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Palaeontology

VOLUME 35 · PART 1 FEBRUARY 1992



Published by

The Palaeontological Association · London

Price £36.50

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A NEW STEM-GROUP CHORDATE FROM THE LOWER ORDOVICIAN OF SOUTH WALES, AND THE PROBLEM OF LOCOMOTION IN BOOTSHAPED CORNUTES

by I. S. WOODS and R. P. S. JEFFERIES



ABSTRACT. The cornute *Procothurnocystis owensi* gen. et sp. nov., from the Upper Arenig of South Wales, is reconstructed and described. Within the chordate stem-group, it probably represents a plesion between that of '*Cothurnocystis fellinensis* Ubaghs, 1969, on the anticrownward side, and that of *Cothurnocystis elizae* Bather, 1913, on the crownward side. On death by burial, the only known specimen of *Procothurnocystis owensi* seems to have swallowed a mouthful of mud. The locomotory cycles of *Procothurnocystis owensi* and *Cothurnocystis elizae* are reconstructed, using hand-powered working models on appropriate substrates of wet clay or wet sand respectively. In its locomotory peculiarities, *Procothurnocystis owensi* probably represents the more advanced condition and *Cothurnocystis elizae* the more primitive.

THE aims of this paper are to reconstruct and describe the Welsh lower Ordovician cornute *Procothurnocystis owensi* gen. et sp. nov., to suggest its phylogenetic position and to reconstruct its locomotion along with that of *Cothurnocystis elizae* Bather, 1913.

The cornutes and mitrates are here regarded as chordates. The arguments for this view can be found in Jefferies (1986, 1990) and Cripps (1988, 1989a, 1989b, 1990).

We have reconstructed *P. owensi* from latex casts by plotting several projections simultaneously on a drawing board. Dorsal and ventral casts of the specimen were made using latex. Most of the drawings were made from these latex casts. The oral region, however, was reconstructed from an early photograph of the holotype.

PHYLOGENETIC METHODOLOGY

The terms 'total group', 'crown group' and 'stem group' still require explanation (Hennig 1969; Jefferies 1979, 1986). The total group of a monophyletic group comprises the living members of the group and all those extinct organisms which are closer related to the living members than to anything else still extant. The crown group of a monophyletic group comprises the latest species population ancestral to all the living members, and all descendants of that population, whether living or dead. And the stem group of a monophyletic group comprises all members of the total group which are not members of the crown group. A stem group is therefore paraphyletic and extinct by definition.

The stem group will consist of the stem lineage and the side branches. The stem lineage comprises all those members of the stem group which are directly ancestral to the crown group, while the side branches are descended from the stem lineage but not ancestral to the crown group. Within the stem lineage, the autapomorphies of the crown group were successively acquired. The stem group can be divided into a series of plesions, each one comprising all those organisms which, so far as can be determined, are equally closely related to the crown group (for this definition of the word plesion, see Craske and Jefferies 1989).

SYSTEMATIC PALAEOLOGY

Superphylum DEUTEROSTOMIA Grobden, 1908
 Subsuperphylum DEXIOTHETICA Jefferies, 1979
 Phylum CHORDATA Bateson, 1886
 (Stem group of the Chordata)
 (Plesion of *Procothurnocystis owensi* herein)
 Genus PROCOTHURNOCYSTIS nov.

Type species. Procothurnocystis owensi sp. nov.

Diagnosis. A *Cothurnocystis*-like cornute with an x plate but no y plate, with the k-, t- and f-spikes convex-bottomed in transverse section and protruding rearwards, a horizontally flexible hind-tail, the stylocone deeply embedded in the fore-tail, two pairs of dorsal fore-tail plates corresponding to each of the 1st–4th pairs of ventral fore-tail plates, and two pairs of ventral plates (dorsal ventrals and ventral ventrals) in the 5th (most distal) fore-tail ring.

Remarks on systematic 'address'. Categorical rank for groups above the species level is arbitrary (Ax 1984, 1987; Craske and Jefferies 1989). It ought therefore to be discontinued except for the genus, which must be kept for nomenclatorial reasons. In the above systematic 'address', the traditional ranks of phylum and superphylum are quoted for the sake of completeness, while subsuperphylum is obtained by interpolation. The omission of all other categorical ranks is intentional.

Procothurnocystis owensi sp. nov.

Plate 1, figs 1–4; Plate 2, fig. 3; Text-figs 1–6, 11–12

1987 '*Cothurnocystis*' sp.; Jefferies in Fortey and Owens, p. 287, fig. 139a–b.

Etymology. This species is named in honour of Dr Robert M. Owens, of the National Museum of Wales, Cardiff, who found the only known specimen and allowed us to describe it.

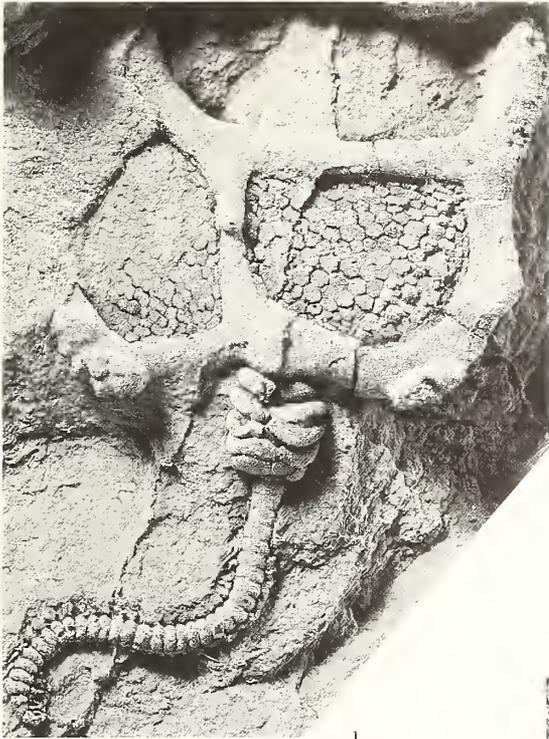
Holotype. The unique specimen is conserved in the Department of Geology, the National Museum of Wales, Cardiff, with the registration number NMW 84.17G.119. It was found in May 1979, by Dr R. M. Owens, of the National Museum of Wales, at locality 24 of Fortey and Owens (1987, p. 109; for map see fig. 2, p. 77), in the upper Arenig Pontyfenni Formation in the disused quarry near the farm of Llwyn-crwn, near the village of Whitland, Dyfed. The exact locality is at 112° and 117 m from the farm (National Grid Reference SN 2399 1795).

The specimen was preserved fully articulated and seemingly in life position. It was presumably killed by sudden burial. A last, enforced mouthful of mud can be seen in a photograph taken, shortly after discovery, at the National Museum of Wales (Pl. 1, fig. 3).

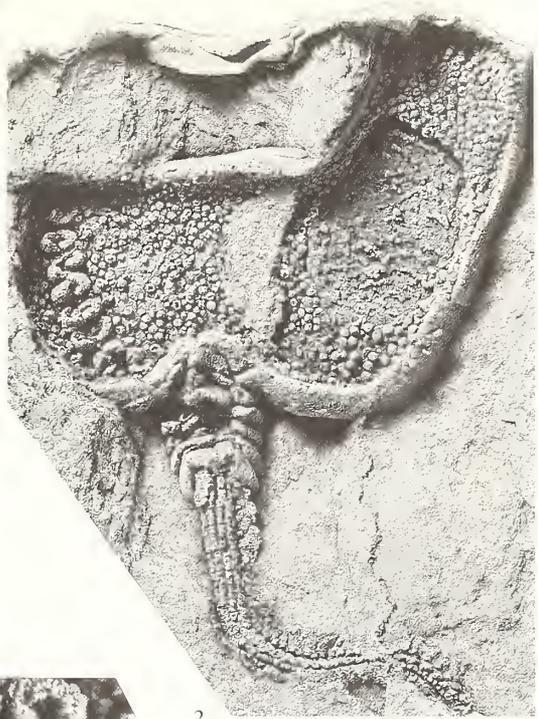
The early photograph of the specimen shows that it was almost complete when found, lacking only the anterior parts of the oral appendages (b and c). However, it has unfortunately since lost much of the oral

EXPLANATION OF PLATE 1

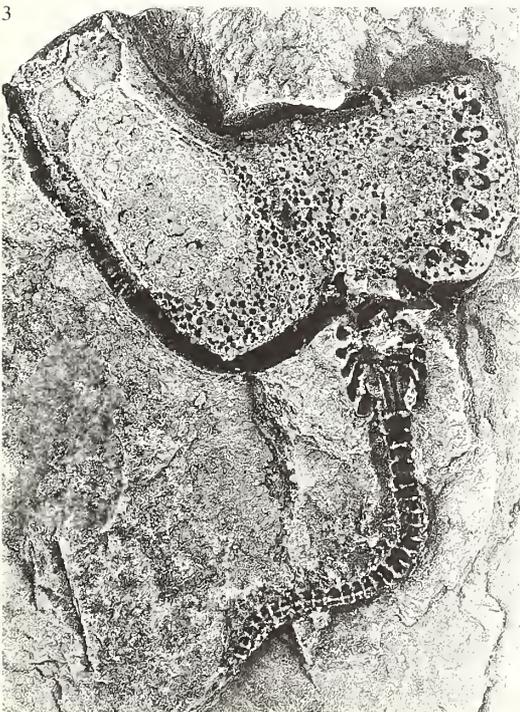
Figs 1–4. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; Whitland, Dyfed; Pontyfenni Fm. 1, latex cast of ventral surface, $\times 4$. 2, latex cast of dorsal surface, $\times 4$. 3, natural mould in ventral aspect, as shown by an early photograph from the National Museum of Wales; note the 'last mouthful of mud' behind the mouth, the presence of plates b, c, v and w and of a single oral spike-shaped plate near the mouth, the infilling of the gonorectal groove and sculpture of the dorsal surface of the stylocone, $\times 4$. 4, latex cast of the branchial region in dorsal aspect; the 3rd, 4th, 5th, 6th and 7th slits show a facet on the anterior U-plate for attachment of the tongue, there being no such facet on the respective posterior U-plate; the platelets of the flexible tongue are visible inside the 8th slit, $\times 16$.



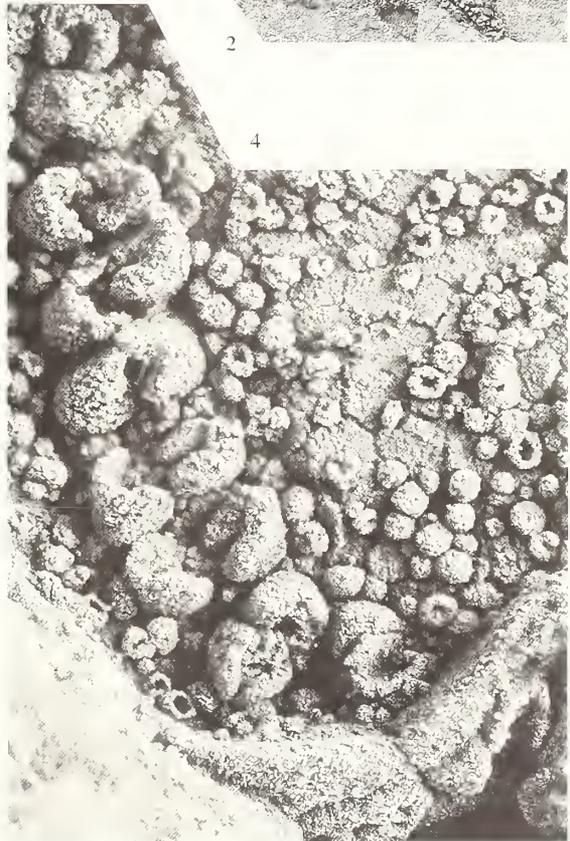
1



2



3



4

region, including the stumps of b and c, the v and w plates, and much of the d plate. The damage is highly regrettable and probably results from the taking of latex casts.

Diagnosis. As for genus.

Description. See anatomical description below.

Stratigraphical occurrence. Lower Ordovician, upper Arenig, Pontyfenni Formation.

ANATOMY OF *PROCOTHURNOCYSTIS OWENSI*

An alphabetical notation (Jefferies and Prokop 1972) is used for the head plates. Plates given the same letter in different cornutes are believed to be homologous.

Procothurnocystis owensi, like all cornutes and mitrates, consists of a head and tail (Text-fig. 1A, E-F). The head is 16 mm at its widest point and the whole animal, if the tail were straightened and excluding the oral appendages (not preserved), is 29 mm long (head 14 mm, tail 15 mm). The head is asymmetrical and boot-shaped and is bordered by a marginal frame of seventeen calcite plates.

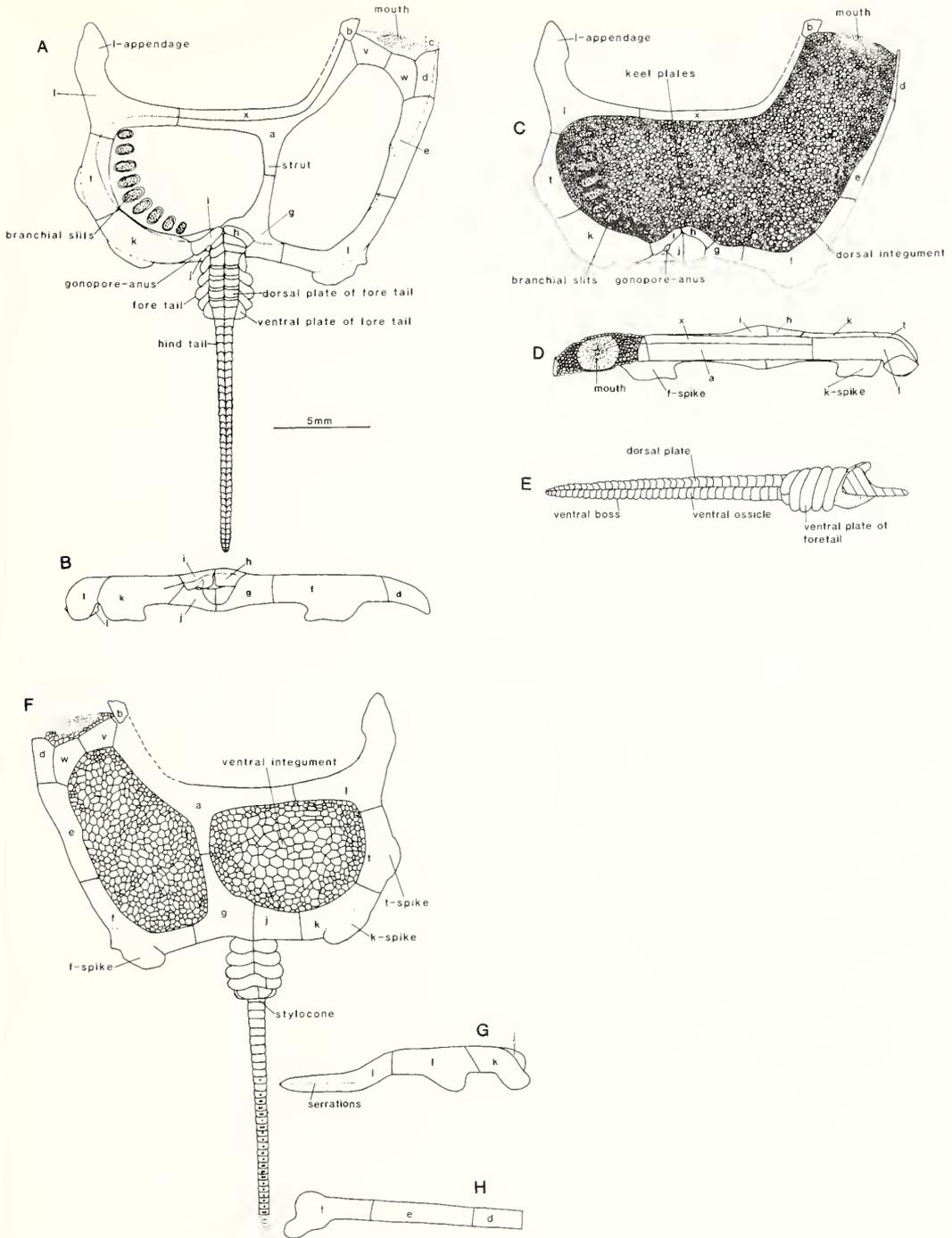
P. owensi is compared here especially with *Cothurnocystis elizae* Bather, 1913 (see Jefferies 1986, fig. 7.2a-b; Jefferies *et al.* 1987, text-fig. 14) which represents the more crownward adjacent plesion, and with '*C. fellinensis* Ubaghs, 1969 (Pl. 2, figs 1-2) which represents the less crownward adjacent plesion.

The ventral and dorsal integuments of the head of *P. owensi* were plated. As in most cornutes, the ventral integument was divided into two by the ventral strut, formed from parts of marginal plates a and g. The plates of the ventral integument were polygonal. Near the marginal frame and strut they were small and elongate, with their long axes parallel to the frame or strut, while in the middle of the two areas of integument they were larger and not elongate.

Dorsal integument. The dorsal integument was plated with numerous small plates, circular in plan view, which rarely contacted one another. A series of nine gill slits exists in the left part of the dorsal integument, near to plates t and k (Pl. 1, figs 2, 4). The smallest dorsal integument plates occur near the plates of the head frame and also around the gill slits. Their small size indicates that the integument was especially flexible in these regions. The plates in the middle of the integument are mostly larger. Some smaller plates occur between the larger integument plates and may represent newly formed plates.

There are three spines on the left part of the dorsal integument, about half way between the anterior and posterior parts of the frame (Text-fig. 1C; Pl. 2, fig. 3). The axes of the spines lie in the fossil approximately parallel to the longitudinal axis of the head. Each spine is widest proximally, pointed distally and about 1 mm long. These spines correspond in position to the left keels of the primitive cornutes *Ceratocystis perneri* Jaekel, 1900, *Protocystites menevensis* Hicks, 1872 (Jefferies *et al.* 1987) and *Nevadaecystis americana* Ubaghs, 1963 (Jefferies 1986, fig. 7.27). Presumably they represent, in some way, vestiges of such a keel. They are termed keel spines and are equivalent to the six 'épines' noted by Ubaghs (1969, p. 47) in a similar position in '*Cothurnocystis fellinensis* (Pl. 2, fig. 2). Neither in '*C. fellinensis* nor in *P. owensi* is there any evidence for keel spines elsewhere on the dorsal integument.

The head frame. Three spikes exist on the ventral surface of the head frame, named f-spike, k-spike and t-spike after the plates which bear them. Unlike *Cothurnocystis elizae*, the lower surfaces of the spikes are convex in transverse section rather than flat. The axis of the f-spike runs rightwards anteriorly. The spike terminates in a rounded protuberance posteriorly while anteriorly it slopes into the contours of the f plate. The k- and f-spikes are both partly visible in dorsal view. The axis of the k-spike runs leftwards anteriorly, but is otherwise similar to the f-spike. The t-spike runs



TEXT-FIG. 1. Reconstruction of *Procothurnocystis owensi* gen. et sp. nov. A, dorsal aspect without integument. B, posterior aspect of head. C, dorsal aspect of head with dorsal integument. D, anterior aspect. E, right lateral aspect of tail. F, ventral aspect. G, left lateral aspect of head. H, right lateral aspect of head, c-appendage omitted.

leftwards anteriorly, but at a smaller angle to the long axis of the cornute than either the f- or k-spikes. The posteriorly directed bosses of the k-, t-, and f-spikes in *P. owensi* are exactly contrary to the usual cornute condition of forward-pointing spikes, as seen, for example, in *Cothurnocystis elizae*.

Plate l is long, being about the same length as in '*Cothurnocystis*' *fellinensis*. It is dorso-ventrally flattened and has sharp lateral edges. There is an abrupt downward kink about 0.4 of the length from its posterior end (Text-fig. 1G), so that the anterior part lay lower than the posterior part.

There are two oral appendages (b and c). Their bases can be seen in the early photograph (Pl. 1, fig. 3) but they are incompletely preserved and their shape is therefore unknown. In the locomotory reconstructions the b and c appendages are based on those of '*Cothurnocystis*' *primaeva* Thoral, 1935 (see Ubaghs 1969, pl. 6, fig. 1).

Plate a forms the ventral part of the median anterior region of the head frame. Its posterior projection which, with part of plate g, forms the ventral strut, is relatively shorter than in '*C.*' *fellinensis* but longer than in *C. elizae*. The anterior bend in plate a of *P. owensi* is less abrupt than that of *C. elizae*.

Plate x is dorsal to plate a. In dorsal aspect, it is shaped like a reversed L, though the angle between the branches is obtuse rather than perpendicular. In having an x plate, *P. owensi* resembles '*C.*' *fellinensis* and differs from *C. elizae*.

The relative positions of plates v, w, d and c are much the same in *Procothurnocystis owensi* as in '*C.*' *fellinensis* and *C. elizae*.

A ridge runs dorso-ventrally on the inner face of plate e, somewhat anterior to the middle of the plate (Text-fig. 1A; Pl. 1, fig. 3). This ridge, and the bend in the x and a plates on the left side of the buccal lobe, probably indicate the position of the posterior border of the buccal cavity.

Plate g is constructed much as in '*C.*' *fellinensis*. Its anterior projection, to form part of the strut, is not as long or slender as the homologue in *C. elizae*.

Plates h and i in *Procothurnocystis owensi* have only a slight area of contact with each other (Pl. 1, fig. 2). Their mutually contacting surfaces are rounded, rather than being sutured as in *C. elizae*. Plates h and i have a strongly convex anterior face and a concave posterior face.

There is no plate y in *Procothurnocystis owensi*, although this plate exists between plates h and i of many cornutes such as *Ceratocystis perneri*, *Protocystites menevensis*, *Phyllocystis* spp. and '*Cothurnocystis*' *fellinensis*. The absence of plate y, and of the median eye which it always carried, is probably a synapomorphy of *P. owensi* with more crownward cornutes.

Plates g and j of *Procothurnocystis owensi* meet in the ventral mid-line of the tail insertion, as is usual in cornutes. Viewed from behind, there would be a gap between plates h, i, g and j (Text-fig. 1B). This gap connected the space inside the head skeleton with the lumen of the fore tail.

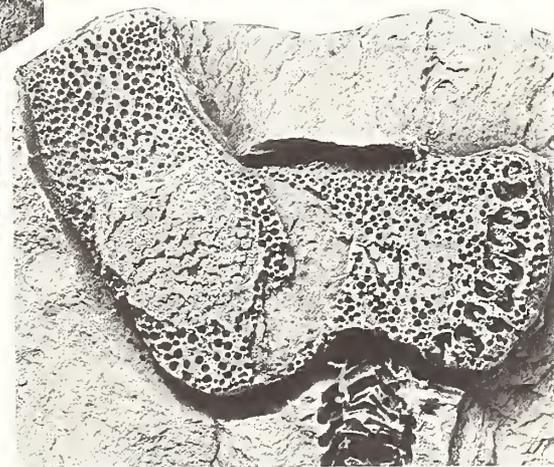
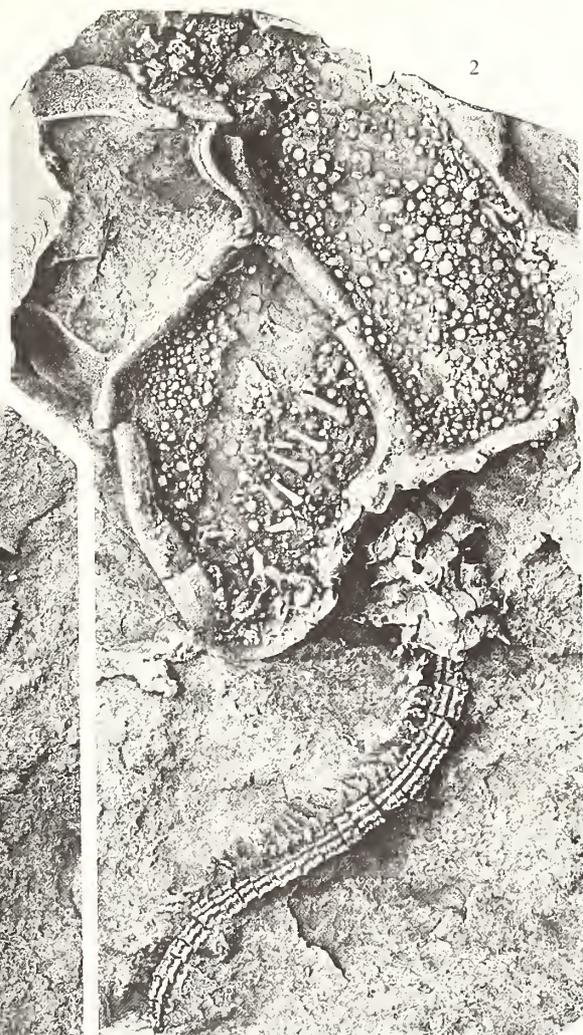
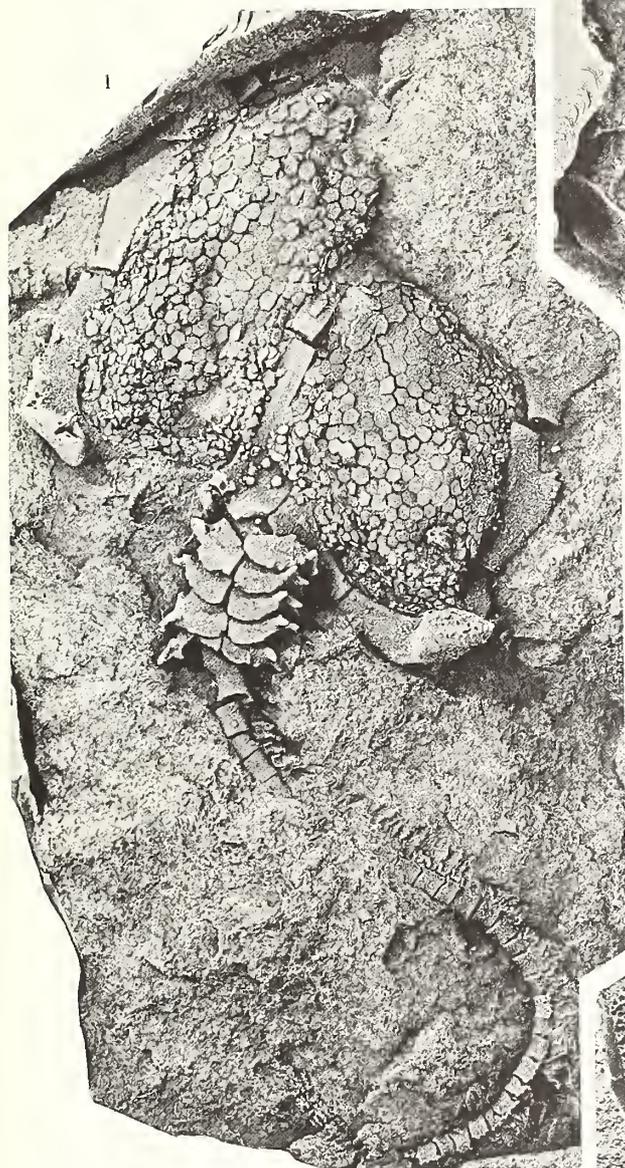
The cross-section of all the marginal plates, except the appendages, is approximately triangular – the medial face is slightly concave and is perpendicular to the convex ventral face while the third, external dorsal face links these two and is also convex. The internal faces of the marginal plates are rarely visible.

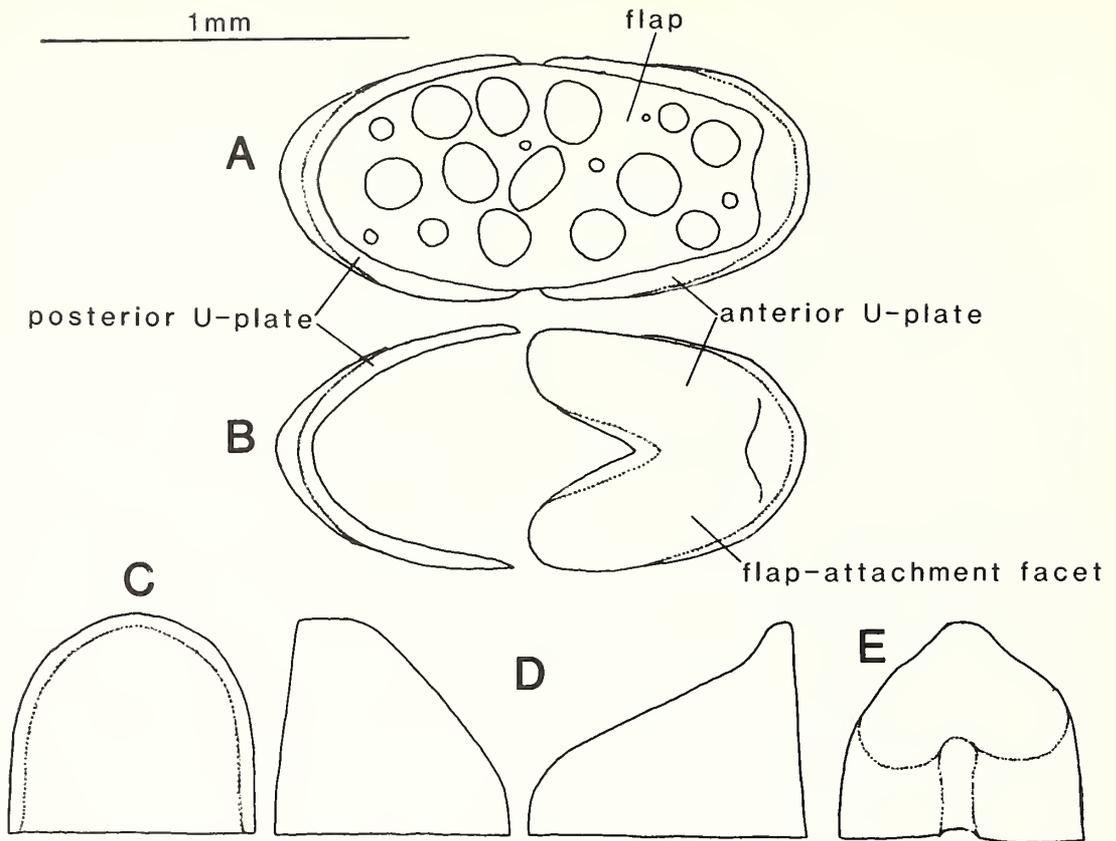
Head openings and branchial skeleton. The openings of the head are anatomically crucial. A series of nine similar openings is situated in the left, 'toe', part of the dorsal integument (Text-figs 1A, C,

EXPLANATION OF PLATE 2

Figs 1–2. '*Cothurnocystis*' *fellinensis* Ubaghs, 1969. Latex moulds of unique specimen and holotype; University of Lyon 508. 1, ventral aspect, $\times 4$. 2, dorsal aspect, note the keel spines and the curvature of the hind-tail (cf. Text-fig. 11/2), $\times 4$.

Fig. 3. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; Whitland, Dyfed; Pontyfenni Fm.; natural mould in ventral aspect in its present condition; note the three keel spines in the left part of the dorsal integument, $\times 4$.





TEXT-FIG. 2. *Procothurnocystis owensi* gen. et sp. nov. Skeleton of a gill slit. A, dorsal aspect with flap in place. B, dorsal aspect without flap. C, posterior U-plate seen from inside branchial slit. D, lateral aspect of the skeleton of a slit. E, anterior U-plate seen from inside slit.

2A-E; Pl. 1, figs 2, 4). Each of these openings is framed by an anterior and a posterior U-shaped plate of approximately equal size, which articulate with each other by touching at the free ends of the U's. There is evidence, in the form of platelets preserved within the paired U-plates (Pl. 1, fig. 4, especially the second opening from the right), that a flexible flap of integument, containing these platelets, was attached to the anterior U in life. The free end of the flap would have extended rearwards to cover the posterior U. The anterior U has a thick dorsal margin and an anterior-dorsal facet, presumably for flap attachment (Pl. 1, fig. 4, especially the 6th and 7th openings from the right). The posterior U has a considerably narrower dorsal margin, with no facet for flap attachment. These openings can readily be interpreted as outlet valves and therefore as gill slits (Jefferies 1986, p. 193).

The position of the mouth in the reconstructions, because of the above-mentioned damage to the specimen, is based mainly on the early photograph (Pl. 1, fig. 3). The latex cast and rock mould of *P. owensi* provide additional data. The early photograph clearly shows at least one plate of the oral pyramid and the positions of plates b, c, v, w and d on a natural mould mainly of the dorsal surface. This evidence of an anteriorly placed mouth is supported by an examination of the dorsal integument of the buccal region, which shows that the mouth did not open there.

A layer of rock, shown clearly in the early photograph (Pl. 1, fig. 3), separates the dorsal and ventral integuments in the region behind the mouth, but not elsewhere. This layer probably

represents a mouthful of mud, swallowed by the animal just before it died. Such a mouthful of mud suggests that *P. owensi* was a deposit feeder, taking in food particles sucked in from the topmost layer of bottom mud or the lowermost layer of water.

The gonopore–anus opens left of the tail (Text-figs 1A–C, 5A; Pl. 1, fig. 2; Pl. 3, fig. 1). The gill-slit series ends just left of the gonopore–anus, as in *Nevadaecystis americana* (see Ubaghs 1963) but unlike *Cothurnocystis elizae*. In *Protocystites menevensis* Hicks, 1872 the gonopore–anus is likewise located to the left of the tail. In the reconstruction of this species given by Jefferies *et al.* (1987) the gill-slit series is shown as extending in front of the gonopore–anus, as in *C. elizae*, but it does not in fact do so, as shown by examining text-figures 10a and 15 and plate 54, figure 1 of that paper. The situation in *P. owensi*, with the gill-slit series stopping just left of the gonopore–anus, being thus found in the anti-crownward plesions of *N. americana* and *P. menevensis*, is probably primitive compared with the condition in *C. elizae*.

Chambers and soft anatomy of the head. Because of the preservation of the fossil, only a limited amount can be said about the internal soft anatomy of the head.

The buccal cavity would be bounded, posteriorly on the left, by the abrupt bend in the a and x plates and, posteriorly on the right, by the almost vertical ridge running down the medial face of the e plate.

The position of the posterior coelom can be inferred only by comparison with *C. elizae* and other cornutes. The infilling of the gonorectal groove can be seen crossing the posterior coelom in the early photograph (Pl. 1, fig. 3), but no other internal features are visible in this region.

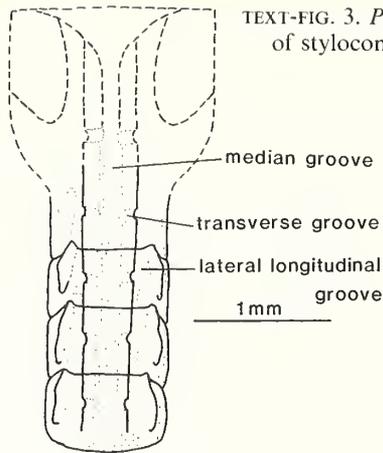
The pharynx was probably the largest chamber in the head. Towards its left end, the row of nine gill slits presumably opened through its roof.

The ridge on the internal mould which represented the infilling of the gonorectal canal is shown to enter the region of the posterior coelom from anterior right in the early photograph of the specimen (Pl. 1, fig. 3). This suggests that the patent part of the right anterior coelom, which would have contained the gonad and most of the non-pharyngeal gut, lay in its invariable cornute position, in the posterior right part of the head (the 'heel' part of the 'boot').

Attachment of the dorsal integument. The dorsal integument would be attached near the upper edge of the medial face of the marginal plates. On some plates, such as x and t, a narrow, horizontally elongate groove is seen at the top of the approximately vertical medial face, and this groove is probably an attachment facet for the dorsal integument. On plates k, i and h, however, the same groove passes onto the dorsal surface of the plates. In the only known specimen, the dorsal integument is still largely attached to the frame but has been pushed down into the head by the weight of overlying sediment. Thus most of the medial face of the marginal plates is obscured by the dorsal integument.

The tail. The tail of *P. owensi* is well preserved in both dorsal and ventral aspect (Text-figs 1A–H, 3–6; Pl. 1, figs 1–3).

The skeleton of the fore-tail (Text-fig. 5) is complicated and differs considerably from the condition normal to cornutes as represented by *Cothurnocystis elizae* for example. Such normal forms show a number of imbricating rings, each comprising a symmetrical pair of large ventral plates and a symmetrical pair of smaller dorsal plates. In *Procothurnocystis owensi*, the fore-tail plates are similarly arranged in rings, there being five such rings altogether. The first three rings are normal, except that there are two pairs of dorsal plates for each ring (Pl. 3, fig. 1), instead of one pair. Probably the anterior pair in each ring, which are much larger than the posterior pair, are homologous with the dorsal plates of other cornutes, whereas the posterior pair represent an autapomorphy of *P. owensi*. The ventral plates of each of these three rings are sutured together in the mid line, while the dorsal plates are not sutured medially but meet at a rounded edge. The ventral plates of the first three rings form, in transverse section, about three-quarters of the circumference of the tail, the remaining quarter being formed from the dorsal plates.



TEXT-FIG. 3. *Procothurnocystis owensi* gen. et sp. nov. Reconstruction of stylocone and of the first hind-tail ossicles in dorsal aspect.

The fourth ring is like the first three, except that the suture between the two ventral plates is left of the midline (Pl. 3, fig. 2; Text-fig. 5C-D).

The fifth ring is different. There is a single pair of dorsal plates, as usual in cornutes, rather than two pairs (Pl. 3, fig. 1). And, on the other hand, there are two pairs of ventral plates, i.e. dorsal ventral plates, and ventral ventral plates (Pl. 3, fig. 2; Text-fig. 5C-D).

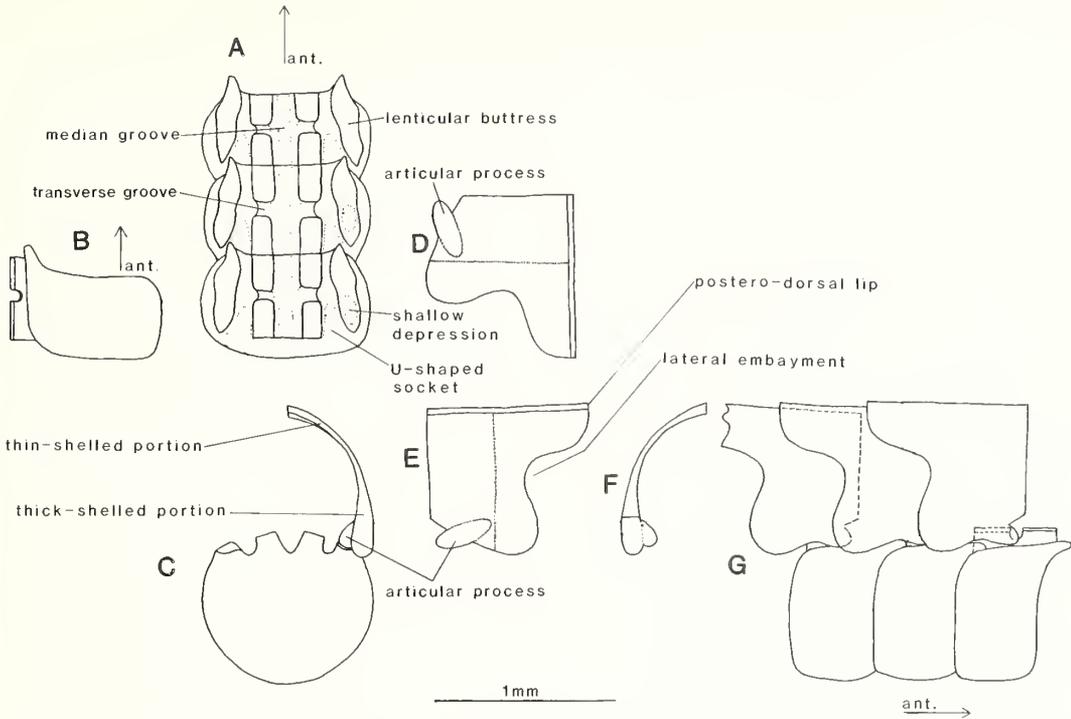
Concerning other points in the fore-tail anatomy, at the front end of the fore-tail two pairs of plates fill the gap between the first ring and plates h and i (Text-figs 1A, 5A-B; Pl. 1, fig. 2). Each fore-tail ring imbricates over its more posterior neighbour. Ventrally the posterior margin of the ventral plates points anteriorly in the midline. In lateral view the posterior margin of the ventral plates is convex posteriorly. Altogether, there are eleven pairs of imbricating dorsal plates in the fore-tail and this is about double the usual number of dorsal plates as seen in *C. elizae* or '*C. fellinensis*'.

As discussed below, the fore-tail has the stylocone deeply inserted into it and the anterior excavation of the stylocone is very shallow. For both these reasons, there would have been very little space inside the fore-tail for muscle (see Text-figs 1A, E-F, 3; Pl. 1, figs 1-3).

The structure of the fore-tail is suited to dorso-ventral flexion in its anterior part, i.e. in front of the anterior end of the deeply inserted stylocone. The dorsal plates are particularly adapted to allow ventral flexion, since their large numbers would allow the dorsal surface to stretch. The posteriorly convex shape of the ventral plates in lateral aspect (Text-fig. 1E) would allow them to flex in a vertical plane.

The stylocone of *P. owensi*, as mentioned, is deeply inserted into the fore-tail – only about one tenth of its length would have been visible from outside when the animal was alive (Pl. 1, fig. 3). This deep insertion is unique among cornutes. The stylocone is vase-shaped, with a slim stem posteriorly and the greatest breadth anteriorly (Text-fig. 3). It overlies the ventral parts of the three most posterior rings of the fore-tail and is itself overlain by the dorsal plates of these three rings. A single pair of dorsal plates, immediately posterior to the fifth ring of the fore-tail, articulate with the stylocone.

The sculpture of the dorsal surface of the stylocone is shown in the early photograph (Pl. 1, fig. 3; Text-fig. 3) and confirmed, in part, by the latexes and specimen in their present state. There is a median groove, believed to have contained the notochord. From this groove in the stylocone extend two pairs of transverse grooves. The precise outline of the stylocone is doubtful. The early photograph shows a pair of large but shallow lateral excavations situated antero-laterally on the dorsal surface of the stylocone. As already said, the anterior median excavation of the stylocone



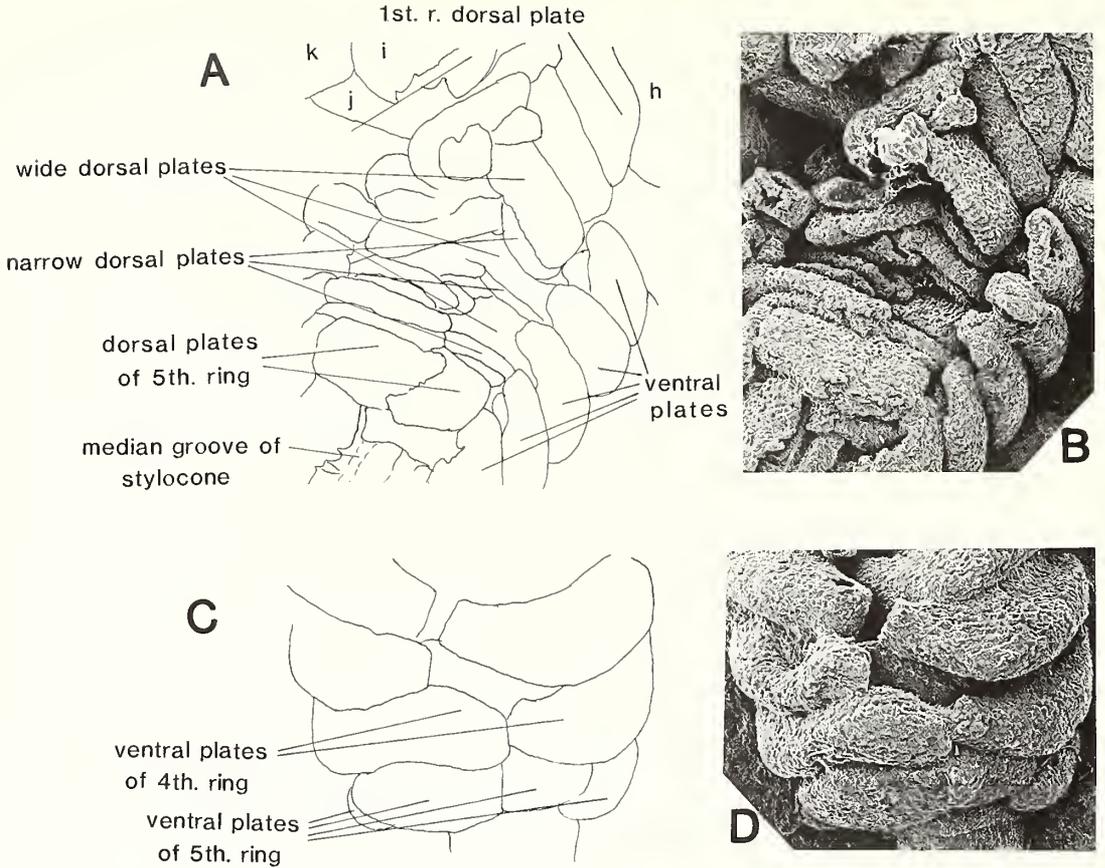
TEXT-FIG. 4. *Procothurnocystis owensi* gen. et sp. nov. Anatomy of the hind-tail. A, dorsal aspect of three hind-tail ossicles. B, right aspect of a hind-tail ossicle. C, posterior aspect of a hind-tail ossicle and of right dorsal plate in life position. D, medial aspect of plate rotated transversely from its life position without movement anteriorly or posteriorly. E, medial aspect of the same plate in its life orientation, rotated 90° from its position in C. F, anterior aspect of the same plate. G, right lateral aspect of three ossicles and three plates.

seems to have been much shallower than in other cornutes. This is shown by the same photograph (Pl. 1, fig. 3).

The hind-tail consists of thirty-five segments. The skeleton comprises ventral ossicles and paired dorsal plates meeting in the midline.

There is one ventral ossicle in each segment of the hind-tail. The sculpture of the dorsal surfaces of the ossicles can be seen in several places (Text-figs 4A, 6; Pl. 1, fig. 2). It consists of a median groove with a pair of ill-defined longitudinal lateral grooves to left and right of it in each ossicle. From the median groove, a pair of transverse grooves run out in each ossicle, to open into the lateral grooves. The longitudinal lateral groove shows a slight deepening at the end of each transverse groove. At the posterior end of each longitudinal lateral groove in each ossicle there is a shallow U-shaped excavation. Lateral to the lateral groove there is a slightly raised lenticular facet, running approximately parallel to the median groove but diverging slightly outwards and rearwards. For each ossicle, the anterior end of the lenticular facet is carried forward as the dorsal surface of an articulation horn and projects somewhat into the U-shaped excavation of the next ossicle in front (Text-fig. 6A-B). Towards the posterior end of the lenticular facet is a shallow elliptical depression, which presumably articulated with an articular process seen on the dorsal plate (Text-fig. 6C-D). The proximal ventral ossicles are roughly semicircular in transverse section whereas more distal ossicles are wider relative to their depth.

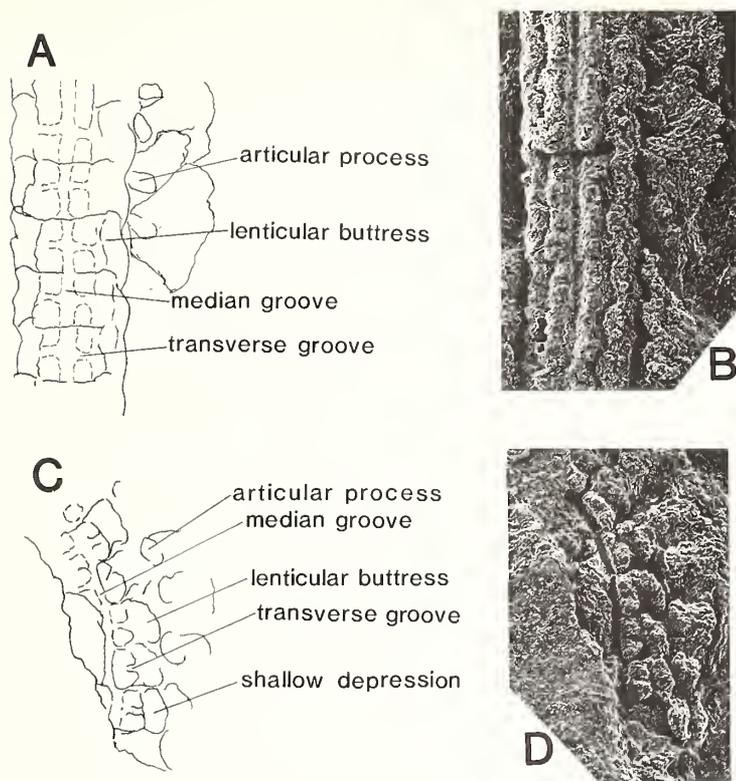
Thus the ossicles articulate together. The nature of this articulation is that, on right and left, an anterior lateral horn (which bears on its dorsal surface the anterior end of a lenticular facet) projects



TEXT-FIG. 5. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; scanning electron micrographs (B, D) and explanatory sketches (A, C) of latex casts of fore-tail; all figures $\times 15.4$. A–B, dorsal aspect; C–D, ventral aspect.

into the shallow U-shaped excavation in the next ossicle anterior (Text-fig. 4A–B, G). The shape of the anterior horns of each ossicle, and their articulation with the next ossicle in front, suggest that a little flexing may have occurred in the vertical plane. However, it is clear from the shape of the ossicles and dorsal plates, and from the posture of the fossil as preserved, that the more distal portion of the tail (ossicles 9–35) could flex much more strongly in the horizontal plane than vertically. The preservation of the fossil also suggests that the hind-tail corresponding to ossicles 1–9 was probably almost rigid in all directions. The junctions between the more proximal ossicles were planar (except for the articulation horns) but it was difficult to assess the curvature of such junctions more distally. In the series of ossicles from 9 to 35 it seems that the tip of the tail could probably be flexed in the horizontal plane through a total of 180° or more, as indicated by the preserved posture of the hind-tail in the fossil (Pl. 1, figs 1–3).

The ventral face of each of the more posterior ossicles is developed as a broadly convex ventral boss. From ossicle 11 rearwards most ossicles have, in addition, small rounded protuberances, usually one but sometimes two, on or near the ventral midline (Text-fig. 1F; Pl. 1, fig. 1). Presumably the ventral bosses and protuberances helped to grip the substrate during locomotion. The protuberances may be homologous with the ventral spikes of more crownward cornutes, e.g. *Reticulocarpos hanusi* Jefferies and Prokop, 1972.



TEXT-FIG. 6. *Procothurnocystis owensi* gen. et sp. nov. NMW 84.17G.119; holotype; scanning electron micrographs (B, D) and explanatory sketches (A, C) of latex casts of hind-tail in dorsal aspect; all figures $\times 15.4$; B, proximal portion; D, distal portion; cf. Pl. 1, fig. 2.

The last four ossicles of the tail decrease progressively in size, so that the width of the last ossicle (No. 35) is approximately 0.4 the width of the fourth from last ossicle (No. 32). Furthermore, the last ossicle appears to be rounded. Hence *P. owensi* has a definite terminal ossicle. This is contrary to the assertion in Jefferies (1986, p. 193) that the end of the tail in cornutes is always abrupt.

The dorsal plates (Text-figs 4C–G, 6; Pl. 1, figs 1–2) consist of a thin-shelled dorsal portion and a thick-shelled ventral portion. The thick-shelled portion had, in lateral aspect (Text-fig. 4D), a convex posterior margin, forming a ventral lobe which overlapped the next plate posterior, while more dorsally the margin of the plate was at first concave in lateral aspect (the lateral embayment) and then convex again at the midline (forming with its antimere a median postero-dorsal process). The lateral embayment, being situated where the tail in transverse section is widest, would allow considerable horizontal flexion while the median postero-dorsal process would tend to prevent dorsal flexion. (This is particularly the case because the median dorsal suture between a pair of plates was long, extending the length of two ossicles.) The anterior margin of each plate was approximately straight in lateral aspect. The dorsal plate was half-U-shaped in posterior aspect so that, when the dorsal plates were paired in life, the inverted U would be complete. The ventral articulation of each dorsal plate is somewhat longer than the ventral ossicle with which it mainly articulates. On the inside of the anterior ventral region of each plate was a boss-like articular process which articulated with the elliptical depression on the lenticular facet of the ventral ossicle. The position of the boss and depression means that each plate overlapped the next posterior plate and

that each plate extended onto the next ossicle behind. The wall of each plate was thicker anteriorly than posteriorly to allow for imbrication with the next plate.

LOCOMOTION

The strange shape of boot-shaped cornutes raises the question of whether they moved and how. Jefferies (e.g. 1986, p. 104) has suggested that, like all calcichordates, they crawled rearwards across the sea floor, pulled by their tails.

In reconstructing possible locomotory cycles for *Cothurnocystis elizae* and *Procothurnocystis owensi*, we first take *C. elizae*. Features probably important in its locomotion are stressed in Text-figure 10 (tail, k-spike, t-spike, l-appendage, b-appendage, c-appendage, f-spike). We recall that spikes by definition are short and ventrally directed, whereas appendages are elongated and directed anteriorly. A rearward direction of locomotion is suggested by the fact that the t-, k- and f-spikes have points or sharp edges anteriorly but blunt ends posteriorly, while the l-, b- and c-appendages slope downwards and forwards. The l- and b-appendages were rigidly fixed to the head, whereas the c-appendage, right of the mouth, was articulated to the marginal frame and would have been able to wag to right or left. The mere left-right asymmetry of the head of *C. elizae* is consistent with rearward locomotion, since asymmetrical objects are directionally stable if pulled, but not if pushed.

The fore-tail of *C. elizae* was adapted to flex laterally, as shown by gaps between the successive rings of major plates of the fore-tail on the right and left but not in the ventral or dorsal midlines. Also the distal half or third of the hind-tail of *C. elizae* seems, because of the horizontally cylindrical junctions between some of the ventral ossicles, to be adapted for bending downwards (Jefferies 1986, p. 202). Such downward flexure would be passive and would result from the elasticity of ligamentary fibres joining the ventral hind-tail ossicles. Straightening of the hind-tail would be an active process, caused by the contraction of muscles in the lumen of the hind-tail. A specimen of the hind-tail of *C. elizae* preserved with the postulated downward terminal flexure is shown in Text-figure 7F.

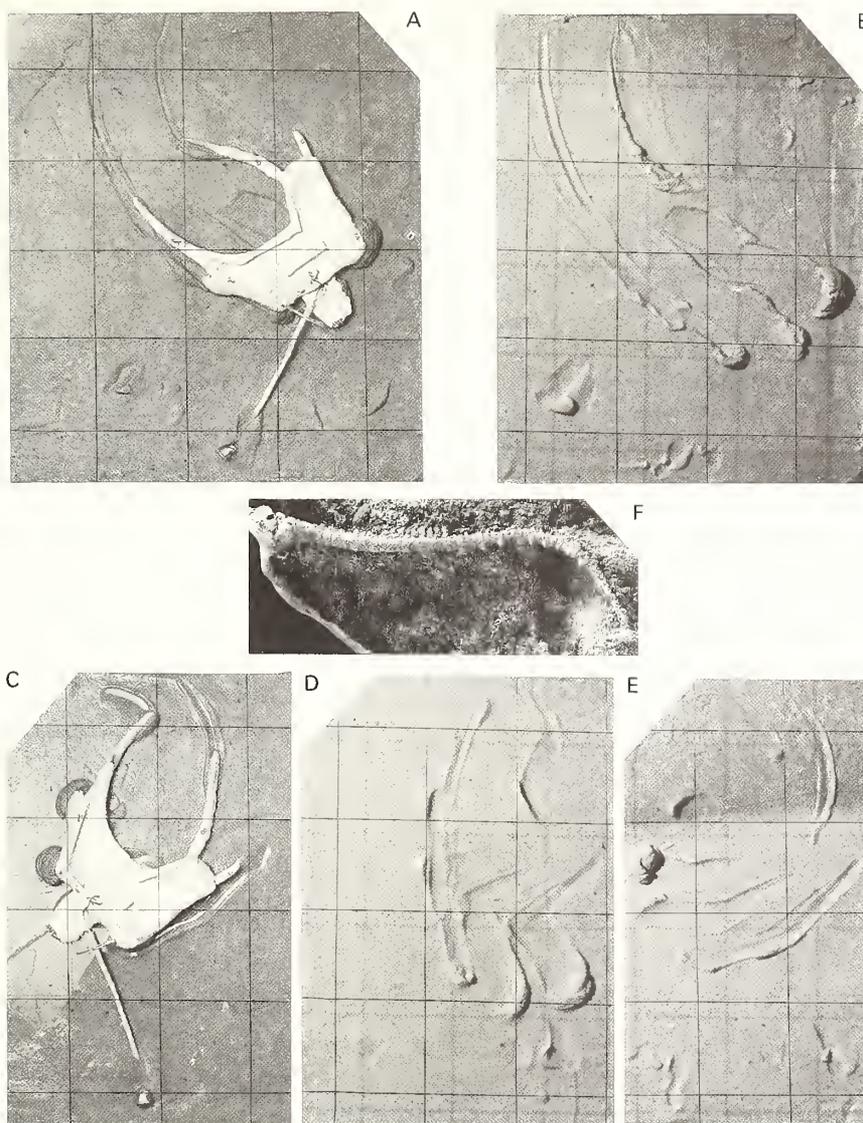
We made a model so as to reconstruct experimentally the locomotory cycle of *C. elizae* (Text-fig. 7A, C). It was about nine times natural size. The head and fore-tail were fashioned from wood and hard-setting resin. They were modelled in three dimensions and were accurate as concerns the ventral and lateral surfaces. The mid- and hind-tail were of stiff plastic-wrapped wire. They were loosely hinged to the head at the tail insertion – in shape the hind-tail curved ventrally in a distal direction, as it probably could in *C. elizae* in life. At the very tip of the tail there was an upwardly directed handle which did not exist in the animal but was experimentally convenient. An imperfection in the model was that the small c-appendage, right of the mouth, was rigidly fixed to the frame, rather than being able to wag to right and left as in the living animal.

We caused the model to locomote across the planar horizontal surface of some water-saturated sand in a shallow square box (Text-fig. 7). When placed on the sand, the model rested on the flat lower surfaces of the spikes and the lower surfaces of the appendages and tail. The ventral integument did not touch the sand.

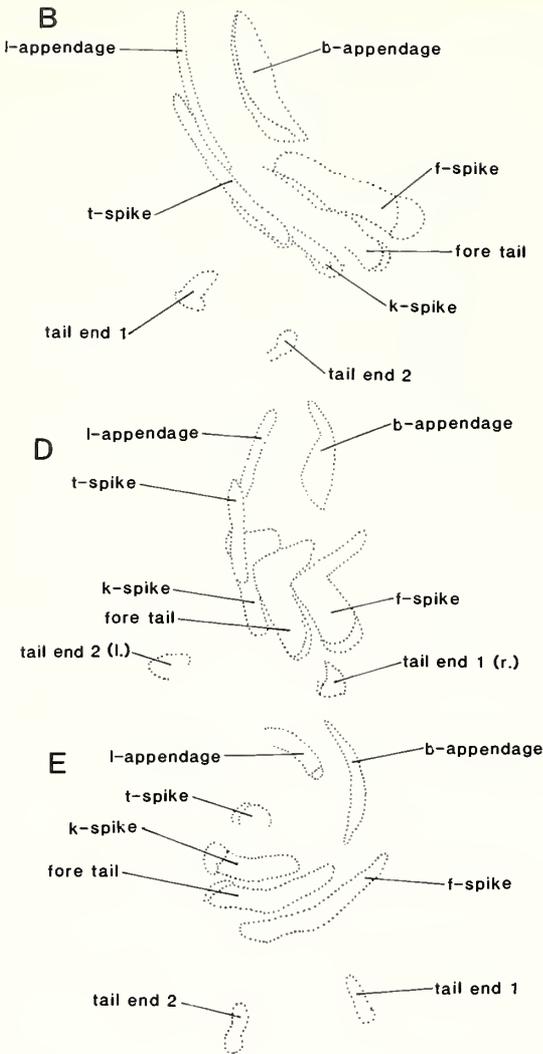
To produce the appropriate movement, the experimenter held the distal end of the tail into the sand by the vertical handle, while pushing gently sideways with one finger on the proximal end of the wire which represented the mid- and hind-tail. By these actions he imitated the ventralward hooking of the distal part of the tail to grip the substrate and the contraction of the left or right fore-tail muscles.

A four-stroke locomotory cycle was worked out using the model of *C. elizae* (Text-figs 7–9). It comprised: (1) a tail-leftward power stroke (Text-fig. 9A); (2) a tail-rightward return stroke; (3) a tail-rightward power stroke (Text-fig. 9B); and (4) a tail-leftward return stroke.

Going into more detail, the cycle starts with the tail-leftward power stroke. The distal part of the hind-tail was inserted into the sediment at the midline and the fore-tail then flexed to its maximum leftward extent, relative to the head (Text-fig. 7A). As mid- and hind-tail thus swung leftward and forward relative to the head, the head yawed anti-clockwise relative to the sea floor, about a region centred anterior to and right of the head. The tracks made by the model in two successive tail-left



TEXT-FIG. 7. *Cothurnocystis elizae* Bather, 1913. A–E, experiments on locomotion; the sides of the grid squares are 100 mm long and the model is about $9 \times$ natural size; for explanation of individual tracks in B, D and E, see Text-figure 8. A, model lying on wet sand after two successive tail-left power strokes – note the piling-up of sand at the f-spike, and to a lesser extent at the k-spike, and the tracks caused by sliding along the l-appendage and by moving perpendicular to the b-appendage. B, tracks after two successive tail-left power strokes. C, model at end of a single tail-right power stroke – note the piling-up of sand at the k- and t-spikes, and the tracks caused by sliding along the b-appendage and by moving perpendicular to the l-appendage. D, tracks after a tail-right power stroke followed by a tail-left power stroke. E, tracks after two successive tail-right power strokes. F, latex cast of specimen BMNH E23197 (Gray Collection) from the type locality of the species, i.e. the Starfish Bed of Harper's (1982) Locality 6, near Girvan, Scotland (Upper Rawtheyan Stage of Ashgill Series), $\times 1.8$; the specimen, in left lateral aspect, shows part of the fore-tail, and the entire mid- and hind-tail, preserved with the sagittal plane parallel to the bedding; the curvature is probably natural and resulted from elastic contraction of ligamentary fibres in the ventral column of ossicles when the dorsal muscles relaxed at death – note the ventral protuberances in the anterior part of the distal half of the hind-tail and the down-turned end of the hind-tail.

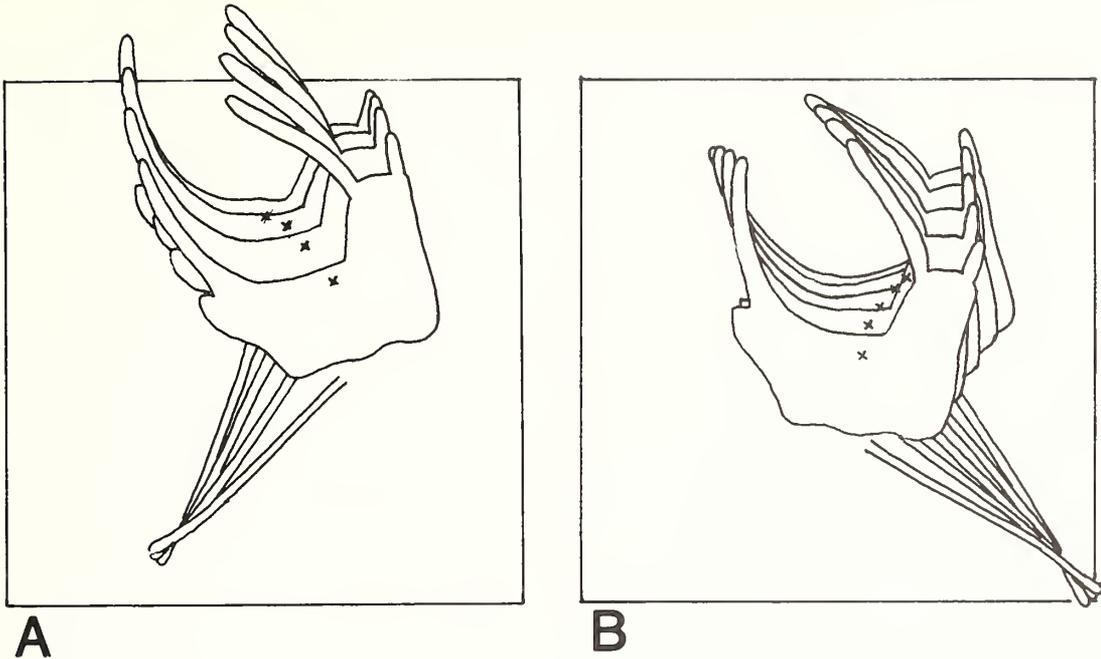


TEXT-FIG. 8. *Cothurnocystis elizae* Bather, 1913. Tracings to explain the tracks shown in Text-figure 7 A-E. The tracings take the same letters as the corresponding figures in Text-figure 7.

power strokes (Text-fig. 7B) show that: (1) sediment piled up behind the f-spike on the right posterior corner of the head, and to a lesser extent behind the k-spike on the left side of the head; (2) the t-spike (likewise on the left) slid rearwards over the substrate; (3) the curved l-appendage (on the extreme left of the head) slid rearwards along its length in the manner of an arcuate sledge runner or ski; and (4) the b-appendage, which was curved in the opposite direction to the l-spike, slid over the sand while rotating leftward and rearward transversely to its own length. Piling-up of sediment shows where the substrate was resisting movement of the head.

In the tail-rightward return stroke, the mid- and hind-tail would swing, entirely in water and without gripping the sea floor, from its extreme left position to the midline.

The tail-right power stroke began when the distal part of the hind-tail was inserted into the sea bottom at the midline. The fore-tail then flexed to its maximum rightward extent, relative to the head (Text-fig. 7C). As a result, the head yawed clockwise, relative to the sea floor, around a centre near the left side of the head at the proximal end of the l-appendage. Tracks made in two successive



TEXT-FIG. 9. *Cothurnocystis elizae* Bather, 1913. Successive positions of the head and tail during the power strokes of the locomotory cycle. Drawings traced from photographs of the model – compare Text-figures 5 and 6; the side of the square represents 300 mm in the model and about 33 mm in life; x marks estimated position of centre of mass of the head. A, tail-left power stroke. B, tail-right power stroke.

tail-right power strokes (Text-fig. 7E) show that: (1) sediment would pile up on the left side of the head against the k-spike and the t-spike; (2) the curved b-appendage would slide rearwards along its own length as an arcuate sledge-runner; (3) the f-spike and the c-appendage (both on the right side of the animal) would slide clockwise over the sediment; and (4) the l-appendage, being curved in the opposite direction to the b-appendage, would rotate rightwards, sliding over sediment transversely to its own length.

In the tail-leftward return stroke, the tail would swing, entirely in water and without gripping the sea floor, from its extreme right position to the midline. The locomotory cycle would then start again.

The c-appendage, as already mentioned, was articulated to the frame in the animal (Text-fig. 10), but not in the model. In life it could probably take up two different positions. Namely, it would wag passively to the right during the tail-leftward power stroke, so that its length was concentric to the curvature of the l-appendage (along which the head was then sliding), and would wag passively to the left during the tail-right power stroke, so that its length was concentric to the curvature of the b-appendage (along which the head was then sliding). By so wagging, it would always present least resistance to the rearward motion of the animal by sliding rearward along its own length. This view of the function of the c-appendage seems more elegant and likely than the opinion of Jefferies (1968, p. 258) who thought that, by waving actively from side to side, it served to stir up the food-rich bottom mud which then would be sucked into the mouth as a suspension.

To generalize, each ventral spike alternated in its mode of action during successive, opposite-sided power strokes – namely it would grip the sea floor strongly during one power stroke and grip it more weakly or slide rearwards over it in the next. Likewise the l and b appendages alternated in their action, sliding rearwards along their curved length in one power stroke and rotating

transverse to their length in the next. The l-appendage and the k- and t-spikes (on the left side of the head) would show one of these modes of action during any one power stroke, whereas the b-appendage and the f-spike (more on the right side of the head) would show the other. The small, articulated c-appendage would, by passive drag, take up one of two alternative positions, so as to resist rearward motion as little as possible.

Speaking quantitatively, we estimated the position of the centre of mass for the head of *C. elizae* by suspending a cardboard silhouette of the head from various hinge points. It probably lay anterior to the midline of the tail insertion, shortly behind the anterior frame, as indicated in Text-figure 9. We measured the motion of the centre of mass during a locomotory cycle on the basis of successive photographs taken of the model lying on the wet sand. If the length of the head is measured from the anterior end of the b-appendage to the midline of the tail insertion, then the centre of mass moved rearwards by 70% of the head length during the total cycle. This rearward translation happened in two equal phases: during the tail-leftward power stroke, the centre was translated 20% of the head length to the right and 35% of the head length rearwards; and during the tail-rightward power stroke, it was translated 20% of the head length to the left, and 35% of the head length rearwards. During each power stroke, the hind-tail wagged through 30° relative to the sea floor, and through 50° relative to the posterior margin of the head frame. Consequently, the posterior margin of the head rotated, relative to the sea floor, 20° during each power stroke – anti-clockwise during the tail-left stroke, and clockwise during the tail-right stroke. (All measurements given are approximate.) Thus in terms of the total movement of the head, whether in translation or rotation, the tail-left and tail-right power strokes were mirror images of each other.

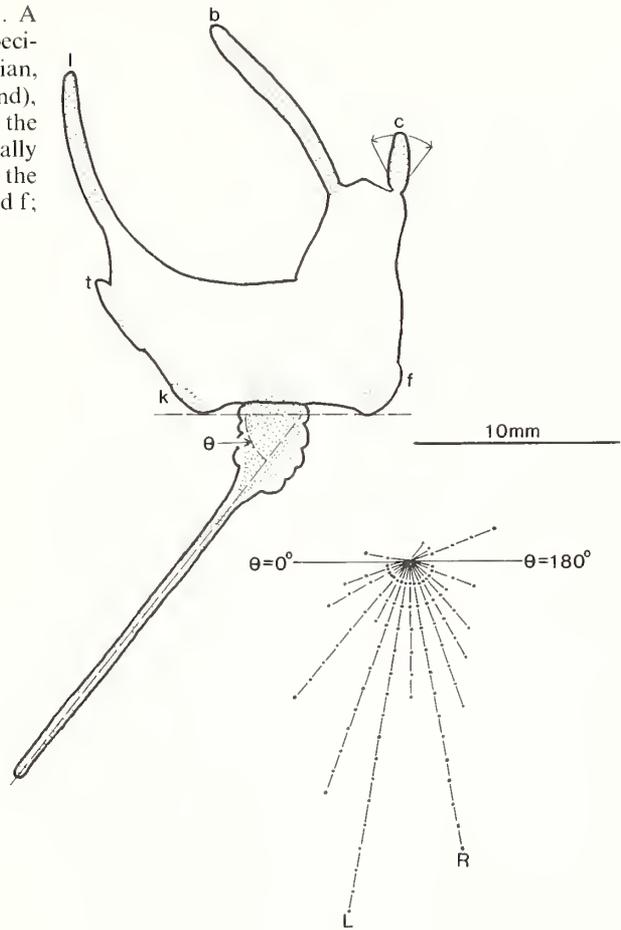
Jefferies (1969, p. 525) recorded the position of the hind-tail relative to the head in ninety-six specimens of *C. elizae* from the Starfish Bed at Girvan (Text-fig. 10). He found that there were two specially frequent positions, situated approximately 10° right of the midline (thirteen specimens) and 10° left of it (sixteen specimens). These positions would correspond, respectively, to the beginnings of the tail-rightward and tail-leftward power strokes. In six specimens the hind-tail extended (to within 10°) exactly rearwards from the midline of the tail insertion. In forty-one specimens it was 5° or more left of the midline; and in forty-nine specimens it was 5° or more right of the midline. These data represent the postures of animals at death by burial. They suggest that the tail-leftward and tail-rightward power strokes were about equally frequent and that the animals tended to die at, or shortly after, the start of a power stroke, presumably because oxygen consumption was highest then.

If this was how *Cothurnocystis elizae* moved, it would have made tracks on the sea floor like those in Text-figure 7. It would be miraculous if such tracks were ever found, however. The fact that so many features of the anatomy of *C. elizae* can be explained by the postulated mode of locomotion, suggests that it really did move in the manner suggested.

Turning to *Procothurnocystis owensi*, the tail, as already mentioned, had several striking features: (1) the posterior part of the hind-tail, approximately distal to ossicle 10, could flex horizontally but probably not, or almost not, vertically; (2) the anterior part of the hind-tail, approximately as far back as the 10th ossicle, probably could not flex in any direction and the same was presumably true of the posterior part of the fore-tail, for in it the stylocone was deeply inserted; (3) the anterior part of the fore-tail could probably flex vertically but not, or almost not, horizontally; and (4) there was little space for muscles in the fore-tail, since the stylocone was deeply inserted into the fore-tail and had a very shallow anterior excavation. The small size of any fore-tail muscles suggests that in *P. owensi*, unlike *C. elizae* and probably most other cornutes, they were not the main motor in locomotion.

The head of *Procothurnocystis owensi* also shows peculiar features. Namely, the tips of the t, k and f spikes project rearwards instead of forwards, and thus in the opposite direction to those of all other known cornutes, and the lower surfaces of the spikes are convex in transverse section rather than flattened. The f- and k-spikes are almost mirror images of each other. Both these spikes are elongate, their long axes converge rearwards and there is an angle of about 70° between the long axis of the fore tail and the long axis of the spike.

TEXT-FIG. 10. *Cothurnocystis elizae* Bather, 1913. A census of observed tail positions in ninety-six specimens from the type locality (upper Ordovician, Ashgill Series, Thraive Glen, near Girvan, Scotland), redrawn and modified after Jefferies (1969); the animal is shown in dorsal aspect but ventrally prominent parts of the head and buried parts of the tail are stippled. Ventral spikes are labelled t, k and f; appendages are labelled l, b and c.



Horizontally flexible hind-tails, revealed by the posture of the animals at death by burial, are known in some other cornutes. Such include '*Cothurnocystis*' *fellinensis* Ubaghs, 1969, *Thoralicystis melchiori* (Ubaghs, 1983) (see Cripps 1988) and *Scotiaecystis collapsa* Cripps, 1988. Wherever observed, this horizontal flexibility is perhaps homologous. Predominantly vertical flexion of the fore-tail on the other hand, is deduced to have occurred in crownward cornutes such as *Reticulocarpos hanusi* Jefferies and Prokop, 1972, and in mitrates. In these forms it is not likely to have been homologous with vertical flexion in the fore-tail of *P. owensi*.

The horizontally curved shape of the hind-tail (Pl. 1, figs 1–3), in the fossil as preserved, from ossicle 10 to ossicle 35, represents about half a wavelength of a sine wave. Probably the posterior part of the hind-tail, as it flexed from side to side, would pivot about the ninth ossicle. Sine waves would pass forward along this laterally flexible region by muscular contraction and relaxation.

We made a scale model of the head of *Procothurnocystis owensi*. It was about eight times natural size and constructed, like the model of *Cothurnocystis elizae*, of wood and hard-setting resin. The shapes of plates b and c in the model were based on those of '*Cothurnocystis*' *primaeva* Thoral, 1935. We did not attempt to model the tail because its mode of action was probably very complicated.

We caused the head to locomote across the surface of water-saturated clay in a shallow square box by placing one finger on the rear part of the head frame and pressing obliquely rearwards and

towards the midline, alternately co-linear with the f-spike on the right or with the t- and k-spikes on the left. The clay was intended to simulate the very soft clayey mud on which *P. owensi* probably lived and died. Unlike *C. elizae*, the head did not rest on the ventral surface of the spikes, but sank down so that the ventral integument and strut rested on the clay while the spikes, much of the l-appendage and the whole of the b- and c-appendages were embedded within it. (We recall that the shapes of the b- and c-appendages are unknown.) Pressing rearwards on the frame in the manner described produced rearward movement with much yaw. Thus, when pulled at the right towards the rear and leftwards, the head would slide readily along the length of the f-spike, while tending to pivot about the k- and t-spikes on the left side of the head. The result was rearward translation and clockwise rotation. When pulled at the left towards the rear and rightwards, the head would slide readily along the common axis of the k- and t-spikes, pivoting about the f-spike on the right side of the head. The result was rearward translation and anti-clockwise rotation. We suggest that this was how the head moved in life. The successive orientations and positions of the head in Text-figure 11 are traced from photographs taken during experiments with the model, whereas the successive positions of the tail are reasonable guesses.

The rearward protuberance of the k-, t- and f-spikes seems to help the spike to slide rearwards through the mud. It is functionally different from the anterior sharp protuberance of the spikes of *C. elizae*, which tended to prevent forward movement by pushing into sediment which the spikes otherwise slid over. The convex lower surfaces of the spikes allowed the spikes to sink into the sea bottom, rather than resting upon it.

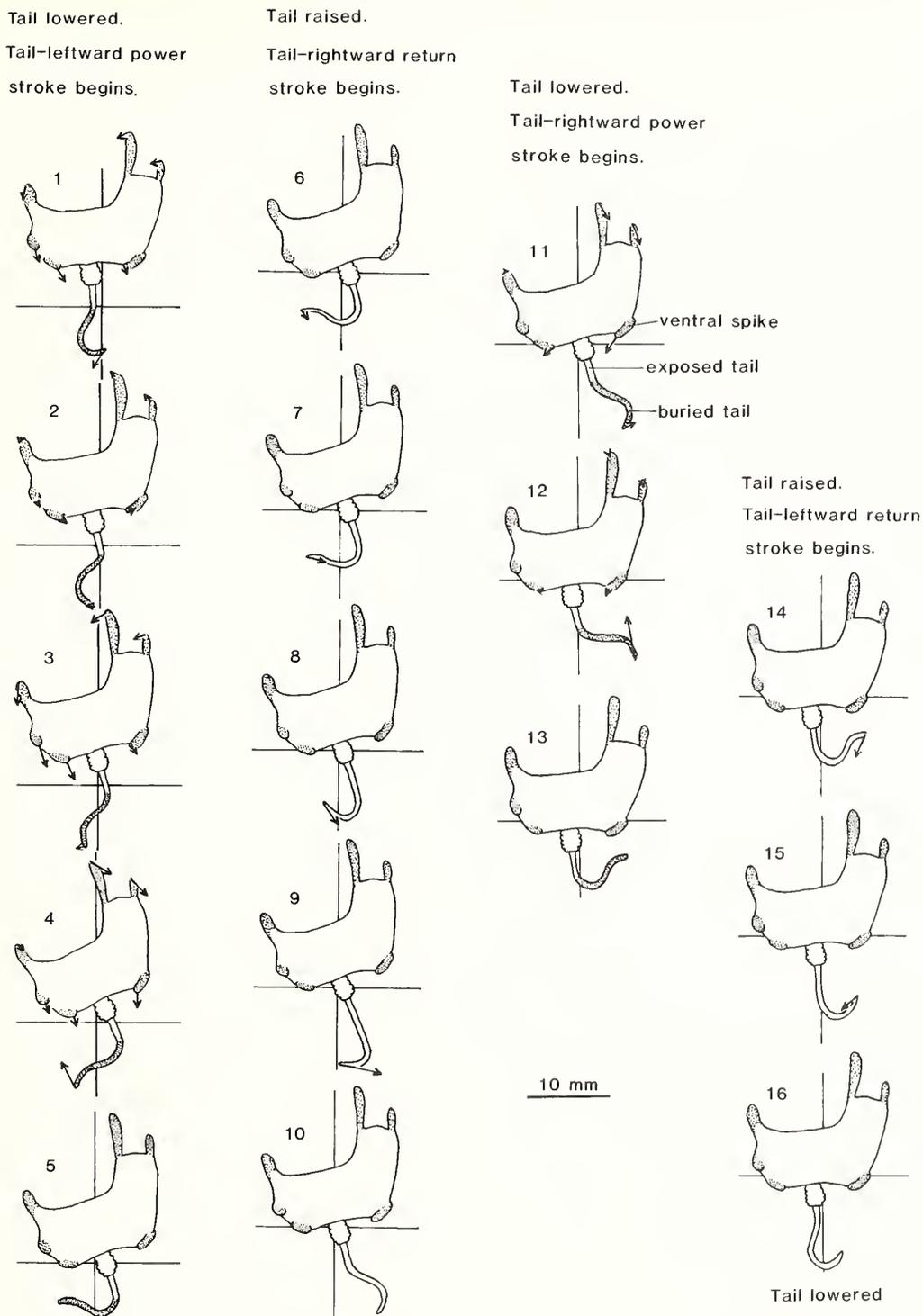
The locomotory cycle (Text-fig. 11) of *Procothurnocystis owensi*, like that of *Cothurnocystis elizae*, probably comprised four strokes: a tail-leftward power stroke, a tail-rightward return stroke, a tail-rightward power stroke, and a tail-leftward return stroke. Unlike *C. elizae*, however, the action of the fore-tail would be confined to raising the mid- and hind-tail out of the mud before a return stroke, and depressing it into the mud before a power stroke. Also the actual motor for locomotion would lie in the muscles of the hind-tail, flexing forwards and leftwards during the tail-leftward power stroke and forwards and rightwards during the tail-rightward power stroke. Force from the flexible part of the hind-tail would be applied to the head by pulling leftwards and rearwards, or rightwards and rearwards, on the distal end of the rigid proximal part of the hind-tail. This rigid part would act as a lever pulling on the head via the fore-tail. In transmitting forces generated by the hind-tail, the anterior part of the fore-tail would behave as a hinge with a horizontal axis, transmitting the horizontal components of force but not the vertical component.

The posture of the hind-tail in Text-figure 9/2 is like that in the only known specimen of '*Cothurnocystis*' *fellinensis* (Pl. 2, fig. 1), while that of Text-figure 9/12 is like that of the only known specimen of *Procothurnocystis owensi* (Pl. 1, figs 1–3). However, the locomotion of '*C.*' *fellinensis* must have differed considerably from that of *P. owensi* since the fore-tail of '*C.*' *fellinensis* looks to have been laterally flexible, the stylocone was not deeply inserted into the fore-tail, and there was no rigid proximal portion to the hind-tail.

As concerns phylogenetic polarity, the locomotion of *Procothurnocystis owensi* is probably advanced compared with that of *Cothurnocystis elizae* in several respects, namely:

1. Several features are unique to *P. owensi* among known cornutes and therefore probably represent the advanced condition in all cases. Such are the deep insertion of the stylocone into the fore-tail, the shallowness of the anterior excavation of the stylocone, the presumed small size of the fore-tail muscles, the more-than-double number of dorsal plates in the fore-tail, the presence of four ventral plates in the fifth ring of the fore-tail (rather than two), and the posterior protrusion of the ventral head spikes.

2. Predominantly dorso-ventral flexion of the fore-tail is not unique to *P. owensi*, for it elsewhere existed in the mitrates and in the most crownward plesions of the cornutes – namely those of *Reticulocarpos hanusi* Jefferies and Prokop, 1972, *Domfrontia pissotensis* (Chauvel and Nion, 1977) and *Prokopocystis mergli* Cripps, 1989. Lateral flexion of the fore-tail, however, is probably primitive for cornutes since it seems to have existed in most of the known species, and in particular in the two least crownward cornute plesions – those of *Ceratocystis perneri* Jaekel, 1900 and of



TEXT-FIG. 11. *Procothurnocystis owensi* gen. et sp. nov. Locomotory cycle, dorsal aspect; the scale bar refers to the fossil, not to the model (which was about $8\times$ larger); the spikes and the buried parts of the tail and appendages are stippled. 1-5, tail-leftward power stroke; 6-10, tail-rightward return stroke; 11-13, tail-rightward power stroke; 14-16, tail-leftward return stroke. The number of stages shown in each stroke is of no significance.

Protocystites menevensis Hicks, 1872. Also it probably existed in the solute *Dendrocystoides scoticus* Bather, 1913, and the solutes represent the paraphyletic group from which cornutes arose (Jefferies 1990). (The best evidence for lateral flexion in the fore-tails of these three animals is that the major plates of the fore-tail alternate with each other, and overlap each other, from right or left, in the ventral midline, and in *D. scoticus* in the dorsal midline as well.) All this suggests that dorso-ventral flexion of cornute fore-tails is advanced compared with lateral flexion. It is unlikely, however, that the dorso-ventral flexion of *P. owensi* is homologous with that of the crownward cornutes and mitrates, since the latter condition seems to have evolved in the chordate stem lineage between the plesions of *Hanusia* and *Reticulocarpus hanusi* (Cripps 1989a), and therefore much more crownward than *P. owensi*. Also the main motor in the locomotion of crownward cornutes, such as *R. hanusi*, lay in its primitive cornute and solute position in the muscles of the fore-tail, not in those of the hind-tail.

3. Lateral flexion of the hind-tail is probably advanced compared with lateral rigidity, since the hind-tail seems to have been laterally rigid in the anti-crownward cornutes *Ceratocystis perneri* and *Protocystites menevensis* and was rigid in all directions in most solutes, including *D. scoticus*. So far as can be discerned, lateral flexibility of the hind-tail may be homologous in all the cornutes that show it. This conclusion is uncertain, however, since the phylogeny of the cornutes is not well known, except near the crownward and anti-crownward ends of the cornute part of the chordate stem group.

The peculiarities of locomotion in *Procothurnocystis owensi* were probably adaptations to a very soft floor – so soft that the head sank into the mud down to the level of the ventral integument so that the spikes, much of the appendages and most of the tail were buried. A punting action, such as *Cothurnocystis elizae* probably used, will work only when the floor is strong enough to grip the end of the punt pole (or the downturned end of the hind-tail). This will mainly be true of sandy or silty sea floors, which do not appreciably weaken when stirred. Indeed, sands become stronger under pressure, so that the terminal hook of the hind-tail would grip the sea floor more firmly if it were deeply thrust into the sand than if inserted more shallowly. Clayey floors, on the other hand, because of thixotropy, lose nearly all their weak strength when stirred. On clayey floors, therefore, a swimming action will be more reliable than a punting action, for it will function even if the sediment loses all strength and becomes a viscous fluid.

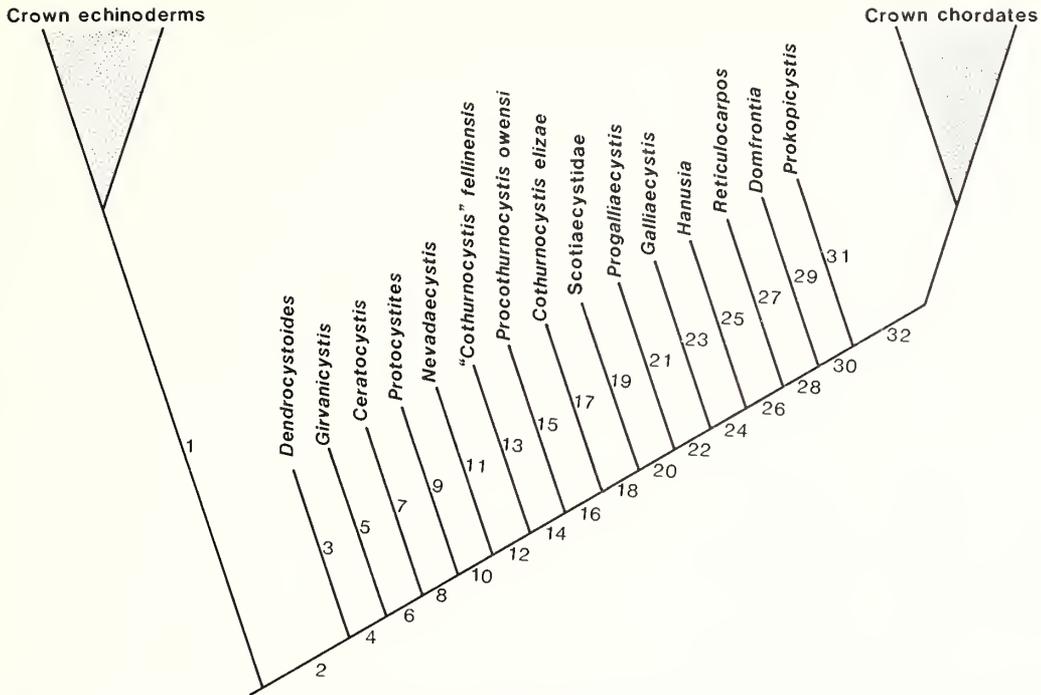
PHYLOGENETIC POSITION OF *PROCOTHURNOCYSTIS OWENSI*

Assuming the plesion series shown in Text-figure 12, then *P. owensi* represents a plesion intermediate between those of '*C. fellinensis*' and *C. elizae*. The relevant features of *P. owensi* can be analysed as follows:

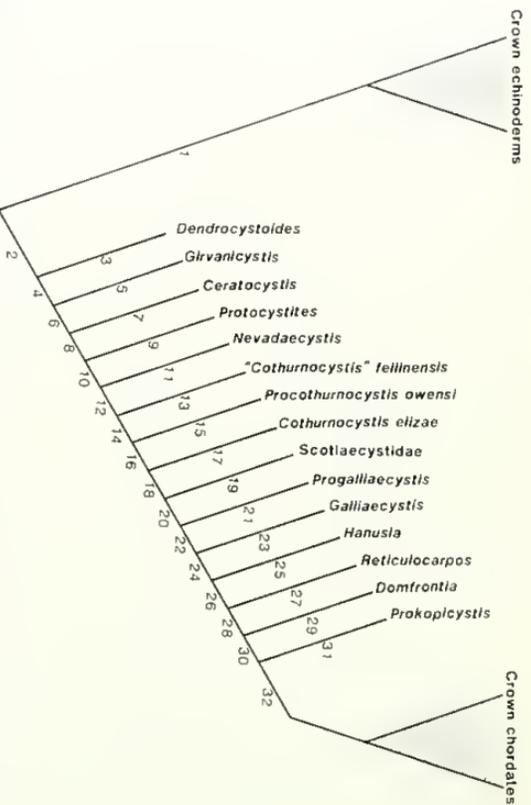
1. Evolutionary novelties which probably arose in the chordate stem lineage just anti-crownward of the plesion of *P. owensi* (between that plesion and the plesion of '*C. fellinensis*' in segment 14 of Text-fig. 12) are only two, namely: loss of the y plate and the contained median eye; and perhaps the reduction of the number of keel spines from six to three.

2. Autapomorphies of *P. owensi*, which would have arisen in segment 15 of Text-figure 12 are: the deeply inserted stylocone; more-than-doubling of the dorsal plates of the fore-tail; the leftward shift of the suture between the ventral plates of the 4th ring of the fore-tail; the increase in number of the ventral plates of the 5th fore-tail ring from two to four; and rearward protrusion of the ventral spikes.

3. Only four evolutionary novelties probably arose just crownward of *P. owensi*, in the chordate stem lineage between the plesion of *P. owensi* and that of *C. elizae*, in segment 16 of Text-figure 12. These are: loss of the x plate; an increase in the number of gill slits from nine to about sixteen; extension of the gill slit series rightwards, so that the gonopore–anus came to open into the outwash of the gill slits; and entire loss of the keel spines from the dorsal integument.



TEXT-FIG. 12. Cladogram of the Dexiothetica to show the relationship of crown-group chordates and crown-group echinoderms to stem-group chordates. Among the latter, two solute plesions are shown (*Dendrocystoides* and *Girvanicystis*) and all the known cornute plesions (*Ceratocystis* to *Prokopocystis*). The numbered segments correspond to evolutionary novelties as follows: 1, echinoderm autapomorphics, e.g. loss of tail, loss of gill slit, sessility, quinquaradial symmetry, mouth in centre of upper surface etc.; 2, tripartition of tail, origin of notochord and brain, gill slit migrates to posterior left position on head; 3, antibrachial process; 4, dorsal plates of head large, complete marginal hinge line; 5, no known changes; 6, solute-cornute transition with loss of arm, loss of water vascular system, migration of hydropore to posterior right of head, migration of gonad, gonopore, and heart to posterior right of head, multiplication of gill slits, paired dorsal plates on hind-tail, stylocone, etc.; 7, no known changes; 8, dorsal surface of head flexible, gonopore-anus left of tail, plate wax divides into w, a and x; 9, very light construction of skeleton; 10, anterior U-plates of gill slits, origin of strut (as thickening of head floor), increased flexibility of dorsal surface of head, plate d included in frame; 11, lateral spread of e-spike and f-spike; 12, ventral surface of head flexible (except for strut), spines on dorsal keels, t plate in frame; 13, no known changes; 14, loss of plate y; 15, autapomorphies of *Procothurnocystis owensi*, such as deep insertion of stylocone in fore-tail, reduction of fore-tail muscles, posterior protuberance of l-, k- and t-spikes; 16, loss of keel spines, loss of plate x, increase in number of gill slits to about 16, extension of gill-slit row anterior to the gonopore-anus; 17, no known changes; 18, loss of plate t, approximate symmetry of plates h and i, overlap of fore-tail plates epsilon and theta over head plates g and j; 19, scotiaecystid autapomorphies, e.g. plate s, interbranchial elements; 20, loss of specialized branchial skeleton and specialized oral skeleton, acquisition of dorsal bar, reduction in length of l-appendage to form an l-spike, horizontal suture between anterior strut plate (m) and a; 21, no known changes; 22, further reduction of l-spike; 23, no known changes; 24, reduction of left side of head to produce a more symmetrical outline, visible distinction between prosencephalon and deuterocephalon; 25, autapomorphies of the genus *Hanusia*, including large plate in dorsal integument, C-shaped section of marginal plates, ribs on l-spike; 26, symmetrical outline for the head, flat ventral surface without spikes or appendages, very small size, abbreviated hind-tail with large spikes on the ossicles and stylocone, peripheral flange, very light histology of skeleton, separation of anterior strut plate from the frame; 27, large depressions in frame for transpharyngeal eyes; 28, ventral convexity of head, dorsal extensions of marginal plates towards the centre of the head, very large plates in dorsal integument, loss of anterior strut plate (m), shield-like expansion of h and i; 29, loss of dorsal bar; 30, strong expansion of tail plates epsilon and theta over plates g and j of the head, gonopore-anus opening into branchial region, loss of major dorsal plates of fore-tail; 31, absence of all but one dorsal integument plate behind the dorsal bar; 32, changes at cornute-mitrate transition including origin of right gill slits, origin of left and right atria, further expansion of epsilon and theta to form part of the head, loss of plates g and j, loss of cornute mid- and hind-tail by autotomy, regionation of mitrate fore-, mid- and hind-tail, origin of inner layer of ventral skeleton, etc.



TEXT-FIG. 12. Cladogram of the Devotheoretical to show the relationship of crown-group chordates and crown-group echinoderms to stem-group chordates. Among the latter, two soluble plesions are shown (*Dendrocystoides* and *Girvanicystis*) and all the known cornute plesions (*Ceratocystis* to *Prakopecystis*). The numbered segments correspond to evolutionary novelties as follows: 1, echinoderm autapomorphies, e.g. loss of tail, loss of gill slit, sessility, quinquetradial symmetry, mouth in centre of upper surface etc.; 2, tripartition of tail, origin of notochord and bran. gill slit migrates to posterior left position on head; 3, antibranchial process; 4, dorsal plates of head large, complete marginal hinge line; 5, no known changes; 6, soluble-cornute transition with loss of arm, loss of water vascular system, migration of hydropore to posterior right of head, migration of gonad, gonopore, and heart to posterior right of head, multiplication of gill slits, paired dorsal plates on hind-tail, stylocone, etc.; 7, no known changes; 8, dorsal surface of head flexible, gonopore-anus left of tail, plate wax divides into w. a and x.; 9, very light construction of skeleton; 10, anterior U-plates of gill slits, origin of strut (as thickening of head floor), increased flexibility of dorsal surface of head, plate d included in frame; 11, lateral spread of c-spine and f-spine; 12, ventral surface of head flexible (except for strut), spines on dorsal keels; 1 plate in frame; 13, no known changes; 14, loss of plate y; 15, autapomorphies of *Procothurnocystis owensii*, such as deep insertion of stylocone in fore-tail, reduction of fore-tail muscles, posterior protuberance of f-, k- and f-spikes; 16, loss of keel spines; loss of plate a; increase in number of gill slits to about 16, extension of gill-slit row anterior to the gonopore-anus; 17, no known changes; 18, loss of plate 1, approximate symmetry of plates h and i, overlap of fore-tail plates epsilon and theta over head plates g and j; 19, scutiacystid autapomorphies, e.g. plate s, interbranchial elements; 20, loss of specialized branchial skeleton and specialized oral skeleton, acquisition of dorsal bar; reduction in length of l-appendage to form an f-spine, horizontal suture between anterior strut plate (m) and a; 21, no known changes; 22, further reduction of f-spine; 23, no known changes; 24, reduction of left side of head to produce a more symmetrical outline, visible distinction between proencephalon and deuterocephalon; 25, autapomorphies of the genus *Hanusia*, including large plate in dorsal integument, C-shaped section of marginal plates, ribs on f-spine; 26, symmetric outline for the head, flat ventral surface without spikes or appendages, very small size; abbreviated hind-tail with large spikes on the ossicles and stylocone, peripheral flange, very light histology of skeleton, separation of anterior strut plate from the frame; 27, large depressions in frame for transpiratory eyes; 28, ventral convexity of head, dorsal extensions of marginal plates towards the centre of the head, very large plates in dorsal integument, loss of anterior strut plate (m), shield-like expansion of h and i; 29, loss of dorsal bar; 30, strong expansion of tail plates epsilon and theta over plates g and j of the head, gonopore-anus opening into branchial region, loss of major dorsal plates of fore-tail; 31, absence of all but one dorsal integument plate behind the dorsal bar; 32, changes at cornute-mitrate transition including origin of right gill slits, origin of left and right arra, further expansion of epsilon and theta to form part of the head, loss of plates g and j, loss of cornute mid- and hind-tail by autotomy, regeneration of mitrate fore-, mid- and hind-tail, origin of inner layer of ventral skeleton, etc.

CONCLUSIONS

Procothurnocystis owensi, from the lower Ordovician of South Wales, is a cornute and hence a stem-group chordate. It is remarkable in several respects. Most noteworthy are the laterally flexible hind-tail, the deep insertion of the stylocone into the fore-tail and the fact that the ventral spikes of the head are convex ventrally in transverse section and protrude posteriorly.

It probably represents a plesion intermediate between those of '*Cothurnocystis*' *fellinensis* and *C. elizae*. It is crownward of '*C.*' *fellinensis* in lacking a y plate and having a reduced number of vestigial keel plates. It is less crownward than *C. elizae*, in that the latter has sixteen antero-posteriorly asymmetrical gill slits, has the gill-slit series extending rightwards in front of the gonopore–anus, has no x plate, and has lost the vestigial keel plates.

The evidence for the soft-part anatomy of *Procothurnocystis owensi* is mostly poor. However, the location of the buccal cavity is clearly defined, the position of the pharynx is partly indicated and the infilling of the gonorectal groove could be seen on the specimen when first found.

The locomotory cycles of *Procothurnocystis owensi* and *Cothurnocystis elizae* are reconstructed on the basis of hand-powered working models. Both species, like all known cornutes and mitrates, would probably move rearwards pulled by the tail. The locomotory cycles, in both species, would be four-stroke: a tail-leftward power stroke; a tail-rightward return stroke; a tail-rightward power stroke; and a tail-leftward return stroke. In *Procothurnocystis owensi*, however, unlike most other cornutes including *C. elizae*: (1) the ventral spikes and the appendages would sink downwards so that the ventral integument would be in contact with the mud of the sea bottom – the rearward protrusion of the spikes would allow them to move more easily through the mud in a rearward direction; (2) the motor in locomotion lay probably in the muscles of the hind-tail, rather than in those of the fore-tail; and (3) the fore-tail muscles would act only to lift the hind-tail out of the mud at the end of each power stroke, and to depress it into the mud at the beginning of each power stroke.

Our work, therefore, has revealed a previously unknown primitive chordate in the Ordovician of Wales, placed it systematically, and allowed us, by using simple hand-driven models, to reconstruct the locomotion of boot-shaped cornutes.

Acknowledgements. We would like to thank Dr Robert M. Owens (National Museum of Wales, Cardiff) for finding the specimen of *Procothurnocystis owensi* and for making it available for study. We are also grateful to Dr David Hardwick (Civil Engineering Department, Imperial College, London) who kindly discussed locomotion of *P. owensi* and *C. elizae* from an engineer's standpoint and inspired us to make models of them. Finally we thank Tony Cripps for many helpful suggestions.

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IAN S. WOODS
21 Lovell Close
Henley-on-Thames
Oxon RG9 2PX

R. P. S. JEFFERIES
Department of Palaeontology
The Natural History Museum
Cromwell Road
London SW7 5BD

Typescript received 3 June 1990

Revised typescript received 15 May 1991

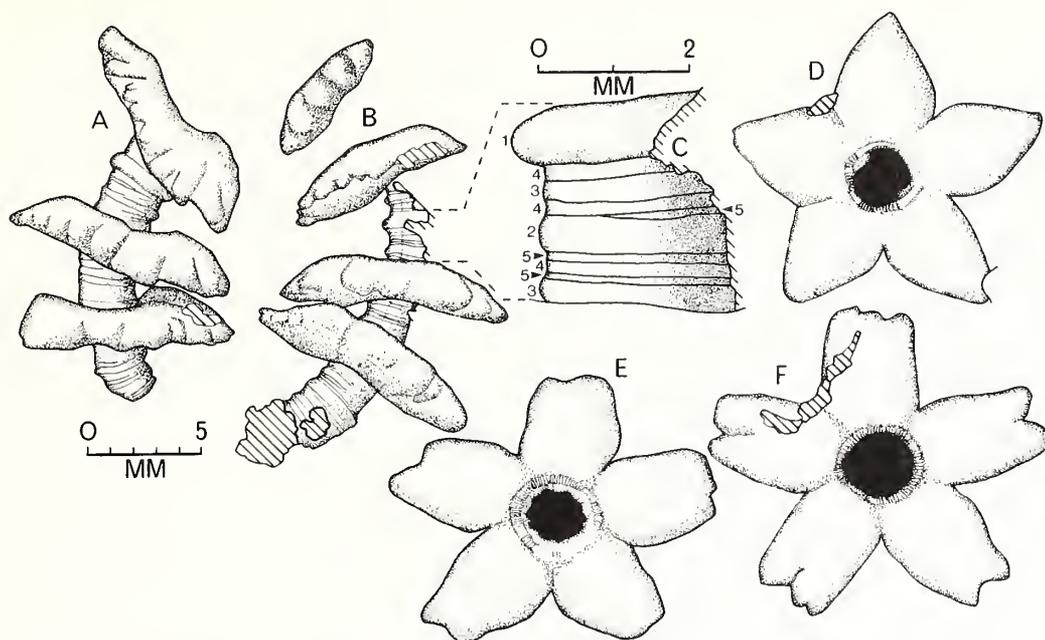
AN UNUSUAL CRINOID COLUMNAL MORPHOSPECIES FROM THE LLANDOVERY OF SCOTLAND AND WALES

by STEPHEN K. DONOVAN *and* NEIL D. L. CLARK

ABSTRACT. Distinctive crinoid columns with pentastellate to serrate circular nodal epifacets are probably derived from rhodocrinitid diplobathrid camerates and are placed in the morphogenus *Floricolumnus* (col.) gen. nov., which is only known from the Lower Llandovery of the British Isles. The type species, *F.* (col.) *girvanensis* sp. nov., is known only from the Newlands Formation of the Girvan district (late A₄ to early B₁). Nodals of this species are inflated; epifacet 'rays' are simple, bifid or multilobate; the column is strongly heteromorphic. *F.* (col.) sp. cf. *F.* (col.) *girvanensis* is from the Gasworks Mudstone of Dyfed (A₃ to early A₄). The presence of this genus in both the North American and South European faunal provinces is compatible with the cosmopolitan distribution of Late Ordovician and Silurian crinoids previously recognized on the basis of complete specimens.

THE Llandovery crinoid fauna is poorly known. For example, only one faunule of this age has been described from the British Isles (Brower 1975). In particular, Lower Llandovery crinoid faunas are rare and only two have, as yet, been documented, from the Cataract Group of Ontario (Eckert 1984) and the Brassfield Formation of Ohio (Ausich 1984*a*, 1984*b*, 1985, 1986*a*, 1986*b*, 1986*c*, 1987; Ausich and Dravage 1988). However, there are two British formations from low in the Llandovery which have produced small, but significant, crinoid faunules (Ramsbottom 1954; Text-fig. 1). The Gasworks Mudstone of the Haverfordwest area, Dyfed, of mid Rhuddanian age (A₃ to early A₄; Cocks *et al.* 1971, fig. 2), has yielded three crinoid taxa: *Pisocrinus* sp. (Family Pisocrinidae); *Macrostylocrinus* sp. (family Patelliocrinidae); and *Dimerocrinites* sp. (family Dimerocrinitidae). A further species of *Dimerocrinites* is known from the Newlands Formation of the Girvan district, Strathclyde, which is of Rhuddanian/Idwian boundary age (late A₄ to early B₁; Cocks *et al.* 1971, fig. 2). The Gasworks Mudstone taxa all represent earliest known appearances of their respective families in the British Isles south of the Iapetus Suture. The presence of *Dimerocrinites* at both localities further suggests a possible similarity of the crinoid taxa, at least at the generic level, in the North American and South European faunal provinces in the Lower Llandovery. This is similar to the pattern seen in the Upper Ordovician before the late Ordovician extinctions (Donovan 1989*a*, table 1), when 100% of crinoid families and 75% of genera occurred in both provinces. Of the taxa known from the Gasworks Mudstone, patelliocrinids and dimerocrinitids are both known from the Cataract Group and the Brassfield Formation, the latter also including a species of pisocrinid (Donovan 1989*a*, fig. 2). This distribution suggests that, by the Lower Llandovery, the crinoid faunas of the North American and South European faunal provinces may have been nearly cosmopolitan, at least at the family level (but also see comments on Silurian crinoid distributions in Holland 1971, pp. 70–71).

A further crinoid taxon common to both the Gasworks Mudstone and the Newlands Formation has been recognized on the basis of large and distinctive columnals, probably derived from rhodocrinitid camerates. Ramsbottom (1954, p. 264) considered these two occurrences to be conspecific, a deduction with which we broadly concur, although the Gasworks Mudstones specimens are few. We have therefore been cautious in comparing the columnals from the two localities.



TEXT-FIG. 2. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov. A-C, holotype. A, BMNH E49740a, lateral view of pluricolumnal. B-C, BMNH E49740b; B, lateral view of pluricolumnal; C, enlargement of part of a noditaxis, with internodal orders numbered. D-F, articular facets of paratype nodals, D, BMNH E49741a. E-F, BMNH E49739b and a, respectively (counterparts). All figures are camera lucida drawings of latex casts; all, except C, at the same scale.

Floricolumnus (col.) *girvanensis* sp. nov.

Plate 1, figs 1-2, 5-6; Text-figs 2-4

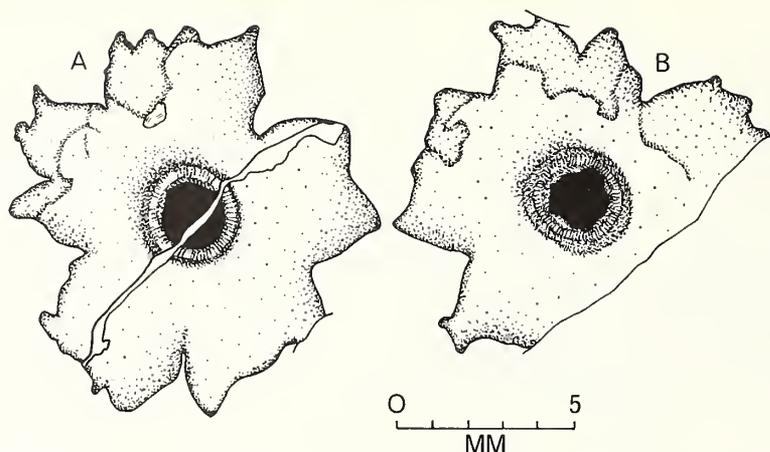
1954 Peculiar crinoid stem (in part); Ramsbottom, p. 264, pl. 12, figs 10-13.

Derivation of trivial name. After Girvan.

Type material, locality and horizon. Holotype, British Museum (Natural History) (BMNH) E49740a-b (counterpart external moulds: Pl. 1, fig. 6; Text-fig. 2A-C); paratypes, BMNH E49739a-b, E49741a-b, Hunterian Museum (HM) E3265/1-5, E3266/1-5, E3481/1-10, E3482/1-23, E3530, E3553/1, E3554-E3556, E3564-E3566, E3643, E3645/1-3, E6062a-b, E6063a-b, E6064a, E6065-E6069, E6071a-b, E6072 (all external moulds with or without counterparts). All specimens are from the Newlands Formation (Llandovery, Rhuddanian/Idwian boundary, late A₄ to early B₁; Cocks *et al.* 1971, fig. 2) of the Girvan district, Strathclyde, Scotland (Cocks and Toghil 1973, pp. 215, 216). It is probable that all specimens come from the type locality, a 'small N-S sandstone ridge on the E side of a small stream 150 m due E of Newlands Farm' (Howells 1982, p. 4), near Dailly, about 11 km ENE of Girvan, Strathclyde, Scotland, GR NS 2775 0434. Howells (1982) considered this locality to be of *Monograptus gregarius* Biozone age (= B₁ to early B₂).

Diagnosis. As for the genus.

Description. Nodals: pentastellate to circular crenulate columnals with a central lumen of pentagonal or circular outline. Lumen surrounded by a conical claustrum (Text-fig. 2E), of pentagonal, circular or crenulate pentagonal outline, which is often partly or completely obscured by sediment. The claustrum of HM E3566 appears to be pentameric, although the epifacet shows no evidence of merism. Claustrum surrounded by a narrow articular facet, of circular or pentagonal outline (Pl. 1, figs 1-2; Text-figs 2D-F, 3-4), comprising



TEXT-FIG. 3. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov. A–B, HM E6062a and b respectively, paratype (counterparts); camera lucida drawings from latex casts.

numerous short, unbranched, fine, radial crenulae. The articular facet is usually conical and continuous with the claustrum (Text-fig. 2E). Where the facet appears to be parallel to the plane of the columnal, it is apparently due to the presence of a low internodal (or internodals) that is still articulated with the nodal (for example, Pl. 1, fig. 2; Text-figs 2F, 4B). Epifacet broad, pentastellate to serrated circular in outline, unsculptured and inflated, so that the crenularium always lies within a depression. The 'rays' of the epifacet vary from being pointed (Pl. 1, fig. 1; Text-fig. 2D) through bifid (Pl. 1, figs 2, ?5; Text-figs 2E–F, 4A) to multilobate (Pl. 1, fig. 6; Text-figs 2A–B, 3, 4B). 'Ray' form is highly variable, but is broadly consistent within any columnal. The outline of the epifacet is often asymmetrical. 'Rays' may be in close contact (Pl. 1, figs 1–2, 6; Text-figs 2–3, 4B) or separated (Pl. 1, fig. 5; Text-fig. 4A). The surface of some epifacets is uneven and coarsely laminar, possibly suggesting secretion of a new stereom layer (Text-fig. 4B).

Internodals: column heteromorphic, with up to five orders of internodals developed and regularly intercalated (Text-fig. 2C). Priminternodals are highest *et seq.* Prim-, secund- and tertinternodals have decreasingly convex latera, while quart- and quintinternodals have planar latera. Articulation is symplectial. An ideal noditaxis of this column would comprise N5453545254535451545354525453545 (notation follows Webster 1974), but is not clearly seen in the available specimens; part of one of the most complete noditaxes from the holotype is illustrated (Text-fig. 2C). HM E3481/10 is poorly preserved, but at least five orders of internodal appear to be regularly intercalated. Columnals are wedge-shaped in the early stages of intercalation (Text-fig. 2C, quintinternodal in middle of figure). The column was obviously highly flexible, as is indicated by the strong curvature of the holotype (Pl. 1, fig. 6; Text-fig. 2A–B). A claustrum is present in the internodals of some pluricolumnals.

Dimensions. Columnal diameter (KD), articular facet diameter (FD) and lumen diameter (LD) were measured, where possible, from all of the available nodals (measurement of KD followed Moore *et al.* 1968, fig. 5G; lumen diameter includes the width of the claustrum). Graphs of KD/FD and FD/LD (Text-fig. 5) showed close correlations between these parameters at the 99% confidence level.

EXPLANATION OF PLATE I

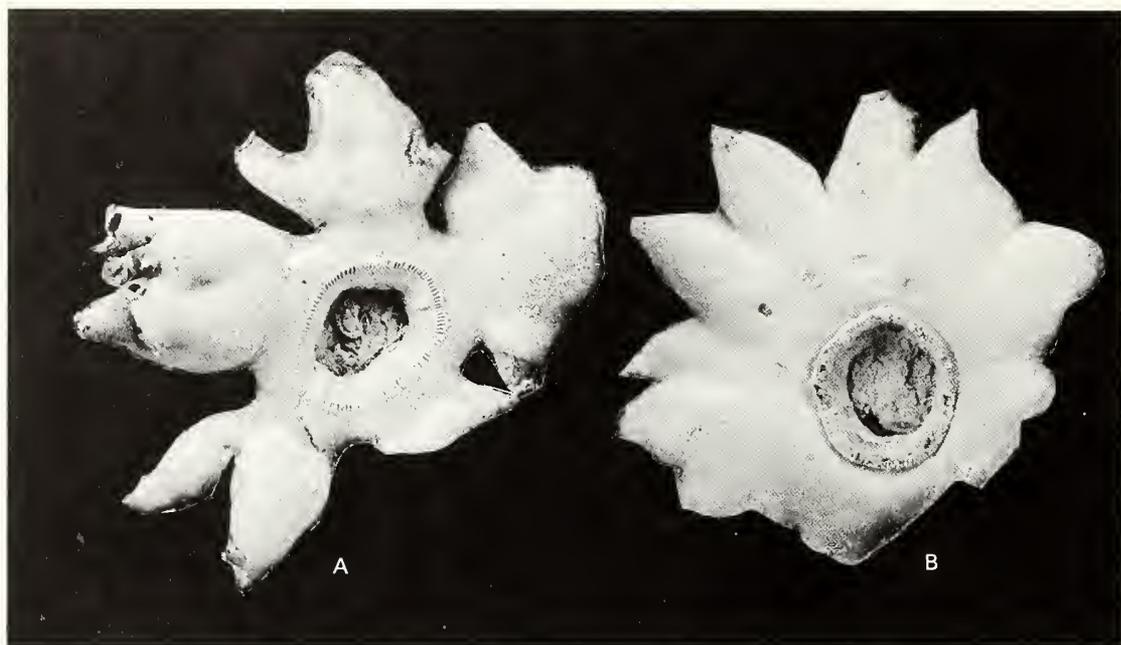
Figs 1–2, 5–6. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov. 1, BMNH E49741a, paratype, $\times 5$. 2, BMNH E49739a, paratype, $\times 5$. 5, HM E6063a, paratype, $\times 5$. 6, BMNH E49740b, holotype, lateral view of pluricolumnal, $\times 4.5$.

Figs 3–4. *Floricolumnus* (col.) sp. cf. *F.* (col.) *girvanensis* gen. et sp. nov. 3, SM A32132, $\times 5$. 4, SM A32131, $\times 4.5$.

All figures illustrate latex casts of natural moulds whitened with ammonium chloride sublimate. All except figure 6 show articular facets (with or without articulated internodals) of nodal columnals.



DONOVAN and CLARK, *Floricolumnus*



TEXT-FIG. 4. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov., paratypes. A, HM E3265/1. B, HM E3482/15. Both figures illustrate latex casts from natural moulds whitened with ammonium chloride. Both $\times 5$.

Floricolumnus (col.) sp. cf. *Floricolumnus* (col.) *girvanensis* sp. nov.

Plate 1, figs 3–4; Text-fig. 6

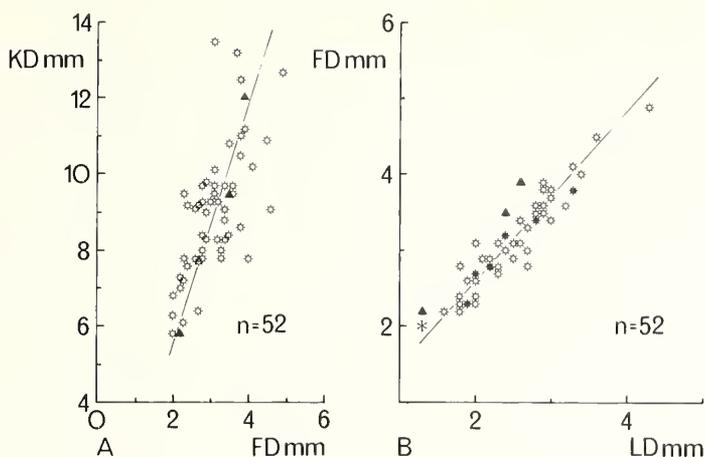
1954 Peculiar crinoid stem (in part); Ramsbottom, p. 264.

Material, locality and horizon. Three specimens, Sedgwick Museum (SM) A32131–A32133, all external moulds without counterparts. All specimens are from the Gasworks Mudstone of Dyfed, southwest Wales (Lower Llandovery, Rhuddanian, A₃ to early A₄; Cocks *et al.* 1971, fig. 2), from near the gasworks, Haverfordwest, opposite the entrance to the quay, NGR SM 9585 1540.

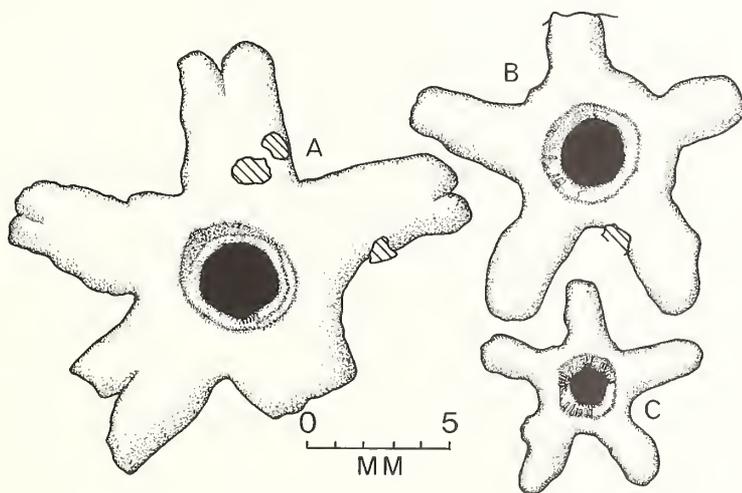
Description. Only known from pentastellate nodal columnals with a central, pentagonal to circular lumen (Pl. 1, figs 3–4; Text-fig. 6). Where the lumen is pentagonal, the lumen angles are rounded. The lumen is surrounded by a crenularium composed of short, fine, unbranched crenulae. The crenularium occurs within a conical depression, with or without a flattened platform adjacent to the lumen. The articular facet is surrounded by a broad, smooth and unsculptured epifacet of pentastellate outline. The 'rays' of the epifacet are blunt and well-rounded, dividing into a pair of blunt projections in the largest columnal (Pl. 1, fig. 3; Text-fig. 6A).

Measurements. These data have been plotted on Text-fig. 5 for comparison with the Girvan specimens. Note that, although the KD/FD data agree well, the FD/LD points consistently plot well to the left of the regression line for *F.* (col.) *girvanensis* s.s.

Discussion. A broad diversity of nodal geometries has been included in *Floricolumnus* (col.) *girvanensis*, but the variation shown is not outside the range of morphologies that might be expected within a single species. It is well known that the majority of crinoid columns show changes in morphology along their length (Moore *et al.* 1968; Ubaghs 1978; for specific examples, see Donovan 1984; Donovan *et al.* 1986). The range of nodal morphologies in *F.* (col.) *girvanensis* is from strongly pentastellate columnals with elongate 'rays' (Pl. 1, fig. 2), through ossicles with



TEXT-FIG. 5. A, plot of columnal diameter (KD) versus articular facet diameter (FD), and B, plot of FD versus lumen diameter (LD) in *Floricolumnus* (col.) *girvanensis* gen. et sp. nov., based on measurements taken from the type specimens. Where the specimens are deformed, original diameters were estimated. Open star = one specimen, closed star = two specimens, asterisk = three specimens. Regression lines are plotted ($FD = 0.31 + 0.31 KD$; $LD = 0.89 FD - 0.29$). Data for *F.* (col.) sp. cf. *F.* (col.) *girvanensis* are plotted as closed triangles.



TEXT-FIG. 6. *Floricolumnus* (col.) sp. cf. *F.* (col.) *girvanensis* gen. et sp. nov. A, SM A32132. B, SM A32131. C, SM A32133. All figures are camera lucida drawings from latex casts.

broader rays (Pl. 1, fig. 1; Text-fig. 4A), to columnals where the 'rays' are so expanded that the ossicles have become near-circular with a serrated outline (Pl. 1, fig. 6; Text-figs 2A-B, 4B). This progression most logically represents the change in columnal geometry from the proximal to the distal regions of the stem, as it is more likely that calcite would have been secreted, rather than absorbed, to alter the outline of the ossicles. At least some nodals have a coarsely laminar appearance, suggesting secretion of an outer calcitic layer.

This interpretation of column morphology begs two questions: what were the functions of these

unusual nodals, and why was it necessary to change their outline down the length of the stem? Three interpretations are possible and each may have made some contribution to the function of the column: protection from predation; improved hydrodynamic lift; and attachment to the substrate. The nodals are always 'spinose', whether pentastellate or serrated, and may have acted to deter predators. However, none of the columnals shows undoubted signs that they may have been regenerating following unsuccessful predation and it is doubted if a crinoid column would have been particularly nutritious, unless the axial canal contained tissues not found in modern stalked crinoids (cf. Jefferies 1968, fig. 5). This is at least possible, as the axial canal of *F. (col.) girvanensis* is broader than that of any extant crinoid, although the function of these tissues is problematic (they are unlikely to have been muscular: Donovan 1989b).

Perhaps more probably, the broad epifacets may have been an aid to hydrodynamic lift to help raise the crown above the substrate (cf. the kite paradigm of Breimer and Webster 1975). Riddle (1989) has recently demonstrated how an unusual column geometry could influence the behaviour of water currents close to a crinoid and, by analogy, it may have been that broad epifacets were an aid to generating lift. However, the more rounded columnals which we interpret as being distal would probably have performed this function more efficiently than the proximal(?) pentastellate columnals.

Attachment of the distal column is the most probable principal function of these serrated and pentastellate nodals. It is a general observation that, although rhodocrinitid columnals are often very common locally (for example, *Balacrinus basalis* (McCoy) in the Onny Valley, Shropshire; Donovan 1986, p. 48), obvious attachment structures are absent. This may indicate that attachment was by a form of non-cirriiferous runner (analogous to cirriiferous runners: Brett 1981) which relied upon frictional contact to help the crinoid maintain its station. Broad epifacets normal to the axis of the column would have acted as a series of drag anchors to prevent the crinoid being transported by a current, enabling the orientation of the crown to change in response to alterations in current direction (the presence of numerous low columnals would have made the column particularly flexible; Text-fig. 2A–B). The serrated distal epifacets of *F. (col.) girvanensis* may have helped the stem to cut down into the underlying sediment and thus gain a particularly good purchase.

Acknowledgements. We thank David Lewis (BMNH) and David Price (SM) for providing latex casts of specimens in their care.

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STEPHEN K. DONOVAN
 Department of Geology
 University of the West Indies
 Mona, Kingston 7, Jamaica

NEIL D. L. CLARK
 Hunterian Museum
 The University
 Glasgow G12 8QQ

AFFINITY OF *TUBIPHYTES*

by ROBERT RIDING *and* LI GUO

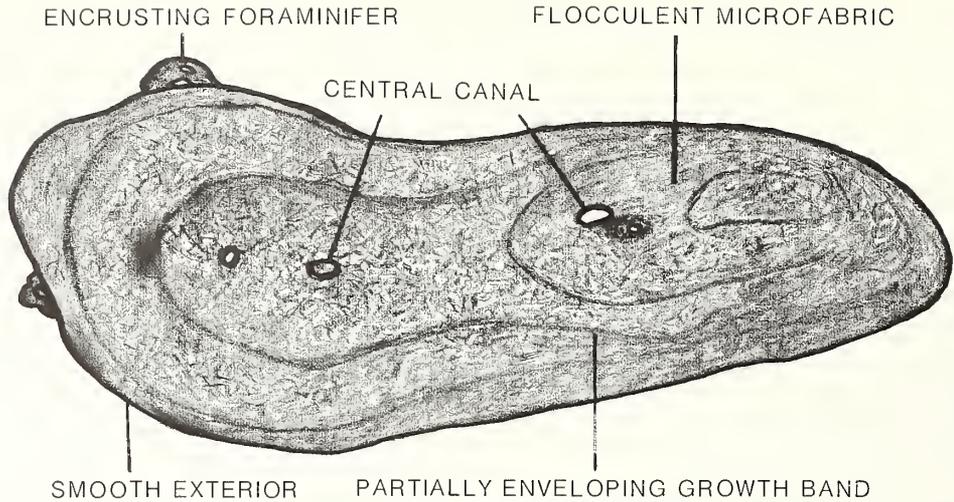
ABSTRACT. *Tubiphytes* Maslov, 1956 is a problematic fossil which ranges from early Carboniferous to mid-Cretaceous and is common in Permian and Triassic reef and other shallow marine carbonate facies. It has been suggested to be a cyanobacterium, hydrozoan, sponge, red alga, foraminifer, and a cyanobacterium-chlorophyte consortium. Its distinctive morphological features include densely flocculent and layered skeletal structure, an axial canal system which may or may not be integral to *Tubiphytes*, and smoothly rounded to encrusting external form. Cyanobacterial and algal affinities are discounted. A foraminiferal affinity cannot be ruled out, but is inconsistent with the morphology and organization of most *Tubiphytes*. The presence of an integral canal system would be consistent with a hydrozoan or sponge affinity, but the absence of other cavities in the skeleton which individuals could occupy does not favour a hydrozoan affinity. There is similarity between the skeletal structure of *Tubiphytes* and that of archaeocyath exothecal tissue and sponge filling tissue. *Tubiphytes* appears to have been capable of colonizing deeper and cooler water than algae with which it may also be associated. The family Nigriporellidae Rigby, containing *Tubiphytes*, is here regarded as belonging to the invertebrates, possibly the Porifera.

TUBIPHYTES is an important late Palaeozoic to Mesozoic reef-building organism which is widely regarded as an alga (Johnson 1963, p. 139; Croneis and Toomey 1965, p. 7; Flügel 1977, pp. 324–325; Flügel 1980, pp. 86–88; Flügel 1981a, p. 153; *Encyclopaedia Britannica* 1983, *Micropaedia X*, p. 167; Sartorio and Venturini 1988, p. 37). However, widely differing opinions concerning its affinity were expressed on the occasion of its discovery, which was made independently in the USSR and the USA during the 1950s. These questions concerning its affinity have not since been resolved. Although generally only a few millimetres in size, this fossil is a major contributor to Pennsylvanian, Permian and Triassic reefs and it is also often present in other shallow-marine carbonate facies. Its systematic position is therefore of ecological and sedimentary as well as evolutionary significance. Here we propose that a poriferan affinity accounts best for the canal system, banded structure, and flocculent skeletal fabric which are the most distinctive features of this genus.

DESCRIPTION

Tubiphytes is commonly irregularly cylindrical in form, or encrusting, with a smooth external surface and a distinctive dark, densely flocculent, internal structure which in detail appears to be composed of an irregular fibrous network. Internal tubes, which have been interpreted either as encrusted extraneous objects, or as a canal-system, are usually present. Spinose peripheral tubes have been reported in one instance (Flügel *et al.* 1984, pl. 31, fig. 6). The skeleton has a layered structure created by bands laid down successively around the central tube or tubes (Pl. 1). Variations in structure, style of encrustation, internal tubes, and inclusions are illustrated by Vachard (1980, fig. 67). *Tubiphytes* typically occurs as small (a few millimetres) individual masses, which may be irregularly branched, and also as thick (up to several centimetres) encrustations, usually on other skeletons such as sponges and bryozoans. Narrow tubiform fossils have also been compared with *Tubiphytes* (Flügel *et al.* 1984, pl. 42, fig. 9). The skeleton is generally very well preserved, sometimes in sharp contrast with associated skeletons (as noted by Rigby (1958, p. 584)) and its simple, smooth, dark appearance makes it conspicuous in thin-section.

Thus, the principal morphological features (Text-fig. 1) are: (a) the enclosed tube system; (b) the delicate, but generally well-preserved, flocculent network-like internal fabric; (c) the banded



TEXT-FIG. 1. Characteristic morphological features of *Tubiphytes obscurus* Maslov. Based on an Upper Permian specimen provided by David Edwards from the massive facies of the Capitan Reef Complex, Bat Cave Canyon, New Mexico, USA.

structure of the skeleton; and (d) the smooth, encrusting form with hemispherical to stolon-like protuberances.

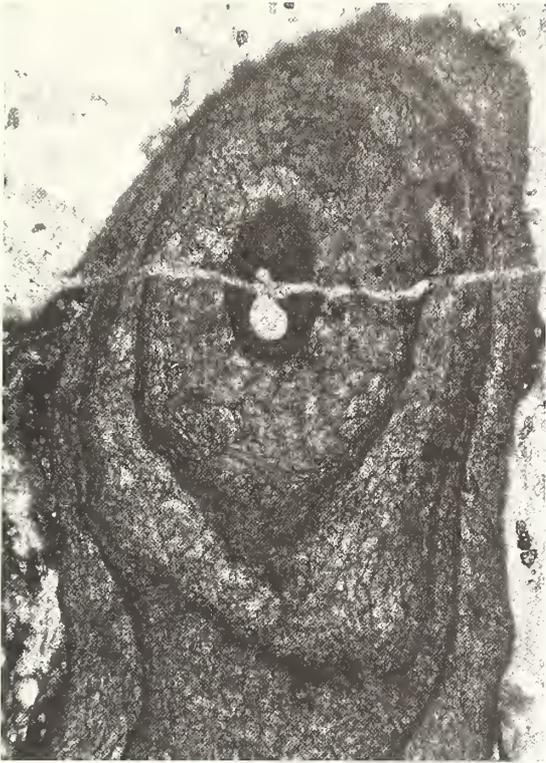
HISTORY OF RESEARCH

Reviews of the progress of information and views concerning *Tubiphytes* have been made by Croneis and Toomey (1965), Flügel (1966, pp. 56–58), Ott (in Kraus and Ott, 1968), Flügel (1981a, 1981b), and Babcock (1977, pp. 17–18, 1986). For further information concerning taxonomy and distribution see also Vachard (1980, pp. 338–343) and Schäfer and Senowbari-Daryan (1983, pp. 126–129). The principal details are as follows.

Maslov (1956, pp. 82–84) placed *Tubiphytes* in *algae incertae sedis* with the tentative suggestion that it could be a cyanobacterium (Schizophyta). Previously, Rauser-Chernousova (1951, p. 17 and pl. 3, figs 1–2) had named this fossil *Shamovella*, from the Kungurian (uppermost Early Permian) reefal sequences of the Sterlitamak–Ishimbay area, 125–150 km south of Ufa in the Bashkir Republic, just west of the southern Urals, providing illustration but not naming a type species (see Maslov 1956, p. 21; Elias 1959, p. 77). Elias (1959, p. 77) regarded *Shamovella* as a *nomen imperfectus* (see also Croneis and Toomey 1965, p. 7). In establishing *Tubiphytes*, Maslov used material from the same Sterlitamak–Ishimbay area that he and Rauser-Chernousova collected. It is clear from the illustration of *Shamovella* by Rauser-Chernousova (1951) reproduced by Elias (1959, pl. 1, fig. 6) that it is the same as *Tubiphytes* Maslov. Meanwhile, in the United States, in rocks of only slightly younger age (the Capitan reef complex of New Mexico and Texas (Newell *et*

EXPLANATION OF PLATE I

Figs 1–4. *Tubiphytes obscurus* Maslov. Upper Permian, massive facies of the Capitan Reef Complex; Bat Cave Canyon, New Mexico, USA; thin-section photomicrographs showing characteristic features of the type-species (see also Text-fig. 1); smooth exterior, dense, dark flocculent internal microfabric, enveloping to partly enveloping growth bands, and central tubular structures. All specimens courtesy of David Edwards. 1, $\times 32$. 2, $\times 18$. 3, $\times 18$. 4, $\times 35$. Note in figure 4 that the central tube resembles a nubeculariid foraminifer (cf. Flügel 1981b, figs 4–5; and Bernier 1984, pl. 21, figs 1–2), although if the short side branches are regarded as tubes then they also resemble sponge oscula (Colin Scrutton, pers. comm. 1990).



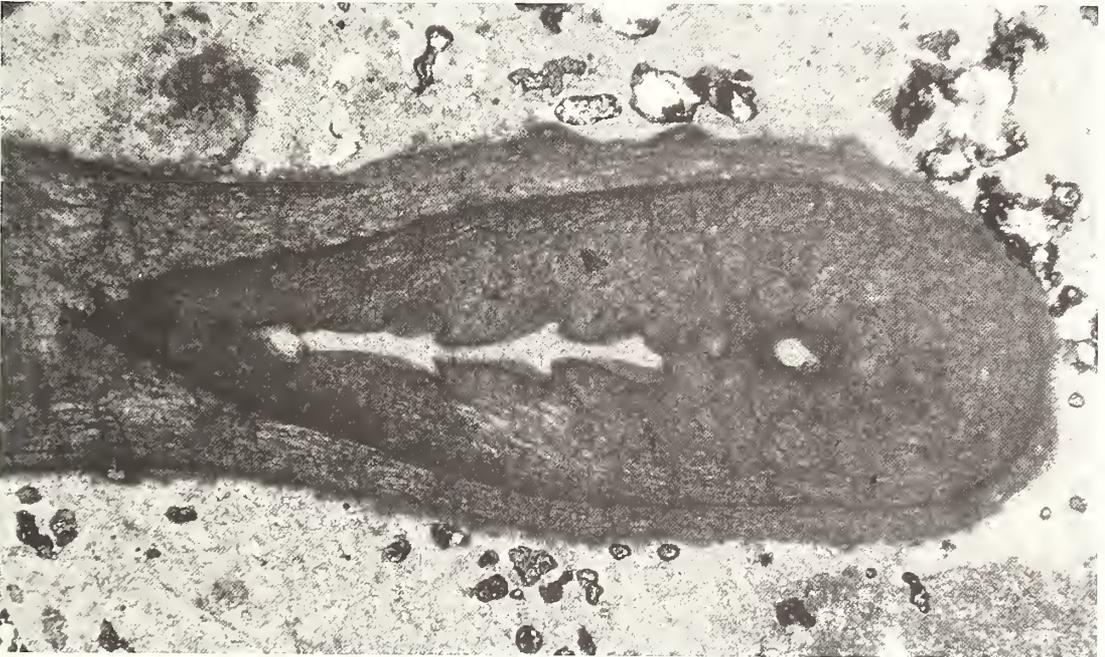
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4

al. 1953, p. 112, pl. 17, fig. 3; pl. 18, figs 1–2, 5–6) and in the Chinati and Glass Mountains of Texas (Newell 1955, p. 307, pls 4–8)), this fossil had been noticed as a frame-building organism. It was not named, but was regarded as a hydrocoralline (= hydrozoan) following advice from J. H. Johnson: 'a problematical encrusting and stoloniferous organism, considered by J. H. Johnson (personal communication) as possibly a hydrocoralline' (Newell *et al.* 1953, p. 112). Newell *et al.* (1953, p. 112) distinguished it from *Solenopora* (see discussion of rhodophyte affinity, below) and Newell (1955, p. 307, pl. 8) noted its 'indistinct internal network suggestive of communicating canals or spicules'.

Shortly after this, Rigby (1958), using material mainly from the middle Permian of Texas, described the same fossil as a new genus, *Nigriporella*, which he placed in a new hydrozoan family, the Nigriporellidae. Konishi (1959) recognized that *Nigriporella* was a synonym of *Tubiphytes*, and also favoured a hydrozoan affinity for it. He noted that it is widespread in the Permian and figured an example from the Lower Permian of Honshu, Japan. Hudson (1960) and Elliott (1962) recorded *Tubiphytes* in the Permian of Oman and northern Iraq respectively, but did not add to views about its affinities.

Although instrumental in first suggesting a hydrozoan affinity to American workers, ten years later Johnson (1963, p. 139) followed Maslov in placing *Tubiphytes* in 'algae of uncertain systematic position', as did Croneis and Toomey (1965). Flügel (1966, p. 56) regarded *Tubiphytes* as a microproblematicum, but in a discussion of affinities mentioned the possibility of a comparison with rhodophytes. This was the first departure from the 'algal' affinities proposed by earlier authors which had actually implied blue-green rather than eukaryote algae.

From this point onwards three strands of opinion can be followed through to the present: sponge/animal, rhodophyte alga, and cyanobacterium or cyanobacterial-chlorophyte consortium. Ott (*in* Kraus and Ott 1968, p. 271) suggested that *Tubiphytes* may be a sponge. Crescenti (1969), describing a new species, *T. morronensis*, from the uppermost Jurassic of the central Apennines in Italy, preferred Maslov's view that it is an *alga incertae sedis*. Homann (1972) and Kochansky-Devidé (1970) supported Flügel's (1966) suggestion of a rhodophyte affinity, although it should be noted that here Kochansky-Devidé was referring not to *Tubiphytes obscurus* Maslov but to *T. carinthiacus* (Flügel), a species originally placed by Flügel (1966, p. 54) in *Hikorocodium* Endo.

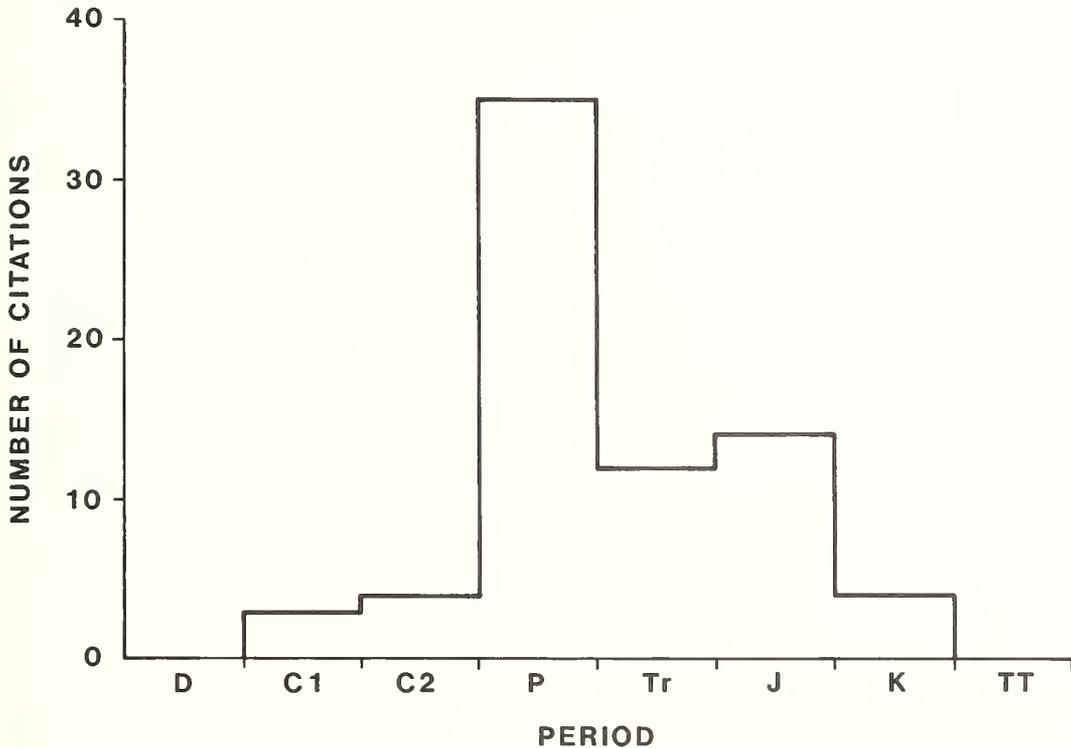
Toomey (1969, pp. 1323–1324) reiterated the possibility of a cyanobacterial origin, and Flügel (1979, p. 578) and Flügel and Flügel-Kahler (1980, pp. 164, 172) also tentatively returned to this opinion. Babcock (1977, pp. 17–18) briefly reviewed the affinities which had been proposed and concluded that neither a hydrozoan nor a cyanobacterial affinity for *Tubiphytes* seemed likely, although later (Babcock 1979, p. 425) he expressed the view that *Tubiphytes* is an animal rather than an alga or cyanobacterium. Flügel (1981a), referring to *T. carinthiacus*, cast doubt on Babcock's (1977, p. 18) criticism of the blue-green algal hypothesis, and echoed Maslov: 'These arguments are not valid if we consider the interwoven threads seen in *Tubiphytes carinthiacus* as remains of trichomes', adding 'The spar-filled "tubes" may belong to another alga, which could have been circumscribed by *Tubiphytes*. Associations of epiphytes consisting of filamentous blue-green algae and filamentous green algae are known from modern environments' (Flügel 1981a, p. 153). Flügel (1983) restated this view that a cyanobacterial-chlorophyte and algal-foraminiferal consortium could be responsible for *Tubiphytes*.

Babcock (1986, pp. 15–17) again reviewed the genus in some detail, emphasizing its problematic nature. In a general systematic treatment of calcified cyanobacteria and algae, Luchinina (in Chuvashov, Luchinina and Shuysky *et al.* 1987, p. 30) placed *Tubiphytes* together with fossils such as *Girvanella* Nicholson and Etheridge. A genus somewhat similar to *Tubiphytes*, *Plexoramea* Mello from the Triassic, which had at times been referred to as *Tubiphytes carinthiacus* (which itself was originally described as *Hikorocodium carinthiacum* Flügel: see Systematic Palaeontology, below) has been compared with both chlorophyte algae and fungi (Flügel *et al.* 1988). *Plexoramea* has a more open internal mesh-like fabric than *Tubiphytes obscurus*. We have drawn attention to the similarity between the microfabric of *Tubiphytes* and that of some archaeocyath tissue (Guo and Riding 1989). The latter is dense, dark, flocculent and also shows banding reminiscent of that seen

in *Tubiphytes*. However, we have not observed a delicately fibrous fabric quite like that of *Tubiphytes*, nor are similar axial canal-systems present and the similarity, although intriguing, remains superficial.

DISTRIBUTION

Tubiphytes ranges from Early Carboniferous to mid-Cretaceous (Text-fig. 2). It first occurs in the Mississippian of Utah, USA (Rigby 1958, p. 586). The youngest record appears to be that of *T. morronensis* by Crescenti (1969, p. 37) from the early Albian (mid-Cretaceous) of central Italy. *Tubiphytes* becomes conspicuous in the Pennsylvanian, where it is best known in the south-western United States (Toomey 1969), and common in the Early Permian (Malek-Aslani 1970; Wahlman 1985, 1988). Newell *et al.* (1953, p. 112) noted the abundance of what later would be recognized as *Tubiphytes* in the Capitan reef complex (see also Achauer 1969; Kendall 1969; Babcock 1977, 1979) and the genus is widely distributed in Permian reefs of the Mediterranean area and elsewhere (Flügel 1984, fig. 4), often in association with another problematical genus, *Archaeolithoporella* Endo (Flügel 1981a). *Tubiphytes* is also important in Middle Triassic reefs (Ott 1967; Brandner and Resch 1981, p. 212), and in the Upper Triassic (Flügel 1981c; Schäfer and Senowbari-Daryan 1983). Jurassic reports include *Tubiphytes* from the middle-upper Oxfordian of Franconia, West Germany (Flügel and Steiger 1981, p. 378), Kimmeridgian of the French Jura (Bernier 1984, p. 524), middle Kimmeridgian and lowermost Tithonian of Franconia (Flügel 1981b), and the middle to upper Jurassic of central Italy (Crescenti 1969, p. 21; Chiocchini *et al.* 1980). Barattolo and Pugliese (1987, pls 32, 40) figure *Tubiphytes* from the middle-upper Jurassic (Callovian-Oxfordian) and Jurassic-Cretaceous (Portlandian-Berriasian) of Capri, Italy. Jansa *et al.* (1982) report *Tubiphytes* from Berriasian-Valangian (early Cretaceous) sponge bioherms of the Scotian Shelf of off-shore



TEXT-FIG. 2. Histogram of published references to *Tubiphytes* by geological period. Data from GEOREF database 1989 and references cited in text.

eastern Canada. Misik (1979, p. 709) reports *T. obscurus* from the Triassic to Neocomian of the western Carpathians without indicating the precise age of the Lower Cretaceous occurrences. Crescenti (1969, pp. 21–22, 37) also recorded *Tubiphytes* from the Lower Cretaceous (up to early Albian) of central Italy.

Although *Tubiphytes* is important in shallow-water limestones, it also occurs in the deeper parts of Permian reefs at Trogkofel in the Carnic Alps (David Edwards, pers. comm. 1989) and at Capitan (Babcock 1977, fig. 16; 1979, fig. 3). At Capitan it also occurs in cryptic reef habitats (J. A. Babcock, pers. comm. 1990). Sponge bioherms containing *Tubiphytes* from the early Cretaceous of the Scotian Shelf are interpreted to have formed at a depth of 60–100 m (Jansa *et al.* 1982). Furthermore, *Tubiphytes* is common in Lower Permian limestones of West Timor (Indonesia), where it is associated with a temperate climate brachiopod fauna (Riding and Barkham in prep.). In this West Timor occurrence, dasycladaleans, gymnocodiaceans, and other algae of warm-water environments are absent and *Tubiphytes* occurs with bryozoans, crinoids and brachiopods. These indications that *Tubiphytes* could inhabit a temperate water environment (West Timor) and also relatively deep (Trogkofel, Capitan, Scotian shelf), and cryptic (Capitan), reefal environments strengthen the view that it is unlikely to be a cyanobacterium (or a green alga).

DISCUSSION

Affinities which have been suggested for *Tubiphytes* include cyanobacterium, hydrozoan, sponge, rhodophyte, foraminifer and cyanobacterium–chlorophyte consortium (Table 1). The distinctive morphological features of the genus include dense flocculent fabric, central tube (canal system?), layered structure, and smooth, simple, external form (Text-fig. 1).

Cyanobacterium

Maslov (1956, pp. 82–84; for English translation see Croneis and Toomey 1965, p. 8) regarded the tube of *Tubiphytes obscurus* as a trace of a stem, or some such extraneous object, which *Tubiphytes*

TABLE 1. Summary of the affinities which have been suggested for *Tubiphytes*, showing the originator (first author), basis for the original interpretation, problems or supporting evidence, and ranking of the affinities in order of likelihood.

Proposed affinity	First author	Original reasons	Problems or support	Likelihood
Poriferan	Ott (In Kraus and Ott 1968)	?	Microfabric resembles sponge filling tissue; growth style (shape, banding) is generally poriferan	1
Foraminifer	Bernier 1984	Morphology of tubular forms	May apply to <i>T. gracilis</i> and <i>T. morronensis</i> but morphology and structure of <i>T. obscurus</i> is inconsistent with a foraminiferal affinity	2 (but does not apply to type-species)
Hydrozoan	Rigby 1958	Canal system	'Canal' may not be integral parts of the skeleton; no zooid receptacle evident	3
Cyanobacterium	Maslov 1956	Microfabric	No close resemblance to known calcified cyanobacterial microfabrics	4
Cyanobacterial chlorophyte consortium	Flügel 1981	?		4
Rhodophyte	Flügel 1966	?	No close resemblance to known calcified rhodophytes	5

encrusted. He therefore concentrated on the delicate irregular meshwork-like structure of the skeleton, which he compared with the trichomes of cyanobacteria. This view has been supported by Flügel (1981*a*, p. 153), particularly with respect to *T. carinthiacus*. Nevertheless, it would seem that the tubes of *Tubiphytes* cannot so readily be disregarded (see discussion of hydrozoan affinity, below). However, the main objections to a cyanobacterial affinity for *Tubiphytes* are that masses of unorientated trichomes are not known to assemble in this fashion, and that it is not the trichomes (the strands of cells) but the enveloping mucilaginous sheath that is the site of calcification in cyanobacteria (Pentecost and Riding 1986, p. 76). This results in solid or tubiform fossils which are comparable with modern calcified cyanobacteria (Riding 1991*a*), but which do not resemble the delicate anastomosing network seen in *Tubiphytes*. Maslov (1956, p. 83) was incorrect when he compared this supposed style of fossilization 'for calcareous blue-green algae with very thin trichomes' with that of *Epiphyton* Bornemann, which is common in the Cambrian. In fact, *Epiphyton* has a dense micritic microfabric in which reports of cells have not been confirmed (Riding 1991*b*). Furthermore, *Tubiphytes* does not exhibit the fabrics, or contain the extraneous particulate material, typical of cyanobacterial oncoids.

Hydrozoan

Tubiphytes is an encrusting organism, and clearly was capable of overgrowing and surrounding adjacent objects. However, it also contains tubes which do appear to be, as even Maslov's name for the genus implies, an integral feature, commonly occupying an axial position in the skeleton. This construction has no analogue among the cyanobacteria or algae. Rigby (1958) was the first to emphasize the tubes. His interpretation of them as representing a canal-system resembling that of hydrozoans, stromatoporoids and sponges is in marked contrast to Maslov's interpretation. Presumably, similar considerations influenced J. H. Johnson's advice to Newell *et al.* (1953, p. 112) suggesting a hydrocoralline (i.e. hydrozoan) affinity for what would subsequently be recognized as *Tubiphytes* in the Capitan reef complex, but this was only a brief personal communication. Rigby's (1958) description of *Nigriporella* is detailed. He regarded the tubes as an integral part of the skeleton, and he discerned similarities with both milleporids and stromatoporoids. He emphasized the 'zooidal tubes connected by a small meandering canal system', identified dactylopores and gastropores (Rigby, 1958, pp. 583–584, text-fig. 2), and particularly compared them with the tubes and canals of milleporids. However, he compared the layered structure of *Nigriporella* with stromatoporoid latilaminae (subsequently, stromatoporoids have come to be widely regarded as sponges, see Poriferan affinity, below). In discussing relationships, Rigby noted that 'Superficially, zooidal tubes of *Nigriporella* resemble canals of sponges', but continued 'chambered tubules and lack of definite skeletal elements akin to spicules make it impossible to class the genus with sponges' (but see Poriferan affinity, below). He concluded, 'Nigriporellids are considered as hydrozoans because of their mode of growth, presence of two types of zooidal tubes, and latilamellar structure' (Rigby 1958, p. 584).

Nevertheless, uncertainties still exist. The tube system of *Tubiphytes* does not generally appear to be so organized as Rigby (1958) described it. The central tube does, in fact, in some cases appear to be an encrusted object, as Maslov (1956) observed (see Foraminifer, below). Also, Rigby's (1958) discussion of hydrozoan versus sponge features needs to be reassessed in the light of subsequent work on fossil sponges. The main feature apparently lacking in *Tubiphytes*, which makes a hydrozoan affinity particularly difficult to support, is a receptacle in which individual zooids could have been housed.

Rhodophyte

Cronis and Toomey (1965), in summarizing the work of the previous fifteen years, contrasted the Johnson/Newell/Rigby hydrozoan view, which was supported by Konishi (1959), with the Maslov/Rausser-Chernousova 'algal' view because it was commonplace at that time to regard blue-greens as algae. However, the idea of an algal affinity in the strict sense, meaning a eukaryote as opposed to a blue-green alga or cyanobacterium, was not actually mentioned until Flügel (1966, p. 58)

tentatively suggested that a rhodophyte affinity might be considered. This was re-stated by Homann (1972, p. 256) for *T. obscurus* and, with respect to *T. carinthiacus*, by Kochansky-Devidé (1970), but has not since been supported. In fact, Newell *et al.* (1953, p. 112) had already compared *Tubiphytes* with *Solenopora*: 'Superficially it has somewhat the general expression of the coralline alga *Solenopora*, forming lamellar expansions, rounded tubercles, and ramose cylindrical branches. Internally the fossil is nearly structureless except for apparently erratic tubular pores or perforations. It is distinguished in thin sections from *Solenopora* by finer and less regular structure and by opacity ...'. The central tube of *Tubiphytes* does not resemble rhodophyte conceptacles (cf. Flügel 1966 and Homann 1972) and the closest comparison that could be drawn with extant calcified red algae would be with the perithallic tissue of crustose corallines, but this has a gridlike appearance which, as Newell *et al.* (1953) noted, is more orderly than that of *Tubiphytes*, and this affinity could not account for the tubes.

Poriferan

Since Rigby's (1958) study of *Tubiphytes*, several fossil groups, including Palaeozoic stromatoporoids (see Stearn 1975; Wood 1987), chaetetids (Gray 1980), and many Mesozoic genera previously attributed to the hydrozoans and tabulozoans (Flügel 1981*b*), have come to be regarded as likely to be sponges. This re-evaluation is both due to discovery of modern analogues, particularly sclerosponges, and to more critical comparative assessment of affinity.

Ott (in Kraus and Ott 1968, pp. 269–273) in a review of the systematics of *Tubiphytes* suggested that it could be a sponge and stated his intention to publish details of this novel suggestion separately. However, this publication did not take place. Several features suggest that *Tubiphytes* could be a sponge. Rigby's (1958, p. 584) rejection of a sponge affinity for *Tubiphytes* on the basis of absence of spicules and presence of chambered tubules is not now valid, but similarities which he noted remain significant. The tubes of *Tubiphytes* do, as Rigby (1958, p. 584) stated, 'resemble canals of sponges'. The banding, which Rigby (1958, p. 583) compared with stromatoporoid latilaminae, also resembles the growth style of sponges (for example, see the enveloping layers of the Wolfcampian calcisponges figured by Wahlman 1988, fig. 9*c*). The flocculent fabric of the skeleton resembles that of exothecal tissue of archaeocyaths (Guo and Riding 1989). It is suggested here that it may be comparable with the vesicular filling tissue of calcisponges (see Hartman *et al.* 1980, p. 208). Furthermore, the smooth encrusting and protuberant external form of *Tubiphytes* is typical of some sponges. However, the apparent absence of external pores is an obstacle to this interpretation.

Cyanobacterial–chlorophyte consortium

Flügel (1981*a*, 1983) suggested that *Tubiphytes* might be a cyanobacterial–chlorophyte consortium, but this interpretation has not been further developed and does not appear to have support from modern analogues.

Foraminifer

Bernier (1984, pp. 523–524) regards *T. morronensis* as a nubeculariid foraminifer. However, this view may be encouraged by the ability of *Tubiphytes* to encrust foraminifers which then become incorporated as a central tube. The Bajocian–Kimmeridgian specimens of *T. morronensis* figured by Crescenti (1969, figs 20–22) show a central tube with constrictions. Bernier's (1984, pl. 21, figs 1–2) illustrations even more clearly show a linear sequence of flask-like swellings which in size and appearance closely resemble uniseriate chamber arrangement in foraminifers. This has also been noted by Vachard (1980, p. 340 and fig. 67 (2)). The miliolacean nubeculariid foraminifer *Nodophthalmidium* Macfadyen has been reported forming the nucleus of encrusting *T. morronensis* from the Upper Jurassic of Franconia, southern Germany (Flügel 1981*b*, p. 136, figs 4–5). Similar morphologies are shown by the 'axial canal-like' structures of specimens from the Upper Permian Capitan Reef Complex (Pl. 1, fig. 4) and from the mid-Permian of eastern Afghanistan (Vachard and Montenat 1981, pl. 2, fig. 3). However, whereas Flügel (1981*b*) interprets *T. morronensis* to be

encrusting a foraminiferal nucleus, Bernier (1984, p. 523) takes the view that the fine tissue of *Tubiphytes* itself is comparable with the wall-structure of miliolid foraminifers, and he compares the whole fossil, both central tube and surrounding dense skeleton, with the nubeculariid genus *Cornuspiramia* Cushman.

The generally much greater thickness of the wall in *Tubiphytes obscurus*, its banded structure and distinctive flocculent, rather than densely micritic, fabric, would appear to preclude the possibility of a foraminiferal affinity. Tubiform fossils with wall-structure resembling that of *Tubiphytes* have been described from the Permian, and it has been suggested that they may be small specimens of *T. gracilis* Schäfer & Senowbari-Daryan (Flügel *et al.* 1984, p. 208, pl. 42, fig. 9). It is therefore possible that some specimens referred to *Tubiphytes* may be foraminifers and this requires clarification. However, there seems little likelihood that *Tubiphytes* itself can be attributed to the foraminifers. The interpretation of Flügel (1981*b*) that nubeculariid foraminifers can act as substrates for encrustation by *Tubiphytes* is accepted here. It is also worth noting that the apparent short side tubes of the axial tube (see Pl. 1, fig. 4) resemble sponge oscula, although if they are actually continuous flanges then they better resemble foraminifer chambers.

Synthesis

Tubiphytes does not appear closely to resemble any extant organism and no convincing parallels can be drawn between it and calcified cyanobacteria or algae. There have been few comparisons made between *Tubiphytes* and other fossils. Examples include the Triassic genus *Plexoramea* (which probably should be classified in the same group as *Tubiphytes*), Rigby's (1958) comparison of *Tubiphytes* with stromatoporoids (a similarity which he did not regard as close), and Maslov's (1956) mention (discounted here) of *Epiphyton*. The significance of the similarity between the skeletal fabric of *Tubiphytes obscurus* and the exothecal tissue of some archaeocyaths (Guo and Riding 1989) is still uncertain.

The canal system, in particular, is crucial to discussion of *Tubiphytes*. If it is integral to the fossil, then it links this genus most closely with animals such as hydrozoans and sponges. An invertebrate affinity is consistent with the ability of *Tubiphytes* to live in relatively cooler (Riding and Barkham, in prep.) and deeper water environments than algae such as dasycladaleans, phylloids, gymnocodiaceans and solenoporaceans, with which it co-exists in shallow warm water environments. In the choice between a hydrozoan or a sponge, the absence of receptacles to house individuals (see Stearn 1982, p. 513) favours a poriferan affinity.

CONCLUSIONS

The widely quoted cyanobacterial affinity for *Tubiphytes*, proposed by Maslov (1956, p. 82) is based on comparison of the flocculent skeletal structure with trichomes. However, this flocculent structure does not have any parallels in known calcified cyanobacteria and algae. There is at present no good evidence to suggest that *Tubiphytes* is a cyanobacterium, alga, or consortium of cyanobacteria and algae. Maslov (1956) believed that the tubes, for which he named the genus, were extraneous objects. It is clear that foraminiferal tubes, for example, can be enveloped by *Tubiphytes*. However, the possibility, documented in detail by Rigby (1958), cannot be ruled out that the tubes represent a canal system which is present as an integral part of the fossil and not as remains of objects which *Tubiphytes* encrusted. The presence of a canal system indicates an invertebrate affinity, particularly hydrozoan or poriferan.

There has been considerable confusion between hydrozoans and sponges in both the Palaeozoic and the Mesozoic. The absence of sites within or upon the skeleton which could have housed individuals is a factor which does not support a hydrozoan affinity. On the other hand, the presence of tabulae across tubes, and also the absence of spicules, which led Rigby (1958, p. 584) to reject a sponge affinity, would not now be regarded as excluding this possibility. The canal system does, as Rigby (1958, p. 584) pointed out, resemble that of sponges, and the other internal and external features of *Tubiphytes* are consistent with a sponge affinity.

Tubiphytes is present not only in the upper parts of reefs and in other shallow-water environments, but also in the deeper parts of reefs such as Capitan (Babcock 1977, 1979) and Trogkofel (David Edwards pers. comm. 1989). There is also evidence in the Permian that it was capable of inhabiting temperate water environments where dasycladaleans, gymnocodiaceans and calcified cyanobacteria were absent (Riding and Barkham in prep.). These environmental tolerances are consistent with an invertebrate affinity.

Tubiphytes obscurus Maslov, the type-species, has a distinctive dense dark skeletal structure. This wall appears to be too thick to be comparable with that of foraminifers (but cf. Bernier 1984, and Flügel *et al.* 1984, pl. 42, 9) and there seem to be no other parallels among late Palaeozoic and early Mesozoic fossils. However, it is similar to the exothecal tissue of Lower Cambrian archaeocyaths, whose systematic position is also problematic but for which a poriferan affinity is now considered likely (see Debrenne and Vacelet 1984).

Therefore, the available evidence does not support a cyanobacterial or algal origin for *Tubiphytes*. Its environmental distribution is consistent with an invertebrate affinity and its general skeletal structure and organization suggest that it is a hydrozoan or sponge, although a foraminiferal affinity cannot be ruled out. On balance, morphological evidence at present indicates that a poriferan affinity is the most likely one for *Tubiphytes*.

SYSTEMATIC PALAEOLOGY

INVERTEBRATA

Phylum ?PORIFERA

Family NIGRIPORELLIDAE Rigby, 1958

Although *Nigriporella* is a junior synonym (of *Tubiphytes*) this does not invalidate the family name (for taxonomic description see Rigby (1958, p. 583)).

Genus TUBIPHYTES Maslov, 1956

- 1951 *Shamovella* Rauser-Chernousova invalid genus
 1956 *Tubiphytes* Maslov, p. 82
 1958 *Nigriporella* Rigby, p. 584

Description. For taxonomic description see Maslov (1956, p. 82). Konishi (1959) recognized that *Nigriporella* is a synonym of *Tubiphytes* although he did not specifically state that it is a junior synonym. Johnson (1963, p. 139) considered that *Tubiphytes* 'closely resembles Johnson's and Konishi's *Retaphycus* from the Mississippian of Alberta (Johnson and Konishi, 1956, p. 103, pl. 7). It appears to differ only in having a coarser texture and a somewhat different growth form.' However, these illustrations of *Retaphycus* show neither the central canal-system nor the layered structure which are typical of *Tubiphytes* and we conclude that they are not related. *Plexoramea* (Mello 1977, pp. 190–192) is, however, similar to *Tubiphytes* (for details see Flügel *et al.* 1988).

Discussion. Seven species referable to *Tubiphytes* have been described:

T. obscurus Maslov, 1956, p. 82, pl. 25, figs 1, 3; pl. 26, pl. 27, figs 1–3; the type-species.

N. magna Rigby, 1958, p. 584, pl. 86, fig. 1.

N. minima Rigby, 1958, p. 585, pl. 86, figs 2–3.

T. carinthiacus (Flügel 1966) Kochansky-Devidé 1970, p. 244, pl. 20, figs 1–2 (= *Hikorocodium carinthiacum* Flügel 1966, p. 54, pl. 10, figs 1–5).

T. morronensis Crescenti, 1969, p. 35, figs 10, 20–22.

T. gracilis Schäfer and Senowbari-Daryan, 1983, p. 128, pl. 10, figs 1, 8.

T. multisiphonatus Schäfer and Senowbari-Daryan, 1983, p. 129, pl. 10, figs 5–7.

Plexoramea cerebriformis has on a number of occasions been confused with *T. carinthiacus* (see Flügel *et al.* 1988). Misik (1979, p. 709) regards *T. morronensis* as a junior synonym of *T. obscurus*.

Acknowledgements. This research was supported by TOTAL and encouraged by André Maurin. David Edwards very kindly provided *Tubiphytes* specimens from Capitan. We are grateful to Thierry Boisseau for drawing our attention to several references. Jack Babcock, Colin Scrutton and Colin Stearn constructively reviewed the manuscript and, together with anonymous reviewers, made many helpful suggestions.

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ROBERT RIDING

LI GUO

Department of Geology
 University of Wales College of Cardiff
 Cardiff CF1 3YE, UK

Typescript received 29 March 1990
 Revised typescript received 24 May 1991

PHYLOGENETIC RELATIONSHIPS OF THE BASAL DINOSAURS, THE HERRERASAURIDAE

by FERNANDO E. NOVAS

ABSTRACT. Herrerasaurids were predatory, obligatorily bipedal dinosaurs recorded in early Late Triassic rocks of South America. It has been suggested recently that the Herrerasauridae constitute a paraphyletic assemblage, but several apomorphic traits in the dorsal, sacral, and caudal vertebrae and the pectoral and pelvic girdles support the monophyly of this group. The relationships of Dinosauria with other members of Ornithodira are considered, supporting the monophyly of the newly recognized clade Dinosauriformes, constituted of *Lagosuchus* + (*Pseudolagosuchus* + (Dinosauria)). The Dinosauria, including Herrerasauridae, Saurischia, and Ornithischia, is diagnosed on the basis of six synapomorphic traits. The hypothesis that the Herrerasauridae constitute the sister-group of the remaining dinosaurs is supported here on the basis of four apomorphic traits uniquely shared by Saurischia and Ornithischia. The recently coined name Eudinosauria is used for the group of dinosaurs including the common ancestor of Saurischia, Ornithischia, and all of its descendants.

THE early diversification of the dinosaurs is documented mainly from Ischigualastian Age (approximately Carnian) beds of South America, which have yielded remains of several taxa commonly considered as the oldest known carnivorous dinosaurs. The Santa María Formation (Southeastern Brazil) has yielded material of *Staurikosaurus pricei* Colbert, 1970 (Galton 1977); and the Ischigualasto Formation (Northwestern Argentina), probably younger than the Santa María Formation (Bonaparte 1982), produced *Herrerasaurus ischigualastensis* Reig, 1963 (Novas 1989a; Sereno and Novas 1990). Almost complete herrerasaurid material recently collected in the latter formation (Sereno *et al.* 1988) strongly suggests that the type specimens of *Ischisaurus cattoi* Reig, 1963 and *Frenquellisaurus ischigualastensis* Novas, 1986 are cospecific with *Herrerasaurus ischigualastensis*, and these are considered as junior synonyms of this last taxon. The supposed occurrence of *Staurikosaurus* in the Ischigualasto Formation, as claimed by Brinkman and Sues (1987), is based on a very poorly preserved specimen that does not exhibit autapomorphies of *Staurikosaurus*. *Herrerasaurus* and *Staurikosaurus* were obligatorily bipedal dinosaurs, 1–5 metres long, with an unusual mixture of both plesiomorphic characters with respect to saurischians and ornithischians, and derived features similar to those of tetanurine theropods (Reig 1963; Benedetto 1973; Gauthier 1986).

Cladistic relationships between *Herrerasaurus* and *Staurikosaurus* are still debated. Both taxa are grouped together in Herrerasauridae by some authors (Benedetto 1973; Novas 1986, 1989a, 1989b), whereas others doubt this arrangement (Galton 1977; Gauthier 1986; Brinkman and Sues 1987; Paul 1988; Benton 1990; Sues 1990). The phylogenetic relationships of *Herrerasaurus* and *Staurikosaurus* with Saurischia and Ornithischia are also debatable. Herrerasaurids have been variously considered to be saurischians with theropod affinities (Benedetto 1973; Galton 1985), carnivorous sauropodomorphs (Colbert 1970), the sister group of Ornithischia + Saurischia (Gauthier 1984, 1986; Gauthier and Padian 1985), and as Dinosauria *incertae sedis* (Novas 1989a).

I will examine two main aspects of Herrerasauridae: do they constitute a monophyletic group, and what are their relationships within Dinosauria?

Abbreviations. FMNH, Field Museum of Natural History (Chicago); MACN, Museo Argentino de Ciencias Naturales (Buenos Aires); MCZ, Museum of Comparative Zoology, Harvard University (Boston); PVL, Paleontología de Vertebrados, Fundación 'Miguel Lillo' (S. M. de Tucumán); PVSJ, Paleontología de

Vertebrados, Universidad Nacional de San Juan (San Juan); UPLR-PV, Paleontología de Vertebrados, Universidad Provincial de La Rioja (La Rioja).

HERRERASAURIDAE AS A MONOPHYLETIC GROUP

The Herrerasauridae was erected by Benedetto (1973) to include *Herrerasaurus* and *Staurikosaurus*, based on numerous resemblances between them. Galton (1977, p. 240) considered both taxa as 'sufficiently different' to be placed in distinct families, and created the Staurikosauridae for the reception of *Staurikosaurus*, a position followed by Brinkman and Sues (1987), Paul (1988), and Sues (1990). Brinkman and Sues (1987) and Sues (1990) considered Herrerasauridae (*sensu* Benedetto 1973) as a paraphyletic assemblage, citing two characters *Herrerasaurus* shares with Saurischia and Ornithischia (exclusive of *Staurikosaurus*): tibia with a transversely expanded distal end, and three sacral vertebrae. However, a transverse expansion of the distal tibia seems to have been attained independently in *Herrerasaurus*, ornithischians, theropods, and sauropodomorphs (Novas 1989a), and contrary to previous interpretations (Reig 1963; Benedetto 1973) *Herrerasaurus* (PVL 2566; PVSJ 104; PVSJ 461) exhibits only two sacral vertebrae, a character probably retained also by *Staurikosaurus* (Galton 1977).

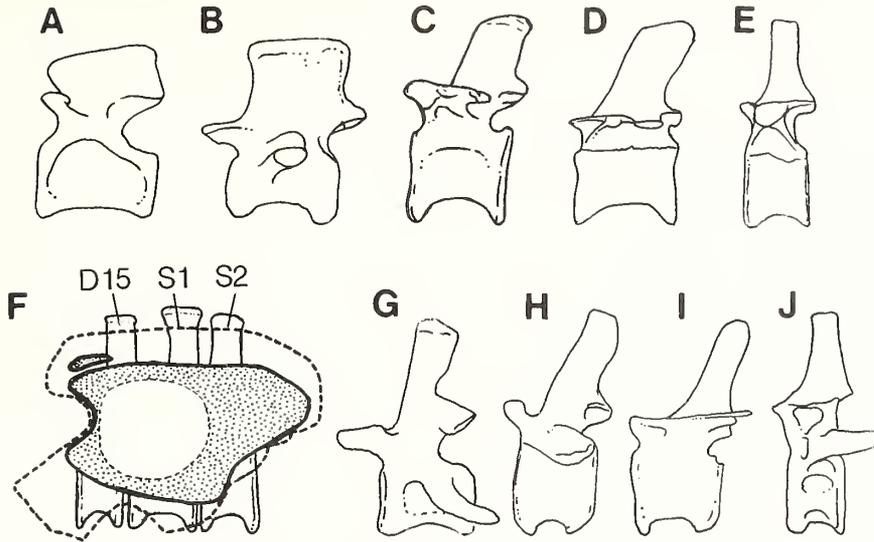
While the evidence supporting the paraphyly of the Herrerasauridae is ambivalent, the monophyletic nature of the Herrerasauridae is supported by the following derived traits uniquely shared by *Herrerasaurus* and *Staurikosaurus*:

A. *Posterior dorsal vertebrae with centra anteroposteriorly shortened (e.g. dorsal 13–15 with length/height ratio less than 0.8)*. Posterior dorsal vertebrae with long and low centra are present in *Lagosuchus* (Text-fig. 1A) with a length/height ratio (L/H) near to 1.95. Proportionately long centra (with respect to depth) seems to be plesiomorphic for Dinosauria, because that condition is present ancestrally in ornithischians (Santa Luca 1980), sauropodomorphs (Huene 1926; Bonaparte 1971; Cooper 1981), and theropods (Welles 1984; Bonaparte 1986), in which the L/H ratio for posterior dorsal vertebrae is > 0.9 (Text-fig. 1B–D). On the contrary, *Herrerasaurus* and *Staurikosaurus* share posterior presacral vertebrae with short high centra, with $L/H < 0.8$ for the thirteen dorsal vertebra (Text-fig. 1E).

B. *Posterior dorsal and first sacral vertebrae with robust neural spines axially shortened, squared shaped in cross-section*. The posterior dorsals and sacral vertebrae of *Lagosuchus* have plate-like, axially long, neural spines (Text-fig. 1A). This condition is ancestral for Dinosauria because it is present in basal ornithischians, sauropodomorphs, and theropods (Text-fig. 1B–D). *Herrerasaurus* and *Staurikosaurus* are derived in that they share posterior dorsal and first sacral vertebrae with stout, anteroposteriorly short neural spines that are quadrangular in cross-section (Text-fig. 1E).

C. *Sacral vertebrae with very deep sacral ribs especially that of the last vertebra, which cover nearly 90% of the medial surface of the iliac blade*. Lightly-built sacral ribs, with those of the last sacral vertebrae dorsoventrally flattened and fan-shaped, are present in *Chanaresuchus* (PVL 4375), *Gracilisuchus* (PVL 4597), *Lagerpeton* (PVL 4619), and *Lagosuchus* (PVL 3870), and represent the plesiomorphic condition for Archosauriformes (*sensu* Gauthier 1984). The fan-shaped ribs articulate with a horizontal ridge running medially on the posterior iliac blade. This condition was retained in Dinosauria ancestrally, being present in early sauropodomorphs (Huene 1926; Cooper 1981), theropods (Welles 1984), and ornithischians (Galton 1974). *Herrerasaurus* exhibits first and second sacral vertebrae with ribs dorsoventrally deep, especially that of the last sacral, which surpass ventrally the medial ridge of the posterior iliac blade and extend towards the rear near the posterior margin of the ilium (Text-fig. 1F). Dorsoventrally deep sacral ribs are also present in *Staurikosaurus pricei* (MCZ 1669).

D. *Proximal caudals with vertical neural spines*. Ornithischians, sauropodomorphs, and theropods appear to have retained the ancestral condition (e.g. *Lagosuchus*, PVL 3871) in that the neural spines of the proximal caudals are posteriorly inclined (Text-fig. 1G–I). Instead, *Herrerasaurus* and *Staurikosaurus* are unique in that they share proximal caudals with vertical neural spines (Text-fig. 1J).

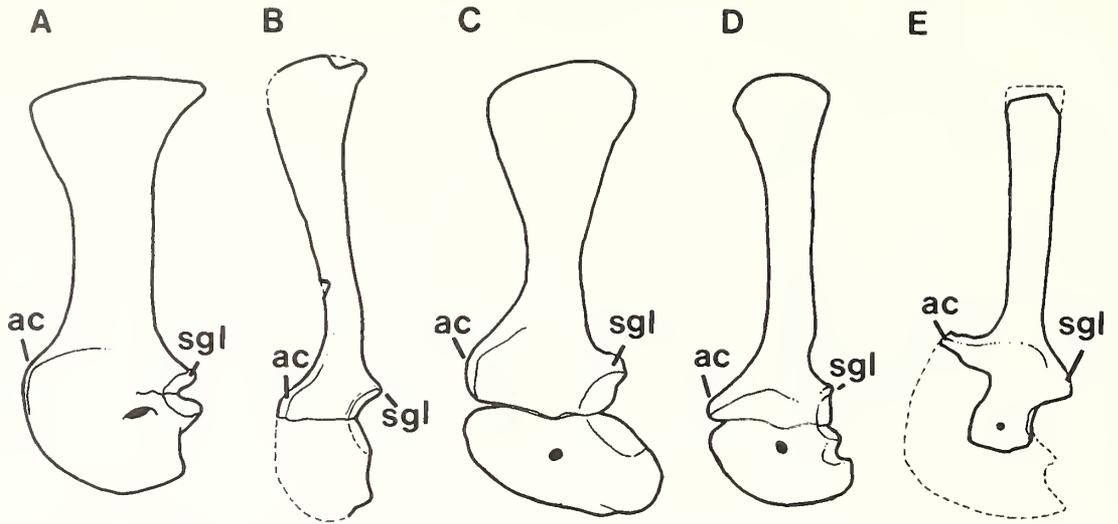


TEXT-FIG. 1. Vertebral column in lateral view of several taxa of Dinosauriformes. Not to scale. A–E, posterior dorsal vertebrae of A. *Lagosuchus*; B. *Heterodontosaurus*; C. *Plateosaurus*; D. *Dilophosaurus*; E. *Staurikosaurus*. F, dorsal fifteen and first and second sacrals of *Herrerasaurus* (PVL 2566) showing sacral rib attachment (stippled) on the ilium (dotted line). G–J, proximal caudal vertebrae of G. *Heterodontosaurus*; H. *Plateosaurus*; I. *Dilophosaurus*; J. *Herrerasaurus* (PVL 2566). A. after Bonaparte (1975); B. G. after Santa Luca (1980); C. H. after Huene (1926); D. I. after Welles (1984); E. after Galton (1977). Abbreviations: D15, fifteenth dorsal vertebra, S1, first sacral vertebra, S2, second sacral vertebra.

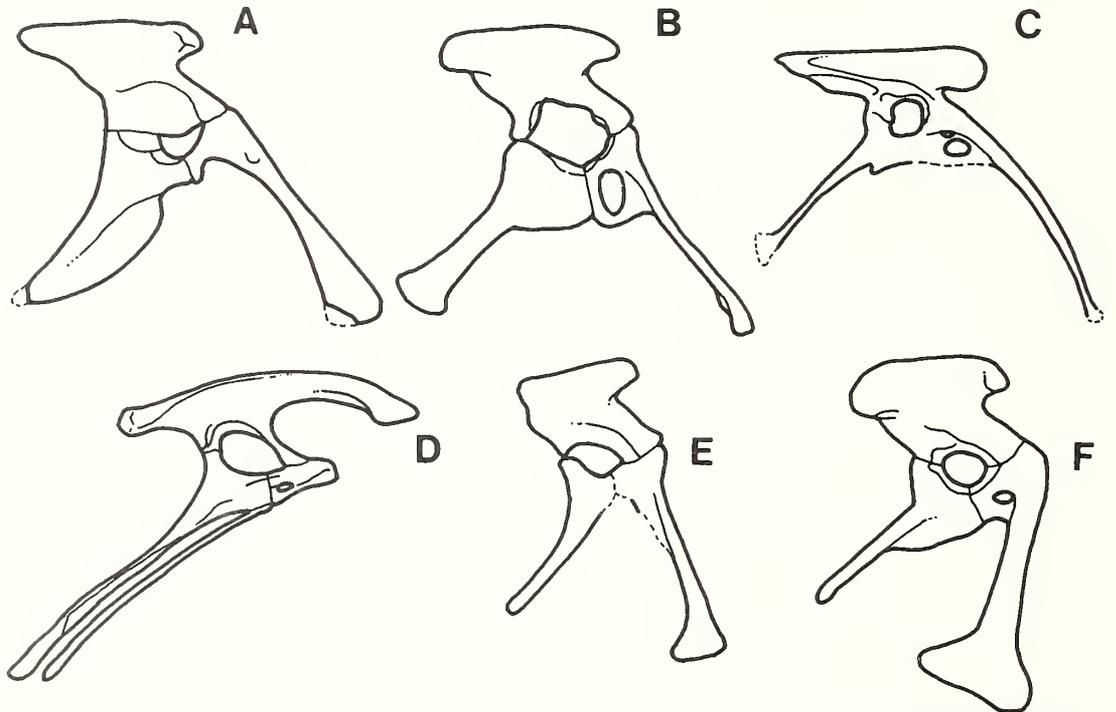
E. Distal caudals with elongated prezygapophyses, overlapping nearly 50% of the preceding vertebra. In Dinosauria ancestrally, distal caudals have short prezygapophyses (Gauthier 1986), surpassing slightly the anterior border of the centrum. This condition is present in *Lagosuchus* (PVL 3871), ornithischians (Thulborn 1972; Santa Luca 1980; Colbert 1981), and sauropodomorphs (Huene 1926). On the contrary, *Herrerasaurus* and *Staurikosaurus* share distal caudal vertebrae with elongated prezygapophyses, that overlap more than half of the preceding vertebrae (Galton 1977; Novas 1986). Theropods exhibit also this derived feature (see Raath 1969), but in the context of the evidence, it is interpreted that elongate prezygapophyses arose independently in Herrerasauridae and Theropoda (Gauthier 1986).

F. Acromial process extends distally with respect to the scapular glenoid lip, and forms nearly a right angle with the scapular blade. In *Lagosuchus* (Bonaparte 1975) and ancestrally in Sauropodomorpha (Huene 1926; Bonaparte 1971), Theropoda (Bonaparte 1986; Colbert 1989), and Ornithischia (Santa Luca 1980; Colbert 1981) the acromial process (ac, Text-fig. 2A–D) occupies approximately the same level as, or is proximal to, the scapular glenoid lip (sgl) and forms a wide curve with the scapular blade. *Herrerasaurus* exhibits an apomorphic condition with a deep acromial process extended distally with respect to the scapular glenoid lip, and defines an angle near to 90° with the scapular blade (Text-fig. 2E). This set of derived features is also seen in an undescribed, fragmentary right scapula of the type specimen of *Staurikosaurus pricei* (MCZ 1669).

G. Distal expansion of the scapular blade strongly reduced. In Dinosauria ancestrally the scapular blade is distally expanded anteroposteriorly (Gauthier 1986), representing more than 27% of the length of the scapula. *Herrerasaurus* (Text-fig. 2E) exhibits a distinct morphology of the scapula (Brinkman and Sues 1987; Novas 1989b), with slender scapular blade anteroposteriorly narrow distally, representing approximately 16% of the length. Colbert (1970, fig. 2) illustrates a distal end of a scapula of *Staurikosaurus*, but the morphology and proportions of this fragmentary bone do



TEXT-FIG. 2. Scapular girdle in lateral view of different taxa of Dinosauriformes. Not to scale. A, *Lagosuchus* (after Bonaparte 1975). B, *Heterodontosaurus* (after Santa Luca 1980). C, *Riojasaurus* (after Bonaparte 1971). D, *Piatnitzkysaurus* (after Bonaparte 1986). E, *Herrerasaurus* (reconstruction based on PVSJ 53 and MCZ 7064). Abbreviations: ac, acromial process, sgl, scapular glenoid lip.



TEXT-FIG. 3. Pelvic girdle of different taxa of Dinosauriformes. Not to scale. A, *Lagosuchus* (after Bonaparte 1975). B, *Plateosaurus* (after Huene 1926). C, *Syntarsus* (after Raath 1969). D, *Heterodontosaurus* (after Santa Luca 1980). E, *Staurikosaurus* (after Galton 1977). F, *Herrerasaurus* (reconstruction based on PVL 2566 and PVSJ 373).

not coincide with the proximal portion of the scapula cited above. The available evidence suggests that the distal end of the scapular blade in *Staurikosaurus* was anteroposteriorly narrow like that of *Herrerasaurus*.

H. *Pubis with distal half anteroposteriorly expanded.* Ancestrally in Ornithodira (e.g. *Lagerpeton*, *Lagosuchus*, and *Pseudolagosuchus*; Bonaparte 1975; Arcucci 1986, 1987) the distal half of the pubis has anterior and posterior margins subparallel in lateral view (in *Lagosuchus* the apparent distal expansion of the pubis in lateral view is due to a light lateral folding of the pubic plate; Text-fig. 3A). Dinosaurs retained such a condition since it can be seen in Sauropodomorpha, Theropoda, and Ornithischia (Text-fig. 3B–D). On the other hand, *Herrerasaurus* and *Staurikosaurus* exhibit unusual pubes with the distal half anteroposteriorly expanded, with anterior and posterior margins distally divergent (Text-fig. 3E–F), defining ‘U-shaped’ pubes in cross-section at the mid-length.

I. *Distinct pubic ‘foot’ anteroposteriorly expanded, more than 25% of pubic length.* In Ornithodira ancestrally the distal end of the pubis is anteroposteriorly flat (e.g. *Lagosuchus* and *Pseudolagosuchus*), a condition retained in Ornithischia (Santa Luca 1980), and early saurischians, which exhibit the distal end of the pubis almost unexpanded (Huene 1926; Welles 1984; Text-fig. 3A–D). One outstanding synapomorphy of the Herrerasauridae is the presence of an enlarged distal pubic ‘foot’ (Text-fig. 3E–F), representing more than 25% of the pubic length (Benedetto 1973).

Based on this analysis, the family Herrerasauridae is considered to be a monophyletic group, which includes *Herrerasaurus* and *Staurikosaurus* and their most recent common ancestor. Since the Staurikosauridae is monotypic, a cladistic diagnosis of this taxon is redundant with that of *Staurikosaurus*, and consequently is phylogenetically uninformative.

SYSTEMATIC PALAEOLOGY

Family HERRERASAURIDAE Benedetto, 1973

Diagnosis. Dinosaurs with posterior dorsal vertebrae with centra anteroposteriorly shortened (e.g. dorsal 13–15 with length/height ratio less than 0.8); posterior dorsal and sacral vertebrae with robust neural spines axially shortened, square-shaped in cross-section; sacral vertebrae with very deep sacral ribs, especially that of the second sacral, which covers almost the entire medial surface of the iliac blade; proximal caudals with vertical neural spines; distal caudals with elongated prezygapophyses, overlapping nearly 50% of the preceding vertebra; acromial process extends distally with respect to the scapular glenoid lip, and forms nearly a right angle with the scapular blade; distal expansion of the scapular blade strongly reduced; pubis with distal half anteroposteriorly expanded; distinct pubic ‘foot’ axially broadened, more than 25% of pubic length.

Comments. None of the synapomorphic traits diagnostic of the Herrerasauridae is seen in *Walkeria* (Maleri Formation, India; Chatterjee 1987), thus dismissing opinions that it is a member of the Herrerasauridae, as claimed by Paul (1988). On the contrary, the available information supports its referral as *Dinosauria incertae sedis* (Novas 1989a). *Aliwalia* (Elliot Formation, South Africa), scantily represented by portions of a femur, was interpreted by Galton (1985) as closely related to *Herrerasaurus* and *Staurikosaurus*, and as a member of the Herrerasauridae by Paul (1988). Nevertheless, the fragmentary femur not only does not share apomorphies with *Herrerasaurus* and *Staurikosaurus* (Sues 1990), but exhibits a prominent anterior trochanter, a derived feature shared by Saurischia and Ornithischia, exclusive of the Herrerasauridae (see below). In my opinion, the type specimen of *Aliwalia rex* is referable as *Dinosauria indet.*, but in the absence of autapomorphic (diagnostic) features, *Aliwalia rex* is best regarded as a *nomen nudum*.

PHYLOGENETIC RELATIONSHIPS OF BASAL DINOSAURS

The phylogenetic relationships and the diagnosis of the Dinosauria have been substantially altered as a result of cladistic studies (e.g. Gauthier 1984, 1986; Brinkman and Sues 1987; Novas 1989a;

Benton 1990; Sereno and Novas 1990). Nevertheless, information resulting from recent studies and the discovery of better preserved specimens and new taxa, challenge those hypotheses and promote re-examination of the characters supporting them. Gauthier (1984, 1986) offered extensive evidence to support the view that Dinosauria, Pterosauria, and *Lagosuchus* constitute a monophyletic assemblage, which he termed Ornithodira. Although this hypothesis gained acceptance among some authors (e.g. Padian 1984; Gauthier and Padian 1985; Sereno and Novas 1990), disagreement remains about the position of *Lagosuchus*. Gauthier (1984, 1986, p. 46) grouped pterosaurs and dinosaurs in the ornithodiran subclade 'Ornithotarsi', with *Lagosuchus* as the immediate outgroup, but the evidence supporting such an interpretation is founded on several apomorphic similarities which are untestable in the available material of *Lagosuchus*. Other characters which Gauthier (1984) cited in favour of a monophyletic 'Ornithotarsi' (e.g. distal tibia transversely broadened; absence of calcaneal tuberosity; simplified intratarsal joint) are absent in the Herrerasauridae, and the tarsal characters in early sauropodomorphs (Novas 1989a); consequently these features are considered apomorphic resemblances independently acquired by pterosaurs, ornithischians, and theropods. A preliminary study of ornithodiran relationships (Sereno and Novas 1990) strongly supports the Pterosauria and *Lagerpeton* (Arcucci 1986) as successively closer sister-groups of the remaining ornithodirans.

In order to study the phylogenetic relationships among dinosaurs and their more immediate outgroups, seventeen derived features in five terminal taxa were analysed using parsimony (see data matrix, Table 1). The character analysis is presented below and the result depicted as a cladogram in Text-figure 6.

TABLE 1. Character data matrix for five terminal taxa of Dinosauriformes. Character states scored for Ornithischia and Saurischia are hypothesized as ancestral for each group. Character numbers correspond to those listed in the text.

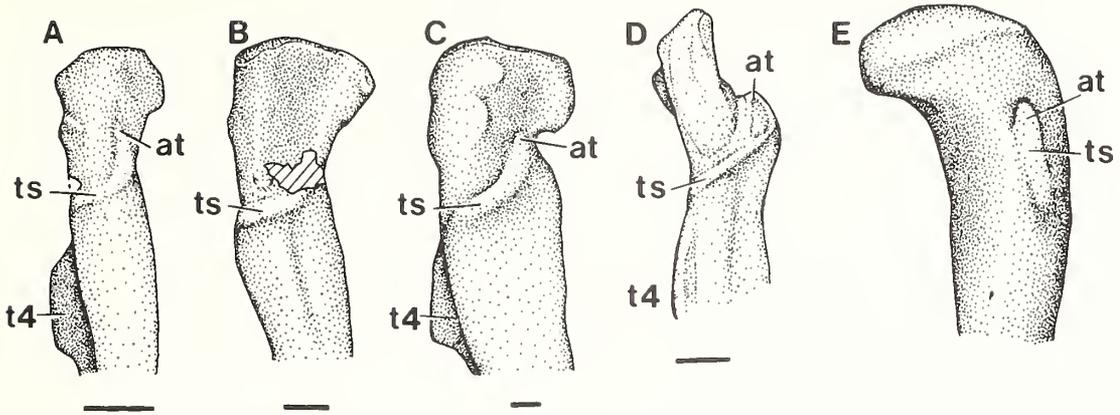
Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Lagosuchus</i>	1	1	1	1	1	0	0	?	0	0	0	0	0	0	0	0	0
<i>Pseudolagosuchus</i>	1	1	1	1	1	1	1	?	0	?	0	0	0	0	0	0	0
Herrerasauridae	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Ornithischia	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Saurischia	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Lagosuchus, *Pseudolagosuchus*, and Dinosauria share the following set of derived traits, absent in Ornithodira ancestrally:

1. subrectangular, distally projected deltopectoral crest on the humerus;
2. presence of a trochanteric shelf on the lateroproximal surface of the femur (Text-fig. 4A-C; see character 17 for comments);
3. anterior trochanter on femur;
4. tibia with prominent cnemial crest;
5. distal tibia with lateral longitudinal groove.

These apomorphies suggest a monophyletic group, **Dinosauriformes** (Novas 1991), that comprises the most recent common ancestor of *Lagosuchus*, Dinosauria, and all taxa stemming from it. Within Dinosauriformes, *Pseudolagosuchus* and the Dinosauria are grouped together in an unnamed taxon, which exhibits the following apomorphies:

6. elongated pubis, nearly as long as the femur;
7. presence of a pyramidal-shaped ascending process of the astragalus, with a posterior subvertical facet and presence of an elliptical depression behind this process.



TEXT-FIG. 4. Proximal portion of the right femur of different taxa of Dinosauriformes. A, *Lagosuchus* (PVL 3871; scale 5 mm). B, *Pseudolagosuchus* (left femur reversed; UPLR-PV 53; scale 5 mm). C, *Herrerasaurus* (PVL 2566; scale 20 mm). D, *Syntarsus* (after Rowe 1989; scale 20 mm). E, *Massospondylus* (after Cooper 1981; not to scale). Abbreviations: at, anterior trochanter, ts, trochanteric shelf, t4 fourth trochanter.

Based on recent studies on dinosaur phylogeny (Gauthier 1986; Brinkman and Sues 1987; Novas 1989*a*, 1989*b*; Sereno and Novas 1990), and as a result of the present analysis, the following features are considered synapomorphic for Dinosauria:

8. increased asymmetry of the hand (phalangeal formula, 2-3-4-5-2);
9. perforated acetabulum;
10. ischium with slender shaft and with ventral 'keel' (obturator process) restricted to the proximal third of the bone;
11. femoral head more distinctly set off from shaft of femur;
12. tibia overlaps anteroproximally and posteriorly the ascending process of the astragalus (i.e. ascending process inserts beneath the tibia), with consequent ventral projection of the posterior process of the tibia;
13. calcaneum with a concave proximal articular surface, fixed to the distal end of the fibula.

The relationships of the Herrerasauridae with the Saurischia and Ornithischia are debatable. Commonly they were included in the Saurischia (e.g. Reig 1963; Colbert 1970; Benedetto 1973; Galton 1977, 1985), based primarily on pelvic morphology. Herrerasaurids share with sauropodomorphs and theropods an elongate, anteroventrally oriented pubis, perforate acetabulum, and an elongate ischium, features frequently used to define a 'saurischian pelvis' (e.g. Romer 1956). Nevertheless, none of these characters constitutes a synapomorphy of Saurischia: the anteroventral orientation of the pubis 'is a basic archosaur patent' (Romer 1956, p. 323), an elongate pubis (nearly as long as the femur) is present also in *Pseudolagosuchus* (Arcucci 1987), here considered as the immediate outgroup of the Herrerasauridae + (Saurischia + Ornithischia) clade; a perforate acetabulum and an elongate ischium are shared not only by herrerasaurids and saurischians, but also by ornithischians. In short, the 'saurischian pelvis' is an assemblage of plesiomorphic characters for Dinosauria (or even more inclusive groups), and does not support close relationships among Herrerasauridae, Sauropodomorpha, and Theropoda.

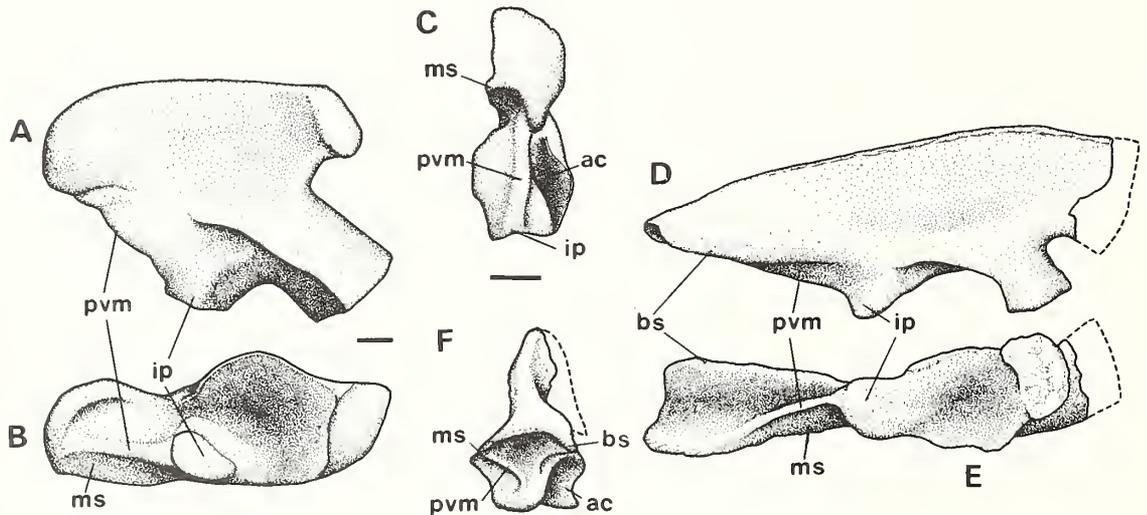
More recently, Gauthier (1984, 1986) and Gauthier and Padian (1985) considered herrerasaurids as the sister taxon of Ornithischia plus Saurischia, but no characters were cited by them in support of such an interpretation. Nevertheless, this hypothesis gained support among other authors (Brinkman and Sues 1987; Sereno and Novas 1990; Sues 1990; this paper), and Brinkman and Sues 1987, Text-fig. 7) listed in favour of such a phylogenetic arrangement 'medial wall to acetabulum less well developed', and 'pedal digit V small'. However, these characters are doubtful.

The geometry and relative development of the medial acetabular wall (expressed as a percentage of dorsoventral depth with respect to the anteroposterior length of the medial acetabular opening) is similar in *Staurikosaurus* (27%), *Herrerasaurus* (32%), and basal ornithischians (33%; Santa Luca 1984, fig. 13); only sauropodomorphs and theropods exhibit a higher ratio (nearly, or more than 50%; Bonaparte 1971; Cooper 1981; Welles 1984), and probably constitutes a synapomorphy of Saurischia. The assertion of Gauthier (1986, p. 46) that the acetabulum becomes fully perforate independently more than once in dinosaur evolution is probably true.

As for the reduction of pedal digit V (because of preservation only metatarsals, exclusive of phalanges, are considered here), a metatarsal V shorter than I is present in ornithischians (Galton 1974) and theropods (Welles 1984; Colbert 1989), but the distribution is problematic in early sauropodomorphs since some of them exhibit a metatarsal V subequal to, or even longer than, metatarsal I (Cooper 1981, table 4). Also, some specimens of *Herrerasaurus* exhibit a metatarsal V slightly shorter than metatarsal I.

Four synapomorphic features shared by Saurischia and Ornithischia are recognized here in support of the outgroup position of Herrerasauridae with respect to the remaining dinosaurs, as depicted in Text-figure 6:

14. *At least three sacral vertebrae.* The sacrum of *Herrerasaurus* (PVL 2566; PVSJ 104; PVSJ 461) is composed of two sacral vertebrae, widely attached to the ilia through the sacral ribs, a condition probably present in *Staurikosaurus* (Galton 1977). In *Herrerasaurus* the last dorsal vertebra (dorsal fifteen) is placed behind the tip of the anterior iliac spine (Text-fig. 1F), but its transverse processes, laterally projected above the first sacral rib, do not articulate with the inner surface of the ilia. On the contrary, saurischians and ornithischians can be distinguished from more remote outgroups in that they exhibit a sacrum with three or more sacrals, a condition convergently acquired in Pterosauria among ornithodirans (Padian 1984). It is hypothesized here that in the common ancestor of Saurischia and Ornithischia, the vertebra that increased the sacral count to three was incorporated from the presacral series, because in several non-dinosaurian archosauromorphs (e.g. *Lagosuchus*, *Lagerpeton*, *Gracilisuchus*, *Chanaresuchus*) and early dinosaurs

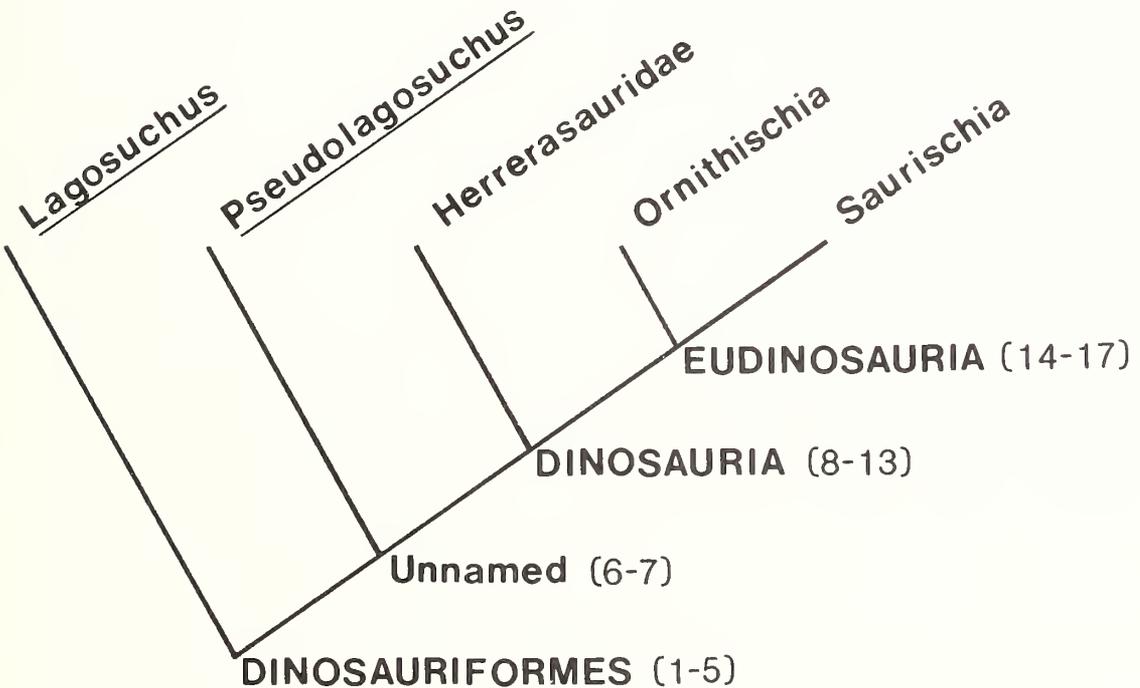


TEXT-FIG. 5. Right ilia in A, D, lateral; B, E, ventral; and C, F, posterior views. A–C, *Herrerasaurus* (A–B, PVL 2566; C, MACN 18.688); D–F, *Torvosaurus* (after Galton and Jensen 1979). Abbreviations: ac, acetabulum, bs, brevis shelf, ip, ischiadic peduncle, ms, medial shelf for sacral rib articulation, pvm, posteroventral margin of ilium. Scale 20 mm.

(*Herrerasaurus*) the placement of the two sacral vertebrae with respect to the ilia is coincident with that of sacrals 2 and 3 of basal sauropodomorphs. In addition, in the archosauromorphs and early dinosaurs mentioned above, the sacral rib of the last sacral vertebra has a similar fan-shaped morphology and it articulates along the medial surface of the posterior iliac blade (Novas 1987, 1989*b*). This evidence refutes the interpretation that in early sauropodomorphs the third sacral vertebra is of caudal origin (Charig *et al.* 1965; Charig 1982).

15. *Presence of a prominent brevis shelf on the lateroventral side of the postacetabular blade of the ilium.* Gauthier (1986, p. 43) recognized this character as a synapomorphy of Ornithodira, but the distribution of the brevis shelf is restricted to Saurischia and Ornithischia among ornithodirans. In Ornithodira ancestrally (e.g. *Lagerpeton*, *Lagosuchus*) the postacetabular portion of the iliac blade is transversely compressed, with the posteroventral margin running from the ischiadic peduncle towards the posterior end of the blade, a condition retained by herrerasaurids (Text-fig. 5A–C). In contrast, saurischians (e.g. Galton and Jensen 1979) and ornithischians (Thulborn 1972; Galton 1974), aside from the posteroventral margin running from the ischiadic peduncle to the posterior end of the blade (pvm), exhibit a distinct and prominent shelf on the lateroposterior margin of the iliac blade, the brevis shelf (bf, Text-fig. 5D–F).

16. *Presence of a prominent anterior (lesser) trochanter on the femur.* In Dinosauriformes ancestrally (e.g. *Lagosuchus*, *Pseudolagosuchus*, *Herrerasaurus* and *Staurikosaurus*) the anterior trochanter is represented by a tiny vertical prominence (at, Text-fig. 4A–C). On the contrary, ornithischians (Thulborn 1972; Santa Luca 1980), sauropodomorphs (Huene 1926; Bonaparte 1971), and theropods (Raath 1969; Rowe 1989) share a prominent proximally projected anterior trochanter. The presence of the anterior trochanter in Ornithosuchidae (Bonaparte 1971) is considered homoplastic with that of Saurischia and Ornithischia.



TEXT-FIG. 6. Cladogram depicting phylogenetic relationships among dinosauriform ornithodirans. Numbers correspond to those listed in the text and scored in the data matrix (Table 1).

17. *Trochanteric shelf reduced to a slight prominence.* In Dinosauriformes ancestrally (e.g. *Lagosuchus*, *Pseudolagosuchus* and Herrerasauridae) the 'trochanteric shelf' (Gauthier 1986) constitutes a prominent posterodistally oriented ridge on the lateroproximal surface of the femur (ts, Text-fig. 4A–C). Ornithischians and saurischians exhibit a derived condition with respect to other dinosauriforms, consisting in a reduction (or even absence) of the trochanteric shelf. In ornithischians, the trochanteric shelf is lacking (Thulborn 1972; Galton 1974), in early sauropodomorphs the trochanteric shelf is represented by a slight, subvertical ridge placed distally to the anterior trochanter (Cooper 1981, fig. 67A), and ancestrally in tetanurine theropods (e.g. *Allosaurus*, FMNH 1505 and P25114) the trochanteric shelf is probably represented by a slight prominence anterodistally oriented. Ceratosaurian theropods (Abelisauridae and robust individuals of *Syntarsus*, *Coelophysus*, *Dilophosaurus*, *Ceratosaurus*; Gauthier 1986; Rowe 1989; Novas 1991; Text-fig. 5D) constitute an exception among saurischians because they show a very prominent trochanteric shelf, even more developed than in Dinosauriformes ancestrally. The distribution of the trochanteric shelf among dinosaurs suggests that in the common ancestor of saurischians and ornithischians this structure was reduced with respect to the plesiomorphic dinosauriform condition, and that among theropods the presence of a strongly developed trochanteric shelf, even more than in Dinosauriformes ancestrally, constitutes a synapomorphy of Ceratosauria (Gauthier 1986; Rowe 1989; Novas 1991).

In short, the character distribution suggests that the Herrerasauridae are the sister-group of Saurischia + Ornithischia, as originally proposed by Gauthier (1984, 1986). In agreement with the analysis presented above, the name **Eudinosauria** (Novas 1991) is proposed for the clade including the common ancestor of Saurischia and Ornithischia and all of its descendants.

DISCUSSION

Cladistic analysis supports the hypothesis that the Herrerasauridae constitute the sister-group of Ornithischia + Saurischia, a clade traditionally named Dinosauria Owen, 1841 (Owen 1842). Implicitly based on that conception Gauthier *et al.* (1989) excluded the Herrerasauridae from the Dinosauria, preserving in such a way the original usage of the term. Nevertheless, since the herrerasaurids were described, virtually all authors have considered them to be dinosaurs (e.g. Reig 1963; Colbert 1970; Benedetto 1973; Bakker and Galton 1974; Bonaparte 1975; Galton 1977; Brinkman and Sues 1987; Paul 1988; Novas 1989a; Benton 1990; Sues 1990). In an influential work, Gauthier himself (1986, p. 44) offered a new combination of Dinosauria, defining them to include Herrerasauridae, Saurischia, and Ornithischia. This last position is maintained here, maximizing the stability and the phylogenetic informativeness of the name of the taxon, the composition of which most authors accept.

Preserving the Dinosauria to include the common ancestor of Herrerasauridae and Saurischia + Ornithischia, and all of its descendants, the name Eudinosauria (Novas 1991) was coined to encompass the common ancestor of Saurischia, Ornithischia, and all of its descendants, the diagnosis of which is based on the presence of at least three sacral vertebrae, a brevis shelf on the lateroventral side of the postacetabular blade of the ilium, a prominent anterior trochanter on the femur, and a reduced trochanteric shelf.

Acknowledgements. I thank L. M. Chiappe, G. W. Rougier and J. F. Bonaparte, Museo Argentino de Ciencias Naturales, P. C. Sereno, University of Chicago, J. A. Gauthier, California Academy of Sciences, K. Padian, University of California; T. Bown, United States Geological Survey, A. L. Cione, Museo de La Plata, and A. M. Báez, Universidad de Buenos Aires, for their valuable criticisms and comments on this manuscript. This research was supported by CONICET and Occidental Exploration of Argentina.

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FERNANDO E. NOVAS

Museo Argentino de Ciencias Naturales
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Typescript received 1 May 1990

Revised typescript received 20 February 1991

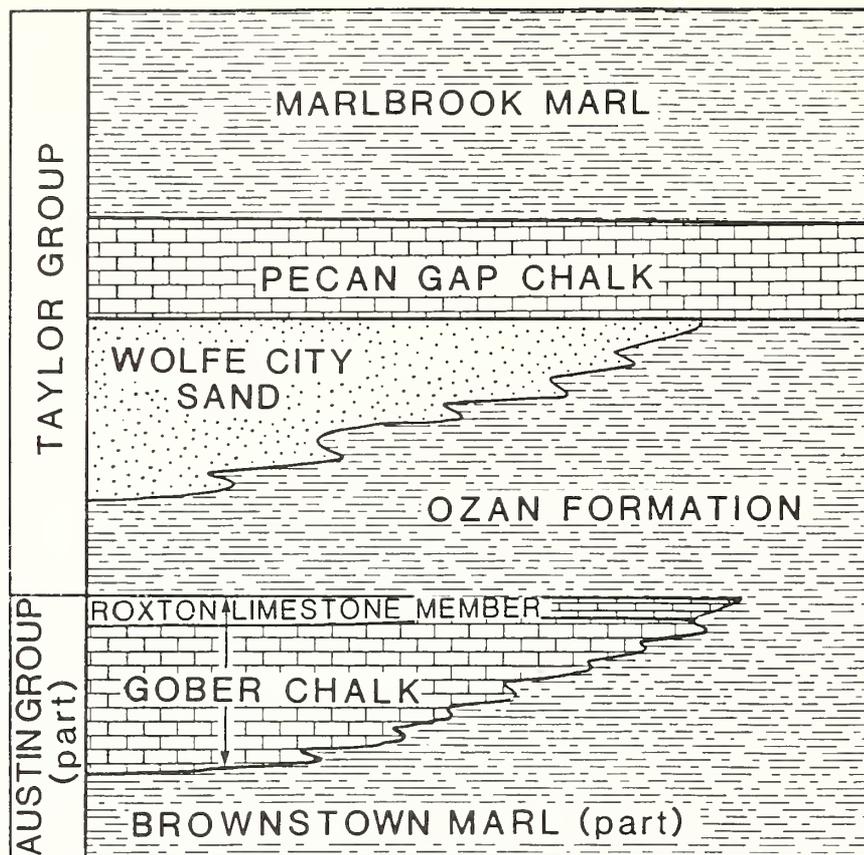
CAMPANIAN TRACHYSCAPHITES SPINIGER AMMONITE FAUNA IN NORTH-EAST TEXAS

by W. A. COBBAN and W. J. KENNEDY

ABSTRACT. A horizon 46 m above the base of the Ozan Formation in the North Sulphur River north-west of Ladonia in Fannin County, Texas, yielded a fauna of *Pachydiscus* (*Pachydiscus*) *paulsoni* (Young, 1963), *Eupachydiscus grossouvrei* (Kossmat, 1898), *Placenticerus* sp., *Menabites* (*Delawarella*) *delawarensis* (Morton, 1830), *M. (D.) danei* (Young, 1963), *M. (D.) vanuxemi* (Morton, 1830), *M. (D.)* sp., *Glyptoxoceras* sp., *Baculites* sp. group of *aquilaensis* Reeside, 1927, *Scaphites* (*Scaphites*) sp. group of *hippocrepis* (DeKay, 1828), *Trachyscaphites spiniger spiniger* (Schlüter, 1872), and *T. densicostatus* sp. nov., together with the bivalve *Inoceramus* (*Endocostea*) *balticus* Böhm, 1909. The presence of *T. spiniger spiniger*, previously known only from western Europe and the USSR, dates the assemblage as early but not earliest late Campanian in a north-west European sense, while stratigraphic relationships to other Gulf Coast Campanian faunas suggest it to be younger than the early Campanian zone of *Scaphites hippocrepis* III and older than the middle Campanian zone of *Baculites mclearnii* of the US Western Interior. The Western Interior lower–middle Campanian boundary and the European lower–upper Campanian boundary are approximately coincident; this level can be dated at 80 Ma approximately on the basis of radiometric dates from Western Interior bentonites.

SCAPHITES SPINIGER Schlüter, 1872 is a large, ornately ribbed, tuberculate scaphite, first described from the 'Mucronaten Kreide' of north Germany, and subsequently recognized as an important marker fossil for the upper Campanian in France, Germany, Sweden, The Netherlands, Poland, European Russia, and Soviet Armenia. Recent works by Schmid and Ernst (1975) and Błaszkiwicz (1980) have clarified its range and value in correlation.

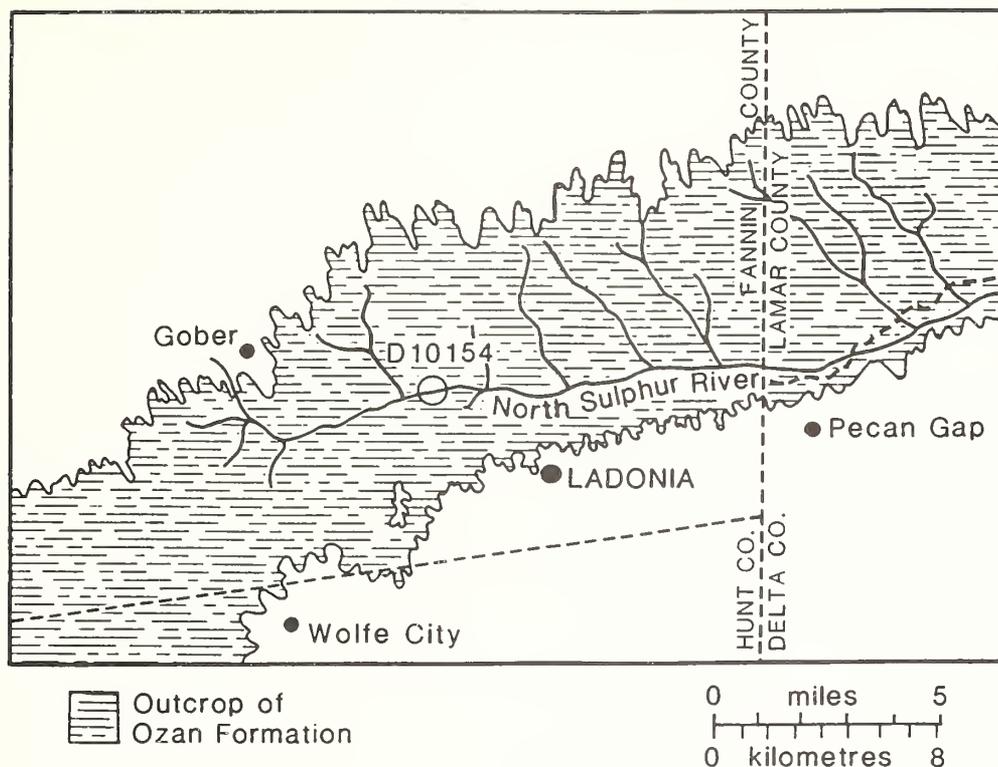
Adkins (1929) described, as *Scaphites porchi* and *S. aricki*, two new species of multituberculate scaphites from the 'upper Taylor formation' of Navarro County, Texas. He compared them to '*Acauthoscaphites*' *spiniger* but dismissed any close relationship, stressing the very compressed shell of '*A*' *spiniger* as one of several distinguishing features, being unaware that Schlüter's figured specimens were crushed. Cobban and Scott (1964) studied multituberculate scaphites from the Campanian of the United States Western Interior, and introduced the genus *Trachyscaphites* with *T. redbirdensis* Cobban and Scott 1964 (p. E7. pl. 1, figs 1–7; text-fig. 3 as type species). They recognized *spiniger* as a further member of the genus and divided it into two subspecies, the nominate one and *T. spiniger porchi* Adkins, 1929. The latter was described from both the Gulf Coast and Western Interior, and provided an important link between the cosmopolitan faunas of the former and endemic ones of the latter. It was not possible to correlate Old and New World *T. spiniger* because it was not known if the subspecies recognized were geographical or chronological in nature. It is therefore of some significance that we have recognized abundant specimens of *Trachyscaphites spiniger spiniger* in the Ozan Formation of north-east Texas (Text-figs 1–2) and can show it to precede *T. spiniger porchi*; they are thus chronological subspecies. Furthermore, *T. spiniger spiniger* occurs with abundant texanid ammonites that have previously been regarded as world-wide markers for the upper lower and middle Campanian (depending on whether a two- or three-fold division of the Campanian is used; there is no general agreement), leading to a review of Campanian ammonite zonation in both the US Gulf Coast and western Europe.



TEXT-FIG. 1. Lithostratigraphic divisions of the upper part of the Austin Group and the Taylor Group in north-east Texas.

STRATIGRAPHIC AND LOCALITY DETAILS

Text-figure 1 shows the lithostratigraphic divisions of the upper part of the Austin Group and the Taylor Group in north-east Texas, modified after Thompson *et al.* (1978) and others. The fossils described here come from the middle part of the Ozan Formation, some 46 m above the base. The term Ozan was introduced by Dane (according to Dane 1929, p. 58, footnote 72) on 10 September 1926, in what is an otherwise anonymous US Department of Interior Memorandum for the Press, No. 8823. The type locality is near Ozan in Hempstead County, Arkansas, and Arkansas outcrops and fossil occurrences are described in detail by Dane (1929). In north-east Texas, beds at this level that are equivalent to the Ozan Formation were termed 'unnamed marl' of the Taylor Group by authors up to and including Adkins (1933), but the term Ozan Formation is now applied to beds above the Gober Chalk and below the Pecan Gap and Annona Chalks (e.g. Geologic Atlas of Texas, Texarkana Sheet, 1966). The sequence is as much as 130 m thick, and consists of light grey-weathering, bluish-grey, calcareous clays with chalky beds and some fine sand units. The material studied here was collected by the late James P. Conlin (Fort Worth, Texas), W. A. Cobban, R. E. Burkholder and others at or close to USGS Mesozoic locality D10154 outcrops in the North Sulphur River 4.1–5.0 km north-west of the centre of Ladonia in Fannin County (Text-fig. 2). This corresponds to locality 15 of Paulson (1960, p. 112) who gives precise details as to how to reach the outcrop ('go 0.5 mi. west of square at Ladonia, Fannin County; turn north 2.0 mi. to North Sulphur River Bridge; walk 1.2 mi. west to the junction of Davis Creek'). The



TEXT-FIG. 2. Locality map for part of north-east Texas showing the source of specimens described in the text.

fossils come from a distinctive glauconitic unit at most a few tens of centimetres thick that overlies a marked omission surface that can be traced widely in the subsurface (Paulson 1960, p. 22) and is here 46 m above the top of the Gober Chalk. The basal unit above the omission surface is a red-weathering, green, glauconitic marl rich in bioclasts. The bed is crowded with black phosphate nodules, many of which are worn moulds of *Baculites* with rarer *Placenticeras*, although bivalves, gastropods and vertebrate debris are the commonest faunal elements. They show many of the complex taphonomic features described in the very similar unit at the Austin-Taylor contact as described by Fürsich, Kennedy and Palmer (1981). In contrast, the fauna described here is an indigenous one, commonly crushed and with original aragonitic shell preserved.

AGE AND CORRELATION OF THE FAUNA

The indigenous ammonite fauna from the Ozan Formation north-west of Ladonia is as follows: *Pachydiscus* (*Pachydiscus*) *paulsoni* (Young, 1963) (frequent), *Eupachydiscus grossouvrei* (Kossmat, 1898) (rare), *Placenticeras* sp. (rare), *Menabites* (*Delawarella*) *delawarensis* (Morton, 1830) (rare), *M. (D.) danei* (Young, 1963) (fairly frequent), *M. (D.) vanuxemi* (Morton, 1830) (rare), *M. (D.)* sp. (rare), *Glyptoxoceras* sp. (frequent), *Baculites* sp. group of *aquilaensis* Reeside, 1927, (abundant), *Scaphites* (*Scaphites*) sp. group of *hippocrepis* (DeKay, 1828) (rare), *Trachyscaphites spiniger spiniger* (Schlüter, 1872) (frequent), *Trachyscaphites densicostatus* sp. nov. (rare). Also present is the distinctive inoceramid bivalve *Inoceramus* (*Endocostea*) *balticus* Böhm, 1909 (Pl. 7, figs 6, 10). No zonation has been developed for the higher Campanian in the Gulf Coast region to date, but Young (1963) proposed the following partial scheme:

ZONE

upper Campanian (part) *Hoplitoplacenticerus marroti*

lower Campanian { *Delawarella sabinalensis*
Delawarella delawarensis
Submortonicerus tequesquitense

At first sight, the North Sulphur River assemblage, with *P. (P.) paulsoni*, *M. (D.) delawarensis*, *M. (D.) danei* and *M. (D.) vauuxeni*, would seem to fall into the *delawarensis* zone, from details in Young's text-figure 3 and list on p. 28 of that work. Unfortunately Young's specimens of these species are not placed in sequence, rather coming from the Gober Chalk (Text-fig. 1) and correlatives in north-east Texas and south-west Oklahoma. Instead, we believe the present fauna to be much younger.

At Roxton in Lamar County, 26.5 km east-northeast of Ladonia, the Roxton Limestone Member at the top of the Gober Chalk yields *P. (P.) paulsoni*, *Anapachydiscus* sp. juv., *Placenticerus placenta* (DeKay, 1828), *Hoplitoplacenticerus* aff. *H. plasticum* (Pauleke, 1907), *Menabites (Delawarella) delawarensis*, *M. (D.)* aff. *vauuxeni*, *Submortonicerus vandaliaense* Young, 1963, *Submortonicerus* sp., *Nostoceras (Eubostriochoceras)* sp. nov., *Baculites haresi* Reeside, 1927, and *Scaphites (Scaphites) hippocrepis* (DeKay, 1828) form III (Cobban, 1969). The North Sulphur River fauna occurs 46 m above this. The Wolfe City Sand (Text-fig. 1) at Wolfe City, 11.5 km south-southwest of Ladonia (Text-fig. 2), yielded the following: *Patagiosites* sp., *Placenticerus* sp., *Hoplitoplacenticerus* sp. nov., *Baculites mclearni* Landes, 1940, *Trachyscaphites spiniger porchi* Adkins, 1929, and *Inoceramus acerbaiddjanensis* Aliev, 1939. The base of the Pecan Gap Chalk (Text-fig. 1) has yielded ammonites at scattered localities around Pecan Gap and Wolfe City (Text-fig. 2), including *Pachydiscus (Pachydiscus)* sp., *Lewyites* sp., *Baculites taylorensis* Adkins, 1929, and *T. spiniger porchi*. Taken together these faunas place the North Sulphur River assemblage in both a US Western Interior and a north-west European context.

Comparison with US Western Interior faunas

Ammonite zonation for the Western Interior Campanian is summarized by Cobban (in press), who recognizes seventeen ammonite zones, with an additional three that may be Campanian or Maastrichtian:

ZONE

upper Campanian (part) { *Exiteloceras jemeyi*
Didymoceras stevensoni
Didymoceras nebrascense

middle Campanian { *Baculites scotti*
Baculites reduncus
Baculites gregoryensis
Baculites perplexus
Baculites sp. (smooth)
Baculites asperiformis
Baculites mclearni
Baculites obtusus

lower Campanian { *Baculites* sp. (weak flank ribs)
Baculites sp. (smooth)
Scaphites hippocrepis III
Scaphites hippocrepis II
Scaphites hippocrepis I
Scaphites leei III

The fauna of the Roxton Limestone Member, with *S. hippocrepis* III and *Baculites haresi*, correlates with the Western Interior zone of *S. hippocrepis* III. The Wolfe City Sand fauna has *Baculites mclearni*, which is restricted to its zone in the Interior. *Trachyscaphites spiniger porchi* is known from the *B. mclearni* zone. *Menabites (Delawarella) danei*, which occurs in both the Roxton Limestone Member and North Sulphur River faunas, occurs in the *Baculites obtusus* zone in the Western Interior near Pueblo, Colorado. *Baculites* sp. group

of *aquilaensis*, differs from *B. aquilaensis* of the Western Interior lower Campanian, such as to suggest it may be younger. The North Sulphur River assemblage thus lies somewhere around the boundary between the lower and middle Campanian provincial substages of the Western Interior.

Comparison with western European faunas

Kennedy (1986 and references therein) reviewed the 'classic' zonation of the Campanian Stage in the type area of Aquitaine, France. The sequence, based on the work of de Grossouvre (1894, 1901) and Haug (1908–1911) and others is:

ZONE	
upper Campanian	$\left\{ \begin{array}{l} \textit{Nostoceras (Bostrychoceras) polyplacum} \\ \textit{Hoplitoplacenticeras marroti} \end{array} \right.$
lower Campanian	$\left\{ \begin{array}{l} \textit{Menabites Delawarella delawarensis} \\ \textit{Placenticeras bidorsatum} \end{array} \right.$

These are scarcely zones in the accepted sense, as ammonites are rare in Aquitaine (Kennedy saw thirteen *P. bidorsatum*, two *M. (D.) delawarensis*, twenty or so *H. marroti* and fourteen *N. (B.) polyplacum*), and ranges are only incompletely known. The presence of forms intermediate between *S. (S.) hippocrepis* II and III in the *bidorsatum* zone, as well as *M. (D.) delawarensis* in the *delawarensis* zone suggests the Sulphur River fauna corresponds to the latter. But *Trachyscaphites spiniger*, common in the Sulphur River fauna, is also known in Aquitaine, from Assize P³ of Arnaud at St Médard de Barbezieux, a unit that yields upper Campanian *marroti* and *polyplacum* zone fossils at other localities.

A better control on the age of *T. spiniger* in Europe comes from the careful work of Schmid and Ernst (1975) working on the White Chalk faunas of north Germany (see also Ernst and Schmid 1979; Schulz *et al.* 1984). They divide the upper Campanian as follows:

- Micraster grümmensis*/*Cardiaster granulosis* Zone (top)
- Belemnitella langei* Zone
- Bostrychoceras polyplacum* Zone
- Galerites vulgaris* Zone
- Pachydiscus stobaei*/*Galeola papillosa basiplaua* Zone
- Echinocorys conica*/*Belemnitella mucronata senior* Zone (bottom)

Trachyscaphites spiniger has been recorded from the top of the *E. conica*/*B. m. senior* zone, but Ernst and Schmid found it to occur first as fragments in the lower part of the *P. stobaei*/*G. p. basiplaua* zone, to be rare in the middle of the zone, with a specimen from the upper *G. vulgaris* zone, while noting records from as high as the basal *B. polyplacum* zone.

There are also detailed records from the Vistula Valley in Poland (Błaszkiwicz 1980), where the following sequence is recognized:

ZONE	
upper Campanian	$\left\{ \begin{array}{l} \textit{Nostoceras pozaryskii} \\ \textit{Didymoceras donezianum} \\ \textit{Bostrychoceras polyplacum} \\ \textit{Neancyloceras phaleratum} \end{array} \right.$
lower Campanian	$\left\{ \begin{array}{l} \textit{Goniot euthis quadrata} \\ \textit{Goniot euthis granulata granulata} \end{array} \right.$

T. spiniger spiniger and subspecies *T. s. posterior* Błaszkiwicz, 1980, first appear in the *N. phaleratum* zone. The subspecies *T. s. posterior* was differentiated from the nominate species because of a smaller number of ribs

running between the tubercles of the same row on the exposed part of the normal spiral and the presence of lateroumbilical tuberculation on earlier sectors of the exposed normal spiral. It also differs on the whole in a smaller degree of freeing the shaft from the phragmocone and in a frequent lack of ribs between the tubercles on the same row on the shaft (Błaszczewicz 1980, p. 32). Loss of ribbing on the body chamber is a feature of subspecies *T. s. porchi*, and in terms of an evolutionary progression, a sequence *T. spiniger spiniger*, *T. spiniger posterior*, *T. spiniger porchi* is perfectly feasible.

What is clear is that *Trachyscaphites spiniger spiniger* marks a low upper Campanian horizon in a north-west European sense, in the broad *H. marroti* zone of the Aquitaine succession, the *P. stobaei*/*G. p. basi plana* zone in north Germany (though reported to have a longer range) and the *N. phaleratum* zone in the Vistula Valley, Poland. This is supported by other, less detailed records from Europe: *T. spiniger sensu lato* is thus known from the lower part of the upper upper Campanian *B. polyplacum* zone in the Kopetdag (Atabekian 1979), upper upper Campanian *Belemnitiella langei* zone of the Russian platform (Naidin 1979), and the lower upper Campanian Zeven Wegen Chalk of the Netherlands (Kennedy 1986; Jagt 1988).

Discussion

The previous review indicates that the first appearance of *Trachyscaphites spiniger spiniger* is a good marker for a horizon low in, but not at, the base of the upper Campanian as the substage is defined in north-west Europe. The North Sulphur River fauna is thus low upper Campanian in a north-west European sense, while the Texanitinae, previously thought to die out at the top of the lower Campanian, extend into the upper Campanian. Use of a *Menabites (Delawarella) delawarensis* zone in the lower Campanian is thus unwise, since the index species clearly extends into the upper Campanian. Correlation with the United States Western Interior is less satisfactory, but the first appearance of *T. spiniger spiniger* is certainly above the zone of *Scaphites hippocrepis* III and below that of *Baculites mclearnii*, so that the lower-middle Campanian boundary in the Western Interior must lie very close to the European lower-upper Campanian boundary. This correlation using fossils also provides an indirect numerical age for the lower-upper Campanian boundary in western Europe, because Obradovich and Cobban (1975) dated a series of bentonites, for which Odin and Obradovich (1982, p. 770) provide recalculated ages. A bentonite from either the top of the *Baculites obtusus* zone or base of the *B. mclearnii* zone gave apparent ages of 79.9 ± 3.2 Ma and 79.2 ± 1.6 Ma. A bentonite bed from the zone of *Baculites* sp. (weak flank ribs) gave 80.0 ± 1.6 Ma. Kennedy and Odin (1982), followed by Hallam *et al.* (1985) and Snelling (1985) gave numerical ages of 83 ± 1 Ma and 72 ± 1 Ma respectively for the beginning and end of the Campanian. The present correlation suggests the age of the European early or late Campanian boundary to be around 80 Ma, so that the early and late Campanian are of disparate durations. The tripartite subdivision of the American Campanian may be more practical (Cobban, in press).

SYSTEMATIC PALAEOLOGY

Location of specimens. All specimens described here are deposited in the National Museum of Natural History in Washington DC, and have USNM catalogue numbers; casts of some are kept at the US Geological Survey at the Denver Federal Center, Denver, Colorado. TMM = Texas Memorial Museum, Austin, Texas. GAB = Geological and Palaeontological Institute of Bonn University.

Conventions. Suture terminology is that of Wedekind (1916) as reviewed by Kullman and Wiedmann (1970): E = external lobe; L = lateral lobe; U = umbilical lobe, I = internal lobe.

Dimensions are given in millimetres, with D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilicus. Figures in parentheses are dimensions as a percentage of diameter.

Order AMMONOIDEA Zittel, 1884

Suborder DESMOCERATAEAE Zittel, 1895

[*nom. transl.* Wright and Wright 1951, p. 18; *ex.* Desmoceratidae Zittel, 1895]

Family PACHYDISCIDAE Spath, 1922

[*nom. transl.* Spath, 1923, p. 39; *ex.* Pachydiscinae Spath, 1922]

Genus and subgenus *PACHYDISCUS* Zittel, 1884

[= *Parapachydiscus* Hyatt, 1900, p. 570; *Joaquimites* Anderson, 1958, p. 218; *Pseudomenuites* Matsumoto, 1955, p. 169]

Type species. *Ammonites neubergicus* Hauer, 1858, p. 12, pl. 2, figs 1–3, pl. 3, figs 1–2, by subsequent designation by de Grossouvre (1894, p. 177).

Pachydiscus (Pachydiscus) paulsoni (Young, 1963)

Plate 1, figs 4–7; Plate 4, figs 7–9; Plate 5, figs 7–8; Text-figs 3A–C, 4B

1963 *Parapuzosia paulsoni* Young, p. 53, pl. 11, figs 3–5; pl. 12, figs 1–4; pl. 15, fig. 10; pl. 17, fig. 9; pl. 19, figs 3–4; text-figs 8a–b; 9g,j,r.

Types. Holotype is TMM 30625, from the Gober Chalk in McCurtain County, Oklahoma. Hypotypes are USNM 441382–441388, from the Ozan Formation of Fannin County, Texas.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
USNM 441382	103.6 (100)	35.2 (33.9)	47.2 (45.5)	0.75	20.4 (19.7)
USNM 441383	67.0 (100)	22.9 (34.2)	31.5 (47.0)	0.72	13.2 (19.7)

Description. We have thirty-six specimens ranging from 33 to 175 mm in diameter. Coiling is moderately involute, with 65% of the previous whorl covered. The whorl section is compressed, with a breadth to height ratio of 0.70–0.75, the whorl section compressed oval, with the greatest breadth just outside the umbilical shoulder. The umbilicus is small and comprises 20% of the diameter. The umbilical wall is low and flattened, and the umbilical shoulder is broadly rounded. Flanks are broadly rounded and convergent to a narrowly rounded venter. Internal moulds are smooth (Pl. 1, figs 4–5), because ornament is produced by thickening of the shell (Pl. 5, figs 7–8; Text-fig. 3A) rather than by folding. Where shell is present, distant, narrow, wiry ribs that number 12–14 per whorl arise at incipient bullae, while other ribs may extend to the umbilical shoulder as mere striae. Additional ribs intercalate both low and high on the flank to give a total of as many as 60 ribs per whorl; the intercalated ones may be as strong as or as weak as the primaries. Ribs are straight and prorsiradiate to the outer flank, then flex forward and are concave, projecting forward over the ventrolateral shoulder, which they cross in a broad convexity. This pattern of ornament is developed in the largest specimens seen that have well-preserved ornament. In the largest specimen itself, the ornament of the inner whorls is particularly well preserved and shows the presence of well-developed very elongate bullae (Text-fig. 3A). Suture deeply and intricately incised; typical for genus.

Discussion. Young (1963, p. 53) referred this species to *Parapuzosia* Nowak, 1913 (p. 350; type species *Sonneratia daubreei* de Grossouvre, 1894, p. 154, pl. 28; see revision in Immel *et al.* 1982, p. 11, pl. 2, figs 9–10; pl. 3, figs 1–2; pl. 4, fig. 2). Young's species is rather a *Pachydiscus* (*Pachydiscus*), differing from *Parapuzosia* in its lesser compression, feebly bullate primary ribs that are close rather than distant, few intercalated ribs of variable length rather than many that are confined to the outer flank, and lack of constrictions on the inner whorls. Its characters are thus pachydiscid rather than puzosiine. *Pachydiscus (P.) paulsoni* is closest to *Pachydiscus (Pachydiscus) duemmensis* (Schlüter, 1872) (p. 52, pl. 16, figs 1–2; see Kennedy 1986, text-fig. 12), from which it differs in the presence of weak bullae, more compressed whorl section and fewer, wider-spaced ribs.

Occurrence. Lower Campanian part of the Austin Chalk, *Submorticeras tequesquitense* zone of Travis County, Texas; *Delawarella delawarensis* zone in McCurtain County, Oklahoma and Little River County, Arkansas, in equivalents of the Gober Chalk; lower Campanian, Roxton Limestone Member at top of the Gober Chalk at USGS Mesozoic locality D6896, Lamar County, Texas, as well as the present occurrence in the middle Campanian Ozan Formation at USGS Mesozoic locality D10154 in Fannin County.

Genus EUPACHYDISCUS Spath, 1922

[= *Mesopachydiscus* Yabe and Shimizu, 1926, p. 172]*Type species.* *Ammonites isculensis* Redtenbacher, 1873, p. 122, pl. 29, fig. 1; by original designation.*Eupachydiscus grossouvrei* (Kossmat, 1898)

Plate 1, figs 8–10

- 1865 *Ammonites ootacodensis* Stoliczka, p. 109 (*pars*), pl. 57 only.
 1898 *Pachydiscus grossouvrei* Kossmat, p. 101 (166).
 1922 *Eupachydiscus grossouvrei* (Kossmat); Spath, p. 124.
 1931 *Pachydiscus grossouvrei* Kossmat; Basse, p. 26, pl. 2, figs 16–17; pl. 13, fig. 3; *non* pl. 3, figs 8–9; *non* pl. 11, fig. 2 (= *E. pseudogrossouvrei* Collignon, 1952).
 1932 *Parapachydiscus grossouvrei* (Kossmat); Collignon, p. 26, fig. 14.
non 1938 *Eupachydiscus grossouvrei* (Kossmat); Collignon, p. 28. (= *Eupachydiscus pseudogrossouvrei* Collignon, 1952).
 1952 *Eupachydiscus grossouvrei* (Kossmat); Collignon, p. 39, pl. 7, fig. 2; pl. 28, fig. 1.
 1955 *Eupachydiscus grossouvrei* (Kossmat); Collignon, p. 40, pl. 7, fig. 2; pl. 28, fig. 1.
 1970 *Eupachydiscus grossouvrei* (Kossmat); Collignon, p. 34, pl. 42, fig. 2307.

Types. Holotype, by monotypy, is the original of Stoliczka 1865, pl. 57, from the Arrialoor Group of Otacod, South India. Hypotype is USNM 441389, from the Ozan Formation of Fannin County, Texas.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
USNM 441389	78.5 (100)	40.3 (51.3)	42.8 (54.5)	0.94	16.4 (21.0)

Description. Coiling is moderately involute, with 70% of the previous whorl covered. The umbilicus is small, comprising 26% of the diameter, deep, with a rounded undercut umbilical wall on the mould. The whorl section is slightly compressed, with broadly rounded flanks and venter. Primary ribs arise singly (and, perhaps, in pairs) from feeble umbilical bullae, while additional ribs intercalate below mid-flank. Ribs are narrow and sharp, and separated by somewhat wider interspaces. They are straight and prorsiradiate to the outer flank, where they flex forward and become concave over the ventrolateral shoulder before crossing the venter in a broad convexity. Total rib number per whorl cannot be determined for certain because of poor preservation but it is estimated at 36. Sutures not seen.

Discussion. The present specimen differs in no significant respects from comparable-sized Madagascan specimens figured by Basse (1931) and Collignon (see synonymy) as well as unfigured material from Madagascar in the collections of the Muséum National d'Histoire Naturelle in Paris and in the Collignon Collection at Dijon.

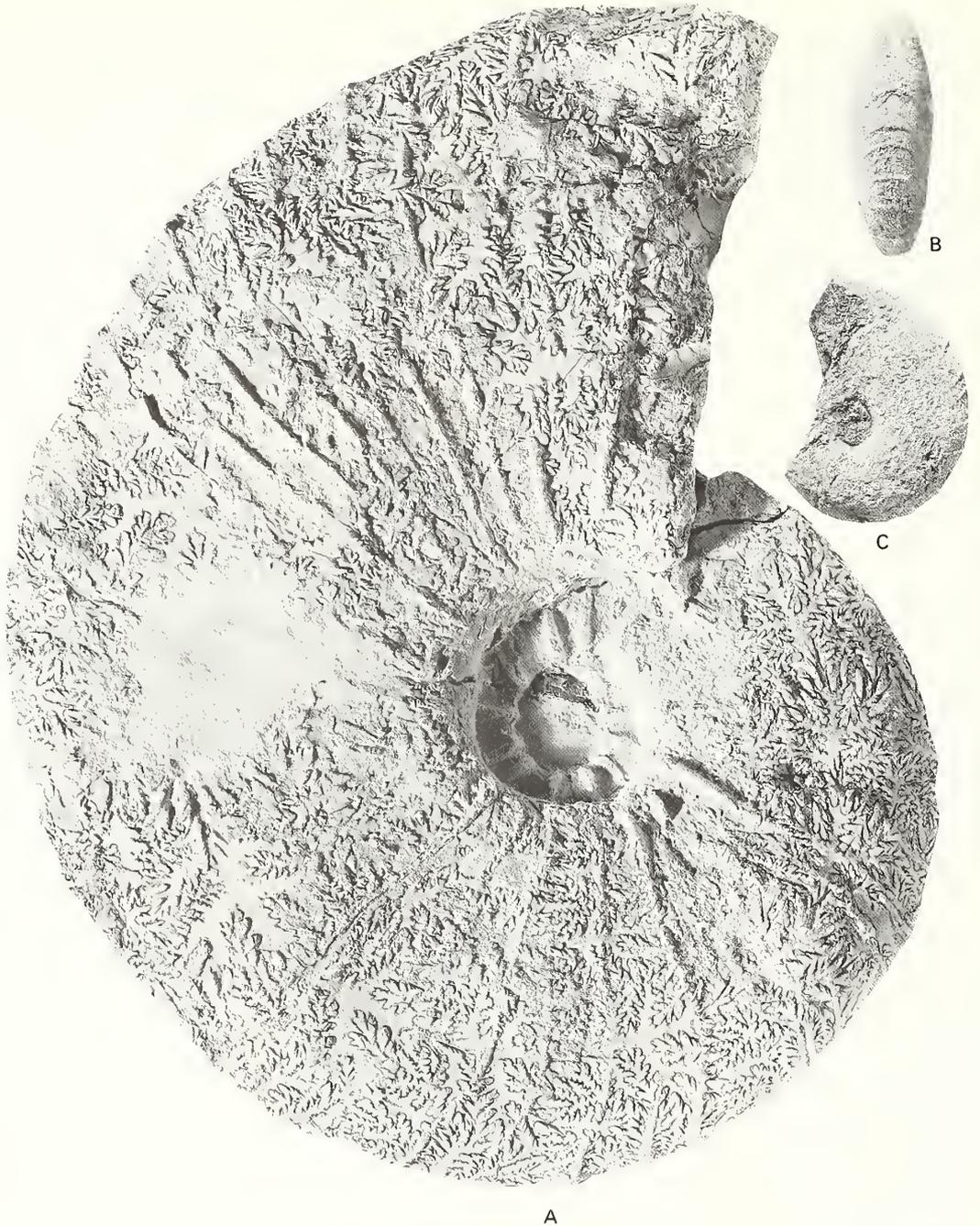
Eupachydiscus jimenezi (Renz, 1936) (p. 3, pl. 2, fig. 4; see also Young 1963, p. 59, pl. 14, figs 1–5; pl. 16, fig. 4; text-fig. 10*k*) has a depressed whorl section and much stronger, distant bullae that give rise to pairs of ribs, with numerous shorter intercalated ribs between bullate ones. *Eupachydiscus gordonii* Young, 1963 (p. 59, pl. 16, figs 1–3; text-fig. 8*e*), a second Texas species, is said to be Santonian. It has twenty umbilical bullae per whorl giving rise to one, sometimes two, ribs, with

EXPLANATION OF PLATE I

- Fig. 1. *Trachyscaphites densicostatus* sp. nov. USNM 441427; paratype; microconch.
 Figs 2–3. *Trachyscaphites spiniger spiniger* (Schlüter, 1872). USNM 441416; microconch body chamber.
 Figs 4–7. *Pachydiscus (Pachydiscus) paulsoni* (Young, 1963). 4–5, USNM 441383, 6–7, USNM 441384.
 Figs 8–10. *Pachydiscus (Pachydiscus) grossouvrei* (Kossmat, 1898). USNM 441389.
 All specimens from the Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas. All $\times 1$.



COBBAN and KENNEDY, *Trachyscaphtes*, *Pachydiscus*



TEXT-FIG. 3. *Pachydiscus (Pachydiscus) paulsoni* (Young, 1963). A, USNM 441387. B-C, USNM 441388. All figures natural size.

about twenty shorter ribs intercalating to give a total of approximately forty-four ribs per whorl. The ribbing is also much sharper than in the present species, but this may be due to differences in preservation. Collignon (1952, 1955) discussed differences between *E. grossouvrei* and other species from outside the United States.

Occurrence. Middle Campanian Ozan Formation of north-east Texas.

Superfamily HOPLITACEAE H. Douvillé, 1890
[for synonymy etc., see Kennedy 1986, p. 56]

Family PLACENTICERATIDAE Hyatt, 1900
[= Hypengonoceratinae Chiplonkar and Ghare 1976, p. 2; Baghiceratinae Chiplonkar and Ghare 1976, p. 3]

Genus PLACENTICERAS Meek, 1876
[for synonymy, see Kennedy and Wright 1983, p. 869]

Type species. *Ammonites placenta* DeKay, 1828, p. 278, pl. 5, fig. 3 (2), by original designation by Meek 1876, p. 426.

Placenticerus sp.

Plate 2, fig. 1

Description. *Placenticerus* is represented by four fragments in the North Sulphur River fauna, the largest and best-preserved (Pl. 2, fig. 1) with a whorl height of 67 mm. Coiling is very involute, with a tiny, deep umbilicus that has a flattened, outward-inclined wall and broadly rounded umbilical shoulder. The inner flanks are broadly rounded, the outer flanks flattened and convergent, the venter narrow and tabulate, with sharp ventral edges. Two of the fragments are smooth; two have umbilical bullae of moderate strength, that number five per half whorl.

Occurrence. Middle Campanian, Ozan Formation, USGS Mesozoic locality D10154, Fannin County, Texas.

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894

[*nom. correct.* Wright and Wright 1951, p. 24 (*pro* Acanthoceratida Hyatt, 1900, p. 585), *nom. transl. ex.* Acanthoceratidae Hyatt, 1900, p. 585, *nom. correct. ex* Acanthoceratidés de Grossouvre, 1894]

Family COLLIGNONICERATIDAE Wright and Wright, 1951

[*nom. subst. pro* Prionotropidae Zittel, 1895, p. 430 (*ex* *Prionotropis* Meek, 1876, p. 453, *non* Fieber, 1853, p. 127; = *Collignoniceras* Brcistroffer, 1947 (unpaged) (= *Prionocyclidae* Breistroffer, 1947 (unpaged) *ex* *Prionocylchus* Meek, 1876, p. 298, ineligible as family type)]

Subfamily TEXANITINAE Collignon, 1948

[*nom. transl.* Wright 1957, p. L429 *ex* Texanitidae Collignon, 1948]

Genus MENABITES Collignon, 1948

Type species. *Menabites menabensis* Collignon, 1948, p. 7 (64), pl. 17, figs 3 and 4; pl. 18, fig. 1, by subsequent designation by Wright 1957 (p. L432).

Subgenus DELAWARELLA Collignon, 1948, p. 64 (19)

Type species. *Ammonites delawarensis* Morton, 1830, p. 244, pl. 2, fig. 4, by original designation.

Menabites (Delawarella) delawarensis (Morton, 1830)

Plate 6, fig. 9

1830 *Ammonites delawarensis* Morton, p. 244, pl. 2, fig. 4.

- 1948 *Menabites (Delawarella) delawarensis* (Morton); Collignon, p. 29 (86) (with full synonymy).
 1986 *Menabites (Delawarella) delawarensis* (Morton, 1830); Kennedy, p. 81, pl. 11, figs 3–4; text-fig. 30 (with additional synonymy).

Types. These appear to be lost, in spite of the observations of Young (1963, p. 111); see Reeside (1962, p. 132) and Kennedy (1986, p. 81). Hypotype USNM 441391, from the Ozan Formation of Fannin County, Texas.

Description. Four specimens between 93 and 120 mm diameter are referred to this species. All are distorted to varying degrees. Coiling is moderately evolute; $U = 30\%$ of diameter with about a third of the previous whorl concealed in the dorsal impressed zone. The umbilical wall is of moderate elevation, flattened and subvertical and notched to accommodate the submarginal tubercles of the previous whorl. The umbilical shoulder is narrowly rounded. Twenty-one sharp umbilical bullae perch on the shoulder, and may project into the interspaces of the previous whorl; they are separated by deep interspaces that notch the shoulder and upper part of the umbilical wall. Broad, straight prorsiradiate ribs arise from these bullae either singly or in pairs and strengthen across the flanks, where they develop into a blunt, bullate lateral tubercle and a much stronger conical submarginal tubercle. A broad rib connects this to a somewhat weaker feebly clavate marginal tubercle, which gives rise to one or a pair of low, broad ribs (the adapical one the weaker) that terminate in strong external clavi. A broad, concave, smooth zone separates these clavi from a blunt siphonal ridge. Suture simple, with broad, bifid E/L and L, U_2 narrower.

Discussion. The North Sulphur River material differs in no significant respects from large collections of New Jersey and Delaware specimens before us. The Texas specimens are somewhat variable in strength of their tubercles versus ribs, notably in the development of the submarginal row. *Menabites (D.) delawarensis* differs from *M. (D.) danei* (Young, 1963) (see below) by the much coarser ribbing and tuberculation of *M. (D.) danei*, in particular the persistence of a strongly trituberculate 'Australiella' stage to as much as 150 mm diameter in Young's species. Of other Texas species, *M. (D.) campaniensis* of Young (1963, p. 113, pl. 64, figs 2, 6; pl. 67, fig. 2; text-figs 24a, 25a) *non* de Grossouvre, 1894, is much more evolute with a much lower whorl expansion rate and widely separated ribs. *Menabites (D.) sabinalensis* (Young, 1963) (p. 112, pl. 54, fig. 2; pl. 63, figs 1, 3, 4; text-figs 20c, 21e, 26c) is strongly and distantly ribbed with weak tubercles throughout and adults that are quadrituberculate.

Occurrence. *Menabites (D.) delawarensis* has generally been thought of as a late early Campanian species, but is here shown to range to the middle Campanian (early later Campanian in a north-west European sense). It occurs in the Merchantville Formation in Delaware and New Jersey (Sohl and Mello in Owens *et al.* 1970), and in the Austin Chalk in Texas where Young used it as an index for the mid-lower Campanian. Young's specimens from Travis County were said to be from unit D of the Burditt Marl. The species also occurs, but is poorly dated, in the Big Bend National Park. We have seen numerous specimens from the Roxton Limestone Member at the top of the Gober Chalk in Lamar County, where it is dated as late early Campanian and the Middle Campanian Ozan Formation at USGS Mesozoic locality D10154 in Fannin County. The species occurs in what are said to be equivalents of the Gober Chalk in McCurtain County, Oklahoma (Young 1963). A single specimen is known from the upper lower Campanian of Aquitaine, France, and it is also recorded from the lower Campanian of Zululand, South Africa and, possibly, Madagascar.

Menabites (Delawarella) danei (Young, 1963)

Plate 2, figs 5–8; Plate 3, figs 1–3; Plate 4, figs 1, 12

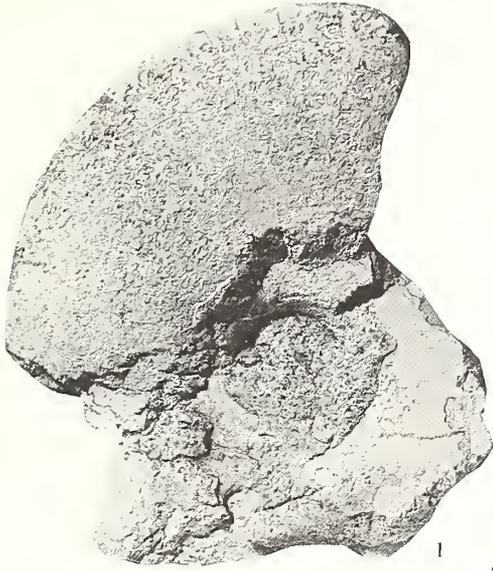
EXPLANATION OF PLATE 2

Fig. 1. *Placenticeras* sp. USNM 441390.

Figs 2–4. *Menabites (Delawarella) vanuxemi* (Morton, 1830). 2–3, USNM 441397. 4, USNM 441398.

Figs 5–8. *Menabites (Delawarella) danei* (Young, 1963). 5–6, USNM 441392. 7–8, USNM 441393.

All specimens from the Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas. All $\times 1$.



- 1929 *Mortoniceras delawareense* (Morton); Dane, pl. 10, figs 1–2.
 1963 *Delawareella danei* Young, p. 114, pl. 57, fig. 6; pl. 62, figs 1–2; pl. 64, figs 1, 5; pl. 65, figs 1–2; pl. 66, figs 3–4; text-figs 24e, 33b.

Types. Holotype, by original designation, is TMM 30646, from 'a formation equivalent to the Gober Chalk' in McCurtain County, Oklahoma, 1.6 km west of the Oklahoma line on the highway from Foreman, Arkansas, to Tom, Oklahoma. Hypotypes USNM 441392–441395, from the Ozan Formation of Fannin County, Texas.

Description. Twelve specimens, ranging from 42 to 160 mm diameter are referred to Young's species. In juveniles up to 70 mm diameter (Pl. 2, figs 5–8), coiling is very evolute with $U = 40\%$ or more of the diameter, deep, and with a flattened, outward-inclined umbilical wall that is notched to accommodate the submarginal spines of the preceding whorl (Pl. 2, fig. 7). The whorls are massive, depressed, reniform in intercostal section with the greatest breadth just below mid-flank and a whorl breadth to height ratio of 1.42. The costal whorl section is polygonal, with greatest breadth at the submarginal spine and a whorl breadth to height ratio of 1.76 in USNM 441393, taken at the basal septum of that spine. There are 7–8 strong umbilical bullae per half whorl, that in places are seen to be the septate bases of umbilical spines. They are separated by deep interspaces that notch the umbilical shoulder and upper part of the umbilical wall, and give rise to single strong, broad, coarse ribs that are slightly prorsiradiate and separated by interspaces of similar breadth or more. Each terminates in a massive rounded submarginal node that is the septate base of a short spine, visible in the inner whorl of USNM 441393 (Pl. 2, fig. 7). These give rise to one or two low broad ribs that connect to coarse external clavi. In a few cases the clavi intercalate, and are not obviously linked to the submarginal nodes. A shallow broad groove separates the external clavi from a coarse, rounded siphonal ridge on the mould, but where shell is preserved on USNM 441393 (Pl. 2, fig. 7), this corresponds to a high, hollow siphonal keel, while the external clavi also seem to have borne a septate spine. USNM 441394 (Pl. 3, figs 1–3) shows this massively tuberculate stage to a slightly larger diameter, with 16 umbilical spines per whorl; there are 17 in USNM 441395 (Pl. 4, figs 1, 12) at an estimated 85 mm diameter. From this diameter onwards the tubercles weaken relative to the ribs (on moulds), with up to 23 ribs per whorl at 140 mm diameter (Pl. 4, fig. 12), and the whorl section becomes less depressed, with costal $wb:wh$ ratios down to 1.3. At a diameter of 70–110 mm the submarginal tubercle splits (Pl. 3, fig. 2; Pl. 4, fig. 12) into a clavate marginal and rounded-bullate submarginal, while a feeble bullate lateral tubercle appears at as little as 70 mm in some specimens (unfigured specimen USNM 441396), but later in others. Suture little incised, with broad, bifid E/L and L and smaller U_2 .

Discussion. The diagnostic feature of *Menabites (Delawareella) danei* is the persistence of the coarsely ornamented trituberculate '*Australiella*' stage prior to acquisition of the pentatuberculate *Delawareella* condition. This, plus the coarseness of ornament, distinguish *M. (D.) danei* from all other North American species.

Occurrence. Lower Campanian, Roxton Limestone Member at top of Gober Chalk in Lamar County, Texas, and presumed equivalents in McCurtain County, Oklahoma (see under *Types*); middle Campanian Ozan Formation at USGS Mesozoic locality D10154 in Fannin County, Texas.

Menabites (Delawareella) vanuxemi (Morton, 1830)

Plate 2, figs 2–4

- 1830 *Ammonites vanuxemi* Morton, p. 244, pl. 3, figs 4–5.
 1963 *Submortoniceras vanuxemi* (Morton); Young, p. 98, pl. 54, fig. 3; pl. 56, fig. 2; pl. 57, fig. 7; pl. 58, fig. 3; pl. 67, fig. 3; pl. 69, figs 1, 2, 6; text-figs 12c,e, 26d–e.
 1980 *Submortoniceras vanuxemi* (Morton); Klinger and Kennedy, p. 232.

Types. Holotype by monotypy is No. 19492 in the collections of the Academy of Natural Sciences.

EXPLANATION OF PLATE 3

Figs 1–3. *Menabites (Delawareella) danei* (Young, 1963). USNM 441394; Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas, $\times 1$.



COBBAN and KENNEDY, *Menabites*

Philadelphia, from the Chesapeake and Delaware Canal, Delaware; refigured by Reeside, 1962, pl. 72, figs 4–5. Hypotypes are USNM 441397 and 441398, from the Ozan Formation of Fannin County, Texas.

Description. USNM 441397 (Pl. 2, figs 2–3) is a poorly preserved juvenile 62.5 mm in diameter, with an umbilicus of 23%, of moderate depth, and with a flattened subvertical umbilical wall and narrowly rounded shoulder. The whorl section is compressed; whorl breadth to height ratio is 0.78, and the greatest breadth is low on the flanks. The inner flanks are broadly rounded, the outer flanks flattened and convergent, the ventrolateral shoulders narrowly rounded. Small umbilical bullae give rise to straight prorsiradiate flank ribs both singly and in pairs, while there are long intercalated ribs. Weak lateral submarginal and marginal tubercles are present on all ribs, as well as small external clavi. A smooth zone separates these from a blunt siphonal ridge. USNM 441398 is a crushed phragmocone 145 mm in diameter, with $U = 30\%$ approximately. Only the older one-half is shown here (Pl. 1, fig. 4). There are an estimated twenty-two small umbilical bullae per whorl that project into the umbilicus. These bullae give rise to narrow, straight, prorsiradiate ribs either singly or in pairs. These are initially very narrow, but strengthen and broaden across the flanks, developing weak lateral bullae, stronger bullate submarginal tubercles, and slightly clavate marginal tubercles. External clavi are strong and approximately twice as numerous as the marginal row, to which they are usually linked by a low, weak rib. The venter is too poorly preserved for adequate description, but seems to have borne a siphonal ridge or keel. Suture poorly exposed; moderately incised, with broad bifid E/L and L; U_2 smaller.

Discussion. Collignon (1948, pp. 30, 43) referred *vanuxemi* to *Submorticeras*, but it is no more than a homoemorphous compressed *Menabites* (*Delawarella*) with weak ornament, as shown by the pattern of ribbing and tuberculation. Compressed whorls, dense crowded ribs and weak tubercles render this species distinct from all other North American *Delawarella*.

Occurrence. Merchantville Formation in New Jersey and Merchantville Formation and Woodbury Clay in the Chesapeake and Delaware Canal according to Reeside (1962), where it is regarded as early Campanian in age. Young (1963, text-fig. 3) shows it occurring in his lower Campanian *Delawarella delawarensis* zone in Texas, but detailed records (p. 100) are less precisely dated although the species is noted from Brewster County and from sandstone beds in the San Carlos area of Trans-Pecos, Texas, and from Uvalde County. References to lower Campanian specimens from the brown bed at the top of the Gober Chalk are from the Roxton Limestone Member and are of late early Campanian age. Young also noted a specimen from the Tombigbee Sand Member of the Eutaw Formation at Plymouth Bluff, Mississippi, but we have not seen this specimen. Ozan Formation at USGS Mesozoic locality D10154 in Fannin County, Texas.

Menabites (*Delawarella*) sp.

Plate 6, figs 1–2

Description. USNM 441399 is a distorted juvenile 43 mm in diameter, with $U = 33\%$ approximately of diameter. There are an estimated thirty-six ribs per whorl that arise singly or in pairs from weak umbilical bullae or intercalate low on the flank. The ribs are straight and prorsiradiate, each bears a weak lateral bulla, a clavate tubercle (either submarginal or marginal) at the inner ventrolateral position and an equal number of external clavi. A smooth ventral zone separates the clavi from a sharp, undulose siphonal keel. Sutures not seen.

EXPLANATION OF PLATE 4

Figs 1–2. *Menabites* (*Delawarella*) *danei* (Young, 1963). USNM 441395.

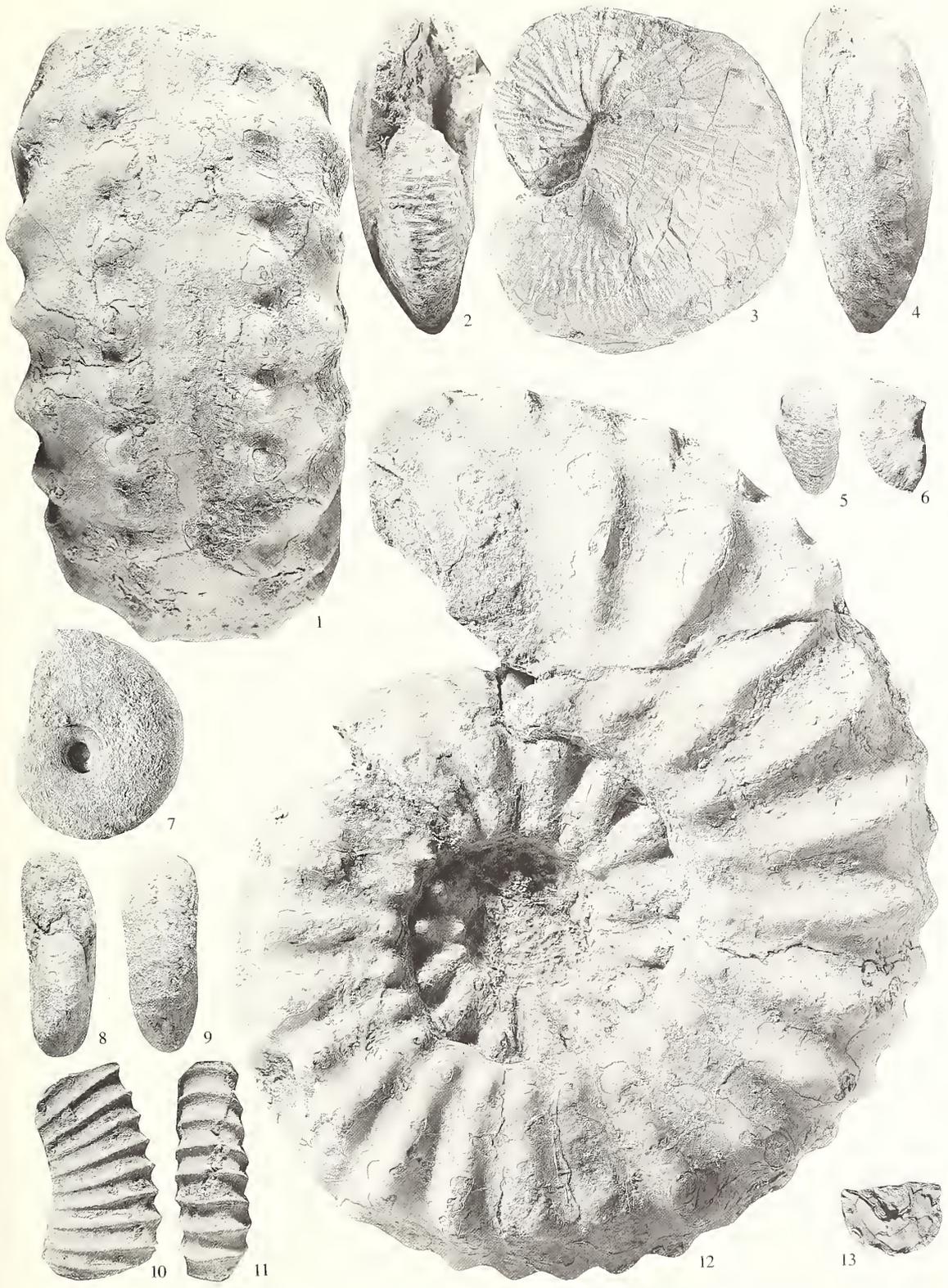
Figs 2–4. *Trachyscaphtites densicostatus* sp. nov. USNM 441426; holotype; macroconch.

Figs 5–6, 13. *Scaphites* (*Scaphites*) group of *hippocrepis* DeKay, 1828, form III of Cobban, 1969. 5–6, USNM 441413. 13, USNM 441414.

Figs 7–9. *Pachydiscus* (*Pachydiscus*) *paulsoni* (Young, 1963). USNM 441385.

Figs 10–11. *Glyptoxoceras* sp. USNM 441400.

All specimens from the Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas. All $\times 1$.



COBBAN and KENNEDY, Campanian ammonites

Discussion. This juvenile, quadrituberculate texanitid corresponds in its ribbing to certain juveniles from the Merchantville Formation of New Jersey, but the latter generally have five rows of node at the diameter of our specimen, and seem to be juvenile *M. (D.) vanuxemi*.

Occurrence. Middle Campanian Ozan Formation at USGS Mesozoic locality D10154 in Fannin County, Texas.

Suborder ANCYLOCERATINA Wiedmann, 1966
 Superfamily TURRILITACEAE Gill, 1871
 Family DIPLOMOCERATIDAE Spath, 1926
 [= Neocrioceratinae Spath, 1953, p. 17]
 Subfamily DIPLOMOCERATINAE Spath, 1926
 [= Scalaritinae Ward, 1976, p. 455]
 Genus GLYPTOXOCERAS Spath, 1925
 [= Neohamites Brunnschweiler, 1966, p. 48]

Type species. *Hamites rugatus* Forbes, 1846, p. 117, by original designation by Spath, 1925, p. 31.

Glyptoxoceras sp.

Plate 4, figs 10–11; Plate 6, figs 5–6; Plate 7, figs 7–8.

Description. The most complete specimen is USNM 441401 (Pl. 5, fig. 9), a crushed composite mould from the marls above the main fauna described here. The specimen consists of just under two whorls of an open planispiral criocone with the whorls barely separated. It and a second specimen show the earliest preserved section to a whorl height of 7 mm to have been finer ribbed than later sections. The latter are represented by 28 fragments with whorl heights of as much as 17 mm. Most are body chambers, which suggests this to be the adult size of the species. The whorl section is compressed oval with a whorl breadth to height ratio of 0.79; the dorsum and venter are broadly rounded, and the flanks somewhat flattened. The rib index is six. The ribs are weak on the dorsum, but strengthen and sweep back over the dorsolateral area. They are sharp, rursiradiate on the flank, and narrower than the interspaces; they strengthen as they cross the venter transversely. None of the specimens shows the suture.

Discussion. Coiling alone distinguishes the present material from other North American species such as *G. ellisoni* Young, 1963 (p. 46, pl. 1, figs 10–14; pl. 73, fig. 9; pl. 78, fig. 6) of the upper Santonian and lower Campanian in Texas, which has straight or only slightly curved shafts and is much larger. *Glyptoxoceras* [*Helicoceras*] *rubeyi* (Reeside, 1927, p. 14, pl. 3, figs 8–10; pl. 5, figs 3–11) has a nearly circular whorl section and prorsiradiate ribs. Closer is '*Hanites*' *novimexicanus* Reeside, 1927 (p. 8, pl. 4, figs 1–6), but this is much larger and has an elliptical coil.

Occurrence. Middle Campanian, Ozan Formation at USGS Mesozoic locality D10154 in Fannin County, Texas.

EXPLANATION OF PLATE 5

Figs 1–6, 10–15. *Baculites* sp. group of *aquilaensis* Reeside, 1927. 1–2, USNM 441404. 3–4, USNM 441405. 5–6, USNM 441406. 10–11, USNM 441407. 12–13, USNM 441408. 14–15, USNM 441409.

Figs 7–8. *Pachydiscus* (*Pachydiscus*) *paulsoni* (Young, 1963). USNM 441386.

Fig. 9. *Glyptoxoceras* sp. USNM 441401.

All specimens from the Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas. The original of Figure 9 is from chalky beds a little higher in the section than the other specimens. All $\times 1$.



COBBAN and KENNEDY, Campanian ammonites

Family BACULITIDAE Gill, 1871
 [Eubaculitinae Brunnschweiler, 1966, p. 24]
 Genus BACULITES Lamarck, 1799

[= *Homaloceratites* Hupsch, 1768, p. 110 (*non binomen*); *Euhomaloceras* Spath, 1926, p. 80]

Type species. *Baculites vertebralis* Lamarck, 1801, p. 103, by subsequent designation by Meek 1876, p. 391.

Baculites sp. group of *aquilaensis* Reeside, 1927

Plate 5, figs 1–6, 10–15; Plate 6, figs 3–4; Plate 7, figs 3–4; Text fig. 4D

1927 *Baculites aquilaensis* Reeside, p. 12, pl. 6, figs 11–13; pl. 8, figs 1–14.

1927 *Baculites aquilaensis* var. *separatus* Reeside, p. 12, pl. 8, figs 15–21; pl. 9, figs 6–15; pl. 45, figs 5–6.

1927 *Baculites aquilaensis* var. *obesus* Reeside, p. 12, pl. 10, figs 1–8.

Types. Figured specimens USNM 441404–441412, from the Ozan Formation of Fannin County, Texas.

Description. We have more than 100 fragments, ranging from 10 to 40 mm in whorl height. The collection is highly variable. At one extreme are very weakly ornamented individuals (Pl. 5, figs 3–6) with a compressed, ovoid whorl section (whorl breadth to height ratio as little as 0.6), and venter only slightly narrower than the dorsum. Ornament is nearly absent on the flanks, and consists of asymmetrically concave growth lines and lirae that cross the dorsum in a broad convexity. They sweep strongly forward on the ventral part of the flanks and intersect the line of the venter at an acute angle, where they strengthen over the ventrolateral region into regular riblets that cross the venter in a broad convexity (Pl. 5, fig. 6). Stronger ornamented individuals (Pl. 6, figs 3–4) have low, broad, shallow, concave ribs that extend across the dorsal two-thirds of the flank, with a rib index of 4. The ribs project strongly forward on the ventral third of the flanks, where they are accompanied by numerous striae and growth lines, all of which intersect the line of the venter at an acute angle. The ribs strengthen again across the venter (Pl. 6, fig. 4), which is crossed by low, broad, convex ribs, that may be accompanied by intercalated ribs so that there are more ventral than flank ribs (Pl. 5, figs 10–11). Other specimens have less compressed ovoid whorl sections (Wb:Wh ratio up to 0.85). Ornament is much coarser, with rib indices of 1.5–2, the flank ribs extending across the dorsum in a broad convexity (Pl. 5, fig. 15), while intercalated ribs are present on the ventral third of the flanks and venter (Pl. 5, fig. 14) or not (Pl. 6, figs 7–8; Pl. 7, figs 3–4). The suture (Text-fig. 3D) is moderately incised, with rectangular bifid lobes and saddles.

Discussion. This large collection of what is a very generalized *Baculites* shows a wide range of intraspecific variation, as is normal in the genus. The ovoid rather than oval whorl section plus style and variation range of ribbing strongly recall the variable *Baculites aquilaensis* Reeside, 1927, and its varieties *separatus*, with distant ribs, and *obesus*, with coarse ribs and stout whorl section. The present material differs from this lower Campanian species in the relatively uncommon incidence of compressed and closely ribbed specimens like the holotype (Reeside 1927, p. 12, pl. 10, figs 1–3), a fact that presumably reflects the markedly younger age of the present material. Our material is best compared to the baculites in the Western Interior lower Campanian zone of *Baculites* sp. (weak flank ribs) (Gill and Cobban 1966, table 2).

When compared with other Campanian species known from the Gulf Coast, the Ozan Formation specimens can be separated from *Baculites taylorensis* Adkins, 1929 (p. 204, pl. 5, figs 9–11) by the

EXPLANATION OF PLATE 6

Figs 1–2. *Menabites* (*Delawarella*) sp. USNM 441399.

Figs 3–4, 7–8. *Baculites* sp. group of *aquilaensis* Reeside, 1927. 3–4, USNM 441411. 7–8, USNM 441410.

Figs 5–6. *Glyptoxoceras* sp. USNM 441402.

Fig. 9. *Menabites* (*Delawarella*) *delawarensis* (Morton, 1830). USNM 441391.

All specimens from the Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas. All $\times 1$.



COBBAN and KENNEDY, Campanian ammonites

strong node-like bullae of that species, lying close to the dorsum, and quite unlike the ribs of our material. *Baculites taylorensis* also has numerous narrow prorsiradiate ribs on the ventral half of the flanks that cross the venter in a broad convexity. *Baculites reduncus* (Cobban 1977, p. 459, figs 2–6), which occurs in the Annona Chalk in Arkansas (unpublished observations by the authors), has a high expansion rate, stoutly ovate whorl section, crescentic ribs on the dorsal half of the flanks but no or very weak ornament on the venter. *Baculites haresi* Reeside, 1927 (= *B. ovatus* var. *haresi* Reeside, 1927, p. 10, pl. 6, figs 5–10; pl. 7, figs 9–10), which occurs at the top of Gober Chalk in north-east Texas, generally has coarse ventral and ventrolateral ribbing only, although a few variants have low, broad, concave crescentic flank ribs with an index of 2 or 3. *Baculites ovatus* Say, 1820 (see revision in Cobban 1974, p. 3, pl. 1, figs 1–32; pl. 2, figs 1–14; pl. 3, figs 1–6, 9–11; text-fig. 4) has an oval whorl section rather than the ovoid one of the present material. Dorsolateral ribs are sparse and distant, whereas ventrolateral and ventral ribs are much more numerous.

Occurrence. Middle Campanian Ozan Formation of USGS Mesozoic locality D10154 in Fannin County, Texas.

Superfamily SCAPHITACEAE Gill, 1871

[*nom. transl.* Wright and Wright 1951, p. 13 *ex* Scaphitidae Gill, 1871, p. 3]

Family SCAPHITIDAE Gill, 1871

Subfamily SCAPHITINAE Gill, 1871

[*nom. transl.* Wright 1953, p. 73, *ex* Scaphitidae Gill, 1871, p. 3]

Genus and subgenus SCAPHITES Parkinson, 1811

[= *Anascaphites* Hyatt, 1900, p. 572; *Jahmites* Hyatt, 1900, p. 572; *Holcoscaphites* Nowak, 1911, p. 564]

Type species. *Scaphites equalis* J. Sowerby, 1813, p. 53, pl. 18, figs 1–3, by subsequent designation by Meek 1876, p. 413.

Scaphites (*Scaphites*) sp. group of *hippocrepis* (DeKay, 1828)

Plate 4, figs 5–6, 13

Types. Figured specimens USNM 441413 and 441414, from the Ozan Formation of Fannin County, Texas.

Description. Two small fragments are part of the final hook of what were probably adult microconchs. They have clavate umbilical tubercles with effaced flank ornament, conical ventrolateral nodes in one (Pl. 4, figs 5–6) and clavate ones in the other (Pl. 4, fig. 13). The venter is ornamented by fine ribs which loop between the tubercles and intercalate. This type of ornament shows these specimens to belong to the same group as the slightly older Campanian species *S. (S.) hippocrepis*, relating to some forms of *S. hippocrepis* III of Cobban (1969, pl. 3, figs 1–6, 12–14). The material is inadequate to determine whether these are very late survivors of *S. (S.) hippocrepis*, or some undescribed form that provides a link between it and the much younger *S. (S.) pumilis* Stephenson, 1941 (p. 426, pl. 90, figs 10–12).

Occurrence. Middle Campanian, Ozan Formation at USGS Mesozoic locality D10154 in Fannin County, Texas.

EXPLANATION OF PLATE 7

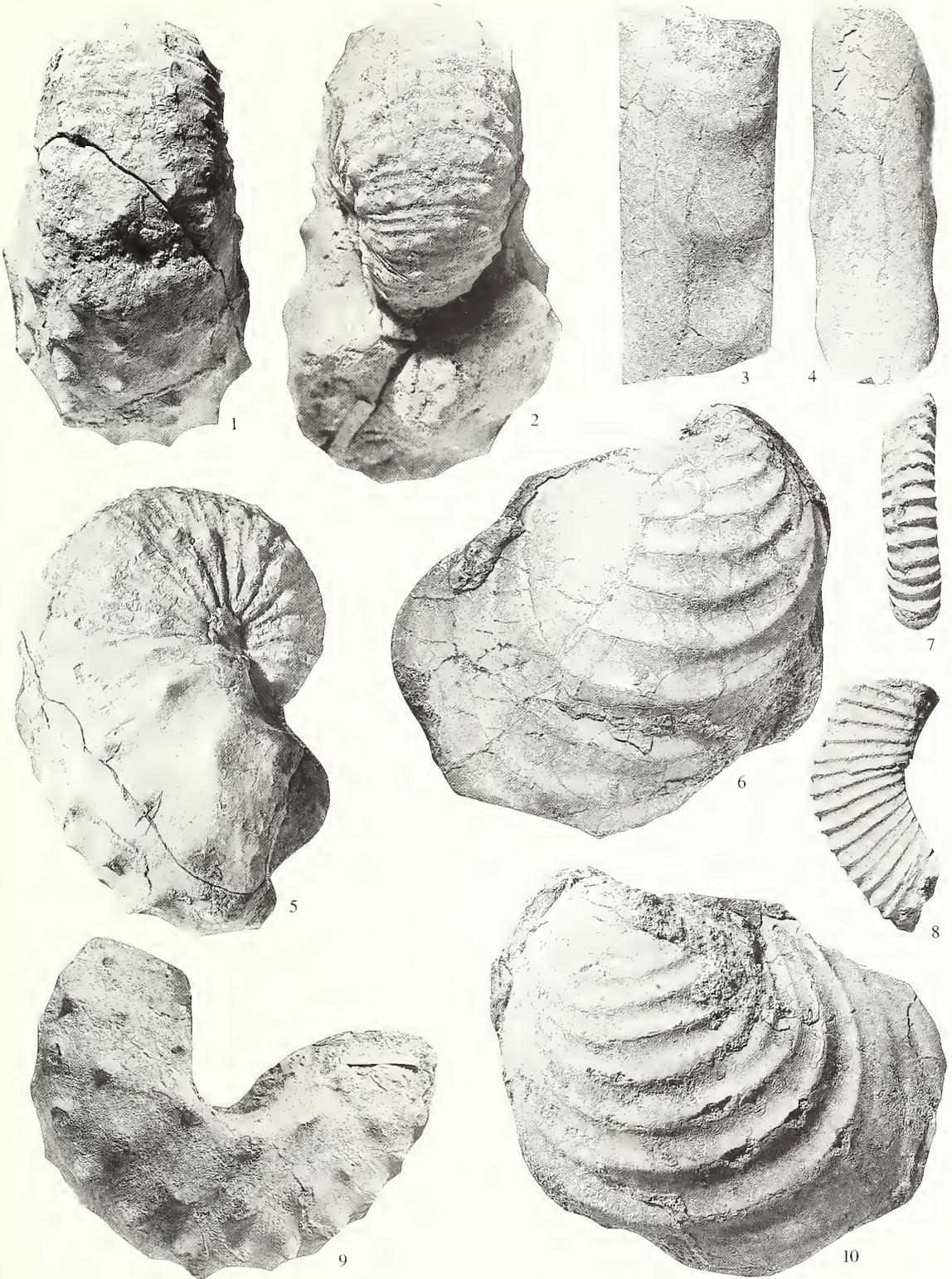
Figs 1–2, 5, 9. *Trachyscaphites spiniger spiniger* (Schlüter, 1872). 1–2, 5, macroconch, USNM 441417. 9, microconch, USNM 441418.

Figs 3–4. *Baculites* sp. group of *aquilaensis* Reeside, 1927. USNM 441412.

Figs 6, 10. *Inoceramus (Endocostea) balticus* Boehm, 1909. USNM 441429.

Figs 7–8. *Glyptoxoceras* sp. USNM 441403.

All species from the Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas. All $\times 1$.



COBBAN and KENNEDY, Campanian ammonites

Genus TRACHYSAPHITES Cobban and Scott, 1964

Type species. *Trachysaphites redbirdensis* Cobban and Scott, 1964, p. E7, pl. 1, figs 1–7; text-fig. 3, by original designation.

Trachysaphites spiniger spiniger (Schlüter, 1872)

Plate 1, figs 2–3; Plate 7, figs 1–2, 5, 9; Plate 8, figs 1–9; Text-fig. 4A

- 1872 *Scaphites spiniger* Schlüter, p. 82, pl. 25, figs 1–7.
 1980 *Trachysaphites spiniger spiniger* (Schlüter); Błazkiewicz, p. 30, pl. 13, figs 1–3, 5, 7 (with synonymy).
 1986 *Trachysaphites spiniger* (Schlüter, 1872a); Kennedy, p. 130, pl. 22, fig. 4; text-fig. 42A–F (with additional synonymy).

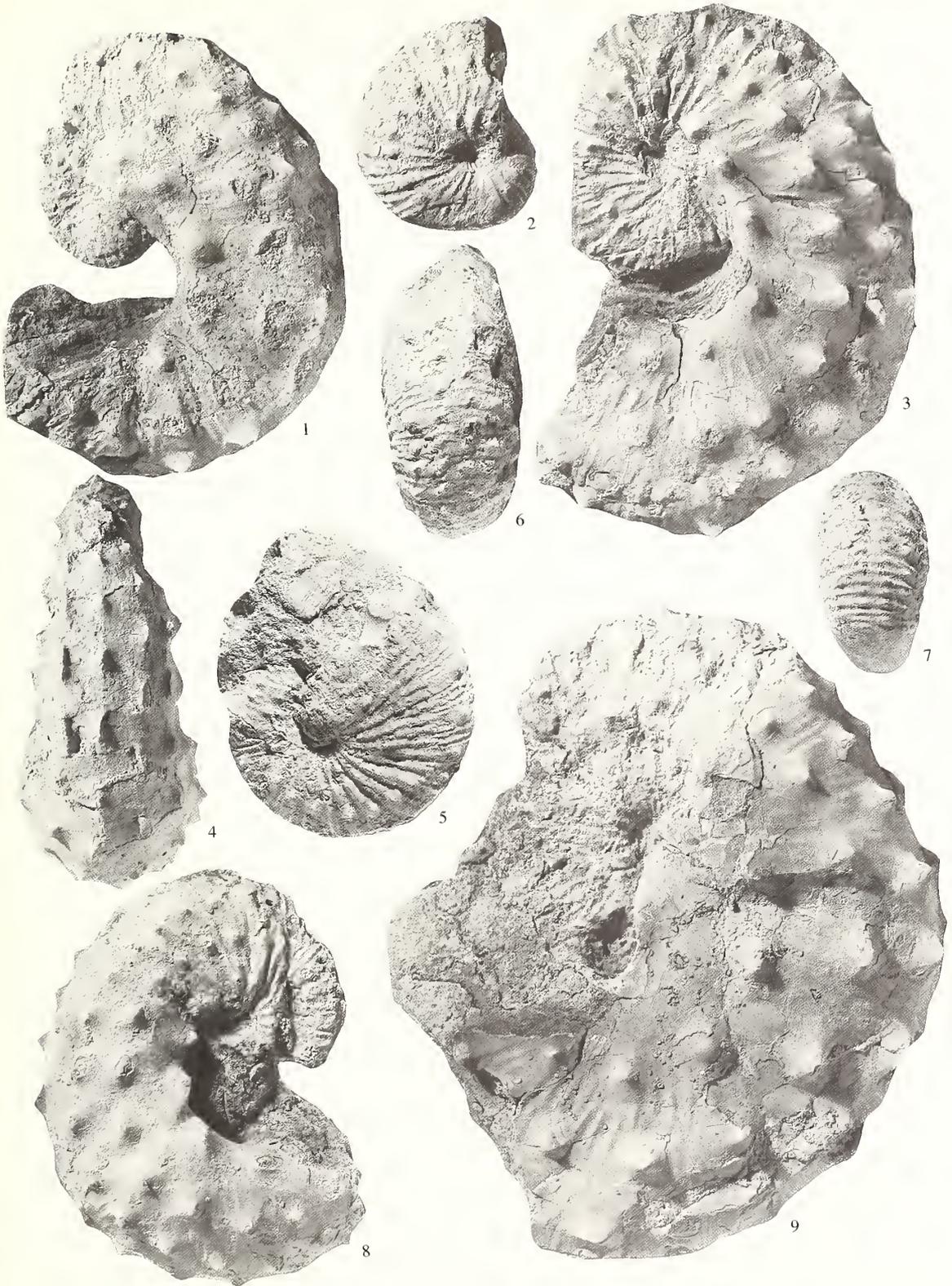
Types. Lectotype, designated by Błazkiewicz 1980, p. 31, is the original of Schlüter 1872, pl. 25, figs 1–3, GPIB unregistered, from the upper Campanian of Darup, Westphalia. Paralectotype GPIB 61a is the original of Schlüter 1872, pl. 25, fig. 4; paralectotype GPIB 61b is the original of Schlüter 1872, pl. 25, fig. 6, both from the upper Campanian Hügélgruppe of Haldem, Westphalia. Hypotypes USNM 441416–441425, from the Ozan Formation of Fannin County, Texas.

Description. Forty specimens are referred to the nominate subspecies, which is strongly dimorphic; twelve specimens are microconchs, ten are macroconchs, and eighteen are unassigned fragments. Microconchs (Pl. 1, figs 2–3; Pl. 7, fig. 9; Pl. 8, figs 1, 3–4, 8) vary from 57 to 87 mm in length. The phragmocone is very involute with a tiny umbilicus comprising less than 10% of the diameter. The intercostal whorl section is compressed to depressed with broadly rounded flanks and venter, and whorl breadth to height ratios of up to 1.1 in undeformed specimens. Delicate, straight, prorsiradiate ribs arise singly or in pairs at the umbilical shoulder without developing a bulla and number about 15 per half whorl. They strengthen across the flank and link to a small conical outer lateral tubercle either singly or in pairs; there are 10–12 such tubercles per half whorl; they give rise to one to three finer ribs, while some non-tuberculate ribs branch at the same level on the flank. These ribs loop to small conical inner ventrolateral tubercles or intercalate between them, and then loop to small conical outer ventrolaterals. The latter generally alternate on either side of the mid-ventral line such that the fine ribs loop or zig-zag across the venter between the tubercles or intercalate between them. There are generally slightly more ventrolateral than lateral tubercles. The body chamber is slender with a concave profile to the line of the umbilical shoulder in lateral view so that the umbilicus of the phragmocone is visible. The umbilical wall is smooth and concave. There are up to seven strong umbilical bullae; nine subspinose, weakly clavate outer lateral tubercles; thirteen subspinose, clavate inner ventrolateral tubercles and a similar number of subspinose, outer ventrolateral tubercles. The tubercles are offset on the flanks, and alternate on either side of the mid-ventral line (Pl. 1, fig. 2; Pl. 8, fig. 7). Numerous delicate prorsiradiate ribs loop between the rows of tubercles or intercalate between them. The number of ribs increases across the flank so that the whole shell surface has a dense covering of ribs. On the venter the ribs loop, zig-zag and intercalate between the ventral clavi. Tuberculation declines markedly before the adult aperture which is well preserved in USNM 441415; there is a marked constriction with a short dorsal rostrum. Macroconchs (Pl. 7, figs 1–2, 5; Pl. 8, fig. 9) vary from 66 to 100 mm long. They differ from microconchs in the form of the body chamber, which has a weak umbilical bulge at the adapical end. The umbilical shoulder follows a straight course in lateral view (Pl. 8, fig. 9) so that much of the umbilicus of the phragmocone is concealed. The umbilical wall is convex, and the umbilical tubercles, rather than being clavate and perched on a sharp umbilical shoulder, are displaced out to an inner lateral position and are bullate. Outer lateral tubercles and inner and outer ventrolateral tubercles are

EXPLANATION OF PLATE 8

Figs 1–9. *Trachysaphites spiniger spiniger* (Schlüter, 1872). 1, microconch, USNM 441419. 2, 7, juvenile, USNM 441420. 3, microconch, USNM 441421. 4, 8, microconch, USNM 441422. 5, 6, juvenile macroconch, USNM 441423. 9, macroconch, USNM 441424.

All specimens from the Ozan Formation 46 m above the base at USGS Mesozoic locality D10154; Fannin County, Texas. All $\times 1$.



COBBAN and KENNEDY, *Trachyscaphtes*

only weakly clavate when compared with those of most microconchs. Suture with deeply incised E/L (Text-fig. 4A).

Discussion. This large assemblage differs in no respects other than preservation from the generally crushed types and other specimens from Germany. *Trachyscaphites spiniger porchi* (Adkins, 1929) p. 205, pl. 5, figs 1–3), of which *Scaphites aricki* (Adkins, 1929) (p. 206, pl. 5, figs 7–8) is a synonym (see Cobban and Scott 1964, p. E10, pl. 2, figs 1–23; pl. 3, figs 1–11; text-fig. 4), differs from the nominate subspecies in having fewer tubercles in all rows on the body chamber and generally lacking the dense ribbing so well-displayed by the present specimens. *Trachyscaphites spiniger levantinensis* Lewy, 1969 (p. 132, pl. 4, fig. 1), from the upper Campanian of Israel, is based on a microconch and is probably a synonym of *porchi*. *Trachyscaphites spiniger posterior* Błaszkiwicz, 1980 (p. 31, pl. 13, fig. 4; pl. 14, figs 1–7; pl. 15, figs 2–3; pl. 30, fig. 2), from the upper Campanian of the Vistula Valley, Poland, was differentiated from the nominate subspecies because of the 'smaller number of ribs running between the tubercles of the same row on the exposed part of normal spiral and the presence of latero-umbilical tuberculation on earlier sectors of the exposed, normal spiral. It also differs on the whole in a smaller degree of freeing the shaft from phragmocone and is a frequent lack of ribs between the tubercles of the same row on the shaft.'

Trachyscaphites pulcherrimus (Roemer, 1841) (see revision in Kennedy and Summesberger 1984, p. 171, pl. 11, figs 1–2, 10–22, pl. 13, figs 2–6) is easily distinguished by the presence of five rows of flank tubercles as well as a siphonal row. *Trachyscaphites densicostatus* sp. nov., described below, has only three rows of tubercles on the phragmocone and sparse, distant umbilicolateral tubercles and more numerous inner and outer ventrolateral rows of tubercles on the body chamber.

Occurrence. Upper Campanian of Germany, The Netherlands, Sweden, Poland, the USSR (European Russia, Soviet Armenia and Kopet Dag); the species is restricted to the lower upper Campanian where precisely dated. In the United States it is best known from the middle Campanian Ozan Formation at USGS Mesozoic locality D10154 in Fannin County, Texas. There is a flattened specimen in the USGS Mesozoic collections at Denver from the Annona Chalk at USGS Mesozoic locality 12889 about 6.4 km east of Clarksville, Red River County, Texas.

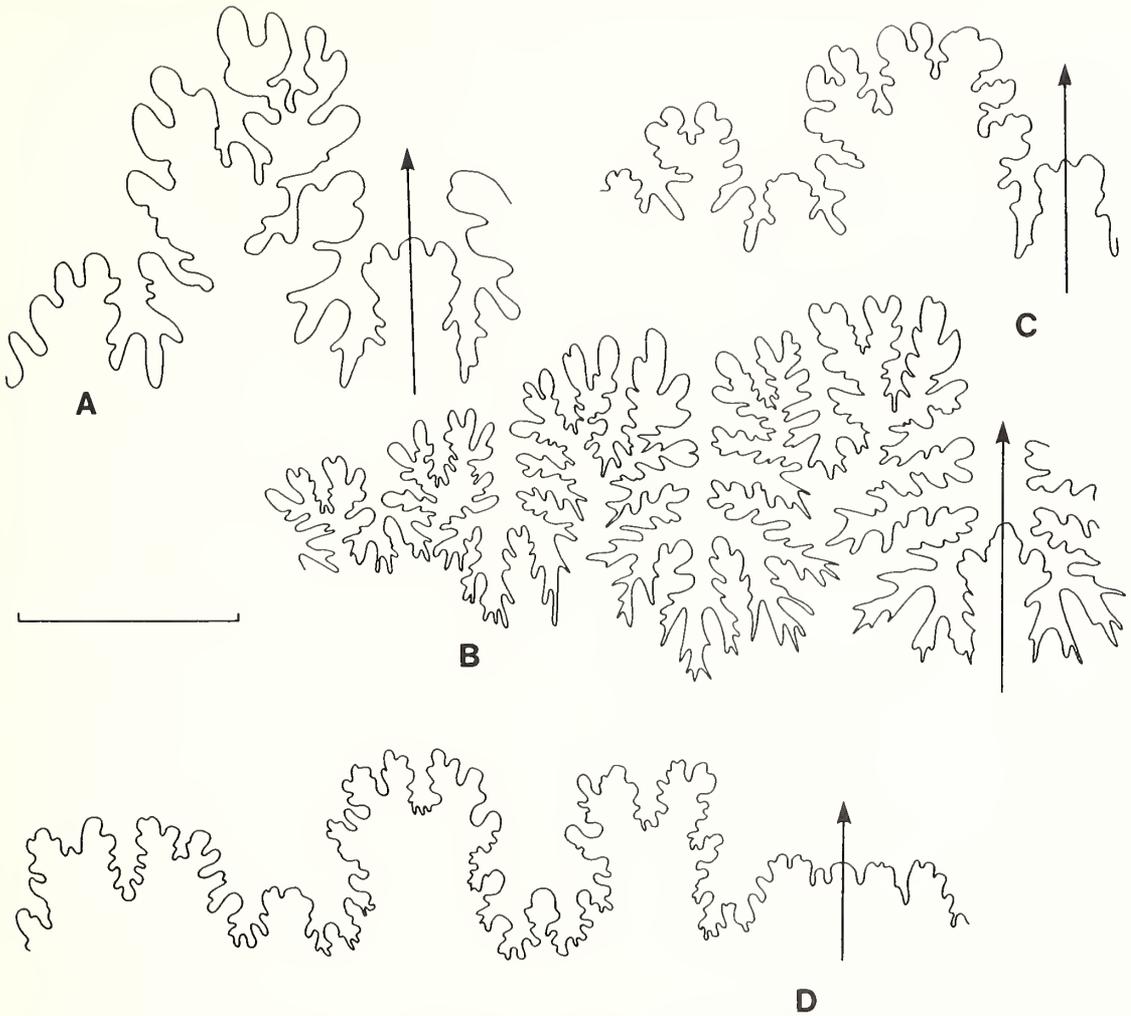
Trachyscaphites densicostatus sp. nov.

Plate 1, fig. 1; Plate 4, figs 2–4; Text-fig. 4C

Types. Holotype USNM 441426, paratypes USNM 441427–441428, from the middle Campanian Ozan Formation at USGS Mesozoic locality D10154 in Fannin County, Texas.

Diagnosis. *Trachyscaphites* with densely ribbed phragmocone that has small conical outer lateral tubercles and inner and outer ventrolateral tubercles; densely ribbed body chamber that has sparse umbilical/umbilicolateral tubercles and more numerous inner and outer ventrolateral clavi.

Description. The species is strongly dimorphic. Paratype USNM 441427 is a complete microconch 50 mm long. The phragmocone is poorly preserved, but shows fine, dense, prorsiradiate ribs arising either singly or in pairs at the umbilical shoulder, and small outer lateral tubercles and inner and outer ventrolateral tubercles linked by one or more ribs with nontuberculate ribs intercalated. The body chamber is slender with a concave line to the umbilical shoulder when viewed in profile, such that the umbilicus of the phragmocone is visible; the umbilical wall is concave, and the shoulder sharply defined. Five coarse umbilical clavi perch on the umbilical shoulder and give rise to groups of narrow prorsiradiate ribs; some nontuberculate ribs intercalate low on the flank. Ventrolateral and ventral ornament is not preserved, but paratype USNM 441428 has from the beginning of the final hook, small conical inner and outer ventrolateral tubercles linked by delicate ribs with others intercalated between; the outer ventrolateral clavi alternate across the venter and are linked by zig-zagging ribs. The holotype, USNM 441426, is an adult macroconch 57 mm long. The phragmocone is very involute, the body chamber short, with a straight umbilical shoulder in side view such that the umbilicus of the spire is occluded. Ornament on the spire consists of dense rounded prorsiradiate ribs that arise at the umbilical shoulder and are feebly flexuous on the flanks, where they increase by bifurcation and intercalation.



TEXT-FIG. 4. External sutures. A, *Trachyscaphites spiniger spiniger* (Schlüter, 1872). USNM 441425. B, *Pachydiscus (Pachydiscus) paulsoni* (Young, 1963). USNM 441384. C, *Trachyscaphites densicostatus* sp. nov. USNM 441426. D, *Baculites* sp. group of *B. aquilaensis* Reeside, 1927. USNM 441406. Bar scale is 10 mm.

Some ribs link to tiny outer lateral tubercles, while others intercalate between. Ribs arise in groups of two or three from these tubercles, and link to small conical outer ventrolateral tubercles or intercalate between them; the outer ventrolaterals are also small and conical and similarly linked to the inner ventrolaterals. Tubercles alternate on either side of the venter, across which they are connected by zig-zagging ribs. The body chamber is ornamented by dense, crowded, prorsiradial, weakly flexuous ribs that arise at the umbilical seam and increase by branching and intercalation across the flanks. Four distant umbicolateral bullae are present, as are 12 inner ventrolateral clavi which connect groups of ribs with several intercalated between. They alternate in position with an outer ventrolateral row where groups of ribs are again linked, with others intercalated. Delicate ribs connect the alternate outer ventrolateral clavi across the venter. Suture moderately incised with broad, asymmetrically bifid E/L and narrower bifid L and L/U (Text-fig. 4C).

Discussion. The combination of delicate ribbing and multituberculation show this species to be a *Trachyscaphites*. The presence of only three rows of tubercles on the phragmocone, disappearance of the outer lateral row and appearance of an umbilical/umbicolateral row on the body chamber

with its numerous crowded flexuous branching and intercalating ribs distinguish it from all other species referred to the genus.

Occurrence. As for types.

Acknowledgements. Most of the figured specimens were collected by the late James P. Conlin, Fort Worth, Texas, who kindly donated them to the US Geological Survey. R. E. Burkholder, formerly of the US Geological Survey, Denver, took some of the photographs. W.J.K. acknowledges the financial support of the Natural Environment Research Council (UK) and the staff of the Geological Collections, University Museum, Oxford, and Department of Earth Sciences, Oxford.

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W. A. COBBAN

US Geological Survey
Denver, Colorado, USA

W. J. KENNEDY

Geological Collections
University Museum
Parks Road, Oxford, UK

Typescript received 6 August 1990

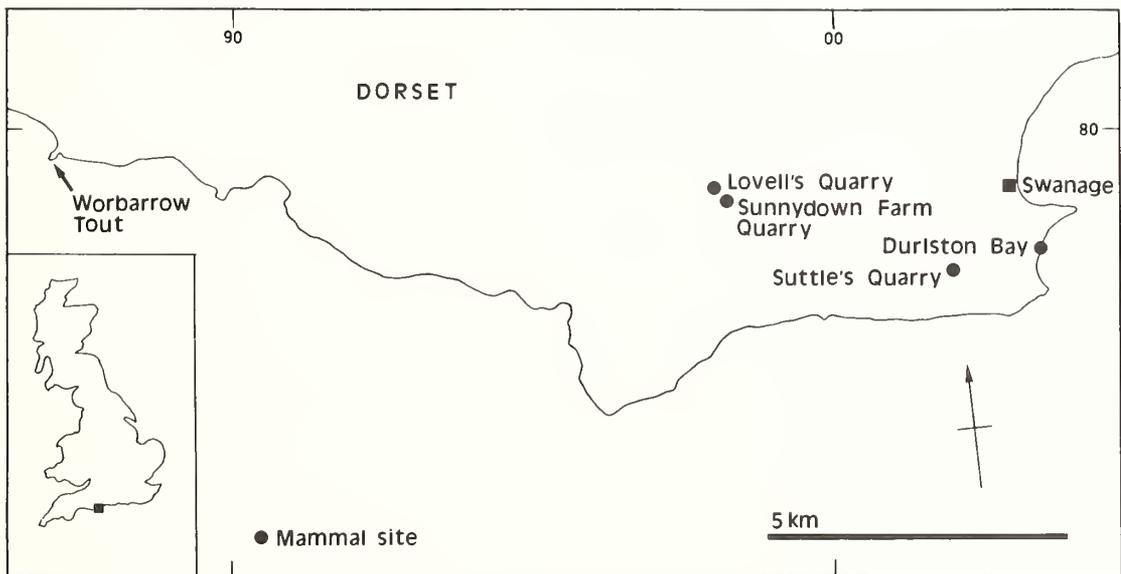
Revised typescript received 13 June 1991

MULTITUBERCULATE MAMMALS FROM THE UPPER JURASSIC PURBECK LIMESTONE FORMATION OF SOUTHERN ENGLAND

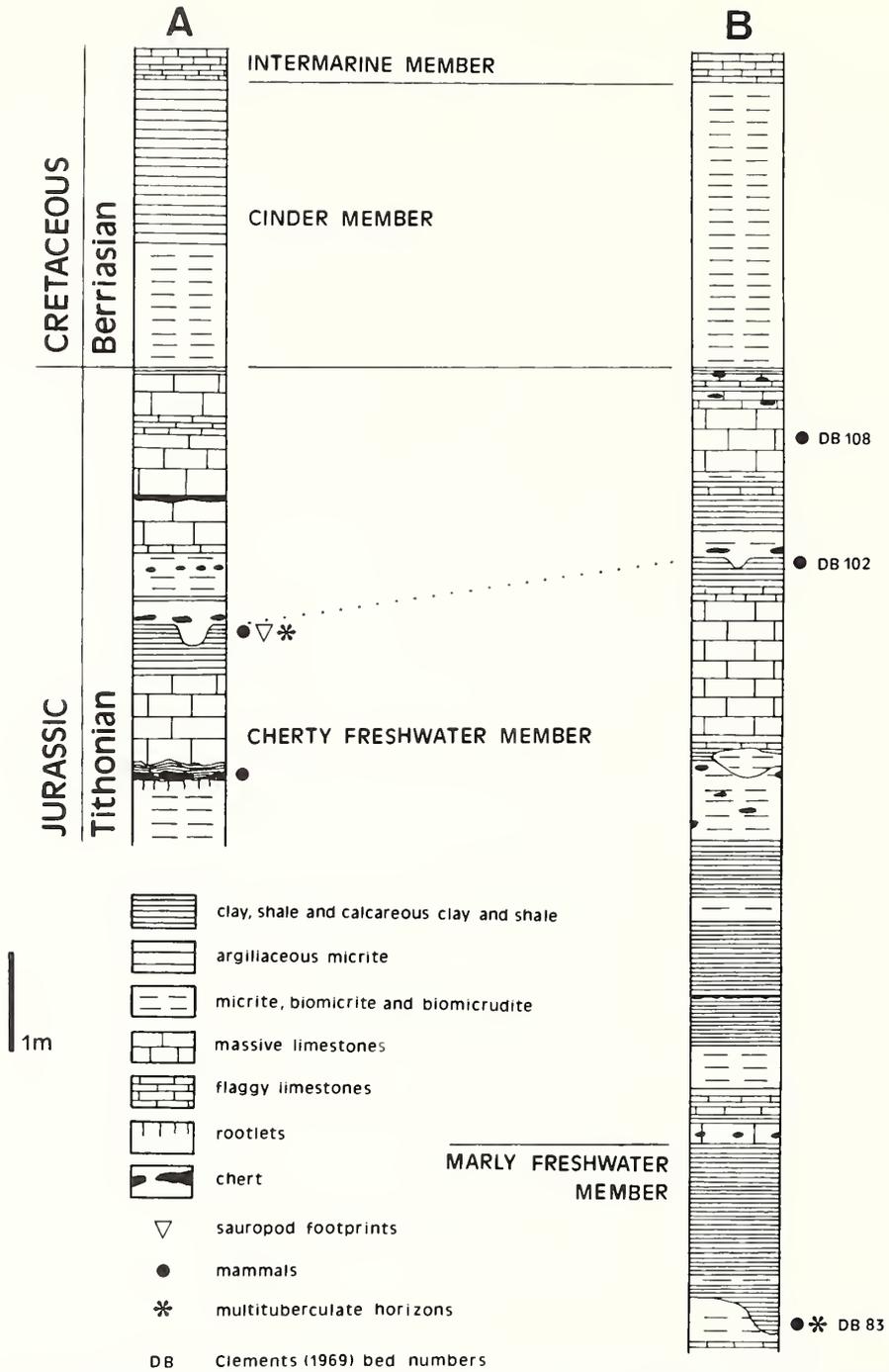
by Z. KIELAN-JAWOROWSKA and P. C. ENSOM

ABSTRACT. The multituberculate suborders: Paulchoffatoidea (Hahn, 1969, new rank) and Plagiaulacoidea (Simpson, 1925), plagiulacoid families Plagiulacidae (with two subfamilies Plagiulacinae and Eobaatarinae) and Allodontidae are re-diagnosed. The Arginbaataridae is assigned to a suborder *incertae sedis*. It is demonstrated that *Plioprion* Cope, 1884, based on lower jaws, is a junior synonym of *Bolodon* Owen, 1871, based on upper jaws. A dentary fragment and twenty-five isolated multituberculate teeth from the Upper Jurassic Purbeck Limestone Formation are described. In one case seven teeth found in one sample are regarded as belonging to the same individual. *Bolodon* and *Plagiulax* Falconer, 1857 are assigned to the Plagiulacinae; the systematic position of *Zofiabaatar* Bakker and Carpenter, 1990 is uncertain; *Ctenacodon* Marsh, 1879 and *Psalodon* Simpson, 1926 are assigned to the Allodontidae. Two taxa are erected: *Gerhardodon purbeckensis* gen. et sp. nov. and *Sunnyodon notleyi* gen. et sp. nov., assigned to the Paulchoffatiidae. An upper premolar with three main cusps, additional cusps, cuspules and pits, is different from any hitherto known and is identified as ?Plagiulacinae gen. et sp. indet. The new taxa are notably smaller than those previously known from the Purbeck Limestone Formation of England, probably the result of the screen-washing method employed in their collection.

THE first significant collection of mammals from the Purbeck Limestone Formation was made by S. H. Beckles from his legendary excavation in 1857 on the cliffs of Durlston Bay, Swanage, Dorset (Text-fig. 1). The excavation was in part due to the encouragement of Richard Owen and was



TEXT-FIG. 1. Map showing the location of the Purbeck Limestone Formation localities mentioned in the text.



TEXT-FIG. 2. Representative stratigraphic sections of the part of the Purbeck Limestone Formation at Sunnydown Farm Quarry (A) redrawn from Ensom (1988), and Durlston Bay (B) based on Clements (1969).

graphically described by Charles Kingsley (1857). Owen had studied the earlier discoveries, which included mammals, made in Durlston Bay by P. B. Brodie and C. Wilcox (Owen 1854). The collection made by Beckles formed the basis of Owen's (1871) account of the Purbeck mammals in the monograph 'Fossil Mammalia of the Mesozoic Formations'.

Since Beckles's pioneering work a number of attempts have been made to relocate his 'Mammal Bed'. Two of these, by H. Willett in 1880 and W. Heap between 1946 and 1949, were recorded by E. W. Willett and H. Willett (1881), and Heap (1958), respectively, who, despite considerable expenditure of time and money, found only five further jaws. From the time of the first discoveries the coastal section has remained the focus of endeavour and further specimens have been recovered by individual collectors and university-based researchers.

The mammalian fauna recovered includes multituberculates (see Hahn 1978*a*, and Clemens and Kielan-Jaworowska 1979 for reviews), which have been described by Falconer (1857, 1862), Owen (1871), and Simpson (1928).

Until now, the principal source of Purbeck mammals is believed to have been the so-called 'Mammal Bed', Bed 83 of Clements (1969), which lies within the Marly Freshwater Member of the Purbeck Limestone Formation (Text-fig. 2). Owen (1871, fig. 4) also records a mammal as coming from the 'Feather Bed', Bed 108 of Clements (1969) which lies in the overlying Cherty Freshwater Member, also of the Purbeck Limestone Formation. Exposures of these strata rarely occur in quarries inland from Durlston Bay. Routine fieldwork in Sunnydown Farm Quarry, Sunnydown Farm, near Langton Matravers, Swanage, Dorset (NGR SY 9822 7880), by one of us (P.C.E., then at the Dorset County Museum) and Dr W. A. Wimbledon (Nature Conservancy Council) during the summer of 1986 led to the discovery of a diverse dinosaur footprint fauna, including the first sauropod tracks to be recorded in the Purbeck Limestone Formation. Subsequent work on the site produced a rich vertebrate fauna of fish, amphibians, reptiles and mammals. Brief accounts of these discoveries were given by Ensom (1987, 1988, 1989).

The collection of Purbeck mammalian teeth so far recovered from the Sunnydown Farm contains members of the Triconodonta, Docodonta, Symmetrodonta, Peramura and Multituberculata. This paper is a description of the multituberculate material so far recovered.

The terminology employed in the present paper is that of Kielan-Jaworowska *et al.* (1987). Abbreviations include: BMNH, Natural History Museum, London (previously British Museum (Natural History)); DORCM, Dorset County Museum, Dorchester, Dorset; PIN, Palaeontological Institute, USSR Academy of Sciences, Moscow; YPM, Yale Peabody Museum, New Haven; I, i, P, p, M, m, upper and lower incisor, premolar and molar, respectively; d, deciduous.

STRATIGRAPHY AND LOCALITIES

Sunnydown Farm Quarry provides an exposure in the upper part of the Cherty Freshwater Member (uppermost Lulworth Beds of Casey 1963) lying below the Cinder Member (Text-fig. 2), the base of which currently marks the boundary of the Jurassic and Cretaceous periods in Southern England (Rawson *et al.* 1978, following Casey 1963).

The Cherty Freshwater Member is represented by a sequence of clays, calcareous clays, biomicrites and biosparrudites. The limestones often contain nodules of chert. The footprints were made in a fine-grained mixture of smectite and illite (West 1988) and are preserved as casts on the base of the overlying cherty biomicrite. This limestone is referred to as the 'Cap' by quarrymen and can be correlated with bed 103 (Clements 1969) in Durlston Bay (NGR SZ 035780) and bed 117 (Ensom 1985) at Worbarrow Tout (NGR SY 869 796). The underlying vertebrate-rich clay can accordingly be correlated with bed 102 in Durlston Bay and 116 at Worbarrow Tout. At the former locality this is *c.* 7.5 m above the 'Mammal Bed' (Clements 1969). Below the underlying 'New Vein' (= bed 101 in Durlston Bay) is a very carbonaceous clay, rich in coprolites and containing a vertebrate fauna which includes mammals, though no multituberculates have so far been recorded.

Following the recovery of mammals from the clay below the 'Cap', samples were taken from the same horizon in Durlston Bay, Suttle's Quarry (NGR SZ 020777) and Lovell's Quarry (NGR SY

980790), 5.25 km and 4 km ESE and 300 m NW of Sunnydown Farm Quarry respectively (Text-fig. 1). All samples collected yielded a similar fauna. The teeth of multituberculates were present in samples from all three quarry sites. Tridactyl dinosaur footprints were present at Durlston Bay, Lovell's and Sunnydown Farm Quarries but not observed at Suttle's Quarry. Sauropod tracks have only been recorded at Lovell's and Sunnydown Farm Quarries. A 1.4 kg sample of clay taken at the equivalent horizon with tridactyl footprints at Worbarrow Tout (11 km WNW) yielded some vertebrate remains though no mammalian remains were observed.

PALAEOENVIRONMENT

The conditions that existed during the deposition of the Purbeck Limestone Formation were generally brackish or freshwater, though there are occasional appearances of an almost normal marine fauna, e.g. in the Cinder and Scallop Members. With a view to establishing the nature of the environments the abundant invertebrate faunas have been the subject of a number of studies.

Examples are the papers on ostracods and faunicycles by Anderson (1985) and the palaeoecology of the molluscs and their relationship to ostracod biostratigraphy by Morter (1984). Carbon isotope ratios were used by Allen and Keith (1965) to study palaeosalinity in these strata.

West (1988) gives a detailed description of both the clay and the overlying limestone at Sunnydown Farm Quarry drawing the conclusion that they were deposited in environments with 'very low' and 'low' salinities respectively. West suggests that the clays represent extensive mud flats bordering a freshwater lake. The presence of dinosaurs is evident from the considerable number of footprints recorded at all sites but one. This would suggest emergent or at least shallow water deposition for the clays. No evidence of mudcracking has been noted in the clays or on the base of the overlying 'Cap'. The remarkable similarities between sediment type and palaeontology observed at the sites on this strike exposure of 16 km give some idea of how extensive this freshwater lake may have been.

The presence of reworked vertebrate material from earlier sediments cannot be ruled out; significant quantities of silicified wood are present in the samples and this is considered to have been derived. The presence within individual samples of teeth, which have come from the same dentition, points to at least some of the material suffering minimal transport within the environment of deposition.

MATERIALS AND METHODS

The samples collected at Sunnydown Farm Quarry consisted of approximately 3 tonnes of clay dug from the floor of the quarry after the 'Cap' bed had been removed. Normally the top 2–4 cm were collected in samples up to c. 35 kg. Each sample was from beneath one or more slabs of the 'Cap'. The slabs were mapped and numbered and the sample sacks carried the same numbers. Single sample numbers were allocated to each sack. Samples were kept separate so that any associations of bones and teeth would be preserved.

The fissured limestone overlying the clay and steep quarry faces on three sides resulted in inevitable contamination of samples though every care was taken to keep this to a minimum. In addition the fractured 'Cap' often spalled lower surfaces which were removed with the clay samples and only recovered later as the coarse fraction during sieving.

The samples were removed from the site and dried before sieving. The first samples were processed through 20 cm brass test sieves down to aperture size of 0.3 mm. A bulk processing machine constructed to the design of Ward (1981) permitted the remaining samples to be sieved with great efficiency through a stainless steel mesh with an aperture size of 0.33 mm. Approximately 5% of the original sample remained after sieving. The residues were graded and then picked under a binocular microscope using a gridded sorting tray. Only a small proportion of the total sample has so far been picked.

The descriptions that follow are based mostly on the new collection housed in the Dorset County Museum, and the specimens described are from the Cherty Freshwater Member of the Purbeck Limestone Formation from three localities: Sunnydown Farm and Lovell's Quarries, both near Langton Matravers, and Suttle's Quarry near Swanage. The specimens from the old collection from the 'Mammal Bed', Marly Freshwater Member, Durlston Bay near Swanage (deposited in the BMNH) are discussed mostly under Comparisons, but scanning electron micrographs of the epoxy resin casts of some of them, and drawings, are published for comparative purposes.

We restrict the synonymies to publications in which the specimens are illustrated.

DIAGNOSES OF SUPRAGENERIC TAXA

The high-level taxonomy of the Late Jurassic and Early Cretaceous multituberculates are misleading. We are aware that the suborders Paulchoffatoidea and Plagiaulacoidea and some of the families assigned to them are possibly paraphyletic groups; however, because of the fragmentary nature of the material we have found it impossible to treat them cladistically. We redefine the suborders Paulchoffatoidea (new rank) and Plagiaulacoidea and the families and subfamilies of the latter, as far as the new material described in this paper allows us to do so. We hope that this material will help in future to recognize the true relationships between these suborders and families.

In the diagnoses given below we use the following abbreviations: All., Allodontidae; Arg., Arginbaataridae; Eobn., Eobaatarinae; multis, multituberculates; Paul., Paulchoffatoidea; Plag., Plagiaulacoidea; Plagn., Plagiaulacinae; Plagd., Plagiaulacidea; Ptil., Ptilodontoidea; Taen., Taeniolabidoidea.

Suborder PAULCHOFFATOIDEA (Hahn, 1969), new rank

Revised diagnosis. Dental formula: 3,1–0,5–4,2/1,0,4–3,2. Differs from Plag. (except Plagn.), Ptil. and Taen. in having I3 3- to 4-cusped. Differs from Plag., Ptil. and Taen. in having M1 without posterolingual ridge or third row of cusps. Differs from Plag. in having M2 with 2–3:3–6 cusps and no anterobuccal wing. Differs from all other multis in having p1–p3 in buccal view oval or quadrangular rather than triangular; p3 almost as long as p4, p3 with a row of buccal cusps. Shares with Plag. parallel-sided p4 (plesiomorphy), but differs in having only 4 serrations in p4. Differs from Plagd., Ptil. and Taen. in having m1 with anterior cingulum with cusps and enlarged buccal cusp. Differs from all multis in having m2 basin-like, with only one anterolingual cusp and in having a rudimentary coronoid. Differs from Ptil. and Taen. (whether from Plag. unknown) in having enamel tentatively referred to as ?aprismatic.

Stratigraphic and geographical range. Middle Jurassic–Early Cretaceous of Europe, Early Cretaceous of North Africa.

Remarks. We assign to this suborder all the taxa from the Late Jurassic of Portugal assigned by Hahn and Hahn (1983) and Hahn (1987, 1988) to the Paulchoffatiidae: isolated teeth identified by Hahn and Hahn (1983) as Paulchoffatiidae, gen. et sp. indet. 3, and tentatively Paulchoffatiidae?, gen. et sp. indet. 4, from the Middle Jurassic of England; *Gerhardodon* gen. nov. and *Sunnyodon* gen. nov. from the Purbeck Limestone Formation of England; *Parendotherium* Crusafont-Pairo and Adrover from the Early Cretaceous of Spain and Hahnodontidae Sigogneau-Russell from the Early Cretaceous of Morocco (Sigogneau-Russell 1991). *Mojo* Hahn, Lepage and Wouters, 1987 from the Upper Triassic of Belgium is poorly known and is not included here. A discussion on the taxonomy of the paulchoffatoid taxa is beyond the scope of the present paper.

Suborder PLAGIAULACOIDEA (Simpson, 1925), Hahn, 1969

Revised diagnosis. Dental formula: 3,0,5–4,2/1,0,4–3,2. Differs from some Paul., Ptil. and Taen. in having I3 2- or 3-cusped. Differs from Paul. in having M1 with an incipient wing-like posterolingual

ridge and smaller number of cusps in M2 (2–3:3). Differs from Paul. but shares with other multis p1–p3 triangular in buccal aspect and p3 without buccal cusps. Shares with Paul. parallel-sided p4 (plesiomorphy), but differs in having p4 1.5–2 times longer than p3 rather than subequal in length and greater number (5–8) serrations on p4. Differs from Paul. but shares with other multis m2 with a middle groove. Differs from Ptil., Taen. and Arg. in having discrete cusps (2–3) in m2 only in a lingual row and incipient cusps in buccal row in Plagd. (more discrete buccal cusps in All.). Differs from Paul. but shares with other multis lack of coronoid bone in known taxa.

Families. Plagiaulacidae Gill, 1872; Allodontidae Marsh, 1889.

Stratigraphic and geographical range. Late Jurassic to Early Cretaceous of Europe, Late Jurassic of North America, Early Cretaceous of Asia.

Family PLAGIAULACIDAE Gill, 1872

Revised diagnosis. Differs from All. in having I3 3-cusped (plesiomorphy); P4 and P5 relatively longer in relation to M1, P4 with a row of buccal cuspules; posterolingual wing in M1 relatively larger; anterobuccal incipient cingulum on M2; p4 about twice as long as p3, with 6–8 serrations; m1 without an enlarged buccal cusp; m2 without obvious buccal cusps, separated only lingually by irregular grooves. Differs from all other multis in having a characteristic ‘ornamentation’ of comma-shaped pits and grooves. Differs from All. and most other multis in a tendency of basal parts of molar cusps to coalesce in peripheral aspect.

Subfamilies. Plagiaulacinae Gill, 1872; Eobaatarinae Kielan-Jaworowska, Dashzeveg and Trofimov, 1987.

Geographical and stratigraphic range. Late Jurassic to Early Cretaceous of Europe; ?Late Jurassic of North America; Early Cretaceous of Asia.

Subfamily PLAGIAULACINAE Gill, 1872

Revised diagnosis. More plesiomorphic subfamily than Eobn., from which it differs in having P5 with buccal cuspules; M1 with smaller posterolingual ridge; lower incisor (in most taxa) with complete enamel, but limited enamel in North American ‘plagiaulacoid’; p4 as a rule with a row of buccal cusps (but single cusp in *Bolodon osborni*); m1 and m2 symmetrical; enamel referred to as ?preprismatic (not gigantoprismatic).

Genera. *Plagiaulax* Falconer, 1857; *Bolodon* Owen, 1871; ?new genera to be erected for ‘*Bolodon*’ *falconeri*, ‘*Bolodon*’ *elongatus* and ?*Zofiabaatar* Bakker and Carpenter, 1990.

Geographical and stratigraphic range. Late Jurassic Europe, ?Late Jurassic of North America.

Remarks. *Plioprion* Cope, 1884 was erected as a monotypic genus to include *Plagiaulax minor* (Falconer, 1857), a species classified by us as *Bolodon minor* (Falconer). We demonstrate that *Ctenacodon ?minor* (Falconer) (Simpson 1928, p. 40, *recte*: *Plioprion ?minor*) is a junior synonym of *Bolodon osborni*. *Plioprion* Cope, 1884 is therefore a junior synonym of *Bolodon* Owen, 1871. Two more species were assigned to *Plioprion* by Hahn and Hahn (1983): *Plioprion ?dawsoni* known from single m2 that according to Clemens (1963) may not be a mammal tooth, and *Plioprion ?falconeri* (Owen, 1871) which is a lower jaw taxon. As the upper teeth of this species are not known, it cannot be demonstrated whether it belongs to *Bolodon* or to a new genus, and we refer to it as ‘*Bolodon*’ *falconeri*. *Zofiabaatar* (Bakker and Carpenter, 1990) from the Morrison Formation of North America, assigned to an uncertain family, is related to the Plagiaulacidae in having p3 reduced in length, as long as a half of p4 (plagiaulacid apomorphy), but shares with Allodontidae a paulchoffatiid-like structure of m1 (plesiomorphy); it is not known whether it shares other features

characteristic of European plagiaulacines. A new subfamily or family should be erected for it. Another North American Morrison Formation 'plagiaulacoid' with limited enamel on lower incisor, recently reported by Engelmann *et al.* (1990), may also be a member of the Plagiaulacidae.

Subfamily EOBAATARINAE Kielan-Jaworowska, Dashzeveg and Trofimov, 1987

Revised diagnosis. Differs from most Plagn. (except North American 'plagiaulacoid') in having limited enamel on the lower incisor, m1 and m2 asymmetrical, shorter lingually than buccally, P5 without buccal cuspules and M1 with more prominent posterolingual ridge. Differs from Paul., Plagn., and Ptil., but shares with Arg. and Taen. gigantoprismatic enamel.

Genera. *Loxaulax* Simpson, 1928; *Eobaatar* Kielan-Jaworowska, Dashzeveg and Trofimov, 1987; ?*Monobaatar* Kielan-Jaworowska, Dashzeveg and Trofimov, 1987.

Geographical and stratigraphic range. Early Cretaceous of Europe and Asia.

Remarks. Kielan-Jaworowska *et al.* (1987) assigned the Eobaataridae to the Taeniolabidoidea because of the limited enamel on the lower incisor and gigantoprismatic enamel regarded as taeniolabidoid apomorphies. They made it clear, however, that the Eobaataridae is very close to the Plagiaulacidae. Limited enamel on the lower incisor has been found recently in a 'plagiaulacoid' from North America (Engelmann *et al.* 1990) and cannot be regarded as a taeniolabidoid apomorphy. Enamel structure in multituberculate taxa is so far poorly understood, and one cannot be sure whether one can make systematic assignments on its basis. Our present comparisons show that the Eobaataridae (*sensu* Kielan-Jaworowska *et al.* 1987) and the Plagiaulacinae (as defined herein) are closer to each other than any of them is to the Allodontidae. Therefore we assign the Eobaatarinae (new rank) to the Plagiaulacidae.

Family ALLODONTIDAE Marsh, 1889

Revised diagnosis. Differs from Plagd. in having 2-cusped I3; P4 and P5 relatively shorter in relation to the length of M1 (plesiomorphy), with one or no buccal cuspules; posterolingual ridge in M1 very small; anterobuccal cingulum in M2 uncertain, possibly lacking; p4 about 1.5 times (instead of twice) as long as p3, with 5–6 serrations and a row of buccal cusps; m1 somewhat Paul.-like in having an enlarged middle cusp in buccal row; m2 with 3: 3 cusps, cusps more discrete than in Plagd., in buccal row clearly separated on lingual aspect, possibly coalesced buccally. No grooves and pits on molars characteristic of Plagd.

Genera. *Ctenacodon* Marsh, 1879; *Psalodon* Simpson, 1926.

Stratigraphic and geographical range. Late Jurassic of North America.

Remarks. The type genus of the Allodontidae is *Allodon* Marsh, 1881, a junior subjective synonym of *Ctenacodon* Marsh, 1879.

Suborder *incertae sedis*

Family ARGINBAATARIDAE Hahn and Hahn, 1983

Revised diagnosis. Differs from all multis in having very large p4 with limited enamel, rotating anteroventrally during the ontogeny over the worn p3 and p2, which disappear. Shares with Paul., some Plagn. and Ptil. lower incisor completely covered with enamel (plesiomorphy). Shares with some Paul. presence of canine (plesiomorphy). Differs from Plgd. and shares with All. P4 and P5 without buccal cuspules. Differs from Plagd. in having distinct conical cusps on lower and upper molars. Shares with Plag. incipient posterolingual ridge in M1. Differs from Plgac. in having molar cusps smooth or weakly striated. Shares with Eobn. and Taen. gigantoprismatic enamel.

Genus. *Arginbaatar* Trofimov, 1980.

Stratigraphic and geographical range. Early Cretaceous of Asia.

Remarks. Kielan-Jaworowska *et al.* (1978) assigned the Arginbaataridae to the ?Plagiaulacoidea, but stated that it differs in the structure of p4 from the plagiaulacoids and from all other multituberculates, warranting inclusion in a suborder of its own. As the upper and lower jaws of Arginbaataridae have not been found together and were only tentatively matched by Kielan-Jaworowska *et al.* (1987), we think that the erection of a new suborder for the Arginbaataridae would be premature.

Discussion

The apomorphies of the Paulchoffatoidea are: ?the structure of I3 with 3–4 cusps; the structure of m1 with anterior cingulum with cuspules and two rows of cusps in which one buccal cusp is clearly enlarged, and the structure of m2 which is basin-like with only one antero-lingual cusp. These types of teeth have not been so far found in the Haramiyiidae, although *Haramiya*, group I bis (Sigogneau-Russell 1989 and references therein), resembles m1 of Paulchoffatoidea. As demonstrated by Krause and Hahn (1990), all paulchoffatiids (including Paulchoffatiinae) have the crown of M2 offset lingually relative to that in M1, as is characteristic of plagiaulacids and all other multituberculates.

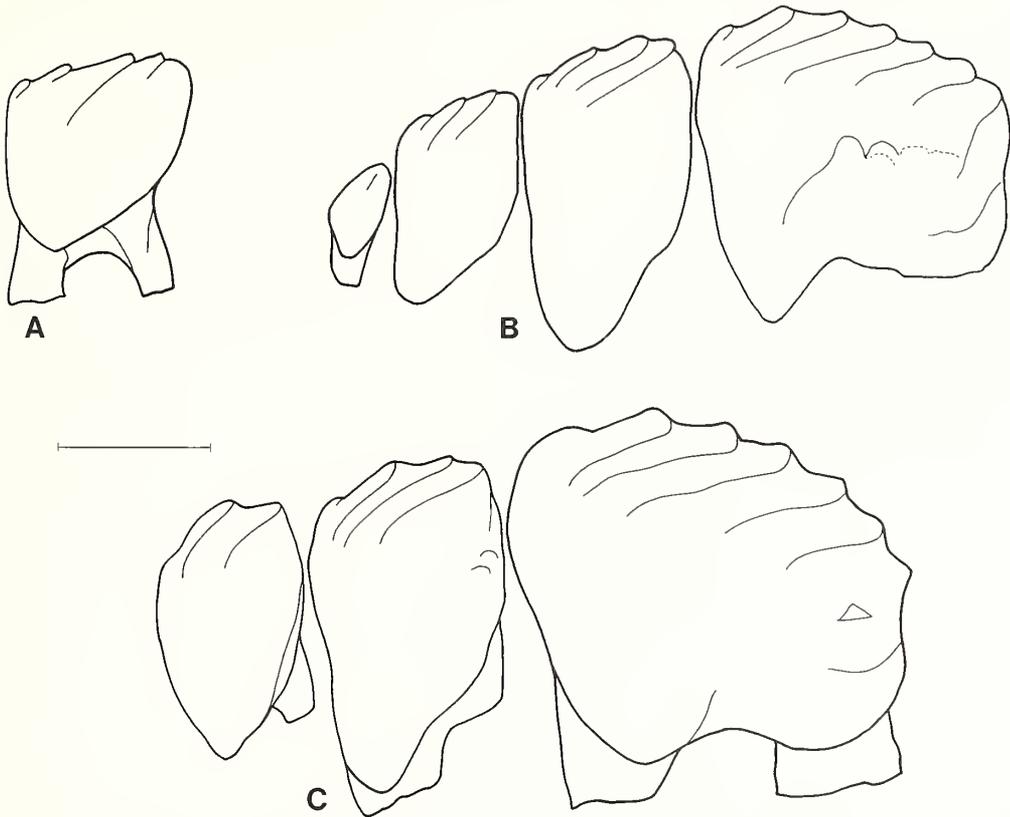
Some of the paulchoffatoid apomorphies are retained in plagiaulacoid taxa, e.g. three-cusped I3 in Plagiaulacidae and somewhat paulchoffatoid-like m1 in Allodontidae, and are primitive characters in these groups.

The apomorphies of the Plagiaulacoidea are: the triangular shape of p1–p3, disappearance of buccal cusps in p3, increase in the number of serrations in P4, increase of the length of p4 in relation to p3, appearance of the middle groove in m2, appearance of the postero-lingual ridge in M1 and reduction of the number of cusps in M2. M1 in Paulchoffatoidea has only two rows of cusps, although in *Henkelodon* (see Hahn 1977, fig. 10) there appears to be a tiny, although uncertain posterolingual ridge, not so obvious as in Plagiaulacoidea (this tooth was referred to by Hahn 1977 as M2, which is M1 – an opinion with which Professor Gerhard Hahn now agrees, personal communication).

The apomorphies of the Plagiaulacidae are: an increase of the length of P4 and P5 in relation to the length of M1, an appearance of an incipient anterobuccal wing in M2, appearance of irregular grooves that divide the buccal rounded ridge in m2 (Text-fig. 4), the ‘ornamentation’ of comma-shaped pits and grooves on the molars. In the structure of the upper premolars and molars the Plagiaulacidae are perhaps most reminiscent of the paulchoffatiid *Henkelodon* (assigned to the Kuehneodontinae, see Hahn 1977), which has a row of buccal cuspules on P4 and P5 in addition to the two rows of cusps. The M2 of *Henkelodon* is not known. Another paulchoffatoid genus that has P4 and P5 similar to those in the Plagiaulacidae is *Kielanodon*, assigned by Hahn (1987) to an uncertain subfamily in the Paulchoffatiidae. The upper molars and lower jaw of *Kielanodon* are not known.

The apomorphies of the Allodontidae are: two-cusped I3 and the presence of two rows of distinct cusps in m2. There are three buccal cusps in m2 in the Allodontidae, separated medially, but it is not certain whether they coalesce buccally. As far as the structure of the lower premolars is concerned the Allodontidae is more plesiomorphic than the Plagiaulacidae, as the shortening of the length of p3 in relation to the length of p4 is smaller than in the Plagiaulacidae. In Allodontidae P4 and P5 are relatively shorter in relation to the length of M1 than in the Plagiaulacidae, which is also a plesiomorphic feature, characteristic of most paulchoffatoid taxa. m1 in Allodontidae is also more plesiomorphic than in the Plagiaulacidae in having an enlarged second cusp of the buccal row (similar to that in Paulchoffatoidea), while in the Plagiaulacidae the two buccal cusps in m1 are of subequal size.

The grooves on molars characteristic of the Plagiaulacidae are also characteristic of (but less



TEXT-FIG. 3. Camera lucida drawings of the lower premolars, buccal view. A, *Gerhardodon purbeckensis* gen. nov., sp. nov.; left ?p3; DORCM GS 19; holotype. B, *Bolodon minor* (Falconer); right p1-p4; reversed, based on epoxy resin cast of BMNH 47729. C, *Bolodon osborni* Simpson; left p2-p4; p4 based on epoxy resin cast of left tooth BMNH 48399, p3 on DORCM GS 202, p2 on DORCM GS 204. Scale = 1 mm.

obvious in) the Argentinean Late Cretaceous *Ferugliotherium* (Bonaparte 1986). The peripheral (buccal, posterior, lingual and possibly anterior) cusps on M1 of *Ferugliotherium* tend to coalesce basally as characteristic of the Plagiaulacidae. The transverse grooves also occur in the molars of ptilodontoids; these are more regularly distributed than in the plagiaulacines and eobaatarines and there is little or no coalescence. In Taeniolabidoidea such grooves are generally absent; even when present they are not as well developed as in ptilodontoids, except perhaps in *Microcosmodon*.

SYSTEMATIC PALAEOLOGY

Suborder PAULCHOFFATOIDEA Hahn, 1969, new rank

Family ?PAULCHOFFATIIDAE Hahn, 1969

Subfamily *incertae sedis*

Genus GERHARDODON gen. nov.

Etymology. In honour of Professor Gerhard Hahn (Marburg) in recognition of his work on multituberculates and Greek *odous*, meaning tooth.

Diagnosis. As for the only species *Gerhardodon purbeckensis* sp. nov.

Gerhardodon purbeckensis sp. nov.

Plate 1, figs 1–5; Text-fig. 3A.

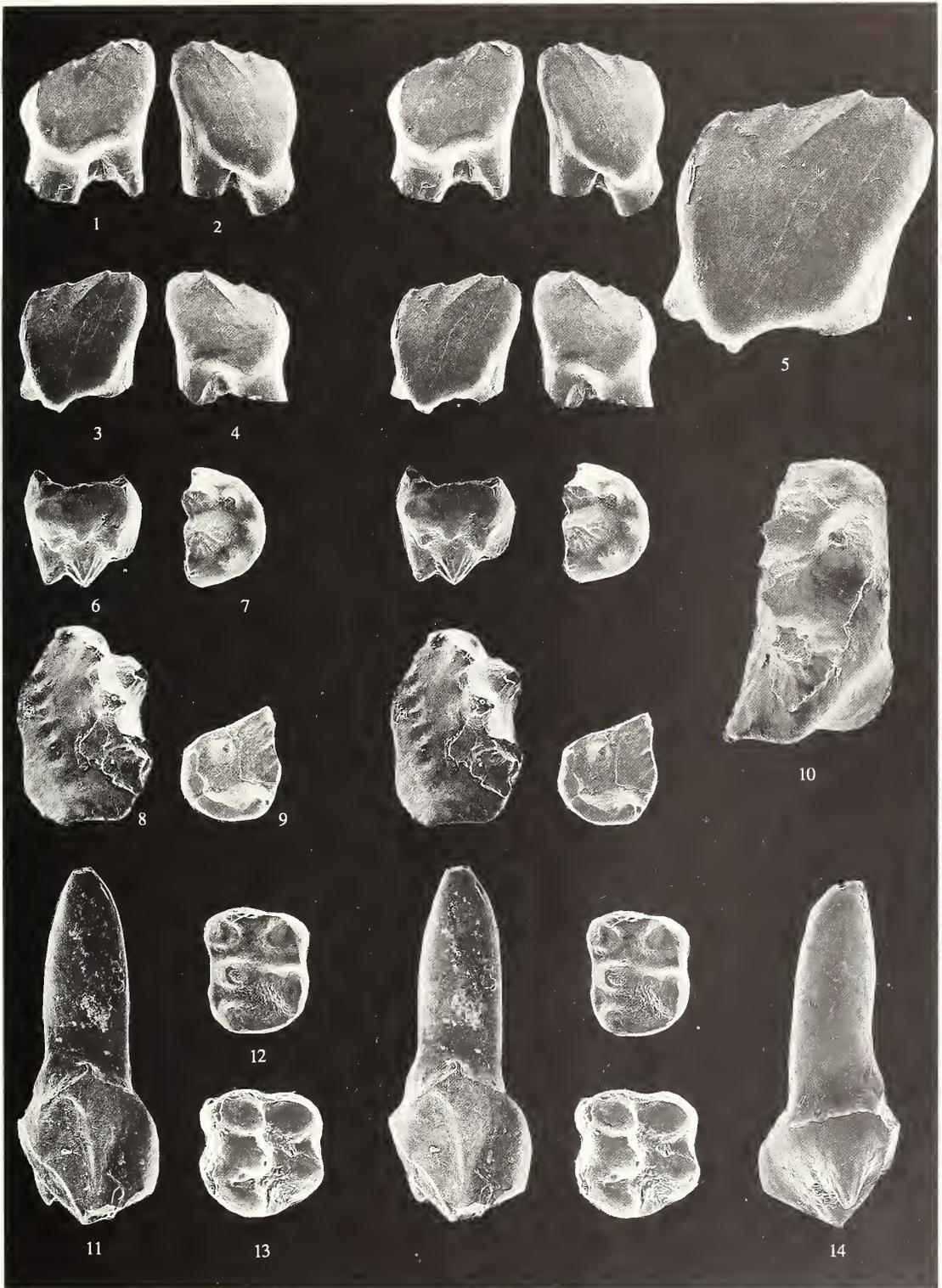
Etymology. Occurring in the Purbeck Limestone Formation.*Holotype.* DORCM GS 19 (sample 95), left ?p3 (Pl. 1, figs 3–5; Text-fig. 3A).*Type horizon and locality.* Purbeck Limestone Formation, Cherty Freshwater Member, Sunnydown Farm Quarry near Langton Matravers.*Additional material.* There are two more specimens in the same sample (no. 95) that may belong to the same individual: DORCM GS 20, a right ?p3 is almost identical to DORCM GS 19 and conspecific with it; DORCM GS 21, the anterior part of a ?right P4 or P5 is described under cf. *Gerhardodon purbeckensis*.*Diagnosis.* ?p3 differs from p3 of *Kuehneodon* and *Guimarotodon* (and possibly from other paulchoffatiid taxa in which this tooth is abraded) in having almost transversal (rather than vaulted) upper margin, in being roughly trapezoidal and slightly longer than high, rather than taller and roughly oval or quadrangular. Differs from p3 in other paulchoffatiid genera in having the distance between the second and third serrations greater than between the others and the third ridge the longest. Buccal cusps which occur in p3 of Portuguese paulchoffatiids are absent.*Description.* Left ?p3 DORCM GS 19, in buccal aspect is irregular, roughly trapezoidal, taller anteriorly than posteriorly, 1.0 mm long and 0.9 mm high. The upper margin is nearly straight, the exodaenodont lobe weakly pronounced. There are four serrations and four weak ridges, the first in both buccal and lingual aspects being hardly discernible. The distance between the second and the third serration is one and a half times longer than between the first and the second and twice as long as between the third and fourth. The ridge of the third serration in both aspects is notably longer and more prominent than the others. The lingual side is less tall than the buccal, roughly oval, and elongated longitudinally. Right ?p3 DORCM GS 20, is almost identical with DORCM GS 19, differing only in having a slightly more elongated exodaenodont lobe; the tooth is 0.9 mm long and 1.0 mm high in buccal aspect.*Comparisons.* The right and left lower premolars of *Gerhardodon purbeckensis* are identified as ?p3, as they do not bear buccal cusps (although buccal cusps are present in p3 of all adequately known Portuguese paulchoffatiids, personal communication from Professor Gerhard Hahn). This ?p3 is closer to p3 of the Paulchoffatoidea than Plagiaulacoidea in being roughly trapezoidal rather than triangular and short rather than tall. In most paulchoffatoid taxa (Hahn 1969, 1978b, 1978c, 1987) the upper margin of p3 has been abraded. It has been well preserved in *Kuehneodon uniradiculatus*

EXPLANATION OF PLATE I

All specimens are from the Purbeck Limestone Formation, Cherty Freshwater Member. Specimen in figure 9 is from Suttle's Quarry near Swanage; all others are from Sunnydown Farm Quarry near Langton Matravers. All are scanning electron micrographs; figure 5 is $\times 40$; all others $\times 20$. Except where stated, all teeth in occlusal view are oriented with anterior margin up.

Figs 1–5. *Gerhardodon purbeckensis* sp. nov. 1–2, DORCM GS 20; right ?p3, lingual and buccal views. 3–5, DORCM GS 19; holotype; left ?p3, buccal, lingual and buccal views. All except figure 5 are stereo-pairs. Figs 6–10, 12–13. cf. *Gerhardodon purbeckensis* sp. nov. 6–7, DORCM GS 21; anterior part of the ?right upper premolar, anterior and occlusal views (in figure 7 anterior margin is to the right). 8, 10, DORCM GS 11; left ?P5, occlusal and buccal views. 9, DORCM GS 15; anterior part of the right m1 (anterior margin downwards). 12–13, DORCM GS 9; left ?M1, occlusal and oblique lingual views. All except figure 10 are stereo-pairs.

Figs 11, 14. ?Plagiaulacinae, gen. et sp. indet. DORCM GS 14; left I3, posterior and anterior views; figure 11 is a stereo-pair.



KIELAN-JAWOROWSKA and ENSOM, *Gerhardodon*, ?*Plagiaulacinae*

(Hahn 1978*b*, text-fig. 9), in dp3 or *Kuehneodon dietrichi* (Hahn 1978*c*, text-fig. 1) in dp2–dp4 of Paulchoffatiidae gen. et sp. indet. (Hahn 1987, text-fig. 6), in *Guimarotodon leiriensis* (Hahn 1987, text-fig. 5) and dp3 of Paulchoffatiidae gen. et sp. indet. (Hahn 1987, text-fig. 6). In all these species p3, p4 and dp2, dp3 and dp4, when known, bear buccal cusps. It is not known whether *Paulchoffatia* had premolars with straight or slightly vaulted upper margins (Kühne 1961; Hahn 1969, 1978*b*). *Paulchoffatia* differs from other paulchoffatiid genera in having a large p2 similar to p3. It is possible that ?p3 of *G. purbeckensis* is p2 of *Paulchoffatia* type or even p4, which has lost the buccal cusps.

cf. *Gerhardodon purbeckensis* sp. nov.

Plate 1, figs 6–10, 12–13; Text-figs 5D, 6C

Material. Several isolated teeth in the collection from the Cherty Freshwater Member of the Purbeck Limestone Formation are similar to those of the Paulchoffatoidea, rather than Plagiaulacoidea. They fit the size of the lower premolars of *Gerhardodon purbeckensis* and may be conspecific with it. We assign them tentatively to *G. purbeckensis*. These are: DORCM GS 15 (sample 05) from Suttle's Quarry near Swanage, anterior part of the right m1, and three specimens from Sunnydown Farm Quarry near Langton Matravers: DORCM GS 21 (sample 95) anterior part of a ?right upper premolar; DORCM GS 11 (sample 4) left P4 or P5; DORCM GS 9 (sample 28), left ?M1.

Description. Right m1. DORCM GS 15 (Pl. 1, fig. 9) only the anterior part of the crown without roots has been preserved. Along the anterobuccal rim there are three cusps, heavily worn in this specimen, the first of which is the largest and is transversely elongated. The next cusp is smaller, the most posterior one is the smallest. Only the first (rounded) cusp of the buccal row has been preserved. This is situated opposite the third of the above described anterobuccal cusps. On the anterolingual margin there is a rounded cusp, worn buccally, the worn surface being confluent with the worn surface of the first anterobuccal cusp. There are two cusps in the lingual row. To the rear of the first lingual cusp the oblique ridges extend from the lingual margin towards the middle of the tooth.

Upper premolars. DORCM GS 21 (Pl. 1, figs 6–7), anterior part of the ?right upper premolar without roots; the preserved part is 0.9 mm wide. There are three small cusps along the anterior margin, two main cusps (which may correspond to the anterior cusps of the middle and buccal rows, the middle being the larger) and possibly one more, smaller and broken lingual cusp. We recognize the rim with three cusps as the anterior one by comparison with P5 of *Paulchoffatia delgadoi* (Hahn 1969) and *Henkelodon naias* (the latter referred to by Hahn 1977, text-fig. 10, as M1) and because this side bears a distinct oval facet (Pl. 1, fig. 6), suggesting the presence of a tooth in front of it. We believe that the tooth is the right one by comparison with *Henkelodon* and with left ?P4 or P5 (DORCM GS 11) described below. In both DORCM GS 21 and DORCM GS 11 there are three rows of cusps and the cusps in the lingual row are smaller than those in the middle row.

Left ?P4 or P5 (DORCM GS 11), (Pl. 1, figs 8, 10; Text-fig. 5D), has its roots broken off; it is 1.5 mm long and 0.9 mm wide; the tooth has a broken anterolingual corner and is badly damaged. The cusp formula is 1:3:27. The row of lingual cusps is directed obliquely upwards when the middle row is placed horizontally. The tooth originally had a row of ?seven small lingual cusps, which are worn out and small oval transverse grooves are preserved between them. There are three large cusps in the middle row, the ultimate one being larger than the first two, which are strongly worn lingually. There is one large cusp in the buccal row, placed opposite the groove between the first and second cusps of the middle row. Along the anterior margin two worn cusps are preserved, but as the anterolingual corner of the tooth is broken off, one can presume that there were originally three cusps as in DORCM GS 21. The enamel is not preserved on the lingual part of the tooth; it is retained on the cusps of the middle row (although worn on the lingual side of the first two cusps) and on the buccal cusp. The cusps on which enamel is preserved are ornamented with radiating ridges. DORCM GS 11 and DORCM GS 21 because of the different state of preservation appear very different at first sight. However, in both teeth there are possibly three minute anterior cusps, and three rows of cusps, the lingual being the smallest. DORCM GS 11 and GS 21 may either represent the same tooth, or one may be P4 and the other P5.

Left ?M1 (DORCM GS 9), (Pl. 1, figs 12–13; Text-fig. 6C), has the roots broken; it is 1 mm long lingually, 0.95 mm long buccally, and 0.85 mm wide. The tooth is roughly rectangular in occlusal view, has rounded angles, and a narrow rim around the first lingual cusp. The cusp formula is 2:3. All five cusps are of almost the same size; the posterior one in the lingual row is slightly smaller. The buccal cusps are worn lingually, the lingual ones subhorizontally. The lingual margin opposite the groove between the penultimate and ultimate

lingual cusps is slightly convex lingually, but an incipient lingual ridge, characteristic of M1 in the Plagiaulacidae, is not developed.

Comparisons. We identify the fragmentary tooth DORCM GS 15 as the first lower molar, because of its similarity to these teeth in the Paulchoffatiidae (Hahn 1987), characterized by a row of anterobuccal cuspules and large first buccal cusp. Its attribution to cf. *Gerhardodon purbeckensis* is entirely tentative, based on size only. The upper premolar DORCM GS 21 was found in the same sample as the holotype specimen (lower premolar) of *Gerhardodon purbeckensis*; as it fits the holotype specimen in size, it may belong to the same individual, and if so, the other upper premolar DORCM GS 11 may also belong to *G. purbeckensis*. These P4 or P5 are reminiscent of P4 and P5 of *Pseudobolodon oreas* (Hahn 1977; Text-fig. 2), and *Henkelodon naias* (Hahn 1977, text-fig. 10, identified by Hahn as P5 and M1), in having three rows of cusps, the single cusp and cuspules in the buccal row being situated anterobuccally. The lingual cusps of P4 in *P. oreas* and *H. naias* are worn, but there were possibly four in *P. oreas*, and as many as seven in cf. *G. purbeckensis*.

DORCM GS 9 is tentatively identified as M1, because like the M1 of *Henkelodon naias* (referred to by Hahn 1977, text-fig. 10, as M2) it has a rectangular shape, two parallel rows of cusps and a small lingual convexity in the posterior part of the lingual margin, which is not developed into a ridge as in the Plagiaulacidae. DORCM GS 9 may be shown to be a right m1 rather than left M1.

Genus SUNNYODON gen. nov.

Etymology. From the locality Sunnydown Farm and Greek *odous*, meaning tooth.

Diagnosis. The same as for the only known species *Sunnyodon notleyi* sp. nov.

Sunnyodon notleyi sp. nov.

Plate 5, figs 3, 10; Text-fig. 5F

Etymology. Named in honour of Mr and Mrs R. F. Notley, the owners of Sunnydown Farm Quarry.

Holotype. DORCM GS 18 (sample 011) right ?P5 (Pl. 5, figs 3, 10; Text-fig. 5F).

Type horizon and locality. Purbeck Limestone Formation, Cherty Freshwater Member, Lovell's Quarry near Langton Matravers.

Diagnosis. ?P5 resembles P5 and P4 of *Paulchoffatia*, *Kuehneodon* and *Kielanodon* in having only two rows of cusps, but differs in having two cusps of the buccal row arranged symmetrically in the middle of the tooth length, and only one anterior and one posterior buccal cuspule. Differs from all known paulchoffatiid taxa in the presence of an incipient lingual ridge, with a small cuspule. In number and arrangement of cusps it resembles *Kielanodon*, but differs from P4 and P5 of that genus in being narrower, roughly oval in shape, and in having differently arranged cusps in the buccal row. Cusp formula 2:4:ridge.

Description. The species to which ?P5 DORCM GS 18 belongs was very small. ?P5 is 0.94 mm long lingually, 0.87 mm long measured along the middle of the buccal row of cusps and 0.67 mm wide across the level of the lingual ridge. There are two cusps of subequal size in the buccal row and two cuspules, one situated anterolingually with regard to the first cusp and the other posterolingually to the second cusp. The four cusps in the lingual row increase in size posteriorly. There is a minute cuspule placed anteriolingually to the first lingual cusp. All the cusps and buccal cuspules are ornamented with radiating ridges. Opposite the furrow between the penultimate and ultimate lingual cusps there is an incipient lingual ridge with a small, pointed cuspule in the middle.

Comparisons. *Sunnyodon notleyi* resembles P4 and P5 of *Kielanodon hopsoni* (Hahn 1987, text-fig. 7) in having four lingual and two buccal cusps. Additional cuspules in the buccal row are arranged in *K. hopsoni* posterior to the buccal cusps, while in *S. notleyi* one is anterior and one is posterior. The unusual feature of this tooth is the presence of an incipient lingual posterior ridge with a single cuspule, a ridge similar to those in M1 in plagiulacoids. However, we think that this tooth is P5 or P4, rather than M1 because of the conical shape of the cusps with radiating ridges, which are characteristic of the paulchoffatoid and plagiulacoid upper premolars and not of the molars. An incipient third lingual ridge similar to that in M1 in plagiulacoids has not been described as yet in paulchoffatoid and plagiulacoid upper premolars, but in almost all previously known paulchoffatoid upper premolars with two rows of cusps, the lingual side has been abraded. DORCM GS 18 does not belong to *Gerhardodon purbeckensis*, as there are other, differently shaped and larger upper premolars in the studied collection that fit better the size of the holotype specimen of *G. purbeckensis*, and which we tentatively assign to that taxon (see also Comparisons under cf. *G. purbeckensis* above).

cf. *Sunnyodon notleyi* sp. nov.

Plate 5, figs 5–6; Text-fig. 5E

Material. DORCM GS 17 (sample 27), ?left P4 or P3 from Sunnydown Farm Quarry near Langton Matravers, Cherty Freshwater Member of the Purbeck Limestone Formation.

Description. ?Left P4 or P3 DORCM GS 17 is roughly oval, with an incurvature on the posterior margin. It is 0.78 mm long lingually, 0.67 mm buccally and 0.61 mm wide. It bears four cusps of subequal size, two in the buccal row and two in the lingual row, the two lingual being placed to the rear of the buccal ones. In addition there is one buccal cuspule placed on the buccal margin, between the two cusps, and one lingual cuspule placed in front of the first lingual cusp. All the cusps are ornamented with radiating ridges.

Comparisons. ?P4 or P3 (DORCM GS 17), was found in sample 27, which also yielded a large I2 (DORCM GS 10), described below as belonging to Plagiulacinae gen. et sp. indet. a, I2. However, the two specimens from sample 27 differ markedly in size, which precludes their assignment to the same taxon. ?P5 (DORCM GS 18) and ?P4 or P3 (DORCM GS 17) may belong to the same species as they fit each other in size and are the only upper teeth of this size in the studied collection. ?P4 or P3 (DORCM GS 17), which we tentatively assign to *Sunnyodon notleyi*, has four cusps and additional cuspules and is of paulchoffatoid rather than plagiulacoid pattern. Of the known paulchoffatoid taxa it resembles possibly most the P3 of *Kielanodon hopsoni* (Hahn 1987, text-figs 7–8), with four cusps, from which it differs in being more regularly oval and in having only two cusps and one cuspule in the lingual row.

Remarks on paulchoffatoid taxa from the Purbeck Limestone Formation of England

The multituberculates previously described from the Purbeck Limestone Formation of England (Falconer 1857, 1862; Owen 1854, 1871; Simpson 1928) are, in our opinion, members of the Plagiulacoidea, although Hahn and Hahn (1983) assigned *Bolodon* and *Pliopriion* to the Paulchoffatiidae (see 'Remarks' under Plagiulacidae below). In the collection from the Cherty Freshwater Member of the Purbeck Limestone Formation described in this paper, in addition to members of the Plagiulacidae that prevail, there are teeth which we assign to the Paulchoffatiidae. We believe that there are at least two paulchoffatoid taxa in the collection studied, a slightly larger one, *Gerhardodon purbeckensis*, and a very tiny one, *Sunnyodon notleyi*.

The holotype specimens of these two taxa and other teeth tentatively assigned to them show a mixture of characters that may be found in almost all paulchoffatoid genera known from the Kimmeridgian or Oxfordian (Helmdach 1971; Mohr 1989) of Portugal, assigned either to the Paulchoffatiinae or to the Kuehneodontinae. Therefore we leave *Gerhardodon* gen. nov. and *Sunnyodon* gen. nov. for the time being in subfamily *incertae sedis*; we cannot rule out that they belong to different subfamilies.

Suborder PLAGIAULACOIDEA (Simpson, 1925), Hahn, 1969

Family PLAGIAULACIDAE Gill, 1872

Subfamily PLAGIAULACINAE Gill, 1872

Remarks. Hahn (1969) divided the Plagiaulacoidea into the Paulchoffatiidae Hahn, 1969 and Plagiaulacidae Gill, 1872 (see also Hahn 1971, 1977, 1978*b*, and Hahn and Hahn 1983), the families which we now regard as belonging to separate suborders. Important differences according to Hahn and Hahn (1983, p. 58) are: the structure of m2 which in the Paulchoffatiidae is 'Becken-förmig gebaut, mit erhöhtem, umlaufendem Rand und nur einen, antero-lingual gestallten Höcker', while in the Plagiaulacidae is (p. 81): 'm2 gebaut wie m1, mit 2 Längs-Reichen von Höckern'; and the structure of I3 which in the Paulchoffatiidae is three-cusped, and two-cusped in the Plagiaulacidae, similar to I2 (but see Diagnoses of suprageneric taxa above). The bulk of the paulchoffatoid genera come from the Kimmeridgian or Oxfordian (Helmdach 1971; Mohr 1989) of Guimarota in Portugal. Hahn and Hahn (1983) assigned to the Paulchoffatiidae, among others, two genera from the Purbeck Limestone Formation of England: *Bolodon* Owen, 1871, based on upper jaws, and *Plioprion* Cope, 1884, based on lower jaws (regarded by us as congeneric). In the material described in this paper seven isolated teeth that we regard as belonging to the same individual were found in sample 61. The M2 found in this sample (Pl. 3, figs 7–8) does not differ at the specific level from that in the holotype specimen of *Bolodon osborni* Simpson (BMNH 47735A, Pl. 3, fig. 9). The lower premolars from the same sample (Pl. 2, figs 4–6) are conspecific with those of *Ctenacodon* cf. *minor* (Falconer) (Simpson 1928, p. 40; see also Pl. 2, figs 3, 7), assigned by Hahn and Hahn (1983) to *Plioprion* Cope. On this basis we regard *Plioprion* cf. *minor* (Falconer) as a junior synonym of *Bolodon osborni* Simpson, and *Plioprion* Cope, 1864 a junior synonym of *Bolodon* Owen, 1871. We assign *Bolodon* Owen to the Plagiaulacinae in Plagiaulacidae (contra Hahn 1969 and Hahn and Hahn 1983) for the following reasons: The crowns in p2 and p3 in *Bolodon* are triangular and tall as characteristic of the Plagiaulacoidea, while in the Paulchoffatoidea the crowns in p2 and p3 are lower, oval or roughly quadrangular. p4 in *Bolodon* is elongated longitudinally, about twice as long as p3 (as characteristic of the Plagiaulacidae), while in the Paulchoffatiidae p4 is as long as p3. Other reasons for assigning *Bolodon* to the Plagiaulacidae are the structure of M2 and m2. In the Plagiaulacidae M2 has the cusp formula 2–3:3 and differs in this respect from that in the Paulchoffatiidae where the cusp formula of M2 is 2–3:3–6 (Hahn 1969, 1971). In m2 of *Bolodon* (Text-fig. 4) and possibly *Plagiaulax* (the only known m2 of the latter, BMNH 47733 is heavily worn, see Falconer 1857, figs 7–10 and Kielan-Jaworowska *et al.* 1987, pl. 8, fig. 1), there are no discrete buccal cusps but only a rounded ridge. m2 in *Bolodon* is reminiscent of those in the Paulchoffatiidae (e.g. Hahn 1969, figs 36–38; 1971, fig. 19; Text-fig. 4B, D) in having a buccal ridge instead of discrete cusps, but differs in having a longitudinal middle groove and two lingual cusps (whereas there is only one in the Paulchoffatiidae). The only known m2 of *Bolodon* is that of *Bolodon minor* (BMNH 47729), now lost (figured by Falconer 1854, fig. 15, and Owen 1871, pl. 4, fig. 9B, as *Plagiaulax minor*). The wear of the specimen and possible inadequacy of the drawings induced Hahn (1969) to believe that this m2 had a structure characteristic of the Paulchoffatiidae. As shown by the well preserved m2 of *Bolodon osborni* (Pl. 3, figs 5–6; Text-fig. 4B), m2 in *Bolodon* differs from that in the Paulchoffatiidae in having a longitudinal groove and two cusps in the lingual row, and from the Allodontidae in the lack of discrete buccal cusps.

Genus BOLODON Owen, 1871

Synonym. *Plioprion* Cope, 1884.

Type species. *Bolodon crassidens* Owen, 1871.

Revised diagnosis. Dental formula: 3,0,5,2/1,0,4,2. Smallest plagiaulacine genus that differs from *Plagiaulax* in having smaller lower incisor and four lower premolars rather than three (both shared

with '*Bolodon falconeri*'). Differs from *Plagiaulax* and '*Bolodon falconeri*' in having smaller number of buccal cusps in p4 (1-?4) rather than ?6. Differs from '*Bolodon elongatus*' in having P1-P3 without prominent posterior cingulum and P1 of subequal size with P2 rather than distinctly larger.

Species. *B. crassidens*, *B. osborni* and *B. minor*. '*Bolodon falconeri*' and '*Bolodon elongatus*' possibly do not belong to this genus.

Remarks. P4-M2 and m1-m2, well-preserved in *Bolodon* species, are unknown or badly damaged in other plagiaulacine genera and cannot be compared. See also the diagnosis of Plagiaulacinae under 'Diagnoses of suprageneric taxa' above.

Bolodon osborni Simpson, 1928

Plate 2, figs 3-7; Plate 3, figs 3-9; Plate 4, figs 3-7, 9-11; Plate 5, fig. 4; Text-figs 3C, 4B, 5B, 6A

1928 *Bolodon osborni* sp. nov. Simpson, p. 45, pl. 3, fig. 6; text-fig. 10.

1928 *Ctenacodon ?minor* Falconer, Simpson, p. 40, pl. 3, fig. 5.

1971 *Bolodon osborni* Simpson; Hahn, text-fig. 14.

1987 *Bolodon osborni* Simpson; Kielan-Jaworowska, Dashzeveg and Trofimov, pl. 10, fig. 3; text-fig. 3A.

Holotype. BMNH 47735A right maxilla with P1, P3-M2, figured by Simpson (1928, pl. 3, fig. 6, text-fig. 10); by Hahn (1971, text-fig. 14); Kielan-Jaworowska *et al.* (1987, pl. 10, fig. 3); and P1. 3, fig. 9; P1. 4, figs 9, 11; P1. 5, fig. 4 in this paper.

Type horizon and locality. Purbeck Limestone Formation, Marly Freshwater Member, Durlston Bay, Swanage.

Other material. BMNH 48399 right dentary from the type horizon and locality, with p1-p4 exposed in lingual aspect (figured by Simpson, 1928, pl. 3, fig. 5, as *Ctenacodon* cf. *minor*, and erroneously referred to in the explanation to the plate as the buccal aspect of the left dentary; Pl. 2, fig. 7) and left p4 registered under the same number, possibly belonging to the same specimen (Pl. 2, fig. 3). The remainder of the material is from the Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnydown Farm Quarry near Langton Matravers, Swanage, Dorset. These are: seven teeth found in sample 61, all left, fitting each other in size and regarded as belonging to the same individual: all in DORCM GS 204, p2; GS 202, p3; GS 201, p4; GS 203, m1; GS 206, m2; GS 207, M2; GS 205 broken I2; GS 4, left m1 (sample 3); GS 1, P2 or P3 (sample 35); GS 3, P2 or P3 (Bulge sample); GS 5, P2 or P3 (Bulge sample).

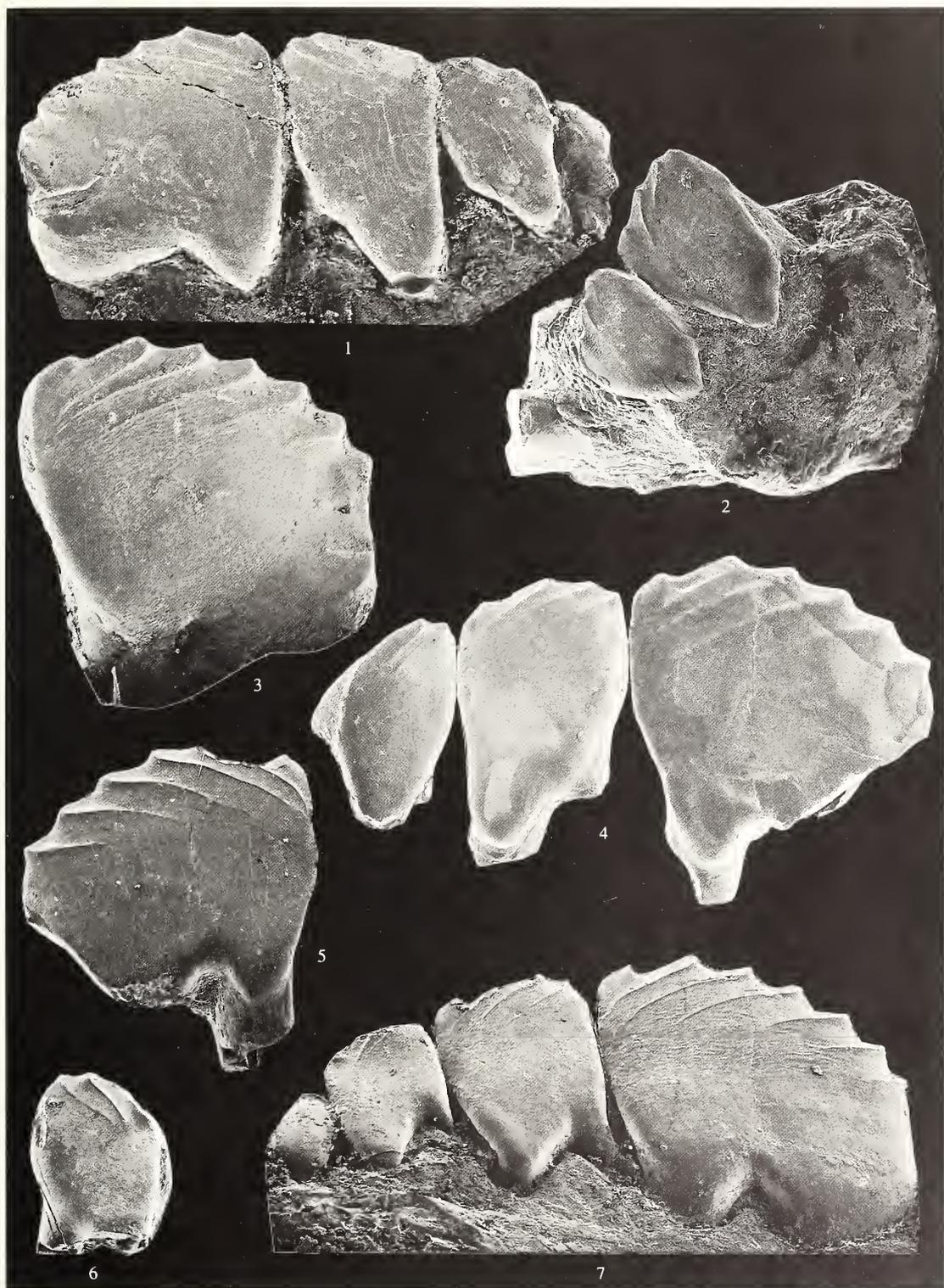
Diagnosis. Shares with *B. minor* 6-7 serrations in p4, but differs from it in being larger (p4 being 2.4-2.7 mm long), in having only a single buccal cusp in p4, ridges on p4 more widely spaced and

EXPLANATION OF PLATE 2

All from the Purbeck Limestone Formation. Specimens in figures 1, 3 and 7 are from the Marly Freshwater Member, Durlston Bay, Swanage; specimens in figures 2, 4-6, are from the Cherty Freshwater Member; specimen in figure 2 is from Suttle's Quarry near Swanage; specimens in figures 4-6 from Sunnydown Farm Quarry near Langton Matravers. All are scanning electron micrographs, $\times 20$.

Figs 1-2. *Bolodon minor* (Falconer). 1, BMNH 47729; epoxy resin cast of the holotype; fragment of the right mandible with p1-p4, buccal view. 2, DORCM GS 12; fragment of the left mandible with broken incisor; p2 and p3, buccal view.

Figs 3-7. *Bolodon osborni* Simpson. 3, BMNH 48399; epoxy resin cast of left p4, buccal view. 4, photomontage of three teeth from the same sample: DORCM GS 204, p2; DORCM GS 202, p3; DORCM GS 201, p4, buccal view. 5, DORCM GS 201; p4, lingual view, part of the upper margin has been broken after the photograph in figure 4 was taken. 6, DORCM GS 204; p2, lingual view. 7, BMNH 48399; epoxy resin cast; right mandible with p1, p2, p3 and p4, lingual view.



KIELAN-JAWOROWSKA and ENSOM, *Bolodon*

p3 relatively larger in relation to p4. Differs from *B. crassidens* in being smaller, in having P4 more parallel-sided with three large cusps in the middle row, a cuspule in front of them and a row of buccal cuspules, rather than two large middle cusps, and a smooth prominent anterobuccal cingulum.

Description. Estimated length of the skull is about 3 cm.

Lower teeth. The lower incisor has not been preserved. p1 is preserved only in BMNH 48399 and is exposed in lingual aspect (pl. 2, fig. 7). p2–p4 from Sunnydown Farm Quarry are shown in pl. 2, figs. 4–6; p2 (DORCM GS 204) has one weak and two distinct serrations, two ridges on the buccal side and three on the lingual side; it is 1.7 mm long and 0.8 mm wide. p3 (DORCM GS 202) is 2.1 mm long and 1.1 mm wide, it has four serrations and all except the first one bear ridges. In buccal aspect a short ridge extends downward from the last serration and there is a minute cuspule below it. The ventral margin of the exodaenodont lobe is very prominent. p4 (DORCM GS 201) is 2.4 mm long and 2.3 mm high and has six serrations, all except the first one provided with ridges. This specimen is incomplete, and the posteroventral part, posterior root and buccal cusp have not been preserved. A single buccal cusp is preserved in the left tooth of BMNH 48399 (Pl. 2, fig. 3). The cusp formula of m1 is 2:2. The tooth is roughly rectangular, but slightly shorter lingually than buccally. m1 (DORCM GS 203) is 1.4 mm long and 1.2 mm wide, while DORCM GS 4 is 1.5 mm long and 1.2 mm wide (Pl. 3, figs 3–4). In DORCM GS 203 the large posterior root is almost completely preserved, the anterior one is broken at the base; in DORCM GS 4 both roots are broken, a small part of the posterior one being preserved. Both cusps in the lingual row are crescent-shaped, with large, roughly triangular surfaces sloping towards the middle groove. In DORCM GS 4 on the first lingual cusp, in front of the main cusp, there is a minute cuspule, which is less prominent in GS 203 because of wear. Both cusps of the lingual row, as preserved in both specimens, are not ornamented. In the buccal row there is an elevated cingulum in front of the first cusp. The first cusp is roughly cone-shaped, with four surfaces sloping down from the tip, the posterior one ornamented with grooves. The second cusp has its tip situated buccally, worn in both specimens and a large crescentic surface, strongly ornamented with irregular grooves, that slopes down anterolingually from the tip. m2 DORCM GS 206 (Pl. 3, figs 5–6) is 1.6 mm long and 1.3 mm wide, roughly oval, with slightly sigmoid anterior margin. Both roots are broken off. The first cusp of the lingual row as preserved in DORCM GS 206 is not ornamented and has three surfaces that slope down from the tip: a crescent-shaped anterolingual, and two roughly triangular buccal and posterior ones. A wide groove divides the two cusps of the lingual row. The second lingual cusp is elongated longitudinally, roughly triangular in occlusal aspect, with the tip situated in the anterior one third of the length. A ridge extends from the tip posteriorly, separating the buccal and lingual slopes. The anterior slope is irregular, ornamented with a crescent-shaped, prominent ridge. The buccal slope was originally ornamented with grooves and ridges; only the first ridge is well preserved. The buccal side forms a prominent rounded ridge, with traces of three minute cuspules in the posterior half. A large surface, conspicuously ornamented with irregular, mostly transverse grooves and ridges, slopes down from the rounded ridge to the middle groove. The anterior part of the buccal ridge is worn.

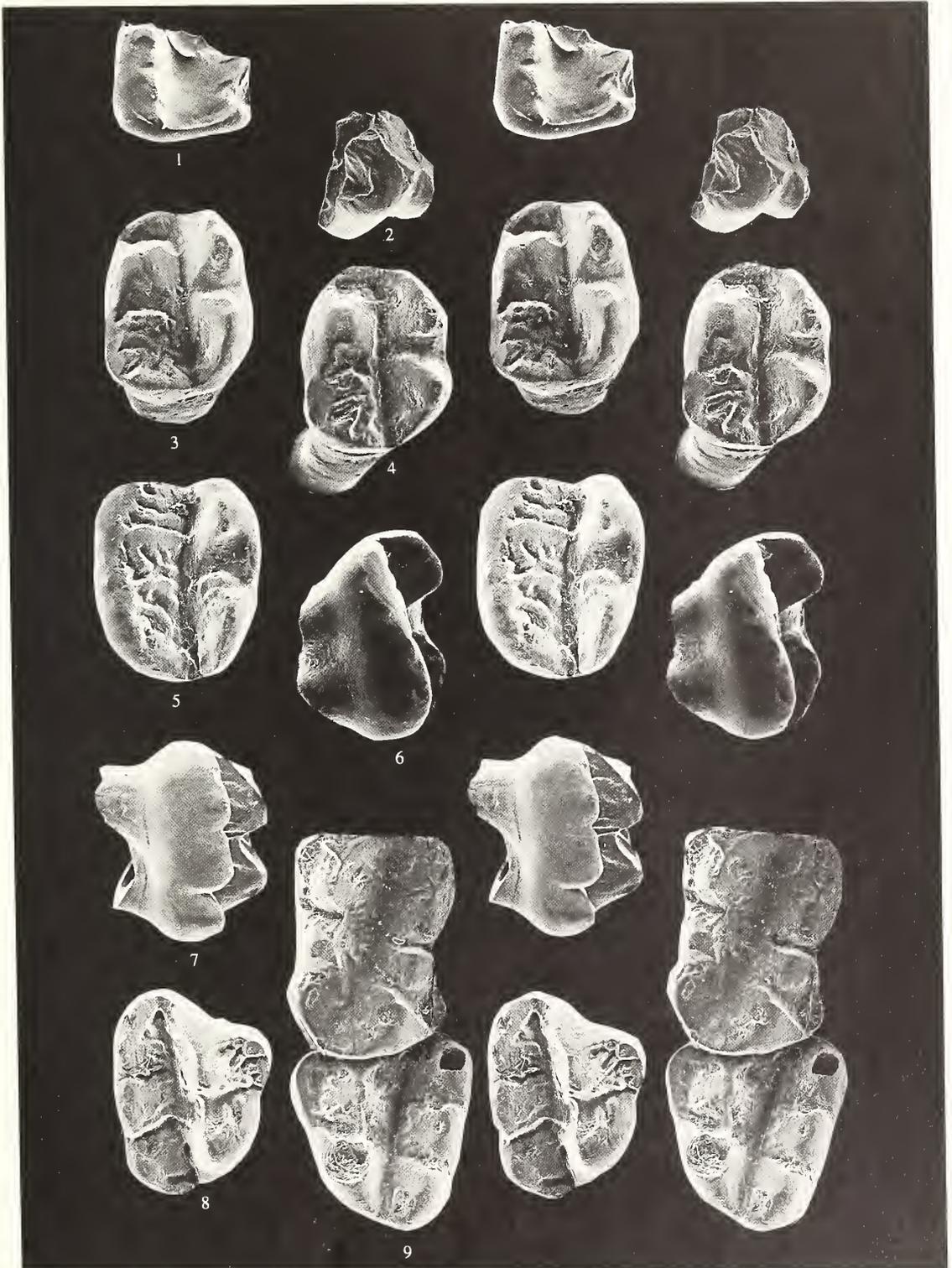
Upper teeth. I1, I3 and P2 are not known. I2 (DORCM GS 205; Pl. 4, fig. 3) is a fragment of the left tooth with broken tip and part of the accessory cusp preserved. It is similar to I2 DORCM GS 8 (Pl. 4, fig. 1) described under *Plagiaulacinae* gen. et sp. indet. a, I2, but is notably smaller. P1, P4, P5 and M1 have been preserved only in the holotype specimen (Pl. 4, figs 9, 11). P3 in the holotype specimen is partly obscured by P4. We identify three specimens (DORCM GS 1, GS 3 and GS 5) as P2 or P3 (Pl. 4, figs 4–7, 10), because they are all two-rooted, although the roots have been broken, and because they roughly correspond in size and

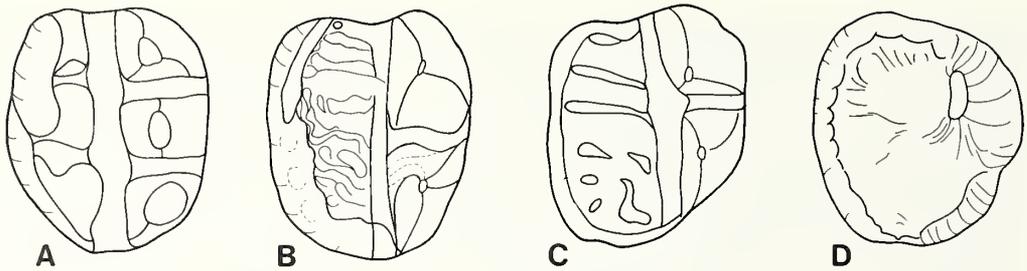
EXPLANATION OF PLATE 3

All are from the Purbeck Limestone Formation. Specimens in figures 1–8 are from the Cherty Freshwater Member, Sunnydown Farm Quarry, Langton Matravers. Specimen in figure 9 is from the Marly Freshwater Member, Durlston Bay, near Purbeck, Swanage. All are scanning electron stereo-micrographs $\times 20$. All teeth are oriented with anterior margin up.

Figs 1–2. cf. *Bolodon minor* (Falconer). DORCM GS 6; posterior part of the right M1, occlusal and lingual views.

Figs 3–9. *Bolodon osborni* Simpson. 3, DORCM GS 4; left m1, occlusal view. 4, DORCM GS 203; left m1, occlusal view. 5–6, DORCM GS 206; left m2, occlusal view and buccal views. 7–8, DORCM GS 207; left M2, lingual and occlusal views. 9, BMNH 47735A; right M1 and M2, occlusal view.





TEXT-FIG. 4. Comparison of the left second lower molars, occlusal views. A, *Ctenacodon scindens* YPM 10366; right tooth, reversed. B, *Bolodon osborni*; DORCM GS 206. C, *Eobaatar magnus*; PIN 3101/53. D, Paulchoffatiidae, gen. et sp. indet. A-C are camera lucida drawings; A, of epoxy resin cast; B-C of original specimens; D is after Hahn 1969, text-fig. 36a, simplified. Scale = 1 mm.

structure to P3 in the holotype, while P2 has not been preserved in the holotype. The posterior cingulum obscured in P3 in the holotype, is well seen in all of them. They are all smaller than P1 of the holotype (Pl. 4, fig. 11) and differ from it in absence of the anterior cingulum.

M2 (DORCM GS 207) (Pl. 3, figs 7-8) appears on the photograph in occlusal view narrower than the holotype specimen (Pl. 3, fig. 9), which is in part due to a slightly different position on the photographed specimens, and possibly has a more sigmoid anterior margin. It is notably longer lingually than labially, divided by a deep longitudinal groove. There is a narrow anterior rim that widens medially and passes onto the first cusp of the buccal row, reaching its tip. The rim protrudes laterally and surrounds the base of the first buccal cusp, which is very irregular in shape. Its tip, as preserved in DORCM GS 207, forms a longitudinal ridge. Four surfaces slope up from the ridge: the anterior one is smooth and forms a part of the anterior rim mentioned above; the buccal one is the largest and surrounded by a rim; the posterior one is steep and small; the lingual one is steep and large; it protrudes anteriorly and reaches the anterior rim. The second cusp of the buccal row is roughly triangular. Three surfaces slope up from its tip: the anterior one is roughly triangular, the posterobuccal is crescent-shaped and convex, and the lingual one is steep. In lateral view the buccal cusps coalesce at the bases. The first cusp in the lingual row has its tip placed posteriorly. Three surfaces slope up from it: the large buccal one which reaches the longitudinal groove; the anterolingual one, which is convex and crescent-shaped, and a very small posterior one. The second cusp is the shortest in the row. Due to wear the tip in DORCM GS 207 has the form of a ridge. There is a large, flat buccal slope and a convex lingual one. Anterior and posterior slopes are hardly pronounced. The third cusp is roughly a mirror-image of the first one, but has its tip situated in the middle. Except for the outer wall all the cusps of the tooth are ornamented with prominent pits and grooves. The grooves on the buccal slopes of the lingual cusps continue onto the lingual

EXPLANATION OF PLATE 4

All are from the Purbeck Limestone Formation, specimens in figures 1-7 and 10 are from the Cherty Freshwater Member, Sunnydown Farm Quarry near Langton Matravers, specimens in figures 8-9 and 11 are from the Marly Freshwater Member, Durlston Bay, Swanage. All are scanning electron micrographs; figures 1-2 $\times 10$, all others $\times 20$. All except 3, 8 and 11 are stereo-pairs. All teeth in occlusal view are oriented with anterior margin up.

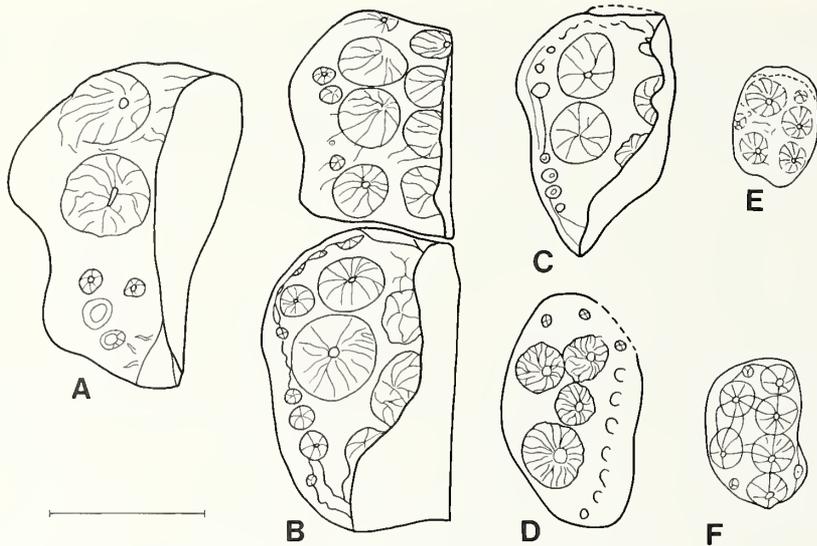
Fig. 1. Plagiaulacinae gen. et sp. indet. a. DORCM GS 8; right I2, lingual view.

Fig. 2. Plagiaulacinae gen. et sp. indet. b. DORCM GS 10; left I2, lingual view.

Figs 3-7, 9-11. *Bolodon osborni* Simpson. 3, DORCM GS 205; broken left I2, lingual view. 4-5, DORCM GS 1; left P2 or P3, occlusal and buccal views. 6, DORCM GS 3; left P2 or P3, occlusal, slightly anterior view. 7, 10, DORCM GS 5; left P2 or P3, buccal and occlusal views. 9, 11, BMNH 47735A; 9, right P3-P5 occlusal view; 11, right P1, occlusal and slightly anterior view.

Fig. 8. '*Bolodon*' *elongatus* Simpson. BMNH 47736; fragment of right maxilla with P1-P3 of the holotype specimen, epoxy resin cast, occlusal view.





TEXT-FIG. 5. Camera lucida drawings of the upper premolars, in occlusal view. A–C, are based on epoxy resin casts, all shown as right teeth, D–E reversed. A, *Bolodon crassidens*; BMNH 47735; P4. B, *Bolodon osborni*; BMNH 47735A; P4 and P5. C, cf. *Bolodon minor*; DORCM GS 7; P5. D, cf. *Gerhardodon purbeckensis*; DORCM GS 11; P5. E, cf. *Sunnyodon notleyi*; DORCM GS 17; ?P4 or P3. F, *Sunnyodon notleyi*; DORCM GS 18; ?P5. Scale = 1 mm.

slopes of the buccal cusps. The most prominent ornamentation is on the buccal slope of the first buccal cusp, where in addition to the pits and grooves there occur prominent ridges.

Variability. The specimens assigned here to *Bolodon osborni* differ slightly in size. In BMNH 48399 p4 is 2.7 mm long (left tooth), and 2.5 mm wide (right tooth, measured in lingual aspect), while p4 DORCM GS 201 is 2.4 mm long. M2 in the holotype specimen is slightly larger than DORCM GS 207. These differences are not greater than those observed in other multituberculate genera and species (see, e.g., Krause 1977, 1982, 1987; Kielan-Jaworowska *et al.* 1987).

EXPLANATION OF PLATE 5

All are from the Purbeck Limestone Formation, specimens in figures 1–3, 5–6 and 8–10 are from the Cherty Freshwater Member, specimens in figures 4 and 7 are from the Marly Freshwater Member. All are scanning electron micrographs, all except figures 4 and 7 are stereo-pairs. Figures 1–2, 4, 7–9, $\times 20$; figures 3, 5–6, 10, $\times 40$. All teeth are oriented with anterior margin up.

Figs 1–2. ?*Plagiaulacinae*, gen. et sp. indet. DORCM GS 2; Sunnydown Farm Quarry near Langton Matravers; ?right P1, P2 or P3, or left canine, occlusal and lingual views.

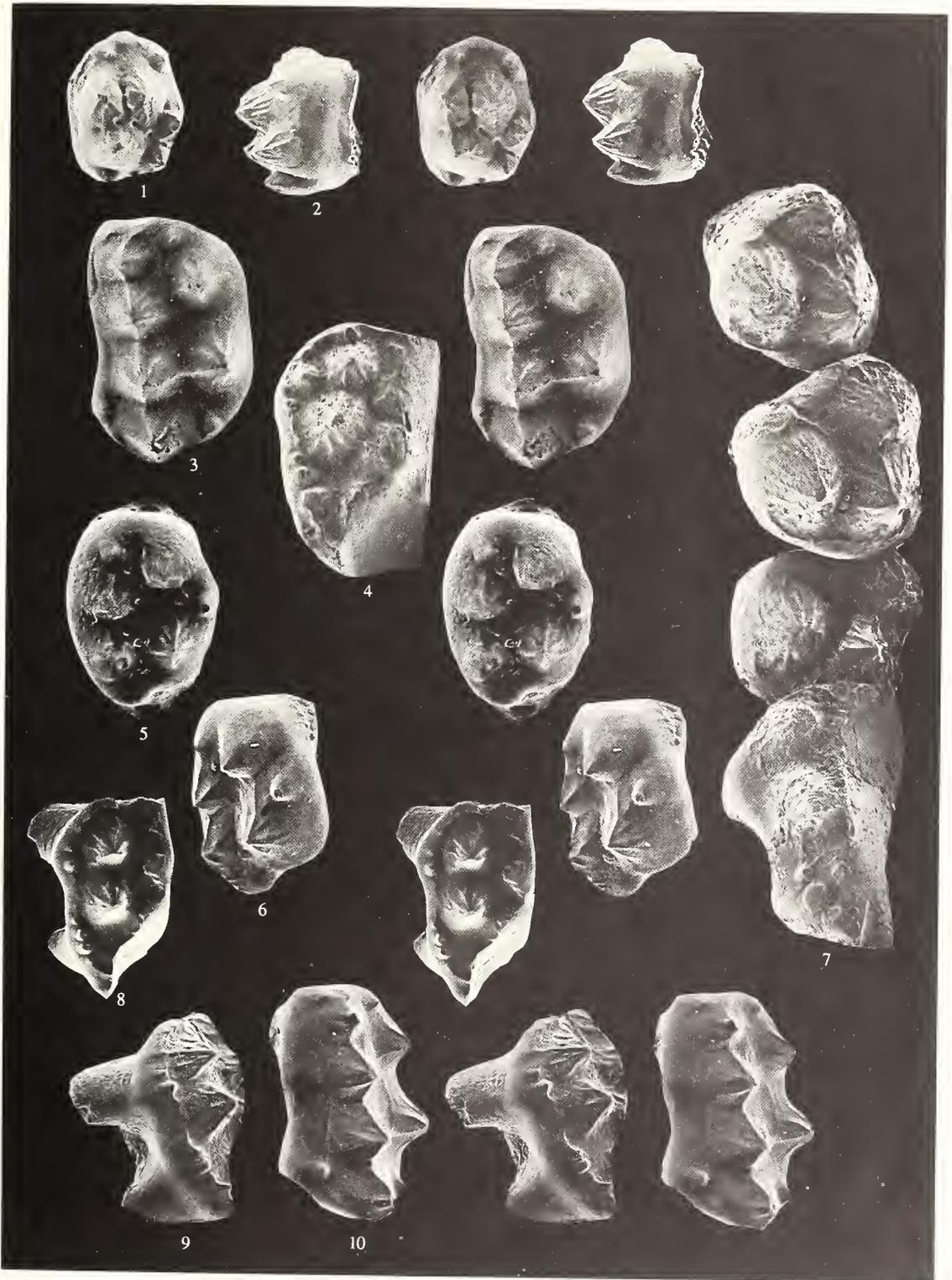
Figs 3, 10. *Sunnyodon notleyi* sp. nov. DORCM GS 18; holotype; Lovell's Quarry near Langton Matravers; right ?P5, occlusal and lingual views.

Fig. 4. *Bolodon osborni* Simpson. BMNH 47735A; epoxy resin cast of the right P5 of the holotype specimen; Durlston Bay, Swanage; occlusal view.

Figs 5–6. cf. *Sunnyodon notleyi* sp. nov. DORCM GS 17; Sunnydown Farm Quarry near Langton Matravers; ? left P3, occlusal and buccal views.

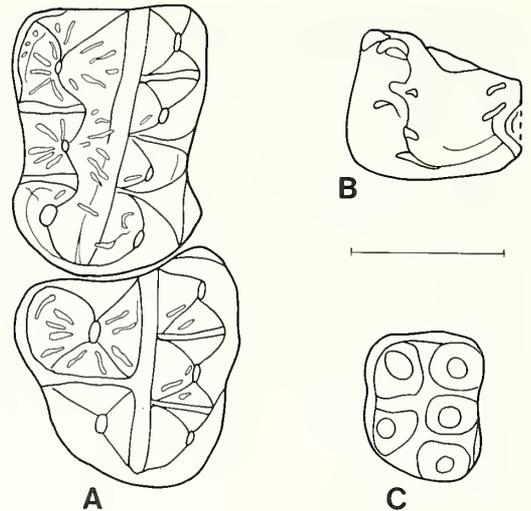
Fig. 7. *Bolodon crassidens* Owen. BMNH 47735; Durlston Bay, Swanage; epoxy resin cast of the fragment of maxilla with P1–P4 of the holotype specimen.

Figs 8–9. cf. *Bolodon minor* (Falconer). DORCM GS 7; Sunnydown Farm Quarry near Langton Matravers; right P5, occlusal and buccal views.



KIELAN-JAWOROWSKA and ENSOM, multituberculate mammals

TEXT-FIG. 6. Camera lucida drawings of the upper molars, occlusal view, all shown as right teeth. C-D reversed, A, based on epoxy resin cast. A, *Bolodon osborni*; BMNH 47735A; M1 and M2; M1 which slightly covers M2 in the specimen has been separated in the drawing. B, cf. *Bolodon minor*; DORCM GS 6; posterior part of M1. C, cf. *Gerhardodon purbeckensis*; DORCM GS 9; ?M1. Scale = 1 mm.



Comparisons. See 'Comparison of Plagiaulacinae species' below.

Bolodon minor (Falconer, 1857)

Plate 2, figs 1-2; Text-fig. 3B

- 1857 *Plagianlax minor* sp. nov.; Falconer, pp. 262-267, 271-272, text-fig. 15 a-d.
 1983 *Plioprion minor* (Falconer); Hahn and Hahn, p. 66, with synonymy, excluding *Ctenacodon* cf. *minor* Simpson 1928.
 1987 *Plioprion?* *minor* (Falconer); Kielan-Jaworowska, Dashzeveg and Trofimov, pl. 10, fig. 3.

Holotype. BMNH 47729, right dentary with incisor, p1-m2 (m2 now lost), figured by Falconer 1857, pl. 3, fig. 15; Owen 1871, pl. 4, fig. 9; Simpson 1928, pl. 3, fig. 4, text-fig. 9; Hahn 1971, text-fig. 2; Kielan-Jaworowska *et al.* 1987, pl. 10, fig. 3, and this paper: Pl. 2, figs 1-2; Text-fig. 3B.

Type horizon and locality. Purbeck Limestone Formation, Marly Freshwater Member, Durlston Bay, Swanage.

Other material. DORCM GS 12 (sample 05) from Suttle's Quarry, Cherty Freshwater Member of the Purbeck Limestone Formation, a fragment of left dentary with broken incisor, p2 and p3; see also P5 and M1 described under cf. *Bolodon minor* below.

Diagnosis. Differs from *B. osborni* and *B. crassidens* in being smaller, the length of p4 being 2.1 mm. Differs from *B. osborni* in having ?four buccal cusps in p4 and the ridges more closely spaced.

Description. See Simpson (1928, p. 38). The lower incisor fragment preserved in DORCM GS 12 is strongly compressed laterally and covered with a thin layer of enamel. p2 and p3 preserved in the same specimen are 1.3 and 1.65 mm high respectively, lower than in the holotype where they are 1.5 and 2.2 mm high.

Comparisons. See 'Comparison of Plagiaulacinae species' below.

cf. *Bolodon minor* (Falconer, 1857)

Plate 3, figs 1-2; Plate 5, figs 8-9; Text-figs 5c, 6b

Material. In the collection from Sunnydown Farm Quarry there are two isolated teeth, right P5 DORCM GS 7 (sample 35) and posterior part of right M1 DORCM GS 6 (sample 35), which belong to *Bolodon*, but are smaller than *B. osborni* and differ from it in details. They apparently belong to *B. minor*.

Description. Right P5 DORCM GS 7 (Pl. 5, figs 8–9; Text-fig. 5C) has both roots broken off and is partly worn. It is 3.25 mm long and 2.2 mm wide. The cusp formula is 2:3. The cusps of the lingual row are strongly worn lingually. The middle cusp is the largest. The cusps of the buccal row are of subequal size and larger than those of the lingual row. The tip of the anterior lingual cusp is placed posteriorly. The tooth is surrounded anteriorly and buccally by a cingulum with small cuspules. Anteriorly the cuspules are developed only as small crenulations. Buccally, opposite the first buccal cusp there are three cuspules, the posterior one being the largest; to the rear of the second buccal cusp there are four cuspules, the penultimate being the largest. The worn lingual surface forms a large vertical wall, which swings buccally opposite the second buccal cusp, producing the pointed end of the tooth crown when seen in dorsal view. All of the cusps are ornamented with radiating striae. The partial right M1 DORCM GS 6 (Pl. 3, figs 1–2; Text-fig. 6B) is possibly somewhat smaller than in *B. osborni*. It has an almost straight posterior margin, rather than convex as in *B. osborni* (pl. 3, fig. 9). A ridge, parallel to the posterior margin extends between the posterior cusps of the buccal and lingual rows. In the preserved fragment, which may represent half of the tooth, there are three small buccal cusps, which suggests that the number of buccal cusps was possibly greater than in *B. osborni*. Two strongly worn lingual cusps are preserved with traces of comma-shaped grooves, characteristic of the molars of *Bolodon*. The crescent-shaped lingual ridge characteristic of *B. osborni* has not been preserved.

Comparisons. See ‘Comparison of Plagiaulacinae species’ below.

Plagiaulacinae gen. et sp. indet. a, I2

Plate 4, fig. 1

Material. DORCM GS 8 (sample 112), right I2 from Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnydown Farm Quarry near Langton Matravers.

Description. I2 (DORCM GS 8) is 8.5 mm long with root, strongly bent anteriorly, flattened laterally and provided with a prominent accessory cusp. The root is closed. The distance between the tips of the main and accessory cusps is 2 mm. The tooth is slightly constricted above the accessory cusp and its width at that point is 1.5 mm, but otherwise the crown gradually passes into the root. The posterior surface of the main cusp is strongly worn.

Comparisons. I2 (DORCM GS 8) is about 1.6 times larger than the fragmentary I2 (DORCM GS 205) (Pl. 4, fig. 3) assigned to *B. osborni*. It may belong to one of the two large plagiaulacine species based on the lower jaws: *Plagiaulax becklesii* or ‘*Bolodon*’ *falconeri* in both of which p4 is about 1.6 times longer than in *Bolodon osborni* (BM 47729). One of these taxa is possibly a counterpart of ‘*Bolodon*’ *crassidens*, while the other is a counterpart of ‘*Bolodon*’ *elongatus*. I2 (DORCM GS 8) is smaller and more bent than I2 in *Psalodon fortis* and has a more prominent accessory cusp (Simpson 1929, p. 26, pl. 5, fig. 3). It differs from I2 in Paulchoffatiidae (e.g. *Kuelneodon dryas*, *K. simpsoni* and *Henkelodon naias*, see Hahn 1977) in being more bent, relatively slender, with a less robust accessory cusp and less prominent difference of the diameter between the crown and the root.

Plagiaulacinae gen. et sp. indet. b, I2

Plate 4, fig. 2

Material. DORCM GS 10 (sample 27), left I2 from Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnydown Farm Quarry near Langton Matravers.

Description. DORCM GS 10 has a complete crown and part of the root preserved. It gradually diminishes in diameter towards the main cusp. At about 0.7 mm from the tip of the main cusp, there is an angulation with a minute lingual accessory cuspule.

Comparisons. I1 in the Plagiaulacidae except for the alveoli and roots has not been described, but the root of I1 preserved in the type skull of *Bolodon crassidens* is very small, much smaller than that

of I2; it therefore seems improbable that DORCM GS 10 is an I1. Among the Paulchoffatiidae Hahn (1969, 1977) described I1 in *Paulchoffatia delgadoi*, *Paulchoffatia* sp. (referred to as *Kuehneodon* sp., Hahn 1977) and in Paulchoffatiidae gen. et sp. indet. In all these cases I1 uniformly narrows towards the tip and there is no angulation or accessory cusplule. DORCM GS 10 described above differs in this respect also from paulchoffatiid I1. It may be I2 of a smaller species than the one to which I2 (DORCM GS 8, Pl. 4, fig. 1) described above belongs.

?Plagiaulacinae gen. et sp. indet., I3

Plate 1, figs 11, 14; Text-fig. 7

Material. DORCM GS 14 (sample 28) left I3 from the Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnysdown Farm Quarry near Langton Matravers.

TEXT-FIG. 7. ?Plagiaulacinae gen. et sp. indet.; DORCM GS 14, left I3; crown view; the buccal side is to the right. Scale = 1 mm.



Description. Left I3 DORCM GS 14, measured in anterior view is together with the root 2.7 mm long, the length of the root being 1.8 mm. The crown strongly overhangs the root. The tooth is three-cusped, compressed anteroposteriorly, 2.4 mm wide and 2.4 mm long in posterior view. The main cusp is steeply worn buccally and more horizontally worn lingually, producing a sharp triangular tip. A prominent anterior cusp is placed on the buccal side of the anterior wall of the crown, lower than the small cusp placed on the lingual side of the posterior slope. The latter is developed as a subhorizontal cingulum, the medial side of which extends upwards as a ridge towards the tip of the main cusp. In posterior aspect the crown is longer than anteriorly, producing a triangular tip upwards. The root is closed and bent posteriorly.

Comparisons. The three-cusped I3 characteristic of DORCM GS 14 occurs in both the Paulchoffatiidae (Hahn 1977) and Plagiaulacidae (Simpson 1928). DORCM GS 14 differs from I3 of all known paulchoffatiid taxa in having only one anterior cusp rather than two, the posterior cusp developed as a ridge, and in being compressed anteroposteriorly. It is more reminiscent of the I3 of *Henkelodon naias* and *Paulchoffatia* sp. (referred to by Hahn 1977, text-fig. 8 as *Kuehneodon* sp., but see Hahn 1978b, p. 183) than that of *Kuehneodon simpsoni*, although the posterior cusp, which is weak in our specimen, is hardly developed in *K. simpsoni*. DORCM GS 14 recalls I3 of *Bolodon crassidens* (Simpson 1928, text-fig. 11) in the arrangement of the cusps, but differs from it in being strongly compressed anteroposteriorly and roughly oval in cross section, rather than triangular, and in having less prominent additional cusps. It is also reminiscent of I3 of *Psalodon fortis* (Simpson 1929, p. 26, pl. 5, fig. 3), which although being two-cusped, is similar to DORCM GS 14 in being compressed anteroposteriorly. In this respect I3 of *P. fortis* differs from I2 which is laterally compressed. Our specimen differs from I3 of *P. fortis* (in addition to being smaller) in the presence of a prominent anterior cusp and a smaller posterior one. Because of this ambiguity we tentatively assign DORCM GS 14 to the Plagiaulacinae.

?Plagiaulacinae gen. et sp. indet., ?upper premolar or canine

Plate 5, figs 1-2

Material. DORCM GS 2 (sample 13) from Cherty Freshwater Member of the Purbeck Limestone Formation,

Sunnydown Farm Quarry near Langton Matravers, ?right anterior upper premolar ?P1, P2 or P3 or ?left canine.

Description. ?Upper premolar (DORCM GS 2) is 1.25 mm long and 1 mm wide in occlusal view. The roots are completely resorbed, but it cannot be excluded that the tooth was single-rooted. If so, it would be a canine rather than a premolar. There are three main cusps, two lingual and one buccal, and three smaller lingual cusps. One of them, the smallest, is placed at the corner of the anterior and lingual margins, the two remaining are on the posterior half of the lingual margin, the first of these being larger than the second. Along the anterior margin there are two minute cuspules, and the trace of a third one between them, while along the posterior margin there are two cuspules, the buccal one larger than the lingual. All the cusps are ornamented with radiating ridges. In grooves between the main cusps and between the two posterior lingual cusps there is an ornamentation of distinct pits.

Comparisons. The upper ?premolar (DORCM GS 2) is reminiscent of P1–P3 in the plagiaulacid genera *Bolodon* and *Ctenacodon* whose three main cusps are arranged similarly. We identify it tentatively as a right tooth, but it might be a left one. If so, the margin described here as anterior would be posterior and additional lingual cusps identified as posterior, would be placed anteriorly. We identify the side with additional cusps as lingual, by comparison with the position of main cusps in plagiaulacid upper premolars, in which two cusps are situated lingually and one buccally. This tooth differs from all the known plagiaulacid upper premolars in having additional cusps lingual to the three main cusps and anterior and posterior cuspules, and in having the pits in grooves between the cusps. Similar (but not certain if homologous) ornamentation (grooves and ‘comma-shaped pits’) occurs in molars of the Plagiaulacinae and Eobaatarinae but was not found previously in the anterior upper premolars. We assign DORCM GS 2 to the Plagiaulacinae, rather than to the Allodontidae or Paulchoffatiidae, because of this ornamentation. Another reason for this assignment is that the Allodontidae do not occur in the Purbeck of England, and the paulchoffatiids known from these beds do not fit the size of DORCM GS 2; they are too small. Additional cuspules on premolars occur rarely in the Paulchoffatiidae (e.g. in *Pseudobolodon* sp., Hahn 1977, text-fig. 3) and in the Plagiaulacidae (e.g. in *Bolodon elongatus*, Pl. 4, fig. 8). In both these taxa there are only two additional cuspules, but no lingual additional cusps as in DORCM GS 2 and the pits characteristic of our specimen are lacking. If DORCM GS 2 was single-rooted then it may be a canine rather than premolar, and the facet for contact with the adjacent tooth, which occurs on the side identified by us tentatively as the anterior one, would be for the contact with the first premolar, so indicating the posterior wall of the tooth. In such a case DORCM GS 2 would be a left rather than right tooth. However, uncontested canines have not been found so far in the Plagiaulacidae, although Hahn and Hahn (1983) tentatively suggested the presence of a canine in *Ctenacodon*. Canines occur in various paulchoffatiid genera, but we believe that the general structure of the described tooth has plagiaulacine rather than paulchoffatiid affinities.

Comparison of Plagiaulacinae species

Six plagiaulacine taxa have been described from the Purbeck Limestone Formation of England. These are: *Plagiaulax becklesii* Falconer, 1857; *Bolodon minor* (Falconer, 1857), assigned by Falconer (1857) to *Plagiaulax*; *Pliopriion falconeri* (Owen, 1871), assigned by Owen (1871) to *Plagiaulax*, and referred to by us as ‘*Bolodon*’ *falconeri*; *Bolodon crassidens* Owen, 1871; *Bolodon osborni* Simpson, 1928; and *Bolodon elongatus* Simpson, 1928.

B. osborni is known from both upper and lower jaws and dentition, and *Ctenacodon* cf. *minor* Simpson 1928 is regarded here as its junior subjective synonym. Three taxa, *Plagiaulax becklesii*, ‘*Bolodon*’ *falconeri* and *Bolodon minor* are based on lower jaws, although upper premolars and molars are tentatively assigned to *B. minor* and described in this paper. Two taxa, *Bolodon crassidens* (Pl. 5, fig. 7; Text-fig. 5A) and *Bolodon elongatus* (Pl. 4, fig. 8), are based on maxillae with incomplete dentitions and the upper molars of both are not known. We agree with Hahn and Hahn (1983) that *Bolodon elongatus* possibly does not belong to the genus *Bolodon* and we therefore refer to it as ‘*Bolodon*’ *elongatus*. Both *B. crassidens* and ‘*B.*’ *elongatus* are relatively large and

correspond in size to the two large species based on the lower jaws. It is thus very probable that one of the large upper jaw taxa is conspecific with '*Bolodon*' *falconeri* and the other with *Plagiaulax becklesii*. If so, there would be four uncontested plagiaulacine taxa in the Purbeck of England (unless the ?upper premolar or canine, DORCM GS 2, described here as ?*Plagiaulacinae* gen. et sp. indet., belongs to a fifth plagiaulacine taxon).

If it were to be demonstrated in the future that *Bolodon crassidens* is conspecific with, e.g., *Plagiaulax becklesii*, then one should reconsider the generic assignment of *Bolodon osborni* and *Bolodon minor*, which would not be congeneric with *Bolodon crassidens*. As long as it cannot be demonstrated unequivocally which upper jaw matches the lower one, these taxonomic decisions cannot be made.

Bolodon minor is the smallest species of the genus. It differs from *B. osborni* in being smaller and in having ?four buccal cusps in p4 (one in *B. osborni*). The differences between p2 and p3 structure are hardly discernible (Text-fig. 3). Upper teeth of *B. minor* are poorly known, P5 DORCM GS 7 (Pl. 5, figs 8–9; Text-fig. 5C) and incomplete M1 DORCM GS 6 (Pl. 3, figs 1–2; Text-fig. 6B) described under cf. *B. minor*, differ from those in *B. osborni*: P5, in having two buccal cusps of equal size, while in *B. osborni* (Pl. 5, fig. 4; Text-fig. 5B) the posterior one is larger, and in having buccal cuspules less differentiated in size; M1, in having a nearly straight posterior margin, while it is convex posteriorly in *B. osborni* (Pl. 3, fig. 9; Text-fig. 6A) and possibly in having more and smaller buccal cusps. In spite of these differences *B. osborni* appears more closely related to *B. minor* than to *B. crassidens* (Pl. 5, fig. 7; Text-fig. 5A) and '*B*' *elongatus* (Pl. 4, fig. 8), from both of which it is also notably smaller. Both these latter species are known only from the anterior premolars. P1–P3 are similarly shaped in *B. crassidens* and in *B. osborni*, but P4 has two large buccal cusps in *B. crassidens* and a prominent cingulum buccal to them without cuspules, while there are three buccal cusps and a cingulum with cuspules in P4 of *B. osborni* (Text-fig. 5A–B). P4 in *B. crassidens* (Text-fig. 5A) more closely resembles P5 of *B. osborni* than P4 (Text-fig. 5B). P1–P3 in '*B*' *elongatus* (Pl. 4, fig. 8) differ notably from those in other *Bolodon* species in having a prominent posterior cingulum, P3 being smaller than P1 and P2, and elongated longitudinally. Lastly, both *B. minor* and *B. osborni* resemble '*Bolodon*' *falconeri* and differ from *Plagiaulax becklesii* in having four lower premolars rather than three.

DISCUSSION

English Purbeck Limestone Formation multituberculate mammals are known from four localities (Text-fig. 1): the previously known locality at Durlston Bay, Swanage, and three new localities (Ensom 1987, 1988): Sunnydown Farm and Lovell's Quarry, both near Langton Matravers, and Suttle's Quarry near Swanage. Multituberculates from the Durlston Bay locality are from the Marly Freshwater Member and those from the three new localities, the Cherty Freshwater Member, all within the Purbeck Limestone Formation. All the multituberculates described from Durlston Bay belong to the *Plagiaulacinae* (see '*Comparison of Plagiaulacinae species*' above).

The new collection from Sunnydown Farm Quarry contains, in addition to some of the taxa previously known from Durlston Bay (*B. minor*, *B. osborni* and two large I2, possibly belonging to *Plagiaulax becklesii* or '*Bolodon*' *falconeri*), two new taxa: *Gerhardodon purbeckensis* gen. et sp. nov., and *Sunnyodon notleyi* gen. et sp. nov., both assigned to the Paulchoffatiidae. In addition we have described I3 assigned to the ?*Plagiaulacinae*, gen. et sp. indet., and an upper premolar or canine identified also as ?*Plagiaulacinae*, gen. et sp. indet. It appears from our study of the collection from Sunnydown Farm Quarry, that the English Late Jurassic multituberculate fauna was more diverse than previously thought. The new taxa differ from those previously known, by, among other features, notably smaller dimensions. This is, we believe, the result of a different sampling method. To find teeth less than 1 mm long (e.g. the holotype specimen of *Sunnyodon notleyi*) when searching for fossils in the outcrops would be difficult, but such small specimens are more readily collected using the washing and screening method adopted by us.

Evaluation of the fauna described in this paper in relation to the Middle to Late Jurassic and

Early Cretaceous multituberculates known from the world (see Kielan-Jaworowska 1974, and Clemens and Kielan-Jaworowska 1979, for earlier reviews) is of interest. The only Middle Jurassic multituberculate specimens so far known are an eroded ?I1 and an eroded ?molar, from Bathonian strata, the former from Oxfordshire (Freeman 1979) and the latter from Dorset (Freeman 1976), where in addition, a small undescribed fragment of what is possibly a multituberculate tooth (DORCM G 10827) was collected by one of us (P.C.E.). Due to the meticulous work of Hahn (1969, 1971, 1977, 1978*a*, 1978*b*, 1978*c*, 1988 and references therein; see also Hahn and Hahn 1983), the Late Jurassic (Kimmeridgian or Oxfordian, see Helmdach 1971 and Mohr 1989) multituberculate fauna of Portugal is well known, five genera being established, all assigned to the Paulchoffatiidae Hahn, 1969. Otherwise, Late Jurassic multituberculate faunas are known from the Purbeck of England (Simpson 1928 and references therein) and the correlative Morrison Formation of North America (Simpson 1929; Bakker and Carpenter, 1990; Engelmann *et al.* 1990). The Purbeck fauna is dominated by the Plagiaulacoidea which first appeared here. We have recognized two families within the Plagiaulacoidea: Plagiaulacidae with two subfamilies (Plagiaulacinae mostly for the European genera, but possibly occurring also in North America, and Eobaatarinae for Early Cretaceous European and Asian genera), and the family Allodontidae for the North American Late Jurassic genera. The genus *Bolodon* assigned by Hahn and Hahn (1983) to the Paulchoffatiidae, in our opinion, belongs to the Plagiaulacidae (Plagiaulacinae). As demonstrated in this study, rare and generally very small surviving members of the Paulchoffatiidae are also found in Purbeck strata.

From the Early Cretaceous (Barremian) (Mohr 1989) of Spain, isolated teeth are known (genus *Parendotherium* and *Plagiaulax?* sp.) assigned to the Paulchoffatiidae and Plagiaulacinae respectively (Crusafont Pairó and Adrover 1966; Crusafont and Gibert 1976; Hahn and Hahn 1983). The Early Cretaceous (Valanginian) English multituberculate *Loxaulax* (Simpson 1928; Clemens 1963; Clemens and Lees 1971) has been placed by Kielan-Jaworowska *et al.* (1987) in the Eobaataridae, regarded by us as a subfamily of the Plagiaulacidae.

Coeval with the Eobaatarinae there occurs in the Early Cretaceous of Asia a highly specialized family, the Arginbaataridae, assigned by us to a suborder *incertae sedis*. A single Early Cretaceous paulchoffatoid m1 assigned to a family of its own – the Hahnodontidae – has been recently found in North Africa (Sigogneau-Russell 1991). A large collection of isolated multituberculate teeth was obtained many years ago from the Albian of Texas (Patterson 1956; Slaughter 1965) and is currently being described by Krause and others (see Abstract by Krause *et al.* 1990). Early Cretaceous multituberculates have also recently been recovered from Cloverly Formation localities in Montana by D. W. Krause and R. Cifelli (personal communication from D. W. Krause to Z.K.-J.).

It follows from the foregoing review that Middle to Late Jurassic and Early Cretaceous multituberculates are scarce and poorly known. The relationships between the suborders Paulchoffatoidea and Plagiaulacoidea and between them and members of the two later multituberculate suborders Taeniolabidoidea and Ptilodontoidea are still poorly understood. We believe that continuing study by one of us (P.C.E.) of samples from the Purbeck Limestone Formation and the resultant study of the morphology and enamel microstructure of the teeth may contribute to a better understanding of multituberculate phylogeny and interrelationships among the multituberculate suborders.

Acknowledgements. Mr W. T. Haysom drew the attention of one of us (P.C.E.) to the quarries at Sunnydown Farm. The excavation of this site was carried out with permission from the owners Mr and Mrs R. F. Notley and was funded by the Dorset Natural History and Archaeological Society who have given permission for the authors to study the material collected. Access to other quarries was granted by Messrs P. Lovell and C. Suttle. The Area Museum Council for the South West gave grant-aid for the sieving machine that was built and installed at the Dorset County Museum by Mr S. M. Etches. The latter, along with S. Baker, A. and P. Blackler, A. Brokenshire, Mrs M. Ensom, S. Riley, R. Road, S. Roles, J. Seabrook, P. Stevens, Mrs J. Thomas and W. Wilblood helped P.C.E. with the excavations. Mrs H. Machen and Mrs C. Cook gave great assistance with the sieving, and G. Bate with the picking of residues.

During the course of this study we compared casts of Late Jurassic multituberculates from England, housed in the BMNH collection, and from North America housed at the YPM collection, sent to Z. K.-J. in 1986 by Dr J. J. Hooker and Professor J. Ostrom respectively. Z. K.-J. was able to study a large collection of casts of various multituberculates housed at the Department of Anatomical Sciences of the State University of New York at Stony Brook, in charge of Professor D. W. Krause. Professors J. A. Hopson (Chicago), G. Hahn (Marburg) and D. W. Krause (Stony Brook) read the manuscript of this paper and provided most useful comments. The SEM micrographs were taken by Z. K.-J. and Ms T. Rolfsen (Institute of Biology, University of Oslo), and the drawings prepared by Mr B. Bocianowski after Z. K.-J. pencil sketches. Research of Z. K.-J. was supported by funds from Norges Allmennvitenskapelige Forskningsråd (grant ABC/LR 441. 90/002). To all these persons and institutions we express our sincere thanks and gratitude. This paper is Contribution No. 363 from the Paleontological Museum, University of Oslo.

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Z. KIELAN-JAWOROWSKA
Paleontologisk Museum
Universitetet i Oslo
Sars gate 1, N-0562 Oslo 5, Norway

P. C. ENSOM
Yorkshire Museum, Museum Gardens
York YO1 2DR, UK

Typescript received 12 September 1990
Revised typescript received 27 February 1991

TWO NEW CORNUTES FROM THE LOWER ORDOVICIAN OF SHROPSHIRE AND SOUTHERN FRANCE

by P. E. J. DALEY

ABSTRACT. Two new cornutes, *Chauvelicystis vizcainoi* sp. nov., and *Prochauvelicystis semispinosa* gen. et sp. nov. are described. *C. vizcainoi*, from the lower Ordovician (Lower Arenig) of the South of France, has previously been synonymized with *Chauvelicystis spinosa* Ubaghs, 1969, and is shown to be the sister taxon of *C. ubaghsi* (Chauvel, 1966). *Prochauvelicystis semispinosa* is found in the Tremadoc stage (lowest Ordovician) of Shropshire, England. It is the smallest known cornute, and has spines along the right marginals of the head and fixed extensions of the marginal plates forming horizontal appendages on the left side of the head. The spines and appendages are for support on a soft substrate and prevention of movement in an unwanted direction during locomotion. It is the most primitive member of the new subfamily Chauvelicystinae.

THE aims of this paper are threefold: (1) to erect a new species, *Chauvelicystis vizcainoi*, for a cornute from the Lower Arenig of the South of France previously described by Ubaghs (1983), but wrongly identified by him with *Chauvelicystis spinosa* Ubaghs, 1969; (2) to describe *Prochauvelicystis semispinosa*, a new genus and species of cornute, and to consider its functional morphology; and (3) to reconstruct the phylogeny of these and related forms.

Cornutes are controversial animals, and their morphology is currently interpreted in three incompatible ways, associated respectively with the names of Ubaghs (1967, 1981), Jefferies (1967, 1986) and Philip (1979). Ubaghs and Philip regard cornutes as echinoderms, but differ in interpretation of their structures, whereas Jefferies, and Cripps (1988, 1989*a*, 1989*b*) regard them as stem chordates; this interpretation will be adopted throughout this paper.

SYSTEMATIC PALAEOONTOLOGY

Superphylum DEUTEROSTOMIA Grobden, 1908
Subsuperphylum DEXIOTHETICA Jefferies, 1979
Phylum CHORDATA Bateson, 1886
(Stem group of the Chordata)
Grade CORNUTA Jaekel, 1900 (rank emended)
Family PHYLLOCYSTIDAE Derstler, 1979
Subfamily CHAUVELICYSTINAE subfam. nov.
Genus CHAUVELICYSTIS Ubaghs, 1969

Type species. *Chauvelicystis spinosa* Ubaghs, 1969

Chauvelicystis vizcainoi sp. nov.

Text-fig. 1

(*non Chauvelicystis spinosa* Ubaghs, 1969, pp. 53–56, fig. 23.)

1983 *Chauvelicystis spinosa* Ubaghs, pp. 40–45; fig. A.

1988 *Chauvelicystis spinosa* Ubaghs; Parsley, p. 348, fig. 26.1.

1988 *Chauvelicystis spinosa* Ubaghs; Ubaghs and Robison, p. 15, fig. 6.

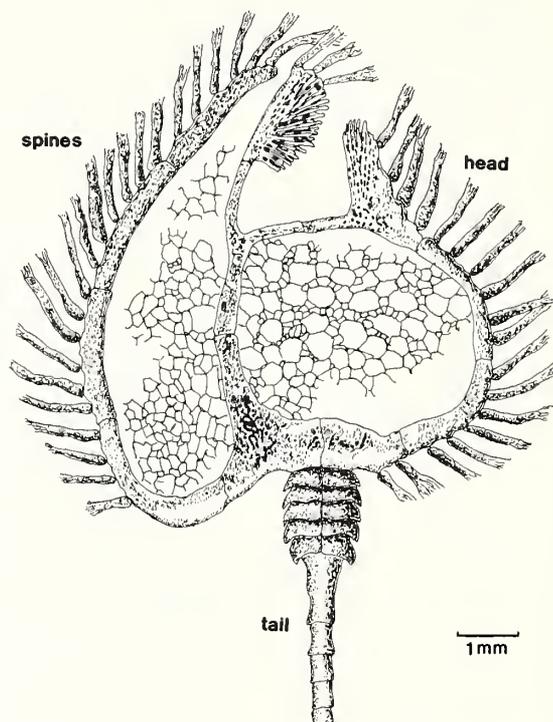
Etymology. The species is named in honour of M. Daniel Vizcaïno of Carcassonne, France, who collected most of the relevant material.

Holotype. Specimen A, Melchior Collection, Laboratoire de Géologie Sédimentaire et Paléontologie, Université Paul-Sabatier, Toulouse, France.

Material, horizon and locality. Two nodules bearing part and counter-part of two individuals, specimens A and B, from level *f* of the Lower Arenig *schistes de St Chinian*, Pech de Cossenon, France, Melchior Collection, Université Paul-Sabatier, Toulouse, France, A quartzite nodule bearing the remains of about five individuals denoted by C1, C2, etc. from Cassagnoles, France, Lower Arenig, level *g*, Courtessole-Vizcaïno Collection, Laboratoire de Géologie Sédimentaire et Paléontologie, Université Paul-Sabatier, Toulouse, France, No. OE9.

Diagnosis. Plate b with oar-shaped horizontal flange of fibrillar stereom with three spines attached to its anterior edge, and a convex spineless left edge; spines surrounding the head are either straight or very slightly curved forwards and blunt, with splayed out ends; distance from the tip of the l-appendage to the base greater than the width of base (Text-fig. 1).

TEXT-FIG. 1. Ventral view of *Chauvelicystis vizcainoi* (after Ubaghs 1983, fig. 11).



Discussion. *C. vizcainoi* differs from *C. spinosa* Ubaghs, 1969, with which it was incorrectly synonymized by Ubaghs (1983), since *C. vizcainoi* possesses an l-appendage, a flange on plate b, an open frame behind the mouth, and blunt-ended spines. In contrast, *C. spinosa* has no l-appendage, no flanges on plate b, a closed mouth frame and pointed spines. *C. vizcainoi* differs from the similar species *C. ubaghsi* Chauvel, 1966, in that the latter has a less strongly curved buccal lobe region of the head, short broadly-based l-appendage and fan-shaped distal region of plate b.

Genus PROCHAUVELICYSTIS gen. nov.

Etymology. *Pro*, before, and *chauvelicystis*, a name given by Ubaghs (1969, p. 53) in honour of the late M. Jean Chauvel, who contributed much to the study of cornutes and mitrates.

Type species. *P. semispinosa* sp. nov. here designated.

Prochauvelicystis semispinosa sp. nov.

Text-figs 3–12

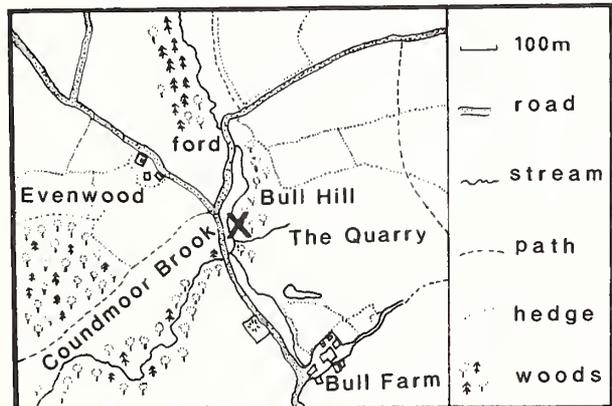
Etymology. *semi*, half and *spinosa*, spined – from the presence of spines on the right side of the head only.

Holotype. British Museum (Natural History), London; BM(MH) E63366 from the Arenaceous Beds of Shropshire, England.

Additional material, horizon and locality. Five further specimens, BM(NH) E63363–E63365, E63367 and E63477. The specimens were collected by Dr R. P. S. Jefferies and Dr R. A. Fortey of the British Museum (Natural History) and Dr R. Owens of the National Museum of Wales in March 1987.

The specimens were found in a soft yellow-green shaly horizon of the so-called Arenaceous Beds, part of the Shineton Shales formation of the Tremadoc stage in Shropshire, England (Stubblefield and Bulman 1927). The Tremadoc is now considered to be of lowest Ordovician age (Norford 1988). The collection site was the low river cliff forming the east bank of the Coundmoor Brook, near Bull Hill Cottage, Harnage Grange, Cressage, Shropshire, UK National Grid reference SJ 555 014 (Text-fig. 2), location C of Stubblefield and Bulman (1927, p. 114).

TEXT-FIG. 2. Locality map redrawn from Ordnance Survey 1/25,000 sheet SJ40/50 2nd series 1979. Collecting site marked 'X'.



The Arenaceous Beds contain no species of the youngest British Tremadoc biozone fauna (that of *Angelina sedgwicki*), but some species of the second youngest biozone fauna (that of *Shumardia (Conophrys) salopiensis*) are present, suggesting that the lower Arenaceous Beds are slightly younger than the *S. (C.) salopiensis* Zone, but probably older than the *A. sedgwicki* Zone (Fortey and Owens 1991).

The Arenaceous Beds show evidence of having been laid down as turbidites and contain a diverse continental-shelf trilobite fauna, but the absence of graptolites implies that deposition was not in the open sea (R. A. Fortey, pers. comm., 1990). The presence of complete trilobites and remains of moulted exoskeletons in the Arenaceous Beds suggests that the fossil assemblages are *in situ*, and have not been transported.

Diagnosis. A cornute with spines on the right side of the head only; left side marginal plates extend horizontally and forward as rigid appendages; a trapezoidal x-plate and somewhat flattened ventral surface.

METHODS AND TERMINOLOGY

Prochauvelicystis semispinosa was reconstructed by drawing the natural moulds and latex casts to scale on a drawing board. Six projections were drawn: dorsal and ventral, anterior and posterior, right and left lateral (Text-fig. 3).

The plate nomenclature follows the system established by Jefferies and Prokop (1972), as revised

in Jefferies, Lewis, and Donovan (1987). This system uses letters or numbers, or a combination of them, to identify homologous plates. A combination of characters implies plate fusion, e.g. plate de is believed to result from fusion of plates d and e.

DESCRIPTION

Head

The head is boot-shaped, but is less asymmetrical than in, for example, *Cothurnocystis elizae* Bather, 1913. As in all cornutes, the skeleton of the head is formed from plates of calcite stereom, histologically identical to the calcite skeleton of echinoderms. The microstructure of this stereom is mainly labyrinthic (see Smith 1980, p. 8 for stereom histology). Text-figures 3 and 5a–b show the general appearance of *Prochaulocystis semispinosa* while Text-figure 4 shows the marginal plates of the head and their nomenclature.

On the left side of the head three similarly sized subtriangular plates, k, t, and l, are prolonged to form appendages (Text-figs 3, 4, 5a–b). The junctions between these plates are small in area and possibly allowed some relative movement. The appendages point forwards and their ventral surfaces are flat.

Plate x is a small trapezoidal plate whose left posterior edge contacts plate l (Text-figs 4, 5a). The anterior face of x touches the posterior part of plate b.

Plate a (Text-figs 3b, 5a–b) is produced posteriorly into a strut process which meets the strut process of plate g. The strut process of a is curved slightly to the right posteriorly and is posteriorly truncated. The mid-part of the left side sutures with the anterior right side of plate l. Anteriorly plate a contacts the posterior margin of plate b. Plate x fits on to a dorsal facet in plate a and covers almost all of the anterior half of the latter plate (Text-figs 4, 5a).

Plate b is a large blade-like plate which frames the left side of the oral region and the buccal cavity (Text-figs 3–4, 5a–b, 6). It is somewhat thickened proximally, but tapers peripherally to a flange of fasciculate stereom. The flange would increase the area of the substrate supporting the weight of the head, thus lessening any tendency to sink in the mud.

Plate c forms much of the right side of the oral lobe and of the buccal cavity (Text-figs 3–4, 6). It is similar in shape to plate b, but smaller and with a less pronounced flange. The relative positions of the sites of attachment of the buccal integument to plates b and c show that the mouth opened obliquely leftwards at about 45° to the longitudinal axis (Text-figs 3, 6).

About 15 spines articulate in a single horizontal row to the outer edge of the right marginal plates (Text-fig. 3). The spines point anteriorly, as do the appendages on the left side of the head. On all of the right marginal plates, the spines are separate from the marginals themselves, and articulate by small tubercles fitting into sockets in the marginals. They may have been capable of active movement, but scars for muscle attachment are not visible. They certainly would have been able to move passively. The row of spines begins posteriorly with the minute hindmost spine on plate g, increase in size along f, and then decrease to two-thirds of this size on the distal part of c. All spines consist of fasciculate stereom (Text-fig. 5c).

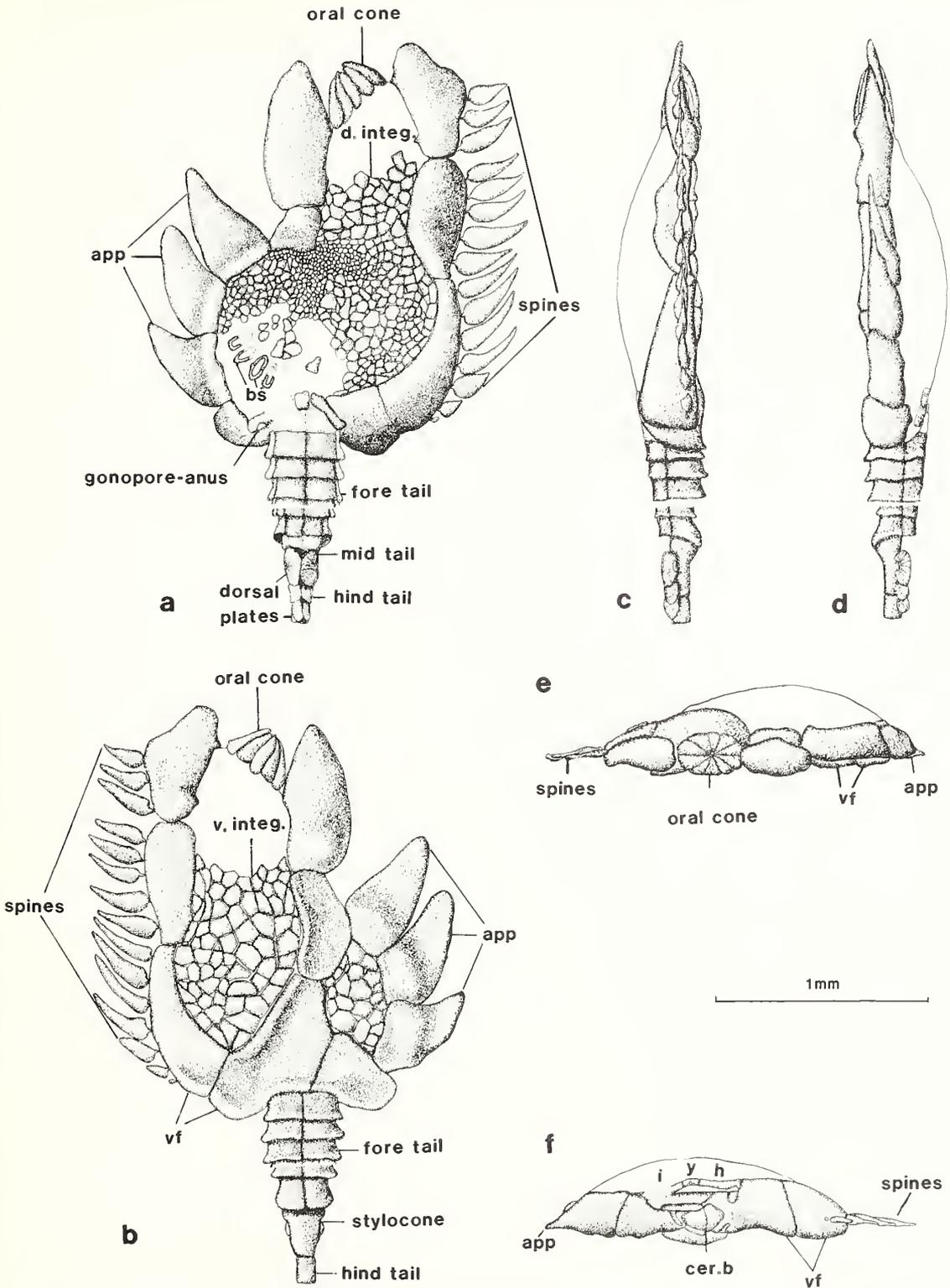
Plate de contacts the posterior part of plate c and probably results from fusion of plates d and e (Text-fig. 7). This plate has on its median surface a pronounced overhang (Text-figs 3a, 5a), the median apex of which probably marks the right posterior angle of the buccal cavity.

Plate f adjoins plate de (Text-fig. 5a). It widens and becomes higher posteriorly, from its low and narrow junction with the latter. It bears a ventral posterior flange and a roughened raised postero-dorsal ridge.

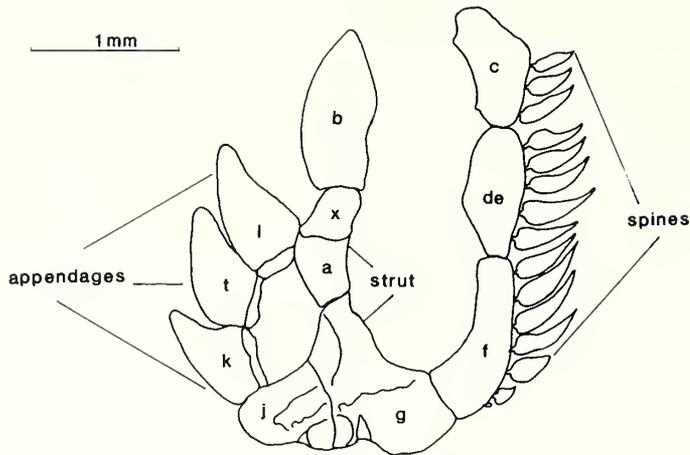
Plate g is the largest plate (Text-figs 5a–b, 8). Its right side attaches to f by a suture of complex curvature which would have prevented any movement. The posterior left part of g is expanded to form a lobe which bears on its ventral outer margin a flange directed downwards posteriorly and continuous with that of f. This flange becomes less pronounced leftwards, and is also absent at the tail-junction. At the latter region g was probably overlapped by the anterior ventral plates of the fore-tail. The right half of the cerebral basin forms a deep excavation in the left half of g lined with microperforate stereom. Just to the right of the basin, and running roughly parallel to its edge, is the reception groove for the tail insertion. As with plate f, the dorsal part of plate g is a raised area of coarse labyrinthic stereom. A right-angled excavation in the left side of the raised area is the attachment site for plate h (Text-figs 5a, 8).

Anteriorly, plate g is prolonged to form the posterior part of the strut. The strut curves leftwards anteriorly and is keeled dorsally, forming two faces sloping away from each other (Text-figs 5a, 8). Ventrally, it bears a shallow depression whose margins are parallel to the outline of the plate (Text-fig. 5b).

Plate j sutures to the left of plate g at a gently curved joint, convex leftwards in dorsal aspect (Text-figs 5a–b, 8). Like g, it has a flange on its postero-ventral edge which decreases in depth medially, disappearing at



TEXT-FIG. 3. Reconstruction of *Prochauvelicystis semispinosa*: *a*, dorsal aspect; *b*, ventral aspect; *c*, right lateral aspect; *d*, left lateral aspect; *e*, anterior aspect; *f*, posterior aspect. Abbreviations: app., appendages; cer. b., cerebral basin; d. integ., dorsal integument; v.f., ventral flanges; v. integ., ventral integument.



TEXT-FIG. 4. Marginal and strut plates of *Prochauvelicystis semispinosa*.

the tail junction. This flange also becomes lower towards the left margin of the plate. As in plate g, a shallow excavation occupies most of the ventral surface of the plate (Text-figs 3b, 5a). The area of raised coarse stereom forming the dorsal external surface of the plate is less pronounced than in g. On the inner face, the gonorectal groove runs leftward from the suture with g and ends in an upward-running groove (Text-figs 5a, 8). Parallel to the gonorectal groove, and anterior to it, is a thin wall of stereom which would have formed the rear boundary of the posterior coelom (Text-figs 5a, 8).

The dorsal tail-junction plates h, y, and i, are poorly preserved. Plate h is long with a straight right portion and a somewhat curved left part (Text-figs 5a, 8).

Plate y is a small element bearing a notch posteriorly (Text-figs 3, 5a). In the cornute *Ceratocystis perneri*, Jefferies (1969, p. 521) suggests that this notch is associated with a nerve leading directly upward from the brain and that it could have been the site of a median eye. The same is presumably possible for *P. semispinosa*.

Plate i is very poorly preserved with only about half remaining (Text-fig. 5a). A poorly defined notch at one end may indicate the dorsal margin of the gonopore-anus. Plate i would overlies the gonorectal groove in life.

The skeleton of the dorsal integument of the head is formed from small rounded polygonal plates of labyrinthine stereom which vary in size in different regions of the head (Text-figs 3a, 5a, 9c). In the buccal cavity region, framed by plates x, b, c and de, the integument plates are larger than those covering the rest of the head, while in a small area adjoining plate x posteriorly, and to the right, they are much smaller (Text-fig. 5a). The dorsal integument in the branchial region is largely missing.

The skeleton of the ventral integument is formed from large polygonal plates of retiform stereom, usually about three to four times as large in area as the dorsal plates of the buccal cavity (Text-figs 2b, 9b, d). Much of the integument has been lost in the specimens both dorsally and ventrally. The ventral integument of the buccal cavity is particularly poorly preserved (Text-fig. 5b).

Openings of the head

The branchial slits open on the dorsal surface of the left part of the pharyngeal region of the head (Text-fig. 3a). The branchial skeleton is poorly preserved with only three or four posterior U-shaped plates, and possibly one anterior U-shaped plate, remaining in specimen E63366 (Text-fig. 5d). The precise number and detailed structure of the branchial elements is thus unknown.

The mouth of *P. semispinosa* would have opened leftward, as indicated by the attachment areas of the buccal integument plates band c (Text-figs 5e, 6). As plates b and c do not meet, the mouth was probably terminal, not dorsal as in *Phyllocystis*. In the mouth region three or four spine-shaped plates along the internal edge of plate b suggest the presence of an oral cone like that of *Cothurnocystis elizae* (Bather 1913, p. 399; Jefferies 1967, pp. 165–166, 1986, pp. 194–195; Text-figs 3a, 5a herein).

The gonopore-anus of *P. semispinosa* opens to the left of the tail-inscription (Text-figs 3a, 5a). A rounded notch in plate i and a notch in plate j in the left posterior part of the gonorectal groove indicate its position.

Chambers of the head

Jefferies (1967, 1968, 1969, 1979, 1981*a*, 1981*b*, 1986) has reconstructed several chambers in the cornute head. These are indicated by changes in the surface texture of the stereom of the internal surfaces of the marginal plates, and also by the nature of the integument plates (Text-figs 3, 5–8).

The buccal cavity of *P. semispinosa* was presumably bounded by the mouth anteriorly, and posteriorly on the right side by the apex of the overhang of plate *de*. On the left posterior side, it could have been bounded by the rearmost right corner of plate *x*. As already mentioned, the dorsal integument of the buccal cavity was plated with larger ossicles than those of the rest of the dorsal surface (Text-figs 3*a*, 5*a*).

The pharynx would have run from the posterior boundary of the buccal cavity to the region of the branchial slits. In the dorsal integument its position is indicated by smaller plates than those over the buccal cavity particularly in a small area contiguous with plate *x* (Text-fig. 5*a*).

The right anterior coelom would lie below the pharynx on the right side of the head. It would have been bounded on its right and posterior sides by plates *f* and *g*, and on its anterior side by a line which runs from the apex of the overhang of plate *de* to a ridge on the dorsal side of *g* (Text-figs 5–8). Plates *f* and *g* show evidence of the presence of this coelom by a denser stereom texture on the ventral part of their internal faces. The line separating these textures was the pharyngo-visceral line which in life would be the boundary between the pharynx and the right anterior coelom (Text-fig. 5*e*). The right anterior coelom is homologous to the right metacoel of the hypothetical *Cephalodiscus*-like ancestor.

The anterior limit of the gonorectal groove is marked by a weak ridge on plate *g* which also forms the left boundary of the right anterior coelom (Text-figs 5*a*, 8). The gonorectal groove is better developed on plate *j*, as described earlier.

The anterior boundary of the posterior coelom is marked by a thin wall of stereom on the anterior side of the gonorectal groove. The right side of this coelom is indicated by a hemispheroidal excavation on plate *g* (Text-figs 5*a*, 8, 9*a*, 10). The posterior coelom would have overlain the gut but it is not clear where its posterior boundary lay.

A left anterior coelom may have been present, but would have been a purely virtual chamber (Jefferies 1967, 1986; Jefferies and Lewis 1978; Jefferies *et al.* 1987). The possible presence of this coelom is inferred from the theory of descent from a *Cephalodiscus*-like ancestor, (Jefferies 1967–1986). It would correspond to the left somatocoel of echinoderms (Jefferies 1986, p. 284).

Tail

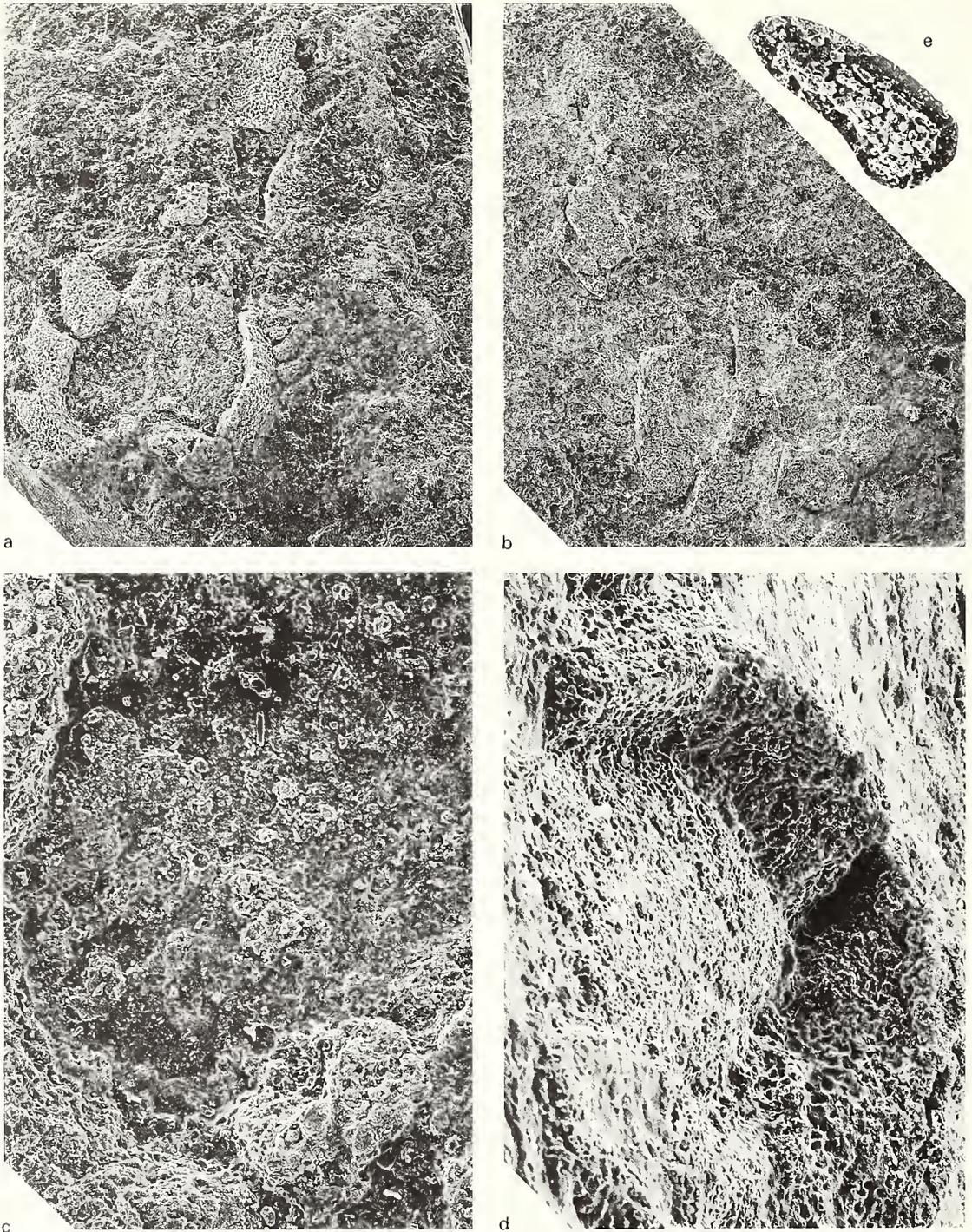
The tail of *P. semispinosa* is poorly preserved, but enough remains for a reconstruction. Apart from the dorsal plates, its skeleton is formed from labyrinthic stereom.

As in all cornutes, the tail is divided into three regions; fore-tail, mid-tail, and hind-tail (Text-figs 3, 11). The fore-tail is attached to the head at the reception grooves, as already described. The usual cornute pattern of articulating rings, each composed of four plates, is present. Ventrally the fore-tail skeleton consists of a series of paired plates. These are in the form of two adjacent hollow quarter-cylinders, whose antero-posterior length is about half the radius. They subtend an angle of a little more than 90° when viewed from behind, and consequently their ascending processes are just visible in dorsal view (Text-figs 3, 9*a–b*, *d*, 10, 12*d*).

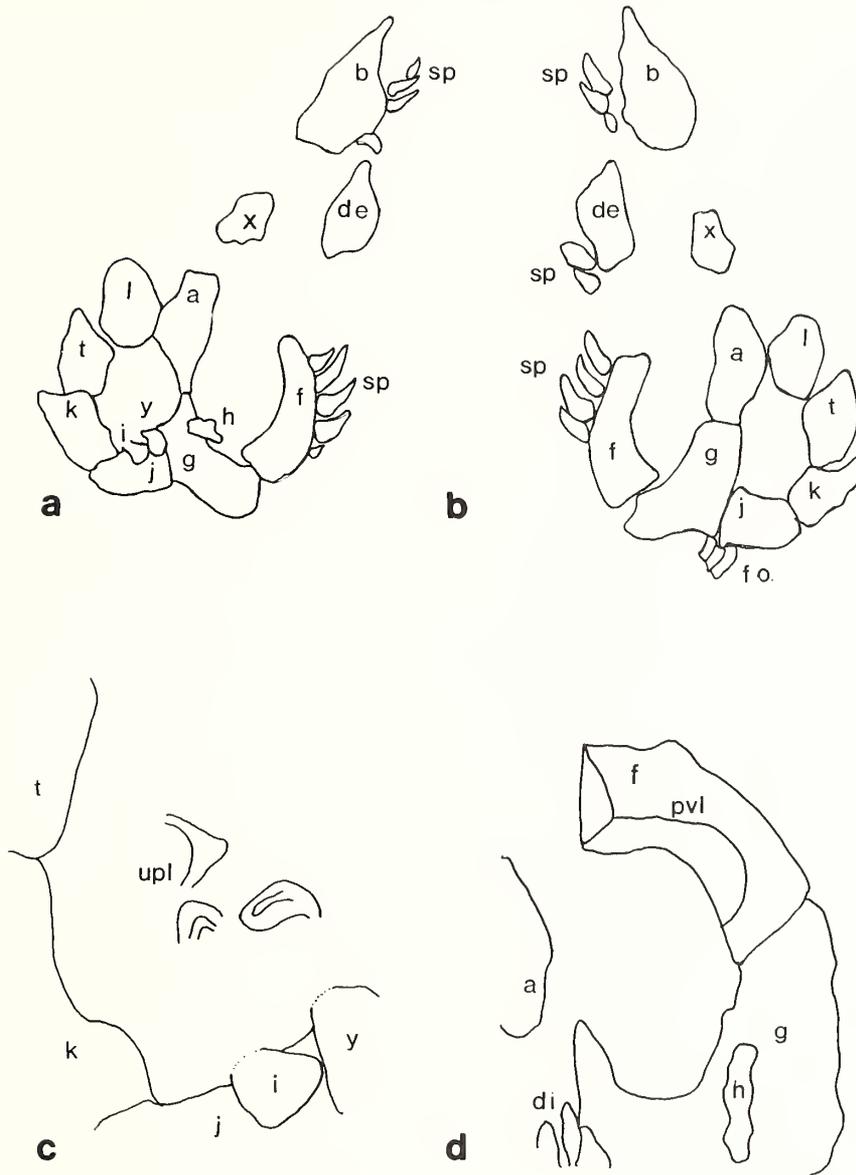
The dorsal plates of the fore-tail are also paired and curved in transverse section (Text-figs 9*a–b*, 10, 11*a–d*). They are somewhat flattened dorsally, and have an almost straight suture where they meet in the mid-line. They curve sharply downward at their margins, where they join the dorsal faces of the ventral plates (Text-fig. 11*d*).

The plates of each fore-tail ring overlap the plates of the ring behind, and each pair of ventral plates is expanded posteriorly. The most posterior fore-tail ring overlaps the anterior part of the mid-tail and shows pronounced rearwardly expanded extensions of the two ventral plates (Text-figs 3*b*, 9*b*). The number of fore-tail rings is unknown, but comparisons with related cornutes suggest that there would have been from five to seven.

The mid-tail includes the stylocone which is shaped like a truncated half-cone (Text-figs 9*a–b*, 10, 11*a–c*). The ventrolateral surfaces of the stylocone, which would have been external surfaces in life, are covered with minute papillae. The dorsal surface is complex in form, with a median groove flanked by a pair of ridges, and these ridges are each interrupted by transverse grooves. Lateral to the ridges, the surface of the stylocone slopes downwards and outwards at an angle of about 15°. The stylocone bears a deep excavation anteriorly, which is triangular in plan view. This excavation is deeper at the anterior end of the stylocone and tapers into the median groove. From its broad anterior part, the stylocone tapers distally. About two-thirds of the way along its antero-posterior length, paired lateral processes exist. It is possible, but not certain, that these swellings may have articulated with dorsal plates.



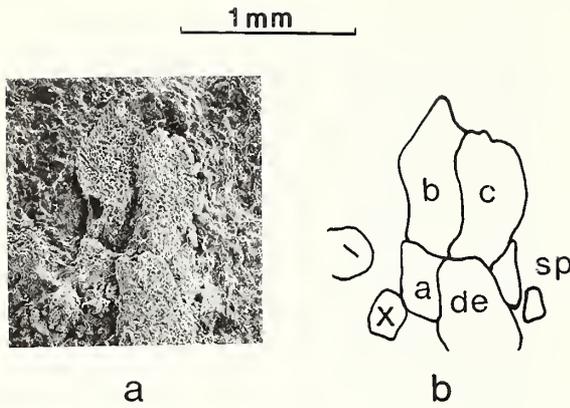
TEXT-FIG. 5. *Prochauvelicystis semispinosa* gen. et sp. nov. Scanning electron micrographs of gold/palladium coated latex casts. All specimens preserved in the British Museum (Natural History). Plate nomenclature and labelling are given in Text-figure 6. *a*, E63366*a*; holotype; showing one individual; plates of the pharyngeal area are dissociated or missing, $\times 20$. *b*, E63366*b*; counterpart of E63366*a*; showing ventral surface, $\times 20$. *c*, Spine of E63366*a*; dorsal view, $\times 90$. *d*, Enlargement of E63366*a*; showing branchial skeleton, $\times 120$. *e*, Internal view of plate *f* of E63366*a*; showing pharyngo-visceral line, $\times 67$.



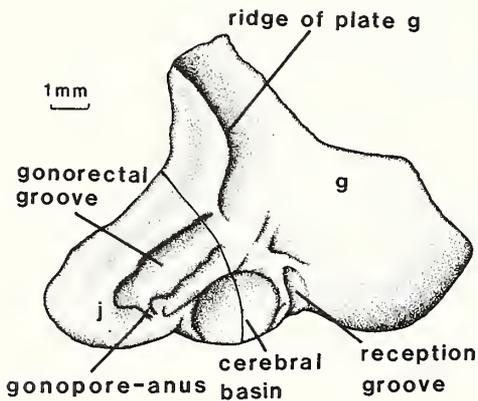
TEXT-FIG. 6. Explanatory tracing of Text-figure 5. Letters represent plate nomenclature except for: di, dorsal integument plates; fo, fore-tail plates; pvl, pharyngo-visceral line; sp, spines; upl, U-shaped plates of branchial skeleton.

The dorsal plates of the mid-tail are elliptical structures of fasciculate stereom with a thickened, roughly semi-circular, ventral articulating surface (Text-figs 3a, 9a-b, 10, 11a-b). The edges are poorly preserved, so that the precise outline of these plates is uncertain. Two pairs of these plates probably covered the distal part of the stylocone.

The hind-tail is very poorly preserved with only one ventral ossicle remaining (Text-figs 9a-b, 11a-c). This seems very like the distal part of the stylocone, with a median groove flanked by a pair of ridges, each of which is interrupted half way along its length by a transverse groove. The dorsal surface on either side of the ridges



TEXT-FIG. 7. *a*, Electron micrograph of BMNH E63365*a*, showing dorsal view of plates *b* and *c*. *b*, explanatory tracing of *a*; letters represent plate nomenclature except for *sp*, spines.



TEXT-FIG. 8. *Prochauvelicystis semispinosa*. Detail of plates *g* and *j* in dorsal aspect.

slopes downwards and outwards. The posterior part of the stylocone and the hind-tail ossicle thus have the same cross-section. The ventral and lateral surfaces of the hind-tail ossicle are papillate as in the stylocone. It is highly likely that a pair of dorsal plates articulated to this ossicle as they did to the stylocone, but these cannot be identified with certainty among the preserved material.

With only one preserved ossicle, the total number of hind-tail ossicles is indeterminate. As the cross-sectional area of the remaining ossicle is about equal to that of the distal end of the stylocone, it is likely that it was part of the proximal hind-tail. The parallel sides of this ossicle suggest that the tail did not taper steeply, and therefore there could have been more than one ossicle in the hind-tail.

FUNCTIONAL MORPHOLOGY

Spines and appendages

Spines and appendages are not synonymous in cornute morphology. Spines are defined as long narrow, pointed structures movably articulated to a marginal plate (Text-figs 3, 5*c*, 11). Appendages are horizontal prolongations of part or all of a marginal plate, fully integral with its structure and therefore not capable of relative movement.

Spines and appendages have different phylogenetic origins. The *k* and *t* appendages are developed from the *k* and *t* spikes of other cornutes, while the *l* appendage is found in the most primitive known forms (Jefferies *et al.* 1987, pp. 442–446). However, the spines are a new development, found only in the genera *Prochauvelicystis* and *Chauvelicystis* (Chauvel 1966; Ubaghs 1969, 1983).

Spines and appendages could support the weight of the head on the substrate, by increasing the weight-bearing surface and thus reducing the load per unit area. This would enable the animal to rest on a soft substrate. In the closely related genus *Phyllocystis*, a peripheral flange fulfilled this function (Ubaghs 1969). Compared to a flange, spines and appendages may have had the advantage that there would be less suction force to be overcome when the animal moved.

If the spines and appendages were purely supportive structures, then they would be expected to be directed radially from the centre of the head. In fact they point forwards. This orientation would hinder movement in a forward direction (Text-fig. 12). It might be suggested that *P. semispinosa* could face into a constant current, and use the spines and appendages as anchoring devices. However, judging by the fine grain of the sediment the environment was usually tranquil so this explanation is implausible. Also, the ability of the spines to fold against the side of the head only makes functional sense if *P. semispinosa* were capable of locomotion.

Locomotion

P. semispinosa was probably able to move actively across the substrate. It is possible to reconstruct the locomotory cycle of *P. semispinosa* from its morphology, although the uncertain number of fore-tail plates and hind-tail ossicles means that any reconstruction is tentative. Cornutes probably moved mainly rearwards, that is, tail first (Jefferies 1986, pp. 204, 213, 232; Jefferies *et al.* 1987, pp. 476–480; Parsley 1988, p. 352; Cripps 1989a, p. 234; 1989b, pp. 73–76; Woods and Jefferies 1992, pp. 1–25). The forwardly directed spines and appendages of *P. semispinosa* seem to confirm this view, as they would greatly hinder forward motion. Furthermore, an asymmetrical shape, such as the head of a boot-shaped cornute, is easier to pull across a surface than to push, as it is directionally stable when pulled, but directionally unstable when pushed.

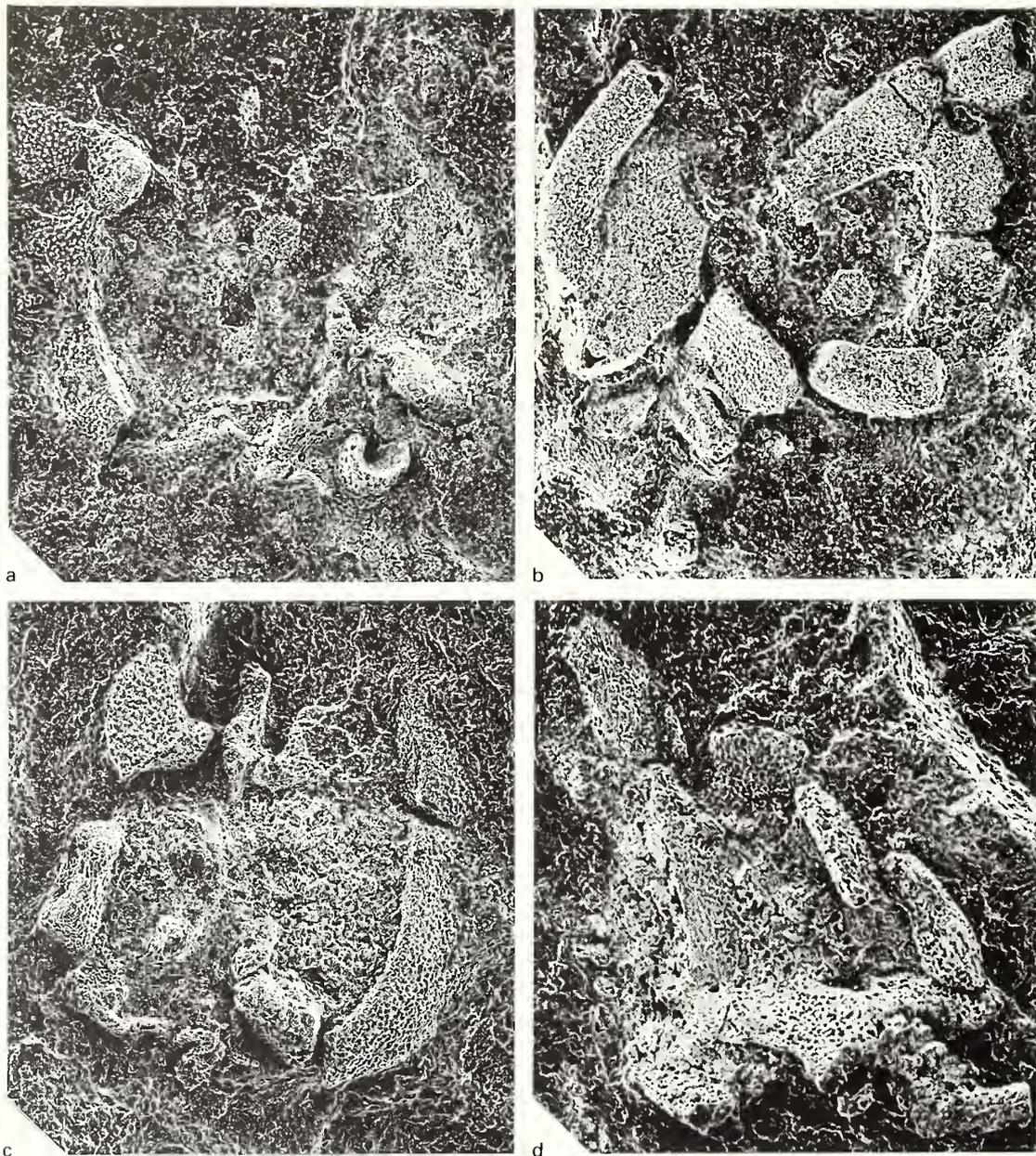
P. semispinosa probably lived on the surface of the mud which formed the sea bed. The mud was likely to have been soft, as implied by its lithology, and by the weight-saving and load-spreading adaptations of *P. semispinosa* itself. Thus *P. semispinosa* could have inserted its tail into the substrate by bending it ventrally, and in doing so exerted a force which would have raised the rear part of the head, and moved the head as a whole rearwards. Horizontal force alone would not have moved the head as the flanges on the postero-ventral margins of plates f, g and j would have held the head firmly in the substrate (Text-figs 3, 5b).

The shape of the fore-tail rings suggests that they could have been displaced ventrally at an angle of 15° to 20° between adjacent rings. If, as seems likely, there were six or seven rings in the fore-tail, then the fully bent fore-tail would have subtended an angle of between 90° and 140° in the vertical plane, enough both to raise the head and pull it along. Similarly, the fore-tail rings could be displaced relatively by about 10° horizontally, giving an overall flexion of 60° to 70°, enough to allow the tail to move from side to side and to change the direction of movement of the head.

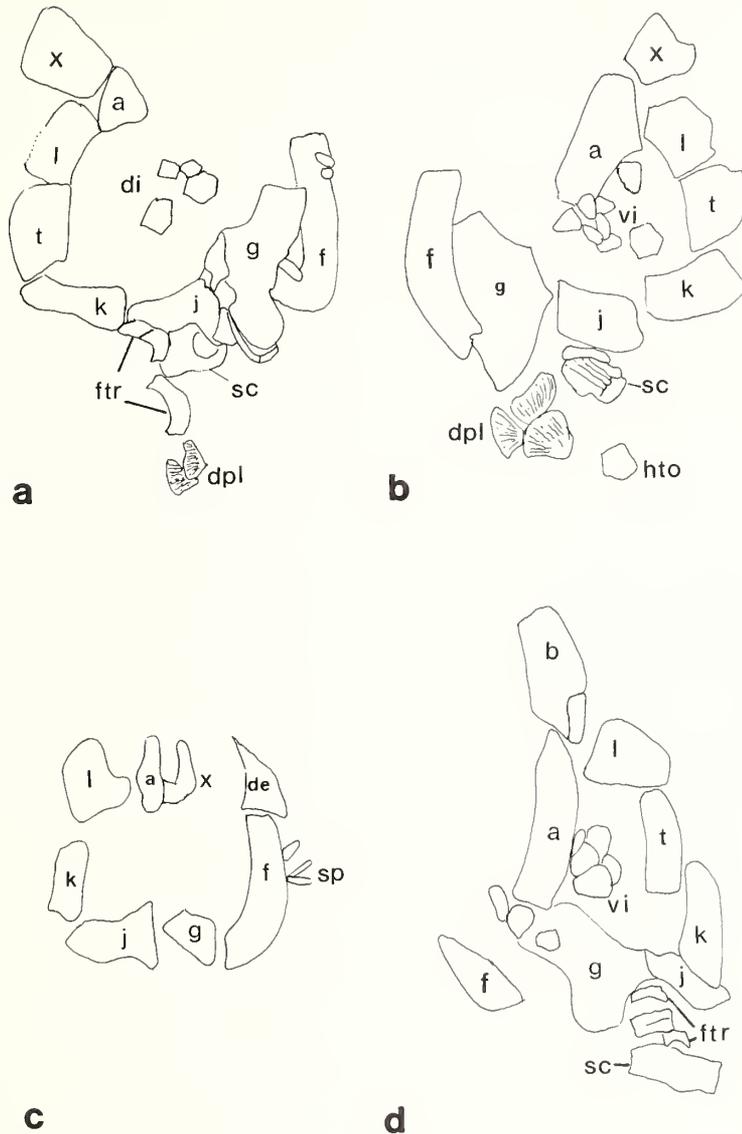
The papillate texture of the ventral surfaces of the stylocone and the hind-tail ossicle probably helped to make the grip on the substrate greater than it would have been had their texture been smooth, a further possible adaptation to living on soft mud.

In the following discussion, the term 'yaw' refers to movement in a horizontal plane about a vertical axis, while the term 'roll' refers to rotation about a horizontal antero-posterior axis. It is assumed that there is no effective resistance from the water, and that both the water and mud are undisturbed by currents. In Text-figure 13a, *P. semispinosa* is shown at rest with the spines extended roughly at right angles to the head. Locomotion started with the tail bending ventrally into the mud, raising the posterior ventral flanges of the head clear of the substrate (Text-fig. 13d) and pulling the head rearward (Text-fig. 13b), causing the spines to lie flush with the right marginal plates. The centre of mass was probably to the right of the axis of symmetry of the tail and so the ventral bending of the tail would have caused the head to yaw anticlockwise as seen from above, and to roll downwards to the right so that it is supported by the right marginal plates (Text-fig. 13c). The combination of roll and yaw would probably have bent the tail to the left (Text-fig. 13c). The appendages of the left side of the head would have been clear of the substrate.

The tail would then have been pulled out of the mud, exerting a forwardly directed force, which



TEXT-FIG. 9. *Prochauvelicystis semispinosa* gen. et sp. nov. Light micrographs of latexes whitened with sublimated ammonium chloride. All specimens preserved in the British Museum (Natural History). Plate nomenclature and labelling are given in Text-figure 10. *a*, E63477*a*; dorsal view of specimen showing marginal plates, fore-tail plates, proximal part of stylocone, dorsal plates and hind-tail ossicle, $\times 20$. *b*, E63477*b*; counterpart of E63477*a*; showing ventral views of marginal plates and hind-tail ossicle, and the distal part of the stylocone, $\times 20$. *c*, E63367*a*; showing dorsal integument, plate f, and a spine, $\times 28$. *d*, E63365*c*; showing left marginals, strut, isolated plates of ventral integument, fore-tail, and stylocone, $\times 19$.

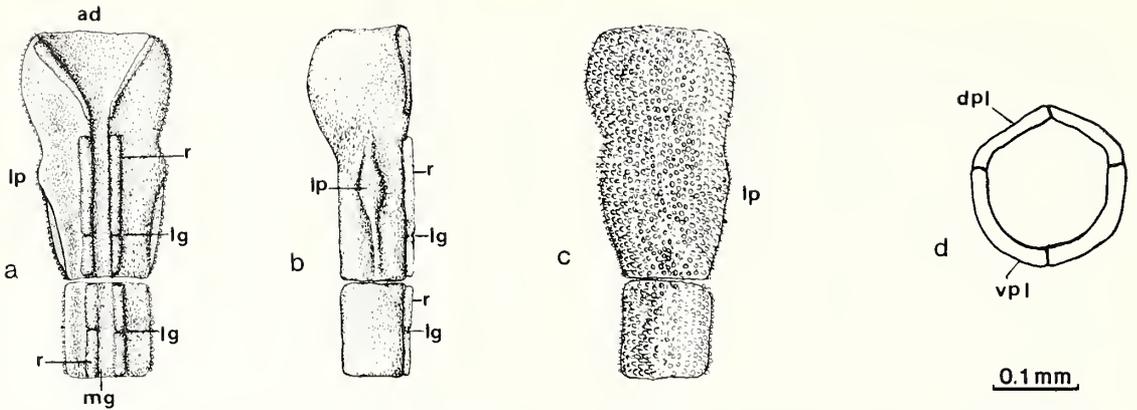


TEXT-FIG. 10. Explanatory tracing of Text-figure 9. Letters represent plate nomenclature except di, dorsal integuments; dpl, dorsal plates of mid and hind-tail; ftr, rings of fore-tail; hto, hind tail ossicle; sc, stylocone; sp, spines; vi, plates of ventral integument.

would have been resisted by the appendages and by the spines, the latter being extended at right-angles to the head (Text-fig. 13e). Rightward horizontal movement of the tail in the water, followed by ventral bending, caused the head both to yaw clockwise as seen from above and to roll down to the left so that it would have been supported by the appendages of the left marginal plates. The head then moved further to the rear and resumed the orientation it had when at rest (Text-fig. 13f-g).

Although the ventral flanges of *P. semispinosa* meant that the posterior part of the head must have been raised at the start of the locomotory cycle, they would have had the advantage of reducing the extent to which the head would have sunk into the substrate.

Could *P. semispinosa* have moved using its spines? Their asymmetric location, absence of obvious

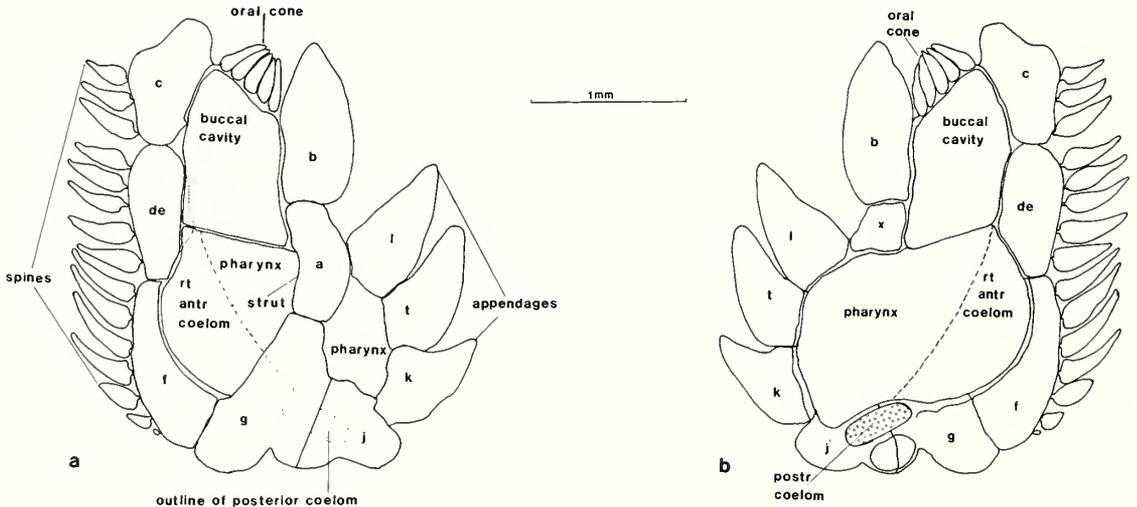


TEXT-FIG. 11. *Prochauvelicystis semispinosa*. Detail of stylocone and hind-tail: *a*, dorsal view; *b*, left lateral view; *c*, ventral view; *d*, cross-section of fore-tail. Abbreviations: ad, anterior depression; dpl, dorsal plates of hind tail; lp, lateral process; lg, lateral groove; mg, median groove; r, median ridge; vpl, ventral plates of hind tail.

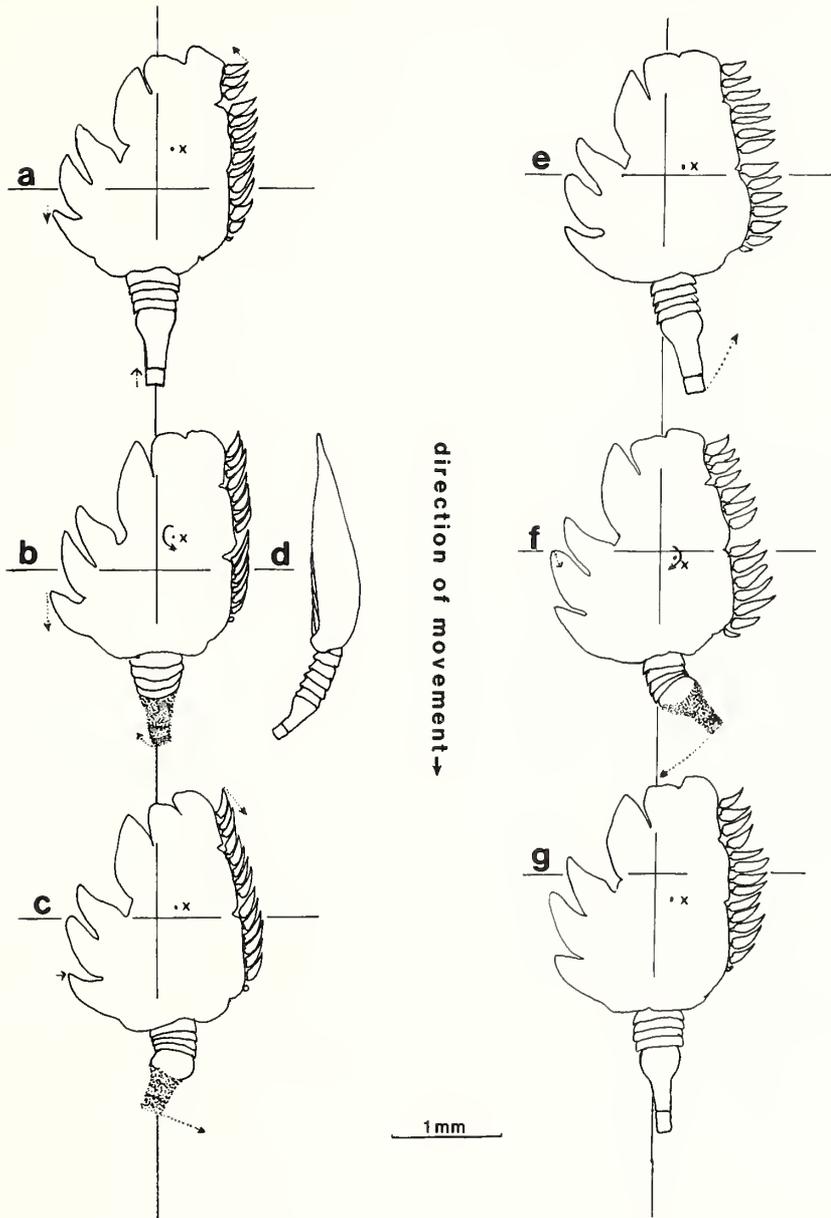
muscle attachments, small size, and weak structure make this unlikely. All but the first of these reasons make it unlikely that the spines could actually raise the left side of the head to overcome the suction effect of the substrate. It seems that the tail was the only active organ of locomotion, and that the head rolled about the ventral surface of the strut to overcome suction during the locomotory cycle.

Some upholders of the aulacophore theory of the cornute tail (Ubaghs 1961, 1969, and subsequent papers; Chauvel 1966, p. 98; Fisher 1982), have suggested that the assumed feeding function of the aulacophore precluded cornutes from being motile. However, Parsley (1988, pp. 351–353) believes that the tail was both a feeding arm and a locomotory structure.

When feeding, *P. semispinosa* would rest on the substrate supported by its spines, appendages, the ventral surfaces of the marginal plates, strut, and the tail. It was very probably a deposit feeder, ingesting detritus and micro-organisms together with some organic material from the lowest layer



TEXT-FIG. 12. *Prochauvelicystis semispinosa*. Reconstruction of the chambers of the head; *a*, dorsal aspect; *b*, ventral aspect.



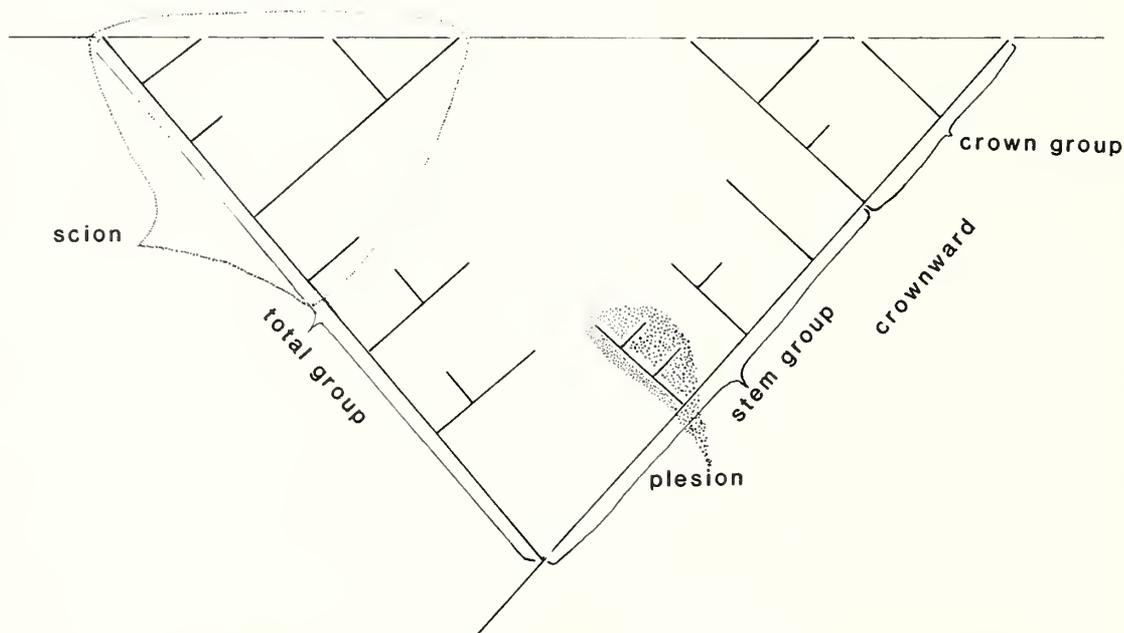
TEXT-FIG. 13. Locomotory cycle of *Prochauvelicystis semispinosa*. Arrows indicate the direction of travel of the point from which they are drawn, their lengths the displacement of the part in question in the next stage in the locomotory cycle. Stages figured are not separated by equal intervals in time but show major features of the locomotory cycle. The two lines at right angles form a space grid and thus show changes in displacement. Stippled parts of the tail are buried in the mud. The centre of mass of *P. semispinosa* is denoted by 'x'. *d*, lateral aspect of *b*, in which the tail raises the head by pushing into the substrate.

of water just above the sea-bed and the topmost layer of the substrate. The oral cone would be opened, and food particles would be ingested using inflowing water currents resulting from the ciliary and muscular action of the pharynx. Excess water and unwanted solid matter would be voided through the mouth, while food passed into the non-pharyngeal gut.

PHYLOGENY

Prochaelicystis semispinosa is a cornute. The cornutes have been shown to be stem chordates (Jefferies 1967–1986; Jefferies *et al.* 1987; Cripps 1988, 1989*a*, 1989*b*), and are thus a paraphyletic group. The term Cornuta (cornutes) can be used to denote a grade of evolutionary organization.

The concepts of crown group and stem group are useful in constructing phylogenies (Jefferies 1979, pp. 449–451; Text-fig. 14 herein). The crown group of any taxon is defined as the latest common ancestral species of all extant forms of a group, plus all descendants of that species, living or dead. The crown group corresponds to the *group of Hennig (1983, pp. 12, 29–30). A stem group is defined as all those extinct taxa more closely related to one crown group than another, but which are not themselves members of the crown group. A stem group and a crown group together form a total group. Given two monophyletic members of a stem group, or plesions (Patterson 1981), the one that is more closely related to the crown group is said to be more crownward. A plesion plus all taxa more crownward than it in the total group forms a scion, which is named after the least crownward plesion in it (Craske and Jefferies 1989, p. 74).



TEXT-FIG. 14. Explanation of the terms stem group, crown group, total group, plesion and scion.

The data matrix in Tables 1 and 2 was used to produce the cladogram (Text-fig. 15) using the computer program Hennig 86, devised by Dr J. S. Farris, of the State University of New York, Stony Brook, New York, USA. Relationships are based on shared derived characters only (Wiley 1981, chapter 3). To polarize the characters of the cornutes, the *Soluta* as described by Caster (1967) and Jefferies (1990) have been used as an outgroup.

The program initially produced 38 equally parsimonious trees from the data matrix. From these, a consensus tree was produced using the method of successive weighting in which characters found

TABLE 1. Characters used in the cladistic analysis of cornutes. The derived state is specified.

1.	Loss of feeding arm.
2.	Association of the gonopore with the anus.
3.	Loss of the water vascular system.
4.	Multiple branchial openings.
5.	Flexible dorsal integument with several separate dorsal plates.
6.	Gonopore–anus opens left of the tail junction.
7.	Loss of hydropore.
8.	Plates w, a and x form plate wax.
9.	Plate y smaller than plates h or i.
10.	Anterior u-plates of branchial skeleton.
11.	Fully flexible dorsal integument.
12.	Strut as a thickening of the floor.
13.	Flexible ventral integument and clearly demarcated strut.
14.	Plate t.
15.	Loss of plates v and w.
16.	Pointed spines on the right side of the head.
17.	Buccal lobe of head curves leftwards.
18.	Spines on left side of the head.
19.	Blunt spines.
20.	Suture between plates b and c forms a mouth frame.
21.	Gonopore–anus opens over tail junction.
22.	L-shaped plate x.
23.	Heart-shaped head with peripheral flange.
24.	Plates b and c fused to form a single plate.
25.	Anterior strut plate.
26.	Posterior u-plates of branchial skeleton.
27.	Separation of plates b and c to give a terminal mouth.
28.	Separate plate x.
29.	Paired dorsal hind-tail plates.
30.	Plate h subequal in size to plate y.
31.	Proximal fore-tail plates overlap onto ventral surfaces of plates g and j.
32.	Plate s.
33.	Interbranchial elements.
34.	Dorsal bar formed from plates a and d.
35.	Specialized plates of the branchial skeleton.
36.	l-appendage.
37.	Optic embayments.
38.	Ventral hind-tail ossicles bear downwardly directed spines.
39.	Convex ventral surface of the head.
40.	Marginal plates of the head expand onto the dorsal surface.
41.	Development of the right pharynx.
42.	Loss of cornute mid- and hind-tail.
43.	Absence of plate y.

to indicate relationships consistently among the initial trees are given higher weight than those that are less consistent (Farris 1969).

In the following discussion, the numbers in square brackets (e.g. [2]) refer to the characters as listed in Table 1, and shown on the cladogram (Text-fig. 15). Nodes on the cladogram are represented by horizontal lines and denoted by capital letters, e.g. node A (Text-fig. 15).

The cladogram shows that the cornutes (node A) are characterized by loss of the solute feeding arm [1], close association of the gonopore and the anus [2], loss of the water vascular system [3],

TABLE 2. Data matrix for the solutes, twenty-three cornute taxa and the mitrates. In the matrix the symbol '1' denotes a derived character state as specified in table 1, '0' a plesiomorphic character state, and '?' the absence of information on the state of a character.

Character nos	1	6	11	16	21	26	31	36	41
Solutes	00000	00000	00000	00000	00000	00000	00000	00000	000
<i>Ceratocystis perneri</i>	11110	00100	00000	00000	00000	01110	00000	10001	000
<i>Protocystites menevensis</i>	11111	11010	00000	00000	11000	01110	00000	10001	000
<i>Nevadaecystis americana</i>	11111	110?1	1100?	00000	?1000	1??1?	??0?1	10?00	00?
<i>Cotlurnocystis primaeva</i>	11111	11011	11100	01000	?1000	?1??0	0000?	10?00	00?
<i>Phyllocystis blayaci</i>	11111	11011	11111	01001	10110	10110	00001	00000	000
<i>P. crassimarginata</i>	11111	11011	11111	01001	10110	10110	00001	00000	000
<i>Milonicystis kerfornei</i>	11111	11010	11111	00001	10101	00110	0000?	00000	000
Domfront cornute	11111	110?0	?1101	00000	?0001	01110	00000	01100	00?
<i>Amygdalotheca griffiei</i>	11111	110?0	11111	00000	?0101	01?10	00000	00?00	000
<i>Chauvelicystis spinosa</i>	11111	11011	11111	11101	01000	1?110	00001	00?00	000
<i>C. ubaghisi</i>	11111	11011	11111	11110	??000	11110	00001	10000	000
<i>C. vizcainoi</i>	11111	11011	11111	11110	?1000	11110	00001	10000	000
<i>Prochauvelicystis semispinosa</i>	11111	11011	11111	10000	00000	11110	00001	10000	000
<i>Cotlurnocystis fellinensis</i>	11111	11011	11110	00000	01000	11110	00001	10?00	000
<i>C. elizae</i>	11111	110?1	11110	00000	00000	11010	00001	10000	001
<i>C. courtessolei</i>	11111	110??	11110	00000	?1000	?1110	0000?	10?00	00?
Scotiacystidae	11111	11010	11101	00000	00000	00111	11101	10000	000
<i>Progalliaecystis ubaghisi</i>	11111	110??	11101	01000	?0001	0?01?	10010	10000	001
<i>Galliaecystis lignieresi</i>	11111	110??	11101	00000	?0001	0?01?	00000	00000	001
<i>Hanusia</i> spp.	11111	110?0	01101	01000	00001	0?01?	00010	10000	001
<i>Reticulocarpos hanusi</i>	11111	110?0	11101	00000	00001	01010	00010	01100	001
<i>R. pissotensis</i>	11111	110?0	01101	00000	00001	0?011	00000	0?111	001
<i>Prokopicystis mergli</i>	11111	110?0	11101	00000	00000	01011	10010	0?111	001
Mitrates	11111	110?0	00001	00000	00000	01001	10010	01011	111

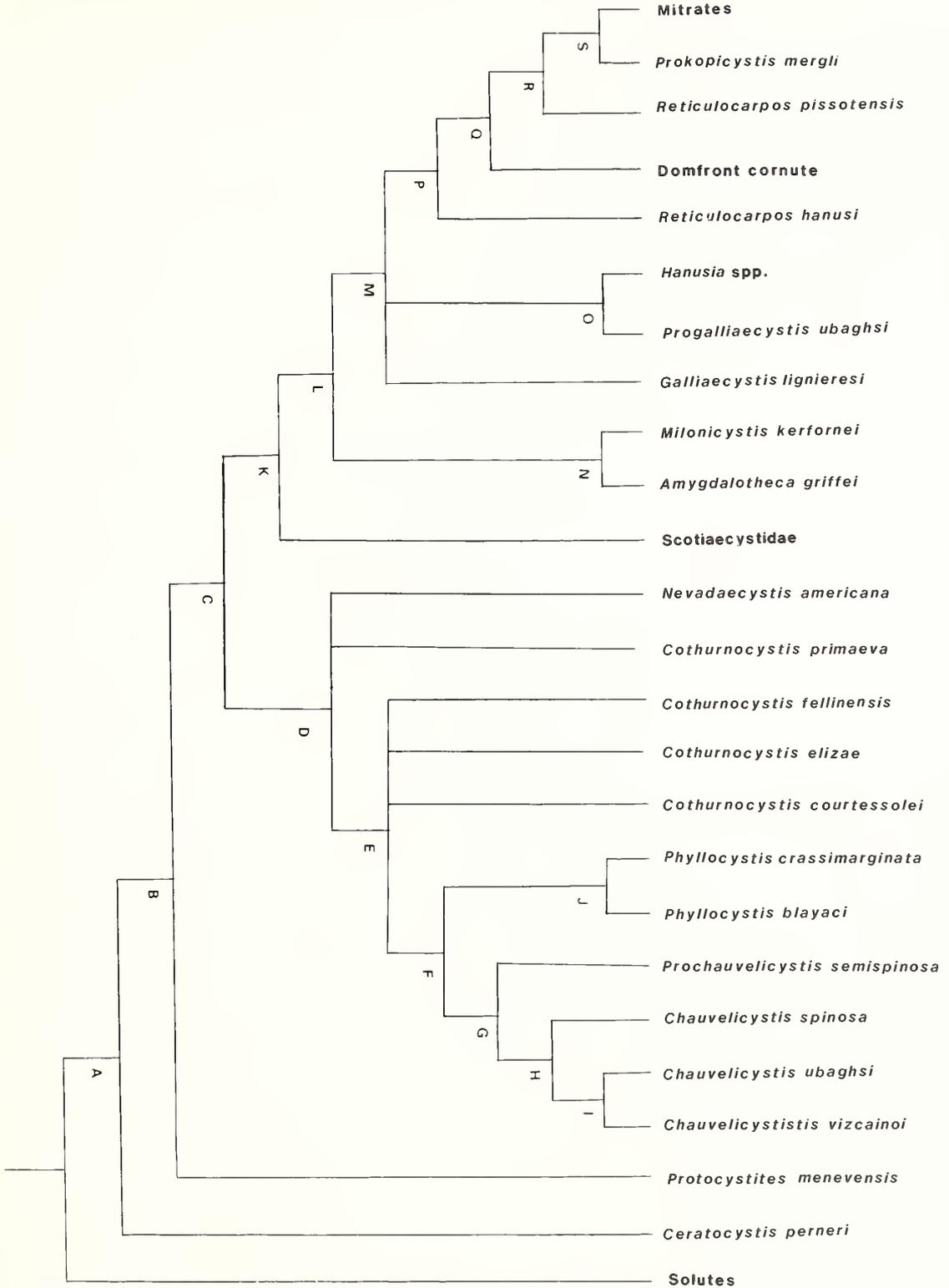
multiple branchial openings [4], paired dorsal plates of the hind-tail [29], separation of plates b and c to form a terminal mouth, and presence of an l-appendage [36].

The most plesiomorphic ('primitive') cornute known is *Ceratocystis perneri* Jaekel, the only cornute to retain the hydropore. The next most plesiomorphic cornute is *Protocystites menevensis* Hicks. It shares six characters with all more crownward cornutes (node B), flexible dorsal integument [5], opening of the gonopore-anus to the left of the tail junction [6], loss of the hydropore [7], plate y smaller than plates h or i [9], posterior U-shaped plates of the branchial skeleton [26] and a separate plate x [28].

All cornutes more crownward than *C. perneri* and *P. menevensis* (node C) share a fully flexible dorsal integument [11], a strut as a thickening of the ventral integument of the head [12], a flexible ventral integument with a clearly demarcated strut [13], and specialized plates of the branchial skeleton [35].

Prochauvelicystis semispinosa and the three species of the genus *Chauvelicystis* Ubaghs form a clade, the subfamily Chauvelicystinae (node G), on the basis of pointed spines on the right side of the head [16]. *P. semispinosa* is the most plesiomorphic chauvelicystine. The genus *Chauvelicystis* (node H) is characterized by the presence of spines on the left side of the head [18]. *C. vizcainoi* sp. nov. and *C. ubaghisi* (Chauvel) are sister taxa (node I) because of their possession of blunt spines [19], leaving *C. spinosa* Ubaghs as the most primitive member of its genus.

The genus *Phyllocystis* Thoral, 1935 (Ubaghs 1969; node J) has two species, *P. crassimarginata* Thoral and *P. blayaci* Thoral, and is characterized by the presence of a mouth frame [20], a heart-shaped head with a peripheral flange [23], and fusion of plate b and c [24]. The genus *Phyllocystis* and the subfamily Chauvelicystinae form the family Phyllocystidae (Derstler 1979, p. 104; node F)

TEXT-FIG. 15. Cladogram of *Prochauvelicystis semispinosa* and other cornutes. Characters are listed in Table 1.

characterized by loss of plates v and w [15], the buccal lobe of the head curving to the left [17] and the opening of the gonopore-anus lying over the tail-junction [21].

The Phyllocystidae form an unresolved four-fold polytomy (node E) with *Cothurnocystis courtessolei* Ubaghs, *Cothurnocystis fellinensis* Ubaghs and *Cothurnocystis elizae* Bather denoted by the presence of plate t [14]. This group forms an unresolved trichotomy (node D) with *Cothurnocystis primaeva*, Thoral and *Nevadaecystis americana* Ubaghs, with the presence of an L-shaped plate x [22].

The family Scotiaecystidae (Caster and Ubaghs, in Caster 1967; Cripps 1988) share plate s [32] and interbranchial elements [33]. The scion of the Scotiaecystidae (node K) is defined by the loss of plates v and w [15], a parallelism with the phyllocystids. *Amygdalotheca griffei* Ubaghs and its sister taxon *Milonicystis kerfornei* Chauvel form the family Amygdalothecidae (Ubaghs 1969, p. 63; node N), characterized by a heart-shaped head with peripheral flange [23], a parallelism with the genus *Phyllocystis*. The amygdalothecids are related to all more crownward cornutes (node L) by possession of an anterior strut plate [25].

Progalliaecystis ubaghsi Cripps and the three species of the genus *Hanusia* Cripps form a clade (node O) with leftward curvature of the buccal lobe of the head [17], separation of plates b and c to give a terminal mouth [27], and a dorsal bar formed by plates a and d [34] (node O). Character 27 has evolved twice, as it is also found at node A. Character 17 is a parallelism with the phyllocystids. The *Hanusia*-*P. ubaghsi* group forms an unresolved trichotomy (node M) with *Galliaecystis lignieresii*, Ubaghs and the scion of *Reticulocarpos hanusi*, Jefferies and Prokop with absence of plate y [43].

The scion of *R. hanusi* (node P) possesses optic embayments [37] and spines on the ventral hind-tail ossicles [38], and that of an undescribed cornute from the Llandeilo of Domfront, Normandy, France (node Q) shares the overlap of the proximal ventral fore tail plates onto the ventral surfaces of plates g and j [31]. The scion of *Reticulocarpos pissotensis* Chauvel and Nion (node R) shares a convex ventral surface of the head [39] and the expansion of marginal plates of the head onto the dorsal surface [40]. *Prokopocystis mergli* Cripps is found to be the sister taxon of the mitrates (Jefferies 1986, ch. 8), from their shared dorsal bar [34], a parallelism with the *Hanusia*-*Progalliaecystis* group.

The mitrates all share development of a right pharynx [41] and loss of the cornute mid- and hind-tail [42]. Jefferies (1986, chapter 8) has shown that mitrates can be referred to the stem groups of the extant chordate subphyla.

CONCLUSIONS

C. vizcainoi is a previously unrecognized species of *Chauvelicystis*, differing slightly from *C. ubaghsi* but more from *C. spinosa*. Together with *P. semispinosa*, it shows that spined cornutes were more diverse and widespread than previously believed.

Prochauvelicystis semispinosa is an unusual cornute because of its small size and the presence of spines on the right side of the head only. Both these features are probably adaptations to living on a soft substrate. The orientation of the spines suggests that *P. semispinosa*, like other cornutes, was actively motile and move rearwards.

P. semispinosa has derived characters in common with the three known species of the genus *Chauvelicystis* and is the most primitive member of the Chauvelicystinae. In its gross morphology, *P. semispinosa* is intermediate between the boot-shaped cornutes of the genus *Cothurnocystis* and the more symmetrical *Chauvelicystis* and *Phyllocystis*. The boot-shaped head is probably a primitive condition inherited from the less crownward cornutes such as *Ceratocystis perneri*. *P. semispinosa* is also primitive in having spines on the right side of the head only, unlike *Chauvelicystis* which has the derived condition of spines on right and left sides of the head. Thus *P. semispinosa* is the primitive sister-taxon of an important clade of cornutes, the first species in this clade known from Britain.

Acknowledgements. I thank Dr R. P. S. Jefferies of the Palaeontology Department, Natural History Museum, for suggesting and supervising the project, also Dr A. Cripps, Dr A. B. Smith, Mr D. N. Lewis, and Dr R. A. Fortey for much useful advice, and Dr D. Hardwick (Civil Engineering Department, Imperial College, London) for discussing locomotion and functional morphology of *Prochauvelicystis semispinosa* from an engineering point of view. Without their help this paper would not have been possible.

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P. E. J. DALEY

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

Typescript received 15 January 1990

Revised typescript received 10 May 1991

NEW CLADID CRINOIDS FROM THE LATE ORDOVICIAN OF GIRVAN, SCOTLAND

by STEPHEN K. DONOVAN

ABSTRACT. Two new species of cladid crinoids are described from the Starfish Bed (Ashgill, late Rawtheyan) at Threave Glen, near Girvan, southwest Scotland; this bed has yielded the most diverse crinoid fauna of any British Ordovician locality. *Euspirocrinus girvanensis* sp. nov. is based on a unique internal mould of the dorsal cup and anal series. The five infrabasal plates form a low circllet, the anal X plate is infolded and the short anal series comprises numerous small polygonal plates, *Dendrocrinus collapsus* sp. nov. is known from five specimens, all external moulds. The anal sac and dorsal cup of this species bear a distinctive ribbed sculpture.

THE Ashgill Starfish Bed of Threave Glen, near Girvan, Strathclyde, Scotland, is the most important crinoid locality in the British Ordovician. In an Ordovician crinoid fauna comprising only about fifty nominal species, a third are known only from this locality (Donovan 1989a). The species that have been described from this horizon are generally well-preserved crowns which retain the proximal column. Preservation is always as moulds. Exceptionally well-preserved echinoderms and calcichordates appear to be limited to a single horizon in Threave Glen (Harper 1982a; 1982b), representing catastrophic entombment of a life assemblage, although contrasting interpretations of the environment of deposition were given in Goldring and Stephenson (1972) and Ingham (1978). Ramsbottom (1961) published the first descriptions of Threave Glen crinoids, recognizing eleven species assigned to eight genera. To this total Brower (1974) added a second species of *Xenocrinus* and Donovan (1989b) described three new species of disparid (the known crinoid fauna is summarized in Table 1). Two further species of cladid from Threave Glen, which were discovered in the collections of the Hunterian Museum (HM), Royal Museum of Scotland (RMS) and the Natural History Museum, London (BMNH), are described herein.

Terminology herein is that of Moore *et al.* (1968), Ubahgs (1978) and Webster (1974). The synonymy annotations follow Matthews (1973).

SYSTEMATIC PALAEOONTOLOGY

Class CRINOIDEA Miller, 1821

Order CLADIDA Moore and Laudon, 1943

Suborder CYATHOCRININA Bather, 1899

Superfamily CYATHOCRINITACEA Bassler, 1938

Family EUSPIROCRINIDAE Bather, 1890

Genus EUSPIROCRINUS Angelin, 1878

Type species. By monotypy; *Euspirocrinus spiralis* Angelin, 1878, from the Wenlock of Gotland (see Franzén 1983, p. 10).

Diagnosis. (Modified from Moore *et al.* 1978, p. T583). Attachment by encrusting terminal holdfast. Column holomeric proximally, pentameric more distally. Dorsal cup conical, bowl-shaped. Five (sometimes three?) infrabasals, five basals and five radials present. Radial and BC basal support the C radial; radianal and CD basal support the anal X; anal X, radianal and C radial support the anal series. Radial facets less than the full width of the plates. Arms branch isotomously and curve inwards. Anal series short.

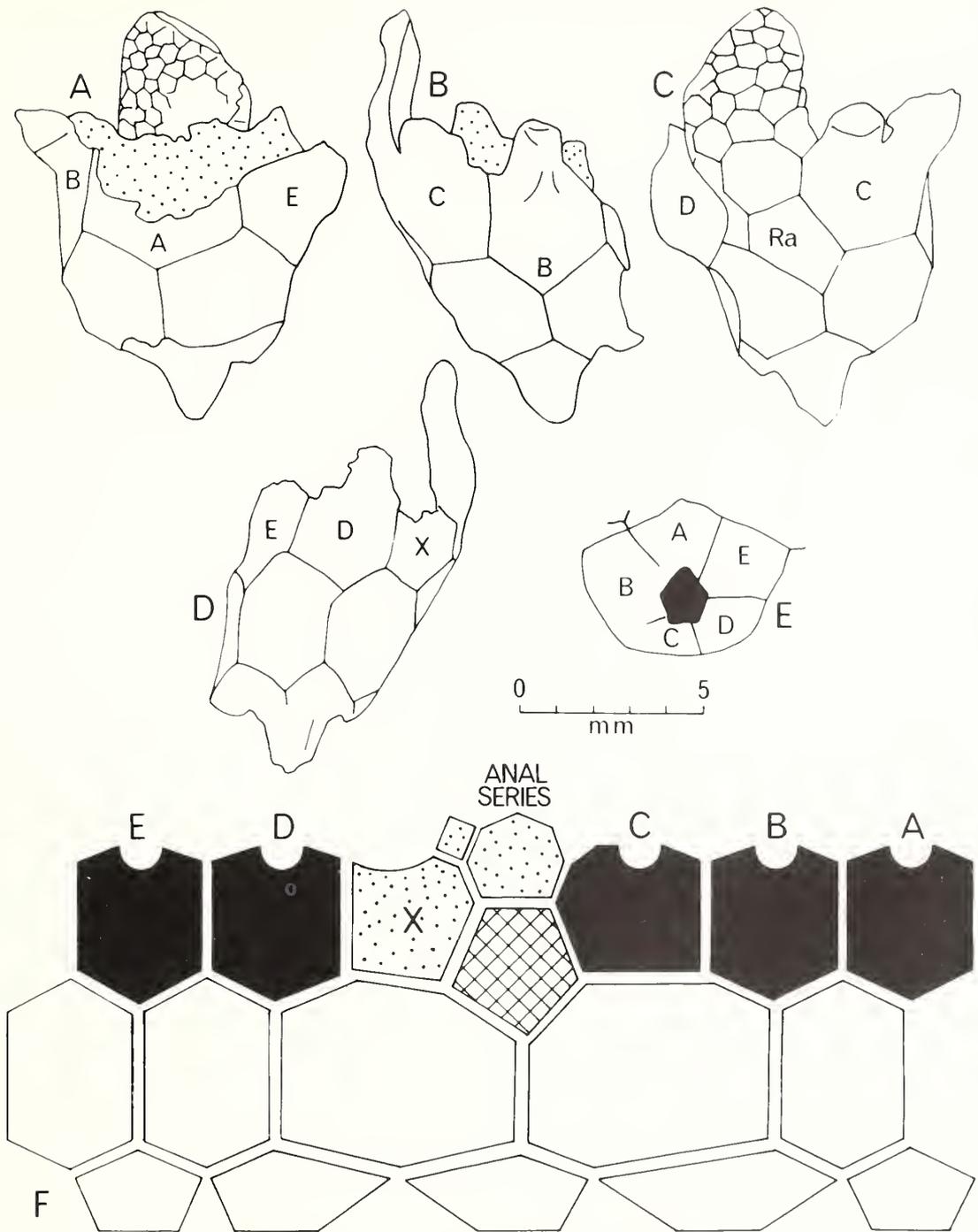
TABLE 1. The crinoid fauna of the Ashgill Starfish Bed, Threave Glen, near Girvan, Scotland.

Order DISPARIDA
Family IOCRINIDAE
<i>Westheadocrinus girvanensis</i> Donovan, 1989b
Family PISOCRINIDAE
<i>Eociceroocrinus sevastopuloi</i> Donovan, 1989b
Family CALCEOOCRINIDAE
<i>Anuloocrinus thraivensis</i> Ramsbottom, 1961
<i>Cremaocrinus drummuckensis</i> Ramsbottom, 1961
Incertae familiae
<i>Clavicularocrinus scoticus</i> Donovan, 1989b
Order CLADIDA
Family EUSPIROCRINIDAE
<i>Euspiroocrinus girvanensis</i> sp. nov.
Family POROCRINIDAE
<i>Porocrinus scoticus</i> Ramsbottom, 1961
Family DENDROCRINIDAE
<i>Dendroocrinus granditubus</i> Ramsbottom, 1961
<i>Dendroocrinus collapsus</i> sp. nov.
Family CUPULOCRINIDAE
<i>Cupuloocrinus drummuckensis</i> Kolata, 1975 (= <i>C. gracilis</i> Ramsbottom, 1961, non <i>C.</i> [= <i>Poteriocrinus</i>] <i>gracilis</i> (Hall, 1847))
<i>Cupuloocrinus heterobrachialis</i> Ramsbottom, 1961
Order TAXOCRINIDA
Family TAXOCRINIDAE
<i>Protaxocrinus girvanensis</i> Ramsbottom, 1961
Order MONOBATHRIDA
Family XENOCRINIDAE
<i>Xenocrinus multiramus</i> Ramsbottom, 1961
<i>Xenocrinus breviformis</i> Brower, 1974
Family PATELLIOCRINIDAE
<i>Macrostylocrinus cirrifer</i> Ramsbottom, 1961
Order DIPLOBATHRIDA
Family RHODOCRINITIDAE
<i>Diaboloocrinus</i> sp.
Incertae familiae
Diplobathrid(?) indet.

Euspiroocrinus girvanensis sp. nov.

Plate 1, figs 1-2; Text-fig. 1

v*1954 *Euspiroocrinus girvanensis* sp. nov., Ramsbottom, p. 44, pl. 10, fig. 5.*Derivation of name.* After Girvan, the nearest town to the type locality.*Type material, locality and horizon.* A unique holotype, HM E3499, part of the J. L. Begg collection; a slightly deformed internal mould of a dicyclic crinoid cup. From the late Rawtheyan (= early Gamachian in North American terminology) Starfish Bed of Threave Glen, Girvan district, Strathclyde (National Grid Reference NS 250 038).*Diagnosis.* *Euspiroocrinus* with low infrabasal circle comprising five plates, narrow radial facets, infolded anal X plate and short, broad anal series, including numerous polygonal ossicles.



TEXT-FIG. 1. *Euspirocrinus girvanensis* sp. nov. A-E, HM E3499; holotype; camera lucida drawings of internal mould of the dorsal cup. A, A ray central. B, BC interray central. C, CD interray central. D, D ray central. E, basal view (axial canal of column shaded). Key: A to E, Carpenter rays; Ra, radialial; X, anal X plate. F, schematic plating diagram of the dorsal cup. Infrabasals and basals unshaded; radials black; radialial cross-hatched; anal series stippled.

Description. Column unknown, but infill of proximal axial canal pentagonal in outline. Five low infrabasals, forming a flattened base to the dorsal cup (Text-fig. 1E), just visible in lateral view. Infrabasal outline pentagonal to hexagonal with a narrow, infolded base adjacent to the axial canal. Five basals, all higher than infrabasals. AB, DE and EA basals high and hexagonal (Pl. 1, fig. 1; Text-fig. 1D), supporting radials. BC basal heptagonal, supporting the B and C radials, and a radianal plate in the CD interray. CD basal heptagonal, supporting the radianal, anal X and D radial. Radial cirplet includes five radials, a radianal, anal X and the next most proximal plate of the anal series. Radials about the same size as basals. All radials, except C, hexagonal (Text-fig. 1B), with an articular facet at the apex of the hexagon, apparently angled away from the oral surface. C radial apparently heptagonal, supporting at least two ossicles of the anal series (Pl. 1, fig. 2; Text-fig. 1C). Radianal small and pentagonal. Anal X about as large as the radianal and hexagonal, but with a free upper surface, folded through about 90°. Anal series short, broad, flattened, lozenge-shaped and multiplied, with rather larger ossicles on the posterior than on the anterior surface (cf. Text-fig. 1A, C). Arms not preserved. Mouth central and ?pentagonal.

Remarks. While it is unusual to erect a new crinoid species on the basis of an internal mould, the plate sutures of this specimen are very obvious (Pl. 1, figs 1–2; Text-fig. 1), so that the geometry of the dorsal cup is more apparent than that of some species known from more ‘complete’ thecae. In particular, attention is drawn to the near-perfect preservation of the internal mould of the anal series.

This specimen has twice previously been examined. A series of photographic plates by James Wright, preserved in the Department of Geology of the Hunterian Museum, obviously formed part of an unpublished typescript, ‘Ordovician Crinoidea from Girvan, Ayrshire’, the text of which is now lost (an associated letter from Wright to Professor A. E. Trueman, dated 14th June 1943, indicates the antiquity of the work). A figure of HM E3499 on one of the plates remains unlabelled and, presumably, unidentified. Ramsbottom (1954) described the specimen and identified it as *Euspirocrinus*, but these observations and conclusions were not repeated in Ramsbottom (1961).

HM E3499 differs from the other cladid genera identified from the Starfish Bed at Threave Glen (Table 1) either in having a different pattern of dorsal cup plating, a contrasting anal series architecture, or both. The plating arrangement of the dorsal cup (Text-fig. 1F) most strongly suggests an euspirocrinid cyathocrinitacean (see Moore *et al.* 1978, fig. 372.3–5). The relative positions of the C radial, radianal and anal X most closely approach *Euspirocrinus* and *Ampheristocrinus*. In the latter, X supports three plates of the anal series, while in *Euspirocrinus* it supports only two. In HM E3499, X supports two plates, one large and one small (Text-fig. 1F), indicating the Threave Glen species to be a species of *Euspirocrinus*.

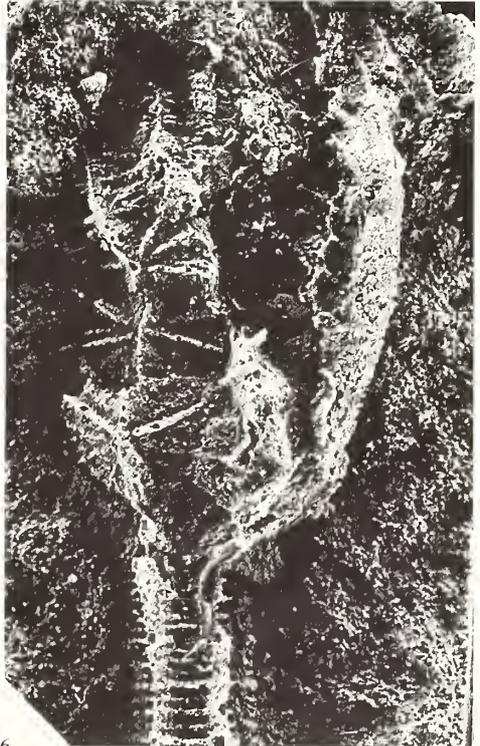
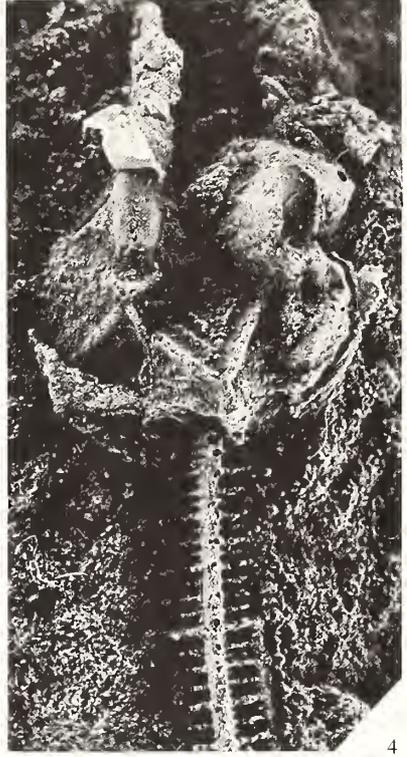
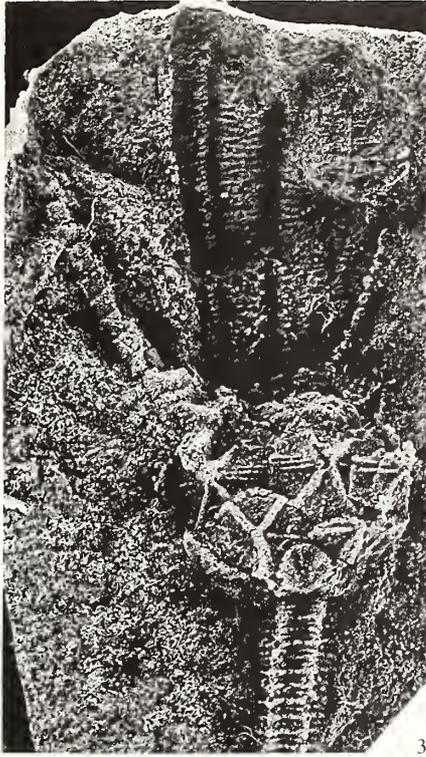
Only four other species of *Euspirocrinus* have been described. The type species, *E. spiralis* has prominent infrabasals that are plainly visible in lateral aspect, radials larger than basals and an anal series incorporating few plates. In *E. cirratus* Strimple, 1963, from the Wenlock of Oklahoma, USA, the infrabasals are apparently fused such that only three are present, the basal plates are small compared with the radials and the radianal is quadrangular. *E. obconicus* Billings, 1885, from the Caradoc of Ontario, Canada, has prominent infrabasals and low, broad radials. *E. heliktos* Ausich, 1986, from the early Silurian of Ohio, USA, also has prominent infrabasals, as well as broad radial facets. Therefore, none of the previously described species of *Euspirocrinus* closely resembles the

EXPLANATION OF PLATE 1

Figs 1–2. *Euspirocrinus girvanensis* sp. nov. HM E3499; holotype. 1, A ray central (cf. Text-fig. 1A). 2, CD interray central (cf. Text-fig. 1C). Both internal moulds, both $\times 4$.

Figs 3–6. *Dendrocrinus collapsus* sp. nov. 3, BMNH E67901b; holotype; proximal column and crown, $\times 5$. 4, BMNH E47326b; paratype; proximal column and dorsal cup, $\times 6$. 5, BMNH E67901a; holotype; crown with well-preserved anal series, $\times 5.5$. 6, BMNH E47326a; paratype; proximal column, dorsal cup and proximal anal series, $\times 6$. All latex casts taken from natural moulds.

All specimens coated with ammonium chloride.



Girvan species. The specimens discussed by Ausich (1986, pp. 728–729, figs 6.8, 6.13) as (?)*Euspirocrinus* sp. are too poorly known for discussion, although it is noted that the radial facets are much wider than in *E. girvanensis*.

Suborder DENDROCRININA Bather, 1899
 Superfamily DENDROCRINACEA Wachsmuth and Springer, 1886
 Family DENDROCRINIDAE Wachsmuth and Springer, 1886
 Genus DENDROCRINUS Hall, 1852

Type species. By monotypy; *Dendrocrinus longidactylus* Hall, 1852, from the Wenlock of New York State, USA.

Diagnosis. (Modified from Moore *et al.* 1978, p. T608). Crown elongate and conical. Cup dicyclic, with five prominent infrabasals, five basals and five radials. Radial directly below C radial. Anal X in radial circlet, supported by CD basal and radial. Anal series comprising large plates posteriorly and proximally only, with several columns of small interlocking plates arranged laterally, anteriorly and distally. Arms slender, uniserial, apinnulate and branching isotomously several times. Articular facets of radials narrow and rounded, angled away from oral surface. Column holomeric or possibly pentameric in some species, heteromorphic proximally, circular, pentagonal or pentastellate in section.

Dendrocrinus collapsus sp. nov.

Plate 1, figs 3–6; Text-figs 2–3

1989a Dendrocrinid sp. nov.; Donovan, fig. 1.

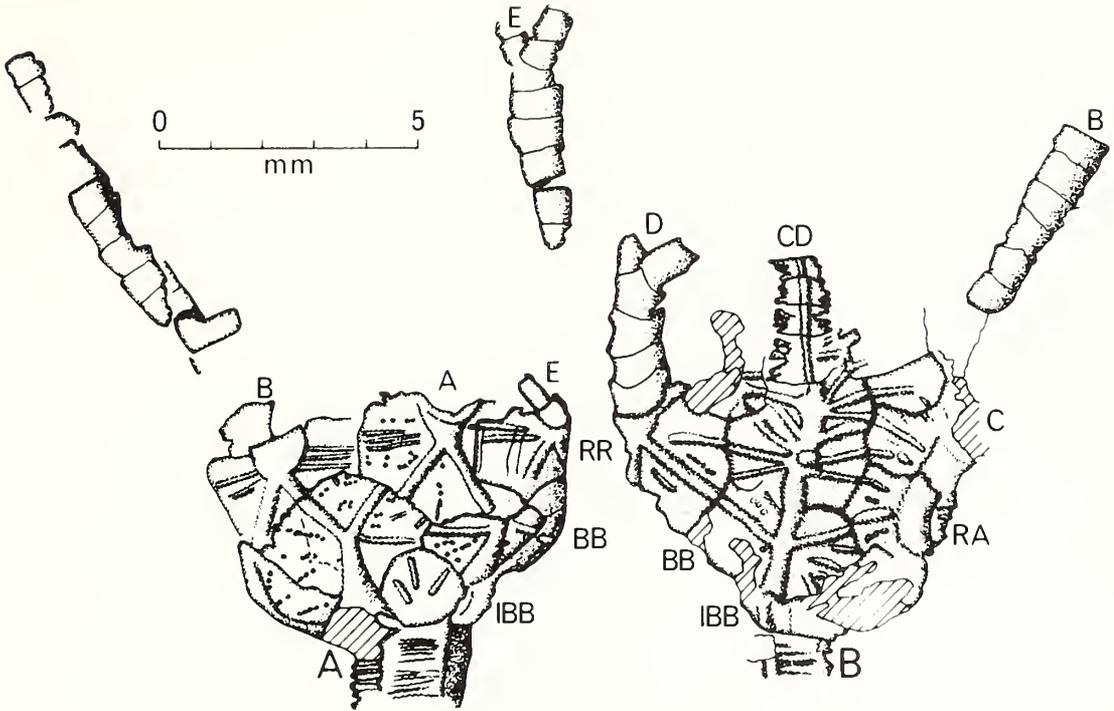
Derivation of name. From the Latin *col*, 'together' and *lapsus*, 'to slide or fall', alluding to the collapsed state of the dorsal cup in all available specimens.

Type material, locality and horizon. Species known from five specimens, four of which are part and counterpart external moulds: holotype, BMNH E67901a–b; paratypes, RMS 1957.1.28 (part and counterpart); BMNH E47326a–b; E67904a–b (anal tube), E68729 (anal tube). Locality and horizon as for *E. girvanensis* above.

Diagnosis. *Dendrocrinus* with slender, elongate pentastellate column, broad, moderately high, bowl-shaped dorsal cup with sculpture of radiating ribs which are particularly strongly developed on the basals, radials and anal X, broad anal sac composed of columns of plates with distinct radiating ribs, and moderately robust arms which branch at least twice.

Description. Attachment structure unknown. Proximal 40 mm of column preserved in the holotype (Pl. 1, fig. 3), while 18 mm is retained by BMNH E47326 (Pl. 1, fig. 4). The stem is slightly curved in both specimens, without any proximal taper away from the base of the cup. Stem pentastellate in section, heteromorphic N212, with nodals higher than priminternodals and secundinternodals. Latera are convex to angular at the angles of the 'star', but are otherwise strongly infolded. The latera of secundinternodals are planar, but strongly infolded, so that the more convex latera of nodals and priminternodals form narrow epifacets and give the stem a ladder-like appearance (Pl. 1, figs 3–4, 6). Features of the articular facet not seen.

Dorsal cup dicyclic (best seen in E67901b; Pl. 1, fig. 3; Text-fig. 2A). Five infrabasals, pentagonal in lateral view (Pl. 1, figs 3, 6; Text figs 2A, 3A–B) and folded under the cup with an angular geniculation. Centre of lateral face of infrabasal depressed parallel to long axis of crinoid. Fine, separated radial ridges or columns of tubercles extend adorally. Sutures between infrabasals correspond to the angles of the column. Five basals, larger than infrabasals, polygonal in outline, apparently hexagonal to heptagonal. Plates raised centrally, from which radiate a few stout ribs in a Y-shaped pattern (Pl. 1, figs 3–6; Text-figs 2–3). Two orders of finer radiating ribs and/or lines of tubercles also present. Five large radials, as large or slightly larger than basals, polygonal (octagonal?) in outline, with an arm facet in the central third of the adoral margin. Arm facet broad and



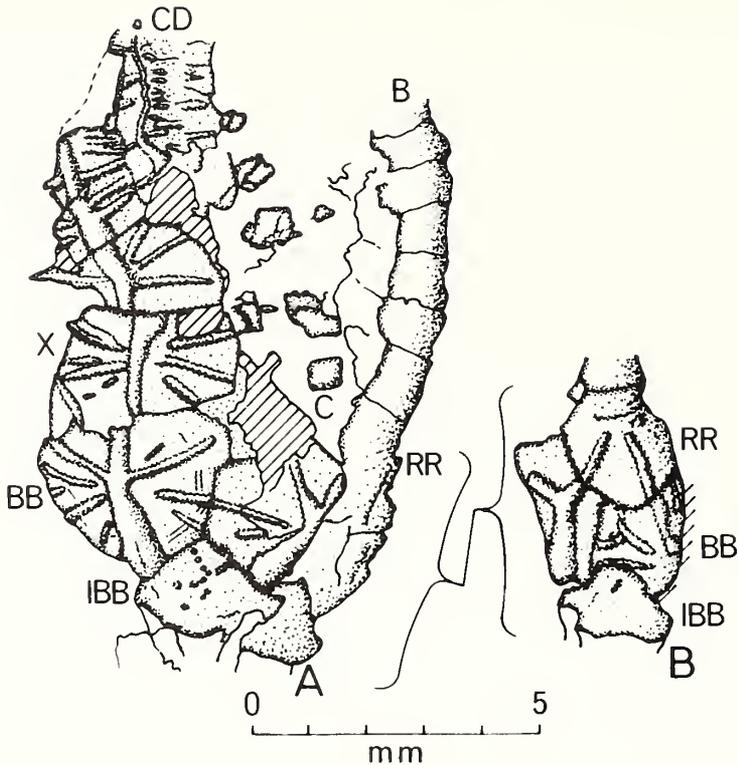
TEXT-FIG. 2. *Dendrocrinus collapsus* sp. nov.; holotype; dorsal cup. A, BMNH E67901b. B, BMNH E67901a; anal X is the large plate in the centre of the figure supported by the CD basal. Camera lucida drawings of latex casts taken from counterpart external moulds. Key: A to E, Carpenter rays; CD, CD interray (part of the anal series illustrated); RR, radials; BB, basals; IBB, infrabasals; RA, radialial. Proximal parts of some arms illustrated.

V-shaped, wider than the U-shaped proximal facet of $1Br_1$. Adoral groove narrow, U-shaped, associated with a broad, shallow V-shaped plate margin. Plate sculpture similar to that of basals.

Anal X supported by the hexagonal(?) basal in the CD interray, on which a particularly large central rib is orientated parallel to the long axis of the crinoid and continues on at least the proximal plates of the anal series (Pl. 1, figs 5–6; Text-figs 2B, 3A), along with more slender, but still pronounced, ribs which radiate from the plate centres. X separates the D and C radials (Text-fig. 2B), the latter being supported by a radialial plate. X and the posterior sides of the C and D radials support a large, complex anal sac composed of few columns of plates with a stellate ribbed sculpture (Pl. 1, figs 3, 5).

Five moderately robust, non-pinnulate, uniserial arms, which are poorly preserved, but which branch at least twice (Text-fig. 2B illustrates the primaxillary in the D ray and also the E ray ?secundaxillary). Primaxillary at $1Br_1$ in E67901a. Primaxillaries about as high as wide. Brachial latera planar and unsculptured.

Remarks. Although specimens of this taxon are partly disarticulated, sufficient morphological detail is preserved to show that this species is undoubtedly a *Dendrocrinus*. Moore *et al.* (1978, figs 394.5, 395.1d) illustrated the plating arrangement of the dorsal cup in the type species, *D. longidactylus*. The large CD basal supports the anal X and both abut the moderately large radialial in the C ray. This radialial supports the C radial. The anal series immediately above X is broad and comprises three columns of plates. The central column is supported by X, while the two flanking columns are supported by the C and D radials (Moore *et al.* 1978, fig. 395.1c). The anal tube comprises multiple columns of plates, each plate bearing a sculpture of radiating ribs. All of these features are seen in *D. collapsus*. The posterior plating geometry is particularly well seen in the holotype (Pl. 1, fig. 5; Text-fig. 2B).



TEXT-FIG. 3. *Dendrocrinus collapsus* sp. nov., paratype, BMNH E47326a. A, dorsal cup with proximal part of anal sac and arm of B ray. B, cup plates of the B ray. Key: X, anal X plate; otherwise as in Text-figure 2. Camera lucida drawings.

A note associated with the paratype specimen BMNH E47326, classifying it as '*Palaeocrinus* cladid', is disregarded. The Girvan species lacks respiratory structures and has a prominent anal sac, features which distinguish it from *Palaeocrinus* Billings *s. s.* (Moore *et al.* 1978, p. T588). The radiating ribs of *D. collapsus* are coarser than those of *Palaeocrinus* (see, for example, Brower and Veinus 1974, pp. 37–61, text-figs 3–7; pl. 5, figs 4–5; pls 6–8; 1978, pp. 451–454, pl. 16, fig. 3; Sprinkle 1982, pp. 154–163, figs 46A–E, H–L, 47; pl. 13, figs 6, 9–11; pl. 14), indicating that they did not serve a respiratory function. *Palaeocrinus s. s.* has no anal sac. Although some species with an anal sac have been assigned to *Palaeocrinus*, these taxa are probably misclassified (Moore *et al.* 1978, p. T588).

Three other species of *Dendrocrinus* have been described from the Lower Palaeozoic of Britain: *D. granditubus* Ramsbottom, 1961, from the Ashgill Starfish Bed at Threave Glen; *D. rugocyathus* Ramsbottom, 1961, from the Slade Beds of Dyfed, Wales; and *D. extensidiscus* Brower, 1975, from the Telychian, late Llandovery Gutterford Burn Starfish Bed of the North Esk Inlier, Lothian, Scotland. *D. granditubus* has a large and distinctive anal sac, composed by very numerous columns of very small plates, which is very different from that of *D. collapsus* (compare Pl. 1, figs 3, 5 herein with Ramsbottom 1961, pl. 4, figs 1–7). *D. rugocyathus* has a strongly ribbed dorsal cup, but the centres of radial and basal plates are raised and disc-like, with short, stout, radiating ribs (Ramsbottom 1961, pl. 3, figs 1–5). Unlike *D. collapsus*, *D. extensidiscus* has a smooth, slender cup (Brower 1975). *D. collapsus* is also distinct from the various species of *Dendrocrinus* known from North America.

Acknowledgements. This paper was written during the period of National Geographic Society grant 4264-90, which is gratefully acknowledged. Keith Ingham (HM), Bill Baird (RMS), Dave Lewis and Andrew Smith (BMNH) kindly loaned and allowed access to specimens. Andrew Smith also permitted use of his photomicroscope equipment. I particularly thank Phil Lane (University of Keele) for taking the photographs used in Plate 1.

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STEPHEN K. DONOVAN

Department of Geology
University of the West Indies
Mona, Kingston 7,
Jamaica

Typescript received 24 July 1990

Revised typescript received 30 May 1991

HOLOTHURIANS IN THE BLUE LIAS OF SOUTHERN BRITAIN

by P. M. GILLILAND

ABSTRACT. In a detailed study of the Blue Lias (Hettangian–Sinemurian) at four localities in southern Britain holothurian sclerites were found in 76% of samples, sometimes in abundance. There are eleven sclerite morphospecies, four of them new, including examples of the Dactylochirotida (Ypsilothuriidae), Dendrochirotida (?Cucumariidae), Apodida (Achistridae, Chiridotidae and Synaptidae), Elasipoda and probably Molpadiida (Molpadiidae). Four types of calcareous ring are described and, where possible, their associated sclerite morphospecies identified. A number of microfossils previously assigned to the class are demonstrated to be non-holothurian including Etheridgellidae and *Rhabdotites*. *Calclamna* and *Binoculites* are recognized as growth stages of the same morphotype and their taxonomy revised. The fauna includes the earliest unequivocal records of the order Molpadiida and families Synaptidae and Ypsilothuriidae. New taxa are *Acutisclerus plagiacanthus* gen. et sp. nov., *Palaeoypsilus liassicus* gen. et sp. nov., *Theelia synapta* sp. nov., *Priscopodatus* sp. nov.?, and the genus *Clavallus*.

The fauna is of limited palaeoenvironmental and biostratigraphical use, although changes in size frequency (*Achistrum monochordata*) and relative abundance (*Binoculites* spp.) are potentially informative for the latter. Assemblages are difficult to recognize possibly due to taphonomic effects. The fauna is broadly similar across northwestern Europe but with regional variations both in sclerite composition and abundance.

ALTHOUGH the first fossil sclerites were described nearly one hundred and fifty years ago (Münster 1843) the study of fossil holothurians today still consists of little more than taxonomic description. This is due to the practical and taxonomic difficulties associated with fossil sclerites. Significant problems do remain concerning the classification of fossil material but there have been several monographic accounts which could provide a basis for considering holothurian palaeobiology and biostratigraphy, e.g. Croneis and McCormack (1932), Deflandre-Rigaud (1962) and Frizzell and Exline (1955). Yet there have been few references to more applied aspects such as palaeoecology (e.g. Mostler 1977), biostratigraphy (e.g. Rioult 1961; Mostler 1972c), and evolution (Pawson 1966). It therefore seemed imperative to undertake a detailed study which from the start set out to investigate the potential information obtainable from fossil holothurians. The present study is an attempt to develop such an approach and does not purport to be a definitive account of holothurians from a particular part of the stratigraphic record.

The Hettangian–Lower Sinemurian part of the Blue Lias in Britain was chosen as the subject of study for several reasons. Most importantly a number of micropalaeontologists have indicated the frequent occurrence of sclerites in this facies. Records include dumb-bell-shaped spicules from Hock Cliff (Henderson 1935) and hooks from the *planorbis*, *angulatus*, and *bucklandi* zones of the Yorkshire Lias (Blake 1876). In an unpublished report, Clements *et al.* (1975) noted the presence of holothurians in several samples from the Blue Lias near Rugby. In addition, the biostratigraphy of the Blue Lias is well documented and there are a number of well described and easily accessible sections available.

Liassic holothurians are also widely known from other parts of Europe, particularly Germany (Issler 1908; Bartenstein 1936; Bartenstein and Brand 1937; Mortensen 1937; Kristan-Tollmann 1986). In France early records included Terquem (1862) and Terquem and Berthelin (1875). Later Rioult (1961) described sclerites from the Lias of Normandy and discussed their possible use in biostratigraphy. Michelson (1972) provided an excellent account of palaeoecology and

morphological variation of holothurian (and ostracod) assemblages from the Lias of the Danish Embayment.

METHODS

Sampling

Hand-sized samples were collected from logged sections at Pinhay Bay (P), near Lyme Regis, SY 320908; Hock Cliff (H), on the River Severn, at SO 726091; Maisemore Cliff (M), also on the Severn, at SO 812216; and Long Itchington quarry (L), near Rugby, SP 419631. Throughout the text sample numbers are prefixed by P, H, M, or L depending on locality. E numbers are British Museum (Natural History) catalogue numbers.

Processing

Several extraction techniques were applied to identical test samples for evaluation. Decanting of disaggregated samples, as recommended by Frizzell and Exline (1955), was not successful. The following method proved the best since samples could be processed relatively quickly and the majority of the material isolated remained well preserved. A hand-sized sample was broken into 0.5 cm fragments, dried in an oven, immersed in kerosene for 30 minutes and, after decanting off the kerosene, immersed in boiling water and left for 1.5–2 hours. The resultant sludge was gently washed through 0.5 cm and 63 μm (240 mesh) sieves with water and a little detergent and dried in an oven. The dried residue was immersed in 10% hydrogen peroxide for 30 minutes, washed through the 63 μm sieve again and dried. A small proportion of the final residue was removed and further cleaned in an ultrasonic tank for 15 seconds. To prevent cross-contamination of samples, all equipment was kept thoroughly clean including dislodging unwanted material from the fine sieve with a powerful jet of water.

Picking

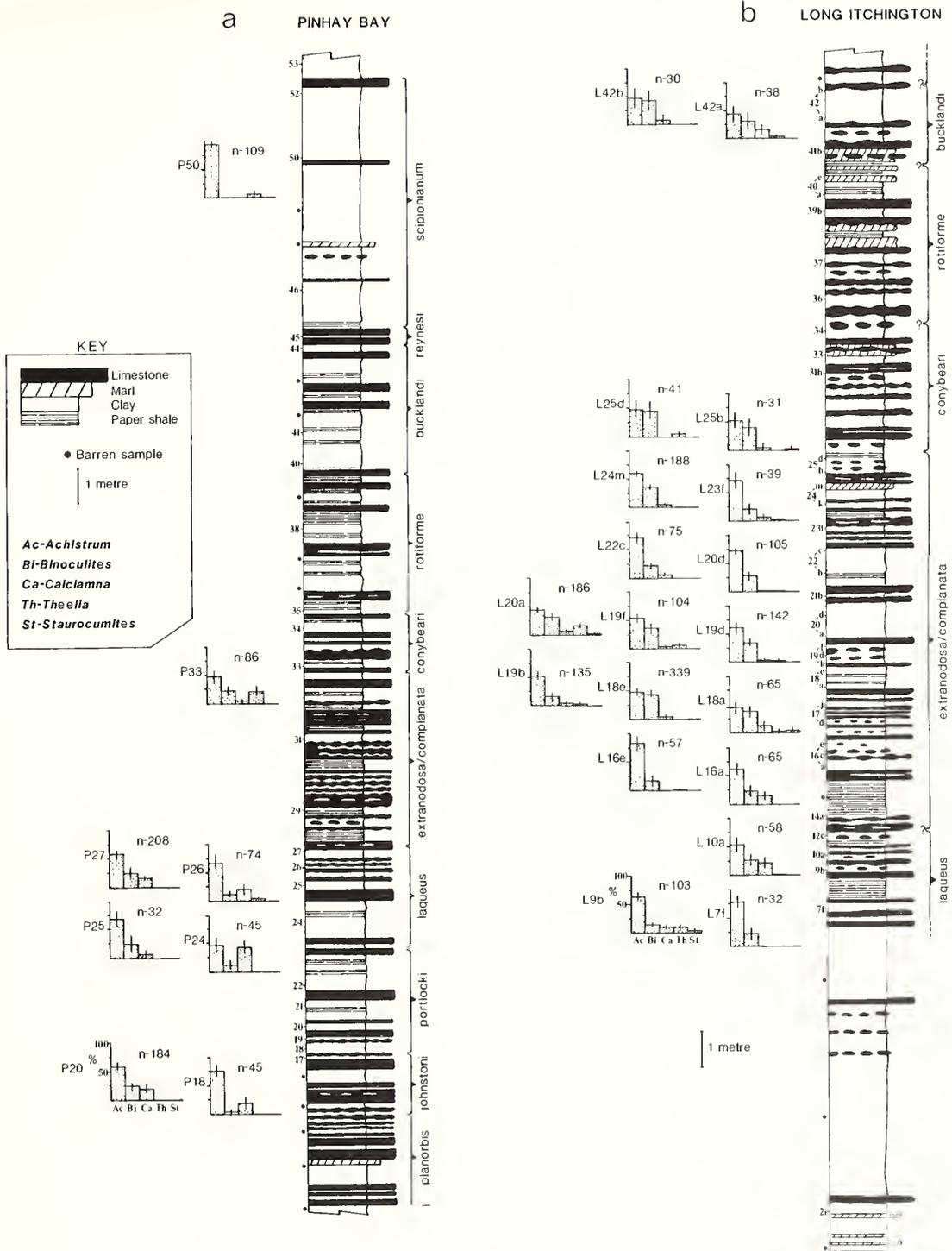
The residue was lightly scattered over an 8 \times 7 cm tray and scanned/sorted under a binocular microscope. Microfossils were transferred and stored on gum-coated Franke slides. In order to determine the relative abundance and co-occurrence of morphotypes the numbers of each type of sclerite were recorded from four 'pickings'. In addition material treated ultrasonically was scanned for excellent specimens.

Most of the measurements were made with a graticule eyepiece binocular microscope. For scanning electron microscopy, spicules were mounted on photographic film, and larger material with 'Evostick' wood glue. These were coated with gold palladium and observed with Hitachi S-2500, Cambridge 100 and Cambridge 180 scanning electron microscopes.

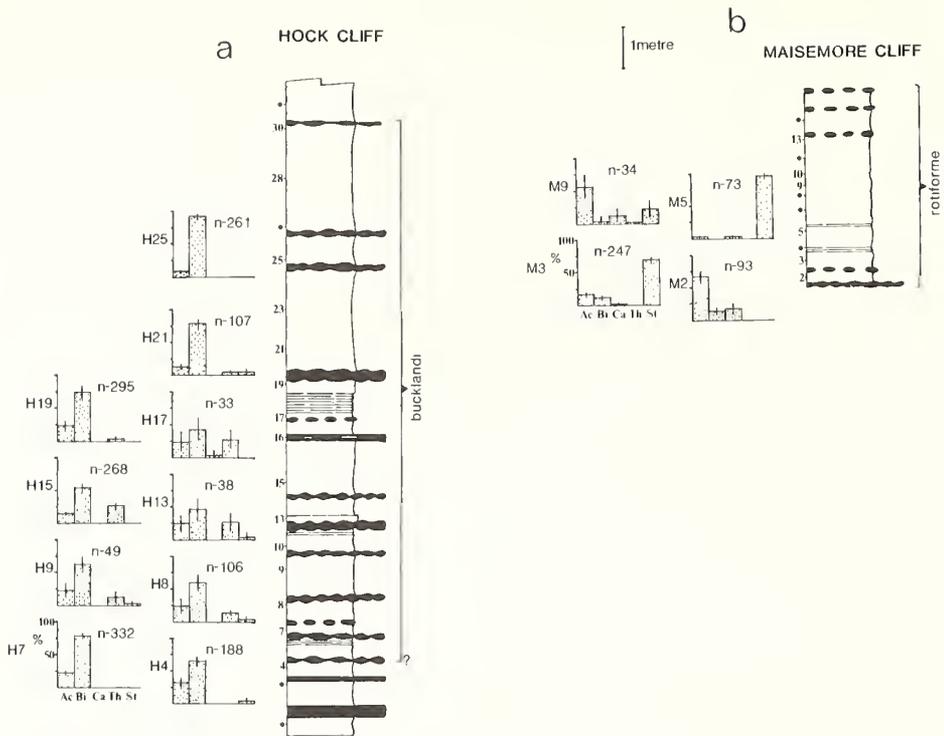
SCLERITE DISTRIBUTION IN THE BLUE LIAS

Occurrence of sclerites

Sample details and numbers of various sclerite types are shown in Text-figures 1–2. Of the 110 samples processed 76% contained holothurian sclerites, some in abundance (> 50 from four pickings). In the remaining 26 samples 23 had few or no other microfossil elements. No relationship could be discerned between the presence or abundance of holothurians, or particular morphotypes, with any other group of microfossils which included echinoid, ophiuroid, asteroid and crinoid debris, ostracods, foraminiferans, bivalves, microgastropods, sponges and fish fragments. Rioult (1961) noted that holothurians were numerous in beds rich in other echinoderms but variable compared with ostracods and foraminiferans. Michelson (1972) reported the co-occurrence of the ostracod genus *Macrocypris* with the highest abundance of holothurian sclerites but an inverse relationship with the genus *Lophocythere*. In the present material non-holothurian components of the microfauna were not studied in such taxonomic detail but no correlation was observed between holothurian abundance and the distribution of different ostracod types.



TEXT-FIG. 1. *a*, Section through the Blue Lias at Pinhay Bay. *b*, Section through the Blue Lias at Long Itchington. Sample numbers used at Long Itchington are after Clements *et al.* (1975). Sections shown with reference to ammonite subzones. Numbers on section are samples; sample numbers on the histograms preceded by P (Pinhay Bay) or L (Long Itchington). Histograms record the relative abundance (mean \pm 2 standard errors) of each major morphotype from samples with a total sclerite complement (*n*) of 30 or more (after '4 pickings').



TEXT-FIG. 2. *a*, Section through the Blue Lias at Hock Cliff. *b*, Section through the Blue Lias at Maisemore Cliff. Sections shown with reference to ammonite subzones. Numbers on section are samples; sample numbers on the histograms preceded by H (Hock Cliff) or M (Maisemore Cliff). Histograms record the relative abundance (mean \pm 2 standard errors) of each major morphotype from samples with a total sclerite complement (n) of 30 or more (after '4 pickings').

Sclerite abundance

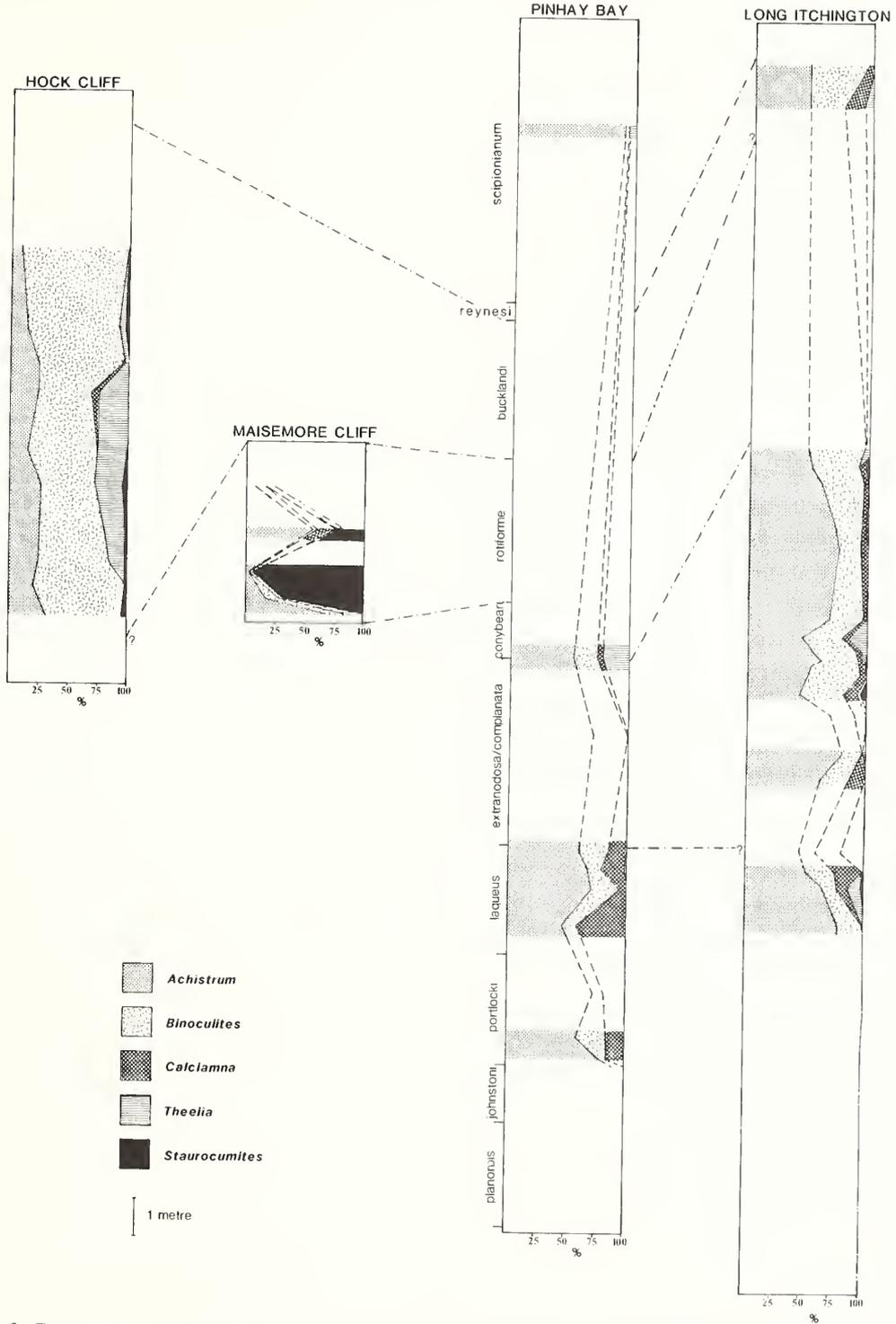
An estimate of the numbers of sclerites per weight of sediment from L18e, the most holothurian rich sample, gave an equivalent of 12250 per 100 g, comparable with the number of ostracod valves. An average figure nearer 4000 sclerites/100 g was calculated for samples in which sclerites were relatively common, i.e. those shown in Text-figures 1–2. This is still significantly higher than the maximum value of 400 sclerites/100 g given by Michelson (1972).

Composition and sclerite association

The most conspicuous elements of the holothurian fauna are 'hooks' – *Achistrum monochordata* Hodson, Harris and Lawson, 'dumb-bells' – genus *Binoculites* Deflandre-Rigaud, 'plates/buttons' – genus *Calclanna* Frizzell and Exline, 'wheels' – genus *Theelia* Schlumberger, and 'tables' – *Staurocumites bartensteini* Deflandre-Rigaud.

The relative numbers of the main morphotypes were recorded to determine whether two or more consistently co-occurred and thus might be considered to form a sclerite assemblage (see Gilliland 1990, Section 2.2.2). For example, if hooks and wheels were possessed by the same species one would expect both to occur in the same samples. A constant ratio between components of an assemblage cannot be assumed. On the other hand an increase or decrease in one morphotype should, at least, be accompanied by a similar change in the other morphotypes, and this should be observable in fossil material.

The relative abundance of sclerites from each section is summarized in Text-figure 3. There is no



TEXT-FIG. 3. Comparison of the relative abundance of the main morphotypes within each section using Pinhay Bay as a reference for correlation (dot-dash lines). Shaded areas are parts of the section with samples containing 30 or more sclerites. Dashed lines indicate extrapolation between the shaded areas but with information included from samples with between 20 and 30 sclerites.

evidence of an association between any of the five major morphotypes. For example, *Staurocumites bartensteini* has a sporadic distribution which does not relate to any of the other four morphotypes and *Binoculites* occurs at Hock Cliff without the presence of *Calclamna*. *Binoculites* generally changes inversely to *Achistrum*, and there is no correlation between the latter genus and *Theelia*.

The relative abundance of morphotypes is useful for constructing a 'faunal profile' within and between sections. This is constructed from the number of discrete sclerites within a standard sample size, but, unfortunately, cannot be related to numbers of individual animals since a *Staurocumites*-bearing species may have more sclerites per individual than an *Achistrum*-bearing species. Similarly, changes in the relative numbers of morphotypes could represent changes in the density of sclerites within a species or between populations. Therefore it cannot be assumed that the predominance of a morphotype is indicative of a dominant species in the living holothurian fauna. Post-mortem sorting of different sclerites is probably not significant (see discussion).

There are some changes within the sections (Text-fig. 3), but, given the sporadic occurrence of sufficient numbers of specimens, particularly from the same periods of time at different sections, little correspondence between sections can be recognized. It is difficult to explain why there are incongruities in the absolute abundance of sclerites: there are no consistent differences in the lithology or associated microfauna of samples in which holothurians are common and those in which they are not.

Whilst faunal/sclerite composition offers little stratigraphic use, broad trends within sections are worth comparing. Sclerite composition during the Upper Hettangian is similar in the Pinhay Bay and Long Itchington sections, i.e. a predominance of *Achistrum*, a significant proportion of *Binoculites/Calclamna*, and a sporadic occurrence of *Theelia* and *Staurocumites*. Further up the section in the *bucklandi* zone at Long Itchington the percentage of the various sclerites remains similar to the lower part of the section. However, at Pinhay Bay, in the *scipionianum* subzone, the composition changes significantly and hooks become more important. At Hock Cliff the situation differs with *Binoculites* (and only a few *Calclamna*) more significant than *Achistrum* and more wheels compared to other localities. The composition at Maisemore Cliff is strikingly different with marked fluctuations in *Staurocumites*, a morphotype which is rare or absent in the other sections. Hence, in spite of the limited data there appears to be evidence of greater geographical than stratigraphic variation.

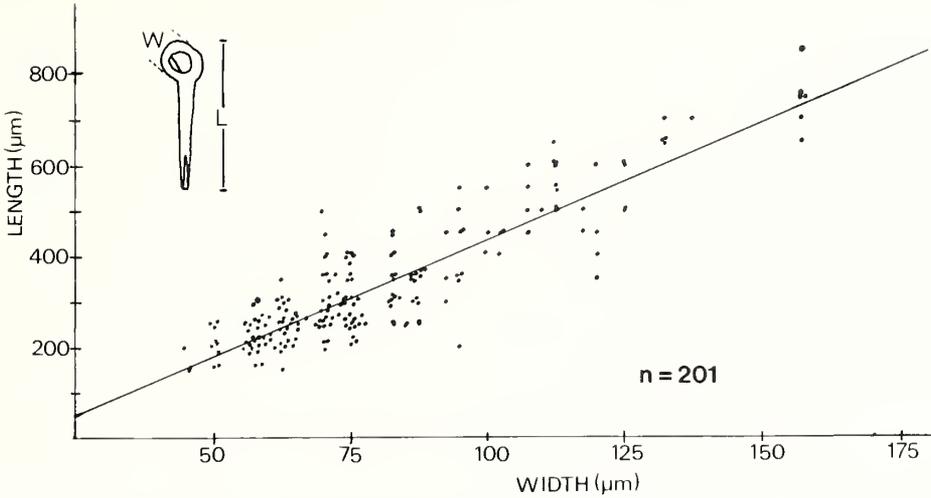
VARIATION OF *ACHISTRUM MONOCHORDATA*

Hooks occur throughout the sections studied and are commonly the most conspicuous type of sclerite (see Text-figs 1–2). All of the hooks can be referred to *Achistrum monochordata*. The morphospecies is present in sufficient numbers to allow an analysis of changes in its morphology.

Initial observations indicated that only size and eccentricity (whether the head lies to the right or left of the shaft) varied appreciably. Most hooks are broken along the shaft so head width was used as a parameter of size, since in intact hooks width correlates well with length (Text-fig. 4). Fifty specimens were picked from samples in which *A. monochordata* was relatively common or abundant. A comparison of the measurements of two sets of fifty hooks from the same sample (L18e) gave an insignificant difference in width ($t = 0.7$ compared with the tabulated value of $t = 1.658$, at $P = 0.05$).

The ratio of left to right 'headed' hooks varied between 0.515 (L24m) and 1.941 (L16). There is no evidence of a relationship between this variation and variation in hook size (the correlation coefficient value for left:right ratio against mean width is 0.04). Indeed the mean widths of left and right hooks are almost identical – left = 106.5 μm , $n = 554$, right = 106.8 μm , $n = 592$, with 4 examples showing no eccentricity. Both left and right hooks occur in the body wall of whole body individuals from the Carboniferous Mazon Creek locality (personal observation).

A change can be seen in hook size over time (Text-fig. 5). All the means from the cluster of high values in the *portlocki-conybeari* period are significantly different from those of the *rotiforme-reynesi* period (at the $P = 0.05$ level) except the 'largest' value of the lower cluster (lower *rotiforme*) and the



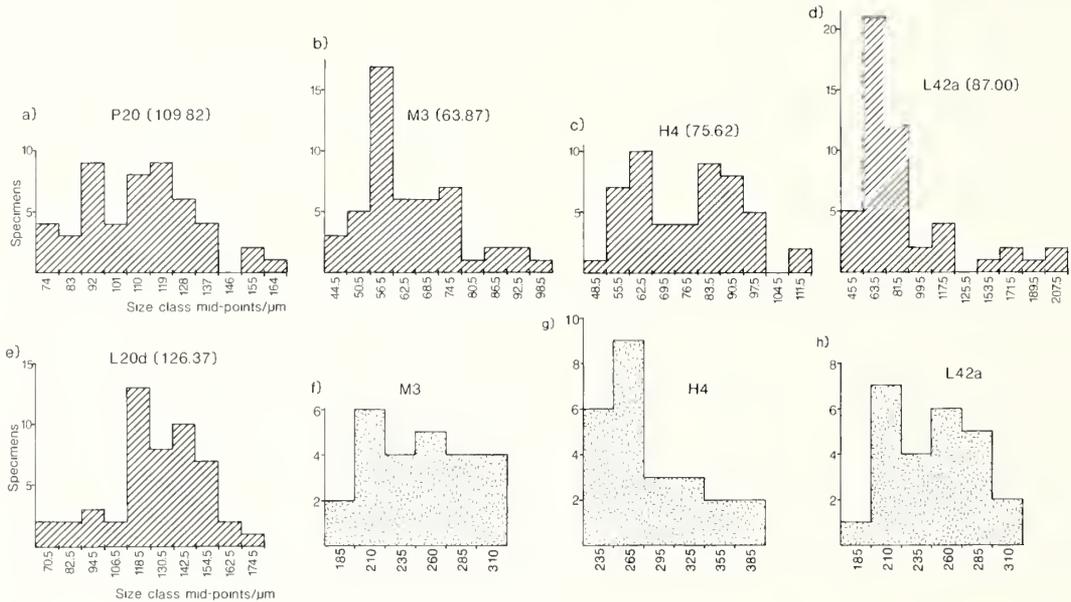
TEXT-FIG. 4. A plot of length against width of head in *Achistrum monochordata*. The regression equation is $Width = 14.7 + 0.1938 \text{ Length}$; $R^2 = 79.2\%$, correlation coefficient = 0.891.



TEXT-FIG. 5. Values of mean width (± 2 standard errors) of *Achistrum monochordata* ($n = 50$) from various samples through the Blue Lias. Question marks indicate samples of uncertain stratigraphic age. \square = Pinhay Bay, \bullet = Long Itchington, \circ = Hock Cliff, \blacktriangle = Maisemore Cliff.

'smallest' value of the higher cluster (upper *portlocki*). The variation appears to be over time rather than between localities (i.e. geographical variation) because samples from Long Itchington occur in both the main groups of values.

The possible cause(s) of the observed trend in hook size are not obvious. Nothing is known about the size of hooks, or analogous Recent sclerites, compared with the size of the individual animal, and it is difficult to envisage a link between the average spicule size and any environmental factors. Post-mortem effects such as sorting can be dismissed because there is no consistent correlation between width frequency distribution and mean size (see Text-fig. 6*a-e*). The observed change in



TEXT-FIG. 6. *a-e*, Size frequency histograms of the head width in 50 specimens of *Achistrum monochordata* from selected samples. Figure in brackets is the mean width. *f-h*, Size frequency histograms of length in 25 specimens of *Binoculites terquemi* from selected samples.

EXPLANATION OF PLATE I

Figs 1–7, 9, 20. *Binoculites terquemi* Deflandre-Rigaud. 1, E27320; H9; *bucklandi* subzone, $\times 105$. 2, E27313; H4; *bucklandi* subzone, $\times 110$. 3, E27321; H9; *bucklandi* subzone, $\times 40$. 4, E27324; L10*a*; *laqueus?* *extranodosa/complanata* subzone, $\times 90$. 5, E27330; L10*a*; *laqueus?* *extranodosa/complanata* subzone, $\times 115$. 6, E27296; L9*b*; *laqueus?* *extranodosa/complanata* subzone, $\times 110$. 7, E27279; L10*a*; *laqueus?* *extranodosa/complanata* subzone, $\times 155$. 9, E27315; L10*a*; *laqueus?* *extranodosa/complanata* subzone, $\times 205$. 20, E27344; H7; *bucklandi* subzone, $\times 70$.

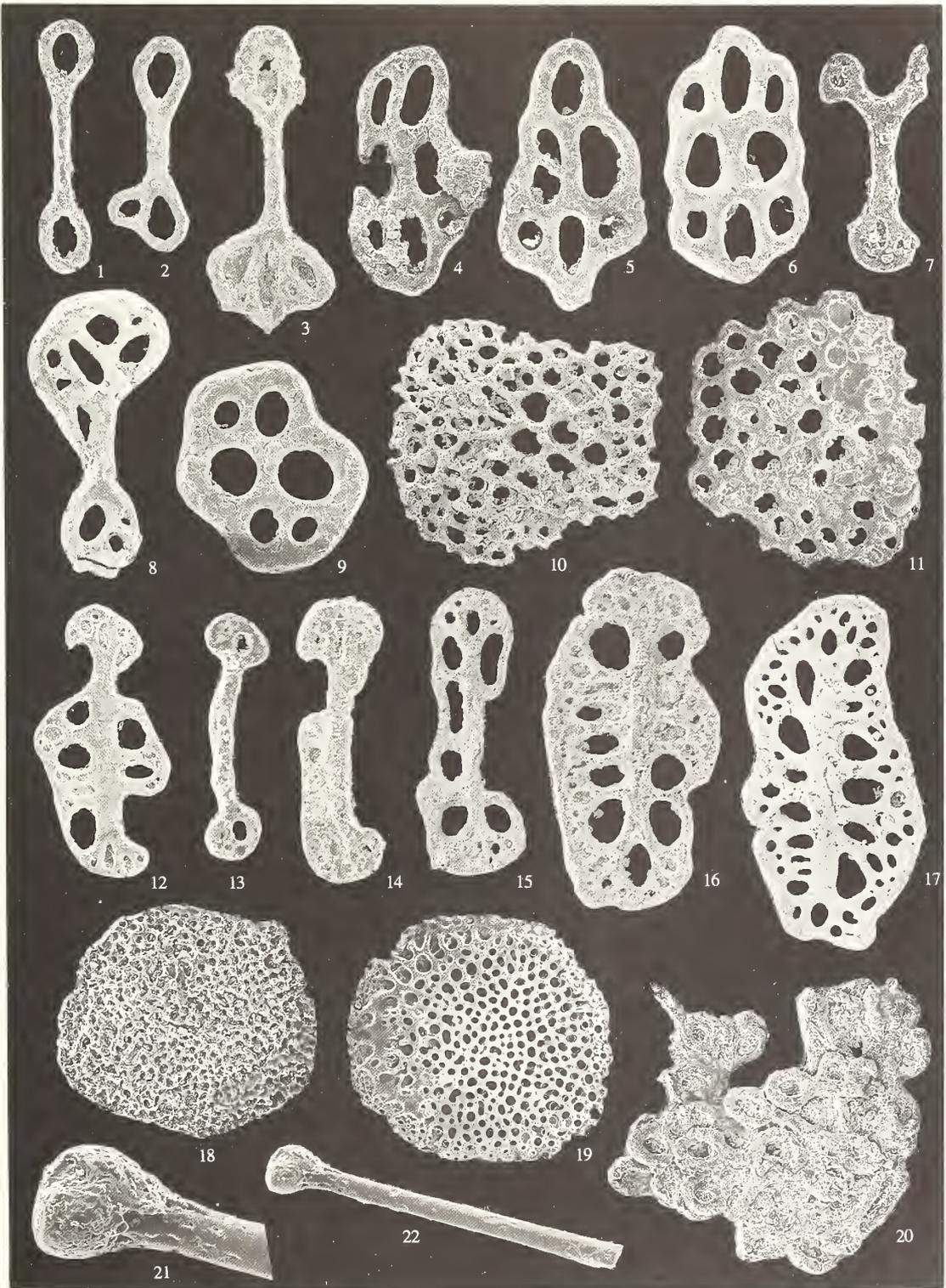
Figs 8, 12–17. *Binoculites jurassica* Frizzell and Exline. 8, E27289; L9*b*; *laqueus?* *extranodosa/complanata* subzone, $\times 105$. 12, E27317; L10*a*; *laqueus?* *extranodosa/complanata* subzone, $\times 100$. 13, E27291; L18*e*; *angulata* zone, $\times 95$. 14, E27292; L18*e*; *angulata* zone, $\times 95$. 15, E27293; L18*e*; *angulata* zone, $\times 95$. 16, E27294; L18*e*; *angulata* zone, $\times 95$. 17, E27305; L24*k*; *angulata* zone, $\times 95$.

Figs 10–11. *Eocaudina*-type plates. 10, E27360; L33*b*; *conybeari?* *rotiforme* subzone, $\times 115$. 11, E27335; H13; *bucklandi* subzone, $\times 145$.

Figs 18–19. *Frizzellus*-type elements. 18, E27404; P27; *laqueus* subzone, $\times 120$. 19, Disc scale of the Recent ophiuroid *Ampholites norvegica*; from 300 m depth; Trondljemfjord, Norway, $\times 120$.

Figs 21–22. *Rhabdotites?* *rectus* Hampton. E27042; Upper Bathonian; Dorset, $\times 230$, $\times 100$, respectively.

H, L, M and P numbers refer to samples. E numbers are British Museum (Natural History) catalogue numbers.



GILLILAND, Blue Lias holothurian sclerites

size may have stratigraphic application but the small size of samples in some parts of the succession makes this difficult to prove. In addition there is a possible cycle of increasing/decreasing size, but this also cannot be confirmed because of the low frequency of hooks in the critical period prior to the *portlocki* subzone.

THE MORPHOGENERA *BINOCULITES* AND *CALCLAMNA*

Dumb-bell-shaped sclerites of the genus *Binoculites* Deflandre-Rigaud are common in the material studied. Three 'species' occur distinguished on the number of holes in the expanded ends (Rioult 1961): *B. terquemi* Deflandre-Rigaud (one hole), *B. irregularis* Frizzell and Exline (< five) and *B. issleri* Deflandre-Rigaud (> five). On the basis of the present material the three taxa are intergradational and can no longer be separated; there are even examples with a different number of holes at either end that could be classified as one of two different 'species' depending on which end is selected (Pl. 1, figs 2–3).

Observations of over 1500 specimens indicate that *Binoculites* and plates/buttons of the genus *Calclamna* are linked in a morphological growth series with the former developing into the latter. However, it is possible that some of the apparent 'early growth stages' had completed growth, i.e. within one individual there was a mixture of *Binoculites*, perhaps restricted to one part of the body such as the tube-feet, together with *Calclamna* at all stages of formation.

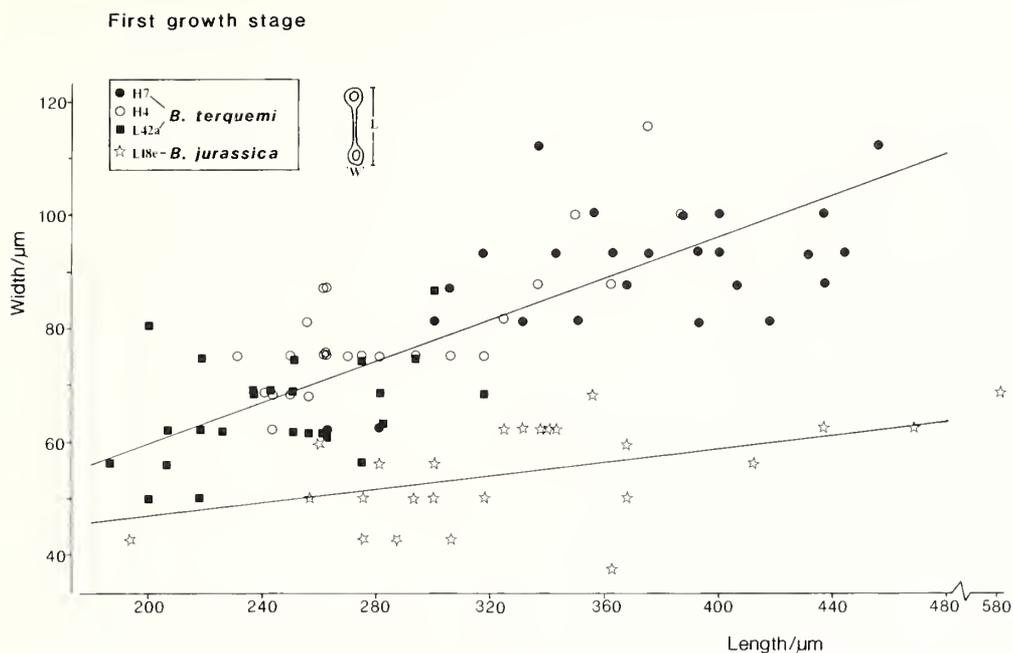
Two different growth series are evident, each derived from a different form of *B. terquemi*. The first, here referred to as 'Calclamna group one', begins with a short *B. terquemi* with relatively wide terminal holes (*B. terquemi* form *beta* of Rioult 1961). Additional holes are added at each end commonly before development of the central holes. Subsequent growth from each end of the 'dumb-bell' and outwards from the shaft produces a cruciform pattern of holes. The 'end product', *Calclamna germanica*, is variable in shape, and the number, size and distribution of the additional holes are also variable. Occasionally a 'bar' has grown across and divided one of the central holes (Pl. 1, fig. 5). Michelson (1972) noted a similar variation in *Calclamna germanica*, but a bar was more frequent in his material.

The second growth series, 'Calclamna group 2', begins with a relatively long and thin *B. terquemi* (form *gamma* of Rioult 1961). This form can usually be identified by the thickness of its shaft, which is nearly as thick as the two ends, and, except in smaller specimens, by a greater length/width ratio (see Text-fig. 7), although a distinction between the two forms of *B. terquemi* cannot always be made. Due to the long shaft section of *B. terquemi* form *gamma* subsequent growth creates two rows of holes along the length of the shaft. The formation of bars is obvious in some specimens and contributes to an increase in the number of central holes. Sometimes the middle part has fully formed before the rest of the sclerite, resulting in the morphospecies *Calclamnella jurassica* Frizzell and Exline (Pl. 1, fig. 12). At the periphery there are many small holes which occur rarely in *Calclamna germanica* (Pl. 1, fig. 17). In a number of examples of 'Calclamna group two' the central shaft and rim of the plate are thicker than the rest of the sclerite.

Elongate plates with two rows of holes are normally included in the morphogenus *Calclamnella* Frizzell and Exline. Here *Calclamnella* is restricted to elongate plates with two rows of holes which lack the terminal holes that are characteristic of *Calclamna*. This distinction is important because the buttons/plates of dendrochirotes are like *Calclamna*, whereas the buttons of aspidochirotes are usually like *Calclamnella* as defined here.

The two growth series result in apparently different morphologies (compare Pl. 1, fig. 6 with fig. 17), but do these represent distinct biological taxa? The formation of bars, increasing hole number, and the occurrence of intermediate forms (Pl. 1, figs 7–8) serve to reduce the distinction between the two series. In the material of Michelson (1972) the proportion of intermediates was evidently quite high. On the other hand the range of variation represented by the two series is not known in any one Recent species. Thus the morphological evidence may indicate two distinct biological species, but is there supporting evidence from their stratigraphic distribution?

The stratigraphic distribution of the two groups offers conflicting evidence. Both types are known



TEXT-FIG. 7. Plot of length (L) against width (W) of the earliest growth stage for *Binoculites terquemi* (regression equation: $\text{Width} = 23.75 + 0.18 \text{ Length}$) and *B. jurassica* ($\text{W} = 35.34 + 0.06 \text{ L}$), $n = 25$ for each sample (see text for discussion of taxonomy).

from the Middle Triassic upwards and have been recorded together (e.g. Issler 1908; Michelson 1972; Gupta and Kachroo 1976; Gheorghian 1976). In this study they have a similar overall stratigraphic range (Text-fig. 8), and in most samples there are specimens from both groups. The relative proportions of each group, however, vary stratigraphically (Text-fig. 8). In the *portlocki-laqueus* subzones there is a mixture of both *Calclamna* groups, followed by an increase in the proportion of 'group two' and then, towards the top, there is almost complete dominance of 'group one'. Within each group the ratio of *Binoculites* to *Calclamna* is markedly different in the lower part of the section, even in the same sample. In the *rotiforme/bucklandi* subzones, at Hock Cliff and Maisemore Cliff, 'group one' is composed almost entirely of *Binoculites terquemi* of variable size which may even represent a third 'group'. Assemblages from the same period at Long Itchington, however, retain the full growth series and resemble those from lower down in the section.

Thus the differences between all stages of each growth series and the quantitative stratigraphic evidence suggest a distinction between two species, whereas the occurrence of sclerites intermediate between both growth series and the gross stratigraphic distribution suggest there is only one species. However, the degree of variation represented by the two series is greater than that known from any recent species. The two groups are therefore separated as two closely related 'biological' species.

The following taxonomic revision is proposed. The *Binoculites* of each species (growth series) can be distinguished as described above. The final stage of 'group one' is *Calclamna germanica* and of 'group two' *Calclamna jurassica*. Both growth series belong to the same genus for which the senior synonym is *Binoculites*. Each growth series must be named after the senior specific synonym within each, i.e. *Binoculites terquemi* and *Binoculites jurassica* respectively. The morphotypes 'Binoculites' (= early growth stage), restricted to those sclerites which have not yet lost the distinctive dumb-bell shape, and 'Calclamna' (= late growth stage) are retained as informal names in order to identify possible significant (geographical/evolutionary?) changes in the ratio of these two stages. For

example, Michelson (1972) recorded very few specimens of the form *Binoculites* amongst more than 1700 of the form *Calclamna* from the Lias of the Danish Embayment. The high percentage of early growth stages at Hock Cliff and Maisemore Cliff is interpreted as geographical variation within the species *Binoculites terquemi*.

ELEMENTS OF THE CALCAREOUS RING

A significant number of elements of the calcareous ring were recovered from the Blue Lias. Fossil records of elements of the calcareous ring are remarkably rare considering the number of described sclerites (Gilliland 1990, Section 5.4). The descriptive terminology used for the gross structure is based on that of Belyaev and Mironov (1977) as outlined in Gage and Billet (1986). Two main types of ring, and two others, can be distinguished.

Calcareous ring Type 1

More than twenty specimens each of radial (Pl. 5, figs. 6–10; Pl. 6, fig. 1; Text-fig. 9f–g) and interradial (Pl. 5, figs. 3–5; Text-fig. 9d–e) elements were found (including BMNH E27415–27419, E27424–27425, E27428, E27439, E27441–27442), from the *extranodosa/complanata*, *rotiforme* and *bucklandi* subzones.

Interradials. The anterior end consists of a well-developed pointed process, relatively large lateral crests and associated small frontal excavations. The whole element tends to be curved with the inner face being concave and the lateral articulation faces inclined inwards (Pl. 5, fig. 3). Associated with the posterior indent is a sunken area on the inner face which shallows anteriorly (Text-fig. 9e). The stereom is typically very dense with thickened trabeculae and small pores (diameter *c.* 10–15 μm) over a large part of the outer face (Pl. 5, fig. 5) but may be comprised of a more open labyrinthic stereom, as in the rest of the outer face and the entire inner face, or a denser, 'knobbly' stereom as on the frontal excavations (Pl. 5, fig. 5).

Radials. There are one or two anterior processes. The first, found in most specimens, is short and broad with a central notch (e.g. Pl. 5, figs 8, 10). The additional process is longer and pointed like that of the interradial (Pl. 5, fig. 8). On the external face a depression lies posterior to the notch of the broader process and, when present, between the two anterior processes. Compared to the interradials, the radials are more elongate, less curved (internally/externally), and the posterior indent may be deeper, but the lateral crests and frontal excavations of both elements are similar. On the inner face the posterior indent extends into a furrow which divides anteriorly into two or three branches (Pl. 5, fig. 7; Text-fig. 9f). The stereom resembles that of the interradial but is consistently more dense on the main part of the external surface (Pl. 5, fig. 8).

Discussion. Although these elements are quite variable they are closely comparable with the calcareous ring elements found in the order Molpadiida. In fact variation in the shape of the Type 1 elements is not unusual in Recent species, where it merely reflects the relative position within the calcareous ring (Hatanaka 1939). The relative length of interradials is also known to vary with age (Hozawa 1936). Hess (1975) described similar examples from the Oxfordian of Switzerland which he also assigned to the Molpadiida.

By comparison with Recent material it is possible to infer some of the soft tissue components of the fossil material. The longitudinal muscle would have inserted onto the notched anterior process of the radial piece (see Text-fig. 9f). The furrow would have housed the anterior extension of the radial canal. This normally divides into three tentacular canals (leading to a total of fifteen tentacles from five radials in Recent molpadiids) and a much smaller radial canal. In the fossil material details of this part were not observed, possibly because the furrow was very shallow and the reduced section of the radial canal may have been too small to have left a preservable trace. Hence it is unfortunately not possible to infer the number of tentacles present in this species. The reduced part of the radial

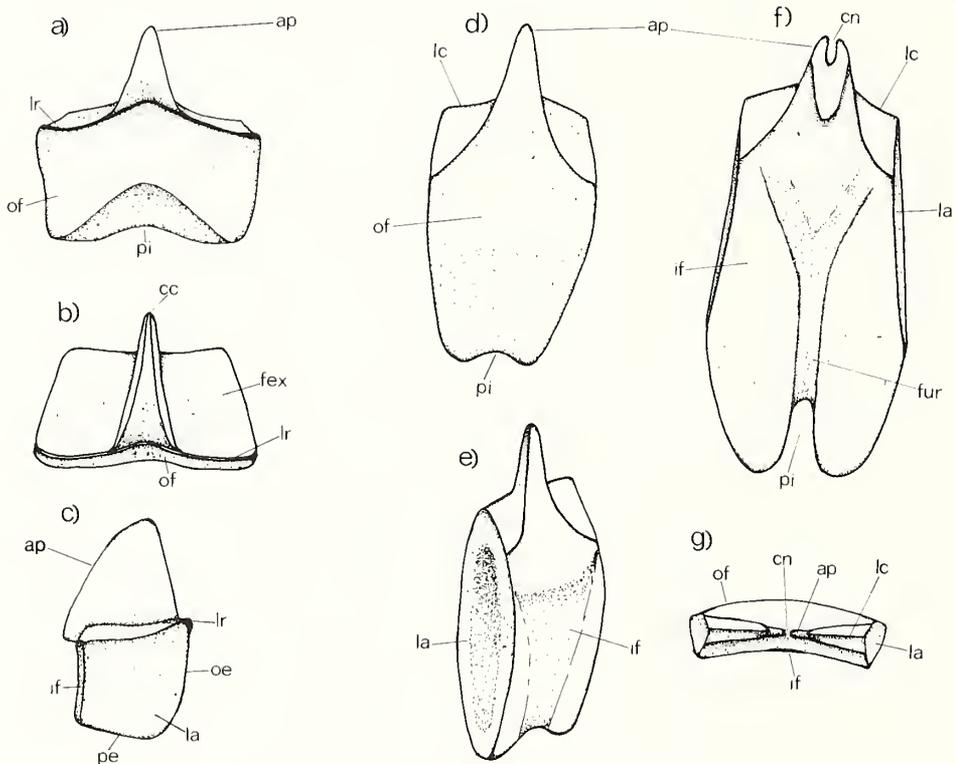
canal would have passed over the front of the radial through the notch of the main anterior process.

Of the four families of Molpadiida the calcareous ring described here is most likely to be derived from the Molpadiidae. In this family the radial elements possess a single posterior process, which is commonly notched, and, in some species, a notch in the anterior process for the passage of the radial canal and nerve. The radial elements of the Caudinidae also have a notch on the anterior process but, by contrast, there are large posterior prolongations (see Heding 1935). The ring elements of the Gephyrothuriidae are different, being short and very broad with anterior ridges rather than processes (Heding 1935). In the Eupyrgidae the posterior process is rudimentary and there is a perforation, rather than a notch, for the passage of the radial canal and nerve (Heding 1935).

Calcareous ring Type 2

More than 25 specimens were recorded, including BMNH E27420–27423, E27440 (Pl. 6, figs 2, 4–5, 8–10; Text-fig. 9*a–c*), from the *laqueus?extranodosa/complanata*, *extranodosa/complanata*, *conybeari*, *rotiforme?bucklandi* and *bucklandi* subzones. The radial and interradial elements are very similar in structure and cannot be differentiated.

There is one, or occasionally two (Pl. 6, fig. 10), prominent anterior process with a well-developed central crest which also projects from the inner face (Pl. 6, fig. 5). The lateral crest, or ridge, is



TEXT-FIG. 9. *a–c*, reconstruction of calcareous ring Type 2, example with one anterior process; *a*, outer face; *b*, lateral view; *c*, anterior view. *d–g*, reconstruction of calcareous ring Type 1; *d*, interradial, outer face; *e*, interradial, oblique view of inner face; *f*, radial, inner face; *g*, radial, anterior view. Abbreviations: ap, anterior process; cc, central crest; cn, central notch; fex, frontal excavation; fur, furrow; if, inner face; la, lateral articulating face; lc, lateral crest; lr, lateral ridge; oe, outer edge; of, outer face; pe, posterior edge; pi, posterior indentation.

usually well developed (Pl. 6, fig. 4). The frontal excavations are relatively large and flat (Pl. 6, fig. 4) as are the lateral articulation faces. The posterior end is slightly concave or indented except in one example in which there is a well-developed process (Pl. 6, fig. 9). The internal face, and sometimes the external face, may be deeply sunken near the posterior edge and shallows to form a ridge anteriorly (Pl. 6, fig. 2). The stereom is openly labyrinthic over the inner and outer faces and towards the anterior process, but thickened at the edges. In some examples the internal face of the anterior process appears imperforate (Pl. 6, fig. 2). The stereom is denser on the frontal excavations (Pl. 6, fig. 8) and the side of the anterior process (Pl. 6, fig. 5).

Discussion. This type of calcareous ring is most similar to that of the Recent family Myriotrochidae (order Apodida). In myriotrochids the radials differ from the interradials by sometimes having a perforate anterior process, of which there is one possible example in the fossil material, and sometimes a double anterior process, of which there is at least one specimen from the Blue Lias (Pl. 6, fig. 10). In addition, a posterior process, as seen in BMNH E27422 (Pl. 6, fig. 9), is found only on radial elements, e.g. as in *Myriotrochus clarki* or *Siniotrochus myriodontus* (Gage and Billett 1986). Even considering this and further variation of Recent myriotrochids, such as the development of the posterior process in *M. clarki*, the gross morphology of the fossil examples is very variable and they may be derived from different myriotrochids. However, for the moment these elements are interpreted as all from one type of ring pending further material.

Amongst Recent myriotrochids two anterior processes occur only on the (dorso-lateral) radials of species which have twelve tentacles (Heding 1935). By inference the fossil species from which Type 2 elements are derived is assumed to have possessed twelve or more tentacles. Hess (1975) described similar myriotrochid elements of the calcareous ring from the Oxfordian of Switzerland.

Calcareous ring Type 3

One specimen, BMNH E27426, was recovered from sample H15 (Pl. 6, figs 3, 6). This has a very similar structure to that of the Type 2 elements, but has two discrete posterior processes which are not confluent with the lateral edges.

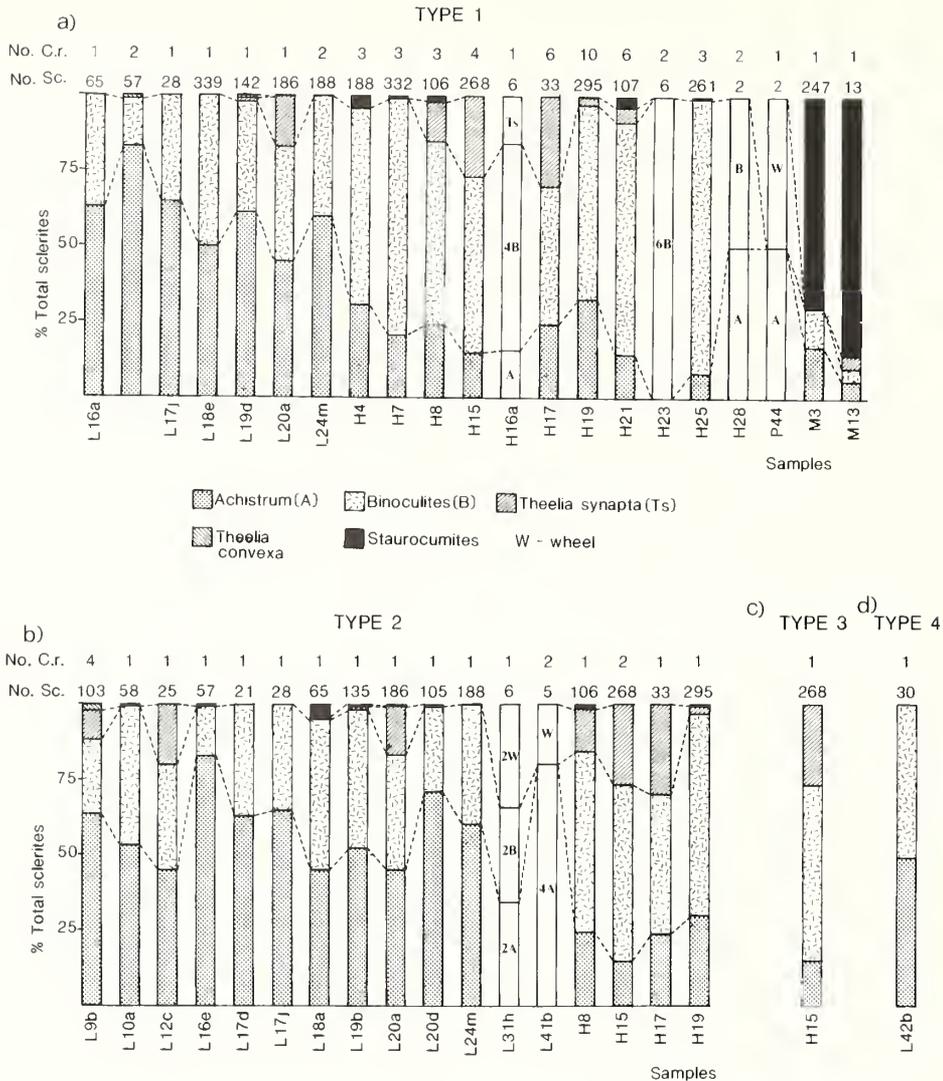
Discussion. The presence of posterior processes suggests that this is a radial element. It is most like the calcareous ring of the Myriotrochidae, by comparison with the Recent fauna and calcareous ring Type 2. It co-occurs in the same sample with several Type 2 elements, including BMNH 27422, of which it may be an aberrant form. However, there are no Recent myriotrochid radials with posterior processes like those seen here. Hence this element is tentatively separated from calcareous ring Type 2.

Calcareous ring Type 4

A single element, BMNH E27427, from a fourth type of ring was found in sample L42b (Pl. 6, fig. 7). Its stereom architecture indicates this is certainly echinoderm in origin. The symmetrical shape of the element, the presence of two apparent lateral faces, and a possible anterior process with a furrow on the internal (?) face and a notch at the end suggest that this is from a holothurian rather than any other echinoderm. Amongst holothurians this fourth type of element is most similar to the radials of some 'simple' types of ring found in the Dendrochirotida, e.g. the Cucumariidae, and the Dactylochirotida.

Relationship of calcareous ring and sclerites

The distribution of the four types of calcareous ring are compared with the more common sclerite components of the holothurian fauna (in Table 1). The percentage on the right indicates the probability of finding a particular morphotype when that type of ring is present in a sample. This is affected by the frequency with which each morphotype is found, i.e. the percentage is high for *Achistrum* because this morphotype is the most common throughout the succession. The left-hand column is more informative, giving an indication of the probability that a particular type of ring



TEXT-FIG. 10. Number of elements of the calcareous ring (No. C.r.), total numbers of sclerites (No. Sc.) and the relative number of the main morphotypes for samples bearing: a, calcareous ring Type 1; b, Type 2; c, Type 3; d, Type 4.

will occur in a sample when a particular morphotype is also present. These percentages are more dependent on the relationship between the calcareous ring and sclerites than the frequency of the sclerites.

In Text-figure 10 the total number of elements of each type of ring is given together with the number of sclerites and the percentage composition of the sclerites. There is large variation in the number of sclerites relative to the number of elements of the calcareous ring (e.g. cf. *Staurocumites*, or total sclerites, with Type 1 in samples H19, M3 and M13), hence there is little point in trying to estimate the number of sclerites per individual of fossil species based on there being usually only 10–12 elements of the calcareous ring in most extant holothurians.

Calcareous ring Type 1 is derived from a molpadiid and probably the family Molpadiidae. In the

TABLE 1. The distribution of elements of the calcareous ring with respect to the most common sclerite morphotypes; bracketed figures are the number of samples in which both the calcareous ring and morphotype are found as a percentage of the total number of samples bearing that particular morphotype (on the left) or calcareous ring (on the right).

Sclerite morphotype	Calcareous ring											
	Type 1			Type 2			Type 3			Type 4		
	%	No. samples	%	%	No. samples	%	%	No. samples	%	%	No. samples	%
Total	(25.0)	21	(20.5)	17	(1.2)	1	(1.2)	1	(1.2)	1	(1.2)	1
<i>Achistrum</i>	(26.0)	20	(95.2)	17	(100)	1	(100)	1	(100)	1	(100)	1
<i>Binoculites</i> / <i>Calclamna</i>	(29.9)	20	(95.2)	16	(94.1)	1	(100)	1	(100)	1	(100)	1
<i>Theelia synapta</i>	(36.4)	8	(38.1)	8	(47.1)	1	(100)	1	(100)	1	(100)	1
<i>Theelia convexa</i>	(33.3)	3	(14.3)	5	(38.5)	—	—	—	—	—	—	—
<i>Stauromamites</i>	(55.0)	11	(52.4)	6	(35.3)	—	—	—	—	—	—	—

Blue Lias fauna the only possible molpadiid sclerite morphotype is *Staurocumites bartensteini*. The simplest interpretation, therefore, is that this morphotype and calcareous ring come from the same species. From Table 1 the most informative data, i.e. the left percentage column, support the association of Type 1 rings with *S. bartensteini*. However, it is surprising to find samples with Type 1 specimens but no *Staurocumites* (Text-fig. 10a).

Calcareous ring Type 2 is most closely comparable with that of the Myriotrochidae, but no distinctive myriotrochid wheels were recovered. However, the calcareous ring of hook-bearing body fossil material from the Carboniferous Francis Creek Shale is most similar to that of extant myriotrochids (personal observation) and hence the structure seen in the Myriotrochidae today may be primitive. Calcareous ring Type 2 is likely to be associated with one of the three apodan morphotypes found in the Blue Lias fauna, but as to which one it is difficult to conclude. *Achistrum* is far more abundant and frequent than either of the two apodan wheels, but the results in Table 1 indicate an association with *Theelia convexa*. A similar problem arises in establishing the sclerite morphotype associated with calcareous ring Type 3; the results in Table 1 favour an association with *Theelia synapta*. Alternatively, the Type 3 element may be an example of calcareous ring Type 2 indicating that this 'myriotrochid-like' calcareous ring was more variable than that of modern myriotrochids.

If the fourth type of ring element is dendrochirote in origin, then the most likely associated morphotype is *Binoculites*, interpreted to be from a dendrochirote, which is more common than other relevant morphospecies, e.g. *Palaeoypsilus*, and the only one to occur in the same sample.

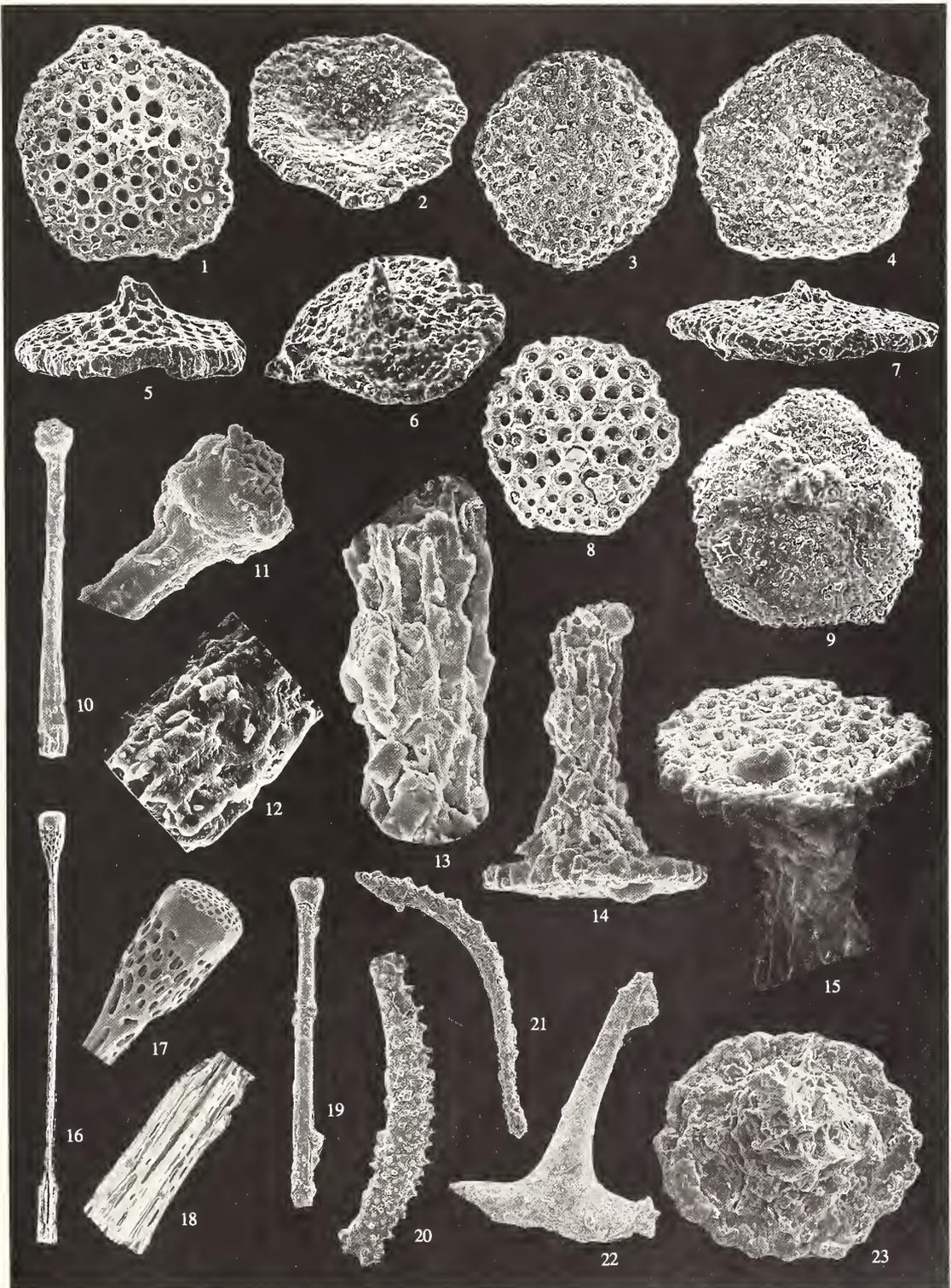
Even considering just the main sclerite taxa there appears to be one type of calcareous ring missing. Furthermore, Types 3 and 4 are each represented by a single specimen and calcareous ring structures are lacking in some samples with abundant sclerites. However, simple observations of Recent holothurians (Gilliland 1990) suggest that the ratio of sclerites to elements of the calcareous ring should be higher than even the most sclerite-laden samples from the Blue Lias. This could be because the relatively robust calcareous ring has a greater preservation potential, and/or post-mortem separation of an original calcareous ring/sclerite assemblage has occurred which is suggested by the variable distribution of the different calcareous ring types.

NON-HOLOTHURIAN 'HOLOTHURIAN SCLERITES'

The family Etheridgellidae. This family incorporates polygonal/subcircular, thickened, imperforate discs sometimes with a granular surface and a 'pseudospire'. Two genera were included in the Treatise, *Etheridgella* Croneis and *Frizzellus* Hampton (Frizzell and Exline 1966). A large number of such plates was recovered from all sections from the *planorbis* zone upwards. Previous authors have expressed doubts about whether these sclerites are from Holothuroidea. Frizzell and Exline (personal communication in Hampton 1958a) stated that plates from Recent ophiuroids were

EXPLANATION OF PLATE 2

- Figs 1–9. *Frizzellus*-type elements. 1, 5, E27388; L12c; *laqueus?extranodosa/complanata* subzone, both $\times 180$. 2, E27395; P25; *laqueus* subzone, $\times 180$. 3, E27392; P22; *portlocki* subzone, $\times 110$. 4, 9, E27377; P24; *laqueus*, both $\times 185$. 6, E27410; P50; *scipionianum* subzone, $\times 180$. 8, E27384; H4; *bucklandi* subzone, $\times 185$. 9, E27073 (in part); *Frizzellus irregularis* Hampton; Upper Bathonian; Dorset, $\times 115$.
- Figs 10–12, 19. *Rhabdotites*-type elements. 10–12, E27336; L7f; *laqueus* subzone, $\times 210$, $\times 590$, $\times 950$, respectively. 19, E27196; M9; *rotiforme* subzone, $\times 95$.
- Figs 13–15, 23. *Palaeoypsilus liassicus* sp. nov. 13–15, Holotype; E27338; H4, *bucklandi* subzone, $\times 400$, $\times 200$, $\times 245$, respectively. 23, Paratype; E27334; H4, *bucklandi* subzone, $\times 295$.
- Figs 16–18. Pedicellarium stalk of the Recent diademid *Centrostephanus longispinus* from the Philippines, $\times 75$, $\times 295$, $\times 295$, respectively.
- Figs 20–21. Curved rods. 20, E27333; L18a; *angulata* zone, $\times 160$. 21, E27364; M3; *rotiforme* subzone, $\times 100$.
- Fig. 22. Anchor-shaped sclerite; E27343; L18a; *angulata* zone, $\times 100$.



GILLILAND, Blue Lias holothurian sclerites

'generically indistinguishable' from *Frizzellus*. Hampton (1958a) argued for their holothurian origin because of the close association of *Frizzellus* with other undoubted holothurian sclerites, and because it appeared to be closely related to *Etheridgella*. However, the association of *Frizzellus* with other sclerites indicates little and furthermore Pawson (personal communication in Lane 1976; Pawson 1980) did not think *Etheridgella* was a holothurian either. Lane himself presented a convincing case for a crinoid origin for some *Etheridgella*-type sclerites from the Pennsylvanian Lane Shale (Lane 1976). Frizzell and Exline (1966) included the complete Devonian fossil *Palaeocucumaria huusrueckiaua* in the Etheridgellidae on the basis of the body wall sclerites. As Lane correctly pointed out, no matrix-free ossicles of *Palaeocucumaria* have been examined and their preservation within the body wall, and published photographs, are not sufficient for a detailed description. It is probable that the original sclerites of this species have acted as the nuclei for the formation of pyrite blebs, hence destroying any morphological details.

Observations of *Etheridgella*-type plates from the Blue Lias indicate that the majority cannot be interpreted as holothurian. The plates are of variable shape, thickness and size, i.e. 160–360 μm . The edges of plates are often irregular implying that their growth had not ceased. Some specimens are opaque and brown in colour, a feature which Lane considered to be an important difference between *Etheridgella* and associated undoubted holothurian sclerites. However, in the Blue Lias examples the colour depends on the thickness of the plates and also varies in the accepted holothurian morphotypes. Sclerites of the *Etheridgella*-type occur together with a variety of other echinoderm material and sometimes in samples with no unequivocal holothurian sclerites, but there is no obvious relationship with any of the other echinoderm classes.

Within the *Etheridgella* material it is possible to distinguish a number of different forms: (a) flat to biconvex plates composed of a multilayered labyrinthine stereom with an average pore size of *c.* 15 μm (Pl. 1, fig. 18); these plates have a granular surface of small knobs; the ultrastructure, size and variation in the shape of these plates compare well with the disc scales of ophiuroids (Pl. 1, fig. 19); (b) squarish, multilayered plates with a smooth surface and more solid appearance compared with type (a) due to thickened trabeculae and occluded pores (Pl. 2, fig. 3); some specimens of *Frizzellus irregularis* are very similar (Pl. 2, fig. 9); (c) strongly concavo/convex, circular plates, imperforate on the concave side and with a stereom meshwork on the convex side (Pl. 2, figs 2, 6); a thin or thick prominent projection is developed from the centre of the stereom structure; plates of this kind are not known in holothurians; and (d) polygonal plates, slightly concave in the centre, with large (*c.* 10 μm) regularly arranged holes in the middle and smaller (*c.* 5 μm) holes towards the periphery (Pl. 2, figs 1, 5); a short projection or spire comprising several struts extends vertically from the central convex area; similar convex plates without a spire may be early growth stages (Pl. 2, fig. 8; a plate with a spire and a single layered stereom is more likely to be holothurian than non-holothurian in origin; however, examples occur which are intermediate in morphology with 'type (a)' plates (Pl. 2, figs 4, 7).

The morphology of (a)–(c) above precludes assigning them to holothurians. Hampton's original material of *Frizzellus irregularis* in the collections of the British Museum (Natural History) shows a similar wide morphological variation. The position of type (d) is uncertain and for the moment it is preferable to classify it as echinoderm in origin rather than specifically holothurian. Some taxa of the Etheridgellidae, at least, seem to be derived from crinoids and ophiuroids.

Rhabdotites-type rods. Frizzell and Exline (1955) recognized two species of the morphogenus *Rhabdotites* Deflandre-Rigaud which are simple, straight to slightly curved rods with a knob at each end. *Rhabdotites rectus* Frizzell and Exline, originally described from the Middle Triassic, is now accepted to be the roveacrinid (somphacrinid) microcrinoid *Osteocrinus rectus* (Kristan-Tollmann 1970).

Rods attributable to *Rhabdotites* were found in several samples from the Blue Lias. These rods are straight, long and thin, with a knob at one end and a slight increase in diameter at the other end (Pl. 2, figs 10, 19). The rods are not solid throughout but composed of stereom meshwork in parts. Over most of the shaft there are grooves which become deeper towards the knob (Pl. 2, fig. 11). The

knob itself is pitted producing a 'pepper-pot' sculpture which may be obscured if poorly preserved. At the opposite end a steorem of longitudinally arranged holes and grooves occurs all the way round.

The ultrastructure of the rods indicates clearly that they are not derived from holothurians or roveacrinids. They do, however, compare closely with stalks of echinoid pedicellaria (i.e. Pl. 2, figs 16–18). The Blue Lias includes a variety of echinoid debris derived from *Eodiadema* and *Diademopsis* and the *Rhabdotites*-type elements are considered to be pedicellarial stalks from one of these two genera.

Some previously described records of *Rhabdotites* are also probably derived from echinoids. Hampton (1957) referred a single specimen (BMNH E27042) from the Upper Bathonian to *Rhabdotites?rectus*. This specimen has a similar ultrastructure to the Blue Lias rods, though this has been largely obscured (Pl. 1, figs 21–22). Likewise, a badly preserved specimen of *R. rectus* with a knob at only one end, described by Zawidzka (1971), should not be accepted as holothurian in origin.

Curved spiny rods. Variably curved rods (Pl. 2, figs 20–21) occur throughout the section. These rods are spiny over much of the surface, or at least along the outer curve, though poor preservation may obscure this.

Curved spiny to smooth rods occur in some Recent holothurians, e.g. the Stichopodidae. However, similar spicules are found in several octocoral groups such as the Alcyonacea and Gorgonacea (e.g. see Bayer 1956; Deflandre-Rigaud 1957). Octocoral rods are more or less strongly sculptured by spines or 'warts', whereas holothurian rods are usually sculptured along one edge and not to the same extent. The Blue Lias examples are most probably octocoral in origin. Specimens in which there appear to be spines along one edge only cannot be accepted as holothurian because they intergrade with more spiny examples and because all the spines except those seen in profile may be obscured if poorly preserved.

Anchor-shaped sclerite. One anchor-shaped sclerite was recovered from sample L18a (Pl. 2, fig. 22). It is about 450 μm long and the shaft is thick, becoming wider and curving round to form two arms at one end. The other end is broken so it is not possible to determine if a 'stock' structure is present or not. Anchor-shaped sclerites occur in both holothurians and other groups, particularly sponges. Holothurian anchors differ from the Blue Lias specimen because the shaft is normally long and slender with the widest section in the middle, and there is a sharp angle between the shaft and the curved arms. The anchor sclerite is more similar to those previously assigned to sponges (see Mostler 1972d).

Eocaudina-type plates. Various echinoderm plates were found throughout the succession (Pl. 1, figs 10–11). Most comprise a single layer of retiform steorem whilst some also have a secondary layer. Holes may be regularly arranged (Pl. 1, fig. 11), or irregularly arranged and variable in size, e.g. 5–50 μm . Such plates are usually assigned to the holothurian morphogenus *Eocaudina*. However, as some authors have noted, *Eocaudina* cannot be considered unequivocally holothurian in origin since these plates are also found in other echinoderms (Frizzell and Exline 1955). In the Blue Lias *Eocaudina* co-occurs with both holothurian and other echinoderm skeletal elements. It seems preferable, therefore, not to accept these plates as holothurian.

SYSTEMATIC PALAEOLOGY

The systematic section is arranged, where possible, in terms of the Recent biological classification. Because of the artificial taxonomy normally employed for fossil holothurian sclerite classification the parafamily Priscopedatidae appears under several different Recent orders and hence, to avoid confusion, is placed in square brackets subsequent to its first appearance.

Class HOLOTHUROIDEA
Order DACTYLOCHIROTIDA Pawson and Fell, 1965
of DENDROCHIROTIDA Grube, 1840
(sometimes united in the sub-class DENDROCHIROTACEA Grube, 1840)
Parafamily PRISCOPEMATIDAE Frizzell and Exline, 1955 *pars*

Type species. *Priscopematatus pyramidalis* Schlumberger, 1890.

Diagnosis. Fossil sclerites in the form of tables or spired plates comprising a perforated base, or disc, and a spire and/or stirrup.

Discussion. In Frizzell and Exline (1966) the Priscopematidae includes tables only, of which there are four genera as distinguished by Deflandre-Rigaud (1962). One of the main diagnostic characters used in their classification was the number of branches in the stirrup and/or spire, being either three (*Dictyothurites*, *Priscularites*) or four (*Priscopematatus*, *Staurocumites*). Soodan (1975) revised the classification, following the addition of *Priscolongatus* Gorka and Luszczewska, 1969, and recognized the new genera *Clarkina*, *Feddenella*, *Fletcherina*, *Hannaina*, and *Sastriella*, using the number of central holes and the shape of the base as differentiating characters. Spired plates were not included in either of these schemes because, in the case of the former, no fossil examples had been found and, in the latter case, because the only definite fossil spired plate had been incorrectly placed in the genus *Priscopematatus*. The parafamily Priscopematidae is enlarged here to include spired plates. Tables occur in four of the six Recent orders of holothurians and the Priscopematidae is therefore polyphyletic. Spired plates are found in several families of the order Dactylochirotida and one family of the Dendrochirotida, the Paracucumidae (Gilliland 1990). Those fossil examples that cannot be referred to one of these orders only are considered first, followed by any that can be.

The spired plates described below are distinct from any existing genus of table, having more than four pillars (tables usually have four or less) which become intertwined. Additionally the disc may have a reticulate network, composed of more than one calcareous layer, that cannot be easily differentiated from the base of the spire. Spired plates are not assigned to a separate parafamily because of their similarity to, and possible morphological intergradation with, certain tables (see Gilliland 1990, Section 2.3.4).

A comparison with Recent spired plates indicates that the differences between the fossil forms are as great as those between Recent genera and they should therefore be placed in more than one morphogenus.

Genus CLAVALLUS nov.

Etymology. From the Latin *clavallus*, club-like, in reference to the shape of the spire.

Type species. *Priscopematatus spicaudina* (Gutschick *et al.*, 1967).

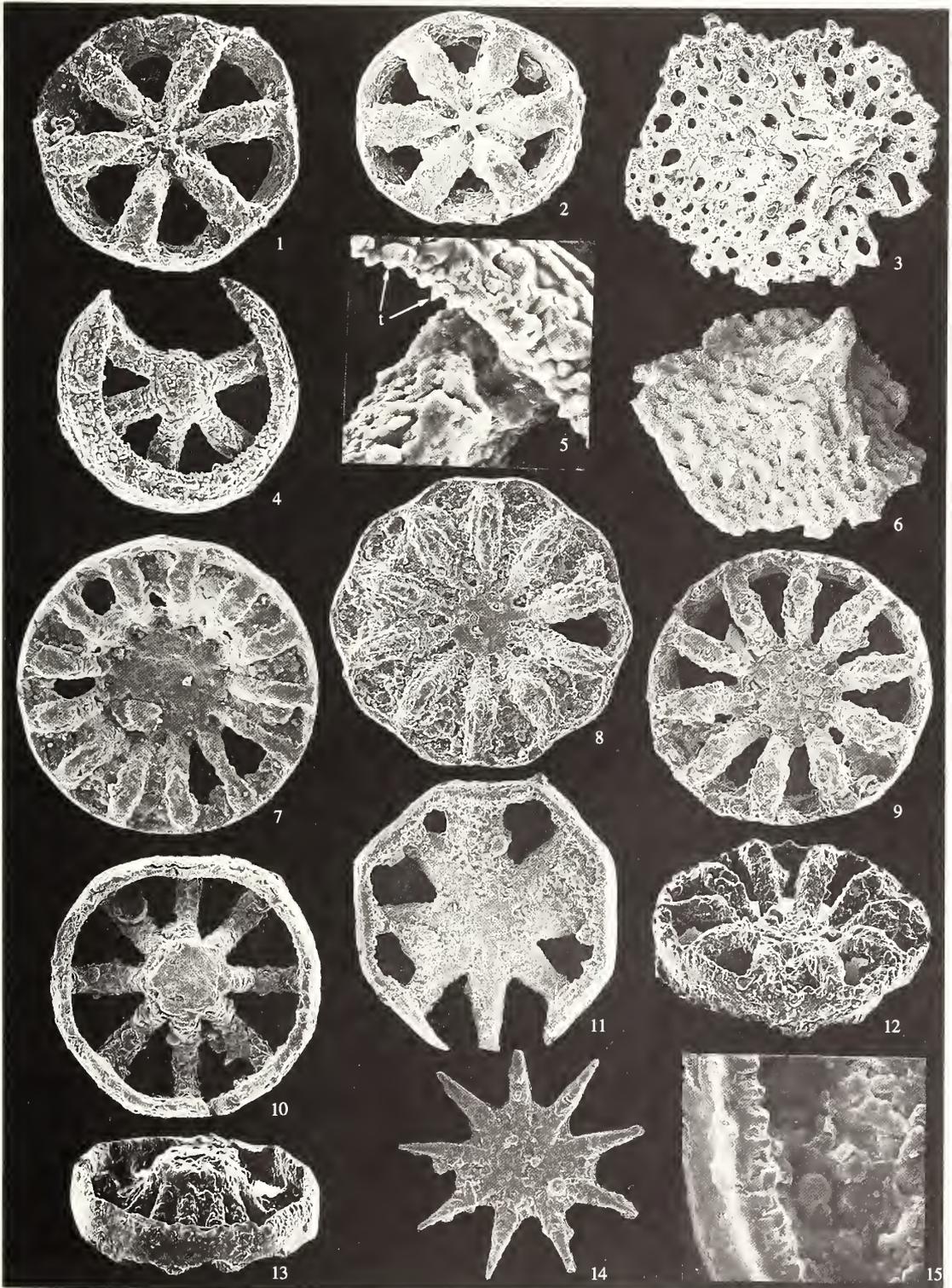
Diagnosis. Plates with a spire that is noticeably expanded in the top third and is placed near to the

EXPLANATION OF PLATE 3

Figs 1–2, 4–5. *Theelia convexa* (Whidborne). 1, E27239; L16e; *angulata* zone, $\times 215$. 2, E27130; L9b; *laqueus?extranodosa/complanata* subzone, $\times 255$. 4–5, E27240; L17j; *angulata* zone, $\times 240$, $\times 1180$, respectively; t = teeth.

Figs 3, 6. *Acutisclerus plagiacanthus* sp. nov. Holotype; E27349; L23f; *angulata* zone, both $\times 110$.

Figs 7–15. *Theelia synapta* sp. nov. 7, Holotype; E27208; L9b; *laqueus?extranodosa/complanata* subzone, $\times 360$. 8, Paratype; E27186; H13; *bucklandi* subzone, $\times 195$. 9, 12, E27256; L20a; *angulata* zone, both $\times 185$. 10, Paratype; E27312; L20a; *angulata* zone, $\times 230$. 11, Paratype; E27159; H15, *bucklandi* subzone, $\times 130$. 13, E27257; L20a; *angulata* zone, $\times 200$. 14, E27183; H15; *bucklandi* subzone, $\times 200$. 15, E27175; H15; *bucklandi* subzone, $\times 740$.



GILLILAND, Blue Lias holothurian sclerites

centre of the plate. The base is composed of a single layer which curves slightly upwards into the base of the spire so that distinct pillars cannot be discerned. The spire is relatively tall compared to the plate diameter (height:diameter ratio > 0.6), smooth, and without obvious perforations over most of its area.

Remarks. This is a monospecific genus. The species is recorded from the Lower Carboniferous (Gutschick *et al.* 1967), the Upper Permian (*P. cf. spicaudina* Mostler and Rahimi-Yazd, 1976) and the Middle Triassic (*P. cf. spicaudina* Mostler, 1968*b*).

Genus ACUTISCLERUS nov.

Etymology. From the Latin *acutus*, pointed, in reference to the spire.

Type species. *Priscopedatus empeldensis* (Kristan-Tollmann, 1986).

Distribution. Lower Lias (Hettangian) of England, and Upper Lias (Pliensbachian) of Northern Germany.

Diagnosis. Round to oval plates with a spire comprising more than four pillars or struts which are bound together in an almost solid network and which converge to a point.

Remarks. *Acutisclerus* differs from Recent forms of spired plates in the way the spire converges to a point. The sculpturing of the spire and the morphology of the disc do not allow assignment to either the Dendrochirotida or Dactylochirotida.

Acutisclerus plagiacanthus sp. nov.

Plate 3, figs 3, 6

Etymology. From the Greek *plagio*, to the side, and *acanthus*, a thorn or spine, in reference to the leaning spire.

Types. Only one specimen, the holotype, BMNH E27349, from the *angulata* zone of Long Itchington.

Diagnosis. Irregularly bound, sub-oval plate perforated by irregularly distributed (i.e. not closely packed) circular to oval holes, with an eccentrically placed spire. The spire has a broad base formed from many (> 4) struts that coalesce and converge to a point. The spire is oblique, rather than perpendicular, to the base plate.

Dimensions. Length of plate, 460 μm ; maximum width, 395 μm ; spire height, 160 μm ; hole diameter, 8–50 μm .

Description. A spired plate comprising a sub-oval base and a 'leaning' spire. The edge of the plate is irregular and probably still developing. The plate is perforated all over by variably sized and irregularly arranged holes, most of which are relatively small ($< 30 \mu\text{m}$) and separated by equally sized struts. The smallest holes are circular while larger holes are oval. The spire rises from the plate at about 60° at about one third along the length of the base plate. The spire is composed of 8 or more struts intermingled with the stereom of the base plate and extending over a wide area of about 170 μm in diameter. The struts coalesce to form a spire of much smaller diameter than its base.

Remarks. *A. plagiacanthus* differs from *A. empeldensis* in that the spire leans obliquely and the base of the spire occupies a relatively larger area.

Order DACTYLOCHIROTIDA Pawson and Fell, 1965
Family YPSILOTHURIIDAE Pawson and Fell, 1965

Diagnosis. Dactylochirotidids with body wall formed of large plates each with a spiny spire.

Remarks. Although there are soft tissue characters which identify ypsilothuriids the structure of the spired sclerites is highly distinctive. In the Vaneyellidae the spire is relatively short.

[Parafamily PRISCOPEMATIDAE Frizzell and Exline, 1955] *pars*
Genus PALAEOYPSILUS nov.

Etymology. After the Recent holothurian family Ypsilothuriidae.

Type species. *Palaeoypsilus liassicus* sp. nov.

Diagnosis. Spired plates consisting of a circular, regularly perforated base, relatively small compared to the height of the spire, and a prominent spiny spire, widest at the bottom, comprising many vertical struts interlocking along the length of the spire.

Remarks. Amongst the spired plates of Recent taxa only those of the Ypsilothuriidae possess a tall, spiny spire. However, the base plate of *Palaeoypsilus* is both smaller than that of Recent ypsilothuriids and has a proportionally taller spire. Hence the specimens described below are assigned to a new genus rather than one of the three existing ypsilothuriid genera. However, *Palaeoypsilus* resembles other ypsilothuriid spired plates with respect to other characters and the irregular edge of the plate suggests that the plate may still be developing.

Palaeoypsilus liassicus sp. nov.

Plate 2, figs 13–15, 23

Etymology. After the Lias.

Types. Holotype, BMNH E27338 (Pl. 2, figs 13–15); paratypes, BMNH E27334 (Pl. 2, fig. 23), E27339; all from the *bucklandi* subzone of Hock Cliff.

Other material. One specimen from the *bucklandi* subzone of Hock Cliff and one from the *laqueus?* subzone of Long Itchington.

Diagnosis. A spired plate with a circular, regularly perforated base and a massive, long, thorny spire comprising many interlocking, vertical struts.

Dimensions. Diameter of base, 140–180 μm ; spire height is greater than the diameter.

Description. Spired plates with a circular base plate and undulating periphery imparting a spiny appearance (Pl. 2, fig. 23). The base is perforated by small, round, regularly arranged and equal-sized holes. A large, robust spire rises centrally and is formed of many interlocking elongate vertical struts connected by crossbars (Pl. 2, fig. 13). The spire is widest at the bottom where additional struts have developed from the base plate. A thorny effect is produced from small outgrowths along the length of the struts (Pl. 2, fig. 13).

Remarks. Recent ypsilothuriid plates are much larger (usually 1 mm or more in diameter) than those of *Palaeoypsilus liassicus*. Recent examples also co-occur with unspired plates, of which there are possible examples in the Blue Lias fauna (see Etheridgellidae and *Eocaudina*-type plates above), and dendrochirotocean irregular rods (Gilliland 1990, Section 2.3.4) of which no examples were recovered. The lack of rods may, however, be due to the rarity of *P. liassicus*.

Order DENDROCHIROTIDA Grube, 1840
Parafamily CALCLAMNIDAE Frizzell and Exline, 1955 *pars*

Diagnosis. Flat to concavo-convex perforate plates, usually thin and rarely multilayered. Shape is

variable and commonly the edge appears to be incompletely formed, i.e. it is highly scalloped. The perforations are not denticulate and there is no socket, strap or spire.

Discussion. Calclamnidae includes a large number of genera some of which cannot be considered unequivocal holothurians, e.g. *Eocaudina*, *Mortensenites* or *Petropegia*. Thus the family may be polyphyletic by inclusion of sclerites from several different echinoderm classes. Pawson (1966) included all Calclamnidae within the order Dendrochirotida but, given the wide occurrence of plates in the Recent fauna, the family is probably also polyphyletic with respect to holothurians. Many of the genera may be assigned to the Dendrochirotida, including *Binoculites* (as defined here). However, *Calclamnella* (as defined here) includes sclerites found in the Aspidochirotida.

Genus BINOCULITES Deflandre-Rigaud, 1952 emend

Type species. *Binoculites terquemi* Deflandre-Rigaud, 1952.

Other species. *B. jurassica* (Frizzell and Exline, 1955).

Diagnosis. Perforate, elongate buttons or plates, usually bilaterally symmetrical, with one or more terminal holes at each end. Between the terminal holes there are either two rows of holes, one on each side of the midline, or just two holes producing a cruciform pattern together with the terminal holes. Early growth stages are dumb-bell-shaped rods in which only the terminal holes are present.

Remarks. The genus *Binoculites* was formerly restricted to the dumb-bell-shaped rods and included in the parafamily Stichopitidae. However, *Binoculites*, so defined, merely represents the early growth stages of plates of the genus *Calclamna* and should be placed in the family to which these plates are assigned, i.e. the Calclamnidae. Following ICZN regulations the generic name *Binoculites* is retained with *Calclamna* Frizzell and Exline, 1955 reduced to synonymy. The genus *Calclamnella* Frizzell and Exline, 1955 is retained for plates similar to *Binoculites*, as defined here, but in which no terminal holes are present. *Binoculites* may be assigned to the Recent order Dendrochirotida and closely resembles sclerites of, for example, some species of the family Cucumariidae.

Binoculites terquemi Deflandre-Rigaud, 1952 emend

Plate 1, figs 1–9, 20

- 1875 'Spicules de tube ambulacraire de radiaires' Terquem and Berthelin (*pars*), p. 109, pl. 9, fig. 9a.
 1876 Crinoid arm segments? Blake, p. 448, pl. 17, fig. 45.
 1908 *Uncinulina polymorpha* Terquem (*pars*); Issler, pp. 95–97, pl. 7, figs 346–350, 352–353, 358–360 (not figs 351, 354–357, or 361–362).
 1932 *Uncinulina polymorpha* Terquem (*pars*); Croneis and McCormack, p. 128, pl. 18, figs. 48–49, 56, 60–63, 65 (not figs 53, 64 or 66–68).
 1935 ?Holothuroidea Henderson, pp. 555–556, text-fig. 3m.
 1936 Anker-Platten Bartenstein, pp. 2–4, text-figs 2a–b, 7 (excluding lower left specimen).
 1937 'Spicules of holothurians' Mortensen, pp. 25–26, pl. 4, figs 8–9, 16–19.
 1937 Holothurien-Ankerplatten Bartenstein and Brand, p. 439, pl. 2A, fig. 24.
 1950 'Nadel (Spicula) einer dendrochiroten Holothurie' Schindewolf, text-fig. 89.
 1952 *Binoculites terquemi* Deflandre-Rigaud, p. 6.
 1953 *Binoculites terquemi* Deflandre-Rigaud; Deflandre-Rigaud, p. 953, text-fig. 11.
 1955 *Binoculites irregularis* Frizzell and Exline, p. 67, pl. 1, figs 16–17.
 1955 *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. 68, pl. 1, figs 19–21 (not fig. 18).
 1955 *Binoculites terquemi* Deflandre-Rigaud; Frizzell and Exline, p. 69, pl. 1, figs 24–26.
 1955 *Calclamna germanica* Frizzell and Exline, pp. 76–77, pl. 2, figs 1–5.
 1955 *Calclamnoidea irregularis* Frizzell and Exline, p. 82, pl. 2, fig. 18.
 1961 *Binoculites issleri* Deflandre-Rigaud; Rioult pp. 130–131, table 1, fig. 8.
 1961 *Binoculites irregularis* Frizzell and Exline, forms β and γ Rioult, p. 130, table 1, figs 7, 16.

- 1961 *Binoculites cf. irregularis* Frizzell and Exline, Rioult, p. 130, table 1, fig. 3.
 1961 *Binoculites terquemi* Deflandre-Rigaud, form β Rioult, p. 129, table 1, fig. 5.
 1961 *Calclamna germanica* Frizzell and Exline, forms α and β Rioult, pp. 132–133, table 1, figs 4, 9.
 1966 *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. U662, text-fig. 529 (3c) (not 3b).
 1966 *Binoculites terquemi* Deflandre-Rigaud; Frizzell and Exline, p. U662, text fig. 529 (3a).
 1966 *Calclamna germanica* Frizzell and Exline; Frizzell and Exline, p. U664, text-fig. 530 (1a–b).
 1968 *Calclamna cf. germanica* Frizzell and Exline; Speckmann, pp. 199–200, pl. 1, fig. 5.
 1972 *Binoculites irregularis* Frizzell and Exline; Michelson, p. 61, pl. 2, figs 2–3.
 1973 *Calclamna germanica* Frizzell and Exline; Michelson, pp. 61–64, pl. 1, figs 1–18; pl. 2, figs 4–8; pl. 3, figs 1–6.
 1978 *Binoculites irregularis* Frizzell and Exline form β Rioult?; Copestake, pl. 32, fig. 7.
 1986 *Binoculites issleri* Deflandre-Rigaud; Kristan-Tollmann, p. 130, pl. 29, fig. 1.

Types. The lectotype (selected by Frizzell and Exline 1955, pl. 1, fig. 24) was originally described by Mortensen 1937 (pl. 4, fig. 8). Mortensen described one other specimen in the syntype series (pl. 4, fig. 9).

Material studied. Over 1500 specimens including BMNH E27267–27272, E27279, E27295–27296, E27301, E27313–27316, E27320–27330, E27344. The material comes from Hock Cliff (*bucklandi* subzone), Long Itchington (?*portlocki*–*reynesi* subzones), Maisemore Cliff (*rotiforme* subzone) and Pinhay Bay (*portlocki*–*laqueus*, *rotiforme*–*sauceanum* subzones).

Stratigraphic range. Middle Triassic (Anisian) to Lower Jurassic (Upper Pliensbachian).

Diagnosis. A species of *Binoculites* which is relatively short and wide. There are usually two prominent holes at either end of the long axis and two larger holes in the central area either side of the mid-line. Additional holes, usually about half the size of the first formed terminal holes, occur at either end.

Dimensions. Fully developed examples vary in length from 150 to 500 μm and in width from 150 to 310 μm . The widest part is normally towards the middle and the width between 50 and 90% of the length. In the earliest growth stage the widest part of the sclerite is at either end and is 20–30% of the length. A few early growth stages were found which are larger (i.e. up to 750 μm in length) than any of the fully developed plates (Pl. 1, fig. 3).

Description. The earliest growth stages are relatively short and wide at the expanded ends (Text-fig. 7) with a large hole in the expanded part. Growth outwards from the expanded ends results in the addition of holes which are still quite large but usually smaller than the first formed hole (Pl. 1, fig. 2). Further accretion proceeds towards the middle from the two ends eventually joining up to form central holes which may be larger than or equal in size to the primary terminal holes (Pl. 1, figs 4, 9). Very small holes may occur around the periphery (Pl. 1, fig. 4). The relative length/width of the plates varies from long and thin to short, wide button-like forms. The orientation of the central holes also varies. Occasionally a bar grows across one of the central holes dividing it in two (Pl. 1, fig. 5).

Discussion. *B. terquemi* is a well-defined species with different growth stages (= previously recognized morphotypes) which can usually be distinguished at all stages of growth from the closely related species *B. jurassica* (see Text-fig. 7 and discussion of the morphogenera *Binoculites* and *Calclamna* above). These differences include the size of the secondary holes at either end, which are quite large in *B. terquemi*, and the number of small holes around the entire periphery, of which there are very few in *B. terquemi*.

Binoculites jurassica (Frizzell and Exline, 1955) emend

Plate 1, figs 8, 12–17

- 1875 'Spicules de tube ambulacraire de radiaires' Terquem and Berthelin (*pars*), p. 109, pl. 9, fig. 9a.
 1908 *Uncinulina polymorpha* Terquem (*pars*); Issler, pp. 95–97, pl. 7, figs 351, 354–357 (not figs 346–350, 352–353, 358–362).

- 1932 *Uncinulina polymorpha* Terquem (*pars*); Croneis and McCormack, p. 128, pl. 18, figs 64, 66–68 (not figs 48–49, 56, 60–63, 65).
- 1952 *Binoculites terquemi* Deflandre-Rigaud (*pars*), p. 6.
- 1955 *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. 68, pl. 1, fig. 18 (not figs 19–21).
- 1955 *Calclammella jurassica* Frizzell and Exline, pp. 78–79, pl. 2, figs 11–13.
- 1961 *Binoculites terquemi* Deflandre-Rigaud, form γ Rioult, p. 130, table 1, fig. 14.
- 1961 *Calclammella jurassica* Frizzell and Exline; Rioult, p. 133, table 1, fig. 13.
- 1966 *Binoculites issleri* Deflandre-Rigaud (*pars*); Frizzell and Exline, p. U662, text-fig. 529 (3b) (not 3c).
- 1978 *Binoculites issleri* Deflandre-Rigaud; Copestake, pl. 32, fig. 4.

Types. The holotype of *Calclammella jurassica*, as figured by Frizzell and Exline (1955; pl. 2, fig. 11), appears not very representative of the species. However, this figure is a poor reproduction of the original plate given in Issler 1908 (pl. 7, fig. 355) which shows the specimen to be characteristic of the species as defined here. The holotype comes from the Upper Sinemurian of Oferdingen, Schwabia, Germany. The paratypes proposed by Frizzell and Exline include further specimens figured by Issler (pl. 7, figs 354, 356) which come from the Lower Hettangian of Nurtigen, Schwabia. All of this material is located in the Geological Institute of Tübingen.

Material studied. Over 750 specimens including BMNH E27271, E27273–27274, E27277, E27280–27282, E27285–27294, E27297–27300, E27303–27311 and E27317–27319. The material comes from Hock Cliff (*bucklandi* subzone), Long Itchington (?*portlocki-conybeari* subzones), Maisemore Cliff (*rotiforme* subzone) and Pinhay Bay (*portlocki-conybeari* subzones).

Stratigraphic range. Upper Triassic (Carnian) to Lower Jurassic (Upper Pliensbachian).

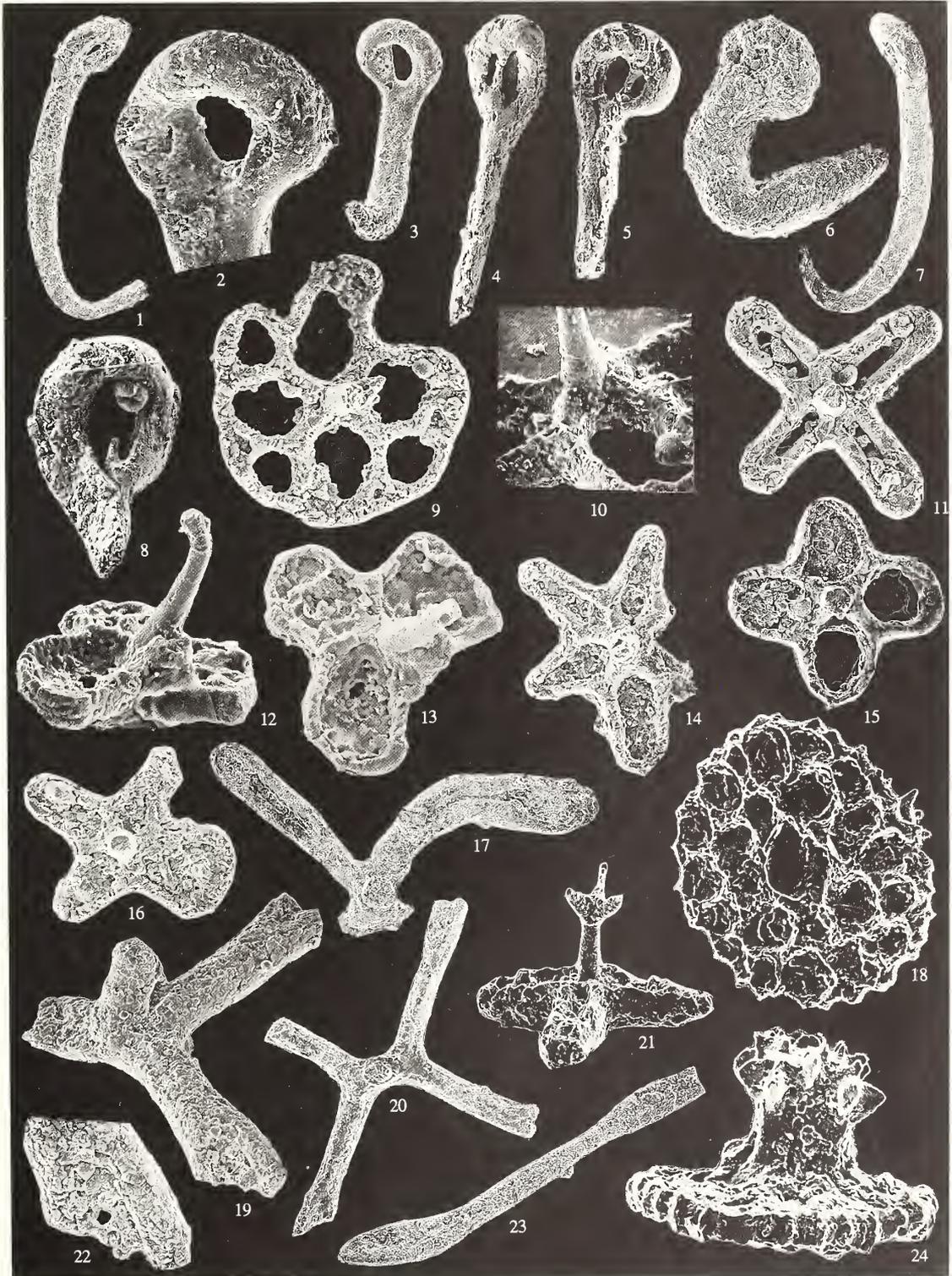
Diagnosis. A species of *Binoculites* which is relatively long and thin. Fully developed specimens have two rows of usually larger holes either side of the mid-axis. In the earliest growth stages the two ends of the rod are very narrow with a single small hole at the mid-axis. Smaller holes occur at the ends of the sclerite and sometimes around the entire periphery.

Dimensions. Fully developed examples vary in length from 380 to 620 μm and in width from 190 to 300 μm . The maximum width is central and varies between 40 and 50% of the length. In the earliest growth stage the widest part is at either end and varies between 10 and 25% of the length. A few early growth stages were found which are smaller, i.e. 195 μm in length, than any of the later growth stages.

Description. The earliest growth stage is relatively long and thin (Text-fig. 7) with a small hole occupying either end (Pl. 1, fig. 13). Further development proceeds as for *B. terquemi*, but results in two rows of holes or, perhaps more accurately, rows with more than one hole per row. The holes in the main (central) area of the

EXPLANATION OF PLATE 4

- Figs 1–8. *Achistrum monochordata* Hodson, Harris and Lawson. 1, E27137; L19b; *angulata* zone, $\times 80$. 2, E27140; H7; *bucklandi* subzone, $\times 300$. 3, E27207; H13; *bucklandi* subzone, $\times 150$. 4, E27123; P50; *scipionianum* subzone, $\times 125$. 5, E27121; P26; *laqueus* subzone, $\times 115$. 6, E27136; L19d; *angulata* zone, $\times 115$. 7, E27128; L17j; *angulata* zone, $\times 120$. 8, E27120; P26; *laqueus* subzone, $\times 140$.
- Figs 9–16, 21. *Stawocumites bartensteini* Deflandre-Rigaud. 9, E27224; M13; *rotiforme* subzone, $\times 235$. 10, E27210; M3; *rotiforme* subzone, $\times 380$. 11, E27266; M3; *rotiforme* subzone, $\times 225$. 12–13, E27221; M3; *rotiforme* subzone, both $\times 385$. 14, E27203; M3; *rotiforme* subzone, $\times 230$. 15, E27265; M3; *rotiforme* subzone, $\times 240$. 16, E27204; M3; *rotiforme* subzone, $\times 230$. 21, E27211; M3; *rotiforme* subzone, $\times 230$.
- Figs 17, 19–20, 22. *Praceuphronides multiperforata* Mostler. 17, E27353; L23f; *angulata* zone, $\times 75$. 19, 22, E27352; L23f, *angulata* zone, $\times 195$, $\times 230$, respectively. 20, E27354; L23f; *angulata* zone, $\times 155$.
- Figs 18, 24. *Priscopodatus* sp. nov.? Holotype; E27342; L9b; *laqueus?extranodosa/complanata* subzone, $\times 585$, $\times 600$, respectively.
- Fig. 23. *Punctatites?* aff. *extensus* (Mostler). E27222; L18e; *angulata* zone, $\times 75$.



GILLILAND, Blue Lias holothurian sclerites

fully developed plate are larger than the terminally placed holes. As in *B. terquemi* the orientation of the central holes varies. The additional 'secondary' holes at the two ends tend to be very small and may continue around the entire periphery.

Discussion. Although *Binoculites issleri* precedes *Calclammella jurassica* by three years the trivial name used here is *jurassica*. This is because *B. issleri* was originally defined on material referable to both *B. jurassica* and *B. terquemi* (as defined here) and the holotype is a form assignable to *B. terquemi* (see Frizzell and Exline 1955, pl. 1, fig. 20). Thus, *B. issleri* is a junior synonym of *B. terquemi*. The oldest available name for the material described here is therefore *Calclammella jurassica*, although the generic name is subordinate to *Binoculites*. *B. jurassica* and *B. terquemi* differ in several ways as discussed above.

Order ELASIPODA Théel, 1882
Parafamily STICHOPITIDAE Frizzell and Exline, 1955 *pars*
Genus PRAEUPHRONIDES Mostler, 1968b

Type species. *Praeuphronides multiperforata* Mostler, 1968.

Other species. The genus includes seven other species: *P. concavus* Mostler, 1972b; *P. complexus* Kozur and Mock, 1972; *P. crassiramosus* Mostler, 1972a; *P. latus* Mostler, 1972b; *P. robustus* Mostler, 1970; *P. simplex* Mostler, 1969; and *Praeuphronides* n. sp. Kozur and Mock, 1972.

Stratigraphical age and distribution. Middle Triassic (Upper Anisian) to Lower Jurassic (Middle Lias) of Austria, Czechoslovakia, Rumania, and the Indian Himalayas.

Diagnosis. Sclerites comprising a rod with four arms in one plane. The distal part of each arm is expanded and bears numerous small holes usually lying within a groove. A large spine or apophysis, with variably developed sculpturing, usually occurs in the centre of the rod.

Remarks. *Praeuphronides* exhibits a wide morphological variation and can be compared with several Recent morphotypes. Mostler (1969) referred *Praeuphronides* to the order Elasiopoda deriving the name from the elasiopod genus *Euphronides* (now *Psychropotes*). Hansen (1975) considered the resemblance to elasiopod sclerites superficial and suggested a closer affinity with the Synallactidae (order Aspidochirotida). *Praeuphronides* resembles synallactid sclerites more, both having four arms in one plane, the arms being perforated and expanded distally, and a single large, central spine. However, there is also gradation between *Praeuphronides* and the fossil morphospecies *Palelpidia* which is accepted by both Hansen (1975) and Mostler (1969) to be elasiopod. For the present, the latter evidence is more compelling and *Praeuphronides* is referred to the Elasiopoda (see Gilliland 1990, Section 5.10.2). The presence of holes within a groove at the end of the arms seems to be restricted to *Praeuphronides*.

Praeuphronides multiperforata Mostler 1968b

Plate 4, figs 17, 19–20, 22.

- 1968a *Praeuphronides multiperforata* Mostler, pp. 8–9, pl. 1, figs 2–3.
- 1968b *Praeuphronides multiperforata* Mostler; Mostler, pp. 430–431, text-fig. 1.
- 1968c *Praeuphronides multiperforata* Mostler, pl. 1, figs 9, 13.
- 1972 *Praeuphronides* cf. *multiperforata* Mostler; Kozur and Mock, p. 11, pl. 5, fig. 2.
- 1972a *Praeuphronides multiperforata* Mostler; Mostler, p. 4 (listed only).
- 1973 *Praeuphronides multiperforata* Mostler; Kozur and Mostler, p. 307 (listed only).
- 1973 *Praeuphronides multiperforata* Mostler; Mostler and Parwin, pp. 12, 20, 30 (listed only).
- 1974 *Praeuphronides* cf. *multiperforata* Mostler; Kozur and Mock, pl. 5, fig. 1.
- 1979 *Praeuphronides multiperforata* Mostler; Mostler, p. 336 (listed only).

- 1980 *Praeephronides multiperforata* Mostler; Donofrio *et al.*, p. 68 (listed only).
 1986 *Praeephronides multiperforata* Mostler; Soodan, pp. 64–65, pl. 1, fig. 1.

Types. Mostler (1968a) based his description on 36 examples from the Anisian 'Schreyeralm, obere Ammonitenlage' from Schreyeralm, Northern Austria, of which one, the holotype, was figured. All the material belongs to the Institut für Geologie und Paläontologie, Innsbruck.

Material. Five specimens (BMNH E27350–27355) from Long Itchington, sample L23f (*angulata* zone).

Stratigraphic range. Middle Triassic (Anisian) to Lower Jurassic (Upper Hettangian; Upper Sinemurian?).

Diagnosis. *Praeephronides* with four large divergent arms. The arms may be of unequal length but are all expanded distally. There is a well-developed groove in the expanded part with two or more rows of fine holes. The central spine is thick, varies in height relative to the length of the arms, and is expanded towards the top with small spines.

Dimensions. Maximum arm length, 239–420 μm ; maximum arm width, 90–120 μm ; spine height *c.* 90 μm .

Description. Flat sclerite comprising a short rod with four diverging arms. The arms are either straight (Pl. 4, fig. 20) or curved (Pl. 4, fig. 17), with arm width increasing distally. Along the expanded part is a groove perforated by two or more rows of small holes (Pl. 4, fig. 22). In the centre of the rod is a massive, circular, solid spine or apophysis which appears to be unsculptured (Pl. 4, fig. 19).

Discussion. Mostler (1968b) has discussed the large variability found in *Praeephronides multiperforata*. The variation seen in the present specimens is not significant. Although all the specimens come from one sample there appears to be nothing unique about the lithology or associated microfauna.

Order APODIDA Brandt, 1835

Parafamily THEELIIDAE Frizzell and Exline, 1955 emend Frizzell and Exline, 1966

Diagnosis. Concavo-convex wheels with spokes, separated by interspoke spaces, connecting a nonquadripartite central portion and an outer rim.

Remarks. Theeliidae includes wheels found in the apodan families Chiridotidae and Myriotrochidae and the larval wheels of the apodan family Synaptidae plus genera, such as *Micradites*, with unestablished affinities.

Genus THEELIA Schlumberger, 1890 emend

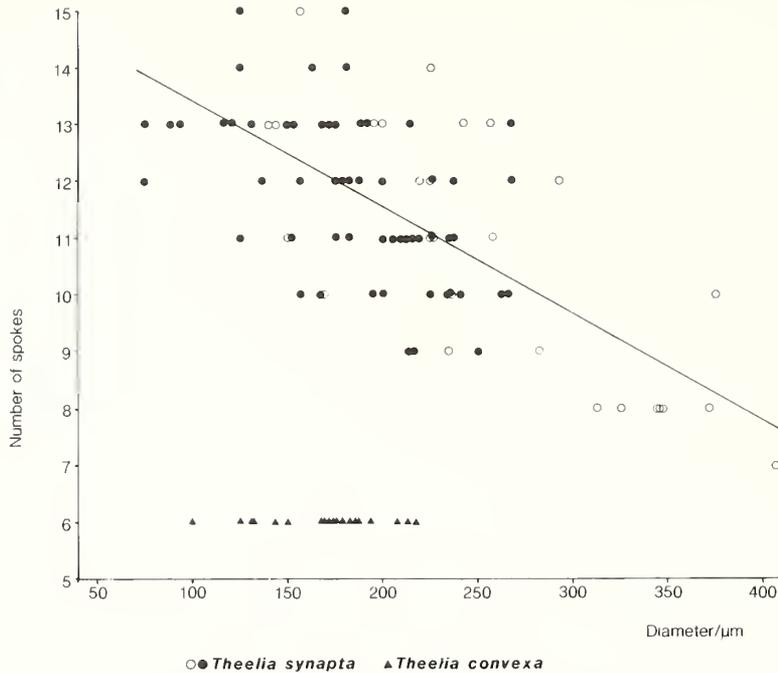
Type species. *Chiridota undulata* Schlumberger, 1890.

Diagnosis. Rim inclined to the plane of the wheel, curving upward and inward, and possessing regularly spaced teeth which do not extend to the periphery. The centre is imperforate, typically with a hemispherical or conical button or tubercle. Spoke number is variable, even within the same species, but is commonly less than ten.

Remarks. In their emended diagnosis Frizzell and Exline (1966) include spoke number as 6–10 but there are species, e.g. *T. convexa* with more than 10 (Lord and Senior 1973) and *T. variabilis* with less than 10 (Zankl 1966), which clearly indicate that this no longer holds.

Two types of wheel-shaped sclerite are present in the Blue Lias. Both occur together in only 5 out of 26 samples and the distribution of the two species is not correlated.

Maximum diameter, spoke number and number of teeth were recorded in order to determine if they were taxonomically diagnostic characters. There were few specimens with teeth visible over the



TEXT-FIG. 11. A plot of the number of spokes against wheel diameter of *T. synapta* ($n = 82$) and *T. convexa* ($n = 11$). The regression equation for *T. synapta* is: number of spokes = $15.3 - 0.0186$ diameter; R^2 value = 48.1%, correlation coefficient = -0.698 (cf. tabulated value of 0.283, at $P = 0.01$). Open circles for *T. synapta* indicate data points from one sample (H15).

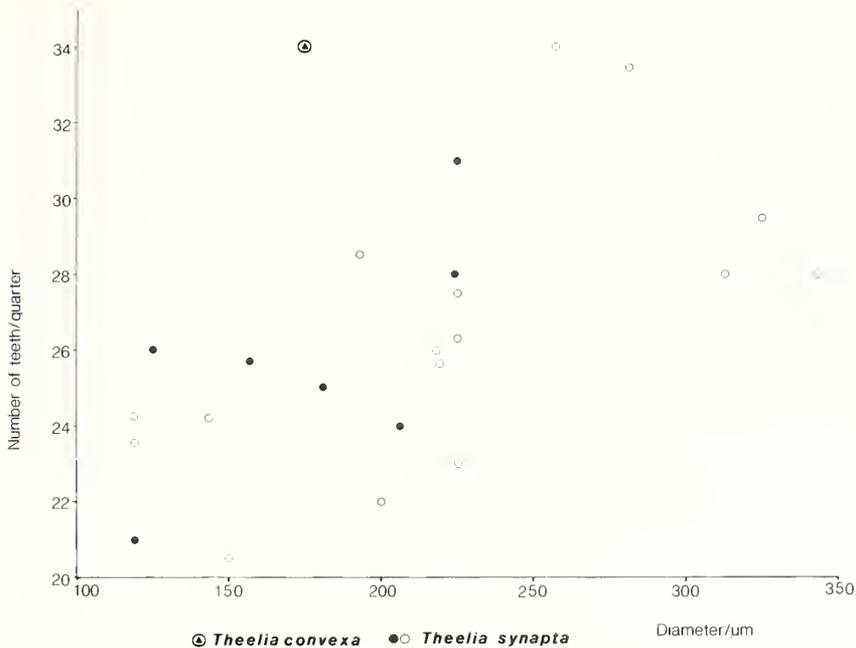
entire circumference so the number of teeth per quarter of the circumference was counted since they are regularly spaced around the inner edge. The relationship between diameter and number of spokes (Text-fig. 11) proved to be taxonomically useful, but that between diameter and number of teeth is not so informative (Text-fig. 12).

Family CHIRIDOTIDAE Östergren, 1907

Theelia convexa (Whidborne, 1883)

Plate 3, figs 1-2, 4-5

- 1883 *Chiridota convexa* Whidborne, p. 537, pl. 19, fig. 14, 14a.
- 1894 *Chiridota convexa* Woodward, p. 590 (check list only).
- 1917 *Chiridota convexa* Whidborne; Upton, p. 115.
- 1935 *Chiridota convexa* Whidborne; Fahrion, p. 12.
- 1936 *Chiridota convexa* Whidborne; Bartenstein, pp. 7-8.
- 1936 *Chiridota heptalampra* Bartenstein, pp. 6-8, text-figs 10a-b, 11a-b.
- 1951 *Chiridotites convexus* Whidborne; Deflandre-Rigaud, pp. 26-27, text-figs 47-48.
- 1951 *Chiridotites heptalampra* Bartenstein; Deflandre-Rigaud, pp. 27-28, text-figs 49-50.
- 1952 *Chiridotites heptalampra* Bartenstein; Deflandre-Rigaud, p. 9.
- 1955 *Theelia convexa* Whidborne; Frizzell and Exline, pp. 116-117, pl. 6, fig. 13.
- 1955 *Theelia heptalampra* Bartenstein; Frizzell and Exline, pp. 120-121, pl. 7, fig. 1.
- 1961 *Chiridotites heptalampra* Bartenstein; Rioult, pp. 142-143, pl. 1, fig. 21.
- 1964 *Chiridota heptalampra* Bartenstein; Frentzen, p. 43, pl. 4, figs 18-21.
- 1965 *Theelia heptalampra* Bartenstein; Kristan-Tollman, p. 18.



TEXT-FIG. 12. A plot of the number of teeth per quarter wheel circumference against wheel diameter in *T. synapta* (circles; $n = 23$) and *T. convexa* (triangle; $n = 1$). Open circles for *T. synapta* indicate data points from one sample (H15). Correlation coefficient for *T. synapta* is 0.631 (cf. tabulated value of 0.537, at $P = 0.01$).

- 1969 *Theelia heptalampra* Bartenstein; Garbowska and Wierzbowski, pp. 533–534, pl. 1, fig. 1; text-fig. 6A–C.
 1969 *Theelia heptalampra* Bartenstein; Gorka and Luszczevska, p. 379, pl. 78, figs 1–3.
 1972 *Theelia heptalampra* Bartenstein; Matyja, p. 240, text-fig. 8.
 1972 *Theelia heptalampra* Bartenstein; Kozur and Mock, p. 22, pl. 11, figs 3–4.
 1973 *Theelia convexa* Whidborne; Lord and Senior, pp. 36–37, pl. 1, figs 1a–b, 3a–c, 4a–f.
 1975 *Theelia* cf. *heptalampra* Bartenstein; Hess, pl. 46, fig. 4.
 1974 *Theelia heptalampra* Bartenstein; Kozur and Mock, pl. 7, fig. 6.

Types. Holotype, Sedgwick Museum J3741, from the Inferior Oolite, Bajocian (Middle Jurassic) of Burton Bradstock, Dorset.

Material studied. More than 20 specimens (including BMNH E27130–27131, E27193–27195, E27239–27240, E27243 and E27258–27259). The material comes from Pinhay Bay (*laqueus* and *conybeari* subzones) and Long Ichington (*laqueus*, *extranodosa/complanata* and *bucklandi* subzones).

Stratigraphic range. Upper Triassic (Upper Norian) to Upper Jurassic (Upper Oxfordian).

Diagnosis. Wheel with 6–11 strongly arched spokes. The hub lies within the plane of the rim which is strongly inclined to the plane of the wheel and is finely denticulate along the inner margin. On the ventral side there is a so-called 'star' formed of thin extensions of the spokes joined together above the hub.

Dimensions. Maximum diameter, 100–219 μm .

Description. Small wheels with a circular periphery and inner rim (Pl. 3, figs 2, 4). The latter is deep, strongly curved over (Pl. 3, fig. 2), and denticulate (Pl. 3, figs 4–5) with many small teeth although these may be difficult

to see due to poor preservation. Six spokes are consistently present (Text-fig. 11) although one badly preserved specimen may have seven spokes (diameter 175 μm). The spokes are relatively thick and either straight or widest in the middle (Pl. 3, figs 1–2). On the ventral side is a so-called ‘star’ comprising thin extensions of the spokes joined together and positioned in a flat plane above the hub. The main part of the hub is dome-shaped and concave below the star. The hub lies below (or within) the plane of the rim on both sides.

Discussion. The holotype is poorly preserved and in the original description Whidborne (1883) makes no mention of the ‘star’, and states that the inner rim is smooth. However, Lord and Senior (1973) included a photograph of the holotype, taken with a light microscope, in which both teeth and a star can be seen. The wheels described here are identical to Lower Bathonian material described in Lord and Senior (1973). Frizzell and Exline (1955, pl. 6, fig. 13*b*) incorrectly showed a low central boss on the ventral side of *T. convexa*.

Theelia heptalampra (Bartenstein, 1936), common in the Jurassic, is identical to *T. convexa* except in having 7, not 6, spokes. In some types of wheels such a small difference in spoke number is insignificant. However, in modern chiridotids it is rare to find wheels with other than 6 spokes. The sample size of the present material is small but there may be one specimen with 7 spokes. Further, Lord and Senior (1973) record *T. convexa* from the Lower Bathonian with 6–11 spokes (6 being the most common). *T. convexa* and *T. heptalampra* are therefore synonymized with *T. convexa* taking priority. *T. mortenseni* Deflandre-Rigaud (*non* Mortensen 1937, pl. 10, fig. 10) is similar to *T. convexa* but possesses larger (and fewer) teeth which is an important character (Rioullet 1961) and distinguishes the two species. Other Jurassic wheels differ significantly in one or a few characters. *T. crassidentata* Deflandre-Rigaud has flat spokes and less numerous and larger teeth, *T. florida* Frizzell and Exline and *T. wartensis* Garbowska and Wierzbowski have a median ridge along the whole length of each spoke, and *T. dentata* Gorka and Luszczewska possesses an undulating periphery, different spoke structure and an irregularly developed star i.e. the ‘arms’ of the star may not necessarily correspond to the centre of the spoke and there is not an extension from every spoke. An irregular star is also characteristic of *T. stellifera* Zankl, an Upper Triassic morphospecies with a wide variation. Kozur and Mock (1972) suggested that the 6-spoked subspecies *T. stellifera bistellata* may be synonymous with *T. heptalampra*, but the consistently irregular 3-armed star of the former distinguishes them. In *T. terquemi* Deflandre-Rigaud the undulating periphery and spokes, which are very wide in the middle, distinguish it from *T. convexa*.

T. convexa is undoubtedly a member of the Recent family Chiridotidae, but is unusual in the large variation in spoke number that it displays.

Family SYNAPTIDAE Burmeister, 1837

Theelia synapta sp. nov.

Plate 3, figs 7–15

Etymology. After the resemblance to the wheels found in the larvae of the Recent family Synaptidae.

Types. Holotype, BMNH E27208, from the *liasicus* zone of Long Itchington (Pl. 3, fig. 7); paratypes, BMNH E27159, E27186 from the *bucklandi* zone of Hock Cliff (Pl. 3, figs 8, 11) and BMNH E27312 from the *angulata* zone of Long Itchington (Pl. 3, fig. 10).

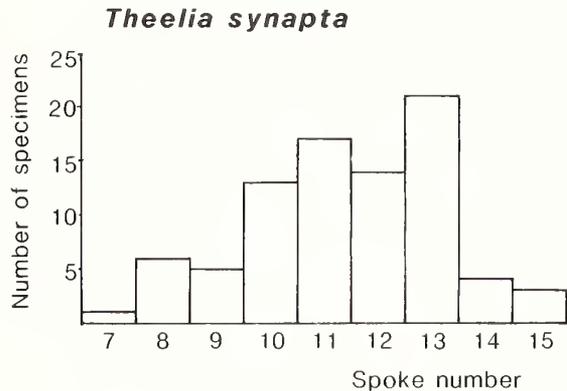
Other material. Over 130 specimens, including BMNH E27141–27192, E27208, E27228, E27230–27238, E27241–27242, E27244–27257, and E27312, only some of which are well preserved. Specimens were found at Pinhay Bay (*laqueus-conybeari* and *bucklandi* subzones); Long Itchington (*laqueus*, *extranodosa/complanata* and *bucklandi*?*reynesi* subzones); Maisemore (*rotiforme* subzone) and Hock Cliff (*bucklandi* subzone).

Diagnosis. Round wheels with small teeth on the edge of the inner rim, a median ridge along the ventral surface of each spoke and a smooth, flat hub on the ventral side.

Dimensions. Diameter of 75–405 μm ($n = 85$); relative diameter of the hub from less than 20% to more than 40% of the wheel diameter but typically 25–35%; number of spokes 7–15.

Description. Round, occasionally polygonal wheels (Pl. 3, figs 7, 11). Outer rim may be undulating (Pl. 3, fig. 8) with the outward-facing convex part corresponding to the interspoke space. Inner edge of the rim usually bears a variable number of blunt-ended teeth (Text-fig. 12; Pl. 3, fig. 15). Rare examples are found in which the whole rim appears to be smooth (Pl. 3, fig. 10). Spoke number ranges from 7 to 15, predominantly 10–13 (see Text-fig. 13). The spokes are strongly arched (Pl. 3, fig. 12) and straight (Pl. 3, fig. 9) or slightly wider in the middle (Pl. 3, fig. 8). Width of the spokes is dependent on their number, but is normally relatively thin. In most specimens there are median ridges along the ventral surface of the spokes (Pl. 3, fig. 8). The ridges are confluent with the hub rather than detached from it to form a 'star'. The ventral surface of the hub is flat and lies below the plane of the rim (Pl. 3, fig. 12). On the dorsal side the hub is rounded to flat and lies in a plane below, or more commonly above, that of the rim (Pl. 3, fig. 13). Ontogenetic stages show strongly tapering spokes which must thicken later in development (Pl. 3, fig. 14).

TEXT-FIG. 13. Frequency distribution of spoke number in the specimens of *T. synapta* used in Text-figure 11.



Discussion. The significance of various wheel parameters, particularly teeth and a central star, are discussed elsewhere (Gilliland 1990). Teeth are often difficult to recognize or appear to be missing in some parts of the rim due to poor preservation. Hence, the presence/absence of teeth may not be a reliable character. However, detailed observation of many specimens, preferably by scanning electron microscopy, should be sufficient to determine whether teeth are consistently absent or not.

A number of previously described wheels with smooth inner rims are similar to *Theelia synapta*. The most similar is *T. immissorbicula* Mostler which is widely distributed in the Upper Triassic (Gilliland 1990). Mostler (1972a) also includes *T. immissorbicula* in a list of Jurassic taxa but there is no indication of the original record. *T. germanica* Kozur, a probable synonym of *T. immissorbicula*, is known from the Lower-?Upper Triassic (Kozur 1969; Soodan 1986). In these two species, however, the inner edge of the rim is consistently smooth and neither has a median ridge on the spokes.

There is a negative correlation between the number of spokes and wheel diameter (Text-fig. 11) as is found in elasipod wheels, but Pawson (1971) found no such correlation amongst synaptid wheels of the giant larva *Auricularia nudibranchiata*. There is also a positive correlation between the number of teeth and diameter (Text-fig. 12) as Zankl (1966) found in *Theelia seniradiata*. Thus the relative number of teeth is a more important character than the absolute number.

The most similar Recent sclerites to *Theelia synapta* are the wheels found in the larvae of the Synaptidae (order Apodida). *T. synapta* is therefore referred to the Synaptidae but, because no anchors or anchor-plates, the sclerites of adult synaptids, have been found in the Blue Lias, it may be considered to be a stem-group synaptid. *T. synapta* differs from Recent synaptid wheels in having a ridge on the spokes and a correlation between diameter and number of spokes.

Family ACHISTRIDAE Frizzell and Exline, 1955

Included genus. *Achistrum* Etheridge.

Stratigraphic range. Middle Devonian to Lower Cretaceous (or Palaeocene?).

Diagnosis. Hook-shaped sclerites with an eye (terminal loop), shank and spear.

Remarks. Hampton (1958*b*) recognized four subgenera of *Achistrum* based on the structure of the eye. Frizzell and Exline (1966) dismissed three of these, as discussed in more detail in Gutschick *et al.* (1967), but raised a fourth, *Aduncrum*, to generic level. However, *Aduncrum* was based on a single specimen found in association with undoubted species of *Achistrum* and is simply an aberrant/broken specimen (personal observation) as suggested by Rioult (1961). Beckmann (1965) erected a new subgenus *Porachistrum* for hooks with a sieve-like partition in the eye. However, Gutschick *et al.* (1967) recovered similar forms (*Achistrum coloculum*) in association with hooks with a more typical eye and did not consider this character merited a separate subgenus.

The family certainly extends as far as the Lower Cretaceous (e.g. Kubiatowicz and Matyja 1977). *Achistrum* was reported by Soodan (1972) from the Palaeocene of India but without a description or figures. Given its significance to the stratigraphic range of the family the Indian record is only tentatively accepted until more details are available.

Genus ACHISTRUM Etheridge, 1881 emend Frizzell and Exline, 1955

Type species. *Achistrum nicholsoni* Etheridge, 1881.

Diagnosis etc. As for family.

Achistrum monochordata Hodson, Harris and Lawson, 1956

Plate 4, figs 1–8

- 1905 *Uncinulina polymorpha* Terquem; Hucce, p. 167, pl. 23, fig. 6*a* (only).
 1935 'Holothuriën-Kalkkörperchen' Eichenberg, p. 318, text-fig. 1 (four specimens top right only).
 1936 'Angelhaken' Bartenstein, pp. 1–2, text-figs 1*a–c*, 6.
 1938 Unidentified sclerites Wicher, pls 1–2 (*pars*), 5 (*pars*).
 1955 *Achistrum bartensteini* Frizzell and Exline, p. 94, pl. 4, figs 5–7.
 1955 *Calcligula? huckei* (in part) Frizzell and Exline, p. 70, pl. 1, fig. 28.
 1956 *Achistrum monochordata* Hodson, Harris and Lawson, pp. 340–341, text-figs 10–11.
 1957 *Achistrum monochordata* Hodson, Harris and Lawson; Hampton, p. 509, text-figs 6–8.
 1958 *Achistrum monochordata?* Hodson, Harris and Lawson; Summerson and Campbell, p. 968, pl. 125, figs 3–7.
 1958 *Achistrum bartensteini* Frizzell and Exline; Said and Barakat, p. 268, pl. 6, figs 1–5.
 1961 *Achistrum monochordata* Hodson, Harris and Lawson; Rioult, pp. 139–140, pl. 1, fig. 2.
 1962 *Achistrum monochordata* Hodson, Harris and Lawson; Fletcher, p. 325, text-figs 6–7.
 1962 *Achistrum bichordata* Fletcher, p. 323, text-figs 1–2.
 1967 *Achistrum monochordata* Hodson, Harris and Lawson; Garbowska and Wierzbowski, pp. 530–531, text-fig. 4*A–M*.
 1967 *Achistrum monochordata* Hodson, Harris and Lawson; Gutschick, Canis and Brill, p. 1471, pl. 187, fig. 30.
 1967 *Achistrum bartensteini?* Frizzell and Exline; Gutschick, Canis and Brill, p. 1470, pl. 187, fig. 32.
 1968*a* *Achistrum bartensteini* Frizzell and Exline; Mostler, p. 14, pl. 2, figs 7–8.
 1969 *Achistrum monochordata* Hodson, Harris and Lawson; Gorka and Luszczewska, pp. 382–383, pl. 79, figs 2–6.
 1971 *Achistrum monochordata* Hodson, Harris and Lawson; Zawidzka, p. 434, pl. 1, fig. 7; text-fig. 2.

- 1973 *Achistrum monochordata* Hodson, Harris and Lawson; Michelson, p. 60, pl. 2, figs 1, 9; pl. 3, fig. 7.
- 1976 *Achistrum* cf. *monochordata* Hodson, Harris and Lawson; Mostler and Rahimi-Yazd, pp. 12–13, pl. 3, fig. 18.
- 1976 *Achistrum monochordata* Hodson, Harris and Lawson; Gheorghian, pp. 59–63, pl. 2, figs 1–2.
- 1977 *Achistrum monochordata* Hodson, Harris and Lawson; Mirauta and Gheorghian, p. 156, no figure.
- 1977 *Achistrum monochordata* Hodson, Harris and Lawson; Soodan, p. 102, pl. 1, fig. 4.
- 1977 *Achistrum monochordata* Hodson, Harris and Lawson; Kubiatoewicz and Matyja, p. 402, text-fig. 1a–b.
- 1978 *Achistrum monochordata* Hodson, Harris and Lawson?; Copestake, pl. 32, fig. 6.
- 1986 *Achistrum bartensteini* Frizzell and Exline; Kristan-Tollmann (in Fischer *et al.*), p. 131, pl. 29, fig. 2.
- 1987 *Achistrum monochordata* Hodson, Harris and Lawson; Soodan and Whatley, p. 169, pl. 1, figs L–M, R–S.
- 1987 *Achistrum bichordata* (Fletcher); Soodan and Whatley, p. 168, pl. 1, fig. F.

Types. Holotype, J. 35785; paratype, J. 35784; Upper Jurassic, Lower Oxfordian (*cordatum* zone), Redcliff, near Weymouth, Dorset, housed in the Sedgwick Museum, Cambridge.

Material studied. More than 2200 specimens including BMNH E27120–27129, E27133–27140, E27207, and E27260–27263. Specimens are recorded from every sub-zone sampled in the period *johnstoni–scipionianum*, and from all four Blue Lias localities.

Stratigraphic range. Lower Carboniferous to Lower Cretaceous.

Diagnosis. Species of *Achistrum* with one or more undivided cross-bar(s) within the eye.

Dimensions. Length 137–845 μm (mean = 339 μm , $n = 201$). Width 35–220 μm (mean = 106 μm , $n = 1200$). The maximum diameter of the shaft near to the head is typically 35–40 μm in larger specimens.

Description. Hooks with a single bar across the eye or rarely with two bars on either side of the eye (Pl. 4, fig. 2). Occasionally the bar is broken in the mid-region to produce 'thorns' (Pl. 4, fig. 8). Almost all hooks exhibit eccentricity which is variable (cf. Pl. 4, figs 4–5). Left- and right-handed specimens are equally common. The head of the hook is usually obviously wider than the shaft and angled slightly in the direction of the spear (Pl. 4, fig. 7). The eye occupies the central and eccentric area of the head and consequently the head is often thicker on the non-eccentric side (Pl. 4, fig. 4). The bar varies in position from subcentral to almost fused with the edge but always on the eccentric side. Between the eye and the spear the shank is usually curved (Pl. 4, fig. 7) although this may be slight. The sharply angled spear is relatively short, compared to the shank, and thins to a sharp point, although exceptions occur (Pl. 7, figs 1, 6). The shaft is typically oval in cross-section (parallel to the plane of the long axis) becoming more circular, and wider, towards the head.

Discussion. The relative importance given to characters for classifying hooks has been discussed extensively (Hampton 1957; Rioult 1961; Garbowska and Wierzbowski 1967; Gutschick *et al.* 1967). Details of the head and eye should be given prominence because these are the most distinctive and easily recognized characters. Characters other than the eye can be useful, however, particularly where poor preservation masks details of the eye. *Achistrum issleri*, which has an empty eye, differs from *A. monochordata* in its circular cross-section and centrally placed (non-eccentric) head. In *A. monochordata* the eye of smaller specimens is commonly infilled but other characters are similar to larger specimens, and, in addition, many small hooks possess a bar (Pl. 4, fig. 3). Rare odd forms (e.g. Pl. 4, fig. 6) should be regarded as aberrant specimens rather than the basis for new morphospecies (e.g. *A. britannica* and *A. warboysensis* Soodan and Whatley 1987). Examples in which the bar has broken, to produce 'thorns', originally assigned to *A. bartensteini*, were correctly synonymized with *A. monochordata* by Rioult (1961).

Hooks with two bars in the eye referable to *A. bichordata* Fletcher, 1962 are infrequent in the present material. Fletcher noted that *A. monochordata* was the commonest morphospecies in his

material. Thus *A. bichordata* is probably a morphological variant forming a small percentage of any normal population of *A. monochordata*. Fletcher recorded other rare hook morphospecies but none was found in the Blue Lias material. Richardson (personal communication in Pawson 1980) noted from body fossil material that more than ten 'species' (= morphospecies) of hooks could be found in one individual. This, together with the distribution of *A. monochordata* and '*A. bichordata*', suggests that biological species possess different morphospecies of *Achistrum* but vary in respect of the dominant type. It is therefore useful to recognize forms of morphospecies, equivalent to former morphospecies, i.e. 'single barred' and 'double barred' forms of *A. monochordata* and to determine the predominating hook type using a large sample. It is possible that the relative size of hooks, e.g. length/width, differs between species. Although there are two distinct size groupings in Text-figure 5, these are unlikely to represent two different species because of the strong correlation between length and width at all sizes (see Text-fig. 4).

Order UNCERTAIN – DENDROCHIROTIDA Grube, 1840 or MOLPADIIDA Haeckel, 1896
[Parafamily PRISCOPEMATIDAE Frizzell and Exline 1955] *pars*
Genus STAUCUMITES Deflandre-Rigaud, 1952 emend

Type species. Staucumites bartensteini Deflandre-Rigaud, 1952.

Diagnosis. Tables with a base of four perforated arms arranged in a cross. Additional holes of equal or smaller size to those in the arms may form between the arms. The spire projects from the centre and is solid with a quadripartite base.

Discussion. The genus appears to be monospecific. Mortensen (1937) considered *S. bartensteini* to be derived from either of the Recent orders Aspidochirotida or Dendrochirotida, but without elaborating. However, this morphospecies appears to have affinities with tables found in both the Recent order Dendrochirotida and the family Molpadiidae (order Molpadiida) (Gilliland 1990).

Staucumites bartensteini Deflandre-Rigaud, 1952

Plate 4, figs 9–16, 21

- 1936 Glitter-Plattchen in Kreuz-Form Bartenstein, pp. 8–9, text-figs 4a–c, 5, 12.
- 1937 Spicule of holothurian Mortensen, pp. 26–27, pl. 4, fig. 10.
- 1952 Unnamed crosses Fischer, text-fig. 19–2–8.
- 1952 *Staucumites bartensteini* Deflandre-Rigaud, p. 6.
- 1953 *Staucumites bartensteini* Deflandre-Rigaud; Deflandre-Rigaud, p. 953, text-fig. 12.
- 1955 *Priscopedatus bartensteini* (Deflandre-Rigaud); Frizzell and Exline, pp. 103–104, pl. 5, figs 4, 6–9.
- 1961 *Staucumites bartensteini* Deflandre-Rigaud; Rioult, pp. 140–141, table 1, figs 10, 18.
- 1964 *Priscopedatus bartensteini* (Deflandre-Rigaud); Zankl, pl. 1, fig. 3f.
- 1966 *Staucumites* cf. *bartensteini* Deflandre-Rigaud; Zankl, pp. 76–77, pl. 5, fig. 3.
- 1966 *Staucumites bartensteini* Deflandre-Rigaud; Frizzell and Exline, p. U667, text-fig. 532(5).
- 1968a *Priscopedatus* cf. *normani* Schlumberger; Mostler, text-fig. 5(2).
- 1968b *Priscopedatus acanthicus* Mostler, pp. 14–15, pl. 3, fig. 1; text-fig. 1.
- 1968b *Priscopedatus staucumitoides* Mostler, pp. 17–18, pl. 3, figs 2–5; text-fig. 2a–d.
- 1968b *Staucumites bartensteini* Deflandre-Rigaud; Mostler, pp. 31–32, pl. 3, figs 6–9; text-fig. 2a–c.
- 1968b *Staucumites horridus* Mostler, pp. 22–23, pl. 3, fig. 10.
- 1968c *Staucumites bartensteini* Deflandre-Rigaud; Mostler, p. 56, pl. 1, figs 4–5.
- 1968 *Staucumites bartensteini* Deflandre-Rigaud; Speckmann, p. 204, pl. 1, fig. 9.
- 1968 *Priscopedatus* sp. 1 Speckmann, p. 202, pl. 1, figs 1, 3.
- 1971 *Staucumites bartensteini* Deflandre-Rigaud; Zawadzka, p. 436, pl. 2, figs 2–5.
- 1971 *Priscopedatus staucumitoides* Mostler; Kozur and Mostler, p. 27.
- 1971 *Staucumites bartensteini* Deflandre-Rigaud; Kozur and Mostler, p. 27.

- 1972 *Priscopedatus acanthicus* Mostler; Kozur and Mock, pl. 6, figs 28–29; also *P. cf. acanthicus*, pl. 6, fig. 27.
- 1972 *Priscopedatus staurocumitoides* Mostler; Kozur and Mock, pp. 13–14, pl. 6, figs 17–22.
- 1972 *Priscopedatus bartensteini* (Deflandre-Rigaud); Kozur and Mock, pl. 6, figs 12–14.
- 1972 *Priscopedatus horridus* (Mostler); Kozur and Mock, pl. 6, figs 25–26.
- 1972 *Staurocumites bartensteini* Deflandre-Rigaud; Mostler, p. 8 (listed only).
- 1973 *Priscopedatus staurocumitoides* Mostler; Mostler and Parwin, p. 12 (listed only).
- 1973 *Staurocumites bartensteini* Deflandre-Rigaud; Mostler and Parwin, p. 12 (listed only).
- 1974 *Priscopedatus acanthicus* Mostler; Kozur and Mock, pl. 6, figs 4–5.
- 1974 *Priscopedatus staurocumitoides* Mostler; Kozur and Mock, pl. 6, figs 1–2.
- 1974 *Priscopedatus bartensteini* (Deflandre-Rigaud); Kozur and Mock, pl. 5, figs 12–13.
- 1974 *Priscopedatus horridus* (Mostler); Kozur and Mock, pl. 5, figs 14–15.
- 1977 *Priscopedatus staurocumitoides* Mostler; Mirauta and Gheorghian, p. 156, pl. 14, figs 1–2, 4, 9.
- 1977 *Priscopedatus horridus* (Mostler); Mirauta and Gheorghian, p. 156, pl. 14, fig. 3.
- 1980 *Staurocumites bartensteini* Deflandre-Rigaud; Donofrio *et al.*, p. 68 (listed only).
- 1986 *Staurocumites bartensteini* Deflandre-Rigaud; Kristan-Tollmann, pp. 131–132, pl. 29, figs 4–9.

Types. The holotype and paratypes were selected by Deflandre-Rigaud (1952), and the holotype figured by her (1953, p. 953, fig. 12), based on material originally described by Bartenstein (1936, figs 4a, c, 5, 12) from the Pliensbachian of Hambühren (N. Germany).

Material studied. More than 300 specimens including BMNH E27198–27206, E27209–27221, E27223–27227, E27229 and E27264–27266, from Maisemore Cliff (*rotiforme* subzone), Hock Cliff (*bucklandi* subzone) and Long Itchington (*laqueus*, *extranodosa/complanata*, *rotiforme* and *bucklandi?reynesi* subzones).

Stratigraphic range. Middle Triassic (Anisian) to the Lower Jurassic (Pliensbachian).

Diagnosis. As for genus.

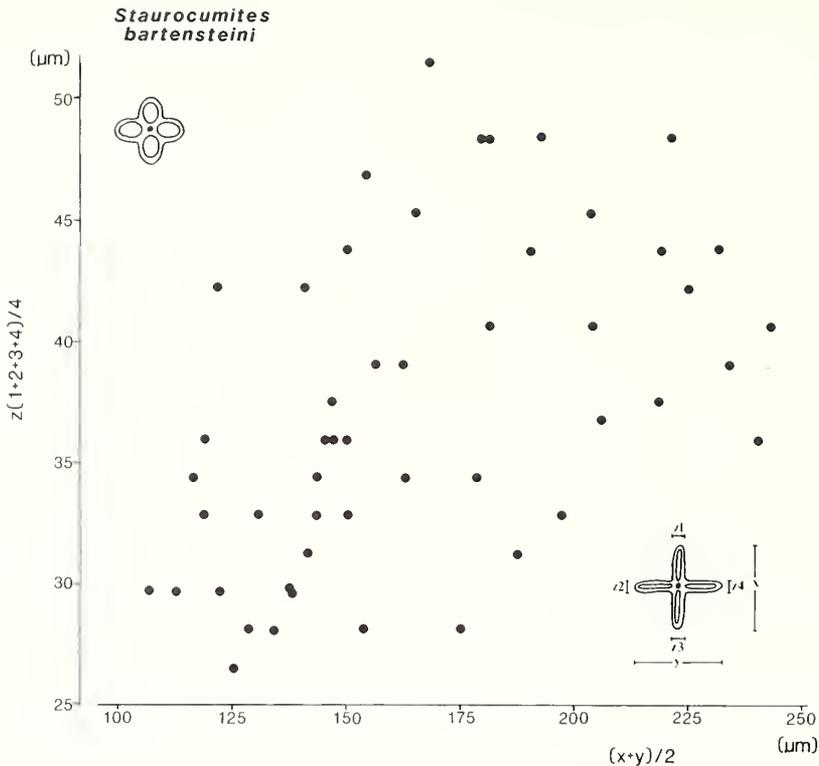
Dimensions. Maximum diameter, 100–255 μm (average of x and y , 105–245 μm); maximum width of arms, 25–56 μm (average arm width, 28–52 μm); see also Text-figure 14; spire height is normally *c.* 40–50% of the diameter.

Description. Tables usually with a quadripartite base composed of four arms each with an elongate hole. Rare examples have additional holes between the main ones (Pl. 4, fig. 9). Other rare forms include three-armed (Pl. 4, fig. 13) and five-armed (Pl. 4, fig. 14) specimens. Length and width of the arms are variable (Text-fig. 14; Pl. 4, figs 11, 15), even within the same specimen and irregularly shaped base plates occur (Pl. 4, fig. 16). The spire is vertical and relatively short but often broken near to the base. One odd example was found with a relatively long spire bent over at the top (Pl. 4, fig. 12). The base of the spire is solid with four faint sloping ridges at the junctions of the arms (Pl. 4, fig. 10). The spire narrows towards the top (Pl. 4, fig. 10) and terminates in three diverging thorns or spines.

Discussion. *S. bartensteini* is a distinctive and widely reported morphospecies. Previous authors have also noted a wide variation in shape (e.g. Mostler 1969, 1972*b*). Rioult (1961) suggested that different forms may be of stratigraphic use, at least in the Lias. This is unlikely since a wide range exists even in specimens from the same sample (Text-fig. 14).

Mostler (1968*a*) erected a new species, *Priscopedatus staurocumitoides*, distinguished from *S. bartensteini* on the presence of more than two (usually three to six) additional holes on the arms, despite showing that the two species simply form a morphological growth series (Text-fig. 2*a–f*). Kozur and Mock (1972, 1974) record both *S. bartensteini* and *P. staurocumitoides* from the Upper Illyrian (Anisian, Middle Triassic) of the same locality. In the present material there were rare examples of '*P. staurocumitoides*'. Clearly the two morphospecies are synonymous.

Mostler (1968*a*) described two other new species *Staurocumites horridus* and *Priscopedatus acanthicus*, both from the same locality as *P. staurocumitoides*. *S. horridus* is differentiated on its thick base plate (i.e. small holes), massive spire and spiny periphery. However, the thickness of the base plate varies in *S. bartensteini* (see Pl. 4, fig. 11) and in *S. horridus* itself (Kozur and Mock 1972,



TEXT-FIG. 14. A plot of the average arm length against average arm width of *S. bartensteini* from sample M3 ($n = 50$).

pl. 6), the spire of *S. horridus* looks no different from that of *S. bartensteini*, and the spiny edge is indicative of continuing growth at the periphery. *P. acanthicus* is simply a form of *S. horridus* in which secondary holes have developed. In addition all these morphospecies have been recorded from the same sample (Kozur and Mock 1974). Mostler (1972*b*) noted the obvious similarity between *S. bartensteini*, *P. staurocumitoides* and *P. acanthicus*, but did not propose any synonymy. The available evidence indicates that *S. horridus* and *P. acanthicus* are also synonyms of *S. bartensteini*.

Kristan-Tollmann (1986) included *Priscolongatus* Gorka and Luszczewska within *Staurocumites*, based on its resemblance to aberrant forms of *S. bartensteini*. This synonymy is questionable since the arms of *Priscolongatus* are solid with holes restricted to the central area, which is concavo/convex rather than flat, and its spire is short and conical, composed of fused pillars, unlike that of *Staurocumites*. *Priscolongatus*, which may extend back to the Middle Triassic, is possibly closely related to *Staurocumites* (Gilliland 1990).

Order UNCERTAIN – DENDROCHIROTIDA Grube or MOLPADIIDA Haeckel
Parafamily PUNCTATITIDAE Mostler and Rahimi-Yazd, 1976

Included genera. *Punctatites*, *Uncinuloides* in part.

Diagnosis. Rod-shaped sclerites with a perforated or non-perforated central area which is commonly the widest part of the rod (occasionally additional arms develop from the central area).

In extreme forms the central area is a short, narrow rod connecting the two wider arms. Some form of slit occurs at either end or over the entire length of the sclerite.

Remarks. The classification, morphological variation and affinities of the Punctatitidae are discussed in detail in Gilliland (1990). *Punctatites* was originally included in the parafamily Stichopitidae and then placed in a separate family. Also included in the new family was the genus *Uncinuloides*. Kozur and Mock (1972), in an extensive revision of *Punctatites*, synonymized *Uncinuloides* with this genus, and certainly a few previously recognized morphospecies, such as *U. diffusus* Mostler, 1971, overlap with taxa previously assigned to *Punctatites*. On the other hand, as discussed in Mostler and Rahimi-Yazd (1976), some other forms of *Uncinuloides* show a morphological gradation with *Uciniulina*, a genus based on rods that may be confused with spicules of non-holothurian groups (Gilliland 1990). Hence, only some species of *Uncinuloides* can be accepted as holothurian sclerites, whilst others may be placed in *Punctatites*.

Genus PUNCTATITES Mostler, 1968 emend Kozur and Mock, 1972

Type species. *Punctatites longirameus* Mostler, 1968c.

Diagnosis. Rods of the Punctatitidae with a smooth edge, usually a prominent perforated slit, and no development of a perforated eccentric area.

Punctatites? aff. *extensus* (Mostler 1968c)

Plate 4, fig. 23

- 1968b *Binoculites extensus* Mostler, pp. 429–430, pl. 1, figs 1–2.
- 1972 *Punctatites extensus* (Mostler); Kozur and Mock, pl. 15, figs 8–9.
- 1972a *Punctatites extensus* (Mostler); Mostler, p. 4 (listed only).
- 1973 *Binoculites extensus* Mostler; Kozur and Mostler, p. 307 (listed only).
- 1973 *Punctatites extensus* (Mostler); Mostler and Parwin, p. 12 (listed only).
- 1979 *Punctatites extensus* (Mostler); Mostler, p. 336 (listed only).

Types. Holotype and paratype from the Upper Triassic, Middle Norian, of Sandling (Northern Calcareous Alps, Austria).

Material studied. One specimen (E27222) from L18e, *angulata* zone of Long Itchington.

Stratigraphic range. Upper Triassic (Middle Norian) to Lower Jurassic.

Diagnosis. A straight form of *Punctatites* with a thin, imperforate mid-region.

Dimensions. Length, 900 μm ; width at the mid-point, 55 μm ; maximum width at the expanded end, 110 μm .

Description. Large rod-shaped sclerite with a narrow middle region (nearly half of the total length) and at either end an elongate expanded area. At one end, which is slightly broken, the sides of the widened area are parallel whilst the other end is ellipsoidal. Within each expanded part there is a sunken area which at the broken end, at least, appears to be perforated.

Discussion. The specimen is slightly broken and the grooved areas at either end are infilled with matrix, obscuring details. However, the presence of a hole at the broken end suggests that the grooved areas are perforated and the sclerite is tentatively referred to *Punctatites*. There are a number of morphospecies of *Punctatites* of which *P. extensus* is the most similar to the example described here. Although the relative length of the central area is variable in *P. extensus*, in forms

in which this is large the rod is thinner than in the specimen described (see, for example, Mostler 1968*b*, pl. 1, fig. 1), and hence assignment to *P. extensus* is tentative until further Blue Lias examples are found.

The affinities of *Punctatites* are uncertain, but probably lie with either the Dendrochirotida or Molpadiidae.

Order UNCERTAIN

[Parafamily PRISCOPEMATIDAE Frizzell and Exline 1955]

Priscopedatus sp. nov.?

Plate 4, figs 18, 24, Plate 5, figs 1–2

Types. One specimen, the holotype (BMNH E27342), from the *liasicus* (*laqueus*?) zone, Long Itchington.

Diagnosis. A table with a round base plate in which two irregular circles of variably shaped holes surround a large central hole. The spire is hollow and formed from four vertical pillars. At the top a Maltese-cross arrangement of spines overhangs the large central hole (Pl. 5, fig. 2).

Dimensions. Diameter, 80 μm ; spire height, 40 μm .

Description. Small, circular table with undulating periphery imparting a spiny effect. In the centre of the base is a large hole surrounded by an estimated eight small holes (Pl. 4, fig. 18). Around the outer part are fifteen to sixteen irregularly arranged holes of variable size and shape but mostly larger than those in the inner circle. Viewed from above the large central hole and inner circle of small holes are obscured by the spire. There are a few tiny holes situated at the periphery between the larger holes (Pl. 4, fig. 18). The spire is shorter than the diameter of the disc and formed from four pillars connected midway up by cross-bars (Pl. 4, fig. 24). At the top of the spire are three layers of spines spread outwards, the lower of which forms a Maltese-cross shape.

Discussion. This is a generalized four-pillared type of table. Fossil examples are not common possibly because of their small size (frequently less than 100 μm in diameter). Deflandre-Rigaud (1962) has described a number of such examples from the Oxfordian of France, the most similar of which are *Priscopedatus heteroporus*, *P. affinis* and *P. spiniferus*. The former has irregularly distributed outer holes, as in the present specimen, but only one circle of these and, in addition, there is a large central hole unobscured by the spire. *P. affinis* differs in having four central holes and only eight large regularly arranged holes around these. *P. spiniferus* also has four central holes, a square-shaped base plate and only one circle of large holes. Because of these differences the present specimen is assigned to a new species. However, due to the poor preservation, and the fact that there is only one specimen, the species is left under open nomenclature until further material is found.

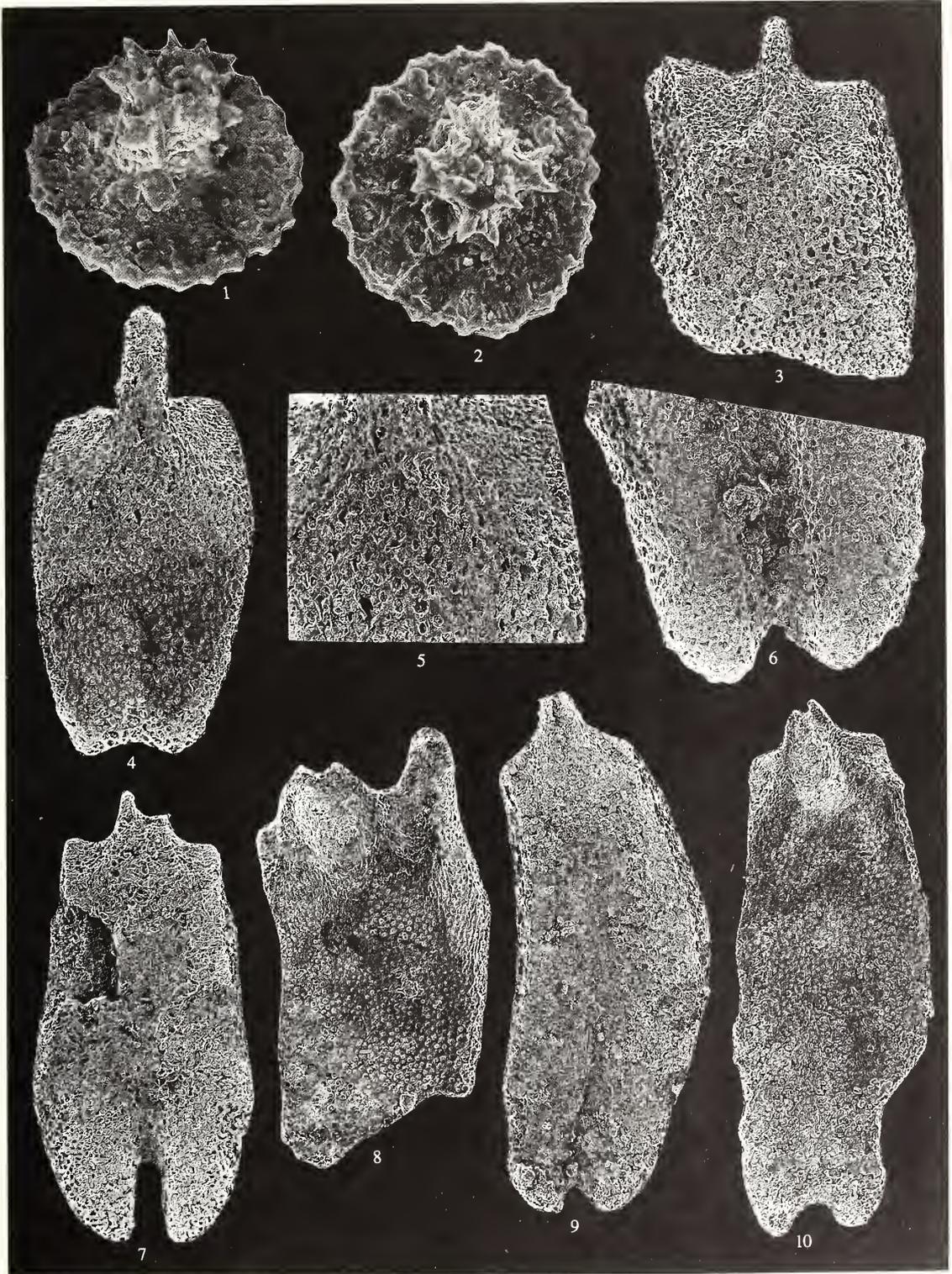
Four-pillared tables are widespread amongst holothurian families (Gilliland 1990). The presence of two circles of holes and the variable size, shape and distribution of the outer holes are characters most frequently found in the tables of dendrochirotes, but may also occur in aspidochirotes. Tables of this kind typically form assemblages with a variety of other sclerite morphotypes but no such association can be identified because of its rarity. Earlier records of four-pillared tables include

EXPLANATION OF PLATE 5

Figs 1–2. *Priscopedatus* sp. nov.? Holotype; E27342; L9*b*; *laqueus*?*extranodosa/complanata* subzone, both $\times 580$.

Figs 3–5. Calcareous ring Type 1 interradials. 3, E27435; L16*e*; *angulata* zone, $\times 85$. 4–5, E27424; H23; *bucklandi* subzone, $\times 70$, $\times 130$, respectively.

Figs 6–10. Calcareous ring Type 1 radials. 6, E27419; H19; *bucklandi* subzone, $\times 105$. 7, E27430; H4; *bucklandi* subzone, $\times 55$. 8, E27417; H19; *bucklandi* subzone, $\times 55$. 9, E27416; H19; *bucklandi* subzone, $\times 55$. 10, E27437; H15; *bucklandi* subzone, $\times 55$.



GILLILAND, Blue Lias holothurian sclerites

Priscopedatus quinquespinosus Mostler and Rahimi-Yazd, 1976, from the Upper Permian, *P. procerus* Mostler, 1971, from the Middle Triassic, and *Solopedatus parvus* Mostler, 1971, from the Upper Triassic, but these are atypical. The latter, for example, resembles the reduced tables of the Recent genus *Labiodemas*. *Priscopedatus* sp. nov.? is the earliest typical example with a prominent four-pillared spire.

GENERAL DISCUSSION

Sorting and preservation

There is little information on the fate of sclerites following death. The rate at which dermal tissue decomposes varies between different holothurians (Schäfer 1972; Pawson 1980; Gilliland 1990). Frizzell and Exline (1955) concluded that most sclerites were deposited near to where the animal lived and the non-holothurian fauna in the present material is generally consistent with this conclusion. For example, various echinoid or ophiuroid elements commonly occur in the same sample. Hallam (1960) concluded that the Blue Lias fauna contains a mixed life and indigenous death assemblage through much of the succession, i.e. a limited taphonomic loss of faunal components but some disturbance following death.

The distribution of elements of the calcareous ring relative to their associated sclerite morphotypes suggests some dispersal took place after death. An absence/scarcity of morphotypes expected to co-occur with *Binoculites*, i.e. dendrochirote rods (Gilliland 1990) or tables, may also indicate differential sorting of sclerites. However, the differences between these various morphotypes are slight and seem unlikely to be significant enough to affect sorting.

Evidence from size frequency distributions is also limited. The length of buttons from the Recent species *Pawsonia saxicola* shows a near normal distribution (Gilliland 1990) and Hampton (1959) obtained a similar result for the buttons of *Holothuria impatiens*. The only information on the expected distribution of hook size is in Sroka (1988) who found a bimodal distribution with a higher peak of smaller specimens. In the Blue Lias material there is no apparent correlation of changes to these predicted size frequencies, as a consequence of sorting, for *Achistrum monochordata* or *Binoculites terquemi* from the same samples (compare Text-fig. 6*b-d*, with 6*f-h*).

Palaogeography

The present investigation, together with previous records (e.g. Blake 1876; Copestake 1978), shows that holothurians were distributed across southern Britain in an area which today extends from Dorset north to Yorkshire, and westward to the Irish Sea. A comparison of the main components of the British Blue Lias fauna with Hettangian and Sinemurian records from Denmark, France and Germany indicates a similar association of sclerites is found across north-west Europe; this also persists through much of the Lias. *Binoculites germanica*, particularly the form *Calclamna*, and hooks are the most widespread and common. There is, however, regional variation. In Denmark and Britain *Achistrum monochordata* occurs in isolation, whereas in France and Germany *A. issleri* and *A. monochordata* occur together. In Denmark *A. monochordata* comprises only about 25% of sclerites (with 75% *Binoculites* form *Calclamna*) compared with a significantly higher proportion (c. 49%) in southern Britain. *Staurocumites bartensteini* is widespread but less common in the Lias

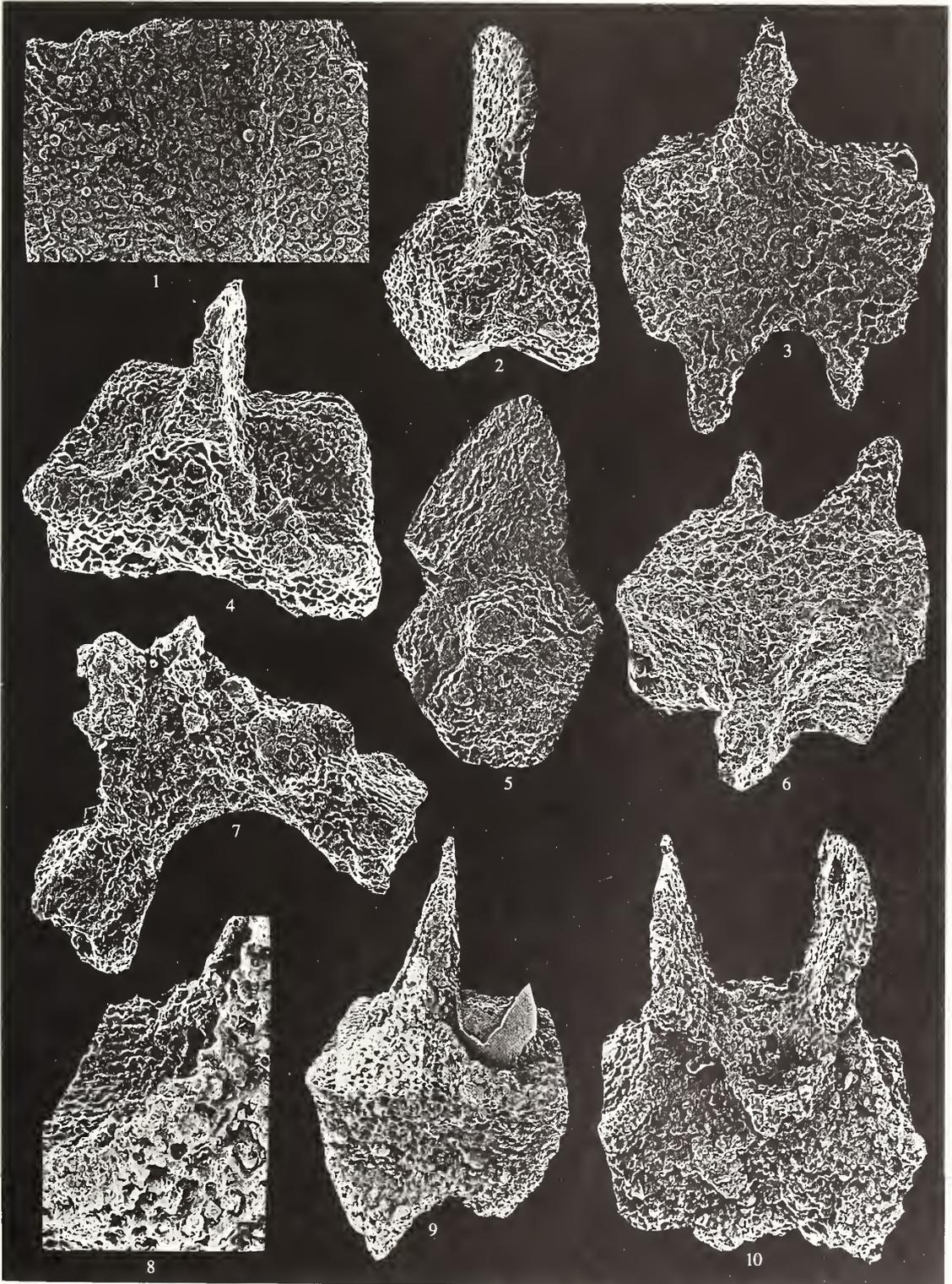
EXPLANATION OF PLATE 6

Fig. 1. Calcareous ring Type 1 radial. E27419; H19; *bucklandi* subzone, $\times 105$.

Figs 2, 4-5, 8-10. Calcareous ring Type 2. 2, 5, E27423; L9*b*; *laqueus?extranodosa/complanata* subzone, $\times 145$. 4, E 27421; L9*b*; *laqueus?extranodosa/complanata* subzone, $\times 130$. 8-9, E27422; H15; *bucklandi* subzone, $\times 145$, $\times 160$, respectively. 10, E27440; L41*b*; *bucklandi?* subzone, $\times 100$.

Figs 3, 6. Calcareous ring Type 3. E27426; H15; *bucklandi* subzone, both $\times 85$.

Fig. 7. Calcareous ring Type 4. E27427; L42*b*; *bucklandi?reynesi* subzone, $\times 115$.



GILLILAND, Blue Lias holothurian sclerites

of both Britain and other regions of Europe. Partly formed *Binoculites jurassica* has a similar geographical range to *B. terquemi* but is less frequent. Fully formed *B. jurassica* have been found only in Denmark and Britain, but the British specimens are more clearly differentiated from fully developed *B. terquemi*. The most significant character of the British holothurian fauna is the presence of wheels which elsewhere in Europe only appear higher up in the Lias (?Sinemurian, Pliensbachian). Thus the southern British fauna included a high proportion of *A. monochordata*, a well developed *B. jurassica* assemblage and the presence of chiridotids and synaptids, compared to other regions. The latter two may indicate a more on-shore assemblage in southern Britain during this period.

Palaeoenvironment

The holothurian fauna from the Blue Lias is quite diverse. Comparison with the distribution of Recent taxa for palaeoenvironmental analysis is limited by the uncertain affinities of some of the morphotypes and the difficulty of restricting others to a taxonomic level below that of a Recent family. Considering the affinities of the fauna, e.g. *Palaeoypsilus* with the Ypsilothuriidae, or *Theelia convexa* and *T. synapta* with the Chiridotidae and Synaptidae respectively, it can be concluded only that the holothurian fauna does not undermine the environmental interpretation of the Blue Lias, i.e. that it was deposited in shallow (no deeper than 150 m), warm (modern tropical-subtropical temperatures) water (Hallam 1960). It is probable, however, that the holothurian fauna from the Blue Lias was composed of a mixture of predominantly shallow water taxa at the lower limit of their distribution and less common deeper water species near to their upper limit.

Holothurians from the Blue Lias have a varied ecology. Dendrochirotes are suspension feeders which either extend their dendritic tentacles from a burrow or cling to a hard/seaweed substratum. Dactylochirotes burrow into unconsolidated sediments feeding on detrital material whilst elasipods plough through the sediment surface. Molpadiids burrow into soft mud and apodans (Chiridotidae and Synaptidae) are commonly burrowers. The activities of the burrowers, particularly vagile chiridotids, would have contributed to disruption of the sediment.

Biostratigraphic aspects

Riout (1961) proposed a zonation of the whole Lias based on twenty-eight holothurian morphospecies, some apparently with a limited vertical range. The morphospecies were grouped into three associations which defined the Hettangian–Sinemurian, the Pliensbachian–lower Toarcian (*temicostatium* subzone) and the middle–upper Toarcian periods. Riout noted the long stratigraphic range of two species of *Achistrum*, but used the absence of hooks as diagnostic of the middle–upper Toarcian, even though both species extended into the Middle Jurassic. Furthermore, two of the four morphospecies used to define the middle–upper Toarcian ‘zone’ were only known from single specimens (*Mortensenites feifeli* and *Calclannoidea protens*) and a third, *Theelia vetusta*, was based on poorly preserved specimens. In addition one of the ‘diagnostic’ taxa for the Hettangian–Sinemurian ‘zone’ is simply an aggregation of *Achistrum* and *Binoculites*.

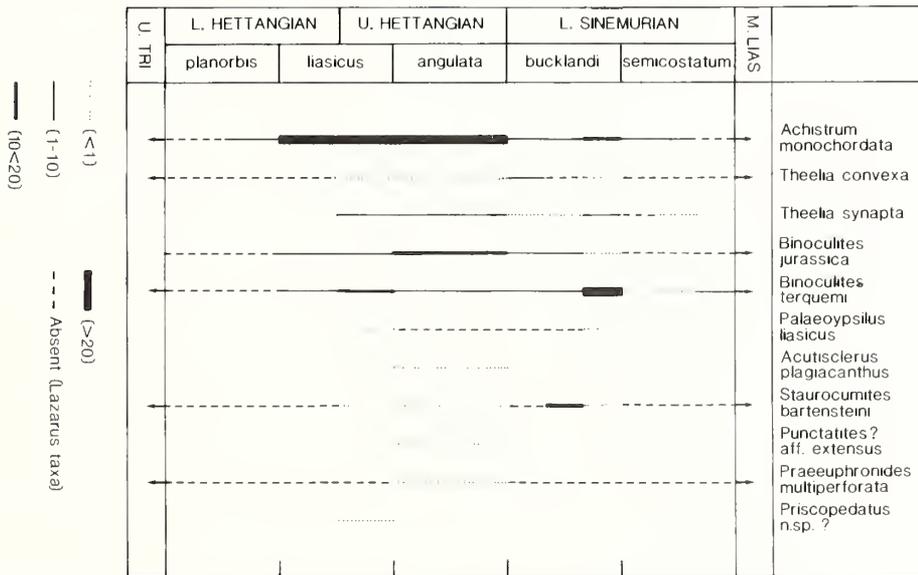
The stratigraphic distribution of the taxa recovered from the Blue Lias of southern Britain is shown in Text-figure 15 and the following changes must be made to Riout’s scheme. *Binoculites terquemi* form τ , *B. irregularis* form τ , *Ambulacrites* (= *Stichopites*) *subrectus*, *Staurocumites bartensteini* and *Theelia heptalampra* (synonymized with *T. convexa*) extend down into the Hettangian or Sinemurian and are no longer restricted to the Pliensbachian–lower Toarcian. In addition, Michelson (1972, pl. 3, fig. 5) figured a specimen of ‘*Calclanna germanica*’ from the Hettangian identical to *Binoculites perforatus*, a morphotype previously thought to be restricted to the Pliensbachian.

These extensions of range together with taxonomic revisions result in a less well defined zonation with only the lower and middle holothurian assemblage zones of Riout still recognizable. The biostratigraphic resolution afforded by sclerites does not compare well with that of many other fossil groups. The Hettangian–Sinemurian is characterized by *Binoculites terquemi* form β , *B. irregularis* and *B. cf. irregularis* (all of which are synonymous), and *Cucumaries mortenseni* and

Mortensenites circularis (both of which may not be holothurian sclerites). The fauna confined to the Pliensbachian–lower Toarcian is now reduced to *Theelia crassidentata*, *T. mortenseni*, *T. rigauda*, *Myriotrochites* (= *Stueria*)? *costifera*, and the curved rods *Ambulacrites* (= *Stichopites*) *terquemi* and *A. (S.) polymorpha* (which are probably synonymous). The Pliensbachian–lower Toarcian may also be recognized by a predominance of wide-armed *S. bartensteini* and the early growth stages of *Binoculites jurassica*.

If biostratigraphic methods other than simple presence/absence are considered, such as general abundance or bio-events, holothurians still have limited application, even on a local scale. For example, the broadly consistent sclerite composition during the Hettangian (Text-fig. 3), whilst not defining this period, may nevertheless be of some use for correlation. However, the variation in sclerite abundance and composition between sections further up the succession during the same periods of time undermines this. At present insufficient sampling also rules out the recognition of holothurian 'bio-events', such as the significant increase in *S. bartensteini* at Maisemore Cliff, although the significant percentage of wheels at Hock Cliff appears to be a local, rather than a widespread, event.

Changes within particular taxa, such as the size change in *A. monochordata* (Text-fig. 5), reveal potentially more useful biostratigraphic trends. The size change observed may even be cyclical but unfortunately there are no data from the *portlocki* zone. The relative abundance of the two *Binoculites* species also varies stratigraphically (Text-fig. 7). The Lower and lower Upper Hettangian



TEXT-FIG. 15. Stratigraphic distribution of the sclerite morphospecies found in the present study. Figures in the key are average number of sclerites per sample for each sub-zone (based on all samples). TRI, Triassic; L, Lower; M, Middle; U, Upper.

have a mixture of both *B. terquemi* and *B. jurassica*, the rest of the Hettangian (the *angulata* zone) has a preponderance of *B. jurassica* and in the Sinemurian *B. terquemi* dominates. In both cases large sample sizes are needed, which limits their application.

Evolutionary implications

Several elements of the Blue Lias holothurian fauna represent important finds with respect to the phylogeny of the class. Of particular note is the presence of *Theelia synapta*, the oldest known apodan wheel which definitely possesses the characters of a synaptid (larval) wheel. This indicates

that the lineage leading to the Synaptidae had evolved by the Lower Jurassic. The Blue Lias *Theelia convexa* are the oldest chiridotid wheels which are closely comparable with Recent forms, i.e. there is a well-developed star structure and a conservative number of spokes. The fauna includes two spired-plate morphospecies, doubling the total number known, and includes the earliest probable representative of the dactylochirote family Ypsilothuriidae. Also, although *Priscopedatus* sp. nov.? is not the earliest known four-pillared table, it is the first typical example and a morphological advance on Triassic forms.

Calcareous ring material is significant simply because of its rarity. If calcareous ring Type 1 is correctly assigned to the Molpadiida then this is the earliest record of the order, in the absence of any unequivocal molpadiid morphotypes. However, the proposed association between Type 1 and *Staurocumites bartensteini* could mean that the earliest record is the first appearance of this morphospecies, i.e. the Middle Triassic (Anisian). Type 1 elements are probably derived from Molpadiidae, indicating that this is the oldest family within the Mopadiida. The similarity of *S. bartensteini* to some dendrochirote tables, however, may indicate a close relationship between the Dendrochirotida and Molpadiida (Gilliland 1990).

Calcareous ring Type 2 is derived from an apodan and possibly a myriotrochid. The absence of associated myriotrochid morphotypes, the data in Table 1, and observations of *Achistrum*- and calcareous ring-bearing complete fossils, suggest that the 'myriotrochid-type' of ring was present in some or all apodan groups at least until the early Jurassic, i.e. the calcareous ring found in myriotrochids today is primitive.

Acknowledgements. I thank Dr A. B. Smith for continued help, encouragement and discussion, and Professor D. Nichols for advice and assistance. I am grateful to Dr R. C. Clements for providing details of the Long Itchington locality, to Dr D. Searle for advice on processing techniques, and Dr M. J. Simms for advice on localities. I thank the EM Unit of the British Museum (Natural History) for providing prints of most of the photographs used. This work was undertaken whilst in receipt of a NERC Studentship which is gratefully acknowledged.

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P. M. GILLILAND

Department of Biological Sciences
Hatherly Laboratories, The University
Prince of Wales Road
Exeter, Devon EX4 4PS

Typescript received 10 September 1990
Revised typescript received 13 May 1991

A TRIASSIC MYGALOMORPH SPIDER FROM THE NORTHERN VOSGES, FRANCE

by PAUL A. SELDEN *and* JEAN-CLAUDE GALL

ABSTRACT. The oldest fossil mygalomorph spider, from the Anisian Grès à Voltzia of the northern Vosges, France, is described as *Rosamygale grauvogeli* gen. et sp. nov. The spider exhibits mainly plesiomorphic characters. It is a tuberculote (*sensu* Raven 1985) and is placed in the Hexathelidae, with some reservations. A ground-dwelling spider, *Rosamygale* was an integral part of the halophilous terrestrial biota of the time. The spiders became entombed in the wet sediment of desiccating pools. The presence of a primitive tuberculote on the southern margins of the Zechstein Sea in the Middle Triassic is evidence for a pan-Pangaeian distribution of the Mygalomorphae prior to the break-up of the supercontinent.

RÉSUMÉ. La plus ancienne araignée mygalomorphe connue provient du Grès à Voltzia, d'âge Anisien, du Nord des Vosges (France). Elle est décrite sous le nom *Rosamygale grauvogeli* gen. et sp. nov. Cette araignée présente essentiellement des caractères plésiomorphes. Elle appartient aux formes 'tuberculote' (*sensu* Raven (1985)) et est rapportée avec réserve aux Hexathelidae. *Rosamygale* qui vivait au contact du sol, appartenait sans doute à la faune halophile de l'époque. Les araignées s'échouaient dans des étendues d'eau en voie d'assèchement et étaient enfouies dans le sédiment argileux. L'existence d'une forme primitive de 'tuberculote' durant le Trias moyen, sur la marge méridionale de la mer du Zechstein, apporte la preuve d'une distribution pan-pangéenne des Mygalomorphae antérieurement à la dislocation du supercontinent.

MYGALOMORPH spiders were first described from the Mesozoic by Eskov and Zonshtein (1990) from localities in the Lower Cretaceous of Transbaikalia and Mongolia. In addition, undescribed mygalomorphs are known from the Cretaceous of Brazil (N. Platnick, pers. comm.). Previously, only Cenozoic fossil mygalomorphs were known (reviewed in Eskov and Zonshtein 1990). Here, a new mygalomorph genus is described, exceptionally preserved in the middle Triassic (Anisian) Grès à Voltzia of the northern Vosges, and is placed in the extant family Hexathelidae. Thus, the fossil record of the Mygalomorphae is doubled, and it is suggested that the infraorder probably had a worldwide distribution before the break-up of the Pangaeian supercontinent.

GEOLOGICAL SETTING

The sediments bearing the fossil spiders, the Grès à meules, form the lower part of the Grès à Voltzia, which belongs to the upper part of the Buntsandstein, of Lower Triassic (Anisian) age (Table 1).

Three facies have been recognized in the Grès à meules Formation (Gall 1971, 1983, 1985): (a) thick lenses of fine-grained sandstone, grey or pink but most often multicoloured, containing land plant debris and stegocephalian bone fragments; (b) green or red silt/clay lenses, generally composed of a succession of laminae each a few millimetres thick, with well-preserved fossils of aquatic and terrestrial organisms; (c) beds of calcareous sandstone with a sparse marine fauna.

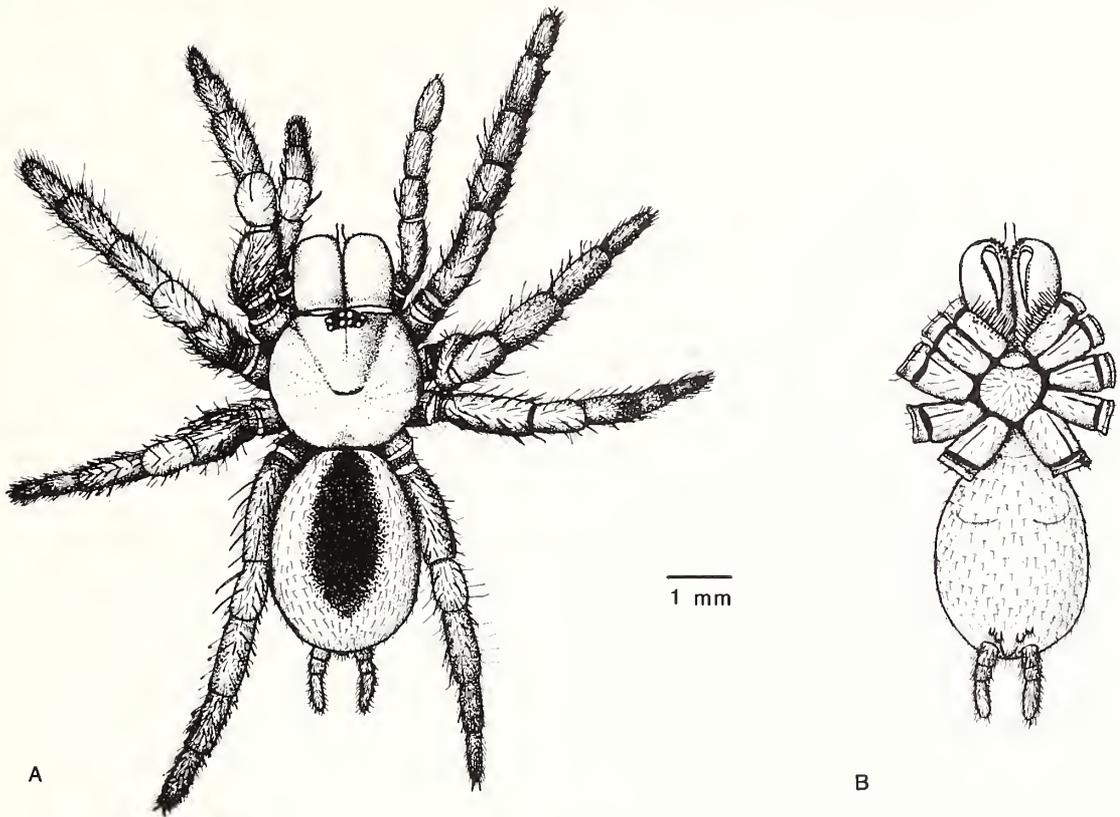
The spiders come from the clay lenses (facies b); the associated fauna includes terrestrial scorpions, myriapods and insects. An aquatic fauna occurs in the same beds, represented by medusoids, annelids, *Lingula*, bivalves, limulids, crustaceans and fish. Land plants are also abundant, comprising horsetails, ferns, and gymnosperms (*Voltzia*). Some animals (e.g. *Lingula*, bivalves) are preserved in life position. Many arthropods (limulids, crustaceans) show, in the same horizon, different larval stages, adults, and moults. Insect egg-strings (Pl. 1, fig. 4), coprolites, and trace fossils are also present. The biota is rich in individuals but poor in species.

TABLE 1. Mid-Tiassic stratigraphy of the northern Vosages, France. *Rosamygale grauvogeli* gen. et sp. nov. occurs in the Grès à meules, the lower part of the Grès à Voltzia of the Buntsandstein Supérieur.

STRATIGRAPHY OF THE BUNTSANDSTEIN IN THE NORTHERN VOSGES (FRANCE)										
MEMBERS AND FORMATIONS				Thickness (m)	Palaeo- environ- ment	Palaeontology				
French nomenclature		German nomenclature				Plants	Inverte- brates	Verte- brates	Traces	
MUSCHELKALK INF.	Niveaux dolomitiques supérieurs		Mittlere und obere Abteilung der Wellenkalkgruppe	15-20	shallow marine		•	•	••	
	Couches à Myacites		Myacitenbänke	30		•••	•	••		
	Grès coquillier		Muschelsandstein	20-30		•••	•	••		
BUNTSANDSTEIN SUPERIEUR	GRÈS À VOLTZIA	Grès argileux		Lettenregion	7-8	deltaic to marine	•	•••	•	•••
		Grès à meules		Werkstein	10-12	coastal fluvial to deltaic	•••	•••	•••	••
	Couches intermédiaires supérieures		Obere Zwischenschichten		15-25	inland fluvial	•	•		•
	Couches intermédiaires inférieures		Untere Zwischenschichten		30					
BUNTSANDSTEIN MOYEN	Zone-limite violette		Violette Grenzzone	4-5	palaeosol	•				
	Conglomérat principal		Haupt konglomerat	20	inland fluvial					
	Grès vosgien supérieur		Oberer Vogesensandstein	150-200		•		•		
	Grès vosgien inférieur		Unterer Vogesensandstein	150-200						
BUNTSANDST. INFÉRIEUR	Grès d'Annweiler		Annweiler Sandstein	50-60	fluvial and playa lake				•	

PALAEOECOLOGY

Evidence from the sediments and fossils points to a deltaic sedimentary environment (Gall 1971, 1983). The sandstone facies corresponds to point bars deposited in strongly sinuous channels; the clay lenses represent the settling of fine material in brackish ponds; the calcareous sandstone results from brief incursions of sea water during storms. The palaeogeographical position for the localities, in the subtropics near the eastern edge of Pangaea, together with the red-beds and the xeromorphic nature of the land flora (Gall 1983), suggest a semi-arid climate in the region. However, the low-

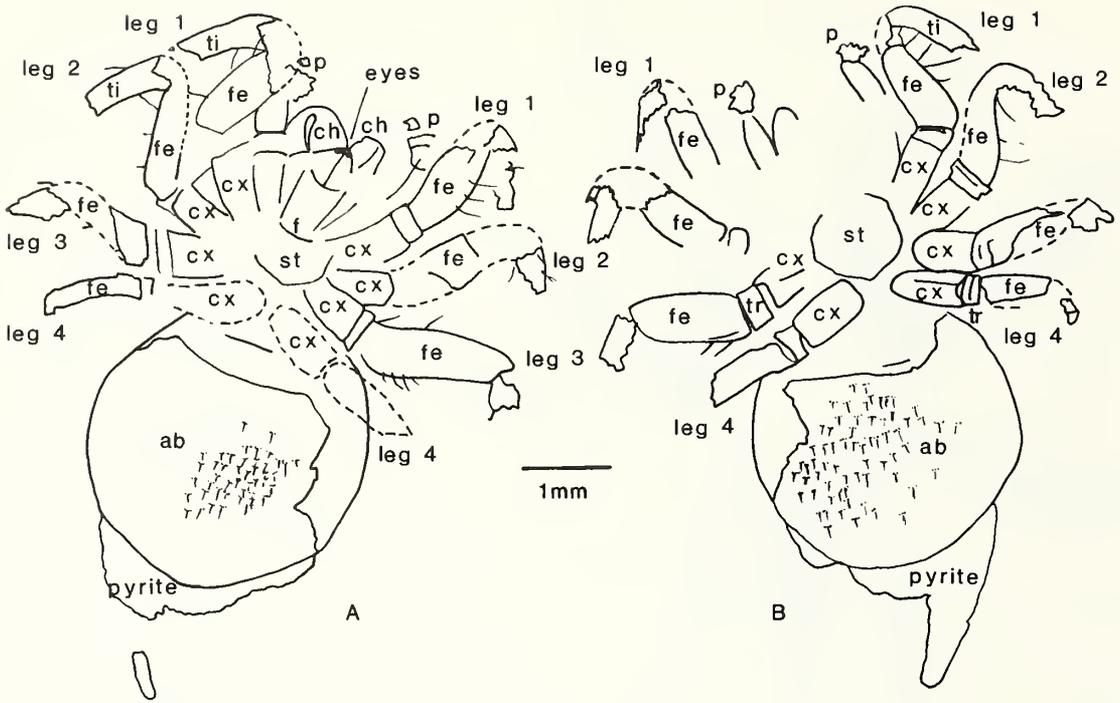


TEXT-FIG. 1. Reconstruction of juvenile *Rosamygale grauvogeli* gen. et sp. nov., based on type series and comparison with living hexathelids. A, dorsal. B, ventral.

lying, deltaic situation suggests that aridity was not severe locally. The climate was probably seasonal; the pools filling during the wet season and evaporating as the dry season approached. Eventually, the pools where the clay lenses were deposited became shallower and dried out completely. This is supported by the presence of desiccation cracks, reptile footprints, salt pseudomorphs and land plants in life position at the top of each clay lens. Also, moving upwards through each lens a transition from aquatic to terrestrial biota is observable (Gall 1983).

The excellent preservation of the terrestrial biota in the clay lens facies, the low energy of deposition, and the presence of *in situ* plant roots indicate that these organisms lived very near the water bodies. No evidence conflicts with the conclusions of Gall (1971, 1983) that the aquatic fauna lived and died *in situ* (i.e. it is autochthonous), and that the preserved terrestrial fossils crawled or fell from the adjacent terrestrial environment to their place of entombment. There is no evidence of drifting of the fossils by water currents. The kinds of plants and animals present, *Lingula's in situ* position, together with the impoverished species diversity, strongly suggest a brackish water community. The euryhaline fauna is typical of transitional environments such as lagoons, pools, and swamps between land and sea, and the dwarfed nature of the stenohaline marine forms supports this (Gall 1983). Such a fauna is adapted to fluctuating conditions of salinity, oxygenation, desiccation, etc. The composition of such restricted communities shows a striking continuity during the course of Earth history.

The spiders evidently inhabited the margins of the stagnant pools where a sparse vegetation grew,



TEXT-FIG. 2. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR11; holotype, part; explanatory drawing for Pl. 1, fig. 1. B, AR11; holotype, counterpart; explanatory drawing for Pl. 1, fig. 3.

grew, dominated by bushes of *Voltzia*, and reed beds formed by horsetails (*Schizoneura*, *Equisetites*). *Rosamygale grauvogeli* is the only known species of spider living in this Triassic landscape.

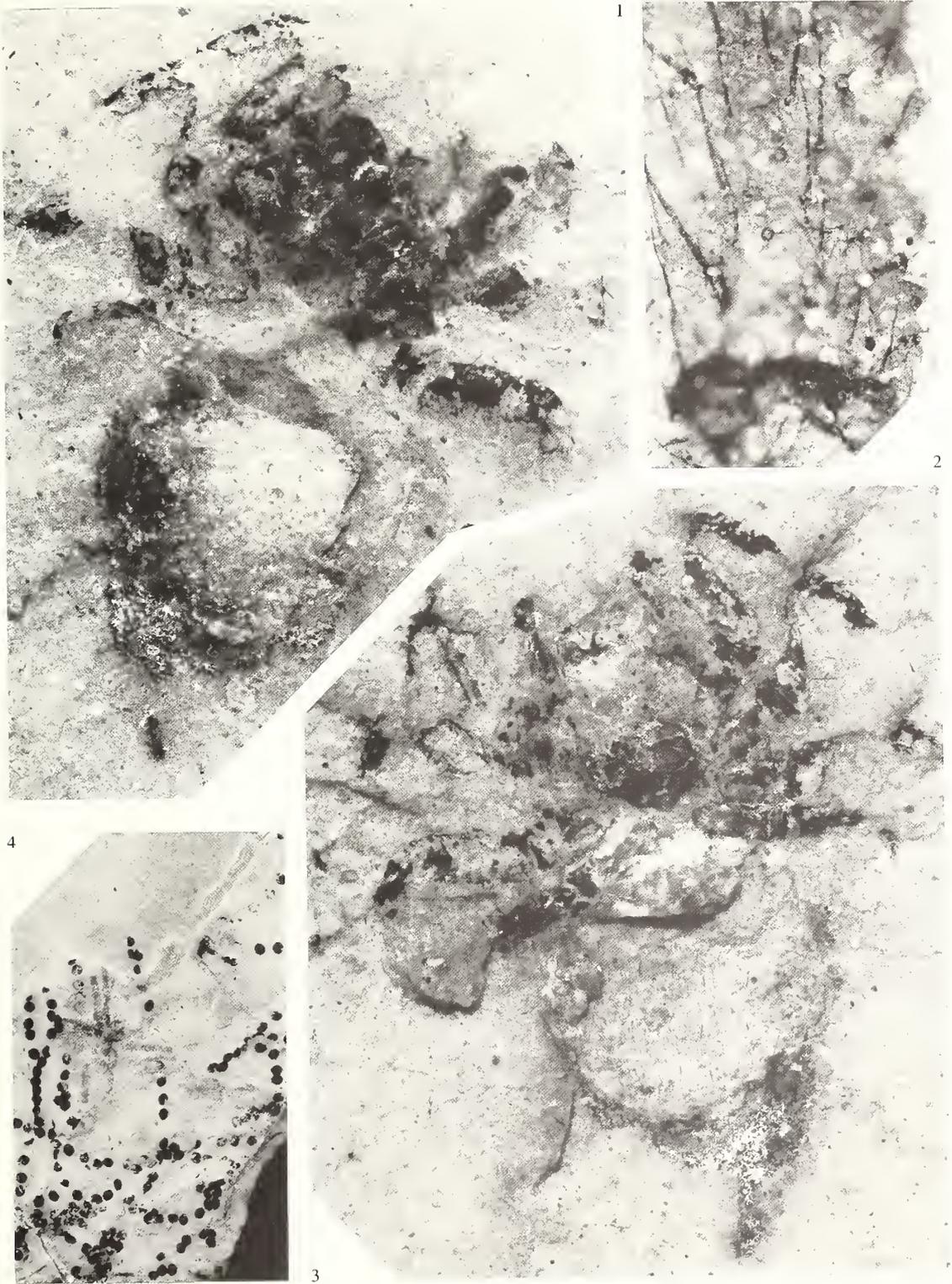
TAPHONOMY

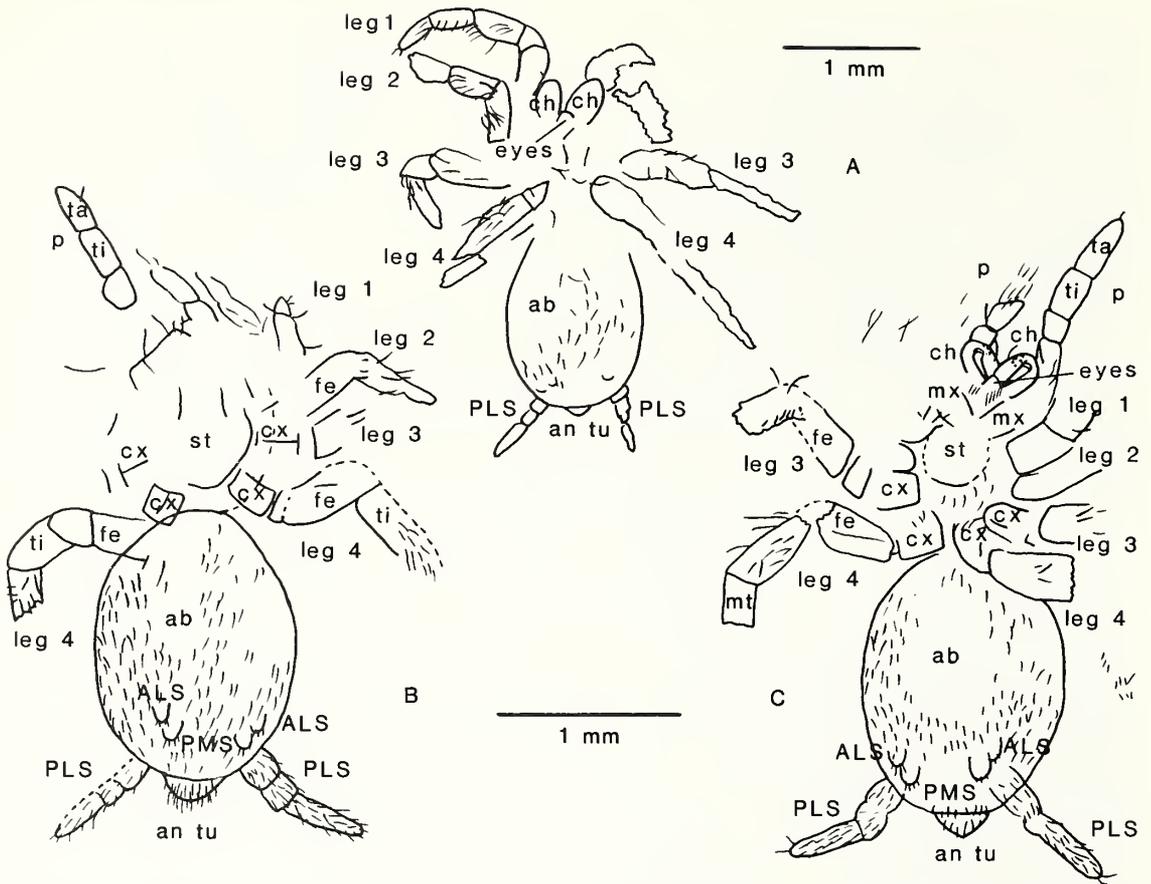
Drying-up of the pools led to death of the aquatic fauna. The abundance of estheriids is significant in that these crustaceans are adapted to swift completion of their life cycle in temporary water bodies. Regular high evaporation rates of the water bodies also favoured deoxygenation, consequent mass mortality of the aquatic fauna and the rapid proliferation of microbial films. Such films may have shielded the carcasses from scavenging activity and created, by production of mucus, a closed environment inhibiting the decomposition of organic material. Later, the deposition of a new detrital load (clay, silt) buried the microbial films and the organisms (Gall 1990).

There are three ways in which the spiders could have been transported to the site of deposition in the ephemeral pools: by water, land, or air. They may have been washed out of the watercourse

EXPLANATION OF PLATE I

Figs 1-4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR11; holotype, part; see Text-fig. 2A for explanation, $\times 15$. 2, AR2; left femur, distal to top, showing various sizes of setae, note similarity of setal follicles to possible trichobothrial bases, $\times 200$. 3, AR11; holotype, counterpart; see Text-fig. 2B for explanation, $\times 15$. 4, PC14; poorly preserved specimen showing common association in rock with strings of insect eggs, *Monilipartus*, $\times 8$.





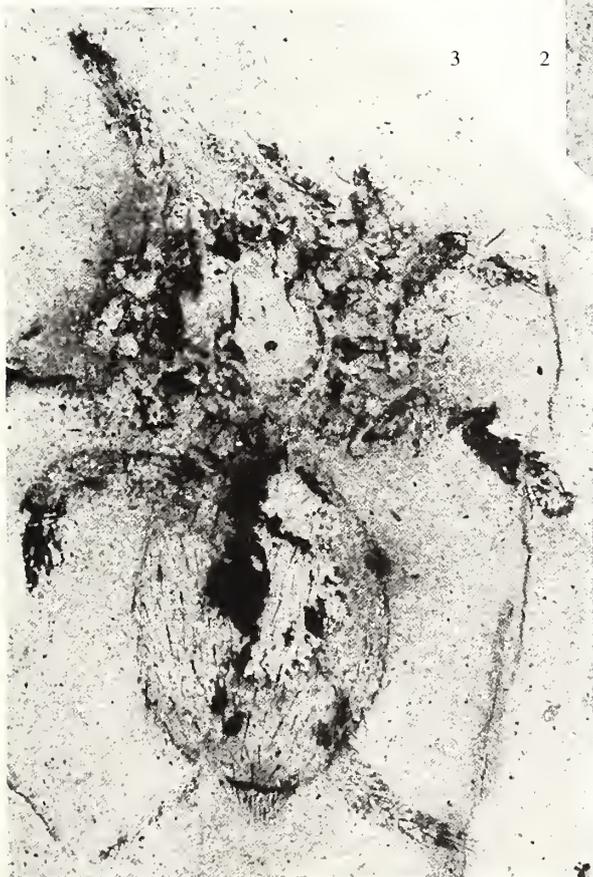
TEXT-FIG. 3. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR5; part; explanatory drawing for Pl. 2, fig. 1. B, AR8; paratype, part; explanatory drawing for Pl. 2, fig. 2. C, paratype, counterpart; AR8; explanatory drawing for Pl. 2, fig. 2.

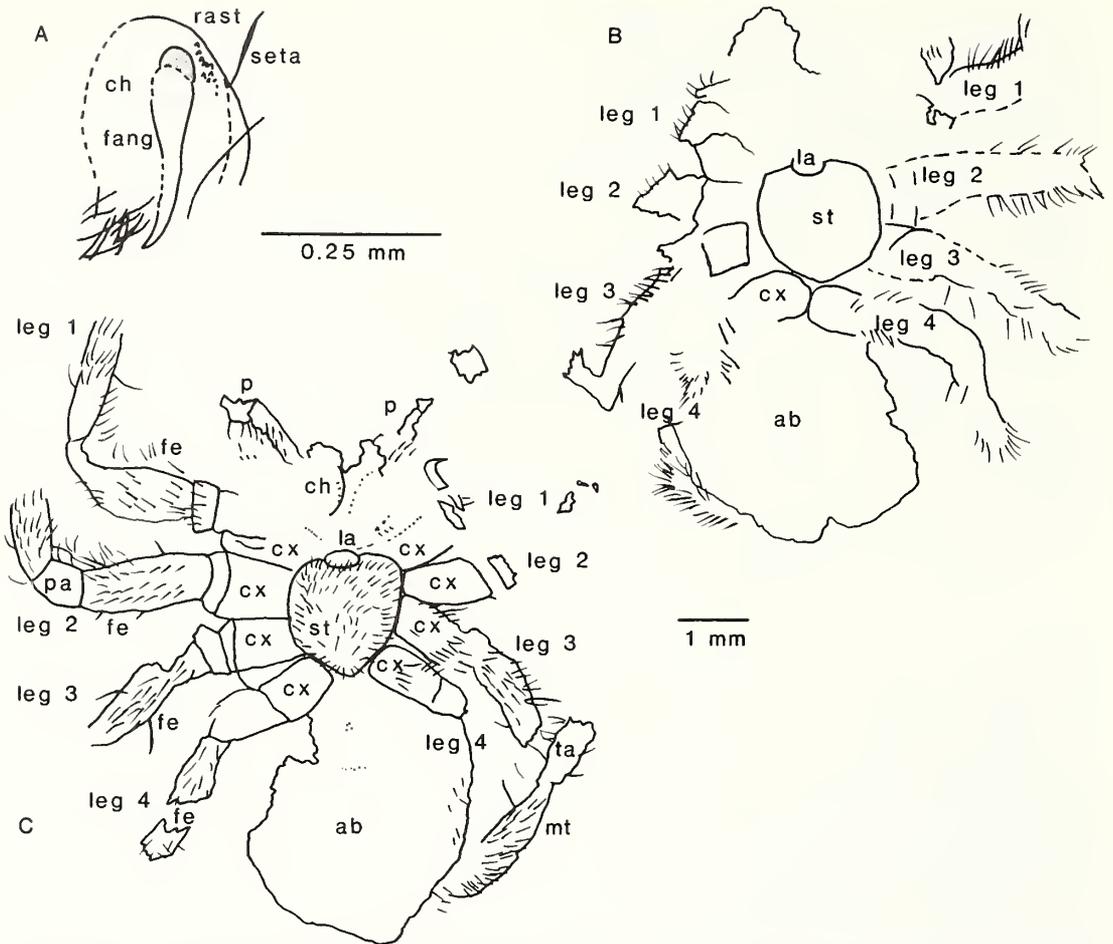
banks, perhaps still enfolded in the silk of their burrow linings or funnel webs; they may have been wandering free at the time and became trapped in the water, mud, or mucilage of the desiccating pools; they may have fallen from the air into the water or mud.

Water. Some of the fossils are preserved with their legs outstretched (Pls 2, 4), typical of spiders which have died in water, whereas the others (Pls 1, 3) show a death attitude with legs flexed around the body; none appears to be distorted by entanglement in silk. The energy of the water in the desiccating pools was low; although the spiders could have been washed in from some distance away and settled out in the lower energy environment, it is likely that there would be some evidence of silk adhering to the bodies, even if only as a distortion on the sediment surface. Extant

EXPLANATION OF PLATE 2

Figs 1-4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France; juvenile specimens. 1, AR5; part; see Text-fig. 3A for explanation, $\times 22$. 2, AR8; paratype, part; see Text-fig. 3B for explanation, $\times 30$. 3, AR8; paratype, counterpart; see Text-fig. 3C for explanation, $\times 30$. 4, AR10; counterpart to specimen figured in Gall (1971, pl. 6, fig. 1), $\times 20$.





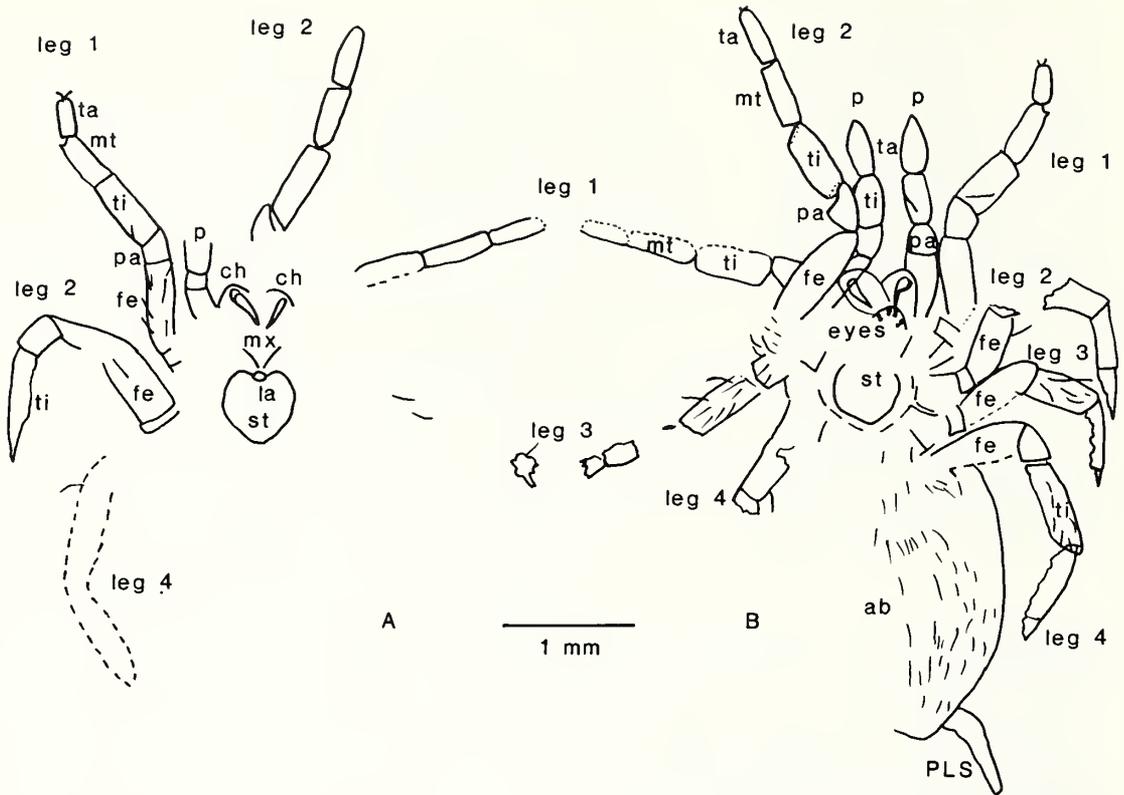
TEXT-FIG. 4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR8; chelicera on left of part; explanatory drawing for Pl. 3, fig. 1. B, AR1; paratype, part; explanatory drawing for Pl. 3, fig. 2. C, AR1; paratype, counterpart; explanatory drawing for Pl. 3, fig. 3.

mygalomorphs living in semi-arid environments commonly construct intricate devices such as bathplug-like trap-doors, levees, and turrets to prevent the inundation of their burrows during flash floods (Main 1982). It seems unlikely that *Rosamygale* could have been washed in during flood periods, and remained intact with little decay, throughout a period of well-oxygenated conditions when an aquatic biota flourished in the water. Moreover, there is no evidence of any other organism now preserved in this facies having been washed in from very far away.

EXPLANATION OF PLATE 3

Figs 1-4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR8; chelicera on left of part (see Pl. 2, fig. 2), mesial to right; see Text-fig. 4A for explanation, $\times 200$. 2, AR1; paratype, counterpart; see Text-fig. 4C for explanation, $\times 11$. 3, AR1; paratype, part; see Text-fig. 4B for explanation, $\times 11$. 4, AR8; chelicera on right of part (see Pl. 2, fig. 2), mesial to left, note patch of triangular teeth mesial to base of fang and part of long setae (both at top left), maxillary setae at bottom, $\times 200$.





TEXT-FIG. 5. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR12; paratype, part; explanatory drawing for Pl. 4, fig. 3. B, AR12; paratype, counterpart; explanatory drawing for Pl. 4, fig. 2.

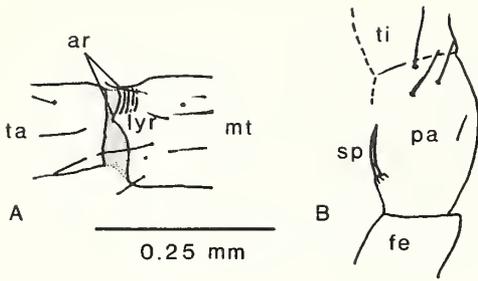
Land. Entrapment of wandering spiders in mud and mucilage is dependent on the habits of *Rosamygale*. During their lives (which may be a number of years for females, over 20 years in some species (Baerg and Peck 1970)), mygalomorphs leave the safety of the nest only for dispersal when young or, if male, to find a mate. Prey capture may involve a dash partly out of the nest; some species make radiating 'trip-lines', others arrange twigs in a radiating pattern from the nest entrance, the purse web of *Atypus* allows the capture of prey from entirely within the closed sac-like web, and other species lure prey inside the nest burrow (Main 1981, 1982, 1986; Coyle 1986). All of these strategies enable mygalomorph spiders to spend the least amount of time and distance outside the web. Therefore, it would normally either be during times of dispersal of young or adult male wandering that a mygalomorph spider would be likely to encounter a natural trap. Main

EXPLANATION OF PLATE 4

Figs 1-4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR12; counterpart; distal metatarsus and tarsus of left side of specimen (see fig. 3), note emarginated distal metatarsus with thorn (bottom left), pectinate paired claws (left one poorly preserved), and small median claw (below right paired claw), $\times 200$. 2, AR12; paratype, part; see Text-fig. 5B for explanation, $\times 22$. 3, AR12; paratype, counterpart; see Text-fig. 5A for explanation, $\times 22$. 4, AR5, counterpart, cheliceral fang, $\times 200$.



SELDEN and GALL, *Rosamygale*



TEXT-FIG. 6. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR12; part; distal metatarsus and proximal tarsus of leg 2 of left side of specimen; explanatory drawing for Pl. 5, fig. 3. B, AR8; part; palp patella of left side; explanatory drawing for Pl. 4, fig. 3.

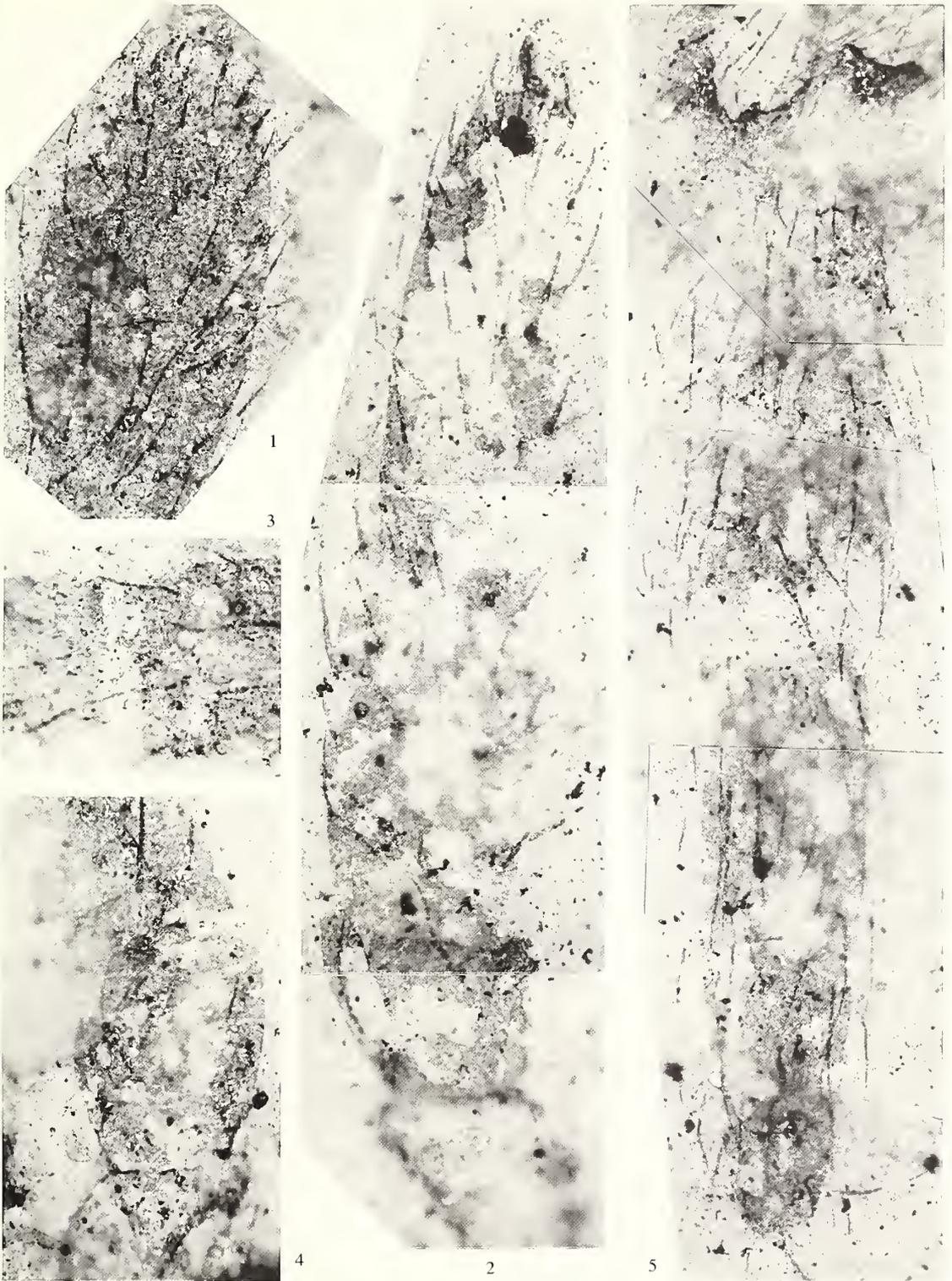
(1982) pointed out that most mygalomorphs adopt strategies for minimizing risk of predation and desiccation during these vulnerable periods. The timing of dispersal and wandering is closely linked with the rainy season: it is easier for the young to start constructing burrows in wet ground, and desiccation of spiders and eggs is avoided when reproduction takes place in humid conditions. Many arid habitat species aestivate, so male wandering must synchronize with female activity. Most Australian mygalomorphs disperse by running along the ground to the nearest suitable new nest site. Clustered populations occur in these species, which may be advantageous if the habitat is suitable (Main 1982). It is likely that male or immature specimens of *Rosamygale* were in the process of dispersal or wandering during a wet season or following rain when they became trapped in the desiccating pools. However, females living in an area which was inundated by standing water would eventually evacuate their tubes, might be unable to reach dry land, and could thus become trapped in the same manner.

Air. Floating on gossamer threads (ballooning) occurs among small araneomorph spiders (principally the erigonine linyphiids in the northern hemisphere), and is also practised by some mygalomorphs. Ballooning has advantages for dispersal in patchy or unstable environments. Mygalomorphs balloon by dangling from a twig on a silken thread until the wind breaks the thread and the spider takes to the air. In contrast, araneomorph ballooners may remain on the substrate, and spin special gossamer threads into the air until the air currents are sufficiently strong, when they let go (Coyle 1983, 1985). The mygalomorph method appears to be more primitive than that of the araneomorphs, since no special gossamer, only dragline silk, is used, and there is little control over the take-off in mygalomorphs (it simply occurs when the silk breaks). An evolutionary progression can be envisaged from dispersal by climbing up vegetation and dropping from draglines, through accidental windblown travel during drops ('rappelling'), to purposeful construction of ballooning platforms as observed in *Sphodros* by Coyle (1983). Coyle (1983) also reported that the mygalomorph ballooning method has been observed in some primitive araneomorphs. Silk has a high tensile strength (it does not break easily) so larger mygalomorphs would be at an advantage during take-off.

Since there was abundant vegetation surrounding the desiccating pools in which the Grès à Voltzia spiders became trapped, it is quite possible that they dropped or were blown from the

EXPLANATION OF PLATE 5

Figs 1–5. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR12; part; palp tarsus (see Pl. 4, fig. 2), $\times 200$. 2, AR8; part; palp of right side, distal femur to tarsus with single claw (see Pl. 2, fig. 2), $\times 200$. 3, AR12; part; distal metatarsus and proximal tarsus of leg 2 of left side of specimen (see Pl. 4, fig. 2), distal to left, superior to top, showing typical superior bicondylar hinge joint and lyriform; see Text-fig. 6A for explanation, $\times 200$. 4, AR8; part; palp patella of left side; see Text-fig. 6B for explanation, $\times 200$. 5, AR8; part; spinnerets of right of specimen (see Pl. 2, fig. 2), ALS (top right), PMS (top centre), and PLS; note distribution of spigots (setae with bulbous bases, see Pl. 6, fig. 4) especially at distal ends of spinnerets, lateral to right, $\times 200$.



SELDEN and GALL, *Rosamygale*

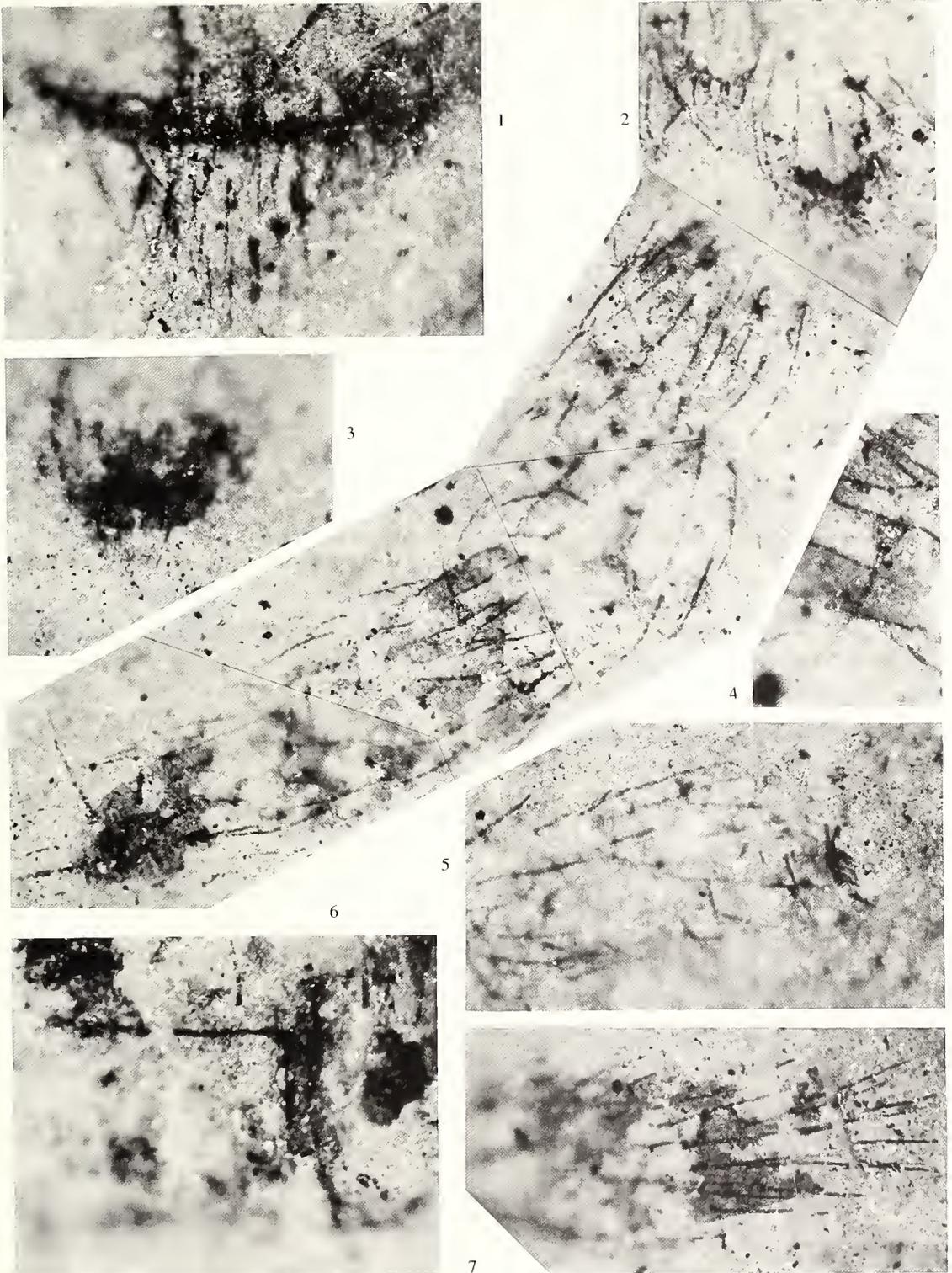
vegetation into the mud. Could *Rosamygale* spiderlings have ballooned? It is thought that mygalomorphs balloon less commonly than araneomorphs not only because of differences in phenology and behaviour but also because of the larger size of most mygalomorph species compared to araneomorphs which balloon regularly. This question was addressed by Coyle *et al.* (1985), who measured the masses and volumes of the ballooning mygalomorphs *Sphodros* and *Ummidia* in comparison with ballooning araneomorphs and the non-ballooning mygalomorph *Antrodiaetus*. They found that whereas the frequency distribution of the ballooning spiderlings was strongly skewed towards those with lighter mass, heavier spiders, up to 6 mg, were also found ballooning. Using the method of volume estimation described in Coyle *et al.* (1985) (volume of a cylinder of body length and diameter carapace width), the *Rosamygale* specimens fall between 1.9 and 27.4 mm³. Using the regression results in Greenstone *et al.* (1985), the estimated masses of the *Rosamygale* specimens would be between about 2 mg and (by extrapolation) 32 mg. However, the masses of the mygalomorphs measured by Coyle *et al.* (1985) were about 35% less than the masses estimated from the regression graph of Greenstone *et al.* (1985). If such were the case in *Rosamygale*, then their masses would have been between about 1.4 and 20.8 mg. Notwithstanding the large mass at one end of this range, it falls within the observed range of mass of ballooning spiders: using sticky traps, Greenstone *et al.* (1987) found that the majority of aeronauts weighed between 0.2 and 2 mg but that the observed range was 0.2 to 25.5 mg. In another study, Dean and Sterling (1985) recorded spiders over 15 mm in length ballooning in Texas. Therefore, it is possible that *Rosamygale* used walking, rappelling, and/or ballooning for dispersal, although there is no evidence that the fossil spider ballooned.

After death in the water, it is likely that terrestrial animals like the spiders and insects would have floated on the surface of the water for some time. Some carcasses were trapped by the mucilage surrounding the insect eggs (Pl. 1, fig. 4). When the water underwent partial desiccation, the bodies of the animals became stuck in the muddy bottom. Subsequently, an influx of detrital mud covered the carcasses; this rapid sedimentation ensured exceptionally good preservation of the fossils.

The spiders are preserved as brown organic cuticle flattened by sediment compaction in most cases. Pyrite occurs in some specimens (Pl. 1, figs 1, 3), which suggests reducing conditions. A peculiarity of a few of the specimens (e.g. Pl. 1, figs 1, 3) is the three-dimensional preservation of the abdomen cast in calcium phosphate. Spider abdomens are covered only in thin cuticle to enable distension, and they are liable to burst even due to changes in osmotic properties of the medium. They are unlikely to be preserved three-dimensionally unless mineralization is rapid. Also, phosphate is a rare casting material in invertebrates. Though phosphate is present in organic tissues, when liberated it is swiftly recycled by other organisms. However, because of the exceptional taphonomic conditions present in the Grès à meules, rapid phosphatization could occur. Phosphatization requires an oxygen-depleted environment and abundant organic matter (Prévôt and Lucas 1990). The microbial film would have sealed the phosphates being released by the decay of the organic matter in the spiders' abdomens, preventing its re-use by other organisms. Acidic conditions produced by decaying organic matter would have released free calcium which combined

EXPLANATION OF PLATE 6

Figs 1–7. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR8; counterpart; anal tubercle (see Pl. 2, fig. 3), ×200. 2, AR8; part; spinnerets of left of specimen (see Pl. 2, fig. 2), ALS (top left), PMS (top right), and PLS; note two segments in basal half of PLS revealed by change in direction of setae, and distribution of spigots (setae with bulbous bases, see fig. 4) especially at distal ends of spinnerets, lateral to left, ×200. 3, AR8; part; anal tubercle (see Pl. 2, fig. 2), ×200. 4, AR8; part; spigot from proximolateral side of distal segment of PLS (see fig. 2), note bulbous base, collar, and setiform hair projecting at high angle to normal setae, lateral down, distal to right, ×400. 5, AR5; counterpart; distal tarsus with pectinate paired claw, ×200. 6, AR8; counterpart, coxa of fourth leg on right of specimen (see Pl. 2, fig. 3), proximal to left, anterior to top, note costa coxalis terminating (on right) in anteroinferior articulation of coxa–trochanter joint, ×200. 7, AR8; counterpart; distal end of PLS of right of specimen (see Pl. 2, fig. 3); compare with part (fig. 2), ×200.



with phosphate to form apatite. Once the phosphatic nodule had formed, it would have prevented flattening of the abdomen during sediment compaction.

MATERIAL AND METHODS

Of thirteen specimens available for study, numbered AR1–12 and PC14, three proved not to be spiders: AR3 is an insect, and AR6 and AR9 are insufficiently preserved for certain identification. The ten spider fossils are preserved as small pieces of cuticle on and just within the fine clayrock. Mainly setae and spines are preserved, which provide an outline of the legs and body, and also of other sclerotized organs such as the chelicerae and parts of the carapace and abdomen. Splitting of the rock has resulted in part of each specimen being preserved on one slab, and part on another. These are termed part and counterpart for convenience, but do not correspond to dorsal and ventral, which are commonly indistinguishable. Comparison of part and counterpart reveals that most of the cuticle is preserved on one slab or the other (compare Pl. 2, figs 2–3 and Pl. 6, figs 2, 7). In addition, a little pyrite is present, and the abdomens and parts of the prosomae of two specimens are infilled with calcium phosphate (Pl. 1, figs 1, 3). Apart from the mineralization, the style of preservation is strongly reminiscent of that of the Lower Cretaceous spiders described from the Sierra de Montsech, Spain (Selden 1989, 1990). Similar methods of study to those used for the Montsech spiders were employed: examination and photography under alcohol at low magnification (less than $\times 200$ on the plates), and oil immersion reflected light microscopy for higher magnification ($\times 200$ or greater on the plates). Drawings were made from the photographs.

Abbreviations used in the Text-figures

ab	abdomen	p	palp
ALS	anterior lateral spinneret(s)	pa	patella
an tu	anal tubercle	PLS	posterior lateral spinneret(s)
ar	articulation	PMS	posterior median spinneret(s)
ch	chelicera	rast	rastellum
cx	coxa	sc	sclerite
f	fovea	sp	spine
fe	femur	st	sternum
la	labium	ta	tarsus
lyr	lyriform organ	ti	tibia
mt	metatarsus	tr	trochanter
mx	maxilla		

MORPHOLOGICAL INTERPRETATION

The reconstruction (Text-fig. 1) is based on morphological details present in the best-preserved, type series of specimens. In addition, information from living hexathelid spiders (e.g. those depicted in Forster and Wilton 1968) was taken into consideration where necessary.

The specimens range up to 6.8 mm in body length (AR1, including chelicerae); some of the best-preserved specimens, AR8 and AR12, are only 2.8 mm long (including chelicerae and anal tubercle). These small specimens are considered to be juvenile on account of the large anal tubercle, widely separated spinnerets (relative to the size of the abdomen), and the lack of spinose armature on the legs. Their palps are well preserved but show no signs of adult male modification. The palps of larger specimens AR1 and AR11, however, appear to end abruptly. This may be due to different preservation of male palps (see below).

The carapace is poorly preserved, only the cephalic lobe and anterior parts being visible in some specimens. The radial arrangement of the coxae suggests that the carapace was broadly oval to subcircular in life. Some unsculptured cuticle of the anterior part of the carapace is present in AR11. The cephalic area is marked by curved sulci which diverge anteriorly, together forming a parabola. AR8 and AR11 show a distinct, procurved line in the position which would be occupied by the fovea (Pl. 1, fig. 1; Pl. 2, fig. 2; Text-figs 3–4). These are not deep, and merge gradually into lines running

towards the anterolateral corners of the carapace. On this evidence, the fovea is reconstructed as transverse and procurved. Longitudinal cracks in AR11 suggest that the cephalic area was raised in life, but not strongly. The ocular region is preserved as a small patch of dark cuticle between the bases of the chelicerae (Pl. 1, fig. 1; Pl. 4, fig. 2). Some specimens show evidence of eyes (AR5, AR11, AR12), from which it is deduced that probably eight were present in two recurved rows. The darkness of the cuticle on the ocular area, which is noticeable even in specimens which lack cuticle of the remainder of the carapace, suggests it was thicker, and possibly raised, in life.

The outline of the sternum is well preserved in a number of specimens (Pl. 1, figs. 1, 3; Pl. 2, fig. 3; Pl. 3, figs 2–3; Pl. 4, fig. 2). It is approximately subcircular, but with a recurved anterior border which accommodates the broad labium (seen in AR1, Pl. 3, figs 2–3). The posterior of the sternum is produced slightly (but does not project between the fourth coxae), giving the whole plate a heart-shaped appearance. At each place where a coxa abuts the sternum, the sternal edge is slightly straightened, giving a slight scalloped appearance. Sigilla cannot be definitely determined in any specimen.

The chelicera (Pl. 2, figs. 2, 4; Pl. 3, figs 1, 4; Pl. 4, figs 2–4) is oval in outline, and broadest distal to the midlength. The chelicerae diverge, but lack flat mesial faces adpressed to each other, which are common in many mygalomorphs. The orthognath fang arises from an anteroinferior position; it is gently curved and almost as long as the body of the chelicera. Small patches of dark cuticle alongside the fang indicate the presence of a row of small teeth. On AR1 and AR8 (Pl. 3, figs 1, 4), an area of dark triangular cuticle patches on the chelicera mesial to the fang base is interpreted as a small rastellum of short teeth. No rastellar lobe is apparent. AR8 also shows a long, gently sinuously curved bristle arising from the mesial face of the chelicera (Pl. 3, figs 2, 4).

The maxilla does not bear a lobe; it is commonly seen as a strong line of dark cuticle (Pl. 4, fig. 3), which suggests that cuspules were present in life. Plate 3, figure 4 shows a row of long bristles arising from the maxilla. The remainder of the palp in small specimens is a typical juvenile palp; patella, tibia, and tarsus are well preserved in a number of specimens. The palp tarsus bears a single claw which appears to be non-pectinate (Pl. 5, fig. 2). In AR8, the palp patella shows a strong, curved spine on the inferior/mesial surface (Pl. 5, fig. 4; Text-fig. 6B); this is very similar to the curved spine present on the tibia of leg 1 of males of many mygalomorphs, used as a clasper during mating. The palps of AR1 and AR11 are not well preserved in these specimens, even though the other appendages are. In the palps of AR1 and AR11 (Pl. 1, figs 1, 3; Pl. 3, figs 2–3), a long podomere (i.e. the femur or the tibia) has an oddly shaped, short piece of the next distal podomere attached, and no more is preserved. It seems strange that the remainder of the palp is not preserved; possibly these are adult males, and the distal parts of the palp were turned laterally so that they are now obscured by the first walking legs; this is supported by the preservation of AR11 (Pl. 1, figs 1, 4; Text-fig. 2). The stiff bristles on the walking legs of the larger specimens (see below) suggest these are males; they could be subadult males, which have swollen but not erupted palpal tarsi, and there is evidence of penultimate males of *Microhexura* wandering or ballooning (Coyle 1981).

The walking legs appear to be approximately equal in length, although the distal podomeres of legs 3 and 4 are not well preserved in any specimen. They are about two-thirds of the length of the body. Leg 1 is slightly shorter than leg 2 in AR12 (Pl. 4, fig. 2, an immature), tarsus 1 being shorter than metatarsus 1, whereas these podomeres are nearly equal in length in leg 2. The podomeres show few modifications, being typical in morphology for the suborder (see, for example, the metatarsus–tarsus joint in Pl. 5, fig. 3). The coxae are well preserved and show a distinct costa coxalis which runs along the anteroinferior surface, terminating in the anteroinferior coxa–trochanter articulation (Pl. 2, fig. 3; Pl. 6, fig. 6). The trochanter shows a groove running anteroposteriorly along the inferior surface. On AR11, this groove appears closer to the distal border of the podomere on more anterior trochanters. The legs are clothed in setae, which are arranged in rows on the femora of larger specimens (Pl. 3, fig. 3). Long, thin, curved bristles, arising at a high angle from the podomere, are numerous on post-trochanteral podomeres of the walking legs, particularly of larger specimens (Pl. 3, figs 2–3; Pl. 4, fig. 2). No definite trichobothria have been observed (it is assumed that trichobothria were present), but some of the setal bases bear a

great similarity to trichobothrial bases (Pl. 1, fig. 2). Some thicker bristles or spines can be seen on the palp patella of AR8 (Pl. 5, fig. 4). Metatarsus 1 of AR12 (Pl. 4, figs 1–2) is emarginated laterally and bears a distinct thorn.

The outline of the abdomen is preserved in most specimens. It is oval in outline, broadest at midlength, and is rather broader in larger specimens presumably due to their greater maturity. The abdomen is clothed in setae. These appear fine in smaller specimens, but relatively shorter in larger ones. The setae arise from small, slightly recurved transverse cuesta-like grooves, seen in internal mould in AR11. AR12 (Pl. 4, fig. 2) shows two pairs of slightly larger setae on the dark patch of cuticle (see later). A patch of dark cuticle covers the anteromedian third of the abdomen. The dark cuticle is oval in shape, but irregular and is not clearly defined at the edges; it is presumed to have been dorsal in life. In AR11 (Pl. 1, figs 1, 3), the abdomen of which is preserved primarily as an internal mould, there are no breaks of slope which would clearly indicate sclerites. Darker colouration in fossil arthropods results from a thicker cuticle (which is commonly correlated with sclerotization and pigmentation in life), for example the *Gilboa* specimens (Selden *et al.* 1991) and the Montsech spiders (Selden 1990). Mygalomorph abdomens usually bear a thin cuticle, though some (e.g. Atypidae, Mecicobothriidae, Microstigmatidae) have one or more dorsal sclerites. When present, pigmentation in living mygalomorph abdomens is not cuticular. So, it is considered that the dark area of cuticle in *Rosamygale* represents sclerotization in which true tergites are not clearly defined. The larger specimens (AR1, Pl. 3, figs 2–3; AR11, Pl. 1, figs 1, 3) do not show the dark area clearly, so it is possible that the sclerotization was present only in early juveniles.

The small specimen AR8 shows the juvenile arrangement of the spinnerets and anal tubercle. In this specimen, the anal tubercle is large, and on either side arise long PLS (Pl. 2, figs 2–3). The PLS is two-thirds the length of the abdomen. The distalmost segment of the PLS is digitiform, half the length of the whole appendage, and there is no evidence of pseudosegmentation. Consideration of the trends of the preserved setae indicates that two segments, approximately equal in length, are probably present proximal to the distalmost segment (Pl. 5, fig. 5; Pl. 6, fig. 2). Thus, it is probable that three segments are present. Anterior to the base of the PLS are two pairs of short spinnerets, the ALS and PMS (Pl. 2, figs 2–3; Pl. 5, fig. 5; Pl. 6, fig. 2). The ALS appear to be very slightly smaller than the PMS; there is no evidence of more than one segment in each of these spinnerets. The anal tubercle (Pl. 6, figs 1–2) is visible in some larger specimens (AR11), but is much smaller in relation to the size of the abdomen than in the juvenile. On all spinnerets, some setae can be seen by their bulbous bases to be modified into silk-producing spigots; these occur distally on ALS and PMS, and distally and laterally along the length of the PLS (Pl. 5, fig. 5; Pl. 6, figs 2, 4, 7).

DISCUSSION

Phylogeny

Raven (1985) produced an important revision of the systematics of the Mygalomorphae, dividing the infraorder initially into two microorders: Tuberculotae and Fornicephalae. He placed Antrodiaetidae, Atypidae, Migidae, Actinopodidae, Ctenizidae, Idiopidae, and Cyrtoucheniidae in Fornicephalae, and all other families in Tuberculotae. Eskov and Zonshtein (1990) re-examined relationships within the Mygalomorphae based on new information from Cretaceous mygalomorphs and a critical assessment of Raven's (1985) character analysis. They recognized two superfamilies within the infraorder Mygalomorphae: Atypoidea (including Atypidae, Mecicobothriidae, and Antrodiaetidae) and Theraphosoidea. At a crude level, the major difference between these schemes lies in Eskov and Zonshtein's allying of Mecicobothriidae with Antrodiaetidae and Atypidae, and, in contrast, their placement of Cyrtoucheniidae near to Hexathelidae and Dipluridae. Our find of a new, older mygalomorph in the Triassic does not have great bearing on these phylogenetic schemes. However, being twice as old as any previously described mygalomorph, the position of *Rosamygale* in the phylogenetic scheme of Mygalomorphae is interesting. The characters of *Rosamygale* which are important in phylogenetic discussion are: the six functional spinnerets, including single-segmented ALS and PMS, and three-segmented PLS with a digitiform

distal segment; the transverse, procurved fovea; lack of maxillary lobes; the wide labium; the large, irregular, dorsal abdominal sclerite; the few, broad teeth constituting a cheliceral rastellum; the tarsi lacking pseudosegmentation, claw tufts and scopulae, with three claws not on a lobe, and pectinate paired claws with numerous teeth.

Presence of six spinnerets is a primitive feature within the mygalomorphs. The ALS are lost in many groups; their retention in Atypidae, Antrodiaetidae, Hexathelidae, Mecicobothriidae, and Microstigmatidae is considered a plesiomorphic condition (Raven 1985). While acknowledging the plesiomorphic nature of ALS retention, Eskov and Zonshtein (1990) used the possession of four and six spinnerets to define theraphosoids and atypoids respectively. However, these authors acknowledged an independent reduction in some atypoids and the retention of six spinnerets by some archaic theraphosoids. The presence of three segments in the PLS was considered plesiomorphic by Raven (1985). Eskov and Zonshtein (1990), on the other hand, proposed that the four-segmented (excluding pseudosegments) PLS possessed by some members of the Mecicobothriidae and Atypidae was the plesiomorphic condition, and therefore that the three-segmented PLS was separately developed by all Theraphosoidea, Antrodiaetidae, and the majority of atypids and mecicobothriids. The digitiform distal segment of the PLS was regarded as plesiomorphic by Raven (1985), and this conclusion was not contradicted by Eskov and Zonshtein (1990). So, we consider that the characters of the spinnerets in *Rosamygale* are in the most plesiomorphic state for the Mygalomorphae, the only possible exception being the three-segmented nature of the PLS.

The shape of the fovea has been used to define a variety of groups within the Mygalomorphae; among those families with six spinnerets, a transverse fovea is found in Atypidae, Hexathelidae, and Microstigmatidae. Eskov and Zonshtein (1990) discussed foveal shape, concluding that, in general, their Atypoidea possess a longitudinal fovea, and the Theraphosoidea a transverse one. Foveae contradicting this generality (e.g. atypids) were considered to resemble the pit found in *Liphistius*, and therefore plesiomorphic. The fovea in *Rosamygale* compares with the Theraphosoidea of Eskov and Zonshtein (1990) but, because of the poor recognition of the fovea in the fossils, it could be a transverse pit.

Atypids bear characteristically elongate maxillary lobes, which Gertsch and Platnick (1980) and Raven (1985) proposed as an autapomorphy for the family. Eskov and Zonshtein (1990) argued that similarly elongated maxillary lobes of some mecicobothriids (considered by Raven to be of different origin from those of the atypids) is a synapomorphy between the Mecicobothriidae and the Atypidae. The absence of such lobes in *Rosamygale* indicates a difference between the fossil genus and these extant families. A wide labium is generally regarded as plesiomorphic.

One or more dorsal abdominal sclerites are known in a number of mygalomorph families (Atypidae, Mecicobothriidae, Microstigmatidae), and have traditionally been considered as homologues of liphistiomorph tergites, and their presence thus plesiomorphic within Mygalomorphae. Eskov and Zonshtein (1990) used the presence of abdominal sclerites as a synapomorphy for their Atypoidea, the only occurrence of such sclerites in their Theraphosoidea being in the diminutive microstigmatids. Certainly, abdominal sclerotization is a feature associated with miniaturized body size in a number of spider families, such as the Oonopidae and Tetrablemmidae. Though small for a mygalomorph, *Rosamygale* is not as small as the microstigmatids, adult males of which range down from 3 mm to less than 1 mm in body length (Raven and Platnick 1981; Platnick and Forster 1982). Nevertheless, the abdominal sclerotization may be related to the small size of the fossil form, and it is possible that it is lost or greatly reduced in adults. The abdominal sclerotization of *Rosamygale* is not very useful as an indicator of affinity, because it could be a plesiomorphic character, a feature of small body size, or both.

The rastellum consists of a group of thorns at the anteromesial corner of the chelicera, and ranges from absent to a distinct lobe bearing long spines. Raven (1986) pointed out that the rastellum varies greatly, even within a family; it is correlated with a burrowing habit (Eskov and Zonshtein 1990). Therefore, the poorly developed rastellum of *Rosamygale* is an indicator of the mode of life of the spider (see below) rather than its affinities. Nevertheless, *Rosamygale* differs from groups with characteristically burrowing habits, such as the Atypidae and Antrodiaetidae, in this respect.

Pseudosegmented tarsi are present, normally in males only, in a number of mygalomorph taxa (Ischnothelinae, Diplurinae, Atypidae, Antrodiaetidae, and some Pycnothelinae, Theraphosidae, and Barychelidae (Raven 1985)). Therefore, the absence of pseudosegmentation in *Rosamygale* suggests it does not belong with these taxa. The tarsi of *Rosamygale* lack claw tufts and scopulae. Claw tufts are known in Theraphosidae, Barychelidae, and a few other, isolated genera (Raven 1985, 1986), and scopulae are present in many groups, including Theraphosidae, Barychelidae, and Nemesiidae. The combination of claw tufts and scopulae was considered as an autapomorphy of the Theraphosidae by Raven (1985). In general, scopulae are thicker and more extensive on the anterior legs than on the posterior, and are generally developed to aid locomotion on smooth surfaces. The absence of these tarsal structures in *Rosamygale* indicates no close relationship with these taxa, the Crassitarsae of Raven (1985). The other tarsal characters of *Rosamygale*, three claws and numerous teeth on the paired claws, also indicate no close relationship with this group.

The discussion above indicates that most characters of *Rosamygale* are in the plesiomorphic state for the Mygalomorphae. Many characters separate the fossil genus from Raven's (1985) Rastelloidina and Crassitarsae (essentially Eskov and Zonshtein's (1990) Ctenizoidina and Theraphosoidina). Sufficient apomorphies in the Atypidae and Antrodiaetidae (e.g. elongated maxillary lobes, rastellum) distance *Rosamygale* from these families, and the derived nature of the PLS distinguish Mecicobothriidae and Microstigmatidae from the fossil genus. *Rosamygale* differs from the described Hexathelidae in the presence of abdominal sclerotization and a small rastellum. Additional features can be used to argue a relationship with the Hexathelidae, and the basal position of *Rosamygale* within Raven's (1985) Tuberculotae. The chelicerae of Atypidae and Antrodiaetidae are much larger in relation to the size of the carapace than in *Rosamygale*. The walking legs are nearly equal in length in *Rosamygale*, whereas legs 1 and 2 are shorter in the Fornicephalae (Raven 1985). Raven (pers. comm. 1990) has suggested that the general appearance of *Rosamygale* (Text-fig. 1) compares most closely with *Bymainiella* Raven, 1978 among living hexathelids. However, it differs from that genus in size (the largest known *Rosamygale* is about the same size as the smallest *Bymainiella*) and compares more closely in this respect with the Microstigmatidae (Raven and Platnick 1981) and the diplurid *Microhexura* (Coyle 1981).

We consider that *Rosamygale* is best placed in the Hexathelidae, differing from all other known members of that family by its possession of sclerotization dorsally on the abdomen (which may be a function of small size and lost in adulthood) and the small rastellum (which functions in digging).

Mode of life

The morphological features of *Rosamygale* discussed above, together with its geological and palaeoecological setting, give good indications of the mode of life of the spider. Mygalomorphs live primarily in warm climates at the present day, although the atypids *Atypus* and *Sphodros* inhabit the temperate palaeartic, and a few reach alpine habitats, for example the diplurid *Microhexura* occurs up to 2300 m elevation in the Pacific northwestern USA (Coyle 1981). Geological evidence (given above) points to a hot climate for the Vosges area in the Anisian, though the near-marine situation and evidence for periodic flooding and drying out suggests the area was humid for at least part of the year.

Many mygalomorphs are noted for their adaptations to arid habitats, being the dominant spiders in such habitats in Australia, and their adaptive strategies have been well documented by Main (1982, and references therein). Behavioural adaptations to reduce desiccation include living in a burrow, aestivation, and dispersal during wet seasons (see above). Morphological adaptations in mygalomorphs to reduce water loss include various cuticular specializations of the abdomen (?wax-secreting disks, reduced pilosity, spiny sclerotized cuticle), and larger body size (Main 1982). Such morphological adaptations do not occur in *Rosamygale*, which may, nevertheless, have used behaviour for drought avoidance. Indeed, the presence of a small rastellum indicates the digging ability of the fossil spider.

Modern hexathelids inhabit wet forest areas (Raven 1978; Main 1981): a few burrow, but most weave a silken tube under stones, logs, bark, litter, and in cracks in the ground. Long PLS are

characteristic of mygalomorphs which construct broad platforms outside their funnel webs for prey capture, and in the mecicobothriids and diplurids the PLS are enormously elongated for this purpose (Gertsch and Platnick 1979; Coyle 1984, 1990). Discussion under TAPHONOMY, above, suggested that *Rosamygale* may have lived in the soft, sandy banks of watercourses, or beneath litter thereon (see reconstruction, fig. 9 in Gall (1985), but note that it is unlikely that the spider climbed trees, except perhaps during dispersal). Like other mygalomorphs, *Rosamygale* probably lived most of its life in its nest, venturing abroad as a juvenile seeking a new nest site, or as a mature or subadult male wandering in search of a mate. The abundant insects (Gall 1983) would have provided a food source for *Rosamygale*. Most of the described forms have aquatic larvae; presumably terrestrial insects were also present; nevertheless, it is conceivable that reliable food sources were present only in humid periods, and that *Rosamygale* aestivated during droughts. Aestivation is common in mygalomorphs which inhabit seasonal habitats (Main 1982). The habitat of *Rosamygale* compares with that of some nemesiids, as described by Main (1981), which are restricted to damp habitats within semi-arid, seasonal climatic regimes.

Biogeography

Apart from the ballooning habit of spiderlings of some species, mygalomorphs are generally good subjects for the study of biogeography because of their sedentary habits (Pocock 1903). At present, hexathelid spiders range from eastern Australia and Tasmania, through New Zealand, to Chile, and one genus, *Macrothele*, occurs in West Africa, southern Europe, India, China, Malaysia, Burma, Vietnam, Japan, and Java (Raven 1985; Snazell and Allison 1989). The related mecicobothriids inhabit western North America and Argentina; the microstigmatids are found in South Africa, South America, and Panama; and the Dipluridae occur in tropical and subtropical regions, mainly southern (Raven 1985). It is not surprising, therefore, that Gondwanaland has been suggested as the original home of this group of mygalomorphs.

Main (1981) discussed the evolutionary biogeography of Australian mygalomorphs. She recognized three evolutionary phases of mygalomorph faunas: (1) ancient (i.e. Mesozoic, early Palaeogene) Gondwanan relicts; (2) less ancient, but autochthonous forms; and (3) Neogene and Pleistocene immigrants. Hexathelids belong to the first group, and this family was discussed in greater detail by Raven (1980). In his biogeographical discussion, Raven (1980) suggested that the ancestor of the family arose in East Antarctica in the early Jurassic, and the group radiated throughout Gondwanaland before it broke up. The presence of *Rosamygale* on the southern shore of the Zechstein Sea in the Middle Triassic indicates that hexathelids, including *Rosamygale*, were probably present throughout Pangaea prior to the break-up of the supercontinent. However, the centre of dispersal of the group is not clear.

Geological history

The only previously described Mesozoic mygalomorphs are a mecicobothriid, an atypid, and an antrodiaetid from the Cretaceous of the Soviet Union, described by Eskov and Zonshtein (1990). Although the diagrams of these specimens are clear, the photographs are poor and the descriptions minimal, so it is difficult to judge the evidence for the assignments of these fossils. However, the placements seem reasonable on the scant evidence presented, and the Cretaceous fossils are quite distinct from *Rosamygale*. Eskov and Zonshtein (1990) discussed the Mesozoic Mygalomorphae in relation to the meagre geological history of the order. Eskov (1984, 1987) had described araneomorphs from the Jurassic which, together with the diversity (i.e. three families) of Cretaceous mygalomorphs, Eskov and Zonshtein (1990) used as evidence for a short 'Age of Mygalomorphs' during the latter part of the early Cretaceous. During this time, they concluded, a range of atypoid mygalomorphs replaced the Jurassic araneomorphs, at least in central Asia. Later, in the Palaeogene, theraphosoids replaced atypoids as the dominant mygalomorphs in the fossil record, but Eskov and Zonshtein (1990) considered that the theraphosoids had been present at low diversity since the early Mesozoic. They linked the faunal changes to changes in flora and insects during the late early Cretaceous.

The fossil record of Mesozoic spiders is currently far too scanty to allow analysis of major events, as Eskov and Zonshtein (1990) attempted, although the evidence so far accumulated does support that of the insects, which indicates trivial extinction of taxa across the Cretaceous–Tertiary boundary. The currently known fossil record of spiders (Selden 1990) begins in the Devonian, with *Attercopus* Selden and Shear, 1991 as the sister taxon to all other spiders. Only liphistiomorphs were present in the Carboniferous (all supposed araneomorphs studied by P.A.S. have so far proved not to be spiders). The present find of a Triassic mygalomorph sits almost centrally within the longest gap (c. 100 Ma) in the spider fossil record, and lends support to the notion that mygalomorphs arose from liphistiomorphs and in turn gave rise to araneomorphs. If an ‘Age of Mygalomorphs’ existed, before the advent of the Araneomorphae, it would have occurred around this time.

SYSTEMATIC PALAEOLOGY

Order ARANEAE Clerck, 1757

Suborder OPISTHOTHELAECOCK, 1892

Infraorder MYGALOMORPHAECOCK, 1892

Remarks. The presence of six spinnerets, posteriorly situated on the abdomen, the PLS consisting of three segments, and the paraxial chelicerae confirm that *Rosamygale* is a mygalomorph spider (for discussion of characters and relationships of spider suborders see Platnick and Gertsch (1976) and Raven (1985)).

Family HEXATHELIDAE (Simon, 1892)

Remarks. The subfamily Hexathelinae of the family Dipluridae (which is the sister-group of the Hexathelidae), was accorded familial status by Raven (1980). It is diagnosed principally by the presence of numerous labial cuspules. *Rosamygale* differs from typical hexathelids in possessing a group of blunt teeth forming a small rastellum on the chelicera, and the probable sclerotization of part of the dorsal surface of the abdomen. In having such sclerotization, *Rosamygale* resembles some of the related mecicobothriids and microstigmatids. The rastellum is an organ used for digging, and though characteristic of the Rastelloidina Raven, 1985, it also occurs in the Tuberculotae where it is not diagnostic. *Rosamygale* is included in this family for convenience and with these reservations; there is no doubt that it is a plesiomorphic tuberculote (*sensu* Raven 1985).

Genus ROSAMYGALE gen. nov.

Derivation of name. Latin *rosa*, a rose (ex Greek *rhodos*, red), from the delicate pink hue of the mineral infill of the abdomen of the specific holotype, reminiscent of the fine rosé wines of Alsace, and French (also obsolete genus name) *mygale*, a bird-eating spider.

Type and only known species. *Rosamygale grauvogeli* sp. nov.

Diagnosis. Hexathelid with six functional spinnerets, ALS and PMS single-segmented, PLS three-segmented; distal segment of PLS digitiform; fovea transverse, procurved; no maxillary lobes; large, irregular, dorsal abdominal sclerite present; cheliceral rastellum consisting of a few broad teeth; tarsi not pseudosegmented, without claw tufts or scopulae; three claws present, not on a lobe, pectinate paired claws with numerous teeth; labium wide.

Rosamygale grauvogeli sp. nov.

Plates 1–6; Text-figs 1–6

1971 Araneida *incertae sedis* Gall, p. 37, pl. 6, fig. 1.

Derivation of name. In honour of the collector of the Triassic spiders of the Grès à Voltzia, Louis Grauvogel.

Material. Holotype AR11; paratypes AR1, AR8, and AR12. Additional specimens: AR2, AR4, AR5, AR7, AR10 (part figured by Gall 1971, pl. 6, fig. 1; not available for this study, counterpart only seen), PC14. All specimens except AR2 consist of both part and counterpart. All are from the Grès à mules, which form the lower part of the Anisian Grès à Voltzia. Localities are as follows (details in Gall 1971): AR1, Adamswiller, Bas-Rhin; AR2, AR4, AR5, AR7, AR12, and PC14, Arzviller, Moselle; AR10, AR11, Bust, Bas-Rhin; AR8, Vilsberg, Moselle. Specimens are deposited in the Grauvogel-Gall Collection, under the care of the Institut de Géologie, Université Louis Pasteur, Strasbourg.

Diagnosis. As for the genus.

Description. Body length up to 6.0 mm. Carapace subcircular, cuticle unsculptured. Fovea transverse, procurved. Eyes probably eight, on a raised lobe.

Sternum oval to subcircular, with recurved anterior edge, posterior projection (but not produced between fourth coxae), and scalloping adjacent to coxae on larger specimens. Labium wider than long, semicircular, possibly overlapping anterior edge of sternum.

Chelicerae robust, about one-quarter length of the carapace, and ovoid in shape (widest towards the distal). Orthognath fang arising from an anteroinferior position and following a gentle, scimitar-like curve to almost full length of body of chelicera. Row of small teeth present along inferior side of the cheliceral body. Small rastellum present, consisting of a few short spines distal and mesial to fang base, not on a lobe. Long bristle apparently arising from mesial side of chelicera.

Maxilla without a lobe, cuspules probably present, bristles present. Immature palp with single, ?non-pectinate claw; curved spine on patella. Legs not elongated, approximately equal in length (leg 1 slightly shorter than others), about two-thirds body length. Coxa with costa coxalis on inferoanterior surface, terminating distally in inferoanterior articulation of coxa-trochanter joint. Coxa 4 without liphistiormorph invaginations. Trochanter unnotched, with inferior groove on inferior surface. Legs covered with smooth setae, and spines on femur, patella and tibia at least. No claw tufts or scopulae. Mctatarsus I with inferodistal spur. Tarsus with curved, pectinate paired claws, small median claw; without pseudosegmentation.

Abdomen oval, broadest at midlength. Cuticle with short setae arising from transverse wrinkles. Large, irregular sclerotized area occupying anteromedian third of dorsal surface. Six spinnerets, all with spigots. ALS and PMS single-segmented; ALS slightly smaller than PMS. PLS long, two-thirds length of abdomen. Distalmost segment of PLS digitiform, half length of spinneret, not pseudosegmented.

Acknowledgements. P.A.S. is grateful to Robert Raven for helpful comments and information on mygalomorphs, to Joe MacQuaker for advice on sedimentary geochemistry, to Fred Coyle for offprints and encouragement, and to The British Council for travel funds in connection with this work.

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PAUL A. SELDEN
Department of Geology
University of Manchester
Manchester M13 9PL

JEAN-CLAUDE GALL
Institut de Géologie
Université Louis Pasteur
1 Rue Blessig, 67084 Strasbourg
France

Typescript received 22 November 1990
Revised typescript received 30 January 1991

THE OCCURRENCE AND PALAEOBIOGEOGRAPHICAL SIGNIFICANCE OF THE FORAMINIFERID *YABERINELLA* FROM THE EOCENE OF OMAN

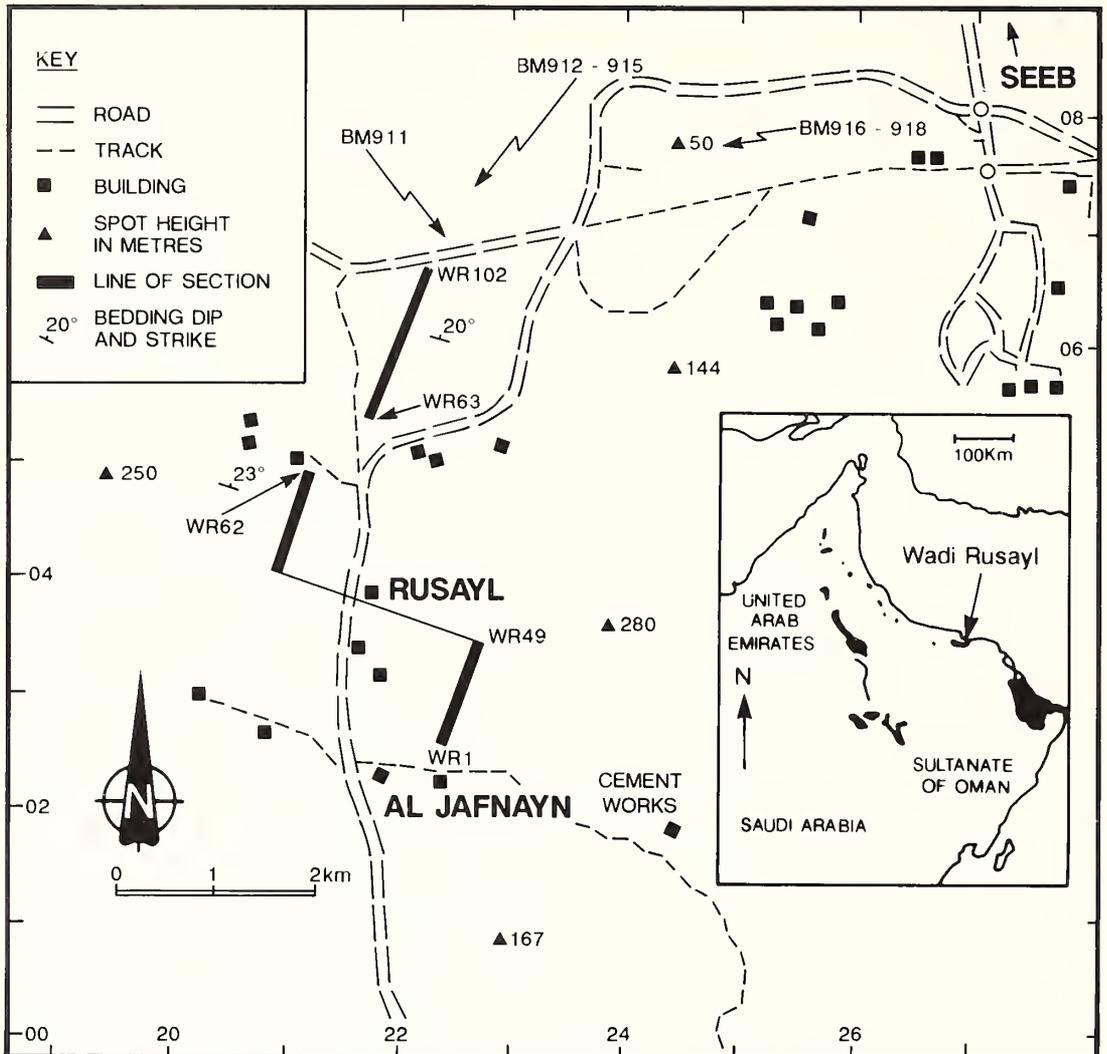
by C. G. ADAMS and ANDREW RACEY

ABSTRACT. *Yaberinella jamaicensis* Vaughan, a genus and species previously regarded as endemic to the Americas, is described from a sample of Middle Eocene (Lutetian) limestone from coastal Oman. The new occurrence is shown to be well within the known stratigraphic range of this species in the Caribbean region. Recently published records of *Austrotrollina*, *Helicostegina*, *Helicolepidina*, *Lepidocyclina*, and *Polytepidina* are discussed briefly in the context of the disjunct distribution of *Yaberinella*. It is considered that since the widely-distributed and relatively well-studied faunas of Middle Eocene carbonate facies are apparently still so incompletely known, the case for provincialism among Palaeogene larger foraminifera is weakened, and published conclusions relating to dispersal routes for some Tertiary genera may well be premature.

DURING recent studies of the Tertiary limestones of eastern Oman (Racey 1988; White 1989) samples were taken from a series of knolls to the east of Wadi Rusayl (Text-fig. 1). One such sample (BM 911) yielded numerous specimens of *Yaberinella jamaicensis* Vaughan, a taxon hitherto thought to be confined to the Americas (Adams 1967; Hottinger 1973). The apparent endemism exhibited by *Yaberinella* was an important factor in the construction of the Tertiary faunal province hypothesis based on larger foraminifera (Adams 1967, 1973), and its discovery in Oman weakens the case for provincialism, at least during Palaeogene time.

The Tertiary succession in the coastal region of Oman has long been known to include strata of Palaeocene to Early Miocene age (Glennie *et al.* 1974; Montenat and Blondeau 1977; Racz 1979). Recent work on the nummulitids by one of us (A. R.) has shown that the upper part of the exposed sequence in the best-known section at Wadi Rusayl is mainly referable to the Middle Eocene (Lutetian). The youngest part of the underlying Seeb Limestone belongs to the *N. benelharnensis* (= *A. spira*) Zone of Schaub (1981), both marker fossils being present (Text-fig. 2). The sample yielding *Yaberinella* was collected from a 'limestone with clasts' (see p. 240), neither the base nor top of which is visible at outcrop. The Seeb Limestone lies below a largely obscured development of Upper Eocene limestone which is itself overlain by the coralliferous Ma'ahm Beds of Oligocene age.

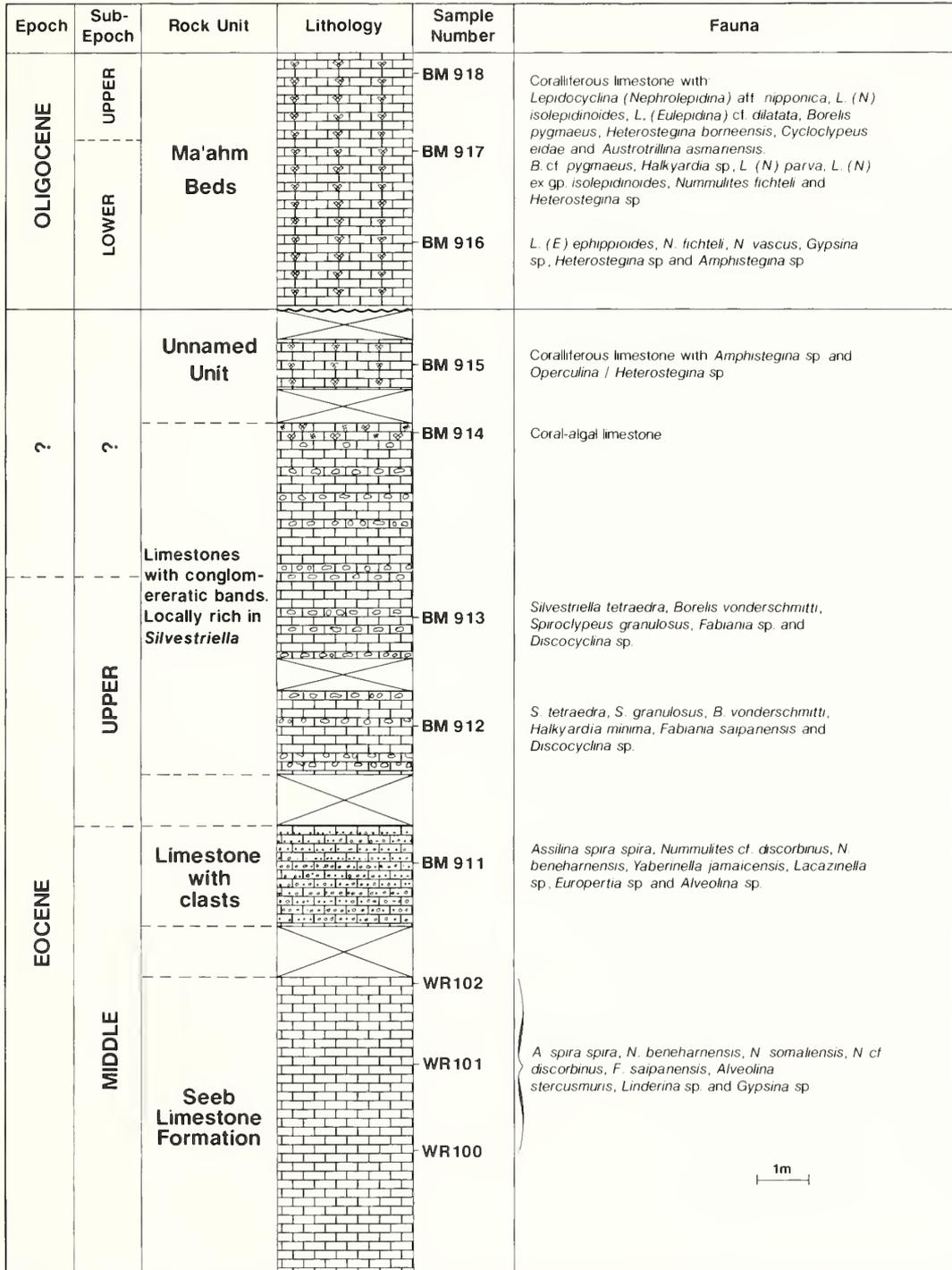
The total thickness of Tertiary limestone in the Wadi Rusayl area is of the order of 580 m, of which 560 m is exposed. With the exception of some 50 m of late Palaeocene limestone at its base, the sequence is Eocene in age, the oldest beds probably being referable to the *Alveolina oblonga* or *A. dainellii* zones of Hottinger (1960; White in prep.). The Middle Eocene part of the sequence is about 450 m thick. Well over 100 samples have been collected from this succession during the last few years, and another 700 have been obtained from beds of equivalent age elsewhere in Oman. Other workers (e.g. Montenat and Blondeau 1977, and various oil company micropalaeontologists) have also examined numerous samples from the Wadi Rusayl area. However, despite this intensive study, *Yaberinella* has not previously been found in Oman, neither has it been reported from the Mediterranean region, the Middle East nor the Indian subcontinent, all areas from which important Middle Eocene limestones (e.g. the Khirthar Limestone, Pakistan) have been described.



TEXT-FIG. 1. Map showing the location of Sample BM 911 in relation to the sampled succession in Wadi Rusayl, Oman.

In contrast to the thick sequence of Palaeocene to Middle Eocene carbonates exposed in Wadi Rusayl itself, the overlying succession (Text-fig. 2) is more varied. The basal 10 m was found to contain a Middle Eocene fauna, younger than anything observed in the main outcrop, and datable as Mid to Late Lutetian. Sample BM 911 yielded *Assilina spira* de Roissy and *Nunmulites beneharnensis* de la Harpe (transported and penecontemporaneously redeposited if not actually reworked) along with *Yaberinella*, while two younger samples (BM 912 and 913) yielded *Borelis vonderschmitti* (Schweighauser), *Calcarina* sp., *Fabiania cassis* (Oppenheim), *Silvestriella tetraedra* (Gümbel), and *Spiroclypeus granulatus* Boussac. These two samples are therefore thought to be from the basal Upper Eocene.

The single sample from which *Yaberinella* was recovered came from a small, isolated outcrop no more than 3 m high and 7 m across: it was collected merely to complete the biostratigraphic sequence, no special importance being attached to it in the field. Not until the rock had been



TEXT-FIG. 2. Schematic stratigraphical column showing the position of Sample BM 911 in relation to the uppermost part of the Middle Eocene, the overlying Upper Eocene, and the Ma'ahm Beds in Wadi Rusayl, Oman.

disaggregated was its palaeobiogeographical significance appreciated, and by then it was too late for special note to be taken of its lithology. The washed and sieved residue was found to contain a large number of small, mostly rounded, mainly discrete, but sometimes aggregated clasts. The igneous components are thought to have been derived from the Semail Ophiolite, and the chert fragments from the Hawasina Series. Since the clasts are not scattered throughout the fragments of limestone in the coarse fraction of the residue, it is considered that they represent a thin band (or bands) of gravel, probably no more than 0.1 m thick. In view of the uncertainty attached to the lithology of this particular sample it is here referred to simply as a 'limestone with clasts'. The foraminifera occur in the carbonate matrix.

SYSTEMATIC PALAEOLOGY

Repository of specimens. All material described and figured in this paper is deposited in the British Museum (Natural History), London (abbreviation BMNH).

Family SORITIDAE Ehrenberg, 1839
 Subfamily FABULARIINAE Ehrenberg, 1839
 Genus YABERINELLA Vaughan, 1928

Type species: *Yaberinella jamaicensis* Vaughan, 1928

Remarks. There is as yet no consensus of opinion regarding the terminology to be employed for the description of the internal structures of *Yaberinella*. Lehmann (1961) referred to ramps, stolons, and attics, but we prefer simpler terms and use only partitions (spiral and transverse), and tubes (central and lateral). The term stolon is, in our opinion, misleading since these structures are not (at least in the type species) simple tubes traversing thick chamber walls, as in the *Lepidocyclinidae* or *Orbitolitidae*, but layers of passages (tubes) delimited by endoskeletal deposits (partitions = 'plates' of Vaughan 1928) within the chamber lumen. The partitions may appear wavy in transverse section. Only in *Y. trelawniensis* Vaughan are the internal partitions greatly thickened (thus resembling chamber walls) as shown by Lehmann (1961, fig. 44), who illustrated tubes ('stolons') traversing massive deposits of endoskeletal material. In *Y. jamaicensis*, these tubes are formed by thin partitions and in cross-section tend to be rectangular rather than circular in shape. Fleury and Fourcade (1987, fig. 4 – explanation) postulate a somewhat different arrangement of tubes but again with greatly thickened partitions as shown by Lehmann (1961).

Although the positions of the chamber boundaries can be seen both on the surface (as sutures)

EXPLANATION OF PLATE I

- Figs 1–10. *Yaberinella jamaicensis* Vaughan, 1928. 1–8, thin sections of megalospheric individuals (1–5, equatorial, BMNH P52263–P52267; 6–8, transverse, BMNH P52268–P52270) showing variation in shape, chamber growth, and proloculus size. Internal structure shows as lozenge-shaped chamberlets in figures 3 and 5 but as chevron-shaped tubes in figures 1 and 2, depending on how the spiral and transverse partitions are cut; Cole's (1952) 'small square chambers' are well seen in figures 5 and 6. 9–10, microspheric individuals; BMNH P52271–P52272 respectively; the sub-annular growth seen in fig. 10 is partly the result of regeneration after test damage. Figs 1–4 and 7, $\times 10$; fig. 5, $\times 11$; figs 6 and 8, $\times 15$; figs 9–10, $\times 10$.
- Fig. 11. *Yaberinella* sp. cf. *Y. trelawniensis* Vaughan, 1929. BMNH P52273; megalospheric form; note the relatively small proloculus, numerous whorls and thick partitions, $\times 15$.
- Fig. 12. *Assilina spira* de Roissy, 1805. BMNH P52274; zonal marker (see Schaub 1981) occurring with *Y. jamaicensis*, $\times 1$.
- Fig. 13. *Nummulites beneharnensis* de la Harpe, 1926. BMNH P52275; zonal marker (see Schaub 1981) occurring with *Y. jamaicensis*, $\times 3$.
- All specimens from Sample BM 911, Eocene, Wadi Rusayl, Oman.



ADAMS and RACEY, *Yaberinella*

and in equatorial section (as clear areas), the 'septa' themselves appear quite structureless and are often seen to be crossed by the spiral and transverse partitions. Septa, as they are normally understood, have not, therefore, yet been observed in this genus. This is probably because the very thin apertural face (the basis of the future septum) has been destroyed by recrystallization in all known specimens.

Yaberinella jamaicensis Vaughan, 1928

Plate 1, figs 1–10

- 1928 *Yaberinella jamaicensis* Vaughan, p. 8, pls 4–5.
 1952 *Yaberinella jamaicensis* Vaughan; Cole, p. 8, pl. 6, figs 1–8.
 1961 *Yaberinella jamaicensis* Vaughan; Lehmann, p. 656, text-figs 43–46, pl. 13, figs 1–4; pl. 14, figs 1–3.
 1969 *Yaberinella jamaicensis* Vaughan; Hottinger, p. 746, text-figs 1–2; pl. 1, fig. 1; pl. 2, figs 1, 2, 4; pl. 3, figs 1–2; pl. 4, figs 1–3; pl. 5, figs 1–6.

Figured material. BMNH P52263–P52270 (thin sections); BMNH P52271–P52272 (microspheric individuals). Sample BM 911 yielded 26 complete specimens and a number of large fragments.

Age. Middle Eocene (Mid Lutetian). Zone of *N. beneharnensis* (= *A. spira*) Schaub (1981). According to Schaub (1981, fig. 23), this is equivalent to the *Chiplragmalithus alatus* Zone (calcareous nannoplankton), which is itself equivalent to Blow's (1979) planktonic foraminiferal zones P10 to 12 (= topmost *H. aragonensis* to lowermost *G. lehnneri*) – see Toumarkine and Luterbacher (1985, fig. 4) and Cavelier and Pomerol (1986, table 1). As mentioned earlier, it is possible that the assemblage is wholly or partly reworked, in which case its age could be slightly younger, *i.e.* Late Lutetian.

Description. Megalospheric generation, based on 16 sectioned and 8 isolated specimens.

Test large, complanate, 4–6.4 mm in maximum diameter and 1.15 mm in maximum thickness. The large subspherical to elongate proloculus (0.70–1.11 mm in maximum internal diameter), is connected to the partitioned chambers by a short neck (*goulot* of Hottinger 1969), usually offset to one side and only rarely visible in equatorial sections. All subsequent chambers are subdivided by two sets of internal partitions, one roughly paralleling the spire (spiral partitions), the other curving back towards the peripheral wall (transverse partitions). Unfortunately, septa are not usually visible in the first whorl, and the total number of chambers in the test cannot, therefore, be determined. The lowermost part of the chamber(s) in the first whorl completely embraces the proloculus. This part of the chamber has the wall of the proloculus as its floor, and the first spiral partition as its roof. It is subdivided by radiating transverse partitions which form the 'small square chambers' described by Cole (1952, p. 8, pl. 6, figs 1, 4–5). The chamber at the end of the first whorl may show from 6–12 spiral partitions. In the present material, the first visible 'septum' occurs at about 1–1 $\frac{1}{3}$ whorls, and is followed by 3–17 (usually about 7) low, planispirally coiled, flaring peneropline chambers, which do not always increase regularly in size. The final chamber is rarely, if ever, complete in the present material. The spiral and transverse partitions are continued throughout the peneropline chambers, but with the transverse divisions becoming more oblique with respect to the spiral set. These are the 'ramps' described by Lehmann (1961) and are thin compared with the diameter of the 'stolons'. In some equatorial sections the two sets of partitions appear to intersect and form numerous lozenge-shaped chamberlets (Pl. 1, fig. 3). In others, the cavities between the partitions appear as tubes ('stolons'). These sets of parallel tubes (0.02–0.06 mm in diameter), are inclined at 80°–130° and give the test a regularly hachured appearance in thin section. Their walls (partitions) are thin (0.20–0.30 mm). The test surface is ornamented by fine ribs running at right angles to the chamber sutures. They are formed by the single layer of narrow, subepidermal tubes which overlie the spiral and transverse tubes of the central region. Although true septa cannot be seen owing to recrystallization, their positions are marked by clear, structureless (recrystallized) areas in thin section. These contrast with the black spiral and transverse partitions which are seen to cross them in places. On the test surface, sutures are sometimes visible as faint depressions. Apertures not observed owing to poor preservation of the distal face of the last chamber.

Microspheric generation. Description based on 1 fairly complete individual and a number of large fragments.

Diameter 8 mm; initial coil of about 3.5 whorls, comprising at least 21 peneropline chambers, 9 of which occur in the last complete whorl. True annular chambers have not been observed, although the ends of the later chambers in large individuals certainly either meet or overlap, thus becoming pseudo-annular (Pl. 1, fig. 10). Proloculus and earliest part of the initial coil not seen in the present material.

Remarks. The relatively small number of specimens obtained from Sample BM 911 show a remarkably wide range in size. Megalospheric individuals are mainly rather larger than the types from Jamaica and have 3–17 peneropline chambers compared with about 9 in Vaughan's figured specimen (1928, pl. 5, fig. 1). Hottinger (1969) recorded individuals from the type area with from 10 to about 15 peneropline chambers. The enormous proloculus, a characteristic feature of this species, is seen in individuals from both Oman and Jamaica. The most complete microspheric individual from Oman is smaller and has fewer chambers than its Jamaican counterparts. The size and layered arrangement of the internal tubes ('stolons') appears to be the same in individuals from the two areas.

One individual (BMNH P52273; Pl. 1, fig. 11) possesses a relatively small proloculus (0.4 mm in maximum internal diameter), thicker internal walls, and a tighter and longer coil than the other specimens. It is therefore referred here to *Y. cf. trelawniensis* Vaughan, a species placed in synonymy with *Y. jamaicensis* by Cole (1952) but regarded as distinct by Hottinger (1969) and Robinson (in press). Hottinger's figures of *Y. trelawniensis* (1969, pl. 5, figs 1–6) also show thickened internal partitions.

Associated fauna. *Assilina spira spira* de Roissy (BMNH P52274; Pl. 1, fig. 12), *Nummulites beneharnensis* de la Harpe (BMNH P52275; Pl. 1, fig. 13), *N. cf. discorbis* (Schlotheim), *Fabiania cf. cassis*, *Alveolina* sp., *Lacazinella* sp., *Eorupertia* sp and miliolids.

Originally described by Vaughan (1928) as having an agglutinated wall, *Yaberinella* was later found by Hans Reichel to be porcelaneous (Lehmann 1961). The internal structure of the adult chambers was analysed by Lehmann (1961, p. 656). In 1969, Hottinger redescribed and figured the two known species and demonstrated their relationship to *Fabularia*, arguing that *Y. trelawniensis* was more primitive and older than *Y. jamaicensis*, a fact confirmed by Robinson (in press) who has found that the range of *Y. jamaicensis* in the Caribbean region approximates to Blow's planktonic foraminiferal zones P12 to early P15, while that of *Y. trelawniensis* is P10 to P13.

It is difficult to relate the various Caribbean records of *Yaberinella* to the single occurrence in Oman because the associated faunas are different in the two areas, and precise control from planktonic foraminifera and/or calcareous nannoplankton is usually lacking. Nevertheless, it is clear that the Oman assemblage occurs well within the stratigraphic range of *Yaberinella* in the Caribbean, and is significantly younger than the oldest known occurrence of the genus. The fact that some individuals resemble *Y. trelawniensis* suggests that the age of this assemblage is P12 to P13, if the ranges cited by Robinson (see above) can be confirmed. The presence of *N. beneharnensis* and *A. spira* confirms that the assemblage in BM 911 cannot be older than P10 to P12, while the faunas in the overlying samples show that it cannot be as young as P15 even if reworking has occurred. A mid to late Lutetian age is therefore certain.

It is clear that the single known occurrence of *Yaberinella* in the Middle East is considerably younger than the earliest Eocene records from the Caribbean area over which there is any planktonic control. It may therefore be inferred that dispersal was from the New to the Old World, presumably by the shortest route (west to east), though in the absence of records from West Africa and the western Tethyan region generally, the direction of movement is uncertain. Hottinger (1969) showed that *Fabularia* may be the closest known relative of *Yaberinella*, but since this genus occurs in both the Tethyan and American regions it does not confirm that *Yaberinella* originated in the Americas.

The most northerly records of *Yaberinella* in the New World are believed to be those from Costa Rica (Eva 1976) and Jamaica (Vaughan 1928, 1929), and the most southerly from the Panama Canal Zone (Cole 1952). This extremely narrow latitudinal range (9°N – 18°N) will undoubtedly be extended by future work.

PROVINCIALISM

The discovery of *Yaberinella* in the Arabian Gulf has cast doubt on the reality of the three main faunal provinces postulated by Adams (1967). Questions had already been raised by certain

unrelated discoveries made during the last twenty years, and these are worth discussing briefly in the present context.

The mixing of American and Tethyan faunas along the western coast of North Africa has been confirmed and extended by Freudenthal's report (1972) of *Helicolepidina* together with typical American species of *Lepidocyclina* from Senegal and Portuguese Guinea. Brun, Butterlin and Monteil (1982) have recently described *Helicostegina* from this area, and Neumann, Ly and Butterlin (1986) reported various American species of *Discocyclina*, *Lepidocyclina* and *Helicolepidina* from Senegal. Of greater palaeobiogeographical significance is, however, the report by Premoli Silva (1986) of *Polylepidina* (reworked into Late Oligocene sediments), in the Nauru Basin, central Pacific. These records indicate that most supposedly endemic American genera were more widespread than was previously supposed. A recent unpublished report of *Proporocyclina* from India will, if confirmed, further reduce the degree of endemicity previously attributed to American Eocene faunas. These records do not, on the other hand, alter the fact that the overall compositions of the larger foraminiferal faunas in the Tethyan, American and Indo-West Pacific regions were different throughout the Tertiary.

The incomplete nature of our knowledge of the Eocene fossil record has been further demonstrated in recent years by the discovery of *Austrotrillina* in limestones of this age in Iran (Rahaghi 1980) and off-shore Tunisia (Bonnefous and Bismuth 1982). *Austrotrillina* is otherwise unknown from sediments older than Oligocene, and has never been reported from Late Eocene strata despite intensive world-wide studies of carbonates of this age. The discovery of *Yaberinella* in Oman indicates, however, that this deficiency may not be significant.

The presence of *Yaberinella* in the Middle East has a twofold significance. First, it removes a generally accepted example of endemism from the larger foraminifera, thus weakening slightly the case for provincialism within this group. Second, it shows that complete reliance cannot be placed on current knowledge of the palaeogeographical distribution of larger foraminiferal taxa. In this context it is worth noting that Skelton and Wright (1987) recorded a similar disjunct distribution (Oman and the Americas) for the Maastrichtian rudist genus *Torreites*.

Clearly, the well-described and abundant Middle Eocene carbonates of the Tethyan region, provide less complete information on the fossil record than is commonly supposed. This is presumably because bedding planes and other depositional hiatuses represent longer intervals of time than do the intervening sediments. The discovery of *Yaberinella* in Oman, of *Austrotrillina* in the Eocene of Iran, of *Lepidocyclina*, *Helicostegina* and *Helicolepidina* in West Africa, of *Polylepidina* in the Pacific, and possibly of *Proporocyclina* in India, indicate that shallow-water limestone faunas are not yet sufficiently well known for areas of origin and dispersal routes of individual taxa to be determined with confidence.

Acknowledgements. Dr Edward Robinson (University of Jamaica) kindly read and made helpful comments on an early draft of the typescript.

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C. G. ADAMS

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

ANDREW RACEY

Geochem Group Ltd
Chester Street
Chester CH4 8RD, UK



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FOSSIL COLLECTING AND SITE CONSERVATION IN BRITAIN: ARE THEY RECONCILABLE?

by DAVID B. NORMAN

ABSTRACT. Collecting fossils for scientific study or as a pastime activity can be a very enjoyable and rewarding experience. However, the motives for collecting fossils, which can range from pure scientific research through hobby collections to commercial enterprise, can present the genuine scientist, hobbyist/collector or legislator with a variety of challenging and conflicting points of view. Imposing legislation which will allow collection through a permit system is appropriate only in a restricted number of cases and is generally regarded as unwieldy, open to abuse and expensive to implement, and may in the longer term damage the scientific value of most sites. However, adopting a totally *laissez-faire* approach to all sites runs the risk of complete loss of fossil localities through over-collection and destruction of specimens. Options for dealing with this paradoxical situation are discussed and some recommendations proposed.

THE history of fossil collecting is one that can be traced some considerable distance into antiquity (Wendt 1968; Rudwick 1976; Dong 1988), but it only assumed high importance in the latter part of the eighteenth and early in the nineteenth century, following the work of Alexandre Brongniart and Baron Georges Cuvier (Rudwick 1976). Such awakenings of interest in the scientific value of fossils favoured fossil collectors, whose skills in finding fossils became sought after by people wishing to develop their own collections and by local and national museums who were anxious to augment their collections for the purposes of display and scientific study.

The Mary Annings (mother and daughter), who opened the very first fossil shop in Britain at Lyme Regis, Dorset, in the early years of the nineteenth century, were very early examples of skilled collectors who made a living out of the desire among relatively wealthy patrons (including the British Museum) for well-preserved fossils; these they were able to collect from the richly fossiliferous clays and limestones exposed along the coastline between Lyme Regis and Charmouth. Many extremely important palaeontological discoveries made by the Annings were bought for private collections or by local and national museums (Rolfe *et al.* 1988). This example is not an isolated one. A contemporary of the Annings, Thomas Hawkins, amassed a very fine collection of large marine reptile skeletons from the same area of Dorset; another, Dr Gideon Mantell, developed a large private museum of fossils from the Sussex area, and was extremely active as a trader of fossils with collectors in other parts of Britain, Europe and the United States. This tradition of collecting and selling and, in some cases, donating fossils to museums (either directly or as bequests) has been maintained, with varying degrees of intensity, down through the years to the present day and has been one of the principal means by which museums have been able to acquire important national and international collections representative of our fossil heritage.

PERCEPTIONS RELATING TO FOSSIL COLLECTORS

Over the past twelve years the subject of fossil collecting and, in particular, the role of commercial and non-commercial fossil collectors has been the subject of lively and, in some cases, acrimonious debate. There have been many claims that geological sites were being destroyed by indiscriminate hammering or over-collection. This culminated in a meeting in London in 1987 on 'The use and conservation of palaeontological sites', organized by the Palaeontological Association and sponsored by the Geological Society, the Geological Curators' Group and the Nature Conservancy

Council (Crowther and Wimbledon 1988). Contrary to expectations, the meeting, at which representatives from all relevant interest groups were present, reached a very broad consensus view on the subject: that *responsible* collecting should be recognized as essential to the geological use and longer-term conservation of most sites (Besterman 1988; Taylor 1988; Knell 1991). Such views have been emphasized recently (Norman and Wimbledon 1988; Norman *et al.* 1990a) culminating in a general policy statement (Norman *et al.* 1990b) concerning the use and conservation of palaeontological Sites of Special Scientific Interest (SSSI).

Sites designated as SSSI are those which have been selected and legally notified as such. To satisfy the legal requirements, documents have to be submitted to the owners/occupiers of the land where the sites have been identified, the relevant local authorities and Government Departments, by the statutory conservation organisations: the Nature Conservancy Council for England (NCCCE), the Countryside Council for Wales (CCW), and the Nature Conservancy Council for Scotland (NCCS). The terms of such notifications are contained within two Acts of Parliament: the *National Parks and Access to the Countryside Act 1949* and the *Wildlife and Countryside Act 1981*; these ensure that SSSI are: (i) given clear geographical locations; (ii) supported by statements of their scientific importance; and (iii) safeguarded by a list of Potentially Damaging Operations (PDOs).

PDOs, introduced by the 1981 Act, provide a most important mechanism for consultation between owners or occupiers and the statutory authorities because they list the types of activity that are thought to be liable to cause damage to the scientific value of the site. Before such activities can be sanctioned negotiations have to be opened with the conservation authorities. A negotiated agreement results in the issuing of a PDO consent form, disagreements are eventually resolved through a Court of Public Inquiry which makes recommendations to the Secretary of State for the Environment who publishes a judgement (*determination*) in due course.

It is clear that palaeontology, and to some extent stratigraphy, is crucially dependent upon collected material, though it should be added that collection is not the absolute be-all and end-all that it used to be. Taphonomic studies which can lead to an understanding of the environment of deposition of fossils require fossils *in situ* rather than *ex situ*, at least in the first instance. Despite such caveats there is no doubt that the scientific disciplines themselves would not now exist in their present form if collecting had not occurred, and they could not develop further without new discoveries. Equally, the areas of land which have been identified as palaeontological and stratigraphical SSSI by the Geological Conservation Review (GCR) could not have been so identified and given a measure of legal protection from the depredations of developers and planners, had not well-documented collections of fossils been made in the past. Between 1977 and 1991 the GCR was funded by the Nature Conservancy Council (the predecessor of NCCCE, CCW and NCCS) to survey and select a comprehensive network of earth science SSSI.

So, the obvious question: if there is widespread recognition of the value of responsible fossil collecting for the use, maintenance and conservation of geological sites within the broad geological community, why should the subject be one which is still at the centre of heated debate? The reason seems to me to be a curious and rather intractable mixture of genuine and intense local concern over the fate of particular favourite sites and their fossils (particularly if these are rare or exceptionally well-preserved), coupled with a fear that the large-scale irresponsible fossil collecting associated with unfettered commercial demands will result in disaster: sites would be pillaged in a mad scramble to obtain a few 'prize' specimens, to be sold for high prices, leaving only rubble and scree behind. Added to this there is the quite widespread belief that most sites can be 'worked out' by a short period of intense fossil collecting.

All three of these factors seem to underlie, to varying degrees, the reactions of many who object to fossil collecting. The importance of each of these factors will tend to vary depending on the type of site at which such events may be occurring. However, there is no doubting the passion with which such views can be held, particularly when the after-effects of such destructive excavations are to hand. In nearly all cases it appears to be the collector with commercial aims who has borne the brunt of criticism in the past. Unpalatable though the thought is, I strongly suspect that the 'commercial collector' is simply the easiest target for criticism because his/her motive for collecting can be

claimed to be straightforward avarice. I do not intend entirely to absolve commercial/professional fossil collectors, who have in some instances caused appreciable degradation of sites. However, as several authors have stated in the past, it is not only commercial collectors who can cause apparent devastation; badly supervised parties of school children, college or university students on field courses are also capable of quite extensive hammering at sites, even if not on the scale of some commercial operations.

THREATS TO PALAEOONTOLOGICAL SITES

Fossil collecting is clearly a threat to fossil sites. However, as a result of the 1987 meeting on palaeontological site use and conservation, it has become accepted generally that it is not the only serious threat. There are four principal categories of threat to such sites: burial, quarrying, misguided conservation and collecting (Black 1988; Taylor 1988).

Burial

One of the primary causes of site loss in the UK is through burial by various means. Burial or general inaccessibility of sites generally takes place through the activities of local authority planners and developers.

At inland sites, in-filling of quarries as part of a waste-disposal strategy is one of the most obvious examples of direct burial. Pre-existing restoration plans for quarry sites can also result in infilling, battering, grading and planting of vegetation on fossiliferous rock faces. (Recent examples include Boon's Quarry SSSI, Webster's Clay Pit SSSI and Clockhouse Quarry SSSI.)

At coastal locations, sea defence and coast protection measures frequently result in schemes which involve the construction of wave-return walls, gabion barrages or rock armour berms in front of eroding cliffs; these are also frequently linked to selective mechanical grading at the top of the cliff and various drainage schemes as part of cliff stabilization measures. Alternatively the cliff may simply be battered with reinforced concrete. The net effect of these actions is either direct, to obscure the cliff section with an impenetrable layer of concrete, or, more indirectly, to reduce erosion at the base of the cliff and promote grading and stabilization of the cliff, culminating in vegetation growth on the previously clear and accessible cliff section (for example at Barton, which is part of the Milford-Highcliff SSSI).

Quarrying

Active commercial quarrying, if located at fossiliferous sites, is a very obvious form of threat. Quarrying removes important fossil specimens as a physical by-product of mining. This threat is most real when excavation is done by remote-controlled heavy machinery, which it is in the vast majority of cases; then important material is inevitably lost. In some cases, localized loss may not be critical, because the beds are laterally extensive and will occur at faces exposed at various locations throughout the quarry and may be left accessible once commercial quarrying has ceased. However, in the case of impersistent beds (channel-fills, fissure-fills, etc.), the entire scientific interest may be lost very rapidly. Equally, if the fossiliferous beds are steeply inclined, quarrying may remove all lateral exposures and leave the scientifically important beds completely inaccessible in the floor of the quarry.

There is also a positive side to quarrying by commercial companies: the very fact of quarrying in the first place made possible many extremely important fossil discoveries. Thus in many instances active quarrying, like natural erosion, is extremely valuable because it constantly serves to renew exposures and makes available previously inaccessible sections of the geological column. Provided that responsible collectors can gain occasional access to new exposures, quarrying can be highly beneficial to palaeontological research.

In a small number of cases commercial quarrying may still depend upon more traditional skills and a less intensive use of heavy equipment. Here it may be possible to establish a code of practice with the quarry owners to (try to) ensure the recovery of a percentage of the fossils that might

otherwise be lost by quarrying (a recent example of this being a code of practice document which has been proposed for Grinshill Quarry, Shropshire). However, such arrangements obviously depend very much on the attitude of the quarry management and the cooperation of the quarrymen.

Misguided conservation schemes

Though rare, there might well be occasions when teams of conservationists could become involved in sites combining biological and geological interests. In such instances there could be a conflict between the interests of the biologists, who might for example be interested in restoring a specific habitat and species mix in an abandoned quarry. Such a scheme might require the infilling and grading of geologically important areas and would thus be inimical to the geological interest of the site. I am not aware of any examples of such a conflict of interests on SSSIs to date.

Equally serious and damaging for geological sites is what might be called the 'civic tidiness effect', which can result in attempts being made to clear what might appear to local council officers to be 'untidy' areas of abandoned quarries (piles of scree, etc.), all of which may be of inestimable value to the practising geologist. This approach is also applied to coastal areas, as in the 'tidying' of a major part of the shoreline at the palaeobotanical site known as Lake (Ham Common SSSI), using gabion blocks, and the grading of the coastal cliff exposures at Bournemouth cliffs, part of Poole Bay SSSI.

Collecting

While responsible collecting is not normally threatening to the scientific interest of the majority of palaeontological and stratigraphical sites, there is a type of site which can be considered vulnerable to collectors, if they act irresponsibly (Norman *et al.* 1990*b*). These are the sites at which fossils are highly localized, such as the examples cited earlier. Classic examples of these are fossiliferous sedimentary infills in fissured limestone; those found in Somerset and South Wales fall into this category. Others can be highly localized beds, such as the famous Granton Shrimp Bed locality in southern Scotland (Taylor 1988).

However, it should be emphasized that these are the exceptions within the full range of palaeontological sites in Britain (Wimbledon 1988), if the SSSI coverage is a fair reflection of the total site coverage, and such special sites deserve special consideration and protection, since they represent a unique and uniquely vulnerable aspect of Britain's natural heritage.

REALITIES AND SOLUTIONS

General statement

Given the generally agreed understanding that responsible collecting is an integral and necessary part of the conservation strategy for any palaeontological site, it must be inappropriate to pursue aims which would end in the hindering of access to the majority of fossil sites. The science of palaeontology will be unable to grow and develop in the absence of source material, and our network of palaeontological sites provides the vital resource for the great part of such activity. Further, in the wider context, it would be unwise to ignore or actively discourage visits to such sites by the general public, whose sympathy and understanding are needed if, in the longer term, our scientific concerns over the heritage value of such sites are to prevail in the political arena.

Consequential loss

If fossils may be removed from sites by responsible means, then it must be accepted that, with the passage of time, the fossil resource at any site will be depleted. This must be considered an acceptable loss, an inevitable consequence of the nature of scientific investigation at palaeontological sites, and indeed many other types of geological site, since their study is in essence field-based. Provided that the more important discoveries made at these sites are properly documented and find their way into museum collections, the scientific knowledge base gains from the loss of the site

resource. Irresponsible collecting resulting in a lack of documentary information for the locality constitutes absolute 'loss', no matter how beautiful the specimen.

Management of loss

Management of the rate and type of loss of material from sites in the British Isles must ultimately depend upon the establishment of widely accepted codes of practice relating to the removal of specimens. The word 'responsible' has been used on a number of occasions in this article, and in several others in recent years, in relation to fossil collecting. It is absolutely vital that a responsible attitude to the collecting of fossils is nurtured in the geological community (in its widest possible sense), simply because we are all dealing with a generally large but nevertheless finite component of our natural heritage. With this idea of responsibility for our natural heritage in mind I would like to offer some recommendations which, if widely adopted, would enable site users to make the most of palaeontological sites in a way that is pragmatic and caters for their various needs. I do this by recognizing that palaeontological sites do not all share the same characteristics. Some are more, and some much less, sensitive to collecting.

Vulnerable versus specimen-rich palaeontological sites

Vulnerable sites. From the point of view of a management strategy for all fossil sites, it is useful to identify those sites which are most vulnerable to collecting pressure. Such sites, as discussed earlier, are relatively few in number and small in geographical extent, when compared to the totality of fossil sites, but by definition contain a rare and limited resource.

In these circumstances it should be regarded as a priority to operate a permit system, in order to ensure that collecting is scientifically justifiable and that suitable repositories will be found for the storage and curation of the specimens, so that they may be studied freely by the geological community at large.

Specimen-rich sites. Many palaeontological sites would appear to have an extensive, though clearly not infinite, fossil resource. In these cases the priority for resource management must be seen in terms of 'husbandry', with a strong emphasis on open access and responsible collecting so that they are used as effectively as is practicable. Within this category of site a clear distinction should be drawn between high erosion and low erosion sites, and it should be recognized that differences in emphasis will be needed in their management, to ensure their long-term viability.

1. High erosion specimen-rich sites. Particularly in areas where there are rapidly eroding sea-cliffs, or in sites which are actively worked quarries (provided permission to collect can be obtained from the quarry firm), the collection of fossils should be regarded as a high priority. High rates of erosion or commercial excavation will inevitably result in high rates of loss of newly exposed fossils, so the more specimens that are collected, and the more regularly these sites are patrolled, the more likely the scientific community is to benefit from at least a percentage of new discoveries. (Examples include regular patrolling of the Oxford Clay brick pits by staff of Peterborough Museum which has resulted in some spectacular discoveries of marine reptiles in recent months. Among natural high erosion sites, museum, amateur and commercial collectors have made some spectacular discoveries in recent years on the southern coast of the Isle of Wight and the coastal cliffs in west Dorset.)

2. Low erosion specimen-rich sites. Inland sites do not generally suffer the high rates of erosion common to many coastal areas or actively worked quarries. In the absence of this 'scouring/refreshing' effect, fossiliferous beds can rapidly be rendered inaccessible, 'worked out' (and exceedingly dangerous) as they disappear beneath a massive overburden. The renowned 'slot' at Ludford Corner was a classic example of this effect though this has since been cut back and made accessible through NCC funding (Rowlands 1989). At such sites, fossil collecting should be done with consideration to the extent of the resource and its accessibility. Agencies such as the newly established Nature Conservancy Council for England, The Countryside Council for Wales and the Nature Conservancy Council for Scotland are empowered to monitor such sites and also administer

funds which may be granted for site clearance and restoration work in order to ensure that such sites remain viable as collecting and study resources.

Principal users of palaeontological sites

Given these distinctions between types of site and the degree and style of collecting that they allow, it is also appropriate to consider the types of 'user'. I distinguish five principal types of users of palaeontological sites: professional/commercial collectors, research scientists, amateurs/hobbyists, student groups, primary and secondary school parties. These are not absolutely clear-cut groups since individuals can be members of several categories simultaneously, or indeed of all if seen from the perspective of a lifetime's work for some individuals.

Commercial collectors. As has been emphasized on a number of occasions (see Taylor 1988; Knell 1991), these users of palaeontological sites have, in most cases, a vested interest in them and the commercial management of the resource, since it can form the basis for their livelihood. Occasionally their excavation techniques are 'responsible', and detailed notes are taken of the location and stratigraphical horizon from which the specimen was collected. The reason for this is two-fold: they realize the scientific value of such information and also its value for identification and ultimately for notional valuation, if intended for sale.

In recent years these collectors have been responsible for several important discoveries of fossils, particularly of large fossil vertebrates; this reflects the fact that large vertebrate fossils can attract high prices in the market place, and that these people are prepared to devote considerable time to developing their skills as collectors. As a consequence commercial collectors are very much in the vanguard of the collecting fraternity. At a time when university, college and museum funds for travel and research are extremely limited, the work of these collectors can be extremely valuable to the science as a whole and should be encouraged, provided that collecting is done responsibly and that research scientists gain access to the material.

The destination of fossils collected depends upon who is prepared to pay. Conflicts or differences of opinion between collectors, museums and academic research workers arise largely because of the mismatch between the commercial aspirations of professional collectors, the perceptions of academic research workers of the value to science of specimens and the limitations on funds faced by museum curators (Rolfe *et al.* 1988).

The ideal result for the scientist is that the specimens should be adequately curated and available for study in a recognized institution – no matter in which country that might be.

The museum curator will stress either the importance of having representatives of the local fossil flora or fauna, or alternatively that their collection provides a national or international overview of a particular palaeontological theme. The nature of the specimen will dictate the preferred approach.

In the case of amateurs and the general public, their concern is more one of the ethics of removal of national natural heritage items by such commercial collectors and their offer for sale on the open market.

Research scientists. With their knowledge and field experience, research scientists can be as competent at finding fossils as professional collectors; they simply lack the time and financial support to enable them to indulge in extended fossil prospecting trips. They too are committed to responsible collecting, since they value the resource they are using. Without it they cannot fulfil their research plans; equally important, without adequate locality and stratigraphic information a new specimen may be rendered virtually worthless from a scientific point of view.

The ideal ultimate destination of such collections is a well-curated museum where the natural heritage may be preserved for posterity.

Student groups. Fieldwork by university and college students at palaeontological sites frequently involves collecting from fossiliferous horizons. Such activities can involve the removal of large quantities of duplicates from sites. The vast majority of these will be lost at a later date, even though

specimens may have extensive field notes attached. This exploitation and subsequent loss, though perhaps understandable in general terms, can pose a considerable threat to some sites.

While it is undoubtedly essential for fieldwork exercises, such as collecting, to be undertaken by all students of the geological sciences, it is seen as increasingly important that students, and particularly their teachers, should take a much more responsible attitude to the resources of sites and the heritage value of material collected (Kneil 1991). Conservation and husbandry of finite resources such as this need to become increasingly a part of the undergraduate curriculum nationally.

Non-commercial collectors, amateurs/hobbyists. As a leisure activity, fossil hunting can be fun, healthy and rewarding and is popular with young and old alike. For the palaeontological research community at large this presents a marvellous opportunity, because amateurs and hobbyists will frequently pass specimens on to museums for identification (for example Mr Bill Walker's discovery of the new dinosaur *Baryonyx walkeri* which was donated to the Natural History Museum).

The primary concern for the curator and research worker, with this sort of activity, is that specimens may be collected without vital locality and horizon information. Education over the matter of specimen collecting, in the form of leaflets, meetings at local clubs and societies and professionally led field trips (such as those organized by the Geologists' Association), can help in this respect.

Primary and secondary school groups. Of increasing importance as a result of the appearance in Britain's schools of the new Government-inspired teaching initiative, the National Curriculum, is the requirement for school children to pay visits to and make collections from geological sites. The potential impact of this type of activity on the fossil resource at many sites is enormous, and is the source of some anxiety within the geological community.

Clearly there is a very great need to establish widely accepted codes of practice among the school teaching profession, concerning the use of sites and the removal of specimens by children during such visits. The problem in this respect is that relatively few of the teachers leading such groups will have a background in geology.

Owners/occupiers. Last, but not least, the users of palaeontological sites must consider the rights of the owners of such sites. As Taylor and Harte (1988) have shown, fossils are regarded as 'minerals' for the purposes of the Law. As a consequence they belong to the person holding the mineral rights to the land – usually the site owner or occupier. For fossils to be collected legally, permission should be sought from the owner of the land prior to collections being made, and title (ownership) may then pass legally to the finder of the fossils, provided this is with the agreement of the owner, and provided that this does not contravene one of the PDOs if this happens to be an SSSI. If fossils are removed from land without permission then this constitutes theft of property, unless of course the material is lying around loose in spoil heaps and trespass is not the means of access (this latter proviso does not apply in Scotland where even apparently abandoned material is owned and remains subject to owner's rights).

In some situations, title to, or ownership of, fossils has been deliberately abandoned by the legal owner as a matter of policy. Along the coast between Lyme Regis and Charmouth in Dorset, the local authority and National Trust, who between them own the coast, have decided to permit fossil collecting as part of a strategy to encourage tourists to the area.

THE FATE OF COLLECTED SPECIMENS

Another source of anxiety and comment within museums relates to the activity of commercial fossil collectors and the loss into private hands of specimens that might otherwise go to scientific collections. In reality this has always happened and will continue, since it is physically impossible to police all sites at all times. In individual cases this may rightly be deplored; however, in many

cases specimens of great scientific importance do eventually end up in national or regional museum collections owing to the responsible actions of these collectors and the relationships that many have established with their own local museums. In some cases it is probably true to say that the scientific value of a specimen may far outweigh its aesthetic appeal (a component of its commercial value) and it will not, as a consequence, attract a high market price, unless museums themselves compete for a specimen and in so doing drive up its price!

Unless scientists are empowered to do all collecting at all times on all sites, a situation which is plainly inconceivable, it is futile to try and prohibit non-scientific collecting of whatever type. The entire community (researchers, curators, collectors) must work collaboratively, obviously within the parameters set by their own professions, in order to ensure that collecting is done responsibly (as befits any element of our national heritage) and that the most scientifically valuable specimens are not lost to science in the long term. Such an approach requires considerable effort and understanding on all sides. Nevertheless, it has been the guiding principle since the time of the earliest collectors.

CONCLUSIONS

In most circumstances the collection of fossils from palaeontological sites is to be encouraged, since this activity will, in the long term, promote the science of palaeontology.

There are a small number of instances where the collection of fossils needs to be regulated and monitored, simply because the fossil resources at some sites are limited and their scientific and heritage value is high. These can be considered to be vulnerable sites.

Strategies relating to the management of the palaeontological resource at specimen-rich fossil sites will vary depending on the degree to which the site is subject to erosional (natural or man-induced) forces.

Collecting practice must be encouraged to be of a uniformly high standard through education and example, as befits specimens that are a component of our natural heritage. And there must be encouragement of attitudes which will foster a willingness to ensure that the scientifically most important specimens are not lost to science in the long term.

The price of fossils, established through commercialized fossil collecting, will continue to cause consternation so long as museums and universities are underfunded (and low priority is given to the acquisition of new fossils): a situation that is unlikely to change in the foreseeable future. Undesirable though it may be to put a monetary value upon any aspect of our natural heritage, it has been argued that there are merits in doing so for fossils. The value may be arbitrary, in most instances, but it may provide a way of raising political awareness among policy makers about an otherwise totally underestimated part of our national heritage.

Acknowledgements. I would like to thank a number of colleagues who have read and commented on earlier drafts of this article, but among them I should like to single out for special thanks Michael Taylor (Leicestershire Museums) and Peter Doyle (Thames Polytechnic), as well as Colin Prosser, Kevin Page and Stefa Kaznowska, all of the Nature Conservancy Council for England.

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DAVID B. NORMAN

Science Directorate

Nature Conservancy Council for England
Peterborough PE1 1UA, UK

Present address:

Sedgwick Museum

Downing Street

Cambridge CB2 3EQ, UK

Typescript received 4 July 1991

Revised typescript received 20 September 1991

APPENDIX

In general terms fossil collecting *per se* cannot, in most circumstances, be considered to be an undesirable activity, whether it is for scientific, educational or commercial purposes. It cannot be stated often enough that, without the activity of collecting, the sciences of stratigraphy and palaeontology would suffer and museums would lose a source of material for display or educational purposes.

There are, however, circumstances, ranging from inappropriate style of collecting (irresponsible use of portable power tools and heavy machinery, unjustifiable large-scale removal of specimens, lack of adequate recording of locality and horizon information with specimens) to the exploitation of vulnerable sites (collecting indiscriminately from isolated sites where the fossils are of extreme rarity), that are both undesirable (for the longer-term viability of sites as a scientific resource) and betray a disregard for the value of the National Natural Heritage (NNH) that is utterly deplorable.

Given these considerations, a general policy statement with regard to fossils and fossil collecting on SSSI has been issued (Norman *et al.* 1990b). An abridged version of this statement, which formed part of a longer statement relating to a specific incident of fossil collecting, is given below:

'The value of palaeontological and biostratigraphical SSSI rests ultimately upon their associated fossils, the sedimentary environment and stratigraphic context. In order for the scientific merit of such an SSSI to have been established, collecting and subsequent scientific study must have occurred. If palaeontological sites are to continue to have scientific relevance (rather than becoming simply a collection of historically interesting locations), further collecting of specimens and their study *must* be ensured.

Given that responsible collecting is a scientifically desirable activity, attention must then be given to the manner in which this is done, and the reasons for it being done.

The *manner* which must be encouraged does not really need to be explained to the audience reading this letter, but is clearly one by which adequate geological records of collections are made for future comparative research purposes (*A code for geological fieldwork*, Geologists' Association, 1975).

The *reasons* for such collecting on SSSI should ideally be scientifically justifiable (part of an individual or group research project, whose aims have been evaluated) and should eventually result in the placement of a proportion of the material (that which is of prime scientific importance, or is published) in a recognised institution (museum) where it can be conserved for posterity and made accessible to others. This "ideal" may not however be practicable in all circumstances. A minority of SSSI may require restrictions on collecting because of the rarity of particular fossils and/or the finite nature of the deposits. At the other end of the spectrum of site quality, SSSI subject to high rates of natural erosion (soft coastal cliffs for example) or high rates of artificial attrition (active working quarries which are known to yield important fossils) may require active promotion of responsible collecting as a means of ensuring that a percentage of the recoverable National Natural Heritage (NNH) is taken before it is lost either through erosion or mechanical destruction.'

A NEW GENUS OF EARLY LAND PLANTS WITH NOVEL STROBILAR CONSTRUCTION FROM THE LOWER DEVONIAN POSONGCHONG FORMATION, YUNNAN PROVINCE, CHINA

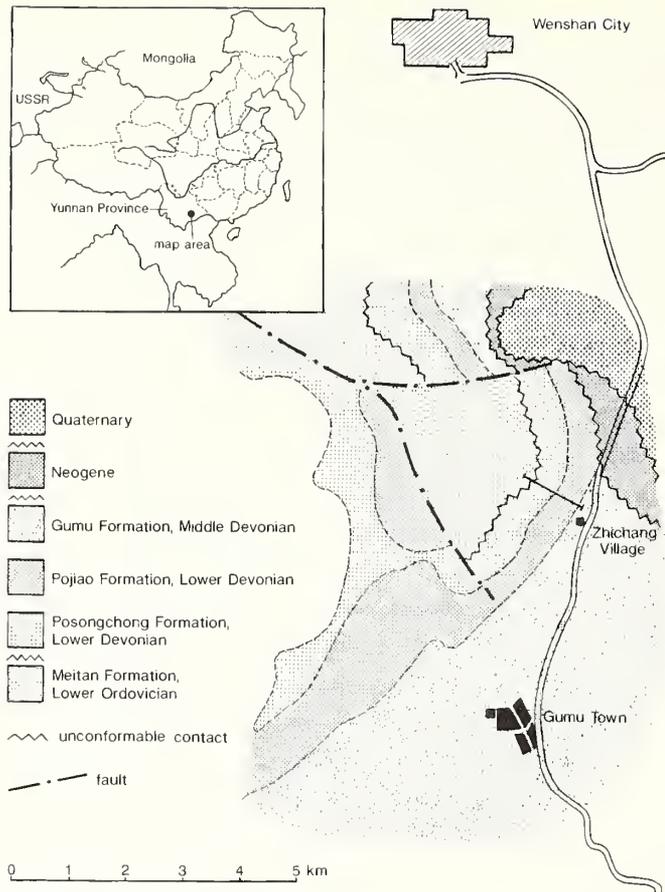
by LI CHENG-SEN *and* DIANNE EDWARDS

ABSTRACT. *Adoketophyton subverticillatum* (Li and Cai) comb. nov. is described from the Siegenian of southern Yunnan, China. It consists of dichotomously branching axes, with terminal compact strobili in which lateral units are inserted oppositely and decussately so that they form four vertical rows. Each unit comprises a stalked, fan-shaped, bract-like appendage bearing an adaxial sporangium with dehiscence into two equal valves. Although such reproductive characteristics parallel those of lycophytes, the shape of bract and absence of microphylls indicate that this plant presents a new combination of characters, presumably within the tracheophytes. It is perhaps closest to the Barinophytales, another group of vascular plants of uncertain affinity. Anatomical information, particularly on the cauline xylem and on the vascularization of the bract (if any) is required before assignment to a higher taxon. These Lower Devonian assemblages from Yunnan include cosmopolitan genera such as *Zosterophyllum* and *Drepanophycus*, but they also contain a high proportion of endemic taxa many of which exhibit novel combinations of characters not yet known elsewhere. Their distinctive nature may thus be evidence for provincialism in early land vegetation.

SOME of the most exciting recent discoveries in early Devonian palaeobotany have come from China (Li 1982; Geng 1983, 1985; Hao 1985, 1988, 1989*a*, 1989*b*). This is particularly apposite as the majority of the evidence for the nature of early land vegetation comes from Laurussia (Boucot and Gray 1982; Edwards 1990*a*, 1990*b*; Edwards and Davies 1990) providing somewhat biased analyses on vascular plant phylogeny, global biostratigraphy based on megafossils, and palaeogeography. Lower Devonian assemblages from Yunnan Province are important because they contain large numbers of specimens, are diverse and come from strata whose ages are being critically assessed (e.g. Hao 1989*b*). They contain cosmopolitan genera such as *Zosterophyllum* and *Drepanophycus* (Halle 1936; Hsü 1966; Cai and Schweitzer 1983; Hao 1985) as well as plants with combinations of characters that do not fit nicely into existing classifications (e.g. Geng 1983; Hao 1988). We describe such a plant here. It was originally named *Z. subverticillatum* by Li and Cai (1977), but their analysis was limited by the small number of fragmentary fossils. This reassessment is based on extensive new collections.

LOCATION AND STRATIGRAPHY

Details of the locality are given in Hao (1989*b*) and Text-figure 1. The fossils come from a hillside exposure, near Zhichang village, Wenshan district, Yunnan Province, of the Posongchong Formation from the horizon with *Stachyophyton yunnanense* Geng (1983) some 70 m below that with *Discalis longistipa* Hao (1989*b*), and 30 m above the base of the formation. There is no direct evidence for the age of these continental deposits containing abundant plants and fish. They overlie unconformably the Meitan Formation containing lower Ordovician fossils and are overlain by the Pojiao Formation with corals and brachiopods. The latter is considered equivalent to the lower part of the Yujiang Formation in Guangxi Province occurring above sediments dated as late Siegenian by conodonts. The Pojiao Formation is thus thought to be Lower Emsian and the underlying



TEXT-FIG. 1. Locality map showing outcrops to south of Wenshan City. Line to north-west of Zhichang village indicates section through Lower Devonian sediments.

Posongchong Formation, late Siegenian in age, although the possibility that it is earliest Emsian cannot be entirely eliminated.

MATERIAL AND METHODS

The matrix is a very fine, slightly micaceous sandstone with rather homogeneous texture and only weak bedding fabric. Depending on the extent of weathering, its colour ranges from cream to buff to yellow-grey, the latter relatively unweathered examples containing fossils with the most coalified material. In most specimens only a coaly dusting remains over an iron-stained impression, whose colour again is variable ranging from pale pink (Pl. 2, fig. 8) to tan to darker brown (Pl. 2, fig. 10). Many strobili retain their three-dimensional form and certain axes and sporangia are infilled with matrix. Casts of spirorbid worms are visible on some fan-shaped appendages (Pl. 1, fig. 5). Permineralizations range from individual cells replaced by limonite or a pink unidentified material, to small areas of replaced axis, to complete strobili replaced by presumed iron oxides (Pl. 1, fig. 4). Cellular preservation is rare (Pl. 4, figs 2-4, 7). Permineralized axes with preserved xylem occur in the same matrix, but not attached to a strobilus.

Coalified material removed on film-pulls or oxidized in Schulze's solution failed to yield cuticles,

spores or xylem. Morphological detail and three-dimensional relationships were achieved by developing specimens with tungsten needles (dégagement), a technique greatly facilitated by the soft texture of the weathered matrix except that coaly material very readily sloughed off. Relatively small rock specimens and permineralized fragments were dried, mounted on stubs and coated with gold prior to SEM examination using a Cambridge 360 SEM. More completely preserved axes and strobili were embedded in a cold setting resin sectioned, smoothed and polished for investigation by reflected light using an Olympus Vanox (Kenrick *et al.* 1991). The photographic equivalent of serial sections at close intervals (Text-fig. 2) was realized by alternately grinding, polishing and photographing an embedded fragment of a strobilus, 1.5 mm long. Grade 600 followed by 800 carborundum were used and approximately 0.1 mm of fossil and sediment removed at each stage so that sixteen serial photographs were obtained. Specimens CBYn 9002001-9002059 are deposited in the Institute of Botany, Academia Sinica, Beijing, China.

SYSTEMATIC PALAEOONTOLOGY

PLANTAE INCERTAE SEDIS

Genus *ADOKETOPHYTON* gen. nov.

Derivation of name. Greek *adoketos*, unexpected or surprising.

Type species. *Adoketophyton subverticillatum* (Li and Cai) Li Cheng-Sen and Edwards comb. nov.

Diagnosis. Distal aerial parts of plant with smooth dichotomously branching axes and terminal strobili composed of compound lateral fertile units. Each unit comprises a bract-like flattened appendage and single adaxially inserted sporangium with two valves and distal dehiscence around convex margin.

Adoketophyton subverticillatum comb. nov.

Plates 1-4; Text-fig. 2

Basionym. *Zosterophyllum subverticillatum* Li and Cai 1977, pp. 24-25, pl. 3, figs 1-3; text-fig. 8.

Type material. Holotype PB 6465 Li and Cai (1977), pl. 3, fig. 2, deposited at the Nanjing Institute of Geology and Palaeontology. As this is a fragmentary specimen, paratype CBYn 9002034a-b (Pl. 1, fig. 3; Pl. 3, fig. 1) is selected to demonstrate features of the strobilar characters in the diagnosis (Institute of Botany, Academia Sinica, Beijing, China).

Stratigraphy. All specimens come from the Posongchong Formation, Zhichang locality, Wenshan District, Yunnan Province, Lower Devonian (?Siegcnian) age.

Diagnosis. As for genus. Vegetative part of plant at least 9 cm tall with smooth axes 0.85 (-1.57)-2.6 mm in diameter ($n = 31$). Parallel-sided strobili with 4 rows of opposite and decussately inserted fertile units up to 90 mm long, the longest with 54 fertile units. Fan-shaped vertically overlapping lateral appendages, 3.2 (-5.6)-10.0 mm maximum width ($n = 76$) with maximum height 3.6 (-15.7)-8.4 mm ($n = 48$), and rigid decurrent stalks, circular in cross-section near base and 0.5 (-0.84)-1.3 mm in diameter ($n = 54$). Vertical distance between appendage insertion 3.2 (-4.9)-7.0 mm ($n = 47$). Sporangia attached to adaxial surface of stalk of appendage, 0.2-1.8 mm from front of insertion, by short stalk 0.11 (-0.6)-1.4 mm wide ($n = 10$) and 0.05 (-0.31)-0.7 mm high ($n = 7$) and covered by subtending appendage. Sporangia of two \pm equal valves, with distal dehiscence along convex margin. Valves sometimes slightly tangentially expanded so that circular to \pm elliptical in face view 1.5 (-2.23)-2.7 mm high ($n = 17$) and 2.0 (-2.7)-3.2 mm wide ($n = 16$) with border 0.08 (-0.2)-0.39 mm wide ($n = 6$). Anatomy unknown.

Description. This is based on almost sixty specimens, the vast majority being fragments of strobili. Attached,

subtending axes are smooth and considerably narrower than the strobili. The longest exhibit sparse more or less isotomous branching with wide (*c.* 50–70°) branching angles (Pl. 4, fig. 1), and little change in axis diameter from base to apex. Associated sterile axes are less regularly branched and may represent the basal regions of *Adoketophyton subverticillatum*. Circinate tips (Pl. 1, fig. 1) in close proximity to some strobili may also belong to *Adoketophyton*. Proximal parts of some strobili have been found, but most are incomplete distally. The longest 'fragment' (Pl. 1, fig. 3) is suggestive of a plant of quite substantial height, but its subtending axis is missing. Each strobilus comprises four vertical rows of overlapping fertile units, arranged in opposite and decussate pairs. The most conspicuous features of the strobilus are the more or less fan-shaped lateral appendages, which were originally described as sporangia by Li and Cai (1977). The variously fractured strobili and the greater number of specimens available for study have revealed the presence of sporangia inserted adaxially on the lateral appendages, and completely covered by them. Thus the strobilus is composed of lateral fertile units. We are reluctant to use the admittedly more convenient term 'bract' for the sterile segment as this has the connotation of a reduced leaf for which we have no evidence. The strobili are parallel-sided and show little change in appendage size or spacing from base to apex although there is limited evidence for slight twisting (Pl. 1, fig. 3).

The appearances of the strobili vary due to differing orientation during compression and plane of fracture. Plate 3, figure 2 shows an example where a single row of complete appendages is visible in abaxial view with members of two adjacent rows partly exposed 'on end'. Two rows of overlapping appendages are apparent in Plate 2, figure 1, while fortuitous fracture (Pl. 1, fig. 2) reveals the components of the fertile unit in longitudinal section. In the first two examples sporangia are usually, but not invariably, found on dissecting away the appendage (see Pl. 2, fig. 3). The latter show some variation in ab- or adaxial (face) view but are similar within a single strobilus. The majority are fan-shaped (Pl. 2, figs 1–6) with parallel-sided stalks expanding into triangular 'laminae' with straight sides and rounded or frayed distal regions. Some are more rounded laterally (Pl. 2, fig. 9) while others are slightly concave (Pl. 2, fig. 1). The position of a sporangium is sometimes marked by a shallow concavity (Pl. 2, fig. 2) and this is also seen in the curvature in the profiles of appendages (Pl. 2, fig. 3). However others are almost straight (Pl. 2, fig. 10). The basal regions of the appendages are revealed by development or seen in fortuitous fracture, being normally obscured by overlapping distal regions. The well-defined relief seen in the 'compression' fossils suggests that the stalks were quite rigid decurrent structures (Pl. 1, fig. 6; Pl. 4, fig. 6), circular in cross-section when free. This was confirmed by the serial transverse sections through the strobilus (Pl. 1, fig. 4; Text-fig. 2) where the axis becomes lobed below the more or less simultaneous departure of almost circular (in cross-section) appendage stalks. That the appendages were inserted in opposite pairs is confirmed in longitudinally fractured strobili (Pl. 1, fig. 2) and by strobilar axes lacking complete appendages (Pl. 1, fig. 6), although in the latter the exact position of superficial representatives is obscured by the decurrent bases. Vertical distances apart appear to be more or less constant within a strobilus, with no evidence for distal crowding although slight decrease is recorded in the longer specimens.

Stalks are inserted at 20–40° angles to the vertical, again with little variation within a strobilus. That between strobili may relate to degree of maturation in that it seems likely that the appendages would have moved abaxially, facilitating dehiscence of sporangia and scattering of spores.

Where parallel-sided the stalks range between 0.5 and 1.3 mm in width; their length cannot be so precisely determined (< 2.5 mm) because each stalk gradually flattens and expands into the blade. In cross-section at transitions they appear crescentic (Text-fig. 2J–P).

The blade itself is thin and rigid, seen as a thin straight or slightly curved line when fractured longitudinally

EXPLANATION OF PLATE 1

Fig. 1–6. *Adoketophyton subverticillatum* comb. nov. Posongchong Fm.; S. Yunnan. 1, CBYn 9002001; strobilus showing two rows of appendages and the appearance of that originally described as *Zosterophyllum subverticillatum*; note stalks of 'bracts' only visible at base and isolated circinate axis, $\times 3$. 2, CBYn 9002002; part of fractured strobilus showing sporangia and 'bracts' photographed under unilateral illumination; longitudinal ridges on sporangia on right of axis represent thickening at margin of sporangium valve, $\times 4$. 3, CBYn 9002034a; paratype; selected to demonstrate variation in strobilar appearance, $\times 1.75$. 4, CBYn 9002059; transverse section through permineralized axis, representative of that drawn in Text-figure 2; note that at this magnification outlines of organs are masked by staining, $\times 7.5$. 5, CBYn 9002015; impression of abaxial surface of 'bract' photographed in unilateral illumination to show spiroribids, $\times 10$. 6, CBYn 9002031; impression with bases of bracts in relief, $\times 4$.



(Pl. 2, figs 8, 10). Its extremities are sometimes irregular, suggestive of the fraying or erosion of less resilient tissues (Pl. 2, figs 2, 4). The slight adaxial curvature of opposing pairs produced a strobilus more or less rounded in transverse section, so that when young it must have superficially resembled an immature *Picea* cone rather than a more sharply angled structure as in a young *Garrya elliptica* inflorescence.

The sporangium is inserted just distal to where the stalk begins to flatten (Text-fig. 2; Pl. 2, fig. 7), up to 1.8 mm from the axis, but the actual junction is not often clearly visible, even when the subtending appendage has been picked away. The sporangial stalk is short and narrow, and often obscured by the sporangial valves (Pl. 3, figs. 1, 4, 6). In face view the latter range from almost circular to tangentially extended (Pl. 3, figs 1–3, 5–8), but are never wider than the subtending appendage at that level. The more pronounced elliptical examples sometimes result from lateral displacement of the valves of a dehiscent sporangium (Pl. 3, figs 5, 7). In side view, sporangia may be strongly flattened as if in section (Pl. 2, fig. 10) or more rounded when folded. The dehiscence line extends around the convex margin (Pl. 2, fig. 7). When sporangia are preserved in side view or are folded, it appears as a slight depression or ridge in the latter (Pl. 1, fig. 2). In certain compressions the margin is characterized by a narrow thicker coalified layer (< 0.39 mm). The possibility that the valves were not identical in size comes from dehiscent examples where the abaxial valve appears taller than the adaxial (Pl. 2, fig. 10), but this slight asymmetry could well result from differential shrinkage following dehiscence. We have failed to isolate any spores.

Anatomical investigations were a disappointment. Superficial cells of the strobilar axis and appendages, replaced by presumably iron oxides, are elongate and the fact that they are preserved suggests that they were thick walled (Pl. 4, figs 3–4, 7). In the radially orientated somewhat narrower cells of the blade, tapering ends are visible under the dissecting microscope, but when such fragments, and those from axes, were examined under the scanning electron microscope no further detail was observed (Pl. 4, fig. 2). Small 'papillae' on the blade may just reflect irregularities in the entombing matrix.

A partly permineralized stalk contained a block of cylindrical 'thick-walled' cells which under high power incident light microscopy gave the impression of being minutely transversely striated and hence tracheid-like. However, the superficial position of these cells and our failure to see any convincing thickenings under the SEM (Pl. 4, fig. 3) suggest that they were part of a peripheral zone of strengthening tissue, whose presence may account for the regularity in sectional appearance of the stalks.

Sections through strobili, while giving important information of relative positions of the fertile parts (Pl. 1, fig. 4; Text-fig. 2) failed to give any extra anatomical detail, except in confirming the existence of thick-walled tissues.

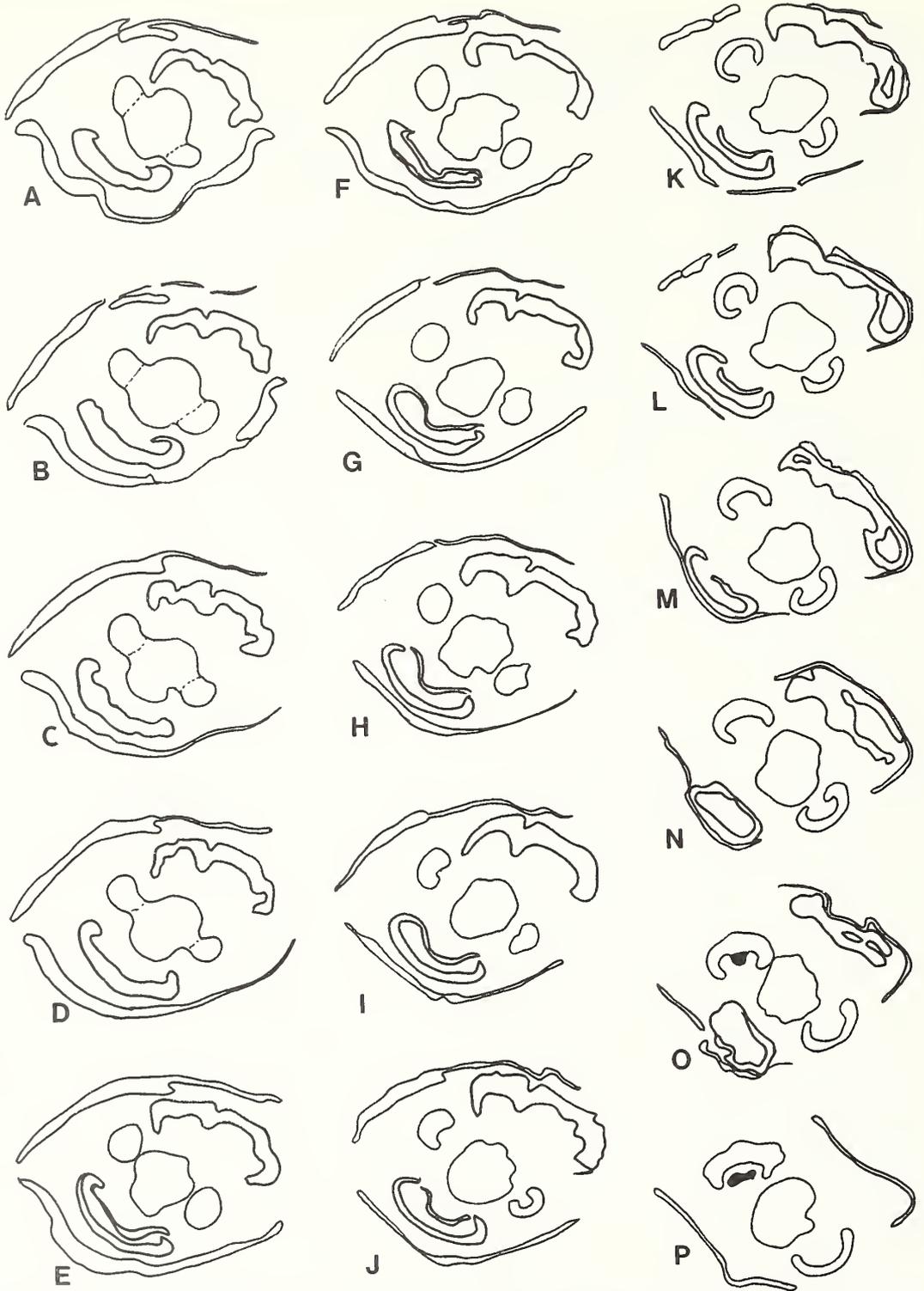
Permineralized axes associated with, but not attached to, the strobili contained centrarch xylem strands, with unusual pitting in the tracheids. We are reluctant to discuss these further here, because we have no unequivocal evidence that they belonged to *Adoketophyton*.

Affinities. Although superficially similar to *Zosterophyllum*, *Adoketophyton* clearly justifies a new genus on the basis of its compound fertile units, a feature not seen in the type genus nor in any other member of the Zosterophyllophytina where sporangia are inserted laterally on the strobilar axis or on aerial branching system, and are not related to any bract-like structures.

EXPLANATION OF PLATE 2

Figs 1–10. *Adoketophyton subverticillatum* comb. nov. Posongchong Fm.; S. Yunnan. 1, CBYn 9002012; abaxial face of exceptionally large 'bract' preserved in fine-grained brown mineral, $\times 3.75$. 2, CBYn 9002048; adaxial face of incomplete 'bract' showing depression originally occupied by sporangium, $\times 8$. 3, CBYn 9002048; bases of 'bracts' in profile and abaxial view, $\times 6.5$. 4, CBYn 9002033; adaxial face of 'bract' showing rock-infilled stalk just below missing sporangium, $\times 9$. 5, CBYn 9002045; abaxial face with bulge marking position of sporangium, $\times 7.2$. 6, CBYn 9002046; adaxial face of 'bract' with remains of sporangium, $\times 6$. 7, CBYn 9002035; impression of sporangium with thickened rims and possible attachment, $\times 9.1$. 8, CBYn 9002004; pale impression with dusting of coaly material showing 'bracts' in vertical section and attached sporangia, $\times 6.25$. 9, CBYn 9002009; small 'bracts' with more rounded outlines, $\times 5.2$. 10, CBYn 9002004; well preserved specimen, with coalified material partly covering orange-brown stained impressions; note the divergent 'bracts'; sporangia towards centre are split into two valves, the abaxial being longer; below there is an uncovered sporangium, $\times 7.5$.





TEXT-FIG. 2. A-P, CBYn 9002059; drawings of successive ground surfaces of T.S. strobilus; note the terete outline of the stalk of the fertile appendage when it separates from the strobilar axis; solid black area indicates base of sporangium, $\times 11$.

Intimate association of a leaf and single sporangium, either borne in its axil or on its stalk, is a lycophyte characteristic and in the vast majority of genera such sporophylls are aggregated into strobili. Superficial reading of the description of the fertile parts in the generic diagnosis of *Adoketophyton* would thus seem to indicate lycophyte affinity. However lycophytes are also characterized by the presence of microphylls, i.e. leaves, which are supplied by a single trace from the cauline stele, there being no leaf gaps. The majority of microphylls are undivided and contain a single vein, but some Devonian examples have divided leaves with correspondingly more complex venation (Bonamo *et al.* 1988). In that *Adoketophyton* has smooth axes, and as far as we are aware, no indication of even incipient leaf traces (cf. *Asteroxylon*), it cannot be assigned to the lycophytes. Further the fan-shaped appendage bearing the sporangium is unlike that known for any Devonian lycophyte sporophyll. With this in mind, plus awareness of our almost complete ignorance of the anatomy of *Adoketophyton*, we do not think that the genus is exhibiting heterobathmy – here seen as advanced reproductive features on unmodified smooth axes. This has been suggested by Schweitzer (1980) for *Drepanophycus spinaeformis*, where the reverse is seen and shoots show cauline stelar and foliar characters of lycophytes (Rayner 1984), but there is no consistent association of microphyll and sporangium in the fertile region. Schweitzer regards *D. spinaeformis* as the most derived member of the zosterophylls, but others have united it formally with *Baragwanathia* and *Asteroxylon* in the Drepanophycopsida (Rayner 1984) or informally in the pre-lycophytes (Edwards and Davies 1990; Li C.-S. in press), the phylogenetic connotation being obvious (Niklas and Banks 1990). In the case of *Adoketophyton*, we consider the compound fertile unit an example of convergence, a similar response to selection pressures relating to protection and nutrition of the sporangium, and that this genus is not representative of the ancestral group that gave rise to the lycophytes (see also Niklas and Banks 1990).

A similar association of sporangium and subtending bract was described by Stepanov (1975) in a new genus, *Uksunaiphyton* of uncertain affinity from the early Devonian of the Kuznetsk Basin, Siberia. Strobili, each comprising a single row of appendages, terminate smooth, bifurcating axes, but the distally curving bract is reconstructed as linear. This appearance may well result from longitudinal fracture of a flattened structure, thus strengthening similarities with *Adoketophyton*, but we would like further information on the Siberian specimens before speculating further on affinities.

The Barinophytaceae is a group of Devonian plants of uncertain affinity in which strobili consist of elongate almost linear lateral appendages each with a single large sporangium. Best known is heterosporous *Barinophyton*, where two rows of alternately inserted appendages are recurved abaxially, with each appendage bearing a sporangium on its concave surface, and twisted so that the two rows of sporangia face each other. The xylem in the cone axis is exarch (Brauer 1980). The strobilus of *Protobarinophyton*, which extends into the Lower Devonian in Siberia, is similarly constructed, but is terminal and solitary, whereas those of *Barinophyton* are pinnately arranged (Brauer 1981). These plants differ from *Adoketophyton* in appendage shape and sporangial insertion. Less completely known and hence putative members of the Barinophytaceae are *Krithodeophyton croftii* (Siegenian, S. Wales, Edwards 1968) and the fructification associated with *Enigmophyton superbum* (Frasnian of Spitsbergen, Hoeg 1942) where strobili comprise two rows of appendages and sporangia. Sporangia of both taxa are thought to alternate with linear bracts, although their exact relationship could not be determined.

In contrast the strobilus of *Stachyophyton yunnanensis* (Geng 1983), found at the same horizon as *Adoketophyton*, has spirally arranged lateral units, each consisting of a linear appendage which bifurcates terminally and to which a more or less elliptical sporangium is adaxially attached. Such examples illustrate the range of complexity (usually underemphasized) in Devonian strobili which we extend further with this description of *Adoketophyton*. However, we are reluctant to assign the new genus to an existing group and leave it under *Incertae Sedis*.

TABLE 1. Species lists from eastern and southern Yunnan Province, China. Stratigraphy based on Liao *et al.* (1978). For endemic genera, see Li (1982); Geng (1983, 1985); Hao (1988, 1989a, 1989b); and Hao and Beck (1991a, 1991b). (? indicates of uncertain taxonomic position; Z, zosterophyll; R, rhyniophyte; T, trimerophyte; * endemic species; † endemic genus).

Xujiachong Fm.	* <i>Zosterophyllum yunnanicum</i> Z * <i>Z. australianum</i> Z † <i>Hsia robusta</i> R <i>Drepanophycus spinaciformis</i>	Pojiao Fm.		Emsian
Guijiatum Fm.	? <i>Z. myretonianum</i> Z	Posongchong Fm.	* <i>Z. contiguum</i> Z † <i>Z. cf. australianum</i> Z † <i>Discalis longistipa</i> Z † <i>Adoketophyton subverticillatum</i> ? † <i>Huia recurvata</i> ? † <i>Stachyophyton yunnanense</i> ? † <i>Gumua zyzzata</i> Z † <i>Eophyllophyton bellum</i> ? † <i>Catenalis digitata</i> ? † <i>Yunia dichotoma</i> T	Siegenian
Xitum Fm.	Various algac <i>Z. sp.</i> Z	~~~~~		
Xiaishancun Fm.		No deposition in Yunnan		Gedinnian
Uppermost Yulongsi Fm.				
Eastern Yunnan		Southern Yunnan		Europe

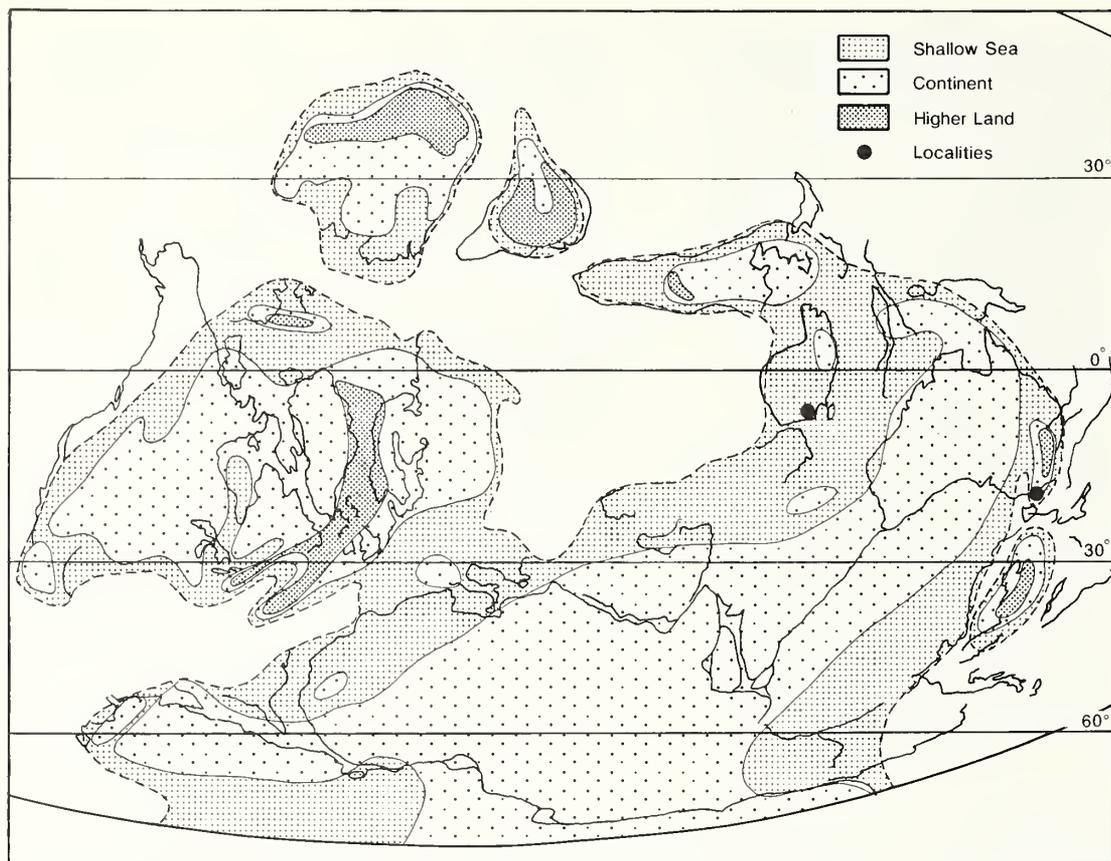
DISCUSSION

The Lower Devonian species list of higher plants from Yunnan Province given in Table 1 is a remarkable tribute to the recent research activity of Li, Cai, Hao and Geng, and will undoubtedly be extended as extensive collecting continues. Edwards and Davies (1990, fig. 16.3), have recently shown an increase in species in the late Siegenian and early Emsian of Laurussia and inclusion of the Chinese data would accentuate this increase in diversity. When analysed in terms of higher taxa in Laurussia (fig. 16.4) it is seen that rhyniophytes and trimerophytes account for some of the increase, but the major contributors are zosterophylls and taxa which cannot be readily accommodated in the three major subdivisions ('other' in fig. 16.6) or 'pre-lycophytes'. This broadly parallels the affinities of the Chinese species in Table 1. Such proliferation of taxa showing novel combinations of characters would seem to be a botanical example for the increase in disparity

EXPLANATION OF PLATE 3

Figs 1-8. *Adoketophyton subverticillatum* comb. nov. Posongchong Fm.; S. Yunnan. 1, CBYn 9002032b; counterpart of base of specimen in Pl. 1, fig. 3; sporangium on lower left is in relief and 'on edge' with dehiscence line visible, $\times 7.2$. 2, CBYn 9002028; part of spike; circular sporangium at top was revealed after removing 'bract'; at bottom is seen typical appearance of entire 'bract' and two rows in profile, $\times 3.8$. 3, CBYn 9002029; part of strobilus with two uncovered sporangia, $\times 5$. 4, 9002037; 'bract' with sporangium, $\times 8.4$. 5, 7, CBYn 9002038; uncovered sporangium; 5 shows attachment and 7, photographed under unilateral illumination, shows overlapping valves, $\times 8.5$. 6, part of spike shown in Pl. 2, fig. 8, $\times 9.3$. 8, CBYn 9002027; two uncovered sporangia near base, and two intact 'bracts' above, $\times 7.6$.





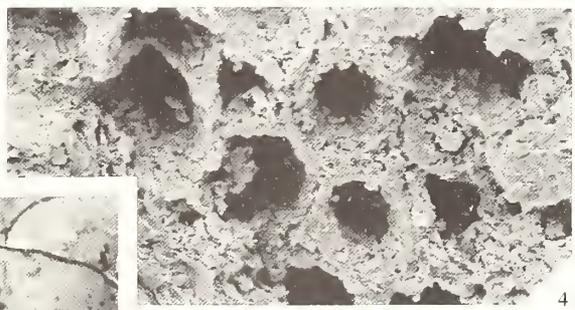
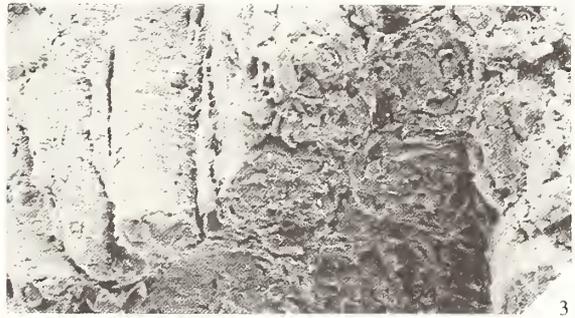
TEXT-FIG. 3. Map showing land masses in Lower Devonian times based on Cocks and Scotese (1991) for the earliest Devonian, but modified in that outlines of certain present-day geographical areas are omitted. Localities are in Yunnan and Australia.

that Gould (1989, pp. 49, 207 *et seq.*) thought symptomatic of the initial radiation of a major group, although when compared with the arthropods in Gould's example, the morphological basis for variation in these relatively simple land plants is far more limited.

The record in Laurussia suggests an initial radiation of land plants (e.g. *Cooksonia*) with isotomous branching and terminal sporangia, archetypal features that severely constrained the extent of variation. Change in mode of branching (apical development) seen early in the Devonian of this

EXPLANATION OF PLATE 4

Figs 1-7. *Adoketophyton subverticillatum* comb. nov. Posongchong Fm.; S. Yunnan. 1, CBYn 9002043; uncovered axes, one of which terminates in a strobilus (arrowed), $\times 1$. 2, CBYn 9002007; permineralized 'bract' showing outlines of superficial cells, $\times 50$. 3, CBYn 9002041; permineralized (? limonite) outer cells of bract stalk; note that the cell surface on the left bears faint horizontal lines, $\times 500$. 4, CBYn 9002041; cells as in 3 but with wall only preserved, $\times 480$. 5, CBYn 9002039b; semi-permineralized strobilus, with stalks in relief and sporangia (e.g. that in face view near base) partially preserved in limonite, $\times 8.2$. 6, CBYn 9002030; impression fossil showing the attenuated bases of the stalks in relief, $\times 5.5$. 7, CBYn 9002041; permineralized cells of superficial layers of stalk, $\times 205$.



palaeoregion was a release from such archetypal constraints with concomitant increase in disparity. There was also anatomical variation, particularly in the nature of conducting tissues, with plants of similar morphology containing water-conducting tissues characteristic of mosses (*Aglaoophyton (Rhynia) major*, D. S. Edwards 1980), of vascular plants or of unique construction (Hueber 1982; Kenrick *et al.* 1991).

Whether or not such a pattern is repeated on a global scale is conjectural as elsewhere we have only tantalizing glimpses of early land vegetation both temporally and spatially. Later Devonian records from China and Australia broadly correspond in that there are some cosmopolitan plants, but they also contain endemics of uncertain affinity. Anatomical data are sparse, particularly in Australia. A difference is that the Chinese plants appear more complex in organization than coeval Laurussian taxa although to date there are relatively few late Siegenian to early Emsian records in the latter area. A small, but diverse, Pridoli assemblage from north-west China contains a single rhyniophytoid with more complex sporangia than found in Laurussia, but has similarity with *Podolia* in the presence of a small 'leafy' axis of uncertain affinity (see Edwards 1990*b*, p. 237 for discussion). Palaeogeographically this Xinjiang record is probably on the Kazakhstan plate complex, and hence some distance away from both Laurussia and South China localities (Edwards 1990*b*, Chen Xu pers. comm.). In contrast, the Ludlow and early Devonian assemblages from Australia occur in the same geographic region (Victoria). For the most part they differ in composition from the coeval Chinese and Euramerican assemblages, but in the late Silurian again show greater complexity in organization than those for Euramerica. The most surprising element in the Ludlow is the pre-lycophyte *Baragwanathia*, also recorded in the Australian Lower Devonian where it is accompanied by *Zosterophyllum australianum*, *Salopella caespitosa*, *S. gracilis*, *Dawsonites subarcuatus*, *Uskiella* sp., *Yarravia oblonga*, and *Hedeia corymbosa*, an assemblage lacking the disparity of the Chinese one.

Recent palaeogeographical reconstructions for the late Lower Devonian (Text-fig. 3) place South China just south of the equator (*c.* 10° S), somewhat further north than the extensive Laurussian localities (10°–30° S) and Australia (20°–30° S) and close to the latter (Cocks and Scotese 1991). In 1987, Raymond included China and South Laurussia as subunits within a major equatorial–middle latitude phytogeographical unit, in an analysis based on plant traits, such as clustering of sporangia, density of spines. A similar result was achieved by Raymond, Parker and Barrett (1985) on distribution of taxa. Current Chinese investigations emphasize the distinctive nature of the Yunnan assemblages, which certainly cannot be attributed to regional taxonomic practices (Banks 1980; Raymond 1987), but sensible discussion on its phytogeographical and evolutionary significance requires further data, and in addition supporting information on dispersed spore assemblages.

Acknowledgements. We are indebted to Hao Shou-gang for his unselfish help and advice. This research was supported from the Science Fund of the Chinese Academy of Sciences via Professor Hsü Sen, Institute of Botany, Academia Sinica, Beijing and also by a small grant from the British Council which enabled Li to visit Britain. Both sources of funding are gratefully acknowledged. We also thank Drs C. R. Scotese, L. R. M. Cocks and W. S. McKerrow for allowing us to use their palaeogeographical reconstructions.

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LI CHENG-SEN

Institute of Botany
Academia Sinica
Xiangshan Beijing 100093

DIANNE EDWARDS

Department of Geology
University of Wales College of Cardiff
P.O. Box 914, Cardiff CF1 3YE

Typescript received 14th February 1991
Revised typescript received 1st May 1991

THE TYPE MATERIAL OF THE JURASSIC CEPHALOPOD *BELEMNOTHEUTIS*

by D. T. DONOVAN and M. D. CRANE

ABSTRACT. The coleoid genus *Belemnotheutis* Pearce, 1842, from the Lower Oxford Clay (Jurassic; Callovian) of Christian Malford, Wiltshire, England, gave rise to controversy and bad feeling between Richard Owen and Joseph Pearce, Gideon Mantell and others. Owen erroneously combined *Belemnotheutis* with an ordinary belemnite rostrum in his reconstructions of the belemnite animal. The type material of the type species, *B. antiquus* Pearce, is catalogued and described in detail for the first time. The species possessed a phragmocone with about 50 chambers, a museular mantle, an ink sac, and ten arms furnished with pairs of hooks and also bearing suckers. Specimens range from about 100 mm to 300 mm in total length.

THE coleoid genus *Belemnotheutis* was described and named by Joseph Channing Pearce (1811–1847) in 1842. It soon became the subject of acrimonious controversy between Richard Owen (1804–1892) on the one hand, and Pearce and his friends on the other. The present contribution gives a summary of the controversy, from published and unpublished material, and redescribes the type material.

HISTORICAL

The famous Oxford Clay locality of Christian Malford was discovered about 1840 during the construction of the Great Western Railway. Pearce heard of the finds in April, 1841 (Pearce 1842, p. 592; where the reference to Cheltenham must surely be a mistake for Chippenham) and visited the locality in the summer of the same year. The fossil cephalopods included ammonites with apertural features preserved and several kinds of coleoids. Fossils were collected and sold by dealers, but Pearce evidently collected his own material. He wrote to Owen (Appendix 1 (1)) on 18 March 1842 '...I remember your kindness when in London and since that period have been collecting ... the Ammonites ... from the Oxford Clay of Christian Malford to the extent of some hundreds of specimens ...'. We cannot know the extent to which he also relied on professional collectors and/or exchange with others for material from this locality. Coleoids were rarer than ammonites and required careful excavation of the clays. Collectors or dealers kept the pit open until at least 1854 (Donovan 1983, p. 485). Dealers sometimes combined more than one imperfect fossil in order to produce a more 'complete' specimen (Donovan 1977, p. 31) and specimens in old collections must always be regarded with this possibility in mind.

Pearce read a paper on his finds to the Geological Society of London on 5 January 1842, published as an unillustrated abstract (Pearce 1842). The full paper was never published, perhaps because the ammonites with 'mouth-parts' which he mentioned had already been described and illustrated by Pratt (1841*a*) (see below). Among the fossils described by Pearce were 'remains of an animal considered to have been probably allied to a Sepia', belemnites, and 'an animal to which he has applied (since the paper was read) the name of *Belemnotheutis*'. The report of Pearce's description of this latter fossil was brief:

'... the lower part is conical, blunt at the apex, and chambered internally like the alveolus of a Belemnite, with an oval siphunculus near the edge of the chambers ... it has a brown thick shelly covering which gradually becomes thinner towards the superior part ... immediately above the chambers is an ink-bag resting on what resembles the upper part of a sepiostaire, and composed of a yellow substance finely striated transversely, being formed

of laminae of unequal density...in some specimens, broken longitudinally through the middle, are exposed long, flat, narrow processes of a different structure...immediately beneath the superior contraction are two long feather-like processes, and one or more which are short, indicating, the author thinks, probably the situation of the mouth.'

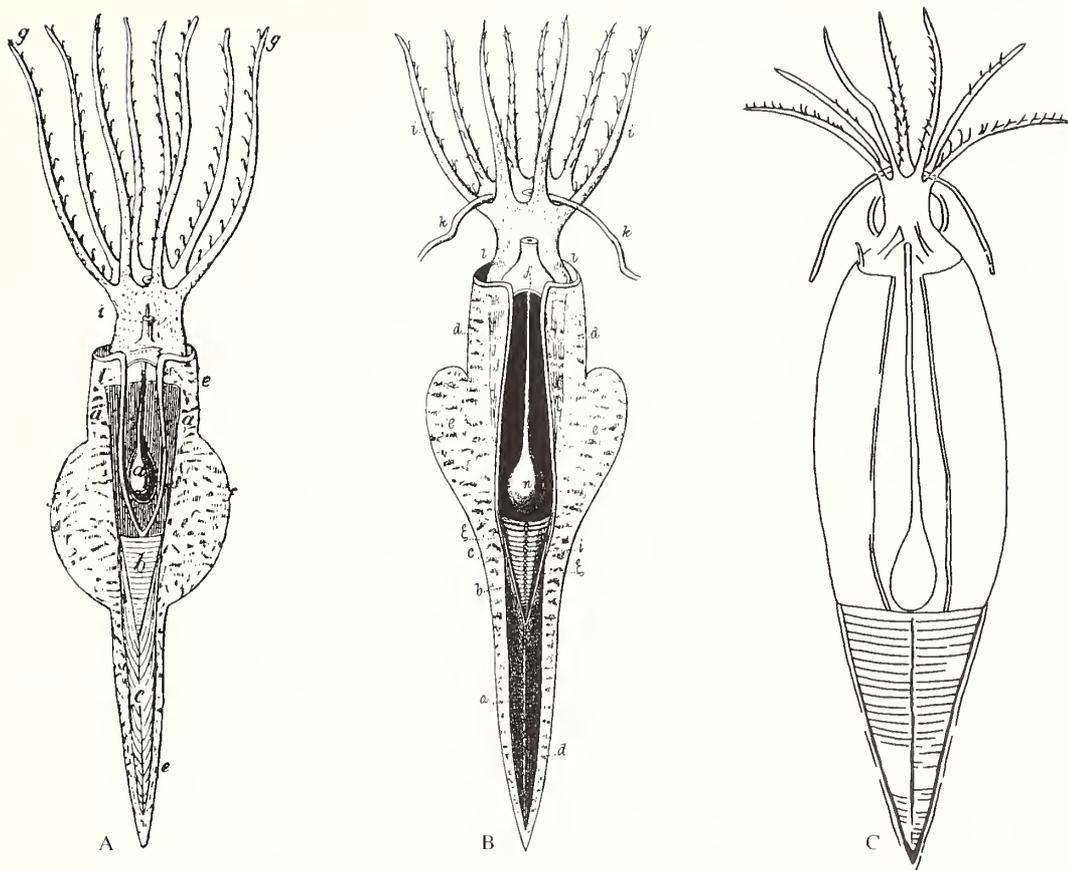
Richard Owen, who had described the first *Nautilus* to be brought to Europe in 1832, and had written the article on Cephalopoda for Rees' *Cyclopaedia*, was present at the meeting (Pearce 1847, pp. 75–76). A year later his wife Caroline noted in her journal for 25 February 1843 'Mr. Pratt, the collector of belemnites, here. A most interesting collection of portions of this long mis-known fossil now in R's possession. The ink-bags, the striated portions of mantle, and tentacles with hooks, all beautifully clear.' (R. S. Owen 1894, I, p. 212). These remarks suggest that Owen had already made up his mind that the new Christian Malford fossils were belemnites. Shortly afterwards he exhibited a specimen obtained by the Marquis of Northampton (Owen 1844, pl. 3 or pl. 5) and one of the Pratt examples (Owen 1844, pl. 4) at the Hunterian Lectures at the Royal College of Surgeons, and in the published version of the lectures there is a reconstruction of a belemnite in which the characters of *Belemnotheritis* are combined with a belemnite guard (Owen 1843, p. 333, fig. 133) (Text-fig. 1A).

Samuel Peace Pratt F.R.S. (1789–1863) is credited with being the first to describe the exceptionally well-preserved ammonites from Christian Malford (Pratt 1841). The ammonites figured in his paper were chiefly specimens in the Bristol Institution collected by Samuel Stutchbury, the curator, and drawn by Stutchbury's assistant W. H. Baily. The majority are now in Bristol Museum. Pratt was induced to present some, at least, of his *Belemnotheritis* material (Owen 1856, specimen nos 25, 28, 30) to the Royal College of Surgeons, London, of which Owen was Conservator. Other specimens were presented to the College by the Marquis of Northampton P.R.S. (Owen 1856, specimen nos 26, 27, 29, 31, 32) and by W. J. Broderip F.R.S. (Owen 1844, p. 65), although the latter were not catalogued as *Belemnotheritis* by Owen (1856). All this material was unfortunately destroyed when the College was damaged during an air raid in 1941.

The fossils mentioned in the last paragraph were described by Owen in a paper read to the Royal Society on 21 and 28 March 1844 (Appendix I, (2)), which was refereed by J. E. Gray (1800–1875) of the British Museum (Appendix I, (3)), and published the same year (Owen 1844). A summary by D. T. Ansted was published by the Geological Society in February 1845 (Owen 1845). Owen made no mention of Pearce's prior paper to the Geological Society, or of his new name *Belemnotheritis*. He included the specimens to which Pearce had applied his name in the genus *Belemnites* and in the species *B. owenii* Pratt. Owen wrote (1844, p. 66) 'the species of Belemnite have been classified according to the modifications of the spathose guard; the one under consideration...was first recognised as a new species by Mr. Pratt, who has honoured me by naming it *Belemnites Owenii*'. This was in fact the first publication of the name (Sherborn 1929, p. 4662).

Owen believed that *Belemnotheritis* phragmocones had become detached from guards before fossilization, and that all such phragmocones had been associated, in life, with a belemnite guard of the common type. He wrote (1844, p. 70): 'The entire phragmocone, with its capsule [i.e. the aragonitic sheath], of these Belemnites from the Oxford clay, has been found not unfrequently isolated and detached, having slipped out of the alveolar cavity of the guard'. Except for this error, Owen gave a detailed and perceptive account of the Christian Malford *Belemnotheritis* and was probably the first to recognize fossilized muscular mantle, giving magnified pictures of the muscle fibres in *Belemnotheritis* and a modern squid (Owen 1844, pl. 7, figs 3–4). He used the presence of an ink sac to infer relationship with the living 'naked Cephalopods' and to classify the belemnites with his Dibranchiata as opposed to the *Nautilus* and the ammonites, in which ink sacs had never been found (Owen 1844, p. 72).

The restoration published by Owen (1844, pl. 8) was similar to that of 1843, with certain details added on the basis of a specimen lent by William Cunnington (now BM(NH) C.5020; Owen 1844, pl. 6). Owen thought that this showed parts of the tentacles, which he added to the restoration (Text-fig. 1B, k, k). It is one of a few specimens which have symmetrical semicircular structures on either



TEXT-FIG. 1. Reconstructions of belemnites and *Belemnotheritis* by Owen and Pearce. A, 'Belemnite restored' from Owen, 1843, p. 598. The rostrum *c* and phragmocone *b* are those of a typical belemnite. The arms with hooks and ink sac are based on *Belemnotheritis*, on account of Owen's erroneous assumption that the *Belemnotheritis* phragmocone had become separated from a belemnite guard. B, reconstruction from Owen, 1844, plate 8. Essentially the same as the 1843 restoration, except that a pair of tentacles *k* has been added. C, MS restoration by Pearce, date unknown, Bristol Museum archives, re-drawn by Colin Stuart.

side of the 'head'. Owen concluded (1844, p. 80) that these were the crystalline lenses of the eyes (Text-fig. 1B, *l, l*). They appear, however to be strips of muscular tissue.

Pearce made a reconstruction which was not published but survives in his papers (Appendix 1, (4)) and is here reproduced as Text-figure 1C. It appears to have been influenced by Owen's 1844 reconstruction (which Pearce had seen, see below) because of the way that the mantle is cut away to show the ink sac, and because tentacles are present. The correct *Belemnotheritis* phragmocone is of course shown and the semicircular structures are placed differently. Mantell published a reconstruction (1848, pl. 14, fig. 1) which shows the correct phragmocone, and lateral fins and tentacles following Owen's second version.

Owen evidently sent a copy of his 1844 paper to Channing Pearce, who wrote to Owen in a letter dated 16 November 1844 (Appendix 1, (5)):

'It has given me great pleasure to read your paper on Belemnites from Christian Malford which you so kindly gave me but I think time will prove that the specimens with hooks belong to a distinct animal without a guard beyond the brown coating which invariably covers the chambers of this singular fossil. I examined this brown covering by Mr.

Bowerbank's glass and he was decidedly of opinion that it was an external surface; you are aware no doubt, I described it as a distinct Genus (*Belemnotheutis*) some time ago in The Proceedings of the Geological Society and I am sorry you did not allude to it.'

Owen must have immediately written to James Scott Bowerbank (1797–1877) about the assertion that the brown coating of the phragmocone was an external surface, for Bowerbank replies to Owen on 20 November 1844 (Appendix 1 (6)):

'We *have* got so far as to be able to pronounce decidedly with the microscope whether a substance be corneous or membranous & that the substance under consideration is neither the one nor the other but composed of prismatic structure radiating from a line passing longitudinally through the body of the Animal & similar in appearance & structure to the bony substance of the Belemnite & this I shall be happy to demonstrate to you upon my own specimens whenever it may be convenient to you to come to my house to see it.'

Bowerbank then wrote of his intention to call at the Royal College of Surgeons in the hope of seeing Owen. They presumably met and discussed Pearce's letter, quoted above, for Bowerbank wrote to Pearce on 2 December (Appendix 1, (7)), with reference to the question of the external surface:

'...I do not recollect the precise words I used but the import of them I well remember & which is: that the substance surrounding the Phragmacones was not "part & parcel" of the chambered portion or phragmacone but in reality equivalent to the solid fusiform belemnite & that it really represented that structure although in a very abbreviated form.'

He went on to say that he had again carefully examined the material and found that its structure agreed exactly with that of the belemnite guard, being composed of polygonal prismatic crystals, and that he had confirmed his original idea that the *Belemnotheutis* specimens

'are in fact neither *more* nor *less* than Belemnites having the spathose guard very much abbreviated, & this extreme shortness no more warrants us in separating it from the Genus Belemnites than the extreme length of *B. tubularis* of the Lias would warrant us in making it the type of a New Genus.'

The conclusion that the sheath investing the phragmocone was homologous with the belemnite guard implied, of course, that Owen was wrong in believing that the *Belemnotheutis* phragmocones had become separated from normal belemnite guards. Bowerbank did not say so in so many words, but did write that 'Mr Owen is in error in making the one with the long spathose guard [*B. owenii*] ... to be the same species....' remarking that he had seen many belemnites with part of the phragmocone, but never one with part of the body preserved, and conversely none of the ones with the body *Belemnotheutis* had a 'long spathose guard'. Thus Bowerbank agreed with Pearce on the technical points but did not support *Belemnotheutis* as a separate genus.

In November 1846 Owen was awarded the Royal Society's Royal Medal in recognition of his 1844 paper on belemnites. The September 1846 number of a new (and short-lived) periodical, the *London Geological Journal*, included (without explanation) a copy of Owen's second reconstruction of the belemnite animal (Owen 1844, pl. 8). This prompted Pearce to send the editor a paper stating 'the facts which appear to me to oppose the conclusion, that these Cephalopoda [i.e. *Belemnotheutis*] are really the animals belonging to the well-known fossil bodies termed Belemnites' (Pearce 1847, p. 75).

The editor, Edward Charlesworth (1813–1893), printed the article in his February 1847 number, together with extracts from Owen's 1844 memoir, and an editorial in which he accused Owen of deliberately omitting from that memoir any mention of Pearce, his material or his study of it. He went on (Charlesworth 1847*a*, p. 81):

'We should not have thought this omission on the part of Prof. Owen required any special notice beyond the reference made to it by Mr. Pearce, were it not that like cases are so common as to constitute an evil of no slight magnitude in the progress of scientific research.'

He gave other examples where he considered that progress had been hindered by uncritical acceptance of the opinions of eminent authorities or the neglect of the views of less well-known

workers, discussing the influence of Deshayes and Agassiz at some length, and finally returning to his original point (Charlesworth 1847*a*, p. 85):

‘Mr. Pearce may have no pretension to compete with Prof. Owen in a knowledge of the organic laws of the Cephalopoda, still his sagacity may be equal to the task of comparing the shell of *Belemnoteuthis* with the phragmocone of the Belemnite-guard, and judging how far the amount of correspondence admits the hypothesis of their being one and the same.’

Pearce’s paper states and expands the microscopic evidence which had been supplied by Bowerbank and which has already been quoted, and emphasizes again that *Belemnoteuthis* had never been found with a belemnite guard attached. The paper was illustrated by lithographs of two examples which Pearce had acquired since reading his 1842 paper [BRSMG Ca5242, Ca5240]. The generic name was now spelt *Belemnoteuthis*. The question of the correct form is discussed below (p. 280). The specific name *B. antiquus* was introduced for the first time, presumably to bring home the fact that the fossils were not *Belemnites owenii* and perhaps also to ensure their separate identity even if the genus *Belemnoteuthis* should be generally rejected.

Joseph Channing Pearce took no further part in the controversy, for he died at Montague House, Lambridge, near Bath, on 11 May 1847. After his death (Appendix 1, (8)) the *London Geological Journal* published a note (Cunnington 1847) from William Cunnington (1813–1906), a well-known Wiltshire fossil collector, who supported Pearce’s claim that Owen’s restoration was a composite animal, but agreed with Bowerbank that the sheath or capsule of *Belemnoteuthis* was the equivalent of the belemnite guard, and that *Belemnoteuthis* was, therefore, not really a distinct genus. He noted the constant presence of two (dorsal) ridges (Owen had thought these were due to crushing of the fossil) and pointed out that they could not have fitted into the circular alveolus of the belemnite. Charlesworth, in an editorial dated 25 May, returned briefly to the subject and recorded that he had just seen new material found by Reginald Mantell near Trowbridge, in which the two ridges were clearly displayed (and, by implication, not artefacts of fossilization) (Charlesworth 1847*b*).

Reginald Neville Mantell, the engineer responsible for building a branch line of the Great Western Railway from Chippenham to Trowbridge, was the son of Gideon A. Mantell (1790–1852). A cutting at Trowbridge exposed the same beds as at Christian Malford, and a section through them was recorded for the first time (R. N. Mantell 1850). G. A. Mantell read a paper on his son’s finds at the Royal Society on 23 March 1848 in which he upheld the distinction between ordinary belemnites and *Belemnoteuthis*, emphasizing that the phragmocone of *Belemnoteuthis* could not have fitted into the alveolus of a belemnite guard. He had written to Owen expressing the hope that Owen would be present, ‘to amend or corroborate my statements’ (Appendix 1, (9)). However, as Mantell noted in his journal (G. A. Mantell, ed. Curwen 1940, p. 221):

‘Royal Society – my paper on Belemnites read. Professor Owen made a most virulent attack on me, ridiculing the communication, and stating it was only fit for a few lines in the “Annals of Natural History”. The Dean of Westminster [William Buckland] corroborated my views, and defended all my statements. The Marquess of Northampton [Spencer Joshua Alwyne Compton, 2nd Marquess] passed a warm eulogium ... to which the meeting which was a full one responded.’

Mantell gave another account of the meeting in a letter to the American geologist Benjamin Silliman (Spokes 1927, pp. 205–206). Charlesworth was also present and five weeks later he wrote from York to James Pearce, Joseph Channing’s father (Appendix 1, (10)):

‘[I] ... felt glad that I had returned the *Belemnoteuthis* ... a drawing and description of it will be embodied in a Memoir of Dr. Mantell’s which is to appear in the Transactions of the Royal Society. This Memoir was read at a late meeting of the Society and followed by a most animated discussion in which all who took part (including Buckland, Bowerbank & others) made a resolute stand against Owen on behalf of poor Channing’s Genus *Belemnoteuthis*. I longed as you may easily imagine to raise my voice in the cause, but not being an F.R.S. I could only have spoken by courtesy, and having so freely used the *Pen*, I thought under all the circumstances it was as well for me to be silent.’

Owen’s behaviour at this meeting was the start of a feud between him and Gideon Mantell which

lasted until the latter's death. It led in turn to misunderstanding and bitterness, among other things about an Elgin reptile, *Leptopleuron* (Benton 1982). Owen had earlier approved of Mantell's geological achievements. In his lectures at the Royal College of Surgeons in 1843 he had said (Owen 1843, p. 5):

'... the young provincial surgeon may be assured by the example of GIDEON MANTELL, that the researches and discoveries in palaeontology and geology, which have added so many honourable titles to that name, are quite compatible with the most extensive, active, and successful practice.'

Mantell's paper was refereed by Charles Lyell and Edward Forbes, who reported (Appendix 1, (11)):

'... We recommend it to be printed in the Philosophical Transactions. In doing so, we neither assent nor dissent from the statements & reasoning therein contained & which are in opposition to those published in the Philosophical Transactions by another distinguished naturalist. As in each case the inferences have been duly considered by the respective authors, we think it desirable that both views of the organic remains in question should be contained in the same publication.'

The paper was duly published about June 1848.

In July 1849 Mantell wrote (Appendix 1, (12)) to Lyell, 'As to the distinct generic characters of Belemnite & Belemniteuthis, no one now (except the great O) disputes it.' Later the same year, Owen opposed a move to award the Royal Society's Royal Medal to Mantell, who wrote in his journal (G. A. Mantell ed. Curwen 1940, p. 246):

'(25 November) Professor Owen has done everything in his power to prevent me obtaining it! [the Royal Medal] What a pity that a man of so much talent and acquirement should be so dastardly and envious. (26 November) Professor Owen ... [claimed] ... my papers in the Transactions were unworthy such an honour! though he received it for his paper on the Belemnite, which has proved to be utterly erroneous.'

Mantell was awarded the Medal for his work on the *Iguanodon*, largely due to the support of Charles Lyell who was on the Council of the Royal Society (G. A. Mantell ed. Curwen 1940, pp. 246–247).

Early in 1850, on 14 February, Mantell read a supplementary paper to the Royal Society, in which he recorded 'uncompressed examples of the distal end of the phragmocones [of *Belemniteuthis*] which must dispel any remaining doubts as to the generic distinction ... being based on natural characters' (G. A. Mantell 1850, p. 395, pl. 29, fig. 7). He also figured (pl. 29, figs 9–10) broken apical ends of two phragmocones which showed that the thin layer enveloping the phragmocone possessed radiating fibrous structure and was thus equivalent to the rostrum or guard of ordinary belemnites.

In 1851, Mantell published his *Petrifactions and their teachings; or, a handbook to the gallery of organic remains of the British Museum* in which he wrote that the *Belemniteuthis* on exhibition '... incontrovertibly prove the correctness of the late Mr. Channing Pearce's opinion, that the soft parts of Cephalopoda found in the Oxford Clay, belong to a genus altogether distinct from the Belemnites with which they are associated' (G. A. Mantell 1851, p. 415) and gave a description of the genus. Referring to Owen's mistaken view, he added in a footnote (G. A. Mantell 1851, p. 460):

'I most studiously endeavoured to avoid giving offence to the eminent anatomist ... whose scientific labours I have so highly eulogized, and have done everything in my power to promote, by placing at his disposal original drawings ... and hundreds of specimens collected by my son; but alas! to doubt Professor Owen's infallibility was a deadly sin, and I have no hope of forgiveness!'

Hostilities continued. In March 1852 the *Quarterly Review* carried an unsigned article with the running head 'Progress of comparative anatomy' (Anon. 1852), a fulsome review in which Owen's position on the belemnite question was still asserted to be the correct one. The article was in fact written by Owen's patron, W. J. Broderip (1789–1859) and the proofs corrected by Owen himself

(A. J. Desmond, pers. comm.). Mantell responded (Mantell 1852) and Broderip (or Owen?) replied in turn (Quarterly Reviewer 1852).

John Morris in the second edition of his *British Fossils* (Morris 1854) accepted Pearce's species *antiquus*, though he gave the wrong reference for it (Pearce 1842) and regarded *Belemniotheutis* as a generic synonym of *Acauthoteuthis* Wagner, 1938, which had been set up for hook-bearing arm crowns from the Lithographic Limestone (Upper Jurassic) of Solnhofen, Germany.

Owen, though he never publicly withdrew his criticism of Pearce and of Mantell, did in fact change his mind. In 1855, in the second edition of his lectures on invertebrates he referred to 'apparently guardless species' (Owen 1855, p. 603, footnote) though he reproduced (fig. 218, p. 598) the erroneous restoration from his 1843 edition. In 1856 was published the '*Descriptive Catalogue ...*' of invertebrate fossils in the Museum of the Royal College of Surgeons of London, cephalopod entries being by Owen (Owen 1856, p. vi), who now followed Morris in accepting *Acauthoteuthis* with *Belemniotheutis* [sic] as a synonym. After mentioning 'the supposition of its having slipped, like No. 13 [a belemnite] from the alveolus of a belemnitic guard of the ordinary structure' he wrote (Owen 1856, p. 1):

'... but, as it appears that the corneo-calcareous capsule is somewhat thicker than in the phragmocone *in situ*, and as several crushed and apparently detached or unguarded phragmocones ... have been discovered in the same formation, a second hypothesis has been propounded, viz. that they have been originally uncomplicated by the normal belemnitic spathose guard, and that they represent a distinct genus or subgenus of the extinct *Belemnitidae*, for which the names *Acauthoteuthis* and *Belemniotheutis* have been proposed, and in the present instance with the specific name of *antiquus*.'

Finally, in his *Palaeontology* (1860, p. 92, fig. 22) Owen illustrated as separate species *Belemnites Owenii*, a guard and phragmocone, and *Acauthoteuthis antiquus* exemplified by a Christian Malford specimen in the British Museum (no. 25966) which was later refigured by Donovan (1977, fig. 6). Owen attributed the species *antiquus* to Cunningham. He was explicit, at last, as to his own change of opinion (Owen 1860, pp. 91–92):

'... further evidence ... has been supplied by the Chippenham fossils, which in all probability are identical in genus, if not in species, with the *Acauthoteuthis* described by Muenster. One of these extraordinary fossils ... is represented in (fig. 22, 2) ... [here follows a description] ... This shell, which is chambered internally, [p. 92] like the *phragmocone* of the Belemnite (fig. 22, 1), has an outer sheath of fibrous structure, one-fourth of an inch thick at the apex, and furnished with two converging ridges on its dorsal side; the external surface, however, is horny (or chitinous), like the pen of the Calamary. These chambered shells occur in great numbers, and are so like the phragmocones of the associated Belemnites, both in structure and proportions, that they were originally described by me as such, and I still view them as evidences of the close affinity of the cephalopod possessing them to the true Belemnite: ...'.

This came too late, unfortunately, to do justice to Pearce, or to Mantell who had died on 10 November 1852.

History of the Pearce Collection

The fossil collection of J. Channing Pearce (1811–1847) remained in the possession of his son until 1 November 1915 when it was bought for £1000 and given to Bristol City Museum. It was kept in store and so escaped the destruction of the greater part of the Museum's geological collection in an air raid in November 1940. The collection includes the material on which Pearce based his genus *Belemniotheutis*, now fully described for the first time. The collection is accompanied by Pearce's MS catalogue. The date of the entries is not known, but is later than the adoption of the spelling *Belemniotheutis* (see below) some time after 1844. The relevant material is listed with notes on the catalogue entries in Appendix 2.

SYSTEMATIC PALAEOLOGY

Subclass COLEOIDEA Bather, 1888

Order BELEMNITIDA Zittel, 1895 (*nom. correct. pro* Belemnoidea)Family BELEMNOTHEUTIDIDAE Zittel, 1884 (*nom. correct. pro* -teuthidae)

Genus BELEMNOTHEUTIS Pearce, 1842

Abbreviations. BM(NH), British Museum (Natural History), South Kensington, London SW7 5BD. BRSMG, City of Bristol Museums and Art Gallery, Queen's Road, Bristol BS8 1RL. Specimen registration numbers with the prefixes Ca, Cb and Cd are in the Bristol Museum and are listed below in Appendix 2.

Spelling of generic name. The generic name *Belemnotheutis* (*sic*) was first published in the *Proceedings of the Geological Society of London* in 1842 (Pearce 1842*a*, p. 593), in the report of a meeting at which Pearce had exhibited some fossils from the Oxford Clay of Christian Malford. It is spelt in the same way in the index to the volume. An unchanged copy of the report was published in the *Annals and Magazine of Natural History* (Pearce 1842*b*). Pearce (1847, p. 75, footnote) said that the name had been suggested by J. E. Gray, who later (1847, p. 206) used the spelling *Belemniteuthis*, probably inadvertently. Owen (1855, p. 602, footnote), more improbably in view of the history given above, also claimed paternity. No species name was mentioned in the 1842 report.

Pearce's paper (1842*a*) was reported in the *Neues Jahrbuch* (Pearce 1843) with the spelling *Belemnoteuthis*. Agassiz ([1845], p. 11) also used this form, and was presumed by Sherborn (1924, p. 681) to have emended the spelling. However, we do not know whether the change of spelling in the *Neues Jahrbuch* and in Agassiz ([1845]) was intentional or a mis-reading for the more familiar *-teuthis*. Although Pearce's original spelling was correctly listed by Sherborn (1924, p. 681) and Neave (1939, p. 413), authors have continued to use the form *Belemnoteuthis*.

If the emendation was intentional it is not justified under the Rules of Zoological Nomenclature now in force. The matter is covered by Article 32(c) 'Incorrect original spelling'. An original spelling is there deemed to be incorrect if (i) it contravenes a provision of Articles 27–31 (which deal with such matters as gender, capitalization, diacritic marks and family-group endings), or (ii) there is clear evidence in the original publication of an error such as a copyist's or printer's error. It is explicitly stated that 'Incorrect transliteration or latinization... are not to be considered inadvertent errors'. Unless an original spelling is incorrect by these criteria, the original spelling is to be preserved.

The form *Belemnotheutis* appears on some of Pearce's MS specimen labels, corrected to *Belemnoteuthis*. Pearce also used the spelling *-theutis* in letters to Owen dated 16 November 1844 and 18 December 1844. This form was therefore used by Pearce at least up to 1844 and was not a scribe's error or a misprint in the Geological Society's *Proceedings*.

We do not know why Pearce used this spelling. We are informed (Alan Griffiths, pers. comm.) that *teuthis* (Gr. τευθίς) is the usual form, but that the form *-theutis* (Gr. θευτις) is recorded once by an Ionic writer. In fact, the form *-theutis* is also used on MS labels dating from the mid-nineteenth century in the Staatliches Museum für Naturkunde, Stuttgart, e.g. *Geotheutis* instead of *Geoteuthis*, and endings such as *-theutis*, *-theutis* and other variants are found for other coleoid genera in nineteenth-century authors. There appears, therefore, to have been equivocation as to the correct form.

We conclude, that whatever the reason for the original spelling, it was intended, and that emendation to *Belemnoteuthis* is not justified by the Rules now in force.

Type species. Pearce's 1847 paper in the *London Geological Journal* was illustrated by two plates (15 and 16) showing specimens now in the Pearce collection at Bristol. Each plate bears the name *Belemnoteuthis antiquus* Pearce, although the specific name does not appear in the text. This was the first publication of the combination *Belemnoteuthis antiquus*. No other species is mentioned. We conclude that the species *Belemnotheutis antiquus* Pearce, 1847 is the type species of *Belemnotheutis* Pearce, 1842 by monotypy (Article 68(d)).

EXPLANATION OF PLATE I

Belemnotheutis antiquus Pearce. BRSMG Ca5240, lectotype, Pearce Collection; dorsal view, $\times 0.75$. (Previously figured by Pearce (1847, pl. 16); for enlarged details see Plate 2.)



Systematic position. *Belemnotheutis* is here included in the Order Belemnitida following Jeletzky (1966, pp. 145–146), Bandel and Kulicki (1988, p. 315) and Peter Doyle (pers. comm. 1990), and in disagreement with the view expressed by Donovan (1977, p. 29). The principal reason for doubt by Donovan (1977) was the aragonitic rostrum of *Belemnotheutis antiquus* compared with the apparently calcitic one of typical belemnites. More recently it appears that the epistrostrum of certain belemnites may be aragonitic (Bandel and Spaeth 1988), so that this distinction loses its force.

Relationship to Acanthoteuthis. The genus *Acanthoteuthis* was proposed by Wagner (1839, p. 94) for coleoids with hooked arms from the Lithographic Limestone (Solnhofener Plattenkalk) of the Solnhofen area, Bavaria. Naef (1922, pp. 180, 252, fig. 91) showed that there were ten arms of approximately equal length. Later finds (e.g. Engeser and Reitner 1981, fig. 5) show that these arm crowns belonged to animals with a shell like that of *Belemnotheutis antiquus*. The chief differences lie in the narrower apical angle of the phragmocone, about 13° (uncrushed), fewer septa (between 40 and 45), and a relatively longer pro-ostracum. The arm hooks are similar to those of *Belemnotheutis antiquus*.

As already noted, early authors (Morris 1854; Owen 1856) regarded *Belemnotheutis* as a synonym of the prior *Acanthoteuthis*. Zittel (1884) separated them but he erroneously regarded *Acanthoteuthis* as an octopod. Naef (1922, p. 186) noted the close similarity between the two genera, and kept them separate principally because of the presence of a well-developed ‘Scheide’ (lit. sheath; ? rostrum) in *Belemnotheutis*; this does not now seem to be a distinction. Engeser and Reitner (1981) kept them separate. It is at least arguable that the differences between the two forms are hardly of generic significance.

Stratigraphical range of Belemnotheutis. The earliest example is from the Kellaways Rock (Lower Callovian; *calloviense* Zone) of Wiltshire, England (BM(NH) 37440). *Belemnotheutis polonica* Makowski from Łuków, east of Warsaw, Poland, comes from a nodule bed of *lamberti* Zone (Upper Callovian) age (Arkell 1956, p. 482). Riegraf (1987) described a crushed phragmocone indistinguishable from that of *B. antiquus* from the Kimmeridge Clay of Kimmeridge Bay, Dorset, England. The exact horizon is not stated but the locality suggests the uppermost Lower, or early Upper Kimmeridge Clay, i.e. *pseudonutabilis* or *gigas* Zone. The youngest example is from the Upper Kimmeridge Clay (Upper Kimmeridgian Stage: ?*pallasioides* Zone) of Kimmeridge, Dorset (BM(NH) C.59184). Doyle (1991, p. 172) records a ?*Belemnotheutis* [phragmocone] from the Nordenskjöld Formation of the Antarctic Peninsula, Antarctica, which would be Upper Kimmeridgian in north European terms. The genus therefore ranges through the greater part of the Callovian, the Oxfordian, and most of the Kimmeridgian Stage. Engeser and Clarke (1988, pp. 137–138) note that the belemnotheutids possibly range up to the Upper Cretaceous on the evidence of ‘*Belemnoteuthis*’ *syriaca* Roger, 1944.

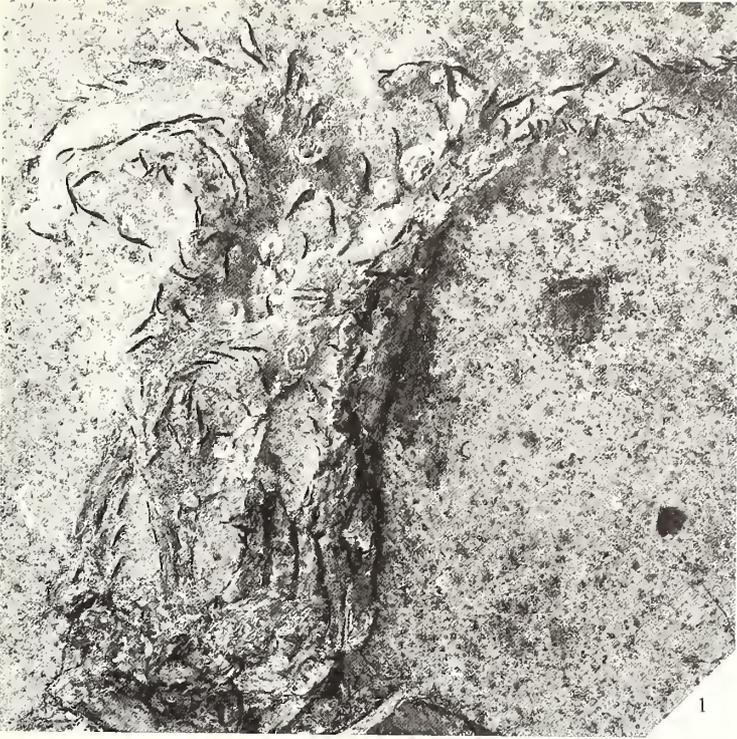
Belemnotheutis antiquus Pearce, 1847

Plates 1–5; Text-figs 2–3

- 1844 *Belemnites Owenii*; Owen, pl. 2, figs 6–8; pl. 3; pl. 4, figs 1–2; pl. 5; pl. 6, figs 1–3; pl. 7, fig. 4 [pars, non Pratt in Owen].
- 1847 *Belemnoteuthis antiquus* Pearce, pls 15–16.
- 1848 *Belemnoteuthis antiquus* Pearce; Mantell, p. 172, pl. 13, figs 1–3, 5.
- 1850 *Belemnoteuthis* Mantell, p. 395, pl. 29, figs 7, 9–10.
- 1851 *Belemnoteuthis antiquus* Pearce; Mantell, p. 459, lign. 100.
- 1852 *Belemnoteuthis antiquus* [Pearce]; Mantell, p. 18, fig. 3.
- 1854 *Acanthoteuthis antiquus* Pearce; Morris, p. 289.
- 1856 *Acanthoteuthis (Belemnoteuthis) antiquus* Wagner and Pearce; Owen, p. 11.
- 1966 *Belemnoteuthis antiqua* Pearce; Jeletzky, p. 78, pl. 16, fig. 2.
- 1977 *Belemnoteuthis antiqua* Pearce; Donovan, p. 27, fig. 6.
- 1991 *Belemnotheutis antiquus* Pearce; Page in Martill and Hudson, p. 156, pl. 31, figs 2–3.

EXPLANATION OF PLATE 2

Figs 1–4. *Belemnotheutis antiquus* Pearce. BRSMG Ca5240, lectotype, Pearce Collection. 1, Arm crown, × 1.25. 2, Detail of hooks and suckers (detail of fig. 3), × 7.8. 3, Parts of two arms, × 4.85. 4, Detail of hooks and suckers, × 6.7.



Type series. The specific name was published in February 1847. Pearce died in May 1847 (see above), and the specimens listed as *Belemnotheutis antiquus* in Pearce's MS catalogue which accompanies his collection in Bristol Museum are assumed to have been available when he wrote his 1847 paper and are therefore syntypes. They are listed and briefly described below (Appendix 2).

Lectotype. The original of Pearce (1847, pl. 16), Pearce no. 160A, now BRSMG no. Ca5240, is here designated the lectotype. It is here refigured (Pls 1–2) and described.

Paralectotypes. The syntypes other than the lectotype become paralectotypes (Article 73(b)(ii); Recommendation 74E). One of the specimens catalogued by Pearce as 160G (now BRSMG Cb3975) is here regarded as doubtfully belonging to the species.

Locality and horizon. All of Pearce's specimens were obtained from the Oxford Clay of Christian Malford in Wiltshire, England, exposed during railway construction about 1840. There is no detailed contemporary description of the occurrence, and the scanty information was summarized by Woodward (1985, p. 32), White (1925, p. 12) and Donovan (1983, p. 485). An approximate National Grid Reference is ST 960777. The zonal horizon is shown by the associated ammonites to be the *phaeimm* Subzone, *athleta* Zone of the Callovian Stage (Donovan 1983, pp. 486–487; Page in Martill and Hudson 1991, p. 156).

Mode of preservation. The *Belemnotheutis* specimens from Christian Malford are remarkable for the preservation of permineralized soft tissues. It is clear that the fossils were preserved in laminated, bituminous shales with an impoverished benthic fauna and little or no bioturbation. In addition to presumed pelagic fishes and cephalopods, Woodward (1895, p. 32) listed two genera of gastropods (including '*Patella*') and three species of bivalves, recorded as *Avicula ovalis*, *Leda phillipsi* and *Pholadomya deltoidea*. These did not necessarily come from the same horizon as the coleoids with permineralized soft parts.

Only the coleoids *Belemnotheutis* and *Mastigophora* (Donovan 1983) show permineralized soft tissues. In the case of *Belemnotheutis*, which possessed an aragonitic phragmocone, isolated phragmocones without associated soft tissue are perhaps five to ten times as numerous in collections as specimens with soft parts. This ratio is clearly an unsafe guide to their original abundance. We do not know, for example, whether the isolated phragmocones and the soft part specimens were found on the same or different bedding planes. Pearce (1842, p. 593) refers to 'four or five bands of laminated clay' but does not specify their fossil content in detail. Fragments of fish and of ammonites on slabs with *Belemnotheutis* soft parts do show that these fossils all occurred together. At Trowbridge, where R. N. Mantell later encountered the same, or a closely similar, horizon, phragmocones were common but well-preserved soft parts were not found (G. A. Mantell 1848, p. 173).

Allison (1988) studied the composition and structure of the fossilized soft parts and offered an interpretation of their preservation. The permineralized tissue is composed of apatite which under high SEM magnification resolves into spheres of 1–2 μm diameter. Allison suggested that the mineralization occurred near the oxic/anoxic boundary after the carcasses sank rapidly into a 'soupy' surface layer of sediment. Mineralization was favoured by high pH but the chemical processes could not be exactly determined. The high pH would of course be consistent with the perfect preservation of the aragonite of the *Belemnotheutis* phragmocones and of the ammonite shells. Allison does not discuss why soft part preservation is not found in fossil groups other than coleoids which were found at Christian Malford.

Description of the lectotype. The phragmocone and rostrum together are 72 mm long and about 30 mm in maximum breadth. The anterior end of the phragmocone is cut off sharply due to preparation. The apical angle is about 36 degrees. The posterior end shows a deep, narrow groove, bounded by rounded ridges, dying out anteriorly. This shows that the specimen is seen from the dorsal side.

The 'body' is preserved as the muscular mantle which extends from about 62 mm forward of the apex of the phragmocone to about 179 mm from the same point. In places it shows transverse striations, 4 or 5 to the

EXPLANATION OF PLATE 3

Figs 1–2. *Belemnotheutis antiquus* Pearce. Paralectotypes. 1, BRSMG Cd22a. Pearce Collection; anterior to phragmocone is hollow left by ink sac, flanked by probable fragments of pro-ostracum, $\times 1$. 2, BRSMG Cd18a, Pearce Collection; dorsal view, $\times 1.25$ (for details see Plate 4, fig. 2, and Plate 5).



millimetre. The anterior end of the 'body' is sharp and is the result of preparation. No detail can be discerned in the 'body'. Near the front end several narrow strips, 1–2 mm wide, lie on the surface of the mantle.

There is a gap between the 'body' and the arm crown, due to preparation. There is no reason to suppose that the arm crown does not belong to the rest of the fossil. The positions of the arms are indicated by double rows of hooks, in some cases associated with suckers (Pl. 2, fig. 1).

There are at least seven arms, possibly more. The bases of the arms are vaguely defined and their exact length cannot be measured; it was probably more than 100 mm. There is nothing to indicate that different arms were of markedly different lengths. Where suckers are preserved there are the same number of pairs of hooks as suckers, but it is not clear whether the hooks are rooted in the suckers, as they sometimes appear to be (Pl. 2, fig. 2). There could have been only one row of suckers per arm. Distal suckers are smaller than proximal ones, the largest being about 2 mm in diameter. Several suckers show what could have been a chitinous ring around the outside (Pl. 2, fig. 4). Mantell (1852, p. 19, fig. 4) illustrated 'three hooks with attached horny rings; from a specimen in the possession of Mr. Cunningham', an interpretation which was doubted, for no apparent reason, by Engeser and Clarke (1988, p. 139). The specimen in question is not known to be extant.

Description of other material. Fossils from Christian Malford were widely distributed during the 1840s and 1850s through dealers and probably by exchange. The following account of *Belemnotheris antiquus* is based on the Pearce material supplemented by that of the BM(NH) and of the Royal College of Surgeons (now lost) published by Owen (1844).

Phragmocone. Isolated phragmocones, almost all from the original Christian Malford locality, are relatively common in old collections. There are eight in the Pearce Collection and about 40 in the BM(NH). Most are crushed and thus visible in two dimensions only. The phragmocone was evidently conical; the transverse section was presumably circular or elliptical, but cannot be ascertained from the material. The angle of the cone at the apex, as measured on crushed specimens, ranges from about 27° to 36°, the mean being about 33° and the standard deviation about 2.42°, based on measurements of 25 well-preserved examples in the Pearce collection and the BM(NH). If conical phragmocones were completely flattened the average apical angle of the uncrushed phragmocones would have been about 21°. One example in which the apex is almost uncrushed (BM(NH) 21449) has an apical angle of 17.5°. In the crushed specimens there often appears to be an increase in the angle of the cone from the apex forwards, but this is probably an artefact caused by greater strength, and therefore less complete flattening, of the apical end.

The uncrushed phragmocone figured by Mantell (1850, pl. 29, fig. 7) has an apical angle of 18°. An uncrushed phragmocone in the Pearce collection (BRSMG Cb3976), preserved in non-laminated mudstone and not certainly belonging to *Belemnotheris*, has an apical angle of 22°. The closely similar phragmocones from Poland, described by Makowski (1952) as *Belemnotheris polonica*, are uncrushed and have apical angles of 20° to 21°.

The overall length of 32 phragmocones measured ranges from 35 to 86 mm. The mean is about 64 mm, but the mode is higher, in the 71 to 75 mm class, so that the distribution is skewed or possibly bimodal. An exceptionally large individual (BM(NH) 88603), not included in these measurements, has a phragmocone around 100 mm long. An even larger specimen in the Pearce Collection (BRSMG Cb3972) appears to be about 300 mm long but is probably compounded of two individuals. Even so these are much larger than other phragmocones of *Belemnotheris antiquus* and are here excluded from the species.

Chambers increase in length from about 0.5 to about 4.0 mm, measured as the distance between suture lines. Twenty measurements on 17 specimens yielded the relationship:

$$y = 0.0516x - 0.0755$$

where y is chamber length and x is distance to the chamber from the apex. There is a positive correlation coefficient of 0.975 between the two measurements. The total number of chambers cannot be counted in any specimen, but is estimated to have been about 50 in large (80 mm long) phragmocones.

EXPLANATION OF PLATE 4

Figs 1–2. *Belemnotheris antiquus* Pearce. Paralectotypes. 1, BRSMG Cd22b, Pearce Collection; arm crown, $\times 1.09$. (For detail of arm hooks see Text-fig. 3b.) 2, BRSMG Cd18a, Pearce Collection; detail of muscles of neck region, $\times 2.4$. (Transversely striated mantle muscle is seen at the bottom of the figure; for whole fossil see Plate 3, fig. 2.)



The siphuncle is not clearly seen in the type material, but the Polish material (Makowski 1952) shows it to have been marginal and ventral. The protoconch cannot be studied in the type material. Apparent differences in the protoconch of Polish material from that of typical belemnites (Donovan 1977, p. 27) have been explained as the result of shell damage during life (Bandel and Kulicki 1988).

Specimens for which the proportion of the phragmocone as part of the total length can be determined are few. They indicate that the phragmocone is about 0.30 of total length including arms.

Rostrum. The apical part of the phragmocone is covered by the rostrum, aragonitic in composition (Donovan, 1977, p. 28; Bandel and Kulicki 1988, p. 304), up to 1 mm thick at the apex in the largest specimens. The thickness diminishes anteriorly so that a little more than half way from the apex to the anterior margin the septal sutures become visible through the thin conotheca. The rostrum has a narrow mid-dorsal groove flanked by rounded ridges, ill-defined on their lateral sides (Pls 2, 5). The position of the groove cannot be determined in the type material, but in *B. polonica* it is mid-dorsal as shown by growth lines which indicate a pro-ostracum in the same position (Makowski 1952, text-figs 7–8). The groove is well marked apically and persists for up to 3/5ths of the length of the phragmocone. Initially angular in section, it becomes flat-bottomed, about 1 mm wide, with fine ribs before dying out. This detail can be seen in a few Christian Malford specimens (e.g. BM(NH) 30460, C.7854) but is better studied in uncrushed examples from the Kellaways Rock (BM(NH) 37440, C.46500–46501) and is well shown by Makowski's enlarged figures (1952, text-figs 7–8).

Owen regarded the paired ridges as accidental, due to crushing. They were correctly interpreted by Cunnington (1847), and by Mantell (1848, p. 175, pl. 14, fig. 4) who wrongly regarded them as ventral in position. Mantell also described and figured (1848, p. 175, pl. 14, fig. 3) a median dorsal (i.e. ventral) ridge but this does seem to have been an artefact of preservation. No such ridge is seen in the uncrushed material of *B. polonica* illustrated by Makowski (1952).

Pro-ostracum. The pro-ostracum is poorly known. The proximal part may be shown by BRSMG Cd16/17, and probable displaced fragments by Cd22a (Pl. 3, fig. 1). The junction of the pro-ostracum with the dorsal margin of the phragmocone is not seen in any specimen, but phragmocones BRSMG Cb3966 and BRSMG Cb3971 show faint oblique growth lines in the right-hand anterior region which appear to be part of a hyperbolar zone.

The length of the pro-ostracum was about 1.2 times the length of the phragmocone, according to the example from the Sedgwick Museum, Cambridge (J24841) figured by Jeletzky (1966, pl. 16, fig. 2). The width is difficult to establish but was substantially less than the width of the flattened phragmocone. There are slight indications that the lateral margins were thickened. If BRSMG Cd16 can be relied on, the pro-ostracum tapered weakly forwards. The Cambridge specimen figured by Jeletzky appears to have a semicircular front end, but growth lines on Makowski's *B. polonica* (1952, text-figs 7–9) show a bluntly pointed end and this is likely to have been so in *B. antiquus*. The pro-ostracum was non-calcareous but its composition has not been determined.

Body. The body of the animal consists chiefly of the muscular mantle, roughly parallel sided but varying in outline according to the amount of disturbance during fossilization, and also modified by preparation. If the body was cylindrical in life and has been perfectly flattened, then the original diameter would have been about 12–14% of the overall length. This estimate cannot be regarded as very reliable.

The muscular mantle is preserved in some specimens as a whitish layer less than 1 mm thick. It bears transverse striations about 0.20 to 0.25 mm apart (Pl. 3, figs 1–2; Pl. 5).

The ink sac lay within the mantle. Its position may be shown by a swelling as the fossilized ink was less compressible than the rest of the fossil (e.g. BRSMG Cd21, Text-fig. 2). In some specimens it has been exposed by the removal of the overlying mantle. The sac lies immediately in front of the phragmocone, and may be about 25 mm long in large individuals. The duct is two or three millimetres across and leads forward to a point near the front of the mantle.

One specimen (BRSMG Cd18a–b) shows a feature near the anterior end which Pearce in his MS Catalogue

EXPLANATION OF PLATE 5

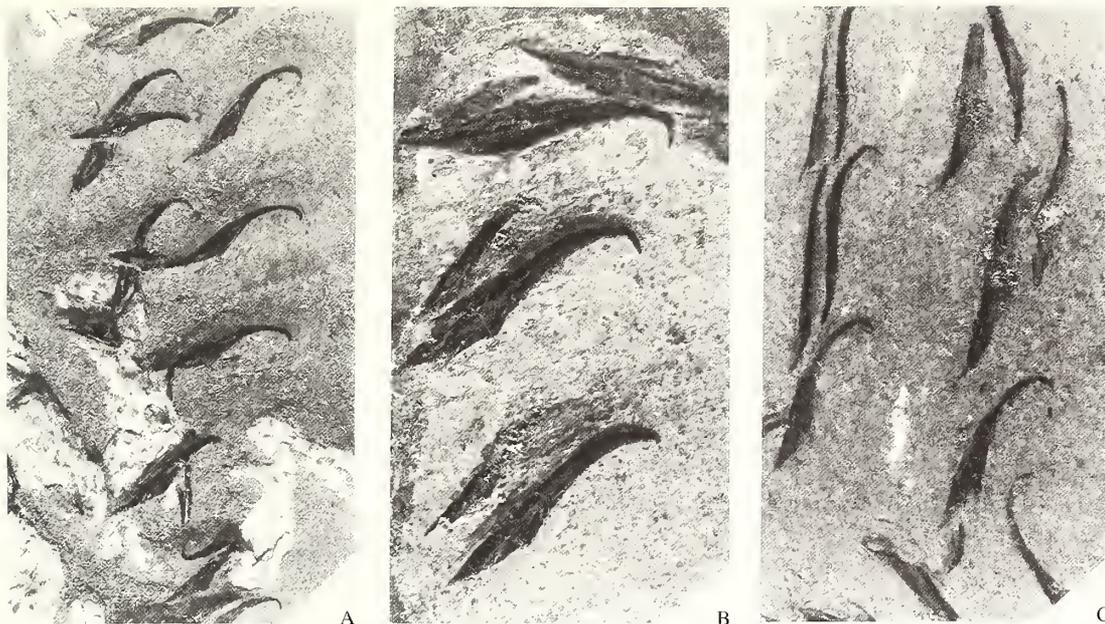
Belemnotheutis antiquus Pearce. Paralectotype, BRSMG Cd18a, Pearce Collection; phragmocone, dorsal view, $\times 2.6$. (Transversely striated mantle muscle is visible at the top of the figure; for whole fossil see Plate 3, fig. 2.)



DONOVAN and CRANE, *Belemnotheutis*



TEXT-FIG. 2. *Belemnotheutis antiquus* Pearce, BRSMG Cd21, paralectotype, Pearce Collection, $\times 1$. The ink sac is visible as a swelling immediately in front of the anterior margin of the phragmocone. For detail of arm hooks see Text-figure 3c.



TEXT-FIG. 3. *Belemnotheutis antiquus* Pearce, paralectotypes. A, BRSMG Cb7661; detail of arm hooks and arm muscle, $\times 4$. B, BRSMG Cd22b; detail of arm hooks, $\times 5.9$; for whole arm crown see Plate 4, fig. 1. C, BRSMG Cd21; detail of arm hooks, $\times 5.8$; for whole fossil see Text-figure 2.

described as 'feathery processes' (Pl. 3, fig. 2; Pl. 4, fig. 2). Examination with the binocular microscope and the SEM shows that this feature is in fact mineralized muscular tissue. It appears to be muscles of the dorsal neck region, and shows some similarity in arrangement to the dorsal neck muscles of the Recent coleoid *Vampyrotheutis* (Young 1964, pl. 5).

Head. The head is not clearly preserved in any of the Pearce specimens. Several BM(NH) specimens show a pair of semicircular strips of tissue, about 2–3 mm wide, on either side of the head (C.5020 figured by Owen 1844, pl. 6, figs 1–3; 25966 figured by Mantell 1851, fig. 100, p. 459; 88603, unfigured). The function of these structures is unknown.

Arms. The greatest number of arms preserved in any specimen (BM(NH) 25966; Donovan 1977, fig. 6) is nine. Assuming bilateral symmetry the original number is thought to have been ten. The arms vary in length according to the size of the individual, but their length is difficult to measure because they are often incompletely preserved, and their bases are usually obscure. They were probably more than 100 mm long in large specimens, about 40% of the total length of the animal including the arms. The arms may be preserved as soft tissue plus paired hooks (e.g. BRSMG Cd22b, Text-fig. 3B) or by hooks alone (e.g. BRSMG Cd21, Text-fig. 3C) showing varying degrees of disturbance from their original disposition. The soft tissue usually appears as a narrow strip two or three millimetres wide. Suckers have been described in the lectotype (above, p. 286).

There is some variation in shape of hooks, some appearing relatively narrower than others (e.g. Text-fig. 3C, left-hand side). This may be due to incomplete removal of matrix. Engeser and Clarke (1988) have discussed arm hooks in fossil and Recent coleoids. The form present in *Belemnotheutis* is found in several species until the late Cretaceous.

Size. As a measure of total size, it is not useful to measure 'mantle length' as with living coleoids. In most specimens the anterior and posterior limits of the mantle arc ill-defined and have generally been modified by unskilled preparation. No clearly-defined head is distinguishable on any example. Total length of specimens has therefore been measured, but is of limited value because of the different configurations in which arms are preserved.

Examples which are more or less complete are rare. The smallest are some poorly preserved examples in the

BM(NH) (24678, 89182, C.2693) which are about 100–120 mm in overall length. Better preserved material ranges from about 135 mm (BM(NH) C.2692, BRSMG Ca5242) to about 250 mm (lectotype), and, exceptionally, about 300 mm (BM(NH) 88603). The ratio between lengths of smallest and largest is thus approximately 1:3, about the same as that between the extreme sizes of phragmocones.

Comparisons. *Belemnotherutis polonica* Makowski, 1952, from the Callovian of Poland, was based on well-preserved phragmocones and rostra only. No soft parts are known. Bandel and Kulicki (1988, p. 314) remark that it is difficult to separate this species from *B. antiquus*. *Belemnotherutis mayri* Engeser and Reitner, 1981, from the Solnhofener Plattenkalk (Lower Tithonian), has a phragmocone with a smaller apical angle than *B. antiquus*, and the arms form a much smaller proportion of the total length.

DISCUSSION

An extended discussion of the relationships of *Belemnotherutis* will not be attempted here, as this will be included in a forthcoming volume of the *Treatise on invertebrate paleontology* dealing with Coleoidea which is now in active preparation. However, it may be remarked that suckers were regarded by Berthold and Engeser (1987) as characteristic of Dibranchiata (in their sense) which exclude, and are treated as a sister group of, 'Belemnoidea'. The presence of suckers in *Belemnotherutis* shows that suckers are not autapomorphic for Dibranchiata *sensu* Berthold and Engeser. Suckers are known in at least two Jurassic teuthids: *Gramadella* (Fischer and Riou 1982) and *Mastigophora* (BM(NH) no. 32352, unpublished). Engeser and Clarke (1988), as mentioned above, have argued convincingly that the arm hooks present in some Recent squids evolved independently of those found in Mesozoic coleoids. However, it is likely that suckers were already present in the common ancestors of the Belemnitida and the living forms.

Acknowledgements. We are grateful to Peter Crowther and Roger Clark at City of Bristol Museums and Art Gallery for facilities to study the Pearce Collection and records. Extracts from the archives of the Royal Society are included by kind permission of the President and Council of the Royal Society. The Owen correspondence is quoted with permission from the archives of the British Museum (Natural History), and the Mantell papers with permission from the Alexander Turnbull Library, National Library of New Zealand, Wellington, New Zealand. We thank Simon Powell and Mike Gray for photography, and Colin Stuart for re-drawing Text-figure 1c. Marion Nixon discussed the type material. Adrian Desmond and Peter Doyle have read and commented helpfully on parts of the typescript, and an anonymous referee added useful suggestions.

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D. T. DONOVAN
Department of Geology
University of Bristol
Wills Memorial Building
Bristol BS8 1RJ, UK

M. D. CRANE
15 Lynwood Avenue
Dunedin, New Zealand

Typescript received 14 September 1990
Revised typescript received 21 June 1991

APPENDIX 1

Archival sources for the historical part of the paper

- (1) Letter from Pearce to Richard Owen dated 18 March 1842. BM(NH) Owen Correspondence xxi, 187–8.
- (2) Journal Book of the Royal Society XLIX, 1843–1859. The drawings to illustrate the paper are filed at PT.75.53–8.
- (3) Gray's report on the paper is filed by the Royal Society at MC 4.20.
- (4) BRSMG, Geology File PEA 5.
- (5) Letter dated 16 November 1844 from Pearce at Bradford [-on-Avon], Wiltshire, to Richard Owen. BM(NH) Owen Correspondence, xxi, 197–198. Photocopy in BRSMG Geology File PEA 7.
- (6) BM(NH) Owen Correspondence, iv, 322–323. Photocopy in BRSMG Geology File PEA 17.
- (7) BRSMG, Geology File PEA 2.

- (8) No. 3 of the *London Geological Journal*, for May 1847, printed a letter on the back cover dated 22 June 1847 and could not have been issued before that date.
- (9) Mantell to Owen 23 March 1848, BM(NH) Owen Correspondence, xviii, 412.
- (10) Letter from Charlesworth to James Pearce dated York, 29 April 1848, BRSMG, Geology File PEA 2.
- (11) Joint report by Lyell and Forbes, in Forbes' handwriting, dated July 1848. Royal Society RR 1.161.
- (12) Mantell, Gideon. Letter, 27 July 1849. Mantell family papers. MS Papers 83: folder 101. Alexander Turnbull Library, National Library of New Zealand, Wellington, New Zealand.

APPENDIX 2

List of specimens of Belemnotheutis in the Pearce Collection, Bristol City Museum, ordered according to their numbers in Pearee's catalogue. All these specimens except the last three are catalogued in the Pearee MS catalogue as Belemnoteuthis antiquus Pearce, from 'Oxford Clay and Kelloway Rock' (sic), the locality being given as 'Nr. Chr. Malford'. For specimens denoted with an asterisk the original MS Pearce labels have the spelling Belemnotheutis, corrected to Belemnoteuthis. Pearee Catalogue numbers are bracketed.

Ca5242 (160*). Small complete individual, 132 mm long. Pearce note reads 'perfect specimen showing the capsule with its chambers, muscular mantle, ink bag, arms & hooks in situ &c it is remarkable that it has lost none of its external surface'. Figd Pearce 1847, plate 15, natural size. Acquired after the Geological Society paper was read, see Pearce (1847, p. 77).

Ca5240 (160A*). Complete specimen. Pearce note reads 'Specimen remarkable for a series of suckers on the inside of each of the arms. It also shows the arms with their hooks exceedingly perfect, the bodies surrounding the eyes, the muscular portion of body and its interior & the perfect capsule with its chambers.' Figd Pearce 1847, plate 16, reversed, and reduced to $\times 0.84$. A piece in the middle of the phragmocone lost since figure. Acquired after the Geological Society paper was read, see Pearce (1847, p. 77). Lectotype here designated.

Cd21 (160B). Rectangular with corner missing, diagonal crack. Complete specimen about 175 mm long. Ink sac and duct. Arms (? 6 or 7) present as hooks only, no tissue preserved. Pearce's note for this group is 'Specimens showing the whole animal with its arms hooks &c remarkably fine, ink bag, muscular mantle, capsule &c'.

Cd22a (160B*). On tablet with Cd22b, Cd23a, Cd23b. Phragmocone (apex missing), 'body', ink sac (disintegrating, leaving impression). Possible broken and displaced pieces of pro-ostracum. Preserved length 193 mm, max. width 52 mm. For Pearce's note see Cd21.

Cd22b (160B*). Arm crown, with soft tissue and hooks. At least 6 arms. For Pearce's note see Cd21.

Cd23a (160B). Rectangular slab with corner detached. On tablet with Cd22a, Cd22b. Counterpart of Cd22a.

Cd23b (160B). Anterior part of body, confused, with parts of 2 arms, some hooks present. Possibly the counterpart of Cd22b.

Cd19 (160C*). Phragmocone (apex missing), mantle, ink sac and duct. A narrower white area in front of the mantle, fragmentary arms with scattered hooks. Pearce catalogue has 'Specimens well preserved & nearly entire showing the ink bag with its duct'.

Cd20 (160C*). Complete specimen 164 mm long. Ink sac, arms with hooks present. For remarks in the catalogue see entry for Cd19.

Cd18a-b (160D). Parallel-sided slab with phragmocone and mantle, dorsal view. Phragmocone shows groove and ridges. Counterpart of anterior half only. Preserved length 148 mm. Pearce catalogue has 'Entire specimen excepting its arms, remarkable for feathery processes passing off from the upper part of the body, and these are studded with little black pointed bodies'. The 'feathery processes' refer to muscular tissue in the neck region (see p. 291). It is not clear what the 'black ... bodies' are.

Cd15 (160E). A nondescript specimen, preserved length 117 mm, excluding possible small fragments of arms. Part of the mantle visible in centre. Neither phragmocone nor ink sac is clearly visible. Pearce's note for the specimens catalogued under the number 160E reads: 'A series of specimens of every part of the animal illustrating its different parts.'

Cd16 (160E). Rectangular slab, on black tablet, with phragmocone (apex missing) and mantle. Preserved length 128 mm.

Cd17 (160E). Rectangular slab on black tablet. Displaced mantle fragments, ink sac. Preserved length 125 mm. Counterpart of Cd16.

Cd24 (160E). On tablet with Cd25. Phragmocone and posterior part of the mantle. Dorsal side.

Cd25 (160E). The counterpart of Cd24.

Cd27 (160E). Part of phragmocone, and ?part of ink sac, displaced.

Cd26 (160E). Anterior end of phragmocone and part of mantle of a small individual. Preserved length 70 mm.

Cb3966 (160E). Complete phragmocone, length 86 mm, width at anterior end 46 mm. Dorsal side, shows apical groove and ridges.

Cb3967 (160E). Complete phragmocone, length 64 mm, width at anterior end 37 mm.

Cb3968 (160E). Phragmocone (apex missing), posterior part of 'body'. Preserved length 131 mm. Broken and jumbled.

Cb3969 (160E). Phragmocone, disturbed pieces of the mantle, fragment of ink sac. Preserved length 113 mm. Dorsal side.

Cb3970 (160E). On a black tablet with Cb3971. Phragmocone. Length 94 mm, width at anterior end 56 mm.

Cb3971 (160E). Phragmocone. Length along mid-like 72 mm, width at anterior end 49 mm.

Cb3972 (160F). Phragmocone, much larger than the others. Probably dorsal side. Length 303 mm, broken apex; estimated 310 mm when complete. However it may be made up from two different individuals; if so, the estimated total length is meaningless.

Cb3973 (160G). On black tablet with Cb3974-6. Apical part of a phragmocone. Pearce note reads 'A series of the capsules with their chambers, uncrushed, showing the natural shape, the siphunculus, and the thickness of the capsule, together with its radiated structure.'

Cb3974 (160G). Apical part of a phragmocone. For Pearce note see Cb3973.

Cb3975 (160G). Phragmocone, not flattened, preserved in calcareous mudstone. Possibly not *Belemnotheritis*. For Pearce note see Cb3973.

Cb3976 (160G). As last.

Cb3977 (-). Phragmocone, in a poor state. Figd Mantell, 1848, pp. 175-176, plate 13, fig. 1.

Cb7661 (-). Much disturbed specimen with phragmocone, mantle, ink sac, arms. Lacks label in Pearce's hand; later Museum label attributes it to Pearce coll. Figd Allison, 1988, figs 2B, 3-4.

Cb7662 (-). Part of mantle and ink sac. Lacks label in Pearce's hand; later Museum label attributes it to Pearce Colln.

SPANISH NEOGENE RHINOCEROSES

by ESPERANZA CERDEÑO

ABSTRACT. Nine genera and fourteen species are recognized among the rhinocerotid remains of the Spanish Miocene and Lower Pliocene. *Protaceratherium minutum* and *Prosantorhinus* sp. are reported in Spain for the first time, and the species *Alicornops alfambrense* has been published recently as a final form in the *A. simorreense* evolutionary lineage. The overall diversity of Rhinocerotidae in the Neogene record of Spain is generally much greater than that of the Equidae. Palaeoclimatic curves for the Spanish Neogene show how rhinoceros diversity depended on the relative humidity and the temperature.

THIS paper reviews the rhinocerotids of the Spanish Neogene, with data from the author's Ph.D. (Cerdeño 1989). Up to now, among Spanish Neogene rhinoceroses, only the fossil remains from the Vallés-Penedés basin had been studied in detail (Santafé 1978a), and they alone have mainly been used as a point of reference.

The fossil material of rhinoceroses comes from 45 Spanish sites, with more than 2000 identified bones, but including only a few cranial remains. These sites have a wide geographical and temporal distribution. They are located in several sedimentary basins: Ebro, Duero, Calatayud-Teruel, with two main areas (Daroca and Teruel), Tajo, and the Eastern and Betic basins. The chronological distribution of the localities ranges through the Miocene and Lower Pliocene (Ruscinian). As can be seen in Text-figure 1, the fossil record is continuous through that time, and only the base of the middle Aragonian is unknown, which is the case for all macromammal groups, not just rhinocerotids. The biozones I have used are those of Mein (1975) and Daams and Freudenthal (1981). Anatomical abbreviations are: I, incisor; Mc, metacarpal; P, premolar.

SYSTEMATIC PALAEOONTOLOGY

Family RHINOCEROTIDAE Owen, 1845

Rhinocerotidae indet. I

The presence of a rhinocerotid in the Lower Miocene of Cetina de Aragón, Zaragoza, is documented only by a distorted McIII whose size and proportions are close to those of the McIII from Paulhiac and Laugnac, France, that Bonis (1973) identified as *Diceratherium pleuroceros*. This name corresponds to *Pleuroceros pleuroceros* as used by Antunes and Ginsburg (1983), Prothero *et al.* (1986) and Guérin (1989). At the moment, it is not possible to assert that the bone from Cetina corresponds to that species, and it is advisable to classify it as Rhinocerotidae indet. I.

Subfamily MENO CERATINAE Prothero, Manning and Hanson, 1986

Protaceratherium minutum (Cuvier, 1822–1825)

The genus *Protaceratherium* has recently been included in the tribe Menoceratini (Heissig 1989) within the subfamily Aceratheriinae, but Prothero and Schoch (1989) consider it as a member of the subfamily Menoceratinae. *Protaceratherium minutum* is the oldest rhinocerotid recorded in the Spanish Neogene. It is known from only two Lower Miocene sites of the Cuenca province, Valquemado and Loranca del Campo. The former corresponds to the MN 2b or Y zone in age and the latter to the MN 3a or Z (Ginsburg *et al.* 1987b). The species is very abundant, with more than 400 remains in Loranca. Among them, there is a cranial fragment

TABLE 1. Biostratigraphical distribution of the European localities with *Protaceratherium minutum*, after Ginsburg *et al.* (1987), Antunes and Ginsburg (1983), Bonis (1973), 1, Mein (1975); 2, Daams and Meulen (1984).

(1)	(2)	Spain	France	Others
4a			Artenay	
3b	A		Beilleaux	Lisboa 1 Chitenay
3a				
	Z	Loranca		
2b			Laugnac	La Chauv
	Y	Valquemado	Selles/Cher	Ulm
2a			Moissac	Budenheim
1	X		Paulhiac Pechbonieu	

which coincides basically with the cranium from Budenheim, Germany, figured by Roman (1924), our specimen being wider in the middle of the occipital face.

The small and slender *P. minutum* shows the upper premolars with a strong lingual cingulum, and there is a bridge of union between protoleph and metaloph whose development is variable. This variation can be observed in the sample from Loranca del Campo, as well as in the French remains from Selles-sur-Cher. Both cases also show the different development of the crochet and crista of the upper premolars. Lower teeth from Valquemado show labial and lingual cingula only on P₂, while at Loranca cingula are present on all the premolars and some molars. The differences among the teeth and the postcranial skeleton of the studied samples of *P. minutum* are mainly referred to size. This is greater in Loranca, where a slightly greater thickness can also be observed.

When the Spanish material is compared with the European data on *P. minutum*, the closest identity is found with the Selles-sur-Cher sample. The French molars are relatively smaller than the premolars and the same also occurs in the Beilleaux sample. The size of the Selles-sur-Cher specimens is closer to those from Valquemado than those from Loranca. This is expected since Selles-sur-Cher is supposed to be almost equivalent in age to the former and older than the latter (Table 1). The trend observed between the two Spanish sites (size increase and slenderness decrease through time) cannot be generalized because younger sites like Beilleaux, France, or Lisbon, Portugal, have smaller-sized specimens than Loranca. The maxillary fragment from Lisbon (Roman and Torres 1907) has been considered as a distinct species, *Protaceratherium tagicum*, because of its smaller size, shorter upper P⁴, and the disappearance of the lingual cingulum at the protocone level (Antunes and Ginsburg 1983). As already stated (Cerdeño 1989), these characters show great variation in the different studied samples. So, the size of the Lisbon teeth exceeds those from Beilleaux. On the other hand, the real length of the P⁴ cannot be measured because the specimen lacks the ectoloph. The discontinuity of the lingual cingulum at the protocone as well as at the hypocone level has been observed in several specimens from Loranca, Selles-sur-Cher, Beilleaux, and Faluns (Touraine, Anjou). This all suggests that the remains from Lisbon do not constitute a distinct species, at least with the present data, and so they are best included in *P. minutum*.

Concerning the postcranial skeleton, the similarity is retained between Valquemado and Selles-sur-Cher and there is also a clear resemblance with the German remains from Budenheim (Roman 1924), whose dimensions are also smaller than in Loranca.

In Western Europe, *Protaceratherium minutum* ranges from the earliest Lower Miocene (Pechbonieu and Cintegabelle, France; Antunes and Ginsburg 1983) to the early middle Aragonian (Artenay, France) (Table 1). Its best representation corresponds to the MN 2-3 or Y-Z-A biozones, with a variation in size that possibly reflects different habitats among the distinct areas where the species has been found.

Later in the middle Aragonian another genus, *Plesiaceratherium*, whose generic characteristics (Yan and Heissig 1986) are basically those of *Protaceratherium*, has been reported in Spain as well as in other Western European countries. I think both genera must be synonymous because it is just the larger size of *Plesiaceratherium* that marks the difference between them. So, *Protaceratherium* has priority over *Plesiaceratherium*. *Plesiaceratherium platyodon* has been found in several middle Aragonian sites of Western

Europe, such as the Spanish sites of Buñol, Valencia (Belinchón 1987), and Can Más, Barcelona (Santafé 1978a). It might be thought that this species is a descendant of *Protaceratherium minutum*.

Subfamily ACERATHERIINAE Dollo, 1885

Alicornops simorreense (Lartet, 1851)

Alicornops alfambrense Cerdeño and Alcalá, 1989

Yan and Heissig (1986) and, more recently, Guérin (1989) and Heissig (1989) have already considered the species *A. simorreense* as the genus *Alicornops*. The definition of this genus would correspond basically with the subgeneric diagnosis (Ginsburg and Guérin 1979) which has been partly reviewed (Cerdeño 1989). One of the characteristics established by Ginsburg and Guérin (1979), the lack of McV, can be clearly refuted by the existence of several well-developed McV in the Spanish sites of Toril-3, Arroyo del Val, and Los Valles de Fuentidueña. At the moment, what really characterizes *Alicornops* is the shortening of the limbs. This genus includes two species, *A. simorreense* and a second one, *A. alfambrense*, recently described from the upper Vallesian of Spain (Cerdeño and Alcalá 1989).

A. simorreense is well known from the upper Aragonian and Vallesian in Western Europe, but it is in Spain that it is best represented with more than 800 remains, among which are three cranial fragments, almost the only ones known for this species. It is widely distributed in the Vallés-Penedés (Santafé 1978a, 1978b), Duero, Tajo, and Calatayud-Daroca basins. Most of the sites are upper Aragonian and Los Valles de Fuentidueña, Nombrevilla, and Relea are lower Vallesian. Only in the Vallés-Penedés basin has *A. simorreense* been reported in the upper Vallesian at Can Jofresa (Santafé and Casanovas 1978).

The cranial fragments of *A. simorreense* come from El Lugarejo, Avila, and belong to an immature individual; Cerro del Otero, Palencia, classified as *Rhinoceros sansaniensis* by Hernández Pacheco and Dantín (1915); and Toril-3, Daroca-Zaragoza, the most complete fragment. As far as can be observed in these fragments, the nasal notch and the anterior orbital edge reach the same level as in *H. tetradactylum* (Guérin 1980) and the processus postglenoideus and posttympanicus are also in contact. The ratio between head and limbs is similar in *A. simorreense* and in the extant species *Rhinoceros unicornis*, *Dicerorhinus sumatrensis*, and *Diceros bicornis* (according to the mean values of Guérin 1980).

The mandible is wide at the symphysis, even for female individuals, as is observed in the two specimens from Toril-3, Daroca, one with small incisors (I_2) (female), and the other one with a much greater I_2 (male).

The upper dentition is larger than in the type specimen from Simorre, France, mainly in P^3 and P^1 . There is an increase in size from the upper Aragonian populations to the lower Vallesian, Los Valles de Fuentidueña, Nombrevilla. The same is observed in the postcranial skeleton. The bones are strong and short, mainly the metapodials, but without being massive bones. There are individual morphological variations in the articular facets and, as in the dentition, size is greater in the lower Vallesian, but this increase is not always very obvious, such as in the astragalus.

By contrast, there is a great deal of postcranial material from the upper Vallesian site of La Roma-2, Teruel, whose morphology is comparable to that of *A. simorreense* but with a significantly different size and robustness (Cerdeño and Alcalá 1989). At the moment, *A. alfambrense* has only been identified from La Roma-2, but some of the French remains from Montredon, classified as cf. *Prosantorhinus* (Guérin 1980, 1988), could be ascribed to *A. alfambrense*. This species would constitute a final stage in the evolution of *A. simorreense*, the species from which it would have been derived, from populations like that of Los Valles de Fuentidueña, where the trend of increase in size and strength can already be noticed. At the same time, other populations of *A. simorreense* seem to increase in size, but retain their proportions, such as the upper Vallesian samples from Vallés-Penedés and the French sites.

Hoploaceratherium tetradactylum (Lartet, 1837)

H. tetradactylum has been reported in upper Aragonian sites of the Vallés-Penedés basin (Santafé 1978a). Moreover, it is present at three other sites in the Madrid area; Paracuellos-5, where it has been recognized previously by Alberdi *et al.* (1985), but on the basis of some bones that really do not belong to this species. With some doubt, because of the scarcity of remains, *H. tetradactylum* is thought also to be present at Cerro de la Plata and Henares-1 (Cerdeño 1989). On the other hand, its presence cannot be confirmed in the Vallesian site of Nombrevilla (Santafé *et al.* 1982) based on the studied sample (mainly dentary remains) which is comparable to that of *A. simorreense* from Los Valles de Fuentidueña.

H. tetradactylum has recently been removed from the genus *Aceratherium* by Ginsburg and Heissig (1989). One of the diagnostic characters indicated by the authors, the semilunate outline of the centrale in the tarsus, does not agree with my own observations on the type material of the species from Sansan, France.

Aceratherium incisivum Kaup, 1832–1834

This species is better documented in the Vallés-Penedés basin than in the rest of Spain. Alberdi *et al.* (1981) recognized *Aceratherium* cf. *incisivum* at Los Valles de Fuentidueña. It is also present in the Teruel area, the upper Vallesian sites of La Roma-2 and Masía del Barbo, and the middle Turolian site of Conclud. The presence of *A. incisivum* at the upper Turolian site of Venta del Moro, Valencia (Guérin 1980; Morales 1984) cannot be supported. The mandible described by the authors does not show the characteristics of the type material from Eppelsheim, Germany (Kaup 1832–1834). The symphysis is narrower and it is more like *Dicerorhinus schleiermacheri* from the latter site. So, this implies that the last appearance of *A. incisivum*, and thus of the subfamily Aceratheriinae in Spain, corresponds to the middle Turolian.

Subfamily RHINOCEROTINAE Owen, 1845

Tribe TELEOCERATINI Hay, 1902

The teleoceratines are not well represented in Spain. There are some reports of the genus *Brachypotherium*, and the presence of the genus *Prosantorhinus* has been established for the first time (Cerdeño 1989).

Rhinocerotidae indet. II cf. *Brachypotherium* Roger, 1904

The oldest remains in the Spanish Neogene related to this group are a few bones and a fragment of an upper I¹ from the Lower Miocene site of Loranca del Campo, Cuenca. These are scarce elements and not significant enough for an accurate identification.

Brachypotherium aurelianense (Nouel, 1866)

Some remains from Rubielos de Mora, Teruel, classified as *Brachypotherium* sp. (Aguirre and Moissenet 1972) seem to correspond to *B. aurelianense*, like those of Molí Calopa (Santafé 1978a). Adding to these reports, *B. aurelianense* has been identified in La Artesilla, Zaragoza, from a few remains that include a wide and short astragalus whose size and proportions indicate its identity.

Rubielos de Mora and Molí Calopa are younger sites than Loranca del Campo within the Lower Miocene, zone A, while La Artesilla is even more recent, corresponding to a lower Aragonian age, the lowest part of zone C, and this indicates the most recent known remains of *B. aurelianense* in Spain. Santafé and Belinchón (1988) noted the presence of *B. aurelianense* at Buñol, Valencia, but these remains are *Prosantorhinus* sp. (see below).

Antunes and Ginsburg (1983) believe that *B. aurelianense* must be included in the genus *Diaceratherium*, keeping the genus *Brachypotherium* just for the youngest species *B. brachypus*. I have in preparation a revision of the French Miocene material of brachypotheres, and I prefer now to maintain *B. aurelianense* in *Brachypotherium*.

Brachypotherium brachypus (Lartet, 1837)

B. brachypus was reported in some upper Aragonian Spanish sites of the Daroca area, Zaragoza (Guérin 1980). The fossil material preserved at Utrecht University indicates the presence of this species at Arroyo del Val-4, Manchones-1, and Manchones-2, despite the general scarcity of remains.

Prosantorhinus sp.

As noted above, another teleoceratine genus, *Prosantorhinus*, has been recognized for the first time in Spain. Checking the lower Aragonian material from Buñol, I found a McIV which caught my attention because of

its great robustness and small size. This bone is not coincident in size or proportions with the French *B. anrelianense*. However, a comparison with two MeIV casts of *Prosantorhinus germanicus* from Sandelzhausen, Germany, supports the idea of the presence of *Prosantorhinus* at Buñol. Certain differences do not permit the identification of the MeIV from Buñol with the German species but, on the other hand, there is some unpublished French material identified as *Prosantorhinus domvillei* (Antunes and Ginsburg 1983, p. 24) with which the Buñol material should be compared.

The MeIV from Buñol also presents similarities with the Lisbon material classified either as *Diaceratherium anrelianensis* or as *Gaindatherium rexmanueli* (Antunes and Ginsburg 1983). The identification of the MeIV as *Prosantorhinus* caused doubts about the correct classification of the Portuguese material. Furthermore, *Prosantorhinus* was also indicated at Lisbon from some dental remains. The Lisbon material must be revised in detail because some of the bones classified as *D. anrelianensis* could belong to *Prosantorhinus*. Besides, the presence of the genus *Gaindatherium* in Lisbon seems very doubtful. A brachypodial postcranial skeleton has never been associated with this Asian genus, contrary to what is stated for *Prosantorhinus* (Heissig 1972, 1974), and possibly the Portuguese postcranial bones assigned to *Gaindatherium* belong to *Prosantorhinus*.

Present data show that *Prosantorhinus* was distributed in Western Europe in sites in Portugal (Lisbon), Spain (Buñol), France (Baigneaux, Artenay, Beaugency, Savigné, La Romieu), and Germany (Sandelzhausen, Steiermark, Georgensgmünd), coexisting in some cases with *B. anrelianense* (La Romieu, Savigné). The Middle Miocene age of these sites ranges from unit MN 3 (Savigné or Les Beilleaux) to MN 5/6 (Georgensgmünd).

Tribe RHINOCEROTINI Owen, 1845

Subtribe ELASMOTHERIINA Bonaparte, 1845

The third group of rhinocerotids recorded in the Spanish Neogene corresponds to the elasmotherines. This group has changed its rank from family to subtribe, according to Prothero and Schoch (1989).

Hispanotherium matritense (Prado, 1864)

The elasmotherines evolved mostly in Asia, but in the Middle Miocene the species *Hispanotherium matritense* appears in the Iberian Peninsula and recently it has been found in France (Ginsburg *et al.* 1987a). First the species (Prado 1864), and later the genus (Crusafont and Villalta 1947) were recognized from dental remains from Puente de Toledo, Madrid. These teeth were characterized by their tendency toward hypsodonty, undulating enamel, and much cement. *H. matritense* has now been recognized in Spain at Dehesa de los Caballos, Plasencia-Cáceres; Torrijos, Toledo; Córeoles, Guadalajara; the Daroca area, Torralba de Ribota, and Tarazona de Aragón, Zaragoza; and recently at La Retama, Cuenca.

The postcranial bones are small and slender and they show great similarity with *H. grimmii*, another species described by Heissig (1976) from the Anatolian Peninsula, Turkey, but larger and slightly less slender.

Other forms with clear affinities to *Hispanotherium* have been described from the Miocene of Asia. Antunes and Ginsburg (1983) have considered them as synonyms of *Hispanotherium* at generic level, while Fortelius and Heissig (1989) place them in *Begertherium*.

The geographic distribution of *Hispanotherium* led Antunes (1979) to propose a migration route through the Alpine Arch from the Asian regions to the Iberian Peninsula. This route has also been proposed for the bovids of the tribe Boselaphini (Moyá-Solá and Alférez, in press). Later, *Hispanotherium* may have reached France from Spain.

H. matritense existed briefly in the Iberian Peninsula. In Spain, it is restricted in the middle Aragonian to the zone MN 4b or D; Córeoles could be older and seems to be included in zone C (lower Aragonian). In Portugal, *Hispanotherium matritense* appears in younger beds corresponding to the MN 5 unit, as well as in France. On the other hand, the Anatolian species has a greater time span through the whole upper Aragonian.

Fortelius and Heissig (1989) present a cladistic analysis of the elasmotherine group, in which *Caementodon* is very close to *H. matritense*, confirmed by my own observations (Cerdeño 1989). I agree also with these authors when they remove *Shemotherium hipsodontus* (Huang and Yan 1983) from the Elasmotherina because this species does not even show the dental characters of the group.

Tribe RHINOCEROTINI Owen, 1845
Subtribe DICERORHININA Ringström, 1924

The taxonomic rank of this group has varied (Heissig 1989; Prothero *et al.* 1986; Prothero and Schoch 1989), even if the subfamily rank is retained by some authors (Guérin 1989). Within Dicerorhinina, the attribution of species like *L. sansaniense*, *D. schleiermachi* or *S. miguelcrusafonti* has also been discussed. For the first of these species I use the generic name *Lartetotherium* as defined by Ginsburg (1974), and I agree with Groves (1983) when he considers that the other European species must be separated from the recent genus *Dicerorhinus* (*D. sinuatensis*).

Dicerorhinina indet.

The oldest representative of the dicerorhines in Spain is a rhinoceros from the lower Aragonian of La Artesilla, Zaragoza. The remains are scarce and non-diagnostic. They are identified as Dicerorhinina because of their global similarities with *Dicerorhinus montesi* from Buñol (Santafé *et al.* 1987). This rhinoceros from La Artesilla corresponds to the Rhinocerotidae indet. III of Text-figure 1.

Lartetotherium sansaniense (Lartet, 1851)

Several Spanish sites have provided scarce remains of *Lartetotherium sansaniense*: Paracuellos-3, Madrid; La Cistérniga, Valladolid; Cerro del Otero, Palencia; Coca, Segovia; and Brihuega, Guadalajara, in the upper Aragonian; and Relea, Palencia; Can Ponsic, Barcelona; and perhaps Nombrevilla, Zaragoza, in the lower Vallesian.

Study of the whole complex, and comparison with the type material from Sansan, France, led to the realization that the dentition is basically identical, but the postcranial skeleton is different (Cerdeño 1986). All comparable bones from the named sites are smaller than the bones from Sansan, and only a pyramidal and a cuboid from Paracuellos-5, Madrid, are closer to their French homologues. These latter two bones were first classified as *Aceratherium tetradactylum* (Alberdi *et al.* 1985), but a later revision suggested a *Dicerorhinus* morphology. It is not easy to interpret these *Lartetotherium* remains. Sansan, as well as Paracuellos-5, are older sites than the others and so there could have been a decrease in size with time. Added to this material of *L. sansaniense*, there are some other older remains (lower Aragonian, zone C) whose morphology and size are also closer to Sansan and their relationship is difficult to establish. This is the case for the remains from Can Más (Santafé 1978; Cerdeño 1986) and the *Dicerorhinus montesi* from Buñol (Santafé *et al.* 1987). Following these authors, *D. montesi* is related to *D. schleiermachi* from the Upper Miocene but it could be more directly related to *Lartetotherium sansaniense*, and even in the same genus. New material of *D. montesi* (the skull and dentition are still unknown) is needed to support this possible relationship.

Dicerorhinus schleiermachi (Kaup, 1832–1834)

Another classical species of *Dicerorhinus*, *D. schleiermachi*, might also be related to *Lartetotherium*. This large species is well represented in the Upper Miocene of Western Europe. In Spain, it is known in the lower Vallesian of the Vallés-Penedés basin and from several localities in the upper Vallesian of the Teruel area like Masía del Barbo and La Roma-2. The abundant bones from La Roma-2 are very large and some of them surpass the maximum values established by Guérin (1980) for this species. Their robustness is also somewhat greater than at other sites. In the Spanish lower Turolian, *D. schleiermachi* is present at Piera, Vallés-Penedés; Puente Minero, Teruel; and Crevillente-2, Alicante. At this last site, the species is very well represented by dental remains, but only three bones have been recovered, contrary to what occurs at La Roma-2 where just six teeth have been found. The species is present through the rest of the Turolian, but is much scarcer. It is known from the middle Turolian of Conclud, Teruel, and the upper Turolian of Las Casiones and El Arquillo, Teruel; Venta del Moro, Valencia; La Alberca, Murcia; and Los Hornillos and El Fargue, Granada. As already commented, the classification of the mandible from Venta del Moro as *Aceratherium incisivum* (Morales 1984) has been modified (Cerdeño 1989). Together with the mandible, there is a very large cuboid that can be assigned to *Dicerorhinus schleiermachi*.

Guérin (1980) classified the metapodials from El Fargue as *Diceros pachygnathus* (he identifies this species at Cenes de la Vega, but the described material comes from El Fargue). This taxonomic determination is not

AGE	STAGE	1	2	LOCALITY	i	a	b	c	d	e	f	g	h	j	k	l	m	n	o	
PLIOCENE	RUSCINIAN		15	Layna															*	
			14	La Calera																*
UPPER MIOCENE	UPPER TUROLIAN		13	El Fargue															*	
				Cenes de la V. La Alberca Venta del Moro Las Casiones El Arquillo																*
	MIDDLE TUROLIAN		12	Crevillente 15															*	
				Los Mansuetos Concud											*					*
	LOWER TUROLIAN		11	Piera											*					*
				Puente Minero Crevillente 2																
UPPER VALLESIAN		10	Can Perellada											*					*	
			Can Jofresa Masía del Barbo La Roma 2									*			*					*
LOWER VALLESIAN	I	9	Can Llobateres							*				*					?	
			Can Ponsic Nombrevilla Chiloeches Los Valles de F. Relea								*					*				?
	H									*			cf					*		
										*										
MIDDLE MIOCENE	UPPER ARAGONIAN	G	7/8	Brihuega							*								*	
				Coca La Cistèrniga Cerro del Otero Andurriales Toril 3							*									*
	ARAGONIAN	F	6	Arroyo del Val		*				*									*	
				Manchones 1 y 2 Armantes 3 Paracuellos 3 Paracuellos 5		*					*				cf					*
MIDDLE ARAGONIAN	E	5	Henares 1										?						*	
			Puente de Toledo Tarazona Torrijos Munébrega 1 Valdemoros 1A Torralba V																	*
LOWER ARAGONIAN	D	4b																	*	
																				*
LOWER ARAGONIAN	C	4a	Córcoles			*	*		*						*			?	*	
			Buñol Can Juliá Can Más Artesilla																	?
	B				III	*														
LOWER MIOCENE	RAMBLIAN	A	3	Rubielos de Mora		*														
				Molí Calopa Loranca																
	Z				II=cf					*										
	Y	2b	2a	Valquemado						*										
				Cetina de A.	I															

TEXT-FIG. 1 Biostratigraphical distribution of the Rhinocerotidae in the Spanish Neogene localities. 1, Daams and Freudenthal (1981). 2, Mein (1975). i, Rhinocerotidae indet.; a, *Brachypotherium aurehanense*/*B. brachypus*; b, *Prosantorhinus* sp.; c, *Plesiaceratherium platyodon*; d, *P. mirallesi*; e, *Protaceratherium minutum*; f, *Alicornops simorreense*; g, *A. alfambrense*; h, *Hoploaceratherium tetradactylum*; j, *Aceratherium incisivum*; k, *Hispanotherium matritense*; l, *Lartetotherium sansaniense*; m, *Dicerorhinus montesi*; n, *Dicerorhinus schleiermacheri*; o, *Stephanorhinus miguelsalazarfonti*.

justified. *D. pachygnathus* has been defined on material from Pikermi, Greece. Bones from this site (Musée Guimet d'Histoire Naturelle, Lyon) show that differences from *D. schleiermachi* from La Roma are limited to the greater robustness of the Greek material. On the other hand, Geraads (1988) has revised the rhinocerotids from Pikermi, and has noted the presence of two forms; *Ceratotherium neumayri* (= *Diceros pachygnathus*) and *Dicerorhinus pikermiensis* (= *Dicerorhinus schleiermachi* var. *orientalis*). This author established cranial differences between these two species, but he could not do the same with the postcranial skeleton (two different morphologies are observed only for some bones). The similarities between the metapodials from El Fargue and *Diceros pachygnathus* are logical since those of *D. pachygnathus* could correspond to the *Dicerorhinus* of Pikermi, a form very close to *Dicerorhinus schleiermachi*, but less slender. Therefore, the bones from El Fargue must be classified as *Dicerorhinus* cf. *schleiermachi* (Cerdeño 1989, p. 350). The main difference between these metapodials and the others is the greater relative length of the MtIII.

Stephanorhinus miguelcrusafonti Guérin and Santafé, 1978

S. miguelcrusafonti is the last species studied among the Spanish Neogene dicerorhines. It has also been described as *Dicerorhinus*, but it corresponds to the Plio-Pleistocene group named *Stephanorhinus* (Groves 1983). This species was defined from the Ruscinian Spanish site of Layna, Soria (Guérin and Santafé 1978), and also recognized at Perpignan, France. Furthermore, the species is identified at La Calera, Teruel (Cerdeño 1989). The skull and mandible are still unknown. The anatomical comparative study of *S. miguelcrusafonti* shows the different slenderness of the Spanish metapodials compared to the Perpignan ones, which have the highest indices. Besides this, there are few morphological differences between *S. megarhinus* and the Plio-Pleistocene species. The Spanish rhinoceros can be distinguished from the common Pliocene European species *S. megarhinus*, mainly by its smaller size. The robustness is comparable or slightly less than in *S. megarhinus*, and only the Perpignan bones are stronger than all other Plio-Pleistocene species. The best knowledge of *S. miguelcrusafonti* could lead to two contrary results. Either it is fully confirmed as a different species, or it becomes a variety of *S. megarhinus*, possibly a subspecies. At the end of the Ruscinian, both forms disappear.

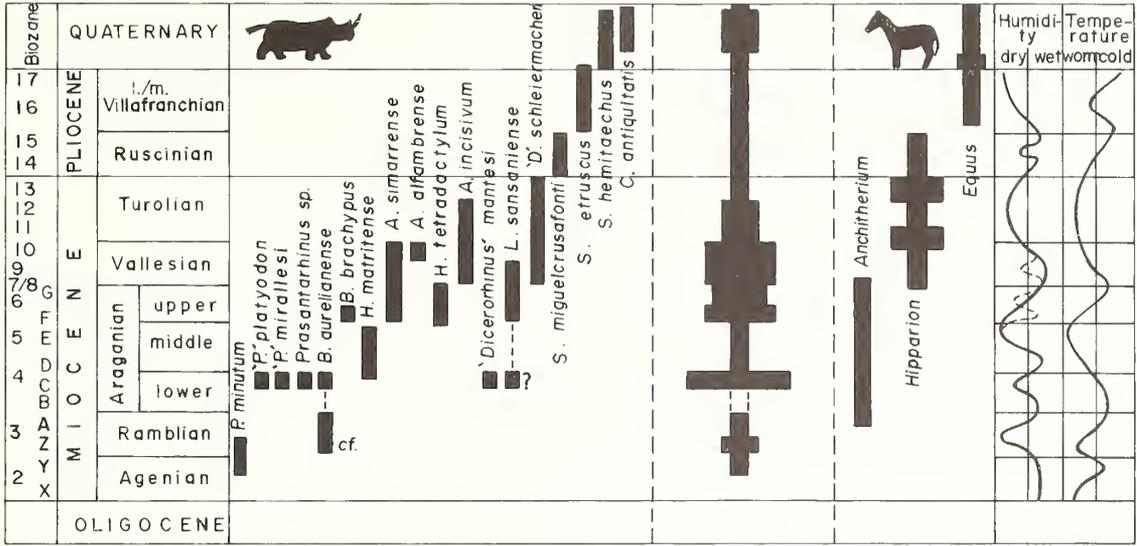
CONCLUSIONS

Nine genera and fourteen species of rhinoceros have been established in the Spanish Neogene. *Protaceratherium minutum* and *Prosantorhinus* sp. are reported in Spain for the first time, and *Alicornops alfambrense* appears in the upper Vallesian as a final stage of the *A. simorreense* evolutionary lineage.

The Spanish Miocene and Lower Pliocene (Ruscinian) are quite well documented for rhinoceroses, and only two biozones are poorly known for macromammals (not only for rhinoceroses): zone MN 2a or X in the Lower Miocene and zone MN 3/4 or B in the early Middle Miocene (lower Aragonian).

Spanish rhinocerotids document several stages that can be grouped as follows:

1. Lower Miocene, zones MN 2b–MN 3a or Y–Z. Characterized by the abundant presence of *Protaceratherium minutum*. This species is coeval with cf. *Brachypotherium* at Loranca del Campo.
2. Lower–Middle Miocene, zones MN 3b–MN 4a or A-(B)-C. Corresponds to a period of highest diversity, but with a rather low numerical representation. There are six species, although no more than four at the same site (e.g. Buñol).
3. Middle Aragonian, zone MN 4b or D. *Hispanotherium matritense* is the only rhinoceros known in the sites of this age, very abundant in localities like Córcoles or Torrijos.
4. Middle–upper Aragonian, zones MN 5/6 or E–F. Rather poorly documented, and apparently only recognized in the Madrid area. Rich sites for macromammal fauna such as Paracuellos-5 have provided only a very few remains of rhinocerotids, compared to the abundance of the equid *Anchitherium*.
5. Upper Aragonian–Vallesian, zones MN 6–MN 10. *Alicornops simorreense* is characteristic at this time. It is widely distributed in Spanish basins with its best representation in Western Europe. It can coexist with *Brachypotherium brachypus* or *Lartetotherium sansaniense*, but always as the predominant species. *A. simorreense* does not appear in Spain during the upper Vallesian, except in the one site of Can Jofresa, Vallés-Penedés basin. However, a probable descendant, *A. alfambrense*,



TEXT-FIG. 2. Schematic representation of the global diversity of the Spanish Rhinocerotidae compared with the diversity of Equidae and global palaeoclimatic changes.

is present at La Roma-2, Teruel basin. In the rest of Western Europe, *A. simorrese* has been identified in the upper Vallesian, but it is possible that a part of this material, as well as cf. *Prosantorhinus* sp. D from Montredon, France (Guérin 1980, 1988), could be related to *A. alfambrense*.

6. Turolian–Ruscinian, zones MN 11–MN 15. Characterized by the decline of the family Rhinocerotidae. Rhinoceroses are abundant in macromammal faunas until the upper Vallesian, but after the Turolian they become more and more scarce. Despite this, rhinocerotids persist until the Upper Pleistocene.

The passage between the last two stages is gradual. In fact, the most characteristic Turolian form, *Dicerorhinus schleiermacheri*, is already present in the upper Vallesian, together with *A. incisivum*. This latter species is occasionally found in the lower and middle Turolian. As early as the latest Miocene (MN 13), *D. schleiermacheri* is the only extant rhinoceros which is replaced by *Stephanorhinus mignelcrusafonti* in the Ruscinian. This one, in its turn, is the only representative of the family at that time and is replaced by *S. etruscus* in the Villafranchian.

All these different stages give us a global temporal distribution which is compared with that of the equids (Text-figure 2). The greatest diversity of the Rhinocerotidae coincides with the development of just one equid, *Anchitherium aurelianense*, a species that hardly varies through the Aragonian. The arrival of the equid *Hipparion*, among other immigrants, occurs at the same time that rhinocerotids begin to decline.

The global distribution of the rhinocerotids can be correlated with the palaeoclimatic curves established by López *et al.* (1987) for the Spanish Neogene (Text-fig. 2), mainly based on micromammals. The predominance of *Protaceratherium minutum* coincides with a warm and wet period which becomes gradually drier and colder. Daams and Meulen (1984) have also established from micromammal faunas a humid environment during the transition Agenian–lower Aragonian. The next stage, with higher diversity, corresponds to both cold and wet maxima in the palaeoclimatic curves. *Hispanotherium matritense* occurs when the conditions become drier, the temperature increases, and the humidity reaches a minimum. This species was well adapted to arid conditions, and it seems that the environment was more advantageous for this rhinoceros than for

other macromammals like the equid *Anchitherium*. This would explain their different representation in the middle Aragonian sites. Later, palaeoclimatic curves show that *Alicornops simorreense* apparently lived in a moderate climate with a global tendency to cold weather with humidity oscillations. The last period is characterized once again by maximum arid conditions in the Turolian which decrease towards the Ruscinian. Possibly, the Turolian aridity favoured *Hipparion* over rhinoceroses which do not regain their previous diversity.

Acknowledgements. This work has been mainly supported by a grant from the CSIC within the Research Project El Plio-Pleistoceno de la cuenca de Guadix-Baza y el corredor Huércal-Overa: evolución faunística y geodinámica. I thank several colleagues for their critical reading of the manuscript. I also thank Dr Kurt Heissig (Universität Institut für Paläontologie und historische Geologie, München) for the useful casts he provided.

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ESPERANZA CERDEÑO

Musco Nacional de Ciencias Naturales
c/ José Gutiérrez Abascal 2
28006 Madrid, Spain

Typescript received 20 March 1990

Revised typescript received 28 November 1990

A NEW SPECIES OF THE HYRACOID MAMMAL *TITANOHYRAX* FROM THE EOCENE OF TUNISIA

by NICHOLAS COURT *and* JEAN-LOUIS HARTENBERGER

ABSTRACT. Dental remains of a new hyracoid mammal, *Titanohyrax tantulus* sp. nov., are described from Eocene deposits at Chambi in Tunisia. This new form is one of very few Palaeogene hyracoid occurrences outside the Early Oligocene Jebel Qatrani Formation of Egypt. Very small size and low crown height reflect the primitive nature of the new species relative to other members of the genus. The Chambi rodent fauna and data from charophytes provisionally indicate an early Eocene age for the locality. *T. tantulus* is thus potentially the oldest known representative of the order Hyracoidea.

TODAY the order Hyracoidea consists of only three closely related genera confined to Africa and the Middle East (Olds and Shoshani 1982). In fact, the living forms are the remnants of a Late Miocene radiation which was the last of three major hyracoid diversifications that occurred during the Tertiary (Rasmussen 1989). The first radiation, which is assumed to have started in the Eocene and was confined to Africa, had resulted in a plethora of genera and species by Oligocene times (Meyer 1978; Rasmussen 1989). Unfortunately, due to the paucity of fossil-bearing sediments of early Palaeogene age in Africa, very little is known about the early stages of this radiation. Although four species of hyrax are known from Eocene sites in Algeria (Sudre 1979; Mahaboubi *et al.* 1986) and hyraxes are reported from Palaeogene localities in Libya (Arambourg and Magnier 1961; Savage 1969) and Angola (Pickford 1986), most of our knowledge about the early evolutionary history of this order comes from the Jebel Qatrani Formation of the Fayum Depression in Egypt (Matsumoto 1922, 1926; Meyer 1978; Rasmussen and Simons 1988). Nevertheless, by this time hyraxes were established in a variety of niches as the dominant African herbivores of medium to large body size (Rasmussen and Simons 1988). As the name suggests, *Titanohyrax ultimus* was by far the largest of these Oligocene forms (Matsumoto 1922) and occurs with two slightly smaller species of the same genus within the Jebel Qatrani Formation of Egypt. A somewhat more primitive species, *T. mougereani*, was reported from the Eocene of Algeria (Sudre 1979), although even at this stage it had already attained great size. We here describe dental remains of a new small hyrax from Eocene deposits in Tunisia which we refer to the genus *Titanohyrax*.

The site from which this material comes is known as the Chambi locality, situated on the northern slope of Jebel Chambi in the Kasserine area of Central Tunisia (Sassi *et al.* 1984; Hartenberger *et al.* 1985). A variety of micromammals have been recovered from lacustrine limestones occurring above a basal conglomerate lying unconformably on marine Late Cretaceous. Insectivores, rodents and primates are presently under study at the Université de Montpellier II (France), while marsupials (Crochet 1986), macroscelidids (Hartenberger 1986) and bats (Sigé 1985) from Chambi have already been reported. The hyrax remains herein described, initially assigned to cf. *Pachyhyrax* and cf. *Saghaterrinn* in a preliminary report about the locality (Hartenberger *et al.* 1985), are the only macromammals thus far recovered from Chambi. All specimens are registered under the prefix CBI and are housed at l'Institut des Sciences de l'Evolution, Montpellier, France.

Concerning the age of the Chambi locality: known gastropods assigned to *Bulinus* sp. indet. and *Palaeocyclolitus* sp. indet. indicate a broad Palaeocene/Eocene age (Sassi *et al.* 1984). Some 30 m above the lacustrine limestones, charophytes have been recovered which are referable to the Bartonian *Raskyella* zone of Europe (Sassi *et al.* 1984). It therefore seems possible that the age of this locality could be from Early Eocene to late Middle Eocene. Of three Eocene mammal-bearing

localities in Algeria, Nementcha is unequivocally of Late Eocene age (Coiffait *et al.* 1984) whereas two other localities, El Kohol (Mahaboubi *et al.* 1986) and Gour Lazib (Sudre 1979), are thought to be of early Middle Eocene age. Based on the observation that rodents from Chambi are clearly more primitive than those from Gour Lazib, Hartenberger *et al.* (1985) suggested an Early Eocene age for this Tunisian locality. Although arguments for the exact age of this locality are at present weak, it is evident that the Chambi fauna is considerably older than the well-known Palaeogene fauna of the Fayum and is plausibly older than the Algerian sites.

SYSTEMATIC PALAEOLOGY

Order HYRACOIDEA Huxley, 1869

Family PLIOHYRACIDAE Osborn, 1899

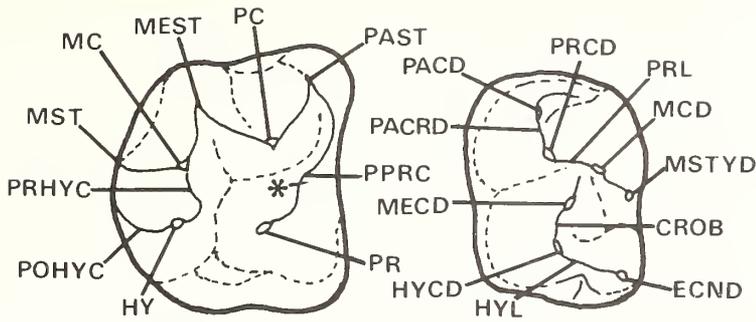
Genus TITANOHYRAX Matsumoto, 1922

Type species. *Titanohyrax andrewsi* Matsumoto, 1922.

Remarks. The genus *Titanohyrax* is today considered to contain four species of medium- to large-sized hyraxes (*T. andrewsi* Matsumoto, 1922; *T. mongereaui* Sudre, 1979; *T. ultimus* Matsumoto, 1922; and *T. angustidens* Rasmussen and Simons, 1988). All species except *T. mongereaui* (Sudre 1979) are known only from the Jebel Qatrani Formation of the Fayum Depression, Egypt (Early Oligocene). Early workers failed to recognize *Titanohyrax* as a distinct genus with the result that its constituent species have had a somewhat complex nomenclatural history. Matsumoto (1922) went some way towards clarifying the problem by recognizing that a lower jaw figured by Andrews (1906) as *Megalohyrax minor* and all those specimens treated as *Megalohyrax* by Schlosser (1910, 1911) were in fact distinct from that genus. He then erected the new genus, *Titanohyrax* Matsumoto, 1922, designating four species: *T. ultimus*, based on four isolated and heavily worn teeth, *T. andrewsi* (Andrews' mandibular specimen), *T. palaeotheroides* (Schlosser's *Megalohyrax palaeotheroides*), and *T. schlosseri* (Schlosser's *Megalohyrax eocaenus*). In the most recent wide ranging review of the order Hyracoidea, Meyer (1978) accepted the validity of *Titanohyrax ultimus*. However, he could recognize no morphological or metrical differences between *T. andrewsi*, *T. palaeotheroides* and *T. schlosseri*; thus he synonymized these three taxa under *Titanohyrax andrewsi*. More recently Sudre (1979) referred a very large upper molar from the Eocene of Hammada du Dra (Gour Lazib), Algeria, to the new species, *T. mongereaui*. Finally, based on recent hyracoid finds from the Early Oligocene of Egypt, Rasmussen and Simons (1988) considered Matsumoto's *T. palaeotheroides* to be morphologically distinct from *T. andrewsi*. As Meyer (1978) had already considered the name '*palaeotheroides*' to be a *nomen nudum* due to Schlosser's inadequate description, Rasmussen and Simons (1988) erected the new species, *T. angustidens*.

Although Matsumoto (1922) and Meyer (1978) have given adequate diagnoses of the genus, a short summary highlighting the way in which molar morphology in *Titanohyrax* differs from that of other Palaeogene genera is presented here (see Text-fig. 1. for explanation of terminology).

Titanohyrax differs from *Geniohyus*, *Bunohyrax* and *Pachyhyrax* in its possession of complete lower molar protolophid and hypolophid and a well-differentiated metastylid. Upper molars further differ from those of both *Geniohyus* and *Bunohyrax* in their possession of more selenodont buccal cusps and trenchant parastyle and mesostyle, and from those of *Pachyhyrax* by the very reduced prehypocrista, absence of spurs on the distolingual surface of the paracone and mesial surface of the distal cingulum. *Sagatherium* differs dramatically from *Titanohyrax* with its absence of lower molar metastylid, very strong prehypocrista, well-developed ribs on the buccal side of both the paracone and metacone and distinctive spurs on the lingual side of very prominent metastyle and mesostyle. Although the lower molars of *Thyrohyrax* possess a metastylid, the entoconid differs from *Titanohyrax* in being mesially very extensive, almost closing the valley between it and the metaconid. In addition, *Thyrohyrax* can be distinguished from *Titanohyrax* in its possession of a very extensive upper molar prehypocrista and folded buccal wall of the protocone. *Titanohyrax* has



TEXT-FIG. 1. Schematic drawing of hyracoid molars showing points of occlusal morphology referred to in the text. Right upper M2 (left) and right lower M2 (right). Orientation: Mesial towards right, buccal towards top (left) and mesial towards top, buccal towards left (right). The following morphological features are illustrated: CROB, cristid obliqua; ECND, entoconid; HY, hypocone; HYL, hypolophid; MC, metacone; MCD, metaconid; MECD, mesoconid; MEST, mesostyle; MS, metastyle; MSTYD, metastylid; PACD, paraconid; PACRD, paracristid; PAST, parastyle; PC, paracone; POHYC, posthypocrista; PPRC, preprotocrista; PR, protocone; PRCD, protoconid; PRHYC, prehypocrista; PRL, protolophid. The asterisk marks the 'paraconular' swelling of the preprotocrista.

most often been confused with *Megalohyrax*. However, unlike *Titanohyrax*, the lower molars of this genus have no metastylid and paraconids tend to be well developed. In the upper molars, buccal styles tend to be rounded and not trenchant with much stronger development of the metastyle. The hypocone and protocone are much more similar in size, and although the protocone lacks a postprotocrista the prehypocrista is much more prominent than in *Titanohyrax*.

Titanohyrax tantulus, sp. nov.

Text-figs 2-3

1985 cf. *Pachyhyrax* and cf. *Sagatherium* Hartenberger *et al.*, p. 649.

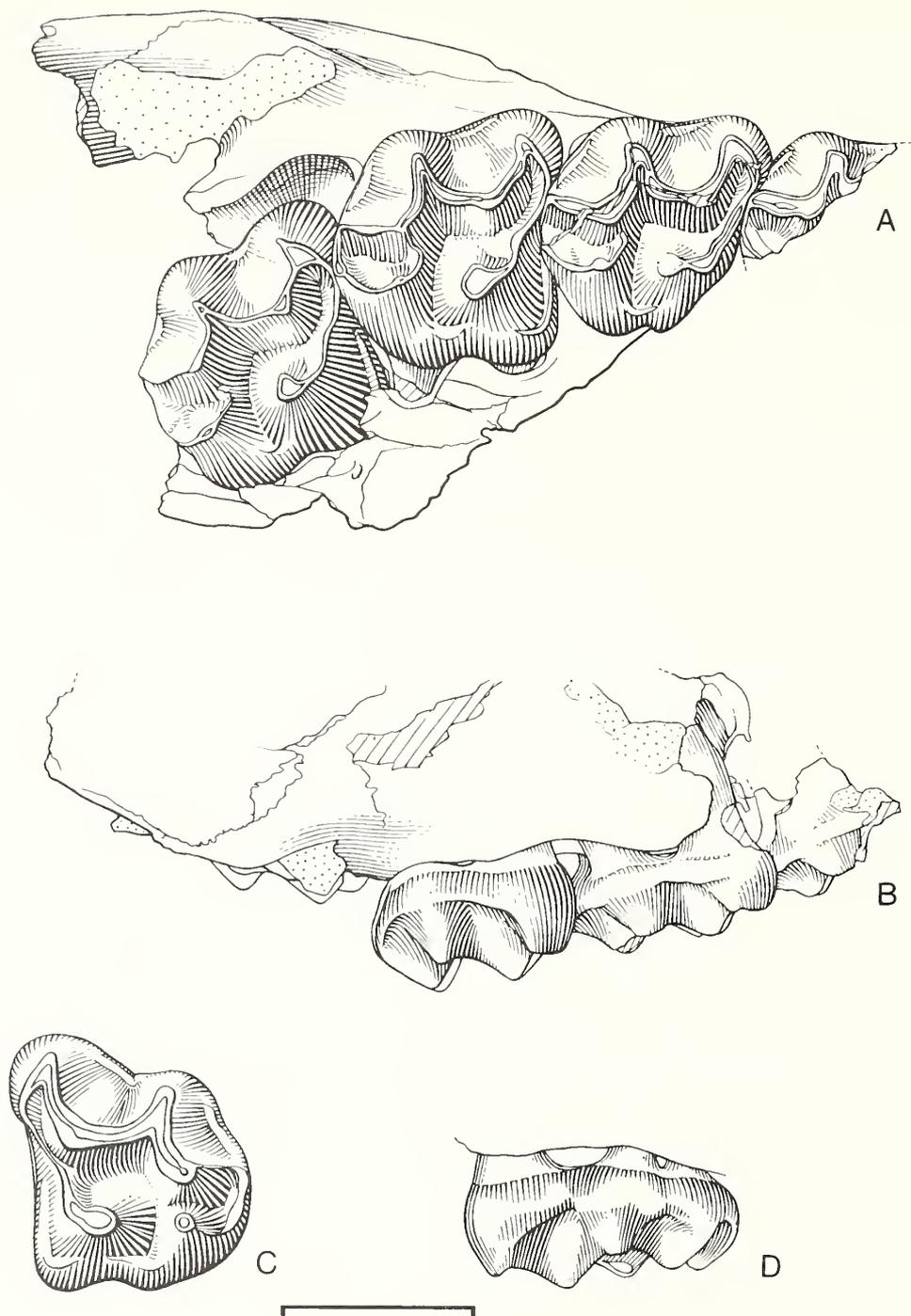
Holotype. CBI 42 right juvenile maxillary fragment with a fragment of DP3 and complete DP4-M2 (Text-fig. 2A-B).

Hypodigm. CBI 27, isolated upper left M3 (Text-fig. 2C-D), CBI 42, lower right M2 (Text-fig. 3A-B), CBI 43, lower left ?molar/premolar (Text-fig. 3C-D), CBI 41, lower right I1 (Text-fig. 3E-F).

Locality and horizon. Northern flank of Jebel Chambi close to Kasserine, Central Tunisia. The Eocene Chambi Formation lies unconformably on marine Late Cretaceous. Specimens come from a 2 m thickness of lacustrine limestone lying about 30 m above the basal unconformity.

Etymology. *Tantulus* (Latin), meaning quite little and referring to the small size of this species relative to other members of the genus.

Diagnosis. *T. tantulus* sp. nov. differs most dramatically from the four previously reported species in its much smaller size, and from all except *T. mongereani* by its very low crown height and basally rounded upper molar styles. Morphologically it differs from *T. ultimns* by its greater differentiation of a metastylid, absence of entostylar development and stronger buccal cingulid. With the exception of size and degree of hypsodonty the lower molars of *T. andrewsi* are probably most similar to *T. tantulus*, although this species still exhibits some minor development of an entostylid. *T. angustidens* is the most distinct member of the genus possessing well-developed upper molar metastyles and long narrow lower molars with extended trigonids. In the possession of a preprotocrista that extends to



TEXT-FIG. 2. *Titanohyrax tantulus* sp. nov. A, CBI 42 right maxilla with fragment of DP3, and DP4-M2 in occlusal view. B, the same specimen in buccal view. C, CBI 27 upper left M3 in occlusal view. D, same specimen in buccal view. Scale = 10 mm.

the parastyle and carries a paraconular swelling. *T. tantulus* is similar to *T. mongereaui*, although it differs from this and all other species in that the buccal side of the paracone is slightly convex as opposed to concave. The absence of entostylar development and the occurrence of a small mesoconid on the cristid obliqua of the lower molars are distinguishing features not reported in any other species of the genus.

Description. The type is a well-preserved portion of a right maxilla from a young individual (Text-fig. 2A-B). DP4 and M1 are in place with M2 erupting from the crypt behind. Morphology from DP4 to M2 is unchanged although there is a normal increase in size distally. The molars are very low-crowned and somewhat trapezoidal in outline, with slightly oblique ectolophs; the width being slightly greater than the length. The parastyle is very strong and marks the most buccally extensive part of the tooth. The mesostyle is strong and compressed mesiodistally near its apex but, in common with the parastyle, becomes more globular towards the base of the tooth. Both the paracone and metacone are lingually displaced with respect to the buccal styles giving the ectoloph a very selenodont appearance. Buccally, the wall of the paracone is slightly convex while that of the metacone is flat. The metacone is more lingually positioned than the paracone, lying lingual and only slightly distal to the mesostyle. A very short postmetacrista descends abruptly in a distal and slightly buccal direction from the summit of the metacone to join the distal cingulum, thus there is no real development of a metastyle.

TABLE 1. *T. tantulus* sp. nov. length (L) and width (W) measurements (mm) of dental specimens referred to in the text.

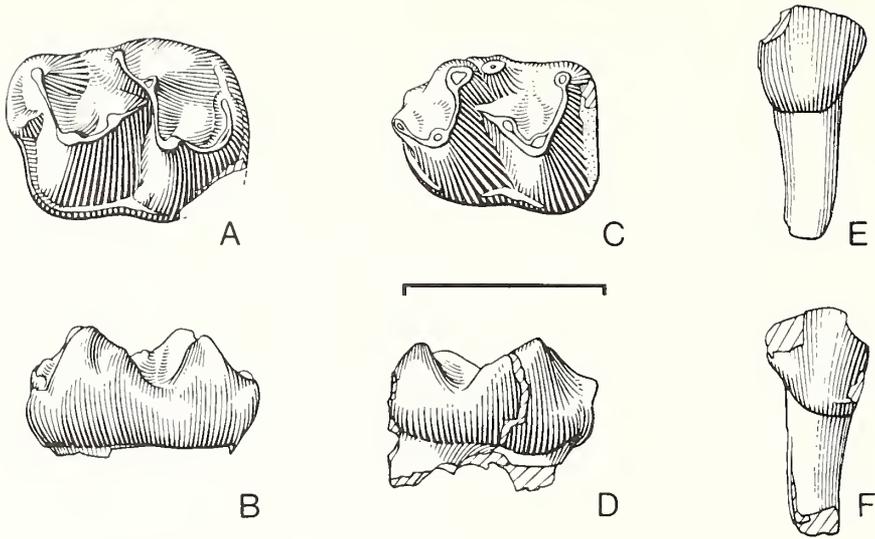
	DP4		M1		M2		M3	
	L	W	L	W	L	W	L	W
Upper teeth								
CBI 42	9.9	10.1	11.1	12.1	11.7	12.4	—	—
CBI 27	—	—	—	—	—	—	12.3	13.0
Lower teeth								
CBI 44	—	—	—	—	11.6	9.2	—	—
CBI 43	—	—	10.2	6.2	—	—	—	—

The protocone is by far the more dominant of the two lingual cusps. It is situated slightly more distally relative to the paracone such that its mesial face slopes shallowly towards the mesiolingual corner of the tooth. The preprotocrista is exceedingly well developed; it extends mesiobuccally to join a lingually trending crest from the apex of the parastyle. At a point midway between the protocone and paracone the preprotocrista is slightly raised to form a small paraconular swelling. There is no development of a postprotocrista. The hypocone is much smaller than the protocone, being mesiodistally compressed and confined to the distolingual corner of the tooth. The prehypocrista is extremely short, buccally directed and abuts the base of the lingually displaced metacone. Descending distally from the hypocone, the short posthypocrista swings abruptly towards the buccal side of the tooth to join the short postmetacrista, thus providing the slightly convex closure to a small distal fossette. Cingula are disjunct around the base of the tooth, being present only at the buccal base of the paracone and metacone, around the mesiolingual base of the protocone and between the protocone and hypocone.

An isolated left upper M3 (Text-fig. 2C-D) is somewhat more trapezoidal in outline. The preparacrista is a little longer and more buccally directed while the hypocone is even more constricted than in the more anterior molars and shows no development of a prehypocrista.

The lower dentition is known only from three isolated teeth. Two molariform teeth are interpreted here as a right M2 (Text-fig. 3A-B) and smaller left M1 or molariform premolar (Text-fig. 3C-D). In addition a single spatulate incisor is known. Spatulate lower incisors were cited as a titanohyacid character by Rasmussen and Simons (1988) in their diagnosis of the genus. Moreover, since *T. tantulus* is the only macromammal known from the Chambi locality this isolated incisor is confidently referred to this species. From the degree of asymmetry it appears to be a right first incisor (Text-fig. 3E-F).

The second molar is essentially bilophodont with strong transverse crests joining the protoconid to the metaconid mesially and the hypoconid to the entoconid distally. A short paracristid descends steeply from the



TEXT-FIG. 3. *Titanohyrax tantulus* sp. nov. A, CBI 44 lower right M2 in oclusal view. B, same specimen in lingual view. C, CBI 43 lower left ?M1 or P4. D, same specimen in lingual view. E, CBI 41 lower right I1 in buccal view. F, same specimen in lingual view. Scale = 10 mm.

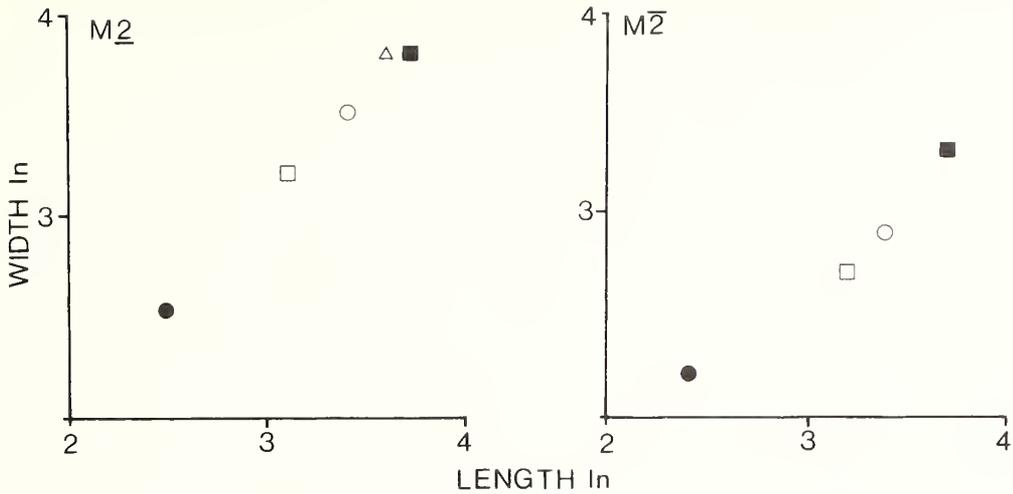
protoconid, curving mesiolingually to merge low down with the mesial cingulum. A very slight swelling of the paracristid occurs just in front of the protoconid and could be interpreted as a vestigial paraconid. The anterior part of the trigonid is greatly reduced and correlates with the poor development of the postmetacrista and virtual absence of a metastyle in the upper molars. The metaconid is well developed and situated almost directly opposite the protoconid. A distinct distolingually trending crest descends a short distance from the summit of the metaconid to end in a prominent metastylid. In the distal part of the tooth, the strong hypolophid is slightly obliquely set due to the somewhat more mesial position of the hypoconid with respect to the entoconid. From the summit of the hypoconid a strong cristid obliqua descends mesiolingually to terminate just buccal of the metaconid base. Just before its termination, there is a small but discrete swelling on the cristid obliqua, more easily visible in lingual view, which is here termed a mesoconid. Cingula are quite well developed on all but the lingual base of the tooth. Distally a crest descends steeply from the back of the entoconid to form a buccally descending distal cingulum. At about the middle of the distal cingulum, a small spur-like hypoconulid is appressed to the distal base of the hypolophid.

The smaller molariform lower tooth is somewhat narrower relative to length than that already described. In addition it exhibits a stronger more mesially directed paracristid terminating in a distinct paraconid, the metastylid is more distally positioned than in the bigger tooth and the buccal cingulum is much weaker and is interrupted around the protoconid and hypoconid.

DISCUSSION

The following features of *T. tantulus* are typical of the genus *Titanohyrax*.

1. Highly selenodont buccal cusps lacking both buccal and lingual ribs with at least proximally trenchant parastyle and mesostyle. Very little development of a metastyle.
2. Protocone much larger than hypocone with strong preprotocrista and no postprotocrista.
3. Hypocone small, mesiodistally compressed with very short recurved prehypocrista abutting the lingually displaced metacone. Short posthypocrista forming the distal cingulum.
4. Mesiodistal compression of the lower molar trigonid basin.
5. Strongly developed metastylid.
6. Spatulate rather than tusk-like lower incisors.



TEXT-FIG. 4. Bivariate plot of upper (left) and lower (right) M2 (log length against width) of species attributed to the genus *Titanohyrax*. Closed circles = *T. tantulus* sp. nov. (measurements in Table 1); open circles = *T. andrewsi* (measurements taken from Matsumoto 1926); closed squares = *T. ultimus* (measurements taken from Matsumoto 1922); open squares = *T. angustidens* (measurements taken from Rasmussen and Simons 1988); open triangle = *T. mongereaui* (measurements taken from Sudre 1979).

The specimens herein described differ most dramatically from all other known members of the genus *Titanohyrax* by their extremely small size (Text-fig. 4). This alone is a sufficient criterion to warrant the erection of a new species. In addition, the upper teeth are very brachyodont with basally rounded styles, features that can be interpreted as primitive with respect to the much more hypsodont Fayum species. Indeed, the much sharper buccal parastylar and metastylar crests in Fayum forms are likely to be a simple correlate of their increased crown height. Further, there are several features observable in this material which have not been reported in previous diagnoses of the genus. The first concerns the great extent of the preprotocrista which is continuous with the buccally directed fold of the parastylar apex. In addition, the preprotocrista exhibits a small 'paraconular' swelling before joining the parastylar crest. Sudre (1979) emphasized both of these features in his description of *Titanohyrax mongereaui* from Algeria. This is also a very brachyodont form with rather globular upper molar styles; however, *T. mongereaui* is more than three times as large as the form from Chambi. In the lower molars, the presence of a small mesoconid on the cristid obliqua has never been reported for the genus although lower molars of *T. mongereaui* are as yet unknown.

As the larger lower molar occludes well with the upper molars, something of the occlusal relationship between the teeth can be deduced. In buccal phase, the metaconid occludes with the mesial face of the protocone while the metastylid occludes with the mesiolingual face of the protocone. The raised edge of the 'paraconular' swelling therefore passes between the protoconid and metaconid to shear against the protolophid. At the end of this phase of occlusal motion, the mesoconid of the cristid obliqua comes to lie in the depression between 'paraconular' swelling and protocone. Recent research has strongly proposed a close phylogenetic linkage between hyraxes and the order Perissodactyla (Fischer 1986; Prothero *et al.* 1988). Although early perissodactyls exhibit well-defined upper molar paraconules, these are always related occlusally to the development of the metastylid (Hooker 1989). Since this is not the case in *T. tantulus*, neither the 'paraconular' swelling nor the metastylid can be homologized with the condition observed in perissodactyls.

Since the 'paraconular' swelling and continuity of the preprotocrista with the parastyle has only been demonstrated explicitly in the huge brachyodont *T. mongereaui* from the Middle Eocene of

Algeria (Sudre 1979), it is tempting to postulate a close phylogenetic link between it and *T. tantulus*. The question as to whether the great disparity in size (Text-fig. 4) reflects phyletic size increase between the two species or an adaptive radiation must, however, remain open; nevertheless, if the data from rodents and charophytes indicating an Early Eocene age for the Chambi locality is substantiated, the former would be a reasonable first hypothesis.

CONCLUSIONS

The discovery of a new diminutive titanohyracid from Eocene deposits of Tunisia extends both the temporal and geographical range of the mammalian order Hyracoidea and increases the size range within the genus *Titanohyrax* substantially. The degree of brachyodonty, relative to Fayum members of the genus, indicates that the Tunisian species is more primitive. Moreover, the suggested Early Eocene age for the Chambi locality (Hartenberger *et al.* 1985) would place *T. tantulus* as the oldest representative yet known of the order Hyracoidea.

Acknowledgements. J.-L.H. wishes to thank Ahmed Ben Saïd (Office National des Mines, Tunis, Tunisia) and Claude Martinez (Office National de la Recherche Scientifique et Technique Outre-Mer, France) for their hospitality and help during field work in Tunisia. B. Marandat prepared the specimens and A. Beaux skilfully made the drawings in Text-figures 2 and 3. Dr A. R. Milner and an anonymous referee improved the typescript. N.C. gratefully acknowledges the financial support of a Royal Society European Postdoctoral Fellowship.

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NICHOLAS COURT

JEAN-LOUIS HARTENBERGER

Institute des Sciences de l'Évolution

USTL Montpellier II

Laboratoire de Paléontologie

U.R.A. 327 du C.N.R.S.

Case Courrier 064, Place Eugène Bataillon

F-34095 Montpellier Cédex 05, France

Typescript received 6 March 1991

Revised typescript received 8 July 1991

SCROLL COPROLITES FROM THE SILURIAN OF IRELAND AND THE FEEDING OF EARLY VERTEBRATES

by BRIAN GILMORE

ABSTRACT. The morphology of scroll coprolites from the post-Llandovery Silurian of Louisburgh, Co. Mayo, Ireland is described. The coprolites occur within relatively fine-grained laminites along with the anaspid agnathan *Birkenia elegans* the dermal scales of *Loganellia*, and the enigmatic '*Glauconome*'. Such a faunal association also exists in the Midland Valley of Scotland. The significance of detritus as a nutrient source and the evolution of particulate feeding among the early vertebrates is examined. By association, *Birkenia* and/or *Loganellia* appear to be the most likely producers. The coprolites in the present study are the oldest known vertebrate spiral coprolites, and the first scroll coprolites to be associated with what are at present considered to be agnathans. The coprolites represent evidence for the early development of valvular intestines, of which the scroll valvular intestine now appears to be the more primitive. These coprolites also provide some of the first definite indications that particulate feeding was of significance among early vertebrates.

IN 1986 in Louisburgh, Co. Mayo, on the west coast of Ireland, a number of small elliptical pellets were discovered in post-Llandovery Silurian laminites. They were identified as spiral coprolites by Dr Douglas Palmer. The collection consists of approximately 160 coprolites, as well as many fragments and degraded coprolitic material.

The existence of coprolites was first noted in 1678 by Lister. Mantell (1822) first proposed an animal origin, which was confirmed by Buckland (1829, 1837), who assigned coprolites from the Lias of southern England to the activities of ichthyosaurs. The conclusions of both Fritsch (1895, 1907) and Neumayer (1904) were that the Permian coprolites they examined represented fossilized valvular intestines. A link between sharks and coprolites was established in 1917 by Woodward. This link was confirmed by Zangerl and Richardson (1963) with their work on the palaeoecology of Pennsylvanian black shales from Indiana. Two conflicting ideas about the formation of coprolites were published by Williams (1972) and McAllister (1985).

Although it was important to examine previous investigations of spiral coprolites, direct comparisons with the coprolites in the present study may not always be useful. Previously all spiral coprolites have been assigned to gnathostomes. The coprolites from Louisburgh are associated with what are at present considered to be agnathans. They are also the oldest vertebrate coprolites as yet described. The composition of the coprolites from Louisburgh is not phosphatic but argillaceous, which contrasts with all previously investigated coprolites whose composition is primarily phosphatic. The majority of previously described coprolites originated from spiral or transverse valves; the coprolites described here were produced by an organism which possessed a scroll or longitudinal valve. Also previously described coprolites do not appear to have suffered the same degree of flattening as the coprolites in the present study.

GEOLOGICAL SETTING

The stratigraphy of the Louisburgh area has been fully dealt with by Maguire (1989). Previously the age of this succession had been the subject of much debate. Subsequently, Palmer *et al.* (1989), by

correlation with the Midland Valley of Scotland, settled on a post-Llandovery Silurian age for the laminites. The Louisburgh/Clare Island succession, approximately 1500 m of siliciclastic sediments, resting unconformably on a metamorphic basement, includes five formations. The basal Kill Sandstone Formation, the Strake Banded Formation, and the Knockmore Sandstone Formation are composed primarily of siltstones and sandstones. The succeeding Bunnamaohaun Siltstone Formation contains the laminites from which the coprolites have been collected. The overlying Glen Pebbly Arkose Formation is composed of coarser sediments and represents the top of the succession.

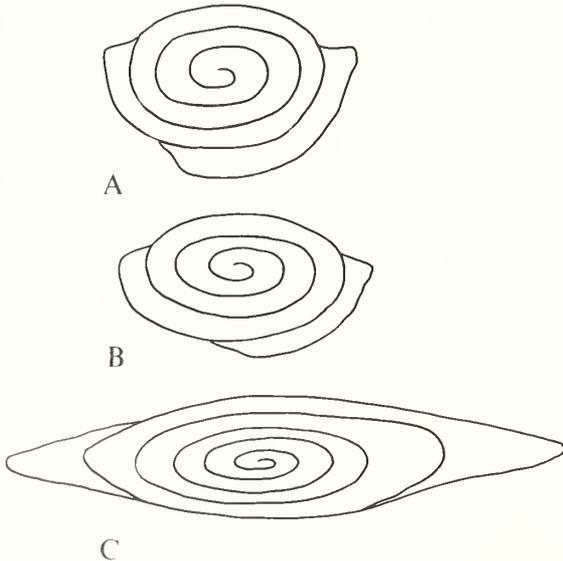
METHODS AND MATERIAL

The coprolites were examined, catalogued and measured. Suitable specimens were sectioned transversely and longitudinally. Extinction patterns were examined under plane polarized light. X-ray diffraction analysis was carried out on separately prepared samples of matrix and coprolitic material. Coprolite models were produced from modelling clay to examine the spiral coiling and deformation due to compression.

Material. Trinity College Dublin: TCD 32412, 32417, 32421, Bunnamaohaun Siltstone Fm., Louisburgh, Co. Mayo. Royal Scottish Museum, Edinburgh: T3827B, T3927, Birkenhead Burn.

DESCRIPTION

The coprolites appear as smooth, grey-brown patches of fine-grained material within the coarser matrix of the laminites. This finer grained nature is confirmed by thin-section studies. There appear to be two natural groups based on the degree of compression. One group contains coprolites which appear completely flattened and are preserved without any internal spiral structure. The second group, which has internal spiral structure (Text-fig. 1), is less numerous and the coprolites appear as bullet-shaped masses with more or less rounded ends. Exfoliation of the outer layers is often visible. Externally no spiral structure is visible in any coprolites, except for very fine sinistral striae visible on the surface of a number of them. Both groups occur side by side on the same bedding surfaces. Many coprolites occur as part and counterpart. All the coprolites display random orientation within the laminites.



TEXT-FIG. 1. Drawings of transverse sections of three scroll coprolites: note the more flattened appearance of the Irish specimen. A-B, T3827B, Birkenhead Burn, Scotland, $\times 10$. C, TCD 32421, Louisburgh, Co. Mayo, Ireland, $\times 30$.

A number of the more suitable three-dimensional coprolites were serially sectioned, perpendicular to the longitudinal axis. The sections appear as simple, continuous dorsoventrally compressed spiral coils around a central axis (Text-fig. 1c). The number of whorls varies from 4 to 6 but is typically consistent within each coprolite.



TEXT-FIG. 2. Transverse section of a scroll coprolite, TCD 32421, from Louisburgh, Co. Mayo, Ireland, $\times 45$. This section, viewed under polarized light, shows the characteristic flattened appearance, the internal spiral coil, extinction of opposite quadrants, and the contrasting grain size between coprolite and matrix, typical of the coprolites sectioned.

The second most striking feature of these sections is the extremely fine-grained nature of the material in the coil. The contrast in grain size with the matrix suggests that some degree of selection occurred prior to defaecation (Text-fig. 2). The longitudinal sections also display this fine-grained texture (Text-fig. 3), but the most noteworthy feature of these sections is the scroll-like coiling consistent with the internal morphology of scroll coprolites (Text-fig. 4). The importance of obtaining longitudinal sections is stressed by Jain (1983). Of all previous investigators, Jain alone describes what he claims to be scroll coprolites; all other authors describe spirally-coiled coprolites.

DETRITUS AND FEEDING

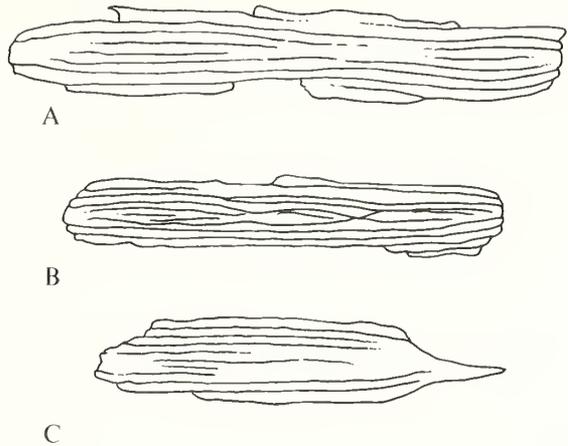
Many of the previous reviews of early vertebrate feeding appear to be in general agreement that sediment or deposit feeding was of considerable significance (Stetson 1928; Parrington 1958; Denison 1961; Ritchie 1964; Moy-Thomas and Miles 1971; Mallatt 1981). All authors are vague about the precise source of nutrition. More recently the importance of organic detritus as a source of food for filter feeders and sediment feeders has been realized (Sorokin 1981). Formed from the decaying remains of organisms, faecal pellets, and terrestrial organic material, these detrital



TEXT-FIG. 3. Longitudinal section of scroll coprolite, TCD 32417, from Louisburgh, Co. Mayo, Ireland. A, polished section of laminite containing the sectioned coprolite mounted in Araldite; the section shows the divisions between different whorls of faecal material extending the full length of the coprolite; surrounding the coprolite are patches of coprolitic material, $\times 3.3$. B, photomicrograph of the right-hand end of the same coprolite showing more clearly the parallel divisions between the 'layers' of faecal material, and the irregularly-shaped patches of coprolitic material beside the specimen, $\times 10$.

particles are the foci of microbial and heterotrophic activity (Fenchel 1970). They serve more as catalysts for energy conversion than as a direct nutrient source for sediment feeders (Conover 1978). The detrital cycle represents an active dynamic system, undergoing constant turnover (Finenko and Zaika 1970).

TEXT-FIG. 4. Drawings of longitudinal sections of three scroll coprolites: note that the divisions between adjacent whorls run parallel for the whole length of the section. A, TCD 32417, Louisburgh, Co. Mayo, Ireland, $\times 4.4$. B, T 3927, Birkenhead Burn, Scotland, $\times 5.7$. C, TCD 32412, Louisburgh, Co. Mayo, Ireland, $\times 7.8$.



The whole cycle is initiated with the introduction of freshly created organic material, from allochthonous and/or autochthonous sources (Sorokin 1978). Rapid colonization of these particles by microorganisms is followed by assimilation of the basic carbon structure of the detrital particle. This metabolism of the 'young' particle becomes less significant as the whole complex matures. The assimilation of dissolved organic matter now becomes of great significance (Khailov and Finenko 1970).

Grazing by protozoans and other members of the meiofauna stimulates bacterial productivity and therefore helps to maintain a high level of metabolism (Briggs *et al.* 1979). The complete detritus/microflora/meiofaunal complex is of great nutrient value (Odum 1970), supplying the protein, amino acid, lipid and carbohydrate requirement of detrital feeders (Parsons and Strickland 1962). Most detritivores do not possess the enzymatic ability to assimilate this material directly. They are therefore dependent on bacteria and fungi to convert the structural carbohydrate into an acceptable form (Briggs *et al.* 1979). Grazing by detritivores stimulates further microbial development by increasing the surface area available for microbial colonization by splitting particles, by resuspension of settled particles, and by the release of metabolites.

The small size of these particles is also significant. There is a peak of biomass available for particulate feeders among the smaller particle sizes (Conover 1981). The percentage of available carbon (non-carbonate carbon) in sediments also increases with an increase in the fine fraction (Zatsepin 1970). Since detritivores are in effect grazing the surface films of micro-organisms on these particles, selection in favour of fine particles will enhance the feeding efficiency and also increase the nutritional intake. Such selectivity is displayed by *Mugil cephalus*, the grey mullet, (Pandian 1975). Odum (1970) demonstrated a decrease in the percentage microbial coverage on detrital particles along the intestine of the mullet.

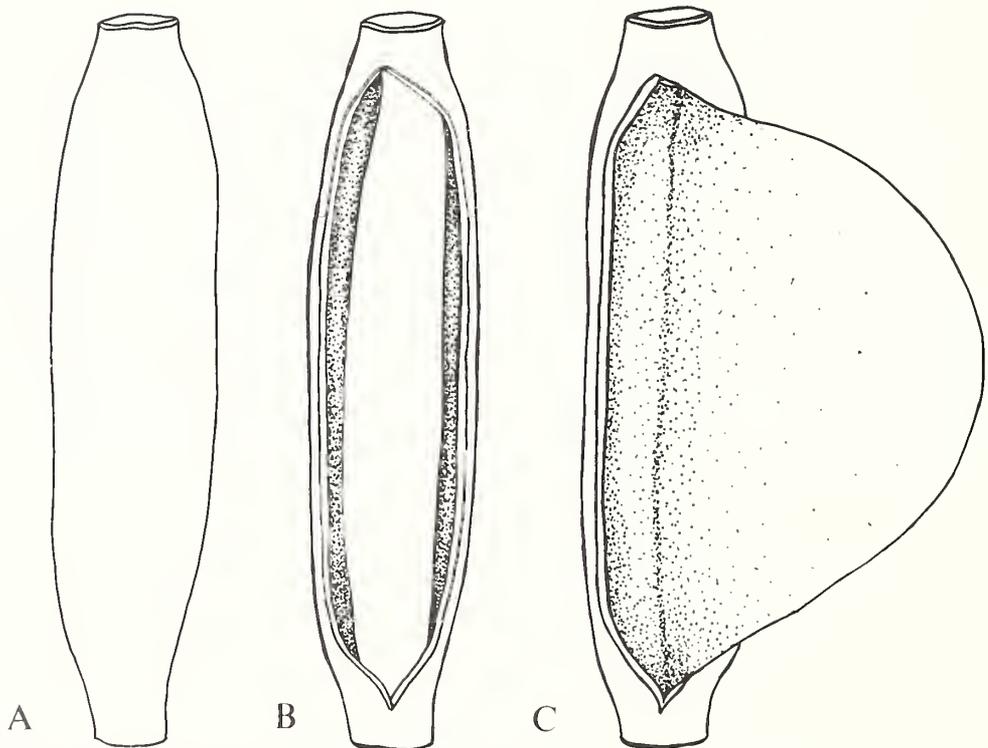
Organic detritus as a nutrient source is widely exploited today, especially by benthic invertebrates and a limited number of highly successful fish including: the milkfish, *Chanos chanos*; mullets, *Mugil* spp.; carp, *Cyprinus* spp.; and *Tilapia* (Odum 1970).

Members of all three invertebrate subphyla of the phylum Chordata – the Hemichordata, Tunicata, and Cephalochordata – feed on detrital particles. A recurring suite of features associated with feeding exists among these protochordates and also the early vertebrates: microphagy (feeding on minute particles), the utilization of mucus for trapping these particles, and the use of a perforated pharynx for filtering the particles. Initially simple filtration of these particles from the water column would probably have been sufficient to meet the nutrient requirements of these organisms. In addition to the above features some of these protochordates possessed a typhlosole (Fee 1925), which is an infolding of the intestinal wall resulting in an increased absorptive surface area.

Fee produced a table (1925, p. 183) showing the distribution of typhlosoles and valvular intestines among primitive vertebrates and fishes, and outlined the decline of such structures among more advanced fishes, concluding that the vertebrate line began with a tendency towards typhlosolar development in the intestine.

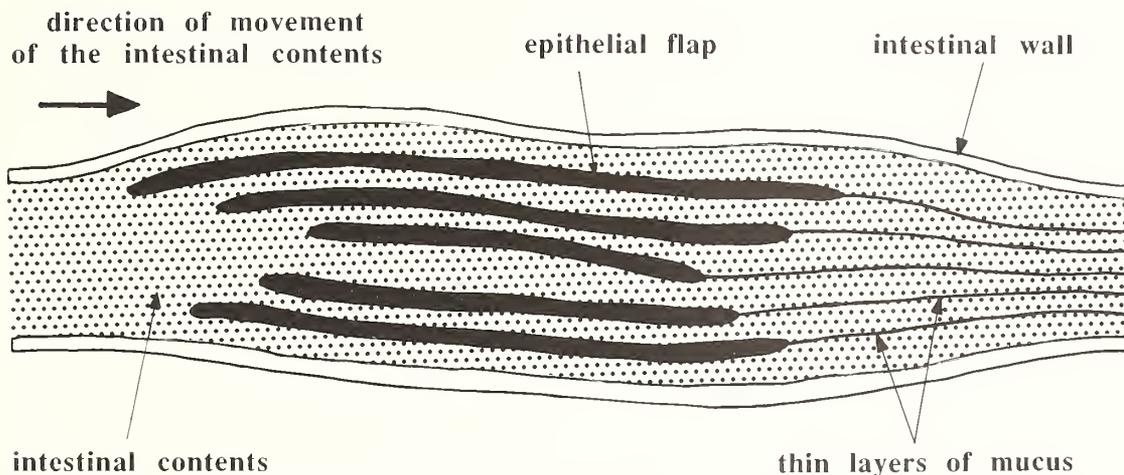
The list of fish groups possessing a valvular intestine includes elasmobranchs, holocephalans, dipnoi, polypterids, holosteans, acipenseroids, and the coelacanth (Fänge and Grove 1979). A reduced form occurs in the lampreys (Hardisty 1979). Fossil fish groups with evidence of valvular intestines are the placoderms, chondrichthyans and possibly acanthodians and actinopterygians (McAllister 1987). Its widespread occurrence testifies to its efficiency. The valvular intestine functions by providing an increased surface area and by slowing down the passage of material, both allowing increased absorption.

Two morphological types of valvular intestine exist, longitudinal or scroll, and transverse or spiral (Owen 1866). Embryologically both begin as simple elongate ingrowths of the intestinal mucosal layer into the lumen of the intestine, resembling a typhlosole. An epithelial flap develops and coils upon itself in the scroll valve, whereas in the spiral valve, the inner layer of the intestinal wall twists spirally around the longitudinal axis of the intestine as the epithelial flap develops, resulting in a more complex structure. As noted by Parker (1885), a huge range of variation occurs in the morphology of spiral valves. Fee (1925, p. 177) suggested that the scroll valve was the first to develop and that the transverse valve developed from secondary modification. The scroll valve which presently exists among some chondrichthyans may have subsequently re-arisen from a transverse type valve (Compagno 1988).



TEXT-FIG. 5. Diagrammatic representation of the dissection and unrolling of a scroll valve. A, intact valve. B, valve opened by a longitudinal incision, coiled epithelial flap visible inside. C, epithelial flap uncoiled and deflected to the right (after McAllister 1987).

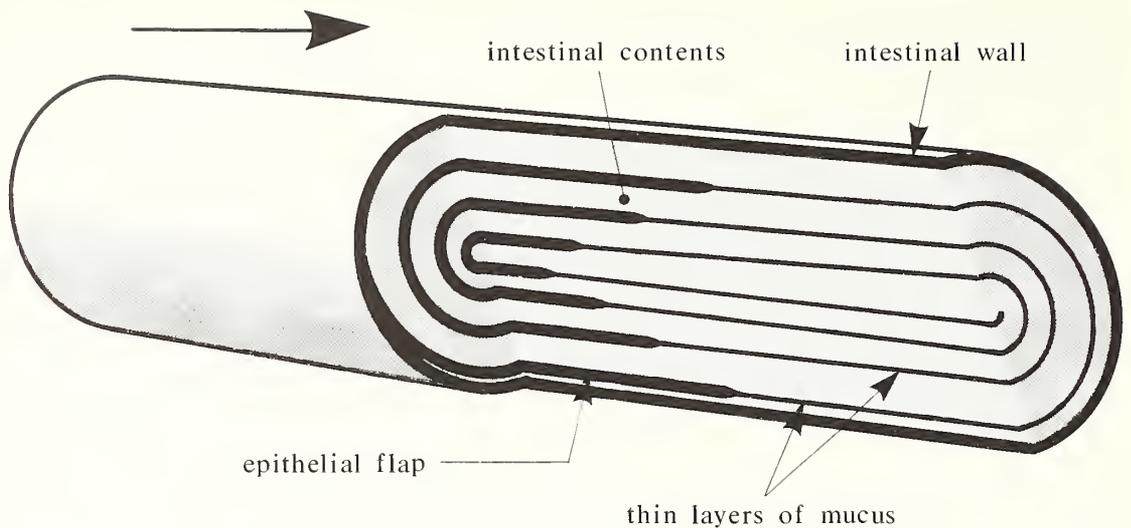
The production of solid faeces by the African lungfish *Protopterus annectans* was reported in 1903 by Bashford Dean. Jain (1981) described the faeces of an Australian lungfish, *Neoceratodus fosteri*. Initially upon expulsion both faeces display spiral structure which slowly begins to uncoil after a period in the water. This has obvious significance for the formation of spiral coprolites. Much of the disagreement in the literature about the formation of spiral coprolites centres on whether a coprolite represents fully extruded faecal material or is an intact valvular intestine packed with partially digested material. This evidence, along with observations by McAllister (1985) of spirally coiled 'cololite' material inside the colon of *Scyliorhinus canicula* (lesser spotted catshark), would seem to suggest that coprolites can represent fully extruded material. A packed valvular intestine, given the right circumstances, would also probably stand a high chance of preservation isolated from any body fossils.



TEXT-FIG. 6. Diagrammatic representation of a longitudinal section through a filled scroll valve. 'Layers' of material appear to become separated by thin layers of mucus as they exit the valve.

As described by Owen (1866) the scroll valve can be unrolled to form a flap of tissue (Text-fig. 5). In its naturally coiled form in the valvular intestine it has the effect of partitioning the intestinal contents. When viewed in longitudinal section the appearance is of discrete layers (Text-fig. 6). When viewed in transverse section the intestinal contents appear as a single continuous spiral coil. The principal direction of movement of the intestinal contents is parallel to the longitudinal axis of the intestine. So, as the material moves posteriorly, the valve terminates and the 'layers', beginning in the centre, come back into contact, separated only by thin layers of mucus. The function of this mucus is lubrication for the passage of the intestinal contents and protection of the epithelial wall. This results in a cylindrical coil of material similar to the coil in the valvular intestine without the epithelial flap (Text-fig. 7). Morphologically the scroll valve functions as a mould which imposes its shape on the material which passes through.

Not all the material passing through the intestine will maintain this spiral form. Only material of the correct consistency will reflect the form of the intestine (Zangerl and Richardson 1963). As these authors point out, information regarding normal faecal output of fish is lacking. It is therefore difficult to speculate as to whether the production of spirally coiled faecal material is the normal condition for fish with valvular intestines. Whether or not it is normal there appears to be an association between detritus, valvular intestines, and spiral coprolites. The scroll coprolites in the present study indicate that the organism responsible possessed a scroll intestinal valve and this represents the earliest occurrence of such a structure. The coprolites also suggest that detritus may have been one of the first major nutrient sources of the vertebrates.



TEXT-FIG. 7. Three-dimensional representation of a filled intestine containing a scroll valve. Diagram shows both longitudinal and transverse sections and the effect of the valve on the separation of the intestinal contents.

POSSIBLE PRODUCERS

The following organisms are the most likely candidates for producing the coprolites:

Agnatha: Anaspida; Cephalaspidomorphi; Heterostraci; Thelodonti.

Gnathostomata: Chondrichthyes; Placodermi; Actinopterygii; Acanthodii.

Others: Eurypterida; unknown faunal element.

A spiral valvular intestine has been proposed for the Carboniferous eurypterid *Cyrtoctenus wittebergensis* from the Witteberg fauna of South Africa (Waterston *et al.* 1985). The reported structure however lies at an angle of 90° to the longitudinal axis of the gastro-intestinal tract. The authors drew a comparison between the spiral structure they encountered and previously described amphipolar coprolites (Williams 1972). Williams, however, suggested that these coprolites originated from palaeoniscoid fish, which also occur in the Witteberg fauna. The proposed feeding methods of most eurypterids (Selden 1984), would not agree with the production of such finely particulate spiral coprolites.

The proposed feeding methods, based on tooth morphology, for the Palaeozoic Chondrichthyes all appear inconsistent with the production of such finely particulate coprolites (Moy-Thomas and Miles 1971; Zangerl 1981). Other evidence concerning food preferences comes from gastro-intestinal contents, gastric residues, and coprolites of Pennsylvanian age, all of which have been examined by Zangerl and Richardson (1963). They concluded that the sharks concerned were feeding mainly on other fish and arthropods.

The morphological adaptations of the earliest gnathostomes, the acanthodians (typical fusiform body, heterocercal tail, large eyes, grasping dentition, large gape), all suggest that they were nektonic and macrophagous and that benthic feeding was not a significant source of nutrition (Denison 1979).

A group with undoubted benthic adaptations is the placoderms. Dorsoventral flattening of the head and thoracic region, dorsal eyes, ventral mouth, and heterocercal tail all indicate this group's benthic mode of life (Denison 1978). From remarkably well-preserved specimens of the Upper Devonian *Bothriolepis canadensis*, Denison was able to determine much of the internal anatomy,

including an extensive valvular intestine. He also suggested that *Bothriolepis* ingested large quantities of detritus (Denison 1941). The first record of a placoderm comes from the lowest Devonian, the Gedinnian of Czechoslovakia and the Dittonian of Britain (Miles 1967), so although potentially capable of producing spiral coprolites it appears unlikely that they were responsible for the Louisburgh coprolites.

The Infraclass Actinopterygii is large and diverse and its members cannot be easily characterized. The first definite record occurs in the Lower Devonian (Schultze 1968), although Gross (1968) has assigned some isolated scales from the Upper Silurian to this group.

Our knowledge of agnathan anatomy and behaviour is still limited. The cephalaspids and the heterostracans, both ranging from the middle Ordovician (Denison 1967; Halstead 1988), display classic bottom-dwelling adaptations including dorso-ventral flattening, ventral mouth, dorsal eyes, and a heterocercal tail (Moy-Thomas and Miles 1971; Märss 1986). However, their absence from the impoverished fauna in Louisburgh would suggest that they were not responsible for the coprolites.

The impoverished fauna from Louisburgh consists of the spiral coprolites themselves, an anaspid agnathan *Birkenia elegans*, and thelodont scales (Palmer *et al.* 1989). The thelodont scales belong to the genus *Loganellia* (Turner pers. comm. 1990). Only a selection of the thelodont scales have been identified so it is possible that other thelodonts may also have had representatives in the Louisburgh fauna.

Thelodonts have 'not received as much attention as other agnathans' (Turner 1973, p. 557). They range from the Arenig Glauconitic Sands of Leningrad (Tarlo 1967) to the Middle Devonian (Ritchie 1963). The body form was a dorso-ventrally flattened cephalothorax and a laterally compressed trunk and caudal region. The tail was hypocercal and there were anal and paired flexible pectoral fins. The orbits were lateral, the mouth sub-terminal and ventral, and they possessed a sensory lateral line system. A body length of 100–200 mm is typical for thelodonts; however, some reached greater lengths, for example *Thelodus parvidens* around one metre (Turner 1986). Yet again the lack of information about the group has hindered any definite conclusions about the life habits of these agnathans. Opinions favour bottom feeding but there is also a possibility of some forms having been nektonic (Märss 1986).

The Anaspida are composed of mainly Silurian forms. They are the most fish-like of all the ostracoderms. Their laterally compressed fusiform bodies, reversed heterocercal (hypocercal) tail and elongate ventrolateral fins probably enabled the anaspids to be rapid and manoeuvrable organisms. Body size ranged from 50 to 300 mm (Halstead 1988), with most not exceeding 150 mm (Moy-Thomas and Miles 1971). Very little direct evidence of their feeding is available; the most common conclusion is that most were particulate feeders. Two anaspids, *Endeiolepis* and a new genus from Kerrera, as yet undescribed, display sedimentary infilling of the intestine (Ritchie 1964). This suggested to Ritchie that ingestion of sediment occurred during feeding.

Another possibility is that some unknown member of the Louisburgh fauna was responsible for the production of the coprolites. Such an organism would have to lack any preservable structure or not have encountered any favourable conditions for preservation, neither of which appears very likely.

From our original list of ten candidates we are left with the thelodonts (*Loganellia*) and anaspids (*Birkenia*) as the groups most likely to include the producer of the coprolites.

DISCUSSION

We know that the aquatic habitat in Louisburgh was probably relatively shallow with low current velocities and anoxic bottom conditions (Maguire 1989). The locality of the water body was within the tropics, and probably in the Southern Hemisphere (Märss 1989). It is not clear exactly what proportion of their lives some of these earliest vertebrates spent here. This habitat may have represented a migration route, a feeding area, a nursery, or perhaps the entire lifecycle occurred here. What appears certain is that the defaecation occurred here or upstream. X-ray diffraction

analysis revealed no compositional difference between the laminites and the coprolites. The implication of this is that the organisms producing the coprolites were ingesting the detrital material which made up the benthic deposits. Of course the final position of the coprolites in the laminites may or may not be close to the feeding site. The coprolites could have either been deposited directly into the laminites as the fish swam over or they could have drifted in if they were sufficiently buoyant (Trewin 1986). The lack of any consistent orientation of the coprolites on the bedding surfaces would suggest that if they did drift they were under the influence of weak or inconsistent currents.

The lack of work on the whole subject of faecal output of modern organisms removes a potentially useful source of information. We can only speculate whether the production of spirally coiled faeces by organisms possessing valvular intestines is a normal or an abnormal occurrence. The production of such spirally coiled faeces would appear to be a coincidental by-product of the shape of the intestine, because it is difficult to imagine any evolutionary benefit to an organism with such an ability. There is also difficulty in interpreting what exactly the measured length of the coprolite represents. Is it the length of the scroll valve? Or the length of the rectum where the coprolite may have spent a brief period before being expelled? Or possibly a combination of both?

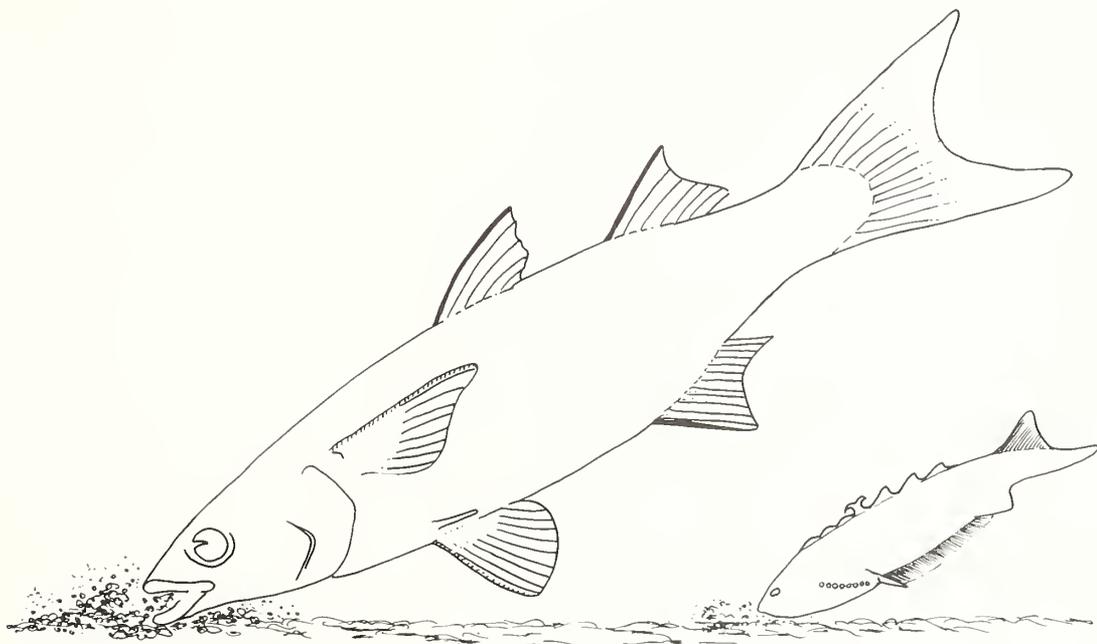
A likely evolutionary sequence can be traced from relatively simple hemichordates through organisms of increasing complexity to the early vertebrates. A recurring suite of features can be followed through this sequence. These features are all associated with particulate feeding and include a filtering pharynx, ciliary and/or muscular pumps for generating feeding currents, the involvement of mucus in the entrapment and transportation of the particles, and an intestine structurally adapted to give an increased absorptive surface area.

Detritus has been demonstrated to be a significant nutrient source for such organisms. As the size and complexity of the organisms increased it was necessary to develop increasingly efficient particulate feeding methods. The increased complexity and mobility which characterized the vertebrate grade allowed a more successful exploitation of detritus as a nutrient source. Within this context the agnathans were the first vertebrates to achieve dominance. The exact phyletic relationship of the Agnatha and the Gnathostomata is as yet uncertain. Their staggered occurrence in the fossil record leads to the general assumption that the agnathans were ancestral. More recently they have been interpreted as sister groups (Hardisty 1979). For the agnathans to achieve this initial domination, in abundance at least, it may have been necessary for them to have had some competitive advantage. I would suggest that, limited as they were to microphagy (Halstead 1982), agnathans were able to expand more rapidly by the continued exploitation of detritus as a pre-existing nutrient source. The gnathostome's ultimate competitive advantage, the acquisition of jaws, required more time for refinement. Indeed the morphological adaptations which can be discerned from agnathan fossil remains appear to concur with this idea. The striking similarity they show to modern detritivores (Ritchie 1963), the discovery of organic-rich sediments in the intestines of some specimens, and now the discovery of these coprolites, all point to the fact that particulate feeding was of significance for early vertebrates.

The existence of spiral coprolites in association with these organisms is not incongruous. Vertebrates began with a tendency towards typhlosolar development of the intestine (Fee 1925). The increased absorptive area of the intestine is a feature which is associated with feeding on detrital sediments, due to the ingestion of large proportions of nutritionally impoverished material (Kapoor *et al.* 1975). The morphology of the coprolites gives us firm evidence that their producer possessed a scroll intestinal valve, whose function was to allow an increase in the uptake of nutrients.

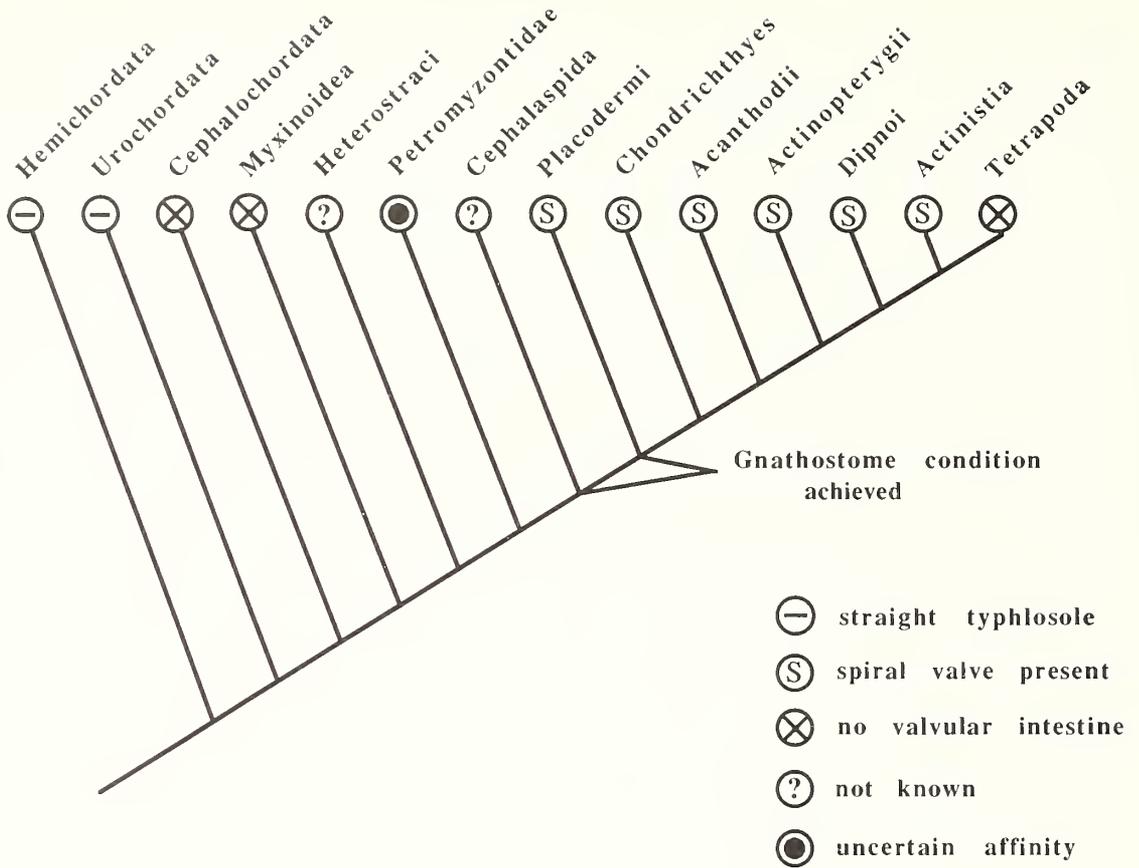
The fine-grained composition of the coprolites relative to the texture of the matrix indicates the occurrence of some degree of selection or filtration. This particle selection/filtration is most likely to have occurred prior to ingestion since this removes the requirement for any major morphological adaptations of the buccal and pharyngeal cavities to produce a complex sieving mechanism. No evidence of such a mechanism has yet been discovered. Pre-ingestional selection of small particles also avoids causing damage to the delicate gill membranes. We know that flexible areas, indicated by a covering of minute scales, were present in the cheek regions of *Birkenia* (Simpson 1988). This flexible buccal region may have been involved with 'blow-suction' feeding as employed today by the

mullet (*Mugil cephalus*). Variation in the time between the blow and the suction phases could effectively regulate the size of particle ingested, the finer material taking more time to re-settle. This is an attractive feeding model since it agrees with both Parrington's (1958) and Janvier's (1987) proposed feeding angle for the anaspids, and may allow feeding without causing bioturbation. No feeding marks have been identified from the laminites. Alternatively a 'soupy' sediment/water interface would also allow detrital feeding while preserving the settled layers below. It is possible to imagine *Birkenia* swimming above the substrate, periodically inclining its body at an angle so that its mouth is close to the sediment, and feeding in such a fashion (Text-fig. 8). An interesting point which may hold some significance is that, inclined at such an angle, the slanting row of gill openings becomes more or less horizontal to the substrate. Mentioned earlier was the probable existence of anoxic bottom conditions in Louisburgh. Therefore such a periodic method of feeding may have been associated with the requirement for an adequate uptake of oxygen.



TEXT-FIG. 8. A comparison of the feeding angles of the mullet, *Mugil cephalus*, (left) and that proposed for the anaspids (right) by Parrington (1958) and Janvier (1987).

The terminally placed mouth of *Birkenia* would have required such an angled approach to benthic feeding. The mouth position of *Loganellia* is thought to have been ventral, just behind the anterior margin of the head, resulting in a horizontal feeding angle. The relative size of the eyes of both organisms indicates potentially divergent approaches to feeding. The larger laterally placed eyes of *Birkenia* may possibly have allowed a more selective approach to feeding and indicate that visual stimuli may have been important. In contrast the eyes of thelodonts usually only appear as small darker stains in the general area where eyes would be expected (Ritchie 1963). Their dorsal situation would prevent visual stimuli from having an important role in food selection. This does not necessarily mean that thelodonts were unselective feeders – they may have possessed other sensory mechanisms involved in food selection, such as sensory barbels as displayed by modern benthic feeding catfish.



TEXT-FIG. 9. Cladogram showing the distribution of typhlosoles and valvular intestines among protochordates, the main fish groups, and tetrapods. Compiled from Fee (1925), McAllister (1987), and with the assistance of Dr Alain Bleick.

The respective size range of the *Birkenia* and *Loganellia*, relative to the coprolites, gives no firm indication as to which was the producer.

When we examine the known distribution of valvular intestines (Text-fig. 9), it appears that the possession of a spiral valvular intestine may in fact be a gnathostome feature, which has been subsequently lost among the tetrapods. Youson (1981) is convinced that vertebrate valvular intestine is not homologous with the structure present in the intestine of the lamprey. Thelodonts, based on scale morphology, may in fact be a sister group of Palaeozoic sharks and so have gnathostome affinities (Turner pers. comm. 1990). If this link can be established it would then strengthen the case for these coprolites being of thelodont origin.

Probably the most satisfying conclusion would be the ability to identify with certainty the organism or organisms responsible for producing the scroll coprolites. The scarcity of evidence reduces the certainty with which such a conclusion can be made. The almost total lack of preserved body fossils and the poorly understood lifestyles of the organisms involved contrive to conceal the identity of the producers. However, these coprolites indicate that the scroll valve was the most primitive type of valvular intestine. They also point to the importance of detritivory among some of the early vertebrates.

Acknowledgements. I would like to acknowledge the assistance and guidance provided by Dr Douglas Palmer. I am also indebted to Professor C. H. Holland for all his considerable help and advice, to Dr Alain Blicek for some interesting discussions, to Dr Euan Clarkson for his encouragement, and to Ms Elaine Cullen and Mr Declan Burke for their help with the illustrations. This research was carried out with the assistance of a Trinity College Research Grant.

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BRIAN GILMORE

Department of Geology
Trinity College
Dublin, Ireland

Typescript received 25 February 1991
Revised typescript received 20 September 1991

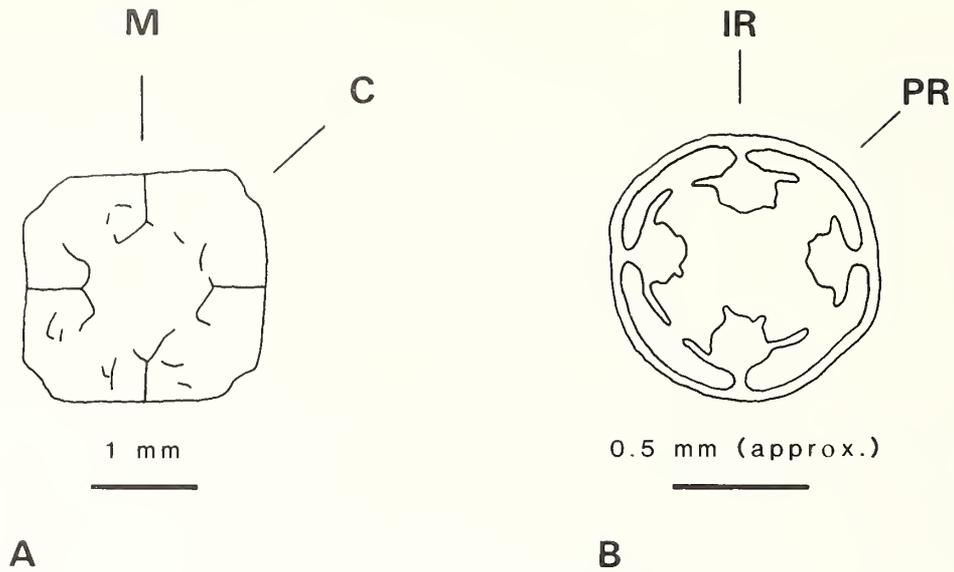
MORPHOLOGY AND PHYLOGENETIC SIGNIFICANCE OF THE CORNERS AND MIDLINES OF THE CONULARIID TEST

by HEYO VAN ITEN

ABSTRACT. The hypothesis that conulariids were closely related to scyphozoan cnidarians is based in large part on interpretations of the morphology of the corners and midlines of the conulariid test. Corners and/or midlines of some or all species of at least ten of the twenty-one currently recognized conulariid genera are internally thickened. Internal midline structures of some or all species of six genera are paired or adaxially bifid. Midlines of one species, *Eoconularia amoena* Sinclair, exhibit features suggesting the presence of a single carina that bifurcates adapturally. Species of five genera exhibit internal structures both at the corners and the midlines. In almost all of these taxa, internal structures at the corners are broader and/or higher than associated midline structures. Internal corner and/or midline structures of some members of two genera are seriated. Conulariid corners and midlines show a number of similarities to soft-part and thecal structures located, respectively, at the scyphozoan perradii and interradii. Nearly all of these similarities are uniquely shared by conulariids and scyphozoans, and corroborate Kiderlen's (1937) hypothesis that conulariid midlines were sites of a gastric septum, homologous to the gastric septa of scyphozoans.

MUCH of the controversy surrounding the analysis of conulariid affinities can be traced to conflicting interpretations of the corners and midlines of the steeply pyramidal, finely lamellar conulariid test. Corners and/or midlines of many conulariids are sites of localized inflection and thickening of the test's inner lamellae (e.g. Wiman 1895; Knod 1908; Reed 1933; Bouček 1939; Van Iten 1991). Based on comparisons of internal conulariid test structures with soft-part and internal thecal structures of scyphozoan cnidarians, conulariid midlines have been interpreted as former sites of a gastric septum, homologous to the gastric septa of scyphozoans (e.g. Kiderlen 1937; Moore and Harrington 1956; Werner 1966*a*, 1966*b*, 1967; Bischoff 1978; Möhn 1984; Van Iten 1991). Scyphozoan septa are normally four in number and lie within one of two mutually perpendicular planes of symmetry, called the interradii. Bisecting the angles between the interradii are two additional symmetry planes, the perradii, that intersect the corners of the rectangular scyphozoan mouth. Conulariid corners, usually situated along two planes that lie more or less midway between two planes containing the midlines, have been interpreted as comparable in position to the scyphozoan perradii. These anatomical relationships are illustrated in Text-figure 1.

This and other hypotheses of homology between conulariids and scyphozoan cnidarians have been questioned by a number of authors (Termier and Termier 1949, 1953; Kozłowski 1968; Oliver 1984; Steul 1984; Mortin 1985; Feldmann and Babcock 1986; Babcock and Feldmann 1986*a*, 1986*b*; Oliver and Coates 1987; Babcock 1991; Yochelson 1991). Yet none of these authors has proposed that conulariid corners and midlines are more similar (and therefore more likely to be homologous) to test or soft-part structures of non-scyphozoan groups. Instead, rejection of the hypothesis that conulariid midlines were sites of a gastric septum has generally been based on claims that (1) conulariids and scyphozoans exhibit fundamental dissimilarities (Termier and Termier 1949, 1953; Kozłowski 1968; Steul 1984; Mortin 1985; Feldmann and Babcock 1986; Babcock and Feldmann 1986*a*, 1986*b*; Babcock 1991; Yochelson 1991); and that (2) similarities between conulariid corners and midlines and features at the scyphozoan perradii and interradii are superficial (Termier and Termier 1949, 1953; Kozłowski 1968; Oliver 1984; Feldmann and Babcock



TEXT-FIG. 1. Transverse cross sections through A, the conulariid *Eoconularia loculata* (Wiman); B, *Craterolophus tethys* Clarke, a stauromedusan scyphozoan. Letter symbols are as follows: M, midline; C, corner; IR, interradius; PR, perradius. Text-fig. 1A taken from Wiman (1895, pl. 5, fig. 11); Text-fig. 1B taken from Kiderlen (1937, fig. 31), with information on scale taken from Gross (1900, pl. 23).

1986; Babcock and Feldmann 1986a, 1986b; Oliver and Coates 1987; Babcock 1991; Yochelson 1991).

The present analysis of conulariid corners and midlines is based in part on new information on the anatomy and occurrence of internal test structures at these sites. In order better to organize our knowledge of this critical aspect of conulariid anatomy, new data on corners and midlines are presented in the context of a general survey of conulariid cross-sectional geometry and internal anatomy. Several previous investigators have also contributed to our knowledge of conulariid corner and midline anatomy. Among the most important earlier studies are Wiman's (1895) paper on *Eoconularia loculata* (Wiman), Sinclair's (1940) paper on *Metacoconularia* Foerste, and Bischoff's (1978) paper on circoconulariids, a group of steeply conical (as opposed to steeply pyramidal)

EXPLANATION OF PLATE I

Examples of conditions of conulariid corner and midline anatomy recognized in the present study (all photos taken with SEM, figure 2 in backscattered electron mode).

Fig. 1. *Simple groove* (SG); inner surface of part of a corner of *Conularia trentonensis* Hall; UMMP 66013; Middle Ordovician; New York, $\times 25$.

Fig. 2. *Carinate groove* (CG); transverse section through a corner of *Climacoconus* sp.; SUI 61531; Upper Ordovician; Iowa, $\times 80$.

Fig. 3. Fragmentary corner of another *Climacoconus* specimen exhibiting two ridges (arrows) interpreted here as parts of a seriated carina; GSC 94786a; Middle Ordovician; Minnesota, $\times 20$.

Fig. 4. *Simple midline* (S); inner surface of part of a midline of *Conularia trentonensis* Hall; UMMP 66013; Middle Ordovician; New York, $\times 25$.

Fig. 5. *Single carina* (SG); inner surface of part of a midline of *Conularia splendida* Billings; the midline carina of this species is often bifid (see text and Pl. 2, fig. 6); UMMP 66123; Upper Ordovician; Iowa, $\times 23$.

Fig. 6. *Paired seriated carinae* (PSC); inner surface of part of one face of an undetermined species of *Climacoconus*, showing pairs of I-shaped ridges flanking the midline; ridges to the right of the midline have been broken and displaced from their original positions; GSC 94785a; Upper Ordovician; Iowa, $\times 30$.



Problematica interpreted by Bischoff (1978) as a taxon within Conulariida. Together with information gathered by previous investigators, results of this study reveal that conulariid corners and midlines are more complex anatomically than has hitherto been realized. Now that our knowledge of conulariid corner and midline anatomy is more complete, we are in a better position to evaluate whether or not similarities between conulariids and scyphozoans are indicative of a close phylogenetic relationship.

MATERIAL AND METHODS

The present study is based on examination of some or all known species of fourteen of the twenty-one currently recognized conulariid genera, supplemented by data presented in previous papers (Barrande 1867; Ulrich 1892; Holm 1893; Wiman 1895; Slater 1907; Knod 1908; Bouček 1928, 1939; Sinclair 1940, 1941, 1942, 1944, 1948; Sugiyama 1942; Bischoff 1978) on members of these and two other genera. Specimens from the following genera were studied: *Anaconularia* Sinclair, *Archaeoconularia* Bouček, *Calloconularia* Sinclair, *Climacocomus* Sinclair, *Comularia* Miller, *Conularina* Sinclair, *Ctenoconularia* Sinclair, *Eoconularia* Sinclair, *Glyptoconularia* Sinclair, *Metaconularia* Foerste, *Notoconularia* Thomas, *Paraconularia* Sinclair, *Pseudoconularia* Bouček, and *Reticulaconularia* Babcock and Feldmann. Information on the identity, location, and age and host horizon(s) of these specimens is presented in the Appendix. Also presented in the Appendix are explanations of repository abbreviations used in the text. Availability of specimens varies widely from genus to genus, with some genera (e.g. *Ctenoconularia* and *Eoconularia*) known only from a handful of specimens, mostly non-preparable types, and others (e.g. *Comularia* and *Paraconularia*) represented by hundreds or even thousands of specimens. Fortunately, type specimens of some of the rare taxa are often broken or exfoliated in such a way as to permit inspection of the test's inner surface.

Depending on the nature of the host matrix, specimens were prepared in one of two ways. Specimens embedded in acid resistant, non-calcareous matrix were sectioned. Sections were cut perpendicular to the specimen's long axis, or parallel to it, along a pair of opposite corners or midlines. Other specimens, preserved in limestone, were embedded in casting resin and then cut in half longitudinally. The two halves were immersed in 10 per cent formic acid until the internal matrix was dissolved, thus revealing the test's inner surface. Wherever possible, specimens were chosen that preserved or were broken near the apertural margin and that tapered to within a few millimetres or less of the apex.

CONULARIID CORNERS AND MIDLINES

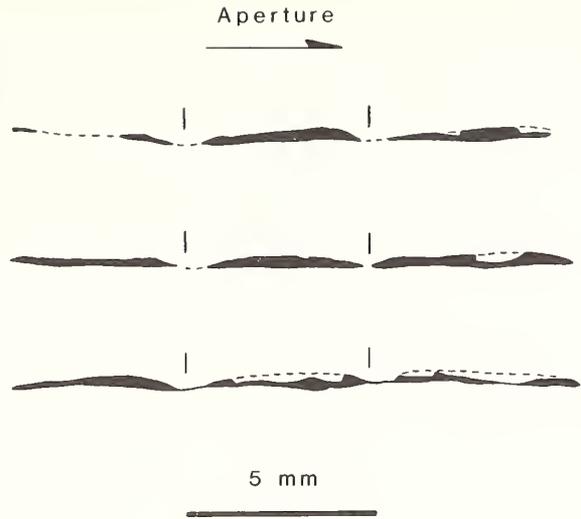
Conditions of conulariid corners

Non-sulcate (NS). Corners of a small number of conulariids appear to have been characterized by the absence of a sulcus or groove. This condition was originally detected in *Anaconularia*, a monospecific genus currently known only from sandstone steinkerns (Barrande 1867; Bouček 1928; Sinclair 1948, 1952). As indicated by present observations and those of previous studies, the corners of all of the 2000 or so steinkerns collected thus far are rounded and show no evidence of a groove or internal test thickening. According to Sugiyama (1942), non-sulcate corners also characterize *Comulariopsis* Sugiyama, a monospecific genus from the Lower Triassic of Japan.

Simple groove (SG) (Pl. 1, fig. 1). Except in the two taxa just mentioned, corners of all conulariids are furrowed by a broad sulcus or groove. In many taxa, this groove is not accompanied by internal test thickening. As indicated by present observations and those of previous studies (Barrande 1867; Bouček 1928; Sinclair 1940, 1941, 1948), this condition characterizes most (and possibly all) currently recognized species of *Metaconularia* and *Pseudoconularia*, and most species of *Comularia*. It also characterizes some species of *Climacocomus*, *Ctenoconularia*, and *Paraconularia* (see Appendix).

Mesially folded groove (MFG). This condition constitutes the sole diagnostic feature of *Notoconularia*, erected by Thomas (1969) to receive three Permo-Triassic species formerly assigned to *Paraconularia*. Although apparently not accompanied by internal test thickening, corner grooves of *Notoconularia* differ from simple grooves in exhibiting an outwardly directed, mesial fold.

TEXT-FIG. 2. Line drawings of longitudinal profiles of three seriated corner carinae in a specimen of an undetermined species of *Climacoconus* from the Elgin Member of the Maquoketa Formation (Upper Ordovician); northeast Iowa, USA; SUI 61534. The midlines of this specimen lack internal structures.



Carinate groove (CG) (Pl. 1, figs 2–3). Corners of a large number of sulcate conulariids exhibit a broadly rounded or keel-like internal carina. This condition characterizes some or all species of *Archaeoconularia*, *Calloconularia*, *Climacoconus*, *Conularia*, *Conularina*, *Ctenoconularia*, *Eoconularia*, *Glyptoconularia*, and *Paraconularia* (see Appendix). Corner carinae here observed are generally more or less continuous and, in many specimens, strongly pigmented. In nearly all taxa they are very prominent (e.g. Text-fig. 3), with carinae of some *Climacoconus* specimens (e.g. UMMP 20560a) locally extending up to about one-third of the distance to the centre of the test cavity.

Evidence of seriation was observed in corner carinae of two specimens of *Climacoconus*. Three carinae in one of these specimens (the fourth carina is not preserved), collected from the Maquoketa Formation (Upper Ordovician) of northeast Iowa, USA, consist of three elongate segments (Text-fig. 2). The segments range from approximately 4–5 mm long and exhibit a gently arcuate longitudinal profile (locally disrupted by breaks sustained during preparation). Consecutive segments along the same carina are separated by a short stretch of non-carinate test, and isolatitudinal segments on different carinae begin and end at approximately the same distance from the apex.

The second specimen (Pl. 1, fig. 3), collected from the Platteville Formation (Middle Ordovician) of southeast Minnesota, USA, preserves portions of two segments of a single carina. This specimen is one of several Platteville *Climacoconus* specimens assigned by Sinclair (1948) to *C. concinnus*, a species that was never published. Although the geometry of the corner carina in other *C. concinnus* specimens could not be determined (due to incomplete preservation and scarcity of available material), midlines of this species are straddled by a pair of seriated carinae, described below.

The arcuate geometry of the ridges described above indicates that they are not the result of breakage or incomplete preservation. The two specimens displaying these ridges show no signs of injury or malformation; their transverse ornament is normal, and their corners diverge more or less continuously, with no apparent constriction at the ends of carina segments. These observations suggest that the carina anatomy displayed by these specimens is not accidental, but a type of seriation.

Conditions of conulariid midlines

Simple (S) (Pl. 1, fig. 4). Midlines of many conulariids are furrowed by a groove and/or exhibit one or two internal thickenings or carinae. Midlines that lack these features are referred to here as simple. Simple midlines characterize species of *Conularia*, *Climacoconus*, *Ctenoconularia*, *Noto-*

conularia, *Paraconularia*, and *Reticulaconularia*. Simple midlines apparently also characterize *Conulariella* Bouček (see for example Bouček 1939, fig. 10).

Outwardly folded (OF). This condition is diagnostic of the genus *Pseudoconularia* (Bouček 1939; Sinclair 1941, 1948). In this taxon, each midline is marked by a low, broad, outwardly-projecting longitudinal fold. As indicated by inspection of figures in Barrande (1867, pls 3–7) and exfoliated areas on the holotype of the only known North American species of this genus (Sinclair 1941; see also Appendix), portions of the test comprised by the fold are non-thickened.

Single carina (SC) (Pl. 1, fig. 5). Midlines of a number of conulariids are sites of a single, broadly rounded or keel-like internal carina. This condition characterizes some or all species of *Archaeoconularia*, *Calloconularia*, *Climacoconus*, *Conularia*, *Eoconularia*, and *Paraconularia* (see Appendix).

In addition to having carinate midlines, the North American species *Eoconularia forensis* Sinclair and *Paraconularia crustula* (White), and the European species *Archaeoconularia fecunda* (Barrande), also possess carinate corners. In *E. forensis*, currently represented by three known specimens (see Appendix), the corner carinae are about four times higher and three times wider than the midline carinae (Text-fig. 3A). Judging from illustrations in Barrande (1867, pl. 8, fig. 9) and Bouček (1939, fig. 2a; Text-fig. 3B herein), the corner carinae of *A. fecunda* are likewise higher and broader than the midline carinae. In *P. crustula*, corner carinae of eight of 18 specimens here examined (see Appendix) are distinctly higher than the midline carinae (Text-fig. 3C), while in the remaining specimens the two sets of carinae are about equally high. (Internal thickening at both corners and midlines was also observed in *Calloconularia strimplei* Sinclair (Pennsylvanian, USA; see Appendix), but due to restrictions on sample preparation the relative sizes of the two sets of internal test structures could not be determined.)

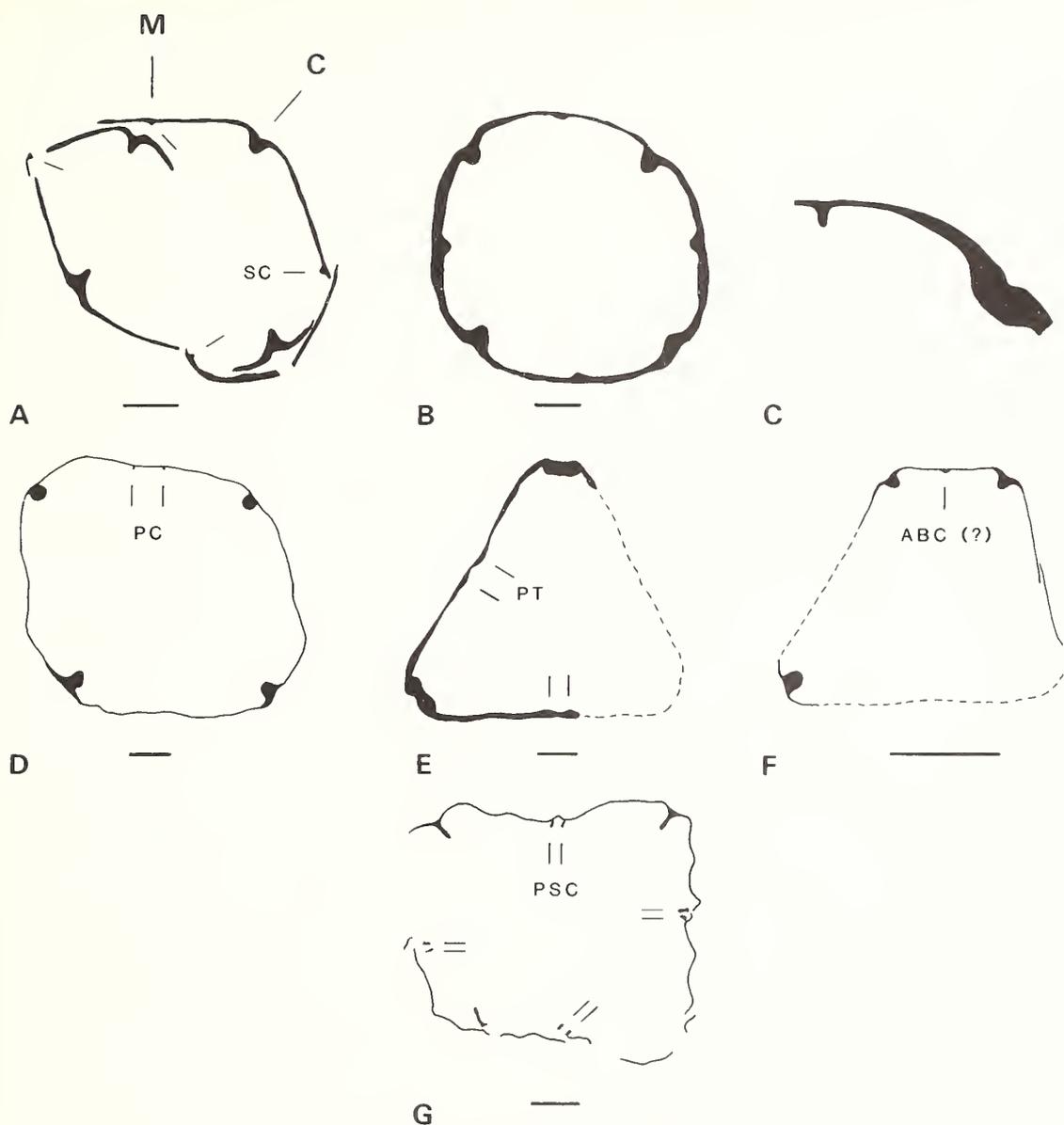
Ulrich (1892, pl. 3, fig. 6a) and Knod (1908, pl. 24, figs 1–2, pl. 31, fig. 3; see also Moore and Harrington 1956, fig. 26) documented a prominent carina at corners and midlines of two specimens collected from the Devonian of Brazil and later identified by Babcock *et al.* (1987b) as *Conularia albertensis* Reed. Babcock *et al.* (1987a, fig. 10B) figured a carinate specimen of the same species from the Devonian of South Africa. In this specimen and the one figured by Ulrich (1892), the carina at the corners is distinctly larger than the carina at the midlines.

Groove with seriated carina (GSC) (Pl. 2, fig. 1). Midlines of *Archaeoconularia* are furrowed by a distinct sulcus (Bouček 1939; Sinclair 1944, 1948), and a very weak groove apparently marks the midlines of *Glyptoconularia*. In the North American species *A. membranacea* (Ringueberg), currently represented by two incomplete specimens (see Appendix), the midlines are also sites of internal thickening. Viewed internally, preserved portions of two midlines of the holotype and most complete specimen (the inner surface of the other two midlines of this specimen cannot be seen) exhibit a series of extremely low, narrow, closely-spaced ridges, running along the crest of the midline groove. The ridges range from approximately 0.4 to 0.8 mm long and are about 0.05 mm wide. They may be more or less contiguous or spaced up to about 0.8 mm apart. Each ridge exhibits a gently arcuate longitudinal profile, with a maximum height near the centre of the ridge of approximately 0.05 mm. Similar ridges occur on portions of two midlines of a fragmentary specimen (BMS 10793) from the same locality.

The geometry of these ridges indicates that they are not artifacts of breakage or incomplete preservation, and the specimens themselves show no sign of injury or malformation. Thus the ridges are probably best interpreted as members of a low, seriated carina.

The corners of *A. membranacea* are sites of a continuous (non-seriated) carina. This structure is substantially higher and broader than the seriated midline carina.

Paired carinae (PC) (Pl. 2, figs 2–4). This condition, previously detected in *Metaconularia* (e.g. Holm 1893; Slater 1907; Sinclair 1940, 1948), apparently also characterizes at least one species each of



TEXT-FIG. 3. Line drawings of transverse sections through conulariids having internal structures at both corners (C) and midlines (M). All scale bars = 5 mm. A, *Eoconularia forensis* Sinclair; GSC 87201. B, *Paraconularia crustula* (White); UMMP 66024b. C, *Archaeoconularia fecunda* (Barrande) (modified from Boucek 1939, fig. 2a). D, *Conularina narrawayi* Sinclair; ROM 18905. E, *Conularina triangulata* (Raymond); GSC 94788. F, *Eoconularia amoena* Sinclair; ROM 23297. G, *Climacoconus* sp.; SUI 61531.

Conularina and *Paraconularia*. It is defined by a pair of low, broadly rounded or keel-like ridges, with members of each pair situated on opposite sides of the midline proper. Paired midline carinae of *Metaconularia* (Pl. 2, fig. 2) diverge towards the aperture, at approximately $1-2^\circ$, and project from about one-fiftieth to one-twentieth of the distance to the opposite midline. They are often strongly pigmented. Carinae of exceptionally complete specimens (e.g. specimens of *M. mammi* (Roy)

and *M. aspersa* (Slater); see Appendix) extend nearly the entire length of the test and are discrete throughout their length. Such carinae show a very gradual, more or less continuous increase in height and width towards the aperture over most of their length.

As noted by Sinclair (1940), some species of *Metaconularia*, for example *M. papillata* (Hall) (Middle Ordovician, New York), exhibit a distinct groove along the midline proper. Observations presented in Barrande (1867, pl. 8, figs 17–18, 20–22) suggest that paired carinae flanking a grooved midline also characterize *Metaconularia? modesta* (Barrande).

Features interpreted here as fragments of paired midline carinae occur in *Conularina narrawayi* Sinclair, currently represented by a single incomplete specimen from Middle Ordovician strata in Quebec (Pl. 2, fig. 3). Paired midline carinae in this specimen are extremely low and narrow. The corners of this specimen are also carinate, but the corner carinae are about five times higher and eight times wider than those at the midlines (Text-fig. 3b).

Inspection of a photograph in Sinclair (1942, pl. 2, fig. 2) suggests that paired carinae also characterize midlines of *Comularina undosa* Sinclair, another species from the Middle Ordovician of Quebec. Unfortunately, the holotype and only described specimen of this species is now missing.

A pair of very low, apparently discontinuous carinae or thickenings were observed in specimens of *Paraconularia chesterensis* (Worthen), currently known from Lower Mississippian strata of the United States (Babcock and Feldmann 1986c). Midlines of two specimens (ISGS/ISM 2489 and UMMP 23955; Pl. 2, fig. 4), collected from lime grainstones in the Chesterian Series of Illinois, are discontinuously straddled by a pair of narrow, dark colour bands. Members of each pair of bands are spaced approximately 1 mm apart and diverge very gradually towards the aperture. As indicated by inspection of sectioned or exfoliated areas (e.g. Pl. 2, fig. 4), each band is associated with very low but distinct internal test thickening. Due to poor preservation or restrictions on preparation, it could not be determined whether midlines of other specimens of *P. chesterensis* exhibit paired tracts of longitudinal thickening like those described above. However, a number of specimens (e.g. specimens from the Edwardsville Member of the Muldraugh Formation of Indiana; LACM 9364) exhibit colour banding at the midlines, and one of these specimens (LACM 9364a) shows internal thickening on at least one side of its only preserved midline.

Paired thickenings (PT) (Pl. 2, fig. 5). This condition characterizes three of the five currently recognized North American species of *Comularina* Sinclair, including the unusual form *C. triangulata* (Raymond), which has three (rather than four) faces (Sinclair 1942, 1948). It consists of a pair of broad, very low, continuous thickenings, one on either side of the midline proper. Although similar to paired carinae, paired thickenings differ from the latter in being substantially

EXPLANATION OF PLATE 2

Additional conditions of conulariid midline anatomy recognized in the present study (all photos taken with SEM, figure 6 in backscattered electron mode).

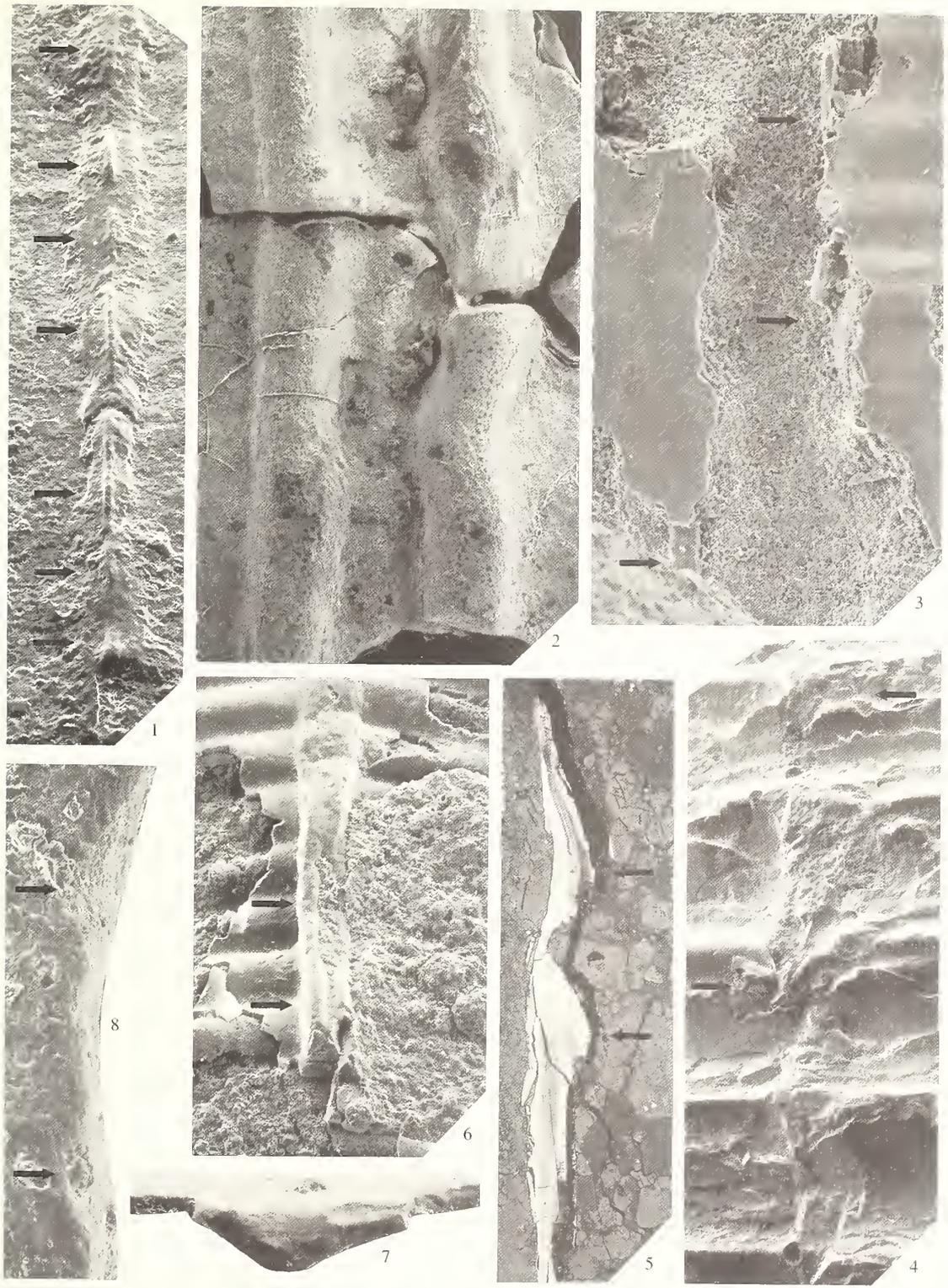
Fig. 1. *Grooved midline with seriated carina* (GSC); part of a series of very low ridges (arrows) along the crest of the inner surface of a midline of *Archaeoconularia membranacea* Sinclair; BMS E10791; Middle Silurian; New York, $\times 20$.

Figs 2–4. *Paired carinae* (PC). 2, inner surface of part of a midline of *Metaconularia* sp.; SUI 37414; Middle Ordovician; Iowa, $\times 25$. 3, fragments (arrows) of paired carinae in *Comularina narrawayi* Sinclair; ROM 18905; Middle Ordovician; Quebec, $\times 80$. 4, fragments (arrows) of discontinuous paired carinae in *Paraconularia chesterensis* (Worthen); ISGS/ISM 2489; Lower Mississippian; Illinois, $\times 20$.

Fig. 5. *Paired thickenings* (PT); transverse section through a pair of midline thickenings (arrows) of *Comularina triangulata* (Raymond); GSC 94788; Middle Ordovician; Quebec, $\times 80$.

Fig. 6. *Low bifid carina* (LBC); inner surface of part of a discontinuously bifid (arrows) midline carina of *Conularia splendida* Billings; UW-BM 73177a; Upper Ordovician; Iowa, $\times 32$.

Figs 7–8. *Single carina, adaperturally bifurcating?* (ABC?). 7, single carina at the broken apical end of one of the faces of the holotype of *Eoconularia amoena* Sinclair; ROM 23297; Middle Ordovician; Quebec, $\times 300$. 8, two carinae (arrows) at the broken apertural end of the widest face of the same specimen, $\times 130$.



VAN ITEN, conulariids

broader and lower. Because known specimens of *Conularina* are broken well above the apex, it is not yet clear whether the thickenings continue as a discrete pair throughout their length or merge adapically to form a single thickening.

As noted in the preceding section, the corners of *Conularina* are also thickened. In all specimens here examined, the corner thickenings are from two to three times higher than those at the midlines (Text-fig. 3E).

Low bifid carina (LBC) (Pl. 2, fig. 6). This condition was detected in specimens of *Conularia splendida* Billings from the Maquoketa Formation (Upper Ordovician) of northeast Iowa, USA. Midlines of these specimens exhibit a low, broadly rounded or carinate ridge, portions of which are often adaxially bifid. Although this is similar to paired midline carinae, the paired crests of low bifid carinae are parts of a single thickening situated on the midline proper, rather than a pair of separate thickenings straddling the midline.

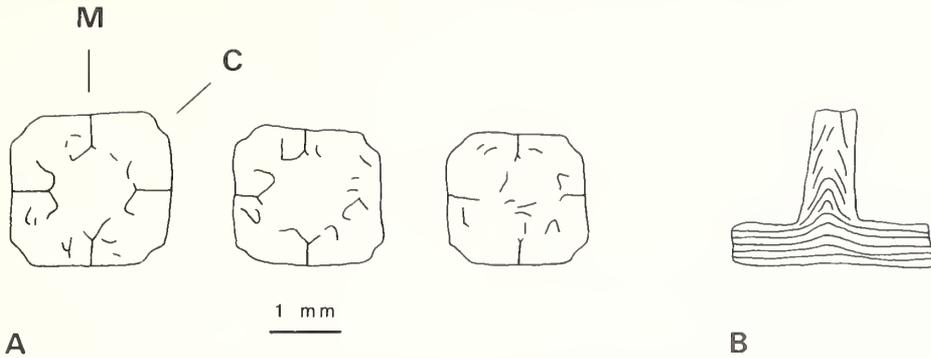
Single carina, adaperturally bifurcating? (ABC?) (Pl. 2, figs 7–8). The existence of this condition, previously detected in certain circoconulariids (Bischoff 1978; see also below), is suggested by inspection of the holotype and only known specimen of *Eoconularia amoena* Sinclair. At this specimen's apical end, now broken, the narrowest face (the specimen exhibits a strongly trapezoidal transverse cross section; see Text-fig. 3F) exhibits a low carina, visible in cross-section (Pl. 2, fig. 7) and indicated on the test surface by a band of strong pigmentation extending along part of the midline. At the opposite end, the widest face exhibits fragments of a pair of carinae, one on either side of the midline proper (Pl. 2, fig. 8). Due to incomplete preservation, it is not possible to determine whether the features detected at the two ends of the specimen are sections through a carina that bifurcates adaperturally, or, for instance, sections through a carina that is discontinuously paired or bifid.

As noted in the preceding section, the corners of *Eoconularia* are strongly carinate. In *E. amoena*, the corner carinae are about three times higher and two times wider than the midline carinae (Text-fig. 3F).

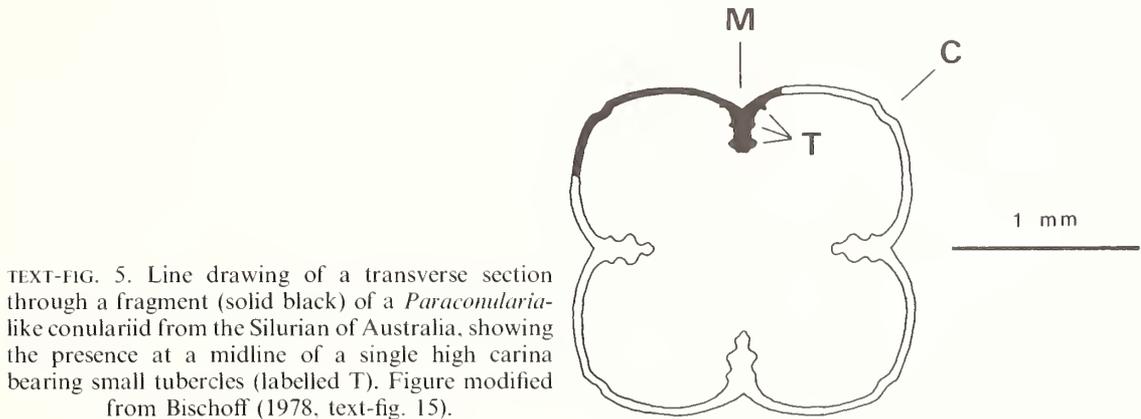
Paired seriated carinae (PSC) (Pl. 1, fig. 6). This condition characterizes specimens of *Climacocopus* collected from Middle and Upper Ordovician strata of the Upper Mississippi Valley, USA and assigned by Sinclair (1948) to one of three species (*C. clermontanus*, *C. concinnus*, and *C. mollis*; see Appendix), all unpublished. The midlines of these specimens are flanked by two files of discrete, closely-spaced ridges. Each ridge is expanded at its ends, making it more or less I-shaped, and extends across a single interspace (the region between the crests of two adjacent transverse ribs). In most specimens, the ridges are strongly pigmented. Members of a pair of files gradually diverge towards the aperture, and the files apparently originate well above the apex. Test material between the two files is thickened. In all four pairs of files, the height and width of the ridges gradually increase towards the aperture.

Corners of the aforementioned *Climacocopus* are sites of a narrow carina. This carina is up to about four times higher than the seriated midline carinae (Text-fig. 3G). As indicated above, a corner carina in at least one fragmentary specimen (GSC 94786a; Pl. 1, fig. 3) shows evidence of seriation. In addition to being higher than segments of paired midline carinae in more complete specimens of the same species, the two preserved corner segments in this specimen were originally several times longer than the midline ridges.

High bifid carina (Text-fig. 4). This condition was discovered by Wiman (1895) in a specimen of *Eoconularia loculata* (Wiman) from the Middle Silurian of Norway (see also Sinclair 1944). Wiman's (1895) three transverse sections (Text-fig. 4A) through this specimen reveal four high carinae whose adaxial portion is strongly bifid. The non-bifid portion of each carina extends about one-third of the way to the centre of the test cavity. From the branching point, the two arms diverge at a high angle and then bend abruptly toward the face. The ends of the arms apparently were free.



TEXT-FIG. 4. Wiman's (1895, pl. 5, fig. 8–11) line drawings of three transverse sections through a specimen of *Eoconularia loculata* (Wiman), showing: A, the presence of a high, adaxially bifid carina at each of the four midlines; B, inflection and thickening of inner test lamellae in the base of one of the carinae.



TEXT-FIG. 5. Line drawing of a transverse section through a fragment (solid black) of a *Paraconularia*-like conulariid from the Silurian of Australia, showing the presence at a midline of a single high carina bearing small tubercles (labelled T). Figure modified from Bischoff (1978, text-fig. 15).

Babcock and Feldmann (1986b) proposed that these features are not carinae, but taphonomic artefacts possibly caused by differential staining of the rock matrix. Although Wiman's (1895) specimen is currently missing (Babcock and Feldmann 1986a), his illustration of the base of one of the midline structures (Text-fig. 4B) clearly shows that it consists of locally inflected and thickened test lamellae, similar to lamellae in carinae observed in other conulariids. Moreover, the midlines were marked by accentuated pigmentation (Wiman 1895, pl. 5, figs 6–7), a feature usually associated with an internal carina. Under these circumstances, and given the indisputable presence of a low bifid carina at midlines of *Conularia splendida* Billings (Pl. 2, fig. 6), it seems wisest to accept Wiman's (1895) characterization of *E. loculata* midlines as accurate.

High tuberculate carina (Text-fig. 5). This condition was detected by Bischoff (1978) in specimens of a *Paraconularia*-like conulariid from the Silurian of Australia. Midlines of this conulariid are marked by a strong, angular sulcus that is associated internally with a single carina that extends about two-fifths of the way to the centre of the test cavity. This carina differs from those discussed above in being covered by small, broadly conical tubercles. The tubercles, arranged on the carina's two flanks, range from about 0.02 to 0.13 mm wide (as measured at their base) and 0.03 to 0.17 mm high (Bischoff 1978).

MIDLINE CONDITIONS OF CIRCOCONULARIIDS

Circoconulariids are represented by abundant but fragmentary material from Silurian and Devonian strata of south-central Australia (Bischoff 1978). Except for their steeply conical (as opposed to steeply pyramidal) shape, circoconulariids are similar to conulariids, consisting of an apatitic, finely lamellar test that is crossed by numerous low, smooth or tubercle-bearing transverse ridges (ribs). In some species, the transverse ribs arch towards the aperture, in such a way as to define eight longitudinal tracts spaced around the test at 45° intervals. Four of these tracts, spaced at 90° intervals, are defined by the summits of segments arching toward the aperture and are interpreted (Bischoff 1978) as homologous to conulariid midlines.

Bischoff (1978) documented five types of internal structures at circoconulariid midlines. Two of these, termed septal ridge and paired septal ridges, are extremely similar, respectively, to single and paired midline carinae of conulariids such as *Paraconularia* and *Metaconularia*. Of the remaining three types of midline structures, two appear to be unique to circoconulariids. The one type that may not be unique to circoconulariids, termed an adaperturally bifurcating low septum, consists of a low carina that splits adaperturally, forming two short branches that diverge at 15–30°. The flanks of this carina (including both single and forked portions) may be smooth or covered by small tubercles, similar to tubercles on the flanks of the midline carina of the *Paraconularia*-like conulariid described above. In some specimens, the midlines show multiple bifurcating septa, arranged in series and with the adapical end of each member of a series situated immediately above the adapertural end of the member below it.

Among the two uniquely circoconulariid midline structures, one structure, similar to multiple bifurcating septa, consists of a series of low, stout, V-shaped ridges, called funnel-shaped septa, that point towards the apex. Individual ridges exhibit a small hole in their adapical end, apparently providing continuous communication between the triangular regions bounded by the two arms of the ridges.

The second uniquely circoconulariid midline structure, termed a septal apparatus, consists of four massive septa that join at the centre of the test cavity, forming a single continuous unit. The sides of each septum exhibit a single longitudinal row of pustules or a coarsely pustulose longitudinal ridge.

SUMMARY OF CONULARIID CORNER AND MIDLINE ANATOMY

Corners and/or midlines of some or all species of at least ten of the twenty-one currently recognized conulariid genera are sites of localized inflection and thickening of inner test lamellae. Internal structures at corners and midlines of most conulariids are smooth; however, the carina at midlines of at least one Australian conulariid, similar to *Paraconularia*, is covered by small tubercles.

Internal midline structures of some or all species of at least six conulariid genera – *Climacoconus*, *Conularia*, *Conularina*, *Eoconularia*, *Metaconularia*, and *Paraconularia* – are paired or bifid. Midlines of *Eoconularia locudata* (Wiman) exhibit an unusually high carina whose cross-sectional geometry is more or less Y-shaped, and midlines of *Eoconularia amoena* Sinclair exhibit features suggesting the presence of a single carina that bifurcates adaperturally.

Corners and midlines of some or all species of five genera – *Archaeoconularia*, *Climacoconus*, *Conularina*, *Eoconularia*, and *Paraconularia* – are both thickened. Except in *Paraconularia crustula* (White), internal corner structures of all such taxa here examined are wider and/or higher than associated midline structures.

Some species of at least two genera – *Archaeoconularia* and *Climacoconus* – exhibit internal corner and/or midline thickenings that are seriated. In *Climacoconus*, where seriation was detected both in midline and corner structures, members of observed corner series are longer and higher than members of observed midline series.

Conulariid midline structures show a number of similarities to midline structures of circoconulariids. Midline structures of both groups represent localized, tetramerally-arranged

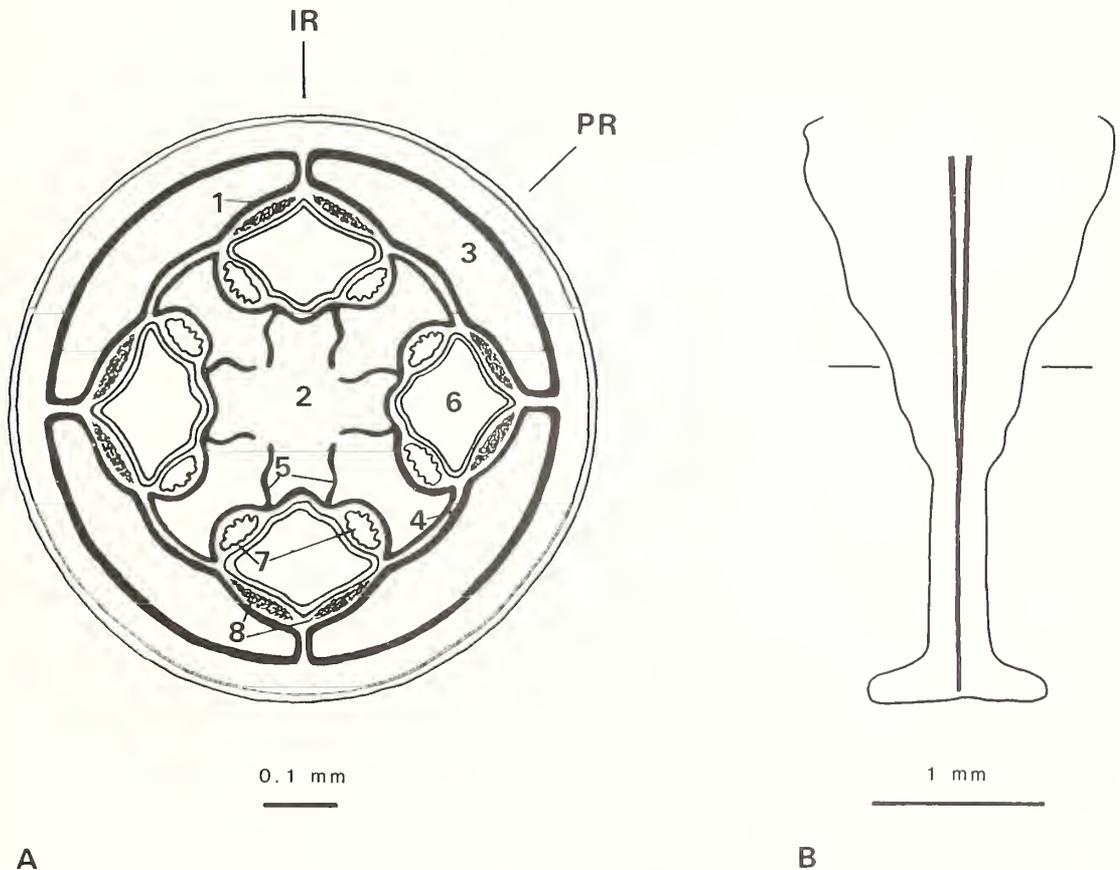
inflections of inner test lamellae, and may be smooth or covered by small tubercles. Two types of midline structures, namely single and paired carinae, occur in members of both groups, and a third type, namely a single carina that bifurcates adapertura, may also be present in both groups.

Together with several other similarities in test anatomy (Bischoff 1978), the similarities outlined above are uniquely shared by conulariids and circoconulariids, and corroborate Bischoff's (1978) contention that these two groups are closely related. For this reason, observed conditions of circoconulariid midlines are regarded here as having a bearing on the interpretation of conulariid anatomy.

SCYPHOZOAN PERRADIAL AND INTERRADIAL ANATOMY

Scyphozoan septa

Except in medusae of the Orders Rhizostomatida and Semaestomatida, the enteron of all scyphozoans is normally subdivided by four radially disposed, longitudinal septa (Hyman 1940). Abnormal individuals may produce two, three, five, or six septa (Hyman 1940; Berrill 1963).



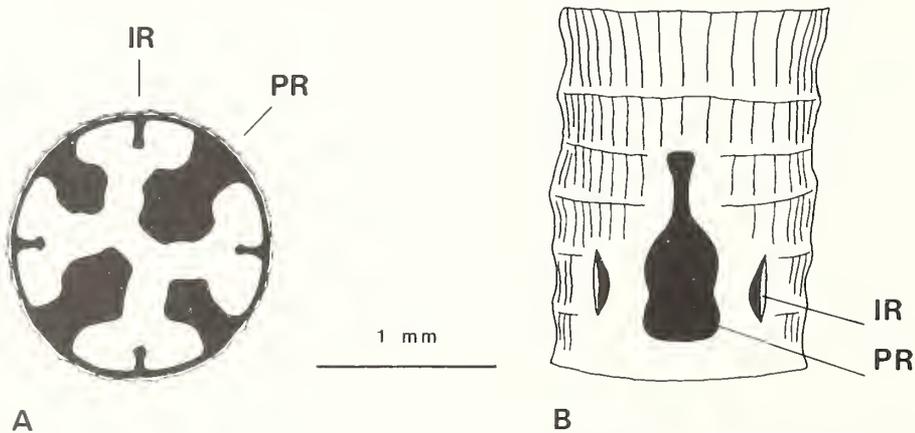
TEXT-FIG. 6. *Craterolophus tethys* Clark, a stauromedusan scyphozoan. A, transverse section near the middle of the polyp. Number symbols indicate the following anatomical features: 1, septum; 2, central stomach; 3, gastric pouch; 4, claustrum; 5, phacellae; 6, peristomial funnel; 7, gonads; 8, retractor muscle. IR and PR stand for interradius and perradius, respectively. B, profile of one of the septal retractor muscles, showing splitting of the muscle to form two strands diverging towards the aperture. Both drawings modified from Gross (1900, pl. 23, fig. 3, pl. 24, fig. 14).

Details of the anatomy of scyphozoan septa have been reviewed by Hyman (1940). Summarizing the main points, each septum is penetrated adorally by a deep, ectoderm-lined, funnel-shaped invagination, the peristomial funnel, that causes the septum to bulge laterally (Text-fig. 6A). In some members of the order Stauromedusida (a group of exclusively sessile scyphozoans), each of the two sides of the septum exhibits a sheet-like longitudinal outgrowth, called a claustrum, that is fused along most of its length with a claustrum of the laterally adjacent septum. The septum's free or adaxial edge exhibits two symmetrically arranged, longitudinal rows, or phacellae, of nematocyst-bearing gastric filaments. Nearer the septum's fixed, or abaxial, edge is a pair of longitudinal, entodermal gonads. Situated still closer to the septum's abaxial edge is a longitudinal retractor muscle, derived from the ectoderm. In most scyphozoans, apparently, the retractor muscle consists of a single tissue bundle; however, in some species of the stauromedusan genera *Craterolophus* Clark and *Lucernaria* Müller, the septal muscle bifurcates adorally (Antipa 1892; Gross 1900; Berrill 1962). In *Lucernaria walteri* Antipa, for example, the muscle splits near the animal's oral end, and the two branches diverge at roughly 20° (Antipa 1892, pl. 17, fig. 1; see also Hyman 1940, fig. 165A); in *Craterolophus tethys* Clarke, the muscle splits nearer the basal end, and the branches diverge at about 2° (Text-fig. 6B).

Coronatid thecal structures

Polyps of the order Coronatida are sheathed in a steeply conical, non-mineralized theca that in some species exhibits internal structures at the interradial and perradial (e.g. Werner 1966a, 1966b, 1967, 1970, 1974, 1979, 1983; Chapman and Werner 1972). The theca is built of numerous, extremely thin (12 nanometres), chitinous lamellae that generally parallel the outer surface of the theca and are grouped in two layers: a thin, outer layer crossed by fine, closely-spaced transverse and longitudinal corrugations; and a thicker, non-corrugated, inner layer. The outer, corrugated layer ranges from about 2 to $4\ \mu\text{m}$ thick and is secreted by soft tissues overlapping the theca's apertural margin. Growth of the outer layer evidently involves extension of the apertural edge of existing lamellae. The inner layer, locally almost $20\ \mu\text{m}$ thick, is secreted by ectoderm of the side of the calyx, which accretes whole lamellae to the theca's inner surface.

In species exhibiting internal thecal structures (Text-fig. 7), the perradial and interradial are sites of a single file or series of discrete, thorn-like longitudinal invaginations of the theca's inner layer. These invaginations, here designated internal thecal projections, are also arranged in whorls, with each whorl consisting of a set of four perradial and four interradial projections. Projections at the



TEXT-FIG. 7. Drawings of internal thecal projections at the perradial (PR) and interradial (IR) of the coronatid scyphozoan *Stephanoscyphus planulophorus* Werner. Drawings modified from Werner (1967, fig. 6b). A, transverse section through a single whorl. B, side view of one member each of a perradial and two interradial files.

perradii are consistently larger (longer, wider, higher) than projections at the interradii, with the perradial projections often extending over half-way to the theca's longitudinal axis. In most species, both sets of projections are smooth; in other species, however, the perradial projections exhibit small tubercles.

COMPARISONS OF SCYPHOZOANS AND CONULARIIDS

The hypothesis that conulariid midlines were sites of a gastric septum, homologous to the gastric septa of scyphozoans, was originally based in large part on comparisons of high, adaxially bifid midline carinae of *Eoconularia loculata* (Wiman) with claustra-bearing septa of stauromedusans such as *Craterolophus tethys* (Kiderlen 1937; Van Iten 1991). As shown in Text-figure 1, both sets of structures are identical in number and arrangement, and show similarities in size (both absolute and relative to the body, or test, cavity) and cross-sectional form. As indicated by previous discussions of other higher taxa (e.g. Jollie 1962; Jones 1985; Barnes 1987), no currently known non-scyphozoan group exhibits soft-part or test structures that more closely resemble *E. loculata* midline carinae than do stauromedusan septa. Coupled with microstructural evidence indicating that the conulariid test was an ectodermal derivative whose growth involved centripetal accretion of whole lamellae (e.g. Bischoff 1978; Van Iten 1991), this suggests that high, adaxially bifid midline carinae, while not directly homologous to stauromedusan septa, were covered in life by soft tissue structures that were homologous to stauromedusan septa.

Midline carinae of other conulariids also exhibit interesting similarities to stauromedusan septa. As noted above in connection with details of septal anatomy, the septal muscle of some stauromedusans consists of a single tissue bundle, while in other stauromedusans the muscle bifurcates adorally. Similarly, conulariids whose midlines are internally carinate exhibit either a single carina, a pair of carinae, or possibly, a single carina that bifurcates adaperturally. Paired midline carinae of relatively small conulariids (e.g. *Conularina narrawayi* Sinclair; Pl. 2, fig. 3) are similar in spacing and angle of divergence to the paired muscle strands of the bifurcate retractor muscle of *Craterolophus tethys*. The geometry of bifurcate midline carinae of the circoconulariid *Garraconularia* Bischoff is similar to the geometry of the retractor muscle of *Lucernaria walteri*, a species in which the paired strands of the muscle's bifurcate portion diverge more rapidly than in *Craterolophus tethys*.

Given that the conulariid (and circoconulariid) test and the scyphozoan septal muscle are both ectodermal derivatives, it seems reasonable to infer that similarities between internal midline structures of conulariid tests and the scyphozoan retractor muscle are indicative of similarity at a more general level of comparison. While test structures at conulariid midlines are not directly homologous to the scyphozoan septal muscle, similarities between these two features could be interpreted as additional evidence that the organization of soft tissues located at conulariid midlines and scyphozoan interradii was fundamentally similar. More specifically, and as proposed earlier by Bischoff (1978), these similarities suggest that the presence of single, paired, or adaperturally bifurcating midline carinae in conulariids (and circoconulariids) reflects the former presence of a septal retractor muscle that could be either single, paired, or adorally bifurcate.

Similarities between internal test structures at conulariid corners and midlines and internal thecal projections at the perradii and interradii, respectively, of coronatid scyphozoans are also important. Both sets of structures consist of tetramerally arranged, longitudinally elongate inflexions of inner lamellae, and may be smooth or covered by small tubercles. Just as coronatid perradial projections are consistently larger (higher, broader, longer) than projections at the interradii, in nearly all conulariids whose corners and midlines are both carinate, internal structures at the corners, interpreted as perradial in position, are broader and/or higher than internal structures at the midlines. (The one species here examined where this size relationship is sometimes not observed, *Paraconularia crustula* (White), is substantially younger geologically than other taxa having carinate corners and midlines (see Appendix), and thus it is possible that departure from the more commonly observed condition represents a relatively derived condition.) Internal test structures of

Archaeoconularia membranacea (Ringueberg) and at least two species of *Climacoconus* are seriated. Although seriation in *A. membranacea* is apparent at midlines only, at least one *Climacoconus* species (Sinclair's (1948) unpublished *C. concinnus*; GSC 94786) shows evidence of seriation at both midlines and corners. Segments of seriated corner and midline carinae in *Climacoconus* are organized in isolatitudinal groups or whorls (currently available specimens of *A. membranacea* are too incomplete to determine if their internal midline structures are arranged in whorls), and, like coronatid perradial projections, segments of seriated *Climacoconus* corner structures are several times longer and higher than segments of seriated midline structures.

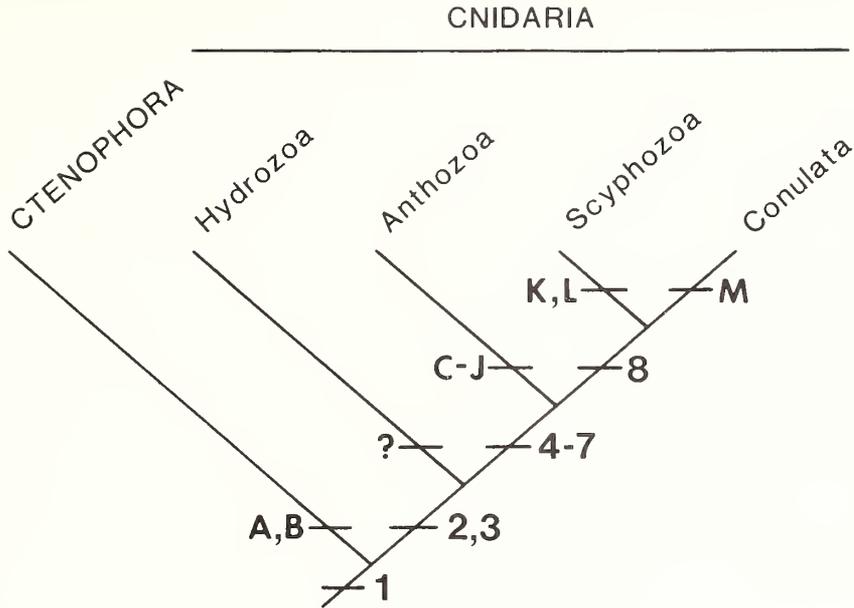
The presence of internal test or thecal structures having the characteristics summarized above is a feature uniquely shared by certain conulariids and coronatid scyphozoans, and thus tends to corroborate the hypothesis that the organization of soft tissues at conulariid midlines and scyphozoan interradial was fundamentally similar. In addition, similarities between internal structures of conulariid tests and coronatid thecae raise the possibility, already suggested by Chapman (1966) and Werner (1966a), that the most recent common ancestor of conulariids and coronatids was a thecate animal having internal thecal projections at the perradial and interradial. Interestingly, conulariids having internal carinae, either continuous or seriated, at both corners and midlines (e.g. *Archaeoconularia fecunda* (Barrande), *Climacoconus*, *Conularina*, and *Eoconularia forensis* Sinclair), are among the earliest (and thus, possibly, least differentiated from a common conulariid/coronatid ancestor) conulariids known.

Finally, just as aberrant scyphozoans produce two, three, five, or six septa, *Conularina triangulata* (Raymond) has only three faces (and hence three midlines), and Babcock *et al.* (1987b) documented a specimen of *Paraconularia missouriensis* (Swallow) with six faces. The only other metazoans resembling conulariids and known to exhibit this array of alternate symmetries are hydrozoan cnidarians (which, for example, show variation in the number of primary branches in the medusa's radial canal system; Werner 1973).

To summarize, conulariid corners and midlines exhibit numerous similarities to anatomical structures located, respectively, at the scyphozoan perradial and interradial. Except for similarities in symmetry patterns (which are also shared with hydrozoan cnidarians), all of the similarities outlined above are uniquely shared by conulariids and scyphozoans, and there is no evidence of greater similarity between conulariid corners and midlines and test or soft-part structures of any non-scyphozoan group. The relatively complex character of similarities between conulariid corners and midlines and scyphozoan perradial and interradial anatomy makes it difficult to dismiss these similarities as superficial or due to convergence. Rather, these similarities suggest that conulariid midlines were sites of a gastric septum, homologous to the gastric septa of scyphozoans. (It should be noted here that Babcock and Feldmann (1986a, 1986b) proposed that the tendency of many conulariids to be distinctly rectangular in transverse cross-section indicates that conulariids were 'bilaterally symmetrical' organisms that exhibited a higher level of anatomical organization than that shown by scyphozoans or other cnidarians; however, 'bilateral (biradial) symmetry' is exhibited by structural elements (e.g. whorls of internal thecal projections) of coronatid thecae (Text-fig. 7A), and thus its occurrence among conulariids in no way weakens anatomical interpretations advocated in this study.)

IMPLICATIONS FOR CONULARIID AFFINITIES

Proponents of the hypothesis that conulariid midlines were sites of a gastric septum interpret conulariids as extinct members of the Phylum Cnidaria, a monophyletic taxon whose extant members are generally thought to include the Classes Anthozoa, Hydrozoa, and Scyphozoa (a number of authors interpret cubozoans, traditionally regarded as a group within Scyphozoa, as a fourth cnidarian class; e.g. Werner 1973; Petersen 1979; Möhn 1984; Brusca and Brusca 1990). Relationships among these three classes (and conulariids) have been subject to widely divergent interpretations (e.g. Jägersten 1955, 1959; Hill and Wells 1956; Marcus 1958; Hadzi 1958, 1963; Hand 1959; Uchida 1963; Thiel 1966; Glaessner 1971, 1984; Werner 1973; Salvini-Plawen 1978;



TEXT-FIG. 8. Cladogram summarizing one interpretation of phylogenetic relationships among conulariids and extant cnidarians. The Phylum Ctenophora is interpreted as the nearest living relative of Cnidaria. Synapomorphies (numbered) are as follows: 1, diploblastic, tentacle-bearing medusa with non-septate digestive cavity having four radially disposed primary branches that bear the gonads; 2, cnidae; 3, planula larva; 4, gastric septa; 5, cnidae-bearing gastric filaments; 6, sex cells ripening in entoderm; 7, mesenchyme cellular; 8, four septa. Autapomorphies (lettered) are as follows (C-J taken from Brusca and Brusca 1990, fig. 43A): A, cydippid larva; B, comb rows; C, loss of medusa; D, hexaradial and octaradial symmetry; E, actinopharynx; F, siphonoglyph; G, loss of cnidal operculum; H, loss of cnidocil; I, cnidae with tripartite flaps; J, cnidae with special ciliary cones; K, rhopalium; L, strobilation; M, apatitic theca. No autapomorphies are shown for Hydrozoa, interpreted by Brusca and Brusca (1990) as a paraphyletic taxon.

Grasshoff 1984; Möhn 1984; Brusca and Brusca 1990; Willmer 1990), and extended analysis of this problem lies beyond the scope of the present discussion. Nevertheless, the presence of four septa in conulariids and scyphozoans may mean that these two groups are more closely related to each other than either group is to anthozoans, which have a greater number of septa, or to hydrozoans, which lack septa. At this point there appear to be no similarities between conulariids and anthozoans or hydrozoans that are not also shared with scyphozoans, and thus there are no similarities that conflict with the hypothesis that conulariids and scyphozoans are nearest relatives. This hypothesis is outlined in Text-figure 8, which also summarizes the more general hypothesis of relationships, favoured by a number of previous authors (e.g. Hyman 1940; Hill and Wells 1956; Hand 1959; Uchida 1963; Brusca and Brusca 1990), that septate cnidarians form a monophyletic group within Cnidaria that excludes hydrozoans.

This and other proposed hypotheses of relationships among taxa within Cnidaria (e.g. medusa-bearing cnidarians form a monophyletic group within Cnidaria that excludes anthozoans; Werner 1973) are in serious need of further testing. Thus far work on this problem has centred largely on analysis of gross anatomical characters such as the presence or absence of septa and the structure of the cnidae (Text-fig. 8). However, additional characters, including the structure of mitochondrial DNA (e.g. Warrior and Gall 1985) and the ultrastructure of sperm (e.g. Hinsch 1974; Schmidt and Hölken 1980), are being explored in some detail, and it will be important to extend this research to cover possible close relatives of Cnidaria such as the Phyla Ctenophora and Platyhelminthes (e.g.

Bayer and Owre 1968; Harbison 1985), one or both of which may be sufficiently similar to Cnidaria to serve as outgroups for cladistic parsimony analysis of relationships within that group.

Needless to say, more work is also needed on conulariids (and circoconulariids), particularly on details of their life history and soft part anatomy. Some of this information may be contained in material from the Hunsrück Slate (Lower Devonian, Germany), which has yielded several pyritized specimens of *Conularia* containing probable relic soft parts (Steul 1984; Van Iten 1989, 1991).

Acknowledgements. This paper is based on part of a Ph.D. dissertation written in the Museum of Paleontology, the University of Michigan, Ann Arbor. I thank the members of my dissertation committee, D. J. Eernisse, D. C. Fisher, K. C. Lohmann, G. R. Smith, and B. H. Wilkinson, for advice and comments on earlier versions of the manuscript. I thank T. Van Iten for printing the photographs, R. S. Cox and R. J. Van Iten for assistance in the field, and R. S. Cox for information on the anatomy of *Metaconularia* specimens in collections of the British Museum (Natural History), London. Permission to borrow or examine museum specimens was provided by T. E. Bolton, M. Carmen, F. J. Collier, N. Eldredge, R. Eng, D. C. Fisher, J. Golden, W. Hammer, A. Horowitz, T. Frest, R. Laub, W. G. Melton, D. Rudkin, R. Titus, and J. Waddington. Their help is greatly appreciated. This study was supported by funding from the Department of Geological Sciences and the Horace H. Rackham School of Graduate Studies at the University of Michigan, Sigma Xi, NSF Research Grant BNS-8521097 to D. C. Fisher, and R. J. and H. B. Van Iten. The scanning electron microscope used in this study was acquired under Grant no. BSR-83-14092 from the National Science Foundation.

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HEYO VAN ITEN
Museum of Paleontology
University of Michigan
Ann Arbor, MI 48109, USA

Present address:

Department of Geology
Gustavus Adolphus College
Saint Peter, Minnesota 56082, USA

Typescript received 2 July 1990

Revised typescript received 28 August 1991

APPENDIX

Conulariids examined in the present study. Letter symbols in parentheses next to a species name indicate conditions of that species' corners and midlines, respectively, and are as follows: NS, non-sulcate; SG, simple groove; MFG, mesially folded groove; CG, carinate groove; S, simple; OF, outwardly folded; SC, single carina; GSC, groove with seriated carina; PC, paired carinae; PT, paired thickenings; LBC, low bifid carina; ABC?, single carina, adaperturally bifurcating?; PSC, paired seriated carinae. N = number of specimens of a given species currently available and/or observed to exhibit conditions listed next to that species' name. Institutions housing examined specimens are as follows: AC, Augustana College, Rock Island, Illinois; AMNH, American Museum of Natural History, New York; BMS, Buffalo Museum of Science, Buffalo; BMNH, British Museum (Natural History), London; BMUW, Burke Museum, University of Washington, Seattle; CM, Carnegie Museum, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; GSC, Geological Survey of Canada, Ottawa; ISGS/ISM, Illinois State Geological Survey/Illinois State Museum, Champaign/Urbana; IU, Indiana University, Bloomington; LACM, Los Angeles County Museum, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard University; NYSM, New York State Museum, Albany; PMNH, Peabody Museum of Natural History, Yale University; PRM, Peter Redpath Museum, Montreal; ROM, Royal Ontario Museum, Toronto; SUI, State University of Iowa, Iowa City; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UMMP*, University of Montana Museum of Paleontology, Missoula; UI, University of Illinois, Champaign–Urbana; UMPC, University of Minnesota, Minneapolis; USNM, United States National Museum, Washington.

Species	Horizon/Age	Locality	Repository	N
<i>Anaconularia</i>				
<i>A. anomala</i> (Barrande) (NS, ?)	Drabov Qtzite (M. Ord.)	Bohemia	MCZ	≈ 760
<i>Archaecoconularia</i>				
<i>A. membranacea</i> Sinclair (CG, GSC)	Rochester Fm. (M. Sil.)	New York	BMS E10791, E10793	2
<i>A. mirifica</i> (Reed) (SG, SC)	Drummock Gp (U. Ord.)	Scotland	GSC 87280a–d	4
<i>Calloconularia</i>				
<i>C. strimplei</i> Sinclair (CG, SC)	Ochilate Gp (Penn.)	Oklahoma	FMNH PE143a	1
<i>Climacocornus</i>				
<i>C. batteryensis</i> (Billings) (?, SC)	Vaurél Fm. (U. Ord.)	Quebec	GSC 29594; PMNH 10367	2
<i>C. bromidus</i> Sinclair (CG, SC)	Viola Fm. (M. Ord.)	Oklahoma	USNM	3

APPENDIX (cont.)

Species	Horizon/Age	Locality	Repository	N
<i>C. bureaui</i> Sinclair (SG, S)	Trenton Gp	Quebec	GSC 17852	1
<i>C. quadratus</i> (Walcott) (CG, S)	Tetreauville Fm. (M. Ord.)	Quebec	GSC 17710-17712	3
<i>C. cf. quadratus</i> (CG, S)	Maquoketa Fm. (U. Ord.)	Iowa	SUI 61534	1
<i>C. rallus</i> Sinclair (CG, S)	Laval Fm. (M. Ord.)	Quebec	GSC 17713	1
<i>C. sp. 1</i> (CG, PSC)	Platteville Fm. (M. Ord.)	Minnesota	GSC 94785a-g	7
<i>C. sp. 2</i> (CG, PSC)	Platteville Fm. (M. Ord.)	Minnesota	GSC 94786a-b; UMMP 20650	4
<i>C. sp. 3</i> (CG, PSC)	Maquoketa Fm. (U. Ord.)	Iowa	GSC 94787; SUI 61531	2
<i>C. urbanis</i> Sinclair (CG, S)	Quebec City Fm. (M. Ord.)	Quebec	GSC 17853	1
<i>Conularia</i>				
<i>C. albertensis</i> Reed (?CG, SC)	Devonian	Bolivia	USNM 409813- 409814	2
<i>C. delphiensis</i> (Maroney and Orr) (SG, S)	New Albany Sh. (U. Dev.)	Indiana	UMMP 66085	≈ 50
<i>C. formosa</i> Miller and Dyer (SG, S)	Stonington Fm. (U. Ord.)	Michigan	UMMP 30369	1
<i>C. milwaukeeensis</i> Cleland (CG, S)	M. Dev.	Wisconsin	UMMP 814	1
<i>C. multicosata</i> Meek and Worthen (SG, S)	Cuyahoga Sh. (L. Miss.)	Ohio	AC I-4160, I-4164; UMMP 804	3
<i>C. cf. splendida</i> Billings (SG, LBC)	Maquoketa Fm. (U. Ord.)	Iowa	SUI 61521-61523; BMUW 73177	7
<i>C. sp.</i> (SC, S)	Cedar Valley Fm. (M. Dev.)	Iowa	SUI 62673-62677, 62683-62693	14
<i>C. subcarbonaria</i> Meek and Worthen (SG, S)	U. Dev.-L. Miss.	USA	FMNH; IUPC; UI	10
<i>C. trentonensis</i> Hall (SG, S)	M.-U. Ord.	USA, Canada	GSC; NYSM; ROM; SUI; UMMP	≈ 100
<i>Conularina</i>				
<i>C. irrasa</i> Sinclair (CG, PT)	Laval Fm. (M. Ord.)	Quebec	GSC 17714	1
<i>C. narrawayi</i> Sinclair (CG, PC)	Laval Fm. (M. Ord.)	Quebec	ROM 18905	1
<i>C. raymondii</i> Sinclair (CG, PT)	Laval Fm. (M. Ord.)	Quebec	GSC 17715	1
<i>C. triangulata</i> (Raymond) (CG, PT)	Laval/Valcour Fms (M. Ord.)	Quebec, New York	CM 2099, 2100, 17714; GSC 17716-17717, 94788-94789	6
<i>Ctenoconularia</i>				
<i>C. obex</i> Sinclair (SG, S)	Platteville Fm. (M. Ord.)	Minnesota	GSC 87193; UMPC 6608	3
<i>C. sp.</i> (SG, S)	Sherman Falls Fm. (M. Ord.)	Ontario	GSC 94784	1

APPENDIX (cont.)

Species	Horizon/Age	Locality	Repository	N
<i>Eoconularia</i>				
<i>E. amoena</i> Sinclair (CG, ABC?)	Sherman Falls Fm. (M. Ord.)	Quebec	ROM 23297	1
<i>E. forensis</i> Sinclair (CG, SC)	Quebec City Fm. (M. Ord.)	Quebec	GSC 1712-1713, 87201	3
<i>Glyptoconularia</i>				
<i>G. gracilis</i> (Hall) (CG, ?)	Tetreauville Fm., Trenton Gp. (M. Ord.)	Quebec, New York	AMNH 789; GSC 94782-94783	3
<i>Metaconularia</i>				
<i>M. aspersa</i> (Slater) (SG, PC)	Ludlow Sh. (Sil.)	England	BMNH G4603, G5373	2
<i>M. calderi</i> Sinclair (SG, PC)	Cobourg/Ottawa Fms (M. Ord.)	Ontario	GSC 9794-9795	2
<i>M. delicatula</i> (Savage) (?, PC)	Maquoketa Gp (U. Ord.)	Illinois	UI X-614	1
<i>M. gibraltarensis</i> (SG, PC)	Manitoulin Fm. (L. Sil.)	Ontario, Michigan	ROM 7537; UMMP 66023	2
<i>M. cf. heymani</i> (Foerste) (SG, PC)	Maquoketa Fm.	Iowa	SUI 62672	1
<i>M. manni</i> (Roy) (?, PC)	Lecthaylus Sh. (Sil.)	Illinois	FMNH PE6252-6256, PE10132, PE23674- 23975, FMNH unnumbered	13
<i>M. papillata</i> (Hall) (SG, PC)	Trenton Gp (M. Ord.)	New York	AMNH 790; MCZ 27809	2
<i>M. sp.</i> (SG, PC)	Dubuque Fm. (U. Ord.)	Iowa	SUI 37414, 62678- 62679	3
<i>M. ulrichi</i> Foerste (SG, PC)	Platteville Fm. (M. Ord.)	Wisconsin	USNM 43087	1
<i>Notocomularia</i>				
<i>N. laevigata</i> (Morris) (MFG, S)	Permian	New South Wales	UMMP 9299	1
<i>Paraconularia</i>				
<i>P. arctica</i> Babcock (?, SC)	Permian	Canada	GSC 90696	1
? <i>P. byblis</i> (White) (SG, S)	English River Fm. (U. Dev.)	Iowa	UMMP 259, 2167	2
<i>P. chesterensis</i> (Worthen) (SG, PC)	U. Miss.	USA	ISGS/ISM 2489; LACM 9364a; UMMP 23955	3
<i>P. crustula</i> (White) (CG, SC)	Pennsylvanian	USA	UMMP 66024a-n; ISGS/ISM 4018, 7865	18
<i>P. missouriensis</i> (Swallow) (SG, S)	L. Miss.	USA	FMNH 1125, 6627- 6628; ISGS 2619; UMMP 26740	5
<i>P. planicostata</i> (Dawson) (SG, SC)	Windsor Gp (Miss.)	Nova Scotia	ROM 29823	14
<i>P. subulata</i> (Hall) (SG, S)	Heath Fm. (L. Miss.)	Montana	CM 34521, 34524, 35000; UMMP* 5613, 5628, 5633	6

APPENDIX (*cont.*)

Species	Horizon/Age	Locality	Repository	N
<i>P. ulrichana</i> (Clarke) (SG, SC)	Devonian	Bolivia	USNM 409842-409843	2
<i>Pseudoconularia</i>				
<i>P. mirifica</i> (Spencer) (SG, OF)	Lockport Fm. (L. Sil.)	Ontario	PRM 1019	1
<i>Reticulaconularia</i>				
<i>R. penouili</i> (Clarke) (SG, S)	Grande Grève Ls. (L. Dev.)	Quebec	NYSM 9412	1

MICROSTRUCTURE AND GROWTH OF THE CONULARIID TEST: IMPLICATIONS FOR CONULARIID AFFINITIES

by HEYO VAN ITEN

ABSTRACT. The conulariid test has been interpreted as homologous to the theca of coronatid scyphozoans, but recently it has been claimed that the conulariid test and coronatid theca are fundamentally dissimilar. This claim is based largely on putative microstructural characteristics of conulariid tests. Examination of sectioned conulariids using scanning electron microscopy reveals that their microstructure is similar to that of the coronatid theca. Analysis of the microstructure and patterns of malformation of healed injuries and growth abnormalities in conulariids indicates that the conulariid test and coronatid theca were also similar in mode(s) of growth and injury repair. Werner's (1966*a*, 1967) suggestion that the ornamental (outer) layer of the conulariid test is homologous to the outer layer of the coronatid theca is problematic. Nevertheless, the conulariid test and coronatid theca can be interpreted as homologous at a more general level of comparison.

RECENT disagreement over the affinities of conulariids has stemmed in part from conflicting interpretations of the microstructure of the conulariid test. Based on examination of thin sections and/or fracture surfaces, most previous investigators (e.g. Barrande 1867; Bouček and Ulrich 1929; Moore and Harrington 1956*a*; Kozłowski 1968; Bischoff 1978) described the conulariid test as built of microscopic, phosphatic or chitinophosphatic lamellae that parallel the surface of the test. Kozłowski (1968) and Bischoff (1978) showed that conulariid test lamellae are less than 10 μm thick and are alternately dense and vacuity-bearing. They and several other authors (e.g. Barrande 1867; Slater 1907; Bouček and Ulrich 1929) reported that the lamellae are arranged in two layers: an outer layer exhibiting transverse ridges or rows of tubercles (the ornamental layer; Kozłowski 1968), and an inner layer that is more or less smooth (the basal layer; Kozłowski 1968). Moore and Harrington (1956*a*) noted that conulariid tests are often very thin, in some cases as thin as 0.056 mm (56 μm). Several other investigators (Bouček 1928; Reed 1902, 1933; Kowalski 1935; Kiderlen 1937) documented tests that are strongly crumpled but unbroken, or that exhibit regular, inward plication of lappet-like structures at their apertural end. This has been interpreted as evidence that such tests were flexible in life (e.g. Moore and Harrington 1956*a*).

Based in part on similarities between conulariids and thecate polyps of the cnidarian class Scyphozoa, several investigators (e.g. Kiderlen 1937; Bouček 1939; Moore and Harrington 1956*a*; Chapman 1966; Werner 1966*a*, 1967; Bischoff 1978) argued that conulariids were scyphozoans or that they were more closely related to scyphozoans than to any other taxon of comparable rank. These authors interpreted the conulariid test as a mineralized theca, produced by ectodermal tissues covering its inner surface. Taking this hypothesis still further, Werner (1966*a*, 1967) proposed that the conulariid test is homologous to the bilayered theca of coronatid scyphozoans, interpreted by Werner (1966*a*, 1967) as direct descendants of conulariids. Werner (1966*a*, 1967) further suggested that the basal and ornamental layers of the conulariid test are homologous, respectively, to the inner and outer layers of the coronatid theca.

The hypothesis that the conulariid test is homologous to the theca of coronatid scyphozoans has been challenged by several authors (e.g. Kozłowski 1968; Mortin 1985; Feldmann and Babcock 1986; Babcock and Feldmann 1986*a*, 1986*b*), all of whom also reject the hypothesis that conulariids and scyphozoans were closely related. Although none of these investigators has argued that the conulariid test is homologous to the test or theca of some non-scyphozoan group, all have claimed

that the conulariid test and coronatid theca are fundamentally dissimilar. Based on examination of tubercle-bearing conulariid tests, Kozłowski (1968) concluded that the tubercles are pierced by a fine canal (choanophyme) that opens at both the base and summit of the tubercles. Kozłowski (1968) interpreted this canal as the former site of a thread-like sensory organ having no homologue in scyphozoans or any other extant taxon. In order to account for the fact that some of the tubercles he examined lacked an opening at their summit, Kozłowski (1968) further proposed that during ontogeny, choanophymes were covered by deposition of lamellae on the test's exterior surface. This led Kozłowski (1968) to conclude that the conulariid test was secreted internally, rather than externally as in scyphozoans and other cnidarians. (More recently, Babcock (1991) argued that specimens examined by Kozłowski (1968) are not conulariids; however, comparison of Kozłowski's figures with conulariid specimens in collections of the University of Michigan Museum of Paleontology satisfied the present author that Kozłowski's specimens are conulariids.)

Kozłowski's (1968) interpretation of conulariid tubercles as perforated structures was refuted by Bischoff (1973, 1978), who reported (Bischoff 1978, p. 298) that 'sections through tubercles (spikes) of well-preserved conulariid test material have...shown that [test lamellae] are continuous over the whole of the tubercles (and adjacent parts of the test), thus excluding the possibility of the existence of a passageway between the interior [test cavity] and the surrounding medium at any stage.' The feature interpreted by Kozłowski (1968) as a canal opening to the exterior is actually a sharp depression in the basal part of conulariid tubercles, which depression is often revealed through severance of tubercles near their base.

Mortin (1985), Feldmann and Babcock (1986), and Babcock and Feldmann (1986a, 1986b) echoed Kozłowski's (1968) conclusion that conulariids represent a group of animals distinct from cnidarians and all other phyla. According to Mortin (1985, p. 12), the conulariid test 'displays various features suggestive of a reasonably complex secretory physiology, probably involving a mantle-like secretory mechanism'. In his opinion (Mortin 1985, p. 13), this 'seems incompatible with a cnidarian affinity for conulariids'. Feldmann and Babcock (1986) and Babcock and Feldmann (1986a, 1986b) proposed that conulariid tests consist of discrete, solid rods embedded within a finely lamellar integument. In their opinion (Feldmann and Babcock 1986, p. 470), 'the rods and multilayered integument form a style of exoskeletal construction unknown in other organisms'. Based on the purported absence of rods in the genus *Metaconularia* Foerste and the species *Conularina triangulata* (Raymond), two taxa traditionally interpreted as conulariids (e.g. Sinclair 1940, 1948; Wilson 1951; Moore and Harrington 1956b; Van Iten 1991a), Feldmann and Babcock (1986) and Babcock *et al.* (1987) concluded that these taxa are not conulariids. Later, Babcock (1991) interpreted *Metaconularia* as a conulariid, for reasons not specified, but he continued to exclude *C. triangulata* (and, apparently, all other members of the genus *Conularina*) from the group.

Finally, Babcock (1990) documented localized, pearl-like swellings in specimens of *Paraconularia magna* (Ries) from the Pennsylvanian of Oklahoma, USA. Calling these structures pearls, Babcock (1991) concluded that their occurrence in conulariids constitutes evidence of a closer affinity with triploblastic taxa than with the diploblastic cnidarians.

OBJECTIVES, MATERIAL, AND PROCEDURE

The purpose of the present study is to evaluate the hypothesis that the conulariid test is homologous to the theca of coronatid scyphozoans by addressing recent challenges to this hypothesis by Mortin (1985), Feldmann and Babcock (1986), and Babcock and Feldmann (1986a, 1986b), and by making additional comparisons with coronatid thecae. A subsidiary goal of this study is to assess the affinities of *Metaconularia* and *Conularia triangulata*. In addition to covering the microstructure of regular features of conulariid tests, this study also addresses the microstructure and patterns of malformation of healed injuries and growth abnormalities. As recognized by previous authors (e.g. Babcock *et al.* 1987; Mapes *et al.* 1989), such features contain information bearing on the mode of growth of the conulariid test and its relation to former soft tissues.

Conulariids examined for this study range from Ordovician to Pennsylvanian in age and are distributed among six of the twenty-one currently recognized conulariid genera: *Climacoconus* Sinclair, *Conularia* Sowerby, *Conularina* Sinclair, *Metaconularia* Foerste, *Paraconularia* Sinclair, and *Pseudoconularia* Bouček. These six genera include the majority of recognized conulariid species, and they provide a comprehensive sample of basic types of conulariid test ornament. Genera not examined here are known only from steinkerns (e.g. *Anaconularia* Sinclair), are extremely rare and represented by non-preparable type specimens (e.g. *Comulariella* Bouček), or consist of species formerly included within one of the six examined genera (e.g. *Calloconularia* Sinclair, *Notoconularia* Thomas).

Methods. Specimens were examined with the aid of an Hitachi S-570 scanning electron microscope. At relatively low magnifications ($< 1000\times$), best results were given by backscattered electron imaging of polished sections, while at higher magnifications best results were obtained using secondary electron imaging of fracture surfaces. The conulariids, all partial specimens broken at both ends, were embedded in Titan casting resin and then sectioned parallel or perpendicular to their long axis. Sections were ground and polished using 600 grit and 0.3 μm aluminium oxide powder, and then cleaned ultrasonically and coated with gold or carbon. All sections are housed in the Museum of Paleontology of the University of Michigan, Ann Arbor, USA, under collection number UMMP 60000. Other specimens referred to in this paper are repositied in collections of the State University of Iowa, Iowa City, USA (SUI).

REVIEW OF CONULARIID GROSS ANATOMY

As conceived by the present author, conulariids are characterized by an apatitic, steeply pyramidal test that usually exhibits four (but in some cases three or six) sides, or *faces*. More or less complete specimens range from less than two to about 20 cm long, though some taxa (e.g. *Metaconularia papillata* Hall; Middle Ordovician, New York, USA) attained lengths of at least 50 cm. At the test's wide end, called the *aperture*, the faces project beyond the ends of the corners, forming a subtriangular or rounded *lappet* that may be folded over the aperture, covering it (Bouček 1928; Reed 1902, 1933; Kowalski 1935; Kiderlen 1937). Tests whose apical end is preserved exhibit a small (less than 1 mm wide), collar-like holdfast (Kozłowski 1968). Other tests, broken some distance above this site, terminate in a smooth, finely lamellar transverse wall, generally referred to as the *schott*.

Tests of almost all conulariids are crossed by numerous transverse ridges, called *transverse ribs*, or by transverse rows of minute, closely-spaced *tubercles*, which are also arranged in longitudinal files. On each face, tubercle rows and, in most cases, transverse ribs arch toward the aperture. As shown by longitudinal sectioning (e.g. Holm 1893; Sinclair 1948), transverse ribs are an expression of trochoidal or sinusoidal corrugation. Transverse ribs of several taxa (e.g. *Conularia*) bear a single row of closely-spaced, hemispherical swellings, similar to the tubercles of taxa lacking transverse ribs. In the former taxa, the region between two adjacent transverse ribs, the *interspace*, often exhibits longitudinal corrugation.

In nearly all conulariids, the corners of the test are furrowed by a prominent sulcus or groove, associated in several corrugated taxa (e.g. *Climacoconus* and *Paraconularia*) with disruption and offset of the transverse ribs. Corners of many conulariids exhibit an internal carina (e.g. Knod 1908; Bouček 1939; Van Iten 1991a, 1992). This carina, which in some specimens projects about one-sixth of the way to the opposite corner, is often strongly pigmented and visible through the test.

With few exceptions, the midline of each face is marked by a groove or by offset or deflection of transverse ribs. Midlines of many conulariids exhibit one of several distinct types of internal carina(e) (Van Iten 1991a, 1992). As in the case of corner carinae, internal carinae at conulariid midlines are often strongly pigmented and visible through the faces.

ANATOMY AND GROWTH OF THE CORONATID THECA

Details of the anatomy and growth of the steeply conical, chitinous theca of coronatid scyphozoans

have been discussed by Chapman (1966), Werner (1966*a*, 1966*b*, 1967, 1970, 1974, 1979, 1983), and Chapman and Werner (1972). Reviewing the main points, the theca fully covers the side of the polyp and has been observed (Werner 1970) to grow up to 8 cm long. The theca terminates adorally in a small, closed, disc-like holdfast, cemented in life to rocks or other firm substrates. The theca's oral, or apertural end is open, but during strobilation the polyp often closes this end by secreting a thin, circular operculum.

Examination of sectioned thecae using transmission electron microscopy (Chapman and Werner 1972) revealed that they are built of numerous, 12 nanometre-thick lamellae, separated from each other by an equally narrow gap bridged by minute processes. The lamellae are grouped in two layers: a finely sculptured, outer layer, about 2–4 μm thick; and a non-sculptured, inner layer, locally almost 20 μm thick. The sculptured, outer layer extends the entire length of the theca and exhibits transverse and longitudinal corrugation, expressed externally as low ridges. Line drawings of longitudinal cross-sections in Werner (1970) show the outer layer alternately thickening and thinning, respectively, at the crests and troughs of the transverse ridges. Although not explicitly stated, it is evidently the case that the exterior surface of the outer layer (i.e. the exterior surface of the theca) is defined by a single lamella, and that outer layer lamellae below the exterior one run parallel to it and, like it, extend the entire length of the theca.

In contrast to the outer, sculptured layer, the inner layer often pinches out a short distance below the aperture. Measurements made on one specimen (Chapman and Werner 1972), about 30 mm long, showed the inner layer narrowing from a thickness of almost 20 μm near the basal disc to a thickness of 2 μm at a distance of 100 μm from the aperture.

In some coronatids, the inner layer exhibits whorls of eight thorn-like structures that project into the thecal cavity and coincide with the polyp's principal planes of tetrameral symmetry (e.g. Werner 1971, fig. 1; Werner 1983, fig. 2). In all whorls, four of the projections are situated at the base of each of the four gastric septa, which lie in one of the two interradial symmetry planes. The other four projections are situated midway between the interradial ones, in one of the two perradial symmetry planes. The perradial projections are consistently larger (longer, wider, higher) than those at the interradia.

The two coronatid thecal layers also differ in the manner in which they are produced. The outer layer is secreted by gland cells in a collar-like zone of modified ectoderm, the junctional secretory band (Chapman and Werner 1972), that is situated at the polyp's oral end. Werner (1979, p. 85) reported that this structure exhibits 'a small transverse groove in which the soft body and rim [apertural margin] of the tubule are intimately connected'. The gland cells that secrete the outer layer are situated within this rim, and it is their activity that allows the thecal margin to keep pace with the lengthening soft body. Given that lamellae forming the outer layer parallel the exterior surface of the theca and extend its entire length, this implies that the outer layer grows by extension of existing lamellae at the apertural margin.

Production of the inner layer is mediated by gland cells in the side of the calyx, below the junctional secretory band. The inner layer grows by centripetal accretion of whole lamellae. Like production of outer layer lamellae, production of inner layer lamellae occurs throughout ontogeny, resulting in sequential addition of whorls of internal thecal projections (with the basalmost whorl added first and more adorally situated whorls added later).

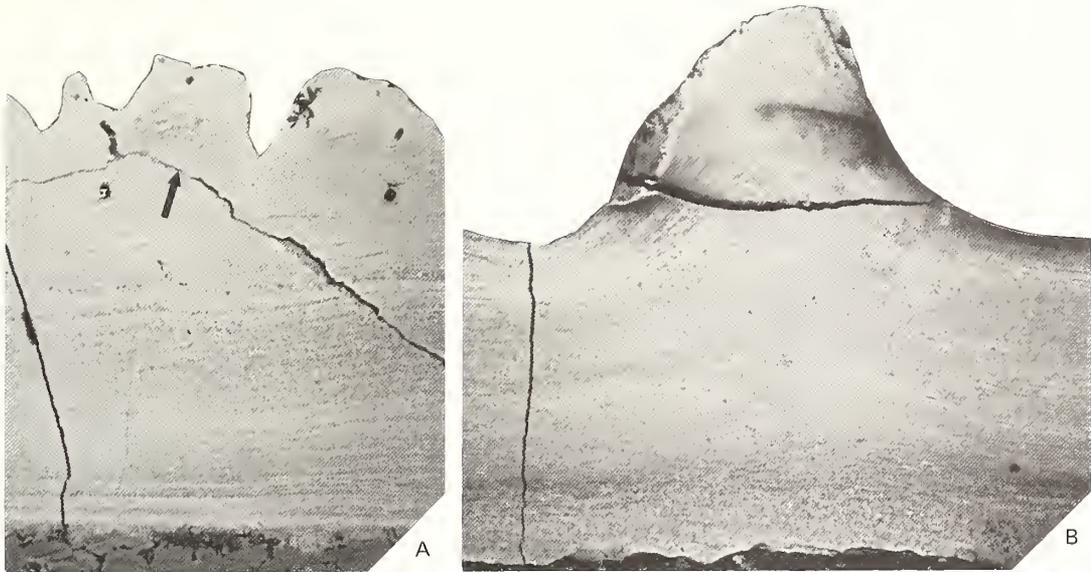
Especially near the aperture, where the inner layer is absent or extremely thin, the theca is highly flexible. Polyps whose theca has been punctured or severed often repair such damage by depositing a thin patch of inner layer lamellae on the inner surface of the theca.

MICROSTRUCTURE OF THE CONULARIID TEST

Observations

Conulariid tests here examined are built of numerous, extremely thin lamellae, alternately dense and vacuity-bearing, that parallel or are concordant with the surface of the test (Pl. 1; Text-figs 1–2). SEM and X-ray diffraction analysis indicate that the lamellae are composed of cryptocrystalline,

carbonate apatite. To determine if an organic component is present, test fragments were dissolved in 5 per cent hydrochloric acid (see Bischoff 1989); however, no such component (which presumably was present in living conulariids) was recovered. None of the specimens examined here preserved the apex or apertural margin, and thus the number and organization of test lamellae at these sites could not be determined.



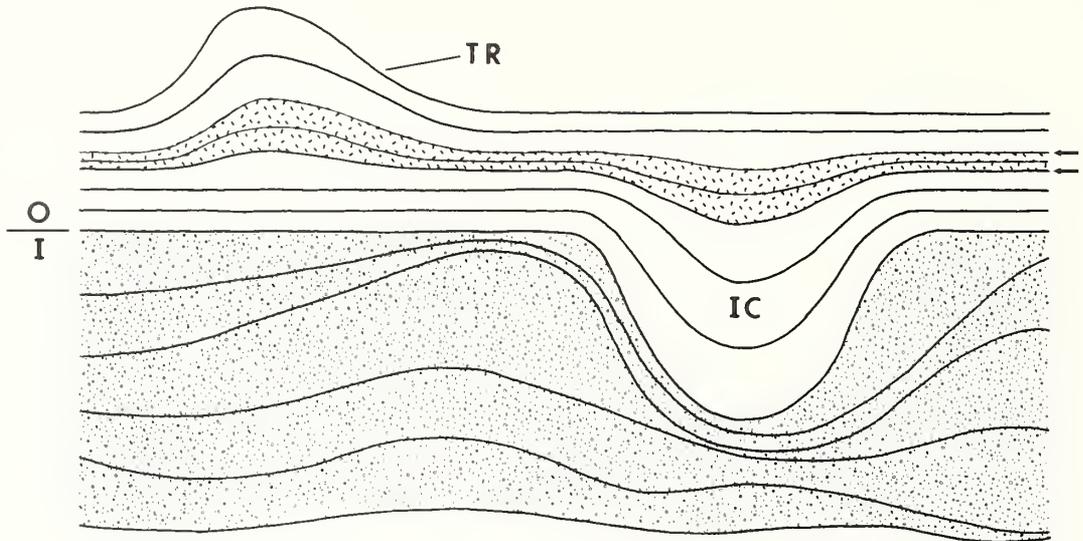
TEXT-FIG. 1. Scanning electron micrographs (backscattered electron mode) of longitudinal sections through conulariid taxa. UMMP 60000. A, *Conularina triangulata* (Raymond); Middle Ordovician, Quebec; note thickening of test lamellae (arrow) in a transverse rib, $\times 420$. B, *Metaconularia* sp.; Middle Ordovician, Galena Group; Illinois, USA; note thickening of lamellae and reduced distinctness of lamellar boundaries in the tubercle, $\times 340$.

Transverse ribs, tubercles and internal carinae, here collectively referred to as test thickenings, represent sites of gradual, symmetrical thickening of individual lamellae (Pl. 1, figs 4–5; Text-fig. 1; see also Van Iten 1991a, fig. 4). Between these sites, lamellae tend to exhibit a uniform thickness of approximately $0.5\text{--}0.7\ \mu\text{m}$ (Pl. 1, fig. 2). Inspection of test thickenings at relatively high magnifications ($> 1000\times$) suggested that lamellae undergoing gradual expansion also split to form additional lamellae.

In some species of *Conularia* and *Paraconularia*, the lamellar fabric is substantially more distinct within the interspaces than within the transverse ribs (Pl. 1, fig. 5). This is due to vacuity-bearing lamellae becoming denser as they pass through the ribs. The same phenomenon was detected in tubercles of *Metaconularia* (Text-fig. 1B), but not in internal carinae.

Relatively thick tests were observed to exhibit two layers, apparently equivalent to the outer (ornamentary) and inner (basal) layers of previous authors (Text-fig. 2). These two layers are particularly distinct in specimens of *Paraconularia crustula* (White), a common species in Pennsylvanian grey shales of the midcontinental United States. As shown schematically in Text-figure 2, the outer layer consists of lamellae that parallel or are in close concordance with the outer or inner surface of the layer, and that participate in the formation of transverse ribs and internal carinae, through gradual, more or less symmetrical thickening. Lamellae participating in the formation of transverse ribs may show reduced distinctness at these sites. Also, whereas lamellae near the outer surface of the layer participate only in the formation of ribs, and those near the inner

surface only in the formation of carinae, lamellae in the central part of the layer may participate in the formation of both types of structures. In contrast to the outer layer, the inner layer consists of lamellae that do not participate in the formation of ribs or carinae, and that often describe irregular, strongly undulatory topographies that are distinctly out of phase with lamellae in the outer layer.



TEXT-FIG. 2. Schematic diagram of part of a transverse section through *Paraconularia crustula* (White). The section passes through a transverse rib (TR) and an internal carina (IC) at a midline. Shown in the diagram are selected lamellar boundaries in a specimen exhibiting highly distinct outer (O) and inner (I) layers. Lamellae in the central part of the outer layer (stippled region marked by arrows) often participate in formation of both ribs and carinae. Diagram based on tracing of individual lamellae in SEM photomicrographs of polished sections through several different specimens. Scale bar = 1 mm.

Discussion

These observations are generally consistent with traditional descriptions of conulariid test microstructure (e.g. Bouček and Ulrich 1929), but they contradict more recent characterizations offered by Feldmann and Babcock (1986) and Babcock and Feldmann (1986a, 1986b). Feldmann and Babcock (1986, p. 469) proposed that conulariid tests consist of 'two separate components', termed integument and rods. Rods are described (Feldmann and Babcock 1986, p. 469) as 'solid, narrow, elongate structures covered by a somewhat flexible, thin, multilayered integument'. According to Feldmann and Babcock (1986 p. 469), '[it] is the rods that, when covered by integument, form the prominent ridges [transverse ribs] across each face of a conulariid'. These authors also proposed that the rods of some conulariids exhibit short projections, called spines, that are oriented perpendicular to the rods and extend into the interspaces (see Babcock and Feldmann 1986b, fig. 2.2).

This interpretation of conulariid test structure is based on the results of low magnification, reflected light and SEM imaging of test material that was not sectioned (Feldmann and Babcock 1986; Babcock and Feldmann 1986a, 1986b). SEM imaging of sectioned material, discussed above,

shows that features interpreted as rods and spines are actually parts of a single, continuously laminated structure. Even in cases where the core of the rib appears to be more or less solid (e.g. Pl. 1, fig. 5), and therefore superficially like a discrete rod, well-defined lamellae on either side of the core 'abut' against it (as opposed to wrapping around it, as implied by Feldmann and Babcock (1986)), and they can be traced through it. Features interpreted as spines arrayed along the rods (e.g. Feldmann and Babcock 1986, fig. 10) are simply crests of the low ridges associated with longitudinal corrugation of the interspaces.

HEALED CONULARIID INJURIES AND GROWTH ABNORMALITIES

Observations

Conulariids exhibiting healed injuries or growth abnormalities have recently been discussed by Werner (1966a, 1967), Babcock *et al.* (1987), Babcock (1988), and Mapes *et al.* (1989). Such features are here assigned to one of two categories. The first category consists of features that have been interpreted as areas of repaired test breakage sustained below the apertural margin, regarded by some authors (e.g. Bischoff 1978; Babcock *et al.* 1987) as a former growth margin. These features are schotts, discussed at length by Sinclair (1948) and Van Iten (1991b), and features analogized by Babcock *et al.* (1987) with embayed injuries (Alexander 1986) on fossil articulate brachiopods. In this paper, features analogized by Babcock *et al.* (1978) with embayed injuries on brachiopods will be referred to as patches.

As seen in external aspect, schotts and patches consist of a more or less circular area of smooth or concentrically rugose test that is surrounded by, and depressed below, rib- or tubercle-bearing test that has been broken (Text-fig. 3). Patches occur on the side of the test and are more or less planar (Text-fig. 3), while schotts cover the apical end and tend to be outwardly convex (e.g. Wilson 1951, pl. 19). Both features may exhibit a small, imperforate dimple or dimple-bearing protuberance, typically located at or near the centre of the area of non-ornamented test (Text-fig. 3). Inspection of sections through schotts (Van Iten 1991b) revealed that they are finely lamellar and extend along the inner surface of the faces proper, toward the aperture. The lamellae parallel the surfaces of the schott, and show no evidence of thickening or reduced distinctness at sites of transverse ribs or tubercles. This suggests that schotts consist of inner-layer lamellae, discussed above. Inspection of fracture surfaces on patches and adjacent test material suggested that patches are similar in microstructure to schotts, and that like schotts they extend for some distance along the inner surface of the faces proper.

Schotts or patches (or both) have previously been documented in *Anaconularia* (schotts; e.g. Barrande 1867), *Archaeoconularia* (schotts; e.g. Barrande 1867; Bouček 1928, 1939; Wilson 1951), *Conularia* (schotts and patches; e.g. Babcock and Feldmann 1986b; Babcock *et al.* 1987), *Paraconularia* (schotts and patches; e.g. Babcock and Feldmann 1986c; Babcock *et al.* 1987), and *Metaconularia* (schotts; Sinclair 1940; Wilson 1951). In this study, patches were observed on specimens of *Metaconularia* as well (e.g. SUI 53089).

The second category of growth abnormalities consists of features interpreted by Babcock *et al.* (1987) as test breakage structures analogous to scalloped and cleft injuries (Alexander 1986) on fossil articulate brachiopods. As described by Babcock *et al.* (1987, p. 99), scalloped injuries are characterized 'by the truncation of one or a few [transverse ribs]', in a manner resembling an angular unconformity (Babcock *et al.* 1987, fig. 7). In their opinion (Babcock *et al.* 1987, p. 99), scalloped injuries 'represent minor [test] damage' sustained along the apertural margin. Babcock *et al.* (1987, p. 99) interpreted cleft injuries as 'V-shaped incisions' into the test that 'have subsequently been closed by the secretion of [test material]'. In their opinion (Babcock *et al.* 1987), cleft injuries were not necessarily sustained along the apertural margin.

Both scalloped and cleft injuries consist of a subtriangular region of abnormally ornamented test that points toward the apex (Babcock *et al.* 1987, figs 7-8; Text-fig. 4 herein). Typically, the region of abnormal ornamentation straddles a midline and consists of one or more ribs or tubercle rows whose central part arches towards the apex, rather than towards the aperture. In cases involving two

or more ribs (or tubercle rows), the degree of departure from normal patterns of arching decreases towards the apertural end of the injury. The lateral margins of the area of abnormal ornamentation are abutted by normally arching ribs or tubercle rows. In addition, ribs or tubercle rows crossing the most apical parts of areas of cleft ornamentation are offset from normally arching ribs or tubercle rows abutting the cleft. Areas of cleft ornamentation differ from scalloped features in showing slight depression of the test surface below the level of laterally adjacent, normally ornamented test; the difference in elevation decreases toward the cleft's apertural end, where the cleft and normally ornamented test are coplanar. Importantly, examination of sections through cleft and scalloped features yielded no evidence of corresponding disruption of internal test microstructure. Test lamellae were observed to pass beneath these features without truncation, offset, or change in number or structure.

These observations suggest that the distinction between scalloped and cleft features is actually one of degree, rather than underlying cause or process. Thus, sites of scalloped ornamentation could be interpreted as responses to relatively minor episodes of injury or irritation, while clefts could be interpreted as responses to more severe episodes.

Cleft (scalloped) ornamentation has previously been documented on specimens of *Comularia* and *Paraconularia* (Babcock *et al.* 1987). In this study, clefts were observed on specimens of *Metaconularia* as well (e.g. Text-fig. 4B).

Interpretations

Schotts and patches. Features similar to conulariid schotts and patches are produced by members of several extant groups, including *Nautilus*, the gastropod *Caecum*, and coronatid scyphozoans (e.g. Chapman and Werner 1972; Bond and Saunders 1989). Members of these groups occasionally undergo perforation or severance of shell or thecal material, which damage is repaired by deposition of new material on the inner surface of the shell or theca. Conulariid schotts and patches probably originated in a similar fashion. Importantly, no case of repaired perforation or severance involving deposition of lamellae on the outer surface of conulariid tests has ever been found.

Cleft ornamentation. Areas of abnormal shell ornamentation similar to cleft ornamentation on conulariid tests have been observed on shells of fossil articulate brachiopods and fossil and living nautiloids (e.g. Alexander 1986; Bond and Saunders 1989). In *Nautilus*, such features are associated with repair of breaks sustained along the growth margin (Bond and Saunders 1989). As noted above, it has been proposed (Babcock *et al.* 1987) that areas of cleft (scalloped) ornamentation on

EXPLANATION OF PLATE I

Scanning electron micrographs of test microstructure in selected conulariids. Figures 1, 4–5 in backscattered electron mode. UMMP 60000.

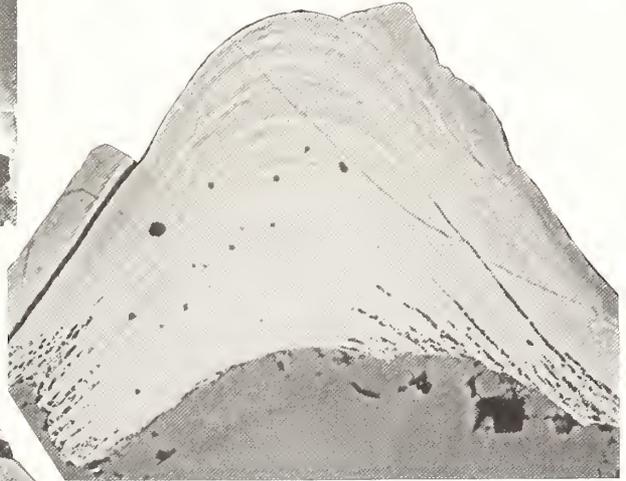
Fig. 1. *Conularia* sp. Middle Devonian, Cedar Valley Formation; Iowa, USA; longitudinal section through an interspace, showing alignment of alternately dense (light-coloured) and vacuity-bearing (dark-coloured) lamellae parallel to the outer surface of the test (outer surface facing top of page, aperture towards the right), $\times 270$.

Fig. 2. *Paraconularia crustula* (White). Pennsylvanian; Oklahoma, USA; detail of test lamellae exposed on a fracture surface within an interspace (outer surface of test towards the left), $\times 4000$.

Fig. 3. *Conularia splendida* Billings. Upper Ordovician, Maquoketa Formation; Iowa, USA; view of part of the exterior surface, showing several broken and exfoliated transverse ribs, interpreted by Feldmann and Babcock (1986) as sites of an internal rod distinct from the fine lamellae, $\times 50$.

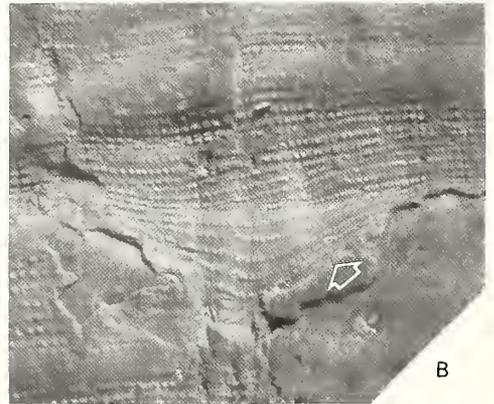
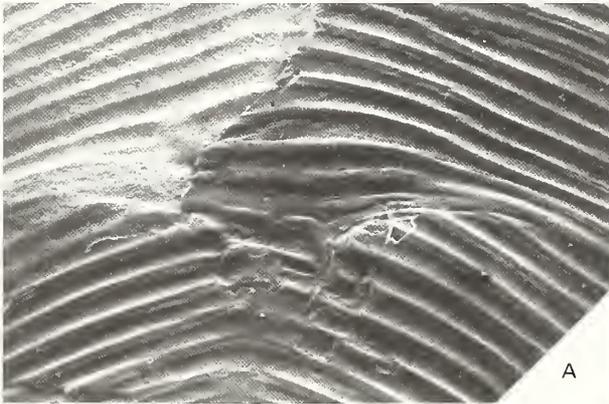
Fig. 4. *Paraconularia* sp. Mississippian; Illinois, USA; longitudinal section through a transverse rib, showing test lamellae passing through the core of the rib (aperture towards the right), $\times 220$.

Fig. 5. *Conularia* sp. Middle Devonian, Cedar Valley Formation; Iowa, USA; longitudinal section through a transverse rib characterized by reduced distinctness of the lamellar microfabric in the core of the rib (aperture towards the right), $\times 290$.





TEXT-FIG. 3. Scanning electron micrograph of a dimple-bearing patch on a face of *Conularia splendida* Billings; Upper Ordovician, Maquoketa Formation; Iowa, USA; SUI 512a, $\times 20.8$.



TEXT-FIG. 4. Examples of areas of cleft ornamentation on conulariid tests (arrows point to the right lateral cleft margin; photos oriented with the aperture towards the top of the page). A, scanning electron micrograph of cleft ornamentation straddling a midline of *Conularia splendida* Billings; Upper Ordovician, Maquoketa Formation; Iowa, USA; SUI 512b, $\times 25$. B, light micrograph of cleft ornamentation straddling a midline of *Metaconularia* sp.; Middle Ordovician, Galena Group; Iowa, USA; SUI 53089, $\times 5.6$.

conulariid tests represent sites of repaired test breakage. However, no microstructural evidence of repaired test breakage was observed in sections through these features. An alternative interpretation of cleft formation will be presented in the following section.

GROWTH AND RELATION TO SOFT TISSUES

Previous investigators (e.g. Bischoff 1978; Babcock *et al.* 1987) have proposed that growth of conulariid tests involved extension along the apertural margin and centripetal thickening. As noted above, comparisons with extant groups such as *Nautilus* and coronatid scyphozoans indicate that schotts and patches probably represent repair structures produced by soft tissues covering the inner surface of the test. The absence of these or similar features on the outer surface suggests that this surface was not covered by test-producing soft tissues, and thus that the conulariid test is an ectodermal derivative. Schotts (and, probably, patches) are similar in microstructure to the inner layer of relatively thick specimens lacking a schott, further suggesting that growth of the faces proper was at least partly mediated by soft tissues covering the inner surface. The structure and arrangement of lamellae within schotts (patches) and the inner layer indicate that these parts of the conulariid test most likely grew by centripetal accretion of whole lamellae.

The same process may also have formed the outer layer, which has been interpreted by some previous authors (e.g. Bischoff 1978) as a product of extension along the apertural margin. Except for the presence of ribs, tubercles and carinae, lamellae in the outer layer are similar to inner layer lamellae. Moreover, lamellae in the outer layer parallel or are in close concordance with the surfaces of the layer, and the outer layer shows no evidence of microstructural features that could be interpreted as growth lines inclined to the lamellae. To be sure, comparisons with extant groups suggest that areas of cleft ornamentation on conulariids reflect progressive healing of damaged or irritated soft tissues lining a former growth margin. However, the absence of corresponding disruption of internal test microstructure further suggests that the healed soft tissues were not involved in the formation of mineralized test material. How, then, could damage to such tissues be expressed as areas of cleft ornamentation on mineralized conulariid tests? One possibility, consistent with microstructural evidence presented here, is that conulariids possessed a set of weakly or non-mineralized lamellae, situated abaxially to the mineralized lamellae preserved in conulariid fossils and produced by soft tissues lining the apertural margin. Repair of breaks in non-mineralized lamellae or localized irritation of soft tissues that produced them might have led to formation of areas of cleft ornamentation, preserved in conulariid fossils by virtue of non-mineralized lamellae having been underplated by mineralized lamellae. Under this scenario, all of the lamellae in conulariid fossils, including both outer and inner layer lamellae, were accreted, whole, to the inner surface of the non-mineralized layer. Given that mineralized lamellae parallel or are concordant with the test surface, this implies that production of mineralized lamellae began late in ontogeny, after extensional growth along the apertural margin had ceased.

To summarize, the conulariid test is an ectodermal derivative produced by soft tissues covering its inner surface and, possibly, apertural margin. Production of mineralized lamellae involved centripetal accretion of whole lamellae. Although extension along the apertural margin is suggested by the occurrence of cleft ornamentation, such growth may have involved thecal material that was not mineralized.

AFFINITIES OF *METACONULARIA* AND *CONULARINA TRIANGULATA*

As noted above, Feldmann and Babcock (1986) and Babcock *et al.* (1987) proposed that *Metaconularia* and *Conularina triangulata* are not conulariids, based on purported differences in test microstructure. However, results of this study show that *Metaconularia* and *C. triangulata* are similar in microstructure (and, at least in the case of *Metaconularia*, injury repair) to genera regarded by Babcock *et al.* (1987) as conulariids. These taxa also display a number of uniquely shared gross anatomical similarities that further support their assignment to a single, monophyletic

group that excludes other organisms. These similarities include: (1) possession of transverse ribs (e.g. *Conularina triangulata*, *Conularia*) or tubercle rows (e.g. *Metaconularia*, *Pseudoconularia*) that generally arch towards the aperture on the faces (Sinclair 1940, 1942, 1948); (2) possession of sulcate corners (e.g. *Metaconularia*, *Conularina triangulata*, *Conularia*) that may be either non-thickened (e.g. *Metaconularia*, *Pseudoconularia*) or internally carinate (e.g. *Conularina triangulata*, *Climacoconus*, some species of *Conularia*) (Sinclair 1940, 1942, 1948; Van Iken 1991a, 1992); and (3) possession of a distinct facial midline associated internally with a pair of longitudinal carinae or thickenings, with members of each pair situated on opposite sides of the midline proper and diverging toward the aperture (e.g. *Metaconularia*, *Conularina triangulata*, certain *Climacoconus*; Van Iken 1991a, 1992).

COMPARISONS OF CONULARIIDS AND CORONATID SCYPHOZOANS

Together with results of previous studies (e.g. Werner 1966a, 1967; Bischoff 1978; Van Iken 1992), results of the present investigation confirm that the conulariid test and coronatid theca share detailed similarities in microstructure, gross anatomy, and mode(s) of growth and injury repair. These similarities can be summarized as follows:

1. theca constructed of numerous, extremely thin ($< 1 \mu\text{m}$) lamellae that parallel or are in close concordance with the surface of the theca and are alternately dense and vacuity-rich;
2. transverse and longitudinal corrugation of lamellae;
3. localized inflection of centripetally accreted lamellae to produce tetramerally arranged, seriated (coronatids and certain conulariids) or continuous (certain conulariids) internal projections or carinae (Bischoff 1978; Van Iken 1991a, 1992);
4. repair of perforation or severance involving deposition of non-ornamented lamellae on the inner surface of the theca;
5. growth involving centripetal accretion of whole lamellae and, possibly, extension of lamellae along the apertural margin.

As indicated by published discussions of other metazoan taxa (e.g. Jollie 1962; Barnes 1987), some of the similarities (similarities 3 and 5) outlined above are uniquely shared by conulariids and coronatid scyphozoans. The present study yielded no evidence of greater similarity between conulariids and tests or thecae of any non-scyphozoan group (e.g. tubiculous polychaete annelids, ascidians, pterobranchs, molluscs). Localized, finely lamellar internal swellings, similar to the pearl-like structures observed by Babcock (1990) in tests of *Paraconularia magna*, occur in the theca of the coronatid *Stephanoscyphus eumedusoides* Werner (see Werner 1974, fig. 4), and thus Babcock's (1991) suggestion that the occurrence of pearl-like structures in conulariids is inconsistent with a scyphozoan affinity for this group seems unwarranted. Although Werner's (1966a, 1967) suggestion that the outer (ornamentary) layer of fossil conulariids is directly homologous to the outer layer of the coronatid theca may be incorrect, the occurrence of cleft ornamentation on conulariid tests suggests that the theca of living conulariids consisted of two layers, similar in origin to the two layers of the coronatid theca.

To summarize, the hypothesis that the conulariid test is homologous to the theca of coronatid scyphozoans is based on detailed similarities in microstructure and mode(s) of growth and repair of injuries. Opponents of this hypothesis have yet to show that the conulariid test is more similar (and therefore more likely to be homologous) to the test or theca of any non-scyphozoan group. Although differences between conulariid tests and coronatid thecae in shape and degree of mineralization have been interpreted as evidence against homology of these structures (Termier and Termier 1949, 1953; Kozłowski 1968; Babcock 1991), the similarities discussed above suggest that these differences can reasonably be interpreted as reflecting descent with modification from a thecate common ancestor.

Acknowledgements. This paper is based on part of a Ph.D. dissertation written in the Museum of Paleontology, the University of Michigan, Ann Arbor. I thank the members of my dissertation committee, D. J. Eernisse, D. C. Fisher, K. C. Lohmann, G. R. Smith, and B. H. Wilkinson, for comments on earlier versions of the

manuscript. Comments by D. C. Fisher and G. R. Smith greatly improved the section on mode of growth. I thank T. Van Iten for printing the photographs, and B. E. Bodenbender for reading earlier versions. Permission to prepare museum specimens was granted by T. E. Bolton, D. C. Fisher, J. Golden, and R. Titus. This study was supported by funding from the Department of Geological Sciences and the Horace H. Rackham School of Graduate Studies at the University of Michigan, Sigma Xi, NSF Research Grant BNS-8521097 to D. C. Fisher, and R. J. and H. B. Van Iten. The scanning electron microscope used in this study was acquired under Grant no. BSR-83-14092 from the National Science Foundation.

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HEYO VAN IJEN

Museum of Palontology
University of Michigan
Ann Arbor, MI 48109, USA

Present address:

Department of Geology
Gustavus Adolphus College
Saint Peter, Minnesota 56082, USA

FIRST FOSSIL FLYING LEMUR: A DERMOPTERAN FROM THE LATE EOCENE OF THAILAND

by S. DUCROCQ, E. BUFFETAUT, H. BUFFETAUT-TONG, J.-J. JAEGER,
Y. JONGKANJANASOONTORN *and* V. SUTEETHORN

ABSTRACT. The first unequivocal fossil dermopteran (flying lemur) is reported here. It comes from the Tertiary Basin (Upper Eocene) of Krabi, Thailand, and appears to be close to the ancestor of the extant forms. Other supposed dermopterans reported previously from North America cannot be referred to this Order.

THE Order Dermoptera Illiger, 1811 is characterized among the mammals by a number of peculiar morphological characters associated with gliding adaptations and by the comb-like lower incisors. The phylogenetic position of the Dermoptera is still obscure, although this order is often classified close to the Primates (Sarich and Cronin 1980). Extant dermopterans have a very restricted geographical range, living only in the forests of south-east Asia where they are represented by two species of the genus *Cynocephalus* Boddaert, 1768: *C. volans* and *C. variegatus* (Walker 1985). The fossil record that until now was attributed to the Order Dermoptera is limited, geographically restricted, and attributed to families distinct from that of the extant genus. Nine species, distributed among seven genera, characterize one extinct family, the Plagiomenidae from the early Palaeocene to the late Oligocene of North America, which has been referred to the Dermoptera (Matthew and Granger 1918; Simpson 1927, 1928, 1937; Rose 1973, 1975; Krishtalka and Setoguchi 1977; Bown and Rose 1979; McKenna 1990), together with one monogeneric family, the Placentidentidae, from the early Eocene of Western Europe (Russell *et al.* 1973, 1982). In other respects, it has been recently suggested that the Paromomyidae (plesiadapiforms) show cranial and postcranial synapomorphies with the extant South-East Asian genus (Beard 1990; Kay *et al.* 1990) but plesiadapiforms have teeth that are very different from extant dermopterans. We report here the discovery of the first fossil dermopteran from the Eocene of South-East Asia. This record represents the only absolutely unambiguous fossil record for the entire Order Dermoptera and for the extant Family Galeopithecidae; it also reinforces the hypothesis according to which plagiomenids and placentidentids can no longer be thought of as dermopterans.

SYSTEMATIC PALAEOONTOLOGY

Order DERMOPTERA Illiger, 1811

Family GALEOPITHECIDAE Gray, 1821

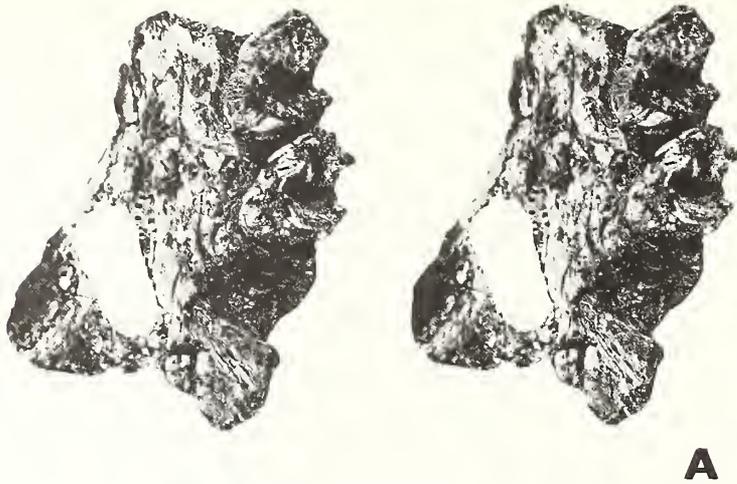
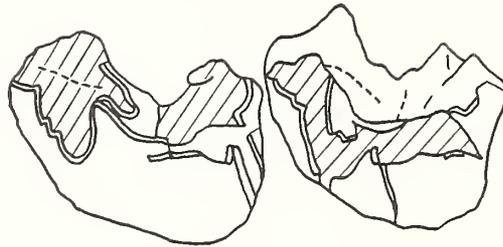
Dermotherium major gen. et sp. nov.

Holotype. A left lower jaw with M_2 and M_3 , No. TF 2580, Collections of the Palaeontological Section, DMR, Bangkok.

Type locality. Wai Lck lignite pit, Changwat Krabi, southern Thailand (latitude, about 8° N; longitude, about 99° E).

Horizon. Main lignite seam of the Krabi Tertiary Basin. Upper Eocene (see Ducrocq *et al.* in press for discussion about the age).

Diagnosis. Resembles the extant genus *Cynocephalus* by its triangular lower molars with the trigonid

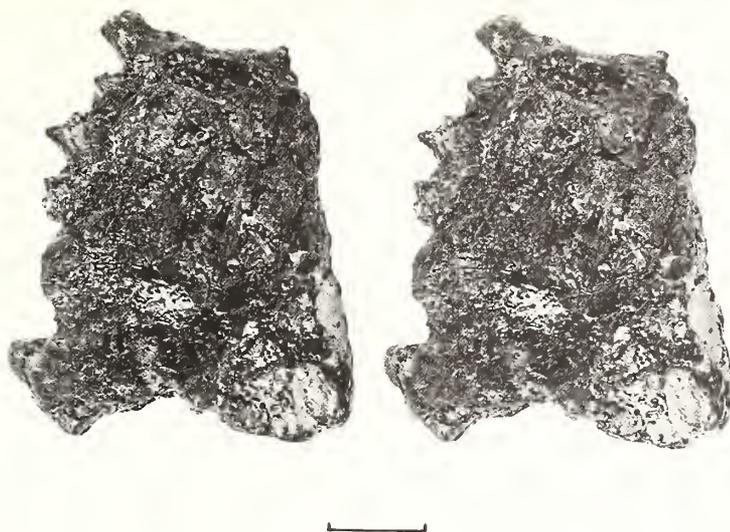
**A****B**

TEXT-FIG. 1. *Dermotherium major* gen. et sp. nov. TF 2580; Upper Eocene of Wai Lek, Thailand; left lower jaw with M_2 - M_3 . A, occlusal view, stereo pair. B, labial view, interpretative drawing. Scale bar, 5 mm.

much narrower than the talonid and compressed antero-posteriorly, its unreduced M_3 with respect to M_2 , its V-shaped and labially salient hypoconid, the presence of a paraconid lingually situated and rather high on the crown, its hypoconulid lingually displaced and close to the entoconid, its rather deep talonid basin, its retro-molar space behind M_3 , its angular area of the jaw strong and ventrally inflated and by its coronoid crest anteriorly directed. It differs from *Cynocephalus* by its larger size, the divergent apices of the anterior trigonid cusps, the presence of the anterior part of the postprotocristid, the shallow talonid basin, the entoconid of the same size of the hypoconulid and by its wrinkled enamel. It is closer to *C. variegatus* by its angular hypoconid with the anterior arm joining the middle of the posterior wall of the protoconid, and by its rather strong paraconid. It differs from *C. volans* by the shape of the hypoconid, the less canted distal wall of its metaconid, and by its entoconid mesial to the hypoconid.

Measurements (in mm): M_2 : Length = 5.45; width = 4.90. M_3 : Length = 5.45; width = 4.65.

Description. The material consists of a partial left lower jaw including parts of the horizontal and vertical rami



TEXT-FIG. 2. *Dermotherium major* gen. et sp. nov. TF 2580; lingual view, stereo pair. Scale bar, 5 mm.

with M_2 – M_3 (Text-figs 1–2). As in *Cynocephalus*, the horizontal ramus enlarges strongly just behind M_3 . In lateral view, the horizontal ramus describes a convex curve below M_2 and M_3 . The anterior border of the ascending ramus is almost vertical.

The third lower molar shows the general structure seen in the extant genus: it is slightly smaller than the second, and in both M_2 and M_3 the trigonid is reduced and the talonid strongly expanded such that the hypoconid occupies a very labial position. The hypoconid is V-shaped with two widely open arms whose anterior one, as in *C. variegatus*, joins the middle of the posterior wall of the protoconid. A paraconid is present, being low and rather lingually situated on the anterior edge of the trigonid: it is weaker in M_2 than M_3 contrary to the condition seen in *Cynocephalus* (Text-fig. 3). There is a lingual notch between the trigonid and the talonid which is deeper on M_2 than on M_3 .

M_3 is the best preserved tooth. Its crenulated enamel shows strong vertical ridges. The trigonid is narrow and the paraconid is reduced and lingually situated. The metaconid is higher than the protoconid and the apices of both cusps are divergent when they are not in both species of *Cynocephalus*. The distal wall of the metaconid is also a little more canted, as in *C. volans*. A protoconid is well differentiated, although short, and is directed towards the disto-lingual part of the tooth. The metaconid and the entoconid are laterally compressed. The talonid is greatly enlarged, with a very labially situated and V-shaped hypoconid. The talonid basin is moderately deep, less than in the two extant species, and the talonid shows three well-differentiated cusps. A small enamel ridge is situated in the valley separating the metaconid from the entoconid; this structure is absent in the extant genus. The entoconid is the highest of the talonid cusps and occupies a more mesial position than the hypoconid, when it is more distal in *C. variegatus* and it is aligned with the hypoconid in *C. volans*. The hypoconulid occupies a lingual position very close to the entoconid on the postero-lingual part of the tooth, and is more robust than the entoconid. In both species of *Cynocephalus*, the entoconid is weaker than the hypoconulid. The entoconid and hypoconulid form a somewhat isolated unit towards the postero-lingual corner of the tooth, and are united by a rather high crest while these cusps are integrated in the crown and more distinct in *Dermotherium*. The hypoconulid also constitutes a small ridge on the postero-lingual wall of the molar although it is not expanded to form a salient posterior lobe as commonly seen among mammals.

The structure of M_2 is rather similar to that of the M_3 although slightly enlarged. Unfortunately, because of the bad preservation, only the entoconid can be clearly discerned on M_2 .

Several characters indicate that this jaw belongs to a dermopteran: the inflated angular region, the relative size of the lower molars, and the configuration of the molar cusps.

DISCUSSION

Previous reports of supposed Dermoptera

The Thai fossil shows affinities with both extant *Cynocephalus* and fossil taxa. There is some confusion about the fossil families and taxa included until now within the Order Dermoptera. For Rose and Simons (1977), this order should include only the families Plagiomenidae and Galeopithecidae, the former, known only from fossils, being the most appropriate known ancestors of the latter. Other authors, for example Carroll (1988), also included the ?Mixodectidae and the Placentidentidae within Dermoptera. This last family is represented by only one subfamily (Placentidentinae) and one species, *Placentidens lotus* Russell *et al.*, 1973, from the Lower Eocene of France. However, it is referred to the Plagiomenidae by Rose and Simons (1977) while Dawson *et al.* (1986) reject the assignment of *Placentidens* to the Order Dermoptera. According to Carroll (1988), the Mixodectidae should include the genera *Eudaemonema* Simpson, 1937 and *Mixodectes* Cope, 1883 from the Middle Palaeocene of North America. Gunnell (1989) does not accept the Mixodectidae within the Order Dermoptera. In his recent work, McKenna (1990) added three new genera (*Tarka* McKenna, 1990, *Tarkadectes* McKenna, 1990 and *Ekgmowechashala* Macdonald, 1963) to the family Plagiomenidae and proposed a new subfamily, Ekgmowechashalinae, for these forms. According to the same author, *Thylacaelurus* Russell, 1954 is not a dermopteran but a lipotyphlan insectivore.

On the basis of basicranial anatomy, MacPhee *et al.* (1989) concluded that plagiomenids were not related to dermopterans and relegated Plagiomenidae and Mixodectidae to Eutheria, *incertae sedis*.

Finally, Beard (1990) and Kay *et al.* (1990) argued for linking plesiadapiforms and Paramomyidae with dermopterans on the basis of postcranial and basicranial anatomy. All fossils previously described as dermopterans should not be placed in that Order (Beard, personal communication), since similarities in dental morphology have been convergently attained.

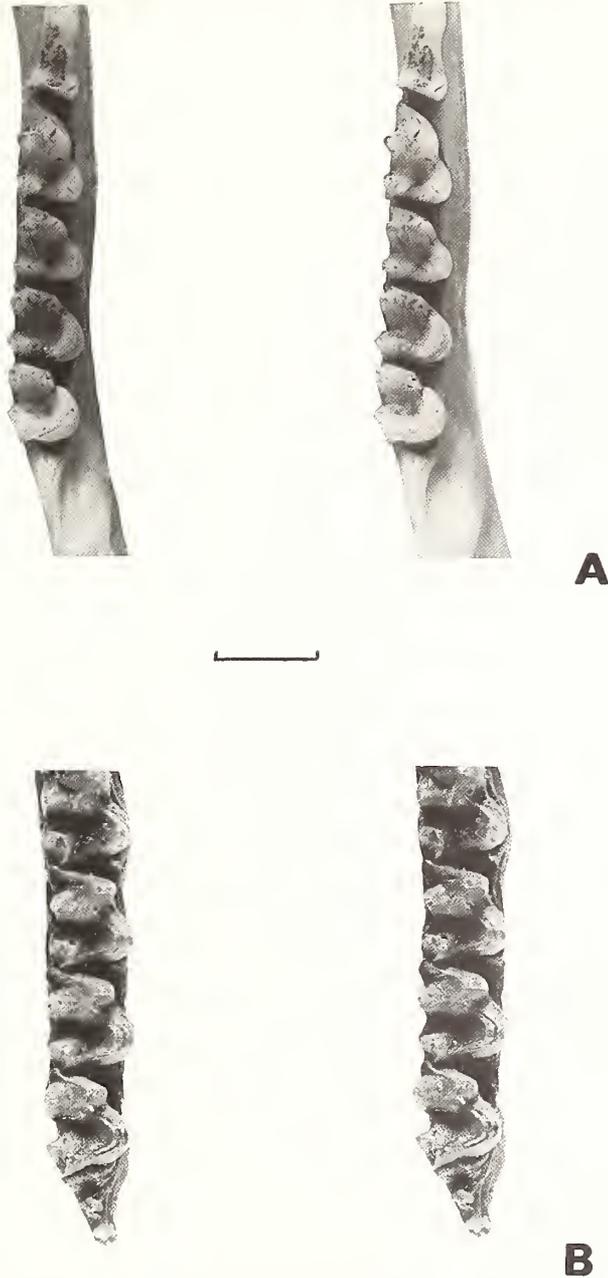
The status of the Asian dermopteran

All the North American fossils previously attributed to the Order Dermoptera, as well as the genus *Microsyops* from early to late Eocene of North America (Gunnell 1989) show a general structure rather different from that of *Dermotherium*. Indeed, they are distinguishable from the Thai fossil in several features: slightly reduced trigonid relative to the talonid, the presence of a hypoconulid which forms a third lobe on the M_3 , possession of a cingulid, and of a paraconid which is generally lost in the Subfamily Ekgmowechashalinae. A system of accessory cuspids also occurs in this latter group, the lingual cusps are distally located with respect to the labial cusps in *Placentidens*, and in this latter genus the trigonid is nearly as wide as the talonid on M_3 .

The M_3 morphology and structure of the Thai fossil is, in general, very different from that of the other fossil genera previously attributed to the dermopterans. *Dermotherium* exhibits the following autapomorphic characters: great size relative to that of the American and European fossil genera, the presence of a labial portion of the protocristid which issues from the protoconid at mid-height and runs disto-lingually towards the talonid basin, lingual cusps laterally compressed, divergent apices of the anterior cusps, and marked antero-posterior compression of the trigonid relative to the talonid.

The Thai fossil shares with extant *Cynocephalus* a triangular outline of the lower molars (M_2 and M_3) which contrasts with the quadrangular lower molars of all other fossils (due to the enlargement of the talonid and the bucco-lingual narrowing of the trigonid). Additional similarities include the presence of a retro-molar behind M_3 , the inflated lower part of the jaw, an anteriorly directed coronoid ridge, absence of a hypoconulid lobe, cingulid and of an entoconulid, a lingually displaced hypoconulid, and a transversely and antero-posteriorly compressed trigonid.

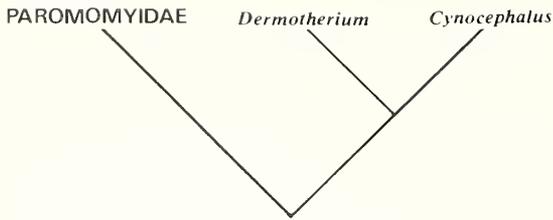
Following the hypotheses of Beard (1990) and Kay *et al.* (1990), we have compared the Thai fossil with the genera of the Family Paramomyidae from North America and Europe (Szalay and Delson 1979). In fact, all these forms are dentally very different from *Dermotherium* in possessing a trigonid as wide as the talonid, a centrally situated hypoconulid, a reduced and elongated M_3 with a



TEXT-FIG. 3. Comparison of right lower dentitions of A, *Cynocephalus volans* and B, *Cynocephalus variegatus*, stereo pairs. Scale bar, 5 mm.

hypoconulid lobe, and in being much smaller in size. If the suppositions of these authors are correct, the Paromomyidae should be a lateral branch of Dermoptera that evolved independently in North America while the Galeopithecidae were evolving in Asia.

It is therefore possible to extend the cladogram published by Beard (1990) by adding the Asian



TEXT-FIG. 4. Cladogram illustrating phylogenetic position of *Dermotherium major* (modified after Beard 1990).

fossil: *D. major* plus the extant genus *Cynocephalus* thus become the sister-group of the Paromomyidae (Text-fig. 4).

Dermotherium is characterized by several peculiar characters which bring it close to *Cynocephalus*:

- trigonid narrower than the talonid and antero-posteriorly compressed;
- disto-lingually displaced entoconid and hypoconulid;
- rather strong and labially salient hypoconid;
- inflated part of the lower jaw behind M_3 ;
- the presence of a rather strong lingually situated paraconid;
- the well-marked retro-molar space;
- the absence of an ectocingulid;
- the presence of a well-marked labial notch between the trigonid and the talonid;
- and the absence of a posterior lobe on the talonid of the M_3 .

These characters, associated with the unreduced M_3 relative to M_2 , suggest that *Cynocephalus* could have had its origin in the form described here.

A comparison with both extant species reveals that *Dermotherium* shows more resemblance to *C. variegatus* (the larger species) because of its size, its angular hypoconid with the anterior arm joining the middle of the posterior wall of the protoconid, and its rather strong paraconid. However, the Thai fossil differs from *C. variegatus* in having an entoconid slightly distally located with respect to the hypoconid. *C. volans* differs from *Dermotherium* in its smaller size, more rounded hypoconid with the anterior arm joining the labial wall of the protoconid, an entoconid that is at the same level as the hypoconid, and by the more canted distal wall of the metaconid.

CONCLUSIONS

Dermotherium major was found associated with a fauna that has been dated as Upper Eocene (Ducrocq *et al.* in press); it is therefore a form that has certainly changed very little over a period of at least 34 million years. This fossil is morphologically very close to the extant genus, and perhaps related to the ancestor of *Cynocephalus*, although our current limited knowledge of *Dermotherium* prevents further precision. Since the Thai fossil is rather different from plagiomenids and placentidentids, the few resemblances that exist between the two families and *D. major* can reasonably be attributed to convergent evolution. The discovery of the Asian fossil is therefore a serious argument for the removal of both Plagiomenidae and Placentidentidae from the Order Dermoptera.

Acknowledgements. We are grateful to Drs K. C. Beard, M. Godinot and J. J. Hooker for their constructive remarks, and Dr M. Tranier for access to recent material. We also thank Drs M. J. Benton, K. C. Beard and K. D. Rose for reviewing our manuscript. This work has been supported by a grant from the 'Mission Paléontologique Française en Thaïlande' of the French Ministry of Foreign Affairs.

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S. DUCROCQ

J.-J. JAEGER

Laboratoire de Paléontologie

USTL

Institut des Sciences de l'Évolution

(URA 327 CNRS)

Place Eugène Bataillon

F-34095 Montpellier cédex 5, France

E. BUFFETAUT

H. BUFFETAUT-TONG

Laboratoire de Paléontologie des Vertébrés

URA 720 CNRS

Université Paris VI, 4 Place Jussieu

F-75252 Paris cédex 05, France

R. HELMCKE-INGAVAT

Y. JONGKANJANASOONTORN

V. SUTEETHORN

Geological Survey Division

Paleontological Section

Department of Mineral Resources, Rama VI Road

Bangkok 10400, Thailand

Typescript received 29 October 1990

Revised typescript received 26 April 1991

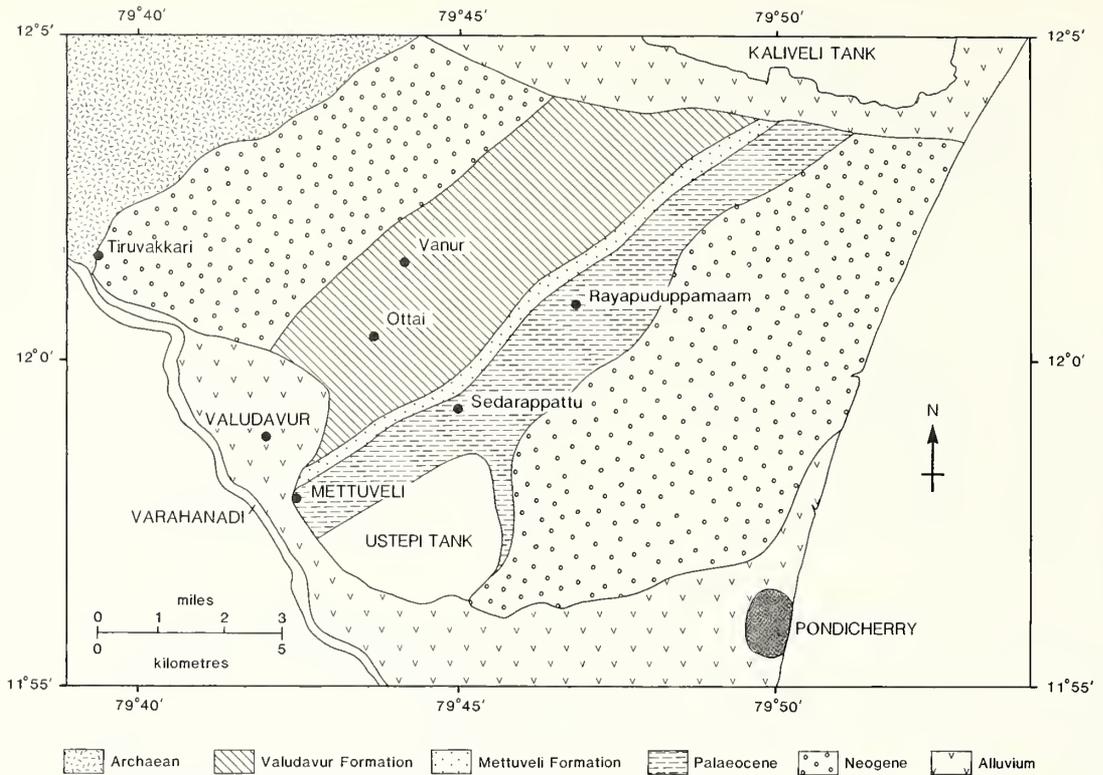
NON-HETEROMORPH AMMONITES FROM THE UPPER MAASTRICHTIAN OF PONDICHERRY, SOUTH INDIA

by W. J. KENNEDY and R. A. HENDERSON

ABSTRACT. The Phylloceratina, Lytoceratina and Ammonitina of the upper Valudavur Formation (Valudavur Group or *Anisoceras* Beds of authors) collected near Pondicherry, south India, are revised on the basis of the collections of the Natural History Museum, London, notably those described by Forbes (1846). Twenty species, referred to thirteen genera, are recognized. The fauna is considered to come from equivalents of a part of the lower Upper Maastrichtian *Belemnitella junior* belemnite Zone of the north-west European sequence, and the lower part of the *Abathomphalus mayaroensis* planktonic foraminiferal Zone. It represents the most diverse Upper Maastrichtian ammonite assemblage known.

EDWARD FORBES'S *Report on the Fossil Invertebrates from Southern India, collected by Mr. Kaye and Mr. Cunliffe* (1846) provided the earliest extensive account of the rich Cretaceous faunas of the subcontinent. The bulk of the material, including thirty-four named species of ammonite, are from what became known as the Valudavur beds or Group, which crop out near Pondicherry (Text-fig. 1). Forbes regarded these rocks as of early Cretaceous age, but d'Orbigny (1850) assigned them to the late Cretaceous, a view that has been generally accepted by subsequent workers. Its precise age based on the ammonites, has been taken as Campanian by many workers, although some have referred it to the Maastrichtian. Micropalaeontological work (e.g. Govidan 1972) shows the beds yielding the Pondicherry ammonites described by Forbes to be high in the Maastrichtian, regardless of how the base of that stage is defined. Increasing knowledge of Maastrichtian ammonite faunas supports this conclusion. The assemblage is of considerable importance for both historical and taxonomic reasons, for it includes the type species of ten genera or subgenera, many of which have cosmopolitan distributions. In all some thirty-two species referred to twenty-four genera or subgenera are recognized from a limited biostratigraphic interval, so that the assemblage is the most diverse Upper Maastrichtian one described to date, exceeding that of the upper part of the Miria Formation of western Australia (Henderson and McNamara 1985, plus unpublished data on heteromorphs), where twenty-six species referred to eighteen genera are known.

The history of the discovery and subsequent debate on the Pondicherry Cretaceous (Text-fig. 1) was reviewed by Blanford (1865). The earliest documented collections were made by Fontannier at an unspecified date, and by Chevalier in 1836 and 1837, who visited the area during the expedition of the French exploratory vessel *La Bonite*, but these were not recorded until 1844. The first published report was by C. T. Kaye of the Madras Civil Service in 1840: 'The existence of a bed of fossiliferous limestone in the neighbourhood of Pondicherry has long been pretty generally known to those who take an interest in such subjects, and some attention was recently attracted to it by several communications in the *Spectator* Newspaper. An observant person, indeed, can hardly fail on being struck with the nature of the stones, which form the paving of some of the streets and steps of many of the houses in Pondicherry, and which are replete, not only with the fragments of innumerable shells, but with many ostreas and other bivalves almost as entire as if they still reposed in their proper element' (Kaye 1840, p. 37). Kaye thereafter describes a short visit, in the company of C. E. Cunliffe, to the source of these paving slabs, at Seedrapett, seven miles (11.5 km) west of Pondicherry (Text-fig. 1), where the stone yielding fossils is described as occurring in large blocks, both on the surface, and immediately below the turf. Kaye figured a baculitid (1840, pl. 1, figs 3-4)



TEXT-FIG. 1. Geological sketch map of the Pondicherry district (modified after Rajagoplan 1964).

and a diplomoceratid (1840, pl. 2, fig. 11) from this locality, together with other elements of the fauna.

Kaye's paper was republished (without the plates), in the *Calcutta Journal of Natural History* (1842a), together with a series of additional notes and comments by Cunliffe (1842), Kaye (1842b), M'Clelland (1842) and Campbell (1842). More accessible is the note by Kaye (1846), where the Cretaceous rocks of Pondicherry, Verdachellum and Trichinopoly were described. Both Kaye and Cunliffe presented their collections to the Geological Society of London; the fish were subsequently described by Egerton (1845, 1846) and the invertebrates by Forbes (1846). His observations on the age of the Pondicherry Cretaceous merit full quotation, as they initiated a century of debate. Forbes (1846, p. 166) noted the remarkable Tertiary aspect of the bivalves, but concluded that rather than indicating such a date, they reflected their earliest appearance, or greatest development in eastern seas. He instead took the ammonites to be the key to the age of the fauna: 'The Pondicherry deposit may be regarded as belonging to the lowest division of the cretaceous system. In it almost all the fossils are new. Such as are analogous to known species are allied to fossils of the lower greensand of English geologists, and Neocomien of the French. In the genus most developed in this deposit, viz. *Ammonites*, three-fourths of the species belong to sections especially characteristic of the "Lower Neocomian" of the Mediterranean basin, whilst of the remainder as many representatives of oolitic fossils occur as of upper greensand species. The resemblance between many of the Pondicherry *Ammonites* and those of Castellane in the south of France is very remarkable' (Forbes 1846, p. 168).

D'Orbigny (1847a) commented on the age of material before him, as well as that described by Forbes, and concluded that it was Turonian in age (p. 507).

The specimens collected from Pondicherry by Chevalier in 1836 and 1837 were illustrated by d'Orbigny (1847*b*; the plates are, however, dated 1846) in Dumont d'Urville (1846–54), without accompanying text. A number of fragments of 'Hamites' were illustrated, most or all of which are synonyms of Forbes's species (d'Orbigny 1850; Kennedy and Henderson in press), together with a spectacular reconstruction of a baculitid, *Baculites ornatus* d'Orbigny, 1847*b*, a synonym of *B. vagina* Forbes, 1846. Three years later, in the *Prodrome*, d'Orbigny placed the Pondicherry ammonites in his Sénonien (1850, pp. 211–216).

Kaye died, at the age of 35, in 1846 (see obituary notice in the *Quarterly Journal of the Geological Society*, 3, 1847, p. xxvi). But collecting continued in the area, and Blanford (1865, p. 7) noted that 'in 1854, Mr. Brooke Cunliffe had, by means of his trained native collectors, obtained a large series of fossils from a hitherto unexplored locality between the original Trichinopoly and Vendechellum fossiliferous sites'. He also described the activities of a series of other collectors in the region. Blanford commenced fieldwork in the Pondicherry area in 1859, publishing his results in 1865, in an account of particular clarity (pp. 151–164). He relocated Kaye and Cunliffe's localities and recognized that the fossils occurred in 'great nodules or fragments of nodules', most of which were unfossiliferous; when fossils did occur, their numbers were vast.

Blanford was unable to obtain a single good ammonite, even though these are the most spectacular fossils in the Kaye and Cunliffe collection. 'I can only attribute my ill fortune to my having come into the field after the locality had been searched by many sharp-eyed collectors, of whose visits the rejected fragments scattered about furnish abundant evidence... In so limited an area the first come will naturally carry off the best prizes. I may notice, however, that the majority of the ammonites that I have seen from Pondicherry are evidently from the same or similar limestone nodules, and in only one or two instances have I been able to identify any as certainly from the overlying conglomerate bed' (Blanford 1865, p. 154). The last is a critical statement, for it indicates the Pondicherry fauna described below to be from a single stratigraphic interval ('a fossiliferous nodule band') and probably from a single locality or limited area near Sydrapet (Sudarampet).

Ammonites from Pondicherry were described by Stoliczka (1863–1866). In his concluding remarks (1866, p. 213), he followed Blanford in recognizing in ascending order, Ootatoor, Trichinopoly and Arrialoor groups in the Trichinopoly district, and Valudavur and Arrialoor groups in the Pondicherry district, taking the Ootatoor and Valudavur groups as one, lower division. Compared with the European succession, he believed the lower Cretaceous (Neocomian) to be absent in South India, with the lowest faunas present agreeing particularly well with the European Gault.

The possibility that the Pondicherry collections contained mixed faunas, and the need for better stratigraphic control, led Warth (1895) to re-examine the area in January and February 1894. He noted the limited outcrop (8 miles (13.2 km) long and 4 miles (6.6 km) wide) and poor exposure, but was able to subdivide the sequence, which he estimated to be some 900 feet (274 m) thick, consisting of predominantly clastic sediments with calcareous concretions:

Arrialoor group of Oldham (Horizons D–F)
Valudavur group of Oldham (Horizons A–C)

Horizon A consisted of white sands with nodules or concretions with burrows below, followed by yellow sands with gravel, and sandy clays with burrowed concretions. No body fossils were found. Horizon B included yellow and white sands with concretions and nodules, yielding body fossils, including baculitids and an ammonite. Horizon C was the source of the Kaye and Cunliffe collection, but Warth saw only concretions lying loose, or embedded in alluvium, and broke up all those he could find that were not incorporated into buildings. Horizon D was characterized as a bed of sandy shale, several feet thick, and full of casts of shells, with a few baculitids and ammonites; Warth noted that shells had been converted to phosphate, or were internal moulds in black phosphate, a preservation quite distinct from that of the Kaye and Cunliffe Collection. Horizon E was characterized by the abundance of nodules of shell limestone, generally lying loose. These

nodules had been used in building, and contained many corals, as well as a few phosphate nodules. Horizon F was characterized by calcareous nodules and burrows, a continuous limestone unit, and sands.

Warth concluded his report with a preliminary list of fossils, identified by Kossmat, in which nine ammonites are recorded from C, *Baculites vagina* and *Pachydiscus* sp. from D, and *Baculites vagina* from E. He stated that Kossmat considered the Pondicherry Cretaceous as belonging to the Ariyalur division, and that the Valudavur group of Blanford must be considered as Ariyalur only.

Kossmat's taxonomic revision of the ammonite fauna of the south India Cretaceous (1895-1898) remains the standard work on the subject. He reviewed the Pondicherry sequence (Kossmat 1897b), where he renamed Warth's divisions (see also Text-fig. 2):

C - Nerinea Beds = Horizon F of Warth

B - Trigonarca Beds = Horizons D and E of Warth

A - Valudavur Beds of Blanford (Anisoceras Beds) = Horizons B and C of Warth

Kossmat recognized twelve of Forbes's ammonite species as co-occurring in Warth's horizon C, and from a re-examination of Forbes's material, concluded that all came from this unit, as did most of the Pondicherry species described by Stoliczka (1863-1866). So far as we can determine, all the ammonites are from Warth's horizon C, the upper part of the Valudavur (*Anisoceras* beds) of Kossmat, and none is from the lower part, Warth's horizon B. Horizon D of Warth, the lower part of Kossmat's Trigonarca Beds, yielded *Pachydiscus gollevillensis* (Kossmat 1897a, pl. 6, fig. 1; 1898, p. 97 (162), pl. 15 (21), fig. 1) renamed *Pachydiscus compressus* Spath, 1922, and *Eubaculites vagina* (not illustrated). Horizon E of Warth yielded (or probably yielded) *Eubaculites vagina* (Kossmat 1897a, pl. 6, fig. 4), *Pseudophyllites indra* (Stoliczka 1865, pl. 58, fig. 2; Kossmat 1897b, p. 59), and

WARTH 1895	KOSSMAT 1897	RAJAGOPALAN 1965	GOVIDAN 1972
HORIZON E	TRIGONARCA BEDS	METTUVELI FORMATION	MAYAROENSIS SUBZONE
HORIZON D			
HORIZON C	VALUDAYUR (ANISOCERAS) BEDS	VALUDAVUR FORMATION	GANSSERI SUBZONE
HORIZON B			
HORIZON A			

TEXT-FIG. 2. Stratigraphic subdivisions of the Pondicherry Cretaceous (modified after Govidan 1972).

Brahmaites brahma. The identity of the *Baculites vagina* illustrated from horizon E is uncertain as it lacks the bituberculate flank ornament of that species, having rather feeble crescentic ribs. Kossmat (1895, pl. 19 (5), fig. 16a–c) figured a large baculite fragment from '1 mile NNW von Rautankupam', a locality placed, with a query, in division E of Warth. This specimen was referred to *Baculites vagina* var. *Otaodensis* Stoliczka by Kossmat, but it has a tabulate venter rather than a fastigiata one, and is *Eubaculites lyelli* (d'Orbigny 1847b) of authors (see Kennedy 1987a for synonymy) of which *carinatus* Morton (1834) is the senior synonymy.

Kossmat analysed in detail the relationship between the Cretaceous deposits of Pondicherry and those elsewhere in south India, and their age, concluding that the Valudavur (*Anisoceras*) and Trigonarca Beds were equivalent to 'the upper Senonian (Campanian, mucronata beds), and the Nerinea beds to the zone of *Nautilus danicus* (danian)' (1897b, p. 70).

A revised lithostratigraphy was published by Rajagoplan (1964, 1965, 1968) (Text-fig. 1), and there are additional palaeontological studies by Furon and Lemoine (1939), Sharma (1953), Rama Rao (1956, 1964), Gowda (1964) and Banerji (1968). The work of Rajagoplan (1968) and Govidan (1972) provided a micropalaeontological dating of the sequence (Text-fig. 2), which is discussed below.

THE AGE OF THE PONDICHERRY FAUNA

Kossmat (1895–1898, 1897b) confirmed beyond doubt the Senonian (late Cretaceous) age of the fossiliferous horizons C, D and E of Warth, and the Tertiary age of F. The precise position of the ammonite faunas has been less certain, and ages of Campanian, Campanian–Maastrichtian and Lower Maastrichtian appear in recent works. Before reviewing this question, the position of the Campanian/Maastrichtian boundary itself requires comment.

The Campanian–Maastrichtian boundary. Birkelund *et al.* (1984) listed six possible markers for the base of the Maastrichtian. As discussed elsewhere, these can be placed in relative sequence (Kennedy and Cobban in press).

- Extinction of *Quadrum trifidum* (nannofossil) (youngest)
- Appearance of *Pachydiscus* (*Pachydiscus*) *neubergicus* (ammonite)
- Appearance of *Hoploscaphites constrictus* (ammonite)
- Appearance of *Belemnella lanceolata lanceolata* (belemnite)
- Extinction of *Globotruncana calcarata* (foraminiferan)
- Appearance of *Globotruncana falsostuarti* (foraminiferan) (oldest)

The most widely accepted boundary for macrofossil workers is the first appearance of *B. lanceolata lanceolata* at the base of its eponymous zone, which we follow here.

There is no widely applicable ammonite zonation for the Maastrichtian; instead, belemnites provide the best macrofossil scale, although its use is limited to northern Europe and parts of the former USSR. It does, however, provide a standard for discussion (see Christensen 1975, 1979, 1988).

- | | | |
|---------------------|---|---------------------------------------|
| Upper Maastrichtian | } | <i>Belemnella casimirovensis</i> Zone |
| | | <i>Belemnella junior</i> Zone |
| Lower Maastrichtian | } | <i>Belemnella occidentalis</i> Zone |
| | | <i>Belemnella lanceolata</i> Zone |

We use Lower and Upper Maastrichtian in this sense here, but note that Schulz (1979) recognized a six-fold belemnite zonation for the Lower Maastrichtian.

It is important to recognize that the Campanian–Maastrichtian boundary based on planktonic foraminifera (e.g. Caron 1985) and nannofossils (e.g. Perch-Nielsen 1985) lies at a much lower level than that based on belemnites or ammonites. The top of the *Globotruncana calcarata* foraminiferal zone and base of the *B. lanceolata* belemnite zone do not correspond, as some recent syntheses show (e.g. Marks 1984; Kent and Gradstein 1985; Bolli *et al.* 1985; Haq *et al.* 1987, 1988). There is as yet no direct correlation between the belemnite and microfossil zonations of the Maastrichtian.

For discussion purposes, we use the following Upper Campanian and Maastrichtian planktonic foraminiferal zonation, after Caron (1985):

- Abathomphalus mayaroensis* Zone
- Gansserina gansseri* Zone
- Globotruncana aegyptiaca* Zone
- Globotruncatella havanensis* Zone
- Globotruncanita calcarata* Zone

As already noted, planktonic foraminiferal workers commonly place the Campanian–Maastrichtian boundary at the base of the *havanensis* Zone. The base of the Maastrichtian as used here (= base of *lanceolata* belemnite zone) is much higher, probably within the *aegyptiaca* Zone.

Age of the Pondicherry fauna. Direct evidence for the age of the Pondicherry ammonite fauna comes from the planktonic foraminifera, described by Govidan (1972, table 1), who recognized a *Globotruncana tricarinata* Zone below, succeeded by a *Globotruncana gagnebini* Zone above, the latter divided into subzones of *Globotruncana gansseri* (older), and *Abathomphalus mayaroensis* (younger). From his faunal lists, Govidan's subzones correspond to the top two zones of the Maastrichtian recognized by Caron (1985) and others. The precise relationship between Warth's horizon C, the source of the ammonites revised here, and Govidan's foraminiferal zonation is not known. Horizon C probably represents the lower part of the *mayaroensis* Zone and cannot be older than *gansseri* Zone (Text-fig. 2). The occurrence of *Gansserina gansseri*, *Heterohelix* cf. *navarroensis* and *Globotruncana* sp. in the matrix of a specimen of *Glyptoxoceras rugatum* (BMNH C51125) collected by Kaye and Cunliffe, determined in thin section by Dr M. D. Brasier (Oxford University), supports this conclusion. A late Maastrichtian age may confidently be ascribed to ammonites from horizon C but the fact that Warth's horizons D and E, referred to the Mettuveli Formation by Rajagoplan (1965), also contain a Cretaceous fauna indicates that a significant time interval separates horizon C from the Cretaceous–Tertiary boundary.

Evidence from the ammonite fauna. We list below our revised nomenclature for species described by Forbes (1846), indicating the original nomenclature in parentheses, and giving known age ranges outside the Pondicherry occurrences, where known.

- Phylloceras* (*Neophylloceras*) *nera* (Forbes, 1846) (*Ammonites Nera* Forbes, 1846, p. 106, pl. 8, fig. 7). Known only from Pondicherry.
- Phylloceras* (*Neophylloceras*) *surya* (Forbes, 1846) (*Ammonites Surya* Forbes, 1846, p. 106, pl. 7, fig. 10). Restricted to the Maastrichtian, extending to the top of the *junior* Zone in Denmark (Birkelund *in press*).
- Phylloceras* (*Neophylloceras*) *decepiens* (Kossmat, 1897a). Known only from Pondicherry.
- Phyllopachyceras Forbesianum* (d'Orbigny, 1850) (*Ammonites Rouyanus* Forbes, 1846, p. 108, pl. 8, fig. 6). Santonian (Madagascar: Collignon 1956, 1966) to high in the *mayorensis* Zone in the Biscay region (Ward 1988).
- Pseudophyllites indra* (Forbes, 1846) (*Ammonites Indra* Forbes, 1846, p. 105, pl. 11, fig. 7; *Ammonites Garuda* Forbes, 1846, p. 102, pl. 7, fig. 1). Upper Santonian/Lower Campanian (*vide* Kennedy and Klinger 1977a) to uppermost Maastrichtian/*mayaroensis* Zone in the Biscay region of France and Spain (Ward 1988).
- Saghalinites cala* (Forbes, 1846) (*Ammonites Cala* Forbes, 1846, p. 104, pl. 8, fig. 4). Maastrichtian, where reliably dated, extending into the upper part of the stage (Kennedy and Klinger 1977a).
- Anagaudryceras Valudavurense* (Kossmat, 1895) (*Ammonites Juilleti* d'Orbigny; Forbes 1846 p. 101, pl. 7, fig. 2). Known only from Pondicherry.
- Gaudryceras kayei* (Forbes, 1846) (*Ammonites Kayei* Forbes, 1846, p. 101, pl. 8, fig. 3). Santonian/Campanian (Kennedy and Klinger 1979) to high in the Maastrichtian in Western Australia (Henderson and McNamara 1985).
- Zelandites varuna* (Forbes, 1846) (*Ammonites Varuna* Forbes, 1846, p. 107, pl. 8, fig. 5). Restricted to the higher parts of the Maastrichtian and extending to the top of the stage on Seymour Island (Macellari 1986; see also Zinsmeister *et al.* 1989).

- Desmophyllites diphylloides* (Forbes, 1846) (*Ammonites diphylloides* Forbes, 1846, p. 105, pl. 8, fig. 8). Lower Santonian (Collignon 1961) to high in the Upper Maastrichtian (Western Australia: Henderson and McNamara 1985).
- Kitchinites pondicherryanus* (Kossmat, 1897). Only known from Pondicherry.
- Hauericeras rembda* (Forbes, 1846) (*Ammonites Rembda* Forbes, 1846, p. 111, pl. 7, fig. 3; *Ammonites Durga* Forbes, 1846, p. 104, pl. 7, fig. 11). Only known from south India.
- B. (Brahmaites) brahma* (Forbes, 1846) (*Ammonites Brahma* Forbes, 1846, p. 100, pl. 8, fig. 1). Upper Maastrichtian, *A. mayaroensis* Zone, based on unpublished occurrences in the Biscay region.
- B. (Anabralmaites) vishnu* (Forbes, 1846) (*Ammonites Vishnu* Forbes, 1846, p. 100, pl. 7, fig. 9). Upper Maastrichtian, on the basis of the occurrence in the 'Calcaires durs lithographiques à Stegasters, route de Gan à Rébenecq' (Basses-Pyrénées) (Seunes 1891, as *Puzosia haugi*; de Grossouvre 1894, as *Gaudryceras planorbiforme*), where it occurs with *Anapachydiscus fresvillensis* (Seunes, 1890a) and *Pachydiscus jacquoti* Seunes, 1890a, a species unknown earlier than the *junior* Zone in Europe (Kennedy 1986c) and extends into the *mayaroensis* Zone in the Biscay region (Ward 1988).
- Pachydiscus (Pachydiscus) neubergicus* (Hauer, 1858) (*Ammonites Chishma* Forbes, 1846, p. 103, pl. 9, fig. 2). Lower Lower Maastrichtian (Kennedy and Summesberger 1984, 1987), lower *lanceolata* belemnite Zone in Europe to low in the Upper Maastrichtian *junior* belemnite Zone (Birkelund 1979, in press). Subspecies *dissitus* extends into the high Maastrichtian in Western Australia (Henderson and McNamara 1985). In the Biscay region it is recorded as extending to the top of the *gansseri* Zone (Ward 1988) and it may extend into the *mayaroensis* Zone (Ward and Kennedy, unpublished).
- Pachydiscus (Pachydiscus) egertoni* (Forbes, 1846) (*Ammonites Egertoni* Forbes, 1846, p. 108, pl. 9, fig. 1; *Ammonites ganesa* Forbes, 1846, p. 103, pl. 7, fig. 8). Known with certainty only from Pondicherry.
- Pachydiscus (Pachydiscus) yama* (Forbes, 1846) (*Ammonites Yama* Forbes, 1846, p. 107, pl. 7, fig. 4). Known only from Pondicherry.
- Pachydiscus (Neodesmoceras) soma* (Forbes, 1846) (*Ammonites Soma* Forbes, 1846, p. 102, pl. 7, fig. 7). Known only from Pondicherry.
- Menuites menu* (Forbes, 1846) (*Ammonites Menu* Forbes, 1846 p. 111, pl. 10, fig. 1). Known only from south India.
- Sphenodiscus siva* (Forbes, 1846) (*Ammonites Siva* Forbes, 1846, p. 110, pl. 7, fig. 6). Known only from Pondicherry. Similar smooth *Sphenodiscus* range through much of the Maastrichtian; in Europe, the analogue, *S. binkhorsti* (Böhm, 1898) first appears in the upper part of the *junior* Zone (Kennedy 1987, p. 178) and ranges to the top of the *casimirovensis* Zone (Machalski and Wolaszczyk 1988).
- Glyptoxoceras rugatum* (Forbes, 1846) (*Hamites subcompressus* Forbes, 1846, p. 116, pl. 11, fig. 6; *Hamites rugatus* Forbes, 1846, p. 117, pl. 11, fig. 2; *Hamites nereis* Forbes, 1846, p. 117, pl. 10, fig. 7). Many doubtful records are based on fragments. Sound well-dated records are Upper Maastrichtian: *junior* Zone in the Maastricht area (Kennedy 1987); high *gansseri* and low *mayaroensis* Zone in the Biscay region (Ward 1988).
- Glyptoxoceras indicum* (Forbes, 1846) (*Hamites indicus* Forbes, 1846, p. 116 [pars], non pl. 11, fig. 4). Maastrichtian of California (Matsumoto 1959a), but imprecisely positioned within the stage.
- Glyptoxoceras tenuisulcatum* (Forbes, 1846) (*Hamites tenuisulcatus* Forbes, 1846, p. 116, pl. 10, fig. 8; pl. 11, fig. 3). A single fragment from Denmark comes from a section that spans the Lower/Upper Maastrichtian boundary (Birkelund in press).
- Glyptoxoceras largesulcatum* (Forbes, 1846) (*Hamites large-sulcatus* Forbes, 1846 p. 117, pl. 11, fig. 1). Known only from Pondicherry.
- Diplomoceras cylindraceum* (Defrance, 1816). The species ranges throughout the Maastrichtian where it is well dated (Kennedy 1987; Ward 1988), and may extend into the Upper Campanian (Matsumoto and Morozumi 1980; Matsumoto 1984; Matsumoto and Miyauchi 1984).
- Phylloptychoceras siphio* (Forbes, 1846) (*Ptychoceras siphio* Forbes, 1846, p. 118, pl. 11, fig. 5). In the Biscay region Ward (1988) shows the species spanning upper *gansseri* and lower *mayaroensis* Zones.
- '*Hamites*' *undulatus* Forbes, 1846 (p. 118, pl. 10, fig. 6). Known only from Pondicherry.
- Enbaculites vagina* (Forbes, 1846) (*Baculites vagina* Forbes, 1846, p. 114, pl. 10, fig. 4). Known only from south India.
- Fresvillia teres* (Forbes, 1846) (*Baculites teres* Forbes, 1846 p. 115, pl. 10, fig. 5). Maastrichtian of California (Matsumoto 1959b, p. 163), but imprecisely positioned within the stage.
- Hoploscaphites indicus* (Forbes, 1846) (*Ammonites? Indicus* Forbes, 1846, p. 114, pl. 8, fig. 9). Known only from Pondicherry.
- Indoscaphites cunliffei* (Forbes, 1846) (*Ammonites Cunliffei* Forbes, 1846, p. 109, pl. 8, fig. 2). In Tunisia,

Pervinquière (1907) described this species from Tebaga and Kalaat es Snam (localities discussed by him in 1903 (pp. 125–126) where it occurs in his unit 13 (1903, fig. 21), 30 m above the highest limestone beds with *Inoceramus* and *Bostrychoceras polyplacum*. Bellier *et al.* (1983) studied this interval at El Kef to the north; if the lithostratigraphic sequence is the same in the two areas, *I. cunliffei* is from the *gansseri* Zone.

Indoscaphites pavana (Forbes, 1846) (*Ammonites Pavana* Forbes, 1846, p. 110, pl. 7, fig. 5). This species occurs with *I. cunliffei* in Tunisia, and similar comments apply.

Discussion. Direct evidence indicates that the Pondicherry ammonite fauna collected by Kaye and Cunliffe comes from a limited horizon which has been variously designated: 'C' of Warth (1895); the upper part of the Valudavur beds of Blanford (1865); the *Anisoceras* beds of Kossmat, and the Valudavur Formation of Rajagoplan (1965, 1968). It probably belongs to the lower part of the *A. mayaroensis* planktonic foraminiferal Zone (Govidan 1972), which is supported by the direct evidence from thin sections described above. Indirect evidence based on comparative stratigraphic data from the Biscay region suggests a horizon either high in the *gansseri* Zone, or low in the *mayaroensis* Zone. Correlation with the belemnite sequence of northern Europe is more difficult, but a horizon somewhere in the lower Upper Maastrichtian *junior* Zone is suggested, based on the limited evidence for the last occurrence of *P. (P.) neubergicus* in Denmark. If correct, the Lower/Upper Maastrichtian boundary as used here (e.g. the *occidentalis/junior* Zone boundary) lies close to the base of the *A. mayaroensis* Zone.

As noted above, a few ammonites are known from division E of Warth (the upper part of the *Trigonarca* Beds of Kossmat) including probable *Eubaculites carinatus* (Morton, 1834). This species seems to have a long stratigraphic range. It first appears in Europe with a diverse ammonite fauna that can be indirectly correlated with the Lower Maastrichtian *sumensis* belemnite Zone of Schulz (1979), which is equivalent to the lower *occidentalis* Zone of general use. Its upper range in Europe extends into the *casimirovensis* belemnite Zone, as indicated by co-occurrence with *crassus* forms of *Hoploscaphites constrictus* (Sowerby, 1817) in southeastern France (Kennedy 1986a), in turn dated as *mayaroensis* Zone (Kennedy *et al.* 1986). This apparent anomaly can be explained by accepting an overlapping range for *E. vagina* and *E. carinatus*, the latter appearing before, and surviving *E. vagina*, with absence of *carinatus* from the beds with *E. vagina* in south India (although occurring above) being a local phenomenon only. An early origin for *E. carinatus* finds support not only in the Lower Maastrichtian in Europe, but also in its abundance in the Owl Creek Formation of Mississippi and Missouri in the USA (Stephenson 1955). This yields a rich nannoflora (Smith and Mancini 1982, 1983) that indicates the *Lithraphidites quadratus* nannofossil Zone, the base of which is within nannofossil zone CC25B of Perch-Neilsen (1985), known to be the age of the first occurrence of *E. carinatus* in Europe (Kennedy and Summesberger 1986).

SYSTEMATIC PALAEOLOGY

Repositories of specimens. The following abbreviations are used to indicate the repositories of specimens mentioned in the text: BMNH, Natural History Museum, London; GSC, Original catalogue numbers of specimens when in the Geological Society of London collections (Blake 1902); MNHP, Muséum National d'Histoire Naturelle, Paris.

Suture terminology. The system of Wedekind (1916) as reviewed by Kullman and Wiedmann (1970), is used here, with E = external lobe, L = lateral lobe, U = umbilical lobe, and I = internal lobe.

Dimensions. All dimensions are given in millimetres, with D = diameter, Wb = whorl breadth, Wh = whorl height, and U = umbilicus. Figures in parentheses refer to dimensions as a percentage of diameter.

- Order AMMONOIDEA Zittel, 1884, pp. 355, 392
 Suborder PHYLLOCERATINA Arkell, 1950, p. 355
 Superfamily PHYLLOCERATACEAE Zittel, 1884, p. 434
 Family PHYLLOCERATIDAE Zittel, 1884, p. 434
 Subfamily PHYLLOCERATINAE Zittel, 1884, p. 434
 Genus PHYLLOCERAS Suess, 1866, p. 76

Type species. *Ammonites heterophyllus* J. Sowerby, 1820, p. 119, pl. 226, by monotypy.

Subgenus NEOPHYLLOCERAS Shimizu, 1934, p. 61

[= *Paraphylloceras* Shimizu, 1935, p. 180 (*non* Salfeld, 1919); *Hyporbulites* Breistroffer, 1947;
Epiphyllloceras Collignon, 1956].

Type species. *Ammonites (Scaphites) ramosus* Meek, 1857, p. 45, by original designation.

Discussion. See Henderson and McNamara (1985, p. 38).

Phylloceras (Neophylloceras) nera (Forbes, 1846)

Plate 1, figs 10–12; Plate 15, figs 1–2; Text-fig. 3A

1846 *Ammonites Nera* Forbes, p. 106, pl. 8, fig. 7.

1850 *Ammonites Nera* Forbes; d'Orbigny, p. 213.

1895 *Ammonites Nera* Forbes sp.; Kossmat, p. 109 (13), pl. 16 (2), fig. 2.

non 1907 *Phylloceras nera* (Forbes); Paulcke, p. 3, pl. 14, fig. 5.

non 1921 *Phylloceras nera* (Forbes sp.) Spath, p. 40 (= *P. (N.) woodsi* Van Hoepen, 1921).

non 1926 *Phylloceras nera* (Forbes); Marshall, p. 134, pl. 19, fig. 4; pl. 26, figs 1–2; (= *P. (N.) marshalli* Shimizu, 1935).

non 1930 *Phylloceras Nera* Paulcke (*non* Forbes); Wetzel, p. 87 (= *Phylloceras (Hypophylloceras) inflatum* Stinnisbeck, 1986).

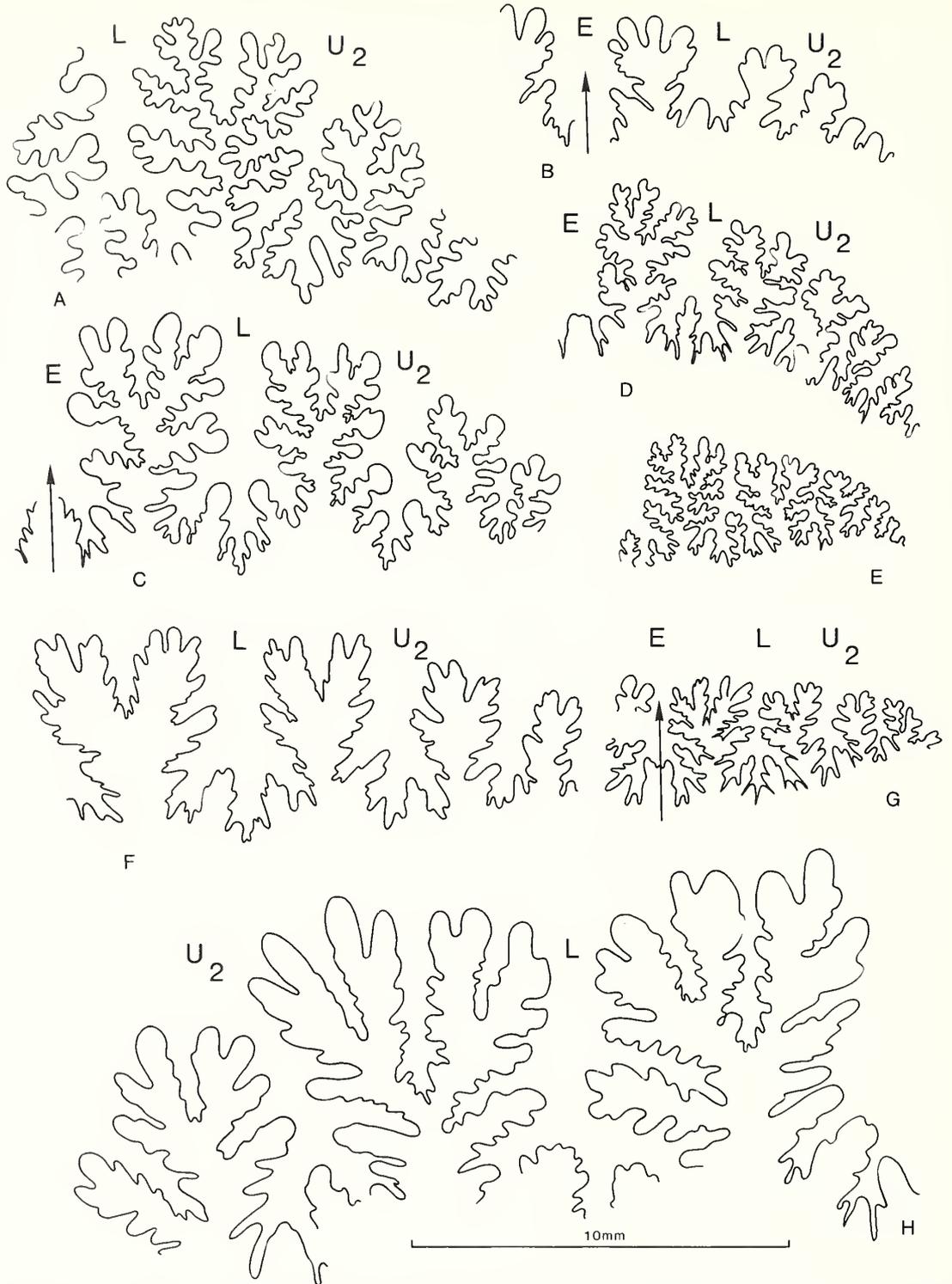
Type. Holotype, by monotypy, is BMNH C22681, the original of Forbes (1846, pl. 8, fig. 7) and Kossmat (1895 pl. 16 (2), fig. 2; GSC R10472, *ex* Kaye and Cunliffe Collection), from the Valudavur Formation, Pondicherry, south India.

Dimensions.

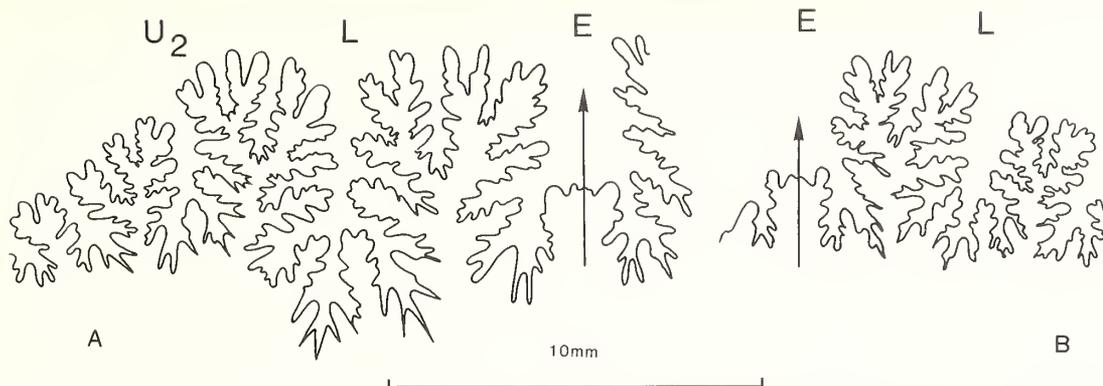
	D	Wb	Wh	Wb:Wh	U
BMNH C22681	19.0 (100)	6.0 (31.6)	10.5 (55.3)	0.57	1.8 (9.5)

Description. The holotype is a largely septate juvenile with, perhaps, the adapical part of the body chamber preserved. Coiling is very involute, with a small umbilicus ($U = 9.5\%$), the umbilical wall steep, passing into a narrowly rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.57, the flanks weakly convex, with maximum breadth below mid-flank, converging to a narrowly arched venter. Ornament is of evenly spaced regular lirae, separated by interspaces of similar width, numbering approximately 100 per half-whorl. They are feebly flexed; straight and retradiate on the inner flanks, swinging forwards on the mid-flank region but straightening and strengthening on the outer flanks, to pass near-straight across the venter. The inner flanks are, in addition, ornamented by broad undulations, four per half whorl, separated by faint, narrow grooves. Suture (Text-fig. 4A) finely divided and deeply incised from an early stage. L is trifold, and deeper than E. U has numerous auxiliary elements, which are arranged on a line that slopes backwards towards the umbilicus.

Discussion. Ribbing is asymmetric across the venter for all of the last whorl, showing the holotype to be malformed to a degree. The immaturity of the holotype, which remains the only specimen confidently assignable to the species, makes comparisons with other taxa difficult. It may be differentiated from the widely occurring *P. (N.) ramosum* (Meek, 1857) by its less flexuous, finer lirae, not projected on the venter (see Henderson 1970, p. 5, pl. 1, fig. 3; text-fig. 2 and Henderson and McNamara 1985, p. 40, pl. 1, figs 1–3; text-fig. 2), but these differences are slight, and larger collections may show the two to be synonyms. The Campanian *Phylloceras nera* of Paulcke (1907,



TEXT-FIG. 3. Sutures of A, *Phylloceras* (*Neophylloceras*) *nera* (Forbes, 1846), BMNH C22681. B, *Saghalinites cala* (Forbes, 1846), BMNH C51054. C, *Phyllopaocyeras forbesianum* (d'Orbigny, 1850), BMNH C51080. D, *Gaudryceras kayei* (Forbes, 1846), BMNH C51050. E, *Gaudryceras valudavurense* (Kossmat, 1895), BMNH C51064. F, *Desmophyllites diphylloides* (Forbes, 1846), BMNH C22682. G, *Pachydiscus* (*Neodesmoceras*) *soma* (Forbes, 1846), BMNH C51039. H, *Hauericeras remsda* (Forbes, 1846), BMNH C51023.



TEXT-FIG. 4. Sutures of A. *Kitchinites pondicherryanus* (Kossmat, 1987), BMNH C47548, B. *Pachydiscus (Pachydiscus) egertoni* (Forbes, 1846), BMNH C51045.

p. 3, pl. 14, fig. 5) is probably a *P. (N.) ramosum*. Maastrichtian material from Quiriquina Island, Chile, has been described as *Phylloceras (Hypophylloceras) inflatum* Stinnisbeck, 1986 (p. 192, pl. 7, figs 7–8; text-figs 16c, 17c).

Occurrence. As for type.

Phylloceras (Neophylloceras) surya (Forbes, 1846)

Plate 1, figs 1–7, 9, 13–14; Plate 15, figs 4–5

- 1846 *Ammonites Surya* Forbes, p. 106, pl. 7, fig. 10.
 1850 *Ammonites Surya* Forbes; d'Orbigny, p. 213.
 1865 *Ammonites Surya* Forbes; Stoliczka, p. 115, pl. 58, figs 5, 5a, 5b.
 1895 *Phylloceras Surya* Forbes sp.; Kossmat, p. 109 (13), pl. 16 (2), fig. 1.
 1895 *Phylloceras surya* Forbes; Steinmann, p. 79, pl. 5, fig. 1.
 1938 *Phylloceras* aff. *surya* (Forbes); Collignon, p. 41, pl. 7, fig. 1.
 1941 *Paraphylloceras* sp. cf. *nera* (Forbes); Spath, p. 42.
 1956 *Epiphyllloceras mikobokense* Collignon, p. 24, pl. 2, fig. 3; pl. 4, fig. 5.
 1971 *Epiphyllloceras geczyi* Collignon, p. 1, pl. 640, fig. 2360.
 1977b *Phylloceras (Hypophylloceras) mikobokense* (Collignon); Kennedy and Klinger, p. 368, pl. 12, fig. 1.
 1977 *Phylloceras surya* (Forbes); Kennedy, text-figs 31.15–16.
 1985 *Phylloceras (Neophylloceras) surya* (Forbes, 1846); Henderson and McNamara, p. 42, pl. 1, figs 7–8, 11–12; pl. 2, figs 1–2; text-fig. 2g (with full synonymy).
 1986 *Phylloceras (Hypophylloceras) surya* (Forbes); Stinnisbeck, p. 193, pl. 7, figs 5–6.
 1989 *Phylloceras (Neophylloceras)* Kennedy, text-fig. 17k–l.

Types. Lectotype, here designated, BMNH C51074, the original of Kossmat (1895, pl. 15 (2), fig. 1a–c); paralectotypes are BMNH C51075, figured by Forbes (1846, pl. 7, fig. 10a–b; GSC R1074), and BMNH C51076–51079 (all GSC unnumbered, ex Kaye and Cunliffe Collection), from the Valudavur Formation of Pondicherry, south India.

Dimensions.	D	Wb	Wh	Wb:Wh	U
BMNH C51076	25.5 (100)	7.3 (28.6)	13.5 (52.9)	0.54	2.2 (8.6)
BMNH C51075	~ 36.5 (100)	11.0 (30.1)	20.0 (54.8)	0.55	3.5 (9.6)
BMNH C51074	~ 100.0 (100)	27.5 (27.5)	66.5 (66.5)	0.41	~ 8.5 (8.5)

Description. The shell is compressed and very involute, with U = 8.5–9.6% of diameter, the umbilical wall low, weakly convex and subvertical, the umbilical shoulder rounded on some specimens but sharply defined on

others. The flanks are weakly convex, converging to a narrowly rounded venter; the greatest breadth is below mid-flank. There are two orders of ribs. Thin ribs separated by wide interspaces arise at the umbilical shoulder on the innermost flank, and number as few as 12 per half whorl in early growth stages, increasing to as many as 20 during later growth. They are feebly prorsiradiate, slightly convex on inner flanks and straight on the outer, declining and effacing by the ventrolateral shoulder. Fine lirae, separated by interspaces of similar width, arise on the inner flanks and follow a similar course to the ribs, but extend to, and strengthen across, the venter. They cover both ribs and interspaces, and number about 100 per half whorl. The suture is deeply incised and very finely divided, with both lobes and saddles having narrow axial zones. L is deeper than E and trifid; U has numerous auxiliary elements arranged on a line that runs straight to the umbilical shoulder.

Discussion. The largest syntype (which has suffered non-lethal injury during life) preserves the beginning of the body chamber, and may be adult. *P. (N.) surya* was discussed at length by Henderson and McNamara (1985), who indicated differences from other species.

Occurrence. Maastrichtian; south India, Madagascar, Zululand (South Africa), Western Australia, Chile, the Biscay region in France, and Denmark.

Phylloceras (Neophylloceras)? decipiens Kossmat, 1895

Plate 1, fig. 8; Plate 15, fig. 3

1846 *Ammonites varuna* Forbes [*pars*], p. 107, non pl. 8, fig. 5 [= *Zelandites varuna* (Forbes, 1846)].
1895 *Phylloceras decipiens* Kossmat, p. 109 (13), pl. 16 (2), fig. 3.
non 1907 *Phylloceras decipiens* Kossmat; Pervinquière, p. 55, pl. 3, figs 10–11.

Type. Holotype, by monotypy, is BMNH C51080, the original of Kossmat (1895, p. 109 (13), pl. 16 (2), fig. 3; GSC R10475, ex Kaye and Cunliffe Collection), a syntype of *Zelandites varuna* (Forbes, 1846), according to Kossmat. It is from the Valudavur Group of Pondicherry, south India.

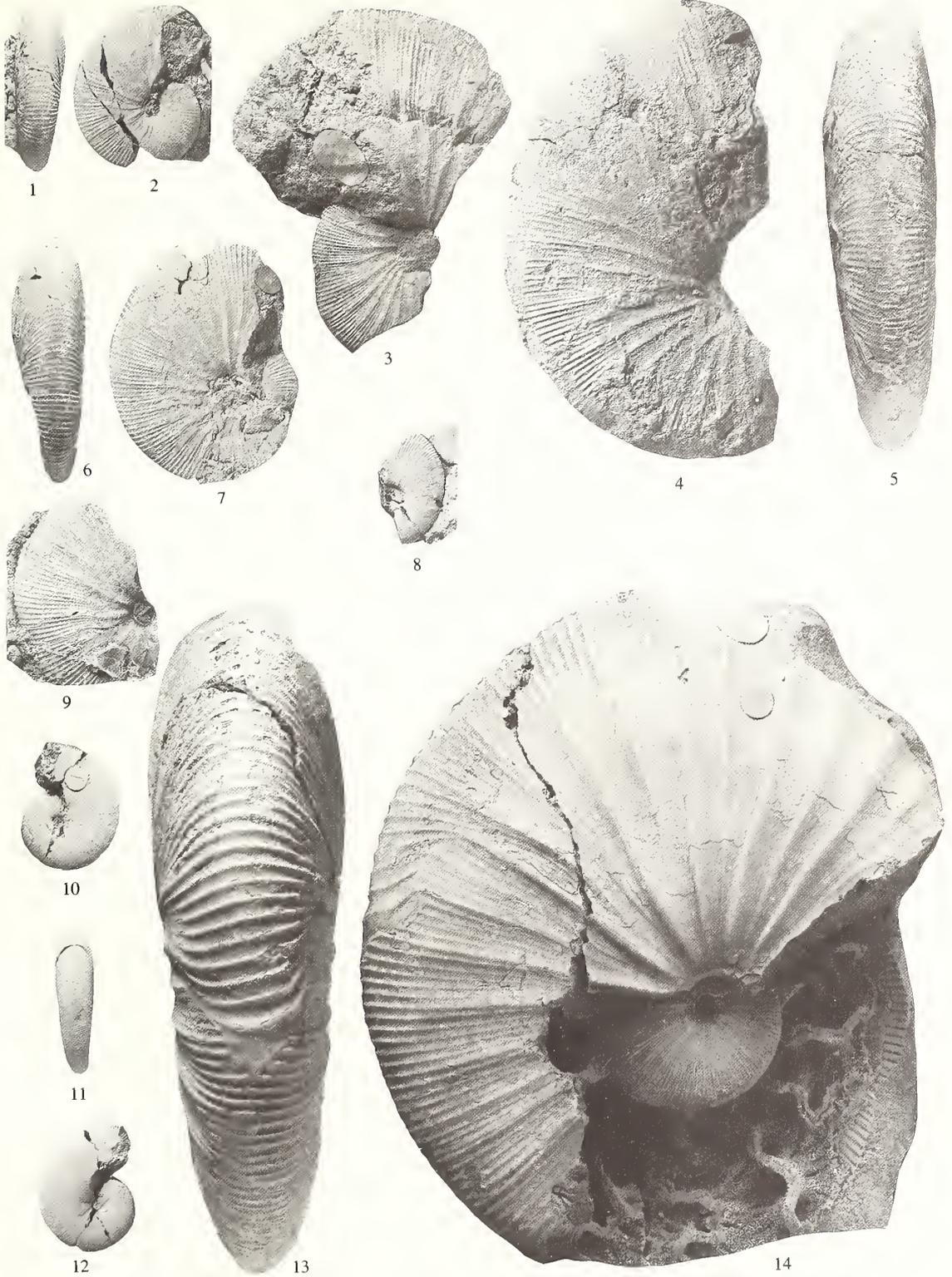
<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51080	~ 15.0 (100)	5.0 (33.3)	7.5 (50.0)	0.67	3.8 (25.3)

Description. The holotype is a partly septate juvenile, with traces of shell preserved. The whorls are depressed during the early growth stages, becoming as broad as high by a diameter of around 5 mm and thereafter increasingly compressed with a whorl breadth to height ratio of 0.67 at 15 mm diameter. The umbilicus is unusually wide for an Upper Cretaceous phylloceratid, comprising 25% of the diameter. The umbilical wall is low and convex, merging with a narrowly rounded umbilical shoulder. The flanks are weakly convex, and converge to a narrowly rounded venter; the maximum whorl breadth is below mid-flank. Fine prorsiradiate lirae, regularly spaced and separated by slightly wider interspaces on the venter, arise at the umbilical shoulder. They are straight on the inner flank, but flex back and are feebly concave on the outer; they pass straight across the venter. The last sector of body chamber shows two feeble folds on the inner flank, separated by wide interspaces. The suture lacks complexity, and is imperfectly exposed. E is broad and shallow, L deep and trifid. U is retracted.

Discussion. Shell form, ornament and suture show *decipiens* to be a phylloceratid, but its generic assignation is unclear to us. The suture is much less complex than that of *Phylloceras (Neophylloceras)* of equivalent size, and the umbilical diameter greater than any species referred to that subgenus; these characters readily distinguish it from other Valudavur species (Pl. 15, figs 1–5).

EXPLANATION OF PLATE I

Figs 1–7, 9, 13–14. *Phylloceras (Neophylloceras) surya* (Forbes, 1846). 1–2, BMNH C51076, paralectotype. BMNH C51077, paralectotype. 4–5, BMNH C51075, paralectotype. 6–7 BMNH C51079, paralectotype. 9, BMNH C51078, paralectotype. 13–14, BMNH C51074, lectotype.
Fig. 8. *Phylloceras (Neophylloceras?) decipiens* Kossmat, 1895. BMNH C51080, holotype.
Figs 10–12. *Phylloceras (Neophylloceras) nera* (Forbes, 1846). BMNH C22681, holotype.
All specimens from the Valudavur Formation of Pondicherry, south India. All $\times 1$.



KENNEDY and HENDERSON, *Phylloceras* (*Neophylloceras*)

The record of Pervinquière (1907) from the Albian of Tunisia is unlikely to be of this species.

Occurrence. As for types.

Genus *PHYLLOPACHYCERAS* Spath, 1927, p. 36

Type species. *Ammonites infundibulum* d'Orbigny, 1841, p. 131, pl. 39, figs 4–5, by original designation.

Discussion. Recent workers have followed Wiedmann (1964) in regarding *Phyllopachyceras* as a synonym of *Partschiceras* Fucini, 1920, or as a subgenus (e.g. Henderson and McNamara 1985). Joly (1970a, 1970b, 1976) concluded that the type species of *Partschiceras* was a *Phylloceras sensu stricto*, and we accordingly afford *Phyllopachyceras* generic status.

Phyllopachyceras forbesianum (d'Orbigny, 1850)

Plate 2, figs 1–12; Text-fig. 3c

- 1846 *Ammonites Rouyanus* d'Orbigny; Forbes, p. 108, pl. 8, fig. 6.
 1850 *Ammonites Forbesianus* d'Orbigny, p. 213.
 1865 *Ammonites Rouyanus* d'Orbigny; Stoliczka, p. 117, pl. 59, figs 5–7.
 1890 *Phylloceras ezoensis* Yokoyama, p. 178, pl. 19, fig. 2a–c.
 1895 *Phylloceras Forbesianum* d'Orbigny sp.; Kossmat, p. 109 (13), pl. 15 (1), fig. 1.
 1903 *Phylloceras forbesianum* (d'Orbigny); Whiteaves, p. 328.
 1921 *Phylloceras ezoense* (Yokoyama); Yabe, p. 54, pl. 8, fig. 2.
 1926 *Phylloceras forbesianum* (d'Orbigny); Marshall, p. 136, pl. 19, fig. 6; pl. 27, figs 3–4.
 1926 *Phylloceras minimum* Marshall, p. 137, pl. 19, fig. 8; pl. 26, figs 5–6.
 1926 *Schluteria rarawa* Marshall, p. 192, pl. 19, fig. 10; pl. 32, figs 7–8.
 1935 *Phyllopachyceras inflatum* Shimizu, p. 178.
 1935 *Phyllopachyceras forbesianum* (d'Orbigny); Shimizu, p. 178.
 1935 *Phyllopachyceras ezoense* (Yokoyama); Shimizu, p. 172.
 1937 *Phyllopachyceras marshalli* Collignon, p. 26.
 1941 *Phyllopachyceras forbesianum* (d'Orbigny); Spath, p. 42.
 1942 *Phyllopachyceras ezoense* (Yokoyama); Matsumoto, p. 674.
 1952 *Phyllopachyceras forbesianum* (d'Orbigny); Usher, p. 52, pl. 2, figs 1–5; pl. 31, figs 11–12.
 1953 *Phyllopachyceras forbesianum* (d'Orbigny); Spath, p. 6, pl. 1, figs 3–5.
 1956 *Phyllopachyceras forbesi* (d'Orbigny); Collignon, p. 26.
 1956 *Phyllopachyceras zelandicum* Collignon, p. 31.
 1962 *Phyllopachyceras forbesianum* (d'Orbigny); Wiedmann, p. 145, text-fig. 10.
 1963 *Phyllopachyceras forbesianum* (d'Orbigny); Jones, p. 24, pl. 41, figs 2, 4–6, text-fig. 9.
 1970 *Phyllopachyceras forbesianum* (d'Orbigny); Henderson, p. 7, pl. 1, figs 2, 4–5 (with additional synonymy).
 1985 *Partschiceras (Phyllopachyceras) forbesianum* (d'Orbigny, 1850); Henderson and McNamara, p. 43, pl. 1, figs 4–6; text-fig. 3f.
 1986 *Partschiceras forbesianum* (d'Orbigny, 1850); Kennedy and Summesberger, p. 184, pl. 1, figs 2–3, 6; pl. 15, figs 3, 6 (with additional synonymy).

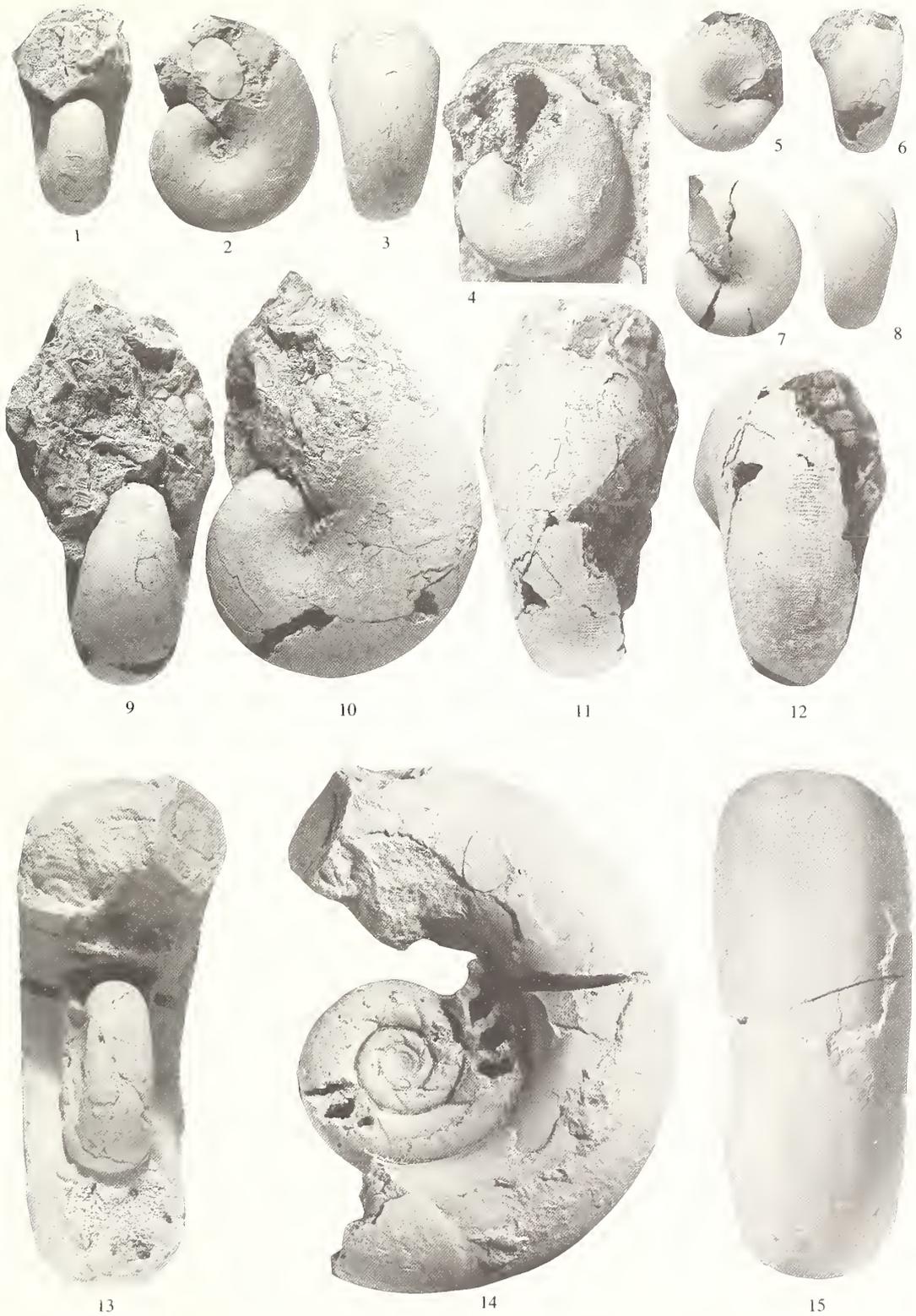
Types. *Ammonites Forbesianus* d'Orbigny, 1850 (p. 213) was introduced as a new name for '*Ammonites Rouyanus* Forbes, 1846, t. 7, p. 108, pl. 8, fig. 6'. Although only one specimen was figured by Forbes, the

EXPLANATION OF PLATE 2

Figs 1–12. *Phyllopachyceras forbesianum* (d'Orbigny, 1850). 1–3, BMNH C51081, lectotype. 4, BMNH C51082, paralectotype. 5–6, BMNH C51083, paralectotype. 7–8, BMNH C82499, topotype (ex. R. Marsham Collection). 9–12, BMNH C51084, paralectotype.

Figs 13–15. *Saghalinites cala* (Forbes, 1846). BMNH C51057, paralectotype.

All specimens from the Valudavur Formation of Pondicherry, south India. All $\times 1$.



KENNEDY and HENDERSON, *Phyllopaichyceras*, *Saghalinites*

indication in d'Orbigny is also to Forbes' description, which refers to more than one specimen so that, contrary to Phillips (1977) and others, there was a type series. We here designate BMNH C51081, the original of Forbes (1846, pl. 8, fig. 6; GSC R10476) the lectotype. Paralectotypes are BMNH 24197, C51082-51086 (GSC unregistered; all *ex* Kaye and Cunliffe Collection). All are from the Valudavur Formation of Pondicherry, south India. Topotypes are BMNH C82499 (*ex* Marsham Collection) and BMNH C3557*a-c*.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51086	9.5 (100)	5.2 (54.7)	4.5 (47.4)	1.16	0.2 (2.1)
BMNH C51083	20.2 (100)	12.0 (59.4)	11.2 (55.4)	1.07	- (-)
BMNH C82499	24.2 (100)	~ 13.5 (55.8)	13.8 (57.0)	0.98	0.5 (2.0)
BMNH C51081	31.5 (100)	18.0 (57.1)	17.8 (56.5)	1.01	0.5 (1.6)
BMNH 24197	45.5 (100)	26.0 (57.1)	28.0 (61.5)	0.92	0.5 (1.1)

Description. Coiling is very involute, with a tiny, deep umbilicus, comprising 2% of diameter, or less. The umbilical wall is low and steep, the umbilical shoulder narrowly rounded, the flanks strongly convex, merging with the broadly rounded venter. The whorl section varies from slightly depressed to slightly compressed. Internal moulds are smooth. Where shell surface is well-preserved, the flanks are covered by dense, straight, prorsiradiate lirae that flex back on the ventrolateral shoulders to cross the venter in broad convexity. As size increases, these lirae are joined by low, distant ribs, most conspicuous on the outer flanks and venter, as in BMNH C510824, the largest paralectotype (Pl. 2, figs 9-11). A striking feature of the lectotype and largest paralectotype is the strengthening of lirae over the siphonal region, producing a coarsely ornamented ventral zone (Pl. 2, figs 11-12). Suture with tetraphylloid saddles (Text-fig. 3c).

Discussion. Henderson (1970) and Kennedy and Summesberger (1986) discussed this species and its synonyms.

Occurrence. The earliest records are from the Santonian of Madagascar (Collignon 1956, 1966) and the Lower Campanian of Spain (Wiedmann 1962). The chief occurrence of the species is in the Upper Campanian and throughout the Maastrichtian. These later records are from south India, Japan, British Columbia, Alaska, California, the sub-Antarctic Islands, Zululand (South Africa), Madagascar, Western Australia, New Zealand, north Germany, Austria, the Biscay region of France and Spain, and the former USSR.

Suborder LYTOCERATINA Hyatt, 1889, p. 7
 Superfamily TETRAGONITACEAE Hyatt, 1900, p. 568
 Family TETRAGONITIDAE Hyatt, 1900, p. 568
 Genus PSEUDOPHYLLITES Kossmat, 1895, p. 137 (41)

Type species. *Ammonites Indra* Forbes, 1846, p. 105, pl. 11, fig. 7, by original designation.

Discussion. See Kennedy and Klinger (1977*a*, p. 180), Henderson and McNamara (1985, p. 49) and Kennedy (1986*a*, p. 18) for recent accounts of this genus.

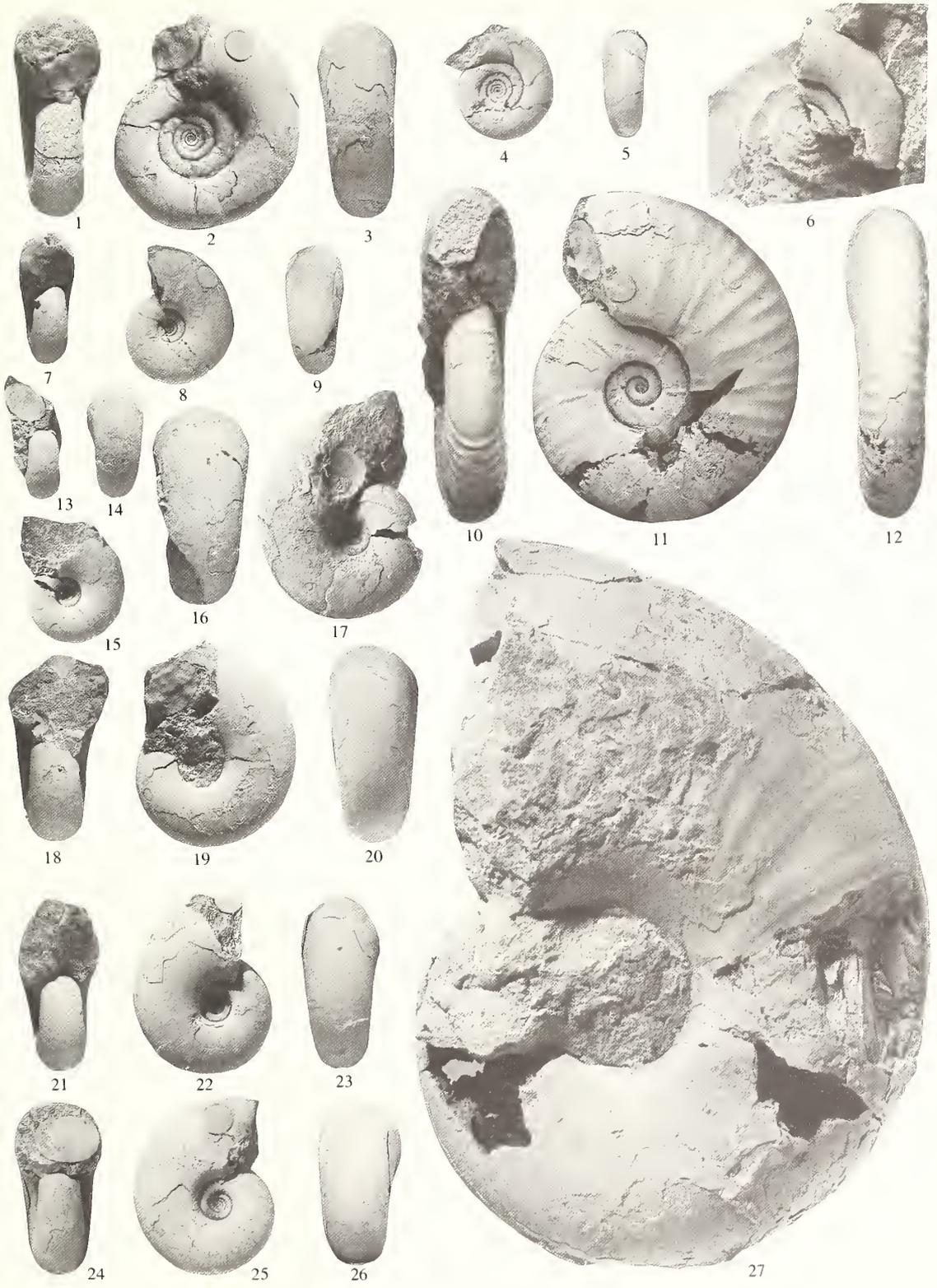
EXPLANATION OF PLATE 3

Figs 1-6. *Saghalinites cala* (Forbes, 1846). 1-3, BMNH C51057, lectotype. 4-5, BMNH C51054, paralectotype. 6, BMNH C3560, topotype.

Figs 7-9, 13-27. *Pseudophyllites indra* (Forbes, 1846). 7-9, BMNH C22676, the holotype of *Ammonites Garuda* Forbes, 1846. 13-15, BMNH C3563*a*, a topotype. 16-17, BMNH C51070, a paralectotype. 18-20, BMNH 24194*a*, a topotype (*ex* Kaye Collection). 21-23, BMNH C82491, a topotype (*ex* Marsham Collection). 24-26, BMNH C51069, a paralectotype. 27, BMNH C51068, the lectotype.

Figs 10-12. *Kitchinites pondicherryanus* (Kossmat, 1897). BMNH C47548, holotype.

All specimens from the Valudavur Formation of Pondicherry, south India. All $\times 1$.



KENNEDY and HENDERSON, Indian Maastrichtian ammonites

Pseudophyllites indra (Forbes, 1846)

Plate 3, figs 7–9, 13–27; Plate 4, figs 1–3

- 1846 *Ammonites Indra* Forbes, p. 105, pl. 11, fig. 7.
 1846 *Ammonites Garuda* Forbes, p. 102, pl. 7, fig. 1.
 1850 *Ammonites Indra* Forbes; d'Orbigny, p. 213.
 1850 *Ammonites Chrishna* Forbes; d'Orbigny [pars], p. 213.
 1977a *Pseudophyllites indra* (Forbes, 1846); Kennedy and Klinger, p. 182, figs 19a–f, 20–22 (with full synonymy).
 1985 *Pseudophyllites indra* (Forbes, 1846); Henderson and McNamara, p. 50, pl. 2, figs 7–8; pl. 3, figs 4–5; text-fig. 5a, 5d.
 1986 *Pseudophyllites indra* (Forbes); Stinnisbeck, p. 199, pl. 8, fig. 4.
 1986b *Pseudophyllites indra* (Forbes, 1846); Kennedy, p. 19, pl. 1, figs 1–5; text-figs 4e, 5a, 6a–e (with additional synonymy).
 1986 *Pseudophyllites* cf. *indra* (Forbes, 1846); Kennedy and Summesberger, p. 187, pl. 1, figs 1, 8; pl. 3, fig. 5; text-fig. 4 (with additional synonymy).
 1989 *Pseudophyllites*; Kennedy, fig. 17b.

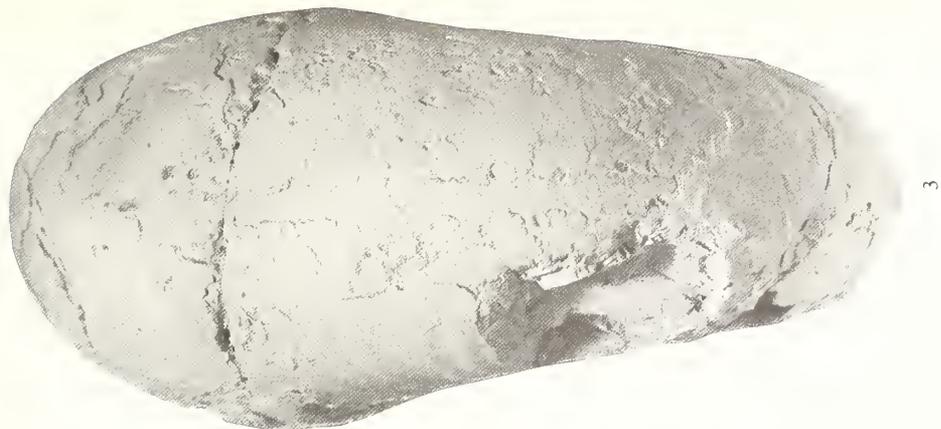
Types. Lectotype, designated by Kennedy and Klinger (1977a, p. 182), is BMNH C51068, the original of Forbes (1846, pl. 11, fig. 7a–b), Kossmat (1895, pl. 16 (2), fig. 9a–b) and others (GSC R10468). Paralectotypes are BMNH C51069, the original of Kossmat (1895, pl. 16 (2), fig. 8; GSC R10469), and BMNH C51070–51073, GSC unregistered, all from the Valudavur Formation of Pondicherry, south India (Kaye and Cunliffe Collection). Topotypes are BMNH 24194a–e (Kaye Collection, 1849), BMNH C82492–82495 (Marshall Collection), and BMNH C3563a–l. The holotype of *Ammonites Garuda* Forbes, 1846 (p. 102, pl. 7, fig. 1) is BMNH C22676 (GSC R10462, ex Kaye and Cunliffe Collection), also from the Valudavur Formation of Pondicherry, south India.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C22678	11.2 (100)	5.8 (51.8)	5.0 (44.6)	1.16	3.2 (28.6)
BMNH C35630	12.8 (100)	6.0 (46.9)	5.2 (40.6)	1.15	3.8 (29.7)
BMNH C22677	13.0 (100)	5.8 (44.6)	4.8 (36.9)	1.20	3.5 (26.9)
BMNH C3563e	14.0 (100)	6.5 (46.4)	5.8 (41.4)	1.12	4.0 (28.6)
BMNH C3563a	16.0 (100)	7.5 (46.9)	6.2 (38.8)	1.21	4.2 (26.3)
BMNH C22676	19.8 (100)	9.0 (45.5)	8.0 (40.4)	1.12	4.8 (24.2)
BMNH C82491	22.5 (100)	11.0 (48.9)	9.5 (42.2)	1.16	4.8 (21.3)
BMNH 24194b	23.8 (100)	10.8 (45.4)	10.0 (42.0)	1.08	5.5 (23.1)
BMNH C51049	26.8 (100)	12.5 (46.6)	11.2 (41.8)	1.1	6.0 (22.4)
BMNH C82493	29.0 (100)	13.8 (47.6)	12.2 (42.1)	1.13	6.2 (21.4)
BMNH 24194a	29.0 (100)	13.2 (45.5)	12.2 (42.0)	1.08	6.0 (20.7)
BMNH C51070	29.0 (100)	14.0 (48.3)	12.5 (43.1)	1.12	6.2 (21.4)
BMNH C51068	110.0 (100)	58.8 (53.5)	54.0 (49.1)	1.1	18.0 (16.4)

Description. Coiling is involute, the whorls rapidly expanding, slightly depressed in juveniles, but slightly compressed in the larger members of the type series. The umbilicus is deep with a high, feebly convex, outward-inclined umbilical wall; the umbilical shoulder is broadly rounded. The flanks are convex, converging to a broadly rounded venter, with maximum whorl breadth just outside the umbilical shoulder. Juveniles are smooth, except for growth lines and striae. These are straight and rectiradial on the umbilical wall, swinging forwards and becoming prorsiradial, straight on the inner flank, but feebly convex on the outer, and crossing the venter in a very shallow concavity. As size increases, delicate folds appear on the flank and venter, paralleling the growth lines. They coarsen markedly on the outer whorl of the lectotype (Pl. 3, fig. 27; Pl. 4) and the venter has a distinctive ornament of low, flat ribs and lirae and striac where the shell is preserved. Suture deeply and intricately subdivided from an early stage, with L deeper than E and asymmetrically bifid.

EXPLANATION OF PLATE 4

Figs 1–3. *Pseudophyllites indra* (Forbes, 1846). BMNH C51068, lectotype; Valudavur Formation; Pondicherry, south India, $\times 1$.



3



2



1

Discussion. The holotype of *Ammonites Garuda* Forbes, 1846 (p. 102, pl. 7, fig. 1), BMNH C22676 (Pl. 3, figs 7–9) is a juvenile of *P. indra*. The present species was discussed at length by Kennedy and Klinger (1977a) and Henderson and McNamara (1985), the latter having more than 70 specimens for study. Kennedy (1986b) and Kennedy and Summesberger (1986) clarified the affinities of the rather poorly preserved Western European material of this species. *P. indra* (and its numerous synonyms) apart, there seem to be two other well differentiated species. *P. teres* (Van Hoepen, 1920) (p. 144, pl. 25, figs 1–2) has a compressed whorl, parallel sides and a subvertical wall, is small, and transitional in certain respects to *Tetragonites* Kossmat, 1895. It is of Santonian date. *Pseudophyllites loryi* (Kilian and Reboul, 1909) and its synonyms *P. latus* (Marshall, 1926) (see revision in Henderson and McNamara 1985, p. 50, pl. 3, figs 1–3, 6–8; text-fig. 5b–c) and *P. skoui* Birkelund, 1965 (p. 37, pl. 3, figs 2–6; text-figs 26–33) have broader whorls that increase at a lower rate, and a spatulate ventral saddle, rather than lanceolate as in *indra*; the recess of the septal lobe is large in *indra*, but small in *loryi*.

Occurrence. Lower Campanian to Upper Maastrichtian. South India, Zululand (South Africa), Madagascar (where it is also recorded from the Upper Santonian), Western Australia, Japan, Sakhalin, Alaska, British Columbia, California, Brazil(?), Chile, The US Gulf Coast, New Jersey, Northern Ireland, Poland, Austria, and southwest France.

Genus SAGHALINITES Wright and Matsumoto, 1954, p. 110

Type species. *Ammonites Cala* Forbes, 1846, p. 104, pl. 8, fig. 4, by original designation.

Saghalinites cala (Forbes, 1846)

Plate 2, figs 13–15; Plate 3, figs 1–6; Text-fig. 3B

- 1846 *Ammonites Cala* Forbes, p. 104, pl. 8, fig. 4.
 1850 *Ammonites Durga* Forbes; d'Orbigny [*pars*], p. 213.
 1977a *Saghalinites cala* (Forbes, 1846); Kennedy and Klinger, p. 168, figs 10a–b, 11a–b, 12d–g, 13a–b, e–k, ?c–d, 14a–f, 15a–f (with full synonymy).
 1977 *Saghalinites cala*; Kennedy, text-fig. 31.17.
 1989 *Saghalinites*; Kennedy, text-fig. 17b.

Types. Lectotype, designated by Kennedy and Klinger (1977a, p. 169) is BMNH C51057, the original of Forbes 1846 (pl. 8, fig. 4; GSC R10466); paralectotypes are BMNH C51054, C51058 (the original of Kossmat 1895, pl. 17 (3), fig. 12, and others); BMNH C3560 is a topotype. All are from the Valudavur Formation of Pondicherry, south India.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51054	15.8 (100)	5.8 (36.7)	4.2 (26.6)	1.38	7.2 (45.6)
BMNH C51057	32.0 (100)	13.5 (42.2)	10.8 (33.8)	1.22	14.2 (44.4)
BMNH C51058	80.0 (100)	29.5 (36.9)	23.2 (29.0)	1.27	37.5 (46.9)

Description. Coiling is very evolute, with a broad, shallow umbilicus (U = 44–47%), about 33% of the previous whorl being covered, the whorls depressed throughout. Early whorls, up to a diameter of 20 mm, have a low, convex, outward-inclined umbilical wall and a broadly rounded umbilical shoulder. On the later whorls the umbilical wall is flattened and subvertical, with the umbilical shoulder more sharply defined. The flanks are weakly convex and convergent, such that the greatest breadth is below mid-flank. The ventrolateral shoulders are broadly rounded to a diameter of about 60 mm, beyond which the venter is distinctly flattened, the ventrolateral shoulders narrowly rounded and the whorl section subquadrate. The venter is feebly concave in the largest specimen (Pl. 2, fig. 15). The mould is smooth, but for constrictions, which number about 5 per whorl. They are retriradiate on the umbilical wall, but swing forwards and are deeply incised on the ventrolateral shoulder, are concave, flexing forwards and straight on the inner flank, flexing back and concave on the outermost flank and ventrolateral shoulder, crossing the venter in a broad shallow convexity. Growth

lines are much stronger where the shell is preserved (Pl. 3, figs 1–3, 6), and constrictions shallower, with adapical collar-ribs. BMNH C51058 is an adult body chamber, with two shallow depressions on the venter, defining low ventrolateral and siphonal ridges (Pl. 2, fig. 15). Additional faint spiral depressions, most obvious on the mould, occur on the outer flank. Suture simple (Text-fig. 3B) with E deeper than L, which is bifid. U weakly retracted on umbilical shoulder and wall.

Discussion. Differences from other species were discussed by Kennedy and Klinger (1977a). It most closely resembles *S. wrighti* Birkelund, 1965 (p. 30, pl. 1, fig. 5; pl. 2, figs 1–5; pl. 3, fig. 1; text-figs 14–25), originally described from West Greenland, but subsequently recorded from Denmark (Birkelund 1979), north Germany (Birkelund 1982) and Austria (Kennedy and Summesberger 1986). Topotypes are shown in Pl. 16, figs 4–6, 9–11; it differs from *S. cala* most obviously in having less flexuous constrictions.

Saghalinites n. sp. of Birkelund (1979, 1982, in press) from the Upper Maastrichtian of Kunrade, the Netherlands, and Denmark is more evolute, with much stronger constrictions.

Occurrence. Where reliably dated, this species is Maastrichtian as in south India and Zululand. There is a doubtful record from Pondoland (South Africa) that may be Santonian or Campanian, and a record from Tunisia (var. *zeugitana* Pervinquière, 1907) that is Santonian. The Antarctic specimens (Howarth 1958, p. 10, pl. 1, fig. 1) are associated with *Gummarites antarcticus*, and here regarded as Maastrichtian.

Family GAUDRYCERATIDAE Shimizu, 1934, p. 67

Genus ANAGAUDRYCERAS Shimizu, 1934, p. 67

[= *Paragaudryceras* Shimizu, 1934, p. 67; *Murphyella* Matsumoto, 1972, p. 208]

Type species. *Ammonites Sacya* Forbes, 1846, p. 113, pl. 14, fig. 9, by original designation.

Anagaudryceras valudavurens (Kossmat, 1895)

Plate 5, figs 1–12; Text-fig. 3E

1846 *Ammonites Julieti* d'Orbigny; Forbes, p. 101, pl. 7, fig. 2.

1895 *Gaudryceras Valudavurens* Kossmat, p. 163 (67), pl. 17 (3), fig. 1.

Types. Lectotype, here designated, is BMNH C51065, the original of Kossmat (1895, pl. 17 (3), fig. 1a–b; GSC R10460); paralectotypes are BMNH C51064, the original of Forbes (1846, pl. 7, fig. 2), and Kossmat (1895, pl. 17 (3), fig. 1c; GSC R10459) and BMNH C51066. All are from the Valudavur Formation of Pondicherry, south India (ex Kaye and Cunliffe Collection).

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51065	12.0 (100)	5.5 (45.8)	3.0 (25.6)	1.83	5.0 (41.7)
BMNH C51066	12.5 (100)	~ 6.0 (48.0)	3.2 (25.6)	1.88	5.0 (40.0)
BMNH C51064	15.0 (100)	6.5 (43.3)	5.0 (33.3)	1.3	6.0 (40.0)

Description. The types are all juveniles, the largest 15 mm in diameter. Coiling is very evolute, with rapidly expanding depressed, inflated whorls. The umbilical wall is convex, sloping outwards and passing into the flanks with no clearly demarcated umbilical shoulder. The flanks are strongly convex, the venter broadly rounded. Ornament is of dense lirae that are straight and strongly prorsiradiate on the inner flank. They break down into even finer lirae on the mid-flank region, and are prorsiradiate on the outer flank, weakly convex, and pass straight across the venter. None of the specimens shows clearly differentiated constrictions, but BMNH C51066 has broad indistinct folds on the flanks up to a shell diameter of about 8 mm. Suture finely subdivided from an early growth stage; L and E of equal depth, U retracted on inner flanks and umbilical wall (Text-fig. 3E).

Discussion. Being juvenile, the types are difficult to compare with other Maastrichtian species, and reference to *Anagaudryceras* rests mainly on the very fine ornament, which distinguishes them from

co-occurring *Gaudryceras*. *Anagaudryceras subtilineatum* (Kossmat, 1895) (see revision in Henderson and McNamara 1985, p. 45, pl. 2, figs 3–4; text-fig. 4a) has a lower expansion rate and distinctive polygyral shell when small, with constrictions and collar ribs. A further species known from the Maastrichtian is *Anagaudryceras politissimum* (Kossmat, 1895) (see Henderson and McNamara 1985, p. 46, pl. 1, figs 9–10; text-fig. 4d); it is only slightly depressed, with collar ribs and weak constrictions. Other Maastrichtian species are discussed by Birkelund (1982) and Matsumoto and Yoshida (1979).

Occurrence. As for types.

Genus GAUDRYCERAS de Grossouvre, 1894, p. 225

Type species. *Ammonites mitis* Von Hauer, 1866, p. 305, pl. 2, figs 3–4, by the subsequent designation by Boule, Lemoine and Thévenin, 1906, p. 183 (11).

Discussion. For synonymy see Kennedy and Klinger (1979, p. 128).

Gaudryceras kayei (Forbes, 1846)

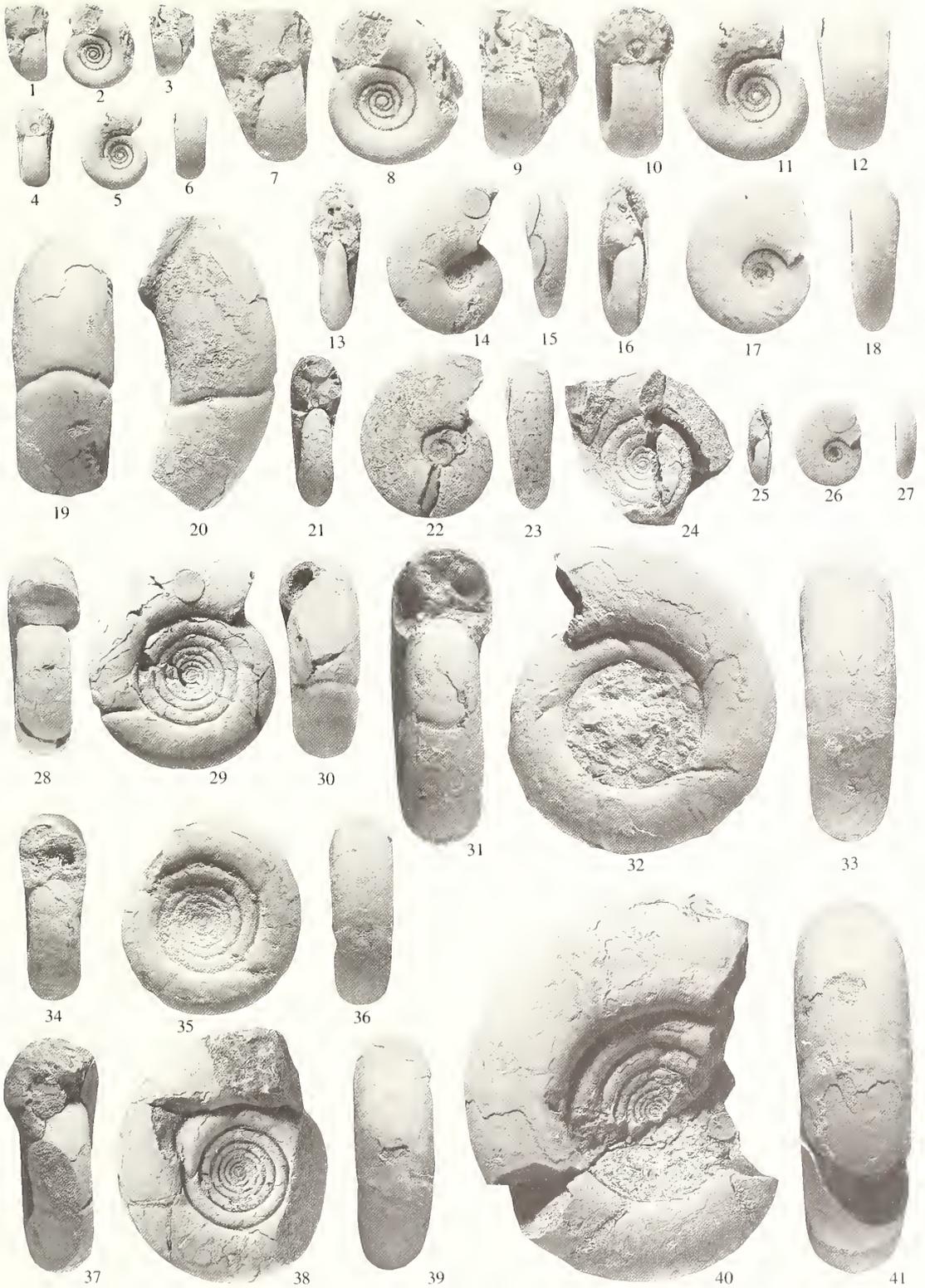
Plate 5, figs 19–20, 24, 28–41; Text-fig. 3D

- 1846 *Ammonites Kayei* Forbes, p. 101, pl. 8, fig. 3.
 1850 *Ammonites Kayei* Forbes; d'Orbigny, p. 213.
 1977 *Vertebrites kayei* (Forbes); Kennedy, text-figs 31.3–31.4.
 1979 *Vertebrites kayei* (Forbes); Kennedy and Klinger, p. 160, pl. 14, fig. 2; text-fig. 5 (with full synonymy).
 1985 *Gaudryceras kayei* (Forbes, 1846); Henderson and McNamara, p. 46, pl. 1, figs 13–14; pl. 2, figs 5–6, 8, 10; text-fig. 4b–c.
 1986 *Gaudryceras* (*Vertebrites*) *kayei* (Forbes); Stinnisbeck, p. 198, pl. 8, figs 2–3; text-fig. 21.
 1989 *Vertebrites*; Kennedy, text-fig. 17a.

Types. Lectotype, by the subsequent designation of Matsumoto and Yoshida 1979 (p. 70) is BMNH C51050, the original of Forbes 1846 (pl. 8, fig. 3a–b; GSC R10461); paratypes are BMNH C51049, the original of Kossmat (1895, pl. 17 (3), fig. 2; GSC R10513), C41501, C51051–51053, C51055 (all Kaye and Cunliffe Collection). Topotypes are BMNH 24193a–b (*ex* Kaye Collection), BMNH C3448–3449, BMNH C3568 (labelled *Ammonites juilleti*), BMNH C82498 (*ex* Marsham Collection). All are from the Valudavur Formation of Pondicherry, south India.

EXPLANATION OF PLATE 5

- Figs 1–12. *Anagaudryceras valudavurens* (Kossmat, 1895). 1–3, 7–9, BMNH C51065, the lectotype. 4–6, 10–12, BMNH C51066, a paralectotype.
 Figs 13–15. *Zelandites varuna* (Forbes, 1846). BMNH C51059, lectotype.
 Figs 16–18, 21–23, 25–27. *Pachydiscus* (*Pachydiscus*) sp. juv. 16–18, 25–27, BMNH C51063, a paralectotype of *Ammonites Varuna*, the measurements of which were given by Forbes (1846, p. 107). 21–23, BMNH C51060, a further paralectotype of *Ammonites Varuna*.
 Figs 19–20, 24, 28–41. *Gaudryceras kayei* (Forbes, 1846). 19–20, BMNH C41501, a paralectotype. 24, BMNH 24193b, a topotype (*ex* Kaye Collection). 28–30, BMNH C51050, the lectotype. 31–33, BMNH 24193a, a topotype (*ex* Kaye Collection). 34–36, BMNH C3558, a topotype. 37–39, BMNH C82498, a topotype. 40–41, BMNH C51049, a paralectotype.
 All specimens from the Valudavur Formation of Pondicherry, south India. All $\times 1$, except figs 7–12, 16–18, which are $\times 2$.



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<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51058	24.0 (100)	9.0 (37.5)	5.6 (23.3)	1.61	13.5 (56.3)
BMNH C3558	30.0 (100)	10.4 (34.7)	7.2 (24.0)	1.44	16.5 (55.0)
BMNH C51050	32.2 (100)	11.0 (29.3)	7.2 (22.3)	1.52	17.0 (56.7)
BMNH C82498	36.5 (100)	12.0 (32.9)	9.2 (25.2)	1.30	18.0 (49.3)
BMNH C51049	55.5 (100)	17.4 (31.4)	14.6 (26.3)	1.19	26.2 (47.2)

Description. Coiling is very evolute, with U = 47–57% of diameter, very depressed in juveniles, with a whorl breadth to height ratio of 1.61, decreasing progressively through ontogeny, to 1.19 at 55 mm diameter. Umbilical wall low, convex, inclined outwards and merging with a broadly rounded umbilical shoulder. The flanks are strongly convex, and merge into the broadly rounded venter. Where shell is preserved, narrow sharp lirae, numbering about 80 per half whorl, are separated by interspaces of variable width. They pass straight across the umbilical wall, and are markedly prorsiradiate on the inner flank, flexing backwards and feebly convex across the mid-flank, concave on the outer flank and sweeping forward on the ventrolateral shoulder to cross the venter in a broad convexity. Constrictions are prominent on internal moulds, are strong, narrow and deep, following a course parallel to the lirae and growth lines; they are irregularly spaced, and number up to five per whorl. Suture line (Text-fig. 3D) with E almost as deep as L, which is broad and trifid. There are numerous auxiliary elements on U.

Discussion. Henderson and McNamara (1985) discussed *G. kayei* in detail, and outlined differences from other species. Their material shows that the juvenile serpenticone stage is succeeded, beyond 75 mm diameter, by a less widely umbilicate one with equidimensional whorls with feebly convex flanks and a more narrowly arched venter. Their Australian specimens have four to seven constrictions per whorl in middle and later growth. *Guadryceras kayei* is intermediate in many respects between *Guadryceras* and the paedomorphic dwarf genus *Vertebrites*, and has been referred to both.

Occurrence. This species first appears in the Santonian of Tunisia, and is also known from the Santonian–Campanian of Pondoland (South Africa), and Mexico, Santonian to Maastrichtian of south India, Campanian of Zululand (South Africa), and Maastrichtian of Western Australia, Chile, California and Madagascar.

Genus ZELANDITES Marshall, 1926, p. 147

Type species. *Zelandites kaiparaensis* Marshall, 1926, p. 147, pl. 20, fig. 9; pl. 31, figs 1–2.

Discussion. For synonymy see Kennedy and Klinger (1979, p. 163).

Zelandites varuna (Forbes, 1846)

Plate 5, figs 13–15; Plate 17, figs 2–3

- 1846 *Ammonites Varuna* Forbes, p. 107, pl. 8, fig. 5.
non 1865 *Ammonites Varuna* Forbes; Stoliczka, p. 111, pl. 58, fig. 1 (= *Z. odiensis* (Kossmat, 1895)).
 1895 *Lytoceras (Guadryceras) Varuna* Forbes sp., Kossmat, p. 161 (65), pl. 16 (2), fig. 4; pl. 17 (3), fig. 8.
 1895 *Lytoceras varuna* (Forbes); Steinmann, p. 84, pl. 5, fig. 2; text-fig. 7.
 1904 *Lytoceras varuna* Forbes; Wilckens, p. 187.
 1930 *Lytoceras (Guadryceras) odiense* Kossmat; Wetzel, p. 89.
non 1938a *Zelandites varuna* (Forbes) var. *japonica* Matsumoto, p. 140, pl. 14, figs 5–7; text-fig. 1a–d.
 1977 *Zelandites varuna* (Forbes); Kennedy, p. 296, text-fig. 31.5.
 1986 *Zelandites varuna* (Forbes); Stinnisbeck, p. 195, pl. 8, figs 5–6; text-fig. 20.
 1986 *Zelandites varuna* (Forbes, 1846); Macellari, p. 14, text-figs 11.11, 11.12, 12.
non 1989 *Zelandites*; Kennedy, text-fig. 17c (= *Pachydiscus* sp. juv.).

Types. Lectotype, here designated, is BMNH C51059, the original of Forbes (1846, pl. 8, fig. 5; GSC R10474); paralectotype BMNH C3567b also belongs here. Of other paralectotypes, BMNH C51080 (Pl. 1, fig. 8) is the

holotype of *Phylloceras* (*Hypophylloceras*) *decepiens* Kossmat, 1895; while several others (e.g. BMNH C51060 (Pl. 5, figs 21–23), C51561–51563 (Pl. 5, figs 16–18, 25–27) and C3567c, are juvenile pachydiscids. All are from the Valudavur Formation of Pondicherry, south India.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51059	23.0 (100)	7.8 (33.9)	10.8 (47.0)	0.72	4.8 (20.9)

Description. The shell is compressed (Wb:Wh ratio = 0.72), with a narrow, shallow umbilicus, the umbilical wall low, and inclined outwards; the umbilical shoulder is narrowly rounded. The inner flanks are broadly rounded, the outer flanks converging to a narrowly rounded venter; the greatest whorl breadth is below mid-flank. Ornament is of growth lines on the shell, and infrequent weak constrictions, 2 to 3 per whorl, most conspicuous on the internal mould. They are rectiradiate on the umbilical wall, prorsiradiate on the inner to mid-flank, but absent on the outer flank. Suture finely subdivided; L bifid and much deeper than E. The external part of U has five bifid minor saddles, the last four following a prorsiradiate straight line.

Discussion. Both specimens referred to this species are wholly septate juveniles; only the paraectotype shows the very fine liration. As noted above, Forbes interpreted this species very widely, including both juvenile pachydiscids and a phylloceratid. *Zelandites varuna* is closely allied to the type species, *Z. kaiparaensis* Marshall, 1926 (see revision in Henderson 1970). It differs in having constrictions restricted to the inner flanks, rather than extending to the ventrolateral shoulder, while the New Zealand species has up to 12 constrictions per whorl. A large specimen from Antarctica (Macellari 1986, text-figs 11.1–11.12) has sparse constrictions, 4 per whorl, that extend out rather farther than in the types of *Z. varuna*. *Z. varuna japonica* Matsumoto, 1938a (p. 140, pl. 14, figs 5–7; text-fig. 1a–d) was differentiated from the Indian types on the basis of its more involute, more compressed shell, without constrictions in the middle growth stage. More obvious is the extension of the constrictions out to the ventrolateral shoulder (Matsumoto 1938a, pl. 14, fig. 5), and their greater number, in which it resembles the type species *Z. kaiparaensis*. Differences in relative proportions are less significant, as noted by Macellari (1986), who regarded *japonicum* as a synonym of *varuna*.

Occurrence. Maastrichtian, south India, Chile, and Seymour Island, Antarctica.

Order AMMONITINA Hyatt, 1889, p. 7

Superfamily DESMOCERATAEAE Zittel, 1895, p. 426

Family DESMOCERATIDAE Zittel, 1895, p. 426

Subfamily DESMOCERATINAE Zittel, 1895, p. 426

Genus DESMOPHYLLITES Spath, 1929, p. 270

[= *Schlüteria* de Grossouvre, 1894, p. 126 (*non* Fritsch in Fritsch and Kafka 1887, p. 33); *Schlütericeras* Collignon, 1938, p. 92 (*non* Hyatt, 1903, p. 110)]

Type species. *Desmoceras larteti* Seunes, 1891, p. 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2–3, by subsequent designation by Spath 1921 (p. 46) as type species of *Schlüteria*, of which *Desmophyllites* is replacement name.

Desmophyllites diphylloides (Forbes, 1846)

Plate 6, figs 1–9; Plate 16, figs 1–3, 7–8; Plate 17, figs 4–7; Text-fig. 3F

- 1846 *Ammonites diphylloides* Forbes, p. 105, pl. 8, fig. 8.
- 1850 *Ammonites diphylloides* Forbes; d'Orbigny, p. 213.
- 1865 *Ammonites diphylloides* Forbes; Stoliczka [*pars*], p. 119, pl. 59, figs 8–9 only.
- 1879 *Ammonites selwynianum* Whiteaves, p. 104, pl. 13, fig. 1.
- 1894 *Desmoceras pyrenaicum* de Grossouvre [*pars*], p. 168, pl. 37, fig. 9 only.
- 1898 *Desmoceras diphylloides* Forbes; Kossmat, p. 108 (173), pl. 19 (25), figs 8–9.
- 1898 *Desmoceras phyllimorphum* Kossmat, p. 110 (175), pl. 19 (25), fig. 10.

- 1907 *Puzosia (Latidorsella) diphylloides* (Forbes); Pervinquière, p. 140, pl. 6, figs 1–2, 7.
 1921 *Schlüteria woodsii* Spath, p. 45, pl. 7, fig. 1.
 1921 *Desmoceras simplex* Van Hoepen, p. 19, pl. 3, figs 11–16; text-fig. 10.
 1921 *Desmoceras crassum* Van Hoepen, p. 20, pl. 4, figs 3, 5; text-fig. 11.
 1931 *Desmoceras diphylloides* (Forbes); Basse, p. 23, pl. 2, figs 3–4.
 1931 *Desmoceras (Latidorsella) diphylloides* var. *besairei* Collignon, p. 15, pl. 2, figs 8–9; pl. 2, figs 5–8.
 1938 *Schlüteria larteti* (Seunes); Collignon, p. 42, pl. 7, fig. 3; text-figs k–l.
 1952 *Schlüteria selwyniana* Usher, p. 63, pl. 5, figs 3–4; pl. 6, figs 1–3.
 1953 *Desmophyllites diphylloides* (Forbes); Spath, p. 21, pl. 2, figs 5–6.
 1955 *Desmophyllites diphylloides* (Forbes); Matsumoto and Obata, p. 121, pl. 24, figs 1–5; pl. 30, fig. 1.
 1958 *Desmophyllites selwynianus* Anderson, p. 215, pl. 40, fig. 2.
 1958 *Desmophyllites siskiyouensis* Anderson, p. 215, pl. 35, fig. 3; pl. 41, figs 1–3.
 1958 *Desmophyllites yoloensis* Anderson, p. 216, pl. 41, fig. 6.
 1959a *Desmophyllites diphylloides* (Forbes); Matsumoto, p. 9, pl. 3, fig. 3; text-fig. 2.
 1961 *Desmophyllites diphylloides* (Forbes); Collignon, p. 61, pl. 25, figs 1–2; text-fig. 2.
 1961 *Desmophyllites diphylloides* var. *besairei* Collignon; Collignon, p. 63, pl. 25, figs 4–6; text-fig. 3.
 1961 *Desmophyllites diphylloides* var. *inermis* Collignon, p. 63, pl. 24, figs 4–5; pl. 25, fig. 3.
 1961 *Desmophyllites diphylloides* var. *lata* Collignon, p. 64, pl. 25, figs 7–8; text-fig. 4.
 1961 *Desmophyllites phyllimorphus* (Kossmat); Collignon, p. 65, pl. 26, fig. 1; text-fig. 5.
 1961 *Desmophyllites larteti* (Seunes); Collignon, p. 66, pl. 26, fig. 2; text-fig. 6.
 1963 *Desmophyllites phyllimorphus* (Kossmat); Jones, p. 34, pl. 10, figs 4–6.
 1965 *Desmophyllites diphylloides* (Forbes); Howarth, p. 388, pl. 11, fig. 3a–b.
 1966 *Desmophyllites diphylloides* (Forbes); Collignon, p. 84, pl. 489, fig. 1973.
 1966 *Desmophyllites diphylloides* var. *besairei* Collignon; Collignon, p. 9, pl. 458, fig. 1870.
 1966 *Desmophyllites diphylloides* var. *inermis* Collignon; Collignon, p. 9, pl. 458, fig. 1871.
 1966 *Desmophyllites diphylloides* var. *lata* Collignon; Collignon, p. 27, pl. 466, fig. 1900.
 1971 *Desmophyllites phyllimorphus* (Kossmat); Collignon, p. 36, pl. 655, fig. 2414.
 1971 *Desmophyllites diphylloides* (Forbes); Collignon, p. 37, pl. 655, fig. 2415.
 1971 *Desmophyllites larteti* (Seunes); Collignon, p. 38, pl. 655, fig. 2416.
 1977 *Desmophyllites diphylloides*; Kennedy, text-figs 31, 33.
 1980 *Desmophyllites diphylloides* (Forbes); Blaseo *et al.*, p. 483, pl. 2, figs 9–15.
 1985 *Desmophyllites diphylloides* (Forbes, 1846); Henderson and McNamara, p. 54, pl. 4, figs 1–4.
 1989 *Desmophyllites*; Kennedy, text-fig. 17d.

Types. Lectotype, by subsequent designation by Matsumoto and Obata (1955, p. 122) is BMNH C22682, the original of Forbes (1846, pl. 8, fig. 8; GSC R10470); paralectotypes are BMNH C22683 (figured by Spath 1953, pl. 2, fig. 5) and BMNH C22684–22685, all from the Valudavur Formation of Pondicherry, south India (ex Kaye and Cunliffe Collection). BMNH C51020 is a topotype.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C22685	9.8 (100)	4.2 (42.9)	5.0 (51.0)	0.84	1.0 (10.2)
BMNH C22684	17.8 (100)	7.8 (43.8)	9.0 (50.6)	0.87	1.8 (10.1)
BMNH C22682	20.0 (100)	8.5 (42.5)	10.0 (50.0)	0.85	2.0 (10.0)
BMNH C22683	20.5 (100)	8.5 (41.5)	10.0 (48.8)	0.85	2.0 (9.8)
BMNH C51020	39.8 (100)	17.0 (42.7)	20.5 (51.5)	0.83	~ 5.0 (12.6)

Description. The type series consists of juveniles only. The shell is slightly compressed, with whorl breadth to whorl height ratios of 0.87 in the smallest specimen and 0.83 in the largest. There is a tiny, pit-like umbilicus. The umbilical wall is subvertical, with the umbilical shoulder narrowly rounded. The flanks are weakly coneave and subparallel, with the greatest whorl breadth around mid-flank; the venter is evenly rounded. The shell surface is ornamented by delicate growth lines (Pl. 6, figs 4–9; Pl. 16, figs 1–3, 7–8), prorsiradiate and straight across most of the flanks but projected forwards and coneave on the outermost flank and ventrolateral shoulder and crossing the venter in a linguoid convexity. There are faint indications of constrictions, and weak collar-ribs, most prominent on the internal mould (Pl. 6, figs 1–3; Pl. 16, figs 1–2). They number up to six per whorl, are straight and prorsiradiate across most of the flank, flexing forwards and crossing the venter in a narrow linguoid convexity. Suture (Text-fig. 3F) with trifid L, equal in depth to E; U with five minor lobes on the dorsal flanks, arranged in a straight reitradiate line.

Discussion. Henderson and McNamara (1985) described this species at length, and had over 30 specimens, septate to nearly 80 mm diameter. Their specimens show constrictions weakening markedly, with parallel flanks (Pl. 17, figs 4–7), as in the largest Indian specimen (Pl. 18, figs 5–6). The type material of *D. phyllimorphum* (Kossmat, 1898) is a compressed example of this species. This and other synonyms were discussed by Henderson and McNamara (1985). *Desmophyllites larteti* (Seunes, 1891) (p. 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2–3; see synonymy in Kennedy and Summesberger 1984, p. 156) is more compressed, with an arched venter (in part perhaps accentuated by crushing), and markedly biconcave constrictions numbering 4–5 per half whorl. The types are shown in Plate 17, figure 9 and Plate 18, figures 1–6, together with the largest Indian specimen (Pl. 17, figs 5–6) and an Australian example of *D. diphylloides* (Pl. 17, figs 4, 7) for comparison.

Occurrence. Lower Santonian to Upper Maastrichtian of south India, Western Australia, Japan, Alaska, British Columbia, California, Argentina, Angola, Pondoland and Zululand (South Africa), Tunisia and southeastern France.

Subfamily PUZOSIINAE Spath, 1922, p. 126

Discussion. For synonymy, see Wright and Kennedy (1984, p. 54).

Genus KITCHINITES Spath, 1922, p. 127

[= *Neopuzosia* Matsumoto, 1954, p. 89; ?*Otiophyllites* Spath, 1953, p. 51]

Type species. *Holcodiscus pondicherryanus* Kossmat, 1897, p. 40 (147), pl. 6 (17), fig. 6, by original designation.

Discussion. See Henderson and McNamara (1985, p. 56).

Kitchinites pondicherryanus (Kossmat, 1897)

Plate 3, figs 10–12; Text-fig. 4A

1897 *Holcodiscus pondicherryanus* Kossmat, p. 40 (147), pl. 6 (17), fig. 6.

1922 *Kitchinites pondicherryanus* (Kossmat); Spath, p. 127.

1954 *Kitchinites pondicherryanus* (Kossmat); Matsumoto, p. 89.

1957 *Kitchinites pondicherryanus* (Kossmat); Wright, p. L366, text-fig. 478.2.

1989 *Kitchinites*: Kennedy, text-fig. 18c–d.

Type. Holotype, by monotypy, is BMNH C47548, the original of Kossmat (1897, pl. 6 (17), fig. 6; GSC unregistered), from the Valudavur Formation of Pondicherry, south India (ex Kaye and Cunliffe Collection).

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C47548	52.8 (100)	14.5 (27.5)	20.0 (37.9)	0.73	16.5 (31.3)

Description. The shell is compressed, coiling moderately evolute, with U = 31.3%, and about half the previous whorl covered. The umbilical wall is low, steep and rather flattened; the umbilical shoulder is narrowly rounded. The flanks are weakly convex, and the venter narrowly rounded; the greatest breadth is below mid-flank. Broad, weak, narrow ribs, about 40 on the last whorl, arise at or just outside the umbilical shoulder or intercalate on the outer flank. They are straight and recti- to feebly prorsiradiate on the flanks, projected forward and concave on the ventrolateral shoulders, and cross the venter in a broad convexity. Occasional long ribs branch on the outer flank. There are five constrictions per whorl, each flanked by collar-ribs, of which the adapical is the stronger. The constrictions arise at the umbilical shoulder, and are straight and prorsiradiate on the flanks, generally truncating one rib. Suture with well-developed minor elements; L deeper than E, and trifid. U with bifid minor lobes, retracted (Text-fig. 4).

Discussion. The holotype is the only known specimen of the species, and consists of phragmocone plus nearly 0.4 whorls of body chamber, and is probably adult. The sparse ribbing, weakly projected on ventrolateral shoulders and venter, distinguishes this species from all others; see reviews in Henderson and McNamara (1985) and Macellari (1986).

Occurrence. As for type.

Subfamily HAUERICERATINAE Matsumoto, 1938*b*, p. 193

Genus HAUERICERAS de Grossouvre, 1894, p. 219

Type species. *Ammonites gardeni* Baily, 1855, p. 450, pl. 11, fig. 3, by original designation.

Discussion. For synonymy see Kennedy (1986*a*, p. 27).

Hauericeras rembda (Forbes, 1846)

Plate 6, figs 10–24; Pl. 17, fig. 1; Text-fig. 3H

- 1846 *Ammonites Rembda* Forbes, p. 111, pl. 7, fig. 3.
 1846 *Ammonites Durga* Forbes, p. 104, pl. 7, fig. 11.
 1850 *Ammonites Rembda* Forbes; d'Orbigny, p. 213.
 1850 *Ammonites Durga* Forbes; d'Orbigny [*pars*], p. 213.
 1865 *Ammonites Rembda* Forbes; Stoliczka, p. 63, pl. 33, fig. 5.
 1865 *Ammonites Durga* Forbes; Stoliczka [*pars*], p. 143, pl. 71, fig. 5, non figs 6–7 (= *Puzosia compressa* Kossmat, 1898).
 non 1871 *Hauericeras rembda* Forbes; Griesbach, p. 63, pl. 3, figs 2–3 [= *H. gardeni* (Baily, 1855)].
 1898 *Desmoceras (Hauericeras) Rembda* Forbes sp.; Kossmat, p. 124 (189), pl. 18 (24), fig. 9.
 non 1906 *Hauericeras Rembda* Forbes; Woods, p. 333.
 non 1907 *Hauericeras Rembda* Forbes; Pervinquierè, p. 167, pl. 7, figs 7–10; text-fig. 69 [= *H. fayoli* (de Grossouvre, 1894)].
 1955 *Hauericeras (Gardeniceras) cf. rembda* (Forbes); Matsumoto and Obata, p. 144, pl. 29, figs 6–7.
 1955 *Hauericeras rembda* (Forbes); Matsumoto and Obata, p. 145, text-fig. 13.
 1971 *Hauericeras rembda* (Forbes); Collignon, p. 37, pl. 655, fig. 2417.
 1977 *Hauericeras rembda*; Kennedy, text-fig. 31. 18.

Types. Lectotype, by the subsequent designation of Matsumoto and Obata (1955, p. 145), is BMNH C51024, the original of Forbes (1846, pl. 7, fig. 3; GSC R10483); paralectotypes are BMNH C51023 and C51025. The figured syntype of *Ammonites durga* Forbes (1846, p. 104, pl. 7, fig. 11) is BMNH C51021, all from the Valudavur Formation of Pondicherry, south India (*ex* Kaye and Cunliffe Collection). BMNH C3567 is a topotype.

EXPLANATION OF PLATE 6

Figs 1–9. *Desmophyllites diphyloides* (Forbes, 1846). 1–3, BMNH C22682, the lectotype. 4–6, BMNH C22683, a paralectotype. 7–9, BMNH C22684, a paralectotype.

Figs 10–24. *Hauericeras rembda* (Forbes, 1846). 10–12, BMNH C51024, lectotype. 13, BMNH C3567, a topotype. 14–16, BMNH C51023, paralectotype. 17, BMNH C51025, paralectotype. 18–21, BMNH C51021, a syntype of *Ammonites Durga* Forbes, 1846. 22–24, BMNH C51022, a syntype of *Ammonites Durga* Forbes, 1846.

Figs 25–26. *Brahmaïtes (Anabrahmaïtes) vishnu* (Forbes, 1846). BMNH C51026, lectotype.

All specimens are from the Valudavur Formation of Pondicherry, south India. Figs 1–20, 22–26 × 1; fig. 21 × 2.



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<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51022	14.8 (100)	4.2 (28.4)	5.0 (33.8)	0.84	5.2 (35.1)
BMNH C51021	18.0 (100)	5.0 (27.8)	6.2 (34.4)	0.81	7.0 (38.9)
BMNH C51025	20.2 (100)	5.5 (27.2)	6.8 (33.7)	0.81	7.4 (36.6)
BMNH C51024	33.0 (100)	7.5 (22.7)	11.2 (33.9)	0.66	12.8 (38.8)

Description. Coiling is evolute, with U = 35–39% of diameter, and about a third of the previous whorl covered, the umbilicus shallow with a steep, feebly convex subvertical wall and narrowly rounded umbilical shoulder. The flanks are feebly convex and subparallel, with greatest breadth around mid-flank. To a diameter of 20 mm, the venter is narrowly rounded on both shell and internal mould. From 20 mm onwards, there is a sharp keel, with a striking flattened crest with polygonal cross-section where the shell is preserved. The keel is poorly differentiated, with a rounded crest on internal moulds. Ornament is either lacking or reduced to obscure growth lines over most of the shell surface; there are traces of three or four constrictions per whorl. These are much more conspicuous on internal moulds. They are rursiradiate on the upper part of the umbilical wall, deeply incised into the flank, convex at mid-flank, concave on the outer flank, and projecting forward across the ventrolateral shoulder to form a ventral chevron. Suture (Text-fig. 3H) with E broad and much shallower than L, which is asymmetrically trifid; U retracted on the inner flanks, umbilical shoulder and wall.

Discussion. As noted by Kossmat (1898), *Ammonites durga* of Forbes represents the early growth stages of *Hauericeras rembda*, prior to development of the keel. This is well illustrated by the largest paralectotype, BMNH C51023, which shows the beginning of a keel developing at 20 mm (Pl. 6, figs 14–16). The syntypes of *durga*, BMNH C51021 and C51022 are both less than 20 mm diameter. *H. rembda* most closely resembles *Hauericeras fayoli* de Grossouvre, 1894 (p. 220 [pars], pl. 27, fig. 3) which is probably from Tercis, Landes, France, and probably of late Campanian age (see revisions in Kennedy and Summesberger 1984, p. 147, pl. 1, figs 8 and 12; pl. 2, figs 4, 13–15, and Kennedy 1986b, p. 27, text-fig. 9a–j). But this is much more evolute, with U = 45%, with constrictions that are sinuous rather than biconvex. The Maastrichtian *H. sulcatum* (Kner, 1848) (p. 8, pl. 1, fig. 3; see revision in Kennedy and Summesberger 1986, p. 27, pl. 1, figs 1–7; pl. 13, fig. 2) has 6 or 7 prorsiradiate constrictions per whorl that are concave, rather than biconcave.

Occurrence. Maastrichtian of south India.

Family KOSSMATICERATIDAE Spath, 1922, p. 134
 Subfamily KOSSMATICERATINAE Spath, 1922, p. 134
 Genus BRAHMAITES Kossmat, 1897, p. 44 (14)
 Subgenus BRAHMAITES Kossmat, 1897, p. 44 (14)

Type species. *Ammonites Brahma* Forbes, 1846, p. 100, pl. 8, fig. 1, by original designation.

Discussion. Two subgenera *B. (Brahmaites)* and *B. (Anabrahmaites)* are recognized, following Henderson and McNamara (1958, p. 67); see also Kennedy (1986b, p. 29)

Brahmaites (Brahmaites) brahma (Forbes, 1846)

Plate 7, figs 1–3; Plate 8, figs 1–11; Plate 9, figs 1–4, 8–16; Text-fig. 5

- 1846 *Ammonites Brahma* Forbes, p. 100, pl. 8, fig. 1.
 1865 *Ammonites Brahma* Forbes; Stoliczka, p. 163, pl. 79, figs 2–4.
 1894 *Hauericeras fayoli* de Grossouvre [pars], p. 220, non pl. 27, fig. 3.

EXPLANATION OF PLATE 7

Figs 1–3. *Brahmaites (Brahmaites) brahma* (Forbes, 1846). BMNH C51029, the lectotype; Valudavur Formation; Pondicherry, south India, ×1.



KENNEDY and HENDERSON, *Brahmaites* (*Brahmaites*)

- 1897 *Brahmaïtes Brahma* Forbes sp.; Kossinat [pars], p. 45 (152), non pl. 8 (19), figs 7-8 [= *Brahmaïtes* spp.].
 1901 *Hauericeras fayoli* de Grossouvre; de Grossouvre, p. 382.
 ?1907 *Brahmaïtes Brahma* Forbes; Boule *et al.*, p. 7 (27).
 1925 *Brahmaïtes Brahma* Forbes; Diener [pars], p. 103.
 non 1938 *Brahmaïtes Brahma* Forbes; Collignon, p. 97 (44), pl. 8, figs 1-2.
 1938 *Brahmaïtes brahma* Forbes; Roman, p. 390, pl. 40, fig. 377.
 1957 *Brahmaïtes brahma* (Forbes); Wright, p. L376, text-fig. 491.1.
 non 1971 *Brahmaïtes brahma* Forbes; Collignon, p. 20, pl. 647, figs 2396-2397.
 1977 *Brahmaïtes brahma*; Kennedy, text-fig. 31.20-21.
 1985 *Brahmaïtes brahma* (Forbes, 1846); Henderson and McNamara, p. 70.
 1986b *Brahmaïtes brahma* (Forbes, 1846); Kennedy, p. 29, text-fig. 10a-k.
 1989 *Brahmaïtes*; Kennedy, text-fig. 17f.

Types. Lectotype, by the subsequent designation of Kennedy 1986b (p. 29) is BMNH C51029, the original of Forbes (1846, pl. 8, fig. 1a-b; GSC R10457); paralectotypes are BMNH C51030, the original of Forbes (1846, pl. 8, fig. 1c; GSC R10458), BMNH C51031-51037, all from the Valudavur Formation of Pondicherry, south India (*ex* Kaye and Cunliffe Collection).

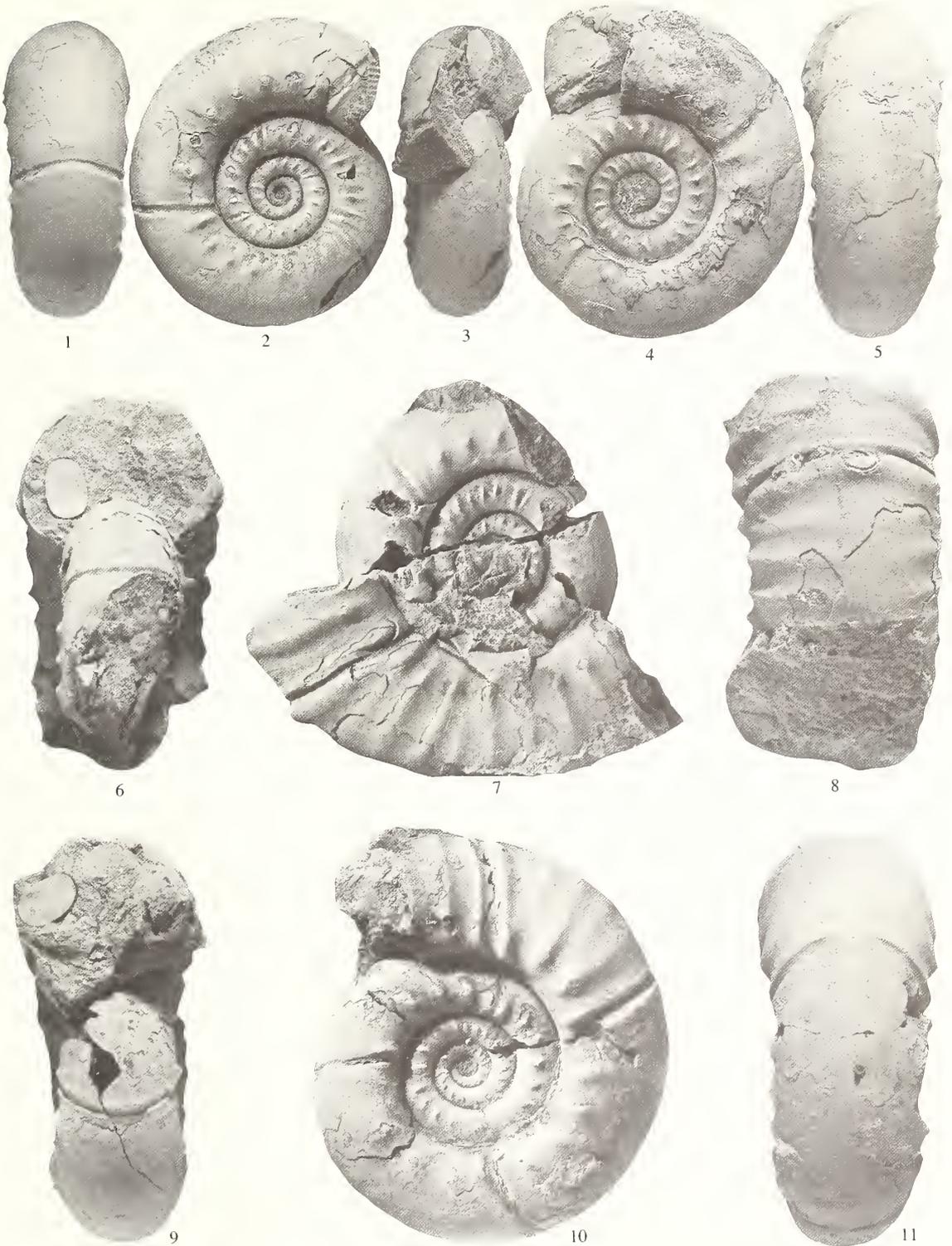
<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH 24195a	15.2 (100)	8.5 (55.9)	4.4 (28.9)	1.93	5.6 (36.8)
BMNH C3564a	15.5 (100)	8.5 (54.8)	4.5 (29.0)	1.90	5.8 (37.4)
BMNH C3564b	16.2 (100)	8.7 (53.7)	4.4 (27.1)	1.98	6.0 (37.0)
BMNH C51034	17.5 (100)	9.8 (56.0)	5.0 (28.6)	1.96	6.2 (35.4)
BMNH C82496	18.0 (100)	9.8 (54.4)	4.8 (26.7)	2.04	6.2 (34.4)
BMNH C51036	18.2 (100)	9.5 (52.2)	5.2 (28.6)	1.82	6.2 (34.1)
BMNH C51037	18.5 (100)	9.8 (53.0)	5.8 (31.3)	1.69	6.2 (33.5)
BMNH 24195b	23.5 (100)	11.0 (46.8)	6.0 (25.5)	1.83	9.0 (38.3)
BMNH C51033	25.2 (100)	12.2 (48.4)	7.2 (28.6)	1.69	9.0 (35.7)
BMNH 24195c	45.5 (100)	19.5 (42.9)	12.0 (26.4)	1.62	20.2 (44.4)
BMNH C51032	49.0 (100)	20.5 (41.8)	13.2 (26.9)	1.50	22.2 (45.3)
BMNH C51035	63.5 (100)	27.4 (43.1)	18.0 (28.3)	1.52	29.5 (46.5)
BMNH C51029	108.0 (100)	35.0 (32.4)	29.0 (26.9)	1.21	56.0 (51.8)

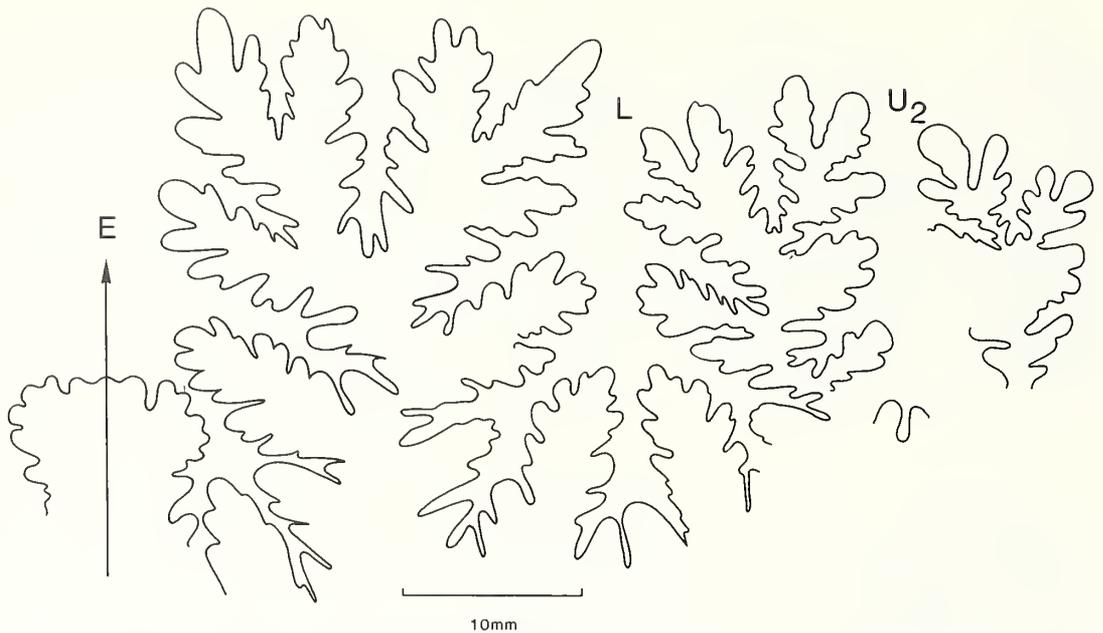
Description. Coiling is very evolute, serpenticone, with a broad umbilicus, U = as little as 33% in juveniles but increasing to 51.8% in adults. The umbilical wall is convex, sloping outwards and merging with a rounded umbilical shoulder. The flanks are low and convex, the venter broadly arched. The greatest whorl breadth is just outside the umbilical shoulder with a whorl breadth to height ratio of up to 2 in juveniles, decreasing to as little as 1.21 in adults. Umbilical bullae are already present at less than 10 mm diameter (Pl. 9, fig. 4), and number 16-22 per whorl. They disappear at a diameter of about 80 mm. The bullae are borne on prorsiradiate ribs that arise high on the umbilical wall and are distant, straight and prorsiradiate, and limited to the flanks at diameters of 60 mm and less. At larger diameters, including those where bullae have been lost, the ribs extend across the ventrolateral shoulder (where they are markedly convex), weakening over the venter, which they cross in a broad convexity; shorter intercalated ribs may also appear. Prominent constrictions, 3 to 4 per whorl, are much more prorsiradiate than the ribs, are deeply incised into the umbilical shoulder, straight on the flanks, projected forward over the ventrolateral shoulder, and cross the venter in a broad convexity (Pl. 7; Pl. 8, figs 1, 9, 11). They are preceded by a strong collar, often raised into a bulla on the umbilical shoulder, and bearing a siphonal bulla at diameters in excess of 90 mm. The suture (Text-fig. 5) is only moderately incised; L is trifold and deeper than E. U has trifold minor lobes, and is retracted on the umbilical wall.

EXPLANATION OF PLATE 8

Figs 1-11. *Brahmaïtes (Brahmaïtes) brahma* (Forbes, 1846). 1-3, BMNH 24195a, a topotype (*ex* Kaye Collection). 4-5, BMNH C51032, a paralectotype. 6-8, BMNH C51031, a paralectotype. 9-11, BMNH C51035, a paralectotype.

All specimens from the Valudavur Formation of Pondicherry, south India. All $\times 1$.





TEXT-FIG. 5. Suture of *Brahmaïtes (Brahmaïtes) brahma* (Forbes, 1846), BMNH C10535.

Discussion. The large suite of specimens available shows the whole of the ontogeny of this species, the lectotype being an adult, with about a whorl of body chamber, and a terminal constriction (Pl. 7). *B. (B.) kossmati* Henderson and McNamara, 1985 (p. 68, pl. 6, figs 11–14; pl. 7, fig. 1; text-figs 9–10) is more widely umbilicate and has a more depressed whorl than *B. (B.) brahma*, and stronger and more numerous ribs when adult.

Specimens described by Kossmat (1897) as *Brahmaïtes brahma* and from the Arialur stage of Trichinopoly belong to other forms; his plate 8 (19), figure 7 is closer to *B. (B.) kossmati* Henderson and McNamara, 1985, but does not develop the distinctive mature ribbing of that species. Kossmat's smaller specimen (pl. 8 (19), fig. 8) has delicate ribs arising in groups from umbilical bullae, quite unlike the present species. *B. (B.) brahma* of Collignon (1938, 1971) from Madagascar have whorl breadth to height ratios of about 1.2 at shell diameters of 50–80 mm, much less than in the type series, suggesting they represent some local form, although Stoliczka (1865) described an equally slender form from Pondicherry.

Occurrence. Maastrichtian of south India and south-western France.

EXPLANATION OF PLATE 9

Figs 1–4, 8–16. *Brahmaïtes (Brahmaïtes) brahma* (Forbes, 1846). 1–3, BMNH C82496, a topotype. 4, BMNH C51036, a paralectotype. 8–10, BMNH C51036, a paralectotype. 11–13, BMNH C51033, a paralectotype. 14–16, BMNH 24195*b*, a topotype.

Figs 5–7, 17–20. *Brahmaïtes (Anabrahmaïtes) vishnu* (Forbes, 1846). 5–7, BMNH C51028, found with the syntypes of *Ammonites Garuda* Forbes, 1846. 17–18, BMNH 24192, a topotype (*ex* Kaye Collection). 19–20, BMNH 83624*a*, a topotype (*ex* Marsham Collection).

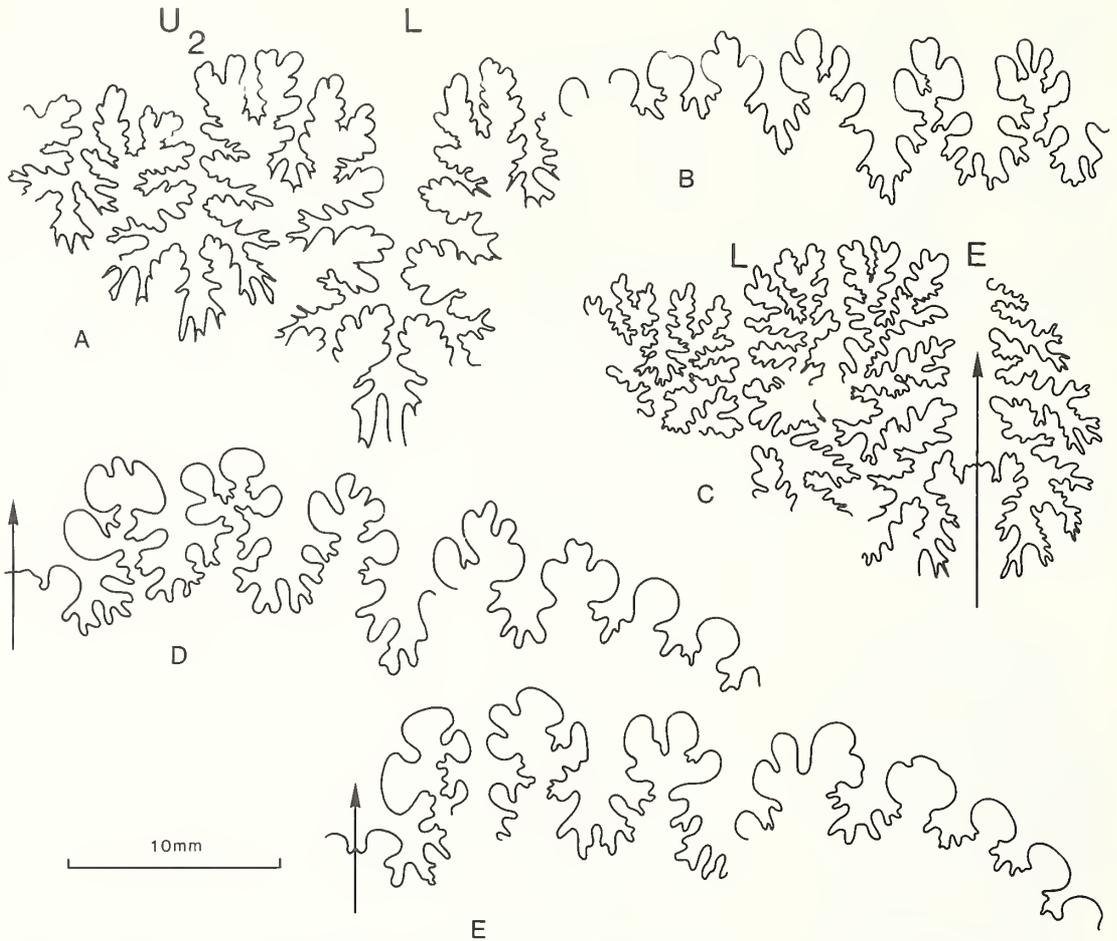
All specimens from the Valudavur Formation of Pondicherry, south India. All $\times 1$.



Subgenus ANABRAHMAITES Yabe and Shimizu, 1924, p. 79

[= *Subbrahmaites* Yabe and Shimizu, 1924, p. 75]

Type species. *Anmonites Vishnu* Forbes, 1846, p. 100, pl. 7, fig. 9.



TEXT-FIG. 6. Sutures of A, *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858), the lectotype of *Anmonites chrislma*, Forbes, 1846, BMNH C51041. B, D, E, *Sphenodiscus siva* (Forbes, 1846). B, D, BMNH C51088, E, BMNH C51087. C, *Menites menu* (Forbes, 1846), BMNH C47550.

EXPLANATION OF PLATE 10

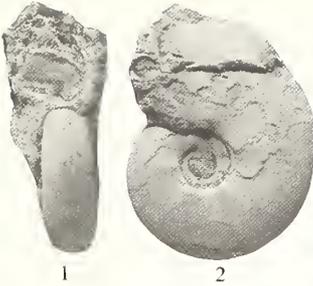
Figs 1–2. *Pachydiscus (Pachydiscus)* sp. juv., cf. *neubergicus neubergicus* (Hauer, 1858). BMNH C51062, a paralectotype of *Anmonites Varuna* Forbes, 1846.

Figs 3–4. *Pachydiscus (Pachydiscus) yama* (Forbes, 1846). BMNH C51040, the holotype.

Fig. 5. *Brahmaites (Anabrahmaites) vishnu* (Forbes, 1846). BMNH C51027, a paralectotype.

Figs 6–8. *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858). BMNH C51047, a paralectotype of *Anmonites Chrislma* Forbes, 1846.

All specimens from the Valudavur Formation of Pondicherry, south India. Figs 1–4 $\times 2$; figs 5–8 $\times 1$.



KENNEDY and HENDERSON, *Pachydiscus*, *Brahmaites*

Diagnosis. *Brahmaïtes* in which umbilical bullae are lacking, whorls equidimensional or weakly compressed, and ribs simple and annular, closely spaced in early growth but widely separated at maturity, with siphonal tubercles.

Discussion. Whorl proportions, lack of bullae and ribbing style set *Anabrahmaïtes* apart from *Brahmaïtes*, and we afford it subgeneric status. *Subbrahmaïtes* Yabe and Shimizu, 1924 (p. 75), with *Brahmaïtes sachalinensis* Yabe and Shimizu, 1924 (p. 78, pl. 13, figs 1–4 as type species) is regarded as a synonym of *Anabrahmaïtes*.

Occurrence. Maastrichtian of south India, southwestern France, northern Spain, Armenia, Sakhalin, and Madagascar.

Brahmaïtes (Anabrahmaïtes) vishnu (Forbes, 1846)

Plate 6, figs 25–26; Plate 9, figs 5–7, 17–20; Plate 10, fig. 5; Plate 17, figs 8, 10–11

- 1846 *Ammonites Vishnu* Forbes, p. 100, pl. 7, fig. 9.
 1850 *Ammonites Vishnu* Forbes; d'Orbigny, p. 213.
 1865 *Ammonites Vishnu* Stoliczka, p. 164, pl. 79, fig. 5.
 1891 *Puzosia haugi* Seunes, p. 20, pl. 15 (6), fig. 1.
 1894 *Gaudryceras planorbiforme* J. Böhm sp.; de Grossouvre [*pars*], p. 231, pl. 34, figs 4–5; pl. 35, fig. 7 [*non* pl. 27, fig. 2, a gaudryceratid].
 1897 *Brahmaïtes vishnu* Forbes sp.; Kossmat, p. 46 (153), pl. 8 (19), fig. 10.
 1938 *Brahmaïtes haugi* Seunes; Collignon, p. 45, pl. 7, fig. 3.
 1970 *Brahmaïtes vishnu* (Forbes); Atabekian and Akopian, p. 37, pl. 2, fig. 6.

Types. Lectotype, here designated, is BMNH C51026, the original of Forbes (1846, pl. 7, fig. 9; GSC R10456); BMNH C51027 is a paralectotype; BMNH C51028 was found with the types of *Ammonites garuda*; all are from the Valudavur Formation of Pondicherry, south India (*ex* Kaye and Cunliffe Collection). Topotypes are BMNH 24192 (*ex* Kaye Collection), and BMNH 83624a (*ex* Marsham Collection).

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51028	11.0 (100)	5.5 (50.0)	2.8 (25.5)	1.96	3.8 (34.5)
BMNH 24192	73.5 (100)	24.2 (32.9)	21.5 (29.3)	1.13	33.0 (44.9)
BMNH 83624a	95.0 (100)	34.0 (35.8)	29.0 (30.5)	1.17	45.0 (47.4)
BMNH C51027	100.0 (100)	31.0 (31.0)	31.5 (31.5)	0.98	44.0 (44.0)
BMNH C51026	107.0 (100)	31.5 (29.4)	32.0 (29.9)	0.98	49.0 (45.8)

Description. The earliest growth stages seen are represented by BMNH C51028 (Pl. 9, figs 5–7), a juvenile 11 mm in diameter. The shell is moderately evolute, with a depressed reniform whorl section, and a near-smooth surface with distant prorsiradiate constrictions, with an associated collar-rib. The inner whorls of larger specimens show coiling to have been more evolute, serpenticone, and ornamented only by growth lines, distant constrictions and associated collar-ribs to a diameter of 20 mm. Beyond this, coiling continues to be very evolute, with a broad, shallow umbilicus ($U = 44\text{--}47\%$), the umbilical wall convex and sloping outwards from the umbilical seam, and merging with a poorly defined umbilical shoulder. The flanks are flattened, and the ventrolateral shoulders and venter broadly rounded. Weak, distant even ribs appear from 20 mm diameter onwards, and arise at the umbilical shoulder, are prorsiradiate and straight to feebly convex on the flanks, effacing on the outer flank and numbering around 40 per whorl. From about 50 mm diameter onwards the ribs coarsen markedly and are of variable strength and spacing, numbering around 20 per whorl. They are narrow, straight to feebly convex, prorsiradiate and annular, weak on the inner flank but strong on the outer flank and ventrolateral shoulders, and weakening over the siphonal region. The ribs weaken markedly on the last part

EXPLANATION OF PLATE II

Figs 1–3. *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858). BMNH C51041, the lectotype of *Ammonites Christna* Forbes, 1846; Valudavur Formation; Pondicherry, south India, $\times 1$.



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KENNEDY and HENDERSON, *Pachydiscus* (*Pachydiscus*)

of the adult shell. Prominent constrictions are present at all ontogenetic stages, generally numbering three per whorl. They are narrow and deep, feebly rursiradiate on the umbilical wall, deeply incised into the umbilical shoulder, and straight and prorsiradiate on the flanks, crossing the venter near-straight and transverse. Each is preceded by a collar, which increases in strength through ontogeny, becoming very coarse in adults, with feeble bullae in some cases. There is a coarse siphonal tubercle, which extends from the rib to interrupt the constriction (Pl. 6, fig. 25; Pl. 9, fig. 19). Suture complex, with L as deep as E and trifold, U trifold, and the umbilical lobe strongly retracted.

Discussion. We can see no significant differences between the holotype of *Puzosia haugi* of Seunes (1891), and the Indian types, apart from differences in preservation, the former, shown in Pl. 17, figs 8, 10, 11, being a composite mould. *P. haugi* was regarded as a synonym to *Gandryceras planorbiforme* of Böhm (1891, pl. 1, figs 11–12) by de Grossouvre (1894, p. 231), but this is a gaudryceratid, as is de Grossouvre's Tercis specimen (1894, pl. 27, fig. 2). *Anabrahammatites sachalinensis* Yabe and Shimizu, 1924 (p. 78, pl. 13, figs 1–4) is even more distantly ribbed than the present species when adult, and lacks the closely ribbed middle growth stage. *Brahmatites mikobokensis* Collignon, 1971 (p. 22, pl. 647, figs 2400–2401) has densely and evenly ribbed, depressed reniform whorls in middle and later growth, with incipient umbilical bullae on internal moulds, the ribbing effacing over the venter, with no siphonal tubercles on internal moulds.

Occurrence. Maastrichtian, south India, Madagascar, south-western France and northern Spain.

Family PACHYDISCIDAE Spath, 1922, p. 132

Discussion. See Kennedy (1986b, p. 30) for a review of the nomenclature problems associated with the dimorphism present in the family.

Genus PACHYDISCUS Zittel, 1884, p. 466
Subgenus PACHYDISCUS Zittel, 1884, p. 466

Type species. *Ammonites neubergicus* Hauer, 1858, p. 12, pl. 2, figs 1–3; pl. 3, figs 1–2, by the subsequent designation of de Grossouvre 1894, p. 177.

Discussion. See Kennedy and Summesberger (1986, p. 188), and Kennedy (1986b, p. 34).

Pachydiscus (Pachydiscus) neubergicus neubergicus (Hauer, 1858)

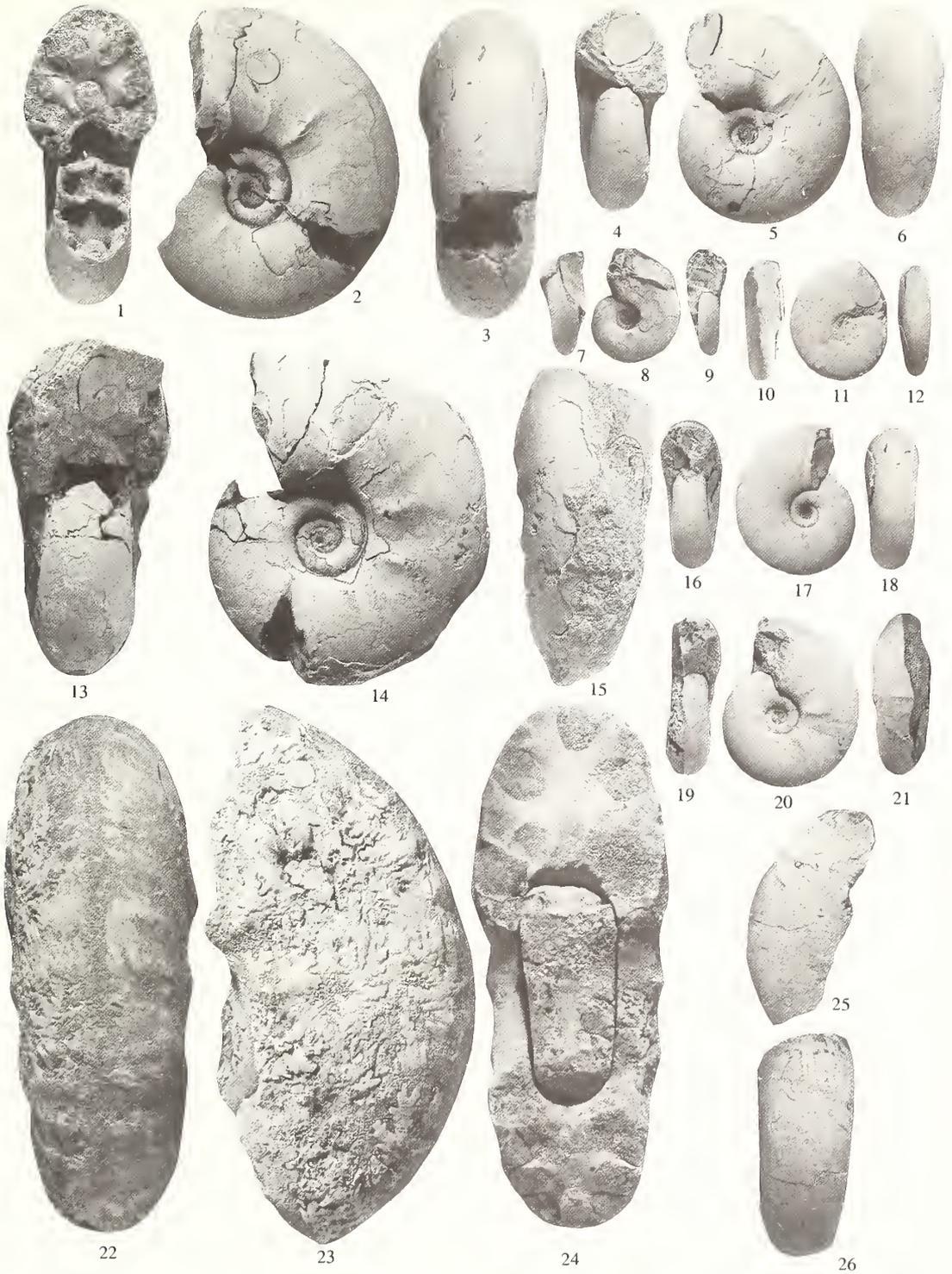
Plate 10, figs 6–8; Plate 11; Text fig 6A

1846 *Ammonites Chrishna* Forbes, p. 103, pl. 9, fig. 2.

1850 *Ammonites Chrishna* Forbes; d'Orbigny, p. 213.

EXPLANATION OF PLATE 12

Figs 1–6, 13–15, 19–26. *Pachydiscus (Pachydiscus) egertoni* (Forbes, 1846). 1–3, BMNH C41042, the lectotype of *Ammonites Ganesa* Forbes, 1846. 4–6, BMNH C51045, a syntype of *Ammonites Ganesa* Forbes, 1846. 13–15, BMNH C51044, a possible syntype of *Ammonites Ganesa* Forbes, 1846. 19–21, BMNH C51046, a syntype of *Ammonites Ganesa* Forbes, 1846. 22–26, BMNH C51043, a paralectotype.
Figs 7–9. *Pachydiscus (Pachydiscus)* sp. juv. cf. *neubergicus neubergicus* (Hauer, 1858). BMNH C51062, a syntype of *Ammonites Varuna* Forbes, 1846.
Figs 10–12. *Pachydiscus (Pachydiscus) yama* (Forbes, 1846). BMNH C51040, the holotype.
Figs 16–18. *Pachydiscus (Neodesmoceras) soma* (Forbes, 1846). BMNH C51039, the holotype.
All specimens from the Valudavur Formation of Pondicherry, south India. All $\times 1$.



- 1858 *Ammonites Neubergeticus* Hauer [*pars*], p. 12, pl. 2, figs 1–3, [*non* pl. 3, figs 1–2 = *Pachydiscus haueri* Collignon, 1952].
- 1986 *Pachydiscus (Pachydiscus) neubergeticus* (Hauer, 1858); Kennedy and Summesberger, p. 189, pl. 2, figs 1–2; pl. 3, figs 1–3; pl. 4, figs 1–5; pl. 5, figs 1, 4–5; pl. 6, figs 1–2, 5; pl. 15, figs 7–8; text-fig. 5a–b [with full synonymy].
- 1986c *Pachydiscus (Pachydiscus) neubergeticus* (Hauer, 1858); Kennedy, p. 34, pl. 4, fig. 3.
- 1986 *Ammonites neubergeticus* Hauer, 1858; Henderson and Kennedy, p. 277.
- 1986 *Ammonites chrishna* Forbes, 1846; Henderson and Kennedy, p. 277.
- 1986 *Pachydiscus chrishna* (Forbes, 1846); Matsumoto in Matsumoto *et al.*, p. 8.

Types. The lectotype of *P. (P.) neubergeticus* is no. 1858.01.6, in the collection of the Geologische Bundesanstalt, Vienna, and is the original of Hauer 1858 (p. 12, pl. 2, figs 1–2). There are three paralectotypes with the same registration number. All are from the Maastrichtian of Neuberger, Steiermark, Austria. The lectotype, here designated, of *Ammonites chrishna* is BMNH C51038, the original of Forbes (1846, pl. 9, fig. 2; GSC R10479); paralectotypes are BMNH C51043 and C51047. All are from the Valudavur Formation of Pondicherry, South India (*ex* Kaye and Cunliffe Collection).

Under the plenary powers of the International Commission on Zoological Nomenclature, *Ammonites neubergeticus* Hauer, 1858, is given precedence over *Ammonites chrishna* Forbes, 1846, whenever the two names are considered to be synonyms (ICZN Opinion 1519, 1989).

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51041	115.5 (100)	33.3 (28.8)	45.5 (39.4)	0.73	33.2 (28.7)

Description. What may be the early growth stages of this species are represented by BMNH C51062, one of the type series of *Ammonites varuna* (Pl. 10, figs 1–2; Pl. 12, figs 7–9). It is 12 mm in diameter, moderately involute with a small, shallow umbilicus, compressed whorls (whorl breadth to height ratio 0.75 approximately) and five umbilical bullae on the outer whorl. BMNH C51038, the lectotype of *P. (P.) chrishna*, is very well preserved, retaining much of its original shell and over half a whorl of body chamber; it seems to be a near-complete adult. Coiling is fairly involute, with about 50% of the previous whorl covered, the umbilicus comprising 28.7% of the diameter, shallow, with a low umbilical wall, sloping outwards from the umbilical seam to a well-rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.73, the greatest breadth around mid-flank, the flanks weakly convex, converging to a rounded venter. There are two orders of ribs on the phragmocone and early body chamber; primaries, which efface on the outer flank but which may be tenuously linked to pairs of secondaries, and secondary ribs confined to the ventrolateral shoulders and venter. The primary ribs are rursiradiate and concave on the umbilical wall and shoulder, and straight and recti- to feebly prorsiradiate on the flanks. They strengthen into long umbilical bullae, and are very distant, numbering 12 per whorl on the last whorl of the phragmocone, and 14 on the outer whorl of the specimen. Secondary ribs arise on the ventrolateral shoulders, are markedly prorsiradiate, concave on the shoulders, strengthened and more or less transverse on the venter, effacing somewhat over the siphuncle. They disappear at a diameter of 95 mm, and number 28 on the last half whorl on which they are present. Suture typical for genus, with L and the first minor lobe on the retracted umbilical lobe trifid.

Discussion. The figured paralectotype (Pl. 10, figs 6–8) is rather worn, but conforms well with the lectotype. The types and additional topotype material of *P. (P.) neubergeticus neubergeticus* were described and illustrated at length by Kennedy and Summesberger (1986), who discussed differences from other species, and showed *neubergeticus* and *chrishna* to represent one and the same species. Differences between *P. (P.) neubergeticus* and other species were also discussed by Kennedy (1986c). *P. (P.) neubergeticus dissitus* Henderson and McNamara, 1985 (p. 72, pl. 7, figs 7, 9; pl. 10, figs 3–6; text-figs 11, 12e, 13c) has inner whorls indistinguishable from those of *P. (P.) neubergeticus*

EXPLANATION OF PLATE 13

Figs 1–3. *Pachydiscus (Pachydiscus) egertoni* (Forbes, 1846). BMNH C51038, the lectotype; Valudavur Formation; Pondicherry, south India, $\times 1$.



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nebergicus (e.g. compare text-fig. 11 in Henderson and McNamara 1985 with Pl. 11, fig. 2 herein). But from a diameter of 85–95 mm onwards, there is an utterly distinct ornament on the late phragmocone of *dissitus* (body chambers are unknown) with many more ventral than umbilical ribs, the subspecies coming to resemble *P. (P.) gollevillensis* (d'Orbigny, 1850) where, however, this dense ventral ribbing occurs throughout ontogeny.

Occurrence. Low Lower to low Upper Maastrichtian of northern Spain, southwestern France, north Germany, Denmark, Poland,¹ Austria, European Russia, the Ukrainian SSR, the Armenian SSR, Zululand (South Africa), Nigeria, Madagascar, Brazil and South India. Subspecies *dissitus* is known only from the Upper Maastrichtian of Western Australia.

Pachydiscus (Pachydiscus) egertoni (Forbes, 1846)

Plate 12, figs 1–6, 13–15, 19–26; Plate 13, figs 1–3; Text-fig 4b

- 1846 *Ammonites Egertoni* Forbes, p. 108, pl. 9, fig. 1.
 1846 *Ammonites Ganesa* Forbes, p. 103, pl. 7, fig. 8.
 1850 *Ammonites Chrishna* Forbes; d'Orbigny [*pars*], p. 213.
 1864 *Ammonites Egertoni* Forbes; Stoliczka [*pars*], p. 104, [*non* pl. 53, fig. 1 = *P. (P.) preegertoni* Collignon, 1955, according to Matsumoto in Matsumoto *et al.*, 1986]; *nec* pl. 53, fig. 2 = *Pseudomenuites stoliczkai* Matsumoto in Matsumoto *et al.*, 1986; ?pl. 53, fig. 3 (suture only); *nec* pl. 53, fig. 4 = *P. (P.) neubergicus neubergicus*.
 1864 *Ammonites ganesa* Forbes; Stoliczka, p. 106, pl. 54, fig. 2.
 1898 *Pachydiscus ganesa* Forbes sp.; Kossmat, p. 96 (161), pl. 15 (21), fig. 2.
 ?*non* 1898 *Pachydiscus egertonianus* Forbes sp.; Kossmat, p. 94 (159), pl. 15 (21), fig. 4.
 1959a *Pachydiscus egertoni* (Forbes); Matsumoto, p. 42, text-fig. 17.
 1959a *Pachydiscus* (s.s.) cf. *egertoni* (Forbes); Matsumoto [*pars*], p. 42, text-fig. 18 only.
 1959a *Ammonites ganesa* Forbes; Matsumoto, p. 45, text-fig. 18.
 ?1985 *Pachydiscus (Pachydiscus) egertoni* (Forbes, 1846); Zaborski, p. 19, text-fig. 19.
 1986 *Ammonites egertoni* Forbes, 1846; Matsumoto in Matsumoto *et al.*, p. 7, text-fig. 2.
 1986 *Pachydiscus*; Kennedy, text-fig. 18e.

Types. Lectotype, designated by Matsumoto, 1959a (p. 42), is BMNH C51038, the original of Forbes, 1846 (pl. 9, fig. 1; GSC R10479); BMNH C51043 is a paralectotype. The lectotype, here designated, of *Ammonites Ganesa* Forbes, 1846, is BMNH C51042, the original of Forbes (1846, pl. 7, fig. 8; GSC R10465); paralectotypes are BMNH C51044–51046. BMNH C51047 is also believed to be a paralectotype, although questioned by Matsumoto (1959a, p. 42). All are from the Valudavur Formation of Pondicherry, south India (ex Kaye and Cunliffe Collection).

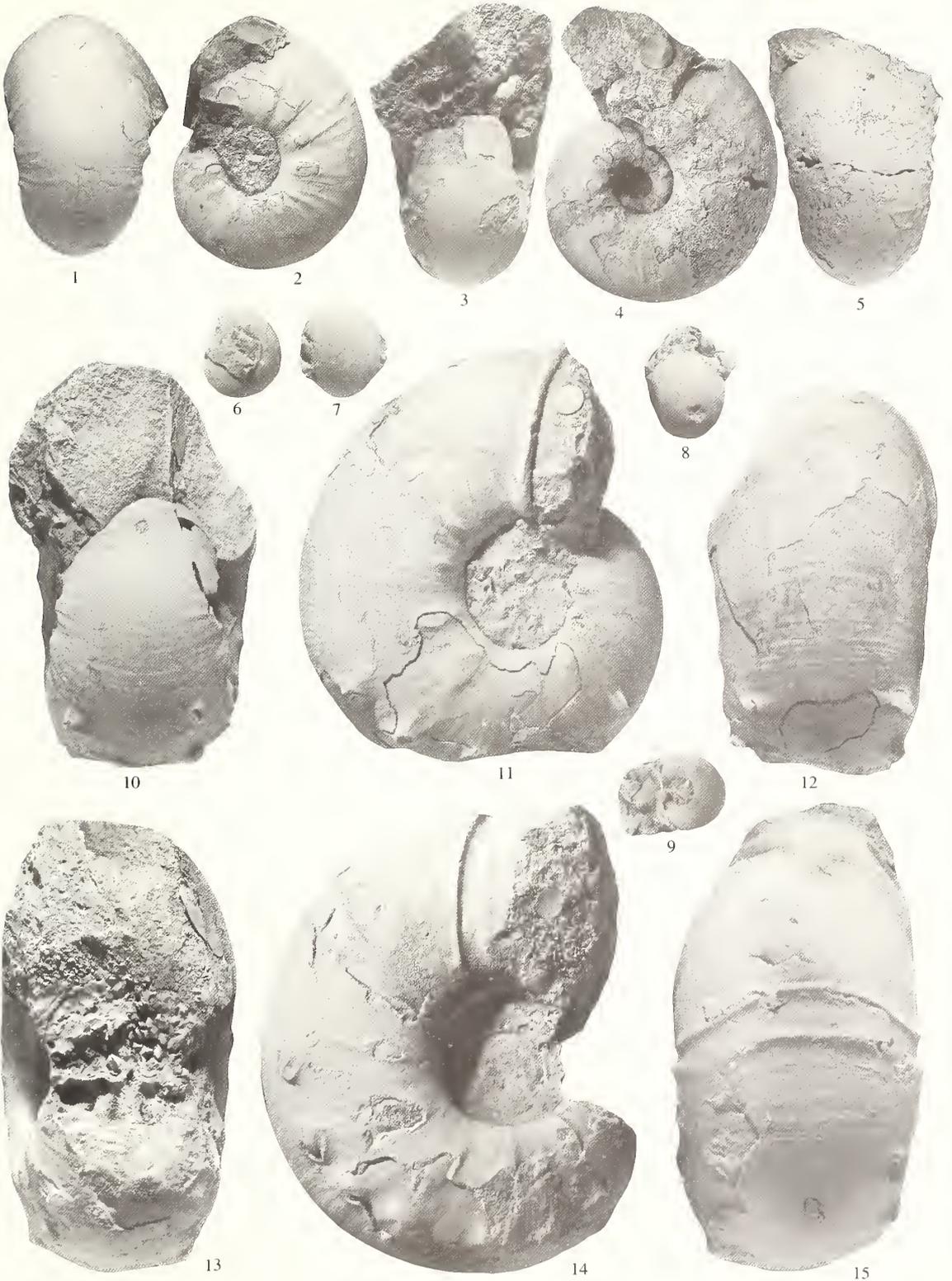
<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C57046	29.0 (100)	13.5 (46.6)	12.8 (44.1)	1.05	7.8 (26.9)
BMNH C51044	43.8 (100)	18.8 (42.9)	18.5 (42.2)	1.02	12.0 (27.3)
BMNH C51042	45.0 (100)	18.8 (41.8)	18.5 (41.1)	1.02	12.5 (27.7)
BMNH C51038	103.0 (100)	38.0 (36.9)	43.0 (41.7)	0.88	28.5 (27.7)

Description. The lectotype and paralectotype of *P. (P.) egertoni* are both phragmocones, the former retaining traces of shell, the latter an internal mould. The coiling is moderately involute, with U = 27.7% of diameter. The umbilicus is of moderate depth, the wall initially steep, but sloping outwards thereafter to a gently rounded

EXPLANATION OF PLATE 14

Figs 1–15. *Menuites menu* (Forbes, 1846). 1–2, BMNH C47551, a paralectotype. 3–5, BMNH C47550, a paralectotype. 6–9, two BMNH unregistered syntypes. 10–12, BMNH C47549, a paralectotype. 13–15, BMNH C51048, the lectotype.

All specimens from the Valudavur Formation of Pondicherry, south India. Figs 1–5, 10–15 × 1; figs 6–9 × 2.



umbilical shoulder. The lectotype has a whorl breadth to height ratio of 0.88 at a diameter of 103 mm. The greatest breadth is below mid-flank, the inner flanks broadly rounded, the outer flanks becoming progressively more convergent as size increases, so that the venter becomes progressively more narrowly rounded.

Juveniles, to a diameter of 45 mm, have 7 or 8 primary ribs per whorl, expanded into umbilical bullae, straight and prorsiradiate on the inner flanks, effacing on the outer. Non-bullate primaries are sometimes intercalated between the bullate ones at this growth stage. Secondary ribs are restricted to the outer flanks and venter, and are only transiently developed, being absent below 45 mm diameter and disappearing at 65 mm diameter in the lectotype; two secondaries separate the primaries at this stage. The lectotype has 12 distant rectiradiate primary ribs on the outer whorl, those on the last part extending to the ventrolateral shoulder but weakening and effacing over the venter. Suture (Text-fig. 4B) typical for subgenus, with deep trifold L and U retracted on umbilical wall.

Discussion. The syntypes of *Ammonites Ganesa* of Forbes (Pl. 12, figs 1–6, 13–15, 19–21) are juvenile *P. (P.) egertoni*, although one, BMNH C51046 (Pl. 12, figs 19–21) has stronger ventral ribbing than the others. It has two thirds of a whorl of body chamber, and a weak terminal constriction. *P. (P.) egertoni* and *P. (P.) jacquoti jacquoti* (Seunes, 1890b) (p. 5, pl. 3 (2), figs 1–3; see revision in Kennedy 1986c, p. 34, pl. 5, figs 3–11, 15–19; pl. 6; text-figs 2d–e; 3o, s; 4b) are closely allied, and Atabekian and Akopian (1969) regarded them as no more than subspecifically distinct. The umbilicus of *egertoni* is smaller, whorls higher with a lower whorl breadth to height ratio, the whorl sides convergent rather than subparallel, with ornament declining from a much smaller diameter. *P. (P.) jacquoti australis* Henderson and McNamara, 1985 (p. 76, pl. 8, figs 1–2, 7–10a; text-figs 12a, 13b, 14, 15a) is a coarser ribbed form that retains secondary ribs to a large diameter; *P. (P.) jacquoti chilensis* Stinnisbeck, 1986 (p. 218, pl. 13, fig. 8; pl. 15, figs 1, 3; text-fig. 28a) seems to be a synonym. Of specimens referred to *Ammonites egertoni* by Stoliczka (1864), his plate 53, figure 1 is *P. (P.) preegertoni* Collignon, 1955, according to Matsumoto (*in* Matsumoto *et al.*, 1986), plate 53, figure 2 is the holotype of *Pseudomennites stoliczkai* Matsumoto, 1986 (*in* Matsumoto *et al.*, 1986, p. 10, text-fig. 5), while the specimen shown in Stoliczka's plate 53, figure 4 seems to be a fragment of *P. (P.) neubergicus neubergicus*. The fragment illustrated by Kossmat (1898, pl. 15 (21), fig. 4) is coarsely ribbed, and may be a *P. (P.) jacquoti*.

Occurrence. Maastrichtian, south India.

Pachydiscus (Pachydiscus) yama (Forbes, 1846)

Plate 10, figs 3–4; Plate 12, figs 10–12

- 1846 *Ammonites Yama* Forbes, p. 107, pl. 7, fig. 4.
 1850 *Ammonites Chrishna* Forbes; d'Orbigny [*pars*], p. 213.
 non 1865 *Ammonites Yama* Forbes; Stoliczka, p. 120, pl. 59, fig. 12.

Type. Holotype, by monotypy, is BMNH C51040, the original of Forbes (1846, pl. 7, fig. 4; GSC R10473), from the Valudavur Formation of Pondicherry, south India (*ex* Kaye and Cunliffe Collection).

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51040	16.8 (100)	5.2 (31.0)	7.0 (41.6)	0.74	4.0 (23.8)

EXPLANATION OF PLATE 15

- Figs 1–2. *Phylloceras (Neophylloceras) nera* (Forbes, 1846). BMNH C22681, holotype.
 Fig. 3. *Phylloceras (Neophylloceras?) decipiens* Kossmat, 1895. BMNH C51080, holotype.
 Figs 4–5. *Phylloceras (Neophylloceras) nera* (Forbes, 1846). BMNH C51076, paralectotype.
 Figs 6–13. *Sphenodiscus siva* (Forbes, 1846). 6–9, BMNH C51088, paralectotype. 10–13, BMNH C51087, lectotype.
 All specimens from the Valudavur Formation of Pondicherry, south India. Figs 1–5 × 2; figs 6–13 × 1.



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Description. The holotype is a juvenile with some test preserved, and septate. Coiling is moderately involute, with $U = 23.8\%$, shallow, with a low, steep but not vertical wall and narrowly rounded umbilical shoulder. The whorls are compressed, with whorl breadth to height ratio 0.74, the flanks feebly convex, converging to a narrowly rounded venter. The shell is smooth, but for a feeble bulla at the largest diameter preserved. Part only of the suture is visible; it is of moderate complexity, with L trifid and U retracted on the umbilical wall.

Discussion. What seems to be the same species is represented by one of the types of *Ammonites varuna*, BMNH C51062 (Pl. 5, figs 21–23). These specimens, by their sutures and (in the holotype of *yama*) presence of umbilical bullae, are juvenile *Pachydiscus* (*Pachydiscus*). There are close similarities to nuclei of *P. (P.) gollevillensis* (d'Orbigny, 1850) dissected from larger specimens (e.g. Kennedy 1986c, pl. 11, figs 1–3), but it is perfectly possible that they belong to any one of a number of Maastrichtian *P. (Pachydiscus)*, including *P. (P.) neubergicus* and subspecies (as suggested by d'Orbigny 1850, p. 213, and by juveniles from Zululand (South Africa) in the collections of the Natural History Museum, London) or *P. (P.) compressus* Spath, 1922. *P. (P.) yama* should, in our view, be treated as a *nomen dubium*. The specimen referred to this species by Stoliczka (1865, p. 120, p. 59, fig. 12) is a much stouter shell, from north-east of Odium, south India (in the text: Coonum in the Trichinopoly Group in the explanation of the plate).

Occurrence. As for type.

Subgenus *NEODESMOCERAS* Matsumoto, 1947, p. 39

Type species. *Pachydiscus (Neodesmoceras) japonicus* Matsumoto, 1947, p. 39, by original designation.

Pachydiscus (Neodesmoceras) soma (Forbes, 1846)

Plate 12, figs 16–18; Text-fig. 3G

1846 *Ammonites Soma* Forbes, p. 102, pl. 7, fig. 7.

1850 *Ammonites Chrishua* Forbes; d'Orbigny [*pars*], p. 213.

1986 *Ammonites soma* Forbes; Matsumoto, in Matsumoto *et al.*, p. 9, text-fig. 4.

Type. Holotype, by monotypy, is BMNH C51039, the original of Forbes (1846, pl. 7, fig. 7; GSC R1046 3), from the Valudavur Formation of Pondicherry, south India.

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C51039	21.5 (100)	8.2 (38.1)	8.5 (39.5)	0.96	5.2 (24.2)

Description. The holotype is a juvenile, with over half a whorl of body chamber preserved, and retaining much of the original shell. Coiling is fairly involute, with $U = 24\%$ of diameter, shallow, with an initially vertical, thereafter outward-inclined umbilical wall, with well rounded shoulder. The flanks are feebly convex and subparallel, the venter broadly rounded, with whorl breadth to height ratio 0.96, the greatest breadth below mid-flank. There are three feeble umbilical bullae on the last whorl of phragmocone. The apertural half of the body chamber bears four weak, irregularly spaced constrictions, of which the last is the strongest. They are rursiradiate on the umbilical wall, straightening on the umbilical shoulder, prorsiradiate and feebly flexuous on the flanks, projected forward on the ventrolateral shoulder, and feebly convex on the venter. They are

EXPLANATION OF PLATE 16

Figs 1–3, 7–8. *Desmophyllites diphylloides* (Forbes, 1846). 1–2, BMNH C22682, lectotype. 3, 7–8, BMNH C22683, paralectotype. Both specimens are from the Valudavur Group of Pondicherry, south India.

Figs 4–6, 9–12. *Saghalinites wrighti* Birkelund, 1965. 4, 12, MGUH 1964.110. 5–6, MGUH 1964.100.9, MGUH 1964.121. 10–11, MGUH 1964.117.

All specimens from the Maastrichtian fauna reworked into the oyster–ammonite conglomerate at the base of the Palaeocene at Nügssuaq, west Greenland, and in the collections of the Geologisk Museum, Copenhagen.

Figs 1–3, 7–8 $\times 2$; figs 4–6, 9–12 $\times 1$.



KENNEDY and HENDERSON, *Desmophyllites*, *Saghalinites*

succeeded by delicate ventral ribs. The constriction next to the aperture has a delicate rib that extends to the umbilicus. Suture with L and U, trifold, U only slightly retracted on the umbilical wall (Text-fig. 3G).

Discussion. Both Stoliczka (1864, p. 106) and Kossmat (1898, p. 94 (159)) regarded Forbes's *Ammonites Soma* as a juvenile of *Ammonites Ganesa*, and thus a synonym of *P. (Pachydiscus) egertoni*. But juveniles of the latter are different in both cross-section and ribbing style (e.g. compare Pl. 12, figs 16–18 with Pl. 12, figs 7–9, 19–21). *Ammonites soma* is a juvenile *Pachydiscus (Neodesmoceras)* in our view, rather than a *P. (Pachydiscus)*, as proposed by both Spath (1953, p. 39) and Matsumoto (*in* Matsumoto *et al.*, 1979, p. 10). The general shell shape is similar to that of *P. (N.) gracilis* Matsumoto, 1979 (*in* Matsumoto *et al.*, 1979, p. 60, notably pl. 10, fig. 2), and juvenile *P. (N.) mokotibense* Collignon, 1952 (p. 81, pl. 28, fig. 2) from Zululand (South Africa) in the collections of the British Museum (Natural History). These species have stouter, more massive shells, with well-developed, distant ventral ribs when young.

Occurrence. As for type.

Genus MENUITES Spath, 1922, p. 123

[= *Besairieites* Collignon, 1931, p. 19; ?*Anapachydiscus* Yabe and Shimizu, 1926, p. 172]

Type species. *Ammonites Menu* Forbes, 1846, p. 111, pl. 10, fig. 1, by original designation.

Discussion. *Memites* has as type species a small form, constricted and bituberculate on the early part of the adult body chamber, and with a markedly constricted adult aperture. Such small forms occur in the same zone of the Upper Campanian of northern Hokkaido (Matsumoto 1984, p. 17, pl. 5, fig. 1; text-fig. 5; *Memites sandai* Matsumoto, 1984) with typical large specimens of the type species of *Anapachydiscus*, *A. fascicostatus* (Yabe, 1921) (Matsumoto 1984, p. 14, pl. 4, figs 1–2; pl. 5, fig. 2; pl. 8, fig. 7; text-fig. 4), and have identical early whorls. There seems little doubt that these are dimorphs. But since the macroconchs of *Memites menu* have yet to be recognized, and might be different from macroconch *Anapachydiscus*, they cannot be yet confirmed as synonyms.

Memites menu (Forbes, 1846)

Plate 14, figs 1–15; Text-fig. 6C

1846 *Ammonites Menu* Forbes, p. 111, pl. 10, fig. 1.

1850 *Ammonites Menu* Forbes; d'Orbigny, p. 213.

EXPLANATION OF PLATE 17

Fig. 1. *Hauericeras rembda* (Forbes, 1846). BMNH C51025, paralectotype; Valudavur Group; Pondicherry, south India.

Figs 2–3. *Zelandites varuna* (Forbes, 1846). BMNH C51059; lectotype, Valudavur Group; Pondicherry, south India.

Figs 4–7. *Desmophyllites diphylloides* (Forbes, 1846). 4, 7, KW21, Oxford University Museum Collections; Upper Maastrichtian Miria Formation Giralda Range, Western Australia. 5–6, BMNH C51020, the largest paralectotype; Valudavur Group; Pondicherry, south India.

Figs 8–9. *Brahmaïtes (Anabrahmaïtes) vislmu* (Forbes, 1846). The holotype of *Puzosia haugi* Seunes, 1891 (pl. 15 (6), fig. 1); Upper Maastrichtian; between Gan and Rébénacq, Pyrénées Atlantiques, France; in the Sorbonne Collections, now housed in the Université Paris VI.

Fig. 10. *Desmophyllites larteti* (Seunes, 1891). The original of Seunes (1891, pl. 13 (4), fig. 2); Upper Maastrichtian; between Gan and Rébénacq, Pyrénées Atlantiques, France; now housed in the Université Paris VI.

Figs 1–3 × 2; figs 4–11 × 1.



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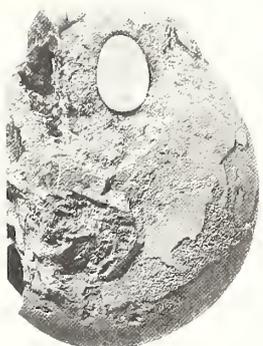
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- 1864 *Ammonites Menu* Forbes; Stoliczka [pars], p. 103, pl. 52, fig. 4, [non fig. 3 = *Pachydiscus Cricki* Kosmat, 1898].
 1898 *Pachydiscus Menu* Forbes sp.; Kosmat, p. 104 (169).
 1922 *Menuites nienu* (Forbes); Spath, p. 123.
 1955 *Menuites menu* (Forbes); Matsumoto, p. 158.
 1957 *Menuites menu* (Forbes); Wright, p. L380, fig. 406.1.
 1977 *Menuites menu*; Kennedy, text-fig. 19.

Types. Lectotype, designated by Matsumoto 1955 (p. 158) is BMNH C51048, the original of Forbes (1846, pl. 10, fig. 1a-b; GSC R10482); paralectotypes are BMNH C47549-47550 (probably the original of Forbes 1846, pl. 10, fig. 1c), BMNH C47551, and three unnumbered nuclei, all from the Valudavur Formation of Pondicherry, south India (*ex* Kaye and Cunliffe Collection). Topotypes are BMNH C3566a-b, and BMNH C82500 (*ex* March Collection).

<i>Dimensions.</i>	D	Wb	Wh	Wb:Wh	U
BMNH C47551	34.2 (100)	22.0 (64.3)	14.4 (42.1)	1.53	8.8 (25.7)
BMNH C47549	61.5 (100)	35.0 (56.9)	26.8 (43.6)	1.31	15.5 (25.2)
BMNH C51048	69.8 (100)	37.8 (54.1)	28.0 (40.1)	1.06	18.8 (26.9)

Description. The lectotype and paralectotype BMNH C47549 are adults and are an estimated 68 mm and 71.5 mm in diameter respectively. Coiling is moderately involute, with U = 25 to 27% of diameter, the umbilical deep, with a high convex wall, sloping outwards to a narrowly rounded umbilical shoulder. The whorl section is depressed reniform, with whorl breadth to height ratio 1.53 at the end of the phragmocone and 1.06-1.31 at the adult aperture. The flanks are strongly inflated, and the venter broadly arched. Prominent umbilical tubercles are present from a diameter of less than 15 mm, and number 11-13 per whorl; they are the flat-topped bases of umbilical spines, none of which survives on the phragmocones (Pl. 14, fig. 2). Fine, crowded irregular ribs, some only a little stronger than growth lines, arise in groups from the umbilical tubercles, and intercalate between the tubercles, covering, together with the prominent growth lines, the whole of the shell surface. They are rursiradial on the umbilical wall, but straight and prorsiradial on the flanks, flexing forwards on the ventro-lateral shoulder, and crossing the venter in a broad convexity. Strong ventro-lateral tubercles, which alternate in position on either side of the venter (Pl. 14, figs 10, 12-13, 15) are developed on the last part of the phragmocone and adapical part of the body chamber, appearing at a diameter of 40 mm. Ribbing weakens on the body chamber, which is densely lirate, and ventral tubercles are absent on the last 90-120°, the umbilical tubercles weakening progressively, but extending much closer to the aperture. Two constrictions are present on the lectotype (Pl. 14, figs 13-15), one 45° before and one immediately preceding the aperture. There is one constriction immediately preceding the aperture (as preserved) in BMNH C47549 (Pl. 14, fig. 11). The constrictions are broad, shallow, feebly concave and prorsiradial on the flanks, sweeping forward on the ventrolateral shoulder, and crossing the venter in a broad, shallow convexity. They are preceded by a narrow, strong, feebly bullate collar-rib, and followed by a weaker, narrow rib. A short, smooth, tubular section of shell separates this rib from the mouth border. The suture (Text-fig. 6c) is florid with deep, narrow, trifid L; U is retracted on the umbilical wall.

What we take to be juveniles of the species are nuclei 7 mm or less in diameter (Pl. 14, figs 6-9); these are even more depressed than the later growth stages, and smooth. One phragmocone, BMNH C82500, shows interrupted growth lines on the venter, recording the site of mantle damage in life.

Discussion. *Menuites menu* is particularly distinguished by the very delicate ribbing, present through most of ontogeny. This alone separates it from species such as *Menuites portlocki* (Sharpe, 1855; p. 30, pl. 17, figs 2-3), from the Upper Campanian of western Europe; *Menuites complexus* Hall and Meek, 1856 (p. 394, pl. 4, fig. 1) from the Upper Campanian of the US Western Interior; *M. ?aff.*

EXPLANATION OF PLATE 18

Figs 1-6. *Desmophyllites larteti* (Seunes, 1891). 1-3, the original of Seunes (1891, pl. 13 (4), fig. 1). 4-6, the original of Seunes (1891, pl. 13 (4), fig. 2). From the Upper Maastrichtian between Gan and Rébénacq, Pyrénées Atlantiques, France; now housed in the Université Paris VI. All $\times 1$.



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complexus of Reeside (1962, p. 122, pl. 69, figs 1–6), from the Upper Campanian of New Jersey; *M. stephensoni* Young, 1963 (p. 57, pl. 15, figs 1–2; text-figs 7*o*, 9*n*), from the Upper Campanian of Texas, which is also much larger; *M. japonicus* Matsumoto, 1955 (p. 158, pl. 31, figs 1–3; pl. 33, figs 2–3; text-figs 4–5), from the Campanian of Japan; *M. naibutensis* Matsumoto, 1955 (p. 164, pl. 33, fig. 1), from an uncertain horizon in Saghalien, and *M. pusillus* Matsumoto, 1955 (p. 165, pl. 32, figs 1–4), from the Santonian of Japan. Closer is *M. sandai* Matsumoto, 1984 (p. 17, pl. 5, fig. 1; text-fig. 5), from the Upper Campanian of northern Hokkaido, Japan. This is the microconch of *Anapachydiscus fascicostatus* (Yabe, 1921) (which specific name has priority). It has a much more depressed, reniform whorl section than *M. menu*, with whorl breadth to height ratio of up to 1:37, fewer umbilical bullae (9 per whorl, versus 11–13), with stronger ribs, and reaches almost twice the size of the Indian species.

Occurrence. As for types.

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894, p. 22

Family SPHENODISCIDAE Hyatt, 1900, p. 585

[= Libycoceratidae Zaborski, 1982, p. 306]

Genus SPHENODISCUS Meek, 1871, p. 298

[= *Austrosphenodiscus* Olsson, 1944, p. 266]

Type species. *Ammonites lenticularis* Owen, 1852, p. 579 (*non* Phillips 1829, pl. 6, fig. 5), by original designation.

Discussion. See Zaborski (1982, p. 315) and Kennedy (1987, p. 176) for recent discussions of the genus. As noted there, the widely distributed smooth or near-smooth *Sphenodiscus*, described as *S. binkhorsti* (Böhm, 1898) in Europe, *S. lobatus* (Tuomey, 1856) in the United States, Mexico, the Middle East and West Africa, and as *S. siva* (Forbes, 1846) in south India, cannot be adequately compared until larger populations have been described. We suspect that they may well prove conspecific, but cannot prove it. Accordingly, we describe the type material of the oldest named species, *S. siva*, below, but defer decisions on the synonymy or otherwise of other species until new collections from the United States and Nigeria before us are fully analysed.

Sphenodiscus siva (Forbes, 1846)

Plate 15, figs 6–13; Text-fig. 6B, D–E

- 1846 *Ammonites Siva* Forbes, p. 110, pl. 7, fig. 6.
 1850 *Ammonites Siva* Forbes; d'Orbigny, p. 213.
 1864 *Ammonites Siva* Forbes; Stoliczka, p. 59, pl. 33, fig. 3.
 1895 *Sphenodiscus Siva* Forbes sp.; Kossmat, p. 178 (82), pl. 22 (8), fig. 2.
 1908 *Sphenodiscus siva* Forbes sp.; Grossouvre, p. 21, pl. 1, fig. 6.
 1977 *Sphenodiscus siva*; Kennedy, text-fig. 31.9–10.
 1982 *Sphenodiscus siva* (Forbes, 1846); Zaborski, p. 315.
 1987 *Sphenodiscus siva* (Forbes, 1846); Kennedy, p. 176.
 1989 *Sphenodiscus*; Kennedy, text-fig. 18*a–b*.

Types. Lectotype, here designated, is BMNH C51087, the original of Forbes (1846, pl. 7, fig. 6; GSC R10481); paralectotype is BMNH C51088, from the Valudavur Formation of Pondicherry, south India (*ex* Kaye and Cunliffe Collection).

<i>Dimensions.</i>	D	Wb	Wh	Wb: Wh	U
BMNH C51087	65.0 (100)	15.0 (23.0)	39.5 (60.8)	0.38	– (–)
BMNH C51088	64.0 (100)	15.0 (23.4)	40.0 (62.5)	0.38	– (–)

Description. Oxycone, with minute umbilicus; greatest preserved diameter 64 mm, whorl breadth to height ratio 0.38. The umbilicus sits in a shallow circumbilical depression. The inner flanks are feebly convex, converging to a sharp venter, the greatest whorl breadth lying well below mid-flank. The surface of the shell, where preserved, is smooth, but for delicate prorsiradiate growth lines, conspicuous close to the umbilical margin only. Suture with shallow incisions (Text-figs. 6B, D-E). E is broad, and shallower than L, which is asymmetrically trifid, and margined by saddles with slender axial zones and phylloid terminations. U has 10 minor lobes in the external part, decreasing in size towards the umbilicus. The first six are asymmetrically trifid and follow a straight, rectiradiate line. Minor saddles on the umbilical lobe have phylloid endings, especially the simpler ones close to the umbilicus. Successive sutures have a tendency to overlap.

Occurrence. As for types.

Acknowledgements. W.J.K. acknowledges the financial support of the Natural Environment Research Council (UK). Support for R.A.H. to work at Oxford was provided by Oxford University Museum, the Department of Earth Sciences and Wolfson College, Oxford, and the James Cook University of North Queensland. We thank Drs S. Anantharaman and K. Ayyasami of the Geological Survey of India (at Hyderabad and Calcutta respectively) for providing us with their unpublished results on the Cretaceous rocks of the Pondicherry area, and Dr M. K. Howarth, Dr H. G. Owen (currently) and Mr D. Phillips (formerly) of the Natural History Museum, London, for allowing us to study collections in their care.

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W. J. KENNEDY

Geological Collections
University Museum
Parks Road
Oxford OX1 3PW, UK

R. A. HENDERSON

Department of Geology
James Cook University
Townsville
Queensland 4811, Australia

Typescript received 20 August 1990

Revised typescript received 20 June 1991

STRUCTURE AND FUNCTION OF THE PECTORAL JOINT AND OPERCULUM IN ANTIARCHS, DEVONIAN PLACODERM FISHES

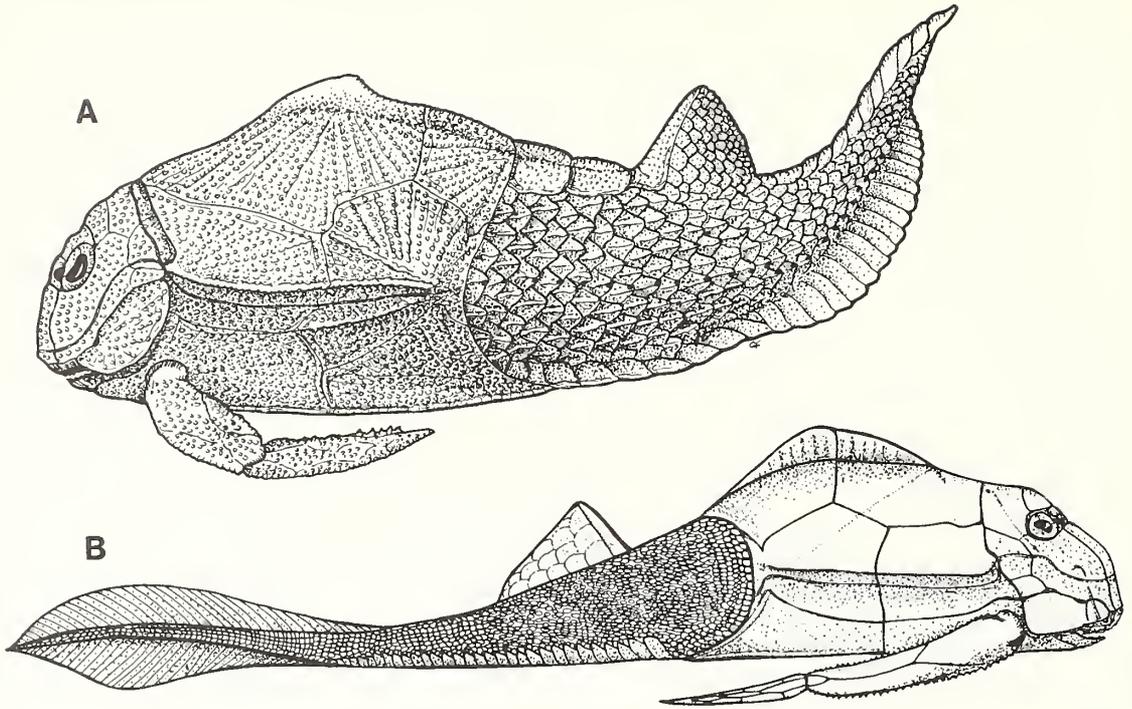
by G. C. YOUNG and ZHANG GUORUI

ABSTRACT. The structure and function of the pectoral fin joint and operculum in antiarchs (Devonian placoderm fishes) are re-examined in the light of new evidence from primitive Early Devonian representatives from South China, and acid-prepared material from the Late Devonian of Western Australia. The characteristic dermal brachial process of advanced antiarchs is absent in *Yunnanolepis*, and rudimentary in *Procondylolepis*. The latter displays a perichondrally ossified articular surface of the scapulocoracoid surrounded by three large foramina, which may be homologized with similar structures in primitive anarthroids. It is proposed that during the evolution of the complex brachial articulation of advanced antiarchs the posterior two foramina fused to form the axillary foramen, which carried nerves and vessels to the fin, but not a muscle. *Procondylolepis* is reinterpreted to have had two proximal dermal articulations on its pectoral fin, which was rotated by an abductor muscle inserting posteroventral and an adductor muscle inserting posterodorsal to the scapulocoracoid articulation. A similar interpretation is applicable to other antiarchs. Manipulation of the fin in acid-prepared *Bothriolepis* indicates that an oar-like swimming function was most unlikely. The same specimen reveals a small groove and opening adjacent to the anterior articulation of the submarginal plate (dermal operculum), which probably contained the spiracular tube.

THIRTY years ago D. M. S. Watson wrote a short morphological paper for *Palaentology* on one of the most widely known groups of Devonian placoderm fishes, entitled 'Some additions to our knowledge of antiarchs' (Watson 1961). The two most striking morphological characteristics of the antiarchan fishes (Text-fig. 1) are their box-like thoracic dermal armour, and their highly modified pectoral fins, which are enclosed in dermal bone to form arthropod-like appendages, sometimes with a distal 'elbow' joint. One of the best-known representatives is the so-called '*Pterichthys*' or winged fish of Hugh Miller (1841) from the Middle Old Red Sandstone of Scotland (genus *Pterichthyodes*, comprehensively revised by Hemmings 1978). The unusual form of the carapace led some early workers to the conclusion that they were dealing with fossilized remains of turtles or beetles (e.g. Anderson 1840), while Romer (1966, p. 24) referred to the antiarchs as 'grotesque little creatures which look like a cross between a turtle and a crustacean'.

Their unusual appearance attracted a number of investigations into their structure and interrelationships, with the revision by Traquair (1894–1914) of Scottish antiarchs resolving most of the questions concerning the general morphology of their dermal skeleton. More detailed monographs on the group were published by Stensiö (e.g. 1931, 1948), and Gross (e.g. 1931, 1941*a*, 1941*b*), and by the time of Watson's (1961) paper the antiarchs were regarded as well known morphologically. Only some special details of functional morphology were apparently outstanding, and two such topics – respiration, and function of the peculiar arm-like appendages – were the subject of Watson's short paper.

In this paper we reconsider the two aspects of functional morphology discussed by Watson (1961) in the context of the increase in knowledge of antiarch systematics and morphology which has ensued over the last three decades. The taxonomic database for antiarchs has increased dramatically in recent years. Gross (1932) listed only seven antiarch genera, but Denison's (1978) handbook included seventeen named genera. A survey of papers recently published or in press shows now there



TEXT-FIG. 1. Reconstructions of two antiarchs. A, *Sherbonaspis hillsi* Young and Gorter, 1981; Middle Devonian; southeastern Australia; left lateral view; actual length c. 200 mm; based partly on restorations in Hemmings (1978). B, *Bothriolepis gippslandiensis* Hills, 1929; Late Devonian; southeastern Australia; right lateral view; actual length c. 380 mm; modified from Long (1983).

are thirty-seven named genera. Thus from the seven genera named in the century since Eichwald (1840) erected the genera *Bothriolepis* and *Asterolepis*, the next half century has seen more than a five-fold increase in presumed taxonomic diversity at generic level. This may be because the middle Palaeozoic vertebrate faunas of extra-European areas, which were regions of Devonian endemism (Young 1981), are now being actively investigated palaeontologically.

The classification used here follows Denison (1978) in recognizing the Placodermi as a major gnathostome group (subclass), containing some seven or more subgroups (orders), of which the Antiarchi and Arthrodira are the two of primary concern in this paper. There are four suborders within the antiarchs (Yunnanolepidoidei, Sinolepidoidei, Asterolepidoidei, and Bothriolepidoidei), but the first may be paraphyletic. It should be noted that in Stensiö's (1959) monograph on the pectoral fin, the term 'Arthrodira' was used in a more inclusive sense than current usage, equivalent to 'Placodermi' as used here. Specimen numbers mentioned in the text indicate repositories by the following prefixes: IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; CPC, Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra, Australia.

PECTORAL FIN

The remarkable arthropod-like pectoral fin of antiarchs, with its complex dermal articulation, is unique amongst vertebrates, and has attracted several detailed descriptions and analyses of function (Traquair 1894; Stensiö 1931, 1948, 1959; Gross 1931; Watson, 1961; Wells and Dorr 1985).

Westoll (1945, 1958, pp. 206–7) considered that the pectoral fin evolved by mobilization during phylogeny of the rigid spinal plate of arthrodires (and by implication that therefore the pectoral fin was not homologous to that of other gnathostomes). This view was rejected by Stensiö (1948, 1959), who showed that in *Bothriolepis canadensis* the fin contained a perichondrally ossified endoskeletal core interpreted as retaining a vestigial articulation with the scapulocoracoid. Surprisingly, in spite of this strong morphological evidence, Westoll's opinion was recently reiterated by Denison (1978) and Wells and Dorr (1985).

The structure of the complex dermal articulation between the pectoral appendage and the anterior ventrolateral plate of the trunk armour has been well known for antiarchs of Middle and Late Devonian age, where it shows little variation. The fin fitted closely around a prominent 'helmet' or brachial process (pbr, Text-fig. 2H), and the presence of this structure has been used to define a major antiarch subgroup, the euantriarchs of Janvier and Pan (1982), including the *Asterolepidoidei* and the *Bothriolepidoidei*.

Structure of the brachial articulation in early antiarchs

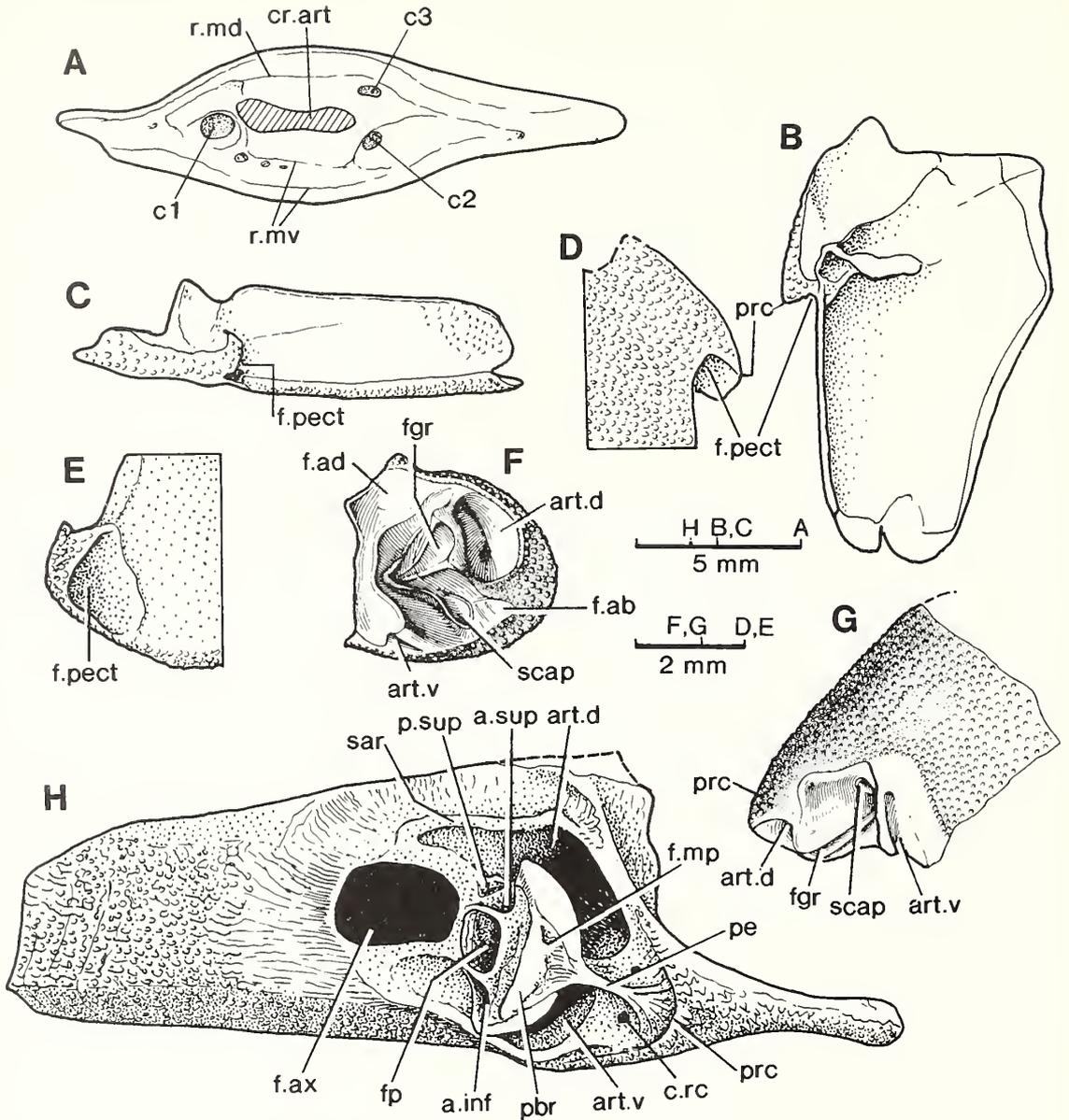
When Watson dealt with this aspect in 1961, the oldest known antiarchs were from the Middle Devonian of Europe. However, in recent years descriptions of older and apparently primitive antiarchs from South China have shown that this structure is not characteristic of the group as a whole. Zhang (1978) and Chang (1980) showed that in the Early Devonian genus *Yunnanolepis* the brachial process of Middle–Late Devonian antiarchs was absent. That this is the primitive condition for antiarchs is indicated by outgroup comparison (the dermal pectoral articulation is not known in any other group of vertebrates), and by the Early Devonian age. Zhang (1984) described another genus, *Procondylolepis*, which had an incompletely developed brachial process (Text-fig. 2F–G), and Ritchie *et al.* (in press) recently suggested that the dermal articulation was rudimentary in another major antiarch subgroup, the sinolepids. *Yunnanolepis*, *Procondylolepis*, and another apparently primitive genus, *Phymolepis*, occur together in the Cuifengshan Formation near Qujing, Yunnan Province. They are of earliest Devonian (Lochkovian, 'Gedinnian') age, making them the oldest named antiarchs. However, undescribed antiarch remains occur in Upper Silurian sediments in the same sequence (see Pan and Dineley 1988, table 6). The sinolepids are best known from the Late Devonian of China (Liu and Pan 1958) and Australia, but Early (?Emsian) and Middle Devonian genera also occur in South China (Zhang 1980; Ritchie *et al.* in press).

These groups provide new information on stages in the presumed phylogenetic transformation of an inferred primitive endoskeletal articulation (between basals of the pectoral fin and the scapulocoracoid), to the largely dermal articulation of advanced antiarchs. Here we consider the structure of the brachial articulation in these early antiarchs, to establish homologies between the various antiarch subgroups. The terminology used here is based on the descriptions of Stensiö (1931, 1948) for *Bothriolepis* and *Asterolepis*, as summarized in Text-figure 2H.

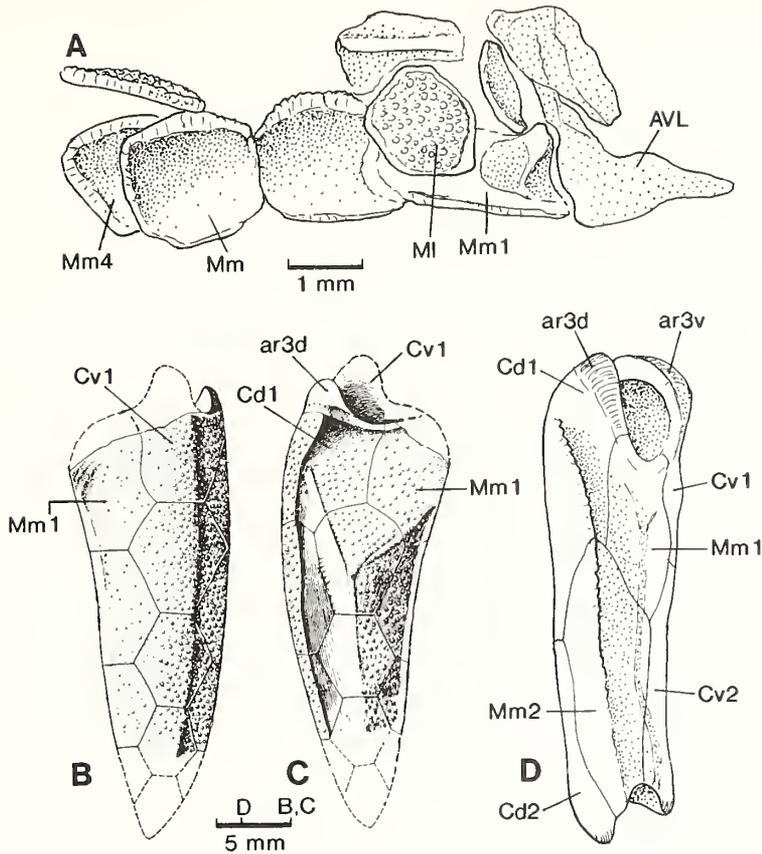
Yunnanolepis. This genus displays what may be considered the primitive condition by outgroup comparison with arthrodires. There is a small pectoral fenestra enclosed by dermal bones of the trunk armour (f.pect, Text-fig. 2B–E). As in arthrodires (Text-fig. 2A) this must have contained the lateral face of the scapulocoracoid and its articular surface for the pectoral fin. It is suggested that the funnel-like vestibule to the pectoral fenestra formed by the surrounding dermal bones could have been a preadaptation to the development of the dermal brachial articulation in other members of the group. The prominent prepectoral corner (prc) has the same morphological position as the prepectoral spines of acanthodians and the prepectoral spinal plate of various other placoderms, and Chang (1980, pl. 3, figs 2–4; pl. 5, figs 2–3) identified an incomplete suture defining a separate spinal element in several specimens of *Yunnanolepis*.

The fin itself is not known in *Yunnanolepis*, but a similar structure may be inferred to that known for the next genus discussed.

Phymolepis. This form is associated with *Yunnanolepis*, and the pectoral fin opening has the same structure (Zhang 1978; see below). In addition a series of small hexagonal plates which covered the



TEXT-FIG. 2. A, external view of the left scapulocoracoid of the arthrodire *Dicksonosteus* (after Goujet 1984). B-E, left anterior ventrolateral plate of *Yunnanolepis* in dorsal, left lateral, ventral, and posterolateral views (B-C modified after Zhang 1978; D-E, showing only the region of the pectoral fenestra, modified after Chang 1980). F-G, pectoral articulation on the anterior ventrolateral plate of *Procondylolepis* in right lateral and ventral views, as figured by Zhang (1984). H, right anterior ventrolateral plate of *Bothriolepis macphersoni* in right lateral view (after Young 1988), with structures of the pectoral fin articulation labelled using the terminology of Stensiö (1931, pp. 92-97). For list of abbreviations see p. 464.



TEXT-FIG. 3. A, Dermal plates of the right pectoral fin as preserved in *Phymolepis* (right lateral view, after Chang 1980, pl. 5, fig. 1; see also Zhang 1978, fig. 11). B–C, left pectoral fin of *Procondylolepis* restored in ventral and dorsal views (modified after Zhang 1984, with proximal elements labelled according to evolutionary rather than positional homology). D, left pectoral fin of a euantiarch in mesial view (*Asterololepis*, after Gross 1931). For list of abbreviations see p. 464.

fin are preserved in one specimen (Text-fig. 3A). This specimen indicates that the arm-like appendage enclosed in dermal plates evolved before a dermal articulation.

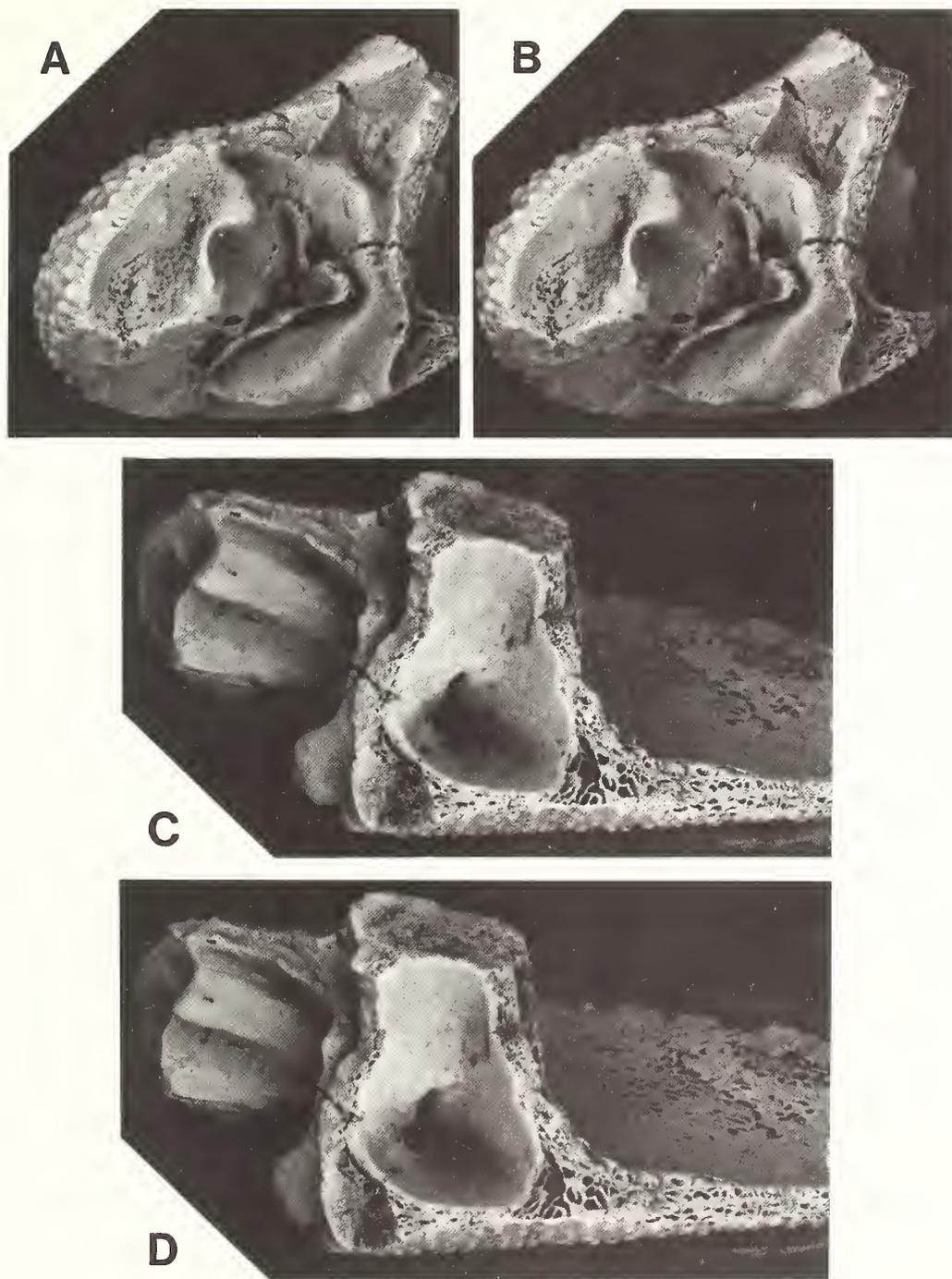
Procondylolepis. The oldest and apparently most rudimentary dermal articulation known occurs in the Early Devonian (Lochkovian) genus *Procondylolepis* Zhang 1984. Several examples of the pectoral fin have been discovered (Text-fig. 3B–C), and the brachial articulation for the fin is commonly preserved on incomplete isolated examples of the anterior ventrolateral plate (Text-figs 4–6), but apart from these the morphology of *Procondylolepis* is completely unknown. As just noted, there is good evidence that the associated genus *Phymolepis* had a similar pectoral fin, but these isolated fragmentary anterior ventrolaterals cannot be referred to *Phymolepis*, because at least one specimen of the latter (Zhang 1978, pl. 6, fig. 5), on which the reconstruction of Zhang (1978, fig. 12) is based, shows a simple pectoral fenestra developed as in *Yunnanolepis*. In other specimens of *Phymolepis* and *Yunnanolepis* this projecting part of the trunk armour is often broken off. In contrast, in *Procondylolepis* it is the only region preserved in otherwise very incomplete anterior ventrolateral plates, because of its much more robust development resulting from the evolution of the rudimentary dermal brachial articulation.

Zhang (1984) analysed the morphological relationship between the pectoral fin elements and the brachial articulation. He identified three distinct pits or grooves on the dermal surface of the pectoral fin attachment of the anterior ventrolateral, which he interpreted as dermal articulations (f.ad, art.d, art.v, Text-fig. 2F). However, on the pectoral fin only one corresponding articular process is known (ar3d, Text-fig. 3B–C), although a second may be inferred on the ventral plate (Cv1). The posterodorsal pit on the anterior ventrolateral (f.ad, Text-fig. 2F) lacks the *siebknocken* texture typical of the dermal pectoral fin articulation in antiarchs, and we now suggest that this may be reinterpreted as a muscle attachment. The remaining two articular surfaces (art.d, art.v, Text-fig. 2F) are assumed to have received two dermal articular processes of the proximal pectoral fin bones, corresponding to the dorsal and ventral articulations of more advanced antiarchs (ar3d, ar3v, Text-fig. 3D). Reinterpretation of the pectoral appendage of *Procondylolepis* as having only two rather than three dermal attachments (Text-fig. 3B–C) permits a more realistic functional interpretation, since, as previously recognized (Zhang 1984), three points of contact would severely restrict the possible movements of the fin. The functional aspect of these articulations is further considered below.

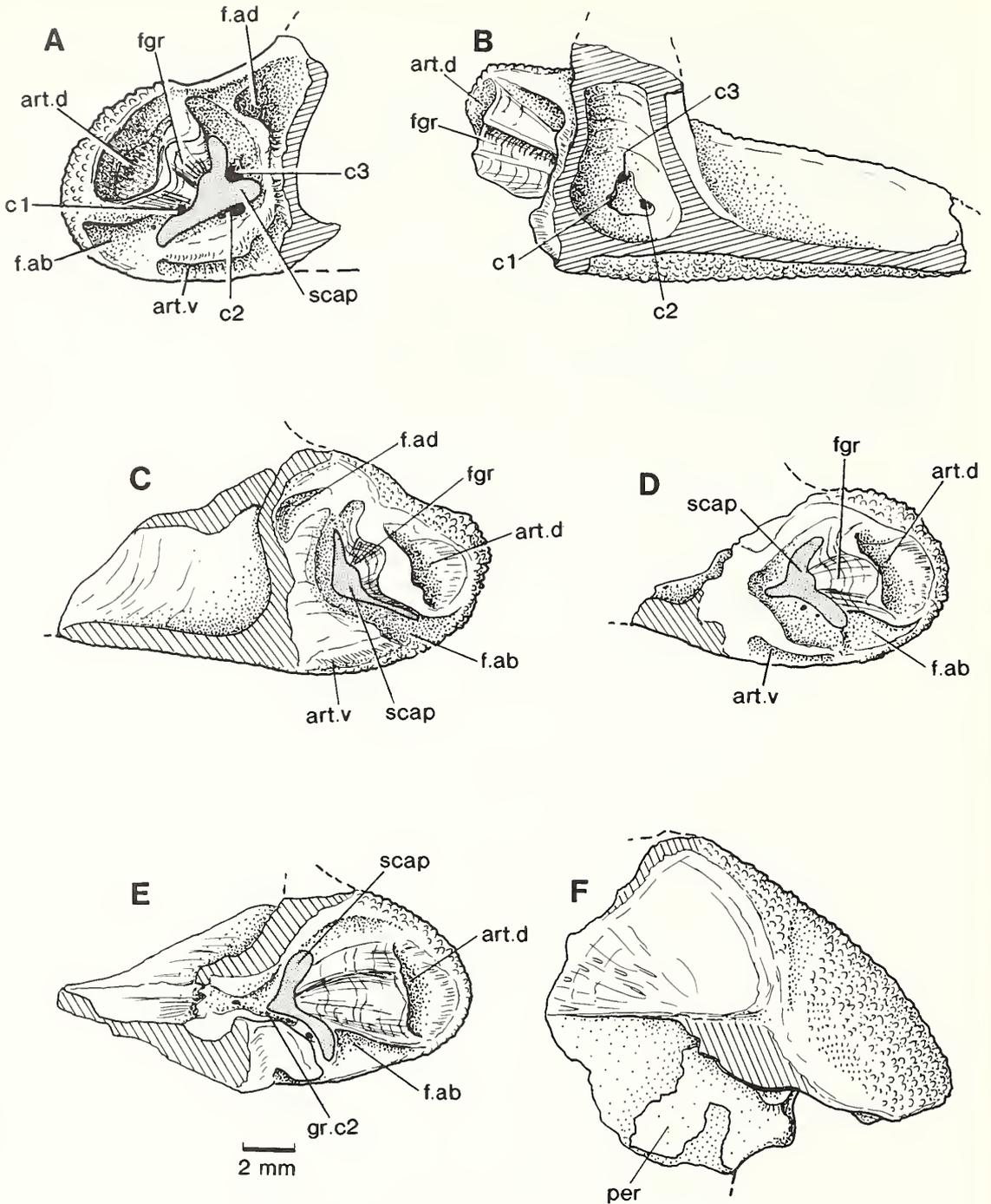
The dorsal articulation on the anterior ventrolateral (art.d, Text-fig. 2F) is developed as a distinct fossa, whilst the ventral is normally a shallow articular groove (art.v, Text-fig. 2F–G). However in some examples referred to *Procondylolepis* (e.g. IVPP.V6941.2) the ventral articulation may also form a small fossa. These structures were fully described by Zhang (1984); we summarize that work here, and illustrate four new specimens of the anterior ventrolateral of *Procondylolepis* showing the joint (IVPP.V6941.10–13). We pay particular attention to the structure in the centre of the fossa articularis formed by a thin lamina of bone, and previously identified as the 'primitive brachial process' by Zhang (1984, fig. 1B; cf. Text-fig. 2F–G). This we now regard as perichondral tissue enclosing the articular surface of the scapulocoracoid (scap, Text-fig. 5).

This bony lamina is normally incompletely preserved with its most distal part broken. It sits in a deep L-shaped cavity behind the strongly projecting prepectoral process (prc). The lamina is best preserved in IVPP.V6941.11, in which the perichondral bone is largely clear of matrix and in articular view is seen to comprise three main lobes (Text-fig. 4A–B; scap, Text-fig. 5A). The small posterior lobe has been lost in other specimens except IVPP.V6941.13 (Text-fig. 5D). Specimen IVPP.V6941.12 has the posterior part broken away to expose the inner extension of the perichondral lamina, constricted mesially and continuous with the laminar bone attached to the inside of the ventral lamina of the anterior ventrolateral plate (per, Text-fig. 5F). The anterior portion of the perichondral lamina is closely attached across the face of the pronounced groove running up the posterior face of the prepectoral process, here termed the 'funnel groove' (fgr, Text-figs 2F–G, 5). However, the perichondral layer is clearly distinguished from the dermal bone by the row of fine pores opening next to its outer surface. These pores go all around the scapulocoracoid, except where enlarged to form three big foramina (Text-fig. 4A–B; labelled c1–c3 in Text-fig. 5A). These have been traced through the bone as follows. The anterior one (c1) opens above the anteroventral lobe, and forms a short external groove running up the prepectoral process beneath the funnel groove (Text-fig. 4A–B). The second (c2) opens beneath the posterior lobe, and the third (c3) above it. The last is the largest foramen. On the inside in IVPP6941.11 is a large opening which also subdivides into three canals (Text-figs 4C–D, 5B). The posterior one is seen on IVPP.V6941.12 to lead to opening c2 (gr.c2, Text-fig. 5E). The dorsal opening leads to c3, and the anterior one, although filled with matrix, can be assumed to lead to opening c1, as labelled in Text-figure 5B.

Sinolepids. Within this group, the pectoral fin articulation is best known in a new Australian genus (Text-fig. 7C), in which it was also apparently of primitive structure (Ritchie *et al.* in press). It comprised a triangular dorsal and a small ventral articular area respectively for the first dorsal and ventral central plates of the pectoral appendage, which pivoted around a single axis passing through these articulations. This is very different from the brachial articulation of more advanced antiarchs (bothriolepidoids, asterolepidoids), because the brachial process was incompletely formed, and lacked a differentiated pars pedalis. The anterior edge of the brachial process was apparently



TEXT-FIG. 4. *Procondylolepis*; IVPP.V6941.11; incomplete left anterior ventrolateral, whitened with ammonium chloride. A-B, left lateral (articular) view, stereo pair. C-D, mesial view, stereo pair, left on top. All $\times 6$.



TEXT-FIG. 5. *Procondylolepis*; incomplete anterior ventrolateral plates. A–B, IVPP.V6941.11; a left plate, in left lateral and mesial views. C, IVPP.V6941.10; a right plate, in right lateral view. D, IVPP.V6941.13; a right plate, in right lateral view. E–F, IVPP.V6941.12; a right plate, in right lateral and dorsal views. Broken surfaces cross-hatched. For list of abbreviations see p. 464.

continuous with the prepectoral corner of the anterior ventrolateral plate, as in *Procondylolepis*. On the assumption that this was not a degenerate condition, the sinolepids also show that the complete brachial process appeared later in phylogeny than the distal joint in the pectoral fin (Ritchie *et al.* in press).

Homology of structural components in early antiarchs

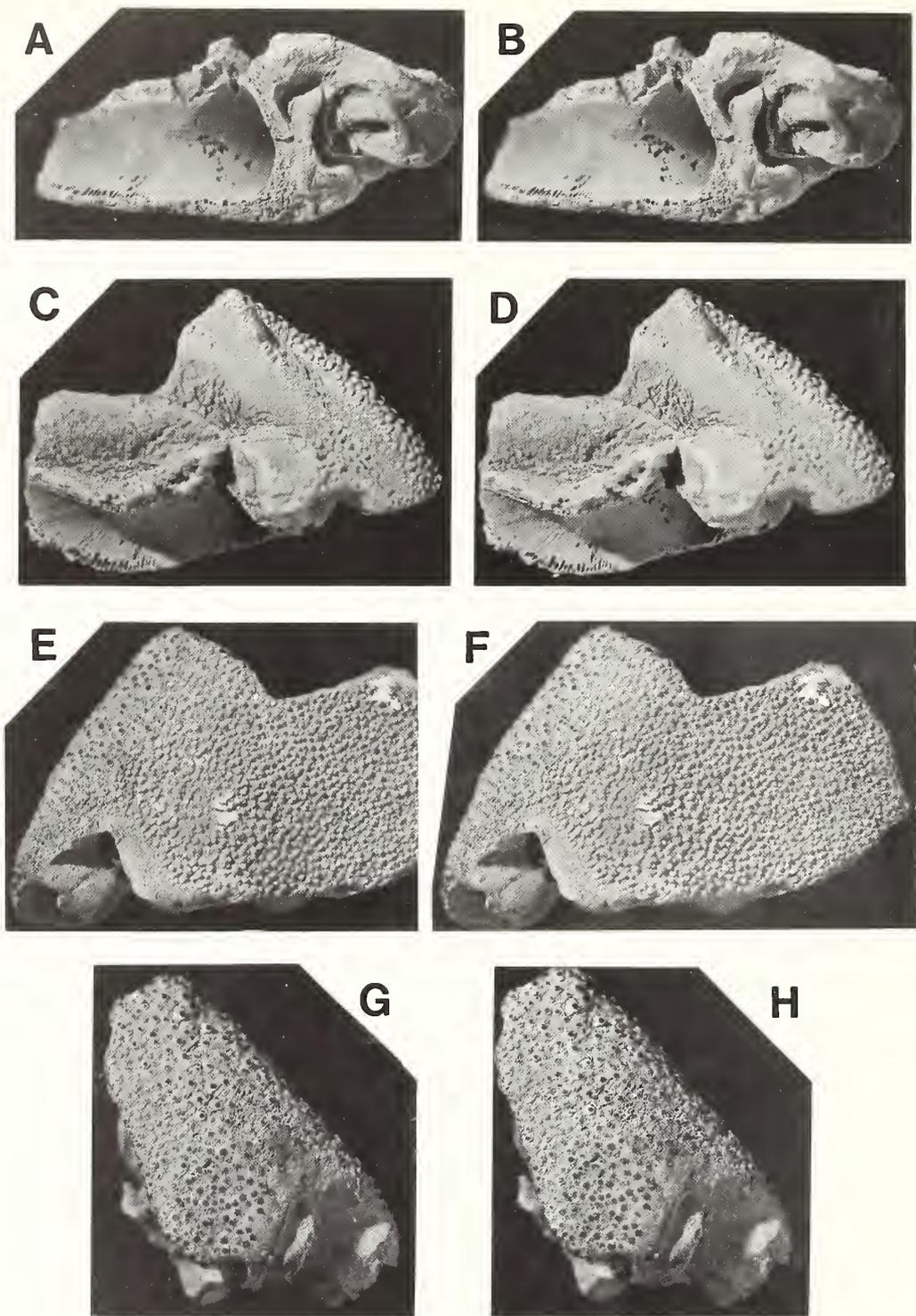
The interpretation of the skeletal features of the pectoral fin articulation of antiarchs is facilitated by comparing the presumed most primitive antiarch condition with that of better-known placoderm groups, such as primitive arthrodires.

Stensiö (1959) identified three types of pectoral fin in placoderms: (i) 'holosomactidial', the type seen in one group of arthrodires (pachyosteomorphs), which is broad-based, with little concentration of radials, suggestive of the embryonic fin structure of sharks, and considered to be the primitive type; (ii) 'merosomactidial', considered to be derived from the previous type by fusion of anterior radials with the endoskeletal shoulder girdle to form the endoskeletal prepectoral process, and modification of covering scales to form the exoskeletal spinal plate of various placoderm groups; and (iii) 'monomesorhachic', the most specialized pectoral fin of any fish, and restricted to the Antiarchi. He considered that this evolved by concentration of the endoskeleton into a single rod encased in a much modified exoskeleton of numerous plates, and with a unique double articulation comprising both exoskeletal and endoskeletal components.

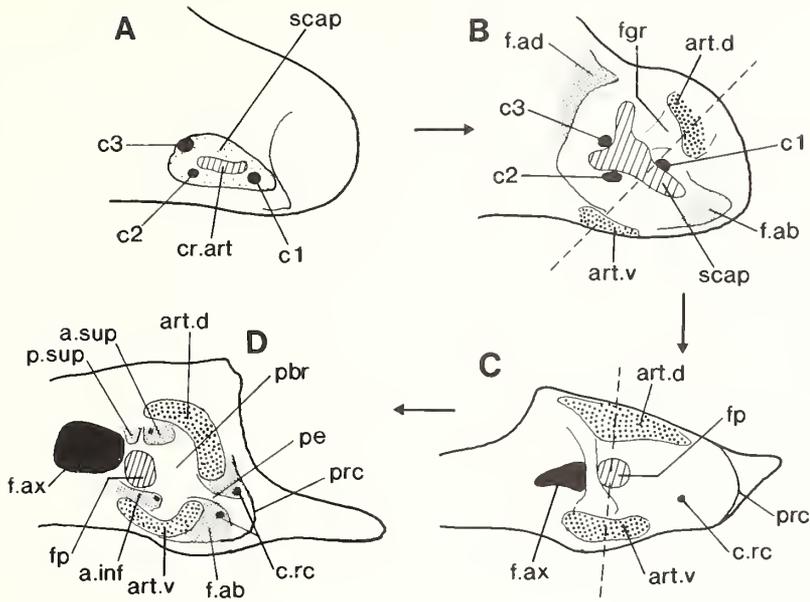
Stensiö (1959, p. 64) could not decide whether the 'monomesorhachic' fin of antiarchs was derived from the 'holosomactidial' or 'merosomactidial' condition, but these cumbersome terms have not been adopted by other authors, and the first two types have neither the significance nor phylogenetic connotation which Stensiö believed. A narrow-based fin is now considered the primitive condition for placoderms generally (for discussion see Young 1986, pp. 12, 47), and within arthrodires Goujet (1984) suggests that three basal elements articulating with the scapulocoracoid was probably the primitive condition, as in chondrichthyans and actinopterygians.

However, other aspects of Stensiö's (1959) interpretation of the antiarch pectoral fin, derived primarily from comparative anatomy rather than observation of fossils, are now supported by new fossil evidence. Stensiö suggested that the endoskeletal component of the pectoral fin articulation was between the proximal end of the endoskeletal bar within the fin (presumably fused basal elements, as identified in *Bothriolepis* by Stensiö 1931, fig. 55), and a special glenoid cartilage which filled the funnel pit, this glenoid cartilage being derived embryologically as a lateral process of the scapulocoracoid, and corresponding to the articular crest of other placoderms. In contrast Watson (1961, fig. 3B) considered the funnel pit to have received the axial skeleton of the fin, but this would have severely restricted its movements. Basing his views on observations of *Bothriolepis canadensis*, Stensiö hypothesized that in adults this glenoid cartilage became completely separated from the rest of the scapulocoracoid, which was situated inside the dermal pectoral girdle.

In *Procondylolepis* the trilobate form of the articular surface to the scapulocoracoid (glenoid cartilage) as just described, and the three major foramina opening around it, may be compared with the structure of the scapulocoracoid in primitive representatives of two major subgroups of arthrodires (phlyctaenioids and actinolepids). Goujet (1984, pp. 68–71) illustrated the articular portion of the scapulocoracoid in *Dicksonosteus* and *Kujdanowiapsis*, both of which have a short horizontal articular crest (cr.art, Text-fig. 2A) surrounded by three major canals, anteroventral, posteroventral, and posterodorsal to the crest (cl–3, Text-fig. 2A). The last may form a notch between the edge of the scapulocoracoid and the dermal border of the pectoral fenestra (Goujet 1984, fig. 71C–D). As pointed out by Goujet (1984, p. 146), the interpretation of the neurovascular supply to the fin in arthrodires is aided by the fact that the pectoral fenestra completely enclosed the fin articulation in dermal bone. Thus all nerves and vessels for the pectoral fin must have traversed the three observed canals. By comparison with modern representatives of other groups (e.g. Marples 1936; Jessen 1972) each canal probably carried both nerves and vessels. Goujet suggested that the anterior canal probably supplied the propterygium, and possibly also the mesopterygium, and may be the homologue of the ventral brachial canal in the acanthothoracids



TEST-FIG. 6. For legend see opposite.



TEXT-FIG. 7. Hypothesized stages in the evolution of the pectoral fin articulation of antiarchs (right articulation illustrated, with anterior end to the right). Arrows indicate suggested direction of transformation series. Heavy stipple, dermal articular surfaces for the pectoral appendage; light stipple, muscle insertion areas. Dashed lines in C-D show suggested axes of rotation of pectoral appendage around dorsal and ventral dermal articulations. A, hypothesized primitive condition, with the scapulocoracoid enclosed in a small pectoral fenestra, and bearing a short horizontal articular crest and three neurovascular canals as in primitive arthrodires, and no dermal articular contact. B, *Procondylolepis*, showing development of anteroventral and dorsal lobes to the articular crest, and muscle attachments to surrounding dermal bone. C, sinolepid (after Ritchie *et al.* in press, fig. 11C), showing posterior migration of dorsal and ventral articular areas to lie above and below circular glenoid cartilage within funnel pit, and coalescence of posterior two canals to form axillary foramen (external opening of rostrocaudal canal not yet identified in this form). D, *Bothriolepis* (a euantiarch), showing enlargement of dorsal and ventral articular fossae as deep subcircular grooves which excavate out the brachial process, associated with differentiation of muscle insertions (cf. Text-fig. 2H). For list of abbreviations see p. 464.

Palaeacanthaspis and *Romundina* (Stensiö 1969, fig. 233; Ørvig, 1975, pl. 5, fig. 8), because of its similar position anteroventral to the articular crest. The posterior canals probably carried the neurovascular supply to the metapterygium. The previously unrecognized posterodorsal canal may have carried a metapterygial vein, because of its large size.

In the light of Goujet's work we suggest a direct correspondence with the three large canals surrounding the scapulocoracoid of *Procondylolepis* described above. The three lobes may indicate persistence of three pectoral fin basals (possibly partly coalesced), with three corresponding neurovascular canals. However, because the distal part of the perichondral lining of the glenoid cartilage is not preserved, the actual shape of the articular area is uncertain. Since the anteroventral lobe passes beneath the anterior canal, whereas in arthrodires the anterior end of the crest is situated

TEXT-FIG. 6. *Procondylolepis*; incomplete anterior ventrolateral plates, all whitened with ammonium chloride. A-B, IVPP.V6941.10; a left plate, in posterolateral view, stereo pair, $\times 3.2$. C-D, IVPP.V6941.10; dorsal view, stereo pair, $\times 3$. E-F, IVPP.V6941.10; ventral view, stereo pair, $\times 3.5$. G-H, IVPP.V6941.11; a left plate, in ventral view, stereo pair, $\times 3$.

posterodorsal to the anterior canal, this anteroventral lobe may be interpreted, together with the dorsal lobe, as a new formation. The central region, extending from the funnel groove to include the posterior lobe, may be suggested as the homologue of the short horizontal articular crest of primitive arthrodires, and thus represents the primitive condition in a hypothetical common ancestor of known antiarchs (Text-fig. 7A).

There are two major morphological differences between the arrangement in *Procondylolepis* and that of primitive arthrodires, but both can be explained in terms of the much constricted dermal pectoral fenestra in these primitive antiarchs. All three neurovascular canals in *Procondylolepis* lie between the surrounding dermal bone and the perichondral lamina enclosing the scapulocoracoid. As noted above, the posterodorsal canal in some arthrodires also lies between the scapulocoracoid and the dermal margin of the pectoral fenestra, although in others it is enclosed within the cartilage like the other two canals. Secondly, the attachment surfaces for the fin muscles are situated on the surrounding dermal bone, whereas in *Dicksonosteus* various ridges and depressions on the scapulocoracoid are interpreted by Goujet as muscle attachment surfaces (r.md, r.mv, Text-fig. 2A). With the constriction of the dermal pectoral fenestra these muscles in primitive antiarchs were presumably displaced to attach on the contiguous dermal bone.

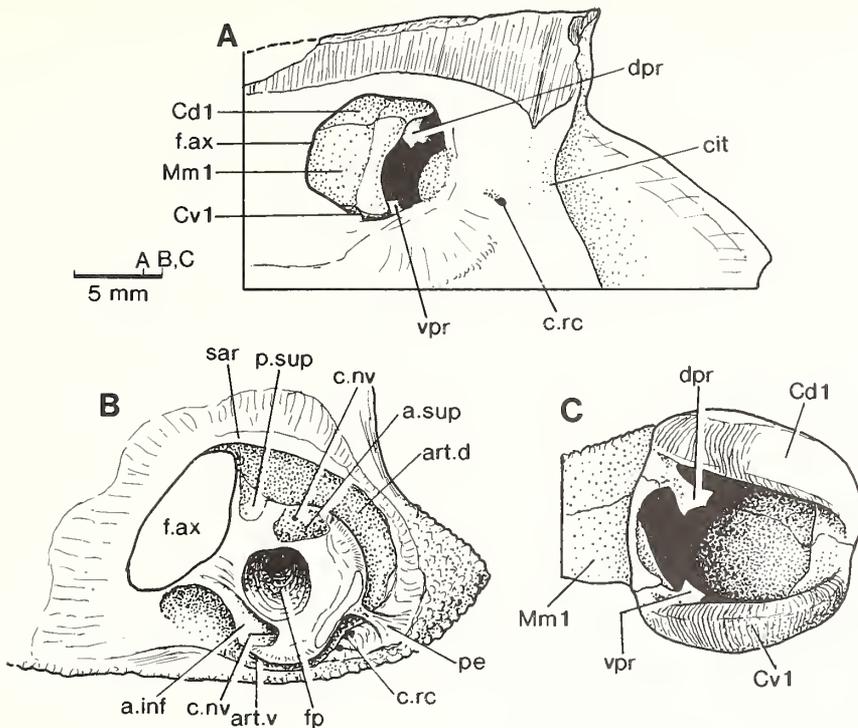
Homology of structural components of the brachial articulation in euantiarchs

The homologies just proposed between the pectoral articulation of a primitive arthrodire (entirely on the scapulocoracoid as in other fishes), and the presumed rudimentary pectoral articulation of *Procondylolepis* (involving a dermal articulation with the pectoral appendage, as in more advanced antiarchs), provide the basis for determining the homology of structural components in the much more complex dermal articulation of euantiarchs, as listed below. It is this fully developed pectoral articulation which defines the Euantiarchi in the sense of Janvier and Pan (1982). In view of the rudimentary nature of the brachial articulation in *Procondylolepis* we cannot agree with the opinion of Pan *et al.* (1987, fig. 51), who include *Procondylolepis* also within the Euantiarchi. The morphological transformations implied by the homologies set out below are summarized in Text-figure 7.

Prepectoral corner (prc, Text-figs 2H, 7C–D). This ornamented lateral projection at the anterior edge of the brachial articulation of euantiarchs is clearly homologous to the ornamented lateral edge of the prepectoral process of *Procondylolepis* (prc, Text-fig. 2G).

Funnel pit (fp, Text-fig. 2H). This unique structure of euantiarchs is a clearly defined conical pit passing through the centre of the brachial process (pbr). It may be of compound origin, with both perichondral and dermal components. In well-preserved acid prepared *Bothriolepis* from Gogo, Western Australia (Young 1984, fig. 7; cf. Text-fig. 8B) it is lined with laminar bone showing concentric striations, which are somewhat reminiscent of the striations across the 'funnel groove' running out from the scapulocoracoid in *Procondylolepis* (fgr, Text-fig. 5). We interpret this groove to be the homologue of the anterior wall of the funnel pit, although in *Procondylolepis* the groove is clearly a dermal structure. We accept the interpretation of Stensiö (1959) that the pit in euantiarchs contained a glenoid cartilage forming the endoskeletal articulation with the pectoral fin. This implies that the walls of the pit may be partly of perichondral origin. In euantiarchs the posterior wall has a distinct lamina lining the pit, which may even be recognized in latex casts of specimens preserved as moulds in sandstone (e.g. Young 1988, pl. 14, fig. 1). We suggest therefore that this is homologous to the posterior perichondral wall of the glenoid cartilage (i.e. external surface of the scapulocoracoid) in *Procondylolepis*. This implies that the trilobed perichondrally-lined space of *Procondylolepis* was contracted and modified during phylogeny into the subcircular or quadrilateral space of the funnel pit seen in euantiarchs. The distinction between the clearly differentiated dermal and perichondral bone layers described above in the funnel groove of *Procondylolepis* is no longer apparent in euantiarchs.

Processus brachialis (pbr, Text-figs 2H, 7D). This most prominent feature of the articulation of



TEXT-FIG. 8. *Bothriolepis* sp.; CPC 25205 (same specimen as described by Young 1984); early Upper Devonian Gogo Formation; Canning Basin, Western Australia. A, inner view of the lateral lamina of the left anterior ventrolateral plate, looking out through the axillary foramen with the pectoral fin in fully adducted position. B, right lateral view of the pectoral fin articulation on the right anterior ventrolateral plate. C, articular view of the proximal end of the left pectoral appendage. For list of abbreviations see p. 464.

euantiarchs we also regard as of compound origin, and without a specific homologue in *Procondylolepis*. We suggest a homology between the dorsal and ventral articular fossae of *Procondylolepis* on the one hand, and euantiarchs on the other (art.d, art.v, Text-fig. 2F–H). We consider the dermal part of the brachial process to have resulted from enlargement of these articular fossae, which excavated out deep hemispherical grooves in the dermal bone. The remaining septum of bone separating these two fossae anteroventrally formed the *pars pedalis* of the brachial process in Stensiö's terminology (pe, Text-figs 2H, 7D), and the 'island' of dermal bone enclosed by these excavations is the *pars condyloidea* of the brachial process (pbr).

Axillary foramen (f.ax, Text-figs 2H, 7C–D). This large foramen in euantiarchs lies directly behind the funnel pit, and is separated from it by a partition made up of the laminar lining of the pit just mentioned, and a connection of smooth bone apparently of dermal origin. Stensiö (1931, 1959) and Gross (1931) considered this foramen to have contained the adductor muscle for the fin, or a tendon of that muscle, and Stensiö (1931, p. 96) noted that the smooth anterior wall of the foramen may have been a trochlea for a strong tendon inserted on the pectoral fin. In sinolepids, however, this partition is a less robust upstanding lamina, more comparable to the posterior perichondral lamina of the glenoid cartilage in *Procondylolepis*, and evidently not developed for tendon attachment. Watson (1961), in noting the small size of the axillary foramen in *Pterichthyodes* compared to that of *Bothriolepis*, suggested that it was much too small for a muscle, and must have contained instead the main nerve and artery for the fin. Since in *Procondylolepis* the three observed canals around the

scapulocoracoid correspond to those in primitive arthrodires, we are led to a similar conclusion to Watson. The two canals (c2, c3, Text-figs 5A, 7B) of *Procondylolepis* are separated only by the posterior lobe of the scapulocoracoid, and we suggest that when this articular surface was modified into a subcircular shape these two canals coalesced into a single larger opening (f.ax, Text-fig. 7C–D), bounded posteriorly by dermal bone, and anteriorly by the perichondral lining of the scapulocoracoid. The much more robust anterior margin of this foramen in euantiarchs, which forms the posterior wall of the funnel pit, may be a thickened perichondral structure, or was perhaps supplemented by a dermal partition.

Rostrocaudal canal (c.rc, Text-figs, 2, 7–8). Stensiö (1931) described and named this structure in *Bothriolepis canadensis*. The canal passes through the base of the internal transverse crista of the anterior ventrolateral plate from an opening just in front of the axillary foramen (Text-fig. 8A). The largest of its several branches opens externally adjacent to the base of the pars pedalis of the brachial process, and other small branches include one passing into the base of the funnel pit. This appears to be a relatively constant arrangement amongst antiarchs. The canal has not been described in *Yunnanolepis* or *Pterichthyodes* (Hemmings 1978; Zhang 1978), but in both *Hyrceanaspis* and sinolepids it is known to open internally between the two divisions of the internal transverse crista (Janvier and Pan 1982, fig. 1c; Ritchie *et al.* in press, fig. 11B). A foramen in the same position is seen in *Asterolepis* (Gross 1931, pl. 5, fig. 4; Karatajute-Talimaa 1963, fig. 11), and in *Yunnanolepis* (Chang 1980, fig. 3b; pl. 3, fig. 2). In acid-prepared *Bothriolepis* from Gogo (Text-fig. 8) the rostrocaudal canal opens internally through a small but distinct foramen in front of the axillary foramen. On both sides it opens anteriorly through the crista, with small foramina passing externally to the muscle depression anterior to the pars pedalis. Two enlarged foramina open above and below the pars pedalis on the left side, and on the right both lie beneath the pars pedalis (Text-fig. 8B). We therefore consider these foramina to have transmitted nerves or vessels to fin muscles inserting in this area, and thus probably to correspond to the anterior canal (c1) of *Procondylolepis*, which was similarly positioned to innervate the main abductor muscle for the fin inserting in the triangular depression immediately anteroventral to the anterior lobe of the scapulocoracoid (f.ab, Text-fig. 5A).

Evolution of the brachial joint in relation to pectoral fin function

Procondylolepis. In primitive arthrodires (Text-fig. 2A) the fin muscles evidently inserted on the lateral face of the scapulocoracoid above and below the articular crest (Goujet 1984). In *Procondylolepis* (and presumably *Yunnanolepis*), with their very restricted pectoral fenestra filled entirely by the articular area of the scapulocoracoid, the muscles must already have formed an attachment on adjacent dermal bone. In *Procondylolepis* an inclined axis passes through the two dermal articulations (art.d, art.v) for the pectoral appendage and the articular surface (scap) of the scapulocoracoid (dashed line in Text-figure 7B). Disposed in a line approximately normal to this axis are the two depressions considered above to have been for muscle insertion; and anteroventral one (f.ab) which would have rotated the pectoral fin outwards and downwards, and a posterodorsal one (f.ad) for an opposing muscle which would have adducted the fin. The fact that the upper dermal articulation (art.d) is a deep pit (Text-fig. 4A–B), which received the articular process of the first dorsal central plate of the pectoral appendage (ar3d, Text-fig. 3B), suggests a pivoting action about this point. The ventral articulation (art.v, Text-fig. 7B) forms a broad shallow groove, indicating some rotation around the long axis of the fin with the dorsal articulation as fulcrum. (As noted above, the ventral articulation in some specimens referred to *Procondylolepis* is also a deep pit similar to that on the dorsal side, which would preclude such a rotating motion). The muscles controlling this rotation may have been more centrally placed, possibly inserting on the scapulocoracoid. Uncertainty about the shape of the distal surface of the scapulocoracoid, and whether it was entirely an articular surface, renders the interpretation difficult on this point.

Sinolepids. Three main changes from the condition displayed by *Procondylolepis* are considered significant (Text-fig. 7C): (i) the dorsal and ventral dermal articulations (art.d, art.v) have migrated

posteriorly to lie essentially above and below the glenoid cartilage contained within the funnel pit (fp); (ii) the funnel pit and contained cartilage have acquired a subcircular shape; and (iii) a single large posterior opening has developed (f.ax). This we suggested above to have formed by coalescence of the posterior two neurovascular canals of *Procondylolepis* (c2, c3, Text-fig. 7B).

The ventral articulation in sinolepids is a deep pit similar in structure to the dorsal one in *Procondylolepis*: this might indicate independent development (Ritchie *et al.* in press). The larger more diffuse dorsal articulation may indicate that any rotation around the axis of the fin was pivoted in this case ventrally rather than dorsally. Alternatively, the dorsal articulation may be considered as more derived than the small articular pit of *Procondylolepis* because the corresponding articular process on the dorsal central plate of the sinolepid pectoral fin is clearly morphologically closer to that of euantiarchs than the corresponding bone of *Procondylolepis* (cf. Zhang 1984, fig. 2; Ritchie *et al.* in press, fig. 15A). The ventral pit-like articulation may likewise be considered more advanced than the shallow groove in *Procondylolepis*.

Euantiarchs. The asterolepidoids and bothriolepidoids are characterized by enlargement of the dorsal and ventral muscle fossae to form deep hemispherical grooves (art.d, art.v, Text-fig. 7D). Because of the close fit of the articular surfaces of the pectoral appendage these must have permitted controlled rotational movement of the fin. Such more complex movements required further differentiation of the musculature. The abductor muscle insertion (f.ab) was apparently subdivided by the pars pedalis (pe), and the adductor insertion was differentiated on the face of the brachial process into superior (a.sup, p.sup) and inferior (a.inf) attachments surrounding the funnel pit. We suggest that the several openings of the rostrocaudal canal (c.rc) above and below the pars pedalis reflect differentiation of the neurovascular supply to service more complex movements of the fin. At least two of the posterior muscle pits also contain foramina for neurovascular canals (c.nv, Text-fig. 8B). The pattern demonstrated here for two species of *Bothriolepis* (*B. macphersoni*, Text-fig. 2H; *Bothriolepis* sp. nov., Text-fig. 8B) is the same as illustrated by Watson (1961, fig. 2) in Scottish *Bothriolepis* material. It may be a synapomorphy of the genus.

As noted above, and contrary to this interpretation, both Gross (1931, p. 41) and Stensiö (1931, 1948, 1959, pp. 64-65) believed that retractor muscles for the pectoral fin had their proximal insertion on the scapulocoracoid within the trunk armour, and passed through the axial foramen to the fin. Distally the muscle insertion was on the endoskeletal rod within the fin, with the muscle passing through the posteromesial corner of the proximal aperture in the fin exoskeleton. In contrast, Watson (1961, p. 215) maintained that the axial foramen was 'quite unsuitable in both size and character to permit the passage of a muscle', and he concluded that 'the whole musculature of the pectoral fin must be internal, lying within the cavity of the fin and in general distal to the helmet process'.

Acid prepared material of *Bothriolepis* from Gogo, Western Australia, in which the complete fin exoskeleton can be manipulated on the brachial process, confirms that the muscle arrangement proposed by Stensiö is most unlikely. In the fully retracted position the fin lies against the trunk armour, and viewed from inside the anterior ventrolateral plate the posterior two thirds of the axillary foramen are obstructed by the proximal end of the first mesial marginal plate of the pectoral fin (Mm1, Text-fig. 8A). This leaves little room for a major muscle to enter the cavity of the fin exoskeleton. This does not preclude insertion of some general adductor musculature on the ridges above and below the axillary foramen (sar, Text-figs 2H, 8B). Like Watson (1961), we regard the axillary foramen as having transmitted the major artery and vein to the fin, consistent with the above suggestion that it was derived in sinolepids by coalescence of the posterior two neurovascular canals of *Procondylolepis*. However, its partial obstruction with the fin fully adducted must mean that, in *Bothriolepis* at least, the space was partly occupied by connective or other soft tissue. As discussed by Zhang and Young (in press), the reason for the large size of the axillary foramen in *Bothriolepis* and *Asterolepis* compared to other forms remains problematic, because it is apparently not correlated with presence of the distal joint, nor length of the proximal segment.

In the same specimen from Gogo two bony projections are preserved on the internal surfaces of

the dorsal and ventral central plates (dpr, vpr, Text-fig. 8), and with the fin adducted these are situated adjacent to the shallow depressions on the posterior face of the brachial process above and below the funnel pit (a.sup, a.inf, Text-fig. 8B). These depressions were considered by Gross (1931, p. 39) and Watson (1961, fig. 2B) to be insertions for retractor muscles, and in the Gogo specimen it is seen that such muscles would have passed across to the processes just described to adduct the fin effectively. The dorsal process has two terminal facets (Text-fig. 8C), perhaps corresponding to the two superior muscle insertion pits on the brachial process.

Watson (1961) interpreted the fin of *Bothriolepis* as capable of twisting about its own axis through an angle of up to 30°. He considered that when the broad dorsal surface of the fin was twisted vertically it would be effective in a swimming stroke, and in the other extreme position (with the narrow outer edge of the fin directed anteriorly) the limb could be brought forward with the least possible resistance from the water. The Gogo specimen shows, however, that in the fully abducted position rotation is not possible due to the triangular section of the pars pedalis, which is much thicker posteriorly than anteriorly. In the fully advanced position of the fin, when its proximal end stands out almost at right angles to the body, the proximal aperture of the fin enclosed the thick end of the pars pedalis, to preclude any rotational or dorsoventral movement (an observation also made by both Gross and Watson). Since it is in the fully abducted position that maximum pull would be obtained in the swimming stroke, it seems most unlikely that the fin was used oar-like to propel the animal through the water. A second point is that oars and oar-like appendages are widest distally, not proximally, and the reverse is the case with antiarch pectoral fins (Wells and Dorr 1985).

Stensiö (1948, p. 154) considered that when fully protracted the fin could not be lowered beneath the horizontal, but in the Gogo specimen it can be lowered to about 25° beneath the horizontal. Rather than some 10° out from the body, as maintained by Wells and Dorr (1985, p. 159), the fully adducted fin fits closely against the lateral wall of the trunk armour, both having the same gentle curvature. Since the greatest mobility of the fin was when it was held back towards the body, it seems more likely that any assistance with swimming involved acting as a hydrofoil by elevating or depressing the narrow leading edge of the fin, causing the fish to rise or fall in the water. The fin may have functioned primarily as a prop or wedge, to fix the animal into crevices or soft sediment on the bottom, either to avoid predators or to provide stability in currents. Secondary functions for the long, primarily protective, pectoral spines in the superficially similar loricariid catfishes include anchoring in strong currents, jostling other fishes for resting places, and crawling and clinging on rocks (Alexander 1965; Wells and Dorr 1985). However the necessity for the fish to prop itself up for breathing (Wells and Dorr 1985, p. 166) seems unlikely if it possessed a spiracle (see below). Another suggestion regarding fin function was that they assisted in pulling the fish through reeds (Gross 1931), but, as noted by Wells and Dorr (1985), modern fishes in this habitat tend to be fusiform, with projections from the body reduced or absent.

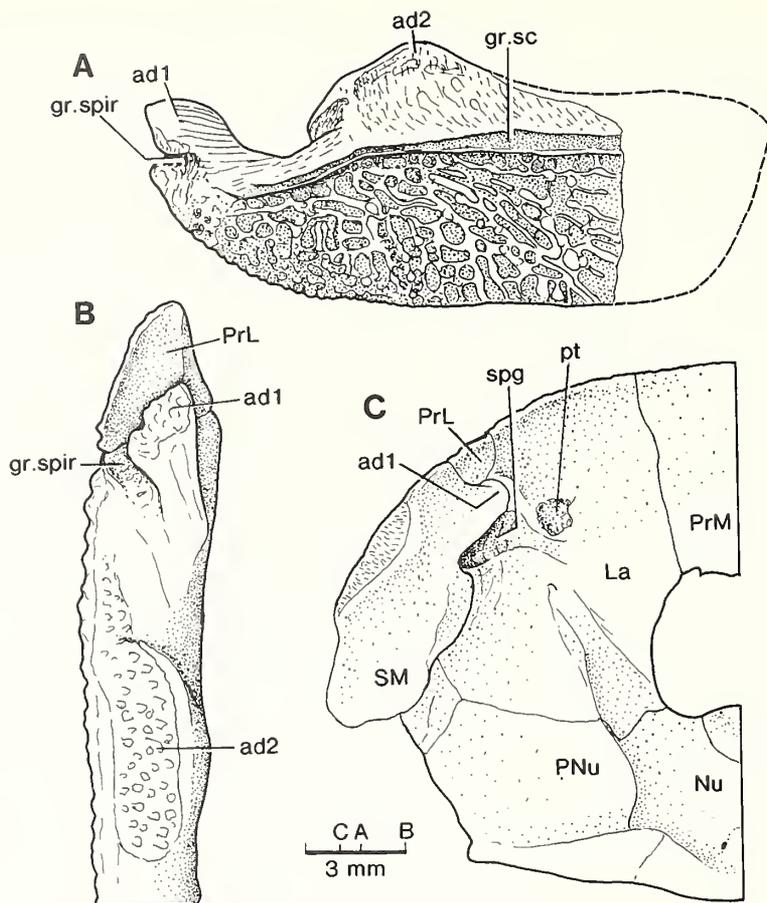
Wells and Dorr (1985) speculated that the appendage may have functioned somewhat like a crutch to enable *Bothriolepis* to walk on the water bottom, in shallows, or even on land. They considered the head and trunk armour to be tightly and rigidly joined, unlike other placoderms, and that this may have had adaptive significance for use on land. However, there was as much movement of the head against the trunk in *Bothriolepis* as in any other placoderm, with the reverse overlap at the postobstacitic (postmarginal) corner (Young 1984, fig. 7) corresponding precisely with that in arthrodires (e.g. Young 1980, fig. 18A). The rigidity of the box-like trunk armour on its own could hardly be an adaptation for walking out of water, since many primitive arthrodires (actinolepids, phlyctaeniids) also possessed an elongate box-like armour. Considering the abundance of *Bothriolepis* remains in some deposits (e.g. Escuminac Bay in Canada), some trace fossil evidence of any excursions across mudflats might be expected.

OPERCULUM

In describing an articulated but slightly crushed specimen of *Bothriolepis pauderi* which included the cheek plates, Watson (1961, p. 218) noted that the 'opercular' plate ('extralateral' of Traquair 1904, and Stensiö 1948; submarginal of Young 1984) had a distinct anterior process passing upwards and inwards into a matching facet on the lateral plate of the skull. On the left side of the specimen behind this process was a distinct notch (Watson 1961, fig. 1c), which he interpreted as having been completely filled by a rounded process seen on the other side of the specimen projecting from the margin of the right lateral plate. Watson thus rejected the interpretation of Stensiö (1947, 1948) that this notch was in fact the spiracular opening. In accordance with Watson's view, Miles (1968) renamed the 'spiracular groove' on the visceral surface of the head shield the 'transverse lateral groove'. Watson also cast doubt on the existence of a separate small cheek plate (Stensiö's 'prelateral' plate) in front of this opercular articulation, even though both Gross (1941a) and Stensiö (1948) had described in detail and figured this small bone for two species of *Bothriolepis* (*B. cellulosa*, *B. canadensis*). Description of acid-prepared *Bothriolepis* from Gogo, Western Australia (Young 1984) confirmed the accuracy of Stensiö's account regarding these small bones, and further study of the same specimen has now cast doubt on Watson's opinion regarding the spiracle in *Bothriolepis*.

This specimen demonstrates the detailed relationship of the main opercular element (the submarginal) to the two small sensory canal bones just in front of the opercular articulation (Young 1984, fig. 1). It was noted that the dermal articulation between the submarginal and lateral plates in *Bothriolepis* is a unique condition amongst placoderms, and that the articulation is supported by a thickened ridge of bone beneath the lateral plate which may have been an extension of the anterior postorbital process of the braincase. In arthrodires (e.g. Young 1979; Goujet 1984) the submarginal has an equivalent position, but is connected to the braincase by articulation between the endocranial anterior postorbital process and a cartilaginous element fixed to the anterodorsal corner of the dermal operculum (submarginal plate). Outgroup comparison indicates that an articulation between a cartilaginous element and the braincase may have been primitively present in antiarchs, to be replaced in bothriolepids by a dermal articulation. A perichondral ossification in the appropriate position has been tentatively identified in the primitive antiarch *Phymolepis* from the Early Devonian of China (Young and Zhang, in prep). Of interest in this connection is the form of the visceral surface of the submarginal plate in *Bothriolepis cullodenensis* figured by Long and Werdelin (1986, fig. 11A), which in place of a dermal process shows an irregular attachment surface not dissimilar to that in some other placoderms (e.g. Young 1986, fig. 14A). Young (1986) considered further the homology of the submarginal attachment in placoderms. Although the cartilaginous element just mentioned has been interpreted by some workers as the epihyal, Young (1986) suggested that it was an additional element (the opercular cartilage), probably derived from the hyoid arch, which in placoderms generally formed a unique type of opercular suspension. This is in contrast to the opercular cartilage in living gnathostomes, which never articulates with the braincase.

The question of a spiracular opening in antiarchs was not addressed by Young (1984), but closer examination of the Gogo material provides new information on this point. The fact that the anterodorsal corner of the submarginal plate in placoderms generally lies adjacent to the exit for the hyomandibular nerve means that a spiracle, if present, would have occupied a similar position. Watson (1961, p. 218) gave as his reason for rejecting Stensiö's interpretation of *Bothriolepis* that 'the spiracle in those fish in which it does occur lies anteriorly and dorsally, and does not form part of the border with which the opercular articulates'. This generalization hardly applies to non-operculate elasmobranchs, and an 'anterior and dorsal' position is not a valid criterion in the case of the highly modified skull morphology of antiarchs. Watson (1961, p. 220) later commented (in contradiction to the quote just given) that any spiracular opening in *Bothriolepis* 'could be expected to come out, either through a special opening in the head shield, or a notch in its border' (that is, in just the position identified by Stensiö). Watson's special pleading led him to the conclusion that



TEXT-FIG. 9. A, *Bothriolepis macphersoni* Young, 1988; incomplete left submarginal plate; Aztex Siltstone; southern Victoria Land, Antarctica. B-C, *Bothriolepis* sp.; CPC 25205 (same specimen as described by Young 1984); early Upper Devonian Gogo Formation; Canning Basin, Western Australia; B, anterior end of left submarginal and attached prelateral plates in dorsal view; C, right half of skull restored in ventral view, with submarginal and prelateral plates attached (cf. Young 1984, pl. 57, fig. 1). For list of abbreviations see p. 464.

because there was no definite evidence for the presence of a spiracle, 'the first gill slit was of full size, and not reduced to its dorsal end alone'. This agreed with the condition which he had earlier (1937) proposed for acanthodians and placoderms, which he grouped together as a major grade of primitive gnathostomes (the 'Aphetohyoidea') characterized by an unmodified hyoid arch. However, there is now much evidence refuting this view for both groups (e.g. Miles 1965, 1973; Miles and Young 1977; Young 1979, 1980, 1986).

The need to re-examine evidence for the presence of a spiracle in *Bothriolepis* arose with the description of a well-preserved submarginal plate of *Bothriolepis macphersoni* from southern Victoria Land, Antarctica (Text-fig. 9A), in which a distinct groove passing laterally around the anterodorsal articular process was identified as possibly containing the spiracular tube (Young 1988, p. 94). A re-examination of the submarginal plate in the acid-prepared Gogo *Bothriolepis* described by Young (1984) revealed a similar groove (gr.spir, Text-fig. 9B), which on reassembly against the skull opens immediately behind the anterior articulation of the submarginal on the lateral plate of the skull. This is exactly the position identified by Stensiö (1948) in *Bothriolepis*

canadensis, but the opening is much smaller than restored by him. It must be recorded that Watson (1961, p. 218) described the same groove in *Bothriolepis panderi* as 'a distinct unornamented groove, clearly recessed below the outer surface of the bone by at least half a millimetre'. Internally this groove is confluent with a deep pocket formed ventrally by the notch between the anterior and posterior dermal attachments between the submarginal plate and the skull, and dorsally by the 'spiracular groove' on the visceral surface of the lateral plate (spg, Text-fig. 9c). Using new evidence of the structure of the jaw cartilages in *Bothriolepis*, Young (1984) concluded that the mandibular joint must have occupied a position just inside the anterior dermal attachment of the submarginal, with the hyoid arch elements immediately behind. In this reconstruction the spiracular groove of Stensiö's (1948) interpretation (spg, Text-fig. 9c) lies in exactly the position expected of the hyoid pseudobranch. We thus consider these various lines of evidence to provide a good indication that there was a spiracle in *Bothriolepis*. In asterolepid antiarchs the submarginal plate has a different morphology from that of *Bothriolepis*, but the dermal attachment to the skull is again subdivided into anterior and posterior areas separated by a shallow notch, which externally is manifested as a small foramen (e.g. Gross 1931, pl. 12, fig. 7). A spiracular opening may thus have been primitively present in antiarchs (or euantiarchs), since it is developed in two major antiarch subgroups.

Finally, some functional aspects of the spiracle may be considered. Stensiö (1948) interpreted the spiracle of *Bothriolepis* as an opening through which water was expelled, this presumably being based on the analogue of modern sharks. But comparison between benthic antiarchs with evidently poor swimming ability and the active predatory habits of most sharks seems inappropriate. We consider it much more likely that the spiracle functioned for the intake of water for respiratory purposes, as is the case in modern batoids. The small ventrally placed mouth and flat ventral surface of the dermal armour in most antiarchs suggest a sluggish benthonic existence, with the weakly developed mouthparts suitable only for soft bottom detritus. In the primitive Early Devonian antiarch *Phymolepis* from South China the normal ornament of fine tubercles on the dermal elements for the upper jaw shows no differentiation at the mouth margin for grasping or biting, and the mouth must have opened in a very restricted space between the suborbital plates forming the dermal upper jaw, and the anterior border of the ventral wall of the trunk armour (Young and Zhang in prep.). The mouth evidently had very limited movement, and opened and closed in a horizontal plane back behind the rostral rim of the skull on the flat ventral surface. In such a position it could hardly have provided an adequate intake for respiratory water during feeding on the bottom. Unlike the suborbital plate, which formed the dermal upper jaw element, the submarginal plate forming the dermal operculum is part of the lateral rather than ventral wall of the armour. Watson (1961, p. 219) commented on the evident mobility of the operculum in *Bothriolepis*, which might be expected in a fish of benthonic habit, where a well-developed opercular pump respiratory mechanism is the norm (e.g. Hughes and Shelton 1962, p. 318). The spiracle would have permitted the intake of clear respiratory water, without interruption to feeding, or the necessity to move from a secure placement on or in the bottom sediment, just as it does in modern batoids.

Acknowledgements. This work was finalized during a visit to Australia by Zhang Guorui in 1989, with the support of an Australian Museum Visiting Fellowship and BMR contract, both of which are gratefully acknowledged. Both institutions are thanked for the provision of working facilities. G.C.Y. acknowledges financial support under the Australian Academy of Science–Academia Sinica Scientific Exchange Agreement for two visits to China in 1981 and 1987, when preliminary work on this project was undertaken, and thanks Chinese hosts for their hospitality, and Dr D. Goujet (Paris) for fruitful discussion on the Chinese specimens. Lu Wenying, Sun Xiaowen, and Yu Xiaobo assisted with translation from Chinese into English, and Dr A. Ritchie, R. W. Brown, H. M. Doyle and A. Haupt are thanked for assistance with preparation and photography. We thank Drs R. E. Barwick, A. Ritchie and Professor K. S. W. Campbell for useful discussion, and K. S. W. Campbell, B. G. Gardiner and D. Goujet for commenting on the manuscript. G.C.Y. publishes with the permission of the Director, Bureau of Mineral Resources, Canberra.

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G. C. YOUNG

Bureau of Mineral Resources
P.O. Box 378
Canberra, ACT 2601, Australia

ZHANG GUORUI

Institute of Vertebrate Palaeontology
and Palaeoanthropology
Academia Sinica
PO Box 643
Beijing 100044, China

Typescript received 6 October 1990

Revised typescript received 27 February 1991

ABBREVIATIONS USED IN TEXT-FIGURES

ad1, 2, anterior and posterior articular processes on SM; a.inf, ventral muscle insertion on brachial process; ar3d, external articular area of Cd1; ar3v, external articular area of Cv1; art.d, dorsal articular depression for dermal process of pectoral fin; art.v, ventral articular depression for dermal process of pectoral fin; a.sup, anterior dorsal muscle insertion on brachial process; Cd1, dorsal central plate 1; Cd2, dorsal central plate 2; Cv1, ventral central plate 1; Cv2, ventral central plate 2; c1-3, foramina piercing scapulocoracoid; cit, crista transversalis interna anterior on AVL plate; c.nv, canal for nerves and/or vessels; cr.art, articular crest on scapulocoracoid; c.rc, rostrocaudal canal; dpr, dorsal process inside pectoral appendage; f.ab, insertion area for abductor muscle of fin; f.ad, insertion area for adductor muscle of fin; f.ax, foramen axillare of AVL; fgr, funnel groove; f.mp, protractor area of brachial process; fp, funnel pit; f.pect, pectoral fenestra; gr.sc, groove for sensory canal; gr.spir, groove on SM for spiracular tube; gr.c2, groove showing course of canal c2; La, lateral plate of skull; M1, plates probably of the lateral marginal series of pectoral appendage; Mm, plates probably of the mesial marginal series of pectoral appendage; Mm1, mesial marginal plate 1; Mm2, mesial marginal plate 2; Mm4, mesial marginal plate 4; Nu, nuchal plate; PNu, paranuchal plate; PrL, prelateral plate; PrM, premedian plate; pt, lateral pit of head-shield; pbr, brachial process; pe, pars pedalis of brachial process; per, perichondral bone layer; prc, prepectoral corner of AVL; p.sup, posterior dorsal muscle insertion; r.md, ridges for insertion of dorsal fin muscles; r.mv, ridges for insertion of ventral fin muscles; sar, supra-articular ridge; spg, spiracular groove on head shield; SM, submarginal plate; vpr, ventral process inside pectoral appendage.

A PRIMITIVE ICHTHYOSAUR FROM THE LOWER TRIASSIC OF BRITISH COLUMBIA, CANADA

by D. B. BRINKMAN, ZHAO XIJIN and E. L. NICHOLLS

ABSTRACT. The primitive ichthyosaur, *Grippia* cf. *G. longirostris* occurs in Lower Triassic beds near Wapiti Lake, British Columbia. The material includes a well-preserved forelimb and a partial foot, and allows for a new interpretation of the homologies of the elements of the carpus and tarsus. Four distal carpals and five metacarpals are present in the hand, the element previously identified as the fifth distal carpal being reidentified as the fifth metacarpal. Similarly, the proximal element of the fifth digit in the foot is reidentified as the fifth metatarsal. The tarsus includes three proximal elements which are identified as an astragalus, calcaneum and centrale, four distal carpals, and five metatarsals. The centrale is lost in later ichthyosaurs. The early evolution of ichthyosaur paddles is reviewed.

CALLAWAY and Brinkman (1989) reported the presence of a primitive ichthyosaur of uncertain affinities in the Lower Triassic Vega Phroso Siltstone Member of the Sulphur Mountain Formation. The only specimen available at that time consisted of disarticulated remains including ribs, a single centrum, and limb elements thought to be from the fore-limb. The ribs and vertebra were mixosaurian, but the presence of an elongate epipodial and circular, plate-like carpal elements indicated that it was more primitive than any known mixosaur. Also, the large size of some of the possible carpal elements raised the possibility that more than one individual was present in this material.

Recently collected specimens from the Lower Triassic Vega-Phroso Siltstone Member show that this material is referable to *Grippia*, although it may be specifically distinct from *G. longirostris*, the only known species of the genus. Well-preserved partial postcranial skeletons document the structure of the presacral vertebral column in this genus and provide a basis for considering the homologies of the tarsal elements in primitive ichthyosaurs and the early evolution of the ichthyosaur hind-paddle. All specimens are housed in the collections of the Royal Tyrrell Museum of Palaeontology (TMP).

SYSTEMATIC PALAEOLOGY

Order ICHTHYOPTERYGIA Owen, 1860
Genus GRIPPIA Wiman, 1929

Type species. *Grippia longirostris* Wiman, 1929.

Distribution. Lower Triassic of Spitsbergen and British Columbia.

Grippia cf. *G. longirostris* Wiman, 1929

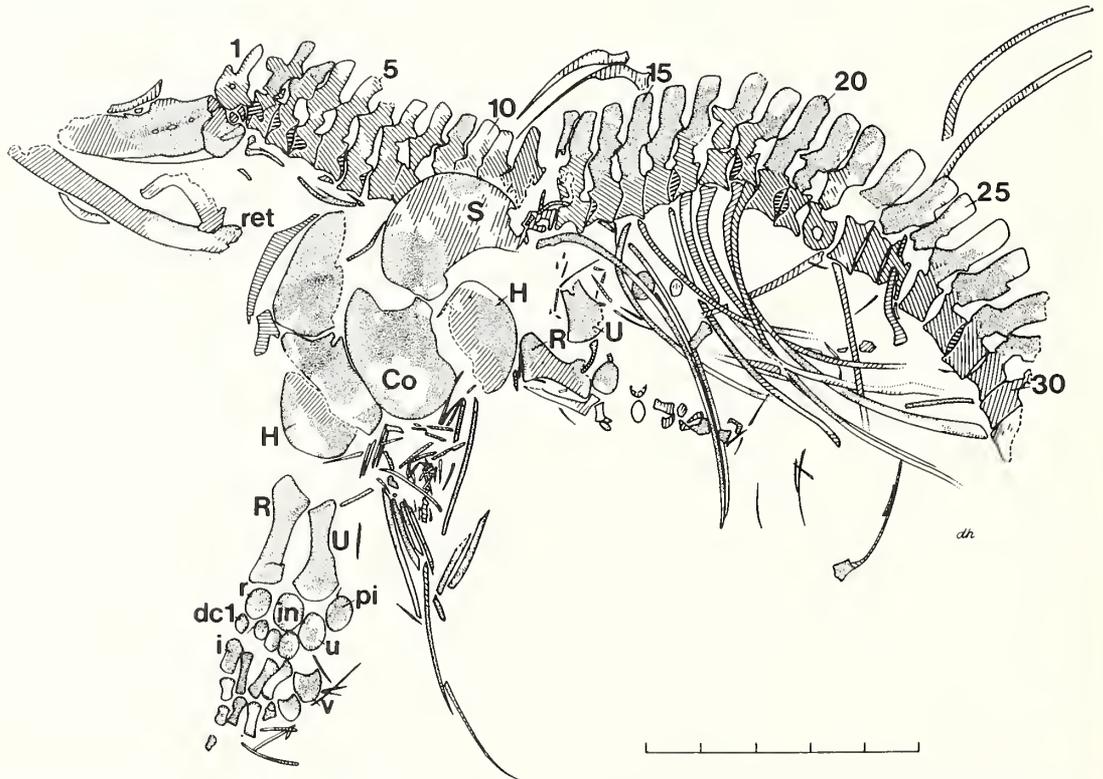
Text-figs 1-5

- 1929 *Grippia longirostris* Wiman, p. 186, fig. 2.
- 1933 *Grippia longirostris* Wiman; Wiman, pp. 1-19, pl. 1-2, figs 3-4.
- 1972 *Mixosaurus longirostris* (Wiman); McGowan, pp. 4-5.
- 1976 *Mixosaurus longirostris* (Wiman); McGowan, pp. 680-681.
- 1981 *Grippia longirostris* Wiman; Mazin, pp. 317-340.
- 1986 *Grippia longirostris* Wiman; Mazin, pp. 314-318.

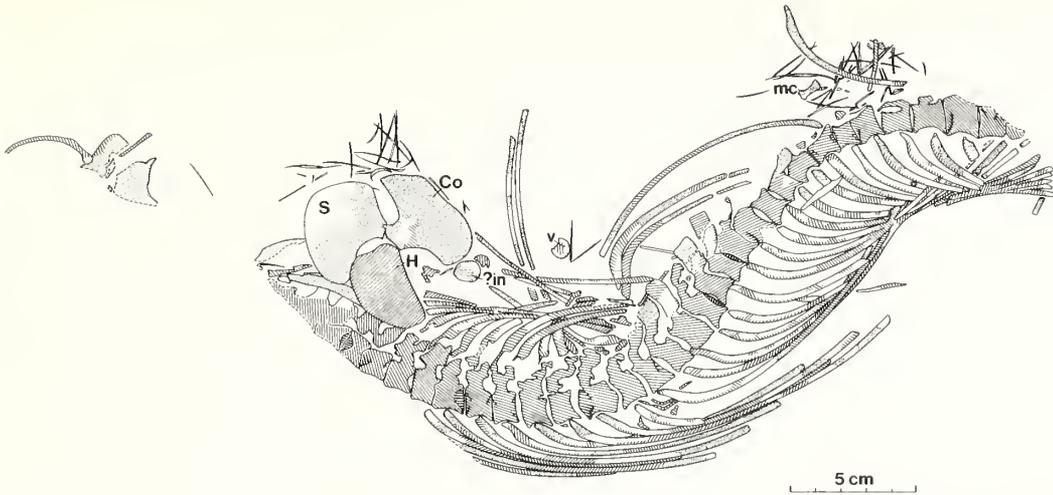
Referred specimens. TMP 89.127.3, a partial skeleton of a single individual including the posterior end of both lower jaws, impression of cheek region of skull, and front part of postcranial skeleton, from south end of cirque designated as D locality; TMP 89.128.5, partial hind limb including most of tarsus, five metatarsals, basal three phalanges of digits one and two, basal two phalanges of digits three to five, and traces of soft tissue, from locality A; TMP 86.152.12, disarticulated remains including ribs, a single (?) dorsal centrum, and elements of the forelimb including ?humerus, radius, and carpal elements, and (?) proximal tarsals, from locality A; TMP 89.127.12, a partial skeleton of a single individual including fragments of posterior end of skull, much of the dorsal region of the presacral vertebral column with ribs of left side in articulation and ribs of right side partially disarticulated, articulated right scapula, coracoid and humerus, and scattered elements of the carpus and metacarpus, from the central portion of D cirque.

Horizon and locality. All specimens are from two localities south-east of Wapiti Lake in east-central British Columbia. Locality A is 54° 31' 35" N, 120° 44' 10" W; and Locality D is 54° 31' 10" N, 120° 43' 19" W. All specimens are from the Lower to Middle Triassic Sulphur Mountain Formation. TMP 89.127.3, TMP 89.128.5, and TMP 86.152.12 are from the Vega-Phroso Member of the Sulphur Mountain Formation and are Early Triassic in age. The exact horizon of TMP 89.127.12 within the Sulphur Mountain Formation is unknown.

Description. Both TMP 89.127.3 (Text-fig. 1) and TMP 89.127.12 (Text-fig. 2) were originally preserved with the skull, but in both cases, only fragments remain. TMP 89.127.3 includes impressions of the cheek region and the posterior end of both lower jaws. Like that of *Grippia*, the cheek region was relatively long and had a distinct emargination. Sutures cannot be identified. Fragments of the posterior end of the skull on specimen TMP 89.127.12 could not be identified with certainty, but may include the lateral edge of the upper temporal opening. The posterior ends of the lower jaws are preserved in TMP 89.127.3. A short retroarticular process was present.



TEXT-FIG. 1. *Grippia* cf. *G. longirostris*, TMP 89.127.3. Abbreviations: Co, coracoid; dc1, first distal carpal; H, humerus; in, intermedium; pi, pisiform; R, radius; r, radiale; ret, retroarticular process; S, scapula; U, ulna; u, ulnare; i-v, first to fifth metacarpals; 1-30, vertebrae number one to thirty. Scale bar is 50 mm.



TEXT-FIG. 2. *Grippia* cf. *G. longirostris*, TMP 89.127.12. Abbreviations: Co, coracoid; dc, distal carpal; H, humerus; ?in, intermedium; S, scapula; v, fifth metacarpal.

Thirty-one vertebrae are present in specimen TMP 89.127.3. The first of these is located just posterior to the cranial elements, so may be one of the first three vertebrae. Except for the first and twenty-second vertebrae, which have rotated 90°, all are preserved in articulation and are seen in lateral view. Thirty-two vertebrae, all from the dorsal series, are preserved in specimen TMP 89.127.12. The first seventeen of these are seen in lateral view, vertebrae number eighteen to thirty are seen in dorso-lateral view, and the last two are again seen in lateral view. Although the complete length of the vertebral column is unknown, these two specimens demonstrate that *Grippia* cf. *G. longirostris* had a long snake-like body.

The shortest vertebrae are the cervicals. The length of the centra increases posteriorly along the column, although both specimens show that at their maximum length, the dorsal vertebrae are higher than they are long (Table 1). Thus the proportions of the centra of *Grippia* cf. *G. longirostris* differ from those of *Grippia longirostris* and other Lower Triassic ichthyosaurs, such as *Utatusaurus hataii* and *Chaolusaurus geishanensis* where some of the vertebrae in the cervical and anterior dorsal region are as long as, or longer than, they are high (Yang and Dong 1972; Shikama *et al.* 1978; Mazin 1981). The third and twenty-first centra in specimen TMP 89.127.3 are preserved in medial cross section, and the twenty-second vertebra in end view. These centra show that the vertebrae are deeply amphicoelous.

The neural arches and spines are clearly visible in lateral view along most of the preserved section of the vertebral column in TMP 89.127.3. Neural arches are preserved along most of the vertebral column of TMP 89.127.12 but only four complete neural spines are present. All four are from the posterior half of the column. As in the dorsal vertebrae of *Grippia longirostris* (Wiman 1933, pl. 1, fig. 9) the neural spines are relatively short and the neural arches are high. The neural arch is highest at the anterior end of the dorsal series and gradually decreases in height posteriorly. The height of the neural spine increases relative to the height of the neural arch, but their combined height does not change relative to the height of the centrum. The width of the neural spine measured antero-posteriorly increases posteriorly along the column. In specimen TMP 89.127.3, the antero-posterior width of the neural spine of the second vertebra is about three-quarters of the length of the centrum, and at the posterior end of the column, the width of the spine is only slightly less than the length of the centrum. The antero-posterior width of the complete neural spines of TMP 89.127.12 is also only slightly less than the length of the centrum.

One cervical rib is present in TMP 89.127.3. This is a short, double-headed rib located next to the second vertebra. Many of the dorsal ribs in specimen TMP 89.127.12 are complete and are preserved in articulation with the vertebral column. These ribs are similar to those of *Mixosaurus* in being long, having a strongly curved proximal third and a nearly straight distal two-thirds. These proportions suggest that *Grippia* cf. *G. longirostris* had a deep, laterally-compressed body. One displaced right rib located near the posterior end of the vertebral column is shorter and more evenly curved. This rib must have come from near the posterior end of the dorsal series, and suggests that the preserved section of vertebral column nearly reaches the sacral region. The

TABLE 1. Measurements of vertebrae of TMP 89.127.3. All measurements are in mm. The length of the centrum is measured at its base and its height is measured at its anterior end; the height of the neural arch is measured from the dorsal edge of the posterior end of the centrum to the postzygapophysis; the height of the neural spine is measured from the postzygapophysis to the tip of the spine.

Vertebra	Length of centrum	Height of centrum	Height of neural arch	Height of neural spine	Width of neural spine
2	4.3	6.2	6.5	5.6	—
3	4.3	6.8	5.7	6.8	2.5
4	4.4	7.4	4.5	7.0	—
5	4.7	6.9	5.0	6.5	3.2
6	6.2	6.7	6.2	6.2	3.0
7	4.5	7.3	7.0	6.3	3.0
8	5.0	7.6	—	6.4	—
9	—	—	6.7	6.7	3.0
10	—	—	6.5	7.6	3.0
11	—	—	—	—	—
12	—	—	—	7.8	—
13	4.8	6.0	6.6	7.8	3.7
14	4.6	5.2	7.0	7.7	4.2
15	5.7	6.7	7.0	8.4	4.0
16	4.5	6.6	7.4	8.6	4.5
17	4.9	6.7	7.3	7.6	4.2
18	5.3	6.7	—	8.2	4.4
19	—	—	—	9.7	5.2
20	5.5	7.5	6.5	10.6	5.2
21	5.3	7.9	5.7	9.4	5.2
22	—	—	—	10.8	5.3
23	5.5	8.5	5.6	10.9	5.7
24	5.8	—	5.8	10.3	5.5
25	—	—	5.6	10.1	—
26	6.1	7.4	5.8	10.2	—
27	6.2	7.2	6.0	10.4	5.7
28	5.8	7.6	5.5	—	—
29	5.7	7.2	—	—	—
30	5.6	6.3	—	—	—

proximal end of four dorsal ribs in specimen TMP 89.127.3 are visible. These are preserved approximately in place adjacent to the twelfth, eighteenth, nineteenth and twenty-second vertebrae, and are all single-headed.

Scattered gastralia are present in TMP 89.127.3. They are generally ichthyosaurian in shape, although their arrangement is uncertain.

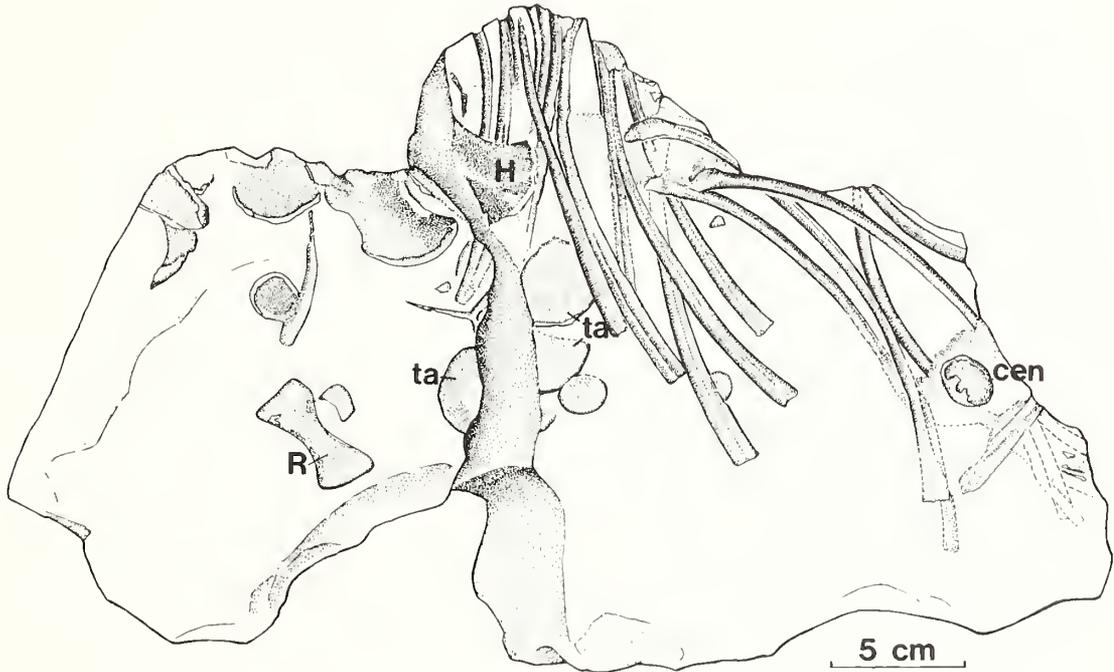
The left scapula and coracoid are complete in specimen TMP 89.127.3, and the right are partly visible. A clavicle and interclavicle are visible anterior to the right scapula, but these are seen in cross-section, so their shape is uncertain. A nearly complete right scapula and coracoid are preserved in TMP 89.127.12.

The shoulder girdle is mixosaurian in its general shape. The coracoid has a greatly expanded ventral plate that narrows to a short peduncle laterally. This peduncle forms both the coracoid portion of the glenoid and the articular surface for the scapula. The scapula has a greatly expanded blade. The ventral edge of the blade is separated from the coracoid, contact between the two elements being restricted to the peduncle of the coracoid.

Both right and left humeri of TMP 89.127.3 are represented by their distal ends and a complete right humerus is present in TMP 89.127.12. These confirm that the element in TMP 86.152.12 tentatively identified as a humerus by Callaway and Brinkman (1989) was correctly identified (Text-fig. 3). The humerus is similar to that of *Grippia longirostris* and *Utatusaurus hataii* in general shape but is more elongate than in those genera. In TMP 89.127.2, the width/length ratio is 0.64, while in *Utatusaurus hataii* this is 0.70, and in *Grippia*

longirostris it is 0.79 (Mazin 1986). The distal articular surfaces can be divided into distinct radial and ulnar portions. The angle between these two portions is 145° , intermediate between that of *Utatusaurus hataii* (152°), and *Grippia longirostris* (133°) (Mazin 1986).

The radius, as in *Grippia longirostris* and *Utatusaurus hataii*, is elongate and has expanded proximal and distal ends. The right radius is well preserved in specimen TMP 89.127.3, and, based on this element, the epipodial preserved in specimen TMP 86.152.12 can be identified as a radius (Text-fig. 3). Surprisingly, the left radius in TMP 89.127.3 is shorter and more robust than the right. In general proportions, the radius is similar to *G. longirostris* rather than *U. hataii*, in that the angle between the proximal articular surface and the shaft of the bone is 56° in both the right radius of TMP 89.127.3 and the radius of TMP 86.152.12 and 67° in the left radius of TMP 89.127.3. The corresponding angle in *G. longirostris* is 57° and in *U. hataii* it is 84° (Mazin 1986).



TEXT-FIG. 3. *Grippia* cf. *G. longirostris*, TMP 86.152.12. Abbreviations: cen, centrum; H, humerus; R, radius; ta, tarsal element.

The right ulna is well preserved and the distal end of the left is present in TMP 89.127.3. As with the radius, this is an elongate bone with expanded ends. The distal end is much more expanded than the proximal, and bears distinct articular surfaces for the intermedium, ulnare, and pisiform. The inner (radiad) border of the ulna is more strongly concave than the external border, giving the element an asymmetrical shape.

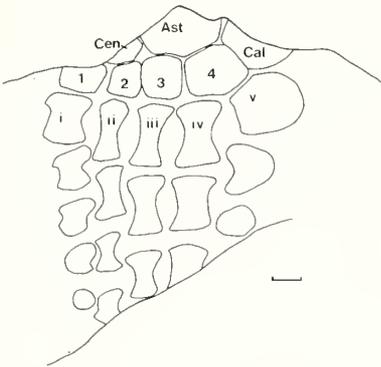
The right carpus is preserved in articulation in TMP 89.127.3. The carpus in TMP 89.127.12 is represented by two of the proximal elements, the fifth metacarpal, and an unidentified metacarpal or proximal phalanx. Specimen TMP 86.152.12 includes several elements that were identified as carpal elements by Callaway and Brinkman (1989). However, some of these are much larger relative to the size of the radius than in specimen TMP 89.27.3, and are reidentified as proximal tarsals (Text-fig. 3).

All the elements of the carpus are plate-like. As in *Grippia longirostris* and *Utatusaurus hataii* the four proximal elements are the radiale, intermedium, ulnare, and pisiform. The intermedium is the largest of these, the remaining three are subequal in size. As in ichthyosaurs generally, the centrale are absent. The four distal elements are identified as the first to fourth distal carpals. The first three are subequal in size and are distinctly smaller than the fourth. The second articulates between the radiale and intermedium, and the fourth articulates between the intermedium and ulnare. The distal carpals are all smaller than the proximal carpal bones.

The first to fourth metacarpals are elongate, slender bones. The fifth metacarpal is a broad, hook-shaped element with an extensive distal articular surface and without a lateral notch. The identification of this element as the fifth metacarpal, rather than the fifth distal carpal, is based primarily on its large size relative to the fourth distal carpal. In primitive reptiles with five distal carpals, the fifth distal carpal is the smallest of these elements. Also, generally the fifth distal carpal is lost before the fifth metacarpal.

The basal three phalanges of the first toe are present. All of these are longer than broad, although the differences in length and breadth decreases distally along the toe. The proximal two elements have a distinct shaft and expanded ends. The third is subrectangular in shape and shows only slightly expanded ends. The second and third digits are represented only by their basal phalanges. These are elongate elements, over half the length of their respective metacarpals and with broadly expanded proximal ends. The basal phalanx of the fifth digit is overlain by the fifth toe. The fifth toe is represented by the basal two phalanges. The first of these is a short, wide element with a broadly concave internal border and a tight notch on the external border. The second phalanx is incompletely preserved but appears to have been a subcircular element.

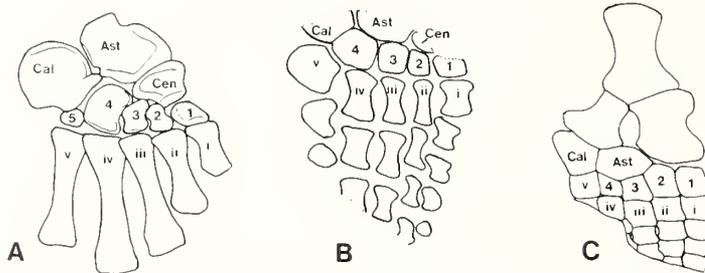
A partial hind-limb is present in specimen TMP 89.128.5 (Text-fig. 4). Three large proximal tarsal elements are incompletely preserved but appear to match some of the elements in TMP 86.152.12 that were previously identified as large carpal elements. Thus these elements are reidentified as the three proximal tarsal elements (Text-fig. 4).



TEXT-FIG. 4. *Grippia* cf. *G. longirostris*; TMP 89.128.5; partial hind limb. Abbreviations: Ast, astragalus; Cal, calcaneum; Cen, centrale; i-v, first to fifth metatarsals; 1-4, first to fourth distal tarsals. Scale bar is 10 mm.

The tarsal elements and phalanges of TMP 89.128.5 are undisturbed, and traces of soft tissue preserved as a faint bluish stain show the extent of the fin. In contrast to the carpus of TMP 89.127.3, the elements of the tarsus of TMP 89.128.5 are closely articulated. This difference is interpreted as a developmental feature associated with the larger size of TMP 89.128.5.

The relative size and position of the elements in the tarsus compares closely with the elements of the tarsus in primitive diapsids (Text-fig. 5A), so despite the incomplete preservation of the three proximal elements, they can be identified as the astragalus, calcaneum and centrale. The astragalus and calcaneum, when complete,



TEXT-FIG. 5. Comparison of the tarsus in primitive diapsid reptiles and early ichthyosaurs. A, *Galesphyrus* from Carroll (1976). B, *Grippia* cf. *G. longirostris*, drawn from TMP 89.128.5. C, *Mixosaurus nordenskiöldii*, drawn from TMP 89.126.5. Not to scale. Abbreviations: Ast, astragalus; Cal, calcaneum; Cen, centrale; i-v, first to fifth metatarsals; 1-5, first to fifth distal tarsals.

would have been the largest elements in the tarsus. The centrale lies between the astragalus and first three distal tarsals. The fourth distal tarsal is the largest of the distal tarsals and lies between, and distal to, the astragalus and calcaneum. The first three distal tarsals are subequal in size, but, as typical in primitive reptiles with a separate centrale, the second is slightly smaller than the first and third.

Five metatarsals are present. The first four are hourglass-shaped. The first is short and broad, its proximal width and length being subequal. The second to fourth are longer. These show an increase in width with the fourth being the widest. The fifth metatarsal is a short, broad, plate-like element. It articulates with the disto-lateral edge of the fourth distal tarsal.

All phalanges are flattened, apparently naturally so. Four phalanges are preserved in the first digit, three in the second, and two in the third to fifth digits. The phalanges of the first digit show a transition from hourglass-shaped to circular. The phalanges of the second to fourth digits are all hourglass-shaped. As with the metatarsals, the phalanges of the second digit are the narrowest, and the phalanges of the fourth digit are the widest. The basal phalanges of the fifth digit is bean-shaped, the second is circular. There is a tendency for the phalanges of the first three digits to form an interlocking structure, with the phalanges of the more medial digits tending to lie lateral to the joints between the corresponding elements of the more lateral digits. This is also the case for the arrangement of the phalanges of the fourth and fifth digits.

Traces of the soft tissue show that the fin was gently tapered. The anterior (leading) edge of the fin is located adjacent to the anterior edge of its bony support. The posterior (trailing) edge extends distal to the posterior edge of the bony support. The presence of unsupported tissue on the distal edge of the fin is a feature that was considered by Robinson (1975) to be typical of fins that are used for underwater flying. Thus although the tarsus and phalanges of *Grippia* cf. *G. longirostris* are morphologically distinct, the hind-limb was functionally specialized for use as a hydrofoil.

Comparisons. Three Lower Triassic ichthyosaurs are well represented by postcranial skeletal material. These are *Utatsusaurus hataii* from Japan (Shikama *et al.* 1978), *Grippia longirostris* from Spitsbergen (Wiman 1929; Mazin 1981), and *Chaohusaurus geishanensis* from China (Yang and Dong 1972). The material described here differs from *Chaohusaurus* and is similar to *G. longirostris* and *U. hataii* in the shape of the humerus and in the presence of a pisiform. The humerus of *Chaohusaurus*, like that of the members of the Shastasauridae and Jurassic ichthyosaurs, has concave pre- and postaxial borders. *G. longirostris*, *U. hataii*, and the Wapiti Lake taxon have a flange on the anterior edge of the humerus giving the element a convex anterior margin. This structure is also seen in *Mixosaurus* and *Omphalosaurus*, and has been interpreted as a primitive ichthyosaurian character because of its wide distribution in primitive ichthyosaurs (Mazin 1986). The presence of a pisiform is a primitive feature in tetrapods, and its absence in *Chaohusaurus* can be interpreted as a derived feature, possibly linking that genus with the Shastasauridae which are characterized in part by the development of a very narrow pectoral fin.

Both *Utatsusaurus hataii* and *Grippia longirostris* are represented by well-preserved forelimb material, and Mazin (1986) has shown that these forelimbs differ in several features. In general, where they differ, the British Columbia specimens conform closely to *G. longirostris* (Table 2). The similarity in the shape of the radius and ulna is particularly striking, and the British Columbia material is referred to the genus *Grippia* on the basis of these similarities.

The British Columbia material differs from *Grippia longirostris* in features of the vertebrae, humerus, carpus, and metatarsus. The cervical vertebrae of the British Columbia taxon are more derived than those of *G. longirostris* in being shorter than they are high. Three cervical vertebrae are known in *G. longirostris* (Wiman 1929; Mazin 1981). All of these have centra that are longer than they are high. The presence of longer cervical centra can be interpreted as a more primitive condition.

The humerus of TMP 89.127.12 differs from that of *Grippia longirostris* in being longer relative to its width and in that the angle formed by the radial and ulnar articular surfaces of the humerus is intermediate between that of *G. longirostris* and *Utatsusaurus hataii* (Table 2). The presence of a relatively longer humerus is probably a primitive feature. The difference in the angle formed by the radial and ulnar articular surfaces is of uncertain polarity.

The carpus of TMP 89.127.3 differs from that of *Grippia longirostris* as reconstructed by Mazin (1986), in that the first three distal carpals are about half the size of the fourth distal carpal, rather

TABLE 2. Comparison of the pectoral limbs of Lower Triassic ichthyosaurs.

	<i>Grippia longirostris</i>	<i>Utatusaurus hataii</i>	<i>Grippia</i> cf. <i>G. longirostris</i>
Width/length ratio of the humerus	0.79	0.70	0.64
Angle between articular surface for the radius and ulna	133°	152°	145°
Angle formed between proximal articular surface and general axis of radius	57°	84°	56–67°
Ulna shape	Asymmetrical	Symmetrical	Asymmetrical
Size of distal carpals relative to the size of the proximal carpals	Equal	Less than half	Less than half
Basal phalanges of fourth digit	—	Broader than long	Longer than broad

than being subequal in size. The condition seen in *G. longirostris* was thought to be primitive by Mazin (1986). If correct, this would suggest that the Wapiti Lake material should be assigned to *Utatusaurus*, which also has a fourth distal carpal that is much larger than the first three. However, primitive diapsids typically have a fourth distal carpal that is large relative to the first three, so the presence of these proportions is better considered to be a primitive feature. Thus if correctly reconstructed, *G. longirostris* would be autapomorphic in the proportions of the distal carpals.

The metatarsus of the British Columbia taxon differs from that of *Grippia longirostris* as reconstructed by Mazin (1981) in that the elements are strongly dorso-ventrally flattened, rather than cylindrical and in the shape of the first and fifth metatarsals. The first is short and wide compared to the second to fourth. In *G. longirostris*, the first four metatarsals are of subequal length. The fifth metatarsal is derived in being a short, hook-shaped element. The element identified as the fifth metatarsal of *G. longirostris* by Mazin (1981) is elongate and cylindrical. In all these features, the metatarsus of the Wapiti Lake taxon can be interpreted as derived relative to *G. longirostris*.

Thus, although the British Columbia material can be identified as *Grippia* on the basis of the similarities in the forelimb, it is not easily referable to *Grippia longirostris*. Of particular note are the differences in the cervical vertebrae and metatarsus which suggest that the new specimens are from a taxon that is derived relative to *G. longirostris*. However, we do not recognize a new species since the skull, which is the best known part of the skeleton of *G. longirostris*, is largely unrepresented in the British Columbia material, and the vertebral column and pelvic limb, which are well known in the Canadian specimens, are incompletely represented in *G. longirostris*. Thus the British Columbia material is referred to as *Grippia* cf. *G. longirostris* at present.

EARLY EVOLUTION OF THE ICHTHYOSAUR PADDLES

Since the limb material of *Grippia* cf. *G. longirostris* provides a much better understanding of the structure of the limbs in that genus, it is possible to reconsider the early evolution of the ichthyosaur limb. The forelimb of *Grippia* cf. *G. longirostris* is slightly more primitive than that of *Utatusaurus hataii* in that more of the basal phalanges remain distinct. In *Utatusaurus hataii*, all the basal phalanges are short, nearly square elements, while in *Grippia* cf. *G. longirostris*, the basal phalanges of the first three digits are much longer than they are wide. Thus *Grippia* cf. *G. longirostris* can be placed at the base of a morphological series showing increased specialization of the fore-limb of ichthyosaurs to form a paddle. This sequence shows that the external and distal elements of the hand were the first to lose their phalanx-like character, and that the most central and proximal phalanges (the basal phalanges of the second and third digits) were the last. *Grippia* and

Utatsusaurus share the loss of the centrale. Whether this is related to the development of aquatic specializations of the limb is uncertain.

The tarsus of *Grippia* cf. *G. longirostris* is the most primitive ichthyosaur tarsus known in that it retains three proximal tarsals and in that the elements of the metatarsus and pes are elongate. Previously the most primitive well-known ichthyosaur tarsus was that of *Mixosaurus* (Text-fig. 5C). The paddle of *Mixosaurus* is primitive relative to other known Triassic ichthyosaur pelvic limbs in that the tibia and fibula retained distinct shafts and were separated from one another (Appleby 1979). However, as in more derived ichthyosaurs and in contrast to *Grippia* cf. *G. longirostris*, the elements of the tarsus and metatarsus in *Mixosaurus* have largely lost their individuality. This has made the homologies of the elements of the ichthyosaur paddle difficult to identify. The three proximal tarsals cannot be the tibiale, intermedium and fibulare. As pointed out by Romer (1956, p. 401), primitive reptiles did not have a distinct intermedium, that element having been incorporated into the astragalus (Peabody 1951).

Callaway (1989) suggested that the two large proximal elements in the mixosaur tarsus were the astragalus and calcaneum, that the centrale was lost, and that the five elements distal to the astragalus and calcaneum were distal tarsals one to five. This proposal largely brought the tarsus of primitive ichthyosaurs in line with that of primitive reptiles, but it was unusual compared to diapsid reptiles in the presence of a large fifth distal tarsal. This was one of the few features that contradicted the hypothesis that ichthyosaurs were derived from diapsid reptiles, a hypothesis that otherwise seems consistent with the morphology of early ichthyosaurs and primitive diapsid reptiles (Tarsitano 1983; Callaway 1989).

The paddle of *Grippia* cf. *G. longirostris* confirms Callaway's (1989) interpretation that the two large proximal elements are the astragalus and calcaneum and that the centrale is lost in the mixosaur tarsus. However, according to the homologies presented here, the tarsus of *Grippia* has four, rather than five, distal tarsals. Based on this, the basal element of the fifth digit in the *Mixosaurus* foot is reidentified as a fifth metatarsal. This reinterpretation removed one of the major obstacles to the hypothesis that ichthyosaurs originated from diapsid reptiles.

Acknowledgements. The authors thank Andy Neuman, Bob Campbell, Anna Curtis, Kevin Lysing, and Ivy Rutzky for assistance in the field during collection of the specimens described here. Dianne Hollingdale drew Text-figures 1 and 2. Donna Sloan drew Text-figure 3, and Bob Campbell drew Text-figure 4. Support for travel enabling one of us (Z.X.) to participate in the field work was provided by the Ex Terra Foundation, Edmonton, Alberta.

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D. B. BRINKMAN

E. L. NICHOLLS

Royal Tyrrell Museum of Palaeontology
Box 7500
Drumheller, Alberta, Canada T05 0Y0

ZHAO XIJIN

Institute of Vertebrate Paleontology
and Paleoanthropology
Academia Sinica, P.O. Box 643
Beijing 100044, P. R. of China

Typescript received 23 January 1991

Revised typescript received 10 June 1991

THE PROGRESS OF QUANTITATIVE METHODS IN PALAEOLOGY

by J. T. TEMPLE

ABSTRACT. The slow progress of quantitative methods in palaeontology during the past decade threatens the survival of palaeontology. Different phenetic and cladistic methods produce different estimates of phylogenetic relations; none of these estimates is *a priori* more authoritative than others; taxonomic and phylogenetic certainty is unattainable, and probabilistic estimates of phylogeny must be accepted. Phenetic methods are well suited to estimating phylogenies from palaeontological data. Objective definitions of taxonomic entities and attribute states are essential in phylogenetic analysis. Outline analysis and landmark analysis are discussed, and the practical advantages of the former are considered to outweigh any resulting loss of homology. Techniques of outline and surface measurement and analysis are reviewed briefly. Temple's (1982*a*) review of ordination methods is supplemented to include standardization of entities, Projection Pursuit, Detrended Correspondence Analysis and Canonical Correspondence Analysis.

An earlier article (Temple 1982*a*) dealt with the use of ordination techniques in palaeontology. The present article, which may be considered a supplement to the earlier one, has a three-fold purpose:

1. to review the progress of quantitative methods in palaeontology during the last decade, and to assess the auguries for the future;
2. to consider quantitative palaeontology in the context of two current methodological debates, namely phenetics *vs* cladistics, and outlines *vs* landmarks;
3. to up-date the earlier article on ordination.

There can be no doubt that palaeontology, if it is to survive into the next century as a serious branch of science, will do so only in so far as it has transformed itself into a quantitative discipline. By its nature, palaeontology contributes primarily to the study of aspects of evolution – variation, speciation, organic diversity, the pattern of change in time – and the evidence that palaeontology brings to bear on these topics carries conviction with scientists in other disciplines only in so far as it is expressed in quantitative terms. To take two examples: polymodality of size or shape can be established only by analysis of frequencies of scores on suitable size or shape indicators; the patterns (or even the existence) of morphological change in fossil lineages or of secular change in organic diversity need to be tested against the models that can be proposed for such data, e.g. random walk with/without drift, trend-stationary process, etc. (Diggle 1990; Nelson and Plosser 1982; Mills 1990).

It must, however, be admitted that the auguries for the change in outlook by palaeontologists essential to the survival of our subject are not good. It is, after all, not many years since the Palaeontological Association gave its annual President's Award to a paper, on assemblage structure of a group of fossils, whose author stated that he had used no numerical methods whatever in his analysis. A recent compendium of palaeontological techniques sponsored by the Association (Briggs and Crowther 1989) gives only the most scanty coverage to quantitative methods. The eyes of the palaeontological world, it seems, still glaze over at the mention of eigenvectors – the word does not, for instance, appear in the index to Briggs and Crowther. It is difficult to be optimistic about the future when most of our colleagues have not yet learned even the vocabulary, let alone the practice, of quantitative palaeontology, after exposure to it during three decades.

Furthermore, the enthusiasm with which cladistic methodology has been embraced by palaeontologists during the past decade (see below) is probably to be explained by the phenomenon

noted in a wider context by Felsenstein (1988a, p. 113), namely that 'young, but traditionally-trained morphological systematists who tended, on the whole, to be uncomfortable with both numerical and molecular methods ... found Hennig's qualitative discussion more accessible than the numerical work which had been slowly spreading for the previous decade'.

Nevertheless, we should not despair, in spite of the disappointments of the past decade. The progress of technology in fields relevant to palaeontology (i.e. image and spatial analysis, data handling, etc.) is now so rapid, and the technology itself is so readily accessible, that notwithstanding its present doldrums palaeontology could still be revolutionized by the turn of the century – but only if we continue to provide the channels for the relevant technology to diffuse into our subject.

PHENETICS VS CLADISTICS

It seems that as far as most palaeontologists are concerned the phenetics vs cladistics debate has been resolved in favour of cladistics – whether for the reason suggested above or not. A mere handful of phenetic studies of fossil groups has been published, and even these few have been virtually ignored by other workers in the relevant fields. Phenetics is definitely not respectable in palaeontology, and word has come down from the mountain to this effect (Gould 1980, p. 110; see also Temple 1982b). On the other hand, a glance at any recent issue of *Palaentology* will reveal cladograms galore. In this respect, of course, our colleagues are by no means alone among taxonomists – see for instance the cladistic triumphalism of Ridley (1985, p. 81) but contrast the more cautious rejection of phenetics by the same author the following year (Ridley 1986, pp. 83–85).

In discussing the respective merits and demerits of cladistics and phenetics it is important to define the two terms accurately, and also to be clear about the purposes for which we are proposing to use these competing methodologies. As to our purposes for using cladistics or phenetics, I presume that nowadays we are not concerned primarily with classification as such, and certainly not with forcing palaeontological data into hierarchically nested Linnaean categories. Rather, we are trying to recover from our data a phylogenetic tree (not necessarily dichotomously branched) in which there is greater genetic interchange, and therefore in most cases greater phenotypic resemblance, along and within rather than between branches. Our task is therefore the same as that of the molecular biologist (Nei 1987, pp. 292 ff.; Felsenstein 1988b). Indeed it is simpler than his, for whereas the molecular biologist attempts to reconstruct the whole tree (including hypothetical nodes, etc.) solely on the evidence of the tips of the branches, we start with a sample of the whole tree, including taxa at or near the nodes, a circumstance that simplifies enormously the reconstruction of the tree.

When we come to define cladistics and phenetics our task is made difficult by the change that has overtaken the former word, from its broad original sense of the study of ancestor–descendant relations between taxa (Cain and Harrison 1960, p. 3; Sneath and Sokal 1973, p. 29) to its restriction to the particular form of cladistic analysis advocated by Hennig (1950, 1966); and also by the changes that Hennig's original concept has itself undergone since 1966, and by the resulting debates between different schools of cladists (Ridley 1986, pp. 86–97), as fierce and bewildering to the outsider as the theological disputes of the fourth century A.D. For present purposes I adopt the following broad definitions of cladistics and phenetics: *cladistics* reconstructs phylogeny on the basis of change in attribute states between ancestral and descendant taxa whose attribute states are specified; *phenetics* does so on the basis of distances (variously defined) between taxa whose attribute states are not necessarily specified (and may be unknown). Since change in attribute states is equivalent to one form of distance (City-block or Manhattan), the difference between the methodologies on these definitions may appear trivial. There is, however, an underlying difference in philosophy between cladistics and phenetics. Cladistics is concerned with discrete attribute states, which are assumed to be independent (Swofford and Olsen 1990, p. 415), and of which the coding either reflects the presumed evolution of the attributes or is determined *a posteriori* by some criterion (e.g. Lipscomb 1990): continuously distributed variables (including statistical means etc.) are difficult to handle by cladistic techniques and lead to results that should be treated with caution (Chappill 1989, p. 231), while some cladistic authors consider them to be inherently unsuitable for

phylogenetic reconstruction (Pimentel and Riggins 1987; Farris 1990). Phenetics, on the other hand, accepts numerical data of any type (including continuously distributed, correlated variables), and requires attribute coding to be objective and to be completed prior to analysis.

Hennig's cladistic methodology (1950, 1966) postulated that the phylogeny of a group of taxa could be reconstructed by observing the distribution of the different (usually two) states of several morphological attributes, on the assumptions: (1) that the evolutionary sequence of states in each attribute is known; (2) that each change of state happens only at a single point in the phylogeny; and (3) that the sequence of states is irreversible. There is no doubt that the rigour which Hennig's methodology has brought to phylogenetic reconstruction has been beneficial, even if it is sometimes difficult to see the intellectual wood for the impenetrable undergrowth of jargon. The logic of determining phylogenies by shared derived attributes is unassailable, and it works very well at the naive level at which it is presented for didactic purposes, e.g. the relations between a small number of hypothetical entities (say, three or four species) based on six or seven attributes in each of which ancestral and derived states can be unequivocally distinguished and all of which suggest a unique phylogeny. The trouble is, of course, that the real world is not as tidy as this. The assignment of ancestral and derived states, although sometimes fairly straightforward and objective, as for chromosomal inversions, is in other cases difficult and controversial or, as for meristic and continuously distributed morphological attributes, inappropriate and simplistic; and in these cases it is disturbing that polarity needs to be incorporated into the analysis at an early stage whereas it would arise more logically (if at all) as output from the analysis itself. Furthermore, as the number of entities and attributes is increased, so there develops a conflict, due to violations of Hennig's assumptions (2) and (3), between the phylogenies suggested by different sets of attributes. This is the problem of homoplasy, or what Felsenstein (1982, p. 381) calls Hennig's dilemma, and Friday (1987, p. 66) non-divergent change. Recent studies of homoplasy quantify the problem and demonstrate convincingly the decline in the consistency index (an inverse measure of homoplasy) with increasing numbers of entities (Archie 1989; Sanderson and Donoghue 1989, text-fig. 1): the decline appears from Sanderson and Donoghue's data to be exponential, and the consistency falls to about 30% for 70 entities. In the face of this problem the pure logic of Hennig's methodology becomes hopelessly compromised by the need to make a subjective choice between the phylogenies supported by different sets of attributes.

These problems in applying Hennig's original methodology have caused many cladists to abandon Hennig's three basic assumptions, no longer assigning ancestral and derived attribute states *a priori* (palaentologists, however, seem reluctant to take this step, except recently Adrain and Chatterton 1990), while acknowledging the extent of homoplasy and seeking the phylogeny that minimizes it. Indeed, some cladists (the so-called 'pattern' or 'transformed' cladists) no longer look upon their cladograms as having phylogenetic significance.

The distinction between cladistics and phenetics has to some extent become blurred by these changes in cladistic methodology. There appears in fact to be a continuous spectrum of phylogenetic techniques (reviewed by Felsenstein 1982; Swofford and Olsen 1990), between overtly cladistic, i.e. based on phylogenetic changes between known or hypothesized attribute states of taxa (e.g. molecular sequence data, discrete morphological data), and pure phenetic, i.e. based wholly on directly observed distances without knowledge of the states that contribute to these distances (e.g. nucleic acid hybridization and immunological comparison data). On this cladistic-phenetic spectrum the phenetic methodologies that have been used in palaeontology (ordinations and dendrograms based on distances derived from attribute state lists) lie towards the phenetic end. Let us examine the two main arguments against using such methods: (1) in replacing the original data matrix by an inter-entity distance matrix, phenetic methods discard valuable information (Farris 1981, p. 22; Penny 1982); and (2) despite the claims of its proponents, phenetic methodology is not objective (Ridley 1986, pp. 39 ff.). There is a third argument based on the non-metric properties of distances, which is of relevance mainly to molecular sequence data and the concept of the molecular clock: for the opposing views see Farris (1981, 1985, 1986) and Felsenstein (1984, 1986, 1988*b*, pp. 530-532).

The first argument against phenetics is a valid but not over-riding objection to those phenetic methods that rely entirely on secondarily-derived distance data both in processing and in presentation. This is true, for instance, of dendrograms, and adds weight to other objections to the use of dendrograms, especially the subjectivity involved in flattening the cylindrical structure of the dendrogram onto the printed page for presentation (Sneath and Sokal 1973, pp. 261–264). The argument also applies to ordination techniques that depend entirely on a secondarily-derived distance matrix, i.e. the various types of multidimensional scaling. It does not, however, apply to ordination by Principal Components, which operates directly on the data matrix, and in which the original data can in principle be recovered from the transformed data that underlie the ordination. Furthermore, it is not an argument that can be used convincingly to discredit phenetics in favour of cladistics, because any loss in phenetic information must be seen in the context of the larger amount of information available to phenetic methods from their ability to handle continuously distributed attributes.

The second argument appears to be two-fold: (1) phenetic methods are sensitive to different choices of distance coefficients and clustering techniques, and (2) the subjective choices forced on the pheneticist in this way vitiate the objectivity claimed for phenetics. The validity of part (1) of the argument must be acknowledged. Recent work (Temple unpublished) shows that the concordance (as assessed, for instance, by nearest-neighbour relations) between distance matrices based on different coefficients decreases as the number of attributes increases. Furthermore, different clustering or ordinating techniques clearly produce different results even when they are operating on the same distance matrix, let alone when operating on different distance matrices. Part (2) of the argument cannot, of course, be used selectively against phenetics, since it applies with equal force to cladistics because of the need to choose between compatibility and the different forms of parsimony for resolving homoplasy: it is a valid inference from (1) only if the pheneticist or cladist accepts the need to make the subjective choice postulated by the argument. It cannot be denied that in the past many pheneticists (including the present author) and cladists have done so, either explicitly or implicitly. The valid response of the pheneticist or cladist to this dilemma, however, is to recognize that different coefficients and techniques produce different estimates of the phylogenetic relations (i.e. different tree topologies); that none of these estimates is *a priori* more authoritative than others; but that probabilities can be assigned to the different nodes and branches according to the frequencies with which they recur in different estimates, and that in this way a probabilistic estimate of the tree can be obtained.

In practice, of course, few pheneticists or cladists are likely to go to the lengths of trying all the available techniques on their data. It is, however, in the spirit of the last paragraph to present an ordination, minimal spanning tree, Wagner tree or dendrogram as no more than the result of applying a particular technique to the data, without claiming to have produced the definitive answer – and I suspect that many pheneticists and cladists do in fact have this attitude towards their results, even if it is not formally articulated. So long as the results are interpreted in this probabilistic spirit, phenetic methods – with their ability to handle meristic and continuous, correlated variables – are well suited to estimating phylogenies from palaeontological data-sets, in which significant inter-attribute correlations are known to occur (e.g. Temple and Tripp 1979, table 3; Temple 1980, table 5). In particular, since palaeontological data are a sample of the whole tree (including nodes or near-nodes), an ordination in which each entity is linked by a minimal spanning tree to its nearest neighbour (however defined) would be expected to converge progressively to the true phylogeny as the density of sampling increases. Applications of this technique (Rowell 1970; Temple and Tripp 1979; Temple 1980) might be criticized (although they do not in fact appear to have been so criticized) for implicit reliance on standardized Euclidean distance as the basis of phylogeny, but it is possible to make such ordinations overtly probabilistic by incorporating phylogenetic relations suggested by different distance measures (cf. Temple and Wu 1990, fig. 2).

We conclude from this discussion that, because of limitations of samples and techniques and because of the widespread occurrence of homoplasy, certainty is not attainable in phylogeny and taxonomy, and whatever methods we use we must be content with probabilistic statements

(Felsenstein 1985; Penny and Hendy 1986; Sneath 1986). In this context the importance of Felsenstein's conclusions cannot be too strongly emphasized: 'The adoption of a methodology that explicitly acknowledges uncertainty is a paradoxical necessity if phylogenetic inference is to be placed on a firm scientific footing' (Felsenstein 1982, p. 399).

Before leaving this topic it is worth remarking that any taxonomic/phylogenetic analysis – phenetic, cladistic or whatever – is only as good as the data on which it is based, and in particular that the objectivity of the results is limited by the objectivity of the original data. It is therefore of the utmost importance that taxonomic entities and attribute states should be defined objectively; and in both respects current palaeontological practice is lax. The most objective taxonomic entity in palaeontology is the topotype sample of a species (Temple and Tripp 1979, p. 234), and the most objective data are thus mean topotypic attribute states of species. In principle, analysis at higher taxonomic levels could be done either (1) by extending the type-concept vertically and representing any taxonomic level by the mean topotype attribute states of its type species; or (2) with some loss of objectivity, by grouping together topotype samples of designated species and calculating the relevant mean attribute states. In practice, neither of these procedures is normally followed, and many taxonomic/phylogenetic analyses in palaeontology are seriously weakened by being based on imprecisely and subjectively delimited 'genera', 'families', etc. As to attribute state definition we need only note that, if attribute states are not precisely and objectively defined, subsequent authors will be unable to repeat or extend the original observations, and not even the most rigorous analysis of such attributes could claim to be scientific.

OUTLINES VS LANDMARKS

The only valid objection that has ever been made to the use of quantitative methods in morphological palaeontology is that they are very time-consuming. This is, of course, no longer true of data-processing, but it is still true of observer-mediated data-gathering, i.e. measurement by an observer using callipers or eye-piece micrometer, and the problem is exacerbated by the need to process large samples in order to obtain statistically robust or significant results (cf. Temple 1987, p. 128). In these circumstances automated measurement is extremely desirable.

The most convenient form of automated measurement is outline analysis, of which at least four types have been used in recent years in palaeontology and related subjects. The first and most extensively used method (e.g. Kaesler and Waters 1972; Healy-Williams 1983) has been polar Fourier analysis. In this method radii are drawn from the centroid of a closed curve (usually at equal angular intervals, say of 5°), and the length of each radius is plotted as a function of the angle of rotation of the radius ($0-360^\circ$) from a zero starting direction. The resulting function is then Fourier-analysed as a sum of trigonometrical functions. Objections to this method are that it cannot be applied to complex curves with re-entrant angles, and that it depends on the identification of the centroid of the closed curve and on the definition of a zero point on the curve. The second type of outline analysis is elliptical Fourier analysis (Giardina and Kuhl 1977; Kuhl and Giardina 1982; Ferson *et al.* 1985). In this, a point travels around the closed curve at constant speed, and the x and y coordinates are separately plotted as periodic functions of time and Fourier-analysed: the curve is then approximated by superimposing a series of orthogonal ellipses (in a manner analogous to the Ptolemaic approximation to the elliptic planetary orbits by superimposing cycles of circles). The third type of outline analysis is eigenshape analysis (Lohmann 1983). Here a point travels around the closed curve at equal increments of arc, and chords are drawn to it from a zero point on the curve. The angles that successive chords make with the tangent at the zero point form a vector characterizing the curve (Zahn and Roskies 1972), and vectors from different curves form a data matrix that is analysed by Principal Components. Both elliptical Fourier analysis and eigenshape analysis are free from the objections to polar Fourier analysis noted above: both can deal with complex curves; neither makes use of the extraneous concept of the centroid; the elliptical Fourier coefficients are independent of the zero point, while Lohmann (1983) avoids the problem by an algorithm for matching the vectors from different original curves. A fourth method, perimeter-

based Fourier analysis, has been introduced recently (Foote 1989). In this, a point travels around the closed curve at equal increments of arc as in eigenshape analysis, but chords are drawn to it from the centroid rather than from the zero point, the lengths and orientations of these chords being separately Fourier analysed. This method also can deal with complex curves, but has the disadvantage of depending on the centroid and a zero point. Of these various methods, elliptical Fourier analysis is the most attractive in principle and was found to perform well by Rohlf and Archie (1984). All four methods, however, are equally liable to the fundamental objections raised recently to the use of outline analysis in morphometrics.

These objections have been cogently stated by Bookstein *et al.* (1982). Briefly, they are that outline analysis obscures homologies. (Full and Ehrlich (1986) direct this criticism specifically at eigenshape analysis and by implication absolve Fourier analysis; but see Rohlf 1986; Ehrlich and Full 1986.) Bookstein *et al.* (1982, fig. 1) illustrate their argument by two circular outlines, one with four equally spaced homologous landmarks, the other with the same landmarks unequally spaced: the two outlines are indistinguishable in their Fourier coefficients (but see below) even though they represent two very different morphologies. The example is striking, but then so is the counter-example of Read and Lestrel (1986, fig. 2) – four equally spaced landmarks linked by two very different outlines indistinguishable by landmark analysis.

There is no doubt that the concept of homology underpins the whole of comparative morphology, and that we should not set it aside lightly. It is not clear, however, that we should restrict our morphometrics entirely to homologous landmarks, as has been done in a series of elegant papers by Bookstein and his collaborators (e.g. Bookstein *et al.* 1985; Bookstein 1986). Quite a lot of useful biometric information is derived from measurements that are not strictly homologous, e.g. the maximum width of a brachiopod or of the frontal glabellar lobe of a trilobite at different growth-stages, the maximum measurable length of a bivalve mollusc without terminal umbones. Furthermore, even in the example given by Bookstein *et al.* (1982, fig. 1) the four landmarks would be likely in practice to disturb the circular outline (as indeed they do in the figure), and if the outlines were sufficiently finely digitized this disturbance would produce differences in the Fourier coefficients between the two cases. Finally, returning to our original theme, there is no doubt that, although algorithms could presumably be devised *ad hoc* to recognize homologous landmarks without observer participation, in the present state of technology outline analysis lends itself much more readily to automated measurement than does landmark analysis.

I conclude that the theoretical objections to outline analysis are not so great as to outweigh the practical advantages of automated measurement that the method offers. There are, however, some important precautions that palaeontological users of outline analysis should observe:

1. standardizing and defining accurately the viewing orientation: this may be relatively easy where the morphology itself defines a plane of symmetry or at least something approximating to such a plane, as in coccoliths, ostracodes, many bivalve molluscs, profile views of brachiopods and trilobites, etc.; it becomes more difficult when we wish to view along (rather than normal to) a plane of symmetry, as in non-profile views of brachiopods and trilobite cephalae (Temple 1972, 1970, pp. 4–6); and it becomes a non-trivial problem, that cannot be solved purely by definition, when we wish to identify the axial view of a trochospiral foraminiferan;

2. defining the reference zero point and/or (depending on the method used) zero direction on the outline;

3. ensuring that size information is not inadvertently lost (by normalizing) early in the analysis: in Fourier methods size information is carried in the coefficients of the zeroth harmonic;

4. using all the information derived from the analysis: in particular, in Fourier analysis the phase angles as well as the amplitudes carry information and should not be discarded as has happened in several palaeontological applications.

Finally, it is important not to lose sight of the fact that most fossils are three-dimensional objects, of which two-dimensional outline analysis can give only an imperfect representation. Three-dimensional measurement and analysis are clearly desirable, and could in principle be done in several different ways, including:

1. characterization by 3 orthogonal profiles;
2. direct, observer-mediated measurement of x , y and z coordinates (Lazarus 1986);
3. several different techniques of automated metrology (Jarvis 1986; Gåsvisk 1987), of which only contouring by holographic interferometry seems yet to have been applied to palaeontology (Elliott and Morris 1987).

Method (1) leads to direct parameterization in terms of 3 sets of Fourier coefficients. Methods (2) and (3) could lead to parameterization in terms of: (a) two-dimensional polynomial or Fourier series (Davis 1986, pp. 405–447) for surfaces equivalent to single-valued distances from a plane of symmetry (e.g. many ostracodes); or (b) spherical harmonics (Jacobs 1974, pp. 310–314; Bomford 1980, pp. 782–787) for surfaces equivalent to single-valued radii from a centroid (e.g. many planktonic foraminifera, acritarchs); or (c) differential geometry (Okamoto 1988), or (d) computerized surface representation methods (Tipper 1979).

ORDINATION TECHNIQUES

A major omission in the earlier article (Temple 1982*a*) was a section on the standardization of entities. The need for such standardization arises from ‘accidental’ differences between entities, particularly from differences in sample size between sites in distributional data. It is possible in some cases to remove the effects of such differences at a later stage of analysis, i.e. as the first eigenvector in Principal Components Analysis by analogy with the growth eigenvector of morphological analysis. The analogy with morphological analysis data is, however, not exact, for whereas a growth eigenvector is usually a direction of increase in all the attributes, the first eigenvector of distributional data may be determined fortuitously by the dominant species in the largest available sample; furthermore, size of an individual is an intrinsic attribute, whereas size of a fossil sample depends on extrinsic factors such as ease/difficulty of collection. For these reasons, although it is possible (indeed desirable) to retain size differences in growth analysis data, it is better for purposes of site ordination to standardize distributional data to a standard size of (say) 100. The constraint imposed on data by standardizing to constant sample size has, however, the undesirable effect of distorting the inter-attribute correlation matrix by inducing spurious negative correlations (this is the ‘closure’ problem encountered in analysis of compositional data in petrology). Ordination of the attributes (i.e. interrelations of taxa) in distributional data should therefore be based on unstandardized data.

Three ordination techniques have become available since the earlier article was prepared, namely, Projection Pursuit, Detrended Correspondence Analysis, and Canonical Correspondence Analysis.

Projection Pursuit (Friedman 1987; Jones and Sibson 1987) is designed to seek out projections (i.e. combinations of attributes) that maximize the inhomogeneity of the data. Projection Pursuit does not yet appear to have been used on palaeontological data, but would be expected to be useful for testing whether morphological variation (size and/or shape) was continuous or discontinuous. As yet, however, Projection Pursuit can apparently handle only fairly small data matrices.

Detrended Correspondence Analysis (Hill and Gauch 1980) is a technique designed to remove an artefact (the ‘horseshoe’ effect) that may appear in ordinations of phyto-sociological data. When vegetation is sampled along an environmental gradient the gradually changing floral composition along the gradient would be expected to show up as a linear seriation of the sites along the first ordination axis, with sites at the environmental extremes furthest apart in the ordination; instead, there is a curvilinear relationship between site scores on the first two (or more) axes, so that the extreme sites are not at the extremes of the ordination. Digby and Kempton (1987, pp. 93–97 – see especially tables 3.2, 3.11, and figs 3.14–3.15) give a very clear account of the phenomenon, which is attributable to underestimation of the distances between sites at opposite environmental extremes and ultimately to a special, quasi-diagonal, form of the data matrix. Palaeontological data matrices of this form arise in biostratigraphy (e.g. Rickards 1976, table 1), and ordinations of such matrices might therefore be expected to lead to horseshoes. This is true, for instance, of the MDSCAL ordination of two pollen sequences by Gordon and Birks (1974, p. 237, fig. 7), and in this case

detrending would probably make more perspicuous the stratigraphical correlation established by Gordon and Birks between the two sequences. The possibility therefore arises of correlating stratigraphical sequences by the scores of the individual horizons on the first axis of a Detrended Correspondence Analysis.

Canonical Correspondence Analysis (ter Braak 1986) is a technique that produces a simultaneous three-fold ordination of *sites* at each of which have been observed the occurrences or abundances of various *taxa* and the values of various (environmental) *variables*: a detrending option is available. This powerful technique clearly has considerable potential in palaeoecological studies, but no applications appear to have been published so far.

Finally, it may be useful to list some relevant general publications that have appeared in the last decade. There are good summaries of ordination techniques by Gordon (1981), Dunn and Everitt (1982), ter Braak (1987), and Digby and Kempton (1987), as well as in the new edition of Davis's invaluable book (1986). Several examples of palaeontological ordination are given in Temple (1987).

Acknowledgements. For criticism of the text I am very grateful to A. R. Milner, B. Roberts, A. W. A. Rushton, G. H. Scott and J. C. Tipper.

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J. T. TEMPLE

Department of Geology
Birkbeck College
Malet Street
London WC1E 7HX, UK

Typescript received 19 December 1990

Revised typescript received 26 April 1991

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