

Baryonyx walkeri, a fish-eating dinosaur from the Wealden of Surrey

ALAN J. CHARIG AND ANGELA C. MILNER

Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD

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SYNOPSIS. The well-preserved skeleton of a large theropod dinosaur, *Baryonyx walkeri* Charig & Milner, 1986, from the Wealden (Barremian, Lower Cretaceous) of Surrey, is described in detail. It is a large theropod with some resemblance to *Megalosaurus* or *Allosaurus*, but is sufficiently different to merit its earlier designation as the type of the new family Baryonychidae. Its distinguishing characters include: the prenasal extension of its snout into a spatulate rostrum, a unique increase in the number of the dentary teeth (which are more than twice as numerous per unit length of jaw as the opposing maxillary teeth), an unusually robust fore-limb, and at least one pair of huge manual talons. Lack of fusion between the components of both skull and vertebrae suggests that this 10 metre long animal was immature.

Few other specimens might be referred to *Baryonyx*: a maxilla fragment of *B. walkeri* is recorded from the Barremian of Spain; two snout fragments from the Aptian of Niger, which are virtually identical to the conjoined premaxillae of *Baryonyx*; two isolated tooth crowns, one from the Hauterivian of East Sussex, and one from Surrey; and seven from the Barremian of the Isle of Wight are compared to the genus. On the evidence of jaws and teeth only, the families Baryonychidae and Spinosauridae (*Spinosaurus*, *Angaturama*, and perhaps *Irritator*) are placed in the superfamily Spinosaurioidea. An investigation of the wider affinities of *Baryonyx*, based on a modified version of Holtz's 1994a data-matrix on the Theropoda, suggests that the Spinosaurioidea is a basal member of the Tetanurae and sister-group to the whole of the Neotetanurae (i.e. the Coelurosauria *sensu* Gauthier plus a variable collection of 'allosauroids'), with *Megalosaurus* and *Torvosaurus* as progressively more distant outgroups.

The associated fossil fauna is dominated by *Iguanodon* and many insects, which lived in the vicinity of a sub-tropical delta. *Baryonyx* was terrestrial, a fish-eater, probably a scavenger, and possibly an active predator of small to medium-sized land animals. It made greater use of its fore-limbs and talons in attack and defence than its jaws and teeth, which were used mainly for seizing fish and entrails. The taphonomy of the holotype suggests that the animal is unlikely to have been transported from elsewhere and probably died where found. Its skeletal remains lay in sediments that were mostly submerged in shallow water but exposed to the air for brief periods; the bones were trampled and broken before fossilization.



Frontispiece *Baryonyx walkeri*, holotype, BMNH R9951; restoration of a living animal in the Wealden landscape. Painted by John Sibbick.

INTRODUCTION

Discovery

The discovery of *Baryonyx* was a major event in the history of British dinosaur palaeontology (Milner & Croucher 1987). Extant faunas of large terrestrial vertebrates invariably include only a small proportion of carnivores, these being at the apex of the food pyramid, and fossil faunas were probably no different. Dinosaur discovery in England goes back more than 300 years (Plot 1677) and includes several finds of a few bones or teeth of carnivores. Until 1983, however, the only significant find of a carnivorous dinosaur had been the partial skeleton of *Eustreptospondylus oxoniensis* (originally placed in the genus *Megalosaurus*), found in Oxfordshire in 1871 and now in the Oxford University Museum. Since the discovery of *Baryonyx*, the partial skeleton of an allosauroid has been described from the Wessex Formation (Wealden) of the Isle of Wight (Hutt, Martill & Barker 1996).

Details of the discovery of *Baryonyx* were published by Milner & Croucher (1987). The enlarged ungual phalanx, the famous 'Claw' originally missing the tip), a second smaller, less complete ungual phalanx and an incomplete haemapophysis, were found on 7 January 1983 by Mr William J. Walker at the Ockley Brick Company's claypit near Ockley, Surrey, and a week later he found the missing tip of the claw. After examining this material at the British Museum (Natural History), we visited the site on 7 February and found large dark-brown bones from the pelvis and hind-limb, lying just beneath the surface of the clay. The physical conditions in the claypit prevented us from collecting the skeleton until the period 25 May to 10 June 1983, when a team of eight from the Department of Palaeontology and a number of volunteers excavated two tonnes of matrix containing bone.

All the remains were found within an oval excavation measuring approximately 5 metres by 2 metres (Fig. 49). Most were encased in nodules of sideritic siltstone, which had been deposited around the bones, but some lay unprotected in soft clay. The skeleton was largely disarticulated and the elements gently scattered, but most of them were still lying approximately in their skeletal position, with the animal's skull at one end and its tail at the other. Some nodules were lifted untreated, some were encased in plaster of Paris and others in expanded polyurethane foam.

Preparation

Preparation of the material was especially difficult because of the hardness of the siltstone matrix, made more intractable by the presence of siderite. A few pieces were subjected experimentally to chemical treatment with thioglycolic acid (which dissolves iron salts but has little or no action on siltstone and other non-ferrous rocks), but it had practically no effect, so most of the matrix had to be removed by mechanical methods. Some field cocoons, the bulk of the rock and the underlying clay were removed rapidly with an industrial shot blaster, a Vacu-Blast Nova 150PB, using plastic shot as the abrasive; as far as is known (R. Croucher and W. Lindsay, pers. comm.) this is the first recorded instance of the use of such equipment for preparing fossils. Rock was also removed with hand tools and with tools powered by compressed air, including diamond-cut circular saws and chisels. For more delicate work close to the bone surface, finely pointed engravers were used under binocular microscopes. Other details of the laboratory work on *Baryonyx* were described by Milner & Croucher (1987).

SYSTEMATIC DESCRIPTION

Suborder **THEROPODA** Marsh, 1881
 Superfamily **SPINOSAUROIDEA** Stromer, 1915
 Family **BARYONYCHIDAE** Charig & Milner, 1986

TYPE-GENUS. *Baryonyx* Charig & Milner, 1986.

DERIVATION OF NAME. From Greek βαρυς, heavy; ονυξ, claw.

DIAGNOSIS. As for genus *Baryonyx*.

Genus **BARYONYX** Charig & Milner, 1986

TYPE-GENUS. *B. walkeri* Charig & Milner, 1986; Early Cretaceous, Surrey, England.

DIAGNOSIS. Monotypic genus, as for species *B. walkeri*.

Baryonyx walkeri Charig & Milner, 1986

DERIVATION OF NAME. For Mr William J. Walker, who discovered the original claw-bone.

HOLOTYPE. Natural History Museum, London: Department of Palaeontology, BMNH R9951.

MATERIAL. The holotype alone; consisting of conjoined premaxillae, conjoined vomers, anterior part of left maxilla, conjoined nasals, left lacrimal, left prefrontal, left postorbital, anterior end of braincase (right frontal, right parietal, right orbitosphenoid, right laterosphenoid), posterior end of braincase together with occiput (both prootics, both opisthotics, basisphenoid, supraoccipital, both exoccipitals, basioccipital), left jugal, both quadrates; both dentaries, both splenials, right surangular, both angulars, right coronoid; some upper teeth *in situ* and many isolated teeth of unknown position in the jaws; axis and 4 further cervical vertebrae, 12 dorsals, 3 or 4 basal caudals, 3 more distal caudals; one axial rib, three other cervical ribs, many dorsal ribs, abdominal ribs, 5 haemapophyses, sternum; both scapulae, both coracoids; both humeri, left radius, left ulna, left pollex with huge ungual, left digit II (complete) or digit III₍₂₋₄₎, other isolated phalanges of both sides; right ilium, both pubes, left ischium; proximal end of left femur and distal end of right, right fibula, right calcaneum, metatarsal fragments, 1 pedal ungual.

LOCALITY. Smokejack's Brickworks (Ockley Building Products Limited, formerly Ockley Brick Company Limited), Wallis Wood, Ockley, near Dorking, Surrey, England. A little below the top of the south-east face, nearest to the works buildings. National Grid reference TQ 113373.

HORIZON. Lower Cretaceous, Wealden Series, Upper Weald Clay; zone of *Cypridea clavata*, near the base of the Barremian; about 7 m below the base of BGS Bed 5c (See Ross & Cook 1995).

DIAGNOSIS. Prenarial region of snout extended into extremely narrow rostrum with spatulate, horizontal expansion at end ('terminal rosette'); snout slightly downturned in lateral view, jaws with sigmoidal margins. Long, low external naris far back on side of

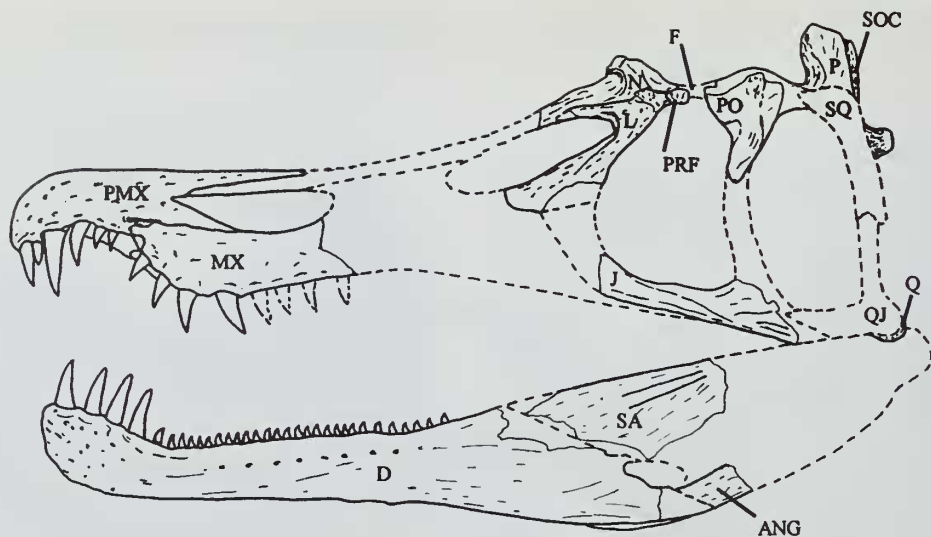


Fig. 1 *Baryonyx walkeri*, holotype, BMNH R9951; reconstruction of skull, from left side. $\times 0.135$.

snout. Complex articulation of premaxilla and maxilla unfused above subrostral notch. Small median knob at posterior end of conjoined nasals, cruciform in dorsal view, with anterior limb of cross drawn forwards into low thin median crest. Occiput deep, with paroccipital processes directed horizontally outwards. Basipterygoid processes descend far below basioccipital, diverging laterally only slightly. Anterior end of dentary upturned in lateral view. 6/7 premaxillary teeth; only 8 maxillary teeth preserved, but probably about 15; 32 dentary teeth, generally smaller than those in the upper jaw, more than twice as numerous per unit length of jaw. Prominent bony wall on lingual side of all teeth. Tooth crowns flattened only slightly labio-lingually, lightly fluted on lingual side; anterior and posterior carinae finely serrated (about 7 denticles per millimetre). Tooth roots exceptionally long and slender. Axis small, with well developed hyposphene. Cervical vertebrae with flat zygapophyses and well developed epiphyses; ends of centra not offset, no upward curve to neck; neurocentral sutures unfused; neural spines generally short, but those of basal caudals expanded into large flattened plates. Cervical ribs short, crocodiloid, slight overlap. Humerus relatively well developed; both ends broadly expanded but flattened, offset 35° against each other; shaft massive, almost straight. Radius stout, a little less than half as long as humerus. Ulna also stout, somewhat longer than radius, with powerful olecranon. Exceptionally large manual ungual phalanx, not laterally compressed, probably from digit I. Pubic foot not expanded. Ischium with obturator flange proximally continuous with anterior margin.

Skull

GENERAL DESCRIPTION (Fig. 1). Despite the limited amount of material available, several interesting observations may be made on the skull. It appears to have been long, at least in its anterior portion. Whereas in other theropods the extreme anterior end of the premaxilla gives rise to the steeply ascending nasal process, forming the anterior margin of the external naris, in *Baryonyx* there is no trace of such a process, and the anterior 170 mm of the conjoined premaxillae form a long low rostrum with a smoothly rounded dorsal surface. Even behind this rostrum there is no ascending process, the

confluent external nares appearing merely as an extensive opening lying well back from the tip of the rostrum and passing horizontally from one side of the snout to the other. The first 130 mm of the rostrum are expanded laterally into a spatulate 'rosette', not unlike that found in modern gavials; the first 70 mm of its lower margin are turned down in lateral view. Behind the 'rosette' the rostrum is remarkably narrow from side to side as seen in dorsal view.

The maxilla fits on to the hind part of the ventral margin of the premaxilla by a complex articulation. The resulting effect is that the line of the upper tooth row, passing backwards from the front of the snout, first rises a little and then, at the junction of the two elements, curves strongly downwards and finally flattens out to run horizontally along the ventral margin of the maxilla. The net effect of this sigmoid curvature is that the front of the rostrum is elevated above the level of the maxillary tooth row, not depressed beneath it. This elevation is reflected in the shape of the upper margin of the dentary, the front 140 mm of which slope strongly upwards towards its anterior end. Nevertheless, in the region of the 5th to 6th premaxillary teeth, the gap between the upper and lower jaws seems to have been much wider than elsewhere and may be termed the subrostral notch.

Other noteworthy general features of the skull are:

1. The deep, narrow shape of the occiput, especially deep below the condyle, the basipterygoid processes greatly lengthened.
2. The great length of the dentary, its dentigerous part very shallow, with well-marked Meckelian groove on the medial surface.
3. The presence of a prominent bony wall on the lingual side of each tooth row.
4. The exceptionally high tooth count (6 premaxillary teeth on the left side and 7 on the right, as contrasted with a more usual count of 5, and 32 dentary, as contrasted with the usual 16 or so). The only other theropods known with more teeth per unit length of lower jaw than in the corresponding length of upper jaw are *Troodon* (Osmólska & Barsbold 1990) and *Pelecanimimus* (Pérez-Moreno *et al.* 1994), and even there the disparity is far less extreme.
5. The much closer packing of the teeth in the dentary than in the opposing part of the maxilla; as a corollary of this the dentary teeth must have been generally smaller (it should be noted

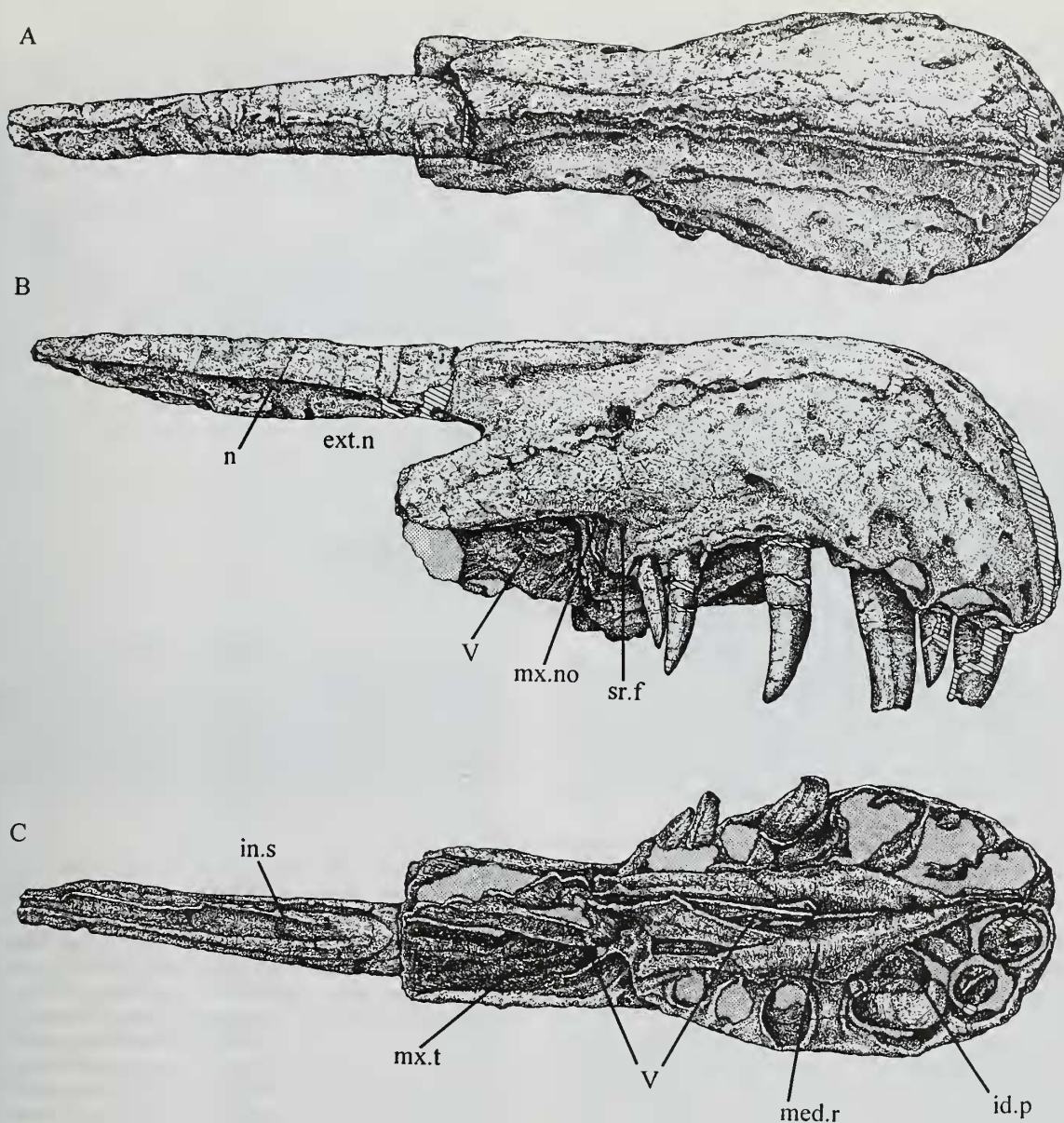


fig. 2 *Baryonyx walkeri*, holotype, BMNH R9951; snout. A, conjoined premaxillae in dorsal view; B, same, right lateral; C, premaxillae in palatal view, showing also vomers. $\times 0.5$.

however, that our knowledge of the maxillary dentition is restricted to the first 7 teeth).

The extremely fragile, laminar nature of the post-dentary bones in the lower jaw.

The lack of co-ossification between the elements, except in the midline and in the braincase.

The last character suggests that R9951, despite its great size, was juvenile, from which we might deduce that the fully mature animal was probably much larger still. The possibility that a member of the spinosauridae (see p. 55) might attain a truly vast size is confirmed by Storer's illustrations (1915) of the dentary of *Spinosaurus aegyptiacus*, an element twice the linear size of that of *Baryonyx*.

REMAXILLA (Fig. 2). Both premaxillae are preserved, firmly

sutured together; the median suture between them is clearly visible on the dorsal surface, though it fades out towards the rear. Both elements are complete anteriorly but broken off behind. The premaxillae (as preserved) are not fused to any other elements; each, however, has (or had) a complex articulation with the maxilla.

The snout is unlike that of most other known dinosaurs, in which an ascending process rises from the very front of the conjoined premaxillae and forms the rounded anterior border of the external nares. Here, by contrast, the snout is long and low; the equivalent process originates 172 mm behind the tip of the snout and is directed almost horizontally backwards. Thus the heavy, robust snout formed by the conjoined premaxillae is seen in lateral view to bifurcate posteriorly into two rami on each side, a short one below (the main body of the premaxilla) and a longer one above (the

'ascending process'); the external naris between them terminates anteriorly in an acute angle. In palatal or dorsal view the snout appears extremely narrow from side to side, and there is a 'waist' between the anterior, dentigerous portion expanded horizontally into a 'terminal rosette' (Charig & Milner 1990) and the two rami, lower and upper, behind.

The lower ramus is broken off transversely not far behind the anterior corner of each external naris, but its full extent on each side of the snout is demonstrated by clear indications of its overlap onto the laterodorsal surface of the left maxilla, indications which suggest that that too was tapered to a point. The dorsal surface of this ramus, forming the floor of the nasal cavity, slopes steeply downward on either side (i.e. it is merely a posterior extension of the side of the snout), but between these slopes is a deep sagittal V-shaped groove.

The upper ramus tapers to a thin spike which presumably met the nasals; it has a smooth outer (i.e. dorsal) surface, but internally (i.e. ventrally), where it borders the nasal cavity, it bears on each side two longitudinal ridges, a low lateral ridge and a stronger medial ridge. Together these produce a shallow lateral groove on each side and a deeper median groove, in the bottom of which the latter suture between the paired premaxillae may still be traced intermittently. These ridges would somehow have supported the internasal septum and associated soft tissues, and the lateral grooves doubtless served for articulation with a forwardly projecting prong from the nasal on each side.

In lateral view the ventral, dentigerous margin of the premaxilla is distinctly downturned, both anteriorly towards the tip and posteriorly towards the articulation for the maxilla; it is smoothly concave between. There is extensive pitting on the outside of the snout, especially towards the tip, which doubtless served for the exit of blood vessels and nerves; a row of nutritive foramina lies just above the bases of the teeth.

In ventral view the terminal rosette has an elongated spatulate shape, around the edge of which lie six dental alveoli on the left side and seven on the right. In these thirteen alveoli only six teeth remain in place, four of them complete to the tip. The first four alveoli on each side are large; nos. 2 and 3 are the largest; nos. 5 to 7 decrease in size progressively. Interdental plates are present, each interrupted by a narrow gap which is rather more posterior than anterior in position.

When the premaxilla is seen in palatal view, the area between the tooth rows on either side appears to be fully occupied by a pair of narrow, transversely rounded 'elements', sutured together in the midline and broken off short just behind the level of the last premaxillary tooth. Each tapers anteriorly to a combined point which abuts against the rear end of a median groove between the medial walls of the first alveolus on each side. Towards the rear each 'element' expands ventrally. From the anterior apex a strongly interdigitating median suture between the two sides pursues a sinuous course backwards for some 30 mm; farther back the interdigitations cease and the two sides are separated by a narrow, elongated, median gap, on either side of which the 'elements' curve out laterally away from each other and then, more posteriorly, almost rejoin. In the region of the anterior half of the median gap their ventral surface is somewhat rugose, suggesting the possible presence in life of a horny pad in the roof of the mouth.

These, however, are not separate elements (despite their close resemblance to vomers) but seem to be integral parts of the premaxilla; they form a pair of stout ridges that support the adjacent tooth rows, lying lateral to them. Posteriorly from the level of the 4th tooth they expand into two vertical flanges, roughly triangular in shape and extending ventrally to an apex just behind the level of the last

(7th) alveolus and then descending again to terminate just behind the subrostral notch.

At the posterior end of the premaxillary tooth row, just below the anterior end of the ventral margin of the lower ramus, is a deep notch which received a rectangular peg-like process on the anterior end of the maxilla. Just in front of this notch lies the subrostral foramen, while just above the notch, in the outer surface of the premaxilla, lie three well-defined pits. A vertical bony buttress separates the notch in front from the anterior end of the deep U-shaped trough behind.

VOMER (Fig. 2C). The ventral (i.e. palatal) surface of the conjoined two lower rami of the premaxilla bears what appears to be a very deep median septum; this divides the concavity of the premaxillary trough into a pair of broad, U-shaped, ventrally facing troughs, each of which received the dorsal edge of the front maxilla. We interpret this as the extreme anterior portion of the paired vomers, fused together to form an extremely slender, vertical lamina which lies in the midline and is clasped between the vertical flanges of the premaxilla (described above). It extends forwards as far as the level of the alveoli for the 4th premaxillary tooth on each side. The central part of this lamina is attached to the roof of the anterior part of the premaxillary trough (though the suture is partly obliterated); anteriorly and posteriorly there is a gap between the dorsal edge of the lamina and the roof of the (inverted) trough. The extreme anterior end of the conjoined vomers tapers to a point and appears to project downwards from the roof of the mouth, in the midline between the premaxillae, an unlikely position that suggests postmortem displacement.

MAXILLA (Fig. 3). All that is preserved is the anterior part of the left maxilla, broken off through the 8th maxillary alveolus. Seen in lateral view, both its upper and lower margins are smooth curves, concave above, and with the lower (dentigerous) margin continuing without interruption around the anterior end; the two margins approach each other posteriorly so that the whole element, though broad from top to bottom in front, narrows appreciably towards the posterior break. Just below the anterodorsal corner the rectangular peg (referred to above under Premaxilla) projects forwards; the maxillary tooth row begins immediately below it and then curves smoothly in a posteroventral direction; when premaxilla and maxilla are placed together in natural articulation there is a small gap of about 20 mm between the last premaxillary tooth and the first maxillary. In *Dilophosaurus* (Welles 1984) this gap in the tooth row is some 40 mm, in an animal which is only about two-thirds the size of the *Baryonyx* holotype. The maxilla extends anteriorly beneath the external naris but is separated from it by the ventral ramus of the premaxilla, so that its most anterior extremity lies some 45 mm farther forward than does the anterior corner of the external naris (in this it contrasts with the condition in *Dilophosaurus*, where there is very little overlap between the two elements and where the most anterior point of the maxilla lies more or less beneath the middle of the naris). Just behind the rectangular peg the medial surface of the maxilla bears a shallow channel running in an anteroventral direction, forming the lateral margin of the external portion of the subrostral canal.

Along the dorsal margin of the lateral face is the long, slightly rugose articular surface for the lower ramus of the premaxilla; it tapers to a point 135 mm behind the front tip of the maxilla and a little way below its dorsal margin. Behind and medial to this, the dorsal margin is smoothly rounded and forms the posterior part of the ventral border of the external naris. The lower margin of the medial face of the maxilla is formed by a stout rounded ridge, lying immediately medial to the tooth row; running above this throughout its length is the articulating surface for the palatine, the anterior

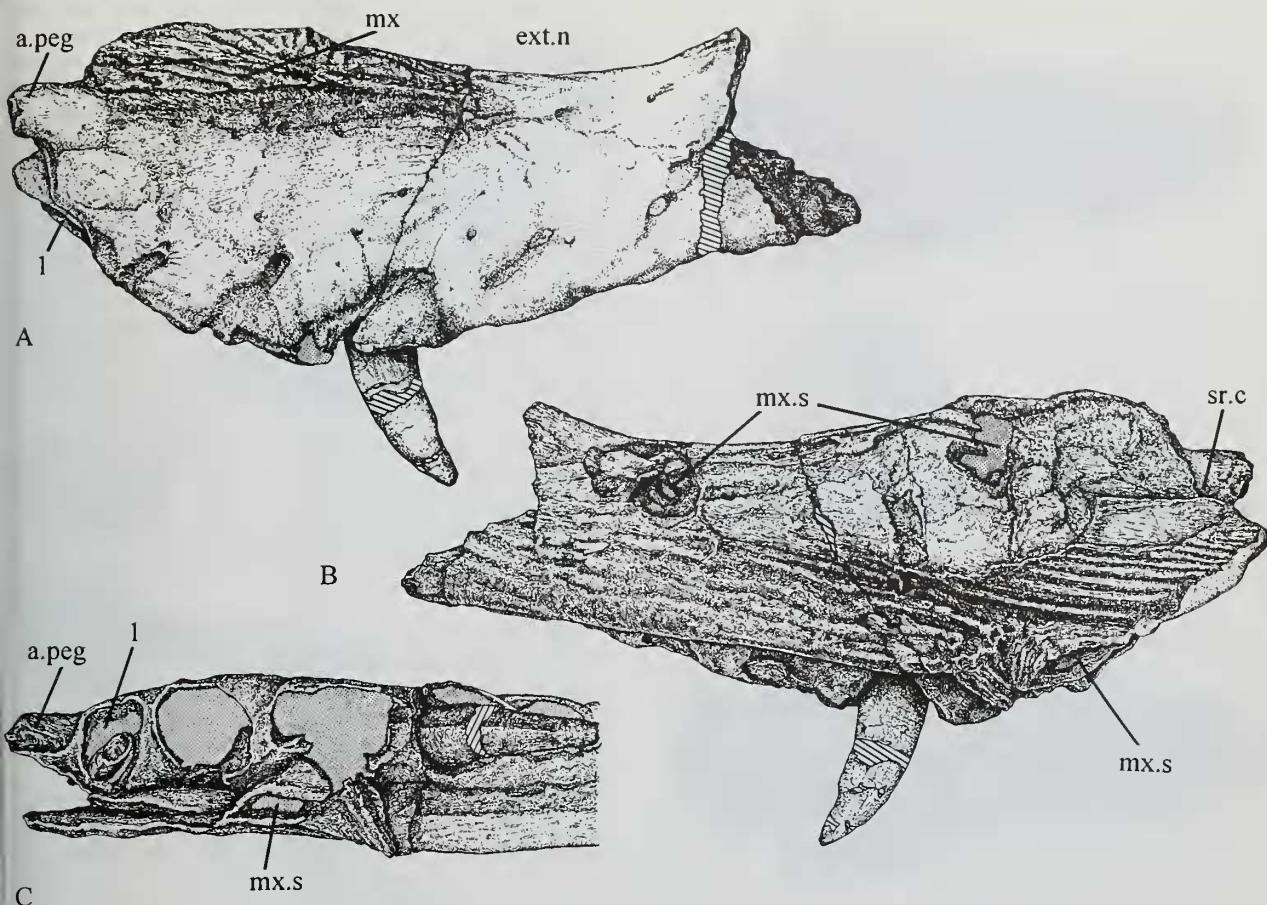


Fig. 3 *Baryonyx walkeri*, holotype, BMNH R9951; left maxilla. A, lateral view; B, medial; C, anteroventral. $\times 0.5$.

portion bearing four prominent longitudinal ridges. Just below the dorsal margin of the medial face lie two large, deep fossae, one above the septum between the 3rd and 4th alveoli and the other above the 6th alveolus. Comparison with other theropod skulls suggests that these may have housed maxillary sinuses.

The most anterior part of the medial face is in fact an anteriorly directed flange (on to the lower half of which run the longitudinal ridges already mentioned). The anterior tip of this flange articulates with a notch on the lateral surface of the anterior process of the palatine (q.v.). The anterodorsal border of the flange forms the medial wall of the internal portion of the subnasal canal.

Seen from below, the anterior/ventral surface of the maxilla is of more or less uniform width. The lateral half of this is occupied by the dental alveoli; the medial half consists posteriorly of the stout rounded ridge referred to above, tapering forwards slightly; anterior to the level of the 4th maxillary tooth this ridge tapers further into the thin medial flange and a less prominent shelf on the inner wall of the flange immediately bordering the medial walls of the alveoli. Also on the medial wall of the flange, behind the shelf, a bony wall surrounds what may well be another maxillary sinus.

On the anterior surface of the rectangular peg is a vertical depression, behind which is the first maxillary alveolus. Altogether there are seven alveoli in the preserved portion of the maxilla; the first four are almost contiguous, separated from each other by only a thick bony wall, but from no. 4 backwards they are more widely spaced. Alveoli nos. 2, 3 and 4 are the largest; nos. 1, 5 and 6 are smaller, no.

7 smaller still. The alveoli are subcircular; no. 4 contains a completely erupted, slightly worn tooth, no. 1 contains only the base of a smaller, broken-off tooth only partly erupted, and no. 6 shows the tip of a newly erupting crown.

We suggested (Charig & Milner 1986, 1990) that there was a mobile articulation on each side between the premaxilla in front and the maxilla behind. We now believe that that suggestion was probably wrong. The anterior end of the maxilla can be fitted neatly into the inverted trough formed laterally by the premaxilla and, medially, by the thin sagittal lamina which appears to be an anterior prolongation of the paired vomers; the rectangular peg on the maxilla then locks into the notch on the premaxilla (Charig & Milner 1986, fig. 1; 1990, fig. 9.2). This complex articulation between premaxilla and maxilla would not permit any movement between those elements, for which, in any case, there is no obvious functional requirement.

NASAL (Fig. 4). The paired nasals are fused together into a single element, although it is possible to detect intermittent traces of the median suture. Three fragments were recovered: the major, posterior, fragment (Fig. 4) was found lodged against the left lacrimal. As preserved, the posterior fragment in dorsal view resembles an arrowhead; it is a narrow triangle, with its apex directed forwards, and from the base (hind end) of this triangle a stubby median process – the ‘shaft’ of the ‘arrowhead’ – projects farther posteriorly and must have articulated with the frontals.

The dorsal (external) surface of the conjoined nasals is raised in

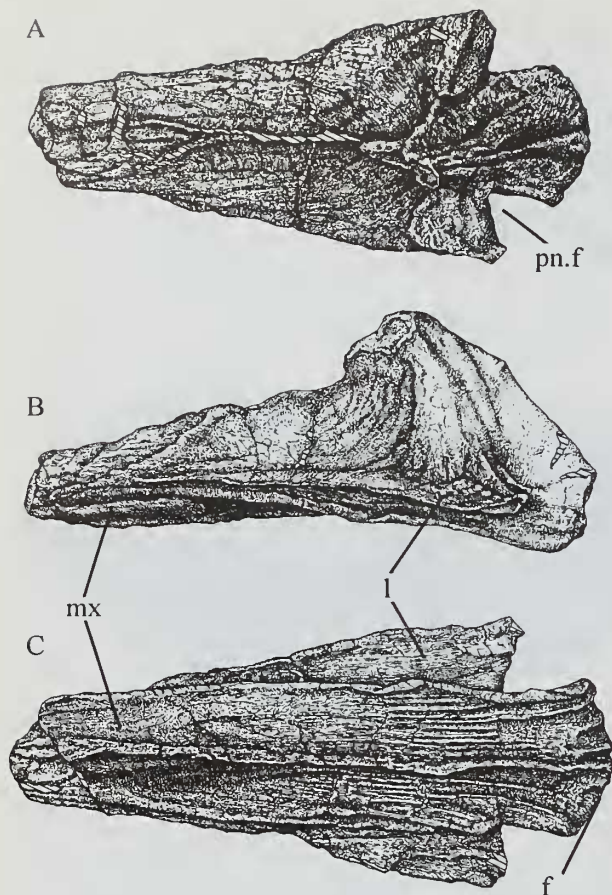


Fig. 4 *Baryonyx walkeri*, holotype, BMNH R9951; posterior part of conjoined nasals. A, dorsal view; B, left lateral; C, ventral. $\times 0.5$.

the midline into a sagittal crest which begins a short way behind the anterior end of the fragment as preserved and continues to its hinder extremity. This is crossed, just anterior to the base of the triangle, by a much lower, rounded transverse ridge; where the two intersect they rise to a tall, prominent peak at the centre of a cruciform excrescence. The anterior part of this sagittal crest is narrow and sharp.

The ventral (internal) surface of the nasals is relatively flat. Paired shallow parasagittal channels, separated by a low median ridge, run the whole length of the fragment and are delimited laterally by sharp ridges running parallel to the mid-line. The parasagittal channels are fairly smooth anteriorly, but more posteriorly bear a series of parallel longitudinal ridges which indicate a firm sutural connexion. The anterior region must have articulated with the ascending process of the maxilla, and the posterior part with an underlying, forwardly projecting process of the frontal; the most posterior part of this surface curves round dorsally so that it faces posteroventrally rather than directly downwards. The lateral extremities are wing-like triangular flat surfaces, the undersides of the lateral portions of the 'arrowhead'. At the extreme posterior end of each lateral 'wing' a very short parasagittal ridge divides the ventral surface into two; the area lateral to this ridge, and, farther forward, the entire width of the surface together form the articulation for the dorsal ramus of the lacrimal. The posterior termination of the lateral wing of the nasal abuts against the anterior face of the dorsal protuberance of the lacrimal (see below). Between the back of the 'arrowhead' and its

'shaft' there lies, on either side, an embayment which must have been part of the margin of a small but distinct fenestra between the nasal, the lacrimal and the prefrontal and frontal. The only theropod we know of that has a fenestra in this position is *Syntarsus* (Raath 1977), for which fenestra Raath proposed the name nasal fenestra¹ although we suggest postnasal fenestra as a more appropriate alternative.

The two more anterior fragments, found in a nearby block (30, Fig. 49) are parallel-sided and triangular in cross-section, the apices being a continuation of the narrow, sharp sagittal crest, little taller than the height at the anterior end of the large fragment. The parasagittal ridge and paired channels continue along the ventral surfaces in line with those on the larger posterior fragment. None of the three fragments join but they indicate that the total length of the nasal was more than 280 mm. Neither fragment shows any trace of a premaxillary articulation at the anterior end.

LACRIMAL (Fig. 5). Only the left lacrimal is preserved. It consists of two rami meeting posteriorly at an angle of about 35°, which encloses the posterodorsal corner of the antorbital fenestra and is considerably more acute than the same angle in other theropods. The nasal (dorsal) ramus is 60 mm long, slender, and tapers to a point; the jugal (ventral) ramus is more than twice as long (155 mm) and stouter.

The dorsal edge of the nasal ramus articulated with the more lateral part of the underside of the nasal bone. The ramus bears a short, horizontal, medially directed lip which underlies the posterior end of its articulation with the nasal. A second, more pronounced lip lies beneath the first one, so that a long narrow groove, some 3 mm wide, is enclosed between the two.

The jugal ramus of the lacrimal projects anteroventrally; its thickened, rounded anterodorsal margin is complete, but its distal half appears to be drawn out posteroventrally into a thinner flange (maximum width as preserved 45 mm), the central part of which is broken off. Its medial surface bears a strong ridge running its entire length and parallel to its dorsal margin. A second ridge is present on the posterodorsal half only, running just below the first ridge and parallel to it, thereby enclosing a deep narrow groove. This groove, continuous with the groove on the nasal ramus, might be supposed to have enclosed the two rami of a V-shaped prefrontal like that found in such theropods as *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993). However, the prefrontal is quite different in *Baryonyx*, small and compact without rami, and could not have articulated with these grooves. The distal end of the jugal ramus of the lacrimal articulated with the main body of the maxilla and, more posteriorly, with the jugal itself.

In the axil of the two rami, on their lateral side, is the deep lacrimal vacuity. Towards the base of this vacuity is the external lacrimal foramen, the outer opening of the lacrimal duct; the internal opening sits in a small pit on the posteroventral surface of the jugal ramus some 40 mm below the posterior termination of the bone. Farther down the same surface are two deep pits, probably foramina, one below the other. These may be the equivalent of the single posterior lateral foramen in *Allosaurus* (Madsen 1976: 20) and

¹The literature is somewhat confused with regard to the position of this fenestra. It is unfortunate that, at present, Raath's dissertation of 1977 is not available to us. Colbert gave a dorsal view of the skull of *Syntarsus rhodensis* (1989, fig. 42B; 'adapted from Raath 1977') which shows the nasal fenestra bordered by nasal, lacrimal and prefrontal; but he did not mention the fenestra in his text. However, Rowe (1989: 129) wrote 'At the junction between nasal, prefrontal and frontal [no mention of lacrimal] is a diamond-shaped opening, termed the nasal fenestra by Raath (1977), that lies just above and rostral [i.e. anterior] to the orbit. This structure is known only in the two species of *Syntarsus*. All this was confirmed by Rowe & Gauthier (1990) and by figs 1C and 1D of Rowe's (1989) paper.

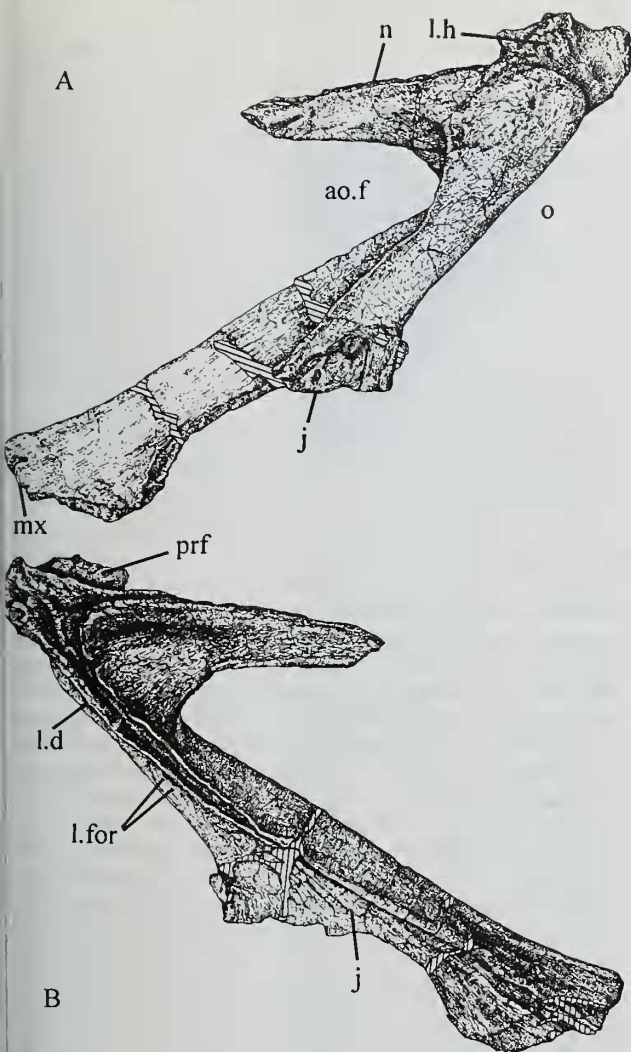


Fig. 5 *Baryonyx walkeri*, holotype, BMNH R9951; left lacrimal. A, lateral view; B, medial view. $\times 0.5$.

Torvosaurus (Britt 1991: 19); another opening on the lateral surface probably connected with one or both of these. At the posterior corner of the lacrimal is a rugose articulation for the prefrontal. Just anterior to the articulation and separate from it, is a dorsal rugose excrescence, about 5 mm high, semicircular in shape, measuring some 20 mm anteroposteriorly and 12 mm across. This may represent the base of a horn core; a similar structure is found in many other herpods, e.g. *Allosaurus*.

PREFRONTAL (Fig. 6). The small, compact and apparently complete left prefrontal proved difficult to identify. It does not have the characteristic V-shape of the typical theropod prefrontal with its two elongated rami (as in, for example *Allosaurus* or *Sinraptor*), nor does either of its rugose articulating surfaces fit convincingly against that of the lacrimal. However, we could not envisage it as any other bone from any other part of the skeleton, and, more persuasively, it was discovered in close association with the nasals and lacrimal in block 2A (Fig. 49; Appendix B). Those two elements had been displaced only a little from their proper relative positions, and the prefrontal was lying, as it should, against the posterior end of the lacrimal.

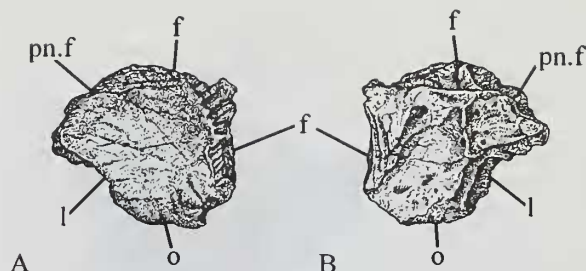


Fig. 6 *Baryonyx walkeri*, holotype, BMNH R9951; left prefrontal. A, dorsal view; B, ventral. $\times 0.5$.

The prefrontal is a thick nubbin of bone, flattened dorsoventrally, with a smooth, slightly concave dorsal surface; seen from above it is roughly isodiametric but of irregular outline. The ventral surface, by contrast, is highly sculptured into ridges and valleys. Anterolaterally the thick margin forms a large, highly rugose facet, which presumably articulated with the posterior end of the lacrimal (although, as stated above, the fit is far from precise). Behind this is a short smooth section of the margin, facing laterally, which would have formed part of the anterodorsal section of the orbital rim.

The posterior part of the margin of the prefrontal forms another articulating facet, only slightly rugose and deeper laterally than medially, which would have abutted against that portion of the frontal that extended laterally between the prefrontal in front and the postorbital behind to reach the orbital rim. The medial surface of the prefrontal is more complex. Dorsally is a deep V-shaped groove, wide anteriorly, tapering posteriorly to an apex, and divided within into two portions by a weak oblique ridge; the anterior portion formed the posterior margin of the postnasal fenestra, the posterior portion articulated with the anterolateral portion of the main body of the frontal. The ventral surface is remarkable only for four parallel ridges running transversely across the finished bone near its posterior margin and for a steep little peak, directed ventrally, at the ventral termination of the lacrimal facet.

POSTORBITAL (Fig. 7). The left postorbital as preserved lacks only its most dorsal portion. As seen in lateral view, it has essentially the shape of a thick lower-case 'y', with the stem of the 'y' (the jugal process) descending posteroventrally and then curving round so that its ventralmost portion is directed steeply downwards. Except dorsally, the margins of the postorbital in lateral or medial view are very thin, almost blade-like.

The anterior half of the lateral surface, curving round medially to form the posterodorsal surface of the orbit, is smooth and convexly swollen throughout its height (i.e., both in its broad dorsal portion and in its narrowing ventral portion). Above the orbit it is weakly rugose, but less so than in *Allosaurus* or *Torvosaurus* (Britt 1991). The posterior half of the lateral surface is weakly concave and leads towards a posteriorly directed flange; the dorsal portion of this flange is broken off but would have articulated with the squamosal, the ventral portion forms part of the anterior border of the lower temporal fenestra. The jugal process is short and square-ended (shorter than the corresponding structures in *Allosaurus* and *Torvosaurus*), and of more or less uniform width. The thick dorsal end of the postorbital is broken off but would have led to a massive facet, directed medially; the greater part of this articulated with the frontal, but a relatively small part articulated at its posterior end with the parietal.

The medial surface is much flatter and, though smooth, is faintly roughened all over. The jugal process bears a distinct vertical

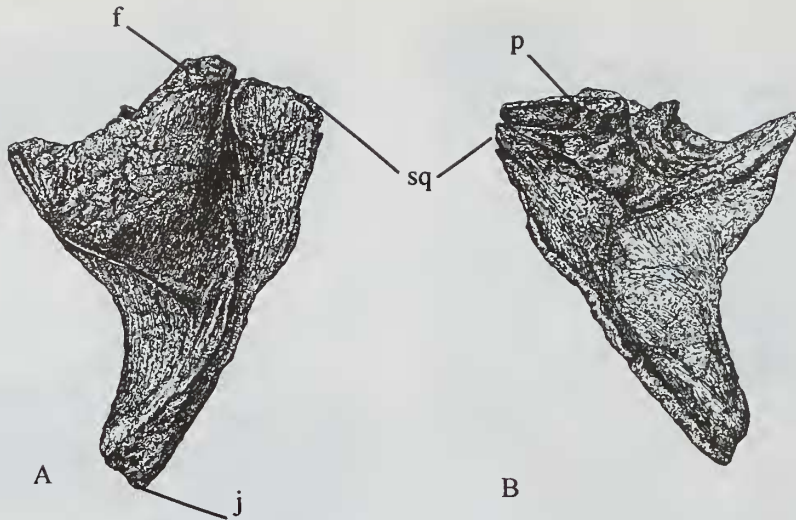


Fig. 7 *Baryonyx walkeri*, holotype, BMNH R9951; left postorbital. A, lateral view; B, medial. $\times 0.5$.

groove, running parallel to its posterior margin. From its posterodorsal region a large process projects mediad, like a flat-topped shelf supported strongly from below by a stout, rounded buttress; this presumably underlay the parietal. Anterior to this a weak concavity faces dorsomedially.

FRONTAL, PARIETAL, AND ANTERIOR END OF BRAINCASE (LATEROSPHEOID, ORBITOSPHEOID) (Fig. 8). A stout plate of bone, very thick and with a smooth surface, and sheared off medially just to the right of the midline, comprises the greater part of the right frontal. It is continuous posteriorly with part of the parietal; a fairly straight line across the bone surface, more or less at right angles to the sagittal plane, may well be the suture between them. The parietal, behind that somewhat dubious suture, extends posteriorly and curves dorsally to form a steep transverse crest, thin from front to back; this crest, some 70 mm high, becomes thinner dorsally and ends in a flat top. The weakly concave ventral surface of the frontal is the ceiling of the posterior part of the orbit. The parietal and frontal together

extend laterally to end in a large and extremely rugose facet for articulation with the postorbital; the parietal forms only the most posterior part of this facet, about one-sixth of its entire length. Along the anterior half of this facet the dorsal surface of the frontal (and presumably of the postorbital too) is raised into a conspicuous protuberance. Anteriorly, the frontal may have contacted the prefrontal, but we cannot be sure of this. Ventrolateral to the frontal (and therefore ventral to the parietal) lies the laterosphenoid.

The laterosphenoid forms the wall of the anterior part of the braincase, thick dorsally but tapering ventrally; in posterior view it is seen in section, behind which a gap separates its broken surface from the anterior face of the prootic (with which it once articulated). Its shape, as preserved, is roughly tetrahedral. In lateral view it appears equilaterally triangular, with one apex directed forwards so that it just reaches the back end of the facet for the postorbital; dorsally it sutures with the parietal, and at its posteroventral corner its surface is extended outwards into a short shelf running more or less parallel with its lower margin. In ventral view it is again triangular, but this time it forms a narrow isosceles triangle with the acute angle directed posteriorly; this surface is part of the internal wall of the orbit. The base of the triangle, at the anterior end, sutures with the frontal, and the anteromedial corner curves round medially to border a large notch which may have served for the emergence of cranial nerves III (oculomotor) and IV (trochlear). Medial to this notch lies a thin, eroded, subtriangular plate of bone, which, according to its general shape and topographical relations, could well be the orbitosphenoid; but it is too poorly preserved to be described properly.

Ventral to the frontal and medial to the laterosphenoid (though separated from the latter by a wide cavity) lies a confused mass of bone and matrix, the identity of which is not clear. As it is, quite fortuitously, almost symmetrical with the right-hand wall of the braincase, it gives the impression that it might be the left-hand wall preserved mostly as a natural mould in matrix: but it cannot be because it lies entirely to the right of the sagittal plane.

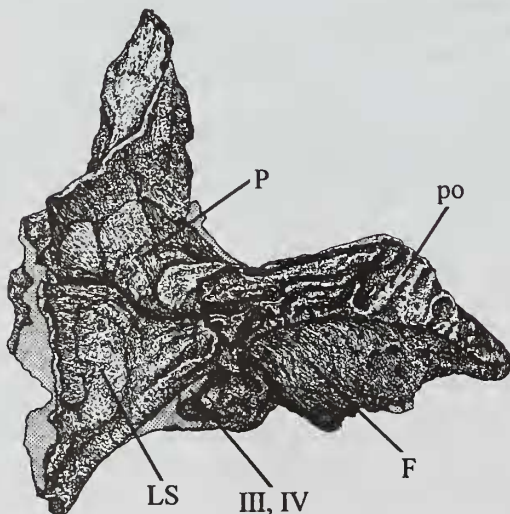


Fig. 8 *Baryonyx walkeri*, holotype, BMNH R9951; right frontal and anterior end of braincase, in lateral view. $\times 0.5$.

POSTERIOR END OF BRAINCASE (WITH OTIC ELEMENTS) AND OCCIPUT (WITH BASISPHEOID) (Fig. 9). The supraoccipital, both prootics, opisthotics and exoccipitals (the latter two elements of the left side detached as a separate fragment), and basisphenoid and basioccipital are preserved. They are described from the posterior forwards

The foramen magnum is semicircular, with a more or less straight lower border and a curved upper border. The lower border lies immediately above the robust, backwardly projecting occipital condyle. Most of the backwardly directed, articulating face of the condyle is formed by the basioccipital; the exoccipitals make only a comparatively minor contribution to this face, namely the dorso-lateral corners, each of which is demarcated from the basioccipital by a straight suture running obliquely. (This suture has separated on the left-hand side.) The dorsal surface of the occipital condyle between the exoccipital sutures on either side is also formed by the basioccipital, which bears a shallow longitudinal depression in the midline; this means that the condyle, seen from behind, has a roughly heart-shaped appearance.

A vertical apron of bone, also part of the basioccipital, extends ventrally from beneath the condyle; it is of uniform width, as wide as the condyle itself, and terminates below in a broad median tongue with a shorter, much narrower lappet on either side. The basisphenoid projects even farther ventrally; this has parallel sides for some distance and then terminates in a pair of processes, the basiptyergoid processes of the basisphenoid, which splay out ventrolaterally. The lower margin of the basisphenoid, between the splayed processes, forms a smooth concave curve. The posterior surface of the basisphenoid, below the median tongue of the basioccipital, is deeply furrowed in the midline; the furrow becomes broader and shallower ventrally and peters out altogether before reaching the ventral margin.

On either side of the foramen magnum/occipital condyle complex lies a horizontally directed lateral wing, the paroccipital process. This is more or less triangular in transverse section, with one face directed posteriorly, another face dorsally and a little anteriorly, and a third anteroventrally. Its medial part is formed by the exoccipital and its more lateral part by the opisthotic; in most dinosaurs those two elements are fused together indistinguishably, but in this specimen an ill-defined suture still demarcates the exoccipital as a slender triangle with its apex directed laterally. The opisthotic extends also ventrally, lateral to the whole length of the basioccipital. At about mid-height of the occipital condyle, on the suture between the exoccipital and the opisthotic and a short distance lateral from the basioccipital, lies a fairly large foramen which is divided in its depth into two separate canals. Recent *Crocodylia* possess several foramina in the same general region, one of which, with exactly the same topographical relationships as the foramen in *Baryonyx*, is likewise divided into two and is unequivocally the vagus foramen; we therefore give that same identity to the 'double' foramen of *Baryonyx*. Iordansky (1973: 226) observed that in the crocodilian foramen vagi 'The medial canal extends to the cerebral cavity and is traversed by the IXth and Xth nerves; the lateral canal extends to the middle ear cavity and contains the Ramus communicans (N. sympathicus) connecting the VIIth and IXth nerves.' [actually Xth and XIth; see Romer 1956: 66]. In *Baryonyx* the external aperture of the smaller canal is dorsomedial in relation to its larger, ventrolateral neighbour. There are two internal apertures within the cavity of the brain stem, just anterior to the foramen magnum; the lower one, lying at the junction of the floor and wall of the cavity, connects with the larger, ventrolateral external foramen, while the upper one, lying behind and a little above its partner, probably connects with the smaller, dorsomedial external foramen. Whether these two are precisely homologous to their crocodilian counterparts is open to question. Meanwhile the dorsomedial part of the anteroventral face of the paroccipital process is overlapped by the prootic (q.v.) below and the supraoccipital (q.v.) above.

The left paroccipital process, i.e. exoccipital plus opisthotic, is present but has been cleanly detached from the rest of the skull. It

lacks the ventral extension and has been distorted to some degree. However, laterally it is more complete than the paroccipital process of the right side, and therefore gives a better indication of the true shape and extent of this structure, of which about 25 mm is missing on the right side (see also Charig & Milner 1986, fig. 2; 1990, fig. 9.4).

The dorsal part of the occiput is contributed by the supraoccipital, which forms (a) the central region of the dorsal margin of the foramen magnum, between the medially directed arms of the opisthotics; (b) the central part of the back end of the skull roof; and (c) arising from the latter, a prominent stout process which, though essentially projecting dorsally, is also inclined a little forwards at its upper end. This process, somewhat compressed antero-posteriorly and is rectangular in shape when viewed from front or rear; its dorsal surface is broadly crescentic. On its posterior surface, on either side of its base, is the external aperture of a canal that has its other end in the upper part of the internal wall of the braincase and presumably served for the passage of a large blood vessel. The basal part of the anterior side of the supraoccipital process, together with the dorsal part of the underlying prootics, forms on each side a strongly furrowed surface which must have sutured with the parietal.

The prootic on either side is a solid, chunky element, forming the wall and floor of this posterior part of the braincase; each meets its fellow along the midline of the floor. A row of foramina for the passage of the cranial nerves runs along the angle between the wall and the floor, effectively dividing the internal and external surfaces of the prootic into an upper part and a lower part (see below, next paragraph). Anteriorly each prootic bears furrowed surfaces for articulation with the laterosphenoid and, more dorsally, with the parietal. Between those articulating surfaces, below the floor of the braincase, is the posterior part of the pituitary fossa; it appears here as two deep median concavities (a smaller above and a larger below, with a saddle between) which penetrate horizontally backwards into the substance of the bone. The posterior wall of the pituitary fossa is the dorsum sellae. On either side of the top of the upper concavity is a large foramen, through which the VIth (abducent) cranial nerve is presumed to have passed forward from the floor of the braincase into the pituitary fossa (see Romer 1956: 67) and thence continued in the same direction to emerge laterally into the orbit (see Osborn 1912: 17).

Externally the upper part of the prootic is applied to the anterior surface of the opisthotic, extending about half-way along the length of the paroccipital process. Its lower margin is a smooth, slightly concave curve, separated from the opisthotic behind by a deep furrow which terminates medially in the fenestra ovalis. Just anteromedial to the latter is a foramen for the VIIth cranial nerve and, farther forward still, a large open notch for the emergence of the Vth. Ventral to these nerve exits the lower part of the prootic forms a large plate-like posterolateral process which is applied to the anterolateral face of the basisphenoid.

On the left side, the opisthotic has become detached from the rest of the braincase; this exposes the cavity of the otic capsule, contained within the body of the prootic. Inside this capsule are two small foramina, both of which lead through into the endocranial cavity to emerge posterior to the large foramen for the passage of the Vth nerve. One of these could well be the duct for the passage of the VIIIth cranial (auditory or acoustic) nerve. These ducts and foramina serve for the passage, not only of blood vessels and lymph ducts, but also of pneumatic openings.

The whole of the ventral portion of this occipital fragment, seen in anterior view, is formed from the basisphenoid with its splayed, downwardly projecting basiptyergoid processes. As stated above, the more dorsal part of the basisphenoid is hidden by the postero-

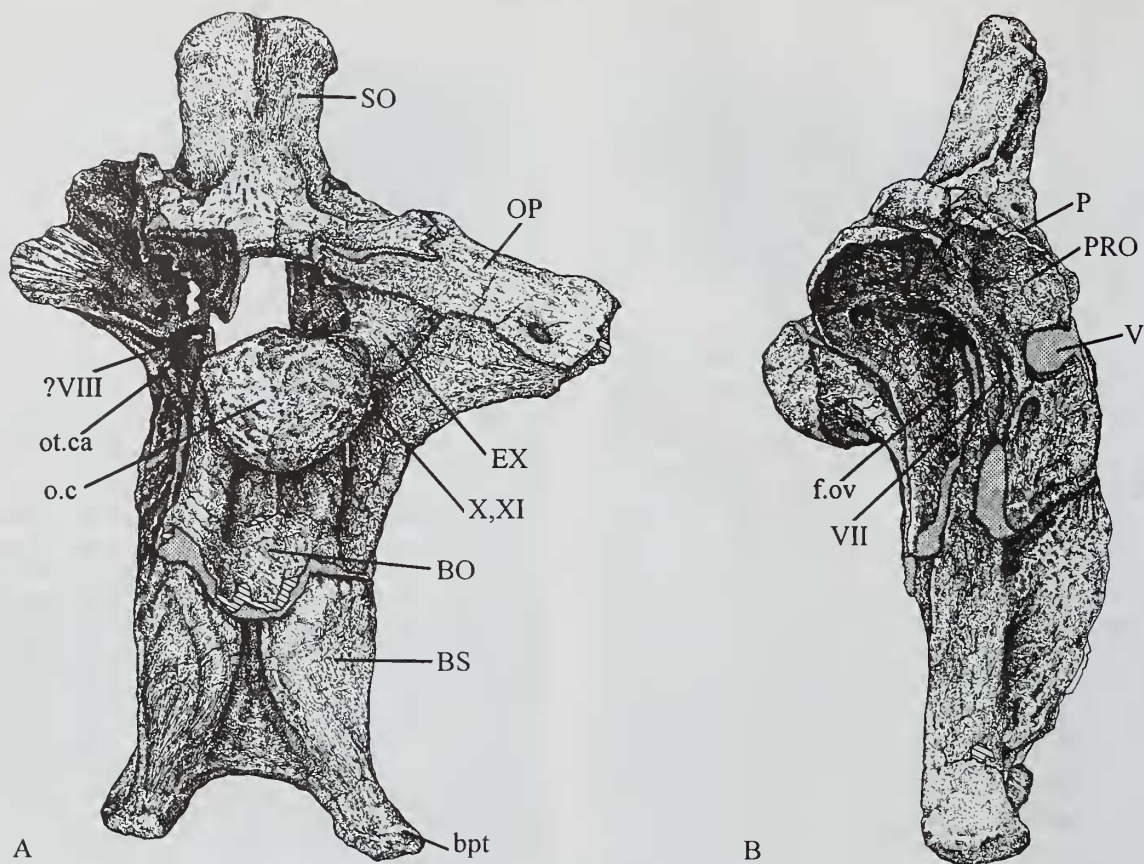


Fig. 9 *Baryonyx walkeri*, holotype, BMNH R9951; occiput and posterior part of braincase, lacking detached left opisthotic. A, posterior view; B, right lateral. $\times 0.5$.

lateral processes of the prootics. In the midline of the anterior surface is an extremely prominent, ridge-like septum which divides ventrally (like an inverted Y) into a pair of ridges, each leading down towards the basiptyergoid process of its side; between the two ridges is a deep cavity. On either side the flat surface of the basisphenoid slopes posterolaterally so that the whole resembles a pitched roof. At the dorsomedial corner of each flat surface, just beneath the posterolateral process of the prootic, is a moderately deep hollow.

JUGAL (Fig. 10). The left jugal is represented by an elongate portion from the centre of the element, lacking what was probably a significant length at either end. In lateral view the lower margin appears almost straight, while the upper margin forms a smooth, shallow, concave curve that is the wide ventral border of the orbit; thus the element is beginning to widen towards the break at either end, the posterior widening being much the larger of the two. The lower margin is generally rounded, the upper margin sharper. The central part of the bone, directly beneath the centre of the orbit, is fairly robust; the ends of the fragment, however, become rapidly thinner towards the breaks (forwards, backwards and upwards).

The lateral surface is more or less smooth except for a weak ridge running diagonally across the suborbital bar, from the upper margin of the bar beneath the front of the orbit to the lower margin of the bar at about the level of the back of the orbit.

The medial surface, by contrast, is distinguished by a series of features. The lower margin is wrapped around to form a strong,

dorsomedially directed flange; this flange is especially well developed beneath the ascending process, and it passes anteriorly and a little ventrally, becoming weaker as it does so, to merge into the lower margin itself beneath the orbit. Beneath the orbit, too, it is flattened, ridged and grooved parallel to its own length to form an articulation that presumably met the ectopterygoid. Posterior to this, where the flange is developed much more strongly, it encloses a deep trough between the main body of the jugal and itself.

The dorsal margin of the suborbital bar is narrowly rounded in front, forms a sharp raised ridge beneath the centre of the orbit, and posteriorly develops a second, slightly lower ridge more or less parallel with the edge of the orbit. Between the two subparallel ridges is a shallow trough. The lower ridge also forms the upper border of the deep trough enclosed by the ventral flange, the trough being at its narrowest at this point. The flange, and therefore the trough which it helps to enclose, taper away to disappear entirely just in front of the break at the hind end. The ventral margin, at this hind end of the bone as preserved, bears a narrow, medially directed shelf which doubtless formed part of the articulation for an anteriorly directed process of the quadratojugal.

The missing anterodorsal corner of the jugal presumably articulated with the maxilla and the posterodorsal corner with the postorbital.

QUADRATE (Fig. 11). Both quadrates are preserved complete, each with a broad transverse articulation for the lower jaw at its ventral

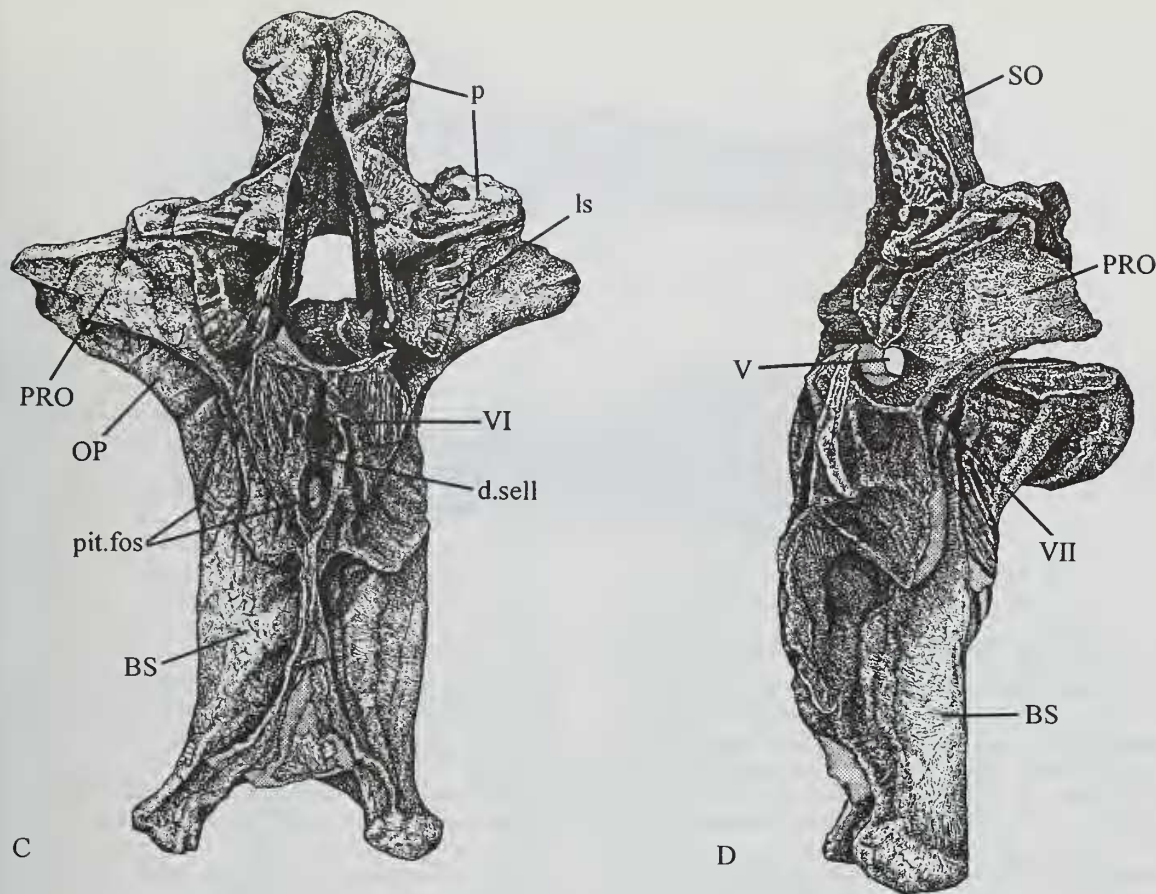


Fig. 9 *cont* *Baryonyx walkeri*, holotype, BMNH R9951; occiput and posterior part of braincase, lacking detached left opisthotic. C, anterior view; D, left lateral. $\times 0.5$.

end. Viewed posteriorly, the quadrate tapers rapidly upwards from the lower jaw articulation into a narrow shaft that swings a little anterolaterally and then dorsally. It terminates in an expanded knob-like head that fitted into the underside of the squamosal; on the lateral side of the head is a small, distinct, slightly concave facet. The lateral surface of the broad basal part of the quadrate forms a large, rugose, kidney-shaped concavity which provided an immovable sutural attachment for the quadratojugal. Higher up the shaft is a laterally directed ridge, its outer end forming a narrow sutural surface, also for the quadratojugal. Between these two quadratojugal attachments lay a large, elongated quadrate foramen delimited medially by the quadrate and laterally by the quadratojugal. This foramen is much larger than the equivalent foramen of *Allosaurus*, which is almost entirely enclosed by the quadrate.

The entire anterior side of the quadrate is extended forwards into a wide pterygoid flange; the medial side of the lower half of this flange was presumably applied to the lateral face of the pterygoid. In *Allosaurus* this flange is directed obliquely towards the midline. The broad quadrate condyle, extending transversely mediad from the quadratojugal facet, is characterized by a screw-like sigmoid swelling; this is anterior in position on the medial side but curves round below the condyle to a posterior position on the lateral side. This surface, which articulated with the lower jaw, is much wider medially than laterally.

Lower jaw (Fig. 12)

Parts of both rami are preserved, including:

Left side: dentary (virtually complete); splenial (fragmentary); angular (partial).

Right side: dentary (a section of the dentigerous bar containing eight alveoli, probably nos. 18–25); splenial (complete); surangular (fragmentary); angular (partial); coronoid (complete).

DENTARY (Figs 13, 14). Of all the elements in the mandible, the left dentary is the best preserved. It was found broken into two: an anterior portion containing the first 26 tooth alveoli and a posterior portion containing the last 6. The broken ends had remained in contact with each other, but the two parts had undergone a relative dislocation to produce a divergence of about 45° from the straight line. Nevertheless, their two ends can be fitted together without the interpolation of any significant missing portion. There were therefore 32 teeth in each complete dentary, 64 in the entire lower jaw.

The anterior two-thirds of the dentary (apart from the terminal expansion) is essentially elongated from front to back and flattened from side to side. Its labial and lingual sides are flat and parallel; the dorsal and ventral margins are nearly parallel, but they do converge a little anteriorly. The dentigerous dorsal surface is also flat and demarcated from the labial and lingual surfaces on either side by a

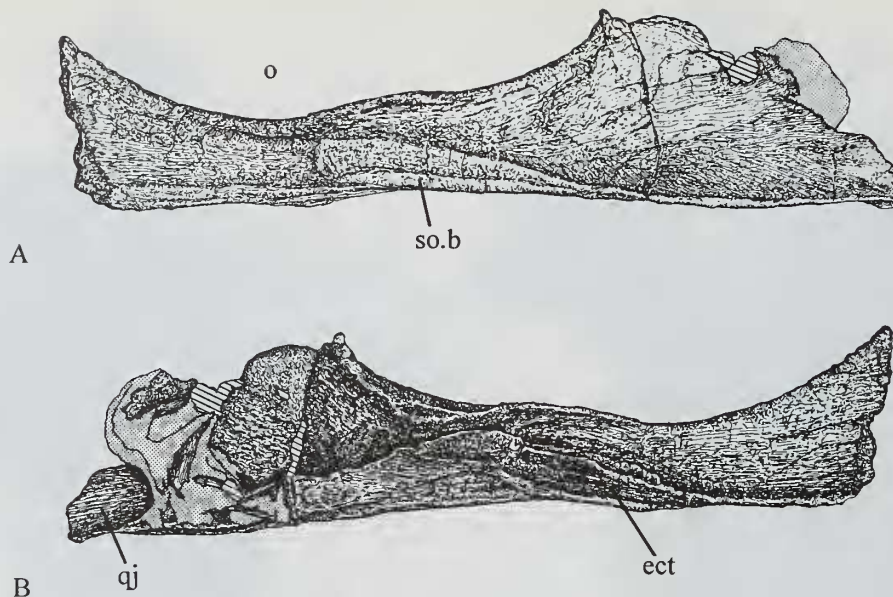


Fig. 10 *Baryonyx walkeri*, holotype, BMNH R9951; left jugal. A, lateral view; B, medial. $\times 0.5$.

right angled corner. The ventral margin is rounded so that it would appear U-shaped in transverse section. Viewed from either side, the dorsal margin is bent significantly upwards as it approaches the anterior end: at about the level of the 9th tooth alveolus it is angled upwards through some 25° and then runs in a more or less straight line to the anterodorsal corner of the bone, i.e. to the region of the 1st tooth. Forwards of the level of the 9th alveolus the dentary starts to expand both vertically and laterally (thereby creating the enlarged 'terminal rosette').

The ventral margin, at the extreme anterior end, passes smoothly into the anterior margin. This region is where the two rami, left and right, joined at the mandibular symphysis. The symphyseal surface,

however, is marked by only a very few short parallel striations on the lingual side of the dentary, suggesting that the symphysis must have been effected through connective tissue only, retaining some mobility between the two jaw rami.

The posterior third of the dentary is altogether much thinner than the anterior part; it has a broader, blade-like appearance, expanded vertically, with the dorsal and ventral margins diverging widely posteriorly. Indeed, the Meckelian groove on its lingual surface widens backwards to the extent that it disappears into a broad, flat surface occupying the entire height of the bone between the dorsal and ventral rims. The labial surface is flat and featureless.

The dorsal and ventral margins of this posterior dentary 'blade'

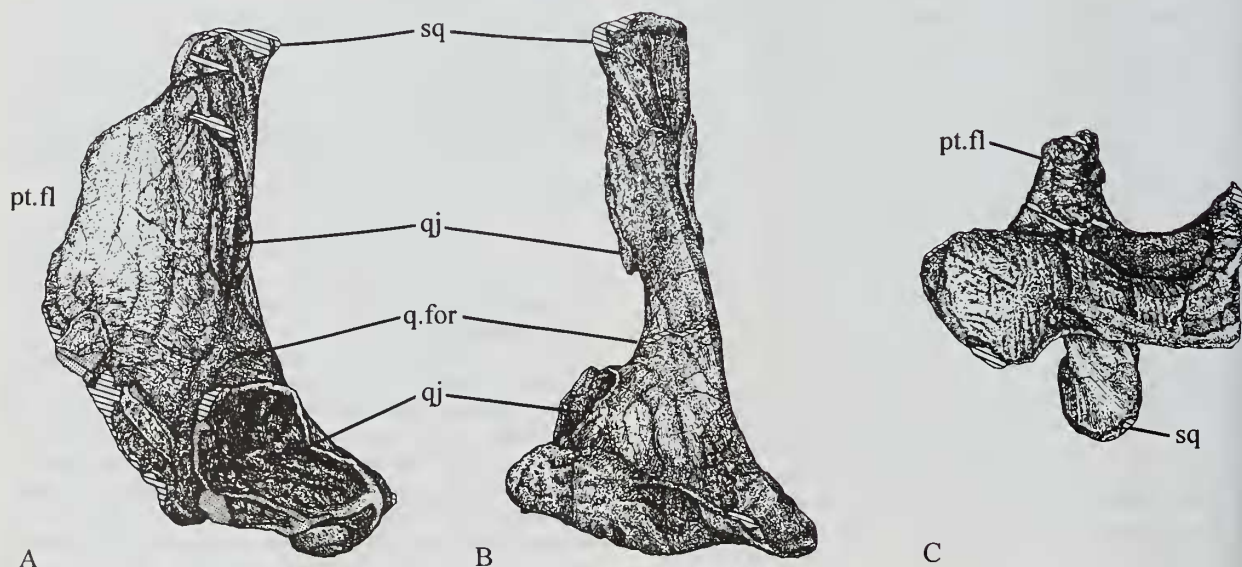


Fig. 11 *Baryonyx walkeri*, holotype, BMNH R9951; left quadrate. A, lateral view; B, posterior; C, ventral. $\times 0.5$.

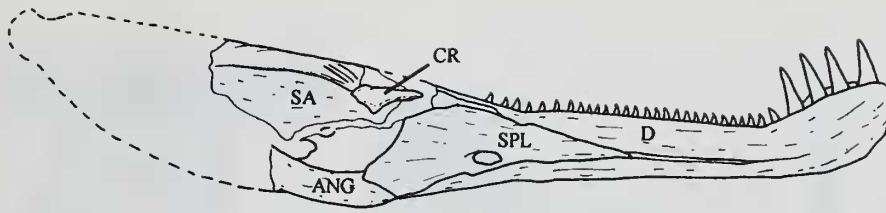


Fig. 12 *Baryonyx walkeri*, holotype, BMNH R9951; partial reconstruction of lower jaw, in medial (lingual) aspect. $\times 0.135$.

are much narrower than are the margins of the stout anterior part of the dentary, but they are still somewhat thickened anteriorly, being backward continuations of the lips of the ever-widening Meckelian groove and continuing to curl round towards each other as distinct overhangs. The dorsal overhang forms a slot for the surangular. As the blade widens posteriorly its ventral lip, which forms a slot for the angular, diminishes and eventually disappears altogether; the form of this fragile posterior end of the dentary is indicated only by an outline that has, in places, been badly damaged and eroded. The ventral margin is nevertheless preserved intact and forms a smooth, slightly convex curve. Its extreme tip (as preserved) is probably not far short of what was once the posterior end of the complete dentary. From that end the dorsal margin of the dentary ascended anterodorsally to the widest point and then descended again forwards, but this part is extremely thin and, as preserved, has an irregularly broken edge. However, at two places on this broken edge there are small lengths of smooth-edged bone of a curved outline, recessed from the general level of the surface, which are doubtless parts of the margins of dentary fenestrae.

In dorsal view the lingual margin of the dentary forms a smooth, gently concave curve, somewhat more marked in front of the 9th alveolus than behind it. The labial margin, by contrast, curves outwards markedly to accommodate the roots of the greatly enlarged first 5 teeth; this swelling produces the mandibular portion of the 'terminal rosette'.

The Meckelian groove runs lengthwise along the lingual surface of the fragment, at a little below mid-height. It has a strongly overhanging dorsal lip and a fairly well-marked ventral lip, the gap between them being 16 mm; the base of the groove is a smooth channel. Anteriorly the groove becomes shallower and narrower, its lips become less pronounced, and it tapers out anteriorly some 60 mm behind the symphysis and beneath the wall separating the 4th and 5th alveoli. Posteriorly, from the 19th alveolus backwards, the lips of the Meckelian groove are themselves grooved and faceted for articulation with the splenial. Indeed, the major part of the lingual surface of the posterior end of the dentary, tapering forwards into the Meckelian groove, served as a slot for the splenial.

The labial surface of the dentary bears a number of foramina, which doubtless served for the passage of blood vessels and/or nerves. There are about 25 scattered over the expanded area at the anterior end, with a much smaller number farther back. There is also a linear series of mental foramina running parallel to the dorsal margin of the bone, lying in a shallow groove at approximately the level of the bases of the alveoli. These do not, however, bear a fixed numerical relationship to the alveoli, being significantly fewer than the latter. They served for the passage of branches of the inferior alveolar nerve and also, presumably, blood vessels. The last foramen of this linear series happens to be on the anterior end of the posterior fragment; behind this the shallow groove continues all the way to the anterior end of the dentary as preserved.

The dorsal border of the lingual surface of the dentigerous region of the dentary is, for most of its length, of approximately the same height as the dorsal border of the labial wall and as the interdental plates. The interdental plates are, therefore, barely exposed in lingual view, unlike the usual theropod condition (e.g. *Allosaurus*).

The alveoli themselves vary in form, from squarish/circular in occlusal view (2nd) to egg-shaped (3rd) to a rectangle twice as broad as long (9th). They vary also in size (see 'Dentition'). They are immediately adjacent to each other so that they are separated by no more than a thin interalveolar wall. The lingual wall of the row of alveoli, i.e. the row of interdental plates, is separated from the dorsal rim of the lingual surface of the dentary by a deep paradental groove (the 'nutrient groove' of Osborn 1912). However, each alveolus communicates with the nutrient groove by means of a slot in its interdental plate, with a foramen at its base. For most of the tooth row these slots are narrow and situated posterolingually (see Fig. 14), but, in the case of the larger anterior teeth nos. 1–5, they are much wider and more anterior in position.

SPLENIAL (Fig. 15). The right splenial is preserved complete save for the fragile dorsal margin and posterior end. The left splenial, by contrast, is very incomplete, the only part of its true margin remaining being a small piece of its posterodorsal corner.

The splenial is a thin, narrow, subtriangular sheet of bone, its apex directed anteriorly, which was slotted into the Meckelian groove on the lingual surface of the dentary. The medial (or lingual) surface of the splenial is distinctly convex dorsoventrally, the convexity being more marked in the posterior half of the bone. The lateral (or labial) surface, facing the dentary, is correspondingly concave. Midway along the length of the element, just above its ventral border, is the moderately large splenial fenestra (= the anterior mylohyoid foramen of Currie & Zhao 1993 and the splenial foramen of Madsen 1976, the latter labelled Meckelian canal in his Plate 9), elongated in an anteroposterior direction. This fenestra is completely surrounded by bone in *Baryonyx* and *Sinraptor* but is in a marginal position in *Allosaurus*; in *Ceratosaurus* it is only small, and in *Coelophysis* and *Dilophosaurus* it is absent altogether.

The medial surface bears a sharp ridge just above its ventral margin, which, by virtue of its overhanging nature, produces a ventral-facing groove that received the dorsally directed, wrapped-around lower margin of the Meckelian groove on the dentary. Anterior to the splenial fenestra this splenial groove is well developed; beneath the splenial fenestra it is very shallow, forming nothing more than a faint lip; behind the fenestra the groove is again distinctly present, but it is narrower and shallower than in the anterior region and posteriorly it fades out altogether into a flat, narrow, ventral margin to the bone.

The dorsal margin of the splenial rises to a 'dorsal process'. Anterior to that the edge of the bone, although a little crushed, is almost straight. Posterior to the dorsal process, the dorsal margin of

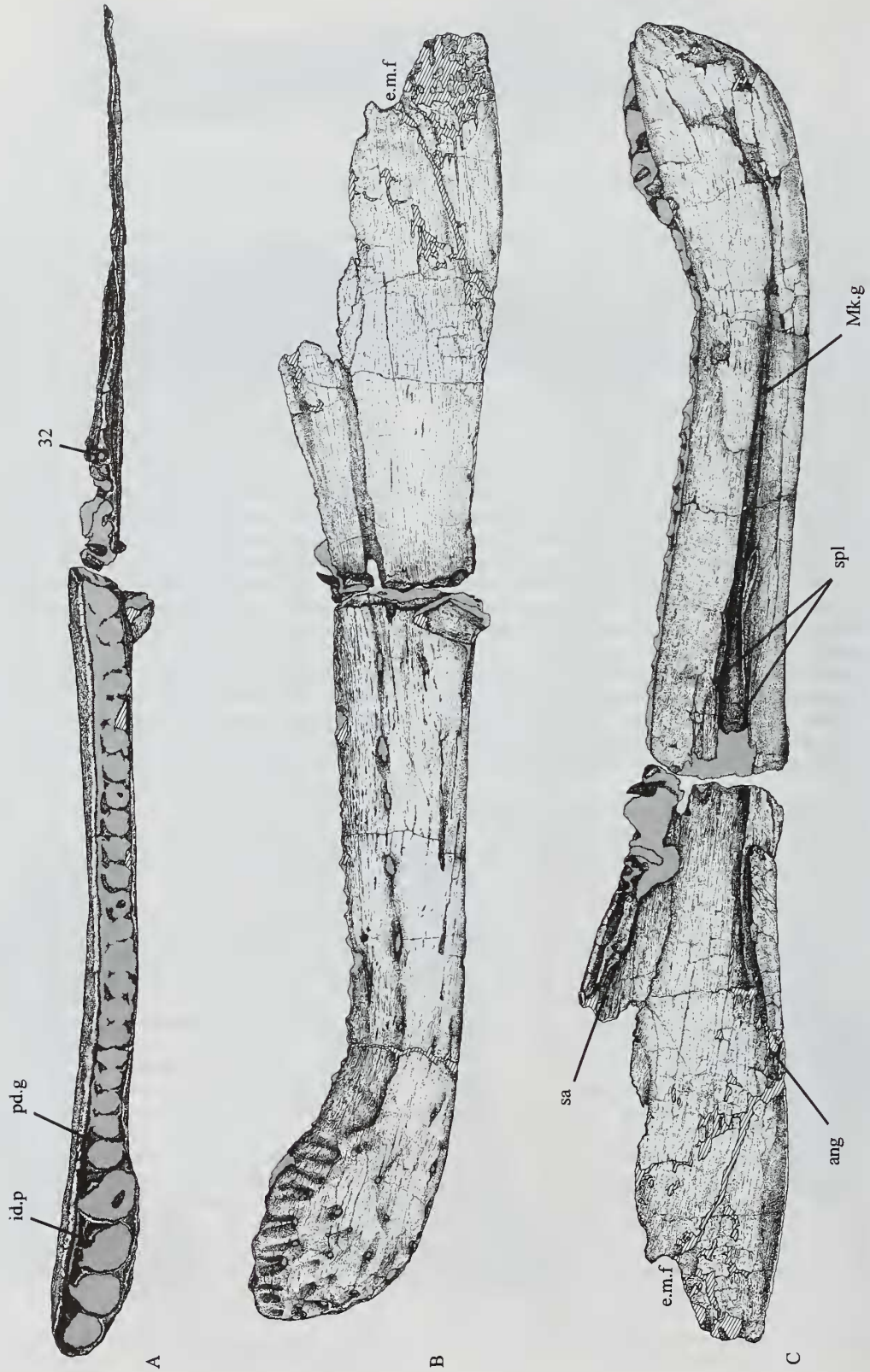


Fig. 13 *Baronyx walkeri*, holotype, BMNH R9951; left dentary. A, dorsal (occlusal) view; B, lateral (labial); C, medial (lingual). $\times 0.33$.

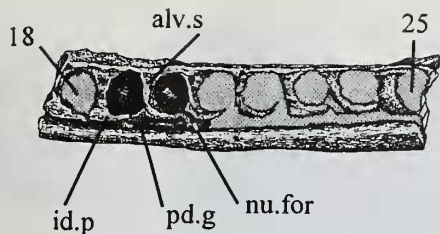


Fig. 14 *Baryonyx walkeri*, holotype, BMNH R9951; part of right dentary, in dorsal (occlusal) view. $\times 0.5$.

the splenial is preserved complete and forms a smooth concave curve, extending posteroventrally and then posteriorly; this, presumably, formed the anteroventral border of the internal mandibular fenestra. The posterior end of the splenial which articulated with the angular is missing.

The anterior tip of the splenial is a flattened tongue that bears strong longitudinal striations on its lateral face. The ventral margin of the latter, just posterior to the splenial fenestra, forms a shelf, which would have received the anterior end of the angular.

SURANGULAR (Fig. 16). Only a large fragment of the right surangular is preserved. This is the central part of the stout upper border of the bone, which itself constitutes the upper border of the posterior half of the mandible as a whole. It consists essentially of a vertical plate, thin and irregularly broken below, which at its upper border is greatly thickened and folded over medially as a brow-like

bar overhanging the deep concavity of the adductor fossa. The bar itself is flattened above into a dorsomedially facing surface, divided by a low central ridge into two shallow parallel channels. This dorsomedial bar narrows posteriorly towards its presumed articulation with the articular, the upper surface loses its twin channels to become smooth and rounded, and the concavity beneath it becomes shallower and disappears just before the posterior break.

A prominent ridge arises in the middle of the lateral surface of the fragment as preserved and runs horizontally backwards, rapidly becoming extremely robust. It terminates at the break but presumably continued backwards as a buttress to the jaw articulation.

ANGULAR (Figs 17A, B). The central portions of both elements are preserved. The right, however, is less complete at either end and adds nothing to description of the left.

The entire angular appears to have been a somewhat boomerang-shaped element, flattened and bow-like and with a pronounced angle in its convex lower border. This lower border is thick and rounded, while the concave upper border is much sharper. The fragment is fairly broad dorsoventrally, but thin and fragile medio laterally. Its anterior end thins anteriorly and is directed a little upwards as well as forwards; its margin appears to be almost complete. The central region, where the blade is narrowest, has a very distinct, weakly concave upper border, which formed the lower margin of the external mandibular fenestra. The posterior end is broken off at right angles to the margins, but the preserved portion clearly indicates that it was both thickening and widening towards the rear.

The medial surface is flat and featureless. The lateral surface, which was applied to other post-dentary elements, is also flat. Posteriorly the thick rounded ventral border is produced laterally

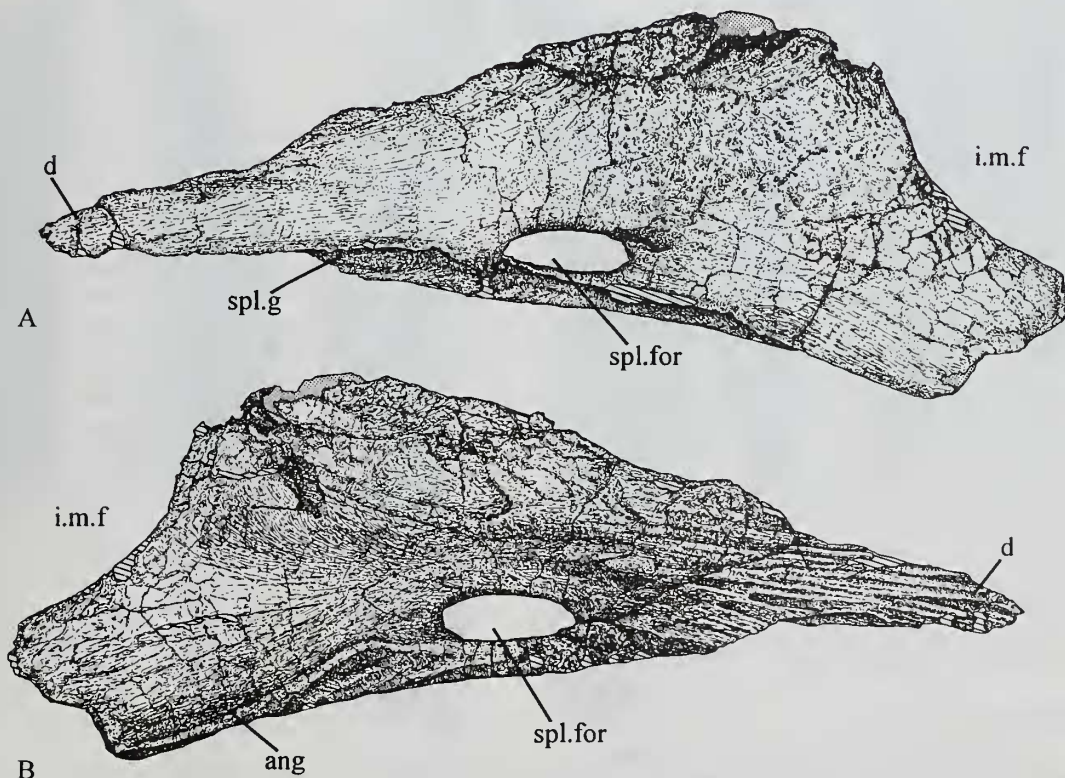


Fig. 15 *Baryonyx walkeri*, holotype, BMNH R9951; right splenial. A, medial (lingual) view; B, lateral (labial). $\times 0.5$.

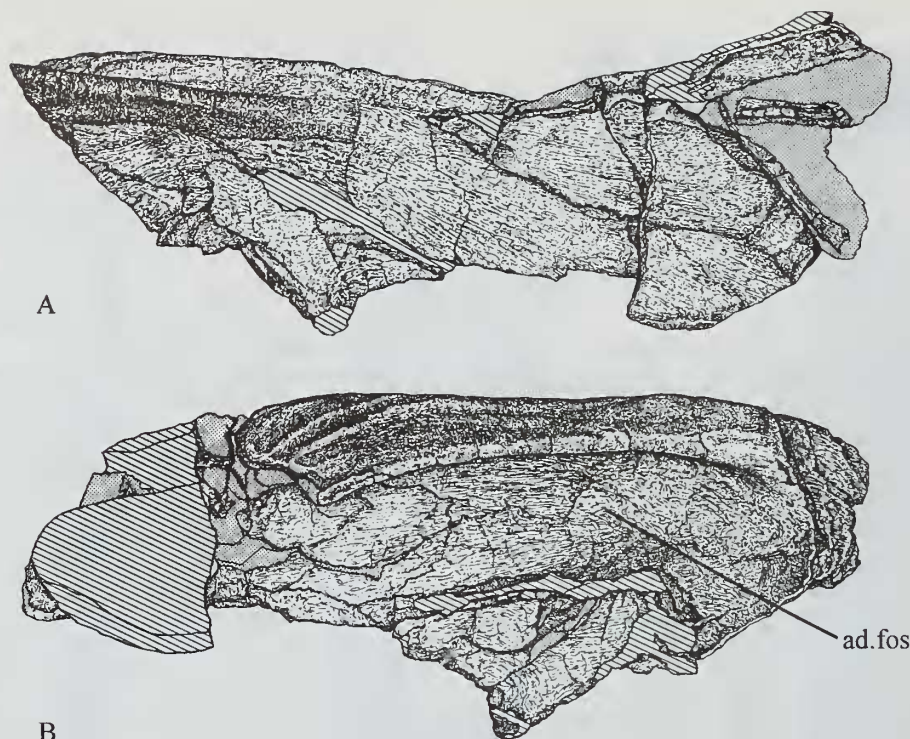


Fig. 16 *Baryonyx walkeri*, holotype, BMNH R9951; right surangular fragment. A, lateral (labial) view; B, medial (lingual). $\times 0.5$.

into a longitudinal flange with a deep ridged groove above it, presumably for articulation with the prearticular. Farther forwards, however, in the region of the angle in the ventral margin, this flange-and-groove becomes transformed into a simple rounded ridge with an elongated shallow depression between it and the angle; still farther forwards the ventral margin becomes much narrower.

The lateral surface of the angular, at the posterior end of the fragment as preserved and just beneath its dorsal margin (i.e. the lower border of the external mandibular fenestra) is depressed below the general level of the surface. The edge of this depression, demarcating it from the general level, runs more or less parallel to the lower margin of the bone in a gentle curve; the depressed area is therefore much thinner than the rest of the blade.

CORONOID (Figs 17C, D). A small, roughly triangular bone, seemingly complete, is presumed to be the right coronoid. The dorsal edge is the longest; the weakly concave posteroventral edge is slightly shorter; the undulating anteroventral edge is the shortest of the three. Both lateral and medial surfaces are generally flat. A broad, laterally facing facet for the prearticular runs along the anteroventral edge. Two somewhat similar facets for the surangular run along the posterior two-thirds of the dorsal edge, with a narrow ridge between them; one faces obliquely laterally and the other, rather narrower, obliquely medially. The concave posteroventral edge is the anterodorsal margin of the adductor fossa.

Dentition (Figs 18, 19)

Most of the teeth preserved are in isolation; a few remain in the premaxilla and maxilla, but none (except for a few tiny replacing teeth) remains in the dentary. They have a general theropod appearance, being simple recurved cones, somewhat flattened labiolingually,

with serrated mesial and distal carinae. At the same time, however, they show a number of characteristic peculiarities:

1. They have very long roots, tapering significantly towards the apex, so that each tooth as a whole is unusually long and slender. This character creates the false impression that the isolated teeth of *Baryonyx* are less recurved than those of most other carnivorous archosaurs. However, the larger tooth crowns are slightly less recurved than the smaller ones.
2. They show only slight labiolingual flattening, much less than in the more blade-like teeth of nearly all other theropods.
3. The carinae are strongly developed, forming, along both mesial and distal edges of the tooth, a distinct ridge with its surface demarcated from the general surface of the crown by a more or less straight line. The carinae run the full length of the crown.
4. Both mesial and distal carinae bear extremely fine denticles, approximately 7 to the millimetre; the only other theropods with comparable denticle count are *Saurornithoides*, with 7–8 per mm (Sues 1978), and *Ricardoestes*, with about 5 per mm (Currie *et al.* 1990). The denticles (Fig. 19) are tall, narrow and sub-parallel-sided, with flat or slightly fluted tops (probably due to wear) and relatively uniform in size, irrespective of the size of the tooth. This condition differs markedly from that shown by theropods in general, where the basal length of the tooth denticles increases with increasing tooth size in linear fashion (Farlow *et al.* 1991). *Spinosaurus* (Stromer 1915), *Angaturama* (Kellner & Campos 1996) and *Irritator* (Martill *et al.* 1996) lack serrations altogether.
5. The lingual surfaces of the crowns are longitudinally fluted (i.e. they bear about 6–8 ridges).
6. The enamel on both surfaces has a finely granular appearance.

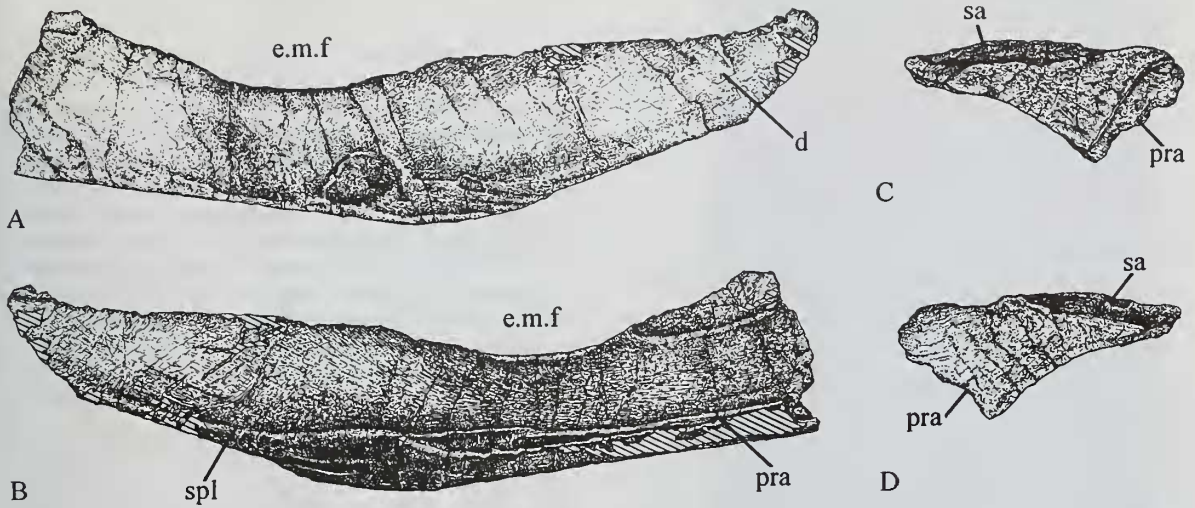


Fig. 17 *Baryonyx walkeri*, holotype, BMNH R9951. A-B, anterior part of left angular; C-D, right coronoid. A, lateral (labial) view; B, medial (lingual); C, lateral (labial); D, medial (lingual). $\times 0.5$.

The only differences between the several teeth preserved are those of size and degree of recurvature. Naturally the size of the actual teeth as preserved varies according to the degree of development of each, but apart from that there is a constant difference between the

sizes of the alveoli, more noticeable in the upper jaw than in the lower. In the premaxilla teeth nos 2 and 3 are the largest, 1 and 4 somewhat smaller, while 5, 6 and 7 form a decreasing series; the largest have twice the diameter of the smallest. In the maxilla the



Fig. 18 *Baryonyx walkeri*, holotype, BMNH R9951; isolated teeth. A, left upper or right lower symphysial crown in (left) labial and (right) lingual views; B, right upper premaxillary or maxillary tooth in (left) lingual and (right) labial views; C, left maxillary or right dentary tooth in (left) labial and (right) lingual views; D, left dentary tooth in (left) labial and (right) lingual views. Natural size.



A



B

Fig. 19 *Baryonyx walkeri*, holotype, BMNH R9951; scanning electron micrographs of tooth crown in Fig. 18C. A, denticles on the mesial carina and the granular texture of the enamel, $\times 30$; B, higher magnification of four denticles from the centre of row in A, $\times 150$.

largest of those in the preserved portion (bearing only the first 7–8 alveoli) is no. 3, from which they diminish fairly regularly in both directions. In the dentary, by contrast, the size of the alveoli is generally much more regular, nos 5–26 forming a straight series of almost uniform diameter; 1–4, however, are appreciably larger, producing a slight swelling corresponding in position to the spatu-

late tip of the upper jaw but much less marked; 27–32 diminish regularly.

Vertebral column

CERVICAL REGION (Figs 20, 21). Five cervical vertebrae are preserved fairly complete, including the axis. Also preserved are the atlantal pleurocentrum (odontoid), the right atlantal neuropophysis, the axial intercentrum, and one cervical rib. The vertebrae were not found in articulation, so they are ordered according to the various morphological trends that they display. If it be assumed that the total cervical count was the usual theropod number, nine, then the vertebrae preserved, in addition to the axis (Ce2), are likely to be Ce3, Ce5, Ce6 and Ce8. Their most important dimensions, together with those of the dorsal vertebrae, are given in Table 1 below.

Table 1 Dimensions of the cervical, dorsal and proximal caudal vertebrae (all measurements are in mm)

	A	B	C	D	E	G	H	I	J	K	L	M
Ce2	50	68	53	52	73	–	–	–	–	–	–	–
(axis)												
Ce3	55e	45	70	65	81	126	90	101	–	–	–	–
Ce5	61	39	80	58idc	74	178	115	117	–	–	–	–
Ce6	67e	44e	84	65	95	179	111	110	–	–	–	–
Ce8	84e	62	95	66e	120	204	99	98	–	–	–	–
D1	75e	80	90	80	91	tbd	–	123	87	16	50	27
D2	103	85	100	78	108	109	115	110	100	14	44	25
D3	85e	65	102	77	92	98	83	119	107	12	39	29
D4	80	65	88	87	90	–	–	–	–	–	–	–
D5	83	72	98	82	92	109	62	62	96	28	62	21
D6	88	73	90e	88	88	117	62	61	134	41	nfr	18
D7	–	–	–	–	–	129	70	63	140	48	nfr	20
D8	82e	74	70	84e	93	–	–	–	–	–	–	–
D10	–	–	–	–	–	140	66	–	–	–	–	–
D11	80	81	tbd	tbd	105	161	73	61	197	80	nfr	18
D13	88	96	100	98e	108	–	–	–	–	–	–	–
D14	104e	96	114	94e	110	184	69	68	201i	86	nfr	19
	A	B	C	D	E	F						
CaA	97	111	111	110	134	33						
CaB	91	99	92	107e	144	32						
CaC	114	112	–	–	140	–						

A, transverse diameter of anterior face of centrum; B, vertical diameter of anterior face of centrum; C, transverse diameter of posterior face of centrum; D, vertical diameter of posterior face of centrum; E, length of centrum below, rim to rim; F, transverse width of centrum at narrowest point (i.e. 'waist') (for proximal caudals only); G, length of neural arch (front of prezygapophysis to back of postzygapophysis; mean of both sides where both are available); H, total width across prezygapophyses; I, total width across postzygapophyses; J, height of neural spine (measured from roof of neural canal at anterior end); K, length of neural spine parallel to body axis (measured from point of divergence of postzygapophyses); L, length of neural spine plus rugosities; M, thickness of neural spine (measured at point of divergence of postzygapophyses); e, estimated; i, incomplete; idc, ignoring deep concavity in upper margin; nfr, no further rugosities; tbd, too badly damaged.

The cervical vertebrae themselves have the following general characters:

The neck as a whole tapers from the back towards the front. The centrum of each vertebra is significantly shorter than those behind it. The transverse diameter of the deeply concave posterior face of each vertebra is likewise significantly less than it is in the vertebra following, but the vertical diameters (except in the axis) remain more or less constant. Thus, while the posterior face of the axial centrum is an almost perfect circle, those of the succeeding verte-

brae become progressively more elongate transversely (See Table 1, p. 30.) This progressive diminution of the vertebrae in a forward direction culminates in a remarkably small axis, its length being only 7.8% of the estimated length of the skull (comparable figures for *Allosaurus*, *Ceratosaurus*, *Coelophysis*, *Deinonychus* and *Dilophosaurus* are 13.6%, 9.8%, 15.7%, 10.8% and 10.6%). Each centrum is constricted in its middle so that it has a waisted or 'hour-glass' shape, but in fact there is no deepening of the floor of the neural canal within each vertebra like that found in some other archosaurs, e.g. '*Mandasuchus*' (Charig MS 1956). The centra are strongly opisthocoelous, the concavity of each posterior face articulating with a great ball-like convexity on the anterior face of the next centrum behind. There are no ventral keels on the centra. However, a faint ventral ridge is present on the posterior half of the axial centrum and on Ce8; the latter occurrence suggests that the undersides of the unknown Ce7 and Ce9 may have been similarly ridged.

Models were made of the missing cervical vertebrae (namely Ce4, Ce7 and Ce9), their dimensions and characters being estimated as intermediate between the actual vertebrae before and behind in the series as ordered by us. When all eight vertebrae (Ce2-Ce9), actual or modelled, were lined up in what we judged to be reasonable natural articulation between the opposing faces of the centra and between the relatively huge zygapophyses, then the neck was more or less straight; there was no sigmoidal curvature of the neck such as is found in many other archosaurs. More precisely, the two faces of each centrum lie parallel to each other; they are not at an angle to each other as in *Allosaurus*, *Ceratosaurus*, *Deinonychus* and many other archosaurs, in which the necks must have curved strongly upwards.

A large parapophysis projects laterally from an anteroventral position on the side of the centrum (except on the axis, see below) and retains that position throughout the series. The distance between the paired parapophysial facets, seen from below, increases as we pass backwards down the neck. This widening is due to the increasing diameter of the centra and affords useful confirmation of the correctness of our ordering. Immediately posterodorsal to the parapophysis lies a pleurocoel, the size of which increases backwards down the series; the left and right pleurocoels of each centrum appear not to communicate with each other across the midline. In Ce3 each side has two adjacent pleurocoels, separated by a septum.

Although in some instances the centrum and neural arch appear to be firmly sutured together, this is not always the case. In Ce5 the two elements were preserved adjacent but separate; they were somewhat distorted, and had to be taken apart in the laboratory and re-set. In Ce8 the centrum and neural arch were preserved completely separate in the same block. In the other vertebrae the line of the neurocentral suture is clearly visible. It runs more or less straight and horizontal and lies about one-third of the way up the sides of the neural canal. The diapophysis is on the side of the anterior half of the neural arch, directly above the parapophysis and the pleurocoel (in contrast to *Allosaurus*). It is flattened dorsoventrally, projects ventrolaterally and scarcely varies through the series. There are no laminae radiating from the diapophysis connecting it with the zygapophyses, which (as already stated) are remarkably large. The postzygapophyses do not diverge more widely from the midline and from each other than do the prezygapophyses.

The neural spines are low, transversely thin, inclined very slightly backwards, and without spine tables. In Ce5-Ce8 the anterior edge of the neural spine bifurcates ventrally into two ridges that diverge towards the left and right prezygapophyses respectively. The posterior edge bifurcates similarly into two ridges that likewise run down

towards the epipophyses. In both cases, just below the point of bifurcation and between the ridges, a massive, rugose, bony protuberance is developed in the midline, projecting respectively anteriorly and posteriorly, and clearly distinct from the neural spine itself. These projections, which doubtless served for the attachment of interspinous ligaments, vary considerably in size and form (see Fig. 20). Epipophyses are massively developed, but by contrast, there are no hyposphenes (except in the axis) or hypantra.

The first two cervical vertebrae, the atlas and axis, differ greatly from the typical members of the series that follow them and must be described individually. The atlantal pleurocentrum forms the odontoid peg that protrudes from the front of the axis. Although it was found firmly attached to the dorsal third of the anterior face of the axial pleurocentrum, it is evident that it is not fused thereto; indeed, on the right-hand side it is somewhat displaced from its natural position. It is of fairly typical form: a hemispherical protruding peg with a flattish semicircular dorsal surface, convexly rounded in front, below, and on either side. Posteriorly these lower surfaces flare out like a collar to form a crescentic articulating surface for the (missing) atlantal intercentrum. At the base of the anterior surface is a small median depression which may well be the notochordal pit. The atlantal intercentrum is missing entirely. It may be presumed that it fitted into the middle third of the anterior face of the axial pleurocentrum.

The right atlantal neurapophysis (the right half of the neural arch of the atlas vertebra) appears in dorsolateral view as a large, roughly trapezoidal, plate-like element that arises dorsally by the shorter of its two parallel sides from what might best be described as a footplate below. It widens dorsomedially towards the longer parallel side, which is virtually straight, but at the same time it curves round more horizontally so that it would have approached the left element in the midline to form a roof over the most anterior part of the neural canal. It also becomes much thinner as it approaches its medial margin, which is so thin as to be almost blade-like. The anterolateral part of the smooth external (dorsolateral) surface is strongly convex in all directions. The internal (ventromedial) surface, which is correspondingly concave and almost as smooth, bears a distinct facet close to its posteroventral edge which articulated with the axial prezygapophysis. The anteroventral margin is concave in profile, smooth, and thickly rounded; it forms the rim of the anterior opening of the neural canal, from which the spinal cord passed forwards into the foramen magnum. The posteroventral margin is thin dorsally but somewhat thicker ventrally.

The base of this trapezium is expanded in two directions into what we have referred to above as a 'footplate': a medial process that extends towards the (missing) atlantal intercentrum, and a lateral process that forms a triangular wing when viewed from above or below. Neither of these processes has been perfectly preserved, both being a little eroded towards their ends. To the best of our knowledge no such lateral process has been reported in any other theropod.

The axial intercentrum is represented by the usual crescentic wedge. Allowing for some distortion, its posterior face fits fairly well into the ventral third of the anterior face of the axial pleurocentrum. Its anterodorsal face, which must have articulated with the missing atlantal intercentrum, is extended forwards into a protuberant lip. Between these two faces, beneath the lip, is the ventral surface, slightly concave from front to rear; on either side it curves upwards and becomes narrower.

The axis itself, with the odontoid attached to its anterior face, is almost perfectly preserved. It is very small compared to the presumed size of the skull. It shows strong opisthocoely (like the other cervicals), and its anterior face possesses a pair of facets, situated ventrolaterally, which articulated with the axial intercentrum. There

is one pair of pleurocoels, again as in the other cervicals. The parapophyses, though present, do not project laterally, and the diapophyses are reduced to small pyramidal tubercles. The neural spine possesses the hatchet-like shape typical of many reptilian axes; the epipophyses are very prominent, and a distinct hyposphene is present.

According to Madsen (1976: 32), in *Allosaurus* the distance from the prezygapophyses to the postzygapophyses, relative to the width, is greater in the anterior cervicals, subequal in the mid-cervicals, and less in the posterior cervicals. In *Baryonyx*, the exact opposite obtains (see Table 1, p. 30).

Madsen also noted (*loc. cit.*) that in *Allosaurus* the epipophyses are long in the anterior part of the series but decrease progressively backwards to only a small ridge in Ce9. The same applies to *Sinraptor* (Currie & Zhao 1993: 2056). In *Baryonyx* the epipophyses are well-developed throughout the series; the longest of all are in Ce8, but those (though still well-developed) are less robust than the epipophyses of the more anterior vertebrae.

DORSAL REGION (Figs 22–26). The material available contains all or part of at least twelve dorsal vertebrae: seven preserved fairly complete, three centra lacking a neural arch (but one with a prezygapophysis and diapophysis) and two neural arches lacking a centrum. Like the cervicals, they were not found in articulation and have been ordered on their various morphological trends. If we assume that the total dorsal count was the usual theropod number, fourteen (making twenty-three presacals altogether), then the vertebrae preserved seem to be: D1, D2, D3, D4 (centrum, left prezygapophysis and diapophysis only), D5, D6, D7 (neural arch diameter only), D8 (centrum only), [D9 missing entirely], D10 (neural arch only), D11, [D12 missing entirely], D13 (centrum only), D14. Additionally, there are other vertebral fragments that we cannot assign to any particular vertebra.

The lengths of the centra (see Table 1) are best measured ventrally, rim to rim. Even so, distortion and damage make it difficult to measure accurately, and some values (denoted with an 'e') are nothing more than reasonable estimates based on the information available. The first eight centra, except for D2 and the missing D7, are of a remarkably constant length, all being in the range 88–93 mm. They are a little longer than the anterior cervicals (73–81 mm), about the same as the mid-cervical Ce6 (95 mm), and appreciably shorter than the posterior cervical Ce8 (120 mm). D2, however, is anomalous in that it too is significantly longer (108 mm). The last four dorsal centra, except for the missing D12, are also longer (105–110 mm).

The lengths of the neural arches, measured from the anterior tip of the prezygapophysis to the posterior tip of the postzygapophysis, are likewise variable. They vary too in respect of the proportion of each to the length of the corresponding centrum. In the cervical vertebrae the neural arches are much longer than the centra so that the zygapophyses, anterior and posterior, project far beyond their centra; in the most anterior dorsals, by contrast, they are scarcely any longer at all. However, from about D5 backwards they gradually increase in length until in the last dorsal (D14) they are 67% longer than the centra. It is interesting to speculate as to the functional significance of these great differences.

Nevertheless, certain general characteristics of the dorsal vertebrae may be discerned. The diameters of the centra are, in general, more constant than the lengths referred to above, but they do display a few individual variations, summarized as follows:

Anterior face, transverse diameters 80–88 mm, varying irregularly, except for D1 75 mm (e) (estimate), D2 103 mm, D14 104 mm (e); vertical diameters, 65–81 mm, increasing steadily from D3 to

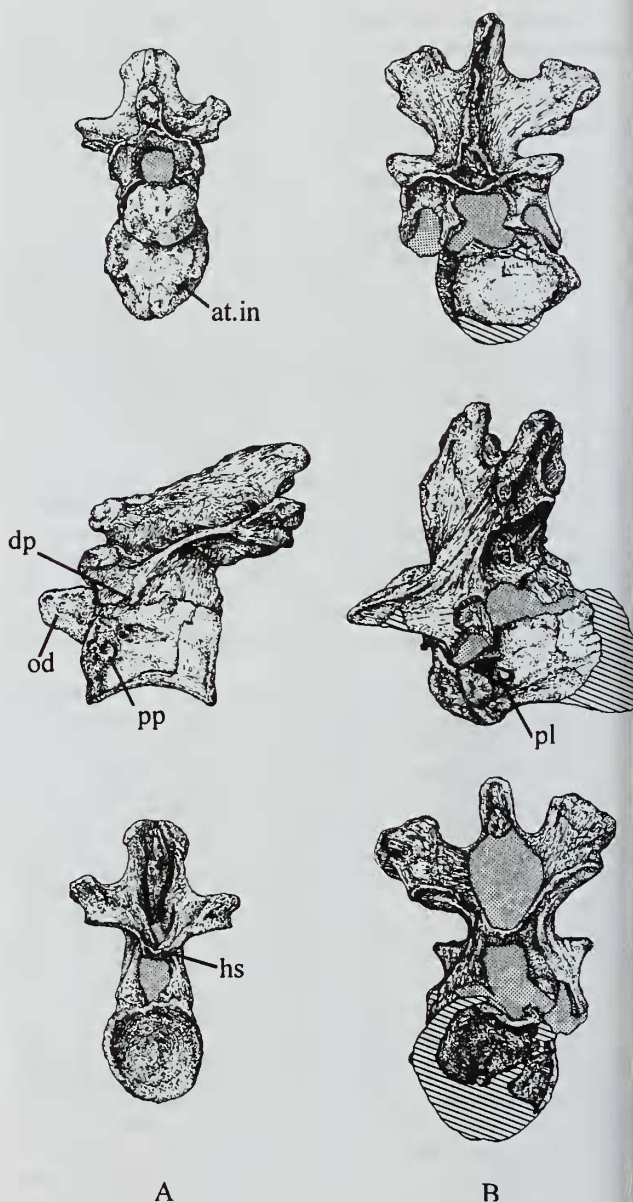


Fig. 20 *Baryonyx walkeri*, holotype, BMNH R9951; cervical vertebrae in (from top downwards) anterior, left lateral, and posterior views. A, axis; B, Ce3, $\times 0.25$.

D11, except for [D1 80 mm, D2 85 mm], D13 96 mm, D14 90 mm.

Posterior face, transverse diameters, 88–102 mm, varying irregularly, except for D8 70 mm, D14 114 mm; vertical diameters, 77–88 mm, varying irregularly, except for D13 98 mm (e), D14 90 mm (e).

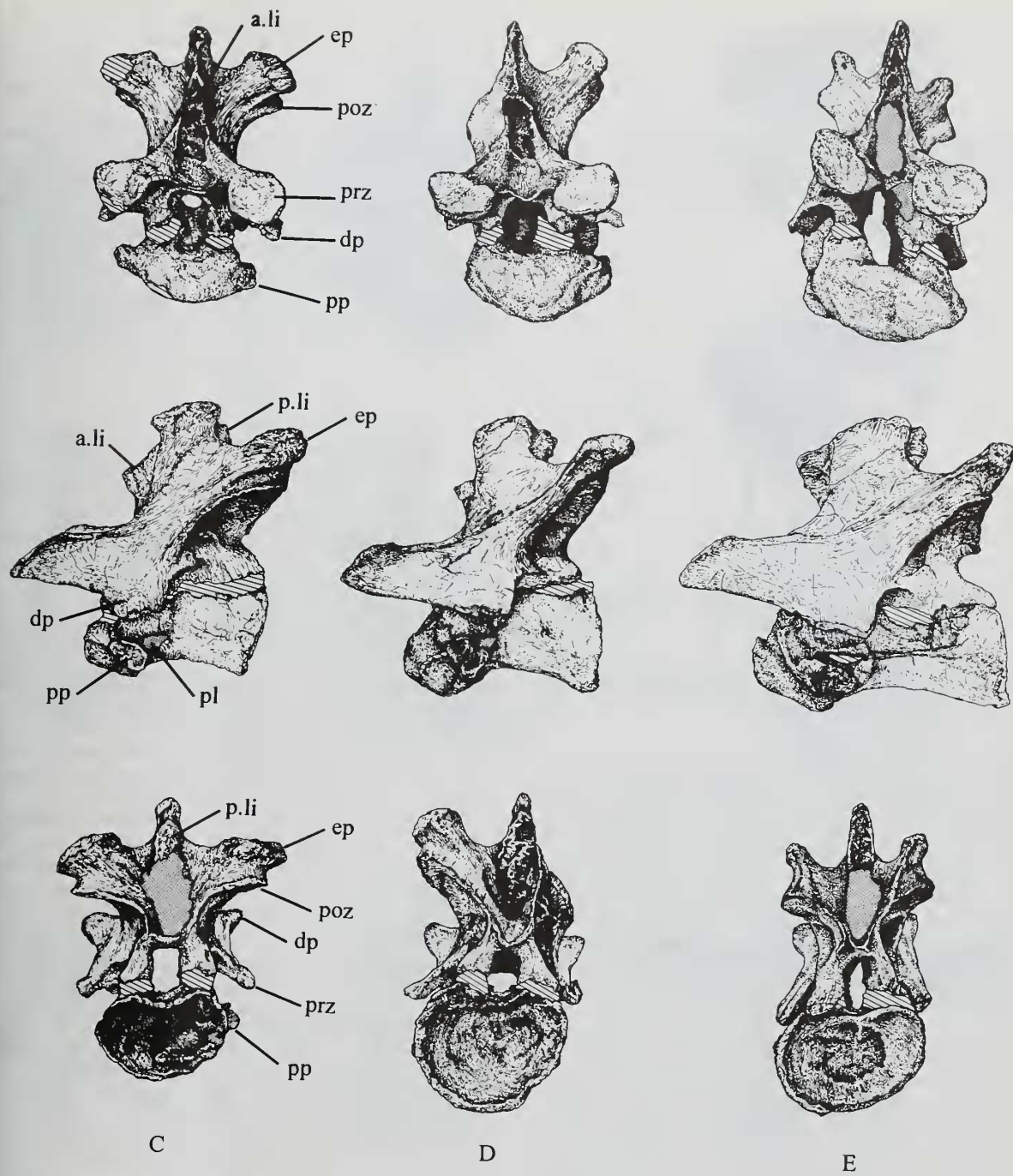


Fig. 20 cont *Baryonyx walkeri*, holotype, BMNH R9951; cervical vertebrae in (from top downwards) anterior, left lateral, and posterior views. C, Ce5; D, Ce6; E, Ce8. $\times 0.25$.

From these figures we may draw the following general conclusions:

- 1. With a few exceptions, the transverse diameters of both faces are greater than the corresponding vertical diameters. Thus the faces are not truly circular but transversely elongate ovals.
- 2. With a few exceptions, the dimensions of the posterior faces are

greater than the corresponding dimensions of the anterior faces with which they articulate (i.e. of the vertebra immediately behind). Individually, however, there seems to be very little or no correlation between the two.

- 3. There is a tendency for the first two dorsal centra (D1, D2) and the last two (D13, D14) to be stouter than the others. This may be

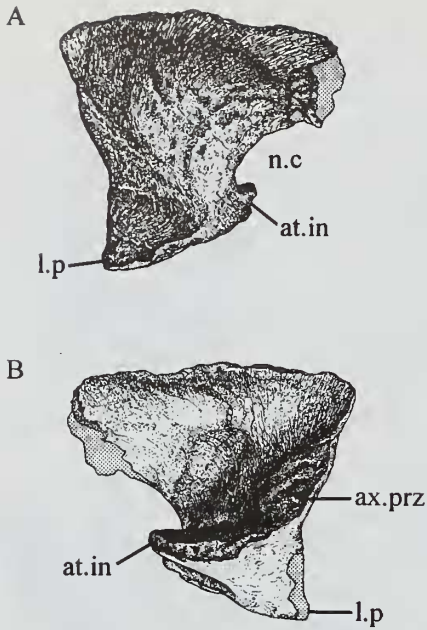


Fig. 21 *Baryonyx walkeri*, holotype, BMNH R9951; right neurapophysis. A, lateral view; B, medial. $\times 0.5$.

correlated with their being positioned in the body directly above the limbs, D1 and D2 in the shoulder region and D13 and D14 immediately in front of the sacrum.

The degree of curvature of the faces of the centra decreases steadily from front to back of the dorsal series. Thus the anterior face is strongly convex (effectively ball-like) in D1-D3, moderately convex in D4, almost flat in D5, completely flat in D6, and slightly concave (where known) in D8-D14. The posterior face is very deeply concave in D1-D5, moderately concave in D6, very slightly concave in D8 and D11, and then (reversing the trend a little) slightly concave again in D13 and D14. Incidentally, these observations provoke a question: why are D4 and D5 so strongly opisthocelous, when the anterior faces of D5 and D6 – with which, of course, they respectively articulate – are, by contrast, almost flat and completely flat respectively?

The tendency to develop a ventral keel beneath the centrum increases rapidly in the anterior part of the dorsal series, reaching its maximum in D4 and D5, but thereafter tailing off posteriorly. D1 bears only a modest ridge, best developed at the anterior end. D2 has a distinct keel, running the whole length of the centrum; D3 is much the same, but the keel is slightly better developed; D4 and D5 continue the trend, with the keel becoming somewhat deeper. In D6 and D8, however, the whole centrum has become 'waisted', the keel has disappeared but there is still a sharp ridge. D11 is very similar, except in that the median ridge is very faint; in D13 it is quite distinct again; and D14 is deeply waisted but its ridge has disappeared altogether.

It is perhaps remarkable that, whereas the faces of the centra of the cervical vertebrae of *Baryonyx* are not 'offset' at all, those of the dorsal vertebrae – especially the first six – lie not perpendicular to the axis of the centrum but at an oblique angle thereto. This 'obliquity' is very pronounced in D1-D3, diminishes progressively in D4 and D5, and becomes more prominent again in D6. It is also present, albeit to only a minor degree, in D8 and D14, but it is entirely absent

in D11 and D13. This phenomenon is generally considered to indicate curvature of the vertebral column. However, the angle of inclination of an articulating face of a centrum, considered alone, does not indicate this; what would produce a curvature of the vertebral column (i.e. angulation between two adjacent vertebrae) would be a *difference* between the two faces of a centrum, or between two faces that articulate with each other in their respective angles of inclination.

As in most archosaurs, the position of the parapophyses varies greatly along the dorsal series; as we pass posteriorly down the series they migrate upwards and backwards, moving from the centrum (D1-D4) to the neural arch (D11-D14). In the intermediate vertebrae (D5-D10) the parapophysis lies across the neurocentral suture and is therefore formed in part by the centrum and in part by the neural arch. In more detail, the position of the parapophysis is as follows:

- | | |
|----------|--|
| D1 | low on centrum, at anteroventral corner |
| D2 | still low, but a little higher |
| D3 | almost at mid-centrum level |
| D4 | anterodorsal at top of centrum, almost reaching neuro-central suture |
| D5, D6 | only top quarter of parapophyseal facet has moved on to neural arch |
| D7 | parapophyseal facet exactly half-way across neurocentral suture |
| D8, D10, | |
| D11 | parapophyseal facet still partly on centrum |
| D13 | functionally, completely on neural arch |
| D14 | wholly on neural arch |

In many other archosaurs the parapophysis continues to migrate posteriorly as we pass backwards down the dorsal series, so that, in the posterior dorsals, it eventually comes to lie on the anterior edge of the transverse process itself. This does not happen in *Baryonyx*, where, even in the last dorsal (D14), the parapophysis remains distinct from, and anterior to, the transverse process.

Like the cervicals, the dorsal centra are equipped with pleurocoels, but these peter out posteriorly. In D1 there is a double pleurocoel, just posterodorsal to the parapophysis. In D2 and D3 there is a single pleurocoel in the same position; in D2 it is longer and slit-like, perhaps because of crushing. In D4 and D5 the pleurocoel lies directly behind the parapophysis; it is an oval opening in D4 and smaller in D5. In D6 there is a deep hollow in the same position, but, since it does not connect with the cavity of the bone, it cannot be a true pleurocoel. In D8 there is a longer, shallower cavity; this has virtually disappeared in D11 and has gone altogether in D13 and D14.

The transverse processes are flat-topped. Each has a sharp anterior edge that swings round to form the anterior horizontal lamina (nomenclature of Britt 1993), a ridge continuous with the lateral edge of the prezygapophysis. A similar ridge, the posterior horizontal lamina, likewise unites the posterior edge of the transverse process with the postzygapophysis. Beneath the transverse process lie two thin but powerful supporting buttresses, one (the anterior infradiapophyseal lamina) running anteroventrally towards the parapophysis and the other (the posterior infradiapophyseal lamina) towards the posterodorsal corner of the centrum. These two laminae, together with the anterior and posterior edges of the transverse process, enclose three deep triangular cavities (the infraprezygapophyseal fossa, infradiapophyseal fossa, and infrapostzygapophyseal fossa respectively). In the more posterior vertebrae of the series the infradiapophyseal fossa contains supplementary buttresses of much weaker construction (one each in D10(?) and D14 but three in D11).

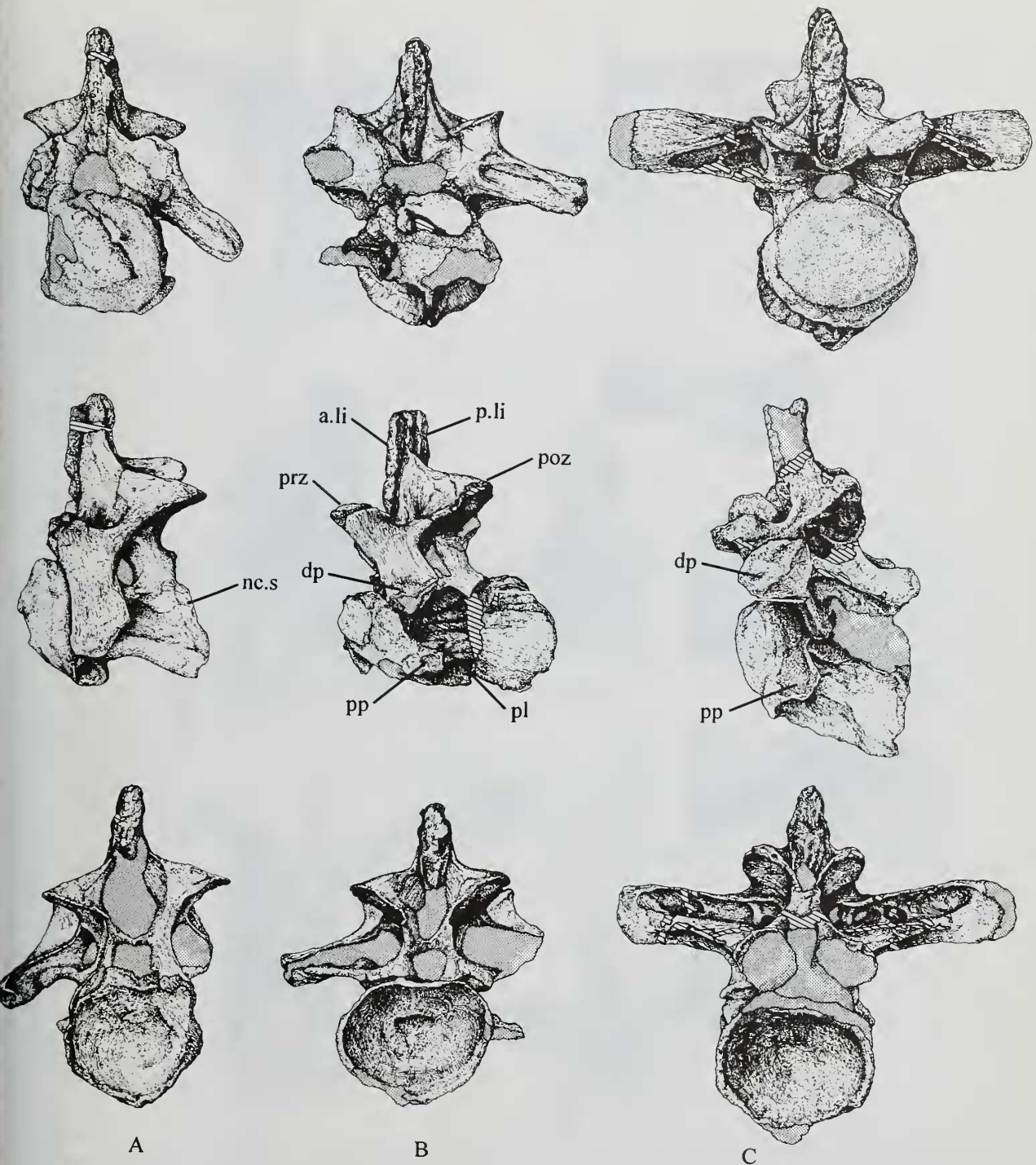


fig. 22 *Baryonyx walkeri*, holotype, BMNH R9951; anterior dorsal vertebrae in (from top downwards) anterior, left lateral, and posterior views. A, D1; B, D2; C, D3. $\times 0.25$.

The lateral projection of the transverse processes from the sides of the neural arch is also directed differently in different parts of the dorsal series. Thus in D1 and D2 they project slightly downwards, in D3 horizontally, in D5 strongly upwards, in D6 a little less steeply upwards, in D7 less steeply still, in D11 very steeply upwards again,

and in D14 less steeply again (much as in D7). In all cases, however, the transverse processes – seen from above – are more or less perpendicular to the body axis; they are angled neither anterolaterally nor posterolaterally.

In the most anterior members of the dorsal series the pre-

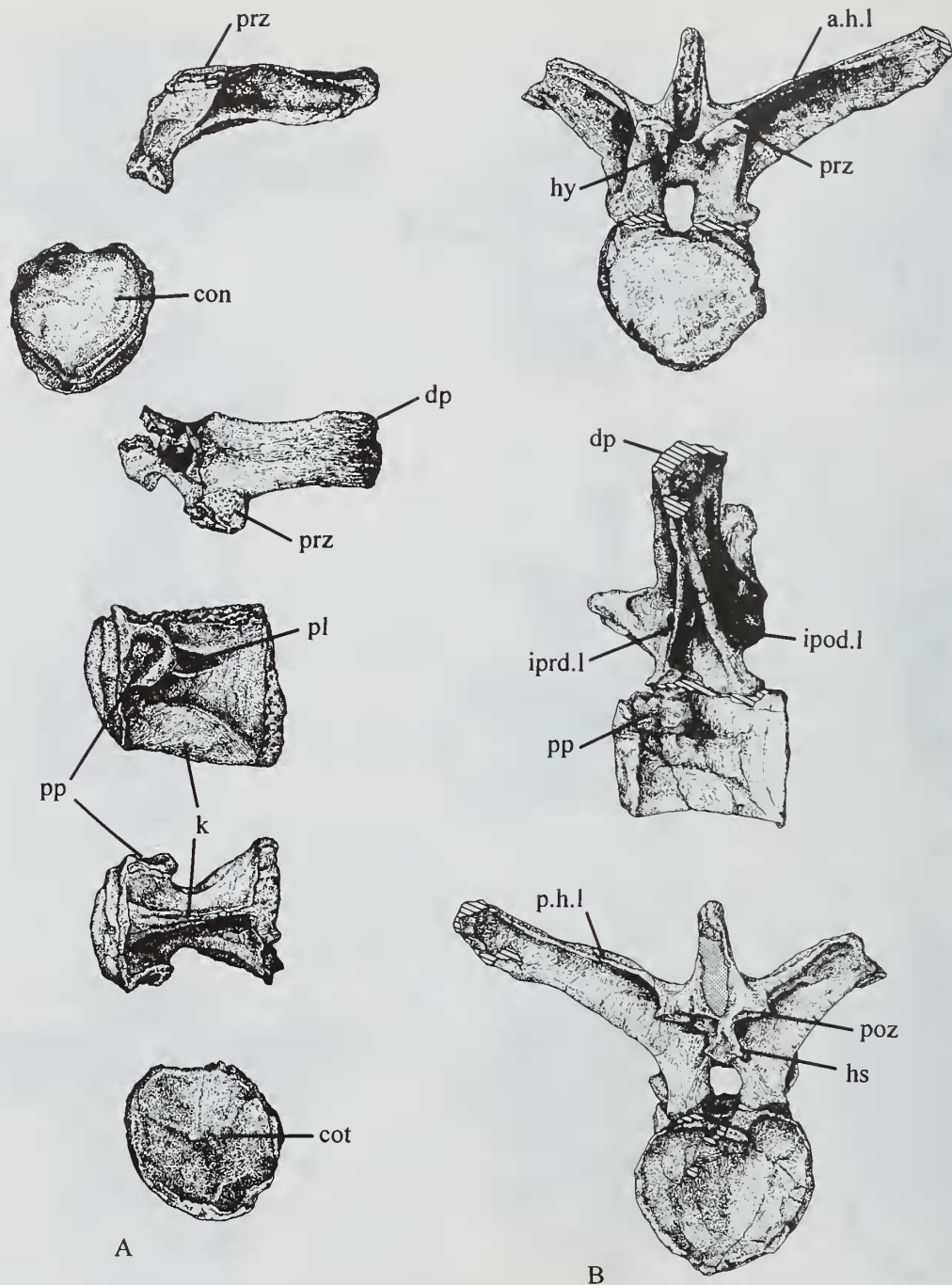


Fig. 23 *Baryonyx walkeri*, holotype, BMNH R9951; 4th and 5th dorsal vertebrae. A, D4 (from top downwards) centrum and left transverse process in anterior view; left transverse process in dorsal view; centrum in left lateral, ventral and posterior views. B, D5 in (from top downwards) anterior, left lateral, and posterior views. $\times 0.25$.

zygapophysis projects directly from the anterior edge of the dorsal surface of the transverse process. The condition in D1 cannot be seen, the relevant part of the vertebra having been broken off, but it is very noticeable in D2 and progressively less so in D3 and D4. In D5 the prezygapophysis has its own separate peduncle.

The distance (if any) between the posterior edge of the transverse process and the postzygapophysis, along the posterior horizontal

lamina, is yet another highly variable parameter. It is, however, impossible to quantify numerically because all the relevant surfaces and edges are rounded, so that there are no fixed reference points from which to take measurements. In D1-D3 there is a considerable (though diminishing) distance between these two structures. In D5-D7 the rear edge of the transverse process (viewed from the side) joins the postzygapophysis approximately at its middle. In D11 it

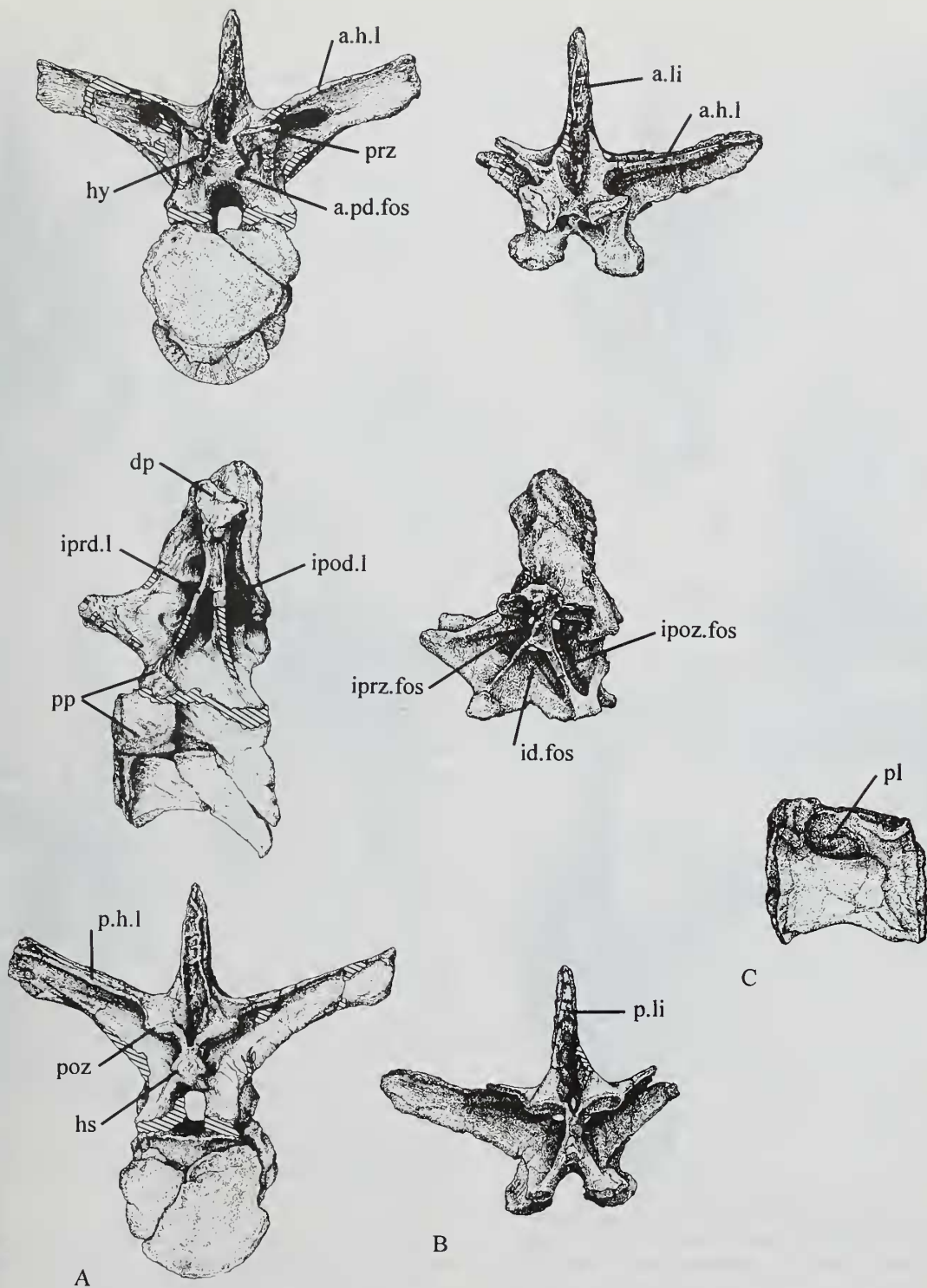


Fig. 24 *Baryonyx walkeri*, holotype, BMNH R9951; 6th-8th dorsal vertebrae. A, D6 in (from top downwards) anterior, left lateral, and posterior views; B, D7 neural arch and spine in (from top downwards) anterior, left lateral, and posterior views; C, D8 centrum in left lateral view. $\times 0.25$.

joins a little way forward of the mid-point, and in D14 it ends just in front of the postzygapophysis.

Baryonyx, like many other large dinosaurs, reduced its weight by developing fenestrations in its neural arches as well as pleurocoels in

its centra. These fenestrations occur in places where the mechanical stresses on the vertebra are not sufficiently great to require complete ossification of the skeletal structure. Essentially, these locations are around the base of the transverse process. Thus, at the proximal end

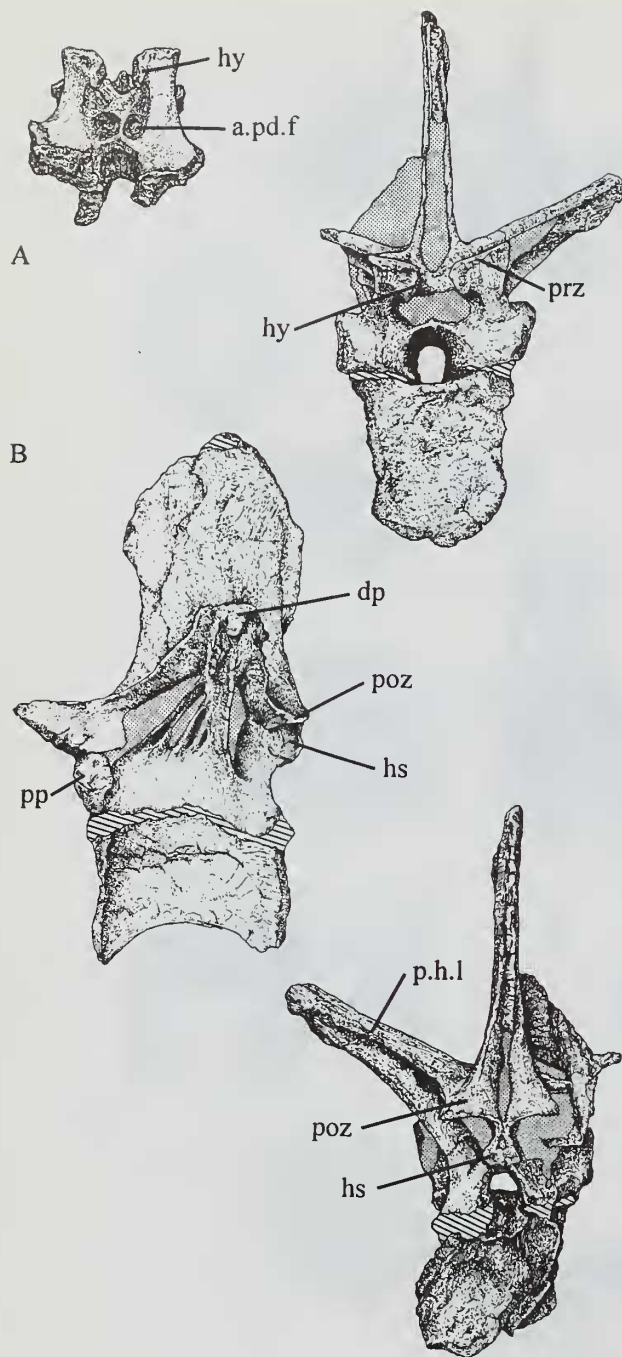


Fig. 25 *Baryonyx walkeri*, holotype, BMNH R9951; 10th-11th dorsal vertebrae. A, D10 neural arch fragment in anterior view; B, D11 in (from top downwards) anterior, left lateral, and posterior views. $\times 0.25$.

of its flat dorsal surface (i.e. at the base of the neural spine) there is what we might call a dorsal fenestration. Underneath the transverse process there are three ventral fenestrations, one at the apex of each fossa – an anterior, a middle, and a posterior – making four fenestrations altogether on each side of the vertebra.

In D4 and D5 the three ventral fenestrations only are present. In D6 and D7 there is also a dorsal fenestration, more pronounced in the

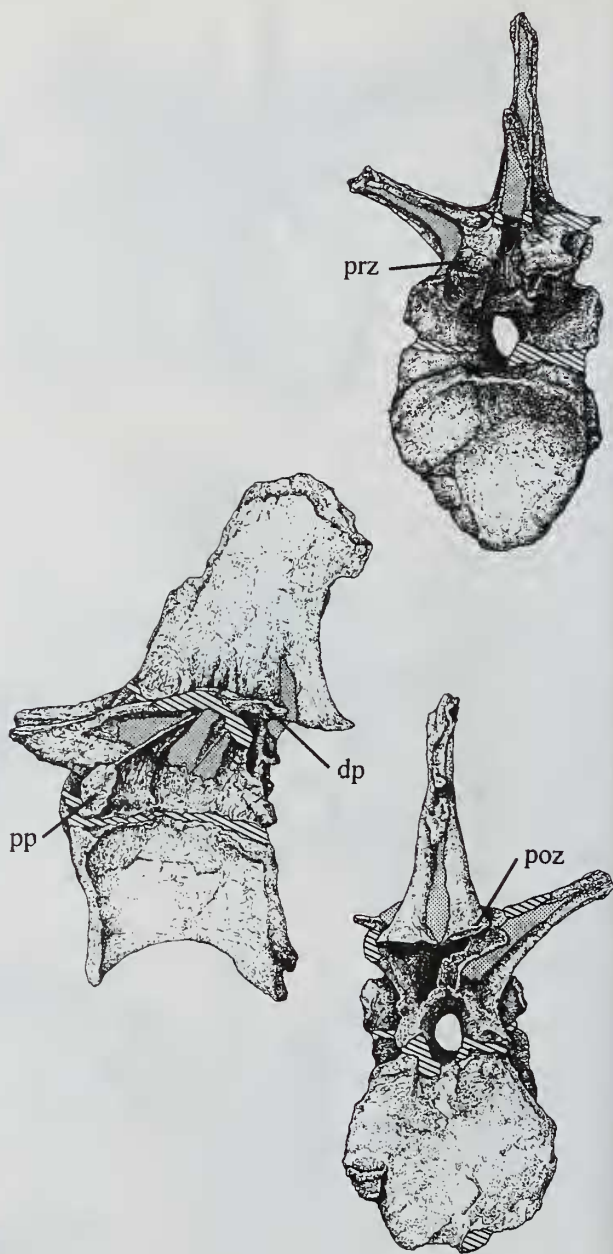


Fig. 26 *Baryonyx walkeri*, holotype, BMNH R9951; 14th dorsal vertebra in (from top downwards) anterior, left lateral, and posterior views. $\times 0.25$.

latter. In D10 the dorsal fenestration appears to penetrate the bone but the three ventral ones do not, for each corresponding fossa contains supplementary buttresses (see above). In D11 the dorsal fenestration is still present but the ventral fossae have not been fully prepared. In D14 the posterior (infrapostzygapophyseal) fossa is a deep pocket.

It is evident throughout the series that, in this specimen at least, the vertebral centra and the neural arches had not co-ossified. In some vertebrae centra and arches had remained together in their proper positions, in others they were still together but relatively

displaced to varying extents, and in yet others they were found completely separate. Their rugose sutural surfaces on either side were unmistakable and generally complete. This lack of co-ossification in the vertebral column confirms our observations on the skull and our suggestion that this particular individual might well be – despite its great size – a juvenile.

The neurocentral suture itself is invariably straight. In D1 the centrum and neural arch were found in their natural relative position. In D2 they are more or less in their proper position but have come slightly adrift. In D3 the neural arch has been tipped forwards by about 45° so that, though still in articulation anteriorly, posteriorly it is separated from the centrum by a wide gap. In D5, D6, D11 and D14 the two components had parted completely but have been re-assembled in the laboratory.

The neural spines increase steadily in height (see Table 1, p. 30) from 87 mm in D1 to 197 mm in D11 and 201 mm incomplete in D14. (There is one exception to this in the case of D5, which at 96 mm complete is shorter than either D2 or D3.) D1 is very slender in lateral view, and D2 and D3 are successively more slender still, all three measuring considerably less in an axial direction than their transverse thickness. D5, however, reverses this trend, and from there on, while the transverse thickness remains much the same, the axial length increases steadily. Thus, in D14 the axial length is four and a half times the transverse thickness. To summarize, the neural spines change from a short stout rod at the front of the series to a tall broad plate at the back.

There are prominent rugosities on the neural spines of D1–D5, projecting in front of and behind the spine itself and of more or less uniform width along its height. They represent the ossified portions of the interspinous ligaments. These have the effect of giving the spine a cruciform cross-section in D1, an appearance which is accentuated in D2. In D3 the cross is transversely wider but not so deep anteroposteriorly; each rugosity projects dorsally above the top of the neural spine proper so as to give a pronounced saddle-shaped appearance in lateral view. In D5 there are still slight rugosities, the anterior being better developed than the posterior; the anterior margin of the spine slopes obliquely posterodorsally, the posterior margin is more or less vertical, and the short dorsal margin is transversely narrow, horizontal, and almost flat. Behind this point there are no more rugosities.

In D6 the anterior margin of the neural spine curves forwards towards the top; the posterior margin is again vertical, in the same plane as the posterior face of the centrum. The top of the spine, however, is much wider than in D5, and in lateral view is pitched like a roof, its apex being appreciably behind its mid-point. D7 is very similar, a little wider still, but with the apex of the roof-like dorsal margin exactly central. The neural spine of D11 is again very similar but a great deal wider, with a more steeply pitched ‘roof’ and with a median flange-like projection on its posterior margin; its widest point is therefore at about half height. In D14 the anterior edge of the neural spine is badly damaged but the base of a forward projection remains; more dorsally there is a very pronounced posterior projection overhanging the postzygapophyses and high above them. This last dorsal vertebra is the only one in which the full height of the neural spine is not preserved, but, even so, it is higher than any of the others. There are no spine tables anywhere in the series.

Another variable character is the angle of inclination (to the horizontal) of the zygapophysial facets (see Table 2), which are usually tilted so as to face dorsomedially (prezygapophyses) or ventrolaterally (postzygapophyses). Again, it is not possible to make precise measurements, but our somewhat crude figures give a good indication of general trends. The inclination tends to decrease as we pass backwards down the series. Note that there can be large

variations between different parts of the column (7°–32°), between adjacent vertebrae (20°–27°), and even between the pre- and postzygapophyses of the same vertebra (7°–18.5°). Nevertheless, it might be supposed that the postzygapophysial angle of a given vertebra should match the prezygapophysial angle of the vertebra behind, with which it articulated. In four of the six cases where there are two adjacent vertebrae with measurable facets there is indeed a close correspondence, with discrepancies of 0.5°, 1°, 1.5° and 2°; another is not too big, at 4.5°; but the worst case is a discrepancy of 13.5°, between the axis and the supposed third cervical, which leads us to suspect that the latter may be badly distorted.

Table 2 Inclination of the zygapophysial facets.

	A	B
Ce2 (axis)	–	18.5°
Ce3	32°	26.5°
Ce5	24°	19.5°
Ce6	20°	15°
Ce8	21°	25.5°
D1	–	20°
D2	24.5°	27°
D3	28°	30°
D5	14°	12°
D6	10.5°	17.5°
D7	15.5°	12°
D10	12°	–
D11	17.5°	7°
D14	7°	18.5°
unnumbered caudal	–	21°

A, angle of inclination of prezygapophysial facets (facing dorsomedially); B, angle of inclination of postzygapophysial facets (facing ventrolaterally).
The angle given is the angle between the zygapophysial facet and the horizontal plane, rounded off to the nearest half-degree. Where measurements can be made on both members of a pair of facets the figure quoted is the mean of the two.

In all but the most anterior dorsals of *Baryonyx* a hyposphene and a hypantrum are well developed. The hyposphene is a large solid median projection between and below the postzygapophyses. Seen from behind it is triangular, with the apex pointing upwards, and on either side a large semilunar facet is directed dorsolaterally. The hyposphene as a whole fitted neatly into the gap between the prezygapophyses of the succeeding vertebra, where its facets articulated with the hypantrum; this latter comprises a pair of similar semilunar facets on the medial sides of the prezygapophysial peduncles, directed ventromedially.

In D1 the prezygapophyses are not preserved, in D2 they are very widely separated, and in D3 slightly less so. It is obvious, therefore, that hypantra were absent. In all three of those vertebrae the hyposphene, if present at all, is the merest rudiment and could not have been functional. In contrast to this, both hyposphene and hypantrum are well developed in D5 and – as far as the state of preservation will permit us to determine – from there on throughout the rest of the dorsal series to D14. Although the hyposphene of D14 is broken off, enough of it remains to indicate unequivocally that there must have been a hypantrum on the first sacral vertebra.

In vertebrae D6–D10 (and perhaps D11) there is a pair of conical pits (peduncular fossae) on the anterior face of the neural arch, immediately above the opening of the neural canal and medial to the bases of the prezygapophyses. In D6 they are fairly widely spaced, circular and shallow. In D7 they are closer together and deeper. In D10 they are very close together, larger and deeper still. Similar pits are present in *Allosaurus* in vertebrae D9–D14, D12 excepted; they are developed best in D9.

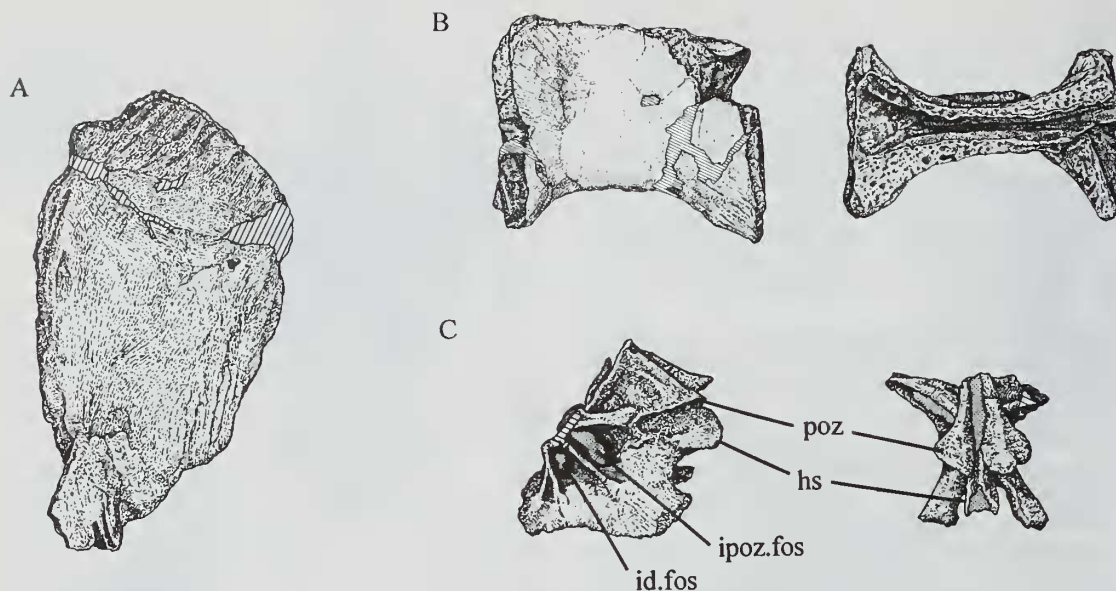


Fig. 27 *Baryonyx walkeri*, holotype, BMNH R9951; sacral/proximal caudal vertebrae. A, neural spine in left lateral view; B, proximal caudal centrum (aB) in left lateral and dorsal views; C, fragment of neural arch of proximal caudal vertebra, in left lateral and posterior views. $\times 0.25$.

CAUDAL REGION (Fig. 27). This region is represented only by the remains of six centra and one neural arch, together with two incomplete neural spines that almost certainly pertain to proximal caudals (or possibly sacrals).

Three isolated centra, though large, show no signs of any parapophyses, diapophyses, buttressing laminae, sacral ribs or pleurocoels. Further, the neural canal running along the dorsal surface of each is very narrow. Taken together, these characteristics suggest that the centra represent proximal caudals. On one of them (referred to below as CaB) the ventral rim of the posterior face is not curved but flattened, as is characteristic of proximal caudals.

There is no way in which the order of these three proximal caudal centra could be determined; indeed, there were probably more than three altogether. We refer to them here simply as Caudal A (CaA), Caudal B (CaB) and the partial Caudal C (CaC), the lettering having no significance as to their place in the vertebral succession.

These centra are of similar diameter to that of the last dorsal, D14, but are much longer; indeed, they are very much longer (134, 144 and 140 mm respectively) than any of the presacral centra (longest preserved is the eighth cervical at 120 mm). Their available measurements are listed in Table 1 (p. 30). They are very strongly 'waisted', with moderately amphicoelous ends; the anterior face is vertically oval (contrast the dorsal centra) and the posterior face is more or less circular. Two of them are reasonably complete up to the virtually straight neurocentral suture and still possess much of the rugose sutural surfaces for the neural arch; the third is only partial, lacking most of the posterior end.

Fragments of three other caudal centra are preserved. The largest consists of the posterior part of a centrum, showing an almost complete articular face measuring 65 mm transversely and an estimated 76 mm vertically. The middle of the face is somewhat hollowed out and its ventral portion bears a large and slightly eroded haemapophysial facet. Enough of the body of the centrum remains to show that it was hollow and strongly waisted and had a somewhat flattened ventral surface.

The other two fragments are too poorly preserved to merit description, but are recognisable as caudals by their small size and flattened ventral surfaces.

An isolated, incomplete, but well-preserved neural arch (Fig. 27C) was found, which can only represent a proximal caudal vertebra, but it does not fit on to any of the proximal caudal centra described above. The posterior edge of its transverse process is well separated from the anterior end of the postzygapophysial facet; in this it resembles the anterior dorsals (for example, D3) and is quite unlike the posterior dorsals, in which those two structures are contiguous. On the other hand, in other characters it is not unlike the posterior dorsals. These are the length of the fragment, which, at approximately 100 mm, is much longer than the total length of the centrum in D3-D8; the infradiapophysial laminae, which are well developed and enclose a deep infradiapophysial fossa; and the powerful hyposphene, which projects farther posteriorly than the postzygapophyses themselves. In any case, the total width across the postzygapophysial facets is only 52 mm, much less than in any dorsal vertebra and they lie in a more or less horizontal plane. Also to be noted is the fact that the ventral margin of the arch, which appears to be complete and to represent the neurocentral suture, curls upwards at the back like the prow of a boat. (For nearest comparison see Welles on the proximal caudals of *Dilophosaurus*, 1984: 124 ff).

A very large, flattened plate of bone, undoubtedly a neural spine, was found (Fig. 27A). It is much larger than any of the neural spines of the dorsal vertebrae as preserved. Another, smaller and less complete fragment of similar form was also found. The anteroposterior length of the larger spine is 142 mm, which is much the same length as the two longer proximal caudal centra (CaB 144 mm, CaC 140 mm) and is therefore very much longer than any other centrum preserved. Both spines were found in Block 43, from the pelvic region of the skeleton, and both possess a characteristic projection (see below) from the posterior or posterodorsal border, not unlike that described above for vertebra D14 (the last dorsal). These

characters, taken together, suggest that the spines in question are from the proximal caudal region of the *Baryonyx* vertebral column or from the otherwise unknown sacral region.

The larger spine is transversely very thin and has blade-like edges; it widens towards its distal end, which may not be quite complete. In lateral view its dorsal profile slopes upwards from either end towards an apex that is situated somewhat behind its middle. From the centre of the posterior part of that profile a symmetrically rounded swelling projects to a distance of about 13 mm. Towards the ventral break of the spine, on its posterior margin, there remains the base of the ridge that ran down towards the right postzygapophysis. Only the dorsal portion remains of the smaller spine; it is about two-thirds the linear dimensions of the larger, is thicker and has a more rectangular distal end. The posterior swelling lies more ventrally than in the larger spine, on what we presume to be the posterior profile.

Ribs

There are numerous rib fragments, mostly of the vertebral ribs but some abdominals too. Many are simply broken pieces of shaft and do not merit description.

VERTEBRAL. These we have arbitrarily classified, for purposes of description, into four groups:

1. Cervical ribs (the left rib of the axis, plus three others, all from the left side, of which only one is complete).
2. Slender uncinat ribs (two) that we tentatively assign to the anteriormost part of the dorsal series (probably D1 and D2).
3. Large, stout non-uncinate ribs (many) that clearly formed the greater part of the dorsal series (probably D3-D11).
4. Significantly smaller, slightly twisted ribs that we assign to the posteriormost part of the dorsal series (probably D12-D14).

CERVICAL RIBS (Fig. 28). The complete cervical rib is of typical 'crocodiloid' form and is tetradial in dorsal aspect. The body of the element is canoe-shaped; a short anterior process tapers forwards and curves mediad, a longer posterior process tapers backwards and is virtually straight. The capitulum and tuberculum are short and stout, with a deep pneumatic pocket between their bases. This is not at all like the cervical ribs of *Allosaurus*, which are typified by a long, ventrally directed spine.

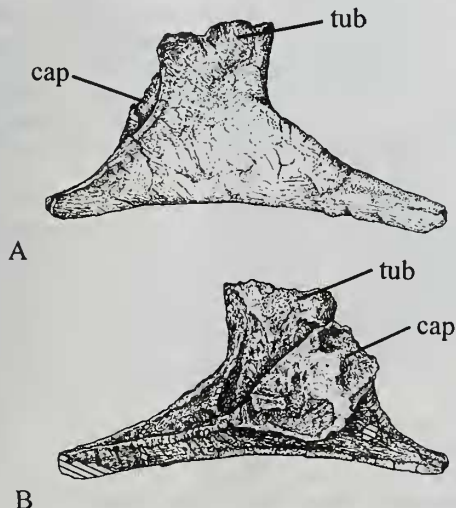


Fig. 28 *Baryonyx walkeri*, holotype, BMNH R9951; left cervical rib. A, lateral view; B, medial. $\times 0.25$.

A fragment of a more posterior cervical rib bears a laterally directed uncinat process, with a pneumatic pocket medial to it as well as the pocket on the medial side of the element. The posterior process is broken off but appears to have been more or less straight.

DORSAL RIBS (Fig. 29). We consider the 'Group 2' ribs to belong to the right side of D1 (first dorsal vertebra) and to the left side of D2 (second dorsal). Each possesses a prominent, keel-like uncinat process on its lateral surface, just below the junction of capitulum and tuberculum (the first dorsal rib of *Sinraptor* also has a vestigial uncinat process). On the medial surface, a short way proximal to this, is a deep circular pit with sloping sides; it lies closer to the posterior margin than to the anterior margin.

The best-preserved, typical ('Group 3') dorsal rib is of the right side and probably belongs to D3 (third dorsal). This robust element comprises a lightly curved shaft, 205 mm as preserved, that terminates dorsally in a short tuberculum; just below the tuberculum a relatively long capitulum diverges medially from the shaft at almost a right angle. (Unfortunately none of the three processes of this triradial bone is complete right to its end.) The ventral profile of the capitulum and the medial profile of the shaft do not form a single smooth curve; the change in direction occurs mainly around the junction. The shaft tapers distally and its distal region is distinctly twisted so that the surface that faces anterolaterally above faces directly anteriorly below. The posteromedial surface of the shaft bears a deep, wide groove that confers an L-shaped cross-section upon the proximal region of the shaft but tapers out distally. The capitulum is subtriangular in section, with a sharp dorsal margin and a stout, rounded ventral margin; its anterolateral surface has a shallow depression running centrally along its length. The medial surface of the tuberculum bears a prominent vertical buttress that disappears ventrally at the junction.

We tried to assign the other ribs in this arbitrary grouping (D4-D11?) to articulation with particular vertebrae but they are too incomplete to be ordered reliably.

The more posterior rib-heads ('Group 4', probably referable to D12 and D13) resemble those of other theropods in that they bear a long capitulum and a very short tuberculum. The tuberculum is reduced to a mere stub less than 20 mm long. There is no intercostal web of bone between the two heads. The presumed last dorsal rib, D14, is short (shaft length 194 mm from a point in the axil between the two rib-heads); its shaft is slender, flattened, convex, almost spatulate distally, with thin edges and a laterally directed tip.

ABDOMINAL (GASTRALIA). Several fragments are preserved. In general, they are pieces of slender, gently curved, tapering shafts, longitudinally grooved on the dorsal surface for articulation with the succeeding element. A few fragments, the two longest being 230 mm and 190 mm, have flattened, spoon-shaped, slightly twisted ends; these are similar to the medial ends of the same elements of *Sinraptor* (Currie & Zhao 1993), which articulate with the gastralia from the opposite side of the body. There are not enough gastralia fragments to determine the number of segments per side (*Sinraptor* has three; tyrannosaurids, *fide* Lambe 1917, have only two).

Chevrons (haemapophyses) (Fig. 30)

Five haemapophyses were found, four of them of very similar size and the fifth somewhat larger. All save one have lost varying amounts of their distal ends.

The one complete haemapophysis is 190 mm long and of fairly typical form. The paired facets which articulated with a caudal

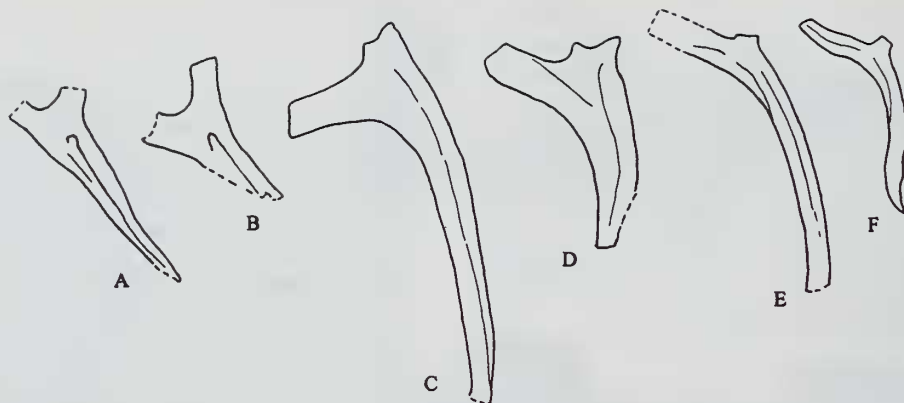


Fig. 29 *Baryonyx walkeri*, holotype, BMNH R9951; isolated dorsal ribs; A, B, anterior; C, D, mid-dorsals; E, F, posterior. $\times 0.17$.

vertebrae are united by a bridge, producing a saddle-shaped proximal end. The paired anterior processes found in *Dilophosaurus* and *Allosaurus* are altogether absent here, in which respect *Baryonyx* resembles *Ceratosaurus*. The distal portion of the bone, beyond the point of union of the two sides, is transversely flattened and expanded into a blade-like structure with a straight anteroventral margin and a concave posterodorsal margin.

Sternum (Fig. 31C)

A fragile plate of bone, in some places no more than 1 mm thick, has broken edges nearly everywhere. However, it is strongly ridged like a tile from the ridge of a pitched roof, with two smooth surfaces lying at an angle of some 40° to one another, suggesting that the fragment is a single median element with a median angulation. At what appears to be its anterior end the bone is considerably thickened; each half has a convexly curved anterior termination, and between the two is a median embayment. Part of the right-hand edge is a true margin which runs diagonally to the midline, thereby indicating that the bone originally widened rapidly towards its thickened posterior end.

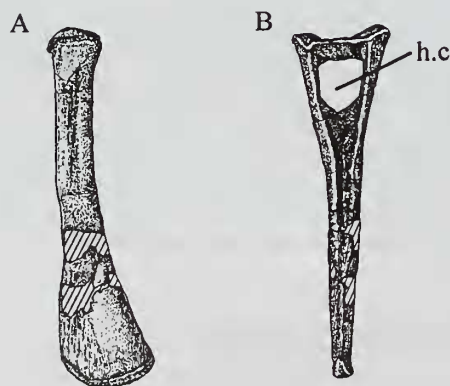


Fig. 30 *Baryonyx walkeri*, holotype, BMNH R9951; isolated haemapophysis. A, left lateral; B, posterior. $\times 0.25$.

Sternal elements have seldom been reported in theropods. In *Sinraptor* (Currie & Zhao 1993) a fragment of a broad plate with a median ventral ridge was found. Some other theropods, e.g. *Carnotaurus* (Bonaparte *et al.* 1990) and *Albertosaurus* (Lambe 1917), have paired, unfused sternals; this could be related to immaturity. The fusion of paired plates into a single median element in *Baryonyx* (despite the lack of co-ossification of the various components of the skull and vertebrae) might suggest the contrary, that the animal was fairly mature.

Pectoral girdle

SCAPULA (Fig. 31A). Both scapulae are preserved incomplete. Whereas the base of the left scapula lacks only part of the acromion process, the base of the right scapula is missing entirely, being broken off transversely a short distance above the glenoid. Both scapulae also lack the dorsal end of the blade, the right seeming to be almost complete distally but its partner rather less so. The following description is based on both.

The scapula is typically theropod in most respects, somewhat curved in anterior or posterior view to fit the shape of the body. The blade is long and strap-like with subparallel sides, although its distal (i.e. dorsal) end is slightly expanded. It is robustly constructed, with rounded edges; the anterior edge is a little thicker than the posterior. The blade thins somewhat dorsally and the edges become sharper, more truly blade-like.

Ventrally the blade expands greatly; it expands anteriorly into the thin (and broken off) acromion process, while the posterior edge thickens gradually in a mediolateral direction. At the same time it expands posteriorly, terminating in the backwardly directed scapular portion of the glenoid fossa and, adjacent thereto, in the ventrally directed facet for the coracoid. The glenoid facet is shaped like a deep inverted U, while the coracoid facet is broad and robust beneath the glenoid but tapers anteriorly towards the acromion process. A straight, distinct ridge is formed where these two facets meet at an angle of about 45° .

In lateral view the ventral margin of the scapula, where it sutures with the coracoid, forms a shallow single zigzag which is reflected exactly in the corresponding dorsal margin of the coracoid (see below).

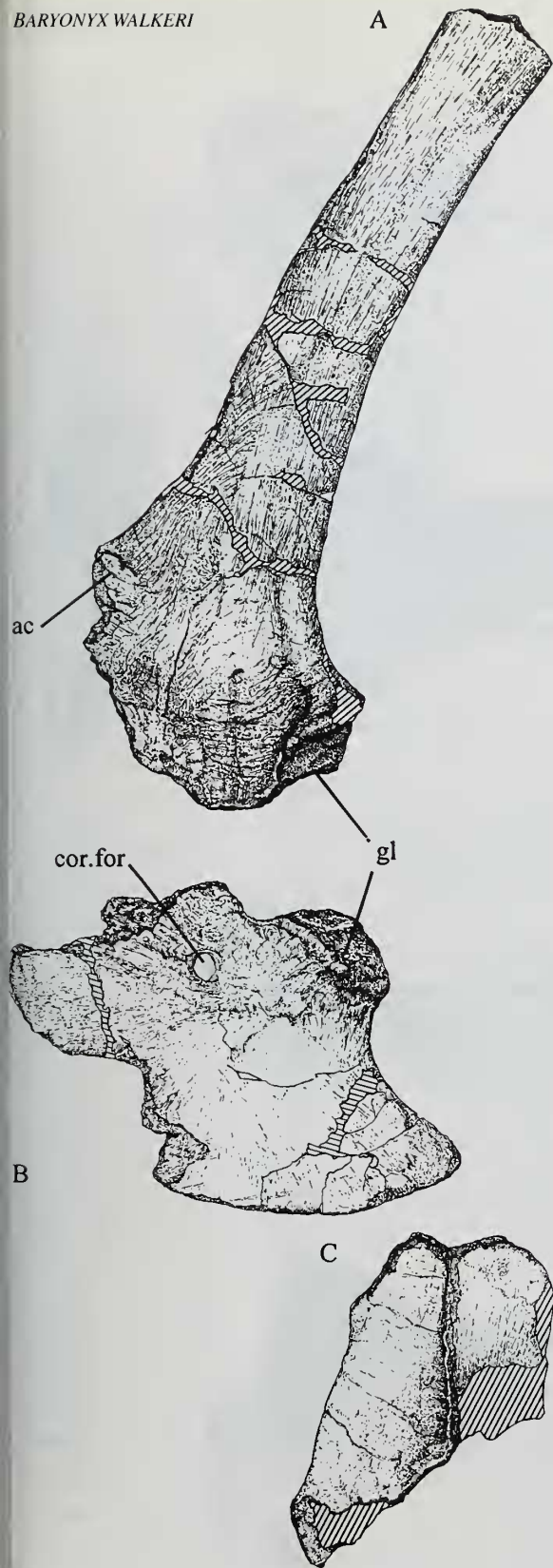


Fig. 31 *Baryonyx walkeri*, holotype, BMNH R9951; elements of pectoral girdle, including sternum. A, left scapula in lateral view; B, left coracoid in lateral view; C, sternum in ventral view. $\times 0.25$.

The thickened posterior edge of the lower part of the scapula, as it approaches the glenoid, bears a low but distinct muscle ridge running parallel to its lateral margin (Welles' 'slight rugosity', 1984: 127).

CORACOID (Fig. 31B). Both coracoids are preserved, but in neither has the anterior region escaped damage. The whole of this region is missing in the right coracoid; in the left, however, sufficient remains to determine its anterior extent but not the shape of the margin.

As usual in theropods, the plate-like coracoid is medially concave and laterally convex, continuing the line of curvature of the adjacent scapula. The perfectly preserved posterior region is shaped like a hatchet and projects directly backwards, not at all towards the midline as in some other theropods. The robust articular region bears dorsally the semicircular glenoid facet and the pear-shaped sutural surface for the scapula, its junction with the medial surface being marked by a prominent rugose ridge. As mentioned above, the line of articulation between scapula and coracoid is zigzag-shaped in lateral view. Ventral to this articulation the coracoid plate is perforated by the coracoid foramen, circular in lateral exposure, pear-shaped in medial exposure and approximately 25 mm in diameter.

Fore-limb

As is typical of theropods, all three major bones are short, relative to the general size of the animal; but they are also remarkably robust and wide, relative to their shortness, with stout shafts and broadly expanded ends.

HUMERUS (Fig. 32). The left humerus is essentially complete, although the medial side of the shaft is somewhat crushed. The right humerus shows a similar state of preservation, but lacks almost the whole of the ectepicondyle (ulnar condyle). The element is 463 mm long (Charig & Milner 1990).

The first impression is of a stout and stubby bone, with two broadly expanded ends connected by a straight and relatively short shaft; the maximal width of the proximal end is 242 mm and of the distal end 183 mm. The two ends, however, are flattened to a significant degree; the distal expansion, in particular, appears very thin in end view. The plane of the distal expansion is offset with respect to that of the proximal expansion by some 30°. At the proximal end there is considerable expansion of the deltopectoral crest on the anterior side, and a greater expansion of the internal tuberosity (the entotuberosity of Welles 1984) on the posterior side. Although the deltopectoral crest projects from the anterior side of the bone, its apical portion is bent round anteromedially so that the lateral surface of the proximal expansion is distinctly convex and its medial surface correspondingly concave.

The distance between the upper end of the humerus and the apex of the deltopectoral crest is approximately 43% of the entire length of the element, while the deltopectoral crest as a whole constitutes 51% of that length. Between the deltopectoral crest and the internal tuberosity lies the head of the humerus, a thickened region that articulated with the glenoid. On the medial surface of the proximal expansion, about half-way between the head and the apex of the deltopectoral crest, is a distinct ridge some 35 mm in length running along a line that is directed towards the centre point of the shaft. This ridge, which is clearly present on both humeri, is a rounded hump distally and tapers proximally to become lower and narrower as it approaches the edge of the bone. To the best of our knowledge, no similar structure has been found elsewhere; it may be a prominent insertion for the pectoralis muscle.

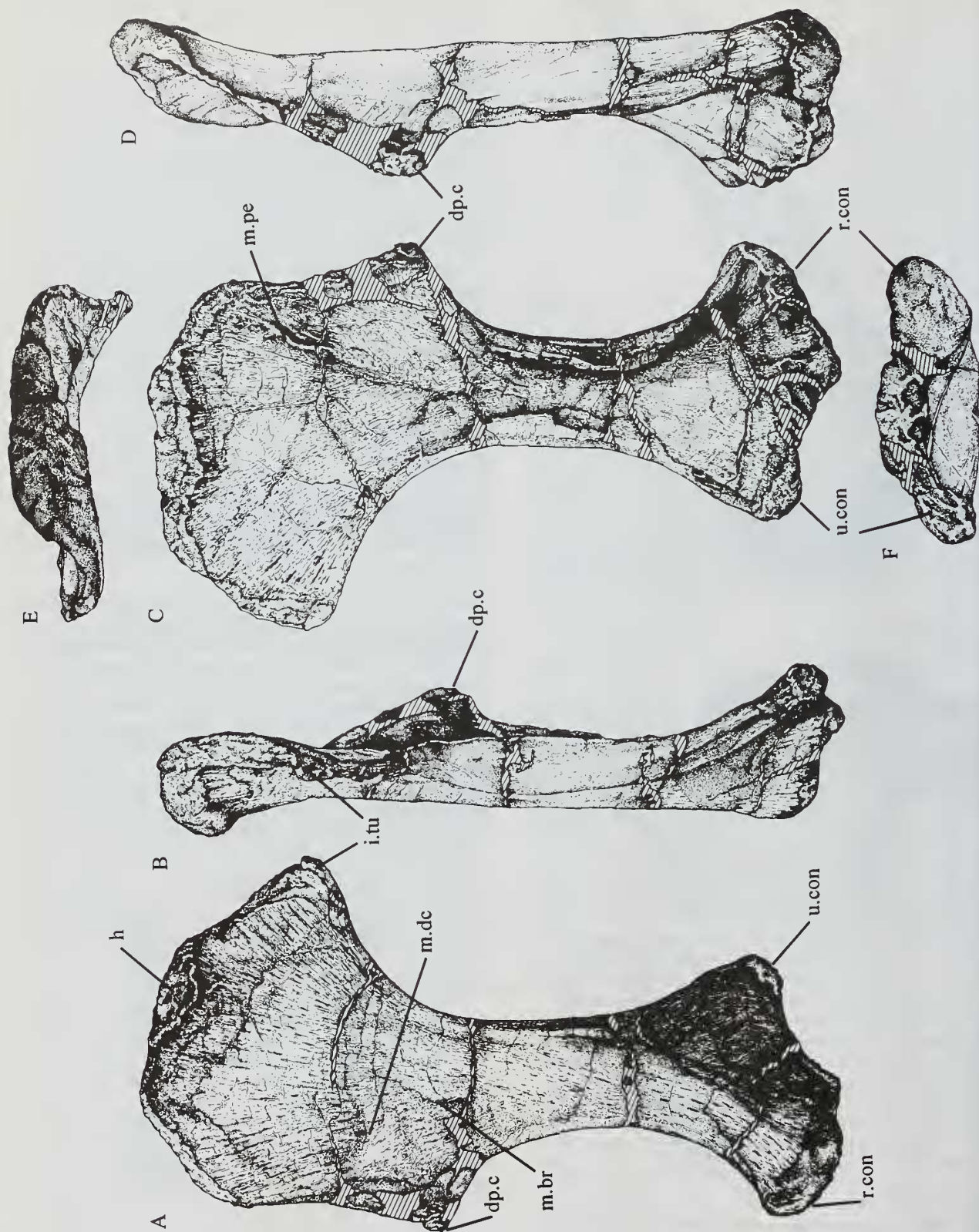


Fig. 32 *Baryonyx walkeri*, holotype, BMNH R9951: left humerus. A, lateral view; B, posterior; C, medial; D, anterior; E, proximal; F, distal. $\times 0.25$.

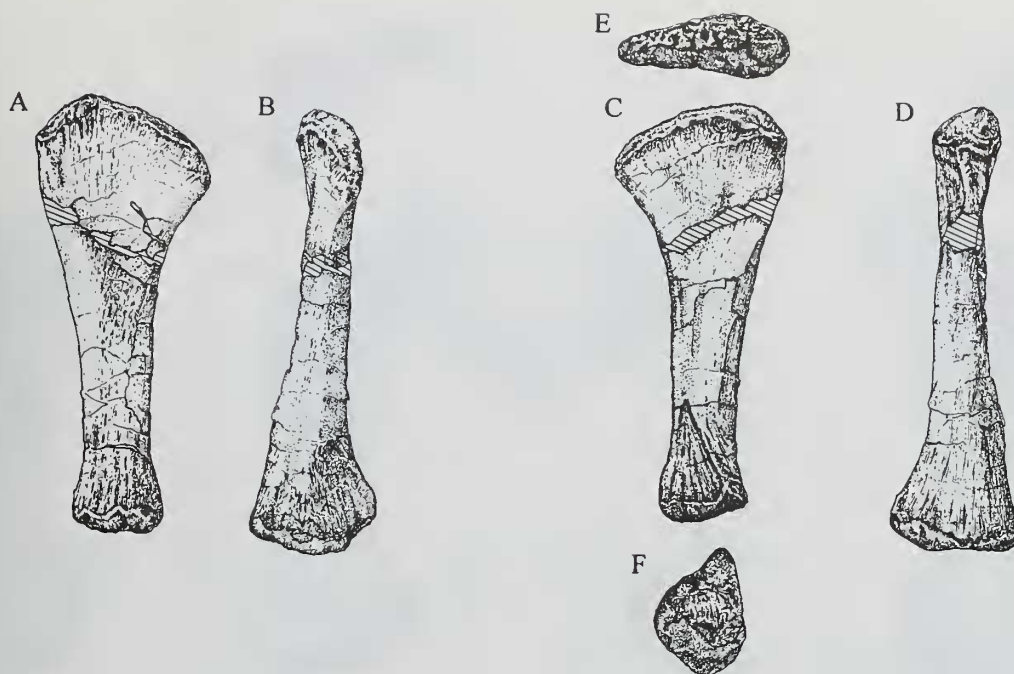


Fig. 33 *Baryonyx walkeri*, holotype, BMNH R9951; left radius. A, lateral view; B, posterior; C, medial; D, anterior; E, proximal; F, distal. $\times 0.25$.

On the lateral side of the proximal expansion, where it begins to narrow into the shaft, are two obvious areas of muscle attachment. Immediately posterior to the apex of the deltopectoral crest is a low, slightly rugose hump; this is presumed to have been the point of insertion of the *deltoideus clavicularis* muscle (cf. Norman 1986: 338). A little lower down and more posterior in position, indeed almost in the centre of the lateral surface, is a large shallow depression with a distinct raised border below and on either side; this probably served as the point of origin of the *brachialis* muscle (cf. Norman 1986, *loc. cit.*).

At the distal end of the humerus the ectepicondyle is well expanded. The lower margins of the entepicondyle and the ectepicondyle form an angle of approximately 45° with each other, and their facets for articulation with the radius and ulna respectively are subequal in length (the ectepicondylar facet being just a little longer). In *Dilophosaurus* the humeral shaft is less straight than in *Baryonyx*, and in *Allosaurus* it is even more curved. The two ends are more offset in *Dilophosaurus* than in *Baryonyx*.

RADIUS (Fig. 33). Both radii are preserved, the left complete but the right lacking a section of the shaft so that the two ends are no longer connected. The radius is a short, straight, stout bone, not distinguished by any remarkable features. It is 225 mm long and therefore only 49% of the length of the humerus. The proximal end is flattened and expanded, its profile being convex in side view; it tapers smoothly into the roughly cylindrical shaft, which continues to taper slightly until it reaches the less expanded distal end. The latter differs from the proximal end in that it is narrower and not flattened; in end view it appears triangular with one corner extended, the longest side (in the plane of expansion) being almost perpendicular to the plane of flattening and expansion of the proximal end. The distal end-surface is perpendicular to the axis of the bone and has a shallow convexity at its centre.

ULNA (Fig. 34). Only the left ulna is preserved, almost complete and 283 mm long; thus it is considerably longer (61% of the length of the humerus) than is the radius. The ulna, unlike the radius, is distinctly bowed. The proximal end bears an unusually powerful olecranon, projecting posteromedially beyond the head of the bone. The articulating surface for the humerus projects anteriorly (making an angle of about 130° with the olecranon projection when viewed from the proximal end) and has a concavely curved anterior profile distal to its apex. The lateral surface of the proximal end actually consists of two surfaces, one facing obliquely forwards and the other obliquely backwards so that they together make a right angle. This angle forms a powerful projection which, unfortunately, has been severely damaged.

The most unusual feature of the ulna is the broad expansion of the distal end. This is essentially in the transverse plane, but the greatest part of the expansion is on the medial side where the bone has been extended anteromedially and, at the same time, somewhat dorsally. Although this medial expansion is distinctly more slender than the central part of the ulna, the bone thickens again towards the medial margin so that the articulating surface is of almost constant width. There is also a rather less prominent anterolateral expansion of the lateral side, but here the bone becomes appreciably thicker, so that this part of the articulating surface is virtually semilunate. The distal profile of the ulna, in anterior or posterior view, is markedly convex.

CARPUS. No recognisable remains of the carpal bones are preserved.

MANUS (Figs 35, 36). The metacarpals too have all been lost, but a few phalanges are preserved (including three unguals), and some are in excellent condition. They include the original and famous 'Claw', i.e. a huge ungual, together with what is probably the phalanx with which it articulated; three phalanges found in articulation

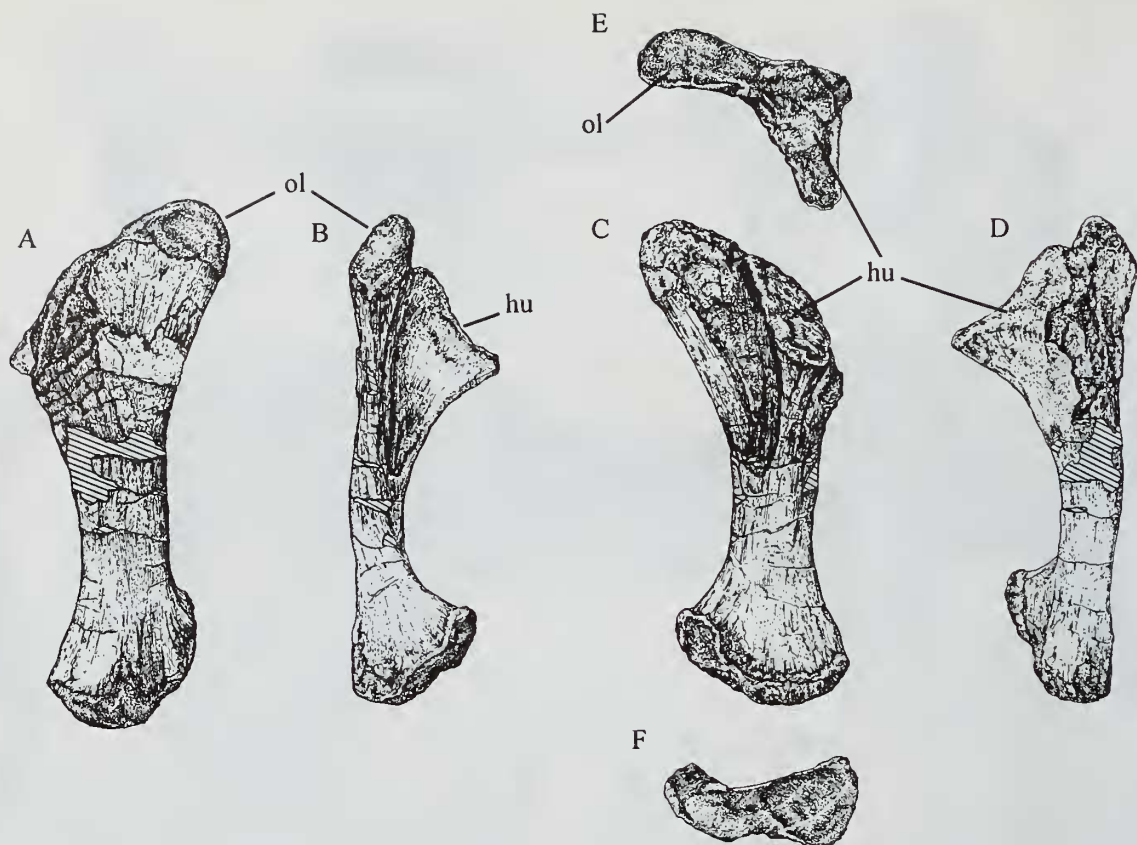


Fig. 34 *Baryonyx walkeri*, holotype, BMNH R9951; left ulna. A, lateral view; B, posterior; C, medial; D, anterior; E, proximal; F, distal. $\times 0.25$.

with each other, of which the most distal is a much smaller ungual; and another four, less complete phalanges. Also preserved are a few more small phalanges which are too incomplete and indeterminate to merit description.

We assume that *Baryonyx* possessed the typical theropod phalangeal formula of 2 : 3 : 4 : (1 vestigial or 0) : 0.

Before describing these phalanges it was desirable to determine:

1. Whether they belonged to the manus or the pes. Non-ungual phalanges from the theropod manus are generally smaller than those of the pes; this comparison, however, requires manual and pedal phalanges from the same individual. Unguals from the manus are more strongly curved than those on the pes. When non-unguals and unguals are found together in articulation, these two indicators should reinforce each other. The precise location of the phalanges within the excavation is another source of helpful information; for example, the only articulated digit found was in Block 27b, which, lying at the head end of the 'dig' (see Fig. 49) and containing also part of the left scapula, was more likely to contain parts of the manus than the pes.
2. Which side they belonged to, left or right. Recognition of which side of the phalanx is medial and which is lateral enables us to determine whether the element in question is from the left side or the right. A study of theropod phalanges illustrated in the literature (e.g. *Allosaurus* figured by Madsen 1976, pls 43 and 44) shows that the lateral profile of each non-ungual phalanx is almost parallel to the sagittal plane but the medial profile is

inclined obliquely, in such a way that the distal breadth is significantly broader than the proximal. Further, a longitudinal groove divides the distal end into two condyles in such a way that the lateral condyle is slightly wider than the medial. As for the unguals, the articulation for the adjacent phalanx is divided into two subequal facets, inclined obliquely to each other and separated by a ridge which begins in a dorsal swelling and then runs ventrally; the swelling and the ridge are a little closer to the lateral margin than to the medial. There is also a slight tendency for the distal tip, in dorsal or ventral view, to be very slightly curved towards the lateral side.

3. Which digit they belonged to and their position within the digit.

Evidence of this nature suggests that all the well-preserved phalanges are of the left manus.

LEFT DIGIT I (POLLEX) (Fig. 35). The attribution of the huge ungual to digit I is no more than a common-sense presumption based on its large size. Indeed, the large size is the only unusual feature of this claw-bone, which measures 310 mm in length around the curved dorsal margin. (The keratin sheath of the claw itself would have been considerably longer.) The slightly eccentric position of the dorsal swelling between the twin facets of the phalangeal articulation suggests that this ungual may be attributed to the left side. The arc of curvature is larger than in an *Allosaurus* of comparable size, i.e. it is less strongly curved. Otherwise this element is a fairly typical theropod ungual of average proportions, almost perfectly bilaterally

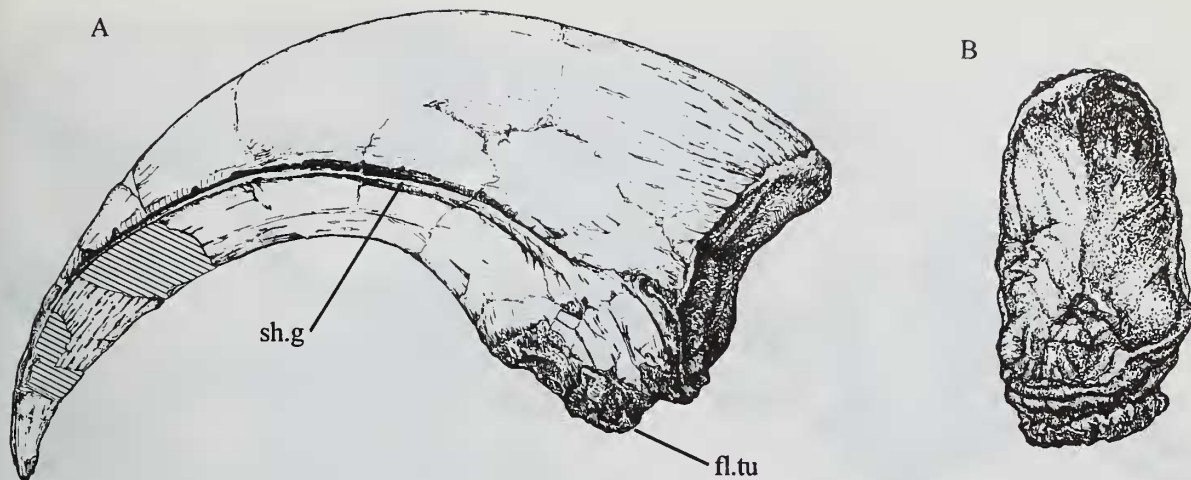


Fig. 35 *Baryonyx walkeri*, holotype, BMNH R9951; ungual attributed to left digit I (pollex). A, lateral view; B, proximal. $\times 0.5$.

symmetrical, very little compressed, smoothly rounded along its length, and sharply pointed. Grooves for the horny sheath run right to the tip, and the flexor tubercle is pinched off more sharply on the medial side than on the lateral.

A distal end of another large phalanx, broken on one side, is probably part of the first phalanx of the same digit. If so, it is with this element that the large ungual articulated. It appears to be a left phalanx, and it compares well with the articulated phalanx described immediately below as the first phalanx of left digit II or the second of left digit III. It has a deep groove between the two condyles, the medial condyle projects obliquely and has a very distinct ligament pit, and the lateral condyle is broken off almost entirely.

LEFT DIGIT II OR III (Fig. 36). The three phalanges that make up this digit were found in articulation; they might be either an entire digit II, or a digit III lacking its basal phalanx. We can try to resolve this dilemma by comparing the bones with the corresponding elements of *Allosaurus* and other theropods. The greater length of the phalanges suggests digit II. On the other hand, the proximal end-surface of the most proximal phalanx of the three (II_1 or III_2 ?) does not have the somewhat irregular, single-faceted form characteristic of a basal phalanx (which would articulate with the distal end of metacarpal II) but has instead the double-faceted form typical of a non-basal phalanx (which would articulate with the pulley-like distal end of phalanx III_1). These elements, in most respects, are standard for a theropod; the ungual, unlike its neighbour on digit I, is not enlarged, its length being estimated (it lacks its tip) at 165 mm. The middle phalanx of the three is appreciably shorter (91 mm) than the most proximal (132 mm). This contrasts with the condition in digit II of *Allosaurus*, where the second phalanx is very slightly longer than the first (Madsen 1976, pl. 45), and in *Deinonychus*, where it is considerably longer (Ostrom 1969: 104). Again, the elements are almost perfectly symmetrical, but a few minor asymmetries indicate that we are here dealing with a finger of the left hand. The most pronounced asymmetry is seen in distal view, where the lateral profile is almost parallel to the sagittal plane but the medial profile is inclined obliquely.

RIGHT UNGUAL II OR III. This element is poorly preserved, it lacks its distal half and its proximal end is badly damaged. Nevertheless, it is apparent that it is a damaged mirror-image of the ungual

attributed to left digit II or III, and is therefore identified as the corresponding right ungual.

RIGHT DIGIT III OR IV. One of the smaller phalanges (length 65 mm) is presumably from a digit III or IV, and the obliquity of its medial profile in dorsal aspect indicates that it comes from the right side.

Pelvic girdle

ILIUM (Figs 37, 38). Only the right ilium is preserved. The remains consist of four substantial unconnected fragments of bone and one natural mould:

1. The pubic peduncle, with the anterior third of the acetabulum.
2. The ischiadic peduncle, with the posterior two-thirds of the acetabulum (there can be no more than a narrow gap between this and fragment no. 1).
3. A large part of the anterior portion of the iliac blade, albeit with no natural edges.
4. Part of the posterior process, with the brevis shelf and brevis fossa, and a large part of the iliac blade dorsal to it.
5. A mould of the medial surface of a large part of the iliac blade, lacking the anterior end; the original natural mould, formed on the rock which underlay the blade in the field, has been reproduced in plaster of Paris via a silicone pull.

The broken end of fragment no. 4 certainly joins on to fragment no. 2, but the loss of what appears to be a few millimetres of material prevents a firm connexion between them. The information afforded by all of the above permits us to describe the ilium as a whole.

The estimated length of the ilium, as preserved, is 835 mm. The material available suggests that the dorsal outline of the blade was a smooth convex curve. The length and precise form of both the anterior and posterior processes are unclear, but the posterior process seems to have tapered posteriad to a slightly pointed, spatulate termination. This process bears three diverging ridges separated by three concavities, i.e. it is triradiate in posterior view. Thus, we have a concave lateral surface, a concave medial surface, and a deeply

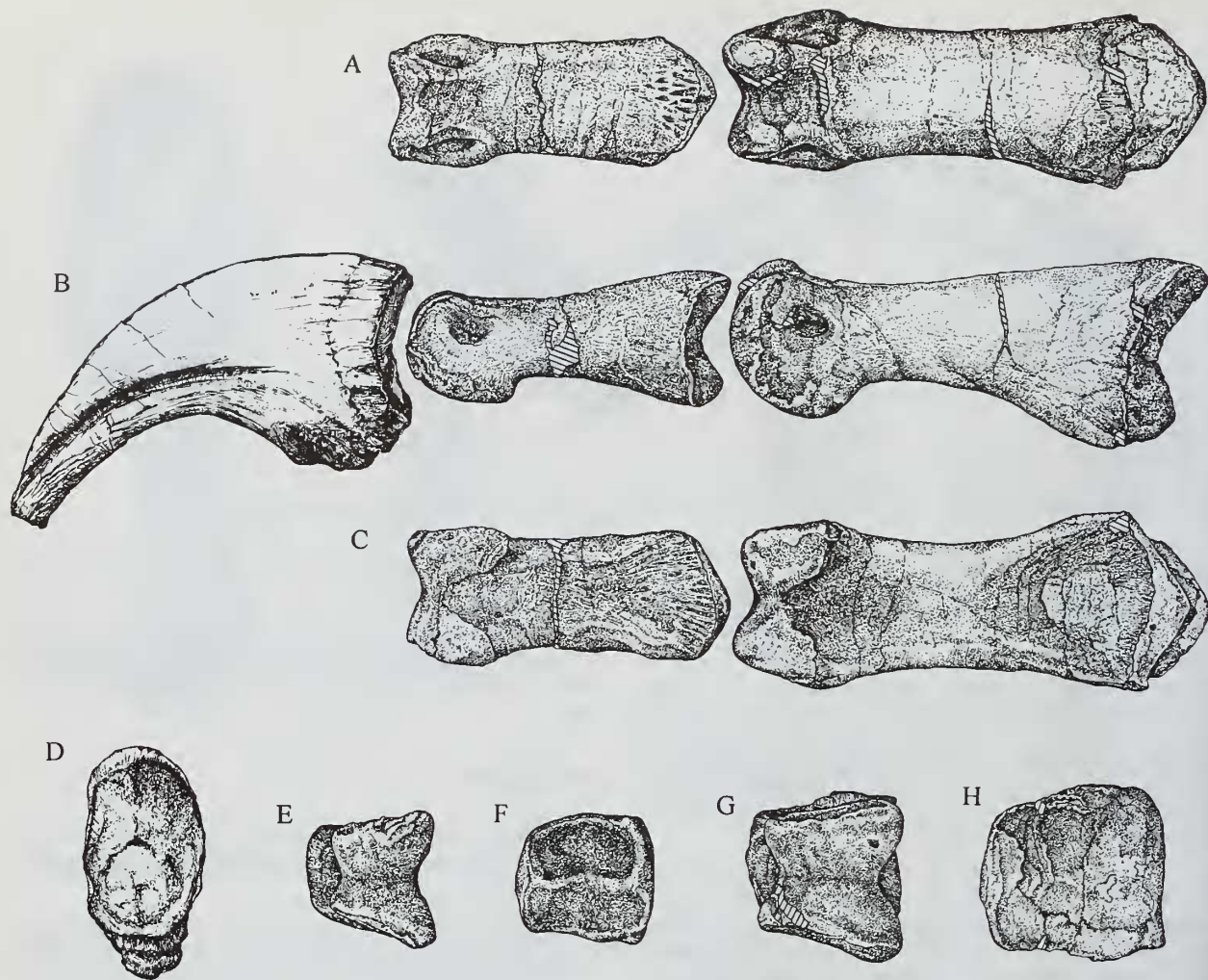


Fig. 36 *Baryonyx walkeri*, holotype, BMNH R9951; three articulated phalanges from digit II or III of left manus. A, proximal and middle phalanges in dorsal view; B, digit with ungual phalanx, left lateral; C, proximal and middle phalanges, ventral; D, proximal end of ungual; E, distal end of middle phalanx; F, proximal end of middle phalanx; G, distal end of proximal phalanx; H, proximal end of proximal phalanx. $\times 0.5$.

excavated ventral surface. This deep excavation is the brevis fossa, and the ventromedially directed ridge which partly encloses it is the brevis shelf. The ventral part of the otherwise concave medial surface is broadly convex, with faint subparallel ridges, and it appears to terminate posteriorly in a pronounced thickening; the rest of the ventromedial blade is very slender. The brevis shelf and the iliac blade are of uniform and approximately equal thickness along their length; the brevis shelf thins towards its ventral edges. The ventrolateral ridge, by contrast, is much stouter and smoothly rounded, and it thickens anteriorly in the direction of the acetabulum.

The iliac blade as a whole is of almost uniform thickness, and its lateral surface is strongly dished anteroventrally where it thickens towards the (missing) anteroventral termination. Further, its medial surface bears two scars for the direct attachment of the truncated diapophyses of the sacral vertebrae: one lies more or less dorsal to the pubic peduncle and is broadly U-shaped, the other lies dorsal to the ischiadic peduncle and is narrow and curved. (The distance between these two scars suggests that there must have been another scar midway between them, where the bone of the blade is missing

and the mould of its medial surface is not well enough preserved to indicate its presence.) These scars have no distinct border, but are characterized by their finely rugose surface, easily distinguishable from the smooth surface of the rest of the blade. It would be expected that the most ventral portion of the blade would bear another row of scars, marking the distal attachment of what are usually called 'sacral ribs' but which generally consist of no more than the capitulum of each rib; each capitulum is attached proximally to the intervertebrally placed parapophysis of its corresponding sacral vertebra and is truncated distally to attach directly to the medial surface of the ilium. In this specimen the most ventral portion of the blade is missing, but the mould of its medial surface shows two prominent and well-defined scars which presumably mark the attachment of the last two sacral ribs.

The pubic peduncle is very robust; its articular surface forms a narrow triangle, the short side being the acetabular edge. The surface of the acetabulum itself, just above this edge, shows a large, deep concavity. The anterior edge of the peduncle, though rounded, is unusually narrow, especially towards the pubic articulation.

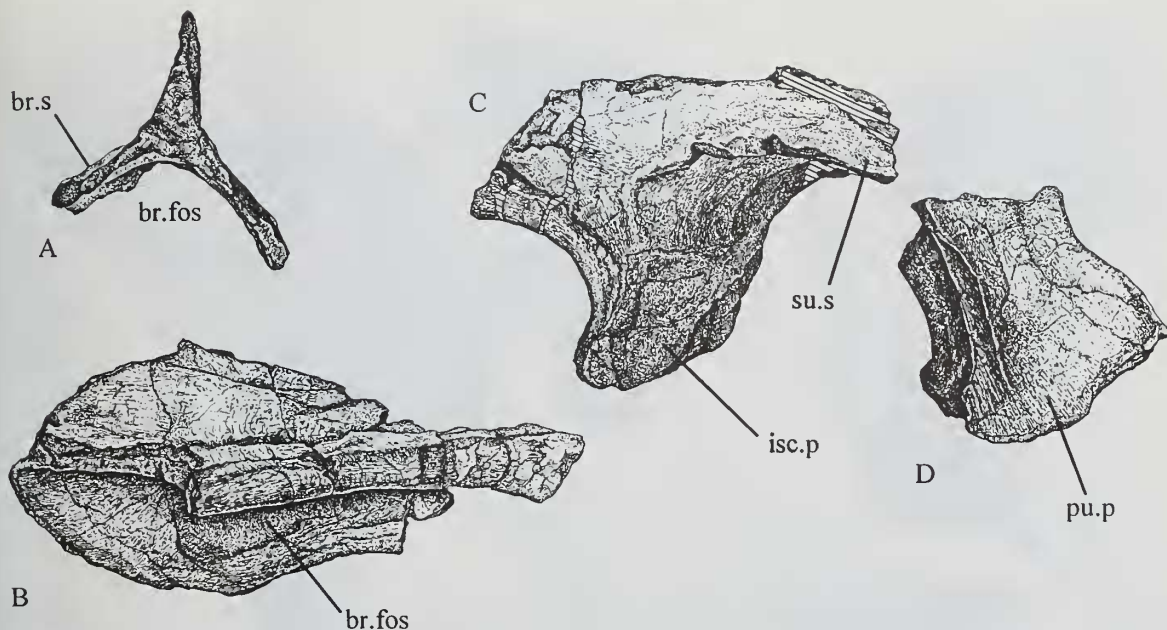


Fig. 37 *Baryonyx walkeri*, holotype, BMNH R9951; right ilium. A, posterior process in posterior view; B, same, ventrolateral; C, ischiadic peduncle, lateral; D, pubic peduncle, lateral. $\times 0.25$.

The ischiadic peduncle is shorter and much more slender. Its articular surface is much smaller, semicircular with its medial corner extended to a point (marking the sharp medial edge of the acetabulum) and extremely rugose. The supra-acetabular crest is well developed and has a sharp lateral edge.

PUBIS (Fig. 39A). One large elongated fragment, 277 mm long, is broken at one end and another fragment, 248 mm long, at both ends; one broken end on each resembles the other so much in size and shape that they are almost certainly parts of the same element, not immediately adjacent to each other but separated by a gap of indeterminate width. Both are stout shafts produced on one side into a broad flange that could well represent part of one half of the 'pubic apron', concave on one side and flat on the other. The fragment with the complete end is probably the distal part of the left pubis, the other fragment is probably the central part of the shaft of the same bone. A third fragment, 251 mm long, has the shape of one end (presumed distal) very like that of the proximal end of the central portion and is likely to be a more proximal piece of the same element. The lengths of the three pieces added together total 776 mm, and we estimate the length of the entire pubis to have been about 1000 mm; this is not unreasonable when compared with the overall length of the entire ilium (about 820 mm). The position of all three pieces on the block (Fig. 48) is fully in accord with this identification.

The acetabular portion of the left pubis is missing entirely. The proximal fragment of the shaft has a thick, rounded lateral edge; the medial border of this proximal part is a true edge, slightly downturned. The medial half of the dorsal surface is distinctly convex, bulging dorsally, and the lateral half is distinctly concave. The bone itself tapers considerably from its proximal end (from 105 mm at the break to a minimum of 71 mm), with its medial and lateral profiles symmetrical and slightly concave. The distal 100 mm or so of this fragment shows, on its medial side, the proximal beginnings of a medial flange, also with a true medial edge; lower down, on the proximal part of the central fragment, this could well have united

with its right counterpart to form a pubic apron (see next paragraph).

The central part of the left pubis is fairly straight and compressed in an oblique transverse plane. Its anterodorsal surface is more or less flat and has a thick rounded lateral edge which widens regularly towards the proximal end of the bone. Its posteroventral surface, by contrast, is strongly concave in transverse section, for it tapers medially into a thin flange. In the more proximal part of the preserved fragment this flange is thicker and is broken off on the medial side, suggesting that it might well have extended farther in that direction to join its fellow in a median symphysis as part of a pubic apron. The more distal part of the flange, however, is extremely slender and has a blade-like medial edge of finished bone, making it less likely that it extended to the midline. This means that a complete apron would have been formed only in the middle section of the pubis.

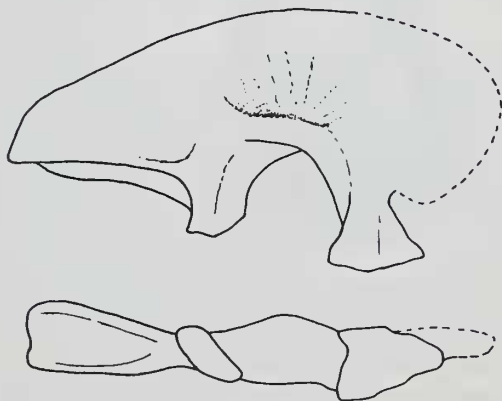


Fig. 38 *Baryonyx walkeri*, holotype, BMNH R9951; reconstruction of right ilium in lateral and ventral views. $\times 0.125$.

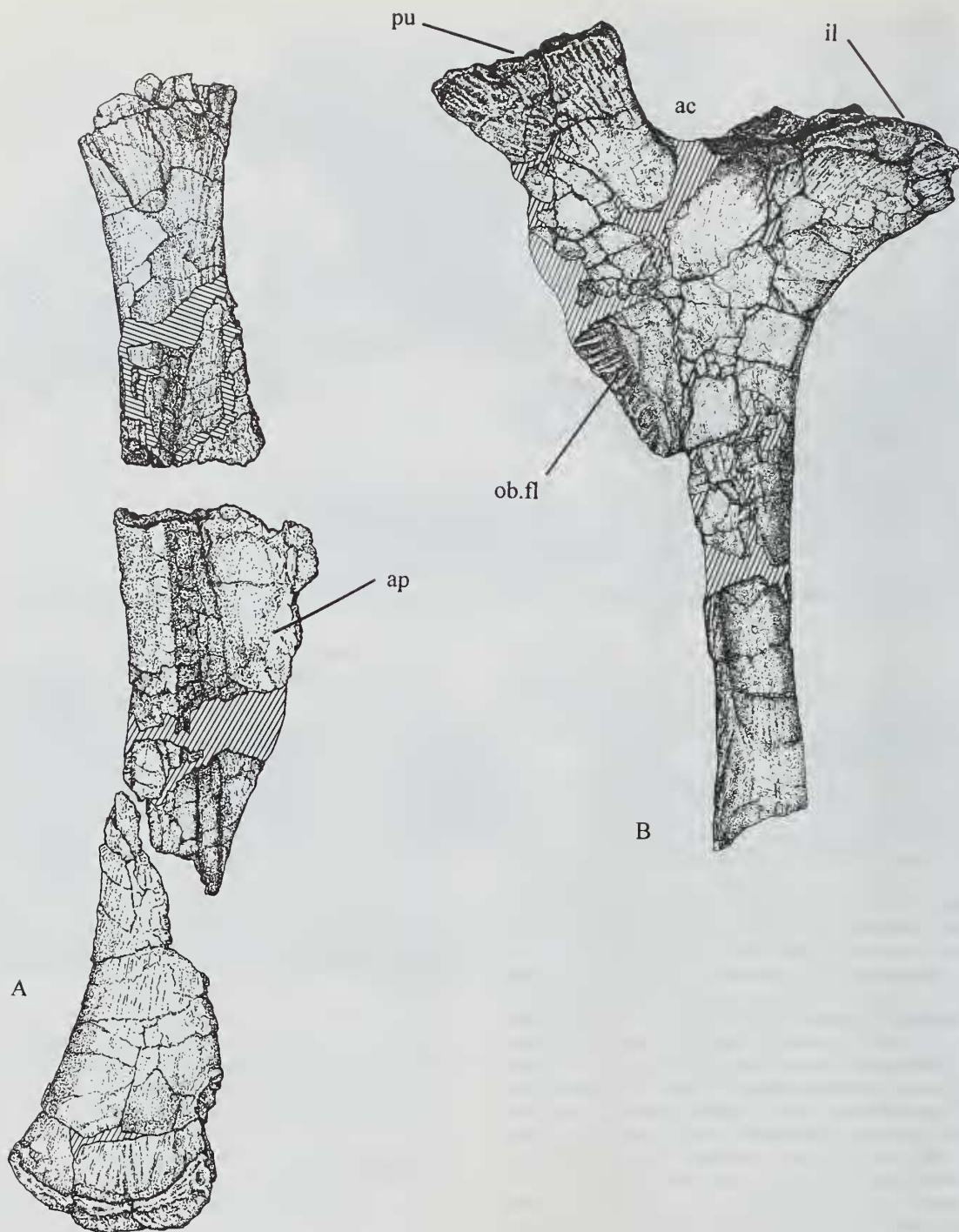


Fig. 39 *Baryonyx walkeri*, holotype, BMNH R9951; ventral elements of pelvis. A, left pubis lacking proximal end, posterior view; B, left ischium lacking distal end, lateral, $\times 0.25$.

The distal part of the left pubis is also flattened, with fairly thick, rounded edges; but it seems likely that the plane of flattening was somewhat different from that of the central fragment, parasagittal rather than transverse, from which we infer that there must have been some degree of torsion between the two pieces. This means that

the two surfaces would have faced medially and laterally respectively, and the positions of the two edges would have been anterodorsal and posteroventral; meanwhile the blade shows a distinct curvature towards the midline as it approaches its distal end. The anterodorsal edge thickens towards the distal end, its medial and lateral margins

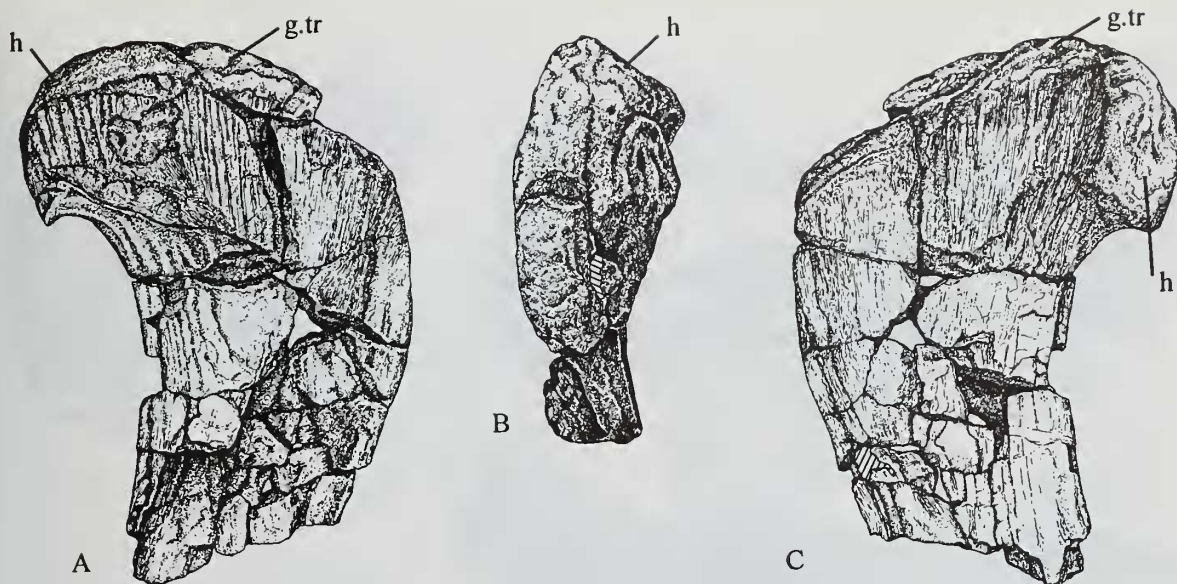


Fig. 40 *Baryonyx walkeri*, holotype, BMNH R9951; proximal part of left femur. A, lateral view; B, proximal; C, medial. $\times 0.25$.

diverging as gentle concave curves; the lateral margin develops a distinct lip, protruding laterally. The profile of the posteroventral edge is weakly concave, so that the pubis expands a little posteroventrally towards the distal end. However, the end itself does not expand extensively either anteriorly or posteriorly to form a 'pubic boot', as it does in many other theropods; indeed the distal profile of the medial or lateral surface forms a smooth convex curve. The medial surface is perceptibly concave towards its distal end.

ISCHIUM (Fig. 39B). A large part of the left ischium is preserved, including most of the shaft (total length of the element as preserved 470 mm). It lacks only the distal end of the shaft and a small part of the anterior edge of the pubic peduncle. Of the right ischium there remain only four fragments of the proximal end, none of which can be fitted together directly; one of them includes the pubic articulation with a small part of the acetabulum, another includes the obturator flange (see below), a third small piece is a further length of the acetabular margin, and a fourth piece is a length of the upper part of the shaft.

The element as preserved is a fairly typical ischium, shaped somewhat like a Y. Between the two peduncles is the most ventral portion of the acetabular ring, narrower in the centre and widening in either direction towards the articulating surfaces for the pubis and ilium respectively; the iliac surface is the larger of the two. Both peduncles (and of course the margins of their articulating surfaces) are convex on their lateral sides and concave medially. Ventral to this region the ischium forms a broad plate which has a stout posterior margin; just below the iliac peduncle this plate is weakly concave between two longitudinal ridges. Towards its anterior margin, below the pubic peduncle, the plate tapers to a slender flange. The ventral part of this flange with its distinctive fluted margin might be interpreted as the equivalent of an obturator process, but the evident absence of any notch or embayment proximal thereto suggests that there was no process projecting anteroventrally, such as is found in *Allosaurus*. There is, however, a slight notch in the anterior edge of the ischium distal to this region; we therefore propose to call this part

of the bone the obturator flange. This condition is very similar to that found in ceratosaurs, in particular *Dilophosaurus* (Welles 1984) and *Carnotaurus* (Bonaparte, Novas & Coria 1990).

The posterior surface of the shaft is broad and flat, but anteriorly it is produced into a thin flange that widens towards the broken distal end. The medial surface of this flange is more or less planar, but the lateral surface is weakly concave.

Hind limb

FEMUR (Figs 40, 41). Both femora suffered extreme damage from clay-winning operations before the presence of the dinosaur skeleton was recognized. The only fragments rescued were (from the left femur) the proximal end with the uppermost part of the shaft, together with the tibial condyle, and (from the right femur) the distal 40% or so of the bone. There was no overlap between the two sides, and it is therefore impossible to make an accurate estimate of the length of the entire element; 1,200 mm is probably a reasonable approximation.

Unfortunately, in this limited material many of the external features had either been destroyed without trace or would have been on regions of the bone that were not preserved; these include the internal and fourth trochanters.

The proximal end of the femur appears not to have been crushed but is nevertheless somewhat flattened anteroposteriorly. The intumed head is oval in outline and its articulating surface is directed, not medially, but rather posteromedially; it is separated from the much larger greater trochanter by a broad U-shaped vertical channel on the posterior side. The greater trochanter is elongated in a mediolateral direction and tapers towards the lateral side, with its anterior surface lightly convex and its posterior surface concave. The lateral edge, narrow proximally, swells out more distally into a distinct protuberance with a convex anterior margin and a straight posterior margin.

The shaft of the femur is more or less circular in cross-section. The distal end shows the usual two condyles, both well preserved;

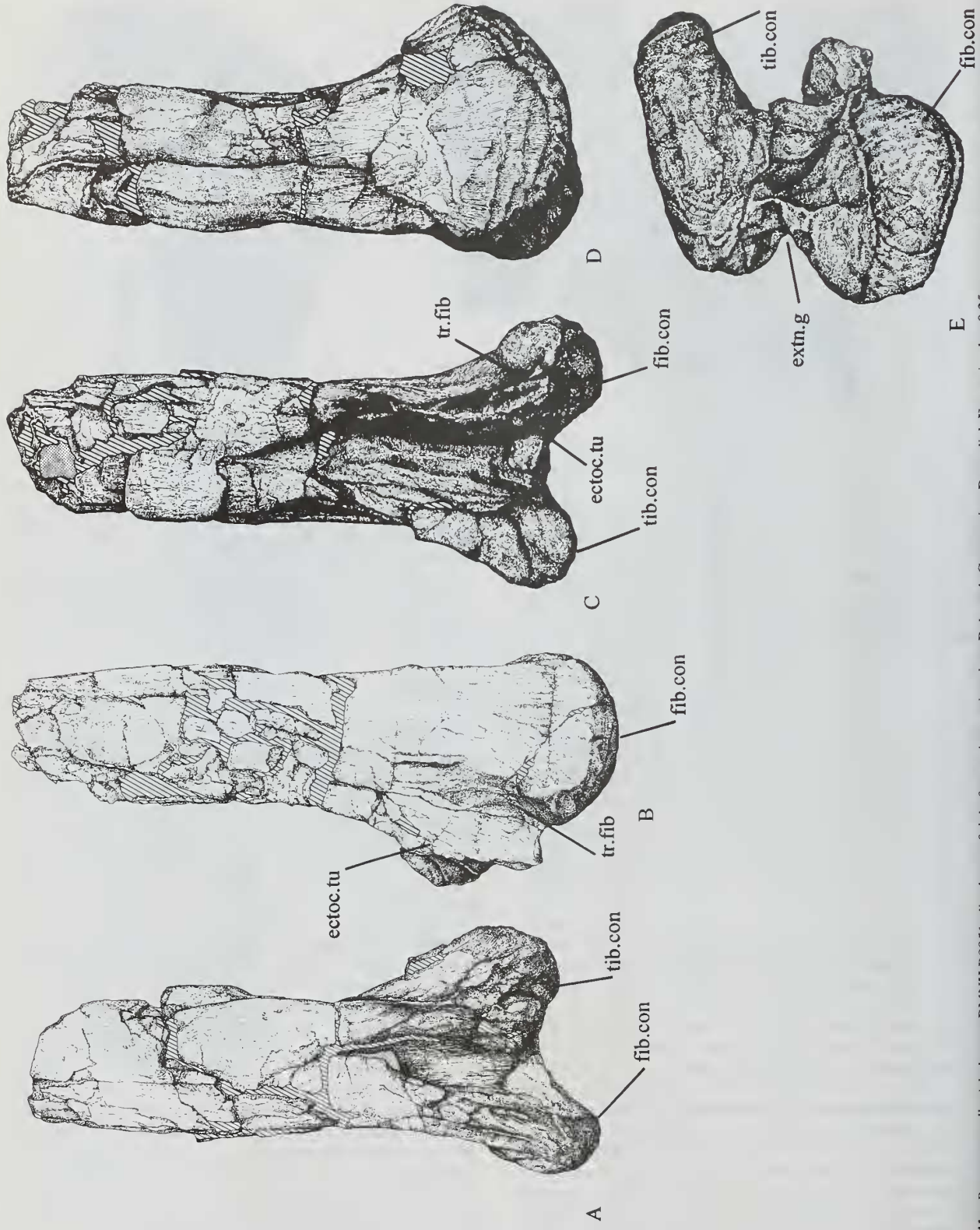


Fig. 41 *Baryonyx walkeri*, holotype, BMNH R9951; distal part of right femur. A, anterior view; B, lateral; C, posterior; D, medial; E, proximal. $\times 0.25$.

the lateral (fibular) extends about 15 mm below the medial (tibial). They are separated by deep intercondylar grooves on both anterior and posterior surfaces; the anterior groove is V-shaped, while the posterior is broader and U-shaped. The tibial condyle, seen in anterior or posterior view, appears to be displaced medially from the line of the shaft; it is greatly expanded anteroposteriorly (though somewhat obliquely) but is relatively narrow from side to side. The fibular condyle, by contrast, lies more or less on the line of the shaft and is less expanded anteroposteriorly. On its posteromedial surface arises a prominent longitudinal flange; this is equivalent to the 'blocky protuberance' described in *Allosaurus* by Madsen (1976: 43) and the 'ectocondylar tuber' described in *Dilophosaurus* by Welles (1984: 137). The deep concavity between this flange and the fibular condyle itself is the trochlea fibularis of Currie & Zhao (1993). A longitudinal groove, deep and V-shaped, runs up the medial surface of the distal part of the shaft; apart from this, the preserved portion of the shaft is in too poor a condition to merit description.

TIBIA. One fragment is recognisable as a distal part of a tibia, but it is too badly crushed to be described.

FIBULA (Fig. 42). The right fibula is in good condition and lacks only its extreme distal end; it is 510 mm long as preserved. The proximal end is broad and flat and expanded anteroposteriorly; the expansion is mostly towards the rear, so that the posterior profile is weakly concave. The lateral surface is weakly convex and the medial surface weakly concave (the latter would have faced the tibia). The elongated, weakly crescentic end-surface is just a little thicker anteriorly than posteriorly. The anteromedial edge of the shaft, just below the head, is slightly thickened for the attachment of the tibiofibular ligaments, but this thickening is less well developed in *Baryonyx* than in *Allosaurus*, *Dilophosaurus* and certain other theropods. Seen in lateral or medial view, the proximal end tapers rapidly distad (with a very weakly concave profile both anteriorly and posteriorly) into a straight, slender, rod-like shaft; the shaft continues to taper more gently, and its anterior and posterior margins eventually run parallel to each other, after which the fragment is terminated by the distal break.

The weak concavity of the medial surface of the proximal end, i.e. the medial sulcus, is continued distad into the medial surface of the shaft, eventually becoming a relatively deep V-shaped trough that terminates suddenly about half-way down the bone (as preserved). Below this the shaft is almost circular in cross-section for a short way but then becomes concave again on the medial side, so that the broken end-surface is clearly crescentic. This medial sulcus is better developed in *Allosaurus*, *Torvosaurus*, troodonts and dromaeosaurs; in *Allosaurus* it is continuous all the way down the shaft.

ASTRAGALUS. A flattened piece of bone compares well with the ascending process of the left astragalus of *Allosaurus*, but is too broken and irregular in outline to merit description.

CALCANEUM (Fig. 43). The right calcaneum is virtually complete. In lateral or medial view it is semilunate, with a weakly concave proximal profile and a strongly convex distal profile. In proximal view, the proximal surface is thick and rounded at the anterior end but tapers to a sharp point posteriorly; the surface itself is weakly concave to receive the distal end of the fibula. The lateral margin of this proximal surface is not higher than the medial margin, in which respect *Baryonyx* is like *Torvosaurus*, but unlike *Allosaurus* and *Sinraptor*.

The lateral surface is almost flat and very slightly dished. The medial surface is convex and bears, at its anterior end, two deep rounded hollows, with a slight protuberance between them. One of

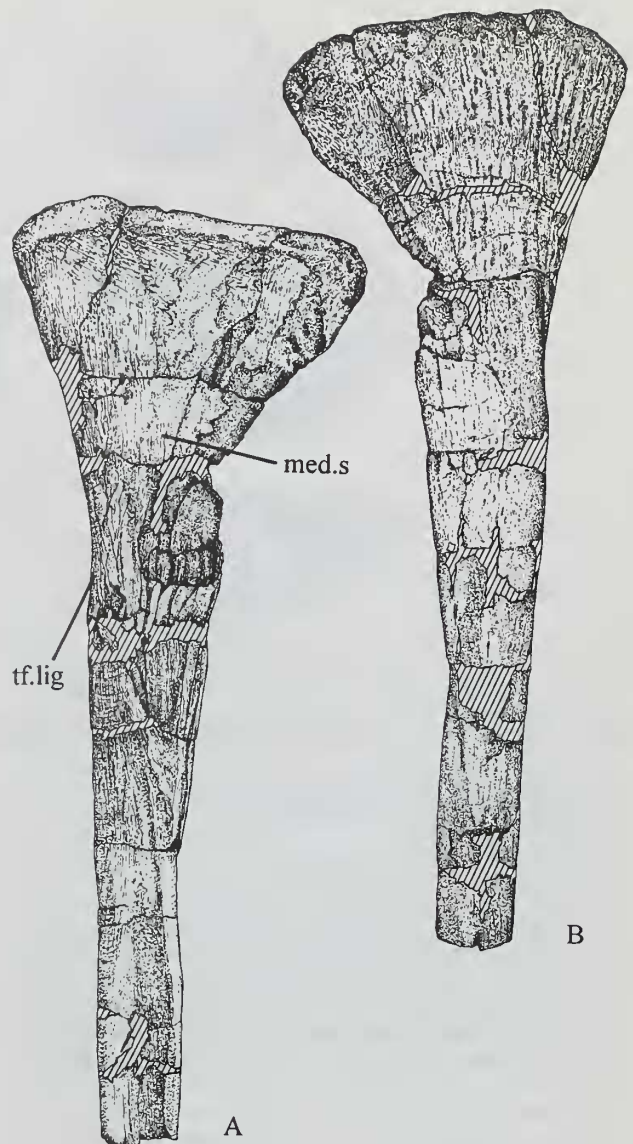


Fig. 42 *Baryonyx walkeri*, holotype, BMNH R9951; right fibula. A, medial view; B, lateral. $\times 0.25$.

these is above and slightly anterior to the other; they are the facets for the two lateral tuberosities of the astragalus, the proximal facet being the larger of the two. The remaining part of the medial surface forms a shallow facet for the reception of the tibia; this facet is much deeper and more cup-shaped in *Allosaurus*.

PES. The collection includes two damaged distal ends of metatarsals, with typical broad, rounded articular surfaces and with fairly well-developed ligament pits. They could be metatarsals II, III or IV of either foot.

Another fragment is the basal part of an ungual from the foot, as indicated by its large radius of curvature and flattened ventral (internal) surface.

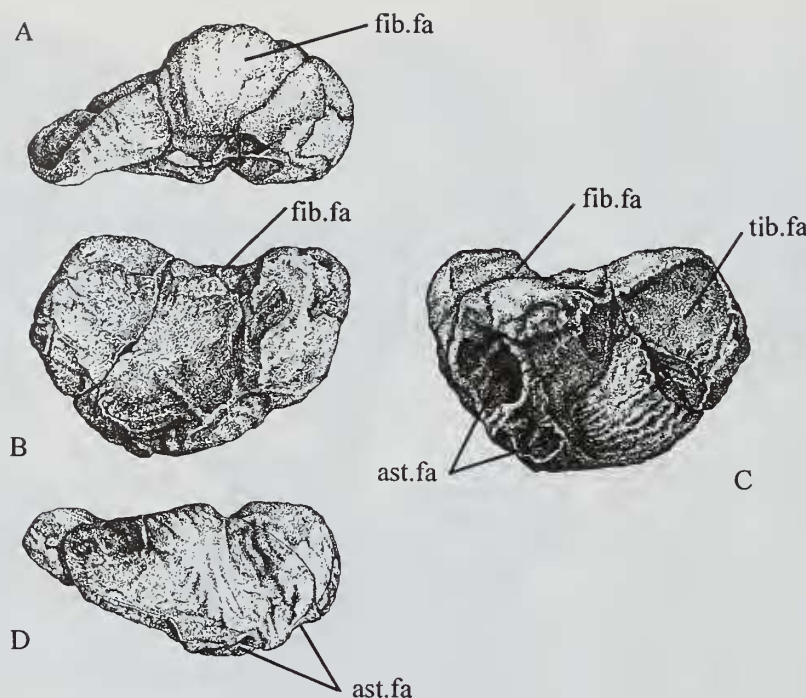


Fig. 43 *Baryonyx walkeri*, holotype, BMNH R9951; right calcaneum. A, proximal view; B, lateral; C, medial; D, distal. $\times 0.5$.

OTHER MATERIAL REFERRED TO THE SAME FAMILY

Taquet (1984) described two fragments from the Elrhaz Formation (Aptian) of Gadoufaoua, Niger, as mandibular symphyses of a spinosaurid (Musée National d'Histoire Naturelle, Paris, MNHN GDF 365 and 366); they were refigured more clearly in Kellner & Campos 1996 (fig. 7). Each is virtually identical to the conjoined premaxillae of the holotype of *Baryonyx* (Charig & Milner 1986; 1990: 139) except in that they possess seven alveoli on each side, not six on the left and seven on the right as in R9951. We consider that these snouts, despite their much younger age, are referable to *Baryonyx* sp. indet.

More recently, Viera & Torres (1995: figs 1–2) referred a left maxilla fragment (Museo de San Telmo, San Sebastian, GA-2065) from the Enciso Group, Barremian of Igea, La Rioja, Spain, to *Baryonyx walkeri*. It is less complete and about 75% of the size of the holotype maxilla but otherwise indistinguishable. The tip, anterior to the 3rd alveolus is missing but complete 8th, 9th and partial 10th alveoli are present confirming that the pattern of evenly spaced subcircular alveoli, gradually decreasing in size, continues further posteriorly than is preserved on the holotype maxilla.

The following isolated tooth crowns are referred to cf. *Baryonyx*; their fragmentary nature and the consequent lack of further information precludes a more precise identification.

Wessex Formation (=Wealden Shales, Barremian), Isle of Wight (Isle of Wight County Museum, Sandown IWCMS 3642 and 5120 from Hanover Point; IWCMS 5122, IWCMS 1995 207–209, University of Portsmouth, UOP.97, all unlocalised) described as possible baryonychid by Martill & Hutt (1996). All these crowns are virtually identical with the teeth of the holotype R9951 in their shape, ornamental

pattern, enamel texture, and possession of finely serrated anterior and posterior carinae with seven or eight denticles per millimetre.

Upper Weald Clay (Barremian), former Ewhurst Brickworks, Surrey (National Grid Reference TQ 108379), a single crown (Maidstone Museum MNEMG 1996.133) collected by Dr E A Jarzembowski in the mid 1980's and reported recently from just below BGS Bed 5c, equivalent to the top of the Smokejacks beds.

Ashdown Sand, (Hauterivian) at Redlands Bricks, Ashdown Works, Scaletts Wood, Turkey Road, Bexhill-on-Sea, East Sussex, National Grid reference TQ60/70 721097, a single crown (Bexhill Museum BEXHM:1993.485), collected by Mr D. Brockhurst in 1993. This crown differs from the Barremian material only in that the carinae do not extend the full distance to the base of the crown.

PHYLOGENETIC RELATIONSHIPS AND SYSTEMATIC POSITION

Our first publication on *Baryonyx* (Charig & Milner 1986) made no suggestions as to the relationships of the genus, beyond the claim that it 'was a typical large theropod in certain respects, resembling, for example, *Allosaurus*'. We nevertheless considered it to be sufficiently distinctive to merit designation as the type-genus of a new family, Baryonychidae. Our second, more detailed publication (1990) confirmed our view of its separate family status; our only other conclusions were that it was not a spinosaurid and that it could not be fitted into Gauthier's (1984, 1986) cladistic classification of the theropods.

Other workers have referred to *Baryonyx* in various contexts. Their assessments of its phylogenetic position were made in the light of one or both of our preliminary descriptions, which were incomplete and contained some errors. Some of those assessments, because

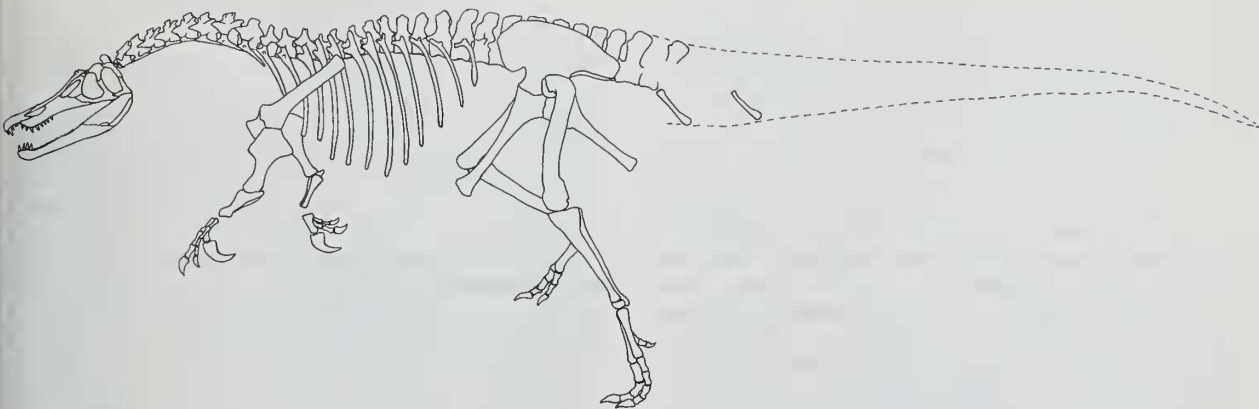


Fig. 44 *Baryonyx walkeri*, holotype, BMNH R9951; reconstruction of entire skeleton, $\times 0.020$.

of this inadequate basis and because of their brevity, scarcely merit discussion. Nevertheless the authors concerned (including ourselves) have generally considered *Baryonyx* to be a close or not-so-close relative of *Spinosaurus*, so that the two genera have often been placed together as a single family (Spinosauridae Stromer, 1915). This has led certain authors (notably Sereno *et al.* 1994) to employ that family as a single unit for the purpose of character distribution analysis.

Bonaparte (1991: 18) suggested a relationship between the Spinosauridae, later fragmentary theropods from Africa (*Carcharodontosaurus* and *Bahariasaurus*), and the South American Abelisauridae; he claimed that the femur of all these forms possessed an anteromedially directed head and a plesiomorphically low lesser trochanter and, if this were true, then they would together represent a major diverse clade (named Neoceratosauria by Novas in 1991), distributed mainly in Gondwana. Holtz (1994a: 1105) cited Bonaparte's work, but misleadingly stated that the Spinosauridae comprised *Spinosaurus* and *Baryonyx*; the latter genus, in fact, was never mentioned by Bonaparte. Holtz also questioned Bonaparte's suggestion, quoting our claim (1990) that *Baryonyx* possessed the tetanuran synapomorphy of an obturator process on the ischium; we now know that to be incorrect – the structure is only a flange. Nevertheless, we agree with Holtz because *Baryonyx* has the femoral head directed medially, not anteromedially, and its other characters are tetanuran rather than neoceratosaurian (see below). Meanwhile Sereno *et al.* (1996), on the basis of new material from the Cenomanian of Morocco, have interpreted *Carcharodontosaurus* as a member of the Allosauroidea.

Elzanowski & Wellnhofer (1992, 1993) proposed a monophyletic group of theropods consisting of *Baryonyx*, *Spinosaurus*, the Troodontidae, *Lisboasaurus* (tentatively identified as a maniraptoran by Milner & Evans in 1991 but reidentified more recently as a crocodylomorph by Buscalioni *et al.* 1996), and *Archaeornithoides* (a tiny fragmentary skull from the Late Cretaceous of Mongolia, described by Elzanowski & Wellnhofer in 1992). This suggestion was based on the following shared characters:

1. Interdental plates absent.
2. Paradental groove present (separating interdental septa from lingual wall of dentary).
3. Lingual wall of dentary lower than labial wall (*Baryonyx*, *Spinosaurus* and *Archaeornithoides* only).

4. Details of articulation between premaxilla and maxilla (*Baryonyx* and *Archaeornithoides* only).
5. Ridge in midline of anterior part of palate (*Baryonyx* and *Archaeornithoides* only).

Elzanowski & Wellnhofer suggested that *Archaeornithoides* was the closest known theropod relative of birds, and that its consistent similarities to *Baryonyx*, *Spinosaurus* and the troodontids narrowed down the ancestry of birds to those theropods that lacked interdental plates and possessed paradental grooves. However, interdental plates are unequivocally present in the dentary of *Baryonyx* (Figs 13, 14), forming a barrier between the alveoli and the paradental groove. Further, since *Baryonyx* does not possess any apomorphous characters of the Maniraptora¹ (in which taxon is placed the Troodontidae), both it and *Spinosaurus* must be far removed from the origin of birds. Another argument against the hypothesis of Elzanowski & Wellnhofer is that *Archaeopteryx* too had interdental plates (as shown by the dentary of the seventh specimen in lingual view, Elzanowski & Wellnhofer 1995). The same is true (Currie 1995) of *Dromaeosaurus*, type-genus of the family Dromaeosauridae, which many authors (most recently Holtz 1994a) regard as the sister-group of *Archaeopteryx*.

Claims of relationship at family level

A minor misunderstanding has arisen over the systematic relationship between (a) *Baryonyx*, (b) *Spinosaurus*, and (c) a partial maxilla from the Upper Cretaceous of Morocco, described and figured by Buffetaut (1989) as *Spinosaurus*. The maxilla of the *Spinosaurus* holotype is known only from a poorly preserved fragment now lost (see below p. 56). Buffetaut was therefore obliged to refer the Moroccan maxilla to *Spinosaurus* on the basis of the only structures common to both specimens, namely the teeth and their alveoli (using, for *Spinosaurus*, dentary teeth and alveoli and isolated teeth). Buffetaut claimed also that *Baryonyx* must be closely related to *Spinosaurus* (basing his evidence both on the original *Spinosaurus*

¹The name 'Maniraptora', proposed by Gauthier (1986: 30) and used by several workers since then, is etymologically wrong. *Manus* (which is Latin, not Greek as stated by Gauthier), meaning *hand*, is a fourth-declension feminine noun with the root *manu-* (see International Code of Zoological Nomenclature, 3rd edition, 1985: 215), not *man-* as Gauthier obviously supposed. His replacement of the English adjective *manual* with '*manal*', *op. cit.*, is presumably based on the same incorrect supposition.

and on the referred Moroccan fossil). He believed that both genera might be in the same family, but concluded that, for the time being, the Spinosauridae and the Baryonychidae should be regarded as separate but closely related. We subsequently argued (Charig & Milner 1990: 131–133, 139) that the Moroccan maxilla resembled *Baryonyx* more closely than it did *Spinosaurus*, and we stated unequivocally that it should be referred to the Baryonychidae as 'baryonychid gen. et sp. indet.'.

Buffetaut (1992), however, listed certain objections to our arguments:

1. We had claimed that his 1989 illustrations of the Moroccan maxilla showed a 'peg-like anterior extremity' and noted also that the posterodorsal rim of the fragment was the 'anteroventral portion of the rim of the external naris', despite the fact that neither of those structures was mentioned in the legend or in his description. Buffetaut subsequently stated (1992) that no evidence of either structure could be seen on the specimen; it seems that we had misinterpreted as true edges the broken edges of the fragment (as seen in the illustrations).
2. We had wrongly accused Buffetaut of misinterpreting the broken posterodorsal rim of the fragment as evidence of an antorbital fenestra, failing to note his comment (1989: 82) that 'no evidence of an antorbital fenestra is visible'.
3. We stated (1990: 32) that the characters common to the Moroccan specimen and to *Spinosaurus* 'can hardly be considered on their own as diagnostic of a particular genus or even a particular family', but we nevertheless included most of them in our list of the important characters which, in combination, typify *Baryonyx*. These statements, however, do not really contradict each other; characters that are insufficiently diagnostic on their own might yet be helpful in combination with others.

Moreover, further preparation and research have shown that our interim accounts of the partly developed *Baryonyx* contained some errors, e.g. we had stated wrongly (1990) that the animal possessed at least one elongated neural spine.

The matter was broken down by Buffetaut into two separate problems. Should *Spinosaurus* and *Baryonyx* be included in the same family? (If the answer is yes, then the family would have to be called by the older family name, viz. Spinosauridae.) The resolution of this problem depends only on material that may be included with near-certainty in one genus or the other, i.e. only on the two holotypes; the Moroccan maxilla is wholly irrelevant. Secondly, is it possible to tell whether the Moroccan maxilla is more similar to *Baryonyx* or to *Spinosaurus*, and if so, which?

Buffetaut (1992) was right in pointing out the incorrectness of the similarities that had caused us to ally the Moroccan maxilla with *Baryonyx* rather than with *Spinosaurus* (Charig & Milner 1990); without those alleged similarities the only structures on which the Moroccan maxilla may be compared with either *Baryonyx* or *Spinosaurus* are the teeth. Table 3 summarizes all relevant comparisons between the teeth of those three forms (as far as is possible with the extremely limited material at our disposal).

On teeth alone it can be seen that the Moroccan maxilla resembles *Spinosaurus* more closely than it does *Baryonyx*, which is what Buffetaut (1989) had originally claimed.

Sereno *et al.* (1994: 270) also proposed a unique family relationship between *Baryonyx* and *Spinosaurus*, based on a cladogram containing 44 characters in 9 terminal taxa, including the Spinosauridae (specifying *Baryonyx* and *Spinosaurus*) and *Afrovenator*, a new theropod of Early Cretaceous age. This relationship was based on the following proposed synapomorphies:

Table 3 Comparisons of teeth of *Spinosaurus* with those of related forms.

	<i>Baryonyx</i>	Moroccan maxilla	<i>Spinosaurus</i>
All teeth:			
curvature	recurved, slightly but consistently	?	hardly recurved at all
serrations	7 to the mm	none	none
fluting	lingual sides of crowns fluted	not mentioned	sometimes very faint, fine vertical striping on enamel towards base
Upper teeth only:			
spacing	widely spaced	widely spaced	?
interdental plates	on both pmx and mx	none	?
labial edge of maxilla	wavy in ventral view	wavy in ventral view	?
Lower teeth only:			
number	32	?	not more than 15
spacing	close together	?	well separated
interdental plates	present	?	absent (<i>vide</i> Stromer and Buffetaut)

1. Elongate prenasal snout. In *Baryonyx* the whole of the snout is elongate; in *Spinosaurus* it is unknown.
2. Specialized anterior dentition, manifested by increase in number of premaxillary teeth. *Baryonyx* has 6/7 premaxillary teeth, which is 1/2 more than the 5 usual in theropods; but, in any case, their number is unknown in *Spinosaurus*.
3. Specialized anterior dentition manifested also by terminal rosette. We coined that term for the horizontally expanded tip to the upper jaw in *Baryonyx*, almost completely surrounded by dental alveoli. The upper jaw of *Spinosaurus* is unknown except for a small fragment of maxilla.
4. Increase in height of dorsal neural spines. This was mistakenly reported in our 1990 publication and is incorrect. In contrast, the dorsal neural spines of *Spinosaurus* are greatly elongated (hence the generic name).

Thus, of the four allegedly synapomorphic character-states, three are unknown in *Spinosaurus* and may therefore be discounted. The last is present in *Spinosaurus* but absent in *Baryonyx*. This means that the synapomorphies of Sereno *et al.* (1994), considered on their own, provide no justification for placing the two genera concerned in the same family.

Consequently, we are now in agreement with Buffetaut in so far as we accept a particular relationship between Spinosauridae and Baryonychidae. However, in the absence of decisive evidence in either direction, the following factors predispose us against synonymising the two families:

1. The material of *Baryonyx* is far more complete than that of *Spinosaurus*, and *Baryonyx* would therefore make a much more informative type-genus for the family in which it is included. More importantly, all of Stromer's (1915) *Spinosaurus* material, housed in Munich Museum, was destroyed in an Allied bombing raid in 1944, and is therefore no longer available for comparisons; nor is there any other material that could be designated as a neotype.
2. The most important distinguishing feature of the Spinosauridae, as suggested by the name, is the elongation of the neural spines on the vertebrae. *Baryonyx* has no such elongated spines. The presence or absence of such spines may have little or no

phylogenetic significance, and it would not be against the International Code of Zoological Nomenclature to call *Baryonyx* a spinosaurid; nevertheless it could be very misleading.

3. The similarities between the two genera, as known at present, are not (in our opinion) sufficiently close to justify their treatment, for cladistic analysis, as a single O.T.U. (operational taxonomic unit).

Also of importance in this connexion are two recently discovered theropods from the Romualdo Member of the Santana Formation (Albian) of the Araripe Basin of north-eastern Brazil. Kellner & Campos (1996) described a fragmentary snout as a new member of the Spinosauridae and named it *Angaturama*. *Angaturama* is especially useful in that it shares certain apomorphic characters with *Spinosaurus*, yet, at the same time, possesses other apomorphic characters that it shares with *Baryonyx* but which could not be demonstrated in *Spinosaurus* itself because of the latter's incompleteness. We therefore believe that, using *Angaturama* as a link, we can justify a closer relationship between the Spinosauridae (*Spinosaurus*, *Angaturama* and the Moroccan maxilla) and the Baryonychidae (*Baryonyx*) than between either of those two families and any other. We further believe that this relationship might be reflected in the classification by placing those two families together in the same superfamily Spinosaurioidea¹ Stromer, 1915, excluding the other genera previously placed there by Sereno *et al.* in 1994 (*Torvosaurus*, *Eustreptospondylus*).

The Spinosaurioidea as defined here is characterized by the following apomorphic characters, unique among the Theropoda:

1. The elongation of the jaws, especially in the premaxillary region.
2. A greater or lesser tendency to develop a terminal rosette (greater in the upper jaw than in the lower).
3. The shape of the front of the lower jaw, turned upwards at the extreme anterior end and constricted transversely just behind that.
4. An increase in the number of premaxillary teeth to seven.
5. Teeth that show a reduction in:
 - (a) the compression of the whole tooth in a labio-lingual direction;
 - (b) the recurvature of the crown (only slight in *Baryonyx*, practically non-existent in *Spinosaurus*);
 - (c) the size of the denticles on the anterior and posterior carinae of the crown (very fine in *Baryonyx*, absent altogether in *Spinosaurus* and *Angaturama*).

The other Albian theropod from Brazil, *Irritator* Martill, Cruickshank, Frey, Small & Clarke 1996, is a partial skull lacking the end of the snout; this makes it difficult to compare with *Angaturama*, except in so far as both genera obviously had elongated jaws, external nares set far back, and teeth that share all the unique tooth characters of Spinosauridae (5. above). It seems very likely that *Irritator* too is a spinosaurid, and even possible that it is a senior synonym (by one month!) of *Angaturama*. Its authors, however, assigned it to the Bullatosauria Holtz, 1994a, a new taxon of maniraptorans that includes the Troodontidae and the Ornithomimosauria.

These characters could, of course, represent independent adaptations to similar diets. On the other hand, it is more parsimonious to

interpret the unique distribution of all seven in the Spinosauridae and the Baryonychidae as indicating a sister-group relationship between those two families. This latter interpretation is consistent with the fact that the degree of reduction shown in the tooth characters (b) and (c) above is significantly less in Baryonychidae than in the much later Spinosauridae, i.e. the characters reflect a trend which seems to have increased greatly during the time interval between the Barremian and the Cenomanian.

The systematic position of *Baryonyx* and its allies within the Theropoda

By far the most detailed analysis of theropod relationships published to date is Holtz's work of 1994a. His computer analysis of the data, based on a matrix of 19 O.T.U.s and 126 characters, produced a single most-parsimonious cladogram (his fig. 4), and a strict consensus cladogram of the six equally parsimonious 'runners-up' (his fig. 5).

Holtz's cladogram agrees in many respects with the cladograms of earlier workers, notably Gauthier's. In some details, however, it differs greatly. The most important difference lies in the positions assigned to the Tyrannosauridae and the Troodontidae, among the most highly derived Coelurosauria (within the Maniraptora and close to the Ornithomimosauria).

We assessed the phylogenetic relationships of *Baryonyx* by incorporating it as an additional, twentieth taxonomic unit into Holtz's data-matrix. It seemed to us, however, that a few of the characters that Holtz had used in his analysis were unsatisfactory and that others were scored wrongly. This opinion has been confirmed independently through the recent publication of criticisms by Clark, Perle & Norell (1994) of several of Holtz's characters (see Appendix C) leading to scepticism of his main conclusion, that the Tyrannosauridae should be placed within the Maniraptora. Our relatively minor modifications of Holtz's analysis have not affected that conclusion.

We deleted 8 characters from Holtz's data-matrix and re-scored a few others, thereby producing a modified data-matrix (Appendix C). All available information on *Baryonyx* (on 57 characters, information on the 61 others being unavailable or too uncertain to be of any value) was added and the analysis run with both the same computer programme (PAUP Version 3.0, Swofford 1990) and with Hennig86 (Farris 1988) and the results compared. PAUP was run under Heuristic and Branch & Bound algorithms and produced six equally parsimonious trees of 228 steps, with a consistency index (C.I.) of 51% and a retention index (R.I.) of 70%. Hennig86, using mh* and Branch & Bound options, gave similar results: six equally parsimonious trees of 234 steps, with a C.I. of 50% and an R.I. of 70%. These figures resemble Holtz's (51% and 71% respectively). Holtz's best cladogram had 244 steps, a few more, but it should be remembered that he used 126 characters as against our 118. All trees were rooted to a hypothetical ancestor on unordered characters.

All these trees (and the corresponding consensus trees) produced by both programmes display topologies that are generally similar to each other and which, in their broad outlines, resemble Holtz's single most-parsimonious cladogram. In all of them there is a monophyletic Ceratosauria arising from the basal node, and, much farther away from the root, a monophyletic Neotetanurae. Between them are three other nodes that give rise to a polyphyletic assemblage that might be referred to collectively and informally as 'basal Tetanurae' (among which *Baryonyx* is placed). The more detailed arrangement of the O.T.U.s was constant within the Ceratosauria but varied from tree to tree within the Neotetanurae; those clades, however, do not concern us here, and discussion of such problems is beyond the scope of the present work.

¹Some confusion surrounds the superfamilial name Spinosaurioidea (which, according to the Principle of Coordination laid down in Article 36(a) of the International Code of Zoological Nomenclature, must retain the same author and date as existing family-group names based upon the same type-genus). Sereno *et al.* (1994) proposed a taxon including *Baryonyx*, *Spinosaurus*, *Torvosaurus* and *Eustreptospondylus*, naming it Torvosaurioidea. However, Sereno *et al.* (1996) changed the name of that nominal taxon to Spinosaurioidea, presumably because the family name Spinosauridae Stromer, 1915 is senior to Torvosauridae.

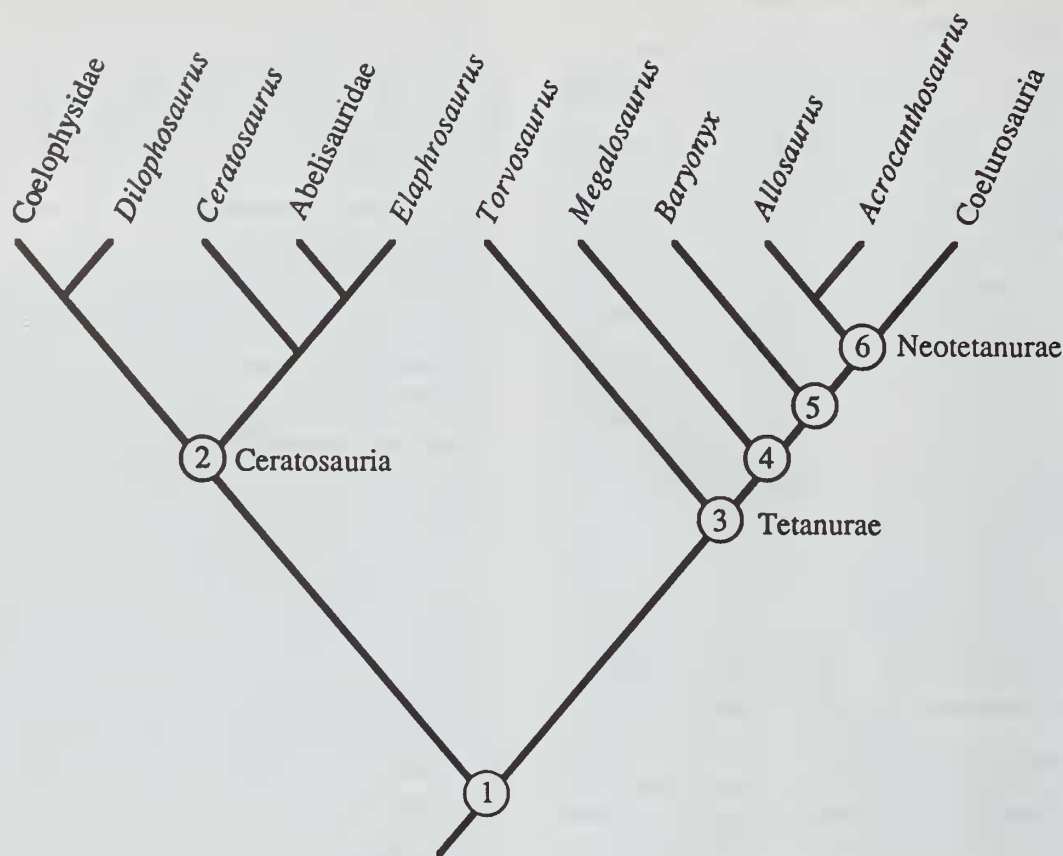


Fig. 45 Cladogram of the Theropoda, based on our modified version of Holtz's data-matrix and including also *Baryonyx*.

In all our cladograms (summarized in Fig. 45) *Baryonyx* is placed as the sister-group of the Neotetanurae Sereno *et al.*, 1994 (=Avetheropoda Paul, 1988), arising from node 5 (numbering of nodes and characters are as used in this work, not Holtz 1994a; for details see Appendix C). The nearest outgroup of the combined clade is *Megalosaurus*, arising from node 4, and the second nearest *Torvosaurus*, arising from node 3. All these taxa (i.e., *Torvosaurus*, *Megalosaurus*, *Baryonyx* and Neotetanurae) together comprise the Tetanurae Gauthier, 1986. If *Baryonyx* were inserted into Holtz's cladogram (his fig. 4) it would split off from the main stem of the Hennigian comb, leading to the Coelurosauria *sensu* Gauthier, between his nodes 6 and 7.

The specific evidence for the position of *Baryonyx* on our cladogram (Fig. 45) is assessed critically below.

At node 3 (*Torvosaurus* dichotomy, Holtz's node 5, Tetanurae) there are fourteen synapomorphies. *Baryonyx* provides positive evidence of only three of those, namely:

50. Dorsal vertebrae pleurocoelous ('unambiguous synapomorphy' of Tetanurae, *fide* Holtz *loc. cit.*).
4. Dorsal vertebrae with transverse processes that are not strongly backturned or triangular in dorsal view (supposedly reversed character).
110. All three pelvic elements not fused together in adults (supposedly reversed character).

At node 4 (*Megalosaurus* dichotomy, Holtz's node 6, unnamed)

there are eight synapomorphies, but unfortunately *Baryonyx* affords evidence of none of them.

At node 5 (*Baryonyx* dichotomy, new node, unnamed) there are five synapomorphies, on only one of which does *Baryonyx* provide data, namely:

96. Coracoid tapers posteriorly ('unambiguous synapomorphy' of Holtz). We thought it unwise to propose a new name for the taxon based on this node; the phylogeny is not yet sufficiently well established.

This evidence is not very convincing. More helpful is the list of synapomorphies for node 6 (dichotomy between *Allosaurus*/*Acrocanthosaurus* and Coelurosauria *sensu* Gauthier; Holtz's node 7; Neotetanurae or Avetheropoda); there are four of them upon which diagnosis of the Neotetanurae is based. In this case, fortunately, *Baryonyx* provides clear evidence to show that it has none of them:

105. Axis with spine table.
117. Manual digit I reduced in length.
88. Obturator process present.
92. Pubic boot pronounced ('unambiguous synapomorphy' of Neotetanurae, *fide* Holtz *loc. cit.*).

Certain characters of *Baryonyx*, though used in Holtz's and our analyses and seeming to be apomorphic for that O.T.U., also occur elsewhere in the cladogram. If our suggested phylogeny is correct,

this means that they must have evolved independently in *Baryonyx* and in the other forms concerned. Examples are:

- 5. Pronounced subnarial gap, indicating a possibly mobile premaxillary-maxillary joint. This gap (renamed the *subrostral notch* in *Baryonyx*, see p. 14) occurs also in certain ceratosaurs, namely Coelophysidae and *Dilophosaurus*, and was therefore considered by Holtz (1994a: 1104) to be an unambiguous synapomorphy for the Coelophysoidea. Rowe & Gauthier (1990: 154) claimed that articulated material shows the premaxillary-maxillary joint of ceratosaurs to be a firm junction, as is also the case in *Baryonyx*.
- 77. Nasals narrow. This occurs also in *Dromaeosaurus*, *Archaeopteryx*, *Tyrannosaurus*, *Troodon* and *Ornithomimus*.
- 13. Parietals projected dorsally. This occurs also in *Ceratosaurs* and *Abelisaurus*.

We considered also the partial analysis of Sereno *et al.* 1994 (in which the synapomorphies are listed only under 'References and Notes'). Those authors did consider *Baryonyx*, though not as a separate O.T.U. but as part of the taxon Spinosauridae (see above, p. 56). Their cladogram (Fig. 46) shows the Spinosauridae as the sister-group of Torvosauridae, arising from node 4 (unnamed, our numbering); those two O.T.U.s together as the sister-group of *Afrovenator*, arising from node 3 (Torvosauroidae); and the Torvosauroidae as the sister-group of the Neotetanurae. The Torvosauroidae and the Neotetanurae together constitute the Tetanurae. We replaced Spinosauridae as an O.T.U. by the genus *Baryonyx* on its own, in an otherwise unmodified data-matrix, then ran the programme as described above (p. 57). This produced a single most-parsimonious tree of 58 steps, C.I. 93%, R.I. 90%, identical to the tree figured by Sereno *et al.* except in that *Baryonyx* occupies the position that was previously occupied by Spinosauridae.

This cladogram requires critical scrutiny. Sereno *et al.*'s (1994) linking of the Spinosauridae (which included *Baryonyx*; Spinosauroidae *sensu* this work) with the Torvosauridae (*Torvosaurus* + *Eustreptospondylus*) to form an unnamed taxon is supported by only two synapomorphies:

- 1. Radius less than 50% of humeral length. This is true of *Baryonyx* (49%), but in *Spinosaurus* neither humerus nor radius is known.

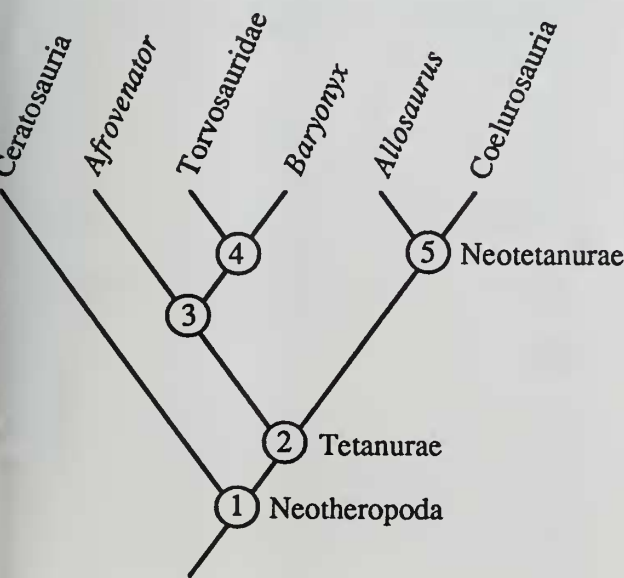


Fig. 46 Cladogram of the Theropoda, according to Sereno *et al.* (1994).

- 2. Manual digit I ungual elongate (three times height of proximal articular end). This is essentially true of *Baryonyx*, where the length of the ungual is more than four times the height of the proximal end: length of ungual measured around the outside of the curve 310 mm, height of end 73 mm. Again, the manus is unknown in *Spinosaurus*.

Thus, while there is no evidence either way for the condition in *Spinosaurus*, it seems that *Baryonyx* and *Torvosaurus* do share two characters. However, such similarities in relative proportions could easily have developed homoplastically and therefore lack phylogenetic significance. Further, while the reduction or absence of a quadrate foramen links *Torvosaurus* with *Afrovenator* (see below), that same foramen is prominent in *Baryonyx*; indeed, it is more of a fenestra than a foramen. Thus there does not seem to be an adequate demonstration of a close phylogenetic link between *Baryonyx* and the Torvosauridae.

Sereno *et al.* (1994) also claimed that this unnamed Torvosauridae + Spinosauridae taxon was the sister-group of their new Saharan theropod *Afrovenator*, ranking the combined taxon as a superfamily and naming it Torvosauroidae (though those same authors, in their 1996 publication, called it Spinosauroidae). This was based on five synapomorphies, all characters of the skull:

- 1. Anterior ramus of maxilla as long anteroposteriorly as tall. In *Baryonyx* the whole of the maxilla as preserved is anterior to the antorbital fenestra and may therefore be presumed to be part of the 'anterior ramus' of Sereno *et al.*; in which case it is several times longer than tall. In *Spinosaurus* practically nothing of the maxilla is preserved and this character-state is therefore unknown.
- 2. Anterior ramus of lacrimal dorsoventrally narrow. In *Baryonyx* this structure, more usually referred to as the nasal or dorsal ramus, shows a condition intermediate between those of *Torvosaurus* and *Allosaurus*. Nothing is known of the condition in *Spinosaurus*.
- 3. Lacrimal foramen small and positioned at mid-length along the jugal ramus. This is confusing in so far as there are three lacrimal foramina in *Torvosaurus* (Britt 1991: 17-19); Britt's photograph of the lacrimal in medial view clearly shows that the large one, which he called the posterior lacrimal foramen, lies one-third of the way down the orbital side of the jugal ramus. In *Baryonyx* also there are three foramina, one large and, close together, two very small ones; the large one lies beneath the junction of the two rami, i.e. at the dorsal extremity of the jugal ramus. The corresponding character-state is unknown in *Spinosaurus*. This proposed synapomorphy is altogether unclear.
- 4. Ventral process of postorbital broader transversely than anteroposteriorly. This character-state is not found in *Baryonyx* and is unknown in *Spinosaurus*.
- 5. Quadrate foramen reduced or absent. *Baryonyx* has a large, prominent quadrate foramen between the quadrate and the quadratojugal. The condition is again unknown in *Spinosaurus*.

In summary, two of the relevant character-states (nos 1 and 2) may be present in *Baryonyx* but it is difficult to have much confidence in them. For the other three (nos 3, 4 and 5) the character is either unclear or in the opposite state. All five characters are unknown in *Spinosaurus*; and none appears in the abbreviated description and diagnosis of *Afrovenator abakensis* published by Sereno *et al.* (1994: 270). We can find no justification for the placing together of these alleged sister-groups.

The net result of our re-working of the analysis of Sereno *et al.*

(1994), with *Baryonyx* replacing Spinosauridae as an O.T.U., is to confirm the systematic position of *Baryonyx* as a 'basal tetanuran', and, at the same time, to cast serious doubts upon any particularly close connexion with *Torvosaurus* and/or *Afrovenator*.

Another cladistic analysis of the Theropoda that deserves brief consideration is that of Russell & Dong (1993: 2122–2125). Many of the O.T.U.s (mostly at family level, but including also *Baryonyx*) were novel, as were many of the synapomorphies proposed, and this resulted in a cladogram that was unusual in several respects. One group, including *Baryonyx*, *Yangchuanosaurus*, *Allosaurus*, dromaeosaurids and tyrannosaurids appeared to be defined 'by the acquisition of horn-like tuberosities along the dorsolateral edge of the skull and relatively large teeth which are few in number' (Russell & Dong, 1993: 2121). In fact, all that appears to pertain to *Baryonyx* in the former connexion is one small tuberosity on the lacrimal. Its teeth (in the lower jaw at any rate) are more numerous than in any other theropod except *Troodon* (Osmólska & Barsbold 1990) and *Pelecaninimus* (Pérez-Moreno *et al.* 1994), both of which are systematically remote from *Baryonyx*. Russell & Dong's analysis does not seem to shed any additional light upon the systematic position of the latter.

Finally, Holtz (1995) published a new phylogeny of the Theropoda in which he proposed a weakly supported monophyletic Megalosauroidae comprising *Afrovenator* + (*Megalosaurus* + *Baryonyx* + *Torvosaurus*).

Conclusions

Our final conclusions on the systematic position of *Baryonyx* are that it should remain as the type-genus of the family Baryonychidae; that its nearest relatives (to be placed in the same superfamily Spinosaurioidea) are the poorly known *Spinosaurus*, *Angaturama* and perhaps *Irritator*; that this group lies within the Tetanurae, close to the base of that taxon, with the Neotetanurae as its sister-group; and that *Megalosaurus* and *Torvosaurus* respectively are progressively more distant outgroups to the combined Spinosaurioidea+Neotetanurae clade.

This is the best that we can do in our present state of knowledge. Our conclusions are subject to the usual caveats:

1. Lists of characters for the same group, drawn up by different authors, are often very different¹ (Charig 1993) and are bound to be far from complete (Panchen 1982).
2. The itemisation of the characters and the scoring of the character-states for the data-matrix require a great number of difficult subjective decisions.
3. Small changes in selection of characters, itemisation and scoring can produce drastic changes in the results of the analysis.
4. Our knowledge of those same character-states in *Baryonyx* is very incomplete, and in certain cases the scoring was likewise difficult.
5. Other authors, generally using very different lists of characters and different O.T.U.s, have produced different cladograms for the Theropoda.
6. The most parsimonious cladogram does not necessarily represent the actual course of evolution (Charig 1982: 414).

At the same time we must point out that, when two or more analyses based on very different lists of characters produce remarkably

similar cladograms, the fact that the shared topology is supported by different rafts of evidence greatly enhances our confidence in its correctness.

PALAEOECOLOGY

In Early Cretaceous times the Weald of Surrey, Sussex and Kent was partly occupied by the Wealden Lake, a large lake of fresh to brackish water that extended westwards into Hampshire. To the north lay dry land in the region of what is now the London conurbation; to the south lay the Anglo-Paris Basin and the open sea. Two large rivers flowed down from the north and north-east to discharge their waters into the lake through a common delta, with shallow creeks and oxbows. The climate was, in modern terms, sub-tropical.

Ross & Cook (1995) have recently reported on the stratigraphy and sedimentology of the Smokejack's locality in particular. The exposure at that site consists of 23 m of Upper Weald Clay, all of it of early Barremian age (estimate of absolute age approximately 130 million years). The *Baryonyx* remains were in fine silty clays of non-marine origin, light olive-grey in colour and containing large irregular nodules of bioturbated sideritic siltstone. The sediments give indications of shallow-water facies (e.g. ripple-marks at the base of the dinosaur level) but show no signs of complete drying out (mud-cracks, erosion etc.), nor is there evidence of braided river deposition; they had obviously settled out of still water (a 'low energy' environment). This lithology, both at the *Baryonyx* horizon and in the beds immediately below, has been interpreted by Ross & Cook as indicating a fluvial and/or mudplain environment with areas of shallow water, lagoons and marsh.

The fossil flora and fauna of the Smokejack's locality as a whole give some idea of the environment in which *Baryonyx* lived (Frontispiece), although it should be remembered that the flora, fauna and total environment all varied significantly at different levels in the sequence. Common plant remains include the fern *Weichselia reticulata* (Stokes & Webb), concentrated locally in layers within the clay and in sideritic lenses, and an aquatic or marsh-dwelling herbaceous plant that grew in monotypic stands. *Bevhalsia pebja* (Hill 1996). Also present were filicopsid ferns, horsetails, club mosses and conifers. Of great importance to the environmental interpretation are the abundance and variety of fossil insects at Smokejack's, 10 orders of which were recorded by Jarzembowski (1984). The exact stratigraphical positions of many of the older finds are not known, but some insects have now been recovered *in situ* from sideritic siltstone lenses at a number of horizons below *Baryonyx* (Ross & Cook 1995). Other elements of the invertebrate fauna were ostracods, isopods, conchostracan and bivalves.

The vertebrate fauna includes sharks, bony fishes (notably *Lepidotes mantelli* Agassiz), crocodiles, pterosaurs, and dinosaurs. Apart from *Baryonyx walkeri*, the only other dinosaur remains yielded by this locality consist of a considerable quantity of material referred to the relatively common ornithomimid *Iguanodon atherfieldensis* Hooley, 1925, and a very few isolated bones of small sauropods. In 1982 we excavated the hind portion of an articulated *Iguanodon atherfieldensis* skeleton at a distance of only about 100 m from the *Baryonyx* site and at approximately the same stratigraphical level. Fragmentary remains of a large *Iguanodon bernissartensis* Boulenger, 1881, were collected in 1988 from a higher level in the sequence.

¹Holtz (1994a) used 126 characters in his analysis of the Theropoda; Sereno *et al.* (1994) used 80 (excluding the Ceratosauria). Even the most generous interpretation could find no more than 17 characters common to both, of which only 4 pertained to the skull and vertebral column.

FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

We (Charig & Milner 1986) have suggested for *Baryonyx*:

- (a) ichthyophagy (a diet consisting mainly of fish) but with the further possibility of a scavenging habit;
- (b) a terrestrial existence; and
- (c) quadrupedality, facultative at least.

DIET AND METHODS OF FEEDING. Kitchener (1987) noted that 'The alternative lifestyle of a scavenger [had] received very little attention' in our paper; he followed this with the full details of our case for a scavenging habit (as presented by us at meetings in Drumheller and Belfast in 1986 but omitted from our publication because of lack of space). Kitchener then went on to state his preference for the idea of a scavenging habit over that of ichthyophagy, a preference which we do not share.

The characters suggesting a scavenging habit, as published by Kitchener, may be summed up as follows:

1. Stance facultatively quadrupedal.
2. Neck long (both 1 & 2 suitable for feeding at ground level).
3. Fore-limbs massively developed, with huge claws (ideal for breaking into a carcass).
4. Snout narrow (well suited to investigating the body cavity of the carcass).
5. External nares placed far back from tip of snout (permitting simultaneous feeding and breathing).
6. Premaxilla and maxilla connected by flexible hinge (allowing freer movement in the restricted space in the body cavity).
7. Teeth slender and finely serrated (for processing the soft viscera).

However, we now know that there is no evidence for characters nos 1, 2 and 6.

Kitchener also put forward one character as evidence against a typical macropredacious habit:

8. Mandible and teeth weakly developed (particularly unsuitable for killing and feeding on large herbivorous dinosaurs). Even crocodilians, after the birds the nearest living relatives of *Baryonyx*, have great difficulty in breaking through the skin of large prey.

He also made two arguments against ichthyophagy:

9. It is unlikely that such a heavy creature 'could have been sufficiently manoeuvrable [*sic*] to catch fast-moving fish'.
10. *Baryonyx* has too many adaptations for fish feeding, viz. fore-limbs for hooking fish and teeth and jaws similar to the fish-eating gavial's; 'one adaptation would suffice'.

In a critical reply to Kitchener, Reid (1987) cited three counter-arguments:

To 3 above: Most available carcasses would probably already have been broken into by the primary predator.

To 8 above: The teeth of modern crocodilians are more or less conical, not adapted to slicing, and are in no way comparable to the bilaterally compressed "steak-knife" teeth of typical theropod dinosaurs. (In fact, the condition in *Baryonyx* is intermediate between the two.)

To 9 above: Large animals, e.g. grizzly bears, are capable of

catching fast-moving fish, at least in shallow water. Techniques analogous to 'gaffing' or trout-tickling could also have been employed.

We add two further comments:

To 7 above: The crowns of the teeth were not slender; in fact, they were less compressed laterally than those of other, more 'typical' theropods.

To 10 above: There is no logic in the argument that, because an animal has two different adaptations that appear to have served the same purpose, neither of them can in fact have served that purpose.

The information that may help us assess the diet and feeding methods of *Baryonyx* is as follows:

1. There is direct evidence of what the animal had been eating. Within its smashed-up rib-cage, in its stomach region, were found:
 - a. Acid-etched scales and teeth of the common Mesozoic fish *Lepidotes* (Fig. 47). These are of especially great significance.
 - b. The disarticulated skeletal remains of a young *Iguanodon* [See Appendix B] showing some evidence of abrasion (and/or etching).
2. There is also circumstantial evidence of the ichthyophagous habits of *Baryonyx*. Modern crocodilians have certain adaptations which are clearly effective in catching and swallowing fishes; analogous characters are found in *Baryonyx*:
 - a. The jaws are long and very narrow from side to side; they are expanded horizontally at the anterior end, with enlarged teeth around the margins of the expansions (Fig. 2). In the upper jaw this spatulate expansion forms a 'terminal rosette', not unlike the corresponding region of the skull of a modern gavial.
 - b. Seen from the side, both upper and lower jaws have sigmoid dentigerous margins (Fig. 1); the upper jaw has a downturned tip and a 'subrostral notch'. Altogether this particular aspect of the animal has an appearance that is distinctly crocodile-like, albeit only superficially so.

These similarities support the idea that *Baryonyx* caught small and moderate-sized fishes in a crocodilian manner, i.e., it seized them with the end of its pincer-like jaws and gripped them transversely in its subrostral notch and lateral teeth; the shape of the jaws and the nature of the teeth accord well with the suggestion that they somehow helped the grasping and manoeuvring of slippery prey. The animal might then have tilted its head back and manoeuvred the fish around so that the fish slid head-first down the gullet into its stomach, as do modern crocodilians. We believe that *Baryonyx* ate fish habitually, though not necessarily exclusively.

Whatever the nature of *Baryonyx*'s preferred diet, the animal seems ill-equipped to have been a typical theropod macropredator of the type that relied largely on short, powerful jaws and blade-like teeth with serrated edges to capture, kill and dismember its prey. This is because:

1. The middle part of each bony ramus of the mandible is wafer-thin.
2. The teeth are only slightly compressed from side to side, thus differing from those of typical macropredacious dinosaurs like *Allosaurus*.
3. The denticles on the carinae of the teeth are remarkably fine (about 7 per millimetre).



A



B

Fig. 47 *Lepidotes* scales, scanning electron micrographs. A, from rib-cage region (Block 44) of the *Baryonyx* skeleton, showing acid-etching of the enamel, $\times 8$; B, from the same horizon and locality but not associated with the *Baryonyx*, showing smooth unetched enamel, $\times 11$.

Conversely, *Baryonyx* possesses characters that suggest different methods of acquiring its food:

1. The jaws are long and narrow, not unlike a pair of forceps. They could have been dipped, either into water to seize relatively small fish, or into the body cavity of a large dead animal to seize the entrails.
2. The external nostrils were lateral and far posterior in position. This would have enabled the animal to continue breathing comfortably even while its snout was still deep in the water or in the body cavity of a carcass.
3. The large and presumably heavy head would have limited the mobility of the neck.
4. The ends of the cervical centra are not "offset"; it is therefore unlikely that the neck would have been held in a sigmoid curve.
5. The cervical vertebrae have well developed epiphyses, but their neural spines are low and lack spine tables. This suggests that the intervertebral muscles were strong and the neck highly mobile, which again would have helped its feeding activities.
6. The humerus is very robust, with both ends broadly expanded. The proximal end in particular is expanded anteriorly into an unusually long and high deltopectoral crest and posteriorly into a well-developed internal tuberosity (compare with other theropods, including *Torvosaurus*). The pectoral girdle too is well developed and there was also an ossified sternum. All this would have facilitated the powerful adduction, abduction (and perhaps rotation?) of the fore-limb as a whole.
7. The radius is relatively short and that too is robust and powerful. The same applies to the ulna without the olecranon, but the olecranon itself is remarkably long; thus the ratio 'length of olecranon/length of ulnar shaft' is exceptionally high. This produced a mechanical advantage (i.e., leverage) when the fore-arm was extended.
8. One manual ungual is enormous; it is of typical theropod form, though somewhat more slender than in *Allosaurus*, and it is not modified into a "sickle" like the enlarged pedal ungual of *Deinonychus* (Ostrom 1969). This was clearly an extremely powerful offensive weapon.

The characters of the fore-limb and manus suggest that the fore-limbs of *Baryonyx* were exceptionally powerful, the fore-arm being capable of exerting great force at the wrist when extended. By activating the enormous claw on the thumb, this would have enabled the animal not only to catch and kill its prey (if necessary), but also to rip and tear it to pieces. In short, the active predation of larger animals and the breaking up of its food were probably performed by the fore-limbs and claws rather than by the jaws and teeth. The enlarged claws could also have been used for 'gaffing', i.e. hooking or flipping fishes out of the water as is done today by grizzly bears.

The fine tooth denticles of *Baryonyx* do not seem to be suitable for the 'rip and grip' cutting action demonstrated by Abler (1992) for more coarsely serrate theropod teeth. Farlow, Brinkman, Abler & Currie (1991) suggested that theropod lateral teeth with very fine denticles might function in a manner indistinguishable from that of smooth-bladed teeth; this might be true of *Baryonyx*. Farlow *et al.* also showed that the lateral blade-like teeth of most theropods displayed a consistent relationship between tooth size and denticle size. They reasoned that a serrated blade might inflict as much damage as a smooth-edged thinner blade but would be less likely to break. Since the blade-like teeth of *Baryonyx* are less compressed than those of most other theropods, the reduction in the size of their denticles might be correlated with their greater robustness.

If we consider the function of the dentition as a whole, all the teeth seem suitable for piercing prey and cutting it smoothly. The long, comparatively straight teeth in the terminal rosette and expanded tip of the dentary also possessed a stabbing function.

Those teeth on the lower jaw that lie below the preserved portion of the maxilla were (on the evidence of the alveoli) smaller, more crowded together, and more than twice as numerous per unit length of jaw as the maxillary teeth that opposed them. A somewhat similar discrepancy is known not only in *Troodon*, which has 15–20 maxillary teeth opposed by 35 in the dentary (Currie *et al.* 1990), but has also been observed in the strange new ornithomimid *Pelecanimimus* (Pérez-Moreno *et al.* 1994). This discordance between the number of teeth in the upper jaw and the corresponding number in the lower is very unusual and, as far as we know, has no analogue among living

reptiles. One might speculate that its functional significance in *Baryonyx* might be somehow connected with the gripping and manipulation of food, the lower teeth forming a closely spaced series of piercing and holding points that opposed the more widely spaced upper teeth.

In connexion with the animal's feeding habits, it should also be mentioned that an apparent gastrolith was found within the rib-cage of the *Baryonyx*.

On balance, we still envisage *Baryonyx* as mainly a fish-eater. It probably crouched on the banks of lakes, creeks and rivers or waded in the shallows (Frontispiece), and it secured its prey by direct seizure with the jaws and perhaps also by 'gaffing'. Small fishes would have been swallowed whole, larger ones broken up by the powerful fore-limbs with their huge claws. Fishing, however, was not the only source of food; there is also:

- 1. Circumstantial evidence that it may well have been both an active predator (using its powerful fore-limbs and claws rather than its jaws and teeth) and/or an opportunistic scavenger.
- 2. Positive evidence (i.e. recognisable bony remains within its rib-cage) that it had eaten a small *Iguanodon*, though whether this was the result of active predation or scavenging cannot be determined.

TERRESTRIALITY. If we accept that fish formed a significant part of the diet of *Baryonyx*, then we must consider the possibility that the animal led an aquatic or semi-aquatic existence. Nevertheless, its anatomy gives no indication of any modifications towards that mode of life. For example, it certainly had no flipper-like modifications of the limbs and it lacked the dorso-ventrally flattened skull with dorsally situated external nares typical of crocodiles. Indeed, the position of the nostrils on the side of the skull would be disadvantageous to an animal spending much of its time in the water. However, *Baryonyx* could probably swim, as can most land vertebrates, despite their lack of any special adaptations.

STANCE AND GAIT. Despite our previous suggestions of quadrupedality (Charig & Milner 1986), the anatomy of *Baryonyx* affords no evidence of a gait any different from that of any other theropod. The length of the humerus of *Stegosaurus*, which is most certainly a quadruped, varies between 43% and 55% of the length of its femur; the corresponding ratio for *Baryonyx* is only 39% (based on an unprejudiced estimate of the femoral length). On the other hand, if *Baryonyx* really was a fish-eater, then it would have been obliged to capture its aquatic prey from a crouching or quadrupedal position, either on the edge of the water or actually in it; and its massive fore-limbs certainly possessed sufficient mechanical strength and adequate musculature for the quadrupedal posture.

TAPHONOMY

The details of the fossilisation of the *Baryonyx walkeri* holotype some of which have already been published in Charig & Milner, 1986) are as follows:

MANNER OF OCCURRENCE. Most of the bones were encased in ideritic siltstone nodules of irregular shape and were directly surrounded by uneven accumulations of extremely fine sand and ilts; such accumulations are not found anywhere else. The rest of the bones lay unprotected in clay.

DEGREE OF ARTICULATION. The bones were largely disarticulated and somewhat scattered.

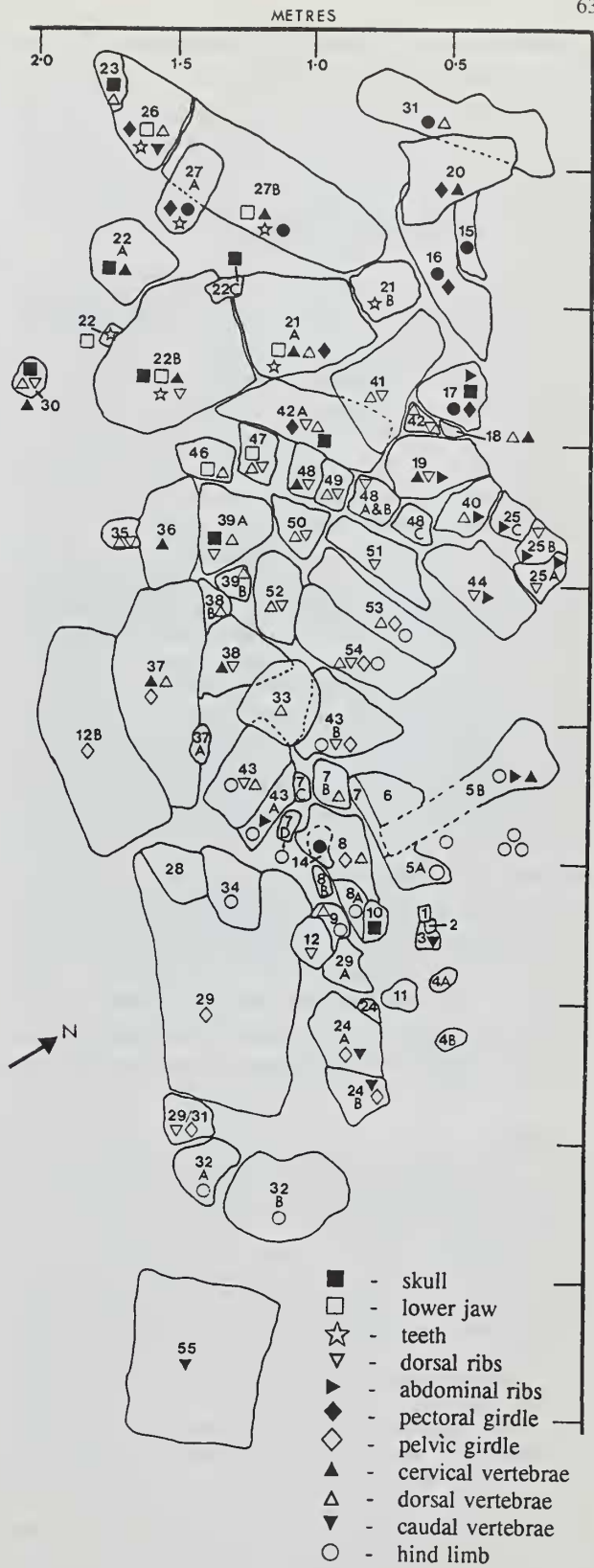


Fig. 48 Plan of the excavation at Smokejack's Brickworks, Ockley, May-June 1983, indicating the *in situ* positions of the numbered blocks and the distribution of skeletal elements.

AREA OF SCATTER. All the bones were found within an area measuring 5m x 2m (Fig. 48).

RELATIVE ORIENTATION OF ELEMENTS. The various elements were generally not far from their natural positions (except for a few that had previously been disturbed by the earth-moving operations). Thus most of the pieces of the skull, pectoral girdle and fore-limbs were at one end of the excavation and most of the pelvic girdle and hind-limbs at the other. (See Appendix B.)

WEATHERING. The degree of weathering of the bones was variable and some were unweathered. The most heavily weathered bones, in particular fragments of rib-shafts and gastralia, show pre-fossilisation splintering, flaking and splitting (stages 2–3 of Behrensmeyer 1978). It should be remembered that the climate of the region was warmer than it is today (more like that of the present-day Mediterranean area) and that the bones lay in a very exposed situation.

DISTORTION AND CRUSHING. Most of the bones were not crushed or distorted to any significant degree, but a few (e.g. the distal end of the tibia) did suffer severe post-mortem distortion.

BREAKAGE. Many of the bones were broken; the skull was in pieces and much of it was missing. However, bones that had lain undisturbed in the clay or in the nodules since fossilisation generally displayed only clean transverse breaks across their shafts, the broken ends showing few signs of weathering or erosion; some were effectively undamaged. In several cases adjacent parts of the same bone, separated by a clean unweathered break, were found in different nodules (for example, both scapulae); after preparation they fitted together precisely. The left dentary had been snapped in half, with the unweathered broken surfaces still in contact with each other at an acute angle. A weathered rib-shaft had been split longitudinally and was preserved with a fragment of another rib wedged at right angles in the gap.

INDICATIONS OF PREDATION OR SCAVENGING. There are no gnaw-marks or punctures produced by the teeth of predators or scavengers.

TEETH. All the lower teeth of *Baryonyx* had fallen out of their sockets, but some of the upper teeth remained in place.

TAIL. The tail was missing almost entirely; all that was found were a few fragmentary vertebrae and haemapophyses, mostly from its base.

Unrelated to all this is the regrettable fact that some of the bones had clearly been broken or severely crushed by mechanical equipment shortly before we collected them.

The deposition of fine-grained sediments around the bones of *Baryonyx* indicates the quiet, low-energy nature of the Smokejack's environment at that particular time; likewise the close association of large and small skeletal elements within a restricted area implies a lack of sorting by currents (Shipman 1981: 31 *et seq.*). These factors suggest that the carcass of the dinosaur was unlikely to have been carried any significant distance by the water, which, in any case, was probably too shallow to float and transport such a huge animal. Indeed, the immediate area of the burial was well suited to be the home territory of a large terrestrial piscivore, catching fish and perhaps scavenging on the mudplain; it might then have become mired in the soft silts, died, and been buried more or less *in situ*.

The excellent preservation of most of the skeletal elements, without evidence of predation or scavenging, suggests that the carcass must have been covered with sediment fairly rapidly. Total decomposition of soft tissues resulted in the disarticulation of the bones, including partial and total separation of centra and neural



Fig. 49 *Baryonyx walkerii*, holotype, BMNH R9951; model of carcass lying on mudbank or in shallow water. Model made by John Holmes.

arches. The differential weathering patterns suggest intermittent surface exposure of parts of the skeleton, either by receding water-level or by shifting of fine sediment. The girdle- and limb-bones, adjacent fragments of which were sometimes encapsulated into separate nodules, had evidently been broken before fossilisation. In particular, the unusual nature of the break in the left dentary suggests trampling by large animals while the bone was buried in shallow sediment (P.J. Andrews, pers. comm.), as does the condition of the split rib-shaft. This interpretation is in accord with the suggested shallowness of the water and sediment, for animals of any size, even the largest, are buoyed up and effectively weightless if the water is deep enough to support them; further, the surrounding sediments would hold the ends of the trampled bones close together and the disarticulated remains would be less liable to wide scattering than they would be at the surface or in clear water. In this context it is interesting to note the observation by Ross & Cook (1995) that the irregular nodules containing swirls of silt and sand at the *Baryonyx* horizon are reminiscent of the red clay, now exposed on the foreshore near Hanover Point on the Isle of Wight, that had clearly been trampled by dinosaurs. Indeed, many of the siltstone nodules found there are casts of large *Iguanodon* footprints, although none of the nodules at Smokejack's resembles footprints.

The total orientation of the bones, disarticulated though they were, suggests that the carcass lay on its back – maybe turned somewhat towards the left (i.e. with its right side uppermost; see Fig. 49). An upside-down position accords with the fact that all the lower teeth have dropped out of their sockets while some of the upper teeth have remained in theirs.

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APPENDIX A. ABBREVIATIONS USED IN THE ILLUSTRATIONS

On all figures stippling denotes matrix; cross-hatching denotes restoration.

III – XI	cranial nerves	gl	glenoid	ot.ca	otic capsule
a.h.l	anterior horizontal lamina	h	head	P	parietal
a.pd.f	anterior peduncular fossa	h.c	haemal canal	pd.g	paradental groove
a.li	anterior ligament scar	hs	hyposphene	p.h.l	posterior horizontal lamina
a.peg	anterior peg	hy	hypantrum	p.li	posterior ligament scar
ac	acromion process	i.m.f	internal mandibular fenestra	pit.fos	pituitary fossa
acet	acetabulum	id.fos	infradiapophysial fossa	pl	pleurocoel
ad.fos	adductor fossa	id.p	interdental plate	pn.f	postnasal fenestra
alv.s	alveolar septum	in.s	internasal septum	po	postorbital articulation
ANG	angular	ipod.l	infradiapophysial lamina	poz	postzygapophysis
ang	angular articulation	ipoz.fos	infrapostzygapophysial fossa	pp	parapophysis
ao.f	antorbital fenestra	iprd.l	infraprezygapophysial lamina	pra	prearticular articulation
ap	pubic apron	iprz.fos	infraprezygapophysial fossa	PRF	prefrontal
ast.fa	facet for lateral tuber of astragalus	is.ped	ischiadie peduncle	prf	prefrontal articulation
at.in	atlantal intercentrum	J	jugal	PRO	prootic
ax.prz	axial prezygapophysis	j	jugal articulation	pro	prootic articulation
BO	basioccipital	k	keel	prz	prezygapophysis
bpt	basipterygoid process	L	lacrimal	pt.fl	pterygoid flange
br.fos	brevis fossa	l.d	lacrimal duct	pu.p	pubic peduncle
br.s	brevis shelf	l.for	lacrimal foramen	Q	quadrate
BS	basisphenoid	l.h	lacrimal horn	q.for	quadrate foramen
cap	capitulum	LS	laterosphenoid	QJ	quadratojugal
con	condyle	m.dc	deltopectoralis muscle	qj	quadratojugal articulation
cor.for	coracoid foramen	m.pe	pectoralis muscle	r.con	radial condyle
cot	cotyle	m.br	brachialis muscle	SA	surangular
CR	coronoid	Mk.g	Meckelian groove	sa	surangular articulation
d	dentary articulation	med.r	median ridge	sh.g	sheath groove
d.sell	dorsum sellae	med.s	median sulcus	SO	supraoccipital
dp	diapophysis	MX	maxilla	so.b	suborbital bar
dp.c	deltopectoral crest	mx	maxilla articulation	SPL	splénial
e.m.f	external mandibular fenestra	mx.no	maxillary notch	spl	splénial articulation
ect	ectopterygoid articulation	mx.s	maxillary sinus	spl.for	splénial foramen
ectoc.t	ectocondylar tuber	mx.t	maxillary trough	spl.g	splénial groove
ep	epipophysis	N	nasal	SQ	squamosal
EX	exoccipital	n.c	neural canal	sq	squamosal articulation
ext.n	external nasal opening	n	nasal articulation	sr.c	subrostral canal
extn.g	extensor groove	nu.g	nutrient groove	sr.f	subrostral foramen
F	frontal	nu.for	nutrient foramen	su.a	supra-acetabular crest
f	frontal articulation	o	orbit	tf.lig	tibiofibular ligaments
f.ov	fenestra ovalis	ob.fl	obturator flange	tib.fa	tibial facet
fib.con	fibular condyle	o.c	occipital condyle	tub	tuberculum
fib.fa	fibular facet	od	odontoid	u.con	ulnar condyle
fl.tu	flexor tubercle	ol	olecranon	V	vomer
g.tr	greater trochanter	OP	opisthotic		

APPENDIX B. LIST OF CONTENTS OF EACH BLOCK

List of elements by field block number.

3	caudal centrum fragment	20	l. cervical rib, l. & r. coracoids	29	ilium fragment, ?l. pubis fragment
5A	<i>Iguanodon</i> humerus, <i>Iguanodon</i> phalanx	21	r. dentary fragment, D1, D2	30	nasal fragments (2), l. quadrate, Ce5, dorsal rib fragments
5B	haemapophysis, gastralia, femur head, astragalus fragment	21A	teeth, l. scapula blade (distal)		
7A	sacral centrum fragment	22A	l. maxilla, nasals, l. lacrimal, l. prefrontal, occiput, teeth, l. cervical rib	31	D3, l. humerus
7B	D5 neural arch (part)			32A	l. femur (distal), r. calcaneum
8	l. ischium, r. ischium head	22B	l. jugal, r. neuropophysis, Ce8, D6 neural arch, l. cervical rib, posterior dorsal rib, gastralia	32B	r. fibula
9	D5 neural arch, D7 neural arch, r. femur (distal)		<i>Iguanodon</i> neural spine	34	l. femur head
10	r. quadrate			36	Ce3
11	<i>Iguanodon</i> , r. femur (distal)	22C	r. frontal/laterosphenoid fragment	37	axis (Ce2), D12–13 (?) neural arch fragment, r. pubic peduncle, r. ischiadic peduncle
12	r. ilium blade	23	premaxillae, dorsal rib fragment		
13*	haemapophysis, ungual phalanx fragment	24A	r. pubis foot	38	dorsal rib fragments
14	two teeth, l. radius, l. ulna		<i>Iguanodon</i> proximal caudal centrum	38B	dorsal rib fragments
15	r. humerus	24B	haemapophyses (2)	39A	l. postorbital, D11 neural arch
16	l. scapula blade, r. radius (proximal)	25	dorsal rib fragments	39B	posterior dorsal rib heads (3)
17	gastralia, r. scapula blade, r. radius (distal)	26	l. dentary tip, teeth, dorsal centrum fragment, proximal caudal neural arch, sternum	40	gastralia
18	D10 neural arch, l. cervical rib	27A	l. dentary, l. & r. splénial, Ce6 centrum, l. manus digit II/III	41	D4 transverse process, dorsal rib heads (4), rib fragments
19	neural spine, dorsal rib fragments (6), gastralia (5), haemapophysis	27B	l. dentary, teeth, l. scapula (proximal)	42	D6 centrum
				42A	D4 centrum, D5 centrum, D6 transverse

	process, D7 neural arch, anterior dorsal rib head, rib fragments, r. scapula (proximal)	47	r. surangular, dorsal rib heads (2) and shaft fragments	54	indeterminate limb fragments, r. femur (distal)
43	D14 neural arch, proximal caudal neural spines (3), dorsal rib fragments	48	Ce6 neural arch, dorsal rib head fragments		D14 centrum, basal caudal centra (2), l. pubis, tibia (crushed), astragalus, distal metatarsal fragments
43	Agastralia, l. fibula proximal fragment	49	D6 centrum, D8 centrum, dorsal rib fragments		<i>Iguanodon</i> left metatarsals II, III, IV, phalanges (3)
43B	dorsal rib fragment, l. distalmost rib, l. pubis (distal)	50	D11 centrum and other centra fragments		caudal centrum fragments (2), haemaphysphes (2)
44	dorsal rib fragments, gastralia	51	<i>Iguanodon</i> dorsal vertebrae	55	
	<i>Lepidotes</i> teeth & scales	52	basal caudal centrum, dorsal rib fragments		
45*	<i>Iguanodon</i> manual phalanges	53	dorsal rib fragments, gastralia, l. pubis fragment, r. femur (distal)		
46	r. angular, dorsal rib heads (4) and shaft fragments		<i>Lepidotes</i> scales		
			<i>Iguanodon</i> supraoccipital, cervical vertebrae,		* Block not marked on plan

APPENDIX C: LIST OF CHARACTERS AND DATA-MATRIX, MODIFIED FROM HOLTZ (1994a)

List of characters employed (the numbers in parentheses at end of each line are Holtz's original character numbers; the publications that follow are those in which these characters were first proposed as synapomorphies).

1. Pubic plate perforated by pubic fenestra below obturator foramen (1; Rowe 1989, Rowe & Gauthier 1990)
2. Distal end of fibula flares to overlap ascending process of astragalus (2; Rowe & Gauthier 1990)
3. Sacral ribs fused to centra in adults (3; Rowe & Gauthier 1990)
4. Cervical vertebrae with transverse processes strongly backturned and triangular in dorsal view (5; Rowe 1989)
5. Pronounced subnarial gap, indicating a possibly mobile premaxillary-maxillary joint (6; Welles 1984, Rowe 1989)
6. Metatarsals proximally co-ossified (7; Osmólska 1981, Rowe & Gauthier 1990)
7. Crista tibiofibularis with sulcus along medial side of base (8; Rowe 1989, Rowe & Gauthier 1990)
8. Axial parapophysis reduced (9; Gauthier 1986)
9. Axial diapophysis lost (10; Gauthier 1986)
10. Axial pleurocoels lost (11; Gauthier 1986)
11. Femoral head directed anteromedially (12; Bonaparte 1991)
12. Premaxilla very deep subnarily (13; Bonaparte 1991)
13. Parietal projected dorsally (14; Bonaparte 1991)
14. Lower temporal fenestra very large (15; Bonaparte 1991)
15. Manual digit III lost (16)
16. Manual unguals with pronounced lip on dorsal edge of proximal articulation (17; Currie & Russell 1988)
17. Parietals fused with laterosphenoids (18; Barsbold 1983)
18. Sternal plates fused (19)
19. Pubic boot longer anteriorly than posteriorly (20)
20. Pubic boot triangular (apex posterior) in ventral view (21)
21. Ilium with preacetabular portion expanded dorsoventrally (22; Gauthier 1986)
22. Astragal condyle with pronounced horizontal groove across anterior face (23; Welles & Long 1974)
23. Supraoccipital crest pronounced (24; Gauthier 1986)
24. Premaxillary-maxillary fenestra (25; Osborn 1912)
25. Insertion area for pterygoideus muscle below mandibular condyle enlarged (26; Gauthier 1986)
26. Lacrimal fenestra present (27; Molnar 1990)
27. Orbit key-shaped (28; Gauthier 1986)
28. Mandibular fenestra reduced (29; Gauthier 1986)
29. Pubic foot projects only posteriorly (30; Gauthier 1986)
30. Pelvis opisthopubic (31; Gauthier 1986)
31. Pedal digit II longer than IV, closer in length to III (32; Gauthier 1986)
32. Obturator process placed distally (33; Gauthier 1986)
33. Ischium not more than two-thirds length of pubis (34; Gauthier 1986)
34. Fourth trochanter lost (35; Gauthier 1986)
35. Proximal caudal vertebrae highly modified (neural spine only in 1-9, box-like centra in 1-5, zygapophysial facets vertical) (36; Gauthier 1986)
36. Prefrontals extremely reduced or lost (37; Gauthier 1986)
37. Frontals separated by an anterior process of parietals (38; Currie 1987)
38. Pedal digit II hyperextensible (39)
39. Ulna bowed posteriorly (40; Gauthier 1986)
40. Furcula present (41)
41. Semilunate carpal present (42; Gauthier 1986)
42. Ischial foot lost (43)
43. Metacarpal III long and slender (44; Gauthier 1986)
44. Ilium with posterodorsal margin curving ventrally in lateral view (45; Gauthier 1986)
45. Coracoid subrectangular (46; Gauthier 1986)
46. Chevrons longer than deep (47; Gauthier 1986)
47. Sacral vertebrae pleurocoelous (48)
48. Quadrate articulation projecting deeply in posteroventral direction (49)
49. Quadrate-quadratojugal articulation mobile (50; Gilmore 1920, Ostrom 1969)
50. Dorsal vertebrae procoelous (51)
51. Humerus sigmoid in anterior view (52)
52. Ilium with preacetabular portion significantly longer than postacetabular portion (53; Currie & Russell 1988)
53. Metatarsals deeper anteroposteriorly than anterolaterally (55; Holtz 1994b)
54. Maxillary teeth lost (56)
55. Fibula with anterior protuberance below expansion (57; Mader & Bradley 1989)
56. Greater trochanter cleft from head (58; Russell 1969)

- 57. Carpals reduced to disc-like structures lacking distinct articular surfaces (59; Gauthier 1986)
- 58. Parasphenoid capsule bulbous (60; Barsbold 1974, Osmólska *et al.* 1972)
- 59. Pterygoid canal present (61; Kurzanov 1976a)
- 60. Metatarsals II and IV contact each other distally on plantar surface (62; Wilson & Currie 1985)
- 61. Frontals long and triangular (65; Currie 1987)
- 62. Arctometatarsus present (66; Holtz 1994b)
- 63. Metatarsus gracile (67; Holtz 1994b)
- 64. Paroccipital process very deep top-to-bottom at root (68; Bakker *et al.* 1988)
- 65. Iliac blades contact along most of dorsal surface (70)
- 66. Ischium bears semicircular scar anteriorly (71)
- 67. Orbit circular and expanded (73)
- 68. Occipital region deflected ventrally (74)
- 69. Endocranium enlarged (75; Russell 1972, Hopson 1980)
- 70. Orbit with pronounced rim (76)
- 71. Lesser trochanter extended by lamella of bone, separate from main body of femur (77; Currie & Russell 1988)
- 72. Cervical zygapophyses flexed (78; Gauthier 1986)
- 73. Subsidiary fenestra between palatine and pterygoid (79; Gauthier 1986)
- 74. Obturator process triangular (80)
- 75. Astragalar ascending process more than one-fourth length of epipodium (81)
- 76. Anterior cervicals broader than deep on anterior surface, with kidney-shaped articular surfaces that are taller laterally than on midline (82; Gauthier 1986)
- 77. Nasals narrow (83; Bakker *et al.* 1988)
- 78. Tertiary antorbital fenestra present (84)
- 79. Anterior cervical zygapophyses elongate (85; Gauthier 1986)
- 80. Jugal expressed on rim of antorbital fenestra (86)
- 81. Number of caudal vertebrae with transverse processes not more than 15 (87; Gatesy 1990)
- 82. Ectopterygoid flange with deeply excavated pocket on ventral surface (88; Gauthier 1986)
- 83. Surangular foramen large (89)
- 84. Cervical vertebrae pleurocoelous (90)
- 85. Obturator foramen lost (91)
- 86. Lesser trochanter placed proximally (92)
- 87. Presacral vertebral column reduced anteroposteriorly relative to femur length (93; Bakker *et al.* 1988)
- 88. Obturator process present (94; Gauthier 1986)
- 89. Basal half of metacarpal I closely appressed to metacarpal II (95; Gauthier 1986)
- 90. Manual digit IV lost (96; Gauthier 1986)
- 91. Tibial shaft with cnemial process arising out of lateral surface (97; Mader & Bradley 1989)
- 92. Pubic boot pronounced (98)
- 93. Astragalar ascending process more than one-sixth length of epipodium (99)
- 94. Tibia with sharp anterolateral ridge for clasping fibula (100; Welles & Long 1974)
- 95. Distal end of fibula reduced (101)
- 96. Coracoid tapers posteriorly (102; Gauthier 1986)
- 97. Occiput, in posterior view, deeper above foramen magnum (103; Bakker *et al.* 1988)
- 98. Surangular with anterior portion deep (105; Gauthier 1986)
- 99. Distal caudals strongly interlocked (106)
- 100. Transition point in tail begins closer to proximal half (107; Gauthier 1986)
- 101. Accessory antorbital fenestra pronounced and round (108; Bakker *et al.* 1988)
- 102. Chevrons attenuated distally (109; Gauthier 1986)
- 103. Last maxillary tooth lies anterior to orbit (110; Gauthier 1986)
- 104. Anterior prong of angular penetrates dentary-splenic cavity (111; Bakker *et al.* 1988)
- 105. Axis with spine table (112; Gauthier 1986)
- 106. Scapula with narrow strap-like blade (113; Bakker *et al.* 1988)
- 107. Interdental plates lost (114)
- 108. Paroccipital root pneumaticised (116; Bakker *et al.* 1988)
- 109. Lesser trochanter aliform (117; Gauthier 1986)
- 110. All three pelvic elements fused together in adults (118; Rowe & Gauthier 1990)
- 111. Premaxillary teeth lost (119)
- 112. Dentary teeth lost (120)
- 113. Number of sacral vertebrae more than five (121)
- 114. Metatarsal IV longer than metatarsal II and closer in length to metatarsal III (122; Holtz 1994b)
- 115. Astragalar ascending process with round external fossa at its base (123; Mader & Bradley 1989)
- 116. Metacarpal I not more than one-third length of metacarpal II (124)
- 117. Manual digit I reduced in length (125; Gauthier 1986)
- 118. Premaxillary tooth crowns asymmetrical in cross-section (126; Bakker *et al.* 1988)

The following characters were used by Holtz (1994) in his data-matrix, but are considered by us to be unsatisfactory:

- 1. Cervical vertebrae with two pairs of pleurocoels (4; Gauthier 1986)
- 2. Tibia and metatarsus elongate (54; Holtz 1994b)
- 3. Occiput deeper above supraoccipital wedge (63; Bakker *et al.* 1988)
- 4. Periotic region with large depression (64; Bakker *et al.* 1988)
- 5. Fenestra ovalis surrounded by large excavation (69; Bakker *et al.* 1988)
- 6. Humerus straight (72)
- 7. Combined premaxillae at symphysis U-shaped (104; Bakker *et al.* 1988)
- 8. Periotic region highly pneumaticised (115; Bakker *et al.* 1988)

O.T.U.s	Character numbers (as listed above)											
	5 65	10 70	15 75	20 80	25 85	30 90	35 95	40 100	45 105	50 110	55 115	60 118
<i>Coelophysis</i>	11111	11111	00000	000??	00000	000?0	00000	00000	00000	01000	00100	00000
	00000	00000	00000	00000	00010	00000	00000	00000	00000	00001	00000	000
<i>Dilophosaurus</i>	01111	01111	00000	000??	00101	011?0	00000	00000	00000	01000	00000	00000
	00000	00000	00?00	00001	00010	00000	00000	00100	00000	10001	00000	000
<i>Ceratosaurus</i>	11110	11000	11110	?00??	10111	10000	00000	00000	00000	00100	10000	0?000
	00000	00000	00?00	00000	00010	00000	00000	00000	00010	00001	00000	000
<i>Abelisaurus</i>	11010	??000	11110	?0000	00101	01000	00000	10000	00000	00101	00?00	0000?
	0?000	00000	00?00	00000	0?010	000?0	11000	01000	00000	10011	001?0	0?0
<i>Elaphrosaurus</i>	1??1?	01000	1????	???0?	00???	???0?	?0?00	?0???	?0?00	0??01	001?0	0???0
	?01?0	0????	00?00	0????	???11	000??	1101?	???11	0?0??	???11	??100	???
<i>Torvosaurus</i>	00?00	0?000	?0?00	0?000	01???	10?00	?0000	?00?0	0000?	0?001	00000	0???0
	?00?0	00?00	?0?00	?000?	???10	?10??	0?010	?000?	001??	?0?00	000?0	0?0
<i>Megalosaurus</i>	0?000	0????	000??	0?00?	11???	??000	?000?	?0?0?	??000	?1??1	00000	0???0
	000?0	?0?00	1??00	?0?0?	??000	01?0?	0011?	0??0?	1?1??	10?10	00000	?0?
<i>Baryonyx</i>	??001	?0000	001?0	00000	??10?	1?000	?00??	???0?	??000	0?001	00?00	0????
	??000	0?00?	?0?0?	01?0?	??01?	??0??	?0???	1??0?	??000	100?0	00???	?00
<i>Allosaurus</i>	00000	00000	00000	00011	11111	11100	00000	00001	00000	01111	10000	00000
	00000	00000	10000	00000	00011	11111	11111	11111	11111	10010	00000	011
<i>Acrocanthosaurus</i>	00?00	00???	0000?	?0?11	??1??	1?000	?0000	?10??	?0???	???01	?00?0	0?0?0
	?001?	00000	10?00	0??0?	01111	111??	11111	?1?11	??0??	??010	?00??	???
<i>Compsognathus</i>	00000	00000	00001	00000	0?00?	00100	00100	?0000	?1000	0?1?0	00000	0???0
	000?0	01000	?0?11	?0000	1?111	11111	?1111	1?111	101?1	10?10	00000	01?
<i>Ornitholestes</i>	00000	00???	00000	00?0?	0?00?	00100	10100	?001?	?111?	00000	10000	000?0
	00000	01000	11?1?	10001	11?11	11111	1??0?	??111	1?1??	?0010	00000	1??
<i>Dromaeosaurus</i>	00000	00000	00000	00000	00000	00011	11111	11111	11111	11111	10000	00000
	00000	00000	01111	11111	11111	11111	11111	11111	11111	100?0	00000	110
<i>Archaeopteryx</i>	00000	00000	00000	00100	00000	00011	11111	1?011	11111	1?0?1	10000	00?00
	000?0	01000	01?11	11111	11011	11111	11111	1?111	111?1	10?00	00000	110
<i>Oviraptor</i>	00000	00000	00000	10100	00000	10000	?1100	10011	11111	01001	10010	10000
	00010	01000	11111	?0111	11011	11111	11111	11011	11?01	11110	11110	11?
<i>Elmsisaurus</i>	00000	00???	0??00	1?000	00???	??000	011??	?001?	?1111	?1??1	?11?0	1??00
	?11?0	??0??	10?11	1??0?	??011	11111	11111	1??0?	??0??	??010	??100	11?
<i>Avimimus</i>	00000	10000	00000	11?00	000??	?0?00	0000?	?001?	?1?0?	?0001	001?0	11001
	?1110	01000	00?01	1??0?	?0011	11111	11111	11???	??001	?1?11	11100	?1?
<i>Tyrannosaurus</i>	00000	00000	00001	01000	00111	10100	00000	01000	01100	01001	00101	11000
	01111	10000	10011	11111	11111	11111	11111	11111	11111	10110	00000	111
<i>Troodon</i>	00000	00???	00000	11?00	00000	00100	00000	00111	111??	?0000	??100	00111
	1111?	?1111	10111	11111	11?11	11111	11111	11111	1111?	?1110	00110	110
<i>Ornithomimus</i>	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00111	11111
	11111	11111	11111	11111	11111	11111	11111	11111	11111	11110	00000	00?