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FRONTAL HEART AND ARTERIAL SYSTEM IN THE HEAD OF ISOPODA

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ZUSAMMENFASSUNG

Untersucht wurde das Blutgefäßsystem im Kopf der Isopoden unter besonderer Berücksichtigung des Frontalherzens (Cor frontale). Die Arbeit basiert auf der Auswertung von Semidünnschnitt-Serien, die von 11 Arten aus 5 Unterordnungen hergestellt wurden.

1. Die Aorta bildet im Kopf zwei Erweiterungen: eine postcerebrale, welche das Magenganglion umgibt, sowie eine praecerebrale im proximalen Bereich der Oberlippe. Von diesen Erweiterungen gehen mehrere Gefäße ab, die vor allem der Versorgung von Gehirn und Antennen dienen.

2. Mit beiden cephalen Gefäß-Erweiterungen sind Muskeln des Darmes eng assoziiert: Ösophagus-Konstriktoren sowie frontale Ösophagus-Dilatatoren verändern bei ihrer Kontraktion das Volumen der praecerebralen Erweiterung, während antero-dorsale Magen-Dilatatoren und Ösophagus-Retraktoren eine entsprechende Wirkung auf die postcerebrale Erweiterung haben.

3. Die Bewegungsweise des Magens deutet auf einen zweiphasigen Pulsationsablauf dieser beiden Gefäß-Erweiterungen hin, welche damit die Pumptätigkeit des Hauptherzens unterstützen. Mehrere einfache Ventilmechanismen verhindern dabei das Auftreten von Hämolymph-Rückströmen. Die funktionelle Koppelung der zwei Gefäß-Erweiterungen läßt es sinnvoll erscheinen, beide zusammen als Frontalherz zu bezeichnen.

INTRODUCTION

Numerous papers deal with the well developed arterial system of the Crustacea (reviews: Maynard, 1960; Giesbrecht, 1921). Special attention has always been directed to the major propulsive organ (primary heart); not only anatomical, but also functional, physiological and neurobiological aspects have been analysed in detail (c.f. references in Maynard, 1960; McLaughlin, 1983). Much scarcer and less comprehensive are descriptions of the so-called accessory hearts (auxiliary pulsatile organs).

Such accessory hearts are mentioned, however, for single species from different crustacean groups as for instance ostracods (Cannon, 1940), copepods (Pickering & Dana, 1838), cirripeds (Cannon, 1947), branchiurans (Grobben, 1908) and malacostracans (see references below). But only the so-called frontal heart (cor frontale of Chun, 1896) in the head of decapod crustaceans has hitherto been the subject of detailed anatomical research (Baumann, 1917; Powar, 1973; Steinacker, 1978, 1979).

In accordance with the last mentioned publications, similar structures in the head of various peracarids have also been called frontal hearts (Hewitt, 1907;

Oelze, 1931; Siewing, 1952, 1953, 1956; Belman & Childress, 1976). But it can not be decided whether or not these "hearts" do really function as auxiliary hearts because detailed investigations of the functional anatomy of the structures in question are lacking.

The aim of this paper is to produce precise anatomical reconstructions of the frontal heart of the isopods, a group of peracarids, which has been particularly little studied in this regard. On the basis of these results, I will attempt to outline a hypothesis of the functional mechanism of this organ.

MATERIALS AND METHODS

Isopods of the groups Oniscidea and Asellota were collected in the environment of Vienna, Austria. For marine species of other suborders, alcohol-preserved material was used. The long storage of some of the specimens proved to have insignificant influence on the condition of the tissues examined.

Adult specimens belonging to the following suborders and families (based on the system of Wägele, 1989) were examined:

- Suborder Asellota Latreille, 1802
    - *Asellus aquaticus* (Linnaeus, 1758)
- Suborder Oniscidea Latreille, 1802
    - Section Diplochaeta Vandel, 1957
        - *Ligidium hypnorum* (Cuvier, 1792)
    - Section Crinochaeta Legrand, 1946
        - *Armadillidium vulgare* (Latreille, 1804)
        - *Cylisticus convexus* (De Geer, 1804)
        - *Oniscus asellus* Linnaeus, 1758
        - *Porcellio scaber* Latreille, 1804
        - *Trachelipus ratzeburgii* (Brandt, 1833)
- Suborder Valvifera Sars, 1882
    - *Idotea baltica* (Pallas, 1772)
- Suborder Sphaeromatidea Wägele, 1989
    - *Sphaeroma calcareum* Dana, 1852
    - *Cymodoce pilosa* H. Milne-Edwards, 1840
- Suborder Cymothoidea Leach, 1814
    - *Cirolana hirtipes* H. Milne-Edwards, 1840

Juvenile instars of *Porcellio scaber* (ca. 2 mm body length) were investigated as well.

The fixed specimens (living animals were fixed with Duboscq-Brasil mixture) were embedded in epoxy resin (ERL-4206) under vacuum impregnation. The objects were serially sectioned (l µm) on an ultramicrotome (Reichert OmU3) with glass knives. The sections were stained with a mixture of azure 2 (1%) and methylene blue (1%) in an aqueous borax solution (1%) at 60 °C for about l min.

RESULTS

For two reasons I will not confine myself to the small area of the frontal heart in the following description. First of all, because the functional mechanism of a heart can better be understood in connection with the arteries leaving the heart. Secondly, because no detailed description of the vessel system in the isopod head so far exists. For the muscles in the head, Scheloske (1977) has given a comprehensive description for *Asellus aquaticus*. Therefore, I will confine myself only to the muscles which are directly or indirectly connected with the frontal heart, and adopt the nomenclature of Scheloske.

Aorta and arteries in the head

The following description refers to the Oniscidea Crinochaeta. The investiated species of this group all have a very similar pattern of arteries. There were no significant differences between the 2 mm long and the adult specimens of *Porcellio scaber*.

Entering the head, the aorta is accompanied by two arteries, which turn laterally and supply the muscles on each side of the stomach. In accordance with Silen (1954) they are called first lateral arteries (lat in figs. 2A,3A).

In the posterior region of the head the aorta gives off a small median dorsal artery, which divides, both endings opening near the dorsal integument (da in fig.3).

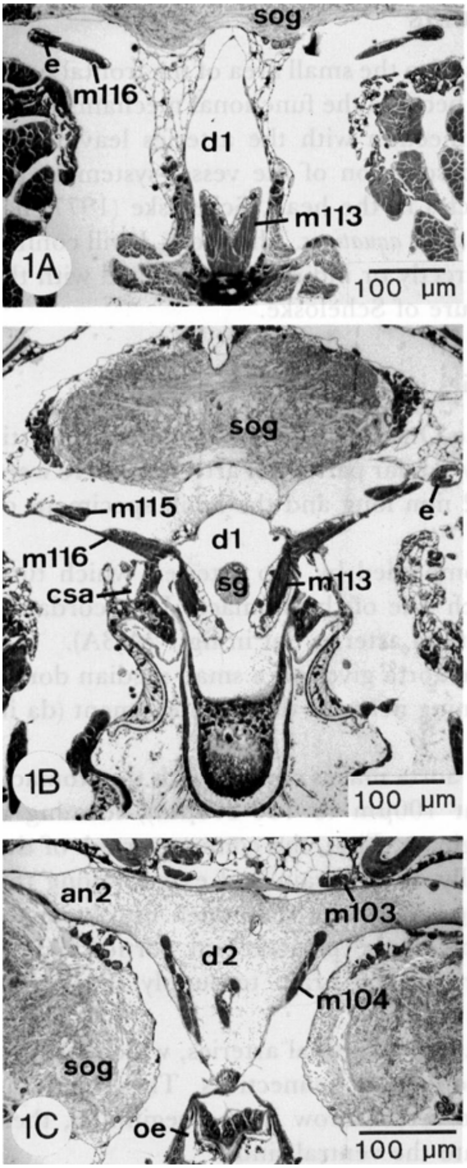
Shortly before reaching the brain, the aorta makes contact with the stomach and increases in diameter (from about 100µm to 150-200µm), forming a dilation from which several arteries originate: First, the common trunk of the two optical arteries which divide dorsally of the brain and extend along the optical lobes towards the eyes (oa in fig.3A), where they open into lacunae.

A second unpaired artery, originating in the postcerebral aortic dilation mentioned above, runs straight forward to the brain to supply this organ (fig.2B). I call this vessel cerebral artery (ca).

The aortic dilation also gives rise to a pair of lateral arteries, which encompass the gut dorsally of the circumoesophageal connectives. These circumstomachal arteries (csa in figs.1,2,3) are very narrow in the beginning, then increase in diameter and finally open into the ventral sinus.

Forward from this postcerebral dilation, the aorta runs downwards into the space left between the posterior margin of the tritocerebrum and the anterior wall of the oesophagus. Then the aorta leaves the oesophagus and forms a second dilation at the basis of the antennae and the labrum. To distinguish it from the first dilation, I will call this the praecerebral aortic dilation. It will be shown below that these two aortic dilations are the main components of the frontal accessory heart in isopods.

The praecerebral aortic dilation again gives rise to a set of arteries, among which the antennal arteries are the most remarkable, with regard to their



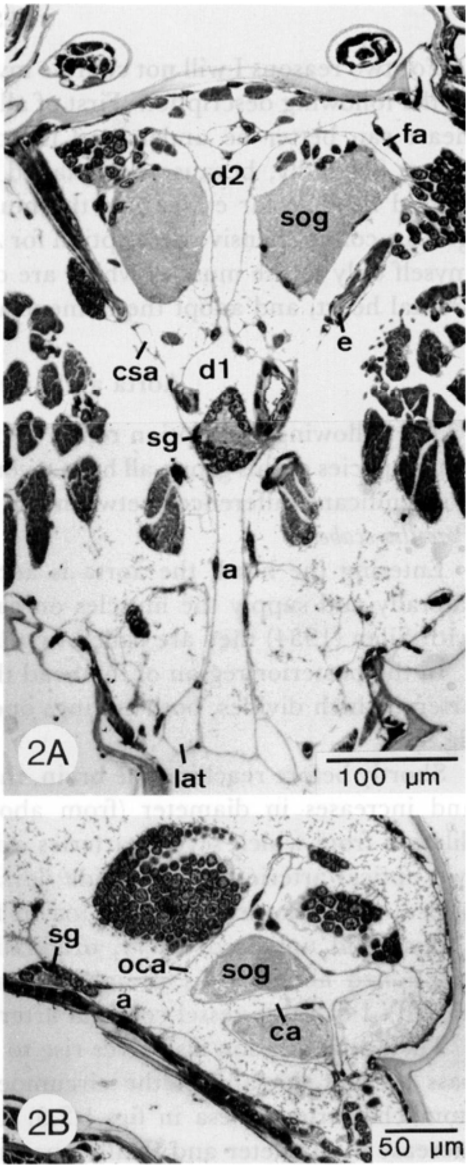


Fig. l. A-C. *Ligidium hypnorum* (Cuvier, 1792), horizontal sections through the head. A, post-cerebral aortic dilation (d1). B, insertion of the muscles m 113 and m 116. C, praecerebral aortic dilation (d2).

Fig. 2. A, B. *Porcellio scaber* Latreille, 1804; Juvenile instar. A, horizontal section through the head, showing the aorta and cuts of the aortic dilations (d1,d2). B, median section with the pericerebral vessel arc. Further abbreviations: a, aorta; an2, antennal artery; ca, cerebral artery; csa, circum-stomachal artery; e, endoskeleton; fa, facial artery; lat, first lateral artery; oca, common trunk of the optical arteries; oe, oesophagus; sg, stomatogastric ganglion; sog, supraoesophageal ganglion.

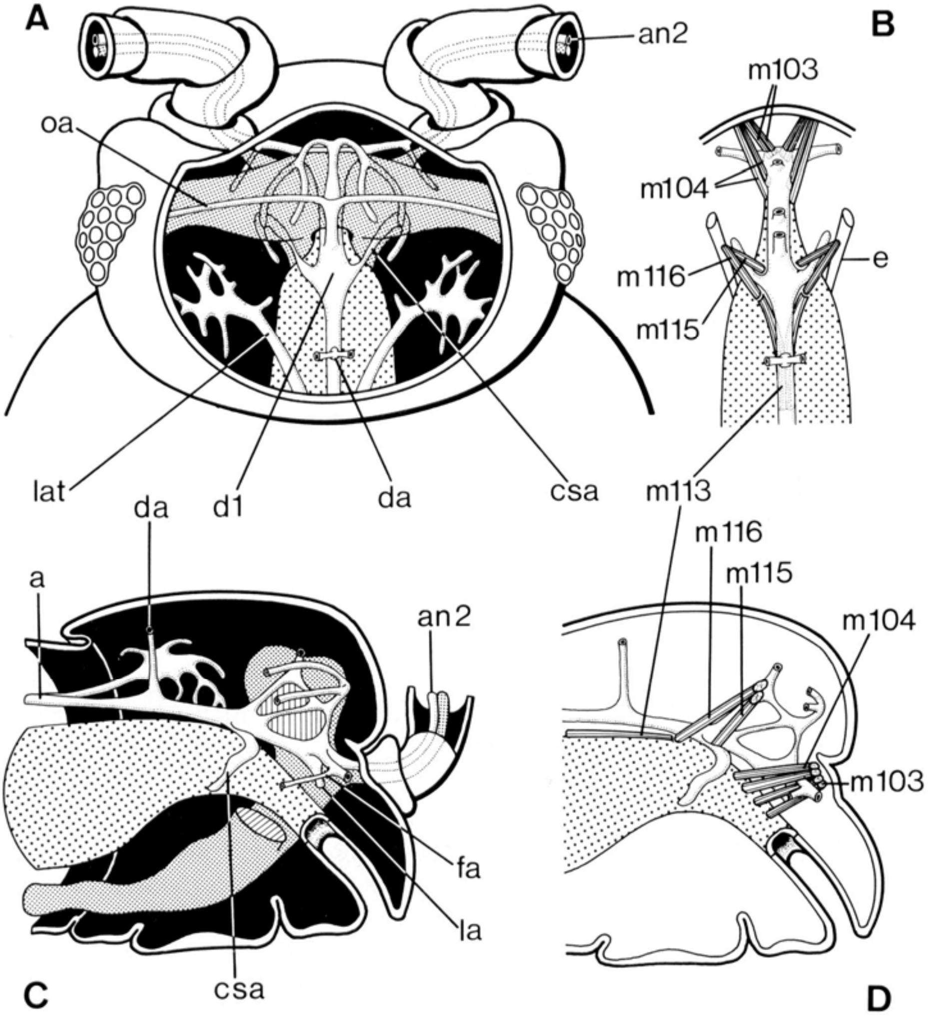


Fig. 3. A-D. *Porcellio scaber* Latreille, 1804, reconstruction of the arterial system in the head and of the muscles connected to the frontal heart. A, opened head in dorsal view; B, detail of A with muscles shown; C, opened head in lateral view; D, detail of C with muscles shown. Coarse screen: alimentary canal; fine screen: nervous system. Abbreviations: a, aorta; an1, antennular artery; an2, antennal artery; ca, cerebral artery; csa, circumstomachal artery; da, dorsal artery; d1, postcerebral aortic dilation; d2, praecerebral aortic dilation; e, endoskeleton; fa, facial artery; la, labral artery; lat, first lateral artery; m, muscle; oa, optical artery; oca, common trunk of the optical arteries; st, stomach.

length: they pass through the antennae all the way to their extreme tips, forming narrow (10-30 µm in diameter) and long tubes (more than 7 mm in *Oniscus*). In all Oniscidea examined, the antennular arteries are reduced. In the proximal region of the first antennal segments, the antennal arteries show remarkable constrictions. These possibly function as valves, as will be discussed below.

Several small arteries branch off from the proximal part of the antennal vessels. They provide the brain, but their pattern is quite variable among the investigated species, so that it seems inadmissible to name them. Only the so-called facial arteries, which are the most conspicuous of these vessels, are constantly present (fa in fig.2A).

Ventrally of the praecerebral dilation, a short median artery runs to the labrum and opens at its base (la in fig.3C). An equivalent artery exists dorsally, which is connected to the cerebral artery and the common trunk of the optical arteries as well, forming two pericerebral vessel arcs (fig.2B).

An oesophageal ring, as described by some authors since Delage (1881), does exist, but its borders are irregular and not defined by continuous membranes.

Differences in other species

Figures 4 and 5 show two species, *Idotea balthica* and *Cirolana hirtipes,* that are rather distantly related to the Oniscidea. Nevertheless the general pattern of arteries is quite the same.

Most similar to the Crinochaeta is the arterial system in *Ligidium*. The only remarkable difference is the lack of any pericerebral vessel arc.

This arc is also missing in all remaining species, which also lack circumstomachal arteries. The dorsal artery is absent in *Asellus* and *Cirolana*. A peculiarity of *Asellus* is that the arteries which are equivalent to the first lateral arteries in other species do not originate from the primary heart in the thorax but from the aorta in the head.

Antennular arteries are absent in *Ligidium,* but exist in all other species. Most variable is the origin of the antennal and antennular vessels from the praecerebral aortic dilation: in *Asellus* the four vessels branch off separately, whereas in *Idotea* a pair of vessels is connected to each of two lateral arteries stemming from the dilation (fig.4). In *Cirolana*, the antennal arteries originate from the dilation separately, whereas the antennular arteries arise from a common, dorsally directed median artery (fig.5).

Muscles associated with the frontal heart

It will be shown below, that the two aortic dilations form a functional unit. Therefore, all muscles connected to any of the dilations are dealt with in this chapter.

In the isopod head, the dilations of the aorta are directly or indirectly connected with five paired and one unpaired muscle:

Firstly, there are four pairs of dilator-muscles. According to Scheloske (1977) they are named m103, m104, m115, m116. The muscles m103 and m104 are oesophageal dilators that have their origin in the dorso-anterior region of the head-capsule. In all species investigated they are divided into separate bundles, some of which pass through the praecerebral aortic dilation (fig.1C), whereas

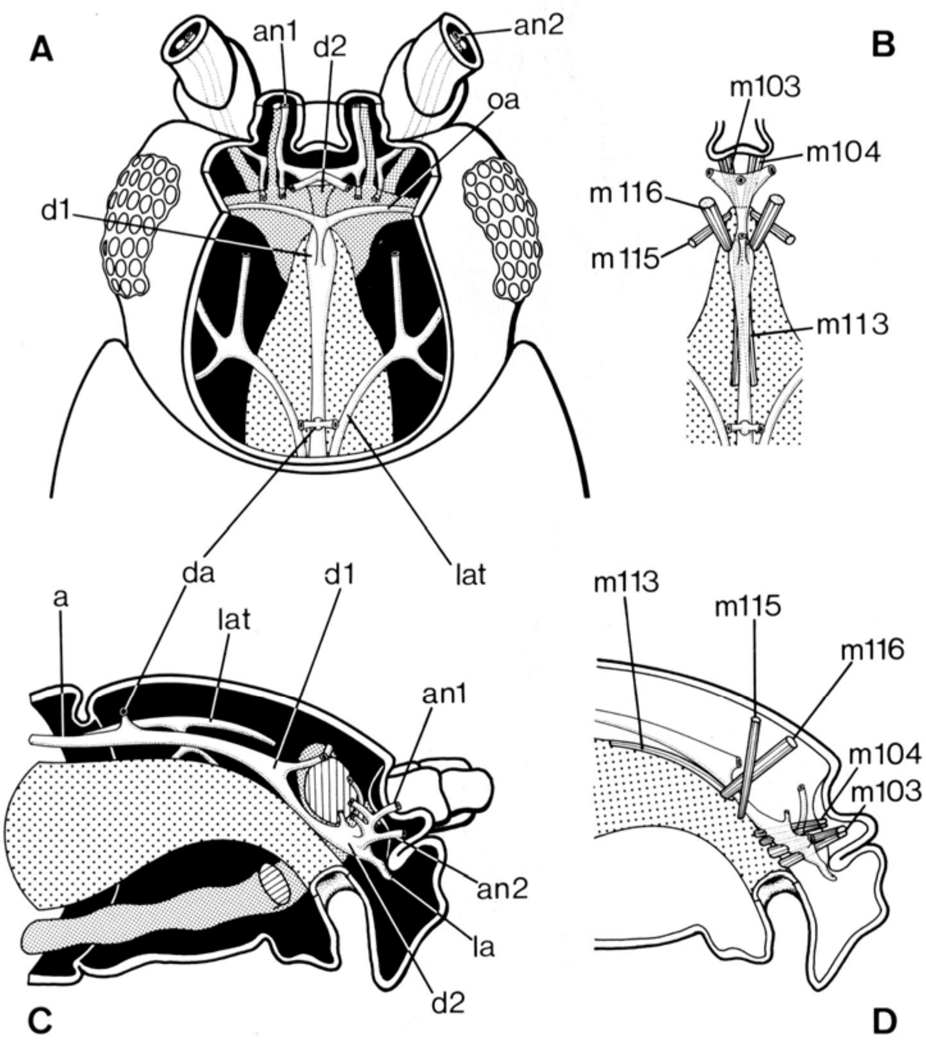


Fig. 4. A-D. *Idotea balthica* (Pallas, 1772). For explanation and abbreviations see fig.3.

others only touch it or have no direct contact. The muscles m115 and m116 are called antero-dorsal dilators of the stomach. In Oniscidea they originate from the frontal arms ("Frontalarme" of Schmalfuß, 1974) of the endoskeleton (e in fig.1); in all other species from the dorsal head-capsule. They insert on the stomach on both sides of the postcerebral aortic dilation, the muscle m116 being directly connected with the wall of the aorta.

Secondly, there are two intrinsic muscles of the gut, m102 and m113. Muscle m102 is the constrictor of the oesophagus and is divided into several flattened bundles, which circle the oesophagus wholly or in part. Muscle m113 is called

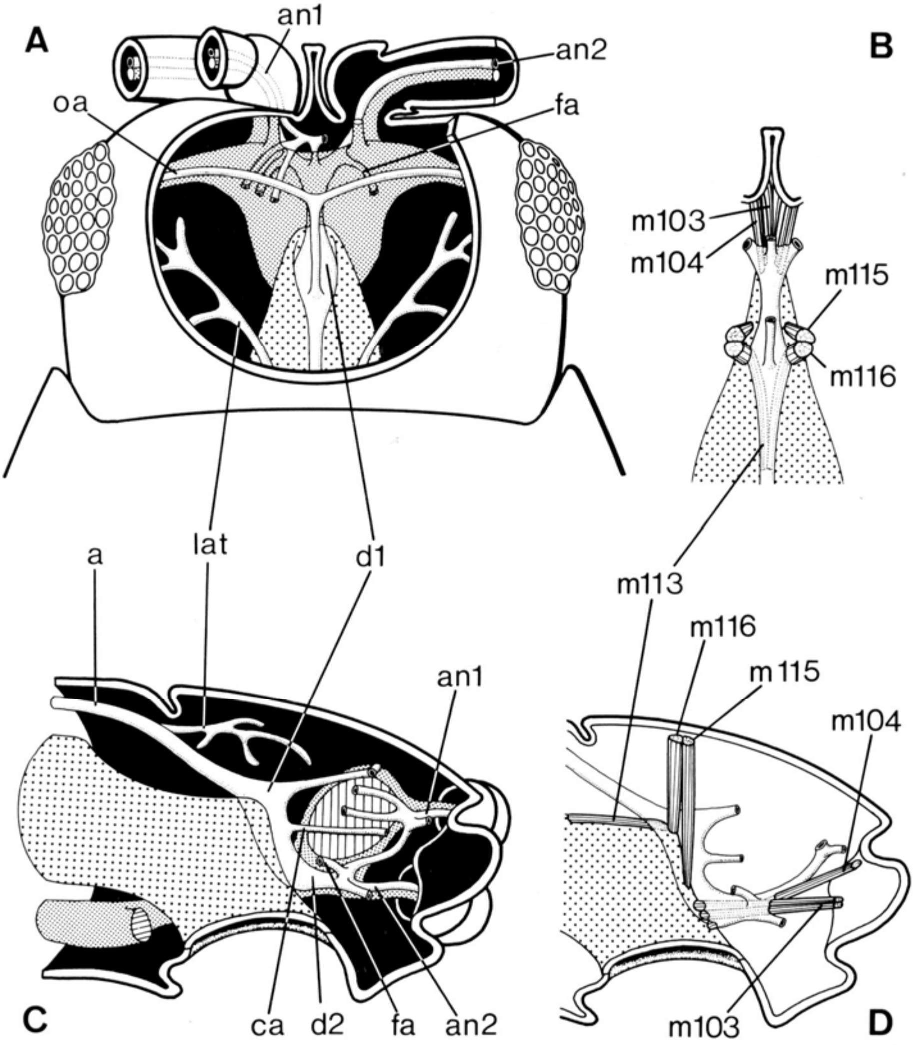


Fig. 5. A-D. *Cirolana hirtipes* H. Milne Edwards, 1840. For explanation and abbreviations see fig.3.

retractor of the oesophagus by Scheloske. It originates in the “Magensklerit 6” (Scheloske, 1976) and runs forward to the dorso-posterior border of the oesophagus. These intrinsic muscles are in contact with the praecerebral and postcerebral aortic dilations, respectively.

DISCUSSION

Anatomy

Though there exists no detailed description of the muscular system in the head of isopods with the exception of the excellent work of Scheloske

(1976, 1977), some authors have dealt with the vessels. Most notable are the investigations on marine “edriophthalmes” of Delage (1881), which were the basis for many ensuing descriptions. Complementary data were published by Hewitt (1907) for *Ligia oceanica* (L., 1758), and Silen (1954), who gave a comparative study of the circulatory system in the Oniscidea. Some errors or misinterpretations of Delage have been rectified by these authors; others persist up to now.

Special attention has always been paid to the postcerebral aortic dilation. It is identical with the “dilation” (Delage, 1881; Hewitt, 1907; Rosenstadt, 1888), “distension” (Zimmer, 1927), “ampulla” (Giesbrecht, 1921) and “sinus oesophagi (Silen, 1954), and has been called frontal heart by some authors (Hewitt, 1907; Maynard, 1960).

The praecerebral aortic dilation has not been described until now for any isopod species.

Nearly all authors followed Delage in describing an oesophageal ring and a subneural artery. Only Hewitt pointed out that he could not find any oesophageal ring of the nature described by Delage. The present investigations show, however, that a haemolymphatic ring does exist, though as part of the lacunar system, according to the definition of Maynard (1960). The same is true for the subneural “artery”, which therefore could better be called subneural lacuna.

Up to now different opinions existed about the presence or absence of a pericerebral vessel arc. Giesbrecht (1921) referred to the examination of marine isopods by Delage (1881), when he stated that probably all isopods lack a “Pericerebralring”. Silen (1954), on the other hand, generalized the existence of such an “arcus cephalicus”, based on the investigation of the Oniscidae. I could find such an arc only in the Crinochaeta.

The functional mechanism of the frontal heart

The two aortic dilations are closely connected instill the stomach and the oesophagus. They lack any intrinsic musculature and can therefore be influenced in their volume by gut-muscles only. So the conclusions on the function of the frontal heart have to be based on the movements of the gut. These have been observed by Scheloske (1976) in *Asellus aquaticus* and can probably be generalized for all isopods, at least for those with plesiomorphic nourishing (Scheloske, 1976; Wägele, 1989).

According to Scheloske (1976), two phases of gut-movement can be discerned. In phase 1, oesophagus and stomach are widened and the food is transported backwards. In phase 2, stomach and oesophagus are constricted and the food is squeezed out at the bottom of the stomach. Consequently, we must assume two phases of frontal heart-pulsation (fig.6): when the oesophagus is widened (fig.6A) the praecerebral dilation is obviously reduced in volume.

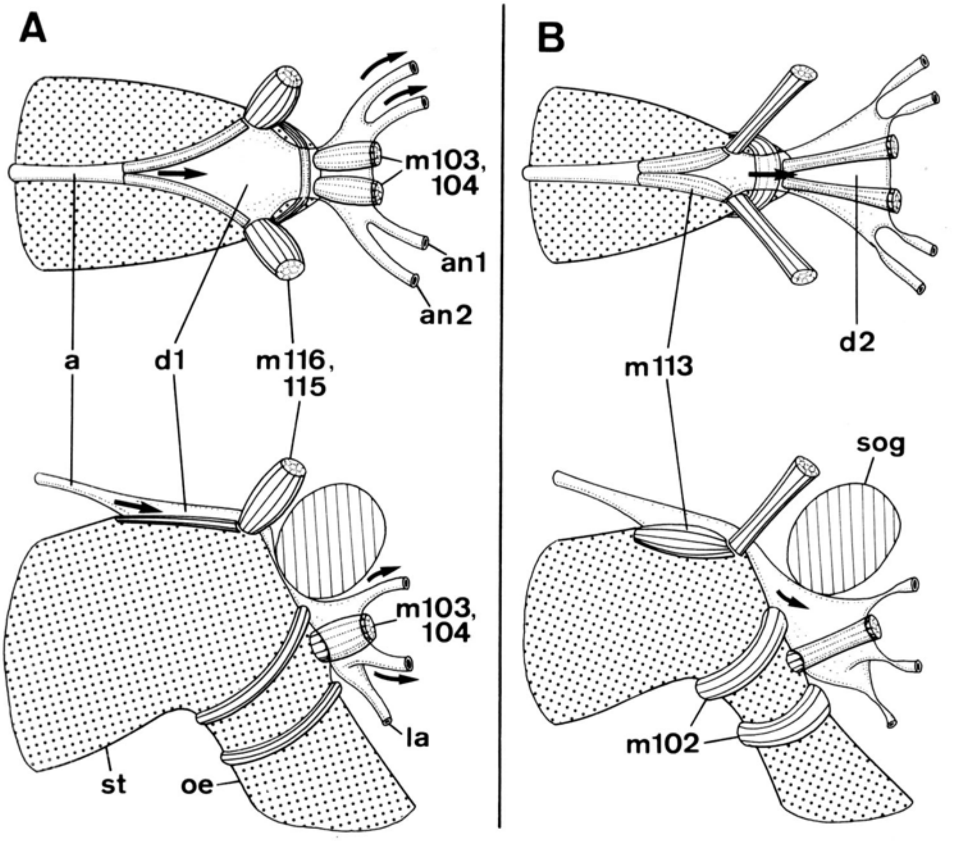


Fig. 6. A, B. Schematic representation of the two phases of frontal heart-pulsation in isopods. Arrows indicate haemolymph-flow. A, phase l, dorsal and lateral view; B, phase 2. Abbreviations as in fig.3. Further explanation in the text.

The space between oesophagus and brain is then closed. As a result haemolymph is pumped into the arteries leaving the praecerebral dilation. At the same time, the dorso-frontal sclerites of the stomach are drawn apart by the muscles m115 and m116. Since the postcerebral dilation lies between these sclerites, it is widened in this phase and filled with haemolymph. The narrow origins of the stomachic arteries in Oniscidea are probably squeezed off by the widened stomach in this phase and can therefore be interpreted as valves. For the optical common artery and the cerebral artery I could not find any valve-structures.

In phase 2 (fig.6B) the praecerebral dilation is widened by the constrictor of the oesophagus (m102). At the same time haemolymph can flow through the space between stomach and brain which is opened by the retractor of the oesophagus (m113) and the muscle m102. The constrictions of the antennal and antennular arteries mentioned above probably collapse by the decreased pressure, and in this way serve as valves. The significance of this phase seems to be confined to the refilling of the praecerebral dilation with haemolymph from the postcerebral dilation.

This functional mechanism of the two aortic dilations makes it clear that the term frontal heart should no longer be confined to the postcerebral aortic dilation, as it has been until now. It should be applied at least to both dilations or, better, include the whole complex of structures connected to them.

Biological significance of the frontal heart

Considering the fact that the arteries in the head of the Crustacea are directly connected with the primary heart by the aorta, the question arises, what purpose the frontal heart serves. This is all the more true, as in Tracheata accessory hearts have only been found in species in which the vessels are separate from the primary heart (Pass, 1991).

One answer could lie in the high resistance offered to haemolymph flow by the well-developed vessel system in the crustacean head, as is argued by Siewing (1956). Hewitt (1907) and Siewing (1956) have further suggested that the posterior position of the heart in some crustacean groups could also favour the development of an accessory frontal heart. Both arguments may be true for the isopods, which often have long antennal, antennular and optical arteries, and of which the heart is shifted particularly far backwards.

Steinacker (1979) has clearly demonstrated that the frontal heart in decapods acts as a “booster pump”, which does not begin to function until some critical level of the main heart function is reached. She ascribes a central role in pressure-regulation to the stomatogastric ganglion, which coordinates the activity of primary and frontal heart. This ganglion has the same position in isopods (sg in fig.2A), which allows the conclusion that the frontal heart has a similar biological significance in this group as in decapods.

Comparative aspects

The vessel system in the head of the other high ranking taxa of the Peracarida and the Anaspidacea is quite similar to that described above for the isopods. Also, the two aortic dilations have been discerned in several species belonging to the Cumacea (Oelze, 1931; Siewing, 1952), Tanaidacea (Siewing, 1954), Anaspidacea (Siewing, 1956) and Amphipoda (unpubl. personal observations). However, the associated musculature shows significant differences, as far as it is described at all (e.g. Siewing, 1954). Therefore, it is unlikely that the functional mechanism of the frontal heart is the same in all these groups. For the same reason it is so far impossible to decide whether all these aortic dilations are homologous or not.

A comparison of the frontal heart of the isopods with that of the scarcely examined Mysidacea and Euphausiacea and the well-investigated Decapoda shows even more anatomical differences. The cor frontale in the latter is chiefly operated by the musculi oculi basales posteriores (Powar, 1973; Steinacker, 1978), that have no equivalent in isopods. Muscles of the stomach and the oesophagus are not connected with the cor frontale in these animals. Furthermore, a praecerebral aortic dilation does not exist, and the antennal vessels do not originate from the aorta, but from the first lateral arteries. So one must recognize that the term frontal heart in all malacostracans is used just as a functional term and does not imply a phylogenetic relationship of these organs.

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REFERENCES

BAUMANN, H., 1917. Das Cor frontale bei decapoden Krebsen. Zool. Anz., **49**: 137-144.

BELMAN, B. W. & J. J. CHILDRESS, 1976. Circulatory adaptions to the oxygen minimum layer in the bathypelagic mysid Gnathophausia ingens. Biol. Bull. Woods Hole, **150**: 15-37.

CANNON, H. G., 1940. On the anatomy of Gigantocypris mülleri. Discovery Repts., **19:** 185-244.

— — 1947. On the anatomy of the pedunculate barnacle Lithotrya. Phil. Trans. Roy. Soc. London, (B)**233**: 89-136.

CHUN, C., 1896. Atlantis. Biologische Studien über pelagische Organismen. Zoologica, **19**: 1-262.

DELAGE, Y., 1881. Contribution à l'étude de l'appareil circulatoire des Crustacés Édriophthalmes marins. Arch. Zool. Exp. Gén., **9**: 1-l73.

GIESBRECHT, W., 1921. Crustacea. In: A. LANG (ed.), Handbuch der Morphologie der wirbellosen Tiere, **4**: 9-252. (Jena).

GROBBEN, K., 1908. Beiträge zur Kenntnis des Baues und der systematischen Stellung der Arguliden. Sitzber. kgl. preuss. Akad. Wiss., **117**: 191-233.

HEWITT, C. G., 1907. Ligia. L. M. B. C. Memoirs, 14. Proc. Trans. Biol. Soc. Liverpool, **21**: 65-100.

MAYNARD, D. M., 1960. Circulation and heart function. In: T. H. WATERMAN (ed.), The physiology of Crustacea, **1**: 161-226. (Academic Press, N.Y.).

MCLAUGHLIN, P. A., 1983. Internal Anatomy. In: D. E. BLISS (ed.), The Biology of Crustacea, **5**: 1-52.

OELZE, A., 1931. Beiträge zur Anatomie von Diastylis rathkei Kr. Zool. Jahrb. Anat., **54**: 235-294.

PASS, G., 1991. Antennal circulatory organs in Onychophora, Myriapoda and Hexapoda: Functional morphology and evolutionary implication. Zoomorphology, **110**: 145-164.

PICKERING, C. & J. D. DANA, 1838. Description of a crustaceous animal, belonging to the genus Caligus, C. americanus. Amer. Journ. Sci., **34**: 226-266.

POWAR, C. B., 1973. The accessory heart of the crab Paratelphusa guerinii (Milne-Edwards). Zool. Anz., **190**: 77-85.

ROSENSTADT, B., 1888. Beiträge zur Kenntnis der Organisation von Asellus aquaticus und verwandter Isopoden. Biol. Zentralbl., **8**: 452-462.

SCHELOSKE, H. W., 1976. Vergleichend-morphologische und funktionelle Untersuchungen am Magen von Asellus aquaticus. Zool. Jahrb. Anat., **95**: 519-573.

— —, 1977. Skelett und Muskulatur des Cephalothorax von Asellus aquaticus (L.) (Asellidae, Isopoda). Ein Beitrag zur vergleichenden Anatomie der Crustacea Malacostraca. Zool. Jahrb. Anat., **97**: 157-293.

SCHMALFUSZ, H., 1974. Skelett und Extremitätenmuskulatur des Isopoden-Cephalothorax. Zeitschr. Morph. Tiere, **78**: 1-91.

SIEWING, R., 1952. Morphologische Untersuchungen an Cumaceen (Cumopsis goodsiri V. Beneden). Zool. Jahrb. Anat., **72**: 522-559.

— —, 1954. Morphologische Untersuchungen an Tanaidaceen und Lophogastriden. Zeitschr. wiss. Zool., **157**: 333-426.

— —, 1956. Untersuchungen zur Morphologie der Malacostraca (Crustacea). Zool. Jahrb. Anat., **75**: 39-176.

SILEN, L., 1954. On the circulatory system of the Isopoda Oniscoidea. Acta Zool. (Stockholm), **35**: 11-70.

STEINACKER, A. 1978. The anatomy of the decapod auxiliary heart. Biol. Bull. Woods Hole, **154**: 497-507.

— —, 1979. Neural and neurosecretory control of the decapod crustacean auxiliary heart. Amer. Zool., **19**: 67-75.

WÄGELE, J. W., 1989. Evolution und phylogenetisches System der Isopoda. Zoologica, **140**: 1-262.

ZIMMER, C., 1927. Crustacea Malacostraca. In: W. KÜKENTHAL & T. KRUMBACH (eds.), Handbuch der Zoologie, **3**: 553-1158. (W. de Gruyter, Berlin).

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