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Cover: This specimen of *Calymene blumenbachii* from the Wenlock of Dudley is mounted in gold, forming the centrepiece of a nineteenth century brooch presented to the Natural History Museum by Miss E. Begg.



# A NEW PRIMITIVE TETRAPOD, *WHATCHEERIA DELTAE*, FROM THE LOWER CARBONIFEROUS OF IOWA

by R. ERIC LOMBARD *and* JOHN R. BOLT

**ABSTRACT.** *Whatcheeria deltae* gen. et sp. nov. is Viséan V3b in age and is represented by the second oldest tetrapod skeletal remains so far described from the Americas exclusive of Greenland. *Whatcheeria* is a primitive tetrapod about 1 m in length including the tail, and is characterized by the following autapomorphies: ornament on cranial dermal bones is absent or extremely light; the parietal foramen is large relative to skull size; the prefrontal forms a thick, raised ridge at the anterodorsal margin of the orbit; and the cleithrum terminates posterodorsally in a robust, posteriorly directed process above a deep notch. *Whatcheeria* is extremely plesiomorphic in retaining: a cheek with long postoccipital portion; a preopercular; lateral line canals that in places are completely encased in bone; a dentary which extends far posteriorly along the adductor fossa; a prearticular that extends anteriorly almost to the symphysis; a toothed adsymphysial; a row of small Meckelian foramina between the prearticular and infradentary bones; a tabular and parietal that are not in contact; a nearly continuous row of teeth on the vomer, palatine and ectopterygoid; a femur with an oblique ridge having a maximum elevation at midshaft; and a pelvis with an area of unfinished bone anterior to the acetabulum.

The phylogenetic affinities of *Whatcheeria* are uncertain at present, but its best placement may be as the first outgroup to the Anthracosauria *sensu* Gauthier *et al.* 1988. This suggestion is supported by the presence of: small post-temporal fenestrae; a tabular horn that continues from the dorsal surface of the tabular; a skull table in which the temporal bones have a strong ventral inflection dorsal to their sutures with the cheek; dermal ornament that, though generally absent, where present is similar to the 'anthracosaur type'; quadrangular orbits; narrow vomers; marginal fangs on the maxilla; an interclavicle with a long parasternal process; and a scapulocoracoid that ossifies from two centres. In the context of this hypothesis of relationships, some of *Whatcheeria*'s observed features are unexpected: pleurocentra that are sometimes composed of dorsally fused antimeres; a region of presacral ribs with flattened shafts and large uncinat processes; and absence of an ossified branchial skeleton.

THE earliest tetrapod remains that can be securely dated come from the Late Devonian, and their very primitive nature suggests that tetrapod origins did not much antedate this time. Eight tetrapod genera represented by skeletal remains have been described from six Devonian localities, in Australia, East Greenland, Russia, Latvia, Pennsylvania and Scotland (Säve-Söderberg 1932; Jarvik 1952; Campbell and Bell 1977; Lebedev 1984; Ahlberg 1994, 1995; Daeschler *et al.* 1994). Lower Carboniferous tetrapods are nearly as rare. Nineteen published localities have produced skeletal remains of about that number of tetrapod genera (Romer 1969; Carroll *et al.* 1972; Smithson 1982, 1985a; Bolt *et al.* 1988; Schultze and Bolt in press). Most of these Devonian and Lower Carboniferous tetrapods are represented by few and/or poorly preserved specimens. Notable exceptions are *Ichthyostega* and *Acanthostega* from the Devonian of East Greenland, and *Greererpeton* from the Lower Carboniferous of Greer, West Virginia, USA. These three genera have provided much of the information upon which our present understanding of the earliest tetrapods rests (Jarvik 1980; Smithson 1982; Clack 1988, 1989, 1994a, b; Godfrey 1989; Coates and Clack 1990, 1991; Clack and Coates 1993).

Four of the Lower Carboniferous tetrapod-producing localities were discovered relatively recently: Dora Open Cast site (= Cowdenbeath), Scotland (Andrews *et al.* 1977); East Kirkton,

Scotland (Wood *et al.* 1985); Goreville, Illinois, USA (Schultze and Bolt in press); and Delta, Iowa, USA (Bolt *et al.* 1988). These localities are important because of their age, the number and quality of specimens produced, and the opportunity they present to collect and prepare early tetrapod specimens with the aid of modern techniques and equipment. Indeed, specimens from these sites have now begun to provide new insights into early tetrapod evolution and will do so for years to come (Wood *et al.* 1985; Milner *et al.* 1986; Smithson 1989, 1994; Bolt 1990; Rolfe *et al.* 1990; Smithson and Rolfe 1990; Clack 1994c; Milner and Sequeira 1994; Smithson *et al.* 1994; Schultze and Bolt in press). We here name and describe briefly a new tetrapod that is represented by numerous and often excellently preserved specimens from the Delta, Iowa locality.

#### LOCALITY AND HORIZON

The Delta locality consists of two adjacent palaeodepressions or collapse structures, exposed in the walls of an inactive limestone quarry. The quarry is in the upper part of a rock unit which has traditionally been referred to as the St Louis Formation (Bolt *et al.* 1988). Studies by members of the Iowa Geological Survey Bureau suggest, however, that only the lower portion of the Iowa 'St Louis Formation' is correlated with the type section of the St Louis Formation, near the Missouri city of that name. The upper part of the Iowa 'St Louis' may correlate instead with the Ste Genevieve Formation (eastern Missouri and western Illinois).

The collapse structures at the Delta site are believed to have developed within the Waugh and Verdi members of the Iowa 'St Louis Formation' during Waugh time (Witzke *et al.* 1990). The Verdi Member records the offlap of an epicontinental sea. The sandstones, shales, and lime mudstones that constitute the overlying Waugh Member lack a definitively marine invertebrate fauna. The Iowa Geological Survey Bureau interprets the depositional environment of the Waugh Member as 'lacustrine, fluvial, and swamp environments in a coastal lowland setting' (Witzke *et al.* 1990, p. 45). The environment of the tetrapod-producing layers within the collapse structures (Units C and D of Bolt *et al.* 1988 and Witzke *et al.* 1990) is interpreted similarly. Thus it is considered to have been primarily lacustrine, fresh-water to brackish, with possible intermittent incursion of marine waters.

In the absence of a normal marine fauna, the age of the Waugh Member has been determined by 'bracketing' it between the Verdi Member of the 'St Louis Formation,' which directly underlies it, and the Pella Formation. The Pella Formation generally overlies the Waugh Member of the 'St Louis Formation' in this area of Iowa, but has been removed erosionally at the Delta site. Foraminiferal and conodont data suggest an age of Viséan V3b for the Verdi Member, and upper V3b to lower V3c for the Pella Formation (Witzke *et al.* 1990; R. M. McKay, pers. comm. 1993). The most probable age for the Delta collapse-structure fills is thus Viséan V3b, i.e. Asbian, c. 340 Ma.

Most of the Delta sink fills have now been excavated, mainly during 1986 and 1988. Over 600 tetrapod specimens were recovered, including about 50 partial skeletons, some nearly complete,

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#### EXPLANATION OF PLATE I

*Whatcheeria deltae* gen. et sp. nov., FM PR 1700, type specimen. Skull in association with pre-sacral vertebral column, partial shoulder girdle, ribs, and partial hindlimb. Skull is in dorsal view, with right cheek and lower jaw visible, left cheek and lower jaw folded under. Note large parietal foramen, and maxillary fangs on both sides; premaxillary fangs are buried in matrix. On the left side of the specimen, a clavicular stem protrudes directly laterally at midlength of the preserved vertebral series; opposite this, on the specimen's right side, the interclavicle and its stem are partly visible, separated by a break. Right femur, tibia and fibula are seen in flexor view on the specimen's right side. Phalanges are visible at posterior end of vertebral series. Scale bar represents 50 mm.



LOMBARD and BOLT, *Whatcheeria*

along with several hundred fish and some invertebrate and plant fossils. All specimens are in the collections of the Field Museum of Natural History and the University of Iowa. Delta fossils are generally well-preserved, and most retain excellent surface and internal detail, even though many have been crushed. The tetrapod described here is by far the most abundant taxon, and may prove to constitute some 90 per cent. of tetrapod specimens. At least two other tetrapods are present in addition: an embolomere, and a colosteid temnospondyl. Both are apparently new. The fish fauna includes the lungfish *Tranodis* (Schultze and Bolt in press), osteolepiform crossopterygians (a rhizodontid and an osteolepidid), acanthodians, elasmobranchs, palaeoniscoids, and the ichthyolith *Cynopodius*.

The description presented here will be expanded when preparation is nearer completion. Approximately 200 specimens of Delta tetrapods have been completely or nearly completely prepared to date, but much remains to be done.

Institutional abbreviations used in this paper are: FM, Field Museum of Natural History; SUI, University of Iowa.

## SYSTEMATIC PALAEONTOLOGY

TETRAPODA *sensu* Gaffney 1979

CLASS, ORDER and FAMILY undesignated

GENUS *Whatcheeria* gen. nov.

*Derivation of name.* From the town of What Cheer, Iowa, USA, home of the discoverer of the Delta tetrapods, Mr M. P. McAdams.

*Whatcheeria deltae* sp. nov.

Plate 1; Text-figures 1–9

*Holotype.* FM PR 1700, skull in association with pre-sacral vertebral column, partial shoulder girdle, ribs, and partial hindlimb (Pl. 1).

*Referred and Cited Specimens.* FM PR 1634 (Text-fig. 1): skull with lower jaws, nearly complete though crushed; atlas, axis, and several additional anterior vertebrae and ribs; part of dermal shoulder girdle. FM PR 1635: skull with lower jaws, articulated partial vertebral column, two scapulocoracoids, humerus (Text-fig. 7B), radius and ulna, plus other appendicular elements; all severely crushed. FM PR 1636: partial skull with several crushed and disarticulated vertebrae. FM PR 1644: block with right and left lower jaw, clavicle, rib, and other elements. FM PR 1651: skull table with frontals, postfrontals, dorsal and ventral sides prepared free. FM PR 1652: partial skull roof with frontals broken off and area around parietal foramen broken out; crushed and incomplete otic capsules present; braincase and both stapes crushed up onto underside of skull roof. FM PR 1701: braincase associated with first three vertebrae. FM PR 1704: left scapulocoracoid with cleithrum. FM PR 1712 (Text-fig. 4): two isolated pleurocentra. FM PR 1740: right half of pelvis (Text-fig. 8) plus interclavicle. FM PR 1745 (Text-fig. 3): seven articulated vertebrae. FM PR 1766: left scapulocoracoid with partial cleithrum. FM PR 1809: large skull with lower jaws, occiput preserved in three dimensions (Text-fig. 2); snout compressed anteroposteriorly and twisted around 90° to left. FM PR 1813: skull and vertebral column, with scattered girdle elements and limbs. FM PR 1814: partial skull with left lower jaw. FM PR 1816: articulated vertebral column, from cervicals approximately through first fifteen caudals, plus limb and girdle elements (pectoral girdle in Text-fig. 6); numerous ribs, some in articulation; associated with braincase and posterior half of skull table. FM PR 1880: left scapulocoracoid with cleithrum, left ilium and ischium, 15 articulated vertebrae and two disarticulated ribs. FM PR 1887: nearly complete articulated vertebral column plus associated pelvis and femur. FM PR 1889: complete rib from mid-presacral region (Text-fig. 5), associated with fragmentary postcranial elements on limestone block. FM PR 1957 (Text-fig. 7A): interclavicle. FM PR 1958 (Text-fig. 9): left femur. SUI 52010: five intercentra, five pleurocentra, including some small complete intercentra.

*Horizon and Locality.* Fills within two adjacent collapse structures formed in the Waugh and Verdi Members of the Iowa 'St Louis' Limestone. Mississippian, Lower Chesterian; correlative with the Lower Carboniferous,

Viséan V3b, Asbian, of Europe. Quarry on land owned by Mr Jasper Hiemstra, SW1/4, SW1/4, section 15, T75N, R13W, Keokuk County, Iowa, USA.

*Diagnosis.* Primitive tetrapod characterized by the following autapomorphies: ornament on cranial dermal bones extremely light, with frontal, parietal, and postparietal unornamented even on largest specimens; parietal foramen large relative to skull size; prefrontal forming thick, raised ridge at anterodorsal margin of orbit, with massive ventral projection on deep surface enclosing a large sinus(?); cleithrum terminating posterodorsally as a robust backwardly-directed process above a deep notch.

*Derivation of name.* After Delta, Iowa, USA, the town closest to the quarry where the type and all other known *Whatcheeria* specimens were collected.

## DESCRIPTION

### *Skull and Lower Jaw*

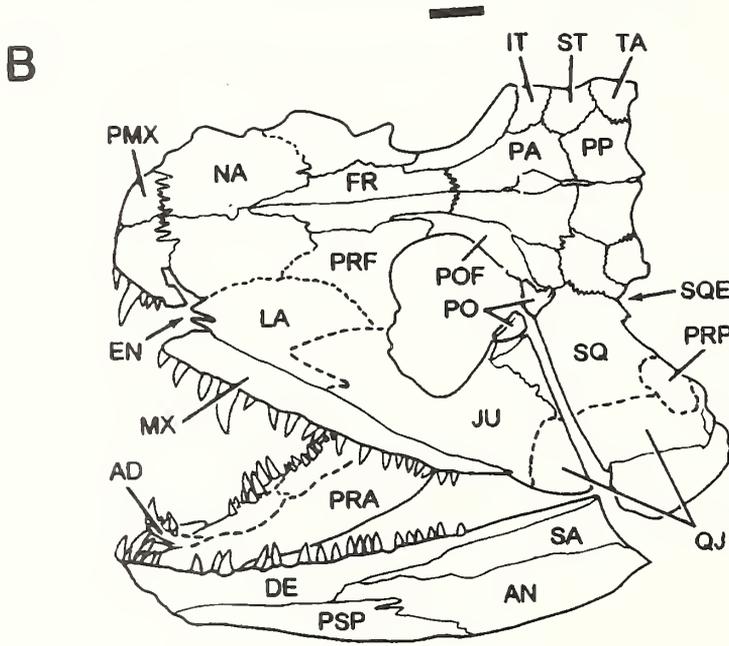
*General features.* Preliminary reconstructions suggest that the skull is high, with a significant degree of lateral compression and nearly vertical cheek. Most *Whatcheeria* skulls that retain the skull table and both cheeks, including the type, are crushed so that one cheek is folded under and the other is splayed out to the side as would be expected from a skull of this shape (Pl. 1; Text-fig. 1). The postoccipital portion of the cheek is very long, placing the jaw joint well behind the occiput. Postoccipital cheek length may be characterized as the horizontal (in the plane of the skull table) distance between the posterior extremities of the quadrate condyles and the posterior margin of the postparietals, divided by overall skull length expressed as horizontal distance from the quadrate condyles to the tip of the snout. On the type specimen, postoccipital cheek length is 21 per cent. of overall skull length. The snout is bluntly pointed rather than broadly rounded, as indicated both by skulls with this region intact and by the well-preserved symphysial region of the lower jaws in FM PR 1809.

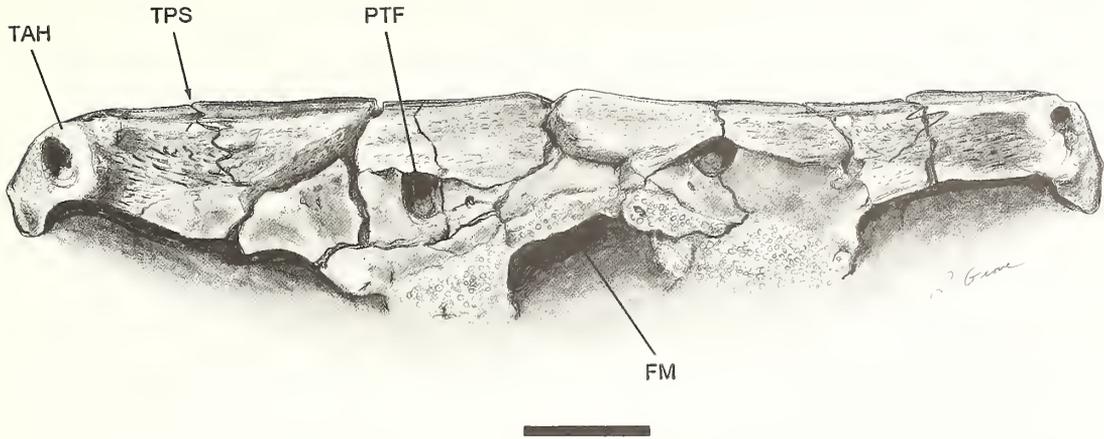
The centres of the large, quadrangular orbits lie at about 60 per cent. of the horizontal distance from the snout to the end of the skull table, as best seen in the holotype (Pl. 1) and FM PR 1634 (Text-fig. 1). Quadrangularity may be accentuated to some degree by crushing but is certainly real, as even isolated jugals and prefrontals always preserve the posteroventral and anterodorsal angles of the orbital margin, respectively. No scleral ossicles have been found. The external naris is far down on the side of the snout, just above the tooth row.

Cranial dermal ornament is very weakly developed. With the exception of the anterior one-half of the lower jaw, the external dermal bones are almost completely devoid of ornament. The course of the cranial lateral line system is indicated by canals completely encased in bone, or by open sulci which may be separated by regions of smooth bone that lack either sulci or canals. A linear array of circular foramina indicates the path of the canal where it is completely enclosed. This condition is best developed in the mandibular line along the anterior two-thirds of the lower jaw, and in the infraorbital line of the lacrimal and jugal. Elsewhere the course of the lateral line is primarily in segments of open sulci, interrupted by short segments of both enclosed canals and smooth bone (Text-fig. 1).

*Skull table.* The skull table comprises paired frontals, parietals and postparietals along the midline, bounded laterally by a temporal series of postfrontals, intertemporals, supratemporals and tabulars. This part of the skull is often found isolated and more or less intact, and is almost always present if any other skull roofing bones are preserved in articulation with one another. There is no tabular-parietal contact; the tabular and parietal are separated by the postparietal and supratemporal. As preserved, the skull table is planar. The posterior margin of the dorsal surface is roughly straight, as are its lateral margins posterior to the orbits. In dorsal view, the lateral and posterior margins are at right angles to one another. The lateral margins are formed by a pronounced ventral flexion which spans the intertemporal, supratemporal and tabular. Anterior to these elements, the skull table narrows sharply where it is incised by the dorsal margins of the orbits (Text-fig. 1).

The midline suture of the skull table is carried on a ridge from the posterior border of the postparietals to the anterior termination of the parietals, where it merges into the surface on either side of the midline. Posterior to the parietal foramen, the ridge broadens slightly. On either side of the midline ridge there is a broad, shallow depression on the postparietal and another on the parietal. The parietal foramen is rimmed by a raised ridge, which is slightly roughened in contrast with the smooth surrounding bone. The opening is exceptionally large,





TEXT-FIG. 2. *Whatcheeria deltae* gen. et sp. nov., FM PR 1809 (partial illustration), occipital region. Abbreviations: FM, foramen magnum; PTF, posttemporal fenestra; TAH, tabular horn; TPS, tabular-postparietal suture. Scale bar represents 10 mm.

and tear-drop shaped with its narrow end posterior. In these features, *Whatcheeria* is similar to *Proterogyrimus* as described by Holmes (1984), though the parietal foramen is larger in *Whatcheeria*. The parietal of the osteolepiform panderichthyid *Elpistostege* is also similar, although the parietal foramen is smaller than in either *Proterogyrimus* or *Whatcheeria* (Schultze and Arsenault 1985).

The 'tabular horn' has in recent decades been an important character in anthracosauroid systematics. In *Whatcheeria* the horn is short, and projects straight backward from the posterolateral corner of the tabular. It has previously been characterized (Bolt *et al.* 1988; Bolt 1990) as being of 'anthracosaur type,' as defined by Panchen (1985, p. 551). Now that more mature specimens are available, this characterization can be recognized as only partly correct. The horn is anthracosaur-like in that its dorsal surface is a continuation of the dorsal surface of the tabular. However, the bifurcation into 'superficial and (small) deep components' described by Bolt (1990, p. 346) reflects size (and perhaps individual variation as well). The largest specimens available, such as FM PR 1809, show that the terminus of the tabular horn is actually a large rimmed pit (Text-fig. 2). In some specimens, the lateral and medial portions of the pit wall are less well developed than the dorsal (especially) and ventral portions, giving rise to a misleading appearance of weak bifurcation. In addition to the rimmed pit that terminates the principal tabular horn, there is usually a smaller raised rugose area on the body of the tabular ventral to the tabular horn (Text-fig. 2). On the left side of FM PR 1809, an exceptionally large individual, a small rugose-surfaced protuberance arises from the dorsomedial side of the base of the tabular horn as well (Text-fig. 2).

*Cheek.* The cheek comprises postorbital, squamosal, jugal, quadratojugal and preopercular. It is particularly well preserved in the type and in FM PR 1813 and FM PR 1634. The jugal is excluded by the maxilla from the ventral margin of the cheek. There is a large squamosal embayment, bounded by the squamosal, supratemporal and tabular. The tabular forms the dorsal and anterodorsal margins of the embayment. The supratemporal

TEXT-FIG. 1. *Whatcheeria deltae* gen. et sp. nov., FM PR 1634 (partial illustration), skull and jaws as preserved. A, indicates surface texture, three-dimensional features and the morphology of the lateral line. Some postcranial elements present on the specimen not illustrated. B, outline drawing to show locations of sutures. Sutures visible on the specimen are solid lines, sutures reconstructed from other material are dashed lines. Abbreviations: AN, angular; AD, adsymphysial; DE, dentary; EN, external narial opening; FR, frontal; IT, intertemporal; JU, jugal; LA, lacrimal; MX, maxilla; NA, nasal; PA, parietal; POF, postfrontal; PO, postorbital; PMX, premaxilla; PP, postparietal; PRA, prearticular; PRF, prefrontal; PRP, preopercular; PSP, postsplenial; QJ, quadratojugal; SA, surangular; SQ, squamosal; SQE, squamosal embayment; ST, supratemporal; TA, tabular. Scale bar represents 10 mm.

forms only a small part of the anterior margin, as can be seen in, for example, the type and FM PR 1634. The cheek portion of the lateral line system preserves the primitive tetrapod pattern (Text-fig. 1).

The cheek-skull table junction of early tetrapods has traditionally been an area of particular functional morphological and phylogenetic interest, because it is often thought to be a kinetic joint inherited from osteolepiform crossopterygians (e.g. Carroll 1988). In *Whatcheeria* this suture is seen in several skulls and numerous separated bones. It shows no obvious characteristics of a mobile joint. On the contrary, the postorbital and squamosal form highly bevelled and interdigitated sutures with the postfrontal, intertemporal and supratemporal.

The preopercular spans the squamosal-quadratojugal suture on the posterior margin of the cheek. Although the sutures with these bones are often obscure, the preopercular can be distinguished from them by the orientation of the lineations on the surface of each. A well preserved preopercular occurs in FM PR 1636, where the suture between it and the squamosal is plainly visible. Another example is in FM PR 1644, which includes an associated quadratojugal and preopercular which have separated but are still in close proximity. The preopercular lateral line canal is represented by an open sulcus.

*Snout.* The snout comprises paired prefrontals, lacrimals, nasals, premaxillae and maxillae. Although a lateral rostral and/or anterior tectal might be expected in such a generally primitive tetrapod, neither has been recovered to date. However, adjacent surface features of the lacrimal and the nasal could indicate a suture with a tectal element.

The external naris is bordered by the maxilla, premaxilla, nasal and lacrimal. The maxilla and premaxilla form the smooth, finished edges of the posteroventral, ventral and anterior margins of the opening. The lacrimal forms only a small portion of the posterior narial margin. In the two specimens (FM PR 1634 and 1814) where the narial margin of the lacrimal is well preserved, it bears a very weakly incised depression. This depression continues for a short distance onto the adjacent portion of the nasal, the bone which forms the entire dorsal margin of the external naris. The nasal is flat to slightly upwardly convex above the opening, and its free margin is fimbriate, with a suture-like morphology. There is never a separate bone associated with this fimbriate area, despite the presence in the Delta collection of at least six prepared specimens that preserve the nasal portion of the external narial margin. It may nonetheless mark a suture, which would presumably be for an anterior tectal that might extend onto the lacrimal; this would be a primitive feature for tetrapods. On the other hand, the fimbriate area of the nasal might be a derived character, which would then be shared with *Archeria* (Holmes 1989) and *Pholiderpeton* (described as *Eogyrinus attheyi* by Panchen (1972)). The maxilla and premaxilla meet in a butt joint below the narial opening, with no sign of bevelling or interdigitation. Rather, the facing surfaces have the appearance of finished periosteal bone.

The prefrontal bears a prominent broad ridge at the anterodorsal corner of the orbit. This ridge is reminiscent of the 'eyebrow' of panderichthyid osteolepiform crossopterygians, in which it is developed on the postfrontal rather than the prefrontal (Schultze and Arsenault 1985; Vorobyeva and Schultze 1991). The undersurface of the prefrontal 'eyebrow' is a massive bony buttress containing spaces (sinuses?) from which small canals appear to open to the orbit via one or more foramina. This deep structure is hidden in almost all available *Whatcheeria* specimens, but is displayed in FM PR 1814. Crushing, combined with the presence of this resistant structure on the underside of the prefrontal, may enhance the prominence of the 'eyebrows' in *Whatcheeria*; it would be interesting to know whether a similar situation prevails in panderichthyids.

The premaxilla bears approximately five teeth + tooth spaces. One or two of these are large alternately replacing fangs, which are separated from the premaxilla-maxilla suture by one or two teeth or tooth spaces. The maxilla bears approximately 33 teeth + tooth spaces. A large fang or fang pair occurs anteriorly, at about positions 6–7 from the suture with the premaxilla. Except for the fangs, premaxillary and maxillary teeth are of similar sizes, decreasing gradually toward the posterior end of the maxillary tooth row. Both premaxillary and maxillary teeth and fangs are circular in cross-section near the base, with the usual labyrinthine appearance; the bases are externally striated. Both teeth and fangs are bluntly pointed and slightly recurved, with the curvature directed both medially and posteriorly.

*Occiput.* The following observations are based mainly on FM PR 1809 (Text-fig. 2), which preserves a relatively complete and undistorted occiput, and on FM PR 1652. The postparietals lack occipital lappets and appear not to be in contact with the exoccipitals, although we have not yet been able to identify either separated exoccipitals, or suture-bounded examples *in situ*. Both FM PR 1652 and FM PR 1809 appear to show the otic capsules in continuity above the foramen magnum. If this observation is correct, the exoccipitals would be physically precluded from contact with the postparietals. Well preserved, small posttemporal fenestrae are present on both sides in FM PR 1809; they appear to have been obliterated by crushing in FM PR 1652. Their

presence thus could be established only from the preservation of the opisthotics in a single specimen, as the several isolated skull tables available to us show no markings on the underside that indicate the existence of posttemporal fenestrae.

*Palate.* The palate is still poorly known; full description will require further preparation. The usual dermal bones are present, namely paired vomers, palatines, ectopterygoids, and pterygoids, plus a median parasphenoid with long cultriform process. The palate is bordered laterally by the premaxilla, maxilla and quadratojugal; the jugal is excluded by the maxilla from contact with any of the palatal bones. The pterygoids meet in the midline, excluding the other paired bones from the small interpterygoid vacuities. The elongate internal naris is bordered by the premaxilla, maxilla, vomer, and palatine.

The vomer, palatine, and ectopterygoid bear a single, nearly continuous row of about 20 teeth, approximately the same size as those of the marginal dentition. This row extends from the anterior end of the internal naris (which it passes on the medial side) to the posterior tip of the ectopterygoid. Only in the region of the vomer-palatine suture is there a slight diastema. Each of these bones also bears an alternately replacing fang pair in line with the other teeth, but no denticles. The palatal surface of the pterygoid is covered by a shagreen of denticles.

*Braincase.* The ossified portion of the braincase in *Whatcheeria* apparently comprises the otic capsules, exoccipitals, basioccipital, and basisphenoid, the latter tightly sutured to the parasphenoid. To date, we have identified eight more or less well-exposed braincases, some isolated and some preserved in association with skulls. Additional examples are demonstrably present in partial skulls, but are almost entirely covered by other bones and thus are not at present available for study.

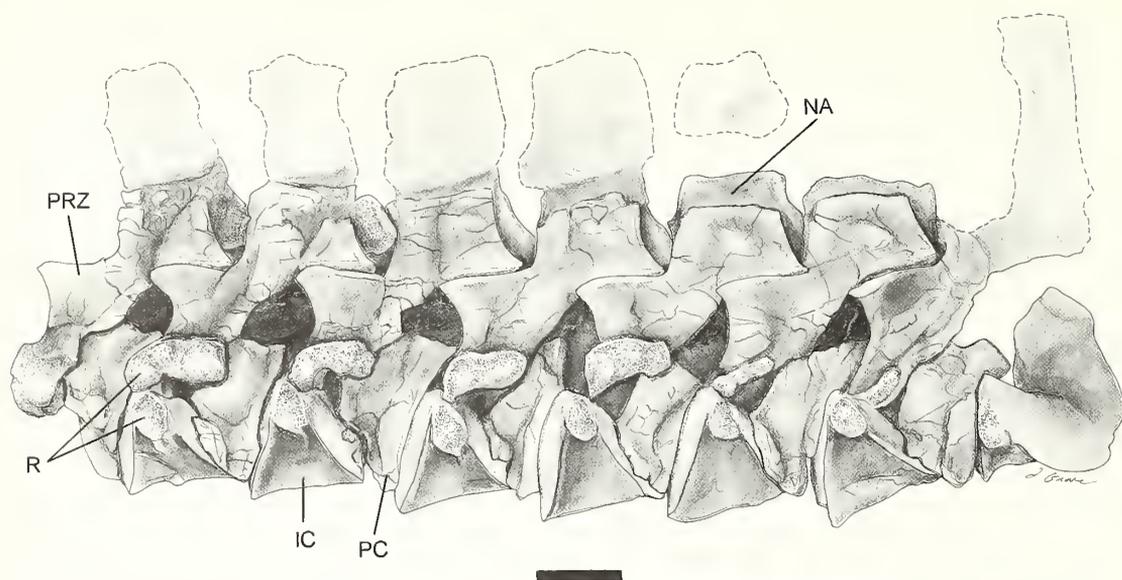
In ventral view, the posterior end of the parasphenoid is a posteriorly open 'U', with its base only a little posterior to the bases of the basiptyergoid processes. The braincases available to us that preserve the basisphenoid-parasphenoid unit in articulation with the basioccipital, suggest that the arms of the 'U' articulated at least as much with the lateral as with the ventral surface of the basioccipital. It appears that the basioccipital contact with the basisphenoid+parasphenoid complex was mostly a butt joint medially, with little overlap except via the arms of the 'U'. The cultriform process probably reached the pterygoids anteriorly. The basiptyergoid processes are very short, and in ventral view are covered by the parasphenoid up to the point where the articular surface begins. The articular surface is unfinished and bifaceted, with dorsal and ventral surfaces each of which is oriented as much laterally as anteriorly.

In FM PR 1651, both stapes are preserved in articulation with the braincase, which is seen in ventral view associated with the underside of the skull table. A single stapes is similarly preserved in FM PR 1816. All three stapes identified to date are badly crushed. The *Whatcheeria* stapes has a stapedia canal, and the ossified shaft as preserved appears flattened but not especially plate-like. However, the true extent of the stapedia shaft is unknown; the ventral margin in the available examples appears to be damaged or unfinished.

*Lower jaw.* The lower jaw has the overall shape common to that of many other early tetrapods, without the deep angle present in many anthracosauroids. There is no retroarticular process or 'coronoid process'. The jaw is composed of 12 bones: dentary, four infradentary bones (splenial, postsplenial, angular and surangular), adsymphyseal, Meckelian bone, three coronoids, prearticular, and articular. Most of the sutures between these bones can be worked out from the numerous mandibles available.

On the external surface, the dentary extends from the symphysis through about two-thirds of the length of the adductor fossa. The infradentary bones are broadly exposed on the lateral surface (Text-fig. 1). Bones definitely participating in the symphysis include a Meckelian ossification, adsymphyseal, and dentary; the sutures surrounding these bones are very clear. The splenial and/or prearticular may contribute as well, but in the specimens prepared to date the borders of the prearticular and splenial are ambiguous at the anterior end of the jaw. The adsymphyseal rests in the symphyseal curve of the dentary; it articulates posteriorly with coronoid I, and laterally with coronoid I, the dentary, and the Meckelian ossification. On the lingual surface the adsymphyseal articulates with the prearticular(?) and Meckelian, and contributes to the symphysis. It bears a row of five to six small teeth along its lateral edge and a pair of marginal-sized teeth lingually.

The limits of the prearticular are clear where it articulates with the articular, coronoids and posterior three infradentary bones. The few large Meckelian fenestrae seen in some embolomeres are absent in *Whatcheeria*. Instead, the prearticular takes part in the formation of seven foramina along its articulation with the infradentary bones. The anteriormost foramen spans the splenial-postsplenial suture; the next four involve the postsplenial, and the last two may involve the postsplenial or angular. The two largest are in the postsplenial series. The suture between the prearticular and the infradentary bones is straight and not interdigitated. This



TEXT-FIG. 3. *Whatcheeria deltae* gen. et sp. nov., FM PR 1745, seven articulated presacral vertebrae as preserved. Abbreviations: IC, intercentrum; NA, neural arch; PC, pleurocentrum; PRZ, prezygopophysis; R, rib articulations. Scale bar represents 10 mm.

contact closely resembles those figured by Jarvik (1980) in *Ichthyostega*, and by Ahlberg *et al.* (1994) in *Ventastega*.

The three coronoids are lenticular in shape. Intercoronoid sutures are oriented longitudinally, running subparallel to the long axis of the jaw rather than transverse to it as is generally the case in osteolepiform fishes. Coronoids one and two bear two sizes of teeth. Each has a single longitudinal row of marginal-sized teeth along its lateral margin. These teeth are tallest in the centre of the row, and separated from the teeth on adjacent coronoid(s) by diastemas centred on the intercoronoid sutures. In addition, each bears a patch of denticles medial to the tooth row. Coronoid three bears marginal-sized teeth in a manner similar to the first two. A large patch of denticles occurs medial to these teeth, however, it is not possible at this time to determine whether they are borne on coronoid three or the prearticular.

Each dentary bears some 30–40 marginal teeth, the size and morphology of which are similar to those of the teeth of the upper marginal dentition. Height of the dentary teeth decreases slightly toward the adductor fossa, but is otherwise uniform. Each dentary has a pair of parasymphysial fangs just lingual to the marginal dentition in the symphyseal curve. The prearticular appears to lack denticles entirely, with the possible exception discussed above.

### *Axial skeleton*

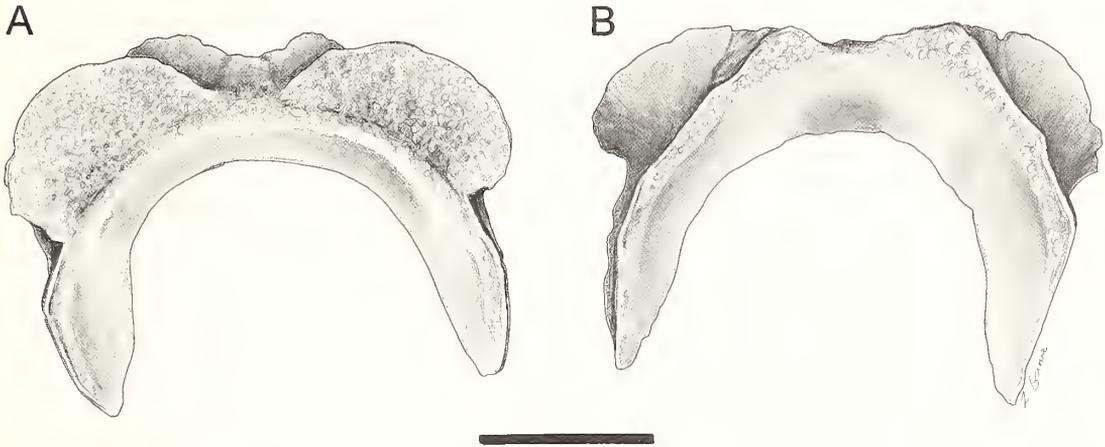
The *Whatcheeria* material includes numerous examples of ribs and vertebrae, including long series of articulated vertebrae representing both presacral and caudal regions. The atlas and axis appear to be present in at least two specimens (FM PR 1634 and 1701), but accurate interpretation of their morphology will require further preparation. Because most of the articulated vertebral material is still unprepared, the composite description below depends primarily on two specimens: FM PR 1700 (Plate 1), and FM PR 1816 (not illustrated). Both have a single long series of articulated and mostly well preserved vertebrae, but neither includes the atlas.

In FM PR 1816, all vertebrae are preserved in lateral view. The single sacral vertebra and rib are unequivocally identifiable. There are 14 caudals, which is less than the full number as shown by other, less completely prepared specimens. Twenty-four presacrals are clearly identifiable, and one vertebra anterior to these is represented by a crushed, featureless but vertebra-sized bony mass associated with a rib. Anterior to that vertebra, a further two are covered by an unidentified bone, but their presence is indicated by partial ribs

which continue the rib series visible on the other anterior vertebrae. The maximum presacral vertebral count for this specimen is thus 27. This is certainly less than the full count, but probably not by much (perhaps three or four at most), as suggested by the size and shape of the anterior ribs. We thus estimate that *Whatcheeria* has about 30 presacrals.

FM PR 1700, the holotype, preserves an articulated series of 22 presacrals, which starts 25 mm behind the skull table and does not include either the atlas or the sacral. The posterior 13 vertebrae in this series are preserved in lateral view, but the anterior portion of the column is twisted so that the first nine vertebrae are preserved in dorsal view, showing little more than their (badly crushed) neural arches.

Typical *Whatcheeria* vertebrae are composed of a crescentic, ventrally thickened intercentrum; paired(?) pleurocentra which extend far ventrally and are often fused dorsally; and a neural arch whose right and left halves are completely fused (Text-figs 3-4). Both pre- and postzygapophyses of presacral neural arches are



TEXT-FIG. 4. *Whatcheeria deltae* gen. et sp. nov., FM PR 1712, pleurocentrum. A, anterior, and B, posterior view. The large articular surfaces for the preceding neural arch are visible in anterior view, the smaller surfaces for the succeeding neural arch in posterior view. Scale bar represents 10 mm.

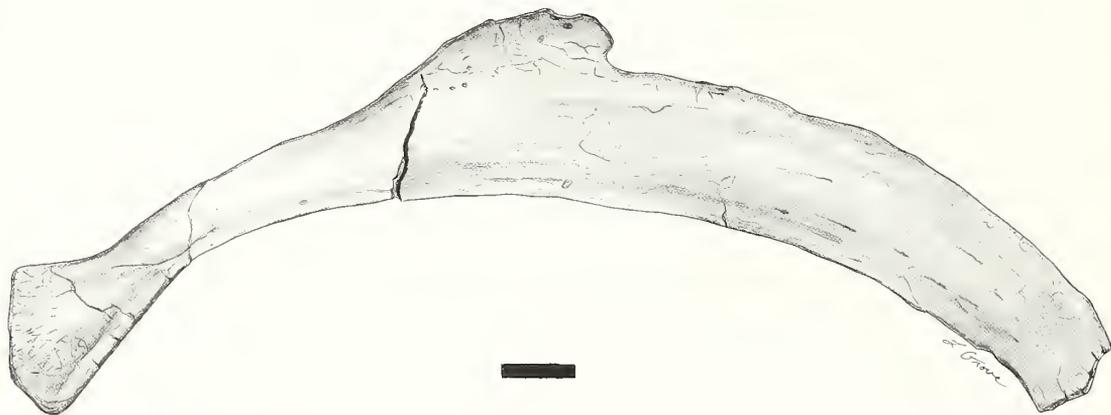
'well developed' in the sense that their cranial-caudal dimension is equal to or larger than that of the neural arch at the same level. Zygapophyses of the caudal vertebrae preserved in FM PR 1816 are also well developed, but diminish significantly in size posteriorly. A supraneural canal is preserved in the neural arch. The neural spines on the caudal vertebrae of FM PR 1816 are slightly (10 mm) taller than those on the presacrals.

The intercentra are not unusual. The dorsally fused pleurocentra, on the other hand, are remarkable. Most of the fused pleurocentra we have seen are separated specimens. Each example bears a large pair of anteriorly facing articular facets for the preceding neural arch, and a small pair for the succeeding one (Text-fig. 4). Fused pleurocentra have been found in a variety of sizes, including some that are quite small. For example, the pleurocentrum in Text-fig. 4 is about 30 mm in greatest diameter, compared with about 15 mm in one of several examples catalogued as SUI 52010. Given that we have a number of articulated *Whatcheeria* vertebral series, it might seem that the frequency and regional variations of fused pleurocentra could be easily determined. However, it is difficult to examine pleurocentra *in situ* in articulated specimens, as this would generally require destructive preparation. We have at present only one *Whatcheeria* specimen that demonstrates some fused pleurocentra as part of an associated vertebral series. In FM PR 1887, four or possibly five dorsally-fused pleurocentra are visible in a disrupted and somewhat scattered region of an otherwise articulated column, just anterior to the sacral vertebra. Three of these are still in close association with the intercentrum, although apparently not fused to it, thus making a bipartite centrum. In articulation, these two central elements form an amphicoelous centrum with a very restricted notochordal opening that is about 20 per cent. of the total centrum diameter. Some *Whatcheeria* vertebrae may be monospondylous: we have recovered an isolated

example tentatively identified as *Whatcheeria*, in which the pleurocentrum is fused to the intercentrum behind it, without trace of suture (FM PR 1886). This specimen is broken in such a way as to make it uncertain whether the pleurocentra were fused across the dorsal midline as well as to the intercentrum. Pleurocentra which fuse dorsally but not ventrally, or are components of a monospondylous centrum as described above, have been described as occurring occasionally in a few temnospondyls (Shishkin 1989).

Presacral rib morphology is one of the most striking features of *Whatcheeria*. FM PR 1700 retains most of the presacral ribs in association with the (preserved portion) of the column (Pl. 1). Most of the presacral ribs are missing in FM PR 1816. It does retain a few in association with their vertebrae, however, at the anterior end of the articulated series and immediately anterior to the sacral vertebra. In addition to the sacral, the first four caudal ribs are present in FM PR 1816. Corresponding vertebrae in FM PR 1816 and FM PR 1700 can be identified based on rib morphology. In FM PR 1816, the most-anterior vertebra whose rib bears a small uncinat process is number 23 anterior to the sacral (sacral vertebra = no. 0). A similar rib in FM PR 1700 is also very near the anterior end of the preserved portion of the column. If this correlation is accepted provisionally, it follows that FM PR 1700 preserves vertebrae from number 6 to number 27 anterior to the sacral, while FM PR 1816 preserves vertebrae number 1 to number 27 anterior to the sacral, plus the sacral itself and the first fourteen caudals.

Changes in *Whatcheeria* rib size and shape, from anterior to posterior, are approximately as follows. We are uncertain whether the atlas bears ribs, but all other presacral vertebrae probably do. Anterior ribs are short, thin, and nearly straight, with a shaft some 2–3 mm in diameter near the head, and not markedly flattened in cross-section. Beginning at vertebra no. 23 anterior to the sacral, the shaft flattens markedly, ribs become longer and strongly curved, and uncinat processes appear proximally, about 20 mm distal to the head. They enlarge rapidly and extend progressively further distally, becoming flanges rather than processes. At the point of greatest development of these flanges, around no. 20 anterior to the sacral, *Whatcheeria* ribs resemble those of *Ichthyostega* (Jarvik 1980), although they are not quite as large (Text-fig. 5). Posteriorly from their point



TEXT-FIG. 5. *Whatcheeria deltae* gen. et sp. nov., FM PR 1889, a rib from mid-trunk as preserved. Scale bar represents 10 mm.

of maximum development, the flanges diminish rapidly. By about no. 11 anterior to the sacral the ribs lack flanges even as 'uncinat processes' and are diminishing rapidly in length and shaft diameter. Ribs immediately anterior to the sacral vertebra are very small, almost rudimentary.

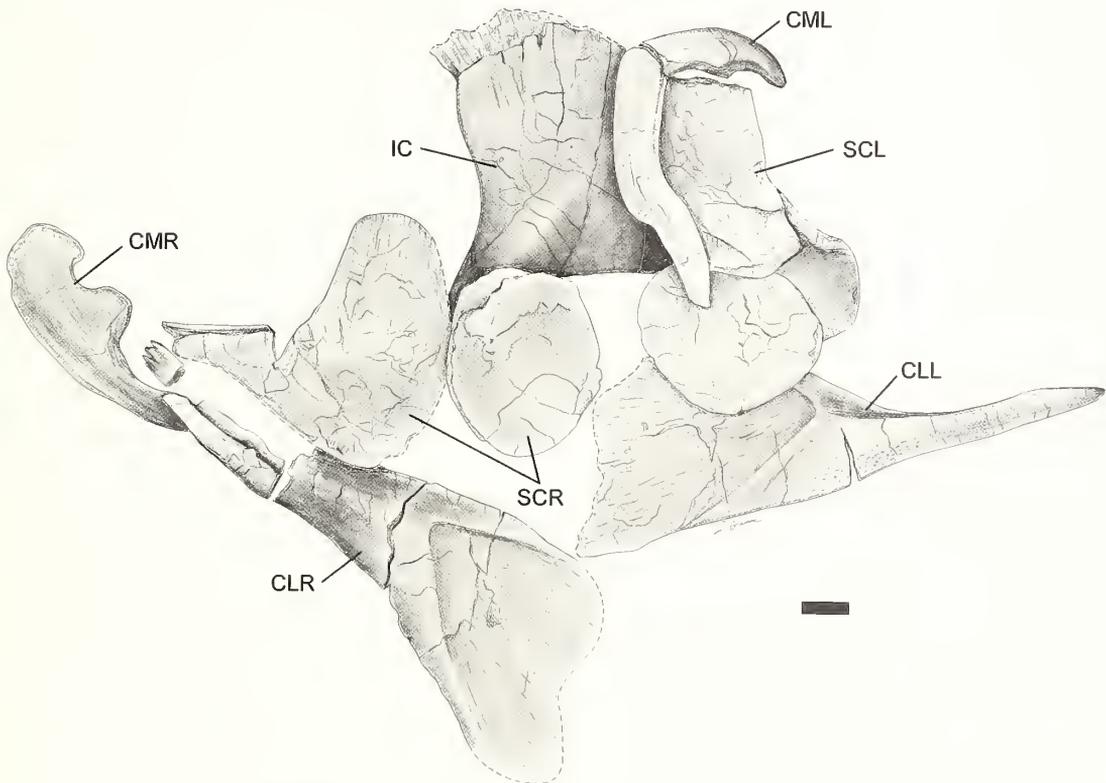
The sacral rib is short and massive, and borne on a greatly enlarged diapophysis. The first caudal vertebra bears a robust, slightly curved rib, whose shaft is semicircular in cross-section with a diameter of about 5 mm. Ribs on caudals 2–4 are slightly larger and longer, and progressively curved more and more strongly posteriorly. The distal half of the fourth caudal rib is angled at about 80° to the proximal half; overall length of this rib as preserved is about 80 mm. Although no ribs are preserved posterior to this point, they might have been present on a few additional caudals; caudal no. 8 is apparently the last vertebra with even a rudimentary diapophysis. The first haemal arch preserved is in association with caudal no. 7, although detached from its intercentrum. Haemal arches probably began anterior to this, as the intercentrum of caudal no. 6 clearly has

the appropriate facet on its posteroventral corner. In FM PR 1816, haemal arches are present on caudals 8–14, which is the last vertebra preserved.

*Appendicular skeleton*

*General.* Relative to overall body size, the limbs of *Whatcheeria* are as large as those of embolomeres and most other early anthracosaurs. Each has well developed tetrapod-type digits. Combined measurements from FM PR 1700, the holotype, and FM PR 1816 indicate that the limbs are of equal length as measured from the proximal end of the propodial to the distal ends of the epipodials. All articulated and most isolated specimens of the pro- and epipodial bones are more or less crushed, through some beautifully preserved three dimensional examples have been recovered as isolated specimens from limestone matrix. No mesopodial elements have yet been recognized, and they may have been unossified. There is no evidence for more than five digits, but the few associated, articulated hands and feet so far available are probably incomplete. All digits are composed of short, flat phalanges, which gives the manus and pes a paddle-like appearance.

*Forelimb.* The pectoral girdle is composed of a midline interclavicle flanked on either side by a scapulocoracoid, clavicle, and cleithrum (Text-figs 6, 7A). The external surfaces of interclavicle, clavicle, and cleithrum are

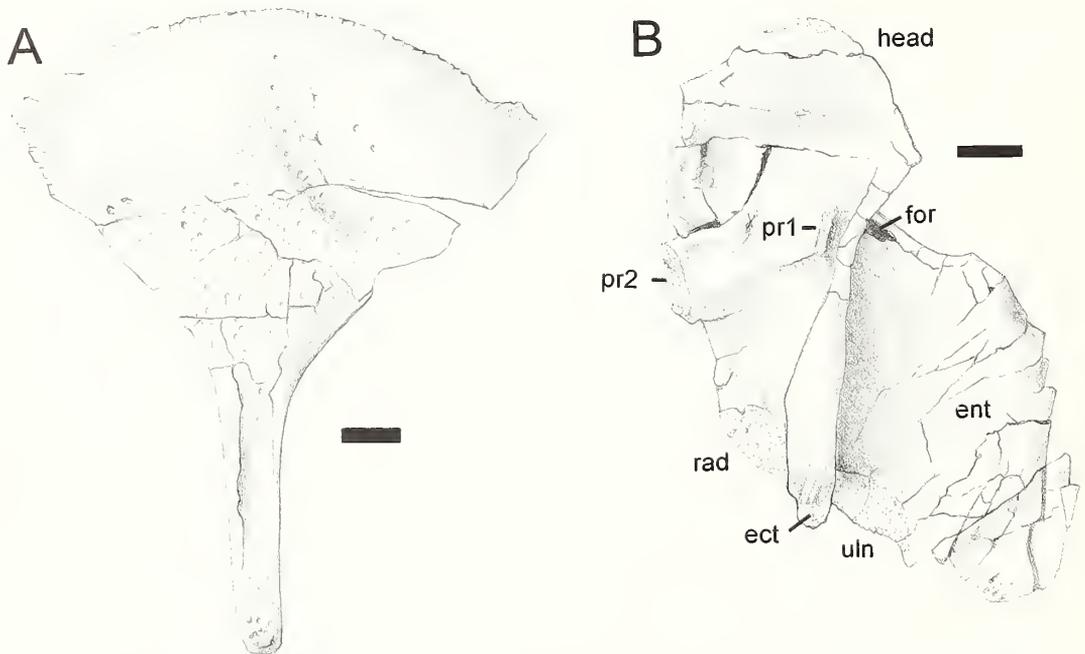


TEXT-FIG. 6. *Whatcheeria deltae* gen. et sp. nov., FM PR 1816, pectoral girdle as preserved. Abbreviations: CLR, CLL, right and left clavicles respectively; CMR, CML, right and left cleithra, respectively; IC, interclavicle; SCR, SCL, right and left scapulocoracoids, respectively. The clavicles are seen in internal view, with anterior roughly towards the bottom of the page. The large, triangular articular depression for the interclavicle is evident on both. The right cleithrum is seen in internal view, the left mostly in anterior view. The interclavicle is exposed in dorsal view. The bone has been rotated by about 90° counterclockwise relative to the other elements, so that its anterior end is roughly towards the upper right of the drawing. The parasternal process lies beneath the other elements present and is oriented towards the lower left of the figure. The right scapulocoracoid is exposed in internal view, the left in external view. Each scapulocoracoid is composed of two ossifications. Scale bar represents 10 mm.

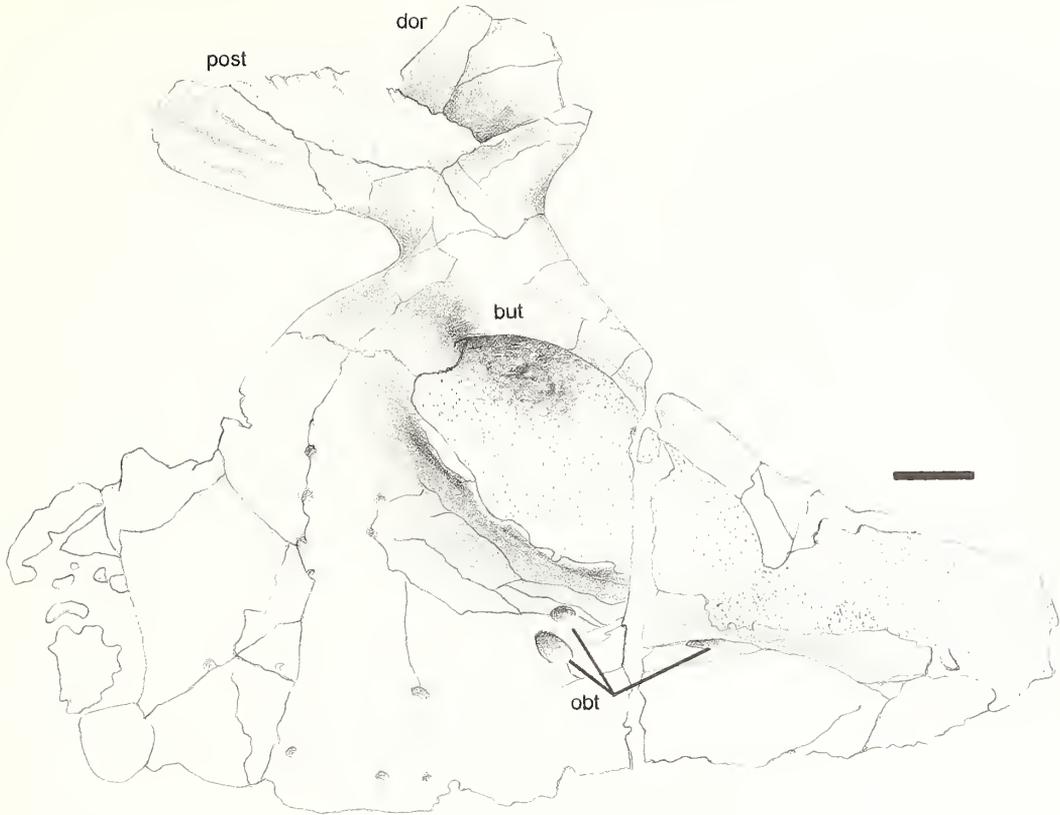
unornamented. The roughly diamond-shaped body of the interclavicle is wider than long, and the long, slender parasternal process is slightly longer than the body. The anterior facets on the external surface of the interclavicle indicate that the clavicles met at the midline at least over the anterior portion of that bone. The cleithrum completely caps the dorsal border of the scapulocoracoid. As an apparently autapomorphic feature of *Whatcheeria*, the cleithrum has a deeply incised, rounded notch in its posterior border. The notch accentuates the blunt-tipped, posteriorly directed process which terminates the cleithrum's posterodorsal extremity. There is evidence for a postbranchial lamina on the cleithrum: FM PR 1766 is a three-dimensional partial scapulocoracoid, which preserves the ventral portion of the cleithral shaft in articulation with the anterior edge of the scapulocoracoid. The anterior edge of the shaft forms a distinct, medially-inturned flange that appears comparable to that described in *Acanthostega* by Coates and Clack (1991). The postbranchial lamina does not appear to extend onto the clavicle.

The scapulocoracoid apparently ossified from two centres, a scapular and a coracoidal. In FM PR 1816 (Text-fig. 6), the scapula and coracoid of each side are preserved as separate but closely associated ossifications. FM PR 1704 is an isolated left scapulocoracoid with the distinctive cleithrum in its normal position. Here the scapulacoracoid is a single piece, with no trace of suture; a deep and apparently natural notch on its anterior border at the dorsoventral level of the glenoid may mark the boundary between two ossification centres. A left scapulocoracoid with similar notch occurs in FM PR 1635, in association with a *Whatcheeria* skull and partial postcranium. Glenoid shape is comparable to that in many other primitive tetrapods: the glenoid is anteroposteriorly elongate and helical. There is a supraglenoid foramen and a supracoracoid foramen, both opening into the subscapular fossa.

Description of the humerus is complicated by the fact that all of the humeri associated with unequivocal *Whatcheeria* remains are crushed, and most are nearly featureless, with poorly ossified proximal and distal ends. The left humerus associated with *Whatcheeria* skeleton FM PR 1635 and prepared in extensor view is a partial exception, in that the caput, capitellum and trochlea, as well as the ectepicondyle and entepicondyle plus some other processes, are all fairly well developed and relatively well preserved. This specimen (Text-fig. 7B)



TEXT-FIG. 7. *Whatcheeria deltae* gen. et sp. nov., pectoral limb elements. A, FM PR 1957, interclavicle in external view. Anterior is to the top of the page. B, FM PR 1635, extensor surface of left humerus. Proximal is to the top of the page. Abbreviations: ect, ectepicondyle; ent, entepicondyle; for, entepicondylar foramen; pr1, process usually identified as a 'latissimus dorsi process'; pr2, process usually identified as a 'deltoid process'; rad, radial articulation; uln, ulnar articulation. Scale bars represent 10 mm.



TEXT-FIG. 8. *Whatcheeria deltae* gen. et sp. nov., FM PR 1740, right half of pelvic girdle. Dorsal is to the top of the page, anterior to the right. Abbreviations: but, acetabular buttress; dor, dorsal iliac process; obt, obturator foramina; post, postiliac process. Scale bar represents 10 mm.

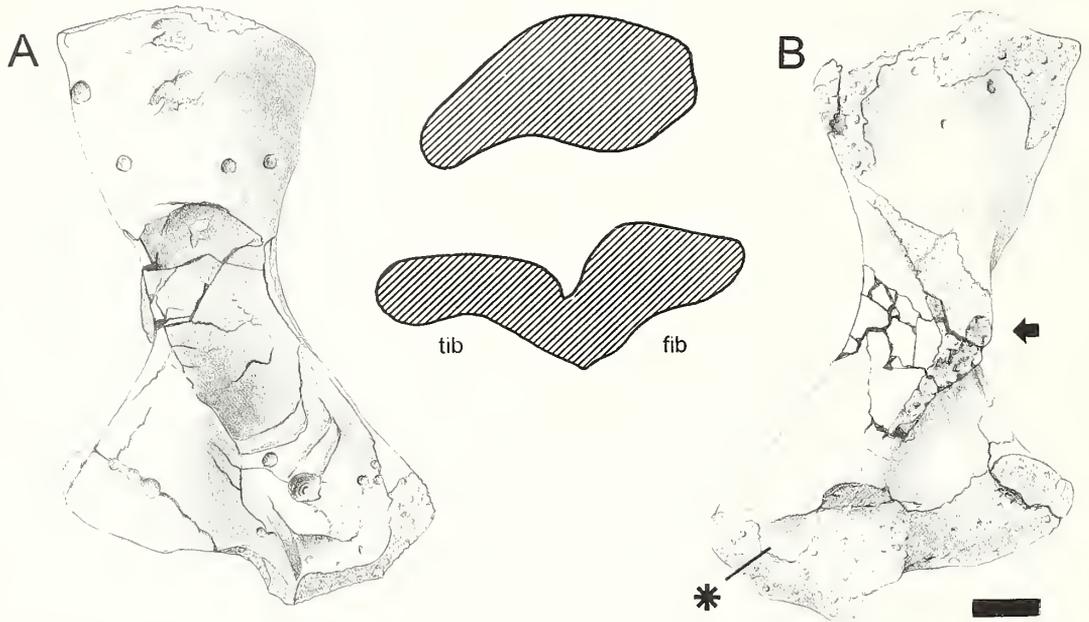
represents the midpoint, in size and ossification, between other definite *Whatcheeria* humeri and some larger and better preserved but unassociated humeri of similar morphology. Although it is thus not established beyond doubt, especially as two other taxa of similar body size are known to occur at the Delta site, we believe that the members of this series all pertain to *Whatcheeria* and base the following description on that belief.

The humerus is the standard early tetrapod L-shaped bone, the shape resulting from the presence of a very large, squared-off entepicondyle. In *Whatcheeria*, both the anteroposterior and proximal-distal dimensions of the entepicondyle are approximately equal to humeral length along the shaft, the latter being, in fact, hardly discernible as such. The ectepicondyle is an exceptionally prominent projection at the distal end of a ridge that begins near the humeral head. On the anterior edge of the shaft there is a distinct 'deltoid' process (pr2, Text-fig. 7B), and a distinct 'latissimus dorsi' process (pr1, Text-fig. 7B) arises from the extensor surface at about mid-shaft; in large specimens, this is developed as a prominent spinous process. The flexor surface bears a very large pectoralis process near its anterior edge (not illustrated). No 'supinator' process can be distinguished. There is a large entepicondylar foramen, but no ectepicondylar foramen. The capitellar and trochlear articular surfaces, for articulation of the radius and ulna respectively, are visible in both flexor and extensor view. The radius and ulna are robust bones, the latter with a well developed olecranon process.

*Hindlimb.* The pelvic girdle has well developed dorsal iliac and postiliac processes (Text-fig. 8). The dorsal iliac process undoubtedly articulates with the markedly robust, short, single sacral rib. The postiliac process is everted from the lateral face of the dorsal process, producing a smooth-surfaced, U-shaped channel between the two processes. Much of the lateral face of the postiliac process is heavily ridged. The ridges run

anteroventrally from the dorsal edge of the process. The acetabulum is anteroposteriorly elongate, strongly concave, and floored by unfinished bone. Posterodorsally, a prominent buttress overhangs the acetabulum. Just posterior to the buttress is a small tongue of finished bone that projects into the acetabulum. Anterior to the acetabulum is a large anteroposteriorly elongate area of unfinished bone separated from the acetabulum itself partly by dorsal and ventral projections of finished bone and partly by an elevated ridge of unfinished bone. The ventral margin of the acetabulum forms a prominent ridge and just ventral to that ridge are three obturator foramina. None of the pelvis prepared so far preserves evidence of the number of ossifications contributing to the pelvic girdle. Neither within the acetabulum nor anywhere else on the girdle have we yet found any trace of a suture. On the other hand, one example of a *Whatcheeria* pelvic girdle (FM PR 1880) includes an apparently independent ilium in lateral view, accompanied by a free bony disc in the expected position of an ischium. Identification of this element is uncertain, as neither it nor the (indisputable) ilium bear any trace of an acetabulum, probably due to immaturity.

The femur is of comparable size to the humerus in specimens where both are preserved (FM PR 1700 and FM PR 1816). All *Whatcheeria* femora that have been prepared to date are more or less severely crushed, like that in the holotype, FM PR 1700 (Pl. 1). An isolated, relatively well preserved femur, FM PR 1958 (Text-fig. 9), compares in all respects with those associated or articulated with definite *Whatcheeria* specimens, and the



TEXT-FIG. 9. *Whatcheeria deltae* gen. et sp. nov., FM PR 1958, left femur. A, extensor surface. B, flexor surface. For each, proximal is towards the top of the page. Between the two drawings are plane projections of the proximal (upper) and distal (lower) regions of unfinished bone. For both, the extensor surface is uppermost. Arrow indicates the approximate highpoint of the adductor crest; asterisk indicates a small region of finished bone discussed in the text; fib, indicates the articular region of the fibula; tib, the same for the tibia. Scale bar represents 10 mm.

following description is based primarily on this example. The shaft is short and stout, and both the proximal and distal ends are expanded. The articulation for the fibula projects further distally than that for the tibia, and flares posteriorly such that the postaxial border of the femur is more deeply concave than the preaxial border. The extensor surface is relatively featureless but is marked by a deep furrow that separates the condyles distally. In FM PR 1958 the marrow cavity of the shaft has collapsed, leaving an elongate depression, and both the proximal and distal ends are marked by linearly arrayed, circular punctures interpreted as tooth marks resulting from scavaging or predation (see below). In flexor view, a prominent oblique ridge, *sensu* Jarvik 1980, begins just between the condyles distally and angles anteriorly and proximally to project beyond the preaxial

border at midshaft (arrow, Text-fig. 9). At this point, the ridge reaches its maximum elevation from the general surface of the shaft. From this apex, the ridge angles posteriorly and proximally and almost immediately bifurcates. The thicker, anterior ridge angles toward the anterior corner of the femoral head but rapidly decreases in height, ending about halfway to the head. The thinner, posterior ridge continues towards the posterior corner of the femoral head whilst gradually decreasing in height. A fossa occupies the area between the two ridges. No ridge or boss occurs in a position equivalent to that occupied by the internal trochanter commonly found in the femora of other Palaeozoic tetrapods. No tooth marks occur on the flexor surface, but a few small foramina are located near the proximal end. The fibular articulation is characterized by a small, strongly concave area of periosteal bone visible in flexor view (\*, Text-fig. 9). This feature occurs less prominently in some other primitive tetrapods; its condition in the Lower Carboniferous *Proterogyrinus* (Holmes 1984) is most similar to that in *Whatcheeria*. The tibia and fibula are similarly robust, with no remarkable distinguishing characteristics (Plate 1).

### *Scales*

A number of scattered, elongate bony scales have been recovered from the site, none in association with articulated *Whatcheeria* skeletal elements. On the other hand, numerous similar or identical scales are associated with the one articulated 'embolomere' skeleton recovered from the Delta site. A colosteid amphibian also occurs at Delta, though no definitely colosteid postcranial remains have so far been recognized. The colosteid *Greererpeton*, from the Lower Carboniferous of West Virginia, has bony scales, though of different morphology from the Delta scales (Romer 1972; Godfrey 1989). The implication, then, is that *Whatcheeria* does not have bony scales and the tetrapod-type scales so far recovered probably belong to the Delta 'embolomere.'

### *Evidence of predation or scavenging*

Both the pelvis and the femur illustrated here show features which we interpret as resulting from predation or scavenging (Text-figs 8–9). Both bones preserve linear arrays of circular depressions. The depressions are sometimes quite deep, and their size and spacing are comparable to those of the alternately replacing marginal dentition of both *Whatcheeria* and the undescribed colosteid at the site. On the extensor surface of the femur, there are two linear arrays at approximately right angles to the long axis: one proximally and one distally. The proximodistal spacing of these arrays is comparable to the head width of *Whatcheeria* obtained from a preliminary reconstruction. The distal array on the femur contains a larger and deeper puncture lying just off the axis of the smaller holes. This is consistent in size and position with having been made by a fang.

## DISCUSSION

For researchers concerned with the origin and early evolution of tetrapods, *Whatcheeria* is in many ways gratifyingly primitive and certainly ancient, representing a period from which few tetrapods have yet been described. It is thus no surprise that its relationships to other tetrapod groups, and the evolutionary history of some of its most striking characters, are far from obvious. Resolution of these uncertainties will require a level of detailed comparative study and cladistic analysis which are beyond the scope of this description. Consequently, the discussion below depends on cladistic studies of early tetrapods published by several other authors. We have relied upon papers with analysis founded on the now almost universal view, which we share, that osteolepiform fishes are the sister group of tetrapods. Within this broad consensus, various authors differ in the groups considered, characters analysed, and polarity assigned to the same characters, and consequently in the cladograms produced. We do not attempt to reconcile those differences here; instead, we confine our discussion for the most part to characters on which there seems to be substantial agreement. More problematic characters are noted and discussed as such.

*Whatcheeria* shows a number of characters that are primitive for tetrapods, but are absent in all but a few of even the earliest known tetrapods. Some of these characters are mentioned in the description above, but we have not attempted to enumerate all of *Whatcheeria*'s primitive characters. The following list provides an indication of its overall primitiveness, but is not intended to substitute for a thorough cladistic analysis.

1. The postoccipital portion of the cheek is long. In *Whatcheeria*, postoccipital cheek length is 21 per cent. of skull length. This is similar to the postoccipital cheek length of various osteolepiforms and primitive, early tetrapods, as calculated by us from reconstructions published by several authors. Thus among osteolepiform fish, postoccipital cheek length is about 19 per cent. of skull length in *Panderichthys rhombolepis* (based on Vorobyeva 1977) and 18 per cent. in *Eusthenopteron fordi* (based on Jarvik 1980). Among early tetrapods, postoccipital cheek length is 14 per cent. in *Ichthyostega* and 13 per cent. in *Acanthostega* (both based on Jarvik 1980); 28 per cent. in *Crassigyrinus* (based on Panchen 1985), which must hold the record for postoccipital cheek length among early tetrapods; 14 per cent., 12 per cent. and 11 per cent. respectively, in the loxommatids *Baphetes kirkbyi*, *Megalocephalus pachycephalus* and *Loxomma acutirhinus* (based on Beaumont 1977); 18 per cent. and 13 per cent. respectively, in the embolomeres *Proterogyrinus scheelei* (based on Holmes 1984) and *Pholiderpeton scitigerum* (based on Clack 1987); and 8 per cent. in the colosteid *Greererpeton burkendorfi* (based on Smithson 1982).

2. Presence of a preopercular. This is known to occur only in *Ichthyostega* (Jarvik 1980), *Acanthostega* (Jarvik 1980; Clack and Coates 1993); *Crassigyrinus* (Panchen 1985), and possibly in *Ventastega* (Ahlberg *et al.* 1994).

3. The lateral line is enclosed in bony canals in some places. Enclosed lateral line canals opening to the surface through spaced holes are universal in osteolepiform fish and occur to some degree in other primitive tetrapods, including the Devonian taxa *Acanthostega* (Jarvik 1980; Clack and Coates 1993), *Ichthyostega* (Jarvik 1980), *Ventastega* (Ahlberg *et al.* 1994) and *Elginerpeton* (Ahlberg 1995) and the Lower Carboniferous *Pholidogaster* (Panchen 1975), *Greererpeton* (Smithson 1982) and *Doragnathus* (Smithson 1980).

4. The dentary extends far posteriorly along the adductor fossa; its extent is comparable to that of dentaries in *Metaxygnathus* (Campbell and Bell 1977) and the loxommatids *Megalocephalus pachycephalus* and *Loxomma rankini* (Beaumont 1977). Only in *Ichthyostega*, which shows the most plesiomorphic state known for tetrapods, does the dentary extend further back (Jarvik 1980).

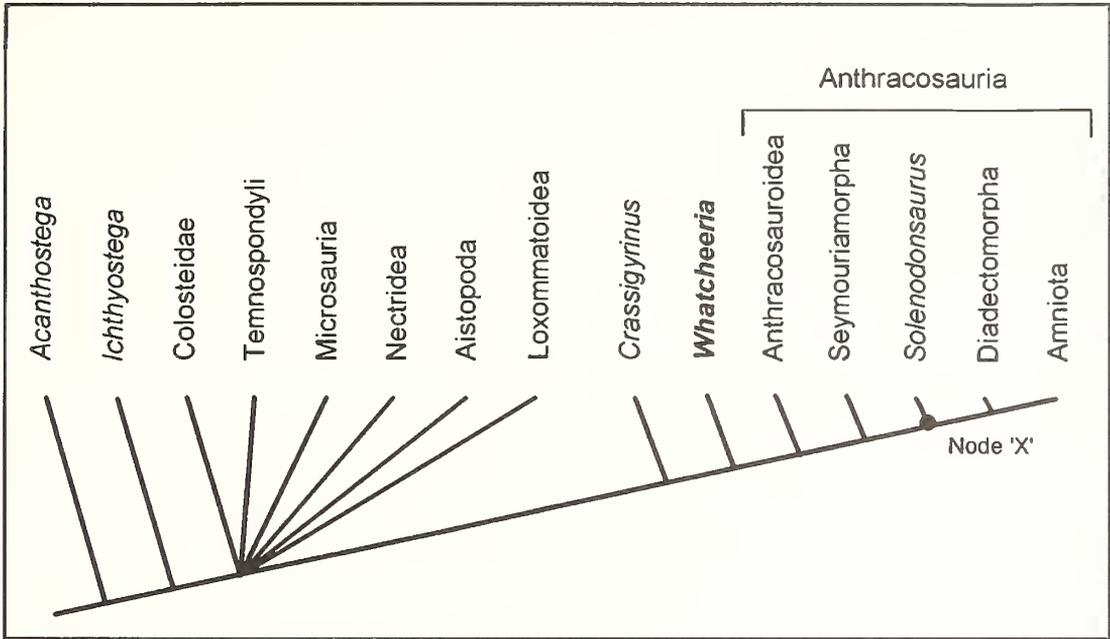
5. The prearticular extends far forward, coming very near to the symphysis and perhaps even participating in it. The prearticular in *Ventastega* also extends far forward (Ahlberg *et al.* 1994), although again it is uncertain whether it participates in the symphysis. It definitely does so in *Ichthyostega* (Jarvik 1980), and the panderichthyid fish *Panderichthys rhombolepis* (Vorobyeva and Schultze 1991).

6. An adsymphysial is present, which is also primitive in bearing teeth. An adsymphysial is very rare in tetrapods, though universal in osteolepiforms. It is present in *Ichthyostega*, where it was sketchily restored by Jarvik (1980), as well as in *Acanthostega* (J. A. Clack, pers. comm.). *Elginerpeton* from the Devonian of Scotland, is interpreted as having a toothed adsymphysial (Ahlberg 1995), as has *Ventastega* (Ahlberg *et al.* 1994), a tetrapod jaw from the Pennsylvanian of Nova Scotia (Godfrey and Holmes 1989) and the Lower Permian embolomere *Archeria* (Holmes 1989).

7. The small and numerous Meckelian foramina are similar to those in the osteolepiform *Panderichthys* (Vorobyeva 1962). Among tetrapods, *Ichthyostega* has been figured with five similar foramina (Jarvik 1980), *Ventastega* with at least three (Ahlberg *et al.* 1994; a minimum estimate, since the figured specimen is damaged), *Caerorhachis* with three (Holmes and Carroll 1977) and *Elginerpeton* with perhaps five, though in this case they are between the Meckelian ossification and the infradentary bones (Ahlberg 1995).

8. The tabular and parietal are not in contact, and in fact are widely separated. This configuration is widespread among early tetrapods, but the condition in *Whatcheeria* is noteworthy because apart from *Crassigyrinus*, it is unique in an animal that appears to have anthracosauroid affinities (see discussion below).

9. Each of the paired palatal bones bears a fang pair, which forms part of a row of about 20 marginal-sized teeth. This arrangement is similar to the condition in *Ichthyostega* and *Acanthostega*, though the distribution on individual bones is different (Jarvik 1980; Clack and Coates 1993; Clack 1994a). Most other Palaeozoic tetrapods have fewer marginal-sized teeth on the palate (or none).



TEXT-FIG. 10. Hypothesis of relationships of *Whatcheeria* to selected Palaeozoic tetrapod groups, as discussed in the text. Position of *Acanthostega* and *Ichthyostega* after Lebedev and Coates (1995). 'Node X' from Gauthier *et al.* (1988).

10. The femur has an oblique ridge on the flexor surface which reaches its maximum elevation at midshaft. This configuration has been described only in *Ichthyostega* among early tetrapods (Jarvik 1980). Indeed, the pattern of ridges and fossae on the flexor surface bears a striking resemblance to those illustrated for *Ichthyostega*. We hypothesize that this morphology is primitive for tetrapods.

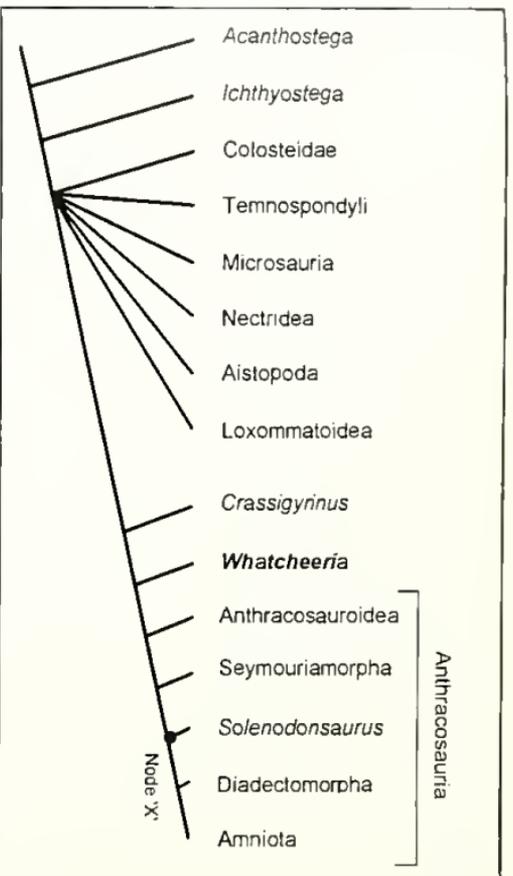
11. The pelvis has a large area of unfinished bone anterior to the acetabulum. This feature has been illustrated for *Ichthyostega* by Jarvik (1980). The general shape of the acetabulum plus anterior unfinished area in *Whatcheeria* and *Ichthyostega* are remarkably similar with respect to proportions, orientation, and details of bony buttresses, including a small tongue of finished bone that projects into the acetabulum at its posterior end next to the large supracetabular buttress. The *Whatcheeria*-*Ichthyostega* configuration may be primitive for tetrapods.

In the absence of a formal cladistic analysis, we will discuss *Whatcheeria*'s relationships first in terms of what it appears not to be, and then in terms of an informal analysis that suggests some groups to which it might be related. To begin, we note that we can identify no synapomorphies of *Whatcheeria* and the microsaurians, nectrideans, or aistopods. Similarly, no synapomorphy convincingly links *Whatcheeria* with temnospondyls. In particular, there is no postparietal-exoccipital contact, which (following Smithson 1985b) is characteristic of both temnospondyls and microsaurians. *Whatcheeria* also does not appear to form a natural group with either or both of two early tetrapod groups that may be called 'temnospondyl-like', namely the loxommatids and colosteids, nor does it share derived characters with any of the Devonian taxa so far described.

We can, however, identify plausible synapomorphies of *Whatcheeria* and Anthracosauria, two of which seem especially convincing:

1. The posttemporal fenestra is small (see discussion in Gauthier *et al.* 1988).
2. The upper surface of the tabular horn is a posterior extension of the upper surface of the tabular, i.e. both lie at the same dorsoventral level (see Panchen 1985).





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Seven additional characters seem to us to suggest a *Whatcheeria*–Anthracosauria relationship, but less convincingly so:

3. The temporal series in the skull table has an abrupt, strong ventral flexure that places the sutures for the cheek bones in a much more ventral plane than those for the midline roofing elements. This produces a characteristic shape of the posterior third of the table, which is also seen in *Crassigyrinus* and early members of the Anthracosauria, notably the anthracosauroids.

4. The cranial dermal bones are almost unornamented. In this respect *Whatcheeria* differs strongly from colesteids and temnospondyls. We consider that the dermal ornament that is present most closely resembles that of anthracosaurs (see description and discussion in Panchen 1985, p. 551). Clack (in press) considers *Whatcheeria*'s ornament comparable to that of the anthracosauroid *Anthracosaurus russelli*. In view of the imprecision with which such a feature is necessarily described, *Whatcheeria*'s (weak) dermal ornament provides only suggestive evidence.

5. The orbits are large and quadrangular. This is also true of *Crassigyrinus* and early members of the Anthracosauria. Loxommatids have a markedly non-circular orbit as well, although in their case due to a large antorbital vacuity which is confluent with the orbit.

6. The vomers are narrow, even though they are primitive in retaining the fang-pair. Gauthier *et al.* (1988) consider narrow vomers to be a synapomorphy at their 'Node X', (Text-fig. 10) and note that it occurs in other anthracosaurs as well. Since 'broad' and 'narrow' are subjective, we consider this character to provide relatively weak support for the proposed relationship.

7. The maxilla has a marginal fang pair. On purely morphological grounds this could just as well be stated as 'Distinct caniniform maxillary tooth...present' (Gauthier *et al.* 1988, p. 125). The difference is subtle, but significant: traditionally, non-amniote early tetrapods have 'fangs', amniotes have 'canines'. Under either name, this feature is characteristic of early amniotes, as pointed out by Gauthier *et al.*, but not unique to them among early tetrapods; for instance, Dilkes (1990) has shown that Lower Permian trematopsid amphibians have two successive (presumably alternately replacing) caniniform teeth in each maxilla.

8. The interclavicle has a long parasternal process. This feature is characteristic of early amniotes, as pointed out by Gauthier *et al.* (1988), but is not unique to them among early tetrapods; for instance, *Ichthyostega* has a similar, though not as pronounced process (Jarvik 1980), as do some microsaur.

9. The scapulocoracoid possesses two ossification centres, one coracoid and one scapular. This is the earliest known appearance of this character, and in an otherwise very primitive animal. Panchen (*in* Panchen and Smithson 1988) cites this character as a synapomorphy of Seymouriamorpha, Diadectomorpha, and Amniota; it has not been described in Anthracosauroidea nor *Crassigyrinus*.

Characters 1–5 in the above list imply, if we have correctly interpreted polarities, a relationship between *Whatcheeria* and Anthracosauria as a whole. Characters 6–9 imply a relationship of *Whatcheeria* with some clade(s) included within Anthracosauria. *Whatcheeria* is not an anthracosaur, as it lacks the tabular-parietal contact that is usually considered one of that group's diagnostic characters. At the same time, *Whatcheeria* lacks such diagnostic characters of Panchen's Palaeostegalia (= *Crassigyrinus*) as minute forelimbs and a deep cheek below the orbits (cf. Panchen 1985). We suggest, therefore, that *Whatcheeria* be regarded for the present as the first outgroup to Anthracosauria, perhaps with *Crassigyrinus* as the outgroup to (*Whatcheeria* + Anthracosauria), as suggested by Bolt (1990).

Three features of *Whatcheeria* are so unexpected as to merit brief discussion in this preliminary description, even though we are uncertain of their implications.

1. We have found an intercentrum fused to its preceding pleurocentrum, as well as several examples of pleurocentral antimeres that are fused to one another dorsally. Fusion of the intercentrum to the preceding pleurocentra corresponds with Shishkin's (1989) 'anteropleural' pattern, of which he finds examples in a few temnospondyls. Pleurocentral fusion above the notochord but without midventral fusion is, so far as we are aware, not common in any other early

tetrapod, although fusion of pleurocentra only on the dorsal side is known to occur as 'occasional co-ossifications in old specimens' of *Eryops* (Moulton 1974, p. 25) and some other temnospondyls (Shishkin 1989). Even in those few temnospondyls where the pleurocentra are normally annular at some growth stage, available evidence indicates that fusion occurred first ventrally, then dorsally (*Doleserpeton*; Bolt 1969). Among anthracosaurs, as well, fusion of pleurocentra has long been considered to occur first ventrally, then dorsally. This opinion is based mainly on centrum morphology of anthracosauroids, particularly embolomeres. Holmes' (1984) description and discussion of pleurocentra in the embolomere *Proterogyrinus* is typical, and we have no reason to doubt his implied conclusion as to the likely ontogenetic sequence of fusion. If *Whatcheeria* really is related to Anthracosauria as we suggest, then its pattern of pleurocentral fusion is especially surprising. Perhaps, however, it should not be. For all practical purposes, the pleurocentrum is unknown in the other taxa that have been hypothesized to be immediate outgroups to Anthracosauria: the Palaeostegalia (*Crassigyrinus*) and the Loxommatoidea. The primitive condition of the anthracosauroid pleurocentrum is therefore uncertain, and it is not impossible that such a pleurocentrum would resemble that of *Whatcheeria*. However, it seems equally possible that other early tetrapods with 'normal rhachitinous' centra will turn out to have the condition found in *Whatcheeria*, if well-preserved specimens are examined with this in mind. At present, the usual assumption is that vertebrae that look 'rhachitinous' in lateral view will turn out to have unfused pleurocentra. But dorsally fused pleurocentra are not easy to recognize in articulated material, as we have found.

2. About half of the presacral ribs have uncinatiform processes. This is discussed by Bolt *et al.* (1988), and Bolt (1990). Such ribs are derived relative to osteolepiform fishes. Whether or not they are primitive for tetrapods as a whole, *Whatcheeria* provides the best evidence to date that they may have been primitive for anthracosaurs.

3. We have been unable to find a branchial skeleton in *Whatcheeria*, despite careful searching. This would normally be unremarkable, as it could be lost post-mortem even if present in life, which seems likely *a priori*. This is, after all, an animal that is manifestly aquatic based on morphology (e.g. lateral line canals) and circumstances of its occurrence. In the very primitive Devonian *Acanthostega*, moreover, ossified branchial arches are retained, apparently along with gill respiration (Coates and Clack 1991), and ossified branchial arches have been described in a number of temnospondyls.

In the case of *Whatcheeria*, however, we feel reasonably sure that an ossified branchial skeleton of primitive gill-bearing morphology was actually absent: we have not discovered it despite having at our disposal numerous articulated cranial remains, including several nearly complete skulls. Although the apparent absence of ossified branchial arches in *Whatcheeria* is unexpected, there is a parallel: Even the earliest representatives of Anthracosauria do not preserve ossified branchial arches as part of a (possible) gill-arch system. This is true even of aquatic species. Panchen (1970, p. 24) noted that 'no trace[s] of any post-hyoid branchial structures are recorded in anthracosaurs' (= Anthracosauroidea of Text-fig. 10). To the best of our knowledge, this is still the case. Where ossified branchial elements occur in anthracosaurs, it is as part of a hyoid apparatus that is greatly reduced and modified from the primitive condition seen in osteolepiform fish. These observations lead us to two tentative conclusions regarding the ecology and relationships of *Whatcheeria*: first, despite its primitiveness and apparent retention of a postbranchial lamina, *Whatcheeria* did not regain gill respiration; and second, the absence of ossified gill bars might be taken as an additional feature indicating relationship of *Whatcheeria* to anthracosaurs.

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# THE EXPERIMENTAL SILICIFICATION OF MICROORGANISMS

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**ABSTRACT.** A number of samples containing microorganisms was silicified at atmospheric and deep-sea pressures with the aim of studying the process of fossilization using SEM and TEM techniques. The samples included a bacteria-fungi-diatom culture, a bacteria-diatom culture, a microorganism-rich water sample from the interface of south-eastern Atlantic deep-sea sediments, and a microbial mat from the surface of other south-eastern Atlantic deep-sea sediments. Silicification commenced with the impregnation of organic material (e.g. cell walls, cytoplasm) by subelectron-microscope-sized crystallites, and the nucleation of spheres of porous hydrated silica within the mucus (extracellular polymeric substances, EPS) of the groundmass. With increasing silicification time the silica precipitates became more electron dense (due to hydrolysis and polymerization) and larger, forming thicker deposits which resulted in an encrusted mammillated surface on the microbial fossils. Eventually, the microorganisms were completely engulfed by the siliceous deposits. The formation of artefacts during fossilization, such as collapsed, silicified cytoplasm, looking like false nuclei in the bacteria, was common. These experiments were undertaken in order to understand the process of silicification in nature. In particular, with respect to the exceptionally well-preserved, silicified microbial mat communities in uppermost Oligocene to middle Miocene sediments from the south-eastern Atlantic, they demonstrated that both the microorganisms and the polymeric slime in which they lived were mineralized. The degree of mineral impregnation and encrustation is related to the availability of the mineralizing ions. The heavily encrusted microorganisms in each of the upper Oligocene to middle Miocene samples from the south-eastern Atlantic Ocean were thus probably subjected to mineralization for a longer period than weakly impregnated/encrusted microorganisms from the same sample.

**REPORTS** of silicified microbial remains, consisting of coccoid and filamentous carbonaceous structures, are relatively common in Precambrian cherts (e.g. Schopf 1974; Awramik *et al.* 1983; Hofmann and Schopf 1983; Walsh 1992). Palaeoecological interpretations suggest that they represent the remains of microbial communities in shallow marine waters which became embedded in a colloidal silica gel and were thus entombed. Observations of silicified microorganisms in Phanerozoic rocks are, however, less common. Fungi in silicified peat of Devonian and Miocene to Pliocene ages were described by Knoll (1985), and possible cyanophytes in silica nodules of middle Cretaceous age by Carson (1988, as reported in Carson 1991). Rare examples of exceptionally well preserved, silicified deep-sea microbial mats in uppermost Oligocene to middle Miocene diatomaceous sediments from the south-eastern Atlantic Ocean (Text-fig. 1) were described by Monty *et al.* (1991) and Westall (1994). These are, to date, the only report of silicified deep-sea bacteria.

It was the discovery of this interesting biota which stimulated the experiments described in this paper. The biota includes isolated microbial filaments, colonies of microbial filaments and a siliceous coating on almost all substrates. The isolated filaments are of various types, ranging from thin filaments 1–10  $\mu\text{m}$  in length and 0.1–0.6  $\mu\text{m}$  in width (Pl. 1) to short, stubby structures 0.3–2.0  $\mu\text{m}$  in length and 0.1–0.5  $\mu\text{m}$  in width. Morphologically, the filaments are straight, bent or wavy and are attached vertically or horizontally to the substrate. The surface texture of the filaments ranges from smooth to highly mammillated. The filaments are sometimes segmented, represented by hollow crusts (Pl. 1, fig. 2), or completely impregnated (Pl. 2, fig. 2). Other clay-coated oval structures of bacterial size containing a 'core' were observed in section (Pl. 2, fig. 4),

but, at the time the microstructures were first described (Westall 1994), could not be interpreted. Their origin is further discussed below and the results of the research described in this paper are used to aid their interpretation.

A large colony of radiating, silicified filaments measuring 10 by 13  $\mu\text{m}$  was found in the uppermost Oligocene sediments. The individual filaments were up to 3  $\mu\text{m}$  in length and between 0.15–0.20  $\mu\text{m}$  in diameter. They were generally smooth-surfaced although part of the colony presented an encrusted appearance.

Associated with the silicified microbial filaments was a siliceous coating on almost all surfaces, in which the microbial filaments were clearly embedded (Pl. 1). The coating was characterized by a smooth to mammillated surface, the latter consisting of microhemispheroidal structures ranging from 0.2–0.7  $\mu\text{m}$  in diameter. Within this coating were some tiny filamentous structures generally < 0.1  $\mu\text{m}$  in length which, sometimes, formed an interlocking network (Pl. 2, figs 1, 3). It was identified as fossilized biofilm by Westall (1994).

The occurrence of the silicified microbial filaments and biofilm in the south-eastern Atlantic sediments was restricted to the almost pure diatomaceous horizons of the pre-middle Miocene interval of the ODP drillsite Hole 699A (water depth 3617 m). More clayey, intervening horizons did not contain such structures. Furthermore, extensive observation of numerous sediment samples of different ages, lithologies and subsurface depths from the southern Atlantic did not reveal such a characteristic association of fossilized microbial filaments and biofilm.

Westall (1994) interpreted the rare silicification of a deep-sea microbial mat community as being due to unusual environmental conditions prevailing in the Southern Ocean in the early–middle Miocene. At this period a prolonged hiatus of 3.5 My was caused by strong current activity related to the development of the Circum Antarctic Current after the complete separation of Antarctica from South America. The strong currents inhibited sediment deposition which led to the formation of a very well developed manganese nodule pavement at the surface of the sediment (some nodules are still visible in the sediment cores; Ciesielski *et al.* 1988). With the diagenetic dissolution of the biogenic siliceous deposits in the sediment column, there was a build-up of dissolved silica in the pore waters. Flux to the water column above would have been strongly inhibited by the presence of the manganese nodule pavement. The high silica concentrations in the pore waters led to the nucleation of silica on any suitable organic surfaces, such as a bacterium wall or the biofilm coating of a sediment particle (N.B. an SEM study of south-eastern Atlantic surface sediment shows that biofilms and microbial mats are common in the deep-sea environment; Westall 1993).

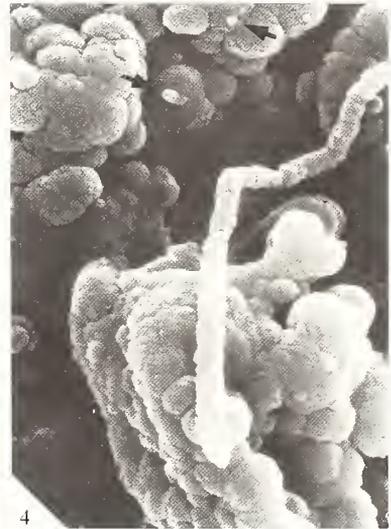
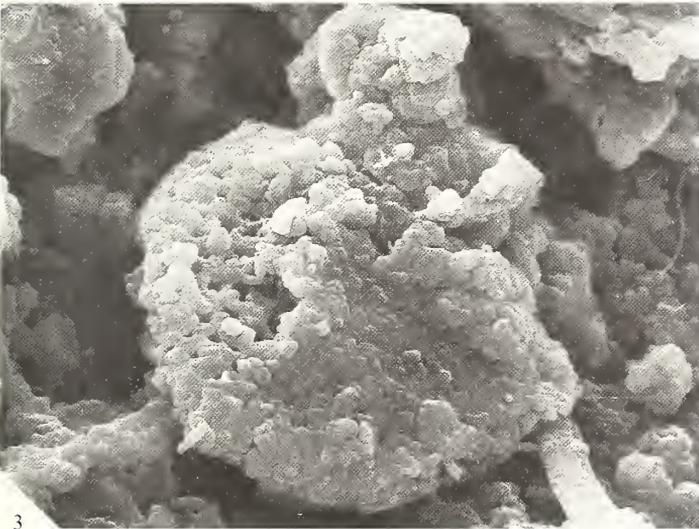
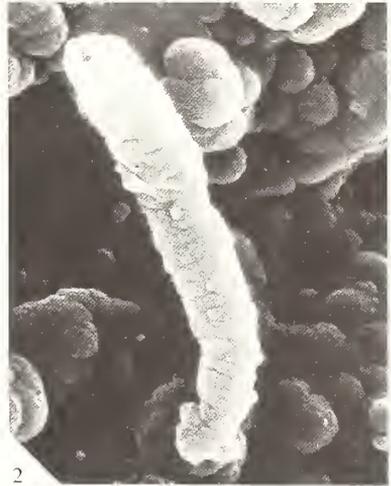
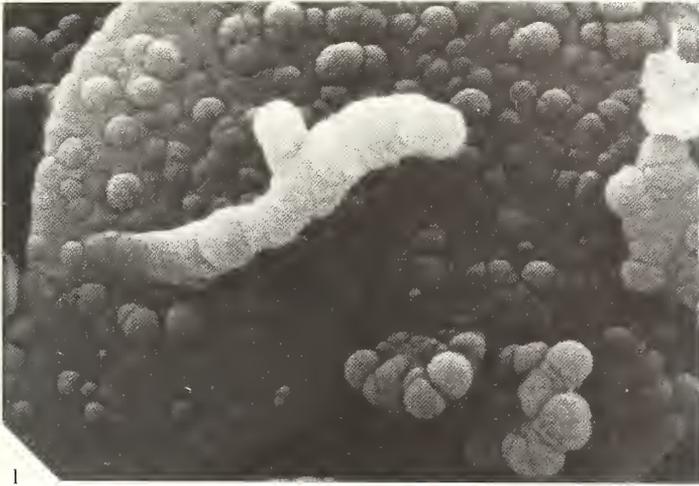
#### PREVIOUS EXPERIMENTAL WORK

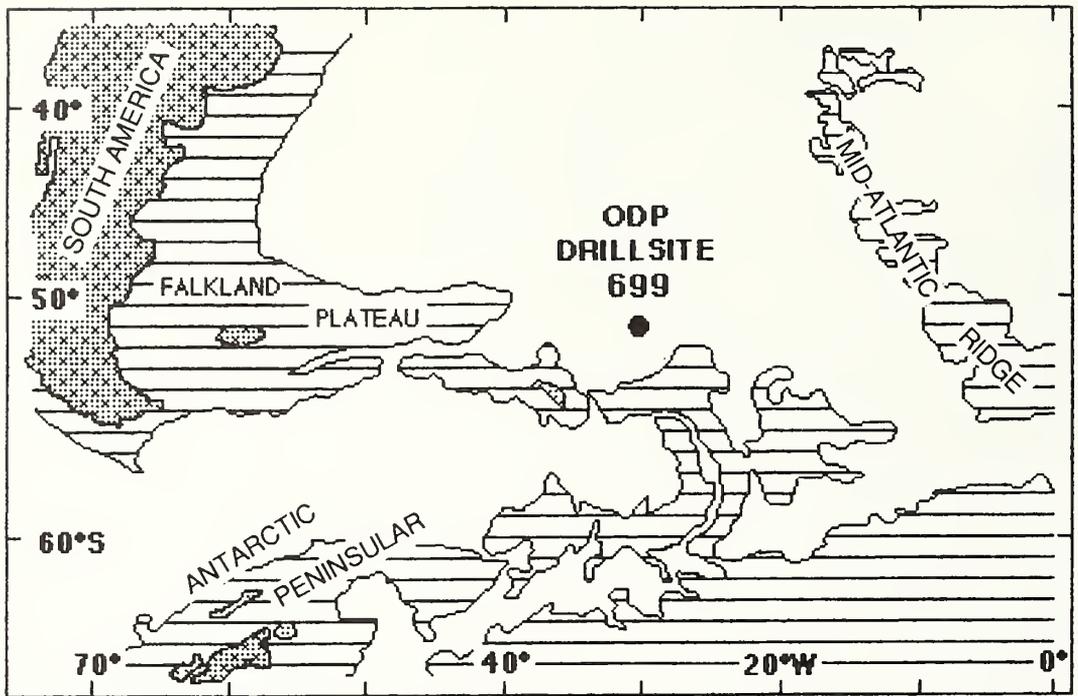
Stimulated by the Precambrian finds, many researchers undertook microbial silicification experiments in order to understand the processes involved (e.g. Oehler and Schopf 1971; Oehler 1976; Walters *et al.* 1977; Francis *et al.* 1978a, 1978b; Ferris *et al.*, 1988). Leo and Barghoorn's (1976) experimental silicification of wood was a major step in this research. These latter authors, as well as Walters *et al.* (1977), Francis *et al.* (1978a, 1978b) and Ferris *et al.* (1988) based their experiments on the impregnation of organic matter by silica. Leo and Barghoorn's (1976) study

#### EXPLANATION OF PLATE I

Figs 1–2, 4, 6. Sample 114-10H-1, 92–94 m (upper Oligocene, SE Atlantic Ocean). 1, silicified filamentous bacterium embedded in silicified mammillated biofilm; note large silica sphere attached to surface of the bacterium;  $\times 15000$ . 2, encrusted hollow filamentous bacterium;  $\times 16500$ . 4, silicified filamentous bacterium; note minute filament heads protruding from silicified biofilm in the background (arrows) and compare with TEM section in Plate 2, figure 1;  $\times 22000$ . 6, small bacterium filament heavily encrusted at one end;  $\times 24000$ .

Figs 3, 5. Sample 114-8H-2, 108–110 m (early-middle Miocene, SE Atlantic Ocean). 3, diatom frustule coated with silicified mammillated biofilm;  $\times 15000$ . 5, small segmented silicified filamentous bacterium;  $\times 22000$ .





TEXT-FIG. 1. Location of the ODP drillsite, Hole 699A, in the south-eastern Atlantic. Depths < 3000 m shaded.

provided a clue as to the processes of silicification in nature: the vehicle for silica impregnation in nature is probably silicic acid in weak solution. The  $\text{Si}(\text{OH})_4$  molecule is small enough to penetrate into organic structures. It becomes attached to functional organic groups, such as the hydroxyl or carboxyl groups of the organic template and, with time and hydrolysis, the hydroxyl or carboxyl bonds are transformed into siloxane bonds. With further hydrolysis and polymerization the material becomes increasingly crystalline. Although bacteria can take up Si, possibly as a replacement for S or P (Heinen 1960; Heinen and Oehler 1979), the experiments of Walters *et al.* (1977) indicate that silicification is a passive process; bacteria simply provide suitable surfaces and surface area for precipitation and mineral nucleation. A summary of the present understanding of the silicification of fossils can be found in Carson (1991).

The earliest silicification experiments were undertaken by Oehler and Schopf (1971) and Oehler (1976), who impregnated microorganisms with silica, and then subjected them to high temperatures (up to 160 °C) and pressures (3000 bars) to simulate the conditions which the Precambrian rocks

#### EXPLANATION OF PLATE 2

Figs 1, 3–4. Sample 114-8H-2, 108–110 m (early–middle Miocene, SE Atlantic Ocean). 1, TEM section through the silicified biofilm coating a diatom frustule (lower part of the photograph); the complex layered construction of the biofilm, penetrated by a minute filament with a clearly tubular internal structure, is clearly observable;  $\times 74000$ . 3, general view of the silicified biofilm coating demonstrating its structured, fibrous, network-like aspect;  $\times 30000$ . 4, two oval bacterium moulds (arrowed), outlined by clay minerals and containing artificial ‘nuclei’;  $\times 52000$ .

Fig. 2. Sample 114-8H-1, 50–52 (early–middle Miocene, SE Atlantic Ocean); section of a bacterium completely permeated by silica attached to a diatom frustule;  $\times 52000$ .



TABLE 1. Samples and methods used in the silicification experiments.

Sample	Origin	Composition	Experi- ment	Conditions			Time
				Pressure (atmospheres)	Tempera- ature (°C)	Light conditions	
1	Culture	Diatoms ( <i>C. fusiformis</i> ) bacteria	2	1	30	Light	2, 4 mo
2	Culture	Diatoms ( <i>C. fusiformis</i> ) bacteria, fungi	1	1	4	Dark	1, 2, 3, 4 w
3	SE Atlantic sediment water interface 5695 m	Bacteria, fungi, yeast diatoms, other	3	500	4	Dark	1, 2, 3, 4 w
			4	500	4	Dark	1, 2, 3, 4 w
4	SE Atlantic microbial mat 3018 m	Bacteria, diatoms, minerals	5	500	4	Dark	1, 3 mo

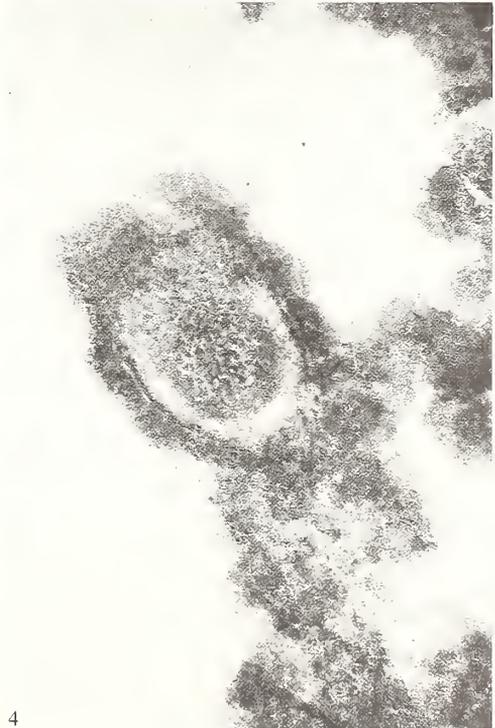
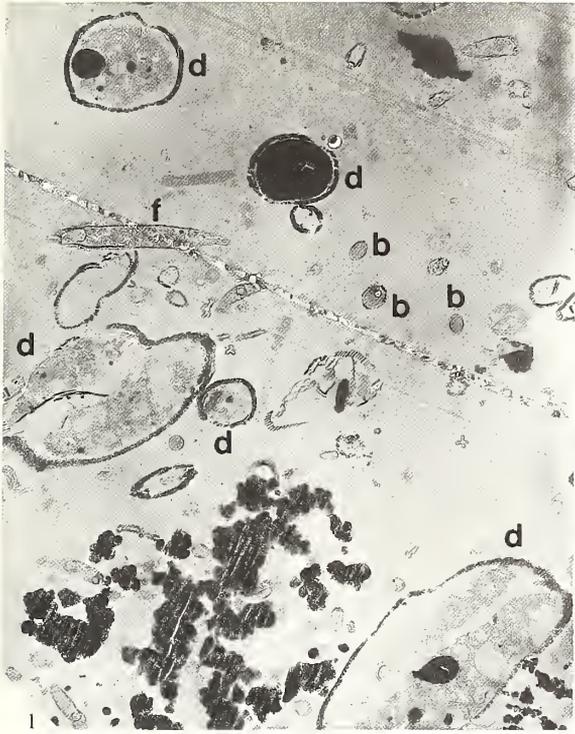
containing the microfossils underwent. Walters *et al.* (1977) and Francis *et al.* (1978*a*, 1978*b*) used an organosilicon solvent and temperatures  $\leq 50$  °C in their experiments, whereas Ferris *et al.* (1988) used a colloidal silica solution at a temperature of 70 °C in order to imitate hydrothermal conditions.

All previous bacteria silicification experiments involved the fossilization of large microorganisms such as cyanobacteria and one spirochete (Oehler and Schopf 1971; Oehler 1976; Walters *et al.* 1977; Francis *et al.* 1978*a*, 1978*b*), although the study of Ferris *et al.* (1988) involved the silicification of the Gram positive *Bacillus subtilis* (Cohn). The rationale for the use of larger bacteria was that these were the kind of organisms identified in petrological thin sections of the Precambrian rocks. Smaller bacteria have, to date, not been identified in these rocks either because of lack of preservation and/or the fact that micrometre and submicrometre-sized structures are almost impossible to observe in thin section.

#### EXPLANATION OF PLATE 3

Figs 1–3. Experiment 1, Sample 2 (1 atmosphere, 1 week). 1, uncontrasted TEM section showing that all diatoms (d), fungi (f) and many bacteria (b) are mineralized; the diatom frustules are more robust and parts of the cytoplasm are replaced by very fine silica (grey areas) or by denser silica (black area or spheres); in the lower part of the photograph there is an aggregate of small porous silica spheres formed in the EPS groundmass;  $\times 4100$ . 2, contrasted TEM section showing a silicified fungal hyphus adjacent to the edge of a diatom frustule; note the finely impregnated cell wall with a thicker accumulation of porous silica at one end; even the cytoplasm has been impregnated with silica; unsilicified bacterium visible, bottom left;  $\times 41000$ . 3, uncontrasted TEM section of a detail of Fig. 1, showing the porous silica spheres engulfing unsilicified bacteria; note silica precipitation on the (unidentified) organic interface at the bottom of the photograph (arrow);  $\times 16500$ .

Fig. 4. Experiment 1, Sample 2 (1 atmosphere, 3 weeks); contrasted TEM section showing silicified Gram negative bacterium, exhibiting the layered wall structure and an artificial 'nucleus', in the process of being engulfed by silica precipitated in the EPS groundmass;  $\times 69000$ .



The research presented in this paper concerns a series of experiments to impregnate and fossilize microorganisms including bacteria, fungi and diatoms. Most of the bacteria silicified were small, in contrast to the majority of the above-mentioned experiments. The process of fossilization was followed in detail using TEM and SEM studies. The first part of this paper concerns the fossilization process at ambient pressures. The second part of the paper deals with fossilization under deep-sea temperature and pressure conditions, the results of which are compared with the fossilized microbial mats of latest Oligocene to middle Miocene age from the south-eastern Atlantic Ocean.

#### MATERIALS AND METHODS

This study is based on experimental fossilizations of a number of different microbial samples.

*Sample 1.* A preliminary experiment to test the chemicals and methods made use of a degrading culture of the marine diatom *Cylindrotheca fusiformis* (Rabenhorst) containing numerous bacteria (cocci, bacilli, very common spirochetes and, rarely, cyanophytes). A degrading diatom culture was chosen because the silicified bacteria from Oligocene to Miocene sediments in the south-eastern Atlantic occurred in almost pure diatomaceous sediments.

*Sample 2.* Another experiment used a similar degrading culture of the same diatom, *Cylindrotheca fusiformis*, which also contained fungi as well as bacteria.

*Sample 3.* A third sample consisted of deep-sea microorganisms from water immediately above the sediment interface at 5695 m water depth from the south-eastern Atlantic (very close to ODP Hole 699A in which the Oligocene–Miocene silicified bacteria were found). The microorganisms at the sediment surface beneath this sample, identified in the laboratory, included Gram positive and Gram negative bacilli, Gram positive cocci, cyanobacteria, fungi (*Phialophora malorum* (Medlar) was identified from a nearby sample), yeast (*Cryptococcus albidus* (Saito) Skinner) and degraded diatom frustules (Westall 1993). Some mineral particles, such as clays attached to the surfaces of bacteria, also occurred in the sample. Bacteria cell counts in the water sample were  $46 \times 10^6$  cells/cc<sup>3</sup> (Westall 1993).

*Sample 4.* The fourth sample was a microbial mat from the surface of deep-sea diatomaceous sediments in the south-eastern Atlantic at 3018 m water depth. Bacteria within the well-developed mat were abundant ( $24 \times 10^6$  cells/g sediment) and included the genera *Acinetobacter* (Brison and Prévot), *Neisseria* (Trevisan), *Streptococcus* (Rosenbach) and *Micrococcus* (Cohn) (Westall 1993). Interestingly, the bacteria in this sample were rarely visible with the SEM because they tended to be hidden by a coat of adsorbed clay minerals or within the aureolae of the diatom frustules (Pl. 12, figs 3–4).

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#### EXPLANATION OF PLATE 4

Figs 1–2. Experiment 1, Sample 2 (1 atmosphere, 1 week). 1, fungal hyphae coated by a biofilm of EPS which also contains fine granules of precipitated silica (granular white areas);  $\times 1400$ . 2, mammillated silica deposit coated by fibrous EPS, with larger silica sphere attached;  $\times 9000$ . 3, detail showing unsilicified spirochetes and seemingly unsilicified bacilli within a fibrous EPS groundmass containing finely granular silica and some small isolated silica spheres (arrow);  $\times 9000$ .

Figs 4–5. Experiment 1, Sample 2 (1 atmosphere, 3 weeks). 4, mammillated silica deposit engulfing a seemingly unsilicified fungal hyphus (arrow);  $\times 1800$ . 5, encrusted hyphae showing hollow internal structure; bacterium in the upper part of the photograph has a slightly rugged, mineralized aspect;  $\times 20000$ .



The nomenclature of the samples from the ODP drillsite Hole 699A in the south-eastern Atlantic, illustrated in Plates 1 and 2, follows from the ODP standard as noted in Ciesielski *et al.* (1988). As an example, Sample 144-699A-10H-1, 92-94: 114 – ODP leg; 699 – drillsite; A – hole; 10H – core (each core is 9.7 m long); 1 – core section (each section is 1 m long); 92-94 – sample depth in cm within each section.

For the silicification of these samples the method of Francis *et al.* (1978a) was used in a modified form. Two series of parallel experiments were undertaken; one at atmospheric pressures, either in the dark at 4 °C (Sample 2) or in the light at 25 °C (Sample 1). The second run involved fossilization at pressures of 500 atmospheres (corresponding with a water depth of 5000 m) and temperatures of 4 °C to imitate average conditions in the deep-sea region of the south-eastern Atlantic. This experiment was undertaken in order to fossilize samples of deep-sea microorganisms, taken from depths of 3700–5600 m, to try to obtain structures similar to those found in ODP Hole 699A (Samples 2, 3 and 4). The samples and experimental procedures used are listed in Table 1.

For the experiments, the excess water in the cultures was removed by centrifugation and the samples were then mixed with TEOS (Francis *et al.* (1978a) noted that a certain amount of water in the sample aided silicification). Each sample, after its respective fossilization time, was centrifuged to remove the TEOS, rinsed with a phosphate buffer and fixed with 2.5 per cent. glutaraldehyde solution in a phosphate buffer for a few days. For electron microscope studies, the samples were rinsed three times with phosphate buffer and post-fixed with 1 per cent. osmium tetroxide overnight and again rinsed three times with phosphate buffer. For the transmission microscope the samples were included in agar and cut into 1 mm cubes for ease of handling. Dehydration using first distilled water and alcohol, then alcohol and propylene oxide was made in percentage steps of 10, 30, 50, 70, 90, 100, 100, 100. The dehydrated samples were impregnated with and, finally, included in Epon resin. Ultrathin sections were made with a diamond blade mounted on a microtome and were contrasted with uranyl acetate and lead citrate. Observations were made with a Zeiss 109 transmission electron microscope. For SEM studies the samples were dehydrated with alcohol and critical-point dried. They were then mounted on brass stubs using silver paint, coated with Au/Pd and observed with a JSM JEOL 5400. Details of sample storage are to be found in the Appendix.

## RESULTS

### *Experiment 1. Sample 2, one to four weeks at 1 atmosphere*

After only one week in TEOS (at 4 °C in the dark) silica precipitation in the sample was quite pronounced (Pl. 3, fig. 1). However, many bacteria seemed to remain unsilicified (Pl. 3, fig. 3), as did much mucus or biofilm (extracellular polymeric substances, EPS, including the degradation products of the microorganisms). The EPS, when observed with the SEM, presented a relatively 'normal' fibrous-web appearance (Pl. 4, figs 1–3) (the term 'normal' is used because EPS in natural sediments prepared for SEM observation often has a fibrous morphology; Westall and Rincé 1994). Some unmineralized bacteria were engulfed by neoformed siliceous masses (Pl. 3, fig. 3).

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### EXPLANATION OF PLATE 5

Figs 1–3. Experiment 1, Sample 2 (1 atmosphere, 2 weeks). 1, uncontrasted TEM section showing details of the silicification of the cytoplasm within a diatom and the thickened frustule wall;  $\times 16500$ . 2, uncontrasted TEM section showing details of a silicified bacterium; note finely reticulate pattern of the silica and the outline of an artificial 'nucleus';  $\times 69000$ . 3, uncontrasted TEM section showing silicified diatom chloroplast in the EPS groundmass; siliceous deposits are larger than in the 1-week old sample and more electron-dense;  $\times 10000$ .

Fig. 4. Experiment 1, Sample 2 (1 atmosphere, 4 weeks); uncontrasted TEM section showing the transformation of silica around a bacterium into small but well-defined spherical structures which form stringers of spheres projecting around the crust;  $\times 69000$ .

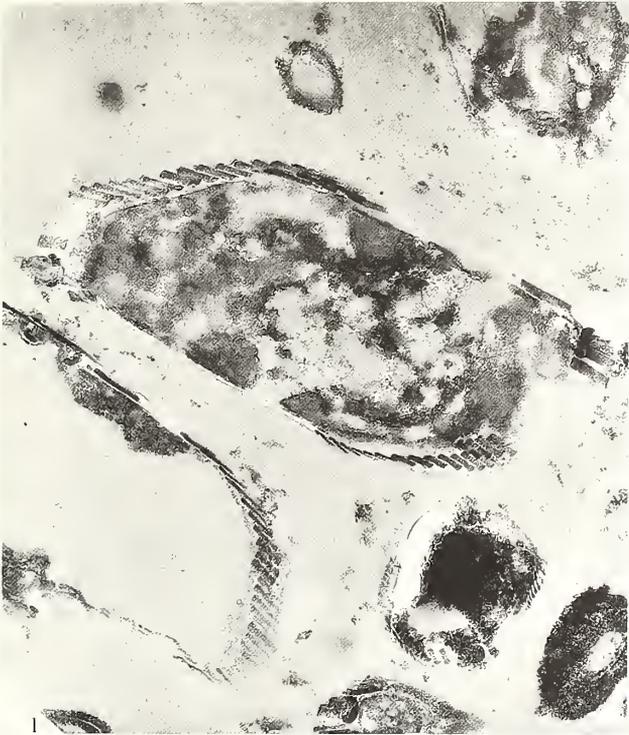


TABLE 2. Results of Experiment 1.

Sample	Pressure (atmospheres)	Time (weeks)	Organic matter preservation	Organic matter mineralized				Mineralization of	
				Bact.	Fungi	Diatoms	EPS	Cell wall	Cytoplasm
2	1	1	Generally very degraded. Many unmineralized cells and EPS. Much unidentified organic matter in the groundmass	Y	Y	Y	Y	Bacteria and fungi partly and completely encrusted. Diatoms encrusted	In diatoms, fungi and bacteria
2	1	2	Most organic matter mineralized. Unidentified organic matter in the groundmass	Y	Y	Y	Y (n.b. much still unmineralized)	Bacteria Fungi Diatoms	Bacteria Fungi Diatoms
2	1	3	Some unmineralized spirochetes. Less unmineralized EPS	Y	Y	Y	Y (including degraded remains of microorgs)	As above	As above
2	1	4	Some degraded, unmineralized bacteria	Y	Y	Y	Y	As above	As above

TABLE 3. Results of Experiment 2.

Sample	Pressure (atmospheres)	Time (months)	Organic matter preservation	Organic matter mineralized			Mineralization of	
				Bacteria	Diatoms	EPS	Cell wall	Cytoplasm
1	1	2	Some unmineralized bacteria and EPS	Y	Y	Y	Fused crust Small silica spheres	Bacteria Diatoms
1	1	4	Rare unmineralized Gram negative bacteria All EPS mineralized	Y	Y	Y	Thick crusts	Not all bact. cytoplasm mineralized Diatoms

Silicification was manifested by the presence of spherical deposits of silica in the groundmass as well as the presence of silicified microorganisms (Pl. 3, fig. 1). The latter were distinguishable from the unsilicified microorganisms in uncontrasted TEM sections because they presented electron dense walls and/or were filled by casts of silica (Pl. 3, figs 1–2); in uncontrasted TEM sections microorganisms without a mineral skeleton, such as bacteria and fungi, are normally poorly defined (Pl. 3, fig. 3). The walls and cytoplasm of the silicified microorganisms seemed to be impregnated by finely crystalline amorphous silica having a porous granular texture (Pl. 3, figs 1–2). Further porous silica, sometimes in the form of  $< 0.2 \mu\text{m}$  spheres, nucleated onto the already permineralized surfaces producing an irregular surface 20–150 nm in thickness (Pl. 3, fig. 2). Silica nucleation on the diatom frustules resulted in a more robust appearance (Pl. 3, fig. 1) (it should be noted that the diatom species *C. fusiformis* is naturally lightly mineralized). In some instances, silica precipitated

TABLE 2 (*cont.*)

Silica precipitation						
Dissem.	Small spheres	Large spheres	Irregular mass	Other	Artefacts	Comments
Y	Y			Unmineralized bacteria trapped in silica deposit	N	Two forms of silica: more dense and less dense (TEM)
Y	Slightly larger		Y	Unmineralized bacteria and fungi trapped in silica	Silica cores from collapsed cytoplasm—look like 'nuclei'	Two forms of silica as above Silica around bacteria exhibits a finely reticulate pattern
Y	Y	Y			False 'nuclei'	Silica mineralizing the cytoplasm is mostly granular: some denser patches in diatoms and fungi
Less	Forming denser silica	Y		Formed of small, coalesced spheres	False 'nuclei' Stringers	

TABLE 3 (*cont.*)

Silica precipitation						
Dissem.	Small spheres	Large spheres	Irregular mass	Artefacts	Comments	
Y	Y	Rare		False nuclei, some with organic coat. Stringers	Silica spheres coated with a monolayer of organic molecules. Reticulate pattern of silica in crust around bacteria	
N	Rare	Y		False nuclei	Thicker crusts 'Clean' aspect of mineralized culture	

within an organism, either as small spheres 0.5–2  $\mu\text{m}$  in diameter (perhaps replacing vacuoles?) or completely filling the cell as an internal cast (Pl. 3, fig. 1). Silica also precipitated on unidentified organic surfaces or interfaces in the groundmass (Pl. 3, fig. 3).

The silica precipitates within the abundant EPS of the groundmass formed loose aggregates of porous spheres ranging from 0.15–0.36  $\mu\text{m}$  in diameter. Some aggregates, however, were formed of larger, fused, electron-dense silica spheres (0.5  $\mu\text{m}$  diameter) with a botryoidal surface (Pl. 3, figs 1, 3; Pl. 4, fig. 2).

Continued degradation of the microorganisms led to an initial increase of organic matter making up the EPS (Pl. 5, fig. 3). However, the organic matter was generally rapidly silicified; already by the second week in TEOS most of the microorganism cells were mineralized but, in the eukaryotes especially, they often exhibited patchy mineralization of the cytoplasm, as if certain organelles

(perhaps the nuclear material) were more easily mineralized than others (Pl. 5, fig. 1). Some silicified diatom organelles, such as chloroplast, were readily recognizable in the groundmass (Pl. 5, fig. 3). The siliceous crust replacing degraded bacteria in some instances exhibited a finely reticulate pattern which obliterated the organic cell wall (Pl. 5, fig. 2). In other cases, the mineralization of the triple-layer wall structure of a Gram negative bacterium was still preserved after three weeks in TEOS (Pl. 3, fig. 4). A few, rare, unsilicified bacteria (generally Gram negative forms) were still observed in the four-week old sample. The TEM sections of the latter sample gave the impression that there was very little EPS but the SEM studies showed that it had simply migrated out of the silicified masses to form a smooth film on the surfaces of the botryoidal deposits (Pl. 8, fig. 1), as opposed to the fibrous web observed at the start of the experiment (Pl. 4, fig. 1).

General indications of increasing silicification with time include the thickening of the siliceous crust around the microorganisms (up to  $0.6\ \mu\text{m}$ ) and increasing crystallization of the silica manifested by: (a) its less porous and more electron dense aspect; (b) an increase in the size of the denser silica spheres (up to  $50\ \mu\text{m}$ ); (c) a decrease in the amount of loosely aggregated siliceous spheres and a corresponding increase in the denser spherical aggregates; and (d) an increase in the size of the silica crystallites nucleating on to the surface of the fossilized microorganisms.

Generally, in the SEM micrographs of the early stages of fossilization the surfaces of the microorganisms, especially the bacteria, looked quite smooth (Pl. 4, figs 1, 3), except for some 10–20 nm sized silica crystallites attached to them, and appeared to be, at least superficially, 'unfossilized'. However, where, for instance, a fungus was broken, it was possible to see that the outer wall was simply a crust (Pl. 4, fig. 5). This underlines the importance of parallel TEM studies which document in more detail the state of fossilization of the microorganisms. The increase in size with time of the crystallites attached to the surface of the fossilized cell walls gave the walls of the microorganisms in the older samples a more rugged, crusty 'fossilized' appearance (Pl. 4, fig. 5). In the TEM sections, the silica forming the crusts around the microorganisms in the older samples consisted of coalesced spheres of silica (60–100 nm) rather than amorphous porous silica (compare Pl. 5, fig. 4 with Pl. 3, fig. 2). In the four-week old sample, stringers of these spheres attached to the outside of the silica crust were common (Pl. 5, fig. 4). They seem to represent artefacts. Another artefact of the silicification process, already apparent in the two-week old sample, was the appearance of cores in the silicified bacteria, formed by the silicification of the collapsed cytoplasm (Pl. 3, fig. 4; Pl. 5, fig. 2). These cores in a fossilized cell could be mistaken for a 'nucleus', which does not exist in prokaryotes.

Lastly, the engulfing of the microorganisms (generally silicified) by the botryoidal aggregates of silica in the groundmass (Pl. 3, fig. 4; Pl. 4, fig. 4) becomes more common with the duration of the silicification process.

The results of Experiment 1 are summarized in Table 2.

#### EXPLANATION OF PLATE 6

Figs 1–4. Experiment 2, Sample 1 (1 atmosphere, 2 months). 1, contrasted TEM section showing a bacterium wall outlined by silica spheres and stringers of spheres radiating from both sides of the wall; faint residues of the reticulate amorphous silica may still be seen (bottom right); a larger silica sphere has started to grow on the crust, left (compare with Pl. 1, figs. 1–3 and Pl. 10, fig. 2); silicified membrane structure around artificial 'nucleus' is clearly visible; remains of organic matter can be seen in the very thin dark outlines of the individual silica spheres (compare with the uncontrasted section in Fig. 2) and as a dark line around the artificial 'nucleus';  $\times 67000$ . 2, uncontrasted TEM section of two encrusted bacteria; the silica around the cell walls has fused but the outer edges are lined with small silica spheres and stringers of silica; the internal part of the cells has been completely replaced by partly fused porous silica spheres;  $\times 67000$ . 3, contrasted TEM section of a bacterium cast retaining the structure of its inclusions; the diatom frustule adjacent is lined with small silica spheres;  $\times 67000$ . 4, contrasted TEM section of an encrusted bacterium wall in which remnants of the organic wall are still visible; note the mass of silica spheres in the background, outlined by fine web-like EPS fibrils;  $\times 67000$ .



1



2



3



4

TABLE 4. Bacteria cell size changes in Experiment 2 (vol.  $\mu\text{m}^3$ ).

	Small bacteria	Large bacteria	Average
Control	0.04	0.37	0.11
2-month	0.04	0.12	0.05
4-months	0.06	0.39	0.25

*Experiment 2. Sample 1, two to four months at 1 atmosphere*

Details of the results of this experiment are listed in Table 3. The silicification phenomena already noted in the previous experiment were further developed after two and four months in TEOS. At the end of the experiment very few bacteria remained unmineralized; only Gram negative cocci and spirochetes continued to resist mineralization (Pl. 7, figs 1–2) and some bacteria were only partly mineralized, even after four months, by spheres or half-moon-shaped silica deposits around the walls (Pl. 7, fig. 2).

The walls of the microorganisms were mineralized by small silica spheres, 20–300 nm in diameter, or fused crusts or casts in the two month sample (Pls 6–7), in strong contrast with the porous granular silica mineralizing the microorganisms in the early weeks of fossilization. Inclusions in the original bacteria (formerly gas or liquid?) were also preserved in casts (Pl. 6, fig. 3). Cores of silicified, collapsed cytoplasm were still common in the bacteria of the two month sample and, in some instances, were coated with an organic layer, thus increasing the (false) nuclear appearance (Pl. 6, fig. 1). Stringers of silica spheres radiating out from the silicified cell wall were also common (Pl. 6, fig. 4).

Organic-coated silica spheres continued to nucleate in the web-like EPS groundmass (Pl. 6, fig. 3), but, after four months, these disappeared and the many tiny spheres coalesced to form fewer, larger organic-coated spheres (Pl. 7, fig. 1). After four months the silica spheres mineralizing the walls of the bacteria coalesced into thicker, electron-dense crusts with a mammillated external surface (Pl. 7). However, electron diffraction of the initial sample and the two and four month old samples did not demonstrate any increase in crystallinity; the silica was, crystallographically speaking, as amorphous after four months as at the start of the experiment.

A general increase in the cell sizes of the mineralized bacteria with time was noted (Table 4), although the average cell volume of the larger bacteria actually seemed to decrease in the two month sample. Francis *et al.* (1978a, 1978b) found that fossilized spirochetes increased in volume whereas cyanobacteria decreased in size upon silicification.

*Experiment 3. Sample 2, one to four weeks, 500 atmospheres*

The results of this experiment are presented in Table 5. At 500 atmospheres and 4 °C (corresponding to general deep-sea conditions at a water depth of 5000 m in the south-eastern Atlantic) the rate of

EXPLANATION OF PLATE 7

Figs 1–3. Experiment 2, Sample 1 (1 atmosphere, 4 months). 1, contrasted TEM section showing heavy mineralization of the diatoms with silica deposition inside the cell walls, forming an almost solid structure; silica spheres around the microorganism fossils are larger and more electron-dense; some bacteria are still unfossilized but, on a few, silica spheres are starting to grow (arrows); note the generally clean appearance of the sample due to the disappearance of the many, small, isolated silica spheres in the groundmass;  $\times 22000$ . 2, contrasted TEM section showing half-moon-shaped silica spheres which have grown around a bacterium such that the bases of the spheres are contiguous with the curvature of the cell; unfossilized spirochete upper right;  $\times 60000$ . 3, uncontrasted TEM section showing a crust formed around a bacterium;  $\times 93000$ .

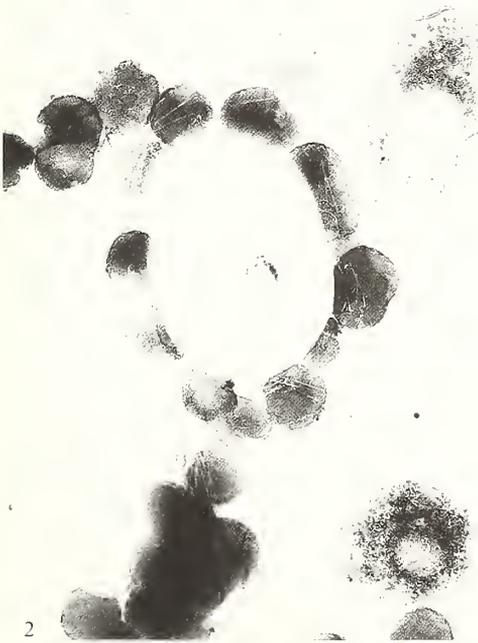
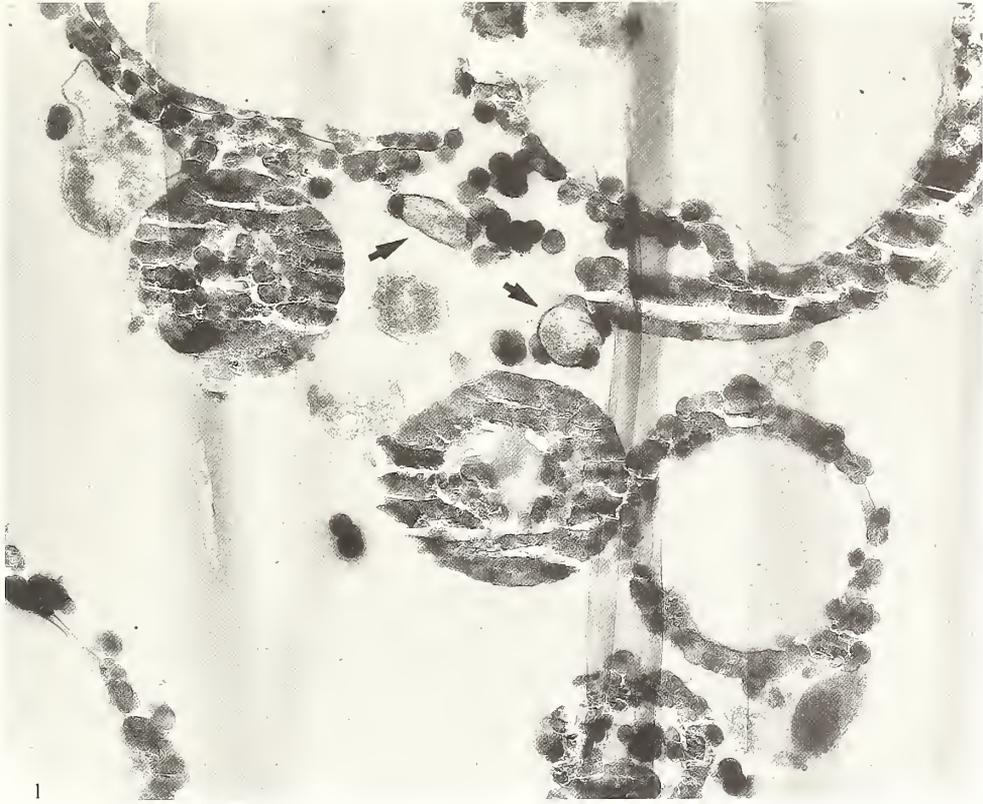


TABLE 5. Results of Experiment 3.

Sample	Pressure (atmospheres)	Time (weeks)	Organic matter preservation	Organic matter mineralized				Mineralization of	
				Bact.	Fungi	Diatoms	EPS	Cell wall	Cytoplasm
2	500	1	Little loose EPS Some unmineralized bacteria.	Y	Y	Y	Y	Not all bacteria or fungi walls mineralized	Not all diatom cytoplasm mineralized
2	500	2	As above	Y	Y	Y	Y	Crusts around bacteria and fungi	Bacteria Fungi Diatoms
2	500	3	Still some unmineralized bacteria	Y	Y	Y	Y	All organisms	All organisms
2	500	4	Everything mineralized	Y	Y	Y	Y	All	All

TABLE 6. Results of Experiment 4.

Sample	Pressure (atmospheres)	Time (weeks)	Organic matter preservation	Organic matter mineralized					Mineralization of	
				Bact.	Fungi	Diatoms	EPS	Other	Cell wall	Cytoplasm
3	500	1	Little unmineralized EPS. Few unmineralized bacteria.	Y	Y	Y	Y	Cyano-bacteria	Almost all bacteria occur as crusts. Thick mineralized glycolalyxes	Mineralized where still present
3	500	2	Still some cell walls unmineralized	Y				Cyano-bacteria	Crusts, clay moulds, glycolalyx	As above
3	500	3	As above	Y					Moulds of bacteria	As above
3	500	4	Large number of unmineralized but degraded bacteria. Some degraded remnants of EPS?	Y	Y	Y	?	?	Eukaryotes	Eukaryotes

silicification of the organic structures was greatly increased, the one week-old sample exhibiting many of the same silicification manifestations as the four week-old, 1 atmosphere sample. There were few unmineralized bacteria and little unmineralized EPS in the groundmass of the TEM sections (Pl. 9, fig. 1), although in the SEM preparations EPS was visible and still had a fibrous

TABLE 5 (*cont.*)

Silica precipitation						
Dissem.	Small spheres	Large spheres	Irregular mass	Other	Artefacts	Comments
Y	Y	Y	Mineralized organisms engulfed by silica sphere mass	Silica crystal?	False nucleus	Bacteria mostly have a granular crust. Diatom cytoplasm already mineralized with dense silica as well as finely granular material
Less		Y	Containing spheres and more dense material		False nucleus Stringers	No small spheres seen
Not much		Y	Bacteria included in irregular mass		Organelles in diatoms. False nuclei Stringers	Not much disseminated silica. Mineralized bacteria starting to lose their identity in the irregular mass. Unmineralized bacteria enclosed in silica mass
Little		Y	Y		Organelles in diatoms and fungi. Stringers on diatoms. Oval, semi-rectangular in groundmass	Bacteria almost disappeared in crystalline silica. Silica mineralizing some fungi has a distinct lattice structure

TABLE 6 (*cont.*)

Silica precipitation					
Dissem.	Small spheres	Large spheres	Irregular mass	Artefacts	Comments
Y	Y	Y	Y	False nuclei	Mineralized thick glycocalyxes around voids (i.e. moulds)
Y					Microorganisms, including bacteria in clay nests are enclosed in large expanses of finely granular to dense silica
			Y	False nuclei	As above
Y	Y		Y		Many bacteria walls remaining in degraded form but other bacteria engulfed by silica have lost their form

aspect (Pl. 8, fig. 2). Over the four week period of the experiment some bacteria were still unmineralized after three weeks but, by four weeks, all microorganisms were engulfed by botryoidal silica deposits and individual silicified bacteria could no longer be distinguished from the engulfing mass (Pl. 9, fig. 2; Pl. 10, fig. 4).



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2	500	2	As above	Y	Y	Y	Y	Crusts around bacteria and fungi	Bacteria Fungi Diatoms
2	500	3	Still some unmineralized bacteria	Y	Y	Y	Y	All organisms	All organisms
2	500	4	Everything mineralized	Y	Y	Y	Y	All	All

TABLE 6. Results of Experiment 4

Sample	Pressure (atmospheres)	Time (weeks)	Organic matter preservation	Organic matter mineralized					Mineralization of	
				Bact	Fungi	Diatoms	EPS	Other	Cell wall	Cytoplasm
3	500	1	Little unmineralized EPS. Few unmineralized bacteria	Y	Y	Y	Y	Cyano-bacteria	Almost all bacteria occur as crusts Thick mineralized glyeocalyxes	Mineralized where still present
3	500	2	Still some cell walls unmineralized	Y				Cyano-bacteria	Crusts, clay moulds, glyeocalyx	As above
3	500	3	As above	Y					Moulds of bacteria	As above
3	500	4	Large number of unmineralized but degraded bacteria Some degraded remnants of EPS?	Y	Y	Y	?	?	Lukaryotes	Eukaryotes

silicification of the organic structures was greatly increased, the one week-old sample exhibiting many of the same silicification manifestations as the four week-old, 1 atmosphere sample. There were few unmineralized bacteria and little unmineralized EPS in the groundmass of the TEM sections (Pl. 9, fig. 1), although in the SEM preparations EPS was visible and still had a fibrous

TABLE 5 (cont.)

Dissem	Silica precipitation				Artifacts	Comments
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Less		Y	Containing spheres and more dense material		False nucleus Stringers	No small spheres seen
Not much		Y	Bacteria included in irregular mass		Organelles in diatoms False nuclei Stringers	Not much disseminated silica. Mineralized bacteria starting to lose their identity in the irregular mass. Unmineralized bacteria enclosed in silica mass.
Little		Y	Y		Organelles in diatoms and fungi Stringers on diatoms Oval, semi-rectangular in groundmass	Bacteria almost disappeared in crystalline silica. Silica mineralizing some fungi has a distinct lattice structure.

TABLE 6 (cont.)

Dissem	Silica precipitation				Artifacts	Comments
	Small spheres	Large spheres	Irregular mass	Other		
Y	Y	Y	Y		False nuclei	Mineralized thick glyeocalyxes around voids (i.e. moulds)
Y						Microorganisms, including bacteria in clay nests are enclosed in large expanses of finely granular to dense silica.
Y			Y		False nuclei	As above
Y	Y		Y			Many bacteria walls remaining in degraded form but other bacteria engulfed by silica have lost their form.

aspect (Pl. 8, fig. 2). Over the four week period of the experiment some bacteria were still unmineralized after three weeks but, by four weeks, all microorganisms were engulfed by botryoidal silica deposits and individual silicified bacteria could no longer be distinguished from the engulfing mass (Pl. 9, fig. 2; Pl. 10, fig. 4).

TABLE 7. Results of Experiment 5.

Sample	Pressure (atmospheres)	Time (months)	Organic matter preservation	Organic matter mineralized			Mineralization of	
				Bact.	Diatoms	EPS	Cell wall	Cytoplasm
4	500	0	Many bacteria either well preserved or already partially degraded. Occurs in diatom aureolae and clay nests. Much EPS: fibrous or partly reticulate. Some EPS on mineral surfaces.					
4	500	1	None observed	Y		Y	Bacteria almost totally disappeared	
4	500	3	None observed	Y		Y		

Initially, most of the bacteria had a 'fresh', smooth appearance when viewed with the SEM, testifying to the fineness of the permeating silica. However, by three weeks many individuals showed visible evidence of fossilization, appearing as broken crusts (Pl. 8, fig. 3) or with large silica spheres attached to their encrusted surfaces (similar to the upper Oligocene to middle Miocene bacteria from the south-eastern Atlantic: compare Pl. 10, fig. 2 with Monty *et al.*, 1991, pl. 4, fig. 4). An increase in the electron density of the mineralizing silica with time was evident (compare Pl. 9, fig. 1 with Pl. 9, fig. 2).

As in the atmospheric fossilization run, with increasing time during the experiment, there was a gradual expulsion of organic matter from within the mineralizing microorganisms and the EPS changed in morphology from being finely fibrous to becoming smooth and stringy (compare Pl. 8, fig. 2 with Pl. 10, fig. 4).

Artefacts appearing within the first week of this experiment included the frequent mineralization of collapsed cytoplasm in bacteria, giving the impression of a false nucleus; stringers of silica spheres appeared around the mineralized cells by the second week. Other types of artefacts occurred in the three and four week samples, for example, regularly-shaped 'tear-drop' structures in the diatoms (Pl. 9, fig. 3) and other more irregular structures within the diatom frustules and in the groundmass (Pl. 11, fig. 1).

#### *Experiment 4. Sample 3, one to four weeks, 500 atmospheres*

This experiment concerned the fossilization of natural deep-sea microorganisms under deep-sea pressure and temperature conditions (Table 6). The organic material was rapidly mineralized although remnants of some unmineralized bacterial walls could still be observed in the three week sample. Bacteria with a thick glycocalyx were particularly susceptible to mineralization with the fossilized glycocalyx reaching 0.2–0.8  $\mu\text{m}$  thickness (Pl. 11, fig. 3). Sometimes only the mineralized glycocalyx or cell wall remained, leaving the inner part of the cell hollow or containing false 'nuclei' (Pl. 11, fig. 4). Where the cytoplasm had not collapsed and had been permineralized, the original inclusions were still visible (Pl. 11, fig. 2). Mineralized Gram negative bacteria, enclosed within the fine grained siliceous deposit, were invariably surrounded by an empty halo, thus creating a cast. However, Gram positive forms were enclosed by an outer crust of silica which was more finely textured than the silica replacing the cytoplasm or that engulfing the microorganisms (Pl. 11, fig. 2).

TABLE 7 (cont.)

Silica precipitation					
Dissem.	Small spheres	Large spheres	Irregular mass	Artefacts	Comments
Y		Y	Y	Spheres with crusts False nuclei	Irregular mass is granular and dense
Y			Y	Full spheres	

In sedimentary environments containing clay minerals, bacteria or colonies of bacteria are invariably coated by clays (Westall and Rincé 1994). Upon degradation of the microorganisms the clay coatings retain their shape but are empty. A number of these empty clay housings were observed embedded within the siliceous precipitate (Pl. 11, fig. 4).

An important observation in the one, two and three week samples was the vast amount of silica precipitated in the groundmass, as disseminated porous granules or as a granular porous mass (Pl. 11, figs 2, 4), or as botryoidal-surfaced electron denser masses, all enclosing the abundant microorganisms. In many cases the engulfed, degraded bacteria were barely recognizable and the SEM study showed that the samples consisted of aggregates of silica spheres coated with fibrous, stringy EPS.

The four week sample seemed to have reacted differently to the TEOS, compared with the other samples. Instead of a few moulds and casts enclosed within a fine-grained porous silica deposit, the sample consisted of large numbers of degraded but apparently unmineralized Gram negative cell walls, as well as unidentifiable, unmineralized organic matter in the groundmass (Pl. 12, fig. 2). Silica spheres formed both on cell walls and within the cells in some of the microorganisms. Botryoidal-surfaced masses as well as irregular masses of disseminated silica granules occurred in the groundmass. On the other hand, eukaryote microorganisms in the sample, such as fungi, did present mineralized cell walls and cytoplasm.

#### *Experiment 5. Sample 4, one to three months, 500 atmospheres*

The deep-sea microbial mat sample (Sample 2285) consisted of a well-developed layer of EPS coating the surface of the diatomaceous sediment and embedding particles within it. Beneath the thick cohesive EPS surface coating, the particles were interlinked and bound together by a fibrillar EPS network. The EPS film was surficial and at a depth of 5 mm in the sediment only a few rare fibrils remained. Although bacteria cells were not observed with the SEM, the epifluorescence counts and TEM studies showed that they were abundant ( $24 \times 10^6$  cells/gm sediment; Westall 1993). They generally occurred coated with clay or within the aureolae of corroded diatom frustules (Pl. 12, figs 3–4).

This particular sample was subjected to long-term fossilization in TEOS under 500 atmosphere pressure. After one month, no organic matter could be distinguished with the TEM; the SEM studies showed that the degraded and denatured organic matter coated the exterior of granular-



TABLE 7. Results of Experiment 5.

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4	500	3	None observed	Y	Y		

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This particular sample was subjected to long-term fossilization in TEOS under 500 atmosphere pressure. After one month, no organic matter could be distinguished with the TEM; the SEM studies showed that the degraded and denatured organic matter coated the exterior of granular-

surfaced aggregates of silica spheres. The silica precipitate formed large expanses of porous granular material which engulfed mineral particles and diatom frustules. The diatom frustules were distinguished in the siliceous precipitate only with difficulty (Pl. 12, fig. 5). Mineralized bacteria were rare and occurred as bacteria-sized moulds (possibly of Gram negative forms, based on a comparison with Sample 3) or as clay moulds. Large, non-bacterial, artificial spheres of silica were common ( $3- > 13 \mu\text{m}$  diameter) as well as spherical or crescent-shaped artefacts, either filled or as crusts of  $0.3-3.3 \mu\text{m}$  diameter (Pl. 12, fig. 6). After three months fossilization at 500 atmospheres, microorganism remains were no longer visible in the granular mass and only minerals such as clays could be distinguished, although artificial spheres, either filled or as crusts were still observed. The results of this experiment are summarized in Table 7.

## DISCUSSION

### *The process of fossilization*

In nature, an important factor in the process of microorganism fossilization is the preservation of the dead cell for a period of time long enough to allow its mineralization. Microorganisms with thick sheaths such as cyanobacteria or the cysts of protists, or with thick glycocalyxes, are more resistant to decay and, therefore, are more readily fossilized (Golubic and Barghoorn 1977; Francis *et al.* 1978a; Knoll 1985; Gerdes and Krumbein 1987). However, the studies of Ferris *et al.* (1988) suggest that the chemical environment of the dead microorganisms may also play an important role, with the binding of Fe ions to cell surfaces effectively retarding the rate of degradation. These authors also put forward the opinion that the preservation of the microorganisms in the experiments of Oehler and Schopf (1971), Oehler (1976) and Francis *et al.* (1978a, 1978b) was due to the denaturation of the autolytic enzymes which naturally degrade a bacterial cell wall upon the death of the organisms. However, they cite no evidence to support their statement. Other factors influencing cell wall fossilization are discussed below.

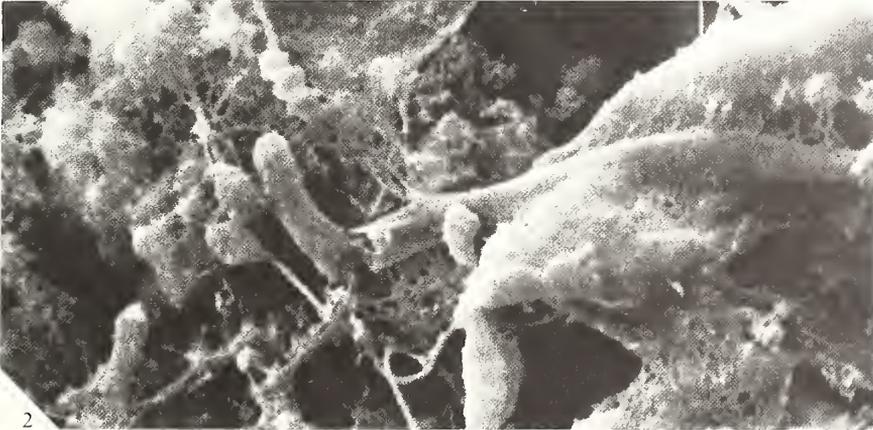
In the experiments described in our paper, the supply of dissolved silica was made readily available in the form of the orthosilicate TEOS. The time delay between cell death and mineralization was, therefore, probably not a limiting factor.

Silicification takes place by the attachment of the silica molecule to a functional group, such as hydroxyl or carboxyl groups of the organic material, i.e. the organic matter serves as a template for the nucleation of silica. Once the initial nucleation has taken place, silica is precipitated by silicic acid polymerization (Leo and Barghoorn 1976). A certain degree of cell degradation may, in fact, increase the number of hydroxyl groups available for silica nucleation (Leo and Barghoorn 1976; Ferris *et al.* 1988); indeed, most of the Proterozoic microfossils present a slightly degraded aspect according to Knoll (1985). Schultz-Lam *et al.* (1993) note that Gram positive bacteria have a higher metal-binding capacity than Gram negative bacteria. This is a result of the former containing more peptidoglycan in their cell walls than the latter. It seems that metals bind primarily to the carboxyl functional groups of the peptidoglycan and teichuronic acids and the phosphoryl groups of the teichoic acids. Could Gram positive bacteria, therefore, be more susceptible to silicification than

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## EXPLANATION OF PLATE 8

- Fig. 1. Experiment 1, Sample 2 (1 atmosphere, 4 weeks); the silica precipitates are volumetrically important enough to almost engulf all organic structures in the sample; the EPS has changed morphology from fibrous to smooth glue-like masses which coat the silica deposits;  $\times 1900$ .
- Fig. 2. Experiment 3, Sample 2 (500 atmospheres, 1 week); fibrous EPS web with mineralized fungal hyphae (note cracked crust in centre) and seemingly unmineralized spirochete;  $\times 15000$ .
- Fig. 3. Experiment 3, Sample 2 (500 atmospheres, 2 weeks); thickly encrusted fungal hyphus with part of a smooth-surfaced, seemingly unfossilized, bacterium, bottom left (arrow); note the still fibrous aspect of the EPS;  $\times 7000$ .



other types of bacteria? Other very important factors to take into account, however, are the physico-chemical conditions of the environment, as there is a very close interaction between microorganisms and their physico-chemical environment (Guerzoni *et al.* 1995). Microbial respiration and metabolic products change conditions, such as pH, within the immediate environment of the bacteria. On the other hand, the physico-chemical properties of the environment and the interactions between cells and the surrounding water are influenced by the nature and properties of the ions present, which affect the hydrophobic balance of the environment (Guerzoni *et al.* 1995).

In the experiments described in this paper, it was noticed that although all the eukaryotes and many of the bacteria were rapidly silicified (within one week at atmospheric pressures), a number of the latter, especially Gram negative forms (mostly spirochetes) in Experiments 1 and 2, resisted complete degradation for long periods and became only partially mineralized after four months' fossilization (at atmospheric pressures). The fact that, when they did silicify, only certain parts of the cell, such as the apices of some bacilli and spirochetes, or certain locations on the walls of some cocci, became mineralized may be related to differences in the composition and hydrophobicity of the heterogenous cell wall. Of the microorganisms which were rapidly mineralized, it appears that the cell wall and, often, all or much of the cytoplasm and internal organs are initially permeated by silica. This would explain the fact that the fossilized microorganisms in the early phases of fossilization often had a smooth rather than rough, encrusted surface when viewed with the SEM, and that individual organelles in the eukaryotes could sometimes still be identified.

Interestingly, not only did the microorganism cells become rapidly silicified but also the EPS in the groundmass. In the early stages of fossilization the volume of EPS in the groundmass actually seemed to increase, probably due to the addition of the degradation products of the microorganisms which, in turn, became rapidly mineralized. In some cases specific organelles, such as chloroplasts from diatoms, could still be distinguished. The importance of macromolecule mineralization rather than simply cellular mineralization in carbonate reefs was noted by Reitner (1993). He studied the formation of modern cryptic microbialites and concluded that 'Calcifying organic macromolecules are mainly responsible for microbialite formation by cementing detrital material' (Reitner 1993, p. 3). In this reef situation,  $\text{Ca}^{2+}$  is bound to the carboxyl groups of the macromolecules which make up the microbial biofilm.

We have seen that organic matter acts as a template for initial silica nucleation but what happens to it during the fossilization process? The experiments demonstrated that most of the degraded cellular material ends up in the groundmass as EPS which, in its turn, becomes fossilized. However, in situations where the microorganisms are rapidly entombed in precipitated silica, often some unmineralized parts of the organic cell wall remain, as a comparison of contrasted and uncontrasted TEM sections shows. This is especially apparent in the high pressure fossilization experiment of Sample 3, which contained microorganisms in water from above the deep-sea sediment surface.

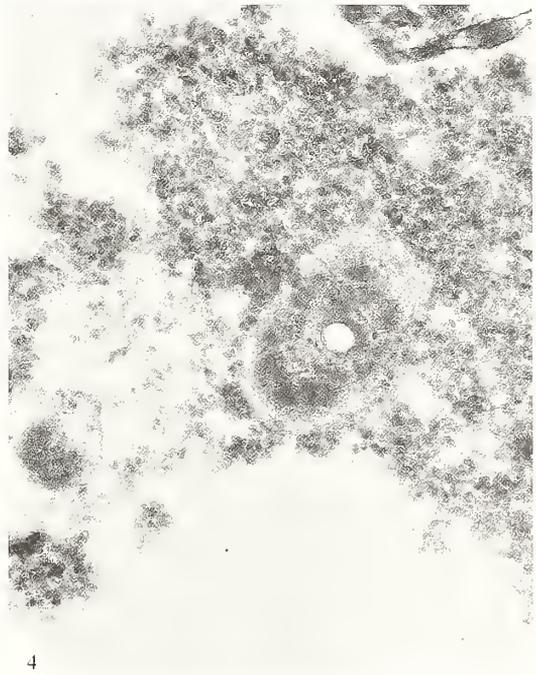
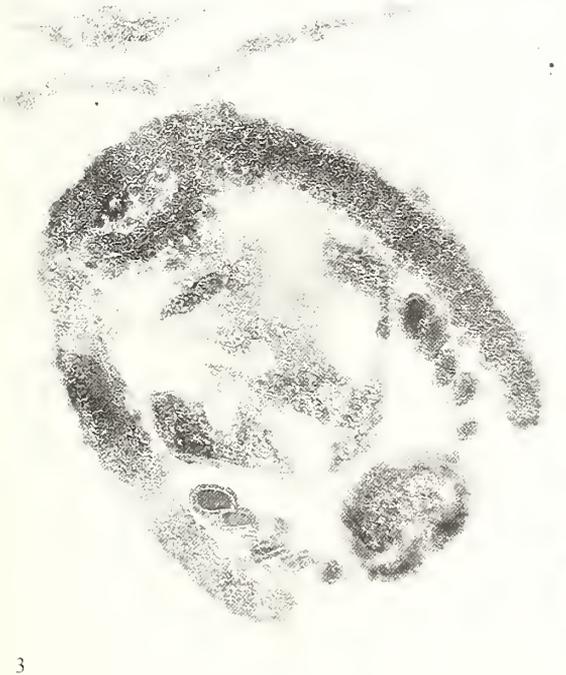
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#### EXPLANATION OF PLATE 9

Figs 1, 4. Experiment 3, Sample 2 (500 atmospheres, 2 weeks). 1, contrasted TEM section showing well encrusted fungus filled with silica and a number of silicified bacteria (moulds and casts, arrows) engulfed in a granular silica deposit;  $\times 10000$ . 4, contrasted TEM section showing detail of a bacterium cast (with inclusion) engulfed in the granular silica deposit;  $\times 41000$ .

Fig. 2. Experiment 3, Sample 2 (500 atmospheres, 4 weeks); contrasted TEM section showing that the silica deposit has completely engulfed all the organic structures; there is also distortion of some diatom frustules, probably as a result of the pressure; bacteria are hardly recognizable – some small oval structures which may be bacteria are arrowed;  $\times 28000$ .

Fig. 3. Experiment 3, Sample 2 (500 atmospheres, 3 weeks); uncontrasted TEM section showing a heavily mineralized diatom with parts of the cytoplasm also mineralized; the symmetrical structures may represent remnants of the frustule wall or may be artefacts; note the more electron-dense aspect of the silica;  $\times 69000$ .



Probably, during the gradual crystallization of the silica, the non-mineralized organic matter is expelled and migrates through the still porous and hydrated precipitate and concentrates at the edges of the silica deposit. In fact, SEM studies invariably show the botryoidal siliceous masses coated with a biofilm of stringy, denatured EPS (Pl. 10, figs 1, 4).

The gradual change in crystallinity of the silica with time, although not crystallographically measurable, was evident in two ways. In the first place the precipitated silica had a less porous and more electron-dense texture when observed with the TEM and, secondly, its morphology changed. Although spheres of relatively electron-dense silica are present in all samples after one week of fossilization (even at 1 atmosphere), most of the early silica precipitates occurred as porous disseminated or loosely aggregated spherules, or as a porous crust around the microorganisms. After a few weeks the disseminated or loosely aggregated spherules in the groundmass consolidated to form botryoidal-surfaced masses and larger spheres, and the uniform porous crusts around the microorganisms became crusts of fused spherules to which other spherules became attached. The size of these spherules gradually increased, resulting in a rough mammillated crust, similar to the bacteria crusts observed in the Oligocene to middle Miocene sediments from the south-eastern Atlantic (Pl. 10, fig. 2). Other studies of silicified microorganisms also noted the mammillated morphology of the mineralized organisms (Oehler 1976) and the mineralizing silica (Knoll 1985).

#### *Silicification artefacts*

One of the most interesting observations from this experiment relates to the effects of continued fossilization with unlimited supplies of dissolved silica. Both the SEM and TEM studies demonstrate that, with time, and especially under pressure, the precipitated silica aggregates engulfed mineralized and unmineralized microorganisms. These aggregates were characterized by the botryoidal surfaces typical of opaline silica. The engulfed organisms were not distinguishable within the silica aggregates with the SEM. Moreover, the TEM sections showed a gradual merging of the silicified microorganisms with the engulfing silica such that, in Experiment 3 (500 atmospheres) after four weeks, bacteria could not be distinguished even in TEM section. In the long-term pressure Experiment 5 (one to three months at 500 atmospheres), even the robust diatom frustules lost their identity and only the clay moulds which used to coat bacteria remained to document the former presence of the relatively abundant microbial community in this deep-sea sediment sample.

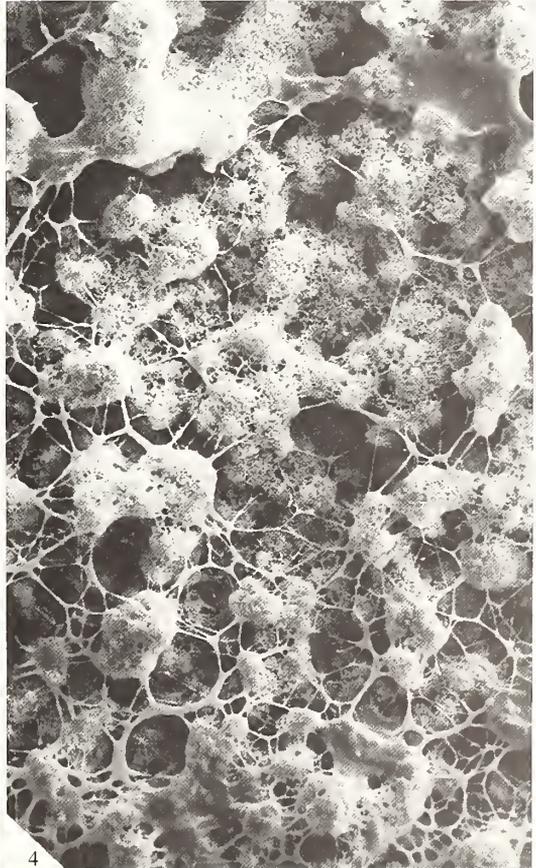
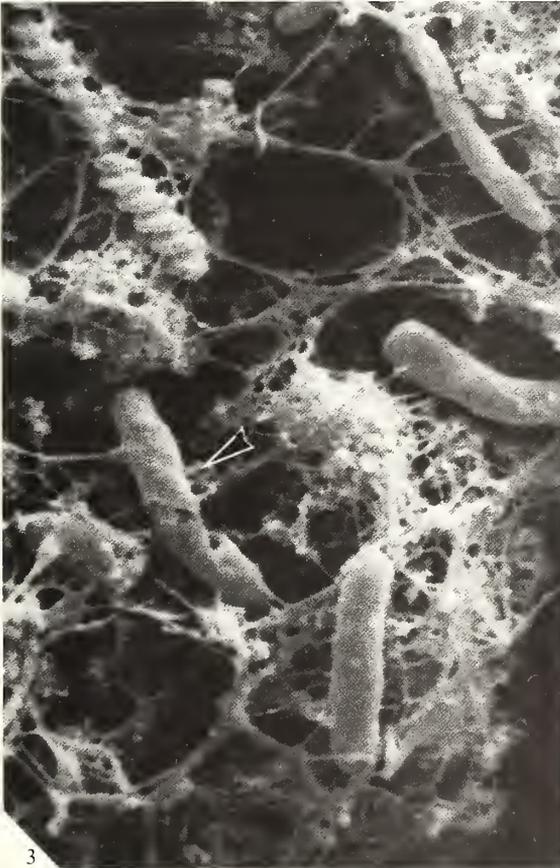
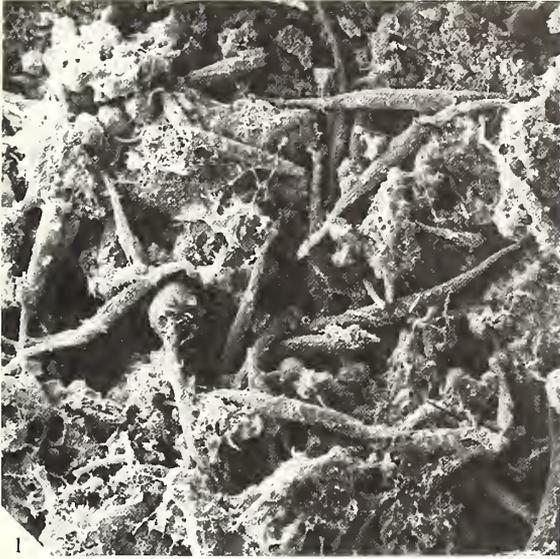
Another silicification artefact was the formation of a silica core in the mineralized bacteria, which looked like an artificial nucleus, resulting from the mineralization of the shrunken, degraded cytoplasm. The occasional presence of an organic membrane around the false 'nucleus' could be due to the adsorption of the excluded organic matter from the silicified cytoplasm onto the siliceous deposit. If such a phenomenon were preserved in the natural fossil record, it could lead to misinterpretation and confusion with eukaryotes. In fact, the formation of artificial 'nuclei' was also noted by Francis *et al.* (1978a), who discussed the implications of such artefacts in the determination of the timing of the appearance of the eukaryotes during the Proterozoic.

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#### EXPLANATION OF PLATE 10

Figs 1–3. Experiment 3, Sample 2 (500 atmospheres, 3 weeks). 1, all the organic structures appear to be encrusted and the EPS no longer has a loose fibrous aspect;  $\times 1000$ . 2, even the bacteria begin to look encrusted and mineralized; this individual displays a remarkable resemblance to the encrusted bacteria in the upper Oligocene–middle Miocene samples from the SE Atlantic (Pl. 1, fig. 3);  $\times 19000$ . 3, the bacteria here have smoother surfaces but the bacterium centre left is broken showing the hollow interior (arrow); note the granular silica deposits still associated with the EPS in the groundmass;  $\times 14000$ .

Fig. 4. Experiment 3, Sample 2 (500 atmospheres, 4 weeks); individual organic structures are no longer recognizable in the mammillated silica deposit; the EPS has taken on a smoother, stringy appearance;  $\times 19000$ .



Other non-microbial structures which formed during the course of our experiments included (1) individual silica spheres (they have previously been misinterpreted as epiphytic bacteria attached to other silicified bacteria, e.g. Monty *et al.* 1991, pl. 4, fig. 6) and strings of spheres attached to the surfaces of the silicified microorganisms, (2) regularly and irregularly shaped objects occurring in diatoms and in the groundmass of Experiment 3, resulting from the mineralization of the degradation products of the microorganisms, as well as (3) the hollow or full spheres in Experiment 5. The last may represent the silicified blobs of the degradation products of the microbial cells, or even the interface along which dissolved organic matter accumulated between a water droplet and TEOS. The mineralization of liquid or gas droplets in nature is not an unusual phenomenon (Gerdes *et al.* 1994).

*Comparison of the experimentally produced microfossils with the silicified bacteria in upper Oligocene to middle Miocene sediments from the south-eastern Atlantic*

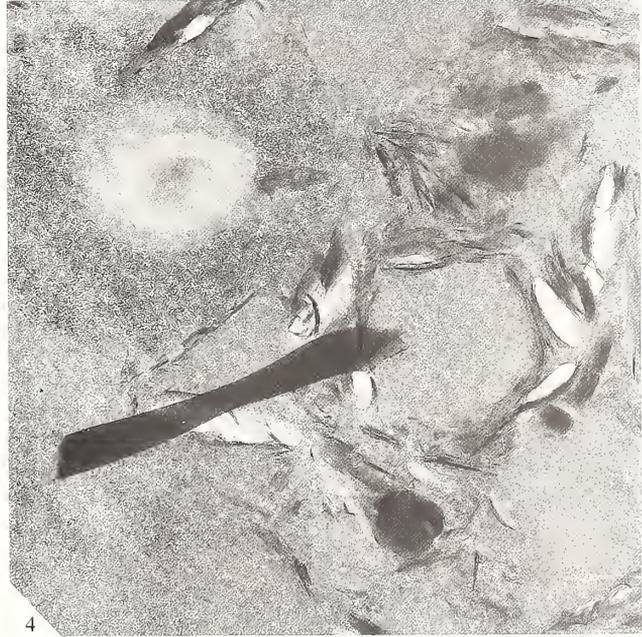
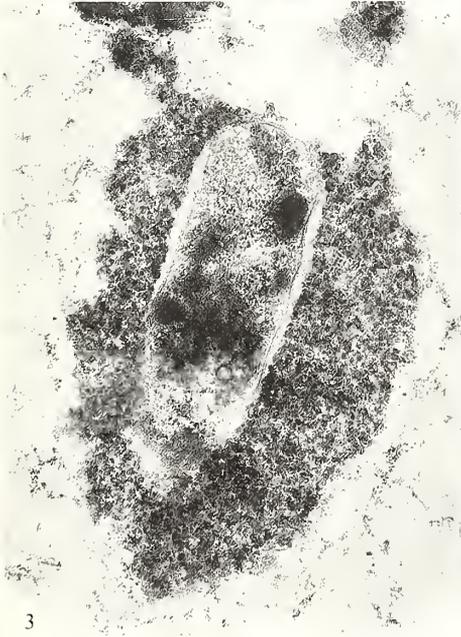
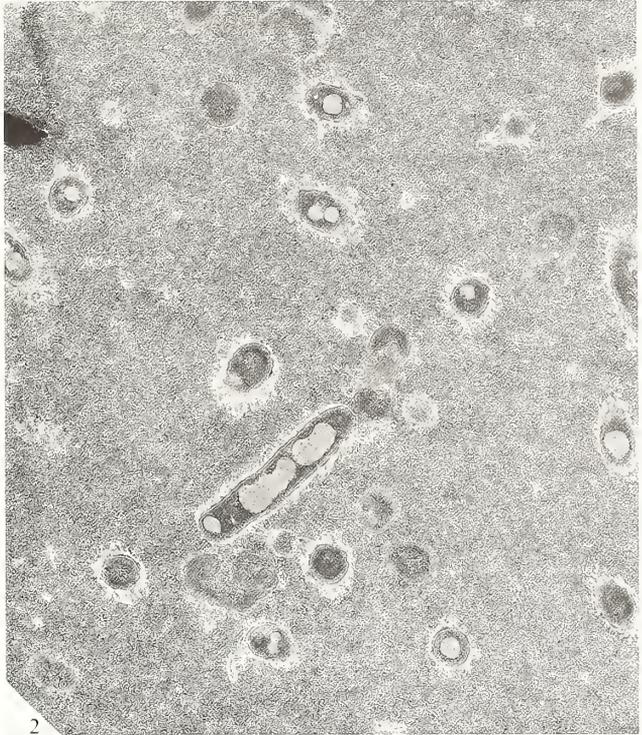
There are a number of similarities and differences between the silicified structures obtained from these experiments and those observed in the upper Oligocene to middle Miocene sediments of the south-eastern Atlantic. In the first place, the botryoidal morphology of the surface of the silicified bacteria is similar. Although most of the Oligocene–Miocene bacteria displayed a rough mammillated crust-like surface, other individuals appeared to be smooth and looked ‘unfossilized’ and ‘fresh’ (Monty *et al.* 1991). Our experiments show that, in the latter case, the fossilization process was probably not very advanced and that the bacteria were probably impregnated by hydrated porous silica, similar to that in the early weeks of the fossilization experiment at atmospheric pressures, or at one week at pressures of 500 atmospheres. The SEM-visible rugged crusts coated with spherical/hemispherical structures, the size of those in the ancient sediments, only formed after a few months of fossilization at atmospheric pressures and after a few weeks at deep-sea pressures.

From this observation it can be concluded that, within a given fossil bacteria-bearing horizon in the upper Oligocene to middle Miocene sediments from the south-eastern Atlantic, bacteria exhibiting a rugged crust were subjected to a longer period of fossilization than those having a smooth surface. Our experiments showed that, for those bacteria recalcitrant to degradation and last fossilized (apparently Gram negative forms), the whole wall was not permineralized by very fine silica. Instead, silica spheres grew at specific locations on their surfaces. This observation may indicate that the smooth-surfaced fossil bacteria of the deep-sea sediments represent permineralized younger bacteria.

As the sediments in which the fossil bacteria were found contained a small amount of other minerals (< 10 per cent.), including clay minerals, and since the pore waters would be carrying many dissolved ions, there is a strong possibility that certain types of bacteria in the microbial mat might have immobilized Fe ions on their surface, which would have retarded their degradation and increased their chances of fossilization (cf. Ferris *et al.* 1988).

EXPLANATION OF PLATE 11

- Fig. 1. Experiment 3, Sample 2 (500 atmospheres, 4 weeks); uncontrasted TEM section showing rod-shaped silica crusts in a diatom which could represent specific organelles or artefacts;  $\times 41000$ .  
 Figs 2–4. Experiment 4, Sample 3 (500 atmospheres, 1 week), contrasted TEM sections. 2, showing many bacteria and other unidentified organic structures embedded in a finely granular silica deposit; the bacteria seem to be in the form of casts outlined by an organic membrane; Gram negative bacteria are outlined by an empty halo;  $\times 16500$ . 3, a Gram negative bacterium with a thick glycocalyx; both glycocalyx and bacterium have been silicified; faint remnants of the layered cell wall may be seen;  $\times 41000$ . 4, the silicified glycocalyx around a bacterium represented by an empty space containing an artificial ‘nucleus’ (upper left); at the centre right a circle of clay flakes forms a mould which marks the position of a completely degraded bacterium (compare with Pl. 12, fig. 3);  $\times 28000$ .



Whereas in the experiments the fossilization process continued until most of the fossilized microorganisms were engulfed in botryoidal silica masses and the bacteria lost their identity, silicification in the ancient deep-sea sediments stopped after the mineralization of the bacteria and the complete coating of all mineral particles in the horizon. Small filamentous structures (part of the original reticular structure of the biofilm?) were engulfed in the botryoidal-surfaced silica coating and bacteria bases were embedded in it, but silica precipitation ceased before the bacteria were engulfed. The cessation of silica precipitation would have occurred when the amount of dissolved silica in the pore waters dropped below a critical concentration.

The formation of artificial nuclei in the experimentally silicified bacteria was noted. Similar structures in clay moulds were observed in the ancient deep-sea sediments from the south-eastern Atlantic (Pl. 2, fig. 4). However, despite innumerable hours of searching, very few of the fossilized bacteria could be identified with certainty in these samples using the TEM. Those that were identified had a completely permeated aspect and were not hollow (Pl. 2, fig. 2).

### CONCLUSIONS

The experiments demonstrated the following.

(1) Not all microorganisms silicify with the same facility; the Gram negative bacteria (especially spirochetes) in Experiments 1 and 2 seemed to be recalcitrant to fossilization, whereas the Gram positive bacteria and eukaryotes (diatoms and fungi) silicified very readily.

(2) The EPS of the groundmass, including organelles such as the chloroplasts of diatoms, was particularly susceptible to silicification.

(3) The resulting morphology of the fossilized microorganisms depended upon the fossilization time and, consequently, the amount of silica available. In the samples observed after only a few weeks of fossilization (those at atmospheric pressures and after one to two weeks at 500 atmospheres), most of the bacteria appeared 'fresh' and 'unmineralized' when observed with the SEM, whereas the TEM studies showed that they were, in fact, impregnated by very finely textured, hydrated silica. Continued fossilization (two to four months at atmospheric pressures and three weeks at 500 atmospheres) gave the microorganisms an encrusted, mammillated, surface morphology, whereas further fossilization resulted in the complete embedding of the microorganisms in a siliceous precipitate and the eventual loss of individual cellular identity.

(4) Artefacts such as silica cores looking like artificial nuclei in the bacteria were common. Other artefacts formed after longer periods of silicification at deep-sea pressures.

(5) Silicification occurred more rapidly under deep-sea pressures than at atmospheric pressures.

Interpretation of the process of fossilization of the upper Oligocene to middle Miocene silicified microbial mats in the south-eastern Atlantic sediments was aided by the observations obtained from the experiments: comparison with the results of the experiment indicated that the microbial

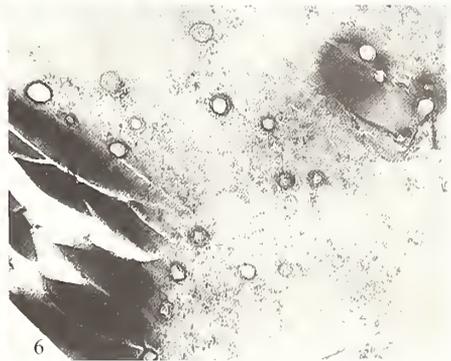
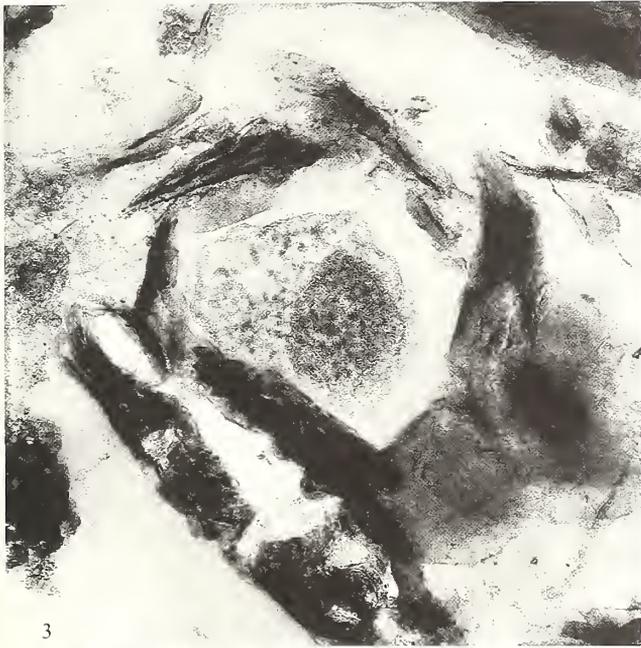
### EXPLANATION OF PLATE 12

Fig. 1. Experiment 4, Sample 3 (500 atmospheres, 3 weeks); uncontrasted TEM section of the moulds of two bacteria containing artificial 'nuclei';  $\times 41\,000$ .

Fig. 2. Experiment 4, Sample 3 (500 atmospheres, 4 weeks); contrasted TEM section of very degraded Gram negative bacteria and other unidentified organic structures with silica spheres growing within the structures and on the walls;  $\times 41\,000$ .

Figs 3-4. Experiment 5, Sample 4 (untreated); contrasted TEM sections. 3, partly distorted bacterium within a clay particle mould; distortion of the bacterium could be a result of the change in pressure between the deep-sea and the laboratory;  $\times 69\,000$ . 4, bacterium within the aureola of a diatom frustule;  $\times 41\,000$ .

Figs 5-6. Experiment 5, Sample 4 (500 atmospheres, 1 month); uncontrasted TEM sections. 5, faint outline of a diatom frustule in the silica deposit;  $\times 28\,000$ . 6, artificial silica spheres, possibly formed around liquid droplets;  $\times 41\,000$ .



community within individual fossiliferous microbial horizons seems to have been silicified continuously during the life of each individual community; older, thickly encrusted bacteria coexisted with younger, smooth individuals. However, the supply of silica was not unlimited because the organic structures were impregnated and encrusted but not completely engulfed by the siliceous deposits.

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## APPENDIX

All samples are stored at the laboratory of the Sezione di Chimica e Tecnologia degli Alimenti of the Dipartimento di Protezione e Valorizzazione Agroalimentare at the University of Bologna. The SEM sample stubs are kept in a dessicator and are listed below.

Sample	Silicification time	Pressure atm	Stub no.
2	1 wk	1	208
	2 wk		215
	3 wk		209
	4 wk		216
	1 wk	500	211
	2 wk		219
	3 wk		220
	4 wk		221
	1 wk		500
3	3 wk	500	213
	1 mth	500	214

TEM sample blocks and sections in numbered boxes are as follows.

Sample	Silicification time	Pressure atm	Resin block	Ultrathin section (* contrasted)
1	0	1	Box 3: 1C	Box 3: 2E, 3A*
	2 mth		Box 3: 1A	Box 3: 6C*, 6D, 6E, 7A
	4 mth		Box 3: 1B	Box 3: 7B*, 7C, 7D
2	1 wk	1	Box 4: 1J, 1K	Box 3: 19E*, 20A, 20B, 20C
	2 wk		Box 4: 1L	Box 4: A1*, A2, A3, A4
	3 wk		Box 4: 1M, 1N	Box 4: A5*, B1, B2, B3
	4 wk		Box 5: 1A, 1B, 1C	Box 3: 14A*, 14B
	1 wk	500	Box 4: 2A, 2B	Box 3: 12B*, 12C, 12D
	2 wk		Box 4: 2C, 2D	Box 3: 12E*, 13A, 13B
	3 wk		Box 4: 2E, 2F	Box 3: 13C*, 13D, 13E
	4 wk		Box 5: 1D, 1E, 1F, 1G	Box 3: 14C*, 14D, 14E, 15A
	1 wk		500	Box 4: 2G
2 wk	Box 4: 2H	Box 3: 15E*, 16A, 16B, 16C		
3 wk	Box 4: 2J	Box 3: 16D*, 16E, 17A, 17B		
4 wk	Box 4: 3L, 3M, 3N	Box 3: 17C*, 17D, 17E, 18A		
4	0	500	Box 4: 2K	Box 3: 18B*, 18C, 18D, 18E
	1 mth		Box 5: 1H, 1J	Box 3: 19A*, 19B, 19C, 19D
	3 mth		Box 3: 2A, 2C, 2D	Box 4: C2*, C3

# THE SUTTON STONE: AN EARLY JURASSIC ROCKY SHORE DEPOSIT IN SOUTH WALES

by M. E. JOHNSON *and* W. S. McKERROW

**ABSTRACT.** The unconformity between Jurassic and Carboniferous carbonates at Southerndown, near Ogmore-by-Sea, Mid-Glamorgan, represents an ancient rocky shoreline which has had a long history of study. Henry De la Beche discussed the ecological details of the unconformity surface, but subsequent debates focused more on the age and depositional setting of the basal Jurassic conglomerate known as the Sutton Stone. Our contribution returns to the theme of faunal development on the unconformity surface. The Jurassic corals, *Allocoeniopsis gibbosa* and *Heterastraea* sp., occur as encrusters of the Carboniferous substrate on a tidal abrasion platform. Serpulid-worm colonies may be observed in life position above the stepped unconformity, but not attached to it. These and other features of a physical and biological nature suggest sporadic preservation in rapidly changing ecological settings during an Early Jurassic marine transgression.

CLIFFS on the Bristol Channel coast at Southerndown, near Ogmore-by-Sea, South Wales, expose segments of a well preserved Jurassic coastline forming part of a small, rocky island (Bradshaw *et al.* 1992, p. 108) composed of thick-bedded Carboniferous Limestone (Wilson *et al.* 1990). The unconformity is overlain by the Sutton Stone (De la Beche 1846), a Lower Jurassic (Hettangian) conglomerate.

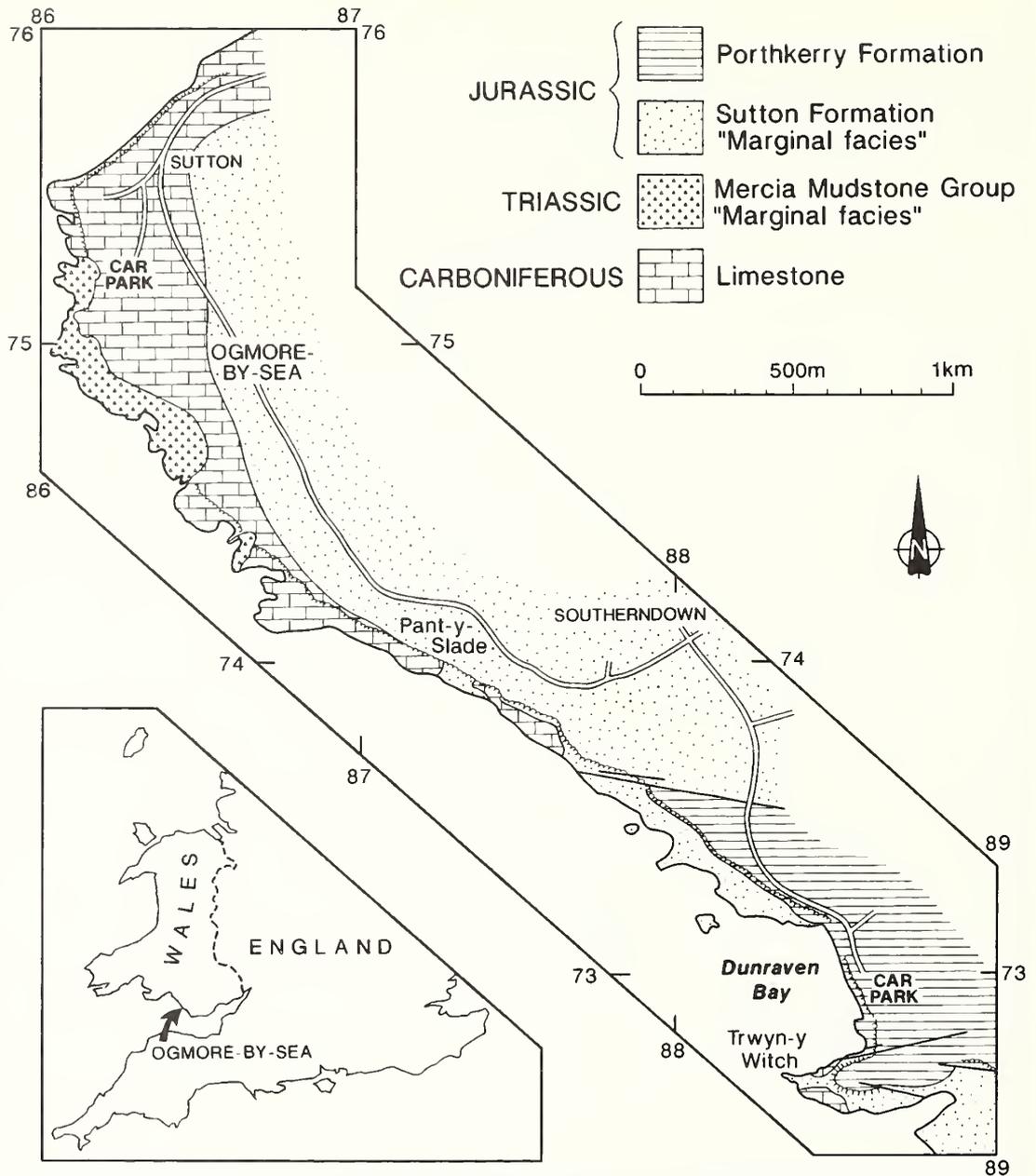
Convincing descriptions of ancient rocky shores in the geological literature are very few. Only 155 references (covering both the Precambrian and Phanerozoic) are cited in the most recent bibliography (Johnson 1992). Among these, only nine citations refer to Jurassic rocky shores, but over half of them relate to the Vale of Glamorgan. In addition, there have been numerous palaeontological publications on the area, and the unconformity has been discussed in many more general works: from Conybeare and Phillips (1822) to Bradshaw *et al.* (1992). The Hettangian rocky shoreline at Southerndown is both the longest studied and most argued about feature of its kind anywhere in the world. Much of the debate has concerned the age of the unconformity, the applicability of stratigraphical units assigned to rocks above the unconformity, the nature of fauna colonizing the shoreline, and the depositional environment on the shoreline.

Despite its intense history of study, the locality still yields additional observations of interest. As an outstanding example of a Jurassic, tidal-abrasion platform, Southerndown is an especially suitable place to look for a fossil community characterized by borers, encrusters, and clingers adapted to life in the surf zone. Faunas associated with submarine hardgrounds are thoroughly reviewed by Wilson and Palmer (1992), but very little is known about the evolution of rocky-shore communities through geological time (Johnson 1988; 1992).

The objectives of this paper are to review the history of research at Southerndown and to report on new discoveries of encrusting organisms on the surfaces of the eroded Carboniferous Limestone.

## LOCATION AND GEOLOGICAL SETTING

On the Heritage Coast south of the Ogmere River, 2.5 km of nearly continuous section show Triassic and Jurassic strata resting unconformably on Carboniferous Limestone. The Triassic rocks are poorly sorted terrestrial breccias, while the Jurassic rocks consist of marine conglomerates and bioclastic limestones. The Triassic breccias are assigned to the Late Triassic Mercia Mudstone Group, because elsewhere in the Bristol Channel area equivalent beds are conformably below the



TEXT-FIG. 1. Map of the coast between Ogmores-by-Sea and Dunraven Bay (modified from Wilson *et al.* 1990, p. 48). The British National Grid lines are indicated on the margins; insert shows position of Ogmores-by-Sea on the coast of South Wales.

Penarth Group of known Rhaetian age (Wilson *et al.* 1990). The Jurassic bioclastic limestones contain Hettangian and Sinemurian ammonites (Hodges 1986).

The Triassic breccias of Glamorgan and Somerset were deposited in valleys with a relief not very different from that of those occurring today in south Glamorgan and the Mendip Hills. However, the deposits at Ogmores are so coarse (with some clasts over 1 m in diameter) and unsorted that they

represent a very different environment from the present; they have been interpreted as flash flood deposits by ephemeral rivers, but they may also be related to contemporary earth movements (Tucker 1977). There are two outcrops of Triassic breccias on the shore at Ogmore (Text-fig. 1); the northern one (extending 850 m from SS 861753 to 864744) appears to have been deposited in a broad irregular valley and the southern one (at SS 866743) is exposed in a narrow valley (less than 100 m wide) with a steep gradient down to the south-west. Both Triassic deposits accumulated rapidly, perhaps 'on a Tuesday afternoon' (cf. Ager 1986, p. 35).

The sub-Jurassic unconformity is very different from the sub-Triassic one, both in its morphology and in the bedded nature of the overlying deposits. Marine planation on the Carboniferous Limestone surface has produced gently inclined platforms on which the basal Jurassic conglomerates rest. The exposed surface near the foot of the gully named Pant-y-Slade (SS 871741; Text-fig. 1) has been termed Platform A (Fletcher 1988); towards the southeast (SS 875378) the basal deposits on this platform overlie topographically earlier deposits on two lower platforms (B and C). All the platforms are generally smooth, except for some channels and ridges towards the southeast limit of Platform A (Fletcher 1988, fig. 3) and a few isolated low rises where the flat-bedded Carboniferous Limestone may extend a few decimetres above the general level. To the south-east, the unconformity descends below sea level in Dunraven Bay. North of the car park in the bay, the high (and dangerous) cliffs are composed of conglomerates and calcarenites of the 'marginal facies' Sutton Formation (Sutton Stone and Southerndown Beds) lying below the offshore facies of the 'Blue Lias' Porthkerry Formation (Wilson *et al.* 1990). To the south of Dunraven Bay, there is a much more pronounced angular unconformity on the promontory of Trwyn-y-Witch (SS 885726), which is best exposed (at low tide) on the south side of the point.

#### PREVIOUS RESEARCH

The earliest reference in the geological literature to the unconformity between Palaeozoic and Mesozoic rocks in South Wales was made by Conybeare and Phillips (1822, p. 31). They described 'horizontal deposits of calcereo-magnesian conglomerates, new red sandstone and lias' as a sequence of formations which 'rest on the back of the most southerly zone of carboniferous lime along the coast from the mouth of the River Ogmore to the Taafé.'

Subsequently, De la Beche (1846, p. 246, fig. 26) compared the basal Jurassic beds above the unconformity in Glamorgan with similar rocks in the English Mendip Hills, where he described the Bajocian shoreline conglomerate as a 'beach-like accumulation'. His illustrations of Jurassic borings in the Carboniferous substrate are the first of their kind in the geological literature. The small borings (1846, fig. 43) are easily referable to *Trypanites*. The shell of a bivalve in a larger boring (1846, fig. 44) is unmistakably *Gastrochaenolites*, a boring by *Lithophaga*. *Trypanites* and *Lithophaga* borings occur at Southerndown (Fletcher 1988, p. 4) as well as in the Mendip Hills.

Less than twenty years after publication of De la Beche's far-ranging report, heated debate broke out regarding the age, geographical setting, and depositional environment of the Sutton Stone. Some aspects of this debate have filtered down to the present day.

Hodges (1986, p. 239) concluded that the Sutton Stone and overlying Southerndown beds of Tawney (1866) should be abandoned as distinct stratigraphical units with independent characteristics, because of their great 'vertical changes in both lithology and colour' and the fact that they cannot be separated palaeontologically. Fletcher *et al.* (1986), on the other hand, considered these units to be suitable lithofacies for distinct nomenclature. Ager (1986) followed Hodges' recommendation in assigning the Sutton Stone and overlying Southerndown Beds to the Sutton Formation.

#### *Age of the Sutton Stone*

Tawney (1866, p. 75) divided the stratigraphical sequence above the unconformity (approximately 30 m thick) into the 'Sutton series' and the overlying 'Southerndown series'. Contrary to De la Beche (1846), the 1.2 m thick basal conglomerate was included by Tawney (1866, p. 73) as part of the 12 m

thick Sutton series. Tawney followed Jones and Tomes (1865) in assigning the beds to the Rhaetian on the basis the supposed range of the bivalve '*Ostrea interstriata*' from the Sutton Stone. This species may now be referred to *Atreta intusstriata* (Emmerich); it is present in both the Upper Triassic and Lower Lias (Lower Jurassic) of Europe (Hodges 1991).

Tawney (1866, p. 81) was the first to describe ammonites from the Sutton Stone on the coast, among them a species he named *Ammonites suttonensis*. Specimens were recovered at a level about 6 m above the base of the unconformity, both at Sutton quarry and Trwyn-y-Witch (Text-fig. 1). Tawney's species is allied with *Caloceras johnstoni* signifying the upper subzone of the *Psiloceras planorbis* Zone (Hodges 1986). The ammonite *Schlotheimia* cf. *thalassica* was later recorded (Trueman 1922) at a horizon about 3 m above the base of the unconformity at Pant-y-Slade. This nominal species is now considered to be a synonym of *S. angulata*, representing the youngest ammonite zone in the Late Hettangian (Hodges 1986). These and other ammonites collected by Hodges (1986) derive from the Sutton Stone near Ogmore, but from horizons well above the basal conglomerate. No ammonites have ever been recovered from the basal conglomerate of the Sutton Stone, but Hodges (1986, p. 239) surmised that the base of the section at Pant-y-Slade was almost certainly in the *planorbis* Zone, possibly extending down into the Upper Rhaetian.

In the first description of corals from the Sutton Stone, Duncan (1866, p. 90) maintained that the Welsh corals had 'nothing in common with any species from Liassic strata', but Bristow (1867) maintained that the age was Early Jurassic, based on the occurrence of '*Ostrea liassica*' and other bivalves. Later, Duncan (1867) recanted his earlier interpretation, though Tomes (1884) still attempted to salvage his argument for a Rhaetian age. All subsequent references to the basal conglomerate of the Sutton Stone assume it is Lower Jurassic in position, except for the possibility (Francis 1959; Hodges 1986) that the base of the section may extend down into the Upper Rhaetian.

#### *Observations on palaeoecology*

Records show that Charles Moore led a field trip to Southerndown in 1866 for the members of the Bath Natural History Club, who collected corals and bivalves from the conglomerate above the unconformity (Winwood 1867). Correspondence with Moore, quoted in Jones and Tomes (1865, p. 191), shows that oysters were found 'attached to Carboniferous Limestone pebbles'. Moore (1877) was also the first to verify that Mesozoic organisms encrusted the Carboniferous Limestone in the Vale of Glamorgan.

The presence of limpets (Tawney 1866, p. 88; Huddleston and Wilson 1892; Strahan and Cantrill 1904) and the top shell, *Trochus*, have also been debated; these are both forms typical of modern intertidal rocky shores.

Although it could be considered that most massive coral species can show an encrusting habit (B. R. Rosen, pers. comm. 1995), this was long a subject for debate. Duncan (1866, 1867) and Moore (1877) recorded numerous corals from the Sutton Stone. Tomes (1884) reported that the coral *Elysastraea fischeri* (this species is now referred to the genus *Heterastraea*) was the only coral (out of 42 species) to encrust clasts of Carboniferous Limestone, and he stated specifically that he had 'not in a single instance met with the *Elysastraea* growing on the floor of Mountain Limestone beneath the Sutton Stone'. Nonetheless, this observation was used to suggest the former existence of coral islands (Tomes 1884, p. 362). Subsequently, Duncan (1886) confirmed the encrusting nature of some corals within the Sutton Stone. In particular, he noted that '*Astrocoenia parasitica* encrusts foreign bodies' (Duncan 1886, p. 105). Reviewing all the evidence available, Arkell (1933, p. 126) concluded that true coral reefs had never formed on Jurassic shores in the Vale of Glamorgan. However, Cox and Trueman (1936, p. 57), considered that a 'distinct coral reef was built' around a small island near Wick.

#### *Jurassic palaeogeography*

Trueman (1920, 1922, fig. 67B) recognized a chain of small islands, and mapped shorelines in the vicinity of Dunraven, Wick, and Cowbridge. The high percentage of calcareous material in the

Sutton Stone was taken as evidence that very little sediment found its way into the coastal deposits, except for that derived directly from the carbonate basement rocks. Geological cross-sections through the islands (Trueman 1922, fig. 68; Wilson *et al.* 1990, fig. 9) suggest that the islands were drowned soon after the end of the Hettangian.

The islands were called St David's Archipelago by Ager (1974, 1986) and their interpretation by Bradshaw *et al.* (1992, p. 109) as islands off the Welsh Landmass is essentially the same as suggested by Trueman (1922). Discovery of marine Jurassic beds in the Irish Sea, however, has greatly reduced the size of the postulated land areas in Wales.

Curiously, recent work lacks any reference to palaeolatitudes. An Early Jurassic (Hettangian) reconstruction of global coastlines by Smith *et al.* (1994, p. 51) indicates a position slightly above 30° N latitude for this part of the British Isles.

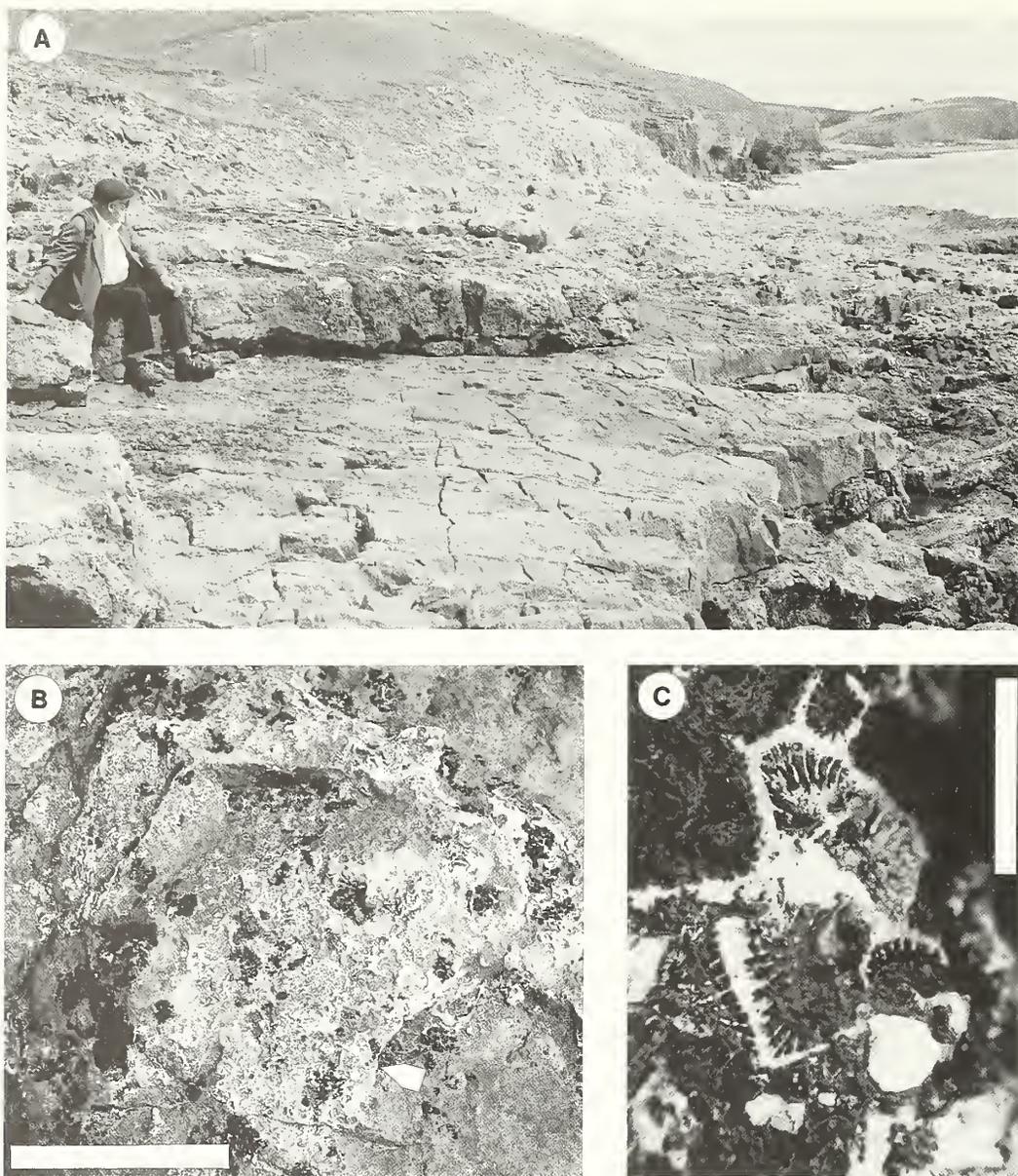
#### *Depositional setting of the Sutton Stone*

The most recent controversy to emerge is without doubt the depositional setting of the Sutton Stone. Ager (1986, p. 35) concluded that it is a debris-flow deposit resulting from a major tropical storm or hurricane which happened 'one Tuesday afternoon'. This notion was based on the argument that the Sutton Stone is a matrix-supported conglomerate with pebbles that float in a fine-grained matrix (see Ager 1993, fig. 9.4). The sort of shingle at Dungeness which was appealed to by De la Beche (1846) as a useful model for the Jurassic basal conglomerate, consists of clast-supported pebbles (see also Ager 1993, fig. 9.3).

Fletcher *et al.* (1986, p. 383) pointed out that a variety of breccias, conglomerates, and skeletal grainstones occurred at different levels and thus the Sutton Stone could not represent a single depositional event. An alternative model was subsequently elaborated (Fletcher 1988, p. 9) in which a suite of different rock fabrics could be produced as a result of cliff collapse and retreat at the back of a wave-cut platform. The origin of some Jurassic features and fabrics at Southerndown were likened to processes on modern carbonate shores, as observed in Puerto Rico (Kaye 1959). Fletcher (1988) concluded that the sculpturing of the Jurassic platform and rocky shoreline at Southerndown took place during still-stands in sea level under conditions of a 2 m tidal range. Under this model, derivation of the Sutton Stone conglomerate by means of day-by-day cliff collapse was also influenced by storm events.

#### VESTIGES OF ECOLOGICAL TIME

Uniformitarian and catastrophic outlooks are popularly portrayed as at variance with one another in assessing the development of the stratigraphical record (Ager 1993). Unconformities and the basal conglomerates typically associated with the transgression of ancient rocky shorelines provide one setting where both outlooks must be accommodated. On one hand, the erosion of an unconformity surface entails day-by-day processes of sedimentary abrasion and hydraulic forcing in the surf zone. The remains of organisms dwelling on ancient rocky shores generally include encrusting, boring, and clinging forms adapted to a high-energy environment, but conveniently preserved *in situ*. Such remains may be found attached to the unconformity surface, itself, or to the clasts which comprise the basal conglomerate. These fossils, as well as erosional surfaces, such as wave-cut platforms and seastacks, represent vestiges of ecological time retained in the stratigraphical record. On the other hand, the shingle fronting a rocky shoreline may be regarded as a deposit most effectively shaped and transported by violent storms. Many authors would agree with Ager (1993) that rocky-shore deposits and their biotas rarely enter the stratigraphical record because of their propensity to be completely eroded away (see review in Hayes *et al.* 1993). Our examination of the unconformity at Southerndown was prompted by the expectation of finding small events on an ecological time scale preserved in the rock record.



TEXT-FIG. 2. Encrusting corals on the unconformity surface near the bottom of Pant-y-Slade (Platform A). A, general view of the exposure, showing the Jurassic Sutton Stone sitting unconformably on the Carboniferous High Tor Limestone. B, slightly raised, but badly weathered, Jurassic coral colony attached to the surface of the Carboniferous limestone; scale bar represents 60 mm; corallum rests below seated figure's left foot in the Text-figure 2A. C, enlargement of individual corallites attributed to *Heterastraea* sp. from the colony shown in Text-fig. 2B; scale bar represents 10 mm; OUM J.55601.

*New discoveries on the unconformity surface*

Near Pant-y-Slade (SS 871741), a thorough search for encrusting organisms now confirms the presence of encrusting corals and bivalves, as well as the annelid boring, *Trypanites*, on the surface

TABLE 1. The Jurassic rocky-shore fauna of the Vale of Glamorgan.

Life style	Platform attachment	Clast attachment	References
Encrusting forms			
Corals			
<i>Heterastraea</i> sp.	×	×	Tomes (1884); this report
<i>Allocoeniopsis gibbosa</i>	×	×	Duncan (1886); this report
Bivalve			
<i>Liostraea</i> sp.	×	×	Jones and Tomes (1865); Moore (1877); this report
Boring forms			
Bivalve ( <i>Lithophaga</i> )			
<i>Gastrochaenolites</i>	×	×	Fletcher (1988)
Annelid			
<i>Trypanites</i> sp.	×	×	Fletcher (1988); this report
Clinging forms			
Gastropods			
<i>Patella suttonensis</i>			Tawney (1866)
' <i>Trochus</i> '			Strahan and Cantrill (1904)

of the Carboniferous Limestone (Text-figs 1–2; Table 1). This search was made on a narrow exposure surface (130 m long but only a few metres wide) of Platform A (Fletcher 1988, p. 3).

Several badly weathered disc-shaped objects are present (Text-fig. 2A). Unlike all the Carboniferous corals observed, they are not planed flat, but are raised above the surface. They are also distinguishable from Carboniferous rugosans (particularly the common genus *Lithostrotion*) by the absence of regularly alternating major and minor septa, the absence of a well-defined outer ring of dissepiments, and septa with irregular, rather than smooth and straight, margins (B. R. Rosen, pers. comm. 1995).

A closer view of one example (Text-fig. 2B) shows an elliptical disc no more than 140 mm in diameter. At higher magnification (Text-fig. 2C), a few corallites are still visible on the surface of the disc, all less than 10 mm across. The open pattern of the corallites, with their clear septal divisions, indicates that the discs are colonial corals preserved in life position. This encrusting form has been identified as *Heterastraea* (B. R. Rosen, pers. comm. 1992). Specimens similar in growth were referred to as '*Elysastraea fischeri*' by Tomes (1884), who noted their clast-encrusting habit.

Other Jurassic examples of encrusting corals, attributed to *Allocoeniopsis gibbosa* (B. R. Rosen, pers. comm. 1992), were discovered on the Carboniferous pavement approximately 70 m northwest of the *Heterastraea* colonies. Again, this observation supports Duncan (1886), who recorded the clast-encrusting habit of a species he identified as '*Astrocoenia parasitica*'. An example of the pavement-encrusting *Allocoeniopsis gibbosa* (Text-fig. 3A) shows good preservation of corallites facing upward in growth position. The margins of the corallum, however, have been worn away.

The discovery of Jurassic corals encrusting the Carboniferous substrate corroborates the original argument by Tomes (1884) that life must have flourished on the unconformity surface before deposition of the Sutton Stone. As the species on the substrate are the same as encrusting species within the Sutton Stone, however, the difference in geological time may not be very significant.

#### *Verification and correction of prior observations*

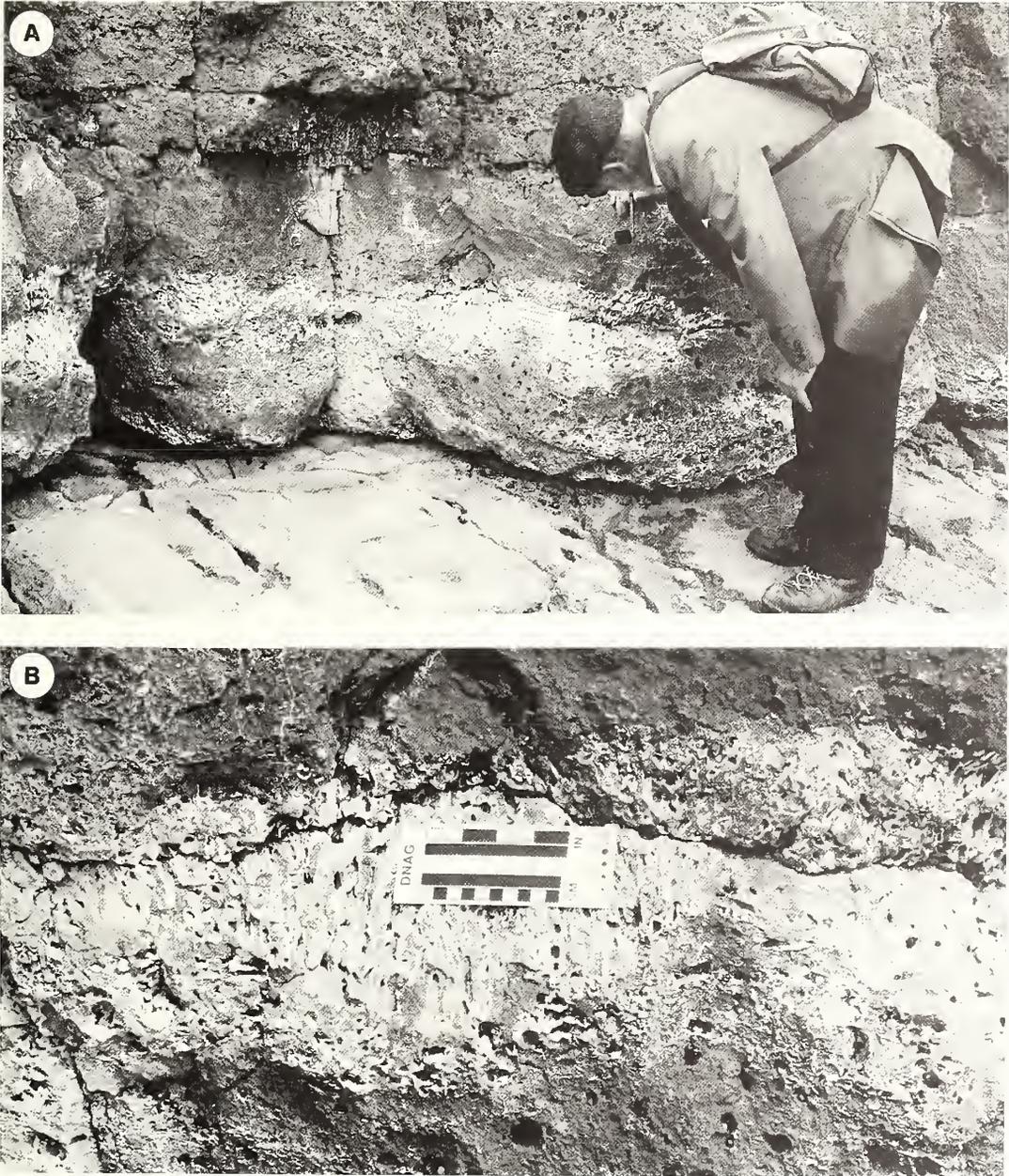
Moore (1877) was the first to record oyster encrustations on the Carboniferous unconformity at Southerndown, but none has been illustrated previously. An attached valve of an oyster (Text-fig. 3B) occurs on the Carboniferous pavement approximately 60 m northwest of the *Heterastraea*



TEXT-FIG. 3. Fossils and physical features on the unconformity surface near the bottom of Pant-y-Slade (Platform A). A, portion of the corallum belonging to *Allocoeniopsis gibbosa* (Duncan) attached to the Carboniferous High Tor Limestone; scale bar represents 10 mm; OUM J.55602. B, attached valve of an unidentified oyster on the same surface; scale bar represents 10 mm. C, tidal rills eroded in the Carboniferous substrate.

colonies. A single valve of *Pecten suttonensis* was also found resting directly on the unconformity surface close to the *Heterastraea* colonies. This species, however, is not considered to have lived attached to the pavement. At a distance 15 to 27 m southeast from the *Heterastraea* colonies, the Carboniferous pavement is bored extensively by *Trypanites*.

To the southeast of Pant-y-Slade on Platform A, the Carboniferous surface exhibits the distinctive tidal rills (Text-fig. 3C), which were first described as channels and ridges by Fletcher



TEXT-FIG. 4. Serpulid colonies in growth position (above Platform B). A, several colonies 300 mm above the Carboniferous substrate. B, enlargement of previous view; scale is 100 mm long.

(1988). The low-sided channels are approximately 1 m wide and 300 mm deep, displaying a consistent orientation. The rills are exhumed from beneath the overlying Sutton Stone.

Only a few metres farther to the south-east, Platform A drops off vertically about 1.5 m to Platform B (Fletcher 1988). It was on this smaller platform that Cope (1971, p. 118) first recorded the occurrence of 'masses of serpulid tubes.' These features were also noted by Ager (1986, p. 30)

as preserved in life position within the Sutton Stone, although he gave the mistaken impression that their colonies rest directly on the Carboniferous Limestone. We observed seven serpulid colonies in the lower part of the Sutton Stone conglomerate above Platform B (Text-fig. 4A–B), spread out over a lateral distance of 2.5 m. On average, each colonial mass is 300 mm in diameter and about 200 mm in height. Six colonies are preserved in life position 300 mm above the unconformity; one occurs only 150 mm above the unconformity surface.

Ager (1986) maintained that these colonies represent the only fossils to be found in growth position in the Sutton Stone of Southerndown. On Platform A, close to the locality with the *Heterastraea* colonies, we observed numerous colonies of cerioid corals in life position within the Sutton Stone at a horizon about 0.5 m above the unconformity surface. On average, these dome-shaped colonies are about 30 to 40 mm in height and 150 mm in diameter, spaced at intervals of approximately 250 mm on a bedding plane. These corals occur at a separate level at least 17.5 mm above the level of the serpulid colonies on Platform B. These occurrences contradict the conclusion by Ager (1986) that the local Sutton Stone is a single, chaotic debris-flow deposit.

#### *Summary of fossil data*

The diversity of the Jurassic rocky-shore community at Southerndown is summarized in Table 1. Seven species are preserved *in situ* on the unconformity surface, *in situ* on clasts in the basal conglomerate, or loose within the Sutton Stone. Due to their encrusting, boring, or clinging habits, these species may be considered fixed elements of the Jurassic rocky-shore community. Other species may belong to this community, but it is difficult to prove their remains were not transported landward from a more offshore setting.

### DISCUSSION

Examples of rocky-shore, intertidal platforms preserved in the geological record are few in number (Johnson 1992). The oldest known possible example is the Precambrian unconformity between the Torridon and Stoer groups in north-west Scotland (Lawson 1976), with exhumed surfaces including a stepped topography with small runnels and channels. Cherns (1982) described tidal erosion surfaces in the Silurian Eke Formation on Gotland, Sweden. These included solution basins comparable with features forming today in coastal karst terrains. Stromatolitic mats developed in some of these basins, and abutted directly against confining side walls. In Israel, Cretaceous disconformity surfaces with *in situ* bivalve borings, which have been partially abraded away, are described by Lewy (1985) as having formed in an intertidal setting. Pliocene and modern abrasion platforms with tidal rills eroded in a contiguous Upper Cretaceous shaley substrate are described by Ledesma-Vazquez and Johnson (1994) from Baja California, Mexico. Like the Israeli disconformities, these intertidal surfaces are bored extensively by bivalves.

In terms of its palaeolatitude, physical topography and range of fossils, a good analogue of the Jurassic platform at Southerndown is the well preserved Pleistocene platform on the shores of Western Australia (Johnson *et al.* 1995). This abrasion platform at the mouth of the Greenough River near Geraldton, exhibits well developed tidal rills eroded in a sandstone substrate. The channel surfaces are uncolonized but the ridge tops are extensively covered by red coralline algae and other encrusters, including oysters, two kinds of serpulid worms, and a scleractinian cup coral. At a slightly higher elevation devoid of tidal channels, the same disconformity surface was colonized by boring barnacles. Gastropods, dominated by robust turbinat shells, were mobile intertidal dwellers on this surface. The entire surface was taken over by a fringing coral reef under transgressive conditions. This Pleistocene disconformity surface has a rocky-shore fauna of at least seven common species. By comparison, the Jurassic rocky shore at Southerndown has an equal number of closely associated species. The main difference between the two systems is that the Jurassic platform seems to lack any encrustations of coralline red algae. Borings on the Pleistocene surface appear to be limited by the success of the coralline red algae as an encrusting cover.

Palmer (1979, p. 214) confirms the occurrence of the long-ranging rhodophyte, *Solenopora*

*jurassica* in Middle Jurassic rocks of England, but the crustose coralline algae, including widely cited forms such as *Lithothamnium*, did not evolve until Late Jurassic time (Wray 1977).

In terms of size, the largest encrusters on the Jurassic unconformity at Southerndown are the colonial corals, here identified as *Heterastraea* sp. and *Allocoeniopsis gibbosa*. Very few examples are known of fossil corals attached directly to non-organic surfaces. The oldest record is from the Upper Ordovician of Hudson Bay, where *Favosites* sp. occurs encrusted on quartzite boulders (Johnson and Baarli 1987) in a rocky-shore setting. Webb (1993) has documented encrustations of another tabulate coral, *Micheliina scopulosa*, on a Carboniferous unconformity in Arkansas. Lower Pennsylvanian corals sit on a karst surface eroded in the Upper Mississippian Pitkin Limestone. An unidentified scleractinian coral is shown by Lescinsky *et al.* (1991, figs 4D–F) to encrust andesite boulders in a rocky-shore setting of Late Cretaceous age in Baja California, Mexico. Octocoral encrusters on gneiss boulders are reported from a rocky-shore setting in the Upper Cretaceous of Bohemia (Zitt and Nekvasilova 1993). The only other coral documented as living as an encruster on an abrasion platform is the scleractinian cup coral, *Rhizotrochus tuberculatus*, reported as the first fossil occurrence from the Upper Pleistocene of Western Australia (Johnson *et al.* 1995). In checking information on corals encrusting non-organic surfaces compiled by Johnson (1992) and Wilson and Palmer (1992), it is evident that the Southerndown locality records one of the earliest instances of scleractinian corals in this habit.

The Cretaceous rocky-shore locality in Baja California also has yielded examples of the pecten, *Lyriochlamys* sp., preserved in life position wedged among boulders (Lescinsky *et al.* 1991, fig. 4A). It is possible that some of the Jurassic pteriod bivalves at Southerndown, such as '*Pecten suttonensis*' or '*Lima gigantea*' may have adopted the same life style. This will be difficult to prove, however, given the nature of floating clasts in the Sutton Stone and parts of the underlying Southerndown Beds.

## CONCLUSIONS

Important observations on the palaeoecology of encrusting oysters and corals in the Sutton Stone of Southerndown were recorded by 19th century paleontologists such as Moore (1877), Tomes (1884), and Duncan (1886). Trueman (1922) placed the unconformity on which the Sutton Stone rests into a much broader context with his seminal description of Early Jurassic islands eroded from Carboniferous carbonates. To this most historic example of an ancient rocky shoreline, we add the first recognition of corals encrusting directly on the unconformity surface and preserved in growth position. The age of the corals *Heterastraea* sp. and *Allocoeniopsis gibbosa* found in this condition, conform with the known Lower Jurassic distribution elsewhere in the British Isles (Negus 1991).

As a time-transgressive facies representing a 'littoral' setting, use of the term Sutton Stone appears to be fully justified as applied particularly to the basal conglomerate resting discontinuously on the unconformity surface. The nature of the eroded platform surface underlying the Sutton Stone and its surprisingly diverse fauna of encrusting, boring, and clinging organisms clearly confirm vestiges of ecological time in the development of this Jurassic rocky shoreline, as suggested by Fletcher (1988). The same argument may be applied to fossil encrustations on clasts and to the preservation in growth position of large coral and serpulid colonies within the Sutton Stone. The mass-flow deposit envisioned by Ager (1986) should not be attributed to a single storm event. Careful reinvestigation of the Southerndown locality indicates that other ancient rocky-shore localities reported in the literature may be expected to yield additional information of palaeoecological value.

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Museum, London) gave us expert advice on the Mollusca. The fossils are left in place at Southerndown, but synthetic replicas are deposited at the Oxford University Museum. Michael G. Bassett (National Museum of Wales) provided many references to the nineteenth century literature on the Lower Jurassic of South Wales. The authors are grateful to Arthur E. Trueman, who taught McKerrow at Glasgow University, and Alfred M. Ziegler, who taught Johnson at the University of Chicago, for passing on their interest in ancient shorelines.

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# ORYCTOCEPHALID TRILOBITES FROM THE CAMBRIAN OF NORTH AMERICA

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**ABSTRACT.** Type and additional specimens of species of *Oryctocephalus*, *Laucastria* and *Oryctocara* are described. Oryctocephalidae have a rostral-hypostomal plate, and hence belong in the Order Corynexochida. Characteristic of the family is the development of lateral glabellar furrows as pits situated inside the axial furrow, and the absence of a border on the pygidium. Two subfamilies are used: Oryctocephalinae, having genal and pleural spines; Oryctocarinae lacking such spines. Species of both groups are found in late Lower to mid Middle Cambrian rocks of North America, Siberia, Asia and Australia, and rare examples occur in South America and Antarctica. Oryctocephalids are typical of deposits in outer shelf and slope areas, in which completely or partially articulated exoskeletons are characteristic. Arrangements of sclerites in such specimens of *Oryctocephalus burgessensis* are considered to result from burial events, not from manoeuvres during exuviation. Compaction and tectonic distortion of specimens in these fine-grained clastic rocks renders questionable some of the characters used in taxonomy.

NEW specimens and the types of two rare oryctocephalids, *Laucastria roddyi* (Lower Cambrian) and *Oryctocara geikiei* (Middle Cambrian), are described, together with the type and additional specimens of *Oryctocephalus reynoldsi*, and well-preserved examples of *O. burgessensis* (both Middle Cambrian). These species of three genera epitomize the morphological range encompassed by the family. The hallmark of an oryctocephalid, as Raymond (1913, p. 716) recognized, is that the glabella had an occipital furrow, and three or four lateral glabellar furrows, each in the form of a pit situated a short distance inside the axial furrow.

Oryctocephalids are found in North America in outer shelf or slope deposits, not in platform sites (Fritz 1990, p. 108). From the late Lower Cambrian *Oleuellus* Zone species of *Laucastria*, *Goldfieldia* and *Arthricocephalus* have been described, and *Chaugaspis* and *Ovatoryctocara* recorded. In the Middle Cambrian species of *Oryctocephalus* (and those referred to *Oryctocephalites* or *Oryctocephalina*) and *Oryctocara* are known from the interval spanning the *Plagiura-Poliella* to *Bathyriscus-Elrathiuu* zones. In the overlying *Ptychagnostus gibbus* Zone (mid Middle Cambrian) the last oryctocephalid, *Tonkinella*, is present. The stratigraphical ranges of species of different genera of oryctocephalids in the Middle Cambrian thus comprise the range of the *Oryctocephalus* Zone in the outer shelf facies (Robison 1976, p. 101, text-fig. 5). In Siberia, eastern Asia, Australia, Antarctica and Argentina (Shergold 1969, text-fig. 2) oryctocephalids are found in Lower and Middle Cambrian rocks of similar facies and range in time. This geographical distribution is independent of the Lower Cambrian olenellid and redlichiid faunal realms (Fortey and Owens 1990, p. 144, fig. 7.2) as is that of the peculiar *Bathynotus* (Whittington 1988, p. 581; Zhao *et al.* 1990). In the Middle Cambrian, burlingiids (Whittington 1994) have a distribution similar to that of oryctocephalids, but also occur in Sweden. Cambrian palaeogeography (Scotese and McKerrow 1990, figs 3–4) points to the isolation of Baltica in high latitudes as having influenced these distributions.

Oryctocephalidae are characteristic of outer shelf sites, many specimens being preserved in fine-grained clastic rocks, and hence flattened; the considerable convexity of the rare limestone preservation of cranidia was described by Fritz (1968, pl. 40, figs 14–16; pl. 41, figs 9–11, 25–27) and Shergold (1969, text-fig. 9). In outer shelf and slope sites, however, articulated dorsal exoskeletons are more commonly found than in open shelf deposits (cf. Fortey 1975; Taylor 1976), so

that the type species of many genera are known from such examples, which may, or may not, have the free cheeks attached. The results of compaction on the outline and lobation of the glabella, and the effects of tectonic distortion, make distinctions between species difficult, either in material from the same or different geographical areas (cf. Shergold 1969, p. 28). They also make questionable the validity of certain characters used in distinctions between genera. For example, is the 'quilted' appearance (Lermontova *in* Vologdin 1940, p. 137) of glabellar lobation, or the sinuosity of the axial furrows in relation to these lobes (used by Shergold 1969, p. 48, in characterizing *Oryctocephalina*) original or partially or wholly the result of flattening a convex cranidium?

Rasetti (*in* Moore 1959, p. O219) included six genera in the Oryctocephalidae, and doubtfully *Cheiruroides* (regarded subsequently as a member of a separate family of Corynexochida by Chang 1963). Rasetti (1952) had earlier described the rostral-hypostomal plate in *Oryctocephalus*, and included this feature, and the lack of a border in the pygidium, as characters of oryctocephalids. He ignored the subfamilies established by Hupé (1953, p. 186; 1955, p. 111) who recognized the two different types of oryctocephalids described herein. These are the *Oryctocephalus* type, having the genal spine and pleural spines on thorax and pygidium, and the *Oryctocara* type, lacking such spines. Hupé also recognized (with question) a third subfamily, to include *Tonkiuella* Mansuy, 1916, with its five thoracic segments and short pygidial axis. Chang (1980), in addition to using these three subfamilies, used *Lancastriinae* Kobayashi, 1935, to include *Lancastria* and other genera. Since 1960 new genera based on Siberian material have been erected, and additional new genera for Chinese Lower and Middle Cambrian species. In Zhang *et al.* (1980) a more elaborate classification is used, which raises oryctocephalids to superfamily rank, and recognizes the spine-bearing and non-spinose forms as separate families, each ranging from Lower to Middle Cambrian. Here I revert to using a single family, with the two subfamilial divisions first recognized by Hupé, because the available information on morphology does not appear to provide diagnostic characters for further subdivision. I attempt here, for brevity, to give in a diagnosis only distinctive, cardinal characters; such characters are not repeated in a diagnosis at a lower taxonomic rank.

Oryctocephalids were placed in the Order Corynexochida in Moore (1959) and by Öpik (1982, p. 6). The protaspis of *Bathyriscus* (Robison 1967; see also Fortey and Chatterton 1988, pl. 17, figs 8, 11, 12, 14–15 (not figs 7, 9–10, 13, 16–19 as given in the plate explanation, in which the names *Bathyriscus?* and *Spencella?* have been transposed in error; B. D. E. Chatterton, pers. comm.), text-fig. 10, 6a–b), has the rostral plate and hypostome fused into a rostral-hypostomal plate. This plate appears to be the cardinal character of Corynexochida, and is associated with the absence of a preglabellar field in later developmental stages, so that in holaspides the frontal lobe of the glabella abuts against the anterior border. Other characters of the protaspis of *Bathyriscus* – the forwardly-expanding glabella, the fossula, proparian suture, and marginal spines – are shared with Ptychopariida (Fortey and Chatterton 1988, text-fig. 10, figs 7a–b, 8a–b). In Ptychopariida the rostral plate and hypostome are separated by the hypostomal suture in the protaspis, and during meraspis development the hypostome becomes natant as a preglabellar field develops. In the meraspis development of Corynexochida (Suvorova 1964, text-fig. 74; Robison 1967; Öpik 1982) intergenal spines may be present, but this is a character shared with Olenellina (Palmer 1957) and Paradoxidoidea (Whittington 1957, fig. 5). Thus, while Robison (1967) first drew attention to the similarities between earliest known developmental stages in Ptychopariida and Corynexochida, the two groups appear to be distinct – the former developing a natant hypostome, the latter retaining from the earliest stage a rostral-hypostomal plate.

## SYSTEMATIC PALAEOLOGY

### Family ORYCTOCEPHALIDAE Beecher, 1897

*Diagnosis.* If the Order Corynexochida is characterized as having the rostral-hypostomal plate present in the smallest known protaspis, and retained into the holaspis stage (and lacking a preglabellar field), then the Oryctocephalidae may be diagnosed as having the glabella with SO

complete, transverse, S1–3 or 4 in the form of pits situated a short distance inside the axial furrow. In many species a pit is developed close to the outer end of the occipital furrow, and a pit is similarly situated in the articulating furrow; thus paired axial apodemes, most conspicuous in the glabella, appear to be characteristic. The pygidium lacks a convex or smooth border, pleural and interpleural furrows extend to the margin; doublure narrow and gently convex.

*Stratigraphical range.* In North America oryctocephalids appear first in the high Lower Cambrian *Olenellus* Zone. The youngest known appears to be a species of *Tonkinella* (Fritz 1971, p. 1168, figs 4, 6) in a deeper water faunule with agnostids at the base of the Eldon Formation. Higher in the Eldon Formation is the Black Band, the fauna of which (Robison 1984, p. 6) is that of the *Ptychagnostus gibbus* Zone. Faunas in Eastern Asia (Chang 1988) include oryctocephalids spanning a comparable range, species of *Tonkinella* being the youngest and occurring at a similar level to that in North America. In the north-east part of the Siberian platform, in the transition to, and in the marine argillaceous facies, oryctocephalids occur throughout the early Middle Cambrian Amgan Stage. Earliest appearing, with paradoxidids, are *Oryctocephalops frischenfeldi* and species of *Ovatoryctocara* and *Oryctocara* (Egorova *et al.* 1976, p. 27, pls 43–46; Astashkin *et al.* 1991, pp. 74, 78, 82), with species of *Oryctocephalus* appearing at this level and higher in the stage (Egorova *et al.* 1976, p. 28, pls 47–53; Astashkin *et al.* 1991, p. 73). In the highest part of the Amgan Stage Astashkin *et al.* (1991, p. 68) record species of *Tonkinella* occurring with *Ptychagnostus gibbus*, *Tomagnostus fissus* and *Paradoxides sacheri*. Thus species of *Tonkinella* appear to be everywhere the youngest oryctocephalids.

*Remarks.* The North American material illustrated herein shows that there were two groups of oryctocephalids. One, typified by species of *Oryctocephalus*, had a genal spine, a spine on the end of each thoracic pleura, and marginal pygidial pleural spines. *Oryctocara* exemplifies species in which there were no marginal exoskeletal spines, and a granulate sculpture. Species of the same two groups have been recognized in Siberia by Russian authors (Lermontova, *in* Vologdin 1940; Tchernysheva 1962; Suvorova 1964), in Australia (Shergold 1969) and in China (e.g. Zhang *et al.* 1980). These two widespread branches of the oryctocephalids are regarded as subfamilies. *Lancastria* is placed in the spinose group, not in a separate subfamily. The position of the long-known *Tonkinella* Mansuy, 1916, species of which are widely distributed (Rasetti 1951, p. 196, pl. 31, figs 13–18; Kindle 1982, p. 10, pl. 1.1, figs 8, 12; Young and Ludvigsen 1989, p. 20, pl. 6, figs 5–11; fig. 6B; Reed 1934, p. 9, pl. 1, figs 3–8, 9?, 10; Tchernysheva 1962, p. 27, pl. 3, figs 1–6), is uncertain. Hupé (1953, p. 186) placed it with question in a separate subfamily, referring to the pygidium, which has a relatively short axis, lacks interpleural furrows, and hence has a radiating arrangement of pleural furrows. Pleural and marginal pygidial spines appear to be absent, but Rasetti (1951, pl. 31, fig. 14) shows a long genal spine, extending beyond the pygidium in his restoration (Rasetti, *in* Moore 1959, fig. 162.6). I therefore prefer to place *Tonkinella* in the spinose group of oryctocephalids, although it lacks pleural spines. McNamara (1986, p. 138, fig. 9) suggested that a paedomorphic reduction in the number of thoracic segments in Middle Cambrian oryctocephalids led to *Tonkinella*; this reduction being accompanied by an increase in relative size of the pygidium, loss of pleural spines, and a decrease in width (tr.) of the free cheek. McNamara also doubted that *Thoracocara* Robison and Campbell, 1974, a progenetic Corynexochida, should be assigned to the Oryctocephalidae, and I share this view. Shergold (1969, p. 56) placed his new genus *Barkleyella* in the Tonkinellinae, but only small cranidia are known, so that its position in the present classification is uncertain.

#### Subfamily ORYCTOCEPHALINAE Beecher, 1897

*Diagnosis.* Genal spine present, facial suture opisthoparian; a single spine arising from the outer end of each thoracic and pygidial pleura.

*Remarks.* *Oryctocephalus*, *Oryctocephalites*, *Oryctocephalina*, *Lancastria*, and *Oryctocephalops* may be placed within this subfamily, probably also *Goldfieldia* and *Tonkinella*; I do not use subfamily Lancastriinae Kobayashi, 1935 (p. 129). The Lower Cambrian *Protoryctocephalus* (Zhang *et al.* 1980, p. 270, pl. 91, fig. 1) clearly belongs here also, but *Oryctocephaloides* (Zhang *et al.* 1980, p. 271,

pl. 96, figs 5–8) has S1 continuous and S2 and S3 faint, and lacks the characteristic oryctocephalid pits. The Lower and Middle Cambrian *Oryctometopus* (Suvorova 1964, p. 252, pl. 29, figs 8–11, text-fig. 75) is known primarily from the cranidium, so that its relationships are uncertain.

### Genus ORYCTOCEPHALUS Walcott, 1886

*Type species.* *Oryctocephalus primus* Walcott, 1886.

*Diagnosis.* Glabella parallel-sided or expanded slightly forward to a maximum anterior width, S1–3 deep pits, S1 pits connected by shallow transverse furrow, S2 and S3 pits may be connected by furrows successively shallower forwards, S4 pits small, faint; anterior margin of rostral-hypostomal plate slightly wider (tr.) than maximum glabellar width. Thorax of seven segments, pygidium with five or six pairs of pleurae.

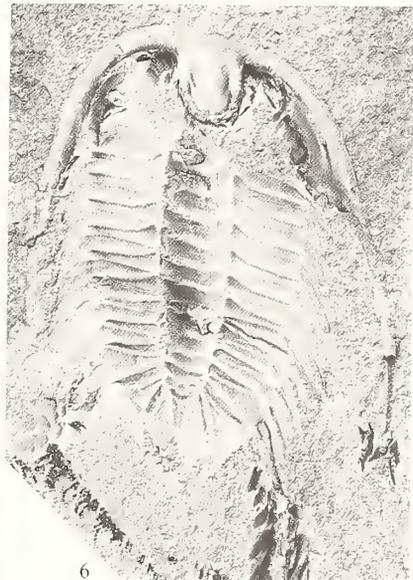
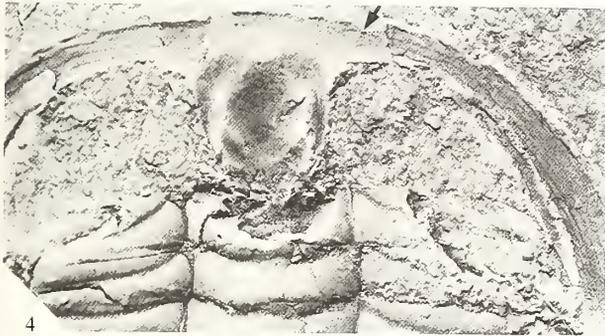
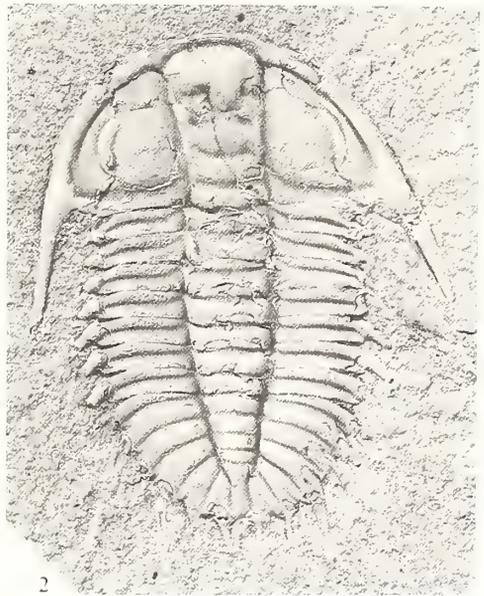
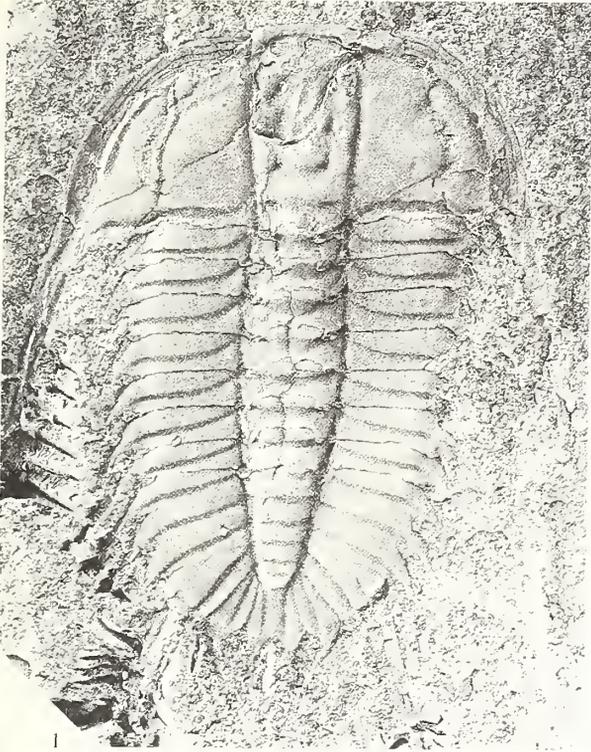
*Remarks.* *Oryctocephalus reynoldsi* is the most completely known species, recognized world-wide, and the diagnosis is based largely upon it. The type species, known only from detached cranidia and pygidia, was redescribed by Palmer (1954, p. 68, pl. 15, figs 1–2; the pygidium by Shergold 1969, p. 15, text-fig. 4) and is from the Middle Cambrian, Pioche Formation, Pioche, Nevada. Fritz (1968, p. 201, pl. 40, figs 14–16) described a damaged cranidium from limestone in the *Albertella* Zone, which retained some convexity, and compared it with *O. primus*.

*Oryctocephalites typicalis* Resser, 1939b (p. 44, pl. 3, figs 1–6; holotype cranidium designated p. 66) is from the 'Langston' Limestone, Wasatch Mountains, Idaho. It is known only from isolated cranidia and pygidia (see Fritz 1968, p. 202, pl. 41, figs 9–11; Shergold 1969, text-fig. 9; Palmer and Halley 1979, p. 84, pl. 13, figs 1–4), and is said to be distinguished from *Oryctocephalus* by the more oval glabellar outline, the maximum width being at a level between S2 and S3; the pygidium has five pairs of pleurae. Shergold (1969, p. 17) sought to characterize *Oryctocephalites* by the pygidium having only five segments, but Palmer and Halley (1979, p. 83) did not accept this. These latter authors stated that in *Oryctocephalites* only the S1 pits are connected by a shallow transverse furrow, whereas in *Oryctocephalus* at least the S1 and S2 pits are connected by transverse furrows. In flattened material such a distinction would be difficult to apply. Until more complete specimens of the species concerned are described, use of the name *Oryctocephalites* will remain problematical.

*Oryctocephalina reticulata* Lermontova, 1940 (in Vologdin 1940, p. 137, pl. 42, figs 3, 3a–b) is the type species of a genus supposedly distinguished by the sinuous course of the axial furrows around inflated portions of the glabella outside pits S1–3. This character is shown in the flattened cranidia illustrated by Tchernysheva (1962, pl. 2, figs 1–8) and by Shergold (1969, pl. 11, figs 2–3; pl. 12, fig. 4). Whether such features result from flattening of a convex cranidium, or are original, is uncertain. Palmer and Halley (1979, p. 83, pl. 12, figs 21–22, 27) use this generic name with question for

#### EXPLANATION OF PLATE I

- Figs 1, 3–6. *Oryctocephalus reynoldsi* Reed, 1899. Middle Cambrian, Stephen Formation, British Columbia, Canada. 1, SM A1425, holotype, north-west slope, Mt Stephen; dorsal view of internal mould;  $\times 5$ . 3, 6, ROM 49966, Mt Stephen; external mould of exoskeleton lacking cranidium, combined with internal mould of rostral-hypostomal plate and doublure; 3, oblique view of rostral-hypostomal plate and adjacent doublure;  $\times 10$ ; 6, entire specimen, ventral view;  $\times 3$ . 4–5, ROM 49968a, internal mould of five anterior segments and detached pygidium, combined with external mould of doublure and rostral-hypostomal plate, Mt Stephen; 4, dorsal view of portion of anterior, connective suture arrowed;  $\times 7$ ; 5, posterior portion of pygidium, inner edge of doublure arrowed;  $\times 7$ .
- Fig. 2. *Oryctocephalus burgessensis* Resser, 1938. Middle Cambrian, Burgess Shale, British Columbia, Canada. ROM 38613, talus in Walcott quarry, internal mould, pleural spines on left side bent upwards so that basal portions appear swollen;  $\times 5$ .



limestone cranidia retaining convexity, which show inflated outer portions of L1 and L2. Tchernysheva referred the type species *reticulata* to *Oryctocephalus*, because it was known only from cranidia. As discussed below, Shergold (1969, pl. 11, fig. 1) had an entire dorsal exoskeleton with this type of glabella, and hence referred it to *Oryctocephalina*. On the other hand, as Shergold recognized, the entire exoskeleton is strikingly like that of *Lancastria*.

*Oryctocephalus reynoldsi* Reed, 1899

Plate 1, figures 1, 3–6

*Holotype*. SM A1425, internal mould of exoskeleton in shale. In all probability Reynolds' collection (Reed 1899) came from the well-known USNM locality 14S, on the north-west side of Mt Stephen (Walcott 1908a); also locality S8d of Rasetti (1951, pp. 76, 128) and locality S of Fritz (1971, figs 1, 6). The collection contains also *Ogygopsis klotzi* (SM A1636, 1638, 1451), *Olenoides serratus* (SM A1440), *Elrathina cordillerae* (SM A1643), *Kootenia dawsoni* (SM A1424), *Bathyriscus rotundatus* (SM A1423), and *Peronopsis montis* (SM A1644). These identifications were made following Rasetti (1951), and indicate his *O. klotzi* faunule and hence the early *Bathyriscus-Elrathina* Zone in the Stephen Formation (Fritz 1971, p. 1164).

*Other Material*. USNM 116238, internal mould, original of Rasetti 1951, pl. 29, fig. 5; external mould, original of Whittington 1992, p. 125, pl. 66; Burgess Shale, Walcott quarry. ROM 49966 to 49968 inclusive, from locality 9 of Collins *et al.* (1983), which also yielded *O. geikiei*; *Glossopleura* Zone, Stephen Formation. ROM 49965, Mt Stephen.

*Stratigraphical range*. Stephen Formation, *Glossopleura* and *Bathyriscus-Elrathina* zones.

*Description*. The holotype (Pl. 1, fig. 1) was illustrated originally only by a drawing. The exoskeleton has been flattened by compaction, compressing the glabella against the external mould of the rostral-hypostomal plate (not mentioned by Reed) and giving an irregular longitudinal infold in the thoracic axis. This compaction rotated the rostral-hypostomal plate slightly clockwise, causing the border to project on the left side in the line of the axial furrow; it also impressed the glabellar pits into the mould of the hypostome.

The glabella appears to expand slightly and evenly forward from the occipital ring to the level of the lateral border furrow, and is then rounded and abuts against the narrow (sag. and exs.) anterior border. The straight, shallow occipital furrow deepens a short distance inside the axial furrow to form an apodeme. The three pairs of deep pits, S1–3, are approximately evenly spaced from each other and the occipital furrow, and are situated a short distance inside the axial furrow. The S1 pits are joined by a shallow transverse furrow. In USNM 116238, and a large, incomplete external mould of a cranidium on ROM 49967, a smaller, shallower S4 is present, situated closer to the axial furrow and opposite the end of the eye ridge. The long, narrow (tr.) curved palpebral lobe is situated far out on the cheek, the anterior branch of the suture curving forward, the posterior directed slightly outward and backward and then curving to cross the posterior border. Eye ridge low, directed inward and forward, lying a short distance inside the lateral cephalic border. This border is wider than the anterior border, convex, underlain by the ventrally convex doublure. The doublure bears four or five strong terrace ridges running subparallel to the margin. The rostral-hypostomal plate (Pl. 1, figs 3–4, 6) was shield-shaped, the middle body of the hypostome convex, divided by a middle furrow, the smaller posterior portion inflated. A low macula, smooth externally, lay adjacent to the inner end of the middle furrow. The lateral border of the hypostome was narrow and convex, and bore terrace ridges parallel to the margin, these ridges curving outward anteriorly, and continuous with ridges on the inner edge of the doublure. The posterior border of the hypostome is convex but is narrower and lower than the lateral border, and bears terrace ridges. The small anterior wing is steeply inclined, without a pit in the external surface and hence presumably there was no wing process. The connective suture appears not only to have bounded the rostral plate, but to have continued along the anterolateral edge of the anterior wing, separating it from the almost vertical inner edge of the doublure. The external surface of the rostral plate bears only a single terrace ridge situated close to the anterior margin, and hence is distinct from the adjacent doublure. The inner portion of the posterior cephalic border is transverse, and outside the fulcrum the posterior margin curves back into the broad base of the genal spine; this spine extends back so that the tip is level (tr.) with the terminal axial portion of the pygidium (Pl. 1, fig. 6).

The thorax has the last three of the seven segments progressively shorter, the axis narrowing. The articulating furrow deepens into a pit a short distance from the axial furrow, an apodeme in line (exs.) with that of the

occipital furrow. The pleura has a wide (tr.) horizontal inner portion, the fulcrum approximately in line (exs.) with the eye lobe, the outer portion of the pleura narrowing rapidly and prolonged by a thorn-like pleural spine; this spine slightly longer on successive segments. Reed (1899) portrayed a short median spine on each axial ring, perhaps based on an irregular infold caused by compaction (Pl. 1, fig. 1); there seems no evidence for such spines. The irregularly broken posterior edge of the inner portion of each pleura, and the posterior cephalic border, is underlain by the leading edge (an articulating flange) of the following segment, and there is a small facet in front of the base of the pleural spine.

The pygidium shows five axial rings and a short terminal portion, the six pairs of pleurae in a radial arrangement, spinose, the last pair directed exsagittally behind the axis. The interpleural division is faint in the first three segments, a strong fold behind the next two segments, a faint sagittal furrow behind the axis. The pleural furrows are relatively broad and deep. The longer fourth segment bears a pleural spine which is wide at the base and extends back far beyond the pygidial margin (Whittington 1992, pl. 66). The doublure of the pygidium (Pl. 1, fig. 5) is a narrow strip, gently convex ventrally, beneath the outermost portion of the pleural region, continuous with the ventral side of the pleural spines. It bears terrace ridges which run concentrically to the margin, the outer ones curving to continue inside the edges of the spines. Thus the base of each pleural spine is seen to have arisen from the entire width of the pleura.

*Remarks.* Shergold (1969, p. 18) described *O. reynoldsi* from the Middle Cambrian of Australia, and very similar material is known from beds of the same age in Siberia (e.g. *O. reynoldsiiformis* in Tchernysheva 1962, pl. 1, figs 1–8) and Korea (Saito 1934, p. 232, pl. 27, figs 17–20).

*Oryctocephalus burgessensis* Resser, 1938b

Plate 1, figure 2; Plate 2, figures 1–7; Plate 4, figure 1

1938b *Oryctocephalus burgessensis* Resser, p. 37.

1951 *Oryctocephalus matthewi* Rasetti, p. 195, pl. 26, figs 4–5.

*Holotype:* USNM 96487, Walcott quarry, Burgess Shale (Rasetti 1951, pl. 26, fig. 2).

*Other material.* GSC collections of 1966 and 1967, from levels between 5 and 14 ft (1.52 to 4.27 m) in the Walcott quarry (Whittington 1971, fig. 3). ROM 38613, 49963–4, from talus in the Walcott quarry.

*Geological horizon.* Middle Cambrian, Stephen Formation, *Bathyriscus-Elrathina* Zone; Walcott quarry in *Ptychagnostus praecurrens* Zone (Robison 1976, p. 104; Conway Morris 1989, fig. 1).

*Remarks.* A single specimen from the Walcott quarry (Whittington 1992, pl. 66) is referred to *O. reynoldsi*. All other specimens from the same locality, loaned to me from the GSC and ROM collections, are here referred to *O. burgessensis*. They are distinguishable from *O. reynoldsi* (compare Pl. 1, figs 1 and 6, with Pl. 1, fig. 2) by the more rounded antero-lateral outline of the cephalon, by the slightly advanced genal spine, and shorter genal and fourth pygidial pleural spines. These characters were not mentioned by Rasetti (1951, p. 194, pl. 26, figs 1–3), who discriminated a second species, *O. matthewi* (Rasetti 1951, p. 195, pl. 26, figs 4–5), in material from the Walcott quarry. This latter species differed supposedly in its shorter pleural and pygidial spines, but I am unable to see such differences in the available sample, nor are they evident in Rasetti's illustrations.

The glabella of *O. burgessensis* shows the deep, round S1–3 pits, the S1 pair joined by a shallow furrow, a faint, small S4 pit anterolaterally (Pl. 2, fig. 2), and an apodemal pit at the distal end of the occipital furrow. A small median occipital tubercle is present close to the anterior margin of the ring. At the fulcrum the posterior border turns to be directed outward and forward, rather than transversely, the angle in the posterior margin obtuse. In some specimens (Pl. 2, fig. 2) this angle is a blunt, backwardly-directed projection. Distally the border runs into the base of the genal spine, which lies in a transverse line with S0. The tip of the genal spine lies in a transverse line with the fifth thoracic segment. The curved thorn-like pleural and pygidial spines show a progressive increase in length from the first thoracic to the fourth pygidial spine, the two pairs inside the fourth pair being shorter (Pl. 2, figs 2, 5–6). The fourth pygidial spine is broad, and, in some specimens, of

length (exs.) less than that of the pygidium (sag.), in others broader and longer. The small triangular facet of the outer portion of the pleural segments, situated in front of the base of the pleural spine, has been exposed in the second, third and seventh segments of the original of Plate 2, figures 1 and 4.

McNamara and Rudkin (1984, p. 171, fig. 13b) described a specimen collected from talus below the Walcott quarry, thought to reveal events during exuviation, because the free cheeks and rostral-hypostomal plate were inverted, directed backwards, and lying to the left of the cranium and thoracopygon. Other such assemblages of exoskeletal sclerites, including an articulated exoskeleton, are shown in Plate 2, figures 1–7 and Plate 4, figure 1 and their arrangement is commented on. No trace of appendages is preserved in any of these specimens, although they were found in layers at the same levels as those yielding soft-bodied fossils such as *Marrella splendens* (Whittington 1971, fig. 5). It is thought (Whittington 1980, p. 129; Conway Morris 1986, p. 424) that the Burgess Shale fossils were buried after transport in a suspension of fine-grained sediment, many coming to rest, as the sediment settled, parallel to the bedding planes. Hence the arrangement of the sclerites in these specimens is not related to moult behaviour but to decay, transport and burial. Before transport, were they carcasses or exuviae (Whittington 1990, fig. 6) held together by the ventral cuticle and articulatory membranes? Partial decay before transport, weakening the links between sclerites, may account for separation of the cranium and some thoracic segments from the rest of the exoskeleton, and events during transport caused the rotation and partial separation of other sclerites. Decay of the remaining soft parts must have taken place after burial. I incline to the view that most, if not all, these specimens were exuviae. On moulting, the facial and connective sutures would have opened to allow egress of the newly-moulted animal, the weakest link in the exuviae being that between the cranium and first thoracic segment (Whittington 1990, p. 35). The elasticity of the ventral cuticle, however, may have brought the edges of the connective sutures back into juxtaposition. Hence, specimens such as the originals of Plate 2, figures 3, 6–7, and Plate 4, figure 1, may have been partially decayed exuviae before transport led to the loss of some sclerites and twisting of others. More complete assemblages of sclerites (Plate 2, figs 2, 5) may have been fresh exuviae before transport, or possibly carcasses.

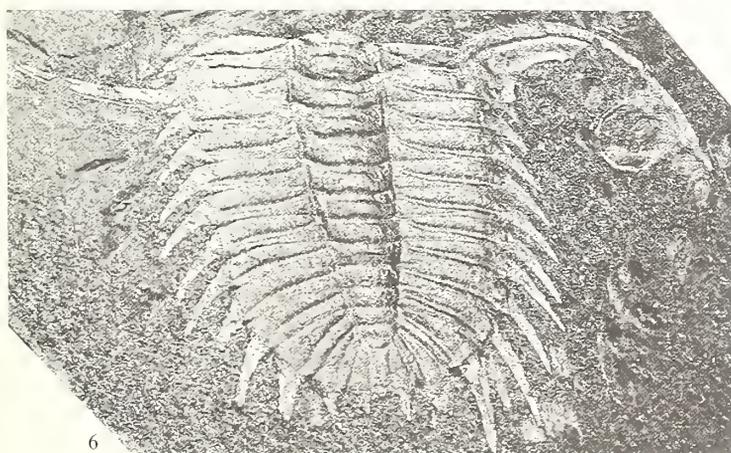
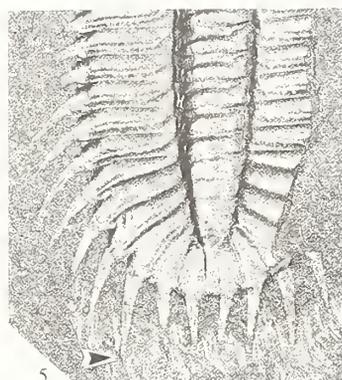
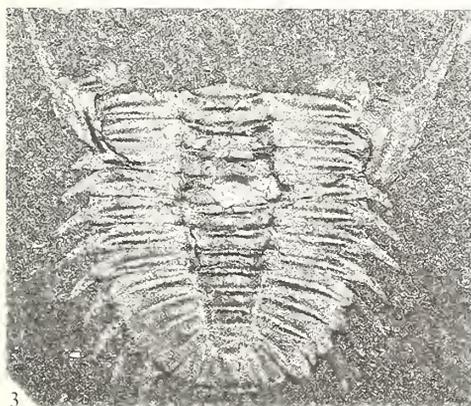
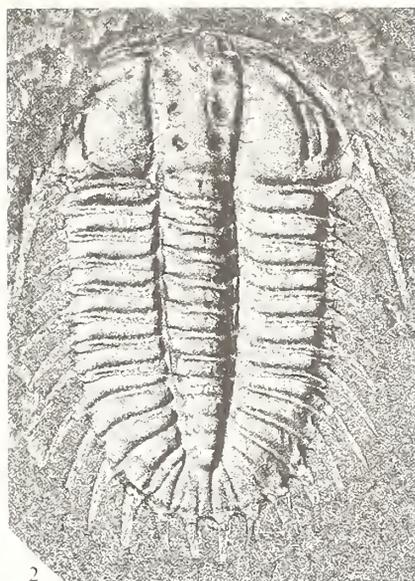
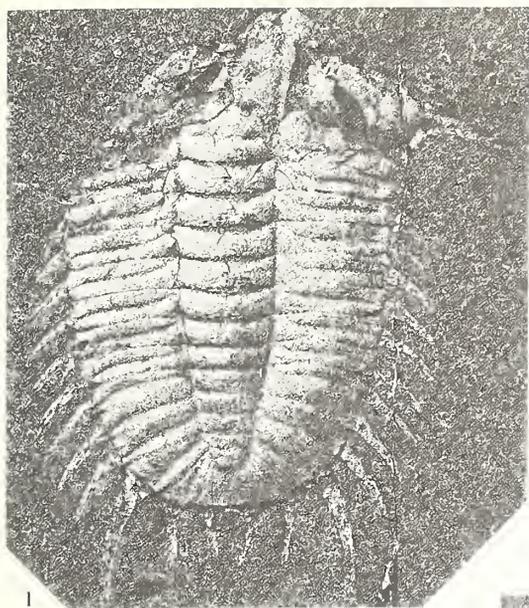
#### Genus LANCASTRIA Kobayashi, 1935

*Type species. Olenopsis rodnyi* Walcott, 1912.

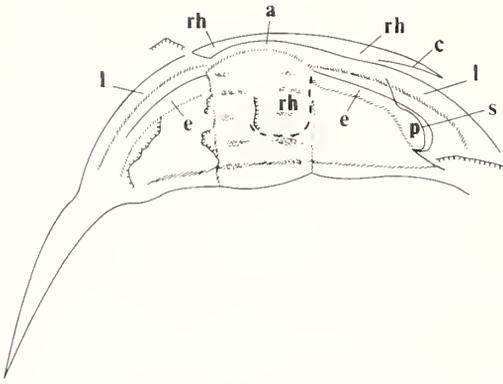
*Diagnosis.* Glabella subparallel-sided, S1–4 pits present, shallow transverse furrow connects S1 pair; eye lobe on outer part of cheek; anterior margin of rostral-hypostomal plate wide, connective suture

#### EXPLANATION OF PLATE 2

Figs 1–7. *Oryctocephalus burgessensis* Resser, 1938. Middle Cambrian, Burgess Shale, British Columbia, Canada. Different arrangements of exoskeletal sclerites chosen from examples found in Walcott quarry; see discussion in text and further example in Plate 4, figure 1. 1, 4, GSC 110749; level 10 ft 4–8 ins (3.15 to 3.25 m), Walcott quarry; 1, exoskeleton with free cheeks displaced, cranium fractured;  $\times 5$ ; 4, enlargement of left side of thorax showing pleural facets (arrowed);  $\times 10$ . 2, 5, GSC 110747; level 5 ft 5 ins to 6 ft 2 ins (1.65 to 1.88 m), Walcott quarry; 2, internal mould of articulated dorsal exoskeleton;  $\times 5$ ; 5, part of external mould showing complete fourth pleural spine of pygidium (arrowed) and narrow marginal band of doublure;  $\times 5$ . 3, GSC 110750, cranium missing, free cheeks and rostral-hypostomal plate linked together, inverted, backward-facing and lying above thoracic segments 1–5; level 10 ft 4–8 ins (3.15 to 3.25 m), Walcott quarry;  $\times 5$ . 6, GSC 110748, cranium missing, right free cheek and rostral-hypostomal plate inverted, left free cheek detached, both cheeks partly beneath segments 1–3; level 10 ft 4–8 ins (3.15 to 3.25 m), Walcott quarry;  $\times 5$ . 7, GSC 110746, cranium and anterior four thoracic segments missing, remainder of exoskeleton articulated and in original relation; level 5 ft 1–6 in (1.55 to 1.77 m), Walcott quarry;  $\times 5$ . Photographed in reflected light, dorsal views.



WHITTINGTON, *Oryctocephalus burgesensis*



TEXT-FIG. 1. *Lancastria rodnyi* (Walcott, 1912). An interpretation of what is preserved in the cephalon of the holotype (Pl. 3, fig. 2). a, anterior border; c, connective suture; e, eye ridge; l, lateral border; p, palpebral lobe; rh, rostral-hypostomal plate; s, facial suture. Hachures show break in slope; dashed line shows outline of hypostome.  $\times 8.5$ .

directed strongly inward. Thorax may be non-fulcrate, of twelve segments, pygidium of four to eight segments.

*Remarks.* As indicated below, specimens from the Lower Cambrian in China, and the Middle Cambrian in Australia, show many similarities to the type species. *Goldfieldia*, known only from rare cranidia, was described from the Lower Cambrian of Nevada (Palmer 1964, p. 7, pl. 1, figs 14, 16–18) and recognized in the early Middle Cambrian of Antarctica (Palmer and Gatehouse 1972, p. 20, pl. 3, figs 7–8). It has the glabella expanding forward, with S1–4 and a small depression at the anterior margin; the anterior border is narrow, the fixed cheek wide. In these latter characters it resembles *Lancastria*. The cranidium described from the Lower Cambrian of northwestern Canada (Fritz 1972, p. 37, pl. 19, figs 20–21) appears to be of a similar type.

*Oryctocephalops frischenfeldi* Lermontova, 1940 (*in* Vologdin 1940, p. 137, pl. 42, figs 1, 1a–c); Tchernysheva 1962 (p. 42, pl. 3, figs 11–14); Suvorova 1964 (p. 246, pl. 28, figs 1–11; pl. 29, figs 1–7, text-figs 73–74) is from the Middle Cambrian, lower Amgan Stage, of the northern and eastern Siberian platform. This species is like *L. rodnyi*, but the glabella expands forward slightly; both species may have twelve thoracic segments and the thorax of *O. frischenfeldi* appears to be non-fulcrate; the pygidium of the latter has only two segments. Suvorova described developmental stages of the meraspid cranidium, which in the earliest stage had long intergenal spines. A rounded projection from the posterior border of the holaspis is the remnant of this spine. Outside this projection the posterior border is directed outward and forward, so that the genal spine is slightly advanced.

#### *Lancastria rodnyi* (Walcott, 1912)

Plate 3, figures 1–5; Text-figure 1

*Holotype.* USNM 58363, counterpart moulds in shale, quarry just west of Fruitville (the name 'Fruitvale' is an error), 2 miles (3.2 km) north of Lancaster, Lancaster County, Pennsylvania.

*Other material.* FM PA 89A, B, counterpart moulds of an incomplete exoskeleton, half a mile (800 m) south

#### EXPLANATION OF PLATE 3

Figs 1–5. *Lancastria rodnyi* (Walcott, 1912). Lower Cambrian, Kinzers Formation, *Olenellus* Zone, Pennsylvania, USA. 1, 4, FM PA 89, half mile (800 m) south of East Petersburg, Lancaster County; 1, latex cast of external mould, dorsal view;  $\times 6$ ; 4, internal mould, dorsal view, arrow indicates possible division between thorax and pygidium;  $\times 6$ . 2, 5, USNM 58363, holotype, Fruitville, north of Lancaster; 2, internal mould, dorsal view, arrow indicates possible division between thorax and pygidium;  $\times 5$ ; 5, latex cast of external mould, dorsal view, tip of arrow on posterior border of cephalon;  $\times 5$ . 3, FM PA 90, cranidium, latex cast of external mould, dorsal view; Donnersville, Lancaster County;  $\times 7$ .



WHITTINGTON, *Lancastria rodnyi*

of East Petersburg, Lancaster County, Pennsylvania. FM PA 90, external mould of cranidium, Donnerville Quarry, Lancaster County, Pennsylvania.

*Geological horizon.* Lower Cambrian, Kinzers Formation, Lower Member, *Wanneria walcottanus* faunule (Campbell and Kauffman 1969), *Olenellus* Zone. In the block containing the holotype is a cephalon, and a small holaspid (with fifteen thoracic segments and the median spine) of *Olenellus* (*Paedeumias*) *transitans sensu* Palmer and Repina (1993, p. 22).

*Description.* The subparallel-sided glabella is divided by a straight occipital furrow (SO) and the pits S1–4, SO and S1–3 equally spaced from each other and the posterior margin, L4 and the anterior glabellar lobe successively slightly shorter (sag. and exs.) than LO–3. An apodemal pit is situated close to the outer end of the SO, the pits of S1–3 situated a short distance in from the axial furrow, the S1 pair connected by a shallow furrow; S4 is a shallower and smaller pit than S1–3, and is situated closer to the axial furrow. Long, curved eye lobe situated close to the lateral and posterior borders, anterior margin in transverse line with L3; palpebral lobe rises steeply from convex cheek. Prominent eye ridge directed inward and forward to axial furrow opposite L4. Anterior border narrow (sag.), convex, widening in front of the axial furrow and merging with the convex lateral border. Broad, shallow depression, the outer portion of the genal field, separates eye lobe and eye ridge from lateral border. Both the depth of this depression, and the convexity of the lateral cephalic border, appear to have been exaggerated by crushing (especially on the left side) of the holotype. Posterior border narrow (exs.), convex, border furrow well-defined; the lateral and posterior borders merging into the broad base of the genal spine, which tapers rapidly, the tip opposite the fifth thoracic segment. Anterior branch of suture curves forward and slightly inward, on to the lateral border; posterior branch of suture directed straight outward and backward. My interpretation of the holotype (Text-fig. 1) is that the rostral-hypostomal plate is partially preserved, displaced to the right and slightly in front of the cranidium. The rostral plate portion was broad (tr.), bounded by a strongly-inwardly directed connective suture. The concave impression on the mid-right of the glabella is part of the hypostomal portion, an external mould which shows a narrow, convex lateral border.

The thorax and pygidium in the holotype (Pl. 3, figs 2, 5) are of nineteen axial rings and pleurae and have a small terminal axial portion. Behind this terminal portion is a short (sag. and exs.) convex area, which bears a pair of short, backwardly-directed spines. A shallow sagittal groove separates these spines; it appears not to be a single plate as interpreted by Shergold (1969, p. 47, text-fig. 16A). Axial rings of uniform length (sag. and exs.), this length reduced progressively posteriorly, narrow (sag. and exs.), articulating furrow with shallow apodemal pit distally, faint lateral inflation of each axial ring, deep pit of articulating process in axial furrow. Pleurae (exclusive of spines), widest at first segment, decreasing progressively in width (tr.) and becoming more strongly backwardly directed, the last pair directed exsagittally. The pleural furrow curves back from the axial furrow, and is then directed slightly obliquely across the pleura. Pleural spines short anteriorly, those of segments 7–16 subequal in length, progressively more backwardly directed, by segment 15 slightly inward, spines of segments 17–19 shorter, the pair behind the terminal piece shortest. A second specimen (Pl. 3, figs 1, 4) has the thorax and pygidium displaced slightly and rotated to the right behind segment 7, and on the left shows 16 segments and the short (sag.) terminal axial piece. The terminal piece bears a pair of short spines. Walcott (1912, p. 245) and Shergold (1969, p. 47) regarded the thorax of the holotype as of nineteen segments, and the terminal piece as the pygidium. Admittedly it is difficult to detect a clear division between thorax and pygidium, but the broken rings of the axis show traces of the articulating half ring beneath the occipital ring and segments 1–12, but no farther posteriorly. Across the doublures of the pleural spines divisions between segments may be seen on segments 6–12, but not farther backward. I conclude that in the holotype the anterior twelve segments composed the thorax, and that the pygidium included seven segments and the terminal piece. The axis in the second specimen shows faint traces of articulating half rings, but clear divisions may be seen on the left side between segments 6–12, suggesting a thorax of twelve segments and a pygidium of four segments and the terminal piece.

In these two flattened specimens the anterior margin of each pleura passes below the edge of the segment in front to form an articulating flange, but there is no evidence of the fulcrum or a fulcral process. I consider it probable that the thorax was non-fulcrate.

An additional specimen (Pl. 3, fig. 3) appears to be that of an incomplete cranidium, showing the pits of S1–3, palpebral lobe and eye ridge, and posterior border.

*Remarks.* This species is very rare in the Kinzers Formation (Campbell and Kauffman 1969), and unknown elsewhere in North America. The holotype of *Oryctocephalina lancastrioides* Shergold, 1969 (pl. 11, fig. 1), from the Middle Cambrian of central Australia, is similar to that of *L. roddyi*,

especially if the latter has been shortened (sag. and exs.) by distortion. Shergold's holotype has the mould of the rostral-hypostomal plate (the hypostomal portion with a narrow, convex border) in place beneath the glabella. His enlargement (1969, p. 12, fig. 4) shows the impression of the inwardly directed connective suture of the rostral portion beneath the cephalic border, indicating that this rostral portion was wide (tr.). Shergold (1969, pp. 48, 51) preferred to refer his species to *Oryctocephalina*, but I consider it more probable that the species *lancastrionides* should be placed in *Lancastrion*.

A species from the Lower Cambrian of China, *Changaspis placenta* (Zhang *et al.* 1980, pl. 89, fig. 11; pl. 90, figs 1–5) is like *Lancastrion roddyi* in glabellar lobation, position of eye lobe, and narrow, convex cephalic border; the thoracopygon in the two species is also similar. The specimens of *C. placenta* show the wide (tr.) rostral plate fused to the shield-shaped hypostome, to form a rostral-hypostomal plate. Species of *Changaspis* are recorded from the Lower Cambrian of the Eastern Subprovince and Chiangnan Belt of the southwest China platform (Chang 1988, p. 55, chart 3), and from the Lower Cambrian of Greenland (Blaker 1986, p. 68, fig. 3).

#### Subfamily ORYCTOCARINAE Hupé, 1953

*Diagnosis.* Exoskeleton lacking genal spine and pleural spines on thorax or pygidium; facial suture opisthoparian, may be gonatoparian, and in *Ovatoryctocara* is proparian; thorax non-fulcrate in certain genera; granulate sculpture in many species.

*Remarks.* In the genera described or discussed below (*Oryctocara*, *Arthricocephalus* and its subgenera, *Sandoveria* and *Ovatoryctocara*) the rostral-hypostomal plate is unknown. However, the absence of a preglabellar field, and the glabella abutting against the narrow (sag. and exs.) anterior border, suggest that the hypostome was conterminant; it may have been fused to the rostral plate. Because the glabellar furrows are developed as pits it remains a reasonable assumption that these forms are oryctocephalids. They also have the characteristic pygidium, lacking a clearly defined border but having probably a narrow doublure.

In the Lower and Middle Cambrian of China many species of Oryctocarinae have been described, including those referred to *Feilongshania* (Zhang *et al.* 1980, p. 272, pl. 91, fig. 3) and *Duyumaspis* (Zhang *et al.* 1980, p. 273, pl. 91, figs 5–6). The type species of these two genera, from the Lower Cambrian, have a relatively much wider axial region than *Oryctocara*. The thorax in *Feilongshania* appears to be non-fulcrate, but in *Duyumaspis* the fulcrum appears to be situated at about half the width (tr.) of the pleura, the outer portion of which is faceted.

#### Genus ORYCTOCARA Walcott, 1908b

*Type species.* *Oryctocara geikiei* Walcott, 1908b.

*Diagnosis.* Axial region narrow, about one-quarter the width of the exoskeleton; glabella parallel sided, S1–3 deep, S4 shallow; eye lobe situated mid-way across cheek. Thorax of twelve segments, pygidium of seven segments; doublure narrow, convex.

*Remarks.* The type material of *Arthricocephalus chauveani* Bergeron, 1899, from the Lower Cambrian of Guizhou (Lane *et al.* 1988) shows that the glabella expands forward slightly; S1–4 are present, S1–3 connected by shallow transverse furrows; the eye lobe is shorter and farther out on the cheek than in *O. geikiei*; and the thorax is of eight segments. Lane *et al.* describe the thoracic pleurae as weakly geniculate, and facets may be present; these authors also describe a narrow pygidial border. In Lane *et al.* (1988, p. 1, fig. 5), a narrow groove forms the lateral and posterior margins of the pygidium; I regard this as the mould of a narrow doublure. Zhang *et al.* (1980) illustrate species of *Arthricocephalus* and *A. (Arthricocephalites)*, which show (e.g. pl. 92, figs 1, 7–8; pl. 93, figs 2, 4) an apparently non-fulcrate thorax and the absence of a pygidial border. The claim (Lane *et al.* 1988) that the hypostome was subquadrate in outline and fused to the doublure

in *Arthrocephalus* is not substantiated by an illustration. *Arthrocephalus* occurs in the late Lower Cambrian of Greenland (Blaker 1986, p. 68, fig. 3; Lane *et al.* 1988, pl. 1, fig. 6); it may also be present in Siberia, if *Oryctocarella* is synonymous as Suvorova (1964, p. 235) suggested.

The Australian Middle Cambrian *Sandoveria lobata* Shergold, 1969 (p. 39, pl. 10, figs 1–11; text-figs 14–15) is distinguished from *Oryctocara* by the forwardly tapering glabella and seven thoracic segments. The glabella has the distinctive pre-occipital (or intervening in Shergold's terminology) lobe and additional rounded, lateral glabellar lobes are preserved in a meraspid cranidium (Shergold 1969, pl. 10, figs 7–8). Similar lateral lobes have been described in *Euarthrocephalus* from the Lower Cambrian of Zhejiang (Ju 1983). In *Sandoveria* S1–4 are present, S1–3 connected by transverse furrows: how far the connections of S1–4 to the axial furrows are real, or the result of flattening, is uncertain. The thoracic segments have the high, crescentic portion of the axial ring (overlying the articulating half ring) as in *Oryctocara*, the anterior and posterior margin of each flat pleura parallel, with no facet developed. The thorax is non-fulcrate, and the pygidium lacks a border.

In the early Middle Cambrian of Siberia species attributed to *Oryctocara* (Tchernysheva 1962, p. 36, pl. 5, fig. 5; Suvorova 1964, p. 236) have been described, and also species of *Ovatoryctocara* Tchernysheva, 1962. The type species *Oryctocara ovata* Tchernysheva, 1960 (p. 220, pl. 51, figs 4–6; proposed in Tchernysheva 1962, as a subgenus of *Oryctocara*) appears to be a distinct genus (Tchernysheva 1962, p. 37, pl. 4, figs 1–5; pl. 5, figs 1–4; Suvorova 1964, p. 242, pl. 27, fig. 17; text-fig. 72; Egorova *et al.* 1976, p. 96, pl. 46, figs 15–16; pl. 48, fig. 17) characterized by the proparian facial suture, the genal angle rounded and lacking a spine, four thoracic segments, the relatively long pygidium with ten to twelve axial rings and ten pleural ribs. The cheeks and pleurae are not granulate, but bear a network of fine ridges. Tchernysheva's illustrations also show that the thorax may have been fulcrate in *Ovatoryctocara*, the fulcrum at about the mid-width (tr.) of the pleura, and the pleura faceted. Two additional species of *Ovatoryctocara* are *O. angusta* and *O. granulata* (Tchernysheva 1962, p. 39, pl. 5, figs 6–12), the latter (Egorova *et al.* 1976, p. 96, pl. 43, figs 15–17) displaying granulate sculpture and a probably fulcrate thorax. *O. granulata* has been recorded (Robison *et al.* 1977, p. 261) but not described, from the late Lower Cambrian of south-eastern Newfoundland.

*Oryctocara geikiei* Walcott, 1908b

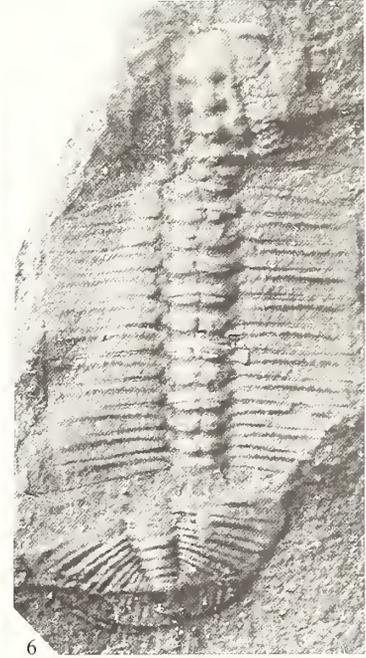
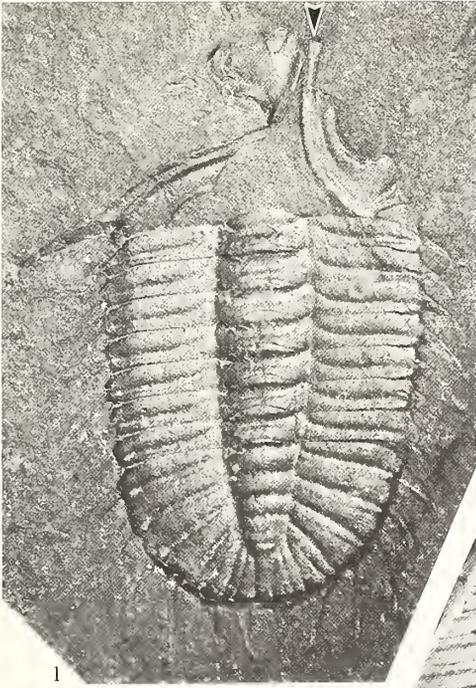
Plate 4, figures 2–3, 4?, 5–9

1908b *Oryctocara geikiei* Walcott, pp. 23–26, pl. 1, figs 9–10.

EXPLANATION OF PLATE 4

Fig. 1. *Oryctocephalus burgessensis* Resser, 1938. Middle Cambrian, Burgess Shale, British Columbia, Canada. Arrangement of exoskeletal sclerites, cranidium missing, right free cheek inverted, rostral-hypostomal plate inverted, left free cheek not inverted (in relation to thoracopygon), both cheeks lie partially beneath segments 1 and 2, connective sutural margin of right cheek arrowed; GSC 110751, Walcott quarry, level 13–14 ft (3.96 to 4.27 m);  $\times 5$ . Photographed in reflected light.

Figs 2–9. *Oryctocara geikiei* Walcott, 1908. Middle Cambrian. 2, USNM 95038, incomplete cranidium; Lakeview Limestone, *Peronopsis bonnerensis* Zone, cement mine just north of Lakeview, Pend Oreille Lake, Idaho, U.S.A.;  $\times 10$ . 3, USNM 53427, external mould of pygidium and fragment of posterior thoracic segment; Spence Shale Formation, *P. bonnerensis* Zone, Liberty Canyon, west of Montpelier, Idaho;  $\times 5$ . 4, USNM 95041 (Resser 1939a, p. 22), small pygidium doubtfully assigned to this species, horizon and locality as fig. 2;  $\times 10$ . 5–6, lectotype, respectively USNM 53428, latex cast of external mould; USNM 53426, internal mould; locality and horizon as fig. 3;  $\times 10$ . 7, 9, ROM 49460, respectively internal mould and latex cast of external mould; Stephen Formation, *Glossopleura* Zone, Mt Stephen, British Columbia, Canada;  $\times 6$ . 8, ROM 49464, external mould, axial region compressed from occipital ring backward, locality and horizon as figs 7 and 9,  $\times 6$ .



*Lectotype* (here selected). USNM 53426, 53428, counterpart moulds of incomplete, crumpled and partially disarticulated exoskeleton, original of Walcott 1908*b*, pl. 1, fig. 9; from the Spence Shale, in Spence Gulch, a ravine running up into Danish Flat from Mill Canyon, about 15 miles (9.37 km) west of Montpelier and 5 miles (3.12 km) southwest of Liberty, Bear Lake County, Idaho, USA.

*Other material.* USNM 53427, external mould of pygidium and fragments of posterior thoracic segments, original of Walcott 1908*b*, pl. 1, fig. 10, horizon and locality as lectotype. USNM 95038, external mould of incomplete cranidium, original of Resser 1938*a*, pl. 1, fig. 22, Lakeview Formation, southern side of Pend Oreille Lake, Bonner County, Idaho (referred to this species in Resser 1938*b*, p. 38; see Resser 1939*a*, p. 14). ROM 49459–61, Stephen Formation, Mt Stephen, locality 9 of Collins *et al.* 1983, the large block that also yielded *Sanctacaris uncata* (Briggs and Collins 1988). ROM 49464, Stephen Formation, beds immediately above locality 9 of Collins *et al.* 1983. ROM 49457–58 from steeply dipping, thin bedded siltstones, Stephen Formation, in a gully west of locality 9. ROM 49462–63, Stephen Formation, south-west shoulder of Mt Field, about 400 m south-west of the peak, at about 2400 m altitude.

*Geological horizon.* Middle Cambrian. The Spence Shale Formation (Robison 1991, p. 94) and the Lakeview Formation yield the fauna of the *Peronopsis bommerensis* Zone (Robison 1976, p. 103), a zone equivalent to the upper *Albertella* and *Glossopleura* zones (Conway Morris 1989, fig. 1). All the ROM localities given above yielded *Glossopleura* sp., *Oryctocephalus* sp. and other trilobites indicative of the *Glossopleura* Zone, present in the basal portion of the Stephen Formation (Fritz 1971, p. 1164).

*Description.* Exoskeleton suboval in outline, maximum width at sixth thoracic segment, axis one-quarter or less of this width (tr.); no genal or pleural spines; pleurae transverse anteriorly, behind about the eighth thoracic segment progressively more strongly backwardly directed. Glabella subrectangular in outline; preglabellar field lacking; narrow (sag. and exs.) anterior border. Occipital ring short (sag. and exs.); occipital furrow with deep pit situated a short distance in from the axial furrow. S1–3 in form of deep rounded pits, situated at equal distances from each other and the occipital furrow, and a short distance inside the axial furrow; shallow transverse furrow connects S1 and S2 pits, fainter furrow connects S3 pits; anterior glabellar lobe about twice length (sag. and exs.) of L3, faint impression of S4 close to axial furrow at about midlength. Glabella abaxial to pits inflated, with incompletely defined, small, circular lateral lobe in front of extremity of occipital ring, and outside S1 pit; whether these lobes are real or the result of the flattening of the glabella is uncertain. Palpebral lobe a low ridge, gently curved and subparallel to axial furrow, situated at about one-third the width (tr. at the posterior margin) out from the axial furrow; anterior end of lobe opposite S4, posterior end opposite mid-L2. Faint eye ridge directed inward and forward to anterior extremity of axial furrow. In the original of Plate 4, figures 7 and 9, the cheeks are displaced inward, obscuring the palpebral lobe. However, the lateral border is partly preserved on the left side, is wider (exs.) than the anterior border, is of uniform width and meets the posterior border at an angle of *c.* 75°. Posterior border defined by forwardly curved border furrow so that it is longest (exs.) medially. Anterior branch of suture directed forward and slightly inward; posterior branch curves outward and backward to cross border close inside genal angle.

The lectotype (Pl. 4, figs 5–6) shows eleven thoracic segments disarticulated from the cranidium, and the pygidium and at least one segment detached and lying behind them. In articulated specimens (Pl. 4 figs 7–9) there appear to be twelve thoracic segments, the interpleural furrows of the pygidium dying out before they reach the margin. A broad (sag. and exs.) articulating furrow separates a narrow, convex axial ring from the strongly convex articulating half ring; apodeme close to the extremity of the articulating furrow. A depression at the posterior margin of the axial furrow is formed at the axial articulating process. The flat pleura shows no evidence of the fulcrum; it is divided by a shallow pleural furrow which curves forward from the axial furrow, is then directed straight outward, to die out just inside the margin. Posterior band longer (exs.) than anterior; narrow marginal band (an articulating flange) lies in front of anterior pleural band and fits below margin of pleura in front. At the extremity pleura is smooth, the margin truncated exsagittally and gently bent down. The anterior and posterior margins of each pleura are parallel, and there is no facet at the anterolateral angle. On the right side of an internal mould (Pl. 4, fig. 7) a groove extends continuously along the edges of the pleurae and pygidium (a corresponding ridge in the external mould). I interpret this structure as the narrow (tr.), convex doublure of pleurae and pygidium.

The subsemicircular pygidium (Pl. 4, figs 3, 7) has six pleural furrows and the shallower, narrower interpleural grooves curving outward and back, the posterior pair directed straight back (exs.) from each side of the sixth axial ring, and enclosing a tiny terminal axial piece and the faint indications of a seventh pleural

pair. Pleural, and especially interpleural, furrows extend out close to the bent-down exoskeletal margin, and there appears to have been a narrow, convex doublure. There was thus no smooth or raised border on the pygidium, and no border furrow.

External surface sculptured with closely-packed granules, most prominent on the genal field and pleural region, less so on the axial region (particularly the glabella), and absent in the furrows.

*Remarks.* The incomplete cranidium (Pl. 4, fig. 2) from the Lakeview Formation appears to belong to this species. An internal mould of a pygidium (Pl. 4, fig. 4) also from the Lakeview Formation, Pend Oreille Lake, is half the size of that of the lectotype, but may represent this species. It has six axial rings and the terminal axial piece, and six pairs of pleurae, with the pleural furrows deep, and is granulate on the anterior and posterior bands.

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*Addendum.* Since this manuscript was completed, F. A. Sundberg (1994, *Corynexochida and Ptychopariida (Trilobita, Arthropoda) of the Elhuanella Biozone (Middle Cambrian), Utah and Nevada. Contributions in Science, Natural History Museum of Los Angeles County*, **446**, 1–137, 93 figs) has described the new genus and species *Opsiosoryctocephalus ophis* and two species of *Tonkinella*. The former is based on small, silicified cranidia, a free cheek bearing a genal spine, and pygidia with marginal pleural spines. The material of *Tonkinella* includes cranidia and pygidia, and is preserved in relief. These species all come from the *Ptychagnostus gibbus* Zone.

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# A NEW EURYPTERID FROM THE LATE ORDOVICIAN TABLE MOUNTAIN GROUP, SOUTH AFRICA

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**ABSTRACT.** An exceptionally preserved eurypterid, *Onychopterella augusti* sp. nov., is described from the Soom Shale Member of the Cedarberg Formation, Table Mountain Group, of Cape Province, South Africa, extending the temporal range of this genus into the late Ordovician and providing the first occurrence in Gondwana. *O. augusti* can be distinguished from related taxa by the shorter proportions of the postabdomen, lanceolate telson, the large anterior projection of podomere seven and the long terminal spine of the sixth prosomal appendage. The level of preservation is such that traces of internal soft tissues, rarely preserved in eurypterids, can be discerned, including muscular tissue associated with the appendages and telson, respiratory structures (areas of branchial chambers), and an apparently spiral valve in the anterior part of the alimentary canal.

THE Table Mountain Group is a 3000 m thick, predominantly arenitic unit that is widely exposed in the mountains of south-western Cape Province, South Africa. A finer grained unit, the Cedarberg Formation, forms a conspicuous recessive marker horizon throughout the area of outcrop, and is divided into two members: the Soom Shale Member and the Disa Siltstone Member (Text-fig. 1). The Soom Shale is up to 15 m thick, and comprises thinly laminated fine siltstones that are black when fresh, but pale grey when weathered. This deposit is becoming well known for producing important and exceptionally preserved fossils, including conodonts (Theron *et al.* 1990; Aldridge and Theron 1993) and naraoiid arthropods (Fortey and Theron 1995). In this paper we report the discovery of two specimens of a new eurypterid, *Onychopterella augusti* sp. nov., one of which has soft tissues preserved.

Both specimens were collected from a locality on the Keurbos farm, about 11.5 km south-east of Clanwilliam, north of Cape Town (Text-fig. 1), where the lower part of the Soom Shale is exposed overlying conformably the diamictites of the Pakhuis Formation. The eurypterids came from loose blocks freed during excavation of the exposure face, so their precise position in the section is unknown. Fossils currently known from Keurbos are not age-diagnostic, but the Soom Shale Member in the Hex River Mountains, some 100 km away, has yielded the trilobite *Mucronaspis olini*, indicative of a late Ashgill age (Cocks and Fortey 1986).

Eurypterids are rare fossils in South Africa. Waterston *et al.* (1985) described the large *Cyrtoctenus wittebergensis* from the Carboniferous Witteberg Group of Cape Province, and two other specimens from Witteberg sediments near Grahamstown, described by Seward (1909), were referred to *Hastimima sewardi* (Strand, 1928) and later, with reservation, to *Hibbertopterus* (Kjellesvig-Waering 1966). Arthropod tracks from the early Ordovician Graafwater Formation, Table Mountain Group, described by Taljaard (1958), Rust (1967) and Anderson (1975) may in some instances be attributable to eurypterid activity (A. Seilacher, pers. comm.). Elsewhere in Africa, eurypterids have been recorded only from farther north; pterygotid fragments were noted from sediments of early Silurian age near Denate in the Atlas mountains of Morocco by Waterlot and Leveque (1960), and carcinosomatid and pterygotid remains were reported from the Acacus Formation (mid Silurian) of Tadrart in Libya (Depitout 1962). Borehole samples from Lower Devonian strata in the Sahara have yielded indeterminate cuticular remains and areas of gill tract

(Taugourdeau 1967, 1978). Depitout (1962) reported abundant eurypterid remains from the upper Silurian of Algeria which he referred to indeterminate pterygotids and *Eurypterus*, although Caster and Kjellesvig-Waering (1964) later suggested that many might be carcinosomatids. A possible pterygotid tergite from northern Libya was recovered from well drilling in the Silurian Tanezruft shale (Kjellesvig-Waering 1964).

Elsewhere in Gondwana, a few eurypterids of Lower Palaeozoic age have been reported from South America. A number of indeterminate tergites and a telson with a serrate lateral margin were described from the Llanvirn of Bolivia by Toro and Pérez (1978). Indeterminate eurypterid remains were also noted from the Yerba Loca Formation (middle Ordovician) of Jachal, Argentina (Ramos and Blasco 1975). *Slimonia boliviana* was described from the Kirusillas Formation (upper Silurian) of Pojo, Bolivia (Kjellesvig-Waering 1973). In the Upper Palaeozoic of Brazil, *Hastimima* has been reported from the Permian of Santa Catarina (see Waterston *et al.* 1985 for review) and Sao Paulo states (Mezzalana 1951), and from the Lower Devonian Picos Formation of Piauí State (Caster 1947). Kjellesvig-Waering (1960), however, concluded that the latter two occurrences were not determinable. Indeterminate remains were noted from the Gamonedá Formation (Lower Devonian) of Tarija, Bolivia (Eldredge and Branisa 1980). *Pterygotus bolivianus*, from the Middle Devonian of La Paz, Bolivia is the only record of a pterygotid from South America (Kjellesvig-Waering 1964). Additionally, a possible adelopthalmid was recorded from the Middle Devonian Punta Negra Formation of San Juan, Argentina (Kjellesvig-Waering 1960).

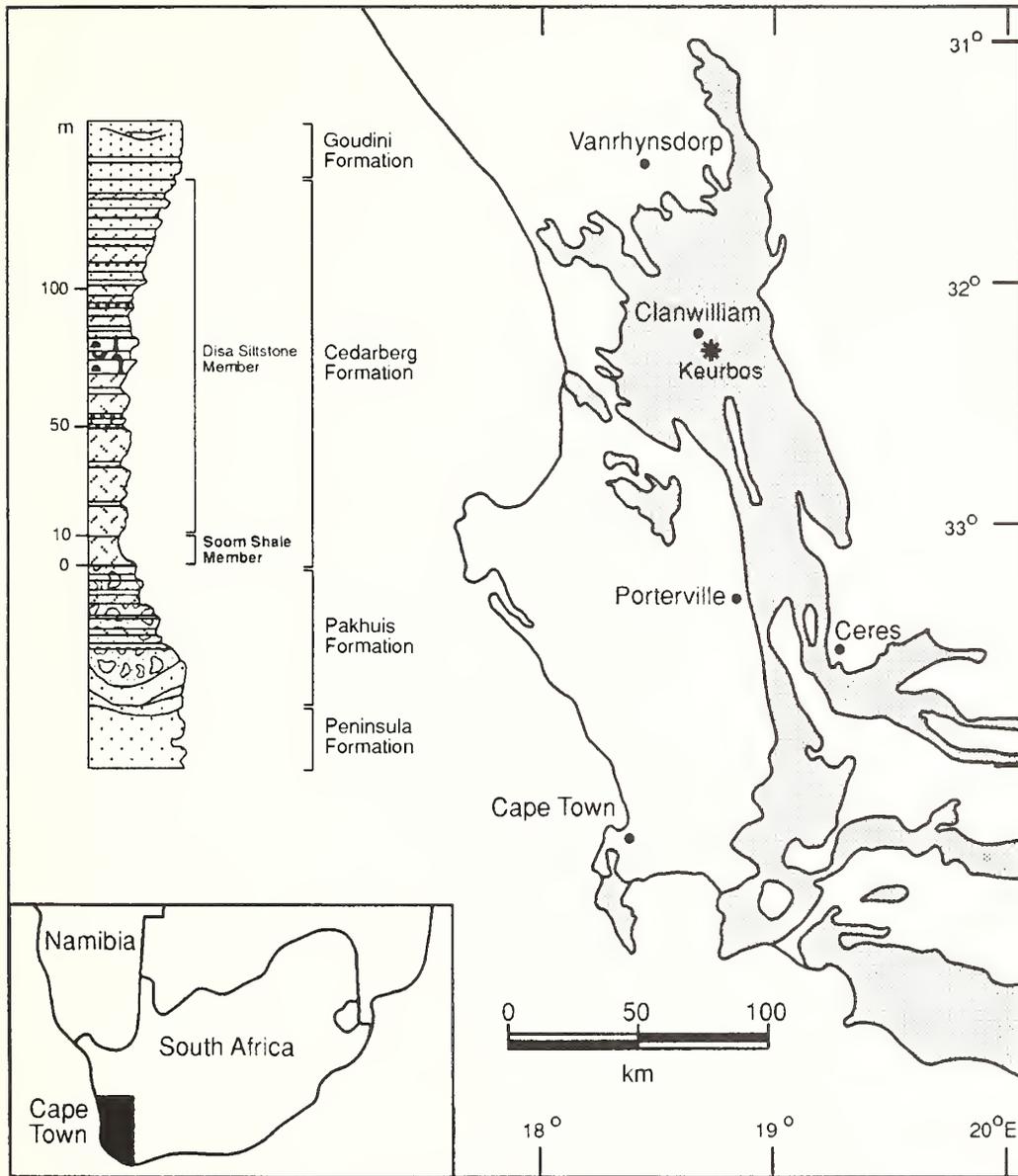
Eurypterid records from Australia, reviewed by Selden (1993), include cuticle fragments from South Yarra, Melbourne, referred to *Pterygotus australis* (M'Coy 1899). Fragmentary specimens, collected at Cootamundra, New South Wales, were referred originally to *Hughmilleria* (Gill 1951), but Caster and Kjellesvig-Waering (1953) later concluded that they were indeterminate, with the largest belonging probably to a pterygotid. An unusual carapace with large eyes and a frilled posterior margin, described as *Melbournopterus crossotus*, was found in upper Silurian siltstones near Heathcote, Victoria (Caster and Kjellesvig-Waering 1953) in association with monograptids. A specimen from the Devonian Gogo Formation, Western Australia was referred tentatively to *Rhenopterus* by Waterston (*in Rolfe* 1966), but awaits formal description. Eurypterid fragments have also been reported from Lower Devonian siltstones at Kinglake West, Victoria (Jell 1992).

Eurypterids previously recorded from the Lower Palaeozoic of Gondwana are all referable to the Carcinosomatidae and Pterygotidae (Plotnick 1983), recognized as representatives of the most marine ecological phase of eurypterids (Kjellesvig-Waering 1961). Until now, *Onychopterella* was known only from the Silurian of North America. The occurrence in the Soom Shale extends its temporal range into the late Ordovician, and provides the first record of the Erieopteridae from Gondwana.

#### MATERIAL AND TERMINOLOGY

The holotype (GSSA C373a, b) comprises the part and counterpart of a complete eurypterid (Pl. 1; Pl. 2, figs 1–3; Text-figs 2–3). The fragile counterpart is broken into two pieces, one of which has been preserved with a clear consolidant to prevent further degradation. The paratype (GSSA C427a, b) consists of part and counterpart, each a single piece, displaying only the incomplete opisthosoma and the distal podomeres of appendage VI on the edge of the block (Pl. 3, figs 1–4; Text-fig. 4). After initial splitting to separate part and counterpart on each specimen, no further preparation was undertaken. The specimens are deposited in the collections of the Geological Survey of South Africa, Silverton, Pretoria (GSSA).

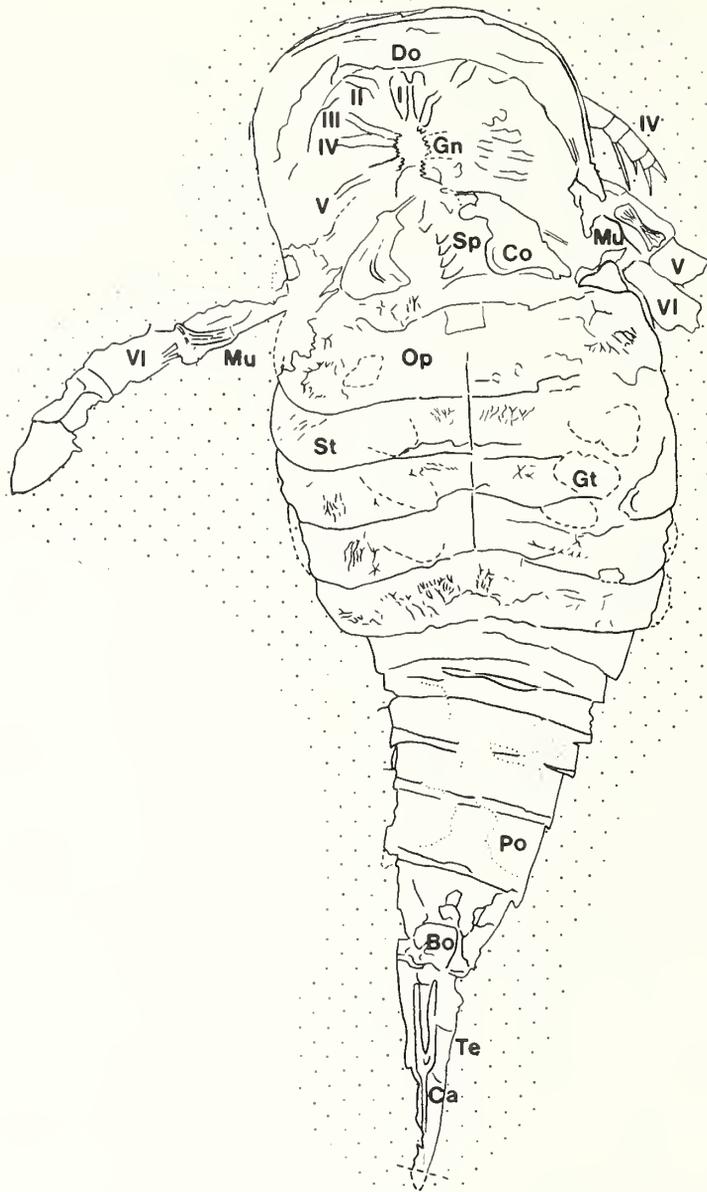
The specimens are described using empirical standards of terminology, following Tollerton (1989) to ensure less subjectivity. 'Prosoma' is used in preference to 'cephalothorax' to describe the anterior tagma, and 'carapace' is used for the dorsal shield of the prosoma. 'Preabdomen' and 'postabdomen' are employed in preference to 'mesosoma' and 'metasoma' respectively, to describe the anterior and posterior units of the abdomen. Prosomal appendages are denoted by Roman numerals, with individual podomeres numbered from proximal to distal.



TEXT-FIG. 1. Map of the south-western region of Cape Province, showing the outcrop of the Table Mountain Group (shaded) and the fossil locality at Keurbos (asterisk). The stratigraphical section shows part of the Table Mountain Group, including the Soom Shale Member.

#### PRESERVATION

The holotype part (GSSA C373a) occurs on a 20 mm thick layer of finely laminated siltstone and consists of an external mould of the ventral surface exhibiting internal features of the prosoma and telson (Text-fig. 2). The taphonomy of fossils in the Soom Shale is currently under investigation, but it seems likely that the soft tissues of the eurypterid have been preserved by early phosphatization.



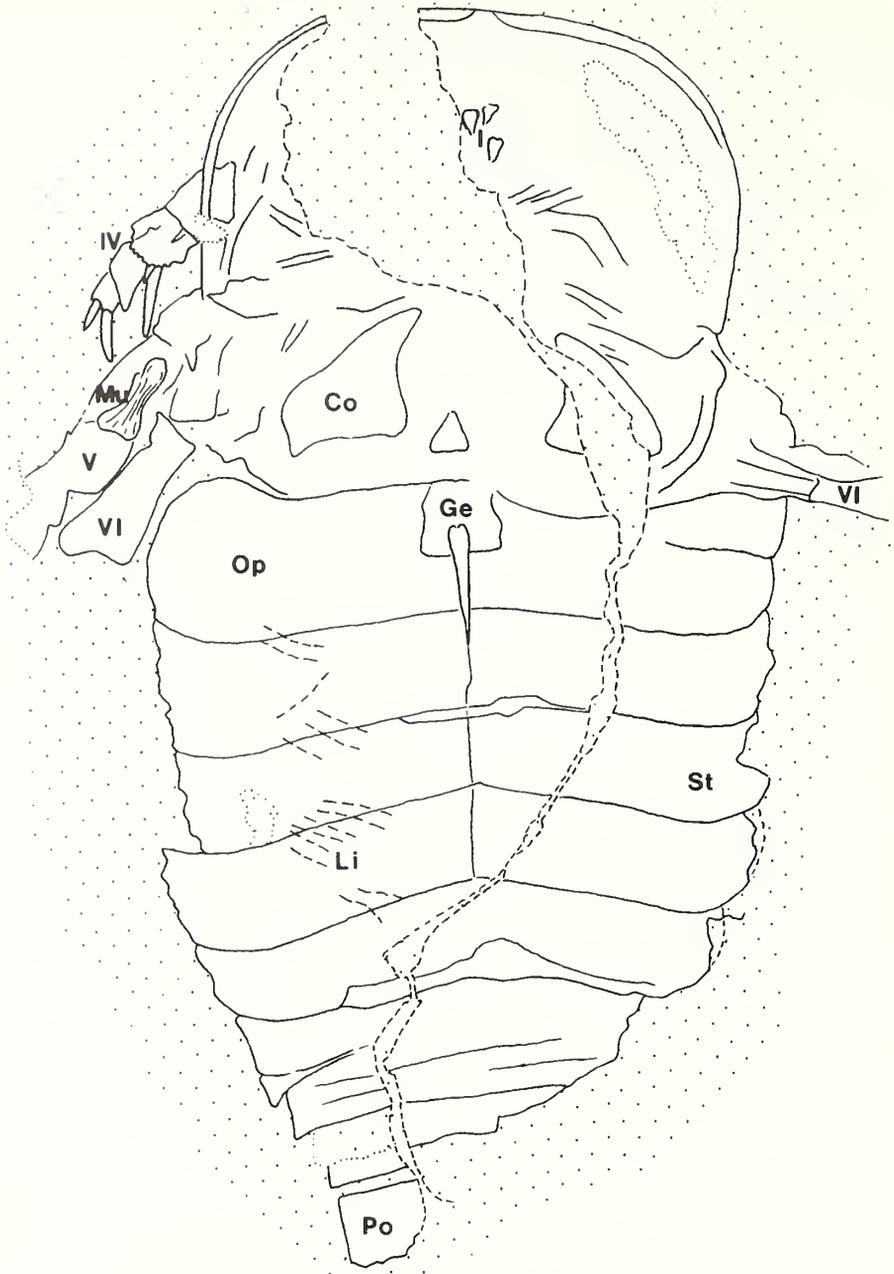
TEXT-FIG. 2. *Onychopterella angusti* sp. nov. Camera lucida drawing of the holotype, GSSA C373a. Prosomal appendages denoted by Roman numerals. Bo, boss-like structure of pretelson and proximal part of telson; Ca, medial carina; Co, coxal muscles of appendage VI; Do, doublure; Gn, gnathobases of prosomal appendages; Gt, gill tract or infilled branchial chambers; Mu, muscular tissue associated with appendages; Op, genital operculae; Po, postabdominal segment; Sp, spiral valve of alimentary canal; St, preabdominal sternite; Te, telson;  $\times 2.5$ .

EXPLANATION OF PLATE I

*Onychopterella angusti* sp. nov.; GSSA C373a, holotype; Soom Shale Member, Cedarberg Formation, Table Mountain Group; Clanwilliam, Cape Province, South Africa;  $\times 2.5$ .



BRADDY *et al.*, *Onychoptarella*



TEXT-FIG. 3. *Onychopterella augusti* sp. nov. Camera lucida drawing of the holotype, counterpart GSSA C373b. Prosomal appendages denoted by Roman numerals. Co, coxal muscles of appendage VI; Ge, trace of proximal part of genital appendage; Li, lineations on infilled branchial chambers; Mu, muscular tissue associated with appendages; Op, genital operculae; Po, small corner of postabdominal segment; St, preabdominal sternite;  $\times 3.5$ .

The majority of eurypterid fossils are exuviae (Clarke and Ruedemann 1912; Stormer 1934) and do not represent dead animals. The very rare preservation of gut structures in some eurypterids has been cited as evidence that these specimens were the remains of dead animals (Kjellesvig-Waering 1958*b*). However, the presence of gut structures cannot be used as the sole criterion to distinguish a moult from a dead animal, because in many arthropods parts of the gut are moulted during ecdysis. Moulded exoskeletons may be found complete, but are frequently preserved as disarticulated remains, dispersed by currents into individual podomeres and tergites. Internal tendonal tissues may be preserved in exuviae, as these are ectodermal in origin (Selden 1981). The preservation of the internal muscular tissues in the holotype indicates that this is the carcass of a complete dead animal. Soft tissues are not recognizable on the incomplete paratype, so we cannot determine whether it is a dead animal or an exuvia.

### MORPHOLOGICAL RECONSTRUCTION

A reconstruction of the dorsal and ventral aspects of *Onychopterella augusti* is provided (Text-fig. 5). The majority of morphological features are preserved on the holotype, enabling an accurate reconstruction of most of the organism, based on this specimen. The shape of the lateral eyes is inferred by comparison with *O. kokomoensis* (Miller and Gurley, 1896) to be reniform (concave outer margin with flatter inner margin); they are approximately one-quarter the length of the carapace and situated in a centrimesial position (see Tollerton 1989). The ocelli are reconstructed as situated slightly posterior to the position of the lateral eyes, near the mid-line of the prosoma, as in *O. kokomoensis* (Clarke and Ruedemann 1912, pl. 25, fig. 2). Despite these authors' statement that the ocelli were not apparent, the artist had noted their position.

Where possible, the anterior appendages (I–V) were reconstructed according to available material, with any unknown parts inferred from *O. kokomoensis*. The reconstruction of appendage VI is based on the paratype (GSSA C427a); the coxae, not present on this specimen, were inferred from the shape of the muscle masses, and from comparisons with the subrhomboidal coxae of *O. kokomoensis*.

The metastoma, not preserved on either specimen, is reconstructed according to that of *O. kokomoensis* as small, approximately one-third the length of the carapace and oval in form, the anterior margin slightly convex and emarginate, a little narrower than the posterior margin.

Only a trace of the proximal part of a genital appendage is preserved on the counterpart of the holotype, and is reconstructed by inference from a specimen of *O. kokomoensis* (Clarke and Ruedemann 1912, pl. 26, fig. 2) as a type A appendage, with paired basal plates, reaching the posterior margin of the third sternite and ending in a tricate termination (Tollerton 1989).

The ventral surface of the opisthosoma can be reconstructed accurately from the holotype but the segmentation of the dorsal surface is inferred from *O. kokomoensis*. The shape of the telson can be determined accurately, although its external morphology is reconstructed according to *O. kokomoensis*, with a single medial carination on the dorsal surface.

The paratype was approximately 143 mm long, by comparison of its proportions with the holotype, although the postabdominal segments of the former are proportionally slightly shorter than those of the latter. This variation is considered solely ontogenetic, the larger individuals having slightly shorter postabdomens.

### RELATIONSHIPS

Two species of *Onychopterella* have been recorded previously, both from North America. They have distinct dolichopteroid or stylonuroid characteristics in that they have slender walking legs and narrow swimming legs, a feature which may be of phylogenetic importance (Kjellesvig-Waering 1958*a*). In this respect, *Onychopterella* is intermediate in form between the Eurypteroidea and the Stylonuroidea.

*O. kokomoensis* is the commonest species in the late Silurian Kokomo eurypterid fauna, Indiana, yet specimens are rare in museum collections. A brief description is given for comparison with *O. augusti*. The body is small and relatively broad, about three and a half times as long as it is wide. The subquadrate carapace, slightly wider than long, has rounded anterior angles and a broad doublure. The lateral eyes are reniform, of medium size, and lie on the anterior half of the prosoma. Appendages III–VI are known, VI being slender and bearing a long terminal spine, more than half as long as podomere 8 and slightly curved. The coxae of appendage VI are relatively small and subrhomboidal in general outline. The oval metastoma is small, measuring little more than one-third the length of the carapace. The genital appendage is seen clearly only in one specimen, reaching the posterior margin of the third sternite with paired basal deltoid plates visible in faint outline. The abdomen is a little wider than the prosoma, the preabdomen as wide as long, the postabdomen relatively short and compact, longer by one-third than the preabdomen. The postabdominal segments increase gradually in length posteriorly, the last being twice as long as the first, but only one-third as wide. The last postabdominal segment is produced into two short broad lobes with blunt extremities. The telson is short and thick (clavate), a little more than one-fifth the length of the body. Ornamentation of the last postabdominal segment consists of small, evenly distributed, sharply angular or pointed scales (Clarke and Ruedemann 1912).

*Onychopterella pumilis* was described from a single, nearly complete, well preserved specimen, displaying the original coloration of the integument, from the lower part of the early Silurian Essex (Edgewood) Limestone in Kankakee County, Illinois (Savage 1916). Only 39 mm long, it differs from *O. kokomoensis* in having proportionally slimmer prosomal appendages, a tapering preabdomen, and a pretelson segment which lacks epimeral prolongations. The telson is spike-like (rapidly contracting) rather than having a slight broadening at the posterior half (clavate) and the lateral eyes are more forwardly placed than in *O. kokomoensis*. The very small size and eye position suggest that this may be a juvenile (Kjellesvig-Waering 1958a), and the differences from *O. kokomoensis* may be solely ontogenetic.

#### FUNCTIONAL MORPHOLOGY

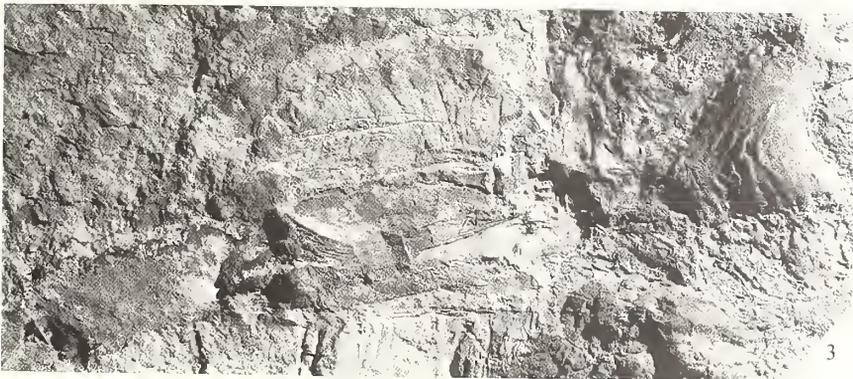
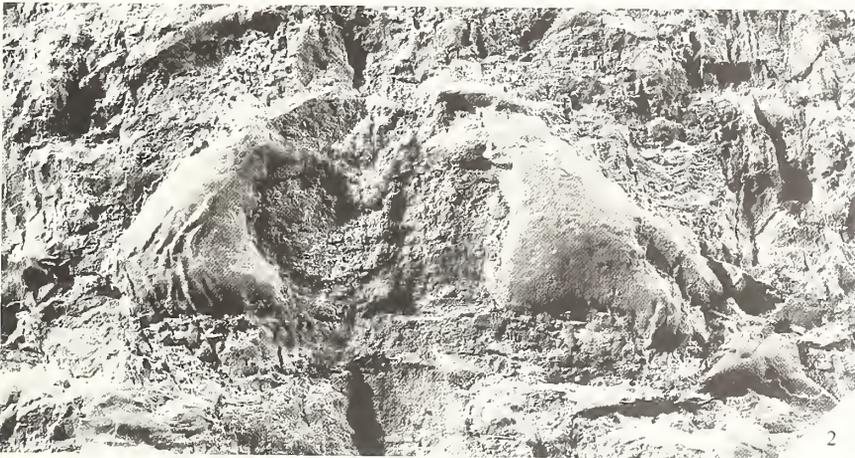
The level of preservation in these specimens is sufficient for the structure of many of the internal features to be discerned, providing information on the functional morphology. The spiral-shaped structure between the two coxal muscle masses of the prosoma probably represents an anterior portion of the gut. The arthropod gut is composed of three parts: the ectodermal stomodeum, comprising the oesophagus and the gizzard; the endodermal mesenteron, formed by the stomach and intestine; and the ectodermal proctodeum, formed by the rectum. In *Limulus*, a related extant chelicerate, food items, after mastication by the gnathobases, are passed down the oesophagus into a grinding chamber, the gizzard. Indigestible particles are regurgitated through the oesophagus, whereas food particles are passed posteriorly through a valve into the stomach. Two pairs of lateral diverticula, forming glandular caeca, secrete digestive enzymes into the stomach through two pairs of ducts. The intestine extends posteriorly into the opisthosoma and waste is egested through a short sclerotized rectum and out through the anus, located on the ventral side of the abdomen, just in front of the telson (Barnes 1980).

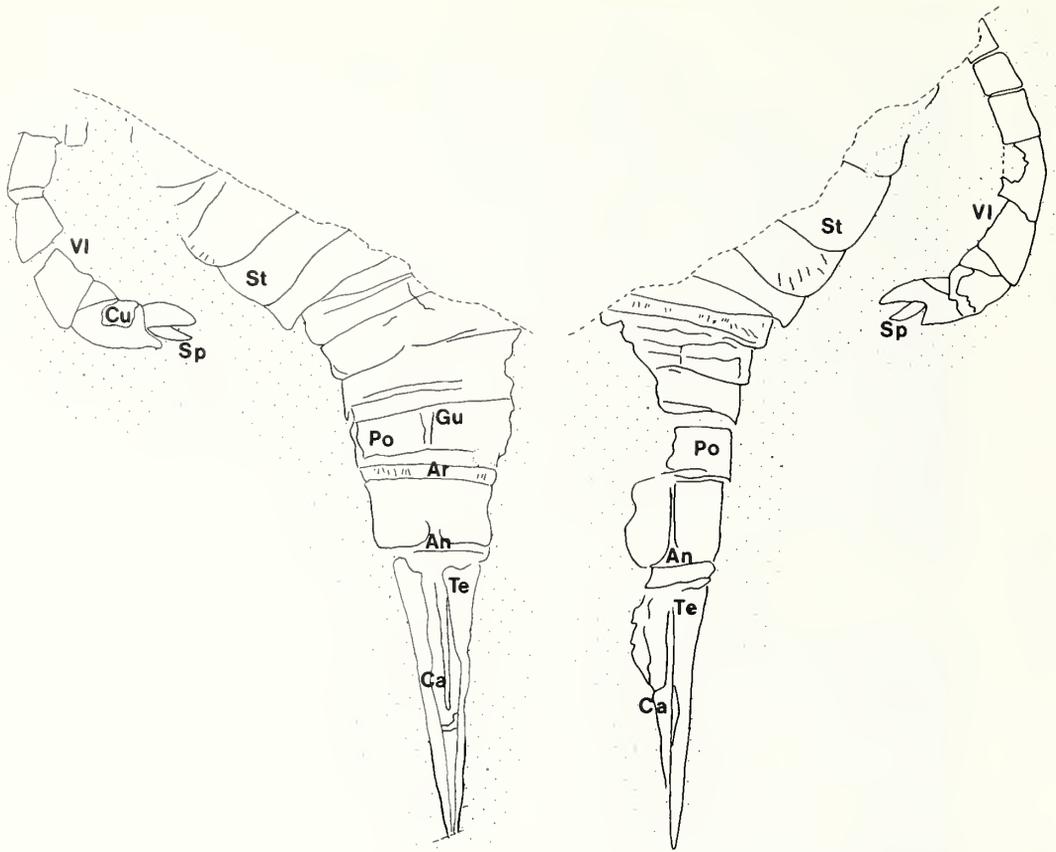
Alimentary canals have previously been described in *Carcinosoma newlini* (Ruedemann 1921; Kjellesvig-Waering 1958b), *Pterygotus (Acutiramus) macrophalmus cummingsi* (Clarke and

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#### EXPLANATION OF PLATE 2

Figs 1–3. *Onychopterella augusti* sp. nov.; GSSA C373, holotype. 1, detail of prosoma;  $\times 3.7$ . 2, coxal muscles of appendage VI with a medial spiral alimentary structure;  $\times 5.5$ . 3, detail of appendage VI: internal musculature and proximal articulation of podomere V;  $\times 5.2$ .





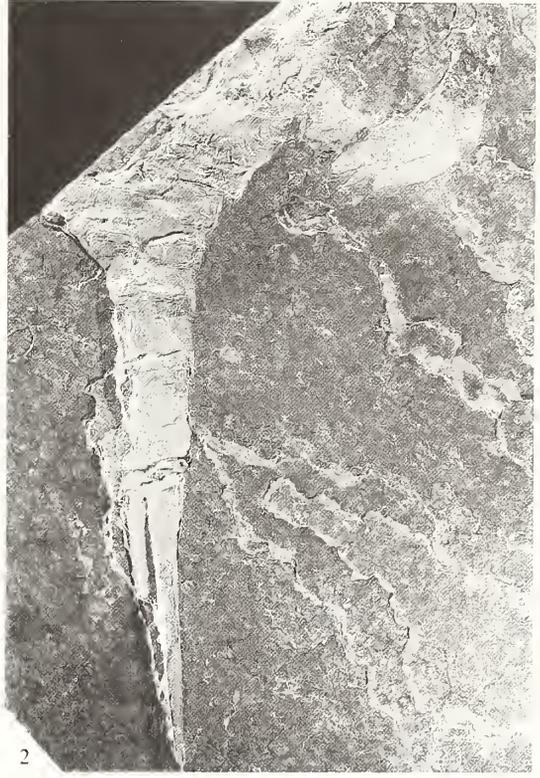
TEXT-FIG. 4. *Onychopterella augusti* sp. nov. Camera lucida drawings of GSSA C427a (right) and GSSA C427b (left). Prosomal appendages denoted by Roman numerals. An, anal opening of pretelson; Ar, arthrodial membrane; Ca, internal mould of medical carina; Cu, patches of cuticle; Gu, posterior portion of gut; Po, postabdominal segment; Sp, distal spine of podomere 8; St, preabdominal sternite; Te, telson;  $\times 1.25$

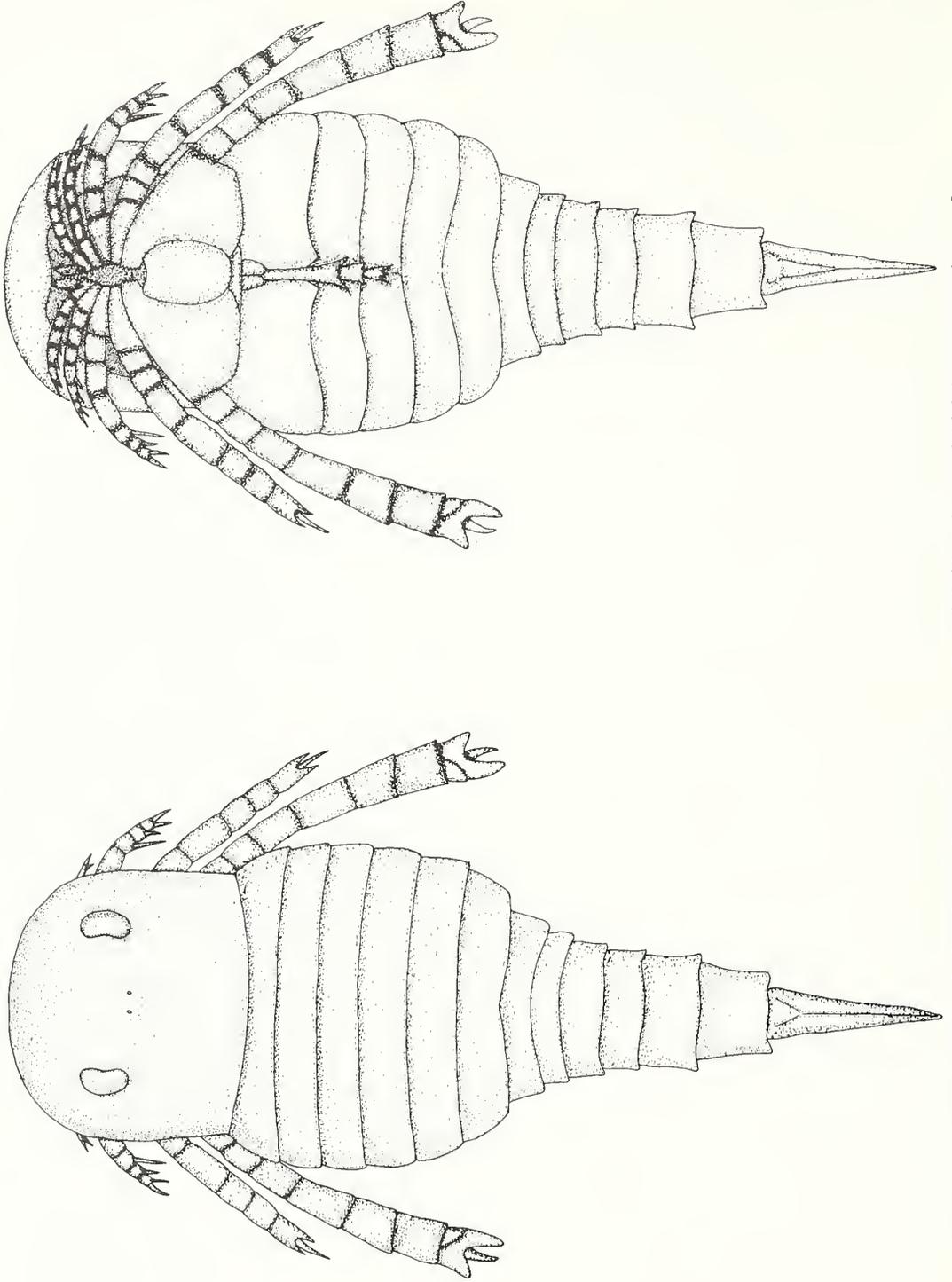
Ruedemann 1912) and *Eurypterus lacustris* (Heubusch 1962), where a depressed tubular structure with several transverse ridges, indicating a spiral morphology, is exposed along the mid-line of the pretelson.

A spiral valve, 80 mm long and consisting of five dextral whorls, was reported in *Cyrtoctenus wittebergensis* (Waterston *et al.* 1985) near the posterior of the prosoma, but no equivalent structure has been described in any other eurypterid. Spiral valves developed independently in various fish groups as an adaptive response to the need to increase the absorptive area of the gut (Williams

#### EXPLANATION OF PLATE 3

Figs 1-4. *Onychopterella augusti* sp. nov.; GSSA C427, paratype. 1, part;  $\times 1.1$ . 2, counterpart;  $\times 1.1$ . 3-4, detail of distal podomeres of appendage VI;  $\times 2.9$ .





TEXT-FIG. 5. *Onychopterella angustii* sp. nov. Dorsal (left) and ventral (right) reconstruction;  $\times 2$ .

1972), although the enterospire occurs towards the posterior end of the digestive tract. It seems reasonable to suggest that similar structures could have evolved in some eurypterid groups for a similar function, although 'the presence of a spiral valve would depend upon the requirements of digestion and absorption which in turn may depend upon such factors as feeding habits and size which vary greatly from one type of eurypterid to another' (Waterston *et al.* 1985, p. 349). The sweep-feeding appendages of *C. wittebergeus* suggest that it was a sediment feeder, and the spiral structure apparently evolved to increase the absorptive area of the gut and to extract food from the sediment. The spiral structure observed in *O. augusti* may have had a similar function, acting as a valve to the mesenteron and increasing the absorptive area of this portion of the gut.

The internal morphology of prosomal appendage VI reveals something of the locomotory capabilities of this animal. The coxal muscles of appendage VI are elongate in an anterolateral orientation, suggesting that these relatively slender legs were maintained in a posterolateral orientation for walking in order to enable sufficient stability around the animal's centre of gravity. In eurypterids the coxae are usually directed transversely, except for the two posterior coxae which have a more posterolateral orientation (Hanken and Stormer 1975). The presence of elongate proximal podomeres and the terminal spine on the sixth prosomal appendage of onychopterellan eurypterids indicates their primitive condition as natatory organs and their functional adaptation to walking (Clarke and Ruedemann 1912).

The prominent boss-like structure at the proximal end of the telson is interpreted as a large area of muscles and tendons used for the articulation of the telson. It appears similar, in many respects, to the enigmatic *Marsupipterus sculpturatus*, known only from its telson, from the Silurian of the Welsh Borderlands (Caster and Kjellesvig-Waering 1955). Originally considered a stylonurid eurypterid, it was interpreted by Rolfe (1963) as a phyllocarid crustacean of uncertain affinity, and was therefore rejected from the Eurypterida by Caster and Kjellesvig-Waering (1964). This species, whatever its affinity, has a large elliptical pouch on the ventral side of the telson, which was attributed a cloacal (storage prior to excretion) function by Caster and Kjellesvig-Waering (1955). However, it is probable that the anus of most eurypterids opened through thin cuticle between the telson and the pretelson, as in *Limulus* (Selden 1984). It is more likely that the elliptical opening of *M. sculpturatus* reflects the presence of a large muscular or tendonal mass similar to that of *O. augusti*, capable of moving the telson to defend the dorsal surface of the eurypterid and enabling overturning while on the substrate. Examination of *M. sculpturatus* from the British Geological Survey collections shows that the cuticle of the ventral surface may have broken away to reveal the opening, which is an internal feature of the telson. The apparent differences in this structure between *O. augusti* and *M. sculpturatus* are regarded as preservational: only the cuticle is preserved in *M. sculpturatus*, revealing a hollow depression, whereas in *O. augusti* the muscular tissues are preserved as an upstanding boss-like structure.

#### PALAEOECOLOGY

Eurypterids are comparatively scarce as fossils, as they typically inhabited marginal marine, deltaic and estuarine environments. *Onychopterella* was thought by Kjellesvig-Waering (1958a) to inhabit brackish and possibly marine water. The mode of life of these eurypterids was undoubtedly nektobenthic; they were capable of swimming but probably lived mostly on the substrate. Clarke and Ruedemann (1912, p. 216) concluded that: 'It was not so well adapted to a swimming lifestyle as forms such as *Eurypterus remipes* as is shown by the relatively small coxae, the less developed and more slender swimming legs, the presence of a terminal spine, obviously used in walking, and the shorter and stouter postabdomen. The extremely broad doublure may indicate an adaptation of the front edge to shovelling or digging.'

The Cedarberg Formation was deposited during a glacioeustatic rise in sea level and probably represents the outwash silt and mud from the retreating ice sheets, deposited in a glaciolacustrine to shallow marine environment (Theron *et al.* 1990). The very fine laminations of the Soom Shale

show no penetrative bioturbation, indicating that conditions were anoxic below the surface. *Onychopterella augusti* is found in association with *Orbiculoidea* and infrequent lingulid brachiopods, orthoconic nautiloids, naraoiid trilobites (Fortey and Theron 1995), conodonts (Theron *et al.* 1990), and various enigmatic organisms. The eurypterid would have been a top predator in this ecosystem, probably feeding on other arthropods, worms and perhaps conodonts.

#### SYSTEMATIC PALAEONTOLOGY

Order EURYPTERIDA Burmeister, 1843

Suborder EURYPTERINA Burmeister, 1843

Superfamily EURYPTEROIDEA Burmeister, 1843

Family ERIOPTERIDAE Tollerton, 1989

*Diagnosis.* Legs II–IV spiniferous, *Erieopterus* type; leg V nonspiniferous, *Eurypterus* type; leg VI swimming leg, *Erieopterus* type (Tollerton 1989).

#### Genus ONYCHOPTERELLA Stormer, 1951

*Diagnosis.* Prosoma subquadrate; walking legs undifferentiated, long narrow, without spines except at distal end; swimming legs inconspicuous, very narrow; pretarsus very long, spike-like; no contraction of opisthosoma; metastoma rounded posteriorly and sub-cordate anteriorly; genital appendage not well known; ornamentation comprises small pointed scales (Miller and Gurley 1896).

*Remarks.* The shape of the telson of *Onychopterella* was described as clavate by Tollerton (1989), but that of *O. pumilis* is styliiform and that of *O. augusti* lanceolate. Therefore telson morphology is here considered a specific, rather than a generic character.

#### *Onychopterella augusti* sp. nov.

Plates 1–3; Text figures 2–5

*Derivation of name.* After August Patrick Pedro, who found the holotype during a collecting trip led by JNT and RJA in 1991.

*Material.* Holotype, GSSA C373a, b: part and counterpart (in two parts); complete prosoma (anterior appendages II–IV complete, V and VI partial), opisthosoma and telson. Paratype, GSSA C427a, b: part and counterpart; incomplete opisthosoma, telson and distal podomeres of appendage VI.

*Horizon and locality.* Late Ashgill, Soom Shale Member of Cedarberg Formation, Table Mountain Group. Keurbos farm, near Clanwilliam, North of Cape Town, South Africa, longitude 18° 58' E, latitude 32° 18' S.

*Diagnosis.* Subquadrate prosoma, broad doublure (approximately one-fifth the length of the carapace), short postabdomen and short lanceolate telson; pretelson lacks epimeral prolongations; appendage VI has podomere 8 drawn into two distal projections, the anterior projection much larger than the posterior, both emarginate with long terminal spine, projecting to the length of the anterior projection of podomere 8.

*Description.* Specimen GSSA C373 (holotype). The body is small (Pl. 1; Text-fig. 2) with a total length of 73.8 mm, approximately three times as long as wide with a first order differentiation of the opisthosoma (Tollerton 1989). The subquadrate prosoma, length 18.7 mm, width at base 21.0 mm, expands slightly anteriorly with a lateral angle of 86°, giving the prosoma something of a horse-shoe shape. The internal structure of the

prosoma can be discerned by colour variations in the internal matrix; the anterior prosomal appendages (I–III), coxal muscles and anterior doublure are preserved in grey against a pale yellow matrix (Pl. 2, fig. 1). There are no details of the eyes or median dorsal ocelli because these are external features. The broad doublure of *Erieopterus* type (Tollerton 1989), clearly evident towards the lateral margins of the carapace, can be followed around the anterior margin where it is slightly concave in the medial region, approximately one-fifth the total length of the prosoma.

Within the medial region of the prosoma, a trace of the coxal gnathobases of appendage VI can be distinguished, those of the right set of appendages more evident than the left. It is not possible to distinguish which teeth belong to which coxa, although the posterior coxal gnathobase appears to bear several teeth. Faint impressions of the anterior appendages project radially away from the oral region; individual podomeres of these appendages are indistinguishable.

The anterior three appendages of the prosoma are poorly preserved, not projecting beyond the lateral margins of the carapace. The chelicerae (appendage I) are preserved as hollow depressions and no details of individual podomeres can be seen. Appendage II is seen best on the left side of the prosoma, projecting forward from the medial region, turning left and following the marginal rim of the carapace, ending in a faint bifid impression. Appendage II on the right side of the prosoma is less clearly preserved as is Appendage III on both sides of the prosoma because it does not project beyond the margin of the carapace and is discernible only as colour variations in the internal matrix.

Appendage IV is best observed on the right side of the carapace, well preserved as a dark grey impression beyond the lateral margin of the carapace. The distal podomeres (4–8) are evident, enabling description, but the more proximal podomeres, within the outline of the carapace, are indistinct. The distal part of podomere 4, preserved length 2.1 mm, width 2.0 mm, shows no evidence of spinosity. Podomere 5, length 2.1 mm, width 2.3 mm, is square, although its distal margin is less clearly preserved; a long spine 2.9 mm long, projecting posteriorly from its distal margin, is covered in small black striae. Podomere 6, length 2.0 mm, width 1.3 mm, has a more rectangular outline. A small spine, length 0.7 mm, projects from its distal margin. Podomere 7, 1.3 mm long and 1.1 mm wide, small and subquadrate in general outline, has a small distal spine, length 1.3 mm. Podomere 8 is short, length 2.0 mm, and spinose, showing traces of small striae.

Appendage V is well preserved beyond the right lateral margin of the carapace, with evidence of the internal musculature, but many of the distal podomeres are missing. Podomere 4, preserved length 2.5 mm, width 2.3 mm, is preserved distally yet is indistinct within the confines of the carapace. Podomere 5, rectangular in outline, 4.5 mm long and 2.1 mm wide, is preserved entirely, displaying evidence of the internal musculature, constricted medially such that approximately one-third of the width of the podomere appears to have been muscular tissue. At the proximal and distal margins of this podomere the muscle tissue expands to the full width of the podomere. Several parallel striations may represent the original muscle fibres. Podomere 6, preserved length 5.9 mm, width 2.2 mm, has a rectangular outline with no evidence of any spinosity. It is partially preserved, its distal part incomplete at the edge of the specimen.

Appendage VI is poorly preserved on the right side of the carapace; only podomere 4 is fully preserved with a trace of the distal margin of podomere 3. No evidence of the proximal podomeres is seen within the carapace, but there are two broadly triangular structures, preserved in a dark grey matrix near the posterior of the prosoma (Pl. 2, fig. 2). The position and size of these structures indicate that they are the large coxal muscles of this appendage. The shape of these coxal muscle masses, as broad as they are long, suggests that these coxae were subrhomboidal in outline. Appendage VI is best preserved on the left side of the carapace (Pl. 2, fig. 3). Podomere 4, preserved length 7.0 mm, width 2.6 mm, projects beyond the carapace, with evidence of the internal musculature constricted medially and expanding distally to the full width of the podomere. Striations inside the podomere may represent original muscle fibres. A convex structure at the distal end of this podomere probably represents a large mass of muscular tissue. The proximal margin of podomere 5 has a notch-like structure, perhaps representing a site of strong articulation with the preceding podomere. An impression of this internal musculature continues into podomere 5, medially constricted and expanding towards the proximal and distal margins. The anterior margin of podomere 5 is broken away and the posterior margin obscured by sediment such that only 5.7 mm of its length and 2.6 mm of its width can be discerned. Of podomere 6, 3.6 mm of its length and 2.6 mm of its width is preserved. Evidence of the internal musculature continuing down the appendage is seen as a medial colour variation. Podomere 7 begins to broaden, reflecting a widening of the appendage into the distal paddle. The posterior and distal margins of podomere 7 are covered by sediment; only 5.2 mm of its length and 5.2 mm of its width are preserved with no evidence of podomere 8 or the terminal spine.

No evidence of the metastoma (post-oral ventral plate) can be seen, but a tubular structure, length 3.1 mm, is identifiable between the two coxal muscle masses of appendage VI (Pl. 2, fig. 2). Four constrictions with

diagonal lineations suggest that this is a sinistral spiral structure and probably represents an anterior portion of the alimentary canal. There is no evidence of a genital appendage.

The opisthosoma is slightly wider than the carapace, expanding to its greatest width in the middle of sternite 2. The preabdomen, a little wider than long, is fully preserved except for the lateral margins of sternites 4 and 5. The genital operculae (sternite 1), length 5.7 mm, width 24.4 mm, are a little larger than the posterior sternites although their anterolateral margins are indistinct. The sternites are several times wider than long, their posterior margins moderately concave in their medial region, their lateral margins broadly rounded. The lengths and widths (at their widest part) of the preabdominal sternites are: sternite 2, length 3.4 mm, width 24.9 mm; sternite 3, length 3.4 mm, width 24.4 mm; sternite 4, length 3.4 mm, width 22.8 mm; sternite 5, length 4.1 mm, width 20.2 mm; sternite 6, length 2.6 mm, width 16.6 mm. The first four sternites have raised areas representing infilled branchial chambers or areas of soft gill tract respiratory tissue (Pl. 1; Text-fig. 2). These ovoid structures, those of the genital operculae being a little smaller than the others, occur on both sides of the body and have parallel, diagonal lineations on them, perhaps representing the internal structure of the lamellate gills (see Manning and Dunlop 1995). Dendritic structures occur over the entire abdomen but are more numerous towards the posterior of sternite 5. These structures most probably represent crenulations in the cuticle due to preservation and do not represent any original internal feature.

The preabdomen is relatively broad until the short postabdomen, where the segments contract gradually to the tapering telson. The postabdominal segments gradually increase their length posteriorly, the last being approximately twice as long as the first, although only half as wide. The dimensions of the postabdominal segments are: segment 1, length 2.6 mm, width 13.2 mm; segment 2, length 3.4 mm, width 11.7 mm; segment 3, length 3.0 mm, width 10.4 mm; segment 4, length 4.1 mm, width 9.3 mm; segment 5 (pretelson), length 5.7 mm, width 7.3 mm. The first few segments of the postabdomen are partially telescoped into one another and the segmentation is somewhat confused. The posterior three segments have areas of sediment pervading their medial region. The posterior lateral margin of each postabdominal segment is produced into small epimera. The distal end of the pretelson has a large boss-like structure protruding from the specimen and extending into the proximal part of the telson. This structure probably represents an area of muscular or tendonal tissue attachment. Posterior to this, two small ridges converge about half-way along the telson and continue as a single ridge to the end. The left hand side of the telson is partly obscured by sediment and the terminal point is missing. The telson, length 13.7 mm, width at base 4.1 mm, approximately one-fifth the length of the body, gradually tapers into a lanceolate shape (Tollerton 1989).

The prosoma of the counterpart, GSSA C373b (Text-fig. 3), has a large medial fracture but the lateral margins of the carapace are evident. The anterior appendages (I–III) are obscured by the internal matrix but the more posterior appendages are apparent. No evidence of the gnathobases are preserved on this specimen as a result of the fracture.

Appendage IV is well preserved on the left side of the carapace. Podomeres 4–8 are preserved beyond the lateral margin but the more proximal podomeres, within the carapace, are indistinct. Podomere 5 shows the long spine projecting from the distal end. Podomeres 6 and 7 have shorter distal spines. Podomere 8 is short and spinose.

Appendage V is represented by podomeres 4–6, well preserved on the left hand side of the carapace; the distal podomeres are missing. Podomere 4 is distally preserved yet indistinct within the carapace. Podomere 5 shows the internal musculature.

Appendage VI is poorly represented on the counterpart. Podomere 4 projects beyond the carapace on the left side; on the right side only podomere 4 and a small corner of podomere 5 can be seen. The coxal muscles are evident towards the posterior of the prosoma, the left one preserved as a shallow depression; the right depression is less clearly evident due to the fracture in the carapace.

The metastoma is not preserved on this specimen. There is a small triangular structure, representing one whorl of the spiral alimentary canal. The genital operculae are preserved and a trace of the proximal part of the genital appendage can be seen, paired basal structures evident, but no detail of the distal part of the appendage is preserved.

The preabdomen is less clearly preserved on the counterpart than on the part. The medial fracture cuts obliquely across the body so that the lateral margins of the sternites are not clearly preserved. The first segment of the postabdomen is almost completely preserved with only its right lateral margin missing. The left half of the second postabdominal segment and only an anterolateral corner of the third are preserved. The more posterior postabdominal segments and the telson are not preserved on the counterpart.

Specimen GSSA C427 (paratype). The part displays portions of the posterior three sternites of the preabdomen, the right half of the postabdomen, the telson and an almost complete sixth prosomal appendage

(Pl. 3, figs 2, 4; Text-fig. 4). Because of an oblique fracture, the anterior half of this specimen and the left lateral margins of the five segments of the postabdomen are missing. The pretelson has a faint impression preserved in the medial region, expanding towards the posterior into a depression, representing the anal opening. All of the telson is preserved except for the left lateral margin.

Appendage VI is well preserved on GSSA C427a, more completely than on the holotype, with the distal seven podomeres present (Pl. 3, fig. 4; Text-fig. 4). Appendage VI is an elongate and slender structure with a prominent spine on the distal margin of podomere 8. Only a small corner of podomere 2 is present. Podomeres 3 and 4 are fully preserved: podomere 3, length 5.3 mm, width 4.5 mm, is square, whereas podomere 4, length 6.0 mm, width 4.9 mm, is more rectangular. The posterior margins of podomere 5, length 7.9 mm, width 5.6 mm, and podomere 6 have broken away. Podomere 6, length 8.6 mm, width 6.0 mm, is relatively long, and widens distally to 6.8 mm. Podomere 7, length 7.1 mm, width 7.1 mm, is somewhat broader than the preceding podomeres. A small triangular podomere, length 3.3 mm, width 2.2 mm (7a), projects off its distal margin. Podomere 8, width 5.6 mm, is elongated into two distal projections, the anterior projection giving this podomere an anterior length of 10.9 mm, twice that of the length of the posterior projection, only 5.3 mm long. The distal margin of podomere 8 is deeply emarginated between these two projections and a long, slightly curved terminal spine, length 4.9 mm, width at base 1.5 mm, projects to the length of the anterior projection of podomere 8. Patches of the original light brown cuticle are preserved on the terminal spine and the seventh and eighth podomeres.

On the counterpart, GSSA C427b, (Pl. 3, figs 1, 3; Text-fig. 4), parts of the posterior three preabdominal sternites are evident. Only a small corner of sternite 4 is preserved. The lateral margins of the anterior two sternites are indistinct, although their lengths can be measured: sternite 5, length 10.1 mm; sternite 6, length 10.1 mm; sternite 7, length 5.2 mm, width 31.4 mm. The postabdomen is more completely preserved on the counterpart than on the part, although the left lateral margin is still indistinct. The dimensions of the postabdominal segments of this specimen are: segment 1, length 4.9 mm, width 26.2 mm; segment 2, length 5.6 mm, width 24.7 mm; segment 3, length 5.6 mm, width 23.2 mm; segment 4, length 5.2 mm, width 19.9 mm; segment 5 (pretelson), length 8.2 mm, width 16.1 mm. Arthroal membrane, 1.5 mm long, can be discerned between the posterior two postabdominal segments. It is highly wrinkled in places, reflecting the easier deformation of this softer cuticle. A medial impression, 1.1 mm wide and slightly concave, is present on the last three postabdominal segments, opening into a depression towards the posterior of the pretelson, representing the gut and anal opening. The telson, length 33.3 mm, width at base 11.2 mm, is more completely preserved than on the part, although the tip is obscured by sediment. Medially, two ridges in the proximal half of the telson, giving an M-shaped cross section, converge approximately half way down its length into a single ridge which gradually thins towards the tip of the telson (Pl. 3, fig. 1). This ridge represents internal soft tissue infilling the mould of the medial carina. Appendage VI is less completely preserved on the counterpart. Only podomeres 4–8 are apparent, together with the distal spine.

*Remarks.* In comparison with related forms, *O. augusti* is of intermediate size, more closely resembling *O. pumulis* in the lack of epimeral prolongations of the pretelson. The proportions of the prosoma and preabdomen are comparable in *O. augusti* and *O. kokouoensis*, although these tagma are a little broader, in proportion to their length, in *O. pumulis*. The postabdomen and telson are a little shorter in *O. augusti* than in the other species. The shape of the telson differs considerably in each taxon: that of *O. augusti* is lanceolate; that of *O. kokouoensis* is clavate (slight broadening in posterior half); and that of *O. pumulis* is long and styliform.

The posterior prosomal appendage is characteristic of these eurypterids, although the distal podomeres are not known in *O. pumulis*. A distinctive feature of *O. augusti* is the morphology of the terminal podomere of appendage VI. The distal margin of this podomere is drawn into two large projections, the anterior much larger than the posterior. The shape of this podomere and the long terminal spine, proportionally much larger than that of *O. kokouoensis*, are distinctive features of this new taxon.

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# OSTRACODA AND PALAEO SALINITY FLUCTUATIONS IN THE MIDDLE JURASSIC LEALT SHALE FORMATION, INNER HEBRIDES, SCOTLAND

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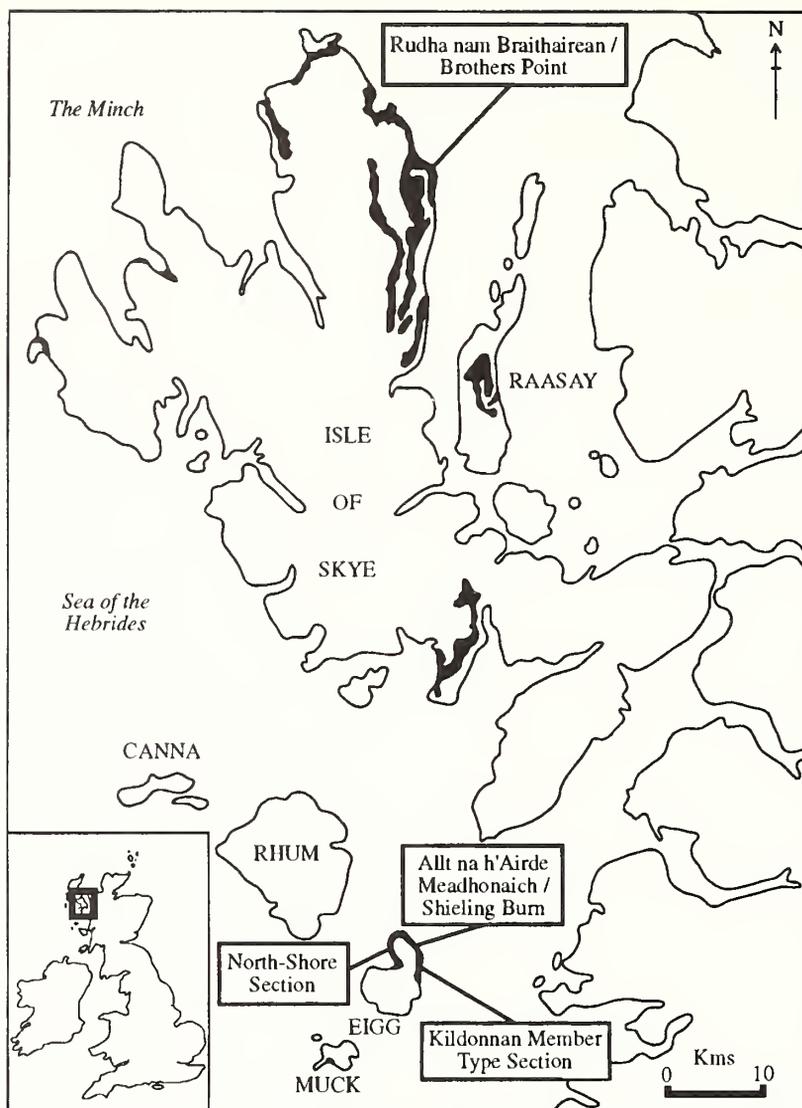
**ABSTRACT.** Molluscs, conchostracans, algae, palynomorphs and, in particular, ostracods are used to define fluctuating salinities in the Lealt Shale Formation, Great Estuarine Group (Upper Bajocian–Bathonian, Middle Jurassic). Salinities ranged from oligohaline (0.5–5‰) to mesohaline (5–18‰). Fluctuations were often rapid, occurring over only 10–20 mm of sediment. The Kildonnan Member of the Lealt Shale Formation is shown to have experienced a more unstable salinity history than the Lonfearn Member of the same formation. The ostracods are shown to provide a more accurate interpretation of the palaeosalinity fluctuations in the sections studied than do the molluscs. Occasionally only integrated studies allow a reasonably viable determination of palaeosalinity. Salinity tolerance ranges are estimated for 26 ostracod species in the sequence studied. Published oxygen isotope analyses of the mollusc *Praemytilus strathairdensis* are shown to correlate well with the salinity fluctuations determined using the ostracod fauna. High abundances of the fresh to brackish water tolerant alga *Botryococcus* correlate with occurrences of freshwater ostracods (*Limnocythere*, *Theriosynoeum* and *Darwimula*), as well as with freshwater molluscs (*Unio* and *Viviparus*), and with conchostracans.

THE aim of this paper is to elucidate the possible palaeoenvironmental significance of the Ostracoda within the Lealt Shale Formation. The paper determines a relative salinity tolerance for each ostracod species from the Lealt Shale Formation and uses these interpretations to detail the palaeosalinity of the depositional environment. Previous studies on the palaeoenvironment using bivalves, gastropods, conchostracans and algae are tested. By the integration of data from all the available faunal evidence a palaeosalinity curve for each section studied is defined.

## THE GREAT ESTUARINE GROUP

The Great Estuarine Group, as defined by Harris and Hudson (1980), is composed of seven formations, all of which were deposited under non-marine to marginal marine conditions (Hudson 1963a, 1966, 1970, 1980; Tan and Hudson 1974; Hudson and Harris 1979; Andrews 1984, 1985; Andrews and Walton 1990). Despite the facies variations manifest in the Great Estuarine Group, the vertical succession is remarkably constant over the entire outcrop, which amounts to c. 90 km in length (Text-fig. 1). Indeed, some individual beds can be traced over the entire outcrop, e.g. the algal stromatolite, which divides the two members of the Lealt Shale Formation, the Kildonnan and Lonfearn members (Hudson 1970, 1980; Harris and Hudson 1980). The Great Estuarine Group has no fully marine sequences within its succession, and, as such, no ammonites with which to date it. A composite dating and correlation (Text-fig. 2) based on palynomorph biostratigraphy, lithofacies correlation and sequence stratigraphy is used to provide a chronostratigraphical framework for the sequence (Wakefield 1991, 1994).

Hudson (1963a, 1966, 1980) and Tan and Hudson (1974) considered that the Lealt Shale Formation was deposited in lagoonal systems which had a direct link to waters of marine salinity;



TEXT-FIG. 1. Location of the outcrop of the Great Estuarine Group (shaded) and of the sections sampled.

an open lagoon in the sense of Hudson (1980). Stable isotope studies (C and O), particularly upon *Praemytilus strathairdensis*, indicate direct seawater–river water mixing (Tan and Hudson 1974, figs 1–2). It was considered that the deposits were not truly estuarine, because this type of environment would not allow the equilibration of  $^{13}\text{C}$  with atmospheric  $\text{CO}_2$  as required to explain the heavy carbon values found, and also because of the wide lateral extent of this very shallow facies (Hudson 1963a).

#### SECTIONS STUDIED

The Kildonnann and Lonfearn members (Harris and Hudson 1980) of the Lealt Shale Formation were originally named the Mytilus and *Estheria* Shales respectively (Anderson 1948; Hudson 1962).

		Ammonite Zones	Ammonite Subzones	Proposed correlation					
Callovian		<i>Macrocephalites herveyi</i>	<i>M. camptus</i>	Staffin Shales Fm	Belemnite Sands Member				
			<i>M. terebratus</i>						
			<i>Keplerites (K.) kepperi</i>						
BATHONIAN	UPPER	<i>Chydoniceras (Chydoniceras) discus</i>	<i>C. (C.) discus</i>	Staffin Shales Fm	Upper Ostrea Member				
			<i>C. (C.) hollandi</i>						
		<i>Oppelia (Oxycerites) orbis</i>				Skudiburgh and Kilmaluag formations			
	MIDDLE		<i>Procerites hodsoni</i>		Duntulm Formation	GREAT ESTUARINE GROUP			
				<i>Morrisiceras (Morrisiceras) morrissi</i>					
				<i>Tulites (Tulites) subcontractus</i>					
		LOWER	<i>Procerites progradilis</i>		No correlation with standard ammonite zones possible		Lealt Shale Fm.	Valtos Sandstone Formation	
				<i>Asphinctites tenuiplicatus</i>					Lonfean Member
				<i>Zigzagiceras (Zigzagiceras) zigzag</i>				<i>O. (O.) yeovilensis</i>	Kildonnan Member
	<i>M. (M.) macrescens</i>								
	<i>P. (P.) convergens</i>								
	Bajocian	<i>Parkinsonia parkinsonia</i>	<i>P. bomfordi</i>	No correlation with standard ammonite zones possible	Lealt Shale Fm.	Elgol Sandstone Formation			
<i>S. truelli</i>									
<i>P. acris</i>									
<i>Stenoceras (Garantiana) garantiana</i>		<i>S. (G.) tetragona</i>	Cullaidh Shale Formation						
		<i>S. (G.) subgaranti</i>							
		<i>S. (P.) dichotoma</i>				Garantiana Clay			

TEXT-FIG. 2. Suggested correlation of the Great Estuarine Group with the standard ammonite zones.

The type sections of the formation are exposed on the islands of Eigg and Skye in the Inner Hebrides off NW Scotland. The type section of the Kildonnan Member is exposed 2.5 km north of Kildonnan, Isle of Eigg [NM 495870] (Harris and Hudson 1980); the dominant lithology is grey, silty shales with monotypic shell beds of the bivalve *Praemytilus strathairdensis*. Other distinctive shelly limestones and sandstones are used to correlate the different parts of the discontinuous exposure (Hudson 1966). Harris and Hudson (1980) show that this section ends with an algal stromatolite. The upper beds of this section (as recorded in Hudson 1966), including the top of Bed 8 and the Algal Bed, lay above a low angle slip plane and have now been largely eroded away. It is unlikely that more than a metre of the Kildonnan Member is missing from the top of the exposure, whilst the base of the exposure is considered to be only a couple of metres above the underlying Elgol Sandstone Formation. The transition from the Kildonnan to the Lonfearn Member is exposed in several sections around the north-west coast of Eigg, particularly at NM 469904–475908. The type section of the Lonfearn Member (Harris and Hudson 1980) is a composite of the exposures seen at Rudha nam Braithairean [NG 526625] and the mouth of the Lonfearn Burn [NG 517551]; the typical lithology is dark grey to brown shales, which often appear black due to metamorphism by the numerous Tertiary sills and dykes. The upper portion of the Lonfearn Member was sampled in the Shieling Burn, Eigg [NM 497888]. The top of the Lonfearn Member, and of the Lealt Shale Formation, is defined at the incoming of *Neomitodon*-dominated siltstones of the Valtos Sandstone Formation (Harris and Hudson 1980).

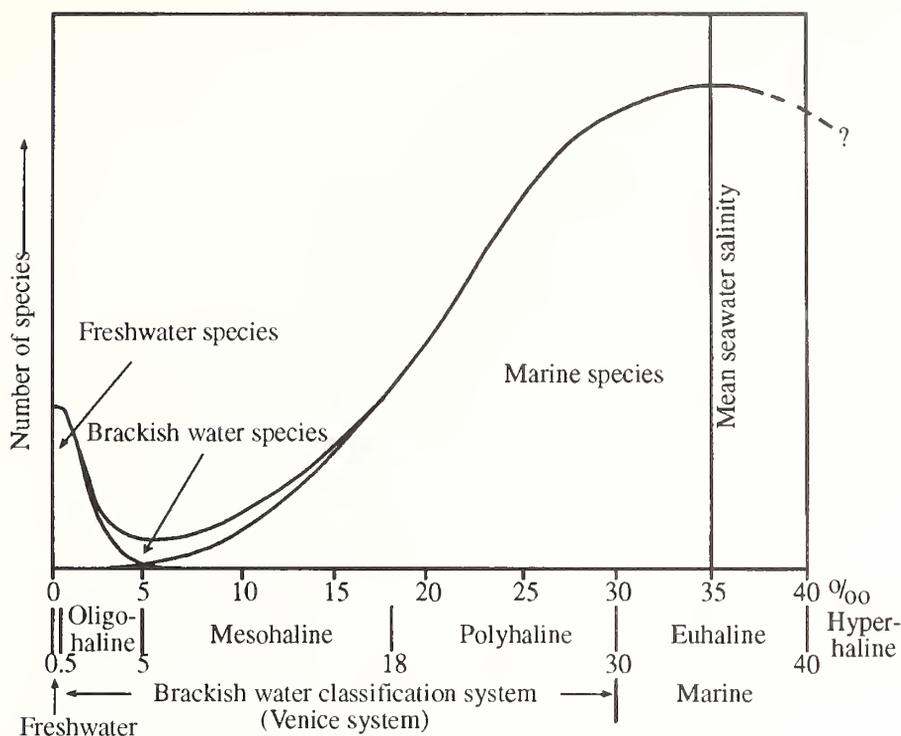
The lithostratigraphical divisions of Harris and Hudson (1980) are used in this paper. The logs for the Lealt Shale Formation sections were supplied by J. D. Hudson, and can be found in the appendix of Wakefield (1991). The logs from the sections exposed on the Isle of Eigg will be published in the 'Small Isles Memoir' of the British Geological Survey (Hudson in press).

#### SAMPLING AND PROCESSING TO OBTAIN OSTRACODS

Samples each weighing approximately 1 kg were collected from the smallest possible vertical thickness, usually 50 mm. Shales, silty shales, clays, mudstones, silty sandstones and sandstones were sampled. Samples were broken into small, 20–30 mm, sized pieces, half of which were placed in a plastic container and covered with a 10 per cent. solution of H<sub>2</sub>O and left overnight. The disaggregated sediment was wet sieved with 2800  $\mu$ m, 850  $\mu$ m and 125  $\mu$ m sieves. These residues were dried, weighed and bagged. Residues were hand picked for ostracods with an 'OO' sable brush using a Wild M8 binocular microscope.

#### THE CLASSIFICATION OF BRACKISH WATERS

All water bodies are complex chemical solutions of various ions. These give rise to salinity, which in turn may affect the distribution of biotas. Salinity is defined as the total ionic concentration, principally of Na and Cl, and is, therefore, defined in terms of chlorinity (Knudsen 1901). The qualitative terms, freshwater, brackish and marine, of the last century were formally quantified by Redeke (1922), Välinkangas (1993) and finally at the Venice Symposium of 1958. Remane (1934, 1958) documented the abundance of species throughout the freshwater to marine salinity spectrum based upon a hypothetical transect from the North Sea into the Baltic Sea (Text-fig. 3). Chlorinity is not considered to be a good method of assessment of salinity values for those brackish water bodies which have no direct connection to the sea. These water bodies may derive their salinity from solutes other than Na and Cl. These types of brackish water bodies are termed athalassic (DeDeckker 1981a). The salinity values and ranges of the Venice system are applied throughout this work. The use of this scale is not intended to imply that Bathonian seawater had a salinity of 35‰, but is used to allow relative changes in salinity to be described.



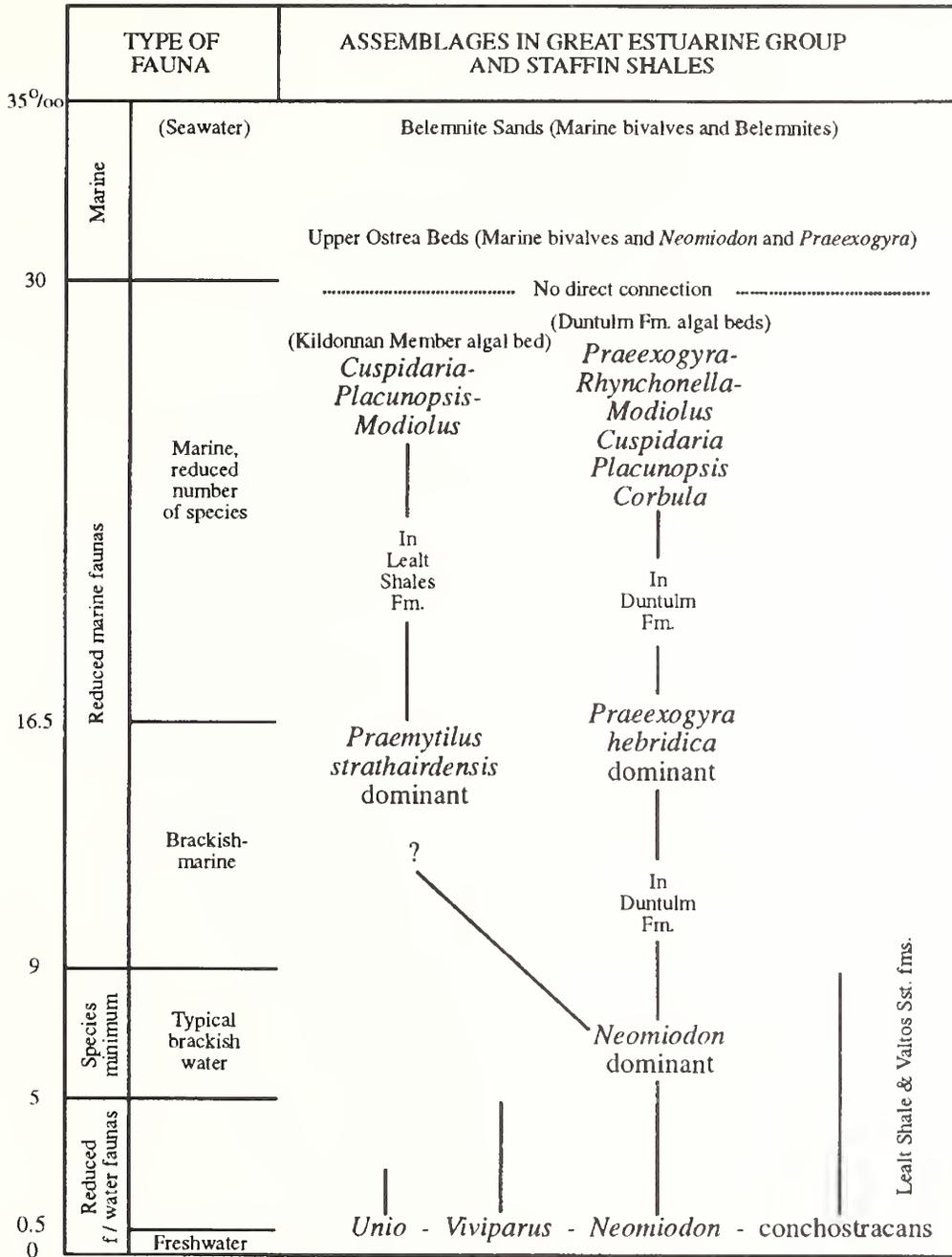
TEXT-FIG. 3. Modified Remane diagram showing the relationship between species diversity and salinity. No precise quantitative significance is implied. The brackish water classification system (Venice System) is shown (after Hudson 1990).

#### PREVIOUS STUDIES ON THE BIOTA OF THE LEALT SHALE FORMATION

The Lealt Shale Formation is the most palaeontologically diverse formation of the Great Estuarine Group. Studies on the molluscan, conchostracan and algal fauna and flora of the Great Estuarine Group (Hudson 1963*a, b*, 1966, 1970, 1980) were preceded by the publication of faunal lists for the Reptile Bed of the Kildonnan Member (Barrow 1908) and for the Great Estuarine Series (Tate 1873). A faunal list for the Lealt Shale Formation is given in Table 1, which also provides details of species authorship. Hudson (1963*a*) established salinity tolerances for the mollusc and conchostracan fauna and hence recognized salinity fluctuations throughout the Great Estuarine Group. A more detailed account of the palaeosalinity of deposition of the Kildonnan Member type section was included in a paper on Hugh Miller's Reptile Bed (Hudson 1966). Such palaeosalinity studies have been refined over the years by the discovery of pseudomorphs after gypsum in the algal bed from the type section of the Kildonnan Member (Hudson 1970), and detailed by stable isotope studies of, in particular, the molluscs and the algal beds (Tan and Hudson 1974; Andrews 1986). Some of the mollusc species of the Great Estuarine Group also occur in China (Yin 1991). Stable isotope analyses of the Chinese specimens have shown that they lived in waters of comparable isotopic composition, and most probably the same salinity, as did the molluscs of the Great Estuarine Group (Yin 1991).

Hudson (1963*a*) argued for a salinity control upon the molluscan and conchostracans faunas, of which the latter has only recently been described taxonomically (Chen and Hudson 1991). This salinity control was reaffirmed in Hudson (1980). Hudson recognized a series of salinity controlled assemblages (Text-fig. 4), which were based upon associations of molluscs and conchostracans, and made assumptions as to the salinity tolerances of each species. These assumptions relied upon





TEXT-FIG. 4. Salinity controlled mollusc and conchostracan assemblages of the Great Estuarine Group and Staffin Bay Shales (modified after Hudson 1963a).

conservatism of the fauna. The co-occurrence of the bivalve *Unio andersoni*, the gastropod *Viviparus scoticus* and conchostracans, contemporaries of which are all known from fresh and oligohaline waters today, supports the initial assumptions. These low salinity forms rarely occur with the bivalve *Praemytilus strathairdensis*, which is considered to be tolerant of mesohaline waters, and

never with the marine bivalves *Placmopsis socialis* and *Cuspidaria ibbetsoni*. Hudson was able to define salinities for the molluscs that he had recorded:

*Unio-Neomiodon-Viviparus* – 0–3‰.

*Neomiodon brycei* as only mollusc = species minimum – 5‰; otherwise euryhaline and highly opportunistic.

*Praemytilus strathairdenis* – lower limit 6–10‰; marine euryhaline; beds which are dominated by small specimens are interpreted as representing the lower end of the tolerance range.

*Placmopsis socialis* – marine, euryhaline around 30‰.

*Cuspidaria ibbetsoni* – marine, euryhaline around 30‰.

These salinity ranges have been corroborated by stable isotope analyses of shells from the various molluscan species (Tan and Hudson 1974). Isotopic analyses of *Praemytilus strathairdenis* from Bed 5 of the Kildonnan Member type section by Tan and Hudson (1974) indicated a mean temperature of growth of 22 °C. This figure was later refined to take into account the likely composition of an ice free Earth, producing a figure of 17–18 °C (Hudson 1980). It was argued that the annual mean water temperature was lower because shell growth had only occurred during the warm summer months, as indicated by detailed shell structure work (Hudson 1968). Tan and Hudson (1974) concluded that *Praemytilus strathairdenis* lived in waters whose salinity was determined by variable mixing of fresh and seawaters giving a direct <sup>13</sup>C–<sup>18</sup>O correlation. When the palaeontological evidence is compared with the life cycle of a typical Recent mussel, such as *Mytilus galloprovincialis* Lamarck, then similarities are evident. Based on detailed life cycle studies, given a summer temperature of 18 °C, then a salinity of 20–25‰ would provide the optimum environmental conditions for growth. The adults of *Mytilus galloprovincialis* are able to survive in salinities as low as 10‰ (Hrs-Brenko 1978).

Recent palynological investigations of the Great Estuarine Group (Walton 1988), have helped to endorse the salinity groupings of the mollusc and conchostracan fauna defined by Hudson (1963a). Walton (1988) found an excellent correlation between high abundances of the fresh to brackish water tolerant planktonic alga *Botryococcus*, the occurrence of the bivalves *Unio andersoni* and *Neomiodon brycei*, the gastropods *Viviparus scotticus* and *Valvata* sp., and conchostracans which were all considered to be tolerant of freshwater (Hudson 1963a). Whilst occasionally abundant with the brackish water tolerant bivalve *Praemytilus strathairdenis*, *Botryococcus* was rare in samples which contained the marine-brackish tolerant bivalves *Tancredia gibbosa*, *Placmopsis socialis* and *Cuspidaria ibbetsoni*.

The mollusc and conchostracan fauna has been used to determine the palaeosalinity of the Great Estuarine Group as a whole (Hudson and Harris 1979). The Lealt Shale Formation was interpreted to have been deposited under variable but generally low salinities (brackish-marine to freshwater). Beds 1–3 of the Kildonnan Member type section, were interpreted to have been deposited under low (fresh–oligohaline; 0–5‰) but variable salinities (Hudson 1966). Bed 5, dominated by the bivalve *Praemytilus strathairdenis*, experienced low brackish-marine salinities (16‰). Beds 6–7 record a general decline in salinity to possibly freshwater conditions in the *Unio* Bed (7a). An increase in salinity is recorded in beds 8–9. The discovery of pseudomorphs after gypsum in the Algal Bed (Hudson 1970, fig. 3) indicates that salinities were hypersaline, at least at times.

Palynological studies of the Great Estuarine Group have only recently been completed (Walton 1988; Riding *et al.* 1991). A brief summary of this work is included to allow a more complete assessment to be made of the Lealt Shale Formation. Only the Kildonnan Member type section and the Lonfearn Member at Rudha nam Braithairean were examined in these works.

In the Kildonnan Member, Riding *et al.* (1991) recorded high levels of gymnosperm pollen; constituting up to 85 per cent. of the palynoflora. The majority of the palynomorphs recorded are non-marine forms. Excepting Beds 6b and 6f, *Botryococcus* was present in almost all samples. Acanthomorph acritarchs, which appear to have tolerated reduced salinities (Walton 1988), occurred with the bivalves *Placmopsis socialis* and *Cuspidaria ibbetsoni* and with marine dinoflagellate cysts. The acritarchs comprised 44.7 per cent. of the palynoflora in Bed 6f. The low diversity dinoflagellate cyst associations are considered to be indicative of marginal marine conditions which were subject

to salinity fluctuations (Riding *et al.* 1991). The Algal Bed contains the highest proportion of pollen, some 97.3 per cent. of the palynoflora.

*Botryococcus* is ubiquitous in the Lonfearn member. Dinoflagellate cysts occur only occasionally, indicating temporary establishments of marginal marine conditions. The lower abundances of peridiphyte spores, compared with those in the Kildonnan Member, suggests that the land areas were less densely vegetated or further away (Riding *et al.* 1991).

Using the palynofloras, Walton (1988) interpreted the Kildonnan Member type section in the following way. Beds 1–6a (inclusive) were deposited under non-marine brackish conditions. Beds 6b, 6c and the base of 6d had a marine influence (acritarchs). The top of Bed 6d records freshwater conditions (*Botryococcus*). Marine influences (acritarchs) are present in Beds 6e and the base of 6f. A return to freshwater conditions is recorded from the top of Bed 6f through Bed 7a. This interpretation compares well with that given in Hudson (1966) and reported earlier in this review.

Little attention has been given to the ostracod fauna from the Lealt Shale Formation. F. W. Anderson (*in* Hudson 1963a, p. 324) noted that the ostracod fauna was dominated by metacyprids. At this time metacyprids were considered to be members of the Limnocytheridae Sars, 1925, and were subsequently raised to subfamily status (Danielopol 1965). Metacyprinae is now considered to be a junior synonym of Timiriaseviinae Mandelstam, 1960, a view with which I agree (see Colin and Danielopol 1978, 1980 for a review of the systematics of the Limnocytheridae). Taking the above into account, and the similarities in external morphology of *Metacypris* Brady and Robertson, 1870 and *Theriosynoecum* Branson, 1936, I consider that Anderson was most probably referring to *Theriosynoecum*. Indeed, many synonyms of *Theriosynoecum* contain species originally assigned to *Metacypris* (see Branson 1966 for examples). However, in Hudson (1966). Gramann and Hiltermann identified, mostly to generic level, ostracods from Bed 3c (*Fuhrbergiella* n. sp.), Bed 5 (*Glyptocythere* cf. *tuberoventina* Brand and Malz; *Glyptocythere* (?) n. sp.; *Progonocythere polonica* Blaszyk; and *Progonocythere* n. sp.), and Bed 6b (*Progonocythere* n. sp.). The occurrence of *Glyptocythere* cf. *tuberoventina* remains unsubstantiated. It is considered that *Glyptocythere* (?) n. sp. is equivalent to *Glyptocythere inversalitera*, *Progonocythere* n. sp. is equivalent to *Progonocythere milleri*, and that *Fuhrbergiella* n. sp. is equivalent to *Fronslarvata chamaeleon*. No palaeoecological interpretation was given for these ostracods.

Only a single foraminifer species has been reported from the Lealt Shale Formation, namely *Anmodiscus tenuissimus* from Bed 6b, Kildonnan Member type section (Hudson 1966). This occurrence can now be extended to include Bed 6 of the Kildonnan Member of the North Shore Section, Egg and from the basal 150 mm of Bed 3 of the Lonfearn Member from Rudha nam Braithairean, Skye. *Anmodiscus tenuissimus* occurs with conchostracans, the bivalve *Neomiodon brycei* and occasionally with small specimens of the bivalve *Praemytilis strathairdensis*, and, as such, it is here interpreted to have been tolerant of low salinity brackish waters (oligohaline to mesohaline; 0.5–10‰).

Chen and Hudson (1991) recorded six species of conchostracan from the Lealt Shale Formation (see Table 1). They are interpreted to have tolerated low salinities (Hudson 1963a) which are below those usually occupied by the bivalve *Praemytilis strathairdensis*. Recent conchostracans tolerate fresh and slightly brackish waters whilst growing and breeding, although they commonly inhabit temporary pools (Tasch 1987).

All of the palaeontological research on the Lealt Shale Formation undertaken to date has substantiated the conclusions of Hudson (1963a, 1966), that the formation was deposited under low but fluctuating salinities. It was these salinity fluctuations that appear to have been the major environmental control upon the faunal and floral occurrences.

#### DETERMINING THE AUTOCHTHONEITY OF OSTRACOD ASSEMBLAGES

Because of the discontinuous growth of ostracods, it is possible to determine the autochthoneity of ostracod assemblages. Most benthic ostracods pass through eight moult stages (instars) between

hatching and maturity. In so doing the ostracod must shed its rigid calcareous valves, and thus leaves a record of its ontogeny for posterity. For each species a record of the moult stages present within a bed gives an insight into the energy conditions of deposition (Whatley 1983, 1988). Each ostracod is measured and plotted on a length:height graph. This allows the different moult stages to be determined. Histograms of the numbers of each moult stage, the age structure of the assemblage, are then used to determine autochthoneity. Sediments deposited under low energy conditions contain ostracod assemblages composed of adults (both dimorphs if present in a particular species) and even the smallest juvenile stages. Due to the large differences in size and hydrodynamic properties of the adults and juveniles, it is unlikely that a low energy thanatocoenosis, as described above, could be constructed by the sequential influences of different hydrodynamic conditions. These types of assemblage are commonest in lacustrine environments (Whatley 1988). Environments with higher energy levels contain ostracod assemblages with incomplete age structures; often only the adults and largest juveniles are present. This age structure is referred to as a high energy thanatocoenosis. Age structures between the extreme end members described above can also be found. These are produced by intermediate energy levels. Allochthonous assemblages often contain only the smallest juvenile stages (Whatley 1983, 1988). As a general rule the smallest juveniles are transported over greater distances than the larger juveniles and adults.

The determination of autochthonous assemblages, as describe above, is further complicated by the preservational state of the ostracods. Oertli (1971) concluded that large numbers of ostracod carapaces within an assemblage indicated a high sedimentation rate. This generalization is overly simplistic and ignores the possible presence of interstitial ostracods, low energy conditions, burrowing habits employed to follow the water table during droughts (DeDeckker 1981b), or of ostracods washed above mean water level during storms (Wakefield 1991). Whatley (1983) noted that ostracods disarticulate their valves during moulting, and that juvenile carapaces indicate infant mortality. The absence of carapaces probably indicates some transport rather than a complete lack of infant mortality. Post mortem carapace preservation depends on hinge structure, valve overlap and whether the adductor muscles contract or relax upon death.

In shallow lagoonal environments, such as those envisaged for the Lealt Shale Formation (Hudson 1963a, 1966, 1980), energy levels would have generally been low. Being so shallow, the environment would easily be influenced by storms. This may explain the lack of the smallest juveniles in the ostracod assemblages studied. Assemblages with adults and a large number of juveniles are common. Assemblages different from this are the exception, some of which have been ascribed to storm deposition (Wakefield 1991). It is these storm-induced mass mortality assemblages which contain large numbers of adults and larger juvenile carapaces, probably as a consequence of rapid sedimentation.

It was not always possible to obtain a large enough number of specimens for accurate age structure studies to be attempted. This was because of variation in the preservation of the ostracods, both within and between sections, as a result of local variation in metamorphism by Tertiary sills and dykes. This was particularly evident in the sections at the Shieling Burn, Eigg, and Rudha nam Braithairean, Skye. For example, calculated recoveries of ostracods per kg of sediment from the Rudha nam Braithairean section varied between a maximum of 18250 and a minimum of 620. These two samples contained the same assemblage (*Limnocythere incerniculum* and *Darwinula pulmo*), with 88–93 per cent. of the ostracod fauna being *Limnocythere incerniculum*. Observations of bedding planes from these horizons indicate that ostracods were equally abundant. It appears, therefore, that variations in preservation are compounded during processing such that many specimens may be effectively destroyed. It was, therefore, in some instances necessary to determine *in situ* ostracods in another way. By counting the number of specimens of each species in an assemblage (each valve represents half a specimen and each carapace one specimen) it was possible to calculate the percentage compositions of each assemblage. In most instances two or three species dominated the assemblage, making up over 80 per cent. of the assemblage, and were considered most probably *in situ*. A qualitative visual check of bedding plane assemblages was carried out at the same time as the counting in order to assess whether adults and juveniles were present for each

species. If only juveniles were present then it was possible to question whether or not the species was *in situ*. Within the Kildonnan Member, and particularly with *Linnocythere incerniculum*, it was noticed that the adults were more prone to damage during processing than the juveniles. This fact exacerbated the problem of determining whether a species was *in situ*. When this method was tried on samples that also had age structure studies carried out, the *in situ* species determined by each method were the same.

## OSTRACOD PALAEOECOLOGY OF THE LEALT SHALE FORMATION

### *Controlling factors on ostracod distribution*

Although it is well known that various physical and chemical environmental variables influence ostracod distribution, e.g. climate, water temperature, water depth, substrate, food supply, salinity, pH and oxygen concentration, it would appear that salinity is most likely to have been the primary controlling factor during deposition of the Lealt Shale Formation.

Most of the variables listed above are considered to have had a negligible affect upon ostracod occurrences in the Lealt Shale Formation. The palaeolatitude has been calculated to have been about 35° N (Smith *et al.* 1973). The climate was warm, with mean annual water temperatures around, or slightly below, 17–18 °C (Hudson 1980). It was wet and there was marked seasonality (Tan and Hudson 1974; Hudson and Harris 1979). It seems highly unlikely that these would have varied across the Hebrides depositional basin, around 90 km from north to south.

The water was probably around 5 m deep (Hudson and Andrews 1985). Water temperature is considered not to have varied with depth because of the shallow nature of the environment (Hudson 1963a; Hudson and Andrews 1987). Numerous shell lags attest to a periodically mobile water column as does the winnowed concentration of bone material in the Reptile Bed (Bed 2) of the type section of the Kildonnan Member (Hudson 1966). The *Praemytilus* in shell beds are often orientated, and were probably deposited in the waning ebb flow after storms. Water movement in shallow environments is likely to disrupt the development of a thermocline. The same process will also prevent the development of salinity stratification, a halocline, (Barnes 1980). A mobile water column also suggests that the water was well oxygenated. Ostracod age structure studies suggest only limited and infrequent transportation of valves. Within the Kildonnan Member some assemblages of the ostracod *Linnocythere incerniculum* have been recorded with both sexual dimorphs and usually five and in one instance seven juvenile stages preserved, indicating stable water conditions and autochthoneity of the assemblages. Only the smallest juveniles have been winnowed out. In other samples containing the same species only juveniles were recorded. These may be low energy thanatocoenoses (see above). All of the ostracods present in the Lealt Shale Formation are considered to have been benthic, e.g. *Darwinula stevensoni* (Brady and Robertson, 1870) is known from Recent ecological studies to be benthic, living either on or in the top 10 mm of sediment (Ranta 1979). For benthic ostracods the substrate is likely to have had an important influence on their distribution. However, no variation of species with differing sediment type was noted in either member of the Lealt Shale Formation. Limestones were not sampled, though shales, silty-shales, clays, mudstones, siltstones, silty-sandstones and sandstones were. Plants are also known to affect the distribution of ostracods (Whatley and Wall 1975). It is not possible to determine exactly what plants, or organic detritus, were present in the Lealt Shale environment on which the ostracods could have lived, and/or fed. Large amounts of organic material are preserved in the shales so food was probably plentiful.

Although *Linnocythere*, *Darwinula* and *Paracypris* all have Recent representatives, the environmental preferences of which can be utilized in palaeoenvironmental studies, most Mesozoic ostracod genera do not. As a consequence, most palaeoecological interpretations of Mesozoic ostracods are based upon morphological similarities with related Recent genera, as well as sedimentary and stable isotope geochemical evidence. Benson (1959) thought that 'most genera are too all-inclusive for detailed ecological work' and that it was 'better to use species...for any paleoecological interpretations'. Sandberg (1965) recognized a small number of genera as

being characteristic of brackish water and consequently placed greater emphasis on the use of genera for palaeoenvironmental and palaeosalinity reconstructions. The large number of ostracod species (eleven from eight genera in the Kildonnan Member and fifteen from ten genera in the Lonfearn Member), and the co-occurrences of species enabled an accurate assessment of relative salinity tolerances for the Lealt Shale Formation. No ostracod species occurs in both the Kildonnan and Lonfearn members, so it is not possible to compare directly the salinity tolerances of species from both members. It was decided not to use the mollusc salinity tolerances of Hudson (1963a) as a basis for defining the relative tolerances of the ostracods, in order to allow an independent determination from the ostracods. However, comparisons with the molluscs were used as a means of checking the relative tolerance ranges of the ostracods detailed below.

#### DETERMINATION OF RELATIVE SALINITY TOLERANCES

Before construction of a salinity tolerance range chart of the Lealt Shale Formation ostracods was attempted, it was necessary to determine which species co-occurred *in situ* (see above). In addition, assumptions were made as to the salinity tolerances of the genera *Theriosynoecum*, *Limnocythere* and *Darwimla*, in order to allow an initial framework upon which to build the relative tolerances of the other ostracod genera and species. It is not possible to determine precise synchronicity in the fossil record, therefore all of the species in a single sample were considered to be synchronous unless evidence to the contrary was available, e.g. as in Bed 3h from the type section of the Kildonnan Member (see below).

The assumption of salinity tolerances for *Theriosynoecum*, *Limnocythere*, and *Darwimla* was based upon studies of both Recent and fossil species. A maximum and a minimum tolerance was assumed for each genus, outside of which it was considered unlikely that the genus could feed, respire and breed. It is known that some ostracods can tolerate enormous variations in salinity, but can only feed and breed over a relatively narrow salinity range (DeDecker 1981a). This assumption of tolerance ranges was not rigorously applied, such that every species of *Limnocythere* had the same tolerance limits. In some cases, it was possible to determine that one species of *Limnocythere*, by its association with ostracods determined to tolerate higher salinities, and the lack of association with another species of *Limnocythere*, had a different tolerance range to the latter species. However, both species' tolerance ranges lay within the generic tolerance range.

These three genera were chosen because they are all either known, or considered to be tolerant of fresh water, and as such only their upper salinity limits vary. Evidence is available to indicate these upper limits with a reasonable degree of certainty. Many of the genera from the Lealt Shale Formation, e.g. *Glyptocythere*, *Acanthocythere* and *Lophocythere*, are considered to have been euryhaline marine. As such both the upper and lower limits of their salinity tolerance could be in doubt.

#### *Salinity tolerance of Theriosynoecum*

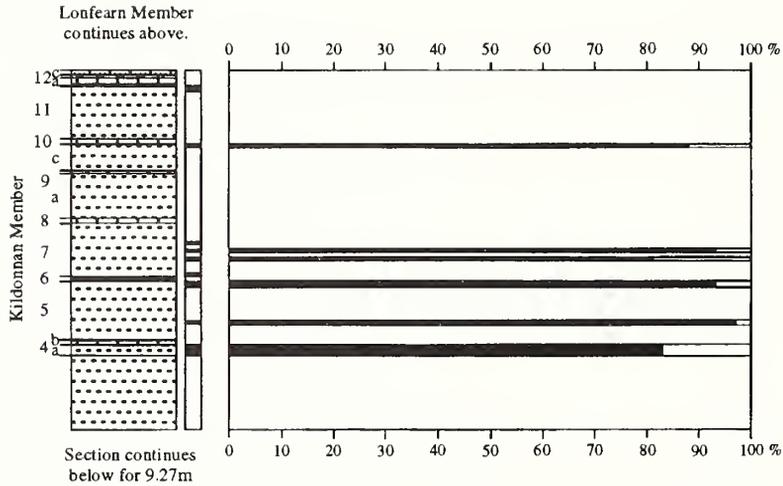
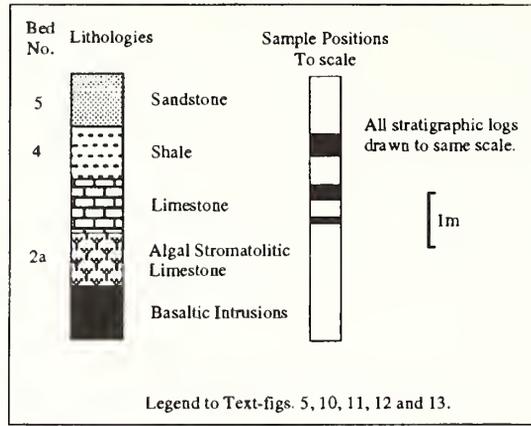
*Theriosynoecum* is known only from the fossil record, having become extinct in the Albian (Cretaceous; Colin and Danielopol 1979). The majority of the evidence as to its salinity tolerance is essentially inference, and often circular, being based upon its association with other assumed freshwater organisms, e.g. *Darwimla* (see below), charophyte oogonia, conchostracans, the bivalve *Unio* and the gastropod *Viviparus*. In this context it should be noted that a Recent charophyte, *Lamprothamnium papulosum* (Wallroth, 1833), has been found growing in saline waters, and still fixing CO<sub>2</sub> up to salinities twice that of seawater (Burne *et al.* 1980). Most charophytes, however, are regarded as being indicative of freshwater. *Gomphodella* is regarded as the closest related, morphologically similar genus to *Theriosynoecum*, and has an upper salinity tolerance of 2.3‰ (DeDecker 1981b).

Only Kilenyi and Allen (1968) give an inferred salinity range for *Theriosynoecum*. Their study of Purbeck and Wealden Ostracoda, following on from the faunicycle investigations of Anderson

*et al.* (1967), indicated a range of 0–7‰. Some ambiguity as to the salinity tolerance of *Theriosynoecum* has arisen during the study of the Purbeck and Wealden Ostracoda. Anderson *et al.* (1967) classify *Theriosynoecum* as an S-phase but primarily brackish water genus. Barker (1966) and Kilenyi and Allen (1968) noted that many of the S-phase genera (*Theriosynoecum*, *Klicana*, *Darwinula* and *Rhinocypris*) also occurred in the freshwater C-phase *Cypridea* assemblages. This indicated that these genera were probably tolerant of fresh to oligohaline waters (0–5‰). Kilenyi and Neale (1978) considered *Theriosynoecum fittoni* (Mantell) to be a freshwater species, a conclusion based upon the stable isotope analyses of Allen and Keith (1965) who measured  $\delta^{13}\text{C}$  values of  $-2\text{‰}$ . Allen and Keith (1965) also studied *Theriosynoecum alleni* (Pinto and Sanguinetti), for which  $\delta^{13}\text{C}$  values of  $+0.48\text{‰}$  were quoted. These results, however, were not based upon measurements on the ostracods themselves, but on bivalve fragments from the same bed, which were not necessarily contemporary. These data were, however, used to argue for a wide salinity tolerance for *Theriosynoecum* in general, although Allen *et al.* (1973, p. 615) did concede the potential inaccuracy in the original statement. Tan and Hudson (1974) analysed *Theriosynoecum conopium* Wakefield and Athersuch, 1990, from Bed 7 of the Kilmaluag Formation type section. They found mean  $\delta^{13}\text{C}$  of  $-1.8\text{‰}$  and mean  $\delta^{18}\text{O}$  of  $-5.9\text{‰}$ , which they considered to suggest transitional to freshwater environments. Isotopic values for  $\delta^{13}\text{C}$  of  $-0.76\text{‰}$  and  $\delta^{18}\text{O}$  of  $-2.95\text{‰}$ , were obtained from a mixed sample of *Theriosynoecum conopium* taken from both Bed 24, Kilmaluag Formation, Camas Mor, Muck, and Bed 3, Kilmaluag Formation, Prince Charles's Point, Skye (J. E. Andrews, pers. comm. 1991). Andrews interprets these results as indicating evaporating 'freshwaters' which were in equilibrium with atmospheric  $\text{CO}_2$ . A tolerance of 0–7‰, as given in Kilenyi and Allen (1968), is used in this work.

#### *Salinity tolerance of Limnocythere*

*Limnocythere* is generally regarded as being indicative of fresh waters. Work on Recent species, however, has begun to unravel the hydrochemical controls on the distribution of *Limnocythere*, and has shown that solute chemistry may be more important than absolute salinity. Carbonel and Peypouquet (1979, 1983) and Peypouquet *et al.* (1979) contended that waters lying on the alkaline or continental saline path of Hardie and Eugster (1970) are dominated by *Limnocythere*. However, Martens (1990), in his study of African rift valley species of *Limnocythere*, did not find any convincing evidence that *Limnocythere* prefers alkaline waters. Many records of the salinity tolerance of *Limnocythere* have been taken from continental settings where Na and Cl are not the dominant salts; athalassic environments, which are often alkaline. *Limnocythere staplini* Gutentag and Benson has been recorded living in salinities of up to 205‰ in Australian athalassic waters (DeDecker 1981a). It should be noted that many Australian *Limnocythere* species inhabit much lower salinities, and are generally only found in permanent water bodies (DeDecker 1983), e.g. *Limnocythere milta* (15.4‰, pH 9.5; DeDecker 1981a) and *Limnocythere mowbrayensis* (< 6‰; DeDecker *et al.* 1982). Alkaline waters are created by anionic enrichment and follow an evaporative path through carbonate, bicarbonate and soda. However, the neutral saline path is governed by cationic enrichment and follows an evaporative path through carbonates, sulphates (such as gypsum) and chlorides. There is little doubt that the waters of Lealt Shale environment lay on the neutral saline path. Tan and Hudson (1974, figs 1–2) used stable isotopic analyses of *Praemytilus strathairdensis* to show a direct mixing of seawater and river water, which could be compared with the work of Mook (1971) on mytilids from Dutch estuaries. The Lealt Shale results indicated that the diluting fresh water was richer in  $^{13}\text{C}$  than the estuaries studied by Mook (1971). This confirmed the idea that the Lealt Shale was deposited in lagoons with a direct link to marine waters which controlled variations in salinity. Hudson (1970) recorded pseudomorphs after gypsum in the algal stromatolitic limestone at the top of the Kildonnan Member. This again adds weight to the argument that the Lealt Shale waters were of a neutral saline chemistry, and that salinity tolerances from species inhabiting alkaline waters may not be applicable in this instance. Forester (1983) was able to show that *Limnocythere* inhabiting lacustrine environments were governed by



TEXT-FIG. 5. Percentage composition of the ostracod fauna containing only *Limnocythere incerniculum* (solid line) and *Darwinula pulmo* (unshaded line), from the Kildonnan Member at Rudha nam Braithairean/Brothers Point, Skye.

solute chemistry rather than by salinity. Again, although of interest, this factor may not be applicable to the Lealt Shale waters as he was studying inland lakes.

Würdig (1983) recorded *Limnocythere* sp. A at salinities of 0–2‰ in the coastal lagoons of eastern Brazil. Wagner (1957) recorded *Limnocythere inopinata* in waters of low salinity (< 3‰). However, Neale (1988) gives the species a tolerance range of 0–33‰ with a preference for salinities below 13‰. Lealt Shale species of *Limnocythere* often occur *in situ* with other freshwater ostracods such as *Theriosynoecium* and *Darwinula* (see discussion above and below). However, the *Limnocythere* species also occur in assemblages where they are *in situ* with genera considered to be tolerant of higher salinities, and with *Darwinula* and *Theriosynoecium* absent. Co-occurrences with *Praemytilus strathairdeusis* indicate that the Kildonnan *Limnocythere* species could tolerate mesohaline salinities. Based on this evidence it is considered that *Limnocythere* had a tolerance range from freshwater into mesohaline salinities, but probably not into polyhaline waters. The range, therefore, is considered for the purposes of this work, to be approximately 0–15‰, although as the discussion above illustrates, *Limnocythere* occurrence is governed by a wide range of chemical

controls, of which salinity is only one. The salinity range given here, when compared with the molluscan fauna with which *Linnocythere* occurs, appears to be plausible, although the range is considered only to be semi-quantitative.

#### *Salinity tolerance of Darwinula*

The salinity tolerance of *Darwinula* can also be based upon studies of Recent species, e.g. *Darwinula stevensoni*. Neale (1988) indicates a tolerance of 0–15‰ for *Darwinula stevensoni*, but notes that it is found at its maximum abundance in salinities of 0–2‰. Hagerman (1967) found that *Darwinula stevensoni* was at its maximum abundance in waters of 3‰ in the Gulf of Finland. This indicates that *Darwinula stevensoni* has a preference for waters of very low salinity. An upper salinity tolerance limit is based upon observations of *Darwinula* in some inland lakes of Australia, where it has been found in salinities of up to 15‰ (Keyser 1977; DeDeckker 1981a). This implies that at very low salinities *Linnocythere* and *Darwinula* are likely to coexist. However, at higher salinities (5–15‰) *Linnocythere* may begin to dominate numerically the assemblage as *Darwinula* approaches its maximum tolerance. This type of association was noted at many levels in the Lealt Shale Formation but particularly in the Kildonnan Member at Rudha nam Braithairean (Text-fig. 5). Here *Linnocythere incerniculum* comprises some 88–93 per cent. of the ostracod fauna, *Darwinula pulmo* being the only other ostracod present in the samples studied. These assemblages have been determined to be autochthonous. Gramann (1971) suggested that some Triassic *Darwinula* species may have had a wider salinity tolerance than Recent species. This conclusion was based upon the association of *Darwinula* with deposits interpreted as having formed in a hypersaline environment. Kilenyi and Neale (1978) felt that these *Darwinula* specimens had not coexisted with the hypersaline conditions; rather they had been killed as the increasing salinity passed their upper tolerance limit, and were then incorporated *in situ* into the evaporites. Other evidence as to the generally low salinities inhabited by Recent species of *Darwinula*, other than *Darwinula stevensoni*, was given by Würdig (1983), in which the following tolerances were given; *Darwinula serricaudata espinosa* Pinto and Kotzian, 1961 (0–3‰); *Darwinula pagliolii* Pinto and Kotzian, 1961 (0–3‰); *Darwinula africana brasiliensis* Pinto and Kotzian, 1961 (0–3‰) and *Darwinula* sp. A Würdig, 1983 (0–11‰).

A salinity tolerance of 0–15‰ with a preference for lower salinities in the oligohaline range, 0–5‰, is used in this work.

#### *Salinity tolerances of the Ostracoda from the Kildonnan Member*

*Darwinula pulmo* was found to occur almost exclusively with *Linnocythere incerniculum*, but often constituted only a small component of the assemblage. In most associations with only these two species, *Linnocythere incerniculum* comprised 90 per cent. of the assemblage. This was particularly evident in the Kildonnan Member sampled at Rudha nam Braithairean (Text-fig. 5). This finding is consistent with the assumed relative salinity tolerances used. *Linnocythere incerniculum* is considered to have tolerated a wider range of salinities (0–15‰) than *Darwinula pulmo* (0–10‰ with a preference for 0–5‰).

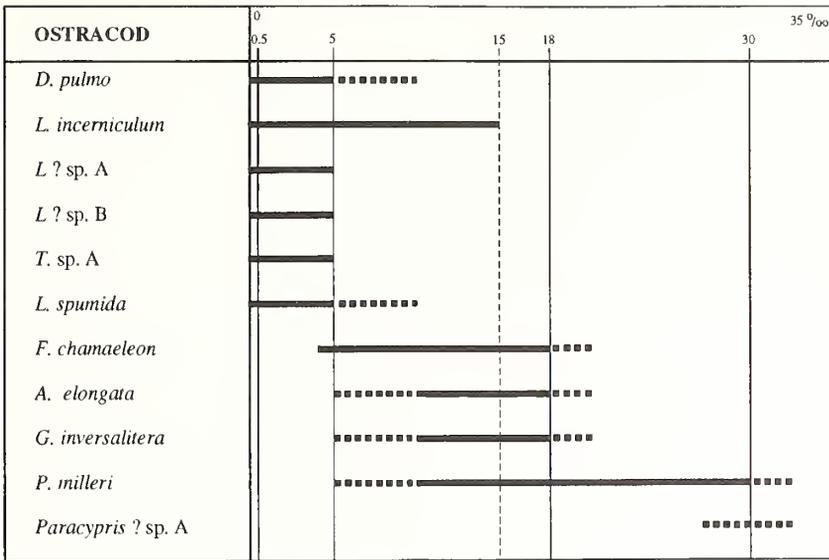
*Linnocythere?* sp. A (one valve), *Linnocythere?* sp. B (two valves) and *Theriosynoecum* sp. A (one valve) were not found in numbers that suggested that they were *in situ*. All were, however, found in association with *Linnocythere incerniculum* and *Darwinula pulmo*, when these latter two species were not considered to be *in situ*. By association, therefore, *Linnocythere?* sp. A, *Linnocythere?* sp. B and *Theriosynoecum* sp. A are tentatively considered to have lived in fresh and oligohaline waters (0–5‰).

*Linnocythere spunida* is also considered to have preferred fresh to oligohaline salinities (0–5‰), but like *Darwinula pulmo* may have tolerated slightly higher salinities. This conclusion is based upon assemblages of *Linnocythere incerniculum* with small but approximately equal numbers of *Darwinula pulmo* and *Linnocythere spunida*. *Linnocythere spunida* was not found *in situ* in any population dominated by the euryhaline marine ostracods defined below, e.g. *Glyptocythere inversalitera*.

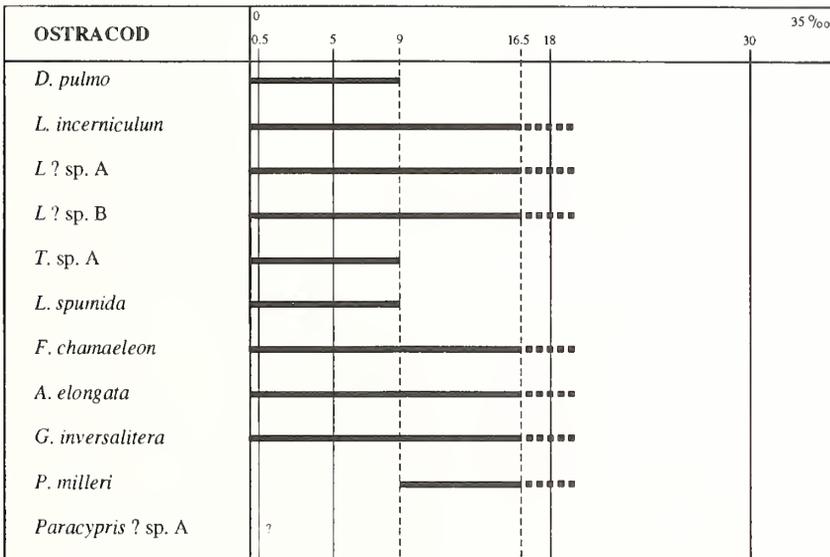
*Fronslarvata chamaeleon* is considered to have been tolerant of mesohaline salinities. This is also the case for *Acanthocythere elongata* and *Glyptocythere inversalitera*. Two of these species are often found in association, but never all at the same time, as their stratigraphical ranges do not overlap (Wakefield 1994, fig. 46). Their lower salinity tolerance limits are, however, considered to have been slightly different. *Acanthocythere elongata* and *Glyptocythere inversalitera* do not appear to have tolerated quite such low salinities as *Fronslarvata chamaeleon*. All three species have been found in association with *Linnocythere incerniculum*, which was considered to have been *in situ* but probably towards the upper limit of its salinity tolerance (15‰). In Bed 4a of the Kildonnan Member type section *Glyptocythere inversalitera* comprises 56 per cent., *Fronslarvata chamaeleon* 21 per cent. and *Linnocythere incerniculum* 20 per cent. of the assemblage. *Linnocythere?* sp. A and *Linnocythere spinida* complete the association (3 per cent.). In the middle of Bed 5e (same locality), the assemblage is composed of *Linnocythere incerniculum* (26 per cent.), *Fronslarvata chamaeleon* (31 per cent.) and *Acanthocythere elongata* (31 per cent.), with *Linnocythere spinida* and *Darwimla pulmo* (8 per cent. and 4 per cent. respectively) not considered to be *in situ*. At the top of Bed 5f (same locality) *Fronslarvata chamaeleon* comprises 49 per cent. and *Acanthocythere elongata* 46 per cent. of the assemblage with *Darwimla pulmo* (5 per cent.) not considered to be *in situ*. Evidence for a lower salinity tolerance of *Fronslarvata chamaeleon* was noted in a sample from the lower half of Bed 5e (same locality) where *Acanthocythere elongata* (3 per cent.) is not considered to be *in situ*, while *Fronslarvata chamaeleon* (51 per cent.) and *Linnocythere incerniculum* (31 per cent.) are considered to be *in situ*. In beds where *Glyptocythere inversalitera* dominates, *Fronslarvata chamaeleon* is generally subordinate. Therefore, *Fronslarvata chamaeleon* is considered to have tolerated salinities as low as 5–10‰, whereas *Acanthocythere elongata* and *Glyptocythere inversalitera* tolerated salinities only slightly below 15‰. *Acanthocythere* and *Glyptocythere* have generally been considered to be indicative of marine conditions, e.g. Morkhoven (1963), Bate (1967), Ware and Whatley (1980, 1983) and Harten and Hinte (1984). However, evidence is now appearing for the general euryhalinity of some species of *Glyptocythere*. Both Stephens (1980) and Sheppard (1981) considered *Glyptocythere guembeliana* (Jones) and *Glyptocythere penni* Bate and Mayes to have tolerated low brackish salinities, but not to have coexisted with *Darwimla* and *Theriosynoecium*. A lower limit of 10‰, therefore, seems reasonable. The upper salinity limit of the three species is more difficult to determine. All three occur in populations where *Linnocythere incerniculum* is not considered to be *in situ* or is absent. This indicates a tolerance above 15‰. In some samples *Glyptocythere inversalitera* dominates over *Fronslarvata chamaeleon* as does *Acanthocythere elongata*, suggesting that *Fronslarvata chamaeleon* did not tolerate as high a salinity as the other two genera. It is not possible on the ostracod evidence alone to determine an upper salinity limit. The fact that neither *Glyptocythere inversalitera* nor *Acanthocythere elongata* are found in assemblages which, by their generic composition, are most likely to have been marine, e.g. with *Lophocythere*, *Looneyella*, *Fastigatocythere*, *Paracypris*, *Pichottia*, *Schuleridea*, may suggest that the highest salinities that they could tolerate were in the polyhaline range (18–30‰).

Both *Progonocythere* and *Paracypris* are generally considered to be marine genera (Bate 1967; Neale 1988). However, in Bed 6, Kildonnan Member, North Shore, Eigg, *Progonocythere milleri* is found in association with *Linnocythere incerniculum*. Although *Linnocythere incerniculum* dominates the assemblage, 81 per cent., as compared with 19 per cent. for *Progonocythere milleri*, male, female and three juvenile stages of *Progonocythere milleri* were present indicating that it was *in situ* and probably able to tolerate salinities lower than 15‰. No samples were found where *Progonocythere milleri* was considered to have co-occurred *in situ* with *Darwimla pulmo*, indicating that the lower limit of its tolerance range was not below 10‰. *Paracypris?* sp. A was never found *in situ*, suggesting that its generic salinity tolerance range was never reached in the exposed parts of Kildonnan Member. The fact that it does not occur *in situ* with *Glyptocythere inversalitera* or *Acanthocythere elongata* confirms the suggestion that it tolerated salinities that were in all probability 30‰ and higher, and that they, in turn, tolerated salinities lower than 30‰.

A chart of the different relative salinity tolerances for the Ostracoda from the Kildonnan Member is given in Text-figure 6. In order to test these salinity tolerances, considering that they were



TEXT-FIG. 6. Inferred relative salinity tolerances of the Kildonnann Member Ostracoda based upon co-occurrences with other ostracods. Solid line indicates preferred salinity tolerance range; dashed line indicates possible further limits of tolerance range.



TEXT-FIG. 7. Inferred relative salinity tolerances of the Kildonnann Member Ostracoda based upon co-occurrences with the mollusc and conchostracan fauna. Solid line indicates preferred salinity tolerance range; dashed line indicates possible further limits of tolerance range.

based upon several assumptions, a similar chart was constructed using the ostracods *in situ* association with the molluscan and conchostracan fauna. The salinity tolerances for the mollusc and conchostracan fauna are those of Hudson (1963a). A comparison of this chart (Text-fig. 7)

with Text-figure 6 indicates a broad similarity of estimated tolerances. Therefore, the relative salinity tolerances of the Ostracoda from the Kildonnan Member are considered to be valid.

*Salinity tolerances of the Ostracoda from the Lonfearn Member*

*Linnocythere spinosa* and *Darwinula phaselus* are usually found in association. As with *Linnocythere incerniculum* and *Darwinula pulmo* in the Kildonnan Member, *Linnocythere spinosa* generally dominated the association, e.g. in Bed 3 of the Lonfearn Member at Rudha nam Braithairean, *Linnocythere spinosa* comprises 89–98 per cent. of the ostracod fauna, *Darwinula phaselus* being the only other ostracod present in the samples. Thus, *Linnocythere spinosa* is considered to have tolerated slightly higher salinities than *Darwinula phaselus*; 0–15‰ and 0–10‰ respectively. These tolerances are the same as those given for *Linnocythere incerniculum* and *Darwinula pulmo* respectively. It is not possible to test this similarity as no ostracod occurs in both members of the Lealt Shale Formation. The fact that the bivalve *Neomiodon brycei* occurs with all four species indicates a close similarity of salinity tolerances or overlap of tolerance ranges.

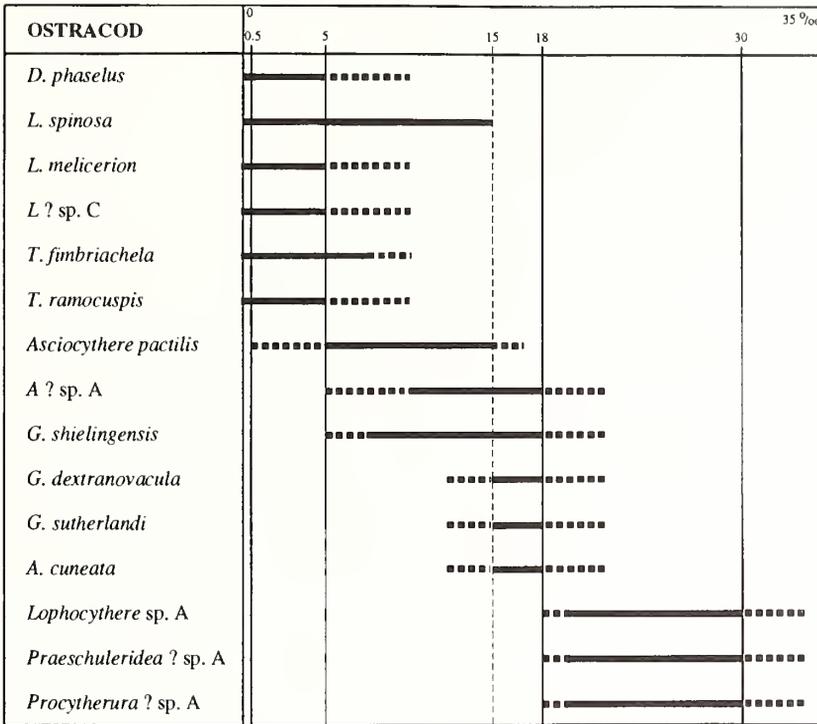
*Linnocythere melicerion*, *Linnocythere?* sp. C and *Theriosynoecium fimbriachela* occur *in situ* with *Linnocythere spinosa* and *Darwinula phaselus*, which is consistent with the assumed salinity tolerances of species of these genera.

*Theriosynoecium ramocuspis* has not been recorded *in situ* with any other Lonfearn Member ostracods. Its salinity tolerance, therefore, is taken to be that preferred by the genus, 0–7‰.

*Glyptocythere shielingensis* was found in some samples to be *in situ* with *Theriosynoecium fimbriachela*, e.g. in Bed 11 of the Lonfearn Member from the Shieling Burn section. Adults and at least three juvenile stages of *Glyptocythere shielingensis* and adults with four juvenile stages of *Theriosynoecium fimbriachela* were recorded in a sample from this bed, indicating that *Glyptocythere shielingensis* could tolerate very low salinities, maybe as low as 5‰. No evidence for faunal mixing has been documented for this horizon. It is not possible to determine an upper salinity tolerance for this species, but the euryhaline nature of *Glyptocythere* suggests that its overall tolerance range may have been large. As previously noted (Stephens 1980; Sheppard 1981), *Glyptocythere* is considered to be highly euryhaline but, until this occurrence, had not been found *in situ* with *Theriosynoecium*. This occurrence may be explained by the findings of Forester and Brouwers (1985), who noted that marine ostracods from Na- and Cl-dominated waters, could survive in fresh waters also dominated by Na and Cl. This may be the case for Lealt Shale waters with their direct sea water/fresh water mixing (Tan and Hudson 1974).

*Glyptocythere dextranovacula*, *Glyptocythere sutherlandi*, *Aalenella cuneata* and *Lophocythere* sp. A generally occur in the same samples. *Glyptocythere dextranovacula* and *Glyptocythere sutherlandi* were used in Wakefield (1991, 1994) to indicate the base of the Lonfearn Member. The association indicates similar salinity tolerances. *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* and *Aalenella cuneata* do not co-occur *in situ* with *Linnocythere spinosa*, indicating a salinity tolerance above 15‰. *Lophocythere* sp. A is never found in large numbers and no adults have been recovered from the samples studied. *Lophocythere* is generally considered to be indicative of marine conditions (Morkhoven 1963; Stephens 1980; Sheppard 1981; Harten and Hinte 1984). These two factors lead to the conclusion that *Lophocythere* sp. A did not tolerate such low salinities as *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* or *Aalenella cuneata*. Although the evidence is not substantial, the lack of association with a demonstrably marine fauna indicates that *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* and *Aalenella cuneata* tolerated salinities in the order of 15–30‰. *Lophocythere* sp. A probably preferred salinities in the upper portion of this range through to fully marine conditions, but this is conjectural. It is reasonably safe to say that fully marine conditions were not experienced in the sections sampled.

*Asciocythere pactilis* co-occurs *in situ* with: (a) *Linnocythere spinosa* and *Darwinula phaselus* in one association (e.g. top of Bed 3 and base of Bed 5, Lonfearn Member, Rudha nam Braithairean, Skye); and (b) *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* and *Aalenella cuneata* in



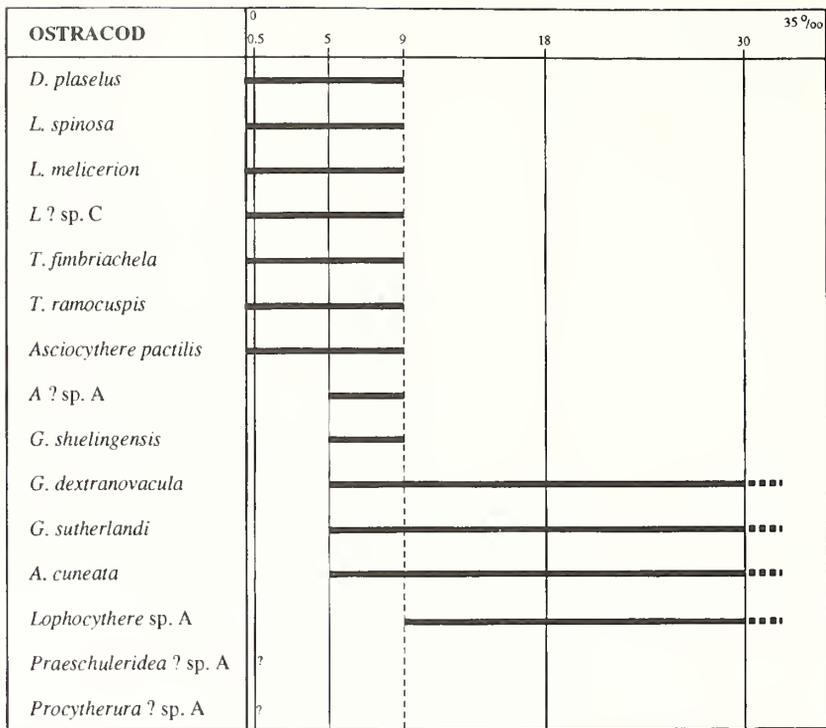
TEXT-FIG. 8. Inferred relative salinity tolerances of the Lonfearn Member Ostracoda based upon co-occurrences with other ostracods. Solid line indicates preferred salinity tolerance range, dashed line possible further limits of tolerance range.

another (e.g. top of Bed 1, Lonfearn Member, Rudha nam Braithairean, Skye). *Ascioythere pactilis*, therefore, would appear to be either highly euryhaline, or to tolerate a narrow salinity band which bridges the gap between the salinity tolerances of the two associations. In the sample from the top of Bed 3, Lonfearn Member, Rudha nam Braithairean, *Ascioythere pactilis* constitutes 58 per cent. of the ostracods present, *Limnocythere spinosa* 35 per cent., *Darwinula phaselus* 7 per cent. along with a single valve of *Praeschuleridea? sp. A* Wakefield, 1994. Males, females and five juvenile stages are preserved of *Ascioythere pactilis* indicating its autochthoneity. This association indicates a tolerance by *Ascioythere pactilis* of salinities higher than those of waters usually inhabited by *Darwinula phaselus*; greater than 5‰. In its association with the higher salinity group *Ascioythere pactilis* occurs in small numbers. A tolerance range of 5–18‰ is used in this work.

*Acauthocythere? sp. A* occurs as a minor constituent of assemblages including *Limnocythere spinosa*, *Darwinula phaselus* and *Limnocythere melicerion* indicating a potential tolerance below 10‰, and perhaps as low as 5‰. It is not possible to determine the upper salinity tolerance limit. This may be similar to that of *Acauthocythere elongata* from the Kildonnan Member.

*Praeschuleridea? sp. A* and *Procytherura? sp. A* occur in small numbers; two valves for each species. Both genera have been found in marine associations (Bate 1967; Ware and Whatley 1980, 1983).

A chart of the relative salinity tolerances of the Ostracoda from the Lonfearn Member is given in Text-figure 8. As with the Kildonnan Member this chart can be compared with one drawn up using *in situ* species co-occurrences with the mollusc and conchostracan fauna (Text-fig. 9).



TEXT-FIG. 9. Inferred relative salinity tolerances of the Lonfearn Member Ostracoda based upon co-occurrences with the mollusc and conchostracan fauna. Solid line indicates preferred salinity tolerance range, dashed line possible further limits of tolerance range.

#### PALAEOSALINITY FLUCTUATIONS IN THE LEALT SHALE FORMATION

Previous interpretations have noted numerous palaeosalinity fluctuations within the Lealt Shale Formation (Hudson 1963*a*, 1966; Hudson and Harris 1979; Walton 1988; Riding *et al.* 1991). It was, therefore, decided to compare the palaeosalinity curves defined by the different faunas present within the Lealt Shale Formation. Palaeosalinity curves were constructed not just for the type section of the Kildonnan Member but also for the Kildonnan and Lonfearn members at Rudha nam Braithairean, Skye and North Shore, Eigg as well as for the Lonfearn Member at Sheiling Burn, Eigg. Few samples were available for study from the last two sections. However, the ostracod occurrences in these two sections proved invaluable in reconstructing the relative salinity tolerances of the ostracods. The Kildonnan and Lonfearn sections exposed immediately north of Elgol, Strathaird, Skye were not included in this study because of the extremely poor record of ostracods from those sections.

The first palaeosalinity curve constructed for each section used the mollusc and conchostracan fauna noted in the samples taken for the ostracod studies. The salinity tolerances suggested for the molluscs and conchostracans by Hudson (1963*a*) and Hudson and Harris (1979) were used. The second palaeosalinity reconstruction uses the ostracod salinity tolerances defined above. When an ostracod species dominated a sample with respect to another, the salinity was taken to be on the dominant species side of their tolerance range overlap. Although this is a logical step to take it need not necessarily represent what actually occurred, but is a best estimate. The size of the error bars produced by the above methods, and the gaps between sample positions, serve to obscure the exact shape of the palaeosalinity curve. The gaps between samples may hold a far more complicated salinity history than that implied by the tie lines, which only indicate a general trend. For the type

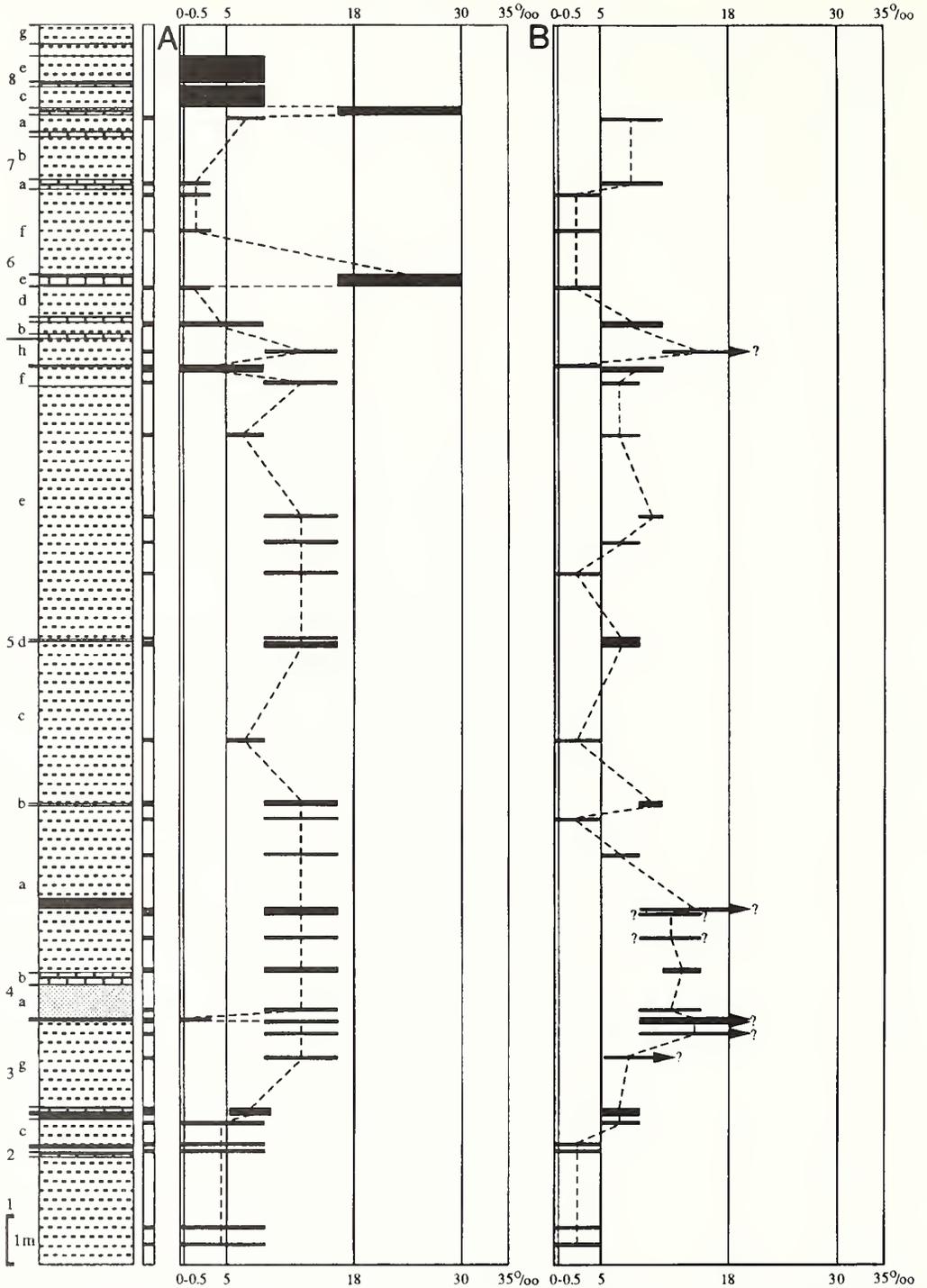
section of the Kildonnan Member and the Rudha nam Braithairean sections a plot is given of the percentage abundances of *Botryococcus* with respect to the total palynoflora; this data is taken from Walton (1988). *Botryococcus* is a fresh to brackish water planktic member of the Chlorophyceae (green algae), high percentages of which can be equated with fresh to brackish waters (Naumann 1922; Hutchison 1957). Finally, an attempt was made to reconstruct a palaeosalinity envelope for the type section of the Kildonnan Member and the Rudha nam Braithairean section using all of the data available.

#### *Palaeosalinity curve for the Kildonnan Member type section*

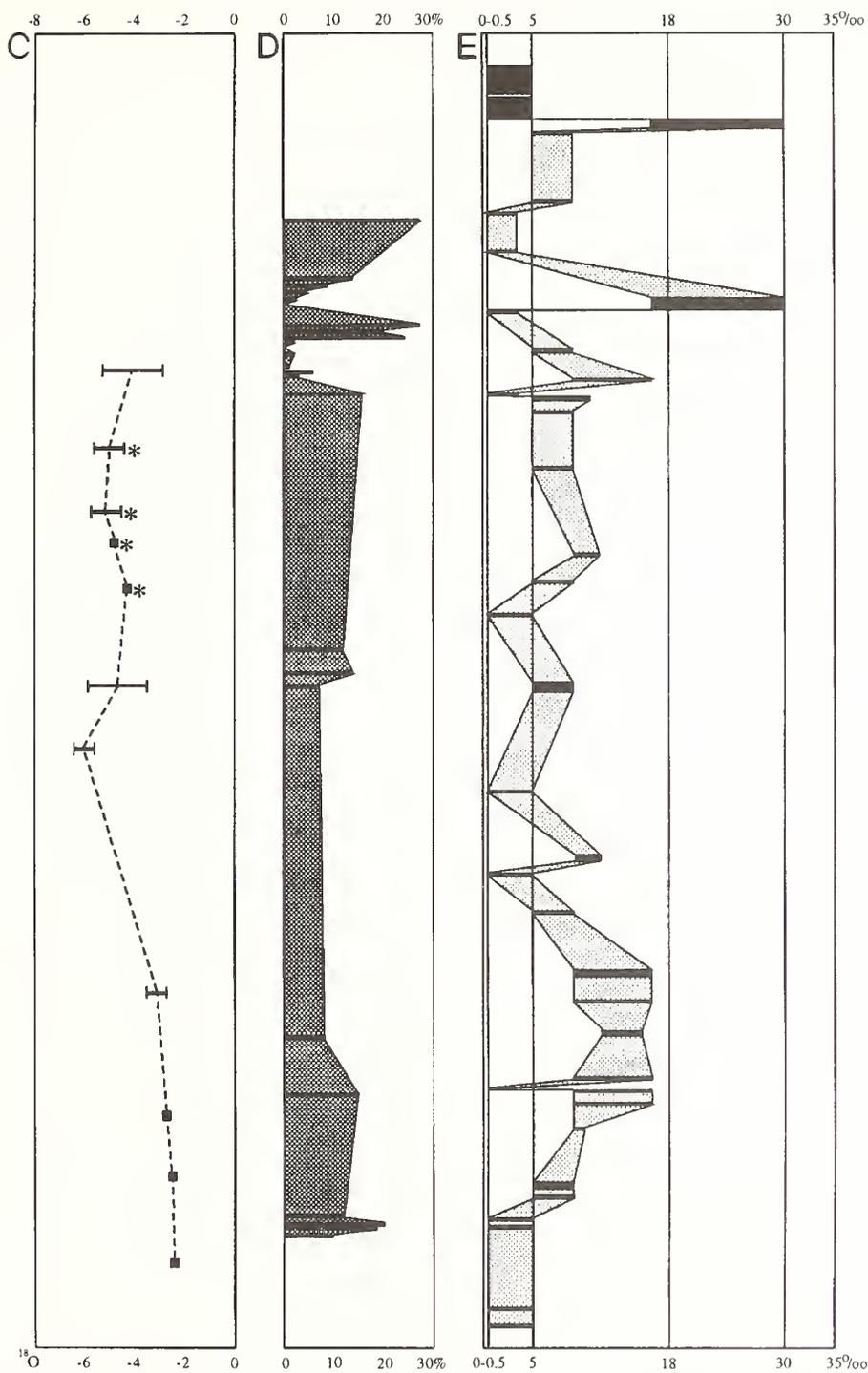
The palaeosalinity curve derived from the molluscs and conchostracans (Text-fig. 10A) in general mirrors that derived from the ostracod fauna (Text-fig. 10B), although there are several subtle differences between the two. These were to be expected considering the differences in the number of species available for each study, which in turn produces differences in the coarseness of the relative salinity tolerances within each group. The ostracods appear, however, in most instances, to allow a more accurate palaeosalinity curve to be defined than is possible using the mollusc and conchostracan fauna.

Both Beds 1 and 3a were deposited under fresh to oligohaline salinities (0–5‰). The faunas of both beds are dominated by the ostracods *Linnocythere incerniculum* and *Darwinula pulmo*, conchostracans, the gastropods *Viviparus scoticus* and *Valvata* sp., as well as fish fragments. An increase in salinity at the top of Bed 3c is indicated by the presence of the ostracods *Fronslarvata chamaeleon* and *Linnocythere incerniculum*, which are accompanied in Beds 3e and 3f by small specimens of the bivalve *Praemytilus strathairdensis*. This salinity increase continues into Beds 3g and 3h, where the ostracods *Fronslarvata chamaeleon* and *Glyptocythere inversalitera*, and the bivalve *Praemytilus strathairdensis* dominate. Salinities were probably around 18‰ but may have been higher. The middle of Bed 3g contains large numbers of fish otoliths as does the base of Bed 5e. Similar concentrations are known from the Oxford Clay and are referred to as coprocoenoses. Otoliths are coated by a thick organic membrane which allows them to pass through the intestines of fish, unlike the other skeletal bones. Otoliths are, therefore, likely to be concentrated preferentially (D. M. Martill, pers. comm. 1991). Some otoliths from Bed 3g were analysed using an X-ray diffractometer by Mr R. N. Wilson (Leicester University), and proved to be composed of the unaltered original aragonite. At present some specimens of these otoliths from Bed 3g are being analysed isotopically (C and O) by T. F. Anderson. It is hoped that this work will increase the information available on water chemistry and probably salinity. Although the *Fronslarvata chamaeleon*, *Glyptocythere inversalitera*, *Praemytilus strathairdensis* fauna is present at the top of Bed 3h, the *Praemytilus strathairdensis* valves are fragmentary, whilst large undamaged specimens of the bivalve *Unio andersoni* (up to 60 mm in length) are present. The undamaged specimens of *Unio andersoni* indicate salinities that were at their highest oligohaline; lower than those estimated for *Praemytilus strathairdensis*. The lower part of Bed 3h is silty and contains thin plasters of *Praemytilus strathairdensis* with *Fronslarvata chamaeleon* and *Glyptocythere inversalitera* visible on the laminations. The upper 10–20 mm of the bed is a *Praemytilus* shell hash, indicating strong current winnowing. Large amounts of phosphatic fish bones and teeth are present as well as specimens of *Fronslarvata chamaeleon* which are difficult to detect amongst the shell hash. It appears that *Unio andersoni* inhabited the shell hash after its deposition and a subsequent reduction in salinity to 0–3‰. *Darwinula pulmo* and *Linnocythere incerniculum* were more obvious and numerous in the shell hash than in the lower portion of the bed. However, the shell hash also contains large numbers of reworked (but most probably indigenous) *Fronslarvata chamaeleon* and *Glyptocythere inversalitera*, which essentially dilute the palaeoenvironmental signature of *Darwinula* and *Linnocythere* when counts of the ostracods are taken. The occurrence, in Bed 3h, of brackish water tolerant palynomorphs corroborates these findings (Walton 1988).

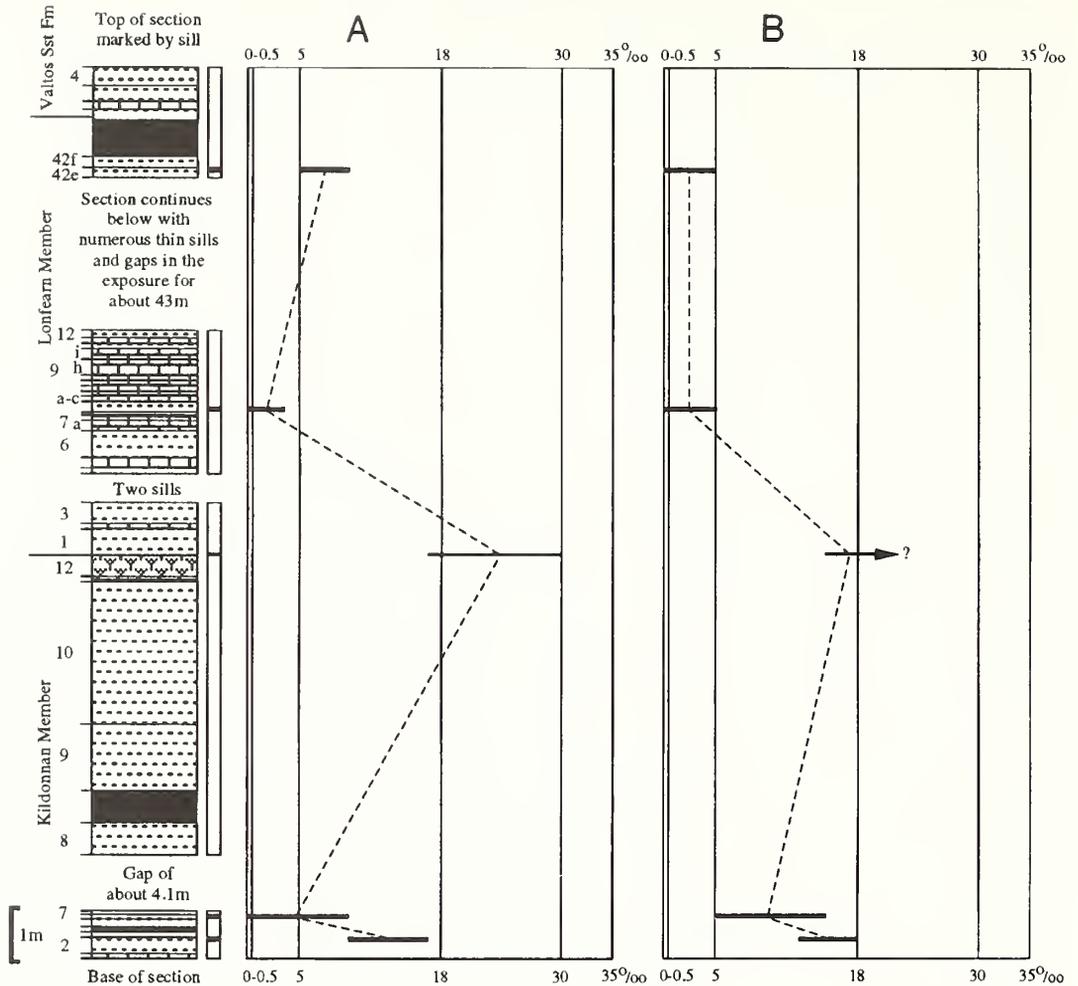
A shale intercalation within the essentially sandy Complex Bed (Bed 4) contains a brackish water fauna composed of the ostracods *Linnocythere incerniculum*, *Fronslarvata chamaeleon*,



TEXT-FIG. 10. Kildonnan Member, Lealt Shale Formation, type section, Eigg. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values of the fauna based upon Hudson (1963a). B, palaeosalinity curve defined using ostracod assemblages. C,  $\delta^{18}\text{O}$  values from *Praemytilus strathairdensis*;



approximate positions of samples analysed are shown; those marked \* were only approximately positioned in the original paper; data from Tan and Hudson (1974). D, *Botryococcus* abundances expressed as a percentage of the total palynoflora; approximate positions of samples are shown; data from Walton (1988). E, composite palaeosalinity curve based on all data.

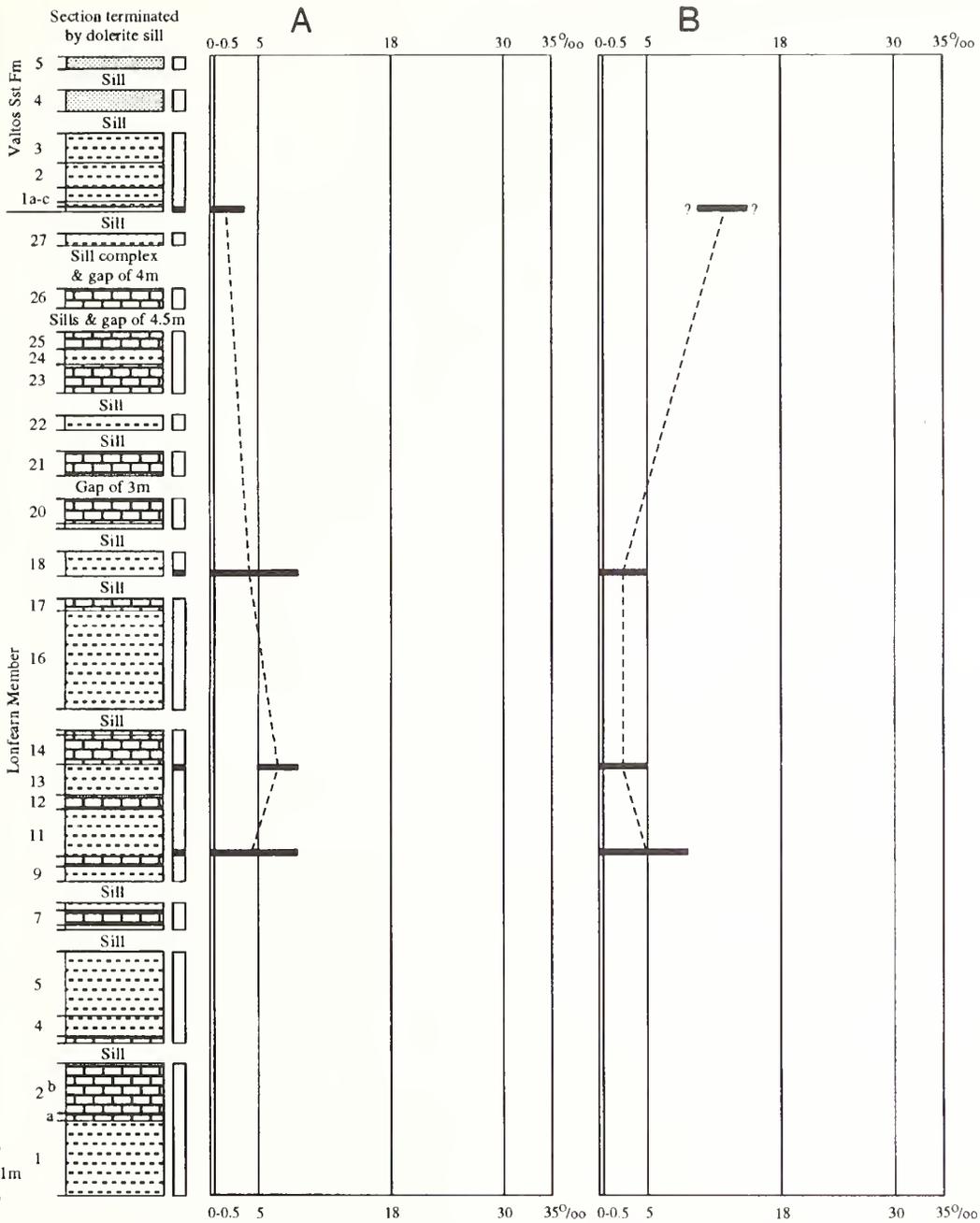


TEXT-FIG. 11. Kildonnan and Lonfearn Members, North Shore, Eigg. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values based upon Hudson (1963*a*). B, palaeosalinity curve defined using ostracod assemblages.

*Glyptocythere inversalitera* and the bivalve *Praemytilus strathairdensis*. Salinities were probably around 15‰.

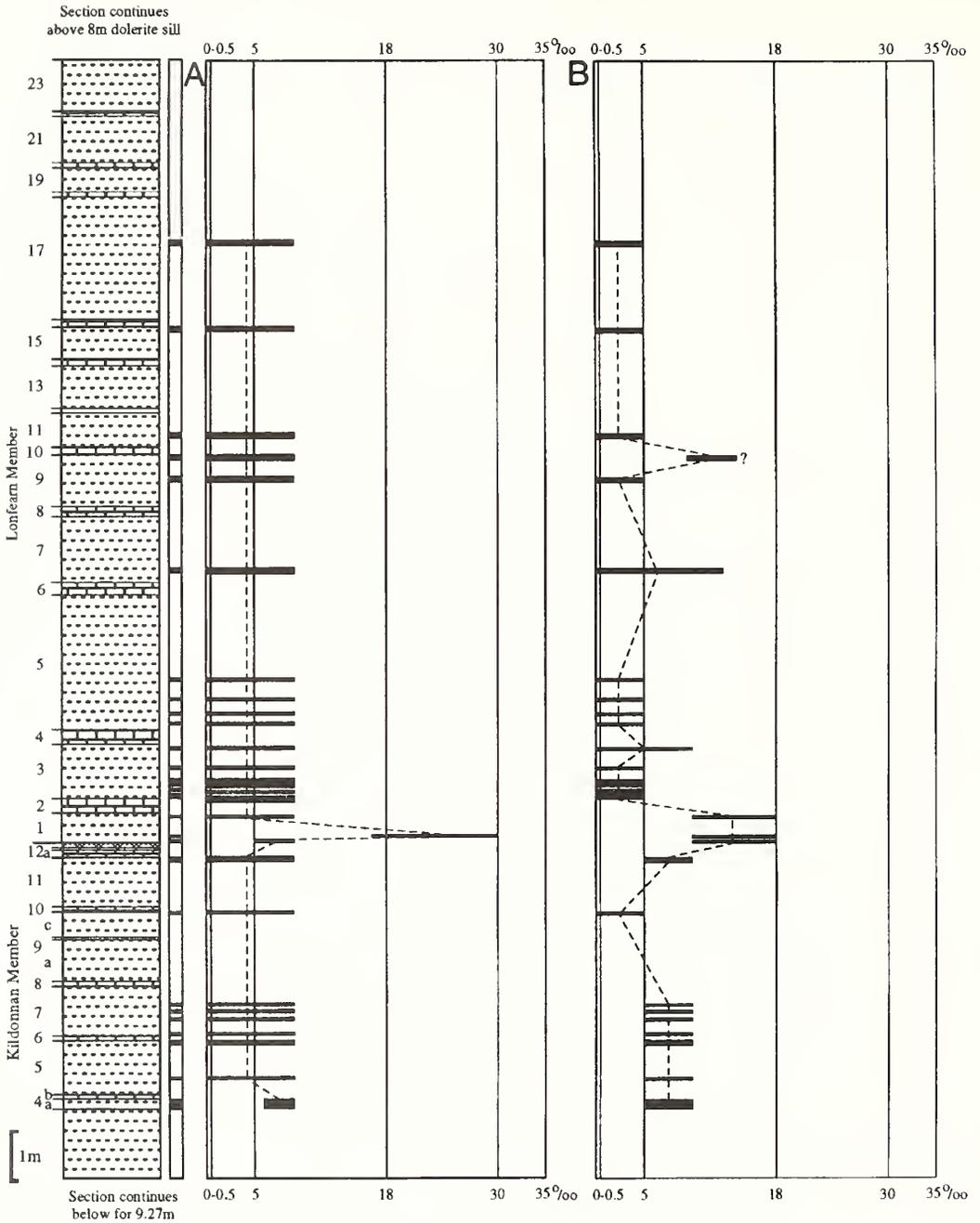
Bed 5, as a whole, has a highly fluctuating palaeosalinity. The mollusc fauna was dominated by the bivalve *Praemytilus strathairdensis*, though the gastropod *Valvata* sp. was occasionally present. It is not possible using this mollusc fauna to distinguish the salinity fluctuations revealed by the ostracod-derived curve as the generally wide salinity tolerance of *Praemytilus strathairdensis* (10‰ to above 20‰) obscures the subtle changes. A strong positive correlation between the palaeosalinity curve defined using the ostracods (Text-fig. 10B) and  $\delta^{18}\text{O}$  values of the bivalve *Praemytilus strathairdensis* (Text-fig. 10C) taken from Tan and Hudson (1974) was observed. Generally 'heavier' oxygen values correlate with higher salinities and 'lighter' values correlate with lower salinities.

Bed 6 records a gradual decrease in salinity with the ostracods *Linnocythere incerniculum* and *Darwinula pulmo* becoming dominant. Walton (1988) noted 'marine' influences, based on the palynomorph flora, in Beds 6b, 6c, the base of 6d, 6e and at the base of 6f. Of these beds only 6b



TEXT-FIG. 12. Lonfearn Member, Shieling Burn, Eigg. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values based upon Hudson (1963a). B, palaeosalinity curve defined using ostracod assemblages.

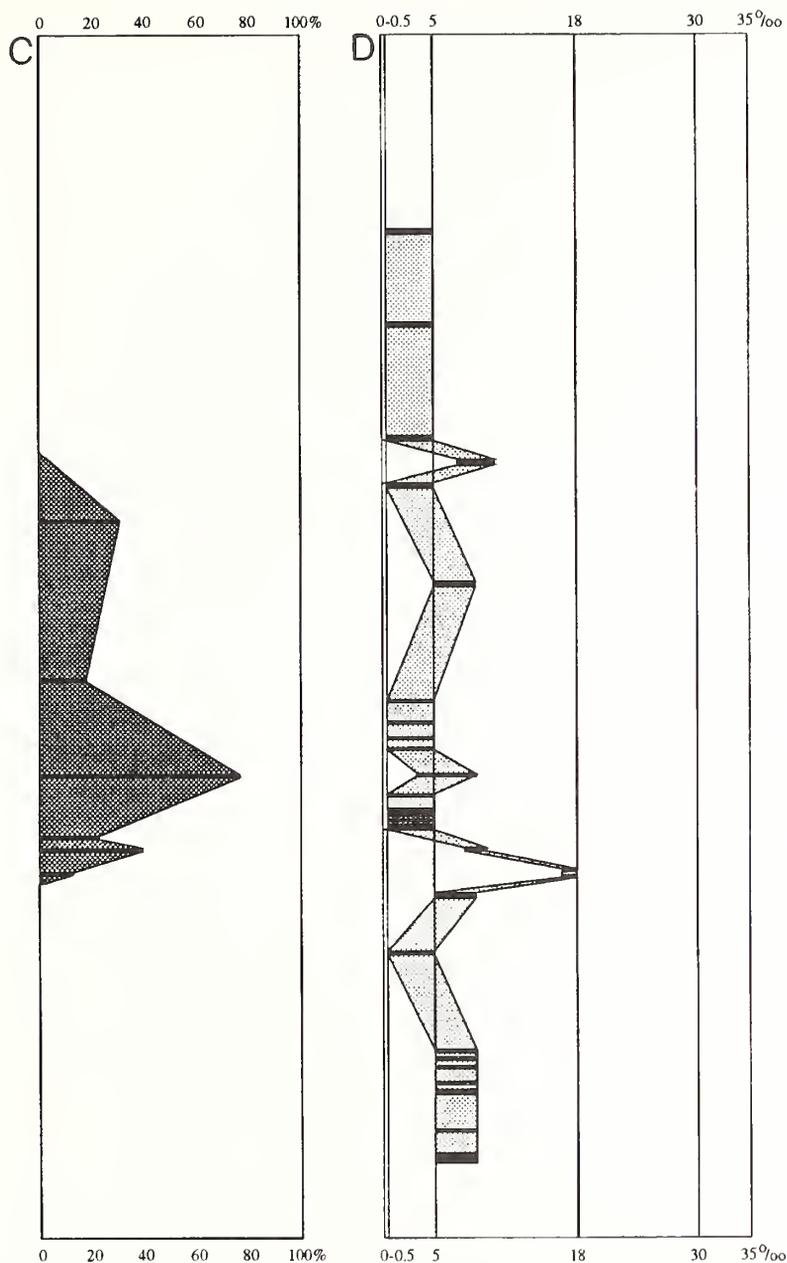
was sampled in this study in the same position as the palynomorph sample site, for which a salinity of around 10‰ is estimated. The *Botryococcus* data (Text-fig. 10D) shows these 'marine' episodes clearly. A negative correlation between palaeosalinity and *Botryococcus* abundances was observed.



TEXT-FIG. 13A-B. For caption see opposite.

Freshwater/oligohaline conditions became fully established in the *Unio* Bed (Bed 7a) where the bivalve *Unio andersoni* occurs with the ostracods *Linnocythere incerniculum* and *Darwinula pulmo*.

A slight rise in salinity is inferred in Bed 8a where *Linnocythere incerniculum* dominates the ostracod fauna over *Darwinula pulmo*. The salinity was probably in the order of 5–10‰. The occurrence of *Neomiodon brycei* as the dominant bivalve is consistent with this conclusion. Bed 8b



TEXT-FIG. 13. Kildonnan and Lonfean Members, Rudha nam Braithairean, Skye. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values based upon Hudson (1963a). B, palaeosalinity curve defined using ostracod assemblages. C, *Botryococcus* abundances expressed as a percentage of the total palynoflora; approximate positions of samples are shown; data from Walton (1988). D, composite palaeosalinity curve based on all data.

contains specimens of the bivalve *Placunopsis socialis*, which is indicative of mesohaline salinities. A return to salinities of around 5‰ is indicated in Beds 8d–g by the occurrence of *Neomiodon brycei* and conchostracans, prior to a rise in salinity before the establishment of stromatolitic

cyanobacterial mats, which cannot be documented in detail at the type section (Harris and Hudson 1980).

*Palaeosalinity curve for the Kildonnan and Lonfearn Members, North-Shore, Eigg*

Very few samples taken from this section, when processed, yielded any ostracods. This was probably a result of metamorphism by the numerous thin sills and dykes intruded into the sediments.

The palaeosalinity curves calculated for the section are given in Text-figure 11A–B. One notable addition to the story of the Lealt Shale Formation is the high salinity fauna recorded from immediately above the Algal Bed. This fauna included the ostracods *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi*, *Aalenella cmeata* and *Lophocythere* sp. A as well as the bivalve genera *Placunopsis* and *Cuspidaria*. The estimated palaeosalinity is at least 20‰, but probably was somewhat higher. The lack of large numbers of the ostracod *Lophocythere* sp. A indicates that the salinity probably did not reach 30–35‰ (see comments in Rudha nam Braithairean subsection about the significance of the ostracod *Progonocythere milleri* recovered from Bed 7 of the Kildonnan Member).

*Palaeosalinity curve for the Lonfearn Member at the Shielling Burn, Eigg*

As with the North-Shore, Eigg section very few samples were available for comparative study of the fauna. The palaeosalinity of the section was in general oligohaline to mesohaline (0.5–18‰). The curves derived (Text-fig. 12A–B) from the molluscs and the ostracods do differ. This is because of the presence of the ostracod *Glyptocythere shielingensis* in the *Unio* shell hash. A similar explanation, but in reverse, to that given for Bed 3h from the type section of the Kildonnan Member may be applicable in this instance.

*Palaeosalinity curve for the Kildonnan and Lonfearn members, Rudha nam Braithairean, Trotternish, Skye*

The Kildonnan Member section is dominated by the ostracods *Limmocythere incerniculum* and *Darwinula pulmo*, the bivalve *Neomiodon brycei*, the conchostracan *Neopolygrapta lealtensis*, the gastropod *Viviparus scoticus*, as well as numerous fish and plant fragments. In all samples *Limmocythere incerniculum* is more abundant than *Darwinula pulmo*, making up 81–97 per cent. of the ostracod fauna (Text-fig. 5). This, combined with the occurrence of the bivalve *Neomiodon brycei* and the conchostracan *Neopolygrapta lealtensis*, indicates a salinity of probably no higher than 10‰.

The ostracod assemblage at the top of Bed 9c is also dominated by *Limmocythere incerniculum* (88 per cent. with a calculated 16230 specimens per kg of sediment) with *Darwinula pulmo* (12 per cent. with a calculated 2290 specimens per kg) subordinate. *Progonocythere milleri* also occurs, making up less than 1 per cent. of the assemblage. A similar level with *Progonocythere milleri* was also found at the type section of the Kildonnan Member (Bed 6b) and in the Kildonnan Member from the North-Shore Section, Eigg (Bed 7). It was suggested by Wakefield (1991, 1994) that *Progonocythere milleri* be used as a marker fossil to enable correlation between the different sections of the Kildonnan Member. In the context of this paper *Progonocythere milleri* indicates an area-wide increase in salinity. This salinity event is only fully recognized in the North-Shore Section, Eigg where both sexual dimorphs and three juvenile stages are preserved, indicating that it was *in situ* and that energy conditions were moderately high as compared with the rest of the section.

The occurrence of *Progonocythere milleri* towards the top of the Kildonnan Member was not the only area-wide faunal event experienced during the deposition of the Lealt Shale Formation. The Algal Bed itself was used as evidence for the area as a whole, the Sea of the Hebrides and Inner

Hebrides basins of Binns *et al.* 1975, acting as one (Hudson 1970, 1980). Immediately above the Algal Bed (basal 50 mm of Bed 1, Lonfearn Member) at Rudha nam Braithairean the ostracod fauna consists of *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi*, *Aalenella cuneata* and *Lophocythere* sp. A, with the bivalve *Neomiodon brycei*. The absence of the ostracod *Linnocythere spinosa* indicates that the salinity was probably above 15‰. Certainly, immediately above the basal 50 mm of Bed 1, the salinity had probably increased to 15–20‰. The fauna here contains the same ostracods but the bivalve *Neomiodon brycei* is subordinate to the bivalve *Quenstedtia?* sp. The change in the bivalve fauna indicates a probable slight increase in salinity between the two levels. It is worth noting that the same fauna and presumably salinity range was also found in Bed 1 of the Lonfearn member at the North-Shore section, Eigg (see above).

From the top of Bed 1 onwards the palaeosalinity remains fairly stable; within the oligohaline range (0.5–5‰). *Linnocythere spinosa* and *Darwinula phaseus* dominate the ostracod fauna with numerous conchostracans and, in the base of Bed 3, occur with the planispiral foraminifer *Ammodiscus tenuissimus*.

Occasionally the salinity increased, such as in Bed 7 and at the top of Bed 9; in Bed 7 the salinity was probably around 10‰ as indicated by the presence of the ostracods *Linnocythere spinosa* (21 per cent.), *Darwinula phaseus* (20 per cent.) and *Linnocythere melicerion* (16 per cent.). However, salinities may have been higher (15‰) to account for the presence of *Acanthocythere?* sp. A (31 per cent.) and *Lophocythere* sp. A (9 per cent.). *Acanthocythere?* sp. A was preserved only as carapaces of the adults, both male and female, and one specimen of a presumed A-1 juvenile, no individual valves being present. The absence of large numbers of juveniles suggests that higher energy conditions may have winnowed out the smaller juveniles. Of the other ostracod species in that sample only *Linnocythere spinosa* (12 per cent. of specimens), and *Darwinula phaseus* (15 per cent. of specimens) have any carapaces preserved. The assemblage of *Linnocythere spinosa* contains adults and several juvenile stages, possibly indicating lower energy conditions than does the assemblage of *Acanthocythere?* sp. A. The assemblage from Bed 7 may represent a mixing of ostracods which lived at different times. *Acanthocythere?* sp. A probably inhabited the sediment first, when energy conditions were higher. *Linnocythere spinosa* only inhabited the sediment after energy conditions had decreased, which may explain the differences in age structure between the two species. It is always possible that the two species co-existed, and that their valves were affected differently by the water currents, such that more juvenile stages of *Acanthocythere?* sp. A were winnowed out.

Bed 9 is dominated by the bivalve *Neomiodon brycei* and the ostracod *Glyptocythere dextranovacula*. Salinities of around 15‰ or above are postulated. This occurrence of *Glyptocythere dextranovacula* corresponds with the complete absence of *Botryococcus* at that level (Walton 1988).

The sampled interval of the Lonfearn Member in general appears to have been deposited under oligohaline salinities. This is supported by the sometimes high abundance of *Botryococcus* (up to 76.3 per cent.; Text-fig. 13C) based upon data from Walton (1988) and Riding *et al.* (1991).

## CONCLUSIONS

The different major components of the biota from the Lealt Shale Formation can all be used in the interpretation of the palaeosalinity of the depositional environment, albeit with varying degrees of precision. The mollusc/conchostracan fauna used by Hudson (1963a) and Harris and Hudson (1980) provides a coarser measurement of the palaeosalinity than does the ostracod fauna. This is probably due to the smaller number of mollusc species (17) when compared with the ostracods (26 in total; 11 in the Kildonnan Member and 15 in the Lonfearn Member, the ranges of which do not overlap but are essentially complementary). With fewer species available for correlation the accuracy with which relative salinity tolerances can be defined is lower. However, the mollusc and conchostracan fauna has one advantage over the ostracod fauna, in that several species are found in both the Kildonnan and Lonfearn members (see Table 1), and, as such, salinities between the two

members can be compared. The difference in the ability to define small scale salinity fluctuations was particularly evident in Bed 5 from the type section of the Kildonnan Member. The bivalve *Praemytilus strathairdensis* dominated the macrofauna, thus reducing the opportunity to detect subtle salinity changes that lay within its large tolerance range (10–20‰). Several salinity fluctuations were noted when studying the ostracod fauna that only became evident with respect to the bivalve *Praemytilus strathairdensis* when its  $\delta^{18}\text{O}$  values were studied. A positive correlation between salinity and  $\delta^{18}\text{O}$  values was noted.

The integration of palynofloristic data also provides valuable information. The percentage abundances of *Botryococcus* proved to be especially useful in the context of the present study. A negative correlation between salinity and abundance is evident.

Text-figures 10E and 13D show the palaeosalinity envelopes for the type section of the Kildonnan Member and the section at Rudha nam Braithairean.

The Kildonnan Member was deposited under generally low but fluctuating salinities. It is considered unlikely that totally freshwater conditions were ever established, and oligohaline salinities were probably more normal. Many of the fluctuations noted were extremely rapid, e.g. Beds 3g–3h, 5f–5g and 6d–6e from the type section of the Kildonnan Member, and in some cases were basin-wide.

The junction between the Kildonnan and Lonfearn members represents a major faunal changeover of ostracod species. No species of ostracod occurs in both members. It would appear that this was because of environmental factors. This boundary is represented in all sections of the Lealt Shale Formation by a stromatolitic algal limestone (Hudson 1970, 1980; Harris and Hudson 1980) representing a basin-wide desiccation event with pseudomorphs after gypsum occurring along many of the algal laminations (Hudson 1970). Immediately after the deposition of the algal limestone the basin was inundated by higher salinity waters, 20‰ or above, with a completely different ostracod fauna from that seen before. However, the bivalve fauna does not change so drastically at the same time. Of the dominant bivalves in the Kildonnan Member only *Praemytilus strathairdensis* fails to occur in the Lonfearn Member.

The Lonfearn Member was deposited under similarly low salinities to the Kildonnan Member. Again freshwater conditions are considered to be unlikely, and oligohaline salinities appear to have been ubiquitous. It appears that the large scale and frequent salinity fluctuations noted in the Kildonnan Member were not repeated during the deposition of the Lonfearn Member.

It is considered unwise to rely on faunal compositions alone, without careful examination of hand specimens, which allow the relationship of species to one another to be noted. This became evident during the study of Bed 3h from the type section of the Kildonnan Member. Here the brackish-marine tolerant bivalve *Praemytilus strathairdensis*, though dominating the fauna throughout the bed, was only seen as shell hash in the upper part of the bed. In the shall hash large specimens of the freshwater tolerant bivalve *Unio andersoni* appeared to be *in situ*. The observation immediately alters the inferred palaeosalinity from brackish-marine to freshwater/oligohaline. This change in salinity was not clearly defined using the ostracod fauna because of the freshwater ostracods (*Limnocythere incerniculum* and *Darwinula pulmo*) inhabiting sediment, the shell hash, with abundant brackish water ostracods (*Glyptocythere inversalitera* and *Fronslarvata chanaeleon*) already in it.

The evidence available from these refined palaeosalinity curves does not detract from the open lagoonal palaeoenvironment, with direct seawater–freshwater mixing, envisaged by Tan and Hudson (1974) and Hudson (1980). The positive correlation between the water chemistry ( $\delta^{18}\text{O}$  of *Praemytilus strathairdensis*) and palaeosalinity, and similar palaeosalinity curves indicated by both benthic (bivalves, gastropods, conchostracans and ostracods) and planktic (*Botryococcus*) biotas confirms the conclusion of Hudson (1963a, 1980) that salinity was the major control on faunal/floral occurrences.

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## APPENDIX

### *Localities and stratigraphy*

(1) Kildonnan Member type section, Eigg [NM 495870]. This section is exposed to the north of Kildonnan on the Isle of Eigg. The section is reached by a narrow cliff path and is exposed on the beach at the start of a beach cliff opposite a distinct shelter stone. The section extends for about 150 m along the shore and is variably exposed from year to year as a result of movement of the storm beach. By the use of distinct marker beds Hudson (1966) was able to construct a composite section. A revised version of this is recorded in Appendix 1 of Wakefield (1991) and in Hudson (in press). The upper portion of Bed 8 and the Algal Bed itself can no longer be seen *in situ* at this locality. These beds lay above a low angle slip plane and have, since their initial recording, been eroded away. The section is best visited at low tide.

(2) Allt na h'Airde Meadhonaich, also known as the Shieling Burn, Eigg [NM 497888]. This stream section running from a dolerite sill with plagioclase phenocrysts on the beach records the upper portion of the Lonfearn Member. The section is interrupted by numerous dolerite sills which have strongly baked the shales.

(3) North-Shore, Eigg [NM 469904–475908]. Only the upper part of the Kildonnan Member is exposed, the base of which is probably equivalent to Bed 5 of the type section. The upper part of the Lonfearn Member is heavily disrupted by numerous sills and dykes, 16–17 m of sediments are

exposed with 16.35 m of sills intercalated. The lower part of the Lonfearn section is relatively undisturbed. This section is best visited at low tide.

(4) Rudha nam Braithairean, also known as Brothers Point, Trotternish, Skye [NG 526625]. This section exposes almost the whole of the Lealt Shale Formation but is intruded by numerous sills, one of which is up to 8 m thick. The upper portion of the Kildonnan Member and the whole of the Lonfearn Member are exposed in the cliff and are accessible with care. The majority of the Kildonnan Member is exposed only at low tide.



# INTERSTIPE WEBBING IN THE SILURIAN GRAPTOLITE *CYRTOGRAPTUS MURCHISONI*

by C. J. UNDERWOOD

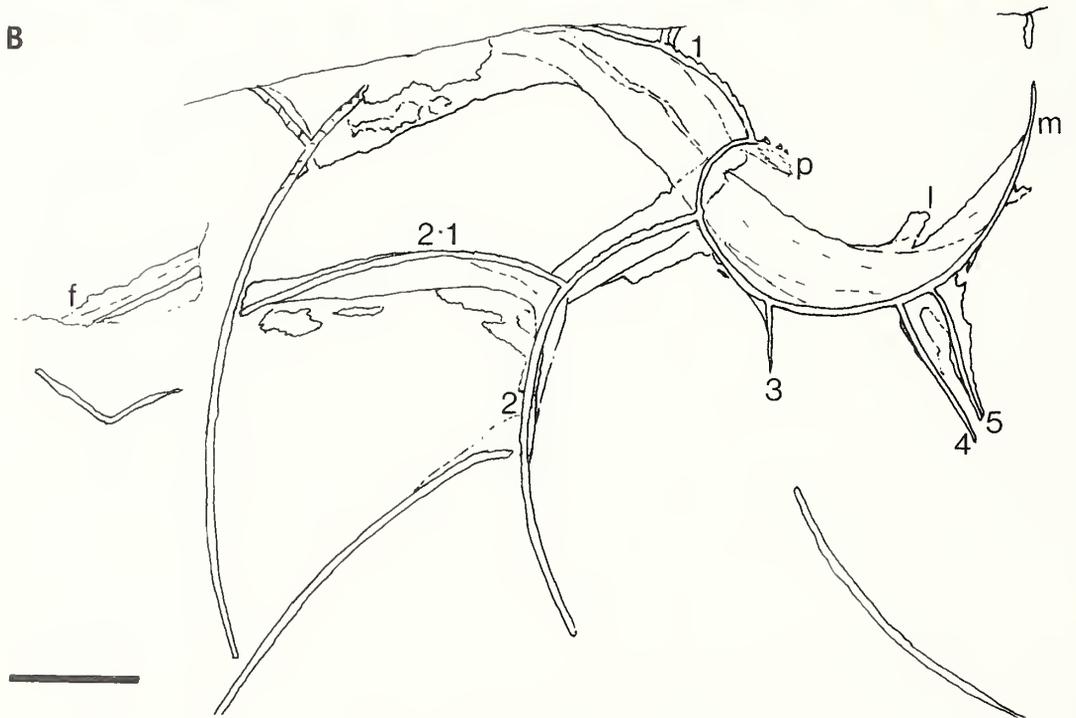
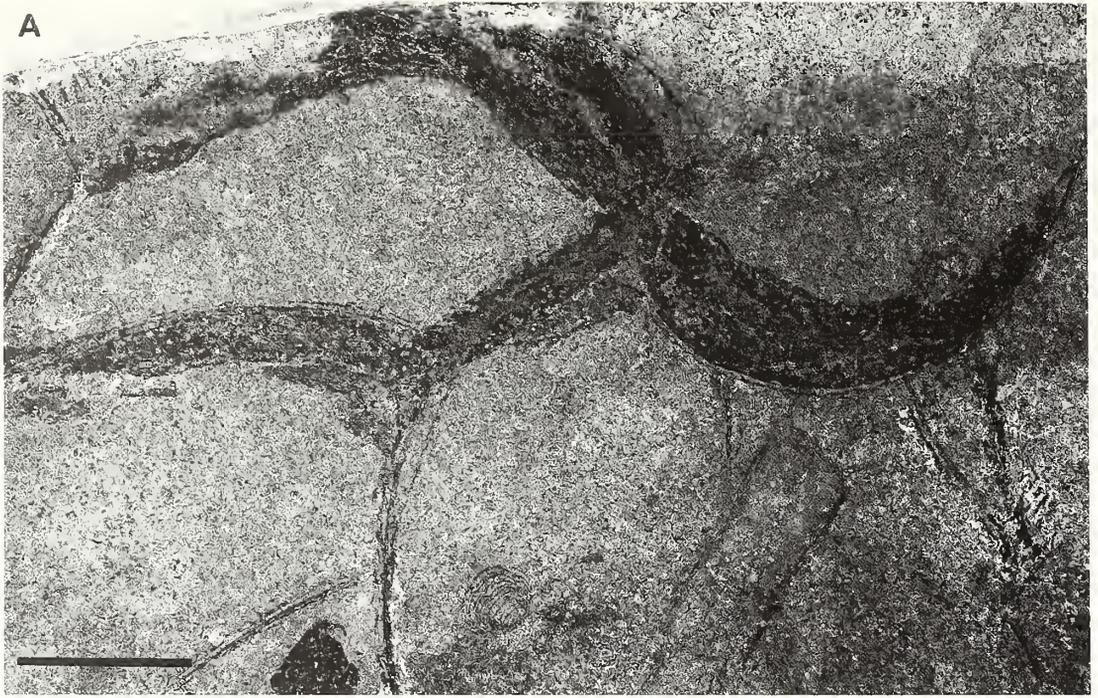
**ABSTRACT.** Although it has long been recognized that the Graptoloidea constituted a diverse group of planktic organisms, the precise hydrodynamics of the various colony morphotypes has been a source of debate. Recent discoveries of specimens of *Cyrtograptus murchisoni* with a complex suite of webs or vanes between the central coiled stipe and the cladial branches have shown that the hydrodynamic modifications of at least this taxon were considerably more complex than previously thought. These webs are composed of very thin peridermal tissue and stretch between the first or second order cladial branches and the main stipe, the webs overlapping to give a screw-like morphology to the rhabdosome. The form of the webbing also has implications for the mode of life and mobility of individual zooids within the colony, as the main areas of web construction are in regions in which the zooids were enclosed within restricted thecal apertures.

AFTER many years of acceptance of graptolites as passive drifters (e.g. Bulman 1970), it has become evident that graptolites were to some extent motile (e.g. Kirk 1990; Rigby 1991; Underwood 1993). The degree and form of this motility is controlled by the hydrodynamic properties of the living rhabdosome (Rigby 1991), which may not necessarily be the same as those of the dead colony as preserved owing to the influence of zooidal and other 'unpreserved' tissues (Underwood 1993). Although no preserved hydrodynamically important parts of zooids (such as lophophores) are known, a number of rarely preserved semi-sclerotized tissues have been recorded. These include proximal webbing in several taxa of anisograptids (Bulman 1970), ancoral periderm in retiolitids (Lenz and Melchin 1987; Bates and Kirk 1992) and a single example of a proximal web in *Cyrtograptus* (Lenz 1974). Such structures are of fundamental importance to the interpretation of the functional morphology of these taxa.

The discovery of three specimens of *Cyrtograptus murchisoni* Carruthers, 1867 with complex interstipe webbing has important implications for graptolite functional morphology and lifestyle. They were found by Mr Brian Beveridge in the *murchisoni* Biozone (Silurian, Wenlock Series) of Buttington Brick Pit, near Welshpool, Powys, Wales (see Cave and Dixon 1993 for locality details). They are preserved as periderm compressions in a grey mudstone, associated with a rich fauna of other *C. murchisoni*, *Monograptus priodon* (Bronn) and *Monoclimacis* sp., along with occasional pelmatozoan material, bivalves and trilobites. None of the specimens has a counterpart. The presence of web-bearing stipe fragments of other individuals of *Cyrtograptus* on two of the slabs suggests that interstipe webbing was normal, but is preserved only under particularly favourable taphonomic conditions. All three specimens are exposed with the sicular or apical surface uppermost, but with the sicula itself missing, and all show sinistral coiling, but it is unclear whether this is characteristic of the taxon. The specimens are deposited in the collection of the Bristol City Museum and Art Gallery, registered as BRSMG Cd2548-2550.

## WEB MORPHOLOGY

A proximal web was described from a specimen of *Cyrtograptus* by Lenz (1974) as a simple sheet of periderm stretched between the main stipe and the first two cladial branches. The far larger and more mature rhabdosomes of *C. murchisoni*, however, show that the web in this species was not a single sheet draped between branches, but a complex series of sheets showing varying degrees of overlap.



TEXT-FIG. 1. For caption see opposite.

Specimen Cd2550 represents a mature rhabdosome, and possesses the most readily recognizable web structure (Text-fig. 1A–B). The webs are present as a series of overlapping sheets, which generally become more extensive towards the central part of the rhabdosome. Many of the webs grade distally from a wide sheet to a narrow flange which becomes difficult to differentiate from the 'normal' stipe, with some suggestion of these flanges being present along almost all of the stipes of the graptolites studied.

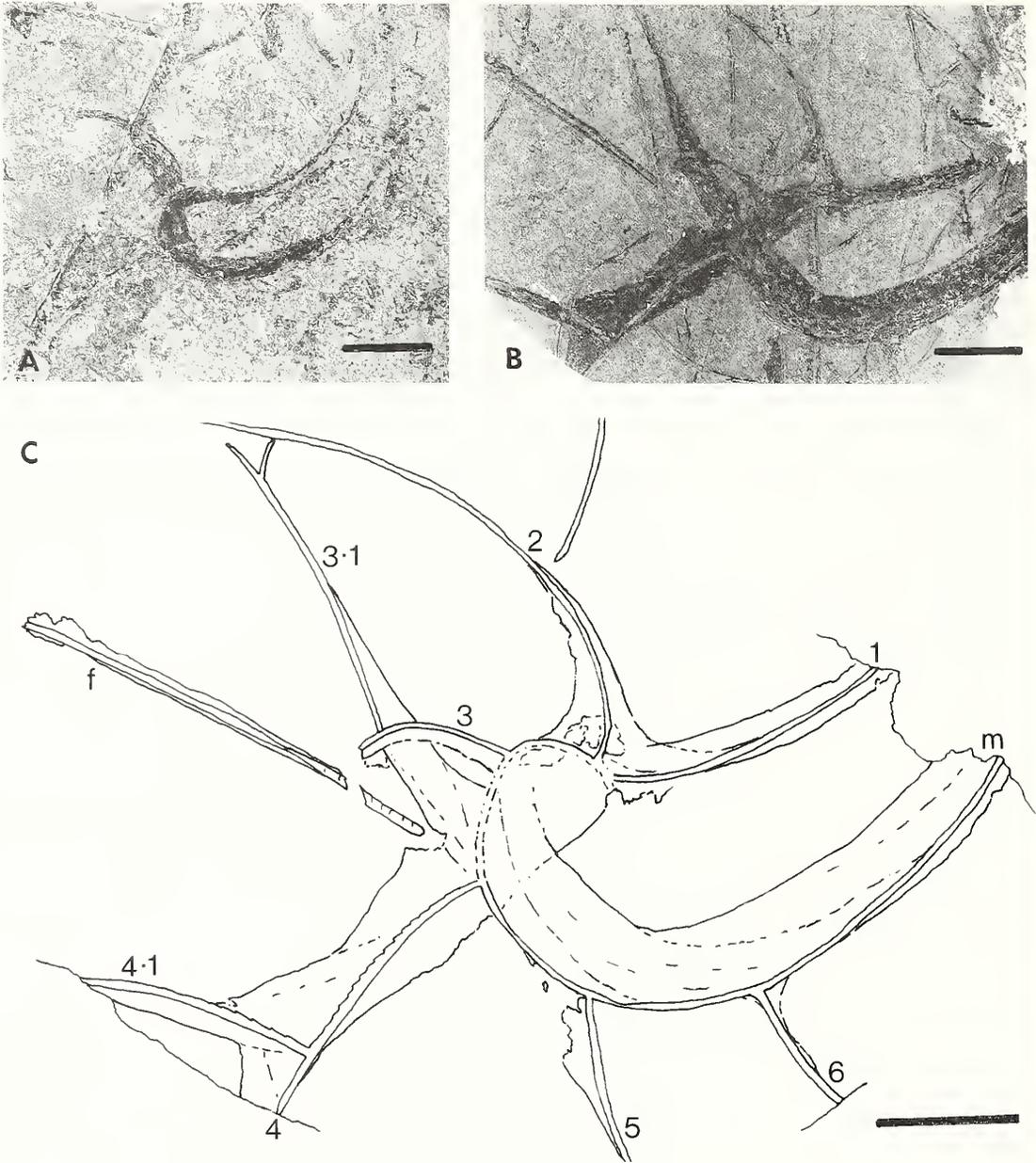
Although very poorly preserved, there is evidence of a small web at the extreme proximal end, stretching probably from the sicula to the first cladium. The webbing over the rest of the primary stipe is broad and extends along its concave edge until the origination of at least the fifth cladium. It appears to be in three distinct overlapping layers, with the more distal layers being overlapped by the more proximal (Text-fig. 3); the most distal of these has a large lobe or irregularity on its trailing edge. The webs along the first cladial stipe are more extensive than along the primary stipe, but also appear to be composed of three overlapping sheets stretched along the concave edge. It appears that these are, at least in part, continuous with webs along the primary stipe. The third major area of webbing is along the second cladial stipe and its second order branches. Less easily interpreted than the other two areas of webs, this appears to consist of two main layers. The better preserved of these is present along the concave and convex sides of the main cladial stipe, as well as forming an extensive web along the second order branch 2·1. This is probably continuous with the second web along the primary stipe. A second, much wider web is also evident along branch 2·1, behind (abscicular to) the aforementioned web. Small webs are also present along the proximal parts of cladial stipes 3, 4 and 5, as well as forming a small process which may mark the position of stipe 6, which is not seen.

The smallest of the specimens, Cd2549, shows the simplest web structure (Text-fig. 2A). There appear to be two webs along the primary stipe, each of which is in continuity with webs along the first two cladial stipes. The longer of these is seen to stretch from 13 mm along the cladial stipe 1, passes over the adscicular ('upper') surface of the primary stipe before extending 35 mm along its concave edge, whilst the second, wider, web extends from the concave edge of cladial stipe 2, passes over the adscicular surface of the earlier web and continues as a wider second web along the primary stipe. A further small area of similar material may indicate an incipient web along the poorly preserved third cladium.

Specimen Cd2548 is the most mature and complex rhabdosome (Text-fig. 2B–C). Although the webs are generally well preserved, the proximal end of the primary stipe has been largely lost with the counterpart, making interpretation difficult. The most proximal webs extend along both sides of cladial stipes 1 and 2 and are then seen to pass across the proximal part of the primary stipe. Although unclear, this then appears to continue along both sides of cladial stipe 4 and branch 4·1. A small area of web is also visible at the base of third order cladial branch 2·1·1 (not seen in figures), showing that in places the web extends over 70 mm from the primary stipe. Cladial stipe 3 appears to provide the origin of two or three webs. One web is present along the concave edge of the first order branch, extending along the primary stipe to just past the origination of cladial stipe 5. A second, wider web is present along the edge of second order branch 3·1. This appears to pass over the asicular surface of all of the previous webs, extending along the concave edge of the primary stipe and attaching to its convex edge close to the origination of cladial stipe 4. It also appears that the main web, which extends along the concave side of the primary stipe, itself probably consisting of two overlapping sheets, may originate in the area of stipe 3. A small web is also present between the convex edges of the primary stipe and cladial stipes 5 and possibly 6.

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TEXT-FIG. 1. *Cyrtograptus murchisoni*, Wenlock Series, Buttington, Powys. BRSMG Cd2550. A, central portion showing the wrinkled and overlapping nature of the dark interstipe webs. B, drawing interpreting the full extent of the webs along the proximal parts of the stipes. Note the small proximal web (p) and the lobe of web material (l). The main stipe (m) is labelled, as are the cladial branches 1–5 and second order branch 2·1. The webbed stipe fragment (f) belongs to another specimen at a lower level in the rock. Scale bars represent 10 mm.



TEXT-FIG. 2. *Cyrtograptus murchisoni*, Wenlock Series, Buttington, Powys. A, BRSMG Cd2549, small rhabdosome, with only two webs visible. B, BRSMG Cd 2548, large and complex rhabdosome. C, drawing of BRSMG Cd2548, showing the complex nature of the multiple, overlapping interstipe webs. The main stipe (m) is labelled, as are the cladial branches 1-6 and second order branches 3-1 and 4-1. The webbed stipe upper left (f) probably belongs to a second specimen. Scale bars represent 10 mm.

A straight stipe fragment with some webbing between cladial stipes 3 and 4 appears to be on a lower lamella in the rock and belongs to a separate specimen.

#### WEB STRUCTURE

The webs appear as dark, vaguely striated films. In places, pyrite polyframboids are present, but these are surface encrustations rather than infills of some hollow structure. The dark material appears to be normal periderm, but is seen to be far thinner than periderm from the stipes and cladia. The striations could represent original structure, but their irregular form makes them more likely to be the manifestation of a wrinkled surface texture. Otherwise there is no evidence for the microstructural composition of the webs. However, as structures obviously post-dating the formation of the thecae, it is likely that they are composed largely or totally of cortical tissue (see Crowther 1981).

The hydrodynamic properties of the web periderm would have been strongly influenced by its rigidity in life. Normal graptolite periderm in life was a rigid material, but far more likely to deform in a ductile than brittle manner (as evidenced by the extreme predominance of buckled over broken stipes in fossil assemblages). The probable wrinkled surface texture of the webs suggests that they were composed of a far more flexible material. This suggestion is supported up by the ease with which the webs twist as they pass from the convex edges of the cladial branches to primary stipe. It is unclear whether the webs represented a loose, flexible sheet or an elastic membrane. Small-scale scalloping along some of the trailing edges of webs could either be a result of contraction of a flexible web or reflect original irregularities in the edge. In specimen Cd 2550 these form a small loose lobe, showing that some original irregularities are present.

#### IMPLICATIONS FOR PERIDERM CONSTRUCTION

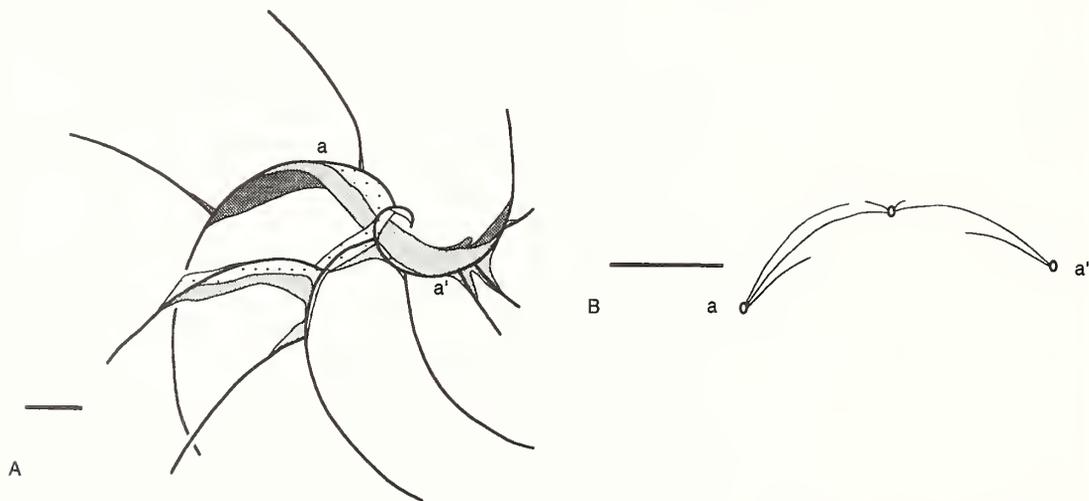
The presence of wide peridermal webs has considerable implications for the manner by which periderm was laid down. The general manner of periderm secretion was for the thecae to be built up by the zooids secreting fusellar tissue, with the subsequent addition of cortical bandages to both outer and inner surfaces (Crowther 1981). Structures such as nemal vanes were built in a similar manner, being constructed by the most mobile, distal, zooids (Urbanek 1973). In all cases, it was probably only the more distal zooids which carried out the construction. The webs in *C. murchisoni*, however, are concentrated at the proximal ends of mature rhabdosomes and must thus have been constructed at a considerable distance from developing zooids. This is shown by an increase in colony size and complexity in the series of specimens Cd2549–2550–2548, with a corresponding increase in area and complexity of the webs. The size of these webs, extending up to 8 mm from the closest zooid, would suggest highly mobile proximal zooids. However, this is not suggested by the thecal morphology. The thecae of *Cyrtograptus*, especially at the proximal end, are hooked with restricted apertures. This modification was almost certainly defensive (Underwood 1993), preventing access by predators, but also probably restricted zooid mobility. Each web also stretches across many thecae, and would have required coordinated activity from all zooids involved for its construction. There are thus three options for the mode of web secretion. (1) The morphology of the webs could easily be accommodated by secretion within a body of extrathecal tissue (e.g. Kirk 1972). This, however, would contradict the need for restricted thecal apertures, and the body of tissue would detract from the hydrodynamic advantage given by the webs, and therefore seems unlikely. (2) Zooids were both considerably more mobile than previously thought, and showed extremely highly coordinated behaviour. They were also small enough to fit through the restricted proximal thecal apertures. (3) It is possible that the unrestricted distal zooids carried out the construction. This would involve high mobility, with zooids needing to have travelled over 100 mm from the growing stipe ends. This mechanism would also have been possible if the thecae below the webs were empty or occupied by non-mobile zooids.

## IMPLICATIONS FOR HYDRODYNAMICS AND FEEDING

It is obvious from the general form of the rhabdosome that the hydrodynamics of *Cyrtograptus* were both complex and closely constrained. It has long been realized that the spiral of the main stipe forms a low, open cone (e.g. Bulman 1970), with it now being evident, owing to the manner in which stipes overlie each other, that the cladial branches diverge at a steeper angle, emphasizing the general conical form. The spiral pattern of the *Cyrtograptus* rhabdosome is itself closely constrained, following a set geometric pattern within each taxon (Huo *et al.* 1986). Within this controlled pattern, the morphology of the interstipe sheets is closely constrained by the spiral geometry of the rhabdosome. Although this was suggested by Lenz (1974) from his observations on a webbed specimen, the small and broken nature of that specimen prevented any firm conclusions.

Physical modelling of the mode of movement of graptolites by Rigby and Rickards (1989) included work on large *Cyrtograptus*, but no allowance was made for the presence of interstipe webbing. The effects of interstipe webs on the hydrodynamics of large multiramous dichograptids were modelled, as the presence of these webs is well known within a range of taxa (Bulman 1970). Dichograptid webs are not, however, directly functionally analogous with the webs of *Cyrtograptus*, as they formed a simple drape between the symmetrical stipes of a planar rhabdosome. This symmetrical webbing in dichograptids would thus have acted simply to increase surface area and reduce the rate of movement, whilst the complex screw morphology of *Cyrtograptus* webs would have controlled the rate of movement, degree of rotation and probably the rhabdosome orientation.

The overlapping nature of the webbing suggests that the hydrodynamic structure was not so much a planar screw controlling water flow over a single curved surface, but more a series of (probably flexible) 'wings' or 'sails' acting to direct water through distinct channels between the stipes (see Text-fig. 3). Along the leading edge of each of these wings was a stipe filled with zooids.



TEXT-FIG. 3. *Cyrtograptus murchisoni*, Wenlock Series, Buttington, Powys. A, diagrammatic reconstruction of BRSMG Cd2550 showing the various layers of interstipe webbing recognized. There is no suggestion that all the webs of the same generation are laterally continuous with each other. B, hypothetical life cross section along line a-a' in A showing the overlapping relationships of the webs. Scale bars represent 10 mm.

Any water through which the central area of the rhabdosome passed thus had to pass through the lophophores of the zooids and the channels between the webs. It is therefore likely that although the webs controlled the flow of water in a purely passive manner, the water flowing over the webs could have been controlled by the zooids.

As filter feeders, the flow of water over the zooids would have controlled the quantity of food

available to the colony. The webs would thus have directly (by directing water over the zooids) and indirectly (by helping control the mobility of the rhabdosome) increased the feeding efficiency of the colony. This would support the idea that *Cyrtograptus* was adapted for highly efficient feeding (Rigby 1991) within deeper, more nutrient-poor waters (e.g. Kirk 1990; Underwood 1993).

The direction of movement of *Cyrtograptus* was assumed by Underwood (1993) to be open end first, the colony acting as an open 'trawl net'. In all three specimens examined, however, narrower webs are present on the adicular surface of wider ones. To get a hydrodynamic benefit from these narrower webs the colony would have had to move adicular (closed) end first. This style of orientation with the point of the cone up-current has been noted within other groups of filter feeders, particularly crinoids (Prof. C. R. C. Paul, pers. comm. 1994). On the largest specimen (Cd 2548), however, one narrow web is seen to pass over the abicular surface of a wider one. It may be therefore, the movement of *Cyrtograptus* was not simply unidirectional, and the colony may have been able to move in a variety of orientations.

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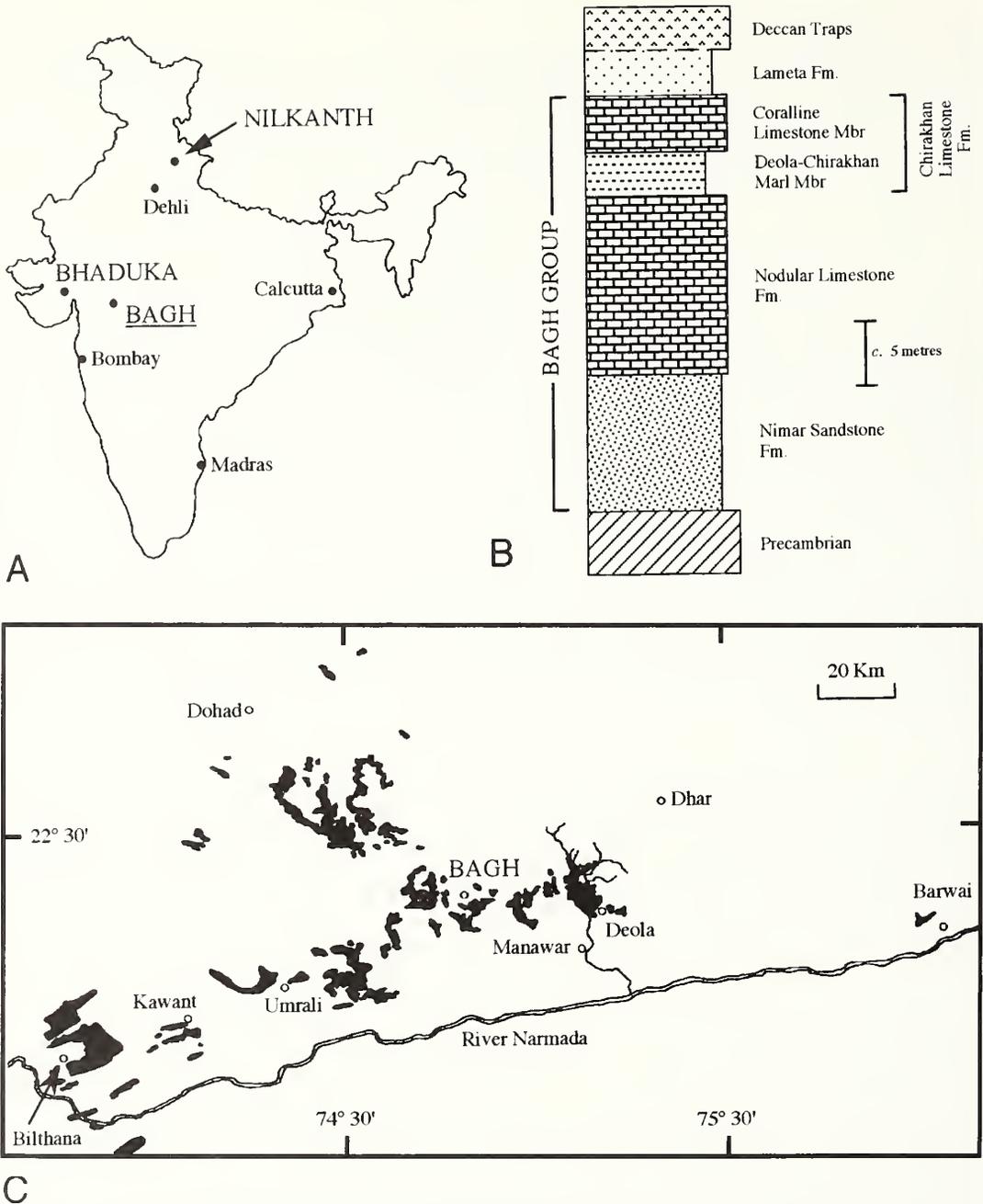
# A NEW CHEILOSTOME BRYOZOAN FROM THE CRETACEOUS OF INDIA AND EUROPE: A CYCLOSTOME HOMEOMORPH

by PAUL D. TAYLOR *and* RAMESH M. BADVE

**ABSTRACT.** The new 'malacostegan' cheilostome *Chiplonkarina* is an unusual genus previously misidentified as a cerioporine cyclostome because of extreme homeomorphy in both zooid-level and colony-level morphology. The type species, *C. dimorphopora*, is the dominant bryozoan in west-central India in the mid-Cretaceous Bagh Group, whose geology is briefly reviewed, and is recorded here for the first time in the Cenomanian of France. A second species, *C. bretoni* sp. nov., occurs in the Lower Cenomanian of France and Germany. In common with many free-walled cyclostomes (and other stenolaemates), the zooids of *Chiplonkarina* are long and tubular, and branches of the dendroid colonies have axial endozones with zooids orientated parallel to the direction of branch extension, bending through almost 90° into the surrounding exozone, where zooids are oriented perpendicular to the branch surface such that their lengthening caused branches to thicken. However, the presence of a cuticular layer in the interzooidal walls, fibrous wall microstructure, and the morphology of the colony base and overgrowths demonstrate that *Chiplonkarina* is a cheilostome. *Chiplonkarina* can be viewed as an early cheilostome 'experiment' in erect growth using a typically stenolaematous growth pattern seldom repeated by the numerous erect cheilostomes that evolved subsequently. The presence of *Chiplonkarina* in the Nilkanth Formation ('Upper Tal Shell Limestone') of Uttar Pradesh, India supports the correlation of these deposits with the Bagh Group and implies a likely Cenomanian-Turonian age.

HOMEOMORPHY in colony-form is pervasive among bryozoans. Even in the absence of well-founded phylogenies of the sort desirable in pinpointing specific instances of homeomorphy, the mosaic distribution of many morphological characters can only be explained by rampant parallel or convergent evolution. Degrees of homeomorphy vary. In some cases, homeomorphic taxa have only a few, particularly conspicuous characters in common, and close scrutiny easily permits distinction between the homeomorphs. In other cases, however, the difference between the homeomorphic taxa is more subtle. Homeomorphy can also be manifested at two hierarchical levels in bryozoans and other colonial animals: colony-level and zooid-level. Notable examples of homeomorphy between bryozoan orders at the colony-level are lyre-shaped fenestrates and lyre-shaped cyclostomes (McKinney *et al.* 1993), and the narrow-branched dendroid colonies which evolved in parallel in trepostomes and cryptostomes (Blake 1980). Homeomorphy at the zooid-level exists, for example, between cheilostomes and the cryptostome *Worthenopora* (Hageman 1991), and between cheilostomes and meliceritid cyclostomes (Taylor 1985).

In this paper, we report a new Cretaceous cheilostome bryozoan which is strongly homeomorphic with cerioporine cyclostomes at both colony- and zooid-levels. *Chiplonkarina* gen. nov. evidently evolved, in parallel, the same geometrical solution as cerioporines (and many other stenolaemates) for growing bushy colonies with cylindrical branches which could thicken proximally towards the colony base where breaking stresses were greatest. This was achieved by having long tubular zooids originating in an axial branch endozone and initially growing parallel to the branch axis at a high rate, but subsequently bending through about 90° outwards into the peripheral exozone where the zooids are perpendicular to the branch surface and growth rate would have been slower. Although a similar colony-form also occurs in the unusual cheilostome *Inversaria* (see Voigt and Williams



TEXT-FIG. 1. A, outline map of India showing locations of the type localities of the Bagh Group in Madhya Pradesh, and of the Bhaduka Limestone (Wadhwan Formation) in Gujarat, and the Nilkanth Formation in Uttar Pradesh. B, generalized vertical section of the Bagh Group and contiguous strata as developed in the Man River Valley near Deola, Madhya Pradesh; thicknesses of the constituent units of the Bagh Group vary considerably and are here scaled approximately according to median values; in some places, the Deola-Chirakhan Marl is absent and the Coralline Limestone rests directly on the Nodular Limestone. C, outcrop pattern of the Bagh Group plus Lameta Formation in the Narmada River Valley centred on the town of Bagh.

1973), most cheilostomes with thick dendroid branches employ frontal budding or other means of self overgrowth to grow thick-branched dendroid colonies, occasionally from an axial bundle of prismatic polymorphic zooids (e.g. *Dysnoetopora*, see Voigt 1970; *Heteroconopeum*, see Voigt 1983).

*Chiplonkarina* is locally common in the Cenomanian of north-west Europe but is much more abundant in the Bagh Group of Madhya Pradesh and Gujarat, west-central India (Text-fig. 1); indeed it is the commonest bryozoan in the Bagh Group, accounting for about 70 per cent. of the bryozoans by volume according to Guha (1987). Branching colonies of *C. dimorphopora* occur in great profusion (Pl. 1, fig. 1) in the uppermost unit of the Bagh Group, the Coralline Limestone, which was formerly used for building temples such as those at Mandu. Bose (1884, p. 71) remarked that the Coralline Limestone '...takes a fine polish, and the thick clusters of branching Bryozoa, of which it is largely made up, give it a most picturesque appearance.'

The principal aims of this paper are: (1) to describe the morphology of *Chiplonkarina*; (2) to establish its taxonomic affinities as a 'malacostegan' cheilostome and its striking homeomorphy with cerioporine cyclostomes (and other dendroid stenolaemates); and (3) to discuss aspects of its growth and functional morphology. Firstly, however, opportunity is taken to summarize aspects of the geology and palaeontology of the Bagh Group of west-central India because almost all of the literature on this important succession has been published in Indian journals which may not be easily accessible elsewhere.

#### GEOLOGICAL SETTING OF THE BAGH GROUP

The Bagh Group was deposited in the Narmada Basin (Trough), an intracratonic trough trending roughly west-east and following the line of the present-day Narmada River in Gujarat and Madhya Pradesh, west-central India (Acharyya and Lahiri 1991). The deposits are exposed in a series of small isolated outcrops (Text-fig. 1), mostly in river valleys to the north of the Narmada River, where erosion has cut through the overlying Lameta Formation and basalts of the Deccan Traps. These exposures extend over a total distance of about 275 km from Barwaha (Barwai) in the east to Naswadi in the west (Ahmad and Akhtar 1990). The outcrop in the Man River Valley near Manawar in Madhya Pradesh reveals the most complete and fossiliferous succession of the Bagh Group (Text-fig. 1B), although the thickest development occurs further west near Rajpipla in Gujarat. The Bagh Group is thought to be the product of a short-lived, eastwards marine transgression by an arm of the Tethys (Chiplonkar and Badve 1973; Jafar 1982). The deposits rest either with strong unconformity on the Precambrian or without obvious break on non-marine Upper Gondwana Group sediments.

#### *Lithostratigraphy*

The large amount of literature on the lithostratigraphy of the Bagh Group chronicles considerable discord between different research schools (summarized by Verma 1969; Guha 1976; Chiplonkar, Badve and Ghare 1977). For example, some authors have excluded the lowermost unit (Nimar Sandstone) from the Bagh Group (e.g. Dassarma and Sinha 1975; Singh and Srivastava 1981; Ahmad and Akhtar 1990), while others have used different names for stratigraphical units exposed in the western and eastern parts of the Narmada Valley (e.g. Poddar 1964; Dassarma and Sinha 1975). The main features of the Bagh Group succession were first established by Blanford (1869, p. 48) who described a section at Chirakhan in the Man River Valley as follows:

Coralline limestone	10 to 20 feet [c. 3–6 m]
Fossiliferous argillaceous limestone abounding in echinoderms ( <i>Hemiaster</i> )	about 10 feet [c. 3 m]
Unfossiliferous nodular limestone	20 feet [c. 6 m]
Sandstone and conglomerate	20 feet [c. 6 m]

Bose (1884) provided a more formal nomenclature when naming the four successive units Nimar Sandstone, Nodular Limestone, Deola-Chirakhan Marl and Coralline Limestone, a scheme retained in essence by Chiplonkar and co-workers (e.g. Chiplonkar, Badve and Ghare 1977). However, alternative names for these four units have proliferated during the past few decades. For example, in the most recent revision of Bagh Group stratigraphy, Ramasamy and Madhavaraju (1993) distinguished three formations: Nimar Sandstone, Karondia Limestone, and Bryozoan Limestone. The Karondia Limestone Formation was originally proposed by Guha (1976) to replace the Nodular Limestone of earlier authors. The Bryozoan Limestone Formation is equivalent to the Barwaha Bryozoan Limestone of Pal (1971), the Chirakhan Limestone Formation of Guha (1976), and the Deola-Chirakhan Marl plus Coralline Limestone of older usage. Some authors (Roy Chowdhury and Sastri 1962; Sahni and Jain 1966) have interpreted the Deola-Chirakhan Marl as a weathering product of the harder limestone but this view is mistaken, as is clear from the differences in faunas between the marl and limestone. There is utility in distinguishing between the marly facies of the Deola-Chirakhan Marl and the typically cross-bedded limestones of the Coralline Limestone (see Chiplonkar, Badve and Ghare 1977) capped by an oyster bed (Chiplonkar and Badve 1980) in the classical sections along the Man River Valley. We therefore recognize these units as separate members of the Chirakhan Limestone Formation (Text-fig. 1B), as did Singh and Srivastava (1981) (the term Barwaha Bryozoan Limestone of Pal (1971) is inappropriate as this unit does not occur in the vicinity of Barwaha). The Nimar Sandstone and Nodular Limestone are retained as formations for the older units because these names are unambiguous and have been widely known since the work of Bose (1884).

The stratigraphical relationship between the Bagh Group and the overlying Lameta Formation, continental deposits with dinosaurian fossils (e.g. Brookfield and Sahni 1987; Mohabey *et al.* 1993), is generally regarded as unconformable, although Raiverman (1975) has suggested that the Bagh Group and Lameta Formation intercalate, and Jafar (1982) believed that they represented facies deposited synchronously.

### Age

The age of the Bagh Group has been a matter of contention, with individual units having been assigned ages ranging from Valanginian to Palaeocene. Although present in reasonable numbers, ammonites in the Bagh Group are mostly poorly preserved steinkerns. The twenty-three named Bagh Group ammonite species point to a Cenomanian or Turonian age (Chiplonkar, Ghare and Badve 1977). The potentially informative inoceramids (of which forty-four nominal species have been distinguished; see Dassarma and Sinha 1975; Chiplonkar and Badve 1976*a*, 1976*b*) are in need of critical comparison with European species of known ages. The echinoid fauna, including *Mecaster meslei* (Peron and Gauthier) which first appears elsewhere in the mid Cenomanian, suggests a mid or late Cenomanian age (A. B. Smith, pers. comm. 1991). Jafar (1982) argued, on the basis of nannofossils, for a late Turonian age (*Eifellithus eximius* Zone) for the entire Bagh Group together with the overlying Lameta Formation. However, the diagnostic coccolith species is difficult to distinguish (J. R. Young, pers. comm. 1993), and some doubt exists over Jafar's age estimate.

Overall consideration of the biostratigraphical data points to a Cenomanian–Turonian age for the Bagh Group, possibly with parts of the Nimar Sandstone at the base of the sequence being Late Albian (Chiplonkar, Ghare and Badve 1977). However, the Nimar Sandstone, as commonly interpreted, is a heterogeneous unit: whereas the upper, more calcareous horizons are marine shallow shelf deposits (Bose and Das 1986) containing marine fossils similar or identical to those found in the overlying limestones, lower levels are fluvial/estuarine (Ahmad and Akhtar 1990), contain plant fossils of Upper Gondwanan affinities, and may be significantly older, perhaps Neocomian (Murty *et al.* 1963; Badve and Ghare 1977; Chiplonkar, Ghare and Badve 1977). Reflecting this upward change towards more marine facies with marine trace fossils, an oyster bed, and a *Jhabotrigonia-Turritella* Bed (Badve and Nayak 1984*a*), the upper part of the Nimar Sandstone, is sometimes recognizable as a separate unit (e.g. Sahni and Jain 1966) called the Amlipura Oyster Bed by Murty *et al.* (1963).

### *Depositional environment*

Bose and Das (1986) interpreted the Nimar Sandstone as a transgressive wave-dominated sequence with upwards fining reflecting deepening of the basin. They regarded the succeeding Nodular Limestone as having been deposited below wave base. Unfortunately, the sedimentology of the carbonate-dominated, fossiliferous upper parts of the Bagh Group has never been studied in detail. The environment of deposition is best simply stated as shallow marine until the necessary research has been undertaken. Guha and Ghosh (1970) inferred a depositional depth of about 20 m on the basis of the bryozoan growth-forms present.

Hardgrounds within the sequence provide evidence of hiatuses in deposition and lithification of the sea-bed. They have been identified at three horizons: (1) at the top of the calcareous Nimar Sandstone at Mahakal, oysters and *Chiplonkarina* colonies are cemented to a hardground; (2) within the Nodular Limestone at Khod-Chikhali, a glauconitized hardground is bored by *Trypanites*; and (3) at the top of the Nodular Limestone at Zirabad, a hardground is bored by truncated *Gastrochaenolites* and encrusted by *Chiplonkarina* and oysters. Nodularity elsewhere in the sequence is suggestive of incipient cementation. From a biological perspective, this early lithification may have been important in creating hard substrates for colonization by epifaunal communities, including animals with hard skeletons whose remains would then have acted as further substrates ('taphonomic facilitation').

Palaeogeographically, the Narmada Valley was probably about 30–40 °S of the palaeoequator during the Cenomanian (e.g. Barron *et al.* 1981; Funnell 1990; Smith *et al.* 1994), although some reconstructions place it within the tropics (e.g. Howarth 1981; Badve and Nayak 1983).

### *Biota*

The rich biotas of the Bagh Group have been described in numerous publications, including general accounts by Chiplonkar and Badve (1973), Dassarma and Sinha (1975), Badve and Ghare (1977) and Chiplonkar, Ghare and Badve (1977). Marine fossils occur abundantly in all units from the upper part of the Nimar Sandstone through to the Chirakhan Limestone. They are particularly numerous and show the best preservation in the Deola-Chirakhan Marl Member in the Man River Valley. Fossils from the higher energy deposits characterizing much of the upper parts of the Nimar Sandstone and the Coralline Limestone Member are typically broken and abraded to varying degrees. Bagh Group body fossils consist predominantly of bivalves (see Dassarma and Sinha 1975; Nayak and Badve 1985 and references therein), gastropods (Chiplonkar and Badve 1972*b*), echinoids (Chiplonkar and Badve 1972*a*), ammonites (see Chiplonkar and Ghare 1977; Ghare 1987 and references therein), bryozoans (see Taylor and Badve 1994 and references therein) and algae (Badve and Nayak 1983, 1984*b*), together with the brachiopod *Malwirhynchia* (Chiplonkar 1938), serpulid worms (Chiplonkar and Ghare 1976*b*), foraminifera (e.g. Rajsheker 1991) and occasional fish teeth (Chiplonkar and Ghare 1974). Burrows and trails are also recorded (Chiplonkar and Badve 1970; Chiplonkar and Ghare 1975; Badve and Ghare 1980), particularly from near the top of the Nimar Sandstone.

## SYSTEMATIC PALAEOLOGY

*Repository abbreviations.* BMNH, The Natural History Museum, London; MACS, Agharkar Research Institute of the Maharashtra Association for the Cultivation of Science, Pune, India; VH, Voigt Collection, Universität Hamburg, Germany.

Order CHEILOSTOMATA Busk, 1852  
 Suborder MALACOSTEGINA Levinsen, 1902  
 Family ELECTRIDAE Stach, 1937  
 Genus CHIPLONKARINA gen. nov.

*Type species.* *Chiplonkarina dimorphopora* (Chiplonkar, 1939), Cenomanian/Turonian, Bagh Group, Madhya Pradesh and Gujarat, India; Cenomanian of Sarthe and Charente Maritime, France; Turonian-?Coniacian of Turkmenistan, Uzbekistan and Tadzhikistan, FSU.

*Other species.* *Chiplonkarina bretoni* sp. nov., Lower Cenomanian of Calvados, France and Westphalia, Germany.

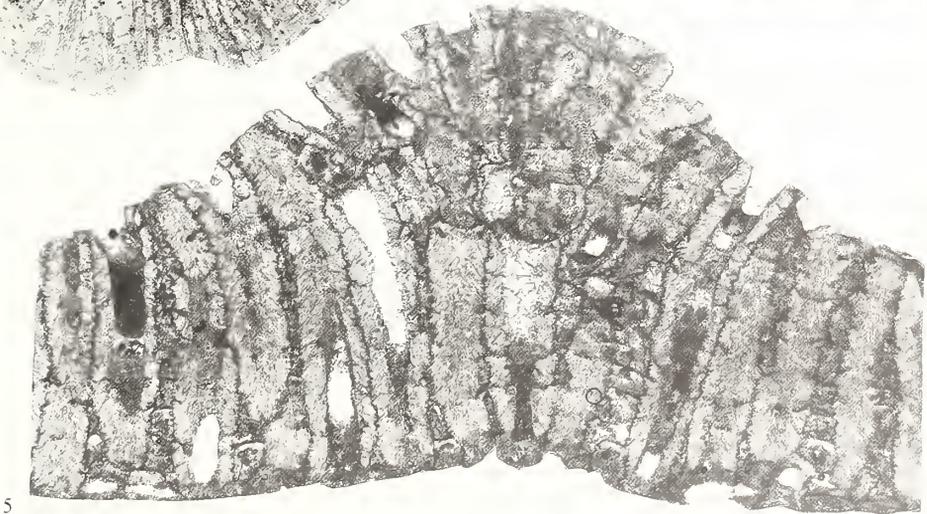
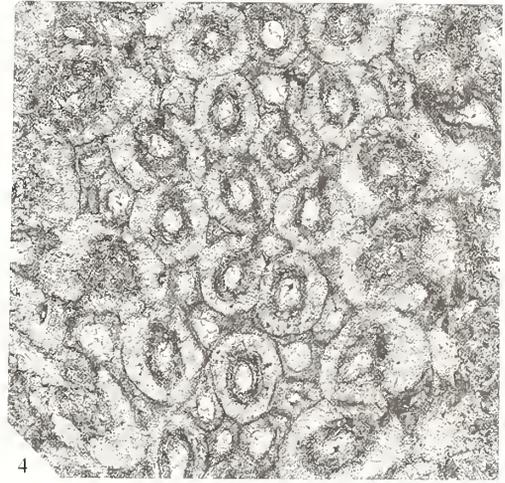
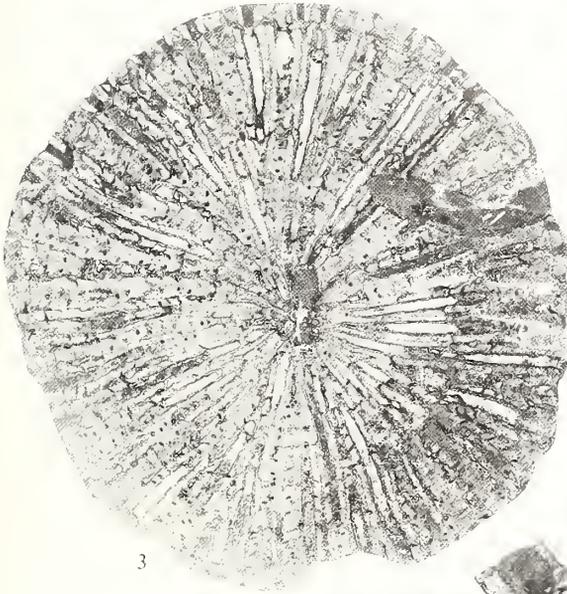
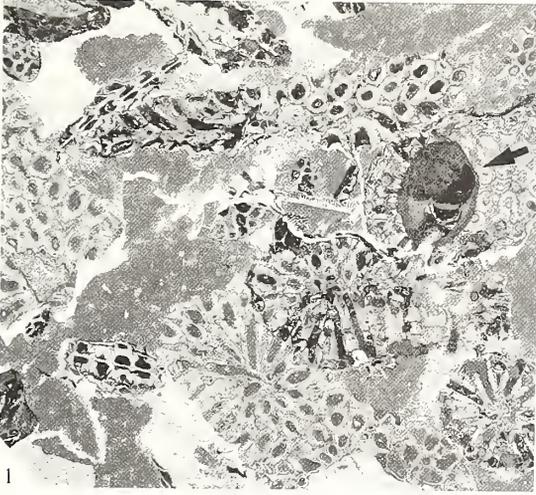
*Derivation of name.* After the late Professor G. W. Chiplotkar (1907–1991), an authority on the Indian Cretaceous (for an obituary, see Badve and Borkar 1991), and author of the type species of this new genus.

*Diagnosis.* Colony developing erect, subcylindrical, bifurcating branches from an extensive encrusting base; early astogeny unknown; erect branches with a narrow, thin-walled endozone surrounded by a thick-walled exozone; zooidal budding concentrated in the endozone; interzooidal walls compound, with the median zooidal boundary being crenulated and often brown in the exozone, interpreted as intercalary cuticle, flanked by a fibrous layer with fibres intersecting the wall surface at about 45°, and occasionally covered by a thinner indistinctly lamellar layer forming a zoecial lining; autozooids long and tubular, oriented parallel to branch growth direction in the endozone, bending through approximately 90° into the exozone to become perpendicular to the branch surface; gymnocyst lacking; cryptocyst narrow, pustulose, not shelf-like but forming a rim continuous with the more proximal parts of the vertical interzooidal walls; opesiae ovoidal, sometimes slightly constricted medially or inverted pear-shaped, occupying a large proportion of the frontal area of the zooid; kenozooids common, irregularly distributed between autozooids, with which they are connected via tunnel-like pores; ovicells and avicularia not observed, presumed absent; pore chambers apparently absent.

*Remarks.* Reasons for assigning *Chiplonkarina* to the malacostegan cheilostomes are given below (p. 649). Superficially, the new genus most closely resembles cerioporine cyclostomes such as *Ceriopora*, *Ceriocava* and *Heteropora* (see Nye 1976), and the Cretaceous cheilostome *Inversaria* (see Voigt and Williams 1973). In thin section, it can be distinguished from cerioporines by the fibrous microstructure of the walls, compared with the lamellar walls of cerioporines, and more particularly by the presence of a crenulated, typically brown layer (interpreted as the remnants of intercalary cuticle; see p. 646) running along the middle of the interzooidal walls. The large larval brood chambers characteristic of cerioporines, are lacking in *Chiplonkarina*. *Inversaria* has exozonal walls with ring diaphragms, calcified cap-like opercula and occasional avicularia, all of which are features not found in *Chiplonkarina*. Fractured interzooidal walls in *Inversaria* show

EXPLANATION OF PLATE I

Figs 1–5. *Chiplonkarina dimorphopora* (Chiplonkar); thin sections photographed in plane polarized light. 1, BMNH D59430 S1; Chirakhan Limestone Formation, Coralline Limestone Member, Badia-Chakrod section, Man River Valley, Madhya Pradesh, India; rock sample crowded with branches including one containing the bivalve boring *Gastrochaenolites* (arrowed);  $\times 14$ . 2–3, BMNH D59436 S1; Chirakhan Limestone Formation, Deola-Chirakhan Marl Member, Sitapuri, Madhya Pradesh, India; 2, exozonal walls with interzooidal pores;  $\times 75$ ; 3, transverse section of thick branch;  $\times 15$ . 4, BMNH BZ87 S1; Upper Cenomanian; Port-des-Barques, Charente Maritime, France; tangential section through thick-walled exozonal zooids with zoecial lining layers;  $\times 48$ . 5, BMNH BZ 2477 S2; Lower Cenomanian (*saxbii/orbigny* zones), Sables et Grès de Lamnay, Lamnay, Sarthe, France; beginnings of erect growth from an encrusting colony base;  $\times 33$ .



median corrugations, suggestive of an intercalary cuticle, but the folds parallel wall growth direction (Voigt and Williams 1973, pl. 2, figs 2–3) whereas those in *Chiplonkarina* are perpendicular. An undescribed genus from the Albian–Cenomanian of southern England resembles *Chiplonkarina* in having stenolaemate-like branches with endozones and exozones, but the exozone comprises short, stacked, box-shaped zooids and not the long, tubular zooids found in *Chiplonkarina*. *Heteroconopeum* Voigt, 1983 from the Turonian has erect branching colonies and zooids somewhat similar in external appearance (Pl. 3, fig. 5) to those of *Chiplonkarina*. However, branch interiors consist of large polymorphic zooids which are overgrown by multilamellar files of autozooids visible on branch surfaces.

Although generally uncommon in the European Cretaceous, *Chiplonkarina* occurs in sufficient abundance in some well-known French localities (notably around Le Mans) to make it somewhat surprising that the genus has not been previously recognized. Examination of the nineteenth century literature reveals only one possible example of *Chiplonkarina*: a species described from Le Mans (Cenomanian) and Grandpré (Albian) by Michelin (1841–48, p. 209, pl. 51, fig. 8a–b) as *Heteropora surculacea*. Reasons for believing that *H. surculacea* may belong to *Chiplonkarina* are the occurrence of widely varying branch diameters in one colony, and the ovoidal shapes of the zooidal apertures. The species was not considered by Walter (1975) when he redescribed the type material of Michelin's Albian and Cenomanian bryozoan species, nor was any material seen during a visit by one of us (PDT) to the MNHM in Paris during 1985. In the absence of Michelin's specimens (and of reliable topotypes), it is impossible to be certain about the affinities of *H. surculacea*.

*Distribution.* Cenomanian–Turonian (?Coniacian) of west-central India, Turkmenistan, Uzbekistan, Tadjikistan and north-western Europe.

#### *Chiplonkarina dimorphopora* (Chiplonkar, 1939)

Plate 1; Plate 2, figures 1, 3, 5–6; Plate 3, figures 1–4; Plate 4, figure 4; Text-figures 2, 5

- ?1884 *Ceriopora dispar* Stoliczka; Bose, pp. 37, 40, 43.
- 1939 *Ceriopora dimorphopora* Chiplotkar, p. 100, pl. 3, fig. 5; pl. 4, figs 2–3.
- 1939 *Ceriopora conoformis* Chiplotkar, p. 100, pl. 3, fig. 3; pl. 4, figs 1, 5.
- 1939 *Ceriopora ellipsopora* Chiplotkar, p. 101, pl. 3, fig. 6; pl. 4, fig. 4.
- 1939 *Ceriocava micropora* Chiplotkar, p. 102, pl. 3, fig. 1.
- ?1967 *Laterocavea*; Tewari and Kumar, p. 37, pl. 3, figs 1, 4–6.
- ?1969 *Ceriopora dispar* Stoliczka; Verma, p. 46.
- ?1969 *Grammanotosoecia talensis* Kumar and Tewari, p. 221 [nomen nudum].
- 1974 *Ceriopora ellipsopora* Chiplotkar; Chiplotkar and Borkar, p. 36.
- 1974 *Ceriopora mamillaria* Chiplotkar and Borkar, p. 36, pl. 1, figs 1–3.
- 1974 *Ceriopora dimorphopora* Chiplotkar; Chiplotkar and Borkar, p. 37.
- ?1974 *Reptomulticava coquandi* d'Orbigny; Chiplotkar and Borkar, p. 37.
- 1974 *Tretocycloecia robusta* Chiplotkar and Borkar, p. 37, pl. 1, figs 4–6.
- 1974 *Ceriocava bhadukaensis* Chiplotkar and Borkar, p. 38, pl. 1, figs 7–9.
- 1974 *Ceriocava grandipora* Canu and Bassler; Chiplotkar and Borkar, p. 38.
- 1974 *Ceriocava micropora* Chiplotkar; Chiplotkar and Borkar, p. 39.
- 1974 *Ceriocava subramulosa* Chiplotkar and Borkar, p. 39, pl. 1, figs 10–12.
- 1974 *Semicea recta* (d'Orbigny); Chiplotkar and Borkar, p. 39.
- 1975 *Ceriopora dimorphopora* Chiplotkar; Guha and Ghose, fig. 2a.
- 1976a *Ceriopora dimorphopora* Chiplotkar; Chiplotkar and Ghare, p. 61, pl. 5, fig. 4.
- 1976a *Tretocycloecia robusta* Chiplotkar and Borkar; Chiplotkar and Ghare, p. 61, pl. 5, fig. 12.
- 1976a *Ceriocava grandipora* Canu and Bassler; Chiplotkar and Ghare, p. 61, pl. 5, fig. 10.
- 1976a *Ceriopora micropora* Chiplotkar; Chiplotkar and Ghare, p. 61, pl. 5, fig. 5.
- 1976a *Ceriocava subramulosa* Chiplotkar and Borkar; Chiplotkar and Ghare, p. 62, pl. 5, fig. 2.
- 1976a *Laterococca tapaswii* Chiplotkar and Ghare, p. 62, pl. 5, figs 7–9.
- ?1977 cerioporids; Mathur, p. 25, fig. 2A–E.
- 1980 *Ceriopora dimorphopora* Chiplotkar; Guha, p. 30, pl. 1, figs 2–8, text-fig. 1b.
- 1980 *Ceriocava nilkanthi* P. Singh, p. 260, figs 28–36.



TEXT-FIG. 2. *Chiplonkarina dimorphopora* (Chiplonkar). Cenomanian/Turonian, Bagh Group, Chirakhan Limestone Formation, Deola-Chirakhan Marl Member, Madhya Pradesh, India. Photographs showing variation in branch diameter. A, thickly branched colony giving rise to a single narrow branch (upper left); BMNH BZ2457; Badia-Chakrod section;  $\times 3.2$ . B-G, range of thick to thin branches from one locality; B, BMNH D59418; C, BMNH D59420; D, BMNH D59421; E, BMNH D59422; F, BMNH D59423; G, BMNH D59424; quarry west of Badia;  $\times 1.6$ .

- ?1985 *Ascopora* sp., Mathur, p. FM70, figs 1-4.  
 ?1985 *Ceriocava nilkanthi* P. Singh, Raiverman and P. Singh, p. FM15, fig. 2e-f.  
 1988 *Ceriocava nilkanthi* P. Singh; P. Singh, p. 103, pl. 1, figs 6-8.  
 1988 *Ceriocava nilkanthi* P. Singh; P. Singh and K. I. Singh, p. 78, pl. 2, figs 6-8.  
 1990 *Ceriocava nilkanthi* P. Singh; V. Singh, p. 30, pl. 3, fig. 5 only, pl. 5, fig. 4.  
 1990 *Diplocava* sp., V. Singh, p. 30, pl. 3, fig. 3 only, pl. 5, fig. 3.  
 1994 '*Ceriopora*' *dimorphopora* Chiplonkar; Taylor and Badve, p. 181, fig. 2A, E-G.

*Type.* Chiplonkar (1939, pl. 3, fig. 5) figured as the holotype of this species specimen number B. H. U. No. B/2 in the collections of the Department of Geology of the Benares Hindu University. As this holotype and other material of *C. dimorphopora* was claimed to be lost, Chiplonkar and Ghare (1976a, p. 61) proposed as neotype specimen No. Gun. 27 in the collections of the Department of Geology at the Agharkar [formerly Maharashtra

Association for the Cultivation of Science (MACS)] Research Institute (ARI), Pune. Unfortunately, Chiplonkar and Ghare's neotype could not be located during February 1991, and has been missing from the ARI collections since 1976. Guha (1980, p. 33), apparently unaware of the paper by Chiplonkar and Ghare (1976a), which he does not cite, subsequently proposed another neotype, 'No. AKG/BRT/H93' in the collections of the Department of Geology and Geophysics, IIT, Kharagpur. Under Article 75 (e) of the Rules of Zoological Nomenclature, Guha's neotype designation is invalid and his specimen cannot replace the lost neotype (J. D. D. Smith, pers. comm. October 1991). Therefore, *C. dimorphopora* lacks a valid type specimen but, as the identity of the species seems uncontentious, it is considered unnecessary to designate yet another neotype.

*Material.* Cenomanian/Turonian Bagh Group, Madhya Pradesh and Gujarat, India. MACS Wal/1 (figured as *Ceriocava grandipora* Canu and Bassler, 1920 by Chiplonkar and Ghare 1976a, pl. 5, fig. 10), Nodular Limestone, Walpur. Gun/1 (figured as *Tretocycloecia robusta* Chiplonkar and Borkar, 1974 by Chiplonkar and Ghare 1976a, pl. 5, fig. 12), Nodular Limestone, Guneri. Kh 26/69 (figured as *Ceriocava subramulosa* Chiplonkar and Borkar, 1974 by Chiplonkar and Ghare 1976a, pl. 5, fig. 2), oyster bed near top of Nimar Sandstone, Khadlu. BW 49/2 (holotype of *Lateroecia tapaswii* Chiplonkar and Ghare, 1976a) and BW 49/3 (paratype of *Lateroecia tapaswii* Chiplonkar and Ghare, 1976a), Chirakhan Limestone, Deola-Chirakhan Marl Member, Barwaha.

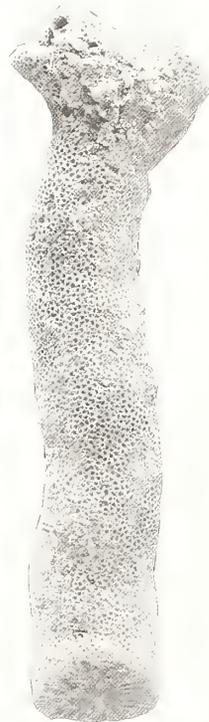
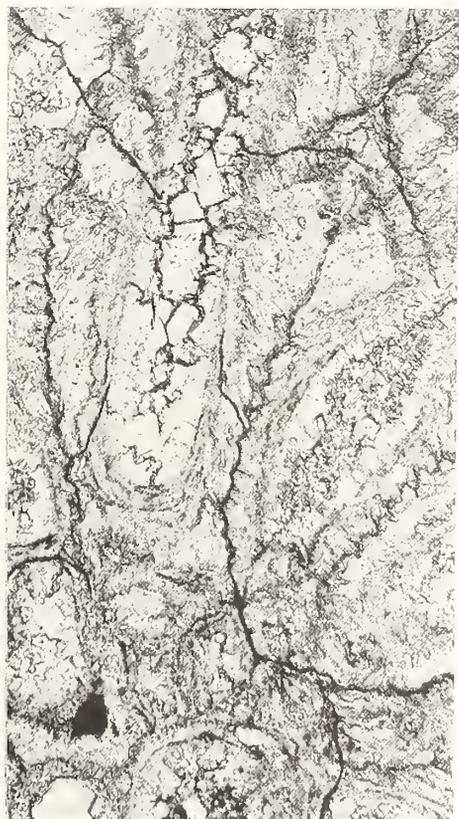
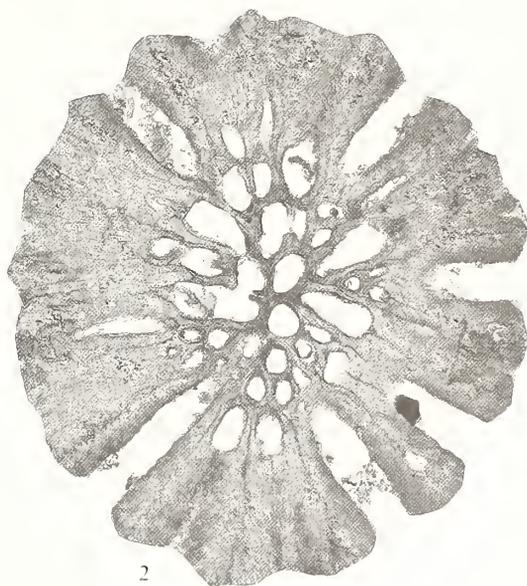
BMNH D59398, D59418–24, BZ 2438–41, BZ 2442 (sample), BZ 2443–4 (thin sections of colony-bases), BZ 2445, BZ 2628 (polished and etched specimen on SEM stub), Chirakhan Limestone, Deola-Chirakhan Marl Member, quarry west of Badia, Man River Valley, Madhya Pradesh. D59399, BZ 2446–51, BZ 2452 (sample), top of Nimar Sandstone, Bilthama, Bharuch District, Gujarat. D59397, D59430 (bryozoan-rich limestone with 2 thin sections), BZ 2453–5, BZ 2456 (sample), BZ 2457, Chirakhan Limestone, Coralline Limestone Member, Badia-Chakrod section, Man River Valley, Madhya Pradesh. D59431 (bryozoan-rich limestone with one thin section), Chirakhan Limestone, Coralline Limestone Member, Hatni River section, Jhabua District, Madhya Pradesh. BZ 2458–9 (samples), Chirakhan Limestone, Deola-Chirakhan Marl Member, Hatni River section, Jhabua District, Madhya Pradesh. BZ 2460, base of Nodular Limestone, Hatni River section, Jhabua District, Madhya Pradesh. D59433 (two thin sections), D59434 (two thin sections), D59435 (two thin sections), D59436 (two thin sections), D59437 (two thin sections), BZ 2461 (thin section of colony base), BZ 2462 (sample), Chirakhan Limestone, Deola-Chirakhan Marl Member, Sitapura, Man River Valley, Madhya Pradesh. BZ 2463, Nodular Limestone, Bhorghat, Man River Valley, Madhya Pradesh. BZ 2464, Chirakhan Limestone, Deola-Chirakhan Marl Member, Chirakhan, Man River Valley, Madhya Pradesh. BZ 2465–7, 2468 (three specimens), Nimar Sandstone, Kholar River section, Barwaha, Madhya Pradesh. BZ 2469 (sample), BZ 2470–2, top of Nimar Sandstone, Pipaldehla, Jhabua District, Madhya Pradesh. BZ 2473 (sample), base of Nodular Limestone, Mahakal, near Bagh Town, Madhya Pradesh. D59432 (rock with thin section), BZ 2474–6, top of Nimar Sandstone, Agarwara, Barwaha, Madhya Pradesh.

Cenomanian/Turonian Wadhwan Formation, oyster bed at top of Bhaduka Limestone Member, Bhaduka, Gujarat, India. MACS Br 1 (identified as *Ceriopora dimorphopora* Chiplonkar by Chiplonkar and Borkar 1974), Br 2 (holotype of *Ceriopora mamillaria* Chiplonkar and Borkar, 1974), Br 3 (identified as *Ceriopora ellipsopora* Chiplonkar by Chiplonkar and Borkar 1974), Br 4 (questionably assigned to *Chiplonkarina dimorphopora*; identified as *Reptonulticava coquandi* d'Orbigny by Chiplonkar and Borkar 1974), Br 5

#### EXPLANATION OF PLATE 2

Figs 1, 3, 5–6. *Chiplonkarina dimorphopora* (Chiplonkar). 1, 3, 5, Chirakhan Limestone Formation, Deola-Chirakhan Marl Member, Sitapuri, Madhya Pradesh, India; 1, BMNH D59433 S1, transverse section through a thin branch (cf. Pl. 1, fig. 3);  $\times 75$ ; 3, BMNH D59434 S1, endozone (lower left) and inner exozone of a transversely sectioned branch showing corrugated inferred remnants of intercalary cuticle and fibrous wall microstructure;  $\times 180$ ; 5, BMNH D59433 S2, tangential section;  $\times 22$ . 6, BMNH D59397; Chirakhan Limestone Formation, Deola-Chirakhan Limestone Member; Badia-Chakrod section, Madhya Pradesh, India; photograph of well preserved branch bifurcating at its distal end;  $\times 3.2$ .

Figs 2, 4. *Chiplonkarina bretoni* sp. nov.; Lower Cenomanian; Carrière du Billot, Notre Dame le Fresnaye, Normandy, France. 2, VH 10565; transverse section;  $\times 50$ . 4, VH 10572; longitudinal section;  $\times 15$ . Thin sections photographed in plane polarized light.

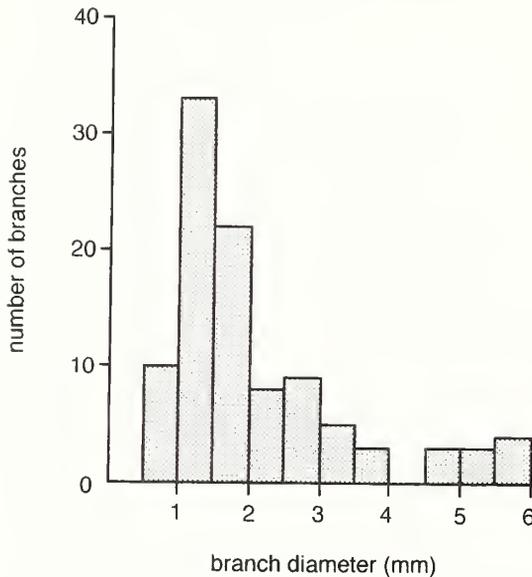


(holotype of *Tretocycloecia robusta* Chiplonkar and Borkar, 1974), Br 6 (holotype of *Ceriocava bhadukaensis* Chiplonkar and Borkar, 1974), Br 7 (identified as *Ceriocava grandipora* Canu and Bassler by Chiplonkar and Borkar 1974), Br 8 (identified as *Ceriocava micropora* Chiplonkar by Chiplonkar and Borkar 1974), Br 9 (holotype of *Ceriocava subramulosa* Chiplonkar and Borkar, 1974), Br 10 (identified as *Semicea recta* d'Orbigny by Chiplonkar and Borkar 1974).

French Cenomanian. BMNH D59401-4, Cenomanian (?Middle), ?Sables du Mans, Le Gasonfier, Le Mans, Sarthe. BZ 2696, Cenomanian, Le Mans. D58966, BZ 2697, Upper Cenomanian, Sables du Perche, Gréze sur Roc, Sarthe. BZ 2477 (two thin sections), Lower Cenomanian (*saxbii/orbigny* zones), Sables et Grès de Lamnay, Lamnay, Sarthe. BZ85-6, 87 (two thin sections), 88-9, Upper Cenomanian, Bed G (of Moreau 1976), Port des Barques, near Rochefort, Charente Maritime.

*Diagnosis.* *Chiplonkarina* with branches of widely varying diameters; autozooids with ovoidal opesia, narrow cryptocysts and apparent polarities that are often neither parallel to branch growth direction nor to the polarities of nearby autozooids; kenozooids numerous, especially in thick branches, intercalated between autozooids.

*Description.* Colony either entirely encrusting, sometimes with a hummocky surface, or more often becoming erect with cylindrical bifurcating branches of highly variable diameter (0.7-11 mm) (Text-figs 2B-G, 3).



TEXT-FIG. 3. Histogram of branch diameter in a sample of one hundred specimens of *Chiplonkarina dimorphopora* (Chiplonkar) collected from the Deola-Chirakhan Marl Member (Bagh Group) of Sitapuri, Madhya Pradesh, India. Note the wide but more or less continuous variation present in this sample.

Encrusting base often extensive, sometimes tubular (cavariiform) as a result of growth around an unpreserved substrate. More than one erect branch may arise from the encrusting base (Pl. 1, fig. 5). Secondary, lateral branches of small diameter often developed, diverging at approximately 90° from the exozone of the parent branch (Text-fig. 2A). Branches divided into an inner endozone with zooids orientated approximately parallel to branch growth direction, surrounded by an outer exozone with thicker-walled zooids orientated approximately perpendicular to branch growth direction and intersecting the branch surface at roughly 90° (Pl. 1, fig. 3; Pl. 2, fig. 1). Endozone narrow, varying from 0.24-0.53 mm in diameter. Exozone broad, accounting for most of the branch diameter, and highly variable in diameter. Wall thickness up to 0.05 mm in the endozone, 0.10-0.25 mm in the exozone. New zooids originate as interzooidal buds, initially triangular and located at triple junctions between existing zooids. Budding occurs in both the endozone and exozone. Distal branch growing tips not observed with certainty, but transversely fractured branches sometimes split along dome-shaped planes in the endozone which may represent former growing tips.

Interzooidal walls compound, interpreted as two exterior walls back-to-back. Median layer of interzooidal walls crenulated in exozone (Pl. 2, fig. 3; Pl. 4, fig. 4; Text-fig. 5), often with a brown deposit; crenulations perpendicular to wall growth direction, with a wavelength of 0.015-0.020 mm. Interzooidal wall microstructure

predominantly fibrous (Pl. 2, fig. 3), the fibres diverging from the crenulations and intersecting the wall surface at about 45°, giving the compound wall a chevron fabric when sectioned longitudinally. Lamellar zooecial lining up to 0.03 mm thick sometimes covering fibrous layer (Pl. 1, fig. 4). Secondary fibrous lining, found in a very few zooids, may represent intramural budding ('regeneration'). Pores (Pl. 1, fig. 2) present in interzooidal walls between autozooids and kenozooids (?lacking in walls between adjacent autozooids), parallel-sided, elongated transversely to wall growth direction, about 0.015–0.030 mm in diameter. Diaphragms very occasionally developed; distinctly U-shaped, concave distally, varying in thickness from 0.01–0.05 mm. Lamellar overgrowths sometimes present, with basal walls 0.015 mm thick giving rise to vertical walls 0.05 mm thick which rapidly attain a 'mature' thickness of 0.10 mm while bending slightly; appreciable endozone lacking in overgrowths.

Autozooids long, club-shaped tubes, moderately thin-walled in the endozone, bending into the exozone and becoming thicker-walled. Endozonal portions of autozooids may exceed 1 mm in length but their full extent and range is impossible to determine. Frontal outline of autozooids (Pl. 3, figs 1–4) on branch surface elliptical, variable in length and width, on average about 1.2 × longer than wide, long axis (?indicating proximal-distal polarity) of variable orientation relative to branch axis in thick branches, but often parallel to axis in thin branches. Opesia occupying most of frontal surface, elliptical, on average about 1.3 × longer than wide, sometimes slightly hourglass-shaped (Pl. 3, fig. 4). No frontal gymnocyst. Cryptocyst narrow, minutely pustulose (Pl. 3, fig. 4), not shelf-like (except in some zooids in lamellar overgrowths) but forming a typically funnel-shaped rim contiguous with the vertical interzooidal walls. Zooidal boundaries slightly grooved (Pl. 3, figs 2, 4). Closure plates and pore chambers not observed, presumed absent.

Kenozooids long, club-shaped tubes, intercalated between autozooids on colony surface. Frontal outline variable, some elliptical, others triangular, rectangular or of a more complex shape with concave sides, smaller than autozooids (Pl. 3, figs 1–4). Cryptocyst and opesia similar in morphology to those of autozooids.

Ovicells and avicularia lacking.

*Dimensions* (frontal dimensions in millimetres of ten autozooids).

	BMNH D59401 (Sarthe)	BMNH D59397 (Madhya Pradesh)
length	$\bar{x} = 0.24$ ; SD = 0.018; CV = 7.4; $r = 0.21$ –0.27	$\bar{x} = 0.28$ ; SD = 0.023; CV = 7.4; $r = 0.24$ –0.30
width	$\bar{x} = 0.20$ ; SD = 0.017; CV = 8.4; $r = 0.17$ –0.23	$\bar{x} = 0.23$ ; SD = 0.026; CV = 11; $r = 0.20$ –0.27
opesia length	$\bar{x} = 0.16$ ; SD = 0.017; CV = 10.8; $r = 0.14$ –0.18	$\bar{x} = 0.18$ ; SD = 0.016; CV = 8.6; $r = 0.17$ –0.21
opesia width	$\bar{x} = 0.12$ ; SD = 0.011; CV = 9.1; $r = 0.11$ –0.14	$\bar{x} = 0.14$ ; SD = 0.013; CV = 8.9; $r = 0.12$ –0.17

*Remarks.* The long synonymy of this species deserves comment. *Chiplonkariina dimorphopora* has been referred to no fewer than seven different cyclostome bryozoan genera and fourteen species. Confusion over its generic assignment undoubtedly stems from a difficulty in applying generic concepts to Mesozoic bryozoans. The erection of so many different species for *C. dimorphopora* is a result of several factors. First is the high variability in branch diameter. *Lateroecea tapaswii* Chiplonkar and Ghare, 1976a, for example, was established for thin-branched specimens. That this variability is not indicative of the existence of more than one species can be seen from the continuous variation in branch diameter found within sampled 'populations' (Text-fig. 3; see also Text-fig. 2B–G, and compare Pl. 1, fig. 3 with Pl. 2, fig. 1), and the occurrence of thick-branched colonies giving rise to lateral branches of narrow diameter (Text-fig. 2A). Specimens with uneven mamillated surfaces have also been given different species names (e.g. *Ceriopora manillarica* Chiplonkar and Borkar, 1974, *Ceriocava bhadukaensis* Chiplonkar and Borkar, 1974), although all of the mamillations observed fall more within the category of irregular bumps than potentially taxonomically significant, regularly-spaced monticules. The importance of this morphological variability has been accentuated by optimism about the possible stratigraphical value of different

morphotypes present in different units of the Bagh Group (M. A. Ghare, pers. comm. 1991). Erection of new names for occurrences of *C. dimorphopora* in the Wadhwan Formation of western Gujarat and Nilkanth Formation of Uttar Pradesh, and ignorance of previous publications have also led to taxonomic proliferation.

Guha (1980) understood the synonymy of the established species of '*Ceriopora*' from the Bagh Group which were known to him, but seems to have been unaware of the paper of Chiplonkar and Ghare (1976a) on bryozoans from the Bagh Group, and that of Chiplonkar and Borkar (1975) on a similar aged fauna from the Wadhwan Formation of Surendranagar District of western Gujarat. The original description by P. Singh (1980) of *Ceriocava nilkanthi*, a nominate species considered herein to be a junior synonym of *Chiplonkarina dimorphopora*, included material from both the Nilkanth Formation ('upper Tals') and from the Coralline Limestone of the Bagh Group. Singh quoted none of the palaeontological papers on the Bagh Group, and made no comparisons between his new species and established bryozoan species from the Bagh Group.

Specimens from the Upper Cenomanian of Port-des-Barques, Charente Maritime, France show some differences when compared with material from India and Sarthe, France. The Port-des-Barques specimens may develop very thick interzooidal walls (0.25 mm), twice the thickness typically found in *C. dimorphopora*, and the autozooids are somewhat larger: measurements made from a tangential section of BMNH BZ87 revealed zooidal lengths of 0.28–0.36 mm and widths of 0.24–0.28 mm (cf. dimensions given above). In view of the intrapopulational variability found in *C. dimorphopora*, however, these differences are deemed insufficient to justify species distinction without support from an intensive biometrical analysis.

*Palaeoecology.* Most specimens of *C. dimorphopora* from the Bagh Group consist of cylindrical branches from broken dendroid colonies (Pl. 2, fig. 6; Text-fig. 2). Despite the relatively robust construction of many colonies, it is rare to find specimens preserving more than one branch bifurcation, whereas the original colonies were probably bushy and would have contained a large number of bifurcations. Both mechanical and biological factors probably contributed to colony fragmentation. Many of the thicker branches contain *Gastrochaenolites* (Pl. 1, fig. 1), indicating boring by bivalves, which undoubtedly weakened the colony and promoted fragmentation. At least some of the branch breakage occurred while colonies were still alive: a thick-branched specimen (BMNH BZ 2445) has a fractured proximal end partly covered by a lamellar intracolony overgrowth. For most specimens, however, there is no such evidence for fragmentation during life and post-mortem breakage cannot be ruled out.

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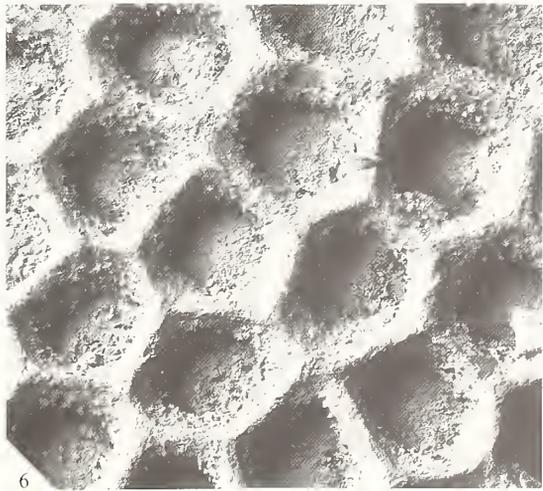
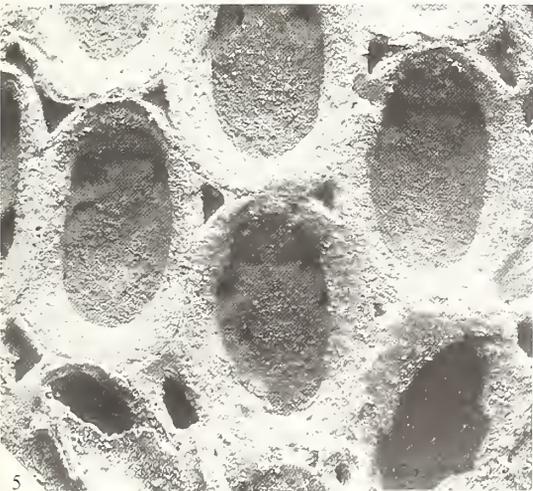
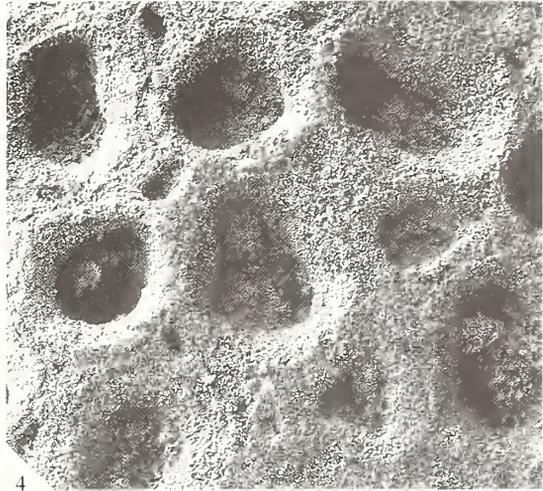
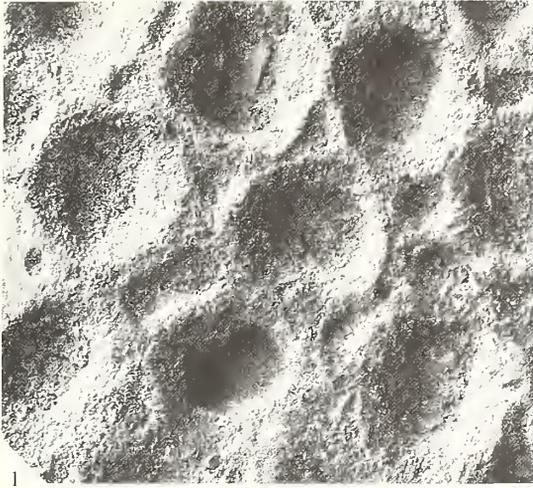
#### EXPLANATION OF PLATE 3

Figs 1–4. *Chiplonkarina dimorphopora* (Chiplonkar). 1, autozooids and space-filling kenozooids in a relatively well-preserved Indian specimen; BMNH D59397; Chirakhan Limestone Formation, Deola-Chirakhan Limestone Member; Badia-Chakrod section, Madhya Pradesh, India;  $\times 80$ . 2, typical coarsely-preserved autozooids and occasional kenozooids from a colony base; BMNH D59399; Nimar Sandstone Formation; Bilthama, Gujarat;  $\times 80$ . 3, autozooids with funnel-shaped 'cryptocysts' and a kenozooid with concave sides (centre) in a French specimen; BMNH D59401; Cenomanian; Le Gasonfier, Le Mans, Sarthe;  $\times 135$ . 4, French specimen with finely pustulose autozooidal and kenozooidal 'cryptocysts'; BMNH BZ 86; Upper Cenomanian; Port-des-Barques, Charente Maritime, France;  $\times 80$ .

Fig. 5. *Heteroconopeum janieresense* (Canu), a 'malacostegan' cheilostome resembling *Chiplonkarina*, showing autozooids with small kenozooids at their corners; BMNH D55536; Turonian; Ruillé-Poncé, France;  $\times 100$ .

Fig. 6. *Ceriocava corymbosa* Lamouroux, the type species of *Ceriocava*, one of the cerioporine cyclostomes to which *Chiplonkarina dimorphopora* has previously been assigned; note the sharp edges of the interzooidal walls; BMNH D59139; Upper Bathonian; St Aubin-sur-Mer, Normandy, France;  $\times 55$ .

Scanning electron micrographs of uncoated specimens imaged using back scattered electrons.



*Distribution.* This species is volumetrically the dominant bryozoan in the Bagh Group (Cenomanian–Turonian, see above) of west-central India and is largely responsible for the term ‘Coralline Limestone’ as applied to the uppermost unit of the Bagh Group where the dendroid branches of *C. dimorphopora* are conspicuous on weathered and polished rock surfaces.

*C. dimorphopora* also occurs in the oyster bed at the top of the Bhaduka Limestone, the youngest unit of the Wadhwan Formation of the Surendranagar District, Gujarat (Chiplonkar and Borkar 1974). The Wadhwan Formation is regarded as a western lateral equivalent of the Bagh Group, and is thus most likely to be of Cenomanian–Turonian age (Chiplonkar and Borkar 1975).

Material of putative *C. dimorphopora* from the Lesser Himalayas (in the vicinity of Nilkanth on Text-figure 1A) is in need of restudy and the following preliminary remarks are based entirely on descriptions and illustrations from the literature. Mathur (1977) figured thin sections of ‘cerioporid’ bryozoans from the Tal Formation of the Garhwal region of Uttar Pradesh which strongly resemble sections of *C. dimorphopora* from the Bagh Group. His sections depict dendroid colonies with thick zooidal walls that have dark middle layers suggestive of the inferred intercalary cuticle found in *C. dimorphopora* from the Bagh Group. The bryozoans described by Mathur were said to be abundant in his Member 3 of the Tal Formation, including the so-called Singtali Formation (Mehrotra *et al.* 1976). There has been considerable debate about the age of the upper parts of the Tal Formation, with one school favouring a Permian and another a post-Palaeozoic (Jurassic–Early Palaeocene) age. The younger age assignment is based on records of various macrofossils (including belemnites) and microfossils, whereas apparent Permian algae, fusulines etc seemingly provide contradictory evidence. I. B. Singh (1981) reviewed the confusion over the age of the Tal Formation and made a clear distinction between older Tal Formation deposits, which are about 2000 metres thick and unfossiliferous, and the overlying Shell Limestone of the Mussoorie-Garhwal area, which is only thirty metres thick (see also Saxena 1985). The Shell Limestone was renamed the Nilkanth Formation by I. B. Singh (1979), although Bhatia (1985) argued that the Shell Limestone constitutes the Tal Formation *sensu stricto* and that, if anything, it is the thick underlying sequence which requires a substitute name. The Nilkanth Formation is interpreted as a high energy carbonate sand bar/shoal complex deposited in a shallow tidal sea (I. B. Singh 1979). It was formed during a marine transgression which flooded an arm of the Tethys along the Subathu-Dogadda Zone, probably contemporaneously with the transgression responsible for marine sediments of the Bagh Group along the Narmada Basin further south (I. B. Singh 1981). P. Singh (1980) described *Ceriocava nilkanthi* from the Nilkanth Formation and also recorded its presence in the Bagh Group. This species is here considered synonymous with *Chiplonkarina dimorphopora*, supporting correlation of the Nilkanth Formation with the Bagh Group, and implying a Cenomanian/Turonian age for the Nilkanth Formation.

European records of *Chiplonkarina dimorphopora* are from the Cenomanian of the Le Mans area, Sarthe, and the Upper Cenomanian of Port-des-Barques, near Rochefort, Charente Maritime, France.

Unregistered material of apparent *C. dimorphopora* from the former Soviet Union was seen recently by one of us (PDT) during visits to the All-Russian Scientific Research Geological Institute (VSEGEI) in St Petersburg, and the Palaeontological Institute of the Russian Academy of Sciences in Moscow. These specimens, which have not been studied in detail, are from the Turonian and ?Coniacian of Turkmenistan,

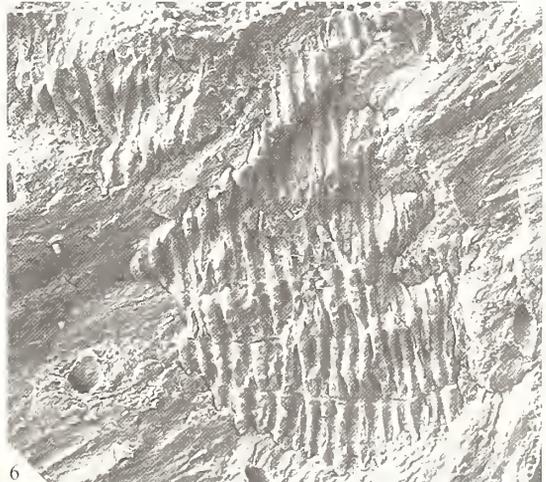
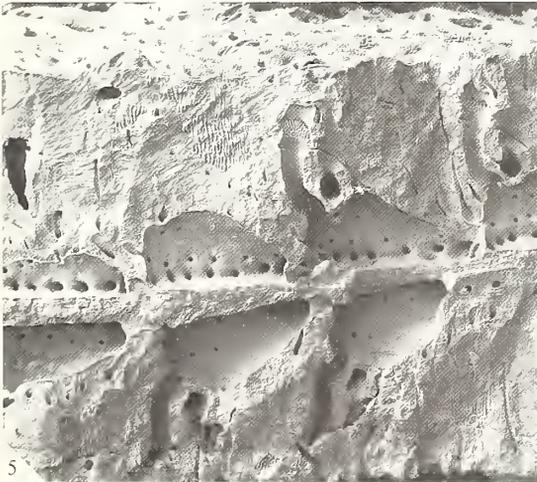
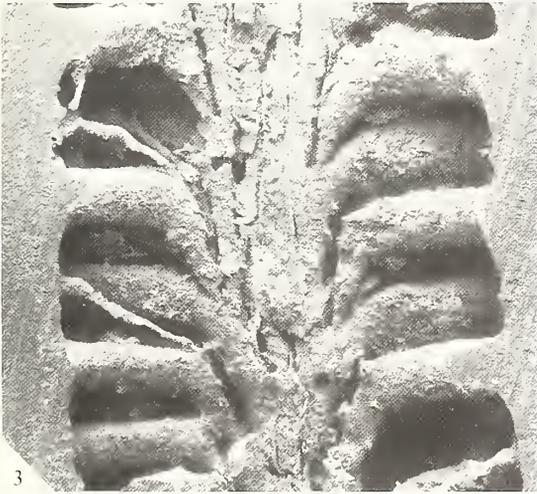
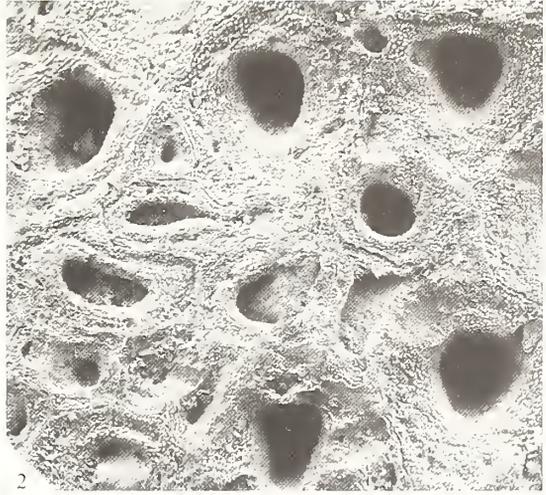
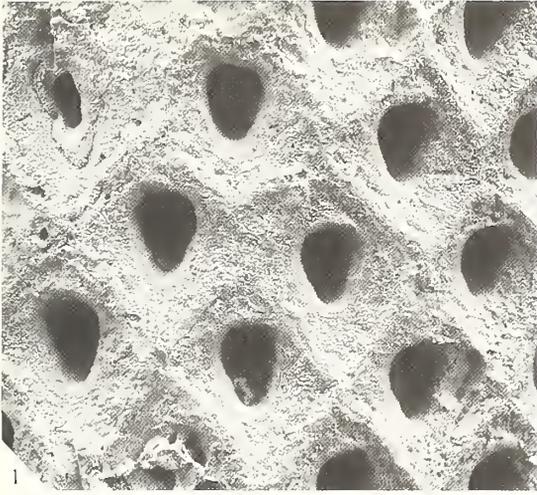
#### EXPLANATION OF PLATE 4

Figs 1–3. *Chiplonkarina bretoni* sp. nov., Lower Cenomanian; Carrière du Billot, Notre Dame le Fresnaye, Normandy, France. 1–2, VH 10373, holotype; 1, group of autozooids showing typical shape of opesia;  $\times 75$ ; 2, overgrowth of small kenozooids; note pustulose ‘cryptocysts’;  $\times 85$ . 3, VH 10383; epoxy mould showing shape of autozooidal chambers; narrow ‘pipes’ at the left may be knozooids;  $\times 50$ .

Fig. 4. *Chiplonkarina dimorphopora* (Chiplonkar); BMNH D59403; Cenomanian; Le Gasonfier, Le Mans, Sarthe, France; detail of transversely fractured branch (branch surface is towards the left) showing corrugations where double interzooidal walls have broken along the line of the intercalary cuticle;  $\times 130$ .

Figs 5–6. *Adeonellopsis yarraensis* (Waters); BMNH 1994. 4. 15. 1; Recent, Otago Shelf (Munida Station Mu 88-29), New Zealand; a cheilostome with corrugations similar to those seen in the interzooidal walls of *Chiplonkarina*. 5, context view of fractured branch showing porous autozooids on either side of the median budding lamina and thick frontal walls;  $\times 37.6$ , detail of frontal wall broken along the line of the corrugated intercalary cuticle;  $\times 200$ .

Scanning electron micrographs of uncoated specimens imaged using back scattered electrons.



Uzbekistan and Tadjikistan. According to T. Favorskaya (pers. comm. August 1994), the species is particularly abundant in the Upper Turonian of Turkmenistan.

*Chiplonkarina bretoni* sp. nov.

Plate 2, figures 2, 4; Plate 4, figures 1–3; Text-figure 4

*Derivation of name.* After Gerard Breton who collected the holotype and other specimens.

*Holotype.* VH 10373, Lower Cenomanian (*carcitanensis* Zone); Carrière du Billot, Notre Dame le Fresnaye, Calvados, Normandy, France; G. Breton Collection. Other bryozoan species present at this locality were tabulated by Voigt (1986).

*Paratypes.* VH 10372, 10374–6, 10383 (epoxy mould), 10564 (twenty-six fragments), 10565–77 (thirteen thin-sections), locality details as for holotype. BMNH BZ 2629–33, Lower Cenomanian, Craie Glauconieuse, Villers-sur-Mer, Calvados, Normandy, France. BZ 2694–5, Lower Cenomanian, Mülheim, Westphalia, Germany.

*Other material.* VH 11650, Lower Cenomanian, Essen, Westphalia, Germany.

*Diagnosis.* *Chiplonkarina* with slender branches; autozooidal opesia inverted pear-shaped, apparent polarity parallel to branch polarity.

*Description.* Colony erect with cylindrical bifurcating branches (Text-fig. 4A) varying from about 1.1 to 2.4 mm in diameter. Branches divisible into a narrow endozone (0.30–0.57 mm in diameter) containing about ten to twenty zooids orientated approximately parallel to branch growth direction, surrounded by an exozone with thicker-walled zooids orientated approximately perpendicular to branch growth direction and intersecting the branch surface at about 90° (Pl. 2, fig. 4; Pl. 4, fig. 3). Wall thickness 0.02–0.03 mm in the endozone, 0.10–0.15 mm in the exozone. Interzooidal walls compound, interpreted as two exterior walls back-to-back. Median layer of interzooidal walls crenulated in exozone (Text-fig. 4B); crenulations perpendicular to wall growth direction, with a wavelength of about 0.020–0.025 mm. Interzooidal wall microstructure in thin section indistinctly fibrous (Pl. 2, fig. 2), the fibres diverging from the crenulations and intersecting the wall surface at about 45°, giving the compound wall a chevron fabric when sectioned longitudinally. Overgrowths occasionally present (Pl. 4, fig. 2), sometimes enveloping tubicolous and other fouling organisms. Lateral branches may be developed at high angles to parent branches. Autozooidal budding, except for that in overgrowths, mostly or exclusively endozonal.

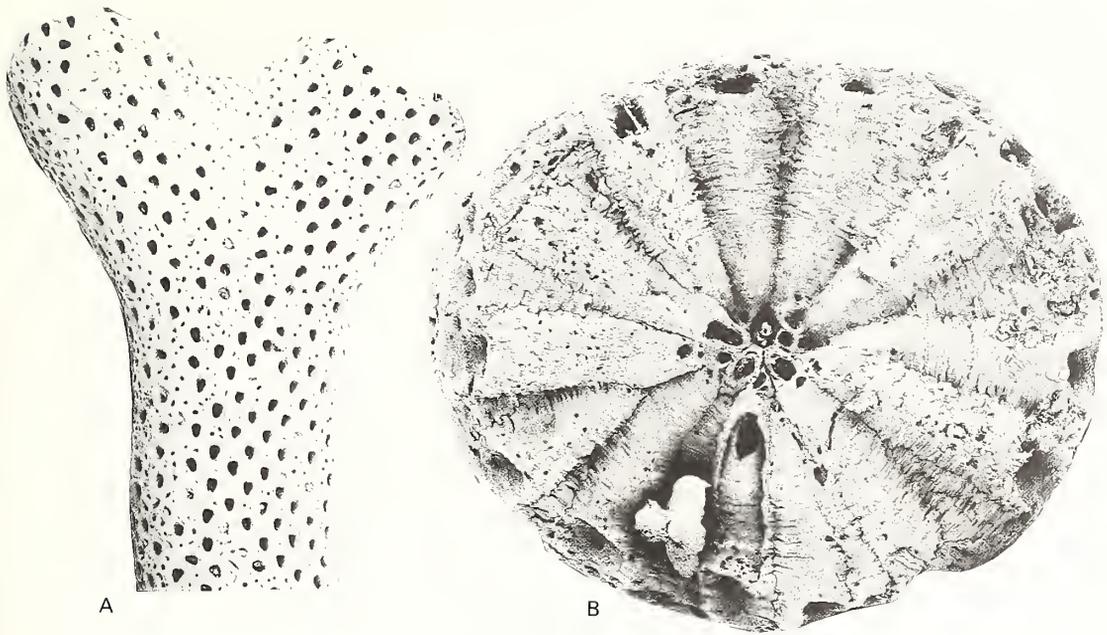
Autozooids tubular, elongate, club-shaped, bending through about 90° from the endozone into the exozone (Pl. 4, fig. 3). Frontal surface hexagonal or diamond-shaped (Pl. 4, fig. 1). Edges of zooids raised, bordered by a groove at the zooidal boundary. Opesia inverted pear-shaped, broadest close to the distal end. Cryptocyst minutely pustulose (Pl. 4, fig. 2), conspicuously funnel-shaped in erect zooids and smoothly continuous with the vertical walls, but more shelf-like in encrusting zooids comprising overgrowths. Closure plates and pore chambers not observed.

Kenozooids occasionally present singly between autozooids in erect branches but more commonly in aggregations at branch bifurcations (Text-fig. 4A), overgrowths, branch anastomoses and around the colony base. They are variable in frontal shape, and smaller than autozooids. Cryptocyst and opesia similar in morphology to those of autozooids.

Ovicells and avicularia lacking.

*Dimensions* (frontal dimensions in millimetres of ten autozooids from VH 10373).

	$\bar{x}$	SD	CV	range
length	0.39	0.020	5.1	0.35–0.42
width	0.33	0.022	6.5	0.29–0.36
opesia length	0.17	0.009	5.6	0.15–0.18
opesia width	0.14	0.009	6.2	0.12–0.15



TEXT-FIG. 4. *Chiplonkarina bretoni* sp. nov. Cenomanian, Essen, Germany; secondary electron micrographs of a coated specimen, VH 11650. A, bifurcating branch,  $\times 11$ . B, fractured distal end of branch showing narrow endozone surrounded by exozone with corrugated zooidal walls,  $\times 35$ .

*Remarks.* This species is characterized by inverted pear-shaped autozooidal opesia which are broadest near their distal ends. Lengths and widths of autozooids are larger than in *C. dimorphopora*, and these dimensions, as well as opesial length and width and branch diameter, are all less variable both within and between colonies than the equivalent dimensions in *C. dimorphopora*. Furthermore, there are generally fewer intercalated kenozooids in *C. bretoni* (although a specimen from the Cenomanian of Essen (Text-fig. 4) has a thicker branch and more abundant kenozooids than the French specimens), the autozooids frequently have a regular, close-packed quincuncial arrangement, and their apparent polarity is invariably parallel to branch length (Pl. 4, fig. 1).

Distal broadening of the opesia (Text-fig. 4A; Pl. 4, fig. 1) is unusual among cheilostomes where the opesia are generally broadest closer to their proximal margins. Correctly orientated branches of *C. bretoni* therefore give the appearance of being upside down, although the forks of branch bifurcations (Text-fig. 4A) and the direction of zooidal growth visible at fractured ends of branches dispel this impression. The unusual shape of the opesia raises the possibility that the zooids of *C. bretoni* may have reversed polarities relative to branch growth direction. For example, in the ascophoran cheilostome families Conescharellinidae and Batoporidae, the small rooted colonies have zooids whose orientation is reversed with respect to the direction of budding of the colony (Cook and Lagaaij 1976). The usual way of ascertaining zooid polarity in cheilostomes is from the positions of the orifice and ovicell, both of which are distal. Unfortunately, *C. bretoni* lacks ovicells, and there are no closure plates that might carry an impression of the operculum, indicating orifice position (cf. closure plates in other cheilostomes, e.g. Taylor 1988, pl. 43, fig. 3). Therefore, the vector of zooidal polarity cannot be confirmed.

*Distribution.* Lower Cenomanian: Notre Dame de Fresnaye and Villers-sur-Mer, Calvados, France; Essen and Mülheim, Westphalia, Germany.

## PHYLOGENETIC POSITION

*Identification of Chiplonkarina as a cheilostome*

Indian specimens here described as *Chiplonkarina dimorphopora* have been repeatedly misidentified in the past as cyclostomes, most commonly *Ceriopora* or *Ceriocava* (Pl. 3, fig. 6). Both of the latter genera are traditionally classified (e.g. Bassler 1953; Nye 1976) within the cyclostome suborder Cerioporina, which ranges from Jurassic to Recent. Cerioporines have long, club-shaped autozooids with a free-walled skeletal organization (i.e. without calcified exterior frontal walls) and fixed-walled gonozooids (i.e. with calcified exterior frontal walls). Colony-form is very often dendroid, comprising subcylindrical, bifurcating branches which have an axial endozone surrounded by an exozone. Skeletal walls are thin in the endozone but become thicker as the zooids bend through about 90° into the exozone. Small polymorphs (kenozooids) are very often distributed between autozooids on the colony surface, although they are rare to absent in the genus *Ceriocava*.

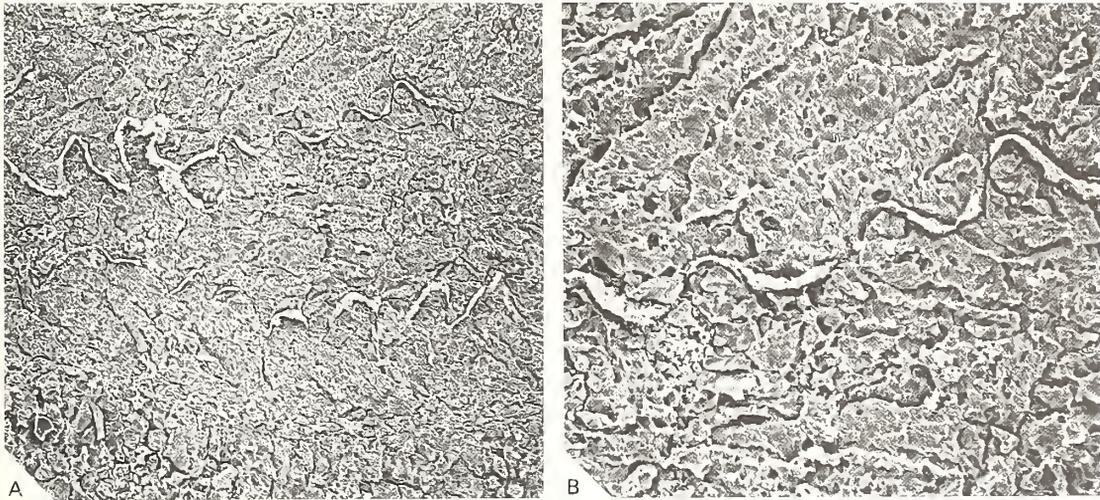
The meliceritid tubuliporine genus *Foricula* is another Cretaceous cyclostome with free-walled, club-shaped autozooids and a dendroid colony-form. *Foricula* has a superficial resemblance to *Chiplonkarina bretoni* but can be distinguished by its calcified opercula, an autapomorphy of the meliceritids (see Taylor 1994).

Except for the absence of gonozooids, which in any case have yet to be discovered in several cerioporines, *Chiplonkarina* has a basic morphology very like that of many cerioporine cyclostomes: autozooids are long, club-shaped and 'free-walled' (in the sense of lacking an exterior, gymnocystal frontal wall), kenozooids are interspersed between the autozooids, and colony branches are differentiated into a thin-walled endozone and thick-walled exozone. However, *Chiplonkarina* has several cheilostome features which show that its identification as a cerioporine, or indeed as a member of any suborder of cyclostomes, is incorrect.

1. *Double interzooidal wall structure.* The duplex structure of the interzooidal walls is the most striking and diagnostic feature demonstrating that *Chiplonkarina* belongs to the Cheilostomata. This is best seen in the exozone where the mid-line of the wall has a corrugated, sutured structure (Pl. 2, fig. 3). The folds are orientated transversely to wall growth direction, and are often associated with a brown coloration interpreted as a remnant of an organic cuticular layer (an intercalary cuticle, cf. Banta 1968). In polished and etched sections viewed using a high resolution SEM, this layer stands out in positive relief (Text-fig. 5), suggesting replacement of the organic material by a non-carbonate mineral. Specimens of *Chiplonkarina* sometimes fracture along the centre of the interzooidal walls where the cuticle was once situated. Such broken surfaces clearly show the corrugations (Pl. 4, fig. 4; Text-fig. 4B). The intercalary cuticle is also manifested on the colony surface by the slight grooves developed at zooidal boundaries (Pl. 3, figs 1–4). There is a clear contrast between the surface appearance of the double interzooidal walls of *Chiplonkarina* and the simple interzooidal walls of cerioporines where the zooidal boundary forms the sharp leading edge of the wall (Pl. 3, fig. 6).

In his detailed and thorough redescription of '*Ceriopora dimorphopora*', Guha (1980, p. 31) noted that '...the outer boundary of the zooecial wall is transversely and irregularly corrugated.... This corrugation makes the suture lines between adjacent tubes serrated.' It is evident from this statement that Guha had observed the position of the intercalary cuticle but did not consider its morphological or systematic significance.

In all known cyclostomes vertical, interzooidal walls are interior walls secreted from both sides by an investing epithelium. Such interior walls lack a cuticular layer, and the walls have a unified structure. Many cheilostomes, however, have interzooidal walls which comprise two exterior walls arranged back-to-back. The calcified component of the wall of one of the zooids is separated from that of the other zooid by an intercalary cuticle which may be folded into corrugations, particularly along zooidal boundaries where frontal thickening is occurring (Pl. 4, figs 5–6; see Banta 1977; Carson 1978), and also basally (Tavener-Smith and Williams 1972, figs 76–77). Duplex interzooidal walls of this type have not been described in cyclostomes; the closest analogue among cyclostomes



TEXT-FIG. 5. Secondary electron micrographs of polished and etched sections of *Chiplonkarina dimorphopora* showing permineralized remnants of the crenulated intercalary cuticle; BMNH BZ 2628; Cenomanian/Turonian, Bagh Group, Chirakhan Limestone Formation, Deola-Chirakhan Marl Member; quarry west of Badia, Madhya Pradesh, India. A, cuticular remnants within opposite walls of a longitudinally sectioned zooid; bryozoan wall calcite and diagenetic calcite filling the zooidal chamber have similar textures in this preparation and cannot be differentiated;  $\times 385$ . B, detail of cuticular remnant;  $\times 950$ .

occurs in the Pliocene species *Blumenbachium globosum* where the colony consists of many subcolonies which at their junctions have back-to-back basal exterior walls with a folded cuticular remnant (Balson and Taylor 1982).

2. *Wall microstructure.* In thin section, the walls of *Chiplonkarina* have a fibrous appearance, the fibres intersecting wall surfaces at angles of  $45^\circ$  or more (Pl. 2, fig. 3). Similar fibrous fabrics are relatively common in cheilostomes (e.g. Ristedt 1977) but are absent or rare in cyclostomes where, when present, fibres are aligned in the plane of the wall and contribute to the laminar appearance of the wall in section (see Boardman *et al.* 1992, fig. 42a–b). Cerioporine cyclostomes have laminated wall microstructures, normally with the laminae parallel or subparallel to the wall surface, although higher intersection angles have been reported from some cerioporines (see Nye 1976, fig. 1E). Therefore, wall microstructure supports assignment of *Chiplonkarina* to the cheilostomes, and not to the cerioporine cyclostomes, but it should be stressed that this evidence must be seen in the light of our limited knowledge of skeletal microstructures and ultrastructures in bryozoans, especially cyclostomes.

3. *Pores in skeletal walls.* Interzooidal walls of *Chiplonkarina* are pierced by pores which are parallel-sided, canal-like structures often orientated obliquely to the wall surface (Pl. 1, fig. 2). In longitudinal sections of interzooidal walls between autozooids and kenozooids, pores may cross-cut the wall fibres approximately at right-angles, 'migrating' proximally with wall thickening. Lines of sectioned pores can then give a chevron appearance.

Both cerioporine cyclostomes and cheilostomes develop pores in interzooidal walls. In cerioporines and other cyclostomes, these pores are characteristically orientated at right-angles to wall surfaces, and generally decrease in diameter towards the centre of the wall where radial spines (seldom seen in fossils) often partly or completely occlude the pore (see Brood 1972; Boardman *et al.* 1992; Taylor and Jones 1993). A greater diversity of pore types occurs among cheilostomes, some

forming distinct pore chambers (or dietellae), and some partly occluded by rosette-plates (or septulae) perforated by many small holes (e.g. Ryland 1970, p. 87). Parallel-sided, canal-like pores are present in the thick interzooidal walls of the cheilostome *Herpetopora* (see Taylor 1988). The pores in *Chiplonkarina* are unlike those of known cerioporine cyclostomes but resemble the pores present in this Cretaceous cheilostome genus.

4. *Colony base and lamellar overgrowths*. The encrusting colony base in *Chiplonkarina* typically extends over a wide expanse of substrate. Zooids in the colony base differ from zooids in erect colony branches by being shorter and more box-shaped. Their endozone is poorly defined and short, comprising thin interzooidal walls which curve upwards for about 0.05 mm from the basal wall before giving way to the thick-walled exozone with interzooidal walls perpendicular to the basal wall. Lamellar overgrowths frequently show a similar structure; i.e. the zooids are short and have an abbreviated endozone. Growing edges of colony bases and overgrowths often have a ragged or stepped appearance. There is no fringing basal lamina.

Cerioporines, like most other multiserial stenolaemates, have colony bases and overgrowths with relatively smooth growing edges. A typically broad fringe of basal wall (or lamina) extends distally from the budding zone, and several ontogenetic generations of stacked new buds may be visible at this common bud.

Lamellar colony bases and overgrowths in cheilostomes are variable in appearance. A common condition, particularly among primitive and/or Cretaceous taxa, is for the growing edge to lack a fringing basal wall and to have an irregular outline as a result of 'intrazooidal budding' whereby new buds are formed discontinuously along the growing edge (see Lidgard 1985).

The irregular, lamina-free growing edges of the colony base and overgrowths in *Chiplonkarina* are more similar to cheilostomes with intrazooidal budding than to any known cerioporine cyclostomes. Furthermore, newly-formed autozooids in overgrowths may have a typically 'membraniporimorph' morphology of the type known in many malacostegan and pseudomalacostegan anascan cheilostomes.

Unfortunately, details of the early astogeny of *Chiplonkarina* are unknown. The morphology of the ancestrula in cerioporines and cheilostomes is very different and would provide important supportive evidence for the ordinal affinities of *Chiplonkarina*. In cerioporines and other cyclostomes, the ancestrula comprises a proximal, bulb-shaped protoecium leading to a distal tube terminated by the aperture. Cheilostomes lack a protoecium, and in most cases have ancestrulae essentially similar in shape to the later zooids in the colony.

5. '*Cryptocyst*'. No true cryptocyst, in the sense of a platform-like interior wall, is present in *Chiplonkarina*. However, the inner surfaces of the two back-to-back exterior walls forming the interzooidal walls constitute a 'cryptocystal rim' visible around the edges of the zooids when seen in frontal view. This cryptocystal rim is densely pustulose (Pl. 3, fig. 4), the gaps between the individual pustules being not much wider than the pustules themselves. Cryptocysts of a similar morphology are widespread among anascan cheilostomes, for example in *Conopeum seurati* (Canu) and *Akatopora circumsaepa* (Uttley) illustrated by Gordon (1986, pl. 1, fig. c and pl. 7, fig. c respectively), and in *Antropora tineta* (Hastings) depicted by Lidgard (1985, pl. 31, figs 2-5). Although the inner wall surfaces of many cyclostomes bear a variety of pustules and spinous processes (see Farmer 1979), these seldom reach the density found in *Chiplonkarina* and appear to be sparse in all cerioporine cyclostomes.

6. *Kenozooids*. Both cheilostomes and cerioporine cyclostomes may develop space-filling kenozooids between the autozooids. These can be of a similar surface morphology in the two groups with the exception that the kenozooids of cerioporines invariably have almost straight edges whereas those of cheilostomes can have concave edges (Pl. 3, fig. 5). Kenozooids with concave edges, resulting from indentation of their outline shapes by neighbouring autozooids, are a common feature in *Chiplonkarina* (Pl. 3, figs 1-4).

These features taken together permit confident assignment of *Chiplonkarina* to the Cheilostomata, and show that the cyclostome-like aspects of its morphology are homoplasies resulting from convergent evolution. Once accepted as a cheilostome, its systematic position within this order must be sought.

#### *Affinities of Chiplonkarina within the Cheilostomata*

Cheilostome bryozoans divide into two morphological grades: anascans and ascophorans. The latter are characterized by zooids with strongly calcified frontal shields, a feature clearly lacking in *Chiplonkarina* which is therefore of anascan grade. Among the anascans, the Malacostega are a primitive paraphyletic grouping of taxa with planktotrophic larvae and lacking the ovicells present in most of the remaining anascans for larval brooding purposes (Taylor 1987). In addition to the lack of ovicells, malacostegans typically have autozooids with simple skeletal morphologies and rarely possess the avicularian polymorphs found in so many other anascans. Ovicells are absent in *Chiplonkarina*, autozooids are relatively simple in form and avicularia wanting. Consequently, *Chiplonkarina* has a malacostegan morphological grade and can be provisionally assigned to the Family Electridae, one of the two recognized malacostegan families. Electrids first appear in the Upper Jurassic and are well-represented in the Cretaceous (e.g. Taylor 1986; Taylor and Cuffey 1992). It should be noted that the Electridae is itself likely to be paraphyletic but that redistribution of the constituent genera among monophyletic families awaits phylogenetic analysis.

*Chiplonkarina* seems likely to be closely related to *Heteroconopenum* (see Voigt 1983; Pl. 3, fig. 5) and to an undescribed cheilostome from the mid-Cretaceous of southern England (mentioned by Larwood 1976, p. 542 as a cheilostome encrusting a ramifying cyclostome colony). Both of these electrids have erect dendroid colonies and autozooids with similar frontal morphologies to those of *Chiplonkarina*.

A close relationship between *Chiplonkarina* and the Upper Cretaceous genus *Inversaria*, although sharing a similar colony-form, can be discounted. *Inversaria* possesses conventional anascan avicularia (Voigt and Williams 1973, pl. 1, fig. 2, pl. 3, fig. 5), suggesting that it is not a malacostegan, although the absence of ovicells in the genus is problematical and may point to an alternative mode of larval brooding. The presence of horned calcified opercula (Voigt 1974) is an autapomorphy of *Inversaria*, and this genus also differs from *Chiplonkarina* in the orientation of the corrugations in the interzooidal walls marking the position of the intercalary cuticle: these corrugations are parallel to wall growth direction in *Inversaria* (Voigt and Williams 1973, pl. 2, figs 2-3) but are transverse to growth direction in *Chiplonkarina* (Pl. 4, fig. 4; Text-fig. 4B).

## DISCUSSION

### *Colony growth*

Bryozoan colonies grow by budding new zooids and/or by lengthening existing zooids. In most cheilostomes, but not in *Chiplonkarina*, zooids are box-shaped, rapidly attain their 'mature' size and do not increase in length during later ontogeny. Therefore, colony growth depends principally on the budding of new zooids, including new zooids budded on top of one another forming multi-layered colonies of increasing thickness. In addition to zooidal budding, the lengthening of existing zooids plays an important role in colony growth in many stenolaemates, as it did in *Chiplonkarina*. The tubular zooids of *Chiplonkarina* continued to grow during their ontogenies and allowed the dendroid colony branches to become considerably thickened. Similar thickening of dendroid colony branches in cheilostome bryozoans is normally accomplished by the frontal budding of new zooids (notably in various 'celleporids', e.g. Voigt 1970), not by the distal growth of existing zooids.

Growth of dendroid (or ramose) branching colonies in bryozoans and other animals necessitates that distal growth rate decreases away from the branch axis (e.g. Key 1990); uniform distal growth rates across the colony surface would produce a hemispherical form. As in dendroid stenolaemates,

*Chiplonkarina* had maximal budding rates and linear growth rates in the axial endozone which forms the distal growing tips of the branches. However, budding was not restricted to the endozone. The substantial enlargement of branch surface area with increasing diameter demanded that zooidal budding continued into the exozone because this increase could not be entirely accounted for by wall thickening, intercalation of kenozooids or enlargement of autozooidal surface area.

Details of the mode of zooidal budding in erect branches of *Chiplonkarina* are unclear. Sections generally reveal new buds first becoming visible at the foci of triple junctions between walls of existing zooids. No mother-daughter relationship is apparent and the pattern of budding corresponds to the interzoecial category defined for dendroid stenolaemates by McKinney (1975). New buds are presumably linked via interzooidal pores, at an early stage in development, to the mature zooids in the colony, but this is difficult to ascertain from sections. At least some of the putative kenozooids intercalated between autozooids in the exozone may be immature autozooids. Careful serial sectioning would be needed to determine whether such 'kenozooids' do indeed develop into autozooids with growth.

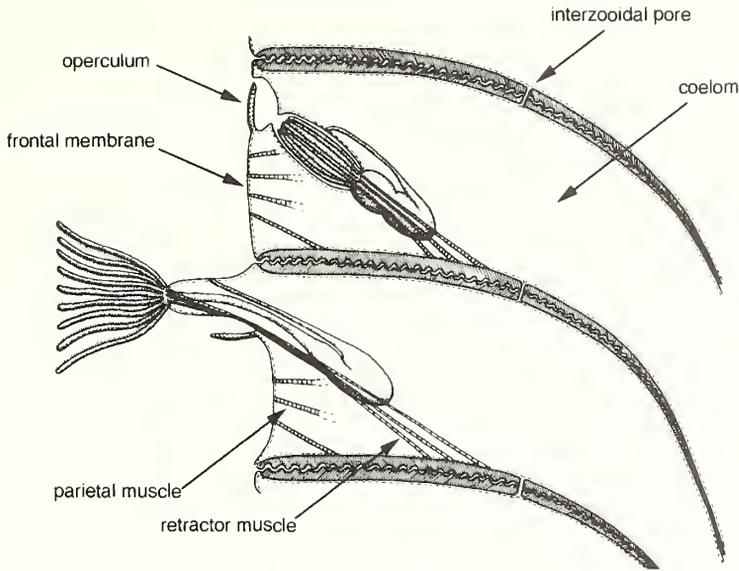
Continued distal (vertical) growth of individual zooids is possible in *Chiplonkarina* because the zooids are open-ended and not constricted by a frontal wall. The absence of a frontal wall permits similar vertical growth in the Recent anascan *Antropora tinca* (Hastings), although to a much lesser degree (Lidgard 1985, p. 278). The gymnocystal or cryptocystal frontal wall developed in most cheilostomes imposes a limit on the upward growth of the zooidal chamber. The frontal wall itself can be thickened, as in many erect ascophorans in which thickened proximal zooids reinforce the colony base (e.g. Cheetham 1971), but the zooidal chamber does not lengthen (excepting peristomial prolongation around the orifice). It seems possible, therefore, that the presence of frontal walls in cheilostomes may have acted as a constraint prohibiting the evolution of more clades with the stenolaemate-like growth patterns found in *Chiplonkarina* and *Inversaria*. Only taxa with negligible frontal walls had the 'preadaptation' necessary to evolve stenolaemate-like dendroid colonies.

With distal growth of the zooidal skeleton, the polypide and associated musculature must also have migrated distally. It is not known whether this migration occurred episodically, perhaps linked to the cycles of polypide degeneration-regeneration which characterizes bryozoans, or more gradually. The skeletal walls show no evidence of periodic changes in thickness suggestive of episodic growth.

#### *Functional morphology*

(a) *Feeding currents.* Branch diameter in *Chiplonkarina dimorphopora* is extremely variable. McKinney (1986) looked at between-species variability in bryozoans with dendroid erect branches (his radial category) and found that branch diameters in species with maculae were significantly greater than in species lacking maculae. Maculae are surface disruptions representing chimneys of excurrent water flow which appear to be necessary in bryozoans with broad surfaces where colony margins alone are insufficient to vent all of the filtered water. McKinney identified a polarization between species with branches less than 2 mm in diameter which are non-maculate, and those with branches more than 2 mm in diameter which are maculate in all stenolaemates and in many cheilostomes. In *Chiplonkarina dimorphopora*, the large, presumably age-related variation in branch diameter means that the species is unusual in spanning the division between these two size categories. Branches of *C. dimorphopora* have a modal diameter of between 1 and 1.5 mm, but range from 0.7 to 11 mm. Maculae cannot be identified in either thin- or thick-branched specimens. It seems likely that thick branches of *C. dimorphopora* would have developed excurrent chimneys with no skeletal expression and perhaps transitory existence. Such chimneys occur in many living cheilostomes (see McKinney 1990 for a review of feeding in bryozoans).

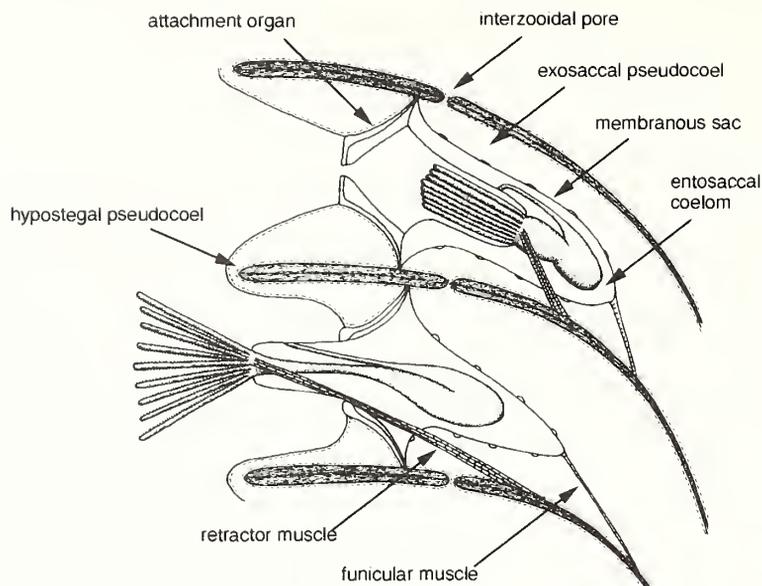
(b) *Soft tissue distribution.* Text-figure 6 shows a reconstruction of soft tissue distribution in *Chiplonkarina* and can be compared with a dendroid cerioporine (or similar free-walled stenolaemate) shown in Text-figure 7. There are two main areas of contrast: the interzooidal walls, and the mechanism of tentacle protrusion.



TEXT-FIG. 6. Reconstruction of soft part morphology in *Chiplonkarina*. Two zooids are shown, one with the tentacle crown expanded and the other retracted.

As noted above, the interzooidal walls of *Chiplonkarina* are duplex structures comprising back-to-back exterior walls including a cuticular layer at the centre of the wall. The two halves of the wall were secreted by discrete epithelia belonging to adjacent zooids. No soft tissue continuity would have existed over the growing ends of the walls (cf. soft tissue connections through pores in the walls which can be inferred). Yet it is clear that growth rates were similar for both sides of the wall. Indeed, the suture-like intergrowth of the medial cuticle implies a close coordination between the neighbouring zooids responsible for wall growth. Interzooidal walls of cerioporines are interior walls lacking a cuticle and secreted by an epithelium which wraps over the ends of the walls and is continuous from one zooid to the next. A hypostegal pseudocoel also links adjacent zooids over wall ends, enclosed by an outer epithelium and cuticle. This more 'integrated' condition presumably does not pose the same potential problems of coordination of growth rates, or of a median plane of weakness formed by the organic cuticle, both of which would have pertained in *Chiplonkarina*.

Anascan cheilostomes, like *Chiplonkarina*, and cyclostomes employ fundamentally different methods for eversion of the tentacles (see Taylor 1981). In both groups, this is accomplished hydrostatically by the contraction of muscles pulling on membranes and forcing coelomic/pseudocoelomic fluids into the tentacle sheath, which then everts and pushes the tentacles out through the orifice. In anascans, the muscles involved are parietal muscles attached to the flexible frontal membrane, which would have occupied most of the frontal surface in zooids of *Chiplonkarina*, and anchored to the lateral or basal walls of the zooid. Two sets of muscles are apparently responsible for tentacle protrusion in cyclostomes: atrial dilator muscles which widen the atrium and force exosaccal pseudocoelomic fluid proximally, and annular muscles of the membranous sac which squeeze the entosaccal coelom. Whereas the typically box-shaped anascan zooid provides a suitably large surface area of depressible frontal membrane, the typically tubular cyclostome zooid furnishes a large surface area of compressible membranous sac. Analogy with living anascans leads to the conclusion that the polypide of *Chiplonkarina* would have been positioned at a shallower depth (i.e. more distally) within the tubular zooidal skeleton than are the polypides of cerioporine cyclostomes. A greater proportion of the older, proximal parts of the zooidal chambers would have been devoid of actively functional soft parts but were presumably still



TEXT-FIG. 7. Reconstruction of soft part morphology in a cerioporine cyclostome with tubular zooids similar in shape to those of *Chiplonkarina*. Two zooids are shown, one with the tentacle crown expanded and the other retracted. Compared with *Chiplonkarina* (Text-fig. 6) note deeper, more proximal location of the polypide within the tubular zooidal skeleton and lesser elevation of the expanded tentacle crown.

filled with coelom and lined by epithelium. Although a few *Chiplonkarina* zooids have calcified basal diaphragms, serving to reduce the length of the living chamber, these are lacking in most zooids, although the existence of non-calcified, membranous diaphragms cannot be ruled out. It is well-known that cheilostome tentacle crowns are characteristically protruded to a greater degree than those of cyclostomes: in cheilostomes, the tentacle sheath may be everted outside the orifice, held on top of the introvert, whereas in cyclostomes the level of the mouth seldom extends beyond the skeletal aperture (cf. McKinney 1988). Therefore, *Chiplonkarina* zooids can be inferred to have had the ability to protrude their tentacles further above the colony surface than cerioporine zooids occupying skeletons of a similar tubular shape.

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# A NEW SPECIES OF CHIMAEROID FISH FROM THE UPPER CRETACEOUS OF THE SARATOV REGION, RUSSIA

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**ABSTRACT.** *Amylodon karamysh* sp. nov. (Chondrichthyes, Holocephali, Chimaeridae) is described from the Early Campanian (Late Cretaceous) of the Saratov Region, Russia. It is based on a single mandibular plate with a relatively short outer margin and four small median tritons. The morphology of the mandibular plate of *A. karamysh* appears to have evolved from the condition in the chimaerid *Ischyodus*, which implies that the shearing-type dentitions of *Amylodon* and *Rhinochimaera* were probably of independent origin.

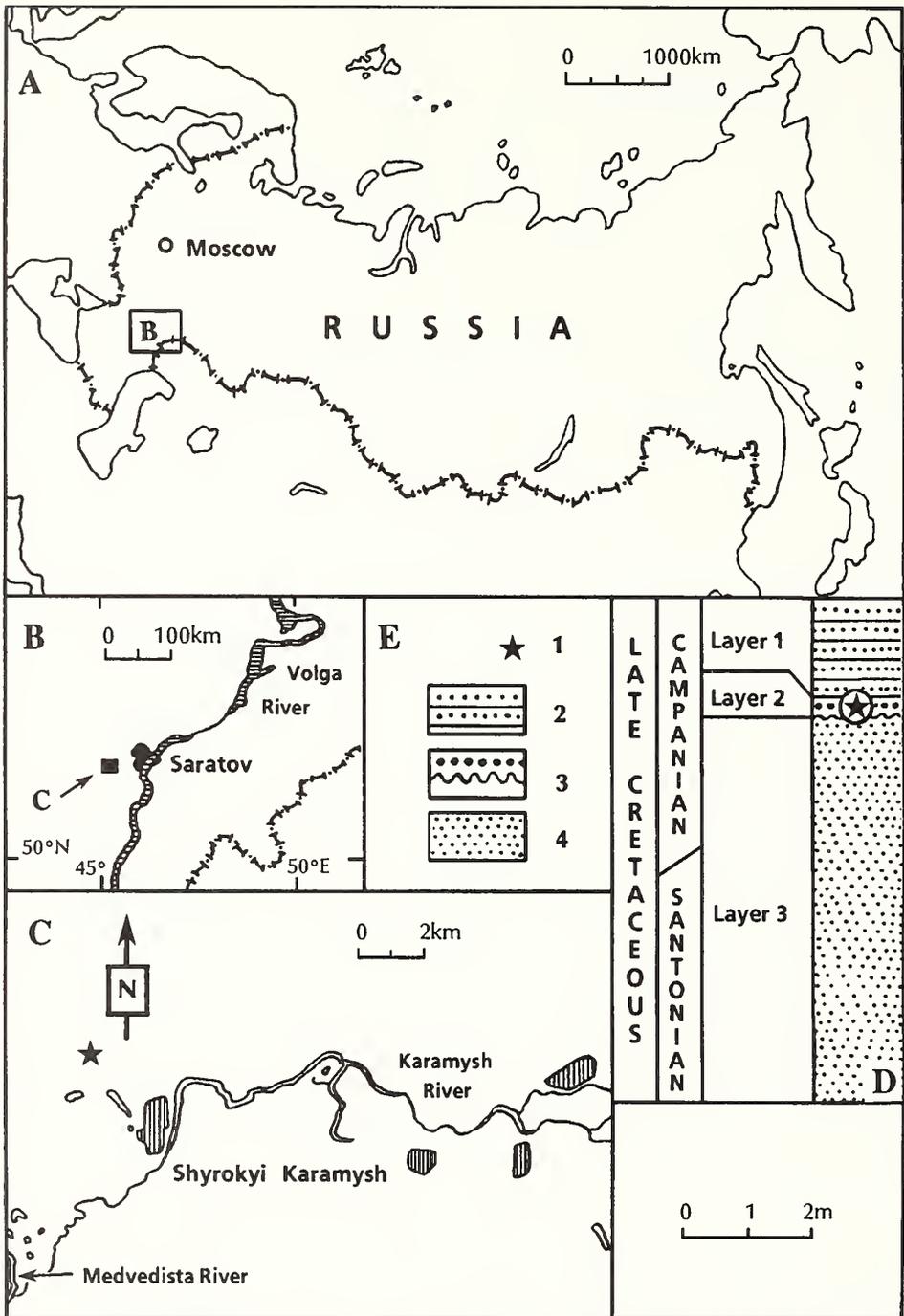
CHIMAEROID fish are a compact group of holocephalan chondrichthyans which now occur in the deep waters of all oceans. However, in the Mesozoic and early Cenozoic, they were widespread and abundant in continental seas and are represented in the fossil record most commonly by their dental plates. Chimaeroids have three pairs of dental plates: vomerine and palatine plates in the upper jaws, and mandibular plates in the lower jaws. Each dental plate consists of a mass of acellular bone in which are set several structures composed of pleromin – the dental tritons. The tritons exposed along the occlusal margin are usually composed of laminated plates of massive pleromin, while those on the lingual surface tend to be elongate parallel columns of vascular pleromin. These vascular tritons occupy most of the lingual surfaces in primitive chimaeroids (*Ischyodus*, *Edaphodon*, *Elasmodus*) and are adapted for crushing. In more derived forms, however, such as *Elasmodectes*, *Amylodon* and *Rhinochimaera*, the vascular lingual tritons are greatly reduced in size or are absent, whereas the occlusal tritons may become more prominent. This type of dentition is associated with a shearing bite. In the following account, the terminology and orientation of chimaeroid dental plates follows the usage of Ward and Grande (1991).

Over the last century, our knowledge of Cretaceous chimaeroids from the territory of the former Russian Empire and USSR has increased greatly. During the nineteenth century, only one genus (*Ischyodus*) was reported from the Cretaceous of Russia (Rogovich 1860; Sinzov 1872). In the most recent published review, seven chimaeroid genera were recorded in Cretaceous vertebrate faunas of the USSR by Glickman *et al.* (1987). These comprised *Ischyodus*, *Edaphodon*, *Elasmodectes*, *Ganodus*, *Chimaera*, a probable callorhynchid (*Callorhynchus* or a new genus), and a rhinochimaerid (*Rhinochimaera*, determined from an egg-capsule, plus a dentition from an undescribed, possibly new, genus). A further chimaeroid genus, *Amylodon*, is reported here for the first time from the Cretaceous of Russia. This genus was known previously only from the Palaeogene of Belgium and England.

## GEOLOGICAL BACKGROUND

The specimen described here comes from the Campanian (Upper Cretaceous) deposits near the village of Shyrokyi Karamysh (51° 21' 3" N, 45° 2' 7" E) in the Saratov Region (Text-fig. 1). The locality is a poor exposure in a ravine. It consists of three beds (Text-fig. 1).

(1) A coarse quartz glauconitic sand, about 6 m thick, containing the bivalve *Syniclonema laeve* (Nilsson), a shark coprolite and teeth and bone fragments of plesiosaurs.



TEXT-FIG. 1. Geographical maps and stratigraphical section of the Karamysh locality. A, map of Russia giving general position of the Saratov Region. B-C, progressive enlargements specifying the position of the locality within the Saratov Region. D, section at the locality. E, key to D. 1, productive horizon; 2, sandstone; 3, phosphatic conglomerate; 4, sand.

(2) A phosphatic conglomerate, up to 400 mm thick, with the bivalves *Monticola* cf. *vesicularis* (Lamarck), the holotype of *Amylodon karamysh* sp. nov., a fragment of a long beak and a mandibular plate of *Edaphodon* sp., several dental plates of *Ischyodus* cf. *bifurcatus* Case, numerous coprolites and shark teeth including *Cretolamna borealis* (Priem), *Pseudoisurus arcuatus* (Woodward), *Eostriatolamia* ex gr. *subulata* (Agassiz), *Pseudocorax laevis* (Leriche), teeth of the teleost fish family Enchodontidae, and the remains of polycotyloid and elasmosaurid plesiosaurs, and mosasaurs.

(3) A quartz glauconitic sandstone, about 1.5 m thick, with fragments of belemnite rostra. In a neighbouring exposure, also near Shyrokyi Karamysh, Bed 3 yields *Belemnitella mucronata* (Schlotheim), the abundant species in the lower part of the Upper Campanian (Bondareva and Morosov 1970). The molluscs from Bed 2 suggest a late Early Campanian age (E. M. Pervushov, pers. comm.). The shark fauna from Bed 2 is also characteristic of the Early Campanian, the same species occurring with *Belemnitella mucronata* in the Early Campanian phosphatic chalks in the Paris Basin (Priem 1897).

### SYSTEMATIC PALAEOLOGY

Class HOLOCEPHALI Bonaparte, 1832  
Order CHIMAERIFORMES Buen, 1926  
Suborder CHIMAEROIDEI Patterson, 1965  
Family CHIMAERIDAE Rafinesque, 1815  
Genus AMYLODON Storms, 1895

*Type species.* *Amylodon delheidi* Storms, 1895, from the Rupelian of Belgium.

*Diagnosis.* Dentition of shearing type. Tritors on the dental plates are very reduced in number and size. On the mandibular dental plate, the median tritor is represented by a few short stripes of vascular pleromin or is absent. The outer margin of the mandibular dental plate is straight.

*Amylodon karamysh* sp. nov.

Text-figure 2

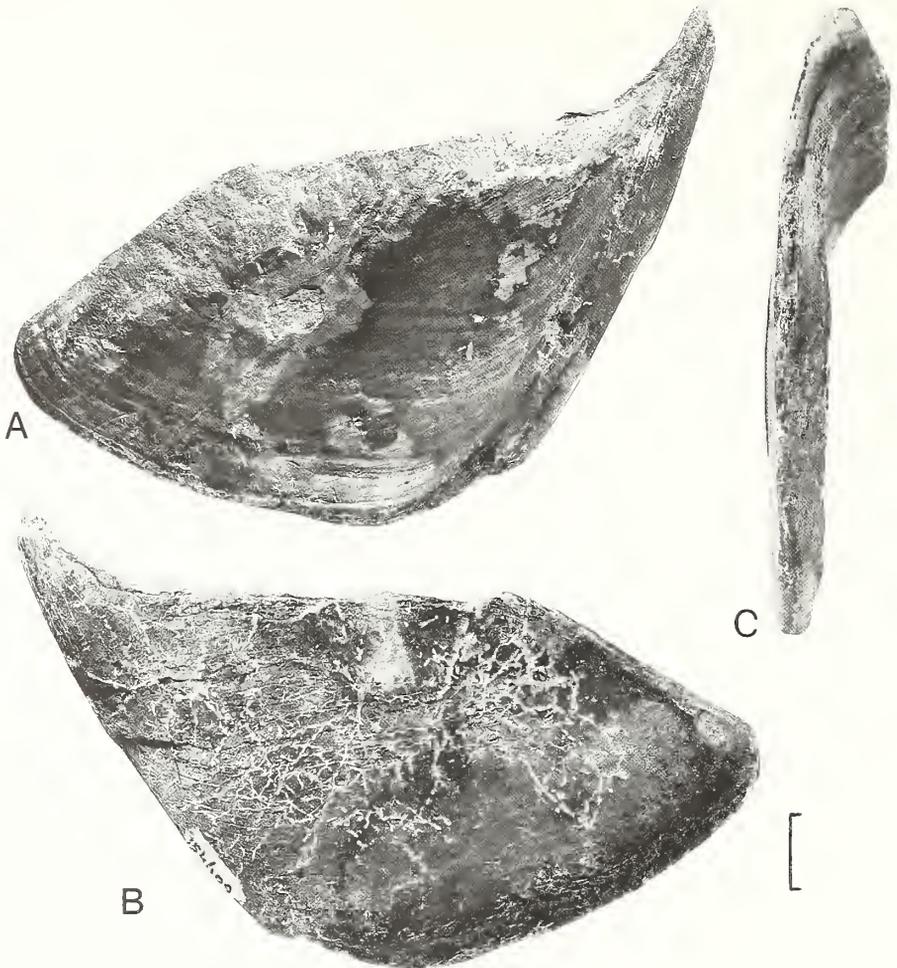
*Derivation of name.* The species is named after the River Karamysh, close to the type locality.

*Holotype.* N 154/109, a left mandibular dental plate, in the collections of the Department of Palaeontology, Saratov State University.

*Locality and horizon.* Shyrokyi Karamysh village, Lysogorsk District, Saratov Region, Russia; latest Early Campanian, Upper Cretaceous.

*Diagnosis.* Large *Amylodon* with mandibular dental plate having a relatively short outer margin (63 per cent. of the total oblique length) and four minute longitudinal median tritors.

*Description.* The mandibular plate (Text-fig. 2) has a distinct beak and wide symphysis. As well as the four median tritors, there is one short stick-like anterior inner tritor on the tip of the beak and another similar tritor on the posterior margin of the plate near the end of the outer margin. The outer margin is somewhat damaged and, consequently, the structure of the outer tritors is unknown. Below the outer margin, the mandibular plate shows a slight thickening which forms a band along the margin. The oblique length of the mandibular plate (from beak tip to caudal extremity) is 104 mm. The angle between posterior and symphyseal margins of the mandibular plate is approximately 28°. The thickness of the dental plate is consistently 7–8 mm throughout its length.



TEXT-FIG. 2. *Amylodon karamysh* sp. nov. SSU N.154/104, holotype left mandibular plate; Lower Campanian, Upper Cretaceous; Shyrokyi Karamysh, Saratov Region, Russia. A, medial; B, occlusal; C, lateral views. Scale bar represents 10 mm.

*Systematic position.* The mandibular dental plate is assigned to the genus *Amylodon* because it has extremely reduced tritons (*contra Ischyodus, Edaphodon, Elasmodus, Pachymylus, Brachymylus, Callorhynchus, Chimaera* and *Harriota*), a straight outer margin (*contra Elasmodectes*), and an upwardly elevated beak (*contra Rhinochimaera*).

*A. karamysh* differs from the type species, *A. delheidi* Storms, 1895 from the Oligocene (Rupelian) of Belgium, in that the former possesses four small median tritons on the mandibular plate, together with a short outer margin. Mandibular dental plates have not been described for *A. eocenica* Woodward and White, 1930, and *A. venablesae* Casier, 1966, from the Eocene (Ypresian) of England (Woodward and White 1930; Ward 1973). However, they resemble those of *A. delheidi* in being mesiodistally narrower; larger specimens have a rounded post-occlusal/basal margin similar to that of *A. karamysh*; and there is no median tritor (David Ward, pers. comm.). A Bartonian mandibular plate assigned to *Amylodon eocenica* by Woodward and White (1930), but removed from that species by Ward (1973) and referred to as '*Amylodon* sp.', differs from the above in possessing a large undivided median tritor and in the shape and position of the anterior inner tritor.

## DISCUSSION

*Amylodon delheidi* was established on the basis of a single mandibular plate of shearing type without tritons on the occlusal surface (Storms 1895, pl. 4, figs 11–12). Woodward and White (1930) considered their Early Tertiary 'Chimaera' *eocenica* to be an intermediate form between Mesozoic chimaeroids with crushing dentitions and the derived Oligocene *Amylodon* and Recent *Rhinochimaera* with purely shearing dentition. The two genera have been assumed to be closely related and both Obruchev (1964) and Ward (1973) have classified *Amylodon* as a rhinochimaeroid. However, the dentition of the Recent *Rhinochimaera pacifica* Mitsukuri (Garman 1904, pl. 8, figs 1–2; Tadashi and Garrick 1979, fig. 1b) differs from that of *Amylodon*. In particular, the beak of the mandibular plate of *Rhinochimaera* is curved downwards and inwards below the vomerine plates, or is straight (Garman 1904, p. 225), whereas it is elevated upwards in *Amylodon*. This suggests that the shearing dentition was derived independently in *Amylodon* and *Rhinochimaera*. *Amylodon* has the same distribution of tritons on the dental plates as the Cretaceous *Ischyodus* and may have evolved from that genus.

There is a trend of increase in the relative length of the outer margin of the mandibular dental plate in *Amylodon* species from the Cretaceous to the Oligocene. In *A. karamysh* (Campanian), the outer margin is 63 per cent. of the oblique length of the mandibular plate; in Ward's *Amylodon* sp. (Bartonian) it is 74 per cent., and in *A. delheidi* (Rupelian) it is 77 per cent. This trend presumably reflects increasing shearing capability in the dentition of this phylogenetic lineage.

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# THE RHYNCHOSAUR *HOWESIA BROWNI* FROM THE LOWER TRIASSIC OF SOUTH AFRICA

by DAVID W. DILKES

**ABSTRACT.** *Howesia browni* is a rhynchosaur (Reptilia: Archosauromorpha) known from a single locality in the *Cynognathus* Assemblage Zone (Beaufort Group: Burgersdorp Formation) near the town of Aliwal North, Eastern Cape Province, South Africa. *Howesia* is diagnosed by the following autapomorphies: (1) multiple rows of small, conical teeth on medially expanded maxillaries that lack longitudinal, occlusal grooves; (2) multiple rows of small, conical teeth on dentaries; (3) a broad ventral process of the squamosal that does not extend below the middle of the lower temporal fenestra; (4) a medial shelf on the quadrate ramus of the pterygoid; (5) contact between the ectopterygoid and jugal reduced to less than half of the distal expansion of the ectopterygoid; (6) deep pockets on the neural arches of the posterior dorsals and sacrals; and (7) posteriorly inclined and tall proximal caudal neural spines. A preliminary phylogenetic analysis demonstrates that Rhynchosauria can be rediagnosed by seven synapomorphies: (1) a beak-shaped premaxilla; (2) a single, median external naris; (3) contact between the premaxilla and prefrontal; (4) depression on the dorsal surface of the frontal; (5) depression on the dorsal surface of the postfrontal; (6) fused parietals; and (7) flat occlusion. *Howesia* is the probable sister taxon to the clade of *Rhynchosaurus*, *Stenaulorhynchus*, *Scaphonyx* and *Hyperodapedon*.

RHYNCHOSAURS are a clade of herbivorous diapsid reptiles of the Triassic Period (245–208 Ma) ranging in bodily length from less than 1 m to approximately 2 m. Rhynchosaur fossils have been found on every major land mass with the exceptions of Antarctica and Australasia. Their abundance in the Middle and Late Triassic indicates that they were a common component of many faunas (Benton 1983a; Benton and Walker 1985; Holtz and Barberena 1994). Detailed descriptions (e.g. Huene 1938; Chatterjee 1974; Benton 1983b, 1990) of the Middle and Late Triassic genera have provided significant data for phylogenetic analyses (e.g. Gauthier 1984; Benton 1985; Evans 1988; Laurin 1991) of Permian and Triassic diapsids. The diet of rhynchosaurs has been hypothesized to be plants (Huene 1939a; Sill 1971; Benton 1983b, 1984) or molluscs (Chatterjee 1974, 1980), but the morphology of rhynchosaurian teeth is different from that of extant vertebrates that eat molluscs, and the unique precision-shear bite of rhynchosaurs is an unlikely method for breaking apart hard-shelled invertebrates (Benton 1983b, 1984). The long, beak-shaped premaxillae probably gathered a variety of plants such as seed-ferns, conifers, cycads, ginkgos, and ferns, which were cut, but not masticated, by the powerful jaws. Roots and tubers were perhaps dug using the hind limb and its large claws.

Far less is known about Early Triassic rhynchosaurs. Three species, *Howesia browni* Broom, 1905, *Mesosuchms browni* Watson, 1912a, and *Noteosuchms colletti* (Watson, 1912b), that are restricted presently to the Middle and Upper Beaufort Group of South Africa, furnish the only information on the early stages of rhynchosaurian phylogeny (Broom 1906, 1913, 1925; Houghton 1921, 1924; Malan 1963; Carroll 1976). The importance of these genera lies in their basal position within Rhynchosauria according to stratophenetic phylogenies (Chatterjee 1969, 1974, 1980) and cladistic analyses (Benton 1987, 1990). Incorporation of basal taxa of a group (plesiomorphic sister taxa) in a cladistic analysis can alter tree topologies and ideas of character evolution, which will in turn affect phylogenetically dependent hypotheses (Donoghue *et al.* 1989). Cladistic studies of diapsids (e.g. Benton 1985; Evans 1988; Laurin 1991) have supported prior arguments (Hughes 1968; Carroll 1976; Brinkman 1981; Benton 1983b) that rhynchosaurs should not be grouped with

rhynchocephalian sphenodontids such as the extant *Sphenodon* in Lepidosauria, as believed traditionally (e.g. Nopsca 1928; Romer 1956; Kuhn 1969). Instead, these studies agree that rhynchosaurs are early members of Archosauromorpha, a clade whose extant members are crocodiles and birds. Thus, data from the South African rhynchosaurs have the potential to modify the composition and diagnosis of Rhynchosauria and alter our conception of the interrelationships of basal archosauromorphs.

Beyond the initial cursory descriptions by Broom (1905, 1906), only selected aspects of the anatomy of *Howesia browni* have appeared in the literature (Haughton 1924; Malan 1963; Carroll 1976). Additional preparation of the three known specimens of *Howesia* has revealed considerable new data, especially of the skull, allowing for the first time a detailed comparison with the other two South African rhynchosaurs and other archosauromorphs. Comparisons with *Mesosuchus* are based upon personal observations of all known material that will be the subject of a forthcoming publication. The Early Triassic rhynchosaur *Howesia browni* is redescribed here, and a preliminary phylogenetic analysis is presented for Rhynchosauria.

Institutional abbreviations are: SAM, South African Museum, Cape Town; BP/1/, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa.

### SYSTEMATIC PALAEONTOLOGY

REPTILIA Laurenti, 1768

DIAPSIDA Osborn, 1903

RHYNCHOSAURIA Osborn, 1903

Genus *HOWESIA* Broom, 1905

*Type species.* *Howesia browni* Broom, 1905

*Diagnosis.* As for the only species.

*Howesia browni* Broom, 1905

Text-figures 1–7

*Revised diagnosis.* Small (total length less than 1 m) rhynchosaurian diapsid that is distinguished from all other rhynchosaurs by the following autapomorphic characters: multiple rows of small, conical teeth with ankylothecondont implantation in medially expanded maxillaries that lack longitudinal, occlusal grooves; multiple rows of numerous conical teeth on the dentaries; broad ventral process of squamosal that does not extend below middle of lower temporal fenestra; horizontal shelf on medial side of quadrate ramus of pterygoid; contact between ectopterygoid and jugal reduced to less than half of the length of the distal expansion of the ectopterygoid; deep pockets on neural arches of posterior dorsal and sacral vertebrae; and tall, posteriorly inclined neural spines of proximal caudal vertebrae.

*Holotype.* SAM 5884 (specimen A), a partial skull with palate and incomplete lower jaws.

*Hypodigm.* SAM 5885 (specimen B), a dorsoventrally crushed skull with a partial palate, braincase, and atlas-axis complex; and SAM 5886 (specimen C), a partial, articulated postcranium consisting of the posterior four dorsal vertebrae, sacrals, first dozen caudals, incomplete pelvic girdles, a partial left hind limb, and a complete right tarsus described by Carroll (1976).

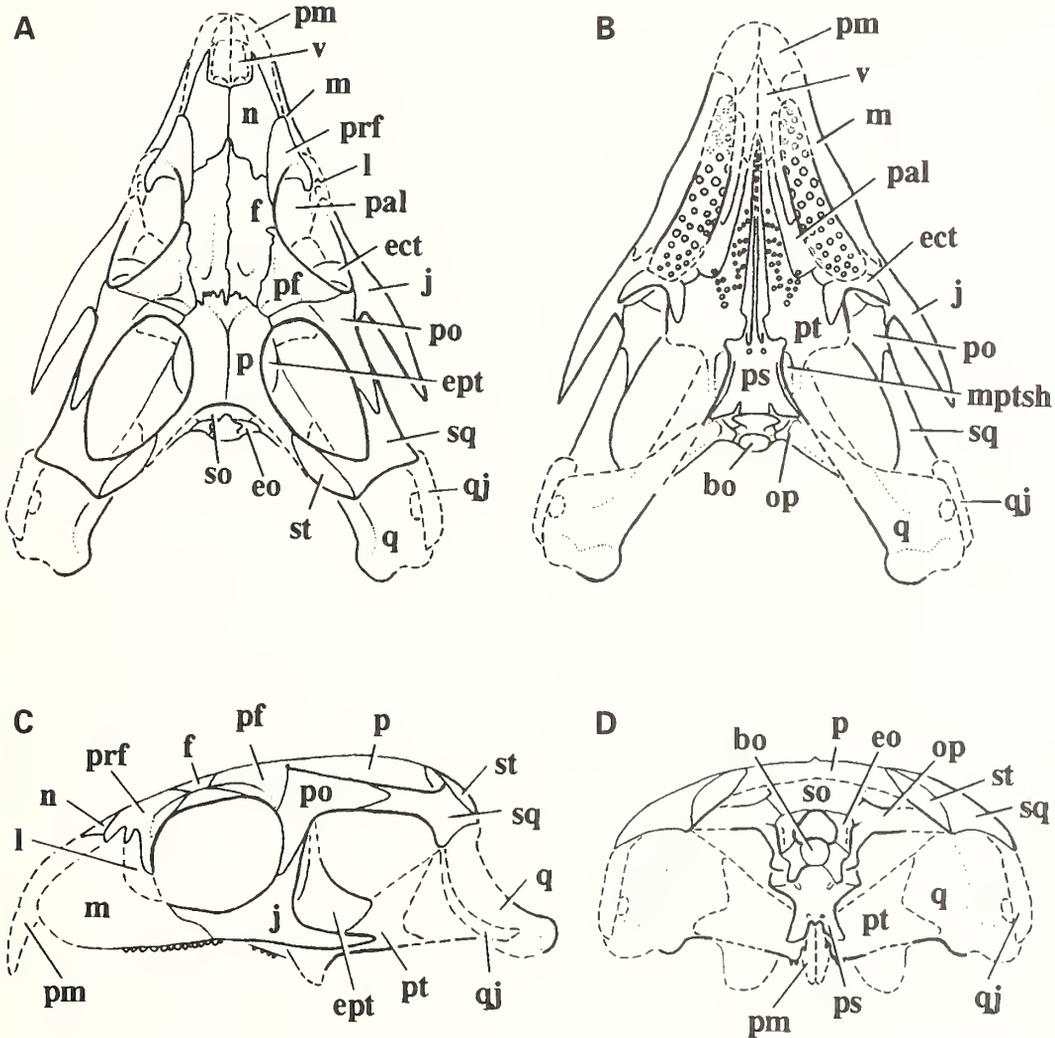
*Locality and horizon.* Precise location is unknown, but near the town of Aliwal North, Eastern Cape Province, South Africa (Broom 1905, 1906). Exposures near Aliwal North are part of the *Cynognathus* Assemblage Zone (Kitching in press) which coincides with the upper two-thirds of the Burgersdorp Formation (Tarkastad Subgroup, Beaufort Group; Keyser and Smith 1979). Age is probably late Early Triassic (Scythian).

*Preparation.* Preparation was undertaken with a pneumatic tool and a pin vice with a tungsten needle. Specimens were impregnated with Glyptal resin. Plaster of paris was used to reinforce portions of SAM 5884 and to embed SAM 5885 to allow preparation of both sides. Latex rubber casts were made of the right dentary teeth and left jugal of SAM 5884 which are preserved as impressions in the matrix.

## DESCRIPTION

*Skull*

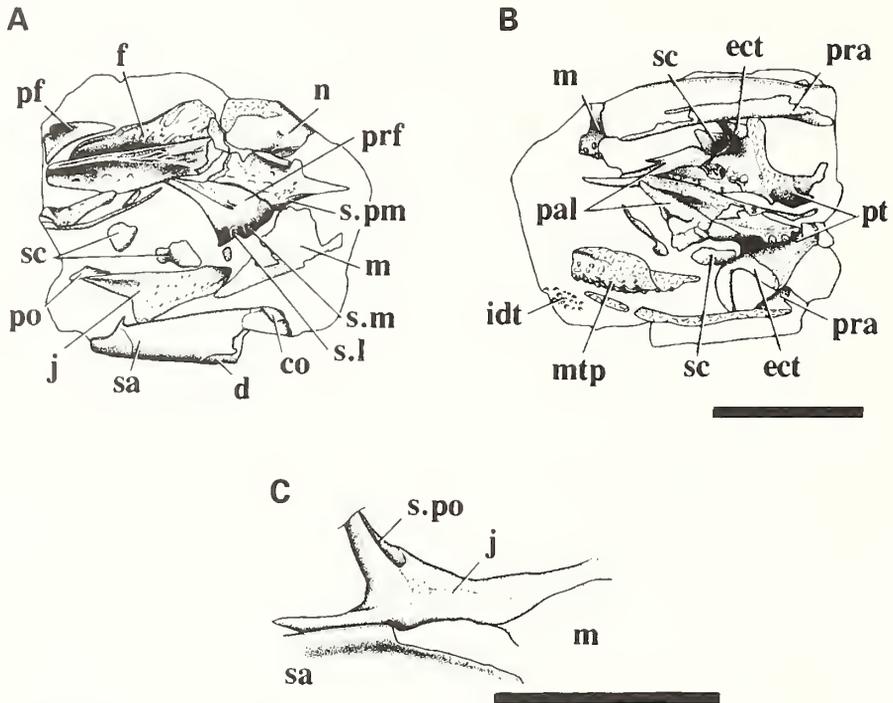
*Restoration of the skull.* Only two prior attempts (Broom 1906; Huene 1939b) have been made to reconstruct the skull of *Howesia*. Both reconstructions depicted a skull similar in its proportions to that of *Sphenodon* and with a complete lower temporal bar. Broom (1906) restored *Howesia* with a blunt snout and laterally placed external nares whereas Huene (1939b) argued that *Howesia* should have a downturned premaxilla as in *Sphenodon*, and positioned a single external naris dorsally along the premaxilla-nasal suture.



TEXT-FIG. 1. Restoration of the skull of *Howesia browni* Broom, 1905; Early Triassic; South Africa. A, dorsal view. B, ventral view. C, left lateral view. D, occipital view. Scale bar represents 20 mm.

Based upon the new cranial data described herein, *Howesia* has a broad skull that tapers gradually to the premaxillae (Text-fig. 1). A downturned, edentulous premaxillary beak is restored, because this morphology is correlated with broad maxillary tooth plates in other rhynchosaurs. The lower temporal bar is incomplete and the lower temporal fenestra is much larger than restored by Broom (1906) and Huene (1939b). The preserved portion of the quadrate suggests that it is a robust element that placed the craniomandibular joint significantly posterior to the occipital condyle in contrast with earlier restorations. A slender quadratojugal is restored, in agreement with *Mesosuchus*, but its existence in *Howesia* is, at present, purely conjectural.

*Dermal bones of skull.* Premaxillae are absent in SAM 5884 and 5885; hence, it is unknown if *Howesia* has a downturned premaxilla, common to all other rhynchosaurs, or premaxillary teeth, as in *Mesosuchus*. Nonetheless, the construction of the nasals, as discussed below, does suggest that the shape of the premaxillae is similar to that of *Mesosuchus* (Haughton 1924).



TEXT-FIG. 2. *Howesia browni* Broom, 1905; holotype, SAM 5884; Early Triassic; South Africa. A, dorsolateral view. B, ventromedial view. C, internal view of left jugal, surangular, and maxilla. Scale bars represent 20 mm.

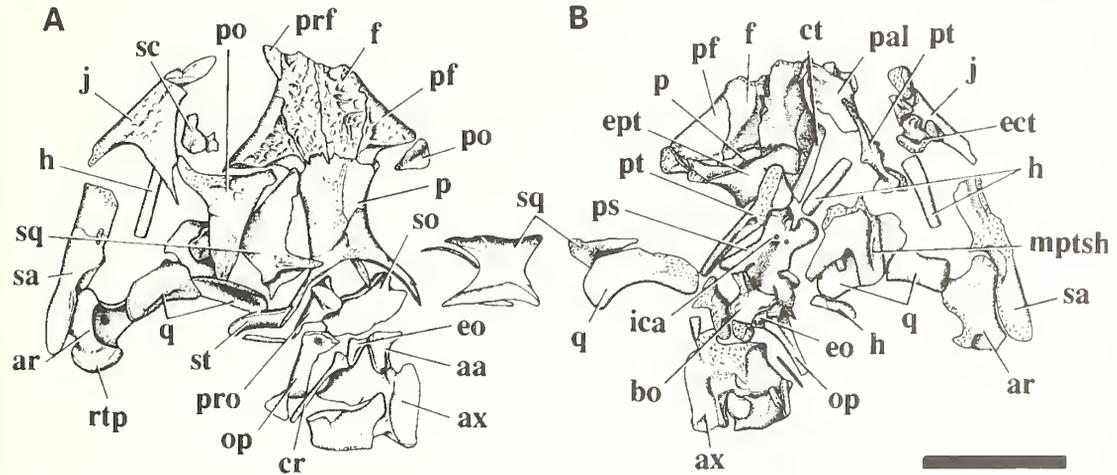
A complete right nasal and a partial left nasal are exposed on the type specimen (Text-fig. 2A). Few differences exist between the nasals of *Howesia* and *Mesosuchus*, and it is clear that *Howesia* has a single, median external naris in agreement with other rhynchosaurs. A sharp ridge along the lateral edge of the nasal demarcates the dorsal surface from a laterally extensive articular region for the posterodorsal process of the premaxilla, as in *Mesosuchus*. The sutural surface for the premaxilla extends to the prefrontal indicating contact between these elements. *Howesia* lacks processes of the nasals like those which project into the external naris in *Mesosuchus* (Haughton 1924) and meet premaxillary processes in more plesiomorphic diapsids. There is a scattering of small pits near the suture with the premaxilla and external naris and a few shallow, longitudinal grooves.

The right maxilla on the type specimen consists of the thin and poorly preserved lateral face and a portion of the medially expanded tooth plate. Owing to the poor preservation, no sculpturing is present.

Three prominent sutural regions for neighbouring bones are visible on the lateral side of the prefrontal: a smaller, posterior, and deeply recessed facet for a narrow dorsal process of the lacrimal; a broader, shallower surface for the maxilla; and a small, anterior facet for the posterodorsal process of the premaxilla. A narrow process of the prefrontal extends along the orbital rim, but does not contact the postfrontal.

Neither skull of *Howesia* has a preserved lacrimal, but its presence is indicated on the type specimen by the articular surface on the lateral side of the prefrontal. Contact between the maxilla and the prefrontal precluded any union between the lacrimal and nasal.

A right jugal (Text-fig. 2A) and an impression of most of the left jugal (Text-fig. 2C) are preserved on the type, and an incomplete left jugal is present on SAM 5885 (Text-fig. 3A). The triadial jugal consists of an anterior



TEXT-FIG. 3. *Howesia browni* Broom, 1905; SAM 5885; Early Triassic; South Africa. A, dorsal view. B, ventral view. Scale bar represents 20 mm.

process that forms the entire ventral orbital rim and is overlapped by the maxilla, a posterodorsal process tapering dorsally along the postorbital, and a posterior process that forms the lower temporal bar. As the completeness of the lower temporal bar in diapsids is a character of phylogenetic significance (Benton 1985; Chatterjee 1986) and it is a point of contention whether or not *Mesosuchus* has a complete lower temporal bar (Haughton 1924; Broom 1925), it is crucial to determine the condition for *Howesia*. Broom (1906) restored *Howesia* with a complete lower temporal bar, arguing that the configuration of the jugal was nearly identical to the jugal of the early reptile *Palaeohatteria* which at that time was thought to be the oldest known diapsid, but recognized later as a synapsid (Williston 1925). He based his claim for a complete temporal bar upon an impression of the left jugal of the type specimen and the incomplete left jugal of SAM 5885. His reconstruction of *Howesia* (Broom 1906, plate XL, figure 1), which appears to be derived largely from SAM 5885, shows, incorrectly, a jugal with a bluntly tipped posterior process that presumably met an anterior process of the quadratojugal. In fact, the left jugal of the type specimen has a complete posterior process that tapers sharply (Text-fig. 2C). In addition, there is no facet on the internal surface of the jugal for the quadratojugal as would appear to be true for other rhynchosaurs with a complete lower temporal bar (Huene 1938; Benton 1983b, 1990). Therefore, the jugal of *Howesia* does not contact the quadratojugal, and the lower temporal bar is incomplete.

Frontals have a longitudinal depression on their dorsal sides that increases in depth posteriorly to a maximum next to the frontal-postfrontal contact. Sculpturing consists of circular to oval pits that are much larger and deeper on SAM 5885.

Postfrontals are distinguished by a marked depression on their dorsal sides situated at the posteromedial corner next to the contact between the frontal, parietal, and postorbital. This depression lessens in depth anterolaterally to the thickened orbital rim. A cluster of shallow pits is present in the postfrontal depression

of the type specimen; those on SAM 5885 are more pronounced and include broad grooves that are oriented towards the orbital rim. Each postfrontal of SAM 5885 has a dorsally facing, smooth region next to the parietal that is continuous with the ventrolateral flange of the parietal, demonstrating that the postfrontal entered the upper temporal fenestra.

Only the left postorbital of SAM 5885 (Text-fig. 3A) is virtually complete. A gently tapering anterodorsal process of the postorbital contacts the parietal and the equally constricted ventral process fits in to a long recess on the dorsal process of the jugal (Text-fig. 2C). The posterodorsal process is broader than the other two processes and tapers sharply. Faint, longitudinal striations on the posterodorsal process and some small pits on the anterodorsal process comprise the sculpturing for this element.

Parietals of SAM 5885 are fused along their common, midline suture which is raised slightly to form a low, but sharply defined ridge. Anteriorly, the ridge divides and extends to the parietal-frontal suture. An apparently rudimentary pineal foramen (Broom 1906) is merely a deep concavity that does not penetrate the parietals. Laterally, the parietals expand into ventrolateral flanges which apparently provided increased surface area for attachment of mandibular adductor muscles. Along the occipital rim, the parietals are drawn laterally and posteriorly into tall, anteroposteriorly narrow wings.

No mention of an element lateral to the parietal wings, other than the squamosal, appeared in Broom's (1906) account of *Howesia*. Haughton (1924) identified supratemporals (tabulars of Broom 1925) in both *Howesia* and *Mesosuchus*, but it is clear, upon comparison of his drawing of SAM 5885 with the specimen, that the elements labelled as supratemporal and squamosal are actually the squamosal and pterygoid portion of the quadrate, respectively. In fact, the genuine supratemporal is not shown in his drawing because it had not been exposed. Only the left supratemporal of SAM 5885 is exposed and is very similar to the supratemporal of *Mesosuchus*. Each is a tall, thin bone that fits into an elongate, occipitally facing concavity on the squamosal and is overlapped marginally by the parietal wing. Consequently, exposure of the supratemporal is primarily occipital and limited to the posterolateral corner of the skull.

The squamosal of *Howesia* (Text-fig. 3A) is a broad, tetradiate element that forms a significant portion of the borders of the upper and lower temporal fenestrae. The ventral process is broad and tapers abruptly to a blunt tip, and its participation in the rear border of the lower temporal fenestra is restricted to only the upper half. In other basal archosauromorphs, the ventral process is either much narrower and extends to the midpoint of the temporal fenestra (*Prolacerta*: BP/1/2675 and BP/1/471; *Euparkeria*: Ewer 1965) or is more robust and extends below the middle of the temporal fenestra (*Mesosuchus*: Haughton 1924; *Proterosuchus*: Welman in press).

*Sclerotic elements.* Fragments of extremely thin bone are present in the orbits of SAM 5884 and 5885 and the suborbital fenestrae of SAM 5884 (Text-figs 2–3). These fragments are evidently the remains of sclerotic rings with each element, judging by the size of the larger fragments relative to the orbit, part of a substantial ring of bone. A sclerotic ring in the orbit of a rhynchosaur was first reported in *Hyperodapedon gordoni* (Benton 1983b).

*Dermal bones of the palate.* Only partial palates remain on SAM 5884 and 5885 (Text-figs 2B, 3B). The pterygoids appear to be united along most of their dorsally expanded medial surfaces, but separate just anterior to the basal articulation. Each palatal ramus of the pterygoids has two narrow fields of large denticles on slightly raised ridges that converge medially at the point of midline pterygoid separation. One field continues anteriorly along the medial edge while the second is directed anterolaterally towards the palatine and the anterior margin of the suborbital fenestra. The transverse flanges of SAM 5884 and 5885 are damaged and it is unknown if teeth were present. The basal process of SAM 5885 is a robust, dorsomedially oriented projection with an articular surface of the basiptyergoid process that faces posterodorsally and slightly medially. A distinctive horizontal shelf that arises from the medial surface of the vertical quadrate ramus (Text-fig. 3B) is autapomorphic for *Howesia*.

The ectopterygoid of *Howesia* is an elongate element sutured along the lateral side of the pterygoid (Text-fig. 2B). Ectopterygoid and pterygoid are joined by a complex interlocking suture in which, in ventral view, the pterygoid overlaps the ectopterygoid for the anterior half of the suture and is in turn overlapped by the ectopterygoid for the remainder. *Mesosuchus* has an identically constructed suture between the ectopterygoid and pterygoid, and a similar configuration has been described recently in the archosauriform *Proterosuchus* (Welman in press). The posterior edge of the ectopterygoid does not reach the transverse flange in these three genera. *Prolacerta* is restored with a more abbreviated ectopterygoid (Gow 1975); however, after examination of the specimen (BP/1/2675) which served as the basis for this restoration, it is clear that the ectopterygoid is incomplete and continued posteriorly along the damaged lateral edge of the pterygoid for an uncertain

distance. Ventrally, the pterygoid of *Prolacerta* does overlap the preserved anterior portion of the ectopterygoid, and the possibility that *Prolacerta* shares a similar sutural pattern with the aforementioned archosauriforms cannot be ruled out. The ectopterygoid has a lunate process that contacted the jugal, but apparently not the maxilla. In contrast with the more robust contact between the ectopterygoid and jugal in *Mesosuchus*, this contact in *Howesia* is restricted to less than half of the lunate process.

The anterolateral row of palatal denticles on the pterygoid continues on to the palatine for only a short distance. Palatine and ectopterygoid are separated along the medial edge of the suborbital fenestra by a wide entrance of the pterygoid.

*Quadrate.* A partial left quadrate remains in SAM 5885 (Text-fig. 3A). The quadrate of *Howesia* is a robust bone with a pronounced posterior emargination, a broad union with the quadrate ramus of the pterygoid, and an apparently equally broad lateral exposure that met the quadratojugal. The strongly emarginated quadrate places the craniomandibular joint posterior to the occipital condyle. *Mesosuchus* has a quadrate with similar proportions.

*Epipterygoid.* A right epipterygoid is exposed in lateral view in SAM 5885 (Text-fig. 3B). It has an expanded, ventrally convex base that rests on the dorsal edge of the quadrate ramus of the pterygoid and a tapering dorsal process (Text-fig. 1C). No significant differences exist between the epipterygoids of *Howesia* and *Mesosuchus*.

*Braincase.* SAM 5885 has a largely complete and well preserved braincase (Text-fig. 3B). There is no evidence of an archosauriform laterosphenoid (Clark *et al.* 1993). The supraoccipital is transversely broad with a slight, median elevation that separates laterally placed, shallow concavities. Its dorsal margin is straight and does not match the strongly curved occipital rim of the parietals, which indicates that the contact between supraoccipital and parietal is displaced anteriorly on to the ventral side of the parietal. The dorsal corners have small facets for articulation with the parietals. Laterally, the supraoccipital has a broad contact with the prootic and opisthotic. Facets along the foramen magnum received the exoccipitals. As these facets do not merge dorsally, it is clear that the supraoccipital enters the foramen magnum. *Howesia* and *Mesosuchus* share similar plate-like supraoccipitals that are different from the inverted V-shaped supraoccipitals of Middle and Late Triassic rynchosaurs.

The triangular plate of the parasphenoid has a pair of large, ventrolateral processes next to its transverse suture with the basioccipital. At the base of the basiptyergoid processes are a pair of foramina for the cerebral branches of the internal carotid arteries. The basiptyergoid processes are stout, project anterolaterally, and expand distally at their joint with the basal processes of the pterygoid. A groove at the base of each basiptyergoid process, anterior to the internal carotid foramina, is probably the vidian sulcus which held the vidian nerve (palatine ramus of cranial nerve VII) and the palatine branch of the internal carotid artery. A thin, dorsoventrally tall cultriform process extends anteriorly for a distance at least equal to the length of the parasphenoidal plate.

The basioccipital forms an occipital condyle that appears to be concave on its posterior surface as a result of poor preservation. It does not appear to enter the metotic foramen because the opisthotic and exoccipital join ventrally.

A left exoccipital lies next to the opisthotic on SAM 5885 (Text-fig. 3A). It has a slender middle region which expands dorsally. Ventrally, a pair of foramina for cranial nerve XII (hypoglossal) lie posterior to the metotic foramen.

The left prootic lies against the parietal wing so that only the dorsal half is exposed to reveal its contacts with the opisthotic and supraoccipital (Text-fig. 3A). The configuration of its articulation with the basisphenoid and the existence of a pila antotica and crista prootica, all argued to be synapomorphies of archosauriforms minus choristoderes (Evans 1990), are unknown.

The left opisthotic has an expanded base where it joins the supraoccipital and prootic. A long, laterally compressed paroccipital process has a slightly enlarged distal end with a blunt face that possibly reached the side of the occiput. The large metotic foramen for cranial nerves IX, X, and XI (glossopharyngeal, vagus, and accessory) and the posterior cerebral vein is formed by the opisthotic and exoccipital. Anterior to the metotic foramen, the opisthotic comprises the posterior border of the fenestra ovalis. A deep fossa extends along the ventral side of the opisthotic from the fenestra ovalis towards the distal end.

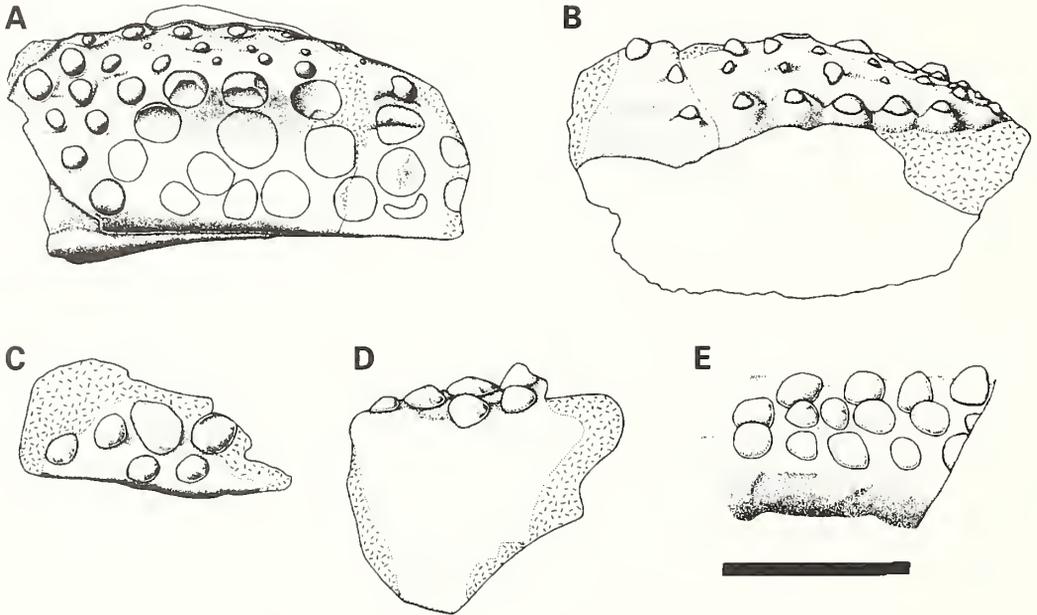
*Lower Jaw.* Little of the mandibles is preserved. SAM 5884 has only the posterior halves of the mandibles (Text-fig. 2), most of which is impression, but this specimen furnishes most information on mandibular sutures.

Only a partial left surangular is present on SAM 5885 (Text-fig. 3). A tiny portion of the dentary, preserved as impression only, is visible on SAM 5884. It evidently tapered to a blunt point between the coronoid and surangular. The coronoid is small and similar to the coronoid of *Mesosuchus* in that it lacks the prominence found in other rhynchosaurs. This prominence on the coronoid is a peak at the level of maximum depth beyond which the profile of the dorsal mandibular margin is slightly concave (e.g. *Hyperodapedon*: Chatterjee 1974). The dorsal margins of the surangulars of *Howesia* and *Mesosuchus* are convex rather than directed posteroventrally as in all other rhynchosaurs. There is no angular preserved, but its impression suggests that it had limited lateral and medial exposures. Virtually the entire inner wall of the adductor chamber is made of the prearticular which expands medially under the articular. SAM 5885 has a partial retroarticular process formed by the articular that is identical to the retroarticular process of *Mesosuchus*. The retroarticular process is robust with a curved posterior margin.

*Hyoid*. Broom (1906) described a pair of elongate bones lying on the palate of SAM 5884 that he interpreted as hyoid elements. These bones are no longer present and were removed apparently by a previous preparator to allow the complete exposure of the palate. Three fragments of elongate, robust bones are scattered among the palatal elements of SAM 5885 (Text-fig. 3) and evidently are the remains of hyoid bones.

*Dentition*. *Howesia* shares with Middle and Late Triassic rhynchosaurs the presence of multiple rows of maxillary and dentary teeth. However, in contrast to the later rhynchosaurs with their precision-shear bite where a ridge of dentary teeth cut in to a groove on the maxilla (Benton 1984), the maxillary and dentary teeth of *Howesia* met along a broad occlusal surface as in captorhinid reptiles such as the Early Permian *Captorhinus aguti* (Rieglés and Bolt 1983).

Portions of the right and left maxillary teeth, an impression of several right dentary teeth, and three left dentary teeth (obscured by the left mandible) are present in SAM 5884 (Text-fig. 2B). A pair of fragments of the left maxilla are separate from SAM 5885 (Text-figs 4A–D, 5). The medially expanded maxilla of *Howesia*

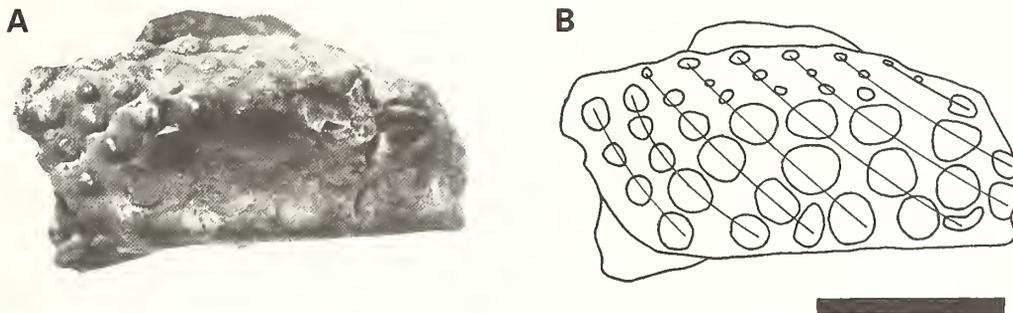


TEXT-FIG. 4. Dentition of *Howesia browni* Broom, 1905; Early Triassic; South Africa. A, maxillary tooth plate of SAM 5885 in occlusal view. B, maxillary tooth plate of SAM 5885 in lingual view. C, fragment of maxillary tooth plate of SAM 5885 in occlusal view. D, fragment of maxillary tooth plate of SAM 5885 in labial view. E, right dentary teeth of SAM 5884 in occlusal view. Scale bar represents 5 mm.

has a strongly convex lingual side and a straight labial side. Teeth are inset from the labial margin as in the other rhynchosaurs with expanded maxillaries. The convex occlusal surface is similar to that of later rhynchosaurs, but lacks a groove. Four rows of occlusal teeth and two rows of lingual teeth are present on the right maxilla of SAM 5884, but this distinction between occlusal and lingual teeth is largely artificial, as noted by Benton (1984) for *Stenaulorhynchus*, because the lingual teeth are part of tooth rows that continue anteriorly on to the occlusal surface.

Unworn occlusal maxillary teeth are conical with a broad base and blunt tip. The largest teeth are present anteriorly and display the greatest wear whereas those at the posterior ends of the tooth rows are smaller and show little or no wear. Enamel covers the entire exposed surface of the unworn teeth.

Teeth of the left maxilla of SAM 5885 are more heavily worn than those of SAM 5884 and reveal more clearly the nature of tooth wear (Text-figs 4A, 5A). Labially facing wear facets are present on those teeth along



TEXT-FIG. 5. Maxillary tooth plate of *Howesia browni* (SAM 5885) Broom, 1905; Early Triassic; South Africa. A, occlusal view. B, line drawing of A to show Zahnreihen. Scale bar represents 5 mm.

the margin between the occlusal and lingual sides of the maxilla. With the exception of a single unworn tooth at the posterolabial corner, all remaining occlusal teeth are worn down to the level of the maxilla. The pattern of these wear facets indicates that the occlusal teeth met a section of the dentary teeth that is narrower than the width of the maxillary occlusal region. Action of dentary and maxillary teeth apparently initially wore down the teeth to the maxillary surface. Occlusion continued with the dentary teeth wearing against bone to create a broad, shallow depression on the maxilla. Unlike the deep, narrow maxillary grooves of later rhynchosaurs, this depression is not a regular feature of the maxilla because it is absent from the similarly sized maxilla of SAM 5884.

Longitudinal rows of dentary teeth of *Howesia* appear to match the orientation of the rows of maxillary teeth (Text-fig. 4E). The three left dentary teeth of SAM 5884 are damaged. Dentary teeth are conical.

Maxillary and dentary teeth of *Howesia* are implanted deeply in bone (Broom 1906; Malan 1963) as shown by natural breaks. Presumably, bone of attachment anchors the deeply rooted teeth, a form of implantation known as ankylotheodont (Chatterjee 1974; Benton 1984) that is found in rhynchosaurs and probably *Trilophosaurus* (Gregory 1945). Histological sections are needed to confirm this supposition for *Howesia*. Unfortunately, specimens of *Howesia* are too few to justify this sacrifice. Worn maxillary teeth on SAM 5885 show radial dentinal tubules in the dentine and occasional circumferential growth lines. The pulp cavities of these teeth are either largely or completely filled by secondary dentine. Thick secondary bone covers the occlusal and lingual surfaces of the maxilla to such an extent that only the tips of the younger teeth emerge above this bone. Wave-like ridges of secondary bone are present in the posterolingual corner.

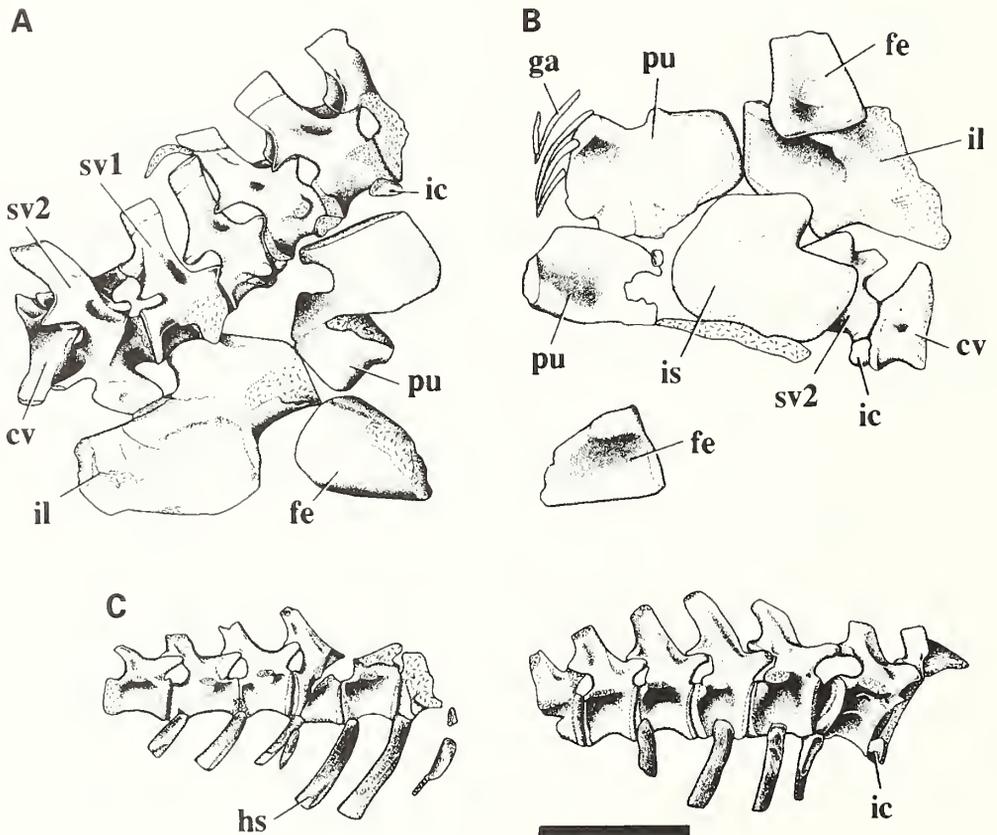
The teeth of *Howesia* are arranged in longitudinal or diagonal Zahnreihen (Text-fig. 5B; Edmund 1960; Malan 1963) and apparently share with other rhynchosaurs an identical pattern of ontogenetic addition (Benton 1984). The left maxilla of SAM 5885 shows this pattern most clearly. Patterns of tooth wear, sizes of teeth, and the wave-like nature of the secondary bone suggest that teeth were added during growth to each Zahnreihe at the posterolingual corner of the maxilla on the lingual side. The smallest teeth in the posterolingual corner with only their tips exposed are the youngest. The convexity of the maxilla (Text-fig. 4B) probably separated the younger maxillary and dentary teeth. Older teeth situated more anteriorly in the rows are larger and worn. Growth of the maxilla was presumably by addition of bone posteriorly to provide space for the new teeth. Each wave-like crest of secondary bone could represent successive phases of growth. As each

crest of secondary bone crosses several Zahnreihen, teeth were apparently added simultaneously to the Zahnreihen. Resorption of bone and loss of teeth probably occurred anteriorly.

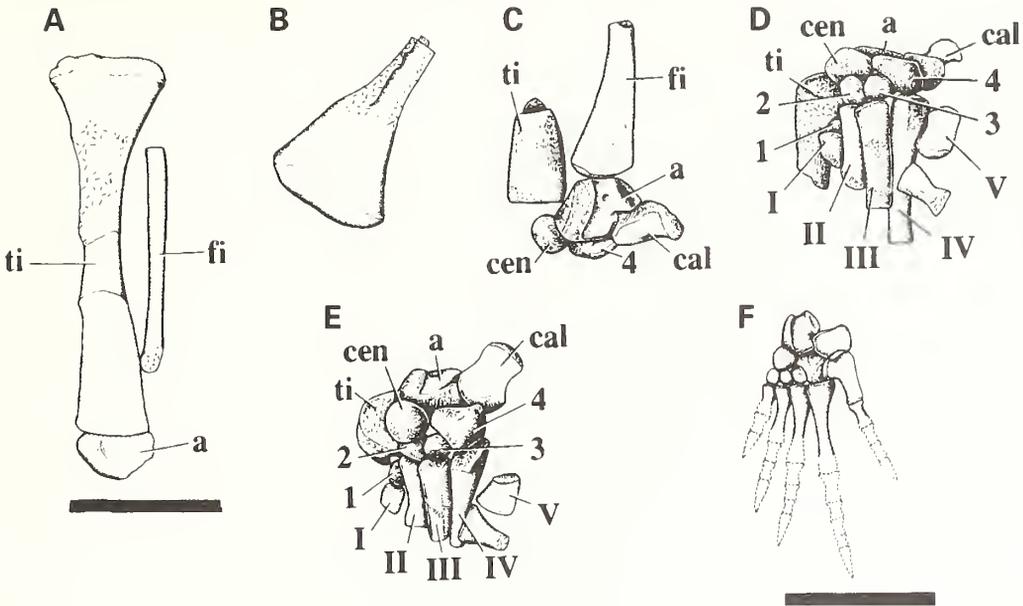
### *Axial skeleton*

*Vertebral column.* Of the atlas-axis complex on SAM 5885, only the left atlantal neural arch and the axis are preserved (Text-fig. 3). The atlantal neural arch has the plesiomorphic amniote morphology of a dorsal arm that forms the roof of the neural canal and a posterior arm that forms the postzygapophysis. A lateral ridge on the posterior arm ends at a broken surface, suggesting the former existence of a posteriorly directed spine, a common feature of early amniotes. There is a large, laterally oriented, circular facet for the proatlas at the junction between the two arms of the atlas arch. The axis has an elongate and dorsoventrally low neural spine that extends forward to overhang the atlantal neural arches. Most of the axial neural spine is extremely thin, but it thickens dramatically at the posterior end, possibly for the attachment of the cervical muscle *M. spinalis capitus*. There is a sharp keel along the ventral margin of the centrum. The anterior one-third of the third cervical vertebrae is in articulation with the axis. The ventral edge of its centrum is rounded gently.

SAM 5886 furnishes all information on the remainder of the postcranium that is known for *Howesia* (Text-figs 6–7). As there is no skull associated with this specimen, the matter of the probable identity of SAM 5886



TEXT-FIG. 6. *Howesia browni* Broom, 1905; SAM 5886; Early Triassic; South Africa. A, right dorsolateral view of posterior presacrals, sacrals, first caudal, pelvis, and proximal femur. B, ventral view of pelvis, second sacral, first caudal, and proximal femur. C, right lateral view of articulated caudal vertebrae. Scale bar represents 20 mm.



TEXT-FIG. 7. *Howesia brownii* Broom, 1905; SAM 5886; Early Triassic; South Africa. A, left tibia, partial fibula, and astragalus in anterior view. B, distal end of left femur in ventral view. C, right pes in posterior view. D, right pes in posteroventral view. E, right pes in ventral view. F, restoration of right pes. Scale bars: A-E (below A) represent 20 mm, F represents 40 mm.

must be addressed first. Broom (1906) argued that SAM 5886 did belong to *Howesia*, and cited as evidence the presence of SAM 5886 in the same horizon as the two partial skulls and an accordance between the morphologies of the pelvis of SAM 5886 and the skull and pectoral girdle of *Howesia*. Neither argument is convincing since both presuppose the non-existence of other vertebrates with similar postcranial morphology. However, there is excellent agreement in general morphology between SAM 5886 and the postcranium of *Mesosuchus*, in particular the pelvis, bifurcate second sacral rib, and tarsus. *Prolacerta* shares these postcranial features with basal rhynchosaurs, but can be distinguished by its narrower, ventrally concave second sacral rib and a tibia that is markedly elongate relative to the femur (Gow 1975). As these features are lacking in SAM 5886, it is likely that this specimen is part of a rhynchosaur. Despite the large number of similarities between SAM 5886 and *Mesosuchus*, there are several differences which indicate that SAM 5886 is not *Mesosuchus* and, indirectly, support assignment of SAM 5886 to *Howesia*, the only other known rhynchosaur from the *Cynognathus* Assemblage Zone. These differences are: the presence of deep pockets on the neural arches of the posterior dorsals and sacrals of SAM 5886 that are absent in *Mesosuchus*; a posterior inclination of the caudal neural spines of SAM 5886 whereas those of *Mesosuchus* are essentially vertical; and the absence on SAM 5886 of a prominent ventral groove on each of the first two caudal centra that is present on *Mesosuchus*. SAM 5886 will, thus, be assigned to *Howesia*, but with the reservation that future discoveries of additional specimens are needed for confirmation.

The posterior four presacrals of SAM 5886 have non-notochordal centra with gently rounded ventral edges (Text-fig. 6). Transverse processes are robust, project significantly beyond the centra, and are directed primarily ventrolaterally and slightly anteriorly. Zygapophyseal surfaces of successive vertebrae meet at an angle of approximately  $10^\circ$  to the frontal plane. A deep pocket is present on the neural arches. Neural spines are tall, and there is no evidence of variation in their height.

*Howesia* has two sacral vertebrae. Construction of the centra, the angulation of the zygapophyses, and shape of the neural spines differ little from the posterior presacrals. The pockets on the sacral neural arches are larger than those on the dorsals.

Length of the tail of *Howesia* is unknown. Caudal centra change little in length along the preserved string of twelve of SAM 5886 (Text-fig. 6) indicating a very long tail of approximately 50 vertebrae as suggested for

*Noteosuchus* (Carroll 1976). *Mesosuchus* probably has a tail of similar length. Later rhynchosaurs have shorter tails composed of between 25 and 30 vertebrae (Huene 1938, 1942; Benton 1983*b*, 1990). A pronounced transverse narrowing of the tail is shown by a significant decrease in the width of the centra past the sixth caudal. The first caudal vertebra has an elongate, blade-like transverse process that projects posterolaterally; all succeeding caudal transverse processes are broken, but it is clear that those past the third caudal project only laterally. Each caudal centrum has a rounded ventral edge that is characterized on vertebrae six to twelve by a sharp, central ridge and flanking, secondary ridges. Shallow depressions on the neural arches that disappear by the ninth caudal are all that remain of the deep pockets on the sacrals and dorsals. There is no apparent change in the angulation of the caudal zygapophyses relative to the dorsals. Neural spines are tall, but much narrower than those of the dorsals, and incline progressively more posteriorly on distal caudals. The caudal neural spines of *Mesosuchus* and *Rhynchosaurus* (Benton 1990) are equally tall, but those of the proximal caudals are vertical in both genera.

Crescentic intercentra are present along the preserved section of dorsals and the proximal two caudals. Haemal arches are elongate with a distal expansion that is greater than at the proximal end. Faint striations cover the haemal arches. The tall neural spines and long haemal spines give the tail of *Howesia* a very deep lateral profile.

*Ribs*. A single cervical rib has an expanded, apparently holocephalous head and a slender shaft (Text-fig. 3A). Both pairs of sacral ribs are fused to the centra (Text-fig. 6A). Only the base of the right first sacral rib is exposed, but it indicates a very robust rib that probably had a firm union with the pelvic girdle. The bifurcate second sacral rib has a greatly enlarged anterior division with a distally expanded, elliptical articular end and a much smaller, blade-like posterior division that does not reach the pelvic girdle.

*Gastralia*. Five posterior gastralia are preserved along the anterior edge of the left pubis (Text-fig. 6B). Each is very thin and narrows towards the body midline.

### *Appendicular skeleton*

*Pectoral girdle and forelimb*. Broom (1906) described and figured a partial shoulder girdle and humerus for SAM 5885. However, these elements are not now present with SAM 5885 nor could they be found in the collections of the South African Museum. It is presumed that they are lost. As illustrated (Broom 1906, pl. 40, fig. 10), the scapula narrows dramatically above the glenoid unlike the much broader scapula of *Mesosuchus*. However, Broom noted that the anterior margin was incomplete, and the narrow scapular configuration is probably an artefact.

*Pelvic girdle*. Each element of the pelvic girdle is enlarged and plate-like with the ilium making the greatest contribution to the acetabulum (Text-fig. 6B). The ilium is very similar to that of *Mesosuchus* and *Noteosuchus* (Carroll 1976) in having a constriction above the acetabulum and a dorsally expanded blade with a larger, posterior expansion. Later rhynchosaurs, with the exception of *Rhynchosaurus* (Benton 1990), have equally developed anterior and posterior extensions of the ilium. Facets for reception of the paired sacral ribs are present on the medial side of the ilium. The facet for the first sacral rib appears larger, and is bounded anteriorly, ventrally and posteriorly by ridges. The facet for the second sacral rib is posterodorsally elongate with an expanded ventral margin which matches the shape of the rib's articular end.

The pubis of *Howesia* is identical to that of *Mesosuchus*, *Noteosuchus* and *Prolacerta* in its possession of a transversely broad, down-turned anterior region and a prominent, ventrally pointing processus lateralis. A large, elliptical obturator foramen is situated near the lateral edge at the level of the downward curvature. The pubes meet medially for most of their lengths, but diverge close to the ischia to border a large, diamond-shaped opening.

The ischium is a posteriorly curved, flat bone. There are few differences between the ischia of *Howesia* and other rhynchosaurs.

*Hindlimb*. As with the pelvic girdle, bones of the hindlimb of *Howesia* are virtually identical to those of the other two Early Triassic rhynchosaurs. Neither femur of SAM 5886 is complete; the left consists of the ends and a portion of the intervening shaft (Text-figs 6B, 7B). Matching the ends to the shaft can give only an

imprecise estimate of femoral length, but it is clear that the femur and tibia were approximately equal in length. Proximally, the articular surface is flat and continuous with the large internal trochanter. There is a slight sigmoidal curvature to the shaft. The distal condyles have only a modest convexity and are equal in size.

The tibia has a broad proximal platform and no cnemial crest (Text-fig. 7A). The shaft is narrowest in the middle and expands slightly at the distal end. The fibula has a narrow shaft and a flattened distal end that is equal in width to the distal end of the tibia.

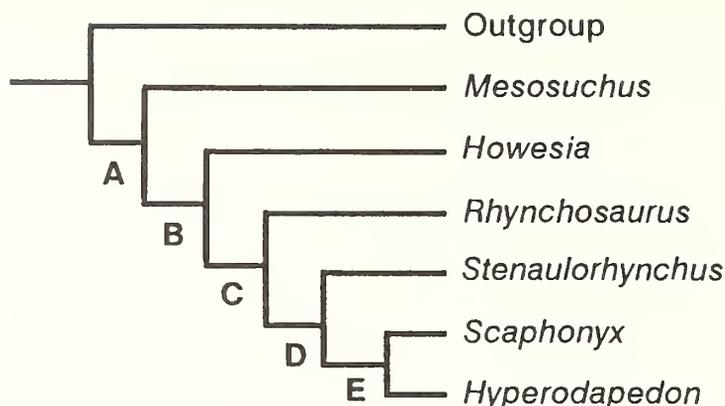
Terminology for the tarsus (Text-fig. 7C–E) follows Carroll (1976) rather than Hughes (1968) and Chatterjee (1974). The proximal end of the hooked fifth metatarsal, illustrated by Carroll (1976, fig. 8), is absent and could not be found in the collections of the South African Museum. The calcaneum has a prominent, laterally directed tuber with an expanded, blunt end. The astragalus has a large, lateral peg that contacts the fibula, and a deep notch immediately below this peg is the medial border of a perforating foramen. As restored by Carroll (1976, fig. 8), three proximal tarsals, the calcaneum, astragalus, and centrale, form a row along the bottom of the crus. However, it is clear that the entire lateral side of the astragalus received the tibia and the centrale should be positioned against the distal side of the astragalus. Consequently, *Howesia* retains the plesiomorphic amniote configuration of only two proximal tarsals, the astragalus and calcaneum (Text-fig. 7F). Four distal tarsals are present. Distal tarsals one to three are smaller than the fourth, and articulate with the entire proximal ends of their respective metatarsals. The centrale and the fourth distal tarsal contact in *Howesia* and *Mesosuchus*. Carroll's restoration of the pes of *Noteosuchus* (Carroll 1976, fig. 6c) has the correct arrangement of tarsals for an Early Triassic rhynchosaur. The first four metatarsals are expanded and overlap proximally. The fifth metatarsal is hooked, but as the proximal half is now missing from SAM 5886, nothing can be added to the description of Carroll (1976).

#### PHYLOGENETIC RELATIONSHIPS

There has been no disagreement in the literature that the Middle and Late Triassic rhynchosaurs form a natural group. With their robust skulls, huge batteries of maxillary teeth, deep lower jaws and toothless beak, these rhynchosaurs are clearly different from any other known reptile. Instead, discussion has centred upon the phylogenetic relationship of the Early Triassic genera to the later 'typical' rhynchosaurs. Broom (1906) recognized close affinities between *Howesia* and the rhynchosaurs *Rhynchosaurus* and *Hyperodapedon* primarily on the basis of their extremely similar dentition, but the possibility of a close relationship between *Howesia* and *Mesosuchus* and the pseudosuchians, the grade of unspecialized thecodonts considered to be ancestral to a variety of archosaurs such as dinosaurs and birds, was soon suggested (Broom 1913). In a classification of early tetrapods (Watson 1917), the thecodontian family Howesiidae was erected to include *Howesia*, *Mesosuchus* and *Proterosuchus*, and the remaining rhynchosaurs were placed as a separate family of rhynchocephalians.

This proposal of a thecodontian ancestry for *Howesia* does not appear to have gained many proponents and was soon forgotten. Instead, it was accepted for many years that the Middle and Late Triassic rhynchosaurs form a group separate from the earlier genera and that *Howesia* with its multiple rows of maxillary teeth lay at the base of their radiation (Huene 1939a, 1939b; Malan 1963; Kuhn 1969; Sill 1970; Chatterjee 1980). Cladistic analyses (Benton 1985, 1987, 1990; Evans 1988) have positioned *Howesia* as the sister taxon to the later rhynchosaurs. However, given the inadequate information in the literature, *Howesia* could play only a minor role in phylogenetic analyses of Rhynchosauria despite its apparent significance. For the first time, there is now sufficient data available for a more rigorous evaluation of the phylogenetic position of *Howesia* within Rhynchosauria.

Only the better known rhynchosaur taxa, *Mesosuchus*, *Howesia*, *Rhynchosaurus articeps*, *Stenaulorhynchus*, *Scaphonyx* and *Hyperodapedon*, are included. Three outgroups were selected from the diversity of known basal archosauromorphs: *Champsosaurus* (Russell 1956; Erickson 1972), *Trilophosaurus* (Gregory 1945), and *Prolacerta* (Gow 1975). Although the relationships of choristoderes such as *Champsosaurus* are uncertain, the taxon is a member of Archosauromorpha (Gauthier 1984; Rieppel 1993). Only a single archosauromorph, *Prolacerta*, was used in the study of Benton (1990); the remainder (*Petrolacosaurus*, *Clandiosaurus*, *Thadeosaurus* and *Yomgingia*) are distantly related basal diapsids that are too far removed phylogenetically for a most parsimonious



TEXT-FIG. 8. Cladogram depicting hypothesis of interrelationships of Rhynchosauria. Polarity of character states was determined through outgroup analysis of *Champsosaurus*, *Trilophosaurus*, and *Prolacerta*, and a hypothetical ancestor constructed to root the tree. Nodes are diagnosed by the following unambiguous characters: **A**, (Rhynchosauria), beak-shaped premaxilla, single median external naris, contact present between premaxilla and prefrontal, depression on dorsal surface of frontal, depression on dorsal surface of postfrontal, fused parietals, flat occlusion. **B**, maxilla with convex occlusal margin, absence of anterior process of nasal projecting in to external naris, presence of maxillary tooth plate, ankylothecondont tooth implantation, maxillary teeth on occlusal and lingual surfaces. **C**, ratio of lengths of frontal and parietal  $\leq 1.0$ , presence of lateral shelf on jugal, absence of palatal teeth on pterygoid, contact between ectopterygoid and palatine to exclude maxilla from suborbital fenestra, a row of three proximal tarsals (astragalus, calcaneum, and centrale), blade and groove occlusion, two grooves on maxilla. **D**, basiptyergoid articulation is posterior to transverse flange of pterygoid, equally large anterior and posterior processes of ilium, ratio of distal femoral width and total femoral length  $> 0.3$ . **E**, midline skull length greater than maximum skull width, robust subtemporal process of jugal with its height  $> 50$  per cent. of its length, single groove on maxilla, depth of lower jaw at adductor fossa  $> 25$  per cent. of total jaw length, maxillary teeth only on occlusal surface, absence of posterior process on coracoid, absence of postaxial intercentra.

determination of the plesiomorphic characters for Rhynchosauria according to Rule 3 of Maddison *et al.* (1984). The present phylogenetic study should be considered preliminary pending the completion of a redescription of *Mesosuchus*.

The data matrix used this study (Appendix 2) is based upon the matrix given in the latest phylogenetic analysis of Rhynchosauria (Benton 1990). The following characters (identified by the same numbering sequence as in Benton (1990) with the prefix B to denote their source) are retained from this data matrix with no modification: B1, B4, B7, B8, B13, B15, B16, B18, B20, B21, B23, B25. Those characters of Benton (1990) included in this analysis with modification and those excluded are discussed in Appendix 3.

A total of 28 characters were used in this study. They were analysed with the program Hennig86 (Farris 1988). All characters were run unordered, and the most parsimonious tree calculated by the implicit enumeration (ie) command.

A single most parsimonious tree (Text-fig. 8) was obtained. It has a length of 32 steps and consistency and retention indices of 0.93. The tree is extremely similar to that of Benton (1990) with the exception of a reversal of the positions of *Rhynchosaurus* and *Stenaulorhynchus*. The explanation for this reversal is found in character B14, the only character that supported the node of *Rhynchosaurus* + *Scaphonyx* + *Hyperodapedon* in Benton (1990). With the polarity of this character corrected in the present analysis, the derived state failed to support a node because it is found in only *Mesosuchus* and *Stenaulorhynchus* and is unknown for *Howesia*.

Seven synapomorphies diagnose Rhynchosauria: (1) a beak-shaped premaxilla; (2) a single, median external naris; (3) contact between the premaxilla and prefrontal; (4) depression on the

dorsal surface of the frontal; (5) depression on the dorsal surface of the postfrontal; (6) fused parietals; and (7) flat jaw occlusion. Discovery of a single, median external naris in *Howesia* confirms previous suggestions that this character is a synapomorphy of rhynchosaurs (Chatterjee 1980; Benton 1985, 1987, 1990; Evans 1988). The only other group of basal diapsids that has a single external naris is the choristoderes, e.g. *Champsosaurus* (Erickson 1972). Characters 3–5 are proposed as new synapomorphies for rhynchosaurs. A contact between the premaxilla and prefrontal is apparently unique to rhynchosaurs among early diapsids although this character state is unknown for *Trilophosaurus* (Gregory 1945). A new burrowing saurian diapsid from the Jurassic of Mexico (Clark and Hernandez 1994) may also have a contact between the premaxilla and prefrontal, but the identification of the prefrontal is uncertain. Depressions are present on the dorsal surfaces of the frontals and postfrontals for all rhynchosaurs, with the possible exception of *Rhynchosaurus* (Benton 1990). *Champsosaurus* appears to have a depression on the postfrontal (Russell 1956; Erickson 1972), but a depression is absent on the postfrontal of the basal choristodere *Ctenioagenys* (Evans 1990). Fusion of parietals has been proposed as a synapomorphy of rhynchosaurs (Chatterjee 1980; Benton 1985). Flat jaw occlusion where maxillary and dentary teeth meet along a broad occlusal surface was not recognized as a rhynchosaurian synapomorphy by Benton (1990) because the character was not separated from the plesiomorphic character state of lateral overlap of maxillary teeth against dentary teeth.

Additional characters that have been proposed as synapomorphies of rhynchosaurs appear to diagnose more inclusive or more restrictive clades than Rhynchosauria. A row of three proximal tarsals (Benton 1985, 1987, 1990; Evans 1988) is a synapomorphy of only the Middle and Late Triassic rhynchosaurs because *Howesia*, *Mesosuchus*, and *Noteosuchus* share the plesiomorphic character of only two (astragalus and calcaneum) proximal tarsals. An anterior position of the occipital condyle relative to the craniomandibular joint (Benton 1990) could diagnose a more inclusive clade than Rhynchosauria because this character is also present in *Prolacerta* (contrary to Gow 1975) and archosauriforms such as *Proterosuchus* (Cruickshank 1972) and *Euparkeria* (Ewer 1965). Evans (1988) added the characters of cervical centra that are shorter than dorsal centra and phalanges that are short in relation to the metapodials. The first character is probably plesiomorphic for diapsids (Laurin 1991) and is not correct for *Mesosuchus*. The second character is not quantified, and appears to be correct only for the Middle and Late Triassic rhynchosaurs.

As concluded in previous phylogenetic studies, *Howesia* is most closely related to the clade of the Middle and Late Triassic genera (Text-fig. 8). *Howesia* shares with these rhynchosaurs five synapomorphies that are primarily of the dentition. Three of these synapomorphies supported the same clade in Benton (1990): ankylotheodont tooth implantation, presence of a maxillary tooth plate (i.e. batteries of teeth), and maxillary teeth on occlusal and lingual surfaces. The remaining pair of unambiguous synapomorphies of this clade in Benton (1990) (frontal shorter than parietal and presence of parietal foramen) fail to support the clade in the present study because the first character is a synapomorphy of only the Middle and Late Triassic genera and the second character is excluded for the reason given in Appendix 3. Two new synapomorphies of *Howesia* and later rhynchosaurs are a maxilla with a convex occlusal margin and the absence of anterior processes of the nasals that project into the external naris. Plesiomorphically, the maxilla of diapsids has a straight occlusal margin whereas *Howesia* (Text-fig. 4B) and later rhynchosaurs have a distinctly convex occlusal margin. *Mesosuchus* retains the plesiomorphic character of narrow anterior processes of the nasals (Haughton 1924) which in other diapsids contact anterodorsal processes of the premaxillae to separate the external nares. These processes of the nasals are absent in *Howesia* and later rhynchosaurs.

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#### APPENDIX 1 - ABBREVIATIONS USED IN THE TEXT-FIGURES

a	astragalus	mtp	maxillary tooth plate
aa	atlas neutral arch	n	nasal
ar	articular	op	opisthotic
ax	axis	p	parietal
bo	basioccipital	pal	palatine
cal	calcaneum	pf	postfrontal
cen	centrale	pm	premaxilla
co	coronoid	po	postorbital
cr	cervical rib	pra	prearticular
ct	cultriform process	prf	prefrontal
cv	caudal vertebra	pro	prootic
d	dentary	ps	parasphenoid
ect	ectopterygoid	pt	pterygoid
eo	exoccipital	pu	pubis
ept	epipterygoid	q	quadrate
ga	gastralia	qj	quadratejugal
f	frontal	rtp	retroarticular process
fe	femur	s.l	suture for lacrimal
fi	fibula	s.m	suture for maxilla
h	hyoid	s.pm	suture for premaxilla
hs	haemal spine	s.po	suture for postorbital
ic	intercentrum	sa	surangular
ica	foramen for internal carotid artery	sc	sclerotic plates
idt	impression of dentary teeth	so	supraoccipital
il	ilium	sq	squamosal
is	ischium	sv1	sacral vertebra 1
j	jugal	sv2	sacral vertebra 2
l	lacrimal	st	supratemporal
m	maxilla	ti	tibia
mptsh	medial pterygoid shelf	v	vomer
		1-4	distal tarsals 1-4
		1-V	metatarsals 1-5

## APPENDIX 2

Description of the characters used in the phylogenetic analysis. The plesiomorphic state is denoted by 0 and derived states by 1 and 2. Characters were polarized using *Champsosaurus*, *Trilophosaurus*, and *Prolacerta* as outgroups.

1. Dimensions of skull: midline length > maximum width (0); midline length < maximum width (1).
2. Premaxilla and anterior part of dentary: teeth present (0); edentulous (1).
3. Shape of premaxilla: horizontal ventral margin (0); beak-shaped (1).
4. External nares: separate (0); single, median naris (1).
5. Premaxilla and prefrontal: no contact (0); contact present (1).
6. Maxilla: horizontal ventral margin (0); convex ventral margin (1).
7. Location of maxillary teeth: only on occlusal surface (0); occlusal and lingual surfaces (1).
8. Maxillary tooth plate: absent (0); present (1).
9. Number of grooves on maxilla: none (0); one (1); two (2).
10. Jaw occlusion: single-sided overlap (0); flat occlusion (1); blade and groove (2).
11. Tooth implantation: subthecondont (0); ankylothecondont (1).
12. Anterior process of nasals: present and project into external naris (0); absent (1).
13. Ratio of lengths of frontals and parietals: > 1.0 (0); ≤ 1.0 (1).
14. Depression on dorsal surface of frontal: absent (0); present and next to sutures with postfrontal and parietal (1).
15. Depression on dorsal surface of postfrontal: absent (0); present (1).
16. Fusion of parietals: absent (0); present (1).
17. Lateral shelf on jugal above maxillary teeth: absent (0); present (1).
18. Subtemporal process of jugal: robust with height > 50 per cent. of length (0); slender with height < 50 per cent. of length (1).
19. Teeth on palatal ramus of pterygoid: present (0); absent (1).
20. Suborbital fenestra: ectopterygoid and palatine do not contact along lateral margin of fenestra (0); ectopterygoid and palatine contact to exclude maxilla from fenestra (1).
21. Location of basiptyergoid articulation relative to transverse flange: coincident with flange (0); posterior to flange (1).
22. Depth of lower jaw measured at maximum height of adductor fossa relative in total length of lower jaw: < 25 per cent. (0); > 25 per cent. (1).
23. Ratio of lengths of dentary and lower jaw: > 0.5 (0); ≤ 0.5 (1).
24. Posterior process on the coracoid: present (0); absent (1).
25. Dorsal margin of ilium: small anterior process and larger posterior process (0); equally large anterior and posterior processes (1).
26. Ratio of distal width of femur and total femoral length: ≤ 0.3 (0); > 0.3 (1).
27. Number of proximal tarsals: two (astragalus and calcaneum) (0); three (astragalus, calcaneum, and centrale) (1).
28. Postaxial intercentra: present (0); absent (1).

## APPENDIX 3

Characters of Benton (1990) included with modification:

B2. Premaxillary teeth: present (0); reduced numbers or absent (1). As the number of premaxillary teeth is unknown for *Howesia*, their reduction in number may be autapomorphic for *Mesosuchus*. Instead, this character is modified to the presence or absence of premaxillary teeth.

B3. Premaxillary shape: straight lower edge, with teeth (0); beak-shaped and toothless (1). The existence of premaxillary teeth and the shape of the premaxilla are separate characters because they do not necessarily occur together in diapsids. For example, *Mesosuchus* has a beak-shaped premaxilla with teeth whereas the outgroup *Trilophosaurus* has a straight-edged premaxilla that lacks teeth. Therefore, this character is reworded to describe only the shape of the premaxilla.

B5. Jugal size: smaller than maxilla (0); larger than maxilla and occupies a large area of the cheek (1). This character is difficult to quantify because it is not stated in which dimensions the jugal and maxilla are to be compared. The robustness of the jugal is expressed instead as a measure of the relative dimensions of the subtemporal process.

B14. Relative length of the dentary: half, or less than half the total length of the lower jaw (0); well over half the total length of the lower jaw (1). Outgroup analysis shows that the polarity of this character should be reversed. A dentary that is greater than half of the total length of the mandible is plesiomorphic for Rhynchosauria.

B17. Jaw occlusion: flat occlusion or single-sided overlap of teeth (0); blade and groove apparatus, where dentary blade(s) fit precisely into maxillary groove(s) (1). The plesiomorphic character state is overlap of teeth during occlusion with flat occlusion and blade and groove occlusion comprising the derived states.

B22. Teeth on the pterygoid: present (0); absent (1). It is uncertain whether this character refers to teeth on both the palatal ramus and transverse flange or only the palatal ramus. It is reworded herein to refer to only the palatal ramus of the pterygoid.

Characters of Benton (1990) excluded from analysis:

B6. Frontal shape: longer than broad (0); broader than long (1). The derived character state is autapomorphic for *Stenaulorhynchus* and is, therefore, excluded.

B9. Parietal foramen: present (0); absent (1). Absence of a parietal foramen is plesiomorphic for rhynchosaurs because it is absent in the outgroups *Trilophosaurus* and *Champsosaurus*, polymorphic for *Prolacerta* (Gow 1975; personal observation), and absent in the basal archosauriforms *Euparkeria* and *Proterosuchus* (personal observation). The presence of a parietal foramen is apparently autapomorphic for *Mesosuchus*.

B10. Supratemporal: present (0); absent (1). This character is excluded because it is uncertain for *Stenaulorhynchus* (Benton 1990) and there is discrepancy in the literature as to whether this bone is absent (Huene 1942) or present (Sill 1970) in *Scaphonyx*.

B11. Shape of the ventral process of the squamosal: narrow and strap-like (0); broad and plate-like (1). This character is not quantified and cannot be determined for the outgroups *Trilophosaurus* and *Champsosaurus*.

B12. Relative position of occipital condyle: approximately in line with the quadrates (0); well in front of the quadrates (1). This character cannot be polarized by outgroup analysis because *Champsosaurus* and *Trilophosaurus* have a third character state of an occipital condyle that is posterior to the quadrates and *Prolacerta* has the supposedly derived state of the occipital condyle anterior to the quadrates. It is necessary to examine the distribution of this character in a broader study of archosauromorphs.

B19. Maximum width of the tooth-bearing areas of the maxilla lying lateral to the main groove: narrower than the medial area (0); equal in width to, or wider than, the medial area (1). It is impossible to code this character for the outgroups, *Mesosuchus*, and *Howesia* because they lack a maxillary groove.

B24. Relative length of the femur and humerus: femur is longer than the humerus (0); humerus is longer than the femur (1). Only *Hyperodapedou* has the derived character state.

B26. Relative size of the centrale: small (0); large, and closely associated with the astragalus (1). The size of the centrale is not quantified, and the distribution of this character becomes identical to that of B25 following correction of the number of proximal tarsals in *Howesia* and *Mesosuchus*.

## APPENDIX 4

Data matrix used in phylogenetic analysis. Numbers (1–28) at the top of each column refer to the characters listed in Appendix 2. A question mark indicates an unknown character state.

Taxon	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Champsosaurus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Trilophosaurus</i>	0	1	0	0	?	0	0	0	0	1	1	0	0	0
<i>Prolacerta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mesosuchus</i>	0	0	1	1	1	0	0	0	0	1	0	0	0	1
<i>Howesia</i>	?	?	?	1	1	1	1	1	0	1	1	1	0	1
<i>Rhynchosaurus</i>	0	1	1	1	1	1	1	1	2	2	1	1	1	?
<i>Stenanolrhynchus</i>	0	1	1	1	1	1	1	1	2	2	1	1	1	1
<i>Scaphonyx</i>	1	1	1	1	1	1	0	1	1	2	1	1	1	1
<i>Hyperodapedon</i>	1	1	1	1	1	1	0	1	1	2	1	1	1	1

Taxon	Character													
	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>Champsosaurus</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Trilophosaurus</i>	0	0	0	?	1	0	0	0	0	0	0	0	0	0
<i>Prolacerta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mesosuchus</i>	1	1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Howesia</i>	1	1	0	0	0	0	0	?	?	?	0	?	0	0
<i>Rhynchosaurus</i>	?	1	1	0	1	1	0	0	0	0	0	0	1	?
<i>Stenanolrhynchus</i>	1	1	1	0	?	1	1	0	1	0	1	1	1	0
<i>Scaphonyx</i>	1	1	1	1	1	1	1	1	0	1	1	1	1	1
<i>Hyperodapedon</i>	1	1	1	1	1	1	1	1	0	1	1	1	1	1



# THE CRANIAL ANATOMY OF THE CAPTORHINID REPTILE *LABIDOSAURIKOS MEACHAMI* FROM THE LOWER PERMIAN OF OKLAHOMA

by J. T. DODICK and S. P. MODESTO

**ABSTRACT.** Study of *Labidosaurikos meachami*, from the Lower Permian Hennessey Formation (Sumner Group) of north-central Oklahoma, reveals the presence of over thirty new cranial characters not present in single-tooth-rowed captorhinids and *Captorhinus aguti*. However, it is uncertain if these new characters represent autapomorphies of *L. meachami* because the skulls of all other large, multiple-rowed captorhinids are poorly known; many of these characters may instead diagnose subclades of multiple-tooth-rowed taxa within Captorhinidae. A suite of skeletal features, including the presence of tooth plates, prominent tooth wear, and the morphology of the skull roof, suggests strongly that *L. meachami* was herbivorous. Propaliny was probably a significant component of the feeding mechanism.

Phylogenetic analysis of the interrelationships of the well known North American captorhinids indicates that *Labidosaurikos meachami* is more closely related to the large, single-rowed *Labidosaurus hamatus* than it is to *Captorhinus aguti*. The sister-group relationship between *Labidosaurikos meachami* and *Labidosaurus hamatus* is supported by fifteen synapomorphies, and is the most robust clade within Captorhinidae. This relationship supports the hypothesis that multiple rows of teeth evolved independently at least twice among captorhinids. *Eocaptorhinus laticeps*, recently assigned to the genus *Captorhinus* as '*Captorhinus* sp.', is formally recognized as *Captorhinus laticeps* (new combination). The phylogenetic analysis indicates that *C. laticeps* and *C. aguti* form a clade, identified here as *Captorhinus*, that is the sister group of the *L. meachami*-*L. hamatus* clade.

THE Permian red-beds of North America are highly fossiliferous and document a diverse terrestrial biota. Members of the reptile family Captorhinidae are common in these deposits, and because of their distinctively hooked snouts, heavily sculptured skull bones, and 'swollen' neural arches, they are among the most distinctive of red-bed fossil taxa. These reptiles occupy a prominent role in discussions of early amniote phylogeny. Although they were once considered the closest fossil relatives of turtles (Clark and Carroll 1973; Gauthier *et al.* 1988; Gaffney 1990), recent work indicates that captorhinids were the first reptiles to have diverged from a lineage that led to the most taxonomically and ecologically diverse reptile group, the diapsids (Laurin and Reisz 1995).

Captorhinid anatomy and interrelationships are known almost exclusively from studies of the Lower Permian genera *Romeria*, *Protocaptorhinus*, *Rhiodenticulatus*, *Captorhinus* and *Labidosaurus*. All these taxa except the last are characterized by small size (skull length under 80 mm), and, except for *Captorhinus aguti*, possess a single row of teeth per jaw (described here as 'single-rowed'). A faunivorous diet has been attributed to these forms (Clark and Carroll 1973; Heaton 1979). Less well known members of the family from younger Permian deposits include the genera *Labidosaurikos*, *Rothianiscus*, *Captorhinikos*, *Gecatogoniphuis*, *Kahueria*, and *Moradisaurus*. All taxa except *Captorhinikos parvus* are large (skull length exceeding 100 mm) and feature 5–11 multiple rows of teeth on medially expanded maxillae and dentaries (henceforth termed 'multiple-rowed'). The dental batteries and the prominent tooth wear suggests strongly that these forms were herbivorous.

One of the best preserved specimens of a large, multiple-rowed captorhinid is the holotypic skull and mandible of *Labidosaurikos meachami*. This specimen, from the Lower Permian Hennessey Formation of Oklahoma, was described briefly by Stovall (1950). He was impressed by the close

resemblance of this captorhinid to *Labidosaurus hamatus*, a large, single-rowed captorhinid from slightly older deposits in north-central Texas.

Several species of large, multiple-rowed captorhinids have been described since Stovall's (1950) work. Despite the apparent close resemblance between *Labidosaurikos* and *Labidosaurus*, recent cladistic studies (Gaffney and McKenna 1979; Ricqlès and Taquet 1982; Ricqlès 1984), have allied the large, multiple-rowed taxa with *Captorhinus aguti*. This postulated sister-group relationship was based solely on the basis of dental characters and suggests that multiple tooth-rows evolved once within Captorhinidae. However, it is unclear at present what significance a monophyletic origin for multiple tooth rows would hold, since the tooth rows in *Captorhinus aguti* are positioned obliquely with respect to the long axis of the jaw, whereas the teeth are aligned with the long axis of the jaw in the large, multiple-rowed taxa (Bolt and DeMar 1975; Ricqlès and Bolt 1983). Furthermore, the recent synonymy of *Eocaptorhinus* under *Captorhinus* (Gaffney 1990) suggests an independent origin for multiple tooth rows in the latter genus, since the former was erected to encompass single-rowed forms otherwise indistinguishable from *C. aguti* (Heaton 1979).

The re-examination of *Labidosaurikos meachami* provided here has three objectives. The first is to provide a thorough description of the cranial anatomy of a large, multiple-rowed captorhinid. All previous descriptions of the cranial anatomy of large captorhinids lack the attention to detail given to those of small captorhinids, and therefore are of limited use in phylogeny and life reconstruction. The second objective is to evaluate the interrelationships of the better known captorhinids using the new cranial information. The resultant phylogeny should help elucidate the origin of multiple tooth-rows in Captorhinidae. Lastly, a brief treatment of the hypothesis of herbivory, attributed to *Labidosaurikos* and other large multiple-rowed captorhinids by Olson (1955, 1971), is presented.

#### MATERIALS

The holotype, OMNH 04331 (formerly MU03-1-S2), is the only known specimen of *Labidosaurikos meachami*. The richly haematitic sediments in which the specimen was deposited are extremely hard and approach the consistency of ironstone. Portions of the skull were cleaned originally by Stovall (1950). Stovall (1950) also removed the lower jaw from the skull, resulting in significant damage to the articular. The braincase was separated from the rest of the skull sometime prior to our study, resulting in loss of bone from the postparietals and the pterygoids. The untouched areas of the specimen were prepared with pneumatic jackhammer, grinder, and pin vice.

The following are abbreviations of the names of the institutions from which specimens were borrowed or examined: FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard University; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; UCLA VP, Vertebrate Paleontology Collections, University of California, Los Angeles.

#### SYSTEMATIC PALAEOLOGY

REPTILIA Laurenti, 1768

EUREPTILIA Olson, 1947

Family CAPTORHINIDAE Case, 1911

Genus LABIDOSAURIKOS Stovall, 1950

*Type species.* *Labidosaurikos meachami* Stovall, 1950.

*Revised diagnosis.* The following description reveals numerous apomorphies that are present in *Labidosaurikos* but are absent in all single-rowed captorhinids and *Captorhinus aguti*. Since these characters cannot be determined faithfully in other large multiple-rowed taxa, they represent ambiguous autapomorphies for *Labidosaurikos meachami*: premaxillary posterodorsal processes short; maxilla dorso-ventrally low in lateral view; septomaxillary facial process present; jugal anterior process deep and transversely thick; jugal medial process bisected ventrally by the maxilla;

postfrontal broad posteriorly; postorbital greatly underlies postfrontal posterior process; squamosal occipital flange lateral portion directed anteroventrally and medial portion expanded slightly posteriorly; parietals domed; supratemporal with distinct dorsal and occipital portions; supratemporal-postparietal contact well developed; squamosal posterior margin notched ventrolaterally; quadratojugal dorso-ventrally tall; quadrate foramen absent; palatine anteromedial process overlies vomer posteriorly; denticles absent from anterior process of pterygoid; basicranial channel present on quadrate flange of pterygoid; epipterygoid with lateral pocket; epipterygoid dorsal process greatly thickened; parasphenoid plate expanded transversely; retractor pit shallow; supraoccipital tall and leans posterodorsally; supraoccipital lateral process feebly developed ventrally; supraoccipital-braincase ossification greatly reduced; paroccipital process compressed dorso-ventrally; paroccipital process sutured to stapedial columella; basioccipital transversely wide; stapedial footplate overlapped by parasphenoid; stapedial foramen relatively small; posttemporal fenestrae large; splenial forms most of jaw symphysis; anterior process of coronoid process short; posteroventral process of coronoid absent.

*Labidosaurikos meachami* Stovall, 1950

Text-figures 1–14

- 1950 *Labidosaurikos meachami*; Stovall, p. 50, pl. 1.  
 1959 *Labidosaurikos meachami*; Seltin, p. 487, fig. 200.  
 1984 *Labidosaurikos meachami*; Ricqlès, p. 13, fig. 3a.

*Holotype*. OMNH 04331, a skull with palate, braincase, and right mandible.

*Diagnosis*. Distinguished from *Labidosaurikos barkeri* Olson, 1954 by the possession of an additional tooth row in both the maxilla and dentary.

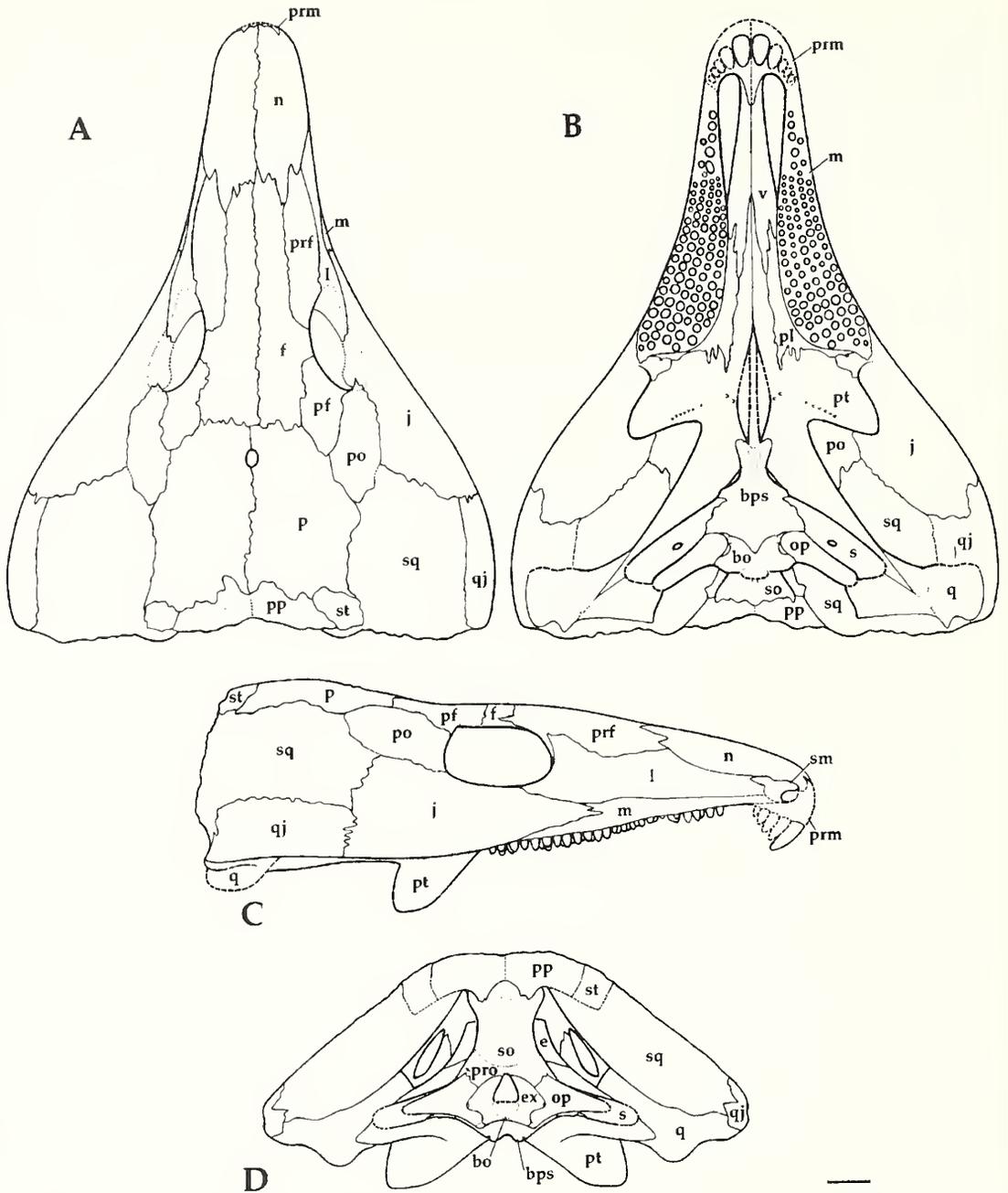
*Horizon and locality*. Collected by J. W. Stovall in 1939 from shales of the Hennessey Formation (Sumner Group), 2.7 km north-east of Crescent, Logan County, Oklahoma; Leonardian, Lower Permian.

DESCRIPTION

OMNH 04331 represents the best preserved cranial material from a large, multiple-rowed captorhinid. Although it is free of distortion, it is missing a large segment of bone from its left half. The high degree of ossification, suggested by the strongly developed external sculpturing and the tightly interdigitating sutures, indicates that the holotype probably came from an adult individual.

The skull (Text-fig. 1) has an estimated total length of about 280 mm. Among captorhinids, only the skull of *Moradisaurus grandis*, with a skull length of 410 mm, is larger (Ricqlès and Taquet 1982). Relative to skull length, the slender snout of *Labidosaurikos* is roughly 25 per cent. longer than those of other captorhinids. Although only one large premaxillary tooth is preserved, the premaxilla of *Labidosaurikos meachami* is reconstructed here with five premaxillary teeth because those of all other captorhinids have four of five teeth that decrease in size posteriorly (with the exception of *Rhiodenticulatus heatoni*, in which the premaxillary teeth are isodont). A relatively long antorbital region has been restored also for *Rothianiscus multidentata* (Olson 1962), but this needs to be confirmed by restudy of the type and referred material. Posteriorly, the skull of *Labidosaurikos* exhibits the broadly flared posterior cheeks characteristic of *Labidosaurus*, *Captorhinus*, and all other multiple-rowed taxa.

In lateral view, the skull (Text-fig. 1c) exhibits the low, wedge-shaped profile of most captorhinids. The maximum height of the skull roof, measured from the top of the postparietals to the base of the quadrate, is approximately 35 per cent. of the length of the skull. In contrast, skulls of single-rowed forms are flat and relatively low; skull height in *Labidosaurus* and *Captorhinus* is roughly 25 per cent. of skull length. The increased height of the skull roof of *Labidosaurikos* contributes to its arched outline in posterior view and may have provided an enlarged internal space for jaw musculature. A high, domed skull roof has been interpreted for other captorhinids. The reconstruction of *Captorhinus aguti* by Fox and Bowman (1966) resembles slightly that of *Labidosaurikos* in posterior view (Text-fig. 1d). However, the skull roof of *Captorhinus* is low and broad



TEXT-FIG. 1. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; reconstruction of skull. A, dorsal view; B, ventral view; C, right lateral view; D, occipital view. Scale bar represents 20 mm.

as in more basal captorhinids (Heaton 1979). Similarly, Clark and Carroll (1973) reconstructed *Romeria prima* (taxonomic emendation of the improperly formed *Romeria primus*, after Heaton 1979) with a tall skull roof, but personal examination of the holotype of *Romeria prima*, MCZ 1963, shows that the skull roof has been elevated by transverse crushing and bending along the squamosal-parietal contact. Olson (1962) restored

*Rothianiscus multidentata* with a lateral profile similar to that given here for *Labidosaurikos*, but the skull table of the former captorhinid was probably not domed (S. Sumida, pers. comm.). Finally, as in other members of the family, the posterior edge of the skull of *Labidosaurikos* is nearly vertical in lateral view, but the braincase is recessed within the skull roof, as seen clearly in ventral view (Text-fig. 1B).

### Skull roof

Although both premaxillae are very poorly preserved, it is clear that each was directed anteroventrally, as in other captorhinids, since the ventral border of the external naris lies at the same level as the ventral border of the maxilla. In contrast with the condition in other early reptiles, where the dorsal process of the premaxilla extends posterodorsally to the level of the external naris, that of *Labidosaurikos* fails to reach even to the level of the anterior narial margin (Text-figs 2–3, 6). Only a single large tooth was preserved in association with the premaxillae. Stovall (1950) restored this tooth immediately below the posterior extent of the external naris, but it was almost certainly the first premaxillary tooth, and, as in other captorhinids, it was succeeded presumably by smaller teeth.

The maxilla (Text-figs 4–6) is the most distinctive cranial element. As in *Rothianiscus* and *Moradisaurus*, the maxilla is greatly enlarged medially, constricting the palate and forming a tooth plate that accommodates six parallel rows of teeth, and is described in detail below. The maximum width of the tooth plate is approximately 25 per cent. of the total length of the bone. Slightly taller teeth, arranged in a single row anteriorly and two smaller rows posteriorly, precede the tooth plate dentition. The maxilla is relatively low in lateral view (Text-fig. 6). In contrast with its great medial expansion, the maxilla is reduced in height laterally, for it has a height-to-length ratio that is roughly one-half that of maxillae in single-rowed captorhinids. The lateral surface of the maxilla can be divided into two regions: anterior to the jugal the external surface is nearly vertical; caudal to this region the maxilla exhibits a lateral flexion of approximately 15–20°. Such flexion marks the beginning of the characteristic cheek swelling found in *Labidosaurus*, *Captorhinus*, and other multiple-rowed captorhinids.

The septomaxilla in most respects resembles closely those of other captorhinids (Text-fig. 6). However, it differs notably in that it has a short, sculptured posterodorsal process that extends onto the skull roof to insert between the lacrimal and the nasal.

The long, narrow lacrimal shares an extensive suture with the jugal that ends well anterior to the orbit (Text-figs 2, 6). The lacrimal and the nasal share a strong overlapping joint; ventrally, an anterodorsal flange of the lacrimal appears to underlie most of the nasal, falling 10 mm short of the internasal suture (Text-fig. 6).

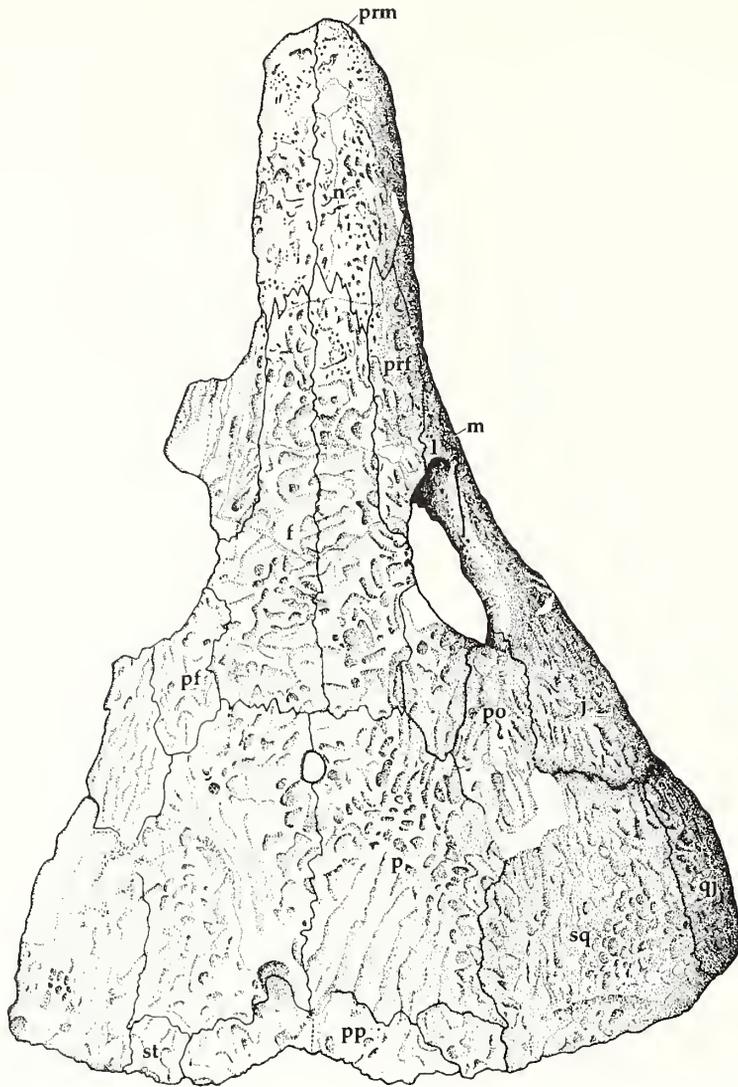
The nasal is slightly broader than those of other captorhinids, and extends ventrolaterally slightly more than half-way down the snout (Text-figs 2–3, 6). In contrast with Stovall's (1950) description, the posterior end of the nasal in both *Labidosaurikos* and *Labidosaurus* is positioned slightly further anterior to the orbits than in other captorhinids, and is undoubtedly related to the presence of a long narrow anterior frontal process in both taxa. Ventrally, the internasal suture is buttressed along a narrow, elevated ridge.

Among captorhinids, the prefrontal of *Labidosaurikos* resembles most closely that of *Labidosaurus* (Text-figs 2–3, 6). The posterodorsal process contributing to the orbital margin is much less acuminate than in other forms. The anterior process of the prefrontal is very long relative to its width and to neighbouring elements; it is approached in relative size only by that found in *Labidosaurus*. Along the anterior orbital margin, the prefrontal has a transversely expanded ventral process that formed an antorbital buttress with the lacrimal.

The frontal is roughly rectangular, and its anterior process is relatively longer and narrower than in all other captorhinids except *Labidosaurus* (Text-figs 2, 4, 6). The frontal lateral lappet, although normally developed dorsally, is overlapped extensively by the prefrontal and postfrontal in ventral view (Text-fig. 4).

Unlike the parietal of other captorhinids, that of *Labidosaurikos* (Text-figs 2–6) is arched in transverse section, such that the paired parietals give the skull roof a slightly domed appearance. Each parietal is also bowed parasagittally, a feature that is accentuated slightly by deformation at the suture shared with the frontal. The elliptical parietal foramen is positioned along the anterior quarter of the interparietal suture, and reflects the anterior displacement of the braincase. The parietal shares overlapping sutures with neighbouring roofing elements that are much more extensive than in earlier captorhinids. As noted by Stovall (1950), the parietal is excluded from the posterior margin of the skull table by the anterodorsal process of the postparietal, a condition found also in *Rothianiscus* (S. Sumida, pers. comm.). The dermal sculpturing most closely resembles that seen in *Labidosaurus*, with which it shares the presence of pits that exceed in size all other pits and grooves. These large pits are found near the parietal foramen and along the suture with the postparietal.

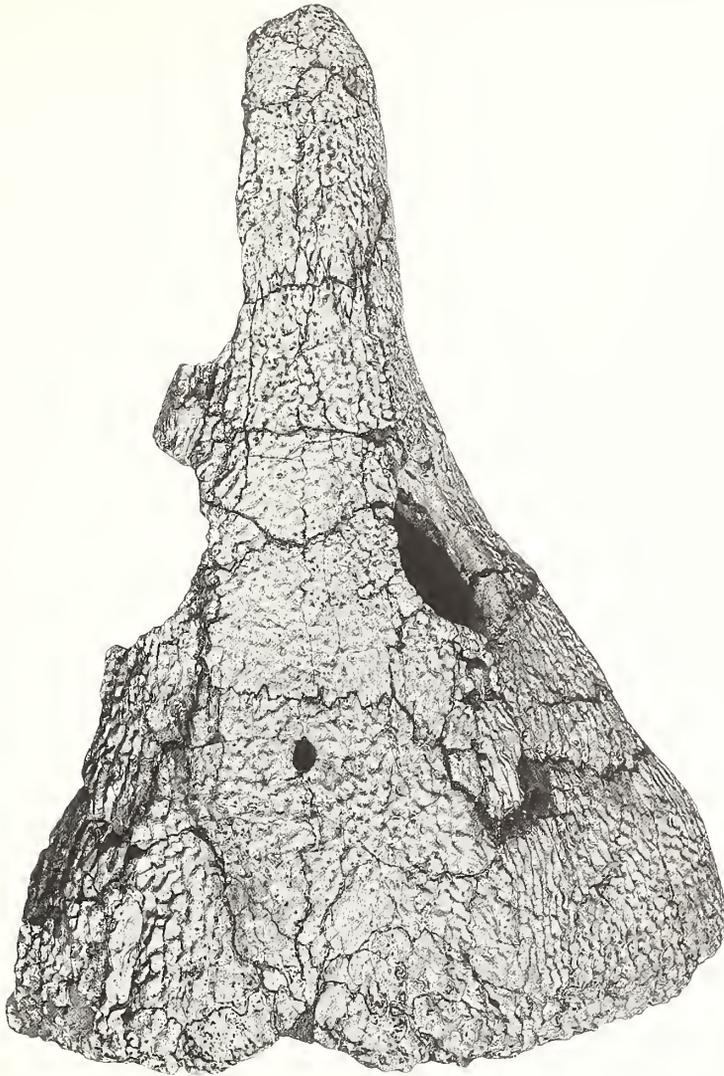
The postparietal (Text-figs 2–4, 7) is unusual in that only the anterior half of the dorsal portion is overlain



TEXT-FIG. 2. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull roof in dorsal view. Scale bar represents 10 mm.

by the parietal, whereas the posterior half is exposed dorsally and is as strongly pitted as the other roofing bones. Accordingly, the postparietals form the median embayment along the occipital margin of the skull roof, as in *Rothianiscus* (S. Sumida, pers. comm.). In contrast, the embayment is formed by the parietals in both *Labidosaurus* and *Captorhinus*. Posteriorly, the postparietal is a flat, lightly scarred plate that is inclined marginally posteroventrally. The anteroventral surface of the postparietal is complex: anterolaterally the postparietal forms a thin flat lamina that underlies the parietal, whereas posteromedially it forms with its mate a stout T-shaped platform that contacted the supraoccipital and the parietal. Unfortunately, when the braincase was removed from the skull, the posterolateral extensions of this platform were damaged. However, enough of the ventral tips of these flanges are preserved in full articulation with the supraoccipital (Text-fig. 7) and demonstrate that they served to strengthen the contact between the skull roof and the occiput.

In most basal eureptiles, the supratemporal is a narrow sliver of bone. In strong contrast, the supratemporal of *Labidosaurikos* (Text-figs 2, 6–7) consists of two plates, joined at roughly 90°. The dorsal portion of the

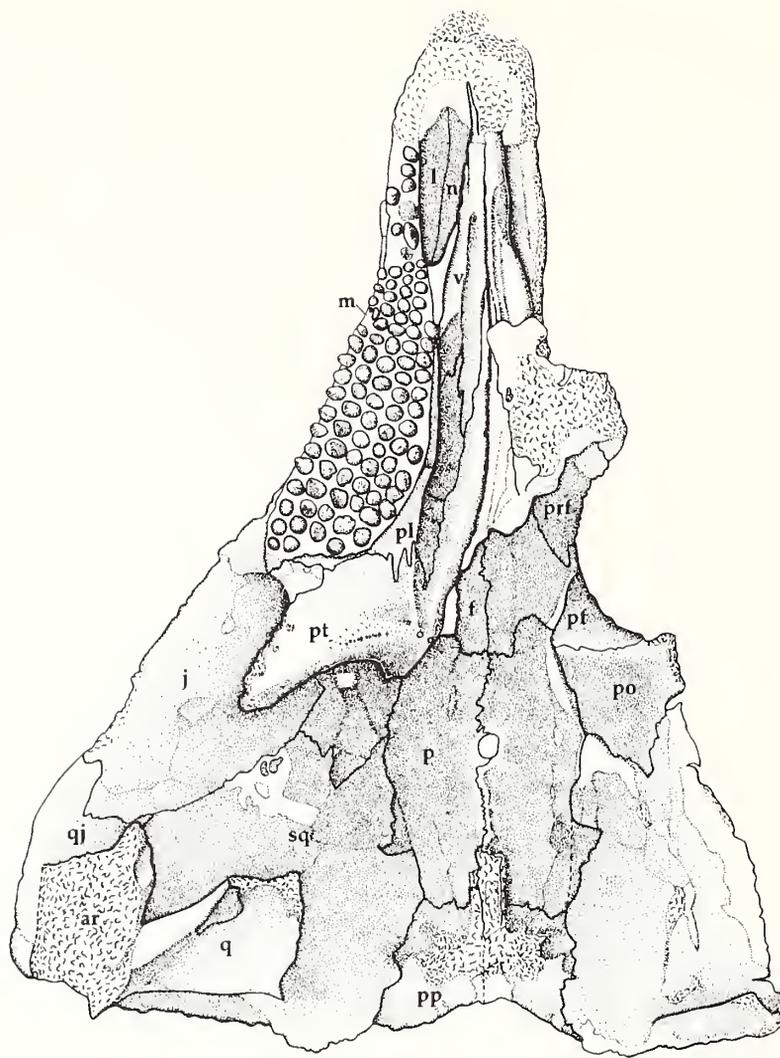


TEXT-FIG. 3. *Labidosaurikos meachamii* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull in dorsal view; for interpretation and scale, see Text-figure 2.

supratemporal does not overlie the posterolateral corner of the parietal as in other reptiles, but instead it overlies the posterodorsal corner of the squamosal. Medially, the supratemporal is sutured firmly to the postparietal.

The postfrontal (Text-figs 2–6) is unique among captorhinids in that the posterior process is relatively broad, plate-like, and more heavily sculptured. Sutures with neighbouring elements in dorsal view are more irregular than in other captorhinids. They are clearly influenced by the pattern of the sculpted pits and furrows, since the sutures occur as gentle curves in ventral view. The free ventral surface of the postfrontal rises slightly posteriorly to form a weak, buttressing ridge along the suture with the postorbital.

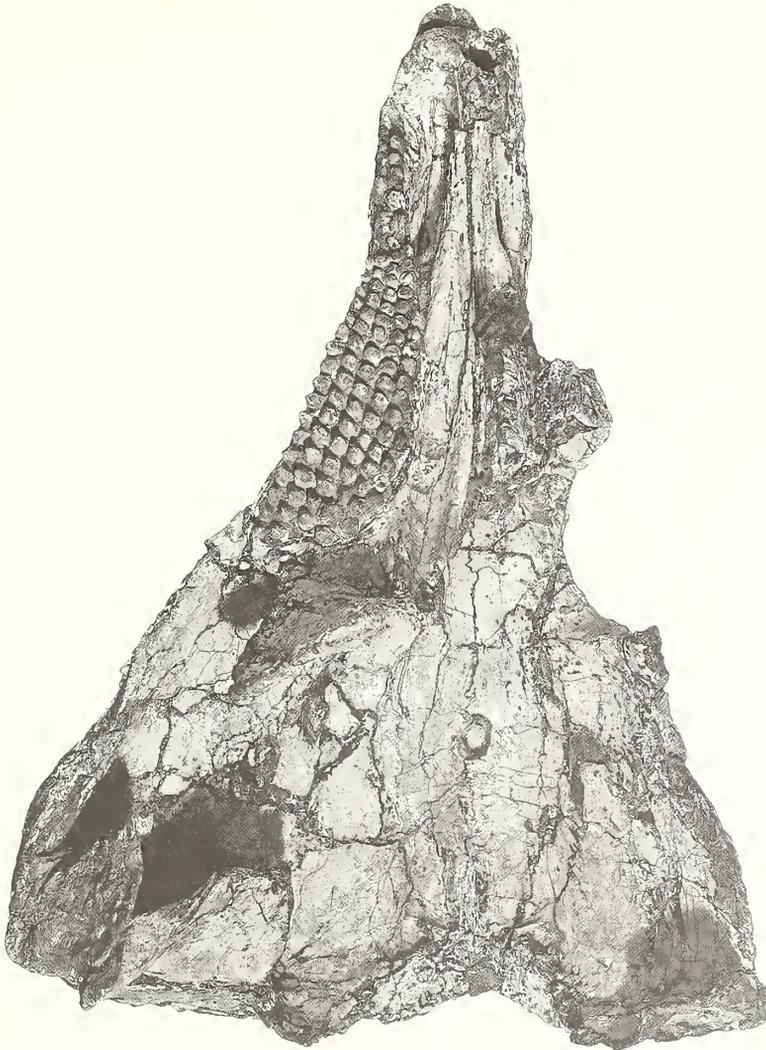
The postorbital (Text-figs 2–6) of *Labidosaurikos* differs little from those of other members of the family, except that a medial triangular flange underlies the posterior process of the postfrontal, and the overlapping suture with the squamosal is strongly developed.



TEXT-FIG. 4. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull roof in ventral view. Scale bar represents 10 mm.

The suborbital ramus of the jugal is extremely tall in lateral view, occupying 40–50 per cent. of the height of the skull in the region of the orbit (Text-fig. 6). Accordingly, the orbital margin is almost straight ventrally instead of concave as in the basal captorhinids. The suborbital process is also very thick transversely, and ends anteriorly with an acuminate tip well forward of the orbit (Text-figs 2, 6). The medial process differs from those of other captorhinids in that it is bisected deeply in ventral view by the posterior tip of the maxilla (Text-fig. 4). The suborbital foramen is relatively tiny. The temporal portion of the jugal is well developed, but does not extend as far posteriorly as in other captorhinids (although it is not as abbreviated as described by Stovall 1950). The dorsal and posterior margins of the temporal portion are deeply overlain by the postorbital and the squamosal and quadratojugal, respectively. The suture with the squamosal is reduced laterally, owing to the slight increase in the height of the quadratojugal. The free ventral margin of the jugal is slightly convex, in contrast with the straight or slightly concave ventral margins of other captorhinid taxa.

In lateral view, the squamosal (Text-figs 2, 4, 6–7) differs little from those of other captorhinid taxa, except that the occipital margin is roughened, and the small posteroventral process extends almost to the ventral



TEXT-FIG. 5. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull without braincase in ventral view; for interpretation and scale, see Text-figure 4.

margin of the skull. The occipital margin of this process is slightly concave posteriorly (Text-fig. 6). The occipital flange is not overlain by the postparietal to the extent seen in the single-rowed captorhinids, and its free edge in posterior view (Text-fig. 7) is slightly less convex in occipital view than in other captorhinids. The flange is also slightly more complex than in other captorhinids: the ventrolateral portion is distinctly plate-like and inclined slightly anteroventrally, whereas the dorsomedial portion is fan-shaped, gently curved, and extends posteriorly beyond the occiput. Laterally, the squamosal overlies the quadratojugal and the jugal to a greater extent than seen in all single-rowed captorhinids except *Labidosaurus*.

The quadratojugal (Text-figs 2, 4, 6–7) resembles those of *Labidosaurus* and *Captorhinus* most closely among captorhinids, except that it has a large, rounded boss that buttresses the lateral condyle of the quadrate, and the quadrate foramen is absent.



visible in the figures. Despite the great medial expansion of the maxillary tooth plate, the palatine maintains its posterior contact with the medial process of the jugal.

The pterygoid (Text-figs 2, 6, 8) retains the triradiate organization characteristic of all early amniotes, but is edentulous except for a narrow band of tiny denticles and small teeth that are aligned along the posterior margin of the transverse flange. The palatine ramus of the pterygoid of *Labidosaurikos* is slender as in *Labidosaurus*, but differs from those of all single-rowed captorhinids in that it is raised slightly above the transverse flange. The transverse flange resembles most closely that of *Labidosaurus* in that its base is relatively narrow, but it is inclined slightly more to the frontal plane, at approximately 70°. The quadrate ramus does not differ from that of *Labidosaurus* or *Captorhinus*, except in size and in the region surrounding the basicranial recess. Here, the pterygoid supports the basicranial portion of the epipterygoid with broad anterior and narrow posterior ridges, and a deep groove runs anteroventrally between the two ridges from the recess.

The epipterygoid (Text-figs 7, 10–11) differs in a number of features from those of single-rowed captorhinids. The columella is a relatively large, transversely flattened pillar that arches slightly posterodorsally. On the lateral surface, a prominent ridge runs down from the base of the columella to the anteroventral corner of the epipterygoid proper. A well defined pocket, of uncertain function, lies immediately posterior to this ridge near the base of the columella. The basicranial recess is inclined posterodorsally, and is slightly more elongate than in other captorhinids.

Among captorhinids, the quadrate (Text-figs 4, 7–8) of *Labidosaurikos* resembles most closely those of *Labidosaurus* and *Captorhinus* in orientation and general proportions. There is no shallow pit on the medial surface of the dorsal lamella to receive the paroccipital process. The condyles cannot be described, because of the *in situ* preservation of the articular.

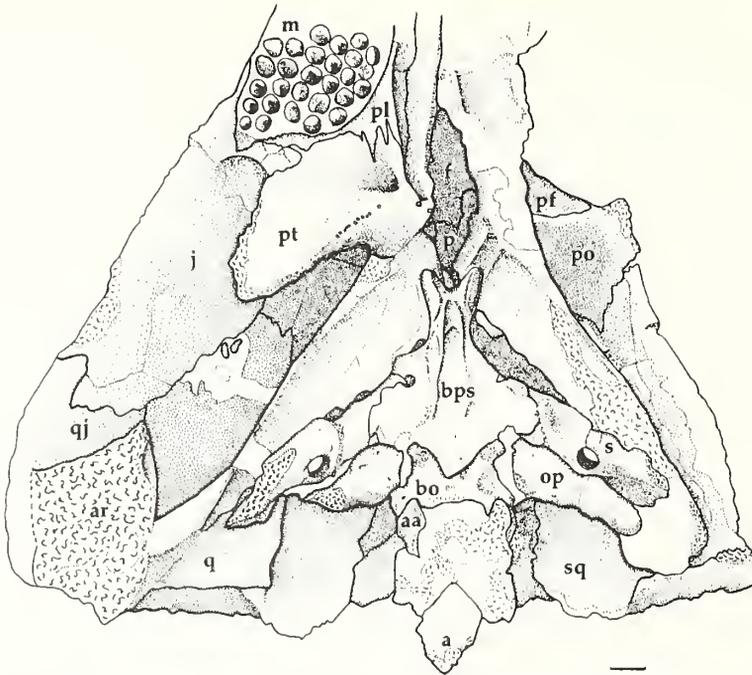
### Braincase

The braincase of the holotype represents the only known material for *Labidosaurikos meachami*. Surprisingly, Stovall (1950) ignored it in his description. A second braincase, assigned originally to *Labidosaurikos* by Olson (1967) and described by MacLean (1970), was later attributed to *Seymouria* (Olson 1979). Of the three major units of the skull, the braincase appears to be the most highly modified from the basic reptilian pattern among captorhinids. In all parts of the skull there is a tendency towards increased ossification and structural reinforcement. However, the braincase of *Labidosaurikos* is unusual in that the sutures between the occipital elements and the rest of the braincase may have been replaced by cartilage; there appears to have been little or no osseous contact between the supraoccipital and the opisthotics and exoccipitals. As reconstructed, the post-temporal fenestra (Text-fig. 1b) is larger and relatively taller than in single-rowed captorhinids, a feature that may be attributed to the increased height of the skull.

Since the parasphenoid and the basisphenoid are fused indistinguishably, the resultant complex is referred to here as the basiparasphenoid. In ventral view, the basiparasphenoid (Text-figs 8–9, 11) is organized in the same manner as in *Labidosaurus* and *Captorhinus*, except that it is considerably wider and distinctly more diamond-shaped. Furthermore, the trough between the cristae ventrolaterales is shallower posteriorly than in those taxa. The basiparasphenoid appears to overlap the stapedial footplate more deeply than in other captorhinids. As in *Labidosaurus* and *Moradisaurus*, the cultriform process projects anterodorsally from between the basiptyergoid processes at roughly 60° to the horizontal plane. Only the base of the process is present, but in relative dimensions this is almost twice as thick transversely and taller anteroposteriorly than those of other captorhinids. The bifaceted basiptyergoid processes are slightly more slender in lateral view than are those of other captorhinids. In ventral aspect, the processes appear parabolic and project slightly laterally. In contrast, those of other taxa appear truncated anteriorly and do not project as far anterolaterally. In lateral view, the sella turcica is greatly constricted between the cultriform process anteriorly and the dorsum sella posteriorly. The clinoid process is poorly developed, such that the retractor pit is much shallower than in other captorhinids. The dorsum sella resembles that of *Captorhinus* (Price 1935), but it is much thicker anteroposteriorly. Its apex is unfinished and was probably topped with cartilage.

Except for its larger size, and the observation that its sutures with neighbouring elements are more serrate, the proötic (Text-fig. 11) differs little from that of *Captorhinus* (Price 1935). Since the supraoccipital was preserved slightly above the remainder of the braincase with an intervening layer of matrix, the nature of the contact between it and the proötic is not clear; the two elements may have been connected via cartilage.

In single-rowed captorhinids, the medial end of the opisthotic resides largely within a concave recess of the exoccipital. There is no indication that an ossified recess exists for the opisthotic of *Labidosaurikos* (Text-figs 7–9, 11) and contact with the other occipital elements was probably completed by cartilage. Ventrally, however, the basioccipital recess is present, but the bones are separated by a distinct gap which suggests that an



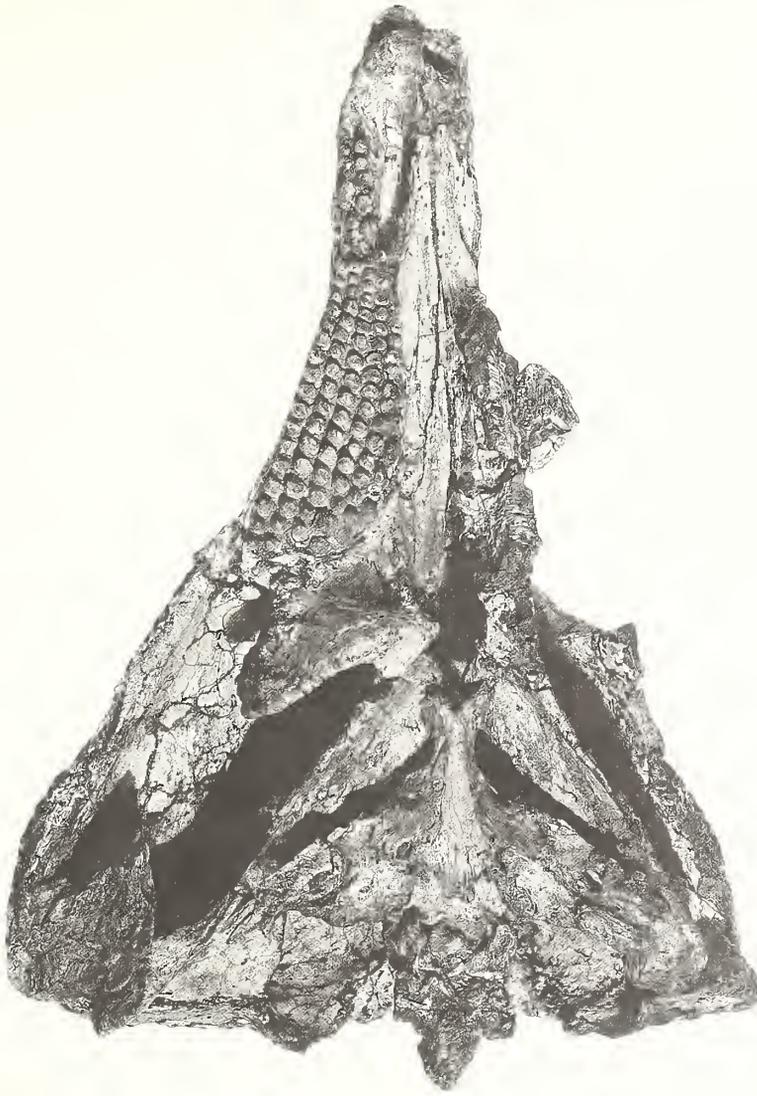
TEXT-FIG. 8. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; braincase and partial palate in ventral view. Scale bar represents 10 mm.

intervening layer of cartilage was present. The paroccipital process is dorso-ventrally flattened and rod-like, with a slightly rounded tip, which probably reflects damage; those of single-rowed captorhinids are circular in cross section, and possess truncated tips. The paroccipital process differs further from those of other captorhinids in that it is sutured to the stapedial columella. Based on their reconstructed dimensions, it is likely that the distal tips of both structures were finished with cartilage that extended posterolaterally to contact the medial surface of the quadrate.

The supraoccipital (Text-figs 7, 11) is greatly modified over the pattern exemplified by *Captorhinus* (Price 1935). Most striking is the absence of a true osseous connection with the rest of the neurocranium. When the skull was collected, the supraoccipital was suspended above the braincase by a bridge of matrix in the position it probably assumed in life. The surrounding elements form a clean, symmetrical margin around the base of the supraoccipital, but there is no apparent bony contact. In most captorhinids, the supraoccipital serves as the major support for the braincase; therefore, it is unusual that portions may have been replaced by cartilage, especially so for *Labidosaurikos*, one of the largest captorhinids. This development suggests that the basicranial articulation and the stapedial-opisthotic complex provided a greater degree of support than in the single-rowed forms. The supraoccipital is distinguished further among captorhinids by its greater height and strong posteroventral lean (Text-fig. 11B). The anterior ascending process and the posterior median ridge of the supraoccipital are better developed than in the single-rowed captorhinids. The lateral ascending process is well developed dorsally, but ventrally it is feebly developed. This is in strong contrast with the condition in *Captorhinus* in which the reverse is true. The lateral ascending process of the supraoccipital features a large opening, of uncertain function, on its dorsolateral edge. No such opening has been reported in other captorhinids.

The exoccipitals (Text-fig. 7) are poorly exposed. Apart from their larger size, they do not differ markedly from those of other captorhinids. The anterodorsal surface of the exoccipital appears to be covered in spongy bone; attachment to the supraoccipital was probably accomplished via cartilage rather than through a sutural contact. As in other early reptiles, the exoccipital was probably fused ventrally to the basioccipital.

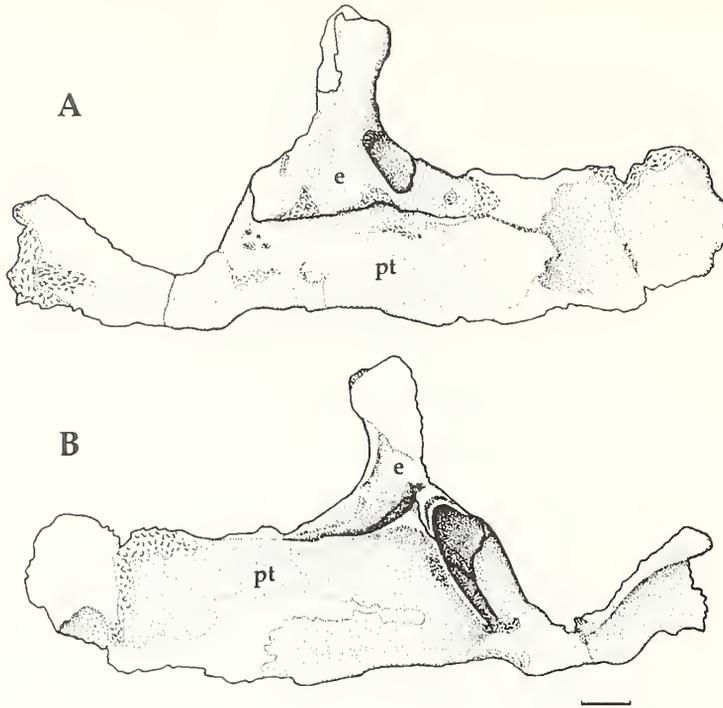
Ventrally, the basioccipital (Text-fig. 8) is much wider with respect to the rest of the braincase than in single-rowed taxa. As in *Labidosaurus*, there is a small, open space between the ventrolateral tuber of the basioccipital and the anteromedial corner of the opisthotic; this space is located immediately ventral to the lagenar recess



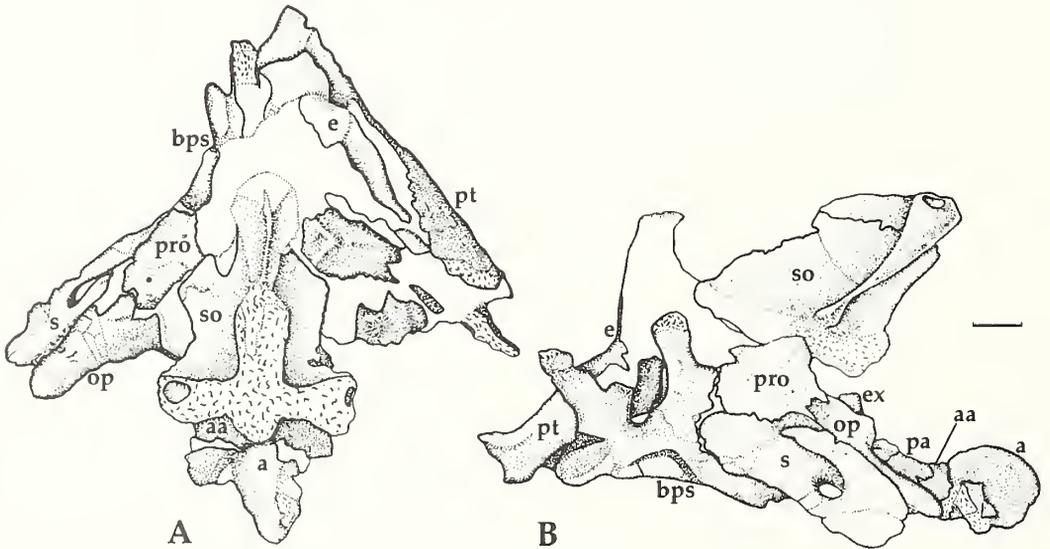
TEXT-FIG. 9. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; skull with braincase in ventral view; for interpretation and scale, see Text-figures 4 and 8.

of the opisthotic in *Captorhinus* (Price 1935). Posterior to the tuber, the basioccipital abuts firmly against the opisthotic. The condyle is absent, and the posterior margin of the basioccipital forms a thin, sharp edge. The absence of the condyle is problematical, since fragments of the atlas-axis complex are preserved in association with the occiput. Remnants of the condyle may have been displaced dorsally and obscured by the surrounding vertebral fragments.

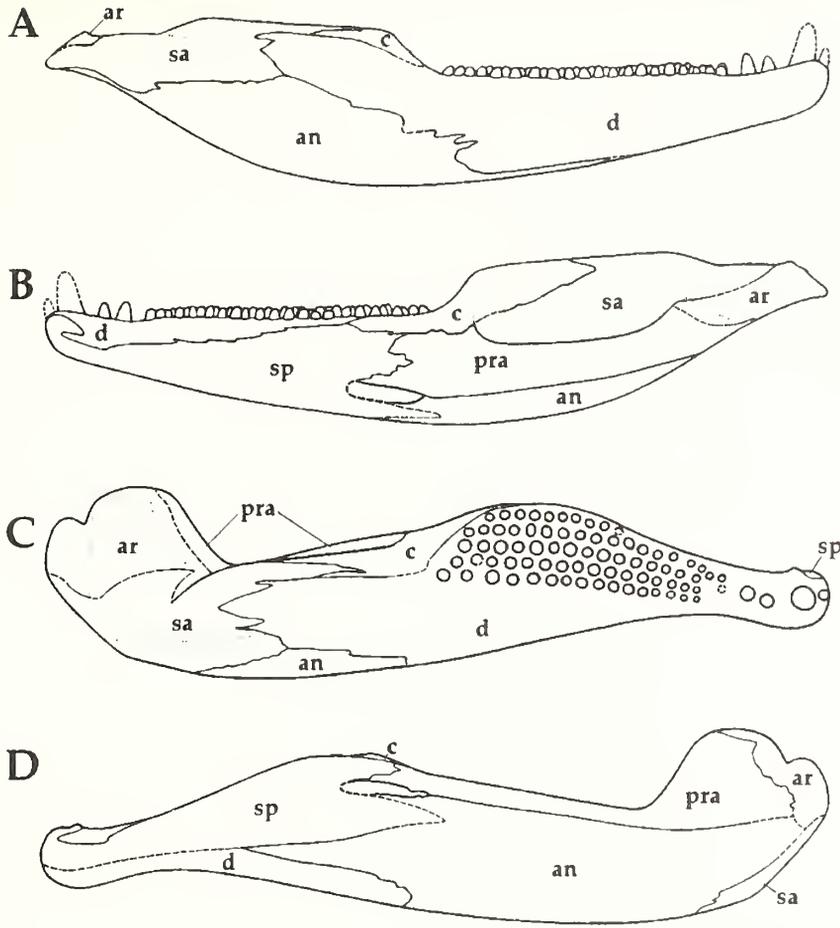
Both stapes are preserved in perfect contact with the braincase (Text-figs 7–9, 11). As in other captorhinids, the stapes is massively constructed, but its footplate is relatively much narrower in lateral view and its columella is deeper antero-ventrally. As in *Labidosaurus*, the stapedia footplate is covered slightly in ventral aspect by the posterolateral wing of the parasphenoid. In *Captorhinus* and most early reptiles, the footplate simply abuts the braincase. The stapedia foramen pierces the columella near the midpoint of the stapes, as opposed to the condition in other captorhinids, where it is positioned immediately distal to the footplate. In



TEXT-FIG. 10. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; epipterygoid and quadrate flange of pterygoid. A, lateral view; B, medial view. Scale bar represents 10 mm.



TEXT-FIG. 11. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; braincase. A, dorsal view. B, left lateral view. Scale bar represents 10 mm.



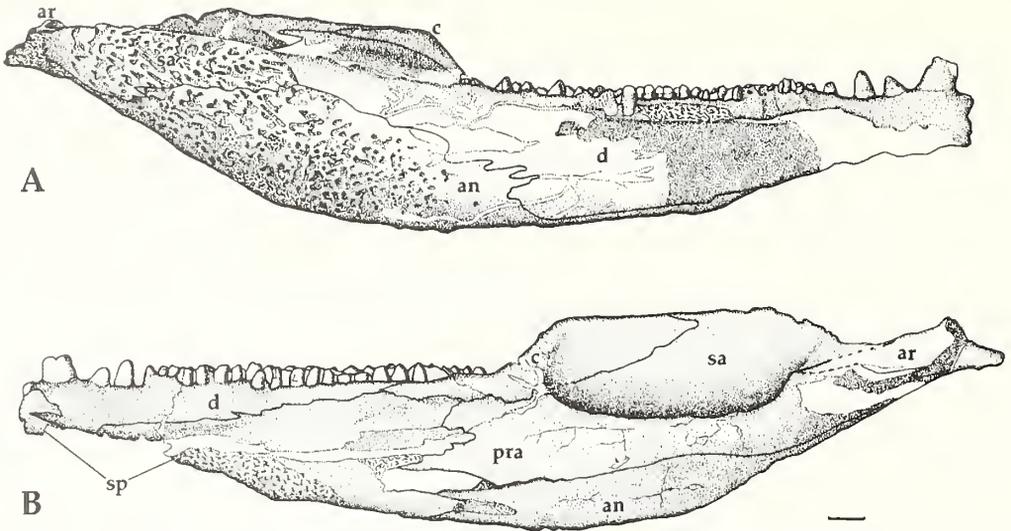
TEXT-FIG. 12. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; reconstruction of right mandible. A, lateral view; B, medial view; C, dorsal view; D, ventral view. Scale bar represents 20 mm.

addition, the stapedial foramen is rounder and relatively smaller than in other taxa. The dorsal process resembles closely that of *Labidosaurus*.

#### Lower jaw

The mandible of *Labidosaurikos* (Text-fig. 12) is remarkably broad for most of its length, and most closely resembles those of *Rothianiscus* and *Moradisaurus* among captorhinids. The maximum jaw width is roughly 14 per cent. of the total length of the jaw, whereas in *Captorhinus* this figure is not more than 9 per cent. The increase in mandibular breadth in *Labidosaurikos* is most apparent when the lower jaw is articulated with the dermal skull roof: its convex labial margin projects as much as 35 mm beyond the lateral edge of the skull, whereas the lower jaws of single-rowed captorhinids are flush with the lateral skull margin. In contrast with its width, the relative height of the mandible is similar to that of other members of the family. In dorsal and ventral views, the mandible has a distinctly sigmoidal outline. A relatively large posterior meckelian foramen (= foramen intermandibularis caudalis of some authors) occupies the lingual surface of the jaw; all single-rowed captorhinids except *Labidosaurus* and an unnamed taxon (FMNH UC 183) feature a small meckelian foramen. Since Stovall (1950) did not describe the mandible, beyond mention of the number of tooth rows present in the dentary, the mandible is described here in detail.

Like the maxilla, the alveolar ridge of the dentary (Text-figs 13–14) is greatly expanded transversely to



TEXT-FIG. 13. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; right mandible. A, lateral view; B, medial view. Scale bar represents 10 mm.

accommodate multiple rows of teeth. Five rows of teeth, aligned along the longitudinal axis of the jaw and curved slightly lingually, interdigitate perfectly with the opposing tooth plate of the maxilla. Four larger teeth precede the tooth plate, among which the second tooth is clearly the largest. Surprisingly, the dentary forms little of the actual sutural surface of the jaw symphysis; this region is overlain almost entirely by the splenial. The posterolateral end of the dentary extends further posteriorly than in single-rowed captorhinids, almost as far as the articulating facet for the jaw suspension. It forms with the surangular a wide lateral shelf at the base of the coronoid process.

In contrast with the condition seen in other captorhinids, where the jaw symphysis is formed equally between the splenial and the dentary, the splenial of *Labidosaurikos* (Text-figs 13B, 14A) forms most of the sutural surface of the symphyseal pad. The symphyseal pad of *Labidosaurikos* is relatively smaller than that of *Labidosaurus* and other single-rowed forms, another characteristic that is shared with *Moradisaurus* (Ricqlès and Taquet 1982). Immediately posterior to the symphyseal pad, the splenial narrows abruptly to a slender neck, but then increases greatly in height and width posteriorly. In ventral view, the splenial dominates the anterior half of the jaw.

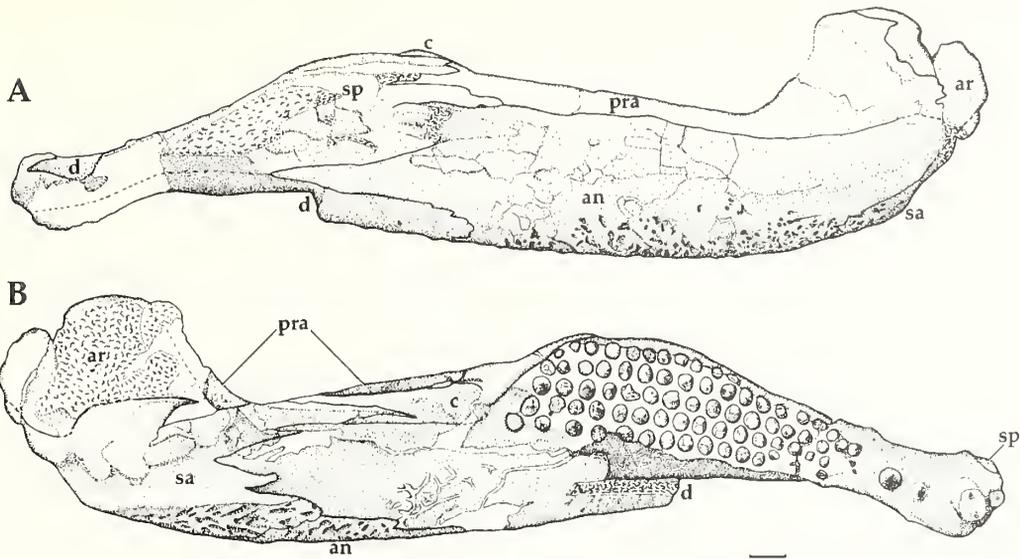
The coronoid (Text-figs 13–14) is modified distinctly over the form seen in most single-rowed captorhinids. The anterior process is short in contrast with the elongate anterior process present in *Labidosaurus* and *Captorhinus*. The posteroventral ramus is completely absent. The posterodorsal process is very deep dorsoventrally, and forms the dorsal ridge of the coronoid process in both medial and lateral views. The posterodorsal process is bifurcated deeply by the surangular in dorsal view.

Dorsally, the surangular (Text-figs 13–14) contributes a sharp ridge to the coronoid process. A broad, lateral shelf projects nearly perpendicularly from the base of the coronoid portion. Posteriorly, this shelf curves medially to form a flat rugose platform for the articular. Ventral to this shelf, the surangular is strongly convex laterally and has a deep overlapping suture with the dentary anteriorly and the angular ventrally.

The angular (Text-figs 13–14) is a large, broadly convex bone that comprises most of the posteroventral corner of the mandible. It is relatively long, approximately equal to the dentary in length. The posterior end, broadly tongue-shaped in ventral aspect, is narrowly acuminate in lateral view, owing to the dorso-ventral flattening of the posterior end of the jaw.

The prearticular (Text-figs 13B, 14) resembles those of other captorhinids, except that the anterior end, contacting the coronoid and splenial, is relatively deeper dorso-ventrally.

The articular (Text-figs 13–14) is compressed dorso-ventrally, a condition shared with *Moradisaurus*. The articulating facet for the quadrate is damaged and there is little surface detail, such that no more than its basic outline is visible. The posterolateral boss of the articular is reasonably preserved and delimits the posterior extent of the facet. The short, broad retroarticular process is similar to that seen in *Labidosaurus*.



TEXT-FIG. 14. *Labidosaurikos meachami* Stovall; Lower Permian; Oklahoma; OMNH 04331, holotype; right mandible. A, ventral view; B, dorsal view. Scale bar represents 10 mm.

### Dentition

Only one premaxillary tooth (not illustrated) is preserved; it is the largest tooth and probably represents the first premaxillary tooth. Stovall (1950) reconstructed it erroneously below the posterior end of the external naris. As in most other captorhinids, this tooth is massive, with an estimated antero-posterior basal diameter of 19 mm and a transverse diameter of 9 mm. It differs from the corresponding tooth in other taxa in that it is slightly recurved.

For descriptive purposes, the maxillary and dentary dentitions of multiple-rowed captorhinids can be subdivided into two areas, multiple (MR) and single row (SR) regions (Bolt and DeMar 1975; Ricqlès and Bolt 1983). Interestingly, there are two short rows in the posterior SR region of the maxilla of *Labidosaurikos* (Text-fig. 4); these teeth do not appear to be part of the tooth plate proper. Otherwise, the teeth here resemble closely those of *Labidosaurus*. As in that genus, there is a weakly developed maxillary caniniform region, but there is no tooth that can be described as a caniniform. The anterior two dentary teeth have been damaged since the original description, but the photographs figured by Stovall (1950) indicate that they projected vertically as in *Labidosaurus*.

As in all large, multiple-rowed captorhinids, the tooth rows of *Labidosaurikos meachami* are nearly parallel to the lateral margins of the maxillary and dentary (Text-figs 4, 14B). Damage to the dentary tooth plate (Text-fig. 13A) reveals that implantation was protothecodont. Apart from the teeth, the tooth plates are covered by recalcitrant matrix, such that there is no direct evidence of MR tooth replacement in *Labidosaurikos*. However, the MR region of *Gecatogomphius kavejevi* features a few resorption pits (R. Reisz, pers. comm.), and is the best evidence for MR tooth replacement in the large, multiple-rowed captorhinids.

The four labial rows of the maxillary tooth plate consist of 17–18 teeth each, whereas the two lingual rows have 14 and four teeth (Text-fig. 4). The MR teeth are isodont pegs. There is a gradual decrease in tooth diameter anteriorly in the four labial rows, but tooth height is fairly consistent. Wear facets are present on most teeth in the MR region. In the outermost maxillary row, wear is confined largely to the lingual surface of each tooth. However, wear is found principally on the labial surface of the innermost maxillary teeth; all intervening maxillary teeth possess wear facets on both lingual and labial surfaces. The small anterior MR teeth are the most severely worn, whereas only a few posterolingual teeth on the edge of the dental platform have escaped wear. There is considerably more wear on MR teeth than on SR teeth, which suggests that they were used for grinding, whereas the SR teeth were probably responsible for simple shearing.

## DISCUSSION

*Phylogenetic relationships*

There have been several phylogenetic analyses of captorhinid interrelationships published recently (Gaffney and McKenna 1979; Ricqlès and Taquet 1982; Ricqlès 1984; Berman and Reisz 1986). All have allied the large, multiple-rowed captorhinids with *Captorhinus aguti* on the basis of dentition alone. However, the above description reveals several non-dental characters shared by *Labidosaurikos* and the large, single-rowed captorhinid *Labidosaurus hamatus* that are not present in *C. aguti*. It is therefore necessary to re-evaluate the interrelationships of *Labidosaurikos*, *Labidosaurus* and *Captorhinus*.

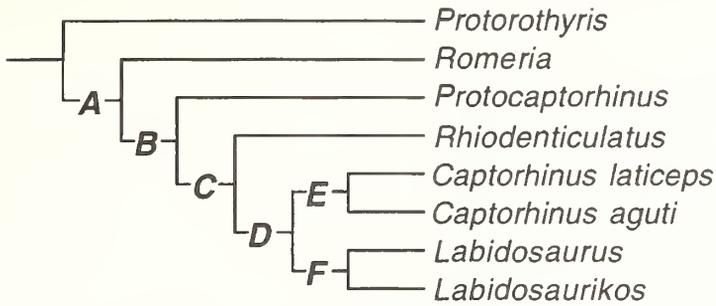
The following taxa form the ingroup: *Captorhinus aguti*, '*Eocaptorhinus*' *laticeps*, *Labidosaurus hamatus* and *Labidosaurikos meachami*. *Captorhinus aguti* is perhaps the best known captorhinid (Price 1935; Fox and Bowman 1966; Ricqlès and Bolt 1983). We also had access to excellent, articulated and disarticulated cranial material referable to this captorhinid that was collected recently from the Fort Sill fissure-fill locality. The genus *Eocaptorhinus* was recently made a junior synonym of *Captorhinus* by Gaffney (1990). Since Gaffney (1990) identified what was formerly '*E. laticeps*' only as '*Captorhinus* sp.', we recognize this single-tooth rowed form as a valid taxon for the purposes of phylogenetic investigation, regardless of its generic identity. The large single-rowed taxon *L. hamatus* has been linked closely with both *Captorhinus* and *Labidosaurikos*. Since the most recent study of the cranial anatomy of this large captorhinid was by Williston (1917), information on this form is taken from MCZ 8727, UCLA VP 3167, and UCLA VP 3200.

The following taxa serve as outgroups: *Rhiodenticulatus heatoni*, *Romeria texana*, *Protocaptorhinus pricei*, and *Protorothyris archeri*. The captorhinid *Rhiodenticulatus heatoni* was described recently on the basis of two skeletons from New Mexico (Berman and Reisz 1986) that were also available to us for examination. The basal captorhinids *Romeria texana* and *Protocaptorhinus pricei* were illustrated and described briefly by Clark and Carroll (1973). The protorothyridid *Protorothyris archeri* (Clark and Carroll 1973) serves as a non-captorhinid outgroup.

Although *Labidosaurikos* appears to share several apomorphies with other large multiple-rowed captorhinids (noted in the description), these forms are omitted from the analysis because they are less adequately known than other captorhinid taxa. These problematic taxa include *Gecatogomphius kavejevi*, a Russian form known only from fragmentary tooth-bearing bones (Olson 1962); *Moradisaurus grandis*, a large African taxon represented by a complete skull, although sutural patterns are unknown (Ricqlès and Taquet 1982); *Rothianiscus multidonta*, distinguished by its rows of massive, occlusally flattened teeth (Olson and Beerbower 1953; Olson and Barghusen 1962), and its congener *R. robusta* (Olson 1965). Similarly, the available literature on the cranial anatomy of *Captorhinikos chozaensis*, *C. valeusis*, *C. parvus* and *Kalmeria seltina* is inadequate by recent standards. Lastly, *Labidosaurikos barkeri*, represented by fragmentary cranial and postcranial materials (Olson 1954), probably represents a junior synonym of *Labidosaurikos meachami* (Seltin 1959). All these taxa need to be restudied, since they are distinguished from one another largely by their dentition or by size (Olson 1954; Seltin 1959; Olson and Barghusen 1962).

Thirty-nine characters were used in the analysis. Several are from previous studies (Gaffney and McKenna 1979; Berman and Reisz 1986), but many are new. No postcranial characters were used, since *Labidosaurikos* is known only from cranial material, and the postcranial skeleton is known adequately only in *Labidosaurus*, *Captorhinus* and *Rhiodenticulatus*. The analysis was run on a Macintosh Quadra 800 computer using the branch-and-bound algorithm of PAUP 3.1, which is guaranteed to find the most parsimonious trees. All characters were optimized using delayed transformation (DELTRAN) and run unordered.

One parsimonious tree was found (Text-fig. 15). It has a tree length of 49 steps and a consistency index of 0.918 excluding uninformative characters. *Labidosaurikos* is most closely related to *Labidosaurus* among the taxa considered here. This relationship is very robust, as 13 more steps are



TEXT-FIG. 15. Hypothesis of relationships for *Labidosaurikos meachami*. Interior branches are defined by the following unambiguous characters: *A* (diagnosing Captorhinidae), premaxillary ventral margin aligned antero-ventrally ('premaxilla hooked' of earlier literature); maxilla posterior end flexed laterally; tabular absent and postparietal transversely elongate; caniniform region present anteriorly on dentary; pineal foramen positioned anterior to midpoint of interparietal suture; maxillary dentition reduced to 25 or fewer teeth. *B*, postparietals partially separated ventrally by supraoccipital; skull table posterior margin straight; retroarticular process present. *C*, quadratojugal square-tipped anteriorly. *D*, maxillary dentition ends posteriorly at level of orbital midpoint; postorbital region expanded laterally; skull table posterior margin with single median embayment; pterygoid transverse flange narrow and tongue-like; parasphenoid with deep groove present between cristae ventrolaterales; mandibular posterior end acuminate; marginal 'cheek' teeth chisel-shaped. *E* (diagnosing *Captorhinus*), jugal medial process positioned dorsally on anterior process; retroarticular process elongate; anterior dentary teeth procumbent. *F*, snout narrow; frontal anterior process long and narrow; supratemporal-postparietal contact well-developed; pterygoid transverse flange narrow; supraoccipital posterodorsal processes tall; occipital condyle positioned anterior to jaw symphysis; large pits present on posterior skull table; mandibular ramus sigmoidal in ventral view; mandibular ramus broad in ventral view; adductor shelf present ventrolateral to coronoid process; meckelian foramen large; coronoid posterodorsal process expanded dorso-ventrally; maxillary caniniform teeth absent; caniniform tooth present anteriorly on dentary with caniniform region absent.

required to break it and unite *Labidosaurikos* with *Captorhinus*. The sister-group relationship between *Labidosaurikos* and *Labidosaurus* is supported by the presence of 15 synapomorphies, listed below. The number of the character is enclosed by parentheses, and derived states other than '1' are enclosed by square brackets. Minus signs indicate reversals, and ambiguous characters are denoted by asterisks:

1. Snout narrow (5).
2. Prefrontal anterior process long (\*6).
3. Frontal anterior process long (-7).
4. Supratemporal-postparietal contact well developed (12).
5. Cultriform process projects anterodorsally at more than 45° to the basal plane (\*20 [2]).
6. Supraoccipital lateral ascending processes tall (22).
7. Occipital condyle anterior to level of jaw suspension (23).
8. Large sculpture pits present on posterior skull table (25).
9. Mandible sigmoidal (26).
10. Mandible broad (27).
11. Lateral shelf present below coronoid process (29).
12. Meckelian foramen large (31).
13. Coronoid posterodorsal process expanded dorso-ventrally (32).
14. Maxillary caniniform teeth absent (35).
15. Dentary caniniform tooth present (38 [2]).

The cladistic analysis supports the hypotheses of Ricqlès and Taquet (1982) and Berman and Reisz (1986) concerning the positions of the basal captorhinids within Captorhinidae. However, our tree differs notably from those of previous phylogenetic studies (Gaffney and McKenna 1979;

Ricqlès and Taquet 1982; Ricqlès 1984) in that *Labidosaurikos* is more closely related to the single-tooth rowed *Labidosaurus* than *Captorhinus*. The close relationship of *Labidosaurikos* and *Labidosaurus* is the most robust proposed for any two captorhinid taxa.

A corollary of our phylogeny is that the origin of multiple-tooth-rows in Captorhinidae is diphyletic. This is not unusual, given that serial repetition of tooth-rows evolved independently in rhynchosaurs. Bolt and DeMar (1975) remarked that their explanation for the development of multiple-tooth-rows in *C. aguti*, reiterated by Ricqlès and Bolt (1983), might require modification if it were to be applied to the *Labidosaurikos* and other large, multiple-rowed captorhinids. Our results suggest that this would indeed be the case, but a detailed examination of tooth-row development and tooth replacement in *L. meachamii* is beyond the scope of the present study.

*Captorhinus aguti* and '*Eocaptorhinus*' *laticeps* are recognized officially here as sister taxa. This sister-group relationship is relatively robust, since three additional steps are required to break it. It supports Gaffney's (1990) recent synonymy of *Eocaptorhinus* under *Captorhinus*. Since Gaffney (1990) abstained from identifying the single-rowed form as anything other than '*Captorhinus* sp.', we therefore recognize formally the new combination *Captorhinus laticeps*. This species of *Captorhinus* appears to be separable from *C. aguti* only by the presence of single rows of marginal teeth, although it is possible that a thorough re-examination of skulls and tooth-bearing elements assigned by Heaton (1979) to '*Eocaptorhinus*' *laticeps* may determine apomorphies distinguishing the former species from the latter. We rediagnose *Captorhinus aguti* by the presence of multiple rows of teeth that are aligned divergently across dental laminae. The sister-group relationship between these two taxa also provides the opportunity to rediagnose the genus itself. *Captorhinus* was diagnosed heretofore by the presence of multiple rows of teeth (Seltin 1959; Fox and Bowman 1966; Clark and Carroll 1973; Heaton 1979), which we interpret instead as an autapomorphy of *C. aguti*. We redefine the genus *Captorhinus* on the basis of the following apomorphies:

1. Alary process of jugal positioned dorsally on medial surface and flush with orbital margin (8).
2. Retroarticular process longer antero-posteriorly than broad (33).
3. Antermost dentary tooth strongly procumbent (39).

Despite the presence of relatively strong relationships between some captorhinid taxa, we have not been able to improve upon certain aspects of captorhinid phylogeny. The weakest part of the tree is the position of *Rhiodenticulatus*, as node C is diagnosed by a single apomorphy. Interestingly, it takes only one more step for *Rhiodenticulatus* to either exchange positions with *Protocaptorhinus*, or for these two taxa to form a clade. Since the anatomy of *Rhiodenticulatus* is reasonably well known, it is entirely possible that future studies on basal captorhinids will alter the position of *Rhiodenticulatus* within Captorhinidae. Furthermore, the status of two characters recognized traditionally as captorhinid apomorphies, the absence of the ectopterygoid and the presence of a medial process of the jugal, is regarded here as ambiguous. Neither character can be determined faithfully in any of the specimens assigned to *Roueria*, whereas only the latter was detected by Heaton (1979) in *Protocaptorhinus*. Re-examination of these two taxa should resolve the uncertainty regarding such problematical characters.

Lastly, we note in the description that *Labidosaurikos* shares several apomorphies with *Gecatogomphius*, *Moradisaurus*, *Rothianiscus*, *Captorhinikos* and *Kahneria*, implying that they form a clade (the 'Moradisaurinae' of Ricqlès and Taquet 1982). However, despite an unprecedented high number of new cranial apomorphies revealed by our redescription, the available literature on other large, multiple-rowed captorhinids is so poor that we could not identify a single unambiguous autapomorphy for *Labidosaurikos meachamii*. These multiple-rowed forms need to be restudied in order to identify unambiguous autapomorphies for *Labidosaurikos meachamii* and to determine the exact relationships of these taxa to *Labidosaurikos* and *Labidosaurus*. Additional work on multiple-rowed captorhinids may result in modifications to the phylogeny presented here, or at least change the distribution of the character states. Furthermore, it is quite possible that future studies may determine that some of the more problematical captorhinid species (those represented by partial, fragmentary remains) may be recognized as junior synonyms of better known taxa.

### Diet

Stovall (1950) refrained from speculating upon the probable diet of *Labidosaurikos*. Indeed, no one has cared to discuss the diet of the large, multiple-rowed captorhinids except Olson (1955, 1971), who regarded them as herbivores. The morphology of the tooth plates and other aspects of the skull support the hypothesis that *Labidosaurikos* was herbivorous.

In general, the tooth plate teeth are relatively small, isodont, and bear prominent wear facets. When the jaws were adducted, the mandibular tooth rows would have rested between maxillary tooth rows. Comprised of relatively small, serially repeated teeth, the tooth plates of *Labidosaurikos* present multiple contact points that could pass one another in a single motion, a feature necessary for shredding fibrous plant material (Throckmorton *et al.* 1981). For shredding to occur, propalinal jaw movement must be possible. Not surprisingly, propaliny has been identified in several early herbivorous tetrapod lineages (Throckmorton *et al.* 1981; King *et al.* 1989; Olson *et al.* 1991). Striation patterns on wear facets have been used to determine the direction of mandibular motion in both reptiles and mammals (Greaves 1973; Weishampel 1983). Unfortunately, no striations are visible on the teeth of *Labidosaurikos* under light microscopy. Evidence for propalinal jaw movement in this reptile instead must be determined from non-dental evidence.

In their investigation of herbivory in dicynodont therapsids, King *et al.* (1989) established the ability of the quadrate to slide antero-posteriorly over the articular as the most important evidence for propaliny. Unfortunately, the articulating surfaces of the quadrate and articular are damaged in the holotype of *Labidosaurikos*, and it is uncertain to what extent propaliny may have been present. Fore-and-aft movement of the lower jaw has been proposed for two other captorhinids. The morphology of the suspensorium in *Moradisaurus* suggests strongly that the lower jaw of that genus was capable of fore-and-aft translation (Rieqlès and Taquet 1982). Similarly, Heaton (1979) suggested that propaliny was also present in *Captorhinus*. However, examination of quadrates and articulators from the Fort Sill locality that are referable to *Captorhinus* suggests that this is not the case. The observation that the articular of *Labidosaurikos* resembles more closely that of *Moradisaurus* than those of more basal captorhinids suggests that the suspensorium of the former genus also may have fostered propaliny. Regardless, determination of whether the jaw articulation of *Labidosaurikos* was osteologically capable of propaliny must await better preserved material.

There is additional osteological evidence that may suggest the presence of propaliny in *Labidosaurikos*. Apart from the jaw articulation morphology, King *et al.* (1989) noted that the adductor musculature must have been arranged appropriately in dicynodonts to effect relative movement of the lower jaw. The antero-posteriorly elongate temporal fenestrae of dicynodonts was interpreted by King *et al.* (1989) to suggest that the jaw adductor muscles originating in the temporal region were angled sufficiently to draw the lower jaw posteriorly. Although the anapsid condition of captorhinids precludes comparison with the synapsid condition of dicynodonts, the temporal region of the skull roof of *Labidosaurikos* does differ from those of *Labidosaurus*, *Captorhinus* and the more basal captorhinids in that it is notably vaulted. This doming, formed mainly by the paired parietals, but expressed also in the unusual posterior expansion of the occipital flange of the squamosal, suggests that the majority of muscle fibres of the adductor mandibulae muscles arising from this region would have inserted onto the coronoid process at an angle of approximately 45° to the horizontal. If this interpretation is correct, this arrangement of the jaw adducting musculature would have served adequately to draw the lower jaw posteriorly in what was presumably the power stroke of propalinal jaw action. The fibres arising from the skull roof were presumably better positioned for effecting and controlling relative movement of the lower jaw than those arising from the palate, which probably served to draw the mandible forwards in recovery. The slightly greater ventral incline of the pterygoid transverse flange of *Labidosaurikos* with respect to the orientation observed for those of *C. aguti* and single-rowed captorhinids supports the latter hypothesis. A more extreme anterior positioning of this flange in dicynodonts was thought by King *et al.* (1989) to be associated directly with propaliny in these synapsids.

The hypothesis of herbivory attributed here to *Labidosaurikos* can be extended to other large,

multiple-rowed captorhinids. The tooth plates of *Captorhinikos*, *Rothianiscus*, *Moradisaurus* and *Gecatogomphius*, although differing from one another and those of *Labidosaurikos* in terms of tooth size, number of tooth-rows and relative size, share a fundamental organization that suggests they were used for the same purpose: the mechanical breakdown of fibrous plant matter. However, additional research on these forms is needed to confirm this hypothesis. Future work on these long-neglected taxa should elucidate further the hypothesis of herbivory attributed to these early reptiles.

*Labidosaurikos meachami* and its multiple-rowed relatives represent the culmination of a series of morphological changes in the family Captorhinidae that resulted ultimately in a worldwide radiation as herbivores. Heaton and Reisz (1981) and Dilkes and Reisz (1986) have commented upon the lack of variation in captorhinid postcranial anatomy with respect to that seen in other early amniote groups. It is quite possible that this conservative nature, associated with an adaptation to herbivory, may have been responsible for the success of the captorhinids during the Permian.

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## ABBREVIATIONS USED IN THE TEXT-FIGURES

a	axis	f	frontal	pf	postfrontal	s	stapes
aa	axis neural arch	j	jugal	pl	palatine	sa	surangular
an	angular	l	lacrimal	prm	premaxilla	sm	septomaxilla
ar	articular	m	maxilla	po	postorbital	so	supraoccipital
bo	basioccipital	n	nasal	pp	postparietal	sp	splenial
bps	basiparasphenoid	op	opisthotic	prf	prefrontal	sq	squamosal
c	coronoid	p	parietal	pro	proötic	st	supratemporal
d	dentary	pa	proatlas	pt	pterygoid	v	vomer
e	epipterygoid	pra	prearticular	q	quadrate		
ex	exoccipital			qj	quadratojugal		

## APPENDIX 1

Description of characters used in the phylogenetic analysis: primitive character states are denoted by 0, and derived states are indicated by 1 or 2.

1. Premaxilla: ventral margin aligned antero-posteriorly (0) or antero-ventrally (1) in lateral view.
2. Maxilla: relatively straight (0) or posterior end flexed laterally (0).
3. Maxilla: posteriormost tooth positioned at level of posterior margin of (0) or positioned at level of midpoint of (1) orbit.
4. Lacrimal: suture with jugal small (0) or well developed (1).
5. Snout: broad, equal to or greater than 35 per cent. of skull length (0) or narrow, equal to or less than 25 per cent. of skull length (1).
6. Prefrontal: anterior process short and tall, approximately equal to the posterodorsal process in antero-posterior length (0) or long and narrow, approximately twice the antero-posterior length of the posterodorsal process (1).
7. Frontal: anterior process short, less than 40 per cent. of the frontal sagittal length (0) or long, approximately 55 per cent. of the frontal sagittal length (1).
8. Jugal: alary process absent (0), present and positioned no higher than the midpoint of the suborbital process of the jugal and distinct from orbital margin (1), or positioned dorsally on the medial surface of the jugal and flush with orbital margin (2).
9. Quadratojugal: antero-posteriorly elongate (0) or short, not extending anteriorly beyond midpoint of postorbital region (1).
10. Quadratojugal: acuminate (0) or square-tipped (1) anteriorly.
11. Postorbital cheek: relatively straight (0) or expanded laterally (1).
12. Supratemporal: contact with postparietal tenuous (0) or well developed (1).
13. Pineal foramen: positioned at (0) or anterior to (1) midpoint of interparietal suture.
14. Postparietal: contacts mate fully along height (0) or dorsally only, postparietals separated slightly ventrally by supraoccipital (1).
15. Postparietal: transversely short with tabular present (0) or transversely elongate with tabular absent (1).
16. Skull table occipital margin: embayed bilaterally (0), straight (1), or with single median embayment (2).
17. Ectopterygoid: present (0) or absent (1).
18. Pterygoid: transverse flange broad-based and distinctly angular (0) or narrow and tongue-like (1) in ventral view.
19. Parasphenoid: deep ventral groove absent (0) or present (1) between cristae ventrolateralis.
20. Cultriform process: extends anteriorly (0), extends slightly dorsally at roughly 15° to the basal plane (1), or extends anterodorsally at more than 45° to the basal plane (2).
21. Supraoccipital: slopes anterodorsally (0), or vertically (1), or is angled posterodorsally (2).
22. Supraoccipital: lateral ascending processes account for half or less (0) or two-thirds or more (1) of the height of the bone.
23. Occipital condyle: at level of (0) or immediately anterior to (1) quadrate condyles.
24. Paroccipital process: short (0) or rod-like (1).
25. Sculpturing: consists of small honeycombing pits and grooves (0) or of pits and grooves with notably larger, randomly positioned pits on posterior skull table (1).

26. Mandibular ramus: relatively straight (0) or sigmoidal (1) in ventral view.
27. Mandibular ramus: narrow, 8 per cent. or less of total jaw length (0) or broad, no less than 14 per cent. of total jaw length (1).
28. Mandibular ramus: posterior end rectilinear (0) or acuminate (1) in lateral view.
29. Mandibular ramus: lateral shelf absent (0) or present (1) below coronoid process.
30. Coronoid: anterior process short (0) or elongate (1).
31. Meckelian foramen: small, antero-posterior length roughly 9 per cent. or less of total jaw length (0) or large, antero-posterior length greater than or equal to 14 per cent. of total jaw length (1).
32. Coronoid posterodorsal process: slender, forms dorsalmost quarter of lateral wall of adductor fossa (0) or deep, forms dorsalmost third of lateral wall of adductor fossa (1).
33. Retroarticular process: absent (0), present and broader transversely than long (1), or present and longer antero-posteriorly than broad (2).
34. Maxillary dentition: tooth stations number 30 teeth or more (0) or 25 or less (1); for multiple-rowed taxa, only those teeth with unobstructed profiles when viewed laterally are considered.
35. Maxillary caniniform teeth: present (0) or absent (1).
36. Multiple tooth rows: absent (0) or present (1).
37. Marginal dentition: 'cheek' teeth conical (0) or chisel-shaped (1).
38. Dentary: teeth isodont (0), caniniform region present anteriorly (1), or caniniform tooth present anteriorly with caniniform region absent (2).
39. Dentary: first tooth oriented mainly vertically (0) or leans strongly anteriorly (1).

## APPENDIX 2

Distribution of character states among the seven captorhinids examined in the analysis. The numbers in the top column (1–39) refer to the characters described in Appendix 1. A question mark indicates that the character state could not be determined because of missing data.

Character number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taxon:																				
<i>Protorothyris</i>	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
<i>Romeria</i>	1	1	0	0	0	0	0	?	1	0	0	0	1	0	1	0	?	0	0	0
<i>Protocaptorhinus</i>	1	1	0	?	0	0	0	1	1	0	0	0	1	1	1	1	?	0	0	0
<i>Rhiodenticulatus</i>	1	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0	0	0
<i>C. laticeps</i>	1	1	1	1	0	0	0	2	0	1	1	0	1	1	1	2	1	1	1	1
<i>C. aguti</i>	1	1	1	1	0	0	0	2	0	1	1	0	1	1	1	2	1	1	1	1
<i>Labidosaurus</i>	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	2	1	1	1	2
<i>Labidosaurikos</i>	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	2	1	1	1	2
Character number:	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
Taxon:																				
<i>Protorothyris</i>	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Romeria</i>	0	?	0	?	?	0	0	0	0	?	?	?	?	0	1	0	0	0	1	0
<i>Protocaptorhinus</i>	0	0	0	1	0	0	0	0	0	?	?	?	?	1	1	0	0	0	?	0
<i>Rhiodenticulatus</i>	?	0	0	?	?	0	0	0	0	1	?	?	?	1	0	0	0	1	0	
<i>C. laticeps</i>	0	0	0	1	0	0	0	1	0	1	0	0	2	1	0	0	1	1	1	
<i>C. aguti</i>	0	0	0	1	0	0	0	1	0	1	0	0	2	1	0	1	1	1	1	
<i>Labidosaurus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	2	0	
<i>Labidosaurikos</i>	2	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	2	0	







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Cover: This specimen of *Calymene blumenbachii* from the Wenlock of Dudley is mounted in gold, forming the centrepiece of a nineteenth century brooch presented to the Natural History Museum by Miss E. Begg.

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# PHYLOGENETIC ANALYSIS AND ORDINAL CLASSIFICATION OF THE BRACHIOPODA

by LARS E. HOLMER, LEONID E. POPOV, MICHAEL G. BASSETT  
and JOHN LAURIE

**ABSTRACT.** The long-standing division of the lophophorate Phylum Brachiopoda into two units of Class rank, the Articulata and Inarticulata, is not supported by phylogenetic (cladistic) analysis. Using the PAUP program, two separate analyses, for seven extant brachiopod orders/suborders and for the combined extant and extinct groups, respectively, are consistent in identifying all chitinophosphatic-shelled stocks as a sister group to the carbonatic-shelled brachiopods, which include both 'inarticulates' and 'articulates' of previous schemes. The chitinophosphatic-shelled stocks are united in the Class Lingulata, but within the Brachiopoda, contrary to the proposals of Gorjansky and Popov (1985). The carbonatic-shelled brachiopods form the Class Calciata, embracing the Subclass Craniformea (including Craniida, Craniopsida, and Trimerellida), and a yet un-named Subclass that includes the Obolellida, Kutorginida, and the 'articulates'. The precise affinities of the kutorginides remain enigmatic, although they are clearly calciate. The proposed relationships suggest that brachiopods are monophyletic and had consistently separate shell chemistries from early in their phylogeny, removing the need for the repeated transformations in biomineralization inherent in previous evolutionary models.

OUR recent outline summary of the higher level classification of the lophophorate Phylum Brachiopoda (Popov *et al.* 1993) recognizes two taxonomic units of Class rank, the Lingulata and Calciata, embracing three units of Subclass rank, the Lingulatea, Craniformea, and 'Articulata'. Such a scheme of systematic classification and nomenclature differs markedly from the previous long-accepted subdivision of the Phylum into the classes Inarticulata and Articulata (e.g. Williams and Rowell 1965, pp. H214-234), and stems essentially from the conclusion that the chitinophosphatic-shelled 'inarticulates' of former classifications constitute a natural group that has little in common with the carbonatic-shelled 'inarticulates', apart from the fact that both lack an articulatory mechanism incorporating a hinge with teeth and sockets and are thus not 'articulates' in the commonly accepted sense, as expounded by Gorjansky and Popov (1985, 1986), Holmer (1991*a*), and Popov (1992).

Following Hennig's (1966, fig. 47; Text-fig 1A herein) original use of a cladistic (phylogenetic) methodology to analyse the phylogeny and systematics of the Brachiopoda, there has been considerable subsequent debate on the subject, in which a variety of theories has been proposed to explain relationships within the Phylum (see Popov *et al.* 1993; Carlson 1995). A number of these subsequent analyses has also employed phylogenetic methods, generally with significantly different results. In the latest of these studies prior to our own work, Carlson (1991, 1995) rejected the revised scope and status of the 'Inarticulata' proposed by Gorjansky and Popov (1985, 1986); some of the points of difference in these analyses and interpretations have already been the subject of preliminary discussion (Carlson 1994; Bassett *et al.* 1994). In this context, it is immediately interesting to note that Hennig's (1966) analysis, which was based on the taxonomically definitive characters of brachiopods propounded by Helmcke (1939, fig. 227), lends strong support to the Gorjansky and Popov model.

The purpose of this paper is therefore two-fold. First, to assess previous cladistic models of brachiopod phylogeny as a means of understanding the differences from and implications for our own model (Popov *et al.* 1993). And then to incorporate any common views into an expanded

discussion of proposed relationships and their nomenclatorial expression. Our analysis is confined to systematic relationships between the major groups assigned conventionally to the Brachiopoda, and does not address the further question of the origins of the Phylum. A number of authors have outlined the current, widely divergent views on this latter question as part of the debate surrounding the origin and early evolution of metazoans as a whole (e.g. Ghiselin 1989; Bergström 1991, fig. 4; Dzik 1991, fig. 4; Schram 1991; Schopf and Klein 1992). Our ultimate conclusion as to brachiopod monophyly is an obvious contribution towards this debate, in support of other recent analyses of phylogenetic relationships within the group (e.g. Rowell 1981, 1982; Carlson 1991, 1995).

*Note.* For brevity and convenience throughout this paper we refer to chitinophosphatic-shelled and carbonatic-shelled brachiopods as phosphatic and calcareous, respectively.

## METHODS

Data matrices (Tables 1 and 2) derived from our selection of what we take to be taxonomically significant characters (see below) have been analysed cladistically using the PAUP program (Phylogenetic Analysis Using Parsimony 3.1.1; Swofford 1993). A total of 40 characters was selected from both extant and extinct brachiopod stocks. The data were analysed separately for the seven extant groups of Order and Suborder rank alone, and secondly for combined characters from the ten living and fossil stocks. In the first analysis the exhaustive search option was used on a data matrix derived from 35 unordered and unweighted characters (Table 1). For the analysis of the combined data, the exhaustive search option was used in analysing 26 unordered and unweighted characters (Table 2).

### *Character selection*

What we take to be diagnostic characters were selected both from the soft-body of brachiopods and from the shell.

Any attempt to reconstruct soft-body anatomy in extinct stocks is clearly interpretative and/or highly speculative. We thus consider it best to make separate analyses of phyletic relationships for the extinct and extant lineages of brachiopods. At the same time, however, we emphasize the point that some features of soft anatomy (mainly the muscle systems, mantle and pedicle) can be inferred confidently in the majority of extinct lineages from an interpretation of shell morphology.

Our work stems initially from our joint evaluation of all the 'inarticulate' brachiopods of previous classifications for the forthcoming revision of Part H of the *Treatise on invertebrate paleontology*; as such, it is beyond our remit, and the scope of this paper, to analyse in detail all the extinct 'articulate' stocks and their relationships. However, because of the implications of relationships between some groups of the 'inarticulates' and the 'articulates' it is necessary to consider some details of the latter, and therefore as representatives of all these groups we use characters derived from the superfamilies Orthoidea and Protorthoidea, based on the commonly held consensus that the earliest Cambrian orthides were among the most plesiomorphic 'articulates' (Williams and Rowell 1965, p. H174; Williams and Hurst 1977, p. 92); in this regard the nisusiids and the calcareous-shelled genera *Kotujella* and *Matutella* were excluded because they require further study before their affinities can be determined.

### *Characters not used*

The limited available knowledge of the ontogeny, and sometimes also the soft anatomy (e.g. nervous system and coelomic partitioning in various 'articulates') of most Recent brachiopods, make it highly speculative to use several features that might otherwise be important for the definition of major clades and their phylogenetic relationships. Thus, for example, the interpretation and homology of subdivisions of the coelom in various brachiopod larvae is a matter of ambiguity, with a separation

into proto-, meso- and metacoel remaining a subject of speculation and numerous different interpretations (Gorjansky and Popov 1985, 1986). The larva of *Neocrania* has as many as four pairs of coelomic sacs (Nielsen 1991), and that of *Terebratulina* only two pairs (Percival 1944). In other calciates, coelomic partitioning has not been investigated. Carlson's (1991, fig. 2; 1995, Appendix 2, character 22) proposed character, based on an imperfect separation of the mesocoel and metacoel, is therefore of doubtful use. The origin of holoperipheral growth in one or both valves is another good example of doubtful homology. We have not used such characters, in an attempt to reduce the influence of homoplasy on the results.

Similarly, unlike some previous investigations, we also question the use of 'functional characters', such as 'large number of gametes released per spawning event', 'larval propulsion accomplished with lophophoral cilia', 'brooding uncommon', etc. Characters of this kind can hardly be homologous and must surely reflect extreme homoplasy; it is difficult to see what use they can have in cladistic analyses. The assumption by Carlson (1991, 1995) that the introduction of a large number of such character conflicts will not outweigh the homologous characters is not proven (see further below, p. 735).

Another complex of rejected characters is related to various plesiomorphic 'absence features', which have been used by some authors for definition of different lineages. We have commented previously on this practice (Bassett *et al.* 1994, p. 3; see also Forey 1990, p. 432), and reiterate our view that it is unsatisfactory to define any group mostly on characters that are absent.

#### *Outgroup selection*

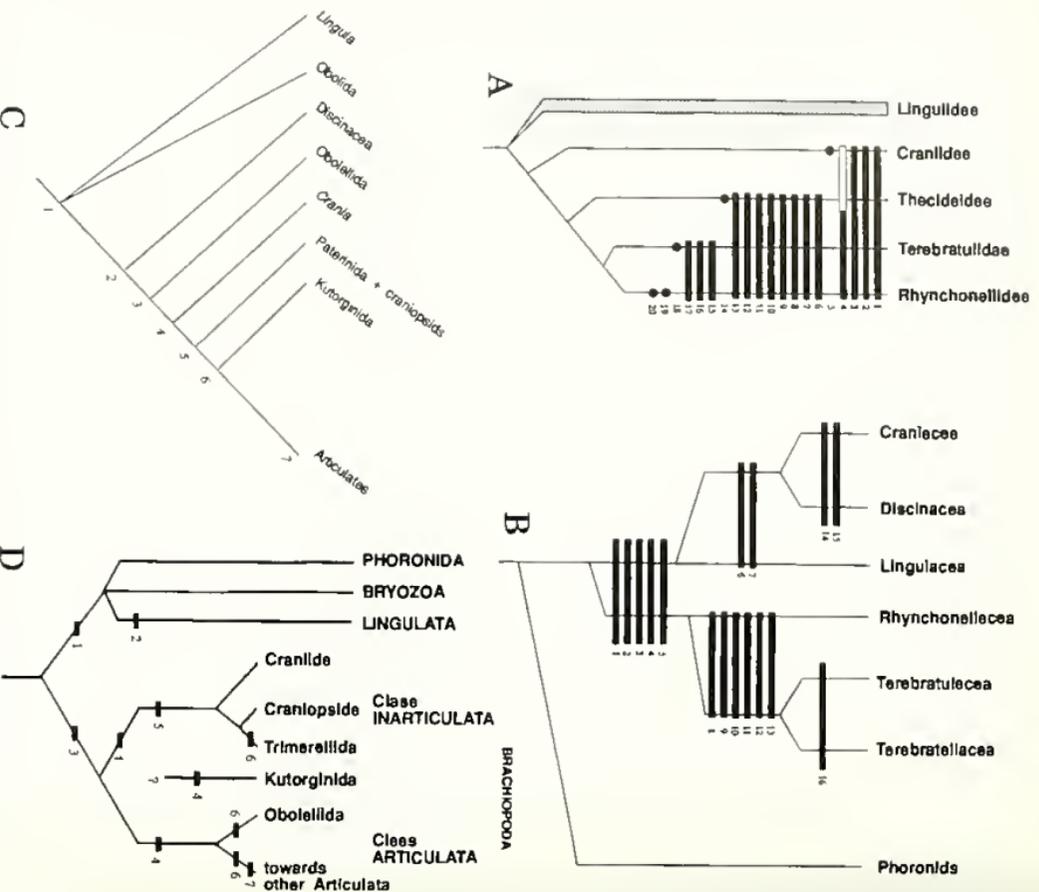
As noted by Carlson (1991, 1994, 1995) the selection of outgroups for determining the polarity of character transformations in brachiopods presents a number of problems. Bryozoans and phoronids are potential candidates, but Carlson (1995) also used Pterobranchia and Sipunculida. Priapulids have also been linked with the brachiopods (Runnegar and Curry 1992; Conway Morris 1994) and might also be outgroup candidates. However, because all these groups lack a bivalved shell, their body plans are fundamentally different and cannot be used to polarize most brachiopod characters.

In our previous analysis (Popov *et al.* 1993) we rooted our trees using a 'phoronid-like' ancestor, apart from the few instances where this group would appear to have derived characters. Notwithstanding the fact that the use of a 'hypothetical' outgroup has validity for some uncertain states (Maddison *et al.* 1984), it can be regarded as a way of *a priori* manipulation of the data set (Carlson 1994); in order therefore to avoid this possibility, in this paper we have chosen to use phoronids as an outgroup.

As noted by Nielsen (1991), brachiopods may not have originated from an ancestor within the Phoronida, but it might be argued that the lophophore anatomy, as well as the nervous system of phoronids, may retain primitive characters. The organization of the brachiopod body plan is dependent largely on its formation within an enclosed filtering chamber (Valentine 1981; Valentine and Erwin 1987), and it is not unreasonable to assume that the characters of the phoronid lophophore, functioning without a filtering chamber, are more primitive.

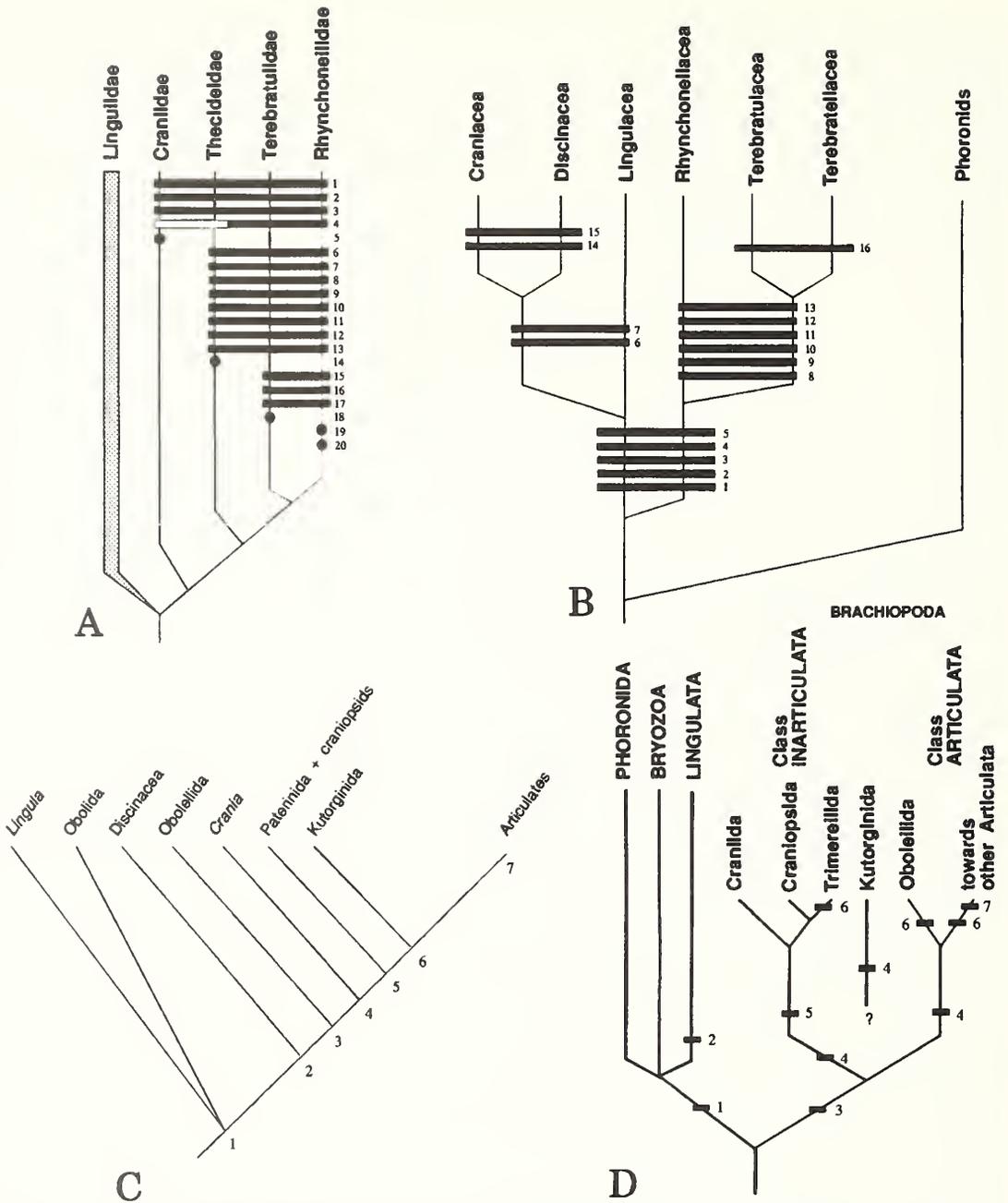
As we have noted previously (Bassett *et al.* 1994), we consider the bryozoans to be less useful as an outgroup. The bryozoan lophophore also functions without a filtering chamber, but is highly modified through a complex process of metamorphosis during ontogeny (Nielsen 1985, 1987). In any event, bryozoans are highly polymorphic in their anatomy and morphology, and it remains extremely difficult to select generalized characters for a 'typical' bryozoan body plan. In this respect, the phoronids constitute a much smaller and more homogeneous group.

Although the choice of an outgroup (or combination of outgroups) obviously influences the result of any analysis, it is not without interest to note that the topology of our proposed cladogram supporting the Lingulata and Calciata (Popov *et al.* 1993; Text-figs 3–4 herein), was also produced in a revised analysis of Carlson's (1995) character state matrix, using the bryozoans, phoronids, pterobranchs, and sipunculids as outgroups (see Text-fig. 5 and discussion on pp. 734–735).



TEXT-FIG. 1 A, Hennig's (1966, fig. 7) cladogram of relationships among the major taxa of the extant Brachiozoa. Synapomorphies shown by bars connecting taxa are: (1) shell consisting of calcium carbonate; (2) anterior part of body parenchymatous; (3) marginal lacuna not developed; (5) dorsal mantle lobes widely separated from the remaining visceral sac; (6) central portion of the shell cavity only partly filled with organs; (7) intestine ending in a blind sac; (8) muscle bundles not penetrated medially by a transverse plate of connective tissue; (9-11) dorsal and ventral mantle lobes united posteriorly, valves articulated by tooth and socket arrangement, dorsal valve with ridges that support lophophores; (14) musculature consisting of only three parts of muscle bundles, the base of the arm of the oldest tentacle is transformed into organs of brood





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## REVIEW AND DISCUSSION OF PREVIOUS CLADISTIC ANALYSES

*Hennig 1966*

The first cladistic analysis of Recent brachiopods was published by Hennig (1966). This was based exclusively on a revised version of 'kinship relationships' [verwandtschaftlichen Beziehungen] among five Recent brachiopod 'families' published in a highly informative, but unfortunately rarely available and little known work by Helmcke (1939, p. 224, fig. 227). The scheme of classification used by Hennig and Helmcke can be reconciled with and transformed readily into the superfamilial system of current usage, and Hennig's proposed cladogram (Text-fig. 1A) corresponds very closely with that derived from our own analysis (Text-fig. 3). The fact that Hennig's selected synapomorphies were based on the extremely detailed and accurate descriptions of Helmcke allows them to be adopted with only minor modification in order to correct a few misinterpretations. For example, Hennig's character 15 (gonads present only in mantle canals) was assumed erroneously by him to be apomorphic only for rhynchonelloideans and terebratuloideans (1966, p. 152). However, it is a characteristic of all calcareous-shelled brachiopods (Williams and Rowell 1965, p. H44).

From his analysis, Hennig concluded that only the 'family Lingulidae' (including discinides) could not be established as a monophyletic group; although not stated explicitly by him, his cladogram implies that these form a kind of 'outgroup' for the calcareous-shelled taxa.

*Rowell 1981, 1982*

Cladograms for both extant and extinct taxa were constructed by Rowell (1981, 1982) as part of a critical analysis of models of polyphyletic brachiopod origins proposed by Valentine (1973; see also Valentine 1975; Wright 1979). Rowell's conclusions support brachiopod monophyly.

For six superfamilies of Recent brachiopods (the Thecideoidea were excluded from the analysis), and with phoronids as an outgroup, Rowell's cladograms (1981, fig. 7, 1982, fig. 4) were based on 16 synapomorphies (Text-fig. 1B herein). Of these, the five characters uniting living brachiopods are: (1), filaments in a single palisade about the lophophore axis; (2), double row of filaments on adult lophophores; (3), brachial lip bounding food groove; (4), two mesocoelic cavities in lophophore; and (5), mantle canals. As discussed by Rowell (1982, p. 305), the structural features of the lophophores of all brachiopods are so similar and are consistently different from those of other lophophorates that it seems most probable that they are true homologies. However, it should be noted that his

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care; (15) gonads present only in mantle lobes; (16) pedicle without a cavity; (17) middle portion of muscles tendonized; (18) right and left arms of the lophophore separated; (19) two pairs of metanephridia; (20) absence of mantle papillae. The nature of the 4th, 12th and 13th synapomorphies is not defined clearly by Hennig. B, Rowell's (1982, fig. 4) cladogram showing the relationships between major taxa of the extant brachiopods. Synapomorphies shown by bars connecting taxa are: (1) filaments in a single palisade about the lophophore axis; (2) double row of filaments on adult lophophore; (3) brachial lip bounding food groove; (4) two mesocoelic cavities in lophophore; (5) mantle canals; (6) hydraulic mechanism for opening valves; (7) presence of larval shell; (8) diductor muscles and hinge mechanism; (9) posterior fusion of mantles; (10) fibrous secondary shell; (11) pedicle as larval rudiment; (12) mantle reversal on settlement; (13) no larval shell; (14) closely comparable oblique internal and oblique lateral muscles paths; (15) holoperipheral growth in both valves; (16) presence of loop. C, Forey's (1982, fig. 4) cladogram derived for eight nested sets of taxa covering both the extinct and Recent stocks (note that definition of the nodes is based in some cases on combinations of characters; see text for further explanation). D, Gorjansky and Popov's (1986, fig. 2) diagram illustrating their view of a diphyletic course of brachiopod evolution. Major autapomorphies and synapomorphies indicated are: (1) schizocoelic coelom, metasomal pouch and settlement on the ventral body wall; (2) bivalved calcium phosphate shell; (3) enterocoelic coelom with reduced metacoel and settlement on the posterior part of the body; (4) bivalved calcareous shell; (5) pedicle and metasome reduced; (6) the origin of articulation; (7) pedicle as cartilaginous stalk and blind alimentary canal.

*Note.* In this Text-figure and in Text-figures 2 and 5 and Table 5 the endings used for brachiopod superfamily names (*acea*) are as used in the original publications by the respective authors; throughout the text we use the ending *oidea* for these same units of Superfamily rank as now recommended generally by the ICZN.

character 2 (Rowell 1982, fig. 4) is a generalization. Thus, in the extant genera of the Lingulata, a double row of filaments occurs in the trocholophe stage, whereas in Recent calcareous-shelled forms a double row of filaments does not develop until the post-trocholophe stage (Williams and Rowell 1965, p. H32; see further below, p. 722).

Eight further synapomorphies were then identified by Rowell (his characters 6–13; Text-fig. 1B herein) that support the traditional two-fold division of brachiopods into inarticulates and articulates, but some of these also require further discussion in the light of subsequent studies. Thus his synapomorphy 7, the presence of larval shell in calcareous and phosphatic shelled 'inarticulates', is not confirmed by recent studies of craniide larvae (Nielsen 1991), and synapomorphy 6 (hydraulic mechanism for opening valves) represents a functional character of doubtful homology (see earlier discussion, p. 715). Although closely comparable oblique lateral muscles are present in these groups (synapomorphy 14) they appear to have some fundamental differences in position and function. In craniides they are attached to the anterior body wall, which is an important difference from discinides (e.g. Bulman 1939, fig. 4).

#### *Forey 1982*

Brachiopods were used by Forey (1982, pp. 125–136) as an example in debating the distinction between and comparative utility of cladograms and phylogenetic trees. His cladogram (1982, fig. 4; Text-fig. 1C herein), which was not based on outgroup comparison, was constructed for eight nested sets of taxa covering both the extinct and Recent stocks, but excluding the acrotretides for which Forey did not identify any unique synapomorphy. Monophyly is identified for the brachiopods as a whole and for the 'articulates', with the 'inarticulates' being paraphyletic.

Of the characters, or groups of characters taken as synapomorphies by Forey, only that in support of his node 1 (branch point) can now be accepted; dorsal and ventral valves secreted by mantle is a character uniting all brachiopods. Node 2 is not supported by either of the listed characters; for example craniides have no pedicle throughout ontogeny (Nielsen 1991), and many linguloids and oboloids are also inequally valved. The presence of a laminar secondary shell layer cannot support node 3 as this feature is present only in craniides, obolellides, and some 'articulates'; in addition there is no delthyrium in craniides and craniopsides. At node 4, the identification of a straight posterior margin to the ventral valve is too vague to be definitive, whilst in any case obolellides have strophic shells to which this character could be applied. Definition of a subapical foramen or open gap (node 5) is similarly tenuous, together with the fact that stocks such as chileides and eichwaldiides have similar primitive openings of uncertain function. This node is also unsupported by the presence of a deltidium, since deltidial structures are variably defined, or absent, in 'articulates'. And finally, the morphology of some obolellide taxa removes support for both nodes 6 and 7. Narrow muscle attachment scars similar to those of 'articulates' originated in obolellides such as *Naukat* (Popov and Tikhonov 1990) and *Bynguanoia* (Roberts and Jell 1990), whilst primitive teeth and sockets were also present in the same group.

Forey (1982, p. 136, caption to fig. 4) makes particular reference to the incongruent placing of the phosphatic shelled Paterinida in his cladogram, where they are interpolated between calcareous stocks. In suggesting that 'placing this group to the left of the obolellids is unparsimonious', he gives no supporting comment, but concludes that 'a division of brachiopods into non-calcareous and calcareous may be over simplistic'. It is pertinent to repeat here that our original summary (Popov *et al.* 1993) was in direct contradiction to this view, and that the present paper is a further exploration of these relationships.

#### *Gorjansky and Popov 1985, 1986*

The phylogenetic importance of shell mineralogy in brachiopod evolution is emphasized by Gorjansky and Popov (1985, 1986) and Popov (1992). These authors do not list synapomorphies for Recent superfamilies, but they can be deduced from the descriptions of phosphatic and

calcareous-shelled taxa in the text; together with the modified cladogram they are reproduced here in Text-figure 1D.

The first two synapomorphies are based on a new interpretation by Gorjansky and Popov of the coelomic subdivision in some brachiopods. Lingulates (discinioideans + linguloideans) would appear to have a mesocoel, restricted to the coelomic spaces in the lophophore (1), and with metacoelic cavities in the remaining part of body (2). These states are regarded as derived for this lineage. The loss of coelomic partitioning in adult 'articulates' also represents a derived feature. In view of limited knowledge of the ontogeny of Recent 'articulate' taxa, as well as craniides, these synapomorphies are regarded here as highly hypothetical. The ambiguous nature of recent information on coelomic partitioning and embryology of extant brachiopods is discussed above (see pp. 714–715).

The fundamental conclusion by Gorjansky and Popov (1985, 1986) that the Lingulata (i.e. all phosphatic-shelled stocks) represent a phylum separate from the Brachiopoda is not now supported by our joint studies. The morphology, anatomy and ontogeny of extant stocks support instead the recognition of two major clades as sister groups within the brachiopods; it is more parsimonious to regard the origin of two different kinds of shell mineralization as a result of initial divergence within the phylum. The subsequent radiation of the lingulate and calciate orders are explained by Gorjansky and Popov in much the same way as in our analysis (see further below).

#### *Carlson 1991, 1995*

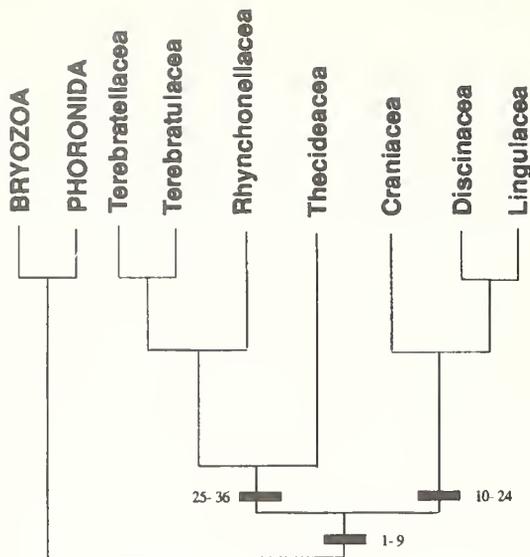
The most exhaustive published analysis of brachiopod phylogeny employing cladistic methodology is that by Carlson (1995), which builds on her earlier preliminary study (Carlson 1991) by considerably revising and expanding the data matrix. In both cases her results support a monophyletic origin for the brachiopods as a whole, and separately for the 'articulates' and 'inarticulates'.

The summary nature of Carlson's 1991 paper precluded a presentation of a data matrix; whilst we note that her detailed 1995 account eliminates some redundant characters and adds other informative features, it remains useful for us to comment separately on both papers as a means of emphasizing our views on the utility or otherwise of various potentially useful characters. Such a discussion is essential in order to understand the fundamental differences in our models and conclusions.

*1991.* In her initial study Carlson produced five different cladograms, but for our purposes discussion can be restricted to the model proposed for the Recent superfamilies (Carlson 1991, fig. 2; Text-fig. 2 herein). Nine synapomorphic characters uniting all brachiopods were proposed. They are: sex usually separate (1); imperfect separation of metacoel and mesocoel (2); pedicle present (3); primary ganglion below oesophagus (4); sensory cells present in juvenile stage only (5); ectodermal epithelium in three distinct zones (6); lophophore palisade bears a single row of filaments (7); lophophore suspended between mantles (8); mantle secreting shell material (9).

Of these, only characters 4 and 8 are acceptable without discussion. The other seven are defined ambiguously or represent what we consider to be plesiomorphic states that characterize not only brachiopods, but also other lophophorates.

The first two characters can be rejected as synapomorphies because they are common within other invertebrates. Character 7 requires clarification in its wording, but we take it to be valid in referring to the single palisade about the lophophore axis as opposed to the double palisade in phoronids. The remaining four features (3, 5, 6, 9) can be used only with emendation. They are not synapomorphic for all brachiopods, but characterize various lineages. It has long been known that the pedicle (character 3) is not homologous in linguloids and discinoids on the one hand and 'articulates' on the other (Williams and Rowell 1965). Character 5 is also ambiguous, because statocysts, for example, are developed in linguloid and discinoid larvae and persist in adults (Chuang 1977). Moreover, lingulate taxa lack sensory organs comparable to those of the 'articulate' larvae. The ability of the mantle to secrete a mineralized shell (character 9) is not a



TEXT-FIG. 2. Carlson's (1991, fig. 2) cladogram showing phylogenetic relationships between the extant brachiopod superfamilies. Synapomorphies are distributed as follows. Brachiopoda: Characters 1-9: sexes usually separate; imperfect separation of metacoel and mesocoel; pedicle present; primary ganglion below oesophagus; sensory cells present in juvenile stages only; ectodermal epithelium in three distinct zones; lophophore palisade bears a single row of filaments; lophophore suspended between mantles; mantles secreting shell material present. Inarticulata: Characters 10-24: development relatively direct; median tentacle of lophophore present initially, then lost; larval propulsion accomplished with lophophoral cilia; large subenteric ganglion only present; one row of adlabial and ablabial filaments on adult lophophore; large number of gametes released per spawning event; brooding uncommon; mantle rudiment does not reverse; ventral and dorsal mantles always discrete; mantle epithelium underlain by thin muscular layer; muscle system complex; laminar shell layer present; valves do not rotate in contact about a hinge axis; pair of teeth and sockets absent; calcareous lophophore supports absent. Articulata: Characters 25-36: coelomic spaces originate by enterocoely, mouth does not originate from blastopore, coelom divided into two principal spaces, the mesocoel and metacoel; postlarval initiation of shell formation; duration of a free-swimming larval stage short; adult lophophore lacks brachial muscles; brachial canal system simple; alimentary canal, pedicle, mixonephridia, and lophophore develop after settlement; gametes develop in mantle canals; gametes released more or less in a single burst; alimentary canal ends blindly; elevator and protractor muscles absent from the lophophore.

characteristic of brachiopods alone, but also of various unrelated invertebrate stocks. And finally, the meaning and implication of character 6 are unclear to us.

Carlson then defines 15 characters as synapomorphies for all 'inarticulates', including craniids. They are: development relatively direct (10); median tentacle of lophophore present initially, then lost (11); larval propulsion accomplished with lophophoral cilia (12); large subenteric ganglion only present (13); one row of adlabial and ablabial filaments on adult lophophore (14); large number of gametes released per spawning event (15); brooding uncommon (16); mantle rudiment does not reverse (17); ventral and dorsal mantles always discrete (18); mantle epithelium underlain by thin muscular layer (19); muscle system complex (20); laminar shell layer present (21); valves do not rotate in contact about hinge axis (22); paired teeth and sockets absent (23); calcareous lophophore support absent (24).

Apart from character 18, none of these characters are acceptable as synapomorphies for the combined calcareous- and phosphatic-shelled 'inarticulates'. Characters 13, 17 and 19 are known only in discinides and lingulides, and are absent or the condition is unknown in craniids. Recent work on the early ontogeny of *Neocrania* (Nielsen 1991) shows that a direct development (character 10) is not a character of craniids, and the absence of mantle reversion (character 17) is probably plesiomorphic for all brachiopods. Craniids have a paired subenteric ganglion rather than a single one as suggested by Carlson (character 13). The presence of a thin muscular layer in the mantle

epithelium of lingulides and discinides (character 19) might indicate the presence of well-developed dermal muscles, and this type of musculature is poorly developed in craniides (Blochmann 1892, 1900). The presence of a median tentacle, lost during later ontogeny, in craniides and lingulates (character 11) appears to be related to the spirolophous lophophore, because it is present also in rhynchonellides (Beecher 1897, p. 106; Rowell 1960, p. 49; Williams and Rowell 1965, fig. 36). Characters 12, 15 and 22 are not features of shell morphology or anatomy, but instead functional processes which, as noted above (p. 715), we consider to be of dubious application in phylogenetic analysis. One row of adlabial and ablabial filaments on the adult lophophore (character 14) is strictly a characteristic of all brachiopods (see also earlier comments on characters in Rowell's 1982 cladogram). With regard to character 20, we have commented previously (Bassett *et al.* 1994) that the use of such extremely generalized characters is of little value in investigating fundamental trends in brachiopod phylogeny; complexity is in the eye of the beholder. The presence of a laminar secondary layer (character 21) is a characteristic only of craniides; the shell structure of lingulides and discinides differs markedly from the laminar shell of craniides and cannot be described in such terms. Problems of denoting similarities based on the absence of any one particular feature (characters 23 and 24) are discussed above (p. 715).

In characterizing the 'articulates', Carlson then lists the following further 12 synapomorphies: coelomic spaces originate by enterocoely (25); mouth does not originate from blastopore (26); coelom divided into two principal spaces, the mesocoel and metacoel (27); postlarval initiation of shell formation (28); duration of free-swimming larval stage short (29); adult lophophore lacks brachial muscles (30); brachial canal system simple (31); alimentary canal, pedicle, mixonephridia and lophophore develop after settlement (32); gametes develop in mantle canals (33); gametes released more or less in a single burst (34); alimentary canal ends blindly (35); elevator and protractor muscles absent from lophophore (36).

The problematical nature of characters 25–29, 32, 34 is discussed above (p. 715). With regard to the brachial muscles in the articulate lophophore (30), they are not lacking but are less organized than in craniides and lingulides, a state that is related apparently to the presence or absence of brachial structures (Williams and Rowell 1965, p. H32), as is the case with the presence or absence of elevator and protractor muscles (36). Mantle canals with gonads (33) are known to be present in all calcareous-shelled brachiopods, including craniides.

1995. The data matrix for Carlson's more detailed analysis of extant brachiopods was built from 112 morphological and embryological characters. In some cases, modifications from her 1991 data set are noted, partly in line with some of our discussion immediately above.

Apart from our own initial study (Popov *et al.* 1993), this thorough analysis by Carlson is the first to present a published data matrix in support of cladograms. Our above review of previous cladistic analyses discusses each of the synapomorphies selected as a means of understanding the resulting theory in the absence of a full matrix. In the case of Carlson (1995) it is more useful to analyse her matrix directly, and in the light of our conflicting results it is more meaningful to do so as a comparative discussion after the presentation of our own analysis (see Discussion, p. 734).

#### DIAGNOSTIC CHARACTERS AND CHARACTER STATES

Our original analysis (Popov *et al.* 1993) of extant brachiopods of Order rank identified 29 diagnostic morphological and anatomical characters as a basis for the construction of a character state matrix. In the light of our continuing studies we have modified the original data set by merging and changing the character coding, while also adding 15 new characters, a combination of which is used in both the analyses presented below. Our revised data take into account published comment on our earlier analysis (Carlson 1994), together with numerous critical points made on initial versions of this manuscript.

*Note.* For ease of cross-reference, bracketed abbreviations of the numbered characters listed below are those set out in Tables 1–3.

TABLE 1. Character State Matrix used in PAUP analysis of characters (1–31, 33–34, 37–38) as listed in the text for the seven extant brachiopod orders and suborders.

Character no.	1	2	3	4	5	6	7a	8	9	10	11	12
Abbreviation	clo	bli	fil	ctl	mfl	man	fus	set	mcl	mar	mas	pds
Phoronida	0	0	0	0	0	0	N	0	N	N	N	2
Lingulida	1	1	2	1	1	1	0	1	0	0	0	2
Discinida	1	1	2	1	1	1	2	1	0	0	0	2
Craniida	1	1	1	1	1	1	2	1	1	1	1	0
Terebratellidina	1	1	1	1	1	1	1	1	1	1	1	1
Terebratulidina	1	1	1	1	1	1	1	1	1	1	1	1
Thecideidina	1	1	0	1	1	1	1	0	1	1	1	1
Rhynchonellida	1	1	1	1	1	1	1	1	1	1	1	1
Character no.	13	14	15	16	17	18	19	20	21	22	23	24
Abbreviation	gab	gon	sta	snt	sup	pmn	dem	obl	ob2	did	olm	lan
Phoronida	U	1	0	0	0	N	1	N	N	N	N	N
Lingulida	1	1	1	1	0	1	1	1	0	0	0	0
Discinida	1	1	1	1	0	1	1	1	0	0	0	0
Craniida	0	0	0	2	0	0	0	0	1	0	1	1
Terebratellidina	0	0	0	1	1	0	0	0	1	1	0	0
Terebratulina	0	0	0	1	1	0	0	0	1	1	0	0
Thecideidina	0	0	0	1	1	0	0	0	1	1	0	0
Rhynchonellida	0	0	0	1	1	0	0	0	1	1	0	0
Character no.	25	26	27	28	29	30	31	33	34	37	38	
Abbreviation	dbv	lpl	ppb	ovm	phs	cal	lsh	css	pun	shr	tee	
Phoronida	N	0	0	0	0	0	0	N	N	N	N	
Lingulida	0	0	0	1	1	0	1	N	N	0	0	
Discinida	0	0	0	1	1	0	1	N	N	0	0	
Craniida	1	0	0	0	0	1	0	1	2	0	0	
Terebratellidina	0	1	1	0	0	1	0	0	1	1	2	
Terebratulina	0	1	1	0	0	1	0	0	1	1	2	
Thecideidina	0	1	0	0	0	1	0	P	1	1	2	
Rhynchonellida	0	1	1	0	0	1	0	0	0	1	2	

### *Lophophore*

The primary feature that characterizes the functional organization of brachiopods is the ability to carry out filtration in an isolated chamber (see also Rowell 1982).

Phoronids have a single coelomic cavity in the lophophore, lacking a brachial lip as well as cartilage-like connective tissue. Despite the considerable morphological similarity of the lophophore in all extant Brachiopoda, there are consistent differences in detail between the main clades. In all extant Lingulata, there is a double row of lophophore filaments in the trochlophore stage (character 3, state 2), whereas in extant Calciata (i.e. Craniformea and 'articulates'), the trochlophore stage has only a single row of filaments (character 3, state 1; see also Williams and Rowell 1965, p. H32). In the phoronid lophophore, a single row of filaments persists throughout the ontogeny (character 3, state 0); this state is also present in the adult stage of Recent thecideidoideans.

TABLE 2. Character State Matrix used in PAUP analysis of characters (6–9, 13, 19–25, 27–40) as listed in the text for the extant and extinct brachiopod orders.

Character no.	6	7b	8	9	13	19	20	21	22	23	24	25	27
Abbreviation	man	fus	set	mcl	gab	dem	obl	ob2	did	olm	lan	dbv	ppb
Phoronida	0	N	0	N	N	1	N	N	N	N	N	N	0
Lingulida	1	1	1	0	1	1	1	0	0	0	0	0	0
Siphonotretida	1	1	1	0	1	1	1	0	0	0	0	0	0
Acrotretida	1	1	1	0	1	1	1	0	0	0	0	0	0
Paterinida	1	0	1	1	0	U	U	U	2	0	0	0	U
Craniida	1	1	1	1	0	0	0	1	0	1	1	1	0
Trimerellida	1	1	U	1	0	0	0	1	1	1	1	0	0
Craniopsida	1	1	1	1	0	0	0	1	0	1	1	0	0
Obolellida	1	0	U	1	0	0	0	1	1	0	0	0	1
Kutorginida	1	0	1	1	0	0	0	1	1	0	0	0	1
Orthida	1	0	1	1	0	0	0	1	1	0	0	0	1
Character no.	28	29	30	31	32	33	34	35	36	37	38	39	40
Abbreviation	ovm	phs	cal	lsh	pss	css	pun	hom	psd	shr	tee	csp	kut
Phoronida	0	0	0	0	N	N	N	N	N	N	N	N	N
Lingulida	1	1	0	1	0	N	N	0	N	P	0	0	0
Siphonotretida	1	1	0	1	0	N	N	0	N	1	0	0	0
Acrotretida	1	1	0	1	1	N	N	0	N	P	0	0	0
Paterinida	U	1	0	1	0	N	N	1	N	0	0	0	0
Craniida	0	0	1	0	N	1	2	0	0	0	0	0	0
Trimerellida	0	0	1	0	N	2	0	0	0	0	0	1	0
Craniopsida	0	0	1	0	N	1	0	0	0	0	0	0	0
Obolellida	0	0	1	0	N	1	0	0	1	P	1	0	0
Kutorginida	0	0	1	0	N	U	U	0	2	0	0	0	1
Orthida	0	0	1	0	N	0	0	0	1	0	2	0	0

Lophophoral muscle fibres are smooth in phoronids (character 5, state 0), but partly striated in brachiopods (character 5, state 1; James *et al.* 1992).

1. Coelomic cavities in lophophore (*clo*).  
States (0) one coelomic cavity; (1) two coelomic cavities.
2. Lophophore palisades and brachial lip (*bli*).  
States (0) two palisades, brachial lip absent; (1) filaments in a single palisade, with brachial lip, bounding a food groove.
3. Arrangement of lophophore filaments (*fil*).  
States (0) one row of lophophore filaments; (1) double row of filaments in the post-trocholophe stage; (2) double row of filaments in the trocholophe stage.
4. Cartilage-like connective tissue in lophophore (*ctl*).  
States (0) absent; (1) present.
5. Muscles fibres in lophophore (*mff*).  
States (0) smooth; (1) striated.

*Mantle*

The presence of dorsal and ventral mantles with coelomic cavities forming a filtration chamber (character 6, state 1) is another distinctive feature uniting all brachiopods, as is the development of mantle setae (character 8, state 1). The latter character was also used by Rowell (1981, 1982). Setae

were previously thought to be lacking in craniids, but Nielsen (1991) identified marginal setae in juvenile *Neocrania*, and they have also been found in the Lower Cambrian 'craniopsid' genus *Heliomedusa* (Jin and Wang 1992) as well as in paterinids from the Burgess Shale (e.g. Whittington 1985). However, marginal setae appear to be absent in Recent thecideidines, and Recent phoronids also lack a mantle with setae.

Mantle lobes that are fused along the posterior margin have been considered to represent a distinctive 'articulate' character (character 7a, state 1 for extant lineages; character 7b, state 0 for extinct lineages; see also Rowell 1982), whereas the phosphatic and calcareous 'inarticulates' have discrete ventral and dorsal mantles (Williams and Rowell 1965, p. H9; Carlson 1991, fig. 2). However, it is apparent that *Lingula anatina* passes through an ontogenetic stage in which the mantle lobes are fused along the posterior margin (character 7, state 1; Yatsu 1902; Williams and Rowell 1965, p. H46). Only in craniids and discinids do the mantle lobes appear to be discrete throughout ontogeny (character 7a, state 2 for extant lineages; character 7b, state 1 for extinct lineages). For the extinct brachiopods with a strophic shell (Paterinida, Obolellida, Kutorginida, Orthida) the absence of setal follicles along the straight posterior margin suggests that the mantle lobes were somewhat modified and might therefore have been fused. Moreover, in view of the absence of any kind of articulatory structures in paterinids, the axis of rotation may have been fixed only by fused mantle lobes.

Differences in the direction of the *vascula terminalia* also differentiate the two main brachiopod lineages. Thus, in lingulates the *vascula terminalia* are directed both peripherally and medially (character 9, state 0), whereas all calcareous stocks have only peripherally directed vascular trunks (character 9, state 1; Williams and Rowell 1965, figs 136, 138).

Reversion of the mantle through ontogeny is a diagnostic character of Recent 'articulate' lineages (character 10, state 1). The available information on the ontogeny of lingulates (Yatsu 1902; Chuang 1977) confirms the absence of reversion in these stocks (character 10, state 0). In the craniids, the change in direction of the larval setae during ontogeny (Nielsen 1991) indicates that some kind of mantle reversion takes place during the complex metamorphosis.

The marginal sinus (character 11, state 0; 'marginal lacuna' of Hennig 1966) is a separate coelomic channel that runs near the mantle edge in *Discinisca* and *Lingula*; it does not appear to be present in calcareous-shelled brachiopods (Hyman 1959, p. 533).

6. Mantles with coelomic cavities forming a filtration chamber (*man*).  
States (0) absent; (1) present.
- 7a. Fusion of mantle lobes (for analysis of extant stocks) (*fus*).  
States (0) fused in embryonic stage, separate in adults; (1) fused along the posterior margin in adults; (2) separate in larvae and adults.
- 7b. Fusion of mantle lobes (for analysis of extinct stocks) (*fus*).  
States (0) no mantle; (1) separate in adults; (2) fused along the posterior margin in adults.
8. Setae (*set*).  
States (0) absent; (1) present.
9. Mantle canals (*mcl*).  
States (0) *vascula terminalia* directed peripherally and medially; (1) *vascula terminalia* directed peripherally only.
10. Mantle reversion (*mar*).  
States (0) absent; (1) present.
11. Marginal sinus (*mas*).  
States (0) present; (1) absent.

#### *Digestive system*

In adult brachiopods there are three types of digestive tracts. In the Lingulata the gut is U-shaped and placed anteriorly close to the right nephropore (character 12, state 2). A U-shaped gut is also present in phoronids (Hyman 1959, p. 245). In *Neocrania* the anus is placed posteromedially

(character 12, state 0; Williams and Rowell, 1965, pp. H17–21). The third type occurs in the ‘articulates’, where the gut is blind (character 12, state 1; Hyman 1959, p. 552).

The attachment scars of the gastroparietal bands (character 13, state 1) can be traced on dorsal valves of various lingulate taxa (paterinides are the only exception) back to the Cambrian (Mickwitz 1896, p. 100; Blochmann 1900, p. 118). This suggests that in the majority of the extinct lingulate lineages the morphology of the digestive tract was probably comparable essentially with that of Recent taxa. These types of scars are lacking in all craniides; in ‘articulates’ the gastroparietal bands never leave attachment scars, and because they do not bear gonads their homology with those of lingulates is questionable and even unlikely.

12. Digestive system (*pds*).

States (0) straight with posteromedially placed anus; (1) straight, blind; (2) U-shaped with anteriorly placed anus.

13. Dorsal attachment of gastroparietal bands (*gab*).

States (0) present; (1) absent.

*Reproductive system*

In Recent craniides and ‘articulates’ the gonads are placed in the mantle canals (character 14, state 0), whereas phosphatic brachiopods and phoronids are characterized by gonads occupying the free edges of the peritoneal bands (character 14, state 1; Hyman 1959, p. 564).

14. Location of gonads (*gon*).

States (0) in coelomic canals; (1) on free edges of peritoneal bands.

*Nervous system*

According to Chuang (1977, p. 53), statocysts develop in lingulide and discinide larvae and persist through ontogeny into the adult stage (character 15, state 1).

The presence of subenteric gangliation in brachiopods distinguishes them from all other lophophorates, but different states occur in each of the main brachiopod lineages (Hyman 1959, p. 560). Lingulates have only one subenteric ganglion (character 16, state 1) and lack a supraenteric ganglion (character 17, state 0); craniides are characterized by the presence of paired subenteric ganglia (character 16, state 2; Williams and Rowell 1965, p. H42); and ‘articulates’ have small transverse supraenteric ganglia (character 17, state 1) and a larger subenteric ganglion (character 16, state 1). These types of gangliation are not present in phoronids (Hyman 1959, p. 239).

A ring nerve formed by the confluence of the peripheral ends of the mantle nerves occurs in the margin of each mantle lobe of lingulides and discinides (character 18, state 1; Hyman 1959, p. 560).

15. Statocysts (*sta*).

States (0) absent; (1) present.

16. Subenteric ganglion (*snt*).

States (0) absent; (1) present, single; (2) present, paired.

17. Supraenteric ganglion (*sup*).

States (0) absent; (1) present.

18. Peripheral mantle nerves (*pmm*).

States (0) absent; (1) present.

*Muscle system*

The muscle system of lingulates is characterized mainly by well developed dermal muscles (character 19, state 1) as well as the presence of transmedian muscles (character 20, state 1) and two or three additional pairs of oblique muscles (character 21, state 0; Rowell *in* Williams *et al.* 1965, p. H273). We do not consider the transmedian muscles to be homologous with any of the oblique muscles in craniides.

Dermal muscles are absent or only weakly developed both in Recent craniides and ‘articulates’ (character 19, state 0) (Rowell *in* Williams *et al.* 1965, p. H273). The craniides have a musculature

that is simpler than that of discinides (Williams and Rowell 1965, p. H28), with only the paired internal oblique muscles being similar to the numerous oblique muscles of lingulates (character 21, state 1). On the other hand, both the paired outside lateral muscles, which are attached anteriorly to the body wall (character 23, state 1), as well as the unpaired *levator ani* (character 24, state 1) are unique to the craniides (Blochmann 1892). This kind of muscle system is also known in the Craniopsida and Trimerellida (Gorjansky and Popov 1985, 1986).

The musculature of 'articulates' consists of three main groups of muscles: paired anterior and posterior adductors, and paired oblique muscles attached posteromedially to the dorsal valve and serving as diductors (character 22, state 1).

Emig (1982, p. 188; see also Williams and Rowell 1965, p. H29) suggested that the dermal musculature in lingulates may be used for the hydraulic opening of the shell, and this was later demonstrated experimentally by Trueman and Wong (1987). Dermal muscles are also well developed in phoronids (Hyman 1959, p. 237). By contrast, they are developed only weakly in *Neocrania* (Hyman 1959, p. 533), and the exact type of opening mechanism is not known, although Gorjansky and Popov (1985, p. 6) suggested that the outside lateral muscles, which attach anteriorly to the body wall (Williams and Rowell 1965, fig. 29), may be used for hydraulic opening of the shell. A similar type of opening mechanism was proposed for lingulides by Gutmann *et al.* (1978), but this is clearly not a viable suggestion because there are no muscles attaching to the anterior body wall in the adult animal.

19. Dermal muscles (*dem*).

States (0) weakly developed or absent; (1) strongly developed.

20. Transmedian muscle (*obl*).

States (0) absent; (1) present.

21. Number of other oblique muscles (*ob2*).

States (0) one pair; (1) more than one pair.

22. Diductor muscles (*did*).

States (0) absent; (1) oblique muscles acting as diductors attached posteriorly to dorsal valve; (2) oblique muscles attached posteriorly to the inner side of homeodeltidium.

23. Outside lateral muscles attached anteriorly to body wall (*olm*).

States (0) absent; (1) present.

24. *Levator ani* (*lan*).

States (0) absent; (1) present.

### *Body wall*

The attachment of the dorsal body wall to the dorsal valve in five separate areas is a character unique to the craniides (character 25, state 1; Beauchamp 1960, fig. 1287) whereas in lingulates, 'articulates', craniopsides, and trimerellides it is attached to only one area (character 25, state 0).

25. Attachment of dorsal body wall to shell (*dbv*).

States (0) attached in five areas; (1) attached to one area.

### *Pedicle*

The pedicle is not homologous within the different lineages of brachiopods (Williams and Rowell 1965, p. H13; see also Carlson 1995, Appendix 2, character 30). In extant lingulides and discinides, the pedicle possesses a coelomic cavity and arises as an outgrowth of the inner epithelium of the ventral mantle, and is attached only to the ventral valve. This feature is diagnostic of all lingulate taxa (character 28, state 1). In 'articulates', the pedicle originates from the larval peduncular lobe (character 26, state 1); in the adult stage it has a core of firm, cartilage-like connective tissue and lacks coelomic cavities (character 27, state 1; Hyman 1959, p. 537). In craniformeans there is no pedicle, nor is there a peduncular lobe in the larva (Nielsen 1991). Based on subdivisions of the coelomic space, Gorjansky and Popov (1985, 1986) have interpreted the anal papilla of the craniides as being homologous with the pedicle of the 'articulates', but supporting evidence is inconclusive.

Nielsen (1991, p. 25) asserted that the larva of *Neocrania* settles on the posterior part of its dorsal side, such that the 'pedicle valve' represents a 'posterior dorsal valve', and the 'brachial' valve an 'anterior dorsal valve'. However, it is difficult to determine where dorsal and ventral meet on the posterior part of a larva lacking a peduncular lobe. This, in addition to the difficulty that Nielsen (1991, p. 21) had in following the fate of the blastopore, makes his interpretation difficult to confirm.

In extinct lingulate taxa, the presence of a *Lingula*-type pedicle is confirmed in some taxa in which the soft anatomy is preserved (e.g. *Lingulellotreta*; Jin *et al.* 1993) and can be deduced convincingly in many taxa in which an impression of the pedicle nerve is retained as a scar (Holmer 1991*b*).

26. Larval peduncular lobe (*lpl*).  
States (0) absent; (1) present.
27. Pedicle forming from posterior part of body (*ppb*).  
States (0) absent; (1) present.
28. Pedicle as outgrowth of ventral mantle lobe (*ovm*).  
States (0) absent; (1) present.

### *Chemical composition of the shell*

There are two main types of brachiopod shell, one in which the predominant inorganic component is calcium phosphate (character 29, state 1), and the other in which it is calcium carbonate (character 30, state 1). In the extant phosphatic-shelled forms, exemplified by lingulides and discinides, calcium phosphate accounts for 74.7–93.7 per cent. of the shell, the remainder being organic material comprising mostly chitin and protein. In calcareous-shelled forms, calcium carbonate makes up 94.6–98.6 per cent. of the shell material in the 'articulates' and 87.8–88.6 per cent. in craniides (Clarke and Wheeler 1922; Vinogradov 1953; Jope 1965); the remainder is organic material, consisting largely of protein.

We have emphasized previously (Popov *et al.* 1993, p. 3) that evolutionary transformations in brachiopod shell chemistry from a phosphatic to a calcareous composition, or *vice versa* (Carlson 1995), are at best weakly founded (Runnegar 1989; Runnegar and Bengtson 1990). Bengtson and Runnegar (1992, p. 450) have also recently reiterated this case in stating that 'there are no convincing examples of a phylogenetic transition from phosphate to carbonate in the history of lineages'. The pattern and timing of biomineralization of the earliest brachiopods remains incompletely known and too poorly understood for defining the polarity (Bengtson 1992, fig. 7.7.1; Bengtson and Runnegar 1992). We therefore separate the two types of mineralization as two characters.

29. Phosphatic mineralization (*phs*).  
States (0) absent; (1) present.
30. Calcareous mineralization (*cal*).  
States (0) absent; (1) present.

### *Shell formation and structure*

Several discrete features of shell formation and structure in both phosphatic and calcareous brachiopods serve in differentiation of major lineages. The initial states of formation show remarkable differences with both extant and extinct lingulate taxa characterized invariably by the presence of a larval shell (character 31, state 1; Holmer 1989). By contrast, craniides (Nielsen 1991) and 'articulates' develop a shell only after settlement (character 31, state 0).

The majority of lingulate taxa are characterized by alternating phosphatic and organic shell layers (character 34, state 2), which become somewhat more complicated in the acrotretides with the further addition of a columnar structure (character 32, state 1; Holmer 1989; Williams and Holmer 1992).

In addition to shell chemistry, craniides, craniopsides and obolellides also have a shell structure fairly similar to that of many of the 'articulate' groups in that they have a periostracum covering

a primary mineral layer consisting of inclined acicular crystallites, and a laminar secondary layer (character 32, state 1; Williams and Wright 1970; Williams 1990, p. 74). Among 'articulate' taxa, a laminar secondary layer is a distinctive character of billingselloideans, strophomenides and other related stocks, whilst a fibrous secondary layer is diagnostic for the Orthida (character 33, state 0). The possible acquisition of an aragonitic shell with its distinctive structure (Jaanusson 1966) is an equally unique character of the trimerellides (character 33, state 2).

An impunctate shell (character 34, state 0) is typical of the majority of Cambrian calcareous brachiopods (*Kotujella* is possibly one of the only exceptions) but according to Williams (1990, p. 71, text-fig. 4F), punctation evolved subsequently several times in 'articulate' lineages. In craniformeans, only craniides have acquired a dendroid punctuation (character 34, state 2; Williams and Wright 1970).

31. Larval shell (*lsh*).

States (0) absent; (1) present.

32. Phosphatic columnar shell structure (*ps*).

States (0) absent; (1) present.

33. Calcareous shell structure (*css*).

States (0) with fibrous secondary layer; (1) with laminar secondary layer; (2) aragonitic.

34. Punctate shell (*pun*).

States (0) impunctate; (1) endopunctate with simple porosity; (2) endopunctate with dendroid porosity.

#### *Modifications of the posterior shell margin*

The presence of a convex homeodeltidium covering the delthyrial opening (character 35, state 1) is a diagnostic character of the paterinides (Laurie 1987).

An open delthyrium is characteristic of both the earliest obolellides (*Obolella*, *Bicia*, *Magnicanalis*) and orthides (*Glyptoria*, *Israeleria*, *Leioria*; character 36, state 1). The various types of delthyrial covers thus probably originated later in their evolution. Several Lower Cambrian 'articulate' stocks with delthyrial covers, such as the nisusiides, have usually been placed within the orthides, but this now seems improbable. *Nisusia* lacks characters such as teeth and brachiophores, and the unusual pattern of its articulation (Rowell and Caruso 1985; Popov and Tikhonov 1990) suggest to us a close affinity with kutorginides.

In all Craniformea, there is no trace of a pedicle opening or gap between the valves in any of the Recent or extinct stocks (character 36, state 0); as in *Neocrania*, this indicates to us that all craniformeans lacked a pedicle.

Shell resorption is a rather rare phenomenon in Lower Palaeozoic brachiopods. It is commonplace within the siphonotretides (character 37, state 1), but the only other documented occurrences within the phosphatic brachiopods are in the acrotretide *Curticia* (Rowell and Bell 1961) and in the lingulide family Dysoristidae (Popov and Holmer 1994). It is also recorded in obolellides (Rowell 1965) and in the cyrtomatodont teeth of 'articulates' (Jaanusson 1971).

The nature of the diverse but primitive articulatory structures is one of the important characteristics of the majority of the earliest 'articulate' lineages (Popov and Tikhonov 1990), but among Lower Cambrian stocks only obolellides (character 38, state 1) and orthides (character 38, state 2) acquired paired deltidodont teeth or denticles on the lateral margins of the delthyrial opening.

In the craniformeans, articulatory structures comprising a cardinal socket and socket plate are found only in the extinct Trimerellida (character 39, state 1; Norford and Steele 1969).

The simplest pattern of articulation, in which the dorsal propareas fit into furrows on both sides of the pseudodeltidium, is known only in the kutorginides (character 40, state 1; Popov and Tikhonov 1990).

35. Homeodeltidium (*hom*).

States (0) absent; (1) present.

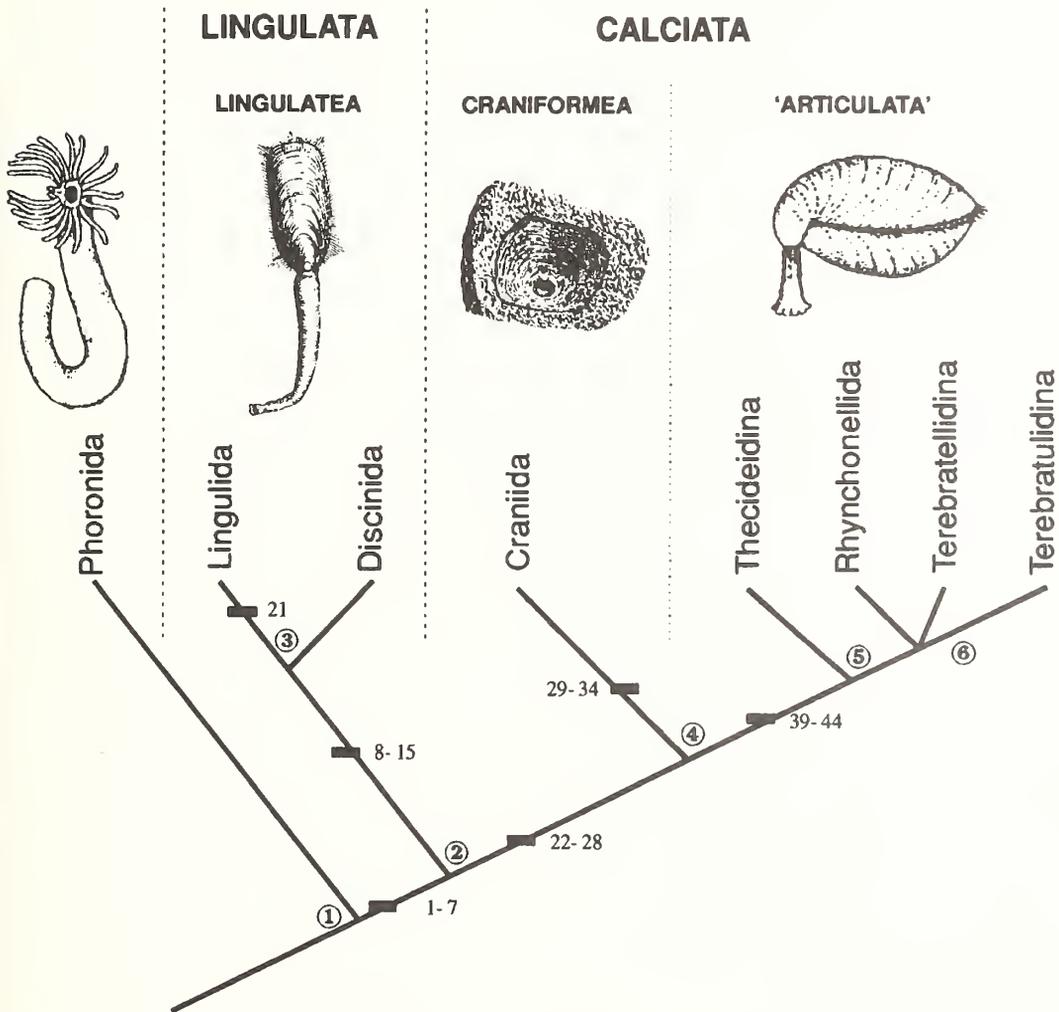
36. Pseudodeltidium and delthyrium (*psd*).

States (0) absent; (1) with open delthyrium; (2) with pseudodeltidium.

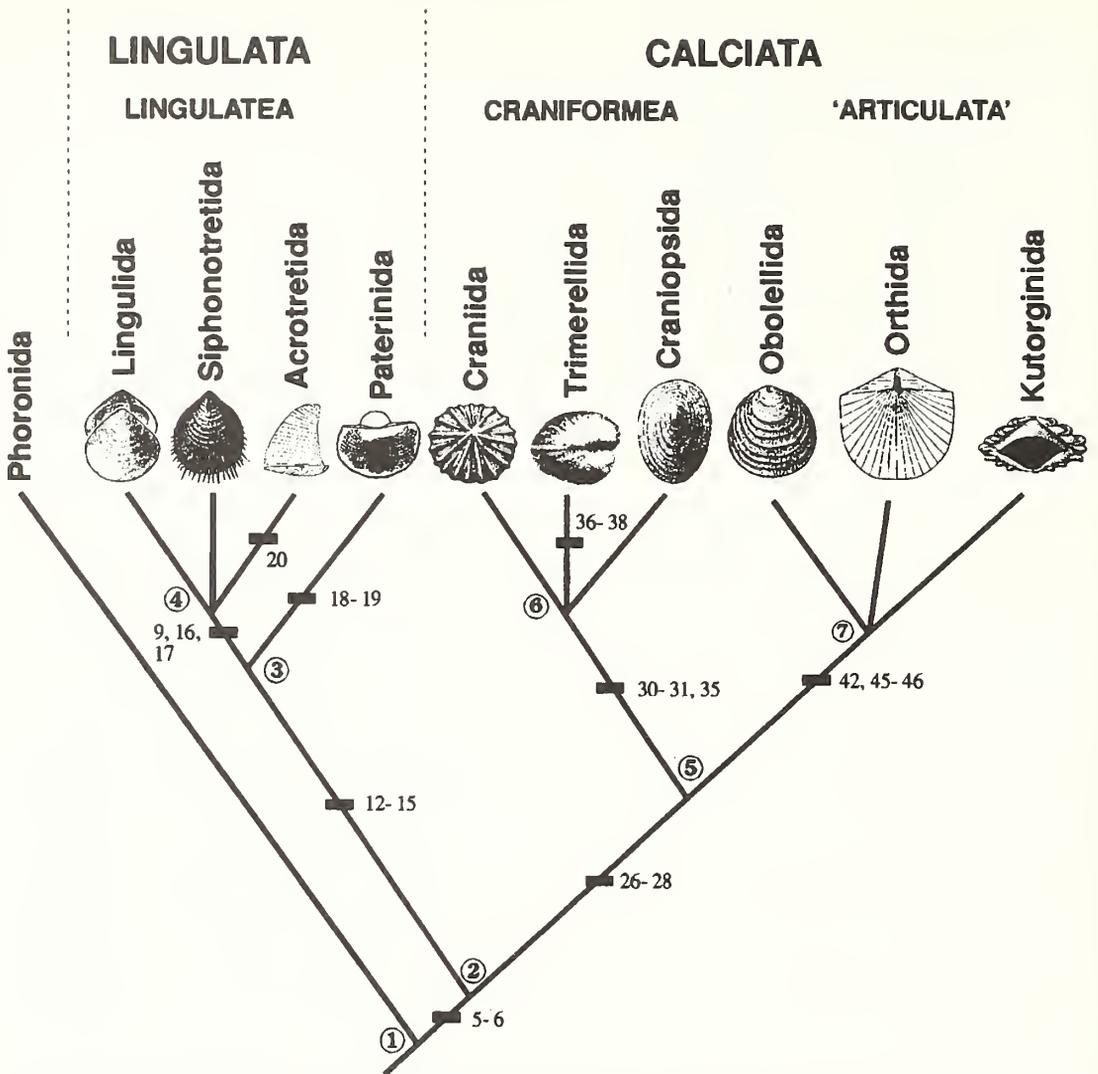
- 37. Shell resorption (*shr*).  
States (0) absent; (1) present.
- 38. Paired teeth and sockets (*tee*).  
States (0) absent; (1) with denticles; (2) deltidiodont articulation.
- 39. Cardinal socket and socket plate (*csp*).  
States (0) absent; (1) present.
- 40. Articulation with furrows lateral to pseudodeltidium (*kut*).  
States (0) present; (1) absent.

RESULTS AND TAXONOMIC IMPLICATIONS

Closely comparable results were obtained in separate analyses of the Character State Matrices constructed for the seven extant brachiopod groups of Order and Suborder ranks (Table 1) and for the combined extinct and extant groups (Table 2). The first computation produced a single tree 42 steps long with a consistency index of 0.952 (Text-fig. 3). For the combined Recent and extinct



TEXT-FIG. 3. Cladogram derived in this study from PAUP analysis of the seven Recent orders/suborders of Brachiopoda; numbered bars denote apomorphic characters summarized in the text.



TEXT-FIG. 4. Cladogram derived in this study from PAUP analysis of the combined extinct and extant orders of Brachiopoda; numbered bars denote apomorphic characters summarized in the t.txt.

stocks 18 trees were generated, each 32 steps long and with a consistency index of 0.938; only the strict consensus tree is presented here (Text-fig. 4). The topologies of both cases are entirely compatible.

Tables 3 and 4 summarize the derived characters produced by these analyses. In a few cases we have chosen not to use potential apomorphies because of problems in determining polarity etc., so that our discussion below focuses on those we take to be acceptable for taxonomic discrimination. Pressure of space precludes a full discussion here of the rejected characters, but they are identified clearly in Tables 3 and 4 and do not affect our overall conclusions.

In the following discussion the numbering of the selected synapomorphies is ordered consecutively to match the numbering on the cladograms derived from them (Text-figs 3-4). Note that this numbering is not therefore the same as that for the characters themselves as set out on pp. 722-729.

TABLE 3. Synapomorphy scheme for internal nodes of the cladogram shown in Text-figure 3.

Node	Character states
1	—
2	1:1, 2:1, 4:1, 5:1, 6:1, 8:1, 16:1
3	3:2, 13:1, 15:1, 18:1, 20:1, 28:1, 29:1, 31:1
Lingulida	7a:0
4	3:1, 8:11, 10:1, 11:1, 12:0, 14:0, 19:0, 21:1, 32:1
Craniida	16:2, 23:1, 24:1, 25:0, 33:1, 34:2
5	7a:1, 12:1, 17:1, 22:1, 26:1, 37:1; 38:2
Thecideidina	8:2
6	27:1

TABLE 4. Synapomorphy scheme for internal nodes of the cladogram shown in Text-figure 4.

Node	Character states
1	—
2	5:1, 6:1
3	20:1, 28:1, 29:1, 31:1
Paterinida	23:2, 35:1
4	7b:1, 9:0, 13:1, 37:1
Acrotretida	32:1
5	19:0, 21:1, 32:1
6	7b:1, 23:1, 24:1
Trimerellida	22:1, 33:2, 39:1
Craniida	25:0, 34:2
7	22:1, 27:1, 36:1
Kutorginida	36:2
Obolellida	38:1
Orthida	33:0, 38:2

For brevity, we cross reference throughout in the following way: character 1, state 1 = 1:1, character 3, state 0 = 3:0 etc. (see also Tables 3–4).

Seven synapomorphies are diagnostic in discrimination of the Recent brachiopods, supporting node 2 in Text-figure 3 and indicative of a monophyletic origin for the Phylum Brachiopoda:

1. Two coelomic cavities in the lophophore (1:1).
2. Filaments arranged in a single palisade about the lophophore axis, with a brachial lip, bounding a food groove (2:1).
3. Cartilage-like connective tissue in the lophophore (4:1).
4. Striated muscle fibres in the lophophore (5:1).
5. Dorsal and ventral mantles with a coelomic cavity forming a filtration chamber (6:1).
6. Mantle with marginal setae (8:1).
7. Single subenteric ganglion (16:1).

At a similar level in the analysis of the combined extinct and extant stocks (Text-fig. 4, node 2), two of the synapomorphies listed above (5 and 6) were generated (Table 4).

Both analyses lend strong support to the recognition of the Lingulata as a natural group within the Brachiopoda (Popov *et al.* 1993; Carlson 1995). The following eight synapomorphies are in support of node 3 for Recent lingulates (Table 3; Text-fig. 3):

8. Double row of filaments in the trochlophore stage (3:2).

9. Dorsal attachment scars of gastroparietal bands (13:1).
10. Statocysts in larvae and adults (15:1).
11. Peripheral mantle nerves (18:1).
12. Transmedian muscles (20:1).
13. Pedicle as outgrowth of the ventral mantle lobe (28:1).
14. Phosphatic mineralization (29:1).
15. Larval shell (31:1).

Four of these synapomorphies (12–15) also support the same point for the combined extinct and extant orders (Text-fig. 4, node 3; Table 4).

The apomorphic character no. 9 also supports the clade consisting of lingulides, discinides, siphonotretides and acrotretides in the combined analysis (Text-fig. 3A, node 4; Table 4) together with two further synapomorphies:

16. Separate mantle lobes in adults (7b:1).
17. *Vascula terminalia* directed peripherally and medially (9:0).

The Order Paterinida appears to be a sister stock of this clade, characterized by two autapomorphies (Text-fig. 4; Table 4):

18. Oblique muscles attached posteriorly to the inner side of the homeodeltidium (23:2).
19. Homeodeltidium present (35:1).

In the combined analysis, the unresolved trichotomy for the Acrotretida, Siphonotretida and Lingulida (Text-fig. 4, node 4; Table 4) cannot be resolved from the characters available. The Order Acrotretida is characterized by a single autapomorphy (Text-fig. 3A; Table 4):

20. Phosphatic shell with columnar structure (32:1).

The Order Lingulida lacks derived characters according to the combined analysis, but in the analysis of Recent stocks a single autapomorphy (Text-fig. 3; Table 3) was found:

21. Mantle lobes fused in embryonic stage, separate in adults (7a:0).

The unity of all calcareous-shelled brachiopods in a clade as a sister group to the lingulates is supported by both analyses. These are the Class Calciata of Popov *et al.* (1993). Six selected synapomorphies (of nine) characterize the extant stocks alone (Text-fig. 3, node 4; Table 3):

22. Double row of filaments in the post-trocholophe stage (3:1).
23. *Vascula terminalia* directed peripherally only (9:1).
24. Mantle reversion developed (10:1).
25. Gonads in the mantle canals (14:0).
26. Dermal muscles weakly developed or absent (19:0).
27. One pair of oblique muscles (21:1).
28. Calcareous mineralization (32:1).

The three last of these were also confirmed in the combined analysis (Text-fig. 4, node 5; Table 4).

Recognition of a Subclass Craniformea (Popov *et al.* 1993) is supported by both analyses, linking the craniides, craniopsides and trimerellides as proposed originally by Gorjansky and Popov (1985, 1986). For Recent craniides this discrimination is supported by six autapomorphies (Text-fig. 3; Table 3):

29. Paired subenteric gangliation (16:2).
30. Outside lateral muscles attached anteriorly to the body wall (23:1).
31. *Levator ani* present (24:1).
32. Attachment of dorsal body wall in five areas (25:0).
33. Calcareous shell structure with laminar secondary layer (33:1).
34. Punctate with dendroid porosity (34:2).

The same separation in the combined extant and extinct taxa (Text-fig. 4, node 6; Table 4) is supported by two of the synapomorphies above (30, 31) and an additional derived character:

35. Mantle lobes separate (7b:1).

This analysis thus indicates that the appearance of separated mantle lobes took place convergently within lingulates and craniformeans.

In the combined analysis, the unresolved trichotomy for the Craniopsida, Trimerellida, and Craniida (Text-fig. 4, node 6; Table 4) cannot be resolved from the characters available.

The Order Craniopsida appears to lack derived characters and it might possibly be closely comparable with the ancestral stock for all craniformeans. It is characterized by a three-layered impunctate shell with a laminar secondary layer, large, submedially placed visceral fields on both valves, a well-developed pleurocoel, and the absence of a pedicle opening. The muscle system of the craniopsides can be interpreted from the pattern observed in craniides (Gorjansky and Popov 1985).

The early divergence of craniformeans and other calcareous-shelled taxa has been confirmed by the recent discovery of craniopsides in Lower Cambrian (Botomian) strata. The genus *Heliomedusa* from Yunnan, China (Jin and Wang 1992) is characterized by a slightly inequivalved shell with mixoperipheral growth of the ventral valve and holoperipheral growth of the dorsal valve. The position of the visceral fields on both valves suggests a relatively large visceral cavity with a well-developed posterior body wall. There is no trace of a pedicle. The mantle canal system was probably pinnate with paired *vascula lateralia* on both valves, and is similar to that of Ordovician craniides like *Pseudocrania*. Marginal mantle setae are also present in *Heliomedusa*.

The Order Craniida includes the only extant craniformeans. The shell morphology of the earliest known Ordovician genera (*Pseudocrania* and *Orthisocrania*) is closely comparable with that of the extant *Neocrania*. A similar muscle system, with paired anterior and posterior adductors, internal oblique muscles and outside lateral muscles attached anteriorly to the body wall, is also present in the earliest representatives of the Order. The presence of the *levator ani* attachment scar on the dorsal valve of extinct taxa suggests a similar position of the digestive tract, with a postero-medially placed anus throughout phylogeny.

The Order Trimerellida is characterized, as are other craniformeans, by the lack of a pedicle opening; they possibly had an open digestive tract with a postero-medially placed anus, indicated by the possible scar of the *levator ani* on the socket plate of the dorsal valve (Gorjansky and Popov 1985). The mantle canal system is characterized by peripherally-directed *vascula terminalia*. The following autapomorphic characters were obtained (Text-fig. 4; Table 4):

36. Oblique muscles acting as diductors, attached posteriorly to dorsal valve (22:1).
37. Aragonitic shell (33:2).
38. Cardinal socket and socket plate (39:1).

The origin and initial radiation of the 'articulates' (as represented here by the orthides) and related calcareous shelled lineages is outside the scope of this paper, but it is possible that the synapomorphies of the extant stocks obtained in our analysis reflect a common origin of the Recent 'articulate' lineages, as a clade that arose after the divergence from the Craniformea (see also Rowell 1981, 1982; Carlson 1991, 1995). The list of proposed synapomorphies (Text-fig. 3, node 5; Table 3) for 'articulates' includes:

39. Mantle lobes fused along posterior margin in adults (7a:1).
40. Digestive system straight, blind (12:1).
41. Supraenteric gangliation (17:1).
42. Oblique muscles acting as diductors, attached posteriorly to dorsal valve (22:1).
43. Larva with peduncular lobe (26:1).
44. Deltiodont teeth (38:2).

Character 42 was also selected in the combined analysis (Text-fig. 4, node 7; Table 4), which suggests that the 'articulate' type of opening mechanism originated convergently in trimerellides (autapomorphy 36) and 'articulates' (synapomorphy 42); the same analysis also produced the following two synapomorphies:

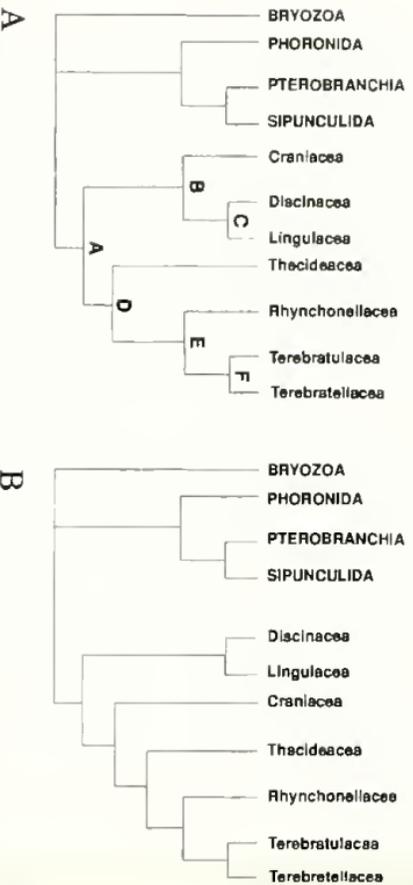
45. Pedicle forming from posterior part of body (27:1).
46. Open delthyrium (36:1).

There is growing evidence that rudimentary articulation developed in parallel within several lineages of calcarees in the early-mid Cambrian, including protorhynchids, mususides, kutoriginides and obolellides (Cooper 1976; Rowell and Caruso 1985; Ushatinskaya 1988; Popov and Tikhonov 1990; Roberts and Jell 1990). In this regard it is worth emphasizing that Cambrian obolellides and kutoriginides are interpreted here as primitive calcaree 'articulates' (Text-fig. 4, nodes 7 and 8; Table 4).

#### DISCUSSION

The scheme of classification summarized in Text-figures 3 and 4 removes the implication inherent in previous subdivision of the Brachiopoda into articulates and inarticulates of repeated evolutionary transformations in shell chemistry, either from a phosphatic to a calcareous composition (e.g. Williams and Hurst 1977) or initially from calcareous to phosphatic as proposed by Carlson (1991, 1995). Experiments with the matrices for our two analyses show that removal of the two characters based on chemical composition (characters 29, 30) does not change the topology of the resulting cladogram in the analysis of the Recent stocks. However, the same change in the combined analysis including the extinct stocks leads to a highly unresolved topology, supporting only two of the nodes (4 and 5) depicted in Text-figure 4, and indicating the need for further studies to resolve such instability.

Carlson (1995) analysed the relationships between seven superfamilies of extant brachiopods, using 112 characters. The topology of her single resulting cladogram (reprinted here as Text-fig. 5)



TEXT-FIG. 5. A, Carlson's (1995) cladogram derived from analysis of 112 characters within seven superfamilies of extant brachiopods. B, Cladogram derived from analysis of Carlson's (1995) 112 characters plus 6 additional characters from our matrix (113-118, Table 5), with a single change in her character 38 (state of Rhynchonellacea changed from 0 to U).

is identical to that published earlier (Carlson 1991; see also above, p. 720), in giving support to the identity of the Class Inarticulata as a monophyletic group. Whilst we do not attempt to analyse all 112 characters used by Carlson, we have already noted the doubtful homology of many 'functional' characters that are used (see above, p. 715). However, some additional comment is also required, because, despite the very large set of characters used in her study, it is apparent that a number of others used in our studies (Popov *et al.* 1993 and herein) are absent from her matrix; in order therefore to test further the stability of her results, we simply added some of these missing characters

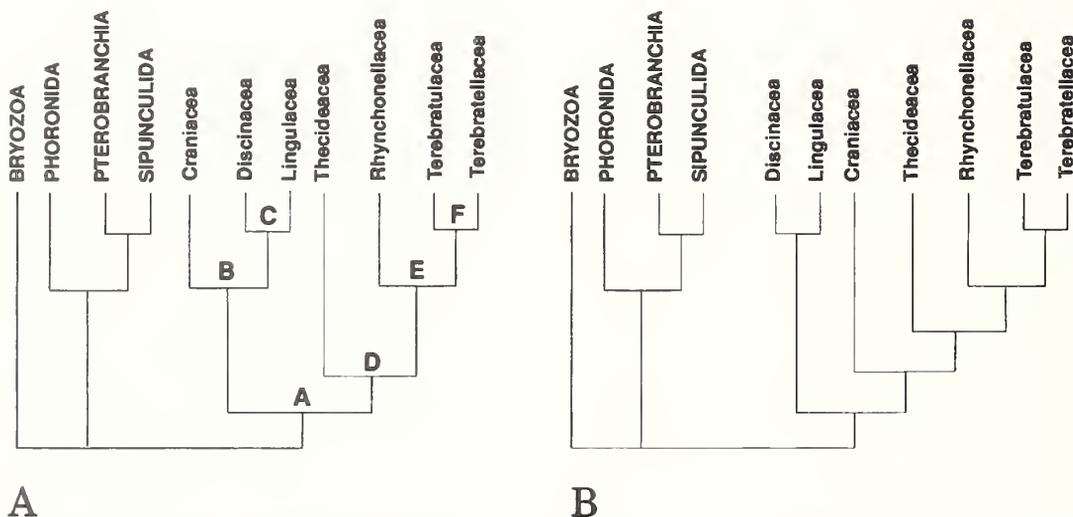


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#### DISCUSSION

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to her otherwise unchanged matrix. For example, the development of dermal muscles (character 113, *dem*; Table 5) does not appear as any of her 112 original characters. The addition of this single character alone is enough to modify the analysis by producing two equally parsimonious trees, with the topologies represented in Text-figure 5A–B. Carlson herself noted that removal of her characters 38 (median tentacle in lophophore) or 40 (internal musculature of adult lophophore) (Table 5), as well as removing data for the thecideoideans completely, also significantly changed the result in producing trees that are consistent with our model. We have already commented (p. 721) on the fact that the development of a median tentacle in the ‘Inarticulata’ might be related to the presence of a spirolophous lophophore, and if we re-code Carlson’s interpretation of the possible presence of a ‘median tentacle’ in rhynchonelloideans (her character 38) to missing (that is, ‘Unknown’), the resulting cladogram also supports our model (Text-fig. 5B). The addition of a further five characters from our matrix (114–118; Table 5) gives yet more strength to the resulting single tree (Text-fig. 5B). This kind of instability in Carlson’s (1995) analysis might possibly be related to the presence of a large number of homoplastic characters (Bassett *et al.* 1994, p. 385). Such effects are probably particularly strong in analyses involving relatively ‘simple’ invertebrate groups with relatively few ‘good characters’ and an ancient geological record (causing problems with outgroups). Unlike vertebrates, for example, the brachiopod body plan does not involve many characters that have a clear-cut homology, and thus it is possible that analyses introducing a large number of homoplastic characters will be more disturbed by this ‘noise’ by comparison with analyses of other groups.

In comparing the conflicting conclusions reached by Carlson and ourselves, recent studies of brachiopod ontogeny and biochemistry lend strong support to our proposals. Nielsen’s (1991) study of the larval development of *Neocrania* indicated that ‘the “articulates” and *Crania* [= *Neocrania*] appear to represent one line of evolution and *Lingula* and *Discinisca* another’. Jope’s (1986) summary of her data on the shell protein and other biochemical characteristics of *Crania* [= *Neocrania*] emphasized a greater similarity to the ‘articulates’ than to the phosphatic-shelled brachiopods. Whilst noting the ‘anomalous taxonomic position of the Craniacea’, Jope (1986, p. 106) stressed that the ‘zoological evidence for connection with the Inarticulata is equally cogent’. Two particular features are given in support of this latter association. These are, the low glycine in the shell protein and the presence of chitin as pads at the site of muscle attachment (Williams and Wright 1970; Jope 1986). However, thin layers of chitin have been discovered in the laminated carbonate shells of molluscs (Weiner and Traub 1984) and Jope (1986) believes that such thin layers will be found eventually in calcareous brachiopods. Although Jope herself recognized the strength of her biomolecular evidence for classifying craniids with the articulates she did not do so, preferring to explain part of this evidence by developing a genetic scenario for the derivation of the Craniida from the phosphatic brachiopods. However, the need for such genetic perturbations is greatly reduced and the biochemical similarities much more easily explained if the Craniformea share a common ancestry with the ‘articulates’. Similarly, the ‘uneasy phylogenetic placement’ of *Lingula* and its phosphatic-shelled relatives pointed out in studies of shell protein by Tuross and Fisher (1989) is resolved by our conclusions. It is unlikely that differences between shell proteins of brachiopods can be explained simply by the different patterns of mineralization of the shell, because the proteinous chain-length of the phosphatic-shelled *Lingula* is comparable with that of bivalve molluscs, but both *Lingula* and the *Bivalvia* differ markedly in this character from *Crania* and ‘articulate’ brachiopods (Jope 1986, fig. 1). The differences are more strongly indicative of a considerable genetic difference between lingulates and calciates.

## CONCLUSIONS

The conflicting patterns of brachiopod relationships reviewed above largely reflect the selection of, and relative taxonomic importance ascribed to characters used in the various analyses; such factors also include the choice and coding of the outgroup. As we have pointed out previously (Bassett *et al.* 1994), a level of subjectivity is inevitable and we certainly reiterate the view that degrees of objectivity cannot be evaluated simply by comparing the size of matrices that support competing

TABLE 5. Character state matrix (see text for explanation) used in PAUP analysis by Carlson (1995). Characters 113–118 (marked as bold text) have been added to Carlson's original 112 characters. The coding of character 38 (marked with **bold**) was changed in one of the analyses run herein.

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Bryozoa	U	0	1	U	U	0	P	1	1	1	1	2	N	0	1	U	0	1	U	1	P	1	U	U	0	N
Craniacea	1	1	1	1	0	1	1	1	2	1	1	0	1	1	1	3	1	1	1	2	1	1	0	2	1	1
Discinacea	1	1	1	1	0	1	U	U	1	U	U	0	1	0	1	3	1	1	U	1	1	1	U	1	1	1
Lingulacea	1	1	1	1	0	1	0	1	1	0	0	1	0	1	0	4	1	1	0	1	1	1	1	0	1	1
Phoronida	2	1	1	0	N	P	P	1	1	1	P	1	3	0	0	0	1	1	2	1	1	1	0	U	0	N
Pterobranchia	1	1	1	1	N	P	1	0	0	U	U	0	2	1	0	0	1	2	1	1	1	1	0	U	0	N
Rhynchonellacea	1	1	1	1	1	1	1	0	2	1	U	2	1	1	P	2	1	2	2	1	2	1	U	1	U	0
Sipunculida	0	U	0	0	N	P	U	0	0	U	1	0	0	P	1	0	0	0	0	0	U	N	U	U	0	N
Terebratulacea	1	1	1	1	1	P	1	0	2	U	U	1	1	1	2	1	2	1	2	2	1	2	1	1	1	0
Terebratulacea	1	1	1	1	1	1	1	0	2	1	U	1	1	1	P	2	1	2	2	1	2	1	U	1	U	0
Thecideacea	1	0	1	1	1	1	1	U	1	1	U	2	1	1	1	2	1	2	1	2	1	2	1	U	1	0
Character no.	26	27	28	29	30	31	32	33	34	35	36	37	<b>38</b>	39	40	41	42	43	44	45	46	47	48	49	50	
Bryozoa	N	N	N	0	0	N	N	1	0	0	0	0	0	0	0	0	0	0	0	0	N	1	0	0	U	
Craniacea	1	1	0	0	0	N	N	1	1	1	1	1	1	2	1	1	0	3	1	1	0	1	2	2	1	
Discinacea	0	0	1	1	1	0	0	1	1	1	2	1	2	1	1	1	0	2	2	1	0	2	0	2	1	
Lingulacea	0	0	1	1	1	0	0	1	1	1	2	1	2	1	1	1	0	2	6	1	0	1	1	2	1	
Phoronida	N	N	N	0	0	N	N	1	1	1	0	0	0	0	0	1	0	0	0	0	0	3	0	1	1	
Pterobranchia	N	N	N	0	0	N	N	2	2	4	0	0	0	0	1	2	0	0	0	0	2	N	1	1	0	1
Rhynchonellacea	U	U	2	1	2	1	1	1	1	1	1	U	1	1	1	1	1	1	3	1	1	1	1	2	U	
Sipunculida	N	N	N	0	0	N	N	0	2	4	0	0	0	0	0	0	0	0	5	1	0	2	0	2	U	
Terebratulacea	U	U	2	1	2	1	1	1	1	2	0	1	0	1	0	1	1	1	3	1	0	1	1	2	1	
Terebratulacea	U	U	2	1	2	1	1	1	1	2	0	1	0	1	0	1	1	1	3	1	0	1	1	2	U	
Thecideacea	U	U	2	0	4	1	N	1	1	3	1	0	U	1	0	1	1	1	4	1	0	1	1	2	U	
Character no.	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	
Bryozoa	0	0	1	N	0	0	0	2	1	1	1	1	2	N	N	N	N	N	0	0	0	0	N	N	N	
Craniacea	1	0	1	0	0	1	0	2	0	0	1	2	1	0	0	1	0	1	0	0	1	1	N	N	0	
Discinacea	1	0	1	0	0	U	0	0	0	0	2	1	1	1	0	1	N	N	0	0	0	N	N	0	1	
Lingulacea	1	0	1	0	1	1	0	1	0	0	2	0	0	3	1	N	N	0	0	0	0	0	N	0	2	
Phoronida	2	0	0	N	1	0	N	2	0	0	0	N	N	N	N	N	N	N	0	0	0	1	N	N	N	
Pterobranchia	0	0	0	N	1	U	0	2	1	0	0	N	N	N	N	N	N	N	0	N	1	N	N	N	N	
Rhynchonellacea	1	1	1	1	1	1	1	0	0	0	1	2	1	2	1	0	N	3	0	1	0	1	1	2	1	
Sipunculida	0	0	0	N	0	0	0	3	0	0	1	2	N	N	U	U	U	0	0	U	0	N	N	N	N	
Terebratulacea	1	1	1	1	1	1	1	0	0	0	1	2	1	2	1	0	N	2	2	2	1	0	1	2	2	
Terebratulacea	1	1	1	1	1	1	1	0	0	0	1	2	1	2	1	0	1	2	2	1	0	1	1	2	2	
Thecideacea	1	1	1	1	1	U	0	2	0	0	1	2	1	1	1	1	N	2	2	1	1	1	0	2	0	

Character no.	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
Bryozoa	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	
Craniacea	1	N	2	1	1	2	0	0	0	N	3	N	N	N	N	N	0	0	0	N	N	1	N	0	N	
Discinacea	1	N	0	0	0	0	0	0	0	N	0	N	U	U	0	0	1	1	1	N	0	0	0	0	0	2
Lingulacea	0	0	0	0	N	1	1	0	0	N	2	0	U	U	2	1	1	1	P	N	0	0	3	1	2	
Phoronida	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Pterobranchia	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Rhynchonellacea	0	2	2	1	N	1	3	2	0	N	0	1	3	2	3	1	2	0	0	2	1	0	1	0	2	
Sipunculida	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Terebratulacea	0	1	1	1	N	1	1	0	P	1	1	1	3	2	2	1	2	0	1	P	1	0	1	0	1	
Terebratulacea	0	1	1	1	N	1	1	1	1	1	1	1	3	1	4	1	2	0	0	0	1	0	1	0	1	
Thecideacea	1	N	1	2	2	1	2	0	0	N	1	1	1	3	2	2	0	2	1	0	N	0	0	0	1	
Character no.	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118								

	dem	mcl	pmn	sta	dbv	lan
Bryozoa	U	N	N	N	N	N
Craniacea	0	0	0	0	1	1
Discinacea	1	1	1	1	0	0
Lingulacea	1	1	1	1	0	0
Phoronida	1	N	N	N	N	N
Pterobranchia	1	N	N	N	N	N
Rhynchonellacea	0	0	0	0	0	0
Sipunculida	1	N	N	N	N	N
Terebratulacea	0	0	0	0	0	0
Terebratulacea	0	0	0	0	0	0
Thecideacea	0	U	U	U	0	0



TABLE 5. Character state matrix (see text for explanation) used in PAUP analysis by Carlson (1995). Characters 113-118 (marked as bold text) have been added to Carlson's original 112 characters. The coding of character 38 (marked with bold) was changed in one of the analyses run herein.

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Bryozoa	U	0	1	U	U	0	P	1	1	1	1	2	N	0	1	U	0	1	U	1	P	1	U	0	N
Craniacea	1	1	1	1	0	1	1	1	2	1	1	0	1	1	3	1	1	2	1	1	0	2	1	1	N
Discinacea	1	1	1	1	0	1	U	U	1	U	U	0	1	0	1	3	1	1	U	1	1	1	U	1	1
Lingulacea	1	1	1	1	0	1	0	1	0	0	0	1	0	1	4	1	1	0	1	1	1	0	1	1	1
Phoronida	2	1	1	0	N	P	P	1	1	1	P	1	3	0	0	0	1	1	2	1	1	0	1	0	N
Pterobranchia	1	1	1	1	N	P	1	0	0	U	U	0	2	1	0	0	1	2	1	1	0	U	0	0	N
Rhynchonellacea	1	1	1	1	1	1	1	0	2	1	U	2	1	1	P	2	1	2	2	1	2	1	U	1	0
Sipunculida	0	U	0	0	N	P	U	0	0	U	1	0	0	P	1	0	0	0	0	0	U	N	U	0	N
Terebratulacea	1	1	1	1	1	P	1	0	2	U	1	1	1	1	1	2	1	2	2	1	2	1	1	1	0
Terebratulacea	1	1	1	1	1	1	1	0	2	1	U	1	1	1	P	2	1	2	2	1	2	1	U	1	0
Thecideacea	1	0	1	1	1	1	1	U	1	1	U	2	1	1	1	2	1	2	U	1	2	1	U	1	0
Character no.	26	27	28	29	30	31	32	33	34	35	36	37	<b>38</b>	39	40	41	42	43	44	45	46	47	48	49	50
Bryozoa	N	N	N	0	0	N	N	1	0	0	0	0	0	0	0	0	0	0	0	0	N	1	0	0	U
Craniacea	1	1	0	0	0	N	N	1	1	1	1	1	1	2	1	1	0	3	1	1	0	1	2	2	1
Discinacea	0	0	1	1	1	0	0	1	1	1	1	2	1	2	1	1	0	2	2	1	0	2	0	2	1
Lingulacea	0	0	1	1	1	0	0	1	1	1	1	2	1	2	1	1	0	2	2	6	1	0	1	1	1
Phoronida	N	N	N	0	0	N	N	1	1	1	0	0	0	0	0	1	0	0	0	1	0	3	0	1	1
Pterobranchia	N	N	N	0	0	N	N	2	2	4	0	0	0	0	1	2	0	0	0	2	N	1	1	0	1
Rhynchonellacea	U	U	2	1	2	1	1	1	1	1	1	1	U	1	1	1	1	3	1	1	1	1	1	2	U
Sipunculida	N	N	N	0	0	N	N	0	2	4	0	0	0	0	1	0	0	5	1	0	2	0	2	0	1
Terebratulacea	U	U	2	1	2	1	1	1	1	2	0	1	0	1	0	1	1	1	3	1	0	1	1	2	0
Terebratulacea	U	U	2	1	2	1	1	1	2	0	1	0	1	0	1	1	1	3	1	0	1	1	2	1	U
Thecideacea	U	U	2	0	4	1	N	1	1	3	1	0	U	1	0	1	1	1	1	4	1	0	1	1	U
Character no.	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Bryozoa	0	0	1	N	0	0	0	2	1	1	1	2	N	N	N	N	N	N	0	0	0	N	N	N	N
Craniacea	1	0	1	0	0	1	0	2	0	0	1	2	1	0	0	1	0	1	0	0	1	1	N	0	1
Discinacea	1	0	1	0	0	U	0	0	0	0	2	1	1	1	0	N	N	0	0	1	0	0	N	0	1
Lingulacea	1	0	1	0	1	1	0	1	0	0	2	0	0	3	1	N	N	0	0	0	0	0	N	0	2
Phoronida	2	0	0	N	1	0	N	2	0	0	0	N	N	N	N	N	N	N	0	N	0	N	N	N	N
Pterobranchia	0	0	0	N	1	U	0	2	1	0	0	N	N	N	N	N	N	N	N	1	N	N	N	N	N
Rhynchonellacea	1	1	1	1	1	1	1	0	0	0	1	2	1	2	1	0	N	3	0	1	0	1	1	2	1
Sipunculida	0	0	0	N	0	0	0	3	0	0	1	2	N	N	N	U	U	U	0	U	0	N	N	N	N
Terebratulacea	1	1	1	1	1	1	1	0	0	0	1	2	1	2	1	0	N	2	2	1	0	1	1	2	2
Terebratulacea	1	1	1	1	1	1	1	0	0	0	1	2	1	2	1	0	1	2	2	1	0	1	1	2	2
Thecideacea	1	1	1	1	1	U	0	2	0	0	1	2	1	1	1	1	N	2	2	1	1	1	0	2	0
Character no.	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Bryozoa	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Craniacea	1	N	2	1	1	2	0	0	0	N	3	N	0	N	N	N	0	0	0	1	N	1	N	0	1
Discinacea	1	N	0	0	0	0	0	0	0	N	0	N	U	0	0	0	1	0	1	N	0	0	0	0	1
Lingulacea	0	0	0	0	N	1	1	0	0	N	2	0	U	0	2	1	1	1	P	N	0	0	3	1	2
Phoronida	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Pterobranchia	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Rhynchonellacea	0	2	2	1	N	1	3	2	0	0	1	3	2	3	1	2	0	0	2	1	0	1	0	2	N
Sipunculida	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Terebratulacea	0	1	1	1	N	1	1	0	P	1	1	1	3	2	2	1	2	0	1	P	1	0	1	P	1
Terebratulacea	0	1	1	1	N	1	1	0	1	1	1	1	3	1	4	1	2	0	0	1	0	1	0	1	1
Thecideacea	1	N	1	2	2	1	2	0	0	N	1	1	1	3	2	0	2	0	1	0	N	0	0	0	1
Character no.	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118							
													<b>dem</b>	<b>mcl</b>	<b>pmn</b>	<b>sta</b>	<b>dbv</b>	<b>lan</b>							
Bryozoa	N	N	N	N	0	N	N	N	N	N	N	N	U	N	N	N	N	N							
Craniacea	2	0	1	N	0	N	N	1	0	N	2	3	0	0	0	0	1	1							
Discinacea	0	0	0	N	0	N	N	2	0	N	1	3	1	1	1	1	1	1							
Lingulacea	1	2	P	N	0	N	N	2	0	N	1	3	1	1	1	1	1	1							
Phoronida	N	N	N	N	0	N	N	N	N	N	N	N	1	N	N	N	N	N							
Pterobranchia	N	N	N	N	0	N	N	N	N	N	N	N	1	N	N	N	N	N							
Rhynchonellacea	0	1	2	1	1	1	N	0	0	1	3	2	0	0	0	0	0	0							
Sipunculida	N	N	N	N	0	N	N	N	N	N	N	N	1	N	N	N	N	N							
Terebratulacea	P	1	2	1	1	2	1	1	0	2	4	2	0	0	0	0	0	0							
Terebratulacea	1	2	P	1	1	2	0	1	0	2	4	2	0	0	0	0	0	0							
Thecideacea	0	1	2	0	2	N	N	0	1	3	U	U	0	U	0	0	0	0							

cladograms. The impossibility of producing a 'complete' character matrix for any group is self-evident, and no resolution can be achieved simply by including large numbers of characters for different groups of brachiopods unless homology can be determined.

From analyses of Recent stocks alone, the fragility of both our cladogram (Text-fig. 3) and that of Carlson (Text-fig. 5A) suggests that either model of relationships could be acceptable. However, when the extinct stocks are also taken into account (Text-fig. 4), it is clear to us that the phylogenetic separation of chitinophosphatic-shelled and carbonatic-shelled brachiopods as sister groups within the phylum has compelling support; not least, it adds considerable weight to the explanation of the pattern of earliest radiation in groups that were previously poorly studied or unknown, but whose morphologies are now becoming increasingly well understood and are giving consistent pointers to these early relationships. New fossil finds, like that of *Heliomedusa* (Jin and Wang 1992) will be one way in which such relationships and the competing models can be further tested in the future. Meanwhile, the evidence from fossils is being backed up increasingly by new data on ontogeny and biochemistry (Bassett *et al.* 1994, p. 386) to demonstrate that previously accepted relationships within the 'inarticulates' are no longer tenable. The implications of relationships of the carbonatic-shelled 'inarticulates' with the 'articulates' cannot be ignored, and neither can the implications for higher level classification within the phylum.

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# ECHINOIDS FROM THE JURASSIC OXFORD CLAY OF ENGLAND

by ANDREW B. SMITH

**ABSTRACT.** The echinoids of the Oxford Clay (Callovian–Oxfordian) of southern England have, until now, remained very poorly known. Three species are described: *Eosalenia jessoni* is shown to be a member of the Aspidodiadematidae, a rare deep-water family of Diadematoidea, and *Trochotiara superbum* and *Disaster moeschi* are both reported from Britain for the first time.

THE Oxford Clay Formation, which extends from the Lower Callovian Calloviense Zone to the Lower Oxfordian Cordatum Zone, is widely developed in southern England. It has been divided traditionally into Lower, Middle and Upper Oxford Clay, but these have now been defined formally as the Peterborough, Stewartby and Weymouth members respectively (Cox *et al.* 1992). The formation is well-known for its beautifully preserved molluscs, especially ammonites, which are both abundant and diverse, and have been studied extensively (Martill and Hudson 1991). In contrast, echinoids from the Oxford Clay have remained almost unknown. In Wright's comprehensive monograph on British Jurassic echinoids, the Oxford Clay and underlying Kellaways Beds are the only formations listed as yielding no echinoids (Wright 1861, p. 434). The first published record of echinoids from the Oxford Clay appears in Penning and Jukes-Browne (1881, p. 7), where *Acrosalenia spinosa*? Agassiz is listed as coming from the Oxfordian St Ives Clays [= Weymouth Member]. Roberts (1892, p. 18) also recorded an *Acrosalenia* from the Oxford Clay of St Ives. However, the first description of an Oxford Clay echinoid did not appear until 25 years later when Gregory (1896) provided a brief description of his new species *Pseudodiadema jessoni*. The only other published record, until recently, was a report of 'crushed Collyritidae' from the Lower Spinosum Clays [= Stewartby Member] of Woodham Brickpit, Buckinghamshire, by Arkell (1939).

The echinoid fauna from the equivalent lithofacies and age in Europe are no better known. Thierry and Néraudeau (1994) point out that the lowest standing diversity of echinoids in the French Jurassic is reached towards the end of the Late Callovian and at the beginning of the Early Oxfordian, coinciding with a sea-level high-stand. Callovian and Oxfordian echinoids do occur more abundantly in facies other than clays, but these have a very different taxonomic composition from the fauna described here.

In 1989, Neville Hollingworth (then at Oxford Polytechnic) started making faunal collections from the Oxford Clay exposed in the ARC quarry at Stanton Harcourt, Oxfordshire. He collected a large number of echinoids, and additional specimens have been collected by Jon Todd (University of Wales, Aberystwyth) and myself subsequently. By far the most common echinoid present at this locality is the irregular species *Disaster moeschi* Desor. This belongs to the family Disasteridae which previously was unrecorded from Britain. In addition, a few specimens of a small regular echinoid, belonging to the rare diadematooid family Aspidodiadematidae, were also collected. These two species were listed in Hollingworth and Wignall (1992, p. 20), and illustrated by Martill (1991) as *Disaster granulatus* (Goldfuss) and *Eosalenia* sp. nov., respectively.

Although larger specimens are inevitably crushed and pyritization often obscures surface detail, preservation of Oxford Clay echinoids can be exquisite. Prompted by the importance of the new finds at Stanton Harcourt and their excellent preservation, additional specimens were sought

amongst museum collections and a third species, this time a true *Pseudodiadema*, was found, along with a number of indeterminate fragmentary spines of cidaroids.

This paper describes the Oxford Clay echinoids and their autecology. The environmental setting and palaeoecology of the fauna from Stanton Harcourt quarry have been discussed in Hollingworth and Wignall (1992), and for the Oxford Clay in general by Martill and Hudson (1991).

#### LOCALITIES AND STRATIGRAPHY

Oxford Clay echinoids are known from the following localities and horizons (stratigraphical nomenclature follows Cox *et al.* 1992):

(a) Woodham Brick Pit, Akeham Street Station, Buckinghamshire [National Grid Reference SP 694183]. Stewartby Member; Upper Callovian, Athleta Zone. Details of the section are given by Arkell (1939) and Callomon (1968).

(b) ARC Quarry, 1 km west of Stanton Harcourt, Oxfordshire [National Grid Reference SP 410048]. The great majority of echinoids comes from the Lamberti Limestone at the top of the Stewartby Member; latest Callovian. However, uncommon specimens of *Disaster* come from immediately beneath, from the Athleta Zone Spinosum Subzone. Full details of this section are given in Hollingworth and Wignall (1992).

(c) Pit just west of the railway station at Warboys, Cambridgeshire [National Grid Reference TL 310818]. Weymouth Member; Lower Oxfordian, Mariae Zone. One specimen is recorded as coming from '4 feet [1.2 m] below the topmost cementstone, i.e. 8 feet [2.4 m] below the Corallian Limestone'. Others are stated to be from 'near [the] bottom' of the pit. Spath (1939) and Callomon (1968) give details of this section.

(d) St Ives Brick Pit [Howe Brick Pit], St Ives, Cambridgeshire [National Grid Reference TL 304718]. Weymouth Member; Lower Oxfordian, Mariae Zone. This section is described in Roberts (1892).

(e) Somersham Brick Pit, 8 km north-east of St Ives, [National Grid Reference TL 373791]. Weymouth Member; Lower Oxfordian. Section details unknown.

#### SYSTEMATIC PALAEOLOGY

Museum repositories are indicated as follows: BMNH = The Natural History Museum, London; OUM = Oxford University Museum, Oxford; SM = Sedgwick Museum, Cambridge.

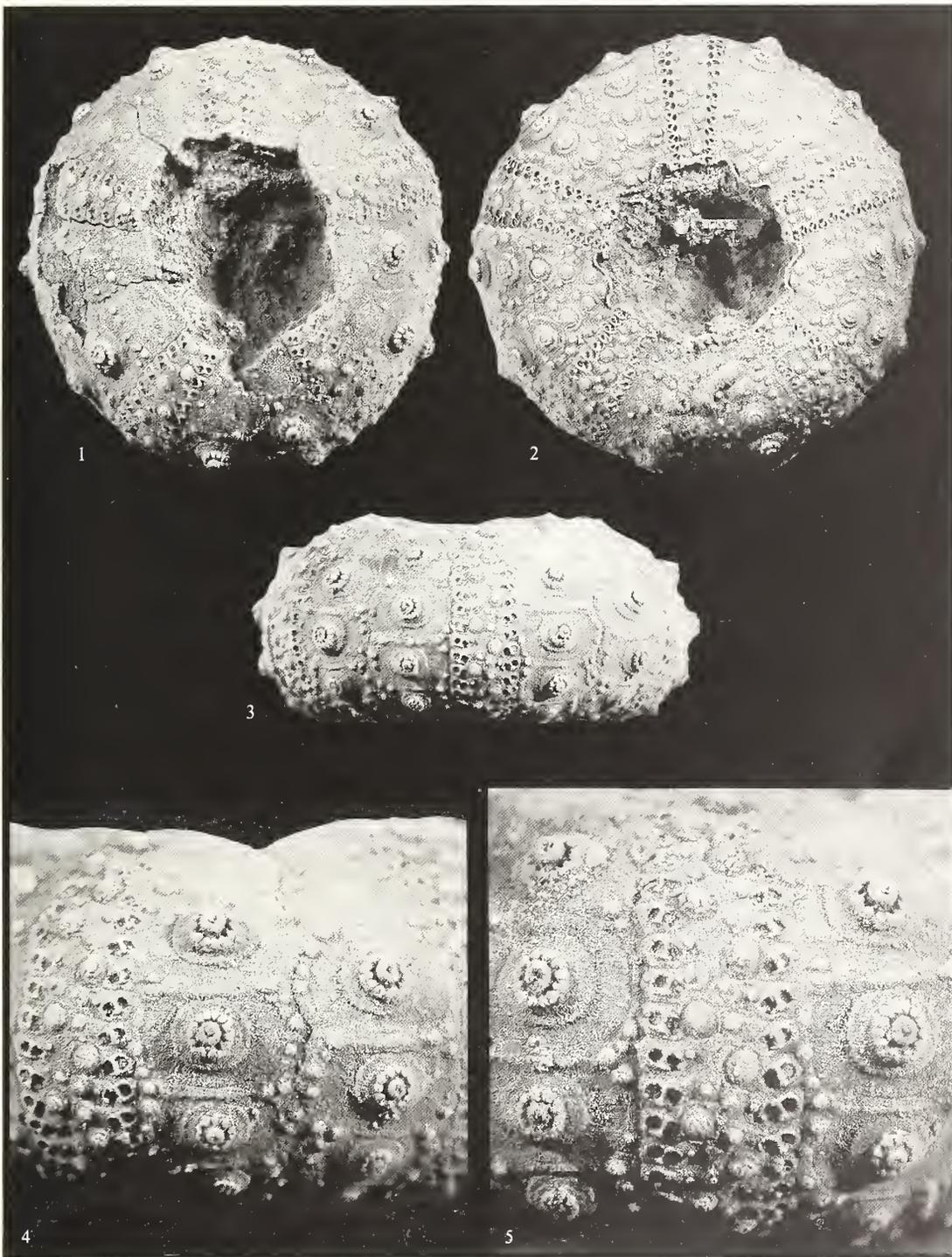
Subclass EUECHINOIDEA Bronn, 1860  
Order DIADEMATOIDA Duncan, 1889  
Family ASPIDODIADEMATIDAE Duncan, 1889

Mortensen (1940) included two extant genera, *Aspidodiadema* Agassiz and *Plesiodiadema* Pomel, and two fossil genera, *Eosalenia* Lambert and *Tiaridia* Pomel, in this family, which clearly belongs to the Diadematoidea, as argued by Smith and Wright (1990, p. 110). Members possess an aulodont lantern and have just ten local buccal plates like all acroechinoids. Apical disc plating is monocyclic, and plates are not sutured to the corona but are imbricate. Primary tubercles are large, perforate and strongly crenulate, whereas miliary tuberculation is sparse, being restricted to the margins of

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#### EXPLANATION OF PLATE 1

Figs 1–5. *Eosalenia jessoni* (Gregory); BMNH EE1294; Upper Callovian Lamberti Zone, Stanton Harcourt, Oxfordshire. 1, apical view; 2, oral view; 3, lateral view; 4, detail of interambulacrum in lateral view; 5, detail of ambulacrum in lateral view. 1–3,  $\times 6$ ; 4–5,  $\times 12$ .



SMITH, *Eosalenia jessoni*

plates. The most diagnostic features of aspidodiadematis are their spine structure and sphaeridial arrangement. Their spines are solid, and the shaft deeply ridged and verticillate. In cross section, they are constructed of an outer ring of stout calcite wedges and a central meshwork that forms horizontal dissepiments (Mortensen 1940, text-figs 6–7). Spines are always very much longer than the test diameter. Sphaeridia are developed uniformly on every plate from peristome to apex, and are placed in small depressions on the lowest of the three elements in each compound plate. They are attached to a small tubercle and hang downwards in life.

The two extant genera differ in their relative development of primary ambulacral tubercles; in *Aspidodiadema*, primary ambulacral tubercles are very large at the ambitus and adorally, occupying virtually the entire compound plate. In *Plesiadiadema*, by contrast, primary tubercles remain small and are restricted to the central of the three elements forming each compound plate.

Smith and Wright (1990, p. 113) were uncertain as to the placement of the genus *Eosalenia* since spines, apical disc, lantern and sphaeridia were all unknown. Specimens of *Eosalenia* from the Oxford Clay, described here, show the highly characteristic development of sphaeridial pits, and associated spines are now also known. On the basis of this new information, there seems little doubt that Mortensen (1940) was correct to place this genus in the Aspidodiadematis. Indeed, the species described below, *E. jessoni* (Gregory), is strikingly similar to *Plesiadiadema* in almost all test details, differing only in having rudimentary interambulacral tuberculation adapically. Lambert (*in* Lambert and Savin 1905) described the ambulacra of *Eosalenia* as being composed of simple plates becoming bigeminate adapically. However, specimens in the Lambert Collection housed in the Department of Geology, Université de Paris VI, have simple ambulacral plating throughout, although occasional elements are expanded and bear larger tubercles (Text-fig. 1B). Exactly the same is true for the *Eosalenia* described here from the Oxford Clay. Thus there is no difference in ambulacral structure that merits separation of *Eosalenia* from *Plesiadiadema*, and the two genera are differentiated solely on the relative development of periapical interambulacral tubercles.

#### Genus EOSALENIA Lambert *in* Lambert and Savin, 1905

*Type species.* *Eosalenia miranda* Lambert *in* Lambert and Savin, 1905, by monotypy, from the Oxfordian of Joyeuse, Ardèche, and Courry, Département de Gard, France and Late Callovian–Early Oxfordian of England. Treated here as a subjective junior synonym of *Pseudodiadema jessoni* Gregory.

*Other species.* *Pseudodiadema varusense* Cotteau from the Pliensbachian of Plan d'Aup, Var, France, and *Pseudodiadema dumortieri* Cotteau from the Bajocian of Saint-Rambert, Ain, France.

*Range and distribution.* Pliensbachian to Oxfordian of France and England. This lineage presumably gave rise to the extant *Plesiadiadema*.

*Diagnosis.* Aspidodiadematis resembling *Plesiadiadema* in ambulacral structure and tuberculation, but with periapical interambulacral plates having rudimentary tubercles only.

#### *Eosalenia jessoni* (Gregory, 1896)

Plate 1, figures 1–5; Text-figure 1

- 1892 *Acrosalenia*, sp. Roberts, p. 18 [listing only].
- 1896 *Pseudodiadema jessoni* Gregory, p. 465, text-fig. a–b.
- 1905 *Eosalenia miranda* Lambert *in* Lambert and Savin, 1905, p. 311, pl. 2, figs 10–14.
- 1911 *Eosalenia miranda* Lambert; Lambert and Thiéry, p. 166.
- 1935 *Eosalenia miranda* Lambert; Mortensen, p. 318, text-fig. 173.
- 1966 *Eosalenia miranda* Lambert; Fell, p. U352, text-fig. 261.4.
- 1991 *Eosalenia* sp. nov. Martill, p. 187, text-figs 7–8.
- 1992 *Eosalenia jessoni* (Gregory); Hollingworth and Wignall, p. 20.

*Types.* The holotype of *P. jessoni* is BMNH E3936, and there are two paratypes, BMNH E3937 and E3938. The holotype of *Eosalenia miranda*, by monotypy, is the specimen in the Gevrey Collection figured by Lambert and Savin (1905). Its whereabouts is unknown. A second specimen, L6.22 in the Lambert Collection at the Université de Paris VI, and identified by Lambert as *E. miranda*, has been examined.

*Material.* In addition to the types, this species is represented by the following specimens: SM J27143a,b, J27149–64, J27165–6, J35958, J46219–21, J48143, J69401; BMNH EE1294 and ? E41896.

*Range and distribution.* In England, the species is known from the Late Callovian, Lamberti Zone, of Stanton Harcourt and the Early Oxfordian, Mariae Zone, of Warboys Pit, Somersham Pit and St Ives (localities b–c above). Poorly preserved regular echinoids from the Late Callovian, Athleta Zone, of Woodham Pit (locality a above) may also belong to this species, although all are too badly affected by pyrite decay to be identified with confidence. The species is also known from the Oxfordian of France.

*Description.* Tests range from about 10 to 14 mm in diameter and 5 to 6.5 mm in test height (height is approximately 50 per cent. of the diameter). The test is circular in outline and wheel-shaped in profile, with the ambitus at about mid-height (Pl. 1, figs 1–3). The diameter of the apical disc is 41–49 per cent. of that of the test, and is circular in outline with small notches both radially and interradially. No plates of the apical disc remain in any specimen.

Ambulacra are narrow and straight-sided, hardly tapering either adapically or adorally. Plating is simple throughout with a primary tubercle developed on approximately every third plate (Pl. 1, fig. 5; Text-fig. 1A–B), although this is not strictly regular and there may be larger tubercles on every second plate adapically. Pore-pairs are small P2-type isopores (as defined in Smith 1978) and show no crowding towards the peristome. There is generally a small secondary tubercle on the plate immediately above that carrying the primary tubercle. The plate beneath each primary tubercle has a shallow sphaeroidal pit associated with a minute granule immediately perradial of the pore-pair (Pl. 1, fig. 5). These sphaeroidal pits are developed regularly on every third plate throughout most of the length of the ambulacrum, being absent only adapically in the largest specimen, where tuberculation also becomes less regular.

Interambulacra are broad, with eight or nine plates in a column. All but the periapical plates carry a large primary perforate, crenulate tubercle. This tubercle is surrounded by a large areole which occupies virtually the entire plate (Pl. 1, fig. 3). A few miliaries lie scattered around the adradial and interradial edges of the plate. Areoles are confluent.

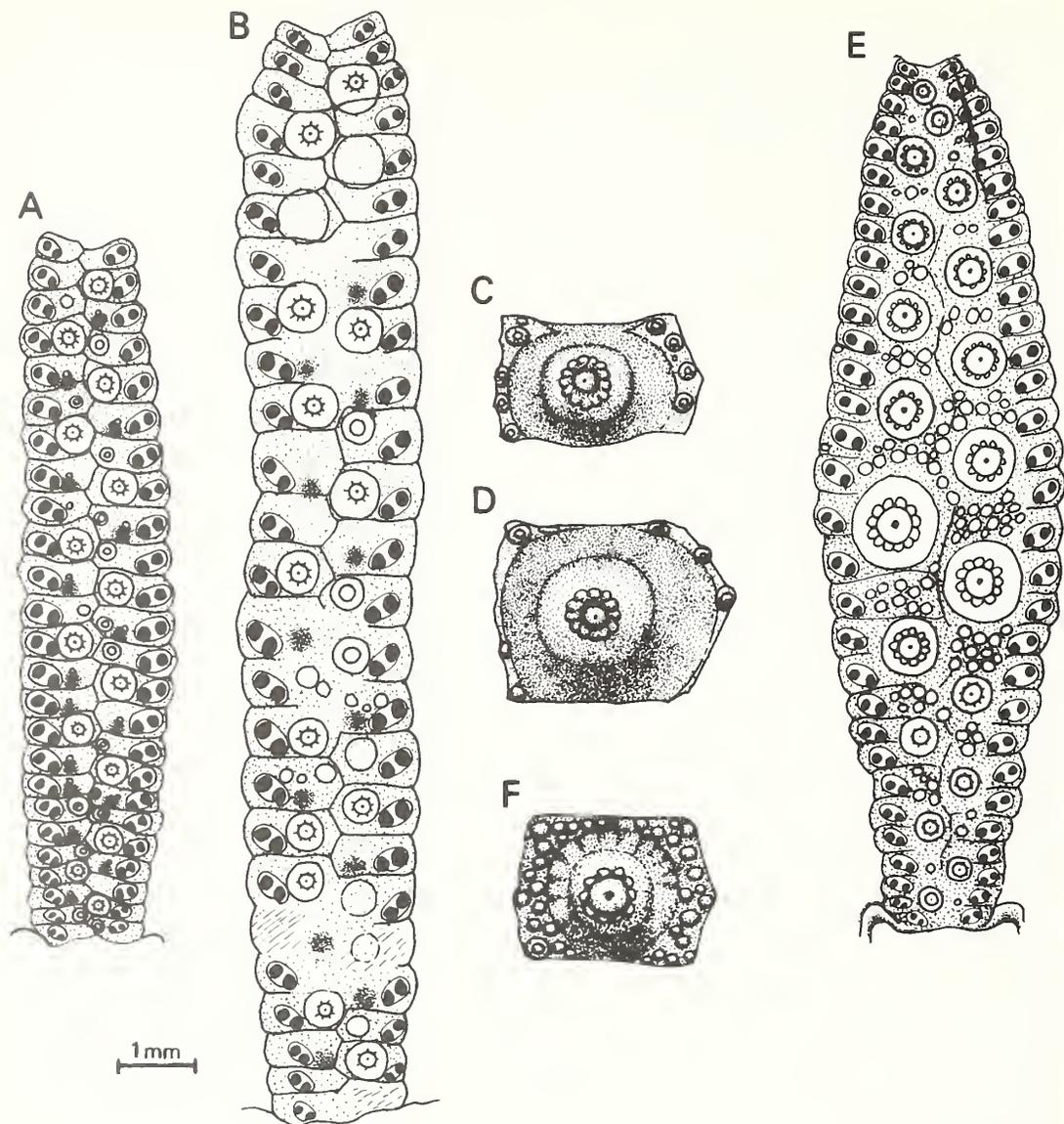
The peristome is slightly smaller than the apical disc, its diameter being about 35–40 per cent. that of the test. Buccal notches are broad and shallow, and give the peristomial edge a very undulose appearance (Pl. 1, fig. 2). Lantern elements and perignathic girdle remain unknown.

Spines are found in association with the test in SM J27143 and J48145. Unfortunately all are broken so that their length in life is unknown. They appear slender and lightly constructed and have no cortex. The shaft is deeply grooved and verticillate, though the thorns are not arranged into well defined whorls. In cross-section, the spine has a relatively large labyrinthine core and an outer ring of wedge-shaped rods. The longitudinal cross section is unknown.

*Remarks.* The species was first recorded from the Oxford Clay of England as *Acrosalenia* in the faunal list given by Roberts (1892). It was recognized as a new species by Gregory (1896), who gave only a brief description and sketch. He failed to realize its true relationships, however, and ascribed it to the genus *Pseudodiadema*. The species was later described under the name *miranda* by Lambert (in Lambert and Savin 1905) from the Oxfordian of Joyeuse, Ardèche, France. Lambert realized that the species was closely related to *Plesiodiadema* and created the new genus *Eosalenia* for it. In addition, a specimen, also Oxfordian in age, in the Lambert collection comes from Courry, Gard, France.

As noted by Lambert and Savin (1905), this species is remarkably similar to extant species of *Plesiodiadema*, differing primarily in lacking primary tubercles on periapical plates. The distinction between *E. jessoni* and earlier *Eosalenia* species is slight, but those from the Pliensbachian and Bajocian have better developed miliary rings around primary interambulacral tubercles.

There is very little difficulty in distinguishing this species from the other Oxford Clay regular echinoid, *Trochotiara superbum* (Agassiz), described below, which differs markedly in its tuberculation and ambulacral structure.



TEXT-FIG. 1. Camera lucida drawings of plating. A-D, *Eosalenia jessoni* (Gregory). A, C, BMNH EE1294; Upper Callovian, Lamberti Zone, Stanton Harcourt, Oxfordshire; A, ambulacrum, from apex to peristome; C, ambital interambulacral plate. B, D, L.6.22 (Lambert Collection, Université de Paris VI); Oxfordian, Courry, Gard, France (specimen identified by Lambert as *Eosalenia miranda* Lambert); B, ambulacrum from apex to peristome; D, ambital interambulacral plate. E-F, *Trochotiara superbum* (Agassiz), SM J27148; Lower Oxfordian, Mariae Zone, St Ives, Cambridgeshire; E, ambulacrum from apex to peristome; F, ambital interambulacral plate.

*Plesiadiadema* is restricted to deep water at the present day and is found between 300 and 3000 m depth (Mortensen 1935). Neither this form nor *Trochotiara superbum* show development of adoral pore-pair crowding, and are thus probably entirely soft-bottom dwellers.

Order PHYMOSOMATOIDA Mortensen, 1904  
Plesion (Genus) TROCHOTIARA Lambert, 1901

A discussion of this genus is given in Smith and Wright (1993), and need not be repeated here.

*Trochotiara superbum* (Agassiz, 1840)

Plate 2, figures 1–5; Text-figure 1E–F

1840 *Diadema superbum* Agassiz, p. 23, pl. 17, figs 6–10.

1882 *Pseudodiadema superbum* (Agassiz); Cotteau, p. 273, pl. 334, figs 1–9.

*Types.* The holotype is M92 in the Agassiz Collection, Museum de Histoire Naturelle de Neuchâtel. It comes from the Oxfordian Marls of Mont Vohayes, Switzerland.

*Material.* The best preserved specimen, on which the following description is based, is SM J27148. Other, less well preserved material includes SM J35954–5, SM J35958, BMNH E4242, and possibly OUM J42906–7.

*Range and distribution.* In England, the species comes from the Early Oxfordian Mariae Zone, of Warboys (locality c above) and St Ives (locality d above). Two poorly preserved regular echinoids from an unspecified level in the Oxford Clay have been found at St Clements and Cowley Field, Oxford, and may also belong to this species. It has not been found at other horizons. In France, it is widely distributed in the Oxfordian, and it also occurs in Switzerland at the same level.

*Diagnosis.* A *Trochotiara* with fine tuberculation and small mamelons. Peristome smaller than apex, its diameter only about 30–33 per cent. of that of the test. Broad naked interradial zone developed adapically.

*Description.* The only well preserved test is 12 mm in diameter and 5.5 mm in height (64 per cent. of the diameter). It is subpentagonal in outline and rather tumid in profile (Pl. 2, fig. 3), with the ambitus a little below mid-height. The circular apical disc opening is rather small for a trochotiariid, with a diameter only 40 per cent. of that of the test. All plates of the apical disc have been lost.

Ambulacra are two-thirds the width of interambulacra at the ambitus and taper both adapically and adorally (Pl. 2, figs 1–2). Pore-pairs are uniserial throughout and there is no pore crowding adorally (Pl. 2, fig. 2; Text-figure 1E). Plates are trigeminate throughout with a large primary tubercle occupying almost the entire compound plate adorally and ambitally. Adapically, the primary tubercles reduce in size gradually and a 2+1 style of compounding is found. Primary ambulacral tubercles are as large as the interambulacral tubercles at the ambitus and have circular, non-confluent areoles (Pl. 2, fig. 4). Miliary granules surround the primary tubercle areoles so as to form a single zig-zag series perradially. There are 30 ambulacral pores and nine primary tubercles in a column.

Interambulacra have 12 plates in a column, which are generally slightly broader than tall. Primary tubercles with circular non-confluent areoles are present on all plates. These are moderately large at the ambitus but become gradually smaller both apically and adorally. Adapically, the primary tubercles are displaced towards the adradial suture. Areoles are typically striated radially (Pl. 2, figs 3–4). Miliaries are well-developed at the ambitus forming a broad interradial zone. Adapically, they become sparse, leaving a broad and well defined naked zone interradially.

The peristome is remarkably small, much smaller than the apical disc, with a diameter only 32 per cent. of that of the test. It is circular and notched by relatively deep and prominent buccal notches (Pl. 2, fig. 2). It is hardly invaginated.

*Remarks.* The species was referred to the genus *Pseudodiadema* by Cotteau (1882). However, the type species of *Pseudodiadema*, *P. pseudodiadema* Agassiz, has a compact dicyclic apical disc which is rather firmly bound to coronal plates, whereas *Diadema superbum* Agassiz has a large pentagonal apical disc scar, and presumably a monocyclic apical disc. It is therefore transferred to the genus *Trochotiara* Lambert, 1901.

The most characteristic feature of this species is the relatively small size of its peristome. In almost all other trochotiariids, the peristome and apical disc are both large, and approximately equal in size. A second distinctive feature of *T. superbum* is the small size of the mamelons on its primary tubercles, although this is less pronounced in the English specimens than in the French. The small peristome, broad flat oral surface, small numerous interambulacral tubercles that decrease gradually adapically, and the well developed interradial naked zone give this species a very distinctive appearance.

Series ATELOSTOMATA Zittel, 1879  
Plesion (Family) DISASTERIDAE Gras, 1848  
Genus DISASTER Agassiz, 1836

*Type species.* *Nucleolites granulosus* Goldfuss, 1826, by subsequent designation of Desor, 1858, p. 201.

*Other species.* There are two other well-defined species, *D. moeschi* Desor, 1858, and *D. subelongatus* (Orbigny), as well as a number of other nominal species.

*Range and distribution.* Known from the Callovian (Middle Jurassic) through to the Barremian (Lower Cretaceous) of Europe and North Africa. The species has not previously been reported from Britain.

*Remarks.* Disasterids belong to the stem group of the Atelostomata and are characterized by their disjunct apical disc plating which, unlike that of collyritids, has only the posterior oculars well separated and posterior to the remainder of the apical disc. In *Disaster*, these posterior oculars border the periproct, which is situated on the posterior surface. Thus, the posterior ambulacra are initiated from the periproct margin and lie at the posterior extremity of the test.

The presence of differentiated peristomial pore-pairs and the arrangement of tubercles suggests very strongly that *Disaster* was a deposit feeder using phyllode tube-feet to collect sediment (Smith 1984). The presence of just a few large pore-pairs rather than a larger number of small pore-pairs is a clear indication that the tube-feet have a broad terminal disc and are utilizing mucus secretion to pick up fine-grained sediment, like most extant holasterids and spatangoids.

The fact that plastronal spines (which provide the forward thrust in modern irregular infaunal echinoids) and lateral oral spines (which provide the digging capability) are so poorly developed argues against *Disaster* having led an infaunal mode of life. So too does the low density of aboral tubercles; it is hard to envisage how such an open canopy of spines could have maintained a water-filled cavity around the test when buried within a mud substratum. However, the subanal tufts of spines are associated with the construction of a subanal drainage channel in living infaunal or semi-infaunal spatangoids (Smith 1984), and *Disaster* clearly had well developed subanal cones of spines. The cones occur very low down, more or less at the base of the test, and once again their function in *Disaster* is problematical. The simplest explanation for them is that they are retained from an ancestral disasterid that inhabited coarser-grained sediments and constructed subanal drainage channels. *Disaster* is thus interpreted as being a secondarily epifaunal detritivore.

*Disaster moeschi* Desor, 1858

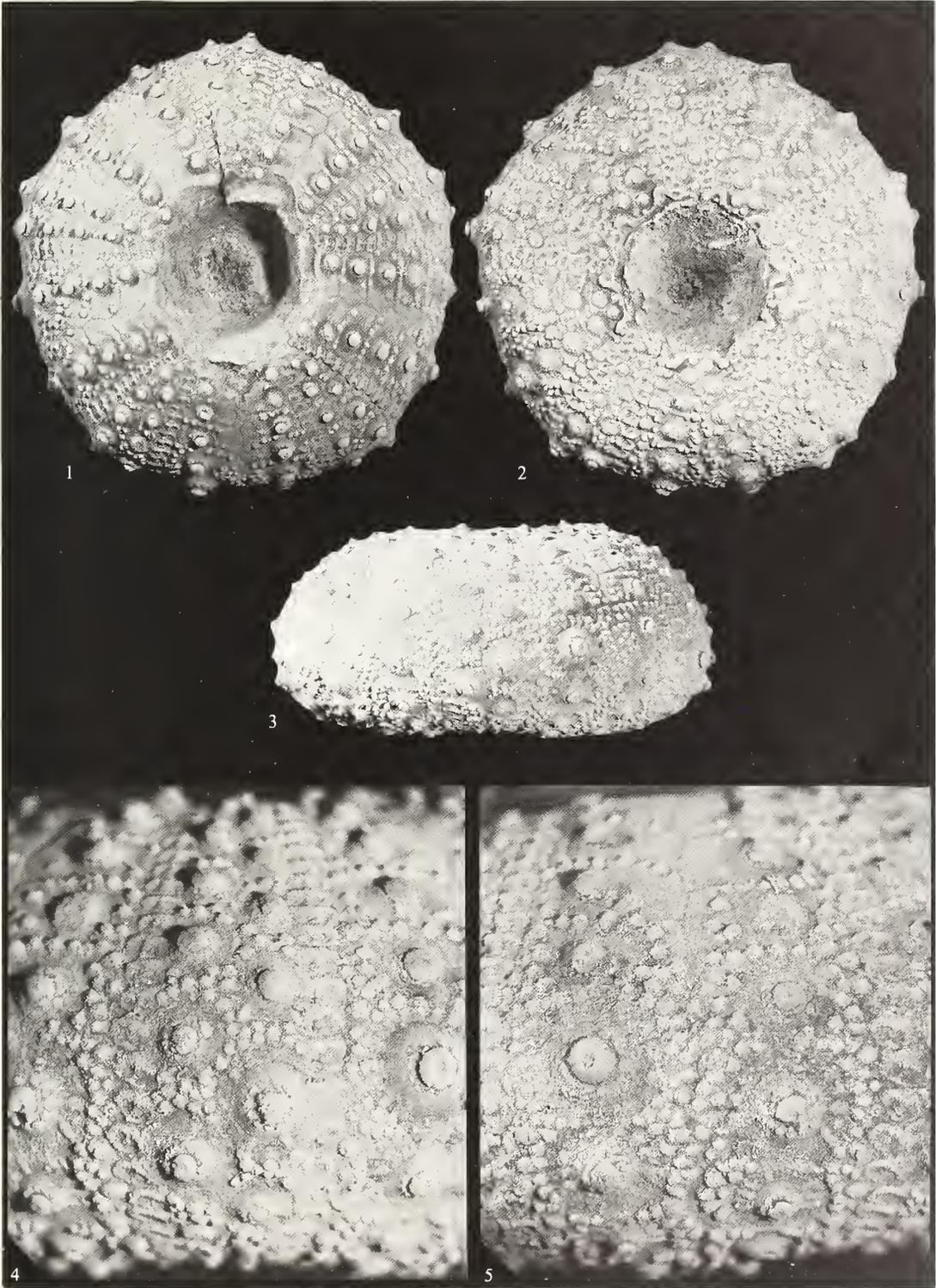
Plate 3, figures 1-6

1858 *Dysaster moeschi* Desor, p. 202.

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EXPLANATION OF PLATE 2

Figs 1-5. *Trochotiara superbum* (Agassiz); SM J27148; Lower Oxfordian Mariae Zone, St Ives, Cambridgeshire.  
1, apical view; 2, oral view; 3, lateral view; 4, detail of ambulacrum in lateral view; 5, detail of interambulacrum in lateral view. 1-3,  $\times 6$ ; 4-5,  $\times 12$ .



SMITH, *Trochotiarā superbūm*

- 1867 *Dysaster moeschi* Desor; Cotteau, p. 107, pl. 24, figs 1–7.  
 1934 *Disaster moeschi* Desor; Beurlen, p. 120, fig. 24a.  
 1963 *Disaster moeschi* Desor; Jesionek-Szymanska, p. 382, pl. 7, fig. 1 [see also for extended synonymy].  
 1991 *Disaster granulosis* (Goldfuss); Martill, p. 187, pl. 35, figs 1–3.

*Type.* The holotype, by original designation, is V63 in the collections of the Museum de Histoire Naturelle de Neuchâtel.

*Material.* A large number of specimens of this species was collected. The description given below is based on BMNH E83558–65 and EE1046–68.

*Range and distribution.* In England, this species is known only from the top of the Late Callovian, Athleta Zone (Spinosum Subzone) and Lamberti Zone of Stanton Harcourt (locality b above; Hollingworth and Wignall 1991), and the Athleta Zone of Woodham Brickpit (locality a above). Elsewhere, it is known from the Early Callovian through to the Early Oxfordian of France, Switzerland and Poland (Jesionek-Szymanska 1963; Thierry and Néraudeau, 1994).

*Diagnosis.* Differs from *D. granulosa* (Goldfuss) in being squatter and broader, in having the apical disc more central, and in having a more squarely truncated posterior with the posterior ambulacra largely restricted to this face.

*Description.* This species is relatively well known and, because the English material is mostly crushed, there is no point in presenting biometric data. However, the English material does preserve excellent surface detail, and this allows tuberculation and pore-pair arrangement to be described in full for the first time.

The apical disc is as in *D. granulosa*, with genital plates 1 to 4 forming a compact ethmophract-style disc. The madrepores are well developed and genital plate 2 is somewhat larger than other genital plates. Gonopores are rimmed (Pl. 3, fig. 5). The posterior oculars are generally lost, but their position is indicated clearly by a pair of notches in the upper corners of the periproct (Pl. 3, fig. 6).

Ambulacral pores are for the most part reduced to rudimentary P1-type isopores (*sensu* Smith 1978) (e.g. Pl. 3, fig. 5). There is no differentiation of aboral petals, and pores in the posterior ambulacra may be simple unipores. Pores remain rudimentary over most of the oral surface also, except adjacent to the mouth where enlarged phylloidal pore-pairs are found. There are approximately three such pore-pairs in each anterior ambulacral column, five in each lateral ambulacral column, and three or four in the posterior ambulacral columns. These pores are considerably enlarged (Pl. 3, fig. 1), and have a very large and swollen interporal partition.

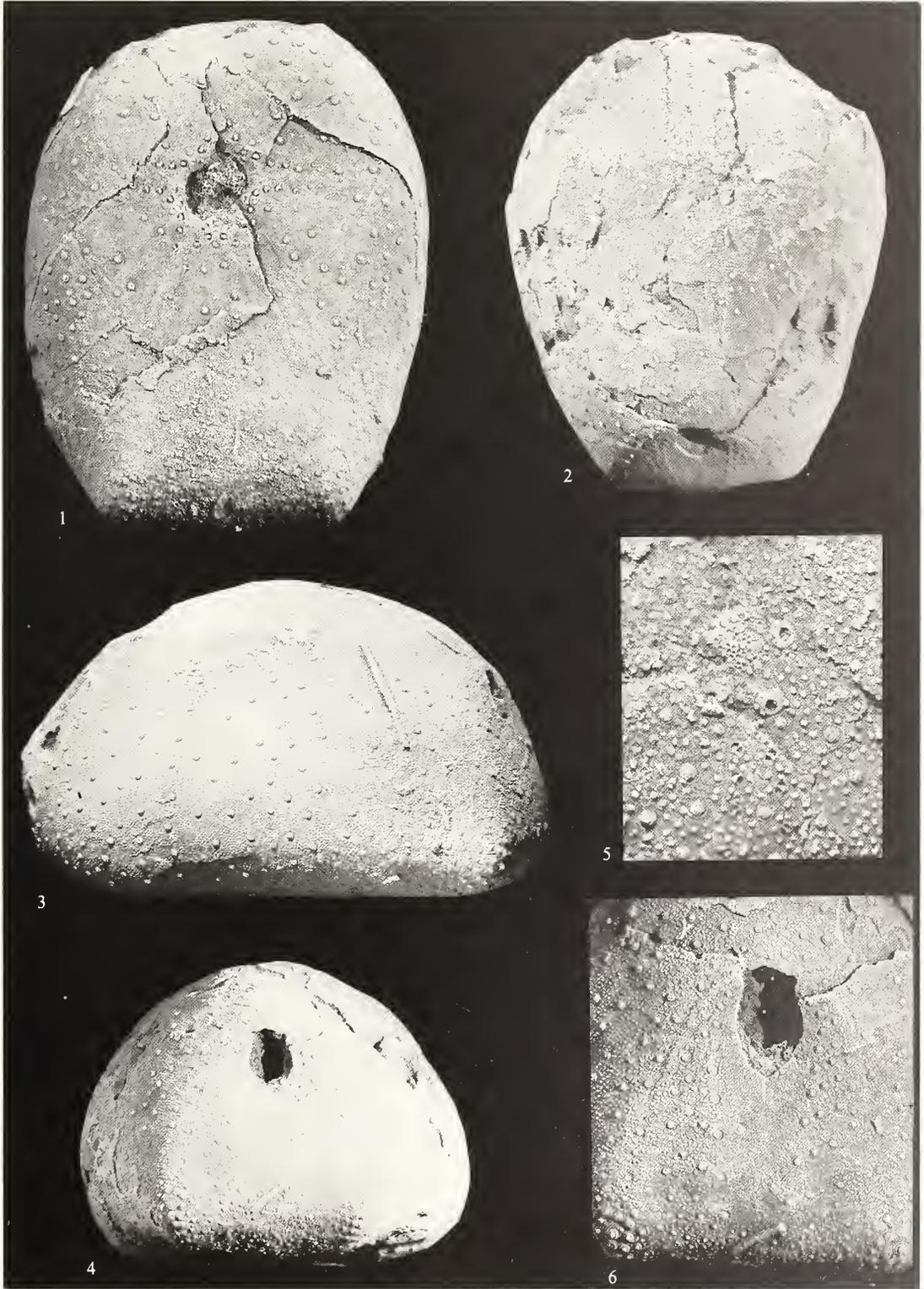
Aboral tuberculation comprises a relatively dense and uniform array of miliaries with a rather sparse scattering of small crenulate and perforate tubercles amongst them (Pl. 3, figs 3, 5–6). Primary tubercle density is about one per mm<sup>2</sup> or less. Areoles are circular in all aboral tubercles. The only place where tubercles become concentrated is on either side of the periproct (Pl. 3, fig. 6) where a vertical band of tubercles with circular areoles is found.

Tubercles are equally sparse over the oral surface, but here there are very few miliaries. Tubercle density increases slightly towards the ambitus, and there is also a ring of tubercles adjacent to the peristome, presumably to help in feeding. The plastron has the highest density of tubercles towards the rear (Pl. 3, fig. 1). Over the plastron and the postero-lateral interambulacra, primary tubercles have asymmetrical areoles that are enlarged towards the latero-posterior, indicating that the spines' power stroke was in that direction. The greatest development of tubercles, however, occurs on the two subanal nodes (Pl. 3, figs 3–4, 6). Here, primary tubercles are larger than elsewhere and so densely packed as to be contiguous. What is more, the tubercles show a distinctly concentric pattern of areole enlargement, areoles being consistently enlarged away from each

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#### EXPLANATION OF PLATE 3

Figs 1–6. *Disaster moeschi* Desor; Upper Callovian Lamberti Zone, Stanton Harcourt, Oxfordshire. 1, 3, BMNH E83558; 1, oral view; 3, lateral view, anterior to the left. 2, 4–6, BMNH E83563; 2, apical view; 4, posterior view; 5, detail of apical disc; 6, posterior view, detail of periproct. 1–4, ×4; 5, ×10; 6, ×8.



SMITH, *Disaster moeschi*

centre. Clearly, *D. moeschi* possessed a well developed pair of sub-anal tufts of spines, and these spines had their power stroke arranged radially outwards.

*Remarks.* *D. moeschi* is very similar to *D. granulosa* (Goldfuss) but is consistently squatter and taller and more truncated posteriorly. Stratigraphically, *D. moeschi* predates *D. granulosa*, and there can be little doubt that the two form a single evolving lineage.

*Acknowledgements.* I thank Neville Hollingworth for first bringing my attention to the occurrence of echinoids in the Oxford Clay and for providing a substantial number of specimens upon which to work, and Beris Cox for drawing my attention to pertinent literature.

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# A LOWER CAMBRIAN CORAL FROM SOUTH AUSTRALIA

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**ABSTRACT.** A Lower Cambrian coral, *Moorowipora chamberensis*, occurs in the Botomian Moorowie Formation near Moorowie Mine in the northern Flinders Ranges, South Australia. The coralla available for study are cerioid, with tripartite cerioid walls characterized by fibrous crystallites belonging to each corallite, separated by dark, fine-grained carbonate. The corallites were built by true individuals (polyps), as evidenced by their contraction to rounded form when clastic sediment was present within the corallum. Tabulae are present, formed as a basal thin, dark layer and upper fibrous layer perpendicular to the upper surface of the plate. The cerioid colonial form with typical coralline wall structure, the presence of short septal spines, the reaction of corallites to influxes of clastic sediment and the construction of the tabulae all indicate that this Lower Cambrian coral may be placed within the anthozoan Subclass Tabulata, albeit with a question mark. This would extend the range of the group considerably.

THE early Cambrian was a time of extensive reef growth, up to the Toyonian or latest early Cambrian extinction. It has been hypothesized that reefs prior to this extinction were constructed principally by archaeocyaths and calcimicrobes (calcareous cyanobacteria), with stromatolite-forming organisms assuming a subordinate role (Rowland and Gangloff 1988). These early, metazoan-dominated ecosystems display many of the features commonly associated with younger Palaeozoic reefs including community zonation, growth into normal wavebase (Rowland 1984; Rowland and Gangloff 1988), and growth interactions that suggest spatial competition. The decline in reef development following the early Cambrian has been attributed to the extinction of archaeocyaths (Copper 1989; Debrenne 1991). It has been presumed that prolific reef growth was not renewed until a new group of preadapted framebuilders evolved, and that this did not occur until Ordovician time, with the first appearance of bryozoans and corals (Sheehan 1985; Copper 1989).

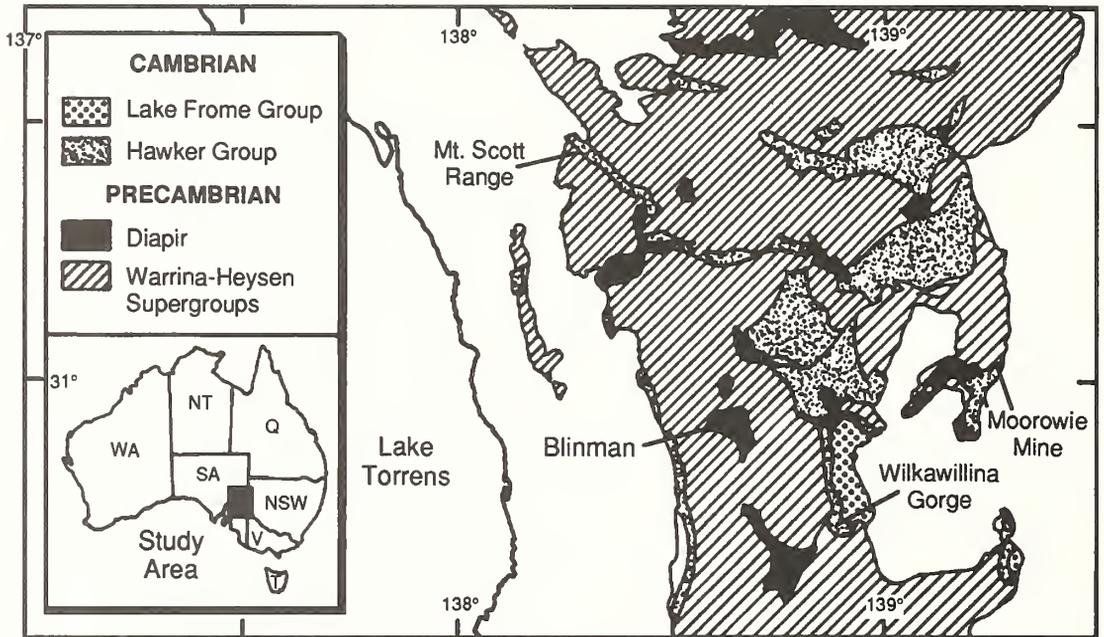
Recent fossil finds in Lower Cambrian strata, however, challenge this common assumption. Two species which may have cnidarian affinities have been reported from reefs in the Botomian Moorowie Formation of South Australia (Lafuste *et al.* 1991; Savarese *et al.* 1993; Fuller and Jenkins 1994). If either of these are genuine tabulate corals, the clade of early Ordovician (Tremadoc, Ibexian) and later Palaeozoic reef corals would have existed prior to the latest early Cambrian (Toyonian) extinction. Alternatively, if these fossils do not belong to the Tabulata, but are cnidarians with skeletal morphologies convergent on tabulate corals, then they represent another group of early Cambrian reef dwellers that went extinct together with the archaeocyaths.

Regardless of their phylogenetic affinity, the two species *Flindersipora bowmani* Lafuste *in* Lafuste *et al.* 1991 and *Moorowipora chamberensis* Fuller and Jenkins, 1994 are significant framebuilding components of Botomian reefs in South Australia. The former, in particular, is a common constituent of Moorowie Formation reefs and is found both as an encruster-binder and as a substrate for attachment by calcimicrobes and archaeocyaths (Lafuste *et al.* 1991; Savarese *et al.* 1993). This paper provides evidence from and further discussion of *M. chamberensis*, which we suggest possesses enough characters diagnostic of tabulate corals to be considered as such, although not unquestionably so. On the other hand, *F. bowmani* has some features in common with corals, but others that question its taxonomic assignment to the Tabulata. We also believe that, as more detailed studies are completed on Lower Cambrian reefs of Australia and correlative reef-bearing

strata in other areas, such as the Cordilleran Region of western North America and the Siberian Platform, other coral discoveries will be made (e.g. Pratt 1991).

#### LOWER CAMBRIAN REEFS OF THE FLINDERS RANGES

Reefs bearing coral-like skeletons occur within the Lower Cambrian Botomian Moorowie Formation and its equivalents in the Flinders Ranges of South Australia (Text-figs 1–2); some of

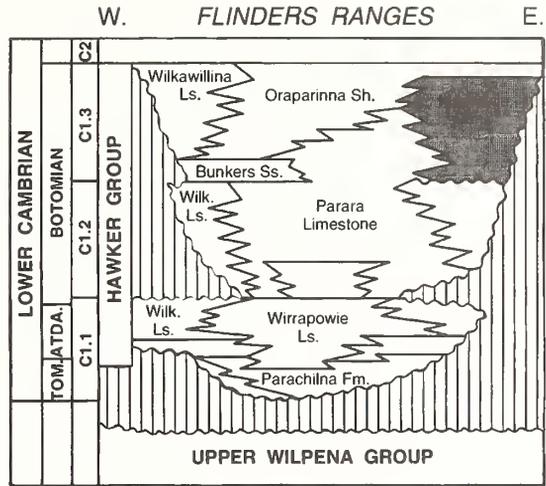


TEXT-FIG. 1. Index map showing location of northern Flinders Ranges within South Australia and location of the Moorowie Mine at the eastern edge of the ranges. Modified from James and Gravestock (1990, fig. 2).

these have been described in detail by James and Gravestock (1990). The Moorowie Formation is geographically limited, and was deposited during the transgressive and highstand phases of the sequence (Gravestock and Hibburt 1991). It is chronostratigraphically equivalent to reef-bearing units elsewhere in the Flinders and Mount Scott Ranges (e.g. the Upper Wilkawillina and Ajax Limestones) and to the Oraparinna Shale (Text-fig. 2). Sediment deposition was influenced by localized synsedimentary tectonics involving diapirism (Coats 1973). Siliciclastic compositions within the Moorowie Formation vary considerably and include red siltstones and mudstones, quartz arenites, coarse arkosic and lithic sandstones, as well as coarse polymict breccias. Associated with these breccias are reefal carbonates including framework boundstones, rudstones, and grainstones. Fossil material discussed here was collected from several levels within the Moorowie Formation at a number of sites located west and south-west of the old Moorowie Mine (Text-fig. 1).

Palaeoenvironmental interpretation of the Moorowie Formation has been treated at greater length by Savarese *et al.* (1993). The hundred metres of exposed strata (Text-fig. 3) represent a non-

TEXT-FIG. 2. Correlation chart of Lower Cambrian, Botomian strata belonging to the Hawker Group, for the Arrowie Basin (Mount Scott eastward to the Moorowie-Yalkalpo Syncline). Simplified from Gravestock and Hibbert (1991, fig. 4).



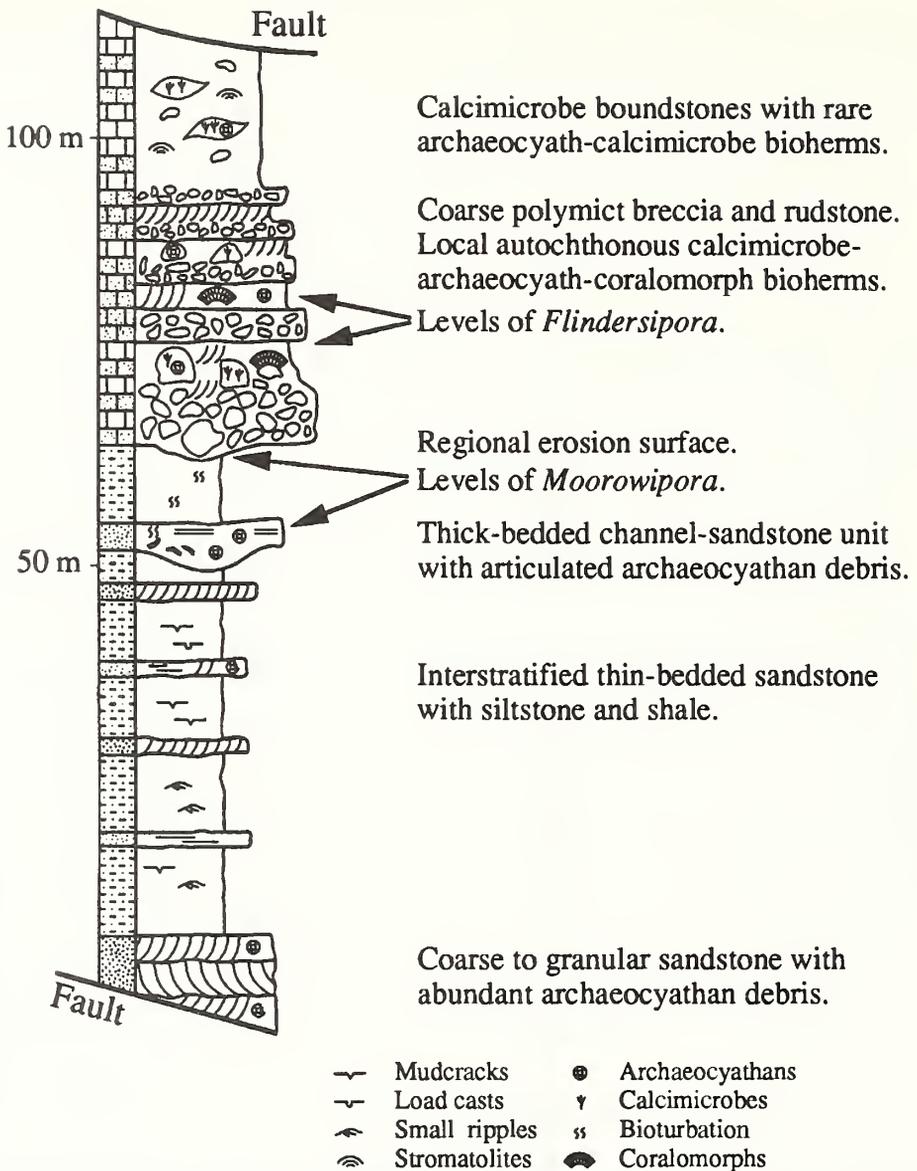
marine to marine transition at the margin of a young seaway. The upper half of the section is composed of interbedded polymict breccias, arkosic, and lithic and quartz arenites which contain marine body and trace fossils and reefal carbonates. The sandstones and breccias are commonly found filling channels. Stratigraphical and sedimentological relationships suggest that these upper strata represent alluvium shed from neighbouring mountain ranges that prograded into the seaway. These deposits have analogues in modern extensional basins and have been called sea-marginal fans (Friedman 1988).

Reef development was founded on these submarine alluvial fans. Alluvial breccias provided a coarse, but stable foundation upon which incipient reef growth could occur during times of sedimentary quiescence. Sedimentation events, if infrequent, did not cause cessation of reef development. Similar sedimentary settings with reef growth have been described from the modern Gulf of Aqaba and Red Sea (Epstein and Friedman 1983; Friedman 1988; Roberts and Murray 1988). Complicating the palaeoenvironmental interpretation of the Moorowie Formation is the presence of reworked reefal carbonates (Text-fig. 3). While some boundstones are clearly autochthonous, others are boulders transported by subsequent alluviation.

The boundstones contain a diverse assemblage of frame-building organisms, with archaeocyaths and the calcimicrobe *Epiphyton* being the most common. Two other calcimicrobes occur, *Renalcis* and *Girvanella*. In addition, stromatolites and sphinctozoan sponges are found, although rarely. Of the coralomorphs, *Flindersipora bowmani* is common (Lafuste *et al.* 1991; Savarese *et al.* 1993). Our discussion of *Moorowipora chamberensis* is based on a beautifully preserved specimen collected in 1992, illustrated by Savarese *et al.* (1993) and herein, and on preliminary study of more than 25 specimens collected in the Moorowie area during August, 1994. The above-mentioned frame-builders occur in complex growth interrelationships (Savarese and Bucklin 1992; Wood *et al.* 1992; Savarese *et al.* 1993), suggesting that competition for space was great on these reefs, as it is on modern ones.

#### CAMBRIAN SKELETAL CNIDARIANS

Cambrian skeletal cnidarians and the origin of the Palaeozoic corals have been summarized by Scrutton (1979, 1984) and by Jell (1984). Their lists of Cambrian fossils include all that have been regarded as formed by corals (the term is here used in the sense of anthozoans with skeleton-forming capabilities). No Lower Cambrian fossils were recognized by either worker as corals specifically belonging to the two principal Palaeozoic groups, the Rugosa and Tabulata. Scrutton (1979, p. 178) used the term 'coralline zoantharians' while Jell (1984, p. 107) suggested that all of the Cambrian



TEXT-FIG. 3. Stratigraphical section of the Moorowie Formation at Moorowie Mine, South Australia. The sequence is fault-bounded, but provides more than 100 m of strata. Modified from Savarese *et al.* 1993, fig. 1.

forms be grouped under the category he named Coralomorpha, rather than using existing groups within the Cnidaria. We agree with Scrutton that all genera (except *Tabuloconus*) described from Lower Cambrian strata prior to 1979 are best referred to as 'putative corals'. Zhuravlev *et al.* (1993) summarized the types of skeletal microstructures that they observed in a number of genera of Cambrian coral-like skeletons, and proposed paths of diversification of this Lower Cambrian fauna. Several other developments have also occurred since Scrutton and Jell published their reviews, and we discuss these and their relevance to the origin and evolution of the skeleton-forming members of the Phylum Cnidaria, Class Anthozoa.

*Tabuloconus kordae* Handfield from the Lower Cambrian of British Columbia and Alaska was

described in detail by Debrenne *et al.* (1987) who clarified the morphology and skeletal microstructure of this anthozoan. Corallites in *Tabuloconus* contain tabulae with a skeletal structure consisting of a basal dark layer and an overlying lighter-coloured fibrous layer (as does *Moorowipora chamberensis* but with a wall structure containing 'different types of microstructural units' (Debrenne *et al.* 1987, p. 5)). These authors found skeletal structures in the walls composed of granular, irregular or fibrous crystals, and, believing that all were biogenic, considered that skeletal secretion in *Tabuloconus* was varied and elaborate. These complications of the skeletal structure are here regarded as most likely to have resulted from diagenetic alteration. We would expect that, when well preserved, the fibrous structure would prove to be original, with crystallites oriented perpendicular to the wall surface. This would suggest a close relationship to *M. chamberensis*, also characterized by this type of fibrous wall structure. The Tabuloconidae (Debrenne *et al.* 1987) then may include this species, but at the present stage of research its familial placement is uncertain.

Of the two species of coral-like fossils from the Moorowie Formation known at present, *Flindersipora bowmani* Lafuste was described fully by Lafuste *et al.* (1991) and discussed by Zhuravlev *et al.* (1993), and *Moorowipora chamberensis* is discussed below. We agree with Scrutton (1992, p. 29) in regarding *Flindersipora* as representing at most an early, somewhat atypical coral-like cnidarian that does not fit well into the Tabulata. However, we regard *M. chamberensis* as having a tabulate coral morphology and place it among the tabulates with reservation, because of the long gap in geological record (Lower Cambrian to Lower Ordovician) between it and the oldest definitive tabulates, as expressed below.

Our specimens of *F. bowmani* fit Lafuste's description very closely. Corallite diameters average 2.5 to 3.0 mm, although sizes are diverse; some were undergoing reproductive fission and are therefore enlarged. Although Lafuste placed the species in the Tabulata, Scrutton (1992, p. 29) referred to it as a 'new Lower Cambrian coralline organism', and rejected both its placement in the tabulates and a common ancestry for the two. Likewise we reject its placement in the Tabulata. The most controversial aspects are the wall and septal structure and the manner of budding. The wall and the plate-like septa have identical skeletal structure, each composed of transverse crystallite fibres; this is different from known skeletal microstructures in tabulate corals. There is no development of a tabulate-like cerioid wall separating individuals within colonies. Septa are apparently present, but their internal structure does not resemble that of septa in Rugosa, or the septal spines of Tabulata. Budding in *Flindersipora*, called fissiparous by Lafuste in Lafuste *et al.* (1991, p. 710), consists of splitting of tubules to form new individuals, each of roughly equal size. The new wall dividing them forms as an outgrowth from the septa, which extends across the axis of the individual to join. Fissiparous division is not characteristic of either tabulate or rugose corals (with the exception of the Tetradiidae, which we feel may not belong within the Tabulata).

The geological record does not contain any *Flindersipora*-like skeletons of younger age. Thus, remarks by Lafuste (in Lafuste *et al.* 1991) on the necessity of rethinking the origins and original characteristics of the Tabulata apparently are unwarranted, as *F. bowmani* seems to be far removed from any direct line of descent leading to the tabulate corals (as observed by Scrutton 1992, p. 31). It should also be stated that Zhuravlev *et al.* (1993, p. 369) noted that no ancestor for the later corals could be recognized among Lower Cambrian coral-like fossils, thus suggesting that they did not consider *Flindersipora* as a true tabulate.

## SYSTEMATIC PALAEOONTOLOGY

### Subclass TABULATA?

#### Family Uncertain

#### Genus MOOROWIPORA Fuller and Jenkins, 1994

*Type species.* By original designation; *Moorowipora chamberensis*, Lower Cambrian, northern Flinders Ranges, South Australia

*Diagnosis.* Small cerioid colonies with complete tabulae, but no mural pores; corallite diameters average from 3.4 to 4.3 mm; corallites generally polygonal, but some are rounded; colonial form may approach subcerioid during part of lifespan; walls fibrous and prismatic in structure, with three layers present, tabulae with dark line at base of structure, overlain by a fibro-normal layer. Spinose projections from walls and from upper surface of tabulae are present; thus there is a suggestion of septal spines as in later tabulate corals.

*Moorowipora chamberensis* Fuller and Jenkins, 1994

Plate 1, figures 1–5; Plate 2, figures 1–4; Text-figures 4–5

1993 Undescribed coral; Savarese *et al.*, p. 918, fig. 2D, F.

1994 *Moorowipora chamberensis* Fuller and Jenkins, p. 231, figs 2–7.

*Holotype.* Museum of South Australia, Adelaide, P34165; from the Lower Cambrian, Botomian, Moorowie Formation, Flinders Ranges, South Australia.

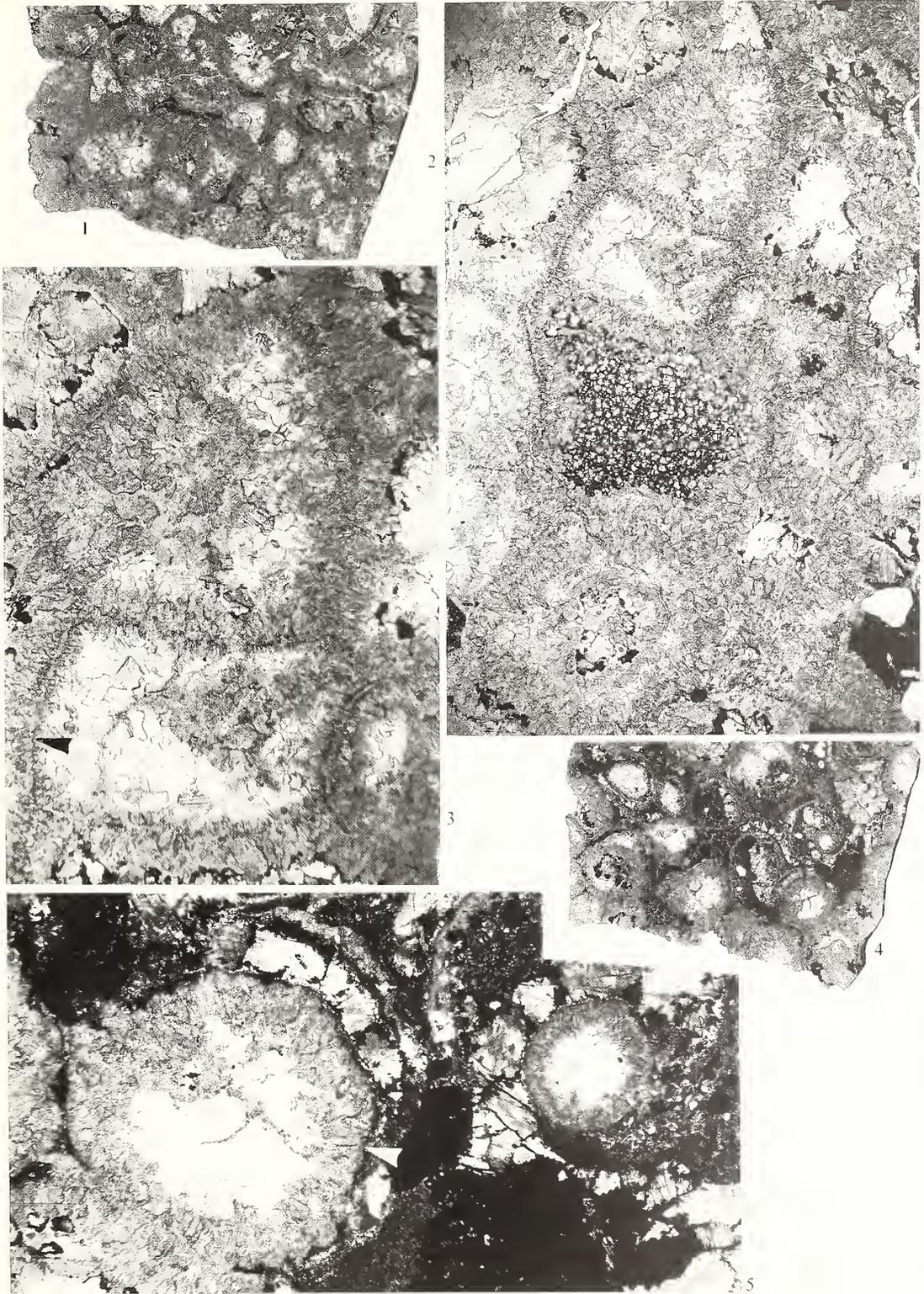
*Material.* The specimen described herein (Museum of South Australia, P34794) is from the Moorowie Formation, Moorowie Mine, South Australia, less than 2 m from a small bioherm (locality: map coordinate UL343707, Arrowie 1:50000 Sheet, map no. 67736-2, Dept of Lands, Government of South Australia, 1987). Five thin sections have been made from this corallum, three transverse and two longitudinal, which are deposited together with all remnants of the colony in the Museum of South Australia, Adelaide, South Australia. More than 25 additional specimens collected subsequently from several levels within the Moorowie Formation (from channel-form lithic sandstones lateral to small bioherms within the medial portion, as well as from the bioherms themselves) in a 10–12 km square area west and south-west of the old Moorowie Mine. Preservation of skeletal microstructure in these specimens is unfortunately not as good as that in the described colony.

*Diagnosis.* Cerioid to subcerioid species; small corallum with polygonal corallites having diameters averaging 3.4 to 4.3 mm and thick, three-layered walls with variably developed septal spines, commonly lacking any; no mural pores present; tabulae complete with basal dark skeletal layer and overlying thick fibrous layer.

*Description.* The best preserved corallum measured approximately 120 mm by 55 mm prior to cutting for thin sections. It was found resting on its side within red calcareous wackestone with abundant haematite-coated, well-rounded quartz grains and rock fragments (Text-fig. 4), and is the specimen figured by Savarese *et al.* (1993, p. 918, fig. D, F). Red silt- and sand-sized sediment is found at several levels within this coral. In transverse section (Pl. 1, figs 1, 4), the corallites appear irregularly polygonal, four- to six-sided, with sides of unequal length. Mature sediment-filled calices from the uppermost part of the corallum are irregularly six-sided, with average corallite diameters (average of maximum and minimum diameters) ranging from 3.0 to 4.3 mm in the cerioid portions of these colonies. Subcerioid, rounded corallites, with sediment surrounding them, are smaller, with average diameters ranging from 2.75 to 4.1 mm. Walls are very thick, ranging from 0.6 to 1.66 mm in total thickness in cerioid corallites (Pl. 1, fig. 2). Wall structure is clearly cerioid: three layers consisting of a fibrous wall (or stereozone) preserved on both sides of the central, finer-grained epitheca (Pl. 1, fig. 3). Where sediment has invaded the colony, corallites are round, and walls are much thinner than in

EXPLANATION OF PLATE 1

Figs 1–5. *Moorowipora chamberensis*; all transverse sections; S.A.M. P34794. 1, overview illustrating cerioid nature of corallum;  $\times 2$ . 2, thick, fibrous walls between corallites and sediment infilled calice in large corallite;  $\times 6$ . 3, cerioid walls between corallites, each consisting of central dense layer with fibronormal peripheral stereozone on each side (arrow);  $\times 10$ . 4, overview of portion of corallum with incursion of sediment causing contraction of individual corallites;  $\times 2$ . 5, enlarged view showing contraction of individuals where in contact with clastic sediment to form smaller diameter, round corallites (arrow);  $\times 10$ .



SORAUf and SAVARESE, *Morowipora chamberensis*



TEXT-FIG. 4. *Moorowipora chamberensis* Fuller and Jenkins, 1994; S.A.M. P34794; external longitudinal view of specimen prior to sectioning, showing the distinct corallites and sturdy tabulae;  $\times 3.3$ .

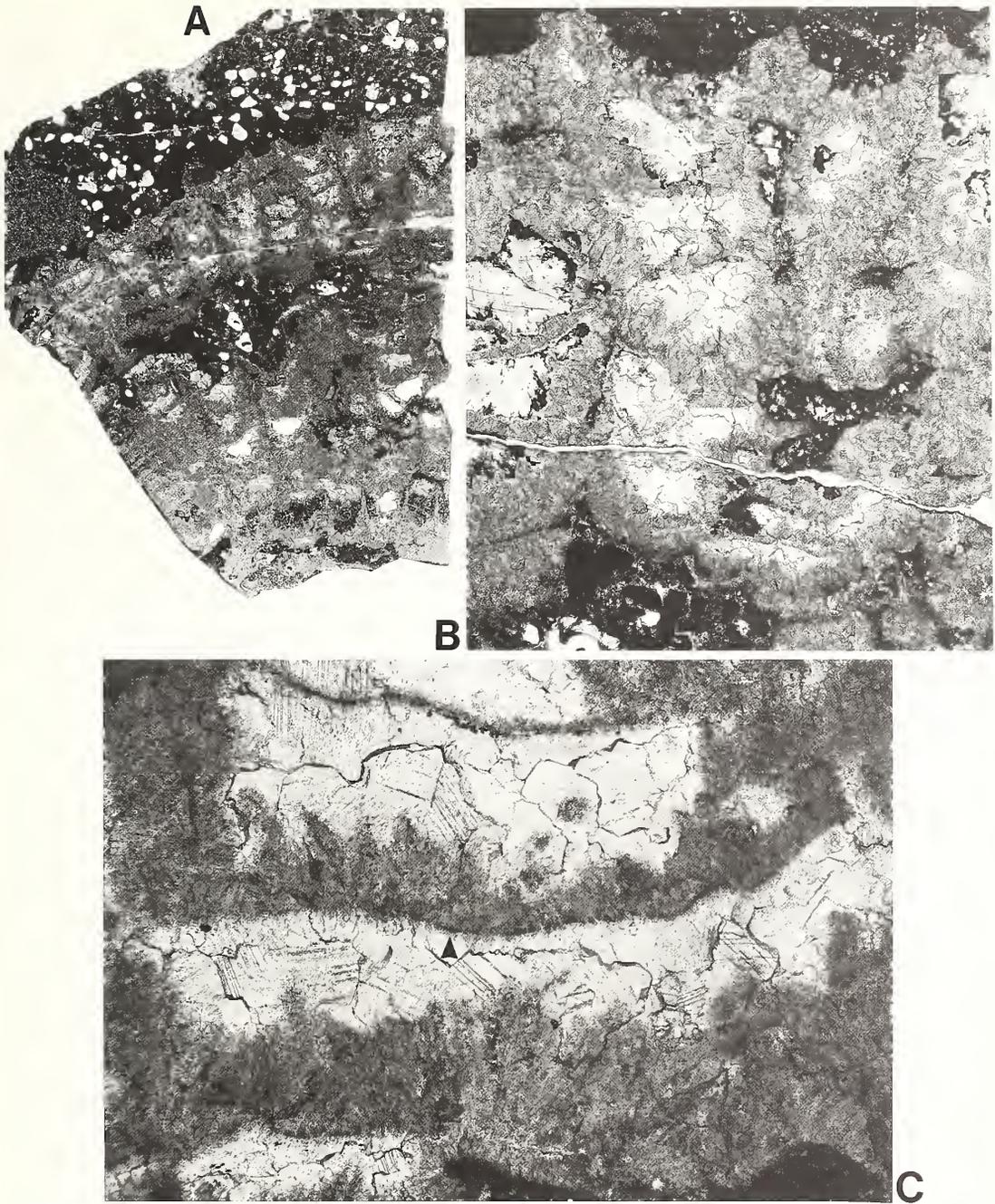
cerioid portions, ranging from 0.35 to 0.75 mm for one fibrous layer plus epitheca (Pl. 1, fig. 5). Wall thickness in cerioid corallites is difficult to measure, because fibrous, spherulitic growth is very luxuriant, and it is not always clear where the wall ends and the thick tabulae begin. Where thick walls are formed, outgrowths of spherulitic clusters of biogenic calcite continue into the corallite as nubs or spines (Pl. 2, figs 1–2). These spines are not as sharply developed, nor do they show the regularity of size, development or arrangement that is typical of septal spines in tabulates later in the Palaeozoic. The type specimen, illustrated by Fuller and Jenkins (1994, figs 2–5) has considerable development of septa (or septal spines), far more than seen in any of our specimens.

In cerioid parts of the corallum, stereozones in adjoining corallites are sometimes separated by red mud; in one, it was seen that the corallite wall was retracted after sediment had lodged between the skeleton and polyp (Pl. 1, fig. 5). Where large amounts of sediment are present within the corallum, individual corallites are separated from each other and are rounded, and corallite walls are much thinner than elsewhere in the corallum. Also, under these conditions, the inner wall or stereozone is thinner, with its fibrous structure formed by smaller, parallel-oriented crystals (Pl. 2, fig. 1). This contrasts with the fibres arranged in recognizable spherulitic clusters where growth was luxuriant in fully cerioid corallites (Pl. 2, fig. 3). Where corallite walls are thin adjacent to sediment, spinose projections on the walls more clearly resemble septal spines (Pl. 2, fig. 1).

In longitudinal section, tabulae are clearly seen to be composed of a basal dark layer and overlying spherulitic fibres (Text-fig. 5A–C). The tops of tabulae are uneven where tabulae are thick, with finger-like to spinose, upward-extending crystal growths. Walls are not always continuous vertical structures, as the fibrous layer of tabulae commonly merges with the stereozone of intercorallite walls (Text-fig. 5B).

*Remarks.* *Moorowipora chamberensis* shares more characters with cnidarian corals than does *Flindersipora*. It is truly cerioid (Pl. 1, figs 2–3), with mature corallites having maximum diameters near 4.5 mm. The tabulate-like features of this coral are as follows:

(1) The cerioid nature of intercorallite walls is typical of massive colonial corals of the Palaeozoic. This is seen where a tripartite wall (epitheca flanked by fibrous layers) separates cerioid corallites (Pl. 1, figs 2–3). The fibrous wall is either composed of slightly diverging crystal fibres of



TEXT-FIG. 5. *Moorowipora chamberensis*; all longitudinal sections; S.A.M. P34794. A, overview of corallum with straight corallites, abundant tabulae, and sediment encapsulated within colonial skeleton;  $\times 2$ . B, enlargement of upper portion of A, showing development of thick tabulae with fibro-normal structure;  $\times 8$ . C, structure of tabulae in second longitudinal thin section, here (arrow) showing thin 'dark line' at base of tabula and luxuriant upward growth of clusters of crystallites above;  $\times 25$ .

interfering spherulitic clusters or parallel calcite fibres normal to the flanks. This bilateral symmetry is regarded as a reflection of the individuality of cnidarian polyps. The skeleton-forming sponges typically do not have a cerioid wall, but rather, 'have a unitary microstructure' (Scrutton 1987, p. 488). Increase in *M. chamberensis* is lateral, as is typical for the Tabulata; this does not occur in the skeleton-forming sponges.

(2) The structure of the tabulae in the corallites is very similar to that in both tabulate and rugose corals occurring later in the Palaeozoic. The tabulae of this Lower Cambrian coral are formed of a thin, dense basal layer and an overlying thicker layer with upwardly oriented spherulitic crystallites forming the bulk of the tabula (Text-fig. 5B-C). This two-layered tabular structure in *Moorowipora* also strongly resembles that of *Tabuloconus* (Debrenne *et al.* 1987, p. 5), and is similar to that seen in later Palaeozoic corals (both Rugosa and Tabulata). This is the structure of dissepiments, the analogous platforms in modern Scleractinia. As shown by Wells (1969) and by Sorauf (1970) these develop by centripetal growth of fine crystallites to form the basal layer, prior to thickening by upward growth of interfering fibrous spherulites. This is very characteristic of coral skeletogenesis.

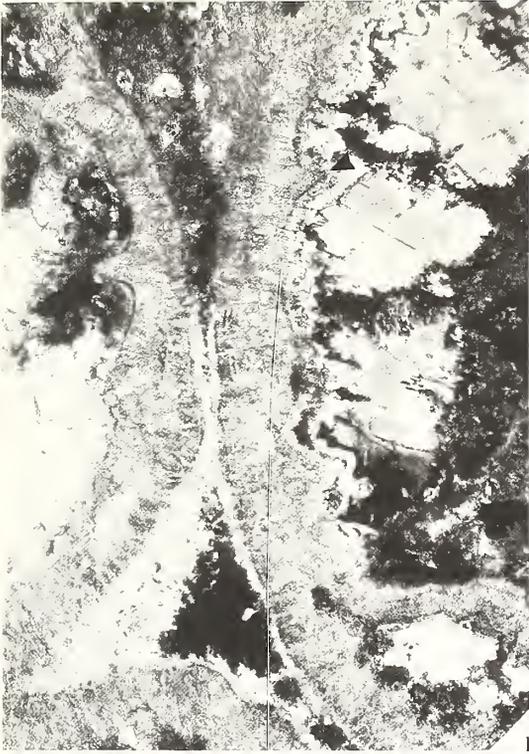
(3) Spines are seen as sharp protrusions on the inside of intercorallite walls, with bases which extend to the exterior surface of the wall (Text-fig. 5A). These do not resemble completely the septal spines of Tabulata, but suggest a similar origin, especially where walls are thin and spines are best defined. Hill (1981, p. F443) noted that septal spines are the most common septal elements seen in the Tabulata and indeed the type considered characteristic of the order.

(4) Another coralline characteristic is observed where terrigenous clastic sediment impinged on the colonies (Pl. 1, figs 1, 4-5). The subsequent contraction, and resultant isolation of individual polyps, led to formation of rounded, tubular corallites separated from one another by sediment. The development of gaps between corallite walls in the Tabulata is interpreted as having an environmental cause, and when they occur they are associated with sediment influxes and appear uniformly across much of the colony (Ross 1953, p. 40). The resulting subcerioid colonial form is commonly seen in Palaeozoic colonial rugose corals where influx of sediment caused retraction of polyps and allowed for sediment-filled spaces between corallites. These Lower Cambrian colonies later expanded laterally to cover this sediment, and the cerioid colonial form was resumed, thus encapsulating muddy red sediment within the corallum. Scrutton (1979, p. 182) noted that this is a typical reaction, and 'deposition by more or less individualized polyps' of skeleton is typical of cnidarians.

(5) The size and configuration of corallites most resembles those in mid-Palaeozoic Tabulata. *M. chamberensis* does not have mural pores as do the cerioid favositid tabulates, and the wall and tabular structure in places is more coarsely fibrous and spherulitic than later tabulate skeletons with their structure of parallel crystal fibres (Pl. 2, fig. 4). However, in *Moorowipora*, when corallites are round and walls are thin, the wall microstructure shows orderly, parallel crystallites (Pl. 2, fig. 1). Mural pores are regarded by Scrutton (1979, p. 182) as having been evolved by favositids later in the Palaeozoic, representing a more integrated colonial state than nonporous tabulate colonies. *M. chamberensis* also has spherulitic, trabecula-like prominences both within walls and on tabular floors (Text-fig. 5C). Development of these spinose projections by upward spherulitic growth of

#### EXPLANATION OF PLATE 2

Figs 1-3. *Moorowipora chamberensis*; all transverse sections; S.A.M. P34794. 1, corallites in contact with infiltrated clastic sediment, with fibro-normal wall structure and weakly developed septal spines (arrow);  $\times 25$ . 2, corallite with extreme rejuvenation (contraction) resulting from influx of clastic sediment. The fibrous nature of the corallite wall and beginnings of septal spines (arrow) is clearly shown;  $\times 25$ . 3, cerioid walls of corallites, fibrous wall structure and septal spines;  $\times 10$ . 4, cerioid part of corallum with small amount of clastic sediment infiltrated. Wall has pulled away from sediment, and wall structure is shown clearly to be composed of fibrous clusters of calcite crystallites (arrow);  $\times 15$ .



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crystals from the top surface of the tabulae may forecast the development of septa by spherulitic growth as septal trabeculae.

The gap in the geological record of fossil corals, between this occurrence and that of the oldest undisputed tabulate, *Lichenaria*, in the Lower Ordovician (Tremadoc, Ibexian; see Scrutton, 1984, p. 111) makes the placement of this coral in the Tabulata somewhat uncertain. However, it is certain that these organisms formed skeleton in ways very similar to those of younger Palaeozoic corals, utilized similar mineralogies, and reacted in similar ways to excessive sedimentation during polypal growth. It seems apparent to us that these are true corals, anthozoan cnidarians with skeletal morphology, at present best placed within the Tabulata.

#### SIGNIFICANCE OF THIS OCCURRENCE

There are a number of ramifications of an Early Cambrian first appearance for tabulate corals. Firstly, given the present criteria used to define the Subclass Tabulata, both *Moorowipora* and *Tabuloconus* could be included, thereby extending its stratigraphical range considerably. Secondly, the existence of Early Cambrian tabulates would require that coral phylogeny (Scrutton 1984; Pandolfi 1989; Zhuravlev *et al.* 1993) be re-evaluated. Skeletonized colonial corals in the Botomian necessitate an Early Cambrian or late Proterozoic ancestor for the group. Thirdly, the lack of coral involvement in reef building in other geographical areas during the Botomian and in the post-Botomian Cambrian world-wide needs to be explained. It is also possible that corals such as these are present elsewhere in the Lower Cambrian and have not yet been recognized. Lower Cambrian coralomorphs have been discovered recently in western Canada (Pratt 1991) and in western United States (Phillip Signor, pers. comm. 1993). A long hiatus in reef growth occurred after the Toyonian extinction (Debrenne 1991) with corals not participating until the early Ordovician.

In addition, the skeletal microstructure of *Moorowipora* has a bearing on the recognition of biogenic and diagenetic skeletal structures. The skeletal structure in *Moorowipora* is typical of many Palaeozoic tabulate corals, and raises the question of whether characteristic skeletal structures do exist in Palaeozoic corals. Zhuravlev *et al.* (1993) did not recognize fibrous skeletal structures in their scheme for radiation of the Lower Cambrian coralomorphs, and thus the occurrence of this type of wall in *Moorowipora* is of considerable significance in understanding early development of the cnidarian skeleton. *Moorowipora* can provide a model of a structural 'starting point' for development of Lower Palaeozoic Tabulata. Regardless of whether *M. chamberensis* is placed within the Tabulata, it should be agreed that these early Cambrian anthozoans were both cerioid and subcerioid in colonial form, and built skeletons in the same fashion as later tabulate corals that lack mural pores. *Moorowipora* and the Ordovician tabulate *Lichenaria* share the cerioid colonial form, fibrous intercorallite walls and presence of tabulae, and both lack mural pores. *Moorowipora* and *Tabuloconus* both have integral and individual corallites, fibrous wall structure, two-layered structure in tabulae, and are both here regarded as possible Tabulata. The presence of Lower Cambrian coral skeletons formed of calcite that was fibrous, spherulitic, and layered in similar ways to skeleton in later Palaeozoic corals indicates that coral-like biomineralization in the Cnidaria evolved first during the early Cambrian radiation, rather than in the Ordovician.

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# PLIO-PLEISTOCENE DEEP-WATER BRYOZOANS FROM RHODES, GREECE

by PIERRE MOISSETTE and NILS SPJELDNAES

**ABSTRACT.** Twenty-one bryozoan species are recorded from the Plio-Pleistocene deep-water marls of the island of Rhodes, Greece. The faunas occur in three sections where they are represented mostly by erect colonial morphotypes belonging to the cyclostomes (11 species) and the cheilostomes (five anascans and five ascophorans). Essentially on the basis of the known bathymetric distribution of the 19 extant species, a depth of deposition of 200 to 600 m is suggested, with a shallowing occurring towards the top of the sections. This is supported by the other fossils (foraminifera, ostracodes, pteropods and trace fossils) found in the same beds. Introduction of bathyal bryozoans from the Atlantic during the late Neogene is also considered.

THE first mention of bryozoans from the Plio-Pleistocene of Rhodes was by Hedenborg (1837), who gave a list of six bryozoans (mostly determined only to genus level) under the heading 'Zoophytes'. The first real description of bryozoans from Rhodes was by Manzoni (1877). This study was based on material from the Deshayes collection, in the Ecole des Mines in Paris. The fauna consisted of 54 species, one of which, *Idmonea hedenborgi*, was new. The next description was by Pergens (1887), who described 60 species, two of which, *Filisparsa delvauxi* and *Pustulopora smitti*, were new. The material for Pergens' description was probably the Hedenborg collection, which came to the Natural History Museum in Vienna in 1865, after the death of Hedenborg. It is doubtful if any of the material described by Manzoni or Pergens came from the deep-water beds mentioned here. No localities are given by Pergens, and none of the localities mentioned by Manzoni, which can be identified, comprises deep-water beds. There have been several references to the occurrence of bryozoans and 'bryozoan marl' in the geological and stratigraphical literature on Rhodes, but no actual information is given. The species described by Manzoni (1877) and Pergens (1887) have been repeatedly referred to by more recent authors, both on Recent and fossil bryozoans, but actual material from Rhodes has not been described.

The late Pliocene and Pleistocene sediments of Rhodes are well exposed, notably on the eastern coast of the island. Three deep-water sections have been studied and a number of samples were taken from various marl beds. They yielded the 21 bryozoan species that are described in this paper.

Most of the palaeoecological interpretation here is based on the known bathymetric ranges of the 19 extant bryozoan species but the distribution of the various zoarial forms is also considered. These colony morphotypes are more or less strictly related to certain environmental factors, among them depth (Stach 1936; Lagaij and Gautier 1965; Labracherie and Prud'homme 1966; Schopf 1969a; Braga 1979; Harmelin 1988; Moissette 1988, 1993; McKinney and Jackson 1989). Bryozoan colonies belong to several erect types: vinculariiform (rigid cylindrical branches), adoniform (rigid, narrow bilamellar branches), reteporiform (rigid reticulate branches), cellariiform (long articulated segments), and catenicelliform (very short articulated segments). Encrusting (membraniporiform), nodular (celleporiform), free-living and cup-shaped (lunulitiform), and conical (conescharellini-form) colonies are also distinguished. The pseudovinculariiform type corresponds with a membraniporiform colony forming a sleeve-like hollow tube once encrusting the stem of an unpreserved organism. Occurrence of these zoarial forms in the Plio-Pleistocene of Rhodes is variable but erect types always dominate, whereas some colony forms are completely absent.

## PLIO-PLEISTOCENE STRATIGRAPHY ON RHODES

The first geologist to erect a detailed stratigraphy for these beds was Hedenborg (1837). A later manuscript edition was utilized by Bukowski (1899). Both Bukowski and other older authors regarded all the beds in question as Pliocene. Later it was realized that the younger beds also included part of the Pleistocene. This complex was named the Sguru Formation by Mutti *et al.* (1970).

Meulenkamp *et al.* (1972) introduced modern lithostratigraphical names. The marine beds were divided into the Pliocene Kritika Formation, consisting of shallow-water, often lagoonal beds, the supposedly Pleistocene Vasfi Formation, consisting mostly of open marine marls, and the youngest, Rhodos Formation, consisting mostly of bioclastic shallow-water limestones.

The field-work carried out since 1976 by the group led by Richard Bromley (Copenhagen, Denmark), Nils-Martin Hanken (Tromsø, Norway) and Stein Erik Lauritzen (Bergen, Norway) has shown that this stratigraphical scheme is too simplified. Bromley and his colleagues are working upon a revision of the stratigraphical nomenclature of these beds, and therefore no new units will be suggested here.

The deep-water beds from which the present material comes have been studied at three localities (for a detailed description, see below): Vasfi, Cape Vagia and Lindos Bay (Text-fig. 1). They are uniform lithologically, and the depth of deposition makes it reasonable to suppose that they were deposited as a continuous unit. The deep-water marls are dark bluish grey and mostly massive due to bioturbation, often with spectacular suites of trace fossils. A few horizons are finely laminated, and have a high organic content.

Palaeomagnetic studies by Løvlie *et al.* (1989) indicate that the Plio-Pleistocene boundary is found in the lower part of the deep-water beds, and thus the thickest part of it is above the boundary, of early Pleistocene age. Because of the problems with precise dating, the other localities are supposed to be of approximately the same age. The dating used here is based upon the hypothesis that, based on the Cape Vagia section, there was a rapid transgression at the end of the Pliocene, reaching its maximum just below the Plio-Pleistocene boundary, and then a slow regression punctuated by climatically induced eustatic cycles. The transgression is so great (more than 600 m) that it cannot be ascribed to ordinary eustasy, but must be a product of local tectonics. Such large vertical movements are known also from other parts of the Aegean Arc, as in Crete (Meulenkamp 1985; Peters *et al.* 1985). As a first approximation, the maximum transgression can therefore be used as a proxy for the Plio-Pleistocene boundary, even if there are some problems resulting from the incompleteness of the sections at the localities.

## DEPTH INDICATORS IN THE DEEP-WATER BEDS

The sediments are extremely fine-grained clays, with more than 90 per cent. of the clastics in the clay fraction. Almost all of the material found in the washed fractions is biogenic, and also the carbonate content is almost completely biogenic, including nannofossils in the clay fraction.

The nature of the faunas in these marls indicates clearly that they were deposited in deep water (> 200 m), but it is difficult to give precise estimates of the depth. This is a consequence partly of the general lack of data about the faunal distribution in this depth interval, and partly of the peculiar local conditions.

The planktonic/benthonic ratio of foraminifera has been used as a depth indicator even if there are certain reservations, as indicated by Zwaan *et al.* (1990). Both their data, and those of Reiss *et al.* (1971) from the coast of Israel, give a depth of about 400 m for assemblages with 50 per cent. planktonic species, a figure which is common in our deep-water marls. In some, but not all the samples, the benthonic foraminifera are dominated by *Uvigerina*, which also indicates considerable depths.

As reported by many authors, the steep topography met with in many parts of the eastern Mediterranean results in extensive transport of shallow-water material down into deeper sediment.

In almost all the microfossil samples in our material, there are obvious shallow-water forms, including epiphytal ones, which evidently have been resedimented. Because of the topography of Rhodes, this is easily explained, even under conditions of much higher sea level.

The ostracodes (including *Polycope* and other deep-water forms) also indicate depths in the same range as the foraminifera, even if it must be admitted that the comparative data for the depth distribution of Mediterranean ostracodes in this depth interval is restricted. None of the true deep-water forms described by Benson (1976) has been found.

*Lophelia pertusa* forms typical deep-water patch-reefs in one of the localities (Vasfi), and has also been reported (Jüssen 1890) from the Lardos locality. This coral is found in about 100 m depth in the cold waters around Norway, and deeper further south. In the Mediterranean it has been reported at depths between 300 m and 800 m, in general deeper than 450 m (Blanc *et al.* 1959; Peres 1967). It should be noted that many observations are on patches of dead coral, which may have lived under other depth conditions. The other faunas found together with *Lophelia* in the Plio-Pleistocene of Rhodes indicate a depth of about 250 m. These intervals also seem to have been cold, and the presence of the corals may be the result of colder bottom water (under such circumstances *Lophelia* is known to grow at shallower depths). Another observation is that the coral patches seem to have started growing on a flat clay bottom, without a solid rock basement. This is not unusual around the coast of Norway and in the uplifted late Pleistocene of Norway, but according to Blanc *et al.* (1959) and Peres (1967) *Lophelia* patches always grow on solid rock, and on ledges in the Mediterranean. Because of these uncertainties, the presence of *Lophelia* can only be used to give a minimum value for our depth estimates.

In some of the beds, found in all three localities, there are numerous pteropods. The most easily visible is *Clio pyramidata*, but in most cases *Limacina* spp. also occur. Conventional data on the distribution of pteropod oozes (Murray and Chumley 1924) affirm that they are found between 700 and 3000 m depth. In some areas (Herman 1971, Indian Ocean) pteropods can be found at much shallower depth (up to 100 m), but the assemblages are rather different from those found in Rhodes. Reiss *et al.* (1971) have pteropods only at 550 m, and Herman (1971) indicates many cores with pteropods in the eastern Mediterranean from depths between 576 and 2897 m. Forbes (1844) reports, from some of the first deep dredging in the Aegean Sea, that white muds rich in pteropods (among them *Clio pyramidata*) are common at depths between 100 and 200 fathoms (= 180–360 m). These observations have not been repeated, but the macrofauna from the same stations has several species in common with those of the pteropod beds in Rhodes, even if many also occur in shallower water. In the fossil localities, the pteropod-rich beds also have high percentages of planktonic foraminifera (typically > 50 per cent.), and many of the foraminifera and ostracodes have recorded depth distributions deeper than 400 m.

The presence of the trace fossil *Zoophycos* which is found both in the Cape Vagia section and at Lindos Bay is also a potential indicator of considerable depth.

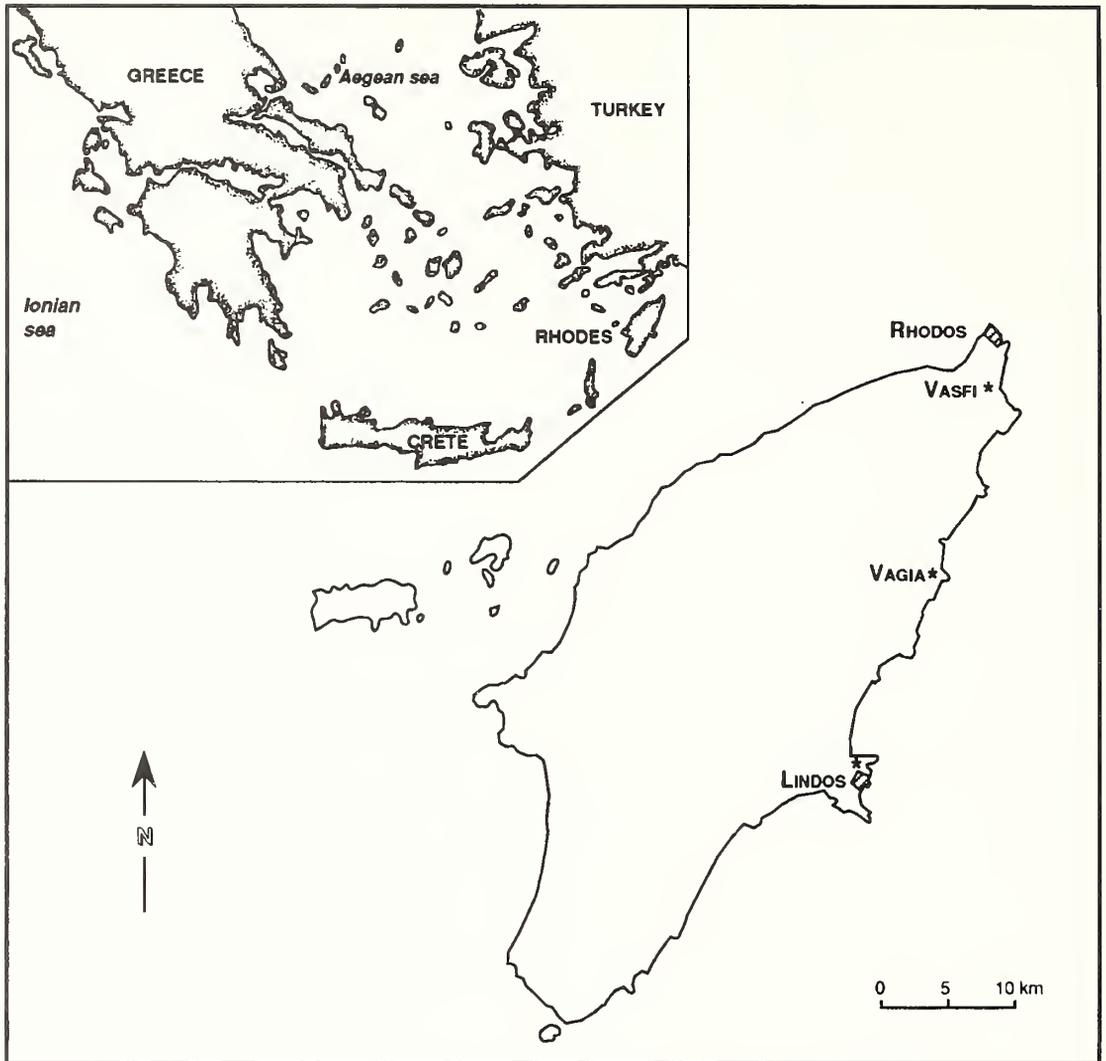
Even if the absolute depth figures are uncertain, the relative values seem to be well established. We regard the pteropod beds to be the deepest (about 600 m), the typical marls to be between 450 and 250 m (based on known depth distribution of foraminifera, ostracodes, and bryozoans), and the *Lophelia* beds are estimated to indicate a depth of about 250 m.

## DESCRIPTION OF THE SECTIONS

### *The Vasfi section*

This section, situated along the eastern coast of Rhodes about 6 km south of Rhodos City (Text-fig. 1), was described by Orombelli and Montanari (1967), Zaccaria (1968), and Sørensen (1984). It was the best known section in the Plio-Pleistocene of Rhodes, and was mentioned repeatedly in the literature, e.g. by Keraudern (1971).

The upper part of the section was logged in detail by one of the authors (NS) and his students in 1976, but shortly afterwards the section was built over by the construction of an hotel. Now only a short section (about 1 m) is exposed at the contact between the coquina and the marl.



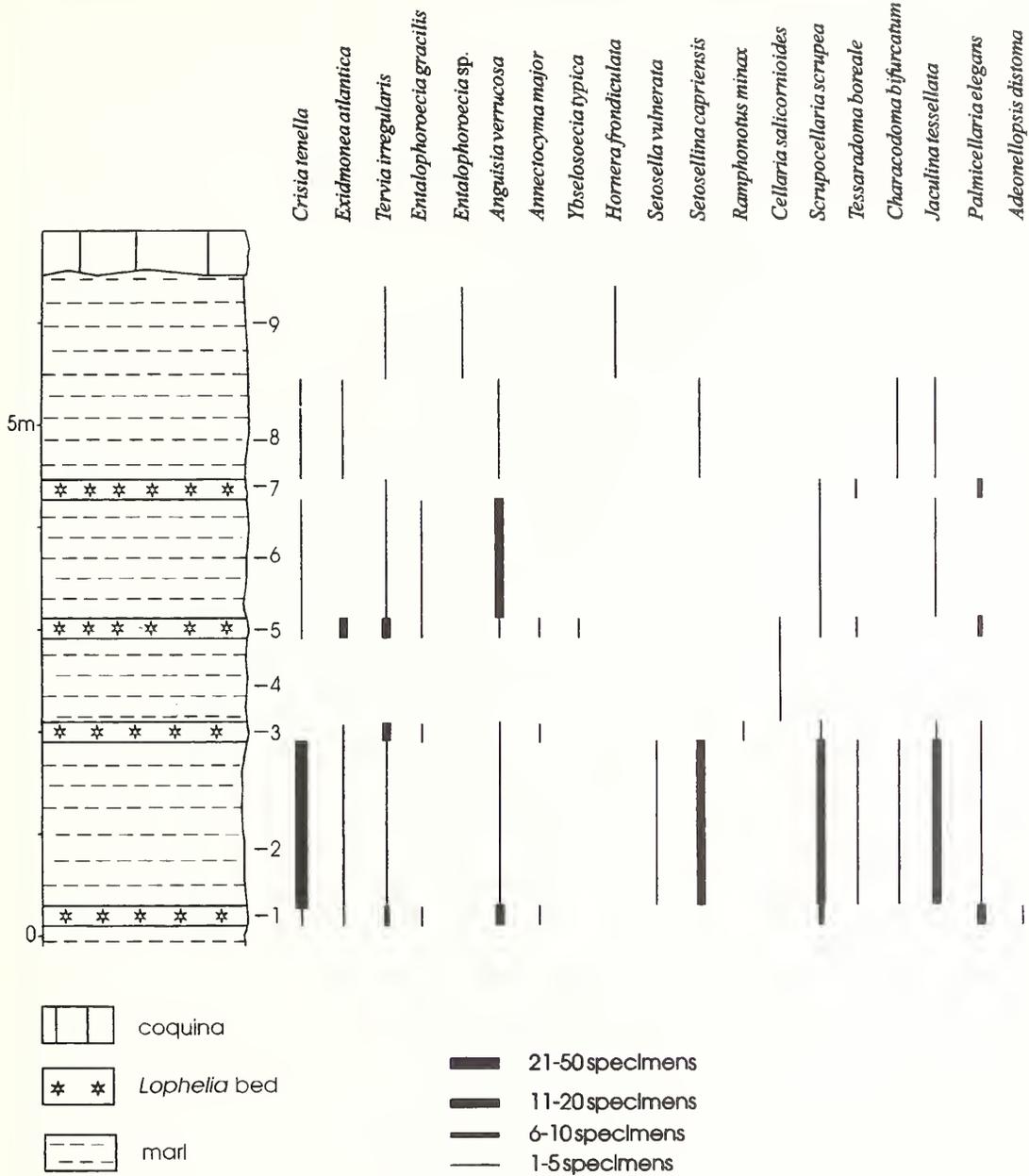
TEXT-FIG. 1. Location map of the three sections on the island of Rhodes.

The lower, unlogged part of the section consists of about 7 m of bluish-grey marl, with a fauna of small molluscs – mostly bivalves – some scaphopods and single corals. This is the typical fauna of these deep-water marls in Rhodes. There are also numerous trace fossils, especially echinoid burrows and *Chondrites*.

The logged section (Text-fig. 2) consists of the same marl, but with four beds of *Lophelia*-thickets. On top, there is a coquinal, impure limestone which grades into a beach-rock. The contact is disconformable, and cuts down into the marl towards the east.

The comparatively sparse macrofauna found in the *Lophelia* patches in Vasfi is also different from that mentioned by Peres (1967) for Recent patches in the Mediterranean. Studies on the microfauna (foraminifera and ostracodes) indicate that the *Lophelia*-beds were deposited at shallower depth, and in colder temperatures than the intervening marls.

The topmost marl beds (about 1–2 m maximum thickness) contain numerous pteropods, and this, in combination with the microfossil data (a high percentage of planktonic foraminifera, with



TEXT-FIG. 2. Distribution of bryozoans in the Vasfi section.

many deep-water forms), indicates deposition at a depth of approximately 600 m. For the other parts of the marl, a depth of about 400 m is estimated, and for the *Lophelia* patches, about 250 m.

The coquina beds above the marl indicate a deposition in shallow water (< 50 m), and a definite Pleistocene age. The age of the marls themselves is either earliest Pleistocene or latest Pliocene. None of the significant guide fossils are found among the microfossils, and *Hyalinea baltica* which is regarded as the guide fossil for the beginning of the Pleistocene, is found only in the coquinal beds,

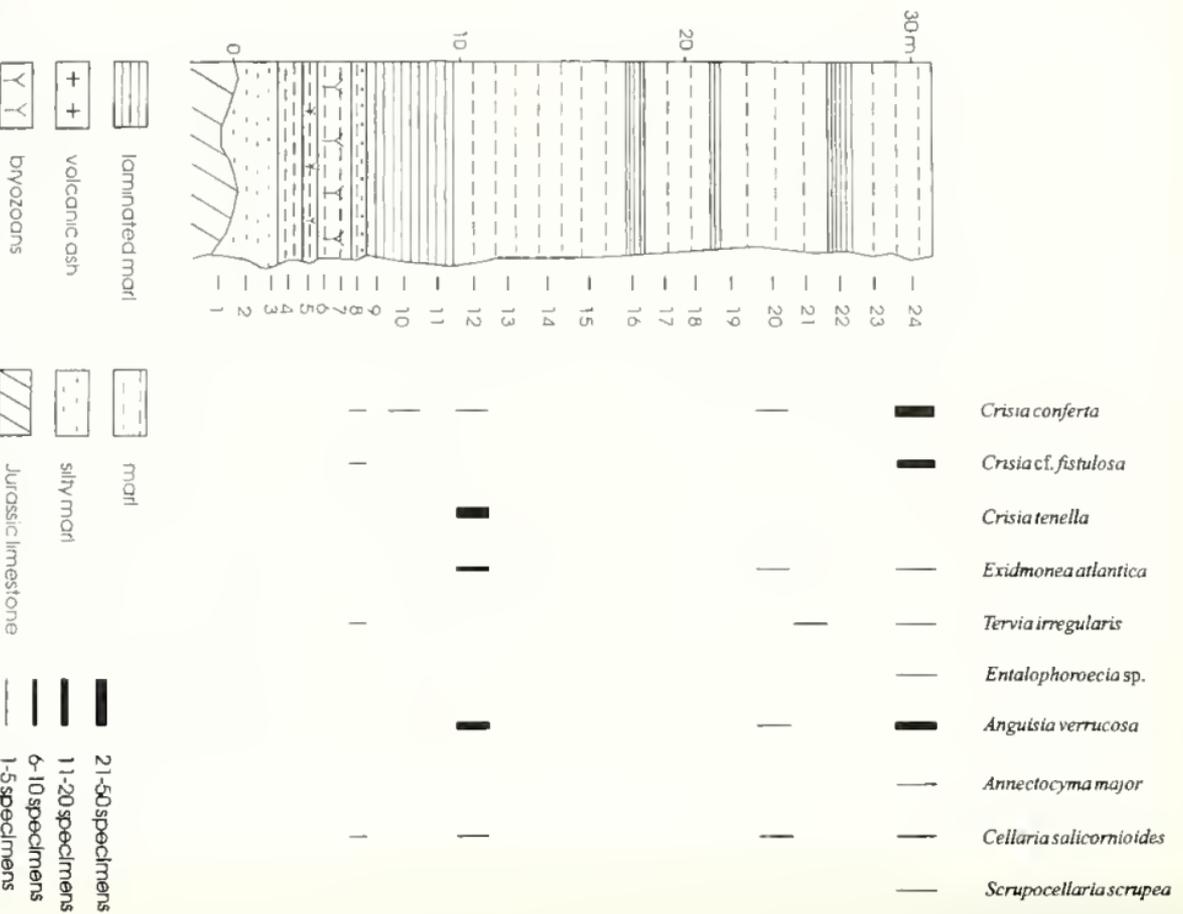




TEXT-FIG. 2. Distribution of bryozoans in the Vash section.

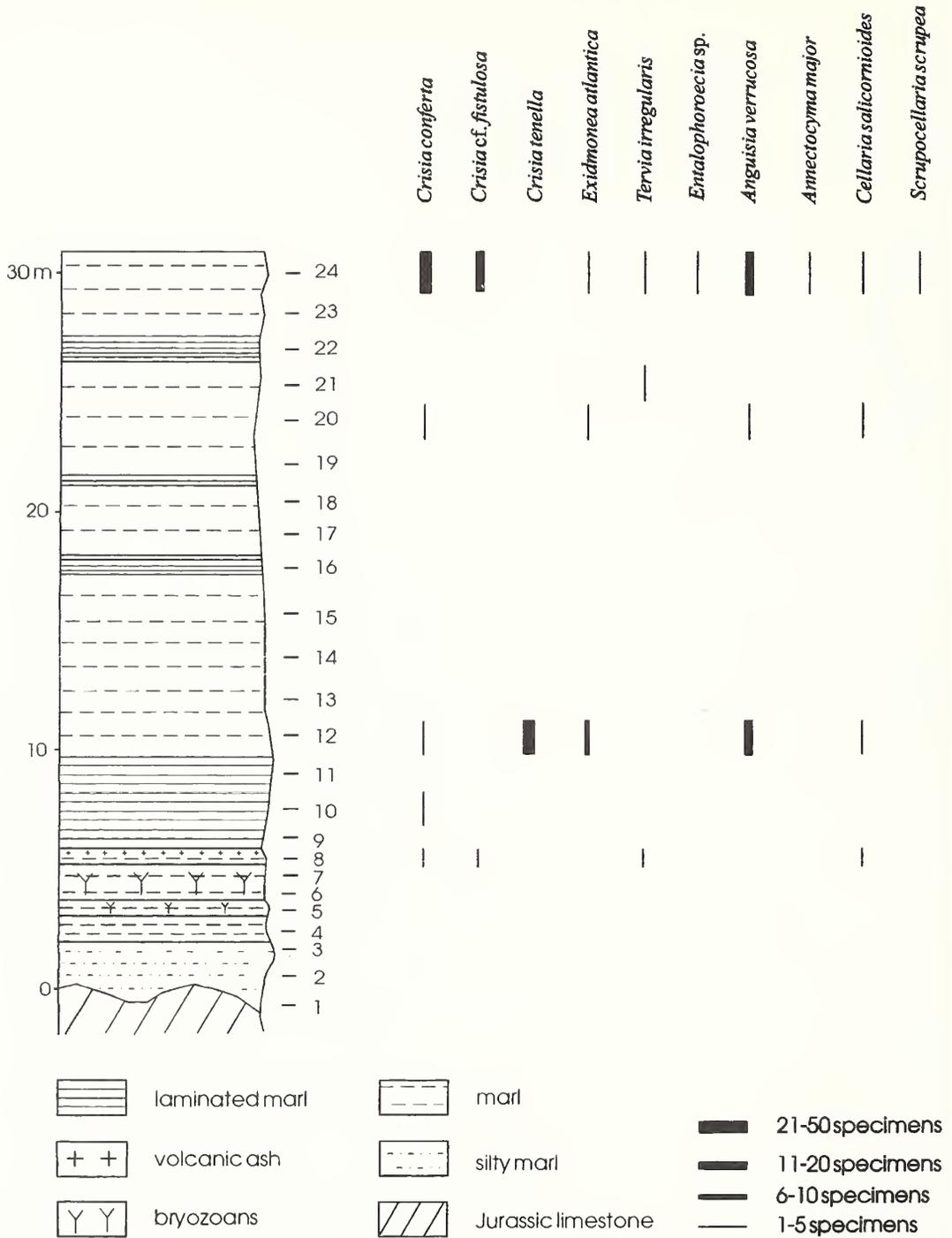
many deep-water forms), indicates deposition at a depth of approximately 600 m. For the other parts of the marl, a depth of about 400 m is estimated, and for the *Lophelia* patches, about 250 m.

The coquina beds above the marl indicate a deposition in shallow water (< 50 m), and a definite Pleistocene age. The age of the marls themselves is either earliest Pleistocene or latest Pliocene. None of the significant guide fossils are found among the microfossils, and *Hyalina haitica* which is regarded as the guide fossil for the beginning of the Pleistocene, is found only in the coquina beds.



TEXT-FIG. 3. Distribution of bryozoans in the Cape Vaga section (samples 1 to 7 include numerous shallow to moderately deep water bryozoans not treated in this paper)





TEXT-FIG. 3. Distribution of bryozoans in the Cape Vagia section (samples 1 to 7 include numerous shallow to moderately deep water bryozoans not treated in this paper).

and (probably as an admixture due to burrowing) in the topmost part of the pteropod-rich marl. If the pteropod-rich beds are taken as indicating the maximum transgression, a comparison with the Cape Vagia section would indicate that the whole section at Vasfi was in the uppermost Pliocene, just below the Plio-Pleistocene boundary. On the other hand, the oscillation in temperature and possibly also depth indicated by the *Lophelia*-beds seem stronger than would be expected from the known late Pliocene glaciations. The stronger oscillations are found only in the upper Pleistocene, and that would be too young for these beds.

#### *The Cape Vagia section*

This locality is a small, south-facing basin on the eastern coast of Rhodes (Text-fig. 1). At the base of the section are Jurassic limestones, intensively bored by *Lithophaga* and other organisms. The lower part of the sequence (Text-fig. 3) consists of marl with fossils (mostly fragmentary) between the boulders and irregularities in the basement, followed by an impure limestone with numerous fossils. Some marl-rich bands are found, and there are numerous trace fossil-horizons. At about 3–4 m above the base there are beds rich in bryozoans, echinoids, brachiopods, and molluscs, especially pectinids. Much material has been washed in from shallower water, including large, bored blocks of limestone (up to 1 m in diameter), fragments of oyster, and red algae, and for this reason, samples 1 to 7 are not studied in this paper.

Above these beds, the clay content increases rapidly, and the top marl includes beds rich in pteropods, and with a high (> 50 per cent.) percentage of planktonic foraminifera. The beds contain some spectacular trace fossils, including *Zoophycos*, found by R. G. Bromley and N.-M. Hanken. These trace fossils are taken to indicate deep water, and in this case the top of the *Zoophycos* is in the pteropod-rich beds, which are estimated to show a depth of about 600 m. They penetrate down into beds which were probably deposited in much shallower depth (about 150–200 m).

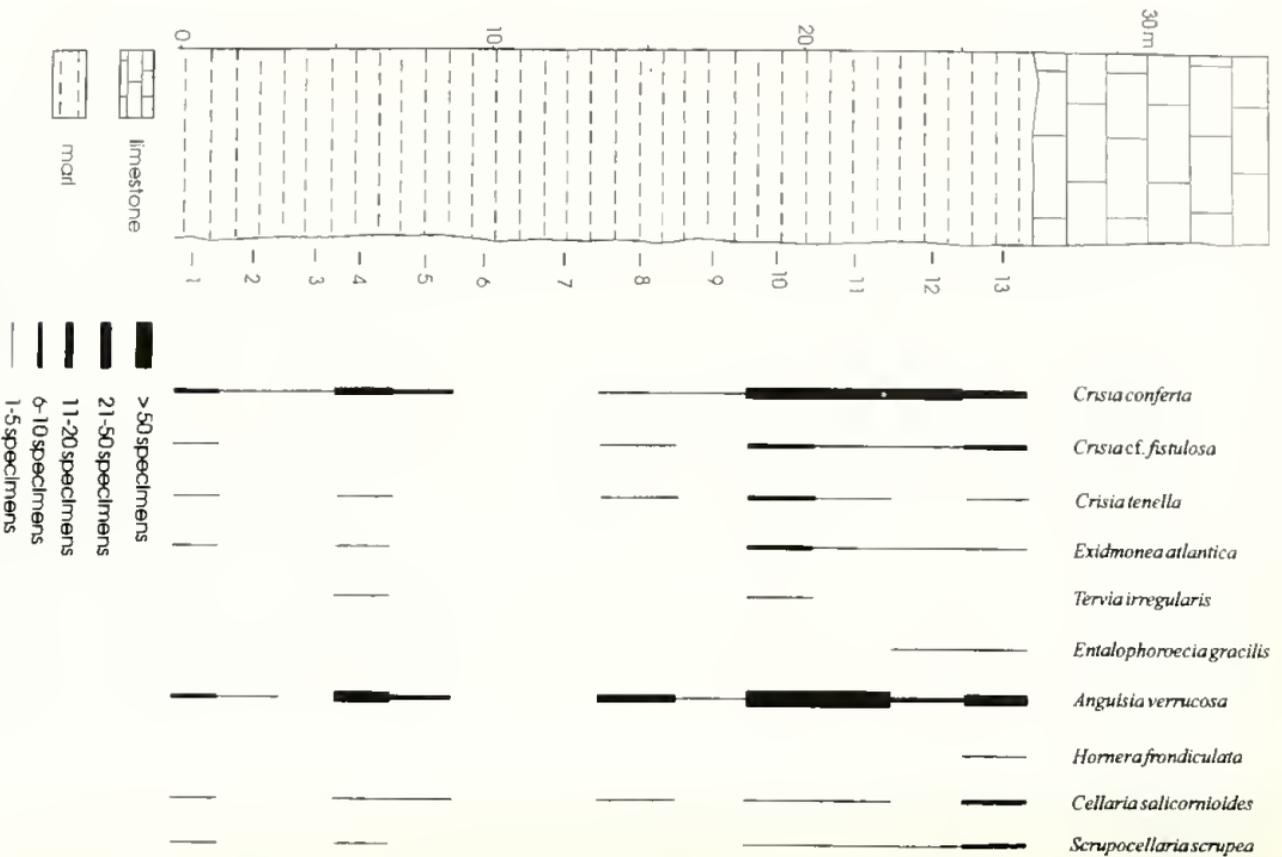
A thin (2–4 mm) red bed, probably a basaltic volcanic ash (Løvlie *et al.* 1989), overlies the *Zoophycos* bed. In the following bed, there are decimetric intervals of laminated, organic-rich beds, some of them with macroscopic plant remains, mostly *Pinus* wood. Most of the section consists of bioturbated marl, with a deep-water fauna dominated by bivalves, scaphopods, solitary corals, and brachiopods. The suggested depth of the lower part of the marl beds is approximately 400 m, decreasing upwards to about 250 m. As usual, there are many microfossils which have been washed in from shallower water, including epiphytic foraminifera.

From the palaeomagnetic results of Løvlie *et al.* (1989) the Plio-Pleistocene boundary should be about 5 m above the ash bed (about 10 m above the base of the section in Text-fig. 3). This indicates that the lower beds and the pteropod-rich beds marking the maximum transgression are youngest Pliocene, and the upper part of the section is Pleistocene. If it is accepted that the normal interval in the top of the section is the Brunhes Chron, this part of the section will be younger than 0.8 Ma.

The model developed from the palaeomagnetic results in this section, which may also be used for correlation with the other sections, demonstrates that the major transgression, which must have been very rapid and of a magnitude which exceeds usual eustatic sea-level changes, started in the very latest Pliocene, reached its maximum (at least 600 m higher than at present), just before the Plio-Pleistocene boundary, and was followed by a very slow, gradual regression.

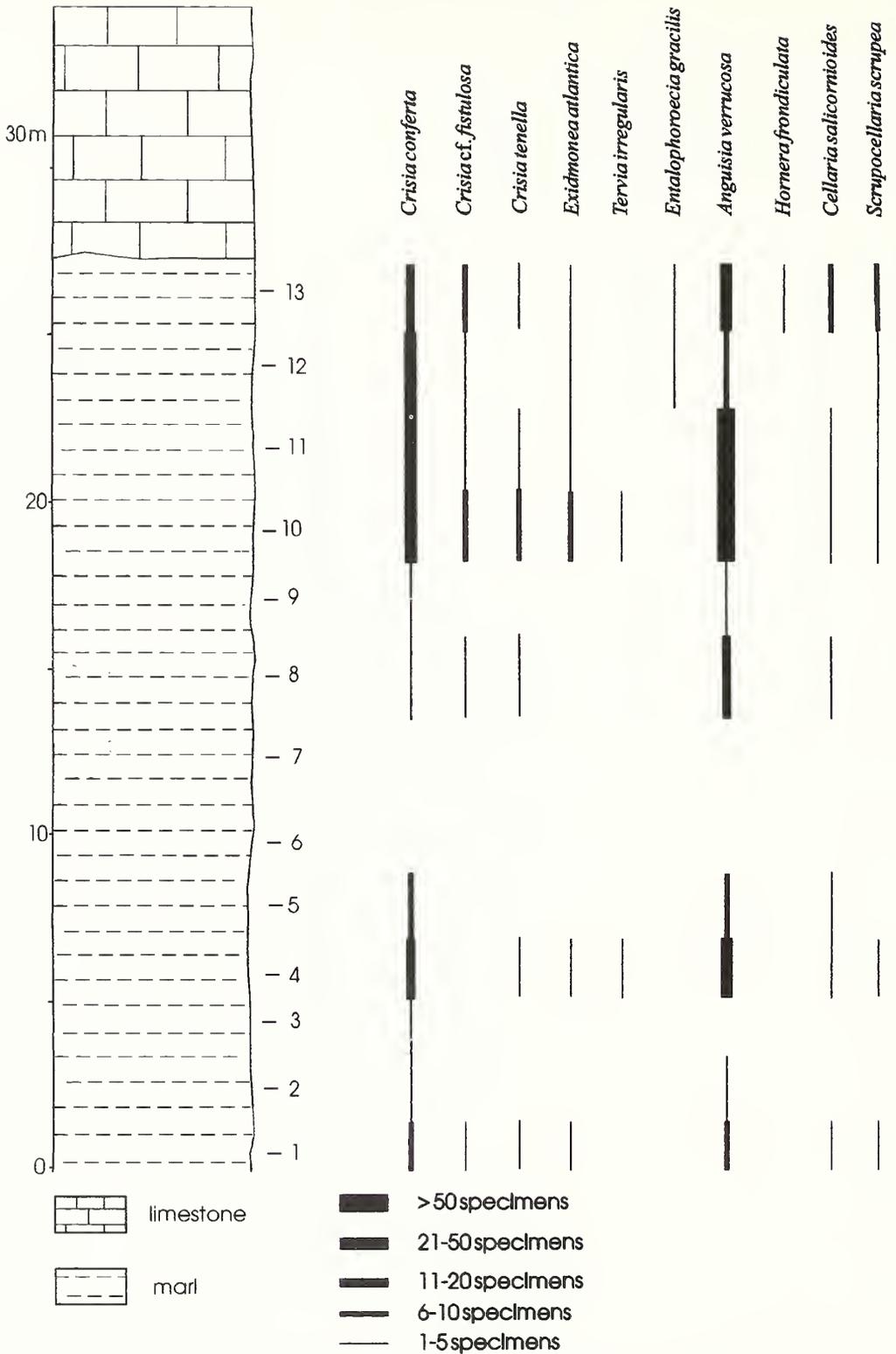
#### *The Lindos Bay section*

Lindos Bay is situated along the eastern coast of Rhodes, a few km north of the town of Lindos (Text-fig. 1). Beginning just above present-day sea-level, the section consists of about 28 m of bluish-grey marl, rich in pteropods and trace fossils (*Zoophycos*). Foraminifera, bivalves, scaphopods and ostracodes are also present, together with decapod, echinoid and fish remains.



TEXT-FIG. 4. Distribution of bryozoans in the Lindos Bay section





TEXT-FIG. 4. Distribution of bryozoans in the Lindos Bay section.

Locally laminated, the marl is mainly massive and well bioturbated. Massive coquinal and bryozoan-rich limestones cap the section, in disconformable contact with the marl (Text-fig. 4).

By comparison with the previous sections, the marls are considered to be uppermost Pliocene. A decrease upwards in the number of pteropod shells and *Zoophycos*, lacking in the last three levels, suggests a progressive shallowing of the deposits from depths around 400 m to approximately 200 m. The coquinal beds above the marl indicate shallow water and a Pleistocene age.

#### MATERIAL AND METHODS

For this study a total number of 39 samples (samples 1–7 of the Vagia section are not considered here) were collected from the marl levels of the three sections. For Vagia and Lindos, 500 g of sediment was weighed and then washed and sieved for each sample, whereas in Vasfi only an approximate weight of sediment was used, c. 100 g. Only 26 samples yielded bryozoans whose fragments were hand-picked from dried residues. The number of specimens belonging to each identified species was counted, and is given in parenthesis in the systematic description ('Material') after each sample number. This results in a semi-quantitative representation of the distribution of the species in the section (Text-figs 2–4).

*Repository.* Figured specimens are housed in the Institute of Earth Sciences, University of Lyon, France (prefixed FSL).

#### SYSTEMATIC PALAEOONTOLOGY

Class STENOLAEMATA Borg, 1926

Order TUBULIPORATA Johnston, 1847 (= CYCLOSTOMATA Busk, 1852)

Sub-order ARTICULATA Busk, 1859

Family CRISIIDAE Johnston, 1847

Genus CRISIA Lamouroux, 1812

*Crisia conferta* Busk, 1875

Plate 1, figures 1–2

1875 *Crisia conferta* Busk, p. 7, pl. 6A, fig. 5.

1990 *Crisia conferta* Busk; Harmelin, p. 1607, figs 2, 12–14.

*Material.* Vagia 8 (2), 10 (3), 12 (4), 20 (1), 24 (31); Lindos 1 (9), 2 (2), 3 (1), 4 (11), 5 (6), 8 (1), 9 (5), 10 (28).

*Morphology.* Colony cellariiiform; internodes rather wide, with eight to twelve zoecia; top of gonozooid generally flattened but sometimes rounded. In some cases, the gonozooid is subdivided into a basal part with flat top, followed by a rounded upper part (Pl. 1, fig. 2). Ooeciostome is of the same diameter but slightly shorter than the peristome of the next distal zooid, both tubes being adjacent or coalescent at their base. Harmelin (1990) noted that *C. conferta* and *C. sigmoidea* Waters, 1916 are probably identical and considered them to be two geographical forms of the same species.

*Occurrence.* Eastern Atlantic (Angola to the Bay of Biscay) at depths from 130 to 850 m, Mediterranean (Gibraltar area) at 110 m. The Mediterranean form, *C. sigmoidea*, has a shallower range: from 5 m in caves to 30 m in coralligenous biocoenosis. This is the first time that *C. conferta* (and *C. sigmoidea*) is reported as a fossil.

*Crisia cf. fistulosa* Heller, 1867

Plate 1, figures 3–4

1867 *Crisia fistulosa* Heller, p. 118, pl. 3, fig. 5.

1879 *Crisia fistulosa* Heller; Waters, p. 268, pl. 23, fig. 3.

1955 *Crisia fistulosa* Heller; Gautier, p. 268.

1968 *Crisia fistulosa* Heller; Harmelin, p. 427, fig. 4: 3–4.

1986 *Crisia fistulosa* Heller; Zabala, p. 607, text-fig. 215.

*Material.* Vagia 8 (3), 24 (12); Lindos 1 (2), 8 (1), 10 (6), 11 (3), 12 (3), 13 (6).

*Morphology.* Colony cellariiform; internodes narrow, each with a small number (three to eight) of long zooecia; gonozooid cylindrical; oeciostome terminal. The specimens from Rhodes are never very well preserved and the specific identification remains uncertain. The possibility that this species was transported from shallower water cannot be excluded. As noted by several authors (Heller 1867; Harmelin 1968; Zabala 1986) *Crisia fistulosa* closely resembles *Filicrisia geniculata* (Milne-Edwards, 1838).

*Occurrence.* Eastern Atlantic (Madeira) but mostly Mediterranean, at shallow depths from 5 to 40 m. This species has never been reported before as a fossil but some citations of *Filicrisia geniculata* (late Oligocene to Recent) may in fact deal with *Crisia fistulosa*.

### *Crisia tenella* Calvet, 1906b

Plate 1, figures 5–6

1906b *Crisia tenella* Calvet, p. 219.

1906c *Crisia tenella* Calvet; Calvet, p. 460, figs 1–2.

1982 *Crisia tenella* Calvet; Harmelin and Hondt, p. 5, pl. 1, fig. 2.

1990 *Crisia tenella* Calvet; Harmelin, p. 1611, figs 2, 15–17, 21.

*Material.* Vasfi 1 (1), 2 (35), 5 (1), 6 (4), 8 (1); Vagia 12 (32); Lindos 1 (1), 4 (4), 8 (3), 10 (8), 11 (2), 13 (2).

*Morphology.* Colony cellariiform; internodes very narrow, each comprising three to twelve zooecia, but five to seven in most cases; basis rami short and thin, always numerous; gonozooid rounded, beginning with a narrow base, erect and oblique to the internode; oeciostome short, dorsal and terminal. Present in all three sections, this species is generally well preserved and is even abundant in some of the samples.

*Occurrence.* Eastern Atlantic (Cape Verde Islands to the Bay of Biscay) at depths from 150 to 1696 m, Mediterranean (Alboran Sea) from 70 to 480 m. This species is also reported here as a fossil for the first time.

### Sub-order TUBULIPORINA Milne-Edwards, 1838

Family TUBULIPORIDAE Johnston, 1838

Genus EXIDMONEA Mongereau, 1970

*Exidmonea atlantica* Mongereau, 1970

Plate 1, figure 11

1847 *Idmonea atlantica* Forbes in Johnston, p. 278, pl. 48, fig. 3.

1966 *Idmonea atlantica* Forbes; Buge, p. 5, pl. B, figs 1–2.

#### EXPLANATION OF PLATE 1

Figs 1–2. *Crisia conferta*. 1, FSL 490.046, internode, frontal view; Vagia 12,  $\times 33$ . 2, FSL 490.047, internode with gonozooid; Vagia 12,  $\times 51$ .

Figs 3–4. *Crisia cf. fistulosa*. 3, FSL 490.048, internode, frontal view; Vagia 24,  $\times 48$ . 4, FSL 490.049, internode with gonozooid; Vagia 24,  $\times 51$ .

Figs 5–6. *Crisia tenella*. 5, FSL 490.050, internode, frontal view; Vasfi 2,  $\times 24$ . 6, 490.051, internode with gonozooid; Vasfi 2,  $\times 73$ .

Figs 7–8 *Entalophoroecia gracilis*. 7, FSL 490.052, branch bearing a gonozooid; Vasfi 1,  $\times 48$ . 8, FSL 490.053, fragment of a branch; Vasfi 3,  $\times 26$ .

Figs 9, 12. *Tervia irregularis*. 9, FSL 490.054, fragment of a branch, frontal view; Vasfi 1,  $\times 51$ . 12, FSL 490.055, detail of the gonozooid with its elliptical oeciostome; Vasfi 1,  $\times 66$ .

Fig. 10. *Entalophoroecia* sp., FSL 490.056, fragment of a branch; Vasfi 9,  $\times 36$ .

Fig. 11. *Exidmonea atlantica*, FSL 490.057, fragment of a branch, frontal view; Vasfi 5,  $\times 40$ .



MOISSETTE and SPJELDNAES, Plio-Pleistocene Bryozoa

- 1970 *Exidmonea atlantica* Mongereau, p. 30, pl. 1, fig. 1; pl. 2, figs 1, 5.  
 1976 *Idmidronea atlantica* (Forbes); Harmelin, p. 182, pl. 32, figs 1–11.  
 1983 *Idmidronea atlantica* (Forbes); Vávra, p. 73, pl. 1, figs 1–4.  
 1986 *Idmidronea atlantica* (Forbes); Zabala, p. 658, text-fig. 235a–d; pl. 28, fig. E.  
 1988 *Idmidronea atlantica* (Forbes); Moissette, p. 48, pl. 6, figs 6–7.  
 1988 *Idmidronea atlantica* (Forbes); Zabala and Maluquer, p. 174, text-figs 569–572; pl. 33, fig. A.  
 1992 *Exidmonea atlantica* (Forbes); Pouyet and Moissette, p. 24, pl. 1, figs 7–8.  
 1992 *Idmidronea atlantica* (Forbes); El Hajjaji, p. 44, pl. 2, fig. 11.  
 1993 *Exidmonea atlantica* (Forbes); Moissette *et al.*, p. 84, figs 3i–j.

*Material.* Vasfi 1 (3), 2 (1), 3 (3), 5 (20), 8 (94); Vagia 12 (7), 20 (5), 24 (1); Lindos 1 (1), 4 (2), 10 (6), 11 (1), 12 (1), 13 (1).

*Morphology.* Colony vinculariiform; fascicles alternating on each side of the median crest, each comprising three to four salient zoecial tubes; dorsal flattened or slightly concave. Although the gonozoid has not been observed, *Exidmonea atlantica* is easily identifiable.

*Occurrence.* Almost cosmopolitan in distribution, this species has been recorded from depths of 10 to 850 m. It has a long stratigraphical range, from the Eocene to the Recent and is particularly well represented in the Mediterranean Neogene.

Family TERVIIDAE Canu and Bassler, 1920

Genus TERVIA Jullien, 1882

*Tervia irregularis* (Meneghini, 1845)

Plate 1, figures 9, 12

- 1845 *Idmonea irregularis* Meneghini, p. 128.  
 1963 *Tervia irregularis* (Meneghini); Malecki, p. 71, text-fig. 30; pl. 3, fig. 11.  
 1972 *Tervia irregularis* (Meneghini); Mongereau, p. 342, pl. 9, fig. 9.  
 1975 *Tervia irregularis* (Meneghini); Vávra, p. 523, pl. 2, figs 3–4.  
 1976 *Tervia irregularis* (Meneghini); Harmelin, p. 163, pl. 26, figs 1–11.  
 1982 *Tervia irregularis* (Meneghini); Harmelin and Hondt, p. 8, pl. 3, fig. 4.  
 1986 *Tervia irregularis* (Meneghini); Zabala, p. 656, text-fig. 234.  
 1988 *Tervia irregularis* (Meneghini); Moissette, p. 49, pl. 6, figs 10–12.  
 1988 *Tervia irregularis* (Meneghini); Zabala and Maluquer, p. 174, text-figs 563–568.  
 1992 *Tervia irregularis* (Meneghini); Pouyet and Moissette, p. 25, pl. 1, figs 11–12.  
 1992 *Tervia irregularis* (Meneghini); El Hajjaji, p. 48, pl. 2, fig. 10.  
 1993 *Tervia irregularis* (Meneghini); Moissette *et al.*, p. 85, fig. 3h, l.

*Material.* Vasfi 1 (9), 2 (1), 3 (14), 5 (11), 6 (1), 7 (2), 9 (1); Vagia 8 (4), 21 (1), 24 (1); Lindos 4 (1), 10 (2).

*Morphology.* Colony vinculariiform; zoecial tubes and their peristomes isolated or clustered in groups of three to five; dorsal convex, with longitudinal lines corresponding with the limits of tubes; gonozoid dorsal, rounded and elongated; oeciostome terminal, elliptical, adjacent to the dorsal, with a curved upper lip. This species is easily identifiable by the clustering of the tubes, the dorsal side, and the gonozoid.

*Occurrence.* Harmelin (1976) considers *Tervia irregularis* as a typical deep-water species, never found above 60 m (60–300 m in the Mediterranean) and even reaching a depth of 2650 m in the Bay of Biscay. It has a vast geographical distribution: eastern Atlantic (Senegal to the Bay of Biscay), Mediterranean, Pacific (Australia) and Indian Ocean (East Africa). It is known from as early as the Eocene from a number of deposits, especially in the Mediterranean realm.

Family ENTALOPHORIDAE Reuss, 1869

Genus ENTALOPHOROECIA Harmelin, 1976

*Entalophoroecia gracilis* Harmelin, 1976

Plate 1, figures 7–8

- 1976 *Entalophoroecia gracilis* Harmelin, p. 100, pl. 7, figs 1–8; pl. 11, figs 1–6.

- 1986 *Entalophoroecia gracilis* Harmelin; Zabala, p. 633, text-fig. 225; pl. 24, fig. E.  
 1992 *Entalophoroecia gracilis* Harmelin; Harmelin and Hondt, p. 614, fig. 1; pl. 2, figs B–C.

*Material.* Vasfi 1 (2), 3 (2), 5 (1), 6 (1); Lindos 12 (2), 13 (3).

*Morphology.* Colony vinculariiform, always slender; zooecial tubes more or less rugose, opening on all sides of the branches; gonozooid forming a simple bulge, generally at the end of a branch; oociostome terminal, of a smaller diameter than the peristomes. This species was only encountered in its erect form, corresponding with deeper habitats than the semi-erect pustuloporian or the creeping stomatoporian colonies (Harmelin 1976).

*Occurrence.* Eastern Atlantic (from the Gulf of Guinea to Brittany) at depths down to 610 m, Mediterranean from 70 to 480 m. This species is reported as a fossil for the first time.

*Entalophoroecia* sp.

Plate 1, figure 10

*Material.* Vasfi 9 (1); Vagia 24 (1).

*Morphology.* Colony vinculariiform; zooecial tubes isolated, always small in number. This species is only represented by two specimens without gonozooids. Specific identification is impossible.

Genus ANGUISSIA Jullien, 1882

*Anguissia verrucosa* Jullien, 1882

Plate 2, figures 1–2

- 1882 *Anguissia verrucosa* Jullien, p. 497, pl. 13, figs 1–2.  
 1977 *Anguissia verrucosa* Jullien; Harmelin, p. 1058, figs 1–2; pl. 1, figs 1, 3.  
 1979 *Anguissia verrucosa* Jullien; Harmelin, p. 414, pl. 2, fig. 3.  
 1982 *Anguissia verrucosa* Jullien; Harmelin and Hondt, p. 7, pl. 1, figs 3–4.

*Material.* Vasfi 1 (11), 2 (3), 3 (2), 5 (3), 6 (18), 8 (3); Vagia 12 (11), 20 (1), 24 (14); Lindos 1 (10), 2 (2), 4 (24), 5 (7), 8 (12), 9 (4), 10 (63), 11 (61), 12 (9), 13 (21).

*Morphology.* Colony vinculariiform, arising from an encrusting uniserial basis; zooecial tubes forming slender bifurcating branches, striated by thin growth lines and verrucous (pseudopores).

*Occurrence.* Eastern Atlantic (200–2018 m) and Mediterranean (500–1525 m). The species created by Neviani (1895) from the Pleistocene of Italy, *A. jullieni*, probably corresponds with an encrusting basis of *A. verrucosa*.

Family ANNECTOCYMIDAE Hayward and Ryland, 1985

Genus ANNECTOCYMA Hayward and Ryland, 1985

*Annectocyma major* (Johnston, 1847)

Plate 2, figure 3

- 1847 *Alecto major* Johnston, p. 281, pl. 49, figs 3–4.  
 1956 *Diaperoecia major* (Johnston); Buge, p. 11, pl. 1, figs 5–6.  
 1976 *Diaperoecia major* (Johnston); Harmelin, p. 79, pl. 1, figs 1–11; pl. 2, figs 1–9; pl. 13, figs 1–10; pl. 14, figs 1–10.  
 1984 *Diaperoecia major* (Johnston); Poluzzi and Padovani, p. 104, fig. 4d.

- 1985 *Amnectocyma major* (Johnston); Hayward and Ryland, p. 1077, fig. 1C–D.  
 1986 *Diaperoecia major* (Johnston); Zabala, p. 623, fig. 222.  
 1988 *Diaperoecia major* (Johnston); Moissette, p. 53, pl. 7, fig. 4.  
 1988 *Amnectocyma major* (Johnston); Zabala and Maluquer, p. 167, figs 492–494; pl. 30, figs A–B.  
 1992 *Amnectocyma major* (Johnston); El Hajjaji, p. 54, pl. 2, figs 4–5.  
 1992 *Amnectocyma major* (Johnston); Pouyet and Moissette, p. 27, pl. 1, fig. 12.  
 1993 *Amnectocyma major* (Johnston); Moissette *et al.*, p. 87.

*Material.* Vasfi 1 (3), 3 (3), 5 (2); Vagia 24 (2).

*Morphology.* Colony membraniporiform, forming irregular dichotomous branches with rugose surface; zoecial tubes often clustered in series of two to four; peristomes moderately protruding. Generally encrusting, this species may also give rise to erect branches, and confusion with *Entalophoroecia* species is then possible (Harmelin 1976).

*Occurrence.* This species has wide geographical and stratigraphical distributions: western and eastern Atlantic (Brazil; Cape Verde Islands to Norway), Mediterranean, and possibly Pacific in the Recent; Mediterranean and eastern Atlantic from the Middle Miocene to the Pleistocene. Its bathymetric range is from 3 to 205 m in the Mediterranean, deeper in the Atlantic (to 362 m off the Spanish–Moroccan coast).

### Genus YBSELOSOECIA Canu and Lecointre, 1933

#### *Ybselosoecia typica* (Manzoni, 1878)

#### Plate 2, figure 4

- 1878 *Filisarsa typica* Manzoni, p. 10, pl. 8, fig. 30.  
 1909 *Filisarsa typica* Manzoni; Canu, p. 115, pl. 14, figs 25–26.  
 1956 *Ybselosoecia typica* (Manzoni); Buge, p. 13, pl. 1, figs 3–4; pl. 2, figs 3–4.  
 1963 *Ybselosoecia typica* (Manzoni); Malecki, p. 76, fig. 33; pl. 5, fig. 1.  
 1965 *Ybselosoecia typica* (Manzoni); Mongereau, p. 317, fig. 1.  
 1974 *Ybselosoecia typica* (Manzoni); Vávra, p. 362, pl. 2, figs 9–10.  
 1984 *Ybselosoecia typica* (Manzoni); Vávra, p. 226, pl. 1, figs 2–3.  
 1988 *Ybselosoecia typica* (Manzoni); Moissette, p. 56, pl. 7, figs 9, 13.  
 1992 *Ybselosoecia typica* (Manzoni); El Hajjaji, p. 56, pl. 2, figs 2–3.  
 1992 *Ybselosoecia typica* (Manzoni); Pouyet and Moissette, p. 28, pl. 2, fig. 4.  
 1993 *Ybselosoecia typica* (Manzoni); Moissette *et al.*, p. 87.

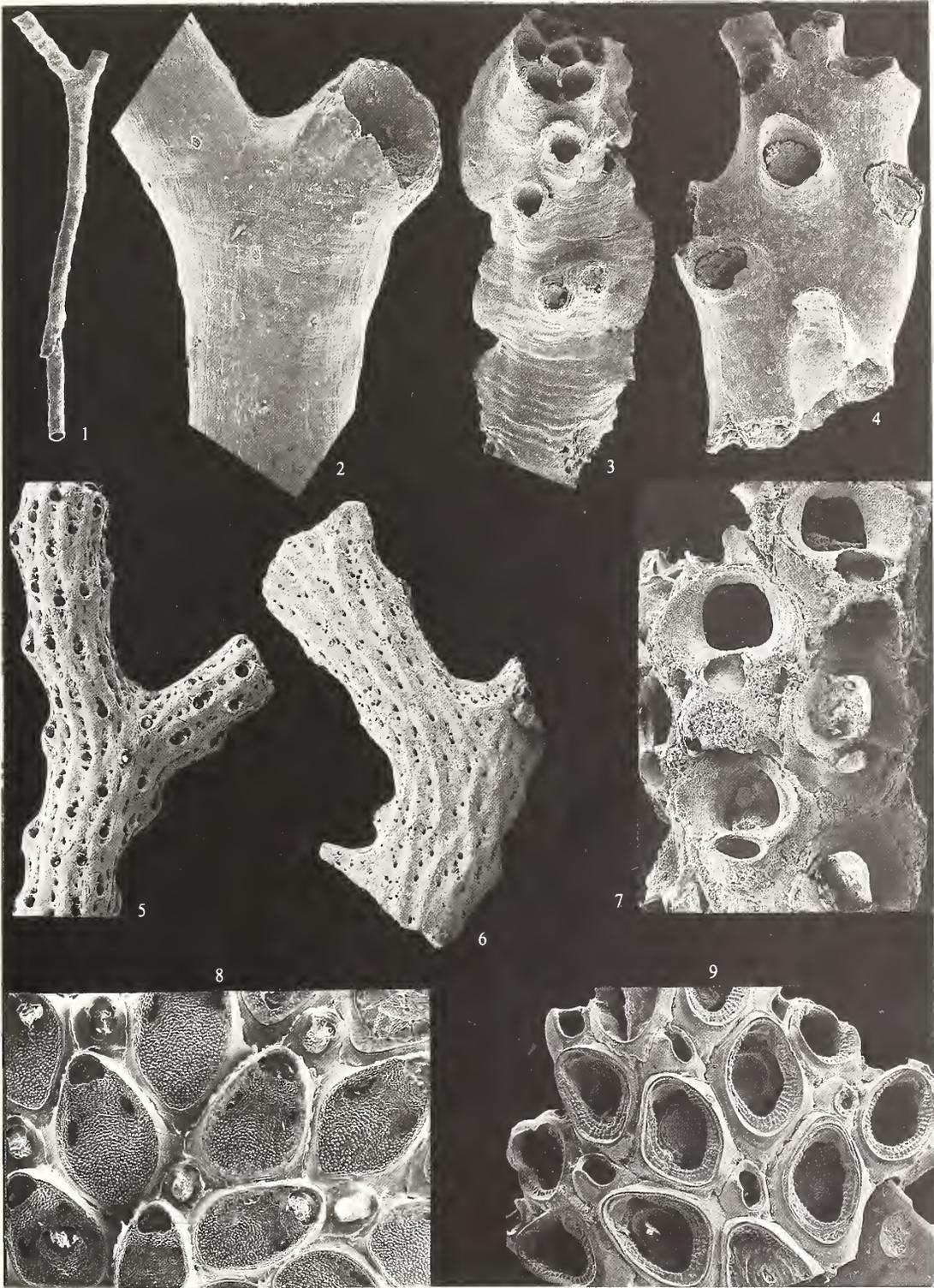
*Material.* Vasfi 5 (1).

*Morphology.* Colony vinculariiform, forming dichotomous and more or less flattened branches; zoecial tubes indistinct, terminated by isolated peristomes of a large diameter; dorsal wall slightly convex, with thin growth lines. This fossil species is easily identifiable by its slightly flattened branches and large peristomes.

*Occurrence.* Eocene to Pliocene, mostly from Mediterranean regions.

#### EXPLANATION OF PLATE 2

- Figs 1–2. *Anguisia verrucosa*. 1, FSL 490.058, bifurcating branch; Vasfi 1,  $\times 24$ . 2, FSL 490.059, detail of a branch; Vasfi 1,  $\times 165$ .  
 Fig. 3. *Amnectocyma major*, FSL 490.060, zoarium with clustered tubes; Vasfi 3,  $\times 32$ .  
 Fig. 4. *Ybselosoecia typica*, FSL 490.061, fragment of a branch, frontal view; Vasfi 5,  $\times 51$ .  
 Figs 5–6. *Hornera frondiculata*. 5, FSL 490.062, fragment of a branch, frontal view; Vasfi 9,  $\times 24$ . 6, FSL 490.063, fragment of a branch, dorsal view; Vasfi 9,  $\times 26$ .  
 Fig. 7. *Ramphonotus minax*, FSL 490.064, fragment of a pseudovinculariiform branch with ovicellate zooecia; Vasfi 3,  $\times 51$ .  
 Fig. 8. *Setosella vulnerata*, FSL 490.065, colony growing in a spiral around the ancestrule on a small shell fragment; Vasfi 2,  $\times 62$ .  
 Fig. 9. *Setosellina capriensis*, FSL 490.066, ancestrular area of a small colony; Vasfi 8,  $\times 94$ .



MOISSETTE and SPJELDNAES, Plio-Pleistocene Bryozoa

## Sub-order CANCELLATA Gregory, 1896

Family HORNERIDAE Gregory, 1899

Genus HORNERA Lamouroux, 1821

*Hornera frondiculata* Lamouroux, 1821

## Plate 2, figures 5–6

- 1821 *Hornera frondiculata* Lamouroux, p. 41, pl. 74, figs 7–9.  
 1963 *Hornera frondiculata* Lamouroux; Malecki, p. 80, pl. 5, fig. 2a–b.  
 1972 *Hornera frondiculata* Auct. forme *frondiculata* Mongereau, p. 329, pl. 5, figs 1–3; pl. 7, figs 1–2.  
 1972 *Hornera frondiculata* Auct. forme *striata* Mongereau, p. 345, pl. 5, figs 8–9; pl. 6, figs 1–4, 6; pl. 7, figs 5–8.  
 1986 *Hornera frondiculata* Lamouroux; Zabala, p. 686, text-fig. 243.  
 1988 *Hornera frondiculata* Auct. forme *frondiculata* Mongereau; Moissette, p. 61, pl. 8, fig. 11.  
 1988 *Hornera frondiculata* Auct. forme *striata* Mongereau; Moissette, p. 62, pl. 8, fig. 10.  
 1988 *Hornera frondiculata* Lamouroux; Zabala and Maluquer, p. 182, text-figs 625–629; pl. 36, figs A–B.  
 1992 *Hornera frondiculata* Auct. forme *frondiculata* Mongereau; El Hajjaji, p. 65, pl. 2, figs 15–16.  
 1992 *Hornera frondiculata* Auct. forme *striata* Mongereau; El Hajjaji, p. 66, pl. 3, figs 1–2.  
 1992 *Hornera frondiculata* Lamouroux; Pouyet and Moissette, p. 30, pl. 2, figs 10–11.  
 1993 *Hornera frondiculata* Lamouroux; Moissette *et al.*, p. 88.

*Material.* Vasfi 9 (1); Lindos 13 (5).

*Morphology.* Colony vinculariiform; zoecial tubes separated by sulci, a vacuole at each end of the protruding peristomes; dorsal sulci little salient, with series of small vacuoles in-between. Depending upon the degree of calcification, two forms of *Hornera frondiculata* were recognized by Mongereau (1972); they are now generally reunited. This species is represented here by a small number of fragments, and only in the highest level of the Vasfi and Lindos sections. Its presence there could be due to a reworking, possibly by bioturbation, of the younger (and shallower) beds of the coquina limestones.

*Occurrence.* Known from the eastern Atlantic (Cape Verde Islands to the Bay of Biscay) and the Mediterranean, *Hornera frondiculata* has been recorded from depths of 30 to 200 m. It has a large stratigraphical range, from the Eocene to the Recent, notably in the Mediterranean realm.

## Class GYMNOLEAEMATA Allman, 1856

Order CHEILOSTOMATA Busk, 1852

Sub-order ANASCA Levinsen, 1909

Family SETOSELLIDAE Levinsen, 1909

Genus SETOSELLA Hincks, 1877

*Setosella vulnerata* (Busk, 1860)

## Plate 2, figure 8

- 1860 *Membranipora vulnerata* Busk, p. 124, pl. 25, fig. 3.  
 1880 *Setosella vulnerata* (Busk); Hincks, p. 181, pl. 21, fig. 7.  
 1882 *Setosella vulnerata* (Busk); Jullien, p. 524, pl. 17, fig. 66.  
 1962 *Setosella vulnerata* (Busk); Gautier, p. 68.  
 1966 *Setosella vulnerata* (Busk); Prenant Bobin, p. 358, text-fig. 117I–IV.  
 1977 *Setosella vulnerata* (Busk); Ryland and Hayward, p. 118, text-fig. 55.  
 1977 *Setosella vulnerata* (Busk); Harmelin, p. 1064, text-figs 13–15; pl. 1, fig. 6.  
 1988 *Setosella vulnerata* (Busk); Zabala and Maluquer, p. 92, text-fig. 133; pl. 2E.  
 1992 *Setosella vulnerata* (Busk); Reguant and Maluquer, p. 144, pl. 1, fig. 6.  
 1993 *Setosella vulnerata* (Busk); Moissette *et al.*, p. 97, fig. 6a–b.

*Material.* Vasfi 2 (2).

*Morphology.* Colony membraniporiform; autozooezia suboval; cryptocyst smooth with a narrow opesiular slit on each side, a little below the semi-circular opesia. A small distal vibraculum is always present over each autozooezium. Two colonies were found in the Vasfi section. They had encrusted small shell fragments and grew in a spiral around the ancestrula (with trifoliate opesia).

*Occurrence.* Western and eastern Atlantic (Gulf of Mexico; Cape Verde Islands to Shetland and Norway), Mediterranean, Indian Ocean (Gulf of Aden). Although presenting a wide bathymetric distribution (30 to 3700 m), this species is typical of deep waters.

Genus SETOSELLINA Calvet, 1906a

*Setosellina capriensis* (Waters, 1926)

Plate 2, figure 9

- 1926 *Cupularia capriensis* Waters, p. 432, pl. 18, figs 8–9.  
 1965 *Setosellina capriensis* (Waters); Cook, p. 182, pl. 1, figs 5–6.  
 1966 *Setosellina capriensis* (Waters); Prenant and Bobin, p. 301.  
 1988 *Setosellina capriensis* (Waters); Zabala and Maluquer, p. 88, text-fig. 111.  
 1992 *Setosellina capriensis* (Waters); Reguant and Maluquer, p. 143, pl. 1, fig. 1.

*Material.* Vasfi 2 (11), 8 (1).

*Morphology.* Colony membraniporiform; autozooezia suboval with a gymnocyst developed in the proximal part only and forming a salient frame around the opesia; opesia oval, surrounded by a granular cryptocyst absent from the more distal part; each autozooezium bears in its distal part a small median vibraculum. The autozooezia of the ancestrular area are almost completely occluded by a calcareous lamina, leaving only a small central pore. This species closely resembles *Setosellina roulei* (Calvet, 1906a). The differences are a smaller zoecial size, a narrower cryptocyst, and a deeper habitat (200 to 2330 m) for *S. roulei*.

*Occurrence.* Eastern Atlantic (Azores and Canary Islands) and Mediterranean, at depths from 55 to 240 m.

Family CALLOPORIDAE Norman, 1903

Genus RAMPHONOTUS Norman, 1894

*Ramphonotus minax* (Busk, 1860)

Plate 2, figure 7

- 1860 *Membranipora minax* Busk, p. 125, pl. 25, fig. 1.  
 1906c *Membranipora minax* Busk; Calvet, p. 388, pl. 26, fig. 2.  
 1962 *Ramphonotus minax* (Busk); Gautier, p. 45.  
 1966 *Ramphonotus minax* (Busk); Prenant and Bobin, p. 271, text-fig. 90.  
 1977 *Amphiblestrum minax* (Busk); Ryland and Hayward, p. 106, text-fig. 46.  
 1986 *Amphiblestrum minax* (Busk); Zabala, p. 263, text-fig. 66.  
 1988 *Ramphonotus minax* (Busk); Moissette, p. 85, pl. 13, figs 4–5.  
 1989 *Amphiblestrum minax* (Busk); Zabala and Maluquer, p. 82, text-fig. 93; pl. 3, fig. B.  
 1992 *Ramphonotus minax* (Busk); El Hajjaji, p. 101, pl. 4, fig. 11.  
 1992 *Ramphonotus minax* (Busk); Pouyet and Moissette, p. 38.

*Material.* Vasfi 3 (1).

*Morphology.* Colony pseudovinculariiform; autozooezia rhomboidal to subhexagonal; gymnocyst and cryptocyst granular, separated by a thin ridge; opesia trapezoidal and rounded. A small avicularium is situated in the centre of the proximal part of the cryptocyst; hyperstomial ovicell globular, with a granular surface and a frontal triangular to circular area. Although generally occurring in its membraniporiform zoarial type, this species is represented here by a small fragment of pseudovinculariiform colony, perhaps corresponding with a deeper habitat. As in Recent material, the specimen from Rhodes presents only one avicularium, whereas other fossil material often shows two avicularia in the distal part of ovicellate autozooezia.

*Occurrence.* Western and eastern Atlantic (Canada and Greenland; Bay of Biscay to Norway), Arctic Ocean, Mediterranean. It is a boreal species widespread in the Atlantic from depths of 25 to 300 m. In the Mediterranean, it occurs between 80 and 145 m. From the fossil record, it is known in the Middle Miocene to the Pliocene, mainly in the Mediterranean region.

Family CELLARIIDAE Hincks, 1880  
Genus CELLARIA Ellis and Solander, 1786

*Cellaria salicornioides* Lamouroux, 1816

Plate 3, figure 1

- 1816 *Cellaria salicornioides* Lamouroux, p. 127.  
1826 *Cellaria salicornioides* Lamouroux; Audouin, p. 236; Savigny, 1827, pl. 6, fig. 7.  
1962 *Cellaria salicornioides* Audouin; Gautier, p. 72.  
1966 *Cellaria salicornioides*? Lamouroux, Savigny-Audouin; Prenant and Bobin, p. 382, text-fig. 124.  
1977 *Cellaria salicornioides* Lamouroux; Ryland and Hayward, p. 124, text-fig. 59.  
1984 *Cellaria salicornioides* Lamouroux; Poluzzi and Padovani, p. 109, fig. 5d.  
1986 *Cellaria salicornioides* Audouin; Zabala, p. 307, text-fig. 84: 3a-e; pl. 3, figs E-F.  
1988 *Cellaria salicornioides* Lamouroux; Moissette, p. 104, pl. 17, figs 1-2.  
1988 *Cellaria salicornioides* Audouin; Zabala and Maluquer, p. 94, text-figs 137-140; pl. 2, fig. H.  
1992 *Cellaria salicornioides* Lamouroux; El Hajjaji, p. 129, pl. 6, fig. 7.

*Material.* Vasfi 4 (1), 5 (1); Vagia 8 (1), 12 (4), 20 (4), 24 (1); Lindos 1 (1), 4 (4), 5 (2), 8 (3), 10 (2), 11 (1), 13 (10).

*Morphology.* Colony cellariiform; slender branches with four longitudinal series of autozoecia; autozoecia subhexagonal, alternating in adjacent series and separated by a thin groove; cryptocyst depressed, finely granular, with a raised marginal rim; opesia semicircular, showing two short lateral denticles on the convex proximal edge; endotoichal ovicell with a small round opening distal to the opesia. The interzoecial avicularium has not been observed on the studied material; however, it is always rare in this species.

*Occurrence.* Eastern Atlantic (from Madeira to Shetland), Mediterranean, Red Sea. It has been recorded from the Atlantic at depths of 0 to 362 m. In the Mediterranean, it occurs between 0 and 150 m. It is known from the fossil record back to the Middle Miocene, essentially in the Mediterranean region, but also in England and Portugal.

Family SCRUPOCELLARIIDAE Levinsen, 1909  
Genus SCRUPOCELLARIA Beneden, 1845

*Scrupocellaria scrupea* Busk, 1851

Plate 3, figures 2-4

- 1851 *Scrupocellaria scrupea* Busk, p. 83, pl. 9, figs 11-12.

EXPLANATION OF PLATE 3

- Fig. 1. *Cellaria salicornioides*, FSL 490.067, extremity of a branch; Vagia 1,  $\times 79$ .  
Figs 2-4. *Scrupocellaria scrupea*. 2, FSL 490.068, fragment of a branch, frontal view. 3, FSL 490.069, ovicellate zoecia. 4, FSL 490.070, fragment of a branch, dorsal view. All Vasfi 1,  $\times 73$ .  
Fig. 5. *Tessaradoma boreale*, FSL 490.071, fragment of a branch, with spiramen and avicularia; Vasfi 5,  $\times 51$ .  
Fig. 6. *Characodoma bifurcatum*, FSL 490.072; Vasfi 8,  $\times 73$ .  
Figs 7-8. *Jaculina tessellata*. 7, FSL 490.073, fragment of the reteporiform zoarium; Vasfi 8,  $\times 33$ . 8, FSL 490.073, detail view of the zoecia and their apertures; Vasfi 8,  $\times 79$ .  
Fig. 9. *Palmicellaria elegans*, FSL 490.074, fragment of a branch showing the cross section; Vasfi 1,  $\times 46$ .  
Fig. 10. *Adeonellopsis distoma*, FSL 490.075; Vasfi 1,  $\times 73$ .



MOISSETTE and SPJELDNAES, Plio-Pleistocene Bryozoa

- 1852 *Scrupocellaria scrupea* Busk; Busk, p. 24, pl. 21, figs 1-2.  
 1880 *Scrupocellaria scrupea* Busk; Hincks, p. 50, pl. 7, figs 11-14.  
 1962 *Scrupocellaria scrupea* Busk; Gautier, p. 90.  
 1966 *Scrupocellaria scrupea* Busk; Prenant and Bobin, p. 432, text-fig. 143.  
 1977 *Scrupocellaria scrupea* Busk; Ryland and Hayward, p. 138, text-fig. 66.

*Material.* Vasfi 1 (6), 2 (15), 3 (3), 5 (2), 6 (2), 7 (2); Vagia 24 (2); Lindos 1 (1), 4 (2), 10 (5), 11 (1), 12 (1), 13 (8).

*Morphology.* Colony cellariiiform; flattened branches with two alternating series of elongated subquadrangular autozoecia; opesia oval, occupying nearly one-half of the zoecium and surrounded by a narrow rim bearing five distal spines (three on the external edge, two on the internal edge); lateral avicularium large and constant; frontal avicularium small and inconstant, mostly associated with ovicells; ovicell rounded, with a smooth surface and a small proximal fenestra; dorsal slightly convex, with a proximal vibraculum on each zoecium. The number of spines is fairly constant on the recovered material. When associated with an ovicell, the frontal avicularium is well developed and in a slightly transverse position.

*Occurrence.* Eastern Atlantic (from Cape Verde Islands to the North Sea), Mediterranean, Indian and Pacific Oceans. This species has a wide bathymetric distribution: from 0 to 500 m in the Atlantic and from 0 to 150 m in the Mediterranean. In the fossil record, it has only been reported before from the Pleistocene of Italy (Neviani 1904).

Sub-order ASCOPHORA Levinsen, 1909  
 Family TESSARADOMIDAE Jullien and Calvet, 1903  
 Genus TESSARADOMA Norman, 1869

*Tessaradoma boreale* (Busk, 1860)

Plate 3, figure 5

- 1860 *Onctopora boreale* Busk, p. 213, pl. 28, figs 6-7.  
 1880 *Porina borealis* (Busk); Hincks, p. 229, pl. 31, figs 4-6.  
 1962 *Tessaradoma boreale* (Busk); Gautier, p. 222.  
 1979 *Tessaradoma boreale* (Busk); Hayward and Ryland, p. 242, text-fig. 104.  
 1988 *Tessaradoma boreale* (Busk); Moissette, p. 123, pl. 20, fig. 5.  
 1988 *Tessaradoma boreale* (Busk); Zabala and Maluquer, p. 142, text-fig. 343.  
 1992 *Tessaradoma boreale* (Busk); El Hajjaji, p. 225, pl. 13, fig. 2.  
 1992 *Tessaradoma boreale* (Busk); Pouyet and Moissette, p. 53, pl. 7, fig. 3.

*Material.* Vasfi 2 (2), 5 (5), 7 (5).

*Morphology.* Colony vinculariiform; autozoecia oval and more or less elongate, the granular frontal bordered by a row of marginal pores; spiramen immediately proximal to the orbicular aperture. Two pairs of small frontal avicularia are generally present: one lateral to the spiramen, the other near the marginal pores. This species varies mainly in the degree of calcification and in the number and position of the avicularia.

*Occurrence.* Western and eastern Atlantic (Florida, West Indies; Cape Verde Islands to Spitzbergen), Arctic, Mediterranean. It occurs at depths of 50 to 3700 m in the Atlantic and down to 1300 m in the Mediterranean. From the fossil record, it is known back to the Upper Miocene, especially in the Mediterranean region.

Family SCHIZOPORELLIDAE Jullien *in* Jullien and Calvet, 1903  
 Genus CHARACODOMA Maplestone, 1900

*Characodoma bifurcatum* (Waters, 1918)

Plate 3, figure 6

- 1918 *Lepralia bifurcata* Waters, p. 96, pl. 12, figs 2-4.  
 1957 *Characodoma bifurcatum* (Waters); Harmer, p. 1006, text-fig. 109; pl. 68, figs 34-36.

*Material.* Vasfi 2 (2), 8 (1).

*Morphology.* Colony vinculariiform; autozoecia quadrangular, with granular frontal; aperture subcircular, limited by two small cardelles in its lower part. One small rounded avicularium is situated on each side of the aperture.

*Occurrence.* *C. bifurcatum* has only been reported before from the Mediterranean, at depths of about 90 m (Waters 1918; Poluzzi and Rosso 1988) and from the Pacific Ocean (Indonesia), at depths of 59–82 m (Harmer 1957). It is most probably a very rare species, both as a fossil and in the Recent.

Family ESCHARELLIDAE Levinsen, 1909

Genus JACULINA Jullien *in* Jullien and Calvet, 1903

*Jaculina tessellata* Hayward, 1979

Plate 3, figures 7–8

1979 *Jaculina tessellata* Hayward, p. 64.

1981 *Jaculina tessellata* Hayward; Hondt, p. 36, pl. 5, figs 4–6.

*Material.* Vasfi 2 (19), 3 (1), 6 (2), 8 (1).

*Morphology.* Colony reteporiform; cylindrical biserial branches joined by thin transverse tubular trabecules; autozoecia subrectangular with a smooth frontal wall; aperture orbicular, incised by a small round sinus. A long and thin mucro is situated on the proximal lip; it bears a small avicularium near its base; dorsal wall smooth, with rare small elliptical avicularia.

*Occurrence.* Eastern Atlantic (Bay of Biscay and Gulf of Cadiz, at depths between 355 and 463 m), Mediterranean (500–509 m). It has only been reported once as fossil, from a Mediterranean Würmian thanatocoenosis (Rosso 1990). This species has not been described before by many authors. Its ecology is also little known.

Genus PALMICELLARIA Alder, 1864

*Palmicellaria elegans* Alder, 1864

Plate 3, figure 9

1864 *Palmicellaria elegans* Alder, p. 100, pl. 2, figs 1–4.

1880 *Palmicellaria elegans* Alder; Hincks, p. 378, pl. 31, figs 7–9.

1962 *Palmicellaria elegans* Alder; Gautier, p. 203.

1979 *Palmicellaria elegans* Alder; Hayward and Ryland, p. 130, text-fig. 50.

1986 *Palmicellaria elegans* Alder; Zabala, p. 409, text-fig. 135.

1992 *Palmicellaria elegans* Alder; Reguant and Maluquer, p. 148, pl. 2, figs 1–2.

*Material.* Vasfi 1 (17), 2 (3), 5 (6), 7 (8).

*Morphology.* Colony vinculariiform; branches composed of two pairs of alternating elongate autozoecia; frontal wall smooth; aperture hidden by a flared peristome with a pointed mucro bearing a small elliptical avicularium on its upper lip. In the fossil material, the peristome is often worn and only the trace of the avicularium is visible near the sunken aperture.

*Occurrence.* Eastern Atlantic (Bay of Biscay, Shetland), Mediterranean. In the Mediterranean it occurs at depths of 50 to 1000 m. As a fossil, this species has been reported before only from the Holocene of Spain (Reguant and Maluquer 1992).

Family ADEONIDAE Jullien, 1903

Genus ADEONELLOPSIS MacGillivray, 1886

*Adeonellopsis distoma* (Busk, 1858)

Plate 3, figure 10

1858 *Lepralia distoma* Busk, p. 127, pl. 18, fig. 1.

- 1962 *Adeonellopsis distoma* (Busk); Gautier, p. 221.  
 1970 *Adeonellopsis distoma* (Busk); Hondt, p. 241, text-fig. 7.  
 1985 *Adeonellopsis distoma* (Busk); Aristegui, p. 425, text-fig. 2.  
 1986 *Adeonellopsis distoma* (Busk); Zabala, p. 391, text-fig. 126; pl. 5, figs E-F.  
 1989 *Adeonellopsis distoma* (Busk); Bishop and Hayward, p. 42, text-figs 172-176.  
 1992 *Adeonellopsis distoma* (Busk); Reguant and Maluquer, p. 145, pl. 1, fig. 9.

*Material.* Vasfi 1 (1).

*Morphology.* Colony adeoniform; autozooezia oval, with one row of marginal pores; primary aperture hidden by a distally developed peristome; frontal wall granular, with a median depression perforated by one ascopore subdivided into eight to twelve small pores; triangular avicularium on the proximal lip of the peristome. The only specimen recovered shows a higher number of ascopores than noted by several authors (eight to twelve instead of five to ten) but the other features are identical. For Gautier (1962), the fossil species *A. imbricata* (Philippi, 1844) and *A. coscinophora* (Reuss, 1848) could be identical to *A. distoma*.

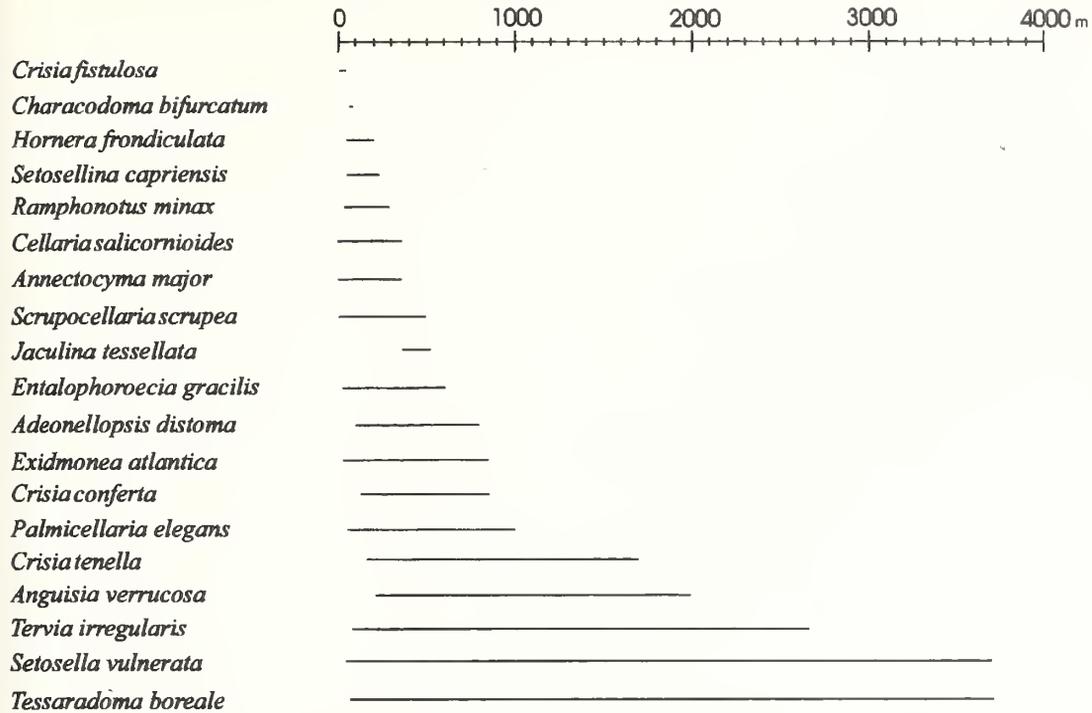
*Occurrence.* Eastern Atlantic (from Madeira to Brittany), Mediterranean, Indian Ocean. This species was found in the Atlantic at depths from 94 to 787 m. In the Mediterranean it is from somewhat shallower depths (100 to 480 m). In the fossil record, it has been reported from the Pliocene of the North Sea basin and from the Holocene of Spain.

#### BRYOZOAN DISTRIBUTION IN THE SECTIONS AND BATHYMETRY

A total of 39 samples was taken from the deep-water marls of the three sections and many of them yielded at least some bryozoan fragments. Only 21 species were found in the collected material: 11 cyclostomes, five anascan cheilostomes, and five ascophoran cheilostomes. Although most of the 19 extant species have a wide bathymetric range (Text-fig. 5) information about depth of deposition may be gathered when combining data for each species (presence/absence and abundance).

In the Vasfi section, all samples yielded at least some bryozoan fragments (Text-fig. 2), but sample four is very poor with only one specimen belonging to *Cellaria salicornioides*. The number of species (19) is moderate: nine cyclostomes, five anascan cheilostomes, and five ascophoran cheilostomes. Erect zoarial types largely predominate with 11 vinculariiforms (*Ramphonotus minax* is in fact a pseudovinculariiform), three cellariiforms, one adeoniform, and one reteporiform, but three membraniporiforms, also occur with very few specimens. The best represented are *Crisia tenella*, *Anguisia verrucosa*, *Scrupocellaria scrupea* and *Jaculina tessellata*. Four other species are less abundant: *Tervia irregularis*, *Setosellina capriensis*, *Palmicellaria elegans* and *Exidmonea atlantica*. Some of the species are only present, or best represented in the *Lophelia* beds: *Tervia irregularis*, *Entalophoroecia gracilis*, *Annectocyma major*, *Tessaradoma boreale* and *Palmicellaria elegans*. From the known bathymetric ranges of the extant species, depths of about 500 to 600 m are inferred for the marl beds, and about 300 to 400 m for the intervening *Lophelia* beds (*Annectocyma major*, a shallower water species, occurs only there). A shallowing probably occurred during the deposition of the upper part of the topmost marl bed (sample eight) with reduction in the number of fragments belonging to deeper water species and appearance of *Hornera frondiculata* (but this species could also have been reworked by bioturbation from the coquina).

In the deep-water part of Cape Vagia section (samples eight to twenty-four of Text-fig. 3) bryozoans are not common and ten samples (most of them corresponding with laminated marl) are barren. The ten species found in this section (eight cyclostomes and two anascan cheilostomes) are represented by a small number of fragments. With the exception of one membraniporiform species (*Annectocyma major*, very poorly represented in the last sample), only erect zoarial types occur: five cellariiforms and four vinculariiforms. Four species are relatively abundant: *Anguisia verrucosa*, *Crisia conferta*, *Crisia* cf. *fistulosa* and *Crisia tenella*. On the basis of the known bathymetric ranges of extant bryozoan species, a depth of 300 to 500 m is suggested for the deposition of the major part



TEXT-FIG. 5. Known bathymetric ranges of the extant bryozoan species found in the Plio-Pleistocene deep-water marls of Rhodes.

of the marls, a shallowing occurring near the top of the section (with shallower water species like *Crisia* cf. *fistulosa* and *Annectocyma major*).

Among the 13 samples taken from the marls in Lindos Bay section, two are completely barren of bryozoans (samples six and seven in Text-fig. 4) and only ten species were found (eight cyclostomes and two anascan cheilostomes). All belong to erect types: vinculariiform (five) and cellariiform (five). Two species (*Anguisia verrucosa* and *Crisia conferta*) are relatively abundant and occur in all or almost all samples. Depths of deposition of 300 to 500 m are indicated by the extant species, with a shallowing to about 200–300 m near the top of the section (presence of *Hornera frondiculata*, and increase in the number of fragments belonging to *Cellaria salicornioides* and *Scrupocellaria scrupea* in the topmost sample).

The indications given by some of the species are dubious, however, since they may either have been displaced from relatively shallow waters (*Hornera frondiculata* is an example), or their exact bathymetric distribution is not properly known. This could be the case of *Crisia* cf. *fistulosa*, *Setosellina capriensis* and *Characodoma bifurcatum*. The reported depth range of *Crisia fistulosa* (5 to 40 m) is definitely too shallow for these deposits, but the corresponding specimens have not been identified with certainty and, if not transported, could belong to another, deeper species or, alternatively, the inferior limit would be lowered with new records for deep-water stations. The depth ranges of *Setosellina capriensis* (55–240 m) and *Characodoma bifurcatum* (59–90 m) are relatively limited and other findings of these rare species could indeed widen their real bathymetric distribution.

#### DISCUSSION

The main features of the deep-water bryozoan faunas studied may be summarized as the following:

- small number of species (one to 11) and fragments (one to 63 but mostly about five) in each 100–500 g sample;
- predominance of the cyclostomes over the cheilostomes (in number of species, eleven to ten, but above all in number of fragments);
- equal number of anascan and ascophoran cheilostomes species;
- strong predominance of erect colonies, rigid or articulated (mainly vinculariiform and cellariiform, but also adeoniform and reteporiform);
- very small number of encrusting species and colonies (setoselliniform and rarer membraniporiform);
- complete absence of mostly shallow-water zoarial forms (catenicelliform and celleporiform, but also lunulitiform);
- lack of conescharelliniform species.

Recent bathyal and abyssal bryozoans (Schopf 1969*b*; Hayward 1979; Cook 1981; David and Pouyet 1986; Gordon 1987) are also represented mainly by erect zoarial forms, with rooted species (cellariiform and conescharelliniform) predominating on the particulate substrates generally occurring in deep-water settings. In the absence of adequate hard substrates, typical encrusting colonies (membraniporiform) are rare and are instead replaced by the deeper setoselliniform morphotype with spiral growth on sand grains or small shell fragments. Among the cheilostomes, anascans are, however, more numerous than ascophorans, and cheilostomes always considerably outnumber cyclostomes, especially in deeper stations (> 1000 m).

Various features of the deep-water Plio-Pleistocene bryozoan fauna from Rhodes (notably abundant cyclostomes and anascan cheilostomes) suggest that deposition took place in the upper-bathyal zone, not deeper than 600 m. Although often found in deep-water assemblages from the Miocene and early Pliocene (Cook 1981; Moissette 1993), conescharelliniform species later disappear from the Mediterranean and so are absent here.

It is difficult to give an absolute depth for the faunas described here, because of the incomplete information about the Recent depth distribution of many of the bryozoans. It is also noteworthy that among the 19 extant species from Rhodes, almost all have a wide bathymetric range: from a few tens of metres to several hundred or even thousand metres (Text-fig. 5). The sporadic occurrence of shallow-water species is best explained by the washing in of such forms from the steep coast; Rhodes does not have a real shelf; depths of 4000 m are commonly found close to the coast, and this makes it difficult to use depth criteria developed for more normal coastal profiles. These species are therefore disregarded in the calculation of the depth of deposition. The relative abundance in a number of samples of mostly deep-water species such as *Crisia tenella*, *Anguisia verrucosa* and *Jaculina tessellata* is considered however to indicate depths of about 200–600 m. Moreover, no deep stenobathic species were found here, as are generally reported from greater depths (> 600 m) in various oceans (Hondt 1975, 1981; Hondt and Schopf 1984; David and Pouyet 1986; Gordon 1987). On the other hand, some indicators (high percentage of planktonic foraminifera, presence of *Lophelia*, *Zoophycos*, and numerous pteropods) point to deeper waters than suggested here.

Harmelin and Hondt (1993) noted that in the Mediterranean there is an upward shift in the depth distribution for some bryozoans. This is particularly the case here since most of the 19 extant species show a deeper depth range in the Atlantic than in the present-day Mediterranean (Harmelin and Hondt 1993). In the Recent, trophic factors, temperature and salinity are responsible for the partial exclusion of deep Atlantic species from the Mediterranean. However, during certain periods of time during the Pliocene and the Pleistocene, exchange of water through the Straits of Gibraltar may have been easier, thus permitting the penetration of bathyal species even into the eastern Mediterranean, where they were able to descend to greater depths. This phenomenon is also observed in various calcified anthozoans, molluscs, brachiopods, crinoids, and serpulid worms, and could be the result of massive cold-water influxes from the Atlantic into the Mediterranean during lower temperature episodes of the Pliocene and Pleistocene, at times when the Mediterranean presented different hydrological features, and when the Straits of Gibraltar were deeper and wider (Barrier *et al.* 1989).

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# BIOHORIZONS AND ZONULES: INTRA-SUBZONAL UNITS IN JURASSIC AMMONITE STRATIGRAPHY

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**ABSTRACT.** Intra-subzonal units, known collectively as 'horizons', are employed in Jurassic ammonite stratigraphy. Two basic types of 'horizon' are used by different authors. In France the unit is commonly employed as a sub-subzonal division which can be termed a 'zonule'. In Britain and Germany, however, the intra-subzonal unit typically used is more closely comparable to a faunal event. These faunal or 'biohorizons' are analogous to the *hemerae* of S. S. Buckman. Zonules, therefore, have a significant time duration, whereas biohorizons have a negligible duration but typically a significant inter-biohorizon time interval. As intra-subzonal units 'horizons' offer the potential for much finer scale correlation of marine Jurassic successions than is possible by any other means. The average zonule duration or biohorizon-plus-gap duration currently possible for the British Jurassic is around 200000 years. Nevertheless, calculations of average duration on a stage by stage basis in the Jurassic suggest that at some levels this figure may be as little as 80000 years.

IN Jurassic chronostratigraphy, a system of chronozones derived from ammonite biozones is used very effectively for correlation purposes. These 'Standard Zones' are discussed fully by Callomon (1965, 1985*b*) and Callomon and Donovan (1974) and their division into subzones is a result largely of historical considerations (the creation of new subzones within existing zones achieves a degree of nomenclatural stability at zonal level).

Jurassic ammonite stratigraphy has now developed beyond the level of subzones to yet smaller divisions known generally as 'horizons'. The origins of the concept of horizons lie essentially in the *hemerae* of S. S. Buckman (1893, 1902). Buckman (1893, p. 479) noted that 'Ammonites have been chosen as the indicators of horizons [in a general sense] and their rapidity in development makes them peculiarly suitable. Therefore, as far as possible, the chronological unit and the ammonite species should go together.'

Buckman had worked on the Middle Jurassic limestones of the Inferior Oolite Group (Aalenian, Bajocian and lowest Bathonian stages) in Dorset and south Somerset and, through very careful layer by layer ammonite collecting, established a very detailed faunal sequence (Buckman 1893). The Inferior Oolite sequence is, however, highly condensed in this area and no one locality contained a complete faunal succession. Many locally developed non-sequences are present and only by considerable cross-correlation was it possible for Buckman to reconstruct a more complete sequence. He realized that the local successions were full of stratigraphical gaps and that each layer with a distinctive ammonite fauna was actually, or probably, separated from others by a time-gap of unknown duration. Each ammonite-bearing layer therefore represented a discrete package of sediment formed during a very short period of geological time.

To use these faunas as correlation tools Buckman (1893, p. 481) created the concept of the 'hemera', taking the name from a Greek word meaning 'day' or 'time'. Each useful fauna from his sequence he identified as belonging to a distinct hemera noting (Buckman 1893, p. 481) that 'successive hemera [*sic*] should mark the smallest consecutive divisions which the sequence of different species enables us to separate in the maximum development of strata.' Unfortunately, however, Buckman managed to discredit much of his early work when he started to derive hypothetically and sometimes inaccurately (e.g. Buckman 1909–1930) hemeral sequences for other parts of the Jurassic.

In the 1920s and 1930s the study of more complete stratigraphical successions than the Inferior Oolite enabled an analogous sequence of small correlative units to be developed by W. D. Lang and

L. F. Spath, for the Lower Jurassic of the Dorset coast (Lang *et al.* 1923, 1928; Lang and Spath 1926). Variably termed 'zones' or 'horizons', these divisions were recognized by the restricted vertical ranges of various nominal ammonite taxa within mudrock-dominated successions of the Lower Lias Group (Hettangian to Lower Pliensbachian stages). Unlike Buckman's hemerae, the small divisions of Lang and Spath formed a continuous stratigraphical sequence with no gaps or overlaps and were therefore effectively rock units, and not time units like hemerae. Later workers, however, such as Spath (1942) and Dean *et al.* (1961), grouped these locally recognizable divisions into larger and stratigraphical coarser units of wider geographical applicability.

The potential to recognize finer correlative divisions than established standard zones and subzones would allow was, however, still recognized. For instance, Callomon (1963, p. 44), in a discussion of the Lower Pliensbachian genera *Liparoceras* and *Beaniceras*, described four successive and clearly distinguishable faunas. These were separated formally as 'Horizons' I to IV. As units identified by discrete faunas, Callomon's horizons were therefore analogous to Buckman's hemerae.

Subsequent development of horizons as intra-subzonal units has, however, been primarily as sub-subzonal units closest to 'conventional' zones and subzones (i.e. very similar to the units used by Lang and Spath for the early Jurassic). This work has been pursued primarily in France and examples are included in Mouterde *et al.* (1970), Cariou (1985) and Corna (1987). Phelps (1985) employed the name *zonule* to distinguish this type of sub-subzonal unit, a term defined by Hedberg (1976) as the smallest division of a chronostratigraphical scale (although the term itself was originally proposed by Fenton and Fenton 1928).

Units analogous to those proposed by Buckman (1893, 1902) have also been used periodically, but often only for specific correlatable faunas within a more conventional zonal sequence (for instance by Callomon 1963 and Callomon and Sykes 1975). It is only relatively recently, however, that this type of unit has once again been used to construct complete correlative sequences. Typically referred to as 'faunal horizons' or 'biohorizons', their use is discussed by Callomon (1985a) and Page (1992) and several schemes are now available for stages or substages of the Jurassic (e.g. Callomon *et al.* 1989; Callomon and Chandler 1990; Dommergues *et al.* 1994).

#### THE NOMENCLATURE AND CHARACTER OF 'HORIZONS'

As discussed above, 'horizons', as quoted in Jurassic ammonite stratigraphy, belong to two basic types:

*Biohorizon* (= '*Faunal Horizon*'). A bed or series of beds characterized by a fossil assemblage within which no further stratigraphical differentiation of the fauna (or flora) can be made (Callomon 1985a), i.e. a biohorizon is effectively defined at both its base and top in a single reference section. Callomon (1985a) suggested that the time equivalent of the chronostratigraphical division of biohorizon could be 'hemera' (this is fully compatible with Buckman's earlier usage of that term). The term biohorizon is preferred here to 'faunal horizon' or simply 'horizon' as its meaning is less potentially ambiguous.

*Zonule*. The smallest component sub-division of a chronostratigraphical hierarchy, defined, as with higher divisions, by a basal boundary stratotype. The term was first applied to standard zonal ammonite stratigraphy by Phelps (1985). Whereas biohorizons tend to be more locally recognizable, Phelps (1985, p. 342) suggested that a sequence of zonules should ideally be useable throughout a palaeobiogeographical province, as are standard zones and subzones.

Biohorizons obviously, therefore, have a number of properties which make them different from conventional chronostratigraphical units, as already noted by Page (1992, p. 134):

1. The recognition of a *biohorizon* is intimately related to the identification of the index *transient species*. A transient is equivalent to a sub-chronospecies, the smallest distinguishable segment of a continuously evolving lineage. Similarly, a biohorizon is the smallest palaeontologically correlatable

segment of geological time. Only the occurrence of diagnostic transient species can confirm the presence of a particular biohorizon, but the general generic or specific composition of a fauna can be a useful guide to recognition.

2. Biohorizons represent discrete but typically very short intervals of geological time, the actual duration of which is not known but is identical to and varies with the times taken to deposit the various defined fauna-containing beds.

3. As the boundaries of most successive biohorizons are not coincident, a significant time gap is potentially present and is shown as an interval between successive units on any correlation diagram.

4. A sequence of biohorizons is established by first constructing a succession of faunal assemblages, and then distinguishing geographically persistent or morphologically distinct associations. These faunas can then form the basis for a defined sequence of biohorizons.

5. Once established, the sequence of defined biohorizons can be integrated with the existing scheme of standard subzones. Nevertheless, the current state of stratigraphical knowledge inevitably means that a subzone may: (a), contain no defined biohorizons; (b), be, for practical purposes, more or less equivalent to a single biohorizon; (c), contain one or more biohorizons, the base of the lowest defining the base of the subzone; or (d), contain one or more biohorizons which may be demonstrably younger than the defined base of the subzone.

6. Biohorizons are usually named in a dual manner, firstly by consecutive numbering and secondly by selecting a suitable transient species as an index.

#### CORRELATING BIOHORIZONS, AND THE LINK WITH ZONULES

Correlation between different biohorizon schemes is more exacting than the correlation between standard zonal schemes in that:

1. Both the bases *and* tops of each biohorizon can be correlated.

2. The intervals between biohorizons can be as important in correlation as the biohorizons themselves. They may also be correlatable in the same way as biohorizons.

3. A biohorizon can be correlated exactly with another by linking their bases and tops. In other instances, however, the correlated unit may be a biohorizon *plus* the interval below and/or the interval above, or even a sequence of biohorizons (which would inevitably include one or more intervals in the correlation).

4. Following on from the above, every line on the correlation diagram has a very specific meaning and may require some discussion in accompanying text; this is the approach followed by Dommergues *et al.* (1994).

5. Exactly correlated biohorizons (e.g. with linked bases and tops) form, to all intents and purposes, time planes, and can be considered as being equivalent to events in event stratigraphy (Callomon 1985a; Page 1992). These faunal events can form extremely valuable inter-regional correlative datums.

The great value of the construction of a sequence of biohorizons is that it effectively defines the observed succession of faunas. As noted by Buckman (1893, p. 481), it is this detailed basic information on faunal sequences which is so important to any future work: '...it may be remarked that the more minute the correlation the better for the student; he can easily dispense with detail; but if such detail as he does need be not given in any paper, he searches in vain for information.' Unfortunately it is this basic information that is so often lacking in many classical works and the contractions of the faunal sequence that are zones and subzones are quoted in discussions of stratigraphy, phylogeny and evolution as though they are the ultimate in resolvable chronology.

Intra-regional or international correlation of biohorizon sequences will establish those units suitable to form the basis for the definitions of a sequence of zonules. As noted previously, zonules should ideally be recognizable throughout a palaeobiogeographical province, as are subzones. The creation of new sub-divisions of existing sequences of standard subzones at the level of zonules helps maintain a degree of nomenclature stability, by removing the necessity to tamper with familiar zonal



and subzonal names and successions in order to achieve an increase in potential correlative resolution. Each defined zonule could contain one or more biohorizons, one of which may or may not be coincident with its defined base (identical to the biohorizon/subzonal relationship described above).

#### THE NATURE OF BIOHORIZONS

It is a remarkable feature of many biohorizons just how widely geographically they can be recognized. For instance, the basal Callovian *kepleri* Horizon of Callomon *et al.* (1989), characterized by the kosmoceratid *Keplerites kepleri* (Oppel) is recognizable in southern England, Germany, Switzerland and also Georgia and East Greenland. The *kepleri* Horizon is an extreme example but several other biohorizons in the Lower Callovian are also recognizable in Britain and Germany (Callomon *et al.* 1989; Mönning 1989), and Britain, south-eastern and eastern France have many Sinemurian biohorizons in common (Dommergues *et al.* 1994).

As noted by Mettraux *et al.* (1992) there is an interplay of supra-regional, regional and local processes underlying these distributions, but it is not always possible to determine readily exact causes. Biological, sedimentological and tectonic effects are involved, but although potential factors may be diverse, a number of key processes appear to facilitate the recognition of most biohorizons. These key processes or factors are:

1. The evolution of one or more ammonite populations/lineages within the biogeographical province under study, leading to the development of distinguishable transients (i.e. sub-chronospecies).

2. The evolution and divergence of related ammonite populations within the basin or province under study (e.g. branching of a lineage or 'true' speciation).

3. The evolution of an ammonite lineage (e.g. genus) present in the province under study, in an adjacent province (or a separated area of the same province), followed by the migration of the new form into the study area (with or without the survival of the local, related population).

4. The presence of morphologically complex and 'rapidly evolving' groups. It is easier to characterize small changes in successive populations of highly ornamented genera than it is to separate successive faunas of morphologically 'simpler' groups. As a consequence, highly ornamented genera will tend to have more distinguishable transients over a given stratigraphical interval than relatively morphologically simpler genera, and therefore will facilitate the recognition of a greater number of biohorizons.

5. The migration into the area being studied, from another basin or province, of a 'new' ammonite population/lineage (i.e. a lineage not present in the immediately preceding biohorizon). This migration may be short-lived (e.g. one transient/biohorizon duration) or may lead to the establishment of a 'local', possibly evolving, population (e.g. surviving for one or more biohorizons).

6. Changes in faunal composition including 'acme-events' (including dominance) of certain lineages, presumably resulting usually from environmental or ecological changes.

7. The periodical or occasional preservation of suitable ammonite faunas resulting from fluctuating or cyclic sedimentary processes, e.g. due to turbiditic sedimentation or Milankovitch cycle-driven sedimentary rhythms.

It is the action of ecological, sedimentological and tectonic controls which preserve snapshots of the basic underlying evolutionary processes listed first above (factors 1-4). The most common and typical combined factors facilitating the recognition and correlation of biohorizons are:

(a). The morphological evolution of an ammonite population in the basin/province under study and the periodical preservation of faunas, thereby leading to the easy separation of successive

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TEXT-FIG. 1. Diagnostic faunal events underlying the identification of Upper Sinemurian biohorizons in Britain (N.B. complete ranges of taxa not shown). The biohorizonal scheme is that of Dommergues *et al.* (1994). Bracketed numbers indicate the nature of the 'event' or process as described in the text under 'The Nature of Biohorizons'.

Stage/Substage		Duration after Harland et al
Tithonian	Portlandian/Volgian	6.5
	Upper Kimmeridgian	
Lower Kimmeridgian		2.6
Upper Oxfordian		2.4
Middle Oxfordian		
Lower Oxfordian		
Upper Callovian		4.2
Middle Callovian		
Lower Callovian		
Upper Bathonian		4.8
Middle Bathonian		
Lower Bathonian		
Upper Bajocian		7.4
Lower Bajocian		
Aalenian		4.5
Upper Toarcian		9
Lower Toarcian		
Upper Pliensbachian		7.5
Lower Pliensbachian		
Upper Sinemurian		9
Lower Sinemurian		
Hettangian		4.5

Zonal Divisions in Britain	Horizons, etc: Britain	
	No. of Potential Divisions	Average Duration
11 SB	13 SB	210,000 years
11 SB	18 SB	
5 SB	17 SB	153,000
7B / 6SB	11B / 9SB	90,000
4B / 4SB	7B / 5SB	
5 SB/B	7 SB	
5 SB	5 SB	120,000
4 SB	7 SB	
8 SB	19 SB	321,000
4 SB	5 SB	
4 SB	4 SB	
9 NW	9 NW	264,000
9 NW	19 NW	
9 NW	11 NW	281,000
7 NW	11 NW	290,000
9 NW	20 NW	
5 NW	10 NW	214,000
10 NW	25 NW	
9 NW	41 NW	120,000
8 NW	34 NW	
6 NW	18 NW	250,000

Zonal Divisions in France	Zonules, etc: France	
	No. of Potential Divisions	Average Duration
9 SM	9 SM	722,000 years
11 ?SB	27 ?SB	96,000
4 SM	12 SM	80,000
6 SM	9 SM	
5 SM	9 SM	
4 SM	10 SM	135,000
5 SM	10 SM	
4 SM	11 SM	267,000
6 SM	8 SM	
4 SM	6 SM	
4 SM	4 SM	352,000
6 SM	18 NW	
4 NW	11 NW	281,000
9 NW	16 NW	
13 NW	17 NW	310,000
6 NW	12 NW	
6 NW	18 NW	188,000
10 NW	22 NW	
9 NW	41 NW	155,000
8 NW	17 NW	
6 NW	12 NW	375,000

TEXT-FIG. 2. For legend see opposite.

transients (i.e. morphological intermediates between observed transients are absent or rare because of non-preservation).

(b). The migration of a 'new' ammonite population into the basin/province under study as a result of the removal of barriers to migration. Migration may be short-lived or may lead to long or short-term establishment of a resident population which evolves and is preserved as above.

As an example of evolutionary and ecological factors in operation, Text-figure 1 shows the Upper Sinemurian biohorizonal sequence proposed by Dommergues *et al.* (1994) interpreted in terms of the key faunal events which facilitate the recognition and correlation of each biohorizon in Britain.

Dommergues and Meister (1991) have further investigated the frequency with which late Sinemurian and early Pliensbachian biohorizons could be recognized in a broader North-West European context and observed phases in which biohorizons were recognizable primarily at basin margins and phases when a basin centre distribution was more apparent. Concluding, Dommergues and Meister (1991, p. 978) noted that factors such as sea-level change, taphonomy and ecological considerations may be controlling these distributions and speculated that 'the comparison with sequence stratigraphy can probably be a valid research program in the future.'

### THE DURATION OF HORIZONS

As intra-subzonal units, the average duration of zonules and the average biohorizon-plus-interval duration, must be, geologically speaking, very short. Callomon (1985*a*) estimated an average figure for this in the Jurassic of 120000 years, based on a general estimation of the number of horizons the system could potentially contain.

There are two great problems with such estimations: firstly, biohorizon and zonule schemes are only available for relatively few stages; and secondly, the available radiometric time scales are relatively crude. The Harland *et al.* (1990) time scale provides a 'standard' framework for estimating the duration and interval length, but tie-points linking radiometric ages directly to the chronostratigraphical scale are few and only five could be used by Harland *et al.* (1990) for the Jurassic, namely at the Tithonian/Berriasian (i.e. Tethyan Jurassic/Cretaceous) boundary (145 Ma), the Kimmeridgian/Oxfordian boundary (153.5 Ma), in the 'mid Bajocian' (168.2 Ma), at the Sinemurian/Hettangian boundary (203.5 Ma) and at the Rhaetian/Norian boundary (within the Upper Triassic; 210.5 Ma). The net result is that stage length and even the position of the base of the Jurassic are frequently 'guestimated' using an averaged figure for the duration of standard ammonite zones. This is obviously highly unsatisfactory and one can only await the development of better Jurassic time-scales. Nevertheless, taking the Harland *et al.* (1990) figures for stage duration as a 'standard' for comparison one can attempt to get some idea of potential relative stratigraphical resolution for each of the Jurassic stages.

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TEXT-FIG. 2. Number of conventional zonal divisions (mainly subzones) compared with actual or potential minimum number of horizons for Jurassic stages and substages in Britain and France (see discussion in text). Estimated average zonule duration or inter-biohorizon interval shown. Abbreviations of faunal provinces: NW = North-West European Province; SM = Sub-Mediterranean Province; SB = Sub-Boreal Province; B = Boreal Province. Sources of information as follows: Hettangian – Lang (1924), Donovan (1956), Whittaker and Green (1983), Bloos (1985), Mouterde and Corna (1991), pers. obs.; Sinemurian – Corna (1987), Corna *et al.* (1991), Page (1992), Dommergues *et al.* (1994), pers. obs.; Pliensbachian – Lang (1928), Howarth (1955, 1956, 1957), Dommergues (1979), Phelps (1985), Dommergues *et al.* (1991). Toarcian – Dean (1952), Howarth (1962, 1973, 1978), Elmi *et al.* (1991), pers. obs.; Aalenian – Contini (1969), Callomon and Chandler (1990), Contini *et al.* (1991*b*). Bajocian – Callomon and Chandler (1990) with later additions for Upper Bajocian (unpublished enclosure with reprints), Contini *et al.* (1991*a*); Bathonian – Arkell (1951–1959), Torrens (1974, 1980), Dietl and Callomon (1988), Westermann and Callomon (1988), Mangold (1991); Callovian – Callomon (1968), Cariou (1985), Callomon *et al.* (1989), Thierry *et al.* (1991), pers. obs.; Oxfordian – Arkell (1935–1948), Sykes and Callomon (1979), Callomon (1989), Cariou *et al.* (1991); Kimmeridgian – Birkelund *et al.* (1983), Hantzpergue (1989), Hantzpergue *et al.* (1991); Tithonian – Cope (1967, 1978), Casey (1973), Wimbledon (1984), Geysant and Enay (1991).

The first problem, relating to the number of 'horizons' in each Jurassic stage, is similarly unresolved. It is straightforward to calculate average durations when published schemes are available, but is obviously more problematical when these have not yet been derived. It is, nevertheless, possible to construct provisional biohorizon sequences when detailed stratigraphical descriptions are available for key ammonite-rich successions. By using such descriptions and deducing a sequence of distinguishable faunas a crude estimate of the *minimum* number of potential biohorizons can be gained.

Using the Harland *et al.* (1990) 'standard' for stage duration in years, and the figures (actual and estimated) for biohorizon or zonule number in each stage, Text-figure 2 has been constructed. This shows the relationship between the resolution available for each substage or stage with conventional zonal units (essentially subzones) and with horizons, as numbers of each unit potentially available. The possible average duration or interval length of each actual or potential horizon sequence is then given (assuming that the Harland *et al.* time scale is close to reality). British and French sequences are compared.

It will be noticed immediately that the calculated biohorizon-plus-interval or zonule duration varies greatly, between a very short 80000 years in the French Oxfordian to a much cruder 722000 years in the French Tithonian. Figures around 200000–350000 years are more typical.

A second and probably more meaningful way of looking at these figures is to attempt an estimation of average duration using the Harland *et al.* (1990) dating of tie-points as a guide. The result is as follows:

Interval	Interval duration	Estimated minimum number of 'horizons'	Average duration of zonule or biohorizon-plus-gap
Base of Kimmeridgian to top of Tithonian	8.5 My	48 (GB)	177000 yrs (GB)
		26 (Fr.)	327000 yrs (Fr.)
'Mid' Bajocian to top of Oxfordian	14.7 My	84 (GB)	175000 (GB)
		89 (Fr.)	165000 (Fr.)
Base of Sinemurian to 'Mid' Bajocian	35.3 My	175 (GB)	202000 (GB)
		154 (Fr.)	229000 (Fr.)
Base of Rhaetian (Triassic) to top Hettangian	7.0 My	18 + 4 (GB)	318000 (GB)
		13 + 4 (Fr.)	412000 (Fr.)

Notes: 1, For convenience the 'Mid' Bajocian tie-point of Harland *et al.* (1990) is taken as corresponding with the Lower/Upper Bajocian boundary; 2, in the virtual absence of latest Triassic ammonoids in Britain and France, a figure of four is used for the correlation resolution of the Rhaetic Stage, derived from the zonation of that stage in southern Europe (Tethyan Realm) of Wiedman *et al.* (1979).

These figures are likely to be more accurate values for average horizon durations and intervals than those of Text-figure 2, but many are certainly still too high as only a minimum value for horizon number is derivable for stages or substages where published schemes do not exist.

Whichever of these, or indeed any other, figures one chooses to use for average biohorizon-plus-interval or zonule duration, there is no doubt that the use of these units can increase greatly the potential resolution of correlation of marine Jurassic sequences. No other correlation method can offer this level of resolution, and certainly not over large distances. Horizons have a real potential to revolutionize all aspects of Jurassic stratigraphical practice and are certainly far more valuable to non-ammonite specialists than is perhaps currently recognized.

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APPENDIX : PUBLISHED BRITISH HORIZONTAL SCHEMES

SUBSTAGE	ZONE	SUBZONE	BIOHORIZON	
LOWER SINEMURIAN	TURNERI	BIRCHI	31: <i>cf. bordoti</i>	
			30: <i>subturneri</i>	
			29: <i>birchi</i>	
			28: <i>pseudobonnardi</i>	
			27: <i>obtusiformis</i>	
		BROOKI	26: <i>hartmanni</i>	
			25: <i>brooki</i>	
			24: <i>sulcifer</i>	
			23: <i>cf. semicostatum</i>	
			22: <i>alcinoeforme</i>	
	SEMICOSTATUM	RESUPINATUM	21: <i>Euagassiceras</i>	
			20: <i>cf. resupinatum</i>	
			19: <i>pseudokridion</i>	
			18: <i>acuticarinatum</i>	
			17: <i>Paracoroniceras</i>	
		LYRA	16: <i>bodleyi</i>	
			15: <i>lyra</i>	
			BUCKLANDI	14: <i>multicostatum</i>
				13: <i>cf. scunthorpense</i>
				12: <i>isis</i>
	11: <i>aff. isis</i>			
	10: <i>scylla</i>			
	BUCKLANDI	ROTIFORME	9: <i>kridion</i>	
			8: <i>caproinum</i>	
			7b: <i>aff. rotiforme</i>	
			7a: <i>rotiforme</i>	
			6: <i>cf. defneri</i>	
	BUCKLANDI	CONYBEARI	5: <i>conybeari</i>	
			4: <i>cf. rotator</i>	
			3b: <i>rouvillei</i>	
			3a: <i>rotarium</i>	
2b: <i>Metophioceras</i> sp. 2				
2a: <i>Metophioceras</i> sp. 1				
1: <i>cf. rougemonti</i>				

TEXT-FIG. 3. Lower Sinemurian Biohorizons (modified from Page 1992).

SUBSTAGE	ZONE	SUBZONE	BIOHORIZON	
UPPER SINEMURIAN	RARI-COSTATUM	APLANATUM	XLI: <i>donovani/simplicicosta</i>	
			XL: <i>aplanatum</i>	
			XXXIX: <i>rectiradiatum</i>	
			XXXVIII: <i>aureolum</i>	
			XXXVII: <i>macdonnelli</i>	
		RARI-COSTATUM	XXXVI: <i>meigeni</i>	
			XXXV: <i>subplicatum</i>	
			XXXIV: <i>boehmi</i>	
			XXXIII: <i>cf. intermedium</i>	
			XXXII: <i>crassicostatum</i>	
		RARI-COSTATUM	XXXI: <i>rari-costatum</i>	
			XXX: <i>rhodanicum</i>	
			DENSINODULUM	XXIX: <i>"Echioceras" sp.3</i>
				XXVIII: <i>radiatum</i>
				XXVII: <i>grp armatum</i>
	XXVI: <i>bispinigerum</i>			
	XXV: <i>lymense</i>			
	XXIV: <i>edmundi/subplanicosta</i>			
	XXIII: <i>delicatum</i>			
	XXII: <i>doris</i>			
	XXI: <i>grp bifer</i>			
	XX: <i>grp oxynotum</i>			
	OXYNOTUM	OXYNOT.	XIX: <i>driani</i>	
			XVIII: <i>gagateum</i>	
		SIMPSONI	XVII: <i>exortum</i>	
			XVI: <i>aff. glaber</i>	
			XV: <i>denotatus</i>	
	OBTUSUM	DENOTATUS	XIV: <i>fowleri</i>	
			XIII: <i>cf. undaries</i>	
			XII: <i>sagittarium</i>	
			XI: <i>aff. arnouldi</i>	
X: <i>blakei s.s.</i>				
STELLARE		IX: <i>stellare</i>		
		VIII: <i>cf. landriotti</i>		
		VII: <i>margaritoides</i>		
		VI: <i>aff. margaritoides</i>		
		V: <i>"Galaticeras"</i>		
OBTUSUM	OBTUSUM	IV: <i>obtusum</i>		
		III: <i>semicostatoides</i>		
		II: <i>cf. confusum</i>		
		I: <i>aff. confusum</i>		

TEXT-FIG. 4. Upper Sinemurian Biohorizons (from Dommergues *et al.* 1994).

SUBSTAGE		ZONE		SUBZONE		ZONULE			
DOMERIAN (pt.)		MARGARITATUS (pt.)		SUBIN- ODOSUS					
									STOKESI
CARDXIAN (pt.)		DAVOEI		FIGU- LINUM	Figulinum		Celebratum		
					Angulatum		Nitescens		
					Crescens		Monestieri		
					Capricornus		Occidentale		
					Lataecosta				
					Maculatum				
		IBEX		LURIDUM		Luridum			
						Crassum			
						Rotundum			
				VALDANI		Lepidum			
						Centaurus		Centaurus	
								Actaeon	
		Valdani		Venarense					
MASSE- ANDUM		MASSE- ANDUM		Aretiforme					
				Masseanum					
JAME- SONI									
JAME- SONI									

TEXT-FIG. 5. 'Mid' Pliensbachian Zonules (after Phelps 1985).

STAGE		ZONE		SUBZONE		BIOHORIZON		
AALENIAN		CONCAVUM		FORMO- SUMI	Aa-16: <i>acanthodes</i>			
					Aa-15: <i>formosum</i>			
					Aa-14: <i>concauum</i>			
		BRADFORDENSIS		GIGAN- TEA	Aa-13: <i>cavatium</i>			
					Aa-12: <i>decipiens</i>			
					Aa-11: <i>gigantea</i>			
		BRADFORD- ENSIS		BRADFORD- ENSIS	Aa-10: <i>bradfordsensis-similis</i>			
					Aa-9: <i>bradfordsensis-baylii</i>			
					Aa-8: <i>bradfordsensis-subcornuta</i>			
		MURCHISONAE		HAU- GLI	Aa-7: <i>murchisonae</i>			
					Aa-6: <i>patellaria</i>			
					Aa-5: <i>obtusiformis</i>			
		OPALINUM		OPALINUM	Aa-4: <i>opalinoides</i>			
					Aa-3: <i>bifidatum</i>			
					Aa-2: <i>lineatum</i>			
OPALINUM		OPALINUM		OPALINUM		Aa-1: <i>opalinum</i>		

TEXT-FIG. 6. Aalenian Biohorizons (after Callomon and Chandler 1990). Abbreviations: Opalin. = Opalinum; Obtusi. = Obtusiformis.

SUBSTAGE		ZONE	SUBZONE	BIOHORIZON	
UPPER BAJOCIAN					
SUBFURCATUM	BANKSI	POL-YGY	Bj-22:	<i>polygyralis</i>	
			Bj-21:	<i>aptous</i>	
	GARRANTIANA	TET-ACR	Bj-24:	<i>garrantiana</i>	
			Bj-25:	<i>tetragona</i>	
	PARKINSONSI	TRUBOM-EL	Bj-26:	<i>acris</i>	
			Bj-27:	<i>truelli</i>	
	SUBFURCATUM	BANKSI	Bj-23:	<i>davidsoni</i>	
			Bj-28:	<i>bomfordi</i>	
	LOWER BAJOCIAN				
	DISCITES	OVALIS	TRIGONALIS	Bj-1:	<i>politum</i>
Bj-2a:				<i>walkeri</i>	
Bj-2b:				<i>rudidiscites</i>	
LAEVUSCULA		LAEVUSCULA	Bj-3:	<i>subsectum</i>	
			Bj-4:	<i>inclusa</i>	
			Bj-5:	<i>romanoides</i>	
SAUZEI		SAUZEI	Bj-6:	<i>'ovalis'</i>	
			Bj-7:	<i>connata</i>	
			Bj-8:	<i>trigonalis</i>	
CYCLOIDES		CYCLOIDES	Bj-9:	<i>ruber</i>	
			Bj-10:	<i>laeviuscula</i>	
			Bj-11:	<i>sauzei</i>	
HUMPHRIESIANUM		HUMPHRIESIANUM	Bj-12:	<i>rhytum</i>	
			Bj-13:	<i>umbilicatum</i>	
			Bj-14:	<i>cycloides</i>	
BLAGDENI	BLAGDENI	Bj-15:	<i>humphriesianum</i>		
		Bj-16:	<i>gibbosum</i>		
		Bj-17:	<i>blagdeniforme</i>		
CORONATUM	CORONATUM	Bj-18:	<i>blagdeni</i>		
		Bj-19:	<i>coronatum</i>		
		Bj-20:	<i>banksi</i>		

TEXT-FIG. 7. Bajocian Biohorizons (after Callomon and Chandler 1990, with later additions for Upper Bajocian). Abbreviations: Bacula. = Baculata; Bomfo. = Bomfordi; Cycloi. = Cycloides; Garant. = Garrantiana; Polygy. = Polygyralis; Tetrag. = Tetragona; Truel. = Truelli.

SUBSTAGE		ZONE	SUBZONE	BIOHORIZON
LOWER CALLOVIAN				
HERVEVI	KAMPTUS	KAMPTUS	V:	<i>kamptus</i> ∞
			VI:	<i>kamptus</i> β
			VII:	<i>polyptychus</i>
			VIII:	<i>metorchus</i>
			IX:	<i>gowerianus</i>
	CURTILOBUS	CURTILOBUS	X:	<i>curtilobus</i>
			XIa:	<i>'gregarium'</i> MS
			XIb:	<i>indigestus</i>
			XII:	<i>tricophorus</i>
			XIII:	<i>galitaei</i>
CALLOVIENSE	CALLOVIENSE	XIV:	<i>calloviense</i>	
		XV:	<i>micans</i>	
		XVI:	<i>enodatum</i> ∞	
		XVIIa:	<i>difficilis</i>	
		XVIIb:	<i>enodatum</i> β	
ENODATUM	ENODATUM	XVIII:	<i>anterior</i>	
		XIX:	<i>enodatum</i> ∞	
		XX:	<i>enodatum</i> ∞	
		XXI:	<i>enodatum</i> ∞	
		XXII:	<i>enodatum</i> ∞	

TEXT-FIG. 8. Lower Callovian Biohorizons (modified from Callomon and Page in Callomon et al. 1989). Abbreviation: Galila. = Galilaei.

# BELEMNITES IN BIOSTRATIGRAPHY

by PETER DOYLE and MATTHEW R. BENNETT

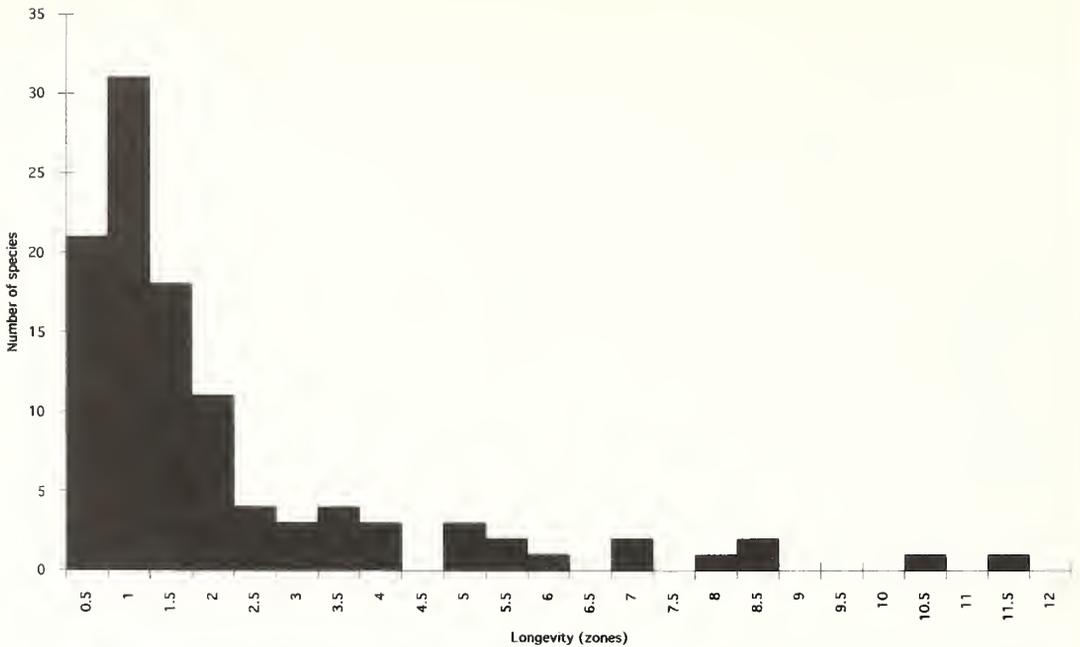
**ABSTRACT.** Belemnites are common fossils in Mesozoic sequences. They have been used as biostratigraphical tools since the nineteenth century, but the only belemnite biozonation in general use is that of the Upper Cretaceous of northern Europe. The potential for broader application of belemnites in biostratigraphy is discussed with reference to first principles. In essence, belemnites are widespread, were relatively fast evolving and largely facies independent, in addition to being relatively simple to identify, abundant and robust. Current belemnite biozonal schemes are discussed in relation to belemnite palaeobiogeographical distribution. It is clear that the greatest potential for intercontinental correlation exists at times of global expansion (e.g. the Toarcian). The scope for development of local or regional belemnite biozonations of stratigraphical value is considerable in uppermost Lower Jurassic through to Upper Cretaceous successions. These are worthy of development, if only for comparison with those based on the undoubtedly excellent, but sometimes uncommon, ammonites.

BELEMNITES have long been regarded as valuable biostratigraphical indicators. For example, William Smith (1816–1819) included at least one characteristic belemnite, *Cylindroteuthis*, from the Clunch (Oxford) Clay in *Strata Identified by Organised Fossils*. In one of the earliest comprehensive reviews of belemnites, Blainville (1827) was well aware of the potential that they had in the correlation of Jurassic and Cretaceous successions. Oppel (1856–1858) described several species which were components of his zonal scheme for the Jurassic as a whole in his monumental *Die Juraformation*. Despite these credentials, and with some notable exceptions (e.g. Lang 1928), the greatest biostratigraphical utility for belemnites has lain with Cretaceous, rather than Jurassic successions. Over the last 150 years or so, a comprehensive scheme for the Upper Cretaceous Boreal Realm (North Temperate of authors) has been developed, with some important early papers (e.g. Strombeck 1855; Schlüter 1870, 1876; Moberg 1885). Continuing research, fully reviewed in Christensen (1988, 1990), illustrates that belemnites are very powerful tools in correlating Upper Cretaceous sequences. Work on other parts of the stratigraphical column has lagged behind, but the development of a similar scheme for the Boreal Lower Cretaceous can also be traced back to the late nineteenth century (Lamplugh 1889, 1896; Pavlow and Lamplugh 1892; Stolley 1911) and research is continuing in this area (Mutterlose 1990). However, overall, relatively few belemnite biozonation schemes exist.

The aim of this paper is to review the current rôle of belemnites in biostratigraphy in order to promote their more widespread use. In order to achieve this aim, it is necessary, first, to examine the fundamental basis of the biostratigraphical utility of belemnites, and second, to review briefly the status of Jurassic and Cretaceous biozonations. This paper is intended to complement two important recent reviews (Christensen 1990; Mutterlose 1990) which have discussed in some detail the belemnite biostratigraphy of the European Cretaceous. As a consequence, the focus of the present paper is towards non-European and Jurassic sequences.

## FUNDAMENTALS OF BELEMNITE BIOSTRATIGRAPHY

In this paper, the term 'belemnite' refers to members of the order Belemnitida, and excludes the Aulacocerida (Devonian–Jurassic). The first true belemnites are considered to have evolved in the Early Jurassic (pending investigation of Triassic records from China), and are taken to have been



TEXT-FIG. 1. Histogram of belemnite species longevity for the Jurassic (Hettangian–Tithonian). Longevity is measured in ammonite biozones. Primary data taken from range charts of Riegaf (1980, 1981).

extinguished with the ammonites at the Cretaceous–Palaeogene boundary. The Bayanoteuthididae, of Palaeogene age, are considered to be dubious belemnoids in need of much further study. Most Palaeozoic records belong to the Aulacocerida.

At its simplest, a good guide or zonal fossil should, ideally, satisfy at least six basic criteria (e.g. Doyle *et al.* 1994). In general, the best guide fossils are those which are: widespread in geographical range, limited in stratigraphical range (i.e. display rapid evolution), independent of facies, abundant, readily preservable, and readily identifiable. The utility of belemnites in biostratigraphy is assessed relative to these criteria below.

### *Geographical range*

Belemnites were widespread from the latter part of the Early Jurassic (Toarcian) until the end of the Cretaceous. Prior to the Toarcian, true belemnites were restricted to Europe (Stevens 1973*a*; Doyle 1994) and are unknown from the Americas, the Southern Hemisphere, and Russia. Lower Jurassic ‘belemnites’ recorded from these areas are actually aulacocerids of the family Xiphoteuthididae (e.g. Hillebrandt and Schmidt-Effing 1981; Doyle 1988; Challinor and Grant-Mackie 1989) and are therefore excluded from this discussion, although they may also prove to be of some stratigraphical value.

Belemnites exhibit provincialism from Toarcian times onwards (Stevens 1973*a*; Doyle 1987*a*), with characteristic Boreal and Tethyan realm faunas developing early and becoming well established in the Mid to Late Jurassic (Doyle 1987*a*). This pattern continued into the Cretaceous, with periodic intermixing of faunas (Doyle 1987*a*; Mutterlose 1988), and changed to a bipolar Boreal and Austral realm pattern in the latter part of the Early Cretaceous (Doyle 1992). These patterns mean that for the pre-Toarcian record, correlation using true belemnites is limited to

Europe. Global correlation is feasible for the Toarcian onwards, but is hampered by the developing provincialism. Intra-realm correlation is possible utilizing near pandemic taxa (e.g. *Neohibolites*, *Hibolites*; Stevens 1973b), and at realm boundaries (e.g. European–Tethyan transition; Christensen *et al.* 1990, 1993).

#### *Stratigraphical range*

Belemnites appeared in the Early Jurassic (Hettangian) and became extinct in the Maastrichtian. Few studies have compiled origination rates for belemnite species, and in general there is insufficient data to estimate an average. Ernst (1964) and Schulz (1979) erected detailed belemnite biostratigraphical schemes for the Upper Cretaceous of Germany, with eight *Gomiotentis* biozones for the Santonian–Lower Campanian (Ernst 1964; Ernst and Schulz 1974) and six *Belemnella* biozones for the Maastrichtian (Schulz 1979). Using these as a basis, Christensen (1995) has estimated that the Upper Cretaceous belemnite biozones may have had durations of *c.* 0.6–0.7 million years. Data for the Jurassic and Lower Cretaceous are more sparse. In one of the few studies dealing with the belemnites from the Jurassic as a whole, Riegraf (1980, 1981) charted the development of the belemnite fauna of the Jurassic of southern Germany. An analysis of his data shows a strongly skewed distribution towards a species longevity of 0.5–1.5 ammonite biozones (Text-fig. 1). These data are crude, but illustrate that for the Jurassic at least, there is a comparable longevity of some ammonite and belemnite species.

#### *Independence of facies*

The life habits of belemnites have been the subject of speculation. Few studies have adequately set out to determine the full range of facies that contain belemnites. Recently, authors have considered that belemnites were nekto-benthic in habitat (e.g. Martill *et al.* 1994). It is clear, however, that their rostra are found commonly in a wide range of facies: in Britain alone, belemnites are abundant in nearshore coarse clastics (e.g. Bearreraig Sandstone Formation, Bajocian), condensed limestone sequences (e.g. Marlstone Rock Formation, Pliensbachian) and shelf mudrocks (e.g. Oxford Clay Formation, Callovian, and Whitby Mudstone Formation, Toarcian), and therefore belemnites may have inhabited a greater range of environments than has previously been documented.

According to Christensen (1976) and Surlyk and Birkelund (1977), Late Cretaceous belemnites of the family Belemnitellidae are common only in nearshore facies. In various nearshore carbonate facies, belemnite populations typically include all growth stages, while in offshore chalks, rostra are rarer and mainly adult. Belemnites are, however, recorded from deeper water facies; for example, Butterworth *et al.* (1988) recorded abundant belemnopseids in offshore and turbiditic facies of the Late Jurassic–Early Cretaceous Fossil Bluff Group of Antarctica. Belemnites occur in deep water facies within a similar setting within the Austral Basin of southern Argentina (Doyle, unpublished data). It is therefore possible to postulate both neritic and pelagic lifestyles for belemnites (cf. Doyle and Howlett 1989, p. 178). This may be supported on simple morphological grounds, as it is likely that belemnites were closer in life-habit to neritic/neritic–pelagic squid than the more specialized and benthic-adapted cuttlefish (Bandel and Spaeth 1988).

#### *Abundance*

Belemnites were abundant in the Mesozoic shelf seas. This is illustrated by the density of their occurrence in many successions, and their presence in a wide range of facies. Indications of this abundance are that mass accumulations of belemnite rostra are relatively common in the fossil record (Doyle and Macdonald 1993), and that belemnites and coleoids in general may well have been the staple food stocks of a range of marine vertebrates (Pollard 1968).

### *Preservation potential*

Belemnite rostra are constructed of low-magnesium calcite (Saelen 1990). They are, for the most part, robust, having served as a counterbalance to the buoyant phragmocone or as a solid support for apical fins, and they are therefore readily preservable. Dissolution of belemnite rostra would take some considerable time to achieve, and in consequence they are often associated with omission surfaces (e.g. Urlichs 1971; Jarvis 1980). Belemnites are often present where ammonites are absent, possibly as a result of the relatively fragile nature and aragonitic composition of the ammonite phragmocone. With care, belemnites may be identified at least to generic level from rostral fragments. This greatly assists in their biostratigraphical utility.

### *Recognition*

Although seemingly difficult to differentiate on morphological grounds, belemnite taxa have a relative simplicity of design which offers the potential for programmed identification of at least generic taxa. Computer programs have been designed with this in mind (R. Moore, pers. comm. 1990). Homeomorphy is subdued in belemnite genera and families, which are readily distinguished by a combination of shape characteristics and such surface features as grooves. Species are distinguished largely by shape, size, ontogenetic development and surface features (e.g. Christensen 1975, 1986). Despite conservatism in overall morphology, belemnite species are no more difficult to determine in practice than many ammonite species (Upper Jurassic perisphinctids, for example).

### *Summary*

Belemnites were widespread neritic or pelagic organisms which had a global distribution from the later Early Jurassic (Toarcian) onwards. Although relatively few studies are available, it seems clear that belemnite species on average had a longevity of 0.5–1.5 ammonite biozones. Belemnites probably inhabited shelf and deeper water environments, and occur in a wide range of marine facies. In general, belemnites are common, readily preserved, and relatively easy to recognize, or at least, no more difficult than some other guide fossils.

Belemnites are ideal guide fossils and have great potential in the development of new biostratigraphies for the Mesozoic. In view of this, the current status and areas of development for belemnite biostratigraphy are reviewed below for the Jurassic and Cretaceous. In each case, a review of the geographical distribution of the belemnites is given to illustrate problems of provincialism and, therefore, wider correlation.

## JURASSIC BELEMNITE BIOSTRATIGRAPHY

### *Palaeobiogeography*

The biogeography of Jurassic belemnites has been reviewed by Stevens (1965, 1973a), Saks and Nal'nyaeva (1966, 1975a), Stoyanova-Vergilova (1982), Doyle (1987a, 1994), Combémoré (1988), Mutterlose (1988), Doyle and Howlett (1989) and Challinor (1991).

Excluding anomalous Chinese Triassic records which require further study (Zhu and Bian 1984), it is apparent that the belemnites first appeared in Europe, and spread during the Late Pliensbachian to Toarcian interval, becoming widespread at this time (Stevens 1973a; Doyle 1987a, 1994). Although many taxa were pandemic (e.g. *Passaloteuthis*), others were endemic, particularly in the high Arctic (Saks and Nal'nyaeva 1975a; Doyle 1987a).

After the extinction of the Passaloteuthididae in the early Mid Jurassic, the development of Boreal and Tethyan faunas became well-advanced. Saks and Nal'nyaeva (1975a) distinguished Arctic and Boreal–Atlantic provinces within the Boreal Realm, dominated by the *Cylindroteuthididae*. In contrast, the Tethyan Realm, extending from the Tethyan Ocean southwards circum-Gondwana, was dominated by the *Belemnopseidae* (Stevens 1973a; Combémoré 1988;

Mutterlose 1988; Doyle and Howlett 1989; Challinor 1991). This pattern continued throughout the Mid and Late Jurassic.

### Biozonation schemes

*Lower Jurassic.* So far, only two formal belemnite biozonation schemes have been erected for the Lower Jurassic; by Stoyanova-Vergilova (1977) for eastern Europe; and Doyle (1990b) for northwest Europe. This is presumably because of the availability of ammonite schemes for this interval (Dean *et al.* 1961). Other papers discussing the biostratigraphical utility of Lower Jurassic belemnites, or giving detailed stratigraphical ranges include Lang (1928), Schumann (1974), Saks and Nal'nyaeva (1970, 1975a, 1975b), Palmer (1972), Riegraf (1980, 1981), Nal'nyaeva (1983, 1984, 1986), Riegraf *et al.* (1984), Doyle (1991) and Doyle and Mariotti (1991).

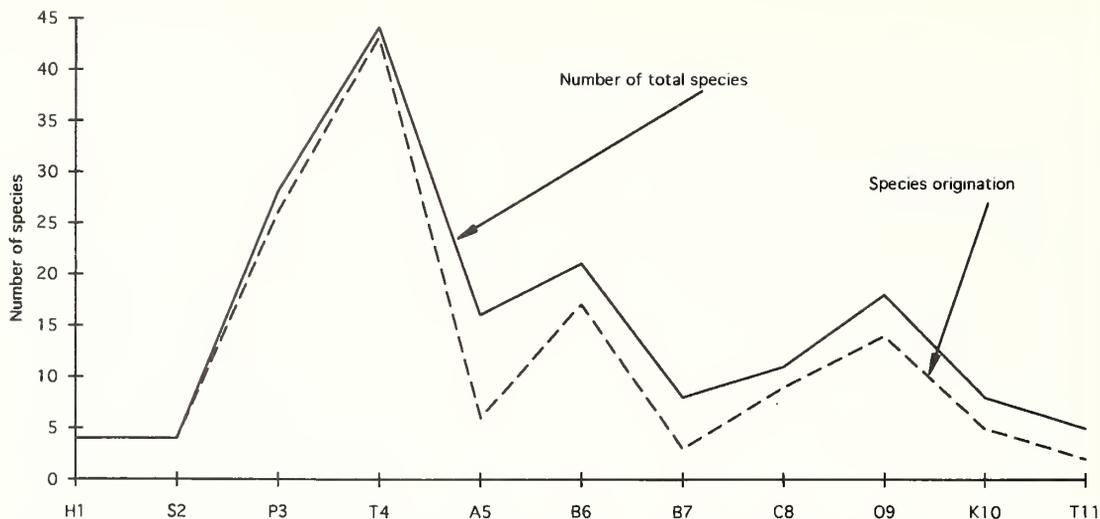
Belemnites are rare in the Hettangian, and so far the only certain record is of the simple genus *Schwegleria* in southern Germany (Text-fig. 2, Schwegler 1962; Riegraf 1980). The Sinemurian

	N.W. EUROPE	E. EUROPE	ARCTIC			GONDWANA
TOARCIAN	B BREVIFORMS	A. SUBTRICISSUS	ACROCOELITES spp.	LENOBELUS spp.	ARCOBELUS spp.	BELEMNITINA
	DACTYLOTEUTHIS spp.					
	A. VULGARIS-S. DORSALIS	ACROCOELITES spp.				
	A. TRISULCULOSUS					
PLIENSACHIAN	P. BISULCATA	P. BRUGUIERIANA				
	Ps. APICICURVATA	Ps. APICICURVATA				
SINEMURIAN	NANNOBELUS spp.	NANNOBELUS spp.				
HETTANGIAN	SCHWEGLERIA spp.					

TEXT-FIG. 2. Belemnite biostratigraphy of the Lower Jurassic. Boxes imply formally erected biozones, range bars indicate useful taxa. Compiled from numerous sources. A, *Acrocoelites*; B, *Brevibelus*; P, *Passaloteuthis*; Ps, *Pseudohastites*; S, *Simpsonibelus*.

holds more promise, with abundant faunas recorded from Europe (e.g. Schumann 1974). Across Europe, this interval is dominated by the distinctive genus *Nannobelus*, and this has prompted Stoyanova-Vergilova (1977) to erect a *Nannobelus* spp. Biozone for Bulgaria, which in practice can be extended to the rest of Europe (Text-fig. 2).

The genera *Passaloteuthis* and *Pseudohastites* (*sensu stricto*) characterize the Pliensbachian Stage (Text-fig. 2). In particular, *Pseudohastites* is an important guide fossil for the Lower Pliensbachian,



TEXT-FIG. 3. Chart of total species (solid line) and species origination (dashed line) for the Jurassic (Hettangian–Tithonian). Species origination is calculated on the number of new species appearing within a stage. Primary data taken from the range charts of Riegraf (1980, 1981). H1, Hettangian; S2, Sinemurian; P3, Pliensbachian; T4, Toarcian; A5, Aalenian; B6, Bajocian; B7, Bathonian; C8, Callovian; O9, Oxfordian; K10, Kimmeridgian; T11, Tithonian.

the distinctive and widespread species *Ps. apicicurvata* (Blainville) being particularly common and a useful guide fossil. The assemblage of taxa first described by Lang (1928) from the Belemnite Marls of Dorset has particular biostratigraphical utility (Palmer 1972). Thus apart from occurring in Europe (Dumortier 1869; Troedsson 1951; Schwegler 1962; Stoyanova-Vergilova 1977; Riegraf 1980), this distinctive fauna is recognizable in East Greenland (Doyle 1991) and Turkey (Doyle and Mariotti 1991). In Europe, the Upper Pliensbachian is distinguished by the ubiquitous species *Passaloteuthis bisulcata* (Blainville) (= *P. paxillosa* and *P. bruguieriana* of authors). Stoyanova-Vergilova (1977) defined a biozone based on this taxon which extends into the Lower Toarcian; this biozone can also be recognized in western Europe (Doyle 1990b). The biozonal index species, and the genus *Passaloteuthis* in general, migrated into Russia (Saks and Nal'nyeva 1970) and the Southern Hemisphere at this time (Stevens 1973a), indicating a possibility for intercontinental correlation with further work.

Analysis of data taken from Riegraf's (1980, 1981) study of southern German belemnites shows that species diversity and origination reached a strong maximum in the Toarcian, with falls in the Middle Jurassic (Text-fig. 3). The Toarcian belemnites have, historically, been well studied in Europe, and therefore the observed diversity may be a 'monographic' artefact of this. However, this is unlikely to be totally the case as it is clear that the Toarcian marks the first widespread geographical dispersal of belemnites outside Europe and its periphery. Thus, for the first time, there is potential for correlation outside Europe. In particular, the migrant genus *Acrocoelites* is widespread, and North European species have been recorded from North America (Doyle 1987a, Challinor *et al.* 1992) and Russia (Siberia: Saks and Nal'nyeva 1975a), although no clear identification of this taxon has been made from Gondwana. *Acrocoelites* forms the basis for the Toarcian zonal schemes of Stoyanova-Vergilova (1977) and Doyle (1990b), which are broadly comparable (Text-fig. 2). In addition, the genera *Dactyloteuthis* and *Brevibelus* (= *Brachybelus* of authors) are distinct Upper Toarcian taxa, although neither are recorded from Siberia. Siberia established itself as a major endemic centre after it was colonized by belemnites in the Toarcian. Endemic genera include members of the Pseudodicoelitidae (e.g. *Lenobelus*) and Passaloteuthididae



Belemnopsidae appeared, and similar taxa spread south into Gondwana at this time (Stevens 1965, 1973a; Challinor 1991). Little published work documents the utility of belemnites in Gondwana and Tethys at this time, and faunal links between these regions are apparent only in as much that the earliest Gondwanan *Belemnopsis* closely resemble examples from Europe (Stevens 1965), but much further study is necessary. *Belemnopsis* from the Bajocian–Callovian interval is distinct in morphology from the later Gondwanan representatives, and therefore holds potential for correlation between the Boreal and Tethyan borders and Gondwana, but much more work is needed to establish true ranges for species.

The Bathonian interval is relatively species-poor (Text-figs 3–4) in both hemispheres. The *Cylindroteuthididae* and *Belemnopsidae* dominated the Boreal and Tethyan realms respectively. In the Southern Hemisphere, endemic *Belemnopsis*-dominated assemblages began to appear (Stevens 1965). In the Boreal Realm, maximum diversity was achieved in the Arctic regions (Saks and Nal'nyaeva 1964, 1975a; Doyle 1987a; Doyle and Kelly 1988) with many species of *Cylindroteuthis* and *Pachyteuthis* (Text-fig. 4). Most were endemic, however, with few having penetrated into the Boreal–Atlantic province (northern Europe). Despite this, widespread taxa such as *Cylindroteuthis puzosiana* (Orbigny), and periodic influxes of taxa such as *Lagonibelus (Holcobeloides) beaumontiana* (Orbigny) are useful indicators in the Callovian and Oxfordian intervals. By the Kimmeridgian and Tithonian/Volgian, belemnites are only common in the Arctic province.

Little recent work has been carried out on the later Jurassic belemnites of southern Europe. Some belemnites have been recognized as having stratigraphical utility (Riegraf 1981; Combémoré and Mariotti 1986), but few comprehensive studies have been completed. Most attention has concentrated upon Gondwana with recent advances in our understanding by Combémoré (1988), Howlett (1989), Challinor (1989, 1990, 1991), and Challinor and Grant-Mackie (1989). These studies build upon the earlier synthesis by Stevens (1965) which developed the concept of a successive development of largely undifferentiated *Belemnopsis* faunas, punctuated by periodic domination by other genera, particularly *Hibolithes* (Text-fig. 4). The concept of the *Belemnopsis uhligi*-complex developed by Stevens allowed for the recognition of a widespread belemnite fauna with much potential for correlation. Recent scrutiny has demonstrated that this 'complex' may in fact be subdivided to give even greater resolution (Challinor 1989).

These works illustrate the possibility of a greater degree of correlation across the Gondwanan continents than was previously known, at least for the Upper Jurassic. For example, Challinor (1990) has recognized the importance of the southwest Pacific belemnite faunas, in Indonesia, New Caledonia and New Zealand. His finely tuned work has enabled a much greater degree of stratigraphical subdivision, and therefore correlation potential, in the south-west Pacific region than has been possible before. Howlett (1989) has identified the value of belemnites in the Antarctic Peninsula region, especially in the correlation of West Pacific faunas. This is the focus of continuing work, especially comparisons with the rich Jurassic faunas of the Antarctic Peninsula.

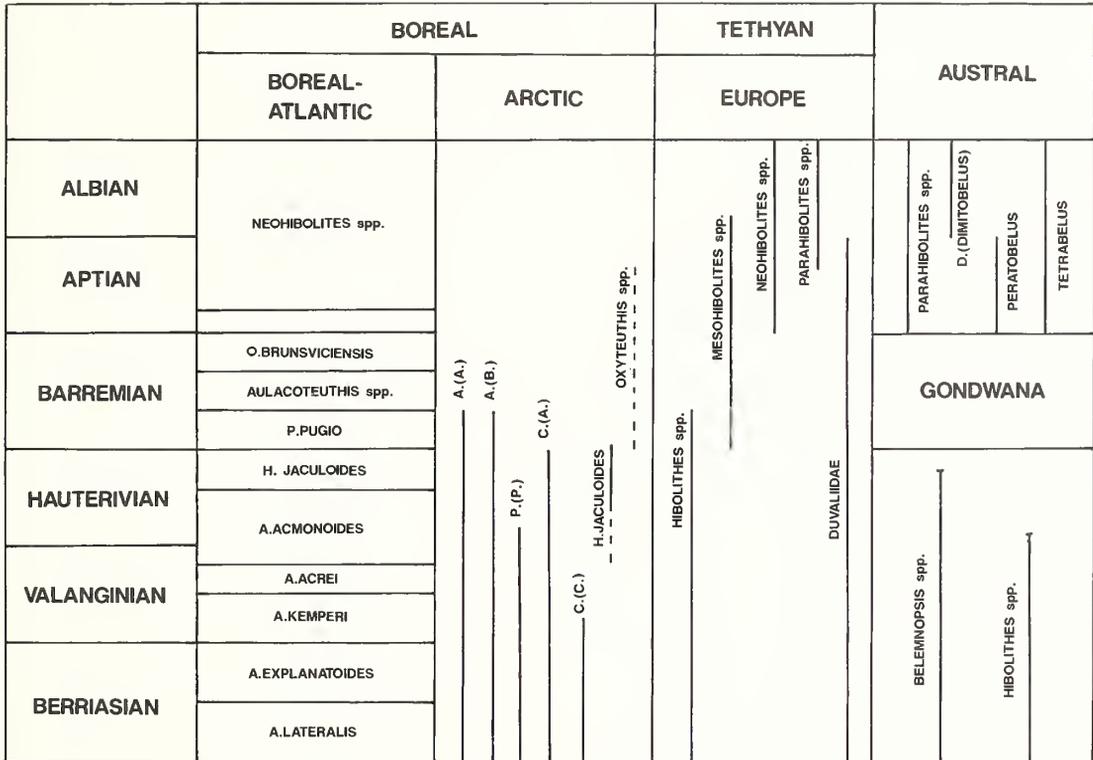
## CRETACEOUS BELEMNITE BIOSTRATIGRAPHY

### *Palaeobiogeography*

The biogeography of Cretaceous belemnites has been summarized by many authors (e.g. Stevens 1973b; Christensen 1976; Mutterlose *et al.* 1983; Mutterlose 1988; Combémoré 1988) and most recently by Doyle (1992), and therefore a detailed treatment is not necessary here. However, in brief, the pattern initiated in the Mid and Late Jurassic continued through to the Early Cretaceous (Hauterivian–Barremian) with the Boreal and Tethyan realms maintained. In the Aptian, a new, entirely endemic, austral belemnite fauna developed, centred on the *Dimitobelidae*, and by the end of the Cenomanian, the Tethyan Realm, as recognized on belemnite evidence alone, cannot be identified. For the rest of the Cretaceous, the pattern was one of an Austral Realm (the *Dimitobelidae*) with a corresponding Boreal Realm (the *Belemnitellidae*) in the north.

Biozonation Schemes

Lower Cretaceous. Biozonations for the Lower Cretaceous have been developed by Lamplugh (1889), Stolley (1911), Pinckney and Rawson (1974), Mutterlose (1983), Howlett (1989) and Challinor (1991). A belemnite biozonation for the whole of the European Lower Cretaceous has been compiled by Mutterlose (1990) (Text-fig. 5). A minor modification of this was suggested by



TEXT-FIG. 5. Belemnite biostratigraphy of the Lower Cretaceous. Boxes imply formally erected biozones, range bars indicate useful taxa. Compiled from numerous sources. A. (A.), *Acroteuthis*; A. (B.), *Acroteuthis (Boreioteuthis)*; C. (C.), *Cylindroteuthis*; C. (A.), *Cylindroteuthis (Arctoteuthis)*; D, *Dimitobelus*; H, *Hibolites*; P. (P.), *Pachyteuthis*; P. (S.), *Pachyteuthis (Simobelus)*.

Mitchell (1992). Papers dealing with the general biostratigraphical utility of belemnites in the Lower Cretaceous include Jeletzky (1964), Saks and Naľnyaeva (1964, 1966, 1975b), Rawson (1972); Combémoré (1973, 1979, 1988), Combémoré *et al.* (1981) and Mutterlose *et al.* (1987).

In Boreal regions, the Lower Cretaceous up to the Barremian is dominated by the Cylindroteuthididae. *Acroteuthis*-dominated assemblages have proved to be of the greatest utility in both Arctic and Boreal-Atlantic provinces, with several species in common (e.g. Jeletzky 1964; Saks and Naľnyaeva 1966, 1975b; Pinckney and Rawson 1974; Doyle and Kelly 1988; Mutterlose 1990) (Text-fig. 5). In the Barremian, the Cylindroteuthididae are common only in the Arctic. In Europe, a detailed biozonation is possible utilizing the Oxyteuthididae (Mutterlose 1983, 1990) (Text-fig. 5).

In the Tethys, *Duvalia* and other representatives of the Duvaliidae have proved valuable as guide fossils (e.g. Combémoré 1979) (Text-fig. 5). Recent records indicate a greater geographical

	BOREAL		TETHYAN	AUSTRAL
	N.EUROPEAN	N.AMERICAN		
MAASTRICHTIAN	BELEMNELLA CASIMIROVENSIS	B. BULBOSA   B. AMERICANA   BELEMNITELLA		D. (DIMITOCAMAX)
	B. JUNIOR			
	BELEMNELLA spp. (6 ZONES)			
CAMPANIAN	B. LANGEI	A. PRAECURSOR		D. (DIMITOBELUS)
	B. MINOR			
	B. MUCRONATA			
SANTONIAN	GONIOTEUTHIS spp. (8 ZONES)	A. GROENLANDICUS		
CONIACIAN		A. COBBANI		
TURONIAN		A. MANITOBENSIS		
CENOMANIAN	A. PLENUS	ACTINOCAMAX	NEOHIBOLITES spp.	DUVALIDAE
	A. PRIMUS			

TEXT-FIG. 6. Belemnite biostratigraphy of the Upper Cretaceous. Boxes imply formally erected biozones, range bars indicate useful taxa. Compiled from numerous sources. A, *Actinocamax*; B, *Belemnitella*; D, *Dimitobelus*.

distribution in the Tethys and Gondwana than was previously recognized for this group (Combémoré 1988; Doyle and Mariotti 1991). Inter-realm correlation of Boreal and Tethyan sequences is hampered by provincialism, but notable migrations of Tethyan taxa northwards and arctic taxa southwards at times of sea level highstand (Rawson 1973; Mutterlose 1979; Doyle 1987a; Mutterlose *et al.* 1987) provide some potential for correlation.

Perhaps the most significant belemnites for inter-regional, inter-continental and even inter-hemisphere correlation in the upper part of the Lower Cretaceous are the rather simple looking members of the genus *Neohibolites* and, to a lesser degree, *Parahibolites*. These genera have almost a worldwide distribution (e.g. Liddle 1946; Hanai 1953; Stevens 1965; Spaeth 1973, 1988; Combémoré 1988; Doyle 1987c), and are already used in the biozonation schemes of Christensen (1990) and Mutterlose (1990) (Text-fig. 5). These taxa are widespread and broadly indicative of the Aptian–Cenomanian interval in many countries (Combémoré *et al.* 1981).

In Gondwana, *Belemnopsis* and *Hibolites* dominate the Lower Cretaceous up to the Aptian, when members of the Dimitobelidae replace them (Text-fig. 5). As with the Upper Jurassic, belemnite biozonations have recently been developed by Howlett (1989) and Challinor (1990, 1991) which demonstrate the utility of belemnites in the correlation of Gondwanan successions. Challinor (1991) recognized that a succession of *Hibolites* species may have utility in the Berriasian–Hauterivian of the south west Pacific, while Crame and Howlett (1988) and Howlett (1989) have identified a late *Belemnopsis* fauna replacing *Hibolites* in the Antarctic Peninsula region in the Valanginian–Hauterivian; this may have implications for correlation with South American

successions (Text-fig. 5). From the Aptian onwards, the Dimitobelidae dominate the Cretaceous of the Southern Hemisphere (Doyle 1992). In these Gondwanan regions, distinct potential for correlation exists, with markers of both local and more widespread stratigraphical utility. Thus, *Tetrabelus willeyi* is a distinctive late Aptian marker for the Antarctic Peninsula (Crame and Howlett 1988), while *Dimitobelus diptychus* is widespread in the Albian, recorded from the Austral Basin of Argentina (Riccardi 1988), Australia (Ludbrook 1966) and Antarctica (Doyle 1987b).

*Upper Cretaceous.* A sophisticated scheme of belemnite biozones has been developed for the Upper Cretaceous, summarized most recently by Christensen (1988, 1990). These papers provide an excellent, comprehensive review and therefore the Upper Cretaceous is dealt with only briefly here. Particularly important are the refined schemes of Ernst and Schulz, erected on the basis of detailed morphological changes observed within lineages of *Goniotoothis* (e.g. Ernst 1964) and *Belemnella* (Schulz 1979). The detail of these and other biozones continues to be refined by Christensen and co-workers (papers in Christensen 1990), such that there is the possibility of widespread correlation across Europe (Text-fig. 6). Similar genera occur in North America, but species are punctuated in their stratigraphical range and are largely endemic, suggesting short-lived migrations from the North European Province (Christensen 1993). Intercontinental correlation is therefore barely possible at this time. However, recent discoveries of belemnitellids from southern France have increased the potential for correlation of Tethyan and Boreal regions (Christensen *et al.* 1990, 1993; Hancock *et al.* 1993) in the Upper Cretaceous.

In the Southern Hemisphere, records of Upper Cretaceous belemnites are relatively rare (Stevens 1965, 1973b; Doyle and Zinsmeister 1988; Doyle 1990a); dimitobelids dominate. The fullest Upper Cretaceous dimitobelid succession is in New Zealand (Stevens 1965), but most species are endemic, making correlations difficult. However, recent discoveries in the Antarctic Peninsula suggest that there may be considerable potential for cross-Gondwanan correlation, even into the Maastrichtian (Doyle and Zinsmeister 1988; Doyle 1990a). Recently collected material from the Santa Cruz Province in Argentina indicates that further inter-regional correlation could be possible in this interval, although much more work is necessary to be able to construct a meaningful biostratigraphy.

## DISCUSSION

From the foregoing, it is clear that belemnites have, in theory at least, considerable potential in biostratigraphy. As neritic or even pelagic organisms, they have a wide distribution. Although many authors have commented on the perceived 'shallow water' habitat preference of belemnites, this is not substantiated by the range of facies and settings from which belemnites have been recorded. Paucity of study may have contributed to their underuse in biostratigraphical studies, but belemnites are common, and more importantly, robust fossils that are relatively easy to distinguish with care. Origination rates based on available data suggest that, in many cases, belemnites have a species longevity which compares well with other zonal indices. All facts considered, belemnites provide an important alternative to ammonites and microfauna/flora in Jurassic and Cretaceous sequences.

Belemnite provincialism represents the greatest problem in inter-regional correlation, and the development of faunal realms in particular hampers such comparisons. 'Event' horizons of rapid geographical expansion can be identified, particularly in the Lower Jurassic (Toarcian), and Lower Cretaceous (Aptian/Albian), but many minor faunal influxes can be recognized, often associated with sea level highstands. The greatest body of information and utility lies in the Upper Cretaceous of Europe, where a very detailed biozonation has been developed over a period of some 150 years. This scheme is in everyday geological use and, with refinement, similar examples, such as the recently developed European Lower Cretaceous biozonation, could increase in importance. This is of particular merit in regions where ammonites or other zonal indices are absent, and in complex tectonic terranes, where belemnites may survive in a better condition than the more fragile ammonites.

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# SOFT-SEDIMENT ADAPTATIONS IN A NEW SILURIAN GASTROPOD FROM CENTRAL ASIA

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**ABSTRACT.** Specimens of the gastropod *Isfarispira septata* gen. et sp. nov., from the Silurian of Central Asia, are characterized by a large, lenticular, multi-whorled shell with a flattened base, a low rate of expansion of the broad whorls, internal septa at intermediate growth stages and a prominent circumbilical flange which closed off much of the umbilicus. These morphological features reflect adaptation to life on a soft substratum, collectively serving to inhibit sinking into the soft sediment by increasing the area of the basal surface. *I. septata* is interpreted as a sedentary, or only infrequently mobile gastropod.

THE presence of an internal plug (or septum) closing off the earliest stages of the shell is not an unusual phenomenon in Palaeozoic gastropod molluscs (Yochelson 1971). Indeed, this morphological feature is not restricted to gastropods, being also documented in the Class Helcionelloida (Rasetti 1957; see Peel 1991a) and the Class Tergomya (Yochelson *et al.* 1973; Webers *et al.* 1992). Several non-molluscan, Cambrian, tube-like fossils, such as *Camarothea* and *Actinothea* (Fischer 1962; Bengtson *et al.* 1990), also developed internal septation.

An internal apical plug or septum in the earliest growth stages of gastropods is usually detectable as a rounded termination of the internal mould, although septa and calcite spar filling the closed-off portion also may be visible in cross sections (see Lindström 1884, pl. 13, figs 30, 36; pl. 15, fig. 5). In contrast to the septa of cephalopods, gastropod septa are not penetrated by a siphuncle or other structure and areas of the shell cavity located adapically of each septum are thus sealed off from the body cavity by the septum itself.

The presence of repeated septa at later growth stages is relatively rare in Palaeozoic gastropods and only a few examples have been documented. Notable amongst these are two Devonian gastropods described by Yochelson (1966, 1971). *Nevadospira* is an open coiled form in which Yochelson (1971) described abundant closely spaced septa in the early and penultimate whorls. Similar septa are known in a variety of other, often loosely coiled, euomphalacean gastropods, although they are not usually as numerous as in *Nevadospira* (Yochelson 1971). *Arctomphalus* has a more tightly coiled, low spired shell form, but Yochelson (1966, 1971) recorded at least ten septa spaced at intervals averaging 2.5 mm. Linsley (1978a) considered *Arctomphalus grandis* to be the male(?) sexual dimorph of *Omphalocirrus goldfussi*; he also described abundant septa in the related omphalocirrid *Hypomphalocirrus*. Illustrations of the rare, open coiled gastropod *Phanerotinus*, from the Carboniferous of the United Kingdom, presented by Morris and Cleevely (1981) indicate the occurrence of septa to within about one whorl of the preserved aperture, with three or four earlier whorls sealed off from the body chamber. The Ordovician to Silurian *Lytospira* also has an open coiled shell with abundant septa in the early whorls (Koken and Perner 1925).

Cook (1993) described abundant internal septa in *Fletcheriawia septata* from the Devonian of Australia. The record is of particular interest in that septation is developed in a tightly coiled, high spired gastropod, in contrast to occurrences of multiple septation in the low spired *Nevadospira*, *Phanerotinus*, *Lytospira*, *Arctomphalus* (= *Omphalocirrus*) and *Hypomphalocirrus*.

Here we describe septation in a large, lenticular gastropod from the Silurian of Central Asia, proposed as *Isfarispira septata* gen. et sp. nov. Together with other features of the shell, such as the broad whorl cross-section, low spire, low rate of whorl expansion, and development of a prominent circumbilical flange, the development of internal septation in *Isfarispira* results from adaptation to life in a soft sediment environment. In general, however, there is no reason to assume any direct correlation between the occurrence of septation in fossil gastropods and soft sediment environments.

While septation indicates withdrawal of the gastropod animal from the early portion of its shell, published descriptions suggest that this withdrawal was a response to several different circumstances.

### GEOLOGICAL SETTING

Specimens described here as *Isfarispira septata* gen. et sp. nov. were collected from the Chorkuin Formation in the Pschemack Mountains of Central Asia which form part of the western segment of Southern Tien Shan (Text-fig. 1). The succession in this area is tectonically deformed into a series of nappes, but includes sedimentary rocks of Middle and Upper Cambrian, Silurian, Devonian and Carboniferous ages. The Chorkuin Formation is of Silurian age, straddling the Llandovery-Wenlock boundary. It is composed mainly of siltstones, but the gastropods are preserved in limestone lenses. All fossils were collected by Irina A. Pianovskaya who also described the section. Associated fossils include the cephalopods *Geisonoceras kureikense* and *Edenoceras hiliferum* (determined by E. I. Miagkova), the graptolite *Monograptus* sp. (?ex group *M. priodon*, determined by G. W. Pianovsky) and the trilobites *Encrinurus punctatus* and *Otarion* sp. (determined by T. I. Hajrullina).

### SYSTEMATIC PALAEOONTOLOGY

Phylum MOLLUSCA Cuvier, 1797

Class GASTROPODA Cuvier, 1797

Subclass PROSOBRANCHIA Milne Edwards, 1848

Order ARCHAEOGASTROPODA Thiele, 1925

Superfamily EUOMPHALACEA Koninck, 1881

Family OMPHALOTROCHIDAE Knight, 1945?

Genus ISFARISPIRA gen. nov.

*Derivation of name.* From the Isfara river, which lies to the east of the type locality in the Pschemack Mountains (Text-fig. 1).

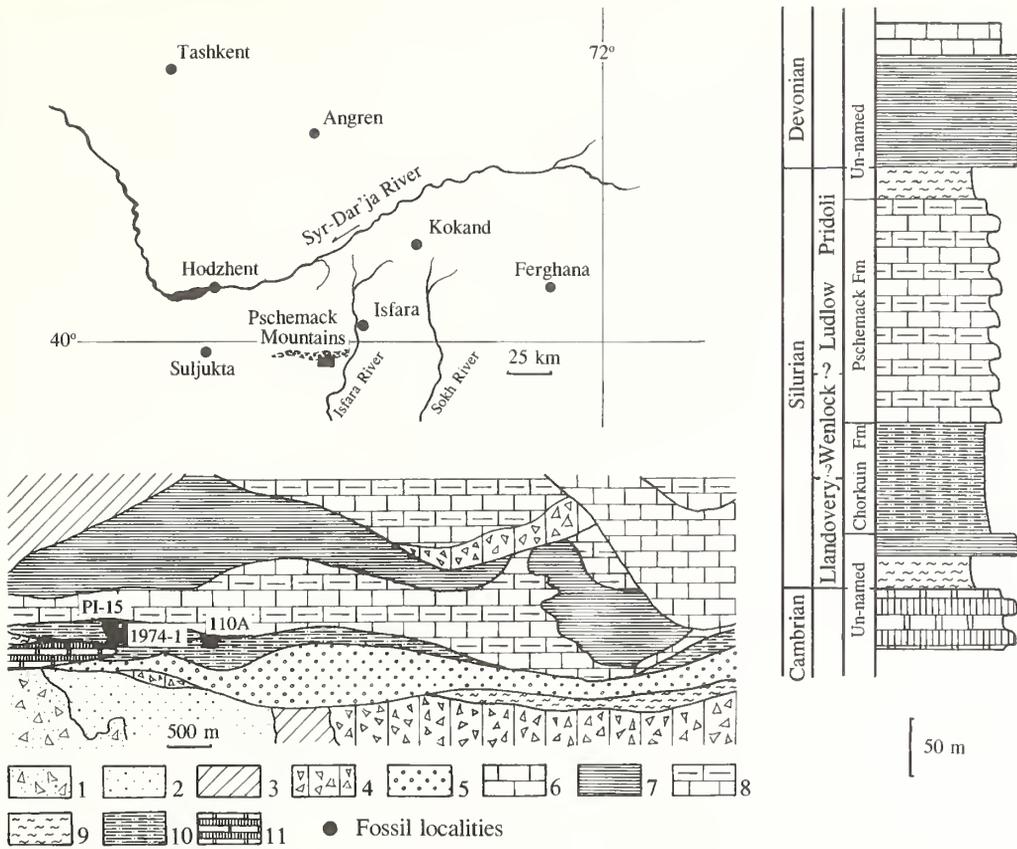
*Type species.* *Isfarispira septata* gen. et sp. nov., from the Chorkuin Formation, Silurian, Central Asia (Text-fig. 1).

*Diagnosis.* Large, lenticular gastropod with more than ten slowly expanding whorls and a radial aperture. Umbilicus largely closed by a blade-like circumbilical flange, extending adumbilically as a continuation of the shallowly convex base. Shell interior with numerous adaperturally concave septa.

*Remarks.* In terms of its lenticular form, *Isfarispira* is morphologically reminiscent of *Liospira* which is widely distributed in Middle Ordovician and Silurian strata (Ulrich and Scofield 1897; Knight *et al.* 1960; Peel 1977). *Isfarispira* is readily distinguished from this genus, however, by its much greater size (more than 80 mm in diameter compared with the 20–30 mm of *Liospira*), greater number of more slowly expanding whorls and absence of the deep peripheral sinus and slit, and resultant selenizone. As in *Isfarispira*, the umbilicus in *Liospira* is often partially or completely closed.

The low rate of whorl expansion invites comparison of *Isfarispira* with Early Ordovician genera such as *Ophileta* and *Ozarkispira*, in particular when the genera are compared in apical view (cf. Knight 1941; Knight *et al.* 1960). *Isfarispira* has a narrower umbilicus, however, with whorls at least twice as wide as high, and the umbilicus is closed by the prominent circumbilical flange; the umbilicus is widely phaneromphalous in the Early Ordovician genera.

*Grantlandispira*, from the Silurian of North Greenland (Peel 1984a), differs from *Isfarispira* in having a higher spired and pronounced cyrtocoid form, although both genera have many whorls. In *Grantlandispira* the umbilicus is almost closed by a massive circumbilical flange, much more robust than the thin circumbilical plate of *Isfarispira*. In addition, ornamentation on the upper



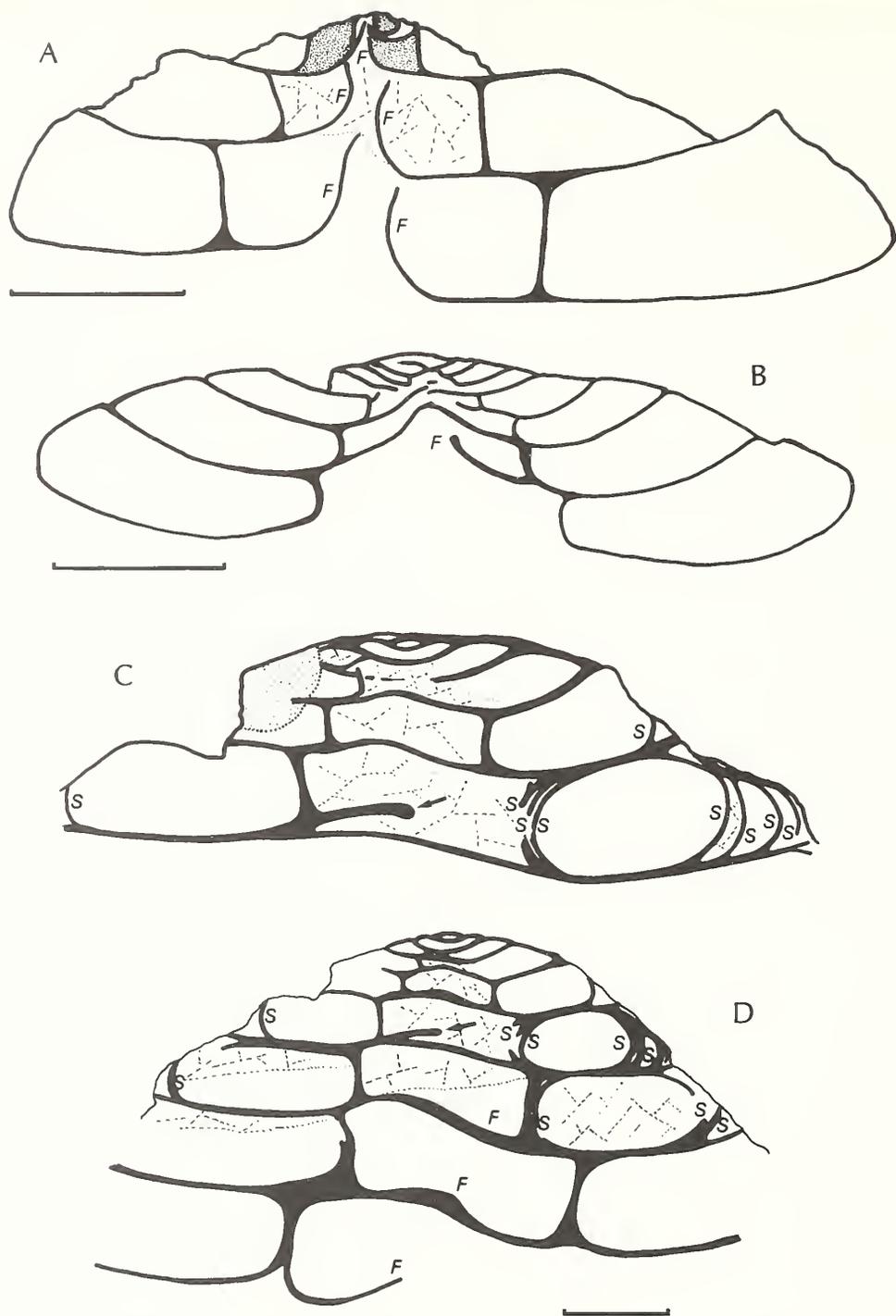
TEXT-FIG. 1. Derivation of *Isfarispira septata* gen. et sp. nov. from the Chorkuin Formation of the Pskemack Mountains, Central Asia; localities are discussed in the text. Lithologies: 1, alluvial deposits; 2, sandstones and gritstones; 3, clays; 4, olistostromes; 5, conglomerates; 6, dolomitic limestones; 7, black cherts; 8, alternations of limestones, clayey limestones and shales; 9, clay shales; 10, siltstones; 11, alternations of cherty rocks and dolomites.

whorl surface of the Greenland genus indicates a sub-sutural sinus which is seemingly not present in *Isfarispira*. Some species of the Devonian *Oreocopia* may also have lenticular shells with a relatively high number of whorls (Pedder 1966) but these can be distinguished from *Isfarispira* by the narrower umbilicus, sub-circular whorl profile and the sub-sutural sinus.

*Planitrochus*, from the Upper Silurian of Bohemia, has a lenticular form, but with fewer whorls than *Isfarispira*; it also is distinguished by its sub-tangential aperture, and the lack of the prominent circumbilical flange (Knight 1941). *Kiaeromphalus*, from the Lower Silurian of Norway (Peel and Yochelson 1976), resembles *Isfarispira* in size and general form. It is distinguished by its more convex whorls with a rounded periphery, and by the open umbilicus.

*Isfarispira* is morphologically quite distinct from other described multi-septate gastropods, such as the open coiled *Nevadaspira*, *Lytospira* and *Phanerotinus* (Koken and Perner 1925; Yochelson 1971; Morris and Cleavelly 1981), the low spired *Omphalocirrus* and *Hypomphalocirrus* (Linsley 1978a) and the high spired *Fletcheriwickia* (Cook 1993).

In the classification of gastropods employed by Knight *et al.* (1960), *Isfarispira* is tentatively assigned to the Omphalotrochidae.



TEXT-FIG. 2. *Isfarispira septata* gen et sp. nov.; Chorkuin Formation, Silurian; Central Asia; camera lucida drawings of polished transverse sections. Scale bars represent 10 mm. A, CSGM 980b, paratype; camera-lucida drawing showing the strongly convex circumbilical flange (*F*) originating from the base of the whorl. Early

*Isfarispira septata* gen. et sp. nov.

## Plate 1; Text-figure 2

*Ophileta?* aff. *perlata* (Hall, 1852); Mironova 1993, p. 7, pl. 1, fig. 1a–b  
*Pycnotrochus viator* Perner, 1907; Mironova 1993, p. 6, pl. 1, fig. 3a–b

*Derivation of name.* With reference to the abundant internal septa.

*Holotype.* Palaeontological Collections of the Central Siberian Geological Museum (CSGM), Novosibirsk, Russia, 980a; Silurian; Chorkuin Formation, locality PI-15, Central Asia (Text-fig. 1).

*Paratypes.* CSGM 980b, from the same collection as the holotype; CSGM 980c, from locality 110A; CSGM 980d–f, from locality 1974-1. Silurian; Chorkuin Formation.

*Description.* At least ten whorls are present. The large lenticular shell is divided into upper and lower surfaces by the prominent peripheral angulation; the shell height varies from three-eighths to about half of the diameter. Sutural indentation is very slight. The sides of the low spire vary from slightly convex, such that the shell is weakly cyrtocoid, to almost flat, but become shallowly concave in the latest growth stage because of an increase in the shell width at the transition to the final whorl. Early growth stages are poorly known. The width of the whorl in cross section, measured perpendicular to the axis of coiling, is about twice the height. The lower (basal) and upper (parietal) walls become increasingly parallel with growth of the shell, such that the two surfaces are both perpendicular to the axis of coiling in the umbilical region in the latest growth stage, but curve slightly adapically as the angular periphery is approached; the base is shallowly convex. The outer whorl surface is very shallowly convex between the periphery and the suture with the previous whorl, more so in early whorls. The final whorl is more noticeably flattened. The umbilical wall is sub-parallel to the axis of coiling and passes angularly into the lower and upper whorl surfaces.

The aperture is radial. Poorly preserved growth lines on the base of the holotype are shallowly convex adaperturally. In the same specimen, very poorly preserved growth lines on the outer whorl surface near the aperture are very slightly concave (adaperturally) as they traverse the outer whorl surface, with adapical obliquity, towards the periphery. Thus, there is a very shallow peripheral sinus, but there is no evidence to suggest the presence of a slit and selenizone. The umbilicus is seen to be wide in cross section but it is closed by a blade-like circumbilical flange which extends from the umbilical shoulder, as a continuation of the base, into the umbilicus. In some specimens, this flange extends across the umbilicus towards the umbilical suture a half whorl previously. In other specimens, the flange curves with increasing convexity towards the axial region. The flange is apparently narrower in the immediate vicinity of the aperture, with a thickened termination, but seems to attain its full extent within a whorl back from the apertural margin.

The shell interior is traversed by abundant septa which are concave adaperturally. In the holotype the body chamber seems to extend over at least one and three-quarter whorls. Adapical of this point, a number of septa are visible but they appear to be irregularly spaced. In cross section, septa are usually visible near the whorl periphery as adaxially concave surfaces which are less angular than the adjacent whorl periphery. The coalescence of septa in the area of the periphery and suture produces a thickening of the shell which gives some internal moulds a slightly gradate profile. The shell itself is seemingly quite thin, relative to the large size of the gastropod, but the flange and umbilical wall appear to be thickened at the aperture in the holotype.

*Remarks.* The small amount of material available illustrates quite considerable variation in the height of the spire. The holotype is relatively low spired, with height being about three-eighths of the maximum preserved diameter. Two paratypes are noticeably more high spired, with a more gradate profile, although the step-like profile has been emphasized by weathering; there are

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whorls are filled with dark calcite spar (stippled); at intermediate growth stages, white calcite spar fills the umbilicus and the tube-like space between the upper surface of the flange and the base of the previous whorl. B, CSGM 980d, paratype; note the development of the circumbilical flange (*F*) about one whorl back from the preserved final growth stage. C–D, CSGM 980c, paratype; showing multiple septa (*S*) and the circumbilical flange (*F*) appearing to cross the umbilicus in the excentric section. Arrows locate the same flange in the enlargement (S) of the apical area. Note the white calcite spar in the umbilicus and as geopetal fills in intermediate whorls; the recrystallized area (stippled) in C is not related to the fossil.

insufficient grounds to suggest that these more gradate forms should be assigned to another species. The specimens, as a whole, are indifferently preserved, particularly with regard to details of the shell exterior.

Mironova (1993) assigned specimens from the same horizon and locality as the holotype of *Isfarispira septata* to *Ophileta?* aff. *perlata* and *Pycnotrochus viator*. Her illustrations show respectively low and higher spired specimens which fall within the range of variation of the current sample. Thus, we have no hesitation in placing Mironova's specimens within *Isfarispira septata*. Her illustration of the base (Mironova 1993, pl. 1, fig. 3b) clearly shows the shallowly convex growth lines and the circumbilical flange.

The relationship of *Isfarispira septata* to *Pleurotomaria perlata* is uncertain. Hall (1852) described the latter species on the basis of imperfect internal moulds from the Lower Silurian of Galt, Ontario, Canada. The scant references to other early reports from North America were summarized by Bassler (1915, p. 747). Hall (1852, pl. 84, fig. 5a-c) clearly illustrated the lenticular form, with numerous slowly expanding whorls, typical of *Isfarispira*, but the nature of the umbilicus, the form of the aperture, and the presence or absence of septa are not known.

Williams (1919, pl. 24, fig. 1a-b) reproduced good photographs of an internal mould also from Galt, Ontario, in apical and umbilical views, but gave no description. The specimen has a maximum preserved diameter of almost 100 mm, measured from the illustration. In umbilical views (Williams 1919, pl. 24, fig. 1b) the internal mould clearly demonstrates the perpendicular relationship of the lower (basal) whorl surface to the umbilical wall, producing a step-like umbilical profile, seen also in *Isfarispira septata*. There is no indication, however, of the presence of a circumbilical flange. Whiteaves (1884, p. 75) did not illustrate Hall's (1852) species, which he knew only from internal moulds from localities at Galt, Hespeler, Elora and Belwood, but commented upon its large size, compressed lenticular form, acutely angular periphery and deep, but rather narrow umbilicus. He did not question its systematic placement with other pleurotomarians, which implies that he believed a peripheral slit and selenizone to be present, although he made no record of such features. Whiteaves (1906, p. 332) quoted from an extract from a letter from E. O. Ulrich suggesting that the species should be referred to *Liospira* which has a well developed peripheral slit and selenizone. In following this practice, Whiteaves reiterated that only poor internal moulds were available to him.

Dolomite internal moulds from localities in the Chicago to Milwaukee region in the collections of the National Museum of Natural History, Washington DC, demonstrate the extremely acute periphery of *Pleurotomaria perlata* and this character serves to distinguish Hall's species from *Isfarispira septata*. Whether or not *Pleurotomaria perlata* should be referred to *Isfarispira*, *Liospira* or another genus must remain an open question until better preserved material is described.

*Preservation and variation in the material.* The holotype of *Isfarispira septata* (Pl. 1, figs. 3, 7-8) is the most complete specimen, but the aperture is not preserved and the upper surface is eroded. Two septa are visible about one and three-quarter whorls back from the preserved aperture (point b in Pl. 1, fig. 8) and seem to

#### EXPLANATION OF PLATE I

Figs 1-8. *Isfarispira septata* gen. et sp. nov.; Chorkuin Formation, Silurian; Central Asia. 1-2, CSGM 980f, paratype; locality 1974-1;  $\times 1$ ; 1, final whorl with spire broken away, in apical view to show the circumbilical flange; 2, in lateral view, the left margin of 1. 3, 7-8. CSGM 980a, holotype; locality PI-15;  $\times 1$ ; 3, umbilical view showing faint growth lines in the lower left quadrant; 7, apertural view showing the shallowly cyrtconoid spire, which becomes concave with the transition to the last whorl, and the prominent septum (a) visible due to removal of parts of the upper surface by weathering; 8, apical view of the weathered specimen, note septa at b (probably marking the adapical termination of the body chamber), a (see also 7) and c. 4-6, CSGM 980d, paratype; locality 1974-1; internal mould;  $\times 1$ ; 4, transverse section (see also Text-fig. 2b) showing cyrtconoid form of early whorls; 5, umbilical view showing sedimentary infill to the umbilicus at a stage when the circumbilical flange was not yet formed; 6, apical view.



delimit the adapical termination of the body chamber; a fill of grey limestone occurs adaperturally of these septa, whereas red-stained carbonate (perhaps partly shell wall) occurs adapically of the pair of septa. A group of three septa spaced at 2–3 mm occurs about half a whorl earlier in ontogeny (point c in Pl. 1, fig. 8), and a single septum is also visible about half a whorl earlier still (Pl. 1, figs 7–8; point a). The presence of other septa cannot be ascertained because of the poor preservation of the upper surface.

Paratype CSGM 980*b* is an internal mould which has been transversely polished through the apex (Text-fig. 2A). The profile is gradate, but this is partly a result of weathering and of thickening of the now removed shell near the periphery of the whorl; septa are not visible. The circumbilical flange is well preserved and curves strongly from the base of the whorl in towards the axial region, where it becomes almost parallel to the axis of coiling. In the latest preserved whorls, sediment has penetrated into the spiral circumbilical cavity formed between the flange and the umbilical wall of the whorl, but this cavity is filled with calcite spar in earlier growth stages.

Paratype CSGM 980*c* (Text-figs 2C–D) is the only specimen available from locality 110A, and occurs in a separate nappe from the localities yielding the other specimens of *Isfarispira septata*. It is a badly weathered internal mould which has been ground down and polished to show a transverse section slightly oblique to the axis of coiling. It is proportionally taller than the holotype and preserves parts of eight whorls. Septa are clearly visible in intermediate growth stages but have not been observed in the earliest or latest growth stages. On account of the excentric section, the circumbilical flange appears to extend across the umbilicus, except at the latest growth stage where it is seen as a short blade protruding into the umbilicus; much of the shell at this growth stage seems to have been dissolved diagenetically. Calcite spar is conspicuous in the umbilicus and whorls at intermediate growth stages, but lime mud fills the latest whorls and also the early whorls. The distribution of lime mud in the early whorls indicates that the apex was perforated, either during or after the life of the gastropod, and that septa were not present or were secondarily destroyed in these early whorls.

Three paratypes were collected from locality 1974-1. One of these (specimen CSGM 980*d*; Pl. 1, figs 4–6; Text-fig. 2B) is a juvenile which has been transversely sectioned. The circumbilical flange is not developed in the final whorl and septa are not visible in the lime mud filling of the shell. A large, transversely sectioned specimen (CSGM 980*e*; not illustrated) shows distinct septa in intermediate growth stages but is too poorly preserved to assess the presence or absence of septa in the early growth stages. Specimen CSGM 980*f* is an internal mould of the final whorl showing the circumbilical flange clearly preserved on its upper surface (Pl. 1, figs 1–2).

#### MODE OF LIFE OF *ISFARISPIRA*

The lenticular form of *Isfarispira* combines a low spire and flattened base to produce a shell with a high surface area, when restored in the presumed living position with the lower surface lying on the sediment surface. The large surface area of the base counteracts sinking into soft bottom sediment and this snow-shoe effect is enhanced by other morphological co-adaptations. Notable amongst these is the shape of the whorl cross section, with maximum extent almost perpendicular to the axis of coiling and thus parallel to the sediment surface (cf. Text-fig. 2). In addition, the prominent circumbilical flange extends deep into the umbilicus to increase the area of shell in contact with the substrate and may serve to exclude sediment from the deeper parts of the umbilicus. Interpretation of the function of the flange is complicated, however, by consideration of its method of formation. Presumably, the flange was produced by an apertural extension of the mantle which partially, or completely, blocked the umbilicus at least during the period of secretion. The absence of the flange from the latest growth stage may indicate that this extension of the mantle was both extensive and possibly even a lasting feature. In such a case, the flange may have supported areas of soft tissue within the wide umbilicus near the aperture, or provided a smooth surface resting on an area of the foot extending beneath the shell in life.

The available small sample indicates quite substantial variation in the form of the circumbilical flange. In the specimen illustrated as Text-figure 2A, the flange is strongly curved and effectively delimits a spiral tube equivalent to the whorl, but located between the umbilical wall of the whorl and the upper surface of the flange. Sediment was probably largely excluded from this circumbilical tube during life. At the present time, the earliest growth stages are filled with calcite spar and sediment is restricted to the latest preserved growth stage. In other specimens, the circumbilical flange is less strongly curved and seems to have extended across the umbilicus towards the previous

half whorl. Again, the presence of calcite spar filling the earliest growth stages may support the interpretation that the flange helped prevent sediment fill of the umbilicus.

Even the large number of whorls and the low rate of whorl expansion can be interpreted in relationship to the 'snow-shoe effect'. The surface area of the base of the shell is naturally increased by a high rate of growth (spiral shell accretion) and a high rate of whorl expansion, but the increase is counterbalanced by a corresponding increase in the volume of the soft parts. This effect is lessened, however, if the rate of growth of the shell, marked by its increase in surface area, is decoupled from the rate of growth of the soft parts. Thus, the low rate of whorl expansion in *Isfarispira* allowed the volume of the gastropod soft parts to increase more slowly than the rate of growth of the shell by spiral accretion, if the animal withdrew from the early part of the shell and lived only in the latest portion. The presence of septa in the interior of *Isfarispira* clearly demonstrates that the gastropod had withdrawn from the earlier (oldest) parts of the shell. In the holotype, septa are visible one and three-quarter whorls back from the aperture as preserved, delimiting the maximum extent of the body chamber. Thus, the earliest eight or more whorls were devoid of living tissue, being filled with water which probably had a slightly lower density than that of the soft parts. Withdrawal of the gastropod from the early whorls, in conjunction with the high rate of spiral growth and low rate of whorl expansion, enhanced shell growth at a minimum cost in terms of the energy requirements of the growing animal.

'Snow-shoe' adaptations are seen in a variety of other Palaeozoic and younger gastropods but different morphological solutions are employed from those described here in *Isfarispira*. Linsley *et al.* (1978) and Peel (1984b, 1986) discussed frilled Palaeozoic gastropods, noting that the flange-like extension of the whorl periphery (as distinct from the flange extending into the umbilicus in *Isfarispira*) may have served either to prop the shell above a solid substratum, as in the recent *Xenophora*, or as a 'snow-shoe' to prevent sinking into soft sediment, as in the familiar Silurian *Euomphalopterus*. Peel (1977, 1978, 1984b, 1991b) suggested that the widely expanded aperture of certain Palaeozoic bellerophonacean gastropods represents expansion of the foot in response to life on a soft substratum. Other expanded bellerophonaceans, such as *Carinaropsis*, lack explanate margins and have thick shells (Peel 1993), indicating a limpet-like existence on harder substrates.

The presence of a radial aperture indicates that *Isfarispira* could not close its shell opening by clamping against the sediment. Shells with this apertural form are often sedentary or only occasionally mobile (Linsley 1977, 1978b) which accords well with the inferred 'snow-shoe' adaptation to life on a soft substrate. *Isfarispira* may have been a ciliary feeder or deposit feeder which only rarely moved to a new location. Some relatively thick-shelled Palaeozoic forms having this mode of life developed a prominent operculum (cf. Linsley and Yochelson 1972, Linsley 1978a), but it is not currently known if a calcified operculum was present in the thin-shelled *Isfarispira*. The presence of a calcified operculum and a thick shell tend to increase the specific gravity of the gastropod animal. The thin shell of *Isfarispira* and the eventual lack of a calcified operculum would have contributed to the 'snow-shoe' effect by keeping specific gravity to a minimum.

#### SEPTATION IN GASTROPODS

The presence of abundant internal septa in such disparate shell morphologies as the open coiled *Nevadaspira*, *Lytospira* and *Phanerotinus*, the thin-shelled and lenticular *Isfarispira*, the thick-shelled but low spired *Omphalocirrus* and *Hypomphalocirrus*, and the high spired *Fletcheriawia* suggests that septation in Palaeozoic gastropods is not associated with a particular mode of life or environment, although it is quite possible that this range of shell forms could have been found in gastropods feeding in a similar manner, for example by ciliary feeding, in different environmental settings.

We concur with Yochelson (1971) in his tentative dismissal of the idea that multiple septation could be a direct response to a need to strengthen the gastropod shell, as has been invoked within the Cephalopoda. Rather he suggested that withdrawal of soft parts 'may allow for greater efficiency in construction of the shell' (Yochelson 1971, p. 239) which, in general terms, agrees with

the interpretation of the various shell features of *Isfarispira* presented here. Morris and Cleevly (1981) noted, without further discussion, that septation allowed withdrawal from, or loss of, the earliest whorls without inconvenience.

In *Isfarispira* it has been shown that withdrawal of the soft parts from the early whorls formed part of an adaptive strategy to life on a soft substrate by increasing the area of the resting surface of the gastropod relative to the volume of the soft parts (the 'snow-shoe' effect). A similar interpretation can be advanced for septation in *Nevadaspira*, *Lytoispira* and *Phanerotinus*, but the operculate *Onphalocirrus* and *Hypomphalocirrus* have dissimilar, thick shells with more rapidly expanding whorls. In this case, withdrawal from the earliest growth stages may simply reflect a body mass of such a shape and size that it no longer required the narrow early whorls; in short, a slightly special case of the general withdrawal from the apical whorls typical of most gastropods. This may parallel the situation in the extant ciliary feeding vermetid *Dendropuma*, where the body mass is relatively short and plump and septa frequently close off earlier parts of the shell (Morton 1965).

Cook (1993) noted that *Fletcheriella*, a high spired form with a thick shell and strongly angulated whorls, lived in high energy environments where the early whorls might be lost while the living shells were rolled along the substrate. Shortening of the body mass and secretion of septa closed off the early whorls which were susceptible to erosion and effectively prevented apical perforation of the shell. Cook (1993) supported his interpretation by reference to specimens lacking the apical portion and with the apex encrusted by calcareous algae, although such features also readily occur after death. Apical perforation may have occurred also in *Isfarispira*, since the earliest whorls in some specimens are filled with lime mud, while intermediate septate whorls are filled with calcite spar (Text-fig. 2C). In the interpreted soft-sediment environment, however, such perforation probably resulted from corrosion rather than erosion. Attempted predation may also produce perforation of the shell apex but durophagous predators at the present day mainly attack the aperture (Vermeij *et al.* 1980, 1981; Vermeij 1982, 1983, 1993). While shell boring predators are known from the latest Precambrian and Cambrian (Bengtson and Yue 1992; Conway Morris and Bengtson 1994), evidence of this and other forms of predation in the Palaeozoic is uncommon when compared with the Mesozoic and Cenozoic (Vermeij 1987). Published records of predation, or attempted predation, on gastropods in the Palaeozoic are rare, although undocumented cases are known to the authors. Peel (1984c) described shell repair in *Euomphalopterus* from the Silurian of Gotland which he attributed to repeated attempted predation. Rohr (1993) and Horny (1993) described cases of shell repair from the Ordovician and Devonian, respectively, which may have had a similar origin.

While septa in all these cases clearly serve to close off earlier (older) parts of the gastropod shell, the causes for withdrawal of soft parts from the early shell are different. Thus, septation provides no single diagnostic character in terms of the mode of life of septate Palaeozoic gastropods, but represents one among many shell features developed in response to varied adaptive strategies.

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# SIZE, BODY PLAN AND RESPIRATION IN THE OSTRACODA

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**ABSTRACT.** Ostracodes are small (0.3–32 mm) bivalved crustaceans with an exceptional fossil record covering the last 540 million years of aquatic life; the group is still represented by nearly 8000 species (Podocopa and Myodocopa). Only two major body plans prevail in the modern fauna if we except the enigmatic punciids. 'Body plan 1' corresponds to ostracodes (Myodocopida, Halocyprida) with a bilateral symmetry, a frontal polarity, a high activity level, an ellipsoidal shape, well designed for moving through water or soft muddy sediment, and (primarily) a circulatory system. 'Body plan 2' corresponds to ostracodes with a ventral or lateral polarity (left/right valve asymmetry). Such organisms (Podocopa) are mostly crawlers (on thoracic legs) on a substratum or within flocculent material, and occasionally remain motionless, simply resting on one valve. The carapace is heavily calcified, bearing strengthening features, and no circulatory features (e.g. a dorsal heart) are present. The living ostracode fauna as a whole has a high diversity at low taxonomic level and conversely a low disparity of body plans. The respiratory and circulatory processes with relation to animal size have been investigated using a scanning electron microscope, microtomed sections, and high-resolution video observations of live specimens. Small ostracodes (0.3 to less than 3 mm) rely exclusively on integumental gaseous diffusion. Larger ones (up to 32 mm) have a dorsal heart, with haemolymph circulation supplementing diffusion. Fewer (e.g. cylindroleberidids) develop additional paired gill-like features, also present in the Triassic. Integumental circulation, evidence for which is preserved as anastomosing features in fossils, is shown to have occurred early in the evolution of Ostracoda, among Ordovician to Devonian leperditicopes, through the myodocope lineage (Silurian to Recent) and also possibly in bivalved arthropods such as the Bradoriida. The post-Cambrian evolution of Ostracoda is believed to have been influenced strongly by either the loss or the conservation of the circulatory system, leading (respectively) to minute organisms confined within a narrow size range (e.g. all living podocope ostracodes) and to larger crustaceans (e.g. living myodocope ostracodes) capable of higher metabolism and free swimming life styles.

THE nearly 8000 described species of living Ostracoda are confined within a surprisingly narrow size range compared with other crustacean groups of comparable diversity (e.g. Copepoda, Isopoda, Cirripedia and Decapoda; Table 1). Thus, the largest known mesopelagic ostracode (*Gigantocypris*; Cannon 1940) is only 60 times bigger in adult size than the smallest deep sea pelagic (e.g. *Archiconchoecia*) and interstitial (see Hartmann 1973) representatives of the group. Comparatively, malacostracan decapods exhibit a much higher size ratio; the Japanese spider-crab (*Macrocheira kaempferi*; Sakai 1970), with thoracic legs spanning over three meters, is about 1000 times larger than the smallest decapods, such as *Pinnotheres laquei*, a commensal pinnotherid crab living within the mantle cavity of brachiopods (Feldman *et al.* in press). If variations of the same amplitude occurred in ostracodes, then a maximum size of at least a metre would be expected.

Exceptionally abundant data from the fossil record show that a comparable size pattern also applies to the 40000–50000 ostracode species (Schram 1986; Maddocks 1992) known from the Lower Cambrian to the present and whose adult size rarely exceeds 1–2 mm (see Benson *et al.* 1961; Scott 1961; issues of the *Stereo-Atlas of Ostracod Shells* from 1973–1994). Noticeable exceptions do exist, however, and relatively larger forms, which may attain several tens of millimetres in carapace length, are common among the Ordovician to Devonian leperditicopes (Berdan 1984; Text-fig. 13), throughout the myodocope lineage from the Silurian (Vannier and Abe 1992) to the Recent, and may be found in very early ancestors of ostracodes such as Lower Cambrian cambriids (see Text-fig. 17; Siveter *et al.* 1994, in press; Williams *et al.* 1994). In this paper, we analyse the

TABLE 1. Size range (in mm), size ratio and approximate number of species in the main groups (subclasses) of living crustaceans. Classification after Bowman and Abele (1982) and Barnes and Harrison (1992a). *a* = maximum adult length; *b* = minimum adult length. In the classification proposed by Barnes and Harrison (1992a), the Subclass Sarcostraca comprises the Order Anostraca, the Subclass Calmanostraca the Order Notostraca and the Subclass Diplostraca the Orders Conchostraca and Cladocera (see Fryer 1987; Martin 1992) (\*) tantulocarids are minute ectoparasites known from two genera (see Boxshall and Lincoln 1983). Eumalacostracan data is given for three major orders only: Amphipoda (1), Isopoda (2) and Decapoda (3).

Class	Subclass	<i>a</i>	<i>b</i>	<i>b</i> : <i>a</i>	Number of species	References
Cephalocarida		2	3.7	~ 2	9+	Hessler and Elofsson (1992), Hessler (pers. comm. 1994)
Branchiopoda	Sarcostraca	15	100	6.7	190	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
	Calmanostraca	30	100	3.3	10	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
	Diplostraca	0.3	18	60	600	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
Rempedia		15	40	2.7	-12	Felgenhauer <i>et al.</i> (1992)
Maxillopoda	Branchiura	3	30	10	200	Overstreet <i>et al.</i> (1992)
	Mystacocarida	0.5	1	2	9	Schram (1986)
	Copepoda	1	250	250	8400	Boxshall (1992)
	Cirripedia	~ 1	300	300	1240	Walker (1992); Hoeg (1992); both pers. comm. (1994)
Ostracoda	Myodocopa	~ 0.5	32	64	650	Maddocks (1992), Morin and Cohen (1991)
	Podocopa	~ 0.3	~ 2.5	9	7000	Maddocks (1992), Benson <i>et al.</i> (1961)
Tantulocarida		?	< 0.3	?	(*)	Boxshall and Lincoln (1983)
Malacostraca	Phyllocarida	4	12	3	15+	Schram (pers. comm. 1994)
	Hoplocarida	10	600	60	500	Schram (pers. comm. 1994)
	Eumalacostraca	5	280	56	6000	Schmitz (1992 and pers. comm. 1994)
	(1) = Amphipoda					
	Eumalacostraca	0.6	400	660	9000	Wägele (1992 and pers. comm. 1994)
(2) = Isopoda						
Eumalacostraca	~ 4?	4000	1000	10000	Barnes and Harrison (1992b)	
(3) = Decapoda						



TABLE 1. Size range (in mm), size ratio and approximate number of species in the main groups (subclasses) of living crustaceans. Classification after Bowman and Abele (1982) and Barnes and Harrison (1992a). *a* = maximum adult length; *b* = minimum adult length. In the classification proposed by Barnes and Harrison (1992a), the Subclass Sarcostraca comprises the Order Anostraca, the Subclass Calmanostraca the Order Notostraca and the Subclass Diplostraca the Orders Conchostraca and Cladocera (see Fryer 1987; Martin 1992). (\*): tantulocarids are minute ectoparasites known from two genera (see Boxshall and Lincoln 1983). Eumalacostracan data is given for three major orders only: Amphipoda (1), Isopoda (2) and Decapoda (3).

Class	Subclass	<i>a</i>	<i>b</i>	<i>b</i> : <i>a</i>	Number of species	References
Cephalocarida	Sarcostraca	2	3-7	~2	9+	Hessler and Elofsson (1992); Hessler (pers. comm. 1994)
		15	100	6-7	190	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
Branchiopoda	Calmanostraca	30	100	3-3	10	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
	Diplostraca	0-3	18	60	600	Martin (1992 and pers. comm. 1994); Barnes and Harrison (1992a)
Remipedia	Branchiura	15	40	2-7	-12	Felgenhauer <i>et al.</i> (1992)
		3	30	10	200	Overstreet <i>et al.</i> (1992)
Maxillopoda	Mystacocarida	0-5	1	2	9	Schram (1986)
	Copepoda	1	250	250	8400	Boxshall (1992)
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	Myodocopa	~0-5	32	64	650	Maddocks (1992); Morin and Cohen (1991)
	Podocopa	~0-3	~2-5	9	7000	Maddocks (1992); Benson <i>et al.</i> (1961)
		?	< 0-3	?	(*)	Boxshall and Lincoln (1983)
Tantulocarida	Phyllocarida	4	12	3	15+	Schram (pers. comm. 1994)
	Hoplacarida	10	600	60	500	Schram (pers. comm. 1994)
Malacostraca	Eumalacostraca	5	280	56	6000	Schmitz (1992 and pers. comm. 1994)
	(1) = Amphipoda	0-6	400	660	9000	Wägele (1992 and pers. comm. 1994)
	(2) = Isopoda	~4?	4000	1000	10000	Barnes and Harrison (1992b)
	(3) = Decapoda					

relation of size to the body plan, the carapace design and to the respiratory processes of Ostracoda, throughout the last 500 million years of evolution of the group.

#### MATERIALS AND METHODS

*Living material.* A nektonic myodocopid species, *Vargula hilgendorffii* (Müller, 1890), was used extensively for documenting the internal (functioning organs, circulatory system) and external (carapace design) features of myodocopid ostracodes (Text-figs 1C–D, 2). Live material was collected at night in December 1993 and March 1994 from shallow water environments (water depth < 5 m) at Tateyama (Boso Peninsula, 35° 00' N, 139° 51' E) along the Pacific Coast of central Japan, and kept in aquaria at the University of Tokyo and Shizuoka University. Repeated observations of live (video recordings, optical binocular microscope) and fixed (SEM) specimens were made through the year. Morphofunctional and behavioural aspects of *Vargula hilgendorffii* were described in Vannier and Abe (1992, 1993). Respiratory features (haemolymph sinuses, circulation, heart) of *Vargula hilgendorffii* and Caribbean congeners have been recently investigated by Abe (1994) and Abe and Vannier (in press). Other species were used for comparative studies:

1. *Conchoecia atlantica* Lubbock, 1856 (Halocyprida; Text-figs 1A–B, 3), *Archiconchoecia striata* Müller, 1894 and *Bathyonchoecia* sp. (both Halocyprida), collected by K. Tachibana from the mesopelagic waters of Sagami Bay (Pacific Ocean; 35° 00' N, 139° 20' E).

2. Undetermined *Conchoecia* species collected (JV) in May 1994 during the sampling cruise of the research vessel Tanseimaru (operation KT 94-07, Ocean Research Institute, University of Tokyo), S of Atsumi Peninsula (loc. EN-03, 34° 13' 86" N, 137° 21' 71" E at about 300 m depth) and at Shima Spur (loc. KN-26, 33° 59' 43" N, 136° 52' 76" E at about 500 m depth) using a 1.5 m diameter conical plankton net (mesh size 0.69 mm).

3. *Leuroleberis surugaensis* Hiruta, 1982. (Myodocopida; Text-fig. 7; Vannier *et al.* in press) recovered from benthic collections off Shimoda, Izu Peninsula, Pacific Coast, Japan (34° 37' 00" to 34° 38' 64" N, 138° 57' 30" to 138° 56' 55" E at depths of 35 to nearly 100 m).

4. *Bicornucythere bisanensis* (Okubo, 1975) (Podocopida; Text-figs 1E–F, 4) from the flocculent muddy bottom sediments (depth approx. 4 m) of Aburatsubo Cove (Pacific Coast of the central part of Japan; 35° 09' 40" N, 139° 37' E, see Abe and Vannier 1991; Abe 1983).

Technical aspects of fixation, observation and microtome sectioning and staining are in Abe and Vannier (in press).

*Fossil specimens.* Ordovician and Silurian leperditicope (see Swartz 1949; Berdan 1984) ostracodes were reviewed, especially those bearing well-preserved anastomosing or radiating features. Among them were:

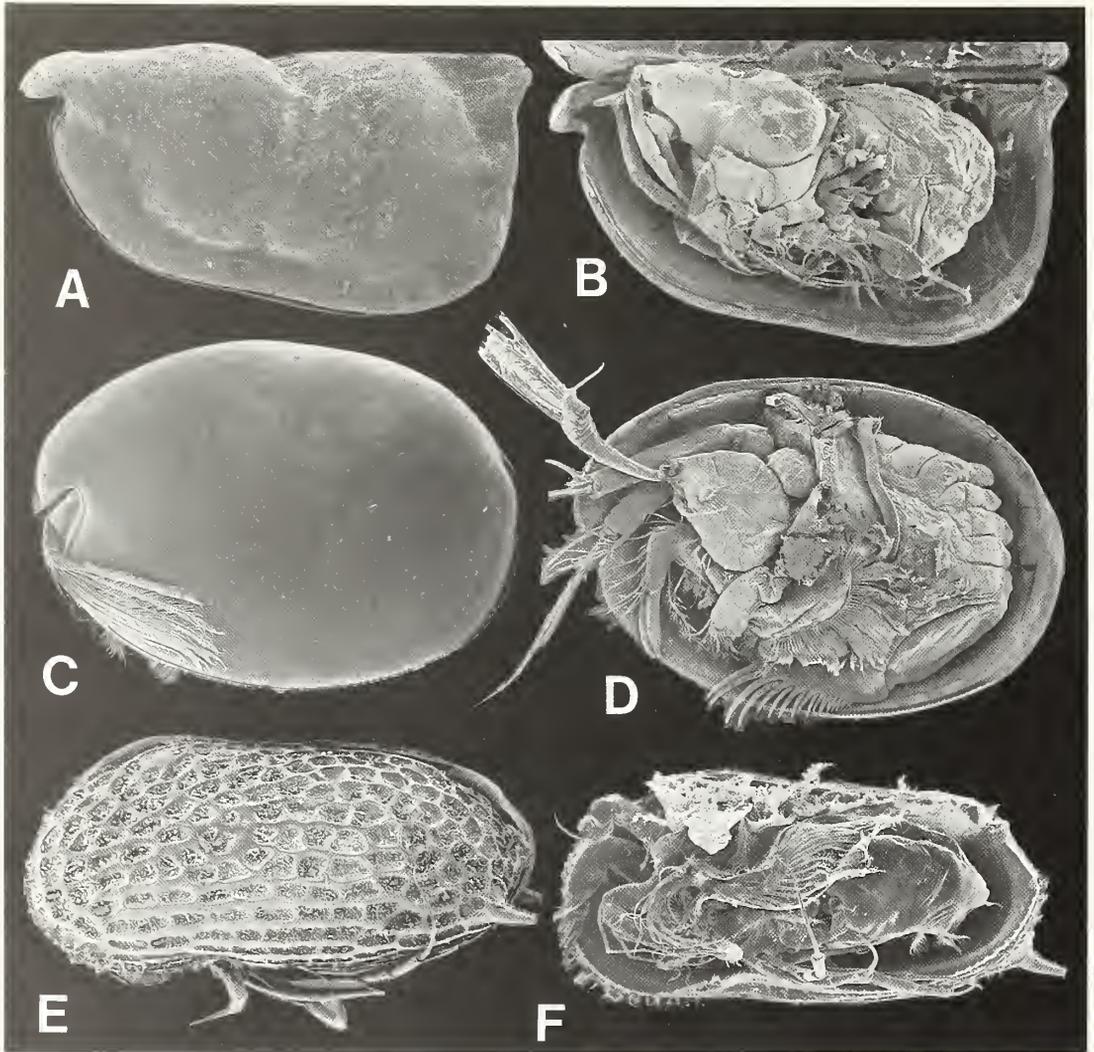
1. *Bivia tumidula* (Ulrich, 1891), *B. linneyi* (Ulrich, 1891), *B. frankfortensis* (Ulrich, 1891), *Teichoichilina jonesi* (Wetherby, 1881; Text-figs 13A, 15E), all from the Middle to Upper Ordovician Lexington Limestone, Kentucky.

2. *Ceratoleperditia kentuckyensis* (Ulrich, 1891) from the Tyrone Limestone, Middle Ordovician, Kentucky; *Kenodontoichilina pustulosa* Berdan, 1984 and *Saffordellina striatella* Berdan, 1984, both from the Ashlock and Bull Fork Formations, Upper Ordovician, Kentucky; *Eoleperditia fabulites* (Conrad, 1843; Text-fig. 14B) from the Platteville Formation, Wisconsin, the Tyrone Limestone and Glade Limestones, Kentucky, and the Lebanon Limestone, Tennessee, all of which are Ordovician in age.

3. *Saffordellina muralis* (Ulrich and Bassler, 1923; Text-figs 13B, 15C) from the Upper Trenton (Middle Ordovician; see Berdan 1984, p. 33) of Nashville, Tennessee.

4. *Isochilina venosculptis* Swartz, 1949 (Text-fig. 15A) from the Pamela Limestone (Middle Ordovician) of Aylmer, Quebec, Canada.

5. *Dihigmoichilina straitcreekensis* Swartz, 1949 from the late Silurian Tonoloway Limestone, Virginia.



TEXT-FIG 1. Internal and external ostracode morphology as exemplified by typical representatives of the orders Halocyprida (A–B), Myodocopida (C–D) and Podocopida (E–F) from the NW Pacific region, Japan. All are scanning electron micrographs of external lateral, and internal (left valve removed) views. A–B, *Conchoecia atlantica* (Lubbock, 1856); FSL 575087; a mesopelagic species from Sagami Bay; adult specimen;  $\times 19$ . C–D, *Yargula hilgendorfi* (G. W. Müller, 1890); a nektobenthic species from shallow water environments; C, FSL 575090; Aburatsubo Cove, Misaki; male specimen;  $\times 23$ . D, FSL 575088; Tateyama; male specimen;  $\times 23$ . E–F, *Bicornucythere bisanensis* (Okubo, 1975); FSL 575089; benthic species from shallow water environments (floculent layer); Aburatsubo Cove, Misaki; male specimen;  $\times 78$ .

None of this material, mostly kept in the collections of the Smithsonian Institution, Washington DC and too fragile (R. Benson, pers. comm.) for transport through the mail, could be obtained for new SEM studies. Our observations are based on the original descriptions and the light photographic illustrations of Swartz (1949) and Berdan (1984).

Type specimens of Devonian leperditicopes from Russia (see Abushik 1990) were borrowed through a loan arranged by Derek J. Siveter, A. Abushik and L. Melnikova (Derek J. Siveter, pers. comm. to JV). Among them, *Leperditia marinae* Abushik, 1980 (Text-fig. 13C–E) from the Lower

Devonian (lower Lochkovian) of Novaya Zemlya (A. Abushik, pers. comm. to JV) and *Moelleritia moelleri* (Schmidt 1883; Text-fig. 13F–H), from the Upper Emsian of Central Ural (A. Abushik, pers. comm. to JV) have been chosen to illustrate the overall morphology (e.g. carapace shape, overlap features) and the size range of leperditicopes.

The Upper Silurian myodocope ostracodes figured here (Text-fig. 16) were collected (JV) in September 1992 from several exposures along the D104 road at Les Buhardières between Andouillé and Saint-Germain-le-Fouilloux, 15 km N of Laval, Mayenne, France. We also refer to the myodocope material described by Siveter *et al.* (1987, 1991), Siveter and Vannier (1990) and Vannier and Abe (1992). Latex casts were made from external moulds of all this Silurian material.

*Gibba kandarensis* Vannier in Galle *et al.* 1995, a beyrichiacean palaeocope ostracode from the Lower Devonian of Immouzer of Kandar, 40 km S of Fes, Morocco (see Galle *et al.* 1995), was examined as an example of an exceptionally large palaeocope (Text-fig. 11).

*Anabarochilina primordialis* (Linnarsson, 1869; see Text-fig 17B and Siveter *et al.* 1993), from the late Middle Cambrian of northern Europe, and a cambriid species (Text-fig. 17A; Siveter *et al.* in press) from the Lower Cambrian Buen Formation of North Greenland are selected examples of early ostracodes of centimetric size and bearing radiating markings.

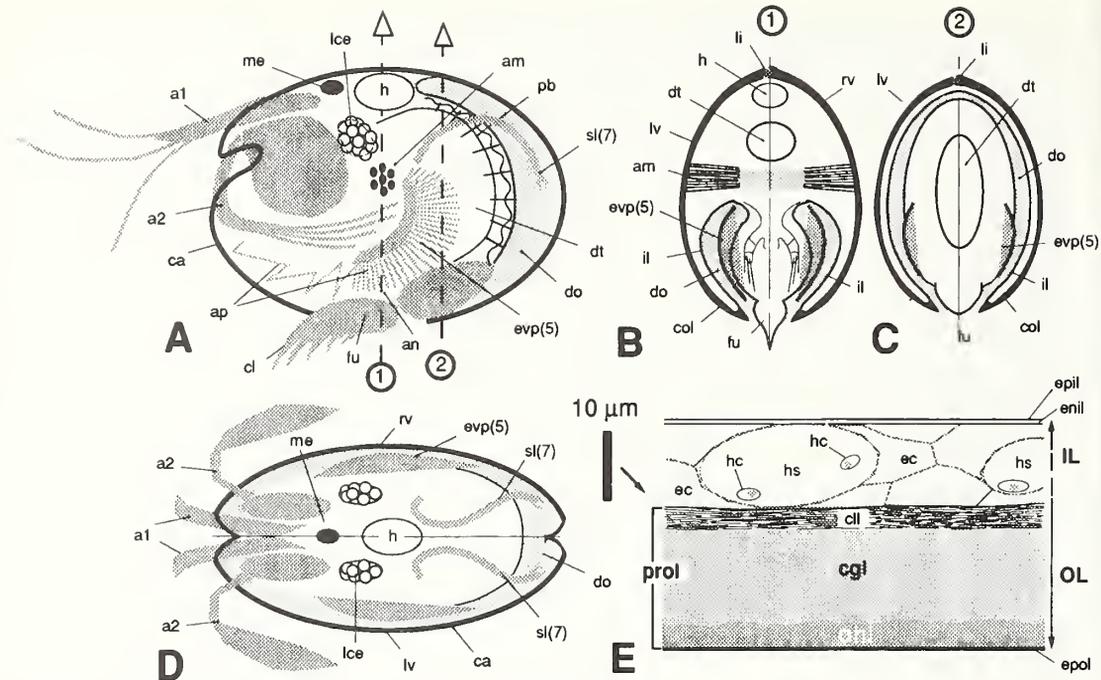
Light photographs of large specimens coated with ammonium chloride, were taken with an Aristophot camera. A Hitachi S2400S SEM was used for electron microscopy. Figured specimens are deposited in the collections of the Université Claude Bernard-Lyon 1, Centre des Sciences de la Terre (FSL), France, the United States Smithsonian Institution, Washington DC (USNM), the Palaeontological Institute, Moscow, Russia (N) and the Sveriges Geologiska Undersökning (GSU), Uppsala, Sweden.

#### BODY PLANS OF LIVING OSTRACODA

Ostracodes are minute crustaceans characterized by a reduction in the number of trunk segments (Swanson 1990); the body (five to seven pairs of appendages) is laterally compressed and entirely enclosed within a bivalved carapace impregnated with calcium carbonate. As in many other crustaceans (see Brusca and Brusca 1990; Gruner 1993), the ostracode carapace is a cuticular fold which originates embryologically from a cephalic segment. It is already well developed as an expansive protective structure in the earliest free-living embryos (Weygoldt 1960, 1993) and forms a bilateral extension of the body (Maddocks 1992; Text-figs 2B, 3B, 4B) that accommodates important cellular compounds and functional systems (e.g. hepatopancreas in podocopes; haemolymph sinuses in myodocopes; Text-fig 8). It is, therefore, neither a shell (e.g. molluscan shell; Crenshaw 1990) nor a simple covering shield-like carapace such as that of notostracan branchiopods (Martin 1992). The uncalcified inner lamella is a continuation of the body integument (see Abe and Vannier in press). Rhythmic and synchronized beatings of specialized appendages (e.g. epipodial ventilatory plates) and appendage movements induce water circulation within the domiciliar cavity as seen clearly from videos of nektobenthic (*Vargula*) and planktonic (*Conchoecia*) species (unpublished data).

Recent ostracodes are commonly subdivided (Barnes and Harrison 1992a) into two subclasses: the Podocopa (about 7000 living species; Orders Podocopida and Platycopida) and the Myodocopa (about 650 living species; Orders Myodocopida and Halocyprida). Using combined electron microscopy, microtomed serial sections, and live video recordings, we analysed the three-dimensional aspects of the anatomy of typical representatives of Myodocopida, Halocyprida and Podocopida as well as the functional anatomy of these organisms. Minor groups (Platycopida, Polycopidae, Thaumatoocyprididae, Punciidae) represented by only a few taxa were not investigated in the present study.

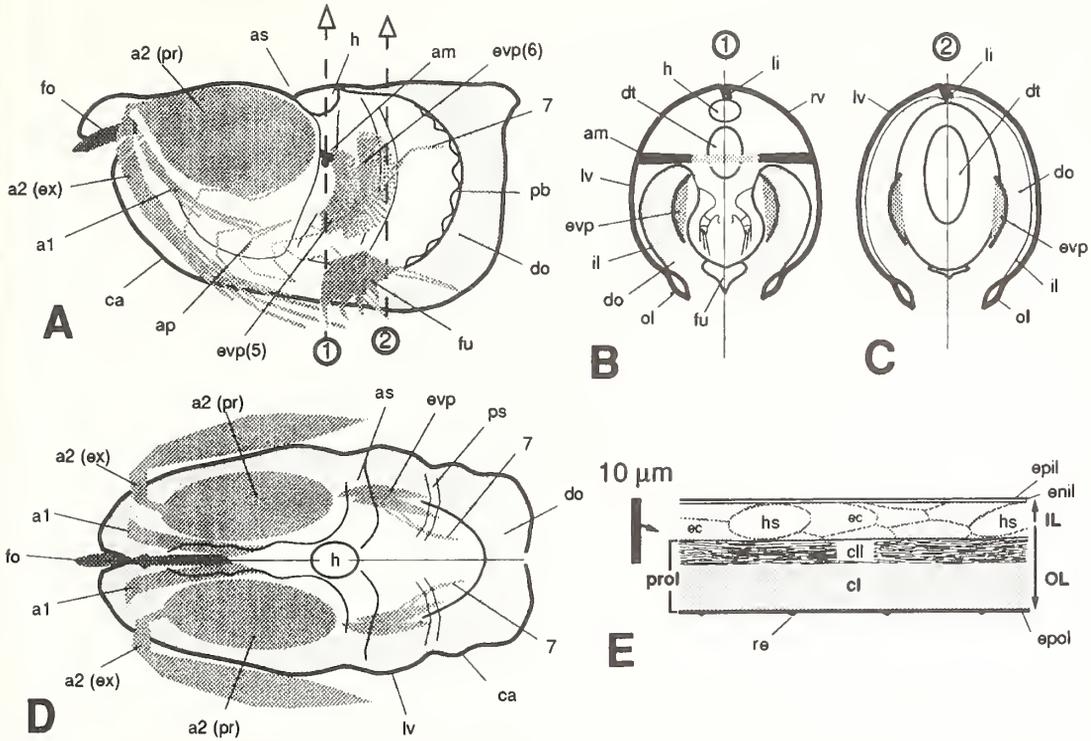
*Myodocopida* (Vargula: Text-figs 1C–D, 2; Leuroleberis: Text-fig. 17). Two pairs of trunk appendages are present, the second one being modified into a pair of multifunctional serpentiform appendages (= 7th limb; see Vannier and Abe 1993). The carapace is ellipsoidal, valves being provided with a rostrum and a rostral incisure allowing well-developed frontal appendages to



TEXT-FIG 2. Anatomy, carapace design and carapace ultrastructure of Recent mydocopid ostracodes, exemplified by *Vargula hilgendorfi* (G. W. Müller, 1890) (Mydocopida, Cypridinidae) from Japan. A, lateral view from left, left valve removed; B-C, simplified transverse sections as indicated in A (① and ②); D, simplified horizontal section; E, schematic cross section through carapace. Animal length approx. 3 mm. Outline of anatomical features simplified from SEM observations and microtomed sections. a1 = 1st antenna; a2 = 2nd antenna; am = adductor muscles; an = anus; ap = 3rd to 6th pair of appendages (not represented); ca = carapace; cel = calcified inner lamella; cgl = coarse granular calcified layer; cl = claw of furca; cll = chitinous-rich laminated layer; col = calcified outer lamella; do = domiciliary cavity; dt = digestive tract; ec = epidermal cells; epil = epicuticle of inner lamella; enil = epicuticle of inner lamella; epol = epicuticle of outer lamella; evp(5) = epipodial ventilatory plate (5th limb); fu = furcal lamella; h = heart; hc = haemolymph corpuscle (haemocyte); hs = haemolymph sinus; il and IL = inner lamella; lce = lateral compound eye; li = ligament; lv = left valve; me = medial eye; ohl = outer calcified homogeneous layer; OL = outer lamella; pb = posterior wall of body; prol = procuticle of outer lamella; rv = right valve; sl(7) = serpentine limb (7th limb).

protrude from the carapace forward and laterally; it is an important functional feature (Vannier and Abe 1992, 1993) involved in swimming and digging activities. A pair of sclerotized furcal lamellae terminates the body posteriorly. Light receptors consist of a medial eye and may include a pair of compound lateral eyes (Huvar 1990). A circulatory system (heart, arteries, haemolymph sinuses; Abe and Vannier 1993b; Text-figs 8, 15) is present. Book gills, usually seven pairs, occur in one particular family, the *Cylindroleberididae* (e.g. *Leuroleberis*; Text-fig. 7) and are interpreted (Vannier *et al.* in press) as the possible remains of lost appendages. The same overall morphology can be recognized in most living mydocopid species and also in the lowermost Mesozoic (Weitschat 1983a, 1983b; Weitschat and Guhl 1994) and Lower Palaeozoic (Vannier and Abe 1992) ancestors of the group.

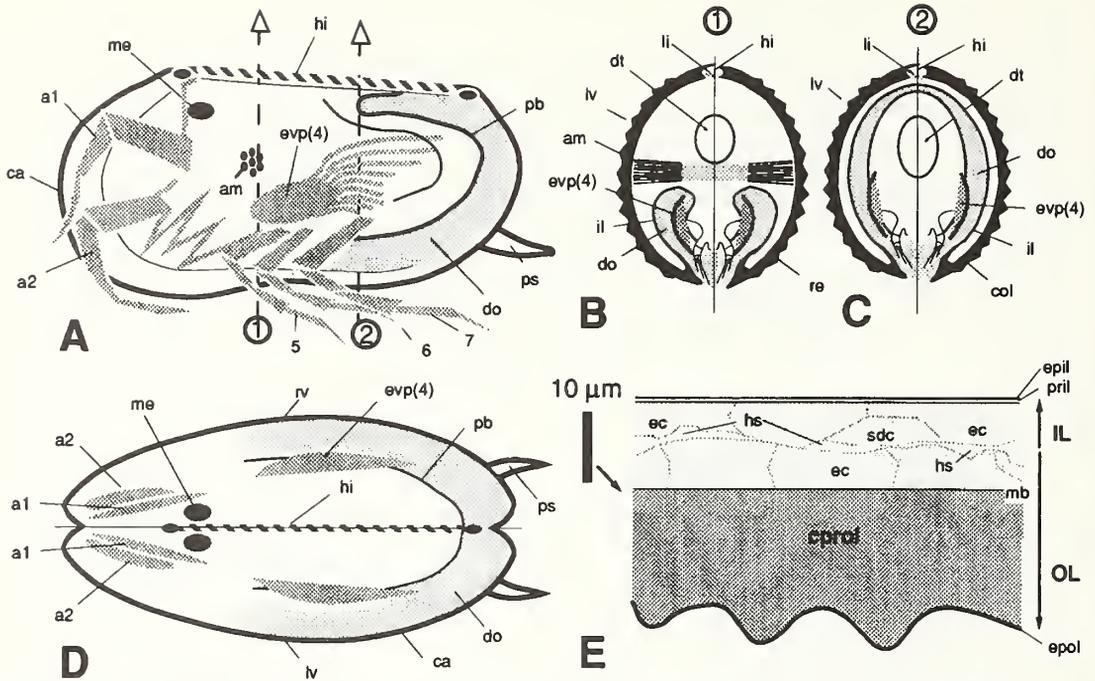
*Halocyprida* (Conchoecia: Text-figs 1A-B, 3). The most distinctive features of halocyprid ostracodes such as *Conchoecia* are 1), the lobation of the carapace expressed as a major constriction



TEXT-FIG 3. Anatomy, carapace design and carapace ultrastructure of Recent halocyprid ostracodes, exemplified by *Conchoecia atlantica* (Lubbock, 1856) (Halocyprida, Halocyprididae) from Japan. A, lateral view from left, left valve removed; B-C, simplified transverse sections as indicated in A (① and ②); D, simplified horizontal section; E, schematic cross section through carapace. Animal length, approx. 3.5 mm. Outline of anatomical features simplified from SEM observations and microtomed sections. Abbreviations (additional to those used in Text-figure 2): a2(ex) = 2nd antenna (exopodite); a2(pr) = 2nd antenna (protopodite); ap = appendages (3rd and 4th pair; not represented); as = adductor muscle; cl = calcified layer; evp = epipodial ventilatory plate; evp(6) = epipodial ventilatory plate (6th limb); fo = frontal organ; ol and OL = outer lamella; ps = posterior sulcus; re = reticulation; 7 = 7th limb.

posterior to the 2nd antenna, and 2), the exceptionally long and straight dorsal attachment of the valves. These two features are unknown in other ostracodes except Palaeozoic archaeocopes, palaeocopes and some mydocopes. The muscular protopodite of the 2nd antenna (Text-fig. 1B) is developed in relation to the free-swimming lifestyle of the animals. The second pair of trunk appendages (= 7th limb) is directed backwards and oscillates along the posterior part of the body (e.g. *Conchoecia*; Text-figs 1, 3; unpublished data from video recordings). These appendages may have the same function as the 7th limbs of mydocopids although they are not serpentiform. Integumental anastomosing channels and a dorsal heart are present, although the integument is much thinner than that of mydocopids (compare Text-figs 2E and 3E). Eyes are missing; the frontal organ protruding from the carapace below the rostrum is assumed to be the main (chemo?) sensory receptor.

*Podocopida* (Bicornucythere Text-figs 1E-F, 4). The lack of anterior rostral features and frontal openings is a distinctive characteristic of podocopid ostracodes. Appendages mainly protrude ventrally through the narrow gape of the valves to accommodate the benthic lifestyle of these animals. The maxillules are derived from head segments and the two pairs of trunk appendages are



TEXT-FIG 4. Anatomy, carapace design and carapace structure of Recent podocope ostracodes, exemplified by *Bicornucythere bisanensis* (Okubo, 1975) (Podocopida, Cytheracea) from Japan. A, lateral view from left, left valve removed; B–C, simplified transverse sections as indicated in A (① and ②); D, simplified horizontal section; E, schematic cross section through carapace. Animal length, approx. 0.9 mm. Outline of anatomical features simplified from SEM observations and microtomized sections. Abbreviations (additional to those used in Text-figure 2): cprol = calcified procuticle of outer lamella; evp(4) = epipodial ventilatory plate (4th limb); hi = hinge; hs = haemocoelic space; mb = membrane; pril = procuticle of inner lamella; ps = posterior spine; re = reticulated ornament; sdc = subdermal cell; 5–7 = 5th to 7th pair of appendages.

transformed into legs for locomotion and sometimes for precopulatory activities (see Abe and Vannier 1991, 1993a). The visual organs derived from the medial eye complex are the only photoreceptors. The epidermal layers of the cuticle lack any differentiated vascular system (see Okada 1981, 1982, 1983; Keyser 1982, 1990) or heart. Furcae are generally poorly developed in comparison with those of mydocopes. The carapace integument is comparatively more heavily calcified in podocopes than it is in mydocopes (see Dalingwater and Mutvei 1990).

*Other groups.* The overall body plan of platycopine ostracodes (Howe *et al.* 1961; Whatley 1991), represented by only two cytherellid genera in the Recent, remains comparable with that of most podocopids. The only distinctive characteristics include a brood chamber defined anteriorly by a vertical ridge, strong clustered adductor muscle scars, a lamelliform furca and the reduction of the two last thoracic appendages. The peculiar appendage morphology of the platycopines may be closely related to the filter feeding (Cannon 1933) and the burrowing mode of life of these animals. A similar adaptation to filter feeding also occurs within the Mydocopa as, for instance, in the cylindroleberidids (Kornicker 1981; Vannier *et al.* in press; JV, unpublished data from scanning electron microscopy and video recordings).

The thaumatocypridid (three genera; Kornicker and Sohn 1976), and the polycopid ostracodes (four genera; Kornicker and Morkhoven 1976) are typically small (1–2.5 mm) mydocopes enclosed within an ellipsoidal, often nearly circular carapace. In spite of a distinctive carapace

design (e.g. no rostrum), these animals have basically the same internal anatomy as that of most myodocopes (Cohen 1982) except that they lack a heart and visual organs. The absence of the 6th and 7th pairs of appendages in polycopids is probably related strongly to the miniaturization of these animals in interstitial habitats (see Hartmann 1973).

The living punciids, represented by *Manawa*, are unique in terms of soft anatomy, carapace design and ontogeny (Swanson 1989a, 1989b, 1990). The carapace of adults has a flattened horizontal life position with appendages extending laterally. The hinge line is long and straight, similar to that of extinct Palaeocopa. Another peculiar feature is the univalved-bivalved transition during the ontogeny, unknown in ostracodes other than in the early Cambrian ancestors of the group (Zhang and Pratt 1993). The affinities of punciids within the Ostracoda (Podocopida or Platycopida?) are still unclear (Swanson 1989b). New collections and video observations of live specimens by one of us (KA, Dec. 1994) are expected to shed new light upon these enigmatic organisms.

*The body plans of Recent Ostracoda.* The term 'body plan' or 'Bauplan' encompasses here the notion of symmetry, architecture and structural range, as well as the functional aspect of the design. Although the internal and external anatomy of the living representatives of Ostracoda may vary greatly in detail, making generalizations difficult, it seems that only two body plans prevail within the modern fauna.

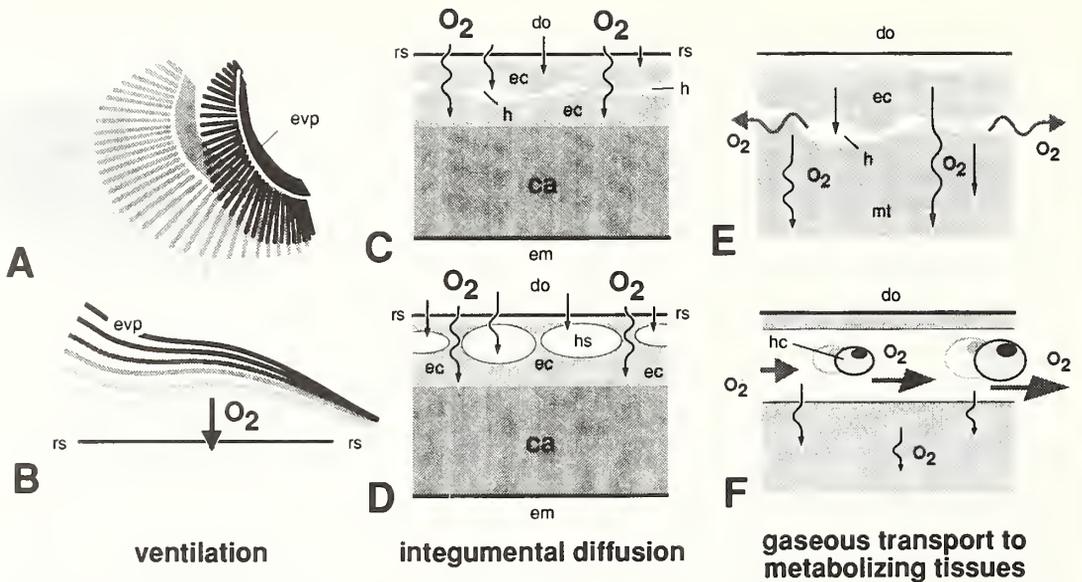
'Body plan 1' corresponds to bivalved crustaceans with a bilateral symmetry and a strong frontal polarity. The anterior part of such animals (e.g. rostrum, antennae) confronts the environment first either when swimming or digging. Nekto-benthic or planktonic organisms have a high activity-level and an ellipsoidal shape well suited for moving through water or soft muddy sediment. Internal and integumental circulation occurs primarily, allowing a larger body size (see below). Most myodocopes (Myodocopida, Halocyprida) fall into this category.

'Body plan 2' corresponds to bivalved crustaceans with a ventral polarity (left/right valve symmetry) or a lateral polarity (left/right valve asymmetry). Such organisms (e.g. Podocopa) are mostly crawlers (on the thoracic legs) on a substratum or within flocculent material, and occasionally remain motionless, simply resting on one valve. The carapace is heavily calcified usually bearing strengthening features. A circulatory system is absent. The physical constraints of gaseous diffusion confine these animals to a small size (see below).

The living ostracode fauna as a whole has a high diversity at low taxonomic level (Table 1) and conversely a low disparity (Gould 1991; Willis *et al.* 1994) in terms of high-level body plans. Judging from the great variety of carapace designs known from the fossil record, one might easily speculate that the diversity of body plans was much higher in the early history of the group, especially in the Ordovician (see Vannier *et al.* 1989). The Cambrian fauna produced unique carapace designs, unknown in present day faunas, e.g. the extinct archaeocopids with interdorsal features (Hinz 1993). However, the lack of information on the soft anatomy of Palaeozoic ostracodes makes it difficult to evaluate the actual magnitude of differences between higher taxa. Whether the disparity among ostracodes was greater in the early Palaeozoic than in the present day has not been clearly determined yet.

## RESPIRATORY FEATURES

*Molecular diffusion.* Most ostracodes (e.g. all podocopes) lack any specialized respiratory organs such as gills, or a heart and circulatory system. Similarly with other minute invertebrates, gas exchange is assumed (McMahon and Wilkens 1983) to take place through the integument of the carapace inner lamella and across the general surface of the body integument (Text-fig. 5A–B, D–E). Ultrastructural studies (Keyser 1990) showed that the uncalcified inner lamella of podocopid ostracodes is not only a respiratory site of exchange but also a preferential area for osmoregulation. The epipodal respiratory plates (Text-figs 1–4) which are well developed in ostracodes, are in no way true respiratory organs comparable with the thin-walled and well vascularized gills of, for instance, malacostracans (Taylor and Taylor 1992); their actual and major function is to ventilate

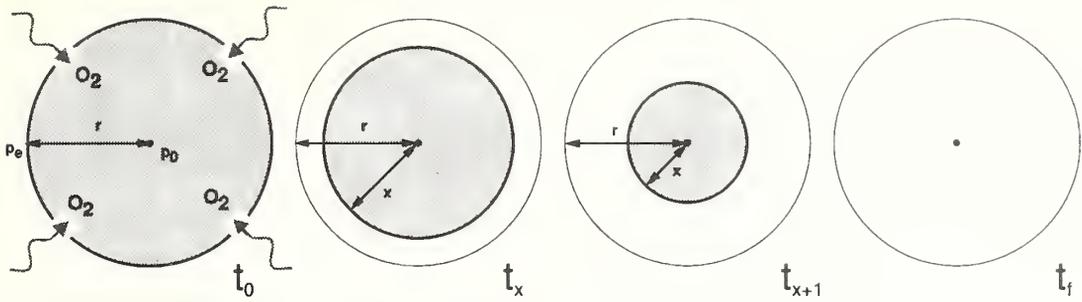


TEXT-FIG 5. Successive steps in the respiratory processes of Ostracoda. A–B rhythmic ventilation (epipodial ventilatory plate) over the surface of integument. C–D, integumental diffusion through the inner lamella (see Text-figs 2–4B–C, E); C, podocopes; D, mydocopes with a circulatory system. E–F, gaseous transport to metabolizing tissues; E, mainly by diffusion in podocopes; F, by fluid convection in mydocopes. ca = calcified part of outer lamella; do = domicilium; ec = epidermal cells; em = external medium; evp = epipodial ventilatory plate; h = haemocoelic space; hc = haemolymph corpuscle (haemocyte); hs = haemolymph sinus; mt = metabolizing tissues;  $O_2$  = oxygen; rs = respiratory surface; vs = ventilatory surface.

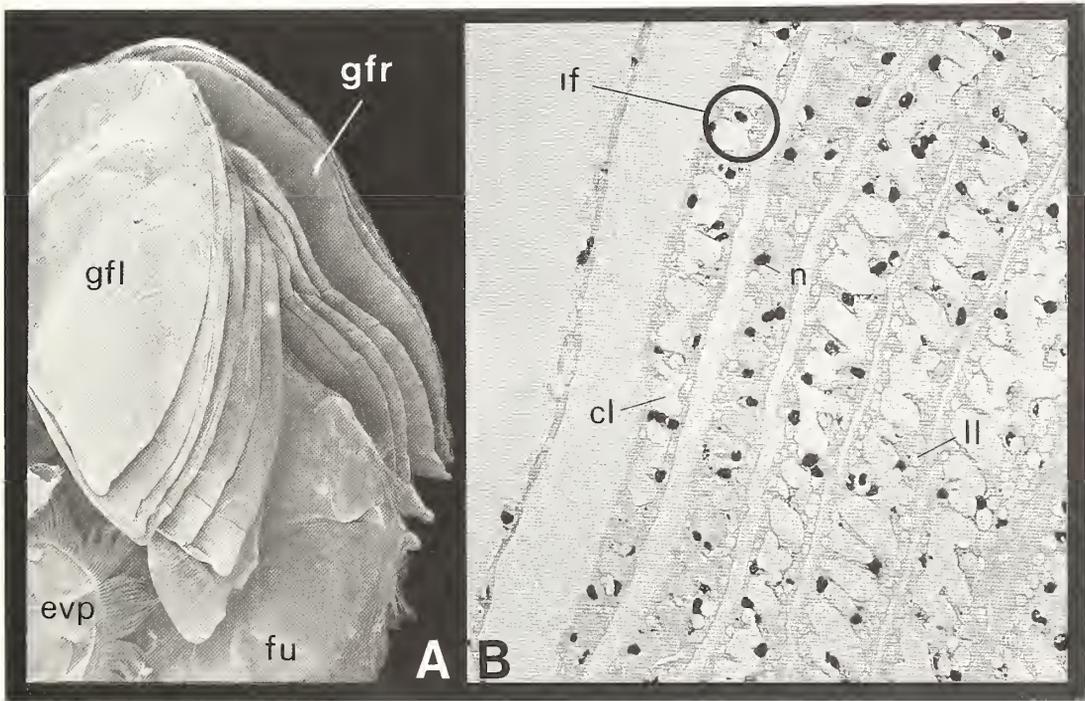
the domiciliar cavity (Abe and Vannier in press), thus creating and maintaining partial pressure gradients between the medium and the respiratory surface. The integument of the inner lamella of the podocopid *Bicornucythere bisanensis* (Text-fig. 4) and the mydocopid *Vargula hilgendorfii* (Text-fig. 2) is uncalcified and consists of an epicuticle (Okada 1982) and a procuticle overlying epidermal cell layers. In *Vargula hilgendorfii*, the integument is as thin as 3–5  $\mu\text{m}$  on the muscular protopodite of the swimming appendages or on the posterior surface of the body and ten times thicker and heavily sclerotized on the furcal lamellae. Gaseous diffusion is obviously facilitated in areas with a thinner integument, in relation to metabolic and functional requirements.

Fluids are present within the carapace of ostracodes even in those lacking a circulatory system (Hartmann 1966). Transmission electron microscope sections of *Cyprideis torosa* (Podocopida; Keyser 1990, fig. 12) and *Hirschmannia viridis* (Podocopida; Keyser 1982, fig. 4) show irregular haemocoelic spaces between the inner and outer layers of epidermal cells (see Text-fig. 4E); similar features are widespread among small crustaceans, for instance in branchiopods (*Daphnia magna*; see Martin 1992, fig. 7). Although their function has not been examined, it is clear that such haemocoelic fluids may increase the effectiveness of diffusion in transferring respiratory gases over short distances.

*Specialized respiratory surfaces.* External integumental folds attached to the dorsal part of the body and usually interpreted (e.g. Kornicker 1981, 1991a, 1991b, 1992, 1994) as gill-like features involved in respiration processes (see Hartmann 1967) are found in cylindroleberidid mydocopid ostracodes. However, no illustrations, using modern techniques, have been published so far. We observed these features in *Leuroleberis surugaensis* from Japan (Text-fig. 7). They consist of a right and a left series

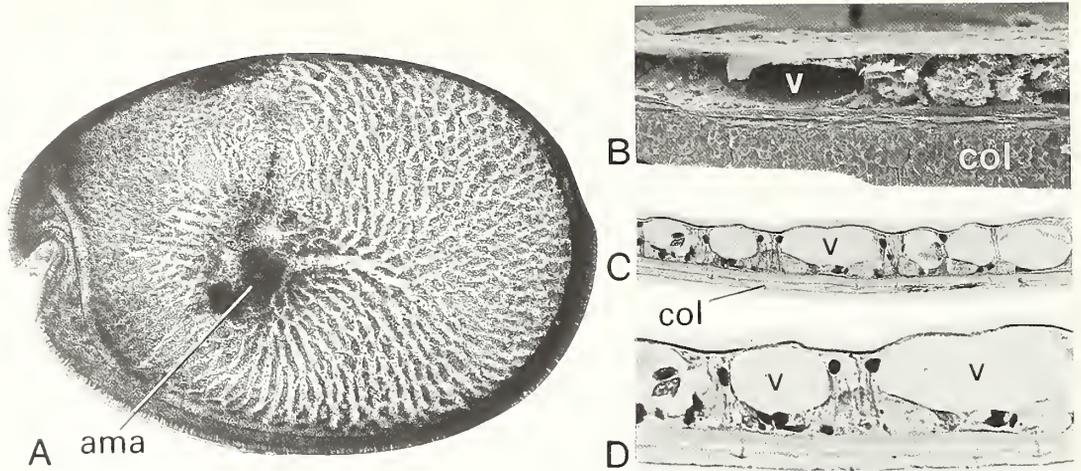


TEXT-FIG 6. Gaseous diffusion of oxygen through the living tissues of a spherical animal (see explanation in text) from the integumental respiratory surface (initial time  $t_0$ ) to the centre of the animal body (final time  $t_f$ ).  $p_e$  = partial pressure of oxygen in the external medium;  $p_0$  = partial pressure of oxygen in centre of animal body;  $r$  = body radius;  $t_0$ ,  $t_x$ ,  $t_{x+1}$  and  $t_f$  = time for each step.



TEXT-FIG 7. Specialized respiratory features in mydocopid ostracodes exemplified by *Leuroleberis surugaensis* Hiruta, 1982, from Shimoda, Japan. A, FSL 575091; scanning electron micrograph showing 7 pairs of book gills on both sides of the posterior part of the body; carapace removed;  $\times 24$ . B, stained (haematoxylin-eosin) microtomed paraffin horizontal section through the gills;  $\times 215$ . cl = central lacunae; evp = epipodial ventilatory plate; fu = furcae (basal part); gf(l) and gf(r) = left and right gills; if = individual fold; ll = lateral lacunae; n = nucleus.

of seven lamellar fold-like extensions of the body integument, each individual lamella representing a large double-sided surface in contact with sea water. In section (Text-fig. 7B), these lamellae show a complex system of central and smaller lateral lacunae surrounded by connective cells, both characteristics suggesting that these are sites for respiratory exchanges. The vascular nature of this



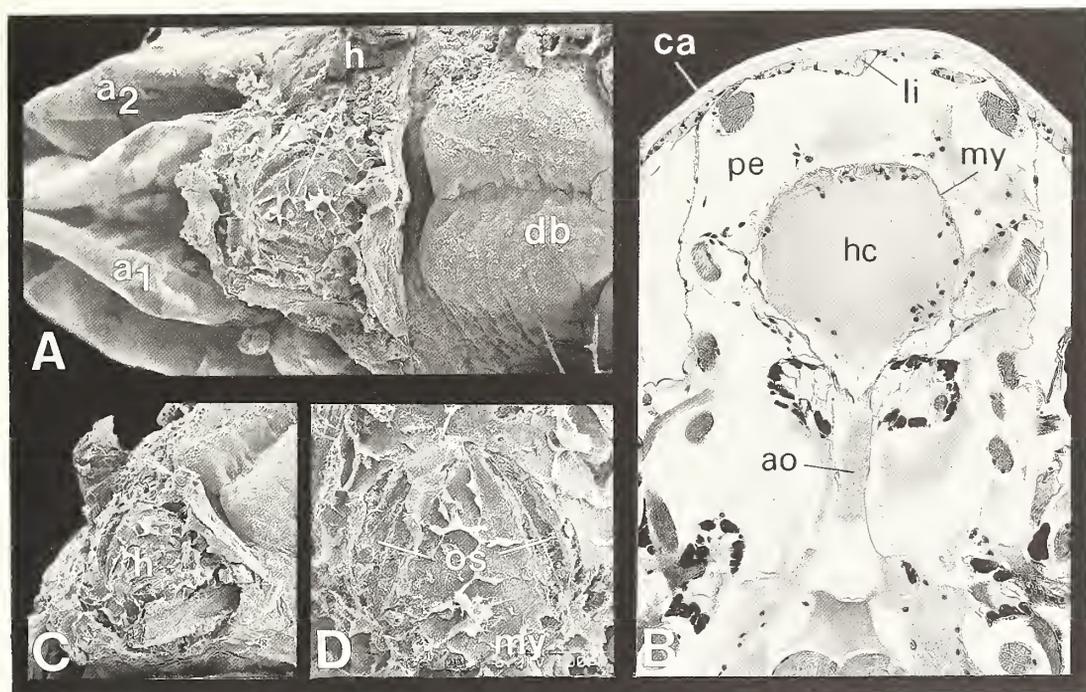
TEXT-FIG 8. Integumental circulatory system of *Vargula hilgendorffii* (Mydocopida, Cypridinidae) from Tateyama, Japan. A, FSL 575092; anastomosing pattern of a left valve (adult female) in transmitted light;  $\times 24$ . B, transverse section through carapace showing vascular features (sinuses); scanning electron micrograph;  $\times 450$ . C–D, stained (haematoxylin-eosin) microtomed paraffin section through carapace (see Text-fig. 2);  $\times 145$  and  $\times 330$ , respectively. ama = adductor muscle attachment; col = calcified outer lamella; v = vascular space (haemolymph sinus).

lacunar network and the flow route of haemolymph through it, have been examined in a separate study (Vannier *et al.* in press). Possible homologues of the paired book gills of Recent cylindroleberidids can be found in lowermost Mesozoic mydocopid ostracodes (Weitschat 1983a, b).

*Circulation.* In larger ostracodes, both Mydocopida and Halocyprida, diffusion obviously remains the basis of gaseous exchanges but is supplemented by internal fluid convection. A fluid (haemolymph) conveying cellular components (haemocytes) was observable both on video recordings and in stained paraffin sections (Text-fig. 5F; Abe and Vannier in press) within the integument of *Vargula hilgendorffii* (Mydocopida) and of *Conchoecia atlantica* (Halocyprida). The anastomosing vascular network present within the carapace of such ostracodes (Text-fig. 8) is part of an integrated circulatory system including a propulsive organ (dorsal heart; Text-figs 9, 12), efferent (aorta) and afferent vessels (e.g. dorsal channel). In *Vargula hilgendorffii* and other mydocopids, the vascular network is always best developed in the posterior half of the carapace (Text-fig. 8A) and this particular area of the domiciliar cavity is assumed to be a preferential site for oxygen uptake, similar to that in other bivalved crustaceans (e.g. Branchiopoda; see Martin 1992, fig. 68). Haemolymph enters the anastomosing network of each valve around the adductor muscle attachment (Text-fig. 8A), through an isthmus which connects the body wall to the inner lamella and then flows radially through the sinuses back to the pericardial cavity of the heart. It is not understood yet how oxygen is transported to the metabolizing tissues, whether it is dissolved in plasma, bound to extracellular pigments such as haemoglobin (Goodwin 1960; Martin 1992) or, less probably, conveyed by the haemocytes. In other crustaceans closely related to Ostracoda, such as Branchiopoda, the extracellular respiratory pigments are not present in haemocytes (Martin 1992).

The living leptostracan phyllocarids possess a comparable circulatory system (Rolfe 1969). The carapace integument is pervaded by a dense network of arched sinuses and marginal channels through which haemolymph flows (video observations; JV unpublished) before returning to the dorsal pericardial cavity. *Nebalia bipes* (see Cannon 1960) from Japan and *Dahlella caldarensis* (see

Hessler 1984) from the East Pacific region are currently being studied for comparison with ostracodes.



TEXT-FIG 9. Heart morphology of *Vargula hilgendorffii* (Mydocopida, Cypridinidae) from Tateyama, Japan. A, C–D, FSL 575093; male specimen, carapace removed; dorsal view ( $\times 60$ ), intermediate anterior view ( $\times 60$ ) and dorsal close-up ( $\times 100$ ) of heart. B, female specimen; stained (haematoxylin-eosin) microtomed paraffin section through carapace; transversal section through heart;  $\times 95$ . a1 = first antenna; a2 = second antenna; ao = aorta; ca = carapace; db = dorsal part of body; h = heart; hc = heart cavity with haemolymph and haemolymph corpuscles (haemocytes); li = ligament; my = myocardium; os = ostium; pe = pericardium.

#### CRITICAL SIZE OF OSTRACODES

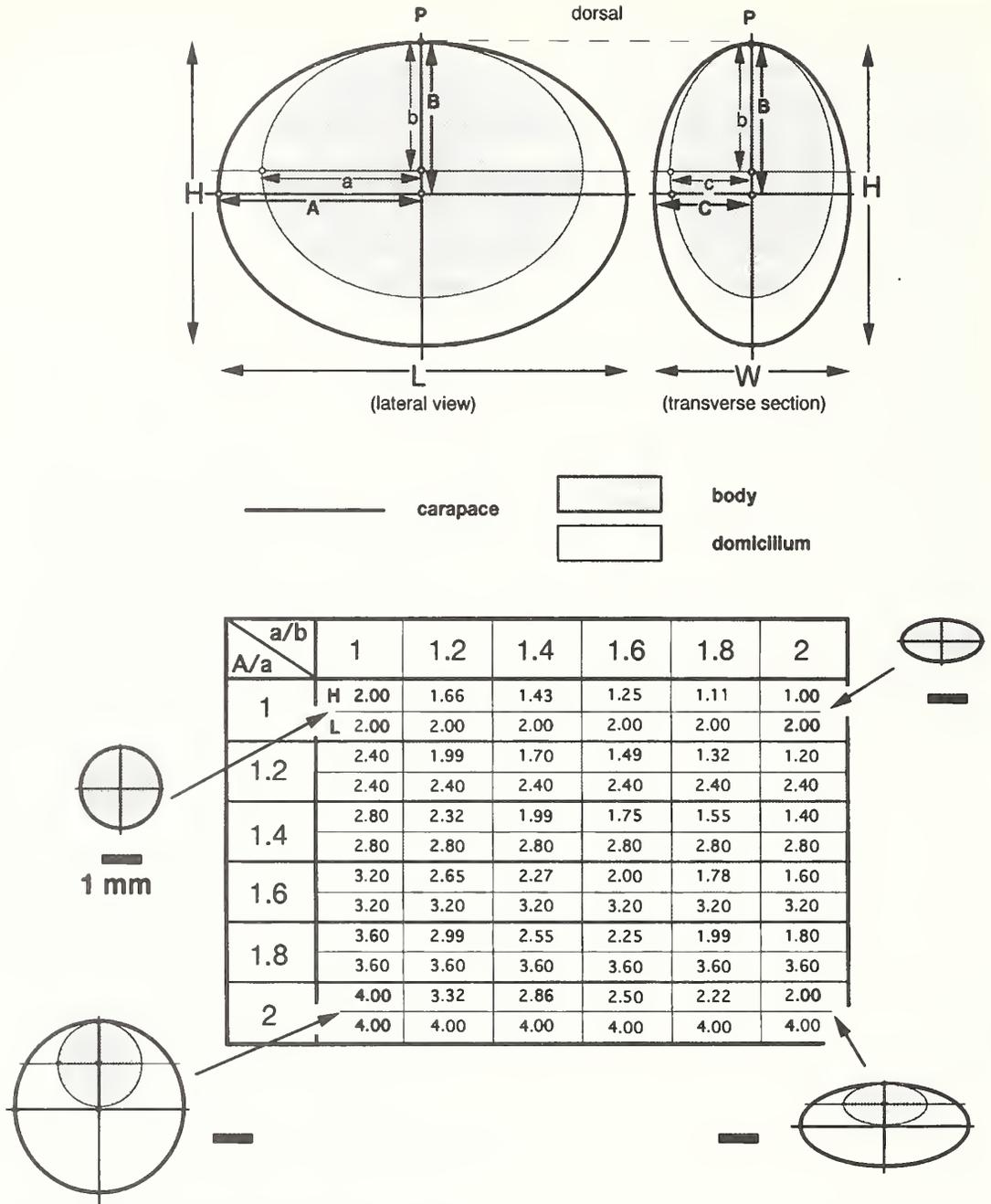
*Ostracodes with no circulatory system.* We considered the theoretical case of an ostracode having an ellipsoidal body (parameters  $a$ – $c$  in Text-figure 10) enclosed within an ellipsoidal carapace (parameters  $A$ – $C$  in Text-figure 10) attached to the body by a single point (P). Although this assumption obviously ignores the actual complexity of ostracodes (e.g. external ornament and appendage morphology), it remains fairly consistent with the average shape of living ostracodes (see Text-figs 2–4). Gaseous diffusion is assumed to occur evenly over the entire surface of the body and at a constant rate through the integument to the metabolizing tissues (Text-fig. 6). Gases such as oxygen diffuse (McMahon and Wilkens 1983) along partial pressure gradients from the outer (integument) to the innermost regions of the body at a rate  $J$  ( $\text{mm}^3 \text{s}^{-1}$ ) given by the equations

$$J = -SK dp/du \quad (1)$$

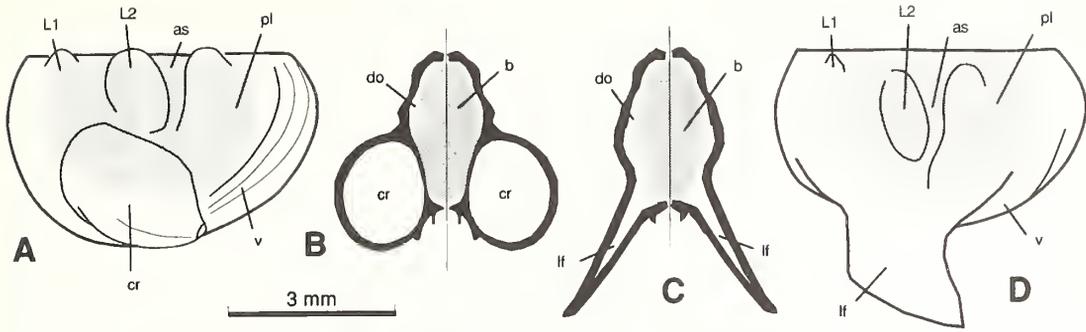
and

$$J = mV, \quad (2)$$

where  $S$  ( $\text{mm}^2$ ) is the area across which the diffusion occurs,  $K$ , a permeability constant ( $\text{mm}^2 \text{atm}^{-1} \text{sec}^{-1}$ ),  $p$ , the partial pressure (atm) of  $\text{O}_2$ ,  $u$ , the distance (mm) over which  $\text{O}_2$  is having to diffuse,  $dp/du$ , the partial pressure gradient,  $m$ , the rate at which  $\text{O}_2$  is used per unit volume of tissue ( $\text{mm}^3 \text{O}_2 \cdot \text{mm}^3 \text{sec}^{-1}$ ) and  $V$ , the volume of tissues ( $\text{mm}^3$ ). These relations apply to many other



TEXT-FIG 10. Maximum carapace size (length  $L$  and height  $H$  in mm) of ostracodes relying on gaseous diffusion only, assuming that 1 mm is the critical distance from integument surface to body centre (see equations and explanation in text). The ostracode carapace and body are considered herein as simple ellipsoidal volumes defined by three parameters:  $A, B, C$  and  $a, b, c$ , respectively, with  $A/a = B/b = C/c, a = 1, a > b > c$ . Figures in table are given for  $a/b$  and  $A/a$  varying from 1 to 2. Lateral outlines of ostracodes are given for extreme values of  $a/b$  and  $A/a$ . The shaded area in the table corresponds to the expected maximum size for most ostracodes ( $a/b$  and  $A/a$  ranging from 1.2 to 2 and 1.2 to 1.6, respectively).



TEXT-FIG 11. Carapace and estimated body size in large beyrichiacean (Palaeocopa) ostracodes, exemplified by *Gibba kandarensis* (see Galle *et al.* 1995) from the Lower Devonian of Morocco. A, D, lateral external views of an adult male and female (left valves), respectively. B–C, simplified transversal section through a male and female carapace. Estimated body volume represented by a shaded area. as = adductorial sulcus; b = body; cr = crumina (brood pouch); do = domicilium; lf = lateroventral flange; L1 = anterior lobe; L2 = pre-adductorial lobe; pl = posterior lobe; v = velum.

invertebrate animals and have been used often by biologists (Alexander 1979; Schmidt-Nielsen 1990; Motokawa 1992) to tackle the problem of maximum body size. If we consider the simplest case where  $a = b = c = r$  (spherical body of radius  $r$ ), then,  $u = r - x$  (radius) at a time  $t_x$  (see Text-fig. 6),  $S = 4\pi x^2$  and  $V = 4/3\pi x^3$ . Equating (1) and (2) we have

$$mV/A dx = K dp.$$

In the present case,  $O_2$  diffuses through the whole body of an ostracode from the integument (partial pressure  $p_e$ ) to the centre ( $p_0$ ).

$$m \int_0^r V/A dx = k(p_e - p_0),$$

$$m \int_0^r x/3K dx = k(p_e - p_0),$$

that is,

$$p_e - p_0 = mr^2/6K.$$

Because  $p_e - p_0$  must be positive (oxygen goes from the periphery to the inside of the body),

$$p_e \geq mr^2/6K$$

$$r \leq \sqrt{(6Kp_e/m)}. \quad (3)$$

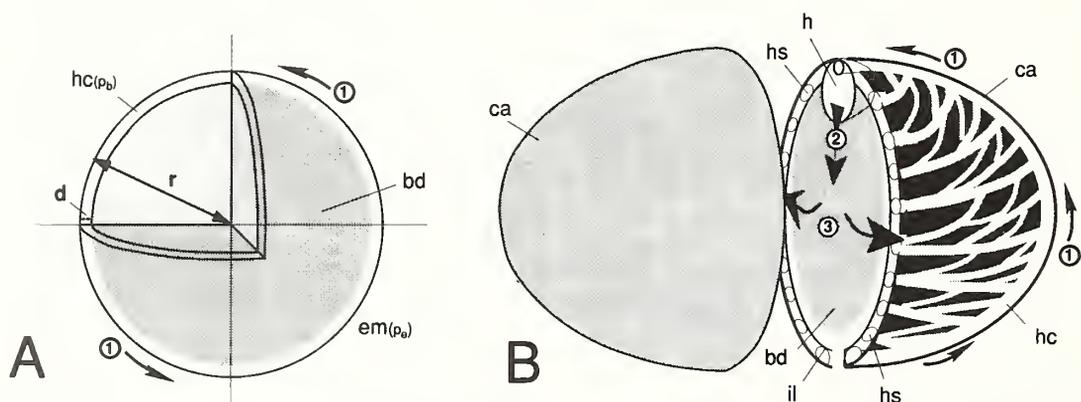
The partial pressure of  $O_2$  in well aerated water is  $p_e = 0.21$  atm;  $K$  and  $m$  are about  $2 \cdot 10^{-5} \text{ mm}^2 \text{ atm}^{-1} \text{ sec}^{-1}$  and  $2.8 \cdot 10^{-5} \text{ mm}^3 \text{ O}_2 \cdot \text{mm}^{-3} \text{ sec}^{-1}$ , respectively (Alexander 1979; Motokawa 1992). The final calculation (3) indicates a critical radius of 1 mm, over which diffusion does not suffice to supply a spherical organism with  $O_2$ . If we suppose that ostracodes have an overall ellipsoidal body shape with  $c < b < a$ , then 'a' should not exceed 1 mm. We estimated (Text-fig. 10) the critical maximum size of ostracodes assuming gaseous diffusion only, for a body ratio  $a/b$ , and for body:carapace ratios  $B/b$  and  $A/a$  varying from 1 to 2. For instance,  $A/a = B/b = 1$  and  $a/b = 2$  (top right figure, Text-fig. 10) corresponds to an elongated carapace of 2 mm length and 1 mm height, entirely occupied by the body mass;  $A/a = B/b = 2$  and  $a/b = 1$  (bottom left figures, Text-fig. 10) give an ostracode of 4 mm in both length and height. These two extreme examples are not expected to be found in nature, nor in the fossil record, and the actual range of critical sizes is likely to be narrower than that envisaged in the whole table (Text-fig. 10). The vast majority of living ostracodes has  $A/a$ ,  $B/b$  or  $C/c$  ratios ranging from 1.2 to 1.6 with a body ratio of about 1.2 to 2. For such organisms the maximum size would approach 3.2 mm long (Text-fig. 10). Our

calculations are consistent with the fact that living podocopes and small myodocopes with no vascular system (e.g. Polycopidae) are all smaller than 3 mm in adult carapace size. The same predictions seem to be applicable to the entire fossil record of the podocope ostracodes (Ordovician to Recent) and to numerous extinct ostracode groups such as *Palaeocopa* and *Binodicopa* (Vannier *et al.* 1989) and to many Cambrian archaeocopes as well. A few exceptions apparently exist. Some beyrichiacean ostracodes (*Palaeocopa*) are known to exceed 5 mm in adult carapace length (Groos and Jahnke 1970; Galle *et al.* 1995; Text-fig. 11). However, this unusually large size is mainly a result of calcified extensions of the carapace such as the inferred brood pouch of females and the large lateroventral flanges of adult males; the body of these ostracodes was obviously much smaller, confined within a relatively narrow ellipsoidal domiciliar space (Text-fig. 11B-C). In such a case, diffusion may have been sufficient to provide the animal with oxygen.

*Ostracodes with a circulatory system.* Simple calculations for invertebrate organisms such as marine worms bearing a simple peripheral circulatory vessel have been attempted by Alexander (1979) and Motokawa (1992), and can be tentatively applied to ostracodes if we consider, again, a theoretical animal with a spherical shape (Text-fig. 12A). This is a relatively close approximation of the actual circulatory system of myodocopid ostracodes in which the anastomosing channels develop over almost the entire surface of the carapace (Text-fig. 12B). Equations (1) and (2) above are used again with  $S = 4\pi r^2$  and  $V = 4/3\pi r^3$  and  $dp/ds = (p_e - p_b)/d$  (see Text-fig. 12A). We have

$$r = 3K(p_e - p_b)/md. \quad (4)$$

The partial pressure of  $O_2$  in the peripheral haemolymph channel ( $p_b$ ) of diameter ( $d$ ) is estimated to be about  $5 \cdot 10^{-2}$  atm by comparison with figures obtained from other small invertebrates (Motokawa 1992);  $d = 3 \cdot 10^{-2}$  mm is consistent with the average diameter of the integumental haemolymph sinuses in *Vargula hilgendorffii* (Abe and Vannier in press). We assume, as before, that the partial pressure of  $O_2$  ( $p_e$ ),  $K$  and  $m$  are about 0.21 atm,  $2 \cdot 10^{-5}$  mm<sup>2</sup>.atm<sup>-1</sup> sec<sup>-1</sup> and  $2 \cdot 8 \cdot 10^{-5}$  mm<sup>3</sup>  $O_2$ .mm<sup>-3</sup> sec<sup>-1</sup>, respectively. Calculations indicate that the maximum possible radius would be 11.4 mm. Consequently, the maximum length of a spherical ostracode having such a peripheral circulatory system is estimated to reach 22.8 mm. This estimation fits surprisingly the actual size range of *Gigantocypris*, the largest known living ostracode with an almost spherical soft carapace about 32 mm long and a circulatory system (Cannon 1940).



TEXT-FIG 12. Peripheral fluid convection in a spherical animal (A) and as observed in *Vargula hilgendorffii* (B), simplified. bd = body; ca = carapace; d = diameter of channel;  $em(p_e)$  = partial pressure of  $O_2$  ( $p_e$ ) in external medium (em); h = heart; hc = haemolymph channel;  $hc(p_b)$  = partial pressure of  $O_2$  ( $p_b$ ) in haemolymph channel; hs = haemolymph sinus; il = inner lamella of cuticle; r = radius; ① = peripheral circulation; ② = circulation from heart to organs; ③ = circulation from organs to anastomosing vascular system.

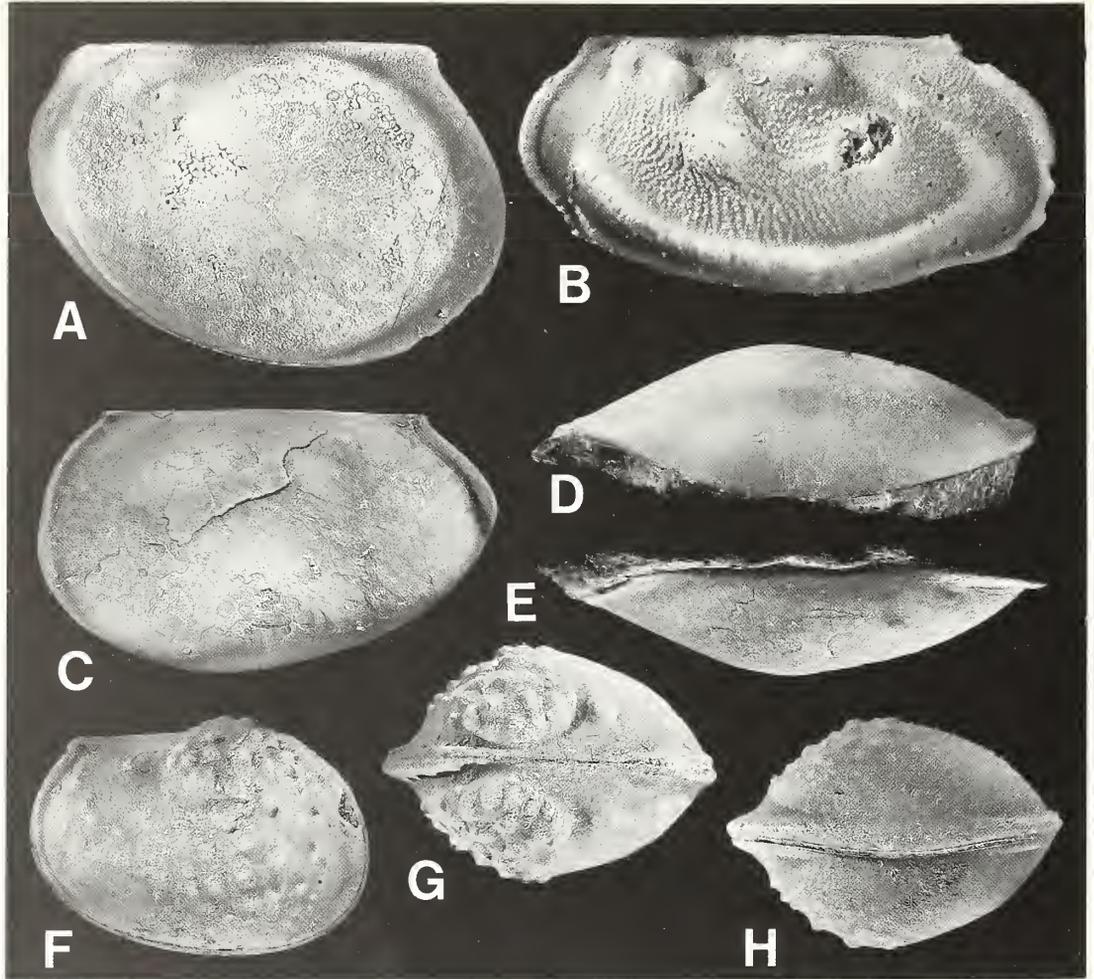
However, a major criticism can be made against such simplistic models and their subsequent predictions of a maximum size. The peripheral circulatory system of myodocopid ostracodes runs between the outer and the inner cuticular lamellae of the carapace and therefore does not supply oxygen directly to adjacent metabolizing tissues other than epidermal cells. It is the efferent system (aorta and secondary vessels and lacunae), well developed in large cypridinid species (e.g. Cannon 1931) which actually delivers oxygen from the heart to the organs (see Text-fig. 12B②, 12B③). If such a system, even though partly lacunar, is dense and efficient enough to bring down the diffusion distances to optimal values, then no maximum critical size exists and ostracodes reaching greater than 32 mm are possible, at least in theory. In fact, the increase of body size in ostracodes with a circulatory system is most probably limited by other constraints such as design (strength of internal and external skeleton) or functional (cardiac pulse and vascular pressure). Leaving apart speculations on ostracode size, fluid convection appears as one of the key features (Abe and Vannier 1993b) which, by augmenting the diffusion processes, most probably allowed ostracodes to range beyond 3.2 mm (see calculations for diffusion only) and to attain a centimetric body size.

*The minimum size of ostracodes.* The smallest known living adult representatives of the group can be found among the interstitial fauna (Hartmann 1973), the deep-marine benthos (Peypouquet 1977; Coles *et al.* 1994 for *Krithe*) and the deep-sea pelagic fauna. Interstitial species (e.g. mesopsammitic organisms with a reduced mobility) belong either to podocopids or myodocopes (Cladocopina, Polycopidae); their body sizes rarely exceed 0.5 mm, usually ranging between 0.1 mm and 0.3 mm (Hartmann 1973). Reduction in the number of appendages, genital and visual organs is a common feature of these microcrustaceans that lack any circulatory system. Extremely small adult sizes also occur in free-living bathyal halocyprid ostracodes such as *Bathyconchoecia* sp. (0.50 mm in adult length) from Sagami Bay, Japan (unpublished data).

*Critical size and depth.* Since the critical body size of an ostracode is proportional to the partial pressure of oxygen in the surrounding medium (equation (3)), we may expect to observe variations of this critical size according to depth. The vertical distribution of oxygen dissolved in sea water, illustrated by profiles (Kester 1975) in the major oceanic basins (NE Atlantic, Indian and NE Pacific Oceans), shows a relatively constant pattern with an oxygen minimum layer (OML) between 750 m and 1100 m and relatively higher O<sub>2</sub> concentrations in deeper waters. For example, in the NE Atlantic (Kester 1975) surface and deep (from 1500 m to 5000 m) waters have comparable values of O<sub>2</sub> concentration (about 250  $\mu\text{mol kg}^{-1}$ ) and consequently of O<sub>2</sub> partial pressure. In this case and according to our model, no significant variation of the critical size is likely to occur between shallow water and deep-sea ostracodes relying on gaseous diffusion. Only those living near or within the oxygen minimum layer may have a smaller critical body size. This prediction, which may have some implications in palaeobathymetry, has to be tested by thorough investigations of the size range of the deep-sea OML species.

#### SIZE, CIRCULATORY AND RESPIRATORY FEATURES IN EARLY OSTRACODA

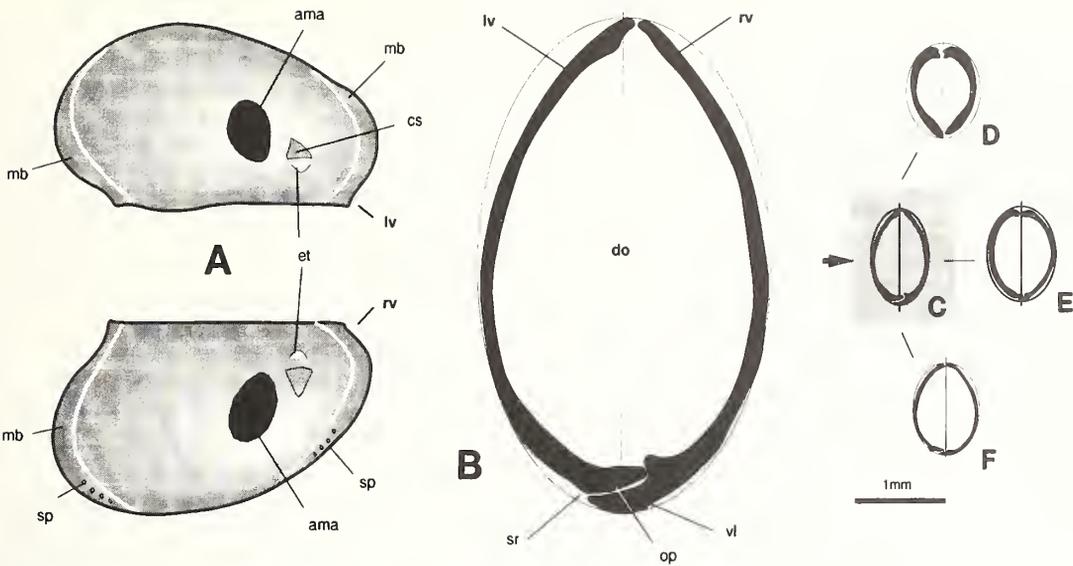
*Leperditicopes.* The extinct Order Leperditicopida (early Ordovician–Upper Devonian; Text-figs 13–14) contains the biggest ostracodes known from the palaeontological and Recent records and is particularly relevant to the problem of size in fossil Ostracoda. Leperditicopes have been reviewed extensively by Berdan (1976, 1984) and Abushik (1990). Apart from the size (adult length from several mm up to 80 mm in *Moelleritia*), the main ordinal characters include (Berdan 1984, p. 4) large adductor muscle scars composed of numerous individual attachment stigmata, a ventral overlap of the right valve over the left, including stop-features, and an inferred eye tubercle (Text-fig. 14A). The postplete lateral outline present in many leperditicopes is most probably a primitive character related to the retral swing of the animal's body within the carapace (Hinz 1993). Although their assignment to Ostracoda was denied by several authors (Swartz 1949; Heidrich 1977), we agree with Berdan (1984), Schallreuter (1978) and Langer (1973), that leperditicopes are true ostracodes.



TEXT-FIG 13. Palaeozoic leperditicope ostracodes. A, *Teichochilina jonesi* (Wetherby, 1881); USNM 338709; Lexington Limestone, Middle Ordovician; Kentucky, USA; left valve (silicified), lateral view;  $\times 4.7$ . B, *Saffordellina muralis* (Ulrich and Bassler, 1923); USNM 41561B, paralectotype; Cathey Formation, Middle Ordovician; West Nashville, Tennessee, USA; left valve, lateral view;  $\times 9$ . C-E, *Leperditia marinae* Abushik, 1980; N 7837-2; Lower Devonian (Lochkovian) of Novaya Zemlya, Russia; right valve in lateral ventral and dorsal views, respectively;  $\times 1.6$ . F-H, *Moelleritia moelleri* (Schmidt, 1883); neotype (housed in the collections of the VSEGEI Geological Institute, Saint-Petersburg, Russia; the material is being revised by A. Abushik); Devonian (Upper Emsian) of the Belaya River, Central Urals, Russia; lateral view of carapace from left, dorsal and ventral views, respectively;  $\times 2.7$ . All are light photographs. A and B reprinted from J. Berdan's negatives.

Leperditicopes share many morphological features with coeval non-lobate ostracodes such as leiocopes (Williams and Vannier 1995), for instance the overlap pattern (Text-fig. 14), the outline of transverse sections and even the shell thickness relatively to the carapace size. The only, but significant difference is size (compare Text-fig. 14B and D-F) and to a lesser extent the shell ultrastructure (see Langer 1973).

Peculiar anastomosing features frequently occur in leperditicopes, most commonly expressed as ridges on the steinkerns or negative markings on the inner surface of silicified valves (e.g. Berdan 1984, pl. 8, fig. 5), more rarely on the external surfaces (Text-fig. 13B). Whether these markings represent former vascular features, with the implication that leperditicopes may have possessed a



TEXT-FIG 14. Overall morphology (A), size, shell thickness and overlap features of Ordovician leperditiid (B–C) and leioCOPE ostracodes (D–F). B–C, *Eoleperditia fabulites*, (Conrad, 1843) from the Ordovician of Wisconsin, USA; D–F, *Baltonotella paraspinosa* (Kraft, 1962), *Hyperchilarina nodosimarginata* Harris, 1957 and schmidtellid gen. nov. from the Middle Ordovician of Oklahoma, USA, respectively. B, D–F, all represented at the same scale (after Williams and Vannier 1995) for comparison of size. C = B but reduced to the same height as D–F for comparison of shell thickness. A–B, after Berdan (1984), modified. ama = adductor muscle area; as = adductor sulcus; cs = chevron scar; do = domiciliary cavity; et = eye tubercle; lv = left valve; mb = marginal brim; op = overlap platform; rv = right valve; sp = stop pits; sr = stop ridge; vl = ventral lappet.

heart, has long been argued (Schmidt 1873; Triebel 1941; Adamczak and Weyant 1973; Langer 1973; Sohn 1974). We provide herein new evidence from detailed comparisons with living ostracodes (Text-fig. 15).

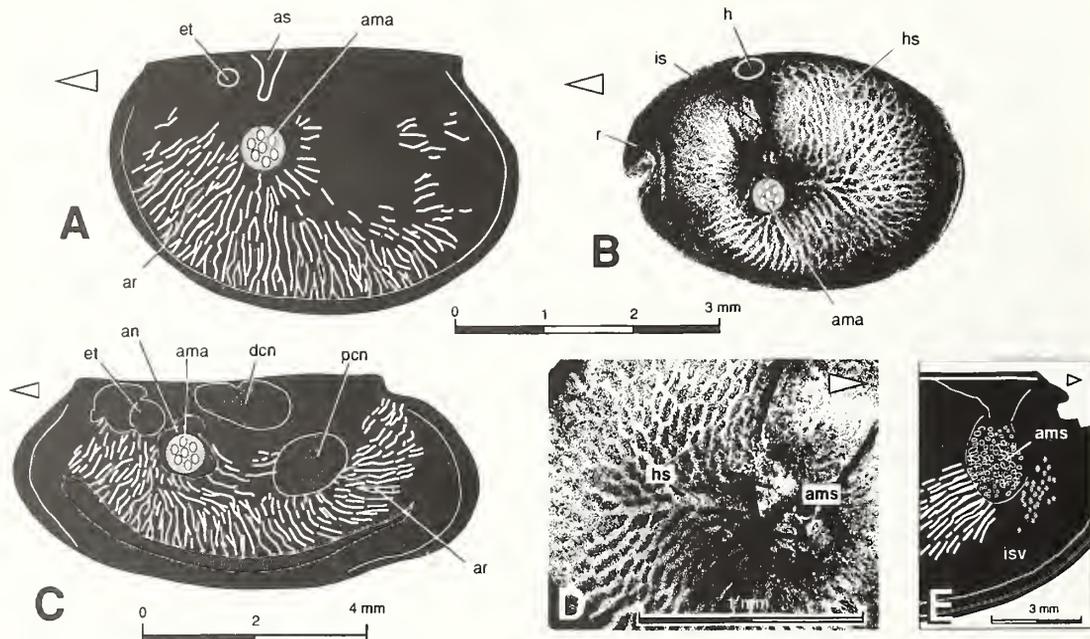
1. The anastomosing markings of leperditicopes radiate from the adductor muscle area toward the periphery of the valve, similar to the integumental sinuses of Recent myodocopes. In living myodocopes, this pattern is a result of the fact that haemolymph enters the vascular spaces of the valve integument in that particular area surrounding the bundles of adductor muscles, then flows radially all the way down to the peripheral channels (Abe and Vannier in press).

2. The radiate network of leperditicopes and living myodocopes (Text-fig. 15A–B) has a similar average density with individual channels comparable in diameter.

3. In leperditicopes, the narrow area situated above the muscle scars lacks any markings and is, therefore, similar to that in living ostracodes. In living animals, this area, which runs between the heart region and the adductor muscle spots, is an attachment area (see Kornicker 1969).

4. Anastomosing markings, as commonly expressed in leperditicopes, are unknown in other groups of non-myodocope fossil Ostracoda, and seem to occur exclusively in specimens reaching over 3 mm in adult carapace length. It is important to note that the same relation of vascularization to large size is observed in living ostracodes. The so-called vascular markings of *Rishona tumida* (Middle Devonian; maximum carapace size 1.8 mm; see Adamczak and Weyant 1973, fig. 2) form a much more intricate network which probably belongs to a different type of shell microstructure. The ramose imprints present on the internal mould of the Ordovician *Cochoprimitia socialis* (c. 4 mm long; Henningsmoen 1954) occur in only some specimens and are thicker than those observed in leperditicopes.

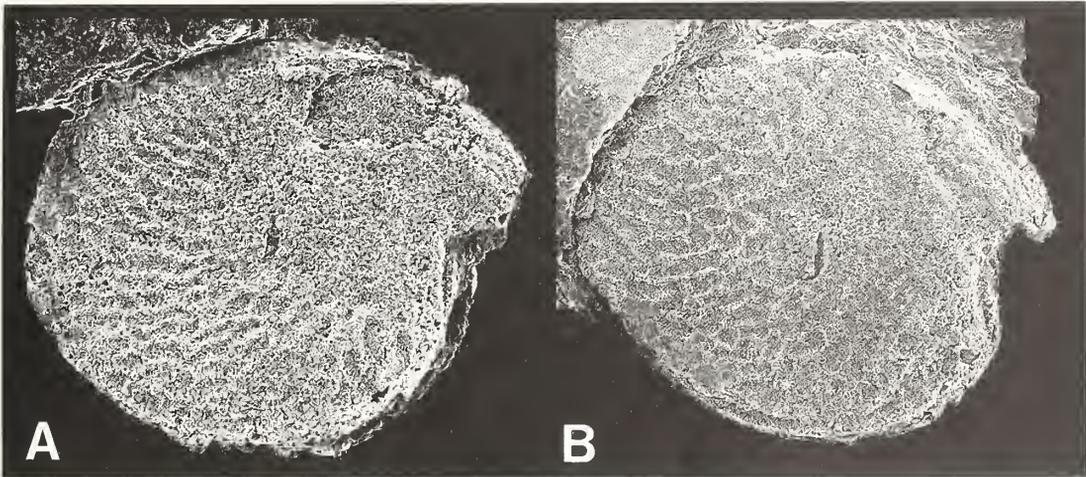
We conclude that Palaeozoic leperditicopes already possessed a vascular system comparable in design and function (for fluid convection) with that of modern ostracodes. Since no information is available on the soft anatomy of these fossil organisms, the presence of a heart (see Sohn 1974) cannot be demonstrated directly. However, almost all crustaceans in which circulatory convection occurs do have a heart. Although the general body movements may, in certain cases, assist haemolymph flow, the heart plays an essential role as the propulsive organ of the circulatory system. Exceptions may be found in some copepods lacking a heart and using valve movements to regulate the direction of haemolymph flow (Maynard 1960). We believe that leperditicopes bearing inferred haemolymph sinuses were also provided with a heart. This organ is likely to have been accommodated dorsally in the upper part of the adductor sulcus (Text-figs 15A–B, 18F).



TEXT-FIG 15. Anastomosing patterns of some Ordovician leperditicope ostracodes compared with the integumental vascular pattern of Recent myodocopids. A, lateral view of a left valve of *Isochilina venosculptis* from the Ordovician of Quebec, Canada; B, D, anastomosing haemolymph sinuses of *Vargula hilgendorffii*, Pacific Ocean, Japan, seen in transmitted light; C, lateral view of the external surface of *Saffordellina muralis* (see Text-Fig. 14B) from the Ordovician of Tennessee (grey shading indicates elevations on the valve); E, inner surface of a silicified valve of *Teichoichilina jonesi* (see Text-Fig. 14A) from the Ordovician of Kentucky, showing the relationships of the radiated markings to the adductorial area. White arrows indicate anterior part of the animal. Adductorial morphology simplified. A, C and E drawn from the original photographic illustrations of Swartz (1949, pl. 66, fig. 13) and Berdan (1984, pl. 11, fig. 2; pl. 8, fig. 5), respectively. ama = adductorial muscle attachment; ams = adductor muscle scars; ar = anastomosing ridges; as = adductorial sulcus; dcn = dorsocentral node; et = eye tubercle; h = heart; hs = haemolymph sinuses; is = isthmus; isv = internal surface of the valve; pcn = posterocentral node; r = rostrum.

*Silurian myodocopes*. Morphological and ecological aspects of the early representatives of Myodocopa have been examined recently in a series of papers (see Vannier and Abe 1992 for complete references). These widespread ostracodes are characterized by a relatively large size (from 3–4 mm up to more than 10 mm in *Entomozoe tuberosa*; see Siveter and Vannier 1990), far exceeding that of all other non-leperditicope Ordovician to Devonian ostracodes. No radial or

anastomosing markings, as typically expressed in numerous Ordovician leperditicopes (Text-figs 14–15), are found in Silurian myodocopes. However, the ornamented pattern of, for instance, the late Silurian bolbozoids shares intriguing resemblances with the anastomosing circulatory pattern of Recent myodocopids such as *Vargula*. The species figured by Siveter *et al.* (1987, pl. 84, fig. 2) as *Bolbozoe* sp. nov. A, has sinuous and bifurcating lines throughout the carapace except on the sulci, the rostrum and the upper part of the bulb. In *Vargula*, circulatory sinuses are similarly much attenuated or absent in the anterodorsal part of the valves. Moreover, the ornament of many bolbozoid species, either reticulated or corrugated, shows clear tendencies to radiate and to bifurcate from the adductorial area (large composite scars) toward the ventral, the dorsal and the posterior part of the valve, which corresponds to the main routes of the circulating haemolymph in *Vargula*. The peripheral convergence of the reticulated/corrugated pattern of bolbozoids (e.g. Siveter *et al.* 1987, pl. 84, figs 2, 7) may correspond, in Recent myodocopids, to the afferent channels, which collect haemolymph before it returns to heart. In this case, the discrete bulbous or triangular features which dorsally terminate the adductor sulcus of *Bolbozoe* or *Entomozoe* (Siveter and Vannier 1990; Vannier and Abe 1992, fig. 2) may indicate the presence of a heart, possibly housed in these small cavities.



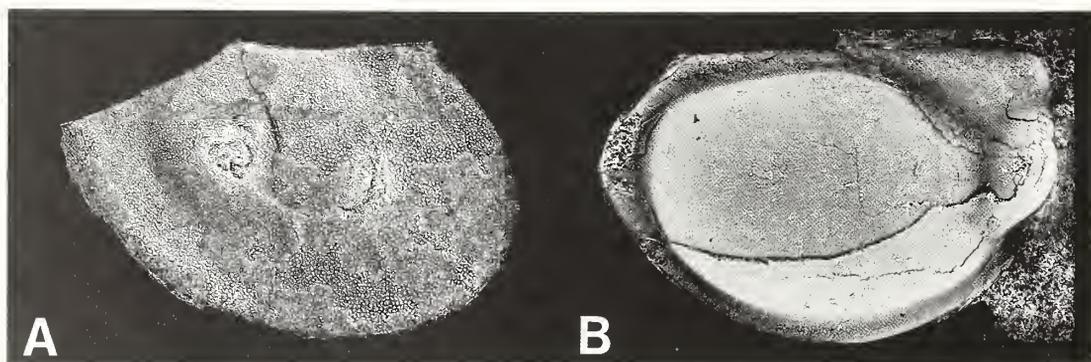
TEXT-FIG 16. Late Silurian myodocopid ostracode (gen. et sp. nov. in Siveter *et al.* 1987) showing external ornament interpreted here as the possible traces of a vascular system (see text for explanation); Lande-Murée Formation; Andouillé, Mayenne, France. A, FSL 575094; B, FSL 575095; both right valves, external lateral views; SEM micrographs of latex casts from external moulds;  $\times 16$ .

Some late Silurian cypridinid-like ostracodes (Text-fig. 16), sharing more obvious similarities (outline, rostrum) with modern myodocopids, also bear an anastomosing 'ornament' which strongly resembles the integumental circulatory network of modern ostracodes. However, the 'ornament' of Silurian myodocopes always appears as positive features on the surface of both casts and steinkerns. This is a major difference from the integumental sinuses of living myodocopids which always run below the calcified layers of the carapace (Text-fig. 8) and are never expressed externally either as grooves or ridges. If the reticulated or corrugated patterns (*sensu* Siveter *et al.* 1987) of early myodocopids represent the trace of a circulatory system, then this system must have had original characteristics in relation to integument. Silurian myodocopids, often preserved as flattened organic-rich imprints in sediments, were probably extremely thin-shelled and poorly calcified ostracodes comparable with living pelagic halocypridids (Text-figs 1A–B, 3). Although very speculative, based on this early stage of our research (thin sections of Palaeozoic specimens are obviously needed), we might envisage that the ornamented network of these ostracodes, if produced

by epidermal layers (see Okada 1981, 1982), also housed circulatory sinuses within the positive features of the polygons. If so, the question still remains as to how such discrete and fragile features may have been preserved in sediment (e.g. Ordovician leperditicopes and Silurian myodocopids). Experimental fossilization of shrimps in the laboratory (Briggs and Kear 1993) indicated that even minute details of soft tissues (e.g. muscles) become mineralized in amorphous calcium phosphate within the first two to eight weeks of the decay processes. The same type of process may account for the '3-D stabilization' of the integumental microstructures of fossil ostracodes, prior to their complete fossilization. In *Vargula* (Text-figs 2E, 9) both internal vessels (e.g. pericardium, aorta) and integumental sinuses are filled with haemolymph. The composition of this fluid is not documented in ostracodes. In larger crustaceans (see Florkin 1960) chemical substances such as inorganic ions, glucids, plasma proteins, coagulable proteins and enzymes have been recognized. If also present in ostracodes, such organic components, still confined in vessels after the animal's death, may be the source for some of the key components of the early mineralization process.

*Mesozoic myodocopes*. Exceptionally preserved phosphatized ostracodes (*Triadocypris*) from the lower Triassic of Spitzbergen (Weitschat 1983a, 1983b; Weitschat and Guhl 1993) reveal a fascinating internal anatomy (e.g. appendages, lateral eyes, 7th limb) surprisingly similar to that of modern myodocopids. However, the shell microstructures (Weitschat, pers. comm.) have not been investigated so far and no evidence is available for the presence or absence of integumental circulatory vessels in these medium-sized ostracodes (carapace length up to 3.1 mm). A recent reconstruction (Weitschat and Guhl 1993) features ciliate protozoans attached to various parts of the integument of the same Triassic species. It is worthwhile noting here that five of these ciliates are found in the dorsal part of the domicilium, which in living myodocopids (e.g. *Vargula*; Text-fig. 9) correspond exactly to the location of heart; they seem to be distributed radially as if they were attached to the outer wall of the pericardium. Continuing scanning electron microscope investigations of this exceptional fossil material may shed light upon this particular problem.

Inferred gill-like features are also found in *Triadocypris* (Weitschat 1983a). They consist of bag-like flattened infolds equally distributed on each side of the body. The quality of preservation of these organs is again good enough to attempt detailed comparisons with Recent homologues. They are most probably similar in morphology and function to the external (intradomiciliar) integumental folds, resembling book gills (Maddocks 1992; Text-fig. 7; Vannier *et al.* in press) in modern cylindroleberidids (Kornicker 1981). These Triassic gills attest to the existence of additional respiratory features implementing diffusion since at least 225 million years ago.



TEXT-FIG 17. Radiating markings interpreted as possible vascular features in Cambrian bivalved arthropods (see text for explanation). A, cambriid bradoriid (Siveter *et al.* in press); Buen Formation, Lower Cambrian; N Greenland; left valve, lateral view;  $\times 5.5$ . B, *Anabaroichilina primordialis* (Linnarson, 1869); GSU 8662, holotype; Middle Cambrian *Lejopyge laevigata* Zone; Djopadalen, Västergötland, Sweden; partly exfoliated right valve showing radiating features on internal mould (see Siveter *et al.* 1993), lateral view;  $\times 6.8$ .

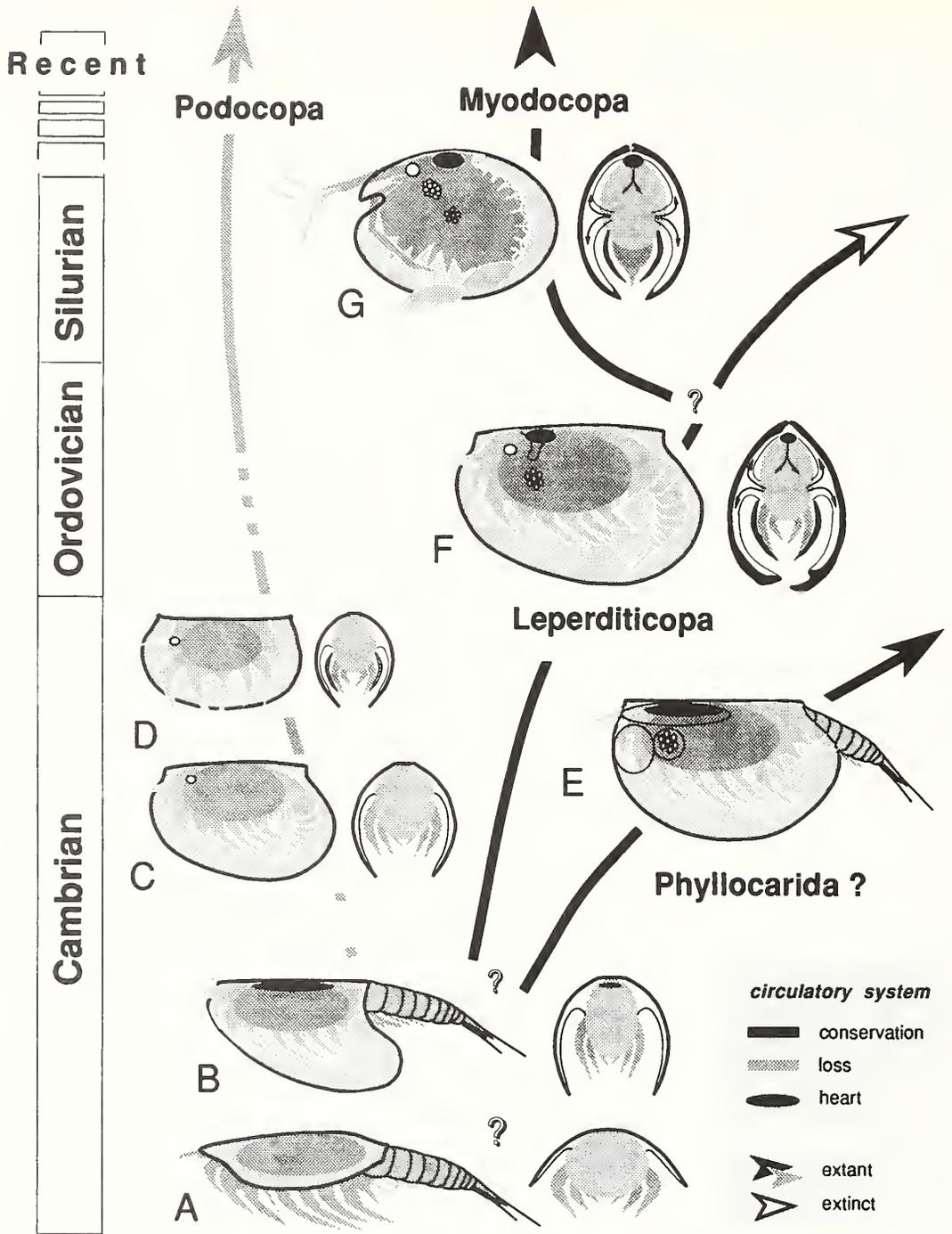
*Ancestry of circulatory systems in ostracodes and other bivalved arthropods.* If our interpretations are correct, circulatory features have existed in ostracodes since at least the Ordovician (Leperditicopa) and occur in the Silurian (Myodocopa); they may be also present in Cambrian bivalved arthropods. *Anabaroichilina primordialis* (Linnarsson, 1869; see Siveter *et al.* 1993; Text-fig. 17B) from the late middle Cambrian of southern Britain, Scandinavia and Australia and the early late Cambrian of Russia reaches a centimetric size and clearly shows on the surface of exfoliated specimens fine anastomosing lines radiating from the adductor muscle scar region. These features are likely to represent the traces of former circulatory sinuses comparable to those of leperditicope ostracodes (Text-fig. 15). However, *Anabaroichilina* shares more morphological traits with phyllocarids than with any other group of bivalve crustaceans or non-crustacean arthropods. For example, the peculiar orientation and design of its inferred circulatory sinuses and the morphology of its nodes have close homologues in Palaeozoic phyllocarid crustaceans (see Rolfe 1969) such as *Carnarvonina venosa* Walcott, 1912 (Middle Cambrian, Burgess Shale, Canada), *Rhinocaris* (Devonian; see Clarke 1893; Rolfe 1969), *Tropidocaris* (Devonian; see Rolfe 1969 and pers. comm.), *Aristozoe* (Devonian; see Barrande 1872; Chlupac 1992, 1994) and, to some extent, *Canadaspis* (also from the Burgess Shale; see Briggs 1978; Whittington 1985). These possible phyllocarid affinities would support the idea (Text-fig. 18E) that the abdomen of *Anabaroichilina* and related genera protruded from the carapace posteriorly or posteroventrally similarly to that of *Aristozoe* or *Canadaspis*. Whether *Anabaroichilina* should be placed within the Phyllocarida, the Ostracoda (Leperditicopa) or the Bradoriida (Williams and Siveter, pers. comm.) is debatable and outside the scope of the present paper.

The oldest record of possible circulatory features comes from several unpublished (M. Williams, pers. comm.; Siveter *et al.* in press) bradoriid arthropods (Cambriidae) from the Lower Cambrian of North Greenland. This material (Text-fig. 17A), of centimetric size, exhibits bifurcating lineations best developed in the posteroventral area of both valves and radiating from central nodes. Comparable features are observed also in Ordovician leperditicopes, especially *Saffordellina* (compare Text-figures 13B and 17A). It seems that integumental circulation can be traced back to the early Cambrian and developed in different lineages of bivalved arthropods, such as the crustaceans, throughout the Lower Palaeozoic.

#### EVOLUTIONARY CHANGES IN CARAPACE DESIGN, BODY PLAN AND RESPIRATORY FEATURES

The earliest Palaeozoic ancestors of Ostracoda were probably small crustaceans with a univalved or a bivalved carapace unable to enclose the body completely, thus differing markedly from all the post-Cambrian representatives of the group. Evidence for this ancestral body plan (Hinz 1993) comes from: 1) the posterodorsal gape of some bradoriid species, suggesting that the abdominal segments of the animal protruded from the domiciliar cavity (e.g. *Aristaluta*, Middle Cambrian; see Hinz 1993); and 2) interdorsal features (a flattened central area demarcated by integumental bends; Müller 1979, 1982), preventing the ventral closure of the valves (Hinz 1993; Hinz-Schallreuter 1993). Hinz (1993) suggested that the gradual reduction of thoracic and abdominal regions of these arthropods, added to the lateral compression of the body and to the increasing biomineralization of the shell, may have set the basis of the body plan of modern ostracodes. The idea that some early lower Cambrian ancestors of Ostracoda were univalved crustaceans bearing a shield-like carapace, is supported by Zhang and Pratt (1993), who demonstrated the univalved-bivalved transition during the early ontogeny of lower Cambrian bradoriids. To some extent, the larval stages of *Manawa* (Recent; Swanson 1989a, 1989b) give a relatively good image of what univalved ostracodes may have looked like.

The profound anatomical changes that are supposed to have taken place in the early stages (Cambrian) of the evolution of Ostracoda have most probably also affected the respiratory features of these organisms. According to Hinz (1993), ancestors of Ostracoda were crustaceans with an elongate and fully segmented body (with head, thorax, and abdomen) protected by a shield-like



TEXT-FIG 18. Main evolutionary changes in the body plan, carapace design and respiratory features of early Palaeozoic (Cambrian to Silurian) Ostracoda and possibly related groups. Simplified lateral views from left and transverse sections through animals; main characteristics of anatomy and respiratory features are indicated for each design (A-G). Lateral views of A-D from Hinz (1993), modified. Arrows in F and G (sections) indicate

carapace of obviously cephalic origin (Text-fig. 18A–B). From a strictly morphofunctional point of view, excluding phylogenetic considerations, this body plan recalls, for example, that of the leptostracan phyllocarids such as *Nebalia*. In *Nebalia geoffroyi* (see Cannon 1960; Schram 1986), the circulatory system has an elongated dorsal heart with series of ostia and a haemolymph sinus extending into the carapace. According to Schram (1986, p. 8), the heart is segmentally derived and the ostia are the remnants of the intersegmental spaces. We suggest in our model (Text-fig. 18) that a comparable system including integumental diffusion and fluid convection (haemolymph) may have existed in Cambrian ancestors of Ostracoda as well. The later reduction of the body, both in terms of size and segmentation (to thorax and abdomen), led to the gradual enclosure of the soft parts within the mineralized carapace. An implication of this new design is the achievement of a closed space, the domiciliar cavity. In such a confined space, ventilation is crucial. Ventilatory plates (e.g. on exopodites or epipodites of thoracic segments) may have developed markedly at that stage, creating and maintaining higher and constant partial pressure gradients over respiratory surfaces (carapace inner lamella and body integument), thus making oxygen uptake more efficient. Müller (1979, 1982) described 'vibratory plates' on the thoracic appendages of *Hesslandona* from the Upper Cambrian of Sweden; this ostracode had a carapace 1–1.5 mm long and a segmented body entirely enclosed within the domiciliar cavity. None of these excellently preserved (by secondary phosphatization of soft anatomy) specimens of *Hesslandona* and related taxa exhibit circulatory or cardiac features. The subsequent reduction of body and carapace size probably brought ostracodes down to the critical size below which gaseous diffusion is sufficient to supply enough O<sub>2</sub>, leading to the partial or total loss of the ancestral circulatory system. The haemocoelic lacunae (Text-fig. 4) still present within the integument of modern podocopes (D. Keyser, pers. comm.) are probably vestigial features and are interpreted tentatively here as the remains of ancient circulatory features.

In our interpretation (Text-fig. 18), some ostracodes, for example the leperditicopes, did not undergo such drastic changes and retained many ancestral characters such as a circulatory system (heart, vessels, sinuses), the postplete shape of the carapace in relation to the abdominal morphology (Text-fig. 18F), and also, possibly, compound visual organs (eye tubercles; Berdan 1984). Circulatory features allowed these organisms to reach an exceptionally large (up to centimetric) size during the Lower Palaeozoic (Cambrian? to Devonian). Silurian myodocopes belong to the same category of ostracodes. In contrast with the leperditicopes, which became extinct by the Devonian, the myodocope lineage (Vannier and Abe 1992) persists through to the present day. The living myodocopids (Text-fig. 2) still have anatomical features, for example the dorsal heart, the strongly arched and well developed curvature of the posterior part of the body, the furcal lamellae, and the compound lateral eyes directly inherited from lower Mesozoic (Weitschat

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possible haemolymph circulation, based on observations of Recent ostracodes (Abe and Vannier in press) and phyllocarids (JV, unpublished). A–B, hypothetical crustacean ancestors (Cambrian) of Ostracoda and possibly related groups. A, shield-like univalved soft carapace; long segmented body; integumental gaseous diffusion only. B, bivalved carapace bearing possible interdorsal features (see Hinz 1993); domiciliar cavity open widely; long segmented body protruding from the carapace through a posterior gape; integumental diffusion; possible circulatory system including an elongated dorsal heart. C, Cambrian bradoriid with reduced body segmentation; bivalved carapace; body accommodated within domiciliar cavity; integumental diffusion; sharp reduction or loss of circulatory system. D, late Cambrian ostracode with more reduced body segmentation; reduction or absence of interdorsum; semi-closed domiciliar cavity with ventilation creating partial pressure gradients of O<sub>2</sub>; integumental gaseous diffusion only. E, Middle Cambrian phyllocarid crustacean(?) based on *Anabaroichilina* (Siveter *et al.* 1993); centimetric size; abdomen protruding from the carapace; inferred dorsal heart and integumental circulation expressed as anastomosing features on valves. Abdomen reconstructed from phyllocarid morphology (Rolfe 1969). F, Ordovician leperditicope; large size up to centimetric; calcified bivalved carapace; ventral overlap features; body accommodated in domiciliar cavity; adductor muscles; intradomiciliar ventilation; inferred dorsal heart and integumental circulation expressed as anastomosing features. G, Silurian myodocopes; large size up to centimetric; calcified, or soft bivalved carapace; body accommodated in domiciliar cavity; adductor muscles; intradomiciliar ventilation; inferred dorsal heart and integumental circulation expressed as anastomosing features.

1983a, 1983b) and probably Lower Palaeozoic ancestors. Circulation may also have allowed myodocope ostracodes to acquire higher metabolic rates, a condition of importance for ostracodes adapted to free-swimming life styles by Silurian times (Siveter *et al.* 1991; Vannier and Abe 1992). The fact that leperditicopes and myodocopes apparently share ancestral characters (Text-fig. 18E-F) brings new information relevant to the pre-Silurian origin and history of myodocopes, considered by many authors (see *Entomozoe* in Siveter and Vannier 1990; Vannier and Abe 1993) to be enigmatic.

### CONCLUSIONS

The early achievement (mid or late Cambrian) of the bivalved design and the probable loss of the circulatory system, implying sharp physical constraints related to respiration, may have confined many representatives of the Ostracoda to within a relatively low and narrow size range, inducing remarkably conservative features among the group up to the present time. The 7000 species of Recent podocopes belong to that category of organisms. In contrast, size constraints were partly overcome by those conserving a circulatory system probably inherited from the early Cambrian arthropodan stock. Thus, large size could develop in several lineages of ostracodes, successively in the archaeocopes (Text-fig. 17A), the leperditicopes and the myodocopes (Text-fig. 18) from the early Palaeozoic through to the Recent (e.g. *Gigantocypris*).

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# DIFFERENTIATING EVOLUTION FROM ENVIRONMENTALLY INDUCED MODIFICATIONS IN MID-CARBONIFEROUS CONODONTS

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**ABSTRACT.** Envirotypes are persistent, environmentally induced, potentially inheritable phenotypes that have not been genetically selected for an environment. Unlike ecotypes, envirotypes do not breed true in different environments. The term ecophenotype should be restricted to phenotypic modifications resulting from disease, injury, physical restrictions on growth or to modifications that develop through use. To distinguish evolution from environmentally induced modifications in conodonts one should consider: (1) number of multielement species in the fauna exhibiting modifications; (2) number of elements in the apparatus displaying modifications; (3) uniqueness of modification; (4) occurrence of modified and unmodified forms; and (5) stratigraphical range of modified form. When applied to the conodont fauna from the Carboniferous Barnett Formation in Texas, these criteria suggest that the geniculatan element is not an envirotypes or ecophenotype of the ponderosiform element, but that two species of *Idioproniodus?* are present. Similarly, when applied to the Pa element of the *Taphrognathus varians* apparatus, the criteria suggest that blade position relative to platform and platform ornamentation is not an environmentally induced feature.

PHENOTYPIC modification may result from evolution of the genotype through mutation, hybridization, or alteration of environmental factors. Differentiating evolutionary changes from environmentally induced phenotypic changes is a long-standing problem, especially for palaeontologists. Many terms describe the environment's influence on a phenotype, but we know of no taxonomically neutral term to describe an environmentally induced, persistent, potentially inheritable phenotype for which there is no evidence of genetic selection for an environment. We propose the term envirotypes.

Populations with modified phenotypes may represent distinct taxa isolated genetically by evolution, or conspecific ecophenotypes, ecotypes, or envirotypes. For extant organisms, breeding experiments and clines may demonstrate relationships among phenotypes. Recently, comparison of DNA sequences has been used to evaluate the genetic relationship between morphologically distinct populations (e.g. Chesney *et al.* 1993). Fossil populations provide a greater challenge because little genetic material is usually preserved, the organisms are deceased and recognition of clines is more difficult.

Conodont-bearing organisms became extinct in the early Mesozoic. Because the nature of the organism is uncertain, no closely related group has been recognized. Skeletal elements, called conodonts, typically display great variability within isochronous as well as chronologically successive populations. Determining taxonomic relationships among various conodont phenotypes provides a unique and difficult challenge.

Recently, several authors have suggested that some forms of conodont represent ecophenotypes (envirotypes herein) rather than genetically distinct species, subspecies or populations (Merrill 1980; Horowitz and Rexroad 1982; Merrill and Bitter 1984; Merrill and Grayson 1987; Merrill *et al.* 1990; Purnell 1992). This paper proposes criteria for evaluating whether modifications to conodont phenotypes represent evolution or environmentally induced changes. In particular, we shall review the suggestion that the form species *Geniculatus claviger* (Roundy) is an envirotypes of the Pb element in the *Idioproniodus paraclaviger* (Rexroad) apparatus and that the form species

*Cloghergnathus globenshii* Austin is an envirotpe of the Pa element in the *Taphrognathus varians* Branson and Mehl apparatus.

#### GENOTYPE, PHENOTYPE, ECOPHENOTYPE, ECOTYPE AND ENVIROTYPE

Genotype refers to an organism's genetic constitution, only a part of which may be expressed. Dominant genes mask recessive genes unless the organism is homozygous for the recessive genes. For example, if the genotype is heterozygous for both giantism and dwarfism genes, the organism will have the potential to be large if the giantism gene dominates or small if the dwarfism gene dominates. Should dominant genes not dominate fully, intermediate features may develop. Some characters are controlled by more than one pair of genes. Interaction of the gene complex will determine the potential expression of the characters. Thus, an organism's genotype is generally much more diverse than features and functions indicate.

Although genes define an organism's potential development, a complex interaction between genotype and environment determines the characters and functions ultimately exhibited. The sum of these characters and functions is called the phenotype. Identical genotypes exposed to different environments may produce different phenotypes. Environmental stimuli can repress development of some features and enhance development of others. For example, coiling direction of some foraminiferal tests seems related to water temperature (Bandy 1960). Above a critical temperature, dextral coiling dominates the population; below that temperature the dominant coiling is sinistral. Other organisms alter spine size, and test or valve shape in response to seasonal changes in water viscosity. Incubation temperature determines gender of some reptiles. Body form, sex and size in some insect species are directly related to the food which larvae are fed. Even phenotypically conservative species may show altered growth patterns and markedly different phenotypes under extreme environmental conditions.

Not all characters or functions may display a great diversity of expression. According to Waddington (1957), some characters are 'developmentally canalized'. Development can proceed in only one direction regardless of the environment. These features will display little, if any, variation in different environments. Other features are 'developmentally flexible'. Development can proceed in a variety of ways. These characters may display great differences in diverse environments. For example, to survive, oysters must develop shells (canalized development), but the shape of the shell is controlled by crowding, light intensity and substrate (flexible development).

Intraspecific variation reflects not only genetic diversity but also the diversity of environments inhabited by a species. Each organism's genetic plasticity establishes modes and limits of response to various environmental conditions. If conditions exceed those limits, the organism can no longer respond adequately. Under extreme conditions an organism may not breed or may die. Self-sustaining populations only occur in habitats where environmental conditions are within the range of response for the organisms composing those populations. Phenotype extinction may not result from only genetic extinction, but also from elimination of environments. Similarly, appearance of new phenotypes may result from new genetic variations through mutation (evolution), hybridization or from environmental change.

An environmentally induced, non-inheritable modification of a phenotype has been called an ecophenotype (King and Stansfield 1985; Hale and Margham 1991). We have problems applying this concept as currently used. Implied in the definition is that each species has a standard phenotype which is altered (modified) by abnormal environmental conditions, thereby producing an ecophenotype. As noted above, all phenotypes are, in part, environmentally induced expressions of the genotype. Different environments may produce different phenotypes from the same genotype. Thus, no phenotype can be considered the standard and all phenotypes could be considered ecophenotypes in terms of being environmentally induced. The phenotype considered the standard is usually the most common form, generally reflecting the most widespread environment, or is the form with nomenclatural priority.

A second problem in applying the ecophenotype concept, as currently used, relates to the non-inheritability of phenotypic modifications. As noted by Schmalhausen (1986), organisms only inherit the *potential* to express structure or function. Without proper environmental stimuli no structure or function can be realized. With proper environmental stimuli any modification can be reproduced, if the genetic potential exists within the organism.

Some environmentally modified phenotypes are extremely stable and persist as long as the environment that induces them exists. These stable, persistent phenotypes show a consistency in form to the extent that some have been identified as distinct species, both modern and fossil. If there was not a genetic basis to these environmentally induced modifications, they would vary greatly with each generation. Therefore persistent, consistent, environmentally induced modifications must be considered potentially inheritable and genetically based. We feel it is inappropriate to call these modified phenotypes ecophenotypes.

The term ecophenotype should be restricted to non-persistent, inconsistent, non-inheritable, environmentally induced phenotypic modifications. This would include modifications from disease, injury, physical restrictions on growth or changes that develop through use (e.g. size of musculature and muscle attachment is partially determined by muscle use). These types of modifications are caused by largely random environmental factors and are clearly not inheritable, although the potential response is. As restricted herein, ecophenotype is similar in concept to phenocopy and variant, except in that some variants can be inheritable.

We found no taxonomically neutral term to describe persistent, consistent, environmentally induced, potentially inheritable phenotypes that are not genetically selected for an environment. The term phenotype is not specific and includes all interactions between genotype and environment including ecophenotype and ecotype. Forma, subspecies, ecospecies and ecosubspecies all imply a taxonomic status (Kenneth 1960; Hale and Margham 1991). Variant does not necessarily imply inheritability (King and Stansfield 1985). Ecotype implies that the population has undergone some genetic selection for an environment that differentiates it from other conspecific populations (Kenneth 1960). Raised in a different environment, ecotypes continue to display phenotypic differences from the population native to that environment. The term morph applies to either an individual of a polymorphic population or a variant (King and Stansfield 1985). In the absence of an appropriate term, we propose *enviotype* for persistent, consistent, environmentally induced, potentially inheritable phenotypes that have not been selected genetically for an environment. Unlike ecotypes, different enviotypes raised in the same environment should produce an indistinguishable range of phenotypes.

Most phenotypes, cited in the literature as ecophenotypes, do not conform to our revised definition of this term and are more properly called enviotypes than ecotypes. Chesney *et al.* (1993) demonstrated that fresh water mussels *Margaritifera durrovensis* Phillips and *M. margaritifera* (Linnè) are conspecific. *M. durrovensis* is the phenotype developed in hard water, whereas *M. margaritifera* inhabits soft water. We would call these enviotypes and not ecotypes because no evidence was presented to show significant genetic differentiation. Lack of breeding experiments also requires that ecophenotypes recognized by Chang and Kaesler (1974), Poag (1978), Wang and Lutze (1986), Brazeau and Lasker (1988), Hove and Smith (1990) and Walton and Sloan (1990) be considered enviotypes. Fossil phenotypes cited as ecophenotypes by Owen and Ingham (1988) and Hauser and Grünig (1993) must be considered enviotypes. Breeding experiments and comparison of DNA sequences, required to demonstrate that populations are ecotypes, are not currently possible with most fossils.

#### DIFFERENTIATING BETWEEN EVOLUTION AND ENVIRONMENTALLY INDUCED CHANGE IN CONODONT MORPHOLOGY

One can determine if extant, modified phenotypes represent distinct taxa or conspecific ecotypes, ecophenotypes or enviotypes through breeding experiments and/or the identification of clines. If a phenotype is raised under a variety of environmental conditions and produces a range of

phenotypes similar to those found in nature living under these environmental conditions, it is obvious that the naturally occurring phenotypes are conspecific. The phenotypes are envirotypes and the various forms do not represent evolutionary change within the species. Using this technique, Schnitker (1974) demonstrated with cloned cultures of *Ammonia beccarii* (Linnè) that *A. parkinsoniana* (Orbigny), *A. advena* (Cushman), *A. beccarii*, *A. catesbyana beccarii tepida* (Cushman), *A. beccarii sobrina* (Shupack), *A. pauciloculata* Phleger and Parker and *A. limnetes* (Todd and Brönnimann) were not true species but only envirotypes (his ecophenotypes).

A cline can demonstrate the close relationship between extreme phenotypes and indicate that end members are conspecific. From a continuous gradation of forms, Poag (1978) concluded that two distinct phenotypes of *Ammonia parkinsoniana* were controlled clinally by variations in temperature and salinity and were not distinct species. Absence of a cline may not be significant. According to Schmalhausen (1986), some modifications attain complete expression at a minimum threshold. Increasing intensity of environmental stimulus does not alter degree of modification. Thus, no cline would be expected. The character either develops fully or is absent.

Comparison of DNA sequences can also be used to demonstrate a relationship between distinct phenotypes. Chesney *et al.* (1993) employed DNA sequences in substantiating that *Margaritifera durrovensis* and *M. margaritifera* are conspecific envirotypes (their ecophenotypes).

Distinguishing between evolution and environmentally induced change is more difficult in fossil populations. Closely related, extant forms should not be used as models in evaluating fossil species. Raup (1972) demonstrated that in some instances the same kinds of differences reflect evolution in one species and environmentally induced change in another.

Clines are also less useful in the fossil record. Lack of spatial and temporal resolution inherent in most palaeontological studies obscures the distinction between isochronous clines and evolutionary sequences. Merrill and Bitter (1984) suggested that morphological changes along a presumed palaeo-ecocline are as likely to represent mixing of end member populations of two closely related species as they are to be ecophenotypes within a species.

Johnson (1981) attempted unsuccessfully to use ontogeny to differentiate 'canalized' and 'flexible' species and thereby identify environmentally induced modifications and evolutionary changes in Jurassic scallops. He proposed that 'developmentally flexible' species should display a decrease in variation with time (ontogeny) in a single environment, but an increase in distinct mean morphologies in different environments. In contrast, he predicted that 'developmentally canalized' species would display few changes.

Conodonts provide a unique challenge in differentiating between evolution and environmentally induced changes. Conodont-bearing organisms have been extinct since the Triassic and the nature of the organism is still uncertain, although many hypotheses have been suggested based upon various unique fossils. No closely related group has been recognized. Although ontogeny is preserved within conodonts, it is not readily accessible because later growth obscures it. Ontogeny is usually interpreted from a size gradation of specimens, despite the problems inherent in this procedure.

We propose the following five criteria to evaluate whether modified conodont phenotypes represent evolution or environmentally induced change (envirotypes). Similar concepts were employed by McKinney and McNamara (1991) in evaluating modified echinoid phenotypes of a species of *Eupatagus*. None of these criteria alone, nor all of them together, can prove that a modified phenotype represents evolution or environmentally induced change. Yet, they do provide a uniform basis for evaluation.

#### *Number of unrelated taxa exhibiting modification*

If more than one unrelated conodont apparatus-species in a sample has similarly modified conodonts, the modifications were probably environmentally induced. It is unlikely that two unrelated species evolving in the same environment would evolve similar modifications

simultaneously and independently. The modified phenotypes are most probably envirotypes or ecophenotypes. If the modification is restricted to only one taxon, this may indicate that only the modified taxon was susceptible to the environmental stimulus or that the modification is genetic in origin.

#### *Number of element types exhibiting modification within an apparatus*

If only one element type of an apparatus was modified, this may suggest evolution, rather than environmentally induced change. Temperature and salinity have been regarded as the environmental stimuli most probably responsible for inducing alterations in conodont phenotypes. Although physical processes could expose one element type to greater stress because of location within the body, chemical or thermal stress would probably influence all conodont-secreting tissues equally. An analogous example can be seen in mammalian teeth. If exposed during development to insufficient nutrients or an over-abundance of an element, such as fluorine, all teeth develop the same 'abnormalities'. A similar situation occurs in bones. For example, rickets affects the entire skeleton, but is most noticeable in load-bearing bones because of the greater stress.

If several or all conodont types within an apparatus are modified, this probably represents environmentally induced change. Mosaic evolution, as shown in conodonts, suggests that it was unlikely for several conodonts in an apparatus to evolve rapidly and simultaneously, or to evolve the same modification. According to Nicoll (1987), Pa elements evolved the fastest, Pb elements more slowly and the remainder of the apparatus was relatively conservative.

#### *Uniqueness of modification*

If the modified phenotype duplicates a common character of conodonts, this may represent an evolutionary trend, parallel evolution, or adaptation to a habitat, rather than an environmentally induced change. If the modification is unique and displays a different microstructure, the modification was probably environmentally induced.

#### *Occurrence of modified forms and unmodified forms*

If modified and unmodified phenotypes of an element co-occur throughout their geographical range, the modification is more probably genetic in origin and may represent an evolutionary change. All forms would have been exposed to the same environmental stimuli. If the environment induced a phenotypic change, all forms having the same genotype would display the modification. Modified and unmodified forms co-occurring indicate that genetically distinct groups (sub-populations) existed.

If phenotypes are isolated or display mixing only along the periphery of their geographical ranges, little information is provided to interpret the relationship between the phenotypes. Peripheral mixing of populations could indicate one of three possibilities: they were distinct, environmentally incompatible taxa throughout most of their ranges; at least one phenotype may have been an ecotype (genetically distinct below a subspecies level); or there was post-mortem mixing.

#### *Stratigraphical range of modified forms*

Modified phenotypes restricted to a single stratigraphical horizon may represent an envirotype developed in a short-lived environment. This would be further supported if the phenotype is restricted to a specific lithology. Modified phenotypes that persist across many stratigraphical horizons and are associated with a variety of lithologies, are more likely to represent evolutionary

change or an environmentally induced change caused by an environmental factor that left no imprint on deposits.

Modified phenotypes that appear periodically could represent envirotypes which only developed when certain environmental factors were present. The modified phenotype could also have been a distinct taxon which periodically migrated into an area when the environment was suitable. Presence or absence would have been environmentally controlled, but the phenotype was not environmentally induced.

#### IS *GENICULATUS CLAVIGER* AN ENVIROTYPIC Pb ELEMENT OF AN *IDIOPRIONIODUS APPARATUS*?

The *Idioprioniodus* apparatus was reconstructed early in the history of conodont apparatus reconstruction, before standard element terminology was established. Each author introduced his own notation or terminology to describe the elements within the apparatus. The resulting multitude of systems can lead to confusion. Text-figure 1 shows the equivalency of terminology of the primary schemes used to describe elements in *Idioprioniodus* apparatuses.

Herein, we follow Klapper and Philip (1971) in developing descriptive terminology based upon form taxonomy for conodont elements. If the form genus name describes sufficiently the conodont element, the name is modified by adding the suffix '-an' to the root of the name. For example, the form genus *Geniculatus* becomes geniculatan. For genera, such as *Polygnathus*, which have scores of morphologically distinct species, the genus name alone is insufficiently descriptive. The trivial name of the appropriate species, modified by adding the suffix '-iform' to the root of the name, is used to describe the conodont. For example, the Pa element of the *Polygnathus communis* Branson and Mehl apparatus is communiform.

Hass (1953) named the form genus *Geniculatus* for specimens recovered from the Lower Carboniferous Barnett Formation in Texas and referred originally to the form species *Polygnathus? claviger* by Roundy (1926). Hass described the conodonts as 'geniculate, asymmetric, massive bar-like units which taper from the vertex toward the anterior and posterior extremities.' Using a size gradation of specimens, he interpreted the ontogeny as beginning with small, fragile, bar-like conodonts and developing into massive elements.

Merrill (1980) noted that not all specimens included in the form species *Geniculatus claviger* (Roundy) developed massive bar-like processes (Pl. 1, figs 1, 4, 11-13). Those lacking this development (Pl. 1, figs 2-3), he referred to as 'ponderosa' elements (ponderosiform herein) because of their similarity to form species *Lonchodina? ponderosa* Ellison. Merrill further reported that, although both geniculatan and ponderosiform elements can co-occur, samples lacking the geniculatan elements interfinger with those containing them in the Barnett Formation. Gencilatan elements are more common in the lower and upper parts of the formation, but are relatively uncommon in the middle third. Because of its distribution and unusual platform development. Merrill (1980), Merrill and Grayson (1987) and Merrill *et al.* (1990) suggested that the geniculatan form is an ecophenotype (herein envirotype) of the ponderosiform elements.

Merrill (1980) and Rexroad (1981) proposed that ponderosiform and geniculatan elements were alternative Pb elements of otherwise identical *Idioprioniodus* apparatuses. In one form, Pb elements were geniculatan and in the other ponderosiform. In 1978, Chauffe informally reconstructed apparatuses from Barnett Formation samples (work unpublished). His reconstructions of *Idioprioniodus*-like apparatuses were identical to those suggested by Merrill (1980) and Rexroad (1981). The apparatus consisted of geniculatan or ponderosiform Pb, neoprioniodan M, hibbardellan (= roundyan) Sa, detortiform Sb<sub>1</sub>, metalonchodinan Sb<sub>2</sub> and ligonodinan Sc elements (Text-fig. 1). In contrast, Sweet (1988, p. 83, fig. 5.31) described and illustrated the apparatus as consisting of digyrate pectiniform Pa (= our Sb<sub>2</sub> metalonchodinan?), digyrate pectiniform Pb (= our ponderosiform), dolabrate M, bipennate Sb, bipennate Sc and alate Sa elements.

Merrill (1980) retained the Barnett Formation *Idioprioniodus*-like multielement species in open nomenclature. However, in the same publication Namy (1980) applied the name *Idioprioniodus*

This paper	Namy, 1980 Merrill and Grayson 1987	Chauff 1983	Robinson 1981 Sweet 1988	Nicoll and Rexroad 1975	Merrill and Merrill 1974	Baesemann 1973 Higgins 1982	Bitter 1972
Pb element ponderosiform	ponderosiform	Pb element "lonchodinan"	Pb element angulate (digyrate pectiniform Sweet, 1988)	paraclaviger element	ponderosa element	B3b element	none
geniculatan	geniculatan						
M element neoprioniodan	conjunctiform	M element neoprionio- dontan	M element dolabrate	conjunctus element	conjunctus element	N element	Ne element
Sa element hibbardellan (roundyan)	subacodiform	Sa element hibbardellan	Sa element alate	subacoda element	subacodus element	B3a element	Tr element
Sb <sub>1</sub> element detortiform	(para) clark- iform	Sb <sub>1</sub> element detortiform	digyrate	clarki element	clarki element	B1b element	P1 element
Sb <sub>2</sub> element metaloncho- dinan	bidentatiform	Sb <sub>2</sub> element metaloncho- dina	digyrate (Pa element? digyrate pectiniform Sweet 1988)	bidentata element	bidentatus element	(N2 Higgins, 1982)	none
Sb <sub>3</sub> element lexingtonensi- form	none	Sb <sub>3</sub> element lonchodinan	bipennate	none	lexington- ensis element	B2 element	none
Sc element ligonodinan	typiform	Sc element ligonodinan	bipennate	typa element	typus element	B1a element	Hi element

TEXT-FIG. 1. Major notation schemes to identify elements in *Idioprioniodus* apparatuses. In Robinson (1983), only Pb and M elements are identified specifically as to shape categories. Symmetry-transition elements are described as ranging from late through digyrate to bipennate. Sweet (1988, fig. 5.31) placed what we interpret to be a metalonchodinan element in the Pa position in the apparatus. We have assigned shape categories to S elements illustrated in Robinson (1983) and Sweet (1988).

*paraclaviger* (Rexroad) in his plate descriptions to a reconstruction containing both ponderosiform and geniculatan elements. There was no discussion in the text and it is unclear if Namy interpreted both of them as elements of one apparatus or as alternative Pb elements within one apparatus type. Namy's plate and plate description were republished in Merrill and Grayson (1987), although within the text the name *I. paraclaviger* was not used. Merrill *et al.* (1990) again employed open nomenclature for the two forms of *Idioprioniodus* apparatuses.

If the geniculatan and ponderosiform elements are ecotypes, ecophenotypes or envirotypes, their apparatuses are conspecific and only one species name is required. If they represent distinct species or subspecies, a nomenclatural distinction must be made. We believe that applying the five criteria proposed herein will provide an objective evaluation of the relationship between the two phenotypes. Analysis results are listed below.

(1) None of the other five multielement species in the Barnett Formation conodont fauna display consistent modifications, as do the geniculatan elements.

(2) Only geniculatan Pb elements of the *Idioproniodus* apparatus are modified. Apparatus elements that would have been associated with geniculatan elements can not be distinguished from those associated with ponderosiform elements. The more rapid evolution of Pb elements, compared with the remainder of the apparatus, would be consistent with the model of mosaic evolution for many conodont apparatuses. *Idioproniodus* may, however, be an exception to this rule, as demonstrated by the more rapid evolution of lexingtonensiform Sb<sub>3</sub> and metalonchodinan (= bidentatiform) Sb<sub>2</sub> elements during the Late Carboniferous.

(3) Modification is the asymmetrical platform development on the Pb element. Platform development on Pa elements is known from the Ordovician through to the Triassic. Although less common on Pb elements, it is not unusual. Platforms developed on form species of *Elictognathus*, *Nothognathella* and others. Merrill (1980), Merrill and Grayson (1987) and Merrill *et al.* (1990) refer to the geniculatan platform as a 'pseudoplatfom' or 'bizarre platform surrogate'. We could find nothing that distinguishes the geniculatan platform from platforms developed on some form species of *Nothognathella*. Microstructure of the geniculatan platform displays normal conodont structure.

(4) Distribution of ponderosiform and geniculatan phenotypes suggests their geographical ranges overlapped only at the periphery. Although there is variation in extent of platform development, it is not possible to demonstrate a cline.

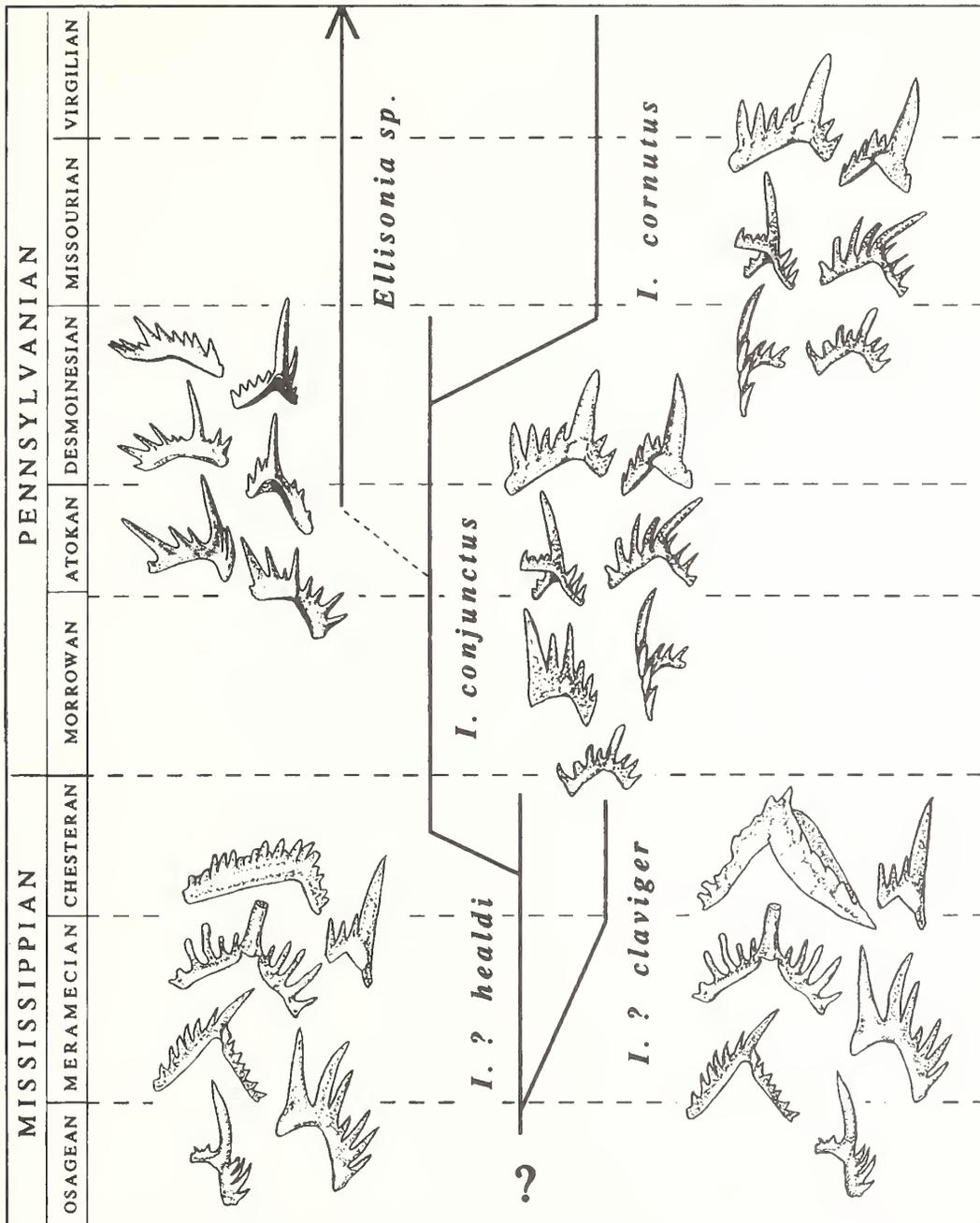
(5) The interfingering relationship displayed by the two phenotypes could have been produced if either phenotype distribution was environmentally controlled or the geniculatan form was environmentally induced.

Thompson and Fellows (1970) reported a similar distribution of form species *Gnathodus cuneiformis* Mehl and Thomas from the Osagean Series of the Midcontinent. *G. cuneiformis* appears only at the bottom and top of several sections although other closely related species of *Gnathodus* occur throughout. Thompson and Fellows interpreted the upper *G. cuneiformis* as a homeomorph of the lower form. From conodont multielement species diversity data, Chauff (1983) reinterpreted the occurrence of *G. cuneiformis*, proposing that the distribution was environmentally controlled by water depth or distance from shore. The species was absent from the part of the section representing maximum transgression.

From our analysis, we find little evidence to suggest that the geniculatan element should be considered an ecophenotype or envirotype. We believe the geniculatan element evolved from the ponderosiform element and does not represent an environmentally induced phenotype. Although we concede that the geniculatan element could be an ecotype, this is a moot point considering available data.

The taxonomic level at which apparatuses with geniculatan Pb elements should be recognized is a matter of subjective interpretation. There is no reliable correlation between morphology and reproductive isolation. At one extreme, sibling species are morphologically identical but reproductively distinct, although their ranges may coincide or overlap. At the opposite extreme, envirotypes, ecotypes and ecophenotypes may be morphologically dissimilar, but are conspecific. There is no reliable guideline determining what differentiates conodont form or multielement subspecies, species and genera.

As a form taxon, *Geniculatus claviger* would be considered sufficiently distinct to be the basis of a form genus. In multielement or apparatus taxonomy, differences within the entire apparatus must be considered. Modification of one element is usually recognized to be of lesser taxonomic importance. We feel the degree of genetic separation indicated by the development of the geniculatan element is sufficiently important to recognize a separate species at this time. We follow Chauff (1983) in questioning the assignment to *Idioproniodus* of multielement species which differ substantially from the type species, *I. cornutus* (Stauffer and Plummer), in element composition. Thus, we recognize two species of questionable *Idioproniodus* in the Barnett Formation: *I. ? healdi* bears the ponderosiform Pb element and *I. ? claviger* contains the geniculatan Pb element.



TEXT-FIG. 2. Phylogeny of *Idioprioniodus* spp. Illustration of *Ellisonia* is redrawn from Sweet (1988); all others original.

PHYLOGENY OF MULTIELEMENT *IDIOPRIONIODUS* SPECIES

The multielement genus *Idioproniodus*, including species assigned with question, is restricted to the Carboniferous. It ranges from Osagean (Lower Carboniferous) to Virgilian (Upper Carboniferous). The ancestor of the genus is unknown. Elements similar to those in multielement *Idioproniodus* occur in Upper Devonian and Kinderhookian (basal Carboniferous) faunas. Few apparatuses have been reconstructed from the Kinderhookian, so it is uncertain if the *Idioproniodus*-like elements are related directly to *Idioproniodus*. Except for the addition of a Pa element, the Upper Devonian apparatus *Cryptotaxis culmunidirecta* (Scott) not only has an identical element composition to *Idioproniodus? healdi*, but many of the elements are also nearly identical. This is not to imply that *Cryptotaxis* is the ancestor of *Idioproniodus*, although they are probably related. However unlikely, one can not discount the possibility that similarity in element composition and form may reflect only similarity of habitat and niche, and little about phylogenetic relationships.

*Idioproniodus? healdi* is the first known *Idioproniodus* species in the Midcontinent and occurs in the Upper Osagean (Text-fig. 2). By the Chesteran, *I.? claviger* appears as a well developed species. It may have evolved as early as Late Osagean or Meramecian from *I.? healdi* by the development of an asymmetrical platform on the Pb element. Nicoll and Rexroad (1975) and Chauff (1983) reported Valmeyeran (= Osagean) ponderosiform (= paraclavigiform) elements with lateral thickenings along the processes. These specimens are large and the thickenings may be 'gerontic features', not the initial stages in the evolution of geniculatan elements. Chesteran *I.? claviger* are not known from the Upper Carboniferous.

Also during the Chesteran, *I.? healdi* evolved into *I. conjunctus* (Gunnell) by addition of a lexingtonensiform [lonchodinan Sb<sub>3</sub>] element to the apparatus. *I. conjunctus* persisted until near the top of the Desmoinesian, where its apparatus gradually lost the Sb<sub>2</sub> metalonchodinan (= bidentatiform) element and evolved into *I. cornutus* (Stauffer and Plummer), the type species for the genus. For a time, both *I. conjunctus* and *I. cornutus* co-existed but, in the Missourian, no *I. conjunctus* remain (Merrill and Merrill 1974). By the Virgilian, faunas contain few elements belonging to *Idioproniodus*. The multielement genus is not known from the Permian.

Sweet (1988) proposed that the multielement genus *Ellisonia*, and possibly *Xaniognathus*, evolved from *Idioproniodus* during the Atokan (Upper Carboniferous). He listed the major differences between contemporaneous *Idioproniodus* and *Ellisonia* as longer and more profusely denticulate processes in *Ellisonia*, and larger basal pit and less prominent zone of recessive basal margin in *Idioproniodus*. In contrast, Bitter and Merrill (1983) suggested that *Ellisonia* possibly evolved from *Magnilaterella*.

Merrill and Merrill (1974) proposed that multielement *Idioproniodus* species were dimorphic. Two similar, yet slightly different apparatuses occur in the same faunas. Horowitz and Rexroad (1982) also suggested that a dimorphic pair was present in their study. One dimorph contained form species *Lonchodina furnishi* and the other *L. paraclaviger* as Pb elements. Restudy of Chauff's (1983) Osagean faunas suggests that a dimorphic pair was present. He illustrated two slightly different Pb elements in his plate 3, figures 26, 30 and 32. From our limited collection, we could not identify dimorphs of *I.? claviger*.

BLADE POSITION ON *TAPHROGNATHUS VARIANS* Pa ELEMENTS AS AN ENVIRONMENTALLY INDUCED FEATURE

Purnell (1992) rejected the practice of establishing taxa on the basis of blade position relative to platform shape and ornamentation on Pa elements from the *Taphrognathus varians* Branson and Mehl apparatus. He demonstrated that blade position changed during 'ontogeny', as interpreted from a size gradation of specimens, and suggested that it may also have been environmentally induced.

From blade position, Purnell (1992) recognized 13 categories of Pa element of the *Taphrognathus varians* apparatus. These he grouped into three distinct morphotypes. For the Bogside Limestone

Member at his locality 10, Purnell plotted category occurrence against an arrangement of samples reflecting a gradient of increasing environmental restriction. Morphotype II, approximately equivalent to form species *Cloghergnathus globenskii* Austin, and Morphotype I were shown to be limited to the most restricted environment, whereas Morphology III ranged into normal marine conditions in this section. Purnell observed that the distribution of morphotypes reflected increasing variability of blade position with increasing environmental restriction, but noted that this was possibly a sampling artefact. He proposed that blade position may have been an environmentally controlled character, an envirotype (his ecophenotype).

Purnell also stated that the three morphotypes were not randomly distributed geographically. American faunas are dominated by Morphotype I, Irish faunas by Morphotype II and his Northumberland faunas by Morphotype III. He found that the morphotypes are not geographically mutually exclusive and show considerable overlap in range of variation.

Unlike the form species *Geniculatus claviger*, we have had limited experience with *Taphrognathus varians* as either a form or multielement species. We have no experience with Purnell's British faunas. Thus, our evaluation of the relationship between these phenotypes is largely from information provided in Purnell (1992).

(1) Purnell cites no modified elements in other multielement species in the fauna.

(2) Only Pa elements in the *Taphrognathus varians* apparatus display modification. Other elements in the apparatus appear to have been vicarious among the three morphotypes and 13 categories.

(3) The modification of the Pa element is the location of blade relative to platform and platform ornamentation. For conodonts, platform ornamentation can be variable or constant depending on the species. In some species platform shape in relation to blade can also vary.

(4) Data presented in Purnell's text-figure 8 indicated that all morphotypes of *T. varians* co-occurred within the restricted and fluctuating environment in the Bogside Limestone Member. Morphotypes I and II appear limited to this environment, whereas Morphotype III ranged into normal marine conditions. Purnell demonstrated no gradation of morphologies along the proposed environmental cline.

These data indicate that Purnell's morphotypes had to be genetically distinct, otherwise different morphotypes would not have occurred in the same environment. Two possibilities exist. In the first, blade position was a genetically controlled (broadly canalized) feature. Distribution of the three genetically distinct morphotypes was environmentally controlled, but not environmentally induced. Morphotypes I and II inhabited mainly restricted habitats, whereas Morphotype III inhabited a wide range of environments. The three morphotypes could co-occur only in restricted environments, as they did in the Bogside Limestone Member.

The second possibility is that blade position was a 'developmentally flexible' feature. Specific morphotypes developed in response to environmental conditions and the genotype of individual organisms. Under normal marine conditions all individuals matured into the range of forms classified as Morphotype III. However, in a restricted environment, some genetic variants (sub-populations) matured into either Morphotypes I or II (Purnell's ecophenotype, our envirotype). The remainder of the population developed as Morphotype III even in restricted environments because they lacked the genetic potential to be altered by the environmental stimuli.

The geographical restriction of Morphotype III to primarily Northumberland faunas argues against Morphotypes I and II being envirotypes induced by a restricted environment. As indicated in the Bogside Limestone Member, Morphotype III occurred in restricted and open marine environments. As such, it should have occurred in, and dominated, all geographical areas containing Morphotype I and II. The near absence of Morphotype III from American and Irish faunas suggests that other factors controlled this morphotype's distribution. It also strongly suggests that Morphotypes I and II were genetically distinct sub-populations dominating large geographical areas encompassing a variety of environments.

(5) All of the morphotypes appear to be long-ranging and not restricted to single time horizons or specific lithology.

We feel the data do not support the assertion that blade position on Pa elements in the *T. varians* apparatus is an environmentally induced character. Sufficient evidence exists to suggest that genetic differentiation among the three morphotypes accounted for their differences in morphology and distribution. They may be considered to represent distinct populations, subspecies or perhaps ecotypes.

The same morphotype distribution of Pa elements of *T. varians* could be explained by low gene flow among genetically distinct populations. Temporary isolation of an initially homogeneous population would allow mutations, such as those controlling blade position, to accumulate and eventually dominate a population and geographical area. When reunited, gene flow between populations may have been limited and diluted by the large existing gene-pool of the indigenous population. If blade position offered no survival advantage, no morphotype would necessarily have become dominant outside the area where it developed. Over time, dispersal of genes introduced into a gene-pool would account for the overlap in range of variation shown within the geographical areas.

### CONCLUSIONS

There is no standard phenotype for an organism. All phenotypes represent the interaction of environment and genotype. The same genotype exposed to different environments may produce different phenotypes. Some phenotypes are stable and persist for as long as the environment exists. These phenotypes must therefore be considered potentially inheritable. As such, they are not ecophenotypes. The name ecophenotype should be restricted to phenotypic modifications resulting from disease, injury, physical restrictions to growth or modifications that develop through use.

Envirotypes are persistent, consistent, environmentally induced, potentially inheritable phenotypes that have not been selected genetically for a given environment. Different conspecific envirotypes bred in the same environment should produce an indistinguishable range of phenotypes.

By considering the number of taxa displaying modifications, number of modified element types within an apparatus, uniqueness of modification, occurrence of modified and unmodified forms and stratigraphical range of modified forms, it is possible to evaluate objectively whether modifications in conodonts represent evolution or environmentally induced changes.

Development of geniculatan from ponderosiform Pb elements represents evolution. The multielement species *I. ? claviger* contains geniculatan Pb elements and *I. ? healdi* has ponderosiform Pb elements. Other elements in the two apparatuses are vicarious. Both species are questionably placed in the genus *Idioproniodus* because their element composition differs substantially from that of the type species, *I. cornutus*.

The *Idioproniodus* lineage begins with *I. ? healdi*. *I. ? claviger* evolved from *I. ? healdi* as early as late Osagean or early Meramecian by the development of the geniculatan Pb element. *I. ? claviger* is not known from the Upper Carboniferous. *I. ? healdi* evolved into *I. conjunctus* during the Chesteran by adding a lonchodinan (lexingtonensiform) Sb<sub>3</sub> element to the apparatus. By the Missourian, *I. conjunctus* evolved into *I. cornutus* by the loss of the metalonchodinan Sb<sub>2</sub> element. The multielement genus *Idioproniodus* is not known from the Permian. *Idioproniodus* spp. may have occurred as dimorphic pairs.

Distribution of morphotypes of the Pa elements of *Taphrognathus varians* suggests that blade position relative to platform and platform ornamentation was genetically controlled, not environmentally induced.

### SYSTEMATIC PALAEOLOGY

Although reconstructed and discussed by several workers, none has provided a synonymy for elements of the *Idioproniodus*? apparatuses from the Barnett and related formations. We employed a conservative approach in synonymizing form species as apparatus elements and restricted our

consideration to Osagean and Chesteran faunas. Only references readily available to us containing adequate illustrations and/or descriptions that permitted identification with some confidence have been included. Synonymies are, therefore, not intended to be comprehensive.

Apparatus element notation follows Sweet and Schönlaub (1975), but has been modified where necessary. Element descriptive terminology is developed along the guidelines established in Klapper and Philip (1971). Specimens are deposited at The Department of Earth and Atmospheric Sciences, Saint Louis University (SLU), St Louis, Missouri 63103, USA.

Phylum CONODONTA Eichenberg, 1930  
 Class CONODONTA Eichenberg, 1930  
 Order CONODONTOPHORIDA Eichenberg, 1930  
 Superfamily HIBBARDELLACEA Müller, 1956  
 Family HIBBARDELLIDAE Müller, 1956  
 Genus IDIOPRIONIODUS Gunnell, 1933

*Form genera.*

- 1933 *Idioprioniodus* Gunnell, p. 265.
- 1953 *Geniculatus* Hass, p. 77.
- 1953 *Roundya* Hass, p. 88.
- 1956 *Neoprioniodus* Rhodes and Müller, p. 698.

*Multielement genera.*

- 1952 *Duboisella* Rhodes, p. 895.
- 1972 *Neoprioniodus* Bitter, p. 68.
- 1973 *Idioprioniodus* Baesemann, p. 703.
- 1974 *Idioprioniodus* Merrill and Merrill, p. 119.
- 1975 *Idioprioniodus* Nicoll and Rexroad, p. 20.
- 1981 *Idioprioniodus* Robinson, p. 149.
- 1983 *Idioprioniodus* Chauff, p. 418.

*Type species.* *Idioprioniodus cornutus* (Stauffer and Plummer, 1932), by subsequent designation (Merrill *et al.* 1987).

*Diagnosis.* Elements Pb = ponderosiform or geniculatan, M = neoprioniodan, Sa = hibbardellan (roundyan), Sb<sub>1</sub> = detortiform, Sb<sub>2</sub> = metalonchodinan and/or Sb<sub>3</sub> = lexingtonensiform, Sc = ligonodinan.

*Remarks.* Determining the variability allowed under the definition of a genus is a problem that multielement taxonomy has not resolved. Each genus must be treated individually. Guidelines used for one genus may not be applicable to another. For example, multielement species of *Bactrognathus* differ primarily in Pa element morphology. Apparatus element composition remained unchanged. In contrast, variation in apparatus element composition has defined species of *Idioprioniodus* (Merrill and Merrill 1974). The difference between *I. conjunctus* and the type species *I. cornutus*, the senior synonym of *I. typus* (Merrill *et al.*, 1987), is absence of the metalonchodinan (bidentatiform) Sb<sub>2</sub> element in *I. cornutus*. Otherwise, the apparatuses are nearly identical.

As earlier multielement species related to *Idioprioniodus* are reconstructed, differences from the type species increase. For example, *I. ? healdi* contains no lexingtonensiform Sb<sub>3</sub> element, but has metalonchodinan (= bidentatiform) Sb<sub>2</sub> elements. *I. ? claviger* is even more distinct. It has the same element composition as *I. ? healdi*, but its Pb element is geniculatan, not ponderosiform. The point at which a species is considered sufficiently distinct from the type species such that it becomes necessary to create a new genus depends upon a palaeontologist's bias.

Some may argue that *I.? healdi* and *I.? claviger* are already sufficiently different from *I. cornutus* that they should be placed in a separate genus. Creating a new genus could obscure the close evolutionary relationship between these species. Yet, placing them in the same genus implies that these species are very similar to the type species.

We have chosen to follow Chauff (1983) and question the assignment to *Idioproniodus* of multielement species which differ substantially from the type species. Thus, we retain *I.? healdi* and *I.? claviger* within *Idioproniodus*, but question the assignment. This will allow us to indicate the close relationship with other species of *Idioproniodus* and also imply that major differences exist with the type species.

Sweet (1988, fig. 5.31) illustrated an *Idioproniodus* apparatus in which he placed what appears to be the metalonchodinan element in the Pa position. We find this to be inconsistent with reconstructions of morphologically similar multielement genera. For example, the apparatuses of *Bactrognathus* and *Cryptotaxis* bear metalonchodinan elements, as well as Pa elements. In both of these apparatuses, the metalonchodinan element is placed within the symmetry transition series. The distinctive shape of the metalonchodinan element evolved probably to perform a specific task within the apparatus. Thus, we feel it is unlikely that the same element morphology occupies different positions in similar apparatuses.

*Idioproniodus* can be distinguished from *Cryptotaxis* and *Bactrognathus* because both of these multielement genera possess Pa elements. See Chauff (1983, p. 419) for additional information regarding differences between these genera.

Voges (1959) named the form species *Geniculatus glottoides* from the 'Dunne Kalkbank an der Grenze Liegende Alaunschiefer/Horizont vorwiegender Lydite'. This form species is unlike *Geniculatus claviger* because its wide platform is concave-up and denticles on the anterior process are small, possibly fused into a low ridge. Voges (1959) did not illustrate any ramiform elements from the fauna containing *Geniculatus glottoides*. Thus, it is not possible to determine if this form species was associated with elements similar to those assigned to the *I.? claviger* apparatus.

*Range.* Osagean through Upper Carboniferous.

### *Idioproniodus? claviger* (Roundy, 1926)

Plate 1, figures 1, 4, 11, 13–14

#### *Pa element.*

- 1926 *Polygnathus claviger* Roundy, p. 14, pl. 4, figs 1a–c, 2a–b.
- 1941 *Bactrognathus inornata* Branson and Mehl, p. 100, pl. 19, figs 14–15.
- 1953 *Geniculatus claviger* Hass, p. 77, pl. 15, figs 10, 12, 14–16, 18–19 [*non* figs 11, 13, 17 = *I.? healdi*; figs 10, 12 cops Roundy, 1926].
- 1956 *Geniculatus claviger* Elias, p. 121, pl. 4, figs B8–B13, B19–B21 [*non* figs B14–18 = *I.? healdi*; cops Roundy (1926) and Hass (1953)].
- ?1957 *Geniculatus claviger* Bischoff, p. 21, pl. 1, figs 2–4 [figs 1, 5–6 may be *I.? healdi*].
- ?1969 *Geniculatus claviger* Druce, p. 60, pl. 8, figs 8–10.
- 1978 *Geniculatus inornatus* Chauff and Klapper, pl. 2, figs 1–2 [cops Branson and Mehl (1941)].

#### *Multielement.*

- 1980 *Idioproniodus paraclaviger* Namy, pl. 5, figs 32–36, 39–42 [*non* figs 37–38 = *I.? healdi*].
- 1987 *Idioproniodus paraclaviger* Merrill and Grayson, p. 72, pl. 7, figs 32–36, 39–42 [*non* figs 37–38 = *I.? healdi*; cops Namy, 1980].

*Diagnosis.* Elements Pb = geniculatan, M = neoproniodontan, Sa = hibbardellan (roundyan), Sb<sub>1</sub> = detortiform, Sb<sub>2</sub> = metalonchodinan, Sc = ligonodinan. Pb elements are arched, have an outcurved anterior process and long, curved posterior process and develop asymmetrical ledges or

platforms along both processes. Denticles are discrete to partially fused. Other elements of apparatus are discussed under Vicarious Elements of *I.?* *claviger* and *I.?* *healdi*.

*Remarks.* From the description and holotype illustration of *Polygnathus?* *claviger*, it is obvious that Roundy (1926) applied the name to a geniculatan element. Thus, the correct name for the apparatus containing geniculatan Pb elements is *Idioproniodus?* *claviger* (Roundy).

The multielement species *I.?* *claviger* is known from the Barnett Formation in Texas and the Caney Shale and Sycamore Formation *sensu* Branson and Mehl (1941) (i.e. the post-Weldon Shale of Ormiston and Lane 1976) of Oklahoma. Possible Pa elements have been identified in Germany (Voges 1959; Bischoff 1957) and Australia (Druce 1969). The specimens illustrated by Bischoff (1957) and Druce (1969) as *Geniculatus claviger* appear to be within the range of variation recognized for the form species. Until the apparatus composition for these elements is demonstrated, we prefer to question their assignment to *I.?* *claviger*. *I.?* *claviger* differs from other species of *Idioproniodus* by the development of a long posterior process and an asymmetrical platform on its Pb element. Some Pb elements resemble the Sb<sub>1</sub> detortiform element, but with a platform and less pronounced cusp.

*Range.* Chesteran (Lower Carboniferous).

*Idioproniodus?* *healdi* (Roundy, 1926)

Plate 1, figures 2–3

*Pa elements.*

- 1926 *Prioniodus healdi* Roundy, p. 10, pl. 4, fig. 5a–b.
- 1926 *Prioniodus* sp. D Roundy, p. 11, pl. 4, fig. 13a–b [*non* fig. 12 = M element].
- ?1940 *Metalonchodina?* sp. Branson and Mehl, p. 172, pl. 5, fig. 15 [possibly an M element].
- ?1940 *Euprioniudina?* sp. Branson and Mehl, p. 171, pl. 5, figs 17–18.
- 1953 *Geniculatus claviger* Hass, pl. 15, figs 11, 13, ?17 [*non* figs 10, 12, 14–16, 18–19 = *I.?* *claviger*; figs 11, 17 cops Roundy (1926)].
- 1956 *Geniculatus claviger* Elias, pl. 4, figs 14–18 [*non* figs 8–13, 19–21 = *I.?* *claviger*; cops Roundy (1926) and Hass (1953)].
- 1956 *Geniculatus longiden* Elias, p. 121, pl. 4, figs D27–D29.
- ?1957 *Geniculatus claviger* Bischoff, pl. 1, figs 1, 5–6 [*non* figs 2–4 = *I.?* *claviger?*].

*Multielement.*

- 1980 *Idioproniodus paraclaviger* Namy, pl. 5, figs 32–38 [*non* figs 32–36, 39–40 = *I.?* *claviger*].
- non* 1981 *Idioproniodus* sp. aff. *I. healdi* Rexroad, p. 11, figs 6–8. [most probably *I. conjunctus*].
- non* 1982 *Idioproniodus healdi* Horowitz and Rexroad, 1982, p. 965, text-fig. 7 (line drawing). [= *I. conjunctus*]
- 1983 *Idioproniodus conleyharpi* Chauff, p. 418, pl. 3, figs 22–23, 25–34.
- 1987 *Idioproniodus paraclaviger* Merrill and Grayson, p. 72, pl. 7, figs 32–38 [*non* figs 32–36, 39–40 = *I.?* *claviger*; cops Namy 1980].

*Diagnosis.* Elements Pb = ponderosiform, M = neoproniodontan, Sa = hibbardellan (roundyan), Sb<sub>1</sub> = detortiform, Sb<sub>2</sub> = metalonchidinan, Sc = ligonodinan. Pb elements are arched and have an outcurved anterior process. Denticles are discrete to partially fused at base. Other elements of apparatus are discussed under Vicarious Elements of *I.?* *claviger* and *I.?* *healdi*.

*Remarks.* Namy (1980) applied the name *Idioproniodus paraclaviger* (Rexroad) to the Barnett Formation apparatus, presumably because of its similarity in element composition to a reconstruction called *I. paraclaviger* by Nicoll and Rexroad (1975) from the Sanders Group. The type specimen of *I. paraclaviger* (holotype of form species *Lonchodina paraclaviger*) was from the Chesterian Glen Dean Limestone, not the Valmeyeran (= Osagean) Sanders Group. Nicoll and

Rexroad suggested that the name *I. paraclaviger* might prove to be inappropriate for the Valmeyeran species.

Norby (1976) restudied the conodont fauna of the Glen Dean Limestone and demonstrated that lexingtonensiform (lonchodinan Sb<sub>3</sub>) elements were probably part of the apparatus containing the type specimen of *Lonchodina paraclaviger*. Although it is possible that apparatuses with and without the lexingtonensiform element co-existed in the Glen Dean Limestone, this cannot be determined from available data. No lexingtonensiform elements have been reported from the Sanders Group or Barnett Formation. Therefore, the *Idioproniodus* apparatus species bearing ponderosiform Pb elements in these strata cannot be the same species as in the Glen Dean Limestone. The name *I. paraclaviger* is inappropriate and another name is needed. Because the apparatus Norby reconstructed is identical in element composition to *I. conjunctus*, the form species name *I. paraclaviger* is a junior synonym of *I. conjunctus*.

Chauff (1983) reconstructed an *Idioproniodus*-like apparatus from the Osagean of the Midcontinent and proposed the name *Idioproniodus? conleyharpi*. It has the same element composition as the apparatus in the Sanders Group and the apparatus containing ponderosiform Pb elements in the Barnett Formation.

Roundy (1926) named *Prioniodus healdi* for a small conodont fragment consisting of a sharp-edged, compressed cusp and one denticle from each process. Holotype illustrations, especially of the lower side, show a marked offset of the processes at the cusp. Hass (1953) placed this form species into synonymy with *Geniculatus claviger* and designated the *P. healdi* holotype as a hypotype for *G. claviger*. Although we have not seen the *P. healdi* type specimen, we believe it represents a ponderosiform element, not a small (immature) geniculatan element. The name *Prioniodus healdi* is senior to *I.? conleyharpi* and the valid name for the Osagean and Barnett Formation multielement species containing ponderosiform Pb elements is *Idioproniodus? healdi*.

Rexroad (1981) and Horowitz and Rexroad (1982) applied the name *Idioproniodus healdi* (Roundy) to conodont apparatuses from the Vienna Limestone Member of the Branchville Formation and from the Glen Dean, Beech Creek and Reelsville limestones (all Chesteran). Because geniculatan Pb elements have not been recovered in the Midcontinent, identification of Chesteran *Idioproniodus* apparatus species depends primarily upon the presence or absence of a lexingtonensiform Sb<sub>3</sub> element. Without the lexingtonensiform element the apparatus is *I.? healdi*; with it the apparatus is *I. conjunctus*. *I. sp. aff. I. healdi* (Roundy in Rexroad 1981) must be considered a dubious designation. Identification was based upon a few fragmentary M, Sb<sub>1</sub> (detortiform) and Sc (ligonodinan) elements. The Vienna Limestone Member is higher in the section than the Glen Dean Limestone, from which only *I. conjunctus* is known. Thus, it is more likely that the elements in the Vienna Limestone belong to *I. conjunctus*, than *I.? healdi*.

*I. healdi*, as reported in Horowitz and Rexroad (1982), is based again on a small number of specimens. From line illustrations in their text-figure 7, it is clear that Horowitz and Rexroad considered the apparatus to contain lexingtonensiform Sb<sub>3</sub> elements. This clearly would be *I. conjunctus*, not *I.? healdi* as defined herein.

#### EXPLANATION OF PLATE I

Figs 1, 4, 11, 13–14. Pa elements of *Idioproniodus? claviger* (Roundy). 1, 4, SLU 507; upper and lower views. 11, 14, SLU 508; upper and lower views. 13, SLU 509; outer lateral view.  
Figs 2–3. Pa elements of *I.? healdi* (Roundy). 2, SLU 510; outer lateral view. 3, SLU 511; inner lateral view.  
Figs 5–10, 12. Vicarious elements of *I.? healdi* and *I.? claviger*. 5, SLU 512; inner lateral view of neoproniodan M element. 6, SLU 513; lateral view of hibbardellan (roundyan) Sa element. 7, SLU 514; inner lateral view of detortiform Sb<sub>1</sub> element. 8–9, SLU 515 and 516; inner lateral view of metalonchodinan Sb<sub>2</sub> elements. 10, SLU 517; inner lateral view of ligonodinan Sc element. 12, SLU 518; posterior view of hibbardellan (roundyan) Sa element.

All specimens from Zesch Ranch; Barnett Formation (Chesteran, Lower Carboniferous). All × 44.



CHAUFFE and NICHOLS, *Idioprioniodus?*

Osagean *Idioproniodus?* *healdi* is discussed in Chauff (1983) under the junior synonym *I.? conleyharpi*. Chesteran *I.? healdi* appears to be identical to the Osagean form. This species differs from other *Idioproniodus* species because it has a ponderosiform Pb element and a metalonchodinan Sb<sub>2</sub> element, but no lexingtonensiform Sb element.

*Range.* Osagean into Chesteran (Lower Carboniferous).

Vicarious Elements of *Idioproniodus?* *claviger* and *I.? healdi* from the Chesteran

Plate 1, figures 5–10, 12

*M elements.*

- ?1926 *Prioniodus* sp. B Roundy, p. 11, pl. 4, fig. 9.
- 1926 *Prioniodus* sp. D Roundy, p. 11, pl. 4, fig. 12 [*non* fig. 13a–b = Pa element of *I.? healdi*].
- ?1953 *Prioniodus ligo* Hass, p. 87, pl. 16, figs 1–3.
- 1953 *Prioniodus inclinatus* Hass, p. 87, pl. 16, figs 10–14 [fig. 12, cop. Roundy (1926)].
- 1956 *Prioniodus?* *inclinatus* Elias, p. 112, pl. 4, figs 4–7 [cops Roundy (1926) and Hass (1953)].

*Sa Elements.*

- 1953 *Roundya barnettana* Hass, p. 88, pl. 16, figs 8–9.
- 1956 *Roundya barnettana* Elias, p. 121, pl. 4, figs 22–23 [cops Hass (1953)].
- 1956 *Roundya* sp. A Elias, p. 121, pl. 4, fig. 26.

*Sb<sub>1</sub> Element.*

- ?1926 *Prioniodus* sp. C Roundy, p. 11, pl. 4, fig. 11 [may be Sc element].
- 1953 *Lonchodina paraclarki* Hass, p. 83, pl. 16, figs 15–16.
- 1956 *Lonchodina paraclarki* Elias, p. 122, pl. 5, figs 6–7 [cops Hass (1953)].

*Sb<sub>2</sub> Element.*

- 1953 *Metalonchodina* sp. A Hass, p. 85, pl. 16, figs 17–18.
- 1956 *Metalonchodina* sp. A Elias, p. 126, pl. 5, figs 8–9 [cops Hass (1953)].
- 1956 *Lonchodina regularis* Elias, p. 122, pl. 5, fig. 20 [figs 19, 21–22 indeterminate].

*Sc Element.*

- ?1926 *Prioniodus* sp. C Roundy, p. 11, pl. 4, fig. 11 [may be Sb<sub>1</sub> element].
- 1953 *Ligonodina roundyi* Hass, p. 82, pl. 15, figs 7–9, ?5–6 [figs 5, 6 cops Roundy (1926)].
- 1956 *Ligonodina roundyi* Elias, p. 126, pl. 5, figs 10–14 [cops Hass (1953)].

*Remarks.* M elements have high, compressed cusps and smaller, discrete to fused denticles on the posterior process. S elements possess discrete, compressed, high, slender, posteriorly reclined denticles. Cusps are similarly shaped but larger and may be marked by lateral ridges. Denticles on the posterior process of the Sa and Sc elements are variable.

Names of other ramiform species proposed by Hass (1953), such as *Ligonodina roundyi*, *Roundya barnettana*, *Prioniodus inclinatus* and *Lonchodina paraclarki*, all of which are part of either the *I.? claviger* or *I.? healdi* apparatus, must be considered *nomina dubia*. These elements are vicarious, occurring in apparatuses with geniculatan or ponderosiform Pb elements. It is impossible to determine to which apparatus species the holotypes of these form species belong.

Bischoff (1957) illustrated several elements, including several Pb elements, which may be part of an *Idioproniodus* apparatus. From data presented in his paper, we could not determine if these elements were associated with the Pb element in an apparatus. Thus, we have not included these elements in the synonymy for vicarious elements.

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# AN ICHTHYOSAUR WITH PRESERVED SOFT TISSUE FROM THE SINEMURIAN OF SOUTHERN ENGLAND

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**ABSTRACT.** A new specimen of ichthyosaur in a carbonate concretion from the Sinemurian (Lower Jurassic) of Black Ven, near Charmouth, Dorset, shows soft tissue preservation. The specimen is indeterminate at generic and specific level. It comprises the posterior portion of the axial skeleton and displays a lunate caudal fin preserved as an organic film. A thin band of phosphatized muscle tissue in the dorsal lobe of the tail indicates that some control of fin attitude was possible despite the absence of axial skeleton in the dorsal lobe. This is the earliest record of an ichthyosaur with an indisputable complete lunate caudal fin. There was a progressive increase in the angle of downturn of the vertebral column in the ichthyosaur tail, from approximately 25° in the new specimen, to approximately 80° in Late Jurassic ichthyosaurs. Ichthyosaurs did not possess typical reptilian epidermal scales.

JURASSIC ichthyosaurs with soft tissues preserved have been described from several localities but are nevertheless extremely rare (Keller 1992; Martill 1993). Such specimens offer a unique opportunity to examine aspects of ichthyosaur morphology, biomechanics, physiology and ecology (Keller 1976; McGowan 1979; Riess 1986; Taylor 1987). The most spectacular specimens are from the *Posidonia* Shale of Baden-Württemberg, Germany from which many complete individuals with body outlines, stomach contents and juveniles within the body have been reported (Fraas 1892; Baur 1895; Hauff 1921; Broili 1942; Hauff and Hauff 1981; Böttcher 1989; Martill 1993). Less well documented examples occur in the Solnhofen Limestone (Upper Jurassic) of Germany (Bauer 1898; Martill 1993).

Despite the abundance of ichthyosaurs in the Lower Jurassic of England, very few specimens have been reported with soft tissues preserved. The best specimens appear to be from the Hettangian of Barrow-upon-Soar, Leicestershire (Lydekker 1889; Andrews 1924; Martin *et al.* 1986; Martill 1987*a*), but these are all incomplete, and are either limb outlines or small patches of organic material associated with the postcranial skeleton. No ichthyosaur with a complete body outline has been recorded from the British Isles. A new specimen from the Lower Jurassic near Lyme Regis exhibits the first ichthyosaur caudal fin to be reported from the British Isles. It is a remarkably preserved arcuate fin with prominent dorsal and ventral lobes and is described in the following account.

## SOFT TISSUE PRESERVATION IN ICHTHYOSAURS FROM ENGLAND

The earliest account of ichthyosaurs with soft tissues preserved is that of Buckland (1836), who described patches of black material associated with skeletons from the Lower Lias of Lyme Regis, Dorset, and from Barrow-upon-Soar, Leicestershire. Buckland noted that the Lyme Regis specimens showed no evidence of scales, and suggested a comparison with the skin of modern frogs. Owen (1840, 1841) reported an ichthyosaur hind paddle with soft tissues from the Lower Lias of Barrow-upon-Soar, and showed that the soft tissues extended well beyond the limb skeleton. However, this is not borne out by Holzmaden specimens, which show the non-skeletal tissue to be restricted to the immediate region of the limb skeleton. Shortly afterwards, Pearce (1846) reported an ichthyosaur from Somerset with an embryo within the area of the trunk, and noted that soft

tissues were associated with the embryo. Mantell (1851) figured the hind limb described by Owen (1840) and commented that a second specimen with soft tissues preserved had been damaged during preparation. Mantell may have damaged the specimen himself, as later implied by Davies (1864) in a report of a further ichthyosaur from Barrow-upon-Soar with associated preserved soft tissues. Coles (1853) noted small black hook-shaped objects associated with an ichthyosaur from the Lias between Upton on Severn and Tewkesbury. He interpreted these as scales within the skin of the ichthyosaur, but it is clear from the figure of the specimen that these objects were cephalopod hooklets in the gut of the animal (see Pollard 1968). Later, Moore (1857, 1862) reported a nodule containing an ichthyosaur with gut contents and preserved soft tissues but provided no locality or horizon data. Subsequently further ichthyosaurs with soft tissues have been reported from Barrow-upon-Soar (Lydekker 1889; Andrews 1924), Lyme Regis (Whitewar 1956), an unknown locality in the Severn Valley (Delair 1966) and the Oxford Clay of central England (Martill 1987*a*, 1987*b*, 1993). Recent surveys of ichthyosaurs with soft tissue preservation are by Martin *et al.* (1986) reviewing the Barrow-upon-Soar material, Martill (1993) reviewing English and German material, and Riess and Frey (1985) incorporating a comprehensive bibliography of ichthyosaurs including exceptionally preserved specimens.

#### MATERIAL

The septarian concretion containing the new specimen was discovered by Mr Chris Moore of Charmouth, on the foreshore in front of the Black Ven landslip between Charmouth and Lyme Regis in Lyme Bay, Dorset (O.S. Grid Reference approximately SY 356931). The lithology and the presence of small *Asteroceras* sp. suggests that the concretion is from the *obtusum* Zone of basal Upper Sinemurian age. Detailed lithological sections for the Lias at Lyme Bay were given by Lang (1914, 1924). The specimen is now housed in the collections of the Yorkshire Museum and is registered as YORYM 1993.338.

The septarian concretion is water-worn and incomplete and composed of a hard, dark grey carbonate mudstone. It measures 340 mm by 270 mm. The plane of splitting passes through the plane of the soft tissue and skeleton of the caudal region of a small ichthyosaur. Septarian cracking is slight, with infills of brown calcite. A few small septarian cracks pass through the soft tissues. The specimen was prepared slightly to expose further soft tissue and the concretion has been partly reassembled (Pl. 1; Text-fig. 1).

#### DESCRIPTION

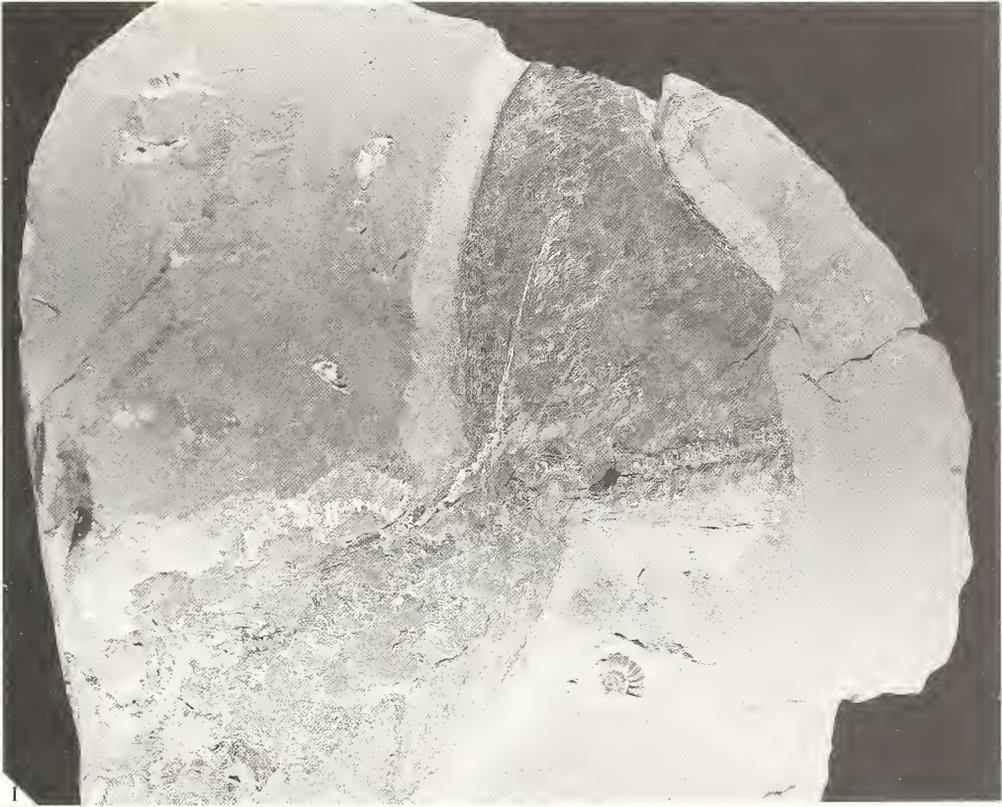
*Axial skeleton.* Only the posterior portion of the axial skeleton is present. It is in articulation apart from a few slightly displaced vertebrae in the region of the tail bend. It is almost certainly part of a complete skeleton, the rest of which is presumably still in the Black Ven landslip. The vertebrae have been split and are visible in section. Ten articulated vertebrae followed by three disarticulated vertebrae are present anterior to the tail bend. Four vertebrae comprise the tail bend, followed by a series of 13 articulated vertebrae extending from the tail bend to the ventral lobe of the caudal fin. A few distal vertebrae are missing. The small size of the specimen suggests that it represents a juvenile individual.

*Soft tissues.* The soft tissues show the distinct outline of a lunate caudal fin and part of the posterior region of the trunk. All soft tissues are compressed and the caudal fin is twisted anti-clockwise in relation to the body as seen from the anterior. The soft tissues comprise two distinct materials: (1), a smooth, black to brown, organic material; (2), buff-coloured, slightly fibrous material, interdigitating with the black/brown material. The buff material is probably phosphatic; although no tests have been performed on it, it closely resembles

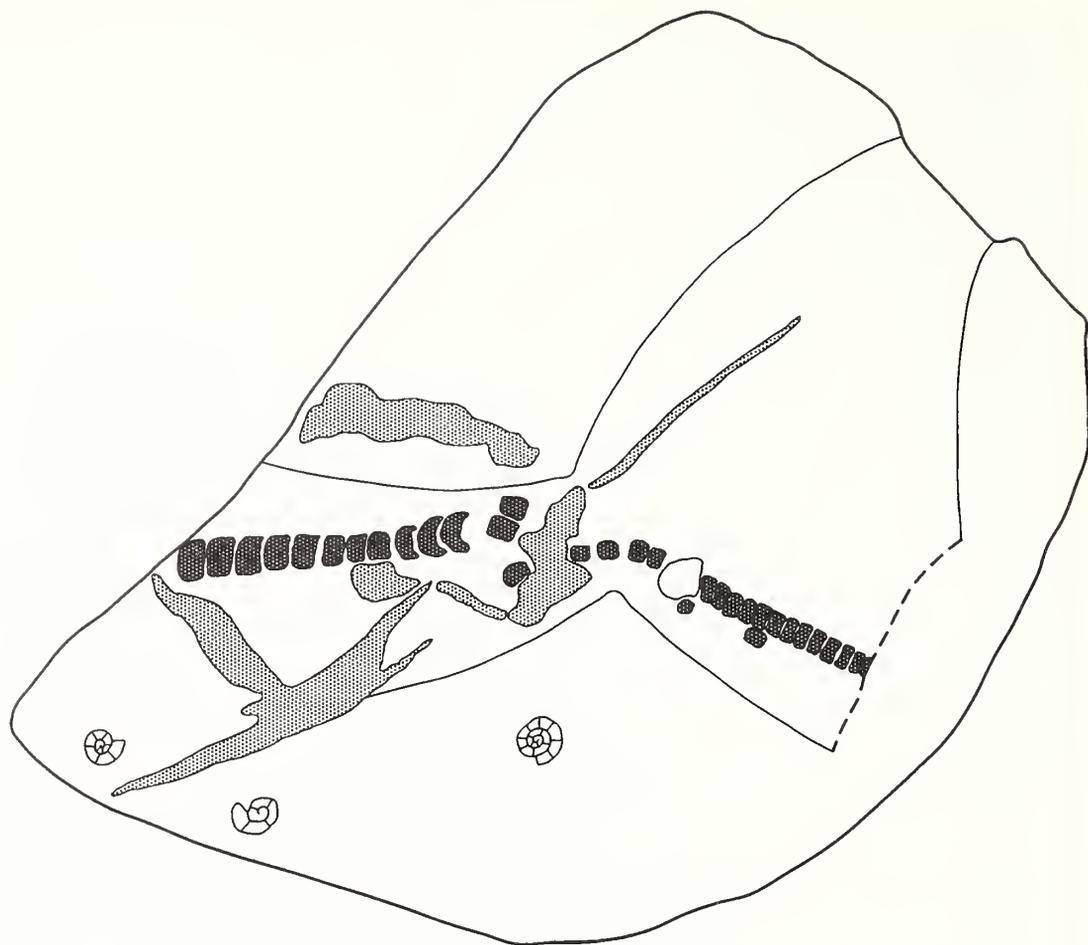
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#### EXPLANATION OF PLATE I

The new soft tissue ichthyosaur specimen; YORYM 1993.338; Lower Lias; Black Ven, Dorset, UK.  
1, *c.*  $\times 0.5$ . 2, high contrast photograph of caudal fin region showing areas of organic material (appearing dark) and areas of ?phosphatic material (appearing whitish); specimen photographed wet, *c.*  $\times 0.75$ .



MARTILL, ichthyosaur



TEXT-FIG. 1. The new soft tissue ichthyosaur specimen; YORYM 1993.338; Lower Lias; Black Ven, Dorset, UK. Sketch illustrating the areas of soft tissue preservation, bones (dark stipple), and late diagenetic calcite (light stipple) in septarian cracks.

phosphatic material found in Holzmaden ichthyosaurs. Both of these materials are known from the *Posidonia* Shale (Lower Jurassic, Toarcian) soft tissue ichthyosaurs (Keller 1992) and from an example of *Ophthalmosaurus* from the Oxford Clay Formation (Middle Jurassic to Upper Jurassic, Callovian–Oxfordian) of central England (Martill 1987b).

In most places the edge of the soft tissue is sharp and defines the shape of the posterior trunk and caudal fin in left lateral view. The edge of the soft tissues has been exposed by preparation, but this has not produced a spurious outline as is the case with some Holzmaden specimens (Martill 1987a, 1993). The ventral margin of the lower caudal lobe is indistinct. The tips of both dorsal and ventral lobes are missing, having extended beyond the present (eroded) boundaries of the concretion.

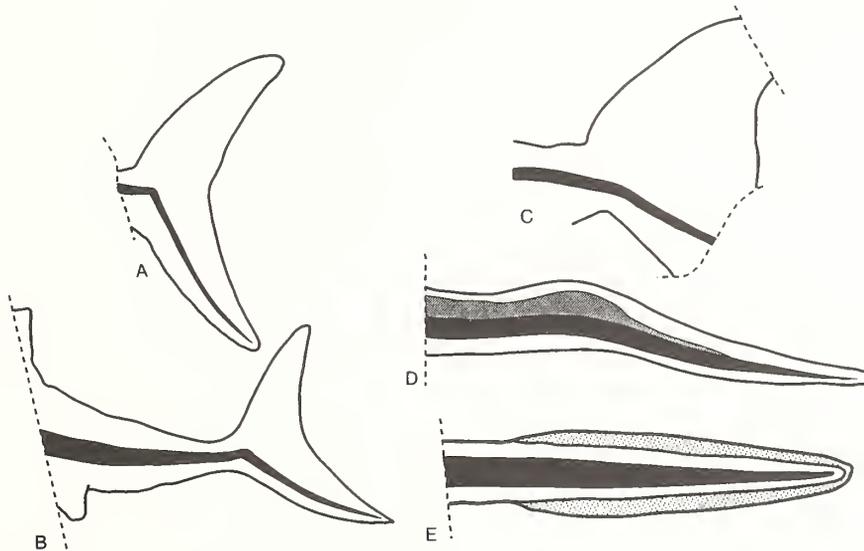
Most of the outline is defined by the distribution of the black/brown organic material. The fibrous buff material is restricted to narrow zones within the central region of each lobe. Buff material is found adjacent to the ventral and dorsal surface of the vertebral column within the lower lobe of the caudal fin. The fibrous nature, colour and aspect of its distribution suggest that this material is most likely to be the phosphatized musculature of the axial skeleton. It resembles phosphatized muscle tissue from fishes of the Cretaceous Santana Formation of north-east Brazil (Martill 1988).

## DISCUSSION

Numerous authors have reported on the occurrence of ichthyosaurs with soft tissues preserved in the Jurassic of England (see above for references). Most of these remains are fragmentary, and none has soft tissues associated with the caudal skeleton.

The new specimen is the oldest known ichthyosaur caudal fin outline. It demonstrates that the complete, lunate outline of the 'typical' ichthyosaurian caudal fin had been achieved by the Sinemurian, an idea that could previously only be postulated on the basis of skeletal elements alone. In addition, the preserved musculature in the dorsal lobe of the new specimen suggests that some degree of control of the shape, rigidity and position of the upper lobe of the tail occurred during locomotion.

It remains unclear as to how the lunate caudal fin of ichthyosaurs evolved. Many Triassic ichthyosaurs, e.g. *Shonisaurus*, had straight tails (Text-fig. 2E), with no distal downturn of the



TEXT-FIG. 2. Caudal fin outlines of ichthyosaurs; vertebral column outlined in black. A, deeply forked caudal fin outline of ichthyosaur gen. et sp. indet., from the Solnhofen Limestone, Upper Jurassic of Bavaria; outline drawn from photograph in Martill (1993, fig. 13). B, caudal fin outline of *Stenopterygius quadriscissus* from the *Posidonia* Shale, Lower Jurassic of Baden-Württemberg, Germany; after illustration in Hauff Museum guide. C, YORYM 1993. 338; outline of caudal fin of the new specimen from the Sinemurian of Dorset. D, supposed caudal fin outline of the Triassic ichthyosaur *Mixosaurus* sp. from Grenzbitumenzone, Ticino, Switzerland; note that the upper lobe of the tail is supported by extended neural spines (shaded dark grey) and that the caudal vertebrae are only slightly downturned. E, supposed outline of caudal fin of the Triassic *Shonisaurus* from Nevada, USA; note that the vertebral column is straight; there is no direct evidence for the dorsal and ventral fins, but biomechanical constraints require them (Riess 1986). Figures D and E are from Riess (1986).

vertebral column (Riess 1986; McGowan 1992). These animals are assumed to have used their tails for lateral undulatory locomotion, as do modern crocodilians (McGowan 1992). The Triassic ichthyosaur *Mixosaurus* has a slightly downturned distal portion of the vertebral column, and also has neural spines of increased height over the region of the tail bend (Text-fig. 2D). This presumably supported an upper caudal lobe, but how much this may have extended beyond the skeleton is unknown as soft tissue specimens do not exist. There is no evidence for increased neural spine height in any of the Lower Jurassic ichthyosaurs, suggesting perhaps that the modified caudal fin of

*Mixosaurus* was not a precursor to the Jurassic ichthyosaur tail condition, as postulated by Jaekel (1904).

The downturn of the vertebral column in the new specimen is only about 25° (Text-figs 1, 2c), although it is difficult to measure accurately because of torsion of the trunk. *Stenopterygius* from the *Posidonia* Shales (Toarcian) consistently has a downturn of between 30° and 50° (Text-fig. 2b), whereas the Solnhofen (Upper Jurassic, Tithonian) ichthyosaur tail shows a downturn approaching 80° (Text-fig. 2a). It is tempting to view this as a gradual increase in the degree of downturn of the vertebral column through the Jurassic, reflecting perhaps increased swimming efficiency, and a response for catching faster-swimming soft-bodied cephalopods and perhaps fish.

A surprising aspect of all ichthyosaur soft tissue specimens is the lack of preservation of typical reptilian scales. This might be attributed to the preserved outline being: (1), a prokaryote mat replacement, resulting in loss of original structural detail; an idea suggested by Martill (1987c) but challenged by Keller (1992); (2), the *in situ* preservation of degraded organic matter preserving only the shape of the ichthyosaur, but no detail; (3), the preservation of a part of the integument below the scaly epidermis; or (4) the preservation of an integument which lacked reptilian scales. The discovery of dinosaur integument from the same formation at a nearby locality (1 km distant) in which typical reptilian scales are well-preserved (Martill 1991) suggests that ichthyosaurs probably lacked typical reptilian scales. Rather than scales, a feature present on the integument of a number of *Posidonia* Shale soft tissue specimens as well as on a Barrow-upon-Soar specimen, is small, ripple-like ridges (Martill 1993, pl. 5, figs 1–6). Although these features may represent artefacts of preservation, they could be original, perhaps having assisted in locomotion, or alternatively, in limiting the opportunities for parasite attachment. Unfortunately these features are not observed on the new specimen.

*Acknowledgements.* I thank Mr Paul Ensom of the Yorkshire Museum for bringing the new specimen to my attention, and the trustees of the Preservation of Industrial and Scientific Material fund (PRISM) for purchasing the specimen, and thus saving it for the scientific community at large. I would like to thank Drs Dino Frey, Jurgen Riess, Arthur Cruickshank and Mr John Martin for thought-provoking discussion. One referee was frank, but nevertheless helpful.

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# ABNORMAL HISTOLOGY IN AN *IGUANODON* CAUDAL CENTRUM FROM THE LOWER CRETACEOUS OF THE ISLE OF WIGHT

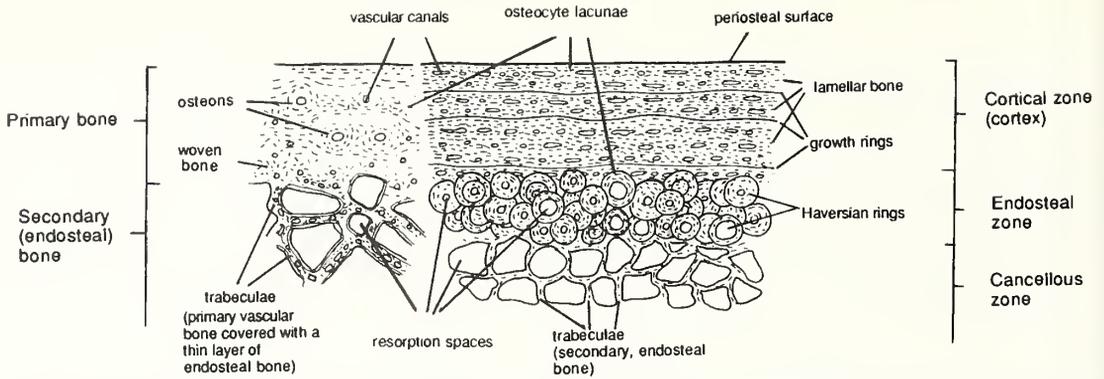
by JANE B. CLARKE *and* MICHAEL J. BARKER

**ABSTRACT.** The abnormal histology of a ?pathological *Iguanodon* (Dinosauria; Ornithischia) caudal vertebral centrum is described and comparisons made with normal iguanodontid histology. The abnormal bone exhibits rapidly generated radial growth patterns; in the cancellous zone, areas of primary bone predominate and there is a distinctive contorted vascularity throughout. The similarities of the observed deformations to known mammalian pathologies such as local trauma, Paget's disease, haemangioma and vitamin deficiency are discussed. Further systematic surveys to ascertain details of dinosaur bone histology and variation are required.

In thin section, dinosaur bones exhibit a range of osteological and histological detail which can be identified readily (Text-fig. 1). The outer edge of *Iguanodon* bones (the cortical zone or cortex) is nearly always vascular, often primary, parallel-fibred bone; the successive layers having built up on the periosteal (outer) surface as the bone grew. However, in some iguanodontid bones, the cortex is composed of primary, parallel-fibred bone which has formed osteons with woven bone in between. Where present, resting lines are visible in the cortex but disappear in the endosteal zone just below the cortex where the bone has been remodelled. In the endosteal zone, the primary bone has been absorbed by osteoblasts, creating resorption spaces. The osteoblasts then reversed their process and deposited secondary bone, starting on the rim of the resorption space and filling it with concentric layers of secondary (endosteal) bone forming distinctive Haversian rings. The collagen fibres are arranged concentrically in these rings and a characteristic extinction cross is observed under crossed polarized light. Osteocyte lacunae (the sites of dead osteoblasts) appear as short black lines, or dots, in thin section. This remodelling continued until the resorption spaces were left empty and the central, sponge-like cancellous zone was formed. In the secondary bone of the cancellous zone, collagen fibres run longitudinally along the remaining strands of bone (trabeculae). At high magnification, these mineralized collagen fibres are clearly visible.

Much of the study of fossil bone thin sections to date has been concerned with the ectothermy/endothemy debate (e.g. Ricqlès 1974c, 1976; Reid 1984b), but also random sections have been cut to compare with modern mammals and reptiles and to describe the detailed histology of dinosaurian bones (Enlow and Brown 1956, 1957, 1958; Enlow 1969; Ricqlès 1969, 1972, 1974a, 1974b; Reid 1984a). Exactly where each type of histology occurs within each bone, the variation between individual bones and variation between species has yet to be ascertained.

The specimens described herein were found on the beaches of the Isle of Wight, having been weathered out of the Wealden Group (Lower Cretaceous) at several locations. There was no indication that there was anything unusual about the *Iguanodon* centrum when it was collected as a 'rolled bone'; its external appearance was consistent with many others found under similar conditions. It was only when sectioned and examined petrographically that unusual features were evident.

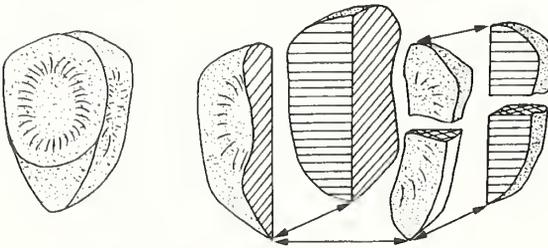


TEXT-FIG. 1. Sketch explaining general histological terminology of a transverse section through a normal fossil vertebrate bone. Not to scale.

### MATERIALS AND METHODS

The material studied comprises four *Iguanodon* (Dinosauria; Ornithischia) vertebral centra. The vertebrae are derived from separate animals but all originate from the seven caudal vertebrae nearest the sacrum (S. Hutt, pers. comm.). In three of the centra (MIWG 5454, MIWG 5385 and IWGMS: 1994: 14) the histology is apparently normal whilst the other (MIWG 7320) is different (abnormal). All the specimens are housed in the Museum of Isle of Wight Geology, Sandown Library, High Street, Sandown, Isle of Wight, PO36 8AF, (MIWG: old accession prefix to 1994 and IWGMS: new accession prefix from 1994 onwards).

Thin sections were prepared longitudinally, transversely and horizontally as shown in Text-figure 2. Detailed tracings of the overall bone patterns were compiled from projected thin sections and composite figures constructed (Text-figs 3–4).



TEXT-FIG. 2. Explosion diagram to show the orientation of the sections cut from the caudal centra. Not to scale.

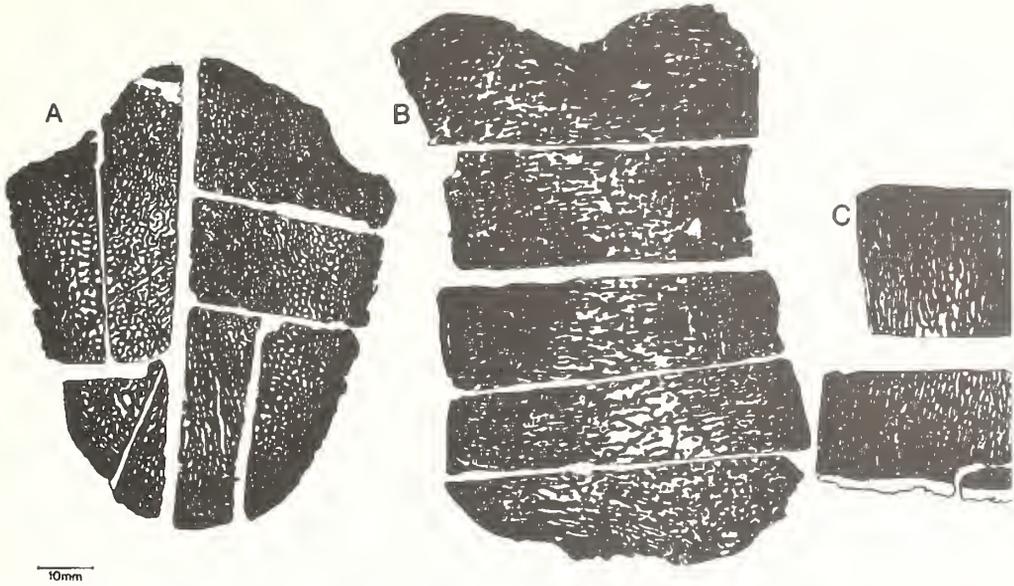
Examination of specimens MIWG 5454, MIWG 5385 and IWGMS: 1994: 14 shows closely similar overall bone patterns and histological detail. Therefore, for descriptive purposes, one centrum, IWGMS: 1994: 14, is used as an example of the normal structure, compared with the abnormal specimen (MIWG 7320).

### DESCRIPTION

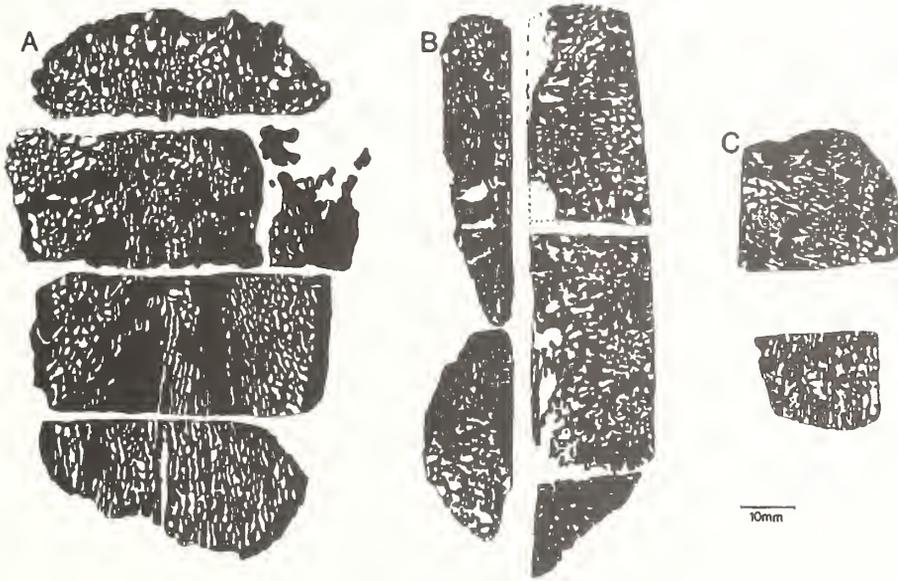
#### *Transverse sections*

*Overall bone pattern.* Sections from the normal centra show the central cancellous zone to be composed of a regular arrangement of trabeculae surrounding voids roughly equal in size (Text-fig. 3A). Some voids in the ventral half of the centrum are elongated radially and one or two radially orientated nutrient canals are also present. As the cortex is approached, the voids become smaller.

The section from the abnormal centrum is very different. Although some post-mortem crushing has occurred, much of the internal structure is still intact and clearly visible (Text-fig. 4A). In the



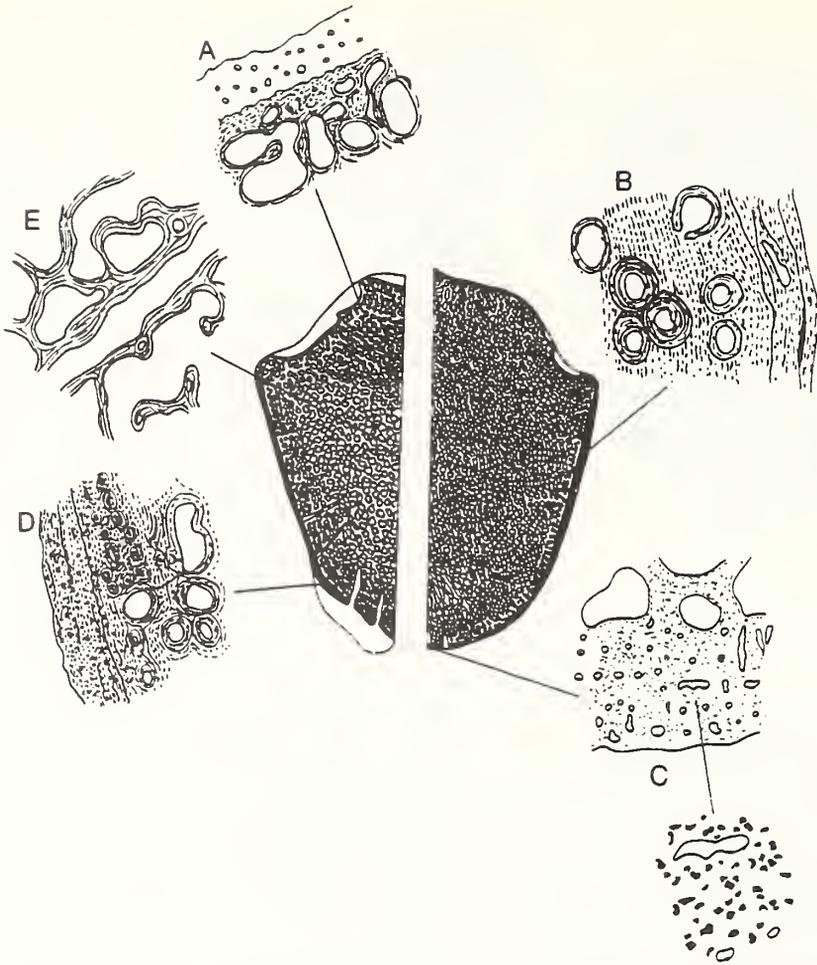
TEXT-FIG. 3. Bone patterns displayed by a normal *Iguanodon* caudal vertebral centrum (IWGMS: 1994: 14). A, transverse section; B, longitudinal section; C, horizontal section. Scale bar represents 10 mm.



TEXT-FIG. 4. Bone patterns displayed by an abnormal *Iguanodon* caudal vertebral centrum (MIWG 7320). A, transverse section; B, longitudinal section; C, horizontal section. Scale bar represents 10 mm.

dorsal half of the centrum, the voids show a similar pattern to the other three centra, although without the same degree of regularity, but in the ventral half, all the voids are radially disposed and are markedly elongated. Six radial nutrient canals are also visible in the specimen.

*Histology.* At the dorsal end of the normal centra, the cortex is composed of fine cancellous bone abutting calcified cartilage (Text-fig. 5A). The trabeculae have a core of primary woven bone

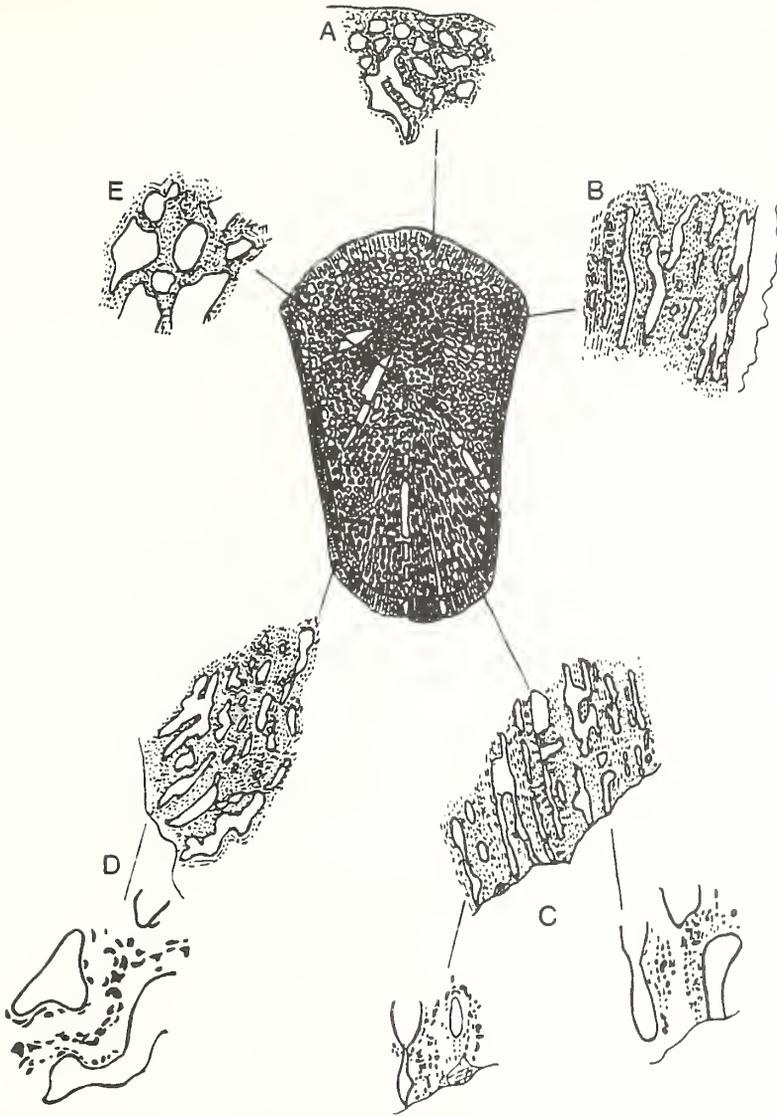


TEXT-FIG. 5. Sketch of a transverse section of a normal *Iguanodon* caudal centrum (IWGMS: 1994: 14), showing histological detail. See text for discussion. Not to scale.

covered by a layer of secondary lamellar bone. A similar area in the abnormal specimen shows the cortex to be composed of fine cancellous bone, composed entirely of primary woven bone with very little secondary lamellar bone (Pl. 1, fig. 1; Text-fig. 6A). The outer edge of the cortex is missing, but the histology of the bone shows none of the regularity displayed by the other three specimens.

Most of the remaining cortex from the normal vertebrae is composed of parallel-fibred vascular primary bone with primary osteons and resting lines (Pl. 1, fig. 2; Text-fig. 5B, D) and one specimen (IWGMS: 1994: 14) also exhibits areas of plexiform bone (*sensu* Ricqlès 1974c). Secondary Haversian rings replace primary bone in the endosteal zone, eventually passing into the cancellous zone where the trabeculae are composed of secondary, lamellar bone with occasional cores of primary bone. The voids which contained blood vessels are arranged in concentric layers. However, the cortex at the extreme ventral end has no resting lines and is entirely primary woven bone (Text-fig. 5C), the resorption spaces grading from small to large on passing into the cancellous zone.

The cortex in the mid region of the abnormal specimen is very vascular (Pl. 1, fig. 3; Text-fig. 6B) and has no resting lines. There is no transition (endosteal) zone; the large resorption spaces of the cancellous zone invade the cortex. The trabeculae are composed of primary cortical bone which still contains primary vascular canals; very little, if any, secondary lamellar bone coats the trabeculae.



TEXT-FIG. 6. Sketch of a transverse section of an abnormal *Iguanodon* caudal centrum (MIWG 7320), showing histological detail. See text for discussion. Not to scale.

At the ventral end, the cortex is composed of woven and parallel-fibred bone and is very vascular with radially orientated blood vessels (Pl. 1, fig. 4; Text-fig. 6C-D). Again, there is no transition zone between the cortex and cancellous zone, the large resorption spaces invading the cortex. The periosteal surface is missing but there is no indication of circumferentially arranged vascular canals. This radially orientated cortical pattern covers the whole of the hemispherical ventral end of the centrum.

The trabeculae in the cancellous zones of the normal vertebrae are composed predominantly of secondary lamellar bone, sometimes bearing a thin core of primary woven bone (Text-fig. 5E). Some post-mortem crushing has occurred in the cancellous zone of the abnormal specimen, but in a central, uncrushed area, the trabeculae are composed mainly of primary vascular woven bone

surrounded by a thin layer of secondary lamellar bone (Pl. 1, fig. 5; Text-fig. 6E). In other areas trabeculae are composed entirely of secondary bone.

### *Longitudinal sections*

*Overall pattern.* In longitudinal section, the normal bones have similar overall bone trabeculae patterns (Text-fig. 3B). The voids in the central part of the cancellous zone are markedly elongate in an anterior-posterior direction. Flanking these larger voids, the trabeculae are arranged in a grid-like pattern (Pl. 1, fig. 6; Text-fig. 7A), particularly in the waist of the centrum where the voids become almost square. In contrast, longitudinal sections of the abnormal specimen show no such pattern (Text-fig. 4B), the voids being irregular without order. Some post-mortem crushing has occurred in the central area, but enough non-brecciated bone remains for any regular structure to have been visible, if it were present.

*Histology.* Within the normal specimens, the trabeculae in the cancellous zone are composed of thin cores of primary woven bone surrounded by layers of secondary lamellar bone (Pl. 1, fig. 6; Text-fig. 7A). In contrast, the trabeculae in the cancellous zone of the abnormal specimen have thick centres of primary woven bone, often containing the cortical vascular canals, surrounded by thin layers of secondary lamellar bone (Text-fig. 8A). Furthermore, in the centre there are thick trabeculae composed of primary parallel-fibred and woven bone (Pl. 1, fig. 7; Text-fig. 8B).

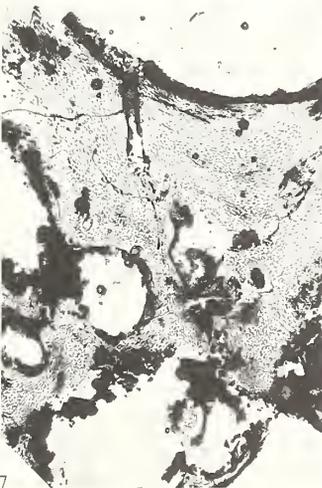
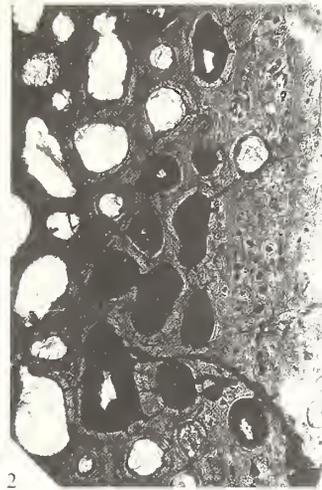
In this longitudinal orientation, all the cortices of the normal specimens are composed of fine cancellous bone which abuts and includes calcified cartilage (Text-fig. 7C–D). In contrast, the cortex at the ventral end of the centrum of the abnormal specimen is radially orientated vascular woven bone (Text-fig. 8C), similar to that observed in the transverse section. The cortical bone in the waist of the centrum is composed of partially compacted cancellous bone (Pl. 1, fig. 8; Text-fig. 8D) which becomes compacted cancellous bone towards the dorsal end (Pl. 1, fig. 9; Text-fig. 8E).

### *Horizontal sections*

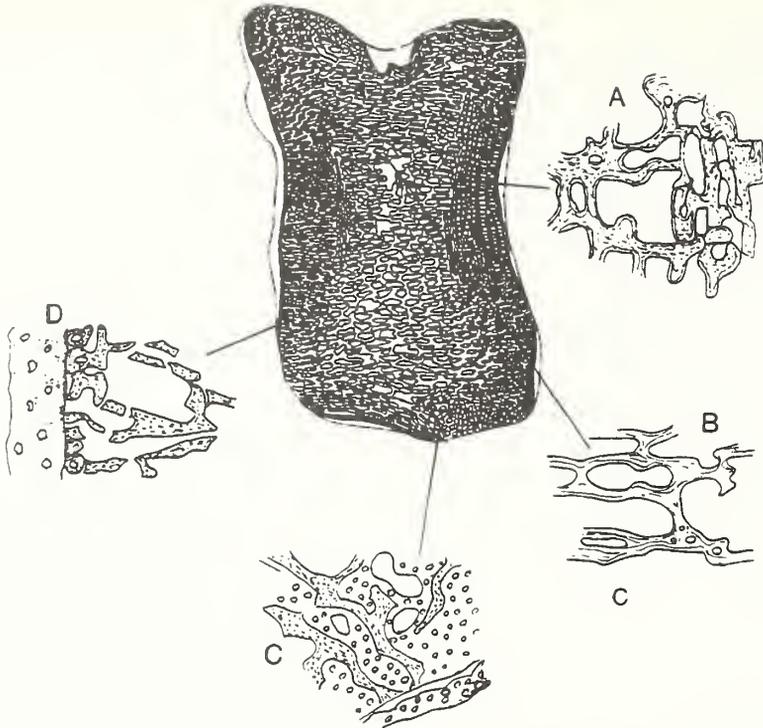
The overall patterns of the trabeculae in horizontal sections of the normal specimens are consistent with those in the transverse and longitudinal sections (Text-fig. 3C) whilst the corresponding sections from the abnormal specimen show continued irregularity (Text-fig. 4C). The histology of all four specimens is exactly comparable with that shown in the transverse and longitudinal sections.

#### EXPLANATION OF PLATE I

Figs 1–9. Thin sections of *Iguanodon* centra. 1, MIWG 7320; near the cortex at the dorsal end of the abnormal centrum; the trabeculae are composed of primary woven bone with little, if any, secondary lamellar bone; periosteal surface at upper right at 30° to the vertical. 2, IWGMS: 1994: 14; cortex from the side of the normal centrum composed of parallel-fibred vascular primary bone with primary osteons and resting lines; note the graduation of small to large resorption spaces away from the cortex; periosteal surface to the right. 3, MIWG 7320; cortex from the side of the abnormal centrum composed of very vascular primary woven bone; note the large resorption spaces invading the cortex; periosteal surface to the right. 4, MIWG 7320; cortex at the ventral end of the abnormal centrum composed of primary woven and parallel-fibred bone; note the high density of vascular canals orientated in a radial pattern and the large resorption spaces invading the cortex; periosteal surface at the bottom. 5, MIWG 7320; trabeculae in the cancellous zone of the abnormal centrum composed of primary vascular woven bone surrounded by a thin coating of secondary lamellar bone. 6, IWGMS: 1994: 14; grid-like pattern formed in the waist of the normal centrum; the trabeculae are composed of a thin core of primary bone surrounded by layers of secondary lamellar bone; dorsal end to the left. 7, MIWG 7320; trabeculae in the centre of the abnormal centrum composed of thick sections of primary woven and parallel-fibred bone. 8, MIWG 7320; cortical bone in the waist of the abnormal centrum composed of partially compacted cancellous bone; periosteal surface at the top. 9, MIWG 7320; cortical bone from the dorsal end of the central dished area of the abnormal centrum composed of compacted cancellous bone; periosteal surface at the top. All × 13, except fig. 6, × 20.



CLARKE and BARKER, thin sections of *Iguanodon* centra



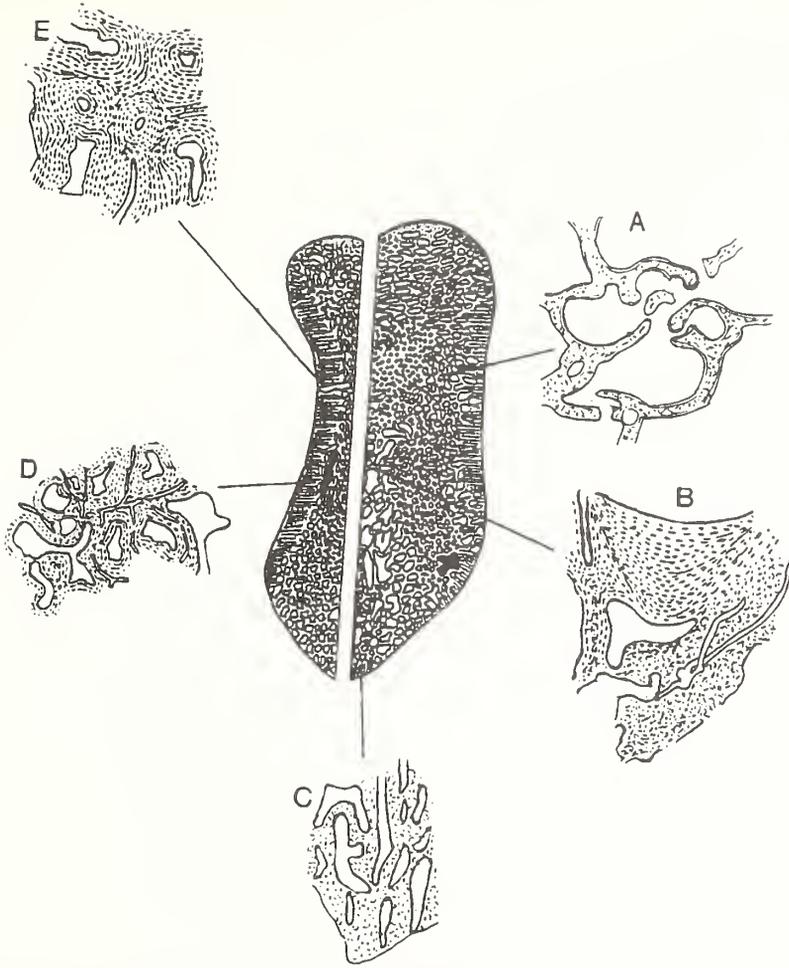
TEXT-FIG. 7. Sketch of a longitudinal section of a normal *Iguanodon* caudal centrum (IWGMS: 1994: 14), showing histological detail. See text for discussion. Not to scale.

#### DISCUSSION

*General.* A sketch of the general histological detail (and its associated terminology) normally observed in thin sections of dinosaur bones is given in Text-figure 1. In the authors' experience, the abnormal bone (MIWG 7320) shows unusual histological detail. Cortical bone at the sides of normal centra is usually parallel-fibred, sometimes with resting lines, with a reasonable density of concentrically arranged vascular canals; while the cortex at the ventral end is sometimes primary woven bone, containing primary osteons. The vascularity of the cortex in MIWG 7320 is unusually high and, together with the presence of woven bone, suggests a high growth rate (Enlow 1969). The radial cortical pattern in the ventral end of the centrum is also highly unusual and again the presence of woven bone, together with the direction of linearity, further suggest abnormally high growth rates (D. Cooper, pers. comm.).

Inside the cortex of iguanodontid vertebral centra, secondary Haversian rings are rare and there is usually a transition zone where primary bone is resorbed and secondary bone deposited. This gradual change is characterized by small resorption holes which become progressively bigger towards the centre of the centrum. In MIWG 7320, large resorption spaces directly invaded the cortex; there is no transition zone where small resorption holes occur.

In the normal iguanodontid centra, the trabeculae in the cancellous zone usually contain a high percentage of secondary, endosteal bone, remodelling having continued until only a thin core (if any) of primary bone remains. Sometimes primary vascular canals are retained in the outer areas of the cancellous zone, but in the centre of the centrum most have been removed by remodelling. In MIWG 7320, the trabeculae throughout most of the cancellous zone are unaltered primary vascular bone surrounded by a thin coating of endosteal bone; there are only small areas in which



TEXT-FIG. 8. Sketch of a longitudinal section of an abnormal *Iguanodon* caudal centrum (MIWG 7320), showing histological detail. See text for discussion. Not to scale.

the trabeculae are composed of secondary endosteal bone. The thick patches of primary bone in the centre of MIWG 7320 are highly unusual; trabeculae in this region are usually thin.

*Aetiology of pathological bone.* It is unfortunate that only a single skeletal element was available for study. However, the comparative histologies described above indicate clearly that bone growth and modification in the MIWG 7320 centrum was unusual.

All features in MIWG 7320 suggest that bone deposition and resorption were abnormally rapid whilst remodelling and deposition of secondary bone was very slow or absent. Most previous pathological studies have been centred on mammals (principally human) so any comparisons must be qualified, however, possible aetiologies are:

(a) Localized trauma during early ontogeny could have caused low grade osteoperiostitis or traumatic arthropathy.

(b) Disease – the bone histology is reminiscent of osteoporosis in mammals, described as ‘decreased bone formation, increased bone resorption or a combination of both’ (Cappell 1964). However, the high rate of growth of primary bone is more akin to Paget’s disease (Osteitis deformans), which is also known to attack only single bone elements. Histological illustrations of

Paget's disease show a remarkable resemblance to the dorsal end of the abnormal specimen (Cappell 1964, pl. 10, fig. 17.28). Another possible cause could be vitamin-related if the condition was pervasive throughout the organism.

(c) Genetic causes – there is, as yet, no means of relating genetic abnormalities to bone histology in dinosaurs. We have observed no evidence to suggest any genetic cause for this condition, although some form of endocrine abnormality remains a possibility again if pervasive throughout the organism.

(d) Haemangioma – the bone was X-rayed and interpreted by a consultant histopathologist and cytopathologist. There is evidence of high turnover of tissue but the overall sectional area percentage of bone does not exceed normal limits and suggests that this is not a true haemangioma (L. Harvey, pers. comm.). Furthermore, although the patterns in the trabeculae bear a similarity to radial sun-burst histologies in some haemangiomas, the radiographs did not reveal the diagnostic striations present in true haemangiomas (Rothschild and Martin 1993).

The specimen described above, shows enough variation from the normal to be considered abnormal, even pathological; the growth structures indicating that something was stimulating the growing mechanisms to an abnormal degree.

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# A REVIEW AND NEW CLASSIFICATION OF THE BRACHIOPOD ORDER PRODUCTIDA

by C. H. C. BRUNTON, S. S. LAZAREV *and* R. E. GRANT

**ABSTRACT.** The authors discuss the large and diverse Upper Palaeozoic strophomenide (*sensu lato*) group of brachiopods, the Productida, the problems inherent in previous classifications and present a new classification with diagnoses down to subfamily and tribe levels. In describing productides it is useful to differentiate between the main corpus (new term) cavity and peripheral cavities. Study of the ways in which the two valves grew leads to more precise identification of the visceral and trail regions of the shell. New data on early productides, from the lower to mid Devonian, has allowed the group to be studied in its complete stratigraphical range, as well as its wide morphological diversity, and has led to the recognition of numerous lineages and homeomorphic relationships. The new classification presented builds on these lineages phyletically and differs markedly from previous classifications in which some similar taxa, now recognized as having different origins, were grouped together. We diagnose two new tribes, the Krotoviini and the Kozlowskiini.

THE order Productida, as here discussed, is made up of the true productidines, strophalosiidines and oldhaminioids, but follows Muir-Wood and Cooper (1960) and Lazarev (1990), for example, in excluding chonetoids, which some researchers (Sarycheva (ed.) 1960) included. This group has long been considered difficult to classify. Davidson (1859) wrote 'the determination and arrangement of British Carboniferous species of *Productus* and *Chonetes* has demanded a lengthened examination, for much confusion still existed among the synonyms,' while Girty (1908) considered that 'as a whole the group has shown unusual plasticity, developing not only widely different types, all referable to the same genus [*Productus*], but also abundant intermediate stages between what one would suppose to be wholly distinct species. In consequence, specific discrimination among '*Producti*' has always been a difficult matter, and authors have shown wide differences of opinion as to where the limits of species should be drawn.' Similarly, Yanishevsky (1918) wrote that the 'group represents perhaps the most complex group of brachiopods, for which it is impractical at the present time to give a clear picture of the generic relationships.' The few genera described in 1918 had risen to 167 by 1960 when Muir-Wood and Cooper published their beautifully illustrated monograph on the Productoidea, in which they wrote that 'No classification...yet produced has proved satisfactory.' With the proliferation of genera since 1960 their classification, used also by Williams *et al.* (1965), has also proved to be unworkable because taxonomic discrimination is not always clear and lineages were seldom considered. Here we offer a classification based on a mix of external and internal characters which persisted during unbroken lineages. We hope this classification can be used to determine taxa, even when less than perfectly preserved.

Lazarev has studied productides since 1974, with contributions on ontogeny (1981), and especially morphological evolution (1985, 1986) and systematics of Devonian taxa of the Strophalosiidina (1989) and Productidina (1990). For over 25 years Brunton has retained an interest in productides, particularly their varied growth features and palaeoecology (e.g. 1965, 1966, 1972, 1982, 1985, and, with Mundy 1988). Grant has dealt with Permian faunas over many years, especially the environmental settings of all productides (e.g. Grant 1963, 1966, 1968, 1972, 1976; Cooper and Grant 1972, 1975).

With the revision of the brachiopod part of the *Treatise on invertebrate paleontology* now under way, we have combined our interests to review classifications of this difficult group and present a

TABLE 1. List of characters, their type (ordered or unordered) and states used in the production of the matrix (Table 2) from which the cladogram (Text-fig. 1) was constructed.

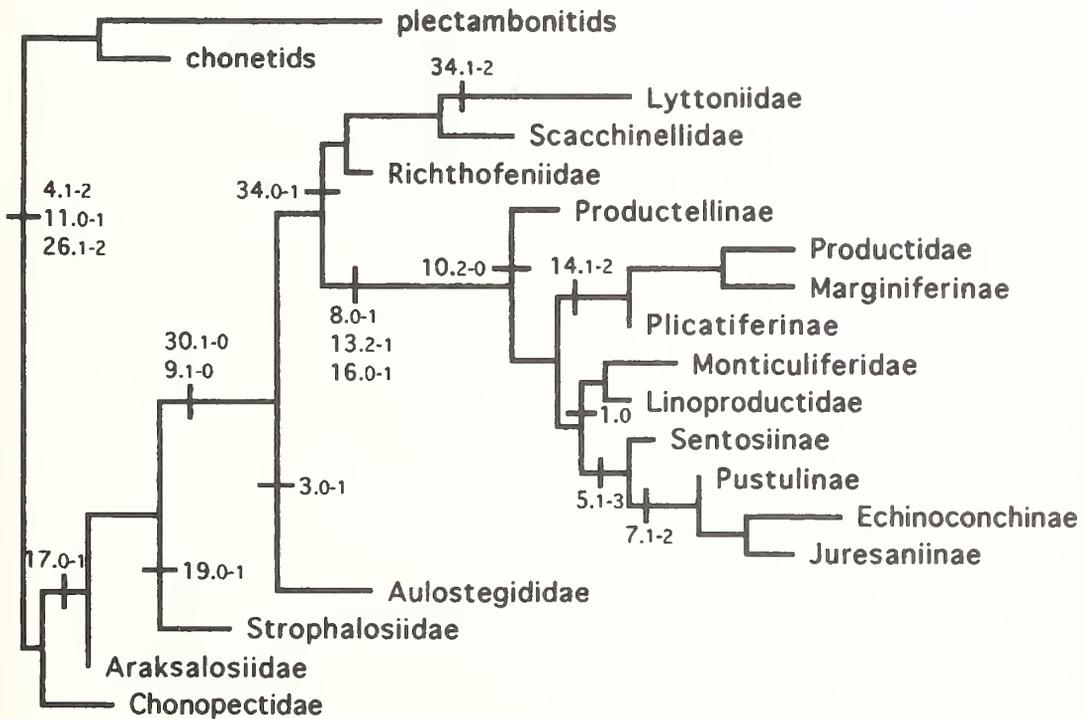
Character	Type	State
1. Fine ribbing	U	Present (0); absent (1)
2. Costae	U	Costate (0); non-costate/smooth (1)
3. Acquisition of costae	U	None (0); anteriorly (1); fully (2)
4. Spines	O	None (0); hinge only (1); general (2); lost (3)
5. Spine distribution	U	None (0); ventral only (1); mostly ventral (2); ventral plus dorsal (3); lost (4)
6. Spine types	U	None (0); thin (1); mostly thick (2); few symmetrical (3); attachment (4)
7. Spine bands	U	None (0); not banded (1); banded (2); bands only anteriorly (3)
8. Interareas	O	Present (0); absent (1)
9. Teeth also post Famennian	O	No (0); yes (1)
10. Corpus depth	U	Shallow (0); moderate (1); deep (2)
11. Aderidia	O	Present (0); absent (1)
12. Dorsal lamellae	U	Absent (0); present (1)
13. Trails	U	Absent (0); long (1); bordering structures (2)
14. Rugae	U	Absent (0); present (1); strong (2)
15. Posterior reticulation	U	Absent (0); present (1)
16. Cardinal process	O	Directed posteroventrally (0); directed posterodorsally (1)
17. Cicatrix	U	Absent (0); present (1)
18. Spine-base swellings	U	Absent (0); present (1)
19. Spines bidirectional	U	No (0); yes (1)
20. Corpus width	U	Small < 20 mm (0); medium/large (1); gigantic > 101 mm (2)
21. Ventral hinge spines	U	Present (0); absent (1)
22. Lateral ridges	U	Absent (0); present (1)
23. Cardinal ridges	U	Absent (0); present (1)
24. Marginal structures	U	Absent (0); present (1)
25. Alveolus	U	Absent (0); present (1)
26. Shell structure	O	Fibrous (0); 'mixed' (1); laminar (2)
27. Cardinal process	U	Not bilobed (0); weakly bilobed (1); strongly bilobed (2)
28. Dorsal platforms	U	Absent (0); present (1)
29. Brachial ridges	O	Absent (0); present (1); weak (2)
30. Brachial ridges area	U	Confined posteriorly (0); widespread + anteriorly (1)
31. Dorsal median septum	U	Absent (0); variable (1); strong (2)
32. Ventral median septum	U	Absent (0); variable (1); strong (2)
33. Dental plates	O	Commonly present (0); absent (1)
34. Profile	U	Concavo-convex (0); conical (1); flat (2)

new one which we hope can be used in the newly revised *Treatise*. We stress that the classification here presented is in a state of development and may not be exactly as will be published in the future brachiopod *Treatise*. We believe, however, that the structure is now sufficiently developed that later changes may be peripheral. The 167 genera described by Muir-Wood and Cooper (1960) has increased to about 500 nominal genera now being considered within the group.

An important weakness in previous classifications was that most of the information was derived from Carboniferous and Permian genera, as few of the Devonian productoid genera were then known and these provided scant evidence for the origin and early evolution of the group. This problem was tackled by Lazarev (1989, 1990) and we now have established productide genera in the

Lower Devonian which can be seen to have their origin in the chonetids (Brunton 1965, 1972; Johnson 1976). More importantly for the classification, increased knowledge of productide evolution in the Devonian allows their morphological trends to be established and these are fundamental to the systematics of the complete group. By the end of the Devonian the major trends of morphological diversity were established, with the separation of the strophalosiidines and three major groups of productidines. Through the Carboniferous and Permian periods recombinations of this diversity, together with some innovations, produced a wealth of genera within lineages, some of which display parallelism in aspects of their morphology. Previously these morphological similarities led to combinations of only distantly related genera in a classification based more on grades of evolution than on clades. Our emphasis is to develop monophyletic lineages of genera from their earliest ancestors and, in this way, to separate genera with superficial similarities into what we believe are more biologically realistic taxa or clades.

In order to provide a more objective assessment of the developing classification 34 characters, well displayed in genera throughout the Productida and belonging to 17 of our proposed family groups, plus 2 outgroups, were subjected to an introductory analysis on a PAUP 3 program. All characters were equally weighted and have from two to four states, and those marked with an 'O' in Table 1 were ordered. The plectambonitoids and chonetidines were specified as rooted outgroups, respectively being distantly related and widely considered (e.g. Johnson 1976) as ancestral to productides, as well as having geologically older representatives. The heuristic search retained a single most parsimonious (non-consensus) tree of length 103 (Text-fig. 1). Despite its provisional



TEXT-FIG. 1. Cladogram tree of 17 family-group taxa within the Productida constructed from 34 characters listed in Table 1. No character was weighted, but those marked 'O' in Table 1 were ordered. The plectambonitids and chonetids were specified rooted outgroups. Synapomorphies are identified by their character number and change of state (see text for further details).

and unrefined nature, the tree clearly separates the Productidina as a monophyletic clade with rather poorly discriminated strophalosiidines forming a more diffuse paraphyletic grouping in which the unusual morphology of the Lytoniidae, Scacchinellidae and Richthofeniidae causes them to be almost separated. The Productidina divides into three groups, the Productoidea (Productellinae to Plicatiferinae), Linoproductoidea (Monticuliferidae and Linoproductidae) and Echinoconchoidea (Sentosiinae to Juresaniinae) (Table 2). The Productellinae, which includes the stem group for all

TABLE 2. Matrix of characters (Table 1) distributed amongst the named taxa.

plectambonitids	1020000010000000--010?010010-1000
chonetids	010111101000000000000101110102210
Lytoniidae	1103400100100000100110000211110012
Richthofeniidae	1102241002102000100110001210201011
Aulostegidae	1112241001102100100110111220101010
Scacchinellidae	11022410021000001001?0100221100211
Strophalosiidae	1102221011102000101000100210112010
Chonopectidae	110211101010010000000001210211010
Araksalosiidae	1102211010100000100000101210111010
Productellinae	1112111100101001000111001210102010
Productidae	1022131102111211000101010221102010
Monticuliferidae	01021111001010101010100000210102010
Linoproductidae	0102111102101101000101010210102010
Sentosiinae	1102313100101101000101000210102010
Pustulinae	1102313102101101010100100210102010
Echinoconchinae	1102312102101201000100110221102010
Juresaniinae	1102313102101101010101111220102010
Marginiferinae	1022231102111111000011010210102010
Plicatiferinae	1102131102101201000111010210102010

productoids, is placed topologically as sister group to all other productidines although, in our classification, it is grouped within the Productoidea (see 7-9 on Text-fig. 3).

A survey of historical studies of productides and full discussions on the methods, character states, origins and evolution of the Productidina is to be found in Lazarev (1990).

Since 1990 we have concentrated mostly upon the large and diverse groups of productoids derived from what were called the Productellidae by Lazarev (1990, fig. 11). Two of us (SSL and CHCB) have in preparation a revision of this stem group family for the Productoidea in which genera are regrouped into subfamilies and tribes according to our view of their evolutionary history. The summary of diagnoses in the appendix herein includes our current views on the Productellidae.

#### METHODS AND CHARACTERS USED IN THE CLASSIFICATION

An important characteristic of the productide shell is its body cavity depth. However, this feature also influences other internal and external features which we need to be able to describe accurately. We find ambiguity in the literature amongst terms describing shell surfaces, such as the 'visceral disc' and 'trails'. There is no uniformity in their use or precision as to what is meant, so we present a system of terms enabling the whole productide shell to be described accurately in a way which is also meaningful to its growth. Productides with a deep shell cavity normally have dorsal valves which are geniculated against the ventral valve. Commonly, growth of the dorsal valve, relative to the ventral valve, was slow. Thus at about half the fully adult curved length of ventral valves, the dorsal valve had virtually stopped growing anteriorly, only adding to the length of its trail. It was at about this half-full-growth stage when the ventral valve commonly changed its growth direction slightly or conspicuously (the geniculation point: Text-fig. 2G), and in many species their surface

ornamentation also changed. This is the stage at which trails first started to develop and from which the two valves grew more or less parallel to each other. Lazarev (1981), dealing with general ontogeny in productoids, and Timms and Brunton (1990), dealing more specifically with growth rates and geniculation in some productoids, suggested that sexual maturity initiated these growth changes. While dorsal valves did not add much to body length (other than for a series of external trails and internal diaphragms in some species), ventral valves continued to grow beyond the 'geniculation point', but commonly with a changed growth spiral so as to become more tightly coiled and with the developing trail more dorsally directed. This pattern of ventral valve growth continued throughout the rest of the brachiopod's life. Growth of both valve trails was along parallel curves and commonly followed a radius of curvature centred on the hinge axis. In some species, during earlier stages of ontogeny, the complete dorsal valve rotated dorsally to some extent and, in so doing, increased the body cavity depth (Brunton 1985). The fully adult ventral valve interior was marked in many species by a ridge onto which the dorsal valve rested when the shell was closed. There is, however, uncertainty in the literature as to what constitutes the trail; whether only the adult regions of shell formed the functional trails, or also the region of the ventral valve which had been a functional trail during earlier stages of growth and by adulthood formed part of the main body of the productide?

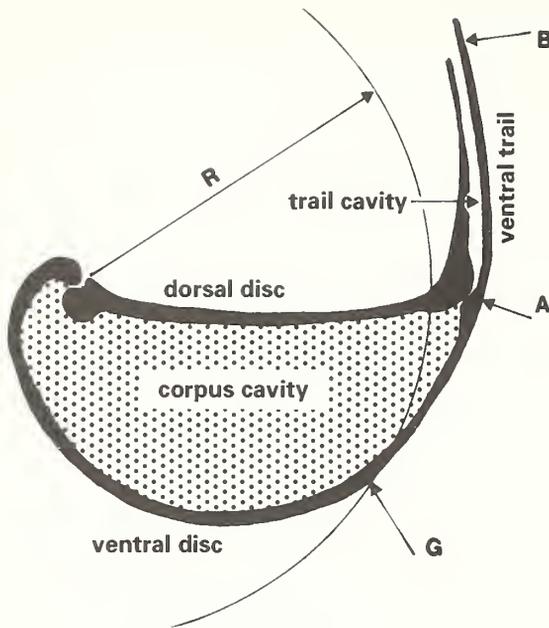
It is not uncommon for the main body region of the shell to be preserved while the ears and trails are lost, and although it may be possible to recognize a point from where ventral trails started to grow and where ornament changes, only the body region can be fully described. Text-figure 2 illustrates a sectional view through a typical deep-bodied productide to which we have added terms we use in describing parts of the shell. We are unable to use the word 'body' in our specific meaning, as it is defined by Williams (1965) to mean the posterior coelomic region containing the main brachiopod organs, other than the lophophore. The terms take into account changes during ontogeny and many are equally useful in describing shallow-bodied productides, i.e. those with a shallow 'corpus' cavity. Indeed, we believe that a clear distinction between 'corpus' and 'peripheral' areas could be equally useful in describing other brachiopod groups, such as some strophomenides or athyrididines. It should be noted, however, that in shallow productides, as there is no strong geniculation in the dorsal valve, the disc lengths of both valves are more similar than in deep shells and their valves grew more closely parallel to each other during ontogeny. In addition there is no universal 'R' value amongst productides; it varies interspecifically, and to a small extent intraspecifically. For instance in a genus like *Overtonia*, each ventral ruga and dorsal lamella was associated with a 'R' value as they grew (Brunton 1985). In *Diaphragmus*, with its preserved series of dorsal trails, the 'R' value is taken at the first-formed dorsal trail and then corresponds with the ventral geniculation point; the subsequent trails correspond to the ventral protrail.

We introduce the following terms (Text-fig. 2):

**Corpus.** That part of the shell comprising the two valves enclosing the posterior body (visceral) cavity plus the mantle cavity (which housed the lophophore in life), but excluding the shelly extensions forming ears and trails. Thus the term can be used to describe surface areas of the shell and the cavity enclosed, as defined above.

**Peripheral cavities.** Cavities peripheral to the corpus cavity, narrowly enclosed between marginal regions of the valves in areas such as the ears or trails in productides or between frills, flanges etc. in athyrididines.

**Protrail** (Latin *pro*, before, and trail). Region of the ventral adult corpus, anterior to the point of geniculation (Text-fig. 2G), which functioned as a trail during earlier growth stages and over which ornamentation commonly changed, resembling that on the true ventral trail. The anterior margin of the protrail can only be defined in adult shells, as the position at which the dorsal valve rested against the ventral inner surface when the shell was closed. In some species this position was marked by internal shell thickening or by less obvious changes in the ornamentation of the inner surface



TEXT-FIG. 2. Stylized section of a closed adult productidine, with deep corpus cavity and trails, showing the terminology used. R – the radius of curvature, centred on the hinge axis, limiting the dorsal and ventral disc lengths, and point G – the geniculation point on the ventral valve at which a major or minor change in growth direction commonly took place; A – the position of rest of the adult dorsal disc against the ventral valve interior; B – the margins of the adult trails. The shell corpus is the dorsal and ventral discs plus the protrail (G–A). These surfaces enclose the corpus cavity (shaded). Totrail – G–B.

(Text-fig. 2A). In terms of growth, the protrail corresponds to the dorsal valve region of marginal ridges or diaphragms, where present.

Totrail (Latin *totus*, complete, and trail). The total length of ventral trail development from the point of geniculation to the valve margin. It is the protrail plus the true ventral trail (Text-fig. 2G–B).

### *The characters*

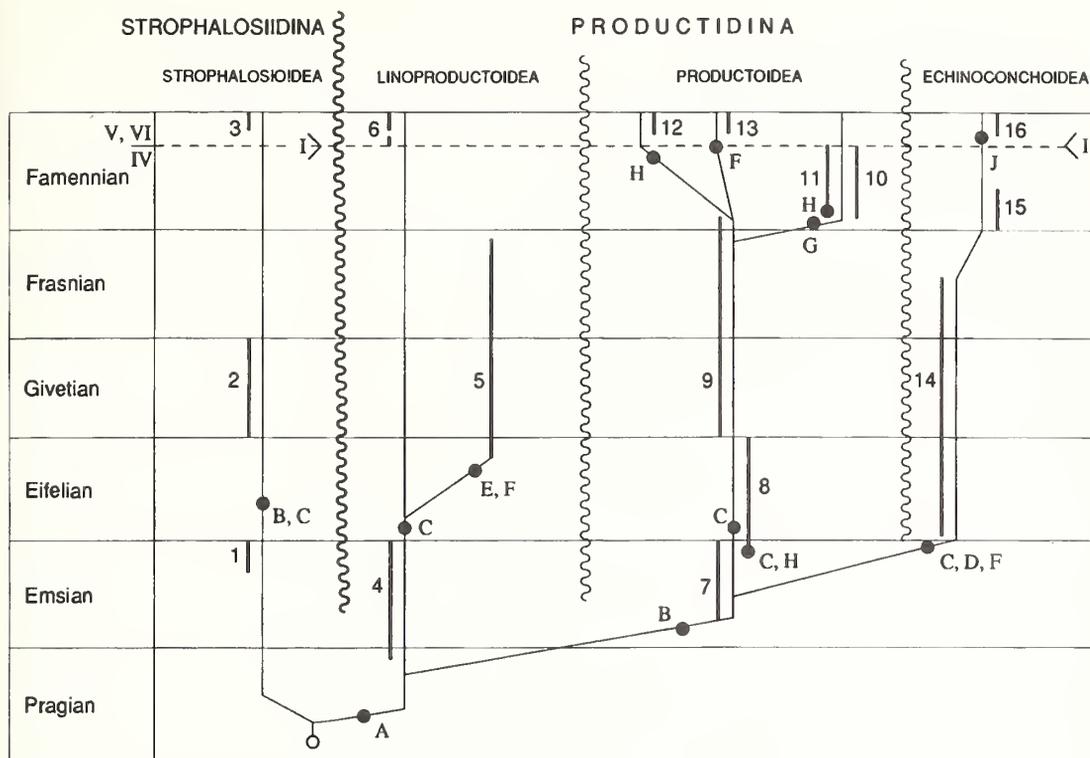
We have attempted to provide a classification which is evolutionary, that is by following lineages, but we recognize that reversals in character trends have occurred.

A process recognized in this classification is that some characters first appeared late in ontogeny, but during evolution appeared increasingly early in the ontogeny of later individuals. Thus, in some productidines, ribbing, for example, may appear first towards the adult anterior valve margins and progressively, through time, has 'spread' posteriorly to cover most or all of the valve or shell. In this way a shell with a smooth umbo, but which is otherwise ribbed, can be identified probably as having evolved from non-ribbed stock.

Emphasis on the importance of some characters has been developed through experience and is used in the classification suggested here. Characters of the greatest importance are those which display ontogenetic and phylogenetic stability; those which arose early in ontogeny and remained throughout the life of the individual, and which also persisted through a long period of time. On the other hand characters that appeared in one or more lineages but lasted only briefly in species of few genera, are of little use in classification above generic level.

The most characteristic feature separating the Productida from their chonetid ancestors is the spread of spines from the hinge line of chonetids to covering the ventral valves of the Productida.

The first apomorphy within the Productida, separating the Strophalosiidina from the Productidina, is the loss of a true interarea in the latter. By a true interarea, we mean growth at the posterior margin which developed at a high angle from the rest of the ventral valve, and in so doing increased valve separation posteriorly. This is in contrast to valve thickening along the posterior margin of some productidines which produced what appears externally like an interarea, but instead

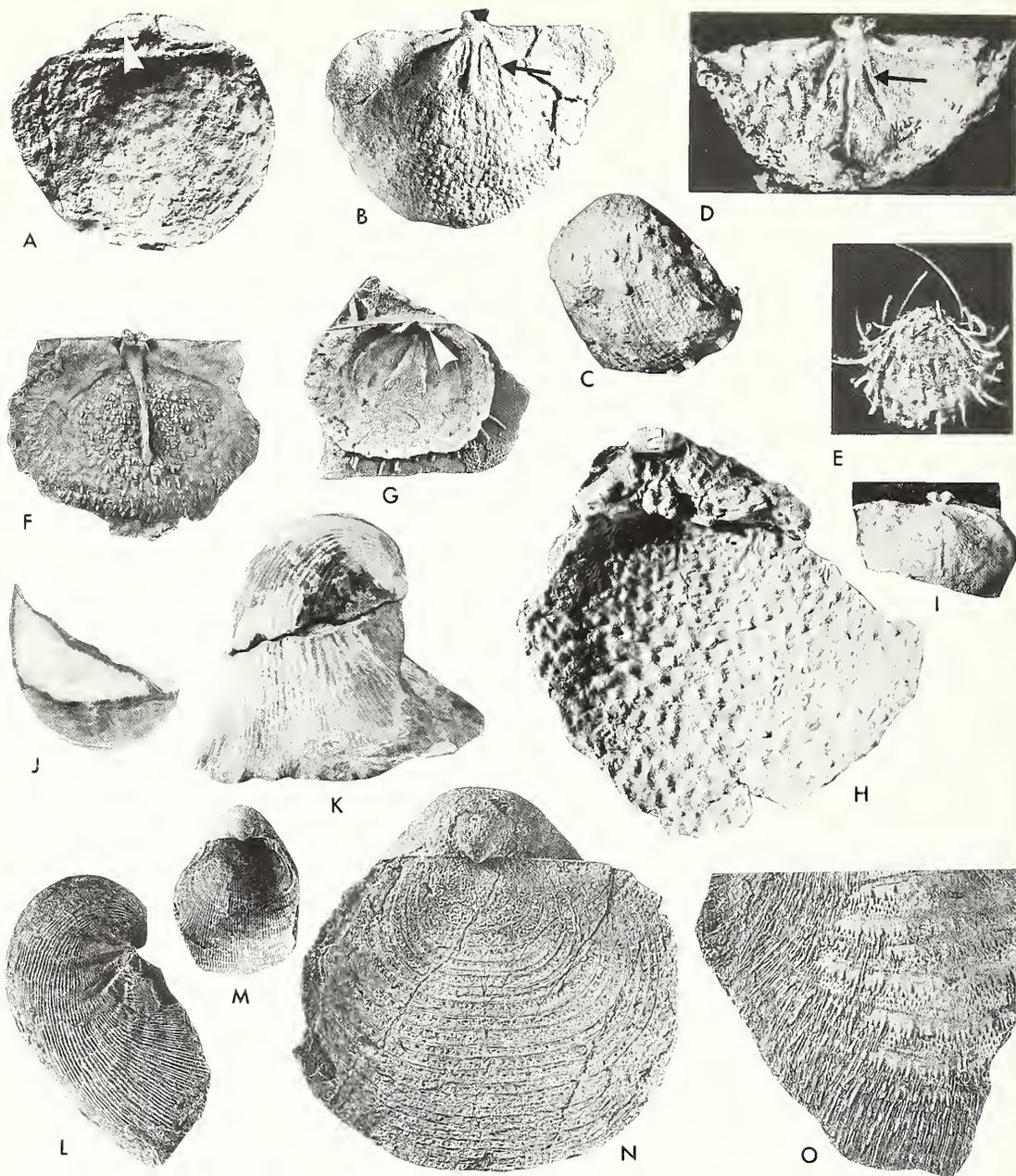


TEXT-FIG. 3. The major morphological changes in Devonian Productida giving rise to the Strophalosiidina and Productidina. Character changes are identified by letters A to J, and the earliest genus in each superfamily, plus others of significance, are numbered 1–16. Characters: A – Loss of interareas. B – Loss of fine chonetid-like ribbing. C – Loss of anderidia. D – Development of dorsal spines (not important in the Strophalosioidea). E – Development of serial dorsal lamellae. F – Development of marginal structures. G – Development of deep corpus cavity. H – Introduction of anterior ribbing. I – Loss of toothed articulation in the Productidina. J – First differentiation of spines into bands. Taxa: 0 – ‘Chonetid’ ancestor from which the spread of spines over the ventral valve gave rise to the Productida. 1 – *Ralia*. 2 – *Devonalosia*. 3 – *Acanthatia*. 4 – *Eoproductella*. 5 – *Devonoproductus*. 6 – *Ovatia*. 7 – *Chattertonia*. 8 – *Spinulicosta*. 9 – *Productella*. 10 – *Ardiviscus*. 11 – *Nigerinoplica*. 12 – *Dorsirugatia*. 13 – *Rugauris*. 14 – *Caucasiproductus*. 15 – *Praewaagenoconcha*. 16 – *Laminatia*.

is a ginglymus with layers of shell material subparallel to the external valve surface. It is noteworthy that anderidia, inherited from the chonetids, which when fully developed probably aided the support of the body wall, are found in species attributed to both the strophalosiidines and productidines (Text-fig. 4B, D) in the Pragian and Emsian (Text-fig. 3, character C), indicating a common ancestry for the Productida.

Text-figure 3 shows the early to mid Devonian evolution of the Productida and the next levels of morphological changes important in their classification. Of fundamental importance in the early stages of evolution, and in dividing the productidines into three basic components are:

1. Preservation of fine ribbing on the valves, inherited from the chonetids, which characterizes the linoproductoids (Text-fig. 4C).
2. Loss of this fine ribbing, producing relatively smooth shells, the productoids (Text-fig. 4E), which in the middle and upper Devonian developed strong costation anteriorly.



TEXT-FIG. 4. A selection of Devonian and early Carboniferous genera from the Strophalosioida (A, F-G), Linoproductoidea (B-C, L-M), Productoidea (D-E, J-K), and Echinoconchoidea (H-I, N-O) showing important features of morphology. ANU: Australian National University, Canberra; B or BB: The Natural History Museum, London; PI: Palaeontological Institute, Moscow; USNM: National Museum of Natural History, Washington, DC, USA. A, *Ralia*; PI 4217/2; Gobi-Altai, Mongolia; Lower Devonian, Emsian; dorsal view; note the interarea and fine radial ribbing;  $\times 3$ . B-C, *Eoproductella*; PI 4114/120 and 4114/121; Tadzhikistan, central Asia; Lower Devonian, Pragian to Emsian; note the anderidia (arrowed) on the dorsal interior and fine ribbing on the ventral exterior;  $\times 4$  and  $\times 3$ . D-E, *Chattertonia*; ANU 18951.1 and 18951.j; New South Wales, Australia; Lower Devonian, Emsian; note the anderidia (arrowed);  $\times 3.5$  and  $\times 2$ . F-G, *Devonalosia*;

3. Appearance of fine, but closely arranged spines also on dorsal valves introduced the echinoconchoids (Text-fig. 4H).

We accord superfamily status to these three groups, being the first level of divisions within the Productidina.

Next in importance is a suite of characters helping to discriminate between families and subfamilies, usually when they appeared for the first time:

I. Depth of the corpus cavity. A useful measure of this is the length of the dorsal valve divided by the maximum depth of the cavity. Those shells with a ratio of three or less are considered as deep (e.g. Text-fig. 4J).

Ia. Shells with shallow corpus cavities are characterized by a concavo-convex lateral profile and trails which are commonly simple and without dorsal geniculation.

Ib. A deep cavity results primarily from a tight spiral curve of the ventral valve, especially of the tottrail, together with geniculation of the dorsal valve anteriorly. This is an important characteristic within the productidines, appearing first in the lower Famennian.

II. The development of marginal ridges at the internal edges of the corpus. These ridges developed progressively through ontogeny at or near the margins of the valves; they separate the corpus cavity from peripheral areas such as ears and trails. Marginal ridges include lateral ridges, ear baffles and subperipheral ridges near the lateral and anterior margins; we include also diaphragms and cinctures. The degree of development of marginal ridges differs among and between groups and in some was associated with the growth of trails. Cardinal ridges, at the hinge, did not function as cavity separations. The relationship between cardinal or lateral ridges and ear baffles can be important, as is the degree of development of these ridges, especially those which served to isolate the corpus cavity posterolaterally.

III. The development of marginal ridges in Carboniferous and Permian taxa may be associated with a series of anteriorly positioned dorsal trails.

IV. The loss of ventral spines at or near the hinge line.

Other characters of varying taxonomic importance and which may recur throughout productide evolution are:

a. The loss of toothed articulation in the Productidina in the Famennian, but its common retention in the Strophalosiidina (Text-fig. 4G).

b. The appearance, early in ontogeny, of a series of trails on dorsal valves.

c. The appearance (in species younger than late Devonian) of ribbing on the disc regions.

d. The development of a strong concentric ornament (lamellae or rugae) over the disc areas. In association with radial ribbing this concentric ornament may produce a reticulate ornamentation posteriorly.

e. Spines became differentiated according to size within concentric bands (Text-fig. 4N–O).

f. Spines became restricted to a few (commonly no more than eight) long and thick halteroid spines, symmetrically placed. These are in addition to small juvenile spines near the hinge or on the ventral umbo, which may be difficult to distinguish.

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USNM 123439c and 123432j; Ontario, Canada; mid Devonian, Givetian; note the posteroventrally projecting cardinal process, interarea and teeth (arrowed);  $\times 3$ . H–I, *Caucasiproductus*; PI 4127/187 and 4127/101; Transcaucasia, Armenia; mid Devonian, Eifelian to Frasnian; note spine bases covering the dorsal valve and long lateral ridges;  $\times 3$  and  $\times 1$ . J–K, *Productus*; BB19691; Derbyshire, England; Lower Carboniferous, Asbian; note the deep corpus cavity (seen in section J showing geopetal structure) and long spreading trail;  $\times 1$ . L–M, *Ovatia*; USNM 124101 and 124103; Oklahoma, USA; Lower Carboniferous, Chesterian; note the fine radial ribbing and lack of dorsal spines;  $\times 1$ . N–O, *Echinoconchus*; BB13629 and B24012; Yorkshire and North Wales; Lower Carboniferous, Viséan; dorsal view (N); part of ventral valve viewed anterolaterally (O); note spine bands on both valves, deep corpus cavity and short trails,  $\times 1$  and  $\times 2$ .

- g. The dorsal adductor scars evolved to a more anterior position, so that the scar plus its trace left a gap between them and the hinge line, which may have accommodated a posterior segment of the mantle cavity.
- h. The development of bordering structures at the valve margins during late stages of ontogeny; these including flanges, gutters, carination and tube-like growths of ventral valves.
- i. The juvenile presence of buttress plates anterior to the cardinal process, retained or submerged by secondary shell during ontogeny.
- j. The development of dorsal muscle platforms raised above cavities. These may be outwardly curving plates from their median fusion with the valve floor, or ones rooted laterally and curved medianly.

Other morphological features, such as a relatively narrow hinge, differentiation of the myophore scars and their dividing ridges on the cardinal process, gigantism (a width of more than 100 mm at the corpus), monticules or the development of strong spines near the dorsal hinge line, are commonly restricted to genera within small subfamilies.

In the Strophalosiidina some of the above characters assume different importance and there are additional features of importance. These include the degree of development of the interareas; the presence of a cicatrix; the development of spines which, on the same area of shell, grew in opposite directions; the loss or retention of toothed articulation; conical valve shape; cystose shell growth; a strong ventral median septum and the presence of a myocoelidium.

The Oldhaminioidea share a pseudopunctate shell with other productides and Liao (1983) reported the presence of rare ventral spines; an observation confirmed by one of use (REG). Another link, with at least some strophalosiidines, is the so-called dorsal valve, which has been shown to be mainly a ptychophous brachidium, with the actual 'valve' reduced to an articulatory process at the hinge (Termier and Termier 1949; Williams 1953; Grant 1972). An important feature amongst Carboniferous taxa is the symmetry of the muscle marks. Later forms are differentiated according to size (and numbers of lateral lobes), orientation of the lateral lobes, presence or absence of a 'hood', orientation of the ventral lateral septa and whether the shell's mode of attachment was by the beak only, by the posterior flap or by major parts of the ventral valve. The nature of the substrate bears upon the form of attachment.

#### POST-DEVONIAN EVOLUTION

By the late Famennian most of the main characteristics of the productidines had developed, as shown in Text-figure 3. Some characters were introduced and reintroduced among and within different evolutionary lineages during the Carboniferous and Permian. For instance, strong radial ribbing appears first in the mid Devonian in *Spinulicosta*, a productellid, on its anterior trail only. Then in the early Famennian, in *Nigerinoplica*, one of the first genera of the Leioproductinae with a deep corpus, ribbing appeared anteriorly but soon was present over much of the corpus. In many productoid groups this ribbing came to a climax, commonly covering the whole shell, by the late Tournaisian, and ribbing persisted through into the Permian. In other productoids there was another 'explosion' of ribbed genera starting in the Artinskian (early Permian). After the introduction of dorsal spines in the echinoconchoids, dorsal spines were introduced independently in several productoid families. Thus, in the early Carboniferous, dorsal spines appeared in examples of buxtoniins, overtoniins and some plicatiferins. In the Permian they reappeared in some species of the Marginiferinae, having been lost from the lineage in middle Carboniferous species. Within the linoproductoids a tubiform ventral valve developed in Carboniferous *Proboscidella* and Permian *Tubaria* and *Siphonosisia*, yet all three were derived from different ancestors (indeed it might be argued that the last belongs in the aulostegoids on account of its deep corpus, rhizoid spines, small cicatrix and widely placed brachial impressions, but an interarea is lacking).

In each of the three productidine superfamilies there are two persistent groups; genera with a shallow corpus and those in which the cavity is deep. However, we recognize also that some taxa

within either of these major groups reverted, via intermediate depths, to the opposite condition. Within the Productidina as a whole there is a general trend towards deepness in the Permian, but some genera demonstrate exceptions to this and reverted to shallow cavities.

During Carboniferous and Permian times morphology changed drastically amongst the entire Productida, contributing to the wide diversity of taxa. Some of the most marked changes occurred amongst strophalosiidines. Hardgrounds and framework reef facies were rare in the Carboniferous but led to morphologies that were reflected in the more common reefs and bioherms of the Permian. The more widespread occurrence of species living on relatively soft sea floors led to a variety of patterns of supporting spines posteriorly and on the venter, and to protective spines at the valve margins throughout ontogeny or only at late stages of growth.

An important adaptation, probably leading to an enlarged lophophore and improved water-circulation system, was the deepening of the corpus cavity, first recognized in some lower Famennian leioproductins, then in echinoconchoids in the Tournaisian, and yet again in linoproductoids in the Viséan. Thereafter, families with deep or shallow corpus cavities are to be found in each of the superfamilies. A Permian adaptation, also interpreted as improving the water circulation system, was the introduction of the falafer brachidium, interpreted as supporting a folded ptychophe (Grant 1972), discovered in some small and cemented species which appear to have lived much as does the Recent *Thecidellina*. This change from the earlier productidine style of lophophore, probably a simple schizophe, took place in the mid Permian, although it is possible that an unsupported ptychophe may have developed in deep strophalosiids in the Upper Carboniferous and persisted well into the late Upper Permian.

In the Permian a few new features appeared in productides: large spines close to the dorsal hinge line in the Horrioniinae; strong bilobation of the shell outline in some of the Marginiferinae and Cooperininae; and monticules (external swellings commonly interrupting radial ribbing) in some of the Monticuliferinae. During the same period there was a diversification among strophalosiidines, with deeply conical ventral valves containing cystose tissues (Richthofenioidea and Scacchinellidae) while a great array of bordering structures developed in the aulostegoids. Other morphologies, having their origins in the Carboniferous, were reworked and extended to create an amazing array of adaptive features, but the group died out by the close of the Permian.

The extinction of brachiopod faunas, particularly the Productida, late in the Permian took place somewhat earlier in North America than farther east in the Tethys region. The regressions led to shallowing and drying which affected the brachiopods living in relatively shallow water particularly severely, so that among productides only *Spinomarginifera* may have survived into the earliest Triassic (data from the Himalayas).

#### CLASSIFICATION AND DIAGNOSES

The classification is hierarchical, so characters are mentioned at their first appearance and may not be repeated at lower taxon levels. Thus, for instance, in the Linoproductoidea the lack of dorsal spines is almost universal and noted at the superfamily level; their presence being noted in the few relevant lower taxa. Thus several taxon levels have to be read to gain the most complete description of a subfamily or tribe. We use the taxon 'tribe' because, in the most diverse and long-ranging families of the Productoidea, we find insufficient taxa down to subfamilies alone in which to accommodate all definable groups within the lineages.

The diagnoses of lower taxa, especially tribes, should be viewed in their stratigraphical context in order to understand the patterns of changes which occurred within families and subfamilies.

Where we include mention of size we follow the convention: shells with a maximum corpus width of up to 20 mm are small; those between 21 and 50 mm are medium; those between 51 and 100 mm are large, and those 101 mm wide and over are gigantic.

In the description of lateral profiles the mention of an 'ideal spiral' means that the growth spiral is not distorted by any geniculation and, in consequence, the corpus cavity can be expected to be shallow.

## Order PRODUCTIDA

*Strophomenides sensu lato* with concavo-convex to planoconvex or conical corpus profiles, commonly with trails; spines on ventral valves or both, rarely reduced to hinge regions or absent from some; dental plates absent; cardinal process bilobate, commonly protruding, with varied recessed myophores; brachial markings commonly present; mantle canals rarely marked; shell substance with crested or sheet laminae and pseudopunctate with taleolae.

## Suborder PRODUCTIDINA Waagen, 1883

Productides lacking interareas or with ginglymus only; toothed articulation absent after latest Devonian; cardinal process directed posteriorly or posterodorsally, not ventrally; brachial ridges reniform, confined posteromedianly.

## Superfamily PRODUCTOIDEA Gray, 1840

Productidines with long trails, other than in early forms; ornamentation diverse, commonly costellate; spines may be absent from ventral hinge area, otherwise widely to closely spaced; dorsal spines commonly absent, when present not widely distributed.

## Family PRODUCTELLIDAE Schuchert, 1929

Shell small to medium sized; dorsal valve concave or, rarely, only slightly concave; ribbing absent from beak or totally; spines varied on ventral valve only and commonly absent from hinge region; corpus cavity shallow, rarely deep in Carboniferous or Permian taxa; teeth present or absent.

## Subfamily/Tribe

**Productellinae** Schuchert, 1929

Ribs rarely developed and then only anteriorly; spines evenly distributed over ventral valve only; corpus shallow; teeth present; lateral ridges and ear baffles lacking; cardinal process lobes divergent, V-shaped dorsally, with pit; dorsal adductor scars commonly non-dendritic.

**Productininae** Muir-Wood and Cooper, 1960

Productellids commonly ribbed, especially ventrally; few spines on ventral valve only, absent from hinge region; corpus cavity shallow, except in some *Paramarginiferini*.

**Productinini** Muir-Wood and Cooper, 1960. Ribbing on ventral valve and concentric lamellae prominent on dorsal valve; ventral profile an ideal spiral; no sulcus.

**Paramarginiferini** Lazarev, 1986. Radial ribbing and, in some, posteriorly reticulate; ventral profile distorted, ventral trail (when present) commonly becoming anteriorly nasute; ventral marginal ridges commonly developed.

**Chonetellini** Likharev, 1960. Outline subtriangular; ventral profile an ideal spiral; ribbing incipient or smooth; commonly nasute.

**Overtoniinae** Muir-Wood and Cooper, 1960

Ribs absent or rarely confined anteriorly on trails; spines scattered equally on both valves, but absent from ventral hinge; corpus depth varied.

**Avoniini** Sarycheva, 1960. Concentric ornament of broad irregular lamellose bands; ventral lateral profile an ideal spiral; corpus cavity shallow to moderate.

**Overtoniini** Muir-Wood and Cooper, 1960. Strong rounded rugae bearing spines; corpus cavity deep; dorsal adductor scars raised.

**Krotoviini** trib. nov. Concentric ornament weak or lacking; ventral profile an ideal spiral; shallow corpus cavity.

**Costispiniferini** Muir-Wood and Cooper, 1960. Concentric ornament weak; ribbing may be present on trails; ventral profile distorted, with shallow to deep corpus activity.

**Institiferini** Muir-Wood and Cooper, 1960. Minute to small shells with relatively deep corpus cavity, bearing concentric ornament and coarse ribbing on trails which are strongly deflected as flanges or gutters; spines on ventral corpus only.

**Marginiferinae** Stehli, 1954

Ribbing dominates concentric ornament (may be reduced in Permian); ventral profile commonly geniculate at start of protrail.

**New tribe** to be described formally elsewhere. Spines on both valves; ribs commonly start anteriorly on corpus with elongate spine bases posteriorly.

**Paucispiniferini** Muir-Wood and Cooper, 1960. Ventral spines only; always ribbed; corpus cavity may be deep.

**Marginiferini** Stehli, 1954. Ventral spines, rarely on both valves; always ribbed, but weakly; commonly with a series of dorsal trails and corpus cavity deep.

**Incisiini** Grant, 1976. Ventral spines only; ribbing absent; hinge narrow; lateral profile an open spiral.

**Plicatiferinae** Muir-Wood and Cooper, 1960

Shell geniculated, with ventral disc only gently convex; corpus cavity moderately shallow to, rarely, deep anteriorly; ribbing lacking, weak or only anteriorly on trails; concentric ornament normally strong, especially rugae; spines sparsely or densely distributed on ventral valves, commonly including near hinge, rarely on both valves.

**Rugaurini** Muir-Wood and Cooper, 1960. Corpus cavity shallow; trail absent or very short; no ribbing; dense spines covering ventral valve, rarely on dorsal valves anteriorly; teeth in oldest taxa; no ear baffles or submarginal ridges.

**Semicostellini** Nalivkin, 1979. Corpus cavity deep; costae on long trails; lateral and marginal ridges commonly well-developed, especially ventrally.

**Plicatiferini** Muir-Wood and Cooper, 1960. Corpus cavity moderately deep; trail long; ribbing absent or weak, only on trails; rugae, or lamellae, strongly developed on corpus; ear baffles in dorsal valve, rarely also in ventral valve.

**Levipustulini** Muir-Wood and Cooper, 1960. Geniculated dorsal valves with short trails; corpus cavity variable; rugae weak or lacking but spines numerous with pustulose bases, commonly on both valves, but lost dorsally in Permian; marginal structures and peripheral cavities reduced or absent.

**Levitusiini** Lazarev, 1985. Relatively large shells with long trails and moderate to deep corpus cavities; ribbing absent, but may be weak, fine radial striations; rugae weak; spines weak and sparsely developed, a row anterior to ears and commonly a ventral median row on weak ridge; weak cardinal ridges; no marginal ridges.

**Yakovleviini** Waterhouse, 1975 [= *Inflatiinae* Sarycheva, 1977]. Commonly medium-sized with thick-shelled ventral valve and moderately deep corpus cavity, becoming shallow in younger genera; ribbing on trails and all but posterior regions of corpus, with 4–6 thick ventral spines; common trend to reduce ear cavities and extend anterior peripheral cavity.

Family **PRODUCTIDAE** Gray, 1840

Commonly deep corpus, rarely moderate or shallow, but then with inflated ventral corpus; spine row(s) near hinge; teeth only in oldest genera.

**Leioproductinae** Muir-Wood and Cooper, 1960

Ribbing commonly absent or weak, never at beak; dorsal spines commonly absent; corpus cavity deep; teeth absent in all but oldest genera.

**Leioproductinae** Muir-Wood and Cooper, 1960. Small to medium-sized; ribbing absent, but commonly with ventral medium weak fold; ventral spines sparse, dorsal spines absent; teeth in early genera.

**Semiproductini** McKellar, 1970. Medium size, with deep corpus cavity and trails; elongate spine bases arranged quincuncially on ventral disc, spines extending onto trail; ribs originate anteriorly on discs and always occur on trails; lateral ridges commonly short, no marginal structures; teeth in early genera.

**Horridoniini** Muir-Wood and Cooper, 1960. Medium or commonly large, thick-walled valves; ribs weak or absent; 1-3 rows of halteroid spines on ventral ears and, rarely, one row near dorsal hinge; rarely other dorsal spines; marginal structures commonly absent.

**Tyloplectini** Termier and Termier, 1970. Ribbed, other than at beak; additional striae dorsally; ventral spines large near hinge and on flanks; probably absent dorsally.

#### **Dictyoclostinae** Stehli, 1954

Medium to large size; trails long, simple; ribbing complete with reticulation posteriorly; ventral spines commonly stout halteroid; dorsal spines absent; dorsal adductor scars positioned posteriorly, close to hinge line; marginal structures absent or weak.

#### **Productinae** Gray, 1840

Small to medium size; trails long, may have bordering structures; ribbing entire, reticulate posteriorly; spines commonly only on ventral valve; marginal structures well developed.

**Productini** Gray, 1840. Ribbing relatively fine; spines thin, numerous on ears; diaphragm associated with series of dorsal trails; dorsal adductor scars may be raised on platforms.

**Spyridiophorini** Muir-Wood and Cooper, 1960. Ribbing coarse, homogeneous anteriorly; spine row on each arched ear; no diaphragm or series of dorsal trails; dorsal adductor platforms well developed.

**Kozlowskiini** trib. nov. Spines variable, but may include few thick halteroid spines; zygidium may be present; marginal ridges associated with series of dorsal trails.

**Retariini** Muir-Wood and Cooper, 1960. Trail non-lamellose, may be tubiform; row of thick spines at base of ventral flank, sparse or absent from dorsal valves; dorsal adductor scars positioned relatively anteriorly.

#### **Buxtoniinae** Muir-Wood and Cooper, 1960

Size varied, but with corpus cavity deep; ribbing on trails and commonly on corpus; spines dense on both valves, but may be restricted anteriorly on dorsal valve; elongate cardinal process pit seldom absent; dorsal muscle scars separated from hinge region.

**Tolmatchoffiini** Sarycheva, 1963. Dorsal trail of varied length; ribbing covering both valves, other than in the early Tournaisian, when umbos smooth; rugae commonly absent, spines on ventral valve not uniformly distributed; cardinal process pit elongate.

**Buxtoniini** Muir-Wood and Cooper, 1960 [= Kochiproductini Lazarev, 1985]. Dorsal trail commonly short, bordering structures (flanges) sporadic; ribs cover both valves, other than in Tournaisian, when smooth posteriorly; rugae irregular, may dominate ribs; spines on ventral valve uniformly distributed, commonly from swollen bases; buttress plates and pit present, but variable.

### Superfamily ECHINOCONCHOIDEA Stehli, 1954

Productidines widest anterior to hinge, with corpus cavity deep in most families; trail commonly very short; spines covering both valves (including at hinge), commonly arranged in concentric bands, recumbent and forming dense mats; ribbing absent.

#### Family SENTOSIIDAE McKellar, 1970

Echinoconchoids having shallow corpus cavity; concentric bands and spine differentiation commonly absent.

#### **Caucasiproductinae** Lazarev, 1987

Sentosiids with teeth and sockets; ventral spines relatively thick, suberect; lateral ridges short, divergent anteriorly.

#### **Sentosiinae** McKellar, 1970

Sentosiids without teeth; spines thin, may have elongate bases.

**Sentosiini** McKellar, 1970. Concentric rugae or lamellae may be as bands anteriorly.

**Bagراسيini** Nalivkin, 1979. Elongate spine bases simulate ribs on both valves.

#### Family ECHINOCONCHIDAE Stehli, 1954

Corpus cavity deep; dorsal trail commonly short; spines thin, commonly in concentric bands, recumbent.

##### **Pustulinae** Waterhouse, 1981

Medium to large size; low rugae; spine base pustules may not be arranged in bands; buttress plates and cardinal process pit absent.

##### **Echinoconchinae** Stehli, 1954

Concentric bands well developed on both valves bearing spines differentiated in size; buttress plates and cardinal process pit absent.

**Echinoconchini** Stehli, 1954. Medium to large; concentric bands cuesta-like in profile, posterior part smooth and narrower than anteriorly where spines differentiated by size; one or two rows of thicker spines posteriorly, thinner rows anteriorly; dorsal adductor scars tend to become raised, crests curve laterally.

**Karavankinini** Ramovš, 1969. Small to medium size; high relief concentric bands, symmetrical in profile, tops bearing concentric rows of spines, distributed by size, separated by wider smooth bands; dorsal adductor scars raised, crests curved medianly, after Serpukhovian.

**Calliprotoniini** Lazarev, 1985. Medium size; concentric ornamentation of low, anteriorly somewhat lamellose bands covered by evenly distributed recumbent spines on each band, grading from large to small anteriorly; lateral ridges strongly developed and extending as submarginal ridges.

##### **Juresaniinae** Muir-Wood and Cooper, 1960

Concentric bands absent or confined anteriorly; spines may be differentiated by size anteriorly; cardinal process pit and buttress plates present in Carboniferous, but lost in Permian genera.

**Juresaniini** Muir-Wood and Cooper, 1960. Quincuncial pustules posteriorly; concentric bands of spines commonly on rest of valves; anteriorly rugose or lamellose.

**Waagenoconchini** Muir-Wood and Cooper, 1960. Corpus with small quincuncially arranged spines and dense mat of long peripheral spines; weak banding anteriorly; trails may be long.

#### Superfamily LINOPRODUCTOIDEA Stehli, 1954

Trail commonly long but simple; ribbing regular, entire and relatively fine, commonly delicately sinuose; ventral spines at hinge and diverse on rest of valve, never few, thick and symmetrical; dorsal valve without spines except grandaurispinins and some giganotoproductins.

#### Family MONTICULIFERIDAE Muir-Wood and Cooper, 1960

Linoproductoids with moderately shallow corpus cavity, rarely very shallow; rugae posterolaterally or irregularly widespread; spines on ventral valve, rarely restricted to hinge region; marginal structures normally absent.

##### **Eoproductellinae** Lazarev, 1987

Small or medium size; both valves or dorsal valve only with fine ribbing; spines on ventral valve only; teeth and sockets present.

##### **Auriculispinae** Waterhouse, 1986 [= Ovatiinae Lazarev, 1990]

Medium size with rounded to elongate outline; spines normally on ventral valve only, with clusters on ears; teeth and sockets absent; marginal structures commonly absent.

**Schrenkiellinae** Lazarev, 1986

Medium size to large, with flattened ventral disc; spines in row near hinge margin only; ribs separated by wider interspaces; rugae may be present.

**Compressopunctinae** Jing and Hu, 1978

Small or medium size, elongate outline, hinge narrow; corpus cavity moderately shallow; valves thin-shelled with complete ribbing and rugae; spines rare, rhizoid; cardinal process a single median ridge (unifid), lateral ridges weak.

**Devonopunctinae** Muir-Wood and Cooper, 1960

Moderately shallow corpus cavity; fine ribbing especially on ventral valve; dorsal valves with concentric lamellae as traces of series of trails; cardinal process pit absent; ear baffles in ventral valve and weak dorsal lateral ridges; weak submarginal ridge in dorsal valve with papillae.

**Gigantopunctinae** Muir-Wood and Cooper, 1960

Gigantic, large or medium size, hinge at greatest width; corpus cavity very shallow; fully ribbed; spines on ventral valve, rarely also on dorsal valves; marginal structures commonly absent; cardinal process pit commonly present.

**Semiplanini** Sarycheva, 1960. Medium size to large, with very thin shell substance; ventral umbo strongly incurved; ribs of various widths; spines on both valves, some on ventral only; cardinal process bilobed or trifold, with median ridges poorly developed; no brachial cones.

**Gigantopunctini** Muir-Wood and Cooper, 1960. Large or gigantic, thick-walled valves; ventral umbo not strongly incurved; commonly ribbed; spines commonly on ventral valve, only rarely on dorsal valve also; cardinal process trifold with median ridge well developed or sole element; brachial cones commonly distinct.

**Striatiferinae** Muir-Wood and Cooper, 1960

Shell large to medium; outline elongate or with tubiform trail, hinge narrow; spines on ventral valve only.

**Striatiferini** Muir-Wood and Cooper, 1960. Large, with very shallow corpus; trails simple; cardinal process of single ridge continuous with median septum.

**Proboscidellini** Muir-Wood and Cooper, 1960. Corpus cavity shallow; hinge narrower than maximum width; ventral trail long and forming tube, irregularly rugose; cardinal process bilobed, lateral and submarginal ridges present.

Family **LINOPRODUCTIDAE** Stehli, 1954

Linoproductoids with deep corpus cavity and distinct trails; commonly no dorsal spines.

**Linoproductinae** Stehli, 1954

Linoproductids without marginal structures or dorsal spines.

**Grandaurispininae** Lazarev, 1986

Linoproductids with thin spines on dorsal corpus; marginal structures and series of trails absent.

**Siphonosiinae** Lazarev, 1986

Linoproductids with elongate outline and short tubiform ventral trail; hinge narrower than maximum width; spines rhizoid, on ventral valve only; marginal structures at borders of both valves [monotypic].

**Anidanthinae** Waterhouse, 1968

Linoproductids with well developed ears and marginal structures; concentric lamellae (series of trails) commonly on dorsal valve.

## Suborder STROPHALOSIIDINA Waagen, 1883.

Productides with interareas in ventral valve only or in both valves; commonly ventrally attached; profile includes conical shape; toothed articulation retained or lost; cardinal process directed ventrally or posteroventrally, never dorsally; brachial ridges commonly extending to disc margins.

## Superfamily STROPHALOSIOIDEA Schuchert, 1913

Interarea in ventral valve or both valves, commonly with cicatrix; corpus cavity shallow; teeth retained; brachial ridges spread widely.

## Family STROPHALOSIIDAE Schuchert, 1913

Outline rounded; strong rhizoid spines over ventral or both valves, may be bi-directional; planoconvex profile, but corpus cavity rather shallow; trails short or absent.

**Strophalosiinae** Schuchert, 1913

Spines on ventral valve only; concavoconvex profile.

**Dasyalosiinae** Brunton, 1966

Spines on both valves; dorsal valve commonly flat.

## Family CHONOPECTIDAE Muir-Wood and Cooper, 1960

Concavoconvex profile; shallow corpus cavity; cicatrix varied; trails short; fine radial ornament, rugae variable; hinge spines plus sparse and fine ventral corpus spines.

## Family ARAKSALOSIIDAE Lazarev, 1989

Interareas short; concavoconvex, shallow corpus cavity; radial ornamentation absent; cardinal process with pit, cardinal and marginal ridges commonly absent.

**Araksalosiinae** Lazarev, 1989

Cicatrix reduced; mat of spines on ventral valve, rarely dorsally, commonly with stout rows at ventral hinge; elongate spine bases may form incipient ribs.

**Donalosiinae** Lazarev, 1989

Cicatrix present, spines relatively thick; concentric ornament may be lamellose.

**Rhytialosiinae** Lazarev, 1989

Cicatrix present; undulose rugae prominent but discontinuous; spines dense on ventral valve, fewer on dorsal valve.

**Quadratiinae** Lazarev, 1989

Pseudodeltidium and chilidium commonly absent; concentric ornament well developed and regular; spines at low angle, rare on dorsal valve; marginal ridges present.

## Superfamily AULOSTEGOIDEA Muir-Wood and Cooper, 1960

Attached permanently by spines or direct cementation; ventral interarea present, dorsal interarea small or absent, no chilidium; trails commonly elaborated or conical in Permian, when corpus cavity became deep; teeth absent; brachial ridges may be restricted.

## Family AULOSTEGIDAE Muir-Wood and Cooper, 1960

Plano- to weakly concavo-convex profile; corpus moderately deep; ventral rhizoid spines prominent; cardinal process trifold or quadrifid; adductor scars dendritic.

**Aulosteginae** Muir-Wood and Cooper, 1960

Elaborated trails; spines numerous, on both valves.

**Chonosteginae** Muir-Wood and Cooper, 1960

Small, with complex valve-like spinose trails at dorsal geniculation.

**Institellinae** Muir-Wood and Cooper, 1960

Corpus rugose to reticulate; trails commonly ribbed with bordering structures of flanges or gutters.

**Agelesiinae** Cooper and Grant, 1975

Corpus outline triangular; ventral interarea reduced; no dorsal spines.

**Rhamnariinae** Muir-Wood and Cooper, 1960

Interarea reduced or rudimentary; spines on both valves; cardinal process lobes strongly divided.

**Echinosteginae** Muir-Wood and Cooper, 1960

Dorsal spines absent; dorsal adductor scars on raised platforms.

## Family COOPERINIDAE Pajaud, 1968

Small; bilobate outline; cemented by large cicatrix, spines or both; hinge teeth and pseudodeltidium absent; dorsal interior with adductor platform and prominent brachial ridges.

**Cooperininae** Pajaud, 1968

Small-sized for family; ventral interarea and cicatrix surrounded by long rhizoid spines; dorsal muscle platforms short.

**Epiceliinae** Grant, 1972

Large for family; hinge narrow with small interarea; ventral spines restricted around cicatrix; brachial ridges multilobed.

## Family SCACCHINELLIDAE Likharev, 1928

Prominent ventral median septum and widely bilobed cardinal process.

**Scacchinellinae** Likharev, 1928

Ventral valve conical with transverse partitions apically; dorsal valve lid-like; deep corpus cavity.

**Tschernyschewiinae** Muir-Wood and Cooper, 1960

Concavo-convex profile; cicatrix common, plus support spines.

## Superfamily RICHTHOFENIOIDEA Waagen, 1885

Ventral valve conical or sphenoid, dorsal valve recessed below ventral margin; ventral valve attached by cicatrix, rhizoid spines, or by both; small interarea present in Upper Carboniferous genera, but lost from Gzhelian onwards.

## Family RICHTHOFENIIDAE Waagen, 1885

Conical; spines rhizoid; ventral myocoelidium.

## Family HERCOSIIDAE Cooper and Grant, 1975

Conical; spines rhizoid; ventral median septum.

## Family CYCLACANTHARIIDAE Cooper and Grant, 1975

Conical; spines rhizoid or absent; ventral muscle callosity.

**Cyclacanthariinae** Cooper and Grant, 1975

Conical; no spines in *Collumatus*.

**Teguliferininae** Muir-Wood and Cooper, 1960

Sphenoid (obliquely conical); spines rhizoid.

**Zalveriinae** Brunton, in press

Sphenoid to low conical; aspinose (other than tip of ventral beak), with shallow corpus cavity.

## Superfamily LYTTONIOIDEA Waagen, 1883

Shells attached by some part of ventral valve; dorsal valve reduced to small posterior region, the hinge and cardinal process; brachial apparatus supporting lophophore and functioning as partial 'dorsal valve' variable.

## Family POIKILOSAKIDAE Williams, 1953

Small shells attached umbonally or by entire ventral valve, often reflecting shape of substrate; ventral diductor scars asymmetrical; brachial apparatus consisting of two major lobes, each with 2–5 variously directed sublobes.

## Family LYTTONIIDAE Waagen, 1883

Ventral adductor scars medial; diductor scars symmetrical.

**Lyttoniinae** Waagen, 1883

Large; attached by ventral surface, beak, or posterior flap; brachial ridges multilobed.

**Rigbyellinae** Grant, subfam. nov.

Small; attached at beak; raised anteriorly; brachial lobes small, few, extending anteriorly.

**Permianellinae** He and Zhu, 1979

Small; attached at beak; bilobed outline; two proportionally large pustulose dorsal lobes directed anteriorly; ventral interior smooth.

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