Sclerolinum major*, from the Caribbean. **A**, **B**, anterior end of animal: **A**, ventro-lateral view; **B**, dorso-lateral view. **C**, opisthosoma. **D**, tubes of *Sclerolinum* species collected from Bransfield Strait, Antarctica. **cpl**, cephalic lobe; **dfu**, dorsal furrow; **gic**, girdle chaetae; **opc**, opisthosomal chaetae; **op1**, first opisthosomal segment; **pla**, plaque; **ten**, tentacle; **tr**, trunk; **vcb**, ventral ciliated band. (Adapted from Southward 1972) [A–C, E.C. Southward; D, A.J. Southward]

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organic matter. Of the three species found in Colombian Basin, southern Caribbean (Southward, E.C. 1972), two live in decaying wood and in mats of plant debris, and one, apparently free-living, in mud, but where plant debris was present. It is not known if *S. sibogae* is associated with submerged wood, but the specimens examined (see Southward, E.C. 1961) came from four deep basins (depths 462–1914 m) among the Indonesian islands, where plant debris might be expected to accumulate. Ivanov & Selivanova (1993) described a new species of *Sclerolinum* (*S. javanicum*), a wood-inhabiting species, from the Java Trench. A record of *Sclerolinum sibogae*, in the Arafura Sea, about 600 km north of Arnhem Land, is the nearest known locality for this family to Australia. The external features of sclerolinids are illustrated in Figure 3.18. Any woody debris collected from the deep sea around Australia should be carefully examined for the fine tubes of sclerolinids.

Subclass VESTIMENTIFERA

Members of the Vestimentifera have tubes that are attached to hard substrata. The tubes may be segmented, with overlapping collars and have a terminal funnel (Fig. 3.3). There is no cephalic lobe. Many tentacles (branchial filaments) are present, grouped in paired lamellae, and make-up the branchial plume; pinnules are present on most filaments. An obturaculum is present; it may seal the tube when the animal is retracted. Its base is among the bases of the branchial filaments, which all arise from the anterior end of the vestimental region (Fig. 3.6A, B).

The short vestimental region has lateral flaps which curl over the dorsal surface. The long trunk is not divided into regions and its surface is scattered with small papillae. There are no girdles of chaetae on the trunk. The short opisthosoma is divided into many short segments, each with numerous chaetae (Fig. 3.6C).

The subclass is divided into two orders: Basibranchia and Axonobranchia. Members of the Axonobranchia are characterised by having branchial lamellae emerging at right angles to the obturaculum, supplied by axial blood vessels running anteriorly along the sides of the obturaculum; the single family, Riftiidae, includes the monotypic genus *Riftia* from the Eastern Pacific. The order is unlikely to occur in Australian waters, and thus is not treated here. The Vestimentifera may also be referred to as the Obturata.

Order BASIBRANCHIA

The order Basibranchia is characterised by having basally organised branchial lamellae, with a blood supply arising from basal blood vessels. It comprises 12 species in six families: Lamellibrachiidae, Escarpiidae, Tevniidae, Ridgeiidae, Alaysiidae and Arcovestiidae (see Table 3.1 for genera and number of species). None is known from Australian seas at present. Only the family Lamellibrachiidae is discussed here as it is the most likely of all the basibranch families to occur in Australian waters.

Family Lamellibrachiidae

Lamellibrachiids are characterised by the pale, smooth outer lamellae of special filaments which protect the branchial filaments; the special filaments lack pinnules and are stouter than the inner pinnulate filaments. The tubes are free-standing, attached posteriorly to rock, or in crevices covered by sediment. The lower part of the tube may be serpentine, often tangled with others in a cluster. The tube wall is stiff and difficult to cut. The anterior end is open, sometimes surrounded by a small funnel (Fig. 3.3C), and the remains of earlier funnels may be seen as slight collars on the tube below. The tubes are whitish or greyish. The posterior end is narrow, about 1 mm diameter, and the width increases to 5–10 mm at the anterior end.

The animal has a white funnel-shaped obturaculum, with a smooth distal surface, surrounded by the two types of branchial lamellae. A low collar covers the lamellar bases. The single excretory pore is detectable in sections only). The lateral vestimental folds remain separate posteriorly. The trunk becomes extremely attenuate posteriorly, and the narrow opisthosoma lies at the extreme hind end of the tube. One genus, *Lamellibrachia*, is known, with five species.

The family was established by Webb (1969) when he described *Lamellibrachia barhami*, a large tube worm collected at 1125 m depth in the North Pacific off California, by a United States Navy submersible. A cluster of tubes was resting on sediment close to rocks, to which the tubes may have been attached. Webb placed the Lamellibrachiidae in a new order, Vestimentifera, in the phylum Pogonophora. Later he described the internal anatomy of *L. barhami* and figured another cluster of its tubes that had been dredged farther north, off Oregon (Webb 1977).

Van der Land & Nørrevang (1975, 1977) described a new species, *L. luymesii*, trawled from 500 m depth off Guyana, in the western Atlantic Ocean. They studied the anatomy of the specimen in detail and decided to refer Vestimentifera to the phylum Annelida. Jones (1985b) later reviewed *L. barhami* and *L. luymesii*, described several new genera and families, classified these into superfamilies and orders, and proposed the separation of Vestimentifera from Pogonophora at phylum level. The ranking of the groups appears to be lower than Jones believed (Southward, E.C. 1988, 1991). The four known species of *Lamellibrachia* show differences in tube form and size, in the shape and length of the obturaculum, the number of sheath lamellae and the proportions of parts of the body (Southward, E.C. 1991).

Lamellibrachiids have been found most frequently on continental slopes, often in association with cold seeps where sulphidic fluids ooze out of sedimentary rocks; locations include seeps off Oregon (Suess *et al.* 1985), in the Gulf of Mexico (MacDonald *et al.* 1989) and at numerous sites around Japan (Kojima, Hashimoto & Ohta 1995). *Lamellibrachia barhami* occurs at a sedimented hydrothermal site in the north-east Pacific (Williams *et al.* 1993; Southward, E.C. *et al.* 1996) and *L. columna* occurs among rocks at a hydrothermal site in the Lau Basin, near Fiji (Southward, E.C. 1991). Both sites appear to offer cool conditions. The family is widespread in the Pacific and Atlantic Oceans and, of all vestimentiferans, its members are the most likely to be found near Australia.

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4. PHYLUM ECHIURA

Stanley J. Edmonds†

DEFINITION AND GENERAL DESCRIPTION

The phylum Echiura comprises a group of non-segmented, coelomate, bilaterally symmetrical, worm-like marine invertebrates. Echiurans have a sausage-shaped muscular trunk and an anteriorly placed extensible proboscis (Fig. 4.1; Pls 11.1–11.6). They are commonly known as spoon worms, a name derived from the function of the proboscis which, in most species, is used to collect sediment from around the burrow.

The saccular trunk is usually light to dark green in colour, or sometimes, reddish brown, and usually bears numerous flat or swollen glandular and sensory papillae. A pair of golden-brown chaetae is usually present on the ventral surface of the trunk, just posterior to the mouth (Fig. 4.2). In a few species a number of chaetae may form a complex; in others, chaetae are absent. One or two almost complete rings of larger anal chaetae surround the posterior region of the trunk in *Urechis* and *Echiurus*, respectively. The proboscis is usually flattened and ribbon-like, but may be fleshy and spatulate. It is highly extensible and contractile, but cannot be withdrawn into the body cavity like the introvert of sipunculans. The distal end of the proboscis is usually truncate or bifid (Fig. 4.1C). In some deep-sea species the proboscis is modified considerably and assists in the collection of food.

The mouth is situated antero-ventrally at the base of the proboscis and the anus is at the posterior extremity of the trunk. Echiurans are detritus-feeders, except for species of *Urechis* which trap very fine particles by secreting a mucous net. A long, convoluted alimentary system lies in the spacious coelom. The very long intestine is attached to the coelomic wall by threads and mesenteries. A special feature of the alimentary system is the collateral intestine or siphon (Fig. 4.2), a narrow tube, that runs parallel to all or part of the intestine.

Nephridia are arranged in pairs (except in one species) and act as gonoducts. Typically, there are one to 10 pairs, but in two genera they are numerous (for example, hundreds in *Ikeda*) and in one unpaired. The nephridia lie in the coelom and are attached to the ventral wall of the trunk. A pair of anal vesicles, which empty into the cloacal region, are thought to be the main organs of excretion. These simple or branched organs open to the coelom through numerous ciliated funnels.

The blood vascular system is closed in all families, except Urechidae, in which it is open, the body cavity being filled with blood. The nucleated blood cells contain haemoglobin. Respiratory gases are exchanged at the surface of the proboscis and trunk, but in *Urechis* anal respiration occurs. The nerve cord is ventral, unsegmented and lacks cerebral ganglia.

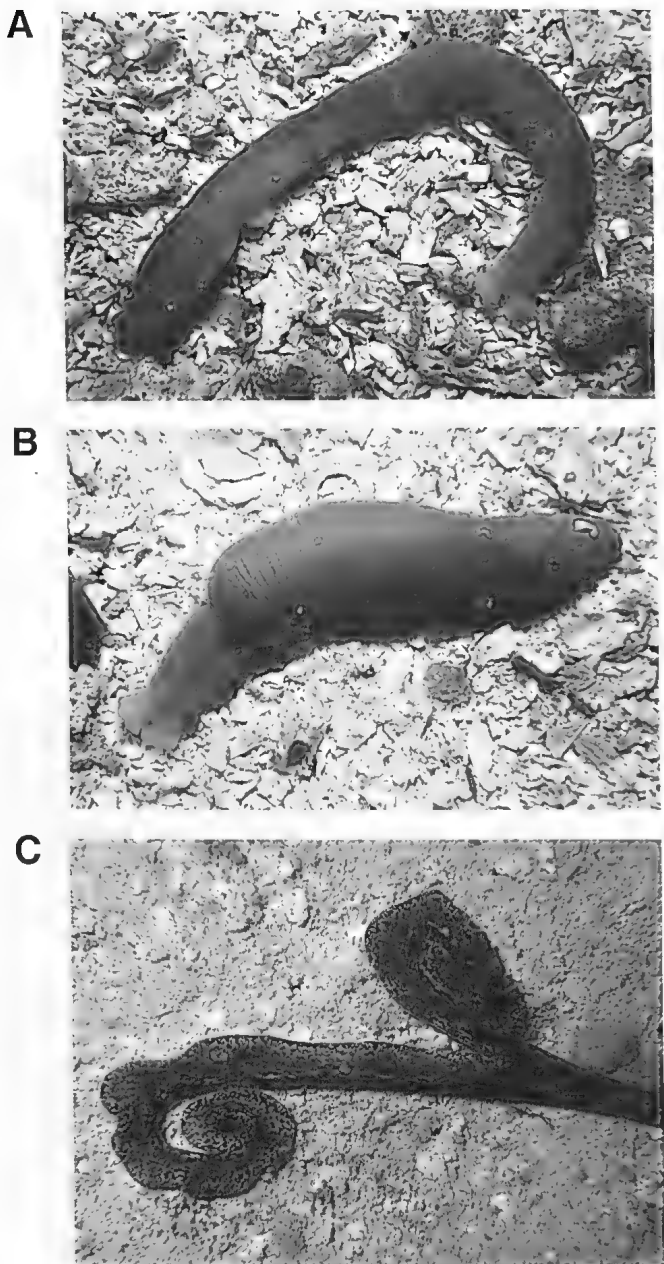


Figure 4.1 Echiurans live in burrows sheltered in a range of habitats from coral and limestone reefs to cracks in wooden jetty piles; usually only the proboscis is visible. **A, B**, an unidentified echiuran, removed from its burrow, in elongated (**A**) and contracted (**B**) forms. The animal was collected from the Solitary Islands, northern New South Wales. **C**, the proboscis of a bonelliid species, shown during feeding over sand.

[A, B, K. Gowlett-Holmes; C, B. Wood]

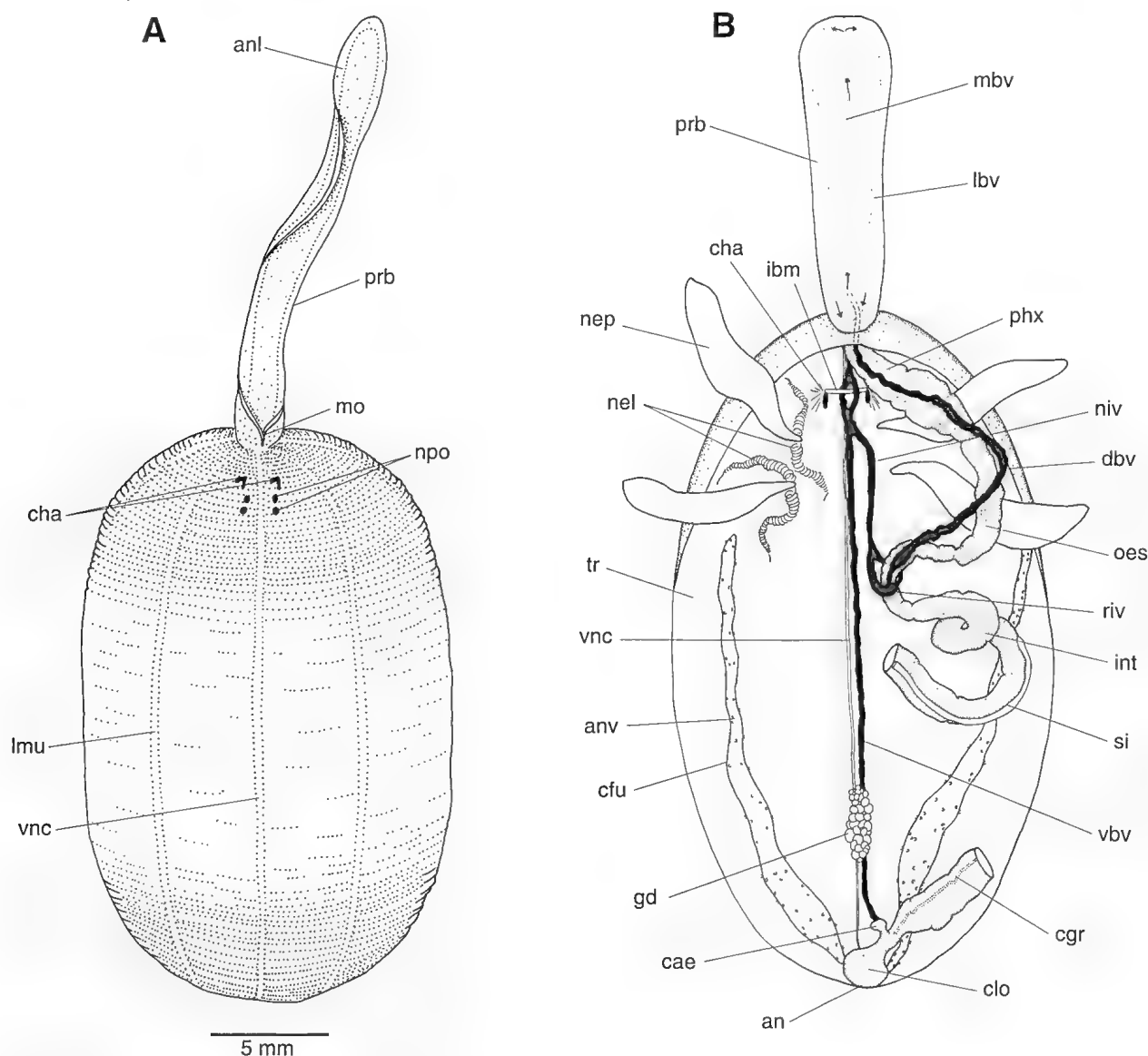


Figure 4.2 General morphology of an echiuran. **A**, external morphology of *Listriolobus pelodes*, ventral view. **B**, generalised internal morphology of an echiuran, dorsal view. Most of the coiled intestine and the nephrostomal lips on one side have been omitted. **an**, anus; **anl**, anterior nerve loop; **anv**, anal vesicle; **cae**, caecum; **cfu**, ciliated funnel; **cgr**, ciliated groove; **cha**, chaeta; **clo**, cloaca; **dbv**, dorsal blood vessel; **gd**, gonad; **ibm**, interbasal muscle; **int**, intestine; **lbv**, lateral blood vessel; **lmu**, longitudinal muscle band; **mbv**, median blood vessel; **mo**, mouth; **nel**, nephrostomal lips; **nep**, nephridium (gonoduct); **niv**, neurointestinal vessel; **npo**, nephridiopores (four are present); **oes**, oesophagus; **phx**, pharynx; **prb**, proboscis; **riv**, ring vessel; **si**, siphon; **tr**, trunk; **vbv**, ventral blood vessel; **vnc**, nerve cord. (A, after Pilger 1993) [A, I. Hallam; B, I. Grant]

The sexes are separate. Mature eggs and sperm pass out through the nephridia and fertilisation is external, except in the Bonelliidae. Cleavage is spiral and the larva is a trochophore. Males and females are indistinguishable externally except in the Bonelliidae. Sexual dimorphism is very marked in bonelliids; the male is minute and usually lives in the female's nephridia. The eggs of bonelliids are fertilised in the nephridia.

Echiurans make burrows in mud and sand, live under rocks, in the shells of molluscs and tests of sand dollars, and in galleries made by other animals in rock and coral. There is no evidence that they are able to bore into rocks as do sipunculans. They are found in tropical, temperate and polar seas and their bathymetric range is wide. Bonelliids have also been collected at abyssal and hadal depths of the oceans (Zenkevitch 1958, 1966).

Fossils with a number of echiuran-like characters are known from the Late Cambrian and the Mid-Pennsylvanian (Jones & Thompson 1977; Glaessner 1979).

HISTORY OF DISCOVERY

The first echiurans to be described were *Thalassema thalasseum* (as *Lumbricus thalasseum*) and *Echiurus echiurus* (as *Lumbricus echiurus*) by P.S. Pallas in 1774 and 1776, respectively, and Rolando described the first bonelliid, *Bonellia viridis*, in 1820. All three were European species.

Early Australian records include those of Haswell (1855), who reported several specimens of *Bonellia* species from the shores of Neutral Bay, Port Jackson (= Sydney) and Saville-Kent (1889) who collected a specimen of *Bonellia* from Cambridge Gulf, Northern Territory. Augener (1903) reported *Listriolobus sorbillans* from Sydney, based on a specimen collected by Dr. Schutte in 1876. Hedley (1906) noticed 'an abundance' of a green bonelliid in a lagoon at Mast Head Island (Capricorn Group), Queensland, and Dakin (1916) collected *Bonellia* species in Western Australia, at the Houtman Abrolhos Islands and at Freshwater Bay in the Swan Estuary.

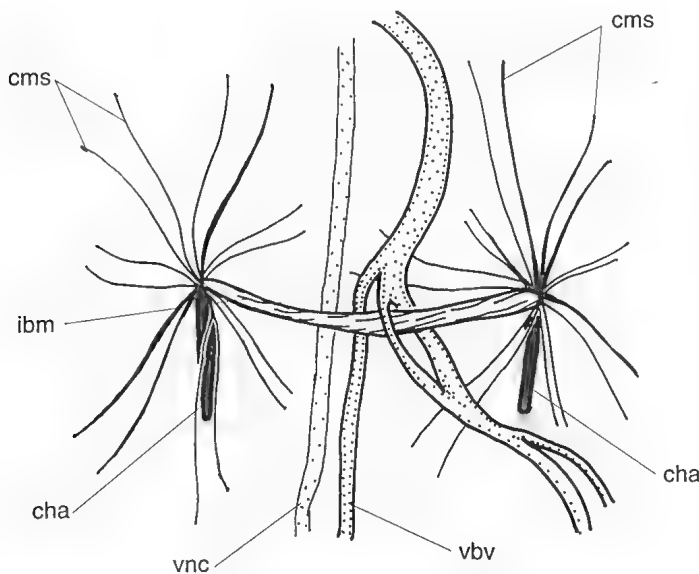


Figure 4.3 Arrangement of chaetae and muscles. The muscle strands originate, internally, on the body wall and insert on the inner end of the chaetal shaft. The interbasal muscle spans the two chaetae, also inserting on the inner end of the chaetae. **cha**, chaeta; **cms**, chaetal muscles strands; **ibm**, interbasal muscle; **vbv**, ventral blood vessel; **vnc**, ventral nerve cord. [I. Grant]

Australians Johnston & Tiegs described *Pseudobonellia biuterina* from North West Island, Capricorn Group, Queensland (1919) and *Metabonellia haswelli* from Sydney Harbour (1920). Fischer (1919, 1921) described *Archibonellia michaelsoni* and *A. mjobergi*, based on single specimens from Western Australia. Monro (1931) identified some of the echiurans collected during the Great Barrier Reef Expedition. More recent work, all taxonomic, has been done by Edmonds (1960, 1963, 1966, 1982, 1987), Nielsen (1963) and Dartnall (1970, 1976). Echiurans are difficult to find and collect and they are not well known in Australia, except for the following species: *Metabonellia haswelli*, *Pseudobonellia biuterina*, *Anelassorhynchus porcellus adalaidensis* and *Ochetostoma australiense*. In the Northern Hemisphere, much experimental research has been done with *Urechis caupo*, *Bonellia viridis* and *Echiurus echiurus*, but so far none has been done in Australia.

The best general account of the phylum is that of Dawydoff (1959). Workers in the group may find useful Stephen & Edmonds (1972), the *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura* (Rice & Todorovic 1975, 1976) and Pilger (1993). The most recent publication on Australian echiurans is that of Edmonds (1987).

MORPHOLOGY AND PHYSIOLOGY

External Characters and Body Wall

The trunk wall may be thick or thin, smooth, or roughened by skin bodies and papillae. It comprises a cuticle, epidermis, dermis or cutis, muscle layers and a coelomic epithelium. The cuticle is non-cellular and covers the whole surface of the animal except the ciliated ventral surface of the proboscis and those small areas where there are sensory cells (Jaccarini & Schembri 1977a). The epidermis is made up of columnar cells, several different kinds of gland cells and sensory cells (Mathew 1976). The dermis is connective tissue containing elastic fibres and may be rich in pigment cells and nerve cells, the latter sending out processes to the sensory cells of the epidermis.

The muscular layers include an outermost layer of circular muscle which overlies a layer of longitudinal muscle and an innermost layer of oblique muscle. The three layers are

usually continuous but in *Ochetostoma*, *Listriolobus*, and *Ikeda* the longitudinal muscles are thickened into bands; in *Ochetostoma*, the oblique musculature between the longitudinal bands forms fascicles (Fisher 1946; Mathew, 1976). A thin peritoneal layer lines the coelom.

Two ventral chaetae are present in most echiurans (Figs 4.2, 4.3). They lie on each side of the nerve cord near the nephridiopores and arise from cells at the base of a chaetal follicle. The latter is a tubular invagination of the epidermis.

In two bonelliid genera, the chaetae are numerous and lie in a genital groove. Chaetae, however, are absent in some Bonelliidae, especially those that live at great depths. In *Urechis*, an almost complete ring of stronger chaetae surrounds the anal region; in *Echiurus* there are two. The action of the ventral and anal chaetae assists an echiuran in burrowing and locomotion.

Proboscis. The proboscis is a muscular organ that extends from the antero-dorsal surface of the trunk near the mouth; it is a preoral lobe (Fig. 4.2). It is capable of great extension, as much as 1.5 m in *Bonellia viridis*, a species with a trunk is 10–30 mm long. Its functions are food-gathering, sensory, respiratory, sometimes locomotory and fossorial. In some species, the proboscis is present only in a reduced form and in others it is easily detached from the trunk while the animal is being collected. It is a fleshy structure, tending to be flat and ribbon-like and is usually either truncate or bifid. The ventral surface is ciliated and serves as a food channel (Fig. 4.4); food particles mixed with mucus are directed along its surface to the mouth by ciliary and muscular action. The dorsal side is not ciliated, except on the leading edge of the lobes of *Bonellia*. When the organ is extended it lies in contact with the substratum from which is derived the term 'spoon worm'. The shape of the proboscis may be considerably modified in some deep-sea species, the mouth being surrounded by massive lips (as in *Prometor*), a funnel-like structure (in *Vitjazema*), and; a collar (in *Choanostomellia*). In *Brunellia* and *Jakobia* the proboscis is oval in cross section for its entire length.

Ventrally and laterally placed series of small cavities, often called the proboscis coelom, are generally present in the proboscis (Fig. 4.4; Menon 1976). The ventral extensions sometimes form anastomosing canals. The proboscis coelom, isolated from the trunk coelom, is lined with a stratified squamous epithelium, although the embryological nature of

4. PHYLUM ECHIURA

the coelom remains unsettled (Pilger 1993). In *Ochetostoma septemyotum*, which bears dendritic projections from the lateral margins of the proboscis, the lateral coelomic channels may undergo extensive branching, suggesting that the function of the channels may then be respiratory. Jaccarini & Schembri (1977a) were unable to find any connecting channel between the coeloms of the trunk and proboscis of *Bonellia viridis*.

Bonellin. Many echiurans, especially bonelliids, are coloured pale to dark green by the presence of an integumentary pigment. In the European species *Bonellia viridis*, the pigment is called bonellin and has attracted the attention of biologists for many years because of its role in the determination of sex in the species and its toxic and protective properties.

The structure and composition of bonellin is now well known. It is a chlorin or tetra-pyrrolic molecule unrelated to chlorophyll (Pelter, Ballantine, Ferrito, Jaccarini, Psaila & Schembri 1976; Pelter, Abela-Medici, Ballantine, Ferrito, Ford, Jaccarini & Psaila 1978). How it is synthesised by *Bonellia* is not yet known (Agius & Jaccarini 1981). According to Bosch (1977), the pigment is contained in star-shaped cells found in the collagen layer of the proboscis and in pigmented cells located beneath the epidermal layers of the body wall. The latter form pseudopod-like projections containing clusters of pigment granules. The projections may eventually separate from their cell body and, when appropriately stimulated, release their bonellin to the exterior.

Bonellin is known to be poisonous to a number of different kinds of organisms and is thought to act as a defensive weapon. It is highly toxic at concentrations as low as 10^{-6} M and rapidly penetrates living structures (Guidici 1984). As long ago as 1931, Michel reported that some species of crabs do not eat the green tissues of *Bonellia* but will readily accept the non-pigmented muscle of the animal. Guidici's (1984) scanning electron microscope studies showed that microbial and encrusting forms of life were absent from the surface of specimens of *Bonellia viridis* although the organisms were plentiful in the environment. Guidici suggested that the toxic properties of bonellin stopped other organisms establishing themselves on *Bonellia*. Bonellin is known to prevent the embryonic development of echinoderms and ascidians and cause the dissociation of sponges. It lyses human erythrocytes

and stops the movement of flagella (Agius, Jaccarini, Ballantine, Ferrito, Pelter, *et al.* 1979). Its action is photodynamic, that is, it acts only in the presence of light and in proportion to the intensity of the light and its duration. It is thought that in the presence of light the pigment triggers the formation of singlet oxygen which then acts on the biological substratum (Guidici 1984). In certain circumstances the pigment can act to the disadvantage of the animal itself. Guidici (1984) reported that *B. viridis* will not live long in an aquarium unless it is shaded from light. In light, it degenerates and dies.

The role of bonellin in the development of sex in *B. viridis* is discussed in the section on Reproduction and Development

Locomotion and Burrowing

Echiurans are able to move slowly over the surface of certain substrata, burrow in sand and mud, move in the tubes which they construct and swim.

Gislén (1940) found that a specimen of *Echiurus echiurus* resting on sand and mud in an aquarium slowly moved until it found a spot where it was able to burrow. The animal progressed forwards by peristalsis-like movements of its body wall and by using its anal chaetae to anchor the posterior region of its body. During digging operations the proboscis lies dorsally against the body wall pointing backwards and seems to play little part in the action. Gislén reported that specimens without a proboscis are able to burrow just as well as complete ones. Digging is a rather complex operation involving both the ventral chaetae and movements of the animal's muscular diaphragm. *Echiurus* swims by twisting its body into spiral coils. Animals without a proboscis can also swim.

Urechis caupo is able to move over a smooth surface by means of peristaltic waves, '... in much the same manner as an earth worm' (Fisher & MacGinitie 1928). An echiuran moves in its burrow in a similar way. In *Urechis*, the proboscis is used to form a hole in the mud. When the excavation is of sufficient size '... the body is drawn ahead by extending the anterior end for anchorage and then drawing up the remainder of the body. This process is continued until the worm completes a U-shaped tunnel open to the surface at both ends'. The tube is enlarged, if necessary, by the scraping

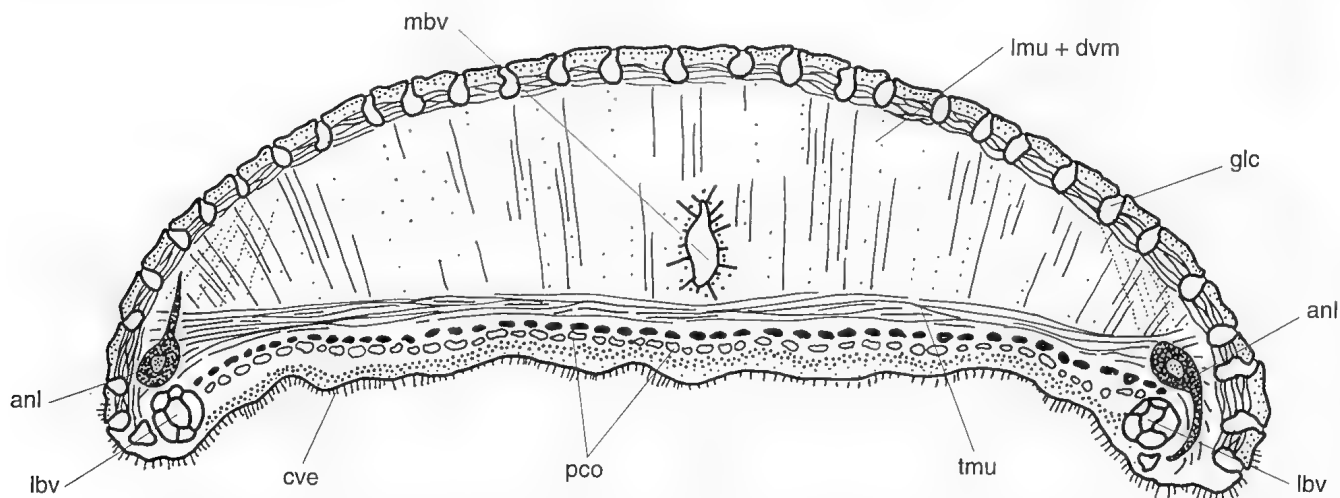


Figure 4.4 Transverse cross-section through the proboscis of *Echiurus* species, dorsal side uppermost. anl, anterior nerve loop; cve, ciliated ventral epithelium; gan, nerve ganglia; glc, gland cells in epidermis; ibm, interbasal muscle; lbv, lateral blood vessel; lmu+dvm, longitudinal muscles and dorso-ventral muscles embedded in a fibrous connective tissue matrix; mbv, median blood vessel; pco, proboscis coelom; tmu, transverse muscles; vbv, ventral blood vessel. (After Baltzer 1931) [I. Grant]

action of the ventral chaetae. Once settled in a permanent home '... its daily activities consist of respiratory movements, obtaining food, cleansing the burrow, and resting' (Fisher 1946).

Bonellia viridis, as found at Malta, does not make its own burrow, but lives in those constructed in rocky substrata, especially by the thalassinoid mud prawn, *Upogebia deltaura* (Schembri & Jaccarini 1978). The burrows, however, are always irrigated by a stream of water, produced by a series of peristaltic waves of its body wall. These animals are also able to move back and forth in the burrow by the wave-like action of the trunk wall.

Chuang (1962a) reported that specimens of *Ochetostoma erythrogrammon* use the distal extremity of the proboscis when they make their burrow and that the trunk plays little or no part in the digging operation.

Early workers thought that a flow of fluid from the coelom of the trunk to that of the proboscis was responsible for the extension of the proboscis of *E. echiurus* (Spengel 1912). Gislén (1940), however, questioned the explanation on the grounds that it did not satisfactorily account for the rapidity of the retraction of the organ. It would take a much longer period of time for the fluid in the proboscis to pass through the tissue joining the proboscis and trunk. Gislén also observed that a proboscis, even when separated from the trunk, was still able to extend.

According to Jaccarini & Schembri (1977a), the proboscis of *Bonellia viridis*, when not extended, lies in a coil in front of the animal (for example, see Fig. 4.5). The successive stages in the extension of a '*Bonellia*' proboscis is shown in Figure 4.5. The forward movement of the organ is produced by the action of numerous, powerful cilia grouped on the dorsal surface of the distal edge of its two lobes, which '... passively drag and uncoil the stem of the proboscis'. No fluid flows between the trunk and proboscis, which is consistent with Bosch's (1979) observation that there is no connection between coeloms of the trunk and proboscis. Jaccarini & Schembri reported that '... the leading edge of the terminal lobes is the sole locomotory organ of the proboscis' and that the mechanism of extension is ciliary and not muscular. They found that the cilia on the leading edge of the lobes are quite different from those on the ventral surface, which are used during food collection. The organ, however, is retracted by the muscular contraction of the longitudinal muscles in the stem. Jaccarini & Schembri also described how *Bonellia* is able to move by using its lobes to fix the animal and then contracting the proboscis stem. They observed in an aquarium that the animal is frequently found out of its burrow and that '... *Bonellia* is far less sedentary than usually thought'.

Digestive System and Digestion

The alimentary canal is a long, much convoluted tube with an anteriorly placed mouth at the base of the proboscis and an anus at the posterior extremity of the trunk. It consists of three general regions: a foregut, the intestine proper of the midgut, and the rectum, cloaca or hindgut.

The foregut, in which the longitudinal musculature lies external to the circular musculature, usually consists of a pharynx, oesophagus, gizzard and crop or stomach, although the distinction between some of the sections is not very clear in some species. The pharynx is often short and bulbous and its walls thick and muscular. The oesophagus also has muscular wells. The gizzard is usually distinguished

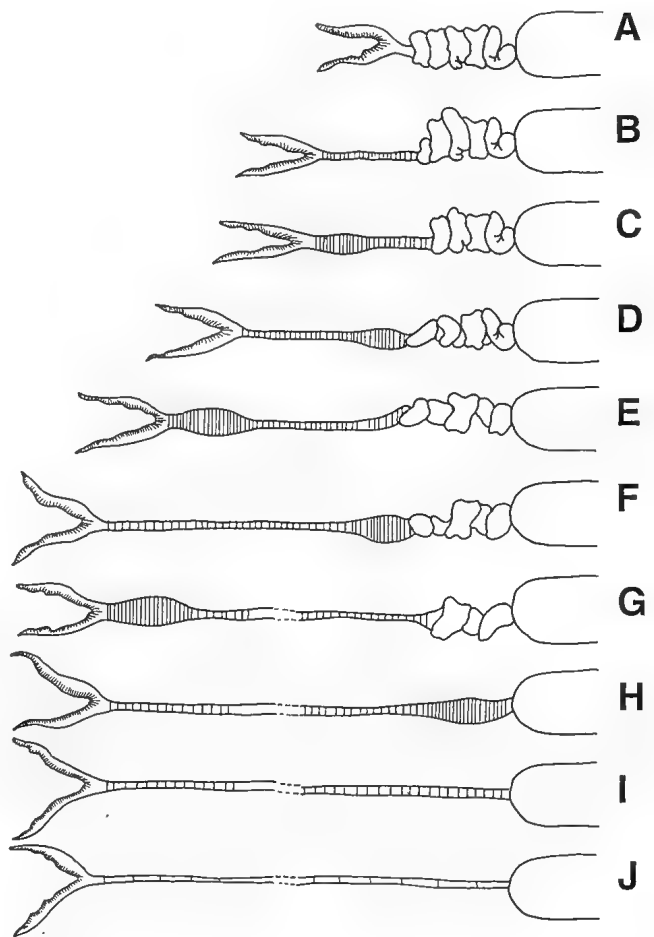


Figure 4.5 Successive stages in the extension of the proboscis of *Bonellia* species. The proboscis can extend up to 1 metre in some species of *Bonellia*. A, the proboscis in its contracted condition; B–I, various stages of extension; J, full extension of proboscis. The arms of the proboscis move forward as a result of the action of powerful cilia lying along the dorsal surface of the leading edge. The stem of the proboscis is moved forward and uncoiled by the action of the cilia and muscular contractions along the uncoiled parts of the stem. Cross-lines on the stem in the diagram indicate areas of contraction and expansion. (After Jaccarini & Schembri 1977a) [I. Grant]

externally by circular striations and the stomach by longitudinal markings, which correspond to the folds of its lining. No masticatory structures are present in the gizzard. The dorsal blood vessel runs along part of most of the dorsal surface of the foregut. The end of the foregut is usually marked by the presence of the ring blood vessel or, in Bonelliidae, the fusion of the dorsal vessel with sinuses in the intestinal wall.

The midgut, in which the circular musculature is external to the longitudinal, is usually long and much contorted. It comprises three sections: pre-siphonal, siphonal and post-siphonal. The canal is usually widest in the mid gut region. The midgut is marked by the appearance of: a ciliated groove or gutter in the ventral wall, and; a conspicuous narrow tube called the 'siphon' or collateral intestine close to the ventral wall of part of the gut and which communicates at both its extremities with the lumen of the gut. A small diverticulum or caecum is sometimes present at the junction of the hind gut or rectum. The siphon is covered with a cutis, its walls contain longitudinal, but no circular musculature, and its posterior extremity often joins the ciliated groove.

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The hind gut is sometimes short and ovoid and is surrounded at its posterior extremity by an anal sphincter. The contents of the anal vesicles are voided into the cloaca and eventually via the anus to the exterior.

Investigations into the physiology of the digestive processes of echiurans are few. Gislén (1940) found that the fluid taken from the mid-gut of fasting specimens of *E. echiurus* was alkaline, that it contained a strong tryptic enzyme that acted on proteins and another enzyme that broke down carbohydrates. The siphon was found to contain a whitish fluid but never any sand grains or food pellets. Its function is not known.

Respiration

Echiurans usually live in a U-shaped tube open at both ends and obtain a supply of oxygen from a current of water that is forced through the tube by a series of peristaltic movements of their body wall. Erythrocytes containing haemoglobin are present in the fluids found in both the circulatory system and in the coelom and an exchange of respiratory gases takes place at the surface of probably both the trunk and proboscis. The circulatory or vascular system of all echiurans, except the Urechidae, is closed and consists of a number of vessels and sinuses. In the trunk are found a comparatively short dorsal vessel, a long central vessel which is associated with the ventral nerve cord for most of the length of the latter and a neurointestinal vessel which connects the dorsal and ventral vessels in the anterior region of the trunk. The posterior extremity of the dorsal vessel is usually joined to the neurointestinal vessel through either a ring vessel or a ring sinus, the exact position of which differs in different species. The ring vessel is probably a 'heart' or propulsive organ and it is commonly placed at the junction of the fore- and midgut. In some Bonelliidae, however, the dorsal and neurointestinal vessels communicate through sinuses in the gut wall when, according to Menon & Dattagupta (1976), the ring sinus is more likely to be a reservoir than a propulsive organ. The position of the ring vessel and sinus in a number of echiurans is shown in Menon & Dattagupta (1976).

Blood flows from the ring vessel into the dorsal vessel and forwards to the median vessel of the proboscis. Blood then moves to the lateral vessels of the proboscis and then posteriorly to the ventral vessel, of the trunk. From the ventral vessel some of the blood flows through the neurointestinal vessel to the ring vessel, so completing the circuit. What happens to the rest of the blood flowing in the ventral vessel is not known with certainty. Menon & Dattagupta (1976) suggested some of it may find its way back to the ring vessel or sinus through a system of sinuses which lie on either side of the siphon.

Nyholm & Borno (1969b) found that the rate of oxygen consumption of specimens of *Echiurus echiurus* living in glass tubes was 0.043 ml/g/h wet weight ($N=19$). For specimens without a proboscis it was 0.046 ml/g/h and 0.012 ml/g/h for the separate proboscis, suggesting that the surface of the trunk is a more important respiratory organ than the proboscis. Chuang (1962b) obtained similar results with 20 *Ochetostoma erythrogrammon*, determining that the oxygen uptake of the detached proboscis of nine specimens averaged only 17.2% of the combined uptake of the trunk and proboscis. It seems likely, therefore, that the proboscis of some species is an accessory but not indispensable respiratory structure especially since some echiurans are able to live for a long time, although they have lost their proboscis (Gislén, 1940). Chuang also showed, by ligaturing the anus of

his specimens, that the hind gut and cloaca of *O. erythrogrammon*, unlike those of *Urechis caupo*, play no part in the respiration of the animal. The lateral margins of the proboscis of *O. septemyotum* are folded and have tree-like outgrowths and those of *Anelassorhynchus sabinus* are frilled. Whether these modifications increase the respiratory ability of the animal is not known.

Brafield (1968) measured the rate of oxygen consumption of whole specimens of *Bonellia viridis* and of the isolated proboscis and the isolated trunk of the same specimens. The oxygen consumption of the proboscis plus that of the trunk corresponded closely to that of the whole animal, a result suggesting that the loss of the proboscis produces '... little physiological stress to the animal'. Brafield also found that the rate of oxygen consumption of the isolated proboscis was two to four times that of the trunk of the same specimens, a different result from that obtained for *E. echiurus* (Nyholm & Borno 1969b) and *O. erythrogrammon* (Chuang 1962b). Brafield (1968) suggested that activity of the numerous cilia of the proboscis compared with the relative inactivity of the trunk might be responsible for the result. In addition, Brafield reported that the rate of oxygen consumption for whole specimens of *Bonellia viridis* in the light was about 30% higher than in darkness. The rate fell when the animals were returned to darkness. He considered that the increase might be due to the increased muscular activity that the animals show when they are placed in the light.

Ditadi & Mendes (1968) showed that the rate of oxygen consumption was significantly higher for mature than for immature *Lissomyema exilii*, and that starvation for as long as 60 days did not significantly alter the rate of oxygen consumption, although body weight decreased. This species is an oxyconformer, its rate of oxygen consumption decreasing as the oxygen tension of the animal's environment falls, and, when carbon monoxide is used to prevent haemoglobin from carrying oxygen, the respiratory pigment in *L. exilii* acts as a storer rather than as a transporter of oxygen.

Manwell (1960) demonstrated that ion-equalised solutions of haemoglobin from the coelomic erythrocytes and the body musculature of *Arhynchite pugettensis* have different oxygen equilibria, the latter having a lower affinity for oxygen than the former. Such information suggests the presence of an 'oxygen transfer system' in which oxygen passes from muscle to coelomic haemoglobin. Manwell hypothesised that either oxygen might pass from the trunk wall to the erythrocytes in the coelom or that anal respiration, similar to that found in *Urechis caupo*, might take place. There does not yet appear to be any evidence in support of the latter suggestion.

The respiration of *Urechis caupo* differs from that of all other echiurans in that it is brought about by means of water forced from the environment into the animal's hind gut by the pumping action of a muscular cloaca. The hind gut of *U. caupo* is a large, thin-walled sac that occupies much of the coelom (for fine structure of hind gut, see Menon & Arp 1992). The coelom is filled with a copious supply of fluid containing haemoglobin-carrying blood cells. Oxygenated water is forced into the hind-gut by a series of pumping movements, without 'exhalation' of the water. From time to time it is discharged through the anus in one 'exhalation'.

Redfield & Florkin (1931) established the respiratory function of the hind-gut by comparing the levels of oxygen and carbon dioxide of the 'inhaled' and 'exhaled' water. They found that the water discharged from the hind-gut contained less oxygen and more carbon dioxide than the water of the aquarium in which the animal lived. The explanation is that oxygen passes to the coelomic blood of the animal via the thin walled hind

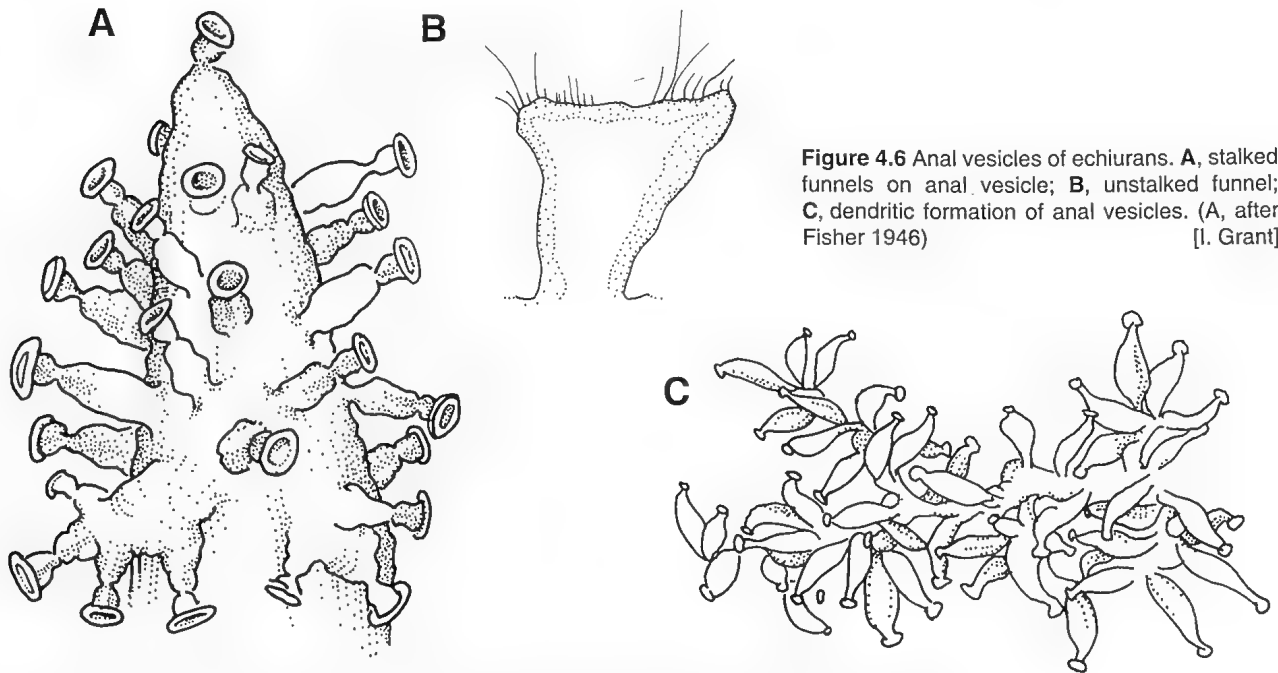


Figure 4.6 Anal vesicles of echiurans. **A**, stalked funnels on anal vesicle; **B**, unstalked funnel; **C**, dendritic formation of anal vesicles. (**A**, after Fisher 1946) [I. Grant]

gut and the contractions of both the body wall and hind gut cause the blood to 'circulate' within the coelom. There are no blood vessels or capillaries within the animal so that its blood system is an open one.

Most of the muscular activity of *U. caupo* is involved in pumping a current of water through its burrow. When the animal feeds the amount of water passing through the burrow increases by about twice to two and a half times that during a non-feeding period (Hall 1931).

Excretion

The chief excretory organs are considered to be a pair of anal sacs or vesicles, symmetrically placed in the posterior region of the body cavity (Fig. 4.2). They discharge their contents into the rectal or cloacal region of the gut. They may be long and tubular or shorter and more sac-like. In bonelliids, however, they often branch, usually becoming tree-like or feathery (Fig. 4.6C). The walls of the sacs, although generally thin, consist of layers of circular and longitudinal muscle and epithelia. Red-brown granules in vacuolated cells are thought to be the end products of catabolism. From the surface of the sacs arise numerous small structures termed ciliated cups or funnels (Fig. 4.6A, B), which open to the body cavity. Sometimes the funnels are stalked. Waste products in the body cavity, it is thought, are directed via the ciliated funnels to the lumen of the anal vesicles and, by contractions of the walls of the latter, through their rectal openings into the posterior gut. From there the wastes are voided.

Fixed and free cells, thought to be excretory in function, because they contain pigmented granules, are found in the walls of the digestive tract, nephridia, anal sacs and body cavity. Ikeda (1907, p. 40) reported the presence of ciliated cells, his so-called 'Töpfchen', in the body cavity of *Ikeda taenioides*. These cells resemble in some ways the swimming urn cells of sipunculans and annelids.

Little experimental research has been conducted on the excretion of echiurans. What role, if any, the nephridia play in the process is not known. Dattagupta & Singh (1976) described the morphology and histochemistry of the anal vesicles and nephridia of a number of echiurans.

Nervous System

The nervous system of echiurans is constructed more or less on the same plan as that of sipunculans and annelids. It consists of a peri-oesophageal collar, a ventral nerve cord (Fig. 4.2), a set of peripheral nerves and sense organs. The peri-oesophageal ring or collar is a very long loop. It arises from the anterior extremity of the ventral nerve cord and follows the lateral edges of the proboscis for its whole length, lying in the connective tissues below the dermis. The anterior part of the collar corresponds to the cerebral ganglia or brain of sipunculans and annelids, although no ganglionic swellings are present in adult animals. Ganglia, however, are said to be observable in the embryos of some species. In *Echiurus*, transverse nervous tissue connects each side of the lateral components of the peri-oesophageal ring.

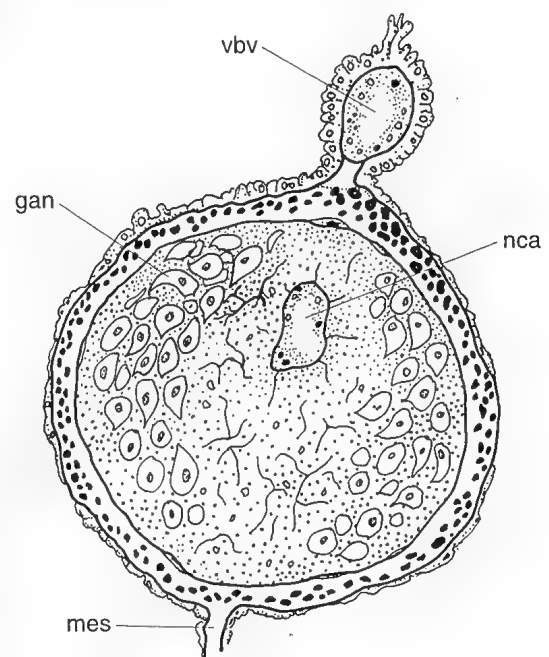


Figure 4.7 Transverse cross-section of the nerve cord of *Echiurus* species. **gan**, nerve ganglia; **mes**, mesentery; **nca**, neural canal; **vbv**, ventral blood vessel. (After Baltzer 1931) [I. Grant]

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The ventral nerve cord runs medially and ventrally the length of the trunk and is attached by a mesentery to the body wall along with the ventral blood vessel (Fig. 4.7). It is unsegmented. In section it shows two groups of ganglia and contains a neural canal.

The peripheral system consists of a series of unpaired, lateral nerves, which arise from each side of the ventral nerve cord. The skin bodies, papillae and sense organs are supplied with nerves from the lateral nerves.

Sensory cells, mostly ciliated are present on the trunk, especially in the region of the thoracic papillae. They are also densely grouped at the lateral edges of the proboscis.

Lawry (1966a) described the neuromuscular system of *Urechis caupo* and reported that the behaviour of the worms in the laboratory seemed unrelated to tidal or diurnal rhythms. Lawry (1966b), however, found that the nerve cord of this species contains a number of pacemaker elements. One, situated in the proboscis, exercises some control over the rest and seems responsible for the generation of descending peristaltic movements of the body wall.

Reproduction and Development

There are no records of asexual reproduction in echiurans. Regeneration of the proboscis, however, has been reported in *Echiurus* (Gislén 1940) and *Bonellia* (Agius 1979).

Reproduction of echiurans is sexual. Males and females look alike and are difficult to distinguish externally, except in the Bonelliidae. In the latter sexual dimorphism is marked, the male being very much reduced in size and living what appears to be a parasitic way of life in, or on the female. What is known about the reproduction and development of echiurans follows largely from the researches of Hatschek (1880) on *Echiurus*, Cann (1886) and Tarrey (1903) on *Lissomyema*, Sawada & Ochi (1962) on *Ikedosoma*, Baltzer (1925, 1937), Herbst (1940), Zurbuchen (1937), Agius (1979), Jaccarini & Schembri (1983) on *Bonellia*, Newby (1940) on *Urechis*, and Pilger (1980) on *Listriolobus*. Dawydoff (1959) gave a good summary of the topic up to 1959 and Gould-Somero (1979) a more recent account based chiefly on *U. caupo*.

The sexes are separate and the gonad, which is unpaired, is situated along the posterior part of a mesentery which runs close to the ventral nerve cord and blood vessel. Gametes in an early stage of development are released into the coelom where they undergo further development. The nephridia, by means of their ciliated nephrostomal lips (Fig. 4.8), are able to distinguish between the different floating bodies in the coelomic fluid and select mature gametes for storage in the organ. Not a great deal is known about the gametic cycles or when they occur. Sawada & Ochi (1962) found that in Japan the eggs of *Ikedosoma gogoshimense* appear in May and June. Pilger (1980) reported that while the gametes of *Listriolobus pelodes* were released during most of the year at southern California, fully grown oocytes were present only in late autumn, winter and spring and that spawning occurred through late winter and spring. Gould-Somero (1975) recorded that the production of eggs in *Urechis caupo* is probably a continuous process.

Fertilisation is external except in the Bonelliidae. Little is known about the mechanism which brings about the release of eggs and sperms at the same time. Mature eggs of some species are distinguished by an indentation at one pole (Fig. 4.9A), a feature which disappears as soon as fertilisation takes place (Fig. 4.9B). Cleavage is spiral and almost equal in *Ikedosoma* (Sawada & Ochi 1962), *Lissomyema* (Torrey 1903) and *Urechis* (Newby 1940), but in *Bonellia*, in which the egg contains more yolk, the third cleavage gives rise to a set of smaller micromeres and another of larger macromeres. As in other protostomes, the blastopore region of the developing embryo becomes the future mouth of the animal.

As far as is known, all echiuran larvae develop into free-swimming and feeding trochophores, that of *Lissomyema* at about 22 hours after fertilisation, of *Echiurus* after about 40 hours (Fig. 4.9C) and of *Bonellia* after about 2–4 days.

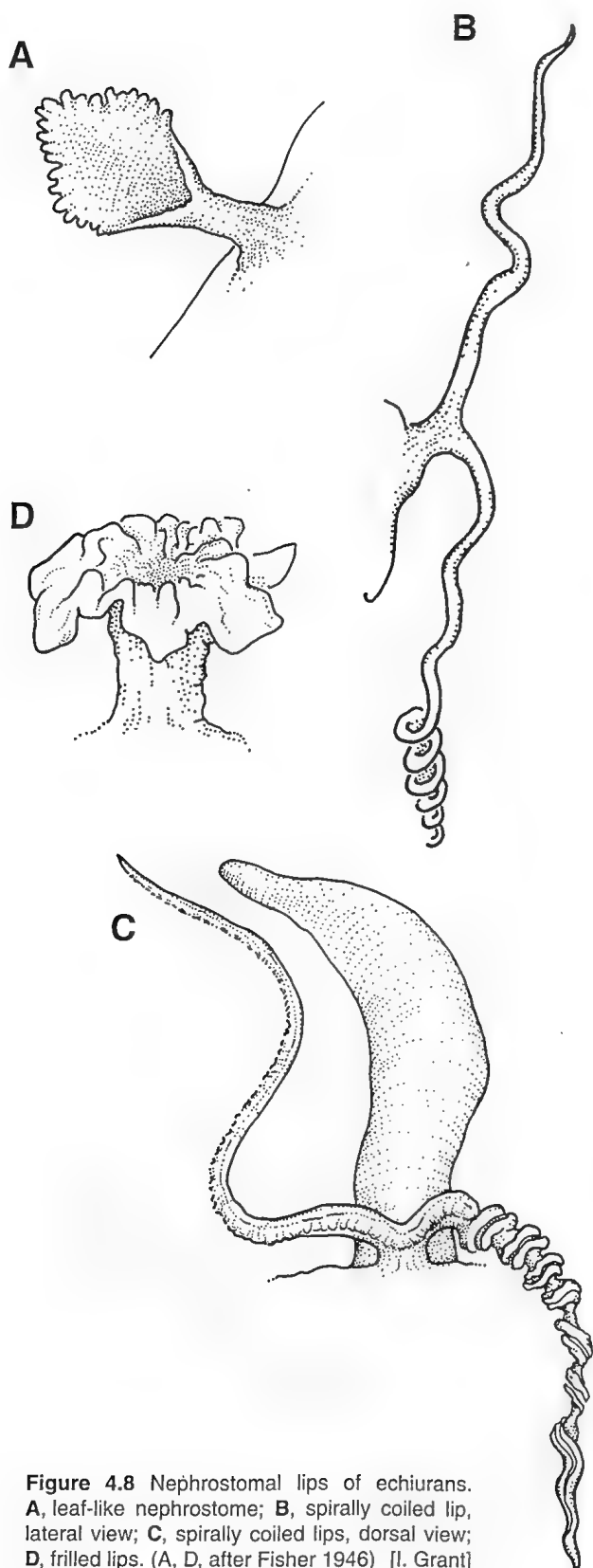


Figure 4.8 Nephrostomal lips of echiurans. **A**, leaf-like nephrostome; **B**, spirally coiled lip, lateral view; **C**, spirally coiled lips, dorsal view; **D**, frilled lips. (A, D, after Fisher 1946) [I. Grant]

During metamorphosis the larva increases in length and organogenesis occurs. No stage corresponding to that of the pelagospaera of sipunculans has been found for echiurans. Eventually the larva settles and begins life as an adult. Pilger (1980) reported that newly settled juveniles of *Listriolobus pelodes* become sexually mature after 6–12 months. Pilger (1977) reviewed the subjects of settlement and metamorphosis in echiurans.

Does segmentation occur during the development of echiuran larvae? The question arises from the researches of Hatschek (1880) and of Baltzer (1917) both of whom reported signs of metamerism in the developing larvae of *Echiurus echiurus* and *E. abyssalis*. There seems, however, to be considerable doubt about the interpretation of their observations. Newby (1940) was not able to find any evidence of metamerism in his developing larvae of *U. caupo*. What appears to be 'segmentation' in young specimens of *U. caupo* is, according to Newby (1940), caused by a series of mucous glands arranged in 12 rings around the developing trunk. Concerning

the matter, Newby (1940 p. 210) said 'the mesodermal bands of echiuroids show no sign of segmentation. The lack of segmentation in the mesoderm considered with the questionable nature of the segmentation of the nervous system and mucous glands ... makes it appear probable that the echiuroids have a primary lack of segmentation'.

Sex Determination in *Bonellia viridis*. The issue of sex determination in *Bonellia viridis*, first raised by Spengel in 1879, has been the subject of much research. A review of the topic is given by Gould-Somero (1975) and a more recent one by Jaccarini, Agius, Schembri, & Rizzo (1983). The generally accepted explanation has followed from the work of Baltzer (1914, 1925, 1931). The larva of *B. viridis* (and other bonelliids, it is assumed) is sexually undifferentiated. If it settles on the proboscis or trunk of a female, the early larva will most probably develop into a male and become adult in about 1–2 weeks. During the development, it moves to the nephridium or gonoduct of the female where it spends the rest of its life as a planariform or vermiform creature, leading the life of a parasite and producing a ready supply of sperm. On the other hand, if an undifferentiated larva develops in seawater without contact with a female, it will probably become a female and reach maturity after about 2 years. Small percentages of males and intersexes may also be produced in conditions without attachment, and of females and intersexes in conditions when there is attachment. Baltzer (1914) demonstrated that larvae, when attached to the proboscis of adult females vitally stained with dyes, take up some of the colouring matter. Zurbuchen (1937) showed that if the time of attachment to the proboscis was reduced more intersexes were produced. Baltzer concluded that a substance present in the proboscis and body wall of the adult female was responsible for the development of the male. Subsequently, the green pigment bonellin was considered to be the masculinising factor.

More recent research has confirmed Baltzer's general conclusions and produced new information as well. Jaccarini *et al.* (1983) showed that sex determination in 83% of all larvae of *B. viridis* depends on the interaction of larvae and their environment, that is, it is metagenic. The sex of the other 17% depends solely on their genetic constitution and is independent of their environment, that is, their sex is syngamic. Jaccarini *et al.* also found that when larvae were cultured in batches in sea-water about 20% became males, whereas if the larvae were cultured singly only 7.5% became males. The increased number of males when cultured in batches causes the interaction between the larvae, Jaccarini *et al.* reporting that up to 20% of the larvae in the batches became attached in pairs. One of the pair becomes a male and the other a female. The experiments of earlier workers were invariably conducted with batches of larvae and consequently did not take interaction factors into consideration. The experiments of Jaccarini *et al.*, except for those specifically dealing with batch cultures, have the advantage of being performed with 'single' specimens.

Experiments using purified bonellin have shown that the pigment has strong masculinising powers. Working with single larvae of *B. viridis*, Jaccarini *et al.* (1983) found, however, that the pigmented secretion produced when an adult female animal is irritated by mechanical disturbance and diluted with sea-water, such that its extinction coefficient at 390 nm was the same value as that of an 10 ppm bonellin solution, gave a significantly higher number of males than either a 10 ppm bonellin solution or tissue extracts of the proboscis or trunk. Why this is so is not yet clear.

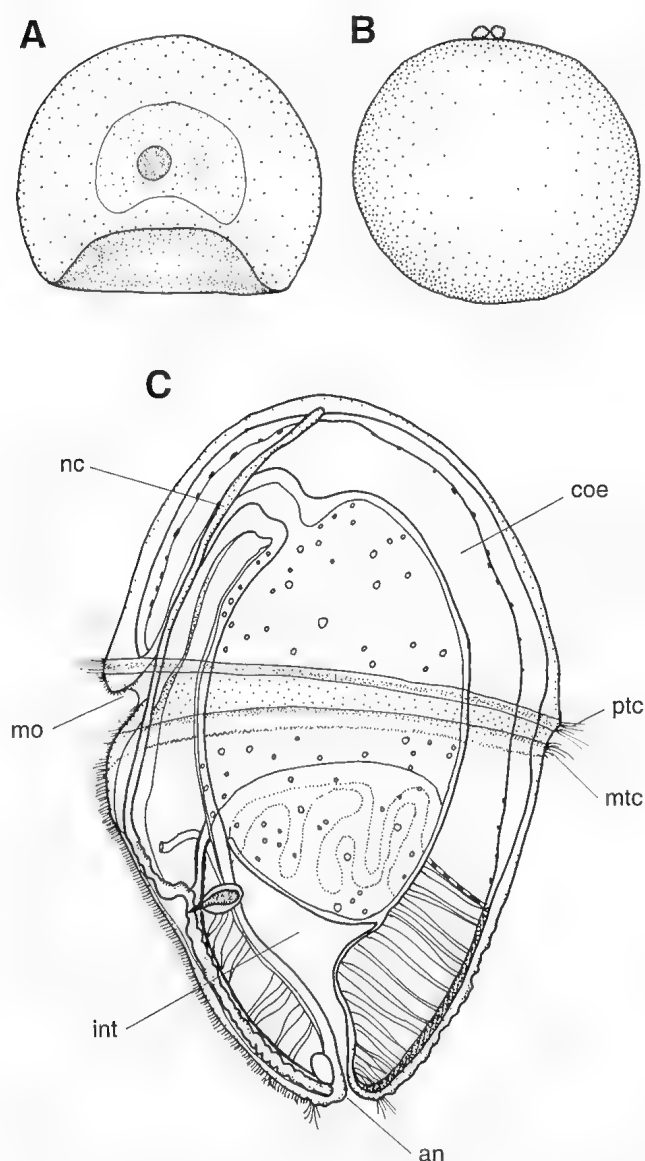


Figure 4.9. A, mature egg of *Urechis caupo* showing characteristic indentation. B, fertilised egg of *Urechis caupo*; the indentation is lost and polar bodies appear. C, trochophore of *Echiurus* species an, anus; coe, coelom; int, intestine; mo, mouth; mtc, metatrochal cilia; nc, nerve cord; ptc, prototrochal cilia. (A, B, after Newby 1940; C, after Baltzer 1931) [I. Grant]

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That the proboscis and trunk secrete a sex determining chemical does not, however, account satisfactorily for all the observed facts about sex determination in *Bonellia*. It has been known for many years (Herbst 1940) that a change in the ionic concentration of the sea-water in which undifferentiated larvae live tends to produce males. An increase in the concentrations of CO_2 , HCl , K^+ ions or traces of Cu^{2+} ions or a decrease in the concentration of SO_4^{2-} ions and of Mg^{2+} ions causes the development of males. This information led Herbst (1940) to suggest that sex determination in *Bonellia* might depend on water balance, dehydration causing the development of males and hydration that of females. What connection exists between the proboscis chemical theory and Herbst's water balance theory, if any, is not known.

NATURAL HISTORY AND ECOLOGY

A number of ecological studies of echiurans have been made in other parts of the world but none in Australia. Fisher & MacGinitie (1928) described the environment of *Urechis caupo*, how the animal digs in mud and sand, its locomotion, its respiratory movements, how it feeds, the commensals that live in its tube and a list of its enemies. Gislén (1940) described the ecology of *Echiurus echiurus*, its digging action, its behaviour in its burrow, its method of respiration, how it feeds and the nature of its food and how it swims. Nyholm & Borno (1969a) published additional information about its nutrition and respiration.

Little information is available about the population densities of echiurans. Barnard & Hartman (1959) described the biomass and community structure on the sea bottom off Santa Barbara, California, finding that *Listriolobus pelodes* was the dominant animal in a large silt-bed at depths of 30–50 m. The biomass of the worms, as shown by profiles in the area, averaged 480 g/m². Fauchald (1971) found that the numbers were very much reduced after a large oil spill in the area. Pilger (1980) made further observations on the natural history of the same species. *Prashadus pirotansis* occurs at densities of one to five animals per m² on the shores of the Arabian Gulf (Hughes & Crisp 1976).

Schembri & Jaccarini (1978) reported *B. viridis* is most abundant on Malta in calcareous rock that borders growths of *Posidonia*. Although the echiuran inhabits tubes made by other animals, especially the thalassinoid crustacean *Upogebia deltaura*, Schembri & Jaccarini suggested that *Bonellia* species may modify its burrow by secreting an acidic mucus and by gentle mechanical action. Inhabiting the burrow is also a number of commensals much like the communities found in the burrows of *Urechis* and *Echiurus*. The writers also outline a suggested food web for the main organisms that inhabit the burrow.

The ecological importance of echiurans is at least four-fold. Firstly, they are detritus-feeders, either directing small particles along the extended proboscis to the mouth or by trapping them in a mucous net which is eventually swallowed. Echiurans are thus decomposer organisms. Secondly, they are eaten by other animals. Fisher & MacGinitie (1928) reported that the larval stages of *Urechis caupo* are eaten by larger marine invertebrates and by a goby, *Clevelandia* sp. and adults by rays in the genus *Myliobatis*. Thirdly, a number of commensals are usually associated with echiurans in their tubes. Some commensals of *Urechis* are a polynoid, *Hesperonoe* species and two pinnotherid crabs, *Scleroplax* species and *Pinnixia* species. Fourthly, they may serve as intermediate or final hosts of a number of parasites, for example, the gregarine *Zygosoma globosum* found in the body

cavity of *U. caupo* (Noble 1938) and the polychaete, *Obligognathus bonelliae* (Fauvel 1923). A few parasitic copepods are known from the digestive tract of echiurans (Illg 1975): *Goidelia japonica* from *Urechis unicinctus* and *Echiurophilus fizei* from the digestive tract of *Anelassorhynchus inansensis*. Further, echiurans may play an important role in sediment bioturbation (Hughes, Ansell & Atkinson 1996).

Feeding Habits

Studies of feeding habits have been made on *Echiurus echiurus* (Gislén 1940; Nyholm & Borno 1969a), *Urechis caupo* (Fisher & MacGinitie 1928), *Ochetostoma erythrogrammon* (Chuang 1962a), *Prashadus pirotansis* (Hughes & Crisp 1976) and *Bonellia viridis* (Jaccarini & Schembri 1977a, 1977c, 1979).

According to Nyholm & Borno (1969a), the food of *E. echiurus* consists of micro-organisms and dead organic matter, like that found on the surface of the sediments where the animal lives. When *E. echiurus* feeds, it extends its proboscis over the surface of the sediment with its ventral side uppermost, using its tip to form a spatula-like structure which slides down into the upper layers of the sediment. The detritus is then directed along the ciliated ventral surface to the mouth and is gradually mixed with mucus. Particles that are too large are rejected by deflection near two ventral swellings, the 'eminences' of Gislén (1940), in front of the mouth. According to Nyholm & Borno '... the mucal strip retains its form through the pharynx and is compressed into pellets upon entering the oesophagus. The pellets contain the same components as those found in the uppermost sedimentary stratum', namely sand grains, diatoms, algal threads, leaves of *Zostera*, infusorians, bacteria and occasionally nematodes and rotifers.

Ochetostoma erythrogrammon feeds at ebb tide in a manner much like that of *E. echiurus*. The animal extends its proboscis over the surface of the mud with its ventral, ciliated surface uppermost and its dorsal, non-ciliated surface on the mud. Sand grains and detritus are collected, trapped in a copious supply of mucus secreted by the proboscis and driven by beating cilia to the mouth. Large, unwanted particles are deflected over the rim of the proboscis by a 'bulge' near the mouth and thus rejected (Chuang 1962a).

Urechis caupo, however, feeds in a very different manner to that of other echiurans. The animal lives in a U-tube through which a current of water is maintained by the pumping action of its body wall. It feeds by 'spinning' in its burrow a transparent, tubular net of mucus which permits the passage of water but which filters out organisms and particles as small as 1 µm in diameter. Fisher (1946) says that, '... if unmolested *Urechis caupo* may continue pumping for an hour before the tube is clogged'. Eventually the net and its catch of food particles are swallowed. Particles that are large are not eaten but are discarded as the mucous net is swallowed. The rejected material is eaten by some of the commensals that inhabit the tube.

When *Bonellia viridis* feeds it extends its proboscis from the burrow and uses its bifid terminal lobes to graze on the surrounding substratum, '... including shallow pockets of detritus in the rocks, the material at the roots of vegetation, patches of sand between the boulders ... or on fronds of attached algae.' It usually feeds at dusk, when it is dark or at dawn (Jaccarini & Schembri 1977c). The ciliation of the proboscis and the importance of cilia in feeding and movement of the animal have been studied in detail by

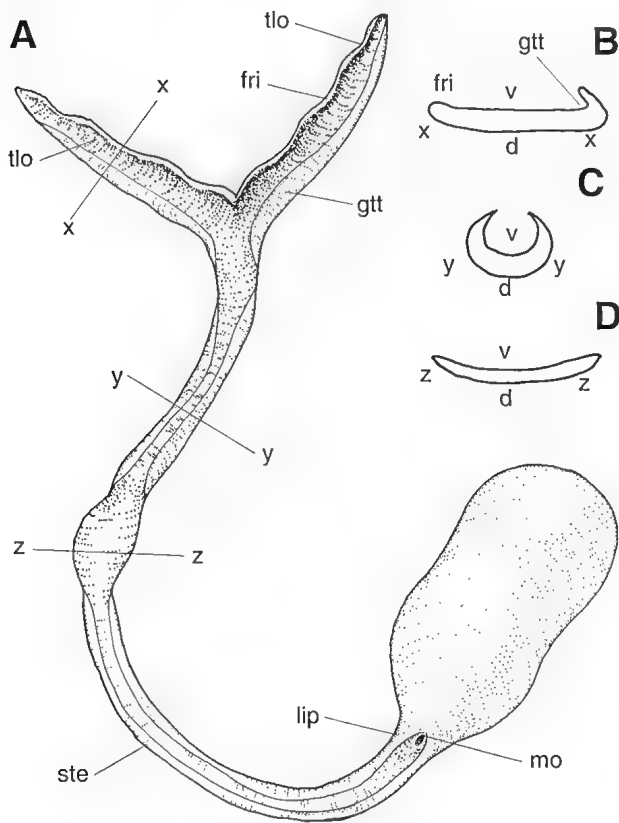


Figure 4.10 Proboscis and feeding action of *Bonellia* species. **A**, ventral view of a female with the proboscis extended showing the external features. **B–D**, transverse sections of the proboscis at different levels as indicated in **A**: **B**, X–X; **C**, Y–Y; **D**, Z–Z. **d**, dorsal; **fri**, fringe; **gtt**, gutter; **lip**, lip; **mo**, mouth; **ste**, stem; **tlo**, terminal lobe; **v**, ventral. (After Jaccarini & Schembri 1979c) [I. Grant]

Jaccarini & Schembri (1977a, 1977c, 1979). Particles smaller than $94 \pm 25 \mu\text{m}$ are directed onto the proboscis by beating of cilia. Particles of size $150 \pm 40 \mu\text{m}$ are picked up by the combined action of cilia and muscles whereas larger particles from $230\text{--}290 \mu\text{m}$ are taken up as a result of muscular activity. The transference of food and mucus from the terminal lobes along the channel or gutter of the stem is caused by the movement of both cilia and muscles. The food is sometimes moulded into a bolus. The experiments of Jaccarini & Schembri (1977c) showed that *Bonellia* is able to select particles, according to both size and quality. They found that the animal spent more time grazing on a plant-enriched substratum than on a clean, unenriched substratum when the latter was used as a control.

BIOGEOGRAPHY

Of 13 known species and subspecies of Australian echiurans: seven have so far been found only in Australia (*Metabonellia haswelli*, *Sluiterina alba*, *Zenkevitchiola brevirostris*, *Protobonellia papillosa*, *Anelassorhynchus porcellus adalaidensis*, *Arhynchite hiscocki*, *Thalassema sydneyense*); one (*Ochetostoma baroni*) is known from the Atlantic, Pacific and Indian Oceans; three (*Pseudobonellia biuterina*, *Listriolobus brevirostris*, *Vitjazema ultraabyssalis*) occur in the western Pacific region, and; two (*Ochetostoma australiense*, *Anelassorhynchus porcellus porcellus*) are known from the Indo-Pacific region. Only one genus (*Metabonellia*) is endemic.

Affinities

The larva of an echiuran is a free-swimming trochophore and its development is similar in many respects to that of the trochophores of sipunculans, molluscs and especially annelids. It is not surprising then that echiurans were for a long time regarded as a class or subphylum of Annelida. From a study of the distribution of guanidine compounds and phosphagens, van Thoi (1976) concluded that echiurans are more like annelids than like sipunculans. Recent molecular phylogenetic analyses using 18S rRNA sequences suggest a close affinity between echiurans and pogonophorans (including vestimentiferans), both of which may be closer to molluscs than to annelids and sipunculans (Winnepenninckx, Backeljau & Wachter 1995). Echiurans are given the rank of a phylum, largely as a result of the researches and advocacy of Newby (1940). Clark (1969), in discussing the affinities of annelids, sipunculans and echiurans, supported Newby's contention that the echiurans constitute a separate phylum.

Hatschek's (1880) claim of incipient metamerism of the mesoderm and coelom of *Echiurus* was treated sceptically by Baltzer (1931) and disregarded by Newby (1940). The modern view (Clark 1969) is that Annelida, Sipuncula and Echiura, although closely related, are separate phyla that arose from a common, unsegmented ancestor, in which the larva was trochophore-like.

FOSSIL RECORD

Two fossils considered to be early echiurans have been reported from other parts of the world.

Coprinoscolex ellogimus was described from the Middle Pennsylvanian Francis Creek Shale (Late Carboniferous) of northeastern Illinois, United States of America (Jones & Thompson 1977). The specimens consisted of a small, scoop-like, flattened, prostomial proboscis and a cigar-shaped trunk. A convoluted gut links an anteriorly placed mouth to a posteriorly placed anus. Faecal pellets seem to be present in the gut. No chaetae, however, show up in the fossil.

Protoechiurus edmondsi was described from a single specimen collected from Kuibis Quartzite, Nama Group, Late Cambrian from South West Africa (Namibia) by Glaessner (1979). The fossil has a cigar-shaped trunk with a spatulate, narrow anterior and a rounded posterior end. A number of ridges (eight?) run longitudinally along the trunk wall and suggest a correspondence with the longitudinal muscle bands of some existing echiurans. No internal characters are discernible.

DISSECTION AND PRESERVATION

The method of collection and preservation of echiurans is similar to that of sipunculans. Collecting species that have tubes in mud is no easy matter. The author's experience of collecting echiurans is limited to a few Australian species. *Metabonellia haswelli* and *Anelassorhynchus porcellus* are easily collected by turning over large rocks in the areas where they are known to occur. Both apparently are able to make tubes in the mud and debris that accumulate under rocks. *Pseudobonellia biuterina* has been found by cracking pieces of dead coral and even from under flower pots standing on a sandy base in a marine aquarium. *Ochetostoma baroni* lives in U-shaped burrows in mud flats and can be dug up at low tides, especially when the animal is about to feed. At such times the long proboscis is stretched out over the surface of the mud. If the posterior end of the tube can be located, then if one digs

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deeply on each side of a line between the anterior and posterior of the tube there is a reasonable chance of collecting a specimen. Patience, however, is required.

When it is collected, place the worm in a plentiful supply of cool sea-water for a couple of hours and shade the animal from light. Do not place more than two animals in a vessel as some species secrete a copious quantity of mucus and the green pigment of *Bonellia viridis* is known to be toxic to a number of other animals, especially in the presence of light.

Echiurans can be narcotised by using the same methods used for sipunculans. It is best to use two lots of formalin when fixing the animals, on account of the large volume of fluid in the coelomic cavity. Store in 70% alcohol.

Dissect specimens on a wax surface under water as for sipunculans, remembering that the ventral side (denoted by the chaetae) should be placed next to the wax. Using forceps, to lift up the body wall, and scalpel, make a longitudinal cut along the dorsal body wall. Echiurans, on account of their long and tangled gut, are not always easily pinned out. A gentle stream of water or alcohol directed from a wash bottle on the internal organs sometimes helps to clear away any gut contents that accidentally spill out during dissection.

CLASSIFICATION

The classification used here (see Table 4.1) is basically that of Fisher (1946, 1949). It differs in several respects from that of Stephen & Edmonds (1972) and incorporates most of the suggestions of Dattagupta (1976), Dattagupta & Menon (1976) and Saxena (1983). It recognises the bonelliids as forming a new order, Bonellioinea (Saxena, 1983), restricts Echiuridae to the genus *Echiurus* and places a number of genera of *Thalassema*-like echiurans in Thalassematidae, something already done by Bock (1942) and Dattagupta (1976). Dattagupta (1976), however, rejected the order Heteromyota. He also erected a number of subfamilies within the phylum. Bisewar (1984) gave a key to the species of *Anelassorhynchus* and Edmonds (1987) to the genera and species of Australian echiurans.

Two echiuran classes are recognised: Echiuridea Fisher, 1946 and Sactosomatidea Fisher, 1946 (spelling emended). All echiurans except the little known species, *Sactosoma vitreum*, belong to the Echiuridea. The Sactosomatidea is distinguished by a body wall with circular musculature either missing or degenerated to a group of fibres and the absence of anal vesicles, siphon, proboscis and chaetae. This class contains a single species, *Sactosoma vitreum*, which has not been recorded from Australian waters and thus is not treated further here. Table 4.2 summarises the distinguishing features of the six families.

Table 4.1 Classification of the phylum Echiura. Families marked with an asterisk (*) have not been recorded from Australian waters. † The author has tentatively placed an undescribed *Ikeda* species from Australian waters in the Ikedidae.

Class ECHIURIDEA									
Order ECHIUROINEA									
Family Echiuridae*									
Family Thalassematidae									
Order BONELLIOINEA									
Family Bonelliidae									
Order XENOPNEUSTA									
Family Urechidae*									
Order HETEROMYOTA									
Family Ikedidae†									
Class SACTOSOMATIDEA									
Family Sactosomatidae*									

Table 4.2 Distinguishing features of the six echiuran families.

Family	Proboscis bifid (+) or not (-)	Longitudinal muscles banded (+)	Oblique muscles fascic. (+)	Marked sexual dimorphism	Vascular system closed (+)	Nephridia paired (+) unpaired (-)	Anal chaeta present (+) absent (-)	Anal sacs tube- or sac-like (+) branching (-)	Genera
Bonelliidae	+(usually)	-	-	+	+	+ or -	-	-(usually)	30+
Echiuridae	-	-	-	-	+	+	+(2 rings)	+	1
Thalassematidae	-	+ or -	+ or -	-	+	+	-	+	8
Ikedidae	-	+	weakly	-	+	-(very numerous)	-	+	1
Urechidae	-	-	-	-	-	+	+(1 ring)	+	1
Sactosomatidae	-	?	?	?	?	?	-	?	1

Key to families of phylum Echiura

- 1(a) Longitudinal musculature of body wall lying between circular and oblique musculature; nephridia usually paired (except in Bonelliidae) and less than 10 pairs2
- 1(b) Longitudinal musculature of body wall lying externally to circular and oblique muscles; nephridia unpaired and very numerous (200–400); specimens very largeIkedidae
- 2(a) Closed vascular system consisting of dorsal, ventral, neuro-intestinal vessels and anterior extensions to proboscis; hind-gut not modified to act as respiratory chamber3
- 2(b) Open vascular system without vessels; hind-gut much enlarged, thin-walled, modified to receive water from cloaca and serving as respiratory organ; proboscis much reduced and scoop-like Urechidae
- 3(a) Sexual dimorphism pronounced; female *Thalassema*-like but male very small (2–10 mm), planarian-like, degenerate and parasitic on or in female; proboscis often bifid; anal vesicles of female branching, sometimes very much so; usually single nephridium (two in *Pseudobonelliia*); ventral chaetae usually two, but sometimes single; absent in some deep-water species Bonelliidae
- 3(b) Sexual dimorphism absent; proboscis not bifid; anal vesicles not branched, but usually tubular or sac-like; ventral chaetae usually two; nephridia paired4
- 4(a) Two almost complete rings of anal chaetae present; a post-pharyngeal diaphragm almost separates coelom into two parts. Echiuridae
- 4(b) Anal chaetae and post pharyngeal diaphragm absent Thalassematidae

Class ECHIUROINEA

The Echiuridea are diagnosed by a body wall with well-developed circular and oblique musculature, an anteriorly placed proboscis and the presence of ventrally placed chaetae. All echiurans, except for one species which belongs to the class Sactosomatidea, are attributed to the Euchiuridea.

The class comprises four orders: Echiuroinea Bock, 1942; Bonellioinea Saxena, 1983; Xenopneusta Fisher, 1946, and; Heteromyota Fisher, 1946. These are distinguished mainly by the arrangements of the body wall musculature, the vascular system and the hind gut.

Order ECHIUROINEA

The longitudinal musculature in the Echiuroinea lies between the outer circular and inner oblique layers. This group shows no marked sexual dimorphism, has a closed vascular system and lacks anal respiration. The nephridia are usually paired and not numerous and anal vesicles are sac-like or tubular, bearing small sessile funnels. The order comprises two families, Echiuridae and Thalassematidae.

Family Echiuridae

Echiurids have two rings of prominent chaetae at the posterior region of the trunk (Fig. 4.11). A post-pharyngeal diaphragm is present and almost separates the coelom into two parts. The proboscis may be long and almost tubular, or shorter and spatulate. There are one to three pairs of nephridia with nephrostomal lips not spirally coiled. The type genus is *Echiurus* Guerin Meneville.

The family contains only one genus, *Echiurus*, comprising four or five species. They are known from the Arctic and Antarctic regions but none has been found in Australia. *Echiurus echiurus* (Fig. 4.11), frequently collected from the cold waters of the northern Atlantic, is one of the best documented echiurans. Gislén (1940) described the ecology and behaviour of the species.

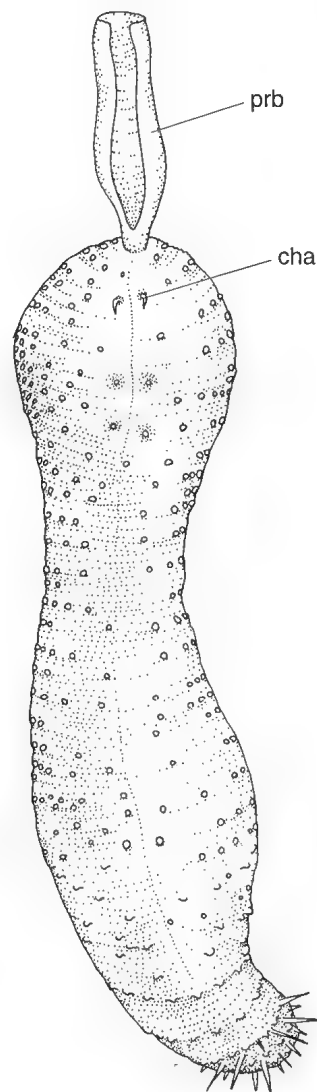


Figure 4.11 Family Echiuridae. *Echiurus echiurus*, ventral view of entire animal. **cha**, chaeta; **prb**, proboscis. (After Baltzer 1931) [I. Grant]

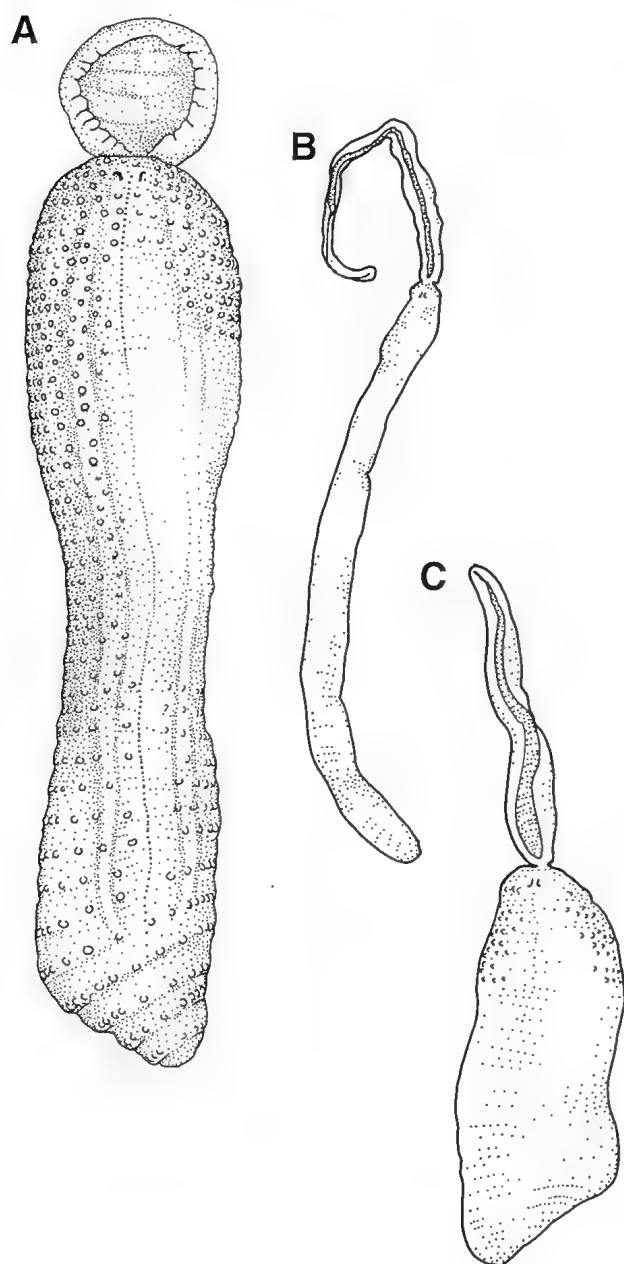


Figure 4.12 Family Thalassematidae. Ventral views of entire animals: **A**, *Listriolobus brevirostris*; **B**, *Arhynchite hiscocki*; **C**, *Thalassema sydneyense*. [I. Grant]

Family Thalassematidae

Thalassematidae lack anal chaetae and a post-pharyngeal diaphragm. The proboscis is usually well developed, sometimes flattened at the tips, but not bifid, and may be easily detached from the trunk (Figs 4.12–4.14; Pls 11.1, 11.2). Thalassematids may be green, reddish or brown. They have one to seven pairs of nephridia, except in *Ikedosoma* and *Prashadus* which may have 20 pairs. The nephrostomal lips may be inconspicuous, leaf-like or elongate and spirally coiled. The longitudinal musculature of the body wall may be continuous (*Thalassema*, *Anelassorhynchus* and *Arhynchite*) or thickened into bands (*Ochetostoma*, *Listriolobus*, *Lissomyema*, *Ikedosoma* and *Prashadus*). Species in all genera except *Lissomyema*, *Ikedosoma* and *Prashadus* have been collected in Australia.

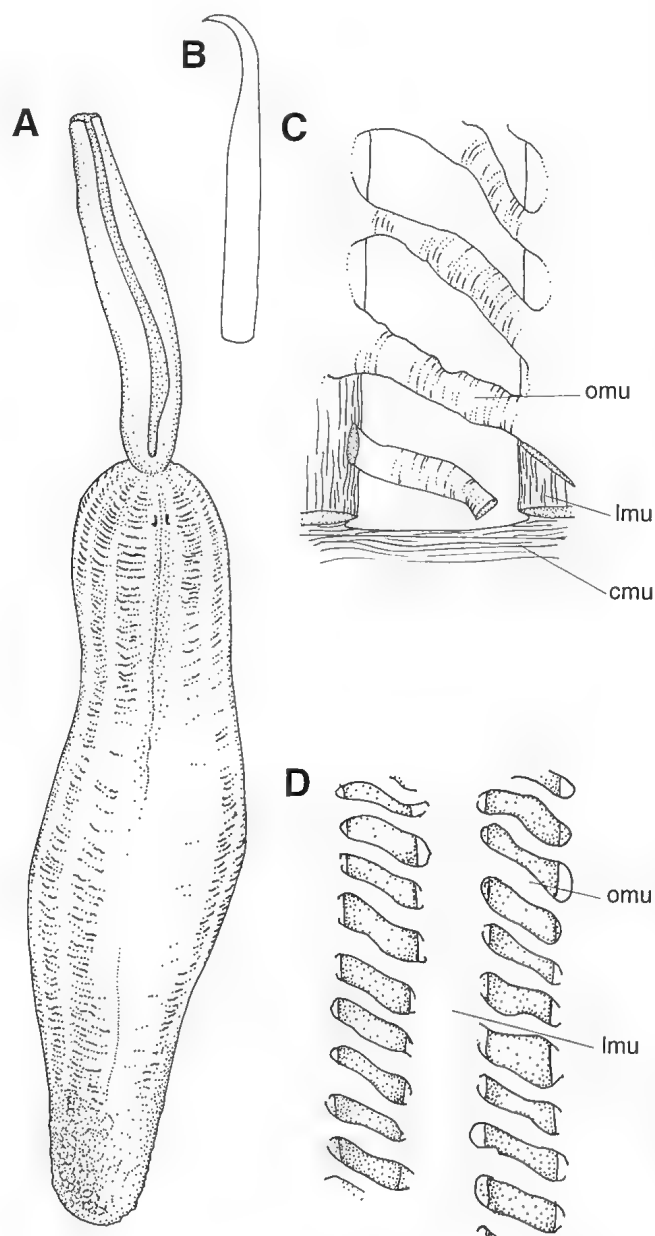


Figure 4.13 Family Thalassematidae. **A**, **B**, *Ochetostoma australiense*: **A**, ventral view of entire animal; **B**, chaeta. **C**, arrangement of innermost layer of oblique musculature in *Ochetostoma* species. **D**, general appearance of the coelomic surface of *Ochetostoma* species. **cmu**, circular musculature; **lmu**, longitudinal muscle band; **omu**, oblique muscle fascicles between bands of longitudinal muscle. [I. Grant]

Thalassematids are more uniform and less diverse in their structure than the Bonelliidae and they tend to live in shallower water (Stephen & Edmonds, 1972). All are detritus feeders. Edmonds (1987) listed and described the Australian species and reported that the most commonly collected members of the family in Australia are *Anelassorhynchus porcellus adalaidensis* (Fig. 4.14A; Pl. 11.1) from Victoria, South Australia and Western Australia and *Ochetostoma australiense* (Fig. 4.13A) from mud flats along the coast of Queensland. Other members recorded from Australia are *Listriolobus brevirostris*, *Arhynchite hiscocki*, *Ochetostoma baroni* and *Thalassema sydneyense*; they are known, however, from only a few specimens.

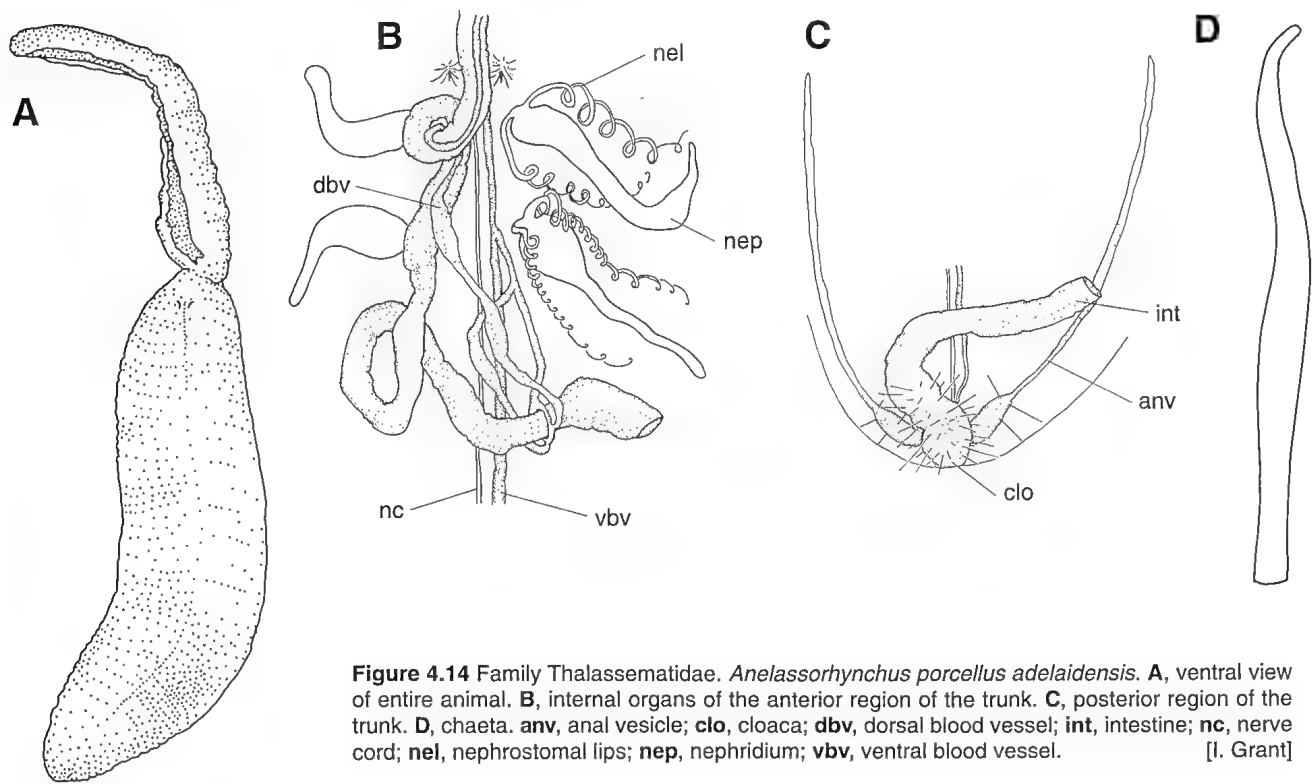


Figure 4.14 Family Thalassematidae. *Anelassorhynchus porcellus adelaidensis*. **A**, ventral view of entire animal. **B**, internal organs of the anterior region of the trunk. **C**, posterior region of the trunk. **D**, chaeta. **anv**, anal vesicle; **clo**, cloaca; **dbv**, dorsal blood vessel; **int**, intestine; **nc**, nerve cord; **nel**, nephrostomal lips; **nep**, nephridium; **vbw**, ventral blood vessel. [I. Grant]

Table 4.3 .Characters distinguishing the genera of Thalassematidae.

Genus	Longitudinal musculature	Oblique musculature	Nephrostomal lips	Nephridia	Position of nephrostome
1. <i>Arhynchite</i> Sato	continuous	continuous	leaf-like	1 pair	basal
2. <i>Lissomyema</i> Fisher	banded	continuous	not spirally coiled	2 pairs	basal
3. <i>Listriolobus</i> Fisher	banded	continuous	spirally coiled	2–3 pairs	basal
4. <i>Ochetostoma</i> Leuckart & Rueppell	banded	fasciculated	spirally coiled	1–7 pairs	basal
5. <i>Anelassorhynchus</i> Annandale	continuous	continuous	spirally coiled	1–3 pairs	basal
6. <i>Thalassema</i> Lamarck	continuous	continuous	not spirally coiled	1–2 pairs	basal
7. <i>Ikedosoma</i> Bock	banded	weakly fasciculated	short spirals	20 pairs or 3–8 groups of 1–4 per group	basal
8. <i>Prashadus</i> Stephen & Edmonds, 1972 (= <i>Rubricelatus</i> Dattagupta & Menon, 1976)*	continuous	continuous	not spirally coiled	8–20 pairs	distal

*The exact family position of *Prashadus* or *Rubricelatus* is not certain; Dattagupta & Menon (1976) placed it in Ikedidae.

Order BONELLIOINEA

In the Bonellioinea, the longitudinal musculature lies between the outer circular and inner oblique layers. Sexual dimorphism is marked, and the male is reduced to a small, planariform, to nematoform animal that lives in or on the female. The female has a closed vascular system. One or two nephridia are present and anal vesicles are usually dendritic or arborescent and bear stalked funnels. There is only one family, the Bonelliidae.

Family Bonelliidae

Bonelliids show pronounced sexual dimorphism. The females have the trunk cigar, ovoid to sausage-shaped, 7–150 mm long and usually light to dark green in colour. The proboscis is often bifid and capable of great extension (up to 1.5 m in *Bonellia viridis*; see Figs 4.15A, 4.16A; Pls 11.3, 11.4). There are one or two nephridia (gonoducts) with either basal

(proximal) or terminal (distal) nephrostomes. Usually two ventral chaetae are present, but in some deep-sea species chaetae are absent (Fig. 4.17A). Anal chaetae are lacking. The two anal vesicles usually branch frequently (Fig. 4.15D, 4.16D). The vascular system is closed, with dorsal and neurointestinal vessels usually connected through capillaries or lacunae in the walls of the intestine.

The male usually lives in a nephridium of the female, but may also reside on the proboscis and body wall or in a specialised tube within the female (Fig. 4.16D). The male is usually very small, 1–6 mm long, but may be up to 20 mm in *Metabonellia*. The body is flat, planariform or nematoform, and lacks pigment and a proboscis; has the alimentary canal, vascular, excretory and nervous systems are much reduced, but the reproductive system is well developed. The body surface is covered densely with multiciliated cells; the coelomic lining is complete in *Bonellia viridis* (Schuchert &

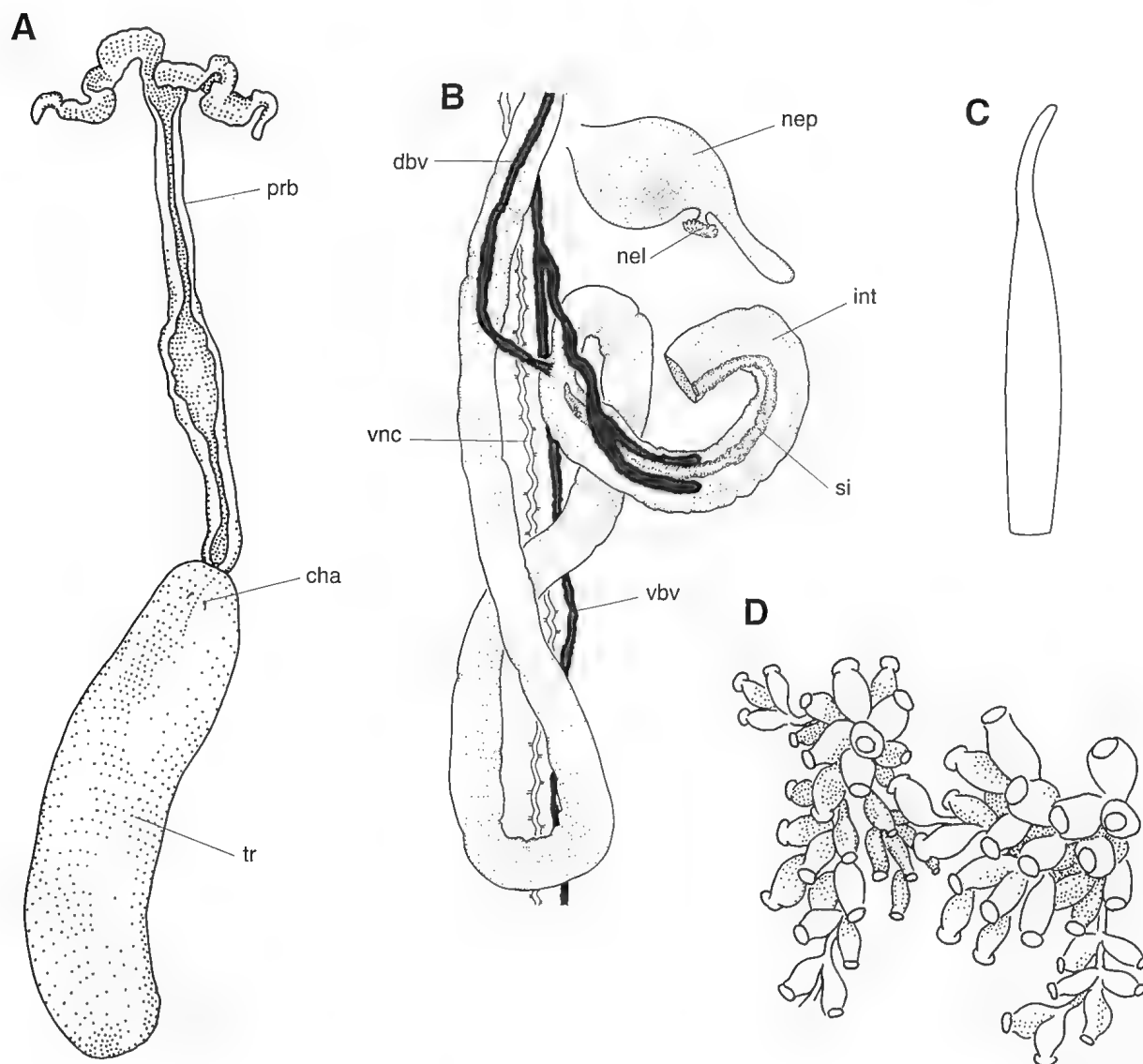


Figure 4.15 Family Bonelliidae. *Metabonellia haswelli*. **A**, ventral view of entire animal with proboscis extended. **B**, internal organs of anterior region of trunk. **C**, chaeta; **D**, section of anal vesicle. **cha**, chaeta; **dbv**, dorsal blood vessel; **int**, intestine; **nel**, nephrostomal lips; **nep**, nephridium; **prb**, proboscis; **si**, siphon; **tr**, trunk; **vbv**, ventral blood vessel; **vnc**, ventral nerve cord. [I. Grant]

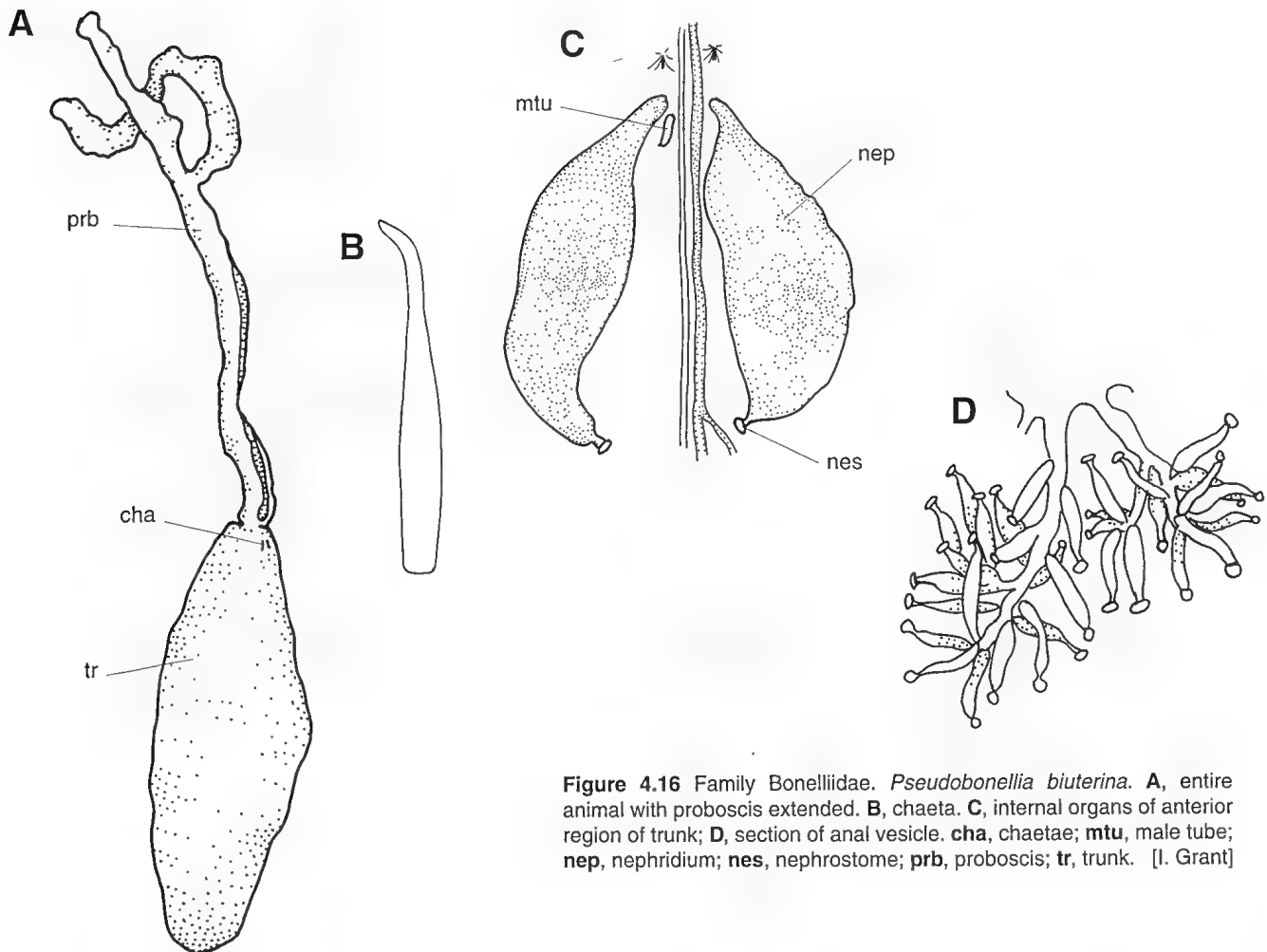


Figure 4.16 Family Bonelliidae. *Pseudobonellia biuterina*. **A**, entire animal with proboscis extended. **B**, chaeta. **C**, internal organs of anterior region of trunk; **D**, section of anal vesicle. **cha**, chaetae; **mtu**, male tube; **nep**, nephridium; **nes**, nephrostome; **prb**, proboscis; **tr**, trunk. [I. Grant]

Rieger 1990). Ventral chaetae may be present or absent. The male is dependent on the female for food and protection. The type genus is *Bonellia* Rolando 1821.

The two most commonly collected intertidal and subtidal, bonelliids in Australia are *Metabonellia haswelli* (Fig. 4.15; Pl. 11.4) and *Pseudobonellia biuterina* (Fig. 4.16). Both are green in colour and have a bifid proboscis capable of great extension. The two are readily distinguished on dissection, the former having a single nephridium and the latter, two nephridia; in *P. biuterina*, the very small male is situated in a small tube between the nephridia.

Bonelliids are tube dwellers; in Europe *B. viridis* is reported to inhabit burrows with multiple exits in rocky substrata (Schembri & Jaccarini 1978). There does not appear to be any record of a bonelliid making its own tube, the burrows inhabited by *B. viridis* often being made by thalassinoid mud prawns of the genus *Upogebia*. In South Australia, *M. haswelli* is often collected by divers from under large boulders that rest on sandy sediments, so that when the boulders are moved the animals float away from their homes. *Pseudobonellia biuterina* has been collected from both coral and limestone formations in Queensland and Western Australia. *Metabonellia haswelli* is known from New South Wales, Victoria, Tasmania, Western Australia and South Australia where it is common.

Bonelliids have also been dredged from the ocean floor at great depths, for example, *Vitjazema ultraabyssalis* (Fig. 4.17D, E) at 9700 m and *Torbenwolffia galatheae* at 8300 m. Four deep-water species, *Zenkevitchiola brevirostris*,

Sluiterina alba, *Vitjazema ultraabyssalis* and *Protobonellia papillosa* were collected off the south coast of Australia by Murina (1978). Descriptions of the animals, in English, are given in Edmonds (1987). Zenkevitch (1966) considered that the Bonelliidae are '... a characteristic community of the abyssal and ultra-abyssal fauna and reach to the greatest depths of the oceans'. He also suggested that the sexual dimorphism of the family and the parasitism of the male are adaptations to life at great depths in a way '... similar to the conditions observed in angler fishes of the order Lophiiformes'.

The determination of sex in developing *B. viridis* has been studied by zoologists for more than 100 years and still engages their attention (see Reproduction and Development). The green pigment bonellin is now known to have lethal effects on a number of organisms and biological processes (see Morphology and Physiology).

The family Bonelliidae is large, comprising about 30 genera. Dattagupta (1976) divided the family into a number of subfamilies.

Order XENOPNEUSTA

The longitudinal musculature in Xenopneusta lies between the outer circular and inner oblique musculatures. Sexual dimorphism is not marked, the circulatory system is open, and the enlarged posterior gut acts as a respiratory organ. The order comprises a single family, Urechidae.

Family Urechidae

Members of the family Urechidae are moderate to very large in size. The trunk is sausage-shaped, rugose and long (up to 500 mm in *Urechis caupo*), but the proboscis short and scoop-like. Two ventral chaetae and one circlet of curved anal chaetae are present (Fig. 4.18). Slime glands open on the anterior part of trunk and near the nephridiopores. Urechids have two or three pairs of nephridia with spirally coiled nephrostomal lips and two large anal vesicles. The vascular system is open. The distal part of the midgut is greatly enlarged and functions as a respiratory chamber, water entering and leaving it through the cloaca and anus. Sexes are separate. The type genus is *Urechis* Seitz.

Urechids differ from other echiurans in their feeding action, that of entrapping fine particles in a slime net, and their method of anal respiration. Probably more is known about the

anatomy, physiology and ecology of the Californian species, *U. caupo*, than any other echiuran. Fisher (1946) described its anatomy, method of feeding and general ecology, Redfield & Florkin (1931) its respiration and Newby (1940) and Gould-Somero (1975) its reproduction and embryology. The family contains only one genus of five species. *Urechis novaezealandiae* is known from New Zealand (Knox 1957), but so far none has been recorded from Australia.

Order HETEROMYOTA

In Heteromyota, the longitudinal musculature of the body wall lies external to the circular musculature. Nephridia are numerous and unpaired, and large anal vesicles are present. The order contains a single family, the Ikedidae.

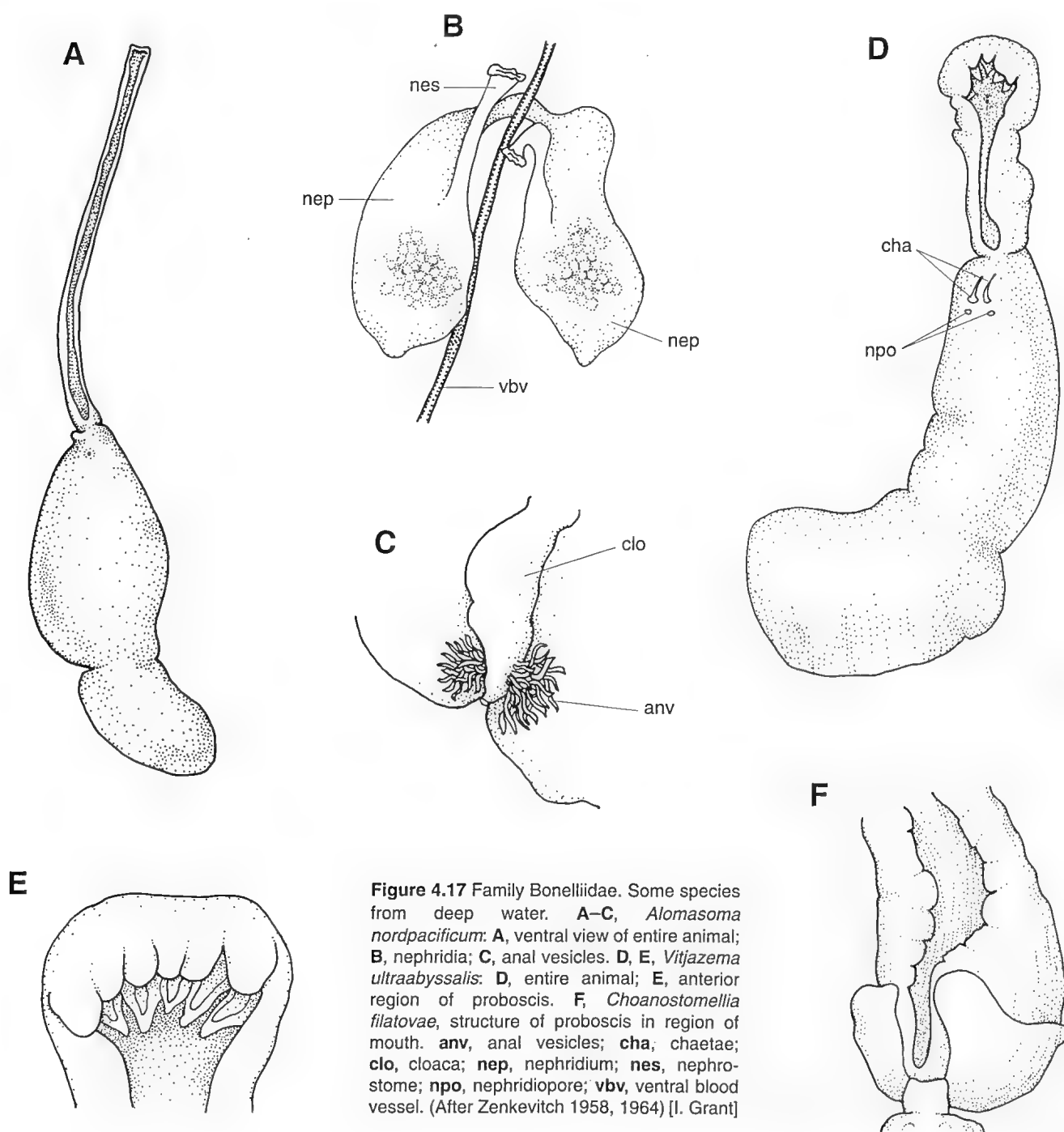


Figure 4.17 Family Bonelliidae. Some species from deep water. **A–C**, *Alomasoma nordpacificum*: **A**, ventral view of entire animal; **B**, nephridia; **C**, anal vesicles. **D, E**, *Vitjazema ultraabyssalis*: **D**, entire animal; **E**, anterior region of proboscis. **F**, *Choanostomellia filatovae*, structure of proboscis in region of mouth. **anv**, anal vesicles; **cha**, chaetae; **clo**, cloaca; **nep**, nephridium; **nes**, nephrostome; **npo**, nephridiopore; **vbv**, ventral blood vessel. (After Zenkevitch 1958, 1964) [I. Grant]

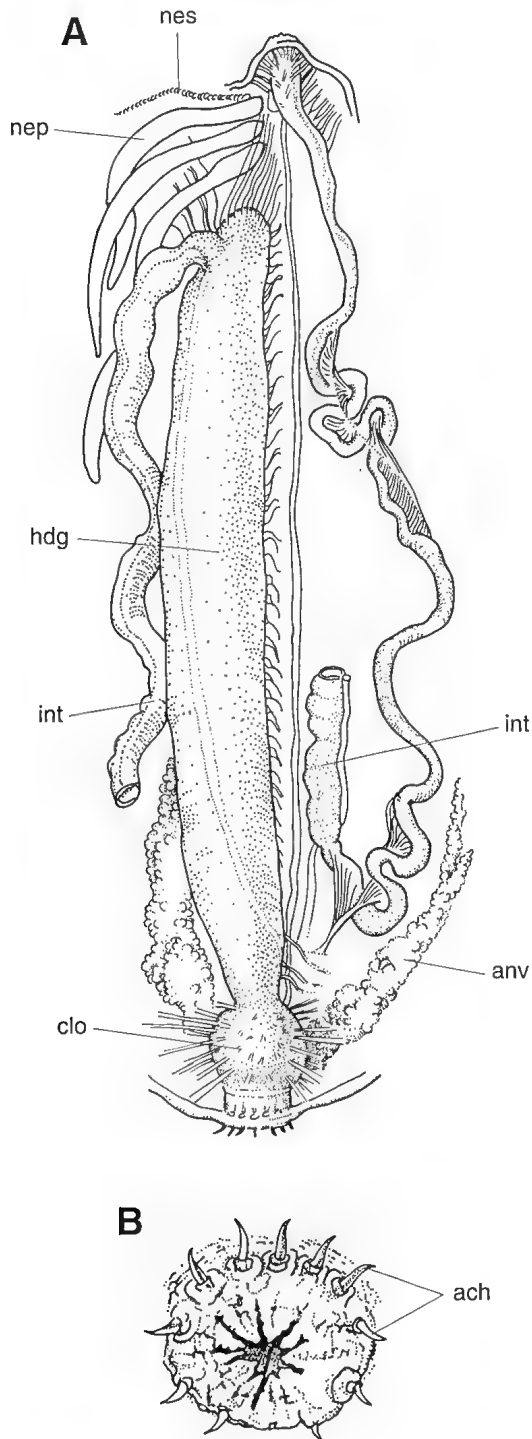


Figure 4.18 Family Urechidae. **A**, morphology of the trunk of *Urechis caupo*. **B**, circlet of anal chaetae of *Urechis* species. **ach**, anal chaeta; **anv**, anal vesicles; **clo**, cloaca; **hdg**, hindgut (respiratory); **int**, intestine (in part only); **nep**, nephridium; **nes**, nephrostome. (After Fisher 1946) [I. Grant]

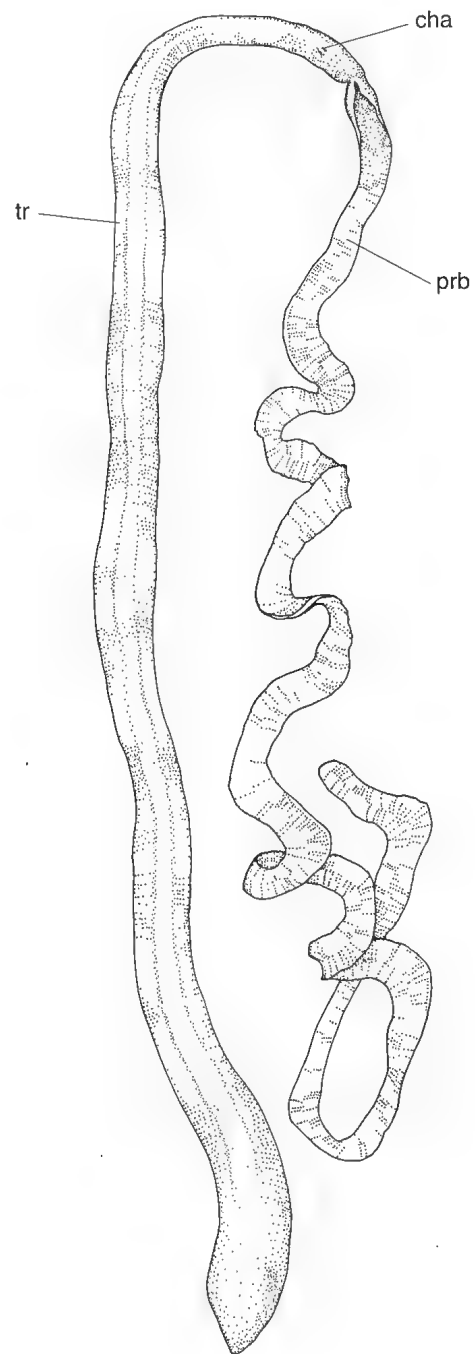


Figure 4.19 Family Ikedidae. *Ikeda taenioides*, ventral view of entire animal. **cha**, chaetae, two present; **prb**, proboscis; **tr**, trunk. (After Ikeda 1907) [I. Grant]

Family Ikedidae

Ikedids are large, the trunk reaching up to 400 mm long and 20 mm wide (Fig. 4.19). The longitudinal musculature of body wall is reported to lie exterior to the circular musculature (Ikeda 1907) and is thickened to form bands (five in *Ikeda taenioides*). The proboscis is very long (up to 1 m in the extended state) and flat. Nephridia are very numerous (more than 200) and unpaired; the nephrostome is situated distally.

The family contains only one species, *Ikeda taenioides*, described from Japan. Edmonds (1987) tentatively identified a large echiuran from Gulf St Vincent, South Australia, as *Ikeda* species. Its trunk was 290 mm long and 7–11 mm wide. Its proboscis was 400 mm long and its surface marked with numerous, transverse brown to black bands (Pls 11.5, 11.6). Five longitudinal bands are present in its body wall. Unfortunately the nephridial and anal regions of the single specimen were badly damaged during collection.

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5. PHYLUM SIPUNCULA

Stanley J. Edmonds†

DEFINITION AND GENERAL DESCRIPTION

The Sipuncula is a group of soft-bodied, unsegmented, coelomate, worm-like marine invertebrates (Fig. 5.1; Pls 12.1–12.4). The body consists of a muscular trunk and an anteriorly placed, more slender introvert (Fig. 5.2), which bears the mouth at the anterior extremity of an introvert and a long, recurved, spirally wound alimentary canal lies within the spacious body cavity or coelom. The anus lies dorsally, usually on the anterior surface of the trunk near the base of the introvert. Tentacles either surround, or are associated with the mouth. Chaetae or bristles are absent. Two nephridia are present, occasionally only one. The nervous system, although unsegmented, is annelidan-like, consisting of a long ventral nerve cord and an anteriorly placed brain. The sexes are separate, fertilisation is external and cleavage of the zygote is spiral. The larva is a free-swimming trochophore. They are known commonly as peanut worms.

Sipunculans live in burrows, tubes and protected places. The trunk may be stout and cylindrical, long and worm-like, globular, pear-shaped, flask-like or twisted into a spiral, and is larger than the introvert. The trunk wall is often thick and highly muscular. The introvert arises at or near the anterior extremity of the trunk and its diameter is noticeably less than that of the trunk. It is a highly elastic organ capable of considerable extension and, at other times, complete or partial retraction within the body cavity. Papillae and glandular and sensory bodies are usually present on the surface of the trunk and introvert; sometimes they are prominent. Hooks and/or spines that are often found on the surface of the introvert assist in food collection. A number of tentacles are associated with the mouth and are involved in both the exchange of respiratory gases and the gathering of food particles. The trunk encloses a large, fluid-filled coelom. Within the coelom a number of retractor muscles (one to four) connect the anterior extremity of the introvert to the wall of the trunk, usually in its mid- or posterior region. A very long alimentary canal lies more or less freely in the coelomic fluid; it comprises: an oesophagus, attached for most of its length by mesenteries to the retractor muscles; the descending and the ascending, spirally wound loops of the intestine, and; a short straight rectum. Attached to the oesophagus is a tubular contractile ('polian' or 'compensatory') vessel which contains fluid and blood cells.

The external openings or nephridiopores of the nephridia are situated ventro-laterally at the anterior of the trunk. The nephridia are involved in excretion and possibly osmoregulation. They also serve as gonoducts. The coelomic fluid contains nucleated blood cells, which carry the respiratory pigment haemerythrin, coelomocytes and

developing eggs or sperm. The nerve cord is ventral and its anterior extremity is connected by two oesophageal connectives to a dorsal cerebral ganglion or brain. Sensory structures such as tactile organs, eyespots, chemoreceptors and a nuchal organ are present in many species. The gonads develop at the base of the ventral retractor muscles and the sexes are separate and difficult to distinguish unless eggs or sperms are present in the coelom. Gametes pass from the coelom to the nephridia through a ciliated nephrostome and from the nephridia to the exterior through a nephridiopore. Fertilisation takes place in the sea and the zygote develops into a free-swimming trochophore larva. In some species, the trochophore undergoes further metamorphosis to form a pelagospaera larva before finally becoming an adult. No signs of segmentation have been observed in any of the developmental stages of the animal.

Sipunculans live in tropical, temperate and polar seas, from the intertidal regions of the shore to the floor of the oceans at depths of 6860 m (Murina 1964; Stephen & Edmonds 1972; Cutler 1977). Fisher (1952) considered that they will live in any protected place that provides access to reasonably clear water and food. According to Cutler (1994), the phylum contains about 150 species. Until recently, the most useful general accounts of the phylum were those of Hyman (1959) and Tetry (1959). Cutler's (1994) monograph updated these works and added sections on their systematics and evolution.

Sipunculans must have been known for centuries to the inhabitants of those parts of the world where the worms were used as food. *Siphonosoma cumanense* (*S. edule*) was eaten by the natives of southern Java (Kohn 1975), *Sipunculus robustus* by the inhabitants of the western Carolines (Sato 1935; Kohn 1975) and *S. nudus* and *Phascolosoma* species by the people of Amoy, China (Chin 1947). Chin's recipe for cooking sipunculans advised prolonged boiling after the addition of salt and vinegar and recommended eating with 'hot mustard'. Whether the worms were eaten by Australian aborigines along the north coast of the continent is not known.

HISTORY OF DISCOVERY

An account of the history of the Sipuncula is given by Hyman (1959). Linné (1767) recognised *Sipunculus* as an order of Vermes. Quatrefages (1847) considered sipunculans, echiurans and priapulans to form a group which he called Gephyrea (*gephyrea* = a bridge), thinking that they were a connection between the annelids and holothurians. The term 'Gephyrea', however, has no status in modern zoological nomenclature (Hyman 1959). Stephen (1965) proposed the name 'Sipuncula' for the phylum, a term which seems to have gained general acceptance.

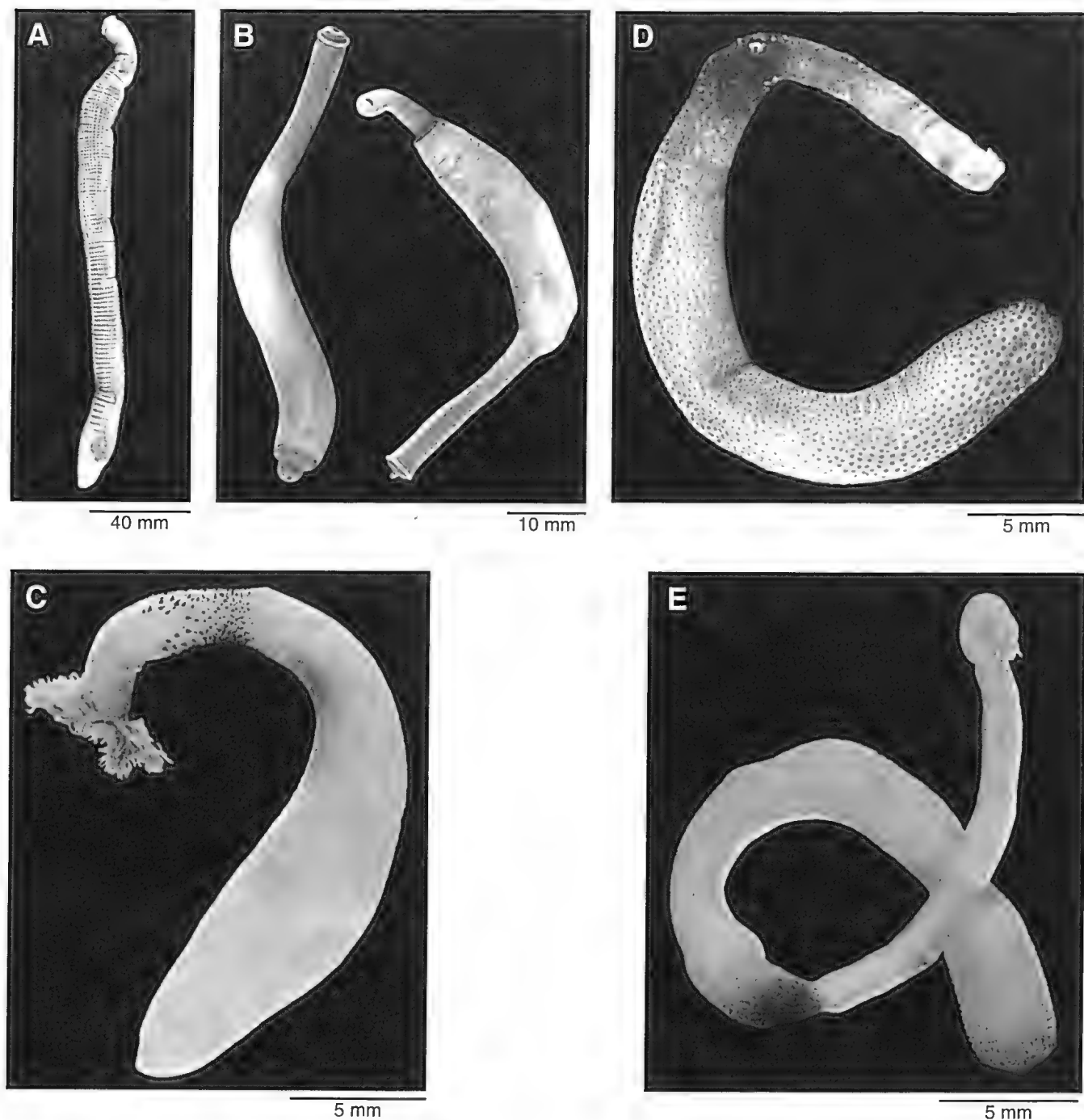


Figure 5.1 External appearance of Australian sipunculans. **A**, *Sipunculus robustus* (Sipunculidae); **B**, *Golfingia vulgaris herdmani* (Golfingiidae); **C**, *Themiste variospinosa* (Themistidae); **D**, *Phascolosoma annulatum* (Phascolosomatidae); **E**, *Aspidosiphon laevis* (Aspidosiphonidae). (A, B, D, from Edmonds 1982; C, E, from Edmonds 1980)

Most of the identifications of Australian sipunculans were made before 1900 by European workers. The first new species described in an Australian journal was *Themiste dehamata* by Kesteven (1903) from the coast of New South Wales. Among the earliest records of Australian sipunculans is that of *Sipunculus heterocyathi* described in 1862 by McDonald, surgeon of HMS *Icarus*, from a solitary coral, *Heterocyathus* species, collected from Moreton Bay, Queensland. Today the sipunculan is known as *Aspidosiphon muelleri*, the name *heterocyathi* having been 'overlooked' (Saiz-Salinas 1986). *Phascolosoma noduliferum* described by Stimpson (1855) was reported from Sydney by Keferstein (1865) and from Nickol Bay, Western Australia by Baird (1868). Keferstein (1865) also reported *Siphonosoma australe* from Sydney.

Baird (1868) recorded *Sipunculus angasi* from Port Lincoln, South Australia, *Sipunculus deformis* from Sir Charles Hardy Island, Great Barrier Reef and *Themiste lageniformis* from Sydney. The first two species are today known respectively as *Sipunculus robustus* and *Siphonosoma cumense*, whereas *T. lageniformis* is still a valid species name. References, mostly taxonomic, to other species are found in Selenka, Man & Bülow (1883), Augener (1903), Kesteven (1903), Fischer (1914, 1919, 1921, 1927), Monro (1931) and Wheeler (1938). Later studies are those of Edmonds (1955, 1956, 1980, 1982, 1986, 1987), Murina (1964, 1972j), Cutler (1977) and Gibbs (1978). Edmonds (1980) listed and provided a key to the Australian species.

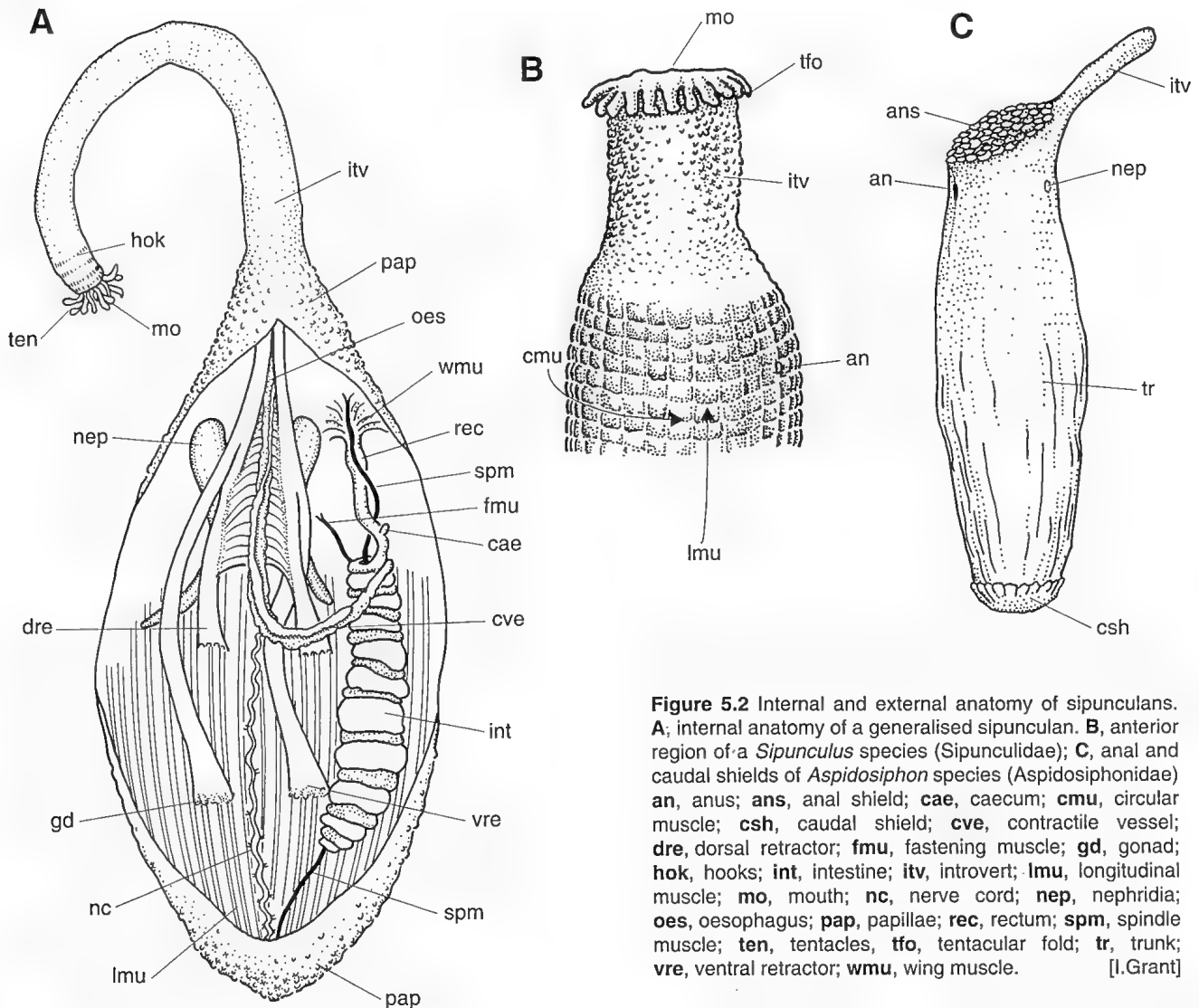


Figure 5.2 Internal and external anatomy of sipunculans. **A**, internal anatomy of a generalised sipunculan. **B**, anterior region of a *Sipunculus* species (Sipunculidae); **C**, anal and caudal shields of *Aspidosiphon* species (Aspidosiphonidae) **an**, anus; **ans**, anal shield; **cae**, caecum; **cmu**, circular muscle; **csh**, caudal shield; **cve**, contractile vessel; **dre**, dorsal retractor; **fm**, fastening muscle; **gd**, gonad; **hok**, hooks; **int**, intestine; **itv**, introvert; **lmu**, longitudinal muscle; **mo**, mouth; **nc**, nerve cord; **nep**, nephridia; **oes**, oesophagus; **pap**, papillae; **rec**, rectum; **spm**, spindle muscle; **ten**, tentacles; **tfo**, tentacular fold; **tr**, trunk; **vre**, ventral retractor; **wmu**, wing muscle. [I. Grant]

Physiological and ecological studies of Australian species are few. Edmonds (1957a, 1957b) published an account on the respiratory metabolism and the catabolism of nitrogen compounds of *Themiste cymodoceae*. Green (1975a, 1975b) published two papers about *Phascolosoma arcuatum*; the 'mangrove sipunculan', one on its annual reproductive cycle and the other on its habits, population structure and feeding patterns. Manwell (1963) showed that the vascular and coelomic haemerythrins of *Themiste cymodoceae* are different by comparing chromatographically ('fingerprinting') the range of peptides formed when the two pigments are digested with trypsin. Worthington (1956) studied the X-ray diffraction patterns of the retractor muscle of *T. cymodoceae*.

MORPHOLOGY AND PHYSIOLOGY

Body Wall and External Characteristics

The functions of the body wall of a sipunculan are protective, secretory, sensory, locomotory, osmoregulatory and, in some species, respiratory and possibly excretory. The wall is usually thick and comprises the layers: cuticle, epidermis, dermis, circular muscle, longitudinal muscle and peritoneum. Sometimes a thin layer of oblique or diagonal musculature is present.

The cuticle is a secretion of the dermis and is composed of unbanded fibres of collagen arranged in orthogonal layers (Moritz & Storch 1970). It is thinnest in the region of the tentacles. Beneath the cuticle lies the epidermis which comprises cuboidal cells, except on the tentacles where the cells are columnar and ciliated. Cilia are otherwise absent from the outer surface of the body wall. The dermis is fibrous and contains connective tissue, and pigment, glandular and sensory cells. The dermis, for example, of some species of *Sipunculus*, *Siphonosoma* and *Xenosiphon*, contains fluid-filled canals, sacs or spaces which open to the coelom via pores (Fig. 5.3). The canals and spaces of *Siphonosoma ingens*, and some other species, are thought to assist in the transfer of oxygen from seawater to the coelomic blood cells (Manwell 1960).

The longitudinal musculature of the trunk wall may be grouped into bands, as in species of *Sipunculus*, *Siphonosoma* and *Phascolosoma*, or may be continuous, as in species of *Golfingia*, *Nephasoma*, *Thysanocardia* and *Themistes*. The circular musculature usually forms a continuous sheet, but sometimes it lies in definite bands, for example, in species of *Sipunculus* and *Xenosiphon*, or in fascicles, as in species of *Siphonosoma*. Both muscle layers of the introvert, however, are continuous. The innermost layer of the body wall, the peritoneum, is a flattened epithelium which gives rise to blood cells, coelomocytes, urn cells and gametes; some parts of it are ciliated.

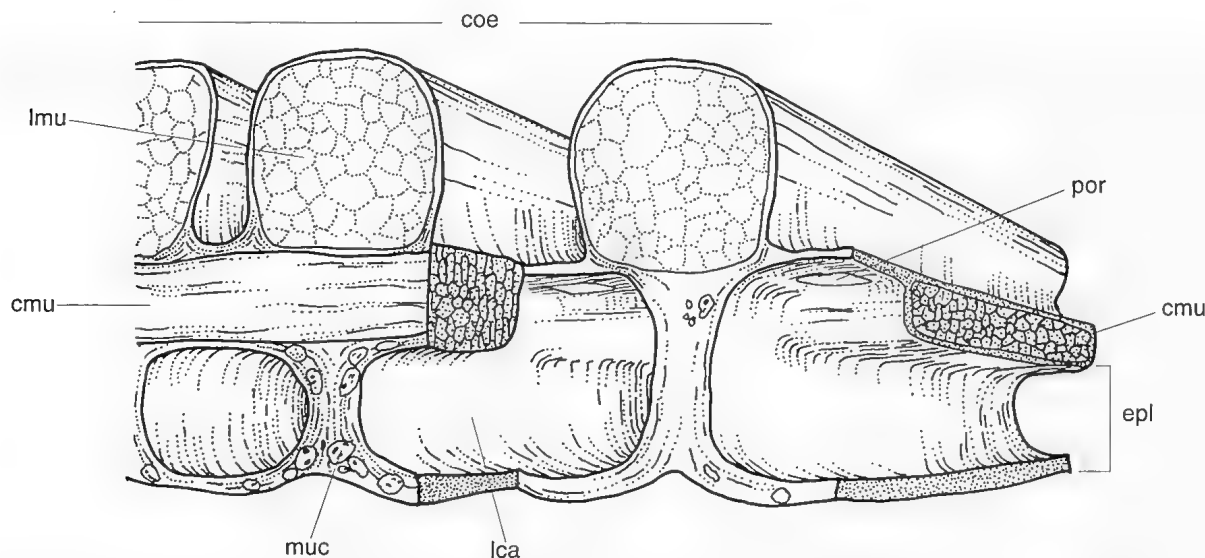


Figure 5.3 Section through the body wall of the trunk of *Sipunculus* species (Sipunculidae), showing position of muscles, coelom and longitudinal coelomic or epidermal canals. **cmu**, circular muscle; **coe**, coelom; **epl**, epidermal layer; **lca**, longitudinal canal; **lmu**, longitudinal muscle; **muc**, muscle cells; **por**, pore or opening connecting the coelom and canals. (After Trueman & Foster-Smith 1976) [I. Grant]

The skin varies considerably in colour and appearance. For example, it is light grey and smooth in *Themiste* and *Golfingia* species, red and reticular in *Sipunculus* species and dark brown and rough in *Phascolosoma* and *Aspidosiphon* species (Pls 12.1, 12.2, 12.3). It may bear papillae on the trunk and introvert, anal and caudal shields and holdfasts on the trunk, and hooks or spines on the introvert. The papillae may be tall, conical, pear-shaped, hemispherical or almost flat. In some genera, such as *Phascolosoma*, papillae may be rounded or mammillate and are often covered with numerous dark brown, polygonal to rounded platelets, and are prominent, especially on the anterior and posterior surfaces of the trunk. A small pore, which communicates with glandular cells in the dermis and epidermis, is present at the tip of the papillae. The composition and nature of the substances secreted by the glandular cells is not known. In some species, they may be lubricatory; for example, a contracted and turgid specimen of *Themiste cymodoceae* is slippery. In rock-boring species the secretions may assist in the decomposition of the substratum. A yellow to dark red anal shield of hardened plates is prominent on the antero-dorsal surface of the trunk of *Aspidosiphon* species and a flat to conical caudal shield is also sometimes present at the posterior extremity. A white, spherical to pineapple-like cap is always found at the anterior extremity of the trunk of *Cloeosiphon* species and a white, truncated to conical structure in species of *Lithacrosiphon*. Prominent, hardened 'holdfasts' are secreted by large glandular papillae on the trunk of many species of *Phascolion* that usually live in the discarded shells of molluscs. It has been suggested that their function is one of fixation (Hyman 1959); Hylleberg (1975), however, considered that their scraping action helps to keep the inside of the animal's shelter clean.

The hooks and spines on the introvert of some species assist in the collection of food by scraping algae from rocks (Rice 1976) and also help to fix some species, for example, *Phascolion* species, when they drag themselves on top of sand, silt or rock (Goreau & Yonge 1968). Introvert hooks in the class Sipunculidea are usually simple, thorn-like hollow structures that are irregularly distributed, but in the Phascolosomatidea they are recurved, usually with an internal structure and marking and closely packed in regularly placed rings. The shape and markings of the hooks often help in the identification of species.

A terminal organ is present in the pelagosphaera larva of some sipunculans and in adult specimens of some species of *Sipunculus*. Its structure and function in pelagosphaera larvae has been studied by Ruppert & Rice (1983). It is a small rounded, knob-like organ joined by a small neck to the posterior extremity of the trunk and contains mucus-secreting, sensory, muscle and tension-bearing cells. The organ is considered to assist the larva in selecting a suitable environment for settlement (for example, rock and not sand), and subsequent adhesion and to augment the animal's food supply by secreting mucus that traps detritus and bacteria. The organ is flexible, enabling the animal to sway with marine currents and permitting it to feed both on the bottom surrounding its point of attachment and in the water column above.

A terminal organ is also found at the posterior extremity of a number of adult *Sipunculus* species, for example, *S. robustus* (= *angasi*), *S. norvegicus*, *S. nudus* and *S. (= Xenosiphon) mundanus* (Edmonds 1955; Åkesson 1958). It is a small sac-like bulb capable of invagination, the condition usually found in preserved specimens. Whether the structure is evaginated or invaginated depends on the pressure of the coelomic fluid in the sac and on the tension of two small longitudinal retractor muscles in the organ (Åkesson 1958). Its function is not known.

Muscles, Movement and Locomotion

Although sipunculans are often regarded as sedentary in their habits, some, especially those that burrow in sand or silt, show considerable activity when they dig. When threatened, most are able to retract their sensitive and probing introvert, often with surprising rapidity.

The introvert is evaginated by contraction of the circular musculature of the body wall and an increase in the hydrostatic pressure of the coelomic fluid. Invagination of the introvert is caused by the contraction of the retractor muscles. These muscles lie within the coelom and extend from the anteriormost region of the introvert to the coelomic surface of the body wall, where they fuse with the longitudinal muscle layer. In some genera, for example, *Sipunculus*, *Xenosiphon*, *Siphonosoma*, *Phascolosoma* and *Golfingia*, there are four

retractors: a ventral pair, lying close to the nerve cord, and a dorsal pair, more remote from the nerve cord. In others, for example, *Themiste*, *Nephasoma*, *Thysanocardia* and *Aspidosiphon*, only a ventral pair is present. There appears to be only one retractor in species of *Onchnesoma*, and may be one to three in *Phascolion* species.

Retractor muscles consist of small, non-striated fibres and very little connective tissue. Prosser, Ralph & Steinberger (1950), Prosser, Curtis & Travis (1951), Prosser & Melton (1954) and Prosser & Spererlakakis (1959) showed that the action potentials of the retractors of *Phascolopsis gouldi* consisted of two components: an all or none spike which fatigues rapidly on repeated stimulation and, a slower wave which facilitates on stimulation. They found, however, that only one type of muscle fibre was present. They concluded that when the animal retracts its introvert it rapidly produces a volley of spikes which cause a quick contraction and then cease. The spikes are then replaced by a more persistent series of slow waves which causes the muscle to remain contracted. Prosser stated 'that conduction in the proboscis retractor of *P. gouldi* is in parallel nerve fibres; that one group of fibres elicits fast all-or-none potentials whereas a second group elicits a gradual end-plate type of muscle potential. Both types of innervation appear to be 'cholinergic'.

The long thread-like spindle muscle is fixed anteriorly in the musculature of the body wall or on the wall of the rectum near the anus. It may or may not be fixed posteriorly at the extremity of the trunk. It traverses and supports the coils of the intestine, determining their length in relation to that of the trunk. Prosser *et al.* (1959) showed that whereas the conduction in the retractor is through nerve fibres, conduction in the spindle muscle is independent of nerves and is produced by mechanical pull from one region to the next. Prosser *et al.* (1959) remarked that the 'muscle is excited to graded responses by quick stretches and is unusually sensitive to mechanical stimulation'.

The burrowing action of *Sipunculus nudus* has been studied by Zuckerkandl (1950) and Trueman & Foster-Smith (1976), and that of *Themiste hennahi* by Tarifeno (1975). Using cinematography and electronic recording devices Trueman & Foster-Smith (1976) determined that *S. nudus* penetrates sand by the forcible eversion of its introvert, brought about by a 'high amplitude pressure pulse of 1.8 N cm^{-2} in the coelomic fluid'. The movement depends on the fact that the trunk wall with its antagonistically arranged muscles encloses a large space filled with almost incompressible liquid. When the introvert is pushed forwards any backward reaction or movement of the animal is prevented by the anchorage of the

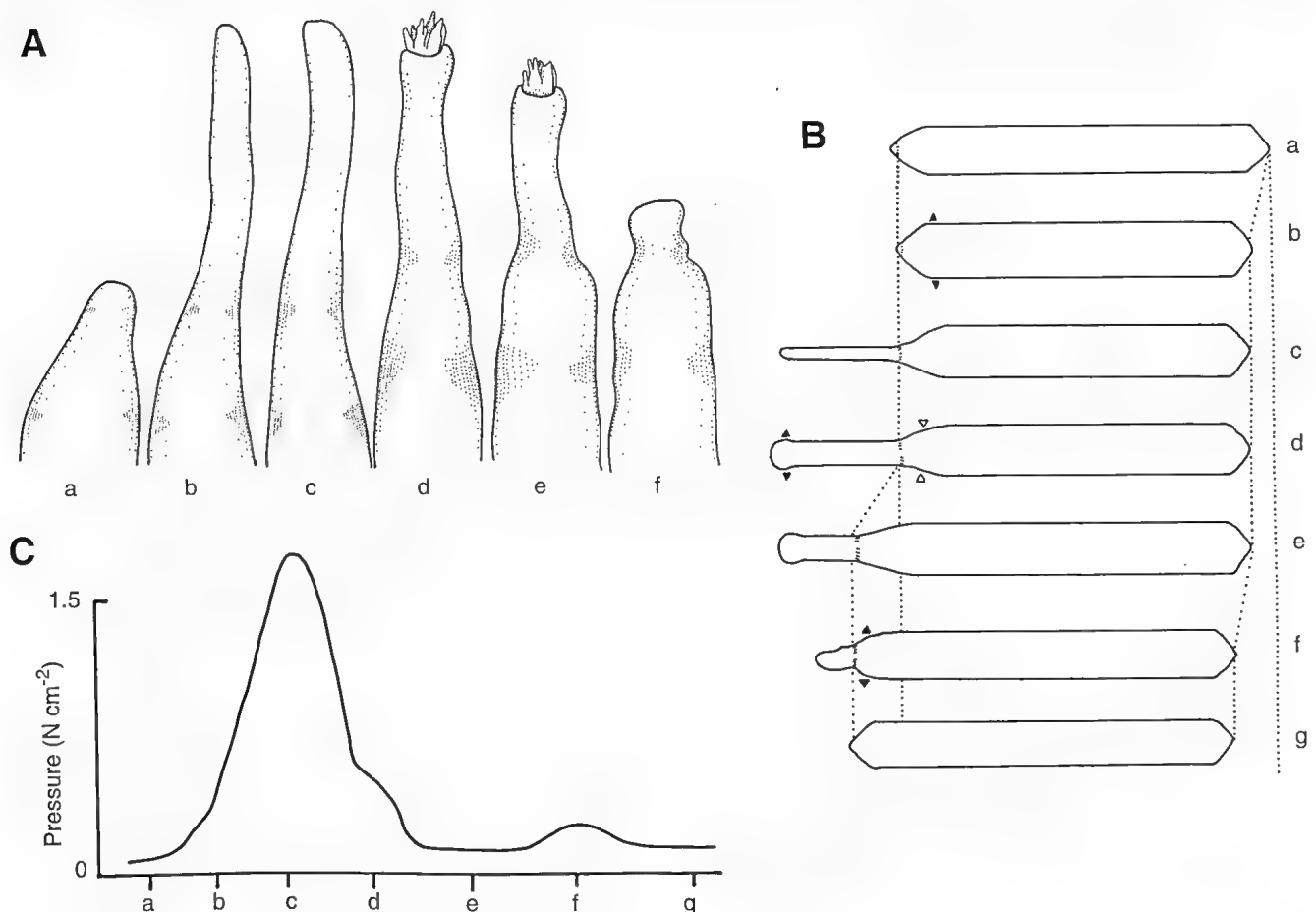


Figure 5.4 A, movement of the introvert of *Sipunculus* species (Sipunculidae) during burrowing - the cycle of activity: a, longitudinal contraction and thickening of trunk before extension of introvert; b, introvert rapidly everted and width of trunk is reduced; c, introvert dilates and tip swells to form an anchor; d, slow retraction of introvert draws trunk forward; e, anterior region of trunk swells, forming an anchor so that the posterior part of the trunk can be drawn forward; f, introvert rapidly retracts without movement of trunk. B, C, movement of the trunk of *Sipunculus nudus* (Sipunculidae): B, diagram of the cycle of digging; C, relationship of the cycle of digging to the internal coelomic pressure. a, resting stage; b, longitudinal contraction of trunk producing high internal pressure for eversion of introvert, $\blacktriangle$ = penetration anchorage; c, introvert everted followed by drop of internal pressure; d, introvert dilated to form a terminal anchorage, ∇ = terminal anchorage; anterior region of trunk becomes thicker causing loss of penetration anchorage; e, anterior region of trunk is pulled forward; f, anterior region of trunk thickens, the introvert retracts rapidly and posterior region of trunk is pulled forward; g, animal returns to a resting condition. Approximate length of cycle is 30 seconds. (After Trueman & Foster-Smith 1976)

trunk ('penetration anchor'). The subsequent anchorage of the introvert by dilation ('terminal anchor') and the relaxation of the penetration anchorage enable the anterior region of the trunk to be drawn forward when the introvert retractors contract. The cycle of events that takes place in the introvert and trunk is shown in Figure 5.4A,B. The pressures developed in the coelomic fluid and the corresponding stages of the digging cycle are related in Figure 5.4C. It may take an animal 5–10 minutes before it reaches a stable position in the sand.

Tarifeno (1975) found that the chances of finding specimens of *Themiste hennahi* in a given locality depend on the relative diameters of the introvert of the animal and the interstices between the particles of the substratum.

Sipunculans have been observed to swim and to make 'defensive movements'. Zuckerkandl (1950) reported that freshly collected specimens of *Sipunculus nudus*, when placed in an aquarium, may swim by regular beat-like flexures of their trunk. Fisher (1954) collected, with the aid of a hand net, swimming specimens of *Sipunculus* species from the Gulf of California. Zuckerkandl (1950) also noticed that 'strongly excited' specimens of *S. nudus* and *Phascolopsis gouldi* in an aquarium sometimes make 'defensive movements', such that the anterior and posterior extremities of the body are rapidly brought together, sometimes even crossing. The coelomic pressures produced at such times were greater than those produced during swimming.

Another form of movement takes place in *Aspidosiphon muelleri* and *Phascolion sirombus*; the former lives in solitary corals and the latter in the discarded shells of molluscs. Both sipunculans are able to pull the coral or shell which they inhabit from one place to another by extending their introvert in the surrounding substratum, using their hooks and tentacles to gain an anchorage and then contracting their introvert. The feeding range of the sipunculan (and coral) is thus increased (Goreau & Yonge 1968).

Osmoregulation

A sipunculan placed in diluted sea water swells and gains weight. Conversely, it shrinks and loses weight when placed in more concentrated sea water. The early work of Adolph (1936) showed: that the body wall of *Phascolopsis gouldi* is permeable to water, but more so to an inward than outward flow; that the body wall is impermeable to salts, and; that the gain or loss in weight is a response to osmotic stress.

Water and salt balance of sipunculans has been well studied since 1936 (see Oglesby 1982 for early references and Cutler 1994). The studies have demonstrated that sipunculans are basically osmoconformers, that is, the osmotic pressure of the coelomic fluid of specimens at equilibrium is close to that of their external medium. Nevertheless, sipunculans are not perfect osmoconformers and have a limited ability to regulate their volume.

Oglesby (1968) studied the osmotic and chloride concentrations of the centrifuged coelomic fluid of *Themiste dyscrita* which had been adapted to a range of salinities. He found that the animal is isosmotic with, or is an osmoconformer in salinities of 188–639 mM NaCl (30–114‰ sea water). In a further set of experiments, Oglesby (1982) showed that the osmotic concentration of the coelomic fluid of *Phascolosoma gouldi*, adapted to salinities from 48–92‰ sea water, is not significantly different from iso-osmoticity. He found, however, that the coelomic fluid is significantly

hypo-ionic to the medium with, respect to Cl^- , 'somewhat hyper-ionic', with respect to Na^+ and 'markedly hyper-ionic' with respect to K^+ .

A number of other factors may be involved in volume regulation, for instance, water and salt excretion by nephridia (Gross 1954; Kamemoto & Nitta 1964) and the transference of osmotically active particles between the tissue and body fluids when hyposmotic stress is imposed (Gross 1954; Virkar 1976a).

Most sipunculans live below the level of low tide and thus are not exposed to variations of salinity. It is possible, however, that those that inhabit tidal flats and intertidal reefs may be subjected to some osmotic stress, especially after heavy rains and flooding. In such situations, their ability to behave as osmoconformers would be an advantage, for example, *Phascolosoma arcuatum* (= *P. lurco*), which lives in or near mangrove flats where it may be cut off from the sea for days (Sasekumar 1974) and at other times be subject to tropical rainstorms. Harms & Dragendorff (1933) studied the osmoregulation of specimens from India and Green & Dunn (1976) of specimens from Malaysia. The latter workers found that animals kept for 64 hours in artificial sea water ranging in concentration from 40–100‰ were 'uniformly iso-osmotic and isotonic (with respect to Cl^-) at equilibrium'. Some differences, however, were noticed with specimens freshly collected in the field. At lower concentrations of the surrounding water the coelomic contents were hyperosmotic and hyperionic, but at higher concentrations the contents were isosmotic and isotonic. Green & Dunn (1976) suggested that, under natural conditions, mud around the animal and in its gut may act as a buffer, thereby allowing it to maintain an osmotic and ionic state different from that of its environment.

Feeding Habits and Digestive System

The gut of sipunculans usually contains sand, mud, small particles of coral or limestone rock, fragments of algae and sea grasses, pieces of molluscan shells, echinoderm exoskeleton and the skeletal parts of diatoms and foraminiferans. This suggests that sipunculans are detritus-feeders, extracting any food contained in whatever they ingest. Chin & Wu (1950) considered diatoms to be an important constituent in the food of a number of sipunculans living at Amoy, China. Rice (1975b) fed larvae of a number of sipunculans on algal cultures of *Phaeodactylum* and *Isochrysis* and the larvae of *Phascolosoma agassizi* on a mixture of diatoms and dinoflagellates collected from tidal pools.

Little experimental work has been done on the feeding behaviour and digestive process of sipunculans. In their study, Peebles & Fox (1933) observed that: although *Themiste hennahi* burrows into perfectly clean sand, it will not ingest any of the sand. Further, its tentacles are sensitive to small particles of food and to traces of chemicals, and the anterior region of its introvert, its tentacles and collar are the most sensitive to contact with foreign substances. It seems likely, then, that the animal is able to exercise some selection as to what it eats. There seems to be little evidence to support the claim that some sipunculans break up coral fragments into smaller particles (Gardiner 1903).

Rice (1976) described two types of feeding behaviour in rock-dwelling sipunculans. Species with long, extensible introverts and short digitiform tentacles feed by extending their introvert from the mouth of the burrow and grazing on the surface of the rock near them. She reported that '*Phascolosoma perlucens*, maintained in the laboratory in intact burrows, has been observed to feed from the surface of the rock on

sediment and detritus. Some particles adhere directly to the tentacles whereas others seem to be scraped off the rock by the small hooks of the introvert'. On the other hand, rock-dwelling species with long filiform tentacles and relatively short introverts such as *Phascolosoma antillarum* and *Themiste lageniformis* make use of a ciliary-mucous mechanism. 'The tentacular crown is extended above the mouth of the burrow and particles adhering to the sticky tentacles are directed by ciliary currents into the digestive tract'. Both *P. perlucens* and *T. lageniformis* are found on the Great Barrier Reef, Queensland (see Cutler 1994).

The structure and histology of the digestive system of a number of sipunculans has been studied: *Sipunculus nudus* (Metchnikoff 1900); *Nephasoma* (= *Golfingia*) *minutum* (Paul 1910); *Golfingia elongata* (Stehle 1953); *Phascolion strombus* (Arvy & Gabe 1952), and; *Phascolosoma arcuatum* (= *lurco*) (Lim 1970). The mouth at the anterior extremity of the introvert opens into a very long tubular gut which for most of its length is wound into a double helix coil (Fig. 5.5A). An anus usually lies on the dorsal surface of the trunk near the base of the introvert. The gut hangs suspended in the coelomic fluid and is usually connected to the coelomic wall of the trunk by mesenteries and/or by fastening and wing muscles. A thread-like spindle muscle, which arises anteriorly either from the body wall near the anus or from the rectum, traverses the coils of the intestine thus supporting them; by extension or contraction it adjusts the length of the coils to the length of the worm (Fig. 5.5A). The spindle muscle may or may not be fixed posteriorly to the trunk wall.

The innermost lining of the tract consists of columnar epithelial cells, sometimes organised so as to form longitudinal folds. Beneath the epithelium nerve cells and muscle fibres are embedded in a mass of connective tissue cells. The outer muscular fibres are longitudinal and the inner circular, an arrangement opposite to that in the body wall. The coelomic surface of the tract is lined with peritoneal cells. Structures known as ciliated pits are present in the walls of the descending loop of the intestine; they may even project out into the coelom like papillae. Cilia lining the pits direct substances secreted at the base of the pit into the lumen of the tract. Another structure called the ciliated groove (Fig. 5.5D) is found in the ventral wall of the intestine of sipunculans. It usually traverses the whole length of the gut and ends at the rectal caecum. Its function is not known. According to Cuénot (1900) and to Andrews (1890), the beating of the cilia in the groove would direct particles and liquids towards the posterior of the gut. The groove itself is reddish in colour, which suggests the presence of haemerythrin or myohaemerythrin.

Stehle (1953) distinguished on histological grounds the following regions in the gut of *Golfingia elongata*: pharynx, oesophagus, crop, stomach, midgut I (= first two thirds of the descending loop), midgut II (= last third of descending loop and first two spirals of ascending loop), hindgut, rectum, caecum. Stehle gave details of the histology of the various sections. The cellular structure of the midgut of *G. elongata* is shown in Figure 5.5B.

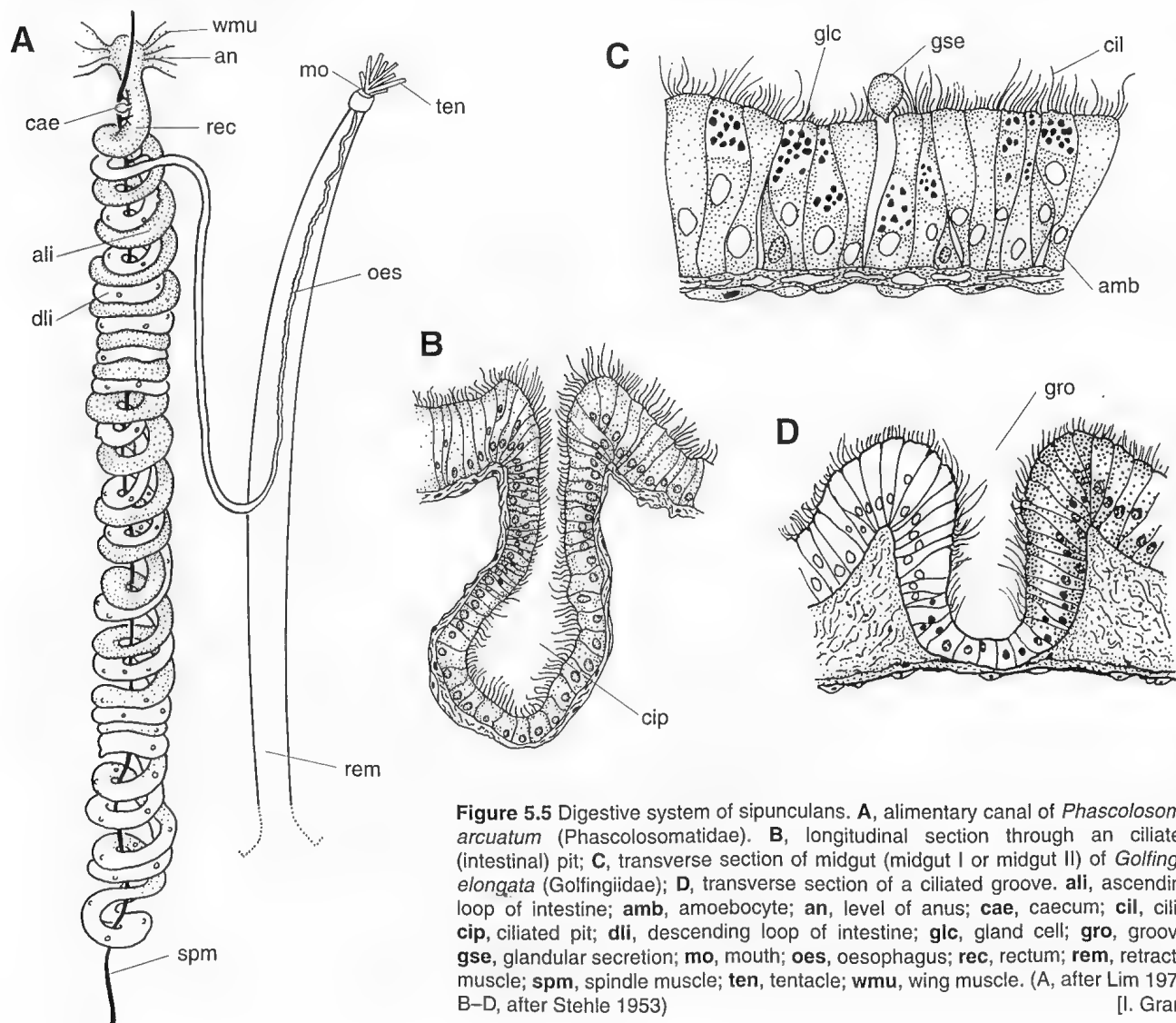


Figure 5.5 Digestive system of sipunculans. **A**, alimentary canal of *Phascolosoma arcuatum* (Phascolosomatidae). **B**, longitudinal section through an ciliated (intestinal) pit; **C**, transverse section of midgut (midgut I or midgut II) of *Golfingia elongata* (Golfingiidae); **D**, transverse section of a ciliated groove. *ali*, ascending loop of intestine; *amb*, amoebocyte; *an*, level of anus; *cae*, caecum; *cil*, cilia; *cip*, ciliated pit; *dli*, descending loop of intestine; *glc*, gland cell; *gro*, groove; *gse*, glandular secretion; *mo*, mouth; *oes*, oesophagus; *rec*, rectum; *rem*, retractor muscle; *spm*, spindle muscle; *ten*, tentacle; *wmu*, wing muscle. (A, after Lim 1970; B–D, after Stehle 1953) [I. Grant]

5. PHYLUM SIPUNCULA

Arvy & Gabe (1952), relying on histochemical techniques, considered that the oesophagus of *Phascolion strombus* was not involved in digestion, since it contained mucus-goblet, but no secretory cells. From the distribution of secretory cells, they concluded that the descending loop is the site of secretion, digestion and absorption and the ascending loop a storage region.

In *Phascolosoma arcuatum*, the mouth opens directly to a bulbous crop and no pharynx is present (Fig. 5.5; Lim 1970). The crop is followed by a stomach, recognisable by its yellow-brown pigmentation. The proximal midgut begins where the stomach ends and consists of most of the descending spiral. Its inner walls are thrown into longitudinal folds and ciliated pits are present. The distal midgut is made up of the extreme posterior part of the descending spiral and the first 20–30 mm of the ascending spiral. The hindgut is distinguished by its larger diameter and lack of ciliated pits. A ciliated groove runs along the inner edge of the spiral or helix. Lim considered that the proximal mid-gut region is the main site of the absorption of digested foods. He observed that digestion was mainly extracellular; the only place where intracellular digestion might occur was in the caecum where food vacuoles were observed in the cells of the mucosa. Lim found it difficult to distinguish between the hindgut and rectum.

Edmonds (1962) concluded that water is absorbed from the gut contents of *Sipunculus nudus* as they pass through the hind gut. The anterior position of the anus of a sipunculan allows wastes to be shed clear of the animal's burrow. Virkar (1976b) reported that *Phascolopsis gouldi* is able to remove C^{14} -glycine from dilute solution in sea water against an apparent concentration gradient and that much of the absorbed amino acid is soon incorporated in complex molecules within the animal. Further details on the digestive system are given by Cutler (1994).

Respiration

The body wall and tentacles are the sites of gaseous exchange in sipunculans. Cutler (1994) summarised information on gaseous exchange and adaptations to anoxia in sipunculans. The tentacles usually consist of a ring or near ring of finger-, thread- or fold-like structures situated near the mouth. The arrangement of the tentacles is important taxonomically: in the class Sipunculidea tentacles encircle the mouth, but in the Phascolosomatidea they form an incomplete ring about the dorsally placed nuchal organ.

A longitudinal furrow imparts a heart-shape to the tentacle in transverse section. The furrowed surface has a thick ciliated epithelium containing mucous cells, whereas the remaining area is covered by an epithelium consisting of cylindrical cells without cilia. Within the tentacles, three longitudinal canals or vessels communicate basally with a ring vessel or sinus which encircles the oesophagus near its anterior extremity. From the ring vessel arises a tubular structure, the contractile, compensatory or 'polian' vessel, which extends along the dorsal side of the oesophagus. Posteriorly it ends blindly. Usually it is single, but in *Sipunculus* and *Xenosiphon* it is double.

In *Thysanocardia* and *Themiste*, diverticula or villi arise from the contractile vessel and project into the coelom. The tentacular vessels, the contractile vessel and its villi, if present, constitute the so called 'vascular blood system' of a sipunculan. The fluid in the system, like that in the 'coelomic system' contains nucleated erythrocytes and coelomocytes.

The fluid in the contractile vessel of some living specimens has been observed to move of its own accord (Hyman 1959) although confirmatory evidence of the motion is scarce.

There is little doubt that the body wall plays a part in respiration. Peebles & Fox (1933) found that the removal of its tentacles was not fatal to *Themiste hennahi*. Manwell's (1960) experiments indicate that the body wall of *Siphonosoma ingens* is involved in the transfer of oxygen. Some sipunculans irrigate the tubes and cavity in which they live by peristaltic-like movements of their body wall. Hylleberg (1969) concluded that the irrigation of the shell of *Phascolion strombus* assists respiration. Pörtner, Heisler & Greishaber (1985) reported on the pumping-like action of the body wall of *S. nudus* when in its tube.

Uptake of oxygen in adult specimens of *Themiste cymodoceae* in sea water in the laboratory at 22°C varied from 4.5–5.5 $\mu\text{l/g/h}$ (wet weight), and that the rate of consumption decreased as the tension of the dissolved oxygen decreased (Edmonds 1957a). More recently Pörtner *et al.* (1985), using more modern techniques, found that at $\text{PO}_2 = 150$ torr, large specimens of *S. nudus* (about 35 g) consumed $0.69 \pm 0.07 \mu\text{mol O}_2/\text{g/h}$. With increasing hypoxia ($\text{PO}_2 = 50$ torr.) oxygen consumption fell to $0.41 \pm 0.08 \mu\text{mol O}_2/\text{g/h}$ or just 60% of the initial consumption.

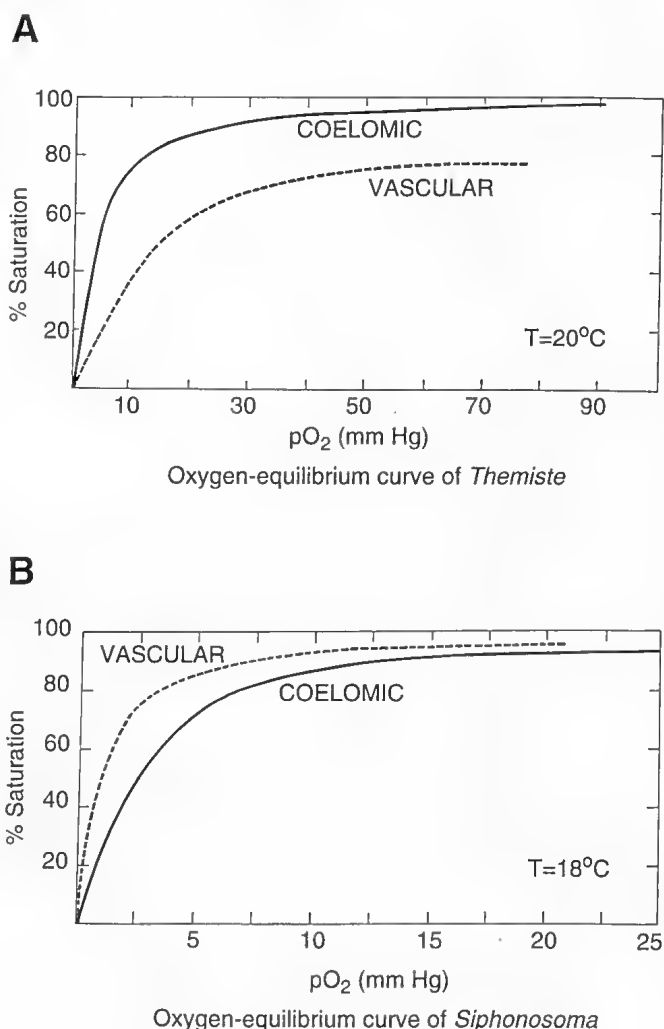


Figure 5.6 The oxygen equilibrium curves of two sipunculans: **A**, *Themiste* species (Themistidae); **B**, *Siphonosoma* species (Sipunculidae). (After Manwell 1960) [I. Grant]

The blood cells of both the vascular and coelomic systems are biconvex, nucleated, disc-like structures and have a diameter of 6–30 μm . They contain haemerythrin as a respiratory pigment; it combines reversibly with oxygen and that increases the oxygen carrying capacity of the blood. When fully saturated at 20°C, 100 ml of the coelomic fluid of *S. nudus* dissolves 1.6 ml of oxygen (Florkin 1933).

In spite of its name, haemerythrin is not a true 'haeme' because its metallic component, Fe, is attached to a protein molecule and not to a porphyrin. The haemerythrin molecule is made up of sub-units, each consisting of two Fe atoms attached to a polypeptide chain of 115 amino acids (Groskopf, Holleman, Margoliash & Klotz 1966a, 1966b). The molecular weight of each sub-unit is about 13 500 (Harrington, Muhoherac, Wharton & Wilkins 1981). Sometimes the haemerythrin molecule is octomeric, comprising eight sub-units, as in the coelomic fluid of *P. gouldi* and *Themiste dyscrita*; trimeric as in the coelomic fluid of *Phascolosoma agassizi*, or; monomeric in the myohaemerythrin of the retractor muscle of *Themiste hennahi* (Harrington *et al.* 1981). Manwell (1963) showed that the vascular and coelomic haemerythrins of a given species may differ slightly in composition in *T. cymodoceae*, *S. ingens* and *P. gouldi*.

In the deoxygenated molecule, haemerythrin is colourless and both iron (Fe) atoms in the subunits are unoxidised or in the Fe^{+2} condition. In the oxygenated state, the molecule is madder or burgundy in colour and the Fe/O_2 ratio is 2:1. Both oxygenated and deoxygenated haemerythrin are easily oxidised to methaemerythrin in which all the metal atoms are in the Fe^{+3} condition and which no longer reacts reversibly with oxygen. Haemerythrin does not show a 'Bohr' effect, that is its oxygen carrying capacity is unaffected by change in pH, and it does not react with carbon monoxide. It thus differs in both these respects from haemoglobin. The oxygen-equilibrium curve of the pigment in *S. nudus* was determined by Marrian (1927) and Florkin (1932). The pigment is 90% saturated at oxygen tensions of 30 mm and 50% saturated at 8 mm. It thus gives up its oxygen only at very low partial pressures, much lower than those that are commonly found in sea water. Additional details are given by Cutler (1994).

What then is the function of haemerythrin? Because sipunculans live in sand, mud, tubes and shells, where the tension of dissolved oxygen may at times be very low, it is possible that the oxygen combined with the haemerythrin is used only when the animal is living in very unfavourable conditions. It may be that the pigment is non-functional when the sipunculan is in well-oxygenated water. When conditions are adverse or when the oxygen tension is low externally, the pigment then may unload its store of oxygen.

Manwell's (1960) experiments show that the blood does transport oxygen in some species. *Themiste hennahi* is a thick-walled sipunculan that lives along the coast of California in sand and mud amongst the roots of *Zostera* species. It has a well-developed system of tentacles, a well-developed contractile vessel and long prominent tubules or villi which extend into the blood in the coelomic cavity. Manwell showed that at a given partial pressure of oxygen the haemerythrin of the coelomic fluid has a greater capacity for oxygen than does the fluid in the contractile vessel (Fig. 5.6A). This means that oxygen, having diffused through the tentacles, is taken up and transported by the vascular haemerythrin into the tubules of the contractile vessel. It then passes to the coelomic haemerythrin on account of the greater capacity for oxygen of the latter at the given tension. It seems, therefore, that the vascular haemerythrin of *T. hennahi* assists

in transporting oxygen from the exterior to the coelomic pigment and that the tentacular surface of the animal is a more important respiratory site than the body wall.

Siphonosoma ingens, on the other hand, is an actively burrowing, sand-dwelling sipunculan. Its tentacles, contractile vessel and villi are comparatively poorly developed. Its body wall is not uniformly thick like that of *T. hennahi*, but is thin because it contains a system of canals that are really extensions of the coelom. Manwell (1960) showed that the vascular pigment of the animal has a greater capacity for oxygen at a given partial pressure than the coelomic pigment (Fig. 5.6B). Thus, the situation is the reverse of that found in *T. hennahi*, and that the body surface is a more important respiratory site than the tentacles in *S. ingens*. Oxygen passes through the thin parts of the trunk wall to the pigment in the coelomic extensions and coelom and then to the vascular fluid. *Themiste hennahi* has been described as a 'tentacle breather' and *S. ingens* as a 'skin breather' (Prosser & Brown 1961). Corresponding similar ecological respiratory adaptations are probably to be found in the Australian species, *Themiste cymodoceae* and *Sipunculus robustus*.

Some sipunculans are capable of anaerobiosis. Peebles & Fox (1933) reported that *T. hennahi* was resistant to a lack of oxygen; Edmonds (1957a) found that *T. cymodoceae* was able to live for days in boiled water through which inert gases were passed, and even in paraffin oil. Oxygen stores in the blood were then found to be depleted.

More recently, Pörtner *et al.* (1984, 1985) studied anaerobiosis in *S. nudus*. They measured the activities of some enzymes involved in its intermediary metabolism and the level of some metabolites found in two situations. The first was during increased muscular activity (functional hypoxia), as when an animal is forced to dig until exhaustion, and the second during prolonged 'environmental hypoxia', as when animals live in places where oxygen levels may be low. They found that although anaerobiosis was only probably small during the usual burrowing activity, nevertheless there was 'a pronounced anaerobic synthesis of ATP', when burrowing extended for longer periods, for example 45 minutes. Octopine was the main end-product. When animals were held for 24 hours in seawater equilibrated with nitrogen, conditions similar to environmental hypoxia, their ATP level scarcely changed and the energy level in the retractor muscle and the body wall was almost the same. Pörtner *et al.* (1984, 1985) concluded that 'the anaerobic metabolism of *S. nudus* is obviously sufficient enough to cover energy requirements during hypoxia periods continuing much longer than those usually occurring in the habitat which last between 2–6 hours'. They also outlined different metabolic ways ATP sources could be maintained during hypoxia.

Excretion

The chief excretory organs of sipunculans are metanephridia (Fig. 5.7). They usually occur in pairs, but are present as a single organ, for example, in some species of *Onchnesoma* and *Phascolion*. They are usually situated on the ventral surface of the coelom at about the level of the anus. They also serve as gonoducts. The metanephridia have two apertures: the nephridiopore which opens to the exterior and the nephrostome which opens to the coelomic cavity. The nephrostome is usually a narrow opening, attached on one side to the coelomic wall and bearing on the other a ciliated lip. A ciliated tube leads from the nephrostome to the lumen of the nephridium. The organ is attached to the body wall at

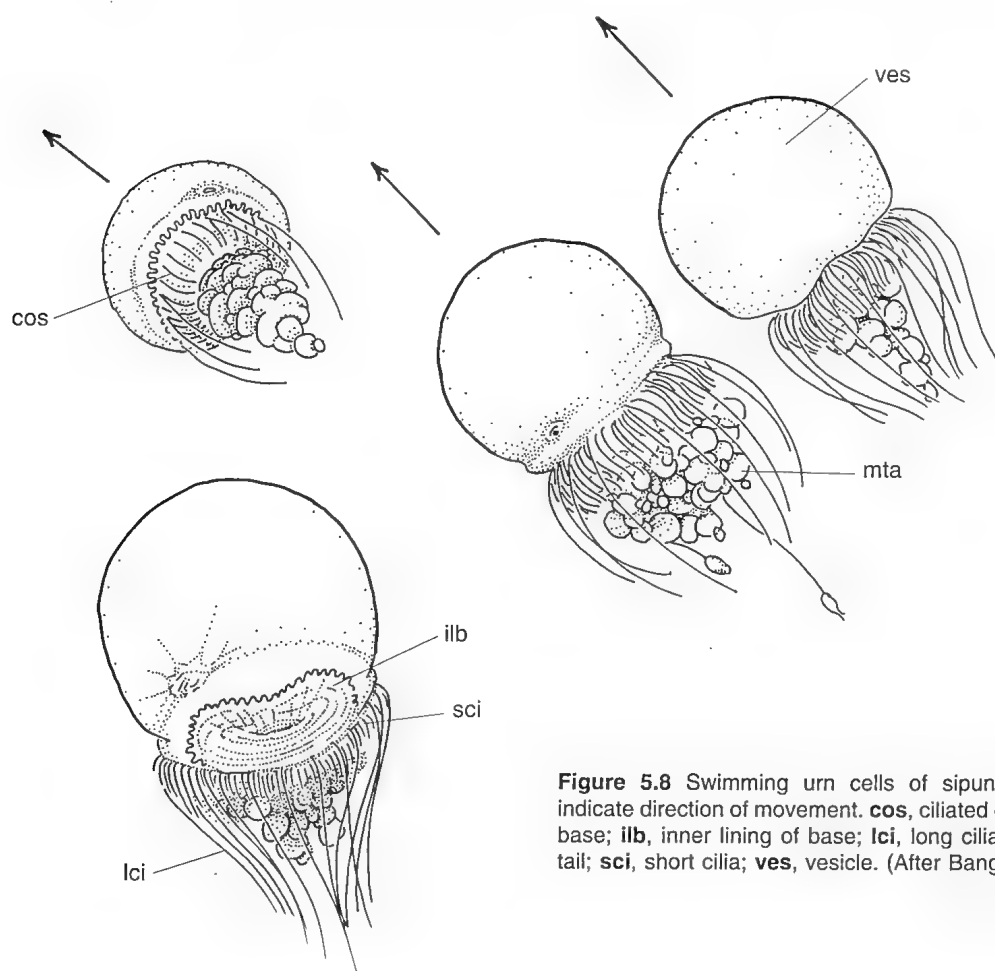


Figure 5.8 Swimming urn cells of sipunculans; arrows indicate direction of movement. **cos**, ciliated outer surface of base; **ilb**, inner lining of base; **lci**, long cilia; **mta**, mucous tail; **sci**, short cilia; **ves**, vesicle. (After Bang & Bang 1980) [I. Grant]

the nephridiopore and, sometimes, by a fine mesentery to the coelomic wall. The sac-like organ hangs more or less freely in the coelomic fluid and is capable of much distension. Its external lining is peritoneal. The nephridial wall consists of connective tissue, layers of circular and longitudinal muscles and internally a peritoneum of large cells often containing pigmented granules.

The excretory role of the organs was established experimentally by Harms & Dragendorff (1933) when they found that fluid withdrawn from the nephridia of *Phascolosoma arcuatum* (= *P. lurco*) contained ammonium salts. The final products of nitrogenous metabolism in sipunculans is excreted as ammonia (Florkin & Dutchateau 1942; Edmonds 1957b). Florkin & Dutchateau (1942) further demonstrated that uric acid is quickly decomposed in the tissues of *Sipunucla nudus*, and that the chain of enzymes uricase, allantoinase, allantoicase and urease is responsible for its decomposition.

Cell debris, foreign particles and intruding bacteria are removed from the coelomic fluid of some sipunculans (for example, *Sipunucla nudus*, *S. robustus* and *Phascolosoma gouldi*) by fixed and free-swimming urn cells (Fig. 5.8). Studies of urn cells include those of Cuénot (1902), Buytendyk (1909), Cantacuzène (1922a, 1922b, 1922c) and Bang & Bang (1962, 1965, 1976, 1980). Both kinds of urn cells share a common origin as fixed cell complexes in the epithelium of the coelomic wall. From time to time fixed cells are pinched off from the coelomic wall to become free-swimming cells. The structure of a free-swimming urn cell is shown in Figure 5.8 and comprises: a vesicle cell; a mucociliated base cell, and; a cluster of small secreting cells attached to the membrane of the base cell (Bang & Bang

1980). As they swim in the coelomic fluid urn cells slowly secrete mucus to which cell debris and other particulate matter adheres. The animal's own (autologous) blood cells are not entrapped. If pathogenic bacteria find their way into the body cavity, however, the urn cells secrete long trails of mucus in which the bacteria are immobilised and isolated. The mucous trails and foreign matter are then cast off as 'brown bodies'. These masses of waste material are commonly found in the coelom and are probably excreted through the nephridia. Cellular defence reactions and phagocytosis by granulocytes in *Phascolosoma* were studied by Dybas (1981). Further information on excretion in sipunculans is provided by Cutler (1994).

Reproduction, Development and Dispersal

An authoritative account of reproduction and development within the phylum is given in Rice (1975a, 1985b) and Cutler (1994). The following outline is based on Rice's detailed reviews.

In sipunculans, the sexes are separate and usually indistinguishable externally. The gonads are narrow, finger-like strands of tissue, situated at the base of the ventral retractors. The younger gametocytes are found proximally on the strand or nearer the base of the retractor than the older ones. Eventually, they are released into the coelom as floating cells where they undergo further growth and development. Close to the time of spawning the gametes move from the coelom, through the nephrostome, to the lumen of the nephridia.

Information is available on the annual gametogenic cycles of four species and on the breeding periods of about 20 (Rice 1975a). Most, however, were studied in the Northern Hemisphere. Green (1975a) found that the tropical species, *Phascolosoma arcuatum*, breeds in Queensland from December to the end of February.

At spawning time, gametes are expelled from the nephridia and fertilisation takes place in the sea. Cleavage is spiral, unequal and holoblastic (all of the egg divides at each cleavage). Gastrulation in species with yolky eggs is epibolic (by overgrowth), but in those with non-yolky eggs and in planktotrophic larvae it is partly epibolic and partly by invagination. With the exception of those species where development is direct and for *Themiste lageniformis*, eventually, a free-swimming trochophore forms, a larva characterised by a ciliate prototroch and an apical tuft (Fig. 5.9A, B). It is a non-feeding larva. In some species the trochophore undergoes further metamorphosis to form a pelagosphaera, a larva unique to sipunculans, 'that swims by means of a ciliated metatroch and in which the prototroch has either been lost or has undergone marked regression' (Fig. 5.9C, D; Rice 1967; Hall & Scheltema 1975). Both the trochophore and pelagosphaera are pelagic.

Rice (1975a, 1981, 1985b) proposed four different categories or patterns of development within the phylum. Species in the first category develop directly, and include such species as *Nephasoma* (= *Golfingia*) *minutum*, *Phascolion cryptum* and

Themiste pyroides. The eggs contain much yolk, the blastulae are solid and gastrulation is epibolic. There is no trochophore larva and the embryo hatches as a small vermiform juvenile.

Development in the other three categories is indirect and always includes one or two pelagic larval stages. Species of the second category, for example *Phascolion strombus* and *Phascolopsis gouldi*, have only one larval stage, a lecithotrophic trochophore (Fig. 5.9A), during development. The eggs contain much yolk, the blastulae are solid and gastrulation is epibolic. The pelagic stage lasts 8 days in *Phascolion strombus* and 8 and 3 days in *Phascolopsis gouldi*, the trochophore then changing into a young worm.

A lecithotrophic trochophore and a short-living lecithotrophic pelagosphaera are always present in the developmental stages of species of the third category; species include *Themiste alutacea*, *T. petricola*, *Golfingia elongata* and *Thysanocardia* (= *Golfingia*) *pugettensis*. Rice (1975a) reported that the lecithotrophic pelagosphaera 'swims for a short time near the bottom, undergoes a gradual loss of cilia and transforms into a vermiform stage'. In *G. elongata*, the egg contains much yolk, gastrulation is epibolic, and the length of the trochophore and pelagic stages are 3 and 2 days, respectively. The corresponding values for *T. pugettensis* are 8 and 13 days. The development of *T. lageniformis*, a well-known species from along the coast of Queensland, and northern and north-western Australia, has been studied by Williams (1972) using animals from a limestone reef in Hawaii. The eggs are very yolky and have a thick gelatinous coat which enables them to adhere to any surface. No trochophoral stage appears during development, the egg hatching directly into a small lecithotrophic pelagosphaera which spends 8–12 days of its existence near the bottom.

The development of species in the fourth category includes both a lecithotrophic trochophore and a planktotrophic pelagosphaera; such species include *Antillesoma agassizi*, *Phascolosoma perlucens*, *P. antillarum*, *P. nigrescens*, *Nephasoma pellucidum*, *Apionsoma* (= *Golfingia*) *misakianum*, *Aspidosiphon fischeri*, *Aspidosiphon parvulus* and *Sipunculus nudus*. Planktotrophic pelagosphaera larvae are known to live for months before changing into adults (Scheltema & Hall 1975; Rice 1981) and this plays an important part in the distribution of many species. The egg of *P. perlucens*, a species known from the Great Barrier Reef, has little yolk, and gastrulation is epibolic. The life of the trochophore is 2.5–3 days and that of the pelagosphaera 30 days (Rice 1975b).

Adult sipunculans are benthic and many species depend on the movement of their non-feeding trochophore larvae for dispersal. Those species, however, which have a pelagosphaera larval stage in their life cycle may be carried great distances before metamorphosis into adults, especially if the pelagosphaera is planktotrophic. The recognition of the different forms or kinds of pelagosphaera larvae, the extent to which they occur in the plankton and their distribution in the ocean currents of the Atlantic Ocean have been studied by marine zoologists during the last 20 years.

Pelagosphaera larvae have been collected along the entire axis of each of the major east-west currents of the North Atlantic Ocean (Scheltema & Hall 1975). Pelagosphaera larvae were present in 75% of 700 samples collected. Laboratory research has shown that cultured pelagosphaera larvae may live for long periods, as much as from 3–8 months before metamorphosis (Scheltema & Hall 1975; Rice 1981). A comparison of the speed of the surface currents and the length of the life of planktonic pelagosphaera indicates that it is possible for West African pelagosphaera larvae to be

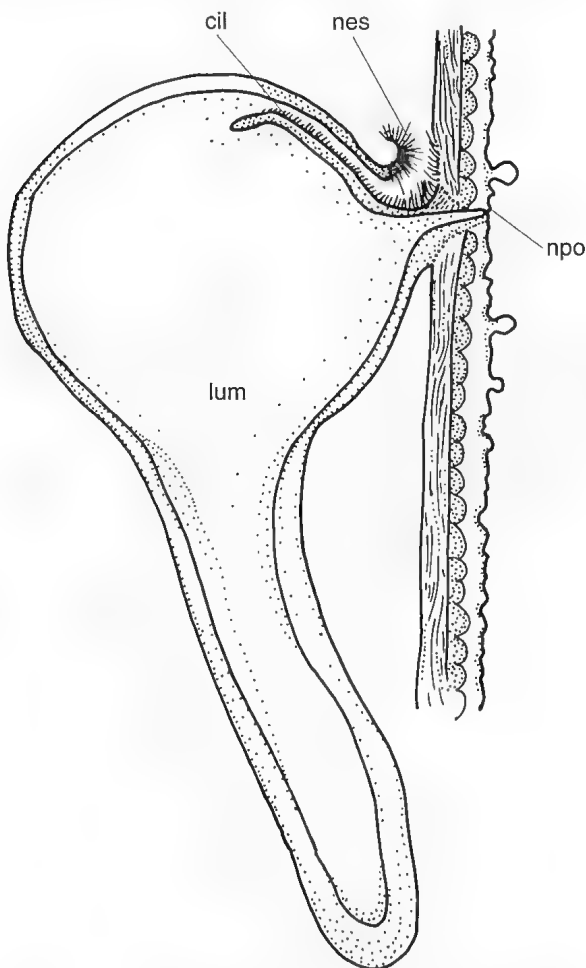


Figure 5.7 Longitudinal section of a sipunculan nephridium. cil, cilia; lum, lumen of nephridium; nes, nephrostome; npo, nephridiopore. (After Shipley 1890) [I. Grant]

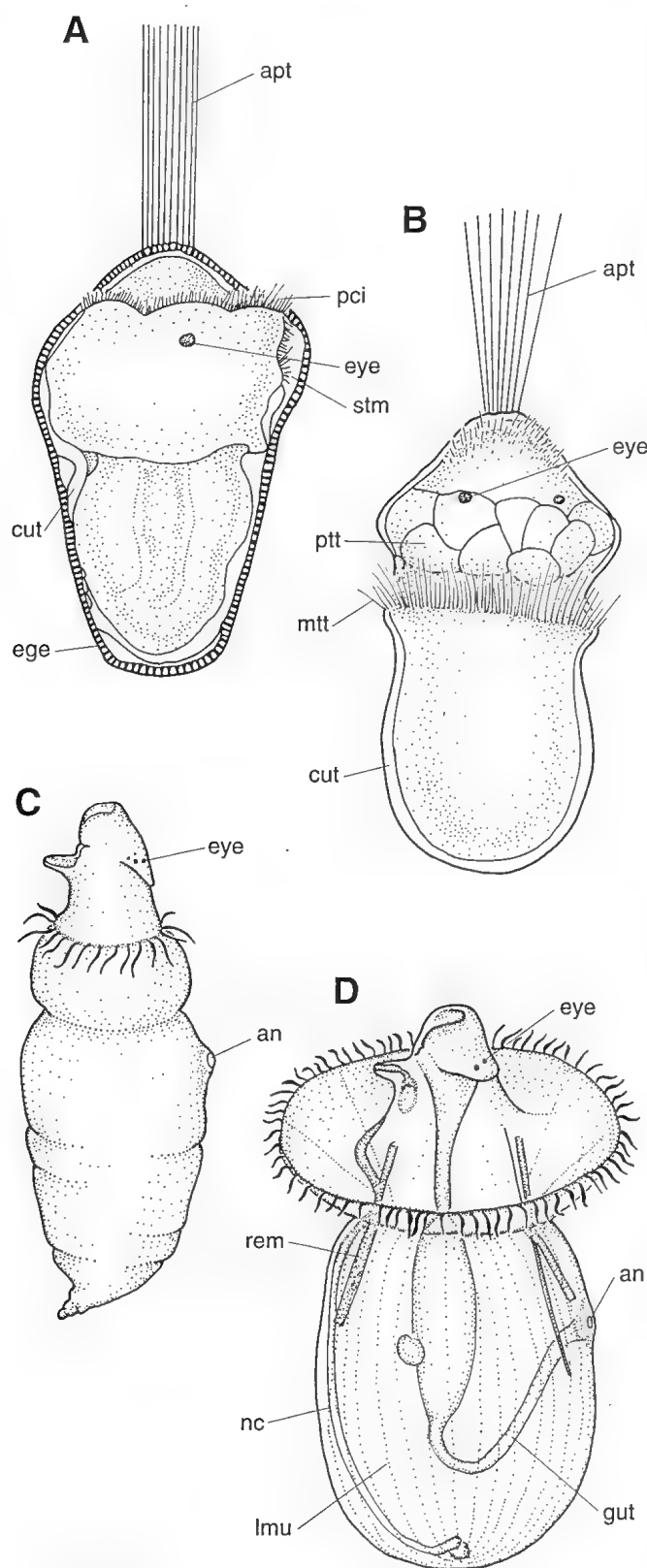


Figure 5.9 Sipunculan larvae. **A**, trochophore of *Phascolopsis gouldi* (Sipunculidae) at 48 hours; **B**, metamorphosing trochophore of *Golfingia vulgaris* (Golfingiidae); the cilia of the prototroch have been lost; **C**, pelagosphaera larva from North Atlantic Ocean, species not known; **D**, pelagosphaera larva of a *Sipunculus* species (Sipunculidae). **an**, anus; **apt**, apical tuft of cilia; **cut**, cuticle; **ege**, egg envelope; **eye**, eye; **gut**, gut; **lmu**, longitudinal muscle; **mtt**, metatroch; **nc**, nerve cord; **pci**, preoral cilia; **ptt**, prototroch; **rem**, retractor muscle; **stm**, stomodaeum. (A, B, after Gerould 1906; C, D, Hall & Scheltema 1975) [I. Grant]

transported across the Atlantic to the shores of America. The chance of this happening is supported by geographical evidence. For instance, the sipunculan fauna of the oceanic islands of the Atlantic Ocean comprises eastern and western Atlantic species rather than endemic species and 30% of the known tropical West African species are found in the West Indies. It seems likely, too, that pelagosphaera larvae are not only the means whereby some sipunculans are widely distributed, but that they also serve as 'genetic carriers' between widely separated populations of sipunculans (Scheltema & Hall 1975; Rice 1981).

Asexual reproduction is known to take place in sipunculans. Rajulu & Krishnan (1969) reported transverse fission and lateral budding in a *Siphonostoma* species and Rice (1970) recorded budding in 15% of *Aspidosiphon elegans* (as *A. brocki*) collected from Florida. Transverse fission has also been observed, but not yet recorded, in a specimen of *Siphonosoma cumanense* collected at Reevesby Island, South Australia, in 1985 by staff of the South Australian Museum.

Åkesson (1958) reported that *Nephasoma* (= *Golfingia*) *minutum* is a protandrous hermaphrodite. The median section of the gonad produces oocytes only, but the more lateral regions give rise to both oocytes and spermatocytes.

Some sipunculans are able to regenerate lost or damaged tissue. The slow regrowth of the tentacles of *Themiste hennahi* was reported by Peebles & Fox (1933) and of the introvert of *Phascolion strombus* and *Nephasoma minutum* by Schleip (1934a, 1934b).

Nervous System and Sense Organs

The nervous system of sipunculans comprises an anteriorly placed cerebral organ or 'brain' connected by two circum-oesophageal commissures to a long ventrally placed, median, unsegmented nerve cord that traverses the length of the trunk (Fig. 5.10). Unpaired lateral nerves arise from the nerve cord, divide and branch so as to almost encircle the body wall. Smaller radial nerves, arising from the ring nerves, form two plexuses in the body wall, one subepidermal and the other subperitoneal. Many skin glands and receptors are connected with the subepidermal plexus. Nerve connections are present between the subperitoneal plexus and the retractors and gut, and between the ring nerves and the nephridia and posterior regions of the gut. The retractors are also supplied with nerves arising from the circum-oesophageal commissures. There is no sub-oesophageal ganglion such as in annelids.

In section, the ventral nerve cord has a cellular part that is ventral and a fibre core that is dorsal; both parts are unpaired. The structure of the cord is uniform and consists of groups of short neurones.

The brain is often oval in shape and may appear to consist of two lobes. Paired nerves from the brain innervate the tentacles, mouth, pharynx, introvert base and the nuchal organ. Detailed histological studies of the brain have been made for *Sipunculus nudus* (Metchnikoff 1900), *P. gouldi* (Andrews 1890) and *Golfingia vulgaris* (Cuénot 1900) and studies of the general anatomy of the nervous system of the following by Åkesson (1958): *Phascolion strombus*, *Golfingia elongata*, *Thysanocardia procera*, *Nephasoma minutum*, *Phascolosoma granulosum*, *S. nudus*, *S. robustus* (= *S. angasi*), *Themiste cymodoceae* and *Onchnesoma steenstrupi* (see also Cutler 1994). The specimens of *S. robustus* and *T. cymodoceae* used in the study were Australian.

A number of sensory organs are associated with the anterior region of sipunculans. A structure known as the nuchal organ is usually well developed in species of *Golfingia*, *Thysanocardia*, *Themiste*, *Phascolosoma* and *Aspidosiphon*. It is a two- to four-lobed cushion of tall, ciliated, columnar epithelium, placed mid-dorsally on the edge of the oral disc. It is best observed in fully extended introverts. It is supplied with nerves from the brain and resembles the nuchal organ of annelids. The function of the organ is not known, but is assumed to be chemoreception.

Photoreceptors and 'eyes' at different levels of complexity are present. The simplest type is an epidermal invagination in the dorsal part of the brain. The lumen of the invagination or ocular tube is filled with solid cuticular material and the cells lining the narrow part of the tube are pigmented. The photoreceptor cells at the base are bipolar. In more highly developed forms, the thickening becomes an elongate structure at the bottom of the tube. In the most developed structures, a spherical or elliptical body is present which, it is thought, may be able to concentrate light waves on the terminals of receptor cells. 'Tentacular eyes' (Åkesson 1958) are present on the aboral surface of the tentacles of *Sipunculus* species. They are composed of tall, columnar epithelial cells and appear as hexagonal structures with an opening in the centre to a cavity within.

Digitate processes are outgrowths from the antero-dorsal margin of the brain and are found in many species of Sipunculidae. They may be short (0.5 mm) and finger-like in *Sipunculus nudus*, longer in *S. robustus*, thread-like in *Siphonosoma ingens*, and cauliflower-like in *S. mundanus*. They contain secretory granules (Åkesson 1958), but their function is unknown. Ward (1891) gave the name 'cerebral organ' to some tissue situated on the anterior margin of the cerebral ganglion of *Sipunculus nudus*. It consists of tall

columnar epithelial cells, often several layers thick, the surface of which is covered with thick cuticle. The structure is more prominent in larval *Sipunculus*. Åkesson (1958) considered it to be a secretory rather than a sensory organ.

Several kinds of sense organs are present on the surface of the tentacles and trunk. Tentacular eyes have already been mentioned. The most common type is made up of a number of fusiform buds of elongated epidermal cells innervated by nerves through their base. The distal extensions of the cells sometimes reach the surface of the animal and often terminate in a cuticular papilla. These sense organs respond to specific stimuli which may be chemical, tactile, thermal or photic.

NATURAL HISTORY AND ECOLOGY

Sipunculans may be abundant at a particular location. Sasekumar (1974) estimated the numerical density of *Phascolosoma arcuatum* at a collecting site in Malaysia as 39 m⁻². Rice (1975c) reported the numbers of *Antillesoma antillarum* and *P. perlucens* in calcareous rock at Puerto Rico to be 415 m⁻² and 101 m⁻² respectively. Hylleberg (1975), in a study of a certain area near Kristienberg, Sweden, found that 90% of 700 gastropod shells dredged at 30 m were inhabited by *Phascolion strombus* and estimated the numerical density of the sipunculan as 60–135 m⁻². He also showed how the numbers of specimens of *Golfingia elongata*, *G. vulgaris*, *Thysanocardia procera* and *P. strombus* along a transect at Gavesik varied down to a depth of 33 m.

Some studies indicated an unequal distribution of males and females in a population. Keferstein (1863) found all of 200 specimens of three different species of *Golfingia* were female and Awati & Pradhan (1936) reported the sex ratio of an Indian population of *Themiste lageniformis* was one male to 100 females. Coles (Rice 1975a) found only two males in 100 specimens of *Thysanocardia pugettensis*, but Rice (1975a) subsequently found in a study of the same population the ratio was 50 females to 37 males with 13 undetermined.

Very little is known about the longevity of sipunculans in their natural habitat. Green (1975a) was unable to detect any age grouping in his Queensland study of *Phascolosoma arcuatum*. A specimen of *Themiste cymodoceae*, distinguished by an injury-marking on its introvert, was observed to inhabit the same spot, wedged between a large moveable rock and some sea grass, for two years at Aldinga, South Australia (S. Edmonds personal observation). As the specimen was large when it was first observed it seems likely that it lived for at least 3 years.

There is no doubt that some species are tolerant of conditions that seem adverse. Green (1975b) found that of 50 specimens of *Phascolosoma arcuatum* kept in aerated seawater for 10 months only two died, only sufficient tap water being added to maintain constant salinity. Harms & Dragendorff (1933) claimed that adults of *P. arcuatum* can be kept 'almost indefinitely' in a pot of mud which is kept moist with tap water. Green (1975b) refers to the species as being 'semiterrestrial'. The presence of coelomic sacs in its body wall probably indicates, with analogy to *Siphonosoma ingens*, the importance of the skin as a respiratory surface (Manwell 1960). The reproduction of the species, however, is dependent on a marine environment.

Edmonds (1980) claimed that sipunculans are related to their environment in at least five ways (see also Cutler 1994). Firstly, they are decomposer organisms, ingesting and chemically breaking down detritus of plant and animal origin.

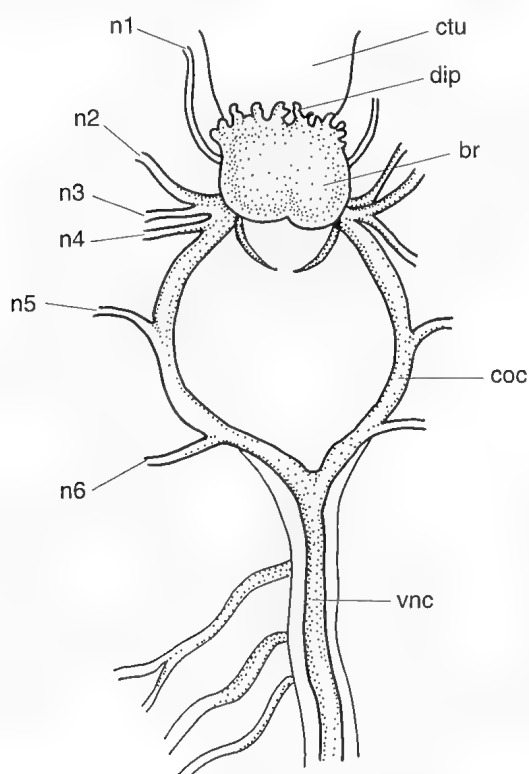


Figure 5.10 Anterior section of sipunculan nervous system. **br**, brain; **coc**, circum-oesophageal connective; **ctu**, cephalic tube; **dip**, digitiform processes; **n1–n4**, nerves to tentacles; **n5**, **n6**, nerves to introvert; **vnc**, ventral nerve cord. (A, after Metchnikoff 1900)

[I. Grant]

Secondly, sipunculans are a source of food for a number of different animals. Kohn (1975) reviewed predation on sipunculans. Some fish eat sipunculans; Kohn listed species from two orders of elasmobranchs and six orders of teleosts known to eat them. Large specimens of *Sipunculus robustus* (for example, South Australian Museum specimen SAM E1849) were found in the gut of some stingrays collected in Port Phillip Bay, Victoria and smaller specimens (for example, South Australian Museum specimen SAM E1072) have been found in South Australia in the gut of the spotted whiting, *Sillaginodes punctatus*.

Only a few invertebrates are known to prey on sipunculans. Kohn (1970) reported that the gastropod *Mitra litterata* preys on sipunculans that burrow in the intertidal reefs at Oahu, Hawaii. In South Australia, *Mitra glabra* have been found to contain the remains of the reef-dwelling sipunculans *Phascolosoma annulatum* (Pl. 12.1) and *Themiste fusca*.

Thirdly, although sipunculans may inhabit the tubes and cavities made by other animals, it is known that some species, especially those belonging to the genera *Phascolosoma*, *Aspidosiphon*, *Cloeosiphon*, *Lithacrosiphon* and *Themiste* are able to construct their own homes in calcareous rock. Such species play an important part in the breaking down of coral and limestone reefs, especially at the outer edges. How soft-bodied animals like sipunculans are able to burrow into hard rock is baffling. Rice (1969), Rice & McIntyre (1972) and Williams & Margolis (1974) have suggested that mechanical abrasion and chemical action are involved. The importance of sipunculans as members of a coral reef community was discussed by Rice (1976). Rice (1985a) has recently described *Phascolosoma turnerae*, a species found boring in wood.

Fourthly, sometimes sipunculans form mutualistic associations with other animals. The association between *Aspidosiphon muelleri* (junior synonyms, *jukesii* and *corallicola*) and solitary corals is probably the best known and is well documented by Rice (1976). On the Great Barrier Reef in Australia, *A. muelleri* is commonly found inhabiting the solitary coral *Heteropsammia michelini*. The sipunculan lives in a spiral cavity in the base of the coral and is able to extend its introvert into the environment through a hole in the cavity. As the worm probes and feeds, the coral is moved from one spot to another. Rice (1976) says 'that through the association the sipunculan is provided with a protective habitat and by movements of the sipunculan the coral is maintained in an upright position on the surface of the substratum and transported to different feeding areas'. The developmental history of the association has also been carefully studied. According to Rice (1976), 'The juvenile *Aspidosiphon*, when 1 mm or less, enters a small, empty, gastropod shell, usually a small *Cerithium*. A coral planula settles on the shell, overgrowing and eventually enclosing it. Only those planulae settling on shells have any chance of survival. Growth of the coral and the sipunculan are well synchronised, the sipunculan enlarging its cavity as a spiral tube in the base of the growing coral while maintaining an opening of the tube on the underside of the coral'. The association is unusual in that it involves three animals, a sipunculan, a mollusc and a cnidarian. A list of some associations between sipunculans and cnidarians and polychaetes is given by Stephen & Edmonds (1972). Some of the copepod associates of sipunculans are listed Illg (1975). The polychaete *Syllis (Toposyllis) armillaris* is usually associated with *Phascolion strombus cronullae*, an Australian sipunculan found in the empty shells of *Gazameda gunni* off the coast of New South Wales. Edmonds (1980) reported that syllids were present in 87% of the shells that contained *Phascolion* species.

Fifthly, sipunculans may contain parasites in their gut, body fluids and tissues. The most commonly found parasitic protozoans are sporozoans, especially gregarines. Some of the records are listed in Stephen & Edmonds (1972) and Jones (1975). Rhabdocoeles have been reported from the gut and encysted metacercariae of unidentified trematodes from different organs of sipunculans. Åkesson (1958) recorded encysted metacercariae in the tentacles of *Sipunculus robustus* from South Australia. Nematodes have been reported from the body cavity of at least three species (Edmonds 1980). Ho *et al.* (1981) reported that sterility can be produced in *Phascolosoma scolops* by an endoparasitic copepod.

Murina (1984) considered that sipunculans comprise four main ecological groups: burrowers that simply swallow the substratum, for example, species of *Sipunculus* and *Siphonosoma*; worms that live in empty shelters and feed on detritus, as in species of *Phascolion*; semi-mobile, waiting sestonophages, that feed on very fine particles of suspended organic matter, for example, species of *Themiste*, and; sessile worms that scrape food from their substratum, such as some species of *Phascolosoma*.

BIOGEOGRAPHY AND AFFINITIES

Within the phylum, almost every possible type of biogeographical pattern known for marine invertebrates occurs, thus making it nearly impossible to generalise. A genus by genus analysis of their distribution and cladogenesis is provided by Cutler (1994).

Many of the shallow warm water species, such as *Phascolosoma perlucens* and *P. scolops*, are very widely dispersed, as are several of the deep cold water species. A few genera have very limited distributions (for example, the monotypic *Phascolopsis* and *Siphonomecus*). Most distributions lie somewhere between these two extremes.

The number of endemic species has been exaggerated due to the inflated number of putative species and may still be artificial as a result of incomplete sampling. The quality of the existing database, and concerns about using both 'tested' and 'untested' endemic species in biogeographical analyses, for example, Murina (1975), are discussed in Cutler (1994). He coupled his discussion of endemism with suggestions about different centres of origin or cladogenesis. In Paleozoic times, when most of the modern genera arose, the shallow Indo-Malayan area did not exist. Rather, the early taxa probably first appeared in the warm, shallow Palaeozoic Panthalassa (or Eo-Pacific) precursor of the Indo-Malayan Archipelago. Other taxa clearly originated in the cooler, younger North Atlantic. The Australian fauna is largely Indo-West Pacific with some circumtropical members.

Based on evidence from palaeontological, biochemical, embryological, immunological and fine-structure data Cutler (1994) concluded that there was an ancestral form common to the sipunculans, annelids and molluscs. In the early Palaeozoic, this form gave rise to the Annelida and a sister taxon that subsequently gave rise to both the Sipuncula and the Mollusca. His model links the least derived mollusc groups (Aplacophora) to the least derived sipunculan genus (*Apionsoma*).

The phylogenetic relationships within the phylum first proposed by Cutler & Gibbs (1985) were modified by Cutler (1994). This included a re-evaluation of the derived nature of six character states: the nuchal tentacles are now considered ancestral to peripherals; the posterior attachment of spindle muscle is now ancestral, and unattached and absent are derived states; complex introvert hooks in rings are ancestral,

scattered or absent hooks are derived and homoplastic (that is, they evolved more than once in different lineages); introvert hooks with basal spinelets are ancestral; the presence of longitudinal muscle bands is homoplastic above family level; the presence of contractile vessel villi is homoplastic above family level; and the loss or fusion of introvert retractor muscles is homoplastic above family level.

Cutler (1994) created a possible evolutionary scenario beginning with his Revised Hypothetical Ancestral Sipunculan that '...had a body wall with a continuous longitudinal muscle layer and no epidermal coelomic extensions. The anterior end of the trunk bore the anus, was without a horny shield, and tapered into the introvert along the same axis. The introvert carried regular rings of sculptured proteinaceous hooks with basal spinelets, and the tentacular crown consisted of a crescent of small nuchal tentacles plus a circumoral collar (cuticular fold). that was the precursor of a set of peripheral tentacles. Internally, the contractile vessel was small and did not have villi. Also present were two pairs of unfused, equal-sized introvert retractor muscles, two nephridia, possibly bilobed, and a complete spindle muscle attached to the posterior end of the trunk. The epidermal organs consisted of only one cell type and one secretory product. This Cambrian population lived in shallow, warm seas and had 10 pairs of mostly telocentric chromosomes ($2N = 20$). The hypothetical ancestor produced an egg with very little yolk and a thin egg envelope that developed into a trochophore. This larva grew into a rather long-lived planktotrophic pelagospaera stage (type IV) and eventually settled to become a juvenile worm.' From this point Cutler described a picture in geological time and space of what might have happened. The synthetic and speculative models presented by Cutler need to be tested by other workers using non-morphological methods.

FOSSIL RECORD

The fossil, *Ottia prolifica* is a long, bilaterally symmetrical worm comprising a proboscis armed with spines and a long unsegmented trunk. It was found in the Burgess Shale material from the Middle Cambrian Stephen Formation of British Columbia, Canada. Walcott (1911) associated the fossil with the Sipunculida and Howell (1962) regarded it as a fossil sipunculan. Banta & Rice (1976), however, in re-describing the fossil, concluded that it represents an early aschelminth rather than a sipunculan.

METHODS OF STUDY

Collecting sipunculans may involve digging in sand and mud, searching in or breaking up limestone or corals, turning over rocks, pulling apart roots of sea grasses, examining discarded shells of gastropods and scaphopods or encrusted serpulid worms and dredging. It is almost impossible to dislodge sipunculans forcibly without seriously injuring them. If they are in sand or mud it is advisable to dig them up with a fork rather than a spade; more whole specimens are then likely to be collected. If the worms live in rock or coral, a sharp blow to the substratum may break it along the fissures, galleries or tubes which they inhabit. They may then be extracted with the aid of forceps. Soaking the rock in weak formalin (0.5%) for 2–12 hours may sometimes free them if the rock is difficult to break. A vice is often required to crack the shell of a mollusc that contains a sipunculan. If the worm lives in the roots of a marine angiosperm it is probably best to dig out a sod of the material and either divide it into smaller pieces or examine the undersurface of the sod for worms. It is nearly always easier to remove them 'tail first'.

Sipunculans should be relaxed or narcotised before fixing, thus reducing the chances of distortion by the fixing agent. Successful relaxation, fixation and preservation can be achieved placing the animals, when collected, and before relaxing them, in a good supply of cool seawater. They may then void some of their intestinal contents. Sipunculans may be relaxed by: placing them in a shallow dish of seawater and either sprinkling over the surface some crystals of menthol or adding, very carefully, a small volume of 80% alcohol in which some menthol has been dissolved; placing them in seawater to which 70% alcohol is slowly added (almost drop by drop if the volume of seawater is small), or; placing them in a 7% solution of magnesium chloride or sulphate. It may be necessary to leave them in the relaxing medium for 2–12 hours. When the animals no longer respond to touch they may be fixed for at least 24 hours in 5% neutral formalin. Sipunculans are usually stored in 70% alcohol.

Information about the internal anatomy of a sipunculan is usually required before it can be identified and is best obtained by dissection. One way of dissecting the animal is to pin it out under water in a dish containing a layer of solidified paraffin wax. In order to do this place the animal ventral side down on the wax (the dorsally situated anus will appear on the upper surface). Using fine scissors or a scalpel and forceps, cut the body wall longitudinally along a line a little to one side of the anus. The body wall should be held up as much as is possible so that the internal structures are not damaged. It is usually necessary to cut almost the whole length of the trunk. The flaps are then pinned back clear of the internal structures. Any coagulated blood or reproductive cells in the coelom can usually be washed away by a gentle stream of water directed from a wash bottle or removed with the aid of forceps. To make a slide mount of sipunculan hooks, a small section of the introvert wall is snipped out, placed on a slide with a drop of glycerine and teased apart with two fine needles. After removing tissue that does not contain hooks, place a cover slip over the preparation. Re-examine under a microscope. It often happens that single hooks or groups of hooks can now be observed. It is essential to lie hooks flat on the slide for drawing or photographing. Papillae can be examined by removing a small piece of skin, placing it on a slide with some glycerine and covering the preparation with a cover slip.

CLASSIFICATION

The classification used in this chapter is that of Gibbs & Cutler (1987). The phylum comprises two classes, four orders, six families and 17 genera (Table 5.1).

Table 5.1 Classification of the phylum Sipuncula (after Gibbs & Cutler 1987)

Class SIPUNCULIDEA
Order SIPUNCULIFORMES
Family Sipunculidae
Order GOLFINGIFORMES
Family Golfingiidae
Family Themistidae
Family Phascolionidae
Class PHASCOLOSOMATIDEA
Order PHASCOLOSOMATIFORMES
Family Phascolosomatidae
Order ASPIDOSIPHONIFORMES
Family Aspidosiphonidae

Key to families of phylum Sipuncula

- 1(a) Horny, hardened or calcareous shield, cap, cone or knob present at anterior extremity of trunk Aspidosiphonidae
- 1(b) Horny, hardened or calcareous shield, cap cone or knob absent from anterior extremity of trunk. 2
- 2(a) Longitudinal musculature of trunk wall thickened to form well-defined bands (which may anastomose) . 3
- 2(b) Longitudinal musculature of trunk wall not thickened into well-defined bands, but forms a continuous sheet. 4
- 3(a) Circular musculature of trunk wall thickened to form bands or smaller fascicles (except in *Phascolopsis*). Body wall of adult with integumental canals or sacs. Tentacles arranged peripherally or as a tentacular fold so as to surround the mouth. Trunk usually cylindrical and sometimes large (70–400 mm). Hooks, if present, simple and not arranged in rows (except in *Phascolopsis*) Sipunculidae
- 3(b) Circular musculature of trunk wall continuous and not in bands. Body wall without integumental canals or sacs (except in *Phascolosoma arcuatum*). Tentacles almost encircle the dorsally placed nuchal organ and do not surround the mouth. Trunk sub-cylindrical, bottle- or flask-shaped. Hooks, if present, complex, recurved, often with characteristic internal markings and arranged in rows. Phascolosomatidae
- 4(a) Single nephridium present. Phascolionidae
- 4(b) Two nephridia present 5
- 5(a) Branching tentacles arise from four to eight stem-like extensions of oral disc. Themistidae
- 5(b) Tentacles not arising from stem-like extensions of oral disc. Golfingiidae

Class SIPUNCULIDEA

Members of the class Sipunculidea have tentacles arranged peripherally so as to encircle the mouth. Introvert hooks, if present, are simple, thorn-like and usually not in rows. The spindle muscle is not attached posteriorly, except in species of *Siphonosoma* and *Siphonomecus*. The two orders within Sipunculidea are Sipunculiformes and Golfingiformes.

Order SIPUNCULIFORMES

Sipunculiformes are distinguished by the presence of longitudinal musculature of the body wall grouped into bands and coelomic extensions (canals or sacs) in the body wall (except in *Phascolopsis*). The order comprises a single family, Sipunculidae.

Family Sipunculidae

Adult sipunculids are generally large, 70–400 mm in length, usually cylindrical, worm-like and often stout (Fig. 5.11A). The longitudinal musculature of the trunk wall is grouped into prominent bands (Fig. 5.11B). The circular musculature, as well, may be grouped into bands or small bundles. The family is distinguished from other families, for example, Phascolosomatidae and Aspidosiphonidae (in part), in which the longitudinal musculature is banded by the arrangement of the tentacles which, if expanded, can be seen to encircle the mouth either in a ring or as a tentacular fold (Fig. 5.11D). Four retractor muscles are present, except in *Siphonomecus*. Either longitudinal canals or integumental sacs are present in the body wall. *Sipunculus*, described by Linné (1776), is the type genus of the family.

The introvert is short in comparison to the trunk, and usually lacks hooks (Fig. 5.11A). If hooks are present, they are simple and thorn-like and commonly not arranged in rows. Figure 5.11C shows the details of the papillae from the surface of the introvert of *Sipunculus robustus*. The contractile vessel may be double (as in *Sipunculus* species) or single (as in *Siphonostoma* species); it usually lacks villi or

tubules. Reproduction and development has not yet been studied in Australian Sipunculidae, but has been described extensively for one European (cosmopolitan) species, *Sipunculus nudus*, (Hatschek 1883; Rice 1985b). The trochophore larva metamorphoses, after about 3 days, to a planktotrophic pelagospaera larva which, drifts in the plankton for about a month, before changing into the adult form. Edmonds (1980) does not list *S. nudus* amongst Australian Sipunculidae. Cutler & Cutler (1985a), however, consider that *S. titubans*, listed from northern Australia by Edmonds (1980), is a junior synonym of *S. nudus*.

Sipunculids burrow in sand and silt and their burrows are neither lined nor permanent. They ingest large quantities of the substratum in which they live and appear to gain much of their food from its contents. It is possible that they may feed from the richer and more superficial layers. Chin & Wu (1950) found that diatoms were an important part of the diet of *S. nudus* in China. Very little is known about the feeding habits of Australian sipunculids.

The family is distributed in the tropical and tropico-temperate regions of the oceans. Two cold water species are known (Murina 1975). The family comprises five genera: *Sipunculus* and *Siphonosoma* are well represented in Australia, whereas *Xenosiphon*, *Phascolopsis* and *Siphonomecus* are not known from Australian waters. Edmonds (1980, 1985) listed 11 species, but according to the taxonomic changes suggested by Cutler & Cutler (1985a), the 10 Australian species in this family are: *Sipunculus indicus*, *S. robustus*, *S. mundanus*, *S. norvegicus*, *S. nudus*, *Siphonosoma cumanense*, *S. australe*, *S. rotumanum*, *S. boholense* and *S. vastum*. The affinities of Australian Sipunculidae are Indo-Pacific.

Order GOLFINGIFORMES

The order Golfingiformes is diagnosed by the presence of longitudinal and circular musculature in continuous layers, and not banded. The order comprises three families, Golfingiidae, Themistidae and Phascolionidae, all of which have representatives in Australian waters.

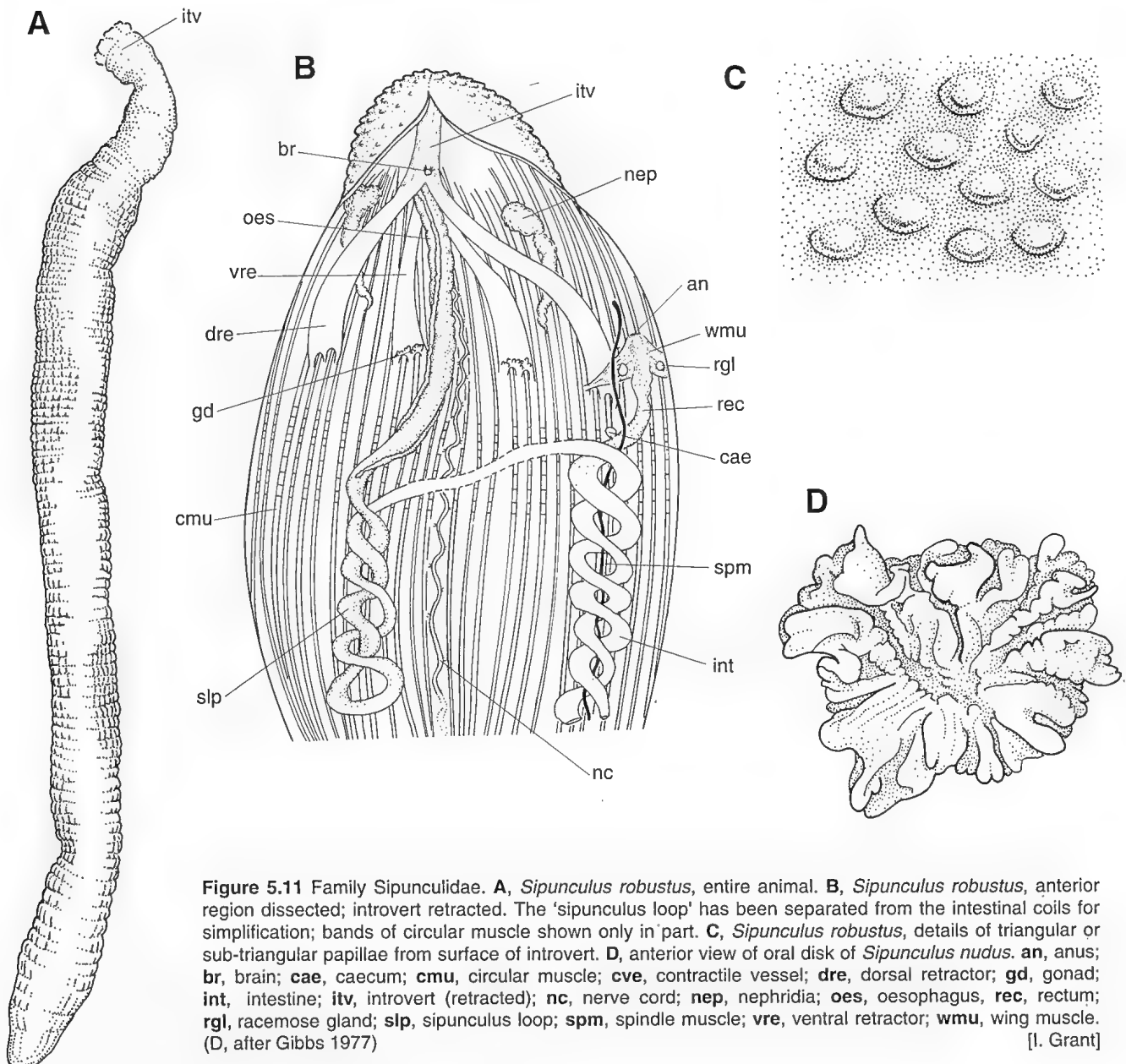


Figure 5.11 Family Sipunculidae. **A**, *Sipunculus robustus*, entire animal. **B**, *Sipunculus robustus*, anterior region dissected; introvert retracted. The 'sipunculus loop' has been separated from the intestinal coils for simplification; bands of circular muscle shown only in part. **C**, *Sipunculus robustus*, details of triangular or sub-triangular papillae from surface of introvert. **D**, anterior view of oral disk of *Sipunculus nudus*. an, anus; br, brain; cae, caecum; cmu, circular muscle; cve, contractile vessel; dre, dorsal retractor; gd, gonad; int, intestine; itv, introvert (retracted); nc, nerve cord; nep, nephridia; oes, oesophagus; rec, rectum; rgl, racemose gland; slp, sipunculus loop; spm, spindle muscle; vre, ventral retractor; wmu, wing muscle. (D, after Gibbs 1977)

Family Golfingiidae

Golfingiids are small to medium-sized sipunculans, with a trunk ranging from 5–100 mm long, and an the introvert of variable length (Fig. 5.12A). Tentacles are always placed peripherally so as to encircle the mouth, but are never borne on stem-like extensions of the oral disc as in Themistidae. The size and number of tentacles may be different in different genera (Fig. 5.12B–E). Spines on the introvert may be present or absent. The longitudinal and circular musculature of the trunk is continuous. Two nephridia are always present. *Golfingia*, described by Lankester (1885), is the type genus of the family.

Since the comprehensive paper on Australian sipunculans produced by Edmonds (1980), the family has undergone considerable revision. Gibbs & Cutler (1987) made several major changes: the genera *Phascolion* and *Themiste* were raised to family status, Phascolionidae and Themistidae respectively, and; the subgenera *Thysanocardia* and *Nephasoma* in Golfingiidae were raised to the level of genus. Gibbs & Cutler (1987) reported that the Golfingiidae comprises three genera, *Golfingia*, *Nephasoma* and *Thysanocardia*.

Several golfingiids are known from southern Australia: *Golfingia margaritacea adelaidensis*, *Golfingia herdmani* and *Nephasoma schuettei*. However, in their revision of *Golfingia* Cutler & Cutler (1987) considered that *G. margaritacea adelaidensis* should be considered as *G. margaritacea* and *G. herdmani* as *G. vulgaris herdmani*. They live in sand, silt and the debris associated with the roots of marine angiosperm plants such as species of *Posidonia*, *Zostera* and *Amphibolis*. Sometimes they are dredged.

The tentacles in *Nephasoma*, may be reduced in number and size (Fig. 5.12C, D). In *Thysanocardia*, the tentacular crown is complex; a ring of peripheral tentacles surrounds the mouth, but in addition, the nuchal organ is enclosed by an arc of nuchal tentacles (Fig. 5.12E). The peripheral tentacles are arranged in paired rows, with extra tentacles forming posteriorly so as to form U-shaped festoons. In *Golfingia*, there are four retractor muscles, but in *Nephasoma* and *Thysanocardia* there are only two. The contractile vessel is simple in *Golfingia* and *Nephasoma*, but in *Thysanocardia* well-developed villi are present. Hooks or spines may be present in *Golfingia* and *Nephasoma*, but are absent in *Thysanocardia*.

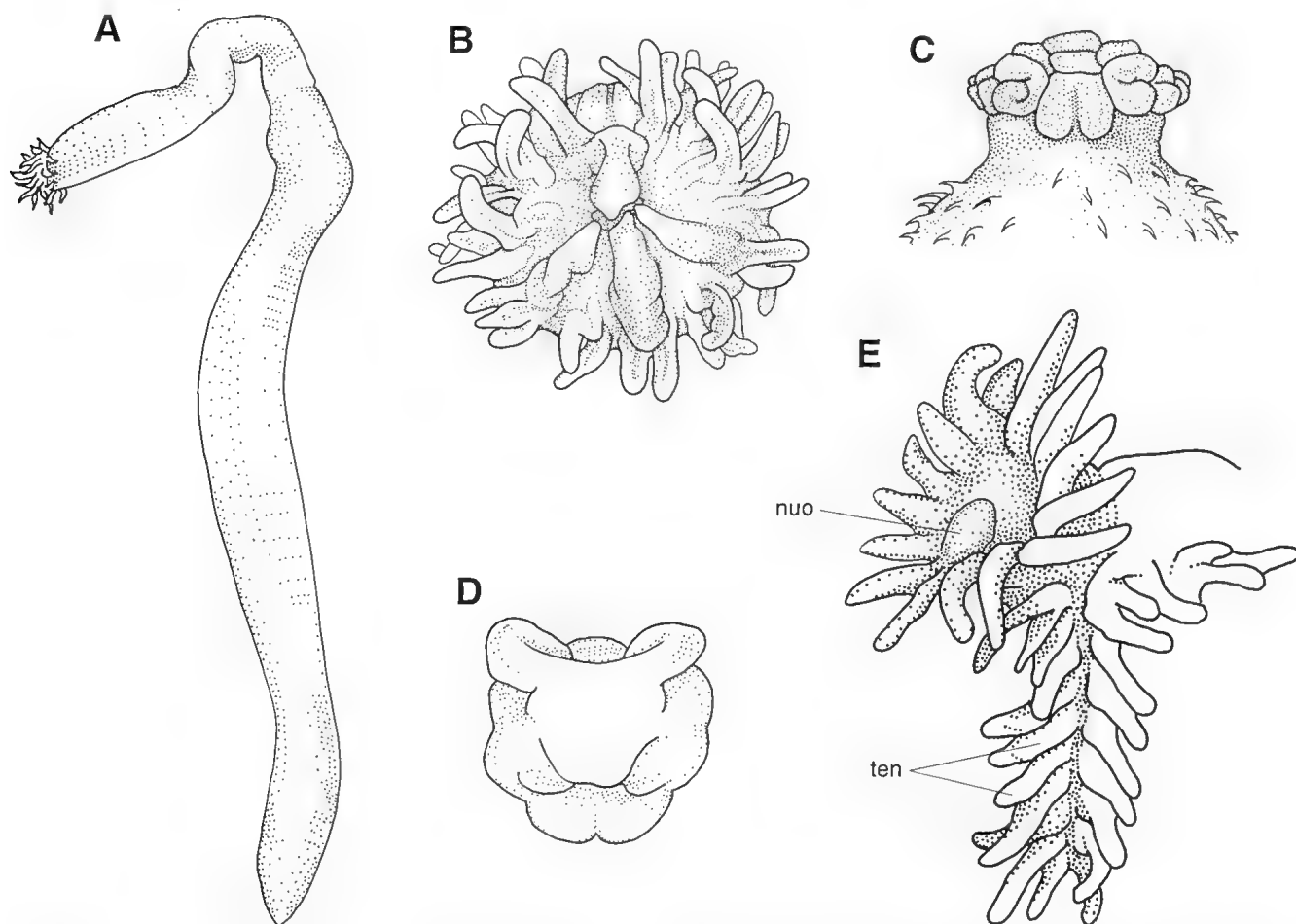


Figure 5.12 Family Golfingiidae. **A**, *Golfingia margaritacea*, entire specimen. **B**, anterior view of oral disk of *Golfingia* species; **C**, dorsal view of anterior region of *Nephasoma abyssorum*. **D**, anterior view of oral disk of *Nephasoma minutum*. **E**, dorso-lateral view of tentacle crown of *Thysanocardia catherinae* showing the nuchal arc and one of 12 festoons. **nuo**, nuchal organ; **ten**, festoon of tentacles. (B–D, after Gibbs 1977; C, after Théel 1905; E, after Gibbs *et al.* 1983) [I. Grant]

Reproduction, embryology and development of several golfingiids, from the Northern Hemisphere, have been studied by Rice (1975a). In *Nephasoma minutum*, development is direct. In *Golfingia elongata*, *G. vulgaris* and *Thysanocardia nigra* [= *G. pugettensis*, according to Gibbs, Cutler & Cutler (1983)], a trochophore and a lecithotrophic pelagospaera are formed during development.

Family Themistidae

Themistids have a trunk which varies in size from 5–170 mm and, in shape from stout and pyriform to long and vermiform (Fig. 5.13A); strongly contracted specimens may be almost globose. The introvert is shorter than the trunk. Tentacles surround the mouth, but arise from the margins of a number of outgrowths of the oral disc (Fig. 5.13B, C). Hooks or spines may be present on the introvert. Both the longitudinal and circular musculature of the trunk are continuous and the external appearance of the body is very smooth. Two retractor muscles are always present and the contractile vessel has well-developed villi. The spindle muscle is not attached posteriorly. *Themiste*, described by Gray (1828), is the type genus of the family, and was for many years known as *Dendrostomum* (describing the branching or dendritic nature of the tentacles). The family comprises the single genus, *Themiste*, which was included in Golfingiidae, but raised to family status by Gibbs & Cutler (1987).

Six species of *Themiste* have been recorded from Australia (Edmonds 1980). All were collected from the littoral region of the shore and all belong to the subgenus *Lagenopsis*, in which the contractile villi are numerous and short. Themistids in Australia live in at least two types of habitat. *Themiste lageniformis* (= *T. signifer*) makes burrows in coral rock. Williams & Margolis (1974) investigated the burrowing mechanisms of sipunculans using *Themiste lageniformis* as an example and Rice (1976) described the ciliary mucous feeding mechanism of this species. *Themiste cymodoceae*, however, lives among the tangled roots of the marine angiosperms *Amphibolis* species and sometimes of *Zostera* species. It is a detritus-feeder and uses its tentacles to direct particles (not always fine ones) to its mouth. *Themiste cymodoceae* lives in a cavity in plant roots; the cavity is gradually excavated by the worm. The sides of the cavity are well compacted and the animal appears to lead an almost sedentary existence. *Themiste cymodoceae* is hardy and 'tough' and, as such, makes a good experimental animal.

Embryology and development have been studied in three species. The development of *T. pyroides*, from Washington, United States of America, is direct (Rice 1967), with a small crawling worm hatching from the egg after 8–9 days. Both a trochophore and a lecithotrophic pelagospaera are involved in the development of *T. alutacea* (Rice 1975a). According to Williams (1972), no pelagic trochophore forms during the development of *T. lageniformis*. The early non-pelagic stage, however, metamorphoses to a lecithotrophic pelagospaera with a terminal organ. The latter changes to a young worm after 8 days.

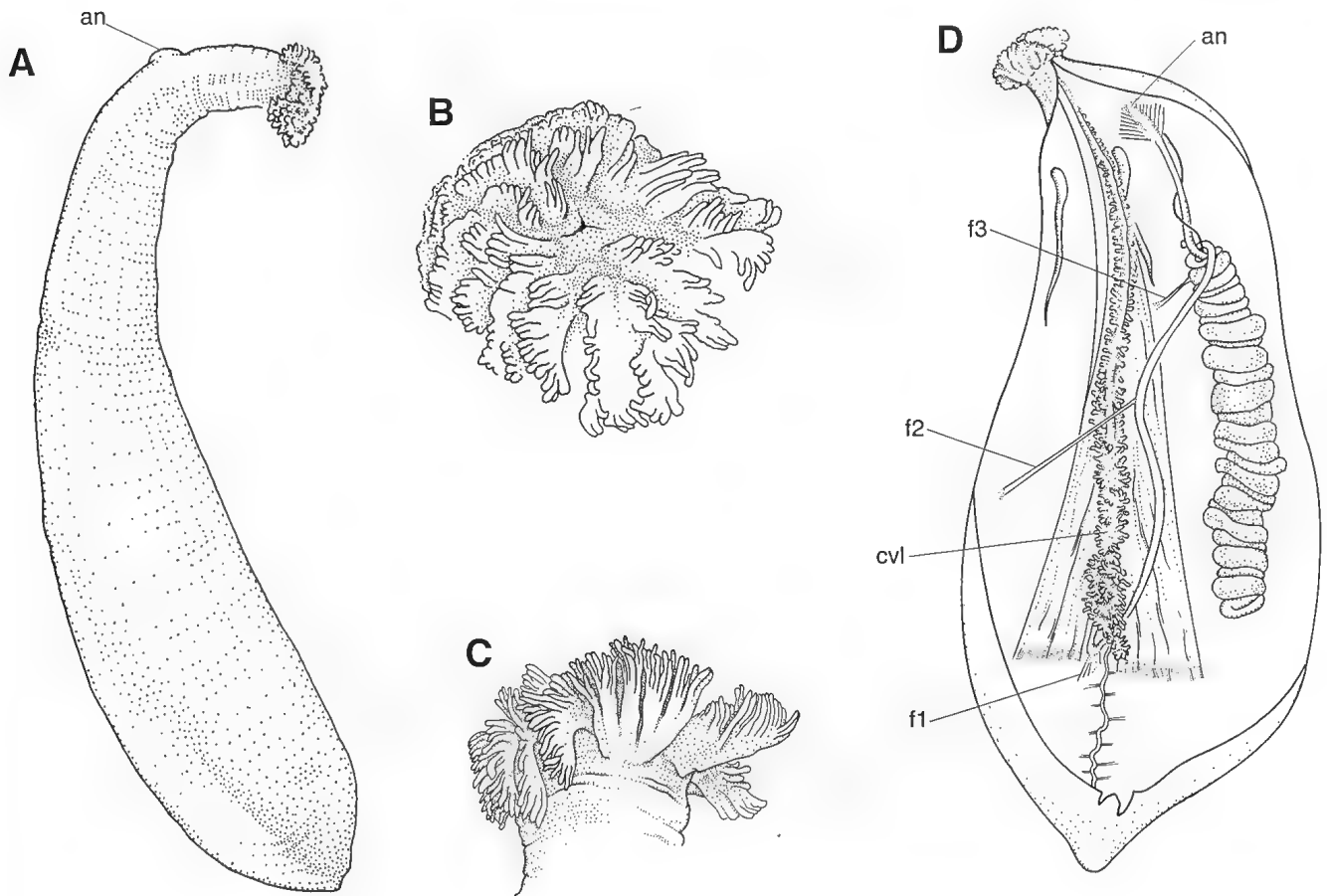


Figure 5.13 Family Themistidae. *Themiste cymodoceae*: **A**, entire specimen; **B**, **C**, branching structure of tentacles showing (**B**) frontal aspect and (**C**) lateral aspect; **D**, dissection showing the contractile villi. **an**, position of anus; **cvl**, contractile villi; **f1–f3**, intestinal fasteners. [I. Grant]

Family Phascolionidae

Phascolionids are small, with a trunk 3–35 mm in length. Their tentacles surround the mouth; rather than borne on stem-like extensions of the oral disc as in Themistidae. Only one nephridium is present, distinguishing members from Golfingiidae in which there are two. The musculature of the body wall is continuous. The family comprises two genera, *Phascolion* and *Onchnesoma*, which differ considerably in size, structure and habitat. *Phascolion*, described by Montagu (1804) is the type genus of the family. In *Onchnesoma* the trunk is very small, less than 10 mm, but the introvert is very long (Fig. 5.14E). The tentacles, usually less than 10, are arranged around the mouth and may be reduced in size or even absent. Only one pair of fused retractor muscles and one nephridium are present. The anus lies on the distal half of the introvert and not on the anterior region of the trunk. The genus has a small number of species; Cutler & Cutler (1985b) in their revision of the genus listed six species and subspecies and provided a key. Edmonds (1980) listed one species dredged off Broken Bay, New South Wales. Cutler (1973) noted that the worms resemble 'a tiny football on a string'.

Phascolion species usually live in the empty shells of gastropods and scaphopods (Fig. 5.14A), less frequently in the empty tubes of polychaetes and in solitary corals; Figure 5.14B, C shows an entire animal of *Phascolion* species removed from its shell. They are commonly collected by dredging. The trunk may be twisted or coiled according the shape of the shell which the animal inhabits. The introvert is of variable length and may be armed with hooks. Characteristic, swollen, papillate structures called 'holdfasts'

are usually present on the body wall (Fig. 5.14D). Formerly they were considered to assist in 'holding' the sipunculan in its shell. Hylleberg (1975), however, found that they help in cleaning the inside of the shell of bacteria and algae. Hylleberg (1969) showed that *Phascolion strombus* irrigates its body wall by a series of peristalsis-like movements. The retractor muscles tend to fuse so that as few as one to four muscles may be present. The contractile vessel lacks villi, except in *P. cirratum*. The gut is often loosely wound and lacks a spindle muscle.

Cutler & Cutler (1985b) and Gibbs (1985) reviewed and provided a key to the species of *Phascolion*; Cutler & Cutler (1985b) also synonymised a number of species. Edmonds (1980) listed four species from Australia: *P. pacificum*, *P. collare*, *P. cronullae* and *P. dentalicolum*. However, *P. cronullae*, from off the coast of New South Wales, may be of only sub-specific status (as *P. strombus cronullae*) and Cutler's (1977) record of *P. dentalicolum*, from the Great Australian Bight, is probably *P. hedraeum* (Cutler & Cutler 1985b).

The embryology and development of two species have been studied: *Phascolion cryptum* (Rice 1975b) and *P. strombus* (Åkesson 1958). The eggs of *P. cryptum* are rich in yolk and have a sticky jelly coating, which enables them to adhere to any surface they contact. Development is direct, after 2 days at 25°C a crawling larva hatches from the egg. Åkesson (1958) reported that the egg of *P. strombus* gives rise to a lecithotrophic trochophore which metamorphoses after 8 days into a small adult. The affinities of the Australian species are Indo-Pacific.

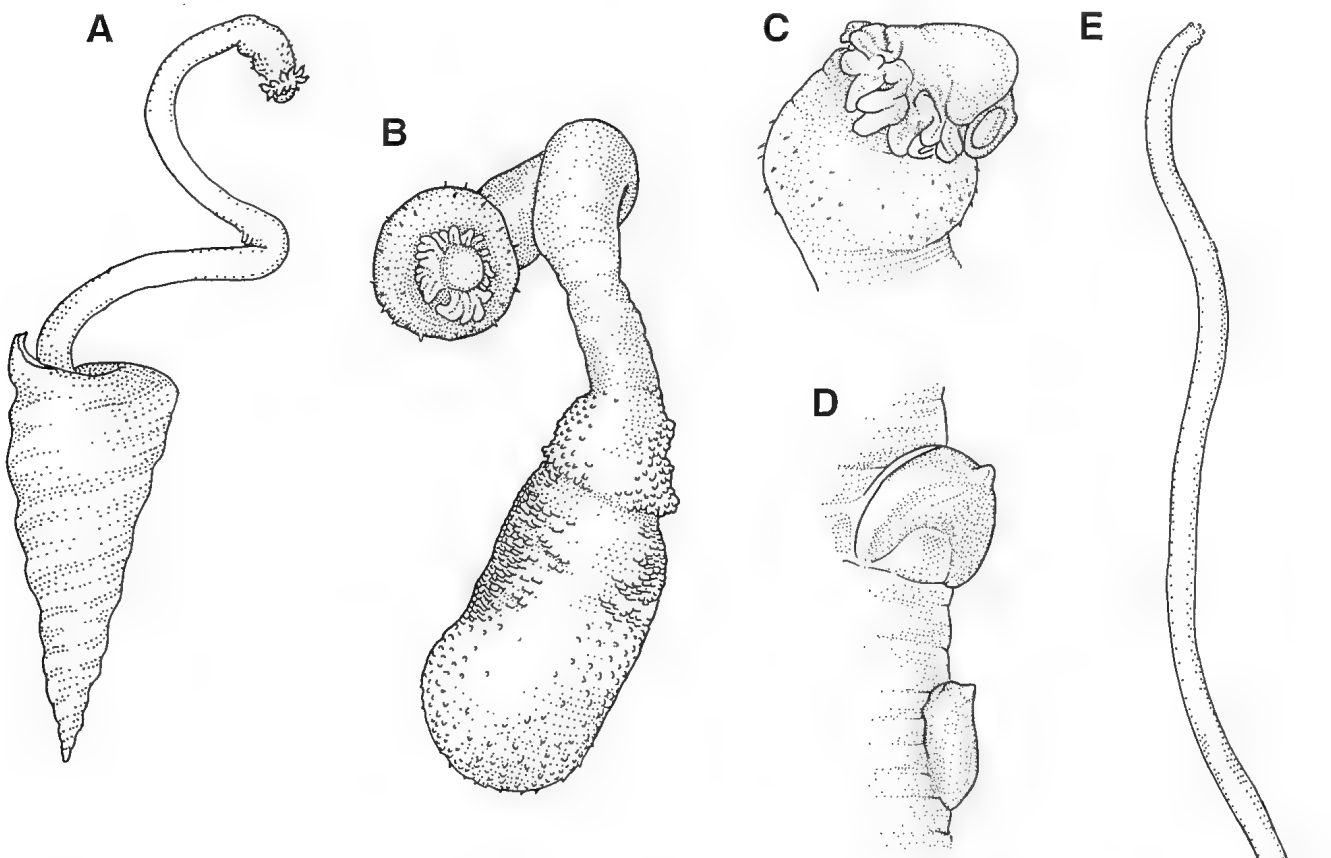


Figure 5.14 Family Phascolionidae. **A**, introvert of a *Phascolion* species emerging from the shell which it inhabits. **B**, *Phascolion* species, entire animal removed from shell. **C**, anterior introvert of a *Phascolion* species; part of anterior oesophagus is everted beyond the mouth. **D**, 'holdfast' papilla of trunk. **E**, *Onchnesoma* species, entire animal (C, D, after Théel 1905) [I. Grant]

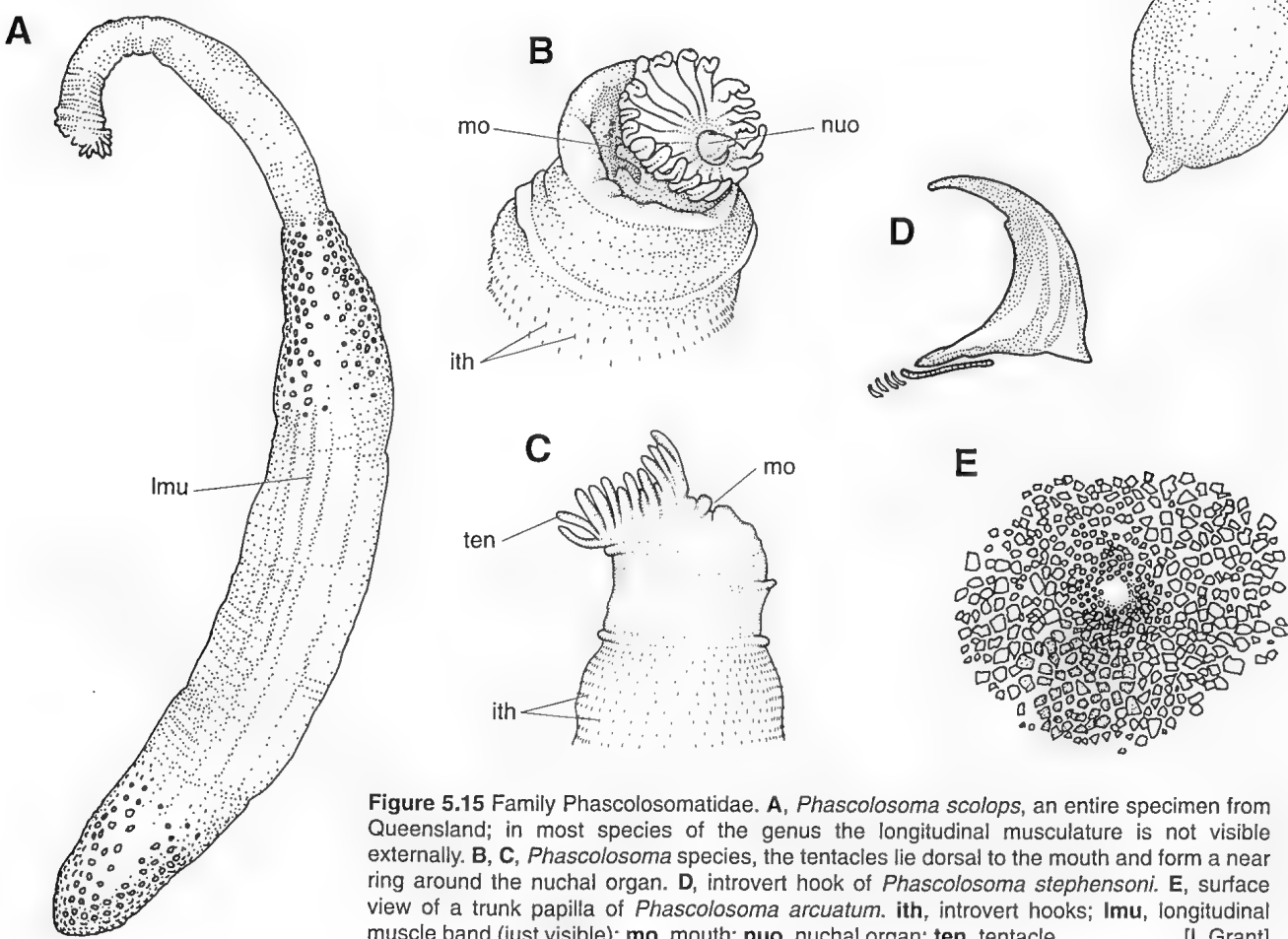


Figure 5.15 Family Phascolosomatidae. **A**, *Phascolosoma scolops*, an entire specimen from Queensland; in most species of the genus the longitudinal musculature is not visible externally. **B**, **C**, *Phascolosoma* species, the tentacles lie dorsal to the mouth and form a near ring around the nuchal organ. **D**, introvert hook of *Phascolosoma stephensoni*. **E**, surface view of a trunk papilla of *Phascolosoma arcuatum*. **ith**, introvert hooks; **lmu**, longitudinal muscle band (just visible); **mo**, mouth; **nuo**, nuchal organ; **ten**, tentacle. [I. Grant]

Class PHASCOLOSOMATIDEA

Members of the class Phascolosomatidea have tentacles that are not peripheral, but are arranged so as to form an arc enclosing the dorsal nuchal organ. Introvert hooks are recurved, usually with internal structure or markings and generally are arranged in rings; introvert hooks are absent in species of *Antillesoma*. The spindle muscle is attached posteriorly. Two orders are included: Phascolosomatiformes and Aspidosiphoniformes.

Order PHASCOLOSOMATIFORMES

Phascolosomatiformes are distinguished by having an anterior trunk which is not modified to form an anal shield and four introvert retractor muscles; includes one family, Phascolosomatidae.

Family Phascolosomatidae

Phascolosomatids (Pls 12.1, 12.4) are small to medium-sized, with a trunk 10–60 mm in length. The body shape may be bottle-, flask- and spindle-like, fusiform, or sometimes subcylindrical (Fig. 5.15A) or, if much contracted, almost rounded. Fewer than 30 finger-like tentacles lie in a near circle dorsal to the mouth (Fig. 5.15B, C) and surround the nuchal organ (since this character is difficult to determine if the introvert is retracted, the anterior region of the organ may have to be dissected). The longitudinal musculature of the trunk wall is grouped into bands which may anastomose; the bands are not always visible externally, but are always revealed on dissection. The introvert and trunk usually bear numerous, pigmented, conical to hemispherical papillae consisting of small plates or platelets (Fig. 5.15E); these are most numerous and largest on the anterior and posterior regions of the trunk. Four retractor muscles are present. The contractile vessel is single and lacks villi, except in *Antillesoma* species. Phascolosomatids are distinguished from aspidosiphonids by the absence of a hard, horny or calcareous anal plate or shield. The type genus is *Phascolosoma* described by Leuckart (1828).

In living specimens, the introvert is capable of considerable extension, but in fixed material it may be half to one and a half times the trunk length. The introvert is usually armed with numerous, closely packed rings of hooks (Fig. 5.15D), which often have a characteristic shape and internal marking. The hooks of some species are thought to assist in scraping algae from rocks (Rice 1976). The identification of species depends on the shape and markings on the hooks and the size, shape and structure of body papillae. The spindle muscle is fastened posteriorly near the extremity of the trunk.

The eggs of most sipunculans are spherical in shape, but those of *Phascolosoma* become slightly flattened ellipsoids during coelomic oogenesis, although initially spherical. The embryology and larval development of a number phascolosomatids has been studied by Rice (1981, 1985b). The trochophore, pelagic for 3–10 days, gives rise to a planktotrophic pelagospaera capable of drifting in the plankton for 1–3 months. Two species studied by Rice (1985b), *Phascolosoma perlucens* and *Apionsoma* (= *Golfingia*) *misakianum*, have been recorded from Australia (Edmonds 1980).

The family, according to Gibbs & Cutler (1987) comprises three genera, *Phascolosoma* (Pl. 12.1), *Apionsoma* and *Antillesoma*; the first is a very large genus and the other two

are very small. *Phascolosoma* species are the most commonly collected intertidal sipunculans in Australia. They live in burrows in limestone and coral reefs, in encrusting masses of tubicolous polychaetes (such as *Galeolaria* species), in clumps of mussels, in rock crevices, under stones and in mangrove flats. Most appear to be detritus-feeders. Edmonds (1980) recorded 11 species from Australian waters; *Phascolosoma kapalum* may also be added to the fauna. *Golfingia misakiana* and *G. trichocephala*, listed by Edmonds (1980), were transferred to *Apionsoma* by Gibbs & Cutler (1987). Phascolosomatids are common especially in the tropical and temperate waters of the world. Australian species are also well known in the western Pacific and regions of the Indian Ocean. Only one is thought to be endemic.

Order ASPIDOSIPHONIFORMES

Members of the Aspidosiphoniformes are distinguished by a modified anterior trunk which forms a hardened anal shield, calcareous knob or cone, and two retractor muscles which may fuse near their base. The order comprises only one family, Aspidosiphonidae.

Family Aspidosiphonidae

Aspidosiphonids are small to medium-sized sipunculans with a trunk of 4–40 mm in length (Pls 12.2, 12.3). They either have a hardened, horny, gold to dark brown anal shield or a white, calcareous knob or cap, both clearly marked off at the anterior region of the trunk (Figs 5.16A, 5.17). The introvert lies ventral to the shield except in the genus *Cloeosiphon* in which it arises from the centre of the cap. Tentacles are small and finger-like and arranged in a near-complete ring around the nuchal organ. The longitudinal musculature is continuous in *Aspidosiphon* (*Aspidosiphon*) and in *Cloeosiphon*, but in bundles (with anastomoses) in *Aspidosiphon* (*Paraspidosiphon*) and *Lithacrosiphon*. Two nephridia are present, as are two retractor muscles which may fuse for much of their length. The spindle muscle is attached posteriorly. The type genus is *Aspidosiphon* (Diesing, 1851).

The length of the introvert is variable, but is usually about as long as or twice that of the trunk. It is covered with numerous rings of closely packed, recurved hooks (Fig. 5.16E, F); spines may be present (Fig. 5.16G). Spines, when present, usually lie in a field posterior to that of the hooks. A hardened caudal shield is often present at the posterior extremity of *Aspidosiphon* (Fig. 5.16C, D; Pl. 12.2). Both anal and caudal shields consist of small to large pigmented plates or platelets. The contractile vessel lacks villi.

The family contains three genera, the diverse and speciose genus *Aspidosiphon* and the two small genera *Cloeosiphon* and *Lithacrosiphon*. *Aspidosiphon* species are almost sedentary in habit and live in discarded shells, solitary corals, in crevices and under rocks and are found boring in coral and limestone reefs where they play a part in the physical disintegration of the environment. They are probably detritus and algal feeders. Embryology and development have been studied in *Aspidosiphon* (*Paraspidosiphon*) *fischeri*, a Caribbean species (Rice 1975b). The egg is oval, but lacks the depressed apices of the eggs of *Phascolosoma* species. Within an hour of fertilisation the egg has divided into four cells and after 10 hours the embryo has begun to swim. After 48 hours the trochophore metamorphoses to a planktotrophic pelagospaera larva, known to live in the plankton for as long as a month.

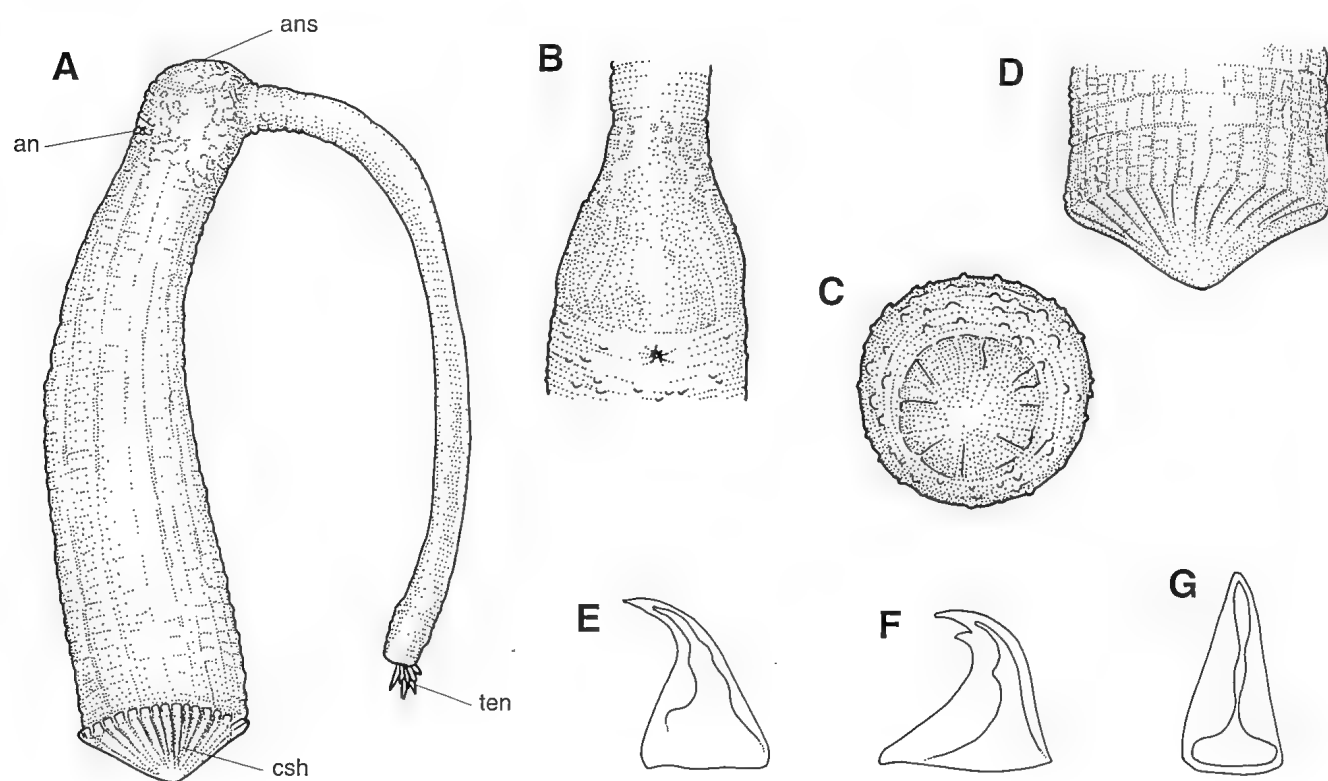


Figure 5.16 Family Aspidosiphonidae. *Aspidosiphon* species. **A**, entire animal. **B**, dorsal view of anal shield showing anus. **C**, **D**, caudal shield: **C**, end-on view; **D**, lateral view showing furrows. **E**, **F**, introvert hooks: **E**, single pointed; **F**, double-pointed. **G**, introvert spine. **an**, anus; **ans**, anal shield; **csh**, caudal shield; **ten**, tentacle. [I. Grant]

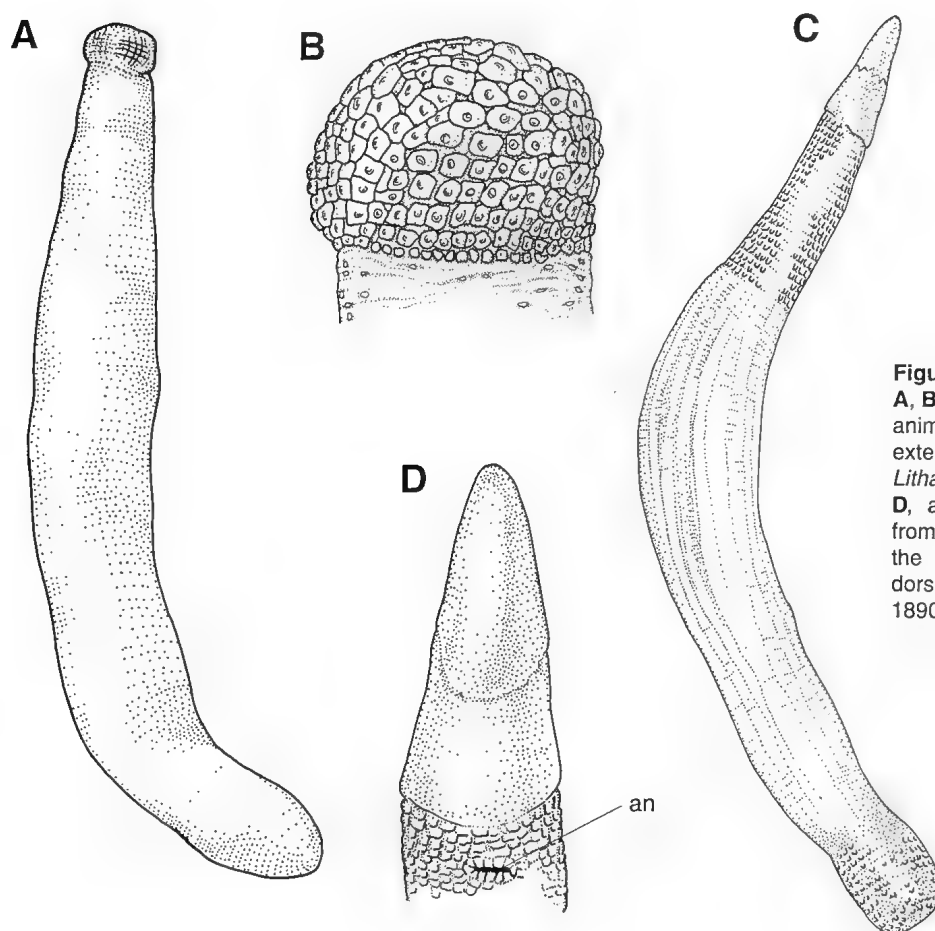


Figure 5.17 Family Aspidosiphonidae. **A**, **B**, *Cloeosiphon aspergillus*: **A**, entire animal; **B**, anterior cap; the introvert extends from the centre of the cap. **C**, **D**, *Lithacrosiphon* species: **C**, entire animal; **D**, anterior cap; the introvert extends from the ventral side of the trunk below the cap. **an**, anus which lies on the dorsal side of the trunk. (C, after Shipley 1890) [I. Grant]

Several species of *Aspidosiphon*, including *A. steenstrupi* (Pl. 12.2) are known from the Great Barrier Reef; others occur on limestone and coral reefs of north-western Western Australia. *Aspidosiphon muelleri* is a common inhabitant of the solitary coral *Heteropsammia michelini* in Queensland.

Edmonds (1980) listed 10 species of *Aspidosiphon*, one of *Cloeosiphon* and one of *Lithacrosiphon* from Australian waters. Aspidosiphonids are inhabitants of tropical and temperate waters, especially the former. The affinities of Australian species are Indo-western Pacific.

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GLOSSARY

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Just as systematics underpins other areas of biological endeavour, a glossary underpins the study of the systematics of a particular group. A good glossary will not only standardise the terms we use and therefore assist in the communication between workers, but also for many terms it is a statement about homologies - if two features are considered homologous then this should be reflected by using the same or a similar name. Use of two quite dissimilar terms for the same structure or concept only leads to confusion (for example, auricle and basal lappet, for the paired processes at the base of the antenna in some sigalionids). Conversely, where it is established that two corresponding structures are not homologous, that is, the structure was not present in the common ancestor, then it may be appropriate for them to be given different names to reflect their different origins. This would apply, for example, to the various existing terms used to describe pygidia of different families (caudal plaque, sternal shield, scaphe) and to the superficially similar muscularised regions of the anterior digestive tract in syllids (proventricle) and spionids (gizzard).

The glossary presented here was initially compiled and edited with the view to standardising polychaete contributions to the text for the *Fauna of Australia*. An early version appears on the Annelid Resources Home Page [at time of publication at <http://biodiversity.uno.edu/~worms/annelid.html>]. It has been expanded by additional terms in the present texts for the Polychaeta, Myzostomida, Pogonophora, Sipuncula and Echiura. Included are all terms used singly or in combination that describe attributes of these taxa, and which in general would require reference to specialist literature. Terms listed in standard dictionaries have been omitted, such as various descriptors (distal, dorsal), or terms which are readily interpreted either from their component parts or their context. Exceptions to these limits are terms which are in everyday use but have a specific meaning for these taxa unrelated to their general use. Many of the terms are defined directly from the present text. The several sources listed below were most valuable in resolving definitions.

abdomen: in polychaetes, body region posterior to the thorax, sometimes followed by a tail.

abyssal: oceanic waters between depths of 4000 m and 6000 m.

achaeitous: without chaetae.

acicula, aciculae: in polychaetes, stout supportive chaeta found internally in projecting parapodial rami.

acicular chaeta: stout, projecting chaeta.

acicular muscle: see oblique muscle.

aciculum: see support rod.

acoelomate: pertaining to animals lacking a coelom.

acrosome: membrane limited organelle at apex of spermatozoon head, covering the anterior surface of the nucleus; secretes enzymes thought to facilitate sperm entry.

action potential: the transient difference in electric potential across the plasma membrane of a nerve or muscle cell on stimulation.

adelphophagy: consumption by a developing larva of nurse eggs present in the same egg capsule.

adenosinetriphosphate, ATP: a source of metabolic energy, widespread in biological systems; comprises adenine, ribose and three phosphate groups.

adhesive plaques: thickened, tanned area of cuticle with a raised margin in pogonophores.

aileron: accessory jaw plate in Glyceridae.

akrotrach (= acrotrach): circlet of cilia anterior to prototroch.

allantoicase: enzyme that catalyses hydrolysis of allantoic acid to urea and glyoxylic acid.

allantoinase: enzyme that catalyses the hydrolysis of allantoin, an oxidation product of urea.

ambulacrum, ambulacral groove: ciliated groove from mouth to tip of each arm pinnule in crinoids; furrow from mouth to tip of each arm in asteroid echinoderms.

amoebocyte: a cell which exhibits amoeboid characteristics in form and behaviour.

amylase: one of a group of enzymes that catalyses the hydrolysis of glycogen or starches to produce sugars.

anaerobiasis: a mode of life in organisms that occupy environments in which oxygen is absent (obligate anaerobiasis) or in low concentration (facultative anaerobiasis).

anal plaque: depressed (or sunken) plate-like pygidium of some maldanids and other polychaetes.

anal vesicles: primary site of excretion in echiurans, a pair of large tubular, sac-like or dendritic organs, linked to the coelom through numerous ciliated funnels.

anastomosing: joining of vessels, ducts, nerves etc to form a network.

annulated: ringed or marked with grooves delineating segments.

annuli (= girdles): pair of chaetigerous epidermal ridges around trunk of perviate and moniliferan pogonophores.

anoxia: a lack of oxygen available for respiration.

antenna, antennae: sensory projection arising from the dorsal, lateral or frontal surface of the prostomium in polychaetes.

antennular auricle: = auricle.

antennular membrane: hood-like membrane between the paleae and the buccal tentacles in Pectinariidae.

apical tooth: see primary tooth.

apical tuft: ciliary sensory organ at the apex of the trochophore larva.

Apicomplexa, apicomplexans: group of parasitic, pathogenic protists, formerly placed in the Sporozoa.

apodous: segments without parapodia.

apomorphy: an advanced or derived feature; compare plesiomorphy.

arborescent: branching like a tree.

architomy: see schizotomy.

arista, aristae: fine hair-like or bristle-like structure in polychaetes.

aristate chaeta: simple chaeta with smooth shaft and a tuft of hairs or a single spine distally in polychaetes.

article: demarcated sections of chaetae or cirri separated by joints in polychaetes.

articulate: jointed, as in antennae, tentacular cirri, palps and dorsal cirri.

achaetigerous: see achaetous.

atoke: non-sexual, unmodified state of an individual in some polychaete groups; pertaining to species which undergo epitoky.

ATP: see adenosinetriphosphate.

atrochal larva: more or less overall ciliated polychaete larva that lacks the ciliary rings of the typical trochophore larva.

auricule: paired ear-shaped processes at the base of an antenna (ceratophore) characteristic of some sigalionids.

Australian region: comprises continental Australia including Tasmania; offshore islands - Macquarie, Lord Howe Island and Cocos (Keeling) Islands; Australian External Territories - Christmas Island, Heard Island, Norfolk Island and Australian Antarctic Territories; and the Australian Exclusive Economic Zone.

autapomorphy: a derived character unique to a particular taxon.

autosynthesis: formation of yolk within the oocyte; compare heterosynthesis.

autotomy: the deliberate loss of body parts; in polychaetes, fragmentation of individuals into two or more parts which regenerate into new individuals.

avicular: beaked; shaped like a bird's head.

axoneme: microtubular structure forming core of cilium or flagellum; comprises two single microtubules, surrounded by nine double microtubules.

B

bacteriocyte: cell in which symbiotic bacteria reside.

basal lappet: = auricule.

benthic: pertaining to the sea floor.

benthonic: pertaining to the benthon or community of organisms that inhabit the sea floor.

biarticulate: with two joints; pertaining to antennae, tentacular cirri, palps and dorsal cirri.

bidentate chaeta: chaeta with two teeth distally.

bifid: distally split in two.

bifurcate chaeta: simple chaeta with two prongs.

bilabiate: with two lips, usually about parapodial lobes.

bilimbate chaeta: simple chaeta with two wings; see limbate.

bioherm: rock mass formed partially or wholly by deposits of sedimentary marine organisms, such as corals or algae.

bipectinate: branching like a feather from a central axis; similar to pinnate, but branches coarser.

biramous parapodium: parapodium with two branches, a notopodium and a neuropodium.

blade: distal, flattened portion of a compound or simple chaeta.

blastomere: cell formed during initial divisions of fertilised egg.

Bohr effect: the decreasing affinity of haemoglobin for oxygen as carbon dioxide concentration increases and pH decreases.

bonellin: a highly toxic green integumentary pigment in echiurans, comprising a chlorin molecule; determinant of sex in boniellids.

boss: small projection or knob-like process in compound and simple chaetae.

brain: ganglionic mass situated at least in part in the prostomium in polychaetes.

branchia, branchiae: in polychaetes, extension of the body wall with a loop of the vascular system; usually well equipped with capillary blood-vessels; in pogonophores, a tentacle bearing pinnules, forming a respiratory organ.

branchial crown: see tentacular crown.

branchiole: see radiole.

bridle: (= frenulum) paired thickened cuticular ridges around forepart of perviate pogonophore.

bristle: see chaeta.

brush-tipped chaeta: see penicillate chaeta.

buccal cavity: mouth cavity.

buccal cirri: cirri in or around the mouth; sensory function rather than feeding (*cf.* buccal tentacles).

buccal organ: anterior part of alimentary canal derived from larval stomodaeum, comprising a complex set of folds, musculature and glands; see pharynx; see also ventral buccal organ.

buccal papillae: extensions of the lip of the proboscis in many proboscidean myzostomes.

buccal tentacles: elongate, grooved, usually ciliated appendages in or around the mouth; palpal derivatives.

bulbus: knob-like structure swollen in appearance.

C

caecum, caeca: blind sac arising from the alimentary canal; applied also to other organ systems, such as nephridia.

calicinate: like the calyx of a flower.

canaliculate: with a (fine) canal or groove.

capillary chaeta: slender, often long, chaeta tapering to a fine point in polychaetes.

capillary, capillaries: see capillary chaeta.

caruncle: projection from the posterior end of the prostomium carrying nuchal organs in polychaetes.

cauda: see pygidium.

caudad: towards the tail.

caudal plaque: flattened pygidium.

centriole: cell organelle at basal end of axoneme of cilium or flagellum; comprises nine triplets of fused microtubules; in myzostome spermatozoa, secondarily at free end of flagellum.

centromere: point on chromosome to which spindle attaches during mitosis.

cephalad: towards the head.

cephalic cage: long, forwardly directed chaetae more or less enclosing the head.

cephalic keel: median ridge on the prostomium or head, as in some Maldanidae.

cephalic peaks: see prostomial peaks.

cephalic plaque: = cephalic plate.

- cephalic plate:** plate-like antero-dorsal surface of the head region in some Maldanidae and Pectinariidae.
- cephalic rim:** flange encircling the head in polychaetes.
- cephalic veil:** see cephalic rim.
- cephalisation:** incorporation of anterior, usually modified cephalised segments, with the head (prostomium/peristomium) in polychaetes.
- cephalon:** see head.
- ceratophore:** basal part of an antenna in polychaetes.
- ceratostyle:** distal part of an antenna in polychaetes.
- chaeta, chaetae:** in polychaetes, a chitinous bristle protruding from a pocket in the body wall; in pogonophores, slender bristle, bearing an oval, serrated head.
- chaetal gland:** (= chaetal sac): in myzostomes and polychaetes, a series of follicles in the parapodium that secrete the support rod, the hook in use, and a varying number of replacement hooks.
- chaetal inversion:** presence, in polychaetes, of uncini on the notopodia rather than the more usual position on the neuropodia.
- chaetiger:** segment bearing chaetae.
- chaetigerous lobe:** that projection or part of the notopodium or neuropodium which bears the chaetae.
- chaetoblast:** cell which forms, together with follicle cell, a chaeta.
- chemoautotroph:** organism able to synthesise organic nutrients from inorganic sources, excluding photosynthesis.
- chevron:** V-shaped chitinised jaw piece at the base of the eversible pharynx in some Goniadidae.
- chlorin:** a saturated porphyrin in which one double bond has been reduced in a single pyrrole ring.
- chlorocruorin:** respiratory blood pigment; changes in colour from green to red with increasing concentration.
- cholinergic:** pertaining to a nerve cell ending that produces or is stimulated by the neurotransmitter acetylcholine.
- chromaphil gland:** see chromatophil gland.
- chromatin:** dark-staining nuclear material comprising DNA and associated bound histones.
- chromatophil gland:** densely staining gland in the ventral pinnule of *Tomopteris*; see also rosette gland.
- chromatophore:** special cell or group of cells carrying pigment.
- ciliated funnels:** see anal vesicles.
- ciliophore:** in polychaetes, distinct area or epidermal patch covered with cilia.
- circular muscle:** muscle layer encircling the body between the epidermis and longitudinal muscle layer.
- circumoesophageal connective:** in polychaetes, tracts of nervous tissue passing down from the brain on either side of the foregut and connecting to the ventral nerve cord.
- circumoral tentacles:** see tentacles.
- cirriform:** slender and cylindrical.
- cirrophore:** basal projection on which a cirrus is mounted.
- cirrostyle:** distal part of a cirrus or tentacle.
- cirrus, cirri:** sensory appendage in polychaetes; usually slender and cylindrical.
- cirrus:** sensory process of body margin in most myzostomatid and some endomyzostomatid species, frequently in pairs; process on medial part of parapodial fold in some Proboscidea.
- clade:** a complete set of taxa with a common ancestor.
- cladistics:** classification of taxa based on lines of evolutionary descent, and, in principle, recognizing only clades.
- cladogenesis:** the divergence within an ancestral species into two or more groups, one or more of which become monophyletic units or species.
- clavate:** club-shaped.
- coelom, coelomate:** body cavity with peritoneal lining; formed in embryonic mesoderm; characteristic of almost all bilateral animals; lined with epithelium termed the peritoneum.
- coelom:** in myzostomes, body cavity formed within, and lined with mesoderm; thought by many to be the lumen of the uterus and associated diverticula, but possibly absent.
- coelomocytes:** amoebocytes present in the coelom, in polychaetes and sipunculans.
- coelomoduct:** a tubule derived from coelomic tissue, connecting the coelom with the external environment; in polychaetes may have a coelomostome; often combined with nephridium and termed nephromixia; nephridium in sipunculans.
- coelomostome:** funnel at the inner end of a coelomoduct.
- cold seep:** emergence of fluid from sedimentary rocks under pressure, such as in regions of continental subduction; may comprise hydrocarbons, such as methane, or water, bearing salts such as sulphides.
- collar:** anterior encircling fold or flap, such as that covering the base of the tentacular crown in Sabellidae and Serpulidae; see also tube.
- collateral intestine:** see siphon in echiurans.
- comb chaeta:** simple chaeta with a comb-like arrangement of teeth on the distal end; present in some Eunicida.
- commensalism:** an association between two species that live together, which benefits individuals of one species without harming those of the other.
- commissure:** a transverse band of neural tissue linking paired ventral nerves or longitudinal nerve tracks; in polychaetes, one of four main tracts of nervous tissue passing through the brain.
- companion chaetae:** in polychaetes, small, simple chaetae, accompanying, or alternating with larger chaetae, usually hooks of some kind.
- compensatory vessel:** see contractile vessel.
- composite chaeta:** see compound chaeta.
- compound chaeta:** chaeta having a terminal portion which articulates with the shaft.
- compressed:** flattened in one plane, usually laterally.
- consecutive hermaphroditism:** change from one sex to another in an individual; may be protandrous, protogynous, or bi-directional.
- contractile vessel:** (= 'polian vessel'; compensatory vessel): in sipunculans, a single, sometimes, double tubular structure extending along the dorsum of the oesophagus, ending blindly; arises from the ring vessel encircling the oesophagus; these, with the tentacular vessels, comprise the circulatory system.
- copragogue:** see faecal groove.
- cordate, cordiform:** heart-shaped.
- crinoids:** echinoderms of the class Crinoidea, termed sea lilies or feather stars.
- cristate:** bearing a ridge or crest.
- crotchet:** see hook.
- crown:** a bilaterally symmetrical branched structure in some polychaetes formed by prostomial palps.
- ctenidium, ctenidia:** in polychaetes, a finger-shaped or flattened structure presumed to have a respiratory function.
- ctenognaths:** polychaetes in which the jaws comprise relatively large basal maxillae and symmetrically arranged rows of numerous anterior denticles in longitudinal series without carriers.

cuticle: thin, non-cellular protective layer produced by and overlying the epidermis in many invertebrate groups; in polychaetes, consists mainly of scleroprotein (not chitin).

cutis: see dermis.

cutting plate: distal part of eunicean mandible.

cysticolous: inhabiting a cyst formed on or within a host.

cytophore: central mass of cytoplasm comprised of cytoplasmic bridges between proliferated opheliid spermatogonia; thought to assist in synchronising the development of the sperm.

cytoplasm: the living contents of a cell, excluding the nucleus.

D

deciduous: pertaining to structures easily autotomised, or shed by the animal as a defensive reaction.

dendrites: branching cytoplasmic processes of sensory cells.

dental formula: in polychaetes, notation showing the distribution of teeth on the crest of a hook or uncinus.

dentate: toothed.

denticle: a minute tooth.

denticulate: finely toothed.

depressed: flattened, usually dorso-ventrally.

dermis: layer of skin underlying the epidermis; comprises connective tissue and a range of other cell types, such as pigment and nerve cells.

desmosome: attachment point (spot desmosome) or line between two animal cells, at which cell membranes are thickened, and the enlarged intercellular space contains connective filaments; see also zonula adhaerens.

detritus: particles of organic origin.

Deuterostomia, deuterostome: primary grouping of bilateral animals characterised by indeterminate cleavage; typical of echinoderms and chordates.

diagonal muscle: obliquely aligned dorso-ventral muscle in the body wall (*cf.* oblique muscle).

diaphragm: muscular partition in pogonophore which separates the forepart and the trunk; develops in juvenile from longitudinal muscle layers; important component of hydrostatic skeleton.

digitiform: finger-shaped.

dioecious: (= gonochorism, gonochoric) pertaining species, in which individuals are either male or female throughout life.

direct developers: embryos that develop completely into juveniles without intermediate larval stages.

diverticulum, diverticula: blind tube(s) or sac-like extension(s) of the lumen of an organ.

dorsal blood vessel: in polychaetes, longitudinal vessel which carries blood forward through the body; situated above the gut.

dorsal cirrus organ: sensory organ, with numerous long cilia at the ventral base of the dorsal cirrus in Eunicida.

dorsal cirrus: in polychaetes, cirrus normally situated on the upper edge of the notopodium.

dorso-ventral muscle: see diagonal muscle.

echinulate: prickly.

ect-aquasperm: spermatozoa that fertilise eggs external to the body.

ectoderm: the outermost layer of germ cells developed during gastrulation.

elytrigerous segment: polychaete segment bearing a scale.

elytron, elytra: dorsal scales found in the scale-worms; homologous with the dorsal cirrostyles.

elytrophore: cirrophore carrying an elytron, as in scale-worms.

endocytotic, endocytosis: process of inclusion of material within a cell via vesicles formed by invagination of the cell's plasma membrane.

endoderm: the innermost layer of germ cells developed during gastrulation.

endothelium: epithelial cells lining the inner wall of the circulatory system.

entire margin: smooth edged; lacking papillae, teeth or other projections.

enteronephridia: blind ciliated canals opening into the stomach.

epiboly: gastrulation process in which presumptive ectoderm grows over and envelops the presumptive endoderm.

epidermis: outer layer of the skin, usually one cell thick in invertebrates; derived from ectoderm.

epigamy: structural modification of an entire adult individual polychaete into a reproductive state or epitoke (*cf.* schizogamy).

episphere: region of trochophore anterior to the prototroch; gives rise to the prostomium in adult.

epitokes: an individual polychaete morphologically modified to leave the bottom to reproduce (epitoky); epigamous epitokes result from the transformation of an atoke to the epitoke; schizogamous epitokes arise by modification and separation from the posterior end of the worm.

erythrocruorins: a group of iron-porphyrin protein respiratory pigments in the blood of invertebrates; sometimes termed haemoglobins.

erythrocytes: nucleated cells in echiuran circulatory system and coelom containing haemoglobin.

eukaryotes: organisms in which the cells have a membrane-bound nucleus, chromosomes comprising DNA, and cellular organelles such as mitochondria.

eversible pharynx: part of pharynx being capable of being extended by turning the inner part outwards.

eversible proboscis: see eversible pharynx.

eye: light receptive organ which usually occurs on the prostomium of polychaetes but may occur elsewhere on the body or appendages.

eyespot: light sensitive structure in several polychaete groups.

F

facial tubercle: projecting ridge or lobe on the upper lip of certain polychaetes, especially scale-worms.

faecal groove: groove, on the posterior region of a tubicolous polychaete, along which the faecal pellets pass before being voided from the tube.

falcate chaeta: distally curved, usually blunt chaeta.

falciform: hook-shaped.

falciger: compound chaeta with a stout, hooked blade or apex, in polychaetes.

fang: in polychaetes, a major tooth-like projection of an uncinus, hook or maxillary plate.

fascicle: a small bundle, of tissue, such as muscle or nerve fibres, or structures, such as chaetae.

felt: matted thin chaetae produced by the notopodia in some species of scale-worms.

fenestrated: with one or more window-like openings; used to refer to the ladder-like arrangement of transparent compartments in the shaft of some polychaete chaetae.

fibrocyte: connecting tissue cell, synonymous with, or derived from a fibroblast.

filamentous: shaped like a fine thread.

filiform: slender and thread-like.

fimbriated: having flattened, leaf-like processes.

flail chaeta: abruptly tapering and distally bent simple chaeta of some orbinids.

flanged chaeta: see limbate or bilimbate chaetae.

foliaceous: thin and leaf-like.

foot: see parapodium.

foregut: anterior, cuticle-lined part of the alimentary canal including the pharynx and oesophagus; derived from the ectoderm; see also stomodaeum.

forked chaeta: see furcate chaeta.

formalin: a solution of formaldehyde in water, used for fixing tissues.

frenulum: see bridle.

frontal palps: anterior, sensory appendages of prostomium in Onuphidae.

frontal peaks: see prostomial peaks.

furcate chaeta: short (usually), bifurcated simple chaeta.

fusiform: cigar- or spindle-shaped.

G

gallicolous: inhabiting galls.

gametocyte: product of division of diploid gametogonium to diploid primary gametocyte; primary gametocyte produces through meiotic division a haploid secondary gametocyte (oocytes and spermatocytes).

gametogenesis: process of gamete formation from the diploid primordial gametogonia to the haploid ova or spermatozoa.

gametogonium, gametogonia: the earliest germ cell(s) in the gametogenic sequence.

gastrotroch: paired or unpaired ventral ciliary bands on body of trochophore larva.

gastrulation: formation of the embryonic ectoderm, mesoderm and endoderm layers.

geniculate chaeta: simple chaeta formed like a bent knee.

genital hook: modified notopodial chaeta used in mating in some Capitellidae.

genital papilla: projection on which a reproductive duct opens.

genital pore: modified nephridial opening.

genital pouch: a pocket-like skin fold between neuropodia in some Spionidae.

giant fibre: enlarged fibre in the nerve cord capable of very rapid conduction of nerve impulses.

gill: see branchia.

girdle: see annulus.

gizzard: muscular, barrel-shaped part of the foregut behind the pharynx in some Spionidae.

glabrous: smooth, glistening.

glial cells: comprise tissue surrounding and supporting neuronal cells.

gonochorism, gonochoric: (= dioecious) individuals are either male or female throughout life.

gonoduct: see coelomoduct; see also nephridia in echiurans and sipunculans.

guanidine: an excretory product formed during protein metabolism (CH_5N_2).

guard: paired delicate chitinous sheaths protecting the tip of some chaetae.

gular membrane: a muscularised septum between two successive anterior segments in polychaetes; divides the coelom into anterior and posterior parts.

gut sinus: thin-walled open chamber of circulatory system around the gut.

gynandry: development of female reproductive system before male system in consecutive hermaphrodites.

H

hadal: oceanic depths exceeding 6000 m.

haemerythrin: respiratory pigment in sipunculans; in different taxa may comprise two, three or eight units of polypeptide attached to two Fe ions.

haemoglobin: intracellular or extracellular iron-protein respiratory pigment in many invertebrates; binds and transports both oxygen and sulphide in pogonophores; respiratory pigment in erythrocytes in echiuran circulatory system and coelom.

harpoon chaeta: stout pointed chaeta with recurved barbs near the tip.

hastate: shaped like the blade of a spear.

head: in polychaetes, collective term used for a structure formed by the fusion of peristomium, prostomium and, in many instances, one or more cephalised segments.

hemigomph: compound chaeta with articulation which re-aligns the tip at close to a right angle to its long axis.

hermaphroditism: presence of functional male and female reproductive systems in an individual, at the same time (simultaneous hermaphroditism) or sequentially (consecutive hermaphroditism).

heterogomph: compound chaeta with articulation which clearly re-aligns the tip obliquely to the long axis of the shaft.

heterosynthesis: exogenous formation of yolk or its precursor which is transported into the oocyte; compare autogenesis.

hindgut: posterior-most region of the alimentary canal, usually short; ectodermally derived.

hispid: minutely hairy; furry, often with reference to chaetae.

histology: the microscopical study of the structure of normal tissues.

holdfasts: swollen, papillate structures on the body wall of *Phascolion* species, inhabitants of discarded mollusc shells; used to clean bacteria and algae off the inside of the shell.

holoblastic: early embryonic cleavage pattern in which cell membranes divide cytoplasm, and yolk, completely; in forms with a small volume of yolk.

homogomph: compound chaeta with articulation which re-aligns the tip at a right angle to its long axis.

homologues: structures of common evolutionary origins, irrespective of functionality, derived from the same structure in the common ancestor.

homology: fundamental similarity in different organisms as a result of their common ancestry.

homoplasy: correspondence in morphology of different organisms as a result of evolutionary convergence or parallel evolution.

hood: in polychaetes, delicate chitinous envelope with a single opening, covering the apex of hooks or other chaetae (see also guards).

hook: in polychaetes, stout-shafted, unjointed, distally-curved chaeta with or without teeth near the apex; in myzostomes, replaceable chaetal component of the protrusible hook apparatus in each parapodium; in sipunculans, recurved and closely packed, or irregularly distributed, simple, thorn-like hollow structures on introvert.

hyaline gland: gland in the pinnules of certain species of *Tomopteris*; usually translucent, sometimes with a yellow spot in the centre.

hydrostatic skeleton: controlled support provided by muscular pressure on body fluids, especially the major venous sinuses; used to modify body or organ shape.

hydrothermal vent: site of emerging, often highly sulphidic hot water, after it has circulated through new crustal rocks at spreading ridges in the deep-sea floor.

hyperionic: internal ionic concentration higher than ambient concentration.

hyperosmotic: internal osmotic concentration higher than ambient concentration.

hypodermic internal fertilisation: transfer of sperm in some polychaetes by attachment to the partner's body wall or by their injection into partner through the body wall.

hypoxia: physiological or environmental state characterised by a low level of dissolved oxygen.

ichnogenus: generic name given to a group of animals characterised by fossilised evidence of their presence, for example, tube, burrow or track; known as trace fossils or ichnofossils.

imbricated: overlapping like tiles.

inquiline: pertaining to a form of commensal symbiosis in which the host primarily provides shelter for the symbiont, even within its body.

intermediate cirrus: in polychaetes, cirriform structure attached to the body wall between the notopodium and neuropodium.

inter-ramal cirrus: in polychaetes, a cirriform structure attached to the notopodium, projecting into the space between the notopodium and the neuropodium.

intersegmental: between segments.

intromittent: structured appropriately for insertion into partner during mating; usually associated with sperm transfer.

introvert: in myzostomes, a retractable protrusion derived either from entire anterior end of the body, often bearing several pairs of buccal papillae (Proboscidea), or from the rear of the oral cavity (Pharyngidea) and lacking papillae; the anterior, protrusible part of a sipunculan; can be retracted, by invagination, completely into the body cavity; see also proboscis.

invagination: in embryology, the folding in of part of the blastula wall, forming a cavity; see epiboly.

iso-osmotic: internal osmotic concentration equal to ambient concentration.

iteroparity: breeding in more than one season, often at regular intervals.

J

jaw formula: see maxillary formula.

jaws: in polychaetes, hardened feeding or grasping apparatus with opposable units situated in the eversible pharynx.

jointed chaeta: see compound chaeta.

L

labial palps: ventral sensory appendages of prostomium in Eunicida.

labidognaths: polychaetes in which the larger pieces of the highly differentiated jaws are located in a pocket with the smaller pieces arranged in semi-circles at its anterior end.

lacuna(e): space(s) or cavity (cavities), usually with reference to those in tissues.

lamella, lamellae: fleshy, flattened or plate-like structure(s).

lanceolate: pointed and shaped like a lance.

lappet: lobe or flap-like projection.

lateral caecum: blind sac arising laterally from the alimentary canal.

lateral lappet: lobe or flap-like projection on anterior segments in Terebellidae.

lateral organs: in polychaetes, small, rounded inter-ramal elevations with stiff projecting hairs; see also dorsal cirrus organ, stereocilia; in myzostomes, sucker-like or pit-like, usually protrusible, organs on the outer part of the ventral body surface, thought to be mechanosensory or chemosensory structures.

lateral shield: glandular area on the lateral venter of thoracic segments in *Polycirrus*; cf. ventral pads.

lecithotrophy: form of development in which larvae generally do not feed, relying on yolk in egg.

ligule: in polychaetes, compressed conical lobe of a parapodium; cf. lobe.

limbate chaeta: in polychaetes, simple chaeta with a flattened wing projecting from one side along much of its distal half; see also bilimbate.

lipase: one of a group of enzymes that catalyses the hydrolysis of lipids or lipoproteins.

lobe: in polychaetes, conical process of a parapodium; cf. ligule.

long-handled uncinus: in polychaetes, uncinus with a long, rod-like basal extension.

longitudinal muscle: in polychaetes, muscle layer running parallel to the long axis of the body, between the circular muscle and the peritoneum; usually arranged in two dorso-lateral and two ventro-lateral bands.

lyre chaeta, lyrate chaeta: see furcate chaeta.

lysosomal enzymes, lysozymes: enzymes important in bacteriolysis; break the glycosidic linkages of mucopolysaccharides and mucopeptides in bacterial cell wall.

M

macromere: one of four large cells formed after the first two divisions of a developing egg; denoted as cells A, B, C and D.

macrotubercle: see tubercle.

madder: colour of dye from root of the herbaceous climber *Rubia tinctorum*.

main fang: see fang, see also primary tooth.

mammillate: pertaining to nipple-like process.

mammiliform: breast-shaped.

manchette: a cylindrical structure in the spermatid comprising microtubules that extend caudally from the posterior margin of the acrosomal cap, and surround the nucleus.

mandible: ventral jaw plate in Eunicida.

manubrium: in myzostomes, a process arising from the distal tip of the support rod of the parapodium, and which guides the movements of the hook.

- maxilla:** dorsal jaw plate in Eunicida.
- maxillary carrier:** posterior support for the maxillae.
- maxillary formula:** summary of the number and arrangement of maxillary plates and teeth in Eunicida.
- maxillary ring:** distal part of the everted pharynx in Nereididae.
- mechanoreceptor:** organ sensitive to mechanical stimuli, such as pressure or stretching.
- medial:** the mid-line regions of the body.
- median:** in the mid-line.
- mesocoel:** pair of coeloms separated by mesentery in forepart of perviate or moniliferan pogonophore.
- mesoderm:** embryonic germ layer derived from the endoderm in triploblastic phyla following gastrulation.
- mesothelium:** a single layer of cells, often squamous in form, lining a body cavity or similar space not exposed to the exterior.
- metacercaria:** endoparasitic fluke larva, derived from cercaria, and precursor of adult fluke.
- metacoel:** pair of coeloms separated by mesentery and trophosome in trunk of perviate or moniliferan pogonophore.
- metamerism, metamer:** segmentation of the body into a series of similar units, termed metamer.
- metanephridia:** in sipunculans, the primary excretory organs, gonoducts and possibly with osmoregulatory function, opening via the nephridiopore to the exterior and through the narrow nephrostome to the coelomic cavity; in myzostomes, term used often, probably erroneously, for ciliated ducts connecting the uterus to the anterior part of the intestine, rarely to the exterior; role in excretion or gamete release is doubtful, but they may expel waste material from the uterus; see also nephridium.
- metastomium:** in polychaetes, rarely used term covering the segmented body between the prostomium/peristomium and the pygidium, but including neither.
- metatroch:** transverse ring of cilia on trochophore, lying posterior to the mouth.
- metatrochophore:** ciliated larval stage of an annelid after segmental proliferation has begun but prior to development of functional parapodia; see also trochophore.
- methanotrophs:** bacteria able to utilise methane as a source of energy and carbon; present in alimentary tract of pogonophores.
- micromere:** small cell resulting from unequal division of cells comprising blastocyst; larger macromeres provide space for the yolk.
- microtubercle:** see tubercle.
- microvilli:** minute, very slender (>0.01 mm diameter) extensions of surface of epithelial cells; in myzostomes on integumental cells, where they penetrate the cuticle.
- midgut:** in polychaetes, central part of the alimentary canal comprising the stomach, when present, and the intestine; in echiurans, long and contorted, comprising presiphonal, siphonal and post-siphonal sections, marked by junctions with the siphon.
- mitochondrion, mitochondria:** small cytoplasmic organelle(s) of various shapes in eukaryote cells; site of the citric acid cycle and oxidative phosphorylation, by which adenosinetriphosphate is formed; probably derived from endosymbiotic bacteria.
- mitraria larva:** larva of oweniid polychaete; swim by ciliary action of an umbrella-like structure.
- moniliform:** beaded or beadlike.
- monophyly, monophyletic:** pertaining to a group of taxa comprising a common ancestor and all its descendants.
- morula:** syncytial mass of spermatozoa in polychaetes.
- mouth:** anterior opening of the alimentary canal; in polychaetes usually anterior opening of fully everted pharynx.
- mucopolysaccharide:** one of a group of polysaccharides comprising repeating disaccharide units and an amino sugar and uronic acid; now termed glycosaminoglycan.
- mucro:** a sharp point or tip on an abruptly tapering structure.
- mucronate:** sharply pointed.
- multiarticulate:** with three or more joints.
- multidigitate:** with many finger-like lobes or projections.
- mutualism:** symbiotic association between two members of different species which benefits both organisms.
- myo-epithelium:** epidermal layer which includes contractile epithelial cells.

N

- nascent:** the state of an atom or molecule, often highly reactive, as it breaks free of chemical bonding.
- natatory:** swimming.
- nectochaete:** developmental stage of an annelid following metatrochophore (up to 20 or so chaetigers); ciliation is reduced and parapodia function in locomotion.
- nematoform:** worm-like.
- nephridial papilla:** projection on which the excretory organ opens.
- nephridiopore:** in polychaetes and sipunculans, the external opening of a metanephridium; see also nephridium.
- nephridium, nephridia:** in polychaetes, excretory organ(s) opening to the exterior via a duct and a nephridiopore; fluid enters the internal end of the more primitive protonephridium through selenocytes; fluid enters the internal end of metanephridium through an open, ciliated funnel termed a nephrostome; in myzostomes, excretory organ comprising ciliated terminal cells, an intracellular tubule and an exit pore; in sipunculans, functions as gonoduct and may store excretory products; in echiurans, functions as a gonoduct, storing eggs or sperm, opening to the exterior through nephridiopore, and internally through a nephrostome, the mouth of which forms nephrostomal lips.
- nephromixia:** combinations in polychaetes of coelomoduct and nephridium termed protonephromixium, metanephromixium and mixonephridium; in protonephromixium, mesodermal components are fused with a protonephridial canal; in a metanephromixium, the mesodermal funnel has become joined with an open nephrostome; in a mixonephridium the coelomic end of the nephridium is completely fused with the funnel of a coelomoduct.
- nephrostomal lips:** tissue surrounding the lips of the nephrostome in echiurans.
- nephrostome:** the opening of a metanephridium to the coelomic cavity; see also nephridium.
- nerve cord:** ventral, segmentally ganglionated nerve trunk passing along the length of the body.
- neurochaeta:** in polychaetes, chaeta of a neuropodium.
- neurocirrus:** see ventral cirrus.
- neurofibrils:** fine proteinaceous longitudinal fibres forming a network within the nerve cell body, axons and dendrites.
- neuropodium, neuropodia:** in polychaetes, ventral branch or ramus of a parapodium.
- neuroseta:** see neurochaeta.
- neurotroch:** longitudinal ventral band of cilia in trochophore.
- notochaeta:** chaeta of a notopodium.
- notocirrus:** see dorsal cirrus.

GLOSSARY

- notopodium:** in polychaetes, dorsal branch or ramus of a parapodium.
- notoseta:** see notochaeta.
- nototroch:** regularly scattered dorsal ciliary bands on body of trochophore larva.
- nuchal cirrus:** see nuchal papilla.
- nuchal epaulettes:** see nuchal organs.
- nuchal organs:** in polychaetes, paired chemosensory structures situated postero-laterally on the prostomium, developed variously as pits, grooves, epaulettes, or elongated ridges; in sipunculans, a two- to four-lobed cushion of ciliated columnar epithelium on the oral disc, resembling the nuchal organ of annelids, and presumed to be chemoreceptive.
- nuchal papilla:** papilla found on the posterior margin of the prostomium of some Phyllodocidae and Spionidae.
- nuchal:** pertaining to the neck.
- nucleoplasm:** the contents of the nuclear envelope within a cell.
- nurse cells:** cells associated with, and providing nutrients to oocytes or spermatocytes during development.

O

- oblique muscle:** muscle attached to the aciculae and chaetae; cf. diagonal muscle.
- obturaculum:** thick, funnel-shaped structure in pogonophores with closely adhering, equal right and left halves; seals the aperture of the tube after withdrawal of the animal.
- occipital collar:** in polychaetes, a prominent fold immediately overlapping the posterior part of the prostomium.
- occipital fold:** see occipital collar.
- occipital lappet:** see occipital collar.
- occipital papilla:** see nuchal papilla.
- occipital:** in polychaetes, pertaining to the postero-dorsal part of the prostomium.
- ocellus, ocelli:** small eye spot(s).
- octopine:** one of the opines, a group of amino acids rarely found in nature; formed during anaerobic synthesis of ATP in *Sipunculus nudus*.
- ocular peduncle:** see ommatophore.
- oesophageal caecum:** in polychaetes, blind sac arising from the oesophagus.
- oesophagus:** posterior part of the foregut connecting the pharynx to the intestine; includes the gizzard or proventricle, and caeca when present.
- ommatidium:** functional optic unit of the compound eyes on the tentacular crown of some sabellidans.
- ommatophore:** projecting structure supporting the eyes, especially in scale-worms.
- oocyte:** female reproductive cell; diploid primary oocyte forms, through meiosis during oogenesis, a haploid secondary oocyte which divides to form an ovum.
- oogenesis:** formation and development of female gametes from diploid oogonia to mature, haploid ova.
- oogonia:** diploid precursor of primary oocytes, derived by mitosis during oogenesis.
- operculum, opercula:** in polychaetes, plug at the anterior end of some tube-dwellers which blocks the tube opening when the worm retracts.
- opisthosoma:** short hind region of the pogonophoran body, divided by septa into many chaetigerous segments; used for burrowing into the sediment by perviate pogonophores.

- oral cavity:** mouth cavity.
- oral ring:** proximal part of the everted pharynx in Nereididae.
- organogenesis:** the formation and development of organs.
- osmoconformers:** organisms in which the osmotic concentration of the internal fluids varies in accordance with the external environment.
- ossicle:** small calcified plate in the exoskeleton of an echinoderm.
- otocysts:** see statocysts.
- oviduct:** tube conducting eggs or oocytes to exterior; in myzostomes, usually applied to posterior portion of uterus dorsal to intestine, alternatively to entire branched lumen of female reproductive system.
- oviparous:** pertaining to deposition of eggs which develop completely and hatch externally.
- ovoid:** shaped like a bird's egg.
- oxyconformer:** an organism in which the rate of oxygen consumption decreases as ambient oxygen tension decreases.

P

- palea, paleae:** in polychaetes, broad, usually flattened chaetae, often with a metallic sheen.
- palmate:** resembling the fronds of a palm.
- palp, palpi:** one of a set of paired, elongate or cushion-like structures arising from the sides of the head; anteroventral and sensory in many 'errant' polychaetes; placed postero-dorsally and used in feeding in spioniform polychaetes.
- palpode:** in polychaetes, tapering anterior projection of the prostomium.
- palpophore:** in polychaetes, basal part of a jointed palp.
- palpostyle:** in polychaetes, distal part of a jointed palp.
- Panthalassa:** the oceanic region surrounding the former supercontinent Pangea.
- papillose:** bearing numerous small, rounded to conical projections.
- paragnath formula:** summary of number and arrangement of denticles on the pharynx in Nereididae.
- paragnath:** sclerotinised denticle on the pharynx in Nereididae.
- paraphyly, paraphyletic:** pertaining to a group of taxa comprising a common ancestor but not all of its descendants; see polyphyly and monophyly.
- parapodial trunk:** in polychaetes, proximal, undivided part of an elongate parapodium.
- parapodium, parapodia:** in polychaetes, one of the two fleshy lateral projections from a body segment, usually bearing chaetae and sometimes greatly reduced; in myzostomes, nearly always five pairs of unarticulated, unbranched appendages with a hook apparatus used for attachment to the substratum and for locomotion.
- paratomy:** see schizotomy.
- parenchyma:** mesodermal tissue surrounding, and filling spaces between organs, muscles and other tissues.
- pectinate:** comb-like; with series of projections arranged like the teeth of a comb.
- pectinate chaeta:** see comb chaeta.
- pedicel:** a short stalk.
- pelagosphaera larva:** pelagic larval form unique to some sipunculans, derived from trochophore, in which the ciliated metatroch is used for swimming and the prototroch is absent or very reduced.

- penicillate chaeta:** in polychaetes, simple chaeta with a brush-like tip.
- peribulbar nerve ring:** in some pharyngidean myzostomes, encircles the muscle bulb within the proboscis and incorporates the cerebral ganglia.
- peristalsis:** rhythmic, directional wave of muscular contraction in a vessel or tube.
- peristome:** see peristomium.
- peristomial cirri:** in polychaetes, paired, elongated cirri on the peristomium.
- peristomium:** in polychaetes, presegmental region of the body surrounding the mouth.
- peritoneum:** serous membrane lining the coelomic cavity.
- pharynx:** in polychaetes, anterior muscular part of the foregut, including the eversible proboscis.
- phosphagen:** creatine phosphate.
- pilose:** covered with very short hairs giving a velvety appearance.
- pinnate:** in polychaetes, feather-like; two rows of pinnules branching from a central axis (*cf.* bipinnate; bipectinate).
- pinnules:** in polychaetes, small side branches, in a feather-shaped process, such as the radiole in Sabellidae and Serpulidae; in pogonophores, an epidermal cell bearing a projection above the surface on the tentacle; in crinoid echinoderms, jointed appendages along each side of the arm.
- pinocytosis:** the process of uptake by cells of particles, large molecules and fluid droplets.
- piriform:** see pyriform.
- planariform:** resembling a flat worm, Tricladida, in form.
- planktotrophic:** larval development in which eggs with little yolk hatch as small, free-swimming trochophores which feed on algae in the water column.
- planula:** a free-swimming, radially symmetrical coelenterate larva.
- platelet:** syncytial mass of spermatozoa in polychaetes.
- plesiomorphy:** primitive retained character; compare apomorphy.
- plume:** numerous pinnulate tentacles arranged on concentric lamellae in vestimentiferan pogonophore.
- plumose:** resembling down; hairy.
- podocytes:** specialised cells which select waste products filtered from the circulatory system and excrete them via the open ducts of the metanephridia.
- polar lobe:** anucleate cell part budding from blastomeres prior to the first three embryonic cell divisions.
- polyphyly:** pertaining to a group comprising two or more taxa derived from distinct lineages.
- polytelic:** pertaining to individuals or species in which adults survive to spawn during two or more breeding seasons.
- polytomy, polytomous:** incompletely resolved node on tree of relationships, where several branches originate together.
- polytypic:** pertaining to a genus with more than one species, a family with more than one genus, etc.
- postchaetal:** posterior to the chaetae; used in relation to parapodial lobes or ligules.
- postsetal:** see postchaetal.
- post-siphonal:** see midgut in echiurans.
- post-trochal:** posterior to the prototroch of the trochophore larva.
- prebulbar nerve ring:** in proboscidean myzostomes, lies anterior to the muscle bulb at the tip of the proboscis, and does not incorporate cerebral ganglia.
- prechaetal:** anterior to the chaetae, used in relation to parapodial lobes or ligules.
- presetal:** see prechaetal.
- presiphonal:** see midgut in echiurans.
- retrochaetal:** anterior to the prototroch of the trochophore larva.
- primary tooth:** larger distal tooth of an unequally bidentate chaeta.
- prionognaths:** polychaetes in which the generally similar jaw-pieces are located in two rows on longitudinal ridges.
- proboscis, proboscides:** in polychaetes, eversible, non-muscular part of the buccal organ (strictly); often used interchangeably with pharynx; in echiurans, a muscular, highly extendable preoral lobe extending from the antero-dorsal surface of the trunk near the mouth, with a role in food-gathering, sensory, respiratory, locomotory and fossorial functions; but cannot be withdrawn into the body cavity like the introvert of sipunculans; see also proboscis.
- proboscis coelom:** ventral and lateral series of small cavities in the echiuran proboscis.
- prostomial keel:** see cephalic keel.
- prostomial peaks:** antero-lateral projections, often chitinised, of the prostomium in some scale-worms.
- prostomium, prostomia:** in polychaetes, anteriormost, presegmental and retrochaetal region of the body, sometimes bearing eyes and antennae; may not be externally recognisable.
- protandry, protandrous:** sequence of sexual stages, from a functional male stage to a hermaphroditic and/or a functional female stage in consecutive hermaphrodites.
- protocoel:** coelom in cephalic lobe of perviate or moniliferan pogonophore.
- protogyny, protogynous:** sequence from a functional female stage to a hermaphroditic and/or a functional male stage in consecutive hermaphrodites.
- protonephridia:** see nephridium.
- Protostomia, protostomes:** primary grouping in bilateral animals characterised by determinate cleavage, in which the fate of cells is pre-determined; found in platyhelminthes, annelids, molluscs and arthropods.
- prototroch:** primary, anterior-most transverse ring of locomotory cilia on the body of the trochophore larva, lying anterior to the mouth; in myzostomes, cilia form a ring of tufts.
- prototrochophore:** see trochophore.
- proventricle, proventriculus:** muscularised region of the anterior digestive tract occurring posterior to the pharynx; with muscle fibres arranged radially; characteristic of the Syllidae.
- proximal:** part of a structure nearer to the base or main body.
- psammophilic:** pertaining to sand-dwelling organisms.
- pseudocompound, pseudojointed:** in polychaetes, pertaining to compound chaeta in which the articulation is incomplete.
- pseudocopulation:** a form of sperm transfer in some polychaete groups involving spermatophores, spermatozeugmata, or free spermatozoa.
- pseudofaeces:** sediment particles transported upwards from feeding depths by a polychaete worm and ejected from the tube; texturally indistinguishable from faeces.
- pseudopod:** cytoplasmic extension used for locomotion and feeding in amoebae and amoebocytes.
- pygidial:** pertaining to the anal region or pygidium.
- pygidial cirrus:** = anal cirrus; cirrus projecting from the pygidium in polychaetes.

pygidium: in polychaetes, post-segmental terminal part of the body surrounding the anus.

pyriform glands: multicellular epidermal glands which secrete chitin and mucopolysaccharides to form the pogonophoran tube.

pyriform: with a broad bulbous base and tapered tip; pear- or onion-shaped.

R

radiole, radii: primary branch in the tentacular crown in Sabellidae and Serpulidae.

radiolar crown: see tentacular crown.

ramose: branched.

ramus, rami: branch, in relation to the dorsal or ventral branch of a parapodium.

raptorial: feeding mode involving snatching, seizing or tearing apart.

receptaculum seminis: seminal receptacle; female organ which receives and stores spermatozoa.

rectum: see hindgut.

redox discontinuity: the boundary between an oxygenated (oxidising) environment and an anoxic (reducing) environment.

reniform: kidney-shaped.

reticulate: pattern or structure forming a network or mesh.

retort organ: club-shaped gland opening into the buccal cavity in Typhloscolecidae.

rhabdomere: photoreceptive element of a compound eye.

ring sinus: see ring vessel.

ring vessel: in echiurans, a vessel joining the posterior end of the dorsal vessel to the neurointestinal vessel forming a ring; probably functions as a 'heart' or a reservoir of fluid; see also see tentacles or contractile vessel in sipunculans.

ringent chaeta: simple, subdistally expanded chaeta with a narrow slit which is internally crenulated or serrated; in Euphrosinidae.

rosette gland: yellowish star-shaped glands in the pinnules of some species of *Tomopteris*; see also chromatophil gland.

rosette: syncytial mass of spermatozoa in polychaetes.

rostrum: in polychaetes, enlarged first tooth or fang of a chaeta, usually a hook or uncinus.

rugose: roughened, lumpy.

S

sabre, sabre-like: in polychaetes, chaeta with a broad curved blade.

scale: see elytron.

scaphe: flattened caudal end in Pectinariidae; see also pygidium, sternal shield.

schizocoelous: pertains to coelomates, in which the body cavity is derived from the splitting of mesodermal blocks.

schizogamous epitoke: see epitoke.

schizogamy: in polychaetes, structural modification of the adult involving the budding off of sexual individuals; see also stolons, epigamy.

schizotomy: in polychaetes, asexual reproduction involving two forms of subdivision of the body and regeneration of the missing parts; in paratomy, a recognisable complete individual forms and then separates from the 'parent' stock; in architomy, the body breaks or fragments without any prior cephalisation.

scleroprotein: one of a group of proteins incorporated into skeletal, connective or epidermal structure.

sclerotinised: pertaining to the hardening of the exoskeleton with the quinone-tanned protein sclerotin.

secondary tooth: in polychaetes, smaller, proximal tooth of an unequally bidentate chaeta.

segment: one of the serially repeated units comprising the trunk; often separated internally by septa.

segmental organ: organs occurring in segmental arrangement; used specifically with reference to nephridia and nephridial ducts.

semelparity: death following a single reproductive season.

seminal vesicle: storage organ for sperm in myzostomes.

sensory buds: epithelial sensory/secretory structures on antennae and cirri.

septum, septa: structural partition(s) or division(s) between two visceral regions, within a haemocoel, or separating two cavities or tissue masses; in myzostomes, formed by the dorso-ventral muscles; in pogonophores, division between segments of the opisthosoma in pogonophores.

sesquiramous parapodium: see sub-biramous parapodium.

sessile: pertaining to organisms attached to or situated directly on the substratum; without a stalk.

sestonophages: consumers of microplankton and organic particles in aquatic systems.

seta, setae: see chaeta, chaetae.

setae: in polychaetes, myzostomes and pogonophores, see chaeta, chaetae; in echiurans, hook-like structures that emerge through the ventral wall posterior to the mouth and elsewhere on the trunk, the latter assisting in burrowing and locomotion.

setal: see chaetal.

setiger: see chaetiger.

setigerous lobe: see chaetigerous lobe.

setigerous: pertaining to setae.

shaft: proximal part of a compound or simple chaeta; or proximal part of a eunicean mandible.

sheath pocket: a diverticulum of the hook sheath in myzostomes.

sheath: in polychaetes, hyaline envelope covering a capillary chaeta.

short-handled uncinus: in polychaetes, uncinus without a long basal extension.

sickle chaeta: simple chaeta with a sickle-shaped blade in some Spirorbinae.

simple chaeta: see unjointed chaeta.

simultaneous hermaphroditism: presence of functional male and female reproductive systems in an individual at the same time.

singlet oxygen: excited state of molecular oxygen $^1\text{O}_2$, formed by many chemical and photochemical processes; especially reactive form.

siphon: in echiurans, conspicuous narrow tube close to the ventral wall of part of the gut; communicates at both its extremities with the lumen of the gut; of unknown function.

siphonal: see midgut in echiurans.

Skolithos: ichnogenus typified by simple verticle or subvertical burrows, termed piperock, formed in shallow, high-energy marine sedimentary environments; probably represents colonies of burrowing suspension-feeders, such as sabellariid polychaetes.

slime glands: used by urechid echiurans to produce a slime net to trap fine particles.

slime net: see slime glands.

solenocytes: in polychaetes, terminal cells at the internal end of a protonephridium; responsible for filtering waste products from the coelomic fluid.

spatulate, spathulate: in polychaetes, simple chaeta with a broadly expanded distal margin; like a spatula; spoon-shaped.

spermathecae: seminal receptacles.

spermatid: haploid, immature precursor of spermatozoon; derived from secondary spermatocyte.

spermatogenesis: process of sperm formation from diploid primordial spermatogonia to haploid spermatozoa.

spermatogonia: the earliest germ cells in the spermatogenic sequence.

spermatophores: in polychaetes and myzostomes, bundles of spermatozoa, all enclosed by a sheath or capsule isolating them from the surrounding environment; see also spermatozeugmata.

spermatozeugmata: in polychaetes, bundles of spermatozoa which are not surrounded by an external covering; may resemble bundles of late spermatids; see also spermatophores.

spermiocyst: in myzostomes, comprises one to three clumps of spermatozoa, at same stage of development, in vacuoles within a cyst cell.

spindle muscle: in sipunculans, a highly muscular, thread-like muscle, inserted anteriorly near the anus or from the rectum; supports the coils of the intestine and adjusts them to length of the worm by extension or contraction.

spine: in polychaetes, a thick acicular or spear-shaped chaeta; may be straight or slightly curved.

spiniger, spinigerous chaeta: compound chaeta tapering distally to a fine point.

spinning gland: gland secreting tube-forming material (threads) present in parapodia of certain scale-worms.

spinous pocket: enlarged, pocket-like serration along the margin of the chaetae of some scale-worms.

spinule: a small spine.

spinulose: bearing small spines.

spiral cleavage: cleavage pattern of early embryonic cells, such that the position of the upper, smaller one of two divided cells is slightly offset from the lower one, forming a spiral pattern.

squamous epithelium: epidermal layer of flattened, scale-like cells.

statocysts: paired epithelial organs at the base of the tentacular crown in sabellids that function in equilibrium and orientation.

stem cells: undifferentiated adult or embryonic cell capable of unlimited division and of giving rise to one or more cell types.

stereocilia: inter-ramal sensory cilia; see also dorsal cirrus organ.

sternal shield: modification of the last segments forming a ventral plate in Sternaspididae; see also pygidium, scaphe.

stolon: in polychaetes, secondary individual *formed by budding, usually from the posterior end, or elsewhere on the body.

stolonisation: form of asexual reproduction involving the formation of stolons.

stomach: glandular and/or muscular region of the midgut of most 'sedentary' polychaetes.

stomodaeum: anterior part of the embryonic alimentary canal formed as an invagination of the ectoderm; see also foregut.

striae: fine parallel marks or lines.

striated: with striae.

stylet: a small pointed tooth-like structure.

stylode: in polychaetes, finger-like projection associated with a parapodium, usually small and distinctly longer than wide.

sub-biramous parapodium: in polychaetes, parapodium with a well-developed neuropodium and reduced notopodium.

suboesophageal ganglion: in polychaetes, nerve centre at the junction of the circumoesophageal connectives and the ventral nerve cord.

subterminal: close to the apex of a structure.

subulate: awl-shaped.

subuluncinus: chaeta with a stout shaft tapering to a slender tip; intermediate between a capillary and an uncinus; see also aristate.

support rod: (= aciculum); in myzostomes, provides support for the parapodium and guides the hook.

symbiont: participant in a mutualistic, commensal or parasitic relationship.

symplesiomorphy: primitive retained character shared by two or more taxa; compare synapomorphy.

synapomorphy: derived character shared by two or more taxa.

synapse: junction between two nerve cells or a nerve cell with another cell type such as muscle.

syncytium: a non-cellular, multinucleate mass of protoplasm.

syngamy, syngametic: fusion of morphologically similar cells.

T

telocentric: with reference to a chromosome with a terminal centromere.

telotroch: girdle of locomotory cilia situated posteriorly on a trochophore larva.

tentacles: elongate structures encircling the mouth in asteromyzostomatid myzostomes, used to anchor the animal to the integument of its host sea star; few to numerous, elongate, vascularised structures extending from cephalic lobe, and primary site of oxygen uptake in pogonophores; in sipunculans, finger-, thread- or fold-like structures either surrounding or associated with the mouth, used for food-gathering and respiration, each with three tentacular vessels, linked to ring vessel encircling the oesophagus; see also palp with reference to feeding palps, and buccal tentacle.

tentacular cirri: in polychaetes, dorsal and/or ventral cirri of parapodia of cephalised segments; often more elongate than those of more posterior parapodia; confused in the literature with peristomial cirri.

tentacular crown: array of elongated appendages on the head in Sabellidae and Serpulidae; used for feeding and respiration.

tentacular formula: notation indicating the arrangement of the tentacular cirri and chaetae; originally used for Phyllodocidae and Alciopidae, now also extended to other families.

tentacular palps: in polychaetes, paired or multiple food-gathering appendages; most are grooved and/or have a longitudinal row of cilia; see also buccal cirri and buccal tentacles.

tentacules: dendritic or finely branched tentacular system in the sipunculan *Themiste*.

tentaculophore: in polychaetes, basal projection on which a tentacle is mounted.

terminal organ: small rounded, knob-like secretory organ in pelagospaera larva of some sipunculans and in some adults of *Sipunculus*; thought to assist the larva in selecting a suitable settlement site, to aid adhesion and trap detritus and bacteria for food.

terminal tooth: see primary tooth.

tessellated: pertaining to a surface with a network of grooves like a tiled wall.

thoracic membrane: thin fold extending from the dorsal part of the collar to the ventral side of the posterior thorax in most Serpulidae.

thorax: anterior region of the trunk in some polychaetes.

tonofilaments: keratin filament linking two epidermal cells via a spot desmosome.

torus, tori: in polychaetes, welt or ridge-like parapodial ramus, often with hooks or uncini.

trabeculae: struts of tissue forming a supportive or bracing framework within a space.

trepan: anteriorly toothed, slightly sclerotinised part of the eversible pharynx of some polychaetes, especially Syllidae.

trichogenic cells: in polychaetes, cells which secrete fine hair-like threads.

triploblastic: the organisation of bilateral animals, which develop from three embryonic germ layers – ectoderm, mesoderm and endoderm.

troch: ring or band of cilia on the embryonic or larval stage, used in locomotion.

trochophore: early, ciliated, free-swimming, planktonic larval stage before segment proliferation begins; in annelids, molluscs, sipunculans, echiurans and bryozoans; in myzostomes, transforms from the initial spherical protrochophore through a trochophore to a pear-shaped metatrochophore.

trophosome: midgut of a pogonophore, and site of symbiotic chemosynthetic bacteria which provide a source of energy for carbon fixation.

truncate: pertaining to a structure that ends abruptly, without tapering.

trunk: in polychaetes, the segmented region of the body between the peristomium and pygidium.

trypsin: a digestive enzyme that catalyses the breakdown of proteins by hydrolysis of peptide linkages.

tube feet: short, external extensions of the echinoderm water-vascular system, coelomic in origin; generally used for locomotion, but for feeding in crinoids.

tube: unbranched, chitin-protein structure secreted and inhabited by pogonophore; hair-like or fibrous in nature, clear, coloured uniformly or patterned; simple or segmented anteriorly, forming a series of collars.

tubercle: knob-like protruberance; often referring to a large (macrotubercle) or small (microtubercle) projection on the elytron of some Polynoidae.

U

unciniger: in polychaetes, segment carrying uncini.

uncinigerous: bearing uncini.

uncinus, uncini: in polychaetes, deeply embedded chaeta of which only its expanded multidentate head protrudes from the body wall; usually arranged in rows transverse to the long axis of the animal; see also long-handled uncinus.

unidentate: distally entire; often pertaining to chaetae.

uniramous parapodium: in polychaetes, parapodium in which one ramus, most frequently the notopodium, is absent.

urease: enzyme that catalyses the breakdown of urea to ammonia and carbon dioxide.

uricase: enzyme that catalyses the oxidation of uric acid to allantoin.

urite: projection from the pygidium.

urn cells: in sipunculans, fixed cells on coelomic wall and free-swimming cells in coelomic fluid that remove cell debris, foreign particles and bacteria.

V

vasa deferentia: ducts carrying spermatozoa from the testes; in myzostomes, male gonoducts carrying spermiocysts to other from vasa efferentia to seminal vesicles or penial ducts.

vasa efferentia: in myzostomes, male genital ducts carrying spermiocysts from testis to vasa deferentia.

vegetal pole: at one end of longitudinal axis of cleavage in the fertilised egg; linked with formation of digestive and associated organs.

venter, ventrum: the lower body surface.

ventral blood vessel: in polychaetes, longitudinal vessel which carries blood posteriorly through the body; situated beneath the gut.

ventral buccal organ: in polychaetes, variable, often complex set of folds, musculature and glands present on the ventral side of many polychaetes; see pharynx.

ventral cirrus: in polychaetes, cirrus normally situated on the lower edge of the neuropodium.

ventral groove: longitudinal mid-ventral furrow.

ventral muscle bulb: see pharynx.

ventral pads: glandular areas on the lateral venter of thoracic segments in some Eunicida, where they replace ventral cirri; compare lateral shields.

ventral shield: glandular segmentally arranged pad on the ventral thorax in some Terebellidae and Sabellidae.

vermiform: worm-like in form.

vestmentum: body region in vestimentiferan pogonophores, on which lateral flaps enfold the anterior part of the body behind the plume.

villus, villi: series of small, digitate tubules arising from the contractile vessel of some sipunculans.

vitellogenesis: formation of egg yolk.

W

winged capillary chaeta: see limbate or bilimbate chaetae.

Z

zonula adhaerens: region of contact with adjacent cells which is continuous around the cell; also termed belt desmosome.

zygote: product of fused haploid spermatozoa and ovum, forming a diploid cell.

zymogen granules: vesicles in glandular cells containing precursors of enzymes.

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FAUNA of AUSTRALIA

POLYCHAETES & ALLIES The Southern Synthesis

This excellent and much needed book presents detailed, well-referenced overviews for a significant portion of the Australian marine worm fauna. Extensively illustrated throughout with high-quality original line drawings of indigenous species, it provides good taxonomic keys to the families, yet is not a taxonomic guide per se. The comprehensive treatment of the phylogeny, taxonomy, classification, history, biology, ecology and zoogeography of polychaete worms and their allies makes this a truly encyclopedic work. As such, it has worldwide relevance to specialists and non-specialists alike; an essential reference volume for everyone interested in polychaetes, myzostomes, pogonophores, echiurans and sipunculans.

Dr Andrew Macfie, Secretary-Treasurer, International Polychaetology Association & Head of Marine Biodiversity, National Museum of Wales, Cardiff, United Kingdom

Maintaining the excellence in text and illustrations established in the Fauna of Australia, this work is much more than an account of the Australian polychaete and allied fauna. The biology of the polychaetes is treated comprehensively, yet provides a review of current knowledge for the general zoological reader for more than 30% of recognised polychaete families. The accounts of the biology of four allied groups, Myzostomida, Pogonophora, Echiura and Sipuncraria, are authoritative. The broad international appeal of the book should ensure its presence in libraries and institutions wherever marine invertebrate biology is studied.

Dr Don Anderson, Emeritus Professor of Biology, University of Sydney, Australia

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