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Cover: SEM of sporangium of *Cooksonia pertoni* ssp. *apiculispora* from Brown Clee Hill, Shropshire. This is the specimen (NMW 94 60G) that confirmed the vascular status of *Cooksonia*; × 70. Photograph published originally in *Nature*, **357**, 683–685, figure 1a.

SMALL SPHERES IN FOSSIL BONES: BLOOD CORPUSCLES OR DIAGENETIC PRODUCTS?

by DAVID M. MARTILL *and* DAVID M. UNWIN

ABSTRACT. Mineralized spherical structures within blood vessels of an archosaurian (possibly pterosaurian) limb bone from the Lower Cretaceous of the Isle of Purbeck, Dorset, England, superficially resemble blood corpuscles, but are shown here to be pyrite framboids. Slightly weathered pyrite framboids in which the outer surface has oxidized, probably to goethite, may resemble nucleated cells when viewed in thin section. Previous records of so-called blood corpuscles within dinosaur bones may also be of a purely diagenetic origin and should be re-examined.

FOSSIL soft tissues have great potential to throw light on the anatomy and physiology of extinct vertebrates such as dinosaurs and pterosaurs, but accurate identification is vital if the true potential of such fossils is to be realized. Fossilized muscle tissues in dinosaurs were noted first by Nopsca (1930), and more recently by Kellner (1996). Preservation of muscle, dermis and structural fibres of the flight membranes in pterosaurs has been reported from the Cretaceous Santana Formation of north-east Brazil (Martill and Unwin 1989), and Martill (1991) reported the occurrence of organically preserved dinosaur skin (as opposed to impressions) on a scelidosaur (early thyreophoran dinosaur) from the Jurassic of southern England. In these examples, the *in situ* position, topography and morphological complexity confirm that they have been correctly identified as skin and muscle tissues.

Workers have also claimed to have recognized blood corpuscles in fossil bones. As early as the beginning of this century, Seitz (1907) and Moodie (1923) described fossilized blood corpuscles from dinosaurs (see also Swinton 1934, 1970). More recently, Abbey (1977) claimed to have found blood corpuscles in dinosaurian remains, while Schweitzer *et al.* (1996) reported the presence of heme compounds, presumably derived from blood, in a specimen of *Tyrannosaurus rex* from the Cretaceous of Montana. Schweitzer and Cano (1994) figured a number of spherical structures within voids of trabecular bones of *T. rex* which they suggested resembled red blood cells, and illustrated a thin section through one of these structures showing a centrally placed 'geometric structure' which they interpreted as the nucleus of a blood cell (Schweitzer and Cano 1994, p. 317, fig. 3a–b).

Below, we outline a number of problems with regard to the preservation and recognition of blood cells in fossil material. Blood cells are highly labile (more so than other reported soft tisues) and, as such, are special; rapid preservation mechanisms are probably required for their incorporation into the fossil record. It is imperative therefore that structures thought likely to represent fossil blood cells are rigorously analysed, especially as a number of diagenetic mineral phases is known to produce structures that could be confused with spherical cells. Unfortunately, many of the early descriptions of so-called fossilized blood cells are based on thin section petrography and, on its own, this technique is not sufficient for their positive identification. As a minimum, we suggest that the following criteria should be satisfied before a blood cell origin is invoked for such structures within bones: (1), strong morphological similarity to the blood cells of given organisms if known; (2), close size comparability to blood cells in extant relatives; (3), high abundance; and (4), presence of characteristic biomarkers (e.g. heme compounds) within the structures analysed.

[Palaeontology, Vol. 40, Part 3, 1997, pp. 619–624]

Here, we present an analysis of some small spheres, discovered in vascular channels within an archosaurian limb bone, which closely resemble the so-called nucleated blood cells figured by Schweitzer and Cano (1994). The purpose of this paper is to draw attention to the fact that a number of mineral species produced during early diagenesis may adopt a spherical habit. Subsequent alteration during weathering produces a morphology which, when viewed in thin section, can be easily confused with blood cells.

MATERIALS AND METHODS

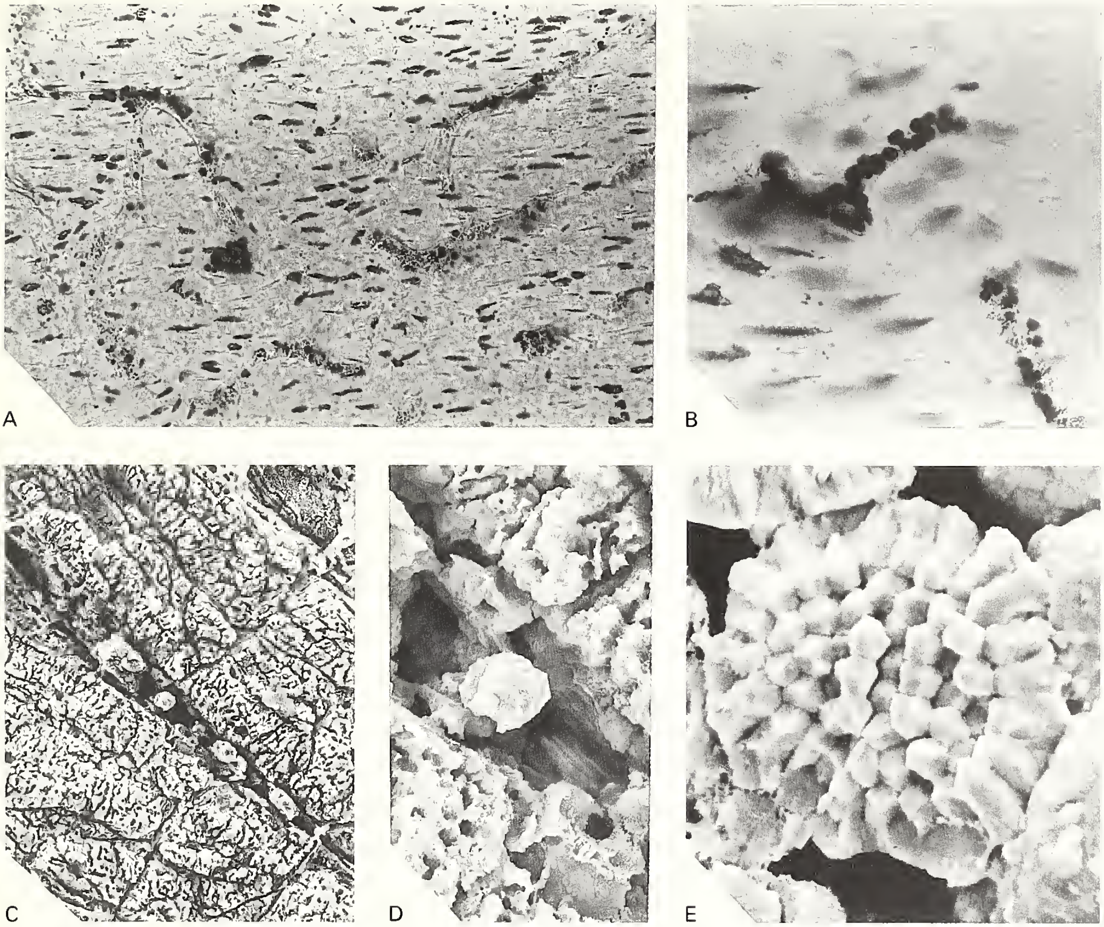
An isolated, elongate limb bone of an archosaurian reptile (possibly part of a tibia of a large pterodactyloid pterosaur) was collected in a block of ostracod-rich argillaceous limestone from the Durlston Formation, Purbeck Group (Lower Cretaceous) on the foreshore at Durlston Bay, Dorset, southern England (Ordnance Survey grid reference SZ040787–SZ035772; University of Cambridge specimen number UMZC T1305). The Durlston Formation is an important source of Lower Cretaceous terrestrial vertebrates (Benton and Spencer 1995; Howse and Milner 1995), and comprises a series of highly fossiliferous limestones and shales deposited in a range of environments from freshwater to marginal marine and hypersaline lagoons (Allen and Keith 1965). The present specimen lacks either articular end, is oval to flattened oval in cross section proximally and subquadrate in cross section distally. As preserved, it is 200 mm long, with a maximum width of 20 mm proximally, tapering to 12 mm distally. The bone wall is between 3 and 5 mm thick, and there is a well-developed central lumen.

Transverse thin sections were made at two points, 30 mm and 160 mm from the proximal end of the bone. A third, oblique section was made at 100 mm. Three additional pieces of the bone were embedded in resin, lightly polished, mounted on flat aluminium stubs and etched in dilute hydrochloric acid for 25 seconds, sputter coated with gold and examined using a Hitachi 250 L Scanning Electron Microscope. Elemental analyses were performed using energy dispersive X ray analysis (EDAX) with a Link AN1000.

OBSERVATIONS

Thin section petrography shows the bone to be well preserved, with osteocyte lacunae and canaliculi clearly visible even at low magnifications (Text-fig. 1A). A large central lumen is filled with brownish/grey sediment containing some ostracod valves. Vascular channels and other void space within the bone is filled with calcite spar, which is easily removed by etching, and euhedral barite in small, discrete patches. These minerals occur as later stage infills. Visible within the smaller vascular channels of the bone are numerous opaque or slightly translucent spherical bodies with a maximum diameter of 20 μm, but mostly with diameters of 5–8 μm (Text-fig. 1B). Although most of the spheres are opaque, a few have reddish brown translucent margins and, superficially, they resemble cells with a dark, centrally placed nucleus similar to those figured by Schweitzer and Cano (1994).

The spheres are resistant to acid etching (Text-fig. 1C), and scanning electron microscopy shows that they have a crystalline surface texture consisting of aggregated cubes, comparable to that of pyrite framboids (Text-fig. 1D), a mineral habit common for pyrite in marine sediments (Hudson 1982). EDAX analysis reveals the presence of Fe and S only in the spherical bodies, and further shows that these spheres are pyrite framboids. The translucent margins of some examples look somewhat smoother and powdery under SEM; this is a result of slight oxidation of their surface to one of the hydrated iron oxides (most probably goethite).



TEXT-FIG. 1. Photomicrographs of thin sections, and scanning electron micrographs of possible pterosaurian limb bone, from the Purbeck Group, Durlston Formation (Lower Cretaceous) of Durlston Bay, Dorset; University of Cambridge UMZC T1305). A, osteocyte lacunae and general fabric of the bone; *c.* ×100. B, as A, showing presence of opaque spherical bodies within microvascular canals of the bone; *c.* ×400. C, scanning electron micrograph of etched surface through bone seen in A; note the framboidal surface texture of the spheres; *c.* ×200. D, scanning electron micrograph of pyrite framboid in C, showing slightly oxidized surface; *c.* ×2500. E, LEIUG DM 70 SEM stub; cross section through pyrite framboid within a coprolite from the Peterborough Member of the Oxford Clay Formation (Jurassic) showing concentric rind of oxidized pyrite, now probably goethite, around unaltered core. When seen in thin section such a structure could resemble a nucleated cell; *c.* ×5000.

DISCUSSION

Fossilized blood corpuscles have been reported in human bone from archaeological sites, where they have been found within vascular canals in bones (Maat 1991; 1993). The preservation of these blood corpuscles is remarkable, in that they appear to be preserved as an organic material, rather than as a mineral replacement, and apart from slight taphonomic damage are morphologically perfect erythrocytes. Here, the morphological complexity is sufficient for the accurate identification of these structures as fossil blood cells, as no diagenetic mineral has to date been reported with a biconcave oblate spheroidal habit. It is clear therefore, that in archaeological materials at least, blood cells can persist for prolonged periods and remain morphologically intact, but such material is comparatively young, and has not undergone intense mineral diagenesis. Putative blood cells from Mesozoic dinosaurs and other extinct groups must have experienced at least 65 million years in the fossil record, and may have been subject to prolonged mineral diagenesis.

Various features may help to identify fossilized blood cells in dinosaurs, pterosaurs and other extinct groups. Reptilian blood cells are ellipsoidal, and so a close morphological resemblance might be expected between fossil and Recent blood cells. Likewise, blood cells are usually of constant dimensions within species (16·9 × 9·9 μm for *Caiman crocodilus*, 23·3 × 13·9 μm for *Sphenodon punctatus*; Saint Girons 1970). The occurrence of numerous similar size bodies might therefore be expected, although morphological transformations and indeed size changes might be produced by taphonomic and diagenetic processes. For example, overgrowths of cryptocrystalline apatite, a mineral species and habit commonly found preserving fossilized labile tissues (Briggs *et al.* 1993), on to a spherical body of only a few micrometres diameter could double the diameter as observed under the electron microscope, and could possibly obscure or even perhaps enhance original surface features. The distribution of putative blood cells within bones or other skeletal elements may also assist in distinguishing between diagenetic products and fossil blood cells, the latter being unlikely to occur, for example, within osteocyte lacunae. Elemental analysis of supposed blood cells may well detect the presence of Fe derived from heme compounds, and S might also be present, released from various amino acids. Incontrovertible evidence of fossil blood might be provided if heme compounds themselves could be detected within the spherical bodies, rather than in bulk bone samples.

Spherical structures have previously been reported from within dinosaur bones in the Wealden Group of the Isle of Wight (Clarke and Barker 1993), but these were composed of siderite, and also barite (Dr M. J. Barker, pers. comm.) and, on the basis of their relationship with other mineral inclusions, these authors concluded that they were of diagenetic origin. Martill (1987) reported the presence of pyrite framboids and euhedral microcrystallites of pyrite within bones of the ichthyosaur *Ophthalmosaurus* sp. from the marine Oxford Clay Formation (Callovian, Jurassic) of central England, that were also of diagenetic origin.

Although the spherical bodies that we describe here from a possible pterosaurian limb bone have a superficial resemblance to a nucleated cell when seen in thin section, and are restricted to vascular channels within the bone, we do not consider that they represent fossil blood cells. Features which support this conclusion include the variable size range (5–8 μm, dimensions somewhat smaller than those of the erythrocytes of modern reptiles; Saint Girons 1970), an elemental composition consistent with pyrite, one of the most abundant early diagenetic mineral phases in marine sediments, and a surface morphology identical to that of framboidal pyrite (Hudson 1982).

Blood corpuscles in dinosaur bone reported in early accounts not based on scanning electron microscopy, e.g. Seitz (1907), Moodie (1920, 1923) and Abbey (1977) may also have been diagenetic products. Seitz (1907) described biconvex structures with flat surfaces as possible fossilized blood corpuscles, but expressed some reservations about this interpretation. His description of the structures is also consistent with the external morphology of pyrite framboids. Likewise, Moodie (1920), after publishing his description of fossilized blood corpuscles, noted that he would not have published his observations, had he been aware of Seitz's (1907) reservations (Moodie 1923).

More recently, Schweitzer (1993) reported the presence of small spherical objects within vascular canals of bones of the dinosaur *Tyrannosaurus rex*. These were described as 'cell-like' and 'primarily of iron' (we suspect that the author meant contained Fe, as analytical techniques using SEM are generally quantitatively unreliable). Later, Schweitzer *et al.* (1996) noted the presence of heme compounds within the same dinosaur specimen. It is therefore possible that some of the Fe from haemoglobin remains as a breakdown product within fossil bone, although this has yet to be demonstrated. It is also possible that Fe from haemoglobin is liberated by bacteria during decay, and becomes available for early pyrite production. However, we suggest that such material should be examined by scanning electron microscopy and EDAX elemental analysis to determine the true nature of any spherical bodies thought to be fossilized blood.

Acknowledgements. We thank Dr Jenny Clack at Cambridge University for allowing us to perform a destructive analysis of the specimen, Mr Clive Trueman for providing some important literature, Mr Roger Pulley and Mr John Davidson for assistance with photography, Mr Geoff Long and Mrs J. Clarke for making the thin sections, and the Department of Geology, University of Leicester, especially Mr Rod Branson, for allowing us the use of their electron microscope and for EDAX analyses. We thank also Dr Mike Barker and two anonymous referees for kindly commenting on the manuscript. DMU is supported by a Royal Society University Research Fellowship. DMM is supported by a University of Portsmouth Senior Research Fellowship.

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ASTRASPIS – THE ANATOMY AND HISTOLOGY OF AN ORDOVICIAN FISH

by IVAN J. SANSOM, M. PAUL SMITH, MOYA M. SMITH
and PETER TURNER

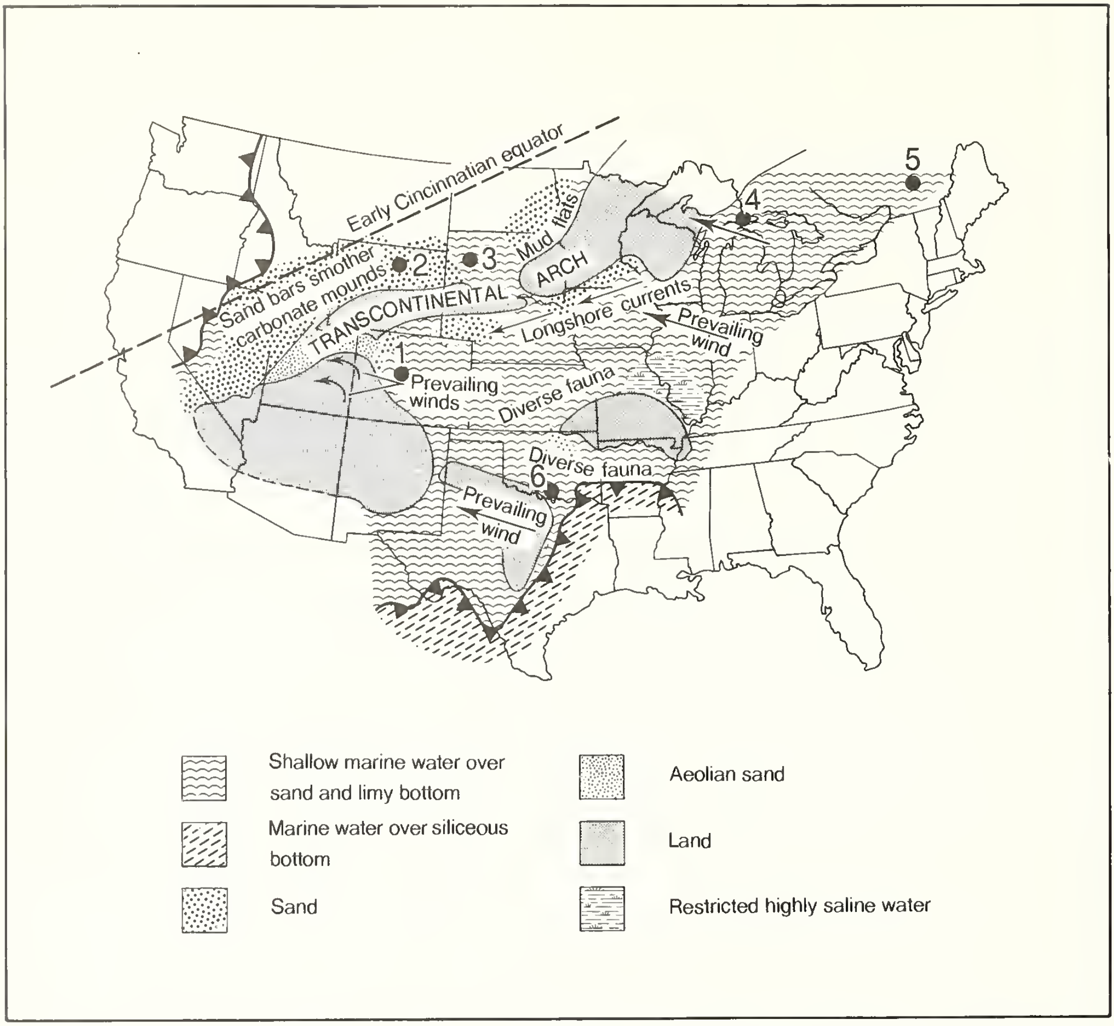
ABSTRACT. A newly discovered specimen of *Astraspis desiderata* Walcott from the mid Ordovician Harding Sandstone Formation of Colorado, USA, is described and represents the third, and most complete, articulated specimen of the taxon recorded to date. *Astraspis* is a pteraspidomorph agnathan with a dorsal headshield formed from polygonal tesserae, and a ventral shield composed of more irregular tesserae. The tesserae are surmounted by star-shaped or smooth, round or ovate tubercles. Well-developed orbits lie directly anterior to a series of eight uncovered, branchial openings which are arranged in a postero-ventrally slanting line. Sensory grooves flank a pineal region on the dorsal headshield. The tail is made up of large rhomboid scales, but the structure of the tail termination remains unknown. Histologically, the hard tissues of *A. desiderata* comprise a basal component of spongy aspidin with large trabeculae and large, irregular soft tissue spaces. Individual tubercles overlie the aspidin and are composed of dentine with an enameloid cap separated by a junctional zone. The dentine is characteristic of *Astraspis* and contains a high density of parallel, fine calibre tapering tubules. *Pycnaspis splendens* Ørvig is considered to be a junior synonym of *Astraspis desiderata* and the genus is monotypic. *Astraspis* has few derived characters in common with other agnathan taxa and is here placed within the monotypic Astraspida, as the sister group of Arandaspida + Heterostraci.

ARTICULATED agnathan specimens from pre-Silurian rocks are extremely rare, with only three localities and five genera recorded world-wide: *Astraspis desiderata* Walcott and *Eriptychius americanus* Walcott from the Harding Sandstone Formation of Colorado, USA (Denison 1967; Lehtola 1983; Elliott 1987); *Arandaspis prionotolepis* Ritchie and Gilbert-Tomlinson and *Porophoraspis crenulata* Ritchie and Gilbert-Tomlinson from the Stairway Sandstone (lower Llanvirn *sensu* Fortey *et al.* 1995) of Northern Territories, Australia (Ritchie and Gilbert-Tomlinson 1977); and *Sacabambaspis janvieri* Gagnier, Blieck and Rodrigo from the Anzaldo Formation (upper Llanvirn *sensu* Fortey *et al.* 1995; Albanesi *et al.* 1995) of Bolivia (Gagnier *et al.* 1986; Gagnier 1993*a*, 1993*b*). Given this scarcity, and the consequent paucity of data concerning the morphological characters of these Ordovician fish, any new data are critical for phylogenetic analyses (Janvier 1996*a*). Most descriptions of *Astraspis* have been based on disarticulated fragments and only two articulated specimens have been recorded hitherto: a headshield, mentioned by Walcott (1892), was figured by Bryant (1936); and a more complete specimen described by Elliott (1987). We describe here an additional articulated specimen of *Astraspis desiderata*, again from the type locality of the species, which constitutes the most complete specimen recovered to date.

The type locality for *A. desiderata* is the Harding Quarry, west of Cañon City, Fremont County, Colorado, USA, but the genus has also been recorded from a number of additional localities along the Ordovician Transcontinental Arch (Text-fig. 1; Ross 1976) in the Harding Sandstone Formation and its lateral equivalents. Accepted records of the genus in addition to the main Harding outcrop are as follows.

1. Bighorn Mountains, west of Buffalo, north-central Wyoming. Although yet to be formally named (Ross *et al.* 1982 denoted the unit as 'Harding Sandstone equivalent'), a microvertebrate fauna comprising *Astraspis* and *Eriptychius* has been recovered (Darton 1907; see comments in Elliott *et al.* 1991).
2. Darton (1909) described specimens of *Astraspis* and *Eriptychius* from the Icebox Shale Member,

[Palaeontology, Vol. 40, Part 3, 1997, pp. 625–643, 4 pls]



TEXT-FIG. 1. Palaeogeographical map of the USA during the mid Ordovician, showing the distribution of known Ordovician vertebrate localities (after Ross 1976, text-fig. 9). 1, Harding Sandstone of Cañon City, Colorado; 2, Bighorn Mountains, north-central Wyoming; 3, Black Hills, South Dakota; 4, St Joseph Island, Ontario; 5, Ouareau River, Quebec; 6, Arbuckle Mountains, Oklahoma.

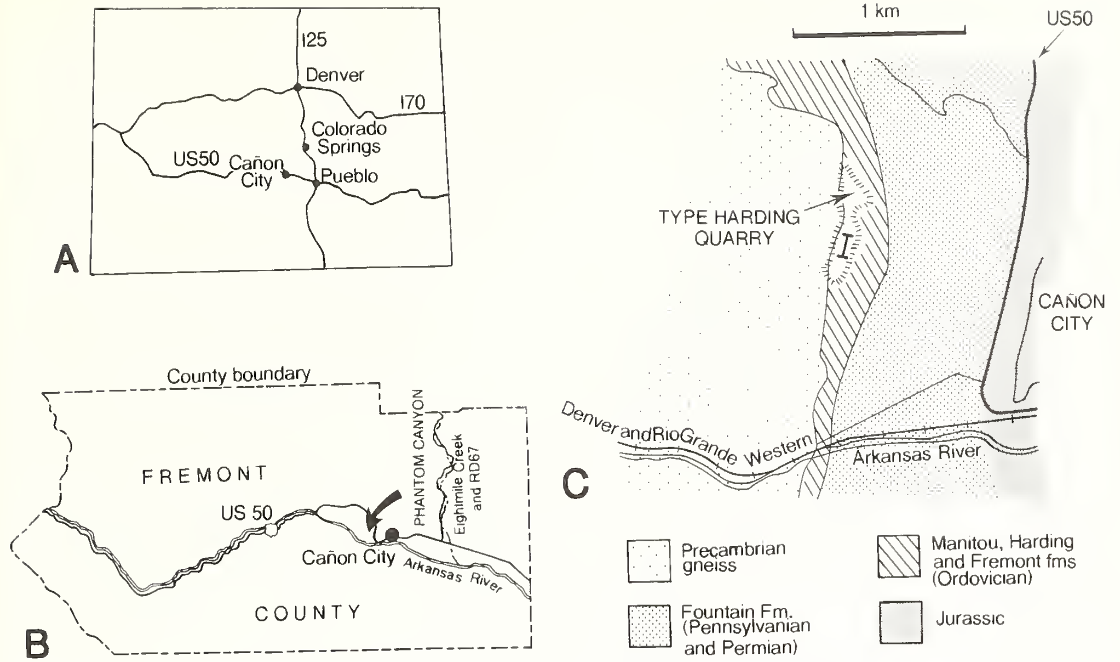
Whitewood Formation of the Black Hills, South Dakota. Boucot and Janis (1983) also mentioned that the Harding Sandstone fauna, consisting primarily of *Astraspis* and *Eriptychius*, has been recorded from Montana and the South Dakota subsurface.

3. Black River Group, St Joseph Island, Ontario, Canada. Darby (1982) recorded a microvertebrate fauna which includes *Astraspis*.

4. Eliuk (1973) has described specimens attributable to *Astraspis* from the Pamelia beds, Black River Group, exposed along the Ouareau River, Quebec, Canada.

5. Ossian and Halseth (1976) reported specimens of *Eriptychius* from the Arbuckle Mountains of Oklahoma. Further collecting may yield specimens of *Astraspis*, since the genus is known from all North American localities from which *Eriptychius* has been recovered.

Astraspis has not yet been recorded outside of North America.



TEXT-FIG. 2. A, map of Colorado; B, map of Fremont County showing the location of the Harding Quarry (arrow); C, geological sketch map of the area around the type locality of the Harding Sandstone (adapted from Taylor *et al.* 1975).

Institutional abbreviations. BU, Lapworth Museum, University of Birmingham, UK; PF, Field Museum of Natural History, Chicago, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

LOCALITY AND STRATIGRAPHY

The Harding Sandstone Formation was first described by Walcott (1892) based on exposures in the Harding Quarry, Cañon City, Colorado (Text-fig. 2). Most subsequent work has concentrated on this area, although some studies (Sweet 1954, 1955; Fischer 1978; Graffin 1992) have encompassed localities elsewhere in the Fremont and Pueblo counties of south-central Colorado. Spjeldnaes (1979) provided a description of the lithologies encountered at the type locality, and a revised sedimentological interpretation of the Harding Sandstone is being prepared by us; preliminary results suggest that the unit in its type area consists of up to six parasequences showing inner shelf to shoreface transitions (Turner *et al.* 1994). The new specimen was recovered from a bedding plane which we interpret as a strandline.

Stratigraphically, the age of the Harding Sandstone is constrained by the locally abundant conodont fauna, which includes *Oulodus serratus* (Stauffer), *Chirognathus duodactylus* Branson and Mehl, *Erismodus quadridactylus* (Stauffer) and *Stereoconus gracilis* Branson and Mehl, suggesting an early Franklinian age (*Phragmodus undatus* Chronozone of Sweet 1984) within the middle Mohawkian – equivalent to the lower middle Caradoc in British terms. The Canadian localities appear to be slightly older than the main Harding outcrop.

The three articulated specimens, two of *Astraspis* and one of *Eriptychius*, previously recorded from the Harding Sandstone came from the type Harding Quarry (Bryant 1936; Lehtola 1983) and the Sturbaum quarries slightly to the north (Denison 1967). The new articulated specimen of *Astraspis desiderata* was found in a small quarry some 150 m due north of the type Harding Quarry on a well-exposed bedding plane which is thought to be the same surface which forms the westerly face of the type quarry.

SYSTEMATIC PALAEONTOLOGY

Class PTERASPIDOMORPHI Goodrich, 1909
Subclass ASTRASPIDA Berg, 1940
Order ASTRASPIDIFORMES Berg, 1940
Family ASTRASPIDIDAE Eastman, 1917

Remarks. Halstead (1993) included both *Astraspis* and *Tesakoviaspis concentrica* Karatajūte-Talimaa, 1978 within the family Astraspididae. Blieck and Janvier (1993) also referred to the latter taxon, quoting the same source, but examination of Karatajūte-Talimaa (1978) reveals that the species was figured but not described in that publication. *Tesakoviaspis concentrica* is a *nomen nudum* and the species figured by Karatajūte-Talimaa (1978, pl. 32, figs 3–7) belongs to a new group of Ordovician fishes with cyclomorial growth, and not to the Astraspida (Karatajūte-Talimaa and Predtechenskyj 1995, p. 55). As currently understood, Astraspida is monotypic and confined to the middle and upper Ordovician of North America.

Genus ASTRASPIS Walcott, 1892

Type species. Astraspis desiderata Walcott, 1892.

Diagnosis. As for the type species.

Remarks. Ørvig (1958) erected *Pycnaspis splendens* for material described from the Bighorn Mountains, Wyoming. He considered the species to be closely related to *Astraspis* but distinguished by supposed histological differences, which included the presence in *Pycnaspis* of the layer later described as pallial mesodentine (Ørvig 1989). Denison (1967) considered the two forms to be representatives of the same genus, but differentiated at species level by both the size and shape of the tubercles and the ornament: *Astraspis splendens* was characterized by larger mushroom-shaped tubercles and *Astraspis desiderata* restricted to plates bearing small, stellate ornament. In our extensive collections of several thousand isolated specimens from localities in Colorado and Wyoming, there are no histological or morphological grounds for considering *Pycnaspis* to be a distinct genus. Furthermore, the collections from the Harding Sandstone and the Bighorn Mountains reveal that the variations in tubercle morphology and size form a continuum. Given the absence of morphological or histological differences, we therefore consider *Pycnaspis splendens* Ørvig to be a junior synonym of *Astraspis desiderata* Walcott.

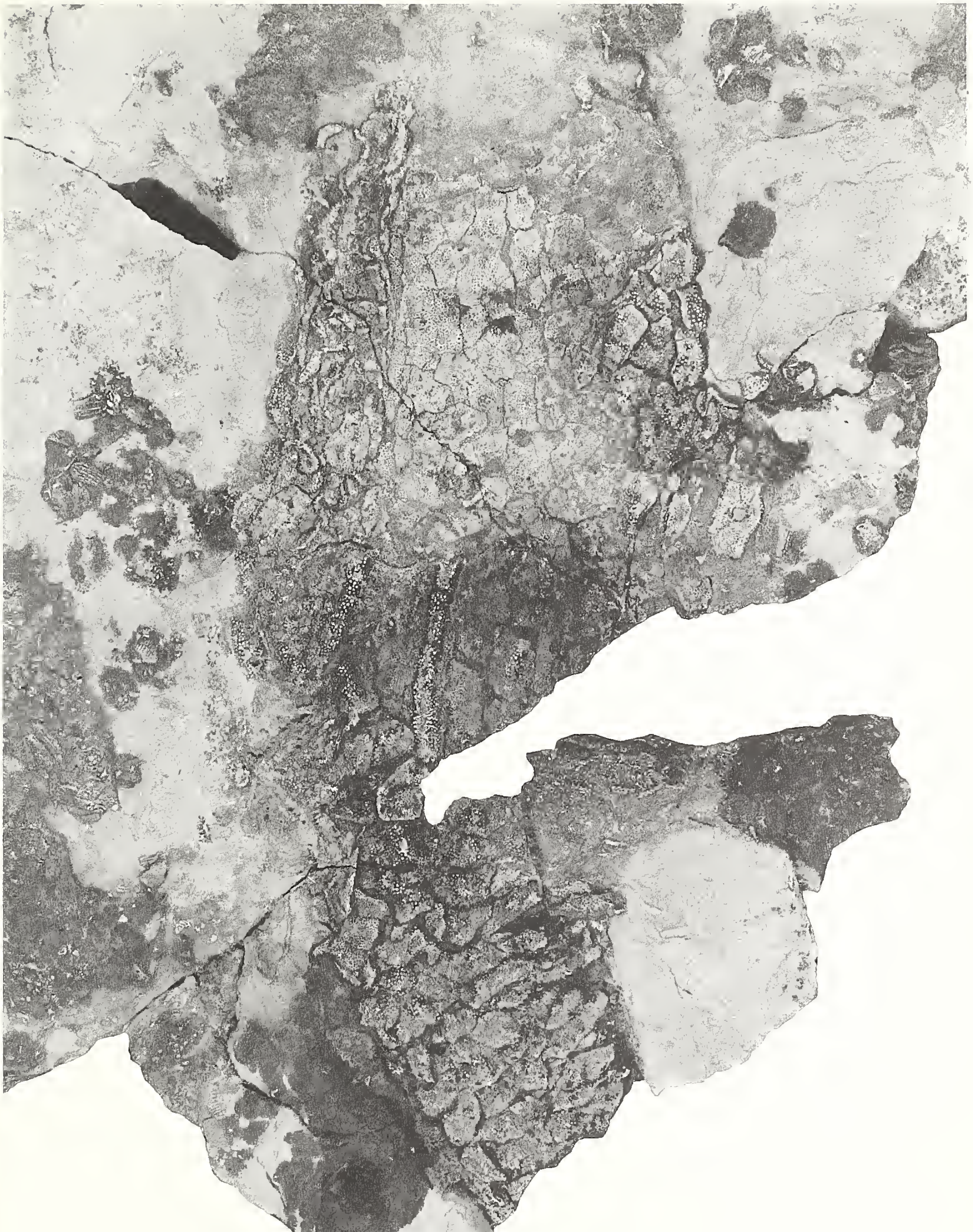
Astraspis desiderata Walcott, 1892

Plates 1–4; Text-figures 3–8

*v1892 *Astraspis desiderata* Walcott, p. 166, pl. 3, figs 6–14; pl. 4, figs 1–4; pl. 5, fig. 3.
v1917 *Astraspis desiderata* Walcott; Eastman, p. 238, pl. 12, figs 5–6.
v1936 *Astraspis desiderata* Walcott; Bryant, p. 416, pls 1–7.
1951 *Astraspis desiderata* Walcott; Ørvig, fig. 22.
1958 *Pycnaspis splendens* Ørvig, p. 7, pl. 1, figs 1–2.

EXPLANATION OF PLATE 1

Astraspis desiderata Walcott, 1892; BU 2472; 150 m north of the Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc; articulated specimen; × 1·5.



SANSOM *et al.*, *Astraspis*

TEXT-FIG. 3. For caption see opposite.

v1964 *Astraspis desiderata* Walcott; Stensiö, p. 177, fig. 32.
v1967 *Astraspis desiderata* Walcott; Denison, p. 164, figs 14–15, 20C, E.
v1967 *Astraspis splendens* (Ørvig); Denison, p. 168, figs 16–19, 20A–B, D, F, 21–25.
1969 *Astraspis desiderata* Walcott; Halstead, fig. 9.
1973 *Astraspis desiderata* Walcott; Lehtola, p. 27, pls 1–2.
1973 ostracoderm tubercles, Eliuk, fig. 2.
*non*1975 *Astraspis*?; Nitecki *et al.*, fig. 7.
1976 ostracoderm tubercles, Winder, pl. 2, fig. 10.
1978 *Astraspis desiderata* Walcott; Fischer, pl. 9, figs b–c.
v *non*1981 ?*Astraspis* sp.; Ethington and Clark, p. 120, pl. 14, fig. 6.
1982 *Astraspis*; Darby, figs 1–3.
v1983 *Astraspis desiderata* Walcott; Lehtola, p. 606, fig. 1.
v1987 *Astraspis desiderata*; Elliott, figs 1–2.
v1987 *Astraspis desiderata*; Halstead, p. 348, fig. 4.
v1987 *Astraspis*; Carroll, fig. 3–4.
v1987 *Astraspis*; Carroll, fig. 3–5.
1989 *Pycnaspis splendens*; Ørvig, p. 438, figs 11–18.
1990 *Astrapididae* [*sic*]; Smith and Hall, p. 298, figs D–E.
v1991 *Astraspis desiderata*; Elliott, Blieck and Gagnier, fig. 2A.
1991 *Astraspis*; Elliott *et al.*, fig. 3A.
v1992 *Astraspis desiderata*; Blieck, fig. 2A–B.
v1992 *Pycnaspis splendens*; Blieck, fig. 2C.

Type material. Thirteen specimens from the Harding Quarry, Cañon City, Colorado, were illustrated in support of the original description of the species (Walcott 1892, pl. 3, figs 6–14; pl. 4, figs 1–4). All were fragmentary and no types were designated. A description of a newly discovered articulated dorsal headshield was made in a postscript footnote (Walcott 1892, p. 167) but it was not figured. This latter specimen was subsequently illustrated by Eastman (1917, pl. 12, figs 5–6) and Bryant (1936, pl. 1). Eastman (1917) noted that the fragmentary material was catalogued under USNM 2351 and that the articulated shield was USNM 8121. Although the dorsal headshield was not figured by Walcott (1892) it is clear that it is a member of the type series, in accordance with ICZN Article 72b, and USNM 8121 is here designated as the lectotype of *Astraspis desiderata*. The fragmentary tesserae and tubercles figured by Walcott (1892, pls 3–4) are designated as paralectotypes.

Locality and horizon. All articulated material comes from the vicinity of the Harding Quarry, Cañon City, Fremont County, Colorado, USA, the type locality for *A. desiderata*. Isolated tesserae have also been recovered from the Bighorn Mountains, Wyoming. Stratigraphically, the Harding Sandstone is of *Phragmodus undatus* Chronozone (middle Mohawkian) age, equivalent to the lower middle Caradoc in British terms.

Diagnosis. Pteraspidomorph agnathan with multiple branchial openings; dorsal and ventral shields composed of fused tesserae, polygonal in outline on dorsal shield and more irregular on ventral shield. Tail composed of large rhomboid scales. Star-shaped and smooth, circular to ovate tubercular ornament on dermal armour, which is formed from enameloid, fine calibre dentine and aspidin.

Description. The anterior region of BU 2472 has undergone dorso-ventral collapse, but the compression of the tail has a lateral component (Pl. 1; Text-fig. 3). The headshield has a preserved length of 73 mm and is around 50 mm wide at its posterior margin, tapering anteriorly with markedly straight sides to 35 mm. The preserved tail is 45 mm long and shows a degree of lateral torsion, perhaps resulting from *post mortem* desiccation of the notochord. The specimen has lost an unknown amount of material from the snout region (we

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TEXT-FIG. 3. *Astraspis desiderata* Walcott, 1892; BU 2472; 150 m to the north of the Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc; camera lucida drawing; specimen is 118 mm in total preserved length. Stippled areas on the unornamented inner surface of the ventral shield represent possible branchial pouches. Abbreviations: co, circumorbital tesserae; lr, lateral ridge plates; mlr, mediolateral ridge; mr, median ridge.

estimate this to be of minor extent, but it does include the oral area) and the posterior of the tail. The total preserved length is 118 mm. The anterior of the specimen largely comprises the interior of the ventral surface, although the exterior of the dorsal shield is seen along the flanks and posterior of the head (Pl. 2, fig. 1). The external surface of the tail is displayed (Pl. 2, fig. 2).

The dimensions of the headshield are extremely close to those of USNM 8121 (Text-fig. 4; Bryant 1936) which has a preserved length of 69 mm and a width along the posterior margin of 51 mm. Five sharp, prominent ridges are present on USNM 8121, with longer median and lateral ridges running anteriorly from the posterior margin for approximately 40 mm. Between the lateral ridges and the median ridge are two shorter structures, 25 mm long, which converge on the anterior end of the median ridge, but do not meet it. BU 2472 possesses only the prominent median ridge flanked by the shorter ridges: only portions of the lateral ridges seen in USNM 8121 are preserved (Pl. 1; Text-fig. 3). Sutured polygonal plates with prominent central tubercles constitute the dorsal headshield of USNM 8121, and, where present, the dorsal tesserae of BU 2472 have the same appearance.

USNM 8121 shows two pairs of tesserae which have a groove running between two rows of tubercles. These linear features lie to the anterior of, and converge on, the median ridge of the dorsal headshield but do not intersect it (Text-fig. 4). They probably represent the grooves for sensory canals. We see no evidence for the additional sensory canals labelled by Stensiö (1964, fig. 32). A prominent sub-circular cluster of tesserae lies on the mid-line of USNM 8121 to the anterior of the median ridge and is suggestive of the presence of a pineal region (Stensiö 1964). One feature of the sensory systems, and indeed the dorsal headshield as a whole, is the lack of precise symmetry developed in the ornament and tessellation (Text-fig. 4).

The ventral headshield, seen in internal aspect in BU 2472, is formed of more irregular tesserae than the polygonal plates of the dorsal headshield. It also seems that PF 5733 is part of a ventral headshield preserved in internal aspect (*contra* Elliott 1987), since the irregular pattern of tesserae is similar to the ventral shield of BU 2472 (Elliott, pers. comm.).

A small arcuate plate, probably a circumorbital tessera, is preserved in cross section towards the anterior of the headshield in BU 2472 (Pl. 1; Pl. 2., fig. 1; Text-fig. 3). Elliott (1987) also interpreted the presence of an orbital region in PF 5733 (Text-fig. 5).

Elliott (1987) identified eight branchial openings on PF 5733, extending from just posterior of the interpreted orbit down the flank of the headshield (here interpreted as the ventral shield) to the postero-lateral edge. The openings are uncovered and delineated by branchial plates attached to elongate rectangular plates on their longest, ventral, margins. Each plate is attached laterally by the shortest margins and the dorsal edge forms a point, producing a sub-triangular opening between each pair of the plates (Elliott, 1987; Text-fig. 5). Plates forming the dorsal margins of the branchial openings are not seen on PF 5733 but are preserved end-on, down the left side of BU 2472 (Pl. 2, fig. 1; Text-fig. 3). These extend posteriorly from the circumorbital plate, and delineate a series of roughly circular structures approximately 5 mm in diameter, representing the upper parts of the branchial openings. In this way, a single plate forms the dorsal margin of each opening whereas the ventral margin comprises two plates.

Elliott (1987), Elliott *et al.* (1991), Gagnier (1995) and Janvier (1996*a*, 1996*b*) all reconstructed *Astraspis* with horizontally arranged branchial openings. However, PF 5733 shows a clear sigmoidal curvature to the branchial plates (Elliott 1987; Text-fig. 5), and the branchial openings in BU 2472 have a slight angular relationship to the lateral margin of the dorsal headshield. In addition, plates of the ventral headshield are seen lateral to those of the branchial area, demonstrating that the branchial plates were not attached to the lateral ridges of the dorsal headshield. Instead they were arranged to form a postero-ventrally slanting line along the side of the animal.

The inner surfaces of the ventral shield tesserae are smooth with pores opening into the basal aspidin. Weakly defined elliptical depressions occur to the right of the midline (Text-fig. 6) and their location, shape and size are suggestive of branchial pouches. To the left of the midline, but slightly offset from the putative

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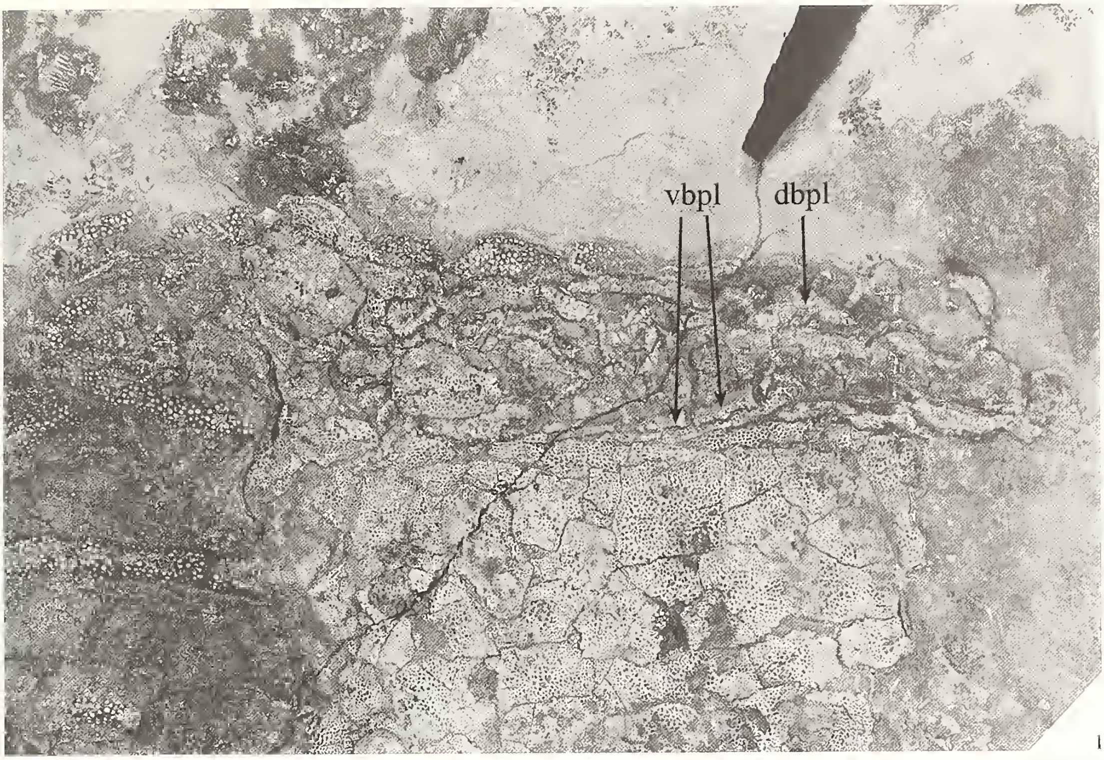
EXPLANATION OF PLATE 2

Figs 1–2. *Astraspis desiderata* Walcott, 1892; BU 2472; 150 m north of the Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc. 1, detail of left branchial region, showing the orbit and branchial plates. To the left the median ridge of the dorsal headshield is clearly seen; the paler area to the right represents the internal surface of the ventral headshield (see Text-figs 3, 6, for labelling). 2, detail of tail. Abbreviations: dbpl, dorsal branchial plate; vbpl, ventral branchial plate. Both ×2.



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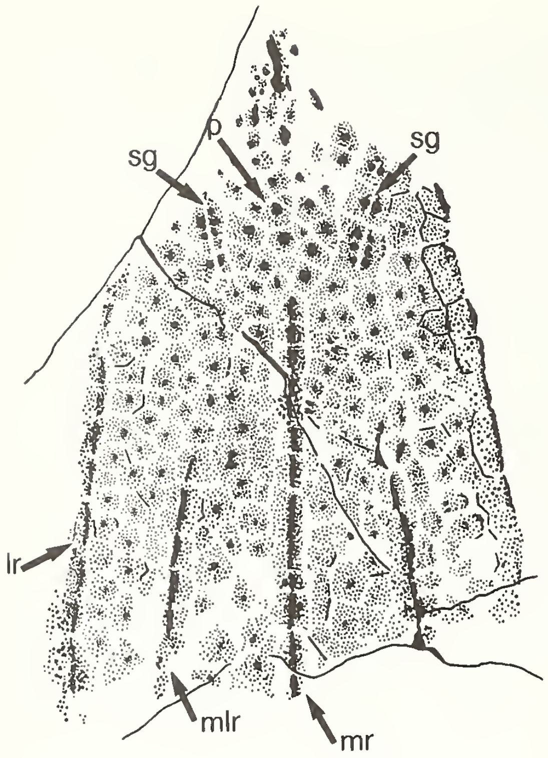
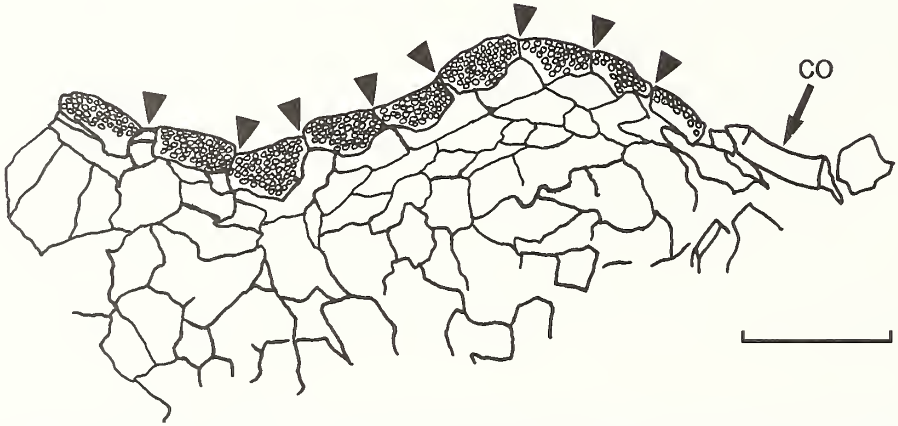
SANSOM *et al.*, *Astraspis*



TEXT-FIG. 4. *Astraspis desiderata* Walcott, 1892; USNM 8121; Harding Sandstone Formation; Caradoc. Specimen is 69 mm in total preserved length. Abbreviations in addition to those used on Text-figure 3: p, pineal region; sg, sensory groove.

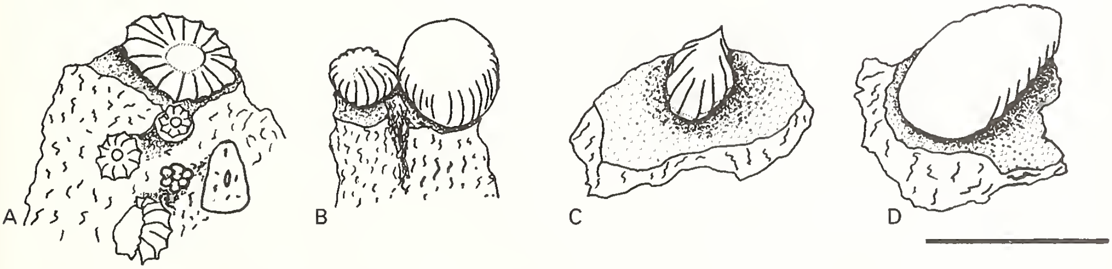


TEXT-FIG. 5. *Astraspis desiderata* Walcott, 1892; PF 5733; Harding Sandstone Formation; Caradoc. Ventral headshield seen in predominantly internal aspect, showing the position of the orbit and eight branchial openings (arrowheads) identified by Elliott (1987, fig. 2). Ornamented areas are the external surfaces of the ventral branchial plates. Scale bar represents 1 mm.

branchial pouches are textured, pitted areas which lack pores through the basal aspidin. They may represent either the sinistral branchial pouches, in different preservational aspect to those on the opposite side, or impressions of a vascularized network associated with the pouches.

The tail of BU 2472 is incomplete, but the preserved portion suggests that *Astraspis* possessed a broad tail, at least 95 mm long. Elliott (1987), basing his observations on PF 5733, reconstructed *Astraspis* with a stubby caudal fin and suggested that the termination was symmetrical in form, in contrast to the reverse heterocercal

TEXT-FIG. 6. *Astraspis desiderata* Walcott, 1892; BU 2472; Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc. Detail of anterior part of ventral shield showing shallow depressions, on the right (arrowed), interpreted as branchial pouches. The textured areas on the left (arrowed) lack pores and may represent either branchial pouches or impressions of a vascular network; ×6.



TEXT-FIG. 7. *Astraspis desiderata* Walcott, 1892; Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc. *Camera lucida* drawings illustrating variations of scale morphology found in sieved samples; only morphologies A and B have been identified on the articulated specimen BU 2472. A, BU 2566; B, BU 2567; C, BU 2568; D, BU 2569. Scale bar represents 1 mm.

type interpreted by Lehtola (1983). It is apparent from a latex peel of PF 5733 that the tail on this specimen is also incomplete, and that the distal tail structure of *Astraspis* remains to be elucidated. The individual scales of the tail are variable in shape, with lateral scales elongated in a dorso-ventral sense and the dorsal scales more polygonal in form (Pl. 2, fig. 2). The dorso-median scales are slightly arched on BU 2472, forming a weakly developed continuation of the median ridge of the dorsal headshield.

A number of different ornaments has been recognized in discrete collections of *Astraspis* dermal plates (Text-fig. 7). However, only two tubercle morphologies are evident on the dorsal surface of BU 2472. Both are circular in outline; one has prominent ridges radiating from a central point, whereas the other has a smooth rounded surface. The latter form appears to be dominant on the tail.

The absence of other scale morphologies observed within collections of isolated material can be explained either by intraspecific variation within the *Astraspis* population or by the presence of additional morphologies on the ventral surface of the animal, the exterior of which is not seen in any of the articulated specimens. Elliott *et al.* (1991; fig. 3A) illustrated a small rhombic scale of *Astraspis* bearing four tubercles from the Swift Current Formation, Ontario, Canada (see Darby 1982 for locality details), but we have yet to recover any specimens with such a regular shape from our extensive isolated collections from the Harding Sandstone.

Histology. The hard tissues of *Astraspis* have been described by numerous authors and a plethora of terms has been applied (cf. Walcott 1892; Bryant 1936; Ørvig 1958, 1967, 1989; Denison 1967; Halstead 1969, 1987; Smith and Hall 1990; Smith *et al.* 1996). Given recent developments in techniques for studying vertebrate hard tissues and a better understanding of the developmental framework, it is appropriate to present a revised description of the tissues.

The dermal armour of *Astraspis* comprises three distinct tissue types. The basal component of the tesserae is typified by a spongy appearance with large trabeculae of aspidin (acellular bone) and open, irregular, soft tissue spaces. In compact areas within this region, the spaces become constricted by the deposition of additional concentric layers of aspidin, forming aspidones. The undersurfaces of tesserae are generally penetrated by pores of up to 0·25 mm diameter (Text-fig. 6).

The tubercles, overlying the spongy or compact basal plate of aspidin, are characterized by two tissues, enameloid and dentine, with a junctional zone between them (Pl. 3, figs 2, 4; Pl. 4, figs 1–2, 5). A substantial part of the tubercle is composed of regular, tubular dentine. This contains extremely fine calibre tapering tubules, each with a maximum diameter of 0·5 μm at their pulpal end (Pl. 3, fig. 4), and generally orientated parallel to each other with occasional cross branches (Pl. 4, figs 3–4). The pulp cavities, large in the new tubercles (Pl. 3, fig. 1), were gradually infilled by dentine during incremental growth, the pattern of which is evident from incremental lines in the dentine (Pl. 4, figs 1–2), some of which are markedly calcospheritic (Pl. 3, fig. 3). The narrow diameter and relatively high density of tubules in the dentine is characteristic of *Astraspis*.

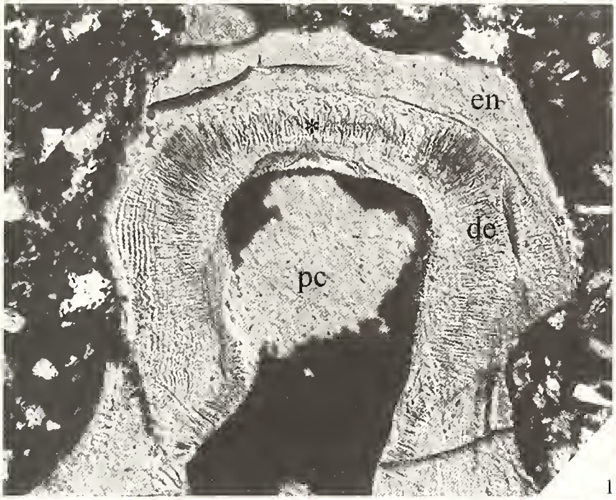
The predominant tissue of the tubercles has been variously described as orthodentine (Denison 1967), acellular bone with fibre bundles (aspidin, Ørvig 1989), or as a unique tissue, astraspidin, sharing characters of both bone and dentine (Halstead 1987). However, the identification of distinct, occasionally interconnected, tubules and a calcospheritic pattern of biomineralization supports the interpretation of this tissue as dentine (Smith and Hall 1990).

A glassy, often sculpted, cap of enameloid surmounts the dentine of the tubercles, sharply truncating incremental lines in the underlying dentine (Pl. 3, figs 1–3; Pl. 4, figs 1–2). The basal region of the cap tissue, the junctional zone, is characterized by a row of wide ascending canals which terminate in finer and finer branches towards the external surface of this cap enameloid (Pl. 4, fig. 2). Some of the finer tubules appear to be continuous with those in the dentine below. Ørvig (1989) referred to this junctional layer, where the wide ascending canals branch into finer tubules, as pallial mesodentine, an interpretation with which we disagree as there is no distinct junction within the capping tissue; instead, there is a sharp boundary between the enameloid and the dentine.

EXPLANATION OF PLATE 3

Figs 1–4. *Astraspis desiderata* Walcott, 1892. 1–3, Harding Quarry, Canon City, Colorado, USA; Harding Sandstone Formation; Caradoc. 1–2, BU 2570. 1, vertical section through growing stellate tubercles with a large pulp cavity and shallow depth of dentine with a high density of parallel tubules; ×189. 2, higher magnification of asterisked area in fig. 1; ×480. 3, BU 2571; pallial dentine has closely spaced incremental lines of Von Ebner which are scalloped in many places where the calcification front has the characteristic calcospheritic pattern (arrows); ×480. 4, BU2269; Bighorn Mountains, Wyoming, USA; 'Harding Sandstone equivalent'; Caradoc; SEM of an etched (1N HCl for 2 mins), polished tubercle; the dentine tubules are relative wide where they open at the pulp surface and narrow to an extremely fine diameter in the pallial dentine; the enameloid is more etch-resistant than the dentine, indicating a more highly mineralized tissue; ×1080. Abbreviations: de, dentine; dt, dentine tubules; en, enamel; pal d, pallial dentine; pc, pulp cavity.

PLATE 3



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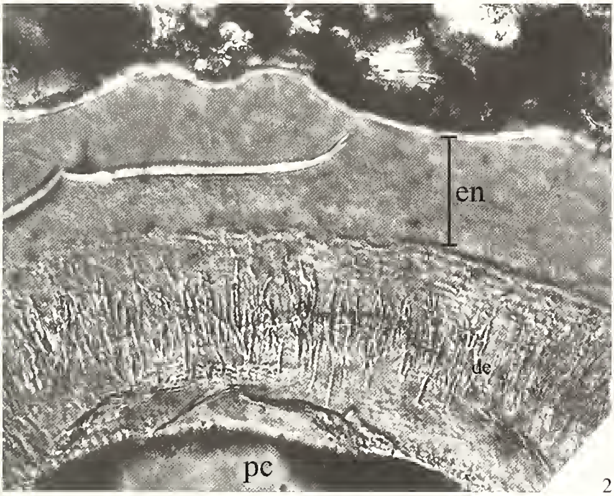

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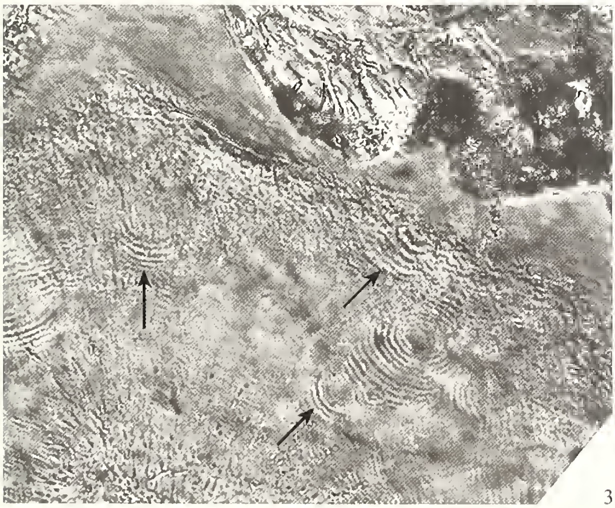

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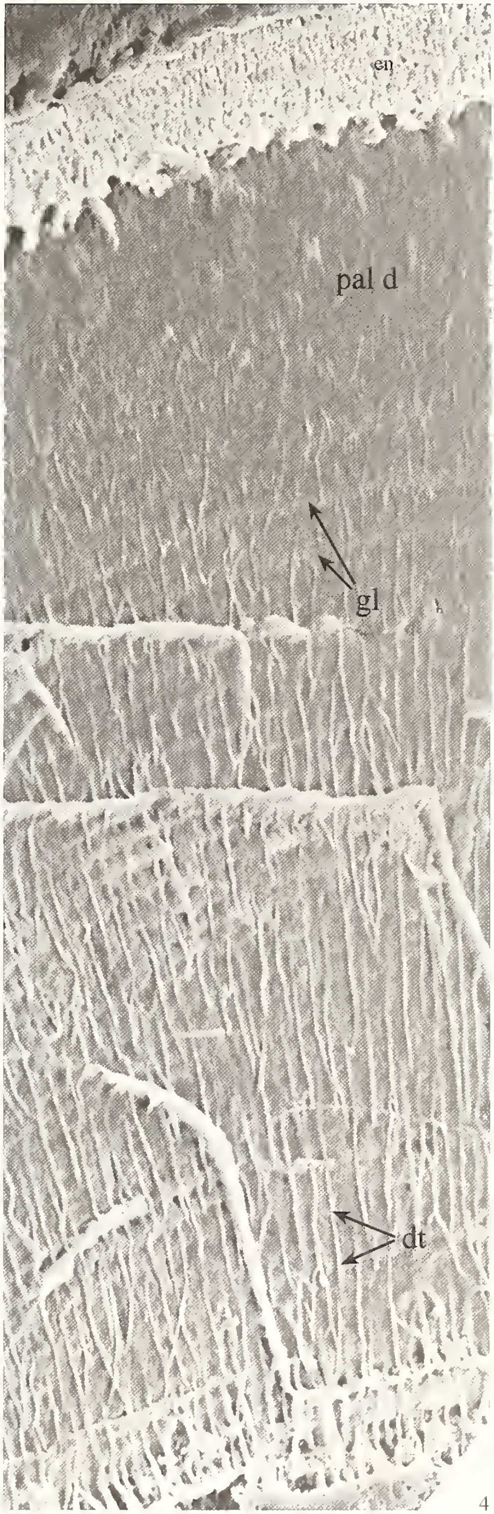

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SANSOM *et al.*, *Astraspis*

CLASSIFICATION OF ORDOVICIAN FISH

Morphological data on Ordovician fish are scarce. Of the five taxa known from articulated remains, only three are sufficiently well preserved to permit reliable reconstructions: *Arandaspis* from the Stairway Sandstone of Australia (Ritchie and Gilbert-Tomlinson 1977), *Sacabambaspis* from Bolivia (Gagnier *et al.* 1986; Gagnier 1989, 1993*a*, 1993*b*) and *Astraspis* (Text-fig. 8). A partially articulated fragment of *Eriptychius* from the Harding Sandstone (PF 1795) represents the rostral part of a headshield with subaponevrotic vessels (Denison 1967; Janvier 1996*b*), but the morphology of the remainder of the body remains unknown. Articulated fragments of *Porophorapsis* were also described by Ritchie and Gilbert-Tomlinson (1977).

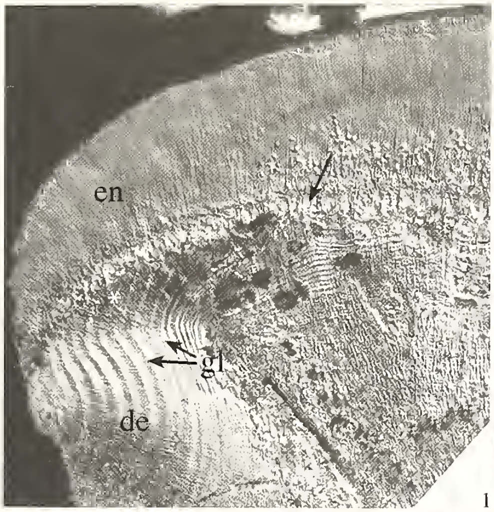
Blieck *et al.* (1991), Elliott *et al.* (1991) and Gagnier (1995) discussed possible relationships between described Ordovician fish and proposed that *Sacabambaspis* and *Arandaspis* are sister taxa within the family Arandaspididae of Ritchie and Gilbert-Tomlinson (1977). They are united by the presence of slanted and closed branchial plates, fused plates forming a headshield with double pineal-parapineal openings, multiple paired grooves for sensory canals on the headshield, and very narrow, elongate, serrated scales covering the trunk and tail.

Astraspis is readily distinguished from the arandaspidids by its possession of eight large gill openings with no cover, and tail scales which are much wider and rhomboid in shape. In addition, *Astraspis* possessed a single pineal region located to the anterior of the median ridge of the dorsal headshield, rather than the paired pineal-parapineal openings of the arandaspids. There is evidence for only a single pair of sensory canals on the dorsal surface of the headshield on USNM 8121 (Text-fig. 4), in contrast to the statement by Blieck *et al.* (1991, p. 14) that '... the canal system is borne in surface grooves it consists of *two pairs* of longitudinal canals together with lateral commisures in a pattern that is very heterostracan in outline' [our italics]. Although a single pair of sensory canals does appear on the reconstruction of Blieck *et al.*, they are not in a position that could be derived from USNM 8121.

The structure of the *Astraspis* tail has yet to be determined with any degree of certainty. Elliott (1987) reconstructed *Astraspis* with a stubby caudal fin, which we consider to be speculative (see *Description* above), and BU 2472 offers no additional information on this point. *Sacabambaspis*, the only Ordovician fish with a preserved tail, has a diphycercal caudal fin (Gagnier 1993*a*, 1995). The elongate caudal spine featured on previous reconstructions of *Sacabambaspis* (Gagnier 1989; Blieck *et al.* 1991; Elliott *et al.* 1991) is now interpreted as the lateral margin of an underlying cephalic shield (Gagnier 1993*a*). *Athenaegis* Soehn and Wilson, 1990, from the Delorme Group (Wenlock) Northwest Territories, Canada, is the next oldest pteraspidomorph fish for which there is conclusive evidence of tail structure. These specimens, classified as cyathaspidid heterostracans, possessed a flexible, symmetrical tail with numerous fin 'rays' that predate similar features in the osteichthyans by some 20 million years (Soehn and Wilson 1990).

EXPLANATION OF PLATE 4

Figs 1–5. *Astraspis desiderata* Walcott, 1892; Bighorn Mountains, Wyoming, USA; 'Harding Sandstone equivalent'; Caradoc; Nomarski differential interference contrast photomicrographs. 1–2, BU 2268; large mushroom-shaped tubercle with a thick layer of enameloid with numerous very fine tubules and a distinct junction (arrow) with the underlying dentine. This junction interrupts the pattern of the prominent, alternating incremental bands in the dentine. Fig. 2 shows the junctional tissue with wide ascending canals and arboriform branches leading to the very fine tubules ending at the cap surface. 3–4, BU 2572; two fields of dentine in a large tubercle where tubules can be seen to branch and when cut across show the high density of tubules per unit area. 5, BU 2573; comparison between enameloid and dentine showing the fine dimensions of both sets of tubules, and the contrasting disrupted and irregular course in the enameloid and the regular branched pattern in the dentine. Abbreviations in addition to those on Pl. 3: ac, ascending canals; gl, growth lines; t, tubule. Fig. 1, × 189; figs 2–5, × 480.



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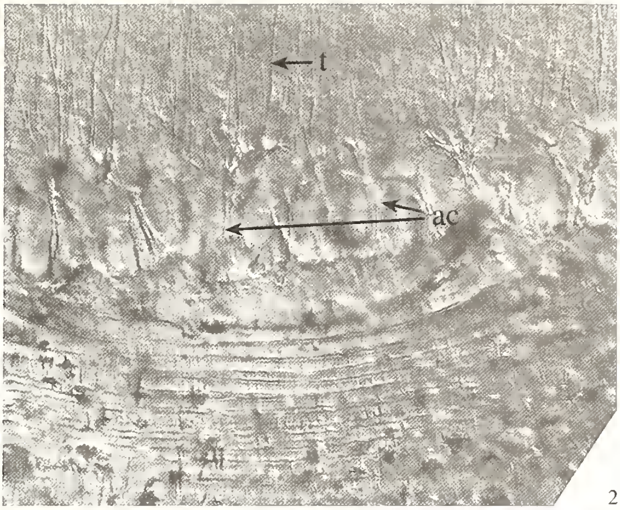

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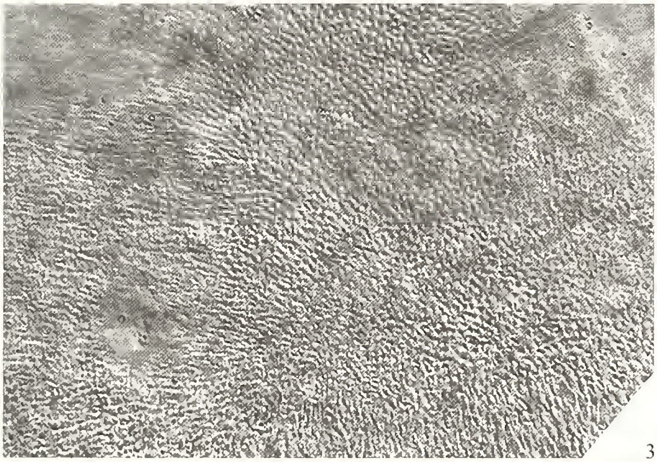

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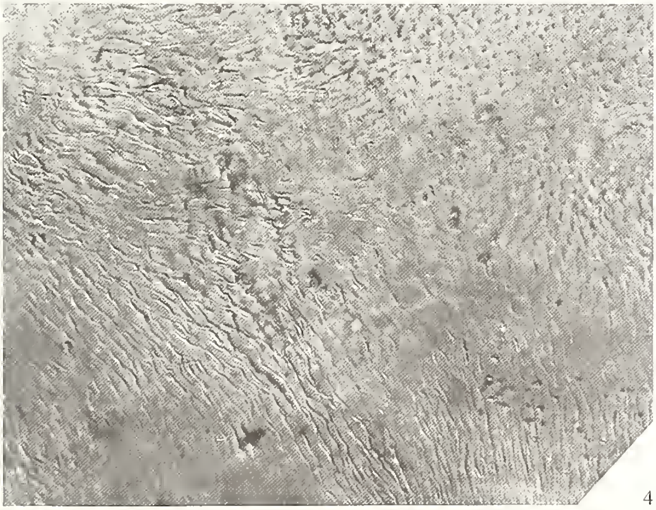

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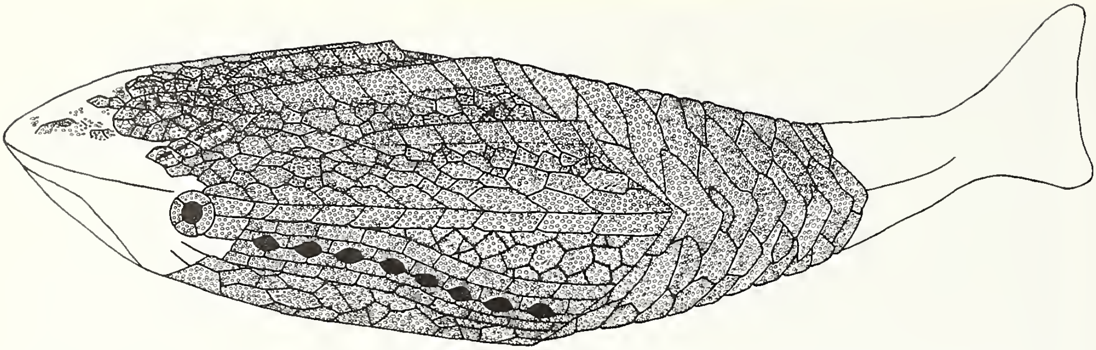
SANSOM *et al.*, *Astraspis*



TEXT-FIG. 8. Reconstruction of *Astraspis desiderata* Walcott, 1892. The tail and rostral areas are schematic since they are not preserved in any of the articulated specimens.

Little is known about the structure of the feeding apparatus in any of the Ordovician taxa. None of the described specimens of *Astraspis* has this area preserved, and the only Ordovician taxon which shows the oral region is *Sacabambaspis*. Gagnier (1993*a*) illustrated the ventral snout of *Sacabambaspis* with multiple rows of oral platelets which appear to have had a scoop-like function, comparable to that postulated for those of later heterostracans such as *Athenaegis* and the pteraspids (see Soehn and Wilson 1990; Janvier 1981, 1996*b*). However, the apparatus does appear to differ between these two groups since the oral plates of the heterostracans are single elongate scales; *Sacabambaspis* possessed composite plates formed from many platelets.

Both Elliott *et al.* (1991) and Blieck *et al.* (1991) claimed that aspidin can be considered to be a character shared by the arandaspidids, *Astraspis* and *Eriptychius*. The absence of histological data from *Arandaspis* and the complex and divergent histologies preserved in *Astraspis*, *Eriptychius* and *Sacabambaspis* suggest that this view is an oversimplification. The only histological character which can be confirmed as common to all forms is a highly vascularized honeycomb tissue which supports the dermal armour. It has been widely assumed that this is an acellular tissue, aspidin, based largely upon hypothetical considerations of the primitive condition in vertebrate hard tissues (Janvier 1981; Blieck *et al.* 1991; Elliott *et al.* 1991; Forey and Janvier 1993), but the available data do not lend firm support to this proposal. Although the honeycombed tissue is clearly acellular in *Astraspis* and *Eriptychius*, that of *Sacabambaspis* contains numerous small cavities, which may represent cell lacunae, and also lacks dentine (Gagnier 1993*a*, 1995). *Astraspis* and *Eriptychius* are readily distinguished in thin section, with significant differences in the nature of the cap material and the types of dentine which form the individual tubercles (Smith and Hall 1990; Smith *et al.* 1996). This suggests that they are not as closely related as has been proposed by Blieck *et al.* (1991). *Eriptychius* may be a primitive true heterostracan (Ørvig 1989; Blieck 1992), although more information about the body plan of this animal is required to confirm this.

Gagnier (1995) stated that dorsal-median scale/skin ridges are present as a uniting feature in all Ordovician taxa, heterostracans and myxinoids. Whilst *Astraspis* has a clearly developed dorsal median ridge on the headshield, this character is not developed prominently on the tail by a series of individual scales, as suggested by the reconstructions of Elliott (1987, fig. 3), Elliott *et al.* (1991, fig. 1B), Blieck (1992, fig. 1C) and Gagnier (1995, fig. 2B).

The development of the lateral line system is a potentially important character which may well provide insight into the relationship of these Ordovician vertebrates to more advanced Siluro-Devonian forms. *Astraspis*, with the lateral line system apparently developed only in the head region, differs from *Sacabambaspis* and the heterostracans, which show evidence for the lateral line system on head and body (Janvier 1996*a*, 1996*b*).

In summary, the significant morphological and histological characters of *Astraspis desiderata* are: dorso-ventrally compressed head; fused polygonal tesserae on the dorsal headshield, irregular tesserae forming the ventral headshield; orbits surrounded by circumorbital tesserae; eight branchial openings arranged in a postero-ventral sloping line; branchial pouches; two dorsal sensory grooves; closed pineal region; articulated, thickened, large, rhomboid tail scales; and enameloid, fine tubular dentine and aspidin.

CONCLUSIONS

Although some of the characters possessed by *Astraspis* may suggest a relationship with true heterostracans, the histology, and the presence of multiple branchial openings indicate a more complex picture. In addition, it is clear from available histological and morphological data that any formal grouping of the Ordovician heterostracan-like agnathans at ordinal level is artificial. Janvier's (1996*a*, 1996*b*) examination of early vertebrates demonstrates that Gagnier's (1993*b*, 1995) redefinition of the class Pteraspidomorphi, to include *Astraspis*, *Eriptychius*, arandaspidids and the heterostracans, does constitute a monophyletic group but one that is united only by the presence of the dorsal and ventral headshields. *Astraspis* has no clearly defined relationship with other groups and, although the heterostracans provide the nearest relatives, Astraspida probably represented an evolutionary *cul-de-sac* within Pteraspidomorphi.

Acknowledgements. Prof. David Elliott (Northern Arizona University) kindly provided high quality photographic prints and latex peels of PF 5733, together with lengthy discussion of the new specimen described here. Prof. Philippe Janvier (CNRS, Paris) is thanked for his helpful comments and advice on our original manuscript. Dr Charles Fair (Bureau of Land Management, Cañon City) is acknowledged for his logistical help whilst we were in the field and Mr Ron Watters gave permission to collect in the type Harding quarries. Dr Jane Keeton (University of Southampton) provided assistance in the field.

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EXOSKELETAL MICRO-REMAINS OF AN ORDOVICIAN FISH FROM THE HARDING SANDSTONE OF COLORADO

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ABSTRACT. Three dimensional scales and fragments of the dermal skeleton from a hitherto little known fish have been isolated from the Ordovician Harding Sandstone of the type area around Cañon City, Colorado, USA, allowing exoskeletal morphology to be correlated with tissue structure and arrangement. Scales with a small crown sculpted into ridges over an extended base exhibit the same histology as material in bone-bed thin sections previously described as 'Vertebrate indet. A' by Denison (1967) and here formalized as *Skiichthys halsteadi* gen. et sp. nov. Possible taxonomic relationships with the osteostracans and primitive gnathostomes, elasmobranchs, acanthodians and placoderms are discussed. The microsquamous exoskeleton exhibits a variety of histological characters: enameloid, mesodentine with odontocytes, basal bone with osteocytes and numerous extrinsic fibre bundles in groups crossing at right angles and inserted at the visceral surface. The suprageneric assignment of *Skiichthys* is uncertain, but a taxonomic relationship to either the acanthodians or the placoderms is likely. The contemporaneous and co-occurring pteraspidomorph agnathans, *Astraspis* and *Eriptychius*, have an exoskeleton of plates and tesserae of acellular bone (aspidin) and tubular dentine and are not closely related to *Skiichthys*.

JAWED vertebrates, in the form of chondrichthyans and acanthodians, have long been thought to have unequivocal first records in the Silurian, but published studies seem to describe relatively advanced forms, rather than stem taxa which would offer firm evidence of phylogenetic links between the major groups of the gnathostomes and their supposed predecessors, the agnathans or jawless vertebrates. Two scenarios have been put forward to solve this problem. The first is that the acquisition of dermal armour occurred independently in the gnathostomes and agnathans, and that this was preceded by a period of diversification of fish lacking mineralized armour and consequently with low preservation potential (Carroll 1987). A second view suggested that the main period of diversification occurred during the Silurian and that 'the evolution of fishes was slow during the Ordovician' (Benton 1990, p. 45). Recent work on the middle Ordovician of North America has yielded data which enable a re-evaluation of these two hypotheses, and has led to the realization that many of the major groups of fish were already components of the marine fauna some 450 million years ago (Sansom *et al.* 1996).

Three-dimensional microvertebrate remains were recovered from the Harding Sandstone utilizing petroleum ether (following the methodology of Swift 1987). Sectioning of isolated scutes has enabled correlation with the classic diagnostic histologies observed in thin sections made from the bone bed horizons within the Harding Sandstone. We describe here a new morphology of micromeric scales, with histology identical to that of 'Vertebrate indet. A' (Denison 1967, p. 185), which forms the basis for *Skiichthys halsteadi* gen. et sp. nov. The characteristics of the distinctive histologies present in *S. halsteadi* are analysed and assessed in relation to higher order taxa, such as osteostracans, chondrichthyans, acanthodians and placoderms. The implications for tissue evolution and developmental models (Smith and Hall 1993) involving putative neural crest cells, already proposed for *Skiichthys* (Smith 1991), can be more realistically evaluated with the new analysis.

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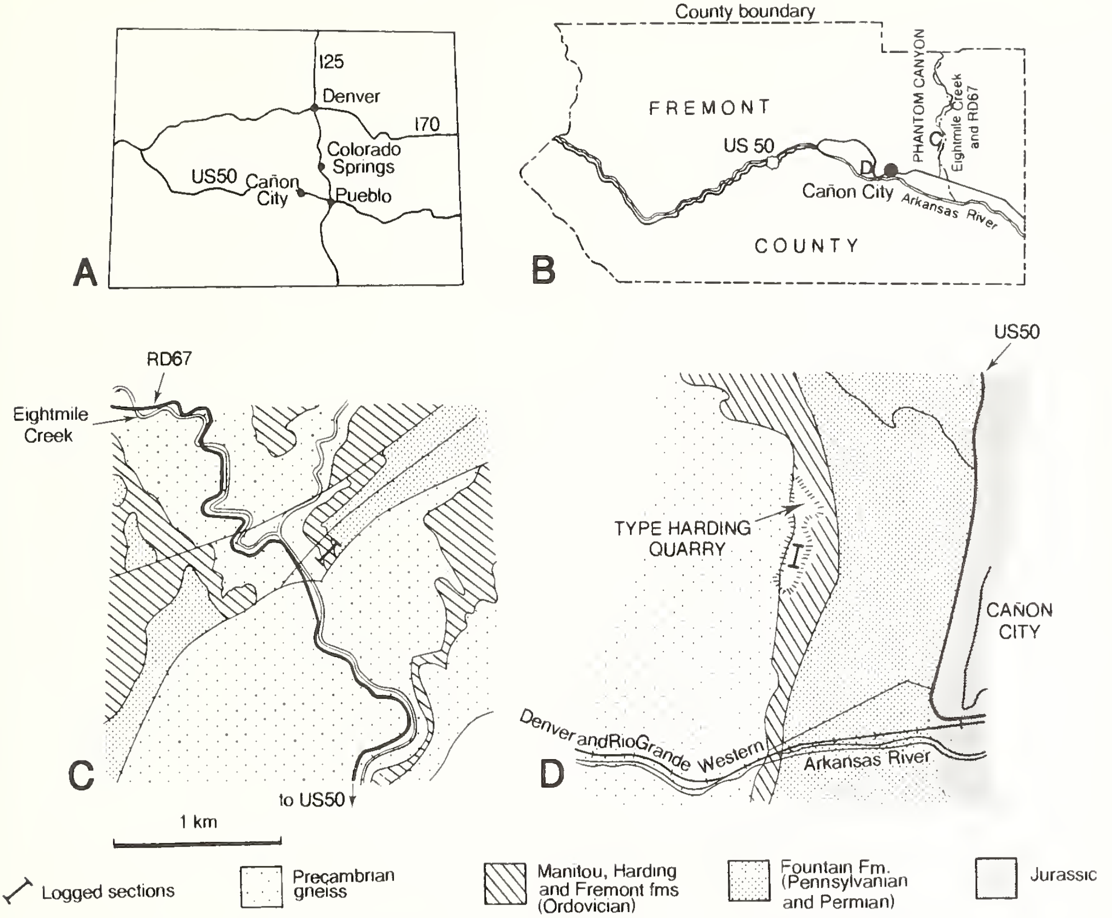
EARLY VERTEBRATE SKELETAL STRUCTURES AND CLADISTIC PHYLOGENIES

Currently accepted phylogenies propose that heterostracans are more primitive than osteostracans and Forey and Janvier (1994) predicted that bone without cells is the primitive vertebrate tissue, a point previously made by Janvier (1981, 1984). Given these hypotheses, it is important to try to establish the phylogenetic position of *Skiichthys halsteadi* as its skeletal tissues are characterized by the presence of cellular bone. The taxonomic position of *Skiichthys* is also crucial to the debate concerning the earliest occurrence of higher taxa, as well as for tissue evolution. Maisey (1988, p. 16) concluded that 'acellular bone is cladistically primitive', and stated that '…the earliest scraps of cellular bone are of uncertain affinity and consequently have no bearing on the present phylogenetic analysis'. Although Forey and Janvier (1994) concluded that cellular bone is an advanced feature, they also confused the issue by stating that 'the presence of cellular bone in the Ordovician vertebrates is an ancient trait of vertebrates' (p. 564). Blieck (1992, fig. 6) placed 'the third vertebrate of the Harding Sandstone' at the stem of clades leading to osteostracans and gnathostomes, in a stratigraphically constrained cladogram depicting early chordate relationships. It has, therefore, become imperative to describe fully the available material in order to assess phylogenetic relationships with other early vertebrates.

PREVIOUS INVESTIGATIONS OF ORDOVICIAN FISH

Examples of mineralized skeletal tissue of Ordovician fish with enclosed cell spaces are extremely rare and only those from the Harding Sandstone of Cañon City, Colorado, USA have been credited as representing cellular bone (Vaillant 1902; Stetson 1931; Ørvig 1951, 1965; Denison 1967; Smith and Hall 1990; Smith 1991). The agnathan taxa *Astraspis* and *Eriptychius* were first described from the Harding Sandstone by Walcott (1892). Subsequent histological studies have shown that the dermal denticles of these forms are characterized by acellular tissues (Bryant 1936; Ørvig 1965, 1989; Denison 1967; M. M. Smith *et al.* 1996; Sansom *et al.* 1997). Denison (1967, p. 185, fig. 26) described and figured sectioned denticles constructed of cellular 'dentine-like and bone-like tissues', characteristic of his 'Vertebrate indet. A'. Smith (1991, fig. 1C–D) identified a similar histology and figured sections of denticles of this Harding Sandstone vertebrate. Both cellular dentine and cellular bone were illustrated within the same denticle, the latter as basal flanges surrounding two, shallow, soft tissue invaginations. Neither Denison (1967) nor Smith (1991) were able to recognize these denticles macroscopically from the sectioned material of tissue retained *in situ* within the rock matrix, but Smith predicted from numerous random section planes of the denticles that the sculptured, enameloid covered crown was multi-crested or ridged and was smaller than, and eccentric to, the bony base. Denison (1967, p. 185) established that 'Vertebrate indet. A' was distinct from *Astraspis* and *Eriptychius* as it was 'constructed in part of a tissue similar to bone' but, while unable to refer it to any known group, he did conclude (1967, p. 186) that 'the mesodentine is most comparable to the superficial tissue of primitive Osteostraci'. Halstead Tarlo (1967) had independently concurred with this opinion, placing it in the Osteostraci, as a tremataspid without further discussion. Smith (1991, pp. 302–303) proposed that the species exhibited '…an early example of a primitively micromeric skeleton' and had both 'bone with osteocytes, and mesodentine with odontocytes' and was, therefore, possibly related to either the acanthodians or the osteostracans. Recently, de Ricqlès (1995, pl. 1, fig. 7) illustrated a specimen of Vertebrate indet. A 'with its base apparently ankylosed upon an aspidin'. However, similar specimens in our extensive new collections lack evidence of aspidin in the base.

Articulated Ordovician fish are extremely rare. The Harding Sandstone has yielded one partially articulated specimen of *Eriptychius americanus* Walcott (Denison 1967) and three incomplete specimens of *Astraspis desiderata* Walcott (Bryant 1936; Lehtola 1983; Elliott 1987; Sansom *et al.* 1997). Articulated specimens have also been described from Australia and Bolivia, but these offer little potential for histological work, being either sandstone moulds (*Arandaspis* and *Porophoraspis*; Ritchie and Gilbert-Tomlinson 1977) or weakly metamorphosed (*Sacabambaspis*; Gagnier *et al.*

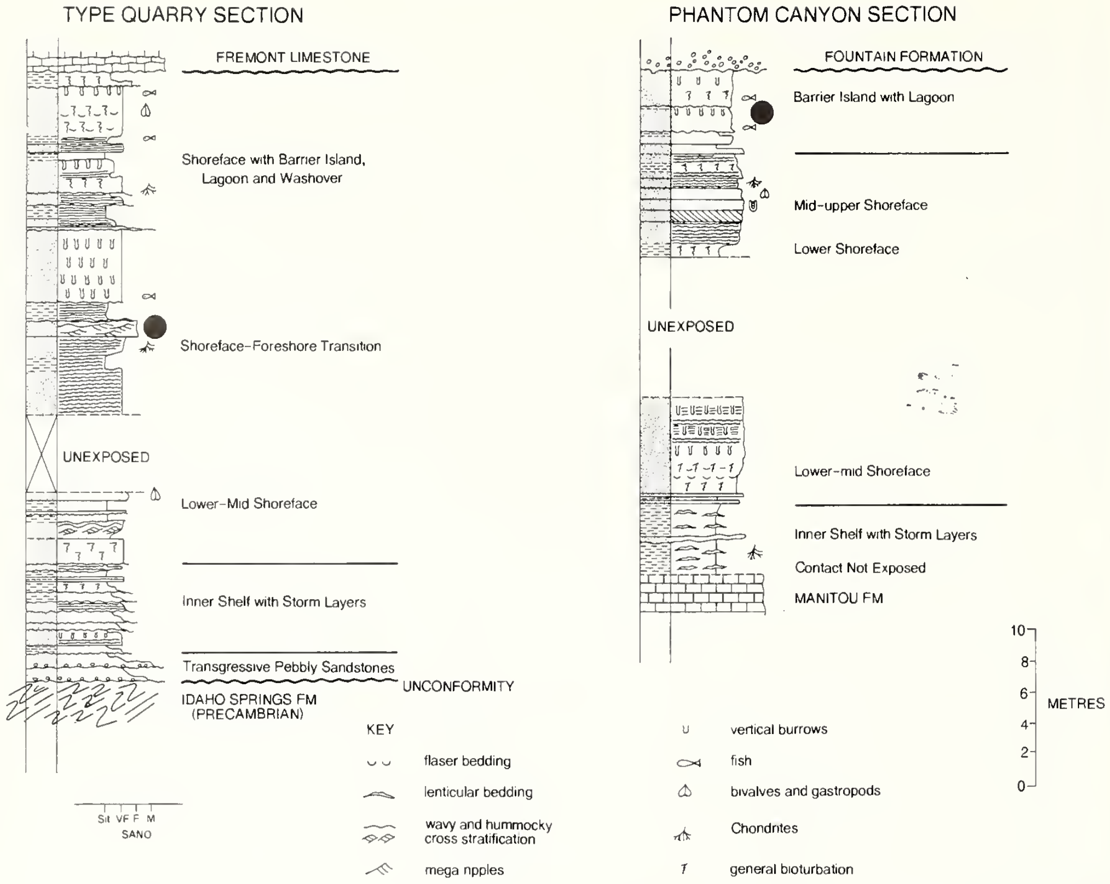


TEXT-FIG. 1. The *Skiichthys*-bearing localities. A, map of Colorado. B, map of Fremont County showing the relative locations of the Phantom Canyon section (C) and the Harding Quarry (D). C, geological sketch map showing the type section of *Skiichthys* in Phantom Canyon (adapted from Wobus *et al.* 1985). D, geological sketch map showing the type quarry for the Harding Sandstone (adapted from Taylor *et al.* 1975).

1986; Gagnier 1993). Disarticulated material, possibly related to *Arandaspis* and *Sacabambaspis*, from the Stokes Siltstone (Llanvirn) in Australia, offers some information on the arrangement of the tissues and their morphology (Gavin Young, pers. comm.), but definitive statements are precluded because of diagenetic alteration. The paucity of articulated remains of Ordovician fish with well-preserved histological features severely restricts the number of characters with which phylogenetic analyses may be made.

TYPE LOCALITY AND STRATIGRAPHY

The Harding Sandstone has its type area around Cañon City, Fremont County, east central Colorado (Text-fig. 1). The unit is dated on the basis of its locally abundant conodont fauna, which places the unit in the early Franklinian (*Phragmodus undatus* Chronozone of Sweet 1984) and correlatable with the lower middle Caradoc in British terms. Although the unit has sometimes been described as fluviatile (Graffin 1992) or estuarine (Fischer 1978), the overwhelming evidence, both palaeontological and sedimentological, is that virtually all of the sequence is marine (Spjeldnaes



TEXT-FIG. 2. Sedimentary logs for the Phantom Canyon section and type Harding Quarry, together with a preliminary sedimentological interpretation. Dots indicate beds known to yield *Skiichthys* specimens. Logs made and interpreted by Dr Peter Turner (University of Birmingham).

1967). In the type area, the Harding Sandstone is characterized by sandstones and siltstones, which represent five or six parasequences representing inner shelf to shoreface transitions, possibly representing part of a barrier island complex (Text-fig. 2; Turner *et al.* 1994).

The Harding Sandstone has a far more diverse fish fauna than has been hitherto documented, and a preliminary study of the palaeoecology of the unit suggests that subtly different palaeoenvironments supported disparate communities of fish. *Skiichthys halsteadi* has been recorded from the Harding Quarry and a section sampled along Phantom Canyon, 1·5 km due west and 8 km north-east of Cañon City respectively (Text-fig. 1). Our preliminary palaeoenvironmental interpretation of the horizons containing *Skiichthys* suggests that the genus lived in extremely shallow water (Text-fig. 2), close to the strandline, and formed a relatively minor part (generally less than 5 per cent.) of a community dominated by *Astraspis* and *Eriptychius*. The scales of sharks, thelodonts (figured by Sansom *et al.* 1996) and as yet unassignable fish, plus conodont elements, complete the vertebrate fauna of the whole Harding Sandstone palaeoenvironment.

Institutional abbreviation: BU, Lapworth Museum, University of Birmingham, Birmingham, UK.

SYSTEMATIC PALAEONTOLOGY

Superclass GNATHOSTOMATA Cope, 1889?
Class INCERTAE SEDIS
Order INCERTAE SEDIS
Family INCERTAE SEDIS

Genus SKIICHTHYS gen. nov.

Derivation of name. From *skia* and *ichthys* (both Greek) for phantom fish, after the type locality in Phantom Canyon, and the elusiveness of three-dimensional material.

Type species. Skiichthys halsteadi gen. et sp. nov.

Diagnosis. The diagnosis follows that of the type and only species, given below.

Skiichthys halsteadi sp. nov.

Plate 1; Text-figures 3–4

v 1967 Vertebrate indet. A Denison, p. 184, fig. 26.
v 1991 'vertebrate indeterminate A' Denison; Smith, figs 1–3.
v 1995 Vert. Indet. A, Smith *et al.*, pl. 1, figs 5–6.
v 1995 Indeterminate Vertebrate A of Denison; de Ricqlés, pl. 1, figs 1–5, 7.
v 1996 Vertebrate indet. A of Denison; M. M. Smith *et al.*, fig. 2D–F.

Derivation of name. After Beverly Halstead who inspired the histological evaluation of this material and made a considerable contribution to the debate on primitive bone-like tissues.

Type locality. Harding Sandstone, Phantom Canyon (lat. 38° 30′, long. 105° 06′), north-east of Cañon City, Colorado (Text-figs 1–2).

Holotype. Isolated scale, BU 2599.

Diagnosis. Fleur-de-lys ornamented scales with markedly flared bases, showing non-areal growth and lacking neck canals, and formed from enameloid, mesodentine and cellular bone.

Description. Minute, individual scales are ovoid, 0·18–2 mm across the base, each with a distinctive *fleur-de-lys* ornamented crown above a more extensive flared base (Text-fig. 3) and without neck canals. The small crown, eccentric on the base, has a central high ridge, flanked by two lower, sub-parallel ridges with shallow furrows between, the three together form a *fleur-de-lys* shape. Some specimens have grooved and botryoidal ornament on these diagnostic ridges (Text-fig. 3F). The ridges of the tubercle are composed of, and shaped by, enameloid, which is confined to the upper part of the tubercle (Text-fig. 4). There is no prominent, organized vascular canal system in the crown, but irregularly arranged dentine canals, possibly containing vascular tissue, predominate in some of the more central regions of the dentine (Text-fig. 4). The bases of smaller, presumably juvenile, scales often have two or more shallow, wide open, soft tissue chambers, opening on the basal surface (pulp cavities; Pl. 1, fig. 1; Text-fig. 4), but the tubercle is without an extensive pulp cavity. A few of the larger scale bases have several enclosed vascular spaces; the surrounding tissue is cellular bone. Known only from microremains, the exoskeleton is microsquamous and the crown is non-growing. The basal bone increased in area after the odontodes formed, but no new odontodes were added. Larger tesserae have not been found, nor any with multiple tubercles on the base.

The superficial, refractile layer of the crown, a type of enameloid about 20–25 μm thick, is translucent and penetrated by numerous, sub-parallel tubules of similar dimensions to those in the dentine (Pl. 1, figs 1–3; Text-fig. 4). The junctional zone at the base of the cap enameloid, where it abuts the dentine, has short, broad tubules branching into the finer tubules that traverse the enameloid to the surface. The subjacent dentine tissue is more extensive and grades into the basal bone tissue; both have cell body-sized lacunae within the tissue (Pl. 1, figs 1–3, 5; Text-fig. 4). The lacunae of the dentine are pear-shaped spaces, leading into one or two directional tubules which continue upwards into an extensive branching network of fine tubules ramifying throughout the dentine. A more concentrated network occurs in a marginal zone just below the enameloid, where some tubules continue across this junction. Faint lines occur in the coronal dentine, indicating the centripetal growth pattern of the tissue (Pl. 1, fig. 1; Smith 1991, fig. 1A–B). This tissue is most typical of mesodentine, a tissue with enclosed odontocyte lacunae and a few directional tubules, all linked by an extensive network of fine branches.

The most basal tissue, continuous with the dentine but extending beyond the base into broader flanges (Pl. 1, figs 1, 5; Text-fig. 4; Smith 1991, fig. 1C), has stellate lacunae with the points extending into canaliculi, these ramify throughout this region in an irregular arrangement linking the lacunae. Some of these canaliculi lead into the shallow cavities opening at the base, and the enclosed vascular spaces. This tissue arrangement is distinctive for the high density of osteocytic lacunae linked by a network of canaliculi, typical of true cellular bone.

All of the basal, cellular tissue has a matrix of broad fibre bundles, closely spaced and running radially from the base towards the crown (Pl. 1, fig. 4; Text-fig. 4). In many section planes, when viewed in polarized light, two sets of these fibres can be observed passing at right angles to each other (Pl. 1, fig. 6). This arrangement is regarded as comparable to the extrinsic matrix fibres of the attachment regions of bone or cementum in scales and teeth. This tissue is assumed to have served to attach these scales to the soft tissue of the dermis.

None of the specimens shows evidence of tesserae or compound scales. The basal tissue varies greatly in amount amongst the scales and has an irregular shape, but always extends beyond the area of the crown (Pl. 1, figs 1, 4). The superficial, glassy layer is thickest over the crests of the ridges, where it contributes to the surface sculpturing and tapers down over the surface of the dentine (Pl. 1, figs 1, 3; Text-fig. 4; Denison 1967, fig. 26A–B; Smith 1991, fig. 1A–C), the tubules within the enameloid are continuous with those of the dentine below, itself with a network of tubules as in mesodentine.

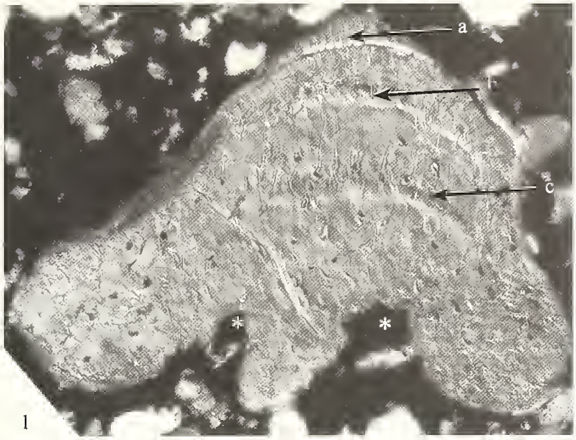
IMPLICATIONS FOR MODELS OF EVOLUTION OF THE DERMAL SKELETON AND POSSIBLE RELATIONSHIPS OF *SKIICHTHYS*

The scales of *Skiichthys* are both distinctive and remarkable for the possession of cellular bone and cellular dentine at a stratigraphically early, and morphologically simple (microsquamous), stage of skeletal organization of the dermal armour. The observation that cellular bone and cellular dentine co-occur suggests that they developed together within the odontogenic complex. In *Skiichthys* it is clear that they do not represent products of an evolutionary transition series from bone to dentine, as has been suggested previously (for reviews see Ørvig 1967, pp. 49–54; 65–79; 97–103; Smith and Hall 1990, p. 324).

In the absence of further information on the body plan of *Skiichthys*, the histology and morphology of the scales assumes a principal role in assessing the phylogenetic relationships of the taxon. The presence of mesodentine and cellular bone are of particular significance, and enable a number of primitive vertebrate groups to be excluded from this discussion.

EXPLANATION OF PLATE 1

Figs 1–6. *Skiichthys halsteadi* gen. et sp. nov.; Harding Quarry, Cañon City, Fremont County, Colorado, USA; Harding Sandstone, Caradoc. The histology of scales from random section planes of the bone bed material; figs 1–3, 5, taken in Nomarski differential interference contrast optics; figs 4, 6, taken in polarized light (polarizer N–S). 1, BU 2608; ortho-transverse vertical section of complete scale crown and partially developed base (arrows a–c show enameloid-dentine junction and two parallel growth contours of the dentine; asterisks mark the vascular cavities). 2, BU 2609; enameloid dentine junction is oblique; tubules in enameloid are continuous with those of the mesodentine; odontocyte lacunae are pear-shaped with coronally directed tubules. 3–4, BU 2610. 3, higher magnification of the crown tissue; enameloid covering with tubules; mesodentine with a marginal network extending from tubules of odontocyte lacunae below. 4, scale with more extensive base in which the direction of Sharpey's fibre bundles is shown by their birefringence as normal to the basal surface. 5, region of the base (close to asterisk in fig. 4) in which osteocytic lacunae and canaliculi are seen in addition to the Sharpey's fibre bundles. 6, BU 2611; example of an extensive scale base sectioned in a plane which shows the alternating, opposite direction of Sharpey's fibre bundles in polarized optics. Figs 1, 4, × 190; figs 2–3, 5, × 480; fig. 6, × 75.



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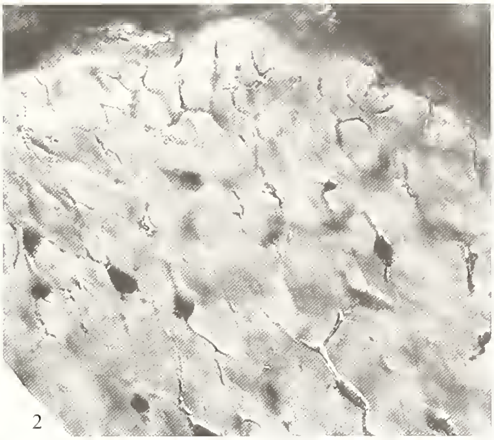

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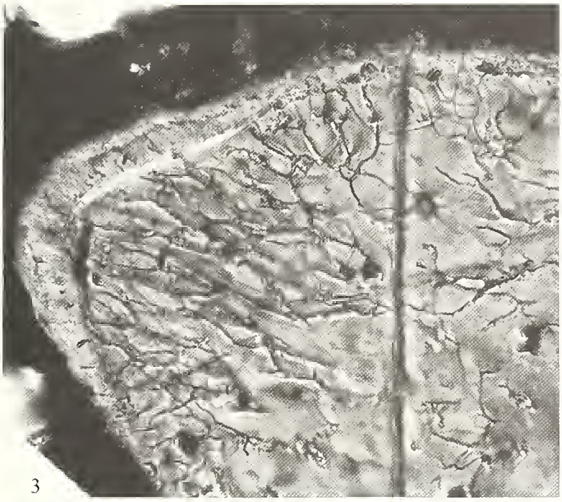

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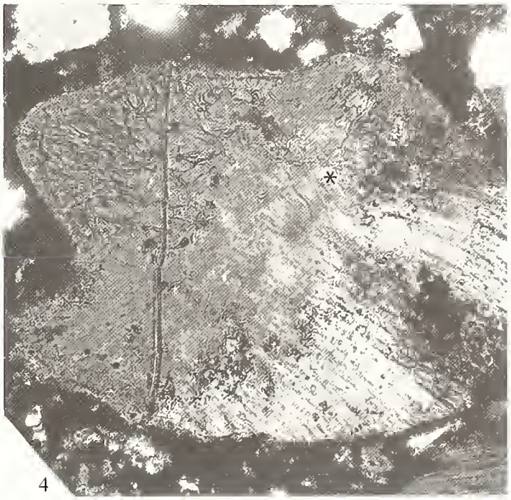

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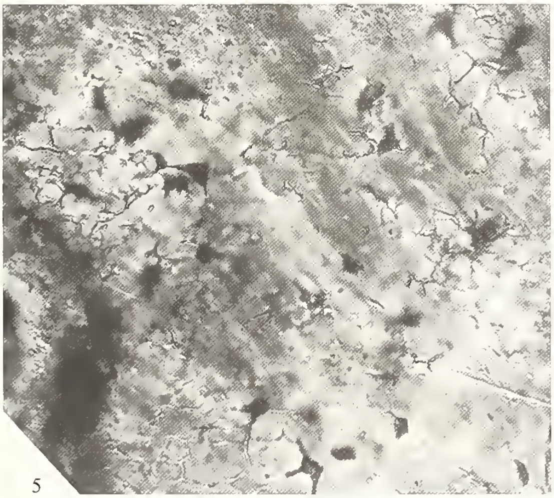

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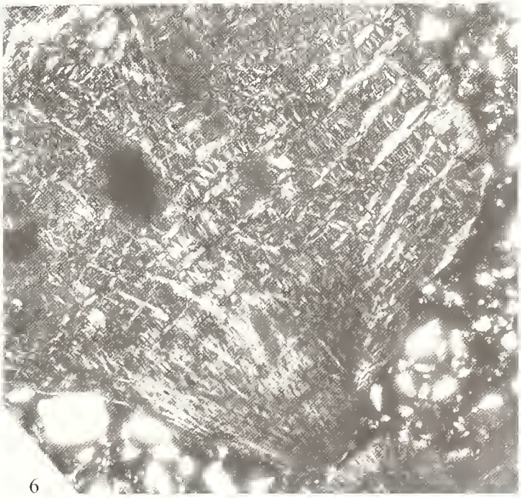

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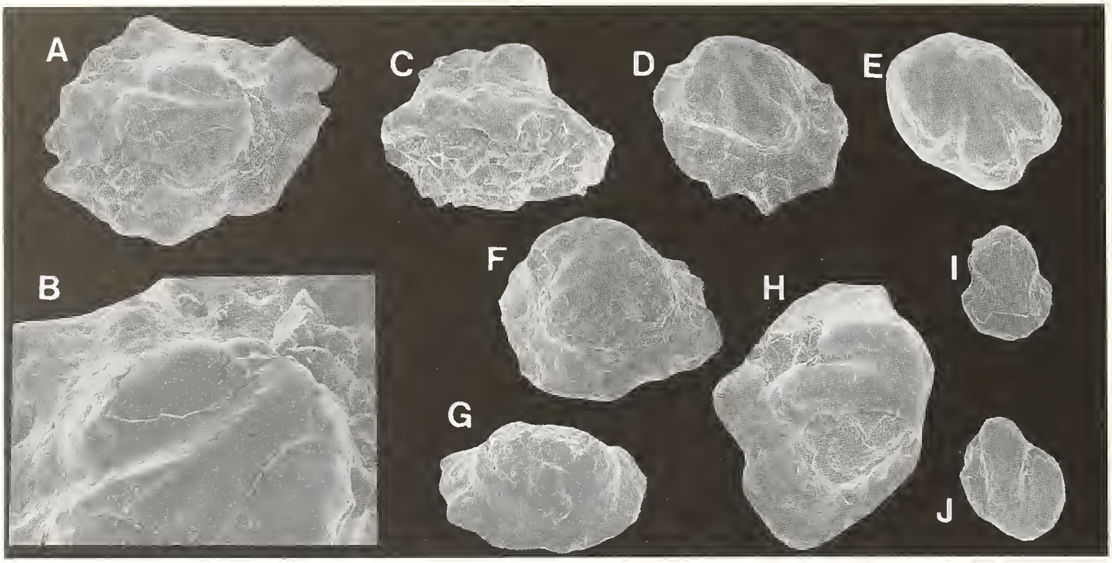
SMITH and SANSOM, *Skiichthys*

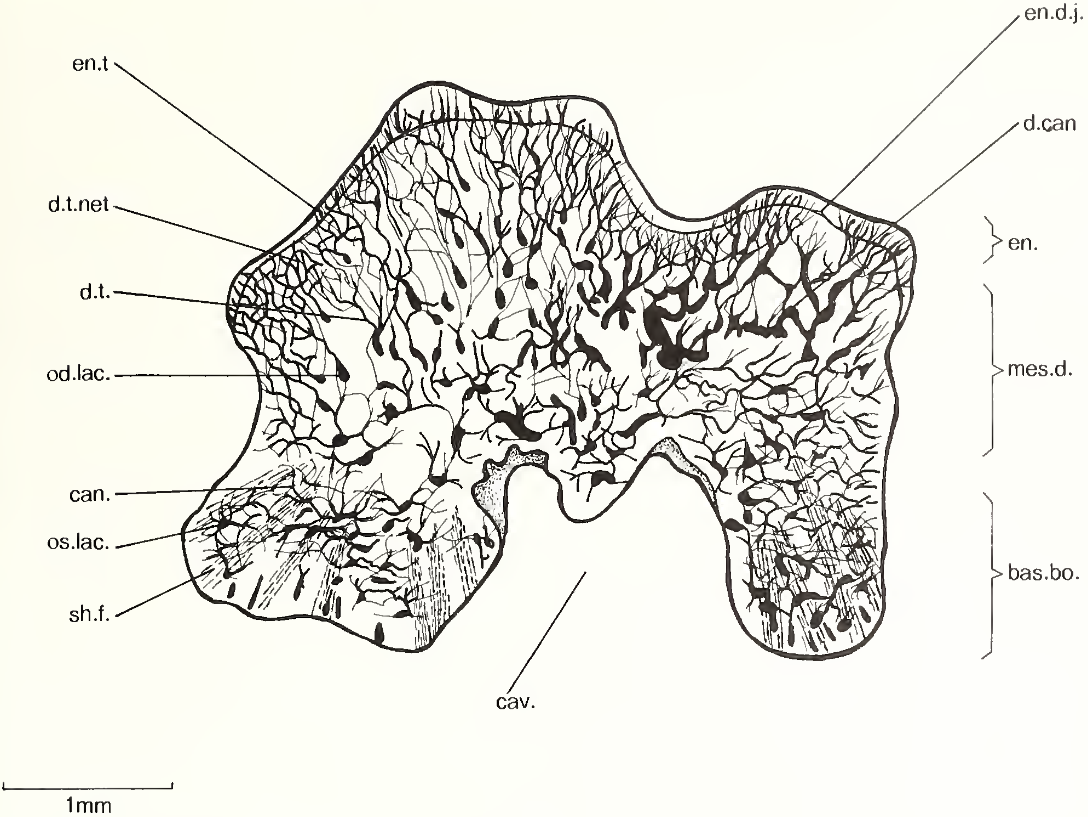


TEXT-FIG. 3. *Skiichthys halsteadi* gen. et sp. nov. A–H, Phantom Canyon, Fremont County, Colorado, USA; Harding Sandstone, Caradoc. A–B, BU 2599, holotype. A, dorsal view; B, detail of cap region where the enameloid has broken away, revealing diagenetically infilled dentine tubule network of the underlying mesodentine. C, BU 2600; lateral view. D, BU 2601; dorsal view. E, BU 2602; dorsal view of specimen with weakly developed base. F, BU 2603; dorsal view of unusual specimen showing botryoidal ornament on *fleur-de-lys* cap. G, BU 2604; dorsal view. H, BU 2605; dorsal view. I–J, Harding Quarry, Cañon City, Fremont County, Colorado, USA; Harding Sandstone, Caradoc; dorsal views of abraded specimens, typical of the preservation seen in material from the type Harding Quarry. I, BU 2606; J, BU 2607. All ×24 except B, ×56.

Ordovician pteraspidomorphs

Astraspis and *Eriptychius*, which co-occur with *Skiichthys* in the Harding Sandstone, have dermal armour formed from acellular bone (aspidin) overlain by tubercles of acellular dentine. However, it is noteworthy that the superficial enameloid of *Skiichthys* is similar to the enameloid found over stellate denticles of *Astraspis*, although it never shows the thickness developed in the larger, mushroom-shaped tubercles also seen in the latter genus (vitrodentine, Denison 1963, p. 145; durodentine, Denison 1967, p. 174). The junctional zone in *Skiichthys*, where enameloid overlies the dentine below, reveals short wide tubules giving rise to several finer branches, many of which lead to the surface of the enameloid. This is identical to the equivalent region in the tubercles of *Astraspis*, figured by Ørvig (1958, fig. 3; 1989, figs 16–18). He interpreted this junctional layer as one with scleroblast cell bodies related to the formation of the outer layer. Ørvig (1958) initially thought that this layer represented the remains of true dentine in *Astraspis*, as he regarded the main tissue of the tubercle as aspidin. Subsequently, Ørvig (1989) considered the junctional layer to be comparable to the ascending dentine canals topped by clusters of branching tubules in katoporid thelodonts and heterostracans, and to the mesodentine of early osteostracans. The junctional layer has also been figured in *Astraspis* by M. M. Smith *et al.* (1996, fig. 1B, E), and Sansom *et al.* (1997), who interpreted the wide tubule spaces as being related to the formation of enameloid, while the dentine below retained another set of cell processes, some of which continue into the enameloid.

Gagnier (1993) noted that the dermal armour of *Sacabambaspis* appeared to lack dentine. Although ovoid lacunae within the hard tissues of *Sacabambaspis* were interpreted as cell spaces, they lack cell processes and bear little resemblance to the cellular bone of *Skiichthys*.



TEXT-FIG. 4. Vertical section through the crown and base of a *Skiichthys halsteadi* gen. et sp. nov. scale, BU 2607, to show the characteristic tissue types, their arrangement and proportions. The crown is mesodentine covered by enameloid, a system of dentine canals is located centrally, and odontocyte lacunae give rise to tubules which terminate in a marginal network and also extend into the enameloid. The base has numerous osteocytic lacunae and canaliculi forming an irregular network, the matrix has many Sharpey's fibre bundles radiating from the visceral surface. Abbreviations: bas.bo., basal bone; can., canaliculi; cav., soft tissue vascular cavity; d.can., dentine canals; d.t., dentine tubules; d.t.net., dentine tubule network; en., enameloid; en.t., enameloid tubules; en.d.j., enameloid dentine junction; mes.d., mesodentine; od.lac., odontocyte lacunae; os.lac., osteocyte lacunae; sh.f., Sharpey's fibre bundles.

Thelodonts

Thelodonts are characterized by discrete, non-growing scales, with distinctive varieties of dentine. All the thelodonts have very weakly developed bases. *Sandivia melnikovi* Karatajūte-Talimaa, 1997, a loganiid thelodont from the Ashgill of Timan-Pechora Province, Russia, and an as yet un-named taxon recovered from the Harding Sandstone (Sansom *et al.* 1996) represent the known records of thelodonts from the Ordovician. Neither of these forms resembles *Skiichthys* in morphology or histological character.

Osteostracans

Denison (1967, p. 185) suggested that the mesodentine seen in *Skiichthys* was 'most comparable to the superficial tissues of primitive Osteostraci', although he did not feel that this was sufficient evidence to assign the taxon to the osteostracans. The presence of cellular bone in *Skiichthys* and the majority of osteostracans would seem to lend support to a phylogenetic relationship. However, *Skiichthys* differs from osteostracans in a number of notable features. We have yet to recover large fragmentary plates carrying the multiple tubercles that would be likely if *Skiichthys* was an osteostracan with a headshield, the preservational potential of which would be high. The scales we have recovered do not show any evidence for the development of tesserae. The osteostracans are characterized histologically by the presence of a continuous superficial layer of dentine and enameloid, containing a pore-canal system (Janvier 1996, pp. 107, 112). *Skiichthys* lacks an organized vascular system, although there are irregularly arranged canals in some areas of the mesodentine. Well-developed attachment fibres are present in *Skiichthys*, but attachment fibres have yet to be described in published accounts of osteostracan histology. In addition, there is no evidence for the presence of any endoskeletal material associated with *Skiichthys*.

The micromeric condition of *Skiichthys*, together with the absence of a well-developed pore-canal system, 'definitively characteristic of the Osteostraci' (Denison 1951, p. 200), would appear to rule out an assignment to this group.

Chondrichthyans

Ørvig (1966) has described mesodentine in the teeth and scales of an elasmobranch *Holmesella* sp. from the Upper Carboniferous of South East Kansas, USA (1966, p. 24, fig. 3B, pl. 5), and added that 'this is a retained primitive character not found in other elasmobranchs'. However, descriptions of the earliest chondrichthyans, including *Elegestolepis grossi* Karatajūte-Talimaa, 1973 from the Upper Silurian of Tuva, *Elegestolepis conica* from the Lower Silurian of Siberia (Karatajūte-Talimaa and Predtechenskyj 1995), and an as yet un-named polyodontode form from the Harding Sandstone (Sansom *et al.* 1996), show dentine with many branching wide and narrow tubules, generally lacking lacunae, and best described as 'arboriform' tubular dentine. Although some examples of mesodentine have been described in *Elegestolepis* scales (Karatajūte-Talimaa 1973, figs 2C, E, 3A–B), and a few lacunae are present in the basal tissue, they were later described as orthodentine (Karatajūte-Talimaa and Predtechenskyj 1995, fig. 8B–F) and the tissue arrangement and morphology are quite different from those of *Skiichthys*. In *Elegestolepis* the crown is non-growing but tissue was added centripetally to the pulp chamber and centrifugally to the small base.

Stratigraphically early elasmobranch scales from the Upper Lochkovian, Ellesmere Island, Northwest Territories, Canada, have been described with irregular branching dentine canals but no mesodentine, although in places there is a network of tubules. There are, however, no enclosed cell lacunae within this tissue (Vieth 1980).

Closely related to the chondrichthyans are *Mongolepis rozmanae* Karatajūte-Talimaa, Novitskaya, Rozman and Sodov 1990 and *Teslepis jucunda* Karatajūte-Talimaa and Novitskaya 1992, from the Lower Silurian of Western Mongolia. These taxa have a very distinctive crown morphology made of an atubular dentine termed lamellin. The base in the latter species is composed of bone with fusiform lacunae but lacking interconnecting canaliculi. These two species again do not have morphological or histological characters in common with *Skiichthys*; most notably their scales are formed from polyodontodes; nor do the other elasmobranch scales, discussed above, compare closely in their histology, morphology or mode of growth.

Placoderms

Mesodentine similar to that seen in *Skiichthys* has been illustrated in the rhenanid placoderm *Ohioaspis tumulosa* Wells (Gross 1973, fig. 2D, F–G). Ørvig (1975, pl. 8, fig. 1, p. 44) also figured and described mesodentine in an acanthothoracid arthrodire, *Romundina stellina* Ørvig; he commented that this is one of the few occurrences in arthrodires of a tissue similar to the mesodentine of osteostracans. Mesodentine is also present in the coronal tissue of tuberculate scales and small tesserae of *Radotina* sp. from the Lochkovian of Podolia, another micromeric acanthothoracid. These microskeletal remains, together with sections of tesserae of *Ohioaspis* and *Romundina*, have been compared with those of *Skiichthys* and the tissue mesodentine found to be similar in all (MMS and Karatajūte-Talimaa, pers. obs.). Osteocytic bone in these forms is also predominant in the middle layer. However, in the placoderm scales there is an obvious system of horizontal canals and pulp cavities, not found in *Skiichthys*, and in those of *Romundina* there is also a layer of spongy bone. Small scales and thin, non-overlapping tuberculate tesserae may be primitive for all placoderms (Denison 1978), as may be mesodentine. As with the osteostracans, *Skiichthys* may be excluded from the placoderms on the absence of any multi-tuberculate tesserae in our collections.

Acanthodians

The tissues of *Skiichthys* share a number of histological features with an undescribed acanthodian from the Middle Llandovery of the Siberian Platform (Karatajūte-Talimaa, pers. comm.) and the Climatiidae, thought to be close to the ancestral shock of Acanthodii (Denison 1979; Long 1995). These include: the presence of mesodentine in the crown (e.g. *Nostolepis* Pander; Gross 1971, figs 2E, 12F, 17M, 18B; and *Euthacanthus* Powrie; Denison 1979, fig. 10A); radially arranged extrinsic Sharpey's fibres in the basal bone; and the presence of bone and dentine with enclosed cell body lacunae interconnected by a network of canaliculi and branching tubules (seen in the undescribed Siberian genus, in *Euthacanthus* and in the ischnacanthid *Gomphonchus* Gross, 1971, fig. 22D). However, the scales of *Skiichthys* differ in not showing strong evidence of areal growth, although in *Euthacanthus* scale growth is only appositional and not superpositional.

Members of the Climatiidae retain many assumed primitive characters, and are thought to be close to the ancestral stock of the Acanthodii (Denison 1979; Long 1995). Among these primitive characters are: a head and trunk covered with small scales, none enlarged, all ornamented by three or four short, converging ridges, superficial mesodentine with no Stranggewebe and a flat base of cellular bone, a pulp-like cavity with no radial canals, and only a little overgrowth in one lateral zone. In *Euthacanthus* (Denison 1979, fig. 10A) the primordial scale is large, backwardly sloping, and added to by a single growth zone which is mainly expressed laterally. The phylogenetic significance of the lack of evidence for areal growth zones and an organized system of radial canals in *Skiichthys* could be considered as a primitive state for acanthodians. The presence of bone cell spaces (osteocytes), dentine cell spaces (odontocytes) and an interconnecting network of cell process spaces, which terminates in the enameloid, are considered as primitive characters of acanthodians, as is the absence of tubules organized into Stranggewebe (Denison 1979).

Larger scales of *Skiichthys* differ from those of all acanthodians described thus far in the presence of vascular spaces enclosed by cellular bone (not aspidin, *contra* de Riqles 1995). The lack of enclosed vascular spaces in later acanthodians either argues against a firm assignment of *Skiichthys* to this taxon, or that the presence of such a vascular system represents the most primitive state for the Acanthodii.

Micromeric condition

The radially arranged coarse fibre bundles in the base of *Skiichthys* (Pl. 1, figs 4, 6; Text-fig. 4), leading from the basal surface into the body of the scale, are similar to those seen in acanthodians (examples include *Gomphonchus* Gross, 1971, fig. 22D; *Diplacanthus* Agassiz; Denison 1979, fig. 10F; *Acanthoides* Agassiz; Denison 1979, fig. 10K), placoderms (e.g. *Ohioaspis tumulosa* Wells; Gross 1973, figs 2A, 7B) and elasmobranchs (e.g. *Holmesella* Gunnell; Ørvig 1966, fig. 2A, pl. 4). These sets of extrinsic fibres functioned as an attachment mechanism, between the scale and the soft tissue of the dermis, known in many hard tissues as Sharpey's fibres, and are a common feature of micromeric scale bases. The progressive mineralization of these attachment fibres was part of the growth process in the basal bone.

CONCLUSIONS

The firm taxonomic assignment of *Skiichthys* depends upon the recovery of articulated remains, or larger fragments, such as spines or tesserae. The available histological and morphological evidence suggests that *Skiichthys* is not an early osteostracan, but could represent a plesion of either the placoderms or acanthodians. Alternatively, *Skiichthys* may represent a new micromeric group, probably within the gnathostome clade. However, as is the case for the contemporaneous shark-like denticles described from the Harding Sandstone by Sansom *et al.* (1996), the absence of positive evidence for the presence of jaws and teeth in *Skiichthys* prevents a definitive assignment to the gnathostomes.

The dermal skeleton of *Skiichthys* is formed principally from cellular mesodentine and cellular bone. These are not the stratigraphically earliest vertebrate hard tissues, Ordovician pteraspidomorphs have acellular aspidin and tubular dentine in their dermal armour, as exemplified in *Astraspis* and *Eriptychius* from the same locality. The demonstration of the Late Cambrian *Anatolepis* Bockelie and Fortey as the earliest non-conodont vertebrate (M. P. Smith *et al.* 1996) implies that acellular tissues are primitive for vertebrates.

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ALL CHANGE AT THE CRETACEOUS–TERTIARY BOUNDARY? ECHINOIDS FROM THE MAASTRICHTIAN AND DANIAN OF THE MANGYSHLAK PENINSULA, KAZAKHSTAN

by CHARLOTTE H. JEFFERY

ABSTRACT. The Maastrichtian and Danian echinoid fauna of the Mangyshlak Peninsula, Kazakhstan is revised on the basis of new collections from three localities representing both a shallow water calcarenite facies and a deeper water chalk facies. The two chalk sections sampled have no biostratigraphically detectable breaks across the Cretaceous–Tertiary boundary.

Sixteen species in 11 genera are recognized, including one new species, *Cyclaster galei*. Of these, 13 species are found only in Maastrichtian strata. The remaining three are found only in the Danian giving an apparent species extinction rate of 100 per cent. across the Cretaceous–Tertiary boundary in Mangyshlak. However, inspection of occurrence data from localities outside Kazakhstan shows that many of these species are in fact longer ranging than the Mangyshlak occurrences alone suggest. If this global data is taken into account the species extinction rate drops to 60 per cent. and the generic extinction rate to 25 per cent. This pattern of local extinction and replacement is repeated in other Cretaceous–Tertiary sections (e.g. in Denmark and at Maastricht).

The Maastrichtian chalk of Mangyshlak contains a diverse echinoid fauna and includes some taxa indicative of shallower water conditions. In contrast, the Danian contains only a small number of exclusively deep water forms. This change in local faunal content may be explained either in terms of a facies shift from shallower to deeper water conditions or by the recolonization of shelf habitats by surviving deep water clades.

GENERATIONS of studies investigating taxonomic diversity through time have identified periods when there was a significant and rapid loss of biological diversity on a global scale. Where the loss has been of large enough geographical and taxonomic proportions, these periods have been dubbed mass extinction events. In all, five extinction events justify this rank. All five have generated a great deal of research interest, both in documenting and in postulating causes for the biological changes. The most recent mass extinction, the end-Cretaceous extinction, is probably the most comprehensively studied. Research has been particularly intensive over the past 20 years, especially since debate was stimulated by Alvarez *et al.*'s (1980) claim that iridium anomalies at the boundary were produced as a result of an extraterrestrial bolide impact.

Previous work on the Cretaceous–Tertiary boundary

Sedimentological and geochemical evidence. Research to date has followed two main avenues. The first has concentrated on the sedimentological and geochemical evidence for an impact and its location (e.g. Bhandari *et al.* 1994). Possible impact sites so far discovered include the Chicxulub crater off the coast of Mexico (Hildebrand *et al.* 1991) and another smaller site off the Indian coast (Negi *et al.* 1993). Further evidence of extraterrestrial bolide bombardment comes from the presence of shocked quartz (Officer 1990), tektites (Smit 1990) and a minimum in the osmium isotope ratio (Peucker-Ehrenbrink *et al.* 1994) in boundary sections. There has also been a great deal of speculation over the way in which the bolide impact and end-Cretaceous extinctions are linked.

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Many differing 'killing mechanisms' have been proposed. Hypotheses have included global darkness caused by debris thrown up by the impact and an associated breakdown of the food chain (Alvarez *et al.* 1980), global cooling again due to the presence of dust in the atmosphere (Pollack *et al.* 1983), and greenhouse warming produced by the volatilization of carbon dioxide from carbonate target rocks (O'Keefe and Ahrens 1989). There have also been suggestions that sulphate, originating from an impact in evaporitic deposits, may have caused acid rain (Weil 1994; Robinson 1995) and surface water acidification (D'Hondt *et al.* 1994). Impact-induced volcanism has also been proposed as a cause of the extinctions (Negi *et al.* 1993; Sutherland 1994).

Palaeontological evidence. The second approach to study of the Cretaceous–Tertiary boundary has focused on the palaeontological evidence for the magnitude and duration of the mass extinction event and how this relates to proposed extinction scenarios. To date, the documentation of biological change has followed two lines: detailed investigations of sections across the boundary, and analysis of regional or global taxonomic compilations. Both approaches have their own inherent problems.

A large amount of work documenting taxonomic change has concentrated on patterns of relative abundances of taxa within so-called complete sections across the boundary (e.g. Hansen *et al.* 1993; Keller *et al.* 1993; van Fossen *et al.* 1995), the aim being to find evidence for the rapidity and duration of the extinction event. However, there are several major problems with this approach. The first is simply that only a small number of continuous boundary sections exist and that many of these are barren of macrofossils. If research was limited to the study of these sections alone, knowledge of taxonomic change across the Cretaceous–Tertiary boundary would be severely restricted. One explanation for this paucity of boundary sections stems from the major sea-level fluctuations and consequent facies changes in the latest Cretaceous. Facies-dependent taxa disappear from the studied section giving a false extinction signal, and it is only by looking in more recent deposits elsewhere where facies similar to those below the boundary occur that the survival of these taxa can be confirmed. Even if a section appears complete and free from facies changes there may still be hiatuses 'hidden' within the section with no lithological expression, and this also can give the impression of many simultaneous extinctions. Indeed, the absence of intervals close to the boundary has been demonstrated by microfaunal studies for many of the classic 'continuous' sections across the Cretaceous–Tertiary boundary (MacLeod and Keller 1991). A further drawback encountered when working at the mm scale is that of reworking. This is particularly pertinent in microfossil studies where arguments continue as to whether fossils collected are still in their original depositional settings (MacLeod and Keller 1992).

The second line of palaeontological investigation has sought to assess the extent of diversity change regionally or globally but with far lower temporal resolution. Such studies have often drawn on data in the form of compendia of occurrences. Compilations of this type very often suffer from problems of inconsistent taxonomic usage (Wingard 1993). Taxonomic disappearances due to artefacts of nomenclature (i.e. the naming of species solely on the basis of their occurrence in a particular stratigraphical level or geographical location) produce 'pseudoextinctions'. A thorough taxonomic revision is therefore a prerequisite for studies of biological turnover. Accordingly, a taxonomic revision of all the echinoid species recorded in the literature from Maastrichtian and Paleocene deposits world-wide is currently underway. This will produce a global database with a uniform taxonomy and with each occurrence as stratigraphically constrained as possible. In order to investigate which clades survived the end-Cretaceous extinction, the data will be set into a sound phylogenetic framework. Inferences about the selectivity of echinoid survivorship at the end-Cretaceous can then be made.

Survivorship selectivity patterns. Despite the volume of work that has been published on the end-Cretaceous mass extinction, relatively little is known in detail about how the marine benthic macrofauna was affected, in terms of both geographical and biological selectivity patterns. Work to date has concentrated on molluscan faunas with varying degrees of extinction selectivity recognized by different workers. No latitudinal bias in extinction intensity has been found among the molluscan groups studied, but only by excluding rudists from the analysis (Raup and Jablonski 1993). This is in contrast to recent microfaunal studies which show a correlation between high latitudes and lower extinction intensities (Keller *et al.* 1993; Elliot *et al.* 1994). However, geographically widespread taxa were less affected over this time period than those with narrow geographical ranges (Jablonski 1986; Jablonski and Raup 1995). Sheehan and Hansen (1986) and Jablonski and Raup (1995) have recorded differences in extinction intensity among bivalve feeding types. In both studies, deposit feeders showed significantly lower extinction rates than did suspension feeders. However, this low overall rate is due to extremely low extinction levels in just two groups, Nuculoida and Lucinoidea (Jablonski and Raup 1995). The preferential survivorship exhibited by these taxa is thus attributable to factors other than, or in addition to feeding strategy (Levinton 1996). Some studies have recorded higher rates of extinction among infaunal and semi-infaunal organisms (e.g. Gallagher 1991). This result is not corroborated by Jablonski and Raup (1995) but it should be noted that rudists were again excluded from their analysis. It has also been suggested that taxa with a planktotrophic mode of larval development fared badly over the Cretaceous–Tertiary boundary (Gallagher 1991). In contrast, Jablonski (1986) recorded similar levels of extinction in gastropods across the Cretaceous–Tertiary boundary regardless of developmental strategy. These examples clearly demonstrate the lack of consensus so far recorded in survival selectivity patterns at this boundary.

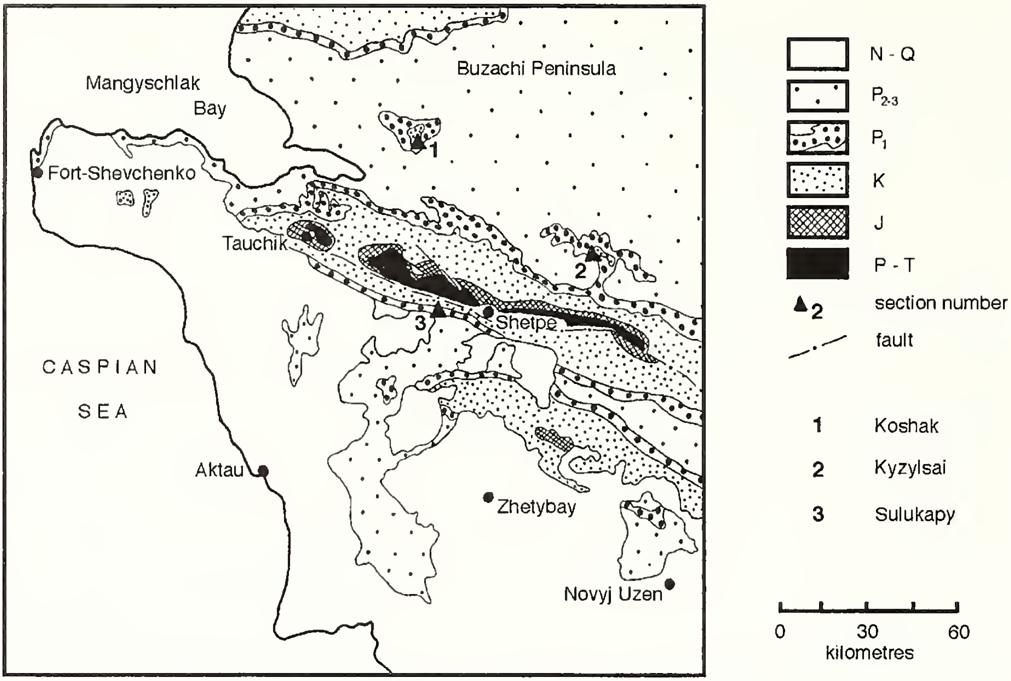
Why study echinoids at the Cretaceous–Tertiary boundary?

Research into other groups of marine benthic macrofauna is necessary if patterns of selectivity are to be clarified. Echinoids are perfect for this type of study: they form an important and diverse component of the marine benthos both before and after the extinction, with some clades surviving; and they are morphologically complex, making them relatively simple to classify taxonomically and phylogenetically. Correlation between morphology and palaeobiology is also good (e.g. Kanazawa 1992), enabling survivorship selectivity of key biological traits to be investigated. Due to a high preservation potential, the fossil record of post-Palaeozoic echinoids is good especially amongst the irregulars (Kier 1977) and fossil echinoids are abundant in differing facies types from the poles to the equator in late Cretaceous and early Tertiary strata. Despite this, the echinoids have yet to be studied extensively outside Russia (e.g. Poslavskaya and Moskvin 1960; Moskvin *et al.* 1980; Moskvin 1989).

Why study the Mangyshlak Peninsula?

The Mangyshlak Peninsula of Kazakhstan is one of only a few localities worldwide where sections without detectable breaks across the Cretaceous–Tertiary boundary contain preserved macrofauna. The other ‘complete’ sections where echinoid faunas are preserved represent different palaeolatitudes and in some cases depositional environments. Deposits in Denmark, Belgium and the Netherlands have a well-constrained stratigraphy and represent both deep- and shallow-water shelf deposition in northern temperate palaeolatitudes (Scotese *et al.* 1988). Sediments accumulated in southern temperate latitudes are represented by fossiliferous sections in Madagascar, but unfortunately there has been very little recent research in this area and detailed stratigraphical work on these sections is yet to be done. Sections across the Cretaceous–Tertiary boundary which represent deposition in the palaeotropics are known from Algeria (Amard *et al.* 1981). However, accurate dating of these sedimentologically undifferentiated sections is exceptionally difficult because of sparse microfossil data and the presence of only a single ammonite species.

In fact, no widely applicable ammonite zonation exists for the Maastrichtian (Hancock *et al.* 1992; Kennedy and Henderson 1993) and the two most widely used biostratigraphical schemes for this stage are based on belemnites (see Christensen 1990) and planktic foraminifera (e.g. Caron 1985). Use of the belemnite scale is restricted to north-west Europe and parts of the former Soviet



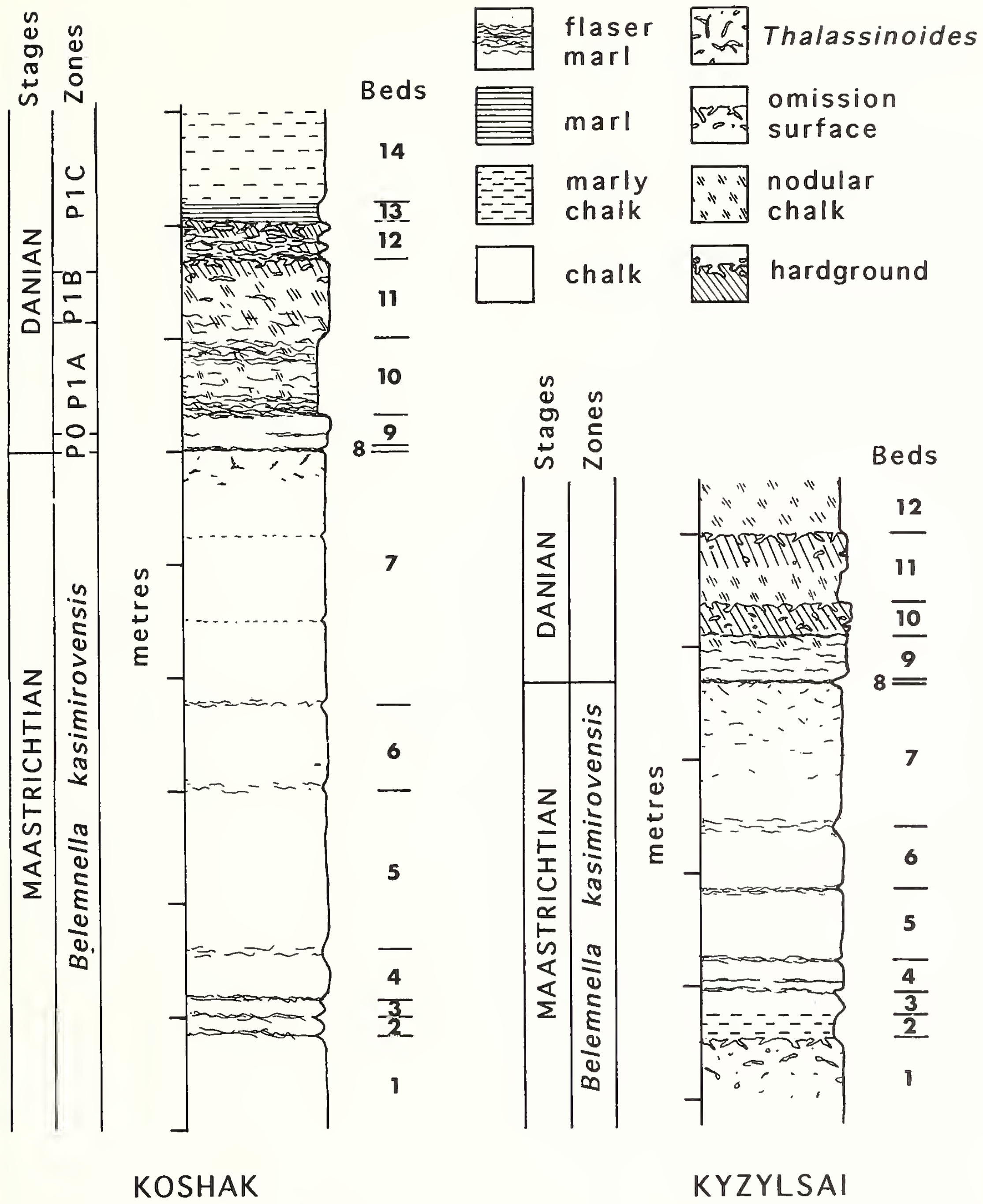
TEXT-FIG. 1. Map of the Mangyshlak Peninsula, Kazakhstan showing the location of the three sections studied. Abbreviations: N–Q, Neogene–Quaternary; P_{2-3}, Eocene–Oligocene; P_1, Paleocene; K, Cretaceous; J, Jurassic; P–T, Permo–Trias.

Union (boreal region) whilst the planktonic foraminiferal zonation is essentially Tethyan. As yet, no direct correlation between the two schemes exists. However, it is known that the Campanian–Maastrichtian boundary as defined by planktonic foraminifera is older than that based on belemnites. In addition, it has been suggested that the Lower/Upper Maastrichtian boundary in the belemnite scheme lies close to the base of the *Abathomphalus mayaroensis* Zone (Kennedy and Henderson 1993). The four-fold division of the Maastrichtian based on belemnites (Christensen 1979) is used throughout this paper for discussion purposes. All the Maastrichtian echinoids described here were collected from the latest Maastrichtian *Belemnella casimirovensis* Zone which, if the assertion of Kennedy and Henderson (1993) is correct, lies within the *A. mayaroensis* Zone.

The Mangyshlak sections have been well dated on the basis of abundant micropalaeontological data. Like the Danish, Belgian and Dutch sections, they represent shelf deposition in northern temperate latitudes. However, the Mangyshlak Peninsula lies much further to the east and at the time of sediment deposition was situated almost in the Paratethys (see Scotese *et al.* 1988). Thus sections here show a somewhat different faunal composition from those in north-west Europe. To date, all the taxonomic work on echinoids from this area has been published in Russian. Standardization with European taxonomy is essential if information on echinoids is to be integrated into a global database.

LOCALITIES AND STRATIGRAPHY

The Mangyshlak Peninsula is situated on the north-east side of the Caspian Sea, 80–100 km north-east of the city of Aktau. A group of three Permo-Triassic inliers form hills running north-north-east–south-south-west along the peninsula. These inliers are surrounded by a periclinal region of Jurassic, Cretaceous and Paleogene strata (Text-fig. 1). The region is semi-arid and provides abundant natural exposures of fossiliferous Cretaceous and Tertiary strata (Naidin 1987). In the



TEXT-FIG. 2. Lithological successions across the Maastrichtian–Danian boundary at Koshak and Kyzylsai (by A. S. Gale). The planktic foraminiferan zones at Koshak were determined by Alfonso Pardo (pers. comm.).

core of the pericline (Sulukapy), close to the outcrops of Permo-Trias, latest Cretaceous and earliest Paleocene sediments were deposited as shallow-water calcarenite facies. Northwards, the succession passes into deeper water chalk facies, which are exposed at Koshak and Kyzyslai.

The material described herein was collected by A. S. Gale, D. J. Ward and J. M. Hancock in May 1994 during an international field symposium on the Cretaceous organized by Russian and Kazakh geologists and led by Professor D. P. Naidin.

Koshak (44° 36′ 55″ N 51° 36′ 45″ E) (Text-fig. 2)

The section at Koshak Hill comprises dry gullies (lower part) and a cliff (upper part) and exposes a total of nearly 20 m of Maastrichtian and 18 m of Paleocene strata. The section was described by Naidin *et al.* (1982) and Naidin (1987). Material for the present work was collected from the lower part of the Maastrichtian section, and from the 9 m straddling the Cretaceous–Tertiary boundary (Text-fig. 2).

The Maastrichtian is developed in a fine white chalk facies, and displays marked rhythmicity on a decimetre scale, probably representing climatic cyclicity in the Milankovitch band. Couplets are defined by burrowed omission surfaces which rest on white chalk, overlain by flaser marl seams. The entire section falls within the latest Maastrichtian *Belemnella casimirovensis* Zone (upper Upper Maastrichtian in the German sense).

The Maastrichtian chalk is overlain by a 10–20 mm thick flasered grey marl (Bed 8) which rests on an omission surface. Nazarov *et al.* (1983) recorded an iridium 'spike' within this bed. *Thalassinoides* burrows (idiomorphic, omission-suite) which contain a dark marl fill, penetrate 0·3 m down into the Maastrichtian Bed 7. Bed 9 comprises firm white chalk containing discontinuous flaser marl partings and is rather unfossiliferous. Bed 10 is a chalk containing many thin wispy flaser marls and abundant echinoids. Beds 11 and 12 are pinkish-grey chalkstone containing abundant debris of calcite fossils and underlie a sharply defined hardground which does not show evidence of boring. Beds 13 and 14 are yellow and marly. Planktic foraminiferan zones were determined by Alfonso Pardo (pers. comm.), and show the Early Danian to be thin but completely represented (P0–P1C). It is not presently possible to determine if any Maastrichtian is missing at Koshak, although the presence of a burrowed omission surface immediately beneath the Danian is suggestive of a minor break at least.

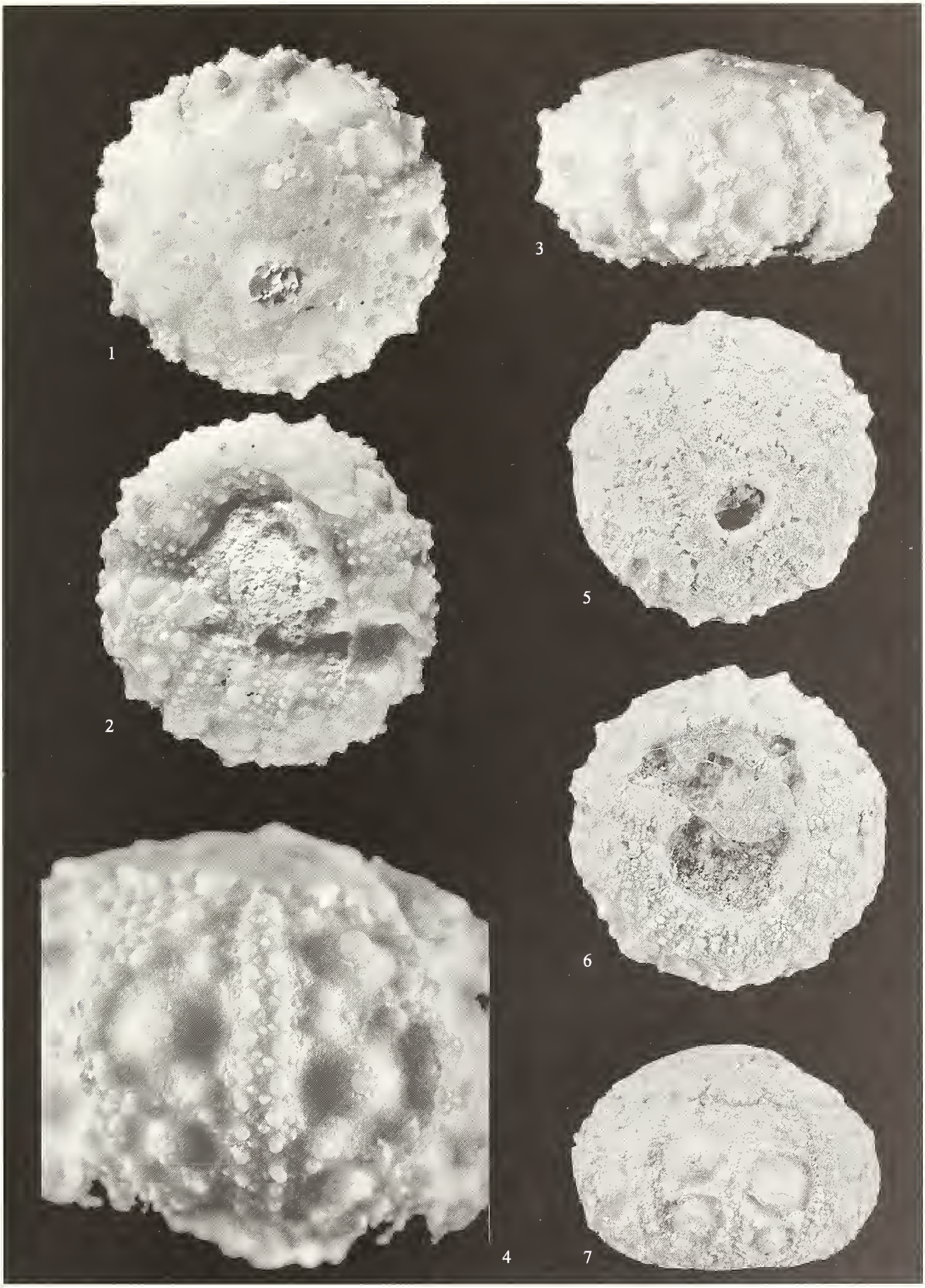
Kyzylsai (Text-fig. 2)

This remote section, exposing approximately 45 m of Maastrichtian chalk and 35 m of Danian chalk and calcarenites, was described by Naidin *et al.* (1982). The upper part of the succession straddling the Cretaceous–Tertiary contact was measured by ASG in 1994 and is shown in Text-figure 2. As at Koshak, the Maastrichtian *B. casimirovensis* Zone is represented by white nannofossil chalks (Beds 1–7) containing flaser marls and an omission surface. The boundary marl is thin and flasered (Bed 8) and is underlain by an omission surface; small limonitized burrows are abundant in the upper 0·65 m of the Maastrichtian. Bed 9 is a chalk containing flaser marls and abundant echinoids, and is overlain by two yellow-pink hardgrounds (Beds 10–11). I have no microfaunal data for this section.

EXPLANATION OF PLATE 1

Figs 1–7. *Salenia belgica* Lambert, 1897; Upper Maastrichtian, Mangyshlak, Kazakhstan. 1–3, BMNH EE5624; 1·0 m below Cretaceous–Tertiary boundary, Kyzylsai. 1, apical view; 2, oral view; 3, lateral view; all ×4, BMNH EE5623; 1·8 m below Cretaceous–Tertiary boundary, Kyzylsai; detail of ambulacrum in lateral view; ×7. 5–7, BMNH EE5629; middle *B. casimirovensis* Zone, Sulukapy. 5, apical view; 6, oral view; 7, lateral view; all ×4.

PLATE 1



JEFFERY, *Salenia*

Sulukapy (44° 08′ 27″ N 51° 54′ 57″ E)

The Late Maastrichtian succession at Sulukapy is exposed where a small stream cuts the Maastrichtian–Danian scarp obliquely. The *B. casimirovensis* Zone (29 m thick) is here developed as a massive calcarenite, a shallow water facies which contrasts strikingly with the chalks at Koshak and Kyzylsai. This facies accumulated over the relatively shallow basement of the Aktau Ridge. The fauna is dominated by belemnites (the zonal species), oysters and echinoids. The contact with the overlying Danian was determined biostratigraphically in the field by finding the upper limit of belemnite records. A sedimentary hiatus is not visible. Echinoids were collected from 10 to 20 m below the Cretaceous–Tertiary boundary.

Institutional abbreviation. BMNH: The Natural History Museum, London.

SYSTEMATIC PALAEONTOLOGY

Order CALYCINA Gregory, 1900
Family SALENIIDAE Agassiz, 1838

Genus SALENIA Gray, 1835

Type species. Salenia scutigera Goldfuss, 1829, by monotypy.

Salenia belgica Lambert, 1897

Plate 1, figures 1–7; Text-figures 3C–D, 4A

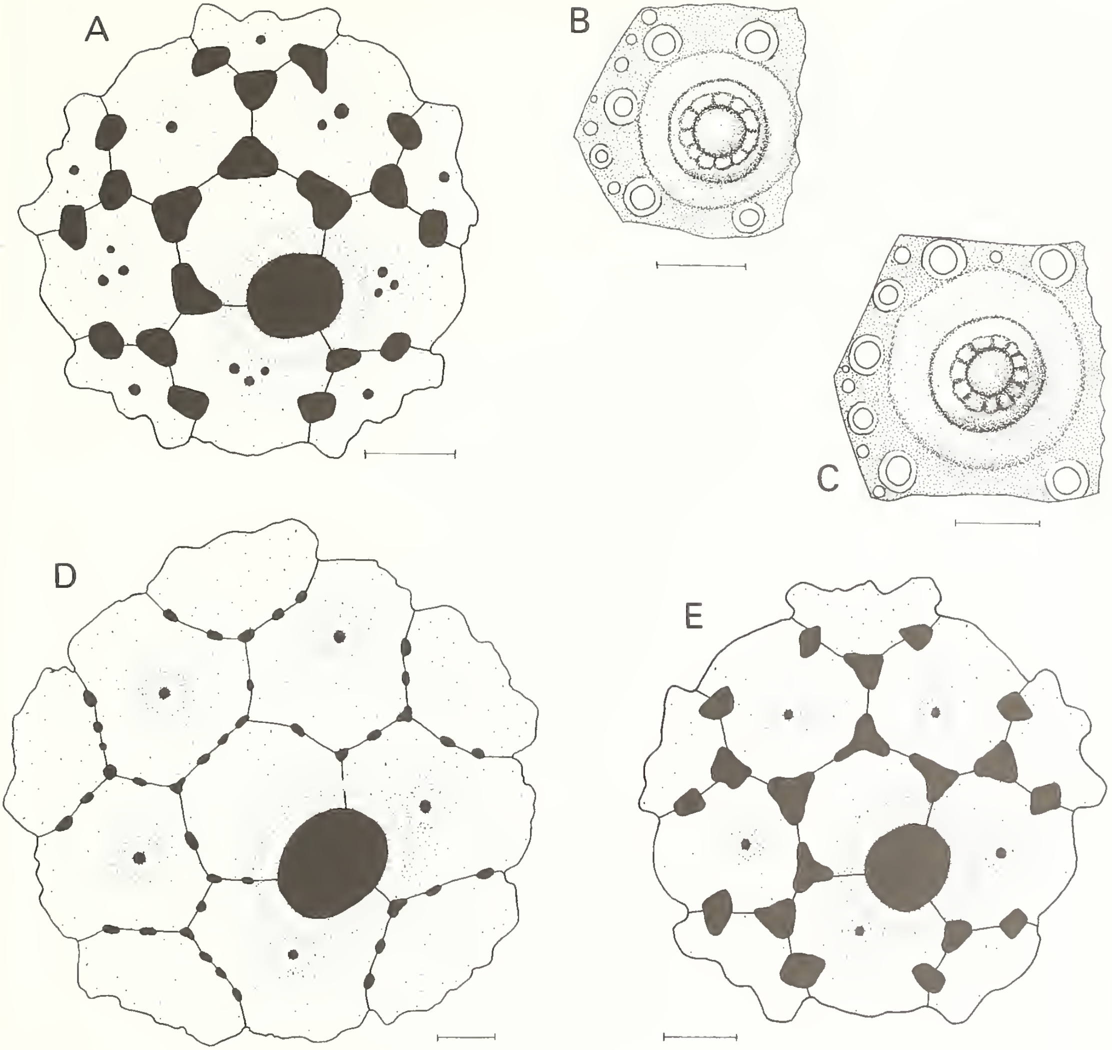
1897	*Salenia belgica* Lambert, p. 150, pl. 3, figs 1–6.
1911	*Salenia belgica* Lambert; Lambert and Thiéry, p. 211.
1979	*Salenia belgica* Lambert; Geys, p. 316 (*pars*), figs 11.3–6.
1982	*Salenia minima* Geys (*non* Desor), p. 266, pl. 29, figs 1–4.
non 1983	*Salenia belgica* Lambert; Kutscher, p. 892, pl. 1, figs 2, 5; pl. 2, fig. 1; pl. 4, figs 3–8 [= *Salenia hagenowi* Nestler].
1987	*Salenia belgica* Lambert; van der Ham *et al.*, p. 21, pl. 2, fig. 2.
1988	*Salenia belgica* Lambert; van der Ham, p. 139, pl. 3, figs 1–4.

Material. Four specimens: BMNH EE5623–EE5624, EE5628–EE5629.

Occurrence. Upper Maastrichtian strata, 1·0–1·8 m below the Cretaceous–Tertiary boundary at Kyzylsai and middle *B. casimirovensis* Zone of Sulukapy, Mangyshlak, Kazakhstan. Elsewhere, the species is recorded from the early Danian of Limburg, the Netherlands and the Mons Basin, Belgium.

Description. Test diameter 13·3–16·4 mm and height 8·5–11·2 mm (64–69 per cent. of test diameter). The ambitus is at mid-height with the test smoothly rounded above and below. The test has broad and flat upper and lower surfaces with the apical disc only slightly convex.

Ambulacra are narrow (13–14 per cent. of test diameter at the ambitus) and almost straight. The plating is predominantly bigeminate with occasional unigeminate plates near the ambitus (Text-fig. 4A). Ambulacral pores are uniserial throughout and are small, well spaced and obliquely positioned. The primary tubercles are uniformly large from the apex to the peristome although they are not contiguous. There are 15 primary tubercles and 24 or 25 pore-pairs per column at 13·3 mm diameter rising to 16 or 17 primary tubercles and 26 or 27 pore-pairs at 16 mm diameter. Smaller secondary tubercles are developed perradially and these form a central zigzag line between the rows of primary tubercles. Sparse miliary tubercles are also present on some plates. The tuberculate zone occupies 67 per cent. of ambulacral width.



TEXT-FIG. 3. *Camera lucida* drawings of *Salenia pygmaea* von Hagenow, 1840, *Salenia belgica* Lambert, 1897 and *Salenia anthophora* Müller, 1846. A–B, *Salenia pygmaea*; BMNH EE5620. A, apical disc; B, single ambital interambulacral plate. C–D, *Salenia belgica*. C, BMNH EE5623; single ambital interambulacral plate. D, BMNH EE5624; apical disc. E, *Salenia anthophora*; BMNH EE5630; apical disc. A and E, scale bars represent 2 mm. B–D, scale bars represent 1 mm.

Interambulacra are approximately three times as wide as ambulacra (41–44 per cent. of test diameter at the ambitus). There are five interambulacral plates per column and all except the most adapical plate carry a fully formed primary tubercle. The primary interambulacral tubercles are large with broad areoles which are confluent throughout, although they decrease in size dramatically towards the peristome. Each primary tubercle is surrounded by seven widely spaced smaller tubercles (Text-fig. 3C). The interradial zone is fairly narrow containing only a few scattered miliary tubercles.

The apical disc is approximately circular in outline, but with the ocular plates protruding slightly beyond the genital plates. There are notches at the margin of the disc between ocular and genital plates. Ocular plate I is always exsert. The disc is 9·4 mm to 12·2 mm in diameter (69–74 per cent. of test diameter) and is fairly thin, although clearly standing above the coronal plates. It is almost flat, although raised a little towards the periproct where there is a distinct rim. The surface of the disc appears smooth, but fine striated ornamentation is apparent under the microscope. Small sutural pits are developed at all triple junctions and additionally at points in between (Text-fig. 3D). Pores are centrally positioned on the genital plates and are surrounded by raised rims. The periproct is almost circular to oval with its longest diameter 13–17 per cent. of test diameter.

The peristome is 38–39 per cent. of the test diameter across. It is very slightly sunken and has small and insignificant buccal slits.

Remarks. This is the first Maastrichtian record of this species despite Geys' (1979) claim that the species is also found in the Maastrichtian of Belgium. The Belgian strata in which *S. belgica* occurs are almost certainly Danian (van der Ham, 1988, p. 139). Despite the slight difference in age between the specimens described here and those already recorded, there are no significant morphological differences.

This species is very similar in overall appearance to *S. hagenowi* Nestler from the Lower Maastrichtian of Denmark and the Isle of Rügen. However, *S. hagenowi* has a more distinctly sculptured apical disc with corrugation towards the margins of the plates, more obvious sutural pits along plate boundaries, and the disc margin is markedly indented at the sutures between the plates.

Salenia pygmaea von Hagenow, 1840

Plate 2, figures 1–4; Text-figures 3A–B, 4B

1840	*Salenia pygmaea* von Hagenow, p. 650, pl. 9, fig. 4.
1911	*Salenia pygmaea* von Hagenow; Lambert and Thiéry, p. 211.
1928	*Salenia pygmaea* von Hagenow; Krenkel, p. 29, pl. 3, figs 14–15.
non 1928	*Salenia pygmaea* von Hagenow; Ravn, p. 41, pl. 5, figs 1–2 [= small specimens of *Salenia anthophora* or *S. selandica*].
1965	*Salenidia pygmaea* von Hagenow; Nestler, p. 982, pls 1–3; pl. 4, figs 1–3.
1973	*Salenidia pygmaea* von Hagenow; Kutscher, p. 111, figs 11–12.
1983	*Salenidia pygmaea* von Hagenow; Kutscher, p. 889, pl. 1, fig. 3; pl. 2, figs 7–11.

Material. Three specimens: BMNH EE5620–EE5622.

Occurrence. Upper Maastrichtian strata, 0·5–2·5 m below the Cretaceous–Tertiary boundary at Kyzylsai, Mangyshlak, Kazakhstan. This species is also recorded from the lower Maastrichtian of the Isle of Rügen, northern Germany.

Description. Test diameter 10·4–13·2 mm and height 6·6–8·6 mm (61–64 per cent. of test diameter). The ambitus lies at approximately 40 per cent of test height from the base and the test is smoothly rounded both above and below. The oral surface is broad and flat whilst the apical surface is somewhat domed (Pl. 2, fig. 3).

The ambulacra are narrow (13–16 per cent. of test diameter at the ambitus) and are approximately straight although becoming slightly sinuous towards the apex. Plating is unigeminate throughout and pore-pairs are arranged in a single column from apex to mouth (Text-fig. 4B). The pore-pairs are well spaced and set very obliquely, becoming smaller on the lower surface. Primary tubercles diminish in size both adorally and adapically away from the ambitus, although they form a fairly contiguous straight line throughout. There are

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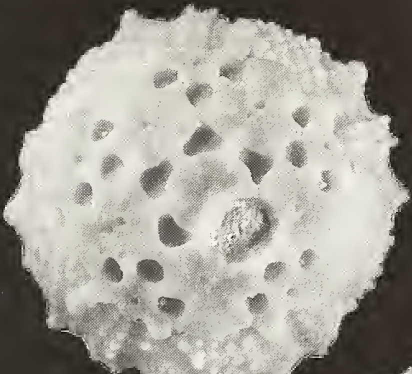
EXPLANATION OF PLATE 2

Figs 1–4. *Salenia pygmaea* von Hagenow, 1840; BMNH EE5621; Upper Maastrichtian, 0·5 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, detail of ambulacrum in lateral view. 1–3, ×4; 4, ×16.

Figs 5–6. *Salenia anthophora* Müller, 1846; BMNH EE5630; Upper Maastrichtian, middle *B. casimirovensis* Zone, Sulukapy, Mangyshlak, Kazakhstan. 5, apical view; 6, lateral view; both ×3.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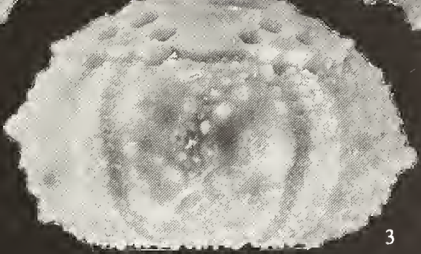
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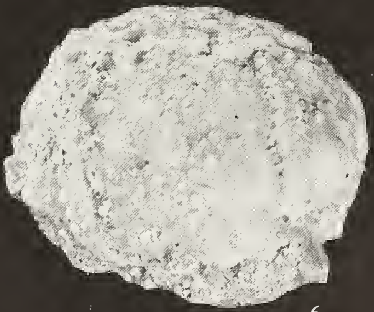
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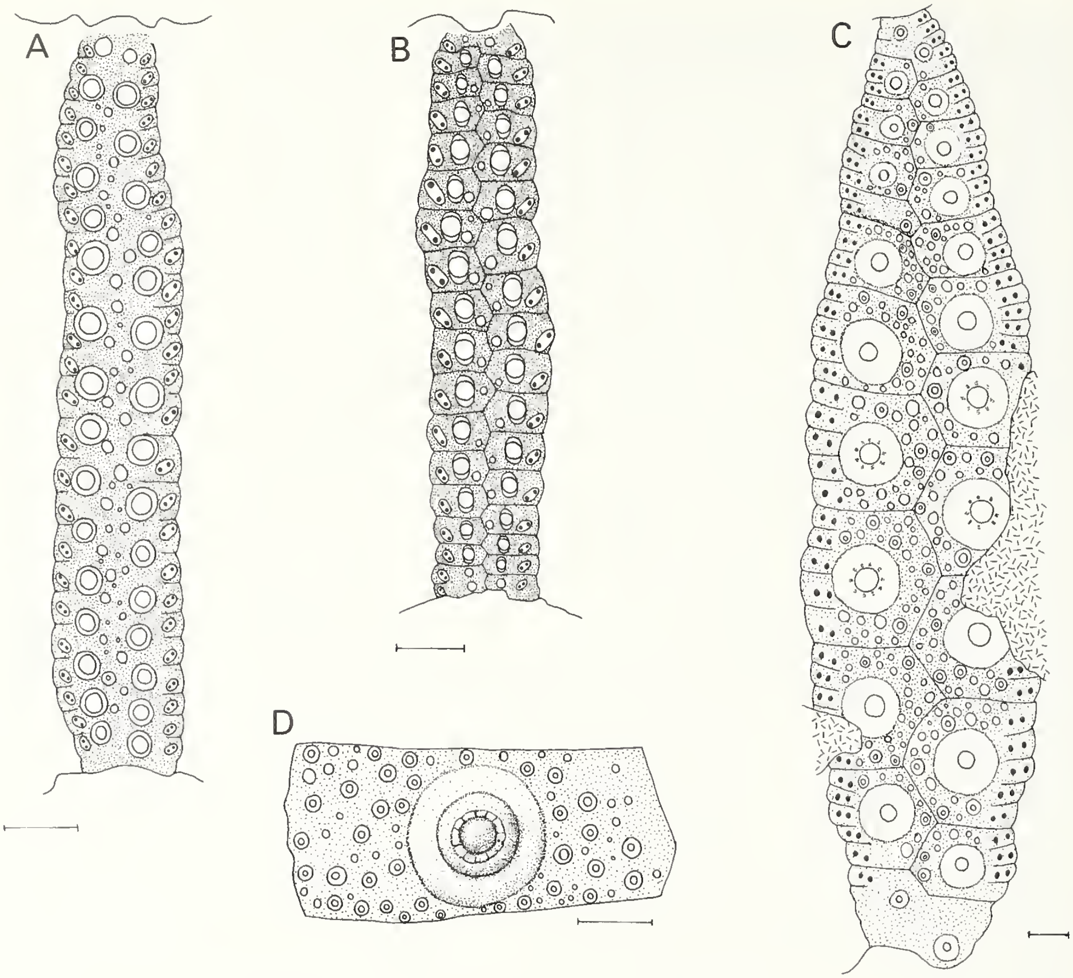

TEXT-FIG. 4. *Camera lucida* drawings of *Salenia belgica* Lambert, 1897, *Salenia pygmaea* von Hagenow, 1840 and *Micropsis* cf. *leridensis* Cotteau, 1856. A, *Salenia belgica*; BMNH EE5623; ambulacral plating. B, *Salenia pygmaea*; BMNH EE5621; ambulacral plating. C–D, *Micropsis* cf. *leridensis*; BMNH EE5631; C, ambulacral plating; D, single interambulacral plate. Scale bars represent 1 mm.

16–18 primary tubercles and 17–19 pore-pairs per column in the ambulacra. Small secondary tubercles are developed perradially and form a zigzag line between the primary tubercles. The tuberculate zone covers 62 per cent. of the ambulacral width.

The interambulacra are 2·7 to 3·2 times wider than the ambulacra (39–43 per cent. of test diameter at the ambitus). There are four interambulacral primary tubercles per column, although the most adapical plate does not carry a fully developed primary tubercle. The primary tubercles are largest at the ambitus and diminish in size substantially towards the mouth. They have broad areoles although these are not confluent. Five well spaced scrobicular tubercles surround the areole of the primary tubercles (Text-fig. 3B) and beyond these is a fairly broad interradial zone with secondary tubercles two abreast and additional scattered miliaries.

The apical disc is approximately circular in outline although with the ocular plates protruding distinctly beyond the genital plates. It measures 77–82 per cent. of test diameter. The disc is fairly thin although obviously elevated above the surrounding coronal plates. The ocular plates are 'bat-shaped' with a distinct central protrusion. Large, subangular sutural pits are developed at all triple junction points and at mid-points where ocular and genital plates are adjacent (Text-fig. 3A). Ocular plate I is exsert in all specimens. The genital plates are slightly sunken centrally where the genital pores lie without distinct rims. Near to each genital pore are two other distinct pits. Pits are also visible at the centres of the ocular plates and the suranal plate. The plates appear smooth but under the microscope show faint radial striations from the sutural pits. The surface is also finely granulated. The periproct is oval with its major axis 14–17 per cent. of test diameter. It is surrounded by a distinct elevated rim.

The peristome measures 77–81 per cent. of test diameter and is slightly sunken. Small buccal slits are present around the margin.

Remarks. S. pygmaea is an easily recognized species due to its unigeminate ambulacra and pitted apical disc.

Salenia anthophora Müller is most similar in overall appearance, but differs in having no small central pits on the ocular and genital plates of the apical disc, and the sutural pits are smaller and less rounded. *Salenia scabra* Nestler has wider ambulacra than either *S. anthophora* or *S. pygmaea* and displays a narrow zone of miliaries separating the vertical columns of primary and secondary tubercles.

Salenia anthophora Müller, 1846

Plate 2, figures 5–6; Text-figure 3E

1846 *Salenia anthophora* Müller, p. 7, pl. 1, fig. 1.
1866 *Salenia bonissenti* Cotteau, p. 202, pl. 15, figs 4–7.
1897 *Salenidia bonissenti* (Cotteau); Lambert, p. 148, pl. 2, figs 13–16.
1911 *Salenia anthophora* Müller; Lambert and Thiéry, p. 211.
1911 *Salenida bonissenti* (Cotteau); Lambert and Thiéry, p. 212.
1928 *Salenia anthophora* Müller; Ravn, p. 44, pl. 5, fig. 4.
1935 *Salenida bonissenti* Cotteau; Smiser, p. 29.
1950 *Salenidia bonissenti* (Cotteau); Kongiel, pp. 311, 321, pl. 1, figs 1–4.
1979 *Salenidia anthophora* (Müller); Geys, p. 313, figs 10.5–6, 11.1–2.
1979 *Salenidia* cf. *bonissenti* (Cotteau); Geys, p. 306, figs 6.3–6.
1983 *Salenidia anthophora* (Müller); Kutscher, p. 891, pl. 1, fig. 1; pl. 2, fig. 2; pl. 3, figs 6–8; pl. 4, figs 1–2.
1983 *Salenidia bonissenti* (Cotteau); Kutscher, p. 890, pl. 1, fig. 4; pl. 2, figs 3–6; pl. 3, figs 1–5.
1987 *Salenidia bonissenti*? (Cotteau); van der Ham *et al.*, p. 21.
1992 *Salenidia anthophora* (Müller); van der Ham and van Birgelen, p. 143, pl. 1, figs 1–3.

Material. BMNH EE5630.

Occurrence. One specimen, collected at Sulukapy, Mangyshlak, Kazakhstan (middle *B. casimirovensis* Zone). Elsewhere the species is recorded from the Lower Maastrichtian of the Isle of Rügen, the Ciply district of Belgium and the Maastricht area and from the Upper Maastrichtian of Poland and Denmark.

Description. The specimen is incomplete, missing the whole of the lower surface of the test as well as some of the sides. Measurements are therefore approximate. The test diameter is *c.* 17 mm and the height *c.* 13 mm (76 per cent. of test diameter). The ambitus appears to be a little below mid-height with the upper surface of the test domed in profile. Ambulacra are narrow, 2·2 mm wide at the ambitus (13 per cent. of test diameter) and slightly sinuous. Plating is unigeminate throughout with the pore-pairs placed obliquely and forming a single series. Primary tubercles are all of a similar size and form a continuous column along the ambulacral length. The tuberculate zone covers 77 per cent. of the ambulacral width. Alternating secondary tubercles are present within the perradial region. Due to the state of preservation, it is impossible to tell the number of tubercles or pore-pairs in each column.

The interambulacra are very broad, 3·7 times wider than the ambulacra (50 per cent. of test diameter at the ambitus). It is impossible to discern the number of primary tubercles in each interambulacral column, but three are discernible in each column between the apex and the ambitus. The tubercles which are visible show broad areoles which do not appear to be confluent. A wide interradial zone covers 35 per cent. of the interambulacral width and this forms a zigzag swathe of secondary tuberculation.

The apical disc is massive. In diameter it occupies 78 per cent. of overall test diameter. It is approximately pentagonal in outline with the 'bat-shaped' ocular plates protruding beyond the genital plates. Large, angular sutural pits are developed at all triple junctions and at mid-points between (Text-fig. 3E). Ocular plate I is exsert. The surface of the apical plates is granular and under magnification shows slight radial corrugation. The genital plates are slightly sunken in the centre where a rim surrounds each centrally placed genital pore. There are no ancillary pits on any of the plates. A rim also surrounds the periproct which is sub-circular in outline. The longest dimension of the anus is 2·5 mm (15 per cent. of test diameter).

The size and degree of invagination of the mouth are not visible.

Remarks. Salenia pygmaea von Hagenow is closest in appearance to *S. anthophora* but differs in having small central pits on the ocular and genital plates, and larger and more angular sutural pits on the apical disc.

Salenia anthophora shows a similar pattern of sutural pitting to that of *S. maestrichtensis* Schlüter, but may be distinguished by its more conical profile and domed apical disc.

Both *S. anthophora* and *S. pygmaea* are easily distinguished from the only other saleniid found in the Mangyshlak sections, *S. belgica* Lambert. This differs markedly in its apical disc structure, predominantly bigeminate ambulacral plate arrangement, thinner, flatter disc with far smaller and less angular sutural pits, and lack of pits on the ocular and genital plates.

Order PHYMOSOMATOIDA Mortensen, 1904
Family PHYMOSOMATIDAE Pomel, 1883

Genus PHYMOSOMA Haime, *in* d'Archiac and Haime, 1853

Type species. Cidaris koenigii Mantell, 1822, by subsequent designation of Lambert and Thiéry, 1911.

Phymosoma granulosum (Goldfuss, 1829)

Plate 3, figures 1–5; Text-figure 5A–B

1829 *Cidarites granulosus* Goldfuss, p. 122, pl. 40, fig. 7.
1855 *Phymosoma granulosum* Goldfuss; Desor, p. 87.
1911 *Phymosoma granulosum* Goldfuss; Lambert and Thiéry, p. 225.
1928 *Phymosoma subconicum* Ravn, p. 59, pl. 6, fig. 5.
?1928 *Phymosoma granulosum* Goldfuss; Ravn, p. 55, pl. 6, figs 3, 6–10.
1934 *Cyphosoma granulosum* (Goldfuss); Tzankov, p. 194.
1973 *Phymosoma koenigi* (Mantell); Kutscher, p. 114, fig. 22 (*pars*).
?1974 *Phymosoma granulosum* (Goldfuss); Savchinskaya, p. 312, pl. 95, figs 7–10.
1980 *Phymosoma granulosum* (Goldfuss); Geys, p. 204, figs 2.1–2.4.
1985 *Rachiosoma granulosa* (Goldfuss); Kutscher, p. 525, pl. 2, figs 7–12 (*pars*).
1985 *Phymosoma koenigi* (Mantell); Kutscher, p. 521, pl. 2, figs 1–6 (*pars*).

Material. Two specimens: BMNH EE5560–EE5561.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. This is a long-ranging species known from the

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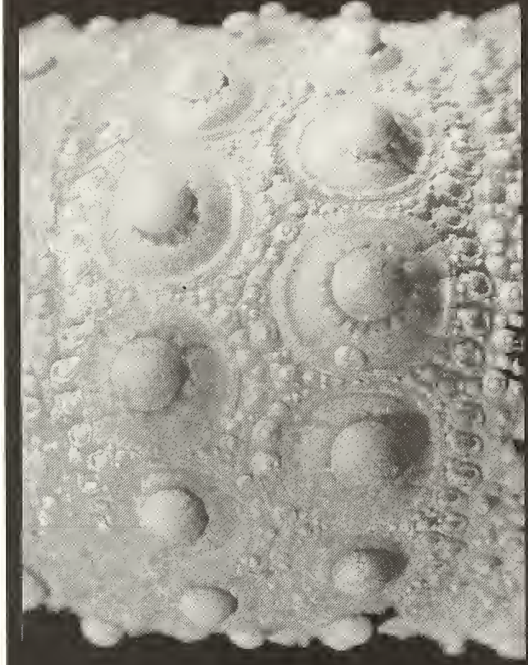
EXPLANATION OF PLATE 3

Figs 1–5. *Phymosoma granulosum* (Goldfuss, 1829); BMNH EE5560; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 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, ×2; 4–5, ×7.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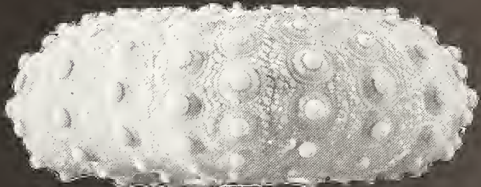
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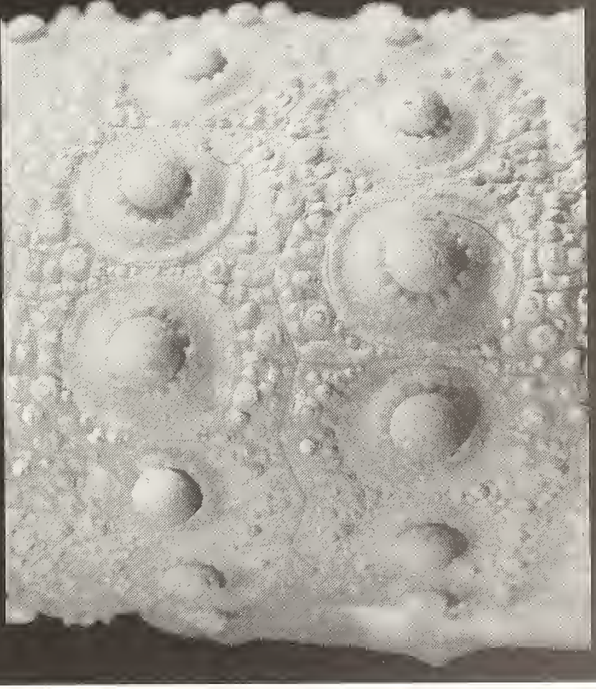
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JEFFERY, *Phymosoma*

Maastrichtian and Paleocene of Denmark. Elsewhere it is found in the Lower Maastrichtian of the Isle of Rügen and in the Lower to Upper Maastrichtian of the Don Basin, Bulgaria, Belgium and the Netherlands.

Description. The specimens are 30·3 mm and 19·2 mm in diameter respectively, and are circular to subpentagonal in outline, with ambulacra at the angles of the pentagon. The test is somewhat flattened with a height 37–38 per cent. of test diameter, and with broad, flat oral and apical surfaces. The sides are uniformly curved with the ambitus at approximately mid-height or slightly above. Ambulacral and interambulacral tubercles are equally developed.

Ambulacra are straight and moderately broad measuring 25–26 per cent. of test diameter at the ambitus. They show phymosomatoid compound plating with five elements in each compound plate at the ambitus (Text-fig. 5A). There is a single large tubercle on each compound plate. These primary tubercles are crenulate and non-perforate and are largest adambitally, becoming smaller both adapically and adorally. In the most adapical plates, the primary tubercle is too small to cover all of the compounding elements and overlies only two or three. There are 11 or 12 compound plates and approximately 53 pore-pairs at 19·2 mm test diameter increasing to 13 or 14 compound plates and 68 pore-pairs per column at 30·3 mm test diameter. The pores are noticeably crowded adorally and adapically where the pore zones also become less sinuous. The pores are partitioned isopores and at the ambitus the pore zone covers 17–18 per cent. of the width of the plates. Miliary tubercles run along the perradius.

Interambulacral zones are 1·3 to 1·5 times wider than ambulacral zones at the ambitus (33–36 per cent. of test diameter). There are 11 or 12 plates per column in both specimens examined. A single large crenulate, non-perforate tubercle with a circular areole is present on each interambulacral plate (Text-fig. 5B). In addition, from the ambitus to the mouth there is a line of small tubercles running along the edge of the plates adjacent to the ambulacra. In the three or four most adoral plates of each column these secondary tubercles are larger and more prominent. Miliary tubercles cover the remainder of each plate. Adapically there are far fewer tubercles and those which are present are appreciably smaller than on the oral surface. A naked interradial zone develops towards the apex.

Apical disc plates are not preserved in either specimen. In diameter, the apical disc occupies 36–39 per cent. of test diameter. Notches are apparent at the interradial sutures.

The peristome is circular with a diameter of 33–41 per cent. of test diameter. A proportionally larger mouth is present in the smaller specimen. Buccal slits are present at the margins of the peristome.

Remarks. Phymosoma corneti Cotteau is closest in appearance to *P. granulosum*. Both have distinctly crenulate primary tubercles and no well developed secondary tubercles. *P. corneti*, however, has extensive zones of miliary tubercles both adradially and interradially, whilst *P. granulosum* has poorly developed miliary granulation and its plates are almost entirely covered by primary tubercles.

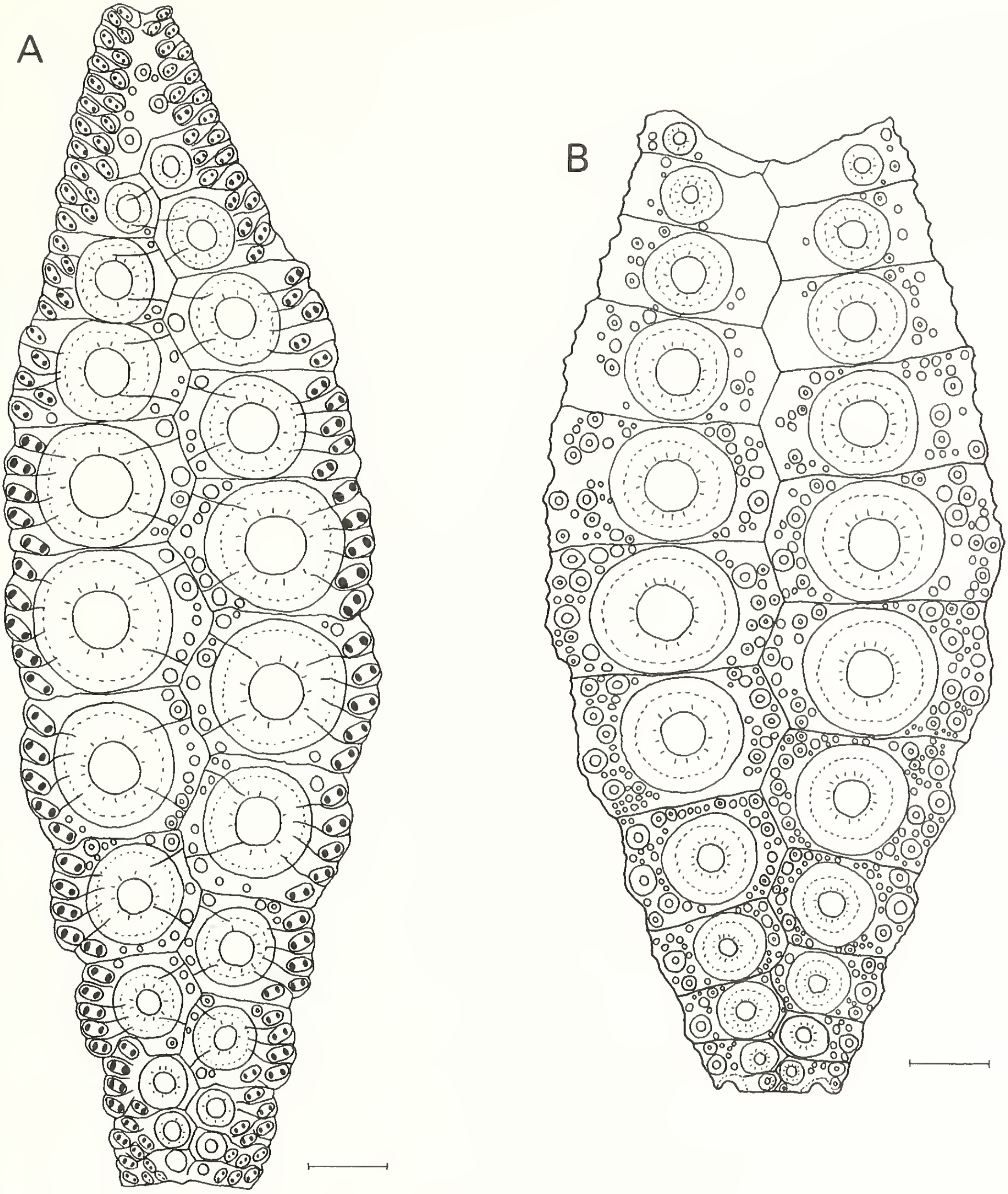
Genus GAUTHIERIA Lambert, 1888

Type species. Cyphosoma radiatum Sorignet, 1850, by original designation.

Gauthieria pseudoradiata (Schlüter, 1883)

Plate 4, figures 1–5; Text-figure 6A–B

1881 *Phymosoma pseudoradiatum* Schlüter, p. 216 [*nomen nudum*].
1883 *Phymosoma pseudoradiatum* Schlüter, p. 24.
1897 *Gauthieria Broecki* Lambert, p. 52, pl. 4, figs 1–5.
1911 *Gauthieria Broecki* Lambert, p. 65.
1911 *Phymosoma pseudoradiatum* Schlüter; Lambert and Thiéry, p. 225.
1928 *Phymosoma pseudoradiatum* Schlüter; Ravn, p. 58, pl. 6, fig. 4.
1935 *Gauthieria radiata* (Sorignet); Smiser, p. 30 (*pars*).
1935 *Gauthieria corneti* (Cotteau); Smiser, p. 31 (*pars*).
1935 *Gauthieria broecki* Lambert; Smiser, p. 32 (*pars*).
1950 *Gauthieria*(?) *pseudoradiata* (Schlüter); Kongiel, p. 314, pl. 1, figs 5–8.
1966 *Gauthieria radiata* (Sorignet); Nestler, p. 1214, figs 1–4.



TEXT-FIG. 5. *Camera lucida* drawings of *Phymosoma granulosum* (Goldfuss, 1829); BMNH EE5560. A, ambulacral plating; B, interambulacral plating. Scale bars represent 2 mm.

1980 *Gauthieria radiata broecki* Lambert; Geys, p. 210, figs 3.3–3.6.
1980 *Gauthieria pseudoradiata* (Schlüter); Geys, p. 212, figs 3.7–3.9, 4.1–4.2.

Material. BMNH EE5625.

Occurrence. Maastrichtian of Kyzylsai, Mangyshlak, Kazakhstan: 2·1 m below the Cretaceous–Tertiary boundary. Elsewhere, it is present in the Lower Maastrichtian of the Isle of Rügen, Belgium and the Netherlands and in the Upper Maastrichtian of Denmark and Poland.

Description. The test is circular in horizontal outline, with a diameter of 12·0 mm and a height of 4·1 mm (34 per cent. of test diameter). The ambitus is a little above mid-height and the test curves smoothly both above and below. Upper and lower surfaces are both broad and flat, although the oral surface is a little less so as the peristome is slightly sunken.

The ambulacra are 3·1 mm wide at the ambitus (26 per cent. of test diameter), tapering orally and ambitally. Compound plates contain three or four elements. Each compound plate carries a large, crenulate, non-perforate primary tubercle covering almost the entire surface of the plate. The compound plates show distinct radial ornamentation, especially close to the ambitus (Text-fig. 6A). Simple plates with densely packed small tubercles alternate with the compound plates. A single row of miliaries separates the primary tubercles ambitally along the perradius. Pore-pairs are uniserial throughout with no phyllode development. There are 35 pore-pairs in each column and these are positioned in weak arcs of five or six along the column length.

Interambulacra are 1·4 times wider than ambulacra at the ambitus (36 per cent. of test diameter). As in the ambulacra, interambulacral plates show distinct radial striations (Text-fig. 6B). Each plate carries a large crenulate, non-perforate tubercle. The primary tubercles on the most ambital plates have broad areoles covering virtually the whole plate. Around the plate margin is a single row of miliary granules. Primary tubercles decrease dramatically in size both apically and orally.

The apical disc is pentagonal and 5·2 mm in diameter (43 per cent. of test diameter), but no plates remain.

The peristome is circular with weak buccal slits. It measures 4·6 mm in diameter (38 per cent. of test diameter) and is very slightly sunken.

Remarks. A distinguishing feature of this species is the pronounced radial ornamentation on both ambulacral and interambulacral plates. Such radial striae are known to be a characteristic of juveniles of several other species of *Gauthieria*, and as all known specimens of *G. pseudoradiata* are small it is possible that they merely represent juveniles of another species. Another characteristic of *G. pseudoradiata* is the marked enlargement of the tubercles on the two or three most ambital plates, a feature also present in *G. middletoni* (Woodward). However, at a similar size to specimens of *G. pseudoradiata*, *G. middletoni* shows less enlargement of the ambital interambulacral tubercles, more developed miliary granulation and no radial ornamentation. It is therefore probable that they do represent two separate species.

Gauthieria pseudoradiata is easily distinguished from the only other phymosomatid found in these Mangyshlak sections, *Phymosoma granulosum*. *P. granulosum* has far coarser tuberculation, moderately strong phyllodes with distinct pore crowding near the mouth and a peristome which is flush with the test. Ambulacral plating also differs. In *Phymosoma*, compound plates are present throughout the ambulacral columns, whereas in *Gauthieria* compound plates alternate with simple elements.

Genus MICROPSIS Cotteau, *in* Leymerie and Cotteau, 1856

Type species. Micropsis desorii Cotteau, *in* Leymerie and Cotteau, 1856, by original designation.

EXPLANATION OF PLATE 4

Figs 1–5. *Gauthieria pseudoradiata* (Schlüter, 1883); BMNH EE5625; Upper Maastrichtian, 2·1 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 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, × 4; 4–5, × 16.

Figs 6–10. *Micropsis* cf. *leridensis* Cotteau, *in* Leymerie and Cotteau, 1856; BMNH EE5631; Upper Maastrichtian, middle *B. casimirovensis* Zone, Sulukapy, Mangyshlak, Kazakhstan. 6, apical view; 7, oral view; 8, lateral view; 9, detail of ambulacrum in apical view; 10, detail of interambulacrum in apical view. 6–8, × 2; 9–10, × 5.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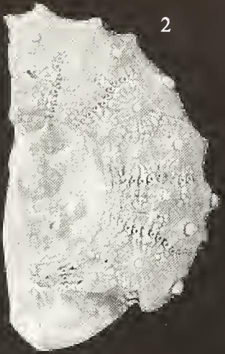
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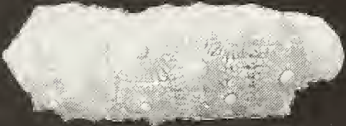
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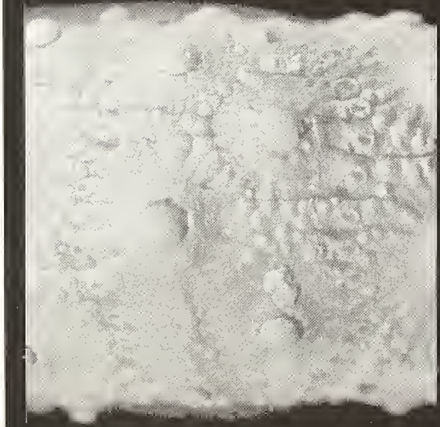
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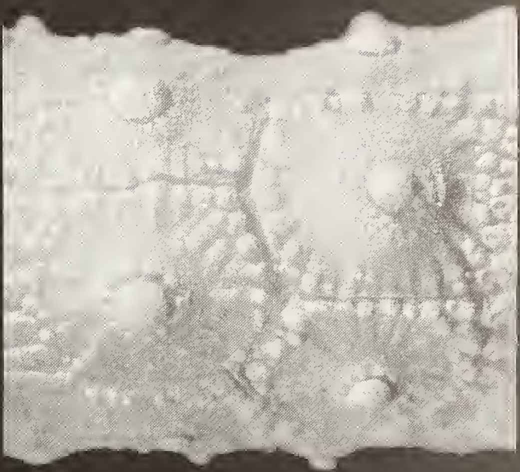
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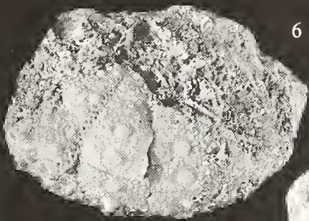
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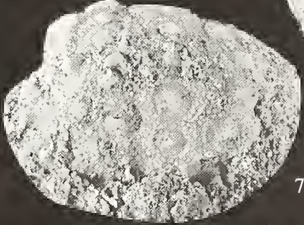
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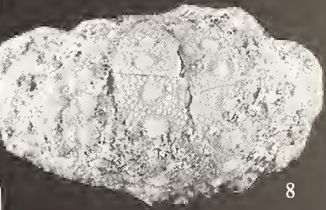
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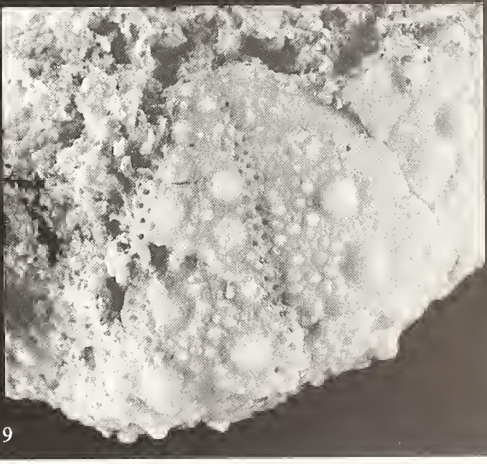
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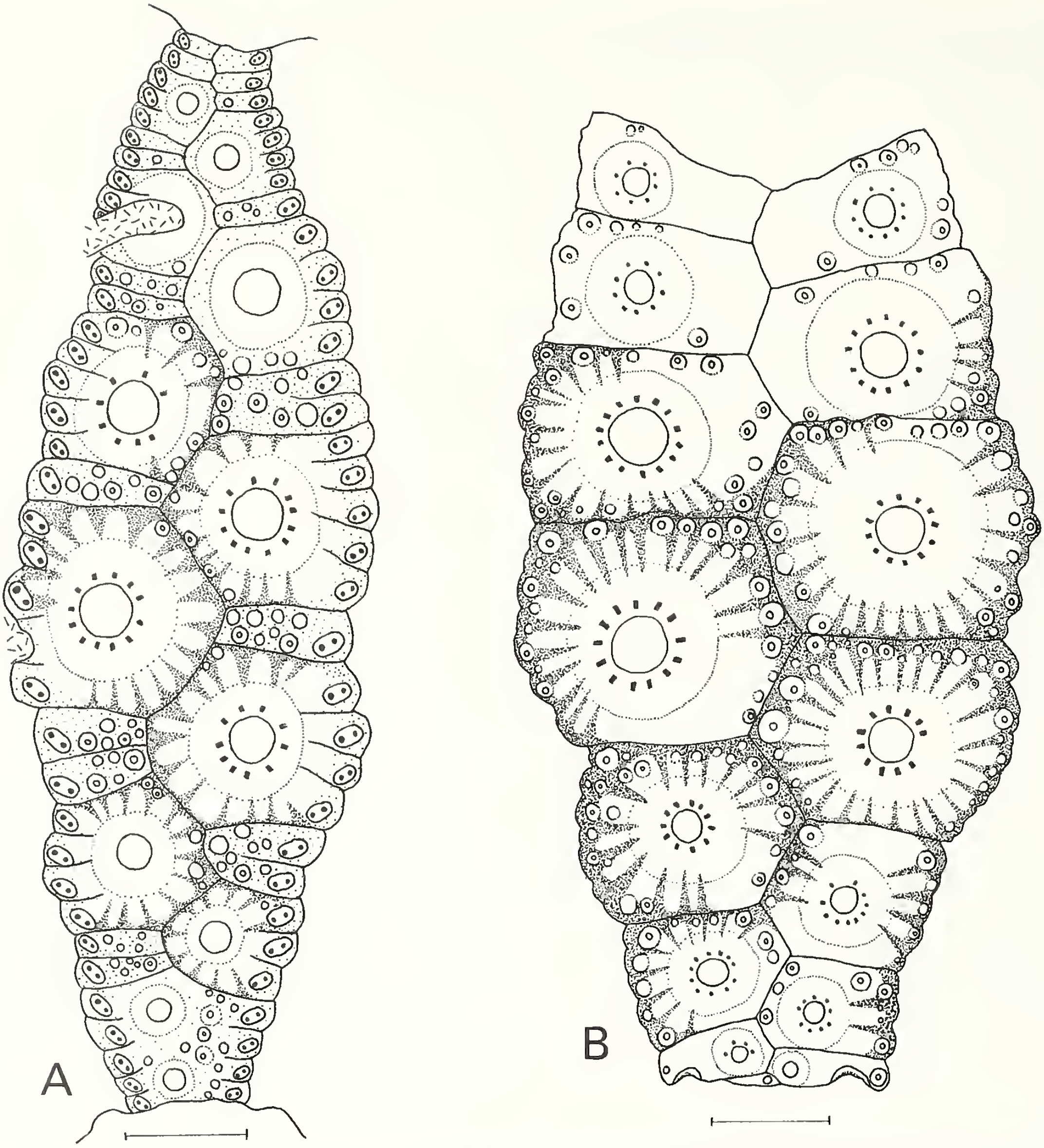
JEFFERY, *Gauthieria*, *Micropsis*



TEXT-FIG. 6. *Camera lucida* drawings of *Gauthieria pseudoradiata* (Schlüter, 1883); BMNH EE5625. A, ambulacral plating; B, interambulacral plating. Scale bars represent 1 mm.

Micropsis cf. *leridensis* Cotteau, 1882

Plate 4, figures 6–10; Text-figure 4C–D

cf. 1882 *Micropsis leridensis* Cotteau, p. 12, pl. 2, figs 8–10.
cf. 1911 *Rachiosoma leridense* (Cotteau); Lambert and Thiéry, p. 221.

Material. BMNH EE5631.

Occurrence. Collected in Late Maastrichtian strata (middle *B. casimirovensis* Zone) of Sulukapy, Mangyshlak Peninsula, Kazakhstan. *Micropsis leridensis* is known only from the Lower Senonian of Lérida Province, Spain.

Description. Only about one-third of the test is preserved. The test measures about 35 mm in diameter and 11·5 mm in height (33 per cent. of test diameter). It is circular in horizontal outline with broad, flat upper and lower surfaces giving it a somewhat wheel-like appearance.

Ambulacral width is 5·7 mm at the ambitus (16 per cent. of test diameter). Compound plates are made up of five elements ambitally but this number is reduced to four and then three adapically (Text-fig. 4c). There are 11 or 12 compound plates per ambulacral column. Each compound plate carries a single primary tubercle. These are non-perforate and only very weakly crenulate. They are of a similar size along the whole of the ambulacral length with an areole of similar width to the diameter of the mammelon. Surrounding the primary tubercles, and especially along the perradius are small secondary tubercles of approximately equal size. There are approximately 53 pore-pairs in each ambulacral column arranged uniserially in weak arcs.

The interambulacra are 1·8 times broader than the ambulacra at the ambitus (29 per cent. of test diameter). The interambulacral plates are of similar height to those in the ambulacra. They are, however, much broader, so that each interambulacral plate is about twice as broad as it is high. Primary tubercles in both ambulacra and interambulacra are equally developed and of similar dimensions. As in the ambulacra, their size diminishes only slightly away from the ambitus with the smallest tubercles adapically. Secondary tuberculation is similar to that found in the ambulacra giving the test an overall granular appearance (Text-fig. 4d).

The apical disc is not preserved, and it is not possible to tell what proportion of test diameter it made up. The shape of the apical system is likewise unknown.

The mouth is small (about 20 per cent. of test diameter), circular and invaginated.

Remarks. Micropsis seems to be closely related to *Porosoma* and *Rachiosoma*. Distinctions between these three genera are based mostly on the structure of the apical system. Consequently, when the apical disc is missing it is difficult to determine the true generic position of a specimen. However, another distinguishing feature of *Micropsis* is its small primary tubercles developed equally in both ambulacral and interambulacral fields. Of described *Micropsis* species, *M. leridensis* Cotteau, from the Senonian of Spain, most closely resembles the specimen from Kazakhstan. It is the only *Micropsis* species to have polyporous plates with five compounding elements near to the ambitus, and shows no enlarged secondary tubercles. Due to age and locality differences between *M. leridensis* and the species described herein, I refer the specimen from Kazakhstan to *M.* cf. *leridensis*.

Order HOLECTYPOIDA Duncan, 1889
Family CONULIDAE Lambert, 1911

Genus CONULUS Leske, 1778

Type species. Conulus albogalerus Leske, 1778, by original designation.

Conulus magnificus (d'Orbigny, 1854)

Plate 5, figures 1–4; Text-figure 7a–b

1854 *Echinoconus magnificus* d'Orbigny, p. 540, pl. 1004.
1921 *Conulus conicus* Breynius var. *grimmensis* Nietsch, p. 41, pl. 11, figs 1–2.
1927 *Conulus magnificus* (d'Orbigny); Ravn, p. 323, pl. 1, fig. 9.
1934 *Echinoconus Raulini* (d'Orbigny); Tzankov, p. 195, pl. 1, fig. 5.
1959 *Conulus magnificus* (d'Orbigny); Poslavskaya and Moskvin, p. 251, pl. 3, fig. 3.
1979 *Conulus grimmensis* Nietsch; Asgaard, table 2.
1986 *Conulus magnificus* (d'Orbigny); Kutscher, p. 325, pl. 1, figs 1–5, text-figs a–b.

Material. Two specimens: BMNH EE5562–EE5563.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. This species is also recorded from the Lower Maastrichtian of northern Germany and the Isle of Rügen, and the Upper Maastrichtian of Denmark, Bulgaria, Crimea and the northern Caucasus.

Description. The test is slightly egg-shaped in horizontal outline, tapering posteriorly and with the widest point 40 per cent. of test length from the anterior margin. The specimens are 42·4 mm and 43·7 mm long and 39·5 mm and 40·1 mm wide respectively. In profile the test has a conical upper surface and a flat base.

The ambulacra are all alike. They are straight, narrow and non-petaloid, with a width approximately 13 per cent. of test length at the ambitus, and tapering towards the apex. Ambulacral pores are alike from the apical system to the peristome except that they become more sunken adorally. On the upper surface of the test, pore-pairs are arranged uniserially and the ambulacral plating is simple. Below the ambitus the pore-pairs form oblique arcs of three and plating is trigeminate.

The interambulacra are approximately three times as wide as the ambulacra at the ambitus (about 43 per cent. of test length). There are four to five ambulacral pore-pairs adjacent to each interambulacral plate and 19 or 20 plates per column in each interambulacrum. There are eight plates separating the peristome from the periproct.

The apical system lies at the highest point of the test. It is slightly longer than wide and tetrabasal (Text-fig. 7B). Gonopores are present on all four genital plates, and the madreporite has numerous additional hydropores. The madreporite is the largest of the plates and is in contact with all three other genital plates. Oculars II, III and IV are well separated. Oculars I and V meet at the midline and are larger than the other three ocular plates.

The peristome is oval in outline and is 1·25 times longer than wide. The axis of elongation runs from the top right to the bottom left. It lies a little anterior of the centre of the oral surface (44 per cent. of test length from the anterior margin) and is very slightly sunken.

The periproct lies in a marginal position, visible both from the posterior and from the oral surface. It is a large transverse oval and is approximately 1·3 times broader than long.

Tubercles are crenulate and perforate. They are denser, coarser, more distinctly sunken and of differing sizes on the oral surface with no differentiation between the ambulacra and the interambulacra. On the upper surface the tubercles from distinct diagonal rows in the interambulacra. Tuberculation is far finer and sparser than on the lower surface.

Remarks. C. magnificus is very similar in size and shape to *C. gigas* Cotteau from the Maastrichtian of the Pyrenees. However, *C. gigas* has a consistently smaller periproct with a longitudinally elongate oval shape which differs markedly from that of *C. magnificus* (Text-fig. 7A, C).

The German specimens described by Nietsch (1921) were larger and less conical than those previously assigned to *C. conicus* (Breynius) and a new subspecies was erected to accommodate them. I have not examined Nietsch's original material. Specimens in the Copenhagen Geological Museum labelled *Conulus grimmensis* are indistinguishable from *C. magnificus*.

Family GALERITIDAE Gray, 1825

Genus GALERITES Lamarck, 1801

Type species. Echinites vulgaris Leske, 1778, by original designation.

Galerites stadensis (Lambert, 1911)

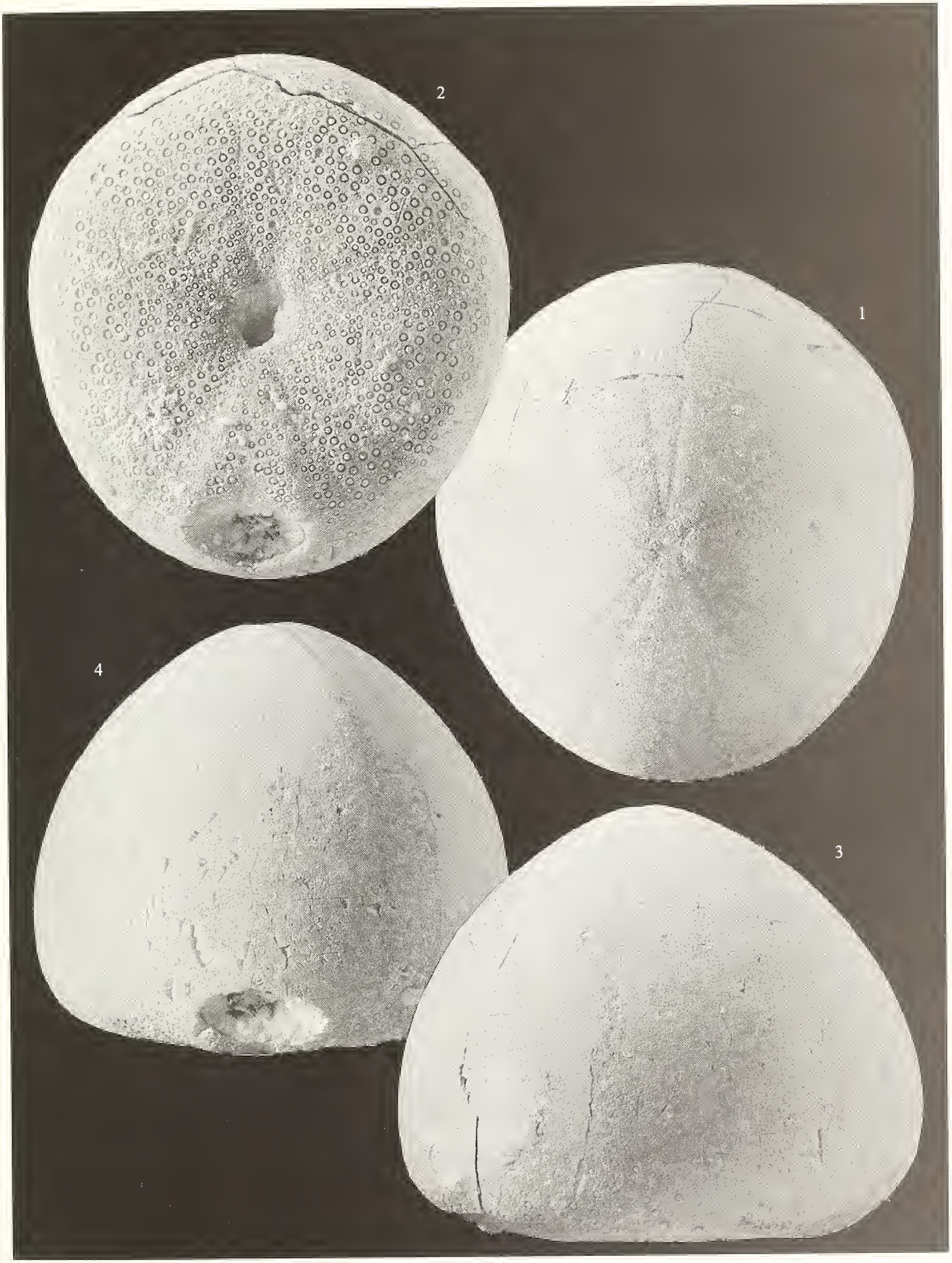
Plate 6, figures 1–9; Text-figures 7D–E, 8

1911 *Echinoconus wollemanni* Lambert, p. 62, pl. 3, figs 19–21.

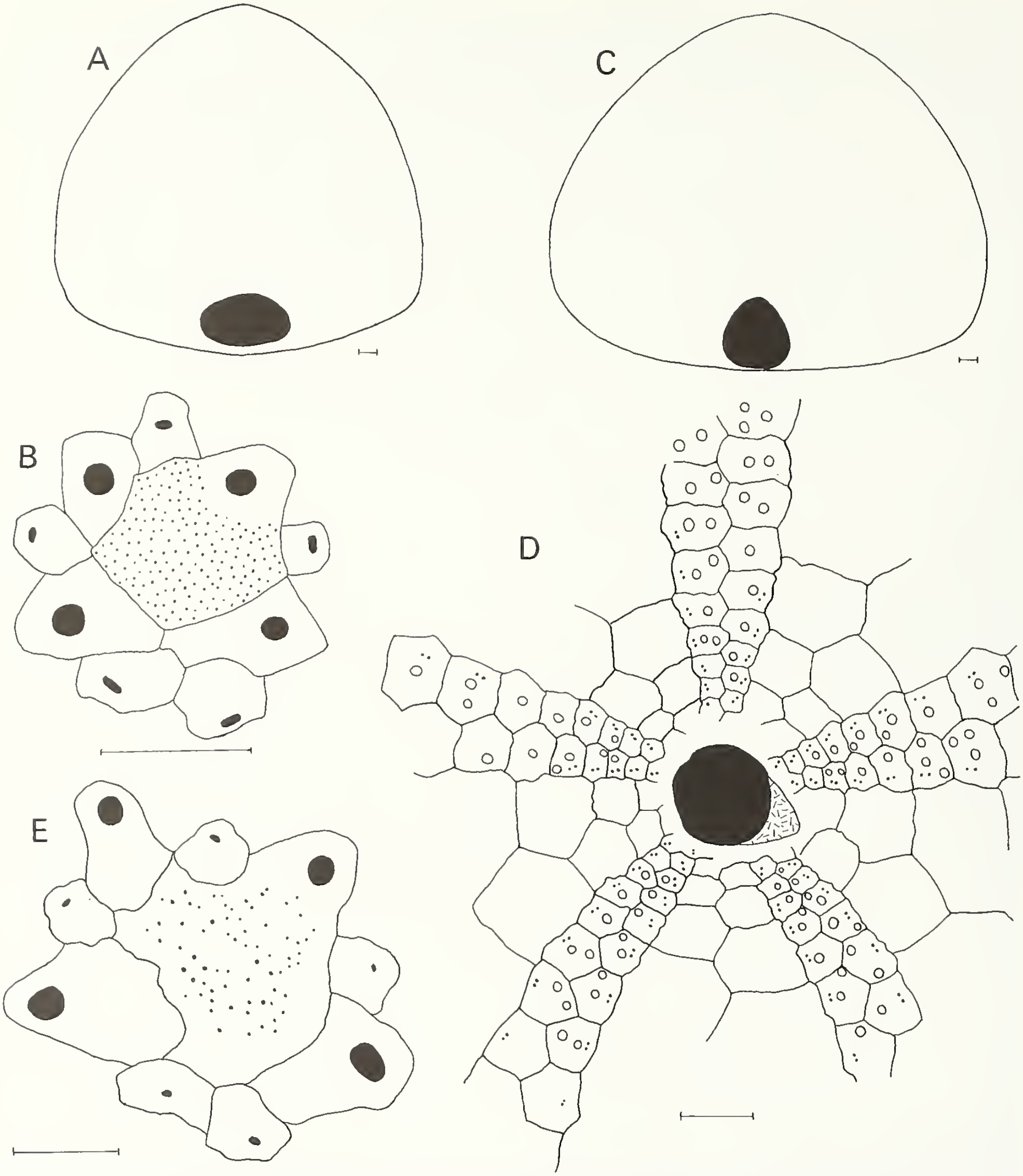
EXPLANATION OF PLATE 5

Figs 1–4. *Conulus magnificus* (d'Orbigny, 1854); BMNH EE5563; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, posterior view; all × 2.

PLATE 5



JEFFERY, *Conulus*



TEXT-FIG. 7. *Camera lucida* drawings of *Conulus magnificus* (d'Orbigny, 1854), *Conulus gigas* Cotteau and *Galerites stadensis* (Lambert, 1911). A–B, *Conulus magnificus*; BMNH EE5563; A, posterior view; B, apical disc plating. C, *Conulus gigas*; Maastrichtian of the Pyrenees; BMNH EE4835; posterior view. D–E, *Galerites stadensis*; BMNH EE5567; D, oral surface plating; E, apical disc plating. A–D, scale bars represent 2 mm. E, scale bar represents 1 mm.

1911 *Echinoconus globulus* var. *stadensis* Lambert, p. 75.
1921 *Echinoconus vulgaris* Leske; Nietsch, p. 33, pl. 9, figs 1–12; pl. 10, figs 1–7, 11.
1927 *Conulopsis globulus* Klein var. *goldfussi* (Lambert); Ravn, p. 326, pl. 2, fig. 3.
1927 *Conulopsis wollemanni* (Lambert); Ravn, p. 327, pl. 2, fig. 8.

1935 *Echinoconus wollemanni* Lambert; Smiser, p. 45.
1959 *Echinoconus vulgaris* Leske; Poslavskaya and Moskvin, p. 252, pl. 3, fig. 4.
?1979 *Galerites globulus* (Klein); Gongadze, p. 70, pl. 6, fig. 3.
1979 *Galerites vulgaris* (Leske); Kutscher, p. 564, pl. 2, figs 6–8.
1985 *Galerites* (*Galerites*) *stadensis* (Lambert); Schulz, p. 54, pl. 6, fig. 2; pl. 10, figs 10–15; pl. 11, fig. 4; pl. 15, figs 1–6.
1987 *Galerites stadensis*?; van der Ham *et al.*, p. 28.
1992 *Galerites* cf. *stadensis*; van der Ham and van Birgelen, p. 149.

Material. Eight specimens: BMNH EE5564–EE5571.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. *G. stadensis* has also been recorded from the Lower Maastrichtian of northern Germany and the Isle of Rügen and the Lower to Upper Maastrichtian of the Maastricht area, Denmark, Georgia, Crimea and the northern Caucasus.

Description. Tests are approximately circular to very slightly elongate oval in horizontal outline. They are more or less domed to conical in profile with a flat base and the ambitus situated just above this. They are 21·3–31·8 mm long and 15·5–26·8 mm high (61–84 per cent. of test length; Text-fig. 8).

Ambulacra are flush and all alike. They are straight and narrow, tapering towards the apex and towards the mouth on the oral surface. At the ambitus they measure between 2·6 mm and 4·1 mm (12–15 per cent. of test length). Pores are small and round with pairs very obliquely positioned especially adjacent to the peristome (Text-fig. 7D). They are identical from apex to mouth except for becoming slightly smaller adorally. Plating is simple throughout and pore-pairs are uniserial along the whole column. Each column contains 37 or 38 plates. The adoral pore angle, as defined by Schulz (1985, p. 14), ranges from 140° to 175°.

Interambulacra are all alike, 2·7–3·5 times broader than ambulacra at the ambitus, measuring between 8·3 mm and 13·3 mm (39–44 per cent. of test length). At the ambitus each interambulacral plate is adjacent to three ambulacral plates. Interambulacrum 5 forms a raised narrow triangular platform between the mouth and anus. There are six or seven plates separating the peristome and the periproct.

The apical system is situated centrally at the highest point on the test. In more conical specimens, it may be sunken slightly below the level of the surrounding coronal plates. It has a greatly enlarged madreporite which is in contact with the remaining three genital plates (Text-fig. 7E). All four genital plates are roughly triangular and carry a gonopore, and the madreporite has numerous additional small hydropores. The apical system is broadest posteriorly where the posterior genital plates are separated by the posterior oculars which meet at the midline.

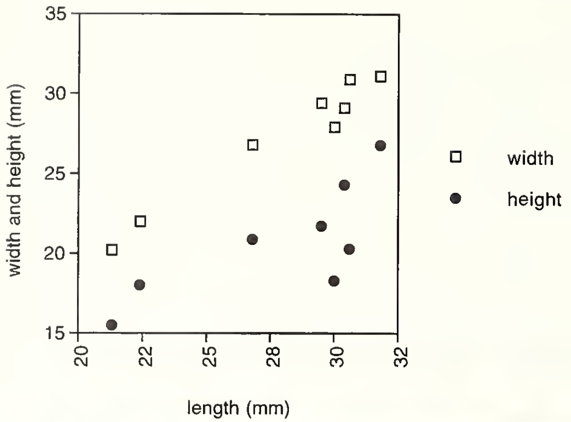
The mouth is situated 37–44 per cent. of test length from the anterior margin. It is circular or very slightly broader than long and is positioned in a deep peristomal well with vertical walls covered by small miliary tubercles. The peristome is fairly small, 1·9–2·8 mm long (7–9 per cent. of test length).

The periproct is situated inframarginally, 28–39 per cent. of test length posterior of the mouth on the raised platform of interambulacrum 5. It is rounded triangular to teardrop-shaped with the widest point posteriorly and is 0·9–1·2 times longer than wide. The length of the periproct is 10–12 per cent. of test length.

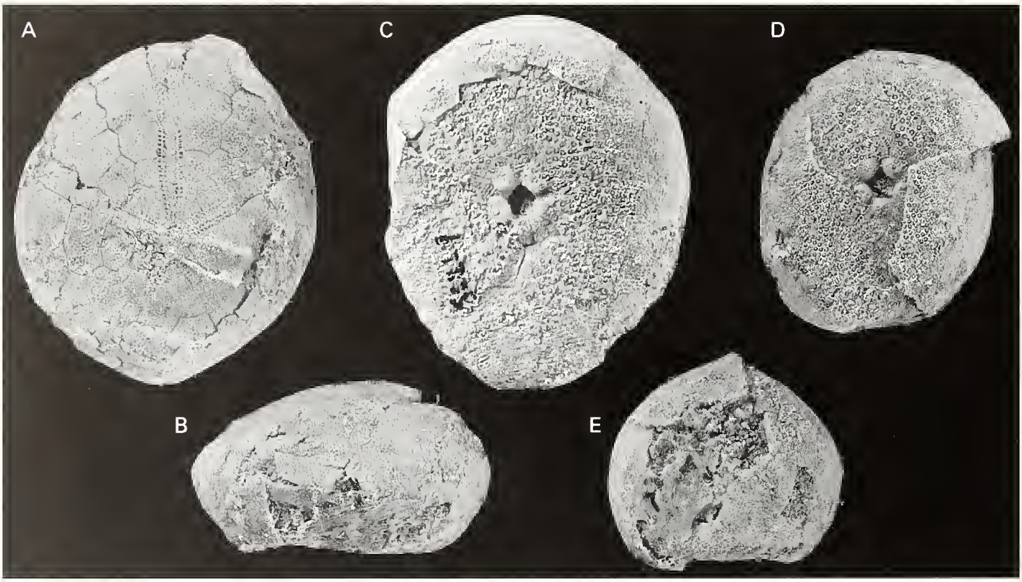
All tubercles are crenulate, perforate and sunken. Over the whole test, primary tubercles with sunken areoles are interspersed with secondary tubercles with mammelons. Dense miliary tuberculation fills all the gaps. On the oral surface the tubercles are larger and more deeply sunken and approximately twice as densely packed as on the upper surface. Tubercles are especially dense immediately adjacent to the mouth.

Remarks. The specimens from Mangyshlak have the vertical peristomal wall characteristic of *G.* (*G.*) *stadensis* which easily distinguishes this species from *G.* (*G.*) *abbreviatus* and *G.* (*G.*) *vulgaris* (Schulz 1985, p. 54).

The adoral 'pore angle' in *Galerites* (Schulz 1985) is a quantitative measure of the straightness of the ambulacra near to the mouth. According to Schulz, the size of this angle is of diagnostic value. Some of the specimens studied have pore angles somewhat smaller than those given for *G.* (*G.*) *stadensis* but within the range given by Schulz (p. 47) for *G.* (*G.*) *vulgaris*. Relative heights and the ratio of ambulacral to interambulacral plates at the ambitus also fall within the range for *G.* (*G.*) *vulgaris*. Schulz described a large number of species and subspecies based upon these characters. However, the diagnostic values of pore angle and relative height often have greatly overlapping ranges and further study may show that many of these taxa should be synonymized.



TEXT-FIG. 8. Biometric data for *Galerites stadensis* (Lambert, 1911).



TEXT-FIG. 9. *Zuffardia* sp.; Upper Maastrichtian, middle *B. casimirovensis* Zone, Sulukapy, Mangyshlak, Kazakhstan. A–B, BMNH EE5634; A, apical view; B, posterior view. C, BMNH EE5632; oral view. D–E, BMNH EE5633; D, oral view; E, posterior view. All ×2.

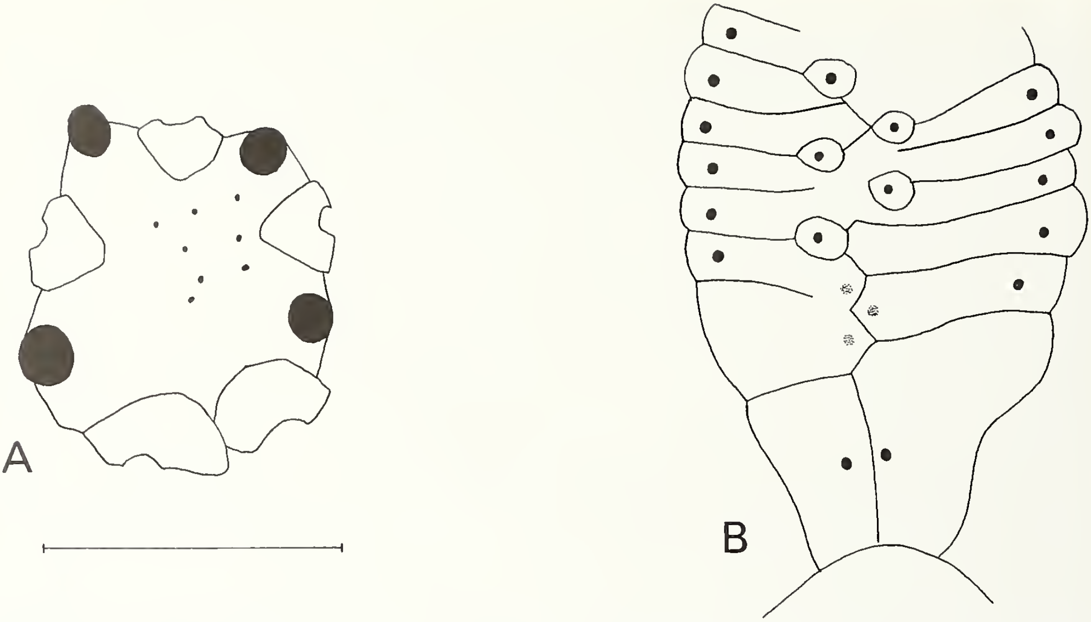
Galerites sulcatoradiatus Goldfuss is extremely similar to *G. stadensis* in overall appearance. They differ only in the larger 'pore angle' of the pore-pairs on the oral surface of *G. stadensis* and in the more distinctly raised triangular area around the periproct. *G. sulcatoradiatus* also has distinct surface tuberculation: primary tubercles are interspersed with pits containing pedicellarial bases which often coalesce.

EXPLANATION OF PLATE 6

Figs 1–9. *Galerites stadensis* (Lambert, 1911); uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1–3, BMNH EE5564; 1, apical view; 2, oral view; 3, lateral view. 4–6, BMNH EE5570; 4, apical view; 5, oral view; 6, lateral view. 7–9, BMNH EE5566; 7, apical view; 8, oral view; 9, lateral view. All ×2.

PLATE 6

JEFFERY, *Galerites*



TEXT-FIG. 10. *Camera lucida* drawings of *Zuffardia* sp. A, BMNH EE5634; apical disc. B, BMNH EE5632; detail of phyllode V. Scale bar represents 1 mm.

Galerites stadensis is easily distinguished from *Conulus magnificus*, the only other holectypoid found in these Mangyshlak sections. *C. magnificus* has its periproct in a marginal position, visible both from behind and below. In addition, the ambulacral plating becomes trigeminate adorally in *Conulus* with the pore-pairs forming arcs of three. Tuberculation also differs: in *Conulus* tubercles are arranged in semi-regular diagonal rows.

Order CASSIDULOIDA Claus, 1880
Family PLIOLAMPADIDAE Kier, 1962

Genus ZUFFARDIA Checchia-Rispoli, 1917

Type species. Pseudocatopygus sanfilippoi Checchia-Rispoli, 1914, by original designation.

EXPLANATION OF PLATE 7

Figs 1–8. *Galeaster bertrandi* Seunes, 1889; Danian, 0·38 m above Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1–4, BMNH EE5596; 1, apical view; 2, oral view; 3, anterior view; 4, lateral view. 5–8, BMNH EE5595; 5, apical view; 6, oral view; 7, anterior view; 8, lateral view. All ×2.

Figs 9–11. *Cardiotaxis heberti* (Cotteau, *in* Cotteau and Triger, 1860); BMNH EE5627; Upper Maastrichtian, 0·4 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 9, apical view; 10, oral view; 11, lateral view. All ×1.

PLATE 7

JEFFERY, *Galeaster*, *Cardiotaxis*

Zuffardia sp.

Text-figures 9A–F, 10A–B

Material. Three specimens: BMNH EE5632–EE5634.

Occurrence. Upper Maastrichtian (middle *B. casimirovensis* Zone) of Sulukapy, Mangyshlak, Kazakhstan. Representatives of *Zuffardia* are known from the Maastrichtian of Libya, Algeria, Oman and the United Arab Emirates as well as from the upper Senonian of southern Iran. It has also been recorded from the upper Paleocene to Eocene of Oman.

Description. The specimens are more or less crushed. They are 19·3–24·6 mm long and 15·1–19·7 mm wide (78–87 per cent. of test length). The test is ovoid in horizontal outline with a smoothly rounded anterior margin and a tapered posterior. In profile, the test is somewhat inflated with the ambitus at about mid-height. The base is flat with slightly rounded margins.

The ambulacra are alike and of equal length. They are flush with the test surface and form long, narrow, poorly developed petals with almost parallel rows of pore-pairs. The petals are open distally and ambulacral plates beyond the ends of the petals are single-pored. Within the petaloid region, the pores of each pair differ in size, the outer pore being more elongate than the inner.

The apical system is situated at the highest point on the test, slightly anterior of centre. The apical region is poorly preserved. However, the apical disc appears to be monobasal with four small gonopores (Text-fig. 10A).

The peristome is positioned a little anterior of centre (43–46 per cent. of test length from the anterior margin). It is pentagonal and invaginated, with the floscelle well developed. There are strong bourrelets and broad single-pored phyllodes with two series of pores in each half ambulacrum (Text-fig. 10B). The phyllodes have six or seven pores in the outer series and three in the inner series. Buccal pores are also present.

The periproct is marginal and of elongate oval shape. It is positioned high on the truncate posterior with a slight projection above it.

Tuberculation on the upper surface is uniform and fairly dense. The tubercles are small with deeply sunken areoles. On the oral surface tubercles are more densely packed and are very slightly larger.

Remarks. This genus appears to be very facies dependent. It is recorded only from the calcarenite deposits at Mangyshlak and from the more sandy, coarse grained calcareous strata of localities outside Kazakhstan.

The specimens available for study are rather more flat-based and have narrower petals than the *Zuffardia* species previously described. However, none of the material is well enough preserved to be designated as holotype of a new species and so is here determined only to generic level.

Order HOLASTEROIDA Durham and Melville, 1957
Family HOLASTERIDAE Pictet, 1857

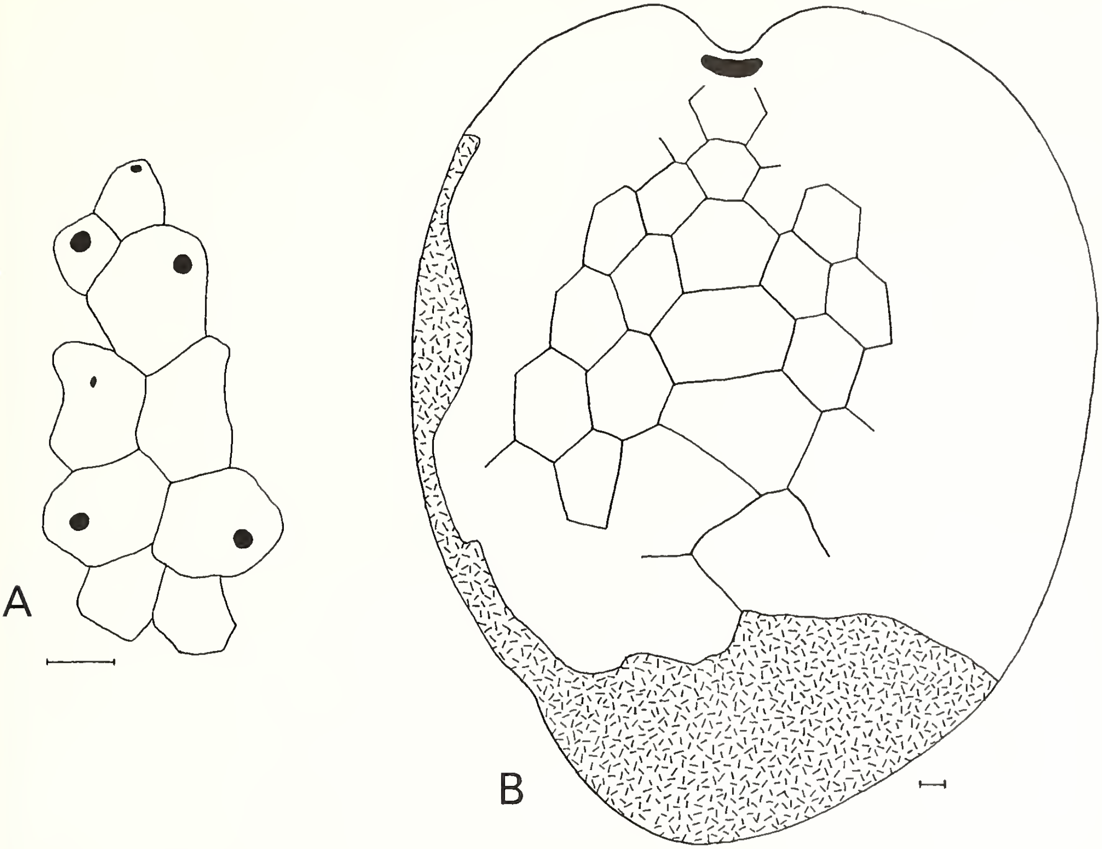
Genus CARDIOTAXIS Lambert, 1917

Type species. Cardiaster peroni Lambert, *in* Peron 1887, by original designation.

Cardiotaxis heberti (Cotteau, *in* Cotteau and Triger, 1860)

Plate 7, figures 9–11; Text-figure 11A–B

1860	*Cardiaster heberti* Cotteau, p. 240.
1874	*Cardiaster heberti* Cotteau, p. 655.
1897	*Cardiaster heberti* Cotteau; Lambert, p. 176, pl. 2, figs 11–12.
1911	*Cardiaster heberti* Cotteau; Lambert, pp. 19, 45, pl. 1, figs 7–9.
1927	*Cardiaster heberti* Cotteau; Ravn, p. 341.



TEXT-FIG. 11. *Camera lucida* drawings of *Cardiotaxis heberti* (Cotteau, *in* Cotteau and Triger, 1860); BMNH EE5627. A, apical disc plating; B, oral surface plating. A, scale bar represents 1 mm. B, scale bar represents 2 mm.

1978 *Cardiotaxis heberti* (Cotteau); Kutscher, p. 627, pl. 1.
1979 *Cardiotaxis heberti* (Cotteau); Asgaard, table 2.

Material. BMNH EE5627.

Occurrence. Upper Maastrichtian white chalk of Kyzylsai, Mangyshlak, Kazakhstan: 1·4 m below the Cretaceous–Tertiary boundary. It is also recorded from the Lower Maastrichtian of the Isle of Rügen, Belgium and the Netherlands, and from the Lower to Upper Maastrichtian of Denmark.

Description. The test is large and heart-shaped. It is 68·9 mm long and *c.* 61 mm wide (86 per cent. of test length). There is a broad and distinct frontal groove which runs all the way to the mouth. The adjoining interambulacra form rounded keels. The test is low (34 per cent. of test length) and flattened, with broad flat oral and apical surfaces. The ambitus is 21 per cent. of test height above the base. The specimen has a very thin test.

The anterior ambulacrum is sunken in the frontal groove and has small, round, non-sunken pores. Each pair is positioned obliquely. The paired ambulacra are flush with the test surface. They are broad at the ambitus and taper substantially towards the apex. The pores are slightly elongate and are identical in both series of the anterior and posterior paired ambulacra. There is a wide, granulated interporiferous zone.

The plastron is made up of a series of single plates placed one behind the other. The labrum is followed by four large single plates which in turn are followed by pairs of alternating plates (Text-fig. 11B).

The apical system is of typical elongate holasteroid structure with four gonopores and ocular plates II and IV meeting at the midline (Text-fig. 11A). The madreporite carries numerous hydropores in addition to its genital pore.

The peristome is situated in an extremely anterior position (8 per cent. of test length from the anterior margin). It is oval, 1·1 times broader than long, and faces anteriorly at the end of the frontal groove. The periproct is not visible.

There is fine and sparse (though regularly spaced) tuberculation on the upper surface. Granulation in between is equally fine and sparse. Larger, more numerous tubercles are present on the oral surface especially along the edges of the plastron and around the anterior margin of the test.

A fairly broad marginal fasciole is visible in parts. It is approximately six miliaries wide and contains inclusions of small tubercles.

Remarks. *Cardiotaxis heberti* is the only representative of this genus found in Maastrichtian strata of Denmark, Rügen, the Maastricht area and the former USSR. It is often found in association with *Cardiaster granulosus* (Goldfuss) from which it may be easily distinguished by its larger, lower and extremely thin test and lack of large adapical interambulacral tubercles. In addition, the plastron of *C. heberti* is made up of the labrum followed by four single plates whilst that of *Cardiaster granulosus* has two single plates after the labrum before the plates become paired and alternate. In *C. heberti*, the peristome is more anterior, situated at the end of the frontal sulcus.

Genus ECHINOCORYS Leske, 1778

Type species. Echinocorys scutatus Leske, 1778, by subsequent designation of Lambert 1897.

Echinocorys obliqua Ravn, 1927

Plate 8, figures 1–3; Text-figures 12, 14B

1927 *Echinocorys obliquus* Ravn, p. 336, pl. 4, fig. 2; pl. 5, fig. 2; text-figs 4–5.
1935 *Echinocorys obliquus* Ravn; Kongiel, p. 36, pl. 3(6), figs 2–3.
1959 *Echinocorys obliquus* Ravn; Poslavskaya and Moskvin, p. 262, pl. 11, figs 3–4, text-fig. 4.
1979 *Echinocorys obliquus* Ravn; Asgaard, tables 1–2.
1979 *Echinocorys obliquus* Ravn; Gongadze, p. 91, pl. 20, fig. 2.

Material. Eighteen specimens: BMNH EE5590–EE5594, EE5600–EE5601, EE5605–EE5613, EE5618–EE5619.

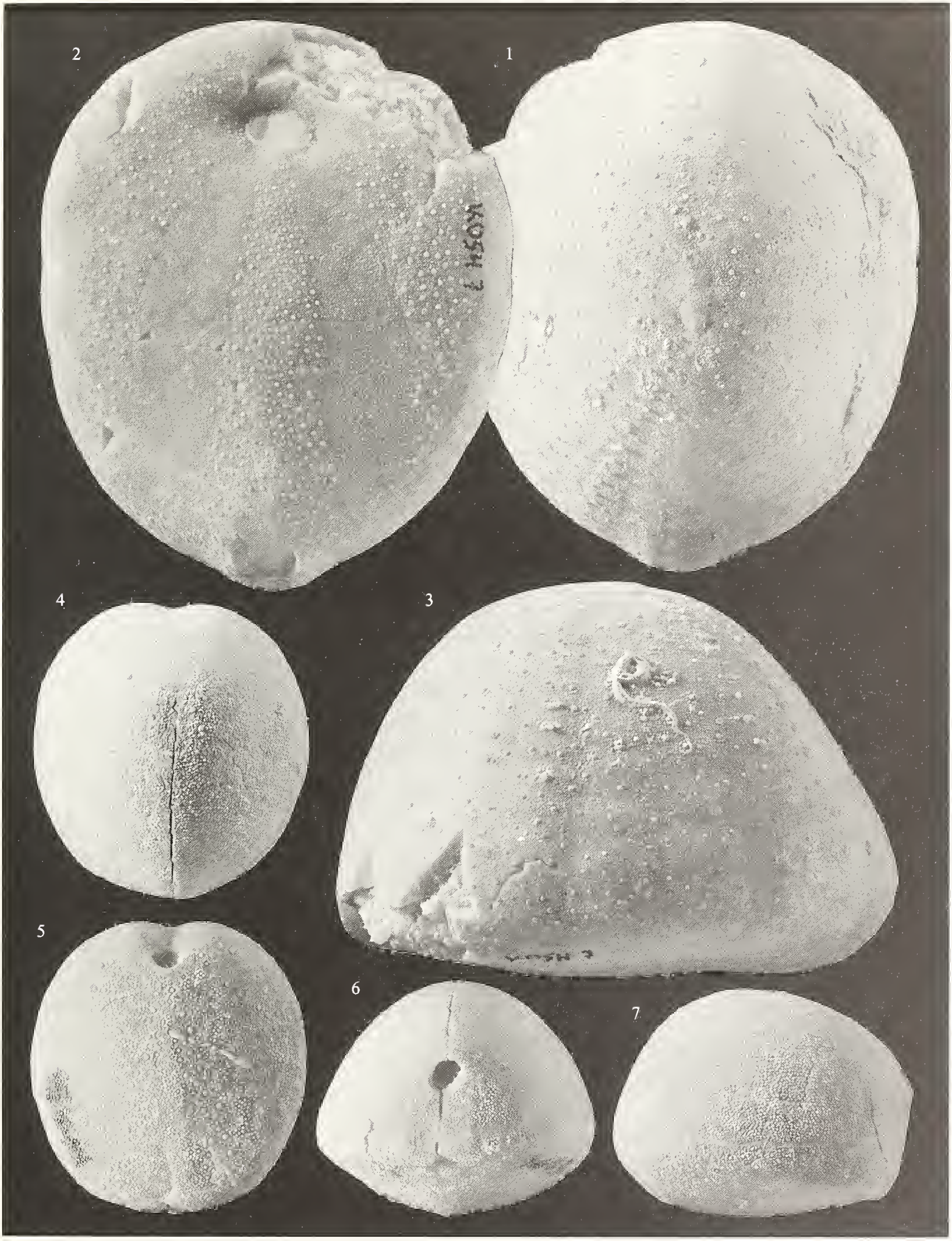
Occurrence. Present in strata from 50 mm below to 0·8 m above the Cretaceous–Tertiary boundary (i.e. predominantly Danian strata) at Kyzylsai and Koshak, Mangyshlak, Kazakhstan. Elsewhere, *Echinocorys obliqua* is known from the Danian of Denmark, Poland, Georgia, Crimea and the northern Caucasus.

Description. This species is remarkably consistent in shape. The test is egg-shaped in horizontal outline with a smoothly rounded anterior margin, tapering towards the posterior. The test is 26·6–44·0 mm long and 23·3–38·7 mm wide (81–91 per cent. of test length). It has a highly vaulted upper surface and a flat base giving it a somewhat rounded sub-conical profile. The height is 16·0–29·8 mm (60–74 per cent. of test length). There is a weak keel running from the apex to the periproct.

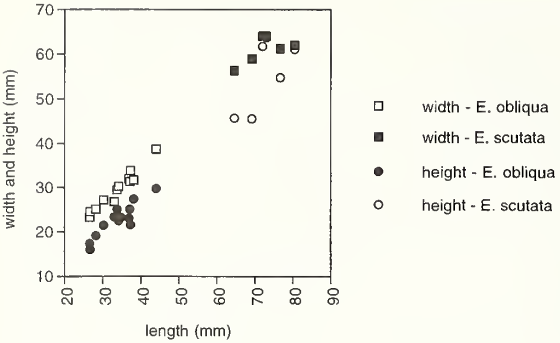
EXPLANATION OF PLATE 8

Figs 1–3. *Echinocorys obliqua* Ravn, 1927; BMNH EE5609; Danian, 0·75 m above Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view. All ×2.

Figs 4–7. *Pseudoffaster caucasicus* (Dru, 1884); BMNH EE5573; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 4, apical view; 5, oral view; 6, posterior view; 7, lateral view. All ×2.



JEFFERY, *Echinocorys*, *Pseudoffaster*



TEXT-FIG. 12. Biometric data for *Echinocorys scutata* Leske, 1778 and *Echinocorys obliqua* Ravn, 1927.

All ambulacra are alike. They are straight and narrow and taper towards the apex. Pores are small and round, becoming smaller still towards the ambitus. They are arranged in slightly oblique pairs at the centre of the ambulacral plates. The interporiferous zone is approximately three times wider than each series of pores. Plating is simple throughout.

The plastron is meridosternous with the labral plate followed by a large single plate and then biserial plating.

The apical system is positioned on the highest part of the test. It is elongate with the anterior and posterior genital plates separated by ocular plates II and IV meeting at the midline (Text-fig. 14B). All four genital plates are similar sized and carry a gonopore. The madreporite also has numerous hydropores.

The peristome is transversely oval and situated anteriorly on the lower surface of the test, 15–19 per cent. of test length from the anterior margin. It is roughly 1·5 times broader than long and is slightly sunken. The mouth is not labiate.

The periproct is marginally positioned, visible both from behind and below. It is small and circular.

Tuberculation is sparse and regularly spaced on the upper surface. The tubercles are small, perforate and crenulate. Granulation in between is equally sparse. On the oral surface tubercles are more abundant. The plastron and anterior and lateral margins show fairly close-packed tuberculation whilst the posterior ambulacral zones are naked.

There are no fascioles.

Echinocorys scutata Leske, 1778

Plate 9, figures 1–6; Text-figures 12, 13A–D, 14A

1959 *Echinocorys pyramidatus* (Portlock); Poslavskaya and Moskvin, p. 259, pl. 8, fig. 2; pl. 9, fig. 1; text-fig. 61.
1959 *Echinocorys ciplyensis* Lambert; Poslavskaya and Moskvin, p. 259, pl. 9, fig. 2; text-fig. 62.
1959 *Echinocorys perconicus* (von Hagenow); Poslavskaya and Moskvin, p. 260, pl. 9, fig. 3; pl. 10, fig. 1; text-fig. 63.
1959 *Echinocorys edhemi* Boehm; Poslavskaya and Moskvin, p. 260, pl. 10, fig. 3; pl. 11, fig. 1; text-fig. 64.
1959 *Echinocorys renngarteni* Poslavskaya and Moskvin, p. 260, pl. 10, fig. 2; text-fig. 65.
1959 *Echinocorys sulcatus* (Goldfuss); Poslavskaya and Moskvin, p. 261, pl. 11, fig. 5; text-fig. 66.
1959 *Echinocorys pyrenaicus* Seunes; Poslavskaya and Moskvin, p. 262, pl. 11, fig. 2; text-fig. 67.
1974 *Echinocorys ovatus* Leske; Savchinskaya, p. 325, pl. 108, figs 2–3.
1974 *Echinocorys ciplyensis* Lambert; Savchinskaya, p. 325, pl. 109, figs 1–4.
1979 *Echinocorys ovatus* Leske; Gongadze, p. 76, pl. 7, fig. 1.
1979 *Echinocorys* cf. *pyramidatus* (Portlock); Gongadze, p. 77, pl. 8, fig. 1.
1979 *Echinocorys conoideus* (Goldfuss); Gongadze, p. 78, pl. 9, fig. 1.
1979 *Echinocorys elatus* Arnaud; Gongadze, p. 79, pl. 10, fig. 1.
1979 *Echinocorys kharagoulensis* Gongadze, p. 80, pl. 11, fig. 1; pl. 12, fig. 1.
1979 *Echinocorys perconicus* von Hagenow; Gongadze, p. 82, pl. 13, fig. 1.
1979 *Echinocorys renngarteni* Poslavskaya and Moskvin; Gongadze, p. 83, pl. 14, fig. 1.
1979 *Echinocorys pyrenaicus* Seunes; Gongadze, p. 84, pl. 15, fig. 1.
1979 *Echinocorys ciplyensis* Lambert; Gongadze, p. 85, pl. 16, fig. 1.

1979 *Echinocorys subglobosus* var. *fonticola* Arnaud; Gongadze, p. 86, pl. 17, fig. 1.
1979 *Echinocorys conicus* (Agassiz); Gongadze, p. 88, pl. 18, fig. 1.
1979 *Echinocorys edhemi* Böhm; Gongadze, p. 89, pl. 19, fig. 1.
1979 *Echinocorys depressus* (Eichwald); Gongadze, p. 90, pl. 20, fig. 1.
1979 *Echinocorys katscharavai* Tsagareli; Gongadze, p. 93, pl. 20, fig. 3.

Material. Six specimens: BMNH EE5577–5579 and EE5615–5617.

Occurrence. Upper Maastrichtian strata (*B. casimirovensis* Zone) of Mangyshlak, Kazakhstan, 12–16 m below the Cretaceous–Tertiary boundary. Elsewhere, *Echinocorys scutata* is known from chalk facies world-wide, ranging throughout the Maastrichtian and Danian.

Description. Tests are oval in horizontal outline and 64·6–80·5 mm long. Maximum width is 77–89 per cent. of test length and occurs just anterior of centre. Test profile is highly variable: it ranges from flat-based and conical to low and exceptionally rounded. Height varies from 66 to 87 per cent. of test length. None of the specimens shows a marked keel.

Ambulacra are as those described for *Echinocorys obliqua* above except that the pore-pairs are not positioned obliquely and the interporiferous zone is much broader in *Echinocorys scutata*. This, however, may just be a function of larger size. Interambulacral plating is also as described above for *E. obliqua*. The plastron is meridosternous.

The apical system is positioned on the highest part of the test. It is of typical elongate holasteroid structure.

The peristome is situated anteriorly, 15–21 per cent. of test length from the anterior margin. It is transversely elongate with no labral projection.

The periproct is situated inframarginally and is visible only from below. It is circular and approximately half the size of the mouth.

Tuberculation on the apical surface is so fine and sparse that the test appears superficially to be tubercle-free. On the oral surface tubercles are far larger and more abundant. As in *Echinocorys obliqua*, tubercles are restricted to the plastron and anterior and lateral margins of the test.

No fascioles are present.

Remarks. The specimens described here are very variable in shape: from flat-based and conical to exceptionally globular (Text-fig. 13). Previous authors have erected a large number of species to accommodate such differently shaped 'varieties'. The six specimens available appear, however, to form a gradational series and, as no structural differences can be distinguished, they are here treated as a single species complex, following van der Ham *et al.* (1987).

Echinocotys scutata and *E. obliqua* are found in different stratigraphical horizons in the Mangyshlak sections (Maastrichtian and Danian respectively). Apart from *E. scutata* always being much larger than *E. obliqua*, they differ most noticeably in the presence of a distinct carina in *E. obliqua* running from the apex to the posterior on the upper surface of the test. *E. obliqua* also has oblique pairs of ambulacral pores and a periproct that is visible both from behind and from below. As noted above some of these character differences may be size-related. However, the studied specimens of *E. obliqua* show a strikingly consistent morphology despite their size differences, and appear to represent a single growth series.

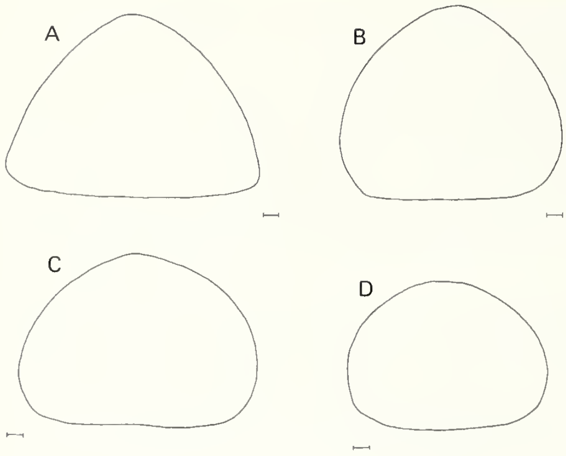
Genus GALEASTER Seunes, 1889

Type species. Galeaster bertrandi Seunes, 1889, by original designation.

Galeaster bertrandi Seunes, 1889

Plate 7, figures 1–8; Text-figures 14F–H, 15

1889 *Galeaster bertrandi* Seunes, p. 822, pl. 27, figs 2–3.
1959 *Galeaster minor* Poslavskaya; Poslavskaya and Moskvin, p. 273, pl. 17, figs 9–10.
1959 *Galeaster sumbaricus* Poslavskaya; Poslavskaya and Moskvin, p. 273, pl. 17, figs 7–8
1960 *Galeaster minor* Poslavskaya; Poslavskaya and Moskvin, p. 58, pl. 2, figs 3–4, 7.



TEXT-FIG. 13. *Camera lucida* drawings of *Echinocorys scutata* Leske, 1778; lateral views. A, BMNH EE5615. B, BMNH EE5579. C, BMNH EE5616. D, BMNH EE5617. Scale bars represent 5 mm.

1960	*Galeaster sumbaricus* Poslavskaya; Poslavskaya and Moskvin, p. 57, pl. 2, figs 1–2.
?1960	*Galeaster dagestanensis* Poslavskaya and Moskvin, p. 59, pl. 2, fig. 6.
1979	*Galeaster* cf. *bertrandi* Seunes; Gongadze, p. 107, pl. 25, fig. 2.
1979	*Galeaster* cf. *minor* Poslavskaya and Moskvin; Gongadze, p. 108, pl. 25, fig. 3.

Material. Five specimens: BMNH EE5588–EE5589, EE5595–EE5596, EE5614.

Occurrence. Danian strata (0·38–0·95 m above the Cretaceous–Tertiary boundary) at Koshak, Mangyshlak, Kazakhstan. *Galeaster bertrandi* was recorded previously from the Maastrichtian of Georgia and the Danian of the eastern Pyrenees. *G. sumbaricus* is also found in the Lower to Upper Maastrichtian of the northern Caucasus and the Transcaspian region, whilst *G. minor* and *G. dagestanensis* are known from the Lower to Upper Danian of Georgia, the northern Caucasus and the Transcaspian region.

Description. The test is heart-shaped in horizontal outline, broadest anteriorly and tapering towards the vertically truncate posterior. The specimens are 15·9–21·2 mm long and 14·2–20·0 mm wide (88–96 per cent. of test length; Text-fig. 15). The distinct frontal groove is deepest at the ambitus and runs all the way to the mouth. On the upper surface it shallows towards the apex. The test is 13·1–16·9 mm high (77–83 per cent. of test length). The ambitus is at one-quarter to one-third height from the base. The test is globular in profile with the upper surface highly vaulted. Both the oral and apical surfaces are weakly keeled posteriorly.

The anterior ambulacrum is sunken in the frontal groove. Its pores are round and minute with each pair situated very obliquely at the adoral centre of the plate. Interambulacral and ambulacral plates of the paired ambulacra are of similar dimensions with one interambulacral plate adjacent to each ambulacral plate. Ambulacral plates are high. Pores in the paired ambulacra are only slightly larger than those of the frontal ambulacrum. The pores of each pair are very close together. Pore-pairs are positioned as in the frontal ambulacrum although a little less obliquely.

The plastron is orthosternous with labral and sternal plates having a fairly broad contact surface (Text-fig. 14H).

The apical system is situated at the highest point on the test, 32 per cent. of test length from the anterior margin. It is of elongate structure with ocular plates II and IV separating the anterior and posterior genital plates. It is difficult to ascertain the position of the posterior ocular plates in many of the specimens. However,

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EXPLANATION OF PLATE 9

Figs 1–6. *Echinocorys scutata* Leske, 1778; Upper Maastrichtian, 12–14 m below Cretaceous–Tertiary boundary, Kyzylsai, Mangyshlak, Kazakhstan. 1–3, BMNH EE5615; 1, apical view; 2, oral view; 3, lateral view. 4, BMNH EE5578; apical view. 5–6, BMNH EE5616; 5, lateral view; 6, oral view. All × 1.

PLATE 9

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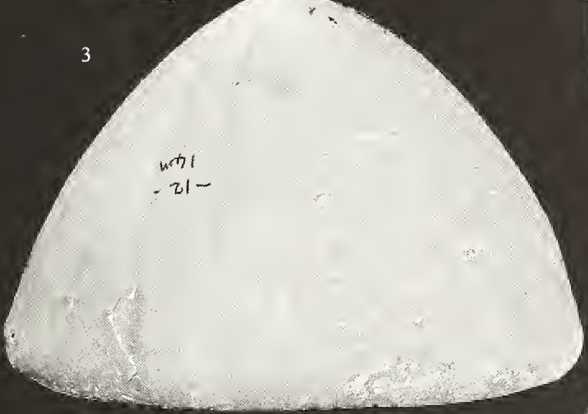

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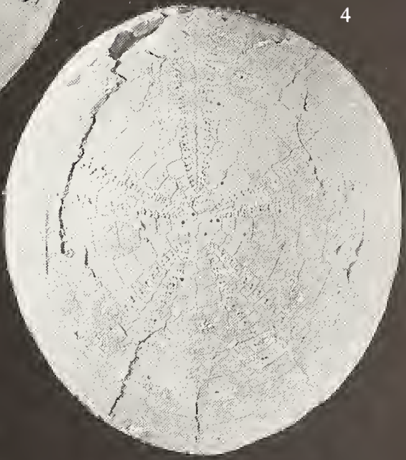

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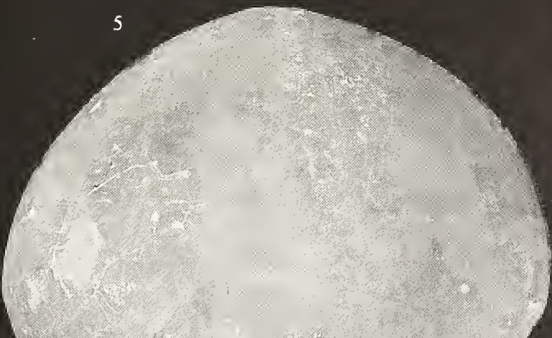
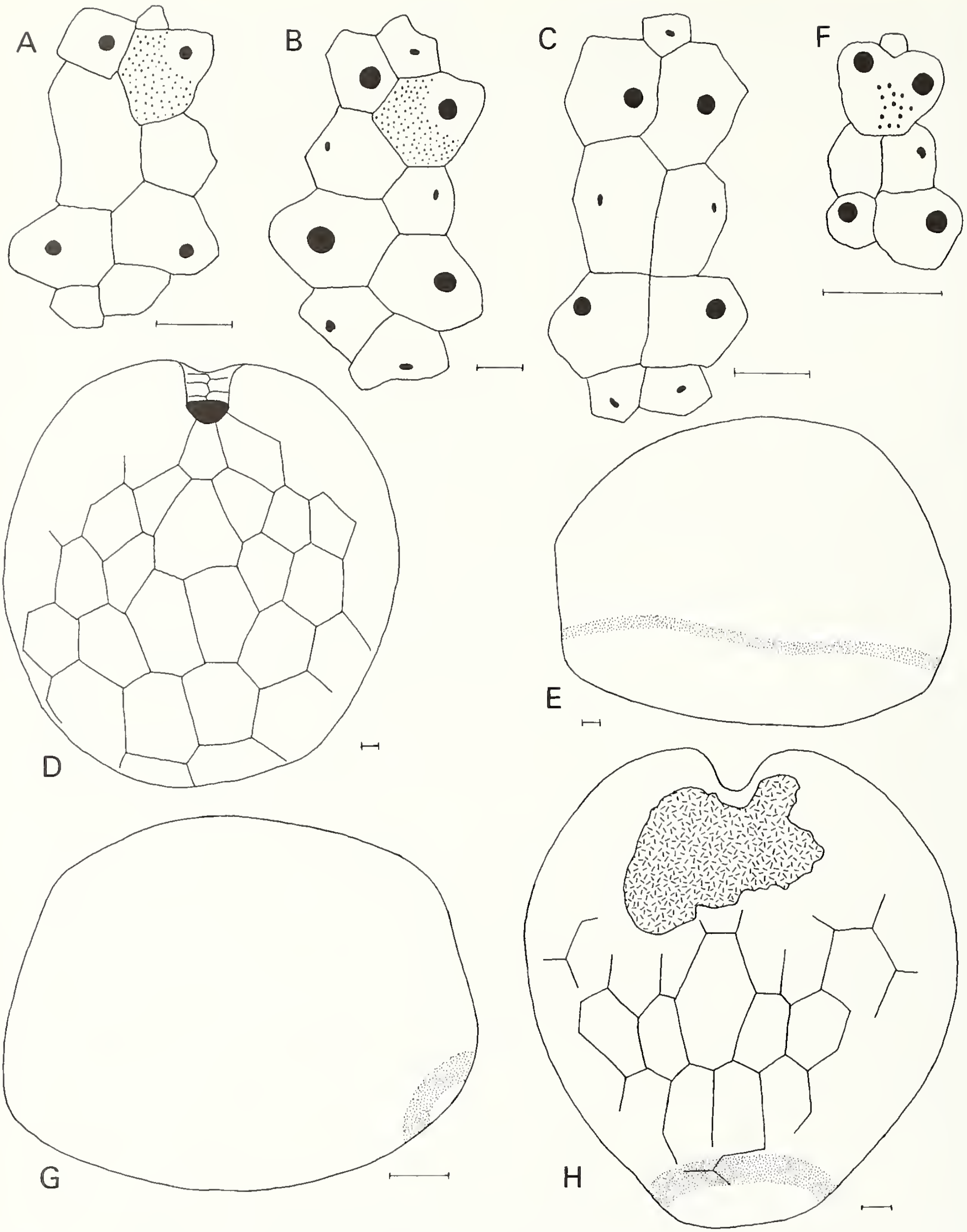


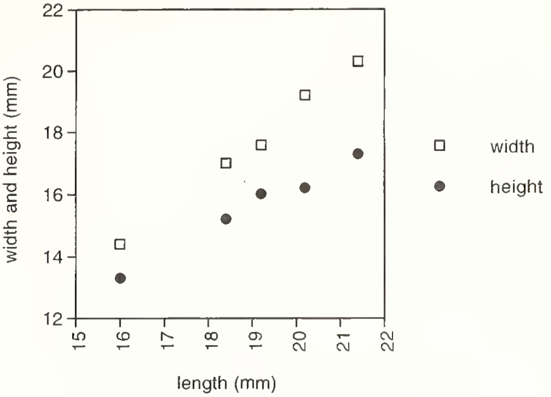
6

JEFFERY, *Echinocorys*



TEXT-FIG. 14. *Camera lucida* drawings of *Echinocorys scutata* Leske, 1778, *Echinocorys obliqua* Ravn, 1927, *Pseudoffaster caucasicus* (Dru, 1884) and *Galeaster bertrandi* Seunes, 1889. A, *Echinocorys scutata*; BMNH EE5579; apical disc plating. B, *Echinocorys obliqua*; BMNH EE5609; apical disc plating. C–E, *Pseudoffaster caucasicus*; BMNH EE5573; C, apical disc plating; D, oral view showing plastron plating; E, lateral view

TEXT-FIG. 15. Biometric data for *Galeaster bertrandi* Seunes, 1889.



where visible, they appear to be disjunct, and not in contact with the posterior genital plates (Text-fig. 14F). Genital plates 2 and 3 are fused and carry several hydropores in addition to the two gonopores. Gonopores are also present on the remaining two genital plates.

The peristome is circular to elongate oval in outline with its greatest diameter 11 per cent. of test length. It is flush with the test and is situated at the end of the deep frontal groove, visible from both the anterior and lower surfaces.

The periproct is situated high on the truncate posterior. It is of similar dimensions to the mouth (10–13 per cent. of test length) and is also circular in outline.

A broad and distinct subanal fasciole is present (Text-fig. 14G–H). It is oval in shape, crossing at the posterior of the sternal plates. It measures 12–15 miliaries across with no inclusions of larger tubercles.

Tuberculation is relatively sparse on the upper surface of the test. Small scattered tubercles are interspersed with fine granulation. Larger tubercles are present immediately adjacent to the apex and dense granulation extends along the centre of the frontal groove. On the lower surface, tuberculation is far denser and the individual tubercles are of greater dimensions. All are perforate, crenulate and not sunken. The largest tubercles are situated along the outer edges of the plastron where their areoles show a preferred enlargement towards the midline and posterior. The ambital area is intermediate in its size and density of tuberculation.

Remarks. *G. bertrandi* differs from *Galeaster carinatus* Ravn in the structure of the plastron. The plastron of *G. bertrandi*, as described above, is orthosternous in construction with the labral plate in broad contact with the following unpaired plate. *G. carinatus*, on the other hand, has a disjunct plastron, with the labrum and sternum separated by the adjoining ambulacra meeting at the midline. However, it has been postulated (David 1988, p. 336) that slight breaks between the labrum and sternum may represent intraspecific variation. In modern taxa, such variation in the degree of separation has been shown to occur with growth (David 1987). Specimens of *G. carinatus* tend to be larger and it could be that this pattern of increasing disjunction is a function of increased size and that the two ‘species’ form part of the growth series of a single species. Poslavskaya and Moskvin (1960) described an even larger species, *Galeaster dagestanensis*. Unfortunately, no details of plastron plating were given. If, with further study, it transpires that this species has a widely disjunct plastron, all nominal species may prove to form part of a single growth series.

The taxonomic confusion surrounding this genus is due in part to the absence of reliable plating information for the named species. Poslavskaya and Moskvin (1960) provided the same text-figures

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showing position of marginal fasciole. F–H, *Galeaster bertrandi*. F, BMNH EE5614; apical disc plating. G–H, BMHN EE5595; G, lateral view showing position of subanal fasciole; H, oral view showing plastron plating. A and G, scale bars represent 2 mm. B–F and H, scale bars represent 1 mm.

with their descriptions of both *G. minor* and *G. sumbaricus*. In this paper, *G. bertrandi* Seunes, *G. minor* Poslavskaya, *G. sumbaricus* Poslavskaya and *G. dagestanensis* Poslavskaya (tentatively) are synonymized as they are distinguished only by subtleties of test shape with no discernible structural differences.

Genus PSEUDOFFASTER Lambert, 1927

Type species. Holaster caucasicus Dru, 1884, by original designation.

Pseudoffaster caucasicus (Dru, 1884)

Plate 8, figures 4–7; Text-figure 14C–E

1884	*Offaster caucasicus* Dru, p. 514, pl. 26, figs 5–10.
1927	*Pseudoffaster caucasicus* (Dru); Lambert 1927, p. 42.
1938	*Pseudoffaster caucasicus* (Dru); Schmidt, p. 78, pl. 25, figs 6–9; pl. 26, figs 6–7.
1938	*Pseudoffaster renngarteni* Schmidt, p. 80, pl. 25, figs 1–5; pl. 26, figs 1–3.
1959	*Pseudoffaster caucasicus* (Dru); Poslavskaya and Moskvin, p. 270, pl. 7, fig. 2.
1959	*Pseudoffaster renngarteni* Schmidt; Poslavskaya and Moskvin, p. 271, pl. 17, fig. 3.
1959	*Pseudoffaster schmidti* Poslavskaya and Moskvin, p. 270, pl. 17, fig. 1.
1979	*Pseudoffaster* cf. *caucasicus* (Dru); Gongadze, p. 104, pl. 24, fig. 2.
1979	*Pseudoffaster renngarteni* Schmidt; Gongadze, p. 105, pl. 24, fig. 3.

Material. Three specimens: BMNH EE5572–EE5574.

Occurrence. Uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan: 14–16 m below the Cretaceous–Tertiary boundary. Elsewhere, *P. caucasicus* is known from the Maastrichtian of Spain and *P. schmidti* and *P. renngarteni* from the Lower to Upper Maastrichtian of the former USSR. *P. caucasicus* and *P. schmidti* are also recorded from Campanian strata of the former USSR.

Description. The test is oval in horizontal outline with a shallow frontal notch and slight posterior truncation. The specimens are 18·9 to 23·3 mm long, with the greatest width, 92–96 per cent. of test length, centrally. The frontal notch is deepest at the ambitus and is traceable all the way to the peristome. The test is somewhat gibbous in profile with a highly inflated upper surface and convex lower surface and with an approximately vertically truncated posterior. The greatest height is 78–82 per cent. of test length, 38 per cent. of test length from the anterior margin. The ambitus is positioned at 27–32 per cent. of test length above the base.

The frontal ambulacrum is sunken. Paired pores are minute, no more than 0·1 mm in diameter, and are positioned obliquely and towards the adoral centre of the plates. The paired ambulacra are flush with the test. The pores are small, round and again positioned towards the adoral centre of the plates. They are hardly oblique. All ambulacra are non-petaloid, straight and taper a little towards the apex.

Ambulacra and interambulacra are of approximately the same width at the ambitus (39 per cent. of test length). The plates are also of roughly the same size with each interambulacral plate adjacent to a single ambulacral plate. The plastron is orthosternous in structure (Text-fig. 14D).

The apical system is positioned at the highest point on the test. It is of typical holasteroid structure – elongate with the anterior oculars meeting at the midline and with four gonopores (Text-fig. 14C).

The peristome is anterior facing, visible from the anterior and lower surfaces and positioned 6–7 per cent. of test length from the anterior margin. It is small and circular, with no labral projection.

The periproct is situated high on the truncate posterior, 49–53 per cent. of test height from the base, under a slight projection. It is circular and of similar dimensions to the peristome.

A distinct narrow marginal fasciole, six to eight miliaries wide, runs below the periproct and is discernible around the complete test margin (Text-fig. 14E). It contains no inclusions of larger tubercles.

Tuberculation on the apical surface is extremely sparse and inconspicuous, although there are tubercles present near the apex, around the ambitus and low down on the interambulacra adjoining the frontal groove. Dense granulation covers the remainder of the upper surface. On the oral surface larger tubercles are present along the edges of the plastron with areoles enlarged latero-posteriorly. Further large tubercles are situated in the remaining interambulacra. Dense granulation fills the spaces between the tubercles. All tubercles are perforate, crenulate and not sunken.

Remarks. P. caucasicus (Dru) and *P. schmidti* Moskvin are both recorded previously only from the Campanian of the former Soviet Union, whilst *P. renngarteni* Schmidt has been collected exclusively from Maastrichtian strata. However, all three have been distinguished merely on subtleties of shape and size and form a gradational series. There appear to be no structural differences on which to distinguish them and consequently they are synonymized in this paper.

Order SPATANGOIDA Claus, 1876
Family MICRASTERIDAE Lambert, 1920

Genus CYCLASTER Cotteau, *in* Leymerie and Cotteau, 1856
[= *Brissopneustes* Cotteau, 1887 (type species *Brissopneustes vilanovae* Cotteau, by original designation); *Isopneustes* Seunes, 1888 (*non Isopneustes* Pomel, 1883)]

Type species. Cyclaster declivus Cotteau, *in* Leymerie and Cotteau, 1856, by original designation.

Remarks. Despite being placed in separate families (*Cyclaster* in Brissidae and *Brissopneustes* in Micrasteridae), *Cyclaster* and *Brissopneustes* differ in their original definitions only in the presence or absence of a peripetalous fasciole. However, several of the species studied have either a partial peripetalous fasciole, which is distinct posteriorly and completely absent anteriorly, or an indistinct peripetalous fasciole most obvious at the ends of the petals and elsewhere made up of miliary tubercles crowded together to varying degrees. There is a complete gradation between those forms with a fully developed peripetalous fasciole and those without. The presence of a peripetalous fasciole is therefore not a reliable diagnostic feature and consequently, *Cyclaster* and *Brissopneustes* are synonymized.

The presence of subanal and peripetalous fascioles has been used as a diagnostic character for Brissidae. As the presence of a peripetalous fasciole has been demonstrated to be impersistent this character is no longer sufficient by itself for familial differentiation. Other differences between Micrasteridae and Brissidae include an ethmophract apical system and mesamphisternous plastron structure in micrasterids compared with an ethmolytic arrangement and an ultramphisternous plastron in the brissids. Since plastron plating is consistently mesamphisternous and the apical system always ethmophract within the *Cyclaster* species studied, *Cyclaster* is here assigned to the Micrasteridae.

The genus *Isopneustes* Pomel (type species *Cyclaster bourgeosi* Cotteau) has four gonopores and a petaloid unpaired ambulacrum. However, Seunes (1888) assigned three-gonopored Cretaceous spatangoids to *Isopneustes*, claiming that the name *Cyclaster* was only applicable to post-Cretaceous species. *Isopneustes* Seunes is thus synonymized with *Cyclaster*.

Cyclaster integer (Seunes, 1888)

Plate 10, figures 1–4; Text-figures 16, 17A–C

1888 *Isopneustes integer* Seunes, p. 798, pl. 28, fig. 1.
1888 *Isopneustes munieri* Seunes, p. 798, pl. 28, fig. 4.
1897 *Brissopneustes danicus* Schlüter, p. 18, pl. 1, figs 1–4.
1926 *Brissopneustes danicus* Schlüter; Ødum, p. 163.
?1926 *Cyclaster brünnichi* Ravn; Ødum, p. 163.
1927 *Brissopneustes danicus* Schlüter; Ravn, p. 349, pl. 4, figs 5–6.
1927 *Cyclaster brünnichi* Ravn, p. 345, pl. 5, fig. 5.
?1933 *Brissopneustes decaryi* Lambert, p. 19, pl. 3, figs 9–10.
1940 *Cyclaster pygmeus* Rouchadze, pp. 129, 155, 176, pl. 3, fig. 7.
1959 *Cyclaster integer* (Seunes); Poslavskaya and Moskvin, p. 291, pl. 26, figs 4–5; text-fig. 107.
1959 *Cyclaster danicus* (Schlüter); Poslavskaya and Moskvin, p. 291, pl. 26, fig. 6; text-fig. 108.
1960 *Cyclaster danicus* (Schlüter); Poslavskaya and Moskvin, p. 70, pl. 5, fig. 6; text-fig. 21.
1960 *Cyclaster integer* (Seunes); Poslavskaya and Moskvin, p. 69, pl. 5, figs 4–5; text-fig. 20.

1979	*Cyclaster danicus* (Schlüter); Gongadze, p. 131, pl. 33, figs 1–2.
1979	*Cyclaster bruennichi* Ravn; Asgaard, tables 1–2.
1979	*Cyclaster danicus* (Schlüter); Asgaard, tables 1–2.
?1979	*Brissopneustes decaryi* Lambert; Tanaka, p. 44, pl. 3, fig. 8.

Material. Thirteen specimens: BMNH EE5581–EE5587, EE5597–EE5599, EE5602–EE5604.

Occurrence. Danian strata (0·37–0·8 m above the Cretaceous–Tertiary boundary) at Koshak, Mangyshlak, Kazakhstan. Elsewhere, this species is recorded from the Maastrichtian of Azerbeijan, the Maastrichtian and Danian of the Pyrenees, the Georgian Republic, the northern Caucasus and the Transcaspian region as well as from the Danian of Denmark and Madagascar.

Description. The test is coffin-shaped with the widest point anteriorly. It is 20·4–28·8 mm long and 16·1–24·3 mm wide (79–89 per cent. of test length; Text-fig. 16). The broad, shallow frontal groove is deepest adapically and shallows to become flush by the ambitus. The anterior margin is smoothly rounded. The upper surface of the test is more strongly vaulted than the lower surface and has a weak keel running posteriorly from the apex to the periproct. The test is 12·2–18·8 mm high (60–70 per cent. of test length).

The unpaired ambulacrum is non-petaloid and lies in a shallow flat-based furrow. Its pores are round, very small and oblique, with those of each pair lying very close together in a hollow separated by a granule. The distance between pore-pairs becomes greater away from the apex and the pore zones diverge strongly. Further from the apex, the pores are situated very low on each plate. The paired ambulacra are petaloid and very slightly sunken. Anterior petals diverge at 110–115° and contain 10–14 pore-pairs. Posterior petals diverge at an angle of 50–60° and comprise 14–18 pore-pairs. Anterior and posterior petals are approximately equal in length. In both pairs of petals, pores are round in the anterior series and a little elongated in the posterior series. Pores are present in ambulacral plates beyond the distal ends of the petals. The interporiferous zone is broader than each poriferous zone.

The plastron is mesaphisternous with a long, narrow labrum (Text-fig. 17B).

The apical system is positioned centrally. It is ethmophract with three gonopores, the madreporite being imperforate but carrying numerous hydropores (Text-fig. 17C).

The peristome is small and transversely oval to kidney-shaped with a thickened rim. It is weakly labiate and lies anteriorly, 25 per cent. of test length from the anterior margin.

The small circular periproct is positioned very high on the truncate posterior.

A distinct subanal fasciole is present. It is six to seven miliaries across and has a simple oval shape in smaller specimens. In larger specimens there is a marked bend under the periproct. A more-or-less distinct peripetalous fasciole is visible in the larger specimens indenting distinctly between the anterior and posterior paired ambulacra (Text-fig. 17A). It is also six to seven miliaries wide although it contains inclusions of large tubercles. This fasciole is lost forward of the anterior paired petals.

The upper surface of the test is covered in dense and quite coarse granulation with sparse, small tubercles interspersed. Tuberculation is denser and coarser on the oral surface especially around the anterior margin of the test and on the edges of the plastron where areoles show a preferred direction of enlargement.

Remarks. Cyclaster vilanovae (Cotteau) is similar in overall appearance, but tapers a little more towards the posterior in horizontal outline. It appears to be slightly more inflated, although the ranges of height as a percentage of test length do overlap between the two species (68–77 per cent. in *C. vilanovae* and 60–70 per cent. in *C. integer*). *C. vilanovae* has a less labiate mouth and paired

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EXPLANATION OF PLATE 10

Figs 1–4. *Cyclaster integer* (Seunes, 1888); BMNH EE5585; Danian, 0·6–0·8 m above Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 5, apical view; 6, oral view; 7, lateral view; 8, posterior view. All ×2.

Figs 5–8. *Cyclaster galei* sp. nov.; BMNH EE5575, holotype; uppermost Maastrichtian, *B. casimirovensis* Zone, 14–16 m below Cretaceous–Tertiary boundary, Koshak, Mangyshlak, Kazakhstan. 1, apical view; 2, oral view; 3, lateral view; 4, posterior view. All ×2.

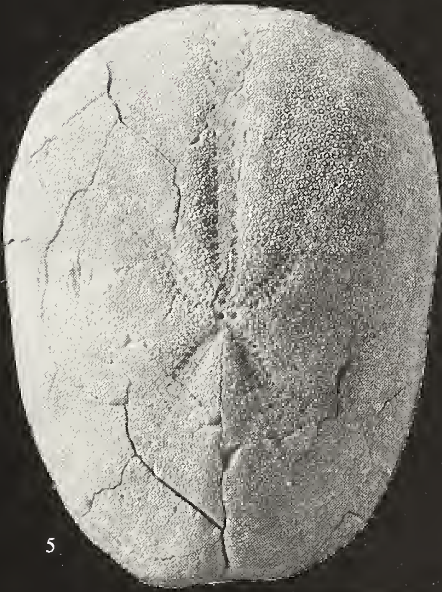
PLATE 10


1


3


2


4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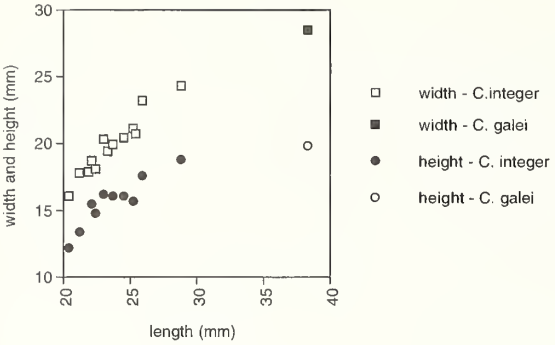
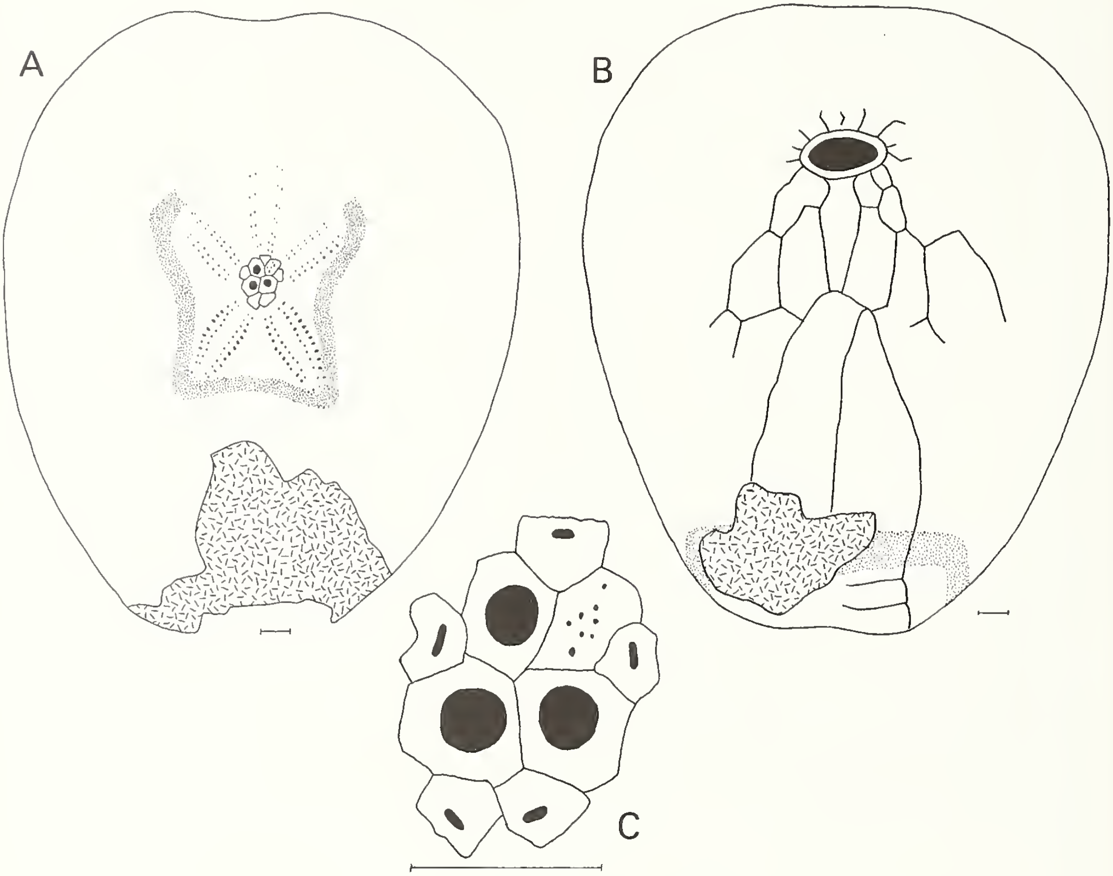
8

JEFFERY, *Cyclaster*

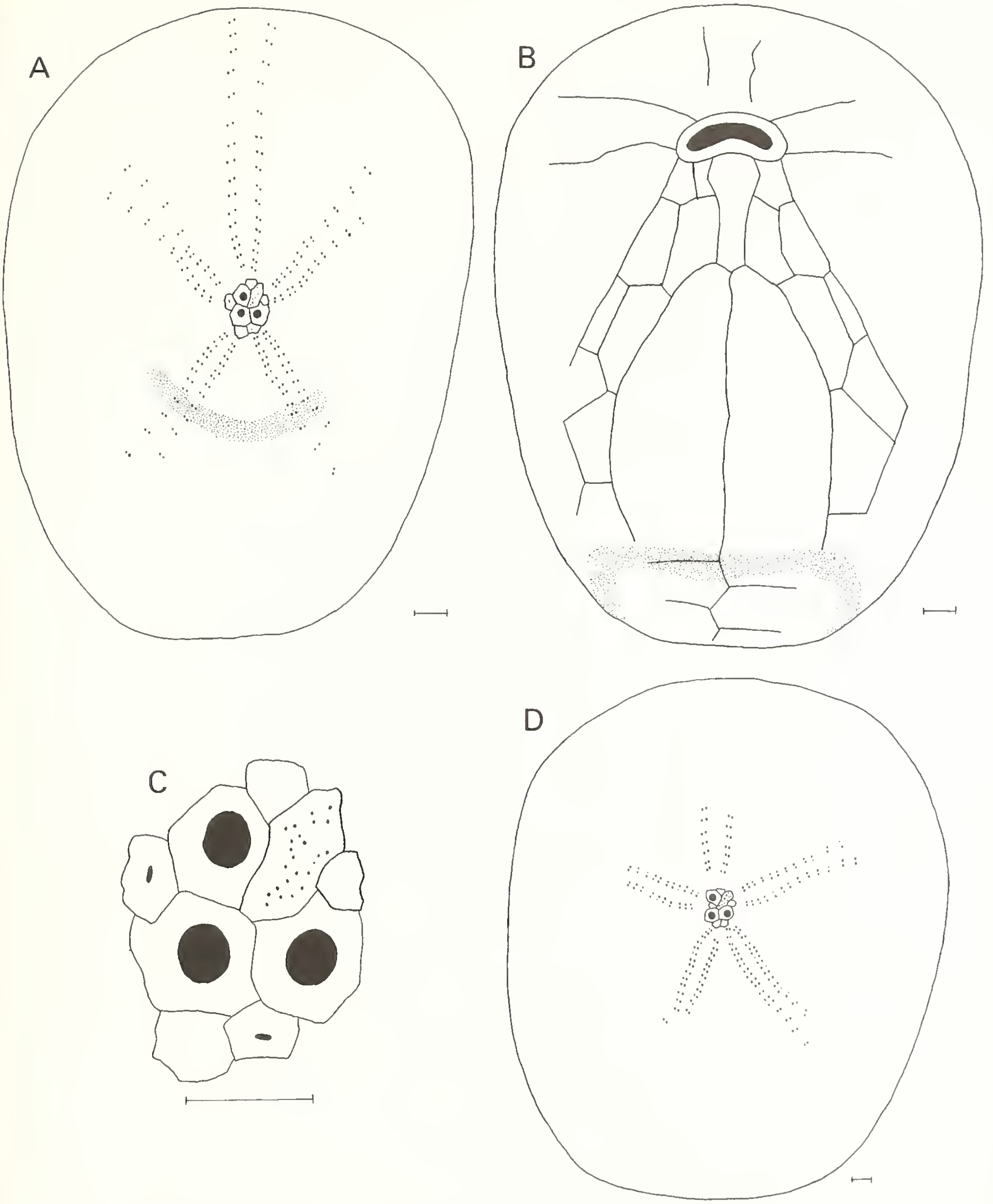


TEXT-FIG. 16. Biometric data for *Cyclaster integer* (Seunes, 1888) and *Cyclaster galei* sp. nov.



TEXT-FIG. 17. *Camera lucida* drawings of *Cyclaster integer* (Seunes, 1888). A–B, BMNH EE5585; A, apical view showing position and extent of peripetalous fasciole; B, apical disc plating. C, BMNH EE5581; oral view showing plastron plating. Scale bars represent 1 mm.

ambulacra that differ from those of *C. integer*. The petals are broader with more elongate pores and a narrower interporiferous zone. Additionally, *C. vilanovae* shows only an indistinct and incomplete peripetalous fasciole which is clearest posteriorly.



TEXT-FIG. 18. *Camera lucida* drawings of *Cyclaster galei* sp. nov. and *Cyclaster suecicus* (Schlüter). A–C, *Cyclaster galei*; BMNH EE5575, holotype; A, apical view showing position and extent of peripetalous fasciole; B, oral view showing plastron plating; C, apical disc plating. D, *Cyclaster suecicus*; Geological Museum, Copenhagen specimen number 2455; lower Danian of Denmark; apical view. A–B, scale bars represent 2 mm. C–D, scale bars represent 1 mm.

Cyclaster galei sp. nov.

Plate 10, figures 5–8; Text-figures 16, 18A–C

Material. Three specimens: holotype, BMNH EE5575, and paratypes, BMNH EE5576 and EE5626.

Occurrence. Two specimens, including the holotype, were collected from the uppermost Maastrichtian (*B. casimirovensis* Zone) of Koshak, Mangyshlak, Kazakhstan, 14–16 m below the Cretaceous–Tertiary boundary. The third specimen was collected from the Maastrichtian (165 m below the Cretaceous–Tertiary boundary) at Kyzylsai, Mangyshlak, Kazakhstan.

Description. The most complete test is 38·3 mm long, with a rounded rectangular shape in horizontal outline. Its greatest width is 28·5 mm (74 per cent. of length) at 9 mm from the smoothly rounded anterior margin, and it tapers a little posteriorly. The greatest height is 19·8 mm (52 per cent. of test length) at the posterior margin. The ambitus is at approximately mid-height. In profile, the test has a truncate posterior and the broad, flattened upper surface of the test has a slight downward slope towards the smoothly convex anterior. The base is slightly convex at the margins.

All five ambulacra are sunken adapically and taper towards the apical system. The anterior ambulacrum is non-petaloid. It runs along a shallow groove adapically which shallows and broadens, becoming flush by the ambitus. Pores are paired throughout but only about 12 sets in the upper 8 mm of the ambulacrum are enlarged. The paired ambulacra are petaloid and open distally. The anterior pair are straight with a very slight forward sweep and are 6·1 mm (EE5575) to 8·3 mm long and 1·2–1·4 mm wide. They diverge at 90°. There are ten pore-pairs in each anterior petal. The posterior paired ambulacra are straight and are 5·3 mm (EE5575) to 7·3 mm long (87–88 per cent. length of anterior petals) and 1·4–1·7 mm wide. They diverge at 60°. There are nine pore-pairs in each petal. Paired pores are apparent beyond the end of the petals although they are much smaller and more widely spaced.

The interambulacral areas are slightly elevated, forming ridges between the petals. All five interambulacra reach the peristome. The plastron is mesamphisternous (Text-fig. 18B) and is 16·8 mm long (44 per cent. of test length). The labrum is elongate measuring approximately 20 per cent. of test length and projects prominently over the peristome.

The apical system is slightly sunken below the surrounding interambulacral areas and lies 17·8 mm (47 per cent. of test length) from the anterior margin. It is approximately twice as long as broad, with the madreporite in contact with the other three genital plates. Oculars I and V abut at the posterior. The apical system is ethmophract and has three large gonopores: the madreporite lacks a genital pore but has hydropores densely distributed over its surface (Text-fig. 18C).

The peristome is positioned anteriorly at 20 per cent. of test length from the anterior margin and is visible in anterior view. It is kidney-shaped with the long axis running transversely and is 4·8–5·6 mm wide and 2 mm long. It has a distinct thickened rim and a labrum that extends prominently over the peristome. The ambulacra are slightly sunken adjacent to the peristome.

The periproct is approximately circular, 3·6 mm high by 3·2 mm wide. It is positioned high on the truncate posterior end of the test.

A broad subanal fasciole is present running below the periproct and composed of 12–14 rows of closely packed miliary tubercles. Within the fasciole is a pair of densely tuberculated areas and three enlarged pore-pairs are present at each lateral edge. Only a short portion of a peripetalous fasciole is visible running just beyond the ends of the posterior petals (Text-fig. 18A). This is an original feature as the tuberculation is well preserved over the whole surface of the test.

Tubercles on the aboral surface are so minute that the test looks superficially tubercle-free. However, the adapical interambulacra are slightly more coarsely tuberculated than the remainder of the upper surface and larger and more closely packed tubercles also run along the borders of the anterior ambulacrum. On the oral surface, the plastron has large, fairly densely packed tubercles with posteriorly enlarged areoles although these do not extend onto the labrum. The periplastronal zones are also tubercle-free but are granular in appearance. All tubercles are perforate and crenulate and slightly sunken.

Remarks. Cyclaster galei has a characteristic oblong outline seen only in two other species: *Cyclaster ruegensis* (Kutscher) and *Cyclaster suecicus* (Schlüter).

Cyclaster ruegensis, from the Lower Maastrichtian of the Isle of Rügen, also has a low test of rectangular horizontal outline and short, virtually flush petals. However, it is much broader than

C. galei with its widest dimension 91–95 per cent. of test length compared with 74 per cent. in *C. galei*. It also has more divergent anterior petals (110° compared with 90° in *C. galei*). All known specimens of *C. ruegensis* are somewhat crushed and damaged with details of the oral surface unclear. *C. ruegensis* has no trace of a peripetalous fasciole.

Cyclaster suecicus (Schlüter), from the Danian of Denmark, is also rectangular in horizontal outline and has paired petals of approximately equal lengths that are open distally. However, the test of *C. suecicus* is broader and more inflated, with a test width of 85–91 per cent. of test length compared with 74 per cent. in *C. galei*. The paired ambulacra are less depressed and the anterior pair are far more divergent in *C. suecicus* (130° compared with 90° in *C. galei*) (Text-fig. 18D). The mouth is also smaller, less labiate and situated in a more posterior position, 24–25 per cent. of test length from the anterior margin. No peripetalous fasciole, however faint or incomplete, is found in *C. suesicus*.

Cyclaster integer (Seunes) is the only other spatangoid found in the Mangyshlak sections. The two species are never found in association, however, as *C. integer* is found exclusively in the Danian and *C. galei* only in the Maastrichtian. The new species differs from *C. integer* in its larger size, more rectangular outline and broader, flatter apical and oral surfaces. The paired ambulacra appear to be open distally in *C. galei* sp. nov. and are also far less divergent than those of *C. integer*. They diverge at an angle of 90° in *C. galei* compared with 110–115° in *C. integer*. The peristome in *C. integer* has a far narrower rim, is less distinctly labiate and is more posteriorly placed at 25 per cent. of test length from the anterior margin. In addition, the labral plate of *C. integer* is far narrower than that of *C. galei* (the labrum is 2·3 times longer than wide in *C. galei* compared with 2·9 times in *C. integer*). A further difference is the presence of a near complete peripetalous fasciole in *C. integer*.

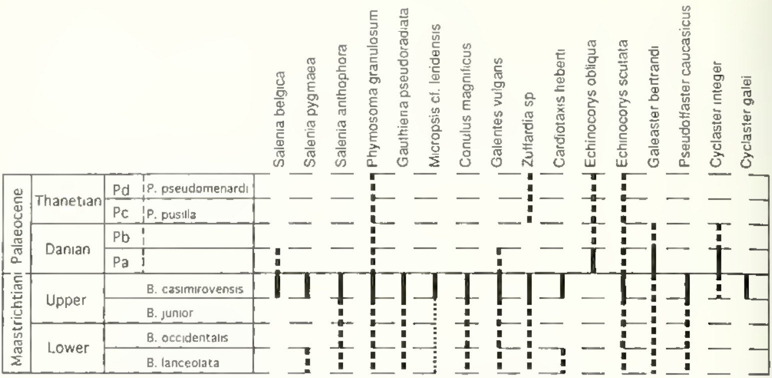
DISCUSSION

All of the taxa described in this paper are stratigraphically confined to either the uppermost Maastrichtian or the lowermost Paleocene in the Mangyshlak sections. Only two genera (*Cyclaster* and *Echinocorys*) appear to pass through the boundary. However, inspection of occurrence data from other localities world-wide shows that many of these species are in fact longer ranging than the Mangyshlak occurrences would suggest (Text-fig. 19).

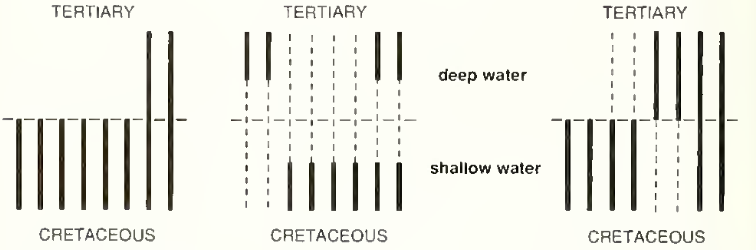
Of the 16 species described, only *Cyclaster galei* sp. nov. is endemic and, if occurrences outside Kazakhstan are taken into account, six of the 15 species present in the Maastrichtian (40 per cent.) survive into the Danian. Thus, the species extinction rate for this fauna at the Cretaceous–Tertiary boundary drops from 100 per cent. to 60 per cent. Although this is lower than some previous estimates for the reduction in marine biodiversity at the species level (eg. 70–80 per cent. extinction estimated by Jablonski and Raup 1995), it is still significant. It should also be noted that the figure of 60 per cent. species extinction is based on actual species occurrence data and not interpolated from rarefaction curves, as in many previous studies (e.g. McKinney 1995). One problem with species data, however, is that species tend to demonstrate a higher level of endemicity than genera, so that generic data may prove more informative.

Of the 11 genera present below the boundary in Mangyshlak, two are also present in the Danian (82 per cent. extinction) but, if world-wide data is considered, this figure drops to 25 per cent. (three out of 12). Again, this is significantly lower than the 50 per cent. generic reduction estimated by Jablonski and Raup (1995) for the Cretaceous–Tertiary turnover. A thorough phylogenetic analysis of these taxa may lead to an even further reduction in the number of apparent extinctions by allowing inferences to be made about the survival of clades. For example, *Conulus* became extinct at the end of the Maastrichtian but has the Paleocene genus *Neoglobator* as a sister group.

The same pattern of local extinction and replacement is repeated in other Cretaceous–Tertiary sections outside of Kazakhstan. Once again, if occurrences away from the studied area are considered, extinction rates are significantly reduced. In Denmark a 56 per cent. extinction across the Cretaceous–Tertiary boundary at the genus level (nine out of 16) is reduced to 25 per cent. (four



TEXT-FIG. 19. Range chart of echinoid species in the Maastrichtian and Paleocene of Mangyshlak, Kazakhstan (solid lines) and world-wide (thick dashed lines). (Thin dashed line denotes presence of species in the stage below.) Pa = nannoplankton zones NP1–2; Pb = nannoplankton zones NP3–4, Pc = planktic foraminifera zone P3, Pd = planktic foraminifera zones P4–P6 (Haq *et al.* 1987).



A) catastrophic event–
no facies change

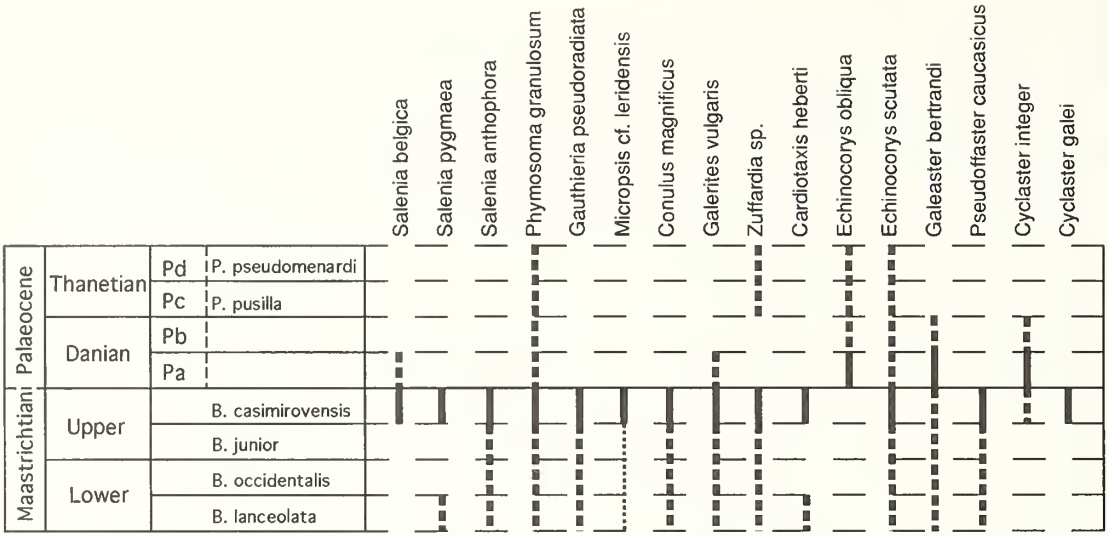
B) facies shift

C) combination of A) and B)

TEXT-FIG. 20. Possible scenarios for the Cretaceous–Tertiary boundary. Solid lines represent occurrences in the studied section; dashed lines represent occurrences elsewhere.

out of 16) if occurrences of taxa outside Denmark are considered, and in the Maastricht area, a loss of 68 per cent. of Maastrichtian genera (19 out of 28) drops to 39 per cent. (11 out of 28).

Can the patterns of taxonomic disappearance at Mangyshlak be explained by sampling alone? Text-figure 19 shows that diversity in the Mangyshlak sections is far greater in the Maastrichtian than in the Danian. This can be explained partially by the fact that two distinct facies types have been sampled in the Maastrichtian (chalk at Koshak and Kyzyslai and calcarenite at Sulukapy) compared with just one (chalk) in the Danian. But even if the three taxa found exclusively in the calcarenites of Sulukapy are eliminated, the diversity difference is still maintained (ten species in the



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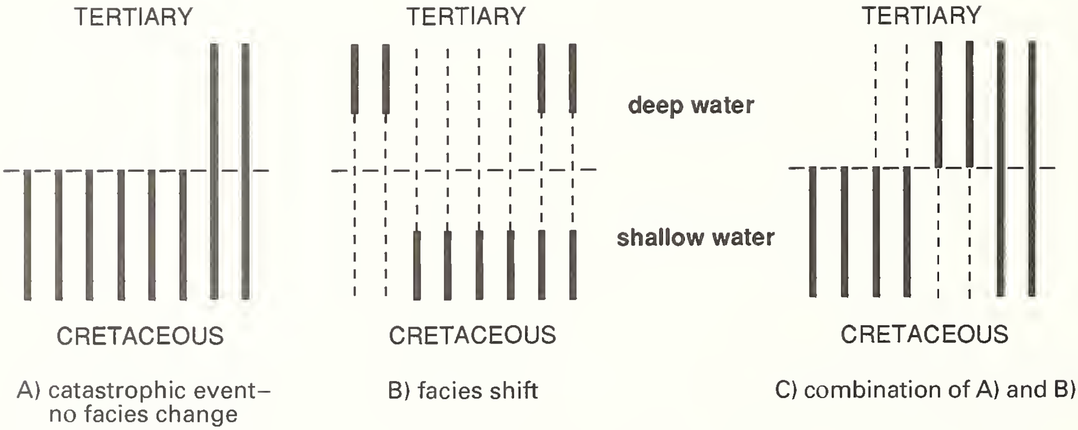

TEXT-FIG. 20. Possible scenarios for the Cretaceous–Tertiary boundary. Solid lines represent occurrences in the studied section; dashed lines represent occurrences elsewhere.

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Maastrichtian and three in the Danian). This is not merely a function of more specimens being collected from the Maastrichtian. In fact, the numbers of Maastrichtian and Danian specimens are about equal with 33 specimens collected from Maastrichtian chalk and 35 specimens from the Danian.

The higher diversity fauna of the Maastrichtian chalk contains a sizeable proportion of regular echinoids which suggests relatively shallow water conditions. The Danian fauna, on the other hand, contains exclusively deep-water irregular forms. It therefore appears that an environmental shift in water depth with little lithological expression has occurred.

If the taxonomic turnover at the end of the Cretaceous had been brought about by some catastrophic event with no associated facies change, the Danian fauna would represent just a surviving percentage of the taxa present in the Maastrichtian (Text-fig. 20A; Hansen 1988). If however, a facies change alone had occurred over this time period, the pattern of survivorship would be very different (Text-fig. 20B). For example, if the Maastrichtian represented deposition in shallower water than the Danian, only species with large depth ranges would be present both below and above the boundary in the studied section. Shallow water forms would migrate or survive elsewhere whilst depth-tolerant species would migrate in from other localities in the Danian. Looking at global occurrence data, there would be no true extinctions. The sections at Mangyshlak appear to represent an intermediate situation (Text-fig. 20C) with a proportion of the taxa becoming extinct, others emigrating from the studied section and others still migrating in.

The study of the echinoid fauna in sections from the Mangyshlak Peninsula clearly demonstrates the problems of sampling and facies change encountered in the study of continuous boundary sections, however complete. Despite these difficulties, similar work needs to be done on other key sections of differing depositional setting and palaeolatitude to discover whether the patterns observed in Kazakhstan are repeated elsewhere. The study of these key sections and the determination of patterns of survivorship selectivity, both in these sections and from phylogenetic studies, will enable us to shed further light on the causes of the biological crisis at the end of the Cretaceous.

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THE EARLY PHYLOGENY OF THE CLASS BIVALVIA

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ABSTRACT. Differences between zoologists and palaeontologists over high-level bivalve taxonomy reflect the hitherto poorly understood early phylogeny of the class Bivalvia. Recent description of a diverse early Arenig fauna and recognition that explosive radiation of early Ordovician bivalves can be correlated with evolution of the filibranch gill within the palaeotaxodonts, together with parsimonious analysis of early bivalve shell characters, has allowed the production of a modified scheme of high-level taxonomy reflecting phylogeny. Shell microstructure has proved of use in detecting phylogenetic links. The subclass Palaeotaxodonta, primitively with prismato-nacreous shells, includes the earliest bivalves and gave rise to the subclass Lipodonta. A new family of palaeotaxodonts, Cardiolariidae, is proposed to include palaeotaxodonts with a modified hinge and probably with filibranch gills; the subclass Palaeoheterodonta, also with prismato-nacreous shells, was derived from these. Radiation from the palaeoheterodonts produced the subclasses Anomalodesmata and Neotaxodonta by the early Ordovician. The Neotaxodonta probably had a shell microstructure with both crossed-lamellar and complex crossed-lamellar elements, and gave rise to the Pteriomorphia, characterized by a calcitic outer shell layer, in early Ordovician times. The shell microstructure of the Neotaxodonta suggests that the Heterodonta evolved from this group, probably by mid or late Ordovician times, but their early fossil record is very poor. A new neotaxodont, *Alytodonta gibbosa* gen. et sp. nov., is described from the lowermost Silurian of Girvan, Scotland. The genus *Babinka* is recorded for the first time from Britain, from the Arenig of South Wales, and the new genus *Homilodonta* is proposed for some mid and late Ordovician palaeotaxodonts from Ireland and North America.

ALTHOUGH bivalves are abundant and varied organisms at the present day and have an excellent fossil record, their high-level classification has been in a state of flux for over a century. This arises from the different series of taxonomic criteria used by various workers; in particular, there is an immediate divergence between the approaches to the problem of high-level classification used by zoologists and palaeontologists. Whilst the former have used many features of soft part morphology and produced different classifications based on different organs, palaeontologists have used shell morphology and those of the soft parts which can be determined from the shell (e.g. musculature). Thus Linnaeus (1758) used the degree of fusion of the margins of the mantle; Lankester (1883) relied on the pedal development, whilst for many zoologists (e.g. Fischer 1880–87; Pelseneer 1889) the gill grade was the definitive criterion in high-level taxonomy of the class. More recently, the stomach type (Purchon 1959, 1960) or labial palp development (Stasek 1963) have been advocated as providing the best taxonomic indicators. For the palaeontologist, however, most of these attributes are not discernible from the fossil shell, although where there are clearly established fossil ancestors of extant forms, it is often possible to draw conclusions as to the nature of certain soft parts. In drawing up bivalve classifications, palaeontologists have used shell form, in particular the dentition (e.g. Neumayr 1884; Bernard 1898), or features of the soft parts which can be deduced from the shell, such as the musculature (e.g. von Zittel 1881–85) or ligament type, together with consideration of the fossil record (e.g. Douvillé 1912) to provide the basis for the high-level taxa. The result has been a conflicting series of classifications of the group (e.g. Starobogatov 1992; Cope 1995).

One of the problems that palaeontologists have faced repeatedly in their quest for a classification of the bivalves is that of homeomorphy. Bivalves are, perhaps unsurprisingly, frequently held up as an example of a group which shows many adaptations of the shell to different modes of life. The

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same shell shapes are repeated in forms which we now recognize cannot be related phylogenetically. This still causes problems; for example, were the Devonian–Recent mytilids derived from the Ordovician–Permian modiomorphoids (as suggested for example by Pojeta 1978) or are the mytilids an unrelated homeomorphic stock which evolved to occupy the same ecological niche? We do not yet know the answer, but the lack of any convincing intermediates (see Carter 1990*b*, p. 273) suggests that the latter explanation may be more likely. Other bivalve characteristics are also homeomorphic; for example, dentition patterns are repeated in unrelated stocks essentially because the number of ways two calcified valves can be articulated is limited. Thus the taxodont dentition of the arcoidean bivalves was for several decades the cause of their direct linking to the nuculoids (e.g. Douvillé 1912; Davies 1947) and this idea was not finally dispelled until Cox (1959) showed that the two stocks were totally unrelated.

One other important tool in the search for fundamental taxonomic criteria in the bivalves has been the advent of shell microstructural studies, made possible through the use of the scanning electron microscope. A major initial monograph by Taylor *et al.* (1969, 1973) showed the potential of such studies as a taxonomic tool; this has been succeeded by many smaller studies of individual fossils or groups. The work has been carried forward more recently in a major compilation by Carter (1990*a*). In the course of these studies, some *caveats* have emerged, for instance that shell microstructures as complex as crossed-lamellar structure can be evolved by unrelated groups of molluscs. Shell microstructure allows other homeomorphies to be detected. For example, the dentition of the heterodonts is at times similar to that of the palaeoheterodonts, so that the two groups have been combined in the subclass Heteroconchia Hertwig, 1895 by some authors (e.g. Pojeta 1978, 1987), although shell microstructure now suggests the two groups are quite distinct and that the similarity in dentition is purely homeomorphic.

The ideal for which to aim, in erecting a high-level taxonomy, is clearly a phylogenetic scheme which uses knowledge of extant bivalves to apply some anatomy to the fossil forms. The *Treatise on invertebrate paleontology. Volume N. Mollusca 6* (Cox *et al.* 1969–71) was a serious attempt at such a scheme but suffered, in particular, because of the lack of knowledge of early fossil forms, and thus details of some of the most fundamental diversifications of the class were lacking. At the time of publication of the *Treatise*, for example, the earliest bivalve was thought to be the Middle Cambrian genus *Lamellodonta* Vogel, 1962; this has been shown subsequently to be a distorted obolid brachiopod (Havlíček and Kříž 1978). However, for more than a decade this spurious bivalve fuelled a major debate about whether actinodont or taxodont dentition was the primitive bivalve condition. Over the past 30 years, however, knowledge of early bivalves has increased dramatically, largely through the works of Pojeta (e.g. 1966, 1971, 1978, 1988) and Babin (e.g. 1966, 1982*a*), and we are now reaching the position of establishing the primary evolutionary pathways along which bivalves diversified.

It is now firmly established that two genera of bivalves existed in the early Cambrian; *Fordilla* Barrande, 1881 and *Pojetaia* Jell, 1980 are now both accepted as belonging to the same family, Fordillidae, which in turn is assigned to the subclass Palaeotaxodonta (Runnegar and Pojeta 1992). These latter authors showed that the shell structure in these forms consisted, at least in part, of nacre prisms, and Carter (1990*b*) showed that a Devonian palaeotaxodont had very similar shell microstructure. From the Middle Cambrian, in addition to *Pojetaia*, two other bivalve genera are known (MacKinnon 1982; Berg-Madsen 1987; Hinz-Schallreuter 1995); all are now accepted as palaeotaxodonts. Berg-Madsen (1987) also recorded a specimen of the mid Cambrian genus *Tuarangia* from an erratic block from Western Pomerania, Poland, which has also yielded the conodont *Westergaardodina tricuspidata* Müller, indicating an early late Cambrian age. This remains the only unequivocal record of a bivalve from the upper Cambrian, but ten species are known from the Tremadoc Series of the Ordovician from three localities (Argentina – Harrington 1938; Australia – Pojeta and Gilbert-Tomlinson 1977, southern France – Babin 1982*a*). The Australian locality was initially recorded as of probable early Arenig age by Pojeta and Gilbert-Tomlinson (1977); however, more recent work has shown that the fauna is of late Tremadoc age (Shergold *et al.* 1991). The Tremadoc faunas include palaeotaxodonts, palaeoheterodonts and cyrtodonts. In the early part of the succeeding Arenig Series, bivalves are now known from five localities world-wide (Cope 1996) and the known fauna totals about 35 species. Of these, the majority come from one locality in South Wales which has recently yielded a bivalve fauna consisting of 20 species belonging to 18 genera (Cope 1996), and includes representatives of the subclasses Palaeotaxodonta, Lipodonta, Palaeoheterodonta, Pteriomorphia and Anomalodesmata. This fauna emphasizes the fact that a significant part of the evolutionary history of the class Bivalvia must have occurred in pre-Arenig times, yet our knowledge of pre-Arenig bivalves is very poor and contributes little to the resolution of the problems of the earliest radiation of the class. The fact that the hitherto described Tremadoc bivalve species include forms which may now be presumed to have been of filibranch gill grade, demonstrates that there must be significant Tremadoc faunas yet to be discovered, and to judge from the fossil record it appears that the Gondwanan shelves are the places where other early bivalve faunas should be sought. Babin (1995) has emphasized the role of the western high latitude Gondwanan shelves in early bivalve evolution, but the Australian Tremadoc faunas show that the low latitude Gondwanan shelves were also important. It is probable that the filibranch gill evolved during the early part of the Tremadoc Epoch and priority should thus go to the search for ancestors of these forms on the peri-Gondwanan shelves, where it seems most likely that they will be found. In contrast, the Laurentian continent seems to be devoid of early Ordovician bivalves; there, rostroconchs occupied the shallow infaunal habitats in much the same way as bivalves did on the Gondwanan shelves. It was not until the mid Ordovician that the bivalves migrated to Laurentia.

Compared with the one known family of bivalves (belonging to one subclass) in the Cambrian, no fewer than 18 families belonging to six subclasses have hitherto been identified as existing before the end of the early Ordovician. The seventh subclass appeared probably by mid or late Ordovician times. Beyond this time, no further bivalve subclasses appeared, and all seven subclasses existing in the late Ordovician are represented at the present day. It is thus clear that the early Ordovician explosive evolutionary outburst represents the most important phase of bivalve evolutionary diversification. Not only did bivalves become noticeably more diverse at this time, and employed an increasing variety of modes of life, but they simultaneously became significantly larger. Compared with the 1–2 mm length of Cambrian bivalves, early Arenig bivalves (apart from the palaeotaxodonts) are regularly 10–15 mm long, and by the Llanvirn Epoch regularly exceed 25 mm. Cope (1995) correlated this increase in size, diversity, and mode of life with the evolution of the filibranch gill. He suggested that amongst the palaeotaxodonts there were forms with a modified hinge indicating an adaptation for greater valve opening commensurate with the acquisition of the feeding gill.

There are demonstrable gaps in the bivalve fossil record because that of the early Ordovician is clearly so incomplete. However, parsimonious analysis of shell characters enables us to reconstruct parts of this cryptogenetic past. Even when the fossil record is more complete, it is often remarkably disjunct; as an example, solemyoid bivalves are unknown from Britain between the lower Arenig and the Lower Carboniferous, although many thousands of bivalves have been collected (and exist in museum collections) from this long interval. Such disjunct fossil ranges provide an added complication to the unravelling of the early phylogeny of some bivalve groups. As a corollary of this, it is clear that the order of occurrence of bivalves in the fossil record cannot be an infallible guide to their respective origins.

The taxonomic scale adopted herein is the same as that of the *Treatise* (Cox *et al.* 1969–71) and of Pojeta (1978, 1987); that is, to treat the major divisions of the class Bivalvia as subclasses. However, I show below that we can now establish plausible phylogenetic links between these major taxonomic units; they are not now discrete entities without connections, as was the case at the time of publication of the *Treatise*. It may be, therefore, that a taxonomically more defensible position would be to regard these major divisions of the class as superorders rather than subclasses.

Subclass PALAEOTAXODONTA Korobkov, 1954

(Pl. 1, figs 1–7, Text-fig. 3)

The palaeotaxodonts include the most primitive living bivalve, the cosmopolitan genus *Nucula*, which has survived, apparently differing little from its Ordovician ancestors. *Nucula* has protobranch gills, a prismato-nacreous shell and a hinge-plate bearing a row of subequal teeth and sockets – the taxodont dentition. It lives as an infaunal sessile deposit feeder.

The fossil record from the early Cambrian through to the early Ordovician suggests that the Palaeotaxodonta were the earliest bivalves, and supports the view that *Pojetaia* and *Fordilla*, not only the earliest unequivocally accepted bivalves but also, in all probability, palaeotaxodontids, could well have given rise to later bivalve stocks. The shell structure of both *Pojetaia* and *Fordilla* has been shown by Runnegar and Pojeta (1992) to be similar to that of a Devonian palaeotaxodont (Carter 1990*b*). Modern nuculoid palaeotaxodonts have a three-layered aragonitic shell: the inner layer consists of sheet nacre, the middle layer of lenticular nacre, and the outer layer is prismatic (Taylor *et al.* 1969). The same three-layered structure also characterizes the Monoplacophora and the Archaeogastropoda, confirming the likelihood that this was the primitive molluscan shell microstructure (Text-fig. 1). However, in contrast to the nuculoids, modern nuculanoid palaeotaxodonts have a homogeneous aragonitic shell (Taylor *et al.* 1969). This change appears to have happened geologically recently, as Cox (1959) reported nacreous structure in a Jurassic *Nuculana*, an observation subsequently confirmed by Taylor *et al.* (1969, p. 68).

The dentition of bivalves is designed to lock the valves accurately on closure, to provide a mechanism allowing rotation along the hinge axis, and to prevent a shearing motion of the valves when open. These characteristics provide bivalves with protection against current action and predation. The taxodont dentitions of the palaeotaxodonts 'provide strong juncture between the valves and in addition oppose rotation in the plane of commissure' (Kauffman *in* Cox *et al.* 1969, p. N173). However, it is clear that the dentition of most of the palaeotaxodonts (e.g. Pl. 1, figs 1–7)

EXPLANATION OF PLATE 1

Fig. 1. *Ctenodonta nasuta* (Hall, 1847); USNM 14718; upper Ordovician, Ottowa, Canada; RV; ×1. Photograph supplied by J. Pojeta. Figured Pojeta 1971, pl. 4, fig. 6.

Fig. 2. *Homilodonta* cf. *regularis* (Portlock, 1843); USNM 162705; middle Ordovician, Kentucky; RV; ×3. Palaeotaxodont figured as *Deceptrix* sp. nov. by Pojeta 1978, pl. 1, fig. 1.

Fig. 3. *Pensarnia laeviformis* Cope, 1996; NMW78. 17G. 1071; latex cast of holotype; figured Cope 1996, pl. 1, fig. 2; Lower Arenig, Llangynog, Carmarthenshire; RV; ×4.

Fig. 4. *Similodonta similis* (Ulrich, 1892); USNM 47037*a*; upper Ordovician, Minnesota; LV; ×5. After Pojeta 1978, pl. 2, fig. 7.

Fig. 5. *Praenucula filistriata* (Ulrich, 1894); USNM 40487; upper Ordovician, Ohio; LV; ×5. Palaeotaxodont figured as *Deceptrix filistriata* by Pojeta 1978, pl. 2, fig. 1. Photograph supplied by J. Pojeta.

Fig. 6. *Myoplusia bilunata perdentata* (Barrande, 1881); Barrande Collection, Národní Museum, Prague; middle Ordovician, Czech Republic. After Babin and Gutiérrez-Marco 1991, pl. 4, fig. 8; RV internal mould; ×5.

Fig. 7. *Nuculoidea lens* Liljedhl, 1983; SGU Type 842; Wenlock, Gotland; holotype, RV; ×3·8. After Liljedahl 1994, fig. 30A. Note central resilifer on the hinge-plate, a Silurian innovation.

Fig. 8. *Ovatoconcha fragilis* Cope, 1996; NMW78. 17G. 1175; lower Arenig, Llangynog, Carmarthenshire; composite mould RV; ×2·5. After Cope 1996, pl. 4, fig. 2. Note large anterior adductor.

Fig. 9. *Psiloconcha grandis* Ulrich, 1894; USNM 46283*a*; upper Ordovician, Ohio; RV; ×1·3. Photograph supplied by J. Pojeta. Figured Pojeta 1988, pl. 17, fig. 1.

Fig. 10. *Solemya radiata* Meek and Worthen, 1860; AMNH 42616; Upper Carboniferous, Ohio; ×1·7. Photograph supplied by J. Pojeta. Figured Pojeta 1988, pl. 22, fig. 1.

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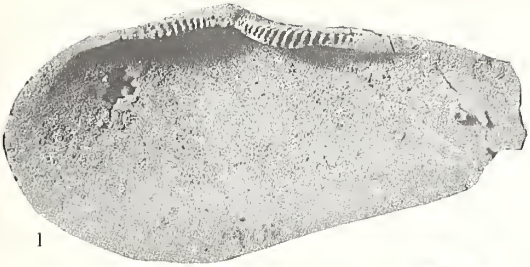
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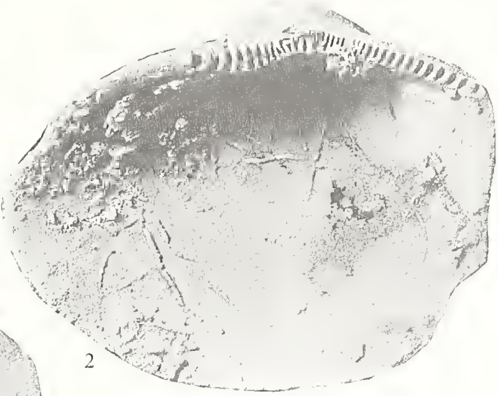
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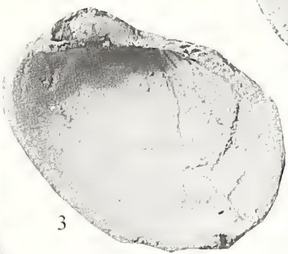
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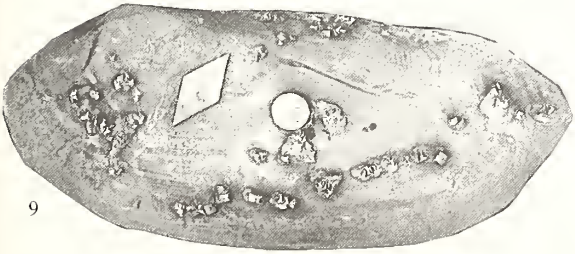
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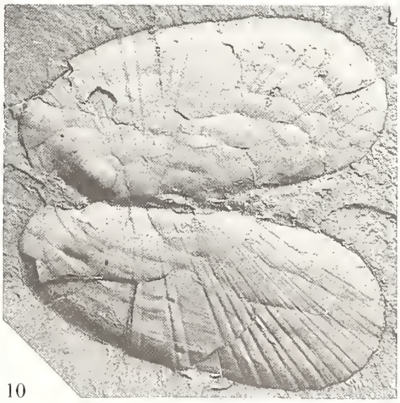
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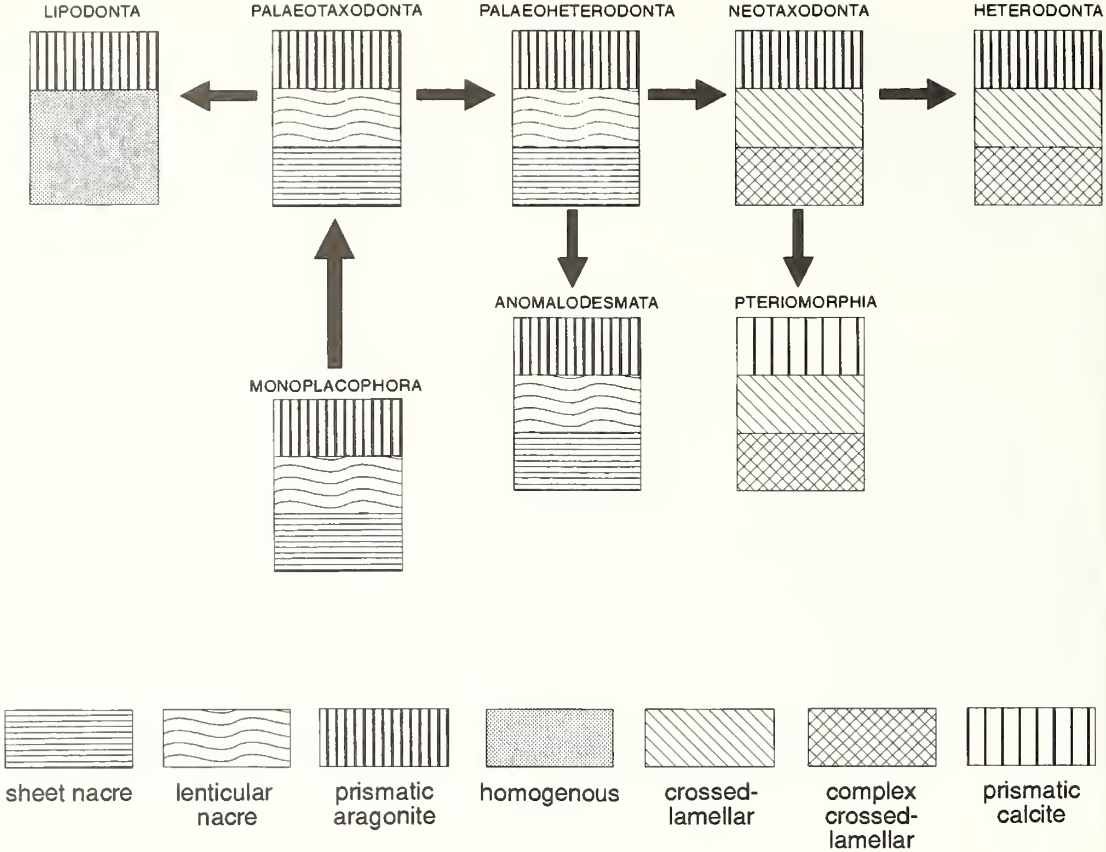
COPE, palaeotaxodonts, lipodonts



TEXT-FIG. 1. Parent shell microstructures of the bivalve subclasses. The forms depicted are those from which all shell microstructures known within each subclass can readily be derived. Thus, in the neotaxodonts (and also in some heterodont families), modern forms have a two-layered shell; this could be readily derived from the presumed parent shell structural type by loss of the outer layer. In the pteriomorphians, many extant forms possess the parent shell structural type; others have extended the calcite to other shell layers, etc.

would only perform in this way with a restricted degree of valve opening. Other palaeotaxodonts (e.g. Text-fig. 3) have a differentiated taxodont hinge which would prevent shearing motions with a greater degree of valve opening.

The palaeoheterodonts can be derived from such a palaeotaxodont ancestor (Cope 1995, and below), and several examples are now known of palaeotaxodonts which have similarly differentiated teeth. Previously (Cope 1995), I suggested that these examples could represent forms in which the hinge mechanism was modified to allow pseudofaeces to be expelled, and could represent the earliest filibranch grade bivalves (see below); these forms could provide ideal ancestors for the diverse early Ordovician palaeoheterodonts. I believe that the fact that all living palaeotaxodonts are protobranch has pre-conditioned our views of extinct forms and thus has hitherto constrained our interpretations of the gill grade of Ordovician palaeotaxodonts. There is no *a priori* objection to the belief that several genera of advanced palaeotaxodonts had filibranch gills. Following this hypothesis, the feeding gill could have been evolved within the palaeotaxodonts and its evolution could well have provided the trigger which unleashed the evolutionary burst amongst the Bivalvia in the earliest Ordovician, presumably during the early part of the Tremadoc.

If the palaeotaxodonts were the earliest bivalves, at least one of the other subclasses must have evolved directly from them. Earlier (Cope 1995), I presented evidence to show that the palaeotaxodonts were the rootstock of the palaeoheterodonts. All extant palaeoheterodonts are of filibranch or eulamellibranch gill grade, and I suggested (Cope 1995) that the filibranch grade evolved within the palaeotaxodonts. This hypothesis removed one of the most awkward obstacles in the way of producing a convincing model of early bivalve evolution. If we accept this hypothesis, it provides a reason for the sudden explosive evolution of the bivalves in the early Ordovician, concomitant with their rapid increase in size and abundance; the development of the feeding gill enabled bivalves to develop their infaunal feeding strategies further and allowed them, for the first time, to develop epifaunal modes of life and to compete, on increasingly equal terms, with the articulate brachiopods.

With the evolution of the filibranch gill, one significant disadvantage accrued: the gill could not differentiate between food and non-food particles, and as water and ciliary currents directed these particles mouthwards, a method of sorting was required unless the animals were to ingest large amounts of useless sediment during normal feeding activity. The solution the bivalves adopted was to eject the sedimentary particles as pseudofaeces, but this material could not be carried away by the already existing internal shell water currents, as these were in the wrong direction, so they employed a vigorous flapping of the valves to expel the pseudofaeces accumulated along the ventral margin of the shell (Cox *et al.* 1969). This, it seems to me, is the reason why differentiated dentition was developed concomitantly with the filibranch gill and with larger size.

It appears most unlikely that the filibranch gill, the more primitive grade of the feeding ctenidium, could have evolved more than once. On the other hand, it also seems clear that the eulamellibranch grade could have evolved several times, as it is found in seemingly unrelated stocks of bivalves. The difference here is that the demibranchs of the filibranch gill, lying as they do in close proximity to each other, are likely to have developed organic connections to each other in different groups of bivalves; this would have resulted wholly from their organic proximity and the consequence is a polyphyletic grouping of bivalves of eulamellibranch grade (as first demonstrated by Ridewood 1903).

A group of early and mid Ordovician–Devonian palaeotaxodonts has now been identified that are united by their differentiated hinge and that are believed to have developed filibranch gills; these are grouped together in the new family Cardiolariidae (see below and Text-fig. 3).

The subclass Palaeotaxodonta is thus here identified as the group which included not only the earliest bivalves, but also that in which the filibranch gill type evolved. *Pojetaia* is confirmed as being close to the ancestral bivalve. It therefore now seems clear that the long controversy over which was the earliest type of dentition, and how the primary radiation of the bivalves occurred is now over. The palaeotaxodonts were the rootstock of the bivalves, and the most fundamental radiation – associated with the evolution of the feeding gill – occurred within that subclass, probably during the earliest Ordovician or possibly latest Cambrian.

Subclass LIPODONTA Cope, 1995

(Pl. 1, figs 8–10)

This subclass includes the extant genus *Solemya* which is an infaunal mobile detritus feeder. Like *Nucula*, *Solemya* has protobranch gills, but differs in its marked anterior elongation with a dominant anterior adductor muscle, and an edentulous hinge. *Solemya* itself has survived little changed since Devonian times. Solemyoids are specialized bivalves adapted to a deeply infaunal habitat, particularly in shallow-water silty muds; they have a much reduced gut, which was the cause of much speculation on their physiology by zoologists, until Cavanaugh (1983) demonstrated that they lived symbiotically with sulphur-oxidizing chemoautotrophic bacteria. Solemyoids have a shell with anterior and posterior gapes which has a thick periostracum that extends ventrally beyond the calcified portion of the valves.

In the *Treatise* (Cox *et al.* 1969), the solemyoids were included as members of the subclass Cryptodonta Neumayr, 1884. Even at the time of publication of the *Treatise*, the members of this subclass appeared an ill-matched medley of forms, whose only factor in common was the lack of knowledge of the hinge. Since 1969, a great deal more information has been obtained on many of these forms and it is now realized that some of them can be assigned to the subclass Pteriomorphia (e.g. Kříž 1979), whilst others include some rostroconchs. Pojeta (1978) suggested that solemyoids were derived from palaeotaxodonts and thus they could be included in the same subclass. He later (1988) figured a series of anteriorly elongated palaeotaxodonts and suggested that these may well have been the origin of solemyoids in the mid Ordovician. Cope (1996) described a new solemyoid, *Ovatoconcha fragilis*, from the Lower Arenig of South Wales, showing that the solemyoids were already a distinct group at this time. Thus Pojeta's claimed intermediate forms could be interpreted either as surviving intermediate stocks, or as a separate mid Ordovician evolution of anteriorly elongated palaeotaxodonts, unrelated to the solemyoids. Another possible early Arenig solemyoid is the *Cymatonota*? sp. figured by Babin (1982*a*, pl. 11, fig. 17) from the Montagne Noire; if this is indeed a solemyoid, the orientation of the shell proposed by Babin (1982*a*, p. 45) would need to be reversed.

As early as 1969, Newell (*in* Cox *et al.* 1969, pp. N212–N213) noted that it was reasonable to conclude that solemyoids were only distantly related to palaeotaxodonts; the only criterion for grouping them together was that they were the only two bivalve cohorts sharing the protobranch gill. Apart from this one feature in common, they 'differ in almost every feature'. With the recognition that some palaeotaxodonts may well have had filibranch ctenidia (see above), it appears that the gill grade now has less of an importance in taxonomy and so this one common factor is of less relevance, except to show that the solemyoids must have originated from the palaeotaxodonts.

Since solemyoids occurred in the early Ordovician, their probable divergence from the palaeotaxodonts must have occurred earlier. In view of this early divergence and their fundamental morphological differences, it is clear that a separate high-level taxon is necessary for the solemyoids. I thus (Cope 1995) introduced the subclass Lipodonta to accommodate them. It is evident that this subclass has had a long geological history. The retention of the protobranch gill and a shell consisting of an outer prismatic layer and an inner homogeneous laminated layer, a microstructural

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EXPLANATION OF PLATE 2

Fig. 1. *Lyrodesma majus* (Ulrich, 1879); USNM 46223; upper Ordovician, Ohio; RV; ×3. Photograph supplied by J. Pojeta. Figured Pojeta 1971, pl. 3, fig. 15. A lyrodesmatid palaeoheterodont.

Fig. 2. *Copidens browni* Pojeta and Gilbert-Tomlinson, 1977; CPC 15593; lower or middle Ordovician; Georgina Basin, NT, Australia; LV, hinge-plate; ×4. Photograph supplied by J. Pojeta. Figured Pojeta and Gilbert-Tomlinson 1977, pl. 28, figs 4–5. A cycloconchid actinodont.

Fig. 3. *Ananterodonta oretanica* Babin and Gutiérrez-Marco, 1985; CUM SP-IV 2 073/OR; lower Llanvirn, Toledo, Spain; holotype LV; ×1. After Babin and Gutiérrez-Marco 1991, text-fig. 9f. A cycloconchid actinodont.

Fig. 4. *Cycloconcha mediocardinalis* Miller, 1874; WM 8893; upper Ordovician, Ohio; RV; ×4. After Pojeta 1971, pl. 2, fig. 16. A cycloconchid actinodont.

Fig. 5. *Actinodonta cuneata* Phillips, 1848; BGS GSM 59825; Upper Llandovery, Marloes Bay, Pembrokeshire; latex cast of RV lectotype; ×1·75. After Pojeta 1978, pl. 4, fig. 9. A cycloconchid actinodont.

Fig. 6. *Colpomya constricta* Ulrich, 1895; USNM 162746; upper Ordovician, Kentucky; ×2·5. After Pojeta 1971, pl. 12, fig. 2. A colpomyid modiomorphoid.

Fig. 7. *Carminodonta crossi* Cope, 1996; NMW78. 17G. 1183; lower Arenig, Llangynog, Carmarthenshire; ×3. After Cope 1996, pl. 3, fig. 8. A cycloconchid actinodont.

Fig. 8. *Modioliodon oviformis* (Ulrich, 1890); USNM 247856; middle Ordovician, Kentucky; ×1·5. After Pojeta 1978, pl. 13, fig. 15. A modiomorphoid palaeoheterodont with a simple pseudocardinal dentition.

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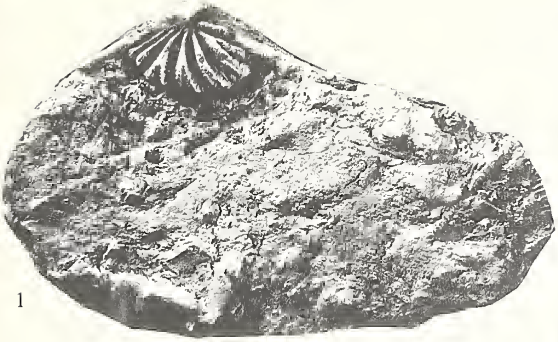

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COPE, palaeoheterodonts

type which could be readily derived from a palaeotaxodont prismato-nacreous shell (Taylor *et al.* 1969, 1973), suggests very early derivation from a palaeotaxodont ancestor, perhaps within the Cambrian; their origin may have preceded the evolution of the filibranch gill among the palaeotaxodonts. The time of origin of the shell microstructure exhibited by modern solemyoids is unknown; Early Palaeozoic forms could well have retained the primitive prismato-nacreous shell microstructure but earlier Cope (1996, p. 989), I presented evidence to show that early Arenig forms had a high organic content in their shell, suggesting the possibility that they already had a thick periostracum.

Lipodonts are essentially edentulous and these forms are included in the superfamily Solemyoidea Adams and Adams, 1857, which contains one family, Solemyidae Adams and Adams, 1857. However, some other forms, which have been related to the solemyoids, possessed teeth, and the extant genus *Nucinella* develops an actinodont-like dentition (Allen and Sanders 1969). Cox *et al.* (1969) assigned *Nucinella* to the family Manzanellidae Chronic, 1952 of the order Arcoida Stoliczka, 1871 (therein placed within the subclass Pteriomorphia) with a query. Allen and Sanders' zoological work suggested, however, that its affinities were solemyoid, and Pojeta (1988) referred it to the family Nucinellidae Vokes, 1956, whilst recognizing Manzanellidae Chronic, 1952 as a separate family within the superfamily Nucinelloidea Vokes, 1956. Pojeta (1988) referred this superfamily to the solemyoids.

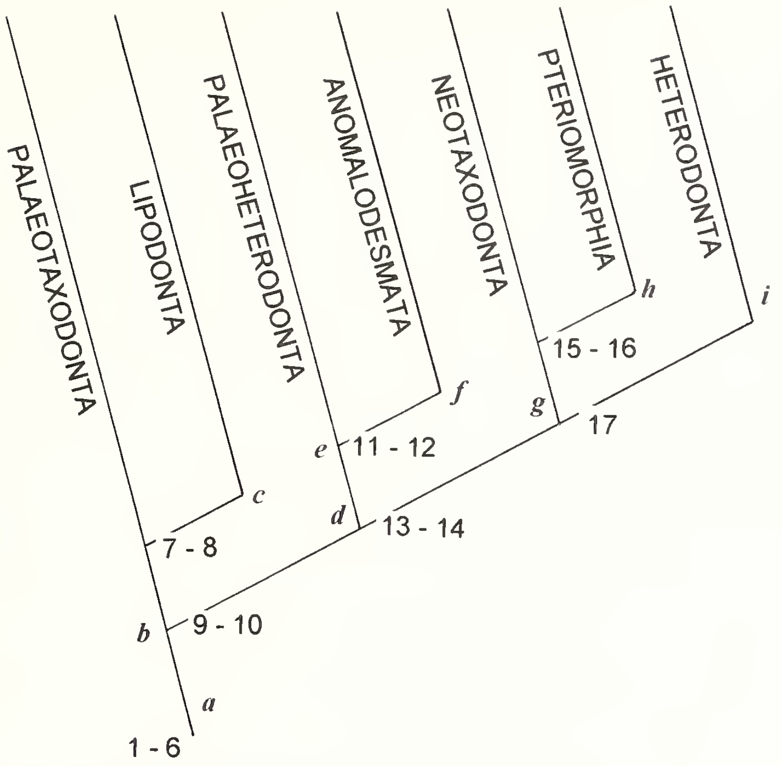
Taylor *et al.* (1973), however, whilst admitting that *Nucinella* had some anatomical resemblances to *Solemya*, reported that other features more closely resembled those of the palaeotaxodonts. Unlike other lipodonts, nucinelloideans have teeth; they also are monomyarian (or have a very reduced posterior adductor). Nucinelloideans have a much smaller shell than solemyoideans; they are usually between 1 mm and 5 mm long; the shell margins do not gape, and the periostracum does not extend ventrally beyond the calcified parts of the shell (Pojeta 1988). Taylor *et al.* (1973, p. 287) reported that the shell structure of *Nucinella* was of similar homogenous type to that occurring in *Nuculana*, but unlike that of *Solemya* or the nuculoideans. Clearly, the affinities of the superfamily Nucinelloidea are not fully resolved, but the balance of evidence suggests to me that both of its families (Nucinellidae and Manzanellidae) are better placed within the palaeotaxodonts as anteriorly elongated forms, possibly derived from the nuculanoids.

On this basis, the subclass Lipodonta remains entirely a rather homogeneous but entirely endentulous group, comprising the single order Solemyoida Dall, 1889, containing one superfamily, Solemyoidea Adams and Adams 1857.

Subclass PALAEOHETERODONTA Newell, 1965

(Pl. 2, figs 1–8; Pl. 3, figs 1–6; Pl. 4, figs 2, 7)

The palaeoheterodonts include the extant genera *Neotrigonia* and *Unio*, but the subclass also includes important fossil forms such as the actinodontoids and the modiomorphoids. The origins of this subclass appear to be in the cardiolariid palaeotaxodonts which, as explained above, were probably of filibranch gill grade. Cope (1995, text-fig. 30.1) demonstrated that the dentition of the Cardiolariidae, in particular of *Cardiolaria* itself (Text-fig. 3), is remarkably similar to that of the palaeoheterodont *Glyptarca* Hicks, 1873 (Pl. 4, fig. 2). Newell (*in* Cox *et al.* 1969, p. N256) designated *G. primaeva* Hicks as type species of the genus which has been subject to misinterpretation because of the inadequate nature of Hicks' type material (lectotype of the type species designated by Carter 1971). Previously (Cope 1996), I figured a new species, *G. serrata*, from rocks of identical early Arenig (Moridunian Stage) age from Llangynog, some 65 km to the east of Hicks' locality, and figured forms with perfectly preserved moulds of the dentition (see also Pl. 4, fig. 2). The similarity of the overlap of the two sets of teeth in *Glyptarca* and *Cardiolaria* is remarkable. *Cardiolaria* is undoubtedly a palaeotaxodont, whilst *Glyptarca*, although a palaeoheterodont, has a posterior tooth developing a pseudo-taxodont separation. Cope (1995) suggested that these genera provide clear evidence of a link between the palaeotaxodonts and the palaeoheterodonts. The



TEXT-FIG. 2. Cladogram showing the postulated relationships between the bivalve subclasses and positions of key genera, families and superfamilies. 1. Prismato-nacreous shell. 2. Protobranch gills. 3. Approximately equal adductors. 4. Two equal valves. 5. Simple opisthodetic ligament. 6. Simple row of teeth on hinge. 7. Anterior adductor dominant. 8. Loss of teeth. 9. Filibranch gill. 10. Differentiated dentition. 11. Loss of teeth. 12. Granulose shell ornament. 13. Duplivincular ligament. 14. Middle shell layer crossed-lamellar; inner layer complex-crossed lamellar. 15. Outer shell layer calcite. 16. Loss of subumbonal teeth. 17. Loss of duplivincular ligament. *a. Pojetaia. b.* Cardiolariidae. *c. Ovatoconcha. d.* Glyptarcoidea. *e. Cosmogoniophora. f. Arenigomya. g. Catamarcaia. h. Cyrtodonta. i.* Crassatelloidea.

overlap of the two sets of teeth appears in the Ordovician only in these two genera; it appears also to be a very rare attribute of bivalve dentition through any part of their geological range. *Cardiolaria* has anterior dentition which displays a similar contrast in size to the posterior dentition as in *Glyptarca*; it lacks, however, the characteristic dorsally divergent arrangement of the anterior dentition of the latter genus. In turn, the dentition of *Glyptarca* is such as would provide an ideal ancestor for the dentition of the neotaxodontids (see below). Thus, the subclass Palaeoheterodonta appears to be readily derivable from the Palaeotaxodonta; it forms the principal plexus of Ordovician filibranch bivalves from which, it is now apparent, two other bivalve subclasses may be readily directly derived.

Some actinodontoideans, such as the family Redoniidae (see Pl. 3, figs 1, 4) have reduced dentition, but the reduction reaches its maximum in the modiomorphoids (Pl. 2, figs 6, 8; Pl. 3, fig. 2), which otherwise appear very close to the actinodontoideans. Pojeta (1978) related the modiomorphoids to the mytilids and suggested that the former may ultimately have been derived from *Fordilla.* He re-introduced Iredale's (1939) group Isofilibranchia as a subclass to include these forms. This suggestion is not accepted herein, as there is no convincing link between the mytiloids and modiomorphoids. Furthermore, the shell structure of *Fordilla* has been shown to be identical to that of *Pojetaia*, resulting in a unification of the two early Cambrian genera in the family Fordillidae (Runnegar and Pojeta 1992); thus *Fordilla* is now regarded as a palaeotaxodont. Some modiomorphoids have teeth of reduced actinodontoid type (e.g. Pl. 2, fig. 8) and thus link clearly with the palaeoheterodonts, whilst in others, teeth are totally missing (e.g. Pl. 3, fig. 2). I find myself in accord with the views of Bailey (1983) who was unable to accept Pojeta's inclusion of the modiomorphoids in the Isofilibranchia. Bailey (1983, p. 200) concluded that the modiomorphoids were best included with the actinodontoids in the subclass Palaeoheterodonta as '*Modiomorpha*... has a heterodont arrangement with weak posterior laterals... other modiomorphoids... have strong posterior elements as part of a continuous actinodont series'. I would agree with Bailey (1983) in regarding modiomorphoids as an example of a bivalve group which has very variable dentition: at times it appears edentulous, at others that of some members is actinodont-like. Like other groups of bivalves, the modiomorphoids were able to repeat different styles of dentition at different times. The fact that the modiomorphoids seem closely allied to the actinodontoid palaeoheterodonts in the early Ordovician suggests that they were directly linked phylogenetically. However, some other occurrences of actinodontoid dentition appear to be unrelated homeomorphies. Thus, some modern solemyoids (see above, for discussion of affinities of these forms) can produce pseudo-actinodont dentition (Allen and Sanders 1969) as also can some modern palaeotaxodonts (Allen and Sanders 1973). These appearances of apparent actinodont dentition imply no more of a phylogenetic link to the actinodonts, than neotaxodontid dentition implies a phylogenetic relationship to palaeotaxodontid dentition – a putative relationship finally refuted by Cox (1959). Thus the presence, or absence, of teeth in the modiomorphoids should be regarded as a feature which appears and disappears. It does not detract from the hypothesis that

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EXPLANATION OF PLATE 3

Fig. 1. *Dulcineaia manchegana* Babin and Gutiérrez-Marco, 1991; CUM PZ-III 2 105/OR; lower Llandeilo, Ciudad Real, Spain; × 2·8. After Babin and Gutiérrez-Marco 1991, pl. 7, fig. 7. A redoniid actinodont with a microcrenulated anterior tooth and single posterior tooth.

Fig. 2. *Modiodonta gothlandica* (Hisinger, 1831); RMMo149878; Wenlock, Gotland; holotype; × 2·5. After Liljedahl 1994, fig. 37G. Internal mould of a modiomorphoid with much reduced dentition.

Figs 3, 6. *Babinka prima* Barrande, 1881; NMW96. 23G. 1*a*; *Bergamia rushtoni* Biozone, Pontyfenni Formation, upper Arenig, Pontyfenni Quarry, Whitland, Carmarthenshire. 3; LV; × 2. 6, close-up to show details of the gill attachment muscle impressions at the end of the pedal muscle scars. The anterior adductor scar is the deeper impression to the left of the print; × 6. Treated herein as an actinodontoid with reduced dentition.

Fig. 4. *Moridunia simplicidens* Cope, 1996; NMW78. 17G. 387; lower Arenig, Llangynog, Carmarthenshire; × 3. After Cope 1996, pl. 5, fig. 6. A redoniid actinodontoid.

Fig. 5. *Goniophora* (*Cosmogonioiphora*) *extensa* Cope, 1996; NMW78. 17G. 1222; lower Arenig, Llangynog, Carmarthenshire; holotype; RV; × 3. After Cope 1996, pl. 4, fig. 5. A modiomorphoid possibly close to anomalodesmatan origins.

Fig. 7. *Arenigomya carinata* Cope, 1996; NMW78. 17G. 1265; lower Arenig, Llangynog, Carmarthenshire; LV; × 3. After Cope 1996, pl. 7, fig. 12. The earliest species of anomalodesmatan known hitherto.

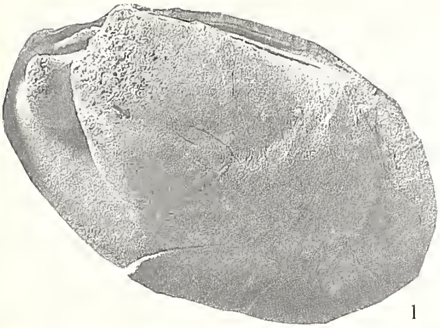
Fig. 8. *Rhytimya radiata* Ulrich, 1895; USNM 102037; upper Ordovician, New York State; RV; × 3. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 15, fig. 1. A form showing the granulose shell texture of many early anomalodesmatans.

Fig. 9. *Orthonota undulata* Conrad, 1841; ANSP 61406; Middle Devonian, New York State; × 1·5. Photograph supplied by J. Pojeta. Figured Pojeta and Runnegar 1985, fig. 11I. An example of a group of Ordovician–Devonian soleniform shells of uncertain affinities; the group may be either anomalodesmatans or modiomorphoid palaeoheterodonts.

Fig. 10. *Cuneamya* sp.; USNM 92331*b*; middle Ordovician, New York State; RV; × 1·5. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 15, fig. 7.

Fig. 2 published with permission from the Lethaia Foundation.

PLATE 3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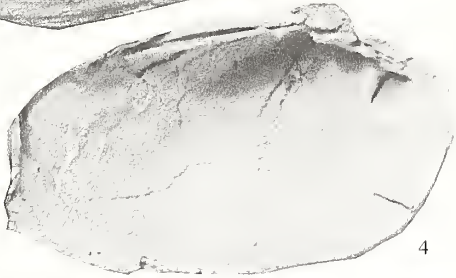
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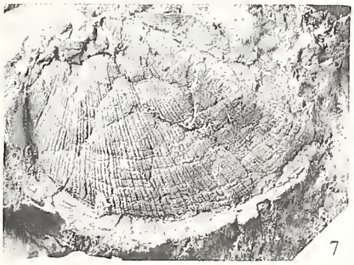
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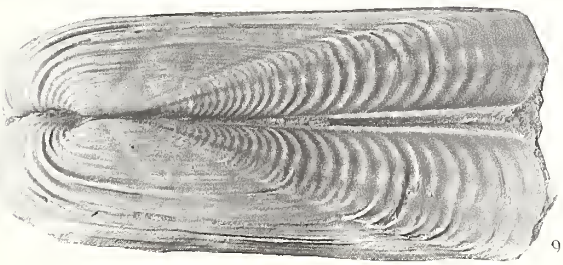
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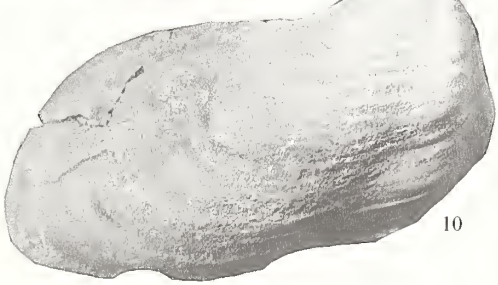
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COPE, palaeoheterodonts, anomalodesmatans the modiomorphoids, with their prismato-nacreous shell, probably evolved from the actinodontoidean palaeoheterodonts which had similar prismato-nacreous shell microstructure. The shell structure of most modern palaeoheterodonts is identical to that of the nuculoid palaeotaxodonts (Taylor *et al.* 1969), supporting their origin from that group (Text-fig. 1).

One extant group of palaeoheterodonts has filibranch grade gills: this is the trigonioids, which can be traced back plausibly to the Ordovician lyrodesmatid palaeoheterodonts (Pl. 2, fig. 1). In turn *Lyrodesma*, first recorded from the middle Ordovician, can be readily derived from the mid Ordovician genus *Tromelinodonta* Babin, 1982*b* and this from *Noradonta* Pojeta and Gilbert-Tomlinson, 1977 (Babin 1982*b*). *Noradonta* shows some similarity in dentition to the cardiolariid palaeotaxodont *Inaequidens* Pojeta and Gilbert-Tomlinson, 1977 (Text-fig. 3F), and may thus link the trigonioids ultimately back to palaeoheterodont origins. The whole lineage is likely to have been of filibranch gill grade if the evolution of the filibranch gill was a unique event. Cox (*in* Cox *et al.* 1969, p. N21) recorded the possible preservation of gills in Jurassic *Laevitrigonia*, based on the evidence of an unpublished nineteenth century plate, apparently showing this feature. Spamer *et al.* (1989, pl. 1) have reproduced the plate illustrating these forms and Whyte (1991) has located several specimens of *Laevitrigonia* showing phosphatic gill supports consistent with filibranch ctenidia.

In the other group of living palaeoheterodonts, the unionoids, all extant members are eulamellibranch. However, Whyte (1992) has demonstrated that while preserved gill structures in Cretaceous unionoids indicate that these forms were eulamellibranch, late Triassic forms had filibranch gills. This constitutes the only example hitherto known of the change from filibranch to eulamellibranch gill grade occurring within a single lineage. However, as first demonstrated by Ridewood (1903), this is a transition which has probably occurred several times in unrelated bivalve stocks, resulting in the polyphyletic nature of the eulamellibranch gill.

Subclass ANOMALODESMATA Dall, 1889

(Pl. 3, figs 7–10)

Anomalodesmatan bivalves are essentially edentulous burrowing forms. Modern anomalodesmatan forms are, apart from one septibranchiate group, of eulamellibranch gill grade; it is thus likely that their ancestors in the Ordovician would have been of at least filibranch grade. Modern anomalodesmatans have three-layered prismato-nacreous shells identical in structure to those of nuculoids (Taylor *et al.* 1973) and it is thus likely that the subclass was derived from forms with prismato-nacreous shells (Text-figs 1–2). This origin must now go back to at least the early Ordovician, following my earlier (Cope 1996) description of the early Arenig anomalodesmatan genus *Arenigomya* (Pl. 3, fig. 7). The first anomalodesmatans are likely to have been of filibranch gill grade, and the eulamellibranch and septibranch forms developed subsequently. Other characteristic features of the anomalodesmatans are the obsolescent hinge teeth, often resulting in an edentulous hinge or, in some cases, a single, rather amorphous tooth beneath the umbo; they never have lateral teeth and commonly have (throughout their geological range) a fine reticulate ornament with a granulose texture developed along the radial ornament and especially where the elements of radial and concentric ornament intersect.

In the early Ordovician, there was one group of bivalves which appears to have all the characters required of an anomalodesmatan ancestor. That group is the modiomorphoid palaeoheterodonts; they are often edentulous, and probably had a prismato-nacreous shell (as in all extant palaeoheterodonts and all fossil forms with the shell structure preserved). Harrington (1938) recorded the modiomorphoid *Cosmogoniophora* from the Tremadoc of Argentina, and Pojeta and Gilbert-Tomlinson (1977) recorded the genera *Colpantyx* and *Xestoconcha*, both colpomyid modiomorphoids, from the late Tremadoc Pacoota Sandstone of the Amadeus Basin of Australia. Modiomorphoids thus appear in the fossil record before anomalodesmatans. Instead of conventional dentition, the colpomyid modiomorphoids have on their hinge what Pojeta and Gilbert-Tomlinson (1977) referred to as a 'blunt articulating device' (Pl. 2, fig. 6) which could again provide a satisfactory link between the modiomorphoids and the anomalodesmatans. In the genus *Arenigomya* (Cope 1996), the hinge structure consists of two spoon-shaped subumbonal structures which would appear to have articulated with each other (see Cope 1996, text-fig. 7). This, however, is rather different from the 'blunt articulating device' in each valve of the colpomyids, which resembles a blunt tooth. It is possible that the structures in *Arenigomya* could have housed an internal ligament, as in some modern anomalodesmatans, and the structure would then be a chondrophore. This is in accord with the hinge structures of modern anomalodesmatan forms.

As far as the origin of the shell ornament is concerned, the modiomorphoid *Goniophora* (*Cosmogoniophora*) *extensa* Cope, 1996 (Pl. 3, fig. 5) has a fine reticulate ornament, and it would require small change to this ornament type to produce the characteristic anomalodesmatan granulose texture. Thus, it appears that all the features of the early anomalodesmatans could be readily derived from a modiomorphoid ancestor, and I believe that there is no need to look any further for the origin of this subclass.

Subclass NEOTAXODONTA Korobkov, 1954

(Pl. 4, figs 1, 3–6, 8–9)

Previously (Cope 1995), I reintroduced the subclass Neotaxodonta for the superfamilies Arcoidea and Limopsoidea which together constituted a restricted order Arcoida. The latter includes several familiar extant forms such as the ark shells and glycymerids. My justification for separating out the superfamilies Arcoidea and Limopsoidea from the subclass Pteriomorphia, as in the *Treatise*, was that extant members of the subclass Neotaxodonta are characterized by their unique combination of duplivincular ligament (secondarily lost in some limopsoids), with a two-layered shell consisting of an outer crossed-lamellar layer and an inner complex crossed-lamellar layer, together with dentitions which are continuous along the hinge-plate. In contrast, the pteriomorphians have a calcitic outer shell layer, dentition which has a subumbonal lacuna, together with a ligament which is primitively duplivincular (although many extant forms have lost it). The origins of the neotaxodonts are believed to lie within the glyptarcoid palaeoheterodonts (Pl. 4, figs 2, 7), from which they differ most significantly in the possession of a duplivincular ligament, but probably also in shell microstructure. The two-layered shell of modern neotaxodonts is most likely to have arisen through loss of the outer aragonitic prismatic layer of a three-layered shell (Text-fig. 1).

In the *Treatise* (Cox *et al.* 1969), the earliest arcoidean is quoted as *Parallelodon*. However, the first occurrence, in the lower Ordovician, reported for that genus was based partly on Newell's placing (*in* Cox *et al.* 1969, p. N256) of *Glyptarca* Hicks, 1873 in synonymy with *Parallelodon*. It has since been shown unequivocally by several authors, including Carter (1971) and Cope (1996, who re-defined *Glyptarca* on the basis of better material), that it is a palaeoheterodont. The fact that its age was early Arenig, rather than Tremadoc as quoted by Newell, has been known since Pringle (1930) demonstrated Hicks' error. The other possible early Ordovician *Parallelodon* is *P. antiquus* Barrois from the upper Arenig of the Grès Armoricain of Brittany. However, Babin (1966, p. 146) reported that Barrois' specimen, on which the dentition was based, was lost, but that a gutta percha mould on which Barrois (1891) based his figure (pl. 3, fig. 3) suggested that the dentition was far less clear than shown in the figure and was 'd'analyse délicate'. It thus seems that this species must be treated with caution until further material is found.

The genus *Catamarcaia* Sánchez and Babin, 1993 from the upper middle Arenig of Argentina (Pl. 4, figs 4, 6, 9) is a form which appears to be close to the ancestral neotaxodont (Cope 1997). This genus has dentition, which could be derived readily from that of a palaeoheterodont such as *Glyptarca* (Pl. 4, figs 2, 7), together with a grooved ligamental area. Sánchez (1995) compared the development of the dentition of *Catamarcaia* with that of *Glyptarca*, pointing out the similarities. However, it should, be noted that this comparison is, in fact, with the glyptarcoid *Hemiprionodonta* Cope, 1996, following the redefinition of *Glyptarca* (Cope 1996). Sánchez and Babin (1993) treated *Catamarcaia* as a pteriomorph lacking the central edentulous space on the hinge-plate, but I would regard that feature as an essential character state for Early Palaeozoic pteriomorphs. Earlier (Cope 1996), I preferred to regard *Catamarcaia* as a palaeoheterodont, but it has since become clear that this genus possesses a continuous subumbonal dentition combined with a duplivincular ligament, which together are the distinguishing feature of the neotaxodonts. Sánchez and Babin (1993, p. 267) declined to assign *Catamarcaia* to a family. I suggest that it could well belong to the Parallelodontidae Dall, 1898, although Sánchez (1995) suggested that it may have been ancestral to that family.

The shell microstructure of *Catamarcaia*, although not preserved, can be reconstructed confidently as three aragonitic layers: an outer prismatic, a middle crossed-lamellar, and an inner complex crossed-lamellar layer. These microsctructures were derived through modification of the three-layered prismato-nacreous structure of its glyptarcoid palaeoheterodont ancestor, although it is possible that the glyptarcoids already possessed such a shell. From such a parent shell microstructure, the shell types of all neotaxodonts, pteriomorphians and heterodonts can be derived readily (Text-fig. 1).

Newell (*in* Cox *et al.* 1969, p. N256) noted that the phylogeny of the Parallelodontidae was 'difficult to determine and poorly understood'; however, the discovery of *Catamarcaia* seems to demonstrate the origin of the group and, moreover, that of the subclass Neotaxodonta. The new genus *Alytodonta* (see below and Pl. 4, figs 1, 5, 8), from the lowermost Silurian, provides a link between *Catamarcaia* and the Wenlock genus *Freja* Liljedahl, 1984 (Pl. 4, fig. 3).

The characteristic taxodont dentitions, exhibited by many neotaxodonts, were responsible for some of the problems of high-level bivalve taxonomy formerly encountered by palaeontologists, particularly those subscribing to the ideas espoused by Douvillé (1912) whose 'sedentary branch' led directly from *Nucula* to *Arca*. This classification was followed by many European palaeontologists and was adopted by Davies (1947) in one of the two then widely available palaeontological textbooks in Britain. The other textbook (Woods 1946) included both *Nucula* and *Arca* in the order Taxodonta. Although the fundamental differences between the two stocks were recognized by Korobkov (1954) in his subclasses Palaeotaxodonta and Neotaxodonta, confusion still clearly persisted in some quarters, and continued until Cox's (1959) unequivocal demonstration that the taxodont dentitions of the arcoids were totally unrelated phylogenetically to those of the nuculoids.

Of the forms included by Cox *et al.* (1969) in the order Arcoida, I have separated out the superfamily Cyrtodontoidea, which is characterized by anterior and posterior teeth, separated by an edentulous area, and retained it in Pteriomorphia, within a new order Cyrtodontoida (Cope 1996). The order Arcoida *sensu stricto*, on the other hand, is characterized by dentition which is

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EXPLANATION OF PLATE 4

Figs 1, 5, 8. *Alytodonta gibbosa* gen. et sp. nov.; BMNH L. 49858; Mulloch Hill Sandstone, Lower Llandovery, Mulloch Hill, Girvan, Ayrshire; holotype, LV. 1, latex cast of internal mould; ×2. 5, internal mould; ×2. 8, enlarged view of hinge region of latex cast to show details of dentition and insertion points of duplivincular ligament beneath umbo; ×3·5.

Figs 2, 7. *Glyptarca serrata* Cope, 1996; lower Arenig, Llangynog, Carmarthenshire. A glyptarcoid palaeoheterodont probably similar to that from which neotaxodonts were derived. 2, NMW78. 17G. 490; RV internal mould with umbo removed to show dentition; ×6·5. Figured Cope 1996, pl. 2, fig. 10. 7, NMW78. 17G. 801; holotype, LV; ×4. Figured Cope 1996, pl. 2, fig. 1.

Fig. 3. *Freja fecunda* Liljedahl, 1984; SGU Type 3379; Upper Wenlock, Gotland; ×12. Detail of RV hinge to show dentition. After Liljedahl 1984, fig. 18I.

Figs 4, 6, 9. *Catamarcaia chaschuilensis* Sánchez and Babin, 1993; middle Arenig, Western Argentina. 4, CEGH-UNC 10530; RV; ×3. 6, CEGH-UNV 10533; latex cast; ×3·66. 9, CEGH-UNC 10530; close-up of anterior dentition; ×7. After Sánchez and Babin 1994, pl. 1, figs 5–7.

Fig. 3 published with permission from Sveriges Geologiska Undersökning. Figs 4, 6, 9, published with permission from the Societa Española de Paleontologia.


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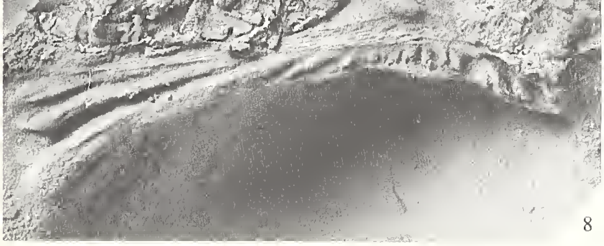
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COPE, neotaxodonts, glyptarcoid palaeoheterodonts continuous beneath the umbo. This leaves the superfamilies Arcoidea and Limopsoidea within the order Arcoida. The latter superfamily is now, however, modified from the entry in the *Treatise*, following the removal of the family Manzanellidae Chronic, 1952 to the Palaeotaxodonta (see above, for discussion of the affinities of the Manzanillidae). One result of this move is that the earliest limopsid is now of late Triassic age (*Hoferia* Bittner, 1894, from the upper Triassic of the Alps).

Subclass PTERIOMORPHIA Beurlen, 1944

(Pl. 5, figs 1–9)

This subclass includes a wide variety of extant forms, such as the oysters, the pectinids and the mussels, that are characterized by shells which have a calcitic outer layer. All groups can be satisfactorily linked phylogenetically to the order Cyrtodontoida (Pl. 5, figs 4–5, 7) which is generally regarded as representing the earliest of the pteriomorphians. The Late Tremadoc Pacoota Sandstone fauna of Pojeta and Gilbert-Tomlinson (1977) includes the hitherto earliest known forms. However, the occurrence of the earliest pterioid in the lower Arenig (Cope 1996) and the earliest ambonychiid in the middle Arenig (Cope 1996) implies that these groups (e.g. Pl. 5, figs 1–2, 6, 8–9) may be of almost equal antiquity. The dentition of the cyrtodontoids, which is characterized by a central edentulous area on the hinge-plate, could have been derived readily from the dentition of the earliest neotaxodonts by loss of the subumbonal dentition. Several authors (e.g. Babin and Gutiérrez-Marco 1991) have noted that there is also agreement between the way in which the teeth of the cyrtodontoids radiate out dorsally from a centre below the hinge-line and the dentition of *Glyptarca*. This dorsally directed divergence was clearly inherited ultimately from the glyptarcoid palaeoheterodonts and, earlier (Cope 1996), I pointed out this significant difference between the actinodontoidean and the glyptarcoidean palaeoheterodonts. It is clear that neotaxodonts form ideal ancestors for the pteriomorphians; the only objection to this hypothesis of cyrtodontoid origins is that it is as yet unsupported by the fossil record. However, as Tremadoc faunas are so poorly known, this is an obstacle that may well be overcome by future finds.

EXPLANATION OF PLATE 5

Figs. 1–2. *Carotidens demissa* (Conrad, 1842). 1, FM 8879, upper Ordovician, Ohio; × 5. LV of a pterioid. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 11, fig. 5. 2, USNM 40554, upper Ordovician, Ontario; LV internal mould; × 1·5. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 11, fig. 12.

Fig. 3. *Myodakryotus deigryn* Tunnicliff, 1987; BGS GSM 22041; Caradoc, Llanfyllin, Montgomeryshire; RV; × 2, Negative supplied by S. P. Tunnicliff. Figured Tunnicliff, 1987, pl. 77, fig. 3. An early limoid.

Fig. 4. *Cyrtodonta huronensis* Billings, 1858; USNM 162715; middle Ordovician, Ontario; RV; × 2. After Pojeta 1978, pl. 8, fig. 2.

Fig. 5. *Cyrtodonta saffordi* (Hall, 1859); USNM 46191*a*; middle Ordovician, Tennessee; RV; × 1·4. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 8, fig. 11.

Fig. 6. *Byssopteria radiata* Hall, 1883; USNM 100540; Upper Devonian, Pennsylvania; lectotype, RV, × 1·15. Showing anterior shortening characteristic of ambonychiids. After Pojeta 1966, pl. 32, fig. 6.

Fig. 7. *Falcatodonta costata* Cope, 1996; NMW78. 17G. 975; lower Arenig, Llangynog, Carmarthenshire; latex cast of holotype, RV; × 3.

Fig. 8. *Ambonychia alata* Meek, 1872, USNM 84928; upper Ordovician, Indiana; RV; × 0·75. After Pojeta 1966, pl. 29, fig. 18. Showing anterior shortening.

Fig. 9. *Palaeopteria* sp.; USNM 162737; middle Ordovician, Kentucky; LV; × 5. After Pojeta 1978, pl. 11, fig. 1. Showing characteristic dentition of early pterioid.

Fig. 10. *Illionia prisca* (Hisinger, 1837); Mo158171; Ludlow, Gotland; lectotype, LV; × 1. After Liljedahl 1991, text-fig. 5c. An early lucinoid heterodont.

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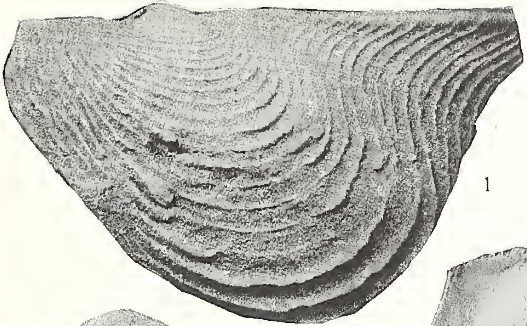
PLATE 5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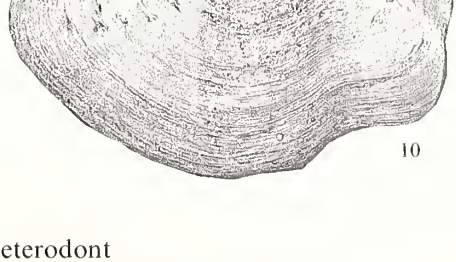
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COPE, pteriomorphians, heterodont

All extant pteriomorphians are of filibranch gill grade and, if the filibranch gill is the monophyletic feature as I claimed previously (Cope 1995), they were derived from a filibranch ancestor in the neotaxodonts.

The presence of a grooved ligamental area, in some cases at least indicative of a duplivincular ligament (see Pojeta 1978; Waller 1978), is another characteristic feature of many pteriomorphians. It is not known in the cyrtodontoid superfamily Falcatodontoidea Cope, 1996 (Pl. 5, fig. 7), but other features of this superfamily link it closely to the cyrtodonts; it appears to have been derived early from the cyrtodontoid stock and to have lost secondarily the duplivincular ligament (as have many of the younger pteriomorphian groups).

Most extant pteriomorphians have a shell with a calcitic outer layer, and some of them (e.g. the oysters) have a predominantly calcitic shell. However, many of them also have crossed-lamellar and/or complex crossed-lamellar structure in their shell (Carter 1990*b*). Previously (Cope 1995), I therefore concluded that the early Ordovician pteriomorphs could well have had a shell which included elements of crossed-lamellar microstructure. It seems probable that crossed-lamellar fabric occurred as a constituent shell microstructure in the neotaxodontoid line at the time of origin of the pteriomorphians because crossed-lamellar or complex crossed-lamellar shells are common to many forms which also possess a duplivincular ligament (neotaxodonts and pteriomorphians). The calcitic outer shell layer of the pteriomorphians thus appears to have developed secondarily from this ancestral shell type. The lucinoid and some veneroid heterodonts (see below) probably provide us with the best clue as to what this may have been, as they consist of three layers: an outer composite prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar layer (Taylor *et al.* 1973). The calcitic outer shell layer of the pteriomorphians seems to have originated by substitution of prismatic calcite for prismatic aragonite, probably through a single mutation, and the crossed-lamellar portions of the shell (or ligament) reflect the original microstructure of the middle and inner shell layer in early Ordovician forms. Indeed, some modern mytiloids and pectinoids retain the presumed parent shell microstructural plan (Taylor *et al.* 1969), as depicted in Text-figure 1. It is likely that the calcitic outer shell layer evolved at about the time of the separation of the Pteriomorphia from the Neotaxodonta, as all pteriomorphian groups, some of which had evolved from the cyrtodontoids within the early Ordovician, have a predominantly calcitic outer shell layer. There are as yet no known early Ordovician pteriomorphs with preserved shell microstructure, although Taylor *et al.* (1973, p. 288) reported that a late Ordovician ambonychiid (e.g. Pl. 5, figs 6, 8) probably had a prismatic calcite outer shell layer.

Other pteriomorphian groups can be derived readily from the cyrtodontoids. The pterioids are now known from the lower Arenig (Cope 1996) and the ambonychiids from the middle Arenig (Cope 1996). The mytiloids seem best derived from the latter group, rather than from the modiomorphoids as preferred by Pojeta (1978) because, in common with all these other groups, they have a shell which is primarily calcitic (but also sometimes including elements of crossed-lamellar and complex crossed-lamellar microstructure; Taylor *et al.* 1969), as opposed to the aragonitic prismato-nacreous shell of the modiomorphoids. Tunnicliff (1987) described the Caradoc genus *Myodakryotus* (Pl. 5, fig. 3), with a morphology intermediate between those of cyrtodontoids and limoids; the genus was assigned to the new family Myodakryotidae within the superfamily Limoidea. Subsequently (Cope 1995, text-fig. 30.3), I suggested how the origin of the later pteriomorphians may be related to these primary radiations.

Since the publication of the *Treatise*, various members of the order Praecardioida Newell 1965, formerly included in the Cryptodonta, have been the subject of further researches (e.g. the major monographical study by Kříž (1979) of the *Cardiola* group) which have demonstrated clearly that they are pteriomorphian forms. Following the *Treatise* classification, they would have been included in the order Arcoida but, in its restricted sense (as used herein, as an order within the Neotaxodonta), they cannot belong there. Kříž (1979) may well have been correct in deriving these forms from the Cyrtodontoida (the latter elevated to ordinal status by Cope (1996)), but they differ in many fundamental ways, including the dentition, from the cyrtodonts, and do not find a natural place within that order. The solution adopted herein is to recognize Praecardioida as a separate order within Pteriomorphia. Some forms included in the *Treatise* in Praecardioida, have been removed subsequently from that group, including the genus *Eopteria* Billings, 1865, shown by Pojeta and Runnegar (1976) to be a rostroconch.

Subclass HETERODONTA Neumayr, 1884

(Pl. 5, fig. 10)

This subclass is the most varied group of living bivalves and includes more than 80 families. It contains many forms familiar on European sea-shores, such as the cockles, razor-shells and myas, and a variety of fossil forms including the Cretaceous rudists. Heterodonts have fused mantle lobes and commonly have siphons; the gills are all of eulamellibranch grade and this subclass appears to be the last major group of bivalves to have evolved. Heterodont radiations are predominantly features of the Mesozoic and Cenozoic; in the Lower Palaeozoic heterodonts are extremely rare fossils and their origins consequently are largely cryptic.

I believe that there are significant differences between the subclasses Palaeoheterodonta and Heterodonta, although some authorities, notably Pojeta (e.g. 1987), combine the two into the subclass Heteroconchia Hertwig, 1895. The palaeoheterodonts are characterized primarily by prismato-nacreous shells and can be derived directly from the palaeotaxodonts (as demonstrated above), whilst the shells of the heterodonts contain both crossed-lamellar and complex crossed-lamellar layers and appear, most probably, to have been derived from the neotaxodonts. There are, of course, major problems in determining the shell microstructure of many fossil forms, particularly those from the Lower Palaeozoic, but probable phylogenetic links, proposed herein, suggest that the palaeoheterodonts and heterodonts should be maintained as distinct entities. All extant heterodonts are eulamellibranch, whilst extant palaeoheterodonts may be filibranch or eulamellibranch (see above).

The complex crossed-lamellar shell structure is shared only by some groups of heterodonts, pteriomorphians and the neotaxodonts; this provides strong evidence for the close association of these subclasses. Previously (Cope 1995), I suggested that although the subclass Neotaxodonta had originated after the acquisition of the duplivincular ligament, it seemed that the Heterodonta must have arisen before this was acquired, as its members lack this feature. I now believe, on the contrary, that this was unlikely, as the neotaxodonts clearly appeared significantly earlier in the fossil record, and the alternative solution, that the heterodonts were derived from the neotaxodonts, is a more parsimonious explanation of the similar shell microstructures in both groups. This view requires that the heterodont line then lost the duplivincular ligament; this is not a serious problem, as several pteriomorphian groups, including the mytilids, the ostreids and the limids, have also lost the duplivincular ligament which their cyrtodontoid ancestors possessed. In addition, some limopsid neotaxodonts have also lost this feature. Thus, it seems that the probable origin of the heterodonts lies within the neotaxodonts and not in the pteriomorphian rootstock as I earlier surmised (Cope 1995). In this view, there is no direct relationship between the palaeoheterodonts and heterodonts. Hertwig's (1895) combination of the two groups in the Heteroconchia, as followed by Pojeta (1987), is ill-founded; their only shared characteristic is a dentition that, on occasion, can be somewhat similar. However, the posterior lateral teeth in the palaeoheterodonts arise from beneath the umbo and the ligament; in the heterodonts, the posterior lateral teeth, where present, usually arise behind the umbo and the ligament. This latter origin of the posterior dentition would be expected if posterior lateral teeth of neotaxodontid type were combined with a shortened opisthodetic ligament as in the Heterodonta.

Reading of the *Treatise* makes it very difficult to decide what the first heterodont was. Cox (*in* Cox *et al.* 1969, p. N113) recorded the earliest form (disregarding *Babinka* – see below) as the lucinoid *Paracyclas* from the upper Ordovician of Scotland although, according to the systematic sections of the *Treatise*, that genus is restricted to the Devonian (Cox *et al.* 1969, p. N512). Cox's record seems to be based on *P. minor*, recorded from Girvan by Hind (1910, pl. 4, figs 32–35); this appears to be lucinoid in shape, but the lack of preserved dentition makes the assignment uncertain.

However, the middle Ordovician–Devonian genus *Cypricardinia* Hall, 1859 is assigned to the cardiniid crassatelloideans (Cox *et al.* 1969, p. N579), making this record earlier. Other records in the *Treatise* may be dismissed more readily; *Redonia*, assigned to the carditoidean veneroids (Cox *et al.* 1969, p. N546) is now agreed to be a palaeoheterodont, whilst *Matheria* Billings, 1858 (Cox *et al.* 1969, p. N566) is regarded as a cyrtodont, as also suggested in its inclusion there (Cox *et al.* 1969, p. N249). Otherwise, the next youngest recorded heterodont is the genus *Illiona* Billings, 1875 from the Silurian (Pl. 5, fig. 10), belonging to Lucinoidea (Cox *et al.* 1969). From these records, it appears that both the crassatelloideans and the lucinoideans have records which go back into the Ordovician, with the possibility that the former appear earlier.

Reid and Brand (1986) showed that all extant lucinoideans live symbiotically with sulphide-oxidizing bacteria, in much the same manner as the lipodontids (see above); they have usually lost the second gill demibranch through paedomorphosis and, like the lipodontids, have a hypotrophied gut. Living lucinoideans are characterized by the lack of an inhalant siphon and are dependent upon the foot to make an adequate inhalant ventilation tube. Reed and Brand suggested that the ancestral lucinoidean was probably already in symbiotic relationship with bacteria and most probably had a eulamellibranch gill; they also suggested that such ancestral types probably lived as shallow short-siphoned suspension feeders, with extensive adductor muscles (a feature which they point out was already possessed by *Fordilla*), and that the Cretaceous–Recent family Ungulinidae Adams and Adams, 1857, as a non-specialized group, may have some of the characters of the ancestral form. As lucinoideans are clearly a specialized group, it is difficult to envisage them as the stem group of the heterodonts, and the crassatelloideans appear more likely candidates. At the moment, therefore, it appears that we cannot identify the origin of the heterodonts, other than to report that their shell microstructures suggest that their origins were from the neotaxodonts.

Taylor *et al.* (1973) showed that modern lucinoideans, and some veneroideans and tellinoideans have a three-layered shell: the outer layer is composite prismatic, the middle layer crossed-lamellar, and the inner layer complex crossed-lamellar; this may well have been the composition of the shell of the early Ordovician neotaxodonts (see above). In other heterodonts, the shell is composed of two layers (Taylor *et al.* 1969, 1973), the outer consists of crossed-lamellar, and the inner of complex crossed-lamellar aragonite microstructures. As lucinoideans are one of the earliest fossil heterodonts, and also widely regarded as the most primitive members of this subclass, it seems likely that the three-layered shell may have been the original heterodont condition, and the two-layered shell derived from this by loss of the outer layer.

McAlester (1965, 1966) claimed lucinoid affinities for the genus *Babinka* Barrande, 1881. However, that form is one of the earliest Ordovician bivalves, being now known from the Tremadoc (Babin 1982*a*), and on that basis alone seems most unlikely to be a heterodont. Indeed, arguments presented herein, suggest that Heterodonta appears to be the most derived bivalve subclass. Of other possible affinities, its dentition could ally it to the cycloconchid palaeoheterodonts, by loss of lateral teeth, as favoured, for example, by Babin (1982*a*). However, Pojeta (1978) suggested that the dentition of *Babinka* was hardly different from that of *Fordilla* and that it could have been directly derived from a *Fordilla*-like ancestor. *Babinka* differs from most other Ordovician bivalves in its multiple pedal muscle insertions, but McAlester's (1965) suggestion that this indicated a direct derivation from a monoplacophoran ancestor, independently of other bivalves (and thus making the class Bivalvia polyphyletic), has been rejected by other authors (e.g. Soot-Ryen 1969; Pojeta 1971). *Babinka* has been recorded widely from rocks of Tremadoc to Llanvirn age and is herein recorded for the first time from Britain (see below and Pl. 3, figs 3, 6). Its early geological appearance makes it difficult to accept *Babinka* as a heterodont. Earlier (Cope 1995), I considered it most likely to be a palaeoheterodont; its multiple pedal muscle insertions are shared by some cycloconchid palaeoheterodonts including *Cycloconcha* Miller, 1874 and *Celtoconcha* Cope, 1996, but also by the nuculoid *Myoplusia* Neumayr, 1884. *Babinka* is certainly not a nuculoid, but several groups of palaeoheterodonts, such as the redoniids and the modiomorphoids, have reduced dentition; I thus concur with Babin (1982*a*) in placing the genus (and the family Babinkidae Horný, 1960) within the order Actinodontoida of the subclass Palaeoheterodonta.

It thus seems that we can exclude *Babinka* from discussions of heterodont origins, in which case, the origin of the heterodonts becomes somewhat more transparent. The shell microstructures which some heterodonts share with the neotaxodonts suggest that these two groups are closely related. The subclass Neotaxodonta appears to have arisen from the glyptarcoid palaeoheterodonts and we now have an early Ordovician genus, *Catamarcaia*, which indicates such a link. The subclass Heterodonta, which evolved somewhat later, probably originated from the neotaxodonts as they share the same shell microstructure; the loss of the duplivincular ligament was a significant feature in this change, and there were concomitant changes in dentition associated with the shortening of the hinge-line. On this reading, the evolution of the heterodonts is a mid Ordovician (or later) phenomenon, and the heterodonts are the most derived of the bivalve subclasses (Text-fig. 2).

CONCLUSIONS

Various factors have contributed towards modifications of the existing schemes of high-level classification within the Bivalvia. The increasing amount of data on bivalve shell microstructures shows that these have considerable taxonomic significance (Text-fig. 1). The consensus of recent work (e.g. Runnegar and Pojeta 1992; Hinz-Schallreuter 1995) suggests that all known Cambrian bivalves were palaeotaxodonts. The discovery of an increasing number of early Ordovician forms has illustrated that the increase in diversity of the class through the early Ordovician represents a truly explosive evolution. The hypothesis that this increase in diversity, coupled with a simultaneous increase in size and abundance of bivalves, could be a direct response to the evolution of the feeding gill, as I proposed previously (Cope 1995), has allowed the construction of new phylogenetic links (Text-fig. 2). The cardiolariids are identified as palaeotaxodonts with differentiated hinge teeth probably indicating the acquisition of the filibranch gill; these form suitable ancestors for the palaeoheterodonts. The lipodonts were evolved from the palaeotaxodonts very early, perhaps during the Cambrian. The modiomorphoid palaeoheterodonts, characterized by reduced dentition, gave rise to the anomalodesmatans in the early Ordovician. One group of palaeoheterodonts, the glyptarcoideans, was characterized by dorsally divergent teeth. Such forms could readily provide the origin of the neotaxodonts by development of the duplivincular ligament. The neotaxodonts, however, had a more sophisticated shell microstructure, which included an outer prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar layer (Text-fig. 1). Early neotaxodonts with this shell microstructure gave rise to: (1) the modern neotaxodonts, which have lost the outer layer; (2) the pteriomorphians, in which the outer layer of prismatic aragonite is replaced by one of prismatic calcite, and which have developed a subumbonal lacuna in the dentition; and (3) the heterodonts, which retained the inherited shell microstructure (although some forms later lost the outer layer), but in which the duplivincular ligament has been lost.

The links between several of the bivalve subclasses now seem to be reasonably well documented, but some problems remain. In order to answer these problems, specific targets should be addressed; initially, the principal efforts should be directed towards increasing our knowledge of the earliest Ordovician faunas, and here the Gondwanan shelves should be the first target area. It has become evident, in the research for this paper, that we know almost nothing about Tremadoc bivalve faunas, yet this was clearly the time when the major diversification of the class occurred. Areas for possible search include north Africa and Argentina. Subsequently, searches must be made for mid and late Cambrian bivalves to fill the disjunct record of early bivalve evolution; it is likely that the subclass Lipodonta was derived from the Palaeotaxodonta before the Ordovician, and even the Palaeoheterodonta may pre-date the Ordovician. For this search, the area under investigation should be widened, as the records of Cambrian forms show them to have been of widespread occurrence and not restricted to the Gondwanan shelves.

Another problem to be addressed is that of the origin of the heterodonts. It may well be that already described Ordovician forms may in future be found to belong to the heterodonts, but the origin of the heterodonts, as the major bivalve cohort of the Mesozoic and Cenozoic, is a subject which requires investigation. The similarity of the shell microstructure in the neotaxodonts and heterodonts suggests that the two are closely related, and that the combination of the palaeoheterodonts and heterodonts within a subclass, Heteroconchia, is engendered purely by some degree of homeomorphy of the dentitions.

The fact that no further bivalve subclasses appeared in the geological record later than the subclass Heterodonta in the mid or late Ordovician, and that all seven subclasses that were then in existence are extant, emphasizes the significance of these early Palaeozoic radiations in the phylogeny of the class Bivalvia.

SYSTEMATIC PALAEONTOLOGY

Class BIVALVIA Linnaeus, 1758
Subclass PALAEOTAXODONTA Korobkov, 1954
Order NUCULOIDA Dall, 1889
Superfamily NUCULOIDEA Gray, 1824
Family CARDIOLARIIDAE fam. nov.

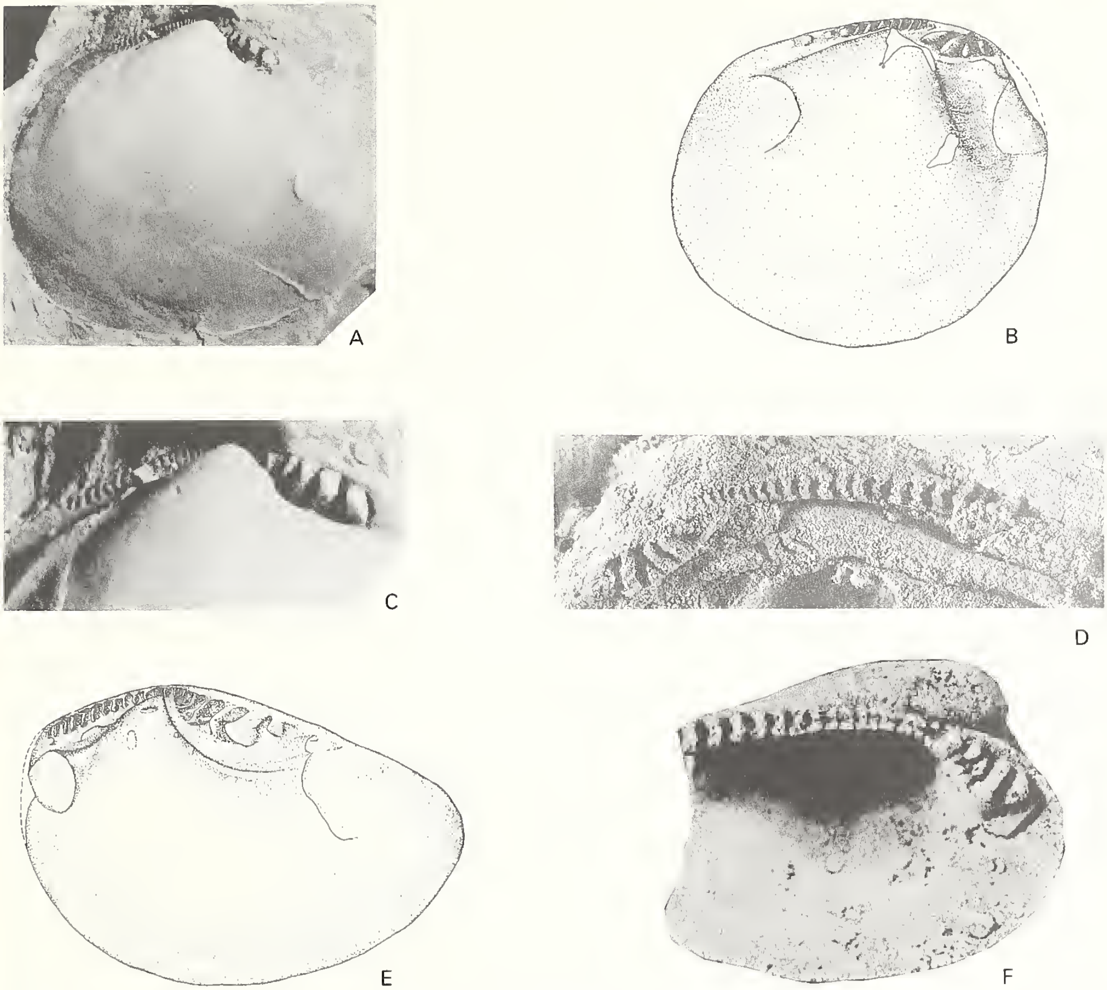
(Text-figure 3)

Diagnosis. Palaeotaxodonts with separate anterior and posterior dentitions, in which the hinge lies along line of posterior teeth; anterior teeth, which may be enlarged, lie below hinge axis. Ligament external, opisthodetic.

Remarks. This new family is proposed for palaeotaxodonts which developed separate anterior and posterior dentitions, with a tendency to overlap subumbonally in some of the more advanced forms. The separate dentitions arose because these forms used their dentition in a way different from that of other palaeotaxodonts. In the cardiolariids, the posterior set of more or less equal teeth acted as the hinge and lies below the external opisthodetic ligament. The separate anterior larger teeth served to locate the valves when they were opened more widely to expel pseudofaeces. Previously, I concluded that this hinge type evolved in response to the evolution of the filibranch gill, probably in the early Ordovician (Cope 1995). In the great majority of palaeotaxodonts, which were clearly protobranch, the equal or subequal teeth (gradidentate; Cope 1995) acted in concert, and the hinge lay parallel with the row of teeth (see Pl. 1, figs 1–7). Although the ligament was originally external and opisthodetic, from the early Silurian onwards many gradidentate palaeotaxodonts developed an internal ligament located centrally on the hinge-plate (Pojeta and Runnegar 1985; e.g. Pl. 1, fig. 7).

The family includes a small number of genera, closely related by their similarly differentiated dentition, which can be described as cardiolariid. This dentition is well shown by *Cardiolaria* itself (Text-fig. 2), the type species of which is *C. barrandei* Munier-Chalmas, 1876. McAlester (1968) designated a lectotype, and figured the type material from the middle Ordovician of the Armorican Massif; McAlester (1968) could not find teeth preserved beneath the umbones in any of the specimens. Babin (*in* Babin and Gutiérrez-Marco 1991, p. 116) examined topotypes showing 'an edentulous space beneath the umbo, between the two sets of teeth. This shows it to be attributable to the genus *Cardiolaria*.' Babin and Gutiérrez-Marco (1991) also figured the closely related species *C. beirensis* (Sharpe, 1853) from the upper Lower Llanvirn to Llandeilo of Spain; they showed that in that form there was clear subumbonal overlap of the anterior and posterior dentitions (see Text-fig. 3). Bradshaw (1970) figured the same species from the Llanvirn and Llandeilo of Finistère; her text-figure 1 showed that at a length of *c.* 5 mm, *C. beirensis* has a continuous dentition, but it is noticeable that there is a discordance immediately anterior to the umbo. Bradshaw (1970, text-figs 2–4) also figured other specimens showing the adult stages and indicated areas of resorption; her text-figure 2 shows a clear overlap between the two sets of teeth.

Another genus grouped herein within the family Cardiolariidae is *Deceptrix* Fuchs, 1919 (which ranges from the mid Ordovician to the Devonian). Forms ascribed to *Deceptrix*, but which do not



TEXT-FIG. 3. Cardiolariid palaeotaxodonts. A, C. *Deceptrix carinata* Fuchs, 1919; lectotype; Lower Devonian, Sauerland, Germany; collections of the Geologisch-Paläontologische Museums der Humbold Universität, Berlin. A, ×4, after McAlester 1968, pl. 6, fig. 1. C, ×6, after McAlester 1968, pl. 6, fig. 3. B, *Cardiolaria beirensis* (Sharpe, 1853); UCNZ K.3; Llandeilo, Finistère; ×5; after Bradshaw 1970, text-fig. 2. D, *Cardiolaria beirensis* (Sharpe, 1853); UCB FSL 550 110; ?upper Llandeilo, Ciudad Real, Spain; ×4·5; after Babin and Gutiérrez-Marco 1991, pl. 3, fig. 5. E, *Praeleda costae* (Sharpe, 1853); UCNZ C.1.b.; Llandeilo, Finistère; ×5; after Bradshaw 1970, text-fig. 7. F, *Inaequidens davisi* Pojeta and Gilbert-Tomlinson, 1977; UT 94496; middle Ordovician, Tasmania; ×5·5; after Pojeta and Gilbert-Tomlinson pl. 5, fig. 7. A, C. Reproduced by permission of the publisher, the Geological Society of America, Boulder, Colorado USA. Copyright © 1968 by the Geological Society of America, Inc. F. Reproduced by permission of the Australian Geological Survey Organisation.

belong to that genus as exemplified by the type species *D. carinata* Fuchs (see Text-fig. 3) have been figured by several authors, particularly Pojeta (1971, 1978) and Tunnicliff (1982). *D. carinata* (refigured by McAlester 1968) and herein (Text-fig. 3) shows a straight row of posterior teeth and a small number of much larger anterior teeth lying below the hinge-line; it is thus a typical cardiolariid and is not related to the gradidentate types which have been figured as *Deceptrix* by Pojeta (1971, 1978) and Tunnicliff (1982). Some of these forms, however, are well described and figured, and in order to prevent further confusion of such forms with cardiolariid palaeotaxodonts, I here propose the new generic name *Homilodonta* (Greek: *homilos* (= crowd) and *odontos* (= tooth), referring to the crowded row of gradidentate teeth on the whole hinge-plate). As type species of the genus, I designate *Arca subtruncata* Portlock, 1843. Tunnicliff (1982, pp. 60–61) revised this species, designated a lectotype and provided admirable illustrations (1982, pl. 9, figs 1–7, 9–11). *Homilodonta* also includes the other species figured by Tunnicliff (1982) under the name *Deceptrix*, and the species figured by Pojeta (1971, pl. 5, figs 19–20; 1978, pl. 1, figs 1–2). One of the latter is figured herein as Plate 1, figure 2. *Homilodonta* is a member of the family Praenuculidae (McAlester 1969) and its gradidentate dentition is unrelated to the cardiolariid type. Another species, figured as *Deceptrix filistriata* (Ulrich) by Pojeta (1978, pl. 2, fig. 1), can be readily included in the genus *Praenucula* Pfab, 1934. It is figured herein as Plate 1, figure 5.

Deceptrix seems distinct from *Praeleda*, good examples of which were figured by Bradshaw 1970 and (under the name *Praenucula*) by Babin and Gutiérrez-Marco (1991). *Praenucula* does not show the two distinct series of teeth arranged at an angle to each other, as noted by Bradshaw (1970) for *Praeleda*, and is thus not a cardiolariid. The Australian genus *Inaequidens* Pojeta and Gilbert-Tomlinson, 1977 (Text-fig. 3F), is another mid Ordovician genus which has a typical cardiolariid hinge and is thus assigned to the family.

If the evolution of the feeding gill in the Bivalvia was a single event, then I believe that it must have occurred early in bivalve evolution. If this important evolutionary step occurred within the Cardiolariidae, its members must therefore have possessed a feeding gill, and the evolution of the differentiated hinge in the Cardiolariidae may be construed as a direct response to the evolution of the filibranch gill and filter feeding. Thus, I have already suggested (Cope 1995) that the genus *Cardiolaria* was a filibranch palaeotaxodont and would now claim the same for all members of the family Cardiolariidae – a conclusion which requires amendment to the diagnosis of the subclass Palaeotaxodonta, as hitherto all its members have been assumed to have been protobranch. On this basis, all bivalve stocks arising directly or indirectly from filibranch palaeotaxodonts must themselves have been of filibranch grade. The eulamellibranch grade ctenidium is thus seen as a polyphyletic feature which evolved separately in distinct filibranch cohorts.

Subclass PALAEOHETERODONTA Newell, 1965
Order ACTINODONTOIDA Douvillé, 1912
Superfamily ACTINODONTOIDEA Douvillé, 1912
Family BABINKIDAE Horný, 1960

Genus BABINKA Barrande, 1881

Type species. *Babinka prima* Barrande, 1881, by monotypy.

Babinka prima Barrande

Plate 3, figures 3, 6

1881 *Babinka prima* Barrande, pl. 266, VI, figs 1–16.
1935 *Babinka prima* Barrande; Thoral, p. 162, pl. 13, figs 4–5.
1954 *Babinka prima* Barrande; Vokes, p. 235, fig. 1.
1960 *Babinka prima* Barrande; Růžička and Prantl, p. 48.
1960 *Babinka prima* Barrande; Horný, p. 480, pl. 1.
1962 *Babinka prima* Barrande; Vogel, p. 235, pl. 5, figs 5–6.
1965 *Babinka prima* Barrande; McAlester, p. 242, pl. 26, figs 3–12; pl. 27, figs 2–5; pl. 28, figs 1–4, 9–14.
1969 *Babinka prima* Barrande; Soot-Ryen, pl. 34, figs 6–8.
1971 *Babinka prima* Barrande; Pojeta, p. 12, pl. 1, figs 12–14.
1977 *Babinka prima* Barrande; Babin, p. 52, pl. 4, figs 1–14; pl. 5, figs 1–3, 6, 9–10.
1978 *Babinka prima* Barrande; Pojeta, p. 242, pl. 14, figs 10–11.

1982*a* *Babinka prima* Barrande; Babin, p. 40, pl. 11, figs 8–9.
1991 *Babinka prima* Barrande; Babin and Gutiérrez-Marco, p. 128; pl. 5, fig. 5.

Material. One specimen, NMW 96. 23G. 1a and 1b (part and incomplete counterpart).

Horizon and locality. From the Pontyfenni Formation, *Bergamia rushtoni* Biozone, Fennian Stage, upper Arenig, at Pontyfenni quarry, Carmarthenshire, South Wales (see Fortey and Owens 1987).

Description. If one accepts the orientation of *Babinka* which was proposed by McAlester (1965), the genus is elongated anteriorly. Starobogatov (1971) disagreed with this interpretation of the orientation but, as shown by Pojeta (1978, p. 242), there are valid reasons for accepting it. The single specimen figured herein (Pl. 3, figs 3, 6) is thus interpreted as a left valve composite mould. The shell is 22·9 mm long and 17·8 mm high, measurements which are similar to those of the larger of the Bohemian type material. The specimen shows well the multiple pedal muscle scars which characterize the genus. On this specimen, some six or seven of these are visible (Pl. 3, fig. 6); according to McAlester (1965), specimens from Bohemia have six pedal muscle scars. Gill attachment muscle impressions are visible at the end of several of the pedal muscle scars; these show up to three small scars for each pedal muscle (Pl. 3, fig. 6). The anterior adductor is very similar in size and situation to that of the type material, being long and elongated dorsally (Pl. 3, figs 3, 6); the posterior adductor is not so well displayed although it clearly conforms in shape and position to that of the species. Unfortunately, no dentition is preserved on this specimen, the hinge area being poorly preserved, but the shape of the specimen and its musculature leave no doubt of the specific assignment.

There is a well-developed commarginal ornament, with some strong growth increments. At the anterior end of the ventral part of the shell, there is a suggestion of a faint radial ornament. The counterpart of the specimen is only partly preserved and shows no additional features.

Remarks. Babinka prima is now recorded from the uppermost Tremadoc and the lower Arenig of the Montagne Noire (Babin 1982*a*), and from the upper Arenig of South Wales; from the Llanvirn of the Czech Republic (Barrande 1881) and the Hesperan Massif of Spain (Babin and Gutiérrez-Marco 1991). *B. oelandensis* Soot-Ryen, 1969, was described from the upper Arenig of Sweden, it differs from *B. prima* in its shape and details of the musculature. This is the first record of the genus from Britain.

Subclass NEOTAXODONTA Korobkov, 1954
Order ARCOIDA Stoliczka, 1871
Superfamily ARCOIDEA Lamarck, 1809
Family PARALLELODONTIDAE Dall, 1898

Genus ALYTODONTA gen. nov.

Derivation of name. From the Greek *alyton* (= continuous) and *odontos* (= tooth).

Type species. Alytodonta gibbosa sp. nov.

Diagnosis. Inflated rounded shell, longer than high with straight hinge-line bearing continuous dentition, with curved anterior pseudolaterals, numerous short pseudocardinals and few long posterior lateral teeth. Ligament amphidetic, duplivincular. Slight posterior alation.

Remarks. Alytodonta is shown by its continuous dentition to be a neotaxodontid and falls into place as a genus intermediate in many characters between *Catamarcaia* Sánchez and Babin, 1993 and *Freja* Liljedahl, 1984. It differs from *Cyrtodonta* (and other cyrtodontids) in lacking a subumbonal lacuna in the dentition. It resembles most closely the early Ordovician *Catamarcaia*, from which it is distinguished by shell proportions and in dentition. *Catamarcaia* has one anterior pseudolateral which is strongly hooked, with its dorsal region parallel to the hinge-line; it has more complex pseudocardinal teeth and has more posterior pseudolateral teeth than *Alytodonta*.

Alytodonta gibbosa sp. nov.

Plate 4, figures 1, 5, 8; Text-figure 4

1910 *Cyrtodonta gibbosa* Salter; Hind, p. 512, pl. 4, fig. 17.
1962 *Cyrtodonta gibbosa* Salter; Vogel, pl. 5, fig. 3.
1984 "*Cyrtodonta*" *gibbosa* Salter; Liljedahl, p. 37, fig. 16F; p. 45, figs 20A, 25D.

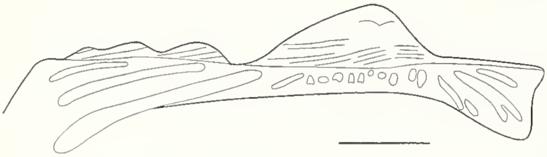
Derivation of name. From the Latin *gibbosus* (= protuberant).

Material. Only the holotype, BMNH L. 49858.

Horizon and locality. From the Mulloch Hill Sandstone, Lower Llandovery, Mulloch Hill, Girvan, Ayrshire.

Diagnosis. As for genus.

Description. The holotype and only specimen known is an internal mould of a strongly inflated left valve, 28·8 mm long and 24·4 mm high, which is weakly alate posteriorly. The umbo projects above the straight hinge-line and is prosogyral. The anterior adductor is small, oval and moderately well impressed. The posterior adductor is much larger, but it is only slightly impressed and its margins are diffuse, so its total extent is not discernible. There is a well impressed small muscle scar immediately anterior to this, which is presumably a posterior pedal retractor. No pallial line is visible.



TEXT-FIG. 4. *Camera lucida* drawing of the hinge region of holotype (BMNH L. 49858) of *Alytodonta gibbosa* sp. nov. Scale bar represents 5 mm.

The dentition (Text-fig. 4) is continuous along the hinge-plate. Three anterior pseudolaterals have two smaller ones interspersed between the posterior two; these probably arose through bifurcation. There are 11 small, rather irregularly arranged, pseudocardinal teeth, the most posterior is elongate. The three posterior pseudolaterals are long and the most dorsal of these is slender, whilst the most ventral is quite thick and blunt (see Pl. 4, fig. 8). The other is intermediate in thickness. The grooved ligamental insertions are clearly visible, both anterior and posterior to the umbo, showing that this bivalve possessed an amphidetic duplivincular liagment.

The internal mould bears impressions of commarginal growth increments, but the anterior ventral marginal area also shows a suggestion of fine radial ornament.

Remarks. Hind (1910, p. 512) referred to this species as *Cyrtodonta gibbosa* Salter. This name, however, appears to be merely a copy from the original label on this specimen in the Gray collection. Unusually, with his description of this species, Hind did not give any synonymy, nor did he refer to any work of Salter where this name can be found. The name as used by Hind is also suspect because the supposed author's name (Salter) was not put in parentheses by Hind. However, Salter never used the generic name *Cyrtodonta*, as he believed (wrongly) that the genus *Palaearca* Hall, 1859 predated it (see Salter 1866). Prolonged search by the writer has failed to find any mention either of the species *Palaearca gibbosa* Salter or of *Cyrtodonta gibbosa*, except by Vogel (1962) and Liljedahl (1984), both of whom merely copied Hind's use of the name. Bigsby (1868) referred to *Palaearca gibbosula* Salter as a manucript name for a species from the Trentonian of western Tasmania, but this species appears never to have been described. I have therefore concluded that *Cyrtodonta gibbosa* is a *nomen nudum* and thus invalid. Since at least three previous authors have used this specific name, I believe the best course is to stabilize the nomenclature, and here propose the name *gibbosa* as a new species.

Liljedahl (1984, p. 37) was the first to point out that this species could not belong to the superfamily Cyrtodontoidea as it had continuous subumbonal dentition, whereas the cyrtodontoids always have a subumbonal lacuna in their dentition, which separates the teeth into discrete anterior and posterior sets. This feature allows the specimen to be assigned to the subclass Neotaxodonta, rather than Pteriomorphia as previously.

Hind's (1910, p. 512) description of the dentition is very inadequate and mentions only two anterior oblique teeth and two long oblique teeth posteriorly. Were it not for his reasonably accurate measurements and figure, it would be difficult to believe that the description of the dentition was in reality from this specimen.

Subclass PTERIOMORPHIA Beurlen, 1944

In my earlier discussion of pteriomorphian taxonomy (Cope 1996, p. 1010), I proposed Cyrtodontida as a new ordinal level taxon to include the superfamilies Cyrtodontoidea Ulrich, 1894 and Falcatodontoidea Cope, 1996. In doing so, however, I overlooked that the Cyrtodontida had been proposed as an order by Scarlato and Starobogatov (*in* Nevesskaya *et al.* 1971) and I am grateful to Mr V. A. Ratter for bringing this to my attention. Although the Rules of Zoological Nomenclature do not apply to taxa higher than the family group level, I nevertheless feel that the authorship of the order Cyrtodonta (which I interpreted in a much more narrow sense than Scarlato and Starobogatov) should be attributed to Scarlato and Starobogatov 1971, *emend.* Cope 1996.

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APPENDIX

Abbreviations used in plate descriptions

AMNH, American Museum of Natural History, Washington DC
ANSP, Academy of Natural Sciences of Philadelphia
BMNH, Natural History Museum, London
BGS, British Geological Survey, Keyworth, Nottingham
CEGH-UNC, Cátedra de Estratigrafia y Geología Historíca, Universidad Nacional di Córdoba
CPC, Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra
CUM, Department of Palaeontology, Complutense University of Madrid
FM, Field Museum of Natural History, Chicago
LV, left valve
Mo, Swedish Museum of Natural History, Stockholm
NMW, National Museums and Galleries of Wales, Cardiff
RM Mo, Swedish Museum of Natural History, Stockholm
RV, right valve
SGU Type, Type Collections, Geological Survey of Sweden, Uppsala
UCB, Université Claude Bernard, Lyon 1
UCNZ, Department of Geology, University of Canterbury, New Zealand
USNM, Department of Paleobiology, United States National Museum, Washington DC
UT, University of Tasmania
WM, Walker Museum Collection at Field Museum of Natural History, Chicago

REVISION OF THE SILURIAN GRAPTOLITE GENUS *RETIOLITES*

by DAVID K. LOYDELL, PETR ŠTORCH *and* DENIS E. B. BATES

ABSTRACT. The three *Retiolites* species, *R. geinitzianus*, *R. australis* and *R. angustidens*, may be distinguished only by differences in their dorso-ventral width (both the maximum attained and the rate of increase from the proximal end). Other characters used previously in specific discrimination are septal bar inclination and meshwork density. The former shows considerable intraspecific variation, with no consistent differences between the species. The latter is dependent upon the astogenetic stage of the specimen examined. Whilst *R. geinitzianus* and *R. angustidens* appear to have been of very widespread distribution, specimens of *R. australis* are known only from north of the Silurian equator. All three species have long stratigraphical ranges (for graptoloids) and are thus of little biostratigraphical utility other than in indicating a Telychian (Upper Llandovery) or Wenlock age.

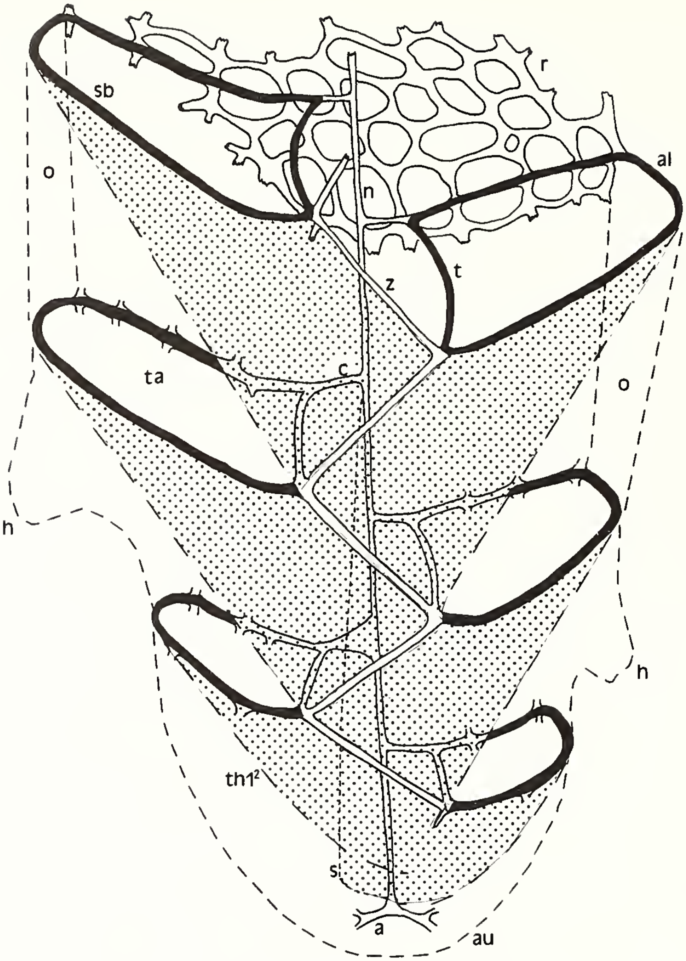
MEMBERS of the graptolite genus *Retiolites* Barrande, 1850 are among the most beautiful and distinctive of all Silurian graptoloids. Surprisingly, despite the wealth of recent publications on Silurian retiolitids (e.g. Bates and Kirk 1978, 1984, 1986, 1987; Lenz and Melchin 1987*a*, 1987*b*; Bates *et al.* 1988; Kozlowska-Dawidziuk 1995), the most recent concerned with the taxonomy of *Retiolites* at the species level was published over half a century ago (Bouček and Münch 1944). Given the considerable and continuing interest in Silurian retiolitids, and the resurgence of studies into high-resolution graptolite biozonation and correlation (e.g. see Koren' 1995), it was clear that a taxonomic revision of the genus was long overdue; this is presented herein.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; BB, Bouček collection, Czech Geological Survey, Prague; BGS, British Geological Survey, Keyworth; BM(NH), The Natural History Museum, London; GSE, British Geological Survey, Edinburgh; L, National Museum, Prague; MV, Museum of Victoria, Melbourne, Australia; N, United Institute of Geology, Geophysics and Mineralogy, Siberian Branch of the Russian Academy of Science, Novosibirsk; NMW, National Museums and Galleries of Wales, Cardiff; PŠ, Štorch collection, Czech Geological Survey, Prague.

SYSTEMATIC PALAEONTOLOGY

Terminology (Text-fig. 1). The terminology used herein is largely that of Bates (1990). The term 'septal bar' (Bates and Kirk 1978) is used for the thick and prominent lists (sb, Text-fig. 1), running at an angle to the rhabdosome axis towards the ventral sides of the rhabdosome. As noted by Kirk (1973, p. 10), the term 'parietal list' (used by Elles and Wood 1908, and more recently by e.g. Bulman 1970; Crowther 1981; Lenz and Melchin 1987*a*; Kozlowska-Dawidziuk 1995) is inappropriate for these structures as they do not enclose any body cavity (e.g. a theca). It is important to appreciate that the septal bars do not mark the junctions of interthecal septa with thecal walls (note that *Retiolites* do not possess interthecal septa). Thecae are rarely preserved, but it has been shown by Holm (1890, pl. 2, fig. 5; Pl. 1, fig. 4), Bates and Kirk (1978, pl. 12, fig. 2) and Lenz and Melchin (1987*b*, fig. 1) that the free ventral walls of the thecae are at a lower angle to the rhabdosome axis than the septal bars (see also Text-fig. 1); the arrangement of thecae depicted by Bulman (1970, fig. 59, 8) in the *Treatise* is incorrect.

[Palaeontology, Vol. 40, Part 3, 1997, pp. 747–762, 1 pl.]



TEXT-FIG. 1. Diagrammatic representation of a *Retiolites* rhabdosome in reverse view, with the ancora sleeve largely stripped away so that the thecal framework is visible. The stippled area represents the (very rarely preserved) thin periderm of the sicula and proximal thecae. The dashed lines on the ventral sides of the rhabdosome show the ventral extent of the obverse and reverse ancora sleeve panels. The lists in solid black are those surrounding the thecal apertures. Abbreviations: a, ancora; al, thecal apertural lip; au, ancora umbrella; c, connecting rod; h, hoods over proximal orifices; n, nema; o, orifices; r, reticulum (ancora sleeve) – only a small part at the distal end of the obverse side of the rhabdosome is shown; s, sicula; sb, septal bar; t, transverse rod; ta, thecal aperture; th, theca; z, zigzag list.

The prominent openings along the ventral sides of the rhabdosome (Pl. 1, fig. 2) should be termed orifices (o, Text-fig. 1) rather than apertures; they are not homologous with the thecal apertures. The latter are somewhat introverted (see Pl. 1, fig. 4; ta, Text-fig. 1). The inclination of a thecal aperture is the angle between the septal bar and the rhabdosome axis.

This paper is concerned only with the gross morphological features of *Retiolites* rhabdosomes; emphasis is placed on the distinguishing features of each species. For fuller descriptions (including micro- and ultrastructural detail) of chemically isolated *Retiolites* material from limestones and carbonate nodules, see Bates and Kirk (1978, 1986, in press) and Lenz and Melchin (1987*b*). The former authors also discussed the affinities, mode of rhabdosome secretion and palaeoautecology of *Retiolites* and other retiolitids (Bates and Kirk 1978, 1984, 1986, 1987, 1992, in press).

Measurements. Measurement of dorso-ventral width, both the maximum attained and the rate of expansion proximally, provides the easiest means of distinguishing between *Retiolites* species. For ease of comparison, measurements of rhabdosome dorso-ventral width are given below at specified distances (in mm) from the proximal end.

Some authors (e.g. Bouček and Münch 1944; Loydell and Cave 1993) considered the inclination of the septal bars to the rhabdosome axis to be of importance in differentiating species. This angle varies considerably intraspecifically (e.g. distally in *R. geinitzianus*, from 35–40° in the specimen illustrated by Loydell and Cave 1993, fig. 9a, to typically 55–60° in specimens from the *murchisoni* Biozone (Sheinwoodian) of Bohemia); it is not a diagnostic feature for any of the three species described below.

Measurements of meshwork density are quoted by several authors (e.g. Bouček and Münch 1944; Bjerreskov 1975), and the species *Retiolites densereticulatus* Bouček, 1931 was erected solely on the basis of its possession of a dense reticular meshwork. Scanning electron microscope studies have shown, however, that meshwork density in *Retiolites* is a function of astogeny, with more mature and 'gerontic' specimens having a denser meshwork (see e.g. Crowther 1981, pp. 92–94, pl. 15, fig. 5; Pl. 1, fig. 5).

Taxa described. Several species originally described under *Retiolites* do not belong in this genus and therefore are not described below. These are the following.

1. *Retiolites grandis* Suess, 1851. A junior synonym of *R. grandis*, *Stomatograptus törnquisti* Tullberg, 1883, is type species of *Stomatograptus* Tullberg, 1883.
2. *Retiolites rete* Richter, 1853. This rare species, recorded only from the lower Telychian of Germany, was placed by Bouček and Münch (1944) in their subgenus *Pseudoretiolites*, a taxon now accorded generic status (see e.g. Lenz and Melchin 1987*a*; Bates and Kirk 1992).
3. *Retiolites perlatus* Nicholson, 1868. Designated type species of *Pseudoretiolites* by Bouček and Münch (1944).
4. *Retiolites perlatus* var. *daironi* Lapworth, 1877. Like *perlatus*, this species is now assigned to *Pseudoretiolites* (e.g. Loydell 1993*b*).
5. *Retiolites perlatus* var. *obesus* Lapworth, 1877. Elles and Wood (1908) placed this in a subgenus of non-ancorate Ordovician 'retiolitid' (*Plegmatograptus*). Přibyl (1948) designated *obesus* type species of his genus *Pseudoplegmatograptus*.
6. *Retiolites macilentus* Törnquist, 1887. Moberg and Törnquist (1909) designated this as type species of their genus *Plectograptus*.
7. *Retiolites nassa* Holm, 1890. Type species of *Gothograptus* Frech, 1897.
8. *Retiolites spinosus* Wood, 1900. Elles and Wood (1908) placed this species in a subgenus (*Gothograptus*); it was subsequently designated type species of *Spinograptus* (see Bouček and Münch 1952).
9. *Retiolites eiseli* Manck, 1917. Designated type species of *Paraplectograptus* by Bouček and Münch (*in* Přibyl 1948; see also Bouček and Münch 1952).
10. *Retiolites praecursor* Kirste, 1919. Originally described from the Aeronian *cometa* Biozone, this species was assigned tentatively to *Pseudoretiolites* by Bouček and Münch (1944). It is from significantly older strata than any described *Retiolites sensu stricto* and Kirste's illustration (pl. 3, fig. 58) suggests that it is highly unlikely that the species should be placed in *Retiolites*.
11. *Retiolites geinitzianus* Barrande var. *maximus* Ruedemann, 1947. The authors have been unable to trace the single specimen assigned to this taxon by Ruedemann. The dimensions are comparable to those of *Stomatograptus grandis*. The horizon is quoted as *convolutus* Biozone (Aeronian), although it is possible (A. C. Lenz, pers. comm. 1996) that Ruedemann had confused '*Monograptus*' *convolutus* (Hisinger) with the Telychian species *Oktavites spiralis* (Geinitz).
12. *Retiolites obliquidens* Obut, 1949. The holotype, illustrated by Obut (1949, pl. 2, fig. 2a–b) and by Obut and Sobolevskaya (1966, pl. 4, fig. 1), is clearly a specimen of *Stomatograptus grandis* (Suess, 1851) *sensu lato*; stomata are prominent, particularly near the proximal end, and the rhabdosome's overall shape and

dimensions also match those of the latter species. Obut (1949, p. 16) stated that the holotype was collected from strata of early Wenlock age. Obut and Sobolevskaya (1966, p. 54) gave a rather different and somewhat more precise horizon for this specimen of '*spiralis* and *grandis*' Biozone (upper Telychian).

13. *Retiolites geinitzianus* var. *liangshanensis* Huo, 1957. This was distinguished by Huo from *R. geinitzianus* only 'by the greater length of the polypary'. Huo's specimens were destroyed during the 'Cultural Revolution' (Loydell 1993*a*), but from Huo's illustrations it seems that the species probably belongs in *Stomatograptus* (and almost certainly not in *Retiolites*).

14. *Retiolites nevadensis* Berry and Murphy, 1975. This species was assigned to *Agastograptus* by Obut and Zaslavskaya (1986) and to *Spinograptus* by Lenz and Melchin (1991) and Lenz (1993). Kozlowska-Dawidziuk (1995) noted differences between Berry and Murphy's species and other *Spinograptus* species, suggesting that *nevadensis* (and *S. apoxys* Lenz, 1993) form a group 'generically separate' from *Spinograptus*. Whatever the species' eventual generic assignment, it seems that it does not belong in *Retiolites*.

15. *Retiolites minutus* Ni, 1978. The type material has been examined recently by one of us (PŠ) and is assignable to *Pseudoretiolites*.

In addition to the above are several other species, originally assigned to *Retiolites* by Eisenack (1951), now placed in the genera *Paraplectograptus*, *Neogothograptus*, *Holoretiolites*, *Spinograptus* and *Plectograptus* (see Kozlowska–Dawidziuk 1995 for details).

Chang and Sun (1947, pl. 1, fig. 9) illustrated what they considered to be a new variety, '*Retiolites geinizianus* [*sic*] var. *spinus* Chang (var. nov.)'. No description was provided, however, and thus this taxon is a *nomen nudum*. The illustration appears to be of a *Stomatograptus*.

Tectonic deformation. Tectonically deformed material which we have not examined personally (e.g. that of Romariz 1962; Schauer 1971; Obut. *et al.* 1988) is omitted from the synonymies below as it is not possible to determine from the illustrations the extent to which the original rhabdosome dimensions have been modified.

Stratigraphical ranges. Ranges quoted appear to apply to all areas except Arctic Canada, from which Lenz and Melchin (1987*a*) reported *Retiolites* from the Homerian Stage (Upper Wenlock). Elsewhere, the extinction of *Retiolites* formed part of the mid Sheinwoodian '*murchisoni* [biotic crisis] Event', recently identified by Štorch (1995) in the Barrandian area of the Czech Republic and undoubtedly of more widespread significance (see e.g. Loydell and Cave 1996).

Order GRAPTOLOIDEA Lapworth, 1873
Suborder VIRGELLINA Fortey and Cooper, 1986
Superfamily DIPLOGRAPTOIDEA Lapworth, 1873
Family RETIOLITIDAE Lapworth, 1873
Subfamily RETIOLITINAE Lapworth, 1873

Genus RETIOLITES Barrande, 1850

(= *Gladiolites* Barrande, 1850, *nom. suppr.* ICZN Opinion 199; *Gladiograptus* Lapworth *in* Hopkinson and Lapworth, 1875; *Dimykterograptus* Haberfelner, 1936)

Type species. *Gladiolites geinitzianus* Barrande, 1850, from the Motol Formation (Wenlock) of Bohemia.

Diagnosis. Sicula represented by virga and virgella, with traces of the prosicular rim; sicular walls normally preserved only as seams. Thecal framework consisting of an obverse nema and reverse zigzag list with connecting rods extending from the former to the thecae. Thecae orthograptid in outline, with introverted apertures; each thecal aperture defined by septal bars laterally, a transverse rod dorsally and a thecal lip ventrally; free ventral walls originate at dorsal transverse rods. Ancora sleeve commences with bifurcation of the virgella to give two primary lists, and further branchings to form the ancora umbrella; ancora sleeve forms two panels covering the obverse and reverse faces of the rhabdosome, panels convex, lists having seams on their external sides; lists making connection with the septal bars by 'plug-hole' junctions, where the inward-facing insertion seam on the septal bar is linked with the outward-facing seam on the ancora sleeve list. The spaces between the sleeve panels and the thecal framework form two external common canals. Ventral edges of the sleeve panels directed laterally, giving a straight appearance to the rhabdosome in lateral profile. Proximal end with distinctive triangular obverse and reverse orifices, and smaller orifices proximal to the lips of the first two thecae. Ventral faces of the rhabdosome formed of two series of orifices, each outlined by the ventral thecal lips and the lateral edges of the ancora sleeve panels; the ancora sleeve panels may extend across the first few orifices.

Remarks. Bulman (1929, p. 181) noted that *Retiolites* was an alternative name proposed by Barrande (1850, footnote, p. 68) for *Gladiolites* Barrande, 1850 'in case *Gladiolites* was not considered sufficiently distinct from *Gladiolus* (since at that time a fossil *Gladiolus* would have been named *Gladiolites*). *Retiolites* has been used, almost without exception, by all writers since Suess (1851, p. 91).'

Haberfelner's (1936) genus *Dimykterograptus* was distinguished from *Retiolites* by the presence of a membrane. However, Haberfelner was observing simply the exceptional preservation of the very thin periderm between the lists of the ancora sleeve. This is sometimes visible in flattened bedding-plane material (see Bouček and Münch 1944, p. 19); its former presence is indicated in isolated specimens by seamed lists (see e.g. Bates 1987, pl. 4, figs 3–4). True orifices in the *Retiolites* rhabdosome occurred only on the obverse and reverse sides at the proximal end (see Bates and Kirk 1984, text-fig. 4g), ventrally, along almost the entire length of the rhabsosome (Pl. 1, fig. 2) and at the distal end of the rhabdosome. Bouček and Münch (1944) were the first to recognize that *Dimykterograptus* is simply a preservational variant of *Retiolites*.

Stomatograptus Tullberg, 1883 has a structure almost identical to that of *Retiolites*, but differs in two major respects: (1) in the presence of stomata, which form prominent pores in the ancora sleeve, often protruding as 'funnels': they form additional orifices, connecting the external common canals with the exterior of the rhabdosome; and (2) in the lateral profile, which is notched in *Stomatograptus*. The ventralmost lists of the ancora sleeve run at right angles to the septal bars (cf. Bulman 1970, fig. 95, 6 and 95, 5). In *Stomatograptus* the ancora sleeve panels do not extend across the proximal ventral orifices.

Retiolites geinitzianus (Barrande, 1850)

Text-figures 2A, D, 3C

vp?1850 *Gladiolites geinitzianus* Barrande, p. 69, pl. 4, figs 24–27 (*non* figs 16, 28–32 [= *R. angustidens*], ?17–19 [lectotype selected by Bouček and Münch 1944, probably = *R. angustidens*], 20–23 [= *Stomatograptus grandis* Suess, 1851 *sensu lato*], ?33 [specimen is lost]).

1851 *Retiolites Geinitzianus* Barr.; Suess, p. 95, pl. 7, fig. 1a–g.

v.1852 *Graptolithus venosus* (n. sp.) Hall, p. 40, pl. A.17, fig. 2a–c.

1883 *Retiolites Geinitzianus* Barr.; Tullberg, p. 41, pl. 1, figs 10–13, 16–17 (?14–15).

p1890 *Retiolites Geinitzianus* Barrande 1850; Holm, p. 18, pl. 2, figs 2–4 (*non* 5 [= *R. angustidens*]).

vp.1908 *Retiolites* (*Gladiograptus*) *Geinitzianus*, Barrande; Elles and Wood, p. 336, pl. 34, fig. 8a, c, (*non* b [= *Stomatograptus longus* Obut, 1949], d [= *R. angustidens*; specimen not traced, Strachan 1971, p. 87]), text-fig. 220a, d–e [cops Holm 1890], f (? c, *non* b [= enlargement of part of pl. 34, fig. 8b]).

1908 *Retiolites geinitzianus* Barrande var. *venosus* (Hall); Ruedemann, p. 469, pl. 29, figs 7–8; pl. 31, figs 6–8; text-fig. 449 [cop. Hall 1852].

1936 *Dimykterograptus boučevi* n. sp. var. *latus* Haberfelner, p. 93, fig. 6.

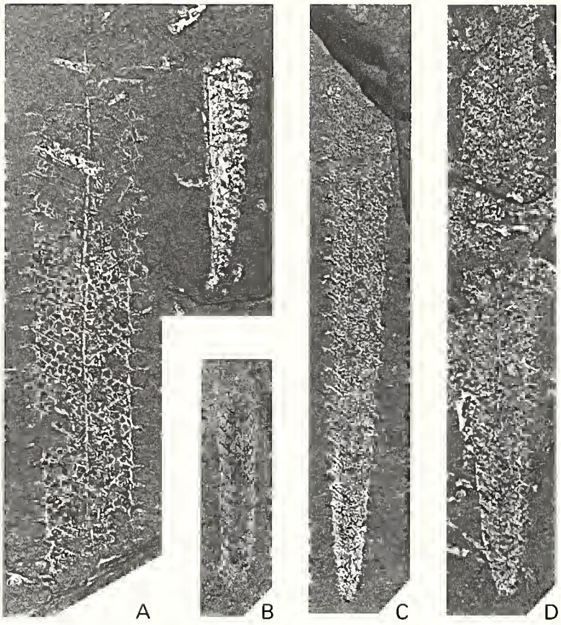
v.1944 *Retiolites* (*Ret.*) *geinitzianus* cf. *angustidens* E. and W.; Bouček and Münch, p. 36, text-fig. 11f–i.

v.1944 *Retiolites* (*Retiolites*) *geinitzianus geinitzianus* Barrande 1850; Bouček and Münch, p. 37, pl. 3, figs 2–5, text-figs 13c–h, 14c–d.

v.1944 *Retiolites* (*Retiolites*) *robustus* n. sp., Bouček and Münch, p. 42, text-figs 12a, 13a–b, 15f.

*non*1966 *Retiolites geinitzianus* Barr.; Eisenack, p. 581, fig. 6 [= *R. angustidens*].

1966 *Retiolites geinitzianus* Barrande, 1850; Obut and Sobolevskaya, p. 15, pl. 3, figs 10–11 (?12–13 [short fragments]), text-fig. 7.



TEXT-FIG. 2. A, D, *Retiolites geinitzianus* (Barrande, 1850). A, holotype of *Retiolites robustus* Bouček and Münch, 1944; L 31629; middle Telychian, Bockendorf-Riechberg, Germany; note tectonic broadening, also affecting specimen of *Monograptus priodon* (Bronn), top right. D, BB 682; Litohlavy Formation, Praha-Pankrác; *tullbergi* (= *crenulata*) Biozone. B, *Retiolites australis* McCoy, 1875; lectotype, MV P12194; Springfield Sandstone, east bank of Maribyrnong River, north of Keilor, Victoria; *griestoniensis* Biozone. C, *Retiolites angustidens* Elles and Wood, 1908; holotype of *Retiolites densereticulatus* Bouček, 1931; L 31386; Motol Formation, Vyskočilka, Bohemia; *insectus* Biozone. All are ×2·5.

p1966	*Retiolites obliquidens* (Obut), 1949; Obut and Sobolevskaya, p. 18, text-fig. 9 (*non* pl. 4, fig. 1 [holotype = *Stomatograptus grandis* Suess, 1851 *s.l.*], fig. 2 [= *Stomatograptus* sp.]).
1967	*Retiolites geinitzianus* Barrande, 1850; Gailite *et al.*, p. 226, pl. 26, fig. 5, text-fig 40.
1967	*Retiolites angustidens* Elles et Wood, 1908; Gailite *et al.*, p. 228, pl. 26, fig. 7, text-fig. 42.
?1967	*Retiolites geinitzianus* Barrande, 1850; Obut *et al.*, p. 79, pl. 7, figs 7–8.
v.1970	*Retiolites geinitzianus angustidens* Elles and Wood; Toghill and Strachan, pl. 105, fig. 8.
1972	*Retiolites geinitzianus* Barrande, 1850; Koren', p. 72, pl. 1, figs 1–4.
1975	*Retiolites geinitzianus geinitzianus* Barrande; Berry and Murphy, p. 98, pl. 14, fig. 1.
1975	*Retiolites geinitzianus geinitzianus* (Barrande, 1850); Bjerreskov, p. 38, pl. 5, fig. F, table 3.
v*non*1984	*Retiolites geinitzianus* Barrande; Chen, p. 48, pl. 6, figs 3–4 [= *Pseudoretiolites dentatus* Bouček and Münch, 1944].
*non*1986	*Retiolites geinitzianus* Barrande; Fu and Song, p. 94, pl. 6, figs 12–13 [= *Stomatograptus grandis* (Suess, 1851)].
1987*b*	*Retiolites*; Lenz and Melchin, p. 354, fig. 1A–E.
.1992	*Retiolites geinitzianus geinitzianus* Barrande; White *et al.*, fig. 7h.
v1993	*Retiolites* sp. nov.; Loydell and Cave, p. 102, fig. 9a.
?1995	*Retiolites geinitzianus* Barrande 1850; Kozłowska-Dawidziuk, p. 281, figs 12A–B, 13.

Neotype. Loydell and Štorch (1996) have applied to the International Commission on Zoological Nomenclature to suppress Bouček and Münch's (1944, p. 37) lectotype selection and to designate as neotype specimen L 31612 (Bouček and Münch 1944, pl. 3, figs 2–4), from the Motol Formation (*Cyrtograptus murchisoni* Biozone) of Vyskočilka, Bohemia.

The choice of lectotype made by Bouček and Münch (1944, p. 37) was unfortunate. The specimen (L 27600) has dimensions comparable to those of *R. angustidens*, but, in being a small, mesial fragment, cannot be assigned confidently to this or any other species. Only those specimens that were figured by Barrande (1850, pl. 4, figs 16–32) are present in the collections of the National Museum, Prague. Of these, only two may, questionably, be assigned to *R. geinitzianus*. These are both short fragments, preserved obliquely, and neither is suitable as a type specimen.The proposed neotype is from the same locality as yielded the lectotype selected by Bouček and Münch.

Material. In addition to the type and figured specimens indicated in the synonymy, several hundred specimens from the Telychian and Sheinwoodian of Wales, Bohemia, Spain and Scotland.

Diagnosis. Broad *Retiolites*; dorso-ventral width increases rapidly from 2·2–3·1 mm (5 mm from the proximal end) to a distal maximum of *c*. 6 mm.

Measurements of dorso-ventral width. All specimens are flattened, with the exception of BGS RCV3332 (very low relief) and BGS RCV7145 (medium relief).* = proposed neotype.

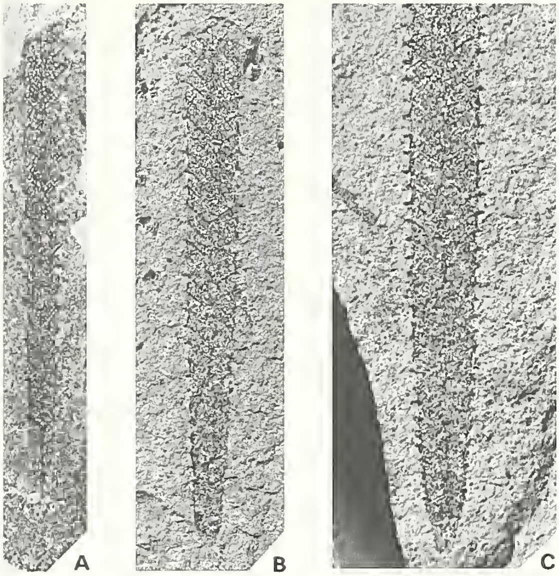
		Distance from proximal end (mm)					
Specimen no.	Biozone	5	10	15	20	30	50
BB 685	*murchisoni*	2·8	3·7	4·1	4·35	5·2	5·5
PŠ 701a	*murchisoni*	2·65	3·45	4·0	4·65	5·1	5·6
PŠ 703	*murchisoni*	2·75	3·9	4·25	5·1	5·1	
PŠ 704	*murchisoni*	2·9	3·55	4·0	4·3	4·5	
PŠ 707a	*murchisoni*	2·7	3·4	4·0	4·25	4·35	
PŠ 708	*murchisoni*	2·95	3·8	4·5	4·9	5·2	5·6
L 28334	*murchisoni*	2·7	3·7	4·25	4·9	5·5	5·95
L 28336	*murchisoni*	2·6	3·25	3·9	4·75	5·1	5·9
L 31612*	*murchisoni*	2·55	3·2	4·2	4·5	5·0	5·9
BGS RCV3332	*centrifugus*	2·5	3·0	3·45	3·35		
PŠ 702	*centrifugus*	2·6	3·4	4·1	4·25	4·6	
BGS RCV7145	*insectus*	2·4	3·1	3·5	3·85		
BB 688	*spiralis*	3·05	3·6	3·7	3·75	3·8	
BB 690	*spiralis*	2·4	3·1	3·65	3·8	4·2	
BGS RCV2402	*spiralis*	2·5	3·2	3·9	4·3	4·6	4·7
BGS RCV2496	*spiralis*	2·5	3·2	3·7	3·85	4·05	
BB 681	*tullbergi*	2·45	3·0	3·7	3·8	3·9	
BB 682a	*tullbergi*	2·2	3·1	3·5	3·8	4·2	
BB 684	*tullbergi*	2·3	3·0	3·5	3·6		
BB 686	*tullbergi*	2·3	3·05	3·8	3·8	4·1	
PŠ 688	*tullbergi*	2·9	3·2	3·95	4·55		
PŠ 689	*tullbergi*	2·25	3·0	3·85	4·1		

Remarks. Elles and Wood (1908) and Toghill and Strachan (1970) identified specimens of *R. geinitzianus* as *R. angustidens* Elles and Wood, 1908. The latter species differs, however, in its more gradual rate of increase in dorso-ventral width (see below). Short, mesial or distal fragments with a width of *c*. 4 mm might be difficult to assign confidently to one or other of these species, however.

In discussion of Hall's (1852) species *venosus*, Ruedemann (1908, p. 471) stated: 'I seriously doubt the specific difference of the American form [*R. venosus*] from *R. geinitzianus*, the genotype of *Retiolites*; for not only are the two exactly alike in dimensions and habit, but they tally also completely in the number of thecae within 10 mm and in their inclination'. He continued, 'We have for these reasons, for the present brought *R. venosus* as a variety under *geinitzianus*, allowing this distinction to stand less by virtue of differential characters than by that of different geographical distribution.' One of us (DKL) has examined Hall's material of *venosus* (AMNH 30957 and AMNH 502179); the specimens are indeed indistinguishable from *geinitzianus* and we follow Bouček and Münch (1944) in treating the two taxa as synonymous. Waterlot (1945, p. 65) considered *R. venosus* to be a senior synonym of *R. angustidens* Elles and Wood, 1908. This is clearly not the case.

Bouček and Münch's (1944) material of their species *Retiolites robustus* (Text-fig. 2A) is tectonically broadened *R. geinitzianus*. The width distally is 6·35–6·45 mm. Bouček and Münch suggested a horizon for this material of around the *crispus*/*griestoniensis* Biozone boundary (= *sartorius* Biozone *sensu* Loydell 1993*a*), but it may be from slightly higher than this (within the *griestoniensis* Biozone).

Obut and Sobolevskaya (1966, p. 18) recognized that SM A.21618 had been assigned incorrectly to *R. geinitzianus* by Elles and Wood (1908, explanations to pl. 34, fig. 8b, text-fig. 220b) and placed this specimen in *R. obliquidens* Obut, 1949 (a junior synonym of *Stomatograptus grandis* (Suess, 1851); see above). The specimen should, however, be assigned to another *Stomatograptus* species,



TEXT-FIG. 3. Proximal ends of the three *Retiolites* species; note the differences in dorso-ventral width. A, *Retiolites australis* McCoy, 1875; holotype of *Retiolites angustissimus* Obut and Sobolevskaya *in* Obut *et al.*, 1967; N 601B/6; Kolyma Formation, north-east Russia; '*spiralis* and *grandis* Biozone'. B, *Retiolites angustidens* Elles and Wood, 1908; PŠ 706; Motol Formation, Velká Ohrada, Bohemia; *grandis* Biozone. C, *Retiolites geinitzianus* (Barrande, 1850); PŠ 702; Motol Formation, Velká Ohrada, Bohemia; *murchisoni* Biozone (Sheinwoodian). All are ×2·5.

S. longus Obut, 1949, which is characterized by a less rapid increase in dorso-ventral width than *S. grandis*.

Loydell and Cave (1993) identified two specimens from Buttington Brick Pit, Wales as belonging to a new species, because of the low angle of the septal bars to the rhabdosome axis. Septal bar inclination is highly variable within *Retiolites* species and these specimens are assigned herein to *R. geinitzianus*.

Stratigraphical range. Telychian Stage (Upper Llandovery), to Sheinwoodian Stage (Lower Wenlock); ?*crispus* Biozone, *sartorius–murchisoni* biozones. *R. geinitzianus* appears to be least common in the upper Telychian, in which *R. angustidens* tends to be the numerically dominant *Retiolites* in graptolite assemblages (see abundance data in e.g. Bjerreskov 1975; Loydell and Cave 1996).

Retiolites australis McCoy, 1875

Plate 1, figure 3, Text-figures 2B, 3A

v.*1875	*Retiolites australis* McCoy, p. 36, pl. 20, fig. 10.
p1934	*Stomatograptus australis* (McCoy); Keble and Harris, p. 181, pl. 22, fig. 5d (*non* fig. 5a–c).
1965	*Retiolites angustidens* (Elles et Wood), 1908; Obut *et al.*, p. 38, pl. 2, fig. 11.
.1966	*Retiolites angustidens* (Elles et Wood), 1908; Obut and Sobolevskaya, p. 16, pl. 3, figs 14–16, text-fig. 8.
.1967	*Retiolites angustissimus* Obut et Sobolevskaya, sp. nov., Obut *et al.*, p. 81, pl. 7, figs 9–11.
1973	*Retiolites angustidens* Elles et Wood, 1908; Kul'kov and Obut, p. 228, fig. 2, 12.
p1978	*Retiolites geinitzianus angustidens* Elles and Wood, 1908; Lenz, p. 33, fig. 15C, H.
1981	*Retiolites geinitzianus angustidens* Elles and Wood, 1908; Bjerreskov, p. 20, pl. 6, fig. 1.
.1981	*Retiolites geinitzianus densireticulatus* Bouček, 1931; Crowther, p. 89, pl. 15, text-fig. 29A.
p.1988	*Retiolites geinitzianus densereticulatus* Bouček; Lenz, p. 1965, pl. 2, fig. 1 (?F2, *non* G–H [= *R. angustidens*]).
1989	*Retiolites geinitzianus densereticulatus* Bouček; Melchin, fig. 13A.

Lectotype. Specimen MV P12194, figured McCoy 1875, pl. 20, fig. 10 (figured herein as Text-fig. 2B); from the Springfield Sandstone, Geological Survey of Victoria locality Ba57, on the east bank of the Maribyrnong River, 1·2 km north of Keilor, Victoria. The associated graptolites are indicative of the mid Telychian *griestoniensis* Biozone (Andrew Sandford, pers. comm.). Keble and Harris (1934, p. 182) referred to this specimen as holotype; McCoy had not designated it as such, however, and, as there are several other syntype specimens (MV P12195), it is more correct to consider the specimen selected by Keble and Harris as the lectotype and those specimens labelled MV P12195 as paralectotypes.

Material. In addition to the lectotype and paralectotypes, all of which are flattened, several three-dimensional isolated specimens from the *sakmaricus* Biozone (upper Telychian, Llandovery), Cape Phillips Formation, Cape Phillips, Cornwallis Island, Arctic Canada.

Diagnosis. Narrow *Retiolites* with a proximal dorso–ventral width of 1·35–1·5 mm (5 mm from the proximal end) increasing gradually to a distal maximum of 2·1–2·4 mm.

Remarks. The lectotype has not previously been illustrated accurately. McCoy (1875, p. 37) noted that 'the lithographer has altered the drawing [pl. 20, fig. 10] so as to render it too gradually and regularly tapering' and that the 'cell boundary lines should diverge at a rather more acute angle and be straighter [than illustrated]'. Keble and Harris's figure (1934, pl. 22, fig. 5d) is inaccurate both in terms of its stated magnification (which suggests a dorso-ventral width of 2·8 mm, cf. the true maximum distal dorso-ventral width in the lectotype of 1·95 mm) and in its failure to portray the basically straight and nearly parallel-sided nature of the rhabdosome margins and the amount of visible detail of the reticulum. Loydell (1993*a*) suggested that '*Retiolites australis* appears, from M'Coy's description and illustrations, to be a senior synonym of *Retiolites angustidens*'. The two taxa are not synonymous, however; *R. australis* differs in its lesser dorso-ventral width throughout its length.

Stratigraphical range. The Australian type material is from the *griestoniensis* Biozone. The range of the conspecific *R. angustissimus* Obut and Sobolevskaya (*in* Obut *et al.*, 1967; Text-fig. 3A) was stated as '*griestoniensis* and *spiralis*' Biozone to '*spiralis* and *grandis*' Biozone. Lenz (1988) illustrated a specimen from the *sakmaricus* Biozone of northern Canada, the same biozone as yielded the chemically isolated specimen illustrated in Plate 1, figure 3. The species has not been reported from the Wenlock, however, and thus its total known range is from the *griestoniensis* Biozone to approximately the base of the Wenlock.

Retiolites angustidens Elles and Wood, 1908

Plate 1, figures 1–2, 5, Text-figures 2C, 3B

vp.1850	*Gladiolites Geinitzianus* Barrande, p. 69, pl. 4, figs 16, 28–32, ?17–19, 33 (*non* figs 20–27) [see synonymy of *R. geinitzianus*].
p1890	*Retiolites Geinitzianus* Barrande 1850; Holm, p. 18, pl. 2, fig. 5 (*non* figs 2–4 [= *R. geinitzianus*]).
p1908	*Retiolites* (*Gladiograptus*) *Geinitzianus*, Barrande; Elles and Wood, p. 336, pl. 34, fig. 8d only [see synonymy of *R. geinitzianus*].
v*.1908	*Retiolites* (*Gladiograptus*) *Geinitzianus*, Barrande Var. *angustidens*, nov.; Elles and Wood, p. 338, pl. 34, fig. 9a–c.
v.1931	*Retiolites geinitzianus densereticulatus* n. var., Bouček, p. 306, fig. 16a.
1936	*Dimykterograptus bončevi* n. sp., Haberfelner, p. 92, fig. 5.
v.1944	*Retiolites* (*Retiolites*) *geinitzianus angustidens* Elles and Wood, 1908; Bouček and Münch, p. 34, pl. 2, figs 1–4, text-figs 11a–e, 12b–e.
?1949	*Retiolites geinitzianus* Barrande var. *angustidens* Elles; Obut, p. 16, pl. 2, fig. 1a–b.
1963	*Retiolites* (*Gladiograptus*) *geinitzianus* var. *angustidens* Elles and Wood; Willefert, p. 26, text-fig. 31.
*non*1965	*Retiolites angustidens* (Elles et Wood), 1908; Obut *et al.*, p. 38, pl. 2, fig. 11 [= *R. australis*].
1966	*Retiolites geinitzianus* Barr.; Eisenack, p. 581, fig. 6.
*non*1966	*Retiolites angustidens* (Elles et Wood), 1908; Obut and Sobolevskaya, p. 16, pl. 3, figs 14–16, text-fig. 8 [= *R. australis*].
1967	*Retiolites densereticulatus* Bouček, 1931; Gailite *et al.*, p. 227, pl. 26, fig. 6, text-fig. 41.
*non*1967	*Retiolites angustidens* Elles et Wood, 1908; Gailite *et al.*, p. 228, pl. 26, fig. 7, text-fig. 42 [= *R. geinitzianus*].
?1966	*Retiolites* ex. gr. *geinitzianus* Barrande, 1850; Obut and Sobolevskaya, p. 19, pl. 4, fig. 3.

v*non*1970 *Retiolites geinitzianus angustidens* Elles and Wood; Toghill and Strachan, pl. 105, fig. 8.
.1975 *Retiolites geinitzianus angustidens* Elles and Wood; Berry and Murphy, p. 99, pl. 14, fig. 2.
1975 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Bjerreskov, p. 38, pl. 5, figs D–E, table 3.
p1978 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Lenz, p. 33, (*non* fig. 15C, H [= *R. australis*]).
*non*1981 *Retiolites geinitzianus angustidens* Elles and Wood, 1908; Bjerreskov, p. 20, pl. 6, fig. 1 [= *R. australis*].
.1982 *Retiolites geinitzianus angustidens* Elles and Wood; Howe, pl. 2, fig. e.
v*non*1984 *Retiolites geinitzianus angustidens* Elles and Wood; Chen, p. 49, pl. 5, fig. 14, pl. 6, figs 6–8 [= *Pseudoretiolites dentatus* Bouček and Münch, 1944], fig. 5 [= indet. retiolitid], figs 10–11 [= *Pseudoretiolites perlatus* (Nicholson, 1868)].
1986 *Retiolites geinitzianus angustidens* Elles et Wood; Fu and Song, p. 94, pl. 7, fig. 2 (? fig. 1).
p.1988 *Retiolites geinitzianus densereticulatus* Bouček; Lenz, p. 1965, pl. 2, figs G–H (?F2, *non* I [= *R. australis*]).
1989 *Retiolites geinitzianus angustidens* Elles and Wood; Melchin, fig. 12C.

Lectotype. Selected by Bouček and Münch (1944); GSE 5629, figured Elles and Wood 1908, plate 34, figure 9a; from the north end of Falbogue Bay, on the west side of Meikle Ross, Kirkudbright Bay, Scotland.

Material. In addition to the type and figured specimens indicated in the synonymy, several hundred specimens from the Telychian and Sheinwoodian of Bohemia, Wales, northern England and Scotland.

Diagnosis. *Retiolites* with dorso-ventral width increasing gradually from 1·8–2·4 mm (5 mm from the proximal end) to a distal maximum of *c*. 4 mm.

Measurements of dorso-ventral width. All specimens are flattened, with the exception of BGS RCV4721 (very low relief).

		Distance from proximal end (mm)					
Specimen no.	Biozone	5	10	15	20	30	50
L 28337	*murchisoni*	1·9	2·5	3·2	3·45	3·9	
BGS RCV4721	*centrifugus*	2·2	2·7	3·0	3·1	3·2	
BB 689a	*insectus*	2·1	2·9	3·4	3·55	3·55	
PŠ 709	*insectus*	2·2	2·95	3·55	3·55		
L 28340b	*insectus*	2·2	2·9	3·2	3·45		
PŠ 706	*grandis*	1·95	2·6	3·0	3·25		
L 28322	*spiralis*	2·4	3·05	3·1	3·5	3·9	
BB 687	*tullbergi*	1·95	2·3	2·65	2·75	2·9	

Remarks. *Retiolites densereticulatus* Bouček, 1931 was considered to be distinct from *R. angustidens* because of its denser reticular meshwork. Meshwork density has been shown to be a function of

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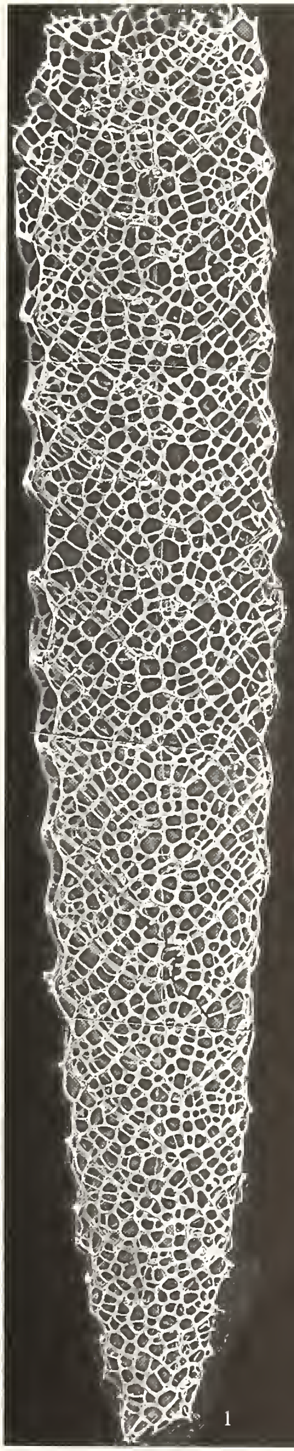
EXPLANATION OF PLATE 1

Figs 1–2, 4–5. *Retiolites angustidens* Elles and Wood, 1908. 1–2, 5, NMW 91.52G.812; Lower Visby Formation, 0·5–1 m below lowest of three main bentonites, 500 m south of Stenkyrkehuks fyr, Gotland. 1–2, obverse and ventral views respectively of rhabdosome; note the orifices opening ventrally (2); these orifices should not to be confused with the thecal apertures (see fig. 4 and Text-fig. 1); both × 15. 5, small part of meshwork, showing lists secreted late in astogeny, causing an increase in meshwork density; × 265. 4, copy (at twice original publication size) of Holm's 1890, plate 2, figure 5; note the presence of a theca, the apertural margin of which runs along the septal bar; the thecal aperture is introverted.

Fig. 3. *Retiolites australis* McCoy, 1875; NMW 91.52G 1330; upper *sakmaricus* Biozone (Telychian), Cape Phillips Formation, Cornwallis Island; × 10.

PLATE 1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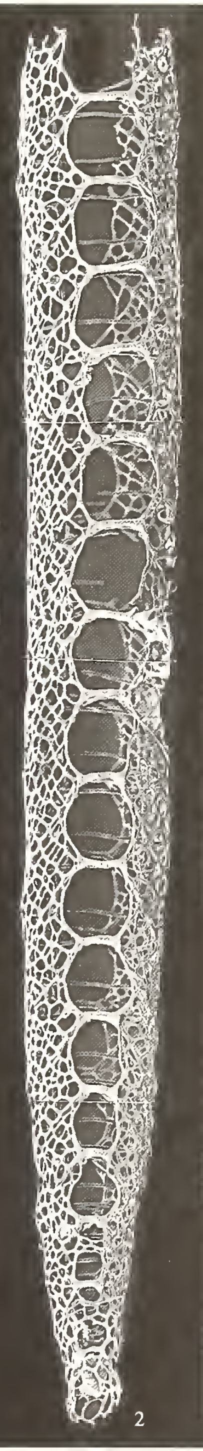
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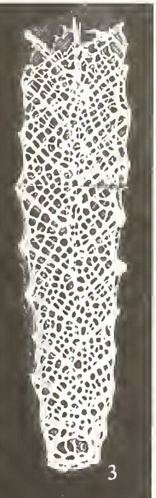
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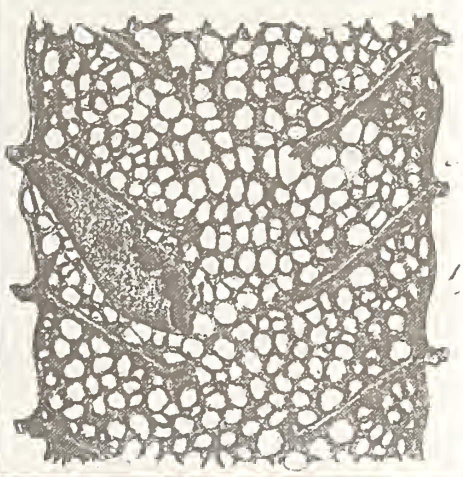
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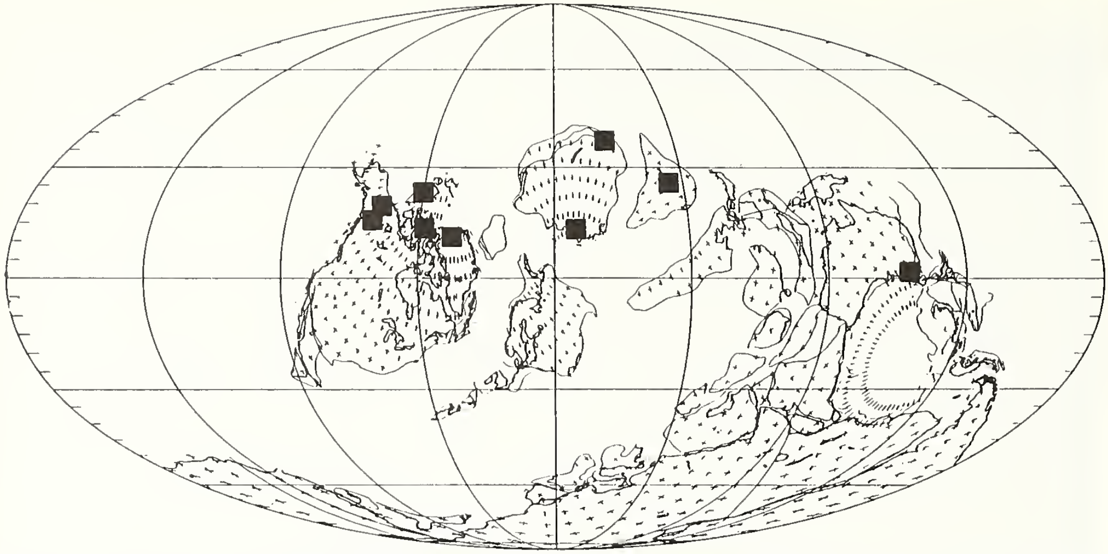
5

LOYDELL *et al.*, *Retiolites*



TEXT-FIG. 4. Localities yielding *Retiolites australis* McCoy (black squares) plotted on Llandovery world palaeogeographical map of Scotese and McKerrow (1990). Note that the position and orientation of Siberia are uncertain (discussions at James Hall Meeting, Rochester, August 1996). The record from Pearya (Bjerreskov 1981) is plotted in north Greenland; collision between Pearya and Laurentia took place late in the Telychian (T. De Freitas, pers. comm. 1996).

astogeny, however (see above), and as the taxa are identical in all respects they are synonymized herein. Incidentally, the lectotype of *R. angustidens* has a reticular meshwork just as dense as that of the holotype of *R. densereticulatus* (Text-fig. 2C). In terms of dorso-ventral width, *R. angustidens* is intermediate between *R. australis* and *R. geinitzianus*.

Bjerreskov (1975) noted a median row of pores on an internal mould of this species and suggested (as had Bouček and Münch 1944) that the genera *Retiolites* and *Stomatograptus* were closely related.

Stratigraphical range. Telychian (*crispus* Biozone; Melchin 1989)–Sheinwoodian (*murchisoni* Biozone).

PALAEOBIOGEOGRAPHY

Specimens of *Retiolites* are encountered in the majority of graptolite collections made from late Telychian and early Sheinwoodian strata throughout the world, although the literature reviewed in the preparation of this paper suggests that the genus was not as common in the seas bordering the various microcontinents that now make up China as elsewhere; here, other retiolitids (particularly species of *Stomatograptus*) appear to have been more common than *Retiolites*.

Whilst both *R. geinitzianus* and *R. angustidens* appear to have had a very widespread distribution, *R. australis* is known only from strata deposited north of the Silurian equator (Text-fig. 4). This restricted geographical distribution matches that of several other late Telychian graptoloids (Melchin 1989, p. 1744).

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CONODONTS FROM THE ORDOVICIAN SHINNEL FORMATION, SOUTHERN UPLANDS, SCOTLAND

by HOWARD A. ARMSTRONG

ABSTRACT. The Shinnel Formation is dominated by over 2 km of quartzose sandstones. It crops out between the Fardingmullach and Orlock Bridge faults, Northern Belt of the Southern Uplands, and is of mid Ashgill age. The interbedded and distinctive Tweeddale Member (previously the Wrae Limestone and Tweeddale lavas) comprises debris flow deposits with clasts of limestone which yield a diverse and abundant conodont fauna, including *Pygodus anserinus*, *Baltoniodus variabilis*, *Periodon aculeatus*, *Protopanderodus varicostatus*, *Spinodus spinatus*, *Eoplacognathus lindstroemi*, *Strachanognathus parvus* and coniform species; an assemblage considered to be of *P. anserinus* Biozone (late Llanvirn (Llandeilian) to early Caradoc (Aurelucian)) age. These conodont faunas are similar to those from the upper Stinchar Limestone from Girvan to the north-west. The deep or cool water, predominantly prioniodontid and panderodontid, conodont fauna is described systematically for the first time. Emended apparatus plans are proposed for *Pygodus anserinus*, *Protopanderodus varicostatus* and *Strachanognathus parvus*.

FLOYD (1996) redefined many of the lithostratigraphical units within the Southern Uplands. The Shinnel Formation (Floyd 1982) is up to 2 km thick and is dominated by quartzose sandstones. Floyd and Rushton (1993) reviewed the biostratigraphy of the formation, referring an interbedded graptolite fauna to the Rawtheyan to Cautleyan, *D. anceps* graptolite Biozone (GBZ). In the Tweeddale area, the Wrae Limestone and Tweeddale lavas (Thirwall 1981) have been included within the Tweeddale Member (Hughes and Boland 1995; Floyd 1996) and are interbedded within the Shinnel Formation. The Tweeddale Member extends for over 20 km along strike to the south-west of Peebles. In its type section at Wrae (NT 1175 3240) it is *c.* 35 m thick but appears to thicken markedly to the north-east of Peebles (Hughes and Boland 1995). The apparently restricted nature of the original depositional environment and re-forestation now mean the Tweeddale Member only crops out sporadically (Text-fig. 1). Limestone occurs as variable sized blocks in a clast-supported debris flow deposit. Clasts range in size from grains to large boulders, which were individually quarried during the late nineteenth century.

James Hutton first discovered fossils in the limestone on Wrae Hill, and this led him to conclude (Hutton 1795, p. 334) that the greywackes of the Southern Uplands were marine in origin. Subsequently the geology of the Tweeddale Member (Wrae Limestone) was described in detail by Peach and Horne (1899), Eckford and Ritchie (1931) and Leggett (1980). Peach and Horne (1899, p. 53) reported a shelly fauna in both the limestone clasts, grit and tuffaceous beds at Wrae Hill, Glencotho, Winkston and Hamilton Hill, and concluded that the deposit was late Caradoc in age. The limestone clasts contain a marine macrofauna of trilobites attributable to the Illaenid-Cheirurid community, (A. W. Owen, pers. comm.), brachiopods, gastropods and crinoids which Clarkson (*in* Leggett 1980, p. 101) attributed to reefal biofacies.

Following the work of Leggett (1980) it has been widely accepted that the clasts within the Tweeddale Member were derived from a volcanic palaeo-high or seamount, accreted to the Laurentian margin from the south. The seamount interpretation relies heavily upon the field observations made by Peach and Horne (1899) who reported a lava flow in association with the limestone conglomerate on Wrae Hill; these field relationships are now obscure. This interpretation conflicts with limited palaeocurrent data from the adjacent greywackes, which suggest a derivation from the north-west, and is further undermined by the absence of limestone deposits in the vicinity

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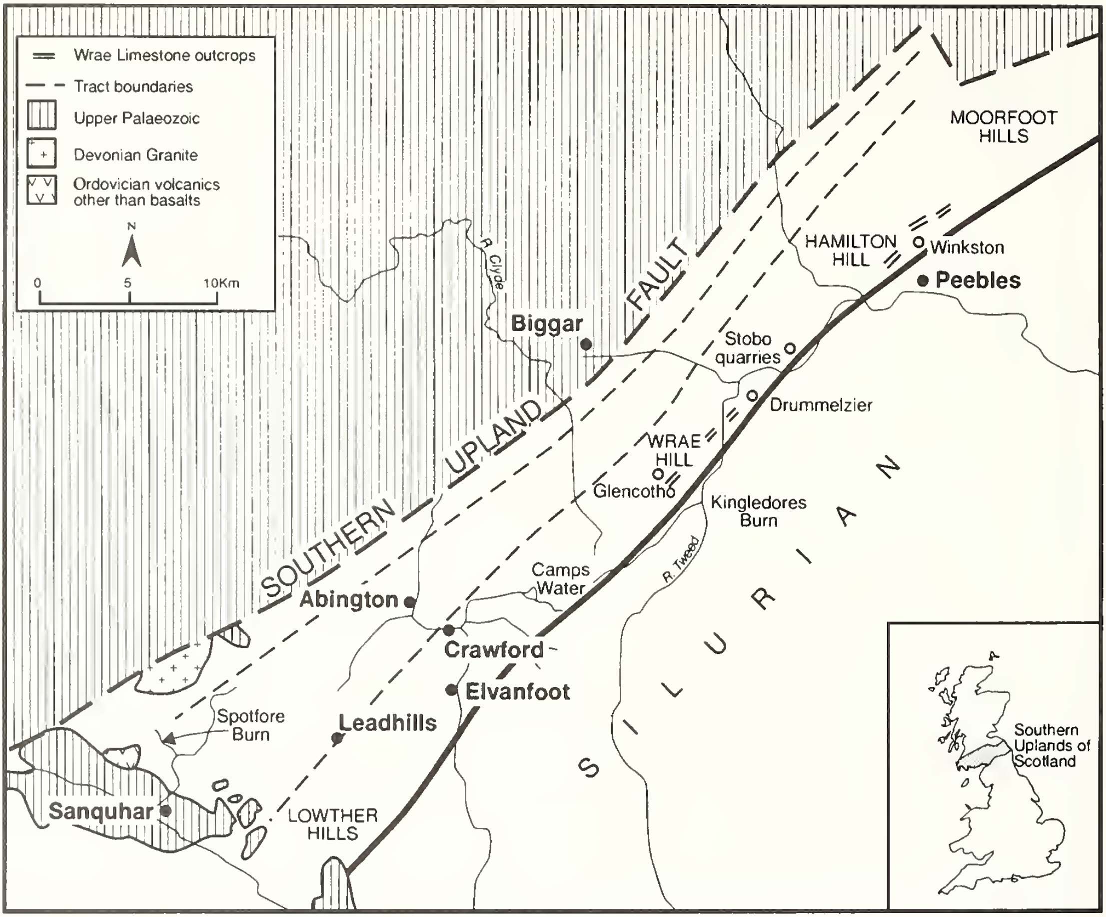


TEXT-FIG. 1. Locality and general geology of the Northern Belt of the Southern Uplands (redrawn from Leggett 1980).

of Bail Hill, the proposed location of the seamount. Regardless of these considerations, the 'Wrae seamount' has often been cited as part of the evidence that the geology of the Southern Uplands is best explained in terms of an accretionary prism (refer to Armstrong *et al.* 1996 for an alternative view). The aim of this paper is to present the first systematic description of conodonts from the limestone clasts. The associated shelly fauna is typical of the northern margin of the Iapetus Ocean and correlations with the shelf succession to the north-west are the most appropriate.

CONODONT STUDIES

Mid Ordovician conodont faunas from the British Isles are relatively poorly known and there is a major difference, at generic level, between the faunas from the series type areas in Wales and the Welsh Borderland, and those from Scotland. Late Llanvirn faunas from Wales are dominated by *Plectodina*, *Icriodella*, *Amorphognathus*, *Panderodus*, *Drepanoistodus* and *Baltoniodus* (Bergström and Orchard 1985) and cannot be correlated directly with Scottish faunas. However, a mid Caradoc, *A. tvaerensis* CBZ (*B. variabilis* Sub-biozone) conodont fauna has been recorded from limestone clasts within the Garn Formation, of the Anglesey terrane, and this includes many species in common with the Tweeddale Member, together with *Complexodus* and *Plectodina* (Bergström 1981*a*).

Ordovician conodonts from the Southern Uplands are known only from the Northern Belt, and have been documented mainly from cherts and shales of mid Arenig, Llanvirn (Llandeilian of Fortey *et al.* 1995) and Caradoc age (see Bergström and Orchard 1985, for a review). Llandeilian (*P. anserinus* CBZ) faunas were first described from red cherts and shales within the Marchburn Formation. Lindström (1957) recorded *P. anserinus* Lamont and Lindström, *P. serra* (Hadding), *Periodon aculeatus* (Hadding) and *Spinodus spinatus* Dzik in association with graptolites. At Ruddenleys [NT 2025 5067] near Leadburn, red cherty mudstones have yielded conodonts (*P. anserinus* CBZ) in close association with dark shales yielding *N. gracilis* GBZ graptolites (Lamont 1975).

Armstrong *et al.* (1990) reported a *Periodon-Protopanderodus* fauna from red shales (Crawford Group, Kirkton Formation *sensu* Floyd 1996) in the Hawkwood Burn [NS 976 254] and, based upon the absence of *Pygodus* and regional considerations, suggested a Llanvirn age. Ethington and Austin (1993) have since extracted four specimens of *Pygodus* sp. from loose blocks of red cherts along strike from Hawkwood Burn, close to Raven Gill. The latter contains exposures of brown and grey cherts and fossiliferous green mudstones of mid Arenig, *O. evae* CBZ age (Lamont and Lindström 1957; Bergström and Orchard 1985). These cherts comprise olistostromes within the Leadhills melange (Hepworth *et al.* 1982; Armstrong *et al.* 1996) and are lithologically, temporally and spatially distinct from the red cherts of the Kirkton Formation. It is therefore likely that the blocks collected by Ethington and Austin (1993) were derived from nearby Kirkton Formation chert outcrops. The red cherts and mudstones of the Marchburn and Kirkton formations are almost certainly correlatives (Armstrong *et al.* 1996).

Smith (1907) and Lamont and Lindström (1957) have recorded probable Llandeilian faunas, including *Periodon aculeatus* and *Spinodus spinatus*, from red shales (Crawford Group, Kirkton Formation) in Morroch Bay [NX 017 252]. Lindström (1957) reported *Periodon* n. sp. aff. *P. aculeatus* (= *P. grandis*, see Löfgren 1978), *Protopanderodus* sp., *Drepanoistodus* sp. and *Dapsilodus* sp. from the Moffat Shale Group, higher in the succession at the same locality. These were associated with *Climacograptus wilsoni* Lapworth, suggesting a Burrellian (mid Caradoc) age.

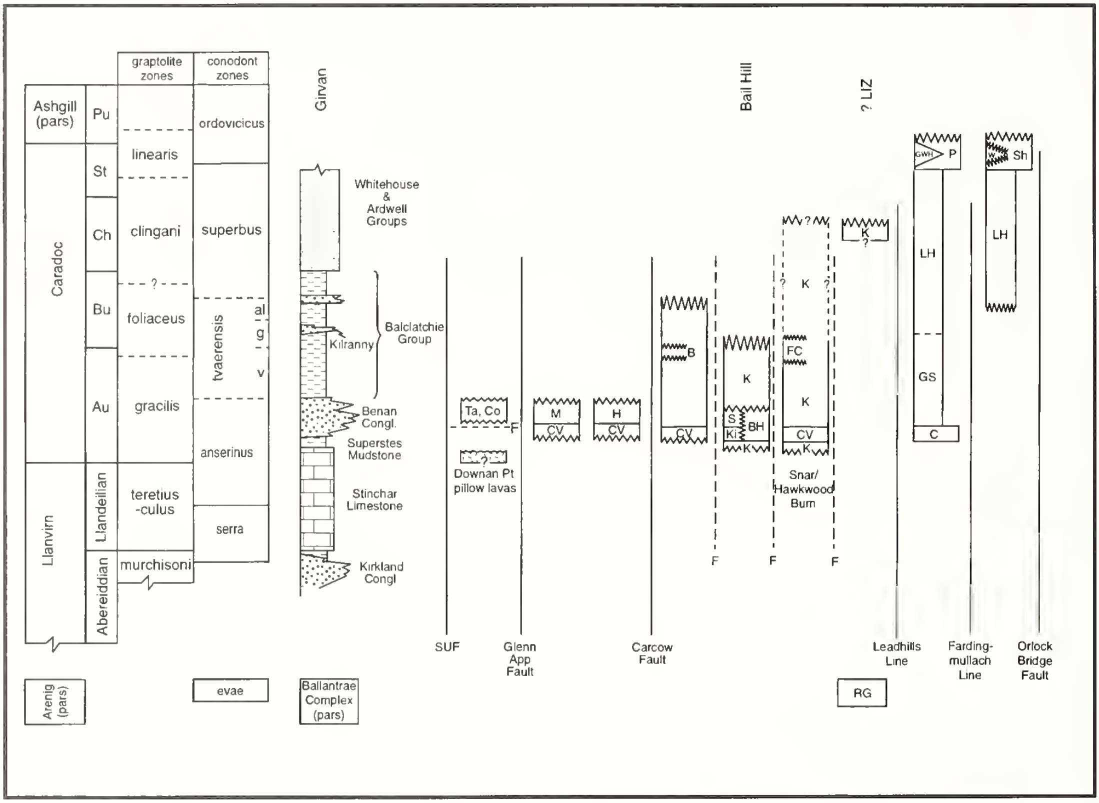
Lindström (*in* Walton 1965) reported ten species of conodont from the Tweeddale Member (Wrae Limestone) at Winkston that Bergström (1981*a*) considered to be the same as those from the Tweed Valley. Bergström *et al.* (1974) listed conodont species from the Tweeddale Member in the Tweed Valley area, from Glencotho Quarry, Wrae Hill and Drumelzier Quarry. They showed that the limestone contains a diverse fauna including *Pygodus serrus* (Hadding), *Periodon aculeatus* (Hadding), *Protopanderodus varicostatus* (Sweet and Bergström), *Spinodus spinatus* (Hadding), *Eoplacognathus* sp., *Strachanognathus parvus* Rhodes and *Prioniodus prevariabilis* (Fåhræus), an association they considered to be of late Llanvirn or slightly younger age. Bergström and Orchard (1985) reported *Polonodus* sp. from the Tweeddale Member. Bergström (1990, table 1) listed additional coniform taxa including *Dapsilodus mutatus* (Branson and Mehl) *Cornuodus*, *Drepanoistodus*, *Walliserodus ethingtoni* (Fåhræus) and *Panderodus*. He also updated his earlier faunal list, omitting *Eoplacognathus* sp. and transferring *Prioniodus prevariabilis* to *Baltoniodus*. From these collections, it has been accepted that the limestone clasts were of late Llanvirn–early Caradoc *Pygodus anserinus* CBZ age (Lamont and Lindström 1957).

Based upon conodont biostratigraphy, the red chert and shales of the Marchburn Formation, Kirkton Formation and limestone clasts within the Shinnel Formation, Tweeddale Member, are all *P. anserinus* CBZ age (see Armstrong *et al.* 1996 for the regional implications of this correlation).

Conodont biozonation

Two main conodont faunal provinces existed throughout the Ordovician, the North American Midcontinent and the North Atlantic provinces (Barnes and Fåhræus 1975). The former was characterized by warm-water, low latitude faunas, the latter by cold-water, high latitude or deeper water faunas. Marked endemicity has resulted in the establishment of separate zonations for each province (see Bergström 1971, 1983; Lindström 1971; Löfgren 1978 for details of the North Atlantic

Province). Conodont faunas from the Southern Uplands are dominated by species considered to be characteristic of the North Atlantic Province and have traditionally been correlated with the standard North Atlantic zonal scheme (Text-fig. 2). In this, the Llanvirn to Ashgill biozones are based on the phylogeny of the rapidly evolving lineages of *Pygodus*, *Eoplacognathus*, *Baltoniodus* and *Amorphognathus*.



TEXT-FIG. 2. Simplified chronostratigraphy, biostratigraphy and lithostratigraphy of the Girvan and Northern Belt areas. The succession between the Leadhills Line and the Fardingmullach Line is a composite of sections to the north-east of Sanquar and at Morroch Bay. Lithostratigraphical terminology for the Southern Uplands succession is that proposed by Floyd (1996). Chronostratigraphy and biostratigraphy are from Fortey *et al.* (1995). Abbreviations: Au = Aurelucian, Bu = Burrellian, Ch = Cheneyan, St = Streffordian, al = *alobatus*, g = *gerdae* and v = *variabilis* Sub-biozones, Ta = Tappins Group, Co = Corsewall Formation, CV and C = Kirkton Formation, chert and volcanics, M = Marchburn Formation, H = Hartree Formation, B = Blackcraig Formation, K = Kirkcolm Formation, S = Spothfore Member, Ki = Kiln Formation of Hepworth *et al.* (1982), now considered a local facies variation of the Kirkcolm Formation, BH = Bail Hill Volcanic Group, FC = fossiliferous conglomerate, LIZ = Leadhills Imbricate Zone, RG = Raven Gill Formation (considered to lie within the Leadhills Imbricate Zone), GS = Glenkiln Shale Formation, LH = Lower Hartfell Shale Formation, P = Portpatrick Formation, GWH = Glenwhargen Formation, Sh = Shinnel Formation, W = Tweeddale Member, SUF = Southern Upland Fault. Snar/Hawkwood Burn section generalized from sections exposed in Snar Water [NS 9085 1685] and the Hawkwood Burn [NS 9770 2540]. The top of the *P. anserinus* CBZ is poorly constrained in the Girvan sequence and most, if not all, the Benan Conglomerate may lie within this biozone.

Bergström (1983) has reviewed middle and upper Ordovician biozonal units. The base of the *P. anserinus* CBZ was originally defined at the first appearance of the nominate species (Bergström

TABLE 1. Abundances of conodont elements found in the Shinnel Formation, Southern Upland, Scotland.

	D153	D156	D159	D160	D208	D209
Baltoniodus variabilis						
Pa		3				
Pb				1		
Pm				2		
Pc				3		
M				5		
Sa		1		1		
Sb				1		
Sc				1		
Belodina sp. indet.						
rastrate						1
Cornuodus longibasis						
ae						1
qa						3
qg						3
qt						3
pf						2
pt						1
Dapsilodus mutatus						
ae		2				
qg		3	1			
pf		9				
Dapsilodus aff. D. obliquicostatus						
ae		2		1		
qg		2		4		
pf		2				
Drepanoistodus suberectus						
ae						2
qg		1		6		4
qt				2		1
qa		4	1	1		2
pf		2		3		1
pt		1	1	2		
Eoplacognathus lindestroemi						
Pa		1		1		
Panderodus sp. indet.						
qa				1		
qg			2	3		2
?qt			1	1	1	
pf		1	1			
Periodon aculeatus						
Pa		43	3	15	1	20
Pb		20	1			2
M		51	1	34	2	51
Sa		17	1	3		7
Sb	1	63	8	25	4	21
Sc		7		7		5
Protopanderodus varicostatus						
ae		8		15		3
qa				3		4
qg		8		27		1
qt		6		5		
pf		4		4		3
pt		9		13		
Pseudooneotodus sp. indet.						1
Pygodus anserinus						
Pa		8	5	39		
Pb		2		8		
Pc		20	2	49		
M		1		17		
Sc		6		1		
Spinodus spinatus		64	5	102		
Strachanognathus parvus						
?ae		32	6	4		1
qa		63	15	2		2
qg		13	2	2		1
qt		18		3		2
?pf		17	1	3	2	3
Walliserodus ethingtoni						
ae				1		1
qg				2		2
Walliserodus aff. W. sancticlairi						
ae		7				
qa		3				
qg		6		3		
?pf		3		1		
Genus and sp. indet.						
Pa				2		9
pb						2
M						1
Sa						2
Sb						11
Total identifiable fragments	1	235	21	123	8	132
Indeterminate fragments	1	180	45	241	12	157
Elements per Kg	2	1942	455	1010	118	400

1971, p. 97). This species is thought to be a direct descendant of *P. serra* and first appeared in the upper Llandeilian (Bergström 1971, p. 150; Fåhræus 1982; Fortey *et al.* 1995, fig. 1). Bergström (1971) subdivided the *P. anserinus* CBZ based upon the evolution of *Baltoniodus variabilis* from *B. prevariabilis*. Dzik (1978) and Bergström (1983) also considered that the transition from *Amorphognathus kielcensis* Dzik to *A. inaequalis* Rhodes occurred at this level, and suggested that an *A. inaequalis* Sub-biozone can be defined on the co-occurrence of *P. anserinus* and *A. inaequalis*. The precise position of the Llanvirn-Caradoc boundary in the North Atlantic conodont zonation remains uncertain. Fortey *et al.* (1995) placed the base of the Caradoc Series (Aurelucian Stage) at the base of the *N. gracilis* GBZ (see Finney and Bergström 1986 for a discussion of this biozone). The base of the Aurelucian evidently falls within the lower part of the *P. anserinus* CBZ (Bergström 1986, 1990; Fortey *et al.* 1995). Bergström (1986, fig. 3) tied the top of the *P. anserinus* CBZ to a level within the mid *N. gracilis* GBZ; consequently, much of the *P. anserinus* CBZ lies within the Caradoc (Fortey *et al.* 1995, fig. 1).

CORRELATION AND PROVINCIALITY

Species from the *P. anserinus* CBZ in southern Scotland are identical to those from coeval strata in eastern North America, such as the Cobbs Arm Limestone, Newfoundland (Bergström *et al.* 1974), the Lenoir Limestone of eastern Tennessee (Bergström 1990), Norway (Hamar 1964, 1966) and Sweden (Bergström 1971; Dzik 1976). The species present in these areas have been categorized as the *Periodon-Pygodus* RSA (Restricted Species Association, *sensu* Bergström and Carnes 1976), characteristic of deeper, cool water, shelf and slope environments, and thought to have contained mainly nektonic taxa. An exception occurs in the Cobbs Arm Limestone of north-eastern Newfoundland, where strata containing this RSA have been interpreted as being of shallow water origin, laid down in a volcanic island setting (Fåhræus and Hunter 1981).

In Scotland north of the Southern Upland Fault, the affinities of all but the deepest water shelly biofacies are Laurentian, even to the end of the Caradoc. Lower Ordovician conodont (Ethington and Austin 1991), brachiopod (Williams 1962; Higgins 1967; Ingham 1978; Bergström and Orchard 1985; Ingham *et al.* 1985; Ingham and Tripp 1991) faunas are characteristic of the American Midcontinent Province centred on Laurentia. Bergström (1971) recorded conodonts from the middle and upper Ordovician of Girvan and later (Bergström 1990) presented a detailed biostratigraphical, palaeoecological and palaeobiogeographical analysis of these faunas. The base of the *P. anserinus* CBZ lies within the upper part of the Stinchar Limestone. The upper part of the biozone (*A. inaequalis* Sub-biozone *sensu* Bergström 1983) is recorded in the overlying Superstes Mudstone (in association with upper *N. gracilis* GBZ graptolites), though the index species is absent. A slightly younger, *Baltoniodus gerdae* Sub-biozone fauna, is known from the Balclatchie Group, near Laggan Burn, Girvan, and occurs in association with *Diplograptus multidens* GBZ graptolites of early Caradoc age (Bergström and Orchard 1985; Bergström 1990). This fauna contains *Periodon aculeatus* and *Spinodus spinatus*, in common with the *P. anserinus* CBZ, but the younger species *Protopanderodus liripipus* Kennedy, Barnes and Uyeno and *Amorphognathus tvaerensis* Bergström are also present (Bergström 1990, fig. 5).

Early Caradoc conodont species from the Scottish deep water sequences to the south of the Southern Upland Fault were cosmopolitan, and are known from similar facies rimming Laurentia, across Baltica and the palaeo-Pacific (Bergström 1990, p. 21). Recent palaeomagnetic data have confirmed the tropical and subtropical location of the Laurentian margin at that time (Trench and Torsvik 1992). The *Periodon-Pygodus* RSA is therefore best considered as an outer shelf and slope, cool water biofacies containing cosmopolitan species, rather than being indicative of a particular faunal province.

EXPLANATION OF PLATE 1

Fig. 1. *Belodina*? sp. indet.; GLAHM Y 357; sample D209, Glencotho Farm; rastrate pf element.

Fig. 2. *Baltoniodus variabilis* (Lindström, 1959); GLAHM Y 358; sample D156, Winkston: Pa element.

Figs 3–8. *Dapsilodus mutatus* (Branson and Mehl, 1933*c*); sample D156, Winkston. 3–4, GLAHM Y 359; anterior and posterior sides of ae element. 5–6, GLAHM Y 360; anterior and posterior sides of qg element. 7–8, GLAHM Y 361; anterior and posterior sides of pf element.

Figs 9–11. *Dapsilodus* aff. *D. obliquicostatus* (Branson and Mehl, 1933*a*); sample D156, Winkston. 9, GLAHM Y 362; ae element. 10, GLAHM Y 363; qg element. 11, GLAHM Y 364; pf element.

Figs 12–23. *Drepanoistodus suberectus* (Branson and Mehl, 1933*b*). 12–16, sample D209, Glencotho Farm. 12–13, GLAHM Y 365; anterior and posterior views of ae element. 14–15, GLAHM Y 437; anterior and posterior views of qg element. 16, GLAHM Y 367; qt element. 17–18, 20–23, sample D160, Winkston. 17–18, GLAHM Y 368; anterior and posterior views of qa element. 20–21, GLAHM Y 370; anterior and posterior views of pf element. 22–23, GLAHM Y 371; anterior and posterior views of pt element. 19, GLAHM Y 369; sample D156, Winkston; qa element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.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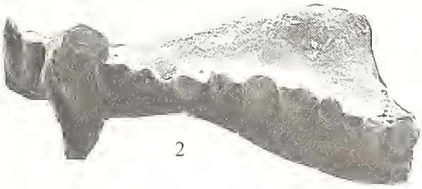
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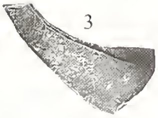
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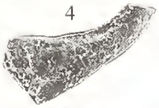
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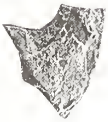
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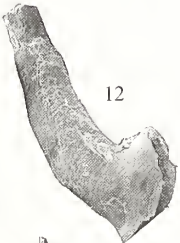
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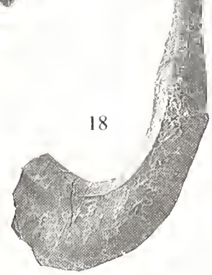
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ARMSTRONG, Ordovician conodonts

LOCALITIES

Localities at Glencotho and Winkston provide the best exposures of limestone. At Glencotho, grey recrystallized limestone boulders up to 3 m across are exposed in a small quarry in the hillside above Glencotho farm (NC 090 294, samples D208–D209). Here they are associated with a matrix of pebbly and tuffaceous breccia. The pebbles are composed predominantly of red chert, basalt and, rarely, mudstone. Limestone boulders are now only exposed for some 10 m along strike to the north-east of the quarry. Leggett (1980) reported limestone clasts up to 30 mm long in a brecciated grit exposed to the south-west of the quarry (in the north bank of a tributary of Glencotho Burn, NC 089 293) but these could not be re-located.

At Winkston, 3 km north of Peebles, several abandoned roadside quarries (NC 2425 4350, samples D156, 159, 160) contain limited exposures and talus screes of breccia, containing limestone clasts up to 0·2 m long. Here the clast-supported matrix is coarse grained and forms more than 50 per cent. of the rock; mudstone, red and grey chert and basalt predominate. Various outcrops on Winkston Hill were described by Peach and Horne (1899, pp. 260–262), including a small outcrop of porphyritic lava. Field relations are not now visible. Leggett (1980, p. 99) noted an apparent fining and diminution of limestone clasts up the hill.

A single sample of calcareous breccia (D153), collected from the Spotfore Burn [NS 789 149], may represent an outcrop of the Tweeddale Member interbedded with the Kirkcolm Formation, between the Carcow and Leadhills faults. This clast-supported breccia has a fine grained matrix; the clasts are predominantly sub-rounded, calcareous mudstone up to 5 mm in diameter. The thin breccia bed crops out in the west bank of the burn, approximately 5 m downstream from a small waterfall. Associated with the breccia, but not in direct contact, are radiolarian cherts and black shales (on the east bank) from which Peach and Horne (1899, pp. 314, 315) reported a graptolite fauna including abundant *Didymograptus superstes* (Lapworth), *Dicranograptus ramosus* (Hall), *Dicellograptus sextans* (Hall) and *Climacograptus scharenbergi* (Lapworth) indicating a probable upper *N. gracilis* GBZ age. The waterfall at this locality is formed from a volcanic agglomerate.

CONODONT FAUNA

Samples up to 2 kg in weight were processed for conodonts using standard techniques, buffering with calcium carbonate and using a 63 μm mesh bottom sieve. Acid resistant, heavy residues were large and underwent magnetic separation prior to picking. Conodonts are abundant and diverse, although generally poorly preserved. Specimens are black with a CAI of 5, indicating they have been subjected to temperatures in excess of 300 °C (Epstein *et al.* 1977). This is consistent with the illite crystallinity data in Oliver *et al.* (1984). The majority of specimens exhibit surficial alteration, best seen as a thin recrystallized mineral film under the SEM. Consequently, specimens are easier to identify and look better preserved under the light microscope. Illustrated specimens are housed in the collections of the Hunterian Museum, with the specimen numbers prefixed by GLAHM Y. The remaining collection is housed in the micropalaeontological collections of the Department of Geological Sciences, University of Durham. Specimen abundances are recorded in Table 1.

SYSTEMATIC PALAEONTOLOGY

The widespread application of multi-element taxonomy has led to the erection of a number of element notational schemes. The scheme proposed by Sweet and Schönlaub (1975), and modified by Cooper (1975), Männik and Aldridge (1989) and Aldridge *et al.* (1995), for platform-ramiform taxa is adopted here as it remains the most widely used amongst conodont workers. The major shape categories and morphological terminology are as detailed by Sweet (1981). Coniform taxa have received less taxonomic treatment and there is no widely accepted terminology for homologous elements within multi-element apparatuses. Sansom *et al.* (1995) have developed a scheme based upon bedding plane and diagenetically fused assemblages of *Panderodus* that appears to be widely applicable to other coniform genera and is employed herein. The major shape categories and morphological terminology used to describe coniform elements follow Sweet (1988) and Sansom *et al.* (1995). Suprageneric classification of conodonts is currently in a state of flux. The scheme proposed by Sweet (1988) and modified by Aldridge and Smith (1993) is employed herein. Synonomy lists are annotated as recommended by Matthews (1973, after Richter 1948). Complete synonomies are given only for emended taxa; shortened synonomies include the original species designation, subsequent important taxonomic changes, British material and the most recent full synonomy lists.

Phylum CHORDATA
Class CONODONTA
Order PRIONIODONTIDA Dzik, 1976
Family BALOGNATHIDAE Hass, 1959

Genus BALTONIODUS Lindström, 1971

Type. Prioniodus navis Lindström 1955*a*, p. 590.

Remarks. Löfgren (1978) argued that *Baltoniodus* should be considered a subgenus of *Prioniodus.* Lindström *et al.* (1974) and Stouge (1984) considered that *Baltoniodus* was well-founded and should be maintained as a separate genus.

Baltoniodus variabilis (Lindström, 1959)

Plate 1, figure 2; Plate 2, figures 2–9

1959	*Prioniodus variabilis* Bergström; Lindström, p. 444, pl. 3, figs 17–19.
1961	*Prioniodus* cf. *Prioniodus variabilis* Bergström; Wolska, p. 56, pl. 5, fig. 2*a–b*.
*1962	*Prioniodus variabilis* Bergström, p. 51, pl. 12, figs 1–7.
1966	*Prioniodus variabilis* Bergström; Hamar, p. 279, pl. 5, figs 2–3, 6.
1971	*Keislognathus gracilis* Rhodes; Bednarczyk, pl. 4, fig. 1.
1976	*Prioniodus variabilis* Bergström; Dzik, text-fig. 24h-1.
1981	*Baltoniodus variabilis* (Bergström); Nowlan, p. 12, pl. 14, figs 10–12, 14–17.
1984	*Baltoniodus variabilis* (Bergström); Chen and Zhang, pl. 2, figs 8–15.
1985	*Baltoniodus variabilis* (Bergström); Bergström and Orchard, pl. 2.3, fig. 2.
1994	*Baltoniodus variabilis* (Bergström); Dzik, p. 84, pl. 19, figs 1–9; text-figs 14c, 15.

Holotype. Prioniodus variabilis Bergström, 1962, p. 51.

Diagnosis. Refer to Bergström and Orchard (1985, p. 58).

Description. A single, complete pastinate Pa element was found in sample D156 (Pl. 1, fig. 2). The inner margin is extended to form a markedly triangular platform when viewed orally. Pb element arched and bipennate, with the anterior process deeper and longer than the posterior; both bear a prominent ledge beneath the denticles (Pl. 2, fig. 2). A short, adenticulate inner lateral process projects beneath and extends up the cusp as a prominent costa. Pc element similar to the Pb element but much more strongly arched; anterior and posterior processes form an acute angle beneath the cusp (Pl. 2, figs 4–5). Pd element arched, bipennate and bowed to the inner side (Pl. 2, fig. 6). Short lateral processes bearing prominent inflation beneath the denticles; anterior process is sharply down-turned, the posterior subhorizontal. Prominent cusp, slightly inclined towards the posterior.

M element tertiopedate, similar to the Sb; the inner lateral process is more sharply directed towards the posterior.

Sa element alate with short posterior process (Pl. 2, fig. 7). Lateral processes sharply down-turned and bear three or four peglike denticles. Sb element tertiopedate, similar to Sa element; inner lateral process much shorter, commonly only bears a single denticle (Pl. 2, fig. 8). Sd element laterally compressed and pyramidal quadriramate, with the processes reduced to rows of denticles.

Remarks. Lindström (1959) first illustrated and recorded this species as *Prioniodus variabilis*, referring the authorship to a manuscript not published until 1962 (Bergström 1962). An apparatus interpretation was provided by Bergström (1971) and all the elements were illustrated by Dzik (1976). This species is distinguished from the older *B. prevariabilis* (Dzik) by the prominent development of the inner margin, and ledges along the process (Dzik 1994).

Family POLYPLACOGNATHIDAE Bergström, 1981*b*

Genus EOPLACOGNATHUS Hamar, 1966

Type species. Ambalodus lindstroemi Hamar, 1964, p. 258.

Eoplacognathus lindstroemi (Hamar, 1964)

Plate 2, figure 1

*1964	*Ambalodus lindstroemi* Hamar, p. 258, pl. 5, figs 1, 4, 7–8, 10–11; text-fig. 5, figs 1a–b, 3a–b, 4a–b.
1971	*Eoplacognathus lindstroemi* (Hamar); Bergström, p. 139, pl. 2, figs 15–18.
1985	*Eoplacognathus lindstroemi* (Hamar); Bergström and Orchard, pl. 2.2, figs 11, 13.

Holotype. Hamar (1964, pl. 5, figs 8, 11); specimen PMO 69791; *Ampyx* Limestone; Ringerike, Norway.

Diagnosis. Refer to that of Dzik (1994, p. 98).

Description. A single fragmentary Pa element bears the characteristic ledge beneath the denticles and an outer lateral process which diverges at a right angle to the anterior process.

Remarks. No ramiform elements have been described for *Eoplacognathus*. The platform elements develop a distinctive ledge beneath the denticles, a convergent feature with members of the Pterospathodontidae. Pb, Pc, Pd and ramiform elements with a prominent ledge are present in sample D160 (Pl. 2, figs 2–9), in association with an *E. lindstroemi* Pa element, but closely resemble elements traditionally included in *Baltoniodus variabilis*.

EXPLANATION OF PLATE 2

Fig. 1. *Eoplacognathus lindstroemi* (Hamar, 1964); GLAHM Y 372; sample D156, Winkston; Pa fragment.

Figs 2–9. *Baltoniodus variabilis* (Lindström, 1959); Winkston. 2–6, 8–9, sample D160. 2, GLAHM Y 373; Pb element. 3, GLAHM Y 374; Sb element. 4–5, Pc elements; 4, GLAHM Y 375; 5, GLAHM Y 376. 6, GLAHM Y 377; Pd element. 8, GLAHM Y 379; Sb element. 9, GLAHM Y 380; Sc element. 7, GLAHM Y 378; sample D156; Sa element.

Figs 10–12. *Panderodus* aff. *P. recurvatus* Rhodes, 1953. 10, GLAHM Y 381; sample D209, Glencotho Farm; qg element. 11, GLAHM Y 382; sample D156, Winkston; pf element. 12, GLAHM Y 383; sample D160, Winkston; ?pt element.

Figs 13–21. *Periodon aculeatus* Hadding, 1913; sample D156, Winkston. 13, GLAHM Y 384; Pa element. 14, GLAHM Y 385; Pb element. 15, GLAHM Y 386; Sb element. 16, GLAHM Y 387; M element. 17, GLAHM Y 388; Sa element. 18–20, Sb elements; 18, GLAHM Y 389; 19, GLAHM Y 390; 20, GLAHM Y 391. 21, GLAHM Y 392; Sc element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.


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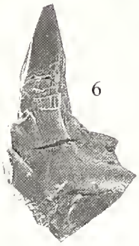
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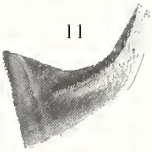
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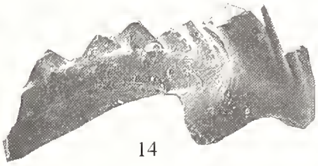
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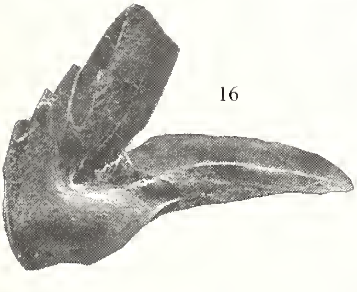
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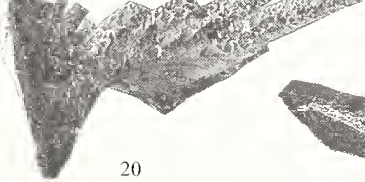
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ARMSTRONG, Ordovician conodonts

Family PRIONIODONTIDAE Bassler, 1925

Genus PERIODON Hadding, 1913

Type species. Periodon aculeatus Hadding, 1913, p. 33.

Remarks. Periodon shares a common apparatus plan with other members of the Prioniodontidae. This is typically septimembrate containing a bipennate Pa, digyrate Pb, dolabrate M, alate Sa, Sb and Sc elements. Two pairs of Sb elements occur in most genera. Dzik (1994) and Armstrong *et al.* (1996) noted homology between the elements of *Periodon* and *Hamarodus* Viira.

Periodon aculeatus (Hadding, 1913)

Plate 2 figures 13–21; Text-figure 3

*1913 *Periodon aculeatus* Hadding, p. 33, pl. 1, fig. 14.
1941 *Loxognathus flabellata* Graves and Ellison, p. 12, pl. 2, figs 29, 32.
1941 *Oistodus prodentatus* Graves and Ellison, p. 13, pl. 12, figs 8, 22–23, 28.
1941 *Ozarkodina macrodentata* Graves and Ellison, p. 14, pl. 2, figs 33, 35–36.
1941 *Loxognathus flabellata* Graves and Ellison, p. 12, pl. 2, figs 29, 32.
1955*b* *Periodon aculeatus* Hadding; Lindström, p. 110, pl. 22, figs 10–11, 14–16, 35.
1957 *Periodon aculeatus* Hadding; Lamont and Lindström, p. 61, pl. 5, fig. 15.
1962 *Falodus prodentatus* (Graves and Ellison); Sweet and Bergström, p. 1227, pl. 170, figs 2–3, text-fig. 2B.
1962 *Ligonodina tortilis* Sweet and Bergström, p. 1240, pl. 171, figs 7–8.
1966 *Periodon aculeatus* Hadding; Sweet and Bergström, pl. 18, figs 1, 3–4; text-fig. 1C, E.
1973 *Periodon aculeatus* Hadding; Barnes and Poplawski, p. 780, pl. 5, figs 15–18a.
1974 *Periodon aculeatus* Hadding; Bergström *et al.*, pl. 1, figs 4–6.
1976 *Periodon aculeatus aculeatus* Hadding; Dzik, fig. 34i–r.
1976 *Periodon aculeatus zgierensis* Dzik, p. 424, pl. 44, figs 5–6; fig. 34e–k.
1978 *Periodon aculeatus* Hadding; Löfgren, p. 74, pl. 10, fig. 1A–B; pl. 11, figs 12–26; fig. 29 (*pars*).
1984 *Periodon aculeatus* (Hadding); Chen and Zhang, pl. 2, figs 1–7.
1985 *Periodon aculeatus* (Hadding); Bergström and Orchard, pl. 2.2, figs 6–7.
1990 *Periodon aculeatus* (Hadding); Bergström, pl. 1, figs 15–16.
1991 *Periodon aculeatus* (Hadding); McCracken, p. 50, pl. 1, figs 13, 20, 22, 25–28; pl. 2, figs 24–27, 31, 34–35.
1994 *Periodon aculeatus* (Hadding); Dzik, p. 111, pl. 24, figs 10–13; text-fig. 31b.

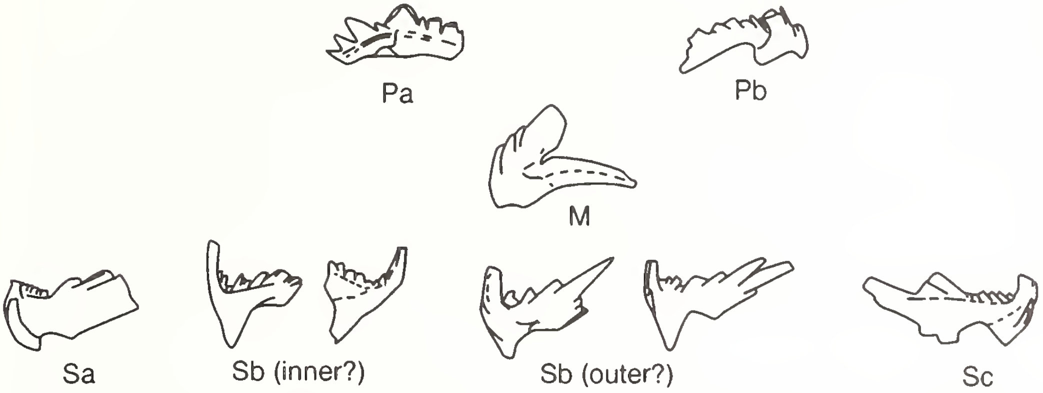
Holotype. Hadding (1913, pl. 1, fig. 14); specimen LO 2353 T (mouldic preservation); *Climacograptus haddingi* GBZ (= *Climacograptus putillus* in Hadding 1913) of Fågelsång, near Lund (upper part of section E15).

Emended diagnosis. A species of *Periodon* with a markedly digyrate Pb; dolabrate M element bearing three to six anterior edge denticles.

Description. Pa element inwardly bowed and angulate; cusp and denticles inclined towards posterior (Pl. 2, fig. 13). Processes of approximately equal length, bearing four to six denticles. Moderate inward flare of basal cavity, directed posteriorly. Pb element digyrate with short anterior process, commonly bearing three or four denticles (Pl. 2, fig. 14). Posterior process longer than anterior, variably bowed downwards and inwards. Pronounced basal cavity flare beneath cusp, directed posteriorly.

M element dolabrate, slightly inwardly bowed (Pl. 2, fig. 16). Anterior margin of the reclined cusp commonly bears three and rarely up to six denticles. Posterior process adenticulate. Weak development of an anticusp on large specimens. Narrow, symmetrically disposed basal cavity flare beneath cusp.

Sa element alate with deep, denticulate processes (Pl. 2, fig. 17). Lateral processes bear two or three short denticles and continue up the cusp as faint costae. Sb element variable in morphology from flat (dolabrate) to inwardly bowed, tertiopedate (Pl. 2, figs 18–20). Posterior process bears up to eight posteriorly inclined denticles; may be outwardly twisted. Inner lateral process developed as two or three, tall denticles, up the edge of the cusp. Outer lateral process reduced to a costa along upper edge of the cusp. Basal cavity flare beneath cusp variably developed, may extend as a ridge along lower margin of the posterior process in large specimens. Sc element similar to Sa but outer lateral process reduced to a costa, rarely a denticulate ridge (Pl. 2, fig. 21). Posterior process has a pronounced downward curvature.



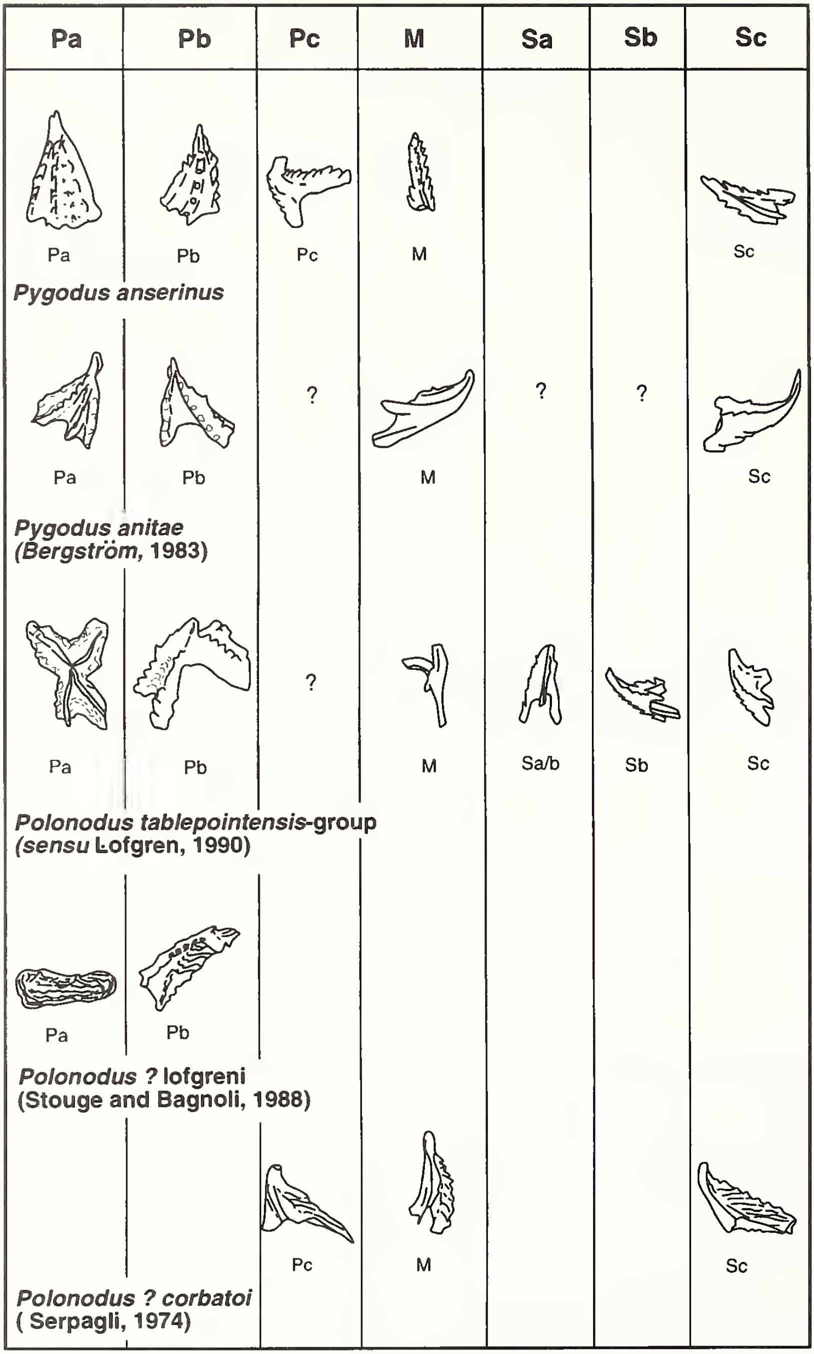
TEXT-FIG. 3. Line drawings of elements placed in the apparatus of *Periodon aculeatus* (Hadding, 1913). Specimens are as figured in Plate 2.

Remarks. Sweet and Bergström (1966) proposed a partial multi-element reconstruction, Bergström *et al.* (1974) included the Pb element and Dzik (1976) proposed the first complete apparatus. Flat and inwardly curved sinistral and dextral morphotypes of the Sb element suggest inner and outer pairs within the apparatus.

Family PYGODONTIDAE Bergström, 1981*b*

Remarks. *Pygodus* appears to have a modified prioniodontid apparatus plan. The family Pygodontidae is retained for conodonts bearing scaphate Pa, pastiniscaphate Pb and bipennate Pc elements. *Polonodus* Dzik also belongs to this family. *Amorphognathus* is not included as it contains a Pd element (Armstrong *et al.* 1996).

The earliest species of *Polonodus* and *Pygodus* have a stelliscaphate Pa and a pastiniscaphate Pb (Text-fig. 4). Historically, phylogenies for this group have been based upon morphological transitions in the Pa element. Löfgren (1990) summarized the current thinking on the evolution of this group. According to Bergström (1983, p. 44) an ancestral, Tremadoc platform conodont, such as *Nericodus* Dzik, 1983, evolved into *Polonodus* and *Pygodus* in the Llanvirn. Löfgren (1990, p. 256), however, considered the ancestry of *Polonodus* to be much more complex. She noted differences in the ramiform elements between the earliest Arenig species, *Polonodus*? *corbatoi* (Serpagli) (equivalent to *Polonodus*? sp. Löfgren, 1985) and the later *P. tablepointensis* Stouge-group (*sensu* Löfgren 1990), which possess ramiforms more similar to those of *Baltoniodus*. No records exist of *Polonodus* between the *O. evae* and *A. variabilis* CBZ and Löfgren (1990, p. 256) concluded that, to derive the later species of *Polonodus* from the early Arenig forms, one must invoke parallel evolution of the ramiforms in the (*Acodus*)-*Baltoniodus* and *Polonodus* lineages. She considered it to be more parsimonious for the *Polonodus*-type platforms to have evolved twice, firstly



TEXT-FIG. 4. Proposed homologies between the elements of *Pygodus* and *Polonodus*. Elements are redrawn: *Pygodus anserinus* (Pl. 4). *Pygodus anitae* Bergström (1983; elements illustrated from Löfgren 1978, pl. 16, figs 5–6, 3 and 4 are from the *E. suecicus* Biozone). Bergström (1983, fig. 6z) figured a possible Pc element but this has well-spaced, peg-like denticles on the posterior process. *P. tablepointensis*-group (*sensu* Löfgren 1978, pl. 16, figs 10 and 9; Löfgren 1990, fig. 1k, 1b, 1f and 1h) from the *A. variabilis* Biozone: *Polonodus*? *lofgreni* in the early Arenig and secondly from *Baltoniodus* in the late Arenig. Members of the *tablepointensis* group have an oistodontiform (M) element (Löfgren 1990, fig. 1K) which is not recognized in *Pygodus anserinus*. It appears more likely that *Pygodus* is directly descended from the *P.*? *corbatoi* group. Until the apparatus of early Arenig *Polonodus* is fully diagnosed, the ancestry of *Pygodus* must remain in doubt.

If iterative appearances of homeomorphic platform elements and relatively conservative ramiform elements are common features of the evolution in prioniodontid clades, then traditional phylogenies must be reconsidered in light of new multi-element reconstructions. The M and ramiform elements gain a new importance in diagnosis and in tracing cladogenesis.

Genus PYGODUS Lamont and Lindström, 1957

Type species. *Pygodus anserinus* Lamont and Lindström, 1957, p. 68.

Pygodus anserinus Lamont and Lindström, 1957

Plate 4, figures 1–7; Text-figure 4

*1957 *Pygodus anserinus* Lamont and Lindström, p. 68, pl. 5, figs 12–13; text-fig. 1a–d.
1958 *Phragmodus* spp. Ethington *et al*., p. 764, text-fig. 1A–D.
1958 *Falodus*? sp. Ethington *et al*., p. 764, text-fig. 1E.
?1958 *Oistodus* cf. *O. parallelus* Pander; Ethington *et al*., p. 764, text-fig. 1F.
1960 *Pygodus anserinus* Lamont and Lindström; Lindström, p. 91, figs 7.1, 7.3.
?1960 '*Arabellites*' *serra* Lindström, p. 95, fig. 7, no. 6.
?1961 *Pygodus anserinus* Lamont and Lindström; Wolska, p. 337, pl. 5, figs 4–5.
1962 *Tetraprioniodus lindstroemi* Sweet and Bergström, p. 1248, pl. 170, figs 5–6.
1962 *Roundya pyramidalis* Sweet and Bergström, p. 1243, pl. 170, figs 7–9.
1962 *Pygodus anserinus* Lamont and Lindström; Sweet and Bergström, p. 1241, pl. 171, figs 11–12; text-fig. 4.
1962 *Haddingodus serra* (Hadding); Sweet and Bergström, p. 1229, pl. 170, figs 1, 4.
1964 *Pygodus anserinus* Lamont and Lindström; Hamar, p. 279, pl. 4, figs 1–4, 11.
1964 *Pygodus* sp. Lindström; Hamar, p. 280, pl. 4, figs 5–8.
1964 *Haddingodus serra* (Hadding); Hamar, p. 266, pl. 4, figs 13, 16.
1964 *Roundya pyramidalis* Sweet and Bergström; Hamar, p. 280, pl. 5, figs 15–16, 20–21; text-fig 4, no. 12.
1964 *Tetraprioniodus lindstroemi* Sweet and Bergström; Hamar, p. 285, pl. 6, figs 4–5.
1966 *Pygodus anserinus* Lamont and Lindström; Hamar, pl. 7, fig. 1.
1974 *Pygodus anserinus* Lamont and Lindström; Bergström *et al*., pl. 1, figs 16–17.
1974 *Pygodus anserinus* Lamont and Lindström; Viira, p. 115, pl. 11, figs 26–27.
1974 *Roundya pyramidalis* Sweet and Bergström; Viira, p. 115, pl. 11, figs 7–8, 11.
1974 *Tetraprioniodus lindstroemi* Sweet and Bergström; Viira, p. 126, pl. 11, figs 9–10, 12.
1974 *Haddingodus serra* (Hadding); Viira, p. 86, pl. 11, fig. 25.
1976 *Pygodus anserinus* Lamont and Lindström; Dzik, p. 440, fig. 29f.
1978 *Pygodus anserinus* Lamont and Lindström; Bergström, pl. 79, figs 1–2.
1979 *Pygodus anserinus* Lamont and Lindström; Harris *et al*., pl. 4, fig. 17.
1983 *Pygodus serra* (Hadding); Ni *in* Zeng *et al*., pl. 12, figs 3–5.
1983 *Pygodus anserinus* Lamont and Lindström; Ni *in* Zeng *et al*., pl. 12, figs 4, 22.
1984 *Pygodus anserinus* Lamont and Lindström; Chen and Zhang, pl. 2, figs 18–21.
1985 *Pygodus anserinus* Lamont and Lindström; Bergström and Orchard, pl. 2.3, fig. 3.
1990 *Pygodus anserinus* Lamont and Lindström; Pohler and Orchard pl. 2, fig. 20.
1994 *Pygodus anserinus* Lamont and Lindström; Dzik, p. 105, pl. 17, figs 7–8; text-figs 26–27.

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elements are from the *P. elegans* Biozone (Stouge and Bagnoli 1988, pl. 11, figs 4 and 1) and *P.*? *corbatoi* (Serpagli) from the *O. evae* Biozone (illustrated from Stouge and Bagnoli 1988, pl. 10, figs 2, 5, 3) are considered together as the *P.*? *corbatoi*-group.

Holotype. Lamont and Lindström (1957, text-fig. 1a–b); specimen LO 3871 T. From grey trilobite-bearing limestone, Gärdslösa Bodar, Öland, Sweden.

Emended diagnosis. A species of *Pygodus* in which the quinquimembrate apparatus comprises stelliscaphate Pa, pastiniscaphate Pb, bipennate Pc element and tertiopedate M element. The ramiform complex is apparently reduced to an Sc element.

Description. Pa element stelliscaphate and triangular in oral view (Pl. 4, figs 1–3). Short, triangular, posterior cusp, markedly inclined towards posterior. Anterior platform bears three prominent, inwardly curved rows of nodes, which lie along the margins and just off-centre. A fourth, incipient row of nodes lies between the outer and inner row. Low ridges may join the nodes across the platform. The inter-ridge areas bear a micro-ornament of small nodes and pock-marks which in a very few specimens are arranged in small circles. The aboral surface is entirely excavated.

Pb element is similar to the Pa element, but lacks the fourth incipient row of nodes (Pl. 4, fig. 4). Platform more inwardly curved; central row of nodes most prominent. Specimens from the Tweeddale Member lack the transverse ridges which join the nodes.

Pc element arched and bipennate, with prominent, posteriorly inclined cusp, deep inwardly directed anterior lateral process and horizontal posterior process (Pl. 4, fig. 5). Base of cusp inwardly inflated, extending to basal margin, bisecting angle between processes. Processes bear eight to ten denticles, fused almost to their tips.

M element tertiopedate, narrow and triangular in posterior view (Pl. 4, fig. 6). Cusp short, posteriorly inclined and often difficult to distinguish from the other denticles. Processes comprise denticulate ridges which run the height of the element. Denticles are as in the Pc element. Posterior process commonly slightly, offset laterally.

Sc element similar in morphology to M element, but strongly, latero-obliquely compressed, posterior process becoming more prominent and sub-horizontal (Pl. 4, fig. 7). Outer lateral process reduced to adenticulate ridge and inner process only slightly bowed inwardly.

Remarks. Lamont and Lindström (1957, p. 68) diagnosed *P. anserinus* as comprising 'a very small cusp and three rows of small, irregular denticles and in big specimens a fourth row', which implies that they considered specimens with three rows of nodes to be juvenile. In the new collections there is no significant size difference between three- and four-rowed specimens, and a range from small to large specimens is present. The incipient fourth row of nodes in *P. anserinus* has since been considered to be a phylogenetic (Bergström 1971, pp. 97, 147) or ecophenotypic (Fåhræus 1982, pp. 4–6) characteristic. Dzik (1994, p. 26) illustrated three- and four-rowed Pa elements from samples 57, 59 and 60 in the Mójcka Limestone at the base of range of *P. anserinus*. Lamont and Lindström (1957, p. 64) and Lamont (1975) recorded both *P. anserinus* and *P. serra sensu formae* from Noblehouse and Ruddenleys from a level high in the *N. gracilis* GBZ and therefore high in the *P. anserinus* CBZ (Fortey *et al.* 1995). The three- and four-rowed *Pygodus* morphotypes would thus appear to co-occur throughout the *P. anserinus* CBZ. Nowlan (1981) and McCracken (1991) applied conferred species status to similar co-occuring elements from the Yukon.

EXPLANATION OF PLATE 3

Figs 1–15, 17–18. *Protopanderodus varicostatus* (Sweet and Bergström, 1962); Winkston. 1–2, 9–15, 17–18, sample D156. 1–2, GLAHM Y 393; ae element. 9–12, anterior and posterior views of qg elements; 9–10, GLAHM Y 397; 11–12, GLAHM Y 398. 13–14, GLAHM Y 399; anterior and posterior views of pf element. 15, GLAHM Y 400; qt element. 17–18, GLAHM Y 402; pt element. 3–8, sample D160. 3–4, GLAHM Y 394; anterior and posterior views of qa element. 5–6, GLAHM Y 395; anterior and posterior views of qg element. 7–8, GLAHM Y 396; anterior and posterior views of qt element, 7 taken before large anticusp was lost.

Fig. 16. *Pseudooneodotus* sp. indet.; GLAHM Y 401; sample D209, Glencotho Farm.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; × 75.


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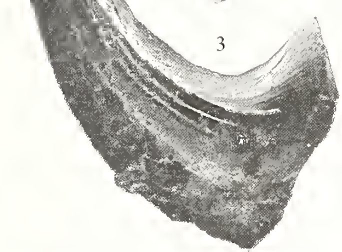
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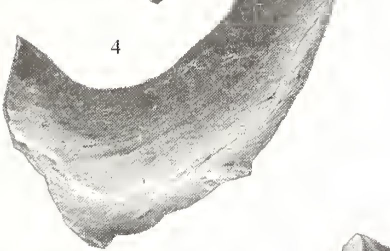
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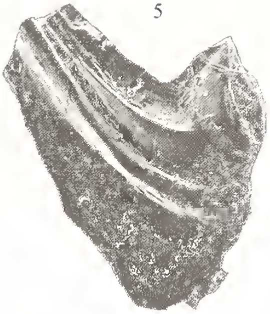
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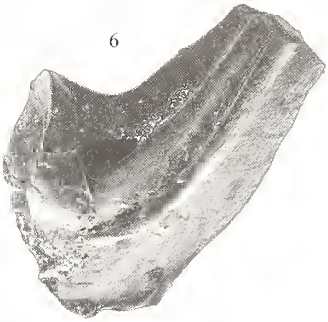
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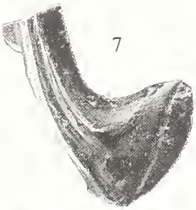
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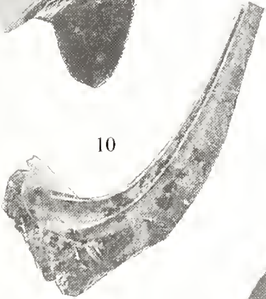
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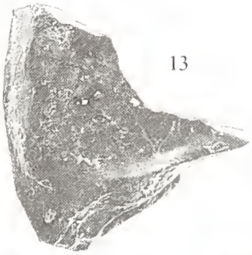
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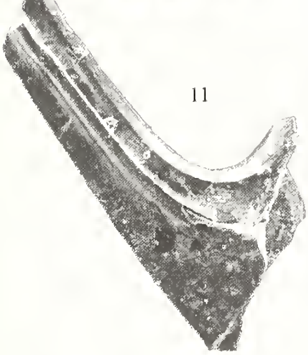
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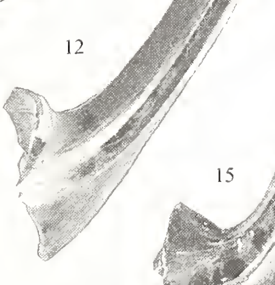
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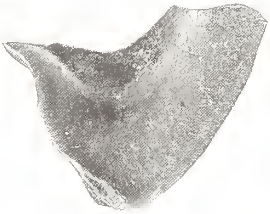


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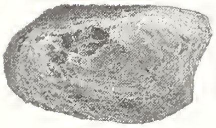
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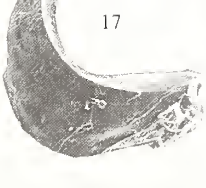
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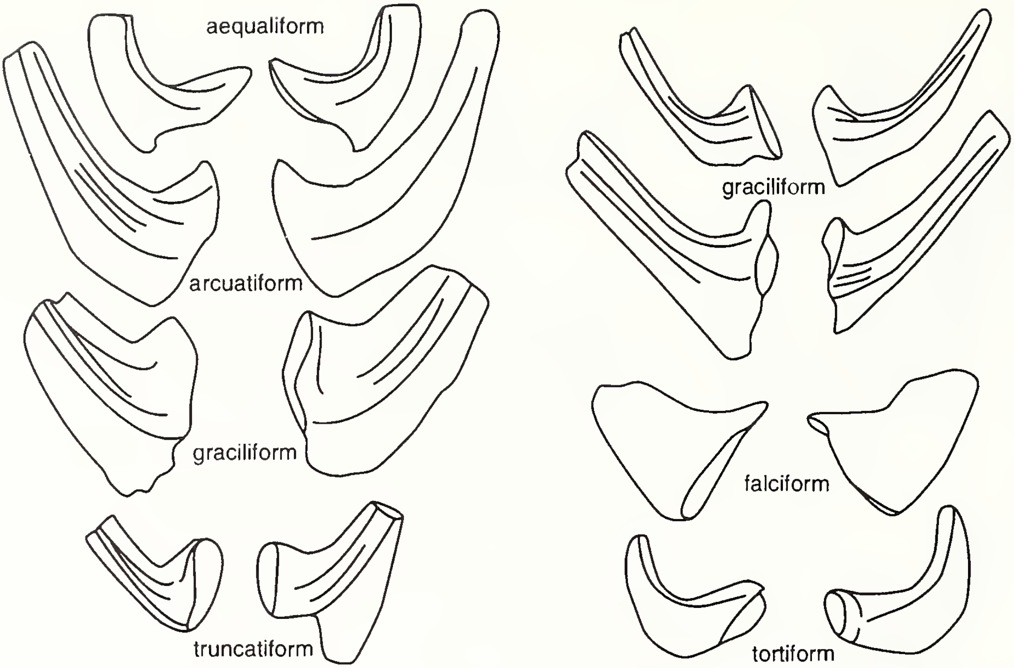
ARMSTRONG, *Protopanderodus*, *Pseudooneotodus*



TEXT-FIG. 5. Line drawings of elements placed in *Protopanderodus varicostatus* (Sweet and Bergström, 1962) and figured in Plate 3. Homologies are suggested with the apparatus plan of *Panderodus* (Sansom *et al.* 1995): graciliform (qg element), truncatiform (qt), arcuatiform (qa) falciform (pf), tortiform (pt) and aequaliform (ae).

Order PROTOPANDERODONTIDA Sweet, 1988

Remarks. Protopanderodontida includes conodonts from a number of clades (Aldridge and Smith 1993) bearing apparatuses comprising longitudinally costate and striated, coniform elements. Most of the members of Protopanderodontida appear to have a panderodontid apparatus plan but lack the incised and torted furrow typical of panderodontids. The homologous structure appears to be formed from well-developed costae.

Family PROTOPANDERODONTIDAE Lindström, 1970

Genus PROTOPANDERODUS Lindström, 1971

Type species. Acontiodus rectus Lindström, 1955*a*.

Protopanderodus varicostatus (Sweet and Bergström, 1962)

Plate 3, figures 1–15, 17–18; Text-figure 5

*1962 *Scolopodus varicostatus* Sweet and Bergström, p. 1247, pl. 168, figs 4–9; text-fig. 1A, C, K.
1962 *Scandodus unistriatus* Sweet and Bergström, p. 1245, pl. 168, fig. 12; text-fig. 1E.

1964 *Scolopodus varicostatus* Sweet and Bergström; Hamar, p. 284, pl. 1, figs 1–2; text-fig. 4, 7a–b.
1964 *Scandodus lunatus* Hamar, p. 281, pl. 2, figs 16–17.
?1966 *Scandodus unistriatus* Sweet and Bergström, Hamar, p. 74, pl. 3, figs 1, 7.
?1966 *Scolopodus insculptus* (Branson and Mehl); Hamar, p. 75, pl. 1, fig. 18; text-fig. 2, 1.
1969 *Scolopodus varicostatus* Sweet and Bergström; Bradshaw, p. 1163, pl. 132, fig. 10; pl. 134, figs 12–13.
1969 *Scandodus unistriatus* Sweet and Bergström, Bradshaw, p. 1161, pl. 135, figs 5–6.
1971 '*Scandodus*' *unistriatus* Sweet and Bergström, Bergström, p. 92, figs 4–5.
1973 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström, p. 272, figs 5–9.
1974 *Scolopodus varicostatus* Sweet and Bergström; Viira, p. 123, pl. 5, figs 23–24; text-fig. 160.
1974 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström *et al.*, pl. 1, figs 9–10.
1978 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström, pl. 79, figs 6–7.
1978? *Protopanderodus* cf. *varicostatus* (Sweet and Bergström); Löfgren, p. 91, pl. 3, figs 26–31.
1978 *Protopanderodus varicostatus* (Sweet and Bergström); Tipnis *et al.*, pl. 8, figs 8, 12.
1980 *Protopanderodus varicostatus* (Sweet and Bergström); Simes, pl. 1. fig. 6.
1981 *Protopanderodus varicostatus* (Sweet and Bergström); Gastil and Miller, fig 2j–k.
1983 *Protopanderodus varicostatus* (Sweet and Bergström); An *et al.*, p. 132, pl. 16, figs 9–12.
1983 *Protopanderodus varicostatus* (Sweet and Bergström); Burrett *et al.*, p. 184, figs C–D.
1983 *Protopanderodus varicostatus* (Sweet and Bergström); Dzik, figs 3–29.
1984 *Protopanderodus varicostatus* (Sweet and Bergström); Nowlan and Thurlow, p. 293, pl. 2, figs 1–3, 8.
1984 *Protopanderodus varicostatus* (Sweet and Bergström); Chen and Zhang, pl. 3, figs 36–38.
1985 *Protopanderodus varicostatus* (Sweet and Bergström); Bergström and Orchard, pl. 2.3, fig. 5.
1987 *Protopanderodus varicostatus* (Sweet and Bergström); Bauer, p. 27, pl. 3, figs 19, 21–23.
1990 *Protopanderodus varicostatus* (Sweet and Bergström); Pohler and Orchard, pl. 2, figs 16–17.
?1990 *Protopanderodus giganteus* (Sweet and Bergström); Pohler and Orchard, pl. 2, fig. 15.
1991 *Protopanderodus varicostatus* (Sweet and Bergström); Marquis and Nowlan, pl. 1, figs 24–25.
1994 *Protopanderodus varicostatus* (Sweet and Bergström); Dzik, p. 74, pl. 14, figs 1–5; text-fig. 11b.

Holotype. *Scolopodus varicostatus* Sweet and Bergström, 1962 from the Pratt Ferry Formation (middle Ordovician), Alabama.

Emended diagnosis. A species of *Protopanderodus* comprising robust, strongly costate q elements with moderately flared bases; acostate pf and costate and strongly curved pt elements.

Description. Symmetrical, aequaliform, continuously upwardly recurved ae element bearing a single costa and deep groove on upper part of each face (Pl. 3, figs 1–2). Upper edge flat. Short base extended upwards as a long heel and downwards as a short anticusp.

Broad, erect, arcuatiform qa element with smooth outer face and multicostate inner (bowed) face (Pl. 3, figs 3–4). Upper and lower edges sharp, the latter extended as an apically narrowing keel. Up to four costae situated in upper half of inner face; outer two most prominent; all costae separated by narrow grooves. Costae terminate short of basal margin. Base extended upwards as a short heel.

Short, recurved, sub-symmetrical, tortiform qt element; upper edge shallowly concave with lateral margins extended as costae; lower edge bears a broad keel which extends downwards as a very prominent anticusp (Pl. 3, figs 7–8). Lateral faces bear two lower and a single upper costa, all separated by deep V-shaped grooves. Costae terminate short of basal margin. Base short and inflated, may bear weakly developed basal wrinkles.

Sub-symmetrical, graciliform qg elements; straight, erect or continuously upwardly curved, with two costae on inner face and three on outer (Pl. 3, figs 5–6, 9–12). Additional minor costae may be present at base of cusp. Major costae extend almost to basal margin. Lower edge with a narrow keel and short anticusp, upper edge shallowly concave and extended upwards as a short heel in straight and erect specimens. The range of morphologies exhibited by these elements suggests that they may have occupied more than one position in the apparatus.

Acostate, falciform pf element; slightly bowed towards inner face (Pl. 3, figs 13–14). Short base; broad cusp with prominent keel on upper edge. Base extended upwards as a sinuously curved heel.

Narrow pt element, laterally compressed, sub-symmetrical, tortiform, continuously upwardly curved (Pl. 3, figs 17–18). Base narrow and twisted inwards. Cusp broadens to midheight before tapering apically. Two costae, close to upper margin on both lateral faces, sub-symmetrically arranged.

Remarks. The pf and ae elements have not been previously included in the apparatus. The specimen figured by Hamar (1966, pl. 1, fig. 18) appears to be an ae element with three major costae crossing the base. *P. varicostatus* ae elements from the Tweeddale Member have only two major costae. Dzik (1994, p. 75) noted that *P. varicostatus* can be distinguished from the younger *P. liripipus*, which has a more broadly flaring base. As reconstructed, *P. varicostatus* has an apparatus plan similar to that proposed for *Drepanodus* by Dzik (1994, fig. 9). The qg elements of *D. robustus* (Dzik 1994, p. 70) have prominent multiple costae on the upper margins, a convergent feature shared with species of *Protopanderodus*.

Genus WALLISERODUS Serpagli, 1967

Type species. Acodus curvatus Branson and Branson, 1947, by subsequent designation of Cooper (1975, p. 995).

Diagnosis. Refer to Cooper (1975, p. 995).

Remarks. Armstrong (1990) reconstructed the apparatus of Silurian *Walliserodus* demonstrating that it possessed a panderodontid plan. It is not clear whether Ordovician and Silurian *Walliserodus* are congeneric.

Walliserodus ethingtoni (Fåhræus, 1966)

Plate 5, figures 10–12.

*1966	*Panderodus ethingtoni* Fåhræus, p. 26, pl. 3, fig. 5a–5b.
1974	*Walliserodus ethingtoni* (Fåhræus); Bergström *et al.*, pl. 1, fig. 12.
1981	*Walliserodus ethingtoni* (Fåhræus); Fåhræus and Hunter, p. 1180, pl. 3, figs 11–16; text-fig. 6A–H.
1994	*Walliserodus ethingtoni* (Fåhræus); Dzik, p. 56, pl. 12, figs 7–10, 15–19; text-fig. 2b.

Holotype. Fåhræus (1966, pl. 3, fig. 5a–5b); specimen LO 4122 T; middle Ordovician; Gullhögen Quarry, Sweden.

Diagnosis. Refer to that of Dzik (1994, p. 56).

Remarks. An incomplete apparatus comprising geniculate ae and sub-symmetrical, recurved qg elements is recognized. These bear the characteristic, paired longitudinal costae of the holotype. Löfgren (1978, p. 114) and Stouge (1984, p. 64) recorded symmetrical and asymmetrical elements.

EXPLANATION OF PLATE 4

Figs 1–7. *Pygodus anserinus* Lamont and Lindström, 1957; sample D156, Winkston. 1–3, Pa elements; 1, GLAHM Y 403; 2, GLAHM Y 404; 3, GLAHM Y 405. 4, GLAHM Y 406; Pb element. 5, GLAHM Y 407; Pc element. 6, GLAHM Y 408; M element. 7, GLAHM Y 409; Sc element.

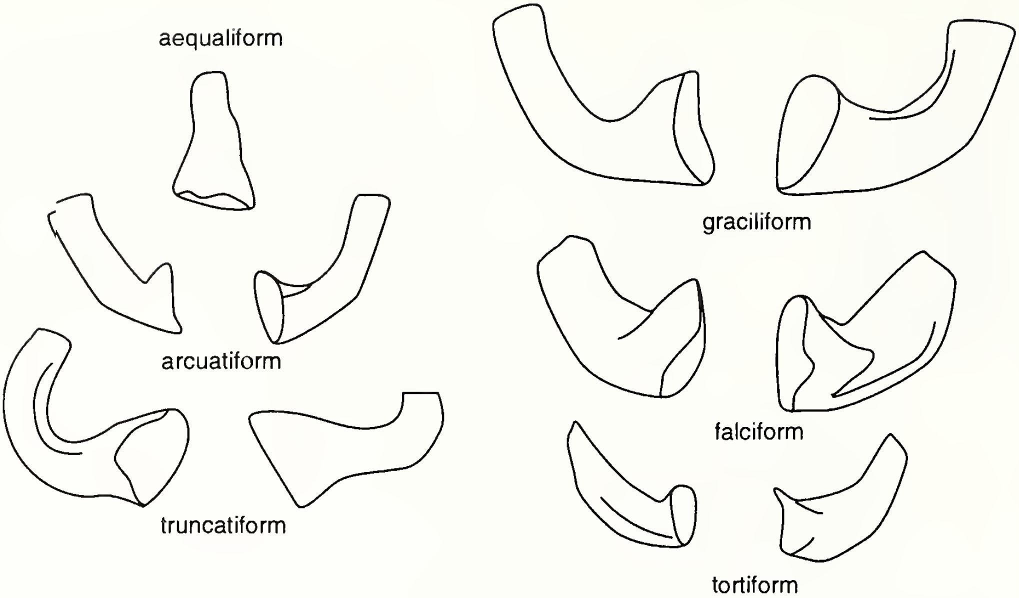
Figs 8–11. *Spinodus spinatus* (Hadding, 1913); Winkston. 8–10, sample D160; 8, GLAHM Y 410; 9–10, GLAHM Y 411. 11, GLAHM Y 412; sample D156.

Figs 12–22. *Cornuodus longibasis* (Lindström, 1955*a*); sample 209, Glencotho Farm. 12, GLAHM Y 413; ae element. 13–14, GLAHM Y 414; anterior and posterior views of qa element. 15–16, GLAHM Y 415; anterior and posterior views of qg element. 17–18, GLAHM Y 416; anterior and posterior views of qt element. 19–20, GLAHM Y 417; anterior and posterior views of pf element. 21–22, GLAHM Y 418; anterior and posterior views of pt element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.

PLATE 4

ARMSTRONG, *Pygodus*, *Spinodus*, *Cornuodus*



TEXT-FIG. 6. Line drawings of elements placed in *Cornuodus longibasis* (Lindström, 1955*a*) and figured in Plate 4. Homologies are suggested with the apparatus plan of *Panderodus* (Sansom *et al.* 1995): graciliform (qg element), truncatiform (qt), arcuatiform (qa) falciform (pf), tortiform (pt) and aequaliform (ae).

Walliserodus aff. *W. sancticlairi* Cooper, 1976

Plate 5, figures 6–9

Remarks. Elements referred to this species comprise thin-walled, deeply excavated cones. The characteristic ae element bears two lateral costae along the lower edge, making it triangular in cross section. A similar element was described as *W.* cf. *W. sancticlairi* Cooper from the Lower Silurian of North Greenland (Armstrong 1990). The arcuatiform and ae elements in the Ordovician species have more prominent upper edge keels. *W. sancticlairi* Cooper consists of slender cones with a similar basal outline but more prominent costae on the ae and arcuatiform elements. Dzik (1994, p. 57) noted that during evolution *W. ethingtoni* elements became more prominently ornamented and thinner walled. The presence of only weakly developed costae in *W.* aff. *W. sancticlairi* appears to distinguish this form.

Family CORNUODONTIDAE Stouge, 1984

Remarks. Cornuodus is currently retained in the Cornuodontidae, but *C. longibasis* appears to have a panderodontid apparatus plan. If this can be confirmed for other species, then this feature and the absence of an incised and torted longitudinal furrow would warrant the transfer of this genus to the Protopanderodontidae Lindström, 1970.

Genus CORNUODUS Fåhræus, 1966

Type species. Cornuodus erectus Fåhræus, 1966, p. 20.

Emended diagnosis. A protopanderodontid with acostate, short, recurved, sub-circular, conical q elements and laterally compressed, keeled pf and pt elements. The q elements have a faint groove along the upper edge. All elements are both faintly microstriate and deeply excavated.

Remarks. Löfgren (1978, p. 49) considered *Drepanodus longibasis* Lindström and *Cornuodus erectus* Fåhræus to be conspecific, and included symmetrical and asymmetrical elements in the apparatus of *Cornuodus longibasis*. *Cornuodus* can be distinguished from *Scalpellodus* Dzik by the less prominent microstriations. Both genera appear to have a panderodontid apparatus plan and are probably closely related. Dzik (1994, p. 61) suggested a close similarity between the apparatus organization of *Cornuodus* and *Dapsilodus*. The panderodontid apparatus plan, and qt and qg elements with a rounded rather than oval cross section would suggest a closer relationship between *Cornuodus* and *Drepanodus*.

Cornuodus longibasis (Lindström, 1955*a*)

Plate 4, figures 12–22; Text-figure 6

*1955*a* *Drepanodus longibasis* Lindström, p. 564, pl. 3, fig. 31.
1966 *Cornuodus erectus* Fåhræus, p. 20, pl. 2, fig. 8a–b; text-fig. 2B.
1967 *Cornuodus erectus* Fåhræus; Serpagli, p. 57, pl. 12, figs 5a–8b.
1967 *Scandodus*? *lanzaensis* Serpagli, p. 95, pl. 26, figs 4a–7d.
1967 *Cornuodus bergstroemi* Serpagli, p. 57, pl. 12, figs 1a–2c.
?1969 *Drepanodus longibasis* Lindström; Bednarczyk, pl. 2, fig. 2.
1970 '*Cornuodus*' *longibasis* (Lindström); Serpagli, p. 43, pl. 7, fig. 2a–b; pl. 20, fig. 12.
1974 '*Cornuodus*' *longibasis* (Lindström); Serpagli, p. 43, pl. 7, fig. 2a–b; pl. 20, fig. 12.
1974 *Protopanderodus longibasis* (Lindström); van Wamel, p. 92, pl. 4, figs 4–6.
1976 *Cornuodus longibasis* (Lindström); Landing, p. 631, pl. 1, figs 12–13, 15.
1976 *Scalpellodus* (?*Cornuodus*) *laevis* Dzik, p. 421, pl. 41, fig. 1; text-fig. 13a–c.
1978 *Cornuodus longibasis* (Lindström); Löfgren, pl. 4, figs 36, 38–42; text-fig. 25A–C.
1978 *Cornuodus bergstroemi*; Löfgren, pl. 2, fig. 37; text-fig. 25D.
1984 *Cornuodus longibasis* (Lindström); Stouge, p. 62, pl. 8, figs 1–8.
1988 *Cornuodus longibasis* (Lindström); Stouge and Bagnoli, p. 114, pl. 1, figs 20–21.
1991 *Cornuodus longibasis* (Lindström); Stouge and Bagnoli, p. 14, pl. 3, figs 3–7.
p1994 *Cornuodus longibasis* (Lindström); Dzik, p. 61, pl. 11, figs 9–13; text-fig. 4a (*non* sp element).

Holotype. Lindström (1955*a*, pl. 3, fig. 31); Upper Planilimbata Limestone (Arenig); Lanna near Orebo, Sweden.

Diagnosis. Refer to Dzik (1994, p. 62).

Description. Conical, entirely excavated ae element approximately twice as long as wide (Pl. 4, fig. 12).

Sub-symmetrical, arcuatiform qa element with short sub-circular base extended upwards as a short heel (Pl. 4, figs 13–14). Cusp circular in cross section, recurved and flexed at midheight. The qt element is similar to qa; truncatiform, strongly recurved particularly above midheight (Pl. 4, figs 17–18). Base more prominently flared and extends downwards as a short anticusp. A shallow groove runs along upper edge. The qg element is difficult to distinguish from qa element (Pl. 4, figs 15–16). Graciliform, basal heel absent, base more circular in cross section and cusp lacking midheight flexure. Faint groove along upper edge.

Falciform pf element with upper and lower edge keels (Pl. 4, figs 19–20). Slightly inwardly bowed, with base inflated on inner side. The pt element is similar to the pf, smaller, with keel only on the lower edge (Pl. 4, figs 21–22). Base more markedly twisted towards inner face.

Remarks. Löfgren (1978) first identified the main element types in *Cornuodus* and the distinction between the species. The qt and qg elements have a very generalized morphology. Dzik (1994, p. 61; fig. 4) included a geniculate 'sp' element in his reconstruction. This type of element has not been found. The pf and pt elements are laterally compressed.

Family DAPSILODONTIDAE Sweet, 1988

Genus DAPSILODUS Cooper, 1976

Type species. Distacodus obliquicostatus Branson and Mehl, 1933*a*, p. 41.

Remarks. The type species has an apparatus which comprises multiple pairs of qg elements, a pair of pf elements and a single ae element (see Armstrong 1990, for a review). Two species of *Dapsilodus* are distinguished, both with the typical apparatus plan.

Dapsilodus mutatus (Branson and Mehl, 1933*c*)

Plate 1, figures 3–8

*1933*c*	*Belodus* (?) *mutatus* Branson and Mehl, p. 126, pl. 10, fig. 17.
1976	*Panderodus* (*Dapsilodus*) *mutatus* (Branson and Mehl); Dzik, fig. 15g–i.
1994	*Dapsilodus mutatus* (Branson and Mehl); Dzik, p. 64, pl. 11, figs 24–26, 31–35; pl. 14, figs 8–9; text-fig. 6d.

Holotype. Branson and Mehl (1933*c*, pl. 10, fig. 17). From the upper Ordovician, Thebes Sandstone, Ozora, Missouri.

Remarks. An apparatus comprising a laterally compressed ae element, qg elements with a large upper edge keel and pf elements which are keeled, small and geniculate. The Silurian species *Dapsilodus obliquicostatus* (Branson and Mehl, 1933*a*) has a similar trimembrate apparatus (Armstrong 1990), including a recurved pf element.

Dapsilodus aff. *D. obliquicostatus* (Branson and Mehl, 1933*a*)

Plate 1, figures 9–11

Remarks. Element morphologies are similar to those in *Dapsilodus mutatus* (Branson and Mehl). The qg lacks the well-developed upper edge keel (Pl. 1, fig. 10). The pf element is recurved and the base is extended upwards as a short heel and downwards as a short anticusp (Pl. 1, fig. 11). These are characters found in the Silurian species *D. obliquicostatus* (Branson and Mehl, 1933*a*). Hamar

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EXPLANATION OF PLATE 5

Figs 1–5. *Strachanognathus parvus* Rhodes, 1955; sample D156, Winkston. 1, GLAHM Y 419; qt element. 2, GLAHM Y 420; ?ae element. 3, GLAHM Y 421; ?pf element. 4, GLAHM Y 422; qg element. 5, GLAHM Y 423; qa element.

Figs 6–9. *Walliserodus* aff. *W. santiclairi* Cooper, 1976; sample D156, Winkston. 6, GLAHM Y 424; ?pf element. 7, specimen 619/30; qa element. 8, GLAHM Y 425; qg element. 9, GLAHM Y 426; ae element.

Figs 10–12. *Walliserodus ethingtoni* (Fåræhus, 1966); sample D209, Glencotho Farm. 10, GLAHM Y 429; ae element. 11–12, GLAHM Y 428; qg element.

Figs 13–18. Gen. et sp. indet.; sample D209, Glencotho Farm. 13, GLAHM Y 430; Pa element. 14, GLAHM Y 431; Pb element. 15, GLAHM Y 432; M element. 16, GLAHM Y 433; Sa element. 17, GLAHM Y 434; Sb1 element. 18, GLAHM Y 435; Sb2 element.

All specimens from the Tweeddale Member, Shinnel Formation (middle Ordovician), Southern Uplands, Scotland; ×75.

PLATE 5

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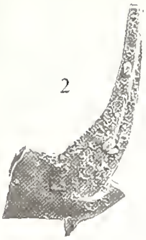

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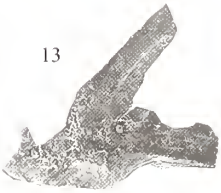

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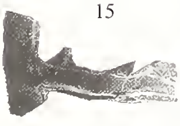

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ARMSTRONG, Ordovician conodonts

(1966, pl. 2, figs 3–9, 13) illustrated identical specimens as *Acodus similaris* Rhodes, from the middle Ordovician of the Oslo region, Norway.

Family DREPANOISTODONTIDAE Sweet, 1988

Genus DREPANOISTODUS Lindström, 1971

Type species. Oistodus forceps Lindström, 1955*a*.

Drepanoistodus suberectus (Branson and Mehl, 1933*b*)

Plate 1, figures 12–23; Text-figure 7

*1933*b*	*Oistodus suberectus* Branson and Mehl, p. 111, pl. 9, fig. 7.
1933*b*	*Oistodus curvatus* Branson and Mehl, p. 110, pl. 9, figs 4, 10, 12.
1933*b*	*Oistodus inclinatus* Branson and Mehl, p. 110, pl. 9, fig. 8.
1933*c*	*Drepanodus incurvus* (Hinde); Branson and Mehl, p. 154, pl. 12, fig. 11.
1955*a*	*Drepanodus homocurvatus* Lindström, p. 563, pl. 2, figs 23–24, 39.
1955*a*	*Drepanodus suberectus* (Branson and Mehl); Lindström, p. 568, pl. 2, figs 21–22.
1966	*Drepanodus suberectus* Branson and Mehl; Bergström and Sweet, p. 330, pl. 35, figs 22–27.
1988	*Drepanoistodus suberectus* (Branson and Mehl); Nowlan *et al*., p. 16, pl. 3, figs 19–22.
1990	*Drepanoistodus suberectus* (Branson and Mehl); Armstrong, p. 130, pl. 22, figs 7–10.
1994	*Drepanoistodus suberectus* (Branson and Mehl); Dzik, p. 78, pl. 17, figs 2–6; text-fig. 12b.

Holotype. Branson and Mehl (1933*b*, pl. 9, fig. 7). From the middle Ordovician, Plattin Formation, Jefferson County, Missouri.

Diagnosis. Refer to Armstrong (1990, p. 130).

Description. All elements have been described previously (see synonomy). In general, specimens from the Tweeddale Member are smaller than at equivalent levels in the Appalachians. The ae element has a broader basal margin than upper Ordovician examples.

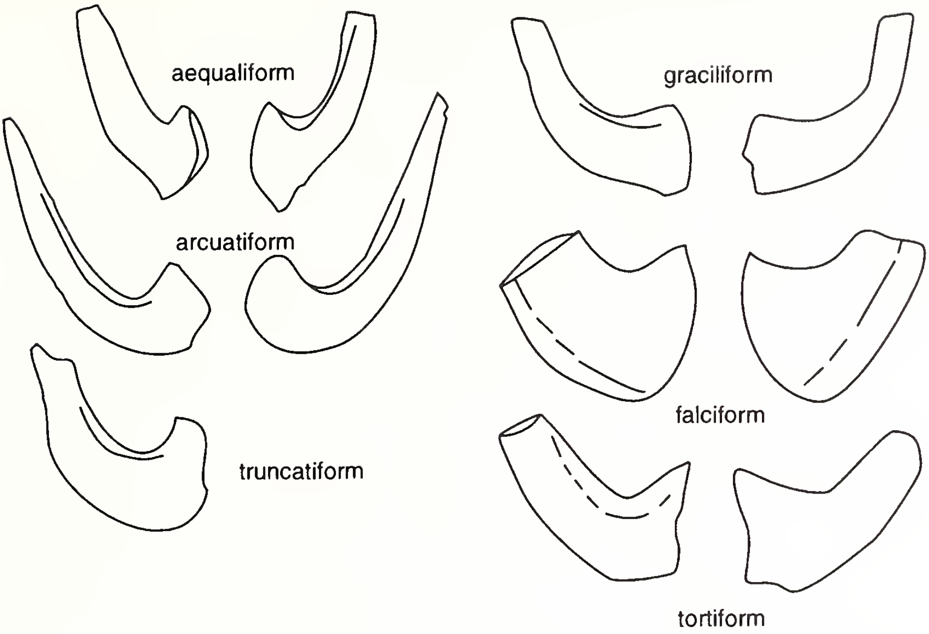
Remarks. A widely known species from the North Atlantic and American Midcontinent Provinces in mid and late Ordovician strata. Considerable variation occurs in the basal outline of the qg, qt and qa elements which Carnes (1975, pp. 129–132), and Bauer (1987, p. 16) divided into three (homocurvatiform) integrading morphotypes.

Family STRACHANOGNATHIDAE Bergström, 1981*b*

Genus STRACHANOGNATHUS Rhodes, 1955

Type species. Strachanognathus parvus Rhodes, 1955, p. 132.

Remarks. Striate coniform elements have commonly been attributed to species of *Scolopodus* Pander, *Staufferella* Sweet *et al*. and *Parapanderodus* Stouge. *Parapanderodus* species appear to have a trimembrate apparatus (Smith 1991, p. 48). The gross similarity in the proposed plans of *Parapanderodus* and *Strachanognathus* suggests that they are members of the same family. Protopanderodontidae contains taxa in which elements in the anterior and posterior domains of the apparatus are morphologically similar. Strachanognathidae is retained for coniform taxa with markedly distinct elements in the anterior and posterior domains. The qt element in these taxa is



TEXT-FIG. 7. Line drawings of elements placed in *Drepanoistodus suberectus* (Branson and Mehl, 1933*b*) and figured in Plate 1. Homologies are suggested with the apparatus plan of *Panderodus* (Sansom *et al.* 1995): graciliform (qg element), truncatiform (qt), arcuatiform (qa), falciform (pf), tortiform (pt) and aequaliform (ae).

closer morphologically to the elements in the posterior domain. In the absence of recognized posterior domain elements *Parapanderodus* is transferred tentatively to the Strachanognathidae.

Strachanognathus parvus Rhodes, 1955

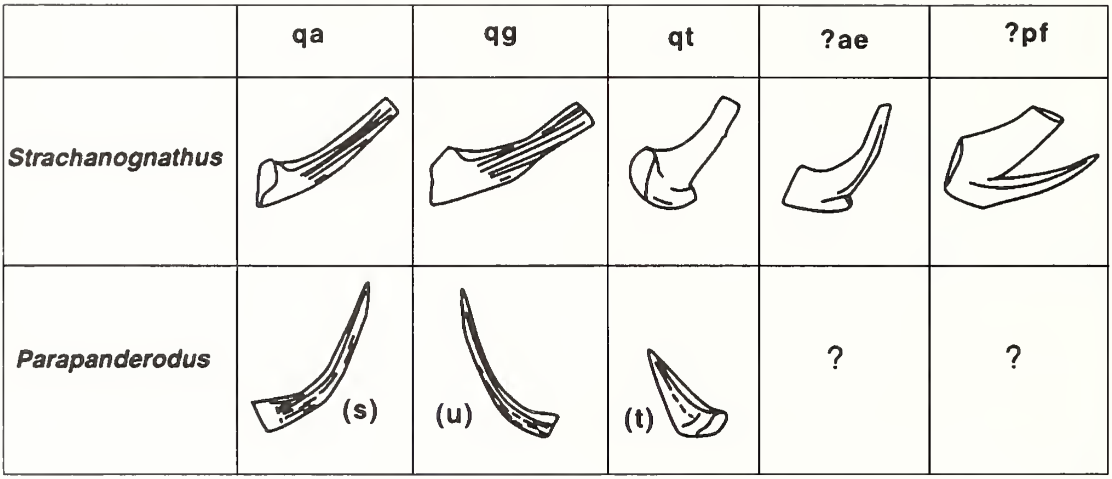
Plate 5, figures 1–5; Text-figure 8

*1955	*Strachanognathus parvus* Rhodes, p. 132, pl. 7, fig. 16; pl. 8, figs 1–4.
1962	*Strachanognathus parvus* Rhodes; Bergström, p. 54, pl. 3, figs 1–6; text-figs 2B, 3H–I.
1964	*Strachanognathus parva* Rhodes; Lindström, p. 140, text-fig. 48K.
1974	*Strachanognathus parvus* Rhodes; Bergström *et al.*, pl. 1, fig. 7.
1976	*Strachanognathus parvus* Rhodes; Dzik, p. 444, text-fig. 14j–k.
1978	*Strachanognathus parvus* Rhodes; Löfgren, p. 112, pl. 1, fig. 29.
1978	*Strachanognathus parvus* Rhodes; Palmeri, p. 27, pl. 6, figs 27–28.
1979	*Strachanognathus parvus* Rhodes; Rhodes; Kennedy *et al.*, p. 550, pl. 1 fig. 24.
1980	*Strachanognathus parvus* Rhodes; Orchard, p. 26, pl. 4, figs 34–35.
1981	*Strachanognathus parvus* Rhodes; Nowlan, p. 13, pl. 3, fig. 18; pl. 5, fig. 5.
1982	*Strachanognathus parvus* Rhodes; Lenz and McCracken, pl. 2, fig. 21.
1984	*Strachanognathus parvus* Rhodes; Stouge, p. 57, pl. 5, fig. 9.
1985	*Strachanognathus parvus* Rhodes; Bergström and Orchard, pl. 2.3, fig. 1.
1990	*Strachanognathus parvus* Rhodes; Bergström, pl. 1, fig. 10.
1990	*Strachanognathus parvus* Rhodes; Pohler and Orchard, pl. 1, fig. 6.
1991	*Strachanognathus parvus* Rhodes; McCracken, p. 52, pl. 2, fig. 36.
1994	*Strachanognathus parvus* Rhodes; Dzik, p. 62, pl. 13, figs 1–6; text-fig. 5.

Holotype. Rhodes (1955, pl. 8, figs 1–4). From the Keisley Limestone, Westmoorland.

Emended diagnosis. Quinquimembrate, comprising short based, laterally compressed elements with prominent cusps show varying degrees of upward and inward curvature. These include an inwardly twisted qa element, recurved ?ae element and bowed ?pf element; all bear a single, keeled and microstriate denticle. Erect qa and qg elements are densely striate.

Description. The ?ae element is similar to qt element, laterally compressed rather than bowed and with recurved cusp (Pl. 5, fig. 2). The qa element is similar to the qg element, base twisted inwards relative to cusp (Pl. 5, fig. 5). Basal cavity with a slight, inwardly and upwardly oblique flare. The qg element is laterally compressed, short based; cusp erect, striate, with upper edge extended as a low keel (Pl. 5, fig. 4). Basal cavity outline symmetrical and lacking flare. The qt element is inwardly bowed; cusp inwardly flexed with faint longitudinal striations (Pl. 5, fig. 1). Prominent groove runs close to and parallels lower edge of cusp. A single large, microstriate denticle fused to lower edge of cusp, with parallel curvature. Upper edge of denticle extended as a narrow keel. Basal cavity narrow with moderate inward flare. The ?pf element is similar to the ?ae element, cusp erect rather than recurved, inwardly bowed (Pl. 5, fig. 3).



TEXT-FIG. 8. Comparison of homologous elements in *Strachanognathus* (proposed herein) and *Parapanderodus* (*sensu* Smith 1991, text-fig. 8). Locations are designated in comparison with *Panderodus* (Sansom *et al.* 1995). The locational terminology applied by Smith (1991) is placed in brackets.

Remarks. The decision of Armstrong *et al.* (1996) to include striate elements in the apparatus of *S. parvus* was based upon comparison with other coniform apparatus plans; co-occurrence and the morphological similarities in the denticles of the qa-qg elements and in the cusps of the pf-pt elements. Both groups of elements bear striations, although these are less obvious in the qa-qg elements. Lenz and McCracken (1982, pl. 2, fig. 21) illustrated an Ashgill q element of *S. parvus* with oblique striations on the denticle. All the elements in the new apparatus reconstruction have been recognized in samples from the Tweeddale Member, the Stinchar Limestone (Bergström 1990) and Ashgill samples from the Dent Group, English Lake District (Orchard 1980; Armstrong *et al.* 1996). Dzik (1994, p. 60) recorded the striate coniform species *Scolopodus peselephantis* Lindström co-occurring with *S. parvus* in samples from the *A. tvaerensis* Biozone, Mójcza Limestone, Poland.

Element location has been assigned *a priori* and is based upon the *Parapanderodus* plan (*sensu* Smith 1991; Text-fig. 9). The diagenetically fused cluster illustrated by Smith (1991, fig. 29c–d) contains in order, a single large 'qa' element, a pair of 'qg' elements, a single, compressed and twisted 'qt' element and a further pair of 'qg' elements. Homology is suggested with the anterior domain of the *Panderodus* apparatus. The posterior domain (pf and pt elements) and ae element are not preserved in the cluster. In the discrete collections of the Tweeddale Member, two additional elements are present. These have been assigned questionably as the ae element and pf element. A pt element has not been recognized.

Order PANDERODONTIDA Sweet, 1988
Family PANDERODONTIDAE Lindström, 1970

Genus PANDERODUS Ethington, 1959

Type species. Paltodus unicostatus Branson and Mehl, 1933*a*, p. 42.

Panderodus aff. *P. recurvatus* Rhodes, 1953

Plate 2, figures 10–12

Remarks. Rare elements attributable to *Panderodus* species are present in all samples, except D153. In the absence of a complete apparatus it is difficult to speciate these, but the general morphology suggests that they belong to a single species. The qg (Pl. 2, fig. 10) and pf (Pl. 2, fig. 11) elements suggest an affinity with *Panderodus recurvatus* Rhodes.

Order and Family Unknown

Genus SPINODUS Dzik, 1976

Type species. Cordylodus spinatus Hadding, 1913.

Remarks. Lindström (1964) recognized a symmetry transition series including three elements previously described as *C. ramosus* Hadding and *C. spinatus* (Hadding). Uyeno and Barnes (1969) added a fourth element to *C. spinatus*. Barnes and Poplawski (1973) described a quadrimembrate apparatus for *C. ramosus*.

Spinodus spinatus (Hadding, 1913)

Plate 4, figures 8–11

*1913 *Polygnathus spinatus* Hadding, p. 32, pl. 1, fig. 8.
1913 *Cordylodus ramosus* Hadding, p. 31, pl. 1, fig. 6.
1976 *Cordylodus spinatus* (Hadding); Dzik, 424, text-fig. 21c.
1981 *Spinodus ramosus* (Hadding); Nowlan, p. 15, pl. 4, figs 18–19.
1985 *Spinodus spinatus* (Hadding); Bergström and Orchard, pl. 2.2, figs 1–4.
1991 *Spinodus spinatus* (Hadding); McCracken, p. 52, pl. 1, fig. 2.
1994 *Spinodus spinatus* (Hadding); Dzik, p. 113, pl. 24, figs 22–25; text-fig. 32.

Holotype. Hadding (1913, pl. 1, fig. 8); specimen LO 2347 t (mouldic preservation); *Climacograptus haddingi* GBZ (= *Climacograptus putillus* in Hadding, 1913) of Fågelsång, near Lund (upper part of section E15).

Remarks. The fragmentary nature of the specimens attributed to *S. spinatus* does not allow an apparatus to be reconstructed. Two categories of elements can be distinguished. 'Coniforms' (Pl. 4, figs 8–10) have long curved cusps and inflated bases; the latter may be extended as a short posterior process. 'Ramiforms' (Pl. 4, fig. 11) develop processes with widely spaced sub-circular denticles and a recessive basal margin. Specimen abundances in Table 1 include all fragments and are thus overestimates.

Genus PSEUDOONEOTODUS Drygant, 1974

Type species. Oneotodus (?) *beckmanni* Bischoff and Sannemann 1958, p. 98.

Diagnosis. Refer to Barrick (1977, p. 57).

Pseudooneotodus sp. indet.

Plate 3, figure 16

Remarks. A single uni-denticulate element was recovered from sample D209. Silurian species of *Pseudooneotodus* have an apparatus which comprises sinistral, dextral and symmetrical uni-denticulate and bi-denticulate or tri-denticulate elements (Armstrong 1990). It is not possible to distinguish species without the full apparatus.

Gen et sp. indet.

Plate 5, figures 13–18

Remarks. Elements attributable to a species of oulodontid-type are present in sample D209. The Pa element (Pl. 5, fig. 13) is similar to that found in *Periodon aculeatus*, although a single denticle on the anterior process is separated from the cusp. The poorly preserved Pb element appears to be bipennate (Pl. 5, fig. 14). The M element is dolabrate (Pl. 5, fig. 15) and two Sb elements are distinguished (Pl. 5, figs 17–18). These are separated on the style of the basal cavity flare beneath the cusp. In the Sb1 this is rounded and in the Sb2 extended as a narrow, short process.

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PALAEOBIOLOGY OF EARLY JURASSIC BAKEVELLIID BIVALVES FROM WESTERN CANADA

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ABSTRACT. Early Jurassic bakevelliid bivalves from the Canadian Cordillera are examined taxonomically, morphologically, and with respect to their biogeographical affinities. Four Early Jurassic species are recognized, which belong to the genera *Bakevellia*, *Gervillaria* and *Gervillella*. One species, *Gervillella leesi*, is new. In addition, *Gervillaria ashcroftensis* (Crickmay) from the Bajocian (Middle Jurassic) of British Columbia and the Lower Jurassic of northern Chile has been included in this study. A functional analysis of the morphologies of the five species reveals characteristic adaptations to distinct life habits. The spectrum comprises endobyssate sediment stickers, an orthothetically attached epibyssate form, and a twisted recliner. From Late Sinemurian to Late Pliensbachian times, the bakevelliid bivalves of the western Canadian allochthonous terranes, Wrangellia, Stikinia and Quesnellia, have strongest affinities to those from northern Chile and Argentina. During this time period Bakevelliidae appear to be absent from cratonal North America. This distributional pattern is consistent with a palaeogeographical position of the terranes closer to the South American Andes than previously assumed.

PALAEOBIOGEOGRAPHICAL studies of Jurassic benthic faunas have always suffered from a lack of detailed and reliable data from western North America. For this reason, one of us (MA) started to revise the Early Jurassic bivalve fauna from the western Canadian Cordillera. As this comprehensive revision is still in progress a palaeobiogeographical analysis of the whole bivalve fauna cannot be carried out at present. Here, we concentrate upon a particular group of benthic organisms, i.e. the bivalve family Bakevelliidae, with the main purposes (1) to document and revise taxonomically the Early Jurassic bakevelliids from western Canada; (2) to interpret their life habits by applying an analysis of functional morphology; and (3) to reconstruct the palaeobiogeographical distribution of the various species.

The endo- or epibenthic, byssally attached Bakevelliidae originated in the Late Permian, flourished during the Early and Mid Jurassic, and became extinct in the Late Cretaceous. They are characterized by a rhombic to trapezoidal outline with a more or less pronounced posterior wing. Ventral to a distinct ligamental area, which bears several ligamental pits, they exhibit various hinge teeth, which may vary considerably in number and shape. Bakevelliid bivalves have been selected here, because (1) they are relatively common benthic elements of Jurassic shelf seas; (2) they occur in a wide range of different lithofacies; and, most importantly, (3) they have been revised recently on the basis of an extensive survey of the published literature and careful examination of museum material (Muster 1995). This latter monograph provides a comprehensive and up-to-date data set that forms an excellent basis upon which to establish the palaeobiogeographical affinities of western Canadian bakevelliids with those from other regions.

GEOLOGICAL FRAMEWORK AND LOCALITIES

The western Canadian Cordillera consists of a collage of various tectonostratigraphical terranes, which were accreted to the western margin of the autochthonous North American craton (e.g. Coney *et al.* 1980). At what time these allochthonous terranes were accreted, and their relative

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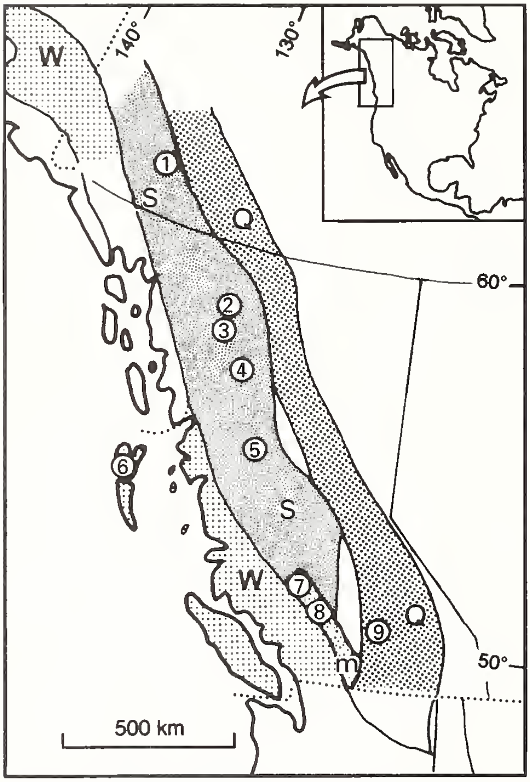
positions prior to docking are still open to debate. In addition to palaeomagnetic analyses, biogeographical data have been used also to place constraints on Early Jurassic palaeogeographical reconstructions of western North America (e.g. Taylor *et al.* 1984; Smith and Tipper 1986; Hallam 1994). We will test whether the distributional pattern of Early Jurassic bakevelliids is consistent with these reconstructions.

The localities which yielded bakevelliid bivalves are situated on three large terranes in British Columbia and southern Yukon. These terranes are, from west to east, Wrangellia, Stikinia and Quesnellia. Additional specimens are available from two small terranes (Cadwallader and Tyaughton terranes) from a tectonically complex region, the so-called 'Methow' Basin, in southwestern British Columbia. Their relationships with other terranes are still controversial. Localities and their corresponding terranes are shown on Text-figure 1 and are listed in the Appendix.



Locality number	Locality name	Lithostratigraphy
①	Laberge	Laberge Formation
②	Cry Lake	Hazelton Group
③	Spatsizi	Spatsizi Group
④	McConnell Creek	Hazelton Group
⑤	Smithers	Hazelton Group
⑥	Queen Charlotte Islands	Sandilands Formation, Fannin Formation
⑦	Taseko Lakes	Last Creek Formation
⑧	Tyaughton Creek	unnamed
⑨	Ashcroft	Ashcroft Formation

TEXT-FIG. 1. Map of western Canada showing allochthonous terranes (stippled) and localities which yielded Early Jurassic bakevelliid bivalves. Allochthonous terranes: m, 'Methow' Basin; Q, Quesnellia; S, Stikinia; W, Wrangellia. Note that locality 7 lies on the Cadwallader Terrane and locality 8 lies on the Tyaughton Terrane.

MATERIAL AND METHODS

The taxonomic part of this study is based on the extensive Jurassic fossil collections of the Geological Survey of Canada housed in Calgary and Vancouver. In addition, type material of western Canadian bakevelliids figures by Crickmay (1930) and Lees (1934) has been examined. For comparison, Early Jurassic bakevelliid type specimens from northern Chile (Aberhan 1994), Argentina (Damborenea 1987; Muster 1995) and Europe (Muster 1995) were examined. Comparisons with other taxa as well as the establishment of geographical range data of species were also aided by the recent revision of backvelliid bivalves (Muster 1995). All figured specimens from western Canada are deposited in the type collection of the Geological Survey of Canada, Ottawa, under the type numbers (prefix GSC) listed in the Text-figure captions.

SYSTEMATIC PALAEONTOLOGY

Order PTERIOIDA Newell, 1965
Family BAKEVELLIIDAE King, 1850
Genus BAKEVELLIA King, 1848

Type species. Avicula antiqua Münster, *in* Goldfuss, 1836 (p. 126, pl. 116, fig. 7); by subsequent designation (King 1850, p. 166); Middle Muschelkalk; Glücksbrunn, Germany.

Subgenus BAKEVELLIA (BAKEVELLIA) King, 1848

Type species. As for genus.

Bakevellia (*Bakevellia*) *waltoni* (Lycett, 1863)

Text-figure 2D–G

*1863 *Gervillia waltoni* Lycett, p. 110, pl. 32, fig. 4.
v1934 *Gervillia* ? cf. *inflata* Schafh.; Lees, p. 42, pl. 4, fig. 2.
v1934 *Bakevellia* (*Neobakevellia*?) *pintadae* Damborenea, p. 126, pl. 1, figs 1–5, text-fig. 4.
v1994 *Bakevellia* (*Bakevellia*) *waltoni* (Lycett 1863); Aberhan, p. 16, pl. 2, figs 10–14, text-fig. 8.
v1995 *Bakevellia* (*Bakevellia*) *waltoni* (Lycett 1863); Muster, p. 38, pl. 5, figs 1–13 [see for extensive synonymy list].

Material. Two left valves from GSC loc. 10246; one right valve from GSC loc. 19376; one left valve from GSC loc. C-81309; one left valve from GSC loc. C-81310; two left valves (GSC 112331 and GSC 112334) from GSC loc. C-81311; one left valve from GSC loc. C-81317; one left valve and one right valve (GSC 112333) from GSC loc. C-81322; three left valves and one articulated specimen from GSC loc. C-81323; one left valve from GSC loc. C-90924; one fragmentary right valve (GSC 112332) from GSC loc. C-90925; and one left valve from GSC loc. C-90930. Specimens are preserved as internal and external moulds; only in one specimen is relict shell material attached to the internal mould. For locality information see Appendix.

Occurrence. All records are from Stikinia; associated ammonites indicate a Sinemurian to Early Pliensbachian age.

Remarks. The most prominent features of *B.* (*Bakevellia*) *waltoni* are its rhombic shape; the presence of an acute anterior ear; a sharply pointed posterior wing; and a hinge consisting of one to four anterior teeth pointing in a postero-ventral direction and one or two elongated posterior teeth, which are oriented more or less subparallel to the hinge margin (Muster 1995). These characteristic features are also present in the studied specimens from western Canada.

Some specimens (e.g. Text-gig. 2F) exhibit external longitudinal grooves and ridges along the dorsal margin of the posterior wing. In this respect they superficially resemble *Pteroperna*, which also is bialate and has a sharply pointed posterior wing. Grooves and ridges along the dorsal margin, however, are also well known in *B.* (*B.*) *waltoni* (e.g. Muster 1995, p. 39, pl. 5, fig. 9). Whilst in *Pteroperna* the ridges appear to be related to the hinge, in *Bakevellia* they represent a thickening of the shell due to a concentration of growth lines in the region where the posterior wing becomes pointed. Furthermore, the main body of the shell of *Pteroperna* is more or less curved, whilst in *Bakevellia* it is always straight.

In contrast to *B.* (*Bakevellia*) *waltoni*, *B.* (*Bakevellia*) *binneyi* (Brown, 1841) exhibits a well rounded anterior auricle and the anterior teeth are arranged in a fan-like manner.

TEXT-FIG. 2. A–C–, H, *Gervillaria pallas* (Leanza, 1942). A, GSC 112327; GSC loc. 14333; internal mould of left valve with relict shell material attached; Pliensbachian, Dewar Peak, British Columbia; × 1. B–C, H, from Joan Lake, British Columbia B, GSC 112328; GSC loc. C-90909; exterior view of left valve; lower Pliensbachian; × 1. C, GSC 112329; GSC loc. C-103307; latex cast of left valve; Pliensbachian; × 1. H, GSC 112330; GSC loc. C-103307; internal mould of right valve of articulated specimen (left valve figured on Text-fig. 2C),

Genus GERVILLARIA Cox, 1954

Type species. Modiola? alaeformis J. Sowerby (1819, p. 93, pl. 251); by original designation (Cox 1954, p. 49); Lower Cretaceous; Isle of Wight, Great Britain.

Gervillaria ashcroftensis (Crickmay, 1930)

Text-figures 3A–D, 5A–B

v*1930 *Gervillia ashcroftensis* Crickmay, p. 48, pl. 3, figs a–c.
v1994 *Gervillaria? ashcroftensis* (Crickmay 1930); Aberhan, p. 17, pl. 3, figs 3a–b, 4, text-figs 10–11.
v1995 *Gervillaria? ashcroftensis* (Crickmay 1930); Muster, p. 53, pl. 9, figs 1, 2a–b, text-fig. 39.

Material. The holotype (GSC 25697) of *Gervillaria ashcroftensis* (Crickmay), which is an articulated specimen from GSC loc. C-186964.

Occurrence. The holotype is from the Bajocian of Ashcroft, British Columbia (Quesnellia).

Description. The shell is slightly twisted and sub-equivalved with the left valve being somewhat more inflated than the right one. The main body of the shell is relatively narrow and curved in a concave-up orientation with respect to the dorsal margin. The anterior part forms a more or less right angle with the plane of commissure. The beak is prosogyrate and almost terminal with a minute anterior auricle in front of it. The posterior wing is large and pointed at its postero-dorsal corner (as can be reconstructed from the growth lines).

The ligamental area exhibits up to six ligamental pits, which are always narrower than the interspaces between them (Text-figs 3B, D, 5A–B). The hinge of the holotype, which is an adult specimen, is completely crenulated. Nevertheless, individual teeth are still recognizable (Text-fig. 5A–B). The left valve (Text-fig. 5A) shows two anterior teeth, with the anterior one being considerably stronger; both are pointing in a postero-ventral direction. The posterior part of the hinge plate carries two elongated posterior teeth, which also point in a postero-dorsal direction. The corresponding right valve of the holotype (Text-fig. 5B) has a single anterior tooth, which is orientated in the same way as in the left valve. In a posterior direction follows at least one elongated posterior tooth. A second posterior tooth might have existed, but, due to intense crenulation in the posterior part of the hinge, is no longer recognizable. We interpret the triangular groove in front of the anterior teeth of both valves as a byssal groove (Text-fig. 5A–B). The pallial line consists of a series of irregularly spaced pits.

Remarks. Even though in western Canada *Gervillaria ashcroftensis* is only known from the Middle Jurassic (Bajocian), this taxon is relevant to our analysis of Early Jurassic bakevelliids, as it occurs in the upper Pliensbachian and Toarcian of northern Chile (Aberhan 1994). Until now the generic status of *G. ashcroftensis* could not be clarified on the basis of Crickmay's description and figures (Crickmay 1930, p. 48, pl. 3, figs a–c). In particular, too little information was available with respect to hinge characters. Therefore, we re-examined the holotype, which exhibits well the hinge in both the right and the left valve.

In the holotype, the slightly sub-equivalved and twisted nature of the shell, together with the complete crenulation of the hinge in adults, permit assignment of this species to *Gervillaria*.

Gervillaria pallas (Leanza, 1942)

Text-figure 2A–C, H

v*1942 *Gervillia pallas* Leanza, p. 155, pl. 4, fig. 1.

Pliensbachian; ×1. D–G, *Bakevellia* (*Bakevellia*) *waltoni* (Lycett, 1863). D, F–G, from the Sinemurian of Mandanna Creek, southern Yukon. D, GSC 112331; GSC loc. C-81311; latex cast of shell interior of left valve; ×1·5. E, GSC 112332; GSC loc. C-90925; latex cast of hinge area of right valve; lower Pliensbachian, Joan Lake, British Columbia; ×1·5. F, GSC 112333; GSC loc. C-81322; composite mould of right valve; ×1·5. G, GSC 112334; GSC loc. C-81311; latex cast of left valve; ×1·5.

TEXT-FIG. 3. *Gervillaria ashcroftensis* (Crickmay, 1930). GSC 25697; GSC loc. C-186964; Bajocian of Ashcroft, British Columbia. A, exterior view of left valve. B, interior view of left valve. C, exterior view of right valve. D, interior view of right valve. All ×0·8.

1987 *Gervillaria*? *pallas* (A. Leanza); Damborenea, p. 135, pl. 2, figs 1–5, text-fig. 7.
1992 *Gervillaria*(?) *pallas* (Leanza); Damborenea, pl. 116, fig. 1a–b.
1992 *Gervillaria*? sp.; Thompson and Smith, pl. 1, fig. 8.
v1994 *Gervillaria pallas* (A. Leanza 1942); Aberhan, p. 18, pl. 4, figs 1a–b, 2a–b, 3a–b.
v1995 *Gervillaria pallas* (Leanza 1942); Muster, p. 60, pl. 10, figs 3a–b, 4–5, text-fig. 43.

Material. One articulated specimen (GSC 112327) from GSC loc. 14333; one left valve from GSC loc. 19365; one left valve from GSC loc. 19373; one right valve from GSC loc. 19374; one articulated specimen from GSC loc. 19395; one left valve from GSC loc. 19397; three left valves, three right valves, and one articulated specimen from GSC loc. 19398; one left valve from GSC loc. 85333; one articulated specimen from GSC loc. 93327; one left valve from GSC loc. 93328; two left valves from GSC loc. C-53514; two left valves from GSC loc. C-81975; two left valves from GSC loc. C-90524; one left valve from GSC loc. C-90664; two left valves and one articulated specimen from GSC loc. C-90902; one left valve and one right valve from GSC loc. C-90903; six left valves and one articulated specimen from GSC loc. C-90905; one left valve (GSC 112328) and one articulated specimen from GSC loc. C-90909; one left valve from GSC loc. C-90924; four left valves and four articulated specimens from GSC loc. C-90925; three left valves from GSC loc. C-90926; three left valves from GSC loc. C-90928; one left valve from GSC loc. C-103198; two left valves from GSC loc. C-103305; and one left valve and one articulated specimen (GSC 112329, GSC 112330) from GSC loc. C-103307. Specimens are preserved as internal and external moulds; only rarely is relict shell material attached to the moulds. For locality information see Appendix.

Occurrence. See above. Associated ammonites indicate an Early Pliensbachian age on Stikinia and a Late Pliensbachian age on Wrangellia and Quesnellia.

Remarks. Gervillaria pallas is characterized by a strongly inequivalved and twisted shell, the left valve being strongly convex, the right valve concave. It exhibits a small anterior ear and a pointed posterior wing. By the presence of two carinae in the left valve, which extend from the umbo to the postero-ventral region of the shell, *G. pallas* can be distinguished from all other Jurassic *Gervillaria* (see also Muster 1995).

Gervillaria pallas was originally described from the Pliensbachian of Argentina (Leanza 1942) and more recently has been documented in detail from the Pliensbachian and Toarcian of Argentina and Chile (e.g. Damborenea 1987; Aberhan 1994). The morphological features of the studied specimens from western Canada agree well with those of their South American counterparts.

In the Canadian specimens, the width of the double carina remains relatively narrow, whilst in South American specimens it commonly widens in adults, although narrow double carinae are known as well (e.g. Damborenea 1987, pl. 2, fig. 4). Therefore we regard this to be a relatively variable feature within a single species.

Genus GEVILLELLA Waagen, 1907

Type species. Perna aviculoides J. Sowerby, 1814 (p. 147, pl. 66); by subsequent designation (Cox 1940, p. 112); Oxfordian; Osmington (near Weymouth), Great Britain.

Gervillella leesi sp. nov.

Text-figures 4A–E, 5D

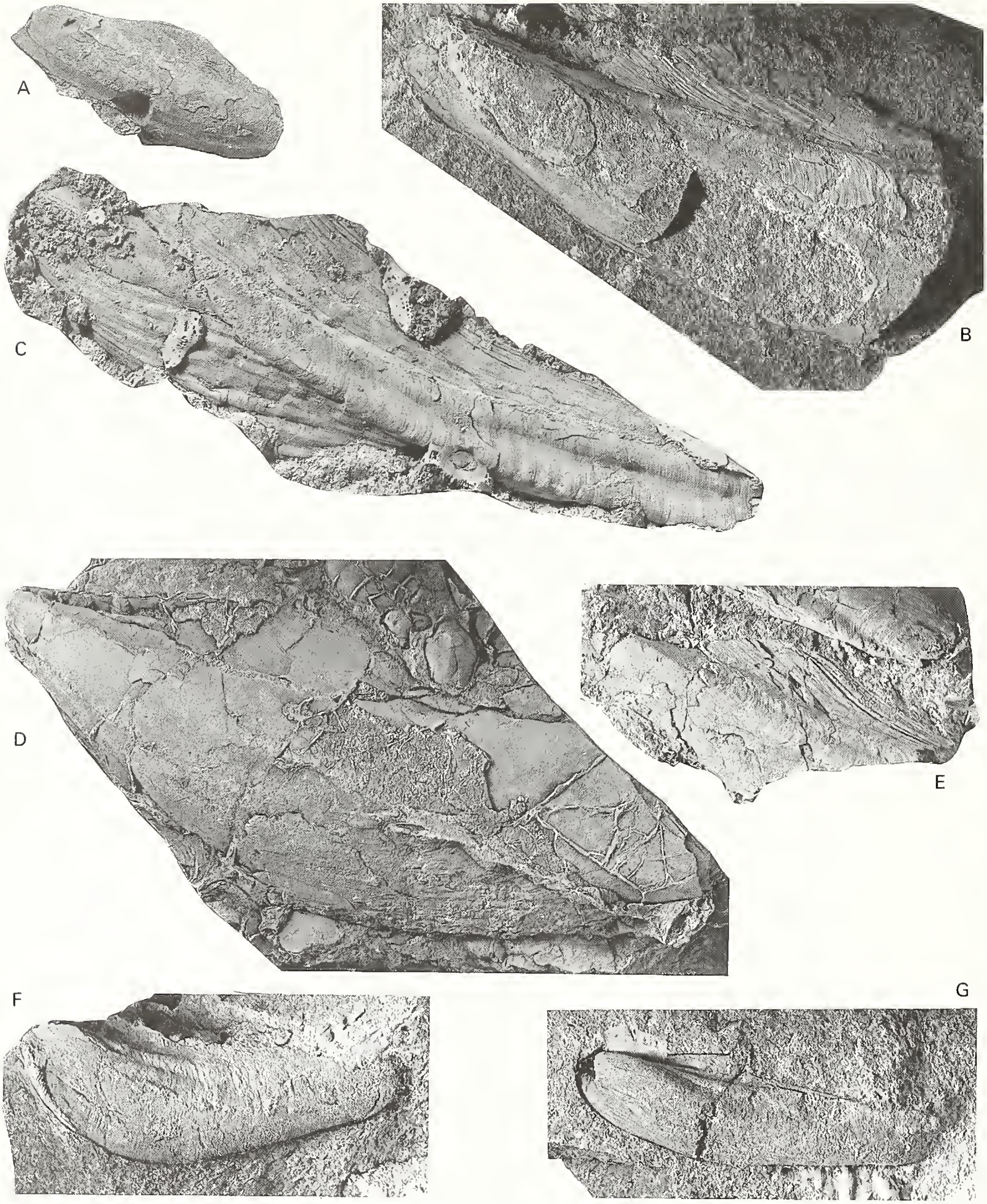
v1934 *Gervillia* sp. nov. Lees, p. 41, pl. 4, fig. 1.

Derivation of name. After Everett J. Lees, who recognized this as a new species.

Holotype. GSC 112324, left valve, figured in Text-figure 4E.

Type locality. Probably upper Sinemurian of Hunter Basin, between Webster and Goathorn creeks, Telkwa Mountains, 54° 31′ N, 127° 05′ W, Smithers map-area, British Columbia (GSC loc. 84187).

Additional material. Two left valves and one articulated specimen (GSC 112321) from GSC loc. 83995; one articulated specimen from GSC loc. 83998; three left valves from GSC loc. 84187; two left valves and one articulated specimen from GSC loc. 88495; five left valves (including GSC 112322) from GSC loc. 88602; one left valve from GSC loc. 88604; five fragmentary valves from GSC loc. 94993; four left valves (including GSC 112323) from GSC loc. 95015; three left valves and one right valve from GSC loc. C-143287;



TEXT-FIG. 4. A–E, *Gervillella leesi* sp. nov. A, GSC 112320; GSC loc. C-157663; internal mould of left valve; Hettangian, Tyaughton Creek, British Columbia. B, GSC 112321; GSC loc. 83995; left valve of articulated specimen; upper Sinemurian, Babine Lake, British Columbia. C, GSC 112322; GSC loc. 88602; latex cast of left valve; upper Sinemurian, Telkwa Mountains, British Columbia. D, GSC 112323; GSC loc. 95015; internal mould of left valve; Sinemurian, McBride River, British Columbia. E, GSC 112324; GSC loc. 84187; exterior and one left valve (GSC 112320) from GSC loc. C-157663. Specimens are commonly fragmented and preserved as internal and external moulds; rarely is relict shell material attached to the moulds. For locality information see Appendix.

Occurrence. See above. Associated ammonites indicate a Late Sinemurian age on Stikinia and a Hettangian age on the Tyaughton Terrane.

Diagnosis. Subequivalved *Gervillella*; double carina running from umbo to postero-ventral corner of shell on both valves and delimiting main body of shell from posterior wing; shell not twisted.

Description. Medium-sized, elongated shell; not twisted. Posterior part of main body slightly curved upwards. Angle between dorsal margin and vector of maximum growth 25 to 30°. Subequivalved, left valve being slightly more convex than right one. Dorsal margin straight, occupying nearly half the shell length.

Anterior ear small and pointed, limited from main body by shallow sulcus. Posterior wing large, obtuse, its posterior margin being slightly concave.

Two well-rounded carinae extend from umbo to postero-ventral corner of shell on both valves. More ventrally placed carina slightly stronger and coinciding with maximum inflation of shell; more dorsally placed carina clearly separates main body of shell from posterior wing. Shallow sulcus present between the two carinae. Carinae developed as shell thickenings and only weakly preserved in internal moulds.

Ligament multivincular. Ligamental area exhibits at least five ligamental pits. Interspaces between them are narrower than pits in anterior half of ligamental area; in posterior direction interspaces increase in width and finally became wider than pits. Hinge poorly known; internal mould of a left valve (Text-fig. 4D) exhibits elongated groove, which is impression of one posterior tooth. Posterior tooth starts below the third ligamental pit and is orientated slightly oblique to dorsal margin.

Outer surface of shell covered by conspicuous growth lines, which bend abruptly when meeting carinae.

Remarks. Within the Bakevelliidae, the presence of one or two carinae is confined to only a few species (*Gervillaria pallas*, *Gervillella araucana* and *Gervillella leesi* sp. nov.), which today are found along the western margin of North and South America. In contrast to *G. leesi*, *G. pallas* is strongly inequivalved and twisted, less elongated, and exhibits a pointed posterior wing. Similarly, *Gervillella araucana* can be separated from *G. leesi* by being inequivalved and twisted. Moreover, it carries only one carina on the left valve and is more strongly elongated.

Gervillella araucana Damborenea, 1987

Text-figures 4F–G, 5C

*1987 *Gervillella araucana* Damborenea, p. 133, pl. 1, figs 6–10, text-fig. 6.
v1994 *Gervillella araucana* Damborenea 1987; Aberhan, p. 18, pl. 3, figs 8–10.
v1995 *Gervillella araucana* Damborenea 1987; Muster, p. 61, pl. 12, figs 3–4.

Material. Three left valves from GSC loc. 85335; two left valves (GSC 112325 and GSC 112326) from GSC loc. 88495. Specimens are preserved as internal moulds. For locality information see Appendix.

Occurrence. All records are from Stikinia; associated ammonites indicate a Late Sinemurian age.

Description. The left valves are very elongated and twisted in an anti-clockwise direction in posterior view. The anterior auricle is well developed and is separated from the main shell by a shallow sulcus. The posterior wing is narrow and obtuse. It is delimited from the main shell by a carina which extends from the umbo to the postero-ventral corner and which is followed ventrally by a shallow sulcus. An internal mould of a left valve (Text-figs 4G, 5C) shows the impression of a short anterior tooth and an elongated posterior tooth, both pointing downwards in a posterior direction.

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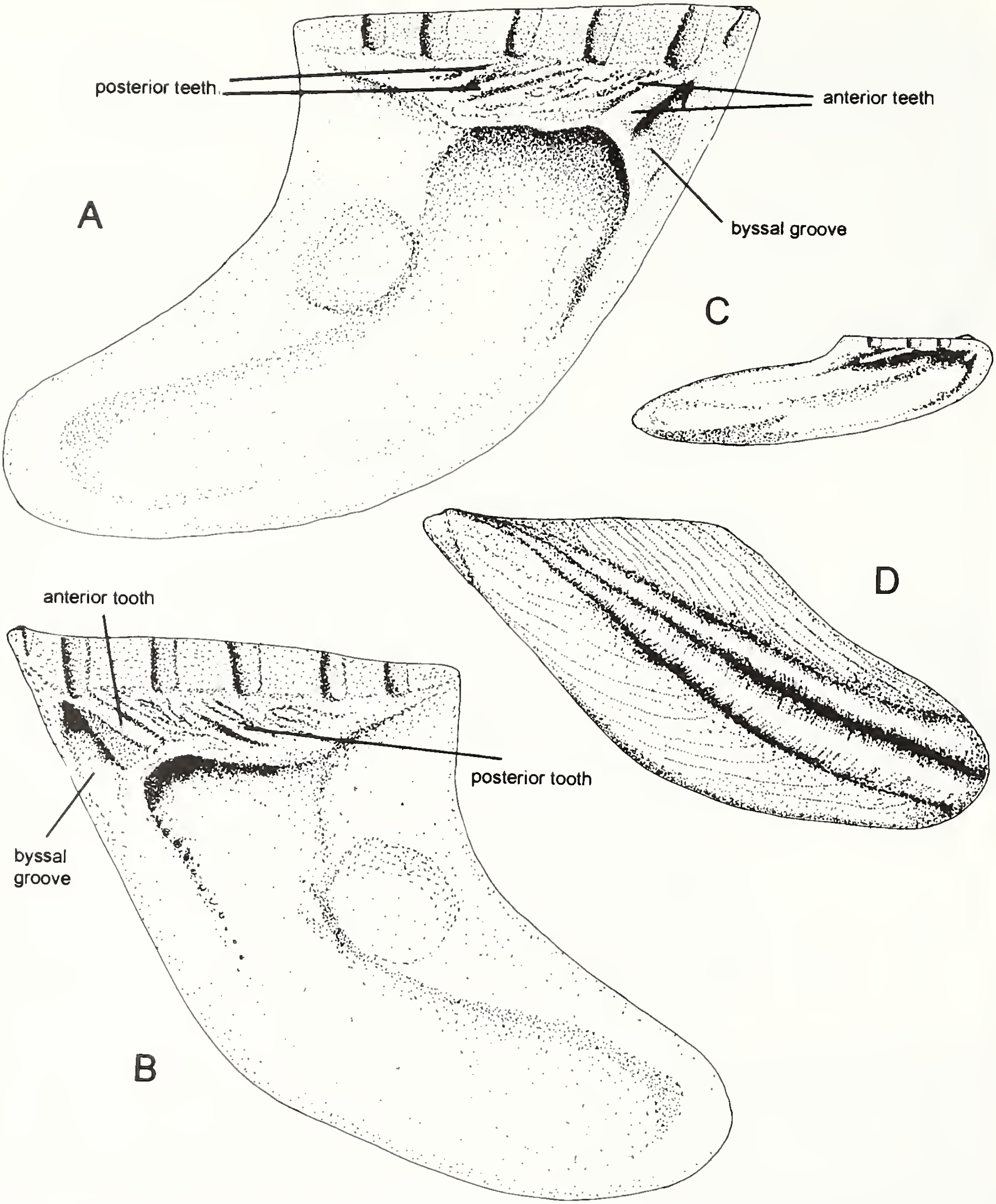
view of left valve; upper Sinemurian, Telkwa Mountains, British Columbia. All × 1. F–G, *Gervillella araucana* Damborenea, 1987; GSC loc. 88495; Upper Sinemurian, Babine Lake, British Columbia. F, GSC 112325; internal mould of left valve. G, GSC 112326; internal mould of left valve. Both × 1·5.



TEXT-FIG. 5. Reconstructions of Jurassic bakevelliid bivalves from western Canada. A–B, *Gervillaria ashcroftensis* (Crickmay, 1930). A, interior view of left valve. B, interior view of right valve. C, *Gervillella araucana* Damborenea, 1987; interior view of left valve. D, *Gervillella leesi* sp. nov.; exterior view of left valve.

Remarks. Gervillella araucana is well known from the Lower Jurassic of South America (e.g. Damborenea 1987; Aberhan 1994) and the studied Canadian specimens cannot be distinguished from South American material.

Gervillella araucana can be separated from all other *Gervillella* by the presence of a single carina, which is only developed on the left valve.

FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

As the youngest known bakevelliid bivalves are of Late Cretaceous age, a direct ecological comparison of fossil with Recent forms is not possible. However, the five species described above exhibit distinct shell features, which allow interpretation of their mode of life from a functional analysis of their morphology. Although this approach might lead to an erroneous interpretation of the autecology of some species, as a rule the results are fairly reliable (e.g. Fürsich 1980). The criteria applied to distinguish between endobyssate and epibyssate life styles as well as orthothetic (oriented with the commissural plane vertically) and pleurothetic (reclining on one side) shell orientations are basically those used by Stanley (1972) and Seilacher (1984).

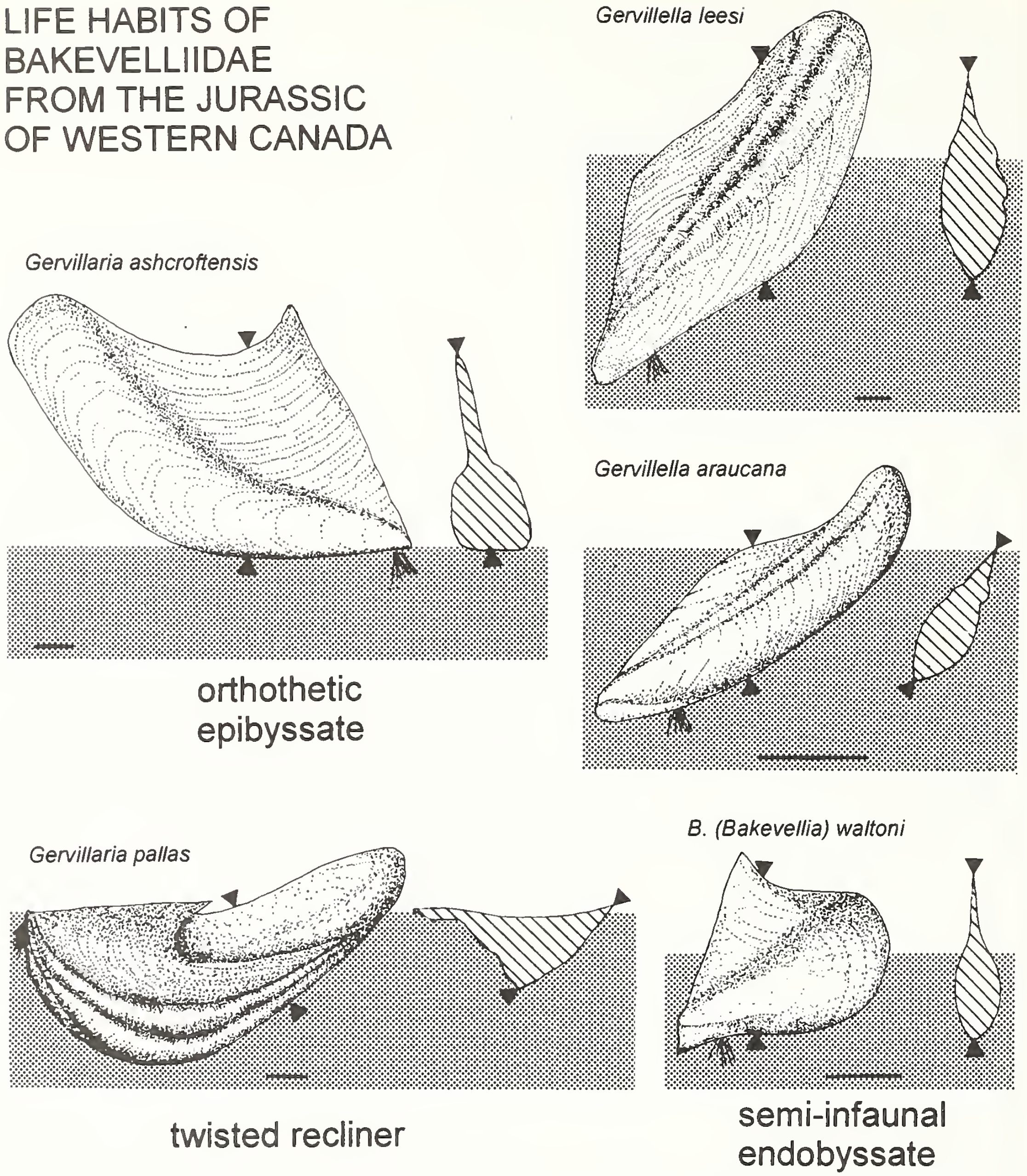
The inferred life habits of Early Jurassic bakevelliids from western Canada are illustrated in Text-figure 6. *Bakevellia* (*Bakevellia*) *waltoni* is reconstructed in a semi-infaunal, endobyssate living position with the sagittal plane more or less vertical as is typical for most known species of *Bakevellia*. This interpretation is based on the nearly equivalved condition, the presence of an anterior auricle, and the absence of appreciable flattening of the ventral margin as well as lack of extensive shell thickening.

A similar endobyssate mode of life can be inferred for *Gervillella leesi*. In addition to the morphological criteria just mentioned, *G. leesi* exhibits a relatively elongate, retrocrescent shell form, which suggests that the species was buried more deeply.

In contrast, *Gervillaria pallas* corresponds well to the paradigm of a twisted recliner (see also McGhee 1978; Savazzi 1981; Damborenea 1987). A highly inequivalved shell and differential thickening of the cup-shaped lower valve in the umbonal region suggest that stabilization in relatively soft substrates was maintained by shape and weight. Adhesion to the sediment was probably increased by the presence of a pair of carinae on the left valve. Furthermore, the large, strongly pointed posterior wing substantially extended the left valve area, which was in contact with the sediment. Due to the strong torsion of the shell, the postero-ventral end emerged above the substrate forming a low angle with the sediment-water interface. Although there is no evidence of a byssal gape, a weak byssus, emerging between the valves at the anterior margin, might have added to the stabilization of the shell.

In terms of morphological characters, *Gervillella araucana* occupies an intermediate position between *Gervillella leesi* and *Gervillaria pallas*. Its elongate form, presence of a well-developed, lobate anterior auricle and lack of ventral flattening suggest a semi-infaunal, endobyssate life position. A weak byssus probably emerged in the antero-ventral region, where the anterior auricle is separated from the main body of the shell by a shallow sulcus on the left valve. Shell torsion and reduction in the convexity of the right valve were probably associated with a slight inclination of the commissural plane towards the left and a shallower position of the shell in the sediment than in *G. leesi*. Again, the presence of a posterior carina in the left valve may have helped to stabilize the shell.

Whilst the species discussed above were either adapted to a semi-infaunal or a reclining mode of life, equipped with an, at best, weakly developed byssus, *Gervillaria ashcroftensis* displays morphological adaptations, which are characteristic of an epibyssate mode of life, with a nearly vertical position of the sagittal plane. These adaptations include (1) the nearly equivalved condition of the shell; (2) a marked thickening of the shell in the umbonal and hinge region of both valves; (3) the presence of a very minute anterior auricle and therefore almost terminal beaks; and (4) antero-ventral flattening of both valves, which lowers the centre of gravity and provides a broad surface for epifaunal fixation. To our knowledge, *G. ashcroftensis* is the only species of the family Bakevelliidae which, presumably, was orthothetically attached to firm and stable substrates with a byssus and the ventral margin resting on the substrate. Therefore, the bakevelliid lineage appears



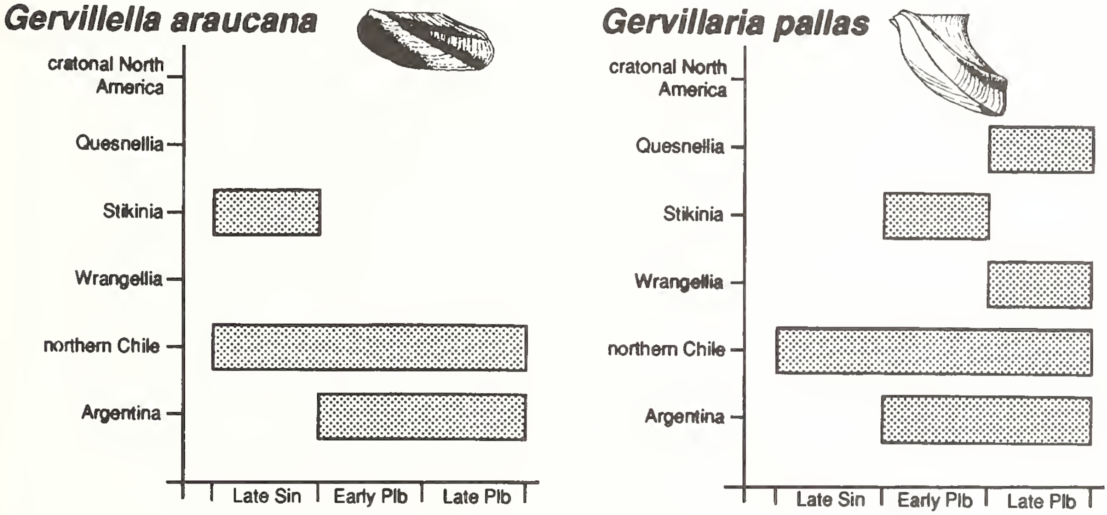
TEXT-FIG. 6. Life habits of bakevelliid bivalves from the Jurassic of the western Canadian Cordillera. Represented are three semi-infaunal, endobyssate sediment stickers, one orthothetically attached, epibyssate form, and one twisted recliner. Reconstructions of life habits are based on an analysis of functional morphology. Scale bars represent 10 mm. For explanations see text.

to be another example in which early forms were endobyssate and epibyssate habits, including that of the pendent *Gervillia*, arose later in phylogeny. This well established evolutionary trend has been documented primarily in Palaeozoic bivalves (Stanley 1972; see also Seilacher 1984).

PALAEOBIOGEOGRAPHICAL AFFINITIES

Distribution of Early Jurassic bakevelliids

The biogeographical distribution of fossil taxa is often plotted on palaeogeographical maps. As the history of the western North American terranes is still debated, however, we refrained from this kind of graphical representation. On the other hand, to plot data points on a present-day geographical map provides a more objective and geologically neutral frame of reference, but fails to illustrate the actual spatial relationships between different areas for various time periods. In the following, we prefer therefore to comment briefly on the spatial distribution of Early Jurassic bakevelliids. In addition, we illustrate area-time charts for two biogeographically interesting species (Text-fig. 7).



TEXT-FIG. 7. Temporal distribution of two conspicuous Early Jurassic bakevelliid bivalves along the eastern Pacific margin. Sin, Sinemurian; Plb, Pliensbachian. Note the faunal similarity between South America and western Canadian allochthonous terranes and the absence of bakevelliids from cratonal North America.

Bakevellia. On a global scale, two species of *Bakevellia* have been recognized from the Lower Jurassic: *B.* (*B.*) *waltoni* (Lycett) and *B.* (*B.*) *binneyi* (Brown). Both occur in mid palaeolatitudes in sediments ranging from fine- to coarse-grained siliciclastics to carbonates. The former appears to have been more widespread, with records from central Europe, Japan, western South America and western Canada (Stikinia). *B.* (*B.*) *binneyi* has been reported only from central Europe and Japan (e.g. Muster 1995).

Gervillaria. Of the five species of *Gervillaria* recognized by Muster (1995) four are known from the Lower Jurassic. *G. ashcroftensis* is reported from the Pliensbachian and Toarcian of northern Chile (Aberhan 1994) and occurs later in the Bajocian of British Columbia, Canada (Crickmay 1930). Similarly, *G. pallas* appears to be restricted to the eastern Pacific margin (Text-fig. 7) being recorded from the Sinemurian and Pliensbachian of northern Chile (Aberhan 1994), the Pliensbachian of Argentina (Damborenea 1987) and from the Pliensbachian of western Canada (Quesnellia, Stikinia and Wrangellia). Both occur in more or less calcareous siltstones, fine- to medium-grained sandstones, and mud- to wackestones. Two further species, *G. alaeformis* (J. Sowerby) and *G. hartmanni* (Münster) have been documented from central Europe and northern Chile, the former also from Japan (e.g. Aberhan 1994; Muster 1995). Again, both species occur in a wide range of sedimentary rocks including shales, marls, sandstones, and wacke- to packstones.

Gervillella. Another bakevelliid, which currently is known only from regions along the eastern Pacific margin, is *Gervillella araucana*. In South America (Argentina, northern Chile) it is represented in rocks of Sinemurian to Pliensbachian age (Damborenea 1987; Aberhan 1994). In the Stikinia terrane of western Canada, *G. araucana* is known from the Sinemurian (Text-fig. 7). The preferred substrates of *G. araucana* were silts to fine-grained sands and what are now packstones. *Gervillella leesi* from the Hettangian of Tyaughton Creek and the Sinemurian of Stikinia appears to be endemic to western Canada, where it is preserved in more or less calcareous siltstones to coarse-grained sandstones. Two further species of *Gervillella*, *G. aviculoides* (J. Sowerby) and *G. lanceolata* (Müster) are confined to the Lower Jurassic of central Europe.

Aguilerella *and* Gervillia. Early Jurassic representatives of *Aguilerella* and *Gervillia* appear to be absent from western Canada and have relatively restricted distributions elsewhere (see Muster 1995). The Late Sinemurian or Pliensbachian specimens from north-western Canada figured as *Aguilerella* sp. by Poulton (1991, pl. 9, figs 1–4, 10–11) are too poorly preserved to allow identification at the generic level.

Andean affinities

According to their palaeogeographical distribution, the five western Canadian bakevelliid species described above can be assigned to one of the following categories: (1) cosmopolitan (*B.* (*Bakevellia*) *waltoni*); (2) endemic to western Canada (*Gervillella leesi*); and (3) restricted to the eastern Pacific margin (*Gervillaria ashcroftensis*, *Gervillaria pallas*, *Gervillella araucana*). Taxa unique to a single sample area and those with a cosmopolitan distribution do not add any information with regard to areal relationships and are not considered further. This also applies to *G. ashcroftensis*, which seems to have been confined to northern Chile during the Early Jurassic. In contrast, *G. araucana* and *G. pallas* are more widely distributed, occurring in several areas along the eastern Pacific margin (Text-fig. 7).

Clearly, our data set is too small to test seriously different terrane reconstructions, but it is interesting to see how it matches with existing models. For this purpose it is necessary to compare the terrane fauna with that from regions with a fixed position relative to the allochthonous terranes. Such areas are the stable craton of western North America ranging from the north-western margin of the Canadian Arctic Islands, northern and eastern Yukon, through the Fernie Basin of north-eastern British Columbia and south-western Alberta, and finally into the United States (e.g. the Sonomia terrane in Nevada, which had accreted to the continent by the Triassic). In the southern hemisphere, Chile and Argentina may serve as stable reference areas for the Early Jurassic.

The distributions of ammonoids (Smith and Tipper 1986) and of the pectinid bivalve genus *Weyla* (Damborenea and Manceñido 1979; pers. obs.) both indicate that the terranes Wrangellia, Stikinia and Quesnellia were in the eastern rather than the western Pacific during the Early Jurassic. This is consistent with the distribution pattern of bakevelliids. Besides their occurrence on the terranes, both *G. araucana* and *G. pallas* were found only in autochthonous western South America (Text-fig. 7). This clearly indicates eastern Pacific affinities and seems to support the idea of a West American bivalve province during the Early Jurassic as postulated by Hallam (1977). Smith and Tipper (1986) also suggested that the terranes were in the northern hemisphere by the Pliensbachian. If correct, we would expect higher similarities in the bivalve fauna of the terranes to those of cratonal North America rather than to those of South America. However, there is not one unambiguous record of an Early Jurassic bakevelliid from the North America craton (pers. obs.; see also Smith *et al.* (1994) for a compilation of illustrated Lower Jurassic bivalves from North America). In part, lack of suitable facies may account for this pattern. Although bakevelliids generally occur in a wide range of different substrates (see above), the Early Jurassic black shales and dark-coloured calcareous mudstones of the Fernie Basin suggest unfavourable, oxygen-poor benthic environments. Moreover, the Early Jurassic bivalve fauna of the Western Interior of the USA is sparsely documented and the apparent lack of bakevelliids may be due to collection failure. Alternatively, the Late Sinemurian to Late Pliensbachian distributional pattern of bakevelliids is also consistent with a position of the terranes closer to the South American Andes, possibly even in the southern hemisphere.

Other bivalves which appear to be restricted to western South America (Chile, Argentina) and the terranes Wrangellia, Stikina and Quesnellia during the Early Jurassic are found, for example, among the pectinaceans. The Hettangian through Toarcian genus *Weyla* is by far the most abundant element in these regions, in terms both of number of individuals and especially, biomass. At least four species of *Weyla* appear to be restricted to these two regions. A detailed biogeographical analysis of Early Jurassic pectinoid bivalves along the eastern Pacific margin is being prepared by one of us (MA) and will provide further clues as to the palaeogeographical history of western Canadian terranes.

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APPENDIX

List of GSC fossil localities in the Canadian Cordillera yielding bakevelliid bivalves. Details include, where available, collector; year; field number; name and short description of locality; NTS: 50000 scale topographical map reference number (with name of 1:250000 scale map sheet in brackets); latitude; longitude; terrane; and age. All collections are deposited in the Geological Survey of Canada.

GSC locality 10246. E. J. Lees; 1930; Laberge area; NTS 105 E(Laberge); Stikinia; (?) Sinemurian.

GSC locality 14333. C. S. Lord; 1945; FT28d; 3·3 km south of Dewar Peak; NTS 94 D(McConnell Creek); Stikinia; Pliensbachian.

GSC locality 19365. J. A. Jeletzky; 1950; Seal Point; NTS 92 E(Nootka Sound); Wrangellia; Late Pliensbachian.

GSC locality 19373. J. A. Jeletzky; 1950; 116/6; Liver Point; NTS 92 E(Nootka Sound); Wrangellia; Late Pliensbachian.

GSC locality 19374. J. A. Jeletzky; 1950; 100/36; Seal Point; NTS 92 E(Nootka Sound); Wrangellia; Pliensbachian.

GSC locality 19376. J. A. Jeletzky; 1950; 115/7; Liver Point; NTS 92 E(Nootka Sound); Wrangellia; (?) Pliensbachian.

GSC locality 19395. J. A. Jeletzky; 1950; 100/56c; Seal Point; NTS 92 E(Nootka Sound); Wrangellia; Late Pliensbachian.

GSC locality 19397. J. A. Jeletzky; 1950; 122/1; Mushroom Point; NTS 92 E(Nootka Sound); 49° 55′ 30″ N; 127° 12′ 10″ W; Wrangellia; Early Jurassic.

GSC locality 19398. J. A. Jeletzky; 1950; 122/4; Hoadley Point; NTS 92 E(Nootka Sound); Wrangellia; Early Jurassic.

GSC localities 83995 and 83998. H. W. Tipper; 1969; F7TD-1s and F8TD-4s; small island north-east of Showshoe Island on Babine Lake; NTS 93 L(Smithers); 54°54′45″ N; 126°10′05″ W; Stikinia; Late Sinemurian.

GSC locality 84187. H. W. Tipper; 1969; F19TD-6; Hunter Basin, between Webster and Goathorn creeks, Telkwa Mountains; NTS 93 L(Smithers); 54°31′ N; 127°05′ W; probably Late Sinemurian.

GSC locality 85333. H. W. Tipper per R. Park; 1970; J6-17-HF; south-west end of Sterret Island on Babine Lake; NTS 93 L(Smithers); 54°55′ N; 126°11′ W; Stikinia; probably Early Pliensbachian.

GSC locality 85335. H. W. Tipper per R. Park; 1970; 20-70P-2F-TD; tiny island south of south-west end of Sterret Island on Babine Lake; NTS 93 L(Smithers); 54°55′ N; 126°10′ W; Stikinia; Late Sinemurian.

GSC locality 88495. T. P. Poulton; 1971; PU-24-71-2F; small island south of Sterrett Island on Babine Lake; NTS 93 L(Smithers); 54°54′ N; 125°10′18″ W; Stikinia; Late Sinemurian.

GSC locality 88602. T. P. Poulton; 1971; PU-40-71-27F; head of Houston Tommy Creek, Telkwa Mountains; NTS 93 L(Smithers); Stikinia; Late Sinemurian.

GSC locality 88604. T. P. Poulton; 1971; PU-43-71-1F; Telkwa Mountains; NTS 93 L(Smithers); Stikinia; probably Late Sinemurian.

GSC localities 93327 and 93328. H. W. Tipper; 1975; F5T-13TD-75 and F14-13TD-75; Dewar Peak; 56°42′30″ N; 126°47′ W; NTS 94 D(McConnell Creek); Stikinia; Early Pliensbachian.

GSC locality 94993. H. W. Tipper; 1977; F8-6TD-77; 20 km south-east of Turnagain Lake; NTS 104 I(Cry Lake); 58°9′ N; 128°58′30″ W; Stikinia; Late Sinemurian.

GSC locality 95015. H. W. Tipper; 1977; F2-17TD-77; 10·5 km west of McBride River; NTS 104 I(Cry Lake); 58°10′ N; 129° W; Stikinia; Sinemurian.

GSC locality C-53514. H. W. Tipper; 1978; 78-TD-ASH-4B; Rattlesnake Hill, north of Ashcroft; NTS 92 I(Ashcroft); 50°46′ N; 121°13′ W; Quesnellia; Late Pliensbachian.

GSC localities C-81309, C-81310, and C-81311. T. P. Poulton; 1979; east of Mandanna Creek; NTS 105 E(Laberge); 61°44′N; 135°41′ W; Stikinia; Sinemurian.

GSC locality C-81317. T. P. Poulton; 1979; east of Mandanna Creek; NTS 105 L(Glenlyon); 62°00′07″ N; 135°48′ W; Stikinia; Sinemurian.

GSC localities C-81322 and C-81323. D. Templemen-Kluit; 1979; east of Mandanna Creek; NTS 105 E(Laberge); 61°44′ N; 135°41′ W; Stikinia; Sinemurian.

GSC locality C-81975. H. W. Tipper; 1979; 79TD-219FA; Joan Lake; NTS 104 H(Spatsizi); 57°29′30″ N; 128°55′00″ W; Stikinia; Early Pliensbachian, Ibex Zone.

GSC locality C-90524. H. W. Tipper; 1981; 81)TD)56)11; south side of Joan Lake anticline, Joan Lake; NTS 104 H(Spatsizi); 57°28′22″ N; 128°56′15″ W; Stikinia; Early Pliensbachian.

GSC locality C-90664. H. Gabrielse; 1981; 81-GA-31-1; 10·5 km north-north-west of headwaters of Conglomerate Creek, Eaglenest Range; NTS 104 H(Spatsizi); 57°29′50″ N; 128°56′ W; Stikinia; Early Pliensbachian.

GSC localities C-90902, C-90903, C-90905, C-90909, C-90924, C-90925, C-90926, C-90928, and C-90930. H. W. Tipper; 1981; 81-TD-5-2a, 81-TD-5-3a, 81-TD-5-3c, 81-TD-52-3A, 81-TD-53-5a, 81-TD-53-4c, 81-TD-53-4B, 81-TD-53-3b, and 81-TD-53-1a; 0·4 km west of Joan Lake camp; NTS 104 H(Spatsizi); 57°29′55″ W; 128°54′12″ W; Stikinia; Early Pliensbchian.

GSC locality C-103198. H. W. Tipper; 1985; 83-TD-39F; south of Nation Peak; NTS 104 H(Spatsizi); 57°37′50″ N; 128°53′30″ W; Stikinia; Early Pliensbachian, Freboldi Zone.

GSC localities C-103305 and C-103307. H. Gabrielse; 1983; 83-GAT-4c and 83-GAT-5b; Joan Lake; NTS 104 H(Spatsizi); 57°29′15″ N; 128°53′20″ W; Stikinia; Early Pliensbachian.

GSC locality C-143287. H. W. Tipper; 1986; 22B-F; south-west of Cardtable Mountain and south of Relay Mountain, Tyaughton Creek; 51°05′14″ N; 122°59′05″ W; NTS 920/2; Tyaughton Terrane; Late Hettangian.

GSC locality C-157663. H. W. Tipper; 1984; 306a; Tyaughton Creek area; NTS 920/2; Tyaughton Terrane; Hettangian.

GSC locality C-186964. C. H. Crickmay; 1926; east slope of Semlin Hill, north of Ashcroft, locality 6 in Crickmay (1930); NTS 92 I(Ashcroft); Quesnellia; Bajocian.

MACHAERIDIANS FROM THE UPPER WENLOCK (SILURIAN) OF GOTLAND

by ANETTE E. S. HÖGSTRÖM

ABSTRACT. Machaeridians, enigmatic animals widespread in Palaeozoic strata, have been known for approximately 130 years but nevertheless remain a little studied and problematical group. Two species of machaeridians (*Lepidocoleus* sp. A and *Turrilepas* sp. A) from the Upper Wenlock of Gotland are described. They occur commonly at Möllbos, with a preservation that allows tentative reconstruction of their morphology and interpretation of the function of the scleritome. The material corroborates the existence of outer sclerites in the Lepidocoleidae and exhibits variability of outer and inner sclerite shape along the body in the Turrilepadidae.

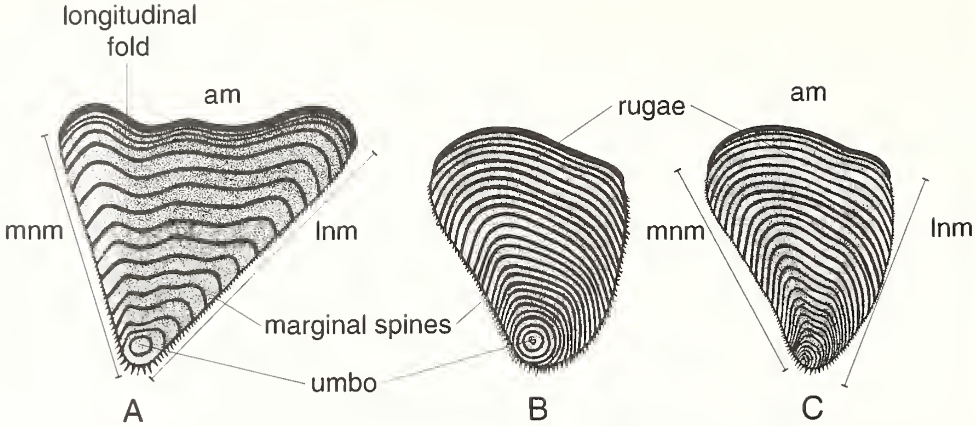
MACHAERIDIANS are a group of problematical, worm-like animals of Palaeozoic age, with an outer skeleton consisting of calcitic sclerites arranged in two or four longitudinal series. The systematics of the group are largely based on T. H. Withers' (1926) monograph of a collection housed mainly in The Natural History Museum. Their phylogeny and affinities are still largely unstudied, but following especially Bengtson (1978), they are considered to be 'metamerically arranged' protostomians with possible close affinities to molluscs, annelids, or arthropods. Recently there has been a renewed interest in the machaeridians, and some important works have been published (Bengtson 1977, 1978; Jell 1979; Dzik 1986; Adrain *et al.* 1991; Adrain 1992).

The Silurian strata of Gotland are comparatively rich in machaeridian skeletal remains, and like many other fossils from this island are often exquisitely preserved. Gotland machaeridians have not been formally described but have been reported quite frequently in the literature (e.g. Aurivillius 1892; Moberg 1914; Hede 1917; Bengtson 1979). A thorough study is thus long overdue. This paper will deal with material from the locality Möllbos 1 in the Upper Wenlock Halla Beds. The purpose is to describe the two most common machaeridians and to introduce some ideas on the appearance and function of their scleritomes. The use of open nomenclature is motivated mainly by the mode of preservation of machaeridians at Möllbos. There is a large amount of isolated sclerites and a number of, often deformed, assemblages. None of these, however, is well suited for the designation of a species, although many previously described taxa have been based on less perfect material.

GEOLOGY

The material is derived from the locality Möllbos 1, representing the middle unit of the Halla Beds, Halla b (Laufeld 1974*a*). The Halla Beds correspond to the Upper Wenlock and consist of thin-bedded strata deposited in shallow water. According to Laufeld (1974*b*), their thickness on Gotland is around 15 m in the north-east (the Hörsne-Gothemshammar area), where three lithostratigraphical units crop out. The lowest unit, a, is 3·5–4 m thick with almost white, oolitic limestone enclosing small bioherms. The middle unit, b, consists of 6–6·5 m of bituminous and argillaceous limestone, also with bioherms. Unit c is the highest and consists of 5 m of argillaceous limestone intercalated with thin laminae of marlstone. This unit is terminated by a discontinuity surface. Towards the south-west the beds decrease in thickness and are replaced by the Mulde Beds of approximately equivalent age.

[Palaeontology, Vol. 40, Part 3, 1997, pp. 817–831, 1 pl.]



TEXT-FIG. 1. Schematic illustrations of the sclerites belonging to *Turrilepas* sp. A. The thick line denotes the accreting margin. A, inner right sclerite with modified apical region. B, modified outer right sclerite. C, unmodified outer right sclerite. *am*, accreting margin; *lnm*, lateral non-accreting margin; *mnm*, medial non-accreting margin. Not to scale.

Möllbos 1 is a low and easily accessible rivulet section, with a lateral extent of around 140 m. The section is located immediately north-west of the dam at the pond. Möllbos 2 is exposed along the same stretch, approximately 150–175 m from the dam.

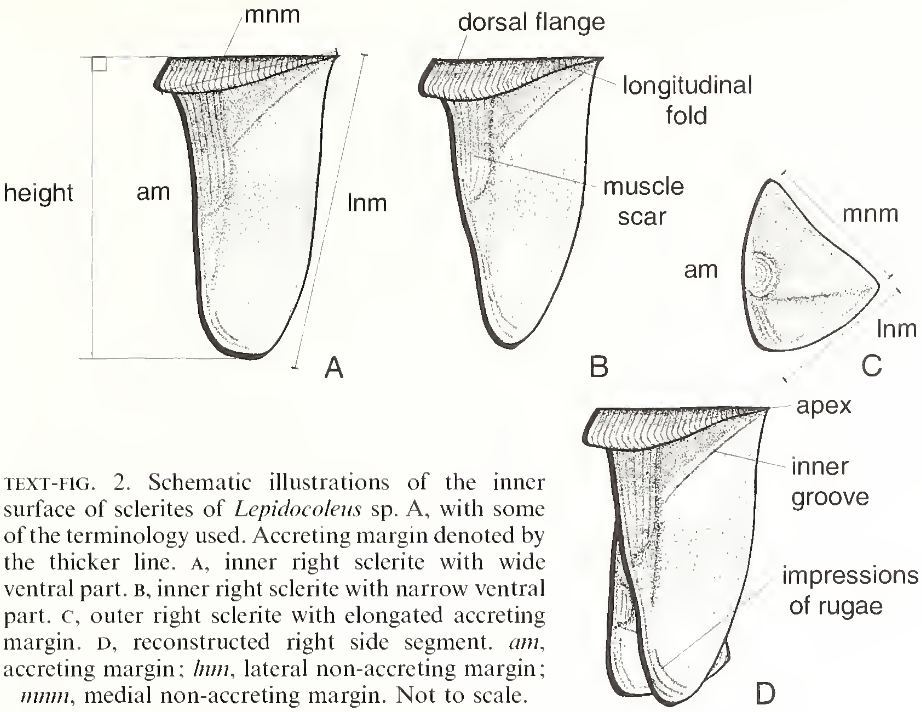
The rocks at Möllbos 1 consist of argillaceous bedded limestone intercalated with thin marly layers; at Möllbos 2 there is a bioherm. Between the bioherm and the bedded deposits there is an area consisting of debris from the bioherm (Hede 1960). This locality has been interpreted as a reef-lagoonal environment (e.g. by Hede 1960). Hede also considered fossils to be scarce at the locality, but subsequent studies on silicified material have shown that the limestone is richly fossiliferous (e.g. Liljedahl 1984, 1985, 1986).

MATERIAL

The material consists of specimens obtained from loose blocks of limestone collected at Möllbos 1, in the summers of 1991 and 1992, and material collected by J. E. Hede in the 1940s, housed in the Department of Historical Geology and Palaeontology, University of Lund. The specimen numbers consist of a prefix followed by a serial number, where PMU stands for the Palaeontological Museum Uppsala University, and LO for the Palaeontological Institute of the University of Lund. Before photography the specimens were lightly dusted with ammonium chloride sublimate.

TERMINOLOGY

The terminology has been adapted from Adrain *et al.* (1991) and Adrain (1992), with a few exceptions. Inner sclerites of the order Turrilepadomorpha are folded at an angle of usually 90°; the fold extends all the way from the accreting margin to the apex. Adrain *et al.* (1991) used the term *longitudinal angle* when referring both to the fold and to the angle of the fold. These will instead be referred to as *longitudinal fold* and *angle of the longitudinal fold*, respectively (see Text-fig. 1). Adrain *et al.* (1991) also used the term *longitudinal angle* when considering outer sclerites in the diagnosis of, e.g. *Turrilepas wrightiana* (de Koninck, 1857); 'length of accreting margin of outer sclerites subequal to length of longitudinal angle of outer sclerites' (Adrain *et al.* 1991, p. 644). Here the usage of *longitudinal fold* is restricted to the inner sclerites. In lepidocoleids the size is given as height of the sclerite and length of the longitudinal fold (Text-fig. 2). The height is measured from the most



TEXT-FIG. 2. Schematic illustrations of the inner surface of sclerites of *Lepidocoleus* sp. A, with some of the terminology used. Accreting margin denoted by the thicker line. A, inner right sclerite with wide ventral part. B, inner right sclerite with narrow ventral part. C, outer right sclerite with elongated accreting margin. D, reconstructed right side segment. *am*, accreting margin; *lnm*, lateral non-accreting margin; *mnm*, medial non-accreting margin. Not to scale.

ventral point to the longitudinal fold, rather than as the length of the accreting margin, since the latter has a somewhat complex morphology in lepidocoleids and is difficult to measure correctly and efficiently. It should also be noted that the term *segment* is used descriptively, without implicit assumptions of the type of metamerism involved.

GENERAL MORPHOLOGY OF SCLERITOMES

Machaeridian scleritomes are of two main kinds, represented by the orders Lepidocoleomorpha and Turrilepadomorpha. The major differences between them lie in the number and arrangement of sclerites and in the presence or absence of a functional dorsal hinge. The universally present muscle scars are currently the best known indicators of soft part anatomy. Jell (1979) reported structures interpreted as head palps in *Plumulites richorum* (Jell, 1979) from early Devonian strata in Australia, but Dzik (1986) presented a more plausible interpretation of the structure, suggesting that the anterior end of the animal had been tucked under the rest of the body with the 'palps' then representing apical parts of inner sclerites.

Lepidocoleomorpha

The lepidocoleomorphs have often been called biseriate machaeridians (e.g. Adrain 1992; in the diagnosis of the order Lepidocoleomorpha) since they have been assumed to possess only two series of sclerites. Dzik (1986), however, reported traces of outer sclerites in *Lepidocoleus ketleyanus* (Reed, 1901), and the present material from Gotland shows this feature in at least part of the scleritome. It is not clear, however, how common it is among lepidocoleids. The inner sclerites of a lepidocoleid are dorso-ventrally elongated, with a distinct dorsal flange constituting the hinge (see Text-fig. 3A for cross section of a scleritome). Adrain (1992) described a special kind of hinge structure in some

TEXT-FIG. 3. Schematic cross sections of the three types of machaeridians discussed in the text. A, species of Lepidocoleidae with outer sclerites, e.g. *Lepidocoleus* sp. A. B, Turrilepadidae. C, Plumulitidae. Not to scale.

lepidocoleids, which he called *tongue-and-groove hinge* (see especially Adrain 1992, fig. 5). This hinge was considered to be a general feature of lepidocoleids, but, as the material from Möllbos shows, there are species without such a structure (they have only relatively large overlapping dorsal flanges). Lepidocoleids are currently the only machaeridians known with a functional hinge. Lepidocoleid scleritomes can be quite long; e.g., *L. ketleyanus* has a minimum of 60 segments. At present there are several types of lepidocoleids classified together, but the resolution of the taxonomic problems lies beyond the scope of this paper.

Turrilepadomorpha

This order includes the quadriseriate machaeridians as traditionally understood. The two families Turrilepadidae and Plumulitidae are separated on the basis of different sclerite arrangement (Jell 1979). Both families have inner sclerites with a distinct longitudinal fold; in at least the turrilepadids there are two morphologies of the inner sclerites. The medial part of one side (usually the left) is larger than the corresponding medial part on the other (usually the right) side (Adrain *et al.* 1991). Outer sclerites, however, are nearly perfect mirror images of each other and are essentially flat. There is a distinct anterior region in both families, with the outer sclerites of the first two segments absent (Adrain 1992). Some have modified outer sclerites in the following two or three segments; until now this feature has only been described in plumulitids (e.g. Barrande 1872; Jell 1979), but turrilepadids from Möllbos exhibit the same kind of modification of outer sclerites (Pl. 1, fig. 8). Turrilepadids have a more-or-less square body cross section resulting from the 90° angle of the longitudinal fold (Text-fig. 3B), except in the anterior region where the fold is only slightly expressed, resulting in a flatter appearance. By segment 5 or 6 the angle of the longitudinal fold is fully expressed (Adrain *et al.* 1991).

In plumulitids the angle of the longitudinal fold is less acute than in turrilepadids, approximately 150° or larger, resulting in a broad ventral body surface and a triangular rather than square body cross section (Text-fig. 3C). Jell (1979, fig. 3c) revised Withers' (1926) erroneous cross section of a plumulitid, but Jell probably separated the sclerites excessively. The sclerites had to overlap if they were to form a total cover of the dorsal side. Plumulitid outer sclerites are considerably larger than their inner ones; in turrilepadids the inner sclerites are somewhat larger.

Preservation

The preservation of machaeridians at Möllbos is commonly very good, but they are usually not silicified as, for example, the bivalves are. Lepidocoleids make up around 80 per cent. of the machaeridians at Möllbos. Most machaeridians at Möllbos are preserved as isolated sclerites, but the locality is also rich in assemblages, especially of lepidocoleids. The higher number of preserved lepidocoleid assemblages is presumably due to their dominance in the fauna and to their ability to close their scleritome fully. There is a difference in the preservation of isolated sclerites on rock surfaces: lepidocoleids almost exclusively expose the inner surface, whereas turrilepadids expose the outer one. This appears to be due to a very thin innermost layer on lepidocoleid sclerites, along which the rock is easily parted. The nature of this layer is currently unknown. When the layer is flaked off, the granulated inner surface appears more distinct than in sclerites with the layer preserved. Turrilepadids from this locality do not appear to possess any such layer, and their granulated inner surfaces tend to adhere to the rock.

SYSTEMATIC PALAEONTOLOGY

Class MACHAERIDIA Withers, 1926
Order LEPIDOCOLEOMORPHA Schallreuter, 1985
Family LEPIDOCOLEIDAE Clarke, 1896

Genus LEPIDOCOLEUS Faber, 1886

Lepidocoleus sp. A

Text-figure 4A–I

Material. Illustrated specimens: LO 7368t, LO 7369t, LO 7365t, LO 7366t, LO 7367t, PMU G1017, PMU G1018, PMU G1019; additional material consisting of seven more-or-less complete assemblages, and approximately 126 isolated, complete or fragmented sclerites.

Description. Inner sclerites usually large and robust, dorsoventrally elongated; all sclerites with ventral part slightly narrower than dorsal one, but some are very much narrower, down to one-third of the length of the longitudinal fold (Text-fig. 4C). Most sclerites have a height of around 5 mm and a length of the longitudinal fold of approximately 2·5–3 mm, but large specimens with a height of 7·5–8 mm are known. Inner surface granulated, with a large, elongated muscle scar, usually around 40–60 per cent. of the height of the sclerite, situated close to the dorsal flange and to the accreting margin of the sclerites (Text-fig. 4A, F). Impressions of the rugae are seen on the inner surfaces on most sclerites; they are often distinct, especially in the muscle scar. Inner groove also distinct, running between apex and muscle scar (as in Text-fig. 4F). Outer surface usually adheres to rock; the rugae are very fine and almost indiscernible, density approximately 5–7 per mm (see Text-fig. 5 for reconstruction of the pattern of rugae). Density of rugae is slightly higher close to the accreting margin and especially in the dorso-ventral direction. Small apical spines are present, but no traces of marginal spines. Dorsal flanges largest anteriorly, but without any tongue and groove-hinge structures as described by Adrain (1992, fig. 5).

Outer sclerites have a roughly triangular outline and are essentially flat (although the largest ones are slightly curved in cross section, in order to fit closely alongside the inner sclerites). Accreting margin very often elongated (Text-fig. 4G), around 3·5–4·5 mm long; lateral non-accreting margin around 4 mm, and medial non-accreting margin 4–5 mm. Inner surface similar to that of inner sclerites except that the muscle scar is smaller and more rounded (Text-fig. 4G–I). Inner groove distinct and running between the ventral part of the muscle scar and the apex (Text-fig. 4G–I). Outer surface not well exposed in the material and therefore the density of rugae can only be estimated approximately, around 5 per mm, very fine as on the inner sclerites (see Text-fig. 5 for reconstruction). Possibly the rugae are also more closely spaced near the accreting margin in the outer sclerites. Outer sclerites show no traces of any apical or marginal spines. Differences in general outline between the outer sclerites may depend on their placement within the scleritome (Text-fig. 4G–I). Total number of isolated outer sclerites recovered from the locality is lower than the number of isolated inner ones, approximately 47 per cent. of 126 sclerites (material too badly preserved for identification has been excluded).

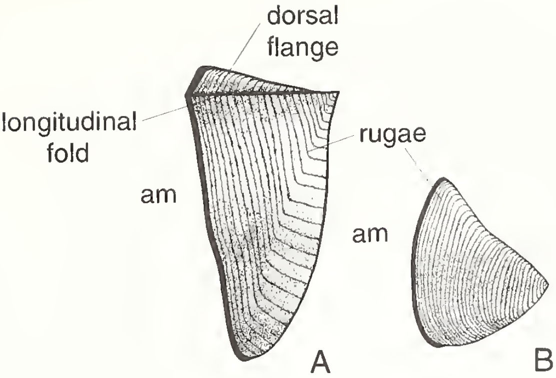
Specimen LO 7368t (Text-fig. 4C–D) partly exposes a cross section, presumably from somewhere along the undifferentiated mid-part of a scleritome. The specimen may be divided roughly into two parts: a posterior part projecting into the rock, only partially exposed, and an anterior part that has been compressed in longitudinal direction so that the segments lie partly on top of one another; hence the estimate of number of segments is slightly uncertain. Approximately 11 or 12 segments are visible in the anterior part but some are badly preserved and exposed. The first seven segments only have left sclerites preserved, exposing their inner surfaces. Best exposed here is sclerite 6, which is a partially complete inner sclerite exhibiting a prominent muscle scar and a narrow ventral part (right arrow, Text-fig. 4C). The following segments, 8–12, have both left and right sides poorly preserved. The most posterior sclerite is the impression of an outer right one (left arrow, Text-fig. 4C) with the muscle scar exposed as a rounded elevation on the surface. A cross section of the assemblage is

TEXT-FIG. 4. *Lepidocoleus* sp. A; Möllbos 1, Halla Beds, Gotland, Upper Wenlock, Silurian, A, LO 7365t; detail of the assemblage; ×4. B, LO 7369t; general view, note outer sclerites (arrows); ×4. C–D, LO 7368t. C, general view of the assemblage; ×5. D, cross sectional view; ×5. E, LO 7366t; inner surface of one right side segment; ×6·5. F, LO 7367t; inner surface of an inner right sclerite; ×5. G, PMU G1019; inner surface of an outer left sclerite; ×8. H, PMU G1017; inner surface of an outer right sclerite; ×6·5. I, PMU G1018; inner surface of an outer right sclerite; note differences in outline from PMU G1019 and PMU G1017; ×6·5.

figured in Text-figure 4D. The right side has slipped dorsally, thus the width of the cross section is narrower than the width of the original scleritome.

Specimen LO 7369t (Text-fig. 4B) derives also from the undifferentiated part of a scleritome. The estimated number of preserved segments is nine or ten. In the anterior portion of the assemblage only displaced and fragmented right sclerites, exposing inner surfaces, are preserved. There are prominent muscle scars exposed in three of them. At least one of the sclerites is an outer one with a more rounded muscle scar, an elongated accreting margin and inner groove (Text-fig. 4B, left arrow). The left side is preserved in the posterior part of the assemblage, where the best exposure of outer surfaces is found. The first segment on the posterior part

TEXT-FIG. 5. Reconstruction of the outer surfaces of sclerites of *Lepidocoleus* sp. A. Thick line denotes the accreting margin. A, inner left sclerite. B, outer left sclerite. *am*, accreting margin. Not to scale.



exposes a complete impression of a large outer sclerite with elongated accreting margin, muscle scar and an inner groove (Text-fig. 4B, central arrow). Beneath this impression the outer surface of an inner sclerite is distinguishable. The following four segments are partly exposed and the spatial relationship between them appears to have been subject to relatively little distortion. Traces of probable outer sclerites are detectable between the inner sclerites (Text-fig. 4B, right arrows).

LO 7365t (Text-fig. 4A) is the largest specimen. Distortion of the assemblage has been quite considerable, producing a splayed-out configuration of the sclerites. The figured part of the assemblage exhibits mostly sclerites from the right side. All but two are nearly completely buried in sediment. These two visible sclerites (Text-fig. 4A, arrows) are one outer and one inner sclerite. The outer sclerite (left arrow) has a distinct muscle scar and an elongated accreting margin; the apical region, however, is not exposed. The inner one (right arrow), situated about two segments posterior to the outer sclerite, is complete except for the lost dorsal flange; a distinct muscle scar and inner groove are clearly exposed. Both sclerites have remains of the thin innermost layer preserved along their non-accreting margins. Posterior to the described inner sclerite, there are two impressions of large, outer left sclerites which have been twisted considerably out of place, so as to attain a reverse orientation in relation to the right-hand sclerites. They expose prominent, rounded muscle scars, inner grooves and elongated accreting margins. Most of the surfaces are covered with the thin innermost layer. The most posterior part (unfigured) of the assemblage has been severely affected by distortion and consists of various fragmented inner and outer sclerites.

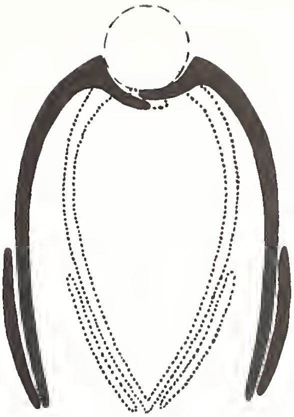
Specimen LO 7366t (Text-fig. 4E) is a small portion of an assemblage. The sclerites of the right side of five segments are preserved. They are compacted on top of each other, resulting in a minimum exposure of all but one segment. The dorsal flanges of all the inner sclerites are broken off. Best exposed is the inner surface of the most posterior segment (Text-fig. 4E). The inner sclerite is broken immediately dorsal and ventral of the muscle scar, thus exposing the outer sclerite beneath it. The inner sclerite shows the muscle scar and the inner groove. Remains of the thin innermost layer are preserved along the lateral non-accreting margin of the sclerite. A set of wrinkles is visible adjacent to the lateral non-accreting margin, oriented roughly in an apical direction. The function of these wrinkles is at present unknown. The outer sclerite is not completely exposed; the muscle scar and dorsalmost parts are concealed beneath the inner sclerite. Clearly visible, though, is the inner groove and quite large portions of the thin innermost layer preserved along the margins. As with the other described assemblages, the outer sclerites are large. The spatial relationship between the sclerites in the specimen is not entirely undisturbed. The specimen has been compacted, and the sclerites seem to have been slightly twisted in relation to each other, thus hiding the muscle scar of the outer sclerite beneath the inner sclerite.

Specimen LO 7367t (Text-fig. 4F) is a separate inner sclerite, and specimens PMU G1017, PMU G1018, and PMU G1019 (Text-fig. 4G–I) are separate outer sclerites.

Reconstruction. The reconstruction proposed here is based on the present material from Möllbos and comparisons with, especially, *L. ketleyanus*. Described specimens LO 7368t, LO 7369t, LO 7365t, and LO 7366t were particularly useful.

Lepidocoleus sp. A has a total length of at least 20–25 segments, and it is only the second known lepidocoleid with outer sclerites. Dzik (1986) reported small outer sclerites in *L. ketleyanus*, but it is not clear whether he considered them to exist throughout the entire scleritome. Neither of the two above species has the anterior end preserved; the posterior end, however, is partly preserved in the large specimen of *L. ketleyanus* from the Much Wenlock Limestone at Dudley, Worcestershire, housed at the Lapworth Museum, Birmingham University (Holcroft Collection, no. 62, figured previously by Withers 1933, pl. 4:4; and Bengtson 1977, fig. 3). In *Lepidocoleus* sp. A the placement of the outer sclerites is uncertain, but comparing the total number of outer and inner sclerites may give some idea of the scleritome organization. The lower number of outer sclerites may be interpreted as a condition where part of the scleritome was composed only of inner sclerites; which part, however, it is not possible to say. There may be a slight taphonomic bias in the count of sclerite types. Outer sclerites were not attached to the soft parts as firmly as inner ones; the muscle was smaller, and the area in contact with soft tissues was also considerably smaller for outer sclerites. Thus the probability for post-mortem dispersal and fragmentation is likely to be somewhat higher for the outer sclerites. This possible difference in preservation may thus affect the number of sclerite types and hence also the reconstruction. Based on comparisons with other machaeridians, it is very probable that the anterior end in *Lepidocoleus* sp. A had modified sclerites. Distinct anterior ends are known from e.g. *Turrilepas wrightiana* (see Adrain *et al.* 1991), *Plumulites richorum* Jell, 1979 and *Lepidocoleus sarlei* Clarke, 1896, i.e. from all three families. The number of segments constituting this anterior end may differ somewhat, and it is not possible to draw any conclusions concerning the number in *Lepidocoleus* sp. A based on the available information. The undifferentiated mid-part section of the scleritome in *Lepidocoleus* sp. A includes *c.* 15–20 segments (a tentative estimate). At least in part of this section, the segments are composed of both inner and outer sclerites. Specimens LO 7368t, LO 7369t, LO 7365t, and LO 7366t have inner and outer sclerites closely associated (Text-fig. 4A–E). The inner ones have a distinctly narrower ventral part (Text-fig. 4A, C), down to one-third of the length of the longitudinal fold. Outer sclerites are large and have an elongated accreting margin. The outer sclerites overlap the inner ones (see especially specimen LO 7366t and LO 7369t where the overlap is clearly exposed, although in LO 7369t only an impression of the outer sclerite is preserved; Text-fig. 4B, E). One segment is reconstructed in Text-figure 2D. The most probable reason for the inner sclerites of *Lepidocoleus* sp. A being narrower in the ventral part is to allow the insertion of the muscle adhering to the outer sclerite. This feature is also of potential value in identifying species where outer sclerites probably were present but are not preserved. The partly preserved posterior end in *L. ketleyanus* shows a continuous decrease in size over several segments (Withers 1933, pl. 4:4; and Bengtson 1977, fig. 3). The posterior structure of *Lepidocoleus* sp. A is probably quite similar. The very last posterior segment is not known. In *L. sarlei* and possibly also in *Lepidocoleus jamesi* (Hall and Whitfield), the pattern of rugae is modified on the minute posteriormost sclerites. The dorsal hinge in *Lepidocoleus* sp. A did not articulate by means of a tongue-and-groove hinge; there are only simple overlapping dorsal flanges. The material does not reveal whether the right side overlaps the left or vice versa. The sclerites do not appear to be enantiomorphic as are those of other lepidocoleids (Adrain 1992). Both sides in *Lepidocoleus* sp. A developed the largest part of the dorsal flange anteriorly, and the continuous hinge appears to be a result of the posterior imbrication of the sclerites. Width of the dorsal depression constituting the hinge is approximately 1–1·5 mm. The resulting cross section of *Lepidocoleus* sp. A is that of a high and narrow scleritome, similar to the cross section of *L. ketleyanus*.

Functional morphology. The cross section of *Lepidocoleus* sp. A resembles that of a bivalve except for the outer sclerites and the hinge structure. Wolburg (1938) reconstructed *Aulakolepos gleidorfense* (Wolburg, 1938) with a ligament positioned in the dorsal depression constituting the hinge, with the assumption that the scleritome functioned more or less like a segmented bivalve. There is no evidence, however, to support the presence of a ligament in the Lepidocoleomorpha. Closing of the lepidocoleid scleritome was presumably accomplished by contraction of the large muscles adhering to the inner sclerites. The opening of the scleritome could not have been accomplished directly by muscle power, as there is no evidence of antagonistic muscles to the ones closing the scleritome. The most probable alternative is the use of hydrostatic pressure. In elongated animals, such as lepidocoleids, a feasible option is the creation of a pressure wave propagating



TEXT-FIG. 6. Schematic cross section of *Lepidocoleus* sp. A illustrating the difference between the closed and the open scleritome. Not to scale.

through the body. Owing to the posterior overlap of the sclerites, the anterior end would be the first part to open.

The overlap of the dorsal flanges would somewhat complicate the process of opening. In bivalves, for example, there is no overlap; the shell halves meet in the hinge. In lepidocoleids the dorsal flanges would have to remain parallel while moving apart in order to achieve a smooth rotation. The movement should follow the outline of an imaginary cylinder placed in the dorsal depression constituting the hinge (Text-fig. 6). A relatively small amount of dorsal rotation (15–20°) will correspond to a ventral opening of approximately 2·5 times wider than the width of the dorsal depression (Text-fig. 6).

The amount of separation of the dorsal flanges is limited by the flexibility of the soft parts and by the apical regions abutting against each other after a certain amount of rotation. The latter may be of importance, especially in lepidocoleids which have a very narrow dorsal depression.

Clark (1964, pp. 31–35) described the general processes for inflation of the body in a simple animal with only circular muscles in the body wall. This, however, is probably not the optimal body organization for lepidocoleids, as the control over smaller parts of the body is low and the result most likely would be a fairly inefficient opening process. Segmentation would give lepidocoleids more possibilities than mere contractions of either end of the body, as it would be possible to employ a small part of the body at a time (Fretter and Graham 1976). This is a controlled and energetically efficient way of opening the scleritome. A drawback is that the maximum pressure in each segment is likely to be low because of the small volume of each segment (Fretter and Graham 1976).

The actual body plan of lepidocoleids (and other machaeridians) is not well understood. The sclerite segments and the muscle arrangement indicates more than a superficial division. Complete transverse coelomic partitions may not be necessary, however, for the opening of the scleritome to function sufficiently well.

Order TURRILEPADOMORPHA Pilsbry, 1916
Family TURRILEPADIDAE Clarke, 1896

Genus TURRILEPAS Woodward, 1865

Turrilepas sp. A

Plate 1, figures 1–8

Material. Illustrated specimens: LO 7371t, LO 7370t, PMU G1020; additional material consisting of three more or less complete assemblages, and approximately 30 isolated, complete or fragmented sclerites.

Description. Large and robust sclerites, inner ones with a length along the longitudinal fold of *c*. 4–5 mm; accreting margin 5–7 mm. Density of rugae approximately 4–5 per mm, total number 18–24. Spacing of the rugae is fairly even over the sclerite surface; there is a tendency for rugae close to the accreting margin to be closer set. The apex (since modified) is also somewhat different from rest. The rugae tend to be quite straight (Pl. 1, figs 2, 5) compared with the more wavy pattern of *T. wrightiana*. Marginal spines number approximately two or three between each ruga; spines larger in apical region than close to the accreting margin (Pl. 1, figs 2, 5). No apical spine on the inner sclerites; instead the umbo is displaced away from the apex producing concentric rugae in the apical region (Pl. 1, figs 3, 5). The rugae are expressed most distinctly when they transect the longitudinal fold and become less distinct on the medial and lateral parts, although the medial part is smoother overall than the lateral one. This apparently corresponds to the pattern of rugae in *T. wrightiana* and *Turrilepas modzalevskae* (Adrain *et al.* 1991). Inflections I_1–I_5 are all present but are not as well expressed as in *T. wrightiana* and *T. modzalevskae*. I_3 is almost indistinguishable, but I_2 and I_4 are also shallower than in *T. wrightiana* and *T. modzalevskae*, resulting in the straight pattern of rugae. Inner surfaces are rarely exposed; where visible the only observed structure is the distinct granulation of the surface.

Outer sclerites occur in two morphologies (Pl. 1, figs 4, 8). The less common form (specimen PMU G1020, Pl. 1, fig. 8, only recovered sclerite of this type) has the umbo placed away from the apex producing distinct concentric rugae in the apical part and also a quite pronounced roundness of the apical region. This is similar to the modified outer sclerites of *Plumulites richorum*, also exhibiting a more rounded shape (Jell 1979). Outer sclerites in *Turrilepas* sp. A usually have a slightly pointed apex but no real apical spine. These sclerites are relatively similar to the outer ones in *T. modzalevskae*. Both *Turrilepas* sp. A and *T. modzalevskae* have shorter accreting margins than *T. wrightiana*, resulting in a more antero-posterior elongated appearance. The size of the modified and unmodified sclerites in *Turrilepas* sp. A is similar; length of medial non-accreting margin 5–7 mm; accreting margin 4–6 mm. The density and total number of rugae differ between the two; modified sclerites have a density of approximately 4–5 per mm (the apex is different because of the modification), total number 20–25; unmodified ones have a density around 5–7 per mm (rugae tend to be closer spaced near the accreting margin), total number 35–45. The density of rugae on the unmodified outer sclerites in *Turrilepas* sp. A is higher than in both *T. wrightiana* and *T. modzalevskae*. Marginal spines approximately four or five between each ruga, larger in the apical region than close to the accreting margin. The rugae on the unmodified sclerites are more distinctly pronounced on the lateral part than on the medial one (Pl. 1, fig. 4). The boundary between the lateral and medial parts appears to correspond to the inner groove of the inner surface. In *T. wrightiana* and *T. modzalevskae* a similar condition seems to exist, although the boundary between the two parts may be situated closer to the lateral non-accreting margin. Inflections of *Turrilepas* sp. A: I_1–I_3 are all quite well defined, I_2 is more distinct than in *T. wrightiana* and seems to correspond to the boundary between lateral and medial parts on these sclerites (Pl. 1, fig. 7). The inner surface is almost never exposed; granulation is virtually the only observed structure on this surface.

Specimen LO 7371t (Pl. 1, figs 1–6) consists of a large portion of an assemblage with the right and left sides exposed, and the dorsal side completely covered by sediment. Mostly outer sclerites are visible, the posterior end is absent and the anterior end appears to have only a few segments missing. The left side of the assemblage (Pl. 1, fig. 1) is *c*. 30–31 mm long, with 21 segments exhibited (numbered from the first one visible). The first segment has only an inner sclerite preserved (Pl. 1, fig. 2). There is no apex preserved and the density of rugae is higher than in the subsequent inner sclerites. The angle of the longitudinal fold is *c*. 120–125° and the sclerite is also smaller than the others (approximately 5 mm, compared with 7–8 mm along the longitudfinal fold). The higher density of rugae, large angle of the longitudinal fold and the smaller size strongly indicates an anterior position in the scleritome. Segment 2 also lacks an outer sclerite and may be similar to segment 1, but this is difficult to judge from the small exposure. Segments 3–7 consist both of outer and inner sclerites, the inner sclerites having a lower density of rugae than the previous ones. Segment 8 has a large inner sclerite with a

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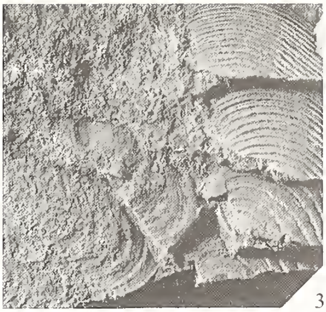
EXPLANATION OF PLATE 1

Figs 1–8. *Turrilepas* sp. A; Möllbos 1, Halla Beds, Gotland, Upper Wenlock, Silurian. 1–6, LO 7371t. 1, general view of the left side; ×3. 2, anteriormost inner left sclerite; ×5. 3, anteriorly placed inner right sclerite with displaced umbo; ×6·5. 4, posteriormost outer right sclerite; ×5. 5, posteriorly placed inner right sclerite with displaced umbo; ×5. 6, general view of the right side; ×3. 7, LO 7370t; impression of an inner right sclerite with displaced umbo and impression of an outer right sclerite; ×4. 8, PMU G1020; right side sclerites, especially outer sclerite with displaced umbo; ×4.

PLATE 1


1


2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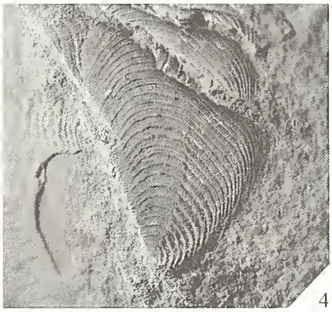
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HÖGSTRÖM, *Turrilepas*

length along the longitudinal fold of at least 7 mm. The rugae are distinctly widely spaced and there are traces of a displaced umbo. Segments 9–20 have only traces or very small parts of the inner sclerites visible. Outer sclerites are present and do not differ much in appearance from each other. The last segment, no. 21, exposes the apical part of an outer sclerite; there is no apical spine present. Marginal spines of the lateral non-accreting margin appear larger and more widely spaced than the spines on the medial non-accreting margin. The right side of the assemblage (Pl. 1, fig. 6) has a length of 29–30 mm, with 21 segments exposed (numbered from the first one visible). Segments 1–2 consist of both inner and outer sclerites, the inner ones are hardly visible and the outer ones are partly broken. Segment 3 exhibits the apical portion of an inner sclerite with displaced umbo (Pl. 1, fig. 3). Widely spaced rugae are also present. The outer sclerite is partly broken, as are the two previous ones. Segments 4–18 are fragmentarily preserved, but still both the inner and outer sclerites are present in all segments and they are apparently uniform. Segment 19 exposes traces of an inner sclerite and a virtually complete outer one (Pl. 1, fig. 4). The apex on the outer sclerite is slightly worn; therefore no spines are preserved there. The marginal spines seem to be larger and fewer on the lateral margin and smaller, more numerous on the medial margin. The pattern of rugae clearly exposes two parts; a lateral part with prominent rugae and a medial part with less prominent rugae. Segment 20 has only the inner sclerite preserved, which has been twisted out of place. This sclerite clearly shows the displaced umbo but has a different pattern of rugae compared with other inner sclerites (Pl. 1, fig. 5). The density of rugae is lower, and the sclerite is also slightly smaller than the other inner ones. The inner sclerite of segment 21 is exposed beneath that of segment 20; it is not entirely complete and it does not correspond in appearance with segment 20 but rather with the rest of the inner sclerites. The outer sclerite of segment 21 has been lost. The left and right sides of the specimen do not match completely in appearance as would be expected in an undisturbed specimen. The left side appears to be derived from a more anterior position than the right. The most reasonable explanation is that the two sides have been displaced relative to each other and that the left side actually does represent a slightly more anterior portion of the scleritome.

Specimen LO 7370t (Pl. 1, fig. 7) is not as well preserved as specimen LO 7371t. It comprises a small part of an assemblage presumably from somewhere along the mid-part of a scleritome. The specimen is *c.* 10–11 mm long with *c.* 7–8 segments preserved. The largest part of the specimen exhibits the dorsal side. Most of the original sclerite material has been worn off, however, making the relationship between the sclerites hard to distinguish. The figured part of the specimen exposes a few right side sclerites preserved as impressions. They have been displaced so as to lie in the direction of a cross section of the assemblage. The most conspicuous of these impressions is the lateral part of an inner sclerite and a complete outer one. The inner sclerite exhibits a distinct displaced umbo and widely spaced rugae. The outer sclerite exhibits a well expressed I_2 and also a difference in distinctness of rugae. Between these two, fragments of additional outer sclerites are visible.

Specimen PMU G1020 (Pl. 1, fig. 8) is a small specimen consisting of *c.* eight right side segments, although most of them are hardly visible. The best exposed sclerite is an outer one with a displaced umbo. The other sclerites are inner ones, and one of them is markedly displaced (Pl. 1, fig. 8); its placement atop the other sclerites results from a backwards slippage. The sclerite derives from one of the anterior segments, as indicated by the position on top of the rest, an angle of the longitudinal fold around 140°, and a higher density of rugae than have the following sclerites.

Remarks. Sclerites with a displaced umbo have previously only been reported from plumulitids, see e.g. Barrande (1872); and Etheridge (1878; although he first considered it to be a turrilepadid); and Jell (1979), where such an umbo is restricted to outer anterior sclerites. Inner sclerites with a displaced umbo, however, are previously unknown.

Reconstruction. The three illustrated specimens (LO 7371t, LO 7379t and PMU G1020) and comparisons with other turrilepadids and plumulitids give a relatively clear picture of the appearance of the scleritome.

Turrilepas sp. A has a scleritome consisting of at least 25 segments and a distinct anterior end as in *T. wrightiana* (Adrain *et al.* 1991). According to Adrain *et al.* (1991), the anterior end in *T. wrightiana* lacks outer sclerites on the two first segments. The inner sclerites of these two segments differ in some ways: they have a higher density of rugae than subsequent inner ones, and they exhibit a larger angle of the longitudinal fold. Not until segments 5–6 does the angle of the longitudinal fold achieve its stable value of 90°. The outer sclerites of *T. wrightiana* are of uniform appearance, however, throughout the scleritome. In plumulitids the anterior structure is similar, but there are species with modified outer sclerites at the anterior end. This is the case for e.g., *P. richorum*, which lacks outer sclerites of the first two segments, whereas outer sclerites of the three subsequent segments have modified apical regions (see Jell 1979 for a detailed description). In *Turrilepas* sp. A the anterior structure is suggested to be as follows. Segments 1–2 consist only of inner sclerites, flatter, and with a relatively high density of rugae. Specimen LO 7371t (Pl. 1, figs 1–6) and PMU G1020 (Pl. 1, fig. 8) have inner sclerites with a higher density of rugae (their angle of the longitudinal fold is larger than 90°, indicating an anterior position). Judging primarily from their size, they do not seem to derive from the very first segment. They are more probably sclerites representing a transition towards the general form of inner sclerites. LO 7371t seems to have lost the outer sclerites of the first segments exposed in the specimen. Segment 3 in *Turrilepas* sp. A presumably had modified outer sclerites (Pl. 1, fig. 8). Due to the fact that only one certain modified sclerite has been recovered, it is not clear in how many segments they were present. They were most probably restricted to the anterior region, as indicated by other species with modified outer sclerites, where they characterize the anterior end of the scleritome. In the turrilepadids this anterior end continues only to segment 5 or 6. Thus the unmodified outer sclerites in *Turrilepas* sp. A appear no earlier than segment 4 and presumably no later than segment 6. By then the inner sclerites have attained the appearance of subsequent ones, and the angle of the longitudinal fold reached the general value of 90° also by segment 6. The largest part of a turrilepadid scleritome is of a uniform arrangement, with a virtually square body cross section resulting from the 90° angle of the longitudinal fold (see especially *T. modzalevskae* in Adrain *et al.* 1991, pl. 2, figs 4–5). The situation in *Turrilepas* sp. A is consistent with this arrangement. The mid-part of the scleriitome in *Turrilepas* sp. A involves at least *c.* 18–20 segments. The posterior end is unknown in *Turrilepas* sp. A as in other turrilepadids. A general decrease in segment size may be the only modification.

Functional morphology. The articulation of the turrilepadid scleritome differs from that of lepidocoleids; turrilepadids were not able to close their scleritome. This is contrary to the opinion of Jell (1979), who considered turrilepadids to be able to close their scleritome fully, like lepidocoleids. Adrain (1992) concluded that it was not very likely that turrilepadids could ever close the scleritome entirely because of the medial overlap and posterior imbrication of sclerites. However, the amount of movement possible in the transverse plane was presumably very small and most likely had very little to do with attempts to close the scleritome. The strong overlap and imbrication of both inner and outer sclerites would prevent all larger movements of the sclerites in that direction. The rugae on all sclerites are asymmetrical, with a form reminiscent of terrace sculptures in burrowing invertebrates (e.g. Savazzi 1994). The steeper sides of the rugae face approximately posteriorly. The distinct pattern of rugae in *Turrilepas* sp. A may be explained partly by the need for reinforcement in areas that otherwise may have constituted weak points. A possible function of the outer sclerites could have been to soften the sediment, either in search for food or perhaps in the process of burrowing, or both. It may possibly be argued that the outer sclerites were used to close the scleritome, at least partly, but considering the arrangement of the scleritome with the overlap and imbrication of sclerites, other functions seem more probable. Besides burrowing for protection, the possibility of enrolling sideways in a manner similar to millepedes should also be considered.

The growth of machaeridian scleritomes holds part of the key to understanding the biology and phylogeny of the group. Adrain *et al.* (1991) suggested that an organism with a fixed number of sclerites grew at the same rate with rugae deposited in an incremental manner. As stated by these authors, this is incompatible with serial addition of segments. Based on the collections in The Natural History Museum (London), this seems to be a plausible hypothesis. Some specimens, however, have sclerites with an aberrant growth pattern which does not conform to incremental growth and such sclerites need to be explained. One such sclerite is figured on Plate 1, figures 5–6; this inner sclerite gives the impression of having been incorporated at a later stage and having achieved its size quite rapidly. A general disturbance of growth should have been traceable on all sclerites at the same intervals. Perhaps this reflects later incorporation of this specific sclerite, but it is not clear whether severe damage led to the replacement of the injured sclerite with a new one or whether it indicates some other aspect of machaeridian growth.

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INTRASPECIFIC VARIATION, DIVERSITY, REVISED SYSTEMATICS AND TYPE OF THE DEVONIAN STROMATOPOROID, *AMPHIPORA*

by COLIN W. STEARN

ABSTRACT. Understanding of the morphological variation and defining characters of the abundant and ubiquitous dendroid stromatoporoid genus *Amphipora* Schulz has been hindered by the loss of the holotype specimen of the type species, *A. ramosa* (Phillips). In the absence of a type, the boundaries of the genus *Amphipora* could only be defined vaguely, yet 12 genera of *Amphipora*-like fossils have been named to constitute the family Amphiporidae Rukhin, and about 175 species of these genera have been described. Assemblages of amphiporids in a single bed show a wide range of variation but are considered to be the remains of a monospecific stand because a comparable range of variation can be demonstrated along the length of single stems. Some highly variable characters have been used to distinguish genera and species. In particular, the expression of the axial canal, nature and presence of peripheral membranes, thickness of skeletal elements, and density of the skeletal network are shown to be of dubious value as criteria for characterizing genera or species.

A neotype for *Amphipora ramosa* is selected from collections made from the Chercombe Bridge Limestone at the Broadridge Wood Quarry, Newton Abbot, Devon, and revised diagnoses of the species and genus are formulated. The presence of distinct pillars in the neotype and all examined specimens from Devon shows that the four genera whose distinctiveness from *Amphipora* was based on the presence of this character, should be regarded as junior synonyms. Four other genera are also placed in synonymy with *Amphipora*. The amphiporid animal is reconstructed as a small, cylindrical, branching, calcified sponge in which the dermal membranes covering the vestibules were locally calcified to form the peripheral membranes and vesicles.

> 'A VAST amount of work remains to be done with respect to the Devonshire organic remains; but I rejoice to know that the task has been placed in the hands of Mr. Phillips who is not only well qualified but ready to overcome every difficulty, and it cannot be long before we are supplied with the fullest and most satisfactory information.' (Lonsdale 1840, p. 729)

Much of the synthetic work on diversity trends in the history of life rests on databases dependant on taxonomic decisions. Until now these large databases have been refined to the generic level but progress towards compilation of species diversity is progressing. The numbers of species and genera recognized in fossil groups commonly depends on the taxonomic philosophies of a few specialists. For the last generation, taxonomic work was driven by the conviction that evolution was expressed in the fossil record as gradual morphological change through time. The refinement of biostratigraphical zonation was a goal that led palaeontologists to recognize smaller and smaller morphological differences as new taxa without clear statements of variability in morphology. The plethora of new taxa generated by this work is illustrated by a survey of the genus *Amphipora* and its relatives. This paper documents the variation in a population of specimens of the genus, suggests that most of the genera distinguished from *Amphipora* by characters shared by specimens in a neotype suite are synonyms, and that the 173 species of these genera that have been described do not reflect the real specific diversity of this taxon.

Fossils of *Amphipora* are strewn through Devonian limestones and dolomites like blankets of broken twigs. In these rocks they are the most abundant and geographically widespread of all

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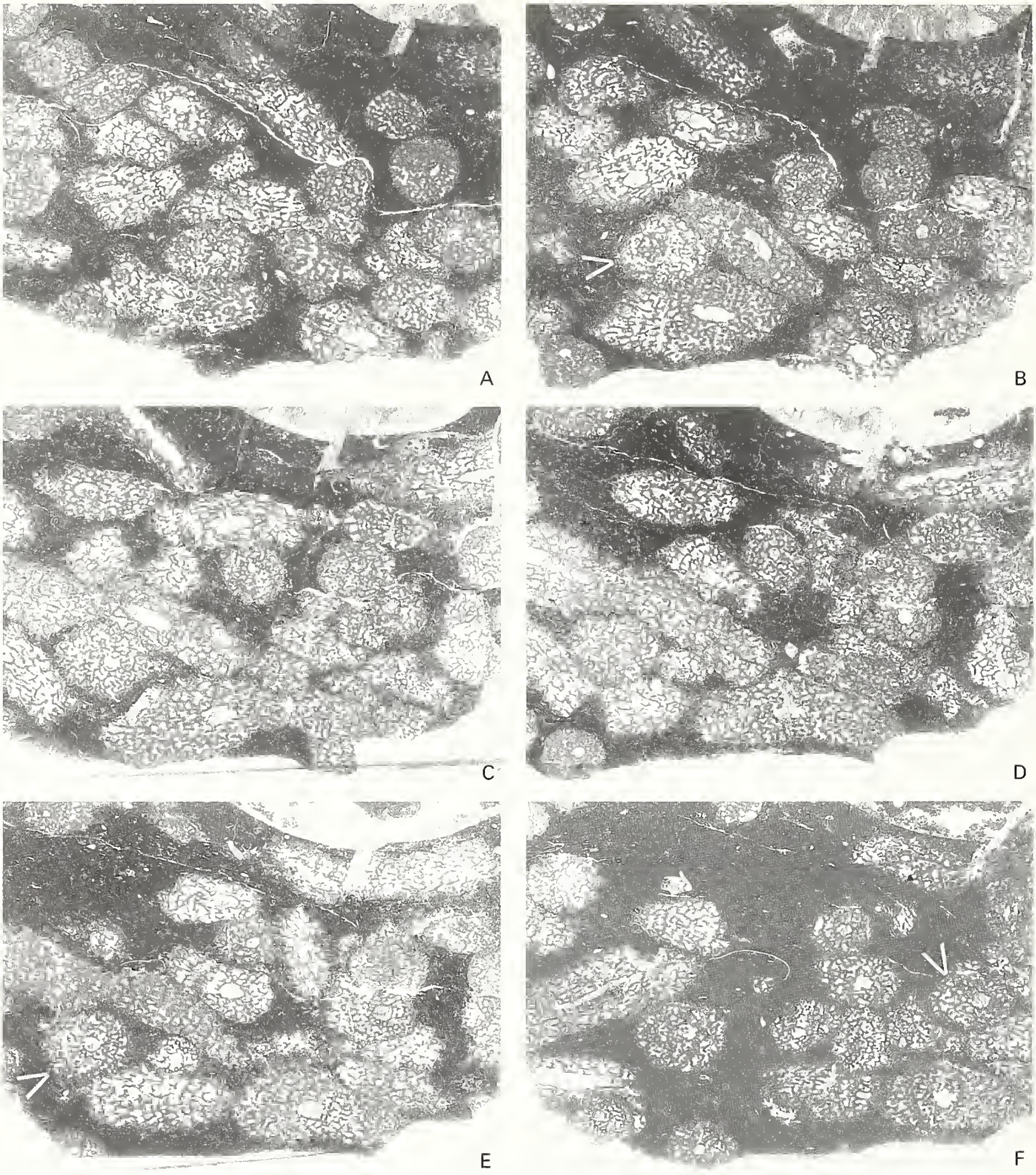
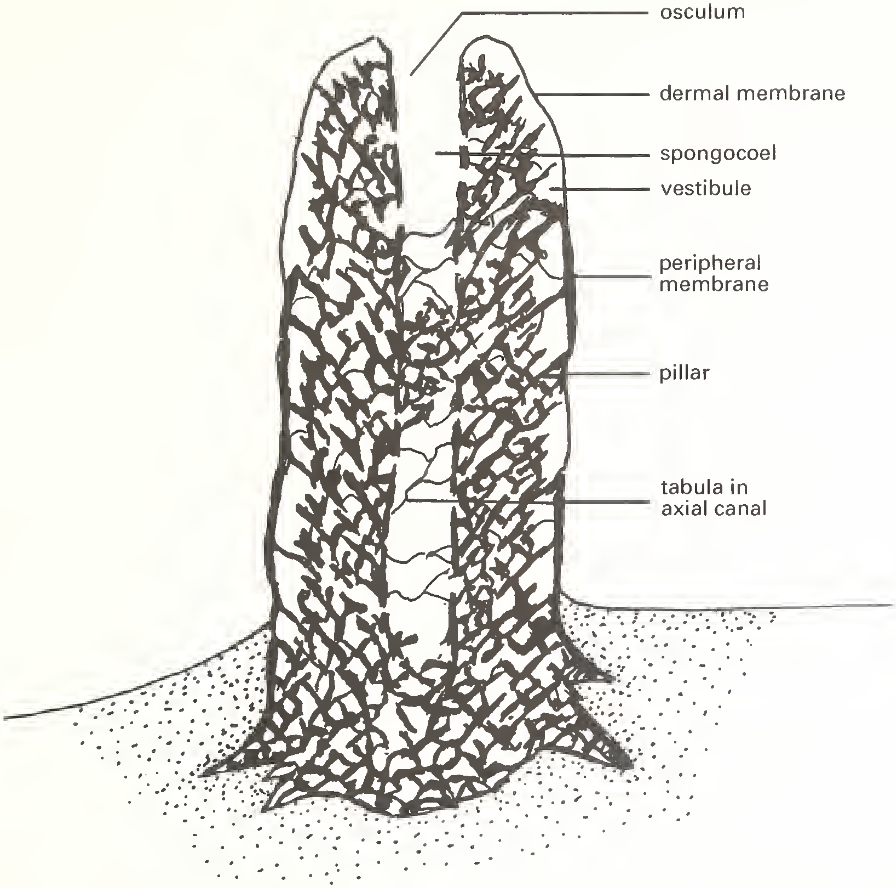


TEXT-FIG. 1. *Amphipora ramosa* (Phillips, 1841); neotype and neotype suite, six serial thin sections from PO 308. The neotype stem is indicated by the V in figures B and E, Broadridge Wood Quarry, Devon. Interval of the sections measured from the first one in parentheses. A, section A1; B, section A2 (1·8 mm); C, section A3 (3·3 mm); D, section A4 (5·1 mm); E, section A5 (6·7 mm); F, section A6 (8·2 mm); see Text-figure 5 for significance of the V. Note the variation in the expression of the axial canal and the pillars in longitudinal and oblique sections. Up/down orientation unknown; all ×2·45.



TEXT-FIG. 2. Reconstruction of *Amphipora ramosa* (Phillips, 1841) as a small sponge rooted in the substrate. The reconstruction of the base is speculative.

macrofossils. The 'twigs' are rarely found in isolation; usually they crowd the bed. Despite their abundance and ubiquity (Text-fig. 1), palaeontologists know little about how these organisms lived, how they should be classified, how the genus should be defined or divided into species. Some of this confusion results from the loss of the type specimens of the type species, *Amphipora ramosa* (Phillips).

Typical amphiporid stems are rods a few millimetres in diameter and are composed of skeletal elements of fibrous calcite defining an irregular network of hard tissue in which concentric elements are obscure, and radial elements are hard to distinguish. The voids, or labyrinthine canals between the elements, open on the periphery in apertures of irregular shape or are covered there by a thin hard tissue membrane held off the surface by delicate processes. The peripheral membrane may be present on only some of the stems or only on some parts of individual stems. A prominent axial canal crossed by dissepiments may or may not be present. Text-figure 2 is a reconstruction of the animal growing from the Devonian sea floor; this is discussed in detail at the end of this paper. Stems more than a few tens of millimetres long are rare but some are as long as 50 mm. Amphiporids occur in rocks of Ludlow age; the earliest *Amphipora* may be as old as Emsian, but the genus is particularly abundant in mid and late Devonian strata. The youngest recorded species of *Amphipora* are found in beds near the base of the Famennian Stage in the Czech Republic and

Russian Urals (Friáková *et al.* 1985). However, the discovery of amphiporids in Strunian (latest Famennian) rocks in western Germany has been noted in the informal literature (Weber 1996, *Fossil Cnidaria and Porifera Newsletter*, **25**(1), 9).

All writers on this genus have commented on the great variability of specimens found preserved together in death assemblages. The most obvious of qualitative differences between stems in an assemblage is in the presence or absence of peripheral membranes and axial canals. Nicholson (1886, p. 110) speculated that the membranes could have been abraded off some specimens or they could be reproductive structures that were present only at certain stages or on certain individuals. Similar alternatives have been discussed by most later writers. Despite the erratic occurrence of the axial canal and peripheral membranes in most assemblages, these features have been used as diagnostic characters to differentiate species.

An astonishing 173 species and subspecies of the genera related to *Amphipora* had been described up to 1991 suggesting that it is much easier to describe a new species of these fossils than to do detailed comparisons with known species.

Since the establishment of *Amphipora* by Schulz (1883), the fossil has generally been considered to belong in the class Stromatoporoidea and, with its related genera, in the family Amphiporidae, Rukhin, 1938. Whether the family should be placed in an order of its own or within another order, such as the Clathrodictyida (e.g. Stearn 1980), remains controversial. No consensus exists on the position of the family within the phylogeny of the stromatoporoids but nearly all the features of their skeletons can be found in other stromatoporoid genera and several genera (see below) appear to bridge the morphological gap between the amphiporids and other stromatoporoid orders. The amphiporid genera are considered in this paper to be sufficiently different from those of the Clathrodictyida, to which they were assigned by Stearn (1980), to constitute a separate order of the class Stromatoporoidea; i.e., Rukhin's (1938) family Amphiporidae is recognized as an order (as was initiated by Webby *et al.* 1993). Cockbain (1984) also suggested that the amphiporids should be separated at the highest level from the rest of the stromatoporoids but did not make a formal proposal.

The cylindrical symmetry of the stems implies that the organism was benthic and interacted with its environment in all horizontal directions. The broken stems may branch dichotomously but no rooting structures or growing tips have so far been positively identified. The organisms are commonly assigned a baffling function in the marine environment (as part of the baffler guild of Fagerstrom (1987)), but they are only rarely found in the upright position of growth as they should be if sediment accumulated around the stems as they 'baffled' the current flow.

Some of the problems in the interpretation of this genus considered here are as follows.

1. In the absence of the type specimens of the type species of the genus, *Amphipora ramosa* (Phillips), how can the typical form of the genus be determined?
2. Are the many displaced stems of amphiporids found together in most deposits remnants of a monospecific stand, and is the variation found within such assemblages indicative of inter- or intraspecific variation?
3. Did the organism pass through a series of developmental stages as it grew – sequential stages exhibiting changes in features, such as peripheral membranes and axial canals, that have been considered to separate different species or different genera?
4. Type specimens of amphiporids have commonly been designated as an assemblage of stems enclosed together in a rock. Should the holotype be a single stem under the Rules of Zoological Nomenclature?
5. Can the organism be reconstructed and the functions of its hard parts interpreted with confidence?

HISTORICAL SUMMARY

The extensive early literature on the amphiporids has been summarized by Lecompte (1952) and Zukalova (1971) and is not reviewed here. Lecompte (1952) emphasized the uniqueness of the genus among the stromatoporoids and observed that the erratic presence of peripheral membranes could not be attributed to mechanical abrasion alone. He suggested that the presence of dissepiments in the axial tube and peripheral cavities indicated an astrorhizal function. He described four new species of *Amphipora* and, from his descriptions, based specific differences on: width of stem, presence of the axial canal, thickness of structural elements, differentiation of pillars, presence and size of peripheral membranes, and nature of the dissepiments in the chambers. Zukalova (1971) listed 63 literature references to species of *Amphipora* in her Table 2. She also plotted (Table 3) the ranges of ratios of diameters of axial canals to branch diameters of the species recognized in these papers. She distinguished specimens as *A. ramosa* from the other five species recognized from Moravia by their ratio of over 1:6; that is, the axial canal is proportionally much smaller than in other species.

Cockbain (1984) has discussed problems concerning *Amphipora*. He described the structure as characterized by 'pillars with lateral processes connecting adjacent pillars', lack of laminae, and an outer wall covering the outside of each branch attached to the ends of the pillars and lateral processes. He regarded the fibrous structure as secondary and interpreted the axial canal as not analogous to an astrorhizal canal. The presence of the canal was not considered to be of taxonomic value. Although his specimens included those with a very thin peripheral membrane clearly separated from the inner structure by a wide vesicle (Cockbain 1984, pl. 7), he considered the membrane as homologous to the other structural elements but only half as thick, and the vesicle as a gallery. He illustrated (Cockbain, 1981, fig. 14) a specimen of *A. rudis* in which the axial canal continues up only one of the branches from a division point, and at another branching the canal is absent for a short distance in the newly formed branch, then forms again.

Dong De-Yuan and Wang Chen-Yuan (1982) introduced two new genera of amphiporids whose generic diagnoses imply that the presence or absence of peripheral vesicles and axial canals is diagnostic at the generic level. Dong De-Yuan and Wang Bao-Yu (1984) introduced another genus, *Tianshanostroma*, that was placed in Idiostromatidae but has many characteristics of an amphiporid. They also established a subfamily, Amphiporina, for several amphiporid genera.

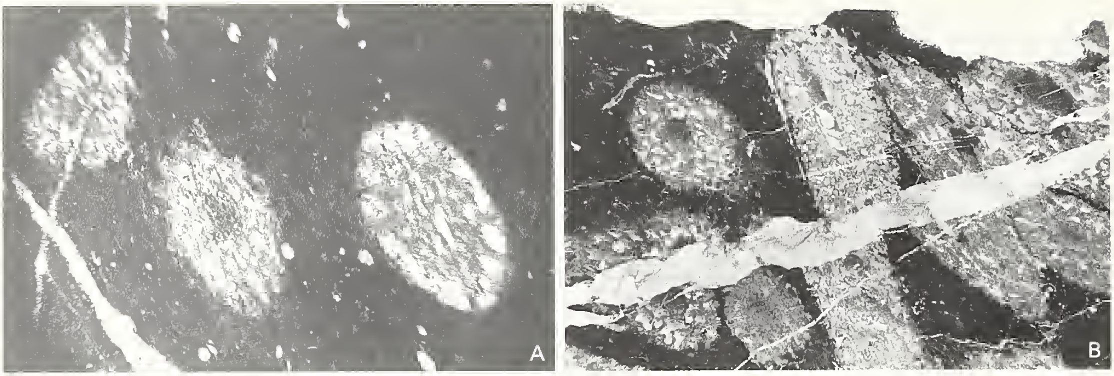
In Bogoyavlenskaya and Dan'shina (1984), Bogoyavlenskaya described six new species of her genus *Stellopora* and assigned the genus to the Actinostromatidae. She referred to the extensions from the pillars in this genus as colliculi and ascribed the voids divided by 'tabulae' to an astrorhizal system. Bogoyavlenskaya also described the new amphiporid genus *Novitella* and placed it in the Gerronostromatidae.

Bogoyavlenskaya (1985) affirmed that *Amphipora* is a stromatoporoid and recognized the axial canal as an astrorhizal canal without horizontal branches. She suggested that some species of the amphiporid *Stellopora* originated as high mamelons on the surface of *Actinostroma* that broke off. She reconstructed *Amphipora* as growing in meadows in shallow water but believed, on the basis of the orientation of the axial canal tabulae, that the stems rolled around like logs on the substrate. She postulated that they were coelenterates that obtained the sunlight they required on all sides by their slow rolling. The occurrence of *Amphipora* communities in the Silurian and Devonian of the Urals was discussed in detail. The genera considered in this paper to be amphiporids are placed by Bogoyavlenskaya (1985) in several different orders.

Makarenko (1988) emphasized the unity of the amphiporids and noted that Bogoyavlenskaya's (1985) division of them into different orders did not take into account their distinctive microstructure. He believed the dendroid growth form that also unites the group to be genetically dictated. Much of his paper is a review of the stratigraphical distribution of *Amphipora* species in the west Siberian region.

LOCATION OF THE TYPE SPECIMEN OF *AMPHIPORA RAMOSA*

The first mention in the literature of *Amphipora* is in Lonsdale's (1840) paper on the Limestones of South Devonshire. In a list of fossils (pp. 737–738) he refers to *Favosites*? *ramosa* from near Chudleigh. The note on this entry reads: '*Favosites*? *ramosa* in the collection of specimens from the Eifel presented to the Geological Society by Mr. Willimott, is labelled *Favosites ramosa* (nob.). It



TEXT-FIG. 3 *Amphipora ramosa* (Phillips 1841). A, specimen in the Geological Survey, London (in 1964, now presumably at the British Geological Survey, Keyworth, Nottingham), numbered 52873, labelled as 'possible syntype'; ×9·7. B, specimen (McGill, Redpath Museum RM 20.5340) from top of the Palace quarry, Chudleigh, Devon, showing the poor preservation but general similarity to the Broadridge Wood Quarry specimens; ×4·85.

was obtained originally from M. Brassart of Bonn. The specimen is evidently not a *Favosites* but its state of decomposition and that of several others kindly lent to me by Mr. Murchison, forbid the characters being properly ascertained. The fossil consists of long slender branches perforated down the centre, and presents a carious [sic] structure resembling that of the genus *Scyphia* [a sponge].'

Phillips (1841) described the stems that were later to be named *Amphipora* as *Caunopora ramosa* from Devonian limestones at Chudleigh and Babbacombe in Devon. Schulz (1883), in describing similar fossils from the Eifel district of Germany, established the genus *Amphipora* using Phillips' species as the type.

Unfortunately Phillips' specimen, the holotype of the species, and hence typical of the genus, cannot be found. I have searched for the specimen at The Natural History Museum, the Geological Survey, London (in 1964), and at the University Museum, Oxford. A specimen then at the Geological Survey (and presumably now at Keyworth) marked 'possibly syntype' does not correspond with Phillips' drawing of the type. It is numbered #52873, cut on five of six sides, and labelled 'pres. Geol. Soc. 1911'. It is accompanied by a slide numbered 52873A (Text-fig. 3A). In a letter of July, 1964 H. Dighton Thomas stated that 'It seems highly improbable that it is a syntype'. Some of Phillips' specimens have been located at Oxford University (J. M. Edmonds, pers. comm. June 1964), for instance Phillips' (1841) plate 10, figure 29c (*Caunopora placenta*), plate 10, figure 28a (*Stromatopora concentrica*), plate 8, figure 23 (*Favosites spongites*), but the specimen of *Caunopora ramosa* is not among them. Colin Scrutton (pers. comm. June 1990) recounted a story, that cannot be authenticated, that some of Phillips' material at Oxford was stolen long ago by thieves who thought they had something of value and was then dumped by them in the River Thames when they realized that they had only rocks.

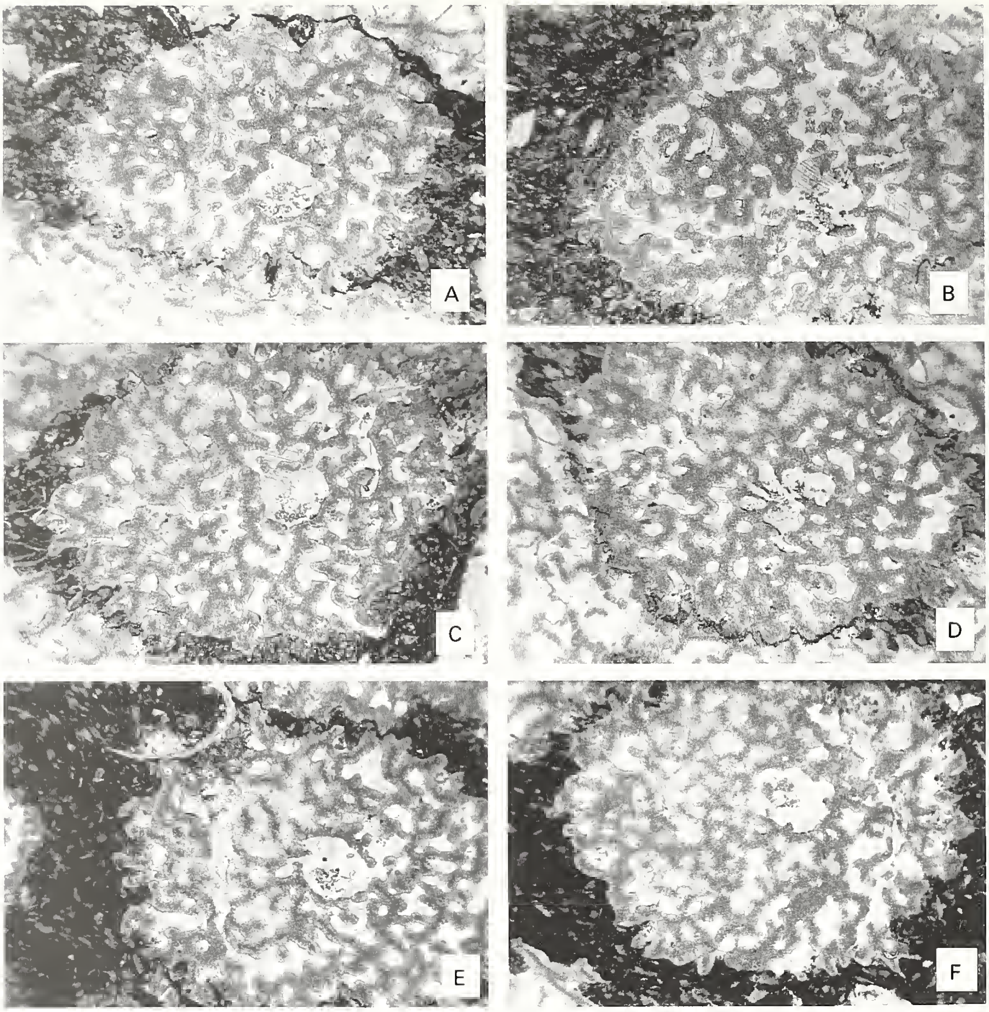
I have examined some specimens (Text-fig. 11A) at the Institut für Paläontologie, Bonn, whose labels suggest they may have been used by Schulz but these do not have the status of types. Most amphiporids are preserved embedded in limestones, but Schulz's specimens from the 'ramosabänke' in the Hillesheim district are preserved weathered out in three-dimensional relief (Schulz 1883, pl. 23, fig. 1) in a light-coloured carbonate that appears to be dolomite. However, the specimens at Bonn cannot be matched exactly with the excellent illustration that accompanies Schulz's paper. Similar exceptionally preserved specimens are in the Nicholson Collection at The Natural History Museum, London, (Nicholson 1886, pl. 9, fig. 1) and must have come from the same bed. Although the outer surfaces of these specimens are preserved in relief, the internal structure of the stems is obscure. Nicholson was the first to use thin sections extensively for the description of stromatoporoids, and his illustrations (Nicholson 1886, pl. 9, figs 1–4; 1892, pl. 29, figs 3–7) of specimens from Hebborn (Paffrath district, Germany) and South Devon (Teignmouth and Shaldon) became the standards by which *Amphipora ramosa* was known. Benton (1979) recorded that the specimens identified by Nicholson as from Teignmouth are labelled on the slides as from Shaldon, a village on the other (south) side of the estuary of the Teign River. However, the genus is based on a typical species that was originally inadequately described and whose characters cannot be determined accurately in the absence of a type specimen.

DESIGNATION OF A NEOTYPE

Phillips' localities for *Caunopora ramosa* were Chudleigh and Babbacombe. The latter is a suburb of Torquay and Colin Scrutton (pers. comm. 1990) suggested that the specimen was a beach pebble. Early collectors in Devon, including Nicholson, collected many specimens from the beaches, particularly at Teignmouth and Shaldon. Since these specimens were Devonian clasts washed out of Permo-Triassic conglomerates on to Recent beaches, nothing can be deduced about their original stratigraphical position. Beds bearing abundant *Amphipora* are exposed south of Chudleigh and particularly at the top of the Palace Quarry (SX 8682 7871; see Scrutton 1969, 1977). A sample for this study was collected there but the preservation is not good and the specimens are sheared, distorted and the microstructure is obscure (Text-fig. 3B). Much better material was collected from two levels in the Chercombe Bridge Limestone at the Broadridge Wood Quarry on the banks of the Lemon River near Newton Abbot (SX 839 711; Scrutton and Goodger 1987). Most of the observations made here on *Amphipora* are based on the Newton Abbot specimens.

Amphipora was clearly an opportunistic species, spreading rapidly in low diversity communities to the exclusion of other taxa when conditions were appropriate. It would seem ecologically unlikely that several species of a single genus (and therefore having similar environmental requirements) would grow in a meadow–like stand in Devonian seas; such stands in modern marine environments are generally almost monospecific and must have resembled modern marine grass communities. However, to establish that the variability seen in different individuals in a random cross section of an aggregate could be present within a single species, this variability must be shown to exist within an individual stem. To investigate this, the stems in the samples were serially sectioned by grinding down a block and recording the polished surface at 0·5 mm intervals by photographs or camera lucida drawings. Because the structure for a short distance into the polished surface can be observed albeit vaguely, such polished surfaces do not give a clear picture of the structure in a single plane. This process also destroyed the specimen. A clearer picture of the structure was obtained by making successive thin sections which could be retained as evidence of the changes along the length of the stem. These were made by cementing the polished block to glass with an ultraviolet-setting adhesive, cutting the block as close to the glass as possible with an Ingram cutoff saw, smoothing the surface by light grinding and recementing the block to make the next section. The closeness of sections is limited by the thickness of the saw blade to about 1·5 mm, but single stems could normally be traced through many cuts by this method (Text-figs 1, 4–5). Variations in the structure were recorded in photographs and drawings made by tracing the structure on enlarged negative prints. In all, 19 thin sections were cut from the suite of the neotype. Random sections of material from Devon, the Eifel and Ardennes, western Canada, and other localities were also examined. Variations in the structure at various stages of growth are best examined in sections that cut the long axis of the stem.

Neotypes. Three blocks of limestone rich in *Amphipora ramosa* were collected from the Chercombe Bridge Limestone at the Broadridge Wood Quarry (SX 839 711). A map of the quarry, its geology, and a stratigraphical section have been published by Scrutton and Goodger (1987). The *Amphipora*-rich beds are of mid Givetian age according to Scutton (1977). Each block was cut into many fragments to make the thin sections. Specimens in the first block collected about 15 m above the quarry base on the path at the east side of the quarry face are designated as the neotype suite and an individual stem, represented by six serial thin sections (PO 308.A1–A6) and the remnant



TEXT-FIG. 4 *Amphipora ramosa* (Phillips, 1841); neotype stem PO 308.A1 to PO 308.A6, six serial thin sections taken from the slides in Text-figure 1 at the intervals recorded in that caption. Position of the stem shown by the V in Text-Figure 1B and 1E. Note the variation along the stem of the axial canal, the proportion of labyrinthine canals and closed spaces, and the thickness of the skeletal elements; × 10.

block from which they were cut, is designated as the neotype and deposited in The Natural History Museum, London, type collection, under number PO 308. The bed from which the neotype sample was taken is about 21 m above the base of section C of Scrutton and Goodger (1987) and is estimated to be about 129 m above the base of the Chercombe Bridge Limestone (Colin Scrutton, pers. comm. 1996). A second block from the other side of the quarry about 1 m stratigraphically below the neotype suite is designated a neoparatype (PO 309) and the sections from it are numbered PO 309.B1–B5. A third block, loose at the base of the quarry, collected by Stephen Kershaw, is micritic and the specimens in it show well-developed peripheral vesicles. This suite of specimens is designated as another neoparatype PO 310 and the thin sections from it are numbered PO 310.C1–4.

Although one stem is designated as the neotype (Text-fig. 4), the assumption is made in this description that all the stems in the neotype asemblage belong to the same species. Serial sections of several stems of the suite (Text-figs 4–7) are illustrated to show that the variation within individuals is comparable to that in individual stems of the suite and justifies this assumption. The use of aggregates of stems to illustrate species of *Amphipora* by authors such as Lecompte (1952) and Zukalova (1971) shows that they also tacitly made this assumption. An additional assumption made in the description is that the stems grew vertically so that the axis defines the vertical dimension.

SYSTEMATIC PALAEONTOLOGY

Class STROMATOPOROIDEA Nicholson and Murie, 1879
Order AMPHIPORIDA Ruhkin, 1938
Family AMPHIPORIDAE Rukhin, 1938

Remarks. Rukhin (1938) included the genera *Amphipora* Schulz, *Idiostroma* Winchell, *Haraamphipora* Rukhin, and *Zelopora* Penecke in the new family. *Idiostroma* resembles the other amphiporids only in growth form and axial canal; its well defined tripartite laminae place it clearly in the Stromatoporellida. *Haraamphipora* is discussed below. *Zelopora* does not occur in Penecke's work and may be a misprint of *Zeapora* Penecke (Berhard Hubmann, pers. comm. 1996). The nature of this fossil is under investigation by Hubmann. It has been considered a bryozoan (Bassler, 1953, p. G236).

Genus AMPHIPORA Schulz, 1883

[= *Amphipora* Schulz, 1883, p. 245; *Haraamphipora* Rukhin, 1938, p. 93; *Paramphipora* Yavorsky, 1955, p. 154; *Vicinustachyodes* Yavorsky, 1961, p. 56; *Stellopora* Bogoyavlenskaya, 1972, p. 27; *Taeniostroma* Dong and Wang, 1982, p. 29; *Columndictyon* Dong and Wang, 1982, p. 29; *Tianshanostroma* Dong and Wang, 1984, p. 269; *Qinghaipora* Dong, 1991, p. 75].

Revised Diagnosis. Skeleton dendroid, branching dichotomously, with axial canal locally absent, locally with well–defined wall, locally poorly defined, opening by pores into the interskeletal network of voids and irregular canals. Skeletal network formed by pillars radiating upward and outward obliquely from axis and short elements extending from, and joining them to form an irregular structure that may in cross section define open or closed spaces. Peripheral vesicles sporadically developed in most species, bounded by an imperforate calcareous membrane supported beyond the skeletal network by extensions of the skeletal elements. Microstructure compact, fibrous.

Remarks. The major change in this diagnosis from those now widely used is in recognition of the importance of the pillars radiating upward and outward from the axial canal and of the intrageneric variability of the skeletal structures. Most of the early illustrations of *A. ramosa* (Phillips 1841; Schulz 1883) and the description of M'Coy (1885) indicate the presence of pillars diverging upward and outward. The impression that such pillars are not characteristic of *Amphipora* may have been given by Nicholson's illustration of specimens from Devon (1892, pl. 29, figs 1–7) and from Hebborn (1886, pl. 9, figs 2, 4) that show these pillars vaguely, if at all. However, oblique sections from the same slide as Plate 9, figure 2 (Nicholson's No. 399) clearly show the radiating pillars (Text-fig. 11B). The pillars have been made a diagnostic generic character of the genera *Stellopora* Bogoyavlenskaya, *Columndictyon* Dong and Wang, *Tianshanostroma* Dong and Wang and *Qinghaipora* Dong. The evidence presented here shows that these four genera cannot be distinguished from *Amphipora* on this basis. Other genera distiguished from *Amphipora* on criteria of questionable validity, because they are expressed to various degrees in most suites of amphiporids, include: *Vicinustachyodes* Yavorsky, *Paramphipora* Yavorsky, *Haraamphipora* Rukhin, *Taeniostroma* Dong and Wang. All eight genera are considered here to be junior synonyms of *Amphipora* Schulz.

Rukhin (1938) established the genus *Haraamphipora* (type species: *H. pachyroides* Rukhin, 1938) on the basis of its thickened skeletal elements, a highly variable feature within individual stems. This genus has generally been considered to be a synonym of *Amphipora* (Yavorsky 1962; Flügel and

Flügel–Kahler 1968; Zukalova 1971). Structural elements of typical *Amphipora ramosa* have an opaque axis coated on both sides by fibrous calcite (Stearn 1977, pl. 3, fig. 3). Yavorsky (1955) distinguished a new genus *Paramphipora* (type species: *P. mirabilis* Yavorsky, 1955) from *Amphipora* on the basis of the absence of this dark axis. In the first and subsequent publications he named 34 new species of this new genus. In all, Russian and Chinese palaeontologists have named 42 species assigned to this genus. Stearn (1966, 1980), Klovan (1966), Flügel and Flügel–Kahler (1968) and Zukalova (1971) have doubted the validity of *Paramphipora* because minor diagenetic changes can obscure the microstructure of *Amphipora*, yielding specimens that would be placed in *Paramphipora*.

In 1961 Yavorsky proposed another amphiporid genus, *Vicinustachyodes* (type species: *V. mirabilis* Yavorsky, 1961). He (Yavorsky 1967) later changed the spelling of the name to *Vicinostachyodes*. The genus is distinguished from other amphiporids by the absence of an axial canal (a feature absent in many specimens of *A. ramosa*). Only Yavorsky (1961, 1967) has named species of this genus and it does not appear in the summary of Soviet genera by Bogoyavlenskaya and Khromych (1985).

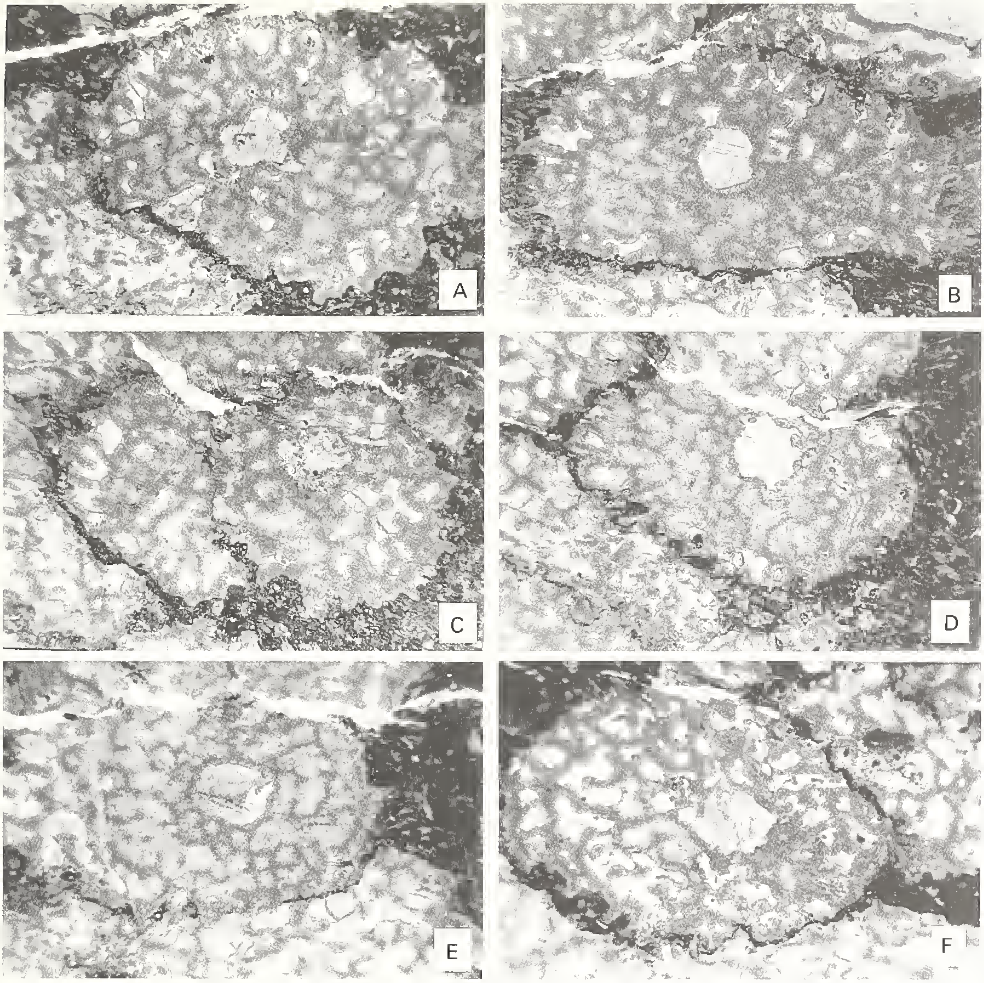
Stellopora Bogoyavlenskaya, 1972 (type species *Amphipora intexta* Yavorsky, 1957) was established for fossils similar to *Amphipora* that in axial section show long pillars radiating upward and outward to the peripheral membranes. Webby *et al.* (1994) commented on the original (Bogoyavlenskaya 1971) naming of this taxa as *Columnoporella* (preoccupied). Although this genus has been used for about 20 species (mostly by Bogoyavlenskaya) its validity is doubtful as evidence presented below shows that the diagnostic pillars are prominent features of *Amphipora ramosa*.

Dong and Wang (1982) proposed two new genera of amphiporids: *Taeniostroma* (type species: *T. yunnanense* Dong and Wang, 1982) and *Columndictyon* (type species: *C. regulare* Dong and Wang, 1982). For the former of these, distinguishing features were listed as irregular skeletal elements without opaque axes, an axial canal, and lack of peripheral vesicles. All these features are known in what is considered here as typical *Amphipora ramosa*. *Columndictyon* is said to be distinguished by the differentiation of the pillars and slightly arched discontinuous laminae, the lack of axial canals and peripheral vesicles (although figures in Dong and Wang's plate 18 suggest that both may be present in the type species). Comparison with the similar genus *Stellopora* is not made in this description (Webby *et al.* 1994). Dong and Wang (1982) also described the new genus *Eostachyodes* (type species: *E. compacta* Dong and Wang, 1982). This genus is not clearly an amphiporid and is classified with the Stachyoditidae by Dong (1988).

Dong and Wang (1984) proposed the amphiporid genus *Tianshanostroma* (type species: *T. xinjiangense* Dong and Wang, 1984). Webby *et al.* (1994) commented on the similarity of this genus to *Stellopora* Bogoyavlenskaya. Like this genus, it has upward and outward radiating pillars best seen in oblique sections. *Qinghaipora* Dong, 1991 (type species: *Q. gracilenta* Dong, 1991) is based on poorly preserved specimens from the Devonian of China. Webby *et al.* (1994) suggested that this genus also could be a synonym of *Stellopora* Bogoyavlenskaya.

The genus *Vacuustroma* Hung and Mistiaen, 1997 (type species: *V. michelini* Hung and Mistiaen, 1997; from *Amphipora* sp. Mistiaen 1988, p. 188), was established for amphiporids with coarsely porous or vacuolate microstructure.

Other genera of Amphiporidae. The first of the amphiporid genera proposed by Bogoyavlenskaya (1965) was *Clathrodictyella* (type species: *Amphipora turkestanica* Lessovaya, 1962). The structure in cross section is much like that of *Amphipora* but in axial section the structural elements appear as upwardly convex cysts vaguely defining laminae that bend down at the periphery. The genus appears to be confined to the Upper Silurian but may extend into the lowermost Devonian. *Euryamphipora* Klovan, 1966, (type species: *E. platyformis* Klovan, 1966) is the only amphiporid with a laminar growth form. The skeleton is a plate of interlaced irregular skeletal elements bordered above and below by marginal vesicles. Cockbain (1984) reconstructed the skeleton as a vertical plate and synonymized the genus with *Amphipora*. Mistiaen (1985) described Frasnian specimens of the genus from Afghanistan as having grown horizontally.

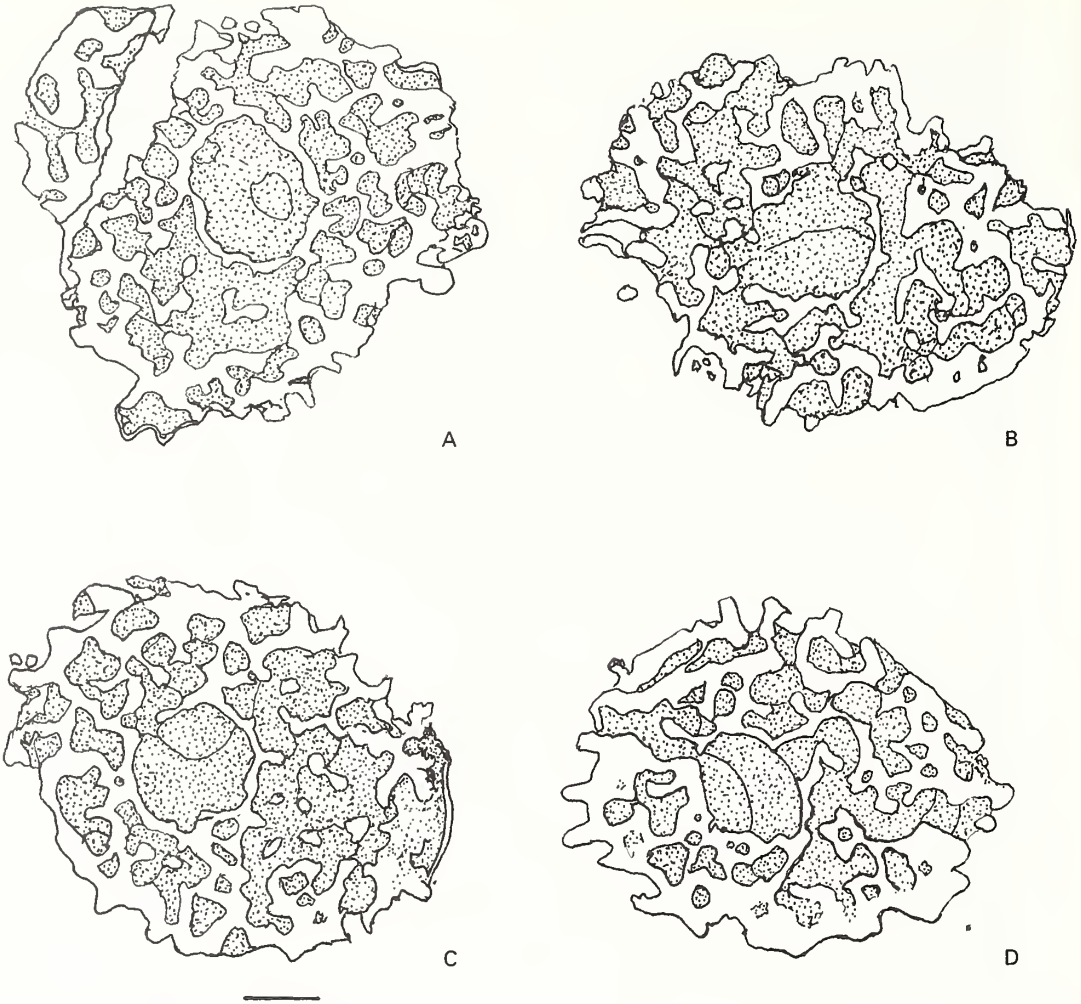


TEXT-FIG. 5. *Amphipora ramosa* (Phillips, 1841); six serial sections from the slides of the neotype suite PO 308.A1 to A6. The location of this stem is shown by the V on Text-figure 1F. Same intervals as for Text-figure 1; ×10.

Bogoyavlenskaya (1984 *in* Bogoyavlenskaya and Dan'shina 1984) erected the amphiporid genus *Novitella* (type species: *Paramphipora tschussovensis* Yavorsky, 1955), although she placed it in the Gerronostromatidae. The cross section is much like that of other amphiporids, with axial canal, peripheral vesicles and irregular structural elements, but oblique sections show gently arched laminae and short pillars confined to interlaminar spaces.

The genus *Eostachyodes* Dong and Wang, 1982 (type species: *E. compacta* Dong and Wang, 1982) resembles *Amphipora* and was described with a group of amphiporids but is probably best classified with the Stachyoditidae, as suggested by Dong (1988).

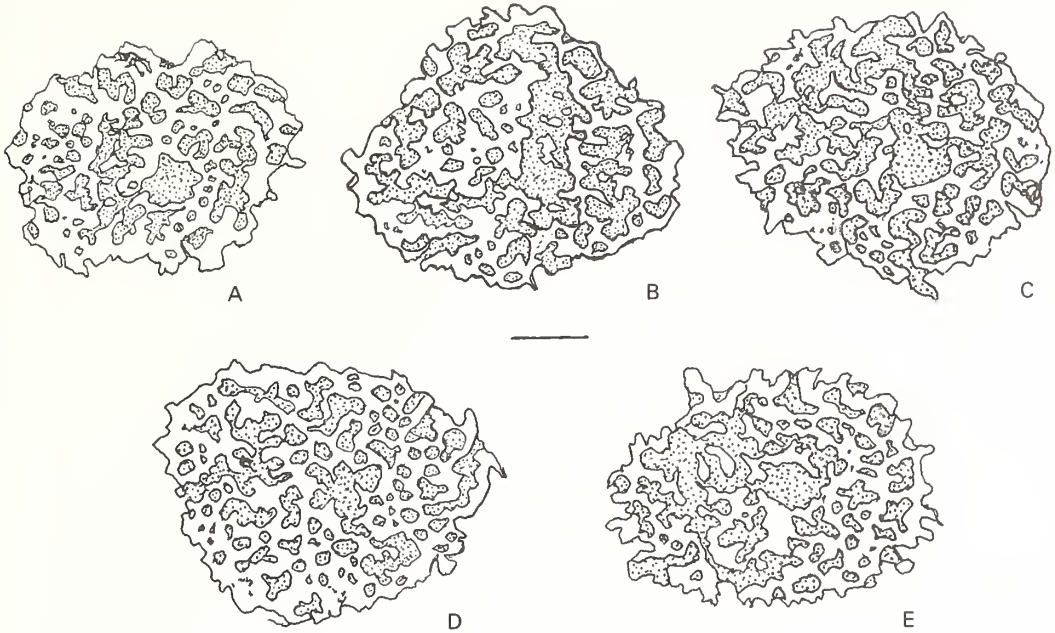
Two other genera related to *Amphipora* have been described but are unlikely to belong in Amphiporidae. *Clavidictyon* Sugiyama, 1939 (type species: *C. columnare* Sugiyama, 1939), from the Silurian of Japan, appears to be an amphiporid lacking an axial canal in transverse section, but has well defined single layer laminae and short post pillars in peripheral parts of the stems. Examination of the type thin section indicates that the species *C. japonicum*, also named by Sugiyama on this



TEXT-FIG. 6. *Amphipora ramosa* (Phillips, 1841); sketches from tracings of four serial thin sections of a stem from the neotype suite but from a set of sections not illustrated in Text-figure 1, showing a more open structure with larger axial canal. A, section PO 308.A10 (0·0 mm); B, section PO 308.A9 (2·0 mm), also illustrated as Text-figure 7D (mirror image); C section PO 309.A8 (3·4 mm); D. section PO 309.A7 (5·0 mm); Scale bar represents 1 mm.

slide, cannot be differentiated from the typical species. Although placed by Stearn (1980) in the amphiporids, *Clavidictyon* seems now better placed in the Clathrodictyida. *Shirdagopora* Lessovaya, 1987 shows superficial resemblance to the amphiporids but can not be placed neatly in any family at present.

The family Amphiporidae can be considered to be made up of the following five genera:
Amphipora Schulz;
Clathrodictyella Bogoyavlenskaya: shows convex cysts in axial sections;
Euryamphipora Klovan: distinguished by plate–like growth;
Novitella Bogoyavlenskaya: shows discrete laminae and short pillars in axial sections;
Vacuustroma Hung and Mistiaen: vacuolate structural elements.
Genera that closely resemble amphiporids but are best placed in other higher taxa include:



TEXT-FIG. 7. *Amphipora ramosa* (Phillips, 1841); sketches from tracing of serial thin sections of the neotype (sections PO 308.A1 to A5). A, from section A1 (0·0 mm); B, from section A2 (1·8 mm); C, from section A3 (3·3 mm); D, from section A4 (5·1 mm); E, from section A5 (6·7 mm). Note that in C most of the internal spaces are continuous. Up/down orientation unknown. Scale bar represents 1 mm.

Clavidictyon Sugiyama: Clathrodictyidae;
Eostachyodes Dong and Wang: Stachyoditidae;
Shirdagopora Lessovaya: *incertae sedis.*

Amphipora ramosa (Phillips, 1841)

Text-figures 1–11

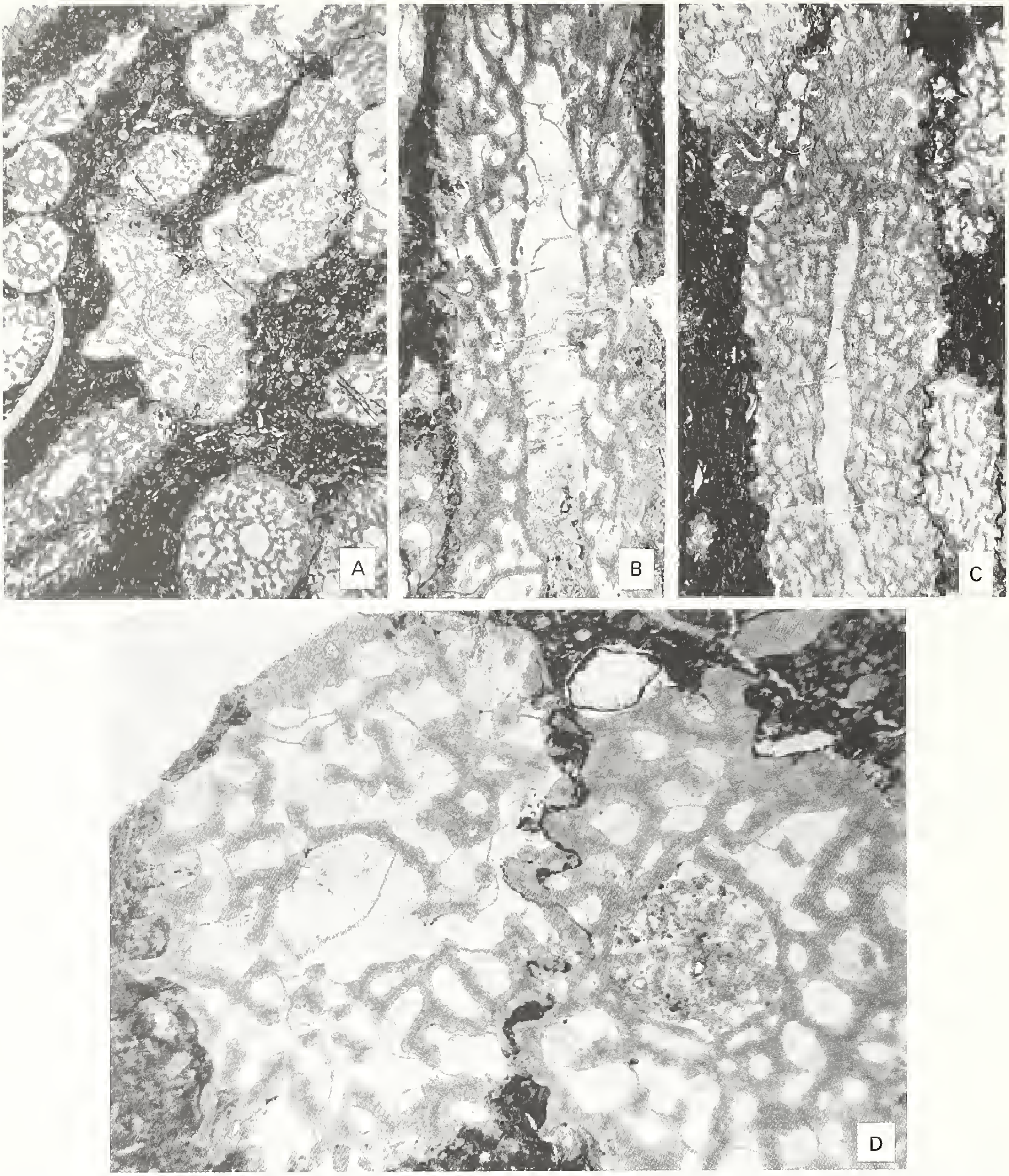
Caunopora ramosa Phillips, 1841, p. 19.

Recently published synonymies of this species include those of Flügel and Flügel–Kahler (1968), Zukalova (1981) and Cockbain (1984). Preparation of a complete synonymy would require the comparison of the nearly 175 described species of amphiporids with the neotype and is beyond the scope of this paper.

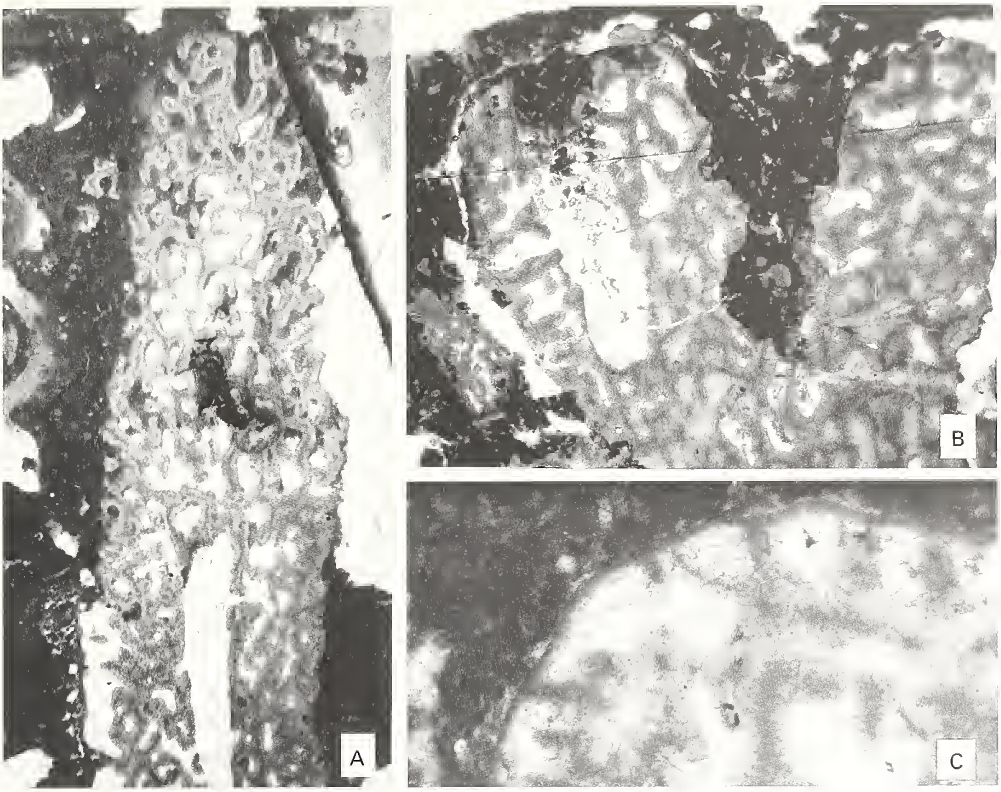
Revised diagnosis. Amphipora with average diameter of about 3·5 mm; wide zone of structural elements; where developed, a narrow axial canal (0·05–1 mm) and zone of peripheral vesicles; well developed pillars at 45°; variable in thickness of skeletal elements, density of their network, and development of axial canal and peripheral membranes.

Description

Skeleton. Stems cylindrical, in all known specimens broken into segments up to 50 mm long, commonly branching dichotomously, rarely showing evidence of lateral budding; without obvious root but some specimens seem to have irregular outgrowths or overgrowths that could be a root system (Text-fig. 8A). Growing tip rarely observed in random sections, rounded with wide, open axial canal into which sediment may penetrate (Text-fig. 9B). Stem diameters show a wide range of values. The mean of 38 measurements of the neotype suite is 3·26 mm (range: 2·0–5·0 mm; standard deviation 0·63 mm).



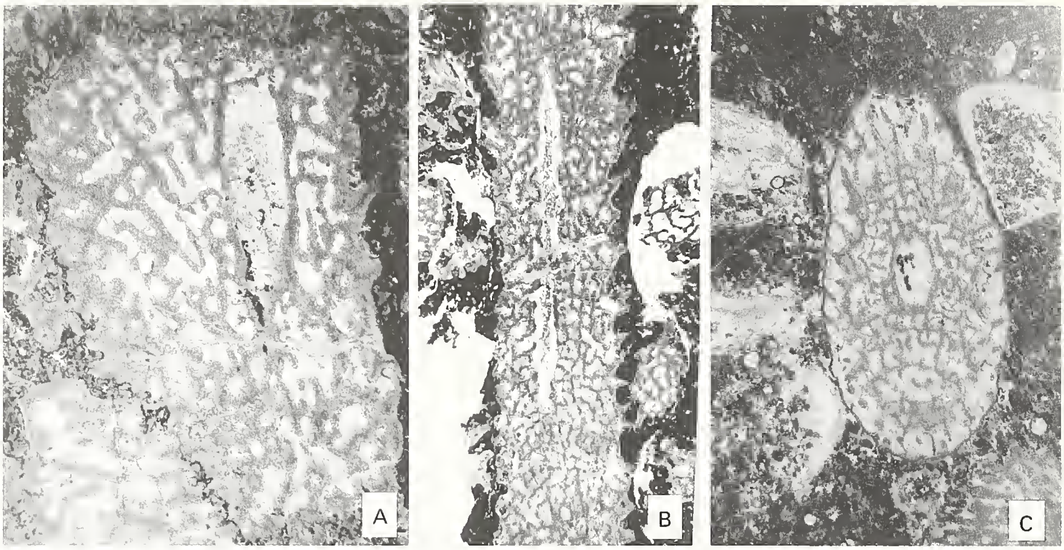
TEXT-FIG. 8. A, *Amphipora ramosa* (Philips 1841)?; specimen from core (McGill Redpath Museum RM 20·5341), Swan Hills field, north central Alberta at 8901 ft [10-34-63-11W5th mer]. Note the outgrowth on the central stem that could be a root structure and the great variation in axial canals and peripheral membranes in a single slide; × 5. B–D, *Amphipora ramosa* (Phillips, 1841). B, neoparatype PO 309.B3; axial section, showing wide axial canal with many pores, well-developed pillars, and a poorly developed peripheral membrane on the middle left; × 10. C, neotype suite PO 308.A15; axial section, showing discontinuous membrane, well developed in the upper right and largely absent below on this side, well-developed pillars holding the membrane, and tabulae crossing the axial canal; × 5. D, section PO 308.A9; cross sections from the neotype suite, showing fibrous microstructure, post-and-bridge construction, dissepiments and tabulae; internal spaces largely open in the stem on the left and closed on that on the right; × 20.



TEXT-FIG. 9. *Amphipora ramosa* (Phillips, 1841); Broadridge Wood Quarry. A, neoparatype PO 310.C6; axial section, showing infilling of upper part by fine sediment and well-developed peripheral vesicle at lower left ending upward without breakage; ×8. B, neotype suite section PO 308.A11; axial section, showing branching and a distal tip with open axial canal infiltrated by sediment; ×10. C, section PO 308.A19; very thin peripheral membrane and narrow vesicle, cross section of neotype suite stem, also showing the fibrous microstructure; ×25.

Axial canal. The canal is present in most stems, obscure or completely unrecognizable in a few, generally bounded by a distinct skeletal wall (Text-fig. 8D), crossed by thin, curved dissepiments of irregular form. Mean of 31 diameters of neotype suite 0·73 mm (range: 0·47–1·0 mm; standard deviation: 0·17 mm). Mean of ratio of axial canal diameter to stem diameter in these specimens 0·22 (range: 0·12–0·39). Canal opening laterally through pores into irregular interskeletal spaces or into canals extending towards the periphery (Text-fig. 8B, D). Highly irregular and locally incomplete tabulae cross the axial canal (Text-fig. 8B–D).

Skeletal network. Skeletal elements commonly 100 to 200 μm thick, possibly diagenetically thickened, highly variable in form and thickness, locally forming an open network in which skeleton forms a small proportion of the stem (Text-figs 4B, 8D), locally almost filling the stem leaving small round interskeletal cavities (Text-figs 4A, 5A–B). In cross section the skeleton appears to be constituted either of isolated pillar-like elements commonly connected by bridges (Text-fig. 8D) or, particularly near the axial canal, of a continuous network inclosing small circular spaces (or canals). Locally the structural elements define and border irregular, tortuous canal systems radiating toward the periphery (Text-figs 4B–C, 8D). Interskeletal spaces crossed by very thin, curved dissepiments (Text-fig. 8D). In axial section the skeleton is cut as an irregular network through which thin pillars curve upward and outward at *c.* 45° from the axial canal to the periphery, commonly supporting the peripheral membranes (if present) at their distal ends (Text-figs 8B–C, 10C). The skeletal network in axial section shows no evidence of parabolic growth lines or structural elements parallel to the growth surface. In oblique sections the pillars are prominent and form an irregular grid with subhorizontal structural elements (Text-fig. 10A, C).



TEXT-FIG. 10. *Amphipora ramosa* (Phillips, 1841). A, section PO 308.A12; oblique section showing the pillars and bridging skeletal elements, neotype suite; × 10. B, section PO 308.A14; axial section, neotype suite, showing complete lack of peripheral vesicles; × 5. C, section PO 308.A15; oblique section showing well-developed thin continuous peripheral membrane, axial canal, and pillars, neotype suite; × 5.

Microstructure. Pillars that are cut across show radial fibrosity (Text-figs 8D, 9C) around a more opaque centre. Linear elements have an opaque axis bordered on either side by a layer of fibrous calcite (Stearn 1977, pl. 3, fig. 3).

Peripheral structures. Three conditions exist at the periphery and more than one condition may exist in a single stem.

1. The structural elements may protrude into the matrix in the absence of a peripheral membrane and the matrix may penetrate a short distance between these elements (Text-figs 1, 4–5). Only rarely does it penetrate deeply into the interskeletal spaces (Text-fig. 9A) that are filled typically with cavity-filling spar. The penetration may be stopped by a transverse skeletal element of normal thickness, a thin dissepiment, or a throat that is too small for the clasts of the grainstone matrix to enter.
2. The structural network is bordered by a membrane of the same thickness as the structural elements (*c.* 100 μm) that incloses vertically elongate spaces as peripheral membranes. These spaces may be impersistent along the length of the stems (Text-figs 8C, 9A).
3. A delicate, continuous peripheral membrane (< 50 μm) surrounds a spar-filled cavity crossed only by the pillar structures that support it and by dissepiments. The width of the inclosed vesicle ranges from one-half to a small fraction of the radius of the stem (Text-figs 8A, 9C, 10C).

The peripheral membranes, where well preserved, appear to be imperforate. Where one is absent (condition 1) canal systems may extend from the axial canal to the matrix by tortuous courses.

Diagnostic features. Within the wide range of variation shown by the neotype suite, what features have potential to be used in distinguishing the species from other species of the genus or differentiating other genera within the family Amphiporidae? The following features that show wide variation within the individual stems or suite here considered to be remnants of a monospecific stand, are certainly not species specific:

1. presence, absence, or form of peripheral membranes;
2. presence, absence, or distinctness of the axial canal;

3. density of the structural network and thickness of the elements;
4. form and abundance of dissepiments.

Features that have potential for separating *A. ramosa* from other species are:

1. the relative constancy of the diameter of the stems;
2. the relatively small diameter of the axial canal and its proportion of the total diameter of the stem;
3. the pillars spreading upward and outward from the axial canal.

Comparison with Phillips' and Schulz's material. Why should the suite of specimens described above be accepted as representative of Phillips' species *Caunopora ramosa*? They are not strictly topotypes because Phillips' only bedrock locality was apparently the ridge of the Chercombe Bridge Limestone south of Chudleigh about 5 km north of the Broadridge Wood Quarry. Evidence that the neotype is representative of Phillips's material can be found in comparisons with nineteenth century descriptions and illustrations of these fossils from Devon (there are no twentieth century studies), specimens from Devon in museums, and topotype material collected from Chudleigh.

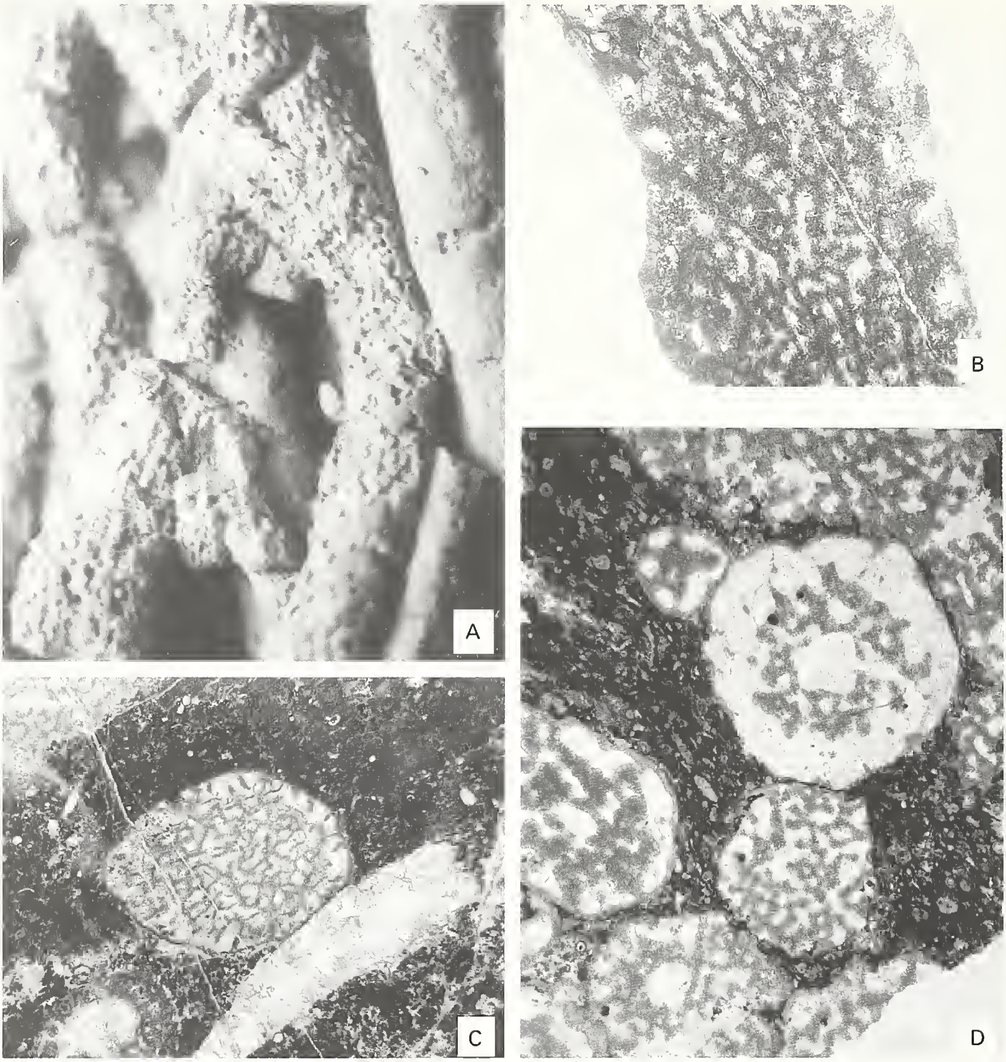
1. Phillips' illustrations (1841, pl. 8, fig. 22a–c) show a stem with relatively small axial canal. The axial section clearly shows the pillars curving upward and outward from the axial canal. Although the diameter of the stems is not given, measurements of the figure suggest that it is about 3·5 mm, (cf. average of 3·26 mm in neotype suite).
2. Schulz's oblique sections clearly show the prominent pillars typical of the neotype in stems 3–4 mm in diameter, peripheral membranes, and a relatively wide structural zone.
3. Specimens from near the type locality, presumably south of Chudleigh, although poorly preserved, show a similar form and range of variation as those in the neotype suite (Text-fig. 3B).
4. M'Coy's (1855, p. 67) description of specimens from Teignmouth mentioned the 'plates... radiating obliquely upwards and outwards from the large central channel to the surface.'.
5. Nicholson's (1892, pl. 29, figs 1–7) illustrations of specimens from Teignmouth show similar, widely varying, proportions to the neotype but do not faithfully represent the pillars. His (1892, p. 225) remarks on the extraordinary variability of Devon *A. ramosa* and his opinion that 'It is most probable that these different forms are really different conditions of a single type...' are strongly supported in this study.

The great variability of the Devon specimens places the validity of the almost 175 species of amphiporids in doubt; their validity must be reassessed. Even a casual survey of these species indicates that the range of variation seen in the neotype specimen and neotype suite includes that of many species described from the Middle and Upper Devonian of various parts the world.

FUNCTIONAL MORPHOLOGY

As mentioned in the introduction, the symmetry and branching of *Amphipora* show that it must have stood upright on the sea floor in underwater 'meadows', but no trace of a root has been described. Possibly, like the aulacerids described by Cameron and Copper (1994), they reinforced their bases by biocementation of the surrounding carbonate substrate. The irregular outgrowths on some specimens encountered in random sections may be a spreading root system or another individual wrapped around a stem (Text-fig. 8A). Their symmetry and branching preclude an existence rolling on the bottom as suggested by Bogoyavlenskaya (1985), nor is there any evidence connecting their occurrence with domical stromatoporoids with high mamelons that broke off.

The distal growing tip has been identified in only two stems of the neotype suite (Text-fig. 9B). In random sections the tortuous course of the stems makes following the axial canal throughout its length in a section almost impossible. In the section illustrated here the tip is rounded, the canal is open at the end and coarse sediment has penetrated into the opening. This configuration and the canals that are evident in some sections radiating from the axial canal directly through the structure suggest that this is a modified astrorhizal system, as suggested by Lecompte (1952). The axial canal has also been shown to open at the end of branches in other cylindrical stromatoporoids, such as



TEXT–FIG. 11. A–C. *Amphipora ramosa* (Phillips, 1841). A, exterior surfaces of a specimen from Schulz's 'ramosabänke' showing some stems with the smooth outer surface of the peripheral membrane, others with open canals; Bonn University, Paläontologische Institut; × 3. B, previously unillustrated tangential section from Nicholson's No. 399 specimen from Hebborn, Germany(Natural History Museum P6071), showing the pillars not clearly illustrated by Nicholson (1886); × 10. C, section PO 308.A15; slightly oblique section, neotype suite, showing thin vesicles and no trace of an axial canal; × 5. D, *Amphipora ramosa* (Phillips, 1841)?; cross sections, Swan Hills field Alberta (as Text-fig. 8A, McGill Redpath Museum RM 20.5341), showing extreme variation in size of stems, complexity of structure, development of the axial canal, and width of the peripheral membranes in a small area; × 10.

Stachyodes. However, unlike the internal structure of other cylindrical stromatoporoids, such as *Stachyodes*, that of *Amphipora* does not preserve successive surfaces parabolic in axial section and parallel to the rounded growing tip.

In nearly all the samples examined, regardless of whether the peripheral membranes are intact, the open space in amphiporids is filled with calcite spar, generally a coarse cavity–filling spar.

Not only are the interstructural spaces (?galleries) filled with spar, the axial canal is also, except at the open end. Since both interior spaces are commonly crossed by dissepiments, I conclude that, like the lower parts of domical stromatoporoids or tabulate corals, they were closed off by the organism as it grew and were empty of organic matter when the organism died. The living tissue was then confined to the upper part of the stem (Stearn and Pickett 1994).

In the specimens studied here, a growth series has not been demonstrated, but variation in the thickness of the structural elements and density of the structure in a single stem is evident (Text-figs 1, 4–5). The thickening of structural elements by overgrowth in the older parts of invertebrate skeletons is well documented in the coralline sponge *Astrosclera* and may also have taken place in *Amphipora*.

Many stems of the neotype suite do not have evident peripheral membranes. In some a membrane clearly separates a narrow vesicle from the matrix, and in many the ends of the structural elements protrude into the matrix. In stems with peripheral membranes in parts of the stem, there is no evidence of breakage at the point where the membrane ends against the structural elements of the stem (Text-figs 8C, 9A). The presence of membranes seems to have some relationship to the matrix in which the stems are embedded. Stems in grainstones rarely have membranes; those in micrites and wackestones commonly have membranes. In the large block collected loose at the bottom of the Broadridge Wood quarry (neoparatype No. PO 310) most of the stems have peripheral membranes. The matrix in these specimens is micritic, finer than that in the neotype, which locally penetrates the interstructural cavities (Text-fig. 9A). Axial sections of this sample show peripheral cavities locally along the length of the stems; these are unbroken where they end against the network of structural elements (Text-fig. 9A). Membranes may be present on one side of a stem and not on the other (Text-figs 8C, 9A). In a sample used for comparison from the Beaverhill Lake Formation (Frasnian) of the Swan Hills area, Alberta, nearly all the stems have peripheral membranes but the width of the cavities they inclose ranges from 0–1000 μm, or from 0–50 per cent. of the radius of the stem (Text-figs 8A, 11D). On the surfaces of Schulz's specimens preserved in three dimensions from the 'ramosabänke' (Text-fig. 11A), the smooth peripheral membrane is present on some parts of the stems and on other parts the rough surface of the ends of the structural elements is evident. In no specimen was an opening seen in this membrane; it appears to have completely sealed the skeleton. From these observations the following conclusions are drawn.

1. The absence of membranes on stems is not everywhere a result of abrasion of the stems, because broken membranes are only rarely found.
2. The development of the membranes is part of the normal growth of *Amphipora*.
3. The membranes did not form only on the base as the organism grew but are sporadically present along some stems.
4. Where present, the membranes sealed off the interior of the skeleton.

Structures possibly analogous to the *Amphipora* membranes have been noted in some other stromatoporoids but their preservation is extremely rare. Nicholson (1886, pp. 59–60) noted the presence of 'a thin apparently structureless calcareous membrane, largely or wholly imperforate' or (p. 110) 'a kind of calcareous pellicle', on several domical and encrusting stromatoporoids. Nicholson (1886, p. 60), Cockbain (1981, pp. 28, 30) and Zukalova (1971, p. 101) reported a thin calcareous membrane on specimens of *Stachyodes*. Structures similar to the peripheral membranes occur in the soft tissue of the coralline sponges *Ceratoporella* and *Stromatospongia* (Willenz and Hartmann 1989). Inhalent water enters a vestibule above the skeleton through microscopic pores in a dermal membrane and passes into the choanocyte chambers within the top of the skeleton. Within the vestibule, water exhaled from the choanocyte chambers is separated from the inhalent water by confinement in a gathering system of tubes analogous to the astrorhizal canals of stromatoporoids. Stearn (1975) has reconstructed domical stromatoporoids with a dermal membrane and vestibule. The calcification of such a membrane as the inhalent surface became non-functional in older or damaged or buried parts of the skeleton would produce a membrane-and-vesicle structure much like that of *Amphipora*. Perhaps such a sealing of the skeleton was required in environments that were rich in fine sediment.

In most deposits the diameter of the stems is relatively constant and strictly axial sections (i.e. those that include the axial canal for much of their length) do not show an increase in width that would be indicative of growth in girth. Such stems are invariably cylindrical. However, some assemblages contain small skeletons of simple internal structure (Text-figs 8A, 11D) that could have been juveniles. In the absence of conical stems, the amphiporid animal is reconstructed as cylindrical throughout its growth (Text-fig. 2) and thin stems are considered to have been unsuccessful and malnourished individuals.

The amphiporid animal can be reconstructed as a small sponge growing in shallow, calm waters periodically swept by storms. The stem was anchored inefficiently by irregular outgrowths at the base or cemented into the substrate. The growing tip had a central opening or osculum that acted as an exhalent pore but extended into a shallow cavity as a spongocoel, blocked below by a tabula. From the spongocoel, collector canals ran irregularly to choanocyte chambers within the structural network. The living tissue was confined to the growing tip; as the soft tissue died, older parts of the skeleton were partitioned off internally by dissepiments and sealed off externally by calcification of the dermal membrane. During growth the exhalent drainage system was at times reorganized so that the walls of the spongocoel broke down and the discreteness of the axial canal was lost. Similar reorganizations of the aquiferous system in living sponges are common and in many stromatoporoids the location of the homologous astrorhizal system was ephemeral. Some of the sponges branched; others remained single. Periodically the *Amphipora* meadows were despoiled by storms that broke the sponges from their bases, fragmented them, and swept them into environments where they did not live. In Devon and western Canada the association of *Amphipora* with grainstones rich in calcispheres suggests that these enigmatic capsules could be related to the propagation of this sponge.

CONCLUSIONS

The large range of variation shown within individual stems of *Amphipora* and suites of specimens preserved together places in doubt the validity of genera separated from the genus and the many species of these genera that have been included in the family Amphiporidae. Description of new taxa in this group should be accompanied by a clear statement of variation along the stem. The illustration of single cross or axial sections is inadequate to establish a new taxon. This study also illustrates that the plethora of generic or specific taxa in the literature may not be a guide to true taxonomic diversity. It suggests that the generic diversity of the family Amphiporidae should be reduced by about one-half.

In concluson, the questions posed at the beginning of this paper can be answered as follows. The typical form of the genus *Amphipora* has been determined by establishing a neotype that is demonstrated to be representative of the original lost type. The small sponge exhibited various configurations of skeletal features as it grew, but these can not be arranged in a growth series. Some of these features have been recognized as of generic rank and most have been recognized as of specific rank. The type specimens of amphiporids cannot be an assemblage of individuals but should be a single stem. The organism can be reconstructed as a small sponge growing in large numbers in shallow marine water.

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DIAGENESIS AND SURVIVAL OF INTRACRYSTALLINE AMINO ACIDS IN FOSSIL AND RECENT MOLLUSC SHELLS

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ABSTRACT. Amino acid analysis was carried out on intracrystalline organic material from fossil and recent mollusc shells from South Wanganui Basin, New Zealand, ranging in age from 3·6 My old to Recent. The absolute abundance of amino acids is highly variable but shows a gradual decline through time due to diagenetic effects. The proportion of peptide-bound amino acids decreases with time, and there is a corresponding increase in free amino acids as proteins are broken down by natural hydrolysis. By 0·5 Ma, most amino acids are free, and the rate of decay of peptide bonds appears to slow appreciably, with small proportions of peptide bound amino acids occurring in shells throughout the time span investigated. The quantities of free amino acids reach a peak between 0·5 and 1 Ma, after which there is a general decrease in most individual amino acids, presumably because they decay or become incorporated into predominantly insoluble geopolymers. Alanine is a notable exception, increasing in older samples because it is a common by-product of the breakdown of other amino acids.

Amino acid data from different species and from shell beds of different ages were compared using multivariate statistical techniques. The results indicate that, despite the effects of diagenesis, the original biochemical distinction between different groups of molluscs (i.e. different proteins within the shell) survives for at least 3·6 My, and may be detectable in older specimens provided sufficient original amino acids remain.

IN order to gain meaningful information from organic molecules in fossil shells, it is necessary to isolate original organic matter which has not been contaminated or replaced by more recent biomolecules. For this purpose, intracrystalline biomolecules are used. These molecules are trapped within the crystals of the shell during biomineralization and are therefore protected from contamination by outside sources until released by decalcification. Many of these molecules may have been actively involved in the process of shell formation by acting as a nucleation site for crystal growth (Lowenstam and Weiner 1989). The molecules which are involved in the biomineralization process are usually proteins and protein-like macromolecules secreted by the cells of the mantle, which form a matrix within and around which calcium carbonate crystals are precipitated (Lowenstam and Weiner 1989). Each protein molecule consists of a chain of amino acids, the order of which is determined by the sequence of nucleotides in the DNA which controls its production. These amino acids are therefore directly related to genotype and may represent useful taxonomic indicators even after the protein sequence has been destroyed (Walton 1992). The interpretation of amino acid data from fossil shells, however, is complicated by the fact that individual amino acids vary in stability, and can decompose at varying rates into other compounds or into other amino acids (Vallentyne 1964, 1968). Hence the amino acid compositions of fossil shells are likely to be less easy to interpret and will reflect complicated amino acid diagenesis reactions as well as original taxonomic variability. The purpose of this paper is to analyse both the peptide bound and the free (i.e. naturally hydrolysed) amino acids from within shells of different ages, in order to investigate the state of preservation of intracrystalline proteins and the extent to which original biochemical differences between taxonomic groups survives the fossilization process.

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TEXT-FIG. 1. Map showing locations of collection sites.

LOCALITIES AND METHODS

Fossil mollusc shells were collected from sea cliffs and inland exposures in the South Wanganui Basin, New Zealand (Text-fig. 1). This area was chosen for its almost continuous sequence of late Pliocene and Pleistocene fossiliferous shallow marine deposits containing abundant mollusc shells. The sequence consists of poorly consolidated layers of sand and mud deposited mainly during interglacials and separated by unconformities associated with glacial marine regressions. Recent mollusc shells were collected from near shore locations and from beaches around the coasts of the North and South Islands of New Zealand (Text-fig. 1).

Well preserved shells of various species were selected from shell beds at different levels in the Wanganui sequence (Text-fig. 2) along with related Recent species. Several specimens were taken from each of 28 shell beds, making 60 specimens in all (Table 1). Each specimen was examined by SEM to check for signs of recrystallization, and XRD analysis was used to check that aragonite shells had not reverted to calcite, as such recrystallization would have allowed contamination of intracrystalline biomolecules. The shells were cleaned of sediment and algae and the ligaments removed. Where necessary the shells were placed in a cool oven at 40 °C to dry out the periostracum which was then removed. Each shell was washed in water then soaked in an aqueous solution of bleach to remove any remaining organic molecules from the surface by oxidation. The shells were then rinsed in clean Milli Ro^{TM} water and left to air dry.

Small carbonate samples were taken from each shell using a small drill with a rotating tip with a diameter of 1 mm. Intercrystalline organic matter was removed from the carbonate powder by

Stage	Substage	Formation	Sample No.
Haweran		Alluvium	
		Rapanui Formation	17,18
		Brunswick Formation	
		Kaiatea Formation	
		Landguard Formation	5,19,20,21
Castlecliffian	Putikian	Putiki Shellbed	
		Mosstown Sand	
		Karaka Siltstone	
		Upper Castlecliff Shellbed	22,23,24
		Shakespeare Cliff Sand	25,26,27,28,29
		Shakespeare Cliff Siltstone	
		Tainui Shellbed	30,31,32
		Pinnacle Sand	
		Lower Castlecliff Shellbed	33,34,35
		Seafield Sand	36,37,38
		Upper Kai Iwi Siltstone	39
		Kupe Formation	8,40,41,42
	Okehuan	Upper Westmere Siltstone	47,48
		Kaikokapu Formation	43,44
		Lower Westmere Siltstone	
		Ophiomorpha Sand	
		Omapu Shellbed	45,46
		Lower Kai Iwi Siltstone	49
		Kaimatira Pumice Sand	50
		Upper Okehu Siltstone	
		Okehu Shell Grit	51,52,53
		Lower Okehu Siltstone	
		Mowhanau Formation	
		Ototoka Siltstone	
		Butler's Shell Conglomerate	54,55
Nukumaruan	Marahauan	Upper Maxwell Formation	
		Mangahou Siltstone	56
		Middle Maxwell Formation	
		Pukekiwi Shell Sand	57
		Lower Maxwell Formation	
		Tewkesbury Formation	
		Waipuru Shellbed	
		Nukumaru Brown Sand	58,59,60
		Mangamako Shellbed	
		Nukumaru Limestone	14
		Ohingaiti Sand	
	Hautawan	Undifferentiated Formations	
		Kuranui Limestone	
		Hautawa Shellbed	61
Waitotaran	Mangapanian	Te Rama Shellbed	
		Parihauhau Shellbed	
		Te Rimu Sand	
		Wilkies Shellbed	62
		Makokako Sand	
		Mangaweka Mudstone	
		Paparangi Sandstone	
	Waipipian	Waverley Formation	
		Upper Waipipi Shellbed	13,65,66
		Middle Waipipi Shellbed	63,67
		Lower Waipipi Shellbed	68
		Snapper Point Shellbed	4
		Rangikura Sandstone	
		Pepper Shell Sand	1,2,3

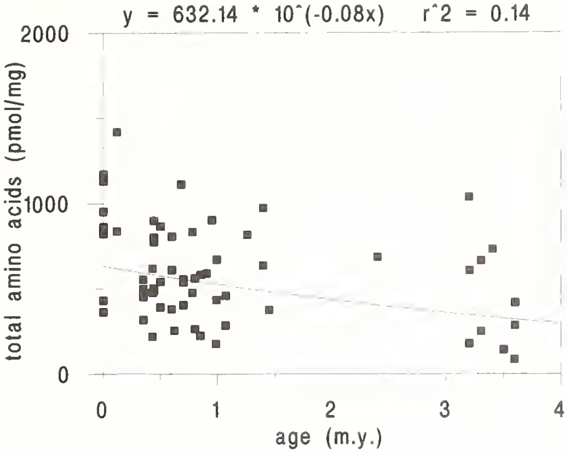
TEXT-FIG. 2. Stratigraphical column of the Wanganui Series, after Fleming (1953) and Abbott and Carter (1991), showing sample points.

TABLE 1. Shell samples 1–60: species, superfamilies, locations and ages.

1. *Maoricardium spatiosum* (Cardiacea) – Pepper Shell Sand (*c.* 3·6 Ma)
2. *Phialopecten marwicki* (Pectinacea) – Pepper Shell Sand (*c.* 3·6 Ma)
3. *Maoricardium spatiosum* (Cardiacea) – Pepper Shell Sand (*c.* 3·6 Ma)
4. *Maoricardium spatiosum* (Cardiacea) – Snapper Point Shell bed (*c.* 3·5 Ma)
5. *Pecten tainui* (Pectinacea) – Landguard Formation (*c.* 0·35 Ma)
6. *Anchomasa similis* (Pholadacea) – Castlecliff Beach (Recent)
7. *Paphies* (*Mesodesma*) *subtriangulata* (Mesodesmatacea) – Long Beach (recent)
8. *Tiostrea chilensis* (Ostreacea) – Kupe Shell bed (*c.* 0·7 Ma)
9. *Paphies australis* (Mesodesmatacea) – Te Rauone Beach (Recent)
10. *Chione* (*Austrovenus*) *stutchburyi* (Veneracea) – Warrington Beach (Recent)
11. *Maoricolpus roseus* (Cerithiacea) – Long Beach (Recent)
12. *Maoricardium spatiosum* (Cardiacea) – Upper Waipipi (*c.* 3·2 Ma)
13. *Patro undatus* (Anomiacea) – Nukumaru Limestone (*c.* 1·45 Ma)
14. *Chione* (*Austrovenus*) *stutchburyi* (Veneracea) – Te Rauone Beach (Recent)
15. *Mactra discors* (Mactracea) – Warrington Beach (Recent)
16. *Spisula* (*Crassula*) *aequilateralis* (Mactracea) – Rapanui Formation (*c.* 0·12 Ma)
17. *Paphies* (*Mesodesma*) *subtriangula* (Mesodesmatacea) – Rapanui Formation (*c.* 0·12 Ma)
18. *Tawera spissa* (Veneracea) – Landguard Formation (*c.* 0·35 Ma)
19. *Tiostrea chilensis lutaria* (Otreacea) – Landguard Formation (*c.* 0·35 Ma)
20. *Pecten tainui* (Pectinacea) – Landguard Formation (*c.* 0·35 Ma)
21. *Zethalia zelandica* (Trochacea) – Upper Castlecliff Shell bed (*c.* 0·43 Ma)
22. *Paphies* (*Mesodesma*) *subtriangulata* (Mesodesmatacea) – Upper Castlecliff Shell bed (*c.* 0·43 Ma)
23. *Venericardia purpurata* (Carditacea) – Upper Castlecliff Shell bed (*c.* 0·43 Ma)
24. *Paphies* (*Mesodesma*) *subtriangulata* (Mesodesmatacea) – Shakespeare Cliff Sand (*c.* 0·44 Ma)
25. *Pecten tainui* (Pectinacea) – Shakespeare Cliff Sand (*c.* 0·44 Ma)
26. *Tiostrea chilensis lutaria* (Ostreacea) – Shakespeare Cliff Sand (*c.* 0·44 Ma)
27. *Paphies* (*Mesodesma*) *subtriangulata* (Mesodesmatacea) – Shakespeare Cliff Sand (*c.* 0·44 Ma)
28. *Venericardia purpurata* (Carditacea) – Shakespeare Cliff Sand (*c.* 0·44 Ma)
29. *Tiostrea chilensis lutaria* (Ostreacea) – Tainui Shell bed (*c.* 0·5 Ma)
30. *Maoricolpus roseus* (Cerithiacea) – Tainui Shell bed (*c.* 0·5 Ma)
31. *Venericardia purpurata* (Carditacea) – Tainui Shell bed (*c.* 0·5 Ma)
32. *Pecten tainui* (Pectinacea) – Lower Castlecliff Shell bed (*c.* 0·6 Ma)
33. *Maoricolpus roseus* (Cerithiacea) – Lower Castlecliff Shell bed (*c.* 0·6 Ma)
34. *Venericardia purpurata* (Carditacea) – Lower Castlecliff Shell bed (*c.* 0·6 Ma)
35. *Venericardia purpurata* (Carditacea) – Tom's Conglomerate (*c.* 0·62 Ma)
36. *Tiostrea chilensis lutaria* (Ostreacea) – base of Upper Kai-Iwi Siltstone (*c.* 0·68 Ma)
37. *Maoricolpus roseus* (Cerithiacea) – Kupe Formation (*c.* 0·7 Ma)
38. *Venericardia purpurata* (Carditacea) – Kupe Formation (*c.* 0·7 Ma)
39. *Paphies* (*Mesodesma*) *subtriangulata* (Mesodematacea) – Kaikokapu Formation (*c.* 0·78 Ma)
40. *Venericardia purpurata* (Carditacea) – Kaikokapu Formation (*c.* 0·78 Ma)
41. *Divaricella* (*Divalucina*) *huttoniana* (Lucinacea) – Omapu Shell bed (*c.* 0·85 Ma)
42. *Amalda* (*Baryspira*) *mucronata* (Muricacea) – Omapu Shell bed (*c.* 0·85 Ma)
43. *Amalda* (*Baryspira*) *mucronata* (Muricacea) – Upper Westmere Shell bed (*c.* 0·8 Ma)
44. *Maoricolpus roseus* (Cerithiacea) – Upper Westmere Shell bed (*c.* 0·8 Ma)
45. *Paphies* (*Mesodesma*) *subtriangulata* (Mesodesmatacea) – Lower Kai-Iwi Shell bed (*c.* 0·9 Ma)
46. *Paphies* (*Mesodesma*) *subtriangulata* (Mesodesmatacea)– Kaimatira Pumice Sand (*c.* 0·95 Ma)
47. *Maoricrypta* (*Zeacrypta*) *monoxyla* (Calyptraeacea) – Okehu Shell Grit (*c.* 0·99 Ma)
48. *Tiostrea chilensis lutaria* (Ostreacea) – Okehu Shell Grit (*c.* 0·99 Ma)
49. *Venericardia purpurata* (Carditacea) – Okehu Shell Grit (*c.* 0·99 Ma)
50. *Maoricrypta* (*Zeacrypta*) *monoxyla* (Calyptraeacea) – Butler's Shell Conglomerate (*c.* 1·07 Ma)
51. *Chlamys gemmulata* (Pectinacea) – Butler's Shell Conglomerate (*c.* 1·07 Ma)
52. *Austrovenus stutchburyi* (Veneracea) – Mangahou (*c.* 1·26 Ma)
53. *Patro undatus* (Anomiacea) – top of Nukumaru Brown Sand (*c.* 1·4 Ma)
54. *Lutraria solida* (Mactracea) – Nukumaru Brown Sand (*c.* 1·4 Ma)

TABLE 1. (*cont.*)

55. *Patro undatus* (Anomiacea) – Hautawa shell bed (*c.* 2·4 Ma)
56. *Crassostrea ingens* (Ostreacea) – Middle Waipipi (*c.* 3·3 Ma)
57. *Lima waipipiensis* (Limacea) – Upper Waipipi (*c.* 3·2 Ma)
58. *Crassostrea ingens* (Ostreacea) – Upper Waipipi (*c.* 3·2 Ma)
59. *Maoricardium spatiosum* (Cardiacea) – Middle Waipipi (*c.* 3·3 Ma)
60. *Crassostrea ingens* (Ostreacea) – Lower Waipipi (*c.* 3·4 Ma)

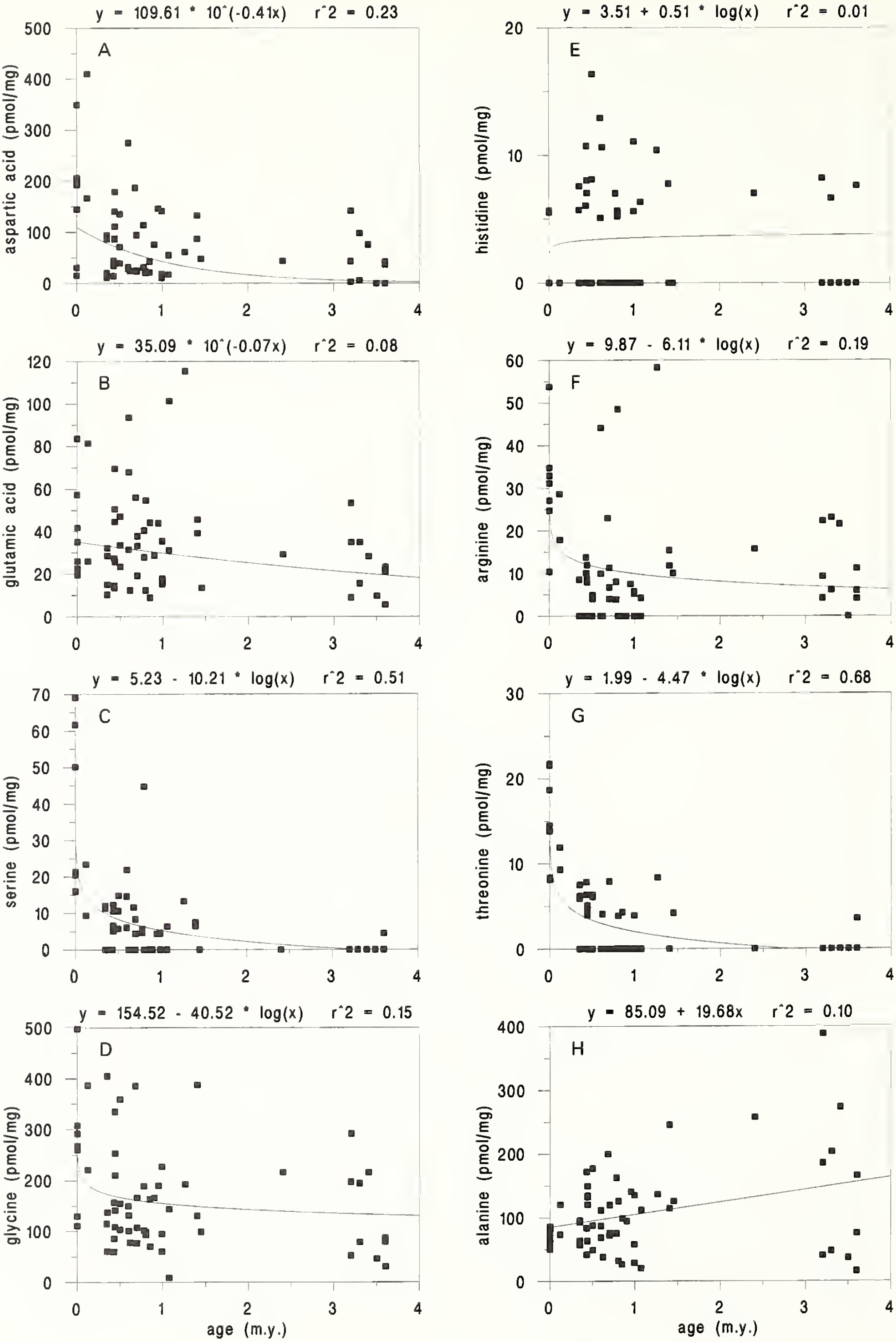


TEXT-FIG. 3. Total intracrystalline amino acids in all samples plotted against sample age.

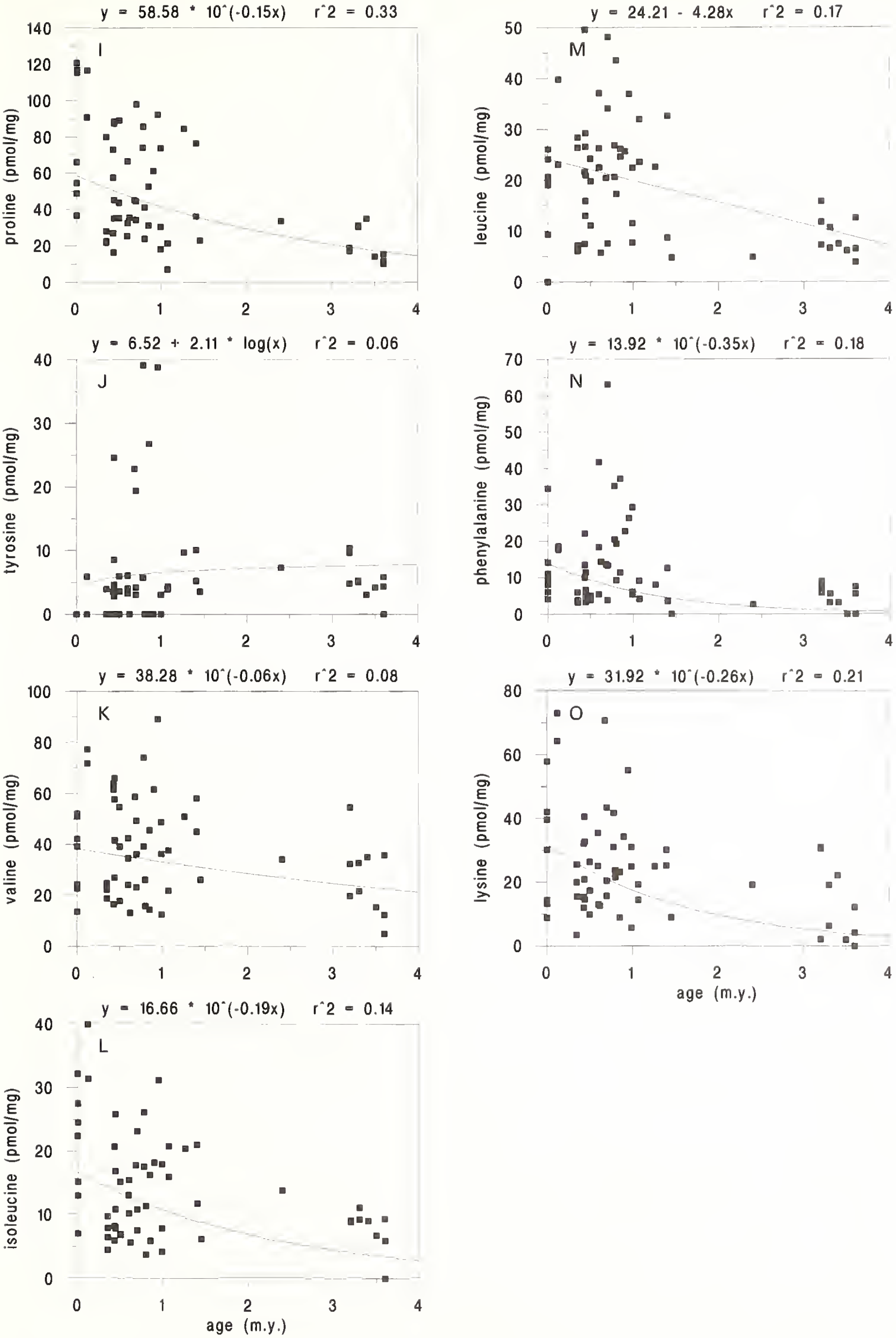
plasma ashing. The samples were dissolved in 2N hydrochloric acid at a ratio of 11 μl per mg of shell and centrifuged to remove insoluble compounds. Analysis was carried out using an Applied Biosystems 420H amino acid analyser. Each sample was analysed both with and without hydrolysis in order to determine the proportion of amino acids present in the free state, i.e. the extent to which the intracrystalline proteins in each shell had been naturally hydrolysed.

Some common proteinogenic amino acids are easily destroyed by hydrolysis. These include asparagine and glutamine (these get hydrolysed to aspartic acid and glutamic acid), methionine and cysteine (these break down due to the oxidation of side-chain sulphur atoms) and tryptophan (this is lost due to the breaking of the carbon double bond present within its ring structure). These reactions are likely to have occurred by natural hydrolysis long before analysis. Therefore, in this study, amounts of original asparagine and glutamine are included in the figures for aspartic acid and glutamic acid respectively, and methionine, cysteine and tryptophan are not quantified. The resulting changes in bulk amino acid composition apply consistently to all samples and therefore do not affect sample relationships. Data are presented as picomoles per milligramme of shell (pmol/mg), which is the form in which the raw data are obtained from the amino acid analyser. This is equivalent to nanomoles per gramme of shell.

The amount of peptide bound amino acids is calculated by subtracting the free amino acids from the total amino acids. Sometimes this results in a negative value, indicating that there are more free amino acids than total amino acids, an impossible conclusion. This problem results from the fact that for total amino acid analysis, peptide bonds must be first hydrolysed using hydrochloric acid. This can result in the total destruction of some amino acids as outlined above. In addition, certain other amino acids may suffer some small losses as a result of this hydrolysis. For example, losses of the amino acids serine, threonine and tyrosine may be of the order of 10–20 per cent. When this problem occurs, and the calculated value for the peptide bound amino acids is negative, the value is taken to be zero.



TEXT-FIG. 4. For caption see opposite.



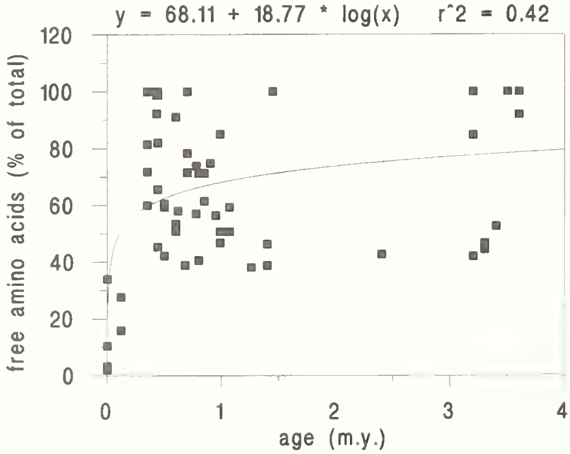
TEXT-FIG. 4. Amount of total individual intracrystalline amino acids plotted against sample age.

The amino acid data were analysed statistically by means of principal component analysis techniques using the program 'Datadesk™' on an Apple Macintosh™ microcomputer. The aim was to investigate the relationships between the amino acid compositions of different samples using a suitable multivariate procedure. In this way a high percentage of the total variance between samples can be expressed on a three dimensional, rotating plot. Groups of samples were chosen that were known to be taxonomically related (e.g. the mollusc superfamilies Cardiacea, Carditacea, Pectinacea, Mactracea, Ostreacea, Anomiacea, Mesodesmatacea, Veneracea and Cerithiacea). Groups of samples from three, four or five superfamilies were plotted together according to their amino acid compositions.

CHANGES IN AMINO ACID COMPOSITIONS THROUGH TIME

The total intracrystalline amino acid compositions of all 60 samples are shown in Text-figure 3. The data reveal a high degree of variability, even in recent samples in which the absolute yield of amino acids ranges from about 400 to 1200 pmol/mg. This level of variability is maintained in fossil samples. Statistically there is an overall decline in abundance through time, but the low coefficient of correlation is testimony to the highly variable nature of the amino acid data. Clearly different taxa of molluscs have very different quantities of proteins present in their shells and this is reflected in the variable yields from related fossil taxa. A gradual decline through time is also seen in most individual amino acids with the notable exception of alanine which increases quite significantly (Text-fig. 4). A few amino acids, such as histidine and tyrosine, are present in such small quantities that the pattern is distorted due to the effect of the detection limit of the amino acid analyser (about 5 pmol/mg), which results in a 'gap' in the results below this value.

Free amino acids are rare in Recent samples, but rapidly become an increasingly important component of the total amino acid yield (Text-fig. 5). Many of the individual amino acids show a pattern of rapid initial increase during the first 0·5 My followed by a gradual decline in older specimens, probably due to the decay of amino acids to form compounds that are not detected by the amino acid analyser (Text-fig. 6). Alanine shows a marked increase over the whole period. The total free amino acids show an initial increase followed by a levelling off as the decline in most individual free amino acids is offset by the increase in alanine, this being the most abundant individual free amino acid. The absolute yield of free amino acids from different specimens is, like the total yield, highly variable. As expected, the rapid initial increase in free amino acids is matched by a rapid initial decrease in peptide bound amino acids (Text-fig. 7). This pattern is seen in most individual peptide bound amino acids except histidine and tyrosine, which are present in such small quantities as to show no pattern (Text-fig. 8).



TEXT-FIG. 5. Free intracrystalline amino acids as a percentage of the total intracrystalline amino acids in all samples through time.

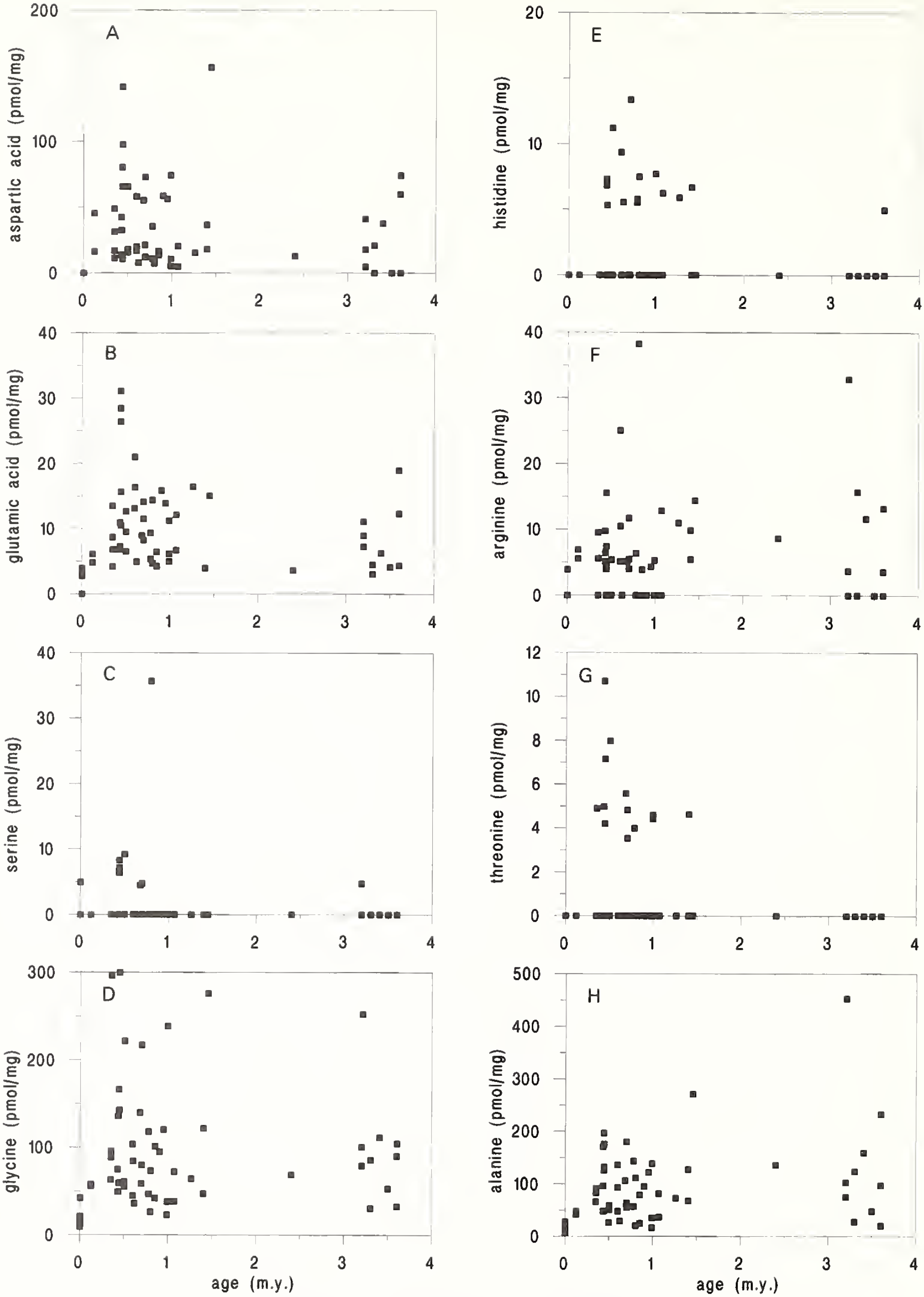
These results are largely as would be expected. The gradual decrease in total amino acids through time is likely to be a function of biochemical reactions which gradually break down some of the amino acids into other compounds which are not detected by the amino acid analyser. In recent shells, the large amounts of peptide bound amino acids and small numbers of free amino acids show that protein preservation is good. The rapid initial increase in free amino acids and corresponding decrease in peptide bound amino acids, however, show that the proteins in fossil shells are poorly preserved as they quickly break down due to natural hydrolysis through time, producing a mixture of free amino acids and other compounds. Most of the peptide bonds are broken within the first 0·5 My. However, some peptide bound amino acids do remain in the oldest samples, indicating that hydrolysis has not been complete and that some peptides may persist for a long time.

These results are consistent with the results of Walton (1992) who found that the proportion of amino acids present in the free state in brachiopod shells rises from negligable amounts in Recent specimens to greater than 58 per cent. by 0·2 Ma, and generally greater than 80 per cent. by 0·5 Ma, showing that brachiopod shell proteins also tend to undergo very rapid initial hydrolysis. Excellent physical preservation therefore, does not necessarily indicate good biochemical preservation (Towe 1980; Weiner and Lowenstam 1980). Previous studies have shown that the rate of this natural hydrolysis is dependent upon many factors: water availability and temperature (and therefore burial history) being amongst the most important (Vallentyne 1964, 1968; Ho 1966). The strength of the peptide bonds, and therefore the rate at which they can be broken, is dependent upon the nature of the residues on either side of the bond (Kleef *et al.* 1975; Kahne and Still 1988; Eglington and Logan 1991). The rate of hydrolysis is also affected by the presence of other biomolecules, such as carbohydrates, which are present within shells (Vallentyne 1964), and metal ions (Ikawa and Snell 1954), both of which tend to speed up the reactions. The speed of amino acid decomposition reactions, therefore, is very difficult to predict and may not relate directly to the thermal stability of individual pure amino acids as determined by Vallentyne (1964).

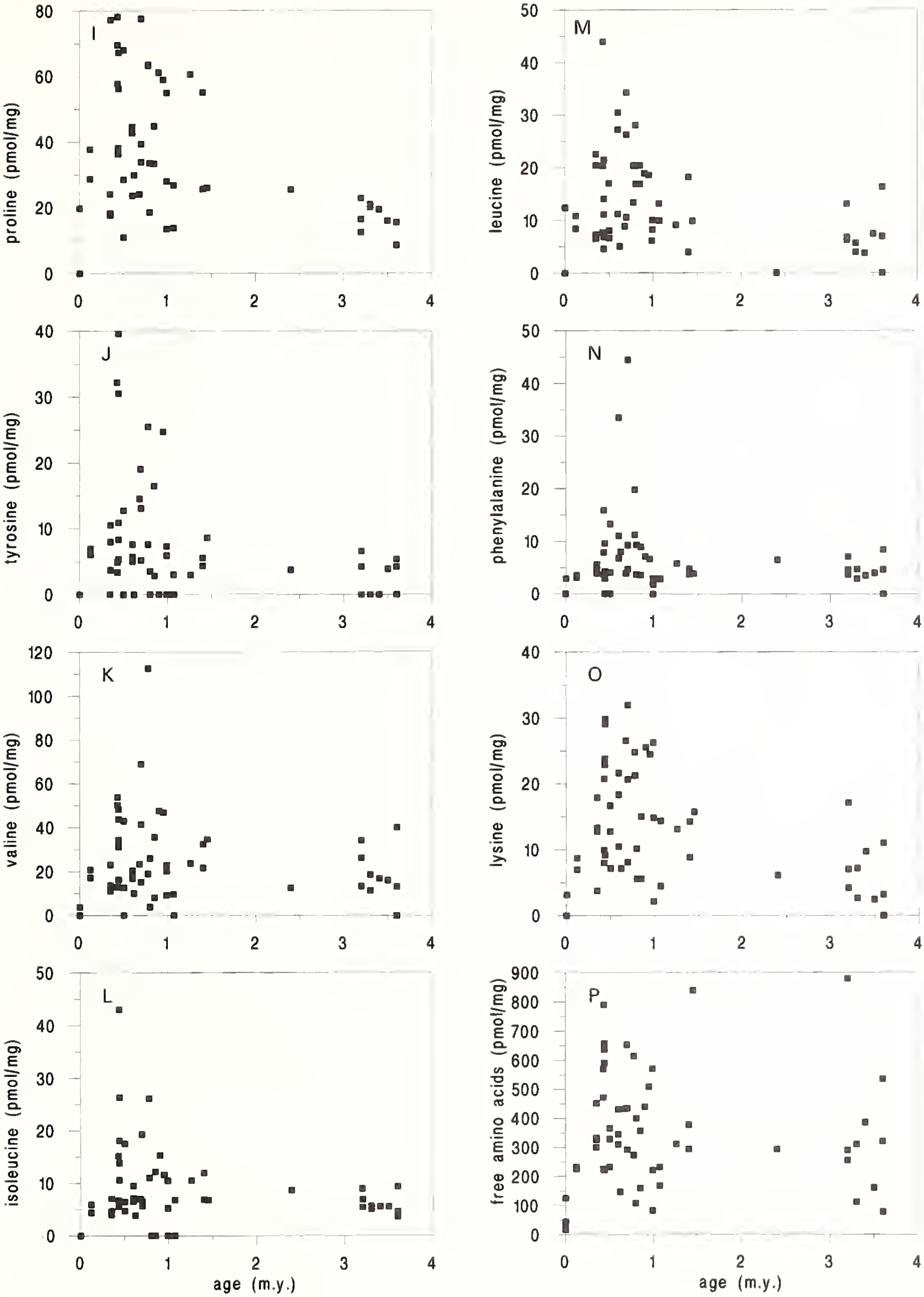
The changes in individual amino acids show that amounts of most amino acids gradually decrease through time as they break down into other compounds. Those which increase through time, i.e. alanine, must be a reaction product, as long as the shell is functioning as a closed system. Alanine is known to be a common product of other amino acid reactions, for instance the decomposition of the relatively unstable amino acids serine, threonine and aspartic acid (Bada and Miller 1970; Bada *et al.* 1978). Alanine is also one of the most stable amino acids (Vallentyne 1964). The production of the proteinogenic amino acid alanine from the decomposition of other amino acids, along with its high stability, explains its anomalously high concentration in these fossils and in others (e.g. Bada and Man 1980).

TAXONOMIC IMPLICATIONS

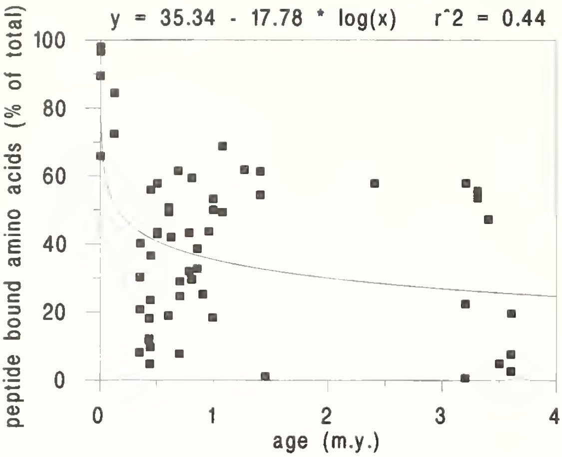
The results of principal component analysis show that samples can be grouped according to their amino acid compositions in ways which reflect their taxonomic groupings (Text-fig. 9). These relationships do not seem to break down due to amino acid diagenesis as the fossils get older, at least within the period examined in this study. This may be because the diagenesis reactions in all samples are very similar, involving the gradual decomposition of most amino acids and the production of diagenetic alanine and various other compounds. Individual standard amino acids break down at different rates experimentally, but in mixtures all the reactions are speeded up and the situation is more complicated because decomposition can occur through many more pathways. Rate depends on temperature, water, the nature of the residues on either side of the bond, and the presence of other compounds (Ikawa and Snell 1954; Vallentyne 1964, 1968; Ho 1966; Kleef *et al.* 1975; Kahne and Still 1988; Eglington and Logan 1991). Some of the amino acids most stable to pyrolysis have been shown to be some of the least stable when fossilized (Jones and Vallentyne 1960). In this study, most amino acids appear to decompose at fairly similar rates despite their differing thermal stabilities. This means that the proportions of most individual amino acids present within shells of different species are relatively unaffected by diagenesis. The process is ubiquitous in



TEXT-FIG. 6. For caption see opposite.



TEXT-FIG. 6. Amount of free individual intracrystalline amino acids plotted against sample age.



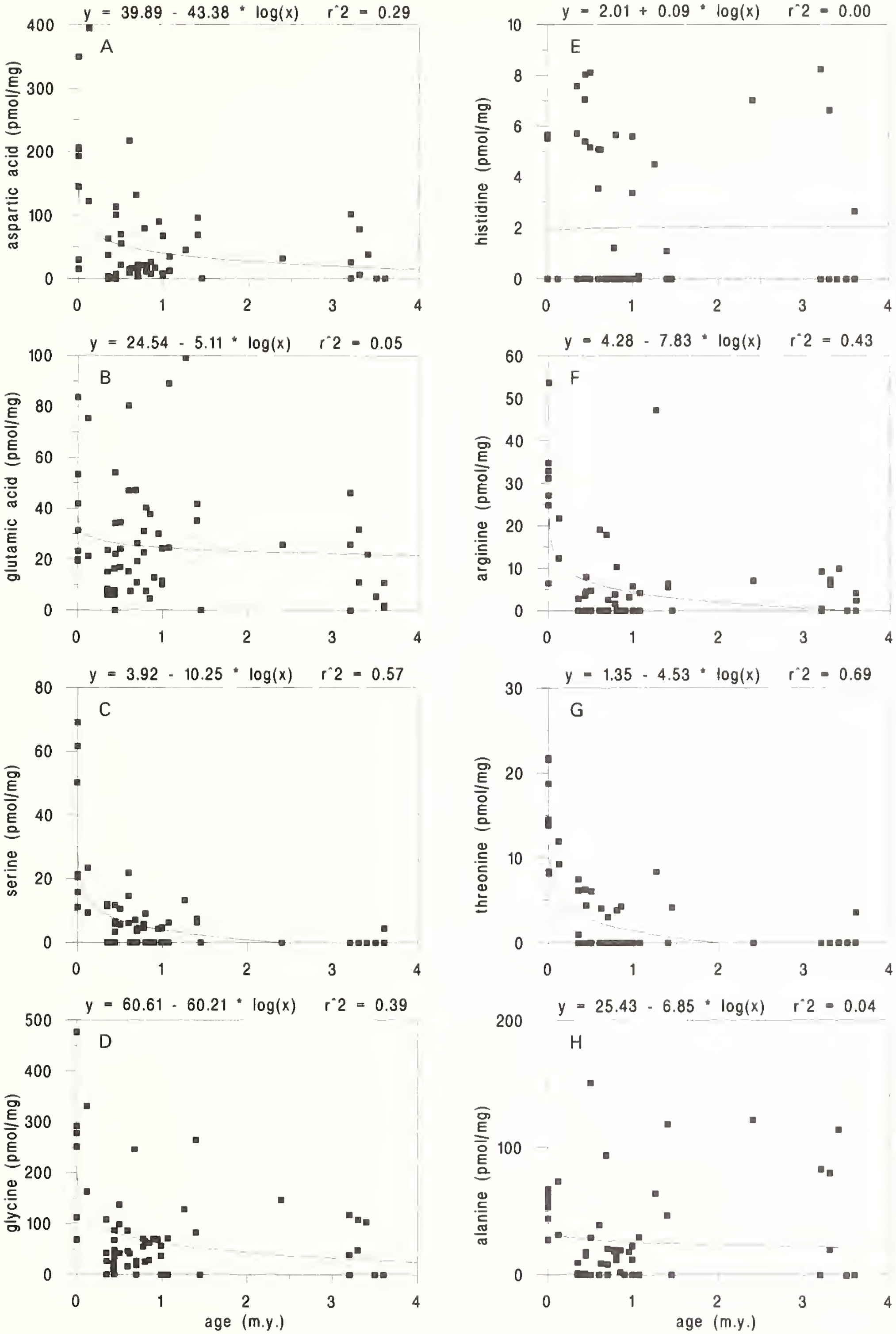
TEXT-FIG. 7. Peptide bound intracrystalline amino acids as a percentage of the total intracrystalline amino acids in all samples through time.

all samples so does not affect relationships, as long as there is enough of the original amino acid left to give a taxonomic signature. When this is finally lost, the taxonomic relationships will quickly break down.

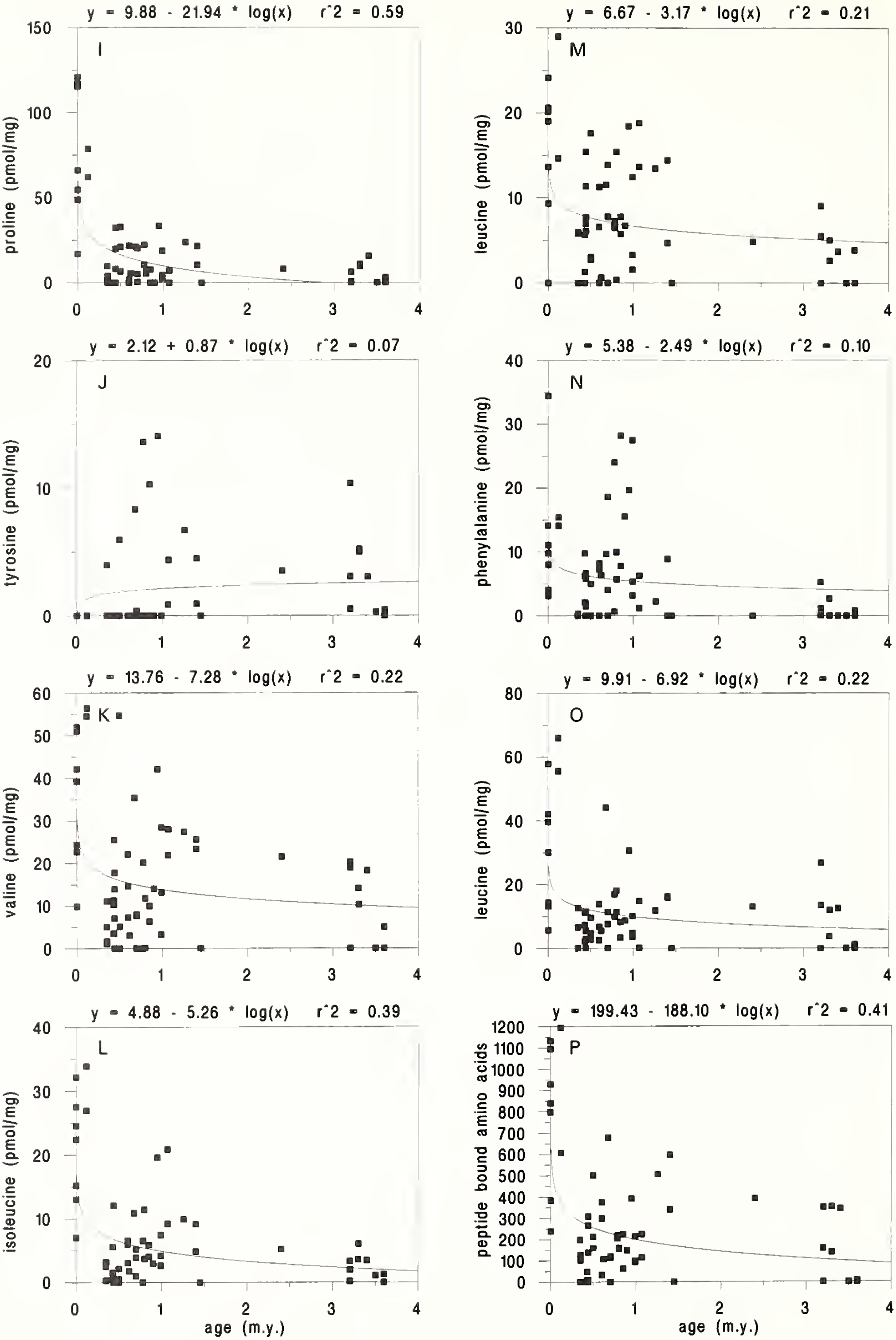
Some morphologically similar groups plot together (Text-fig. 9). For example, samples from the superfamily Ostreacea (*Tiostrea chilensis lutaria* and *Crassostrea ingens*) and Anomiacea (*Patro undatus*) all have an oyster-like appearance. Although the order of amino acids in the shell matrix proteins is derived directly from the DNA and therefore reflects genotype rather than phenotype, the shell morphology is in turn controlled by the shell matrix proteins (Lowenstam and Weiner 1989), so would be expected to follow the same relationships. Therefore, it is interesting to speculate that whilst the overall genotypes of unrelated species may be very different from each other, in cases of similar shell morphology in unrelated species the sections of DNA which control the production of shell matrix proteins may be very similar. This may be a case of reconvergent evolution, resulting in the reconvergence of the morphologies of species that had previously diverged. Therefore, the use of amino acids from shell matrix proteins, although it reflects genotype, may only reflect the part of the genotype which controls shell morphology. The taxonomic relationships inferred from intracrystalline amino acids, therefore, may only reinforce relationships already inferred using the physical measurements of shell morphology. Walton (1992) showed that the intracrystalline amino acid assemblages of recent brachiopods reinforced existing (morphological) taxonomy. However, considering the lack of soft parts available from fossils, and the general lack of preserved DNA, the intracrystalline amino acid compositions of hard parts may nontheless be one of the best indications of genotype available in the fossil record.

CONCLUSIONS

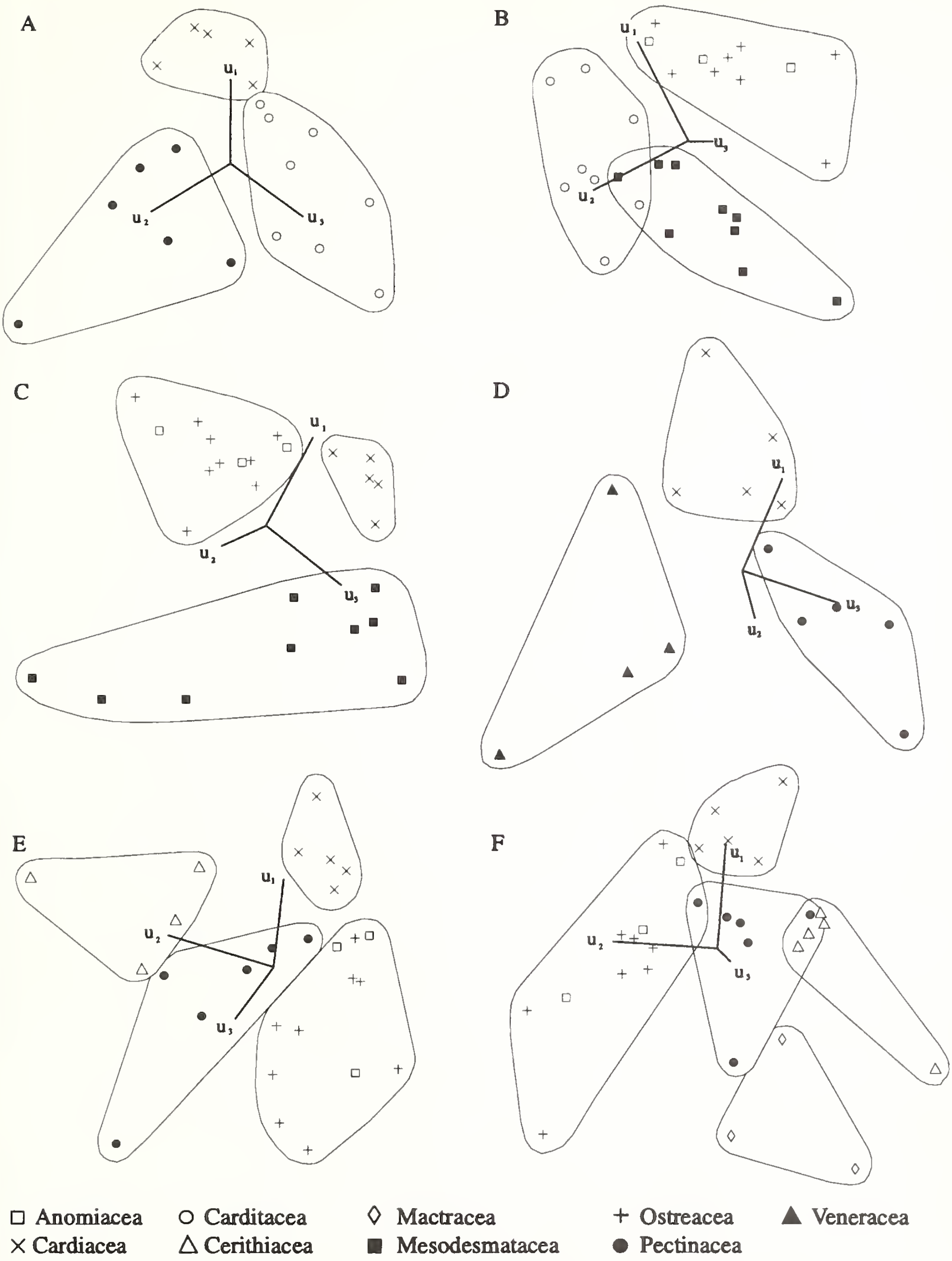
There is a gradual decline in most intracrystalline amino acids through time as they decompose to other compounds. Alanine shows an increase (at least over the time scale of this study) because it is a common product of other amino acid decomposition reactions. In Recent shells, most amino acids are still peptide bound and the number of free amino acids is small. However, most of the peptide bonds are broken within the first 0·5 My. Free amino acids are therefore at a maximum at about 0·5–1 Ma after which there is a decline, except in alanine which continues to increase as other amino acids are broken down. The amino acid diagenesis reactions are fairly ubiquitous in all samples and most intracrystalline amino acids decompose at quite similar rates. Taxonomic relationships can still therefore be inferred from intracrystalline amino acid compositions even after amino acid diagenesis reactions, as long as there is enough original amino acid left to give a taxonomic signal. The results of multivariate analysis of the amino acid compositions of different species tend to reinforce morphological taxonomy.



TEXT-FIG. 8. For caption see p. 868.



TEXT-FIG. 8. Amount of peptide bound individual intracrystalline amino acids plotted against sample age.



TEXT-FIG. 9. Three dimensional rotating plots of the first three principal components of amino acid data for various mollusc superfamilies. A, Cardiacea, Carditacea and Pectinacea. B, Carditacea, Mesodesmatacea, Ostreacea and Anomiacea. C, Cardiacea, Mesodesmatacea, Ostreacea and Anomiacea. D, Veneracea, Cardiacea and Pectinacea. E, Pectinacea, Cardiacea, Cerithiacea, Ostreacea and Anomiacea. F, Mactracea, Pectinacea, Cerithiacea, Cardiacea, Ostreacea and Anomiacea.

APPENDIX 1: TOTAL INTRACRYSTALLINE AMINO ACIDS (pmol/mg)

Sample	Age	Asp	Glu	Ser	Gly	His	Arg	Thr	Ala	Pro	Tyr	Val	Iso	Leu	Phe	Lys	Total
1	3·6	0	5·58	0	30·47	7·66	5·97	0	15·98	9·96	0	4·99	0	3·88	0	0	84·49
2	3·6	36·33	21·01	4·44	78·39	0	11·19	3·56	165·9	15·45	4·35	35·83	9·32	12·58	7·52	12·2	418
3	3·6	42·11	23·26	0	87·23	0	4·13	0	75·39	11·58	5·85	12·33	5·94	6·49	5·53	4·17	284
4	3·5	0	9·6	0	46·23	0	0	0	36·61	14·01	4·19	15·3	6·77	6·14	0	2	140·9
5	0·35	94·43	32·2	12·05	137·1	0	8·42	6·2	95·63	21·75	3·98	22·25	7·94	28·36	3·65	25·52	499·5
6	0	15·52	22·67	15·89	130	0	27·16	8·38	78·36	54·54	0	22·66	13·01	20·61	8	13·23	430·1
7	0	144·6	19·47	21·39	260·3	5·51	31·17	21·57	70·05	116·9	0	51·01	27·52	19·03	11·05	57·84	857·4
8	0·7	94·79	19·18	4·34	166·2	0	11·32	7·88	119·7	34·24	3·06	36·17	7·52	7·53	3·86	20·48	536·3
9	0	193	41·84	61·71	498·3	5·68	34·8	21·75	86·23	115·4	0	42·12	22·41	20·14	14·13	14·43	1172
10	0	349·7	83·72	69·14	308·2	0	53·8	18·71	81·7	66·14	0	39·26	15·21	0	4·09	42·08	1132
11	0	30·44	35·13	16·1	111·1	0	10·43	8·14	54·99	36·79	0	13·6	7·05	26·06	6·05	8·85	364·7
12	3·2	3·19	8·91	0	52·47	0	4·17	0	40·24	17·12	4·78	19·76	9·16	7·24	7·13	2·18	176·4
13	1·45	47·9	13·47	0	99	0	10·02	4·19	126	22·82	3·58	26·13	6·17	4·78	0	8·99	373
14	0	204·3	57·31	50·15	268·1	0	32·94	13·85	50·5	48·83	0	24·35	24·54	9·34	9·75	30·13	824·1
15	0	206·9	26·01	20·46	292·5	0	24·73	14·51	65·39	120·9	0	52·06	32·2	24·16	34·44	39·65	953·8
16	0·12	167	26·07	9·4	221	0	17·9	9·29	73·97	90·77	5·93	71·84	31·42	23·08	17·64	73·04	838·3
17	0·12	410·5	81·58	23·46	386·6	0	28·67	11·91	120·7	116·6	0	77·19	39·99	39·8	18·51	64·27	1420
18	0·35	20·38	15·09	0	60·67	5·71	8·61	5·88	56·91	79·91	0	24·81	9·77	7·16	5·91	15·51	316·3
19	0·35	11·16	10·34	0	404·6	0	0	0	63·93	22·54	0	24·27	4·48	6·09	3·18	3·45	554·1
20	0·35	86·24	28·66	11·37	115·2	7·58	0	7·51	92·47	27·98	0	18·71	6·47	26·41	3·81	19·94	452·3
21	0·43	34·04	27·38	0	157·2	0	10·08	0	171·8	57·49	0	64·07	8·22	49·57	22·08	15·33	617·2
22	0·43	44·09	14·57	0	85·64	6·05	13·78	7·83	83·33	73·12	3·56	61·47	20·76	21·63	10·04	32·08	478
23	0·43	14·48	13·45	0	59·65	0	0	6·32	41·96	26·85	0	16·48	5·96	7·42	13·45	12·05	218·1
24	0·44	87·79	25·69	5·07	253·5	8·04	8·55	5·11	149·7	88·55	8·53	57·74	16·85	20·93	6·64	32·72	775·4
25	0·44	86·26	25·77	10·54	140·8	0	0	0	132·1	16·41	0	27·02	10·9	26·54	5·8	20·99	503·2
26	0·44	140·7	50·48	12·29	334·7	0	0	0	134·4	35·1	4·64	41·45	7·99	12·97	4·41	20·91	799·9
27	0·44	178·9	69·58	11·75	210·7	7·05	11·95	3·94	120·9	87·22	24·62	66·06	25·89	29·23	11·46	40·55	899·8
28	0·44	111·1	44·68	6·61	107·2	10·74	7·94	4·41	63·43	45·13	2·84	41·7	7·84	15·92	3·25	14·59	487·3
29	0·5	135·7	33·56	10·62	359·3	0	0	6·08	177·4	43·67	5·97	54·7	6·93	11·13	3·77	17·39	866·2
30	0·5	71·28	47·12	14·9	102·5	8·12	4·77	0	48·74	35·2	0	17·71	6·82	19·76	4·28	9·88	391·1
31	0·5	39·41	23·51	5·8	154·8	16·36	3·82	6·33	87·64	89	3·59	39·09	15·2	24·21	5·02	26·37	540·1

32	0·6	275·4	93·56	21·87	149·7	0	0	0	111·2	25·35	4·02	34·53	13·08	37·1	5·44	35·54	806·7
33	0·6	28·98	31·53	6·05	100·6	5·09	9·93	0	68·41	32·37	3·29	24·17	10·21	26·31	18·32	13·07	378·4
34	0·6	31·58	67·97	14·6	131·8	12·91	44·17	0	86·67	66·45	6·09	42·4	15·45	22·48	41·76	25·06	609·4
35	0·62	24·32	12·41	0	77·5	10·65	0	4·09	37·9	35·39	0	13·12	5·66	5·67	14·34	12·64	253·7
36	0·68	186·9	56·06	11·58	385·0	0	22·95	0	199·8	45·09	22·85	58·75	17·84	20·42	13·63	70·78	1112
37	0·7	23·43	37·75	0	107	0	3·89	0	71·99	44·44	4·2	23·1	10·85	48·14	13·33	15·75	403·9
38	0·7	24·9	33·3	8·31	76·53	0	6·63	0	75·5	97·82	19·42	49·17	23·18	34·1	63·06	43·44	555·4
39	0·78	114·1	40·41	4·61	188·5	0	8	0	163	85·5	39·1	74	26·11	26·84	20·42	41·78	832·3
40	0·78	31·34	27·93	5·74	101·6	7·01	3·9	0	75·11	74·08	5·72	39·19	17·58	20·6	35·21	31·04	476
41	0·85	42·71	44·21	0	163·3	0	0	4·29	98·32	52·49	26·78	45·55	16·24	26·13	37·16	23·22	580·4
42	0·85	20·96	8·79	0	69·94	0	0	0	26·66	31·09	0	14·44	5·91	24·66	11·44	8·97	222·9
43	0·8	23·64	12·23	0	92·57	5·66	0	3·87	31·74	23·88	0	15·73	3·7	17·24	9·33	23·73	263·3
44	0·8	20·61	54·74	44·71	98·4	5·2	48·55	0	125·8	40·94	0	26·11	11·4	43·52	19·28	21·54	560·8
45	0.9	75·73	28·74	0	165·7	0	0	0	94·51	61·14	0	61·61	18·25	25·67	22·69	34·28	588·3
46	0·95	146	43·94	4·36	190·1	0	7·52	0	140·4	92·24	38·78	89·1	31·18	37	26·27	55·19	902·1
47	0·99	10·18	15·12	0	59·83	5·6	0	0	28·49	18·02	0	12·53	4·21	11·49	5·37	5·77	176·6
48	0·99	141·6	35·46	4·44	227·1	0	5·17	0	135	30·23	3·06	36·22	7·84	7·71	6·13	31·05	671
49	0·99	18·6	17·64	4·67	94·75	11·1	5·72	3·91	57·64	73·76	3·1	48·76	17·93	22·43	29·3	24·95	434·3
50	1·07	17·06	101·3	0	7·96	6·35	0	0	20·26	6·88	4·37	37·59	20·84	31·99	9·13	19·31	283
51	1·07	54·79	31·19	6·3	143·8	0	4·23	0	111·6	20·93	3·93	21·91	16	23·56	4·16	14·52	456·8
52	1·26	60·59	115·5	13·26	192·7	10·41	58·26	8·39	136·4	84·51	9·7	51·03	20·46	22·55	8·02	24·99	816·7
53	1·4	132·6	45·66	6·39	387·5	0	15·39	0	245·7	36·09	10·04	45·04	11·73	8·68	3·56	25·25	973·6
54	1·4	86·81	39·17	7·48	130·2	7·77	11·85	0	114·1	76·49	5·27	58·05	21·04	32·66	12·59	30·1	633·6
55	2·4	44·18	29·32	0	216	7·03	15·75	0	257·5	33·6	7·32	34·14	13·87	4·86	2·68	19·23	685·4
56	3·3	98·32	34·88	0	194·3	0	23·08	0	203·6	30·3	5·21	32·71	11·18	6·61	3·17	19·13	662·5
57	3·2	43·03	34·87	0	197·3	8·24	9·25	0	185·7	18·8	10·37	32·3	8·86	15·83	8·93	31·04	604·5
58	3·2	142	53·4	0	291·9	0	22·32	0	388·3	17·04	9·64	54·54	8·9	11·75	5·79	30·56	1036
59	3·3	5·96	15·47	0	78·57	6·64	6·09	0	47·25	30·97	5	21·6	9·29	10·69	5·58	6·35	249·5
60	3·4	75·49	28·25	0	215·5	0	21·57	0	273·3	34·96	3·05	35·06	9·09	7·45	3·15	22·18	729

APPENDIX 1: TOTAL INTRACRYSTALLINE AMINO ACIDS (pmol/mg)

Sample	Age	Asp	Glu	Ser	Gly	His	Arg	Thr	Ala	Pro	Tyr	Val	Iso	Leu	Phe	Lys	Total
1	3·6	0	5·58	0	30·47	7·66	5·97	0	15·98	9·96	0	4·99	0	3·88	0	0	84·49
2	3·6	36·33	21·01	4·44	78·39	0	11·19	3·56	165·9	15·45	4·35	35·83	9·32	12·58	7·52	12·2	418
3	3·6	42·11	23·26	0	87·23	0	4·13	0	75·39	11·58	5·85	12·33	5·94	6·49	5·53	4·17	284
4	3·5	0	9·6	0	46·23	0	0	0	36·61	14·01	4·19	15·3	6·77	6·14	0	2	140·9
5	0·35	94·43	32·2	12·05	137·1	0	8·42	6·2	95·63	21·75	3·98	22·25	7·94	28·36	3·65	25·52	499·5
6	0	15·52	22·67	15·89	130	0	27·16	8·38	78·36	54·54	0	22·66	13·01	20·61	8	13·23	430·1
7	0	144·6	19·47	21·39	260·3	5·51	31·17	21·57	70·05	116·9	0	51·01	27·52	19·03	11·05	57·84	857·4
8	0·7	94·79	19·18	4·34	166·2	0	11·32	7·88	119·7	34·24	3·06	36·17	7·52	7·53	3·86	20·48	536·3
9	0	193	41·84	61·71	498·3	5·68	34·8	21·75	86·23	115·4	0	42·12	22·41	20·14	14·13	14·43	1172
10	0	349·7	83·72	69·14	308·2	0	53·8	18·71	81·7	66·14	0	39·26	15·21	0	4·09	42·08	1132
11	0	30·44	35·13	16·1	111·1	0	10·43	8·14	54·99	36·79	0	13·6	7·05	26·06	6·05	8·85	364·7
12	3·2	3·19	8·91	0	52·47	0	4·17	0	40·24	17·12	4·78	19·76	9·16	7·24	7·13	2·18	176·4
13	1·45	47·9	13·47	0	99	0	10·02	4·19	126	22·82	3·58	26·13	6·17	4·78	0	8·99	373
14	0	204·3	57·31	50·15	268·1	0	32·94	13·85	50·5	48·83	0	24·35	24·54	9·34	9·75	30·13	824·1
15	0	206·9	26·01	20·46	292·5	0	24·73	14·51	65·39	120·9	0	52·06	32·2	24·16	34·44	39·65	953·8
16	0·12	167	26·07	9·4	221	0	17·9	9·29	73·97	90·77	5·93	71·84	31·42	23·08	17·64	73·04	838·3
17	0·12	410·5	81·58	23·46	386·6	0	28·67	11·91	120·7	116·6	0	77·19	39·99	39·8	18·51	64·27	1420
18	0·35	20·38	15·09	0	60·67	5·71	8·61	5·88	56·91	79·91	0	24·81	9·77	7·16	5·91	15·51	316·3
19	0·35	11·16	10·34	0	404·6	0	0	0	63·93	22·54	0	24·27	4·48	6·09	3·18	3·45	554·1
20	0·35	86·24	28·66	11·37	115·2	7·58	0	7·51	92·47	27·98	0	18·71	6·47	26·41	3·81	19·94	452·3
21	0·43	34·04	27·38	0	157·2	0	10·08	0	171·8	57·49	0	64·07	8·22	49·57	22·08	15·33	617·2
22	0·43	44·09	14·57	0	85·64	6·05	13·78	7·83	83·33	73·12	3·56	61·47	20·76	21·63	10·04	32·08	478
23	0·43	14·48	13·45	0	59·65	0	0	6·32	41·96	26·85	0	16·48	5·96	7·42	13·45	12·05	218·1
24	0·44	87·79	25·69	5·07	253·5	8·04	8·55	5·11	149·7	88·55	8·53	57·74	16·85	20·93	6·64	32·72	775·4
25	0·44	86·26	25·77	10·54	140·8	0	0	0	132·1	16·41	0	27·02	10·9	26·54	5·8	20·99	503·2
26	0·44	140·7	50·48	12·29	334·7	0	0	0	134·4	35·1	4·64	41·45	7·99	12·97	4·41	20·91	799·9
27	0·44	178·9	69·58	11·75	210·7	7·05	11·95	3·94	120·9	87·22	24·62	66·06	25·89	29·23	11·46	40·55	899·8
28	0·44	111·1	44·68	6·61	107·2	10·74	7·94	4·41	63·43	45·13	2·84	41·7	7·84	15·92	3·25	14·59	487·3
29	0·5	135·7	33·56	10·62	359·3	0	0	6·08	177·4	43·67	5·97	54·7	6·93	11·13	3·77	17·39	866·2
30	0·5	71·28	47·12	14·9	102·5	8·12	4·77	0	48·74	35·2	0	17·71	6·82	19·76	4·28	9·88	391·1
31	0·5	39·41	23·51	5·8	154·8	16·36	3·82	6·33	87·64	89	3·59	39·09	15·2	24·21	5·02	26·37	540·1
32	0·6	275·4	93·56	21·87	149·7	0	0	0	111·2	25·35	4·02	34·53	13·08	37·1	5·44	35·54	806·7
33	0·6	28·98	31·53	6·05	100·6	5·09	9·93	0	68·41	32·37	3·29	24·17	10·21	26·31	18·32	13·07	378·4
34	0·6	31·58	67·97	14·6	131·8	12·91	44·17	0	86·67	66·45	6·09	42·4	15·45	22·48	41·76	25·06	609·4
35	0·62	24·32	12·41	0	77·5	10·65	0	4·09	37·9	35·39	0	13·12	5·66	5·67	14·34	12·64	253·7
36	0·68	186·9	56·06	11·58	385·0	0	22·95	0	199·8	45·09	22·85	58·75	17·84	20·42	13·63	70·78	1112
37	0·7	23·43	37·75	0	107	0	3·89	0	71·99	44·44	4·2	23·1	10·85	48·14	13·33	15·75	403·9
38	0·7	24·9	33·3	8·31	76·53	0	6·63	0	75·5	97·82	19·42	49·17	23·18	34·1	63·06	43·44	555·4
39	0·78	114·1	40·41	4·61	188·5	0	8	0	163	85·5	39·1	74	26·11	26·84	20·42	41·78	832·3
40	0·78	31·34	27·93	5·74	101·6	7·01	3·9	0	75·11	74·08	5·72	39·19	17·58	20·6	35·21	31·04	476
41	0·85	42·71	44·21	0	163·3	0	0	4·29	98·32	52·49	26·78	45·55	16·24	26·13	37·16	23·22	580·4
42	0·85	20·96	8·79	0	69·94	0	0	0	26·66	31·09	0	14·44	5·91	24·66	11·44	8·97	222·9
43	0·8	23·64	12·23	0	92·57	5·66	0	3·87	31·74	23·88	0	15·73	3·7	17·24	9·33	23·73	263·3
44	0·8	20·61	54·74	44·71	98·4	5·2	48·55	0	125·8	40·94	0	26·11	11·4	43·52	19·28	21·54	560·8
45	0.9	75·73	28·74	0	165·7	0	0	0	94·51	61·14	0	61·61	18·25	25·67	22·69	34·28	588·3
46	0·95	146	43·94	4·36	190·1	0	7·52	0	140·4	92·24	38·78	89·1	31·18	37	26·27	55·19	902·1
47	0·99	10·18	15·12	0	59·83	5·6	0	0	28·49	18·02	0	12·53	4·21	11·49	5·37	5·77	176·6
48	0·99	141·6	35·46	4·44	227·1	0	5·17	0	135	30·23	3·06	36·22	7·84	7·71	6·13	31·05	671
49	0·99	18·6	17·64	4·67	94·75	11·1	5·72	3·91	57·64	73·76	3·1	48·76	17·93	22·43	29·3	24·95	434·3
50	1·07	17·06	101·3	0	7·96	6·35	0	0	20·26	6·88	4·37	37·59	20·84	31·99	9·13	19·31	283
51	1·07	54·79	31·19	6·3	143·8	0	4·23	0	111·6	20·93	3·93	21·91	16	23·56	4·16	14·52	456·8
52	1·26	60·59	115·5	13·26	192·7	10·41	58·26	8·39	136·4	84·51	9·7	51·03	20·46	22·55	8·02	24·99	816·7
53	1·4	132·6	45·66	6·39	387·5	0	15·39	0	245·7	36·09	10·04	45·04	11·73	8·68	3·56	25·25	973·6
54	1·4	86·81	39·17	7·48	130·2	7·77	11·85	0	114·1	76·49	5·27	58·05	21·04	32·66	12·59	30·1	633·6
55	2·4	44·18	29·32	0	216	7·03	15·75	0	257·5	33·6	7·32	34·14	13·87	4·86	2·68	19·23	685·4
56	3·3	98·32	34·88	0	194·3	0	23·08	0	203·6	30·3	5·21	32·71	11·18	6·61	3·17	19·13	662·5
57	3·2	43·03	34·87	0	197·3	8·24	9·25	0	185·7	18·8	10·37	32·3	8·86	15·83	8·93	31·04	604·5
58	3·2	142	53·4	0	291·9	0	22·32	0	388·3	17·04	9·64	54·54	8·9	11·75	5·79	30·56	1036
59	3·3	5·96	15·47	0	78·57	6·64	6·09	0	47·25	30·97	5	21·6	9·29	10·69	5·58	6·35	249·5
60	3·4	75·49	28·25	0	215·5	0	21·57	0	273·3	34·96	3·05	35·06	9·09	7·45	3·15	22·18	729

APPENDIX 2: FREE INTRACRYSTALLINE AMINO ACIDS (pmol/mg)

Sample	Age	Asp	Glu	Ser	Gly	His	Arg	Thr	Ala	Pro	Tyr	Val	Iso	Leu	Phe	Lys	Total
1	3·6	0	4·4	0	32·81	5	3·57	0	19·76	8·43	0	0	3·7	0	0	0	77·67
2	3·6	59·84	19·04	0	104·5	0	13·26	0	232·6	15·48	4·25	40·11	9·42	16·31	8·47	11·03	534·3
3	3·6	74·3	12·35	0	90·35	0	0	0	96·67	8·52	5·38	13·24	4·65	6·88	4·69	3·22	320·3
4	3·5	0	4·12	0	52·7	0	0	0	47·48	15·96	3·89	16·04	5·65	7·37	3·99	2·46	159·7
5	0·35	31·31	8·69	0	94·96	0	5·62	0	86·02	17·66	0	11·14	4·7	22·54	4·47	12·81	299·9
6	0	0	2·74	0	17·45	0	0	0	24·96	0	0	0	0	0	0	0	45·15
7	0	0	0	0	9·24	0	0	0	7·94	0	0	0	0	0	0	0	17·18
8	0·7	72·9	8·26	0	217·3	0	11·7	4·82	180	33·77	13·03	68·94	6·51	10·54	4·67	20·62	653·1
9	0	0	0	0	21·21	0	0	0	18·88	0	0	0	0	0	0	0	40·09
10	0	0	0	0	16·18	0	0	0	20·5	0	0	0	0	0	0	0	36·68
11	0	0	3·77	4·93	42·13	0	3·97	0	27·66	19·78	0	3·78	0	12·4	2·91	3·14	124·5
12	3·2	4·7	11·13	4·77	100·5	0	3·7	0	74·28	22·81	4·26	26·24	8·99	13·07	7·08	7·05	288·6
13	1·45	156·4	15·05	0	276·3	0	14·4	0	271·1	25·97	8·57	34·68	6·82	9·87	3·87	15·71	838·7
14	0	0	3·91	0	16·15	0	0	0	6·24	0	0	0	0	0	0	0	26·3
15	0	0	2·73	0	14·56	0	0	0	6·63	0	0	0	0	0	0	0	23·92
16	0·12	45·25	4·82	0	57·84	0	5·6	0	42·18	28·69	7	17·21	4·42	8·44	3·55	7	232
17	0·12	16·16	6·08	0	55·66	0	6·95	0	47·18	37·79	6·04	20·77	6·01	10·81	3·13	8·68	225·3
18	0·35	16·91	6·8	0	62·99	0	9·55	4·9	82·8	77·16	10·51	23·08	7·07	7·31	5·6	17·88	332·6
19	0·35	11·3	4·2	0	296·4	0	0	0	65·85	24	8	23·21	4·2	6·5	3·91	3·8	451·4
20	0·35	48·75	13·5	0	88·62	0	5·62	0	91·24	18·23	3·72	13·69	3·99	20·4	4·15	13·31	325·2
21	0·43	32·42	10·97	0	135·8	7·31	6·44	4·97	170·7	69·58	3·38	53·78	6·7	43·92	15·86	8·01	569·8
22	0·43	42·28	6·76	0	74·78	6·83	9·79	10·71	96·06	78·16	32·17	50·22	15·16	20·32	7·92	20·73	471·9
23	0·43	13·77	7·28	0	49·2	0	5·12	0	47·92	57·81	4·9	12·98	5·53	7·69	3·68	9·86	225·7
24	0·44	80·38	26·4	8·29	166·6	0	15·56	7·15	131·8	56·22	30·52	43·76	26·3	13·99	0	29·86	636·9
25	0·44	97·67	31·09	7·17	166·2	0	4·9	0	197	36·27	8·32	31·11	43·04	11·09	0	23·79	657·7
26	0·44	141·7	28·44	6·38	299·7	0	3·97	0	175·5	38·2	10·88	34·34	18·08	6·86	2·92	22·86	789·8
27	0·44	65·66	15·66	0	142·7	0	7·41	4·2	125·6	67·25	39·6	48·25	13·81	21·5	9·65	29·02	590·3
28	0·44	10·61	10·52	0	59·2	5·34	0	0	48·26	36·9	5·36	16·22	10·58	4·55	4·28	9·14	221
29	0·5	65·33	9·55	0	221·7	0	0	0	26·4	10·87	0	0	6·43	8·03	4·1	12·74	365·2
30	0·5	15·76	12·65	9·19	60·51	0	0	0	50·52	28·42	0	12·64	4·71	17·01	13·3	7·16	231·9
31	0·5	17·84	6·48	0	55·52	11·2	5·42	7·97	58·41	67·96	12·71	42·9	17·47	6·61	0	16·71	327·2

32	0·6	57·98	13·17	0	103·5	0	5·14	0	136·2	23·55	5·7	19·92	6·51	30·5	6·82	21·59	430·6
33	0·6	19·79	16·37	0	84·31	0	10·5	0	93·08	42·82	5·02	16·89	7·14	27·2	11·05	10·46	344·6
34	0·6	16·88	21	0	44·89	9·36	25·09	0	47·36	44·52	7·6	20·28	9·5	11·22	33·53	18·31	309·5
35	0·62	7·67	4·89	0	36·05	5·57	0	0	28·98	29·81	0	10·04	3·88	5·06	8·03	7·14	147·1
36	0·68	55·18	8·93	4·47	139·6	0	5·12	5·57	105·9	24·03	14·51	23·35	6·99	8·87	3·92	26·55	433
37	0·7	12·01	11·5	0	79·67	0	5·46	0	63·69	39·36	5·18	15·1	5·67	34·28	9·26	8·12	289·3
38	0·7	21·25	14·13	4·71	58·77	13·37	4·04	3·53	55·04	77·57	19·04	41·49	19·28	26·28	44·45	31·99	434·9
39	0·78	35·34	9·38	0	117·9	5·54	6·39	3·98	143·3	63·25	25·46	112·4	26·14	20·34	19·78	24·74	614
40	0·78	10·56	5·33	0	46·54	5·79	0	0	56·62	63·55	7·62	18·93	11·03	13·36	11·21	21·26	271·8
41	0·85	16·46	6·42	0	101·2	0	0	0	78·79	44·77	16·48	35·61	12·19	20·35	8·92	14·99	356·2
42	0·85	13·77	4·2	0	41·94	0	3·92	0	24·62	33·28	2·84	8·13	0	16·88	3·65	5·56	158·8
43	0·8	7·14	4·67	0	26·26	0	0	0	20·19	18·42	0	3·91	0	16·89	3·65	5·56	106·7
44	0·8	9·51	14·43	35·66	73·15	7·47	38·22	0	111·2	33·42	3·53	26	0	28·05	9·32	10·17	400·1
45	0·9	58·57	15·89	0	94·83	0	0	0	94·96	61·11	0	47·54	15·27	18·92	7·11	25·57	439·8
46	0·95	56·14	13·9	0	120·2	0	4·31	0	122·2	58·86	24·69	46·95	11·58	18·58	6·6	24·49	508·5
47	0·99	5·15	4·97	0	23·08	0	0	0	16·18	13·51	0	9·3	0	8·18	0	2·16	82·53
48	0·99	74·18	11·25	0	238·7	0	5·29	4·42	138·2	27·95	7·3	23·09	5·22	6·12	2·95	26·24	570·9
49	0·99	10·58	6·11	0	37·91	7·71	0	4·6	35·1	54·9	5·92	20·34	10·5	10·01	1·79	14·83	220·3
50	1·07	4·91	12·16	0	38·16	6·23	12·83	0	36·67	26·72	0	9·6	0	13·17	2·85	4·46	167·8
51	1·07	20·3	6·69	0	72·07	0	0	0	81·66	13·8	3·04	0	6·79	9·92	2·97	14·36	231·6
52	1·26	15·55	16·46	0	64·13	5·91	11·03	0	72·51	60·56	2·98	23·66	10·53	9·1	5·8	13·1	311·3
53	1·4	36·6	3·97	0	122	0	9·89	0	127·5	25·57	5·56	21·67	6·9	3·96	4·79	8·89	377·3
54	1·4	17·99	3·98	0	47·03	6·68	5·45	4·63	67·51	55·06	4·31	32·47	11·89	18·22	3·74	14·23	293·2
55	2·4	12·83	3·63	0	68·89	0	8·69	0	135·9	25·38	3·79	12·59	8·68	0	6·49	6·09	292·9
56	3·3	20·96	3·08	0	85·71	0	15·73	0	123·5	20·88	0	18·64	5·16	3·98	4·71	7·19	309·6
57	3·2	17·6	9·02	0	79·3	0	0	0	102·5	12·39	0	13·36	5·5	6·76	3·69	4·2	254·3
58	3·2	40·83	7·26	0	252·5	0	32·93	0	452·8	16·42	6·57	34·24	6·93	6·22	4·66	17·11	878·5
59	3·3	0	4·51	0	30·54	0	0	0	27·31	19·98	0	11·4	5·75	5·67	2·91	2·62	110·7
60	3·4	37·64	6·31	0	111·5	0	11·69	0	159·2	19·29	0	16·84	5·65	3·76	3·57	9·71	385·1

APPENDIX 2: FREE INTRACRYSTALLINE AMINO ACIDS (pmol/mg)

Sample	Age	Asp	Glu	Ser	Gly	His	Arg	Thr	Ala	Pro	Tyr	Val	Iso	Leu	Phe	Lys	Total
1	3·6	0	4·4	0	32·81	5	3·57	0	19·76	8·43	0	0	3·7	0	0	0	77·67
2	3·6	59·84	19·04	0	104·5	0	13·26	0	232·6	15·48	4·25	40·11	9·42	16·31	8·47	11·03	534·3
3	3·6	74·3	12·35	0	90·35	0	0	0	96·67	8·52	5·38	13·24	4·65	6·88	4·69	3·22	320·3
4	3·5	0	4·12	0	52·7	0	0	0	47·48	15·96	3·89	16·04	5·65	7·37	3·99	2·46	159·7
5	0·35	31·31	8·69	0	94·96	0	5·62	0	86·02	17·66	0	11·14	4·7	22·54	4·47	12·81	299·9
6	0	0	2·74	0	17·45	0	0	0	24·96	0	0	0	0	0	0	0	45·15
7	0	0	0	0	9·24	0	0	0	7·94	0	0	0	0	0	0	0	17·18
8	0·7	72·9	8·26	0	217·3	0	11·7	4·82	180	33·77	13·03	68·94	6·51	10·54	4·67	20·62	653·1
9	0	0	0	0	21·21	0	0	0	18·88	0	0	0	0	0	0	0	40·09
10	0	0	0	0	16·18	0	0	0	20·5	0	0	0	0	0	0	0	36·68
11	0	0	3·77	4·93	42·13	0	3·97	0	27·66	19·78	0	3·78	0	12·4	2·91	3·14	124·5
12	3·2	4·7	11·13	4·77	100·5	0	3·7	0	74·28	22·81	4·26	26·24	8·99	13·07	7·08	7·05	288·6
13	1·45	156·4	15·05	0	276·3	0	14·4	0	271·1	25·97	8·57	34·68	6·82	9·87	3·87	15·71	838·7
14	0	0	3·91	0	16·15	0	0	0	6·24	0	0	0	0	0	0	0	26·3
15	0	0	2·73	0	14·56	0	0	0	6·63	0	0	0	0	0	0	0	23·92
16	0·12	45·25	4·82	0	57·84	0	5·6	0	42·18	28·69	7	17·21	4·42	8·44	3·55	7	232
17	0·12	16·16	6·08	0	55·66	0	6·95	0	47·18	37·79	6·04	20·77	6·01	10·81	3·13	8·68	225·3
18	0·35	16·91	6·8	0	62·99	0	9·55	4·9	82·8	77·16	10·51	23·08	7·07	7·31	5·6	17·88	332·6
19	0·35	11·3	4·2	0	296·4	0	0	0	65·85	24	8	23·21	4·2	6·5	3·91	3·8	451·4
20	0·35	48·75	13·5	0	88·62	0	5·62	0	91·24	18·23	3·72	13·69	3·99	20·4	4·15	13·31	325·2
21	0·43	32·42	10·97	0	135·8	7·31	6·44	4·97	170·7	69·58	3·38	53·78	6·7	43·92	15·86	8·01	569·8
22	0·43	42·28	6·76	0	74·78	6·83	9·79	10·71	96·06	78·16	32·17	50·22	15·16	20·32	7·92	20·73	471·9
23	0·43	13·77	7·28	0	49·2	0	5·12	0	47·92	57·81	4·9	12·98	5·53	7·69	3·68	9·86	225·7
24	0·44	80·38	26·4	8·29	166·6	0	15·56	7·15	131·8	56·22	30·52	43·76	26·3	13·99	0	29·86	636·9
25	0·44	97·67	31·09	7·17	166·2	0	4·9	0	197	36·27	8·32	31·11	43·04	11·09	0	23·79	657·7
26	0·44	141·7	28·44	6·38	299·7	0	3·97	0	175·5	38·2	10·88	34·34	18·08	6·86	2·92	22·86	789·8
27	0·44	65·66	15·66	0	142·7	0	7·41	4·2	125·6	67·25	39·6	48·25	13·81	21·5	9·65	29·02	590·3
28	0·44	10·61	10·52	0	59·2	5·34	0	0	48·26	36·9	5·36	16·22	10·58	4·55	4·28	9·14	221
29	0·5	65·33	9·55	0	221·7	0	0	0	26·4	10·87	0	0	6·43	8·03	4·1	12·74	365·2
30	0·5	15·76	12·65	9·19	60·51	0	0	0	50·52	28·42	0	12·64	4·71	17·01	13·3	7·16	231·9
31	0·5	17·84	6·48	0	55·52	11·2	5·42	7·97	58·41	67·96	12·71	42·9	17·47	6·61	0	16·71	327·2
32	0·6	57·98	13·17	0	103·5	0	5·14	0	136·2	23·55	5·7	19·92	6·51	30·5	6·82	21·59	430·6
33	0·6	19·79	16·37	0	84·31	0	10·5	0	93·08	42·82	5·02	16·89	7·14	27·2	11·05	10·46	344·6
34	0·6	16·88	21	0	44·89	9·36	25·09	0	47·36	44·52	7·6	20·28	9·5	11·22	33·53	18·31	309·5
35	0·62	7·67	4·89	0	36·05	5·57	0	0	28·98	29·81	0	10·04	3·88	5·06	8·03	7·14	147·1
36	0·68	55·18	8·93	4·47	139·6	0	5·12	5·57	105·9	24·03	14·51	23·35	6·99	8·87	3·92	26·55	433
37	0·7	12·01	11·5	0	79·67	0	5·46	0	63·69	39·36	5·18	15·1	5·67	34·28	9·26	8·12	289·3
38	0·7	21·25	14·13	4·71	58·77	13·37	4·04	3·53	55·04	77·57	19·04	41·49	19·28	26·28	44·45	31·99	434·9
39	0·78	35·34	9·38	0	117·9	5·54	6·39	3·98	143·3	63·25	25·46	112·4	26·14	20·34	19·78	24·74	614
40	0·78	10·56	5·33	0	46·54	5·79	0	0	56·62	63·55	7·62	18·93	11·03	13·36	11·21	21·26	271·8
41	0·85	16·46	6·42	0	101·2	0	0	0	78·79	44·77	16·48	35·61	12·19	20·35	8·92	14·99	356·2
42	0·85	13·77	4·2	0	41·94	0	3·92	0	24·62	33·28	2·84	8·13	0	16·88	3·65	5·56	158·8
43	0·8	7·14	4·67	0	26·26	0	0	0	20·19	18·42	0	3·91	0	16·89	3·65	5·56	106·7
44	0·8	9·51	14·43	35·66	73·15	7·47	38·22	0	111·2	33·42	3·53	26	0	28·05	9·32	10·17	400·1
45	0·9	58·57	15·89	0	94·83	0	0	0	94·96	61·11	0	47·54	15·27	18·92	7·11	25·57	439·8
46	0·95	56·14	13·9	0	120·2	0	4·31	0	122·2	58·86	24·69	46·95	11·58	18·58	6·6	24·49	508·5
47	0·99	5·15	4·97	0	23·08	0	0	0	16·18	13·51	0	9·3	0	8·18	0	2·16	82·53
48	0·99	74·18	11·25	0	238·7	0	5·29	4·42	138·2	27·95	7·3	23·09	5·22	6·12	2·95	26·24	570·9
49	0·99	10·58	6·11	0	37·91	7·71	0	4·6	35·1	54·9	5·92	20·34	10·5	10·01	1·79	14·83	220·3
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53	1·4	36·6	3·97	0	122	0	9·89	0	127·5	25·57	5·56	21·67	6·9	3·96	4·79	8·89	377·3
54	1·4	17·99	3·98	0	47·03	6·68	5·45	4·63	67·51	55·06	4·31	32·47	11·89	18·22	3·74	14·23	293·2
55	2·4	12·83	3·63	0	68·89	0	8·69	0	135·9	25·38	3·79	12·59	8·68	0	6·49	6·09	292·9
56	3·3	20·96	3·08	0	85·71	0	15·73	0	123·5	20·88	0	18·64	5·16	3·98	4·71	7·19	309·6
57	3·2	17·6	9·02	0	79·3	0	0	0	102·5	12·39	0	13·36	5·5	6·76	3·69	4·2	254·3
58	3·2	40·83	7·26	0	252·5	0	32·93	0	452·8	16·42	6·57	34·24	6·93	6·22	4·66	17·11	878·5
59	3·3	0	4·51	0	30·54	0	0	0	27·31	19·98	0	11·4	5·75	5·67	2·91	2·62	110·7
60	3·4	37·64	6·31	0	111·5	0	11·69	0	159·2	19·29	0	16·84	5·65	3·76	3·57	9·71	385·1

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Cover: SEM of sporangium of *Cooksonia pertoni* ssp. *apiculispora* from Brown Clee Hill, Shropshire. This is the specimen (NMW 94 60G) that confirmed the vascular status of *Cooksonia*; × 70. Photograph published originally in *Nature*, **357**, 683–685, figure 1a.

GUIDELINES FOR COCCOLITH AND CALCAREOUS NANNOFOSSIL TERMINOLOGY

by JEREMY R. YOUNG, JAMES A. BERGEN, PAUL R. BOWN, JACKIE A. BURNETT, ANDREA FIORENTINO, RICHARD W. JORDAN, ANNELIES KLEIJNE, BRIGITTA E. VAN NIEL, A. J. TON ROMEIN *and* KATHARINA VON SALIS

ABSTRACT. The descriptive terminology applicable to coccoliths and other calcareous nannofosils is reviewed and revised. A listing of about 400 terms is given with brief explanations and explanatory figures. General terms are given first, followed by terms for specific taxonomic groups. Appendices list terms we have not used and summarize terms, such as caneolith, which have been proposed for particular types of coccoliths.

THE descriptive terminology of coccoliths evolved on an *ad hoc* basis until the 1950s. Then, the development of electron microscopy stimulated a major revision and introduction of new terms in a co-operative effort (Braarud *et al.* 1955*a*, 1955*b*; Halldal and Markali 1955; Hay *et al.* 1966). This concentrated on the standardization of names for the distinctive types of coccoliths found on coccospheres, e.g. placolith, caneolith. Subsequent work on diverse fossil coccoliths led to a different approach concentrating on element-level structure. The appropriate terminology was synthesized during a Round Table Session at the Rome 1970 Plankton Conference (Farinacci 1971).

There has been intensive research on coccoliths since 1970 and so the existing guides have become obsolescent. In response to this, a terminology workshop was held during the International Nannoplankton Association (INA) conference in Prague, 1991. Following this, a working group was set up and a two-day workshop held in London in 1992. Various publications have resulted from these discussions. Young (1992*a*) discussed new recommendations on controversial topics. Burnett and Bown (1992) provided a check-list for systematic descriptions. Van Niel (1994) reviewed in depth the descriptive terminology of nannoconids. Jordan *et al.* (1995) provided a glossary for living Haptophyta, including cytological terms and an overview of taxonomic concepts. The present paper represents the main proceedings of the working group, and is a synthesis of the descriptive terminology applied to coccoliths and other nannoliths based on its discussions.

In addition to the workshop discussions, this paper is based on a wide range of published sources including Braarud *et al.* (1955*a*, 1955*b*), Halldal and Markali (1955), Farinacci *et al.* (1971), Black (1972), Hay (1977), Okada and McIntyre (1977), Romein (1979), Aubry (1984, 1988*a*, 1988*b*, 1989, 1990), Theodoridis (1984), Perch-Nielsen (1985*a*, 1985*b*), Bown (1987), van Heck and Prins (1987), Varol (1989, 1992), Young (1989), Kleijne (1991, 1992, 1993), Young and Bown (1991), Young and Westbroek (1991), van Niel (1992), Heimdal (1993), and Winter and Siesser (1994). General works consulted include Brown (1954), Gower (1954), Fowler (1965) and Stearn (1983).

ORGANIZATION

The main text is organized into thematic categories covering different aspects of coccolith morphology. This is followed by a section on special terms needed for particular taxonomic groups. The paper is confined to the calcareous structures and does not consider organic components;

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terminology for these is reviewed in Jordan *et al.* (1995). Synonyms which we have not included in the main text are discussed in Appendix 1.

The terms recommended are italicized in the main text and given short explanations, the primary purpose of which is to explain the use of the term to coccolith workers, not to give a rigorous dictionary definition, still less an encyclopaedic explanation. The figures are meant to clarify the logic, but for various reasons not all terms are illustrated. For many terms, genera or species that show the feature particularly well are cited; good sources for illustrations of these taxa are Perch-Nielsen (1985*a*, 1985*b*) and Winter and Siesser (1994).

For terms which have been coined specifically for coccoliths (e.g. placolith) the original author is given in curly brackets {}; this information is mostly from Hay *et al.* (1966).

CHOICE OF TERMS

The general objective of the work is to summarize existing terminology rather than to create a new system. Nonetheless, in order to enhance precision it has been necessary in several cases to select between synonyms, or to assess the utility of obscure terms and, in a few cases, to coin new terms. The following principles have been used as guides.

Need. The purpose of specialist terminology is to make life easier for the reader, not for the author. The convenience of any terminological innovation should be weighed against the danger of producing unintelligible jargon.

Priority. Accepted usage must be respected. First usage and/or original definition is particularly important, but not necessarily binding.

Etymology. Words should not be given meanings that conflict with their etymology.

Ambiguity. Common words should not be given meanings that conflict with their normal meaning, or with their general scientific meaning, or that are more restrictive than a non-expert might reasonably anticipate (e.g. use of bar for structures with a particular optical orientation).

Obscurity. Obscure technical terms that are hard to remember and the meaning of which it is virtually impossible to guess (e.g. areolith), should be avoided, unless they are liable to be used so often that they will become part of routine vocabulary (e.g. placolith).

Synonyms and homonyms. As far as possible, only one term should be used for any given concept (poetic variation is not recommended). Equally, any given term should only have one meaning in a given context.

Where we have selected from possible alternatives, the others are discussed in Appendix 1 with a reference to it in the text – e.g. 'alternative spelling nanoplankton, see Appendix 1'.

GENERAL TERMS

Nannoplankton {Lohmann 1909} – plankton 2–63 μm in diameter (alternative spelling nanoplankton, see Appendix 1). Informal grouping including coccolithophorids, *Thoracosphaera*, chrysophytes, etc., but excluding the bacterial picoplankton.

Calcareous nannoplankton – nannoplankton with calcareous tests.

Nannofossil {?*Stradner* 1961} – fossil < 63 μm in diameter, excluding fragments and juveniles of larger fossils.

Calcareous nannofossil – nannofossil formed of calcium carbonate.

Coccolithophorid {Lohmann 1902} – calcareous nannoplankton belonging to the division Haptophyta (alternative term coccolithophore; see Appendix 1).

Coccosphere {Wallich 1860} – test of coccolithophorid (not necessarily spherical).

Coccolith {Huxley 1868} – calcareous structure formed by coccolithophorid.

Haptophyte – unicellular alga belonging to the division Haptophyta, includes all coccolithophorids (alternative term prymnesiophyte; see Appendix 1).

Nannolith {?Perch-Nielsen 1985*a*} – calcareous nannofossil lacking the typical features of calcareous dinophytes, heterococcoliths or holococcoliths and so of uncertain affinity (see also Young 1992*a*; Young *et al.* 1994). The division between coccoliths and nannoliths varies between authors and is liable to revision as new data become available. N.B. This rather restricted definition of the term has little etymological justification, but has been widely used, e.g. Perch-Nielsen (1985*a*, 1985*b*), Bown (1987), Aubry (1989). (The terms heliolith and ortholith provide an alternative basis for sub-dividing the calcareous nannofossils; see Appendix 1).

Heterococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of crystal-units of variable shape and size. Crystal units typically arranged in cycles with radial symmetry.

Heterococcolithophorid – cell with coccosphere of heterococcoliths.

Holococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of numerous minute ($< 0{\cdot}1\ \mu$m) crystallites all of similar shape and size (N.B. Many of the terms below are not applicable to holococcoliths, and there is a separate section for specific holococcolith terms).

Holococcolithophorid – cell with coccosphere of holococcoliths.

Combination cell {Thomsen *et al.* 1991} – cell with both hetero- and holococcoliths. N.B. These are thought to represent a transitional state between heterococcolithophorid and holococcolithophorid phases of the life cycle.

COCCOSPHERE RELATED TERMS

1. *Descriptive terms*

These are based largely on Okada and McIntyre (1977).

Monomorphic – all coccoliths of similar type (e.g. *Coccolithus*).

Dimorphic – coccoliths of two discrete types (e.g. *Scyphosphaera*).

Polymorphic – coccoliths of more than two discrete types (e.g. *Syracosphaera pulchra*).

Varimorphic {new} – coccosphere with coccoliths whose size and/or morphology varies according to position on the coccosphere (e.g. *Helicosphaera*).

Dithecate – with two discrete layers of coccoliths of different types (e.g. *Syracosphaera pulchra*).

Endotheca – inner layer of coccoliths of dithecate coccosphere.

Exotheca – outer layer of coccoliths of dithecate coccosphere.

Monothecate – with a single layer of coccoliths (e.g. *Scyphosphaera*).

Multilayered – with two or more layers of coccoliths but no differentiation into endo- and exotheca (e.g. *Emiliania*, *Florisphaera*, *Coccolithus pelagicus phase hyalinus*).

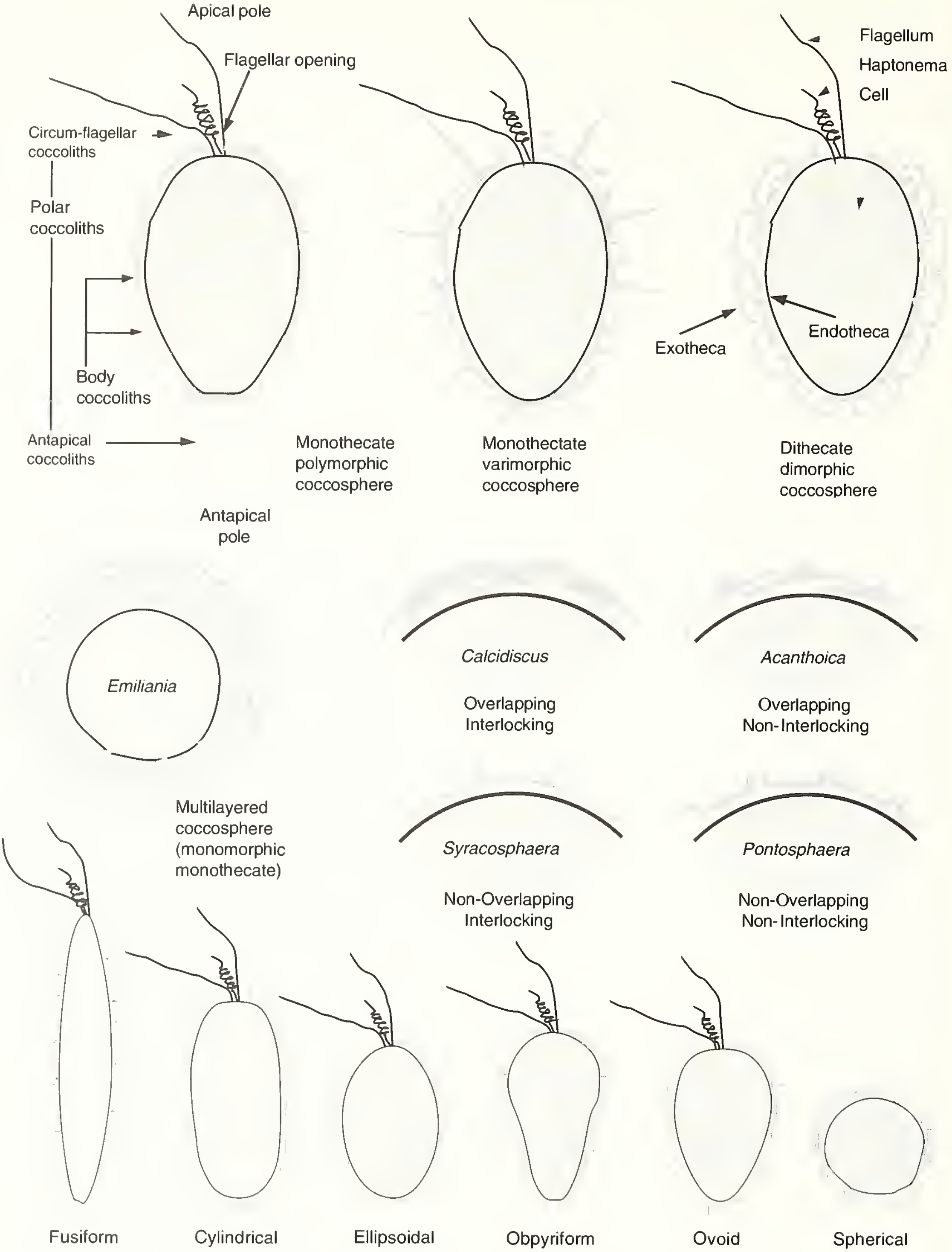
Xenosphere {new, from Greek *xenos*, stranger} – anomalous coccosphere containing coccoliths normally regarded as forming on quite discrete species (e.g. *Emiliania huxleyi* and *Gephyrocapsa oceanica*; Winter *et al.* 1979). N.B. These are very probably artefacts, the term is suggested specifically to suggest the abnormal nature of these structures.

Shape – coccospheres are three-dimensional so their shape should be described using appropriate terms for solid objects. Useful terms include: *cylindrical*, *ellipsoidal*, *fusiform* (elongate with tapering ends), *obpyriform* (inverse pear-shaped), *ovoid* (egg-shaped, i.e. one end broader than the other), *spherical*. See also Heimdal (1993) and Jordan *et al.* (1995).

2. *Orientation*

Apical pole – end of coccosphere with flagellar opening.

Antapical pole – opposite end of coccosphere.



TEXT-FIG. 1. Coccosphere related terms.

Antapical coccoliths – coccoliths occurring at antapical pole.

Body coccoliths – coccoliths other than polar coccoliths.

Circum-flagellar coccoliths/apical coccoliths – coccoliths occurring around flagellar opening (alternative term stomatal coccoliths; see Appendix 1).

Flagellar opening – opening in coccosphere through which the flagella and haptonema pass.

Polar coccoliths {Kamptner 1937} – coccoliths occurring at poles of coccospheres.

3. *Coccolith arrangement*

Overlapping – adjacent coccoliths overlap.

Non-overlapping – adjacent coccoliths arranged with edges directly abutting rather than overlapping.

Interlocking – adjacent coccoliths interlock.

Non-interlocking – adjacent coccoliths do not interlock.

N.B. Interlock and overlap are separate phenomena, and can occur in any combination (see Text-fig. 1).

4. *Informal taxon-based terms*

As with coccoliths (see below), various terms have been coined to refer to coccospheres of particular taxonomic groups. These do not need any special definition, beyond noting the taxonomic groups included. Examples are as follows.

Braarudosphere – Braarudosphaeraceae
Helicosphere – Helicosphaeraceae

TERMS FOR ENTIRE COCCOLITHS

1. *Orientation*

Proximal – directed toward centre of coccosphere/cell. On nannofossils this is usually assumed to be the concave side, but cannot always be determined.

Distal – directed toward outer surface of coccosphere/cell.

Horizontal – perpendicular to proximo-distal direction.

Vertical – proximo-distal direction.

Internal/inner/inward – toward centre of coccolith.

External/outer/outward – away from centre of coccolith.

Longitudinal – direction parallel to long axis of an elliptical/elongated coccolith.

Transverse – direction parallel to short axis of an elliptical/elongated coccolith.

End – edge of coccolith parallel to short axis.

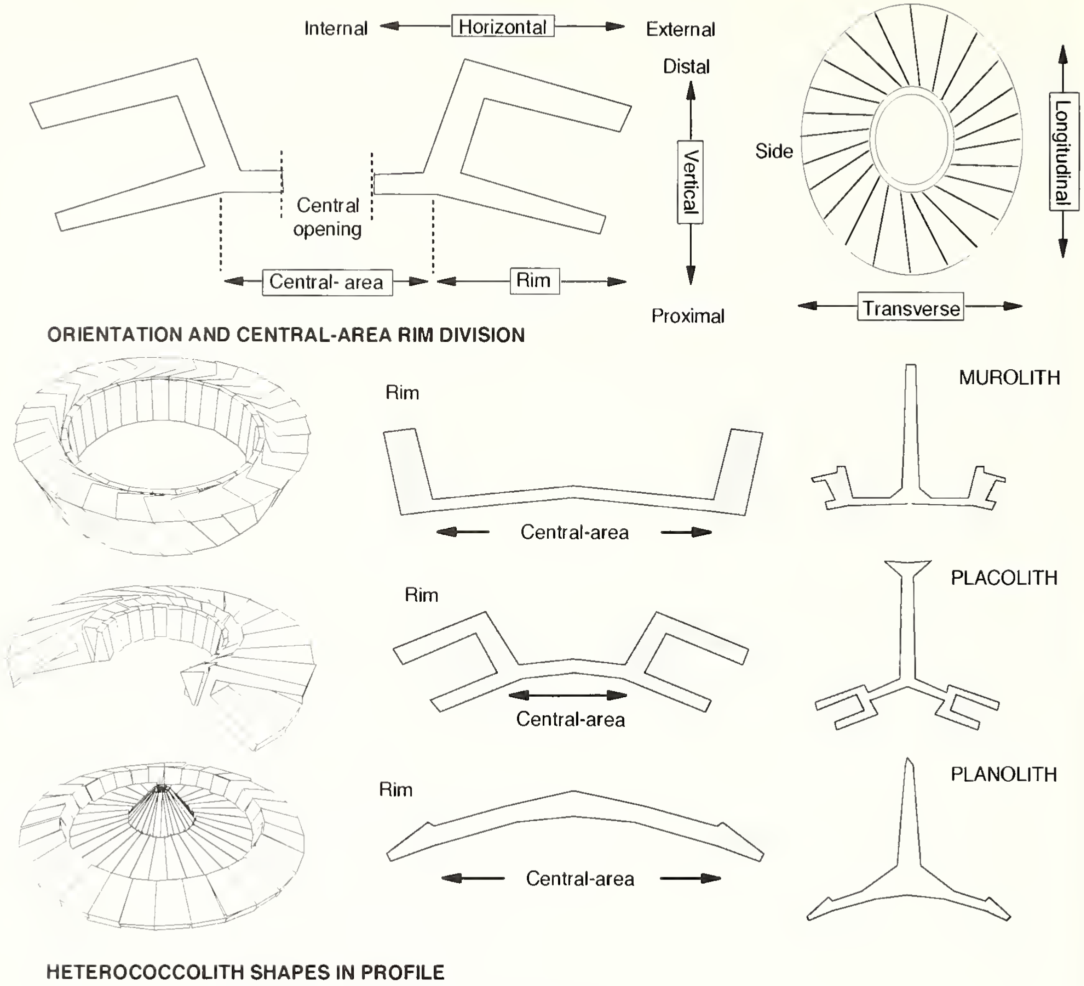
Side – edge of coccolith parallel to long axis.

Length/width/height – maximum dimensions of coccoliths in the longitudinal, transverse and vertical directions respectively.

2. *Parts*

In the vast majority of heterococcoliths there is an outer part which is somewhat higher than the inner part of the coccolith. This provides a convenient basis for starting any description of the shape and structure of coccoliths. It also is in large part a reflection of the coccolithogenesis process; growth outward and upward from the proto-coccolith ring forms the rim whilst growth inward forms the central area.

Central-area – inner part of coccolith, enclosed by the rim. Usually characterized by less regularly cyclical elements than the rim and by inward element growth. May be entirely closed, or include a central opening. N.B. We recommend hyphenating central-area since it has a special meaning.



ORIENTATION AND CENTRAL-AREA RIM DIVISION

HETEROCOCCOLITH SHAPES IN PROFILE

TEXT-FIG. 2. Coccolith orientation, basic parts and shape in profile.

Rim – outer part of coccolith, usually characterized by regular cycles, some vertically directed structures and outward element growth (alternative term marginal area; see Appendix 1). N.B. Use of this term was agreed after considerable discussion at the workshops.

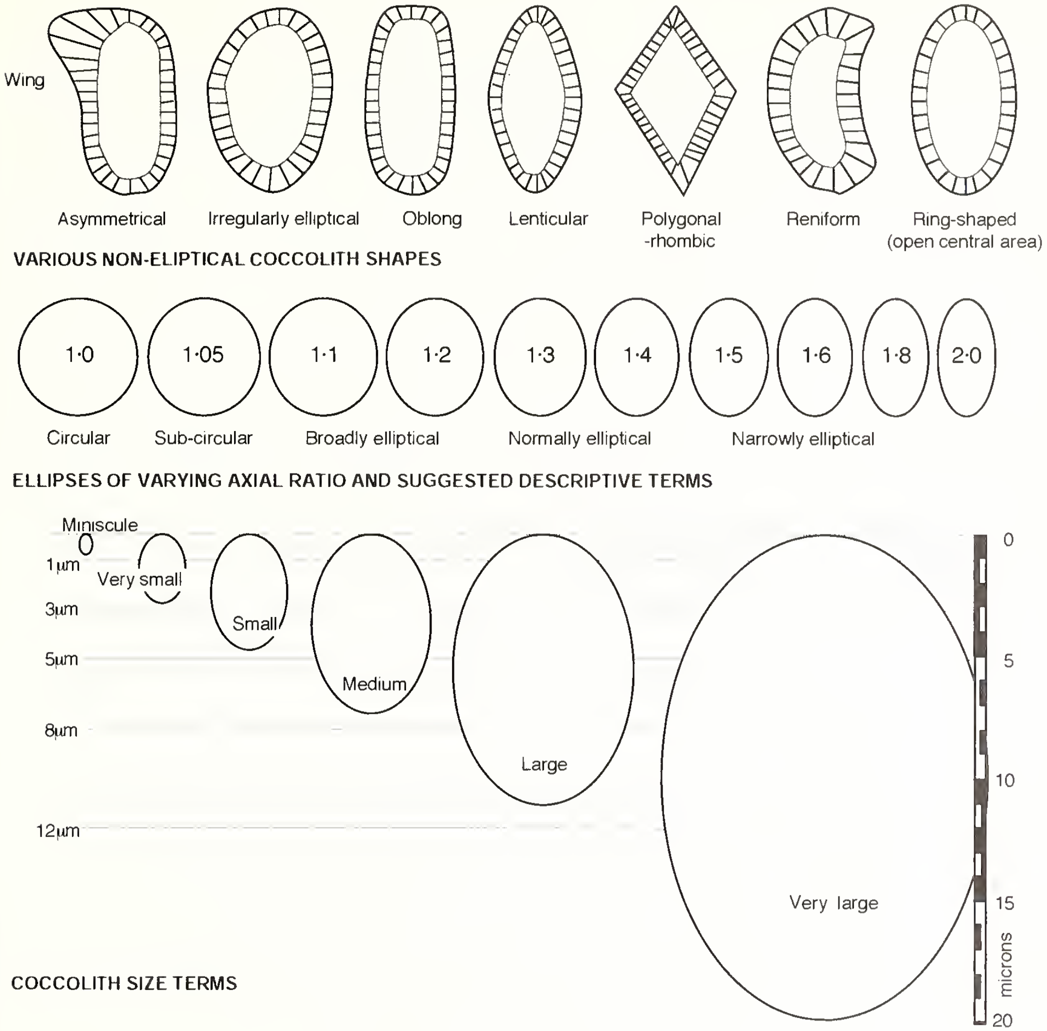
3. Profile – coccolith shape in vertical cross section

Although there is a very wide range of coccolith shapes, the three types listed below recur frequently in disparate groups (see also Young 1992*a*). They are probably homoeomorphic adaptations for organizing coccoliths on the cell. Intermediates between the types occur, and any of them can occur with or without processes. These terms have no taxonomic implications.

Planolith {Young 1992*a*, from latin *planus* flat} – rim not elevated (e.g. *Rhabdosphaera*, *Discoaster*).

Murolith {Young 1992*a*, from latin *murus* wall} – rim elevated but without well-developed shields (e.g. *Zeugrhabdotus*, *Pontosphaera*). (Discolith has been used in this sense; see Appendix 1).

Placolith {Lohmann 1902} – rim has two, or more, well developed shields (e.g. *Coccolithus*).



TEXT-FIG. 3. Coccolith sizes and shapes.

4. *Outline – coccolith shape in plan view*

Axial Ratio (abb. AR): ratio of length to width. Suggested descriptive terms, for elliptical coccoliths, are: *circular*; *sub-circular*; *broadly elliptical*; *normally elliptical*; *strongly elliptical.*

Asymmetrical – without bilateral symmetry, due to a wing or similar structure.

Elliptical – continuously curved with two axes of symmetry. Close to, but not necessarily an exact, mathematical ellipse (alternative terms *oval*, *ovoid*; see Appendix 1).

Irregularly elliptical – with an approximately elliptical shape but departing noticeably from regular form.

Lenticular – symmetrical form intermediate between a rhombus and ellipse, i.e. with pointed ends (e.g. *Syracosphaera prolongata*, *Stradnerlithus*).

Oblong – symmetrical form intermediate between a rectangle and ellipse, i.e. with curved ends but sub-parallel sides (e.g. *Calciopappus caudatus*, *Ellipsolithus macellus*). N.B. This is recommended botanical use (Stearn 1983).

Polygonal – with straight sides (triangular, pentagonal etc., e.g. scapholiths, *Corollithion*) (alternative term *geometric*; see Appendix 1).

Reniform – concavo-convex, kidney-shaped (e.g. *Nephrolithus*).

Ring-shaped – circular or elliptical, with narrow rim and open central area (e.g. *Cricosphaera*, *Manivitella*).

Wing – local extension of rim (e.g. *Helicosphaera*, *Kamptnerius*).

5. *Coccolith size*

Coccolith size is normally given as maximum dimension in plan view, i.e. length. The following sequence of terms is suggestions, based primarily on appearance under the light microscope.

Minuscule (< 1 μm), *very small*, 1–3 μm; *small* 3–5 μm; *medium* 5–8 μm; *large* 8–12 μm; *very large* > 12 μm.

6. *Informal taxon-based terms for entire coccoliths*

Many terms, defined originally as descriptive morphological terms, have become restricted taxonomically. For instance most authors would agree that the term helicolith should be restricted to coccoliths of Helicosphaeraceae, and not to any unrelated homoeomorphs. These terms are useful in many contexts, for example where it is important to distinguish between the organism and the coccolith/nannolith, or for describing polymorphic coccospheres. In general these terms are more widely used by workers on living coccolithophores than by palaeontologists. Comprehensive reviews are given by Tappan (1980), Chretiennot-Dinet (1990), Heimdal (1993), Siesser and Winter (1994) and Jordan *et al.* (1995).

We do not give detailed definitions here, since, essentially, they are defined by the characteristic morphology of the taxa on which they are based. New terms of this sort can be formed by adding to an appropriate generic root either the suffix -lith (e.g. sphenolith) or the suffix -id plus coccolith, murolith, planolith, or placolith (e.g. reticulofenestrid coccoliths).

Only modern usage is given here and many terms have undergone a complex evolution of meaning so that literature usage needs to be interpreted with caution; this applies particularly to the terms cricolith, cyrtolith, discolith, rhabdolith, and tremalith.

Caneolith {Braarud *et al.* 1955*a*, 1955*b*} – Syracosphaeraceae, endothecal coccolith. (N.B. The terms complete/incomplete caneoliths have been used; see Appendix 1).

Cricolith {Braarud *et al.* 1955*a*, 1955*b*} – Pleurochrysidaceae, ring-shaped placolith.

Cyrtolith {Braarud *et al.* 1955*a*, 1955*b*} – Syracosphaeraceae, exothecal coccolith.

Discolith {Huxley 1868} – Pontosphaeraceae, murolith without flanges.

Helicolith – Helicosphaeraceae, coccoliths with helical flange.

Lopadolith {Lohmann 1902} – high rimmed equatorial murolith of *Scyphosphaera*.

Osteolith {Halldal and Markali 1955} – whorl coccoliths of *Ophiaster*.

Pappolith – Papposphaeraceae.

Podorhabdid coccolith – Podorhabdaceae.

Protolith – Stephanolithaceae, Parhabdolithaceae (cf. Bown 1987).

Rhabdolith {Schmidt 1870} – Rhabdosphaeraceae, planoliths with or without spines.

Scapholith {Deflandre and Fert 1954} – *Calciosolenia*, *Anoplosolenia* (alternative term rhombolith).

Tremalith {Lohmann 1913} – Hymenomonadaceae, vase-shaped murolith.

Reticulofenestrid coccolith {Young 1989} – *Reticulofenestra* and descendants.

Coccolithid placolith {Jordan *et al.* 1995} – Coccolithaceae.

(N.B. See also the sections on nannoliths and holococcoliths, and Appendix 2, for related terms).

ULTRASTRUCTURE RELATED TERMS

1. Types of ultrastructural component

These are based largely on Young and Bown (1991).

Element – apparently discrete component of a coccolith. This is an observational term; several elements may unite to form a crystal-unit.

Crystal-unit – a group of elements from different cycles in crystallographic continuity. These are the fundamental components of coccoliths and their identification is a key objective of ultrastructural reaserch.

Segment – one symmetrically repeated part of the coccolith, including elements from each cycle, consisting of one or more crystal-units.

Lamina – platy sub-structure within a crystal-unit (e.g. *Braarudosphaera*).

Contact-surface – plane of contact between two elements (alternative term attachment surface; see Appendix 1).

Suture – trace of contact-surface on surface of coccolith.

Cycle – ring of elements or crystal-units.

Tier – one of a set of vertically superposed cycles (e.g. *Arkhangelskiella*, *Lapideacassis*).

2. Element shapes

N.B. a,b,c are three orthogonal axes, with any orientation.

Block – nearly equidimensional element (abc).

Tile – broad and thin element (ab > c. N.B. *Plate* has been used in this sense but we prefer to use it for larger structures, not for single elements).

Lath – elongate and wide element (a > b > c).

Rod – elongate and narrow element (a > bc)

Wedge – tapering nearly equidimensional element.

Petal/petaloid element – tapering broad and thin element.

Ray – tapering elongate and wide element.

Spine – tapering elongate and narrow element.

Granule – small and irregular or variably shaped element (e.g. blanket elements of *Helicosphaera*, spine-forming elements of *Cretarhabdus*). N.B. *Crystallite* has been used in this sense but we prefer to use it only for holococcolith elements.

3. Element modifications

Curvature – curving of elements. *Laevogyre* – elements curve to the left when traced radially outward. *Dextrogyre* – elements curve to the right when traced radially outward. *Straight* – elements not curved.

Node – block-shaped projection from element.

Keel – lath-shaped projection from element.

Ridge – rod-shaped projection running along element.

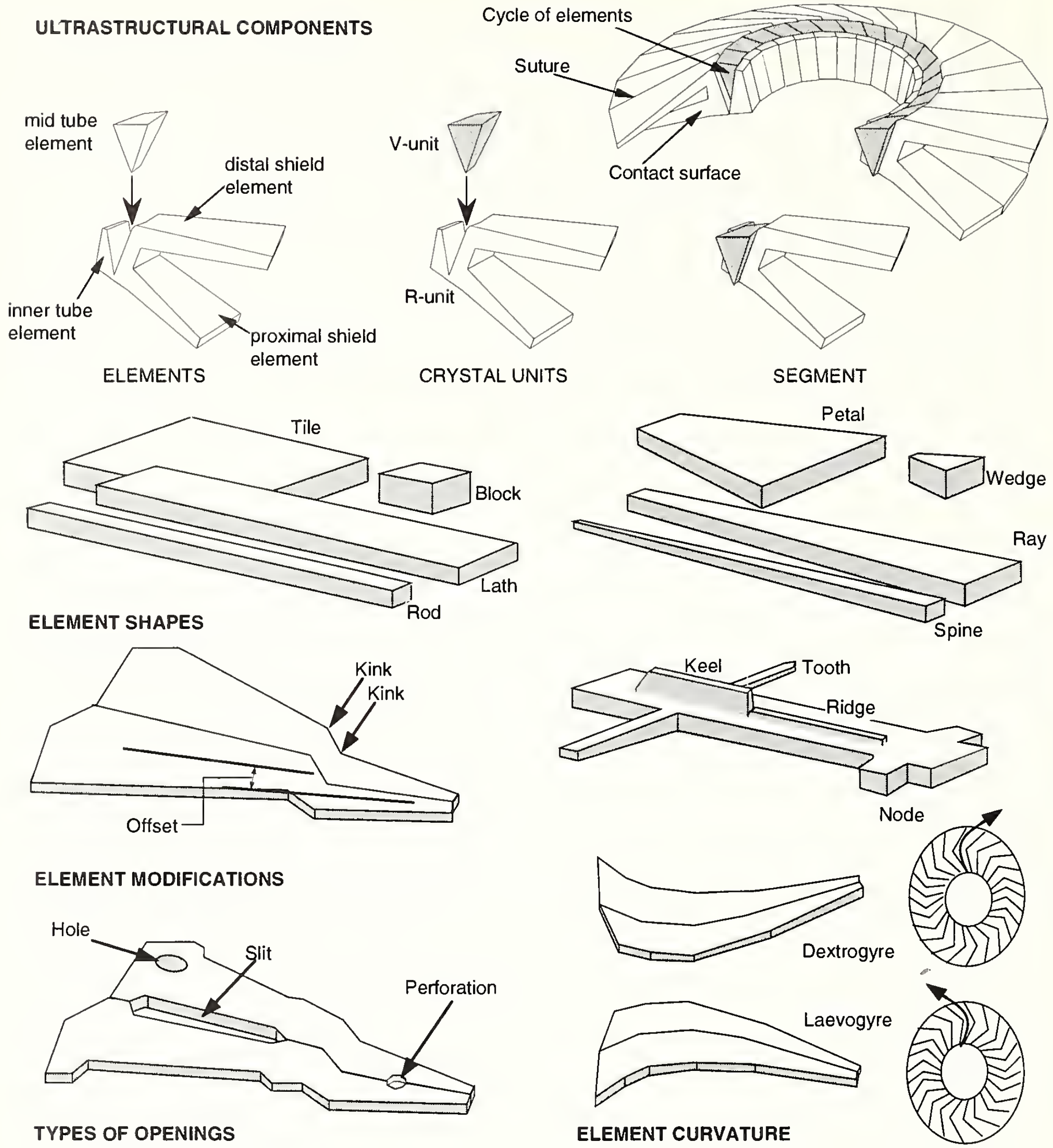
Tooth – rod or wedge-shaped projection from element.

Kink – angular bend in element.

Offset – displacement of an element from radial growth due to a double kink.

4. Special structures

Scissor-structure {Young 1992*b*} – crystal-unit structure formed of two elements growing at only slightly different angles, and forming a two-layered shield (e.g. *Coccolithus* upper and lower proximal shield elements; Text-fig. 6) or tube (e.g. *Toweius* inner and outer tube elements; Text-fig. 6).



TEXT-FIG. 4. Ultrastructural components, elements shapes, element modifications, openings and curvature.

Cross-over zone {Young 1992*b*} – belt around which two cycles of crystal-units cross (this usually corresponds to the proto-coccolith ring, e.g. *Coccolithus*; Text-fig. 6).

5. *Openings*

Canal – narrow elongate opening within a coccolith or nannolith (Text-figs 10, 14).

Cavity – broad opening within a coccolith or nannolith (Text-figs 10, 14).

Common opening – opening formed by several individuals, i.e. the space within a coccosphere or group of associated nannoliths.

Depression – pit on the surface of a coccolith or nannolith.

Hole {Farinacci 1971} – opening running through one element (e.g. *Pemma basquensis*).

Opening – general term for any space not filled by elements.

Perforation {Farinacci 1971} – small opening between two or more elements.

Slit – elongate perforation (e.g. *Emiliania*).

TERMS FOR DESCRIBING COCCOLITH RIMS

1. *Parts of rims*

Each of these parts may be formed of a single cycle of elements, part of a cycle or several cycles.

Shield – broad (sub-)horizontal structure (placoliths).

Tube – (sub-)vertical structure between two shields (placoliths).

Wall – (sub-)vertical structure not associated with shields (muroliths).

Flange – (sub-)horizontal protrusion from rim.

Collar – (sub-)vertical protrusion from rim (may occur on proimal or distal surface).

Crown – discontinuous/beaded collar.

2. *Directions on the rim*

These are based largely on Black (1972).

Radial – direction in the surface of the baseplate perpendicular to its margin: *inward-outward* – toward-away from centre.

Tangential – direction in the surface of the baseplate parallel to its margin.

Clockwise/dextral/right – *anticlockwise/sinistral/left* – senses of direction as seen in distal view. We recommend: use of *clockwise/anticlockwise* as the clearest of these terms for general purposes; use of *dextral/sinistral* when it is wished to emphasize particularly that this is the orientation as seen in distal view.

Vertical – direction perpendicular to the baseplate: *up/down* distal-proximal directions.

Flare and *taper* – divergence of orientation from horizontal/vertical in the radial direction. *Flare* surfaces diverge upward, producing *obconical/funnel-shaped* bodies. *Taper* surfaces converge upward, producing *conical bodies*.

3. *Element arrangement as seen in side view*

Imbrication/inclination – divergence from horizontal in the tangential direction. Imbrication is applicable to a cycle of elements, inclination to individual elements.

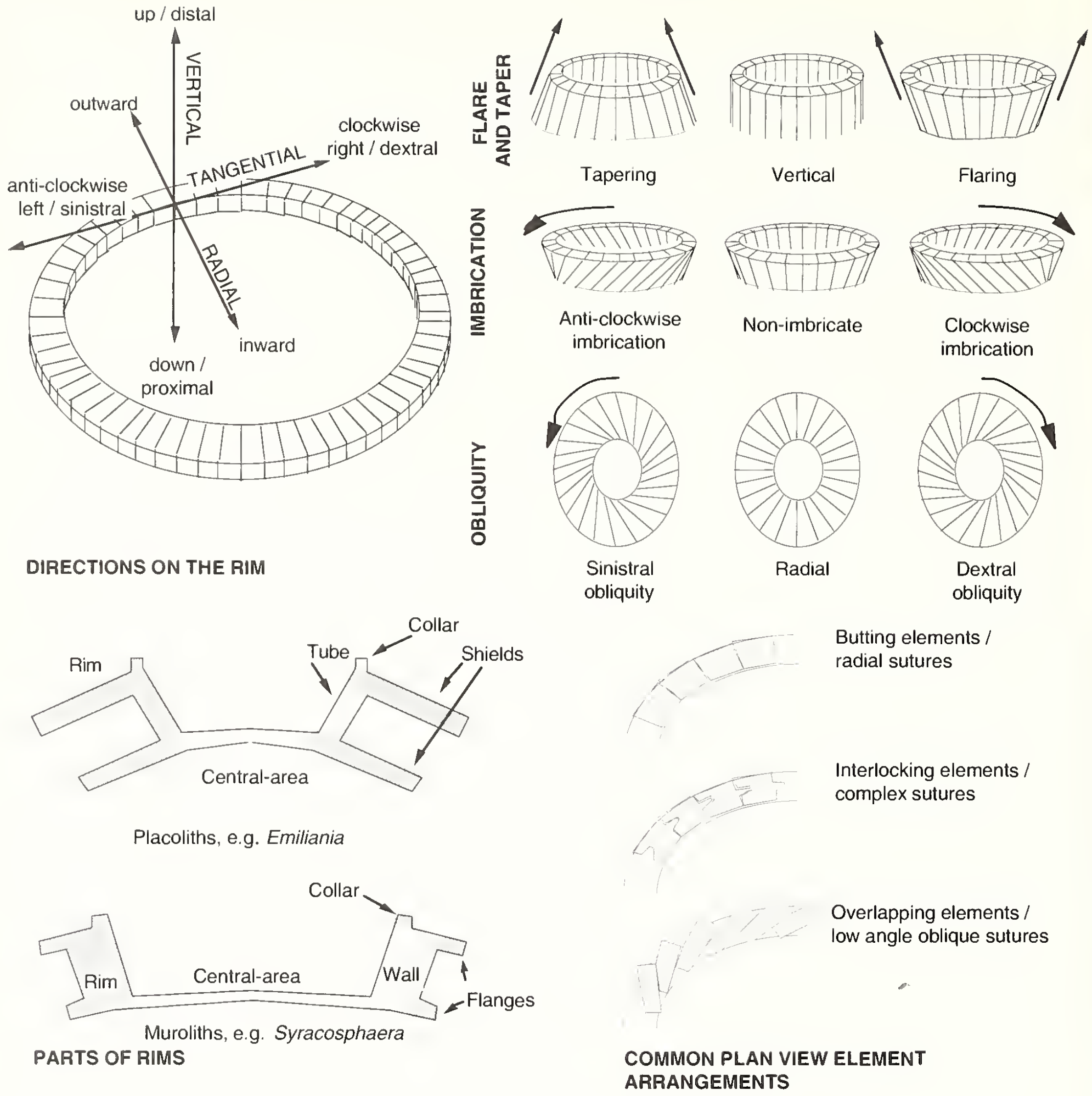
Clockwise/anticlockwise imbrication – offset of upper part of element from lower.

Imbrication angle – angle of contact-surface from the *horizontal*. *High-angle* – sub-vertical contact-surfaces. *Low-angle* – sub-horizontal contact-surfaces.

Zeugoid rim – rim with high-angle imbrication, and without distinct shields (alternative terms loxolith rim, zygodiscid rim; see Appendix 1).

4. *Element arrangement as seen in plan view*

Obliquity – horizontal divergence from radial direction (alternative term precession; see Appendix 1).



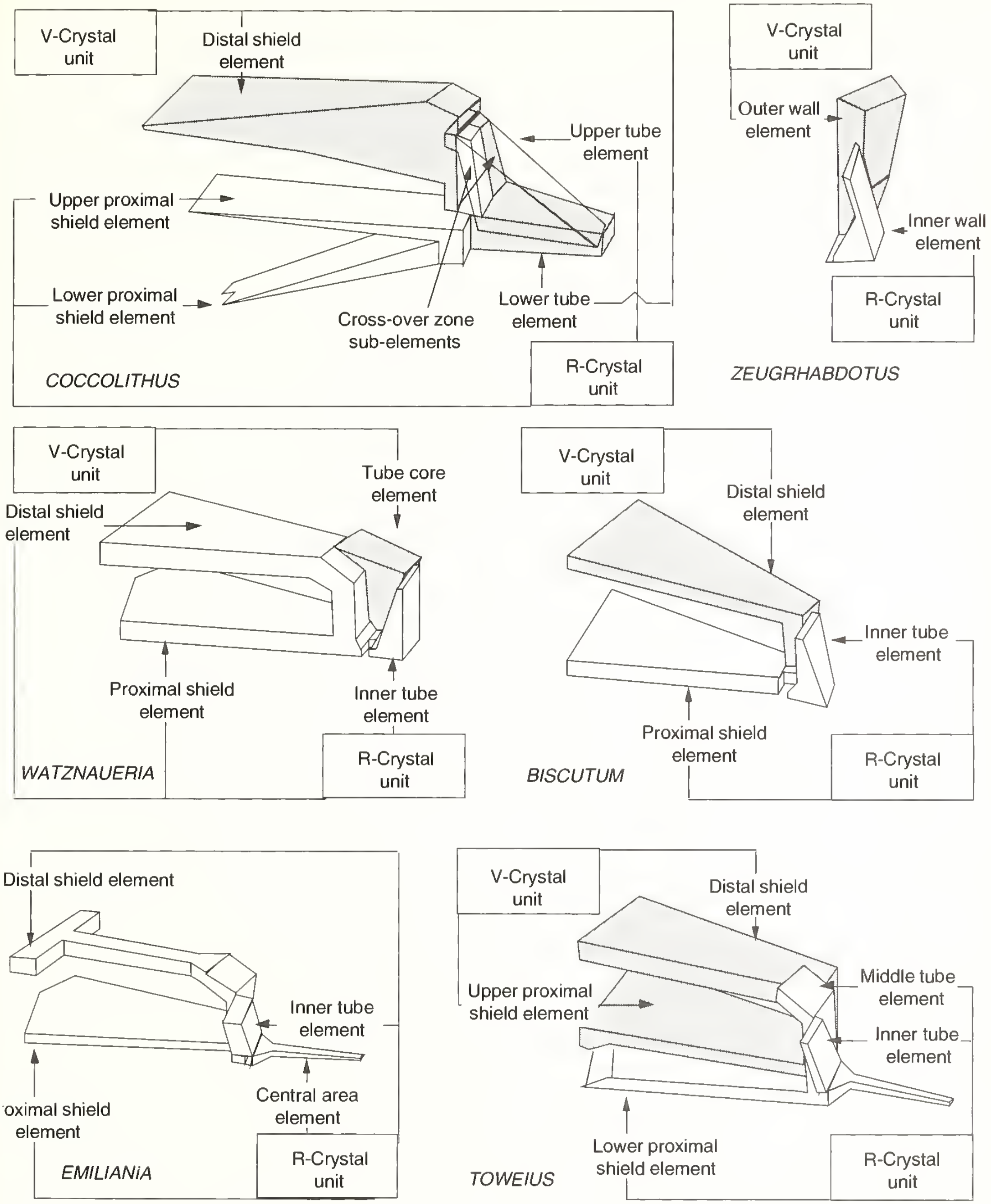
TEXT-FIG. 5. Terms for describing rim structures.

Dexral/sinistral obliquity – deflection from radial of outer part of element relative to inner part, as seen in distal view. Note that elements will show opposite apparent senses of obliquity in distal and proximal view. This can be described as follows: a dextrally oblique cycle displays clockwise obliquity in distal view but anti-clockwise obliquity in proximal view.

Butting – elements with simple (sub-)radial sutures.

Interlocking – elements with complex sutures.

Overlapping – elements with low angle oblique sutures (N.B. This pattern has been described occasionally as imbrication, but we prefer to use imbrication for description of vertical structures).



TEXT-FIG. 6. Terms for identification of elements – with interpreted homologies. Each figure represents one segment of a coccolith. The six examples are representative of major heterococcolith groups. Since the structure of many other coccoliths has not been worked out in detail yet, comparable terminology cannot yet be given for them.

5. *Identification of elements*

For description and discussion, the various elements/cycles of elements need to be identified. This is best done by reference to the location of the elements using the set of orientation and structure terms given above. Examples are given in Text-figure 8. Element shape is not recommended as an alternative since it is easily altered by diagenesis, intra-specific variation and evolution.

CENTRAL-AREA STRUCTURES

1. *Structural types*

Conjunct {Young 1992*a*} – formed from crystal-units of the rim structure, such as *Gephyrocapsa* (bridge and grill), *Helicosphaera sellii* (bar), *Kamptnerius* (plate), *Watznaueria biporta* (bar) (alternative term optically continuous structure; see Appendix 1).

Disjunct {Young 1992*a*} – formed from crystal-units discrete from the rim structure. such as *Arkhangelskiella* (plate), *Coccolithus pelagicus* (bar), *Helicosphaera seminulum* (bar), *Watznaueria britannica* (bar) (alternative term optically discontinuous structure; see Appendix 1).

2. *Orientation in profile*

Basal – occurring on the proximal surface.

Elevated – occurring above the proximal surface.

Vaulted – cone-shaped, rising from the rim toward the centre.

Longitudinal – parallel with long axis of (elliptical) coccolith.

Planar – flat, not vaulted.

3. *Orientation in plan view*

Transverse – parallel with short axis of (elliptical) coccolith.

Diagonal – inclined relative to axes. Angle should be measured from transverse direction: *low angle* – near to transverse direction; *high angle* – near to longitudinal direction.

Dextral/sinistral – inclined to the right/left of the long-axis as seen in distal view. N.B. As with element obliquity the terms dextral/sinistral are preferred for decribng orientations which appear different in proxmal and distal view.

Relative width – width of central-area relative to rim width: *wide* – central-area width more than twice rim width; *normal* – central-area width one to two times rim width; *narrow* – central-area width less than rim width.

4. *Structures spanning central-area*

Arm – part of crossbar, bridge or cross running from centre of coccolith to edge of central-area (alternative terms limb, spoke; see Appendix 1).

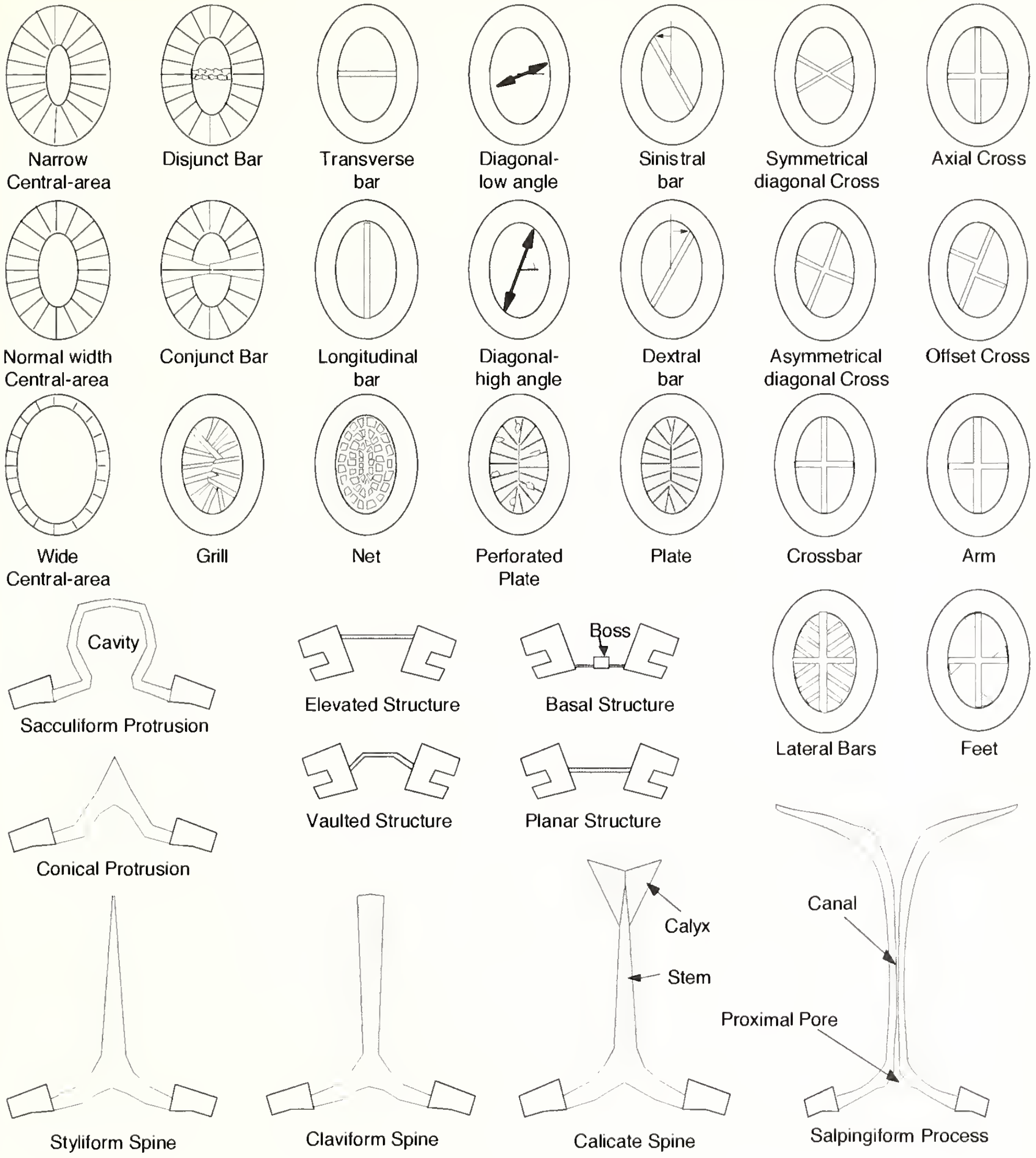
Bar – any elongate central-area structure. N.B. This is a general term. When it is useful to be more specific, terms such as longitudinal bar, cross-bar, and arm can be used (alternative term jugum; see Appendix 1).

Blanket – covering of small elements on distal side of central-area (e.g. *Helicosphaera*, *Coccolithus*).

Bridge – elevated bar spanning the central-area (e.g. *Gephyrocapsa*).

Cross-bar – bar spanning the central-area.

Cross – pair of cross-bars meeting in centre. *Axial cross* (abbreviation +), cross-bars longitudinal and transverse. *Diagonal cross* (abbreviation X) cross-bars diagonal; may be *symmetrical* or *asymmetrical* relative to the axes. *Offset cross* – cross with an offset between the arms of one, or both, of the crossbars (e.g. *Chiasmolithus*).



TEXT-FIG. 7. Central area structures.

Foot – broadening of bar as it meets the rim (e.g. *Cruciplacolithus tenuis*).
Lateral bar – bar running from rim to a cross bar (e.g. *Retecapsa*).

5. *Structures closing central-area*

Central opening – opening at centre of coccolith, may be spanned by bars or other central-area structures, but not by a continuous structure such as a grill or plate.

Closed central-area – central-area without a central opening.

Grill – system of bars closing central-area (e.g. *Emiliania*).

Net – mesh-like structure closing central-area (e.g. *Reticulofenestra*, *Cribrosphaerella*) (alternative term cribrate central-area; see Appendix 1).

Open central-area – central-area without any structures.

Plate – continuous or nearly continuous structure closing central-area.

Perforated plate – plate with perforations (e.g. *Arkhangelskiella*).

6. *Processes*

Calyx – flaring structure at tip of process (e.g. *Podorhabdus*, *Papposphaera*).

Boss – low process, height similar to or less than width (alternative term knob; see Appendix 1).

Process – general term for any structure rising from the central-area.

Protrusion – broad low process, with height similar to width, and width near that of entire central-area. Types: *conical* – cone-shaped protrusion (e.g. *Acanthoica*); *sacculiform* – sac-like protrusion with more-or-less rounded upper part (e.g. *Algirosphaera*). (N.B. *labiatiform* has been used for the elongate double-lipped sacculiform protrusions; see Appendix 1).

Spine – elongated process, height greater than width (alternative term column; see Appendix 1). Types: *styliform* {Halldal and Markali 1955} – spine tapers toward the distal end; *claviform* {Halldal and Markali 1955} – spine has blunt end, without calyx. (N.B. helatoform has been used for nail-shaped processes; see Appendix 1); *calicate* – spine is surmountd by a calyx; *salpingiform* {Braarud *et al.* 1955*a*, 1955*b*} – spine (or protrusion) trumpet-shaped (e.g. *Discosphaera*).

Stem – part of process below calyx.

Cavity – wide opening within process (e.g. *Podorhabdus grassei*, *Algirosphaera robusta*).

Canal – narrow opening running along length of process.

Proximal pore – opening of canal, on proximal side of central-area.

CRYSTALLOGRAPHY

1. *Crystallographic orientation*

Calcite c-axis orientation can be summarized using the following terms, based on Young and Bown (1991), and Young *et al.* (1992). N.B. Actual orientations depart significantly (up to 30°) from true vertical and radial.

V-unit {Young and Bown 1991} – crystal-unit with sub-vertical orientation of c-axis.

R-unit {Young and Bown 1991} – crystal-unit with sub-radial orientation of c-axis, relative to its point of origin (nucleation) on the proto-coccolith ring.

T-unit {new} – crystal-unit with sub-tangential orientation of c-axis (e.g. Braarudosphaeraceae, Polycyclolithaceae).

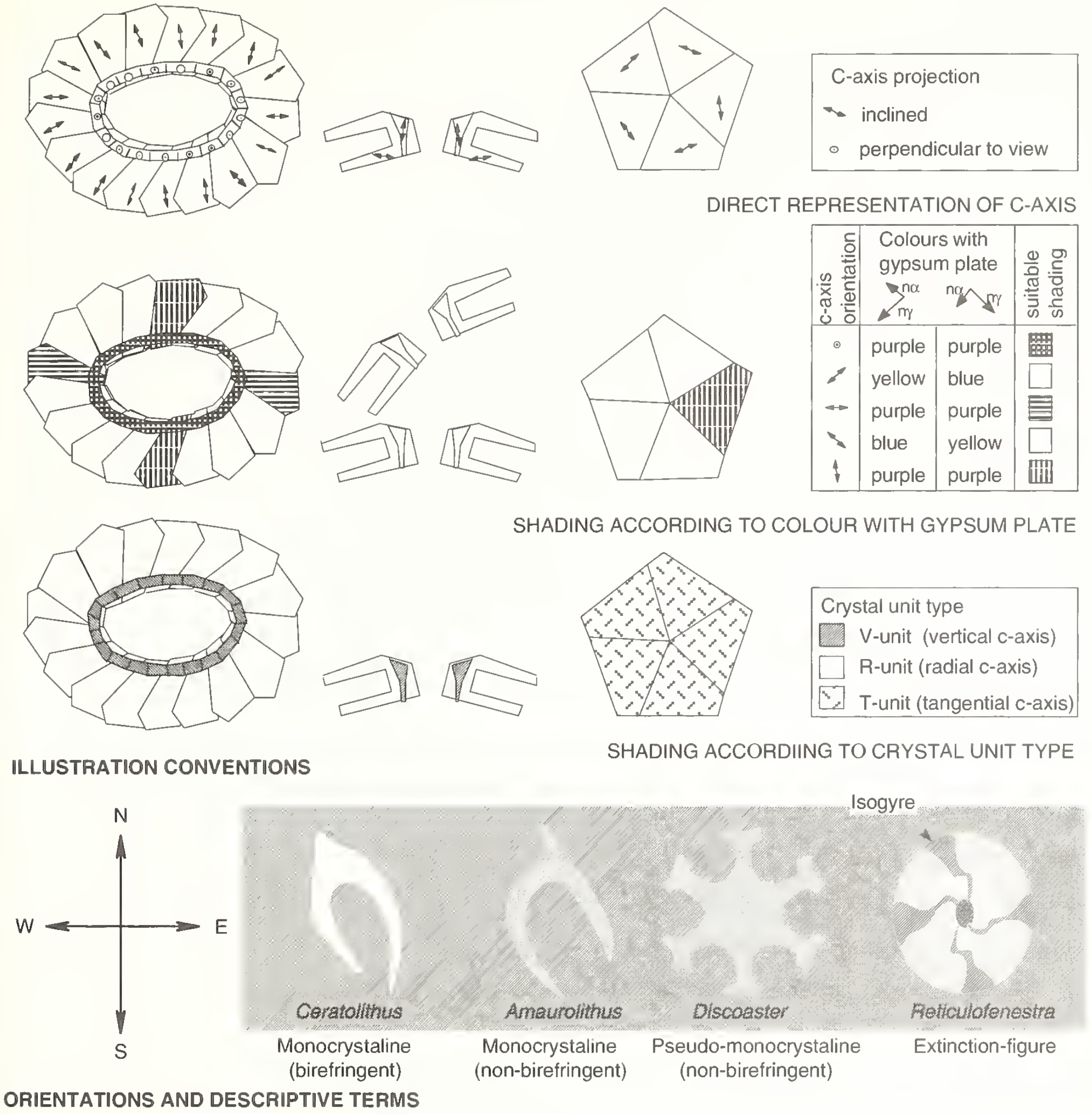
Compound – formed of several crystal-units. such as in *Micula*, *Discoaster*.

Pseudo-monocrystalline – formed of several crystal-units with parallel c-axes, but non-parallel a-axes, such as in *Discoaster*. These behave optically as single crystals, but will not fuse into a single crystal during overgrowth.

Monocrystalline – formed of a single crystal-unit, and so all elements have identical crystallographic orientation of c- and a-axes and overgrow as one unit, e.g. apical spine of *Sphenolithus heteromorphosus*, entire nannoliths of *Florisphaera*, *Marthasterites*, *Minylitha*, *Ceratolithus*.

2. *Graphical conventions for indicating crystallographic orientation*

Symbols – a single symbol per element can indicate c-axis direction (Text-fig. 8).



c-axis orientation	Colours with gypsum plate ↘nα nγ↙	nα↗ ↘nγ	suitable shading
⊙	purple	purple	▦
↗	yellow	blue	☐
↔	purple	purple	▤
↘	blue	yellow	☐
↕	purple	purple	▥

TEXT-FIG. 8. Crystallography: the diagrams showing illustration conventions are based on *Watznaueria* (plan and side views) and *Braarudosphaera*; the figures in the dark box represent the appearance of nannofossils in the light microscope, with cross-polarized light.

Shading – to illustrate directly observations made with a gypsum plate, hatching can be used – vertical and horizontal for parts in extinction (purple). Diagonal for birefringent parts (blue and yellow). The direction of diagonal hatching should of course be based on the c-axis orientation and since the gypsum plate orientation varies between microscopes the relationship between observed colour (blue, yellow) and c-axis direction has to be determined for each microscope.

Unit type shading – for illustrating structure it is convenient to apply the same shading to all the elements of one crystal-unit cycle in all views of the nannolith. For this the following scheme is recommended: V-units stipples; R-units blank; T-units dashes.

3. *Light microscopy based terms*

Birefringent/non-birefringent – appearing bright/dark between cross-polars. N.B. A coccolith or part of a coccolith can only appear non-birefringent in one orientation (when the c-axis is vertical), so these terms should not be used without explicit description of specimen orientation; e.g. 'discoasters are non-birefringent in plan view'.

Extinction-figure – appearance of a specimen in cross-polarized light, particularly pattern of isogyres.

Isogyre – dark line in cross-polarized light caused by elements in extinction.

North/South, East/West – orientations relative to the microscope body.

INTRASPECIFIC VARIATION

1. *Primary coccolith variation*

As a general principle, styles of variation should be described without reference to inferred causal factors; e.g. 'heavily calcified *E. huxleyi*' is preferable to 'cold-water morphotype'. Terms used here are largely based on Young and Westbroek (1991), Young (1994).

Normally formed – with typical form.

Abnormally formed – departing from normal form in some way, includes all the categories below.

Degree of completion/ontogenetic variation – variation in degree to which the coccolith has grown. (N.B. terms such as juvenile and mature are not recommended for use in this context). *Coccolithogenesis* {Outka and Williams 1971} – process of coccolith development and growth. *Proto-coccolith ring* {Young 1989} – earliest stage of coccolith growth, crystal-units simple without differentiation of elements. *Incomplete coccolith* – elements differentiated but incompletely grown. *Complete coccolith* – all elements fully grown.

Teratological malformation – abnormal form developed as result of irregular growth. N.B. The use of the term malformation to describe other types of variation (e.g. degree of calcification, or growth) is not recommended.

Degree of calcification – primary variation in amount of biogenic calcite incorporated in a coccolith. *Under-calcified* – coccolith with elements markedly thinner than normal for the species. *Normally calcified* – coccolith with elements of normal thickness for the species. *Over-calcified* – coccolith with elements markedly thicker than normal for the species.

2. *Secondary alteration of coccoliths – diagenetic and water-column effects*

Overgrowth – secondary inorganic growth of calcite on elements.

Etching – secondary inorganic dissolution of calcite from elements. Descriptive scheme, {from Roth and Thierstein 1972; Roth 1983}.

X, Excellent preservation – coccoliths appear pristine.

E1, Slight etching – serrate outlines, partial dissolution of delicate structures.

E2, Moderate etching – irregular outlines, dissolution of most delicate structures and species.

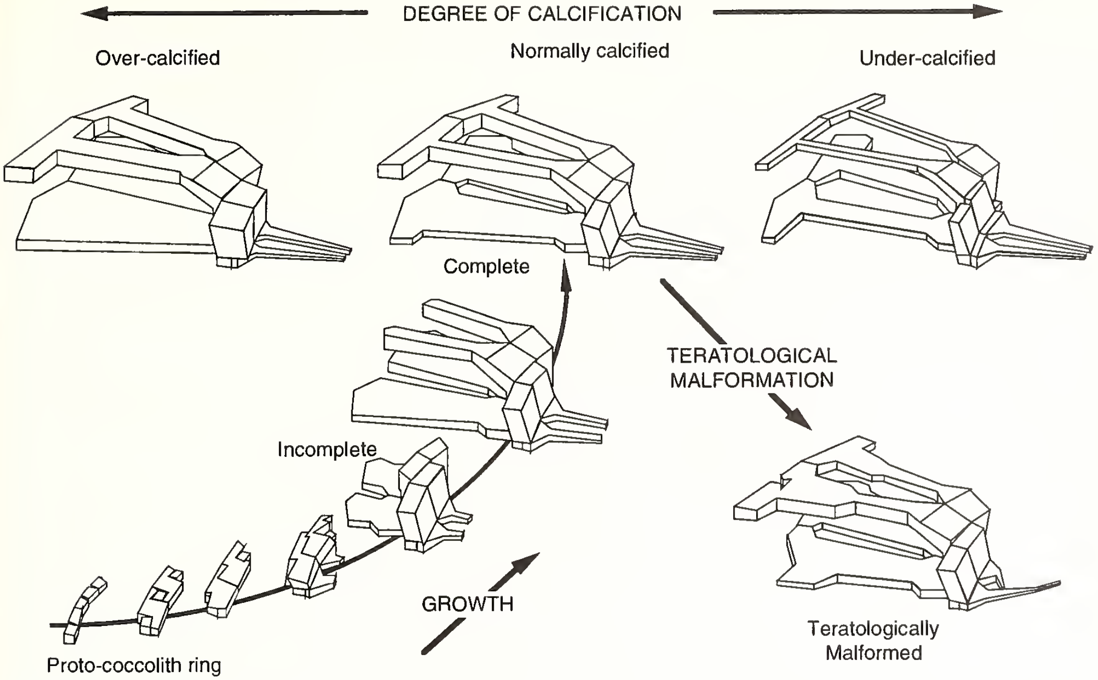
E3, Strong etching – much material fragmented, only resistant species left.

O1, Slight overgrowth – overgrowth of shield and central-area elements noticeable but does not obscure details.

O2, Moderate overgrowth – many elements with large overgrowths, many details obscured.

O3, Strong overgrowth – only overgrown elements, identifications very limited.

N.B. Overgrowth and etching commonly both occur in the same sample: this can be shown by codes such as E1-O2. This scheme is primarily for light microscopy; successful electron microscopy requires preservation grades E1, X or O1.



TEXT-FIG. 9. Intraspecific variation. The sub-figures each represent two segments of *Emiliania huxleyi*. The figure only represents primary, biologically induced, variation. Secondary etching and overgrowth can be superimposed on this primary variation, particularly in fossil specimens.

NANNOLITH SHAPES

Nannoliths display a wide range of shapes, including the following types which all occur independently in more than one group. These shape terms are independent of structure, e.g. tetraradiate nannoliths may be formed of one, four or many crystal units.

Dibrachiate – consisting of two sub-parallel arms joined at one end. Includes *horseshoe*, *arrowhead*, and *arcuate* shapes (e.g. *Ceratolithus*, *Amaurolithus*, *Ceratolithina*, *Ceratolithoides* – except *C. verbeekii*).

Compact – more-or-less equidimensional nannoliths. Includes *conical* (e.g. *Sphenolithus*), *obconical* (i.e. inverted cone-shaped, e.g. *Conusphaera*), *cylindrical* (e.g. *Fasciculithus*) and *cubic* (e.g. *Micula*) shapes.

Rod-shaped – elongate, and apparently without a basal disc. Includes *bladed* (e.g. *Lithraphidites quadratus*, *Triquetrorhabdulus carinatus*) and (*sub-*)*cylindrical* (e.g. *Microrhabdulus*) shapes.

Radiate – with radial *symmetry*. N.B. the number of crystal-units may be larger or smaller than the number of rays.

Triradiate – three-fold radial symmetry (e.g. *Marthasterites*, *Trochasterites*).

Tetraradiate – four-fold radial symmetry (e.g. *Micula*, *Quadrum*, *Nannotetrina*).

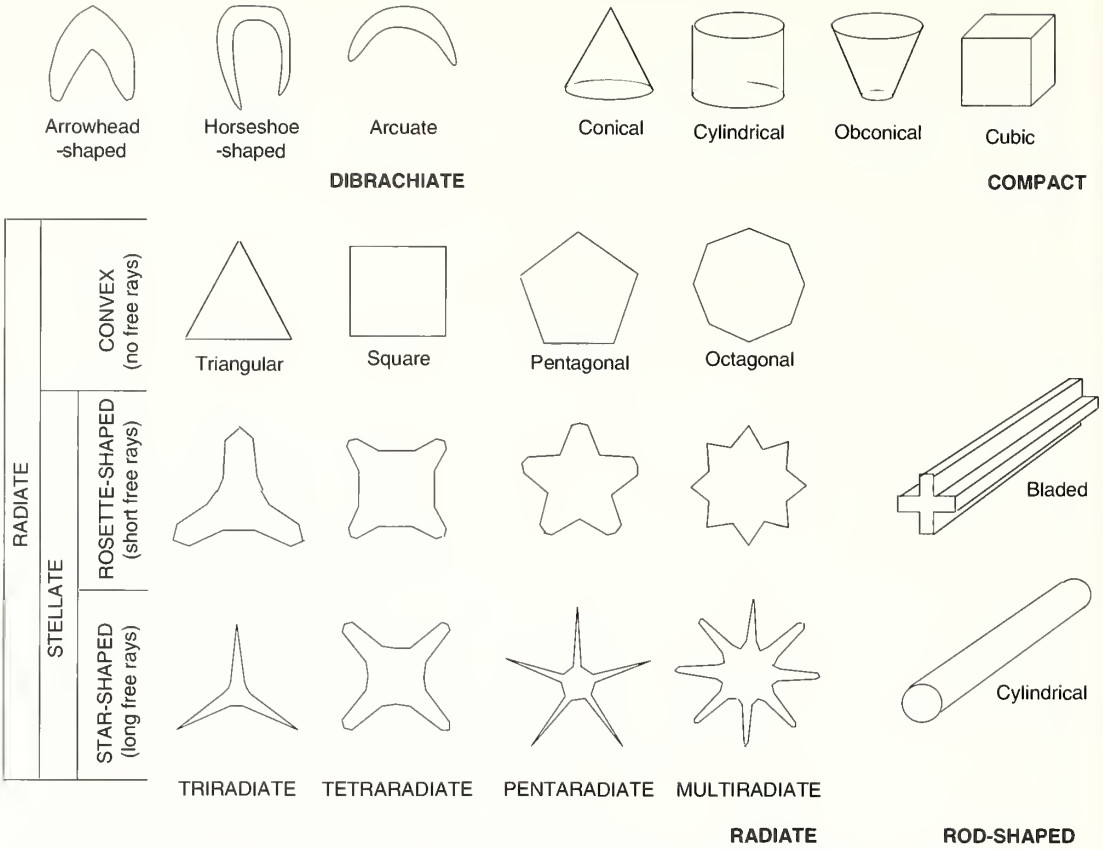
Pentaradiate – five-fold radial symmetry (e.g. *Goniolithus*, *Braarudosphaera*).

Multiradiate – more than five-fold radial symmetry (e.g. many *Discoaster* spp.).

Central body – core part of radiate nannolith where elements are in contact.

Free rays – parts of radiate nannolith extending beyond central body.

Short free rays – length of free rays is less than radius of central body, resulting in a *rosette-shaped* outline.



TEXT-FIG. 10. Nannolith shapes. These terms relate solely to the shape of the nannoliths, not the structure. A cubic nannolith might be formed of one, four, eight or many crystal-units.

Long free rays – length of free rays is greater than radius of central body, resulting in a *star-shaped* outline.

Convex outline – without free rays (e.g. *Braarudosphaera*). Including e.g. *triangular*, *square* and *pentagonal* shapes.

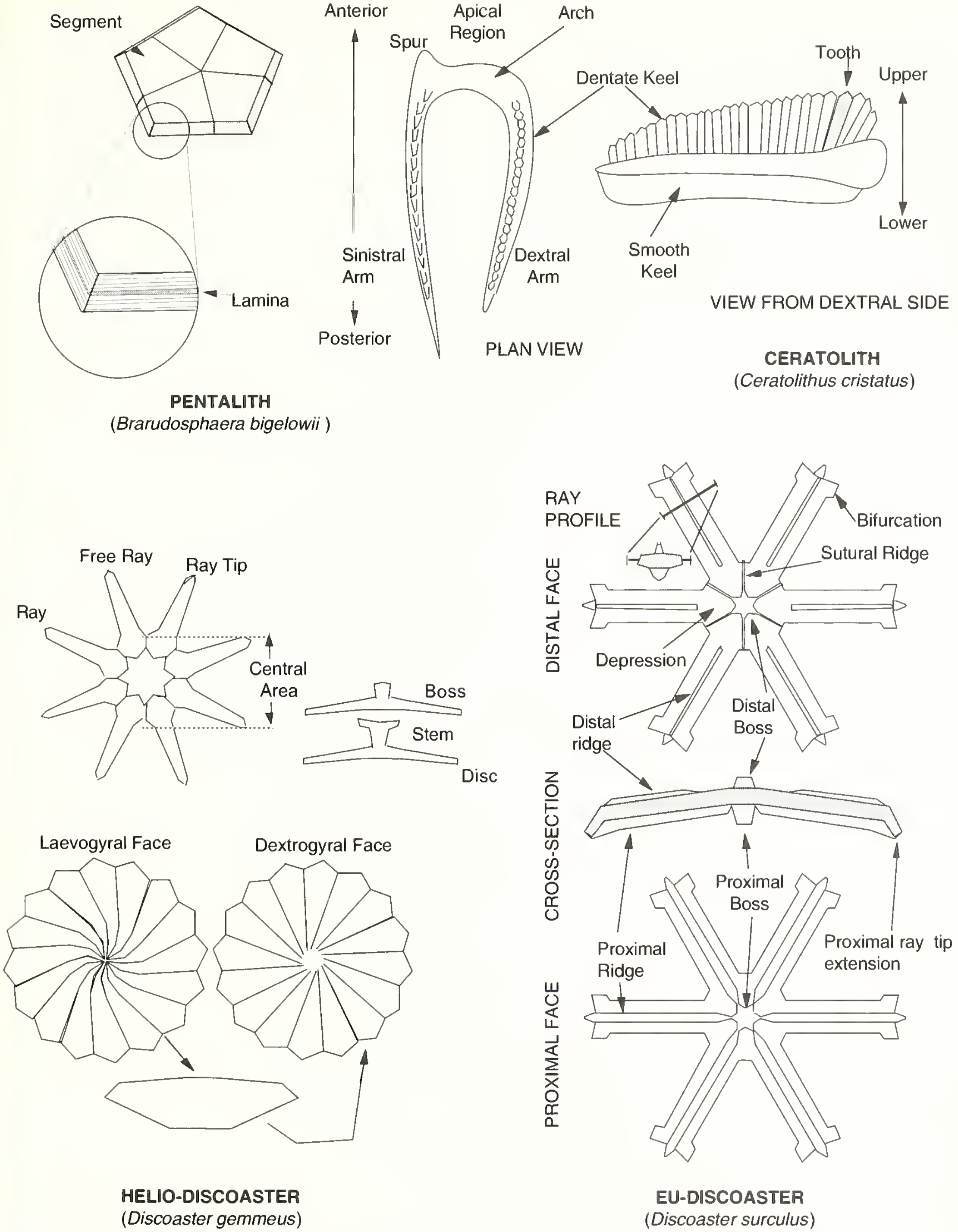
Stellate – with free rays (e.g. *Micrantholithus*, *Discoaster*). Including *rosette* and *star-shaped.*

TERMINOLOGY FOR SPECIFIC HETEROCOCCOLITH AND NANNOLITH GROUPS

For most groups, the general terminology outlined above provides all the terms needed. Some groups, however, have special features which require additional terms, as outlined below. Lapideacassid nannoliths are not covered here: their morphology and sytematics are reviewed by Perch-Nielsen and Franz (1977), and Perch-Nielsen (1985*b*). Terminology for Rhabdolithaceae is mainly covered above, but see also Kleijne (1992). Aubry (1984, 1988*a*, 1988*b*, 1990) reviews terminology for many Cenozoic groups.

Braarudosphaeraceae (*Jurassic–Recent*)

Informal taxon-based name. Pentalith {Gran and Braarud 1935} – nannolith formed by Braarudosphaeraceae (N.B. does not include other nannoliths formed of five elements, e.g. *Discoaster pentaradiatus*).



PENTALITH
(*Brarudosphaera bigelowii*)

CERATOLITH
(*Ceratolithus cristatus*)

HELIO-DISCOASTER
(*Discoaster gemmeus*)

EU-DISCOASTER
(*Discoaster surculus*)

TEXT-FIG. 11. Special terms applied to Braarudosphaeraceae, Ceratolithaceae and Discoasteraceae. N.B. The terms applied to the description of heterococcoliths may also, where appropriate, be applied to these groups, and *vice versa*.

Lamina – plate-like sub-element of segments.

Segment – one of the five component parts of a pentalith. They appear to be single crystal-units.

Ceratolithaceae (*Late Miocene–Recent*)

Informal taxon-based name. Ceratoliths – dibrachiate nannoliths formed by Ceratolithaceae. Includes *Amaurolithus* nannofossils; does not include the ring-shaped exothecal heterococcoliths.

Orientation. Upper/lower – the more-ornamented surface is designated upper. This division is arbitrary, but it is useful since there is a consistent polarity to structures. With careful through-focussing it is possible to distinguish the two sides by light microsopy. N.B. The terms distal/proximal should not be used since ceratoliths appear to be either intracellular or wrapped around the cell (Norris 1965).

Anterior/posterior – closed end is designated anterior.

Left/right – based on upper view, looking toward anterior end.

Apical region – anterior end of ceratolith; hence terms such as *apical node*.

Arch – part of apical regon connecting the two arms.

Arm – rod-like extension back from apical region.

Rod – rod-shaped structure attached to the nannolith (e.g. *Amaurolithus bizarrus*).

Spur – projection from apical region.

Keel – lath-like structure running along an arm. *Dentate keel* – keel formed of sub-parallel teeth. *Smooth keel* – keel without teeth.

Tooth – rod-like sub-element of a keel.

Wing – plate-like extension from main body of nannolith (e.g. *Amaurolithus ninae*).

Discoasteraceae (*Paleocene–Pliocene*).

Informal taxon-based name. Discoasters – nannolith formed by Discoasteraceae.

Eu-discoaster – typically Neogene and usually star-shaped discoasters, with planar contact surfaces between elements.

Helio-discoaster – typically Paleogene and usually rosette-shaped discoasters, with curved contact surfaces.

N.B. These terms are useful even if formal taxonomic division into the genera *Eu-discoaster* and *Helio-discoaster* is not made. The differences between them are given in Theodoridis (1984) and Aubry (1984).

Orientation. In virtually all discoasters, there are consistent differences between the two faces (Stradner and Papp 1961; Prins 1971; Romein 1979; Aubry 1984; Theodoridis 1984; Self-Trail and Bybell 1995). Many of the Neogene eu-discoasters consistently have one concave and one convex face and, by analogy to coccoliths, these faces have been termed *proximal* and *distal* (e.g. Theodoridis 1984). The two sides are also consistently characterized by various other structures; in particular there are usually sutural ridges on the distal side (Text-fig. 11). These structures can be used to separate the proximal and distal faces of planar eu-discoasters.

In helio-discoasters the rays are usually curved, so *laevogyral* and *dextrogyral* faces can be distinguished. Moreover, the curvature is usually stronger on the laevogyral surface. It is not, however, certain which of these faces corresponds to the proximal face in eu-discoasters, and they have varying relationships to discoaster concavity. Hence, the terms proximal and distal have been applied rather inconsistently in this group (compare Stradner and Papp 1961, Prins 1971 and Romein 1979) and are, perhaps, better avoided.

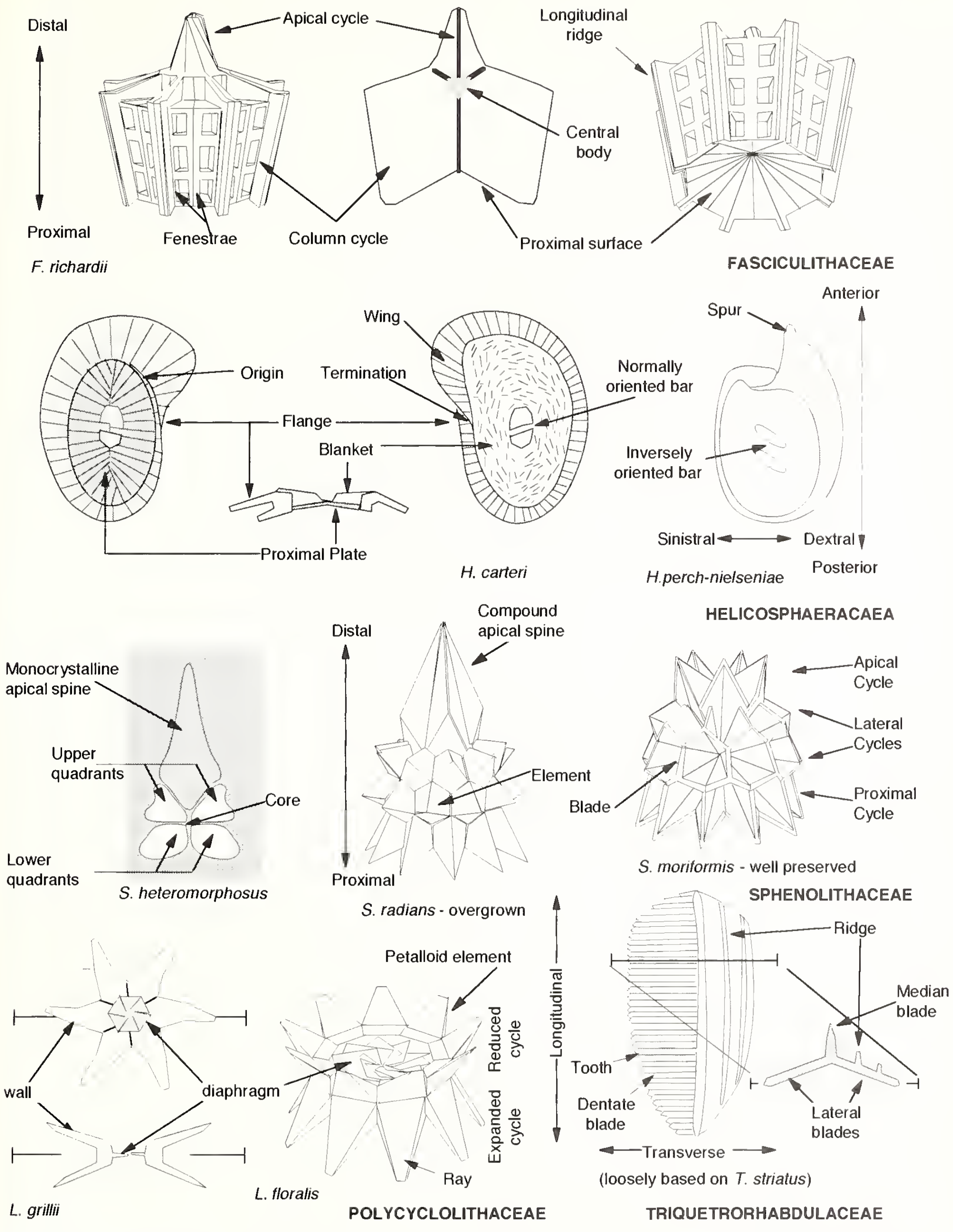
Ray – disc element.

Free ray – part of ray protruding beyond central-area.

Ray tip – outermost part of ray.

Bifurcate tip – ray tip divides into two *bifurcations* (e.g. *D. variabilis*).

Simple tip – ray tip without bifurcation or proximal extension.



TEXT-FIG. 12. Special terms applied to Fasciculithaceae, Helicosphaeraceae, Polycyclolithaceae, Sphenolithaceae and Triquetrorhabdulaceae. N.B. The terms applied to the description of heterococcoliths may also, where appropriate, be applied to these groups, and *vice versa*.

Proximal extension – continuation of the ray downward from the tip (e.g. *D. brouweri*).

Central-area – portion of discoaster with rays in contact.

Contact-surface – surface between adjacent elements (alternative term attachment surface; see Appendix 1).

Disc – main part of discoaster, excluding bosses or stems.

Boss – low distal or proximal protrusion from centre of disc (alternative term knob; see Appendix 1).

Rosette-shaped – discoaster with short free rays (Text-fig. 10).

Segment – ray and associated boss or stem elements.

Stem – high distal or proximal protrusion from centre of disc (e.g. *Discoaster kuepperi*).

Star-shaped – discoaster with long free rays (Text-fig. 10).

Sutural ridge – ridge running along suture.

Fasciculithaceae (*Paleocene–Early Eocene*)

Informal taxon-based term. Fasciculith – nannolith formed by Fasciculithaceae.

Orientation. The concave end of the nannolith is assumed to be proximal.

Apical cycle – distal cycle of fasciculith. (Alternative term cone, see appendix).

Central body {Romein 1979} – optically distinct body occurring in the centre of fasciculith.

Column cycle – proximal cycle of fasciculith, usually forms most of the fasciculith.

Fenestra – regular depression on fasciculith.

Longitudinal ridge – ridge parallel to length of fasciculith.

Proximal surface – lower surface of fasciculith.

Helicosphaeraceae (*Eocene–Recent*)

Informal taxon-based term. Helicolith – nannolith formed by Helicosphaeraceae.

Orientation. The asymmetry of helicoliths allows more precise description of orientation than for most other coccoliths.

Anterior – end with origin of flange and usually with broader flange on distal side often with distinct wing or spur (alternative term pterygal; see Appendix 1).

Posterior – opposite end to anterior (alternative term antipterygal; see Appendix 1).

Detxral/sinistral – right/left sides of helicolith as seen in distal view with anterior end upwards. As with other uses, the terms dextral/sinisral are recommended in place of left/right for terms referring to one particular orientation. The wing, when present, is on the sinistral side.

Bar – structure crossing central opening. Types:

- *Conjunct* – developed from rim elements (e.g. *H. carteri*) (alternative terms optically continuous bar, bar, bridge; see Appendix 1).
- *Disjunct* – formed from elements discrete from the rim (e.g. *H. intermedia*) (alternative terms optically discontinuous bar, bridge, bar; see Appendix 1).
- *Normally oriented* – diagonal bar with dextral orientation; i.e. rotated to the right of the long axis in distal view/anterior end on opposite side to the wing.
- *Inversely oriented* – diagonal bar with sinistral orientation; i.e. rotated to the left of the long axis in distal view/anterior end on same side as wing. N.B. Use of the terms normal/inverse is a ubiquitous convention based on their relative abundances.

Blanket {Theodoridis 1984} – mass of elements forming distal cover.

(*Helicoid*) *flange* – rim structure of helicolith (shield is also used by some workers).

Origin – location of first/shortest elements of flange on the proximal side.

Proximal plate – inward radiate elements on proximal side of central-area.

Spur – spike-like expansion of flange near its termination (e.g. *H. recta*).

Termination – location of last elements of flange on the distal side.

Wing – broad expansion of flange near its termination (e.g. *H. carteri*).

Polycyclolithaceae (*Cretaceous*)

Informal taxon-based term. Polycyclolith – nannolith formed by Polycyclolithaceae. Varol (1992) gives a review of the group.

Orientation. Clear distal/proximal polarity has not been demonstrated, so these terms should be avoided.

Diaphragm – plate-like central cycle of elements

Wall – outer part of nannolith, typically formed of two superposed cycles of elements.

Reduced/expanded cycle – smaller/larger of the two wall cycles.

Ray, *petalloid*, *block* – typical shapes of wall elements.

Sphenolithaceae (*Paleocene–Pliocene*)

Informal taxon-based term. Sphenolith – nannolith formed by Sphenolithaceae.

Orientation. The concave end of the nannolith is assumed to be proximal/basal.

Apical cycle – upper part of sphenolith, formed of most steeply inclined cycle of elements. Types: *Monocrystalline* – formed of one crystal-unit; e.g. *S. heteromorphosus*, *S. belemnos*. *Duocrystalline* – formed of two crystal-units; e.g. *S. distentus*, *S. furcatulithoides*. *Compound* – formed of several crystal-units; e.g. *S. radians*, *S. abies*.

Apical spine – elongate extension of apical cycle.

Base – all of sphenolith except the apical spine.

Blade – one of three sub-parts of an element, seen only in well preserved material.

Core – centre of radiation of elements.

Element – basic component of sphenoliths, each element appears to be a single crystal-unit.

Lateral cycles – cycles between apical and proximal cycles, not always present.

Proximal cycle – lowermost cycle of elements.

Upper/lower part – part above/below the core.

Triquetrorhabdulaceae (*Oligocene–Pliocene*)

Orientation. There is no obvious proximal/distal differentiation.

Longitudinal – parallel to length of nannolith.

Transverse – perpendicular to length of nannolith.

Blade – one of the three main sub-parts of the nannolith.

Dentate blade – blade with transverse sub-structure of rod-shaped teeth.

Lateral blade – one of two broader blades nearly in the same plane (e.g. *T. rugosus*).

Median blade – narrowest of three blades.

Ridge – subsidiary longitudinal structure on a blade (e.g. *T. challengeri*).

Wing – blade greatly extended in transverse direction (e.g. *T. finifer*).

Tooth – rod-like part of a dentate blade.

HOLOCOCCOLITHS

1. Terms for parts of holococcoliths

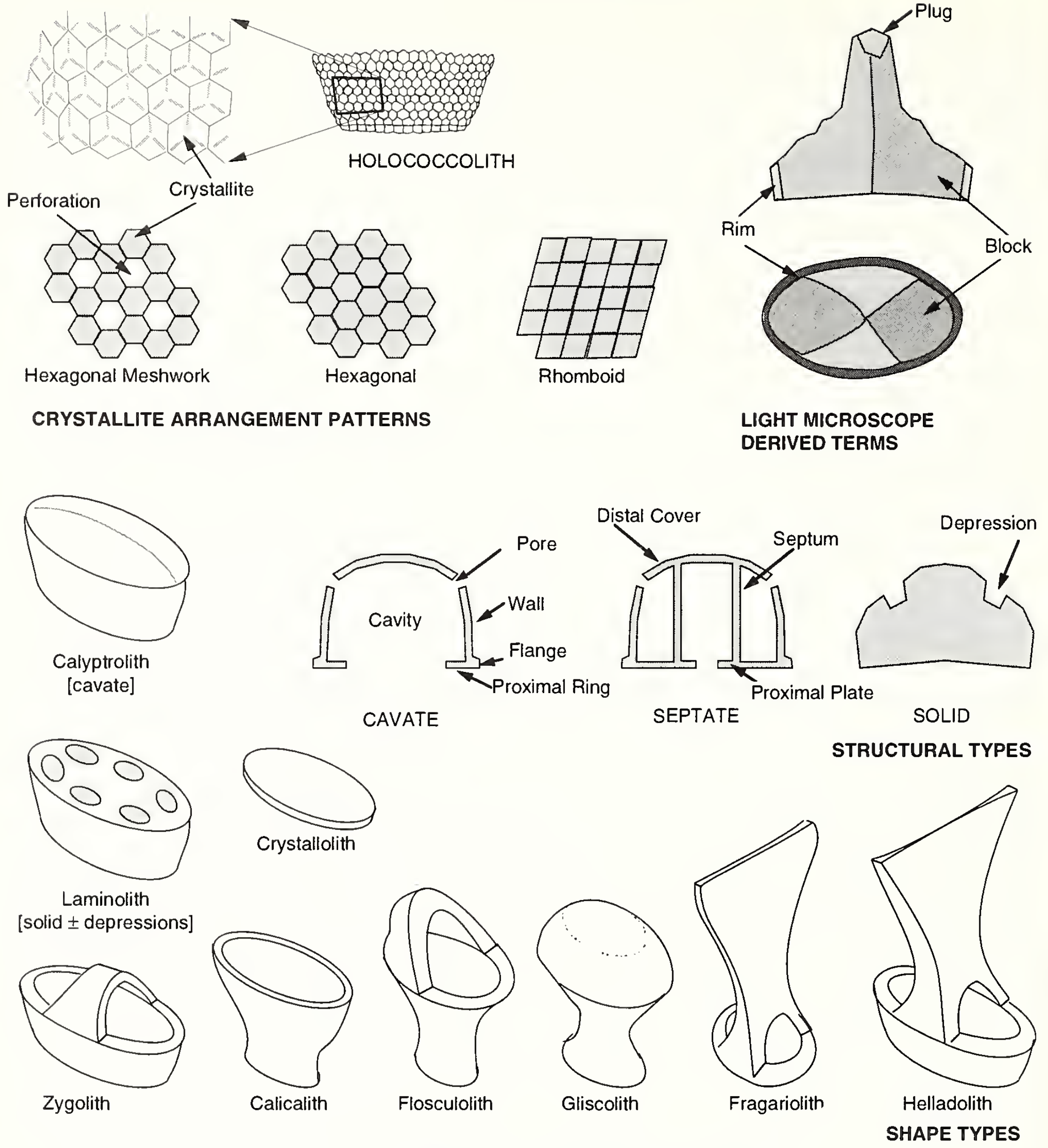
Block – zone of holococcolith that behaves in cross-polarized light as one unit.

Cavity – open central part of holococcolith, not filled by crystallites (e.g. *Calyptrosphaera*, *Zygosphaera*).

Crystallite – individual minute crystal.

Crystallite arrangement – pattern of crystallites visible on a surface. Types: *hexagonal*, *hexagonal meshwork*, *rhomboid*.

Depression – pit on surface, not opening into a cavity.



TEXT-FIG. 13. Special terms applied to holococcoliths.

Distal-cover – distal layer(s) of crystallites, covering cavity (may merge into rim or be discrete from it).
Perforation – opening in wall the size of one crystallite.
Plug – distally positioned block (e.g. *Lucianorhabdus*).
Pore – opening in wall larger than one crystallite (e.g. *Gliscolithus*).
Proximal flange – sub-horizontal protrusion from base of rim.
Proximal-plate – proximal layer(s) of crystallites (nearly) covering base of coccolith.

Proximal-ring – proximal layer(s) of crystallites confined to edge of coccolith.

Rim – peripheral zone discrete in cross-polarized light from the main blocks (typically rim elements have radial c-axes).

Septum – layer(s) of crystallites forming internal wall.

Wall – layer(s) of crystallites forming sub-vertical structure.

2. *General terms for description of entire holococcoliths*

Cavate – with large cavity inside rim (e.g. *Calyptrosphaera*).

Septate – space inside rim is subdivided by septa (e.g. *Syracolithus quadriperforatus*, *Anfractus harrisonii*).

Solid – coccolith consists essentially of a single mass of crystallites without distinct cavity, or septa, with or without depressions, perforations, or pores (e.g. *Syracolithus catilliferus*) and possibly many fossil holococcoliths.

3. *Morphological types*

For holococcoliths, unlike heterococcoliths, there are not many useful structural characters, and the special shape terms (e.g. calyptrolith, helladolith) describe morphotypes that almost certainly occur independently in different taxa. So, these terms are purely descriptive terms and independent from taxonomy. They are not much used by palaeontologists and we do not recommend the creation of new terms for fossil holococcolith types. See also Norris (1985), Kleijne (1991) and Jordan *et al.* (1995).

Calicalith {Kleijne 1991} – open cavate, without distal cover (e.g. *Calicasphaera*).

Calyptrolith {Lohmann 1902} – domal cavate, with nearly continuous distal-cover (e.g. *Calyptrosphaera*).

Crystallolith {Braarud *et al.* 1955*a*} – disc-like solid holococcolith formed of one or two layers of crystallites, with low rim (e.g. *Coccolithus pelagicus* phase *hyalinus*).

Flosculolith {Kleijne *et al.* 1991} – cavate with distal opening partially closed by a vaulted distal-cover (e.g. *Flosculosphaera*).

Fragariolith {Kleijne 1991} – proximal plate directly surmounted by blade-like process (e.g. *Anthosphaera fragaria*).

Gliscolith {Norris 1985} – cavate with bulbous distal part (e.g. *Gliscolithus*).

Helladolith {Heimdal and Gaarder 1980} – similar to zygolith but with bridge expanded distally into double-layered leaf-like process (e.g. *Helladosphaera*).

Laminolith {Heimdal and Gaarder 1980} – solid holococcolith formed of several (more than two) horizontal layers of crystallites, with or without perforations/pores (e.g. *Syracolithus catilliferus*).

Zygolith {Kamptner 1937} – with bridge-shaped distal-cover (e.g. *Homozygosphaera*).

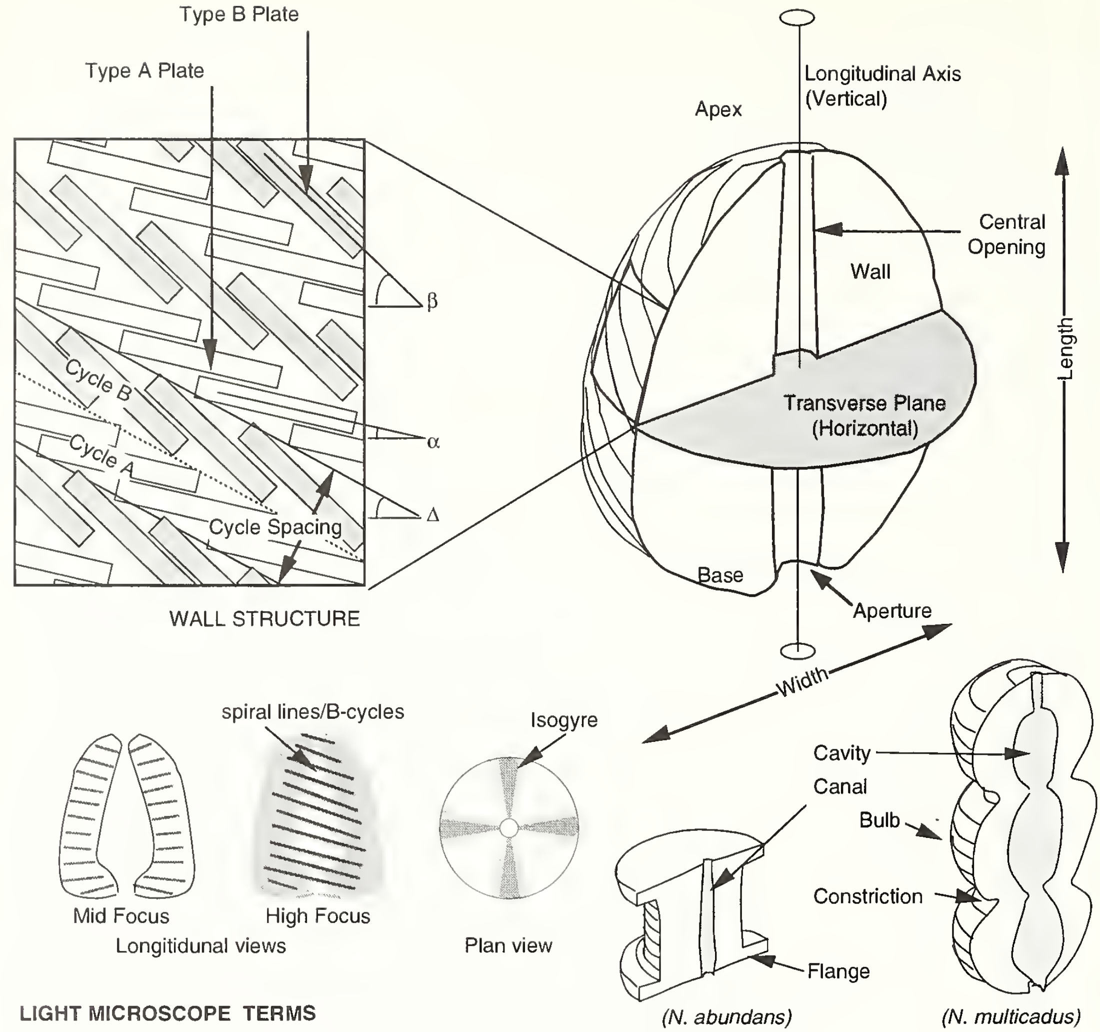
NANNOCONACEAE

Nannoconaceae is a monogeneric group of rock-forming Late Jurassic to Late Cretaceous nannoliths of uncertain affinities. The terminology applicable to *Nannoconus* is reviewed in detail by van Niel (1994), and the following is a list of key terms only.

Informal taxon-based term. Nannoconid.

1. *Associations*

Groups of associated nannoconid individuals have been found by various workers: Trejo (1960); Colom (1965); Ozkan (pers. comm.). These associations have only a very small common opening and may represent colonial groups of cells (cf. many diatoms) rather than single organisms (cf. typical coccospheres).



TEXT-FIG. 14. Special terms applied to holococcoliths.

Association {van Niel, 1994} – a group of systematically arranged individuals.

Twin {van Niel 1995} – two nannoconid individuals joined at their ends, with ridges and grooves extending across the contact surface.

2. *Orientation*

Rosette {Noël 1958} – association of nannoconids lying side-by-side with their longitudinal-axes radiating from a central point. N.B. It is possible that all rosettes are spherical, but the term sphere is not recommended since this has not been demonstrated, and since nannoconid associations may not be strictly comparable to coccospheres.

Longitudinal axis – axis of rotational symmetry of nannoconid.

Transverse plane – plane perpendicular to the longitudinal axis.

Horizontal – directions within the transverse plane.

Vertical – directions parallel to the longitudinal axis.

Pole – end of nannoconid, point of emergence of symmetry axis: *apex* {Bronnimann 1955} – pole in *N. steinmannii* at narrower end of specimen; *base* {Bronnimann 1955} – pole opposite to apex (broader end in *N. steinmannii*).

Longitudinal view – view of nannoconid parallel to longitudinal axis.

Plan view – view of nannoconid perpendicular to longitudinal axis.

3. *General terms*

Central opening {Kamptner 1931} – opening running longitudinally through the nannoconid. Types: *canal* – narrow, < 1 μm; *cavity* – wide, > 1 μm; *aperture* {Kamptner 1931} – expression of the central opening at the ends of the specimen.

Bulb {Trejo 1960} – a distinct swelling of the outline (e.g. *N. borealis* – single, *N. paskentiensis* – double, *N. multicadus* – triple).

Constriction {Deflandre and Deflandre-Rigaud 1962} – external indentation of the wall, between bulbs.

Flange {Stradner and Grün 1973} – horizontal projection around the end of nannoconid. N.B. Flanges may be symmetrical or asymmetrical in end view, and may be present at one or both ends of the specimen.

Wall {Kamptner 1931} – structure enclosing the central opening.

4. *Structure*

Nannoconids appear to be formed of two types of plates arranged in alternating cycles (van Niel 1992). These cycles appear to spiral around the wall but the precise geometry is not yet clear.

Plate {Stradner and Grun 1973} – basic structural element of nannoconid, single sub-triangular platy crystal (alternative term wedge; see Appendix 1).

Type A-cycle {van Niel 1992} – cycle of plates inclined at a lower angle (*angle* α to the horizontal). These are birefringent in longitudinal view (Perch-Nielsen 1988).

Type B-cycle {van Niel 1992} – cycle of plates inclined at a higher angle (*angle* β) to the horizontal. These cycles are non-birefringent in longitudinal view and form the dark *spiral lines* observed in cross-polars in longitudinal view (Kamptner 1931; Deflandre and Deflandre-Rigaud 1962; Perch-Nielsen 1988).

Angle Δ {van Niel 1992} – angle of the A cycle/B cycle contact to the horizontal. N.B. This is the only angle measurable by light microscopy.

Cycle spacing – repeat distance between cycles perpendicular to angle Δ, i.e. combined thicknesses of A and B cycles.

CALCISPHERES

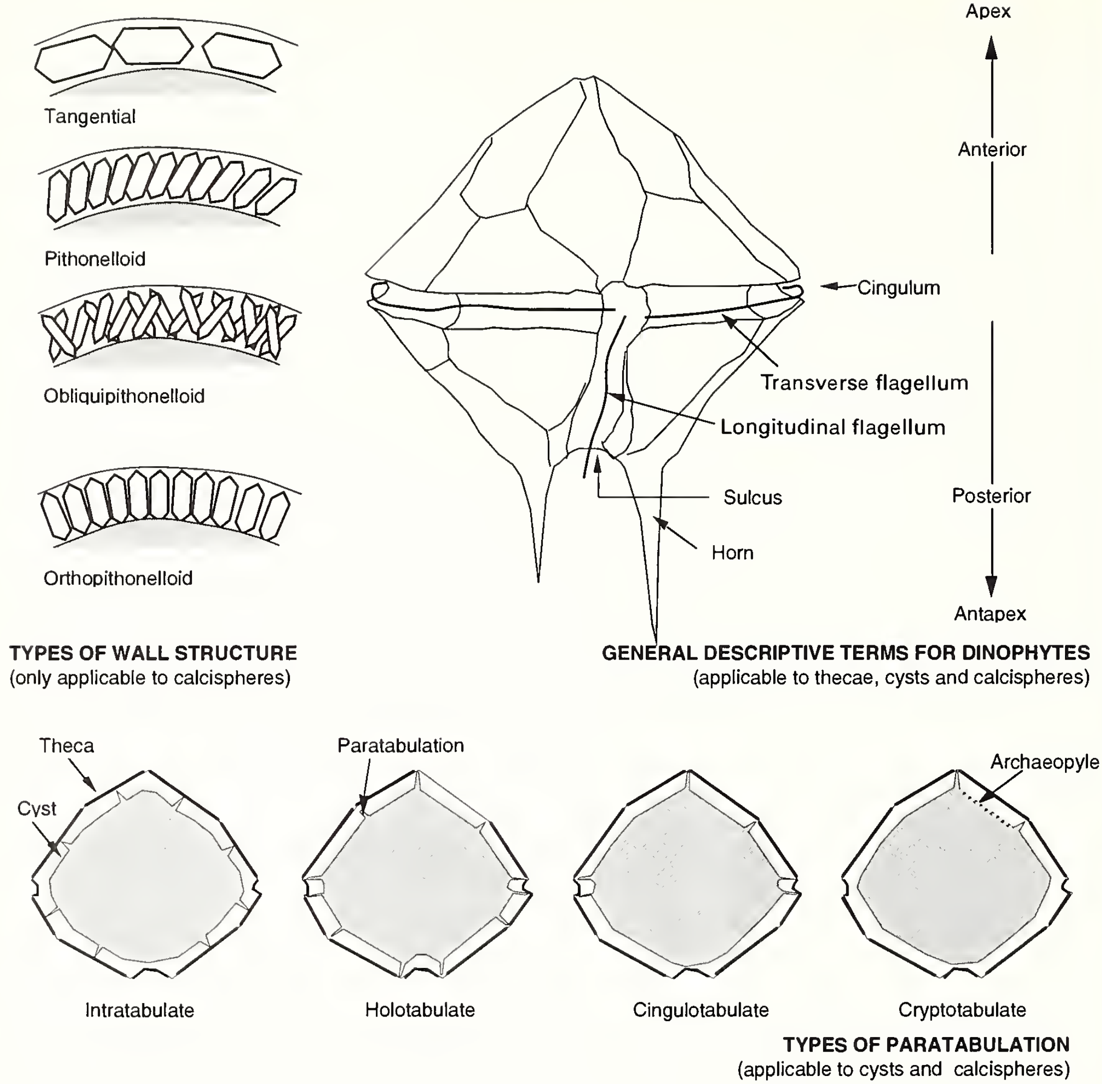
Palaeozoic calcispheres are of uncertain affinity and are not discussed here. Most Mesozoic and Cenozoic calcispheres are now believed to be dinoflagellate cysts. Keupp (1991) gave an English-language synthesis of this group; Janofske and Keupp (1992) gave a brief overview. These workers regard wall structures as the primary basis for classification. Williams *et al.* (1978), Sergeant (1982) and Evitt (1985) summarized the terminology for describing organic-walled cysts, much of which can be directly applied to calcispheres. Only the most important, relevant terms are included here.

1. *Orientation*

Dinoflagellates have clearly differentiated ends, shown by shape, flagellar disposition, behaviour, etc. Swimming direction is conventionally used to determine front and rear.

Apex/anterior end – front of dinoflagellate when swimming, usually pointed. Almost always contains the archaeopyle.

Antapex/posterior end – rear of dinoflagellate when swimming, usually flaring.



TEXT-FIG. 15. Terms used in the description of calcispheres. N.B. Calcispheres are formed by dinoflagellates and their terminology is independent of that used for other calcareous nannoplankton.

Ventral side – side of dinoflagellate with longitudinal flagellum and sulcus.
Dorsal side – side opposite longitudinal flagellum and sulcus.

2. *General terms*

Calcisphere – hollow, typically spherical, calcareous nannofossil. Whereas coccospheres are composite structures formed of numerous coccoliths, calcispheres possess a continuous wall.

Cyst – wall formed around dinoflagellate during non-motile, non-vegetative stage. These often show paratabulation but are continuous structures, except for the archaeopyle if present. Most calcispheres are thought to be cysts; however, the thoracosphere of *Thoracosphaera heimii* is formed during the vegetative stage and so is not a cyst.

Dinoflagellate – informal taxon-based term for member of the phylum Dinophyta.

Theca – non-resistant organic wall of motile vegetative stage of dinoflagellates, composite structures formed of plates.

Thoracosphere – informal taxon-based term for calcisphere formed by *Thoracosphaera*. N.B. *T. heimii* has a wall structure of large elements (*c.* 1 μm) with their c-axes tangential to the wall, and randomly aligned.

3. *Wall types*

Oblique/obliquipithonelloid – formed of elements with their c-axes oblique to the wall and variably aligned relative to each other (e.g. *Obliquipithonella multistrata*).

Pithonelloid – formed of elements with their c-axes oblique to the wall and sub-parallel to each other (e.g. *Pithonella sphaerica*, *P.ovalis*).

Radial/orthopithonelloid – formed of elements with their c-axes perpendicular to the wall (e.g. *Calciodinellum*, *Rhabdothorax*).

Tangential – formed of elements with their c-axes tangential to the wall (e.g. *Fuetterella conforma*, *Thoracosphera heimii*).

4. *Paratabulation features*

Archaeopyle – opening for excystment.

Operculum – plate covering the archaeopyle.

Paratabulation – structures on the cyst of a dinoflagellate reflecting the tabulation of the theca. Paratabulation may be developed on the inner or the outer surface of calcispheres.

Cingulum – sub-equatorial channel occupied by the transverse flagellum.

Sulcus – furrow occupied by longitudinal flagellum.

Horn – protrusion from either end of dinoflagellate.

5. *Paratabulation types*

Holotabulate – paratabulation of ridges or edges on the cyst corresponding to plate boundaries on the theca.

Intratabulate – paratabulation of processes on the cyst corresponding to plates on the theca.

Cingulotabulate – paratabulation confined to cingulum and archaeopyle.

Cryptotabulate – paratabulation confined to archaeopyle.

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APPENDIX 1: TERMS THAT WE HAVE NOT USED

The following terms have been used previously in nannoplankton literature but are not used here, for the reasons outlined. In these notes, the term is defined briefly, using our terminology. Then the reason for our not using it is given (see also the introductory section on the choice of terms).

Attachment surface – Contact-surface between two elements. Superfluous synonym; contact-surface seems more objective.

Bar/Bridge (*sensu* Aubry 1988) – as per Theodoridis (1984), but with opposite meanings.

Bar/Bridge (*sensu* Theodoridis 1984) – synonyms of disjunct and conjunct bar, especially for helicoliths. We consider these terms confusing. Also they are of limited application, whereas the terms disjunct and conjunct can be applied to any central-area structure, not just bars.

Coccocylinder {Covington 1985} – cylindrical coccosphere. Superfluous term, numerous coccospheres are aspherical and there is no utility in coining numerous shape related terms.

Coccolithophore – synonym of coccolithophorid, which has priority (see Jordan *et al.* 1995).

Column – often used as a synonym of spine, which we prefer.

Cone – alternative to apical cycle, for fasciculiths. This cycle only forms a conical structure in a few species so we prefer the more neutral term apical cycle.

Complete/incomplete caneoliths {Halldal and Markali 1955} – endothecal coccoliths of *Syracosphaera* with, respectively, three and two flanges. The distinction is useful but there is no real need for these rather obscure special terms. Also, we prefer to use the terms complete and incomplete to describe degree of completion of growth of coccoliths.

Cribrate central area – obscure alternative to net.

Discolith – this term has been used widely for coccoliths with elevated rims but no shields, i.e. muroliths as defined here. We prefer murolith since discolith has also been used with the different sense of 'a coccolith belonging to Pontosphaeraceae'. In addition, the word discolith is potentially misleading.

Geometric – unsuitable alternative of polygonal. Ellipses and circles are just as geometric as are triangles or pentagons.

Heliolith/Ortholith {Deflandre 1950} – these terms for coccolith types were originally defined on the basis of the crystallographic orientation of the main elements. Ortholiths – dominant elements large, with vertical or tangential c-axis orientation (e.g. *Discoaster*, *Braarudosphaera*). Helioliths – dominant elements have approximately radial c-axes giving a 'sphérolithique' appearance (e.g. *Watznaueria*, *Reticulofenestra*). This concept is of limited use since most heterococcoliths are composed of both vertical and radial crystal-units, whilst for many nannoliths the concept of radial and vertical are unclear. As a result, there has been only limited agreement between authors who have used these terms as to which taxa should be included in which group – compare Deflandre (1952), Tappan (1980), Aubry (1984, 1988*a*, 1988*b*, 1990).

Jugum – synonym of bar. Obscure and superfluous.

Knob – synonym of boss, especially for discoasters. We prefer boss, and it has more general application.

Labiatiform {Halldal and Markali 1955} – elongate double-lipped sacculiform protrusion. Unnecessarily specialized term, applying to only one taxon, *Anthosphaera robusta*.

Limb/spoke – synonym of arm. We prefer arm and it has been applied more widely.

Loxolith rim – synonym of zeugoid rim, which we prefer.

Marginal area {many authors} – rim. We prefer rim since it is more suitable for forming complex terms (e.g. proximal rim element), and because marginal area suggests an unimportant feature whereas this is the most important part of many coccoliths.

Nanofossil, Nanoplankton – synonyms of nannofossil and nannoplankton. Both nano- and nanno- are etymologically valid prefixes derived from the greek word *nanos* (dwarf). We prefer nanno- on the following grounds: (1) general usage, as noted by the Oxford English Dictionary (2nd edition, 1989), nearly all palaeontologists use nannofossil and many biologists use nannoplankton so this is the *de facto* 'correct' spelling; (2) priority, this was the spelling adopted by Lohmann (1909), when he coined the term nannoplankton; (3) differentiation, the SI use of nano- implies 10^{-9} (e.g. nanometre).

Optically continuous/discontinuous structure – essentially synonyms of conjunct and disjunct. We prefer the latter as they are shorter and less potentially misleading.

Oval, ovoid – often used as synonyms of elliptical, but these terms more accurately mean egg-shaped and so are very rarely applicable to coccoliths.

Pterygal, meta-pterygal, pre-pterygal, anti-pterygal {Theodoridis 1984} – orientation terms for helicoliths. Elegant but too obscure for practical use.

Precession {Black 1972} – alternative to obliquity for description of element orientation in plan view. The common scientific use of precession is related to orbital motions which are not analogous to the element orientation. Hence the special use of this term for coccoliths is obscure.

Prymnesiophyte – alternative to haptophyte. Green and Jordan (1994) showed that Haptophyta, rather than Prymnesiophyta is the correct division level name; it follows that haptophyte is preferable to prymnesiophyte as the informal name for members of the division.

Rhombolith {Halldal 1954} – synonym of scapholith. Both are often used; we follow Braarud *et al.* (1955*a*, 1955*b*) in using scapholith.

Stomatal opening and *stomatal coccolith* {Halldal and Markali 1955} – circum-flagellar coccoliths. Stomata implies mouth, and so has unwanted functional implications.

Wedge {Bronnimann 1955} – element of a nannoconid. Bronnimann also used the term plate and this is preferred since it better describes the shape of nannoconid elements as shown by electron microscopy.

Zygodiscid rim – synonym of zeugoid rim, which we prefer.

APPENDIX 2: SUMMARY LISTING OF -LITH WORDS

Numerous special terms have been coined for particular types of coccoliths. These are now used in varying senses, in particular some are used as purely descriptive terms applicable to coccoliths of widely varying structure and taxonomic affinity (e.g. placolith), whilst others are now used only as informal taxon-based terms, i.e. for the characteristic coccoliths from one particular taxon. These terms are, consequently, described in different parts of the main text. For ease of reference, they are all listed here, in alphabetical order. Only the modern/recommended meaning is given here. Readers should be aware that many of these terms have been used in varying ways in the literature. Terms not used in the main text are given in square brackets, [ ].

[*Areolith*] {Norris 1985} – cap-shaped holococcolith with interior ridges and areolae.

[*Asterolith*] {Sujkowski 1931} – obsolete term for stellate nannoliths.

Calicalith {Kleijne 1991} – tube-shaped holococcolith, flaring, open distally.

Calyptrolith {Lohmann 1902} – cap-shaped holococcolith.

Caneolith {Braarud *et al.* 1955*a*, 1955*b*} – endothecal murolith (+/– flanges) of Syracosphaeraceae.

Ceratolith – horseshoe shaped nannolith of Ceratolithaceae.

Coccolith {Huxley 1858} – plate-like calcareous component of haptophyte cell-covering, homologous with organic scale.

[*Cribrilith*] {Halldal and Markali 1955} – perforate murolith of Pontosphaeraceae; in effect a synonym of discolith and so superfluous.

Cricolith {Braarud *et al.* 1955*a*, 1955*b*} – ring-shaped placolith with narrow shields of Pleurochrysidaceae.

Crystallolith {Braarud *et al.* 1955*a*, 1955*b*} – planar holococcolith, rim weak.

[*Cyatholith*] {Kamptner 1948} – obsolete, alternative to placolith.

[*Cyclolith*] {Kamptner 1948} – obsolete, circular placolith.

Cyrtolith {Braarud *et al.* 1955*a*, 1955*b*} – exothecal planolith or inverted murolith of Syracosphaeraceae.

Discoaster – stellate nannolith of Discoasteraceae.

Discolith {Huxley 1868} – murolith of Pontosphaeraceae (has also been used for muroliths in general).

Fasciculith – compact, top-shaped nannolith of Fasciculithaceae.

Flosculolith {Kleijne *et al.* 1991} – flaring, tube-shaped holococcolith, with distal opening partially closed by a vaulted roof.

Fragariolith {Kleijne *et al.* 1991} – holococcolith with simple basal ring and leaf like process

Gliscolith {Norris 1985} – tube-shaped holococcolith with bulbous distal part.

Helicolith – coccolith with helical flange of Helicosphaeraceae.

[*Heliolith*] {Deflandre 1950, Aubry 1984, 1988*a*, 1988*b*, 1990} – heterococcolith with c-axes of main elements radial.

Heliolith – stellate nannolith with birefringent central area, of *Heliolithus* (Paleogene).

Helladolith {Heimdal and Gaarder 1980} – tube-shaped holococcolith with bridge developed into leaf-like process.

Heterococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of crystal-units of complex shape.

Holococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of numerous minute ($< 0{\cdot}1$ μm) crystallites all of similar shape and size.

Laminolith {Heimdal and Gaarder 1980} – laminated disc-shaped holococcolith +/− pores.

Lepidolith {Halldal and Markali 1955} – simple planolith, formed of two elements, of *Gladiolithus*.

Lopadolith {Lohmann 1902} – elevated murolith of *Scyphosphaera*.

Murolith {Young 1992*a*} – any heterococcolith with elevated rim but without well-developed shields

Nannolith {?Perch-Nielsen 1985} – calcareous structure lacking the typical features of hetero- or holococcoliths and so of uncertain affinity.

[*Ortholith*] {Deflandre 1950; Aubry 1984, 1988*a*, 1988*b*, 1990} – nannolith or holococcolith with c-axes of main elements tangential or parallel.

Osteolith {Halldal and Markali 1955} – femur-shaped circum-flagellar coccolith of *Ophiaster*.

Pappolith {Norris 1983} – murolith of Papposphaeraceae.

[*Pentagolith*] {Farinacci *et al.* 1971} – pentagonal coccolith with more than five elements, e.g. *Goniolithus*. These are so rare that the term is redundant.

Pentalith {Gran and Braarud 1935} – stellate nannolith with five segments, of Braarudosphaeraceae.

Placolith {Lohmann 1902} – any heterococcolith with two or more well-developed shields.

Planolith {Young 1992*a*} – any planar heterococcolith, rim not elevated.

[*Porolith*] {Deflandre 1952} – obsolete term for perforate element of *Thoracosphaera*.

[*Prismatolith*] – obsolete term for imperforate element of *Thoracosphaera*.

Protolith {Bown 1987} – murolith with non-imbricate rim of Stephanolithaceae, Parhabdolithaceae.

Rhabdolith {Schmidt 1870} – planolith (+/− spine) of Rhabdosphaeraceae (also has been for spine bearing coccoliths in general).

[*Rhombolith*] {Halldal 1954} – alternative term for scapholith.

Scapholith {Deflandre and Fert 1954} – rhombic murolith of Calciosoleniaceae.

Sphenolith {Deflandre 1952} – nannolith of Sphenolithaceae.

Tremalith {Lohmann 1913} – vase-shaped murolith of Hymenomonadaceae.

Zygolith {Kamptner 1937} – tube-shaped holococcolith with bridge.

REINTERPRETATION OF THE LOWER ORDOVICIAN CONODONT APPARATUS *PAROISTODUS*

by ANITA M. LÖFGREN

Abstract. The lower Ordovician conodont genus *Paroistodus* has previously been interpreted as a two-element apparatus, although with wide variation among its 'drepanodontiform' elements. Collections of conodonts from a series of Swedish sections include almost 75000 elements of four successive species of *Paroistodus*: *P. numarcuatus* from the upper Tremadoc, *P. proteus* from the uppermost Tremadoc and lowermost Arenig, *P. parallelus* from the lower Arenig, and *P. originalis* from the lower middle Arenig to the lower Llanvirn. These species are probably those best known of the genus, and it is shown here that they all have a seven-element apparatus, closely comparable to that of *Drepanodus*.

Nicoll (1990) established a seven-element apparatus model for *Cordylodus angulatus* Pander and some other species of the same genus, the earliest conodonts with ramiform (denticulate) elements. That investigation showed the importance of large collections of elements when making such reconstructions. His careful and detailed descriptions of all element types recognized in *C. angulatus* enabled me not only to identify these in my own collections, but also to find what I consider to be the homologous elements in the coniform (non-denticulate) apparatus of *Drepanodus arcuatus* Pander. Although my interpretation of apparatus reconstructions of these two species differs slightly from those of Nicoll (1990, 1994, 1995, p. 253), his investigations put me 'on the right track'.

The apparatus for *Drepanodus arcuatus* arrived at is also close to that suggested by Dzik (1994). It is intriguing that *Cordylodus*, with a stratigraphical record from the Upper Cambrian to the upper Tremadoc, and *Drepanodus arcuatus*, which first appeared in the Tremadoc, should have such similar element arrangements. The element model in these early taxa should be close to the original seven-element conodont apparatus. The next step was to test this model for other Tremadoc taxa. As *Paroistodus* is the genus that most closely resembles *Drepanodus*, observations were concentrated on *Paroistodus numarcuatus* and its successors.

In faunas with *D. arcuatus* and *P. numarcuatus*, the Pb elements in particular, and also some of the S elements of the two species are very similar. Like *Drepanodus*, *Paroistodus* has a recurved Sa (symmetrical) element, unlike the suberect Sa elements of *Paltodus* and *Drepanoistodus*. This investigation was started by looking for those elements in the earliest species of *Paroistodus*, the Tremadoc *P. numarcuatus*, that were homologous with those distinguished in *D. arcuatus*. On discovering these, similar homologies were sought in the later species *P. proteus* (Lindström), *P. parallelus* (Pander) and *P. originalis* (Sergeeva). A general septimembrate model for *Paroistodus* was thus produced, which is presented below.

MATERIAL

The conodont elements used for the apparatus reconstructions presented here are from Ordovician (Tremadoc to Llanvirn; Text-fig. 1) rocks from various parts of Sweden. Localities from which material has been used are: Kalkberget, Kloxåsen and sections in the Brunflo area (Löfgren 1978)

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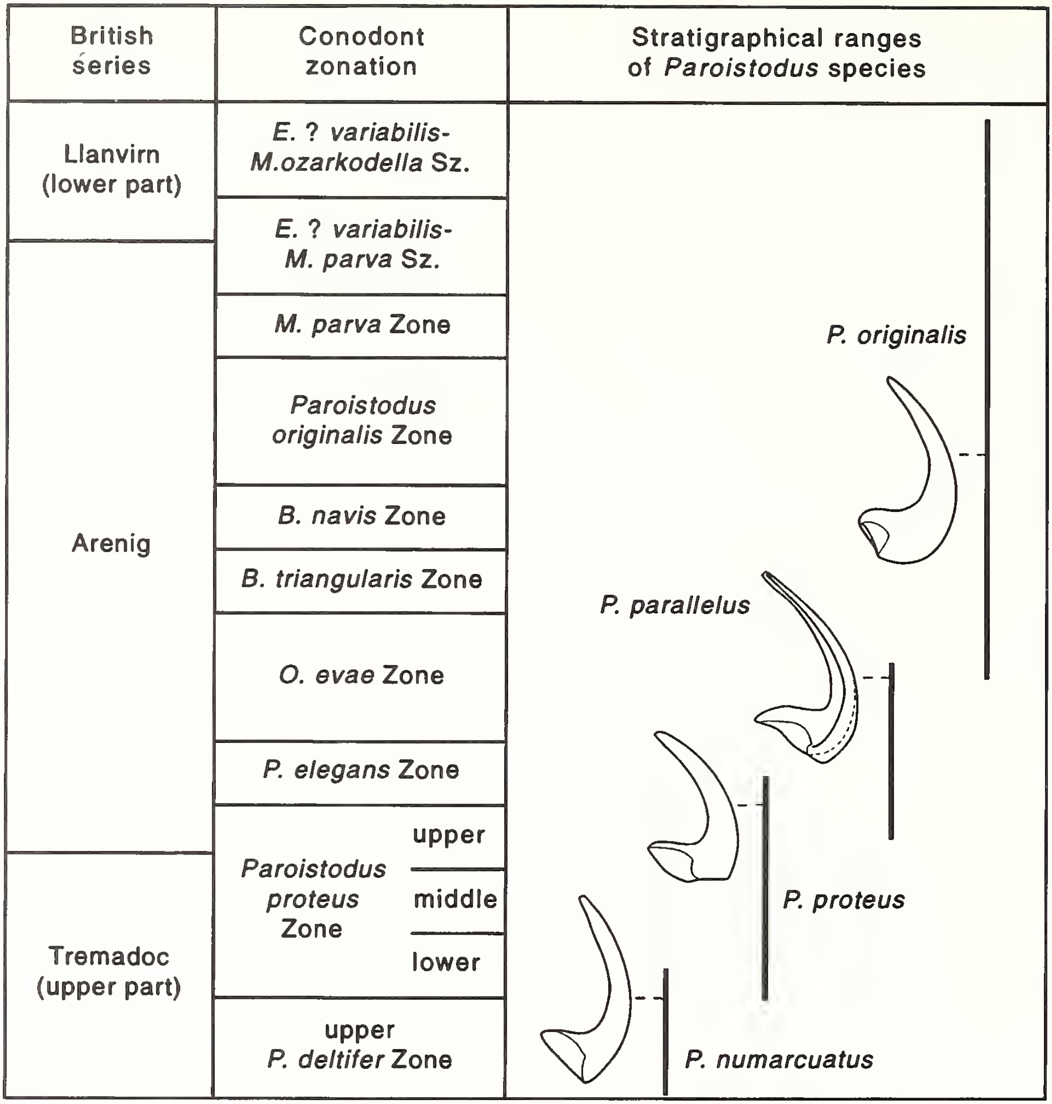


TEXT-FIG. 1. The four successive species of *Paroistodus* in Baltoscandia and their stratigraphical ranges.

and Sommartjärnen (Löfgren 1993*b*) in Jämtland; Finngrundet in the Bothnian Bay (drill core, Löfgren 1985); Sjurberg, Fjäcka and Djupgrav (Löfgren 1994), Talubäcken (Bergström 1988; Löfgren 1995*b*), Rävanäs, Kårgärde and Leskusänget (locations in Löfgren 1995*a*) in Dalarna; Gymninge (Löfgren 1993*b*) and Lanna (Löfgren 1995*b*) in Närke; sections at Hunneberg (Löfgren 1993*a*), Gullhögen, Hällekis and Orreholmen (locations in Löfgren 1995*b*), Brattefors (Teves and Lindström 1988) in Västergötland; Gillberga and Sandvik on North Öland (location in Löfgren 1995*b*) and Ottenby on South Öland (locality description in Tjernvik 1956).

In total, almost 75000 elements of *Paroistodus* were studied. The samples yielding these elements were treated slightly differently over a 25-year period, but those heavily relied upon for the reconstructions and calculations of element ratios were treated with buffered acetic acid (method described by Jeppsson *et al.* 1985) and the residues washed through a 63-micrometer screen.

The preservation is variable; specimens from Leskusänget and Brattefors are in almost pristine condition, while those from Ottenby very often are broken, with some element types more seriously damaged than others. Elements from Hunneberg have been thermally altered, with CAI values (see Epstein *et al.* 1977) varying from 5 to 8; those from Jämtland have a CAI between 3 and 4. All other elements have CAI values of 1–1·5 (almost unaltered).

THE *PAROISTODUS* APPARATUS

Nicoll (1990, 1995) extended the designation system (P, S, and M elements) originally established for younger, ozarkodinid genera (see Sweet 1988 for review) to *Cordylodus* and *Drepanodus*, and it is used herein also for *Paroistodus*. Only well preserved natural assemblages could definitely prove that the element arrangement in these taxa was sufficiently similar to that of, for instance, the upper Ordovician prioniodontid *Promissum* (cf. Aldridge *et al.* 1995) to allow the same designations to be used. The very detailed analyses and comparisons of morphological characters in several taxa made by Nicoll (1990, 1995), however, seem to me to justify such usage. Homologies can be clearly demonstrated to exist between *Cordylodus* and coniform genera such as *Drepanodus* (Nicoll 1990, 1995). Current investigations confirm that the P, S, and M element notation system is applicable also to some other early coniform genera, such as *Rossodus* Repetski and Ethington (Huselbee 1996), *Paroistodus* (herein) and *Paltodus* Pander (Löfgren, unpublished data). For the more advanced coniform genera, such as *Panderodus* Ethington, comparisons using the P, M, and S designations are far more difficult, and alternative notations such as those proposed by Sansom *et al.* (1995) are more useful, at least for the time being.

General characteristics of the element types

Having homologized element types for *Cordylodus angulatus*, *Drepanodus arcuatus* and *Paroistodus numarcuatus* in a few samples with abundant and well preserved specimens (Text-fig. 2), I considered the three succeeding species of *Paroistodus*: *P. proteus*, *P. parallelus* and *P. originalis*. On checking through all the collections for the four *Paroistodus* species and comparing their elements, it soon became clear that seven element types could be distinguished, not only in *P. numarcuatus*, but also in each of the other species. A general description of these element types is given below; for details of each species, see the systematic section.

M element. Geniculate, i.e. there is a sharp angle between the oral edge and the posterior edge of the cusp. The cusp and the posterior part of the aboral margin are subparallel. The cusp is bent inwards in many specimens. The element is makellate *sensu* Nicoll (1990, p. 533).

Pa element. Element with one flatter and one more convex side. Details of convexity of the sides, costae and carinae agree with those of the elements in the S series. Most distinctive of this element type is the notch and flare in the aboral margin on the outer side.

Pb element. With a flaring basal cavity, opening to the inner side.

Sa element. Symmetrical, with rather bulging sides. The cusp is at least slightly reclined or recurved, in contrast to Sa elements of *Paltodus* and *Drepanoistodus*.

Sb element. Slightly asymmetrical where the anterior margin is flexed inwards and there is only a small difference in convexity between the inner and the outer side. The distal part of the cusp can be twisted.

Sc element. Almost symmetrical. The base is flat and rhombic in side view and the asymmetry amounts only to a small difference in convexity between the sides.

TEXT-FIG. 2. Comparison of element types in *Cordylodus*, *Drepanodus* and *Paroistodus* from the upper *Paltodus deltifer* Zone. A–G, *Cordylodus angulatus* Pander, 1856; Orreholmen, sample Vg89-B1. A, M element; LO 7219t. B, Pa element; LO 7220t. C, Pb element; LO 7221t. D, Sa element; LO 7222t. E, Sb element; LO 7223t. F, Sc element; LO 7224t. G, Sd element; LO 7225t. A–C, × 50; D–G, × 60. H–N, *Drepanodus arcuatus* Pander, 1856; Brattefors, sample Vg84-26. H, M element; LO 7226t. I, Pa element; LO 7227t. J, Pb element; LO 7228t. K, Sa element; LO 7229t. L, Sb element; LO 7230t. M, Sc element; LO 7231t. N, Sd element; LO 7232t. H–K, M–N, × 60; L, × 65. O–U, *Paroistodus numarcuatus* (Lindström, 1955); Orreholmen, sample Vg89-B1. O, M element; LO 7253t. P, Pa element; LO 7254t. Q, Pb element; LO 7255t. R, Sa element; LO 7256t. S, Sb element; LO 7257t. T, Sc element; LO 7258t. U, Sd element; LO 7259t. O–Q, × 65; R–U, × 70.

Sd element. Strongly asymmetrical. The anterior margin and the anterio-basal corner are strongly flexed to the inner side, making the entire element concavo-convex.

White matter. In elements of *Paroistodus* white matter fills the entire cusp and base, except at the antero-basal corner and bordering the basal cavity. More extensive areas of hyaline material are thus only present in elements with drawn-out antero-basal corners, for instance Sd elements of *P. originalis.*

Previous interpretations of the apparatus

The apparatus reconstruction for *Paroistodus* given here is not the first attempted. Generally, most authors agree upon which specimens to include in respective species, but have suggested that the elements formed a simpler type of apparatus than the one described here.

Lindström (1971, p. 46; 1973, p. 327) described *Paroistodus* as having two element types, drepanodiform and oistodiform (= geniculate). In addition to these, van Wamel (1974, p. 78) distinguished a scandodiform type, clearly equivalent to the Pb element described here.

Barnes *et al.* (1979) concluded that *Paroistodus* belonged in their Type IIIC category, lacking an erect element type, and basically being a two-element apparatus. Subsequent authors including Bergström (1981) also considered the apparatus bimembrate, although Dzik (1983, fig. 4) indicated up to four element types in the apparatus, but without comment. Sweet (1988, p. 55, text-fig. 5.8) described *Paroistodus* as a bi- to quadrimembrate apparatus but the illustration does not indicate the kind of element categories that I have discerned.

The attribution to *Paroistodus* of elements otherwise referred to *Dapsilodus* Cooper, 1976 or to *Besselodus* Aldridge, 1982 is most probably erroneous (but see discussion in Nowlan *et al.* 1988). Details in element morphology as well as general apparatus type distinguish these taxa from *Paroistodus* as understood here. For an up-to-date interpretation of the apparatuses of *Besselodus* and *Dapsilodus*, see Sansom *et al.* (1995).

Element ratios

The number of each element type in an apparatus can be determined with certainty only in natural clusters or bedding-plane associations of conodont animals. No such assemblages have been found from the kind of coniform apparatus represented by *Paroistodus* except possibly the cluster described by McCracken (1989) as *Protopanderodus* n. sp. A. As noted by Nicoll (1995, p. 253), this is actually a *Drepanodus*. In that cluster there seem to be more than seven elements, among them a P pair. Better known clusters of ramiform and platform elements in Carboniferous ozarkodinid conodonts are usually interpreted as having 15 elements (Aldridge *et al.* 1987), and the giant *Promissum pulchrum* from the upper Ordovician of South Africa had 19 (Theron *et al.* 1990; Aldridge *et al.* 1995), including four pairs of P elements and two pairs of Sb elements.

Studies of isolated element collections and natural assemblages led Sansom *et al.* (1995) to reconstruct the coniform apparatus of *Panderodus* as having 17 elements. Earlier attempts at calculating relative ratios of element types in collections of separated coniform elements from dissolved limestone samples include those of Lindström (1971) and Löfgren (1978). Lindström's (1971, figs 9–12) diagrams show a ratio between drepanodontiform and oistodontiform elements of 2:1 or less, except for one large sample with *P. proteus* which has a ratio of 2·53. My own earlier calculations (Löfgren 1978, pp. 68–70) also led to ratios of 2:1 or even less. Apparently, oistodontiform (M) elements are often much over-represented, as these ratios would imply three or more pairs. The large sample with the 2·53 ratio gives an indication of two M pairs. It is also obvious, both from Lindström's (1971) and Löfgren's (1978) diagrams, that there is a wide variation in ratios from sample to sample, suggesting that preservational aspects may play a decisive rôle in the retrieval of different element types. Lindström (1984, p. 37) discussed hydrodynamic sorting of conodont elements that could lead to distorted ratios and Broadhead *et al.* (1990) and McGoff (1991) performed practical studies of this. Different abilities among element types to withstand crushing is probably also an important distorting influence on their ratios. I have observed that in all but the best preserved collections of *Paroistodus*, Sd elements in particular are much underrepresented and/or broken compared with the other, less concavo-convex S element types. To at least approach the 'true' element ratios one must choose particularly well preserved samples for calculations.

Among my collections, some are consistent with a *Paroistodus* apparatus of 4M, 2Pa, 2Pb, 1Sa, 4Sb, 2Sc and 2Sd elements (17 elements in all). Among these samples are D85-1 (Sjurberg; 509 elements of *P. proteus*), Nä87-1 (Gymninge; 1046 elements of *P. parallelus*) and Nä94-13 (Lanna; 583 elements of *P. originalis*), whilst other samples with rich and well preserved *Paroistodus* faunas indicate higher M ratios. To my knowledge, only one reconstruction so far has suggested more than one pair of M elements. *Gamachignathus* McCracken, Nowlan and Barnes, 1980 was interpreted as having two pairs of M (= e-1 and e-2) elements, although Aldridge *et al.* (1995) preferred a Pc or Pd position for the e-2 element type. However, there are apparatuses with three or four pairs of P elements; apart from *Promissum* from the Ordovician (Aldridge *et al.* 1995), there are some Silurian genera, e.g. *Pterospathodus* and *Pranognathus* (see Männik and Aldridge 1989), with this apparatus model. As M elements and Pb elements are very similar in some species of *Paroistodus*, it is conceivable that one pair of M elements could have functioned like Pb elements.

EVOLUTIONARY TRENDS IN *PAROISTODUS*

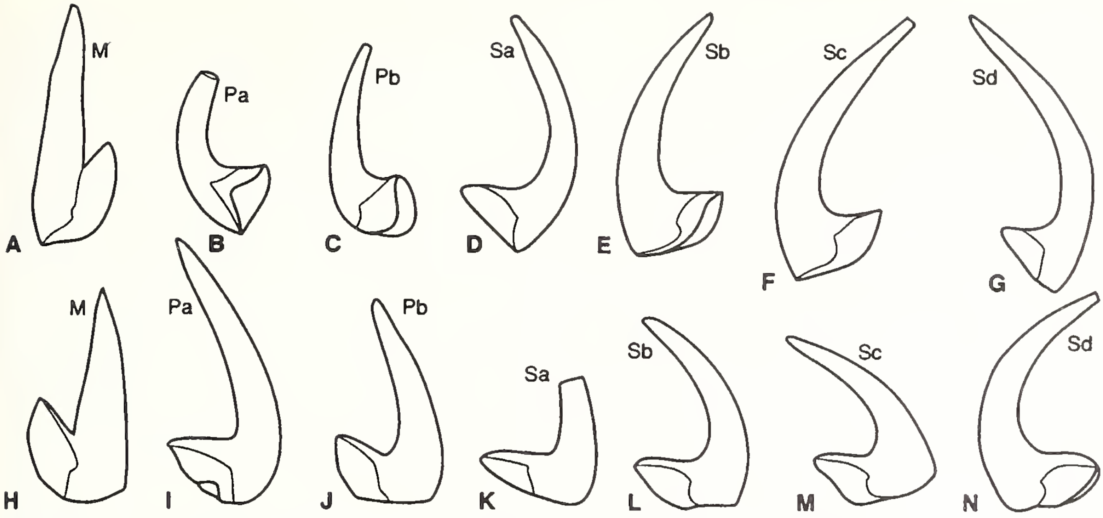
With four successive species of *Paroistodus* present in the same area, some general observations about direction of change in the genus can be made.

Inverted basal cavity. This feature occurs because younger lamellae do not cover older ones antero-basally. The character, which is also present in, for example, species of *Protopanderodus*, was noted and described in some detail by Lindström (1955, p. 537). It is present in specimens of all the *Paroistodus* species studied, but is extremely rare in *P. numarcuatus*, becoming successively more common in all element types in the younger species.

Similarities between element types. As discussed above, the elements of *P. numarcuatus* can be compared in detail with the homologous elements of *Drepanodus arcuatus*. In both these apparatuses the seven element types are quite distinct, possibly with the exception of some S elements. In particular, the Pa and Pb elements are very dissimilar with, in each species, the Pb elements being scandodontiform and morphologically closer to the M elements than to the Pa elements or the S series. Starting with *P. proteus* the Pa and Pb elements become progressively more similar, at the same time converging morphologically with the S series. In *P. originalis*, the youngest species investigated here, there is a striking resemblance between Pa and Pb elements in some long-based populations (cf. Text-fig. 5I–J). In populations with shorter-based elements, however, the two P elements remain more dissimilar, particularly where in some Pb elements the cusp is much more strongly reclined than in the corresponding Pa element (Pl. 1, fig. 19). Possibly, the convergent trend in P elements continues, as one of my youngest *Paroistodus* faunas includes a (probable) Pb element (juvenile) that resembles those of the S series (Pl. 1, fig. 16).

Lateral flattening of elements. In *P. numarcuatus* the sides of the elements, particularly those in the S series, tend to bulge laterally. The later species, *P. proteus* and *P. originalis*, lack lateral carinae and the sides are flatter, especially in the latter. Interestingly, this trend is present also in *Drepanodus arcuatus*, where Arenig specimens are noticeably flatter than Tremadoc ones.

The 'horridus' *trend.* Dzik (1983) postulated that the denticulated Llanvirn species '*Cordylodus*' *horridus* Barnes and Poplawski had connections with *Paroistodus*. An instance where denticles



TEXT-FIG. 3. *Camera lucida* drawings of elements of *Paroistodus*. A–G, *P. numarcuatus* (Lindström, 1955); Brattefors, sample Vg84-26. A, M element (same as Text-fig. 4A). B, Pa element (same as Text-fig. 4C). C, Pb element (same as Text-fig. 4F). D, Sa element (same as Text-fig. 4G). E, Sb element (same as Text-fig. 4H). F, Sc element (same as Text-fig. 4J). G, Sd element (same as Text-fig. 4I). H–N, *P. proteus* (Lindström, 1955); Sjurberg, sample D85-1. H, M element (same as Text-fig. 4L). I, Pa element (same as Text-fig. 4Q). J, Pb element (same as Text-fig. 4N). K, Sa element (same as Text-fig. 4O). L, Sb element (same as Text-fig. 4T). M, Sc element (same as Text-fig. 4U). N, Sd element (same as Text-fig. 4AB).

developed on the oral edge in *Paroistodus* was described by Löfgren (1995*a*) from the early Arenig *Oepikodus evae* Zone at Talubäcken, Dalarna. Another example is '*Drepanodus*' *cordylodiformis* Lehnert, 1995 from the older *Prioniodus elegans* Zone in the San Juan Formation of Argentina. Recently, Albanesi and Barnes (1996) described the transition from *Paroistodus originalis* to *P. horridus* in the lower Llanvirn in the San Juan Precordillera. It thus appears that the development of denticles on the oral margin of elements of *Paroistodus* occurred more than once. In '*Cordylodus*' *horridus* both P and S elements are denticulated (cf. Stouge 1984, pl. 1, figs 1–11) and mimic 'real' *Cordylodus* in their basal shape. Their corresponding M elements closely resemble those of *P. originalis* (cf. Stouge 1984, pl. 5, figs 1–4).

SYSTEMATIC PALAEONTOLOGY

The synonymies give only those references pertinent to the description of the respective apparatus. For fuller synonymy lists of *Paroistodus numarcuatus*, *P. proteus* and *P. originalis*, see Lehnert (1995), and for *P. parallelus*, see Stouge and Bagnoli (1988).

The figured specimens are deposited in the type collection of the Department of Geology, University of Lund, Sweden.

Genus PAROISTODUS Lindström, 1971

Type species. *Oistodus parallelus* Pander, 1856.

Age and distribution. Tremadoc to lower Llanvirn, pandemic.

TEXT-FIG. 4. Elements of *Paroistodus*. A–K, *P. numarcuatus* (Lindström, 1955); Brattefors, upper *Paltodus deltifer* Zone, sample Vg84-26. A–B, M elements; LO 7233t; LO 7234t. C, Pa element; LO 7235t. D, Pb element, outer side; LO 7236t. E, Pa element, inner side; LO 7237t. F, Pb element, inner side; LO 7238t. G, Sa element; LO 7239t. H, Sb element; LO 7240t. I, Sd element, inner side; LO 7241t. J, Sc element, inner side; LO 7242t. K, Sd element, outer side; LO 7243t. A–H, J, × 70; I, K, × 65. L–AB, *P. proteus* (Lindström, 1955); upper *P. proteus* Zone. L, N–R, T–W, AB, Sjurberg, sample D85-1. M, S, Z, Gullhögen, sample GB81-0FK. X, Y, AA, Diabasbrottet, Hunneberg, sample Vg86-12. L, W, M elements; LO 7271t; LO 7280t; × 70. M, Pa element, inner side with additional anterior edge; LO 7295t; × 60. N, R, Pb elements; LO 7272t; LO 7276t; × 70. O, Sa element; LO 7273t; × 75. P–Q, Pa elements, inner and outer side; LO 7274t; LO 7275t; × 75. S, Sa element; LO 7296t; × 60. T, Sb element; LO 7277t; × 75. U, Sc element, outer side; LO 7278t; × 80. V, AB, Sd elements, outer and inner side; LO 7279t; LO 7281t; × 75. X, Pb element; LO 7244t; × 65. Y, Pa element; LO 7245t; × 65. Z, Sb element; LO 7297t; × 60. AA, Sd element; LO 7246t; × 70.

Paroistodus numarcuatus (Lindström, 1955)

Text-figures 2O–U, 3A–G, 4A–K

1955	*Drepanodus numarcuatus* Lindström, p. 564, pl. 2, figs 48–49 [Sd and Sa elements], text-fig. 3I.
1955	*Acodus pulcher* Lindström, p. 546, pl. 2, fig. 38 [Sd element, holotype].
1955	*Drepanodus amoenus* Lindström, p. 558 (*pars*), pl. 2, fig. 26 [only; Sc element, holotype].
1955	*Oistodus parallelus* Pander; Lindström, pl. 4, figs 27–29, text-fig. 3N [only; M element].
1955	*Scandodus pipa* Lindström, pl. 4, fig. 38 [only; Pb element].
1971	*Paroistodus numarcuatus* (Lindström); Lindström, p. 46, fig. 8.
1981	*Paroistodus numarcuatus* (Lindström, 1955); Lindström, p. 227, *Paroistodus* pl. 2, figs 7–8.

Material. Approximately 15000 elements.

General description. In contrast to later *Paroistodus* species, elements of *P. numarcuatus* only very rarely have 'inverted basal cavity' lines antero-basally.

Sa element. Prominent carina present on each side of the recurved cusp. Both its anterior and posterior edges are sharp and the carinae are thickest anteriorly. They begin on the base, abutting against the basal cavity as seen in lateral view. The antero-basal corner is thin, with an angle of *c.* 100° between the anterior edge and the aboral margin. The aboral margin meets the slightly arched oral margin at an angle of *c.* 45°. The basal cavity is restricted to the posterior three-quarters to four-fifths of the base, and it bulges symmetrically on either side.

Sb element. More compressed laterally, and has a shorter and straighter oral edge than the Sa element. It is concavo-convex, the anterior margin facing the inner side and the antero-basal corner thin and slightly flexed inwards. The basal cavity has an inner bulge, the cusp is recurved, and its upper half is often somewhat rotated inwards.

Sc element. More compressed laterally than any of the other elements; the anterior edge of the cusp and the aboral edge of the base form a right angle. The element is almost symmetrical and the cusp strongly recurved.

Sd element. The anterior edge is strongly flexed inwards, making the entire element concavo-convex. In some elements an additional edge has developed anteriorly on the base. The base is short and the carinae are unevenly developed: strong on the outer, much weaker on the inner side. The cusp is recurved and bent inwards.

Pa element. The cusp is recurved and both sides are carinate. The anterior edge is flexed inwards on the base and in some elements an additional edge has developed anteriorly, as in the Sd element. The basal cavity flares towards the outer side, the aboral margin having the characteristic indentation of Pa elements.

Pb element. The cusp is very slightly recurved and each of its lateral sides has a prominent carina somewhat posterior to the mid-line. The anterior edge is slightly flexed towards the inner side. The cusp is only about twice as long as the base, and has a tendency to be bent inwards. The oral margin has a sharp edge, which does not reach the aboral margin. The basal cavity is wide and flaring, particularly towards the inner side. The element is similar to the Pb (pipaform) element of *Drepanodus arcuatus* but has a proportionally longer oral margin and shorter cusp.

M element. The sides of the cusp are carinate and often more bulging than in later representatives of the genus. The cusp is more strongly bent inwards than in the other *Paroistodus* species. In some populations a narrow extension of the basal cavity almost reaches the antero-basal corner, but is laterally pinched and the inner face of the base undulates. The element figured by Lindström (1955, pl. 4, figs 27–28) as *Oistodus parallelus* is a good example of this.

Remarks. In his description of multielement *P. numarcuatus*, Lindström (1971) included *D. amoenus*, with which I concur, except that I believe that one of his illustrated specimens (Lindström 1955, pl. 2, fig. 25) belongs to *Drepanoistodus* (as discussed by Löfgren 1994, p. 1365). Lindström (1971) also included in *P. numarcuatus* the specimens of *O. parallelus* listed in the synonymy above, but not *Acodus pulcher*. One of the illustrated elements of *Scandodus pipa* in Lindström (1955, pl. 4, fig. 38) is a Pb element of *P. numarcuatus*. In that publication, the holotype and other illustrated specimens of *Scandodus pipa* are homologous elements of *Drepanodus arcuatus*.

Stratigraphical occurrence. Tremadoc; upper *Paltodus deltifer* Zone to the lowermost subzone of the *Paroistodus proteus* Zone. The species co-occurs with its successor, *P. proteus*, in the lowermost part of the *P. proteus* Zone.

Paroistodus proteus (Lindström, 1955)

Text-figures 3H–N, 4L–AB

1955 *Drepanodus proteus* Lindström, p. 566, pl. 3, figs 18–21, text-fig. 2a–f, j.
1955 *Oistodus parallelus* Pander, 1856; Lindström, p. 579 (*pars*), pl. 4, fig. 26 (only).
1971 *Paroistodus proteus* (Lindström); Lindström, p. 46, fig. 8.
1981 *Paroistodus proteus* (Lindström, 1955); Lindström, p. 233, *Paroistodus* pl. 2, figs 5–6.

Material. Approximately 17000 elements.

General description. The basal cavity is restricted to the posterior half of the base in the S and Pa elements. Oral keels are better developed in S and P elements and 'inverted basal cavities' are more common in all element types of *P. proteus* than in *P. numarcuatus*.

Sa element. Biconvex, with the lateral sides only moderately bulging, with less prominent carinae than in *P. numarcuatus*. As seen in lateral view the basal cavity is drop-shaped with a poorly defined tip close to the oral margin. The base has a drawn-out antero-basal corner and the aboral margin makes a smooth curve up to the slightly arched and keeled oral edge. The angle between the oral edge and the posterior edge of the cusp is *c.* 90°. The distal part of the cusp is slightly reclined to recurved.

Sb element. There is an asymmetry in this element, as the anterior margin is slightly flexed inwards. In a few specimens the distal part of the cusp is slightly twisted. The outline of the base is similar to that in the Sa element, but the cusp is usually more recurved in the Sb element.

Sc element. Almost symmetrical with flat sides. The outline of the base is rhombic, thereby resembling that in the corresponding element in *Drepanodus arcuatus* ('sculponeaform' element). The base is proportionally longer in an antero-posterior direction than in the other S elements, the oral edge is long and straight and the cusp is reclined to recurved.

Sd element. This is the most asymmetrical of the S elements in that the entire anterior margin is flexed to the inner side, making the element concavo-convex. The inner side is flat, whilst the outer one has a prominent carina. The basal cavity bulges almost equally on either side. The antero-basal corner can be seen only on the inner side. In a few elements there is a short additional anterior edge on the outer side of the base. The cusp is strongly recurved.

Pa element. The lateral outline of the base is similar to that in Sa, Sb and Sd elements. The aboral margin of the base has an indentation and flare on the outer side as in corresponding elements in other taxa. The basal cavity bulges, particularly to the outer side, and the antero-basal corner is flexed inwards. As in some Sd elements, an additional anterior edge may be present on the base. The cusp is slightly recurved, more prominently carinate on the outer than on the inner side, and the angle between the oral edge and the posterior edge of the cusp is *c.* 80°.

Pb element. This has similarities to the M element, but the transition from the oral edge of the base to the posterior edge of the cusp constitutes a smooth curve, and not a sharp angle as in the M elements. The angle between the oral edge and the cusp is usually more than 60°, and the basal cavity flares towards the inner side. The outer side of the reclined cusp is carinate, the inner side considerably flatter.

M element. The cusp is less inclined towards the inner side and more compressed laterally than in *P. numarcuatus*, but there is a rather weak central carina on the inner side and a stronger one posterior of the mid-line on the outer side. The antero-basal corner is thin, often broken or sightly flexed to the outer side. On the base, larger elements often display 'inverted basal cavity' lines. In some populations the base is typically squat and the cusp rapidly tapering. The element illustrated by Lindström (1955, pl. 4, fig. 26) as *Oistodus parallelus* is a good example.

Remarks. Lindström's (1955, p. 566) description included P and S elements, but he described the M elements together with those of *Paroistodus numarcuatus* and *P. parallelus* as *Oistodus parallelus*. The holotype is an Sa element with the characteristic basal shape described above. The Sa element in his text-figure 2j is similar, but more laterally compressed. The short-based element illustrated by Lindström (1955, pl. 3, fig. 19; text-fig. 2d–f) is an Sd element, as is that in his text-figure 2a–c, with its inwardly flexed anterior margin and short additional antero-lateral costa on the outer side. The specimen in Lindström's (1955) plate 3, figure 18 is a typical Pa element with its notched aboral margin, while his plate 3, figure 21 is a Pb element. He (p. 566) even commented on the similarity of this Pb element and '*Oistodus parallelus*' (= M elements of *Paroistodus*). Later, Lindström (1981, *Paroistodus* pl. 2, fig. 6) also included one of these illustrated elements (Lindström 1955, pl. 4, fig. 26) in *P. proteus*, as I have done above. Thus, all element types, except the flat-sided, square-based Sc element and the nearly symmetrical Sb element, were illustrated and described by Lindström (1955).

Stratigraphical occurrence. Upper Tremadoc to lower Arenig; from the base of the *P. proteus* Zone to the *Prioniodus elegans* Zone. The species co-occurs with *P. numarcuatus* in the lowermost subzone of the *P. proteus* Zone and with *P. parallelus* from the uppermost part of the *P. proteus* Zone to the (lower) *P. elegans* Zone.

Paroistodus parallelus (Pander, 1856)

Plate 1, figures 1–12, 17, 21; Text-figure 5A–G

1856 *Oistodus parallelus* Pander, p. 27, pl. 2, fig. 40 [M element].
?1941 *Acodus expansus* Graves and Ellison, p. 8, pl. 1, fig. 6 [Sa element].
?1941 *Oistodus pandus* Branson and Mehl; Graves and Ellison, pl. 1, fig. 34 [Sd element].
1955 *Distacodus expansus* (Graves and Ellison, 1941); Lindström, p. 555, pl. 3, figs 13–17, text-fig. 2g–i [Sa, Pb and Sb elements].
1955 *Oistodus parallelus* Pander, 1856; Lindström, p. 579 (*pars*), pl. 4, figs 30–31 [only; M element].
1971 *Paroistodus parallelus* (Pander); Lindström, p. 47, fig. 8.
1973 *Paroistodus parallelus* (Pander, 1856); Lindström, p. 329, *Paroistodus* pl. 1.

Material. About 9000 elements.

General description. The P and S elements have deeper basal cavities than in the other *Paroistodus* species and their lateral sides are costate. Characteristically, the basal cavity extends to more than half of the length of the base. There is an extensive area of inverted basal cavity anteriorly in most elements.

Sa element. This has equally strong costae, one on each side, and the basal cavity bulges symmetrically on either side. The costae extend from close to the aboral margin to the upper part of the recurved cusp. Basally, the costae are directed posteriorly, high up on the cusp more laterally. The antero-basal corner can be angular or rounded off. The oral edge is arched and strongly keeled.

Sb element. Similar to the Sd element in that the anterior edge is flexed inwards, but its antero-basal corner is less sharply inwardly flexed and its basal cavity less flaring. Its asymmetry consists mainly of a different degree of convexity of its inner and outer side.

Sc element. The base is square in lateral view, the aboral margin usually meeting the anterior edge of the cusp in an angle of *c.* 90°, but in some instances it is rounded off. The cusp is recurved. The costa on each side of the laterally flattened element is less strong than in the other S and P elements, and is sometimes less well developed on one side than on the other.

Sd element. Highly asymmetrical, having the anterior margin, including the antero-basal corner, flexed inwards, making the element concavo-convex. The distal part of the cusp is slightly rotated to the outer side. The costa on the outer side is stronger than that on the inner side. The oral margin is strongly arched and keeled, and the basal cavity flares almost equally to each side.

Pa element. Seen from the outer side the Pa element most closely resembles the Sa element. The Pa element can be distinguished by the indentation of the aboral margin on the outer side, and by the more lateral direction of the costae on its base.

Pb element. Has a costate inner side, the costa beginning on the base and continuing on the strongly reclined cusp. The outer side is broadly carinate or more weakly costate than the inner side. The angle between the oral edge, which is prominently keeled, and the posterior edge of the cusp is usually less than 60°.

M element. Very similar to the corresponding element in *Paroistodus proteus* and *P. originalis*. In some populations the outer side of the element has a bulge basally. According to Pander's (1856) original drawing and description the cusp is quite sharply carinate. In many instances in my collections, however, the cusp is only weakly carinate, particularly on the inner side.

Remarks. Lindström (1971, p. 49) explained that he chose to combine Pander's (1856) type, an M element, with the other elements here described as *P. parallelus*, rather than with younger ones (those referred here to *P. originalis*) as there were no species of similar age to *P. originalis* among those described and illustrated by Pander (1856). I agree with Lindström, but note that even if most of my M elements are less sharply carinate than in Pander's (1856) drawing, it makes sense that in at least some populations of this species the costate S and P elements were accompanied by sharply carinate M elements. The elements described and illustrated by Graves and Ellison (1941) from the Marathon Formation of Texas and tentatively included in the synonymy list could belong to this species or to a closely related one. A closer study will be needed of most Laurentian reports of *Paroistodus* to demonstrate whether they represent Baltoscandian taxa, or parallel forms (the latter seems to be the case in *Drepanoistodus*, for example).

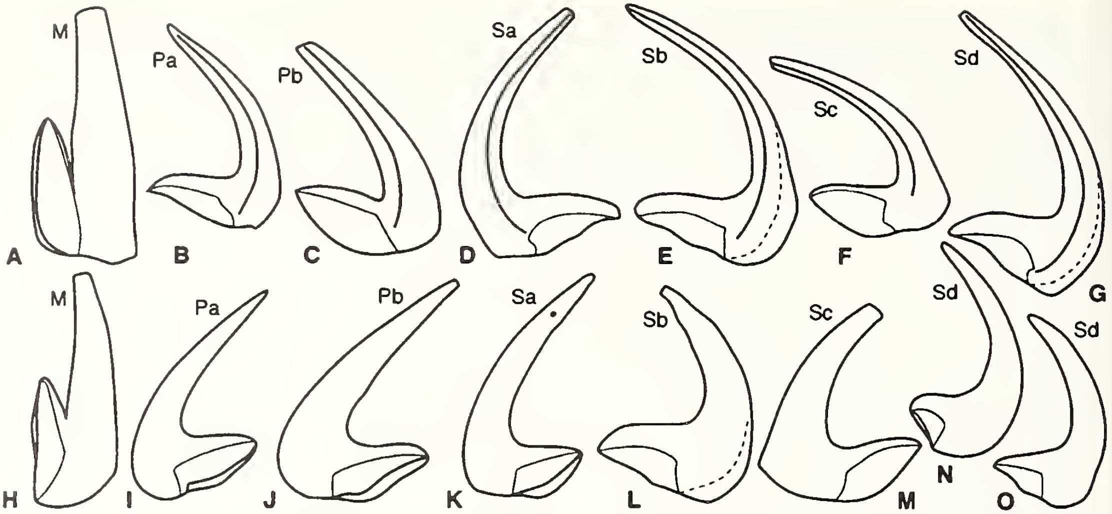
Stratigraphical occurrence. Arenig: from the uppermost *Paroistodus proteus* Zone to the upper middle *Oepikodus evae* Zone. The taxon co-occurs with its predecessor, *P. proteus*, in the uppermost subzone of the *P. proteus* Zone to the lower *P. elegans* Zone, and (rarely) with its successor, *P. originalis*, in the upper middle *O. evae* Zone.

EXPLANATION OF PLATE 1

Figs 1–12, 17, 21. *Paroistodus parallelus* (Pander, 1856); *Oepikodus evae* Zone. 1–2, 4–7, 10–12, 17, 21, Gymninge, sample Nä87-3. 3, 8–9, Orreholmen, sample Vg89-B4. 1, 8, M elements; LO 7282t; LO 7247t. 2–4, Pa elements; LO 7283t; LO 7248t; LO 7284t. 5, Pb element; LO 7285t. 6, Sa element; LO 7286t. 7, Sc element; LO 7287t. 9–10, Pb elements; LO 7249t; LO 7288t. 11, Sd element, inner side; LO 7289t. 12, Sb element, inner side; LO 7290t. 17, Sb element, outer side; LO 7291t. 21, Sd element; LO 7292t. 1, ×50; 2–5, 7–8, 10, 17, 21, ×65; 6, 12, ×60; 9, 11, ×70.

Figs 13–16, 18–20, 22–33. *Paroistodus originalis* (Sergeeva, 1963). 13–15, 18, 20, 22, 24–26, 28, 31, Orreholmen, sample Vg84-10, *P. originalis* Zone. 16, 33, Kårgärde, sample H6, upper *E.*? *variabilis* Zone. 19, Gillberga, sample Ö194-8, *P. originalis* Zone. 23, 29–30, Kårgärde, sample L4, *P. originalis* Zone. 27, 32, Gillberga, sample Ö194-9, *P. originalis* Zone. 13, 24, M elements; LO 7260t; LO 7266t. 14, Pa element; LO 7261t. 15–16, Pb elements; LO 7262t; LO 7298t. 18, Sd element; LO 7263t. 19–20, Pb elements, LO 7299t; LO 7264t. 22, Sb element, inner side with costa; LO 7265t. 23, Sd element; LO 7250t. 25, 28, 30, Sa elements; LO 7267t; LO 7269t; LO 7252t. 26, 29, Sb elements; LO 7268t; LO 7251t. 27, 33, Sd elements; LO 7293t; LO 7300t. 31–32, Sc elements; LO 7270t; LO 7294t. 13, 16, 23–24, 26–27, 29, 31–32, ×60; 14, 18, 20, 22, 33, ×70; 15, 19, 28, ×75; 25, ×65; 30, ×55.

LÖFGREN, *Paroistodus*



TEXT-FIG. 5. *Camera lucida* drawings of elements of *Paroistodus*, showing the outline of the basal cavity. A–G, *P. parallelus* (Pander, 1856); *Oepikodus evae* Zone, Gymninge, sample Nä87-3. A, M element (same as Pl. 1, fig. 1). B, Pa element (same as Pl. 1, fig. 4). C, Pb element (same as Pl. 1, fig. 5). D, Sa element (same as Pl. 1, fig. 6). E, Sb element (same as Pl. 1, fig. 12). F, Sc element (same as Pl. 1, fig. 7). G, Sd element (same as Pl. 1, fig. 11). H–O, *P. originalis* (Sergeeva, 1963); *P. originalis* Zone; H–M, O, Orreholmen, sample Vg84-10. N, Gillberga, sample Ö194-9. H, M element (same as Pl. 1, fig. 13). I, Pa element (same as Pl. 1, fig. 14). J, Pb element (same as Pl. 1, fig. 20). K, Sa element (same as Pl. 1, fig. 25). L, Sb element (same as Pl. 1, fig. 26). M, Sc element (same as Pl. 1, fig. 31). N, Sd element with small basal cavity (same as Pl. 1, fig. 27). O, Sd element with normal basal cavity (same as Pl. 1, fig. 18).

Paroistodus originalis (Sergeeva, 1963)

Plate 1, figures 13–16, 18–20, 22–33; Text-figure 5H–O

1963 *Oistodus originalis* Sergeeva, p. 98, pl. 7, figs 8–9, text-fig. 4 [the holotype (pl. 7, fig. 8) is most probably an Sd element, while the element in pl. 7, fig. 9 and text-fig. 4 seems to be an Sa element].
1971 *Paroistodus originalis* (Sergeeva); Lindström, p. 48, fig. 8.
1981 *Paroistodus originalis* (Sergeeva, 1963); Lindström, p. 231, *Paroistodus* pl. 2, figs 1–4.

Material. About 33000 elements.

General description. In this species there are specimens with basal cavities of approximately the same depth as in elements of *P. proteus*, but also, and often co-occurring with the deep-based elements, there are specimens with very shallow basal cavities. I have not been able to discover whether these two forms belonged to separate populations (there are intermediate forms), and for the present they will be treated together. Anteriorly, all element types have a wide zone of 'inverted basal cavity'. Some populations have costate rather than carinate sides.

Sa element. The cusp is more strongly laterally compressed than in corresponding elements of older taxa of the genus. In some populations the element is very similar to the homologous element of *P. proteus* with an angular antero-basal corner with the basal cavity occupying about half the length of the base. In most populations, however, the basal cavity is shallower, the antero-basal corner is rounded off and it has a wide section of thin translucent material. The cusp is recurved.

Sb element. The anterior edge is flexed to the inner side and the distal part of the cusp bent inwards. In long-based specimens the antero-basal corner is angular, in short-based ones it is well rounded.

Sc element. The base appears angular in side view, and the entire element is laterally flattened. The cusp is recurved and has a strong anterior keel. The antero-basal corner is rounded in a few specimens. There are no short-based Sc specimens, but some elements have a very restricted basal cavity which occupies much less than half the length of the base.

Sd element. Concavo-convex, as the cusp and the entire anterior edge are bent inwards, but in contrast with the homologous element in *P. parallelus* the cusp is rarely rotated. The antero-basal corner is rounded, and the basal cavity bulges, particularly to the inner side. The oral margin is keeled and arched.

Pa element. Similar to the Sa element, but its cusp is more strongly recurved. The anterior edge is slightly flexed inwards and the characteristic indentation of the aboral margin is present, although weaker than in the older *Paroistodus* species.

Pb element. Similar to the M element, but the oral and posterior edges of the cusp are more divergent (*c*. 60°) and separated by a smooth curve rather than a sharp angle. In contrast to earlier species of the genus, the oral edge may be slightly arched, particularly in short-based specimens. The base is expanded on the inner side.

M element. Some of these elements are practically indistinguishable from those of *P. proteus* or *P. parallelus*, but in *P. originalis* the base is generally lower and the cusp is proportionally shorter. Some populations have more distinct mature M elements with a prominent carina on each side and a well-rounded antero-basal corner with a wide, thin edge, slightly flexed outwards. The illustration in van Wamel (1974, pl. 7, fig. 17) of '*Oistodus parallelus*' is an excellent example of this.

Remarks. Specimens of *P. originalis* are uncommon above the *P. originalis* Zone. Those from the overlying *Microzarkodina parva* Zone agree in all details with those from older strata. The youngest representatives come from beds of Llanvirn age in Dalarna (the Kårgärde section) and from latest Arenig strata in Öland (the Gillberga section), and are rare. Most of them are juvenile and thus difficult to assess, but they appear to fall within the limits of variation of *P. originalis*. This taxon, or a similar one, is also present in the upper Arenig and lower Llanvirn of Laurentia and Argentina, often found associated with elements of '*Paroistodus horridus*' (cf. Löfgren 1995*a*, and discussion above).

Stratigraphical occurrence. Arenig to lower Llanvirn; from the upper part of the *Oepikodus evae* Zone to the *Eoplacognathus*? *variabilis-Microzarkodina ozarkodella* Subzone. The species co-occurs rarely with its predecessor, *P. parallelus*, in the upper middle *O. evae* Zone.

Acknowledgements. The investigation was supported by a grant from the Swedish Natural Science Research Council as part of the project 'Early Ordovician conodonts in Sweden'. Many students at the Department of Geology in Lund helped with sampling and picking of conodont samples through the years. Britt Nyberg, Lund, and Mikael Calner, Lund, ably assisted respectively with artwork and with SEM photographic work. The manuscript has benefited from comments by Maurits Lindström, Stockholm, and two anonymous referees and the English was improved by Roger Cooper, Lower Hutt, New Zealand. To all of these, my warmest thanks.

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BOREOPRICEA FROM THE LOWER TRIASSIC OF RUSSIA, AND THE RELATIONSHIPS OF THE PROLACERTIFORM REPTILES

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Abstract. *Boreopricea funerea* from the Lower Triassic of northern Russia is a prolacertiform diapsid, superficially similar to *Prolacerta* from the Lower Triassic of South Africa. The skull is damaged, but relatively complete. The lower temporal bar is absent. Some parts of the skeleton of *Boreopricea*, in particular some of the vertebrae and the foot, are well preserved, and offer clear evidence of prolacertiform affinities. Nineteen species of prolacertiform have been described. Their affinities are difficult to resolve because available specimens for many of the taxa are incomplete. A series of cladistic analyses shows the existence of a tanystropheid clade (*Tanystropheus*, *Tanytrachelos*), to which are allied *Cosesaurus*, *Malerisaurus*, *Boreopricea*, and *Macrocnemus* as successive outgroups. A new synapomorphy of prolacertiforms may be the tight association of astragalus, calcaneum, centrale, and distal tarsal 4 in the ankle, with the centrale in contact with the tibia.

Boreopricea *funerea* was erected by Tatarinov (1978) on the basis of a single complete skull and skeleton of a small reptile from the Lower Triassic of Arctic Russia. Tatarinov (1978) identified *Boreopricea* as a 'prolacertilian' and a member of the family Prolacertidae. Since then, systematists (Benton 1985; Evans 1988) have assumed that this genus was a prolacertiform, and it has been assigned a position in cladograms close to *Prolacerta* and *Macrocnemus*.

The purpose of this paper is to describe *Boreopricea*, to illustrate the material, to clarify some details of its anatomy, and to consider its relationships. This redescription is necessary since Tatarinov's (1978) description was incomplete, poorly illustrated, and incorrect in parts.

Institutional abbreviation. PIN, Palaeontological Institute, Moscow.

SYSTEMATIC PALAEONTOLOGY

Class DIAPSIDA Osborn, 1903
Superdivision NEODIAPSIDA Benton, 1985
Division ARCHOSAUROMORPHA von Huene, 1946
Order PROLACERTIFORMES Camp, 1945
Family PROLACERTIDAE Parrington, 1935

Genus BOREOPRICEA Tatarinov, 1978

Boreopricea funerea Tatarinov, 1978

Text-figures 2–15

Holotype. PIN 3708/1, a nearly complete skull and skeleton, lacking the pelvis, the posterior dorsal vertebrae and anterior caudals; collected in 1972 by the Nenetska (Region) Geological Party, from Kolguyev Island, Arkhangel Province, Arctic Russia (49°E 68°S), Borehole No. 141 at 1112.3 m depth (Text-fig. 1); Vetluzhian Series, Induan, Lower Triassic.

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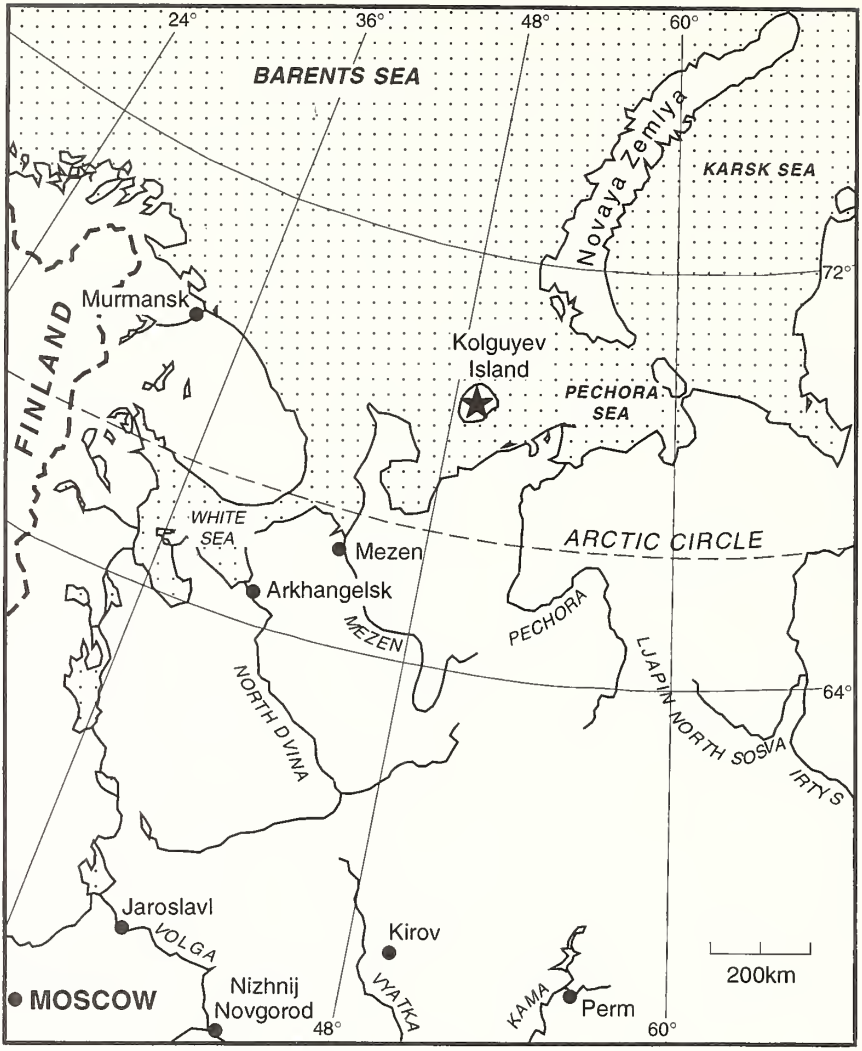
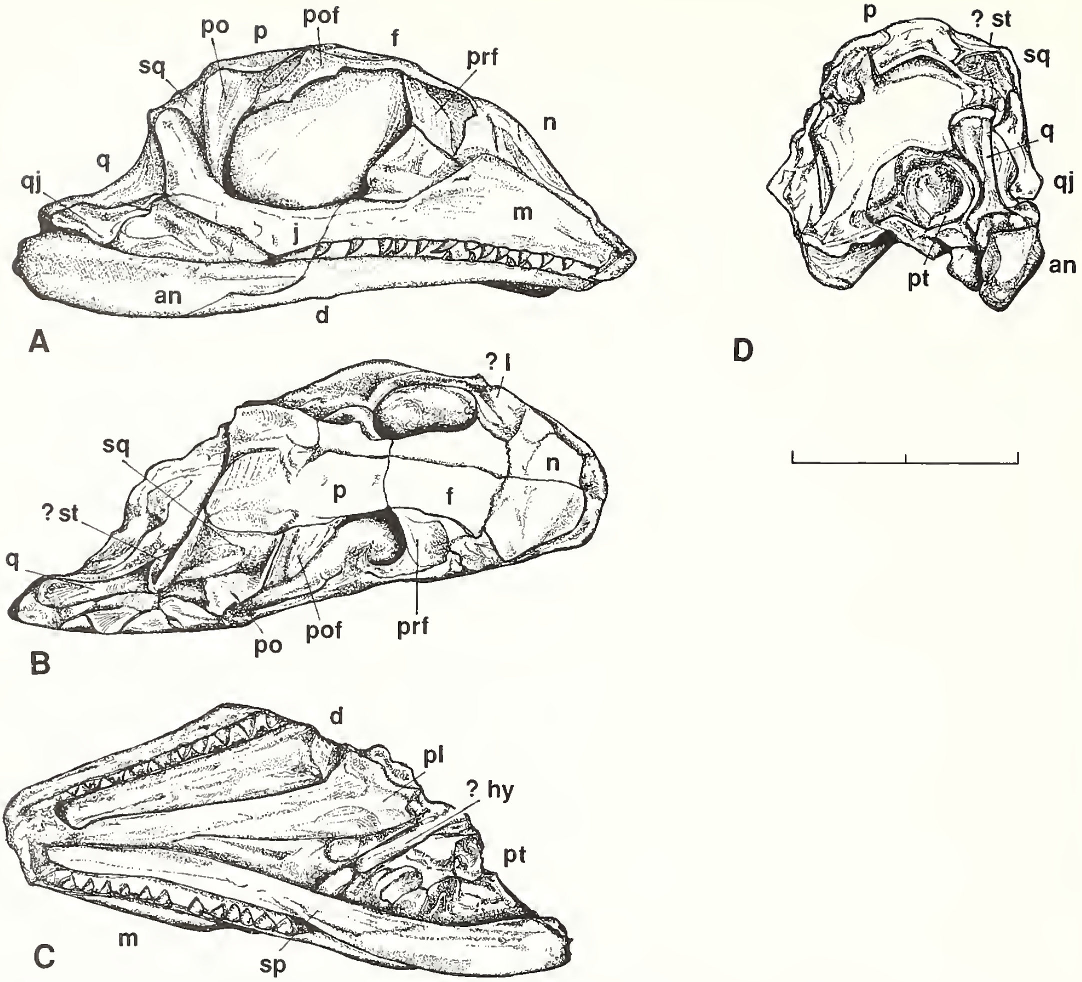


TEXT-FIG. 1. Map of the northern region of the Russian Platform and the Arctic coastline, showing location of the find of *Boreopricea* on Kolguyev Island.

Other material. Tatarinov (1978, p. 511) indicated the existence of a second specimen, PIN 3708/2, 'the anterior end of the muzzle', but this specimen could not be located for the present study.

Diagnosis. A prolacertiform, characterized uniquely by a jugal-squamosal contact. Other synapomorphies: straight fronto-parietal suture; posterior process on jugal absent; quadratojugal tall and with reduced anterior process; posterior dentary teeth lie anterior to posterior maxillary teeth; more than seven cervical vertebrae; metacarpal 3 is equal in length to, or longer than, metacarpal 4; foramen between astragalus and calcaneum absent; second phalanx on digit 5 of foot is long compared with other phalanges. Each of these synapomorphies is shared by other prolacertiforms, but no other taxon has the same character combination.

TEXT-FIG. 2. Type skeleton of *Boreopricea funerea* Tatarinov, 1978 (PIN 3708/1), as currently curated, mounted on card. Pencil outlines indicate bones that are now missing. Scale bar represents 10 mm.

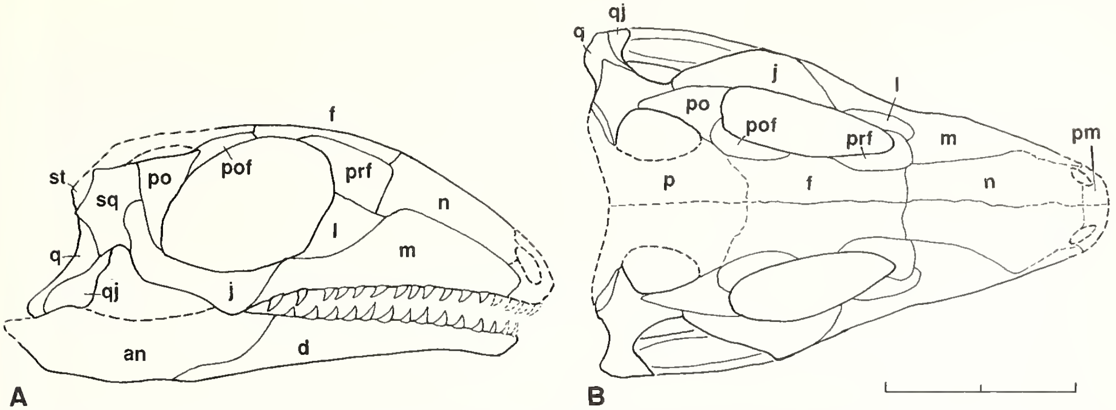


TEXT-FIG. 3. *Boreopricea funerea* Tatarinov, 1978. Skull of PIN 3708/1, as originally preserved, drawn from casts, in right lateral (A), dorsal (B), ventral (C), and occipital (D) views. Abbreviations: an, angular; d, dentary; f, frontal; hy, hyoid element; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pl, palatine; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sp, splenial; sq, squamosal; st, supratemporal. Scale bar represents 10 mm.

Description

General. The type specimen (Text-fig. 2) is rather less complete than indicated in Tatarinov's (1978) description, since some damage has occurred since then (I. V. Novikov, pers. comm. to MJB, 1993). The specimen was prepared out of the matrix by M. F. Ivakhenko, and the perfectly preserved individual bones of the skeleton were attached to a piece of card in natural arrangement, according to their locations in the rock. Since the time of preparation, the skull has been crushed flat, hence obscuring some detail of bone contacts, and certain elements of the postcranial skeleton have been removed from the card, and some have been lost. A plaster cast of the skull indicates its original uncrushed condition, and this was used as a basis for the illustrations (Text-figs 3–4). Where possible, bones were removed from the card for study on all sides.

Measurements of the skeleton indicate a total length of 440 mm, composed of a 29 mm long skull (tip of snout missing), a presacral column length of 170 mm, an estimated sacral length of (?) 10 mm, and a tail length of 230 mm. The estimates of lengths of portions of the vertebral column are based on the limited evidence of the sporadically preserved vertebrae combined with measurements determined from the arrangement of the



TEXT-FIG. 4. *Boreopricea funerea* Tatarinov, 1978. Reconstruction of skull, based on PIN 3708/1, in lateral (A) and dorsal (B) views. Unknown regions, shown by dashed lines, are based on *Prolacerta*. Scale bar represents 10 mm.

elements on the specimen card. These measurements are rather less than those given by Tatarinov (1978, p. 511), who indicated a skull length of 36 mm and a total length of about 450 mm.

Skull. The skull (Text-figs 3–4) is complete, except for the tip of the snout, the left cheek region, and most of the occiput (braincase, posterior part of parietals, posterior part of left mandibular ramus). The lower jaws are in natural articulation. The orbit is large, and the bones surrounding it may be distinguished on the right in the cast, although they are a little displaced. There appear to be two temporal fenestrae, a small upper one, and a lower one bounded on three sides, but with an incomplete lower temporal bar. Only the posterior margin of the nares can be distinguished, where they are bounded by the nasal and the premaxilla, but the nasals are crushed down on to the top surface of the palate, thus obscuring some detail.

There is no trace of the premaxillae, either in the specimen or in the cast of its original condition, although Tatarinov (1978, p. 508) describes these elements. The remainder of the series of paired midline bones of the dermal skull roof is more clearly seen (Text-fig. 3A–B). The nasals are broad elongate elements, shorter and broader than the slender frontals, which are about 1·2 times the length of the nasals. At the anterolateral margin of each nasal is an elongate rounded excavation, representing part of the posterior margin of the naris. Nasals and frontals are quadratic elements, and a short lateral margin of each frontal enters the margin of the orbit. Only the anterior part of the (?) fused parietals may be seen, and there is no indication of a parietal foramen. Postparietals and tabulars are not preserved. A possible supratemporal on the right-hand side is a narrow displaced element behind the upper temporal fenestra, running from the margin of the parietal to the contact of the quadrate and squamosal. Tatarinov (1978, p. 508) records details of the ventral surfaces of the dermal skull roofing elements, and of occipital elements, but none of these may be seen now in the specimen, or in the cast.

The maxilla (m, Text-fig. 3A–C) is a long bone forming the side of the snout, rising to a rounded high point in front of the orbit, and extending back to contact the jugal. Both maxillae can be seen to bear teeth, and there are marked blood vessel/nerve pits on the surface of the bone above the tooth row. The jugal (j, Text-fig. 3A) is lost from the specimen now, and can be seen only in the cast. It is a boomerang-shaped element in the lower posterior angle of the orbit, and it shows no sign of a posterior process beneath the lower temporal fenestra, merely an oblique angulation. This angle is smooth, and does not appear to be broken. Unusually for reptiles, the jugal appears to contact the squamosal with an elongate process (Text-figs 3A, 4), instead of being separated by the postorbital.

The prefrontal is a small crescent-shaped element in the anterior angle of the orbit, seen only on the right in the cast (prf, Text-fig. 3A–B), but now missing from the specimen. The bone is displaced downwards from its original position, and shows the process that lay under the frontal. The lacrimal is not clear on the right-hand side, but may be indicated by the flat area in the lower anterior angle of the orbit below the prefrontal. An indication of the lacrimal duct may be detected here. On the left-hand side of the cast, a complex structure in the anterior part of the orbital margin is probably composed largely of the lacrimal and its process to the palatine.

The right postfrontal is a displaced triangular slip of bone (pof, Text-fig. 3A–B), showing a long contribution to the posterodorsal orbital margin, and contacting the postorbital. The left postfrontal is crushed. The right postorbital is a triangular element, a little larger than the postfrontal, and with a curved orbital margin, a short posterior process which touches the squamosal, and a long contact with the jugal, clearly seen in the cast because of the displacement (po, Text-fig. 3A–B). The left postorbital may be represented by a curved element that is displaced medially, and seen in the cast, but not now in the specimen.

The elements of the posterior angle of the skull may be seen only on the right-hand side (Text-fig. 3A–B, D). The squamosal is a rectangular flat element that lacks evident processes. The quadratojugal is a small triangular bone slip, with no sign of an anterior process below the lower temporal fenestra. The quadrate is a narrow oblique element which extends from an expanded dorsal contact with the squamosal (? and supratemporal) to the articular condyle. The quadrate slopes sharply backward from the squamosal contact. These details can now only be seen in the cast, and not in the specimen.

In the palate (Text-fig. 3C), the premaxillae, maxillae and vomers cannot be seen in the specimen or in the cast, although Tatarinov (1978, p. 509) gave detailed description of all palatal elements. The palatines are difficult to distinguish, but appear to be elongate elements that contact the medial margins of the maxillae above the tooth rows, and are widely separated in the midline, with no evidence now of a midline contact. The right pterygoid shows the anterior and ectopterygoid processes and, in occlusal view, the deep quadrate process curving back to contact much of the medial face of the quadrate. There is no indication of a sphenethmoid, as identified by Tatarinov (1978, p. 510).

The braincase and epipterygoid are absent.

The reconstructed skull (Text-fig. 4) is based on the cast and on the specimen. The circumorbital and temporal regions were restored by moving cut-out bone shapes back to their original articulations. The top of the snout is crushed in both the cast and the specimen, and the nasal was lifted back to its original position. The anteriormost part of the snout, and the parietals, were based on *Prolacerta*.

Mandible. Both mandibular rami are present in the cast, but only the anterior half of the left ramus (Text-figs 3–4). In the specimen, the posterior part of the right ramus is now damaged, and the left ramus is missing. The mandible is narrow and shallow, exhibiting a sigmoid curve in ventral view. The dentary is a low straight element, which presumably bore teeth, but the dorsal margin is concealed within the skull. The splenial is essentially a medial element, but forms the ventral portion of the anterior part of the mandible, and extends some way up the lateral face of the left mandible in the cast. The splenial symphysis is missing. The sutures delimiting the angular, surangular, and prearticular are unclear. The articular and Meckel's canal cannot be seen, and it is not possible to determine whether there was a coronoid process.

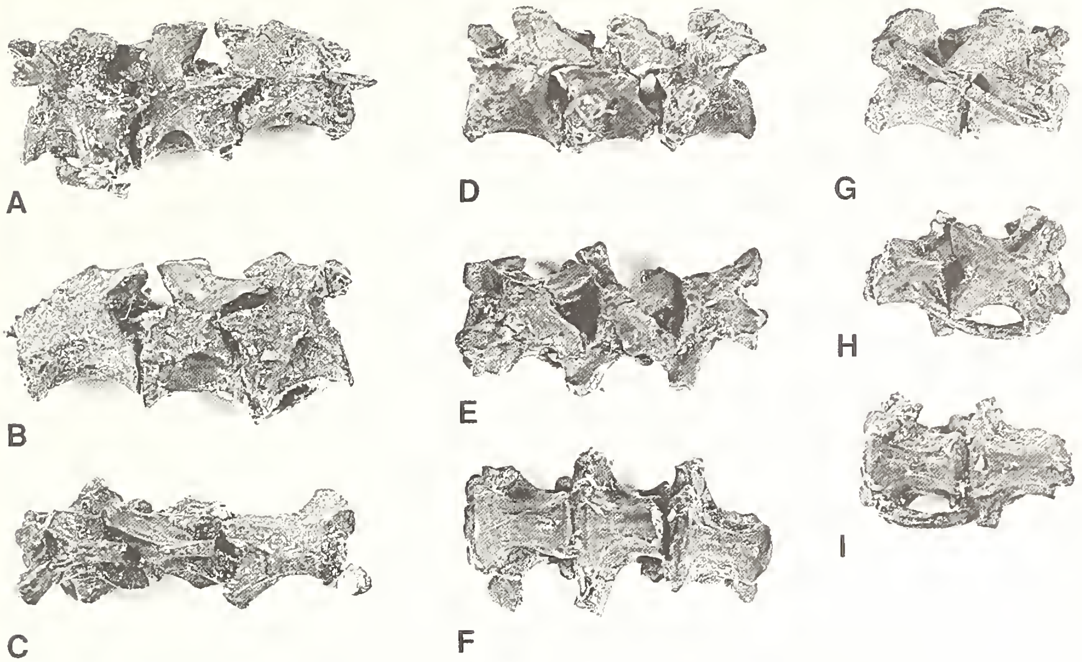
Dentition. The right maxilla bears about 15 teeth (Text-fig. 3A, C), but when intervening gaps are included, the count may be 20–25. There are 13 or 14 teeth and gaps on the left maxilla. Dentary teeth cannot be seen. Tatarinov (1978, p. 510) indicated the presence of 'up to 40 teeth in the upper jaw, seven of which are in the premaxillary [and] about 35 teeth in the lower jaw', none of which can now be confirmed. The maxillary teeth are conical, slightly recurved, and have sharp points. They appear to be arranged with alternating teeth and gaps. The preservation of the specimen makes it difficult to determine whether the teeth sit in sockets; they appear to be surrounded by arcs of bone laterally, and to sit in a groove that is partially open on the medial side.

Tatarinov (1978, pp. 507, 510) described extensive midline rows of teeth on the vomer and pterygoid, but there is no evidence for teeth on any of the palatal elements.

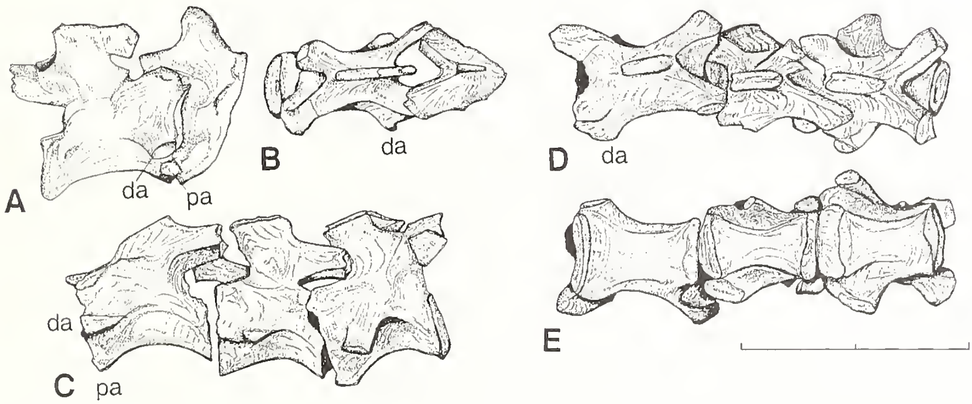
Hyoid elements. A possible hyoid element is represented in the cast by a narrow rod-like bone (?hy, Text-fig. 3C), 5 mm long and 0·3 mm wide, below the right pterygoid, but is no longer visible in the fossil.

Axial skeleton. There are five cervical, nine dorsal and 29 caudal vertebrae, beautifully preserved, some of them still in articulation (Text-figs 5–8). The sacral vertebrae are absent.

The five cervicals appear to follow in sequence, but do not include either the atlas or axis. Hence, these five are probably presacrals 3–7 or 4–8, as suggested by Tatarinov (1978, p. 510). The anteriormost complete vertebra (3 or 4) is elongate and narrow (Text-fig. 6A–B), 7 mm long, with a constricted centrum that is arched high in the middle, and lacks a ventral keel. The articular faces of the centrum appear to be flat and subcircular, the anterior being broader than the posterior. The neural canal is broad. There is a double rib attachment surface (diapophysis and parapophysis; da, pa, Text-fig. 6A–B) at the anterior margin of the centrum, clearly seen on the left. The zygapophyses project a short distance in front of, and behind, the



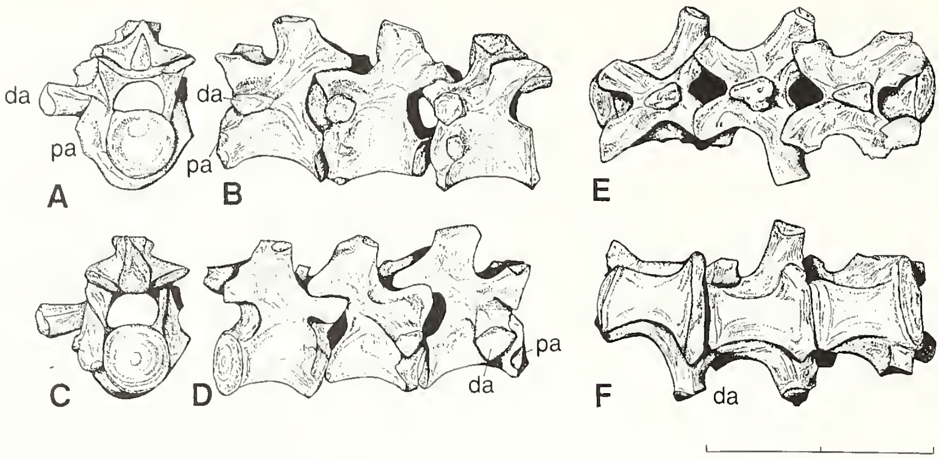
TEXT-FIG. 5. *Boreopricea funerea* Tatarinov, 1978. Vertebrae of PIN 3708/1. Cervical vertebrae 5 or 6 to 7 or 8, in right lateral (A), left lateral (B), and dorsal (C) views. Three anterior dorsal vertebrae, in left lateral (D), dorsal (E), and ventral (F) views. Two anterior dorsal vertebrae, with attached rib fragment, in left lateral (G), dorsal (H), and ventral (I) views. All × 2·5.



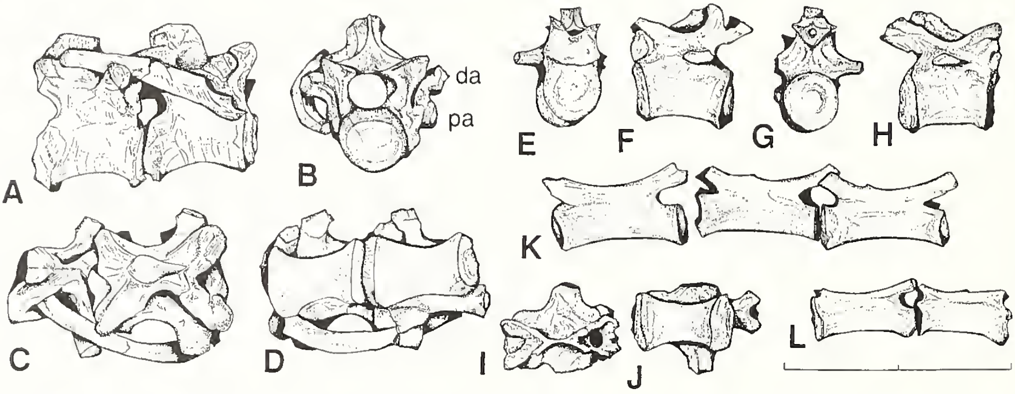
TEXT-FIG. 6. *Boreopricea funerea* Tatarinov, 1978. Cervical vertebrae of PIN 3708/1. Cervical vertebrae 3 and 4 or 4 and 5, in right lateral (A) and dorsal (B) views. Cervical vertebrae 5 or 6 to 7 or 8, in left lateral (C), dorsal (D), and ventral (E) views. Abbreviations: da, diapophysis; pa, parapophysis. Scale bar represents 10 mm.

centrum, and the zygapophyseal facets are angled at about 40° above horizontal. The neural spine is narrow, long (3·5 mm), and low, but the dorsal portion is apparently incomplete.

The three posterior cervical vertebrae 5/6–7/8 (Text-figs 5A–C, 6C–E) are slightly shorter, 5·5–6 mm long, and their centra are slightly broader than in the anterior cervicals. The rib attachment faces form a well-marked sub-triangular area on the anterior lateral margin of the centrum, with the parapophysis located somewhat ventrally, and the broader diapophysis projecting some distance laterally, especially in cervical 7/8 (da, pa,



TEXT-FIG. 7. *Boreopricea funerea* Tatarinov, 1978. Anterior dorsal vertebrae 5 or 6 to 7 or 8 of PIN 3708/1, in anterior (A), left lateral (B), posterior (C), right lateral (D), dorsal (E), and ventral (F) views. Abbreviations as for Text-figure 6. Scale bar represents 10 mm.

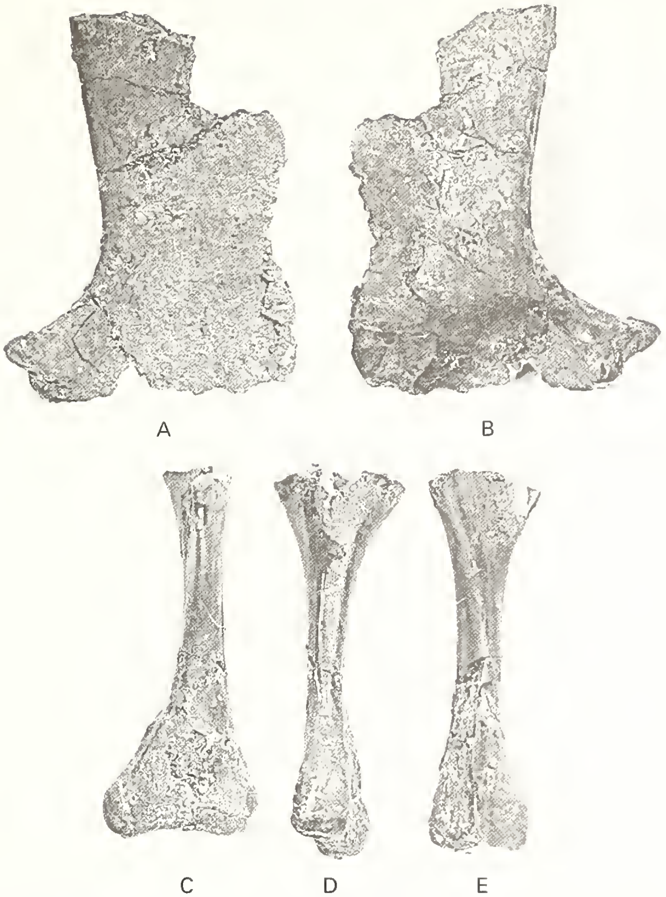


TEXT-FIG. 8. *Boreopricea funerea* Tatarinov, 1978. Dorsal and caudal vertebrae of PIN 3708/1. Anterior dorsal vertebrae, with attached rib fragment, in lateral (A), anterior (B), dorsal (C), and ventral (D) views. Anterior caudal vertebra 4 or 5, in anterior (E), left lateral (F), posterior (G), right lateral (H), dorsal (I), and ventral (J) views. K, mid-caudal vertebrae *c.* 19–21, in left lateral view. L, posterior caudal vertebrae *c.* 34–35, in left lateral view. Abbreviations as for Text-figure 6.

Text-fig. 6C–D). The zygapophyses spread more laterally than in cervical 3/4. The neural spines show a narrow dorsal spine table which is slightly expanded.

There are five well preserved anterior dorsal vertebrae, in a set of three and a set of two (Text-figs 5D–I, 7, 8A–D). Centra are shorter (5 mm) and broader than in the cervicals. The posterior articular face of the centrum is circular, but the broader anterior face is cordate to circular in outline. Both faces are amphicoelous. The centra are narrowly constricted and lack ventral keels. All show a small parapophyseal facet, now quite distinct from the laterally projecting transverse process (diapophysis) which had a sub-triangular lateral articular face (da, pa, Text-figs 7, 8B). The zygapophyses spread widely laterally, and their articular faces are set at an angle of only 20° above horizontal. The neural spines are short and low, and provided with a triangular spine table, with the tip of the triangle pointing back. A set of three poorly preserved posterior dorsal vertebrae show similar features, but no trace of a parapophysis.

There are 29 caudal vertebrae, each preserved whole or in part (Text-figs 2, 8E–L). These caudals are possibly 4–5, 7, 11–15, 16–22, 25–29, 30–32, 34–38, and 41, based upon their locations as glued on to the specimen card.



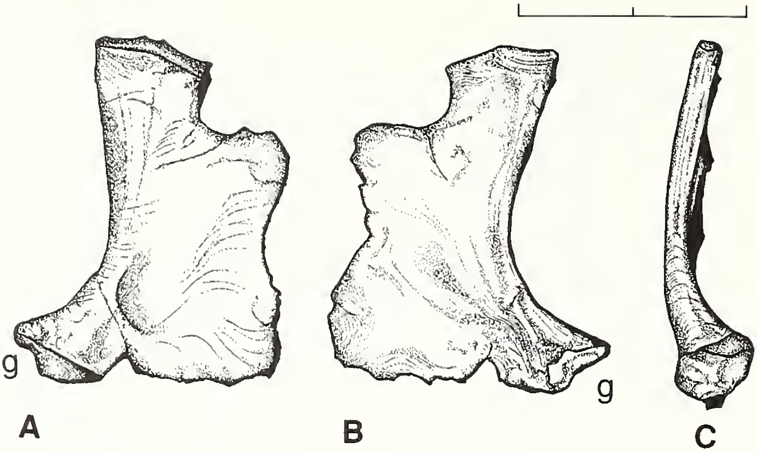
TEXT-FIG. 9. *Boreopricea funerea* Tatarinov, 1978. Scapula and humerus of PIN 3708/1. Right scapula, in lateral (A) and medial (B) views. Partial left humerus, lacking the proximal end, in anterior (C), dorsal (D), and ventral (E) views. All × 3·0.

The numbering, and narrowing of centra towards the more posterior elements, suggests that there were originally about 50 vertebrae in the tail.

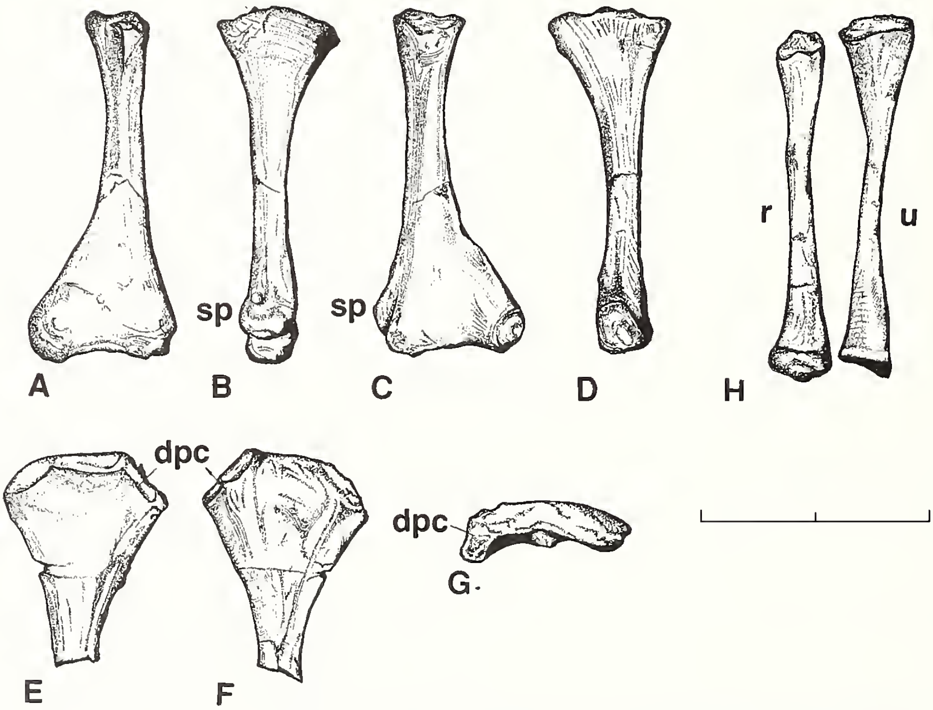
The anterior caudals 4 and 5 (Text-fig. 8E–J) are short, with centra 4–4·5 mm long. The centrum is spool-shaped, but not as constricted as in presacral vertebrae, and the anterior and posterior articular faces are the same size. Distinct low transverse processes project horizontally. The neural spine and zygapophyses are incomplete. Caudal 7 (Text-fig. 2) is more complete, with a 4 mm long centrum. The vertebra shows a neural spine that slopes well back, and has a triangular spine table with an anterior point. The zygapophyses are small and articular faces are nearly horizontal. The anterior and posterior margins of the centrum have a broad rim, but there is no clear haemapophyseal facet. Tatarinov (1978, p. 511) reported a haemapophysis in contact with a caudal vertebra, but that bone is now lost. More posterior caudals (Text-fig. 8K–L) have slightly longer centra, 5–5·5 mm, but much lower and narrower. The neural spine blends with the postzygapophyses, and the transverse process disappears by caudal 16. The zygapophyseal facets become tiny.

A number of narrow rib shafts is preserved (Text-fig. 2), apparently associated with middle and posterior dorsal vertebrae, but the articular heads are not present. Some isolated rib heads are present with the specimen, but there is no evidence now for their correct assignment. Cervical, sacral and caudal ribs are now missing in the specimen.

Appendicular skeleton. Elements of the shoulder girdle, forelimbs and hindlimbs are preserved, but the pelvis is absent (Text-fig. 2). Some of the limbs bones in particular are remarkably well preserved, and it appears that

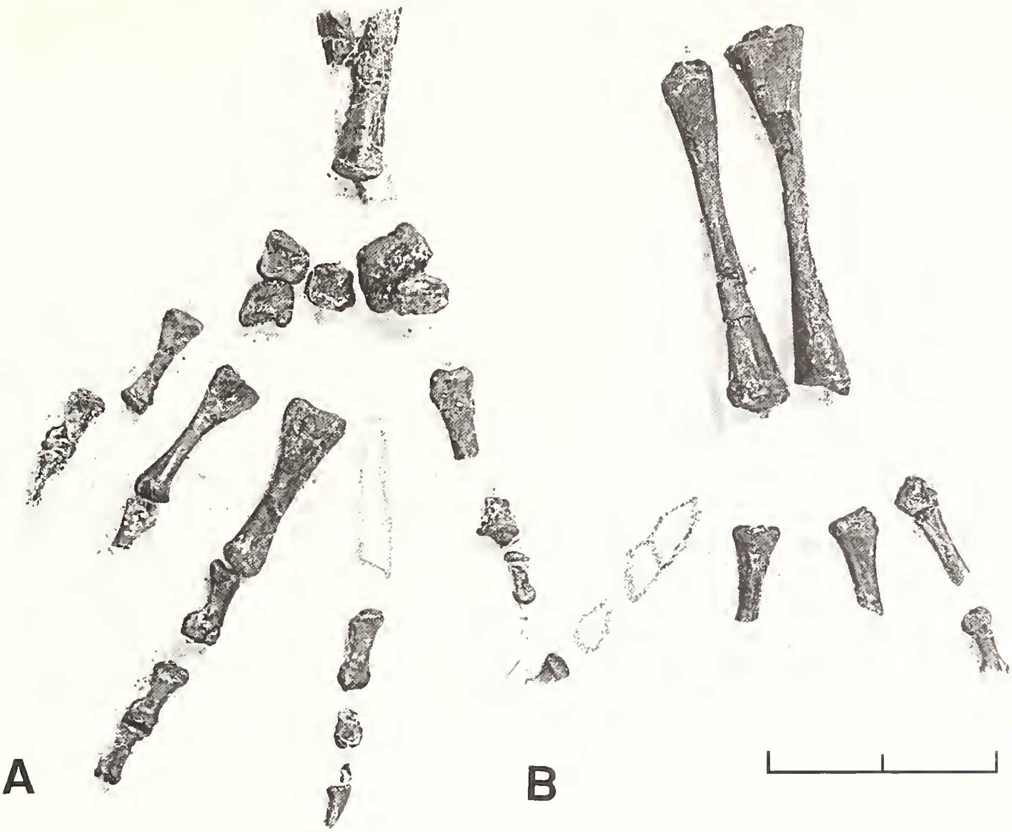


TEXT-FIG. 10. *Boreopricea funerea* Tatarinov, 1978. Right scapula of PIN 3708/1, in lateral (A), medial (B), and posterior (C) views. Abbreviation: g, glenoid. Scale bar represents 10 mm.



TEXT-FIG. 11. *Boreopricea funerea* Tatarinov, 1978. Forelimb elements of PIN 3708/1. Left humerus, lacking proximal end, in anterior (A), dorsal (B), posterior (C), and ventral (D) views. Proximal end of right humerus, in dorsal (E), ventral (F), and proximal (G) views. H, left radius (r) and ulna (u) in posterior view with proximal end at top. Abbreviation: dpc, deltopectoral crest; sp, supinator process. Scale bar represents 10 mm.

the hands and feet were complete, including every wrist and ankle bone, and every phalanx. Some of these elements are now missing. Tatarinov (1978, p. 511) described a clavicle, interclavicle, and an ossified sternum, but none of these elements can be located now.

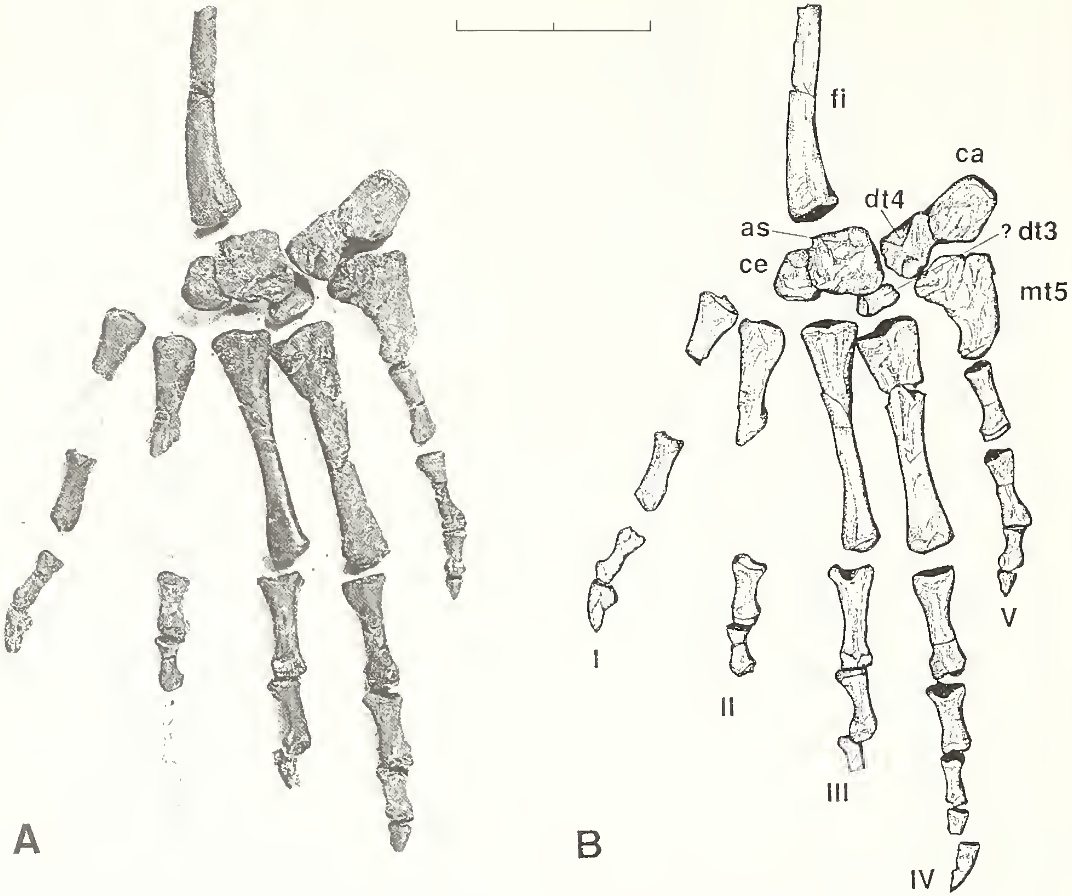


TEXT-FIG. 12. *Boreopricea funerea* Tatarinov, 1978. Right (A) and left (B) hands of PIN 3708/1, as stuck on the card. Individual elements are shown in a mixture of ventral and dorsal aspects. Pencil outlines indicate bones that are now missing. Scale bar represents 10 mm.

The two scapulae are broad elements, apparently quadratic in lateral view, but the thin dorsal and posterior margins are incomplete. The right scapula (Text-figs 9A–B, 10) is better preserved. It measures 16·5 mm high and 12·5 mm long. The whole scapular blade is thin, and it curves outwards, when seen in anterior view. The thicker anterior margin is deeply curved behind the broad glenoid. The articular face of the glenoid is triangular, with the point facing backwards (g, Text-fig. 10). The putative coracoid has a larger glenoid face, also triangular, and with the point facing backwards. Behind it, the bone is thin, and bears a small coracoid foramen. The thin ventral and posterior margins of the putative coracoid are incomplete.

The forelimb is represented (Text-fig. 2) by a nearly complete left humerus (shown as if the right-hand element, and with proximal and distal ends reversed, by Tatarinov 1978, fig. 2), the proximal end of the right humerus, the radius and ulna (complete on the left side only), and both hands (neither complete, but more so on the right side).

The nearly complete left humerus (Text-figs 9C–E, 11A–G), 17 mm long, has broad proximal and distal ends, set at right angles to each other. The distal end bears two condyles, for the radius and the ulna, separated by a constricted middle portion. There is a moderate supinator process (sp, Text-fig. 11B–C) with an ectepicondylar groove (not entepicondylar, as indicated by Tatarinov 1978, p. 511). There are no foramina. The shaft is approximately circular in cross section. The proximal end is more completely seen in the right humeral fragment (Text-fig. 11E–G), which shows a slender deltopectoral crest, projecting at an angle of about 100° from the proximal articular face (dpc, Text-fig. 11E–G). The ventral face of the proximal end of the right humerus is deeply concave, while the dorsal face is somewhat crushed. Comparison of the two incomplete humeri yields an original total length of 21 mm, with the proximal end (right side) 8 mm wide and the distal end (left side) 7 mm wide.

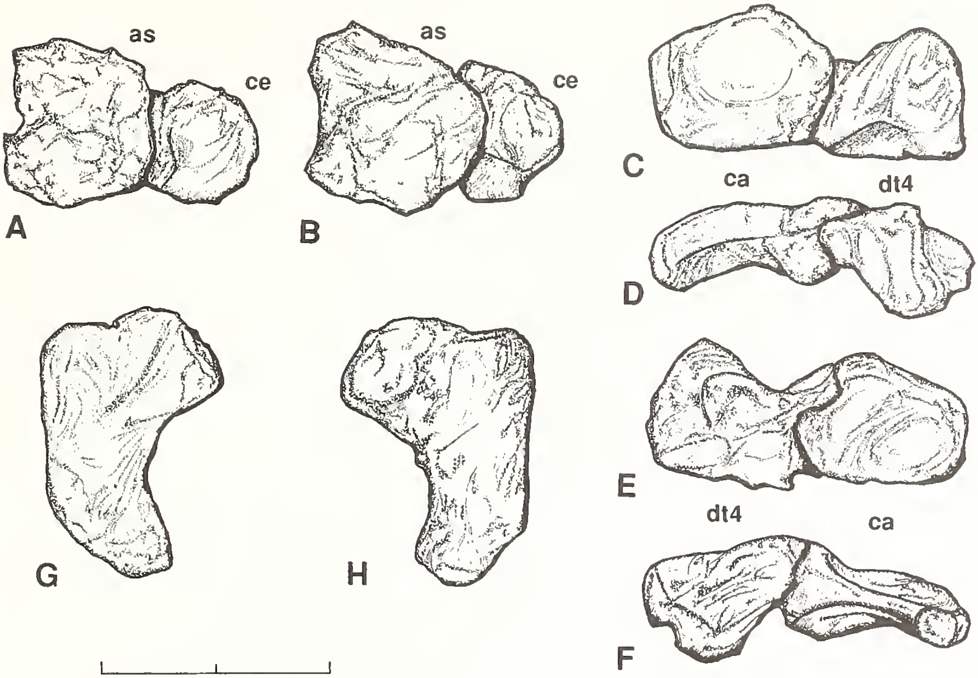


TEXT-FIG. 13. *Boreopricea funerea* Tatarinov, 1978. A–B, right foot, as stuck on the card, of PIN 3708/1, showing partial fibula, the four main tarsal bones, all five metatarsals, and most of the phalanges. Abbreviations: I, II, III, IV, V, digits 1, 2, 3, 4, and 5; as, astragalus; ca, calcaneum; ce, centrale; dt3, third distal tarsal; dt4, fourth distal tarsal; fi, fibula; mt5, metatarsal 5. Pencil outlines indicate bones that are now missing. Scale bar represents 10 mm.

The left ulna and radius (Text-figs 2, 11H) are 17 mm and 16·5 mm long respectively. Both elements are slightly curved rods with a narrow 1 mm wide shaft, and expanded flattened ends which overlap in natural articulation. The proximal end of the ulna (3·5 mm) is broader than the proximal end of the radius (2 mm), but the distal end of the ulna (2 mm) is narrower than the distal end of the radius (3 mm), as is usual in amniotes.

There are five small carpal elements in the wrist of the right hand (Text-fig. 12A), but these are too small and featureless for identification. The hands are secured on the card in ventral view, even though the rest of the skeleton is arrayed in dorsal view; hence digit 1 lies laterally and digit 5 is medial. Metacarpals 1–3 and 5 of the right hand, and 1, 2, and 4 of the left (Text-fig. 12B) indicate that metacarpal 3 was longest, and 2 was a little shorter. Eleven phalanges, including unguals on digits 1 and 4, are present in the right hand, and ten phalanges in the left, including unguals on digits 1 and 5. It is not clear whether all the elements are now in their correct positions, and a phalangeal formula cannot be given.

Two femora are preserved (Text-fig. 2), a partial right lacking the distal end, and a nearly complete left, 25 mm long. The bone appears to be hollow, the left femur showing a calcite core in a broken area of the shaft. The distal end of the left femur is broader (5·5 mm) than the proximal (4 mm). The proximal end shows a sub-



TEXT-FIG. 14. *Boreopricea funerea* Tatarinov, 1978. Elements of the tarsus of the right foot of PIN 3708/1. Astragalus and centrale in close apposition, in dorsal (A) and ventral (B) views. Calcaneum and distal tarsal 4 in close apposition, in dorsal (C), distal (D), ventral (E), and proximal (F) views. Metatarsal 5 in dorsal (G) and ventral (H) views. Abbreviations as for Text-figure 13. Scale bar represents 5 mm.

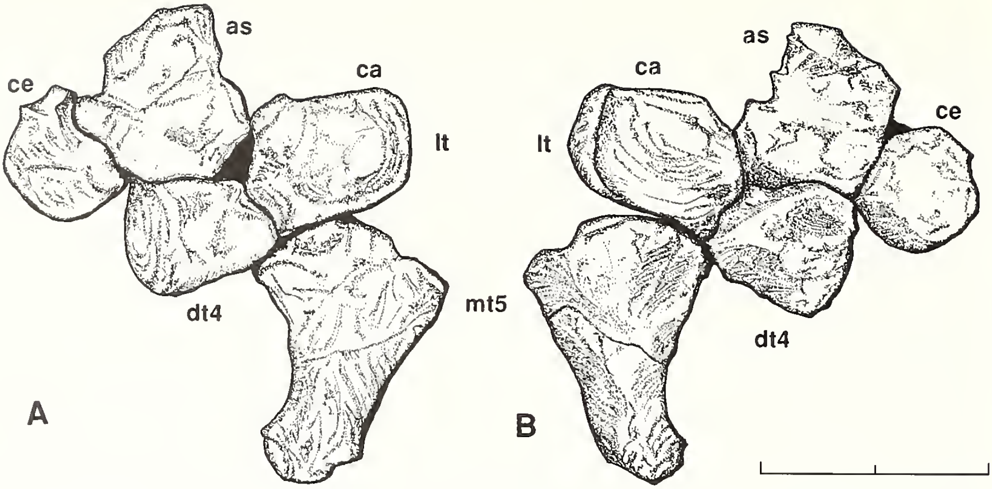
circular articular face, while the distal end is probably more elliptical in outline. The shaft of the left femur shows a slight sigmoid bend, when viewed from above or below.

The lower hindlimb is represented by most of the left tibia, the distal end of the right fibula, and a proximal fragment of the left fibula (Text-fig. 2). The tibia has a broad sub-triangular proximal end, 5 mm wide, and a low cnemial crest. The specimen is 17 mm long, and shows the beginnings of a distal expansion, so it may have been about 20 mm long when complete. The fibula is a slender flat element, 2 × 1 mm proximally and 3 × 2·5 mm distally. The right fibula shows a clear curve in the shaft.

The foot is preserved incompletely on the left, but is nearly complete on the right (Text-figs 13–15), and the description is based entirely on the latter. The foot is glued in ventral view on the card, and digit 1 lies laterally, digit 5 medially, but individual elements are secured variously in dorsal and ventral views. The proximal part of the ankle appears to consist of four elements arranged in two pairs, a centrale and astragalus (= intermedium) and a distal tarsal 4 and calcaneum (= fibulare). In both cases, the elements fit tightly together and cannot be separated, but lines of contact are still visible.

The centrale is a hemispherical element with a concave lateral facet that fits snugly over the medial margin of the astragalus (Text-figs 13, 14A–B). The astragalus is a larger quadratic element that bears two distal articular surfaces, one for the calcaneum, and one for distal tarsal 4. The articulation with the calcaneum may have been more extensive than shown in Text-figure 15, since part of the lateral margin of the astragalus is broken off. The centrale bears a proximal articular face for the tibia, whilst the astragalus contributes to this tibial contact, as well as meeting the fibula.

The calcaneum (Text-figs 13, 14C–F) is of equal depth to the astragalus at the point of articulation. There does not seem to be a foramen between astragalus and calcaneum. The lateral tuber (lt, Text-fig. 15) is 3·5 mm long, almost rectangular, and curves slightly upwards. Both dorsal and ventral surfaces of the tuber are smooth and slightly concave. The calcaneum articulates with distal tarsal 4, although the nature of this articulation is obscured by their firm connection. Distal tarsal 4 shows two distal articular facets (Text-fig. 14D), one sub-rectangular and the other sub-triangular, the former for contact with metatarsal 5. It is not clear how the latter



TEXT-FIG. 15. *Boreopricea funerea* Tatarinov, 1978. Reconstructed tarsus of the right foot of PIN 3708/1 in ventral (A) and dorsal (B) views, showing the likely pattern of fit of the four main proximal tarsal elements and metatarsal 5. Abbreviations as for Text-figure 13; lt, lateral tuber. Scale bar represents 5 mm.

facet articulated with the other ankle bones, since the full series of distal tarsals is unknown. A small bean-shaped distal element is present, probably distal tarsal 3.

The approximate equivalence in size of the astragalus, calcaneum, centrale, and distal tarsal 4 is a feature shared with *Prolacerta* (Gow 1975) and *Macrocnemus* (Rieppel 1989), and the particular arrangement of these four elements, including the contact of centrale and tibia, may turn out to be a prolacertiform synapomorphy. It is not included here in the cladistic analysis until a more detailed study of other prolacertiform specimens can be carried out.

The hooked fifth metatarsal (Text-figs 13, 14G–H), 6·5 mm long, bears an ovoid proximal articular surface with a sharp edge ventrally and a rounded facet dorsally. This surface articulates with distal tarsal 4 and the calcaneum. The dorsal rounded articulation of metatarsal 5 may have allowed this element to bend up more than down. Distally, the fifth metatarsal narrows and is bounded by a straight lateral margin and a hooked medial margin.

Most of the other toe bones are present. Metatarsals 1 and 2 are incomplete distally, 3 to 5 are complete. Metatarsals 3 and 4 are slender elements, 12·5 mm and 13·0 mm long, with flattened expanded proximal and distal ends and a shaft that arches dorsally. Metatarsal 4 is longest, then 3, then perhaps 2, 1, and 5 in order of diminishing length. Sixteen phalanges are present, and these include small pointed unguals on digits 1, 4 and 5. The phalanges have been stuck on card rather inaccurately, since they indicate the unlikely phalangeal formula of 3-3-3/4-4-4. Tatarinov (1978, p. 511) indicated a more typical reptilian phalangeal formula of 2-3-4-5-4 (illustrated as 2-3-4-5-5 in his Text-fig. 2).

RELATIONSHIPS AMONG PROLACERTIFORMS

Previous work

Until recently, the prolacertiforms were of uncertain affinities. Some, or all, taxa were assigned by Romer (1966) to Euryapsida, as basal relatives of the plesiosaurs and ichthyosaurs. Other authors regarded the prolacertiforms, as their name implies, as 'pre-lizards' on the basis of a variety of shared characters, summarized by Wild (1973, 1980). An affinity with archosaurs was hinted at by Cruickshank (1972), and Gow (1975) explicitly noted the close relationship of *Prolacerta* with archosaurs. Benton (1983, 1984, 1985) listed synapomorphies of prolacertiforms and archosaurs, and he suggested that their closest outgroups are Rhynchosauria and *Trilophosaurus*, the whole forming a clade termed the Archosauromorpha (von Huene 1946). Evans (1988) confirmed this view, and added *Megalancosaurus*, Thalattosauria, Kuehneosauridae (tentatively), and Choristo-

TABLE 1. The species of prolacertiforms, arranged in stratigraphical sequence. Main descriptive accounts for each taxon are noted.

- Late Permian (Kazanian):
  - *Protorosaurus speneri* Meyer, 1856; Kupferschiefer, Germany (Seeley 1888).
- Early Triassic (Scythian):
  - *Boreopricea funerea* Tatarinov, 1978; Vetluzhian Series, Kolguyev Island, Russia (Tatarinov 1978).
  - *Kadimakara australiensis* Bartholomai, 1979; Rewan Formation, Queensland, Australia (Bartholomai 1979).
  - *Prolacerta broomi* Parrington, 1935; *Lystrosaurus* Zone, South Africa (Gow 1975; Evans 1986); Fremouw Formation, Antarctica (Colbert 1987).
  - *Prolacertoides jimusarensis* Young, 1973; Xinjiang, China (Young 1973).
  - *Trachelosaurus fischeri* Broili and Fischer, 1916; Buntsandstein, Germany (Broili and Fischer 1916).
- Mid Triassic (Anisian):
  - *Tanystropheus antiquus* von Huene, 1905; Oberer Buntsandstein, Unterer Muschelkalk, Germany (Ortlam 1967; Wild 1973); Gogolin Beds, Poland; Unterer Muschelkalk, Netherlands (Wild and Oosterink 1984).
  - *Rhombopholis scutulata* (Owen, 1842); Bromsgrove Sandstone Formation, Warwick and Bromsgrove, England (Benton and Walker 1996).
- Middle Triassic (Ladinian, or Anisian/Ladinian boundary):
  - *Cosesaurus aviceps* Ellenberger and Villalta, 1976; Montral-Alcover, Tarragona, Spain (Ellenberger 1977; Sanz and Lopez-Martinez 1984).
  - *Macrocnemus bassanii* (Nopcsa, 1930); Grenzbitumenzone, Switzerland and Italy (Peyer 1937; Kuhn-Schnyder 1962; Rieppel 1989).
  - *Tanystropheus longobardicus* (Bassani, 1886); Grenzbitumenzone, Switzerland and Italy (Wild 1973, 1980).
  - *Tanystropheus conspicuus* Meyer, 1855; Oberer Muschelkalk and Lettenkeuper, Germany (Wild 1973, 1980) [? = *T. longobardicus*].
  - *Tanystropheus meridensis* Wild, 1980; Meridekalk (Lettenkeuper), Switzerland (Wild 1980).
- Late Triassic (Carnian):
  - *Malerisaurus langstoni* Chatterjee, 1986; Tecovas Member, Dockum Formation, Texas, USA (Chatterjee 1986).
  - *Malerisaurus robinsonae* Chatterjee, 1980; Maleri Formation, India (Chatterjee 1980).
  - *Tanytrachelos ahynis* Olsen, 1979; Dan River Group, North Carolina and Virginia, USA (Olsen 1979).
- Late Triassic (Norian):
  - *Langobardisaurus pandolfi* Renesto, 1994; Calcare di Zorzino, Cene, northern Italy (Renesto 1994*a*).
  - *Megalancosaurus preonensis* Calzavara, Muscio and Wild, 1980; Calcare di Zorzino, Cene, northern Italy (Renesto 1994*b*).
  - *Tanystropheus fossai* Wild, 1980; Argillite di Riva di Solto, northern Italy (Wild 1980).

dera to the clade. Recent analyses have confirmed this pattern (e.g. Chatterjee 1986; Rieppel 1989; Laurin 1991; Renesto 1991, 1994*a*, 1994*b*).

Relationships within the clade Prolacertiformes have proved harder to establish. The Late Permian *Protorosaurus* has generally been indicated as the most plesiomorphic member of the group (Benton 1985; Evans 1988), and the Mid and Late Triassic *Tanystropheus* and the Late Triassic *Tanytrachelos* have been paired as sister-taxa. However, the Mid Triassic *Macrocnemus* has shuttled between close alliance with the Early Triassic *Prolacerta* and *Tanystropheus*, while the position of

TABLE 2. Characters used in the assessment of the phylogenetic relationships of the prolacertiforms. Some of these characters were proposed by Benton (1985) and Evans (1988). The postulated plesiomorphic (0) and apomorphic/derived (1) states of each character are noted.

Skull characters:

1. Dorsomedial process of premaxilla: extends between narial openings (0); reduced (1).
2. Relative length of nasals and frontals: nasals shorter than frontals (0); nasals longer than frontals (1).
3. Fronto-parietal suture: interdigitating (0); straight (1).
4. Pineal foramen: present and relatively large (0); reduced or absent (1).
5. Lacrimal contact with nasal: present (0); absent (1).
6. Lacrimal extent: element runs forward from the orbit (0); restricted to the orbital rim in lateral view (1).
7. Postfrontal dimensions: substantial tripartite element (0); short element lacking clear processes (1).
8. Posterior process of postorbital: does not extend beyond back of lower temporal fenestra (0); extends back beyond the posterior margin of the lower temporal fenestra (1).
9. Ventral ramus of squamosal: present, and extends below quadrate head (0); reduced and cotyle formed for quadrate head (1).
10. Posterior process of jugal: present (0); absent (1).
11. Quadratojugal shape; an indicator of whether there is a complete lower temporal bar: low and with anterior process (0); tall with reduced anterior process (1).
12. Quadratojugal: present (0); absent (1).
13. Supratemporal: present (0); absent (1).
14. Relative positions of posterior terminations of tooth rows: posterior dentary teeth lie level with, or behind, posterior maxillary teeth (0); posterior dentary teeth lie anterior to posterior maxillary teeth (1).
15. Numbers of premaxillary teeth on each side: seven or fewer (0); more than seven (1).
16. Pterygoid flange teeth; present (0); absent (1).

Postcranial characters:

17. Numbers of cervical vertebrae: seven or fewer (0); more than seven (1).
18. Numbers of cervical vertebrae: fewer than ten (0); ten or more (1).
19. Relative lengths of mid and posterior cervical and dorsal vertebral centra: cervical centra subequal in length to dorsals (0); cervical centra longer than dorsals (1).
20. Cervical neural spine shape: short and tall (0); long and low (1).
21. Ovoid spine-table on top of neural spine: absent (0); present (1).
22. Cervical ribs: short and stout (0); long and slender (1).
23. Neural spines of dorsal vertebrae: short and slender (0); tall and rectangular (1).
24. Trunk intercentra: present (0); absent (1).
25. Attachment of ribs to posterior dorsal vertebrae: not fused (0); fused (1).
26. Scapula shape: tall, and larger than coracoid (0); low, and subequal in size to coracoid (1).
27. Entepicondylar groove or foramen in humerus: present (0); absent (1).
28. Radius length relative to humerus: radius 80–90 per cent. length of humerus (0); radius 40–65 per cent. length of humerus (1).
29. Intermedium in carpus: present (0); absent (1).
30. Centralia in the manus: present (0); absent (1).
31. First distal carpal: present (0); absent (1).
32. Relative lengths of metacarpals 3 and 4: metacarpal 3 shorter than 4 (0); metacarpal 3 equal in length to, or longer than, 4 (1).
33. Relative lengths of metacarpals 1 and 5: shorter than metacarpals 2 and 4 (0); similar in length to metacarpals 2 and 4 (1).
34. Ilium length relative to ischium: longer (0); equal or shorter (1).
35. Preacetabular buttress on ilium: absent, or insignificant (0); well-developed (1).
36. Thyroid foramen in the pelvis: absent (0); present (1).

TABLE 2. (*cont.*)

37. Pubis shape: broad (0); narrow and waisted (1).
38. Femur shape: sigmoidal (0); straight (1).
39. Length of tibia relative to length of femur: tibia shorter than, or subequal to, femur in length (0); tibia longer than femur (1).
40. Foramen in ankle between astragalus and calcaneum: present (0); absent (1).
41. Lateral calcaneal tuber: absent (0); present (1).
42. Pes centrale: present (0); absent (1).
43. First distal tarsal: present (0); absent (1).
44. Second distal tarsal: present (0); absent (1).
45. Relative lengths of metatarsals 4 and 5: metatarsal 4 less than three times length of metatarsal 5 (0); metatarsal 4 more than three times length of metatarsal 5 (1).
46. Metatarsal 5 shape: L-shaped (0); symmetrical and very short (1).
47. Relative length of second phalanx on digit 5 of foot: short (0); long (1).
48. Postcloacal bones: absent (0); present (1).

Malerisaurus has been unclear. Other less well known taxa have been even harder to place. Apart from the practical problems of study of many of these taxa (see below), there seems to be rampant homoplasy within the group.

Materials and methods used in the analysis

Nineteen species of prolacertiforms, in 14 genera, have been described, and these range in age from Late Permian to Late Triassic (Table 1). The material upon which each of these taxa has been established is highly variable, some (e.g. *Protorosaurus*, *Prolacerta*, *Macrocnemus*, *Tanystropheus longobardicus*, *Malerisaurus robinsonae*, *Tanytrachelos*, *Megalancosaurus*) being founded on extensive and relatively complete skeletons, whilst the others are known from less substantial material. The least well known of the listed taxa are *Prolacertoides*, *Tanystropheus antiquus*, *T. fossai* and *Rhombopholis*. The preservation of *Macrocnemus*, *T. longobardicus* and *Tanytrachelos* as compressed fossils makes character determination difficult. The assignment of Mid and Late Triassic material from the Germanic Basin to species of *Macrocnemus* and *Tanystropheus* has also been problematical. In particular, most specimens assigned to *T. antiquus* and *T. conspicuus* are isolated, and there is often little evidence for affinities other than geological age. Wild (1980) may be right in suggesting that *T. conspicuus* is synonymous with *T. longobardicus*, and that *T. antiquus* may belong to another genus.

For the present cladistic analysis, 48 characters that vary among the prolacertiform taxa (Table 2) were tested. Polarities of characters were determined by reference to close outgroups, and three genera were chosen as outgroup taxa for the analyses, namely *Youngina* (Gow 1975), *Rhynchosaurus* (Benton 1990), and *Trilophosaurus* (Gregory 1945). These three taxa were chosen to include a close outgroup of Archosauromorpha (*Youngina*), and two non-prolacertiform archosauromorphs (*Rhynchosaurus*, *Trilophosaurus*). Each is plesiomorphic within its group, and each has been described in some detail. None of these three showed the plesiomorphic state for all characters.

Many of the characters used in previous cladistic analyses of diapsid relationships proved to be ill-defined, hard to code, or redundant. Nonetheless, many of the remaining characters are not entirely satisfactory, falling into a variety of categories: (1) characters based on relative lengths, which could be size-dependent in part (characters 2, 19, 26, 28, 32–34, 39, 45); (2) characters based on absence (?losses) of features, which could have arisen several times independently (characters 10–13, 16); (3) characters based on presences and absences of wrist and ankle bones, which may be prone to individual variation in patterns of ossification (Rieppel 1989), and indeed may be heavily subject to the vagaries of preservation (characters 29–31, 40–44). Despite these problems, it would be wrong to reject all such characters as suspect; it is better simply to regard them as provisionally

TABLE 3. Matrix of binary character-state codes for prolacertiforms. The taxa are listed in Table 1, and the characters in Table 2. Uncertain and unpreserved states are given as '?', and inapplicable characters as 'N'.

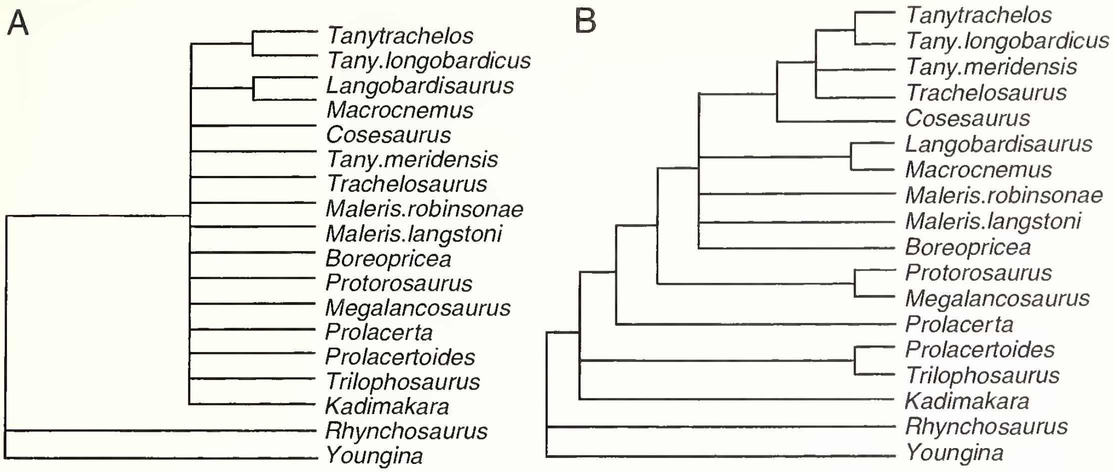
	Skull characters				Postcranial characters						
	1 5	10	15		21	26	31	36	41	46	
Youngina	01000	00100	00010	0	00000	00000	00000	00110	00000	00000	00
Rhynchosaurus	00001	00000	00000	0	00000	00100	00001	10100	01000	00000	00
Trilophosaurus	0001?	?0000	???00	1	00000	01000	01000	00010	00001	00000	00
Megalancosaurus	?????	????0	????0	?	00110	?1?10	1100?	1101?	01001	00001	1?
Protorosaurus	?100?	0?0??	?????	0	10110	11000	00000	?11?0	00001	00010	?0
Boreopricea	?01?0	00001	1001?	?	1011?	?1?00	00???	10???	?0011	0??00	1?
Kadimakara	??000	00010	1001?	?	?????	?????	?????	?????	?????	?????	??
Prolacerta	11000	00001	10010	0	10111	11000	00000	00010	00101	00000	00
Prolacertoides	?1??0	0????	?????	1	?????	?????	?????	?????	?????	?????	??
Trachelosaurus	?????	????0	????0	?	11111	1110?	?????	???1?	?0???	?????	??
Tanystropheus antiquus	?????	?????	?????	?	10111	11???	?????	?????	?????	?????	??
Rhombopholis	?????	?????	?????	?	???11	11???	?????	???1?	?0???	?????	??
Cosesaurus	?????	???10	10?01	?	1011?	11101	?0???	100??	00010	01111	1?
Macrocnemus	0?001	00001	10001	0	10111	11101	10000	00011	10100	00110	?0
Tanystropheus longobardicus	11101	11010	11000	0	11111	11?11	00111	10101	10000	11111	11
Tanystropheus meridensis	00000	01010	N10?0	0	??11?	1????	?????	?????	?????	?????	??
Malerisaurus langstoni	???0?	????0	?????	?	1011?	?1100	00???	??010	000??	?????	??
Malerisaurus robinsonae	00010	11000	00100	0	10111	?1100	00???	??010	00011	11100	??
Tanytrachelos	01010	11110	???00	1	11111	11111	11???	1111?	1010?	11111	11
Tanystropheus fossai	?????	?????	?????	?	???1?	1????	?????	?????	?????	?????	??
Langobardisaurus	0????	?????	????0	?	10110	10?11	100??	00??1	10010	0??10	0?

phylogenetically informative, and to look for further systematic work on prolacertiform anatomy to reveal further details.

All prolacertiform taxa were coded, as far as possible, yielding a character-state data matrix (Table 3). The high proportion of missing data is evident, and this suggests that a search for the most parsimonious tree (MPT) would be unlikely to produce a valid result (Smith 1993; Swofford 1993). The data were analysed by PAUP (version 3.1.1; Swofford 1993), using the exact branch-and-bound algorithm that is guaranteed to find all MPTs. Where more than one MPT was produced, consensus trees were obtained by the strict and Adams techniques.

The missing data are unevenly spread in the matrix (Table 3), with some taxa being complete enough that all, or nearly all, characters could be coded, whilst others, such as *Prolacertoides*, *Tanystropheus antiquus*, *Rhombopholis* and *T. fossai*, exhibited fewer than 10 per cent. of characters. There are two approaches for dealing with large quantities of missing data. One is to cull poorly coded taxa, as was done for example by Fraser and Benton (1989), on the basis that cladistic analyses based on high quantities of missing data are likely to produce poorly resolved, or spurious, phylogenetic trees, and the analytical runs may last for immense amounts of time. The problem with this approach, as pointed out by Wilkinson (1992), is that it makes no distinction between characters that offer useful phylogenetic information and those that do not. Certain characters may be crucial in identifying the position of a taxon with respect to a particular node in the cladogram, and even very poorly coded taxa may reveal such characters. An example is *Prolacertoides*, which has only 8 per cent. of states coded, but the four codable states together cannot be matched with any other taxon.

The second approach, used here, is to apply 'safe deletion rules' (Wilkinson 1992; Wilkinson and



TEXT-FIG. 16. Cladograms showing the relationships of prolacertiforms, based on an analysis of the data matrix in Table 3, using the exact branch-and-bound technique in PAUP 3.1.1. *Youngina*, *Rhynchosaurus* and *Trilophosaurus* are outgroups. Redundant taxa (*Tanystropheus antiquus*, *T. fossai*, *Rhombopholis*) are omitted (see text). Strict (A) and Adams (B) consensus trees of the 450 MPTs. Tree statistics: length, 95; consistency index, 0·474; homoplasy index, 0·526; retention index, 0·561; rescaled consistency index, 0·266.

Benton 1996) that remove redundant information, but retain all phylogenetically informative entries. The sequence of deletions is as follows:

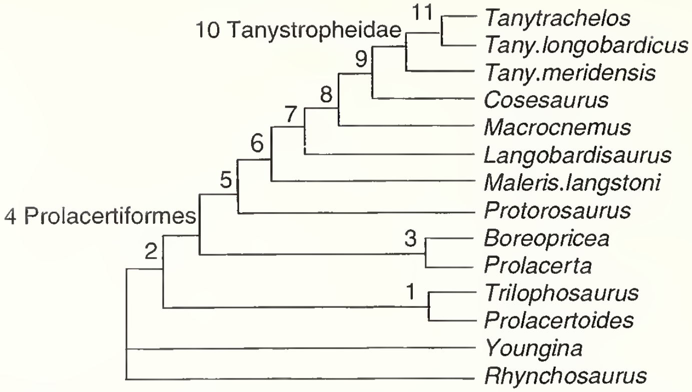
1. Remove all autapomorphies of individual species: there were three of these (characters 13, 29–30).
2. Remove all taxa that contribute nothing to the analysis since they are identical in every known respect to another more substantially coded taxon. Three poorly coded taxa, *Tanystropheus antiquus*, *T. fossai* and *Rhombopholis*, were deleted at this point since the first is identical in coded sites to *Macrocnemus* and other taxa, and the last two are identical, so far as one can tell, to *Prolacerta*, *Macrocnemus* and *Malerisaurus robinsonae*.

Wilkinson (1994) noted that the consensus trees commonly produced by PAUP are unsatisfactory. The strict consensus method is insensitive since it includes only those branching points that are found in all MPTs, and excludes all others, even those that are found in a majority of cases. The Adams consensus method is ambiguous since it includes all nestings that are common to all MPTs, but the topology of the consensus tree does not occur in all MPTs. Hence, Wilkinson (1994) proposed a Reduced Adams Consensus (RAC) method, in which the ambiguity of matching the Adams consensus tree to the MPTs from which it was constructed is obviated. The RAC technique involves selective pruning of taxa that contribute to polytomies until those polytomies disappear. Taxa were pruned according to the rules given by Wilkinson (1994) until a single fully-resolved RAC was obtained, but with the proviso of deleting as few taxa as possible.

Results

The first analysis, with autapomorphies (characters 13, 29–30) and redundant taxa (*Tanystropheus antiquus*, *T. fossai*, *Rhombopholis*) deleted, yielded many MPTs. The strict consensus tree (Text-fig. 16A) shows pairings of *Macrocnemus* + *Langobardisaurus* and *Tanystropheus longobardicus* + *Tanytrachelos*, whilst all other prolacertiforms form an unresolved polytomy with *Trilophosaurus*, a supposed outgroup taxon. *Youngina* and *Rhynchosaurus*, the other two outgroup taxa, form an unresolved trichotomy with the prolacertiform clade.

The Adams consensus trees (Text-fig. 16B) shows the pairings just noted, but is resolved further, with pairings of *Trilophosaurus* + *Prolacertoides*, and *Megalancosaurus* + *Protorosaurus*. The Adams tree also shows a tanystropheid clade, consisting of species of *Tanystropheus* and *Tanytrachelos*,



TEXT-FIG. 17. Reduced Adams Consensus tree produced according to the methods of Wilkinson (1994), by manipulation of the taxa that contribute to polytomies in the original Adams consensus tree (Text-fig. 16B). Additional deleted taxa were *Kadimakara*, *Megalancosaurus*, *Malerisaurus robinsoni* and *Trachelosaurus*. Tree statistics: length, 78; consistency index, 0·577; homoplasy index, 0·423; retention index, 0·629; rescaled consistency index, 0·363. Nodes are numbered, and clade names given for nodes 4 and 10 (see text). Bootstrap values (for 1000 replicates) were less than 50 per cent. for all nodes except 2 (72 per cent.) and 11 (68 per cent.).

with *Trachelosaurus* possibly associated. This clade is nested in a larger clade which includes *Cosesaurus*, *Macrocnemus*, *Langobardisaurus*, *Malerisaurus* and *Boreopricea*.

The Adams consensus tree (Text-fig. 16B) was incompletely resolved, so taxa contributing to the four polytomies were deleted to produce a single fully resolved RAC. The deleted taxa were *Megalancosaurus*, *Kadimakara*, *Trachelosaurus* and *Malerisaurus robinsoni*. The last three taxa contributed to three of the polytomies, and their deletion resolved those nodes. After these deletions, *Megalancosaurus* shifted into a tetratomy with *Protorosaurus*, *Boreopricea*+*Prolacerta*, and a clade of the six tanystropheids and *Macrocnemus*. Deletion of *Megalancosaurus* dissolved that tetratomy, and yielded a single MPT (Text-fig. 17). These procedures produce a RAC tree exhibiting the three properties identified by Wilkinson (1994) as essential: unambiguity, nonredundancy and informativeness.

In the fully resolved cladogram of prolacertiform relationships, the enigmatic *Prolacertoides* appears as the sister group of the outgroup taxon *Trilophosaurus*, as discovered by Evans (1988). *Boreopricea* and *Prolacerta* pair as sister groups and they appear next in the cladogram. The group Prolacertiformes is defined here as *Boreopricea*+*Prolacerta* and *Tanytrachelos*, and all taxa included in the cladogram (Text-fig. 17) between these three. *Protorosaurus* does not appear as the basal prolacertiform. This is surprising since it predates all other members of the clade by at least 10 My, and initial cladistic studies (Benton 1985) suggested that it was the most plesiomorphic form. However, slight variants of the cladogram, for example with *Malerisaurus langstoni* deleted instead of *M. robinsonae*, show *Protorosaurus* as the basal prolacertiform. This confirms Evans' (1988) finding of an unresolved position for this taxon. In the presence of the deleted taxa, *Protorosaurus* is apparently a sister group of the unusual *Megalancosaurus*, and those two appear in a more derived position in the cladogram (Text-fig. 16B) than *Prolacerta*.

The Triassic prolacertiforms are outgroups to the tanystropheid clade (Text-fig. 17). There is no evidence for the pairing of *Prolacerta* and *Macrocnemus* suggested by Benton (1985) and others. The present study does not permit clear division of the Prolacertiformes into subgroups, although a family Tanystropheidae, consisting of the species *Tanystropheus longobardicus* and *T. meridensis*, and *Tanytrachelos*, but excluding '*T.*' *antiquus*, may be recognized. *Boreopricea* here is a basal prolacertiform, but in other solutions, for example with *Malerisaurus langstoni* instead of *M. robinsonae* deleted, *Boreopricea* forms part of the macrocnemid/malerisaurid/tanystropheid clade, an assemblage of generally younger forms, as suggested by Evans (1988).

This cladogram is not uniformly stable. Only two of the nodes (Text-fig. 17) achieve bootstrap values in excess of 50 per cent.: nodes 2 (72 per cent.) and 11 (68 per cent.) This offers some measure of confidence in the reality of the clade containing Prolacertiformes and *Trilophosaurus* (node 2) and the clade consisting of *Tanystropheus longobardicus* and *Tanytrachelos* (node 11). All other branching points in the favoured tree (Text-fig. 17) require further investigation.

The effects of the safe deletion procedures are dramatic. When analyses were performed with the full data set (Table 3), PAUP ran for more than 2 weeks on a Macintosh Power PC, and still did not complete the analysis. With the three redundant taxa, *Tanystropheus antiquus*, *T. fossai* and *Rhombopholis*, deleted, the run lasted for less than 30 minutes (Text-fig. 16), and the final RAC run (Text-fig. 17) lasted for 2·03 seconds.

Clade definitions

Many of the characters used in the analysis have variable distributions across the favoured cladogram (Text-fig. 17), and they do not define any clades uniquely (characters 2–3, 5, 15, 18, 31–35, 38–41, 43, 45). Characters 13, 29 and 30 are autapomorphic. Certain characters define nodes as follows (these are assigned to the smallest possible clade, and some might turn out to define larger clades when more complete material is available).

Node 1: ?4 (pineal foramen reduced or absent; also in *Tanytrachelos*); 16 (pterygoid flange teeth absent; also in *Tanytrachelos*); ?28 (radius 40–65 per cent. length of humerus; also in *Tanytrachelos*).

Node 2: 23 (neural spines of dorsal vertebrae tall and rectangular; reversed in *Langobardisaurus*).

Node 3: ?1 (dorsomedial process of premaxilla reduced; also in *T. longobardicus*); 10 (posterior process of jugal absent; also in *Macrocnemus*); 14 (posterior dentary teeth lie anterior to posterior maxillary teeth).

Node 4: Prolacertiformes: 11 (quadratojugal tall and with reduced anterior process); 17 (more than seven cervical vertebrae); 19 (mid and posterior cervical centra longer than dorsals); 20 (cervical neural spine long and low); 22 (cervical ribs long and slender).

Node 5: 45 (metatarsal 4 more than three times length of metatarsal 5).

Node 6: 24 (trunk intercentra absent).

Node 7: 26 (scapula low and subequal in size to coracoid); 27 (entepicondylar groove or foramen on humerus absent; reversed in *Tanytrachelos*); 36 (thyroid foramen in pelvis); 37 (pubis narrow and waisted; reversed in *Cosesaurus*).

Node 8: 21 (ovoid spine table on top of neural spine; also in *Boreopricea*); 44 (second distal tarsal absent).

Node 9: 9 (ventral ramus of squamosal reduced and cotyle formed for quadrate head); 32 (metacarpal 3 is equal in length to, or longer than, metacarpal 4; also in *Boreopricea*); 43 (first distal tarsal absent); 46 (metatarsal 5 symmetrical and very short); 47 (second phalanx on digit 5 of foot long; also in *Boreopricea*).

Node 10: Tanystropheidae: 7 (postfrontal is a short element lacking processes); 12 (quadratojugal absent).

Node 11: 6 (lacrimal restricted to the orbital rim in lateral view); 18 (ten or more cervical vertebrae); 25 (ribs fused to posterior dorsal vertebrae; also in *Langobardisaurus*); 42 (pes centrale absent); 48 (postcloacal bones present).

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THE FIRST RECORDED TRIGONIOIDOIDEAN BIVALVE FROM EUROPE

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ABSTRACT. The non-marine bivalve superfamily Trigonioidoidea has been considered to be restricted to the Cretaceous of east Asia. It is a distinctive taxon of unionoids, characterized by separated anterior adductor and anterior pedal retractor muscle scars, and an ornament which typically comprises chevron-forming ribs. Well preserved bivalves (with chevron-forming ribs) from the Wealden Group (Barremian and ? Upper Hauterivian, Lower Cretaceous) of the Isle of Wight (southern England), which had previously been assigned to the unionacean unionoids, were re-examined and separated anterior adductor and anterior pedal musculature recognized. The combined character states of musculature, ornament and hinge teeth indicate affinity to the trigonioidid genus *Nippononaia*. However, placement in the established subgenera *N.* (*Nippononaia*) and *N.* (*Eonippononaia*) is precluded by the distinctively larger angle produced by the specimens' chevron ornament. Therefore, a new subgenus, *N.* (*Subnippononaia*), and a new species, *N.* (*S.*) *fordi*, are proposed to accommodate them. This constitutes the first confirmed record of the superfamily Trigonioidoidea outside of east Asia.

THE non-marine bivalve superfamily Trigonioidoidea (?Mid Jurassic to Late Cretaceous) is a distinctive group of unionoids. Representatives of the superfamily are characterized by separated anterior adductor and anterior pedal retractor muscle scars; their distinctive ornament of chevron-forming ribs and (usually) crenulated hinge teeth. The classification used herein follows that of Sha and Fürsich (1993) except that the ending -oidea is used in the superfamilial name. Previous records indicate a distribution restricted mainly to Asia (i.e. the eastern seaboard of the Panthalassan Ocean). Several authors have recorded isolated occurrences of the superfamily from America (Reeside 1957), North Africa (Mongin 1963) and northern South Australia (Ludbrook 1985) but in the absence of the diagnostic musculature, Sha and Fürsich (1993) placed all of these records from outside of Asia in Unionoidea rather than Trigonioidoidea.

Sha (1989) and Sha and Fürsich (1993) recorded bivalves from the Wealden Group (Lower Cretaceous) of the Isle of Wight, off the south coast of England, which have characteristic trigonioidoidean V-shaped ribs on the mid-flank area and reversed V-shaped ribs on both the anterior and posterior areas. The latter authors commented upon the similarity of the hinge structure to that of the Asiatic trigonioidid *Nippononaia* but, since the muscle scars in the Isle of Wight specimens were considered to be feeble and no separation of the anterior pedal retractor scar was observed, they were likewise placed within the superfamily Unionoidea although a similarity to the ancestral trigonioidid *Danlengiconcha* Liu, 1978 (?Mid Jurassic to Early Cretaceous) was noted. Sha and Fürich (1993) further suggested that all non-Asiatic records of Trigonioidoidea should be re-assigned to Unionoidea because, contrary to the diagnostic character state of Trigonioidoidea, all the non-Asiatic taxa which they reviewed showed coalescence of the anterior pedal retractor muscle scar with the anterior adductor muscle scar. Moreover, they suggested that the morphological similarity and contemporaneity of the non-Asiatic forms with the Asiatic trigonioidids *sensu stricto* indicated a common ancestry and parallel evolution, rather than morphological convergence.

We describe here well-preserved material from the Isle of Wight, amongst which an internal mould clearly shows separate anterior pedal and adductor muscle scars, thereby warranting placement in Trigonioidoidea. Using the character states proposed by Sha and Fürsich (1993) for

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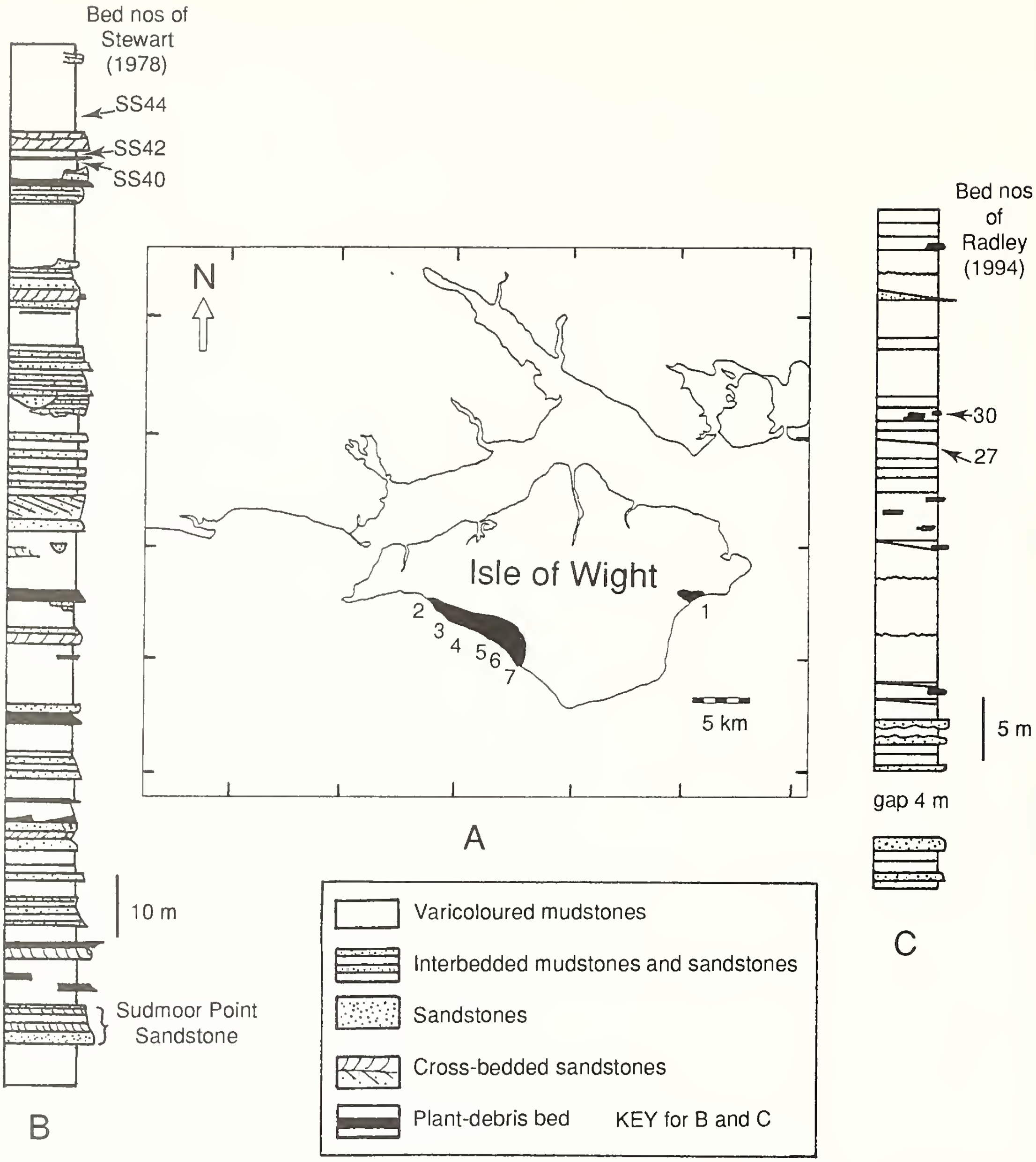


TEXT-FIG. 1. A, outcrop of the Wealden Group (coloured black) on the Isle of Wight, and localities. Key: 1, Yaverland; 2, Compton Bay; 3, Sudmoor Point; 4, Chilton Chine; 5, Brighstone Bay; 6, Cowleaze Chine; 7, Atherfield. B, composite lithological log of the Wessex Formation (Wealden Group) from the south-west coast of the Isle of Wight, after Stewart (1978). C, lithological log of the Wessex Formation (Wealden Group) at Yaverland, Isle of Wight, after Radley (1994).

the classification of this superfamily, we propose the new subgenus *Nippononaia* (*Subnippononaia*), described below, to accommodate this new material.

The Wealden Group of the Isle of Wight (see Text-fig. 1A) comprises the Wessex Formation (formerly known as the Wealden Marls; Daley and Stewart 1979) and the overlying Vectis Formation. The specimens described herein all come from the Wessex Formation which, where exposed, comprises up to 180 m of varicoloured mudstones and sandstones interleaved with plant-debris beds, all of fluvial/overbank origin and deposited in a mosaic of subtropical coastal alluvial environments (Stewart 1978; Stewart *et al.* 1991; Text-fig 1B–C). The formation probably dates wholly from the Barremian (Early Cretaceous) but, based on palynomorphs, possibly also the Late Hauterivian (Allen and Wimbledon 1991). The trigonioidid bivalves occur in both varicoloured overbank mudstones and plant-debris beds throughout the formation. They are preserved as either internal and external moulds (often the internal moulds have smooth listric surfaces along which some internal shear has taken place) or as neomorphic calcite shell replacements. No trigonioidid specimens have been recovered from the Vectis Formation which, for the most part, was deposited under brackish lagoonal conditions and consequently contains a depleted unionoid fauna.

SYSTEMATIC PALAEONTOLOGY

Order UNIONOIDA Stoliczka, 1871
Superfamily TRIGONIOIDOIDEA Cox, 1952 [nom. corr. Kolesnikov, 1977]
Family TRIGONIOIDIDAE Cox, 1952
Subfamily TRIGONIOIDINAE Cox, 1952

Genus NIPPONONAIA Suzuki, 1941
Subgenus SUBNIPPONONAIA subgen. nov.

Derivation of name. From *Nippononaia* Suzuki, 1941, the east Asian genus to which the new subgenus is allied.

Type species. *Nippononaia* (*Subnippononaia*) *fordi* sp. nov.

Diagnosis. Medium-sized bivalve, rectangular/oval in outline, with submedian chevron-forming V-shaped ribs. Both anterior and posterior reversed chevron-forming ribs flank submedian sets. Submedian chevron sets of V-shaped ribs (VA) meet at 30–35°. Distinct and separate anterior pedal muscle scar present.

Remarks. *N.* (*Subnippononaia*) subgen. nov. is distinguished from other subgenera of *Nippononaia* by the larger angle (VA) between the limbs of the submedian V-shaped ribs on the valve flanks. Other recorded subgenera of *Nippononaia* are *N.* (*Nippononaia*) Suzuki, 1941 (VA < 20°) and *N.* (*Eonippononaia*) Guo, 1981 (VA 20–25°); see discussion below.

Nippononaia (*Subnippononaia*) *fordi* sp. nov.

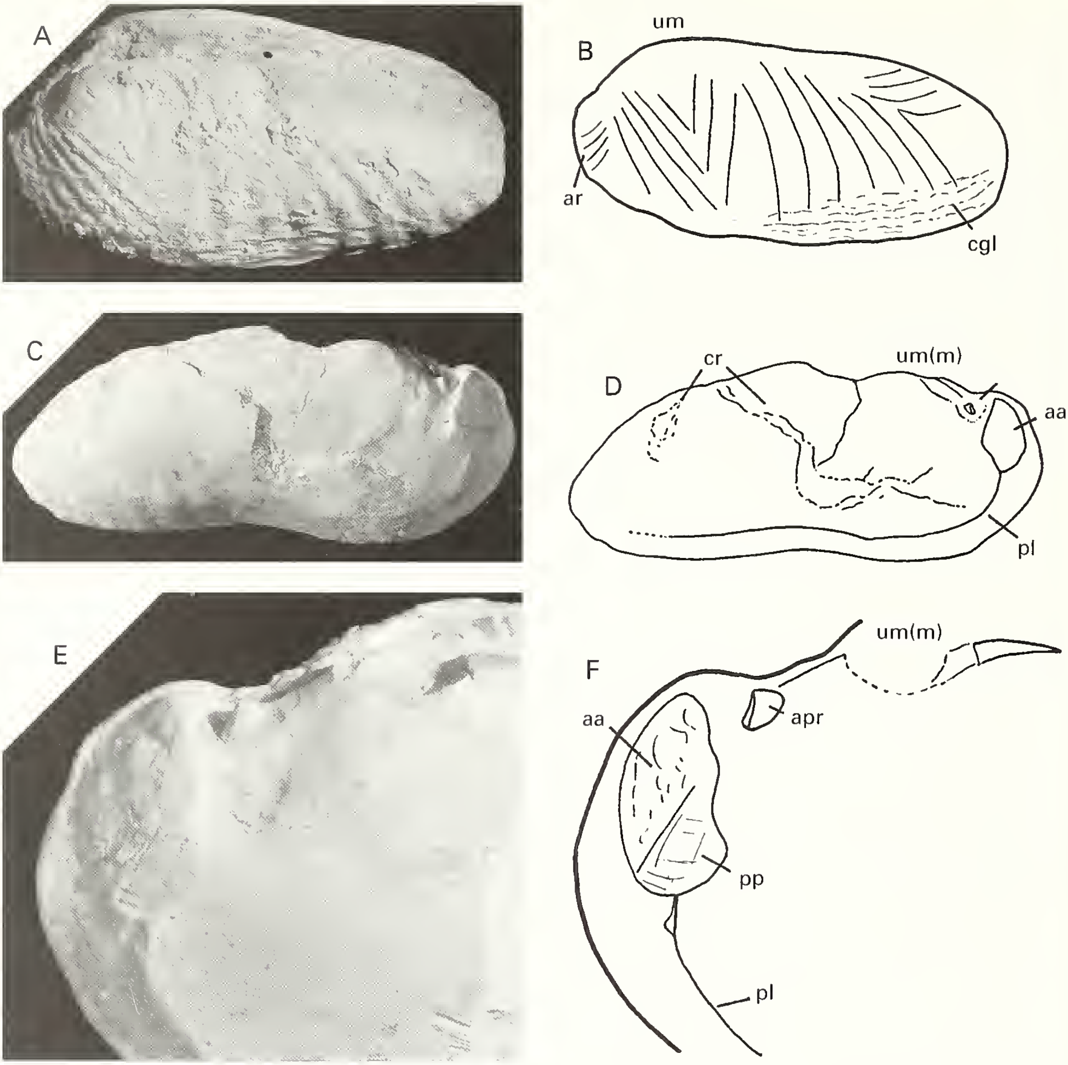
Text-figure 2A–F

1993 *Nippononaia* sp. nov., Barker and Munt, p. 44.

Derivation of name. The late Richard Ford, of Yarmouth, Isle of Wight, in recognition of his contribution to the collective knowledge of that island's palaeontology.

Diagnosis. As for subgenus.

Holotype. Museum of Isle of Wight Geology, Sandown, Isle of Wight, IWCMS: 1995.68 (Text-fig. 2A–B). Neomorphosed calcitic shell showing the external morphology of the two valves but with some slight distortion. From plant debris bed 27 or 30 of Radley (1994), Wessex Formation, Wealden Group, Yaverland foreshore, Isle of Wight.



TEXT-FIG. 2. *Nippononaia* (*Subnippononaia*) *fordi* sp. nov.; Barremian, Wessex Formation, Isle of Wight, England. A–B, IWCMS: 1995.68, holotype, Yaverland. A, left valve, (oblique view). B, left valve, (perpendicular view), indicating the opposed sets of chevron-forming ribs. C–F, IWCMS: 1995.214, paratype, Brighstone Bay. C–D, internal mould of right valve showing musculature. E–F, anterior musculature of left valve. Abbreviations: aa, anterior adductor scar; apr, anterior pedal retractor scar; ar, anterior ribs; cgl, crenulated growth lamellae; cr, areas of crushing; pl, pallial line; pp, pedal protractor scar; um, umbo; um(m), umbonal infill missing. A whitened with ammonium chloride; all photographs taken with an Olympus SZ-PT. A–D, × 2·3; E–F, × 6·5.

Paratypes. IWCMS: 1995.214 (Text-fig. 2C–F). Internal mould showing muscle scars. From plant-debris bed SS40 or SS42 of Stewart (1978), Wessex Formation, Wealden Group, Brighstone Bay, Isle of Wight; MIWG 7321 from a plant-debris bed above the Sudmoor Point Sandstone, *c*. 600 m north-west of Chilton Chine; MIWG 6962 from a shell bed on the foreshore south-east of Chilton Chine; MIWG 21, 7001 and 7342 from plant-debris beds 27 and/or 30 of Radley (1994), Yaverland foreshore and cliff, and MIWG 5816 from a lenticular plant-debris horizon near the top of bed SS44 of Stewart (1978), west of Cowleaze Chine. All specimens are housed in the Museum of Isle of Wight Geology, Sandown, Isle of Wight.

Additional material. Four further specimens (UOP 18/9–12) are housed in the Department of Geology, University of Portsmouth. These were collected from overbank deposits during the excavation of a brachiosaurid dinosaur, *c.* 10 m below the top of the Wessex Formation, north-west of Cowleaze Chine. It has not been possible to locate material reportedly held in the collections of The Natural History Museum, London (Sha 1989 pp. 78–79; Sha and Fürsich 1993, p. 155).

Measurements. Holotype IWCMS 1995.68 (external shell): H (maximum height) = 16·1 mm; L (maximum length) = 30·4 mm; D (anterior end to umbo) = *c.* 8·0 mm; I (inflation of valves) > 8·5 mm (specimen slightly crushed). Paratype IWCMS 1995.214 (internal mould): H = 11·3 mm; L = 26·2 mm; D – not measurable; I > 5·9 mm (specimen slightly crushed).

Description. Medium-sized bivalve, rectangular/oval in shape, with only moderate inflation of the valves. The hinge details are imperfectly known, but a simple pair of corresponding teeth (RV) and sockets (LV) are indicated from silicone-rubber casts taken from an internal mould. Sha and Fürsich (1993) noted that specimens in The Natural History Museum (London) had smooth or very weakly crenulated teeth. There are no submedian teeth. Anterior muscle scars comprise a large anterior adductor conjoined to a large pedal protractor scar. A separate small anterior pedal retractor muscle scar is sited above and behind the adductor scar (see Text-fig. 2E–F). The posterior adductor scar is very weak. The pallial line is strong, but there is no pallial sinus. A high degree of variability occurs in the detail of the valve margins. The following description is based upon the more common morphs. The antero-dorsal margin is initially straight but becomes convex distally. The margin then forms a continuous convexity through the anterior to the antero-ventral margin. The ventral margin may be flat, concave or convex but is always crenulated. The postero-ventral margin is tightly convex. The posterior margin may be flat, shallowly concave or shallowly convex. However, it is distinctively angled to the postero-ventral extremity at *c.* 53°. The posterior margin terminates abruptly at its meeting with the postero-dorsal margin, which is flattened and slopes gently up to the umbo. The postero-dorsal margin forms a slight claustra (i.e. one or two lamellar ridges), carrying an opisthodetic external ligament.

The exterior ornament of the flank comprises five or six sets of chevron-forming ribs. The limbs of the inner sets are straight but the outer sets are arched. These inner (submedian) sets of ribs are centred directly below the umbones and close ventrally. Both the anterior and posterior sets of chevron-forming ribs close dorsally. The main submedian sets have a VA of 30 and 35°. The ornament becomes diffuse and less prominent in mature specimens.

The umbones are slight and set between one-third and one-quarter of the shell length from the anterior margin. A rounded carina is generated behind the umbones and extends to the postero-ventral extremity. The postero-ventral area is concave from behind the umbones to the postero-ventral extreme. The flanks of the shell at the confluence of the chevron sets are also shallowly concave, rising to a gently convex anterior area. The flanks are at best only moderately inflated.

Remarks. N. (*Subnippononaia*) *fordi* displays the clear separation of the anterior adductor and the anterior pedal muscle scars, which is diagnostic of the superfamily Trigonioidoidea (Cox 1952; Sha and Fürich 1993). This is contrary to the observations of Sha and Fürsich (1993), who considered that separate anterior pedal retractor, and anterior adductor scars could not be detected in this taxon or other non-Asiatic bivalves previously attributed to Trigonioidoidea. The earliest description of the superfamily Trigonioidoidea (= Trigonioidacea) was apparently that given by Kolesnikov (1977) but application of Article 36 of the ICZN ascribes the nominal status to Cox, 1952. The distinctive ornament of the shell exterior, comprising submedian and reversed posterior and anterior V-shaped ribs, suggests an affinity with the Asiatic trigonioidid genus *Nippononaia*.

Sha (1989) considered that trigonioidoidean genera can be distinguished by the angle produced by the submedian chevron ribs (VA). With the exception of the genus *Trigonioides* (*Wakinoa*) Ota, 1963, none of the Asiatic genera has VA ranges that coincide with that of the specimens described herein. However, affinity with *Trigonioides* is precluded by the absence of submedian teeth in the new species.

Based upon differences in the angle VA, the genus *Nippononaia* has been subdivided into two subgenera, *N.* (*Nippononaia*) and *N.* (*Eonippononaia*) (see Guo 1981). In *N.* (*Nippononaia*) (type species *N. ryosekiana* Suzuki, 1941, from the Aptian of Japan), the VA is less than 20°, with an ornament consisting of fine, tight chevron ribs. The hinge teeth are also feebly crenulated. *N.* (*Eonippononaia*) Guo, 1981 has a VA of 20–25° and almost smooth hinge teeth.

Recorded non-Asiatic occurrences of bivalves of similar exterior ornament and age include *Nippononaia asinaria* Reeside, 1957 from the Aptian of Colorado. This species is broadly oval in outline, the chevron ribs are stronger than on *N. ryosekiana*, with posterior ribs sub-horizontal. Sha (1989) considered *N. asinaria* to be distinct and he created a new, monospecific genus, *Asinarianaia*, to accommodate it. Additional records noted by Sha (1989) are from Africa (*Subplicatounio flatterensis* Mongin, 1963 – Lower Cretaceous) and from South Australia (*Pledgia eyrensis* Ludbrook, 1985 – Upper Albian or Cenomanian), both with similarities to the trigonioidid genus *Plicatounio*. Sha (1989) and Sha and Fürsich (1993) in referring to these non-Asiatic occurrences of the 'so-called Trigonioididae' were not convinced as to their affinities. However, they considered that their similarity to, and contemporaneity with, the true Asiatic trigonioidids implied the existence of a common ancestor for all these taxa.

Stratigraphical distribution. Wessex Formation, Wealden Group, Barremian and ?Upper Hauterivian, Lower Cretaceous.

FUNCTIONAL MORPHOLOGY OF *SUBNIPPONONAIA*

Within Palaeoheterodonta, chevron ornament is found in the orders Unionoida (all members of Trigonioididae and some members of Unionoidae) and Trigonioida (some members of Trigoniidae) Within Unionoidae, such ornament is commonly found on juvenile specimens and subsequently on the umbonal region of adult specimens which have not suffered dissolution. However, there is a number of genera in which the ornament is continued on mature shells. Amongst these, the Recent African genus *Nyassunio* has tight 'W'-shaped ribs on the posterior of the shell; these become more diffuse and shallower anteriorly. Functional comparison can be made with the trigoniids, notably the Early to Late Jurassic *Vaugonia* (see Stanley 1977) which was adapted to life in mobile substrates, and also the Early Jurassic to Eocene myoid *Goniomya*. Complex ribbing increases the shell surface area which in turn increases the organism's hold in the substrate, thereby reducing the risk of exhumation. Analogy can also be made with the divaricate ornament of the extant lucinid genus *Divaricella* (Stanley 1970) which is used in a saw-like motion during burial. However, this is a disc-like taxon unlike the more elongate *N.* (*Subnippononaia*).

In extant unionoids, the outer shell layer is protected by a periostracum, one of the primary functions of which is to protect the outer shell layers from dissolution, a major problem for molluscs inhabiting calcium carbonate-depleted fresh water. Dissolution pitting can be seen around the umbonal region of the holotype of *N.* (*Subnippononaia*) *fordi*. This indicates that although a periostracum was probably present, the umbonal regions were typically exposed through either microbial degradation, ageing of the proteins of the periostracum (as in extant unionids) or abrasion, thereby allowing dissolution in the oldest parts of the shell.

As *Subnippononaia* lacks a pallial sinus, short siphons are indicated and only shallow burrowing could have been achieved. We can infer that the mode of life of *N.* (*Subnippononaia*) *fordi* was similar to that of trigoniids and unionoideans, namely infaunal and mobile, but lying largely concealed in the substrate. However, sedimentological and biostratinomic settings indicate that *N.* (*Subnippononaia*) *fordi* mainly, or exclusively, inhabited floodplain lakes and ponds. It was never very abundant, and occurs as both articulated specimens and as isolated valves.

ASSOCIATED WEALDEN FAUNA

Amongst the Mollusca, only viviparid and physid gastropods, and unionid bivalves have been recorded from the Wessex Formation (Radley 1994). Morter (1978) suggested that the British Barremian unionids may be conspecific with those described by Cornuel (1874) from the Wassay region of France. Ancestry from stratigraphically lower horizons is unlikely since there is only limited faunal continuity between the pre-Barremian Weald Clay and Hastings Beds of the Weald Sub-basin, and the stratigraphically higher and geographically separated Wessex Formation. The 'gull-wing' ornamented unionid *Protelliptio gualteri* (J. de C. Sowerby, 1836) which ranges from the Weald Clay into the Wessex Formation may be the only species to do so, although *Unio compressus* (J. de C. Sowerby, 1828), found in the Hastings Beds, reoccurs as a Lazarus taxon in the Vectis Formation (late Barremian–early Aptian). *Unio elongata* Cornuel, 1874 and *U. cornueliana* (d'Orbigny, 1850) can be confirmed as 'Wassay' species which are found in the Wessex Formation. *Unio valdensis* (Mantell, 1844) was re-examined by Mongin (1961) and placed in the genus *Margaritifera* but later returned to *Unio* (Mongin 1963). *Unio valdensis* is distributed throughout the Barremian of Europe and into North Africa.

PALAEOBIOGEOGRAPHY

Trigonioidoidea as recognized by Sha and Fürsich (1993) comprises 17 genera whose present day distribution encompasses Japan, South Korea, Mongolia, China, Laos, Thailand and the central Asian part of the former USSR. The oldest records (Middle to Upper Jurassic) are from China and belong to the subfamily Martinsonelliinae. The earliest record for the subfamily Trigonioidinae (which includes the genus *Nippononaia*) is from the Upper Jurassic of Japan (Matsukawa and Ido 1993). To judge by the recorded occurrences, the superfamily Trigonioidoidea attained a wider geographical distribution (mainly southward) during the Early Cretaceous. For example, in south-west China, *N.* (*Eonippononaia*) occurs in the Berriasian to Barremian; during the Aptian and Albian, *N.* (*Nippononaia*) occurs as part of the *Trigonoides-Plicatounio-Nippononaia* fauna (Ma 1994). The superfamily is also found in the Early Cretaceous (undivided) Middle Khorat Subgroup of eastern Thailand (Kobayashi 1984). Given the morphological similarity of *N.* (*Subnippononaia*) to *N.* (*Eonippononaia*) and their relationship in time, the documented southward migration of the group must also include a rapid westward migration and subsequent isolation of the stock in Europe giving rise to *N.* (*Subnippononaia*) by the Barremian. If *Nippononaia asinaria* Reeside, 1957 can be demonstrated to be trigonioidoidean (as yet, its musculature is unknown), a continued westward migration with subsequent allopatric speciation could have produced the Aptian taxon in Colorado.

During the Early Cretaceous, southern England comprised two sedimentary sub-basins, the Wessex and the Weald, both of which were sites of essentially non-marine 'Purbeck–Wealden' deposition from the Berriasian to the Barremian or Early Aptian (Allen and Wimbledon 1991). *Nippononaia* (*Subnippononaia*) *fordi* is recorded solely from the Wessex Sub-basin, within the higher (Barremian and ?Late Hauterivian) part of the alluvial Wessex Formation. The new taxon is found associated with other geographically more widespread unionoid species, mainly found in France but in one case (*Unio valdensis*) into North Africa (Mongin 1961). Like most freshwater bivalves, unionoids would have been restricted to long-standing and permanent bodies of water. Such bodies of water suitable for the migration of freshwater bivalves must have existed between at least Europe, North Africa and South-east Asia and possibly North America. It is unknown whether fossil unionoids reproduced in a similar manner to extant representatives, namely via glochid larvae requiring obligate fish hosts.

CONCLUSIONS

By the early Cretaceous, a wider distribution than previously recognized had been achieved within the superfamily Trigonioidacea. *Nippononaia* (*Subnippononaia*) *fordi* subgen. et sp. nov., described herein, represents the first record of the superfamily Trigonioidoidea from Europe. *Nippononaia*

(*Subnippononaia*) *fordi* from the Barremian (and ?Late Hauterivian) Wessex Formation of the Isle of Wight is found associated with other unionoid species which extend into France and North Africa. This confirmation of the existence of trigonioidid bivalves outside of east Asia clearly necessitates the re-examination of previous non-Asiatic records from North America, Africa and Australia.

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LATE ORDOVICIAN GRAPTOLITES FROM THE NORTH AMERICAN MIDCONTINENT

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ABSTRACT. Although relatively uncommon in the dominantly calcareous upper Ordovician (Cincinnatian) sedimentary rocks in the North American Midcontinent, graptolites have been recorded from many localities during some 150 years of study. A revision of these faunas, the first general review for half a century, is based on new collections from about 20 key localities as well as on museum specimens. These epicontinental faunas are locally rich in individuals but diversity is low, with only about 20 species recognized herein. Widely recorded, but poorly known and commonly misidentified species, such as *Amplexograptus manitoulinensis* (Caley), *Climacograptus putillus* (Hall) and *Rectograptus peosta* (Hall), are redescribed based on type and topotype material. Some stratigraphically important species, such as *Climacograptus nevadensis* Carter, *Dicellograptus complanatus* Lapworth, and *D. gravis* Keble and Harris, previously unknown from the Midcontinent, are also described along with a few other, more common and well-known species. Several Cincinnatian species are shown to have a previously unrecognized biostratigraphical utility. The graptolite zonal succession recognized by Riva in New York–Quebec can be applied readily to many of the sections studied, and a bipartite subdivision of the *A. manitoulinensis* Biozone appears feasible. Conodonts make it possible not only to classify the sections in terms of Atlantic conodont zones but also to establish ties between graptolite and conodont zones. Most Midcontinent graptolite faunas represent the endemic Laurentian Biofacies that differs significantly from the cosmopolitan Oceanic Biofacies of marginal areas of Laurentia. Overlap between these in Oklahoma allows correlation between separate graptolite zonal schemes. The new biostratigraphical data are used for regional correlations and for assessment of sequence stratigraphy.

FOR well over a century (since Hall 1865), geologists have collected and studied graptolites from the Cincinnatian (upper Ordovician) strata of the North American Midcontinent. Despite the long history of these studies, several important aspects of these graptolites, including the taxonomy of many species and their precise stratigraphical ranges, have remained very poorly known. This has prevented not only modern assessments of the regional palaeobiogeography and palaeoecology of these faunas but also the use of some species as reliable guide fossils. Early studies, such as those by Ruedemann (1908, 1947), Ruedemann and Decker (1934), and Decker (1935*a*, 1935*b*), documented large and apparently diverse faunas from the south-central United States. Although representing the standard of North American graptolite research during the first half of this century, these works lack several important aspects of modern taxonomic approach, such as extensive use of proximal end development for classification (Mitchell 1987). Furthermore, little, if any, attention was paid to the effects of preservation on the morphology of the rhabdosome, and no attempts were made to isolate specimens from the matrix by means of acid treatment. More recent work on upper Ordovician graptolites in the north-central Midcontinent is limited to descriptions of faunas from single outcrops (e.g. Werner and Echols 1958; Berry 1966, 1970; Berry and Marshall 1971) and of the ultrastructure of a few taxa (Berry and Takagi 1970, 1971; Herr 1971; Berry 1974). More detailed studies have been carried out in the Cincinnatian type area in the vicinity of Cincinnati in Ohio, Kentucky, and Indiana (Text-fig. 1), by Erdtmann and Moor (1973), Bergström and Mitchell (1986, 1990, 1992), Mitchell and Bergström (1977, 1991), Crowther and Bergström (1980), and Goldman and Mitchell (1991), and in the middle and upper Ordovician of Oklahoma (Arbuckle and Ouachita Mountains) from which Finney (1986) provided important information on the stratigraphical distribution of graptolites.

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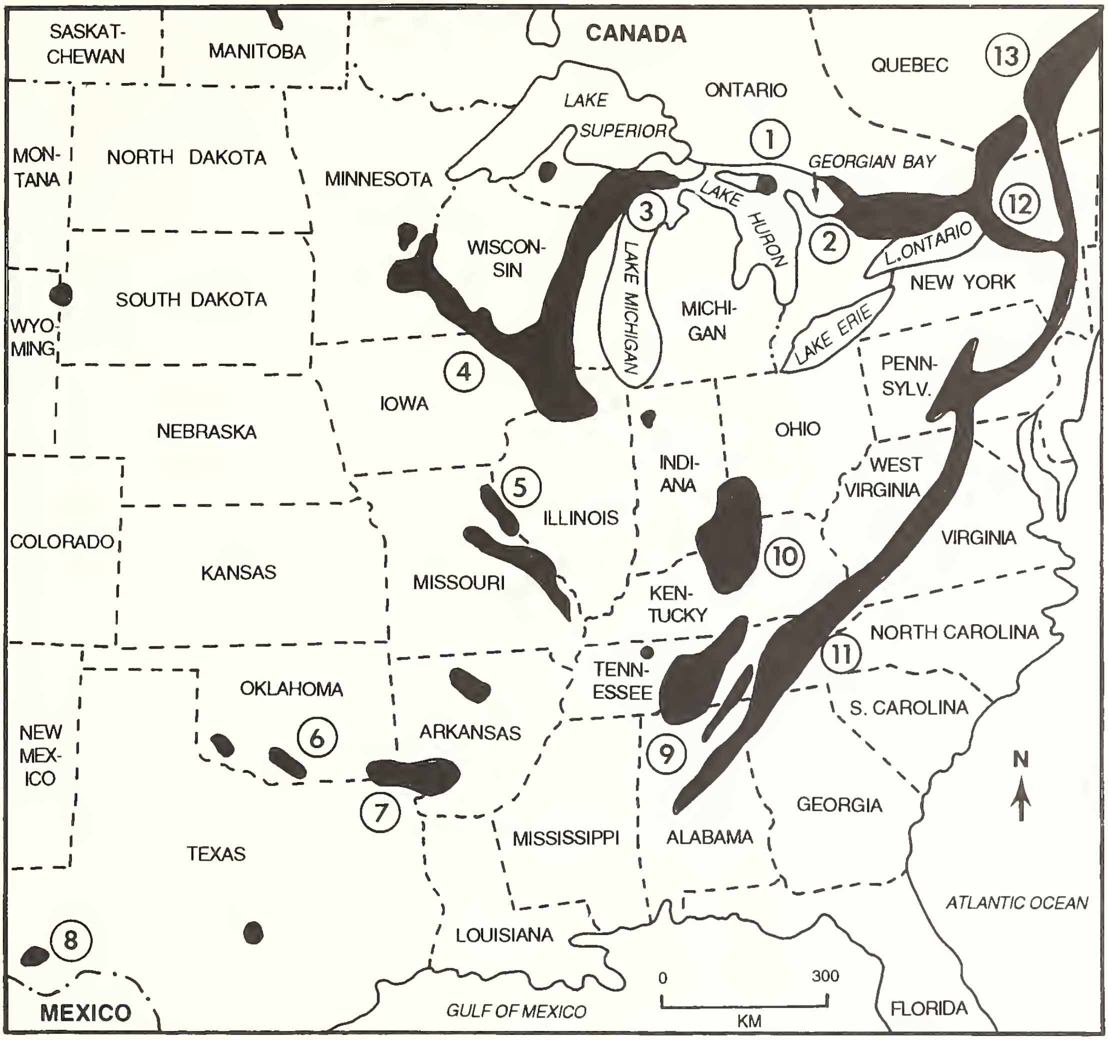
The present paper presents a comprehensive re-examination of the upper Ordovician graptoloid faunas of the North American Midcontinent, and is the first to be attempted for the whole of this vast region since that of Ruedemann (1947). Although Ruedemann's monograph on North American graptolites is still an indispensible source of information, it is out of date in several respects, especially taxonomically. Our investigation covers all the principal upper Ordovician outcrop areas from the Appalachians in the east to the Mississippi Valley in the west, and from Oklahoma in the south to southern Ontario in the north (Text-fig. 1). No upper Ordovician graptolites are known from the Nashville Dome in central Tennessee. We have not investigated the relatively few upper Ordovician graptolites described from the Canadian Arctic (Melchin 1987) nor those from Quebec and New York (Riva 1969, 1974, 1988) which are reasonably well known. Those of the Marathon uplift in western Texas were described by Goldman *et al.* (1995).

The importance of an investigation such as this one lies well beyond the need of a taxonomic reappraisal. For instance, the dark graptolitic shales, and associated carbonate rocks that were deposited over much of the Midcontinent during the late Ordovician (Bergström and Mitchell 1992) record a widespread transgressive event, which has been regarded as eustatic (see, for instance, Witzke and Kolata 1988), and it is marked as a prominent inflection point on numerous sea-level curves based on outcrop studies of North American upper Ordovician successions (see, for instance, Sloan, *in* Sloan 1987; Witzke and Kolata 1988; Johnson 1989; Ross and Ross 1992; Raatz and Ludvigson 1996; Witzke and Bunker 1996). Clearly, an accurate biostratigraphical framework is essential for reconstructing the timing and synchroneity of late Ordovician sea-level fluctuations but thus far, little up-to-date graptolite biostratigraphical information has been available from the Midcontinent for precise correlation of its many key sections, both regionally and internationally. Also, detailed geological data on the upper Ordovician graptolitiferous shales have the potential to be of economic importance because these strata are thought to be the source rocks of the many significant hydrocarbon occurrences in the upper middle Ordovician of the North American Midcontinent.

Conodonts have proved very useful for local and regional correlation of upper Ordovician rocks in the North American Midcontinent, and extensive biostratigraphical work using these fossils have been carried out since the 1950s (for summaries, see Sweet 1979*a*, 1979*b*). However, several regional correlation problems have not been satisfactorily resolved. We have collected samples for conodont work at key graptolite localities, and wherever possible, also assessed published data, in several cases based on restudy of collections made by previous workers. Considerable effort has been devoted to establishing direct ties between the graptolite and conodont biostratigraphy because an integrated graptolite-conodont biostratigraphy clearly has potential of providing a considerably greater stratigraphical resolution than those based on either of these index fossil groups alone (Bergström 1986).

MATERIALS AND METHODS

The present study is based on examination of many museum and some private graptolite collections as well as extensive new collections made at about 20 key localities. Virtually all significant upper Ordovician graptolite occurrences in the Midcontinent are included, and thousands of specimens have been examined. Locality information is given in the Appendix, and graptolite species identified from 20 stratigraphical sections are listed in Table 1. For the graptolite biostratigraphical classification we follow, with one exception (eastern Oklahoma), the zonal scheme advocated by Riva (1969, 1974) that can be applied readily to the study sections. Conodont-bearing units are classified in Atlantic conodont zones (Bergström 1986). The more detailed conodont zonal scheme introduced by Sweet (1984), which is based on graphic correlation, is currently not applicable to the sections discussed herein because only one of these is included in his network of correlated sections. Finally, the term 'upper Ordovician' is used herein for the stratigraphical interval of the Cincinnatian Series following long established practice in North America (Ross *et al.* 1982).



TEXT-FIG. 1. Distribution of Ordovician outcrop areas (black) discussed in the text. Key to areas: 1, Manitoulin Island, Ontario; 2, south shore of Georgian Bay, Ontario; 3, Upper Peninsula of Michigan; 4, Upper Mississippi Valley, Minnesota, Wisconsin, Illinois, and Iowa; 5, eastern and south-eastern Missouri; 6, Arbuckle Mountains, Oklahoma; 7, Ouachita Mountains, Oklahoma and Arkansas; 8, Marathon region, West Texas; 9, Nashville Dome, central Tennessee; 10, Cincinnati region, Ohio, Indiana, and Kentucky; 11, Appalachians, Alabama to Vermont; 12, Mohawk Valley and adjacent areas, New York State; 13, Saint Lawrence Lowlands, Quebec. The North American Midcontinent extends from just west of the Appalachians to beyond the left margin of the map. Note that some coastal state names are omitted because of lack of space.

BIOSTRATIGRAPHY

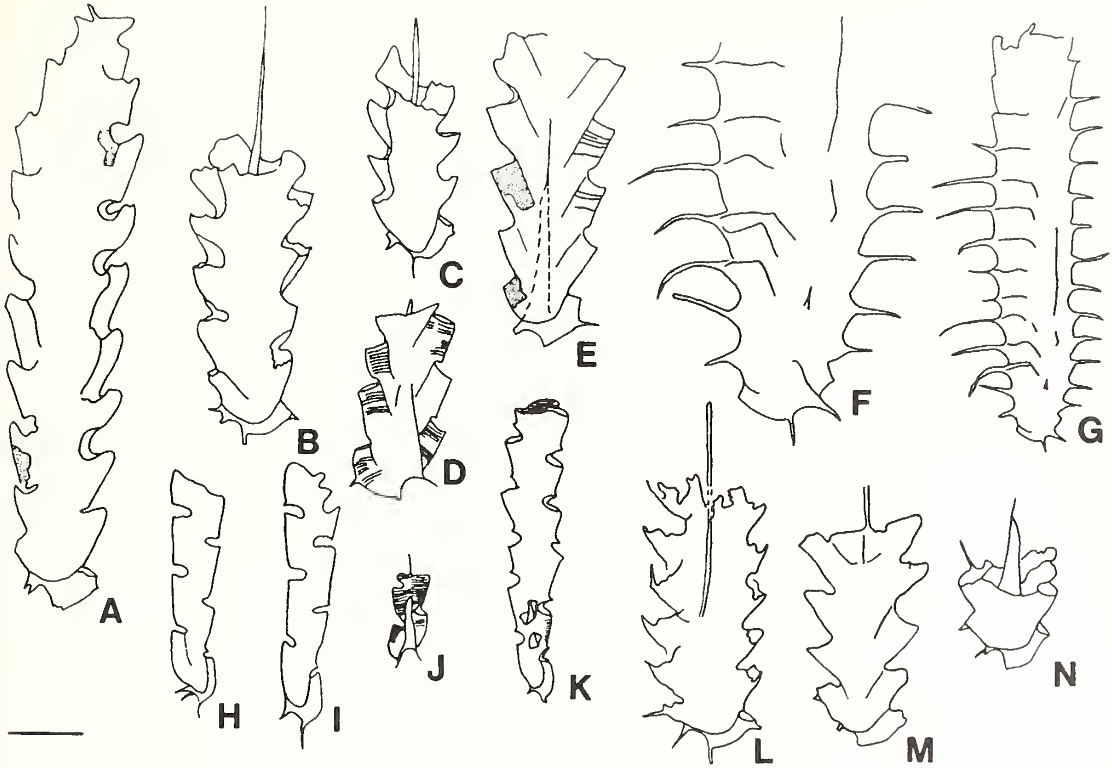
Manitoulin Island and Georgian Bay, Ontario

Graptolite biostratigraphy. An important succession of upper Ordovician graptolite-bearing rocks, including the Collingwood Member of the Lindsay Formation and the Blue Mountain and Georgian Bay formations, occurs in Ontario (Text-fig. 1, areas 1 and 2; Russell and Telford 1983; Lehmann *et al.* 1995). Caley (1936) published descriptions of some upper Ordovician graptolites from outcrops on Manitoulin Island and Senior (1991) recorded several species from exposures and cores of coeval strata along the south shore of Georgian Bay. On Manitoulin Island, the Collingwood Member is a grey-weathering, black, non-calcareous shale (in contrast with its carbonate-rich equivalent along the south shore of Georgian Bay) that contains (Text-fig. 2) numerous specimens of *Geniculograptus typicalis magnificus* (Twenhofel), '*Glyptograptus*' *lorrainensis* (Ruedemann), *Orthograptus quadrimucronatus* (Hall), *O. spinigerus* (Elles and Wood), and *Rectograptus amplexicaulis* (Hall), an association indicating the upper part of the *G. pygmaeus* Biozone. A similar association, which also includes *G. typicalis*, was recorded by Senior (1991) from the Collingwood Member in exposures at Craigleith near the south shore of Georgian Bay.

The overlying Blue Mountain Formation is a blue-grey to brownish shale, a large part of which weathers to clay, with subordinate calcarenitic and calcilutitic beds. Although graptolites are locally abundant, diversity is low, with only *Amplexograptus manitoulinensis* (Caley) (Text-fig. 5A–I), *Orthograptus quadrimucronatus*, and *O. eucharis* being present. The first appears about 10 m above the base of the Blue Mountain Formation at its type locality along the creek on both sides of Highway 6, about 5 km south of Little Current, and is the only graptolite present through the next 2–3 m of section. It has a similar range in drill-cores from the Little Current area. It has not been found at higher levels in the Blue Mountain Formation, nor in the overlying Georgian Bay Formation on Manitoulin Island. Senior (1991) reported the species as abundant in a 10 m interval in the uppermost Blue Mountain Formation, and a questionable specimen about 20 m above the base of the formation, in a drillcore from the Campertown area near the south shore of Georgian Bay. This species has a slightly longer, although still short, range in the St Lawrence Lowland and Anticosti Island successions described by Riva (1969; for the St Lawrence Lowland sections, see also Walters 1977 and Walters *et al.* 1982) and in the Arbuckle Mountains of Oklahoma, where it appears in the middle part of the Viola Springs Formation (Finney 1986). The occurrences in eastern North America and in Oklahoma appear to be nearly synchronous with respect to the stratigraphical range of other important index species such as *Climacograptus putillus* (Hall), *Dicellograptus complanatus* Lapworth, *Geniculograptus pygmaeus* (Ruedemann), and *G. typicalis magnificus*. The short stratigraphical range of *A. manitoulinensis* in these sections may well reflect the total range of this species and not only its local acme. However, in view of the very short range of this species at its type locality, and the lack of close graptolite control of the upper and lower boundaries of the *A. manitoulinensis* Biozone on Manitoulin Island, a reference locality of this biozone will have to be selected elsewhere. Because *A. manitoulinensis* has not been found in the lowermost Blue Mountain Formation on Manitoulin Island and south of Georgian Bay, we tentatively refer that interval to the uppermost *C. pygmaeus* Biozone.

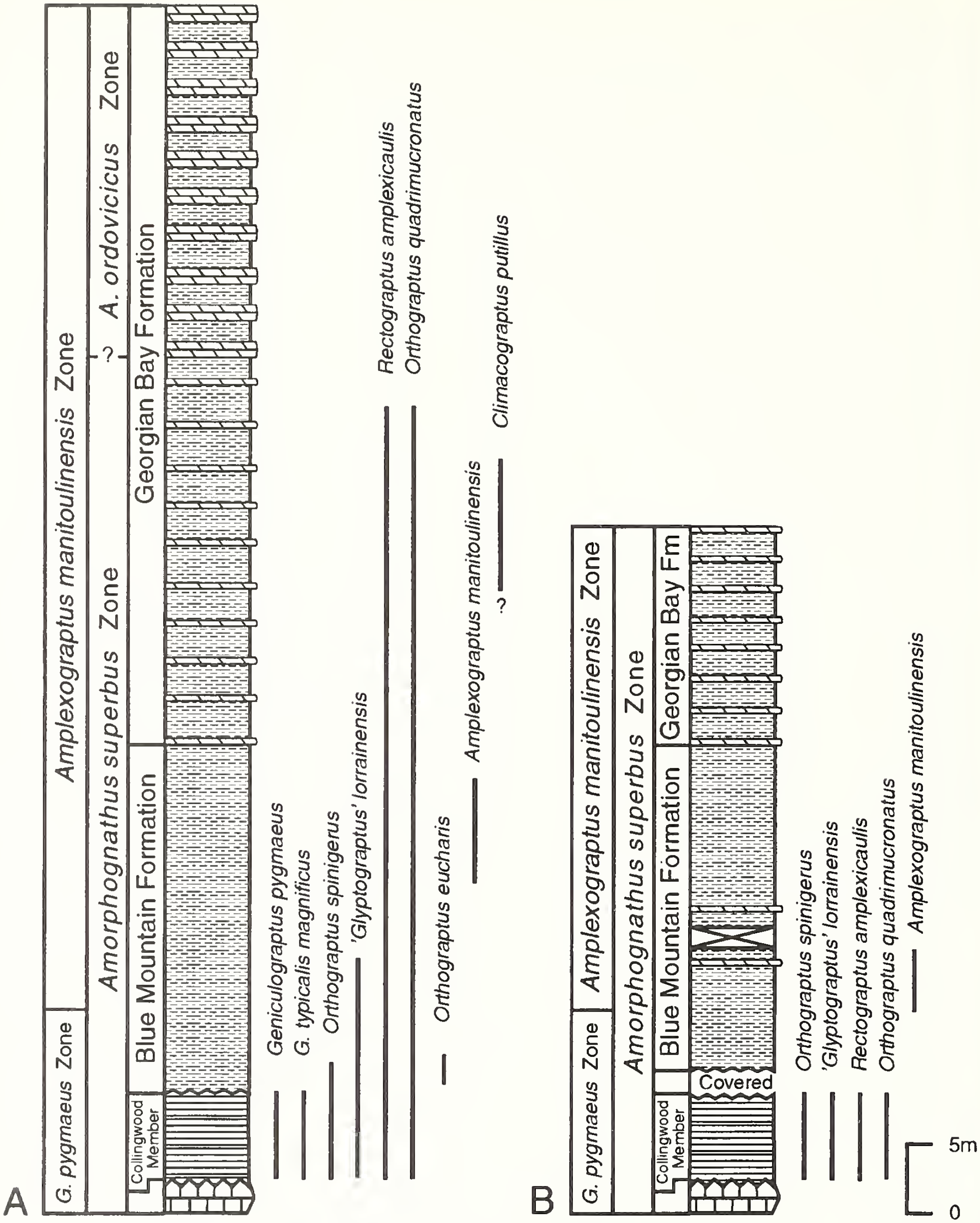
On Manitoulin Island, the Georgian Bay Formation comprises a thick sequence of interbedded grey shales and limestones that grade upward into dominantly carbonates. The contact with the underlying Blue Mountain Formation is drawn at the level of the lowermost bed of a conspicuous group of 20–60 mm thick limestone beds (Johnson *et al.* 1983). The lower portion of the Georgian Bay Formation at the shore exposure at Gorrel Point has yielded *C. putillus* (Text-fig. 5J–Z), *O. quadrimucronatus*, and *R. amplexicaulis* (Text-fig. 3). *Diplograptus similis* and *Diplograptus foliaceus gorrelensis* described by Caley (1936, pp. 66–68) from Manitoulin Island are clearly junior synonyms of *R. amplexicaulis* and *O. quadrimucronatus*, respectively. The succession of graptolite species on Manitoulin Island resembles that in coeval strata in the St Lawrence Lowlands and in the subsurface of Anticosti Island (Riva 1969, 1974; Walters 1977; Walters *et al.* 1982), where *A. manitoulinensis* is likewise succeeded by *C. putillus* (*Pseudoclimacograptus* cf. *P. clevensis* of Riva 1969, 1974; *P.* aff. *clevensis* of Walters 1977) in the upper portion of the *A. manitoulinensis* Biozone below the level of appearance of *D. complanatus*. Based on this, we interpret the upper Blue Mountain and lower Georgian Bay formations to represent the *A. manitoulinensis* Biozone. No graptolites diagnostic of Riva's (1969, 1974) *D. complanatus* Biozone are yet known from Manitoulin Island.

Conodont biostratigraphy. The Collingwood Member has not yet yielded biostratigraphically diagnostic conodonts. Calcareous interbeds in the graptolite-bearing shales of the lower part of the



TEXT-FIG. 2. Graptolites of the *Geniculograptus pygmaeus* Zone. A–C, '*Glyptograptus*' *lorrainensis* (Ruedemann); OSU 48501–48503. D–E, *Rectograptus amplexicaulis* (Hall); OSU 48504–48505. F–G, *Orthograptus spinigerus* (Elles and Wood); OSU 48506. All from the Collingwood Member, Lindsay Formation; Sheguindah, Manitoulin Island, Ontario. H–K, *Geniculograptus pygmaeus* (Ruedemann); OSU 48507–48510; H–I, Collingwood Member, Lindsay Formation; Craigleith Provincial Park, Ontario. J–K, isolated uncompressed specimens; Groos Quarry Formation; Bichler Quarry, Groos, Michigan. L–N, *Orthograptus quadrimucronatus* (Hall); OSU 48511–45512; Collingwood Member, Lindsay Formation; Manitoulin Island, Ontario. Scale bar represents 1 mm (except for fig. G where it represents 2 mm).

Blue Mountain Formation (Text-fig. 3) along the creek near Highway 6 about 5 km south of Little Current contain, along with other conodont species, *Amorphognathus superbus* (Rhodes), *Aphelognathus politus* (Hinde), *Icriodella superba* Rhodes and *Periodon grandis* (Ethington). Essentially the same species association, which clearly represents the *A. superbus* Biozone, ranges upward through the lower 40 m of the Georgian Bay Formation. The precise level of the top of the *A. superbus* Biozone has not yet been established, because the index of the overlying *A. ordovicicus* Biozone, *A. ordovicicus* Branson and Mehl, has not yet been recovered from Manitoulin Island. However, based on the relations between the conodont biostratigraphy and the ranges of shelly macrofossils elsewhere in the Midcontinent, this zonal boundary is likely to be in a poorly exposed interval about 50–60 m above the base of the Georgian Bay Formation. The Manitoulin Island succession is important in terms of conodont-graptolite zone relations in providing direct evidence that the upper part of the *A. superbus* Biozone is coeval with the lower part of the *A. manitoulinensis* Biozone at the type locality of the latter graptolite species. It is appropriate to note that our new conodont data from the Blue Mountain and lower Georgian Bay formations are more detailed than, but in general agreement with, those presented by Barnes *et al.* (1978).



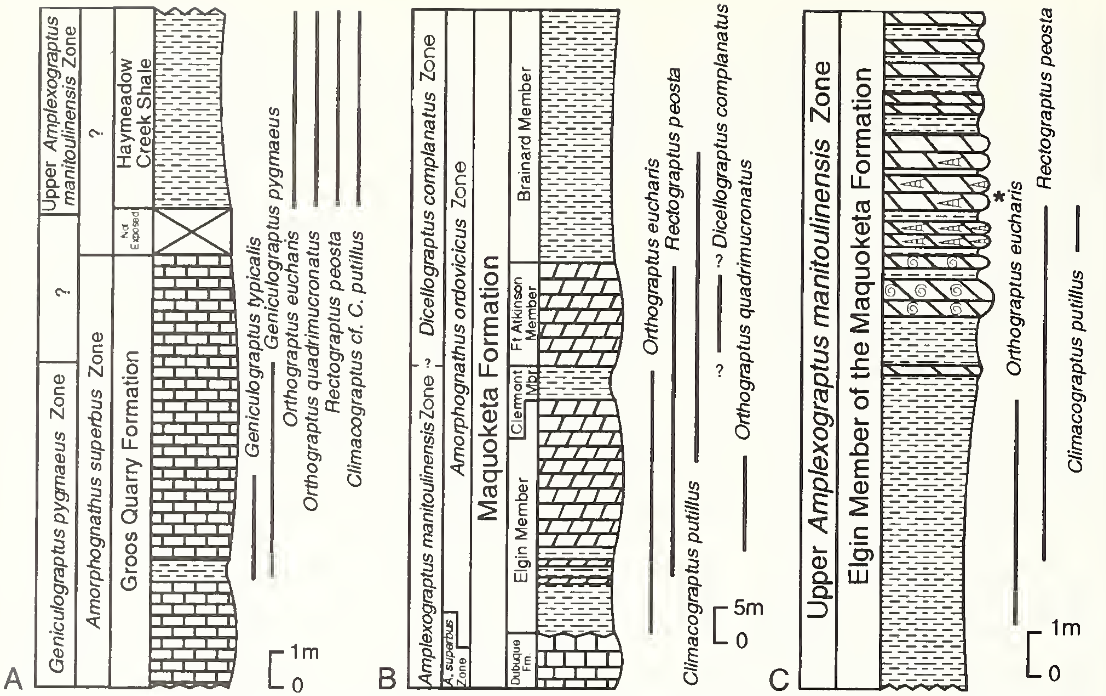
TEXT-FIG. 3. Stratigraphical columns illustrating the upper Ordovician graptolite ranges and graptolite and conodont zones in drill-cores and exposures on Manitoulin Island, Ontario. A, Ontario Geological Survey Core OGS-83-5; from near Little Current. Range of *Climacograptus putillus* is projected from its occurrence in the Gorrel Point section. B, succession at the type locality of *A. manitoulinensis* about 5 km south of Little Current. Near this locality the Collingwood Member rests directly on the Precambrian Lorrain Quartzite.

The Upper Peninsula, Michigan

Outcrops of graptolitic late Ordovician rocks are known from two areas in Delta County, Michigan, in the vicinity of Escanaba and along Haymeadow Creek (Text-fig. 1, area 3). Graptolites were recorded from shaly strata along Haymeadow Creek by Hussey (1952) and the fauna was subsequently discussed in more detail by Berry (1970). These beds, now known as the Haymeadow Creek Shale, have variously been considered to be the uppermost member of the 'Trenton Formation' or 'Trenton Group' (Hussey 1952) or the lowermost member of the Bill's Creek Shale (Hussey 1926). Hussey (1952) noted that the contact between the Haymeadow Creek Shale and the underlying limestone succession is not exposed anywhere in northern Michigan but he believed that only a thin succession of strata was missing at Bichler Quarry at Groos, 8 km north of Escanaba. Hussey (1952) classified the entire limestone succession in Bichler Quarry as the Groos Quarry Member, but Templeton and Willman (1963) referred these rocks to the Dubuque Formation, which they suggested was probably exposed in its entirety there. However, the lithological similarity to the Dubuque Formation of the Upper Mississippi Valley is not striking and, because the Bichler Quarry succession differs substantially also in age from the typical Dubuque Formation, we believe the latter formational designation is inappropriate. Following Ross *et al.* (1982), we prefer to use the term Groos Quarry Formation for these strata that are likely to be of post-'Trenton' age.

Graptolite biostratigraphy. Limestones from the upper part of the Groos Quarry Formation at Bichler Quarry (Text-fig. 2J–K) yielded three-dimensional specimens of *Geniculograptus pygmaeus* and *G. typicalis*, suggesting a *G. pygmaeus* Biozone age. At its type locality along Haymeadow Creek, the Haymeadow Creek Shale is a grey-weathering, chocolate-brown shale with sparse graptolites. A re-assessment of its graptolite fauna based on our new collections and those housed at the University of Michigan shows that it includes only *Climacograptus* cf. *putillus* (*C. pygmaeus* of Berry 1970) (Text-fig. 5AA), *Orthograptus eucharis*, *O. quadrimucronatus*, and *Rectograptus peosta*, a species association indicating the *A. manitoulinensis* Biozone (Text-fig. 4A). The lack of exposure of the contact between the two units prevents us from determining whether a hiatus exists at that level. Although it is possible that the graptolites from Bichler Quarry represent a low diversity fauna coeval with that in the Collingwood Member of Ontario (Senior 1991), the Haymeadow Creek section does not contain the typical lower *A. manitoulinensis* Biozone fauna such as is present in the Blue Mountain Formation of Manitoulin Island and in the Lorraine Group siltstones and shales of New York (Ruedemann 1925, 1947) and Quebec (Riva 1969, 1974; Walters 1977; Walters *et al.* 1982). It is also of interest to note that Ruedemann and Ehlers (1924) recorded *Geniculograptus pygmaeus* and a variety of *R. amplexicaulis* from slabs of shale and limestone in till near Newberry, Lucas County, about 140 km north-east of Escanaba. They interpreted these rocks as coeval with the Collingwood Formation (or Member) in southern Ontario, a unit which has been widely identified in the subsurface of the Michigan Basin (Hiatt and Nordeng 1985). Berry (1970) indicated that the Newberry rocks, which are not known to crop out *in situ*, were coeval with the Haymeadow Creek Shale (*A. manitoulinensis* Biozone) but we interpret them to be older than this unit at its type locality and to represent the *C. pygmaeus* Biozone. The Newberry rocks may be equivalent to the Groos Quarry Formation, or possibly, to the unexposed lowermost portion of the Haymeadow Creek Shale.

Conodont biostratigraphy. No conodonts are yet known from the type section of the Haymeadow Creek Shale but Votaw (1980) recorded specimens from the upper portion of the Bill's Creek Shale in the Escanaba region, including *Icriodella superba*, *Oulodus ulrichi* (Stone and Furnish), *Pseudobelodina vulgaris vulgaris* (Sweet) and *Rhipidognathus symmetricus* Branson, Mehl and Branson. This species association probably represents the *A. ordovicicus* Biozone or, possibly, the uppermost *A. superbus* Biozone. Samples from the Groos Quarry Formation in Bichler Quarry contain a relatively sparse and biostratigraphically poorly diagnostic conodont fauna, including Pa and Pb elements that probably belong to *A. superbus*, along with *Belodina confluens* Sweet,



TEXT-FIG. 4. Stratigraphical columns illustrating the upper Ordovician graptolite species succession, and graptolite and conodont zones on the Upper Peninsula of Michigan and in the Upper Mississippi Valley. A, composite section of Bichler Quarry, Groos, Michigan and the Haymeadow Creek Shale at its type locality. The contact between the Groos Quarry Formation and the overlying Haymeadow Creek Shale is not exposed and the thickness of the unexposed interval is not known. B, composite section of the Maquoketa Formation in north-eastern Iowa (after Witzke and Kolata 1988). Graptolite ranges compiled from cores and exposures in Illinois, Iowa and Minnesota. Occurrence of *D. complanatus* is projected from its inferred stratigraphical position in north-western Illinois. C, graptolite ranges in the Elgin Member of the Maquoketa Formation at Graf, Iowa. This is the type locality of *Climacograptus putillus* (Hall) and *Rectograptus peosta* (Hall). Asterisk indicates upper limit of graptolite collections made during the present investigation.

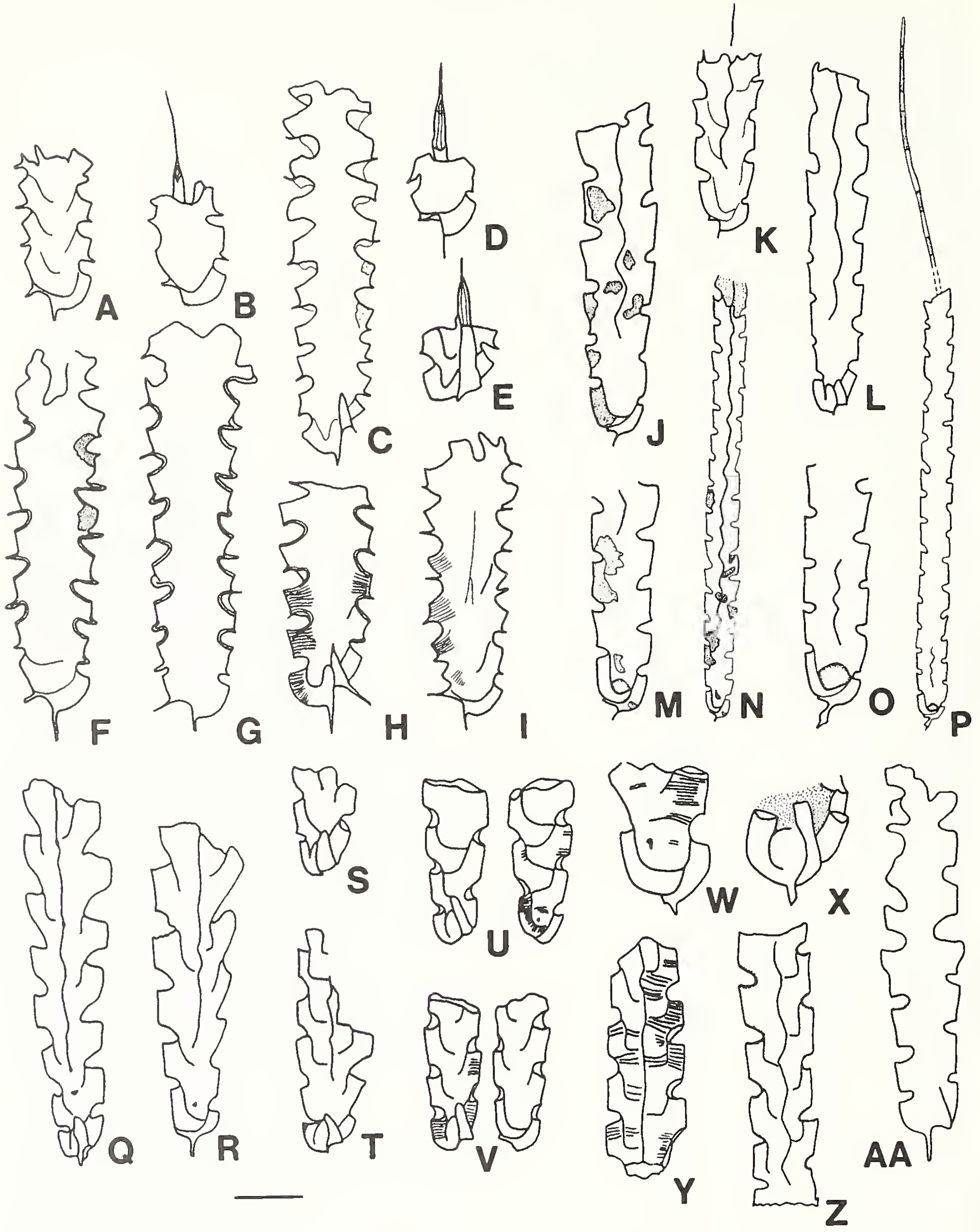
Protopanderodus liripipus Kennedy, Barnes and Uyeno, and *Periodon grandis*. We interpret this fauna as probably representing the *A. superbus* Biozone (Text-fig. 4A). This is in agreement with the graptolite evidence. The graptolite and conodont evidence suggests that the Groos Quarry Formation is probably older than the Dubuque Formation and represents an interval within the middle Edenian to the middle Maysvillian portion of the Cincinnatian standard succession.

Upper Mississippi Valley in Iowa, Minnesota, Wisconsin, Illinois, and Missouri

The Cincinnatian Maquoketa Group (commonly considered to be a formation in Iowa, Wisconsin, and Minnesota and a group in Illinois and Missouri) forms the topmost part of the Ordovician succession in the Upper Mississippi Valley (Text-fig. 1, area 4). The Maquoketa Group (Formation) disconformably overlies the carbonates of the Dubuque Formation in north-western Illinois and east-central Iowa where its dominant lithology is brown graptolite-bearing shale, which grades laterally in all directions into shallow-water trilobite-dominated micrites (Kolata and Graese 1983; Witzke and Kolata 1988). This facies distribution was apparently influenced strongly by the continued development of the east-central Iowa Basin, a prominent depression that was formed during the time of deposition of the underlying Galena Group (Witzke and Kolata 1988). In north-western Illinois the lower part of the Maquoketa Group is classified as the Scales Formation, the basal part of which consists of dark brown fissile shales (the Argo-Fay Bed) that grade upwards into olive-green shales and dolomites (Kolata and Graese 1983). The Scales Formation grades westward and north-westward into the limestones and shales of the Elgin and Clermont members of the Maquoketa Group (Formation) in Iowa, Minnesota, and westernmost Illinois (Text-fig. 4B). There seems to be no disconformity at the top of the Dubuque Formation in southern Minnesota (Leverson *et al.* 1979) where the Dubuque Formation grades into the Elgin Member of the Maquoketa Formation. The Clermont Member is overlain by the Fort Atkinson Member (or Formation) that consists of massive, yellow, cherty dolomites and limestones with interbedded shales. The overlying Brainard Member and the Neda Formation (Kolata and Graese 1983) have yielded no graptolites in outcrops. However, we have seen numerous specimens of *Climacograptus putillus* in the Brainard Member in the Iowa Geological Survey drill cores W7206 (Box 26) and W30792 (Boxes 8 and 9) from central Iowa (Witzke 1987). For comprehensive recent reviews of the stratigraphy of the Maquoketa Group, especially in Illinois, see Kolata and Graese (1983) and Witzke and Kolata (1988).

Graptolite biostratigraphy. In north-eastern Iowa, southern Minnesota, and north-western Illinois (Text-fig. 1) graptolites are most abundant in the brown shale facies of the Elgin Member, although they also occur in the argillaceous carbonates in this member. One of the many graptolite-bearing exposures in the Upper Mississippi Valley deserves special mention, namely the road-cut through the Elgin Member near the Little Maquoketa River at Graf, Iowa (Text-fig. 4C). At this locality, the type locality for *Climacograptus putillus* (Hall, 1865), the Elgin Member consists of a remarkable phosphatic dolomite with countless graptolites and cephalopods. Indeed, near the middle of the exposed succession there are 1–2 m of dolomitic and phosphatic limestone that is a 'graveyard' of the orthoconic nautiloid *Isorthoceras sociale* (Miller and Youngquist). For a detailed recent description of this section, see Witzke and Glenister (1987). The graptolites are very well preserved as three-dimensional phosphatic moulds. This locality was apparently at the heart of the east-central Iowa Basin where a local upwelling of phosphate-rich water (Witzke and Glenister 1987) may have resulted in plankton 'blooms' (including graptolites) upon which the cephalopods might have fed. Our graptolite collections from Graf (Text-fig. 4C) include *Climacograptus putillus* (Text-fig. 5Q–T, W–Z), *Orthograptus eucharis* (Hall) and *Rectograptus peosta* (Hall). In Illinois, the Argo-Fay Bed of the Scales Formation (lowermost Maquoketa Group) has yielded abundant specimens of *O. eucharis* and no other species, but higher parts of the formation have also produced *R. peosta*. In Iowa and Minnesota, the Elgin Member of the lower Maquoketa Formation contains *C. putillus*, *O. eucharis*, *O. quadrimucronatus* and *R. peosta*. Particularly important biostratigraphically is a collection of *D. complanatus* from the Fort Atkinson Formation at Savannah, north-western Illinois, housed at the Museum of Comparative Zoology at Harvard University. Unfortunately, our efforts to find additional specimens of this index species in the Maquoketa Group exposures in the Savannah area were unsuccessful.

Graptolites from exposures of the Maquoketa Shale in north-eastern Missouri (Text-fig. 1, area 5) were described by Werner and Echols (1958), and Berry and Marshall (1971). Werner and Echols (1958) described three-dimensional phosphatic moulds of *C. putillus* that were collected from the lower Maquoketa Shale at Castlewood, 24 km south of Saint Louis. Text-figure 5U–V, Y illustrates similar specimens of *C. putillus* collected by us from a locality near Castlewood, along Highway 21. Berry and Marshall (1970) illustrated specimens identified as *Climacograptus mississippiensis* and *Orthograptus truncatus* var. *socialis* from an exposure of Maquoketa Shale along Interstate-55 near Barnhart, Missouri. Our collections from this locality contain *Climacograptus tubuliferus* (Lapworth) and *R. peosta*. The occurrence of these species suggests an upper *A. manitoulinensis* to lower *D. complanatus* Biozone age for the Maquoketa Shale in north-eastern Missouri. The low



TEXT-FIG. 5. Graptolites from the *A. manitoulinensis* Zone. A–I, *Amplexograptus manitoulinensis* (Caley); OSU 48513–48521; from the Blue Mountain Formation; 5 km south of Little Current, Manitoulin Island, Ontario. J–Z, *Climacograptus putillus* (Hall); OSU 48522–48536; M–N, same specimen; O–P, same specimen; J–P, from the Georgian Bay Formation; Gorrel Point, Manitoulin Island, Ontario; Q–T, W–Z, fully three-dimensional diversity graptolite fauna contains elements of both the endemic Laurentian Biofacies and cosmopolitan Oceanic Biofacies of Goldman *et al.* (1995).

As a whole, the species associations found in the Maquoketa Shale of the Upper Mississippi Valley match those found in the upper *A. manitoulinensis* Biozone and lower *D. complanatus* Biozone of Quebec (Riva 1969, 1974; Walters 1977; Walters *et al.* 1982) and they are also similar to those we record above from coeval strata on Manitoulin Island. We conclude that in the Upper Mississippi Valley, the lowermost portion of the Maquoketa Shale is referable to the upper *A. manitoulinensis* Biozone, and that higher parts of the unit, especially the Fort Atkinson Formation, are coeval with the *D. complanatus* Biozone.

Conodont biostratigraphy. Conodonts have long been known from the Upper Mississippi Valley in Iowa, Minnesota, Wisconsin, and Missouri, and reports have been published on those from the late Ordovician Dubuque Formation (Ethington 1957; Webers 1966; Clark and Babcock 1971), the Cape Limestone (Sweet *et al.* 1975), and the Maquoketa Group (Formation) (Branson and Mehl 1933; Glenister 1957; Webers 1966; Froming 1971; Thompson and Satterfield 1975). Apart from graphic correlation studies by Sweet (1984, 1987), little recent information is available on the upper Ordovician conodonts of this important region, and the vertical ranges of most taxa are not well documented. New collections from the Dubuque Formation, Cape Limestone, and lower Maquoketa Shale (Formation) at several localities have clarified the ranges of several key species. Of particular significance is the common occurrence of representatives of the *Amorphognathus superbus–A. ordovicicus* lineage in the Dubuque Formation and the Cape Limestone. The appearance of *A. ordovicicus* in the very uppermost Dubuque Formation at several localities in Iowa and Minnesota is taken as the base of the *A. ordovicicus* Biozone. The occurrence of, amongst others, *A. superbus*, along with *Belodina confluens*, *Columbodina occidentalis* Sweet, *C. penna* Sweet, *Icriodella superba*, *Periodon grandis*, *Protopanderodus liripipus*, and *Rhodesognathus elegans* (Rhodes), through most of the Dubuque Formation shows that these strata belong in the upper part of the *A. superbus* Biozone (Text-fig. 4B). Conodonts from the lowermost Maquoketa Formation, including the basal phosphatic bed, include *A. ordovicicus* (Glenister 1957; Webers 1966) indicating the *A. ordovicicus* Biozone. The lower Maquoketa Formation was assigned above to the upper *A. manitoulinensis* Biozone, and hence the base of the *A. ordovicicus* Biozone is below the top of the latter graptolite biozone. Stratigraphically higher parts of the Maquoketa Formation have yielded a not very diagnostic conodont fauna. Sweet's (1979*b*) record of *Plectodina florida* Sweet from the Clermont and Brainard members is of both biogeographical and biostratigraphical interest because this is a widespread species in the *A. ordovicicus* Biozone in the western Interior of North America.

At localities in east-central Missouri, the Cape Limestone yields *A. ordovicicus* (Sweet *et al.* 1975) and other species of the *A. ordovicicus* Biozone, whereas in south-eastern Missouri (Cape Girardeau County), where the Cape Limestone is substantially thicker, the lower part represents the *A. superbus* Biozone (Bergström, unpublished data). It would appear, based on both conodonts and graptolites, that not only is the Cape Limestone-Maquoketa Formation contact in Missouri at a closely similar stratigraphical level as the Dubuque Formation-Maquoketa Formation contact in Iowa and Minnesota, but also, that the relations between graptolite and conodont zones are the same in the two regions.

Arbuckle and Ouachita Mountains, Oklahoma

The late Ordovician strata in southern Oklahoma were deposited in two distinctly different

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phosphatic moulds; from the Elgin Member of the Maquoketa Formation; Graf, Iowa; U–V, Y, from the Maquoketa Shale; road-cut along Highway 21, 24 km south-south-west of St Louis, Missouri. AA, *Climacograptus* cf. *putillus* (Hall); UMMP 57361; flattened specimen from the Haymeadow Creek Shale; Haymeadow Creek, Michigan. Scale bar represents 1 mm (except for figs N and P where it represents 5 mm and figs W and X where it represents 0·5 mm).

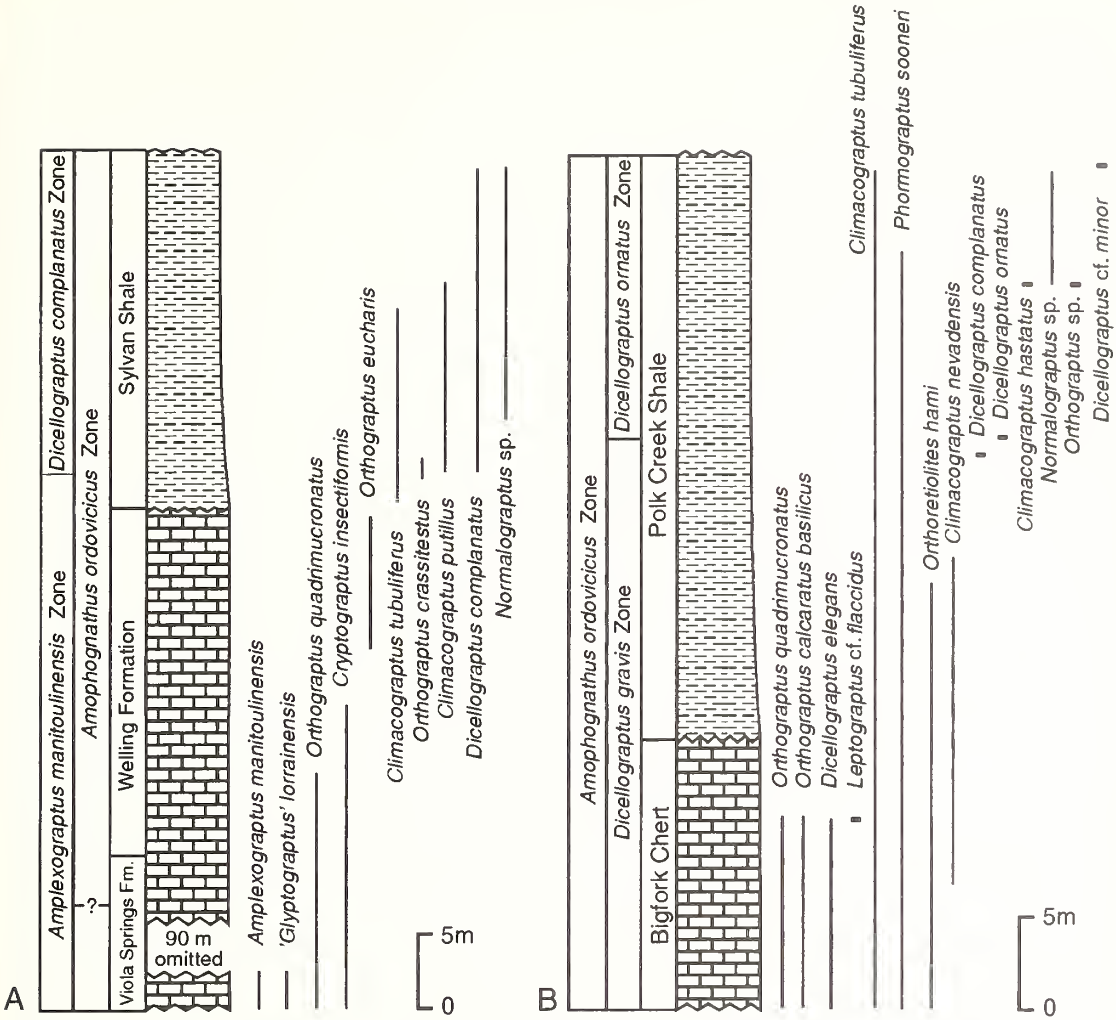
environments (Finney 1986, 1988). In the Arbuckle Mountains (Text-fig. 1, area 6), the carbonates of the Viola Group and the clastics of the overlying Sylvan Shale were laid down in an epicratonic setting within, and along, the southern Oklahoma aulacogen (Hoffman *et al.* 1974). The transition from the Viola Group limestones, which includes the Viola Springs and Welling formations, to the deeper-water Sylvan Shale represents a similar transgressive succession as the replacement of the Galena Group carbonates by the Maquoketa Group shales in the Upper Mississippi Valley. However, as is shown below, the carbonate-shale transition is stratigraphically higher in Oklahoma than in the former region. In the Ouachita Mountains in eastern Oklahoma (Text-fig. 1, area 7), the equivalents to the Viola Group-Sylvan Shale are the Bigfork Chert and Polk Creek Shale (Finney 1986), which represent a different depositional regime, namely a deep basin off the southern margin of the North American craton (Finney 1986, 1988). There are marked biofacies differences between the graptolite faunas of the two regions, which have been brought into rather close juxtaposition by late Palaeozoic thrusting.

Graptolite biostratigraphy. Pioneer studies of graptolites from the Arbuckle and Ouachita Mountains of southern Oklahoma were published by Ruedemann (1908, 1947), Ruedemann and Decker (1934), Decker (1935*a*, 1935*b*, 1936), and Whittington (1954, 1955). Based on comprehensive new collections, Finney (1986, 1988) revised the graptolite biostratigraphy of the Viola Group and Bigfork Chert. We have studied numerous collections from this region, including the type collections at the University of Oklahoma in Norman, Finney's collections, and collections made in recent years by Dr C. E. Mitchell. In the present contribution our discussion is centred on the upper Ordovician portion of the Oklahoma successions; for pertinent information about aspects of the middle Ordovician graptolite biostratigraphy of the Viola Group, see Finney (1986) and Bergström and Mitchell (1986).

In the Arbuckle Mountains, the uppermost Viola Springs Formation and the overlying Welling Formation contain (Text-fig. 6A), amongst other species, the biostratigraphically diagnostic species *A. manitoulinensis* and *O. eucharis* (Finney 1986; Goldman 1995), indicating that this interval belongs to the *A. manitoulinensis* Biozone. Collections from the Sylvan Shale made by Finney and examined by the senior author contain *Climacograptus putillus*, *C. tubuliferus*, *Dicellograptus complanatus*, *D. gravis* Keble and Harris, *Normalograptus* sp. nov., and *Orthograptus crassitestus* (Ruedemann). This association suggests a correlation with the *D. complanatus* Biozone as developed in north-western Europe (Skoglund 1963; Williams 1982*a*, 1982*b*, 1987), at Trail Creek, Idaho (Carter and Churkin 1977; Goldman *et al.* 1995), in the Marathon area, West Texas (Goldman *et al.* 1995), and in the northern Appalachian Basin (Riva 1969, 1974). Also, this interval of the Sylvan Shale corresponds to the *D. gravis* Biozone (Ea4) of the succession in Victoria, Australia (VandenBerg and Cooper 1992). Collections from the lowermost Sylvan Shale do not contain *O. crassitestus*, *C. putillus*, and the particularly significant species *D. complanatus* (Text-fig. 6A), and it is possible that this interval is coeval with the very uppermost part of the *A. manitoulinensis* Biozone.

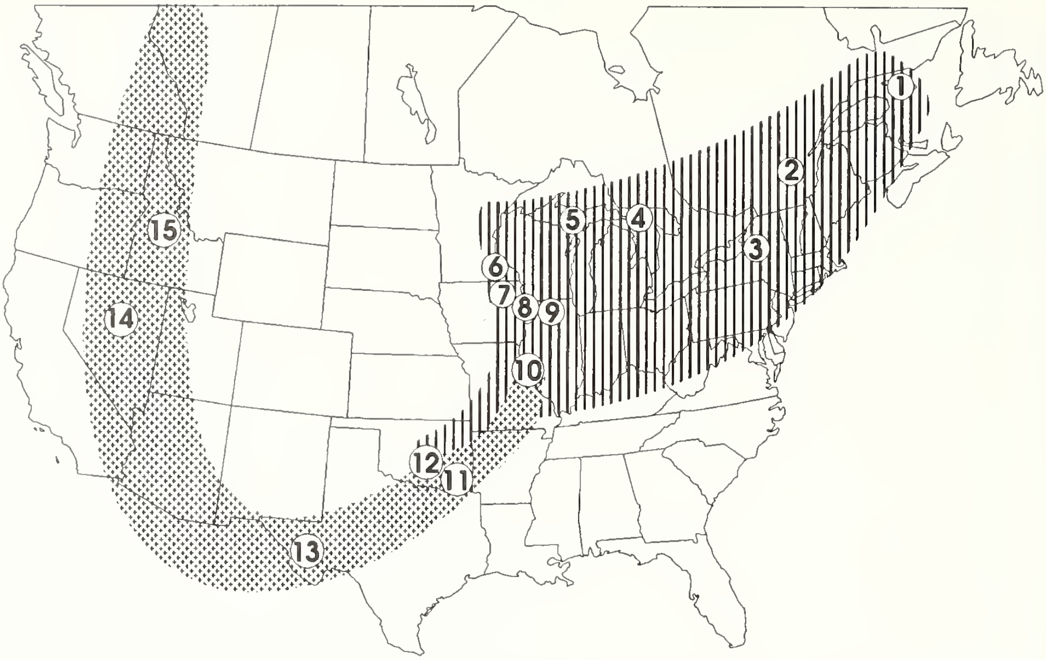
The Polk Creek Shale of the Ouachita Mountains contains a typical deep-water Pacific Province graptolite fauna (the cosmopolitan Oceanic Biofacies of Goldman *et al.* 1995). Graptolites from the Stringtown Quarry (Finney 1986), identified by the senior author, include (Text-fig. 6B) the following (distances above the base of the Polk Creek Shale): 8–10 m: *Climacograptus nevadensis* (Carter), *C. tubuliferus*, *Orthoretiolites hami* (Whittington); 14·6 m: *C. tubuliferus*, *D. complanatus*; 15·5 m: *C. tubuliferus*, *Dicellograptus ornatus* (Elles and Wood); 24 m: *Arachniograptus laqueus* Ross and Berry, *Climacograptus hastatus* T. S. Hall, *Normalograptus* sp., *Orthograptus* sp.

These collections indicate correlation with the *Dicellograptus gravis* and *Dicellograptus ornatus* biozones (Ea4 to Bo2) in the Victorian succession (VandenBerg and Cooper 1992) and the upper *Pleurograptus linearis* to *Dicellograptus anceps* biozones of southern Scotland (Williams 1982*a*, 1982*b*, 1987). The species association is virtually identical to those of the lower Maravillas Formation of West Texas (Berry 1960; Goldman *et al.* 1995) and the coeval portion of the sequence at Trail Creek, Idaho (Carter and Churkin 1977).



TEXT-FIG. 6. Stratigraphical columns illustrating the upper Ordovician graptolite successions, and graptolite and conodont zones in the Arbuckle Mountains and Ouachita Mountains, Oklahoma. A, Arbuckle Mountains sequence; graptolite ranges in the Viola Springs and Welling formations after Finney (1986). B, Ouachita Mountains sequence; graptolite ranges in the Bigfork Chert after Finney (1986).

Conodont biostratigraphy. Conodonts from the middle–upper Ordovician Viola Group (Amsden and Sweet 1983), and the upper Ordovician Sylvan Shale in the Arbuckle Mountains have been described by, among others, Oberg (1966), Sweet (1983), and Dresbach (1983), and a conodont-based graphic correlation of the Viola Springs Formation and the Welling Formation was published by Sweet (1984). Of biostratigraphical significance in the Viola Springs Formation, which is approximately 200 m thick, is the presence (Dresbach 1983) of *A. superbus* near the level of appearance of *A. manitoulinensis* in the middle part of the formation (Finney 1986). Typical specimens of *A. ordovicicus* have been collected from an interval in the topmost portion of the formation in the long section along Interstate-35 on the south side of the Arbuckle Anticline (Dresbach 1983; see also Goldman *et al.* 1995). Samples from the 80 m thick interval between the occurrences of these zonal index species have yielded (Dresbach 1983), amongst others, *Columbodina*



TEXT-FIG. 7. Distribution of late Ordovician graptolite biofacies in United States and adjacent parts of Canada. Vertical ruling and stippling represent the Laurentian Biofacies and the Oceanic Biofacies, respectively. Numbered localities and areas are as follows: 1, Anticosti Island, Quebec; 2, Saint Lawrence Lowlands, Quebec; 3, Mohawk and Black River valleys, New York State; 4, Manitoulin Island, Ontario; 5, Upper Peninsula of Michigan; 6, Rifle Hill Quarry, southern Minnesota; 7, Postville, Iowa; 8, Graf, Iowa; 9, northwestern Illinois; 10, Saint Louis region, Missouri; 11, Ouachita Mountains, eastern Oklahoma; 12, Arbuckle Mountains, Oklahoma; 13, Marathon region, west Texas; 14, central Nevada; 15, Trail Creek, Idaho. Note that the two biofacies overlap in the Arbuckle Mountains. Map adapted from Finney (1986) and Goldman and Bergström (1995).

penna, *Icriodella superba*, *Plectodina florida*, and *Pseudobelodina inclinata* (Branson and Mehl), an association that is diagnostic of either the uppermost *A. superbus* Biozone or the lowermost *A. ordovicicus* Biozone. Although the precise level of the base of the latter remains undetermined, it is clearly below the base of the Welling Formation, and well below the top of the *A. manitoulinensis* Biozone; the base of the overlying *D. complanatus* Biozone is taken at the level of appearance of its zonal index, in the lowermost part of the Sylvan Shale (Text-fig. 6A). Evidently, the base of the *A. ordovicicus* conodont Biozone is within the upper *A. manitoulinensis* graptolite Biozone also in the Arbuckle Mountains succession (Text-fig. 6A).

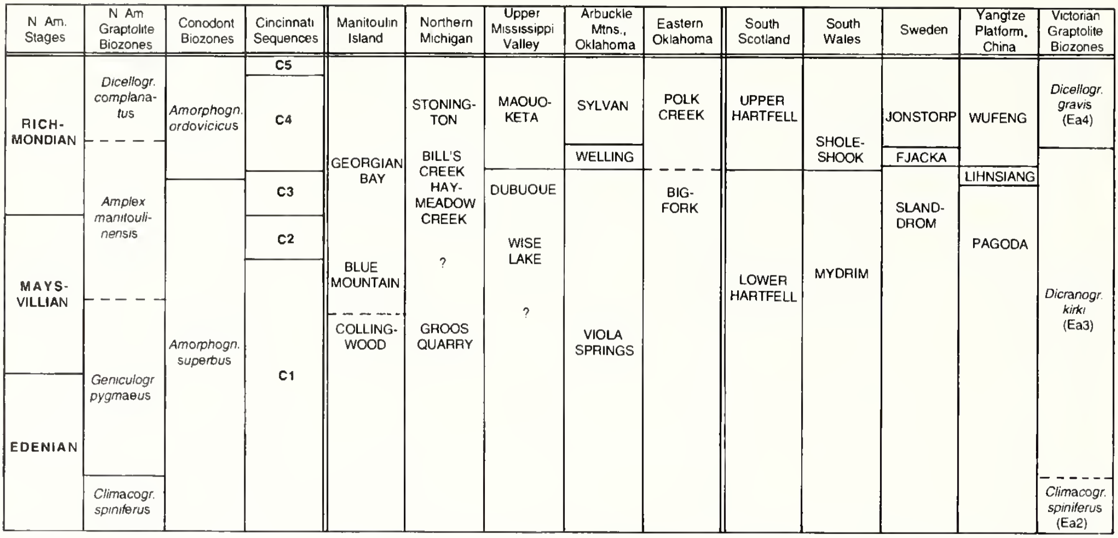
Most samples from the graptolite-bearing Bigfork Chert at Stringtown Quarry, eastern Oklahoma contain few, and biostratigraphically undiagnostic conodonts. However, a sample from the upper third of the unit includes, among others, *A.* cf. *ordovicicus* and is likely to represent the *A. ordovicicus* Biozone. This agrees well with the graptolite biostratigraphy in this section (Finney 1986; also see Text-fig. 6B).

The Cincinnati region in Ohio, Kentucky and Indiana

It is outside the scope of this paper to deal with the relatively well-known graptolites of this important outcrop area (for a general summary, see Bergström and Mitchell 1986), but some comments on the graptolite-conodont zonal relations are in order. Currently available data indicate that the base of the *G. pygmaeus* Biozone is about 25 m above the base of the basal Cincinnatian Edenian Stage in strata belonging to the *A. superbus* Biozone (Mitchell and Bergström 1991). Zonal conodonts occur in close association with zonal graptolites in the lower half of the *G. pygmaeus* Biozone in numerous sections in this region (Text-fig. 1, area 10) and there can be no doubt about the graptolite-conodont zone relations in this interval. The base of the overlying *A. manitoulinensis* Biozone is established less precisely, but unpublished drill-core data suggest that it is about 80 m above the base of the *G. pygmaeus* Biozone near the middle of the Maysvillian Stage in strata of the *A. superbus* Biozone (Text-fig. 8). Of particular interest for the correlation of the type Cincinnatian Series is the appearance of typical representatives of *A. ordovicicus* along with *Periodon grandis*, *Rhodesognathus elegans*, and *Icriodella superba* in the uppermost Arnheim Formation (in an interval also referred to as the Dillsboro Formation) of the lower Richmondian Stage in eastern Indiana (MacKenzie and Bergström 1993, 1994; Goldman *et al.* 1995). The uppermost Arnheim Formation populations of *Amorphognathus* also contain transients to the evolutionary ancestor of *A. ordovicicus*, *A. superbus*. Moreover, only the latter species has been found in stratigraphically older parts of the Cincinnatian. Based on these facts, we interpret the level of appearance of *A. ordovicicus* in the uppermost Arnheim Formation as being its first occurrence in the Cincinnatian succession and that level is taken to mark the base of the *A. ordovicicus* Biozone. In the excellently exposed sections near Brookville, Indiana, *A. ordovicicus* is associated with *Arnheimograptus anacanthus* (Mitchell and Bergström), a graptolite species that elsewhere (see, for instance, Walters *et al.* 1982) is restricted to the *A. manitoulinensis* Biozone. Although absence of zonal graptolites currently makes it impossible to locate the *A. manitoulinensis*-*D. complanatus* zonal boundary precisely in the type Cincinnatian, the facts at hand clearly suggest an overlap between the lower part of the *A. ordovicicus* Biozone and the upper part of the *A. manitoulinensis* Biozone in this succession. This is in agreement with the relations between conodont and graptolite zones in the Upper Mississippi Valley and Oklahoma successions described above.

Graptolite biofacies

Recently, Goldman *et al.* (1995) distinguished two distinct late Ordovician graptolite biofacies within the tropical Pacific Province in Laurentia, namely an *Oceanic Biofacies* characterized by a mixed fauna containing cosmopolitan elements of the epipelagic and mesopelagic biotopes, and a *Laurentian Biofacies* characterized by epipelagic and endemic cratonic taxa. The graptolite faunas of the Laurentian Biofacies occur in the Appalachian Basin, on Manitoulin Island and the Upper Peninsula of Michigan, and in most other parts of the North American Midcontinent. In successions representing this biofacies, Riva's (1969, 1974) upper Ordovician graptolite zone succession is readily applicable. The Oceanic Biofacies is present in the Canadian Rocky Mountains, the Great Basin, the Marathon region of West Texas, and the Ouachita Mountains of Oklahoma and Arkansas. Sequences having this biofacies are best subdivided using the zonal scheme of Victoria, Australia (VandenBerg and Cooper 1992). The Viola Group and Sylvan Shale in the Arbuckle Mountains of Oklahoma contain some elements of both biofacies, including *Amplexograptus manitoulinensis*, *Climacograptus putillus*, *C. tubuliferus* and *Dicellograptus complanatus*, which allows for correlation between the two zonal schemes. The regional distribution of these biofacies in United States and southern Canada is illustrated in Text-figure 7. The Oceanic Biofacies forms a parabolic arc from the Rocky Mountains in Canada across the Great Basin and the Marathon region in West Texas to the Ouachita Mountains in Oklahoma. The cosmopolitan mesopelagic species characteristic of this biofacies, including *C. tubuliferus*, *C. nevadensis* and most dicellograptids and dicranograptids, are off-shore species that generally are not present on the craton (Finney 1986; Goldman *et al.* 1995). However, the widespread late Ordovician transgression, which is recorded by dark shales over much of the Midcontinent (Bergström and Mitchell 1992), allowed several of these mesopelagic species to migrate into the continental interior. Examples of such migrations are the occurrences of *C. tubuliferus* and *D. complanatus* in the Sylvan and Maquoketa shales.



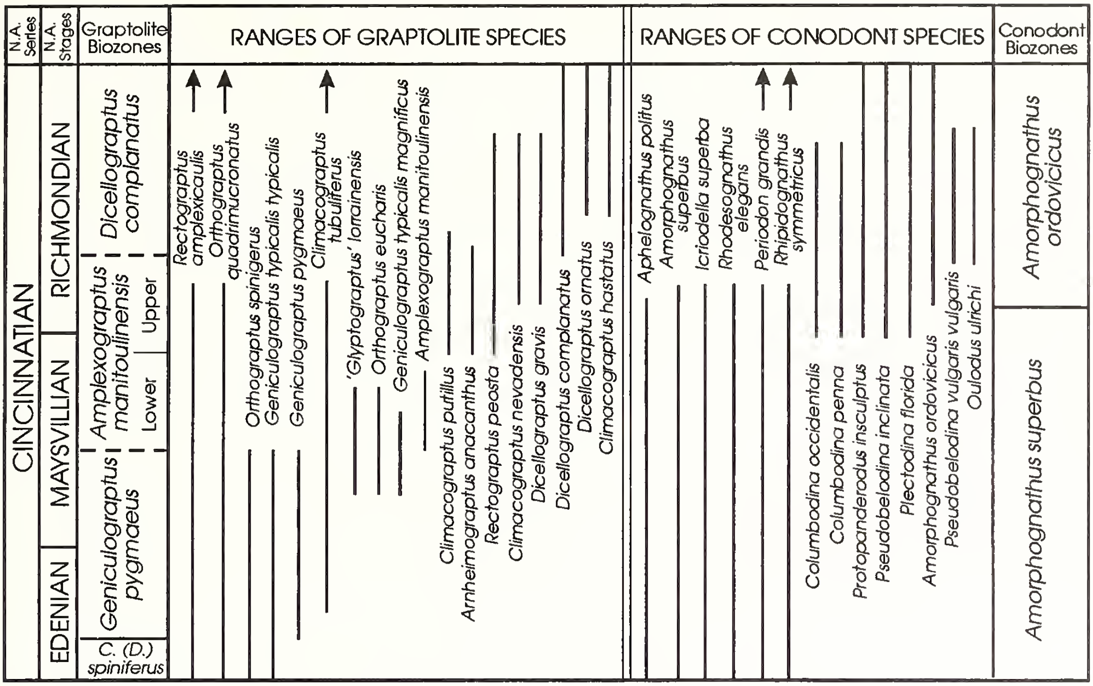
TEXT-FIG. 8. Correlation of North American and Victorian upper Ordovician graptolite biozones with conodont biozones, sequence stratigraphical units in the Cincinnati region, and formations in the North American Midcontinent, southern Scotland, South Wales, Sweden and the People's Republic of China.

The Laurentian Biofacies is present in most of the eastern and central parts of North America. A typical development is in the dark shales and overlying flysch of the Taconic foredeep in New York and Quebec (Riva 1969, 1974). The cosmopolitan epipelagic elements of this biofacies (for instance, *Orthograptus quadrimucronatus* and *Rectograptus amplexicaulis*) occur abundantly at many localities in the continental interior, usually in single-species associations, and in many cases in storm deposits. Endemic species such as *Climacograptus putillus* and *Amplexograptus manitoulinensis* are present more sporadically in the Midcontinent. In the Saint Lawrence Lowlands of Quebec, where the full vertical ranges of these endemic species are best represented, the late Ordovician transgression, so apparent in the Midcontinent, is largely masked by the deposition of clastics eroded from the Taconic orogen.

Areas where these two biofacies overlap, such as the Arbuckle Mountains in Oklahoma, are of particular significance in that their successions provide the opportunity to establish ties between the two disparate zonal schemes. Our interpretation of the relationships between the various units studied by us, the zonal succession recognized in Victoria, Australia (VandenBerg and Cooper 1992) and that established by Riva (1969) is illustrated in Text-figure 8.

Summary of the upper Ordovician graptolite biostratigraphy of the North American Midcontinent and international correlation

Text-figure 9 gives the vertical distribution of the graptolites and conodonts discussed herein, and adds some significant new information to similar compilations published by Bergström and Mitchell (1986) and Goldman *et al.* (1995). It shows that several relatively common Midcontinent species have a narrow stratigraphical range and hence are useful biostratigraphically within the interval of the *G. pygmaeus*, *A. manitoulinensis*, and *D. complanatus* biozones. Of biostratigraphical interest also is that a bipartite subdivision of the *A. manitoulinensis* Biozone appears possible. The upper part has a characteristic species association, including several species absent in the lower part, such as *Climacograptus putillus*, *C. nevadensis* and *Rectograptus peosta*. The biozonal index, *Amplexograptus manitoulinensis*, appears to occur mainly in the lower part of the biozone, whereas *Arnheimograptus anacanthus* and *C. putillus* are most common in, but not restricted to, the upper part. It is premature



TEXT-FIG. 9. Known vertical ranges of graptolite and conodont species in the Edenian through Richmondian succession in the North American Midcontinent. Graptolite zone designations after Riva (1969, 1974). Note that it is possible to subdivide the *A. manitoulinensis* Biozone into a lower and upper part based on the vertical distribution of several species.

to propose formal designations for these units but they seem to have biostratigraphical utility in the Midcontinent successions.

It is also appropriate to note that, because there are several successions in which graptolites and conodonts occur together, it has been possible to establish some new ties between the zonal schemes based on these groups. In all the sections studied, there is close agreement between the graptolite and conodont biostratigraphy. Of special importance for regional correlation is the fact that the new data are consistent with recently published interpretations (Bergström and Mitchell 1992; Goldman *et al.* 1995) that the base of the widely recognized *A. ordovicicus* conodont Biozone is coeval with a level in the upper *A. manitoulinensis* graptolite Biozone.

The data now at hand, which lead to a correlation considerably different than those presented in some recent papers (e.g. Ross *et al.* 1982), are useful for correlations between the Midcontinent sections and with some coeval successions in other parts of the world (Text-fig. 8). The relations between Midcontinent sections are discussed above, and brief comments are given below on their relations to key successions in Europe. For additional comments on the correlation between important upper Ordovician graptolite successions in North America, Australia, southern Scotland, and Sweden, see Goldman *et al.* (1995).

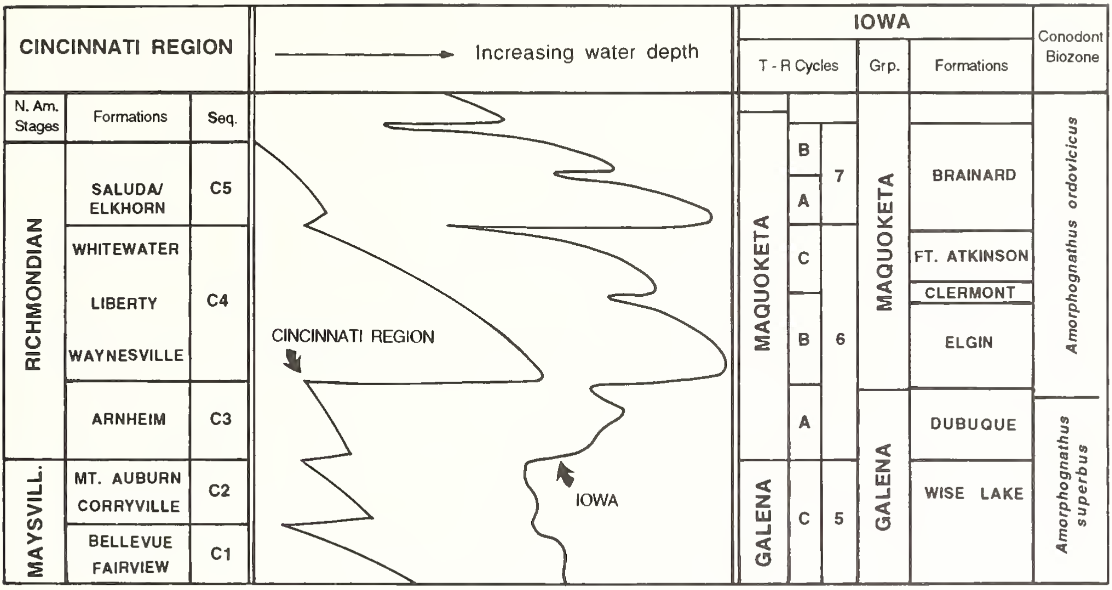
Scotland. The classical upper Ordovician graptolite succession of the Moffat region in southern Scotland, recently re-investigated by Williams (1982*a*, 1982*b*, 1987) and Zalasiewicz *et al.* (1995), has *Dicellograptus complanatus*, *Climacograptus tubuliferus*, *Orthograptus quadrimucronatus* and *Rectograptus amplexicaulis* in common with the Midcontinent faunas. Only a relatively small number of conodonts, which are preserved on shale surfaces and therefore difficult to identify, has been found. Of particular interest are Barnes and Williams' (1988) records of *Amorphognathus superbus* from the Lower Hartfell Shale (*P. linearis* Biozone) and *A. ordovicicus* from the lower Complanatus Band in the Upper Hartfell Shale (*D. complanatus* Biozone) at Dob's Linn. Although their identifications of these key species are based on the platform (Pa) rather than the more diagnostic holodontiform (M) elements, the reported occurrences are in agreement with the graptolite-conodont zone relations elsewhere.

South Wales. Graptolite faunas that are coeval with those of the Hartfell Shale have recently been recorded by Zalasiewicz *et al.* (1995) from a new road-cut along the A40 about 3 km west of Whitland, that exposes the Mydrim Shales and the overlying Sholeshook Limestone. The Mydrim graptolite species associations differ markedly from those of southern Scotland and the North American Midcontinent, the only species in common with the latter being the relatively long-ranging *Rectograptus amplexicaulis* and *Orthograptus quadrimucronatus*. Interestingly, C. R. Barnes (pers. comm. 1995), who is describing the conodont succession at this locality, has discovered *A. ordovicicus* in the lower Sholeshook Limestone just above an interval with graptolites considered to represent the *P. linearis* Biozone. Hence, the graptolite-conodont zone relations appear to be the same as those known elsewhere in this upper Ordovician interval.

Sweden. As described by Bergström and Mitchell (1986, fig. 6) and Goldman *et al.* (1995, fig. 6), the boundary between the *P. linearis* and *D. complanatus* zones in the Swedish succession is taken to coincide with the boundary between the Fjäcka Shale and the Jonstorp Formation. Specimens of *A. ordovicicus* have previously been recorded from the Fjäcka Shale but recently, the junior author has discovered numerous specimens of this zonal index in the upper part of the Slandrom Limestone in a previously unstudied section at Skålberget, Dalarna, central Sweden. Although the Slandrom Limestone has yielded no biostratigraphically diagnostic graptolites and the *P. linearis* graptolite fauna in the overlying Fjäcka Shale has little in common with coeval Midcontinent graptolite faunas, the conodonts provide a close correlation link with the latter region.

SEQUENCE STRATIGRAPHY AND SEA LEVEL CHANGES

In a recent study, Holland (1993; see also Holland and Patzkowsky 1996) defined five sequence boundaries in the upper Ordovician in its outcrop area in Ohio, Kentucky, and Indiana (Text-figs 8, 10). Of particular interest here is his C3/C4 sequence boundary, which coincides with the base of the Waynesville Formation in sections studied by us near Brookville in eastern Indiana. This sequence boundary is just above the base of the *A. ordovicicus* Biozone, and it is overlain by shaly strata representing a deeper-water facies deposited during a prominent sea-level rise that Holland (1993) interpreted to be eustatic. Based on conodont biostratigraphy, the base of the C4 sequence would correspond with the base of the Maquoketa Group in the Upper Mississippi Valley, which represents a change from the relatively shallower-water depositional environments of the carbonates of the Galena Group to the relatively deeper-water environments of the shales of the lower Maquoketa Group (Text-fig. 10). In Michigan and on Manitoulin Island, the corresponding horizon is probably within unexposed intervals of the Bill's Creek and Georgian Bay formations, respectively. Based on conodont biostratigraphy, the equivalent horizon in the Arbuckle Mountains of Oklahoma could be at the base of the Welling Formation, but further studies are needed to clarify whether it can be recognized with certainty. Apparently, the boundary between the Slandrom Limestone and the Fjäcka Shale in the Swedish succession represents a flooding surface of a closely similar, if not identical, age as the base of the C4 sequence. Furthermore, in the well-known succession in the Yangtze Platform region of China, the upper Pagoda Limestone has yielded conodonts of the upper *A. superbus* Biozone (Chen *et al.* 1995) and the overlying Wufeng Shale



TEXT-FIG. 10. Comparison of late Ordovician bathymetric curves from the Cincinnati region in Ohio, Kentucky, and Indiana (after Holland 1993), and Iowa (after Witzke and Bunker 1996). Note the similarity between these curves, especially in the timing of major transgressive-regressive events, which suggests that these reflect eustatic sea level changes.

contains graptolites coeval with the *D. complanatus* Biozone and conodonts of the *A. ordovicicus* Zone. In many sections, these formations are separated by the Linhsiang Formation, a thin unit of nodular limestone that has not yet produced zonal conodonts or graptolites. It would seem that the C4 sequence boundary could correspond to either the base, or more probably, the top of the latter formation but further biostratigraphical study is needed to clarify this. At any rate, the biostratigraphical and depositional data at hand from several continental plates appear to support the idea that the C4 sequence boundary indeed represents a eustatic transgression. The base of the C4 sequence is not the only level in the successions investigated that may reflect eustatic sea level changes. Although there are significant differences between some of the recently published Midcontinent upper Ordovician bathymetric curves, which is in agreement with the observation by Johnson *et al.* (1989, p. 43) that 'cyclic sequences attributed to eustatic sea-level changes have been the subject of much lively debate', two such curves, namely that of the Cincinnati succession by Holland (1993), and that of the Iowa sequence of Witzke and Bunker (1996), are of particular significance in this investigation. These curves, which are based on extensive recent studies in two regions separated geographically by a distance of about 700 km, are compared in Text-fig. 10. Their vertical alignment follows the revised correlation between the successions in the Cincinnati region and the Upper Mississippi Valley presented herein, and no change in the original curve shapes has been made. This comparison between the inferred changes in bathymetry in the two regions shows several important similarities apart from the significant transgression at the base of the Waynesville (base of the C4 sequence) and the base of the Maquoketa (base of the T-R (transgressive-regressive) cycle 6B) referred to above. These include: (1) the base of the C3 sequence appears to correlate with the base of the Maquoketa T-R cycle 6A; (2) the C4 sequence corresponds to the T-R cycle 6B-6C; (3) the C4/C5 sequence boundary appears to correspond to the base of the T-R 7A-B cycle; and (4) the top of the C5 sequence seems to correlate with the top of the T-R cycle 7. Lehmann *et al.*

(1995) observed that some recent interpretations of late Ordovician sea-level changes in the Cincinnati and Upper Mississippi regions were in conflict, but our biostratigraphy-based comparison shows a striking general similarity between recently published bathymetric curves of the successions studied in the two regions. This is noteworthy in view of the fact that these curves reflect subjective, mainly lithology-based interpretations by different investigators working in two widely separated regions. We interpret this similarity as indicating that eustatic sea-level changes exercised a very significant bathymetric control during the deposition of the late Ordovician sediments in these regions.

SYSTEMATIC PALAEONTOLOGY

Repositories for figured and cited material are abbreviated as follows: AMNH, American Museum of Natural History, New York; BU, the Lapworth Museum, University of Birmingham, UK; GSC, Geological Survey of Canada, Ottawa; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; OSU, Orton Geological Museum, Ohio State University, Columbus, Ohio; and USNM, United States National Museum, Washington, D.C.

Suborder VIRGELLINA Fortey and Cooper, 1986
Superfamily DIPLOGRAPTOIDEA Lapworth, 1873, emend. Mitchell, 1987
Family DICRANOGRAPTIDAE Lapworth, 1873
Subfamily DICRANOGRAPTINAE Lapworth, 1873, emend. Finney, 1985

Genus DICELLOGRAPTUS Hopkinson, 1871

Type species. By subsequent designation (Gurley 1896, p. 70); *Didymograpsus elegans* Carruthers, 1867, p. 369, pl. 2, fig. 16a.

Dicellograptus complanatus Lapworth, 1880

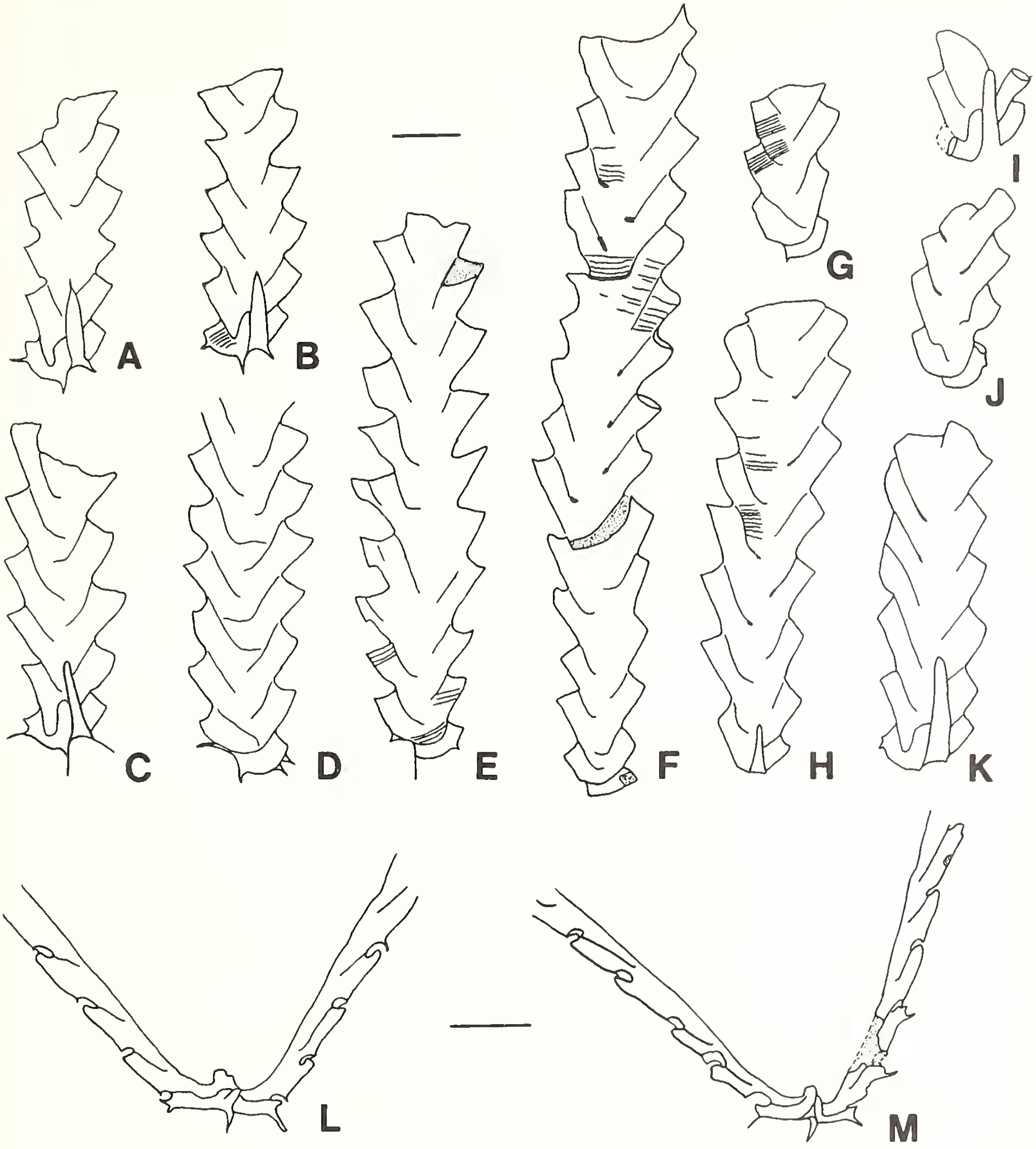
Text-figure 11L–M

1880 *Dicellograptus complanatus* Lapworth, p. 160, pl. 5, fig. 17a–17e.
1904 *Dicellograptus complanatus* Lapworth: Elles and Wood, p. 139, pl. 20, fig. 1a–1d; text-fig. 84a–e.
1908 *Dicellograptus complanatus* Lapworth: Ruedemann, p. 294, pl. 18, fig. 1; text-figs 208–209.
1935*b* *Dicellograptus complanatus* Lapworth; Decker, p. 702 (*partim*), fig. 1a–e (*non* fig. 2g).
1947 *Dicellograptus complanatus* Lapworth; Ruedemann, p. 376, pl. 62, figs 4–10.
1963 *Dicellograptus complanatus* Lapworth; Skoglund, p. 33, pl. 1, fig. 3; text-fig. 10A–E.
1970 *Dicellograptus complanatus* Lapworth; Toghill, p. 12, pl. 4, figs 1–5; pl. 5, figs 1–5; pl. 6, fig. 1; text-figs 2g–l, 4b.
1983 *Dicellograptus complanatus* Lapworth; Koren' and Sobolevskaya, p. 101, pl. 25, figs 5–9; text-fig. 31.
1987 *Dicellograptus complanatus* Lapworth: Williams, p. 71, figs 3a–h, 5a–c, 6g.
1991 *Dicellograptus complanatus* Lapworth; Williams, p. 589, pl. 1, figs 12–13; text-fig. 71–q.

Lectotype. BU 1072b, designated by Toghill (1970, p. 13); Lower Complanatus Band, Dob's Linn, Scotland.

Material. Two complete specimens and numerous stipe fragments from the Sylvan Shale, Sycamore Creek, southern Oklahoma (collected by S. C. Finney), and four specimens (MCZ 9428–9431) from the Fort Atkinson Formation, Maquoketa Group, town of Savannah, Carroll County, Illinois.

Description. Stipes are 0·4–0·5 mm wide at the aperture of th2^1, increasing to an average of 0·7 mm wide distally; stipes diverge at an angle of approximately 60°. Thecae simple, numbering 5–7 in the proximal 5 mm,



TEXT-FIG. 11. A–K, *Rectograptus peosta* (Hall, 1861); OSU 48537–48541, 48595–48600; A–E, flattened specimens; Fort Atkinson Formation, Maquoketa Group; Savannah, Illinois; F–K, fully three-dimensional phosphatic moulds; Elgin Member, Maquoketa Formation; Graf, Iowa. L–M, *Dicellograptus complanatus* Lapworth, 1880; MCZ 9429–9430; Fort Atkinson Formation, Maquoketa Group; Savannah, Illinois (drawings of L–M by C. E. Mitchell). Scale bars represent 1 mm.

decreasing to 4–6 in 5 mm distally, with long, straight supragenicular walls. Th1^1 and th1^2 diverge horizontally from the sicula and bear prominent mesial spines; th2^1 grows horizontally and then bends sharply upward, while th2^2 grows continuously upward. Mesial spines commonly present on second and third thecal pairs.

Thecal apertures slightly introverted proximally, becoming nearly horizontal distally. Axil slender and rectangular.

Remarks. The four specimens (MCZ 9428–9431) labelled *Dicellograptus* cf. *D. complanatus* now appear to be misplaced (F. Collier, pers. comm. 1994). The specimen label lacks precise locality information and the name of the collector, and the present authors were unable to find additional specimens from exposures at Savannah. Lithological descriptions of the slabs containing the specimens provided by C. E. Mitchell (pers. comm. 1994), who had previously examined and identified the material, matched precisely the lithology of the sections we examined at Savannah. Figures of the specimens (Text-fig. 11L–M) were generously donated by C. E. Mitchell. Based on these we feel that the specimens represent *D. complanatus*.

Dicellograptus complanatus was revised and redescribed by Williams (1987), and our specimens agree well with his description.

Stratigraphical and geographical occurrence. Dicellograptus complanatus is the key index species of the eponymous biozone in Europe (Skoglund 1963; Nilsson 1977; Williams 1982*b*, 1987) and North America (Berry 1960; Riva 1969, 1974), and it has also been reported from Russia (Keller 1956; Koren' and Sobolevskaya 1983). *D. complanatus* is a cosmopolitan mesopelagic species, and part of the Oceanic Biofacies of Goldman *et al.* (1995).

Dicellograptus gravis Keble and Harris, 1925

Text-figure 15D

1925 *Dicellograptus gravis* Keble and Harris, p. 516, pl. 70, fig. 2a–b.
1972 *Dicellograptus alector* Carter, p. 46, pl. 1, figs 9, 11–12, 15; text-fig. 2a, g.
1977 *Dicellograptus alector* Carter; Carter and Churkin, p. 18, pl. 3, figs 8, 12–13, 17.
1987 *Dicellograptus alector* Carter; Williams, p. 77, figs 4b, 5d–h.

Syntypes. Geological Survey of Victoria nos 24004 and 24085, from the upper Eastonian (Ea 4) at Mt Easton, Victoria. Specimen 24085 is here selected as the lectotype.

Material. One well preserved specimen from the lowermost Sylvan Shale in Rayford Quarry (Section Q of Alberstadt 1973), southern Oklahoma (collected by S. C. Finney).

Description. Axial angle approximately 30°. Axil rectangular and stout. Stipe width 0·56 mm at the level of the $th1^1$ aperture, increasing to 0·92 mm at the aperture of $th8^1$. $Th1^1$ and $th1^2$ with apertural spines; all subsequent thecae with prominent mesial spines. Supragenicular walls with a distinct bend at the position of the mesial spine. Thecal apertures strongly introverted proximally, less so distally. The free portion of the sicula missing, apparently from resorption.

Remarks. We follow Cas and VandenBerg (1988) in synonymizing *Dicellograptus alector* with *D. gravis*.

Stratigraphical and geographical occurrence. Dicellograptus gravis is the nominal species for Ea4 in the Victorian graptolite succession (Cas and VandenBerg 1988). Goldman *et al.* (1995) suggested that the *D. gravis* Biozone is also an appropriate name for Carter and Churkin's (1977) *C. tubuliferus* Biozone as well as for the coeval part of Zone 13 of Berry (1960) in the basal Maravillas Formation of the Marathon region in West Texas. Williams (1987) recorded the co-occurrence of *D. gravis* with *D. complanatus* in the Mill Formation, Upper Whitehouse Group, at Myoch Bay in the Girvan area, Scotland.

While this is the only species of *Dicellograptus* occurring in S. C. Finney's collections from the lower Sylvan Shale at Rayford Quarry, other sections of Sylvan Shale have yielded numerous specimens of *D. complanatus*. *D. gravis* is a cosmopolitan mesopelagic species and part of the Oceanic Biofacies of Goldman *et al.* (1995).

Family DIPLOGRAPTIDAE Lapworth, 1873, emend. Mitchell, 1987
Subfamily CLIMACOGRAPTINAE Frech, 1897, emend. Mitchell, 1987

Genus CLIMACOGRAPTUS Hall, 1847, emend. Mitchell 1987

Type species. By original designation; *Graptolithus bicornis* Hall, 1847.

Remarks. Considerable confusion continues to plague the taxonomy of several middle and upper Ordovician *Climacograptus* species. The primordial astogeny of such biostratigraphically important taxa as *Climacograptus caudatus* Lapworth, *Climacograptus tubuliferus* Lapworth, *Climacograptus nevadensis* Carter, and *Climacograptus putillus* (Hall) has been variously interpreted (see, for example, Mitchell 1987; Riva 1988; Riva and Ketner 1989) with resultant taxonomic obfuscation.

Mitchell (1987, p. 361, text-fig. 5) described and illustrated the primordial Pattern D astogeny of *Climacograptus caudatus* based on three-dimensional isolated growth stages from the Viola Springs Formation in southern Oklahoma. The salient characters of Pattern D astogenetic growth include a short, broad sicula bearing only a virgella, and a characteristic prosicula composed of only one or two vertical rods that merge with the nema. Th1^1 grows down along the sicula and then turns sharply upward with its metatheca pressed against its protheca. Th1^2 is prosoblastic and grows across the reverse side of the sicula in a broad symmetrical arch. The crossing canal of th2^1 appears as a small hood that fuses along the sicula axis with an upward-growing flange from the crossing canal of th1^2. This fusion of hood and flange is marked by a short list and accompanies the differentiation of the prothecae of th2^1 and th2^2. In mature or semi-flattened rhabdosomes, Pattern D astogeny can be recognized by the broad, evenly rounded arch formed by th1^2 on the reverse side of the sicula, and by a distinct dimple in the position of the list formed by the fusion of the th2^1 crossing canal with the upward-growing flange from th1^2 (Text-fig. 5U, W). Other taxa exhibiting Pattern D primordial astogeny referred to *Climacograptus* by Mitchell (1987) include *C. tubuliferus*, *C. putillus* and *C. styloideus*.

Riva (1988), believing that *C putillus*, *C. tubuliferus*, *C. styloideus*, and *C. nevadensis* possess Pattern H primordial astogeny, referred these species to a new genus, *Scalarigraptus* (a junior synonym of *Normalograptus* Legrand, 1987). Additionally, Riva, *in* Riva and Ketner (1989) established the monotypic genus *Ensigraptus* for Pattern D climacograptinids lacking spines on their first two thecae, with *Climacograptus caudatus* as type species. Williams (1991) noted that in specimens of *C. tubuliferus* figured by Williams and Bruton (1983, fig. 15a, n) th1^2 showed early downward growth, a feature consistent with Pattern D proximal development but not found in Pattern H (in which th1^2 grows directly upward from th1^1), and re-assigned *C. tubuliferus* to *Climacograptus*. It is appropriate to note that Riva, *in* Riva and Ketner (1989) did not discount the possibility that better preserved specimens of *C. tubuliferus* might reveal Pattern D primordial astogeny. Williams (1991) also chose to retain *C. caudatus* in *Climacograptus*, but did not synonymize *Ensigraptus* with *Climacograptus*. We agree with Williams' (1991) revisions and think that the presence and number of spines on the proximal thecae are important characters for differentiating species but are not consistent enough to define genera. We are not convinced that the loss of proximal thecal spines occurred only once in the evolutionary history of *Climacograptus*, and it may well represent a character 'acquired' independently by several species.

Goldman *et al.* (1995) illustrated well-preserved specimens of *C. nevadensis* from the lower Maravillas Formation of the Marathon region that clearly exhibit Pattern D development. We retain *C. nevadensis* in *Climacograptus* and redescribe it based on additional material from the Polk Creek Shale of Oklahoma. Topotypes and other specimens of *Climacograptus putillus*, an often misidentified species, also exhibit Pattern D early astogeny and are redescribed below.

Climacograptus nevadensis Carter, 1972

Text-figure 13E–G

1963 *Climacograptus* aff. *C. innotatus* Nicholson; Churkin, pl. 2, fig. 27.
1972 *Climacograptus innotatus nevadensis* Carter, p. 47, pl. 1, figs 1, 8; text-fig. 2b–f.
1992 *Normalograptus tubuliferus nevadensis* (Carter); VandenBerg and Cooper, fig. 10b.
1995 *Climacograptus nevadensis* (Carter); Goldman *et al*., figs 2a–c, 3a–c.

Holotype. USNM 164439, from the Jacks Peak Formation of the Valmy Group, Chicken Creek, Elko County, Nevada.

Material. Twenty specimens, from exposures of the Polk Creek Shale at the Stringtown Quarry, southern Oklahoma. Comparative material from the lower Maravillas Formation in the Marathon region, West Texas was also examined.

Diagnosis. Pattern D climacograptine with prominent genicular flanges; rhabdosome septate, widens gradually throughout. Nema long, thin; virgella also long and thin.

Description. Rhabdosomes up to 10 mm long, gradually increasing in width from an average of 0·8 mm at the aperture of $\mathrm{th}1^1$ to a maximum of 1·6–1·8 mm distally. Thecae climacograptid, numbering 7–8 in the proximal 5 mm, decreasing in number to 5·5–6·5 in 5 mm distally. Supragenicular walls 0·4–0·45 mm long proximally, increasing to 0·6–0·65 mm distally with a prominent flange or spine up to 0·6 mm long at their base. Thecal apertures shallow, semicircular, slightly everted. Nema long and thin. Virgella moderately long and slender. Primordial astogeny is Pattern D of Mitchell (1987).

Remarks. *C. nevadensis* can be differentiated from *C. tubuliferus* by its distinct genicular flanges, shorter rhabdosome, wider proximal end, and thin as opposed to broad nema. It may be separated from *Paraclimacograptus innotatus* by its Pattern D (as opposed to Pattern I) primordial astogeny, or in poorly preserved material, by its much wider proximal end.

Stratigraphical and geographical occurrence. *Climacograptus nevadensis* is common in Ea3 to Ea4 strata of the Victoria (Australia) graptolite succession (VandenBerg and Cooper 1992), the lower Maravillas Formation of West Texas (Goldman *et al*. 1995), and in the *D. gravis* Biozone of Idaho and Nevada (Churkin 1963; Carter 1972; and see Goldman *et al*. 1995 for a revision of the late Ordovician graptolite zonation). *C. nevadensis* is a cosmopolitan mesopelgic species and part of the Oceanic Biofacies of Goldman *et al*. (1995).

Climacograptus putillus (Hall, 1865)

Text-figures 5J–Z; Plate 1, figures 1–2, 7

1865 *Graptolithus putillus* Hall, pp. 27, 44, pl. A, figs 10–12a.
1908 *Climacograptus putillus* (Hall); Ruedemann, p. 415 (*partim*), figs 368–370 (*non* 371–377).
non 1913 *Climacograptus putillus* Hall; Hadding, p. 49, pl. 3, figs 15–17. [= *Normalograptus haddingi* (Glimberg, 1952)].
1925 *Climacograptus putillus* (Hall); Ruedemann, p. 60 (*partim*).
non 1935 *Climacograptus putillus* (Hall); Thorslund and Asklund, p. 18, pl. 1, fig. 6 [= *Normalograptus haddingi* (Glimberg, 1952)].

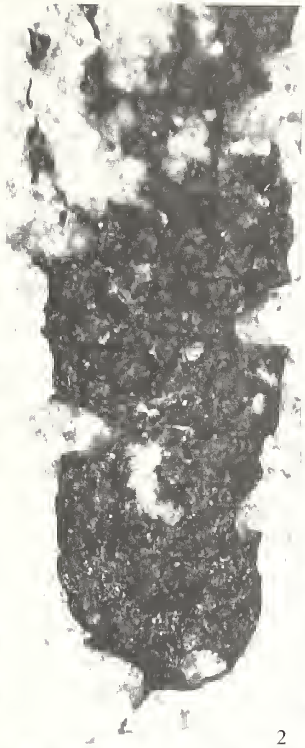
EXPLANATION OF PLATE 1

Figs 1–2, 7. *Climacograptus putillus* (Hall, 1865); 1–2, OSU 48525; Georgian Bay Formation; Gorrel Point, Manitoulin Island, Ontario; × 15 and × 45. 7, OSU 48527; Elgin Member, Maquoketa Formation; Graf, Iowa; × 18.

Figs 3–6. *Amplexograptus manitoulinensis* (Caley, 1936); OSU 48561, 48513, 48521, 48562; Blue Mountain Formation; 5 km south of Little Current, Manitoulin Island, Ontario; note pattern G proximal end development and the prominent genicular flanges; × 50, × 30, × 25 and × 18.

PLATE 1


1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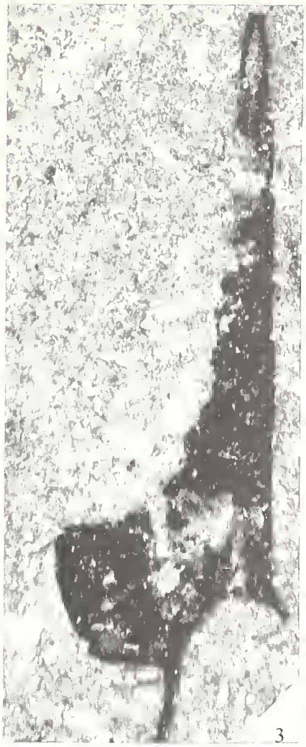
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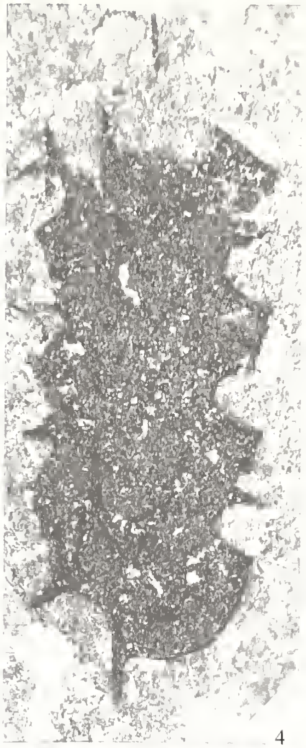
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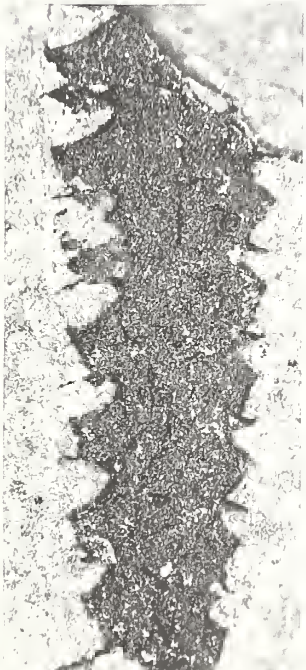
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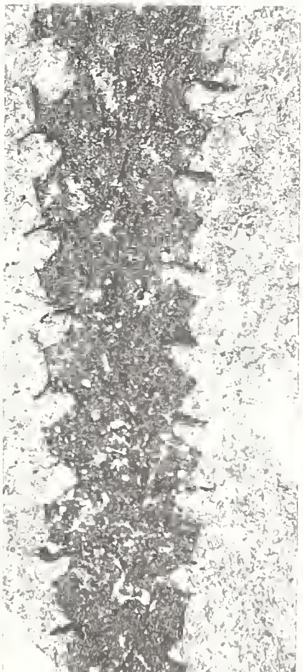
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7

GOLDMAN and BERGSTRÖM, *Climacograptus*, *Amplexograptus*

1935*b* *Climacograptus putillus* (Hall); Decker, p. 706, figs 1m–o, ?2m.
1935*b* *Climacograptus ulrichi* (Hall); Decker, p. 707, fig. 2e.
1947 *Climacograptus putillus* (Hall); Ruedemann, p. 434, pl. 72, figs 29–42.
1958 *Climacograptus putillus* (Hall); Werner and Echols, p. 1026, figs 1–2.
1969 *Pseudoclimacograptus* cf. *P. clevensis* Skoglund; Riva, p. 526, fig. j–k.
1977 *Pseudoclimacograptus* aff. *P. clevensis* Skoglund; Walters, p. 948, pl. 4, figs D–E.

Lectotype. Not yet designated.

Material. Over 100 specimens preserved as internal phophatized moulds from Hall's (1865) type locality near Graf, Iowa; approximately 50 internal phophatized moulds isolated from the Lower Maquoketa Shale near Saint Louis, Missouri; and 12 specimens from the Georgian Bay Formation on Manitoulin Island, Ontario. Additional, but less well preserved material was collected from the Haymeadow Creek Shale in the Upper Peninsula of Michigan, and from the Sylvan and Polk Creek shales of Oklahoma (given to the authors by S. C. Finney).

Diagnosis. Rhabdosome short, narrow ($< 1{\cdot}2$ mm), parallel-sided, with a gently undulose median septum. Thecae climacograptine, slightly everted, with straight genicula. Sicula with a short, stout virgella; th1^1 and th1^2 without spines. Proximal development representing Pattern D astogeny.

Description. Rhabdosome up to 16 mm long (excluding the nema), widening from 0·6–0·7 mm at the level of th1^1 aperture to a maximum of 0·8–1·0 mm at the level of th6^1. Thecae climacograptine, numbering 6–7 in the first 5 mm, decreasing to 5–6 in 5 mm distally, having straight supragenicular walls parallel to the rhabdosomal axis. Supragenicular walls 0·35–0·45 mm long in the second thecal pair, increasing to 0·58 to 0·68 mm long distally. Thecal apertures semicircular, horizontal to slightly everted, and shallow, occupying less than one-quarter of the total rhabdosome width. Sicula exposed on the obverse side of the rhabdosome for an average of 0·54 mm, bearing a short, stout virgella, with a prosicula composed of a single vertical rod that merges with the nema. Sicula aperture 0·2–0·25 mm wide. Length of the entire sicula unknown. Proximal development follows Pattern D primordial astogeny. The broad rounded arch of the th1^2 crossing canal, and the distinct dimple of the position of the list formed by the fusion of the th2^1 crossing canal with the upward growing flange from th1^2, are shown clearly in well preserved specimens (Pl. 1, figs 1–2, 7). A gently undulose median septum begins at the level of the second or third thecal pair. A long slender nema is present in some specimens.

Remarks. Hall's (1865, pl. A, figs 10–12a) type specimens of *Climacograptus putillus* are distal fragments from an exposure of the Elgin Member of the Maquoketa Formation near the Little Maquoketa River at Graf, Iowa (Text-fig. 4C). The Elgin Member at this locality is remarkably phosphatic and the graptolites are preserved as spectacular three-dimensional phosphatic moulds. Riva (1974) noted that Ruedemann (1908, 1925, 1947) had great difficulty in distinguishing between various small graptolites with climacograptine thecae and had referred specimens of several different taxa to *C. putillus* (e.g. *Normalograptus brevis* (Elles and Wood) and *Geniculograptus pygmaeus* (Ruedemann)). Riva (1974) restricted *C. putillus* to Hall's (1865) upper Ordovician material but did not redescribe it, and later (Riva, 1988) referred *C. putillus to Scalarigraptus* (a junior synonym of *Normalograptus*).

We have collected numerous complete specimens of *C. putillus* from the type locality. These specimens (Text-fig. 5Q–T, W–Z), as well as others from the Maquoketa Shale near Saint Louis, Missouri (Text-fig. 5U–V, Y), and from the Georgian Bay Formation on Manitoulin Island, Ontario clearly show a Pattern D primordial astogeny. We therefore retain *C. putillus* in *Climacograptus*. Specimens described as *Pseudoclimacograptus* cf. *P. clevensis* by Riva (1969) and *Pseudoclimacograptus* aff. *P. clevensis* by Walters (1977), recovered from well cores and outcrops of late Odrovician strata in the Saint Lawrence Lowlands and on Anticosti Island in Quebec, are morphologically identical to *C. putillus* specimens collected from the Georgian Bay Formation on Manitoulin Island (Text-fig. 5J–P), and also, although exhibiting preservational differences, to the phosphatic moulds of this species from the Upper Mississippi Valley. Specimens that agree generally with the morphology of *C. putillus*, but are too poorly preserved to show the undulose median septum or proximal end details, occur in the Sylvan Shale of Oklahoma (Ruedemann 1908; Decker 1935*b*).

Stratigraphical and geographical occurrence. Climacograptus putillus first appears in the uppermost *Amplexograptus manitoulinensis* Biozone in the Saint Lawrence Lowlands of Quebec and on Anticosti Island (Riva 1969, 1974; Walters 1977) and Manitoulin Island. Exposures of the lower Maquoketa Group (Formation) in the Upper Mississippi Valley also yield specimens of *Orthograptus eucharis*, *Rectograptus peosta*, and, at one locality (Savannah, Illinois), *Dicellograptus complanatus*. This suggests an age of upper *A. manitoulinensis* to lowermost *D. complanatus* biozone for the lower Maquoketa Group (Formation). *C. putillus* is not known outside Laurentia (specimens assigned to *C. putillus* by Hadding (1913) and Thorslund and Asklund (1935) from the middle Ordovician of Sweden belong to *Normalograptus haddingi* (Glimberg, 1952)). It is an endemic epipelagic species (Goldman *et al.* 1995).

Climacograptus tubuliferus Lapworth, 1876

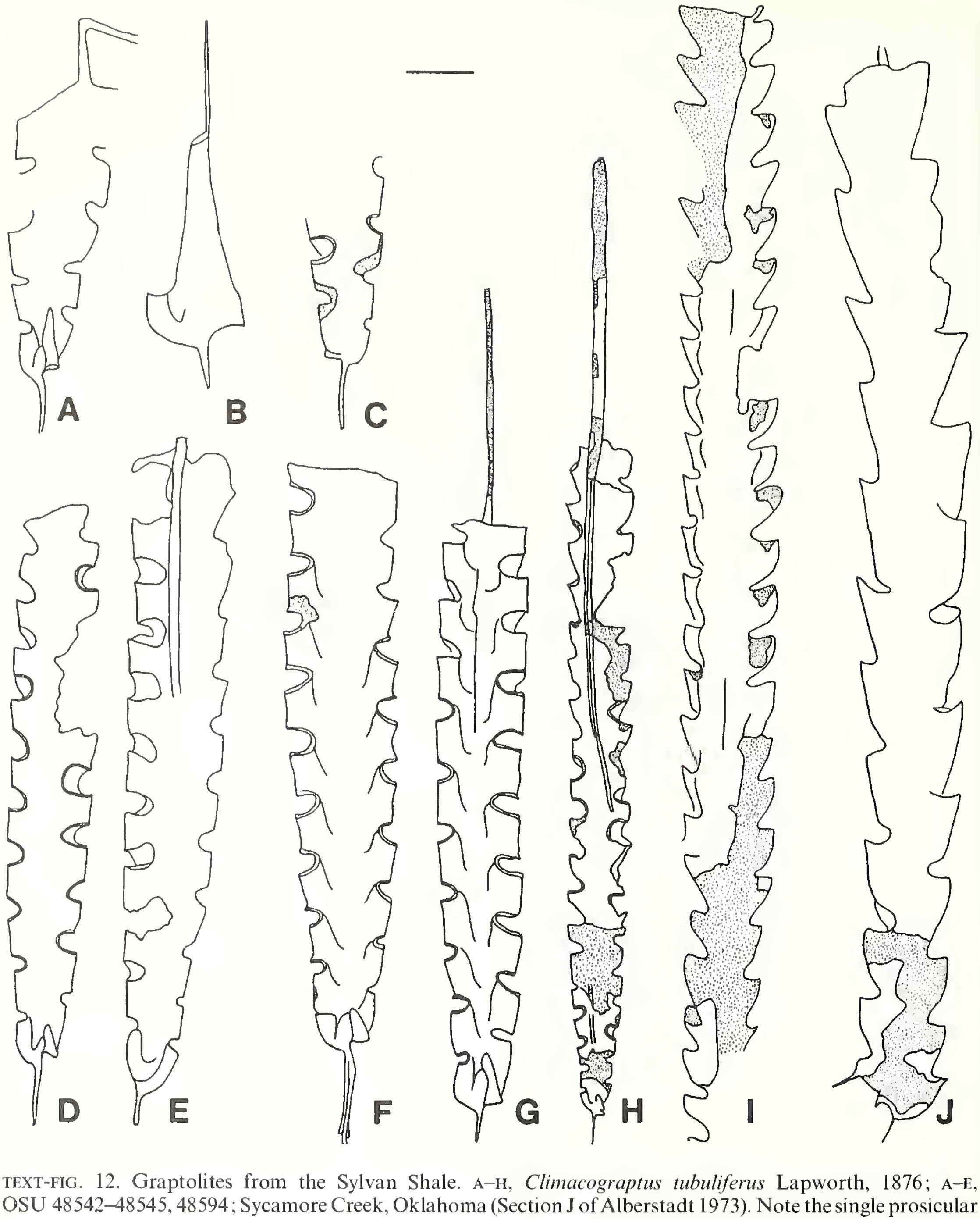
Text-figures 12A–H, 13A–D, I–K, Plate 2, figures 1–3

1876	*Climacograptus tubuliferus* Lapworth, pl. 2, fig. 49.
1877	*Climacograptus scalaris* var. *tubuliferus* Lapworth; Lapworth, pl. 6, fig. 33.
1902	*Climacograptus tubuliferus* Lapworth; Hall, p. 55, pl. 13, fig. 5; pl. 14, fig. 4.
1906	*Climacograptus tubuliferus* Lapworth; Elles and Wood, p. 203, pl. 27, fig. 8a–d; text-fig. 134a–c.
1908	*Climacograptus mississippiensis* Ruedemann, p. 414, pl. 28, figs 12–13; text-figs 366–367.
1908	*Diplograptus crassitestus* Ruedemann, p. 354, text-fig. 299.
1908	*Climacograptus ulrichi* Ruedemann, p. 413, text-fig. 364.
1935*b*	*Climacograptus mississippiensis* Ruedemann; Decker, p. 704, figs 1j–l, 2l.
1935*b*	*Diplograptus crassitestus* Ruedemann; Decker, p. 702, figs 1f–i, 2h.
1947	*Climacograptus tubuliferus* Lapworth; Ruedemann, p. 440, pl. 75, figs 54–56.
1947	*Climacograptus mississippiensis* Ruedemann; Ruedemann, p. 431, pl. 74, figs 3–9.
1947	*Diplograptus crassitestus* Ruedemann; Ruedemann, p. 415, pl. 71, figs 3–9.
1955	*Climacograptus tubuliferus* Lapworth; Harris and Thomas, p. 40, pl. 1, figs 10–12.
1960	*Climacograptus tubuliferus* Lapworth; Berry, p. 85, pl. 19, fig. 5.
1963	*Climacograptus tubuliferus* Lapworth; Ross and Berry, p. 132, pl. 10, figs 1–2.
1977	*Climacograptus tubuliferus* Lapworth; Carter and Churkin, p. 23, pl. 7, fig. 5.
1982*a*	*Climacograptus tubuliferus* Lapworth; Williams, p. 245, fig. 11a–n.
1983	*Climacograptus tubuliferus* Lapworth; Williams and Bruton, p. 170, figs 12c–e, 15a–n.
1983	*Climacograptus tubuliferus* Lapworth; Koren' and Sobolevskaya (*partim*), pl. 41, figs 1–3; text-fig. 51 (*non* pl. 40, figs 6–11).
1986	*Climacograptus tubuliferus* Lapworth; Finney, p. 453, fig. 13a, c.
1987	*Climacograptus tubuliferus* Lapworth; Williams, p. 80, figs 4f, h–i, 6g, 7o–q.
1988	*Scalarigraptus tubuliferus* (Lapworth); Riva, fig. 2i–j.
1989	*Normalograptus tubuliferus* (Lapworth); Riva, *in* Riva and Ketner, p. 87, figs 10a–i, 11a–e.
1991	*Climacograptus tubuliferus* Lapworth; Williams, p. 593, pl. 1, figs 2–4, ?5; text-fig. 8a–c.
1995	*Climacograptus tubuliferus* Lapworth; Goldman *et al.*, figs 2D–E, 3D–F.

Lectotype. BU 1193 g, designated by Riva (*in* Riva and Ketner 1989, fig. 10h); from the Lower Hartfell Shale (*Pleurograptus linearis* Biozone) of Hartfell Spa, southern Scotland.

Material. Fifty specimens from the Sylvan and Polk Creek shales of southern Oklahoma (collected by S. C. Finney); holotype and paratype material of *C. mississippiensis* and *D. crassitestus* (USNM 54268, 242263, 240638, 340636) also from the Sylvan Shale; and the holotype of *C. ulrichi* (USNM 54276a–b) from the Maquoketa Shale near Spencer, Missouri.

Diagnosis. Large, Pattern D climacograptine with a long, thick nema commonly exhibiting a three-vaned structure. Rhabdosome widening gradually from a very narrow proximal end. Virgella long, commonly lodged within a short tubular downgrowth of the sicula (parasicula). Rhabdosome widening gradually from 0·64 mm proximally to 2·5 mm distally.



TEXT-FIG. 12. Graptolites from the Sylvan Shale. A–H, *Climacograptus tubuliferus* Lapworth, 1876; A–E, OSU 48542–48545, 48594; Sycamore Creek, Oklahoma (Section J of Alberstadt 1973). Note the single prosicular rod in B, indicating Pattern D proximal development. F–G, holotype and paratype of *Climacograptus mississippiensis* Ruedemann, 1935*b*; USNM 54268, 242263; USGS collection 241; near Davis, Oklahoma; specimens in partial relief and slightly compressed laterally. H, USNM 240638; same locality as F–G. I–J, *Orthograptus crassitestus* (Ruedemann, 1908); H, paratype, USNM 240638; same locality as F–G; specimen flattened. I–J, holotype and paratype; USNM 54266, 235604; USGS collection 241; near Davis, Oklahoma. In addition

Description. Proximal end very narrow, characterized by Pattern D primordial astogeny. Thecae with slight outward inclination, straight to slightly rounded supragenicular walls, and numbering 6–7 in 5 mm proximally, decreasing to 4–5 in 5 mm distally. Thecal apertures horizontal, semicircular, and narrow. Rhabdosome displaying a delayed median septum, beginning at the seventh thecal pair. Nema long, wide, and often displaying a three-vaned structure (Text-fig. 13A–B). Virgella long, narrow, commonly enclosed within a short parasicula.

Remarks. The holotype and paratypes of *Climacograptus mississippiensis* Ruedemann (USNM 54268 and 242263, respectively; Text-fig. 12F–G) are well preserved specimens of *C. tubuliferus* in partial relief. Hence, *C. mississippiensis* is a junior synonym of *C. tubuliferus*. Similarly, the holotype (Ruedemann 1908, p. 413, fig. 364) of *Climacograptus ulrichi* Ruedemann (USNM 54276a) is a specimen of *C. tubuliferus*, although several specimens on the reverse side of the slab appear to be referable to *C. putillus*. Paratypes of '*Diplograptus*' *crassitestus* Ruedemann on the slab USNM 240638 (Ruedemann 1908, p. 354, fig. 299; Text-fig. 12H) also belong to *C. tubuliferus*. However, the holotype (USNM 54266), and other paratype specimens of '*D*'. *crassitestus* (Text-fig. 12I–J) belong to the *Orthograptus calcaratus* species group and are redescribed below.

Climacograptus tubuliferus can be differentiated from *Climacograptus caudatus* Lapworth by its narrower proximal end, wider three-vaned nema, delayed median septum (specimens of *C. caudatus* are septate from the third thecal pair), and its shorter, less well developed parasicula. An accurate assessment of the differences between *C. tubuliferus* and *C. styloideus* Elles and Wood requires a revision of the latter using well preserved and large populations of specimens.

Stratigraphical and geographical occurrence. Climacograptus tubuliferus is an abundant element in the cosmopolitan mesopelagic Oceanic Biofacies of Goldman *et al.* (1995). It is common in the Lower Hartfell Shale of Scotland (*Pleurograptus linearis* Biozone; Williams, 1982*a*), the lower Maravillas Formation of West Texas (Zone 13 of Berry 1960; the *D. gravis* Zone of Goldman *et al.* 1995), the Sylvan and Polk Creek shales of Oklahoma, and in the *D. gravis* through *C. uncinatus* zones in Victoria (VandenBerg and Cooper 1992). An offshore, deeper water species, it is absent from the Appalachian Basin and most of the craton in North America.

Subfamily ORTHOGRAPTINAE Mitchell, 1987

Genus AMPLEXOGRAPTUS Elles and Wood, 1907

Type species. By original designation; *Diplograptus perexcavatus* Lapworth, 1873.

Amplexograptus manitoulinensis (Caley, 1936)

Plate 1, figures 3–6; Text-figure 5A–I

1875 *Diplograptus hudsonicus* Nicholson; Nicholson, p. 38, fig. 15 [suppressed specific name; ICZN opinion 1561].
1936 *Climacograptus manitoulinensis* Caley, p. 65, fig. 1.
1947 *Climacograptus manitoulinensis* Caley; Ruedemann, p. 431, pl. 73, fig. 55.
1969 *Climacograptus manitoulinensis* Caley: Riva, p. 526, fig. 6g–h.
1973 *Amplexograptus* aff. *A. prominens* Barrass; Jackson, p. 2, fig. 2b, e–f.
1977 *Climacograptus manitoulinensis* Caley; Walters, p. 937, pl. 3, figs a–b, g.
1986 *Climacograptus manitoulinensis* Caley; Finney, fig. 8o–p.
1988 *Pseudoclimacograptus manitoulinensis* (Caley); Riva, fig. 5g–j.

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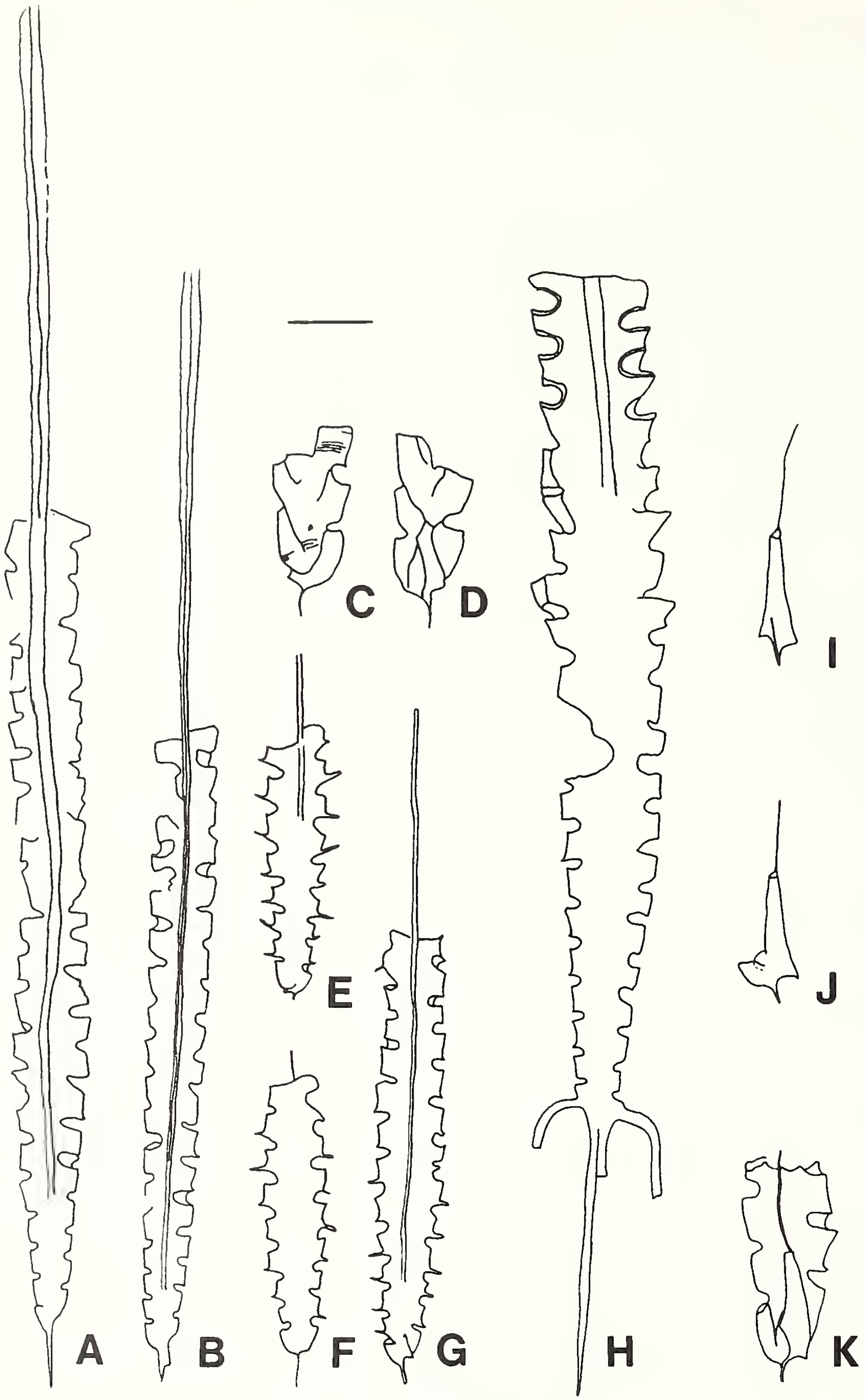
to *C. tubuliferus* and *O. crassitestus*, USGS collection 241 contains many fragments of *Dicellograptus complanatus*. Scale bar represents 1 mm (except for fig B where it represents 0·5 mm and figs H–J where it represents 2 mm).



TEXT-FIG. 13 For caption see opposite.

Type specimen. Caley (1936, fig. 1) illustrated three specimens, but designated no holotype. From these we select the middle one in his figure 1 as the lectotype. According to Caley (1936, p. 66) his specimens were collected at Lot 12, concession XII, Howland Township (which is near Highway 6 about 5 km south of Little Current), and deposited in the Royal Ontario Museum, Toronto.

Material. Several hundred topotype specimens from the Blue Mountain Formation along the creek that crosses Highway 6, 5 km south of Little Current, Manitoulin Island, Ontario, Canada.

Diagnosis. Rhabdosome short, narrow, aseptate; thecae amplexograptid, with short, outwardly inclined supragenicular walls, and very prominent genicular flanges. $\mathrm{Th1^1}$ is U-shaped, and lacks a spine. Primordial astogeny is Pattern G of Mitchell (1987).

Description. Rhabdosome short, generally with less than 15 thecal pairs and less than 10 mm long; widens from 0·80–0·90 mm at the level of the $\mathrm{th1^1}$ aperture to 1·15–1·25 mm at $\mathrm{th6^1}$; long specimens reach a maximum width of 1·5 mm. Thecae amplexograptid, with short, outwardly inclined supragenicular walls and large prominent genicular flanges; closely packed, numbering 8–9 in the first 5 mm, decreasing to 7–8 in 5 mm distally. Supragenicular wall lengths vary from 0·28–0·36 mm at $\mathrm{th1^1}$ to 0·40–0·44 mm distally. Thecal apertures everted, lacking lappets. Sicula with a virgella and paired anti-virgella spines, 1·80–2·0 mm long, and exposed for an average length of 1·0 mm on the obverse side of the rhabdosome. Prosicula short with very prominent vertical rods and thin periderm. $\mathrm{Th1^1}$ growing down along the sicula and then turning upward in a broad smooth arch, and lacking the sub-apertural or mesial spine characteristic of most amplexograptids.

Remarks. Riva (1987*b*) recognized *Climacograptus manitoulinensis* Caley, 1936 to be a junior synonym of *Diplograptus hudsonicus* Nicholson, 1875. However, because the latter name had not been used for more than a century, he applied to the ICZN in 1987 (Case 2596) for a conservation of the former, widely used, species name, and the ICZN ruled in his favour in 1989 (ICZN Opinion 1561).

Riva (1987*a*) placed *A. manitoulinensis* in *Paraclimacograptus* Přibyl along with *A. decipiens* (Riva) based on the prominent genicular elaborations and spineless $\mathrm{th1^1}$ exhibited by these species. The type species of *Paraclimacograptus*, however, is *P. innotatus* (Nicholson), a Silurian species with Pattern I early astogeny. Thus, neither *A. manitoulinensis* nor *A. decipiens* (specimens of which exhibit Pattern G development) belong to *Paraclimacograptus*. *A. manitoulinensis*, *A. decipiens*, and *A. prominens* Barrass are differentiated from all other *Amplexograptus* species by their prominent genicular elaborations and spineless $\mathrm{th1^1}$. Specimens of *A. manitoulinensis* can be differentiated from those of *A. decipiens* by their possession of genicular flanges as opposed to paired genicular spines, and from those of *A. prominens* by their Pattern G as opposed to K proximal astogeny, lack of lappets and much narrower rhabdosome.

Stratigraphical and geographical occurrence. Amplexograptus manitoulinensis is the predominant element and nominal species of Riva's (1969, 1974) *A. manitoulinensis* Biozone. It has been reported by Walters (1977) from the Nicolet River Formation of the Saint Lawrence Lowland of Quebec, and by Finney (1986) from 113 m above the base of the Viola Group at Rayford Quarry (Alberstadt's (1973) Section Q) in southern Oklahoma. *A. manitoulinensis* has not been recorded from outside North America and belongs to the Laurentian Biofacies of Goldman *et al.* (1995).

Genus ORTHOGRAPTUS Lapworth, 1873

Type species. By original designation; *Graptolithus quadrimucronatus* Hall, 1865.

Remarks. Relationships between the taxa within *Orthograptus* have historically been based on thecal morphology. Elles and Wood (1907, p. 220) divided *Orthograptus* into three informal groups:

TEXT-FIG. 13. Graptolites from the Polk Creek Shale, Stringtown Quarry, Oklahoma. A–D, I–K, *Climacograptus tubuliferus* Lapworth, 1876. OSU 48546–48552. E–G, *Climacograptus nevadensis* Carter, 1972; OSU 48553–48555. H, *Climacograptus hastatus* Hall, 1902; OSU 48556. Scale bar represents 2 mm (A–B, E–H) or 1 mm (C–D, I–K).

the *quadrimucronatus* group (specimens whose thecae bear paired apertural spines and are rectangular in cross section), the *calcaratus* group (specimens whose thecae bear paired apertural horns and are sub-rectangular in cross section), and the *truncatus* group (= *amplexicaulis* group, see Riva 1974; specimens whose thecal apertures lack elaboration and are oval in cross section). According to Elles (1922) these groups also had separate ancestries; she believed that the *quadrimucronatus* group evolved from a species of *Glossograptus*, and the *calcaratus* and *amplexicaulis* groups from *Glyptograptus* (now *Hustedograptus*) *teretiusculus*. Elles' suggestion of a polyphyletic origin for *Orthograptus* is consistent with the view of evolution by orthogenesis that was pervasive in graptolite studies during the first half of this century.

Ruedemann (1908, 1947) also believed that there was a close phylogenetic relationship between the spinose orthograptids of the *quadrimucronatus* group and *Glossograptus*, and placed them within that genus. His (1908, 1947) classification was not, however, adopted outside North American (e.g. Harris and Thomas 1955), and was subsequently abandoned there as well (Berry 1960; Ross and Berry 1963). Přibyl (1949), concerned about the apparent polyphyletic origin of *Orthograptus*, erected *Rectograptus* to include the non-spinose *calcaratus* and *amplexicaulis* group orthograptids. Use of Přibyl's genus has been sporadic.

The problem with all the preceding classifications is that they were based on phylogenies constructed from thecal characters and not astogenetic similarity. Mitchell (1987) reunited all three groups within *Orthograptus*, recognizing a common ancestry based on a similar early astogeny (Pattern G). He (1987, p. 378) rejected the segregation of the non-spinose orthograptids into *Rectograptus*, noting that the 'taxon is defined on the basis of the loss of a single, relatively simple character, and there is no reason to assume that such a loss should be unique'.

We agree with Mitchell's (1987) contention that the absence of a character is a poor basis for establishing a new taxon; however, a close examination of the morphology of the *amplexicaulis* group orthograptids shows sufficient differences from the morphology of other *Orthograptus* taxa (particularly in the proximal end) to warrant its inclusion in a separate genus. The proximal end of *Rectograptus amplexicaulis* bears a striking resemblance to that of *Amplexograptus* (Riva, 1987*a*, p. 929; Text-fig. 14C–D). The initial three to six thecal pairs in *R. amplexicaulis* are geniculate and strongly resemble the early thecae in specimens of *Amplexograptus*. In both taxa, th1^1 grows down along the sicula and then turns upward in a rather sharp 'U', its aperture facing upward as opposed to outward as in *Orthograptus*. Th1^2 grows horizontally across the base of the sicula on the reverse side of the rhabdosome and then turns sharply upward, its aperture being either in contact with the sicula or very close to it, leaving only a short portion of its metatheca exposed in the obverse view. Th1^1 has a prominent mesial spine and th1^2 does not bear a spine. The sharp upward bends in the first two thecae impart a rectangular shape to the proximal end in *Rectograptus* and *Amplexograptus* (Text-fig. 14A–D). Additionally, *Rectograptus amplexicaulis* is aseptate (the *quadrimucronatus* and *calcaratus* groups are generally septate), and the thecal margins are straight and everted, as opposed to being lobate and horizontal.

In *Orthograptus*, the first two thecae grew upward at a much gentler angle than in *Rectograptus*, causing their apertures to face outward and not upward, and th1^2 has a much longer portion of its metatheca visible on the observe side of the rhabdosome. Th1^1 and th1^2 both have apertural spines

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EXPLANATION OF PLATE 2

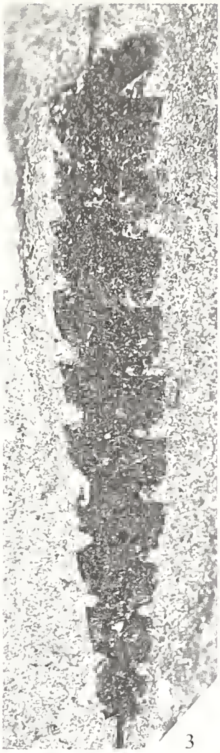
Figs 1–3. *Climacograptus tubuliferus* Lapworth, 1876; Sylvan Shale; Sycamore Creek (Section J of Alberstadt 1973), Arbuckle Mountains, Oklahoma; 1–2, OSU 48563; note pattern D proximal end development; ×10 and ×25. 3, OSU 48564; ×10.

Figs 4–8. *Rectograptus peosta* (Hall, 1861); 4–5, OSU 48540, 48537; Fort Atkinson Formation, Maquoketa Group, Savannah, Illinois; ×18. 6–8, OSU 48565–48567; three-dimensional internal moulds; Elgin Member, Maquoketa Formation; Graf, Iowa; ×25, ×13 and ×35.

PLATE 2


1


2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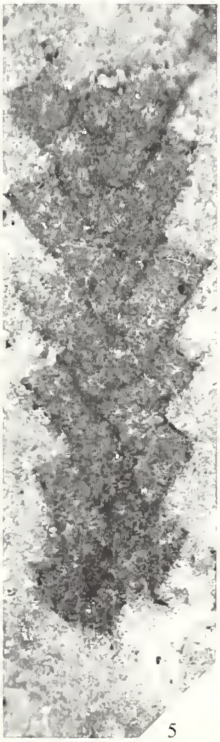
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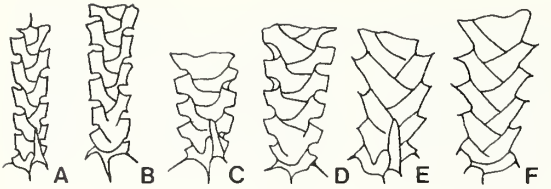
GOLDMAN and BERGSTRÖM, *Climacograptus*, *Rectograptus*



TEXT-FIG. 14. Obverse and reverse views of the proximal portion of specimens representing three different genera with Pattern G early astogenetic development. A–B, *Amplexograptus praetypicalis* Riva; C–D, *Rectograptus amplexicaulis* (Hall); E–F, *Orthograptus quadrimucronatus* (Hall). Note that the proximal end in *Rectograptus* is of similar size to that of *Orthograptus* but of similar shape to that of *Amplexograptus*. *Rectograptus* and *Amplexograptus* share a spineless th1^2, amplexograptid proximal thecae, and a short exposure of th1^2 in obverse view. These characters are not restricted to the species illustrated but occur consistently in these genera.

(although the th1^2 spines were secondarily lost in the youngest end members of the *O. quadrimucronatus* lineage). The more gentle curvature of the first two thecae as they turn upward imparts a smoother, more rounded shape in the proximal end of *Orthograptus* that contrasts sharply with the rectangular proximal end of *Rectograptus* and *Amplexograptus* (Text-fig. 14A–F).

Thus, although *Orthograptus*, *Rectograptus* and *Amplexograptus* all have Pattern G astogeny, the proximal ends of specimens of *Rectograptus* and *Amplexograptus* share several characters not found in *Orthograptus*. Whilst obviously closely related, *Rectograptus* and *Amplexograptus* also exhibit important differences. In *Rectograptus*, only the first few thecae are amplexograptid, whilst most of the rhabdosome is composed of straight orthograptid thecae. Additionally, although the early thecae of *Rectograptus* are geniculate, they do not bear the prominent lappets common in species of *Amplexograptus* (Riva 1987*a*). Therefore, we deem *Rectograptus* to be a valid genus and revise its diagnosis below.

Orthograptus crassitestus (Ruedemann, 1908)

Text-figure 12I–J

1908 *Diplograptus crassitestus* Ruedemann, pp. 334 (*partim*), text-fig. 300; pl. 25, fig. 6; *non* text-fig. 299.

1947 *Diplograptus* (*Mesograptus*) *crassitestus* (Ruedemann); Ruedemann, pp. 415 (*partim*), pl. 71, fig. 3; *non* figs 4–9.

Holotype. USNM 54266, from the Sylvan Shale, 3·2 km north of Dougherty, Oklahoma.

Material. Holotype and paratypes (USGS collection 241 made by E. O. Ulrich) from the above locality.

Remarks. The material of *Orthograptus crassitestus* examined by us is too poor to permit a detailed description, but several observations may be made. The type material includes two distinct species. The holotype and two paratypes (USNM 235604–235605) are orthograptids with Pattern G or K proximal astogeny (the preservation is too poor to differentiate between these two similar developmental patterns). The rest of the material (e.g. USNM 240638) belongs to *Climacograptus tubuliferus*. Specimens of *O. crassitestus* exhibit a long, slender, gradually widening rhabdosome with long, gently sinusoidal thecae. The thecae lack cusps or spines and are inclined at a very low angle to the rhabdosome axis. *O. crassitestus* is reminiscent of *O. fastigatus* Davies and *O. thorsteinssoni* Melchin, with the exception of an apertural spine on th1^2 that is lacking in the latter two species. Ruedemann's specimens are also similar in morphology to specimens of '*Glyptograptus*' *altus* Ross and Berry. The phylogenetic relationships among this group of upper Ordovician orthograptids are presently obscure and in need of further study.

Stratigraphical and geographical occurrence. *Orthograptus crassitestus* is known only from the Sylvan Shale of Oklahoma. Specimens of *C. tubuliferus* and *D. complanatus* co-occur with *O. crassitestus*, suggesting that it occurs in the *D. complanatus* Biozone.

Orthograptus eucharis (Hall, 1865)

Plate 3, figures 1–5; Text-figure 15A–C

1865 *Retiograptus eucharis* Hall, p. 16, pl. 14, fig. 9.
1995 *Orthograptus eucharis* (Hall); Goldman, pp. 530, figs 15·6–15·7, 17·1–4 [with full synonymy].

Holotype. GSC 13623 (synrhabdosome), from the Pointe Blue Shales on Lake St John, Quebec.

Material. Hundreds of flattened and isolated three-dimensionally preserved specimens from the lowermost Maquoketa Group (Formation) in the Upper Mississippi Valley, and several flattened specimens from the Haymeadow Creek Shale of northern Michigan.

Diagnosis. *Orthograptus* with small, narrow, parallel-sided, aseptate rhabdosome that tends to narrow distally; th1^1 with apertural spine, th1^2 lacking a spine, subsequent thecae with paired apertural spines. Periderm attenuated. Primordial astogeny is Pattern G of Mitchell (1987).

Description. Rhabdosomes short (rarely more than ten thecal pairs), narrow, parallel-sided, maintaining a mean width of 0·9 mm throughout or narrowing distally; aseptate; thecae inclined to the rhabdosome axis at an angle of 35–40°; th1^1 with single apertural spine, th1^2 lacking a spine, subsequent thecae with paired apertural spines. Sicula averages 1·96 mm in length and 0·33 mm in apertural width, and is visible in observe view for a mean distance of 0·92 mm before becoming enclosed within the rhabdosome. Periderm attenuated, especially along the free ventral walls of the thecae.

Remarks. This species has been revised by Goldman (1995).

Stratigraphical and geographical occurrence. *Orthograptus eucharis* is the most common graptolite in the lower Maquoketa Group (Formation). It is abundant in both the dense black shale (Argo-Fay Bed) that marks the base of the Maquoketa Group in north-western Illinois (Kolata and Graese 1983) and in the Elgin Member in north-eastern Iowa and southern Minnesota. In Quebec, Michigan, and Oklahoma, specimens of *O. eucharis* occur in the uppermost *G. pygmaeus* to *A. manitoulinensis* Biozone (Riva 1969, 1974; Finney 1986). *O. eucharis* is unknown from outside North America and is an endemic epipelagic species and part of the Laurentian Biofacies of Goldman *et al*. (1995).

Orthograptus quadrimucronatus (Hall, 1865)

Text-figures 2L–N, 14E–F

1865 *Graptolithus quadrimucronatus* Hall, p. 144, pl. 13, figs 1–10.
1877 *Diplograptus quadrimucronatus* (Hall); Lapworth, p. 133, pl. 6, fig. 20.
1907 *Diplograptus* (*Orthograptus*) *quadrimucronatus* (Hall); Elles and Wood, p. 223, pl. 28, fig. 1a–d; text-fig. 145a–f.
1936 *Diplograptus foliaceus gorrelensis* Caley, p. 66, fig. 2.
1947 *Glossograptus quadrimucronatus* (Hall); Ruedemann, p. 452 (*partim*), pl. 78, figs 1–2; (*non* figs 3–5).
1995 *Orthograptus quadrimucronatus quadrimucronatus* (Hall); Goldman, p. 525, figs 10·1–10·19, 11·1–11·6, 15·1–15·5, 17·5–17·9 [see for full synonymy].

Syntypes. GSC 1898a–b, d from the Pointe Blue Shales on Lake St John, Quebec.

Material. Several specimens from the Georgian Bay Formation on Manitoulin Island, and the lower Maquoketa Group in the Rifle Hill Quarry, Fillmore County, Minnesota.

Diagnosis. Orthograptus with short single apertural to sub-apertural spines on th1^1 and th1^2; subsequent thecae with paired apertural spines, none of consistently unusual length; rhabdosome septate, gradually widening. Primordial development is Pattern G of Mitchell (1987).

Remarks. This species has been revised recently by Goldman (1995).

Stratigraphical and geographical occurrence. Orthograptus quadrimucronatus is common in the *C. americanus* through *A. manitoulinensis* biozones in North America. It also occurs ubiquitously in the upper middle and upper Ordovician world-wide. Due to its rather long range, *O. quadrimucronatus* has limited biostratigraphical utility. Specimens collected from the Georgian Bay Formation and from the Lower Maquoketa Group (Formation) are from the *A. manitoulinensis* Biozone. *O. quadrimucronatus* belongs to the cosmopolitan epipelagic Oceanic Biofacies of Goldman *et al.* (1995).

Genus RECTOGRAPTUS Přibyl, 1949

Type species. By original designation; *Graptolites amplexicaule* Hall, 1847.

Revised diagnosis. Rhabdosome aseptate, with amplexograptid proximal thecae and orthograptid distal thecae; th1^1 with mesial to subapertural spine, other thecae non-spinose; thecal apertures smooth, straight, non-lobate, lacking spines or cusps; proximal end amplexograptid-like with th1^1 and th1^2 sharply upturned imparting a rectangular shape. Primordial astogeny is Pattern G of Mitchell (1987).

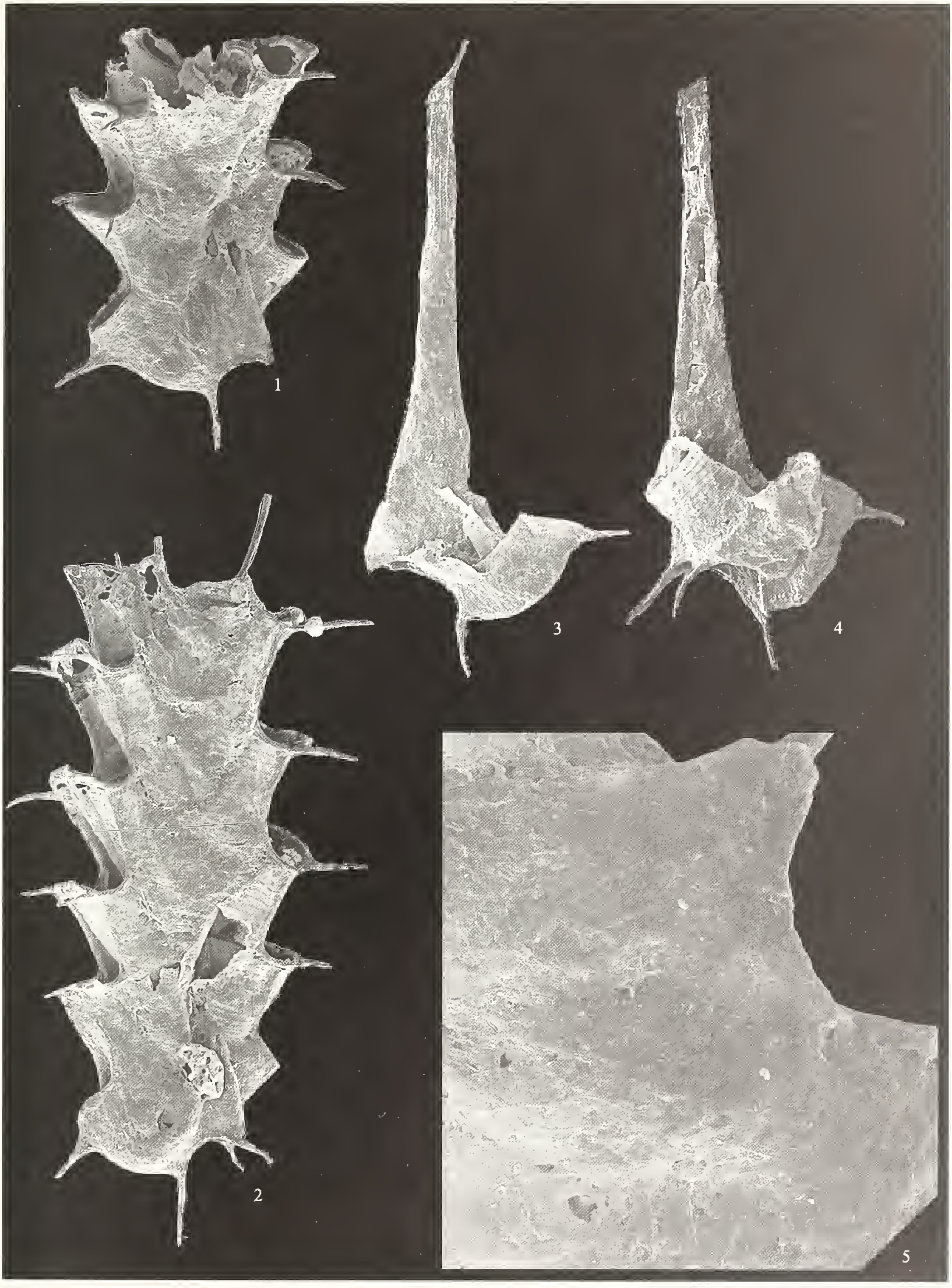
Rectograptus peosta (Hall, 1861)

Plate 2, figures 4–8; Text-figure 11A–K

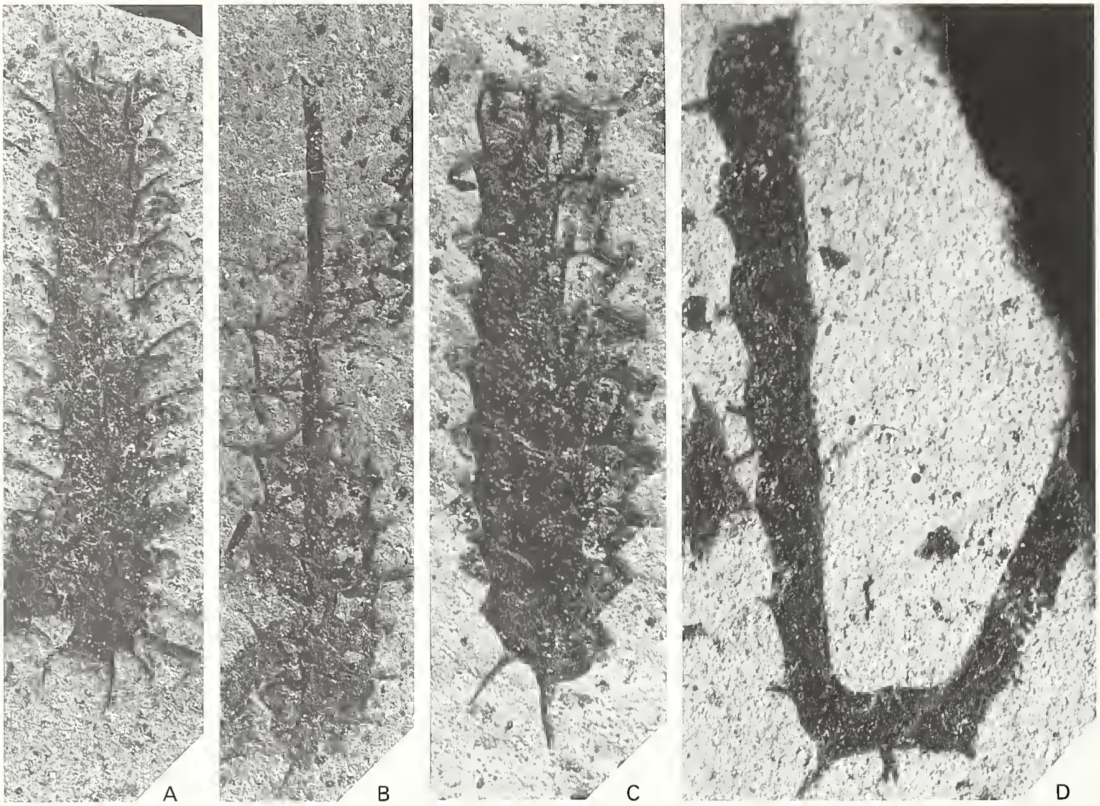
1861	*Graptolithus* (*Diplograptus*) *peosta* Hall, p. 17.
?1861	*Retiolites gracilis* Roemer, p. 31, pl. 5, fig. 1.
?1880	*Diplograptus socialis* Lapworth, p. 166, pl. 4, fig. 13a–c.
1895	*Graptolithus* (*Diplograptus*) *peosta* Hall; Whitfield, p. 47, pl. 5, fig. 12.
?1907	*Diplograptus* (*Orthograptus*) *truncatus* var. *socialis* (Lapworth); Elles and Wood, p. 237, pl. 29, fig. 7a–e; text-fig. 157a–d.
1908	*Diplograptus peosta* (Hall); Ruedemann, p. 372, pl. 25, fig. 17.
1915	*Diplograptus peosta* (Hall); Hadding, p. 16, pl. 2, figs 12–14.
1947	*Diplograptus* (*Glyptograptus*) *peosta* (Whitfield); Ruedemann, p. 408 (*partim*), pl. 69, figs 22–25, ?figs 26–27, 28a; *non* pl. 69, figs 28–31.
?1963	*Orthograptus truncatus* var. *socialis* (Lapworth); Ross and Berry, p. 151, pl. 11, fig. 21.
?1963	*Orthograptus gracilis* (Roemer); Skoglund, p. 46, pl. 4, fig. 6, pl. 5, figs 5, 7, text-fig. 11 [includes synonymy list of *O. gracilis*].
?1970	*Orthograptus truncatus socialis* (Lapworth); Toghill, p. 24, pl. 13, figs 7–9, pl. 16, fig. 7.
1971	*Orthograptus truncatus* var. *socialis* (Lapworth); Berry and Marshall, p. 256, text-fig. 3a–c.
?1987	*Orthograptus socialis* (Lapworth); Williams, p. 81, figs 7c–m, 8f–h.
?1991	*Orthograptus socialis* (Lapworth); Williams, p. 595, pl. 2, figs 16–17; text-fig. 91–n.

EXPLANATION OF PLATE 3

Figs 1–5. *Orthograptus eucharis* (Hall, 1865); SEM photomicrographs; Elgin Member, Maquoketa Formation, Clermont, Iowa. 1–2, OSU 48568–48569, × 45. 3–4, OSU 48570–48571; note the upward growing flange from th1^1 that meets the th1^2 crossing canal to construct the th1^2 protheca; × 60. 5, OSU 48572; note cortical bandages; × 190.



GOLDMAN and BERGSTRÖM, *Orthograptus*



TEXT-FIG. 15. A–C, *Orthograptus eucharis* (Hall, 1865); OSU 48557–48559; Elgin Member, Maquoketa Formation; Postville North Quarry, Iowa; note the reduced periderm; × 12. D, *Dicellograptus gravis* Keble and Harris, 1925; OSU 48560; lower Sylvan Shale; Rayford Quarry, Oklahoma; note the mesial spines present on the thecae, and the distinct bend of the supragenicular wall; × 15.

Type specimen. Not yet designated.

Material. Over 100 specimens from outcrops of the lower Maquoketa Group (Formation) in Iowa and Illinois (see Table 1).

Diagnosis. Slender *Rectograptus* species, aseptate, widening from 0·84–1·00 mm at the th1^1 aperture to 1·16–1·36 mm at the sixth thecal pair, to a maximum of 1·56 mm in long specimens. Th1^1 bears a single apertural spine; th1^2 and subsequent thecae are spineless; thecae straight, simple, with everted apertures, inclined to rhabdosome axis at a low angle (approximately 25°).

Description. Thecae number 7–8 in the proximal 5 mm, decreasing to 5–6 in 5 mm distally in long specimens. Sicula 1·88–2·0 mm long, exposed on the obverse side of the rhabdosome for about half its total length. Primordial astogeny is Pattern G of Mitchell (1987).

Remarks. A plethora of species similar to *R. peosta* have been described from North America and Europe (e.g. by Elles and Wood 1907; Ruedemann 1947; Ross and Berry 1963). Many of these taxa have undoubtedly been erected on the basis of preservational differences, stratigraphical position and national origin. A lack of definable characters makes the task of sorting out their taxonomy

TABLE 1. Occurrence of upper Ordovician graptolite species at each of the investigated localities in the North American Midcontinent. Numbers correspond to localities in Appendix.

	Locality																		
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Dicellograptus complanatus	.	.	.	.	.	.	.	.	.	.	X	.	.	.	X	X	.	.	X
Dicellograptus gravis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.
Amplexograptus manitoulinensis	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Climacograptus nevadensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.
Climacograptus putillus	.	X	X	cf	.	.	.	.	X	.	.	.	X	.	.	X	.	.	.
Climacograptus tubuliferus	.	.	.	.	.	.	.	.	.	.	.	.	.	X	X	X	X	.	X
Geniculograptus typicalis	X	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geniculograptus pygmaeus	X	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Orthograptus crassitestus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	X
Orthograptus eucharis	.	X	.	X	.	X	X	X	X	X	.	X	.	.	.	.	.	.	.
Orthograptus quadrimucronatus	.	X	X	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.
Orthograptus spinigerus	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rectograptus amplexicaulis	.	X	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rectograptus peosta	.	.	.	X	.	.	.	.	X	X	X	X	.	X	.	.	.	.	.
'*Glyptograptus*' *lorrainensis*	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Normalograptus sp. nov.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	X	X	X	.
Orthoretiolites hami	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	X	.	.	.
Phormograptus sooneri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.

troublesome. *Rectograptus peosta* can be differentiated from *R. amplexicaulis* (Hall) by its shorter sicula, more slender rhabdosome and lower angle of thecal inclination. *R. peosta* is similar in its dimensions to *Rectograptus socialis* (Lapworth) and is probably a senior synonym of that taxon. Also, *R. peosta* is closely similar to, and may be conspecific with, *R. gracilis* (Roemer), which occurs in coeval strata in Baltoscandia (Skoglund 1963). Compared with the latter, *R. peosta* appears to have a slightly narrower rhabdosome and the thecae are inclined to the rhabdosome axis at a slightly smaller angle (25° versus 35°), but the significance of these small differences needs further evaluation.

Stratigraphical and geographical occurrence. *Rectograptus peosta* is common in the *A. manitoulinensis* and *D. complanatus* biozones in North America, and in the *D. complanatus* Biozone of Scotland (Williams 1987). *R. peosta* is a cosmopolitan epipelagic species and occurs in both Oceanic and Laurentian biofacies of Goldman *et al.* (1995).

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APPENDIX: GRAPTOLITE LOCALITY DETAILS

1. Eastern Boundary of Craiglieth Provincial Park, south shore of Georgian Bay, Craiglieth, Ontario; Collingwood Member of the Lindsay Formation.
2. Ontario Geological Survey Drill Core 83-5 and exposures along Highway 6, 5–7 km south of Little Current, Manitoulin Island, Ontario; Collingwood Member of the Lindsay Formation, Blue Mountain and Georgian Bay formations.
3. Gorrel Point, shoreline bluffs, 4 km north-east of Gore Bay, Manitoulin Island, Ontario; Georgian Bay Formation.
4. Haymeadow Creek, northern part of Sec. 19, T. 42 N., R. 20 W., Upper Peninsula of Michigan; Haymeadow Creek Shale.
5. Bichler Quarry, Sec. 1, T. 39 N., R. 3 W., Groos, Upper Peninsula of Michigan; Groos Quarry Formation.
6. Rifle Hill Quarry, NE1/4 NW1/4 sec. 35, T. 102N., R. 12 W., Fillmore County, Minnesota; Elgin Member, Maquoketa Formation.
7. Exposure along a small creek beneath County Highway B 60, SW1/4 NW1/4 sec. 35, T. 95 N., R. 7 W., 1·6 km east of Clermont, Fayette County, Iowa; Elgin Member, Maquoketa Formation.
8. Postville North Quarry, SW1/4 SW1/4 sec. 16, T. 96 N., R. 6 W., Allamakee County, Iowa; Elgin Member, Maquoketa Formation.

9. Graf railroad cut, S1/2 NW1/4 SW1/4 sec. 29, T. 89 N, R. 1 E., Dubuque County, Iowa; Elgin Member, Maquoketa Formation.
10. Illinois Central Railroad Cut, SW1/2 NE1/4 SW1/4 sec. 26, T. 29 N., R. 2 E., Scales Mount, Jo Davies County, Illinois; Scales Formation, Maquoketa Group.
11. Outcrop in bluff, north of intersection of State Route 84 and U.S. Route 52, SW1/2 SW1/4 NW1/4 sec. 11, T. 25 N., R. 3 E., Savannah, Carroll County, Illinois. Fort Atkinson Formation, Maquoketa Group.
12. Mt Carroll Quarry, north side of U.S. Route 52, SW1/2 NE1/4 SW1/4 sec. 10, T. 24 N., R. 4 E, 4 km south-west of Mt Carroll, Carroll County, Illinois; Scales Formation, Maquoketa Group.
13. Road-cut along Highway 21, 24 km south-south-west of St Louis, Missouri; Maquoketa Shale.
14. Road-cut along Interstate 55, just north of the Barnhart (Highway M) interchange, SW1/4 SE1/4 sec. 19, T. 42 N., R. 6 E., Jefferson County, Missouri; Maquoketa Shale.
15. Amis Construction Company Quarry, north end of Black Knob Ridge, centre of the N1/2 sec. 16, T. 1 S., R. 12 E., Stringtown, Atoka County, Oklahoma; Bigfort Chert and Polk Creek Shale.
16. Sycamore Creek, Section J of Alberstadt (1973), sec. 27, T. 3 S., R. 4 E., Troy Quadrangle, Oklahoma; Sylvan Shale.
17. Ideal Cement Quarry, sec. 36, T. 3 N., R. 5 E., Alhoso Quadrangle, near Lawrence, Oklahoma; Sylvan Shale.
18. Rayford Quarry, Section Q of Alberstadt (1973), sec. 28, T. 1 S., R. 2 E., Dougherty Quadrangle, Oklahoma; Sylvan Shale.
19. U.S. Geological Survey Collection 241, Middle of sec. 34, T. 1 S., R. 2 E., approximately 3 km north of Dougherty, Dougherty Quadrangle, Oklahoma; Sylvan Shale.

FISH OBLIQUE TO BEDDING IN EARLY DIAGENETIC CONCRETIONS FROM THE CRETACEOUS SANTANA FORMATION OF BRAZIL – IMPLICATIONS FOR SUBSTRATE CONSISTENCY

by DAVID M. MARTILL

ABSTRACT. A large number (> 1 per cent.) of fossil fish from the Santana Formation (?Albian, Lower Cretaceous) of north-east Brazil, occurs at a high angle, or even vertical, to bedding. Petrographic and taphonomic analyses of such occurrences indicate that the laminated argillaceous sediments were soupy and allowed sinking dead fish to penetrate the sediment to depths greater than the total body length of the fish. Density contrasts between the dead fish and the surrounding sediment were negligible, and penetration was largely a result of acceleration due to the high density contrast between the fish and the water column. A commonly recurrent angle of fish to bedding of approximately 45° reflects the gliding angle achieved during forward descent with pectoral fins extended.

CONCRETIONS containing exceptionally well preserved fish from the Romualdo Member of the Santana Formation are extremely abundant on the slopes of the Chapada do Araripe, in the states of Ceará, Pernambuco and Piauí, north-east Brazil (Martill 1993*a*). At several localities around the plateau (Text-fig. 1), fossil fish occur preserved in three dimensions and at a high angle to the bedding in early diagenetic, calcium carbonate concretions. Such a specimen was first illustrated by Martill (1988), and many more were figured by Maisey (1991). Maisey recognized two concretion types where fossils lay at an angle to the bedding. In one (his type 'K' transgressive concretions) the entire fish lies oblique to bedding, whereas in the second type (his type 'I' partly transgressive concretions) only the skull lies oblique to bedding, the remainder of the fish lying parallel to the bedding plane. He also noted that the first type of concretion contained mostly specimens of *Rhacolepis*, whereas the second type of concretion contained mostly large specimens of *Vinctifer* and *Brannerion* (Maisey 1991, p. 67). I can add that large specimens of *Cladocylus gardneri*, *Enneles audax* (= *Calamopleurus cylindricus*) and *Araripelepidotes temnurus* also occur commonly in type 'I' concretions.

Two distinct hypotheses have been advanced to explain these occurrences (Maisey 1991, p. 67). The model proposed for the type 'I' concretions is accepted herein and I merely make a few additional observations. However, I offer an alternative explanation for the generation of type 'K' concretions based on observations of new specimens using thin section petrography, and on extensive field observations.

Specimens are housed in the following institutions: FMNH, Field Museum of Natural History, Chicago; LEIUG, University of Leicester, Department of Geology; UOP, University of Portsmouth, Department of Geology.

SEDIMENTOLOGY OF THE CONCRETION HORIZON

The Romualdo Member concretions occur in a series of grey-green to dark grey, laminated, slightly silty mudstones which were deposited in a restricted lagoon with connections to an epeiric sea. The muds are composed of approximately 75 per cent. smectite, 20 per cent. illite and 5 per cent.

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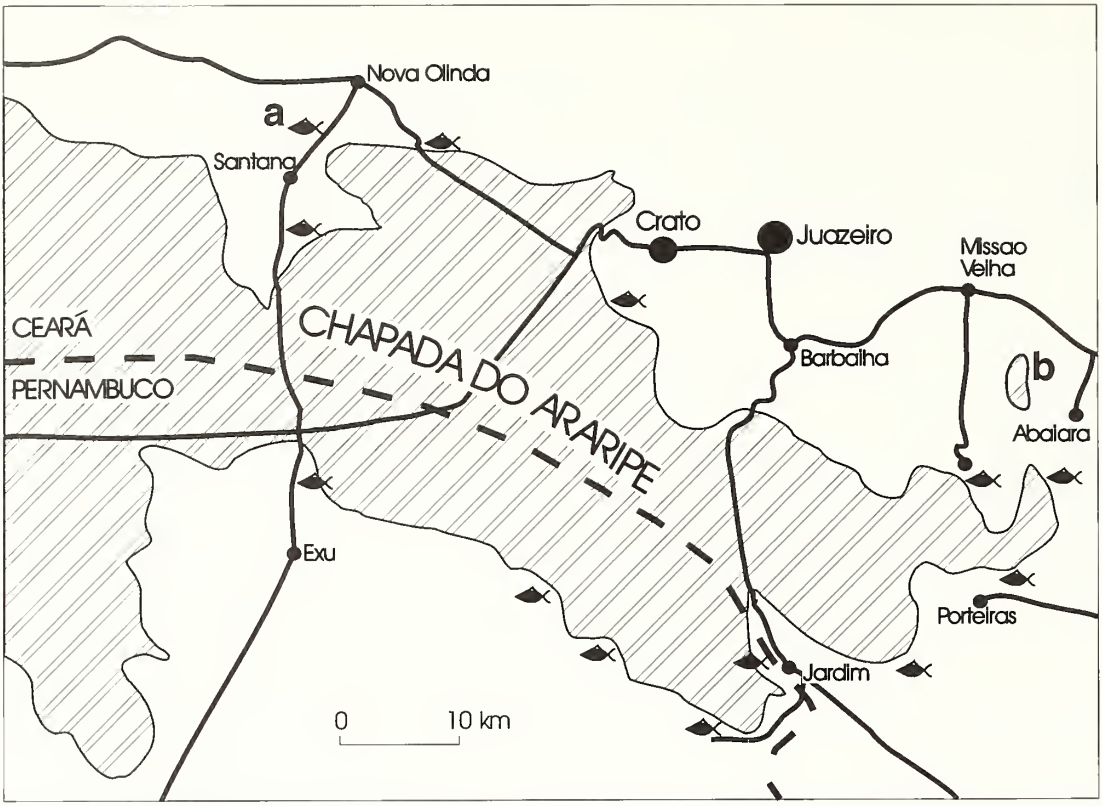


TEXT-FIG. 1. Simplified map of the eastern end of the Chapada do Araripe (shaded area), Brazil, with the main fossil bearing concretion localities indicated by a fish symbol. Localities discussed in the text are: a, Mina Pedra Branca, b, Serra da Maozina.

kaolinite (Berthou *et al.* 1990). The member rarely reaches more than 4–5 m thick, but is laterally extensive occurring over an area of at least 6000 km^2. Ostracods are abundant at some horizons and may even produce thin, impersistent, ostracodal limestones. Septarian concretions occur at intervals, sometimes in discrete bands, but some also appear to be randomly distributed. The concretion-bearing part of the sequence rests on a series of fluviodeltaic and lacustrine sands and silts, with palaeosols and rootlet horizons. The Romualdo Member passes upwards into slightly micaceous, blue/grey shales with thin bands of gastropod limestone rich in *Paraglauconia* and with rare echinoids.

The palaeosalinity of the concretion-bearing part of the sequence is in doubt, but deposition was probably under rather brackish conditions (Martill 1993*a*). It is highly likely that salinities fluctuated considerably with the seasons, a hypothesis based on the presence of mass mortality assemblages of young fishes. Many of the fish species found in the concretions have been reported from coeval fully marine deposits elsewhere (Moody and Maisey 1994). The salinity has important implications, both for palaeoenvironmental interpretations of the fauna and also for the behaviour of the sediment, as salinity plays an important rôle in clay particle flocculation (see below).

THE CONCRETIONS

The concretions containing fish skeletons preserved oblique to bedding are irregularly ellipsoidal, and commonly range from 150 to 400 mm long by 50 to 150 mm wide. The outer surface of the concretion is commonly weathered light brown, with a friable, highly oxidized zone rich in selenite crystals which readily breaks away from the main body of the concretion. Lamination is conspicuous on the weathered surface, but is enhanced after light etching in 10 per cent. acetic acid. The unweathered concretions from Serra da Maozina (Text-fig. 1) are dark grey internally and are usually devoid of other fossils, whereas those from Santana do Cariri are usually a lighter grey and commonly contain coprolites, some with ostracod inclusions. These colour differences probably reflect differing degrees of weathering, rather than any lithological difference between localities. In many concretions laminations cut across the long axes of the concretions, commonly at an angle of 30–45°. In hand specimens laminations are more pronounced in concretions from Santana do Cariri than those collected from Serra da Maozina (Text-fig. 2), but etching with 10 per cent. acetic acid shows that laminations are present in all of these. Cut or split concretions commonly reveal an enclosed fish which is always three-dimensional if the fish is at a high angle ($> 20°$) to the bedding, but often shows collapse features if the fish is at a low angle ($< 20°$) to bedding (Text-fig. 3). In all of the three dimensional specimens, the body cavity of the fish is filled with calcite cements and crystal-lined cavities are often present (Text-fig. 4). Laminations within the concretion body vary in thickness from 1 to 4 mm, and thicker laminae may be present. The laminae are often discontinuous, and may be flexed over and under inclusions such as coprolites (Text-fig. 5). Laminae may reach the body wall of the fish, but there is usually a zone of homogenous sediment between the laminated part of the concretion body and the body wall (Text-fig. 6). This zone is best developed in front of the skull and is often wider around the caudal region of the fish. The axial skeletons of three-dimensional fish may be articulated, but often are disarticulated. When disarticulated, the axial skeleton is often geopetally stacked (Text-figs 4A, 7). The mouth of the fish may be open and infilled with homogenous sediment (Text-fig. 2A–B) and sediment may also be present within the body of the fish and in the gill arches (Text-fig. 2B).

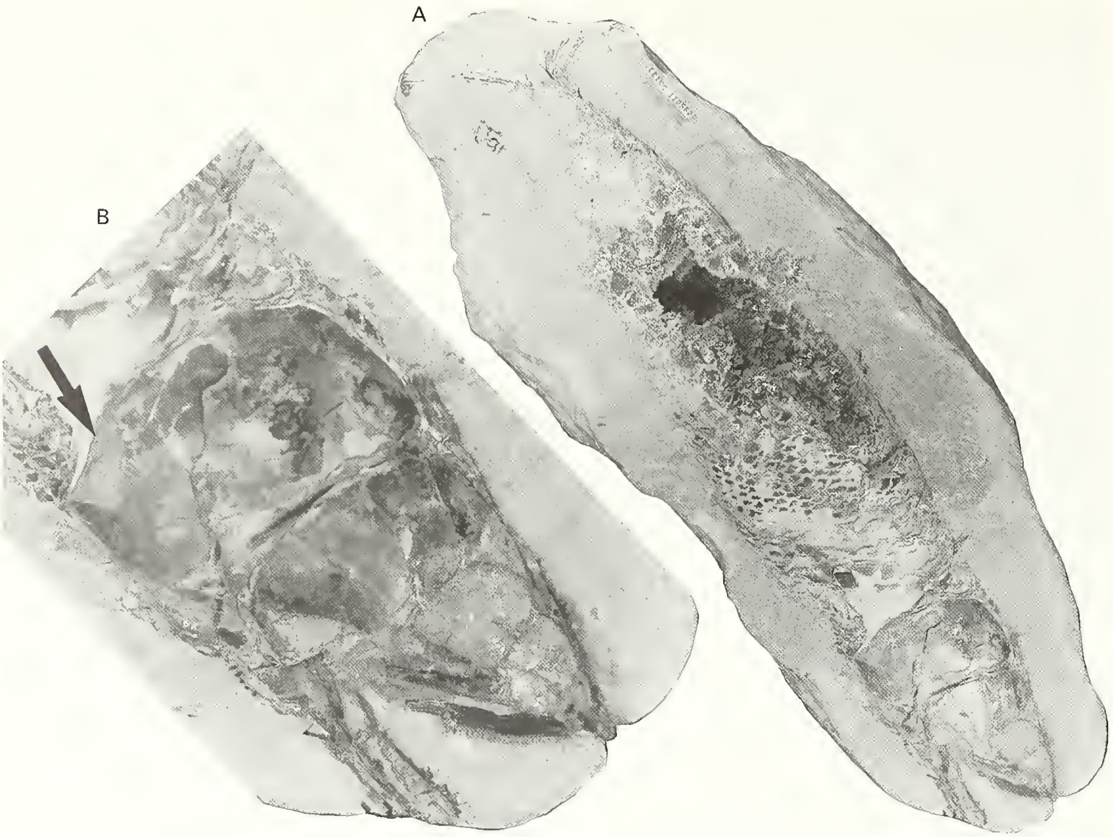
TAPHONOMY OF OBLIQUE FISH

Specimens of *Rhacolepis* preserved oblique to concretion laminae are invariably complete, with the body wall often preserved in three-dimensions over most of its length. The body wall is commonly ruptured, usually along spiralled scale row boundaries, and portions of the body wall and the vertebral column may be telescoped over each other (Text-fig. 7). In most cases, where such ruptures have occurred, sheets of scales have been inserted into the anterior scale row. This may occur in several places on the body, but is usually more common anteriorly. At the point of rupture, sediment may extend into the body cavity (Text-fig. 8; see also Martill 1988, pl. 4, fig. 1a–b). Sediment within the body cavity can have a very sharp boundary with later calcite infills (Text-fig. 4A–B), but in some cases the boundary is irregular, or somewhat diffuse (Text-fig. 8).

The extremities of the enclosed fish may project beyond the concretion boundary, but in most cases it is only the most anterior part of the skull and the distal parts of the caudal fins that do so. As no specimen described herein was observed by the author *in-situ* the preservational style of portions of the skeleton that lay beyond the concretion boundary cannot be documented. Specimens of fish found in the same shales as the concretions, but not enclosed within the concretions are usually highly compressed.

The pectoral and pelvic fins may extend beyond the body, as in life position, but are usually folded back somewhat (Text-fig. 9E), and the dorsal fin is often preserved in the raised position (Text-fig. 10). The strongly forked caudal fin may be slightly closed, but is planar and extends posteriorly from the caudal peduncle as in life. The mouth may be open or closed. The opercula are usually preserved flat against the skull, although in some specimens they may be open (Text-fig. 11). Anteriorly, the body wall cross section is usually nearly round and entire, but posteriorly it may be flattened with opposite sides (upper and lower surfaces) pressed into each other. Even in the most three-dimensional specimens there is usually some indication of flattening of the body wall (Text-fig. 12).

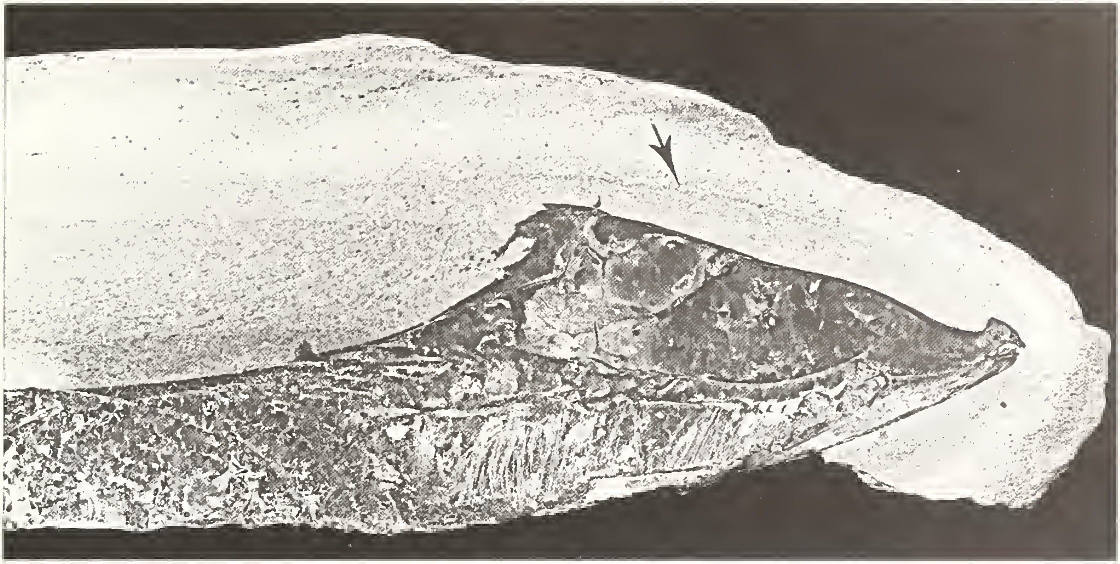
Internally, the skeleton may be fully articulated, especially within the skull, and even the finest gill rays may remain attached to the gill arches (Text-figs 3, 10). The postcranial skeleton may show



TEXT-FIG. 2. Near complete, three-dimensional, partially articulated fish, cf. *Rhacolepis* sp. (LEIUG 110562), enclosed in an early diagenetic carbonate concretion from the Romualdo Member, Santana Formation of Santana do Cariri, Brazil. The skeleton is at a high angle to bedding with the skull pointing downwards. A, entire concretion showing complete fish with damaged dorso-lateral region revealing large gas-filled body cavity, × *c*. 0·4. B, detail of skull showing sediment-filled mouth and fractured suboperculum exposing sediment-filled gill chamber (arrowed); × 1·2.

marked disarticulation where isolated bones or sections of the postcranial skeleton have fallen away from their original position (Text-figs 3, 6, 8). Martill (1988) and Maisey (1991) noted that this skeletal collapse was often geopetal (Text-figs 4A, 7). Within the fishes, soft tissues are commonly preserved as replications in calcium phosphate (Martill 1988, 1994), and are particularly well mineralized adjacent to the body wall and in the gills (Martill *et al.* 1992; Wilby 1993). A phosphatic coeleolite is commonly present in the gut trace (Maisey 1991; Kellner *et al.* 1994; Text-fig. 10). Stomach contents, usually arthropods and smaller fishes (Wilby and Martill 1992), may also be present in fish preserved oblique to bedding (Text-fig. 13). I have found no evidence of predation or scavenging of the oblique fish (they are about as perfectly preserved specimens as one could hope to find), and the cause of death remains a topic for investigation. The high local abundance is suggestive of mass mortality.

Three dimensional fish sub-parallel to bedding. A significant number of three-dimensionally preserved fishes in the concretions are found sub-parallel to the lamination. Nevertheless, careful examination reveals laterally cross-cutting relationships with the laminae (Text-fig. 3) and many of the features described above are to be seen. Maisey (1991) described a number of fish in which only



TEXT-FIG. 3. Median longitudinal section through anterior portion of trunk (partially collapsed) and skull (three-dimensional) of cf. *Rhacolepis* sp. (UOP 96/1), block e of Text-figure 9, from the Romualdo Member, Santana Formation, Serra da Maozina, Ceará, Brazil. The lower margin reflects the original shape of the body wall of the fish, whereas the upper margin in the trunk region has collapsed geopetally following the escape of decomposition gases and the collapse internally of the supporting skeleton. A faint trace of the sediment lamination can be seen flexing down to occupy the space vacated by the escaping gases (note that the more prominent band, arrowed, is a liesegang effect produced during Recent weathering).

the head was oblique to bedding while the trunk lay parallel to the lamination. He attributed this occurrence to collapse of the body onto the sediment surface after partial intrusion of the skull into the sediment. A comparable mode of preservation has been reported for ichthyosaurs from the Posidonia Shales (Lower Jurassic) of Germany (Martill 1993*b*). In the case of the Santana fishes, the skull is commonly at a low angle to the bedding (although high angle examples are known; P. Wilby, pers. comm.) and upside down. Although this relationship may reflect a low angle of entry as the carcass intruded the sediment, it may also be due to post-intrusion rotation of the skull caused by leverage as the body collapsed.

DIAGENESIS

The diagenesis of fish in the concretions of the Romualdo Member has been discussed by Martill (1988). Several generations of carbonate cement fringe the bones, the earliest of which is also the cementing agent of the concretion. These cements are light grey or buff coloured and rarely reach a thickness of more than 2 mm (Text-fig. 4B). This layer may be overlain by a brownish drusy calcite cement reaching a thickness of 2–3 mm. A much thicker layer of black calcite overlies these cements and may fill all available void space (Text-fig. 4A). However, many specimens have vuggy cavities in which this black cement forms small dog-tooth crystals (Text-fig. 2). Some concretions with large vuggy cavities may contain an even later infill of coarsely crystalline white or clear calcite. Barite and celestine may also be present (Martill 1988) (Text-fig. 10). The generally bluish-dark grey colour of the concretions at Serra de Maozina is due to minor amounts of finely disseminated pyrite.

The relationship of the early cements to ingressed sediment is noteworthy. Some sediment within the body cavity appears to overlie some of the calcium phosphate replacing soft tissues. This may represent sediment that was deposited onto soft tissues that were subsequently phosphatized, but

TEXT-FIG. 4. Longitudinal section through a three-dimensionally preserved specimen of cf. *Rhacolepis* sp. (UOP 96/2), from the Santana Formation, Romualdo Member of Mina Pedra Branca, Ceará. See also Text-figures 5–6. A, complete section showing fine-scale lamination within the early diagenetic carbonate concretion, collapsed internal skeletal elements with overgrowths of calcite and larger coarse calcite crystals (dark appearance) filling the body cavity; the lower arrow shows a broad zone of unlaminated sediment in front of the fish skull; the upper arrow shows that laminations extend to the body wall and are deflected downwards slightly; × *c.* 0·5. B, non-laminated sediment inclusion within body cavity fringed with early cement; × 8.

at least some may have been deposited onto soft tissue which had already undergone very early phosphatization (Wilby 1993).

MODELS TO ACCOUNT FOR FISH PRESERVED OBLIQUE TO BEDDING

Existing model for type 'K' concretions (Maisey 1991). Maisey (1991, pp. 76–78) figured a number of examples of three-dimensional fish preserved oblique to bedding and interpreted this occurrence as a result of the fish becoming bloated due to a build up of decomposition gases and then sinking to the bottom. Maisey considered that retention of three-dimensionality was a result of early calcification of the soft tissues. He also argued that a protracted period of burial of the fish lying on the bottom 'end up' was required (Maisey 1991, p. 78). Thus, in the Maisey model, the soft tissues of the fish must effectively be fossilized and all skeletal elements, notably the scales and soft fin-ray segments, must be bound to the carcass to prevent any disarticulation occurring while awaiting burial. Further, it must be assumed that no scavenging took place. Although it is perfectly plausible to explain a lack of macro-scavenging by invoking anoxia, anaerobic bacteria can certainly

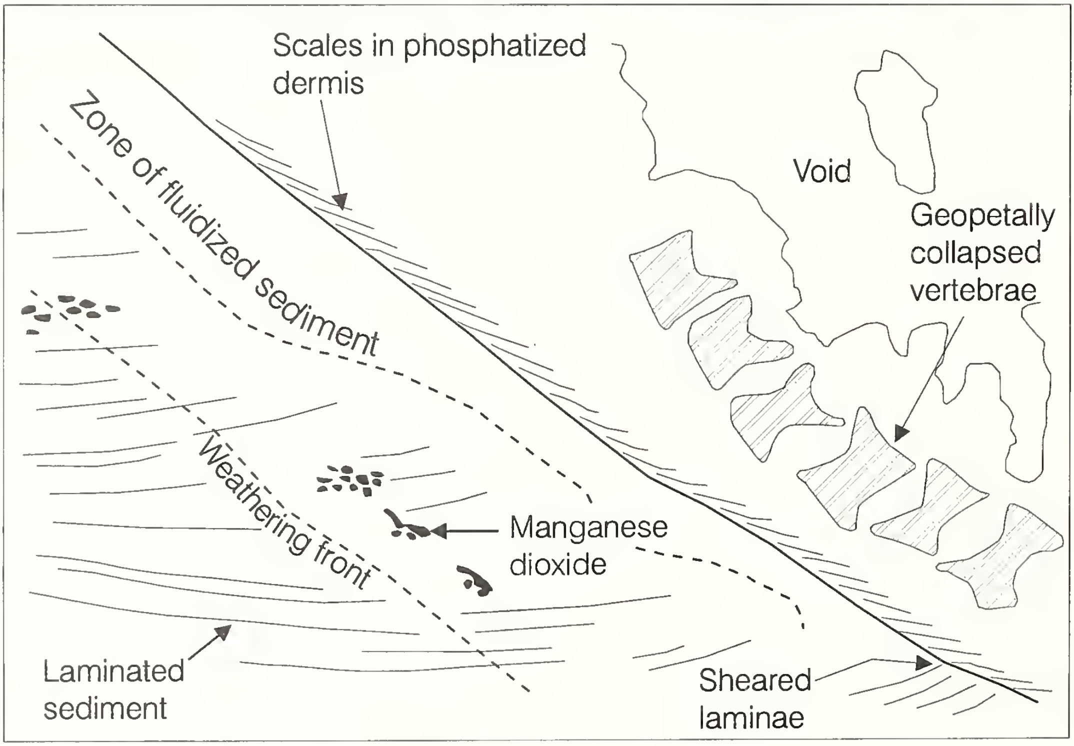
TEXT-FIG. 5. Detail of UOP 96/2 (for details see Text-fig.4) showing small coprolite with ostracod inclusions, in which laminated sediment drapes over and under the coprolite. This is a characteristic feature of elements that fell to the lagoon floor, but did not penetrate the sediment; × *c*. 3.

operate under such conditions and cause decay (Allison 1988). Furthermore, the presence of disseminated pyrite clearly attests to the presence of sulphate-reducing bacteria. It should also be noted that there are no primary sedimentary structures, such as sediment shadows or attenuation of laminae at high points, indicating that sedimentation occurred around an object projecting from the bottom.

Other taphonomic features are also incompatible with Maisey's model. A bloated fish carcass would only float until the body wall was ruptured. Thus, three-dimensionality due to bloating was probably achieved on the lagoon floor, but failed to refloat the carcass. Not all of the three dimensional oblique fish show phosphatization of the soft tissue, and those that do often only have small areas of soft tissues preserved. Those fishes that do show extensive soft tissue preservation are often flattened (see Martill 1988, pl. 1).

The mud-dive model. Clearly, the exceptional preservation of such fossils requires an explanation. It is evident that the fish were arriving on the sea floor intact and that they underwent burial before any scavenging could occur. Scavenging could have been prevented by: (1) exclusion of macro-scavengers by conditions such as hypersalinity or bottom water anoxia; and/or (2) sinking of the carcass into extremely soft (soupy) sediment. The existence of anoxic conditions on the lagoon floor was probably of frequent occurrence as infaunal benthos is exceedingly rare in the concretion layers and disseminated pyrite is abundant. The degree to which anoxicity extended upwards into the water column is unclear. Certainly, benthic invertebrates are uncommon and are usually restricted to a few horizons where small bivalves are often found in high density, but low diversity (1–2 spp.). However, this low diversity may be due to other factors, because benthic fish with high oxygen demands, such as the elasmobranchs *Iansan* and *Tribodus*, as well as some presumed benthic

A



B

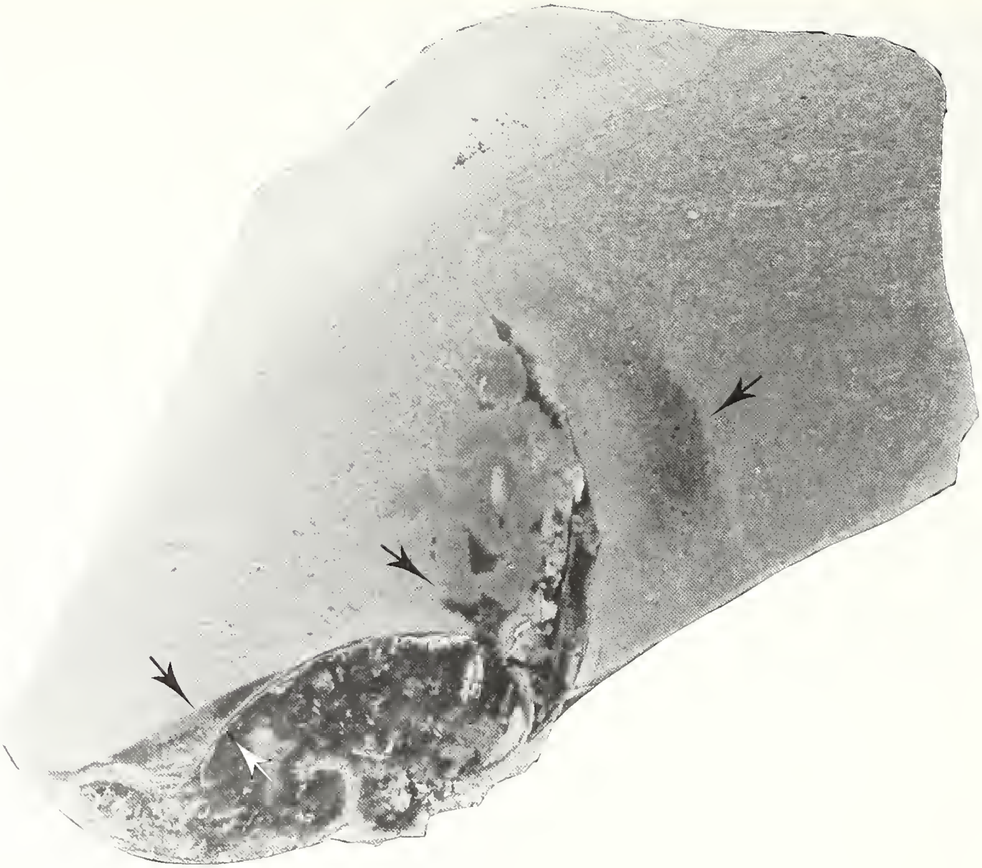
TEXT-FIG. 6. For caption see opposite.

TEXT-FIG. 7. Skull and anterior portion of the trunk of cf. *Rhacolepis* sp. (UOP 96/3) in dorsal view enclosed in a carbonate concretion at an angle of 25° to the bedding; Santana Formation, Romualdo Member (?Albian, Lower Cretaceous) of the Santana do Cariri area; the body wall behind the skull has collapsed and 'sheets' of scales, arrowed, have telescoped anteriorly; × 1·2.

osteichthyans with durophagous dentitions (for example, the pycnodonts *Neoproscinetes* and *Iamanja*) occur quite commonly. Salinities may also have reached high levels, and although no evaporites are reported from this part of the succession, they are important in subjacent parts of the sequence. Even if elevated salinities and anoxia did occur, these factors alone cannot account for the unusual attitude of the fish in the concretions.

The presence of intact laminae extending almost to the body wall of the carcass, with no thickening or thinning of the laminae in the region of the fish, shows that the fish did not influence the nature or style of the accumulating sediment. The sharp truncation of the laminae where they

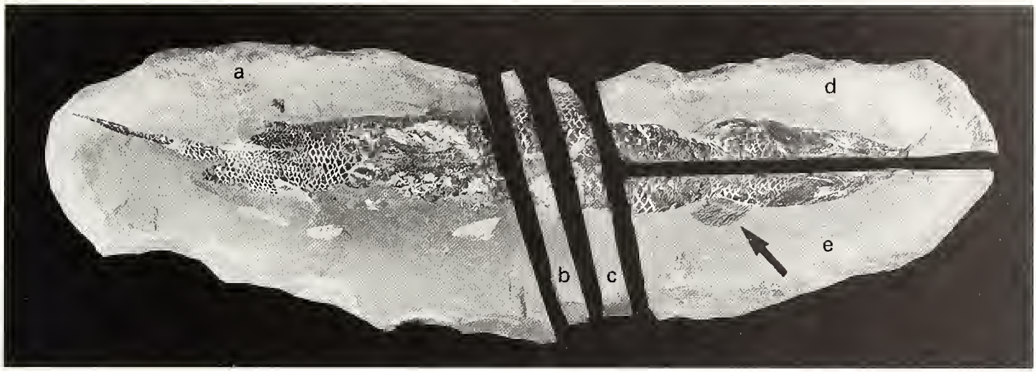
TEXT-FIG. 6. A, magnified contact between the body wall of the fish and the sediment in UOP 96/2 (for details see caption to Text-fig. 4). Note that the laminae are not in contact with the body wall; rather there is a zone of fluidized sediment of variable thickness between the laminated portion of the concretion and the fossil inclusion. The light material between the scales (arrowed) is phosphatized dermis; × *c*. 3. B, outline diagram of A, highlighting features alluded to in the text.



TEXT-FIG. 8. Cut surface of block c of Text-figure 9. The lower surface of the body wall of the fish is intact, but the upper surface has collapsed geopetally. Non-brittle failure of the trunk scales internally resulted in the parting of the body wall (white arrow) from the surrounding sediment (black arrow opposite). This occurred with little or no deformation of the sediment, suggesting that the sediment was not behaving in a fluid manner when the body wall collapsed. Fluidized deformation of sediment on the right side of the body wall has occurred (black arrows to right), in which all primary lamination has been disrupted; ×4.

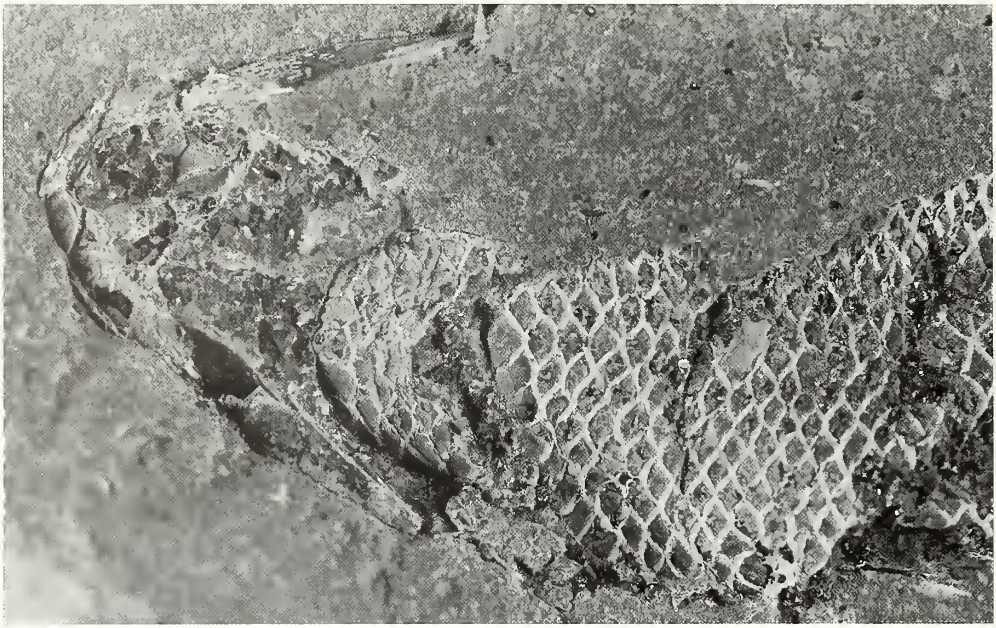
do meet the body wall is convincing evidence of intrusion of the fish into the sediment. The thin zone of homogenized sediment anterior to the fish skull, within the mouth and adjacent to the body, clearly shows that the fine lamination had been disrupted in the vicinity of the fish. For this to occur the sediment must have behaved in a fluid manner, but only for a short period.

A chronology of taphonomic and diagenetic events. It is usually assumed that the fish in the concretions died within the water column and sank as a dead carcass, but it is also possible that some may have died within the sediment, perhaps burrowing as a response to stress, as do some lungfishes, such as *Protopterus* and *Lepidosiren* (Bannister 1987). For those fish that did die in the water column, death was followed by at most only a very short post-mortem drifting phase, as floating carcasses decay, and rapidly disarticulate (Schäfer 1972). The lack of scavenging of the three-dimensional fish is also indicative of a very short period of post-mortem drifting. The dead fish descended (in many examples, upside down) like a glider to the floor of the lagoon, but at a steep angle of descent (around 45° in some examples). On hitting the soft substrate, the fish penetrated



TEXT-FIG. 9. Three-dimensionally preserved, collapsed skeleton of cf. *Rhacolepis* sp. (UOP 96/1) within early diagenetic carbonate concretion; Romualdo Member, Santana Formation, Serra da Maozina, Ceará, Brazil; viewed ventrally; ×0·75. Note that the pectoral fins project out from the body wall (arrowed) indicating lithification before compaction; had compaction occurred prior to lithification the fins would have become pressed against the body. This specimen has been cut to reveal the internal sedimentary and taphonomic features shown in Text-figures 3 and 8.

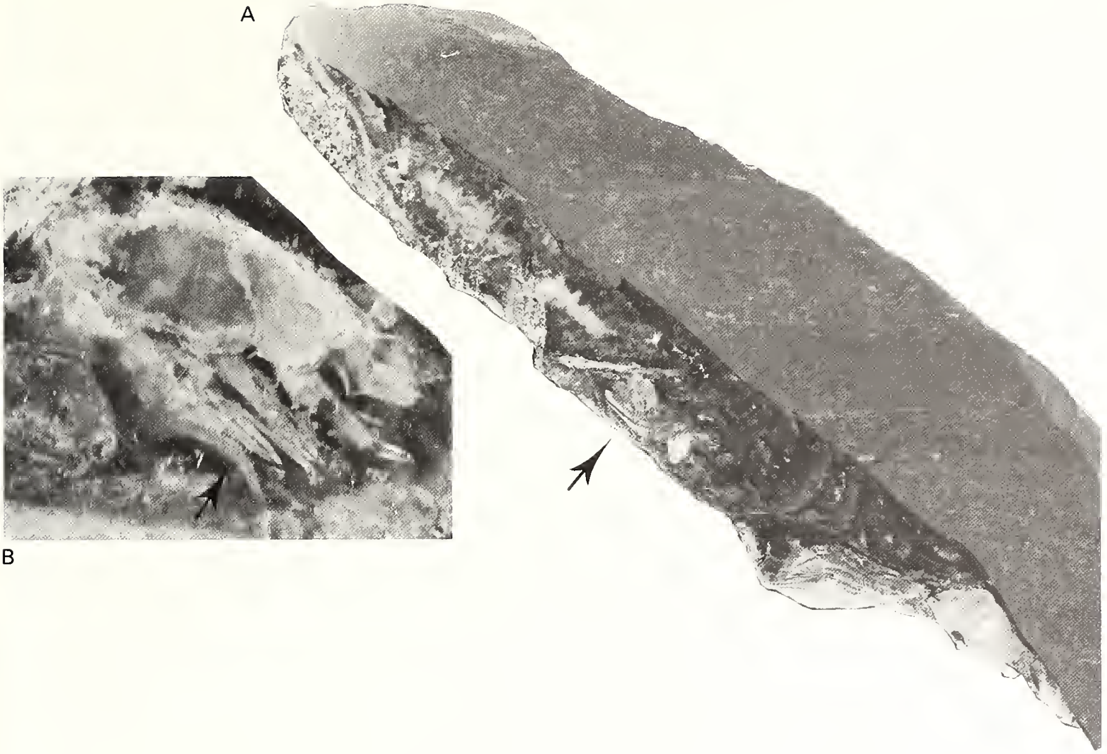
TEXT-FIG. 10. Longitudinal cross section through a specimen of cf. *Rhacolepis* sp. (UOP 96/4) from the Romualdo Member, Santana Formation, Serra da Maozina, Ceará, Brazil. Note that the dorsal fin projects into the sediment, and has not been folded posteriorly during penetration into the sediment (broad arrow). There is a large phosphatic coeleolite in the gut (upper thin arrow) and a baryte infill in the skull (lower thin arrow); ×*c*. 1.



TEXT-FIG. 11. cf. *Rhacolepis* sp. (UOP 96/5) in typical Romualdo Concretion from Santana do Cariri. Note the opercula in slightly open position and the telescoping of the body wall. The open opercula might suggest that the fish was still alive when it penetrated the sediment, and that as the opercula were opened during breathing, fluidized sediment invaded the buccal cavity. × *c*. 1·5.

TEXT-FIG. 12. Thin section of cf. *Rhacolepis* sp. (FMNH PF 10765) cut vertically through the trunk; from the Romualdo Member of the Santana Formation, precise locality unknown. Note that the laminae in the sediment have deformed plastically downwards into the body cavity, but that the laminae are truncated (arrowed). The truncation must have predated the plastic deformation and occurred as the fish penetrated the sediment; × *c*. 1·5.

the sediment at the same angle. If the mouth was open, sediment filled the buccal cavity and spread over the gill arches and invaded the gill filaments. During penetration, the velocity reduced, due to friction and the change in density contrast, and the fish carcass would have come to rest. Decomposition of the soft tissues occurred, with the resultant gases bloating the carcass, and soft tissue phosphatization commenced in some specimens. If the overall density of the fish carcass



TEXT-FIG. 13. A, longitudinal cross section through cf. *Rhacolepis* sp. (UOP 96/6), showing a gut filled with three-dimensionally preserved crustaceans in which soft tissues have been replaced by calcium phosphate (arrowed). × *c*. 1. B, detail of crustacean, probably a decapod, showing well-preserved appendages (arrowed). Once again, the presence of stomach contents in good condition indicates that the fish penetrated the sediment very shortly after death, or perhaps even while still alive; × *c*. 10.

decreased with the build-up of gases, some reverse movement may have occurred, but would have been minimal due to the braking action of the backward-pointing scales and fins. As gas pressure built up and the body wall weakened due to continued decomposition, the gas may have burst through the body wall and invaded the surrounding sediment, leaving a trail of disturbed laminae. The loss of gas allowed the confining sediment to collapse the body wall, sometimes bringing both sides together.

Decomposition of the soft tissues continued and liberated elements of the axial skeleton, small components of which fell geopetally within the body cavity. Any rupturing of the body wall allowed the ingress of sediment. The clay rich sediment may have behaved plastically, flexing into cavities rather than flowing. The proliferation of sedimentary bacteria and resultant early lithification, by calcite, of the surrounding sediment halted further collapse of the body wall. Soft tissue decomposition was probably completed after only a few weeks (Martill and Harper 1990). Commencement of calcite cementation on to all internal surfaces, including skeletal elements, probably occurred at an early stage and may have accompanied some soft tissue decomposition (Briggs and Wilby 1996). Precipitation of calcite resulted in cementation of ingressed sediment within the body cavity of the fish. Calcite also crystallized poikilotopically within the phosphatized soft tissues. Septarian cracking of the larger concretions was probably also an early event, as has been demonstrated for early diagenetic concretions in some black shales (Martill and Hudson 1989). Later calcite cements remain to be dated, but some fill septarian cracks as well as lining larger vuggy cavities within the fishes. At an even later stage baryte and celestine filled some of the remaining cavities, although not in all concretions, suggesting perhaps that there is geographical and stratigraphical control on their distribution. Finally, compaction of sediment surrounding the concretion occurred, usually resulting in compression of any elements of the fish skeleton that projected beyond the limits of the concretion. It should be noted that the fish were introduced into a medium in which diagenetic reactions were already taking place. Most probably, the fish penetrated into the zone of sulphate reduction, as pyrite is present as a very early phase. Locally, bacterial activity within the sediment would have been increased by the sudden addition of abundant nutrients, thus fuelling further diagenetic reactions, including concretion formation.

SUBSTRATE CONSISTENCY

The lack of bioturbation in the Romualdo Member concretions, and the presence of millimetric scale lamination might seem inconsistent with the former existence of a soupy substrate. Rhoads (1970) noted that soupy substrates are often generated by the accumulation and bioturbation of faecal pellets by infaunal deposit feeders. This has been observed in Recent tidally dominated mud systems (Rhoads 1970) and has also been claimed for Jurassic organic-rich mudrocks, such as the Peterborough Member of the Oxford Clay (Hudson and Martill 1991). So, can soupy substrates be produced without bioturbation? Unconsolidated sediments can exist in three physical states: fluid plastic or soft, and firm bonded. The physical state is controlled by, amongst other things, the water content. For a dead fish to have penetrated the sediment, the sediment must have behaved in a fluid manner at the point of impact. The liquid limit for clays is highly variable, but commonly occurs at water contents of around 135 per cent., while the water contents of sediment at the sea floor may be around 190 per cent. (Skempton 1970). However, when water contents are lower, sediment can still behave in a fluid manner if pore water pressure is increased locally, as for example when an object impacts with it.

As soon as a descending fish hit the sediment the impact shock-wave caused disintegration of weak inter-clay particle bonds allowing the clays to behave in a fluid manner. This was especially marked at the sediment surface, and a zone of homogenous sediment, the result of liquefaction, is better developed at higher levels within the concretions (Text-fig. 5). Liquefaction of the sediment is also more marked just anterior to the skull, at the impacting site. In all cases, the zone of liquefaction surrounding the fish is narrow (rarely more than 10 mm thick), all lamination is disrupted, and the sediment has become homogenized. In some specimens, the zone of homogenized sediment adjacent to the body wall in the middle of the trunk where the sides are almost parallel is absent. In this region the laminae appear to have been sheared (Text-figs. 4A).

The depth of the zone in which the sediment could be liquefied may have been variable within the basin. In the largest known specimen in which the entire fish has entered the sediment it had penetrated to a depth of 250 mm (Text-fig. 2). After penetration, the sediment could become plastic, as ageing allowed new clay bonds to be produced. This probably occurred relatively rapidly, since in some cases plastic deformation of the surrounding sediment can be seen where body wall collapse has occurred and laminated sediment has filled the space without entering the fluid phase (Text-figs 8, 12).

After impact, excess pore fluid pressures could dissipate and the sediment returned to the plastic state. Evidence for this is found in the Romualdo concretions where the body wall of the fish has parted from the sediment surface to leave a void. The sediment clearly remained largely undeformed except for some slight bending of laminae as the gaps between the sediment margin and the body wall of the fish are now filled with later spar cements (Text-figs 8, 12).

DISCUSSION

Soupy substrates can conceal carcasses from the activities of macroscavengers and allow their rapid introduction into a zone of mineralization. The rich bacterial biota within the 'soup' may profit from the introduced organic matter, resulting in rapid early diagenetic reactions conducive to the exceptional preservation of articulated, three-dimensional skeletons, sometimes with preservation of soft tissues. Soupy substrates, or 'soup grounds' can be recognized in the fossil record by a variety of taphonomic features, including fossils occurring at high angles to bedding when this is not likely to be a true-life position and by cross-cutting relationships to laminations. In addition, evidence for very soft sediment may be found in the traces left by gas bubbles that escaped from decomposing carcasses. Soup grounds can also act as 'store houses', accumulating large numbers of exceptionally preserved fossils over prolonged periods. Thus the Romualdo Member concretions are both a fossil conservation *Lagerstätte* and a fossil concentration *Lagerstätte*.

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A NEW METHOD FOR EXTRACTING PLANT AND INSECT FOSSILS FROM LEBANESE AMBER

by DANY AZAR

ABSTRACT. The extraction of fossil plants and insects from Lebanese amber is possible by dissolving the amber in chloroform. The fossils can be prepared like Recent material and mounted in Canada Balsam. This method enables better observation of the morphological details of the fossils.

LEBANESE amber, well known as the oldest amber with insect inclusions (Whalley 1980; Poinar 1994), is found in various outcrops in Lebanon: Jezzine, Daher El Baidhar, Safa (pers. discovery), Barouk (pers. discovery), Ghineh (pers. discovery), Bireh, Ain Treize, Mayrouba, Mdeirij/Hammana and Kfar Niss.

The amber used for the present study comes from Mdeirij/Hammana and is preserved in clay-sandstone from the upper Neocomian–basal Lower Aptian C1/C2, *c*. 120 Ma (Dubertret 1951, 1955; Schlee and Dietrich 1970; Schlee and Glockner 1978). Although insects are very common at this outcrop, their presence has not yet been reported in the literature. Lebanese amber is supposed to be formed from araucarian conifers (Cano *et al.* 1993) and usually occurs as very small pieces, less than 1000 mm^3. Inclusions are commonly very difficult to study because of the presence of dark zones and of numerous impurities in the amber. A new method of extraction of the various inclusions has therefore been developed to improve the study of such material.

Extracting fossil organisms has been attempted by Galippe (1920) from various types of amber (Cenomanian of France, Upper Eocene Baltic amber, Miocene French amber from Savoie and some African Recent copal). He noticed that after immersion in ether for four days the amber became smooth and could be cut into small fragments but was not completely dissolved. Larsson (1978) noticed that alcohol softens and partly dissolves Baltic amber, but that the fossils were destroyed with the amber.

Although successful attempts to extract DNA from a weevil (Coleoptera: Nemonychidae) in Lebanese amber have been made by Cano *et al.* (1993), the direct extraction of fossils has never been achieved. It seems that the great majority of fossil insects and plants from Lebanese amber are true inclusions with well-preserved organic remains, unlike Baltic amber.

METHOD OF EXTRACTION

Lebanese amber was washed with a mixture of water and Javel water (NaClO) which facilitated clay suspension. Pieces of the amber were examined under immersion in glycerin (Whalley 1980) or alcohol (60 per cent.) plus glycerin (40 per cent.); the alcohol spread through cracks in the amber and gave better visibility. After selecting pieces with inclusions, these were filed down with emery paper (no. 400, 500 and 600 metal; Akra, pers. comm.; Melky, pers. comm.) until the amber became transparent; then a coat of acetone varnish or Canada Balsam was put over the samples. The finest details of the insects could then be clearly seen, allowing identification of the material. Examination under cedar oil gave satisfactory results.

First attempts at extracting plant and insect remains were made using heat, without success; when the amber was exposed to a heat source, it cracked and burnt. Eventually, organic solvents were tried. Some of them were ineffective (ethanol, butanol). Others made the amber soft (aceton,

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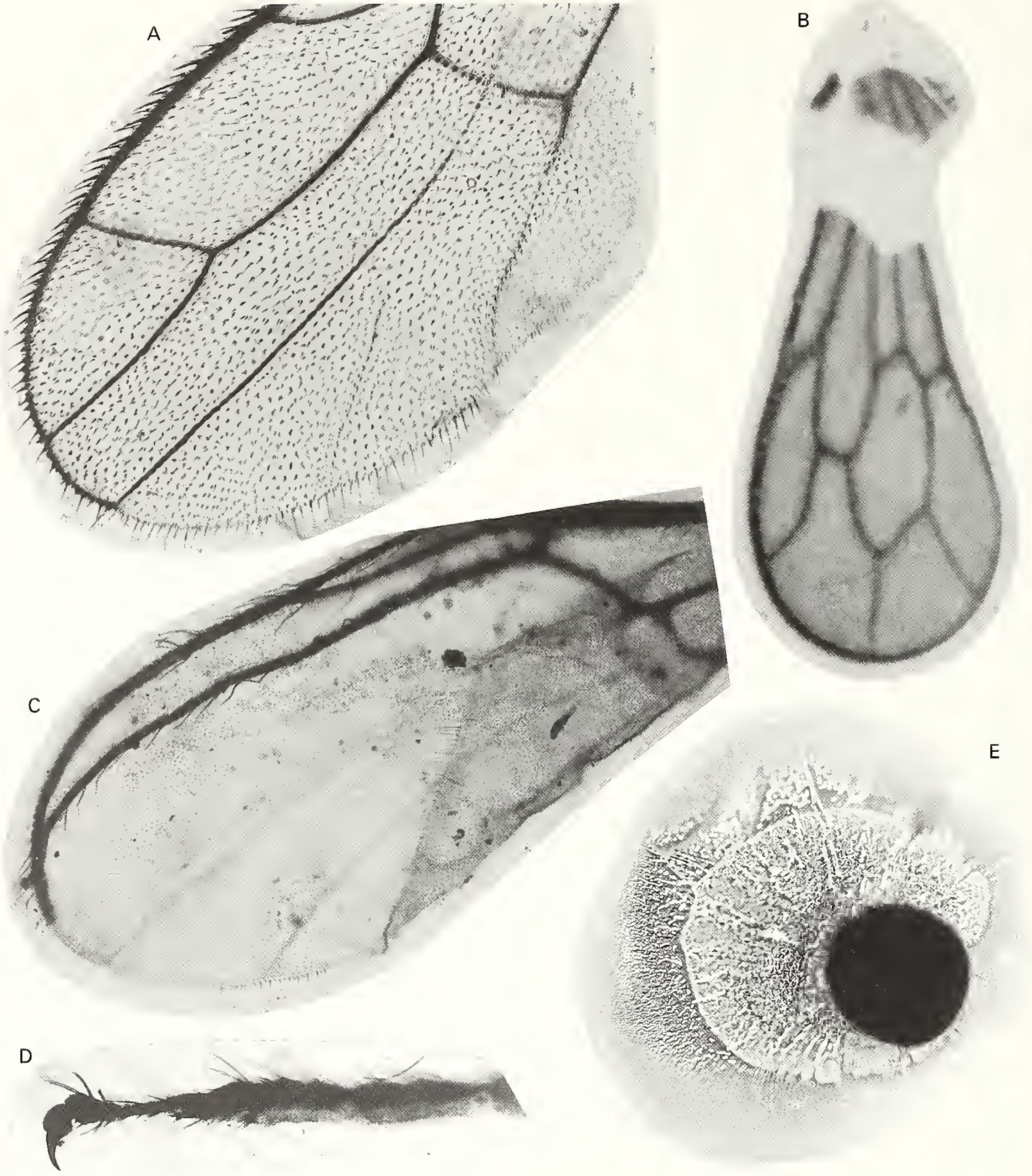

TEXT-FIG. 1. Examples of fossil dissolved out of Lebanese amber using chloroform; Mdeirij/Hammana, Lebanon; upper Neocomian–lower Aptian. A, wing fragment of fly (Diptera: Empidae?); × 160. B, wing fragment of a hemipteran (Enicocephalidae); × 60. C, wing of fly; × 135. D, fragment of insect; × 35. E, undetermined seed; × 85.

toluen, trichloro- 1, 1, 1 ethan). Only chloroform gave satisfactory results, dissolving the amber in less than two hours. The amber was put in chloroform in a completely sealed receptacle, to avoid evaporation of the solvent. The plant and insect remains flocculated and settled from the solution and were prepared on microscopic slides in Canada Balsam. Until now, we have only used imperfect fragments in order not to lose good specimens.

Articulated fragments of the insects from amber were fragile but, with some care, the specimens could be extracted in their entirety (Text-fig. 1A–D). The method gave excellent results for the direct study and manipulation of insect structures such as wings, heads, abdomens and genital apparatuses. Extracted fossils keep their softness as well, just as if they were freshly collected. Putting plant residue in Javel water for 30–60 minutes clarified the tissues for mounting on microscopic slides (Text-fig. 2E). Plant cells and even nuclei were then visible.

The dissolved amber can be recovered by exposing the solution to open air for several days, but the amber will not regain its initial properties. Small amber fragments can be assembled into bigger ones using a small quantity of chloroform.

The present method is of great interest for the future study of the insect fauna of the Lower Cretaceous amber of Lebanon because it allows the direct examination of the fossils. It becomes possible to observe the finest structures, which are otherwise often very difficult to see. Also, fossil material is directly accessible for DNA analysis, with a minimal risk of contamination. It would be very interesting to verify if ambers from other origins could also be dissolved in chloroform.

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HEXAPHYLLIA: A SPINY HETEROCORAL FROM LOWER CARBONIFEROUS REEF LIMESTONES IN DERBYSHIRE, ENGLAND

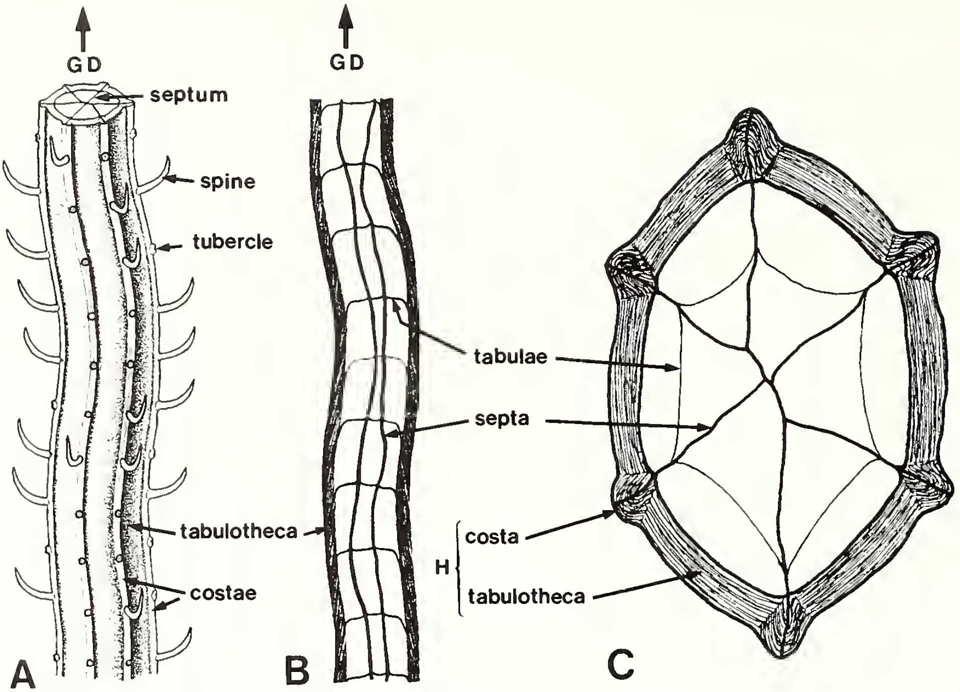
by PATRICK J. COSSEY

Abstract. Exceptionally well preserved and abundant corallites of *Hexaphyllia* are recorded from limestones of the Lower Carboniferous Castleton Reef Belt, north Derbyshire, UK. Details of corallite morphogenesis are presented and the growth attitude of corallites is determined. Tabulae curve down at their margins and fuse together to form the tabulotheca. Conversely, spines curve upward and point in the direction of corallite growth. Soft tissue reconstructions infer the presence of polyps sitting exposed upon and totally enclosing the distal tips of the corallites, with polyp lobes extending down their sides. Much of the corallite is therefore regarded as endoskeletal in origin. Rows of spines projecting from between the polyp lobes gave some degree of protection to the exposed polyps. Assemblages of corallites from different positions in the reef show notable differences in morphology. Variations in shape, wall thickness and tabulae spacing are attributed to contrasting growth rates at different positions within the reef. Examination of approximately 1300 corallites from two localities in the reef reveals the presence of a single species, *Hexaphyllia marginata* (Fleming), which shows considerable intraspecific variation. Systematic studies indicate that criteria used to distinguish *Hexaphyllia* species in the past are invalid and that the majority of previously described taxa are junior synonyms of *H. marginata*. Heterocoral mode of life is discussed in the light of observations made on this species.

The heterocorals are a very unusual and highly distinctive coral group ranging from the Lower Devonian to the Upper Carboniferous. Typically solitary, but rarely weakly colonial, their ontogeny is characterized by unique methods of wall formation and septal insertion. Corallites were elongate and are commonly preserved only as short fragments. The tabulae which are well-spaced in the axial region of the corallite, bend through an angle of almost 90° towards the corallite edge, thicken, and fuse to form the wall between the peripheral edges of the similarly thickened septa. The septa commonly project through the wall and form longitudinal ridges or costae on the external surfaces of corallites. These may occasionally be adorned with a delicate ornament of spines or tubercles (Text-fig. 1). Although relatively uncommon during the earlier part of their range, the distribution of heterocorals during the early Carboniferous was world-wide. They are particularly well known in Europe and south-east Asia, and specimens are found in a wide variety of sedimentary facies. Heterocorals are also common in some reef limestones (Mundy *in* Ramsbottom 1978; Mundy 1980; Cossey 1983; Sugiyama 1984). Although Schindewolf (1941) originally suggested that they led a pseudoplanktic existence attached to seaweeds, more recent work indicates that the heterocorals were benthic sessile forms during their adult life (Różkowska 1969; Cossey 1983; Sugiyama 1989; Weyer 1995*a*, 1995*b*). However, further work on heterocoral ecology and mode of life will be required before the group is to be fully understood.

The first appearance of heterocorals in the stratigraphical record is that of *Tetraphyllia devonica* described by Yoh *et al.* (1984) from the Lower Devonian (Emsian) of south-eastern Yunnan, China. Recently, however, Tourneur and Herrmann (in press) questioned the systematic affinity of *T. devonica* and suggested that their own discovery of *Stellaphyllia* from Mid Devonian (Eifelian) strata in the Cantabrian Mountains of northern Spain represents the earliest heterocoral on record. Other significant Devonian occurrences are from the Upper Devonian, with the appearance of *Oligophylloides* and *Mariaephyllia* (Famennian) in the Holy Cross Mountains in Poland

[Palaeontology, Vol. 40, Part 4, 1997, pp. 1031–1059, 3 pls]



TEXT-FIG. 1. Heterocoral morphology as typified by *Hexaphyllia*. A–B show corallites reconstructed with spines and tabulae in their correct orientation with respect to the growth direction. A, external view of corallite. B, longitudinal section. C, transverse section. GD, growth direction; H, heterotheca.

(Rózkowska 1969), Morocco and the Rheinisches Schiefergebirge, Upper Franconia and Thuringia in Germany (Weyer 1995*a*). Heterocoral diversity and abundance increased in the early Carboniferous, with the early introduction of *Hexaphyllia* and *Heterophyllia* in the late Tournaisian–early Viséan, but it was not until the Asbian that the heterocorals reached their acme (Sutherland and Mitchell 1980; Cossey 1983). Records of both *Heterophyllia* and *Hexaphyllia* continue in the Upper Carboniferous (Wilson 1960; Perret and Vachard 1977; Igo and Kobayashi 1980; Sutherland and Mitchell 1980; Lin and Peng 1990; Weyer and Polyakova 1995) along with *Anomalophyllia* (Tourneur *et al.* in press), until the group finally became extinct part way through the Namurian, during the Chokierian – H_1 Zone (Metcalfe *et al.* 1980). Further details of the geographical and stratigraphical distribution of heterocorals are detailed in Weyer (1967), Sutherland and Mitchell (1980), Wang (1980), Cossey (1983), Poty (1983) and Sugiyama (1984).

The systematic position of the group has for a long time been uncertain. Early workers regarded the heterocorals as belonging either to the Rugosa (Roemer 1880; Thomson 1883; Neumayr 1889; von Zittel 1924) or the Scleractinia (Duncan 1867; Stuckenberg 1904), but others were less sure (M'Coy 1851; Milne Edwards and Haime 1852; Kunth 1869; Carruthers *in* Lee 1909; Hill 1938–41, 1956). Later work on septal insertion patterns led Schindewolf (1941) to conclude that the heterocorals were of neither rugosan nor scleractinian affinity and a new order was established for the group, namely Heterocorallia.

Many different models of septal insertion for the group have been suggested (Yabe and Sugiyama 1940; Poty 1978*a*, 1978*b*, 1981; Lafuste 1979; Sutherland and Forbes 1980; Sugiyama 1984; Fedorowski 1991) and details of heterocoral microstructure are well known (Lafuste 1981, 1987; Karwowski and Wrzolek 1985, 1987; Wang 1988; Rodriguez 1989; Wang *et al.* 1989). Despite this, the relationship of Heterocorallia to other coral groups is still unknown. Similarities in the morphology of *Oligophylloides* and the rugosan *Pseudopetraia* led Hill (1981) to suggest that Heterocorallia may have evolved from a rugose coral stock in the Devonian. This theme was further developed by Fedorowski (1991, 1993) who suggested that Heterocorallia be placed alongside a new order, Calyxocorallia (containing *Pseudopetraia*), in a major new cnidarian subclass, Dividocorallia. This view was subsequently challenged by Wrzolek (1993*a*) who argued that since critical septal insertion evidence is lacking in Fedorowski's (1991) account, the phylogenetic relationship between Heterocorallia and Rugosa must remain unclear.

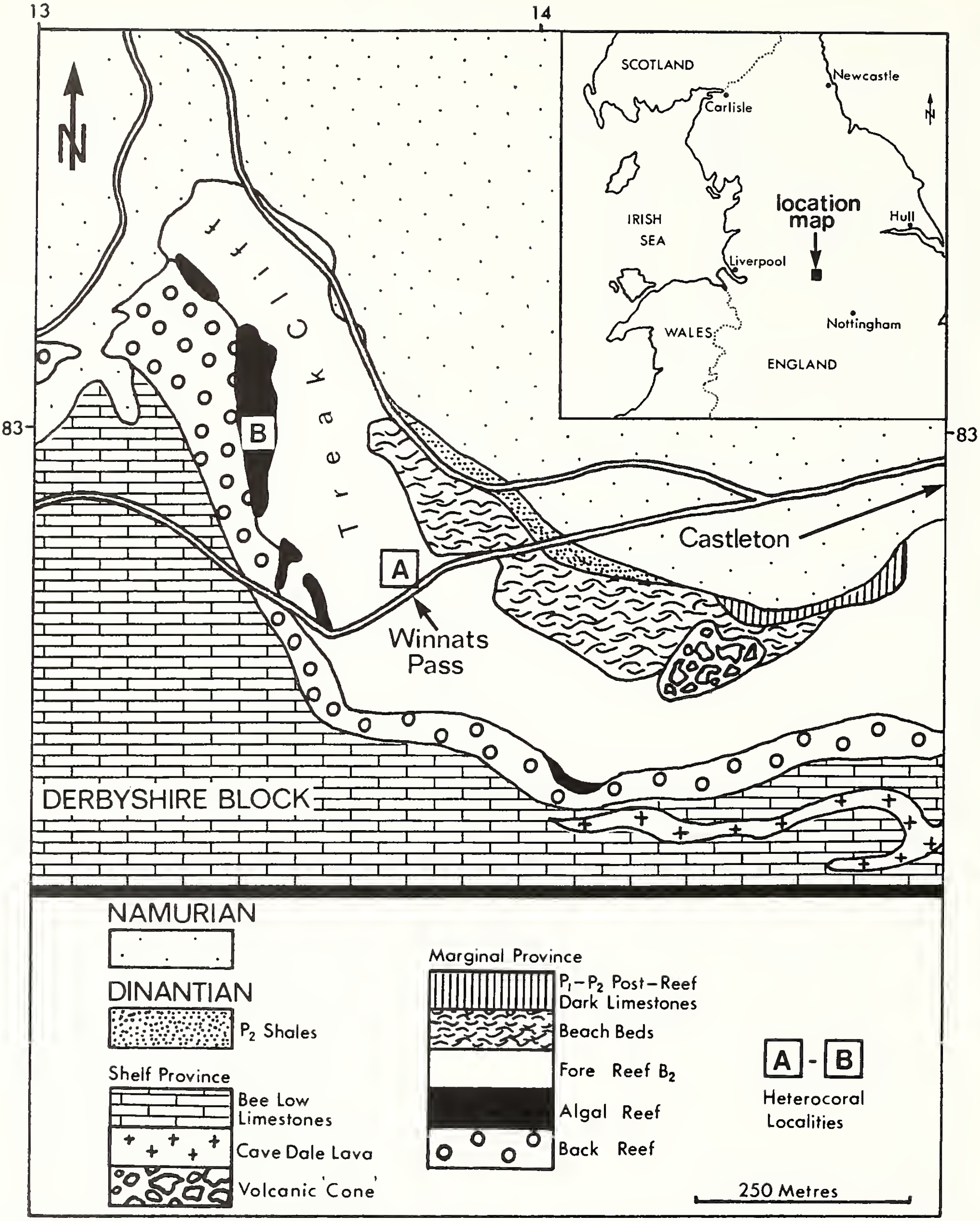
In Europe, only four well-established heterocoral genera are known. These are *Hexaphyllia* Stuckenberg, 1904 – heterocorals with only six septa, based on material from Russia and Scotland; the thicker walled, multiseptate forms *Mariaephyllia* Fedorowski, 1991 and *Oligophylloides* Rozkowska, 1969 – both from Germany and Poland; and *Heterophyllia* M'Coy, 1849 – based on material from Derbyshire. The great morphological variation in heterocoral populations was first appreciated by Young (1868, 1869) who, in a meticulous study of material from Scotland, clearly demonstrated the synonymy of *Heterophyllia mirabilis* and *H. lyelli*, two species that were originally described by Duncan (1867) and later transferred to *Hexaphyllia* by Stuckenberg (1904) and Robinson (1917). Sadly Young's pioneering work was criticized by established authorities at the time and its significance with respect to heterocoral research has largely gone unrecognized. Further details of intraspecific variation in heterocoral populations have been recorded, most notably in *Hexaphyllia* (Poty 1978*a*, 1981; Sugiyama 1984; Herbig 1986; Rodriguez and Comas-Rengifo 1989), but the relevance of this work to species definition in *Hexaphyllia* has yet to be fully evaluated.

In recent years many new heterocoral taxa have been described from south-east Asia, including more than 40 new species of *Hexaphyllia* from various parts of China (Jia and Xu 1975; Jia *et al.* 1977; Yu *et al.* 1978; Wang 1980; Xu 1981; Wang and Ye 1984; Lin and Wu 1985; Huang and Ma 1986; Lin *et al.* 1992; Liu and Su 1992; Lin and Yuan 1994). So far, few have questioned the validity of these new taxa, but, as Fontaine *et al.* (1991) suggested, probably far more species of *Hexaphyllia* have been described than are actually represented by the material. Concerns expressed by Rodriguez and Comas-Rengifo (1989) and Fedorowski (1991) regarding the validity of *Hexaphyllia* indicate that a review of the genus is long overdue.

Although general aspects of heterocoral morphogenesis are well known (Fedorowski 1991), our detailed understanding of corallite development and growth direction stems largely from work on the genus *Oligophylloides* (Rózkowska 1969; Sutherland and Mitchell 1980; Wrzolek 1980, 1993*b*). Comparable studies of other heterocoral genera have not hitherto been published. This paper considers the morphogenesis, systematics and palaeoecology of *Hexaphyllia* and is based on by far the richest and best preserved heterocoral fauna so far discovered in England. Exceptional preservation has facilitated a reconstruction of the *Hexaphyllia* polyp and, for the first time, spine orientation is defined in relation to corallite growth in both *Heterophyllia* and *Hexaphyllia*. The present paper is based on the observation of approximately 1300 corallites observed in hand specimen (42 per cent.), peel section (51 per cent.), and thin section (7 per cent.).

LOCATION AND FIELD OBSERVATIONS

The heterocorals which form the basis of this account are of early Carboniferous (Asbian) age and originate from two localities in Upper B_2 reef limestones of the Castleton Reef Belt, north Derbyshire (Text-fig. 2). Locality A (SK 13758270) is situated in fore-reef limestones near Winnats Pass and Locality B (SK 13478302) occurs in limestones of the algal reef complex at the top of Treak Cliff (Wolfenden 1958; Stevenson and Gaunt 1971; Broadhurst and Simpson 1973). Although the exact age equivalence of the two localities cannot be demonstrated (see discussion in Cossey 1983), their contemporaneity is assumed in this account. Records of heterocorals are also known from the



TEXT-FIG. 2. Geology of the Castleton Reef Belt in north Derbyshire indicating the position of heterocoral localities referred to in the text (modified after Stevenson and Gaunt 1971; Cheshire and Bell 1977).

shelf province Bee Low Limestones (the lateral equivalent of the Castleton Reef Belt deposits) but are uncommon (Cossey 1983). Further details concerning the stratigraphy and palaeoecology of the Castleton Reef Belt have been documented by Parkinson (1965) and Timms (1978).

Locality A. The heterocorals occur in fossiliferous, bedded limestones, which Stevenson and Gaunt (1971) recognized as characteristic of their fore-reef facies. The material consists of over 1100, exceptionally well preserved corallites of *Hexaphyllia* concentrated in thin layers, up to 10 mm thick (Pl. 1). Most corallites were found oriented in a subparallel position with respect to each other and lying with their long axes in the plane of the bedding. Some corallites oriented at an angle to the bedding and with spines curving upwards appeared to be in life position. These features suggest that the corallites may have been 'nesting' in a relatively protected niche within the fore-reef and subsequently concentrated in layers by winnowing, either as result of current activity, or by wave/storm surge. The associated fauna is dominated by the disarticulated, colour-banded, pectenoid bivalve *Streblochondria elliptica* (Phillips), described in detail by Shaw (1970), buxtoniid brachiopods, delicate fenestrate bryozoans and goniatites (see Text-fig. 12).

The preservation of so many corallites from this locality is attributed to the early formation of a radiaxial fibrous mosaic (Bathurst 1971). Unfortunately however, the development of this neomorphic fabric (Kendall and Tucker 1973) has resulted in the modification of primary textures to such an extent that details of the corals' microstructure and of the original sediment matrix are largely indeterminable (Cossey 1983; and see Pl. 2, fig. 1; Pl. 3, fig. 7).

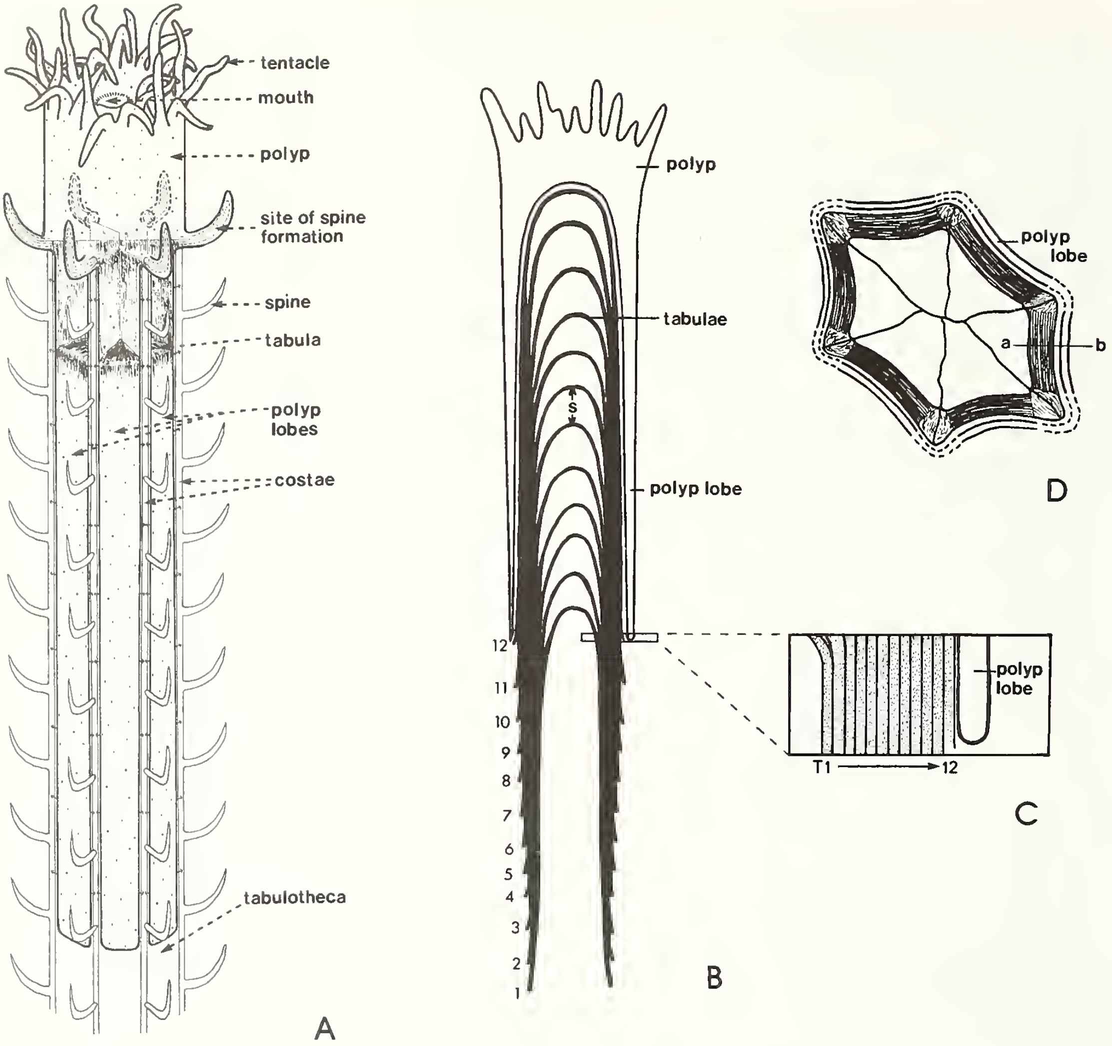
Locality B. The heterocorals occur in massive fine-grained micritic limestones and are associated with limestones from which Wolfenden (1958) described stromatolites of the *Collenia-Cryptozoon* type. Stevenson and Gaunt (1971) later referred to these deposits as of 'algal reef' facies. The material from this locality includes approximately 200 *Hexaphyllia* corallites, many with tubercles, but only a few with spines, and a solitary specimen of *Heterophyllia ornata* M'Coy, also with spines (Pl. 2, fig. 8). The majority of corallites were found lying prone and with their long axes oriented subparallel to the strike of the reef crest. These features suggest that corallites were transported a short distance from their growth position by currents prior to deposition and that during this time their spines were removed by mechanical abrasion. The associated fauna is dominated by *in situ* colonies of *Siphonodendron* spp. (see Text-fig. 13). Although neomorphic effects have also modified the sediment fabric from this locality, the original limestone appears to have been either a biomicrite or a poorly washed biosparite.

Further details of the taphonomy and palaeoecology of the assemblages are given by Cossey (1983), complete with faunal lists from both localities.

MORPHOLOGY

Early growth and orientation

Details of the early ontogeny in heterocorals are scarce since corallites are usually found as small, solitary, fragmented lengths and juvenile corallites are rare. Defining the growth direction of corallites has also proved difficult for, as reference to the literature indicates, heterocorals have been figured in completely different orientations, by various authors. However, a clearer view of heterocoral growth has emerged in recent years with the discovery of what has been widely regarded as weakly colonial coralla in which juvenile offsets have been observed branching away from larger adult corallites (Weyer 1995*b*; Tourneur *et al.* in press; Tourneur and Herrmann in press). Studies of *Oligophylloides* by Rózkowsa (1969) and Wrzolek (1980), for example, indicate that juvenile corallites developed broad bases where they connected with the adult corallites, and that the tabulae curved peripherally downwards in relation to the growth direction as they fused to form the wall.

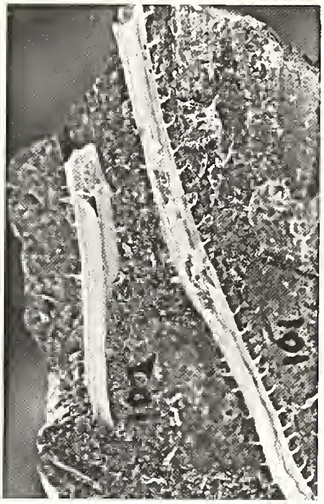


TEXT-FIG. 3. Polyp reconstruction. A, *Hexaphyllia* corallite with polyp in life position. Note the development of polyp lobes extending down the outside of the corallite and the presumed site of spine formation near the top of the polyp. B–D, determination of polyp lobe length in *Hexaphyllia*. The length of the polyp lobes is derived by multiplying the tabulae spacing distance (s) by 11 (see text for further explanation). B, longitudinal sketch section through polyp and corallite. C, enlarged part of B showing 12 fused tabulae (T1–12) in the wall structure. D, cross section of corallite illustrating the lamellar fabric of the wall resulting from the peripheral fusion of the tabulae (a–b = line of the section illustrated in C).

EXPLANATION OF PLATE 1

Figs 1–8. *Hexaphyllia marginata* (Fleming, 1828); Winnats Pass (locality A), Castleton Reef Belt, Derbyshire; all from Upper B_2 (Asbian) fore-reef limestones. Figs 2 and 5–7 illustrate the attachment of juveniles to adult corallites and in fig. 8, the relationship between spine and tabulae can be discerned. 1, MM LL10919; ×3. 2, MM LL10911; ×3. 3, MM LL10920; ×5. 4, MM LL10919; ×9. 5, MM LL10911; ×7. 6, MM LL10912; ×7. 7, MM LL10910; ×8. 8, MM LL10920; ×13.

PLATE 1



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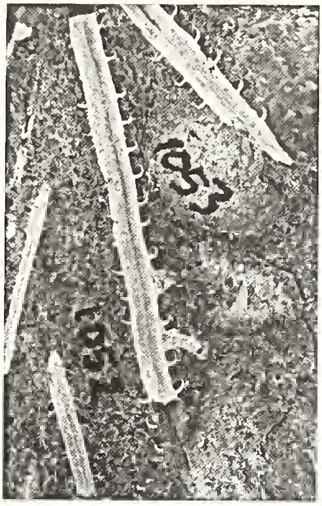

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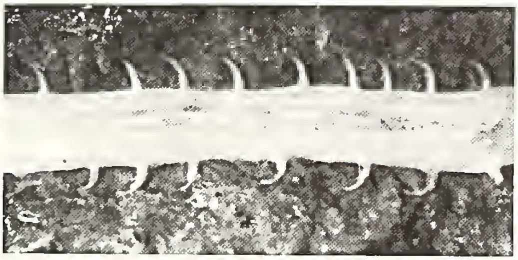

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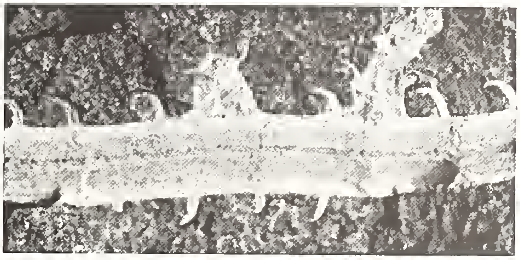

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COSSEY, *Hexaphyllia*

Branching of this kind has also been observed in *Heterophyllia* by Duncan (1867, pl. 31, fig. 6*a*) and in *Radiciphyllia* by Sugiyama (1984, pl. 7, fig. 1*b*; text-fig. 17). In these examples, evidence that the developing offsets originated from the parent corallites to which they are attached is obvious, since the morphology of the adult is usually strongly modified in the zone of contact between them.

So-called 'branching phenomena' may also be recognized in the present account (Pl. 1, fig. 2) but evidence that the juvenile offsets arose from the subdivision of adults by an asexual budding process is difficult to prove. Here, the angle of divergence between juvenile and adult is quite variable and occasionally two offsets diverge from a 'parent' in different directions (Pl. 1, figs 5–6). In addition, there is no obvious change in the morphology of the adult at its contact with the juvenile (Pl. 2, figs 3, 5–6; Pl. 3, figs 2, 4), the contact surface between juvenile and adult is extensive, and the spines of adult corallites are sometimes enveloped by the offsets (Pl. 1, figs 5, 7; Pl. 2, fig. 6). These features suggest that the relationship between the juvenile and adult corallite is more likely to have developed as a result of an encrustation process rather than from budding. In such examples the juvenile corallites would clearly represent the very earliest stages in corallite development formed after the settlement of planula larvae on the adult corallite substrates, their broad expanded bases forming 'talons' analogous to those described in other heterocoral genera by Rózkowska (1969) and Wrzolek (1980). This conclusion does not, however, preclude the existence of budding in *Hexaphyllia*; it merely draws attention to the difficulty in distinguishing between the phenomenon of branching by asexual budding from that of attachment by larval encrustation.

Regardless of their origin, such associations between young and adult corallites have enabled the direction of tabulae curvature to be fixed in relation to the growth direction. The tabulae which are widely spaced along the corallite axis curve peripherally downwards in the opposite direction to that of corallite growth (Pl. 2, figs 3, 5–6). In hand specimen (Pl. 1, fig. 8) and in thin section (Pl. 2, figs 6–7), spines were observed curving consistently in the opposite sense to that of the tabulae and pointing upwards in the direction of corallite growth. A similar relationship between tabulae and spines was also noted in *Heterophyllia* (Pl. 2, fig. 8) in which spines are recorded for the first time (and see Pl. 3, fig. 1). Text-figure 1A–B illustrates the correct orientation of *Hexaphyllia* in it life position.

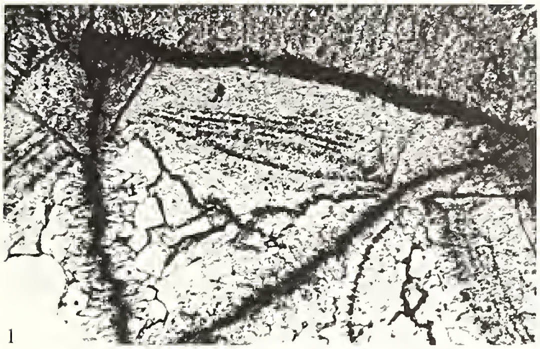
Details of septal insertion are difficult to establish, since insertion was initially extremely rapid and subsequently very slow. Either four or five septa appear in some corallites before they have reached 4 mm in length (Pl. 2, fig. 5; Pl. 3, fig. 2). In some corallites as few as three septa occur (Pl. 3, fig. 9).

EXPLANATION OF PLATE 2

Figs 1–8. Heterocorals from the Lower Carboniferous, Castleton Reef Belt in North Derbyshire. All specimens are of Upper B_2 (Asbian) age.

Figs 1–7, *Hexaphyllia marginata* (Fleming, 1828). 1–3, 5–7, from the fore-reef at Winnats Pass (locality A). 4, from the algal reef at Treak Cliff (locality B). Figs 1–2 and 4 show the development of tabulae in the wall structure. 1, transverse thin section, MM LL10907b; ×47. 2, transverse thin section, MM LL 10908; ×38. 4, transverse peel section, MM LL10900a; ×39. Figs 3, 5–6 show young corallites growing away from adult corallites to which they are attached. From such specimens the curvature of the tabulae may be fixed in relation to the growth direction. 3, transverse peel section, MM LL10909k; ×9. 5, transverse peel section, MM LL10909aa; ×15. 6, transverse peel section, MM LL10909d; ×14. Figs 6–7 illustrate the relationship between spine curvature and tabulae curvature. 7, transverse peel-section, MM LL10906a; ×14.

Fig. 8. *Heterophyllia ornata* M'Coy, 1844; MM LL10900e; algal reef at Treak Cliff (locality B). Note that the relationship between spine curvature and tabulae curvature is the same as that in figures 6–7; longitudinal peel-section; ×15.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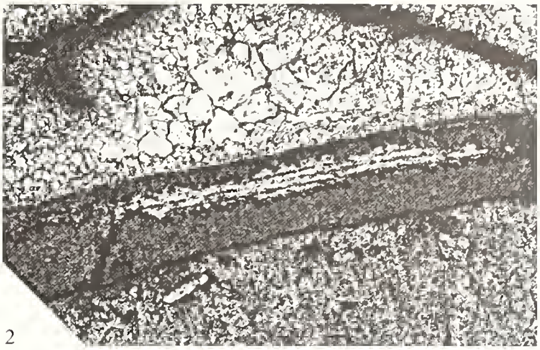
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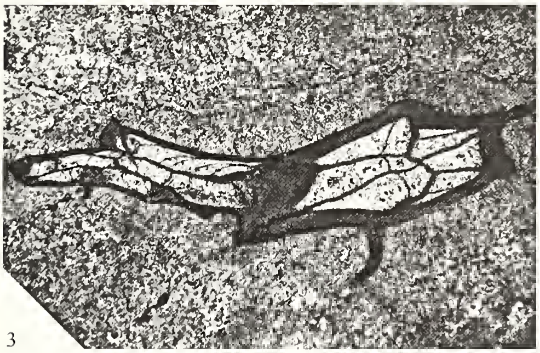
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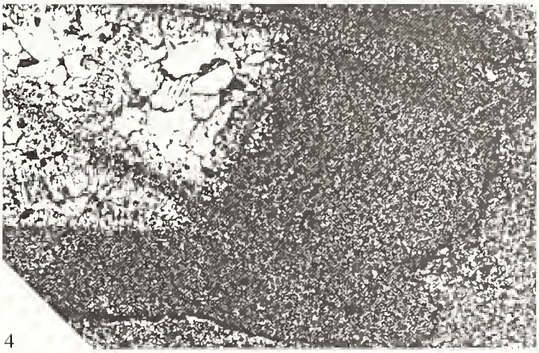
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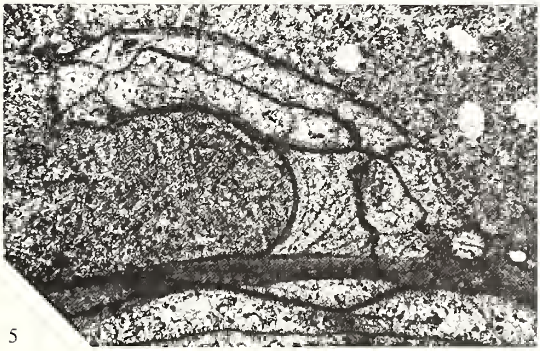
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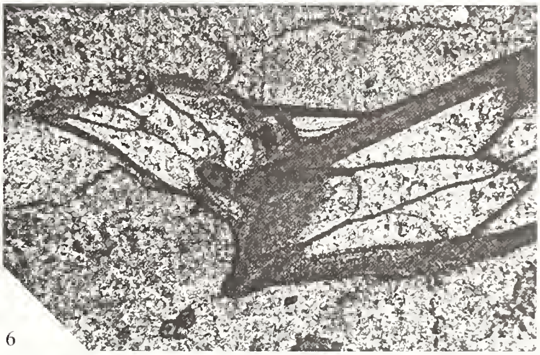
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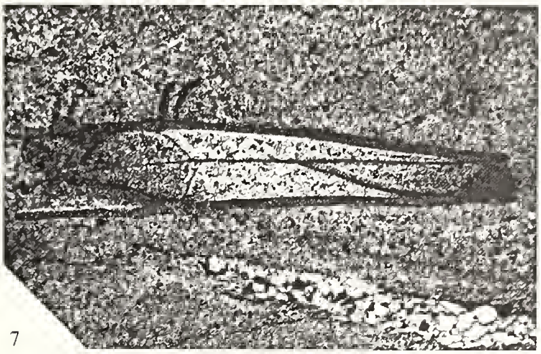
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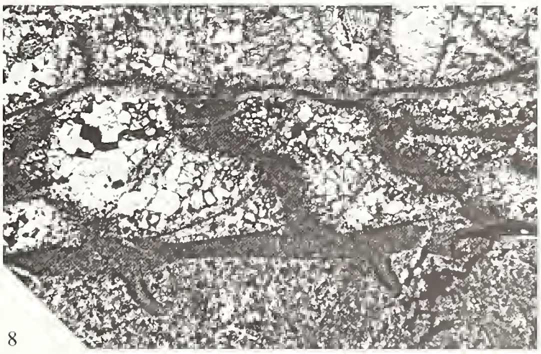
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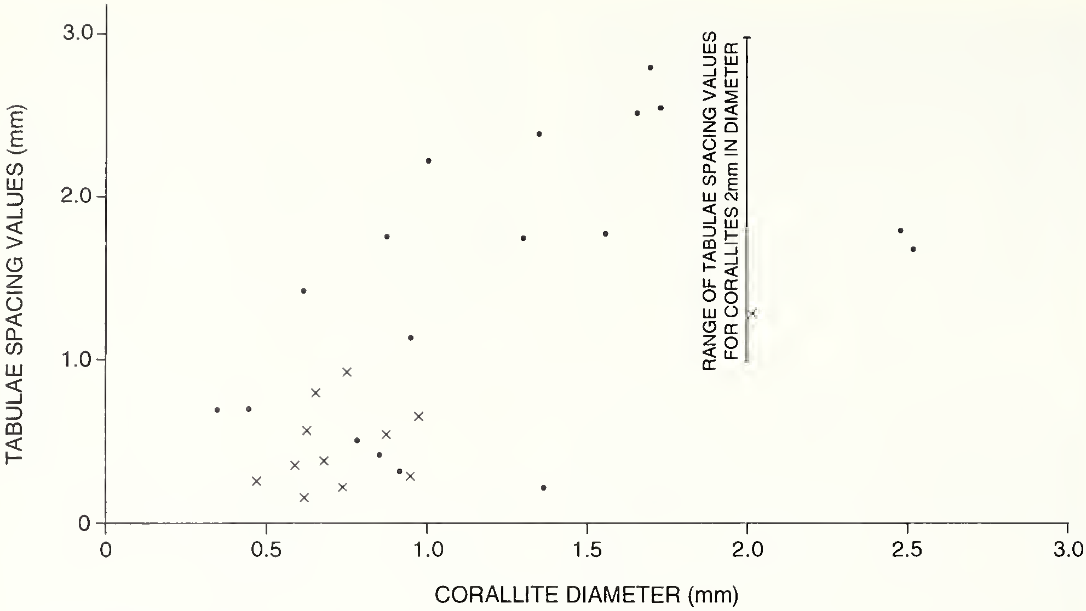
COSSEY, *Hexaphyllia*, *Heterophyllia*



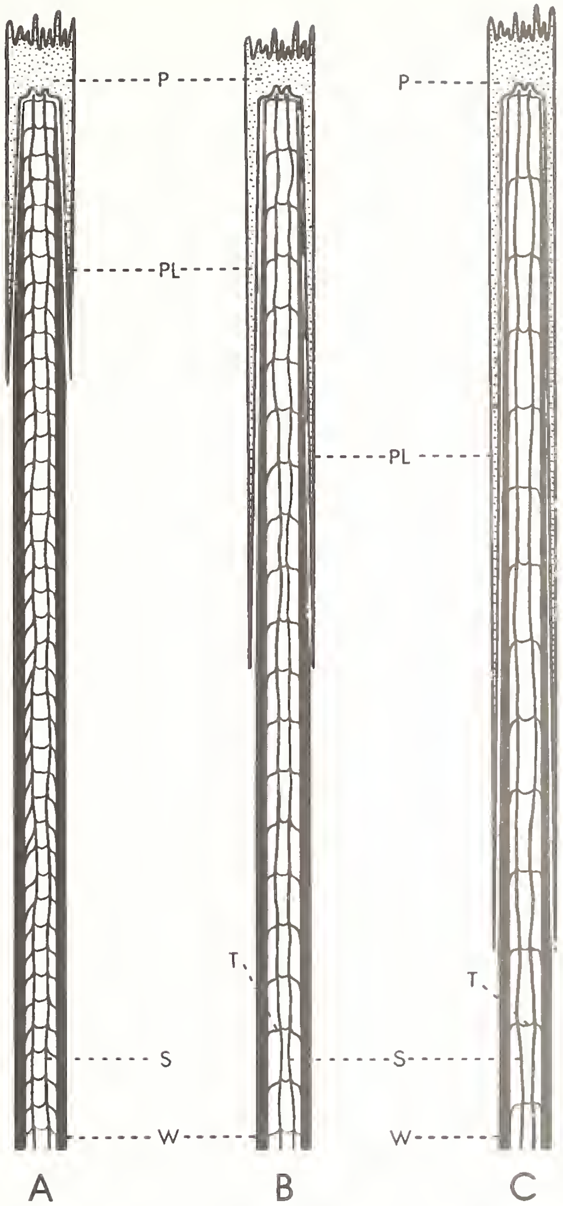
TEXT-FIG. 4. The relationship between corallite diameter and tabulae spacing in *Hexaphyllia marginata* (Fleming, 1828). Dots represent corallites from the fore-reef (locality A) and crosses corallites from the algal reef (locality B). Note that for corallites 2 mm in diameter the tabulae spacing value ranges from approximately 1–3 mm.

Reconstruction of the polyp

It now seems likely that in all heterocoral genera the tabulae curve peripherally downwards away from the corallite axis before fusing to form the corallite wall (Wrzolek 1980; Cossey 1983; Fedorowski 1991). The implication of this unique method of wall formation is significant in that the corals would have lacked a protective cup-like calyx. Furthermore, polyps would have sat exposed upon the tapered growing ends of corallites (referred to as distal cones by Wrzolek 1980, 1993*b*) and with soft polyp tissue extending down the outside of the corallite forming the wall (the tabulotheca). The corallites were therefore largely endoskeletal in origin. In *Hexaphyllia*, the expanded peripheral ends of the septa commonly project beyond the outer edges of the tabulotheca to form the costae and spines. In order to allow for the secretion of the tabulotheca, it is necessary to invoke the presence of up to six polyp lobes extending down the outside of the corallites between the costae (Text-fig. 3A–B). Clearly, the exposed polyps would have been extremely vulnerable to attack from predators were it not for the presence between the polyp lobes of upward curving spines. Protection is therefore seen as the primary function of the spines. For further details relating to the secretion of spines and costae, see Cossey (1983).

The extent to which corallites were enclosed by the polyps and the length of polyp lobes can easily be determined, if only by indirect means. Wrzolek (1993*b*) used trigonometry to calculate the height of the distal cone in heterocorals using the apical angle (the angle between the corallite axis and the peripheral edges of the tabulae) and the vertical separation distance of the tabulae at the corallite axis. The height of the distal cone corresponds exactly to the length of corallite enclosed and thus directly to the length of the polyp lobes. Figures were obtained by Wrzolek (1993*b*) for *Oligophylloides*, *Heterophyllia*, *Longlinophyllia* and *Hexaphyllia* of 2–188 mm, 7 mm, 7 mm and 11 mm respectively. Another convenient method of calculating the polyp lobe length and the method used here, uses the number of tabulae fused in the wall at any given level in the corallite

TEXT-FIG. 5. Determination of polyp lobe length in *Hexaphyllia*. A, based on a spacing of 1 mm between tabulae. B, based on a spacing of 2 mm between tabulae. C, based on a spacing of 3 mm between tabulae. P, polyp; PL, polyp lobes; S, septa; T, tabula; W, wall.



and the average tabulae spacing value at the corallite axis (Cossey 1983). Detailed observations of *Hexaphyllia* corallites seen in thin section (Pl. 2, figs 1–2, 4) indicate that for corallites approximately 2 mm in diameter the established number of fused tabulae in the tabulotheca is 12. Reference to Text-figure 3B–D indicates that for such corallites the polyp lobe length must equate to the distance between the corresponding 12 tabulae at the corallite axis or 11 times the average distance between tabulae. Text-figure 4 indicates that in corallites of 2 mm diameter the average tabulae spacing value ranges from 1–3 mm. Accordingly, the length of polyp lobes in *Hexaphyllia* can be calculated as 11–33 mm (Text-fig. 5).

The existence of polyp lobes and their progressive movement up the sides of corallites during growth can be envisaged from Text-figure 11A, where the component tabulae in the wall structure may be seen overlapping one another like slates on a roof.

Morphometrics

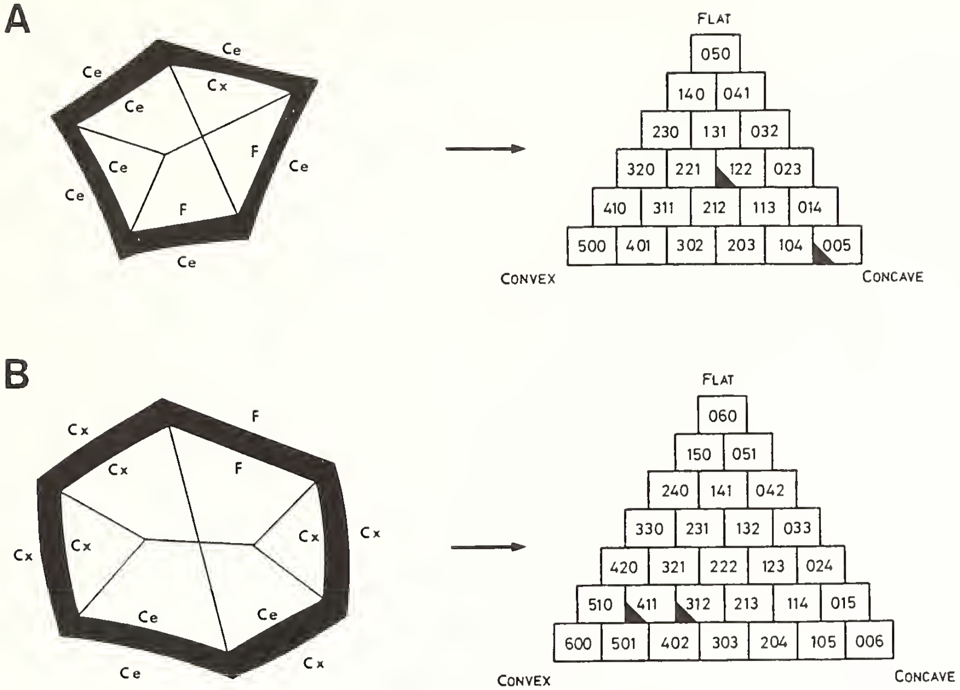
Wall shape and thickness. The shape of any corallite is determined by the shape of its wall. Wall shape can be defined by two ratios. The inner wall shape ratio defines the shape of the inner wall, whilst the outer wall shape ratio defines the shape of the outer wall. In each case, the number of wall-sections that are respectively convex (Cx), flat (F) and concave (Ce) is expressed by the ratio Cx:F:Ce. Text-figure 6 indicates how wall shape ratios are determined and how pyramid diagrams can be used to define different corallite shapes. Definition of wall shape ratios for the Castleton material indicate that the shape of *Hexaphyllia* corallites from both localities in the reef belt is continuously and widely variable (Text-fig. 7). Although cylindrical, prismatic and stellate corallite shapes were found at both localities, cylindrical forms were more prevalent in the algal reef and stellate forms more common in the fore-reef (Pl. 3, figs 14–15). Where cylindrical forms are present the inner walls are commonly more convex than the outer walls. This suggests that cylindrical forms were not the product of corallite abrasion prior to burial.

Variations in wall thickness were also noted between the two localities. Text-figure 8 indicates that wall thickness increased as corallites grew larger and that individuals from the algal reef developed slightly thicker walls than those from the fore-reef.

If (as discussed earlier) the age equivalence of the two localities is assumed, then the functional significance of these morphological variations is striking. The thicker-walled and relatively robust, cylindrical corallites from the algal reef were better suited to life in more turbulent, shallow water close to the reef crest while the more delicate, thinner-walled, stellate corallites are more likely to have lived at greater depths on the fore-reef in less turbulent conditions.

Corallite diameter. Size-frequency plots indicate a wide but continuous range in corallite diameter for *Hexaphyllia* corallites at both localities in the reef belt (Text-fig. 9). In each case the range in corallite diameter is broadly similar, but specimens from the fore-reef have a slightly greater range (0·1–2·6 mm) than those of the algal reef (0·2–2·2 mm). A normal size distribution is indicated in the plots from the fore-reef. The plot for individuals with six septa from the algal reef shows a pronounced bimodal distribution with two prominent peaks, occurring at the 0·9 mm and 1·7 mm corallite diameter marks respectively. The gap between these two peaks represents an absence of corallites with a diameter of 1·2–1·3 mm. Various explanations for this bimodal distribution were suggested by Cossey (1983), including: the presence of more than one corallite generation; the presence of more than one species; the selective removal of the 1·2–1·3 mm diameter corallites; and rapid growth through the 1·2–1·3 mm size range producing corallites with short, tapered sections along their length.

Although the last hypothesis was originally favoured by Cossey (1983), it is now regarded as an unlikely explanation for the bimodality described, since corallites in the 1·2–1·3 mm diameter range are now known to occur (from locality A described here, and see Poty 1978*a*, 1981; Herbig 1986; Rodriguez and Comas-Rengifo 1989) and in none of these cases has a corallite showing tapered growth been directly observed. Bimodal distributions in other heterocoral assemblages have, however, been recorded and these have been interpreted as indicating the presence of more than one species (Poty 1978*a*, 1981). In such examples, morphological differences other than corallite diameter are used to support the argument. Since no other morphological differences were noted in corallites from the algal reef, the presence of more than one species is unlikely to be the cause of the bimodality described. Bimodality arising from the presence of two generations is also doubted

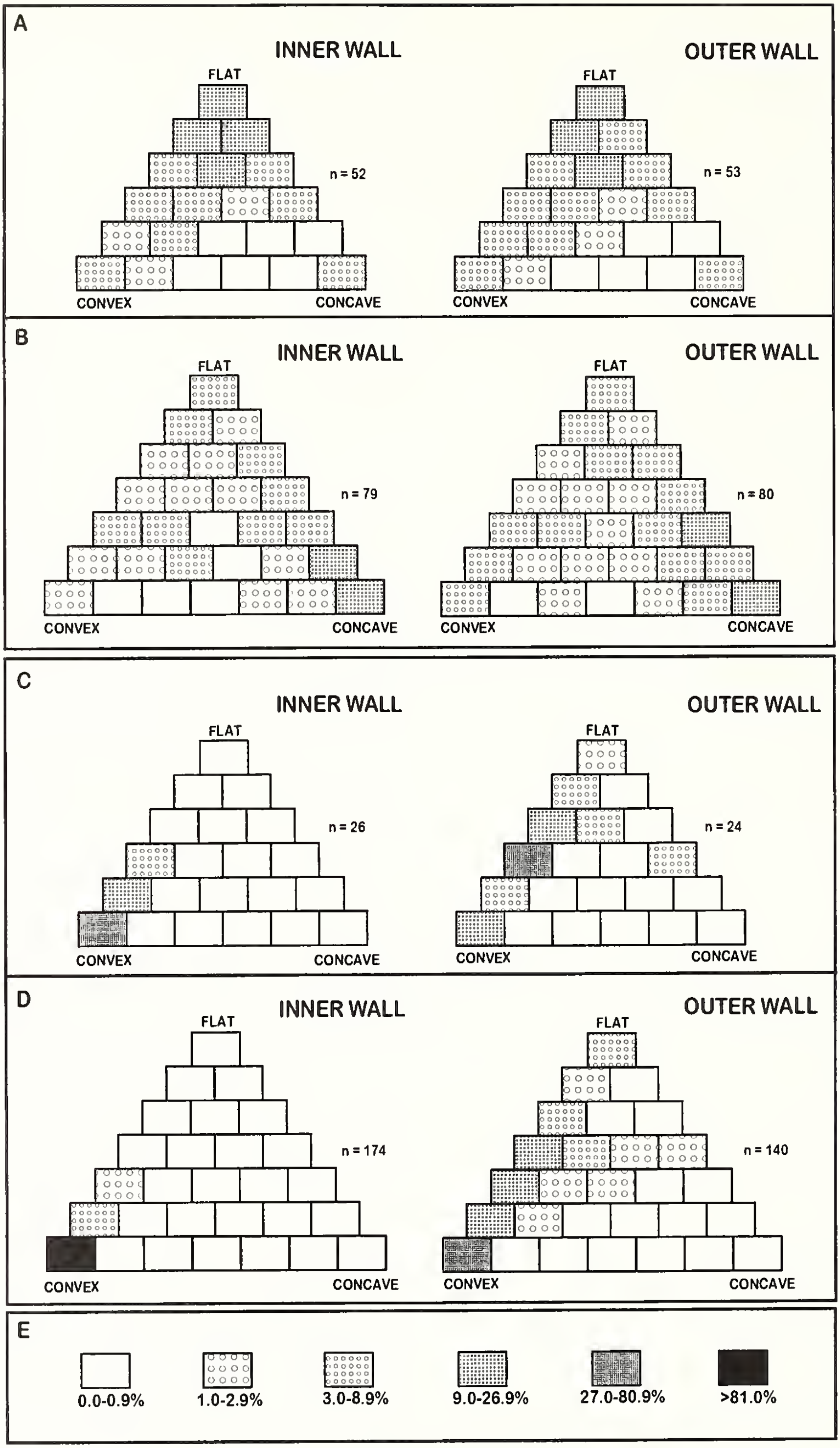


TEXT-FIG. 6. The definition of corallite shape in *Hexaphyllia*. The shape of any corallite is determined by two ratios, an inner wall shape ratio and an outer wall shape ratio. The number of wall sections that are respectively convex (Cx), flat (F) and concave (Ce) is defined by each ratio. Pyramid diagrams can then be used to plot the wall shape ratios for any given number of corallites. In the examples illustrated both inner and outer wall shape ratios are plotted on the same pyramid diagram – although they are usually plotted separately (see Text-fig. 7). A, corallites with five septa, an inner wall shape ratio of 1:2:2 and an outer wall shape ratio of 0:0:5. B, corallites with six septa, an inner wall shape ratio of 3:1:2 and an outer wall shape ratio of 4:1:1.

since, in an assemblage of fragmented corallites, specimens in the 1·2–1·3 mm diameter range and representing the earlier stages in growth of the larger individuals, would still be expected. The explanation favoured here for the bimodal distribution is that corallites in the 1·2–1·3 mm diameter range were selectively removed by currents. The same process may also explain how corallites became aligned parallel to the strike of the algal reef and had most of their spines removed.

Spine spacing and tabulae spacing. Reference to Text-figures 4 and 10 indicates that as corallite size increases, so do the spacing distances of tabulae and spines. In corallites of the same size, the variation in both parameters is both wide and continuous. In 1·2 mm diameter corallites for example, the tabulae spacing value ranges from 0·2–2·3 mm and the spine spacing distance from 1·0–1·8 mm. In addition, the spacing between tabulae is significantly higher in corallites from the fore-reef than in those from the algal reef (Pl. 3, figs 5, 8).

The differences in tabulae spacing, wall thickness and shape noted above, reflect morphological adaptations to life at different positions within the reef caused by differences in growth rate and changes in the shape of the polyps' calicoblast layer during the skeletal secretion. These differences in turn reflect a response to variations in water depth, turbulence, the rate at which corallites settled in the sediment, sedimentation rate, or, a combination of these factors. Further details relating to the morphological differences between the two assemblages are discussed in detail elsewhere (Cossey 1983).



TEXT-FIG. 7. For caption see opposite.

SYSTEMATIC PALAEONTOLOGY

Order HETEROCORALLIA Schindewolf, 1941
Family HETEROPHYLLIIDAE Dybowski, 1873

Genus HEXAPHYLLIA Stuckenberg, 1904

Type species. Hexaphyllia prismatica Stuckenberg, 1904 (p. 72, pl. 3, fig. 5a–d) from the Lower Carboniferous of central Russia.

Emended diagnosis. Elongate, cylindrical or prismatic heterocorals with up to six sides and a maximum of six septa which meet at or near the axis. The peripheral edges of the septa may thicken and project through the wall to form longitudinal ridges or costae along the side of the corallite. The costae may be adorned with tubercles or spines which curve distally in the direction of corallite growth. Whilst the internal structure of the costae, spines and tubercles appears to be continuous with the septa, their external structure appears to form an extension of the tabulotheca. The tabulae are complete and slightly domed structures near the axis, but turn downwards peripherally and fuse together between the distal edges of the septa to form the tabulotheca. Corallite diameters and tabulae spacing values are continuously variable parameters.

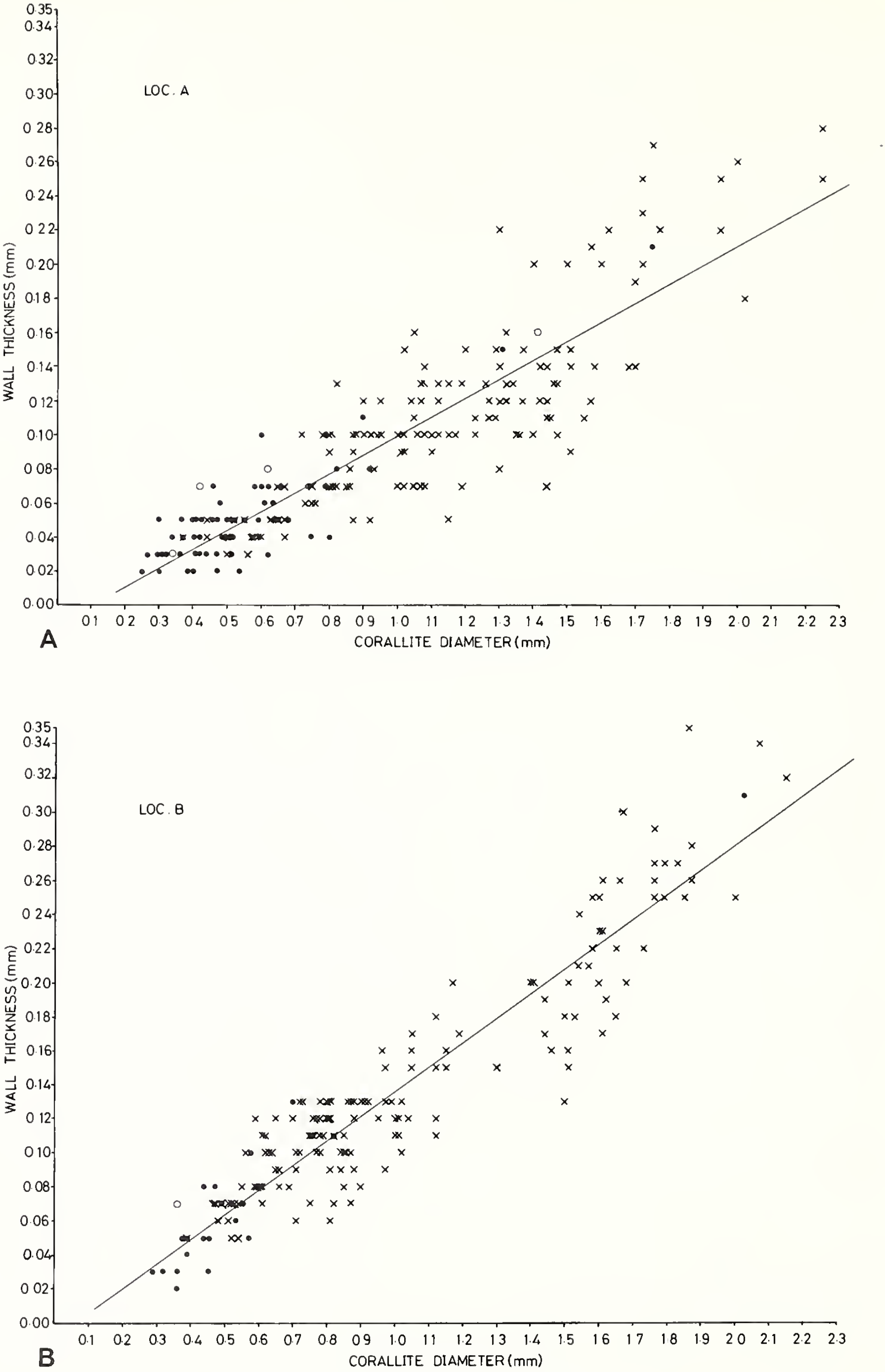
Remarks. The genus was erected for those heterocorals possessing only six septa and was based on *Hexaphyllia prismatica* from central Russia. Later, Poty (1978*a*, 1981) demonstrated that some heterocorals with six septa were simply juveniles of the multiseptate *Heterophyllia* and more recently, Rodriguez and Comas-Rengifo (1989) described populations of *Hexaphyllia*? in which the number of septa ranged from four to ten, but six-septal forms predominated. For such reasons the validity of the genus *Hexaphyllia* was questioned by Rodriguez and Comas-Rengifo (1989) and Fedorowski (1991). With the exception of a single specimen of *Heterophyllia ornata* (see Pl. 2, fig. 8) none of the remaining 1300 corallites from Castleton possessed more than six septa. In view of this and because six-septal forms are the norm, representing more than 80 per cent. of both assemblages, the generic status of *Hexaphyllia* is upheld in this account. Although the presence of spines in both *Heterophyllia* (Pl. 2, fig. 8; Pl. 3, fig. 1) and *Hexaphyllia* (Pl. 1) may indicate a closer relationship than previously suspected, the exact systematic relationship between the two genera remains unclear.

Hexaphyllia marginata (Fleming, 1828) emend.

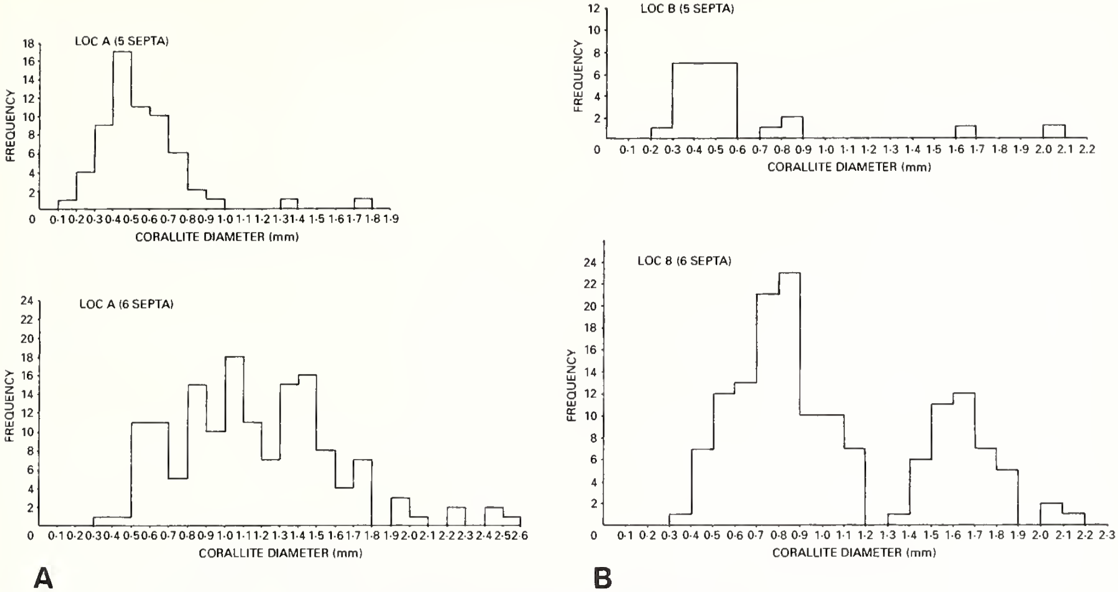
Plate 1, figures 1–8; Plate 2, figures 1–7; Plate 3, figures 2–15; Text-figure 11A–D

1828	*Lithostrotion marginatum* Fleming, p. 508.
1844	*Serpula hexicarinata* M'Coy, p. 169, pl. 23, fig. 28.
1867	*Heterophyllia M'Coyi* Duncan, p. 645, pl. 31, fig. 3a–c.
1867	*Heterophyllia Lyelli* Duncan, p. 646, pl. 31, fig. 4a–c.
1867	*Heterophyllia mirabilis* Duncan, p. 646, pl. 31, figs 5a–h.
1904	*Hexaphyllia prismatica* Stuckenberg, p. 72, pl. 3, fig. 5a–d.
1917	*Hexaphyllia mirabilis* (Duncan); Robinson, p. 178.
1939	*Hexaphyllia elegans* Yabe and Sugiyama, p. 500, pl. 26, figs 1–3; text-fig. 1.
1939	*Hexaphyllia japonica* Yabe and Sugiyama, p. 501, pl. 26, figs 1b–c, 4–5.
1971	*Hexaphyllia mirabilis* (Duncan); Mihaly, p. 54, pl. 1, figs 1–5; pl. 2, figs 1–3.
1975	*Hexaphyllia guangxiensis* Jia and Xu, p. 94, pl. 2, figs 5a–b.

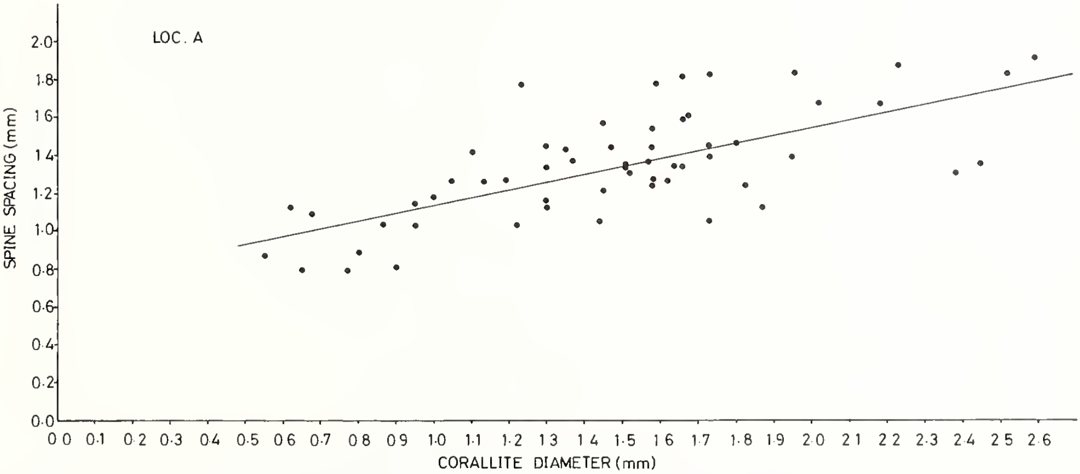
TEXT-FIG. 7. Pyramid diagrams illustrating wall shape variations in corallites of *Hexaphyllia marginata* from the Castleton Reef Belt. A, corallites from the fore-reef (locality A) with five septa. B, corallites from the fore-reef (locality A) with six septa. C, corallites from the algal reef (locality B) with five septa. D, corallites from the algal reef (locality B) with six septa. E, scale – in which the number of corallites with a specific wall shape ratio is expressed as a percentage of the total number of corallites plotted in each diagram.



TEXT-FIG. 8. For caption see opposite.



TEXT-FIG. 9. *Hexaphyllia marginata* (Fleming, 1828) – size frequency plots. A, corallites from the fore-reef (locality A). B, corallites from the algal reef (locality B).



TEXT-FIG. 10. The relationship between corallite diameter and the spine spacing distance in corallites of *Hexaphyllia marginata* from the fore-reef (locality A).

1977 *Hexaphyllia zhongguoensis* Xu; Jia *et al.*, p. 243, pl. 60, fig. 9a–b.
1977 *Hexaphyllia guixiensis* Kuang; Jia *et al.*, p. 243, pl. 60, fig. 11a–b.
1978 *Hexaphyllia transversa* Yu, Lin, Huang and Cai, p. 47, pl. 14, figs 1a–b, 2–3; pl. 15, figs 5–6.
1978 *Hexaphyllia tenuis* Yu, Lin, Huang and Cai, p. 49, pl. 14, figs 5a–b, 6–7.
1978 *Hexaphyllia elongata* Yu, Lin, Huang and Cai, p. 49, pl. 14, figs 12a–b, 13; pl. 15, fig. 7.

TEXT-FIG. 8. The relationship between corallite diameter and wall thickness in *Hexaphyllia marginata*. A, corallites from the fore-reef (locality A). B, corallites from the algal reef (locality B). Note how wall thickness increases at a greater rate in corallites from the algal reef. Circles – corallites with four septa; dots – corallites with five septa; crosses – corallites with six septa.

1980 *Hexaphyllia concavia* Metcalfe *et al.*, p. 25, pl. 3, figs 13, 15.
1980 *Hexaphyllia xizangensis* Wang, p. 43, pl. 1, figs 1–2.
1980 *Hexaphyllia quighaiensis* Wang, p. 43, pl. 1, fig. 3.
1980 *Hexaphyllia quilianshanensis* Wang, p. 44, pl. 1, fig. 7.
1980 *Hexaphyllia jiangdaensis* Wang, p. 45, pl. 1, fig. 11.
1981 *Hexaphyllia minor* Xu, p. 46, pl. 1, figs 8a–b, 9.
1981 *Hexaphyllia yangchunensis* Xu, p. 46, pl. 1, figs 10a–b, 11a–b
1981 *Hexaphyllia crassa* Xu, p. 46, pl. 1, figs 6, 7a–b.
1981 *Hexaphyllia marginata* Poty, p. 73, pl. 34, fig. 17.
1981 *Hexaphyllia mirabilis* Poty, p. 72, pl. 34, figs 15–16.
1984 *Hexaphyllia yabei* Sugiyama, p. 42, pl. 1, figs 1a–8b; pl. 2, figs 1a–4; pl. 4, figs 3–5; text-figs 4b, 9.
1984 *Hexaphyllia inflata* Sugiyama, p. 60, pl. 3, figs 1a–9; text-fig. 12.
1984 *Hexaphyllia forcipis* Wang and Ye, p. 34, pl. 6, fig. 3a–b.
1984 *Hexaphyllia majaiaobaensis* Wang and Ye, p. 35, pl. 6, fig. 5a–b.
1984 *Hexaphyllia tenuiformis* Wang and Ye, p. 34, pl. 6, fig. 6.
1985 *Hexaphyllia longlinensis* Lin and Wu, p. 273, pl. 1, figs 9a–b; 10; text-fig. 1.
1985 *Hexaphyllia tenuis longhuoensis* Lin and Wu, p. 273, pl. 1, figs 11a–b, 12–13.
1985 *Hexaphyllia gigantea crassotheca* Lin and Wu, p. 273, pl. 1, figs 7a–b, 8.
1986 *Hexaphyllia elegantula* Huang and Ma, p. 17, pl. 4, figs 1, 1a–b.
1986 *Hexaphyllia weiningensis* Huang and Ma, p. 15, pl. 3, fig. 1a–b.
1986 *Hexaphyllia irregulare* Huang and Ma, p. 16, pl. 3, fig. 14a–b.
1986 *Hexaphyllia hexagonae* Huang and Ma, p. 17, pl. 4, figs 8a–b, 9–10.
1986 *Hexaphyllia cylindrica* Huang and Ma, p. 17, pl. 4, figs 12a–b, 13a–b, 14.
1986 *Hexaphyllia curta* Huang and Ma, p. 17, pl. 3, figs 19a–b, 20.
1986 *Hexaphyllia clina* Huang and Ma, p. 15, pl. 3, figs 4a–b, 5.
1992 *Hexaphyllia asymmetrica* Liu and Su, p. 476, pl. 1, fig. 1a–b.
1992 *Hexaphyllia extensa* Liu and Su, p. 477, pl. 1, fig. 3a–b.
1992 *Hexaphyllia spinalus* Lin, Huang, Wu, Peng and Qiu, p. 41, pl. 3, figs 1a–2b; text-fig. 1.44.
1992 *Hexaphyllia multitabulata* Lin, Huang, Wu, Peng and Qiu, p. 41, pl. 3, figs 3a–4b; text-fig. 1.45.
1992 *Hexaphyllia yui* Lin, Huang, Wu, Peng and Qiu, p. 43, pl. 3, fig. 8a–b; text-fig. 1.48.
1992 *Hexaphyllia flexus* Lin, Huang, Wu, Peng and Qiu, p. 44, pl. 3, fig. 7a–b; text-fig. 1.49.
1992 *Hexaphyllia crassotheca* Lin, Huang, Wu, Peng and Qiu, p. 44, pl. 3, figs 11–12; text-fig. 1.50.
1992 *Hexaphyllia fractiflexus* Lin, Huang, Wu, Peng and Qiu, p. 45, pl. 4, fig. 1a–b; text-fig. 1.51.
1992 *Hexaphyllia aboloformis* Lin, Huang, Wu, Peng and Qiu, p. 46, pl. 4, figs 2a–b; text-fig. 1.55.
1994 *Hexaphyllia lata* Lin and Yuan, p. 935, figs 2·5–2·6.

EXPLANATION OF PLATE 3

Figs 1–15. Heterocorals from the Lower Carboniferous, Castleton Reef Belt in North Derbyshire. All specimens are of Upper B$_2$ (Asbian) age.

Fig. 1. *Heterophyllia angulata* Duncan, 1867; USDES HCS 270; slopes of Middle Hill above Giants Hole; transverse thin section; ×10.

Figs 2–15. *Hexaphyllia marginata* (Fleming, 1828). 2–4, 6–8, 10–13 and 15, from the fore-reef at Winnats Pass (locality A). 2, MM LL10909k; juvenile corallite attached to adult, transverse peel-section; ×9. 3, MM LL10907a; six-septal form with spines, transverse peel section; ×6. 4, MM LL10907b; juvenile corallite attached to adult, transverse thin section; ×11. 6, MM LL10914a; corallite with four septa, transverse thin section; ×62. 7, MM LL10914a; five-septal form with spine, transverse thin section; ×37. 8, MM LL10909k; corallite with widely spaced tabulae, transverse peel section; ×23. 10, MM LL10917; corallite with four septa, transverse thin section; ×27. 11, MM LL10918a; five-septal form, transverse peel section; ×10. 12, MM LL10916; spiny corallite with six septa, transverse thin section; ×6. 13, MM LL10917; spiny six-septal form, transverse thin section; ×7. 15, MM LL10915a; transverse thin section; ×13. 5, 9, 14, from the algal reef at Treak Cliff (locality B). 5, MM LL10902b; corallite with closely spaced tabulae, longitudinal peel section; ×26. 9, MM LL10901a; corallites with three and five septa, transverse thin section; ×27. 14, MM LL10900b; transverse peel section; ×9.

PLATE 3

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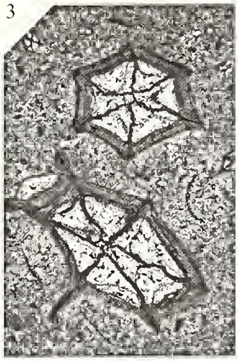

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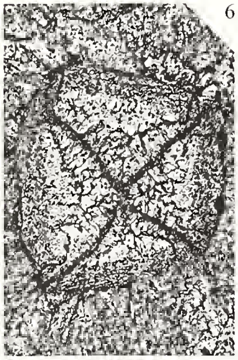

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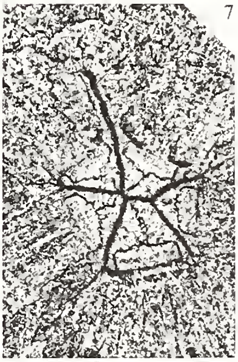

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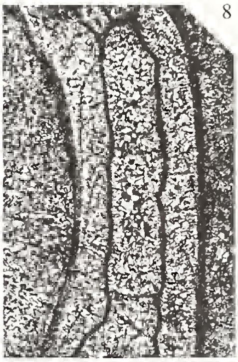

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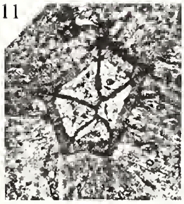

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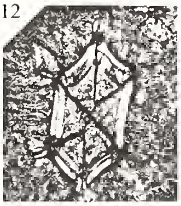

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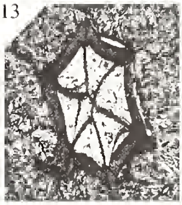

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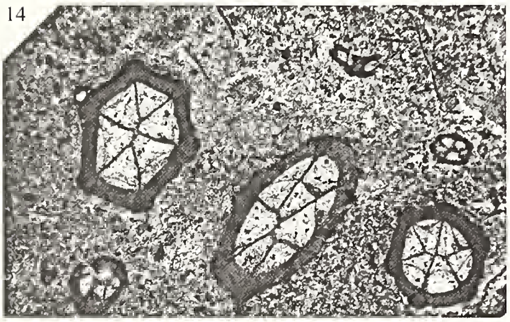

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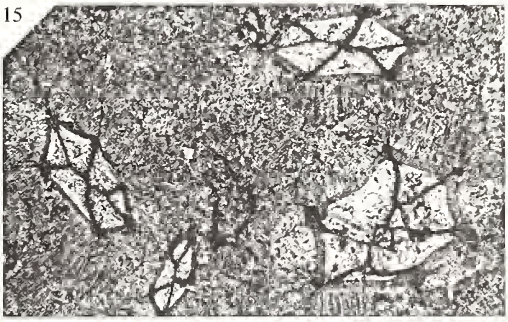
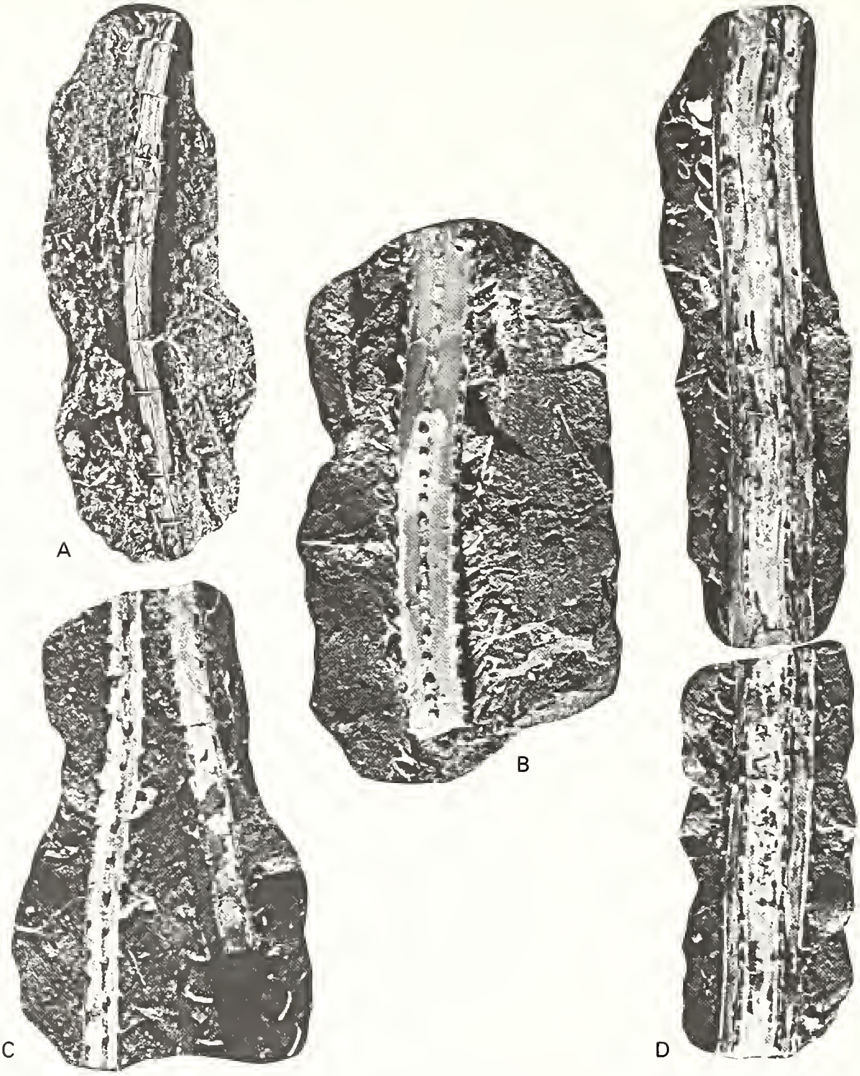


COSSEY, *Heterophyllia*, *Hexaphyllia*



TEXT-FIG. 11. *Hexaphyllia marginata* (Fleming, 1828) from the Lower Carboniferous of Scotland. A, NMS G 1979.1.30; Petershill Formation, D_2 (Brigantian), near Bathgate, West Lothian; note that the wall is composed of overlapping plates (tabulae) resembling roof tiles; × 2·4. B–D, Lower Limestone Group, (Brigantian), Craigenglen, Campsie, near Glasgow. B, GLAMG 01-53cu (1·1); × 5. C, GLAMG 01-53cu (1·2); × 5. D, proposed neotype, GLAMG 01-53cu (2); × 5.

Type material. The type material of *Lithostrotion marginatum* Fleming 1828, and *Heterophyllia Lyelli*, *H. M'Coyi*, *H. mirabilis* of Duncan (1867) is untraceable (Hill 1938–41; Kato 1971; Khoa 1977). The type of *Serpula hexicarinata* (M'Coy, 1844) is inadequate for the revised concept of the species described in this account. A suggested neotype for *Hexaphyllia marginata* is GLAMG O1-53 cu (2) from the John Young Collection (Text-fig. 11D).

Additional material. Approximately 1300 corallites collected by the author from Lower Carboniferous (Asbian) reef limestones at Winnats Pass and Treak Cliff in the Castleton Reef Belt, North Derbyshire, England (Text-fig. 2), deposited at The Manchester Museum (MM); 70 corallites from the John Young Collection, Kelvingrove Museum, now part of Glasgow Art Gallery and Museum (GLAMG); 15 corallites from the Hunterian Museum, Glasgow and ten corallites from the Horsfield Collection, Department of Earth Sciences, University of Sheffield (USDES); the type specimen of *Serpula hexicarinata* M'Coy, 1844, from the National Museum of Ireland, Dublin; the Jameson Collection in the Royal Museum of Scotland, Edinburgh (RSM); and other heterocoral collections from the Palaeontology Department, The Natural History Museum, London, and the British Geological Survey at Keyworth (Nottingham) and Edinburgh.

Emended diagnosis. As for the genus.

Description. The earliest stage in ontogeny is marked by an encrustation. The proximal end of each corallite forms an expanded 'talon-like' structure attached to an adult corallite of the same species. Septal insertion is initially rapid and difficult to define in the talon, and subsequently very slow. Typically, individuals have from three to six septa, the number of septa increasing with corallite size (Text-fig. 8). Although corallites with three to four septa are rare (Pl. 3, figs 6, 9–10), individuals with five to six septa (Pl. 3, figs 7, 9, 11–13) are very common. Corallite diameter ranges continuously from 0·1–2·6 mm. Corallites usually occur as fragments up to 89 mm long. Fragments are seldom perfectly straight and are often slightly sinuous (Pl. 1, fig. 1). Kinked corallites which show a dramatic changes in growth direction also occur (Pl. 1, fig. 3). The length of the unfragmented corallites is likely to have been considerable. Curved spines or tubercles (the abraded remnants of spines) may develop on the costae and are usually well spaced (Pl. 1, figs 1–2, 4; Text-fig. 10). Occasionally, two or three spines may issue from a common spine base (Pl. 2, fig. 7). Spines were recorded on corallites of all sizes from 0·25–2·59 mm including forms with four to six septa. Tabulae are domed and well-spaced along the corallite axis, but turn downwards peripherally and fuse together between the distal edges of the septa to form the thick wall structure. Tabulae spacing values range continuously from 0·2–3 mm (Text-fig. 4). Observation of transverse sections through the wall structure indicates that up to 12 tabulae may have fused together to form the tabulotheca (Text-fig. 3B–D; Pl. 2, figs 1–2, 4). Between the distal edges of the septa the shape of the wall is highly variable. Corallites may be stellate, prismatic or cylindrical in appearance according to whether the walls are respectively, either concave, flat or convex (Text-figs 6–7).

Remarks. The suggestion that *Heterophyllia lyelli* Duncan, 1867 and *H. m'coyi* Duncan, 1867 are species of *Hexaphyllia* was originally suggested by Stuckenberg (1904). Subsequently, another of Duncan's species, *H. mirabilis*, was transferred to the genus by Robinson (1917). Later, Hill (1938–41) identified *H. lyelli* (Duncan) as the junior subjective synonym of *Lithostrotion marginatum* Fleming.

Large numbers of *Hexaphyllia* species have since been described, particularly from China (Jia and Xu 1975; Jia *et al.* 1977; Yu *et al.* 1978; Wang 1980; Xu 1981; Wang and Ye 1984; Lin and Wu 1985; Huang and Ma 1986; Lin *et al.* 1992; Liu and Su 1992; Lin and Yuan 1994), where the recognition of different taxa is based on subtle differences in morphology and where intraspecific variation appears not to have been considered. Criteria used in the definition of *Hexaphyllia* species include: the presence or absence of spines or tubercles; wall thickness and shape; corallite diameter; the shape of the costae; the density of tabulae along the corallite axis.

Intraspecific variation in Heterocorallia was first noted by Young (1868, 1869) who demonstrated convincingly the synonymy of *H. lyelli* and *H. mirabilis* of Duncan (1867). Duncan's original descriptions suggested that *H. mirabilis* had a corallite diameter of 1 mm, the tabulae were widely spaced, the walls slightly convex, occasionally concave and the costae narrow but commonly adorned with spines or tubercles, and that *H. lyelli* had a corallite diameter of 2·5 mm, the spacing between the tabulae was 'average', the walls slightly concave and the costae large but with only occasional tubercles, pits and grooves. Young (1868) examined heterocorals from the same locality as Duncan and found corallites ranging in diameter from 0·6–2·5 mm, with one corallite tapering from 1·3–2·5 mm along its length. He also demonstrated that corallites of all diameters from 0·6–2·0 mm possessed spines and that the tubercles were merely eroded spine remnants. In addition, wall shape and tabulae spacing were seen to be highly variable.

In recent years, intraspecific variation in *Hexaphyllia* populations has become more widely recognized. Fontaine *et al.* (1991) described significant variations in wall shape, and considerable differences in corallite diameter have been recorded by other workers (Poty 1978*a*, 1981; Herbig

1986; Rodriguez and Comas-Rengifo 1989). Additionally, Sugiyama (1984) noticed significant variations in tabulae spacing and corallite diameter.

In this account, a wide and continuous range in corallite morphology has been demonstrated in both *Hexaphyllia* populations described from the Castleton Reef Belt. Corallite diameters range from 0·1–2·6 mm and, if corallites from the J. Young Collection are considered, this range is extended up to 3·9 mm. Spines occur on corallites of all sizes from 0·25–2·6 mm and the spacing between tabulae ranges from 0·2–3·0 mm. The presence or absence of spines or tubercles, or differences in size or shape of the costae, is attributed to the effects of pre-burial erosion. Corallite shapes vary and may be either cylindrical, prismatic or stellate according to whether the walls are predominantly either convex, flat or concave. As a result, corallites from both assemblages in the reef belt are regarded as variants of a single species and, since many previously described *Hexaphyllia* species fall within the limits of variation described in the Castleton material, the synonymy list in this account is extensive, including as many as 51 pre-existing taxa. Most of the criteria used to distinguish *Hexaphyllia* species in the past are therefore thought to be invalid.

This work supports the original conclusions of Young (1868, 1869) and echoes the sentiments expressed by Fontaine *et al.* (1991, p. 66) who stated that in all probability far 'too many species of *Hexaphyllia* have been recognized'.

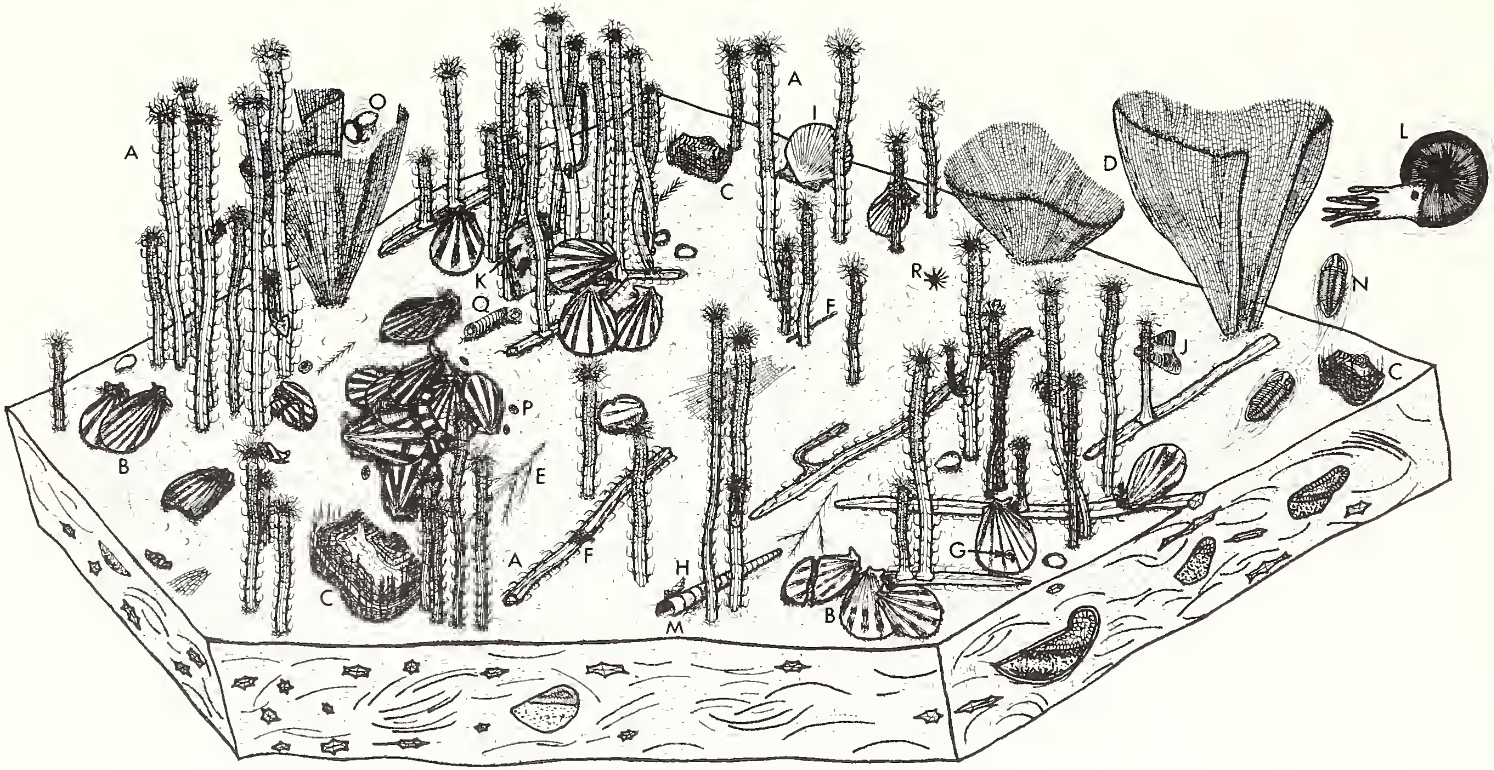
MODE OF LIFE AND FUNCTIONAL MORPHOLOGY

Reference to the literature indicates that heterocoral mode of life is incompletely comprehended. The debate so far has centred upon the extent to which the heterocorals may have been either pseudoplanktic or benthic at different stages in their life, and how they may or may not have been attached to different substrates in either of these two situations. In order that the group may be better understood, details regarding their geographical distribution, functional morphology and facies associations have to be considered.

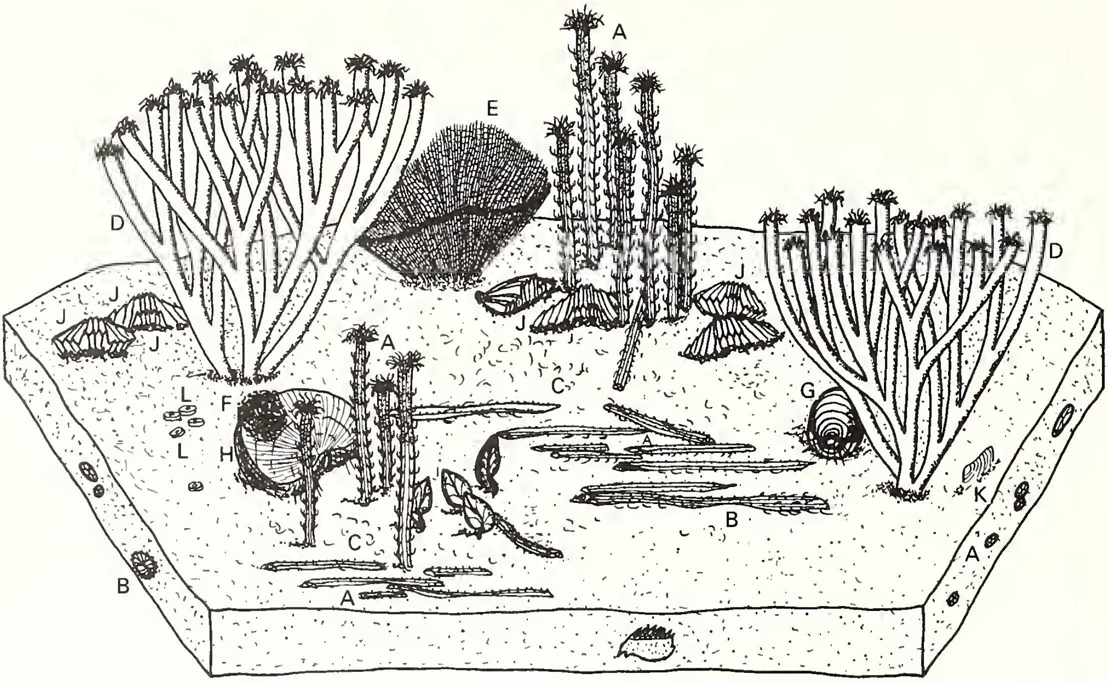
The earliest reference to heterocoral mode of life was made by Schindewolf (1941) who suggested that, on the basis of their scattered distribution, corallite length and the presence of spines in some species, the Carboniferous genera *Heterophyllia* and *Hexaphyllia* led a pseudoplanktic existence attached to seaweeds. Later, Różkowska (1969) reasoned that heavily built taxa possessing 'talons' (e.g. *Oligophylloides*) were likely to be part of the sessile benthos. The idea that *all* heterocorals were benthic during their adult life was originally proposed by Cossey (1983). In developing this view, Sugiyama (1984, 1989) argued for the existence of two separate benthic groups (one 'attached' and the other 'sessile'), the two being distinguished from one another on the basis of whether or not the septa projected through the corallite wall and carried spines. Forms with septa penetrating the wall (e.g. *Heterophyllia*, *Hexaphyllia* and *Pentaphyllia*) were assumed to have been 'attached' by the cementing tips of spines to hard objects, such as rocks, shells, other heterocorals or dendroid rugose corals. Other genera that lacked wall-penetrating septa and spines (e.g. *Radiciphyllia* and *Oligophylloides*) were presumed to have been cemented directly to the sea floor by talon-like attachments. More recently, Lin, Wu and Qiu (1992) suggested that some heterocorals might even have been nektic in habit although supporting evidence for this assertion is unclear.

Functionally, the heterocorals appear to have been much better suited to a benthic rather than a planktic mode of life. In shallow surface waters their lengthy, delicate and sometimes highly ornamented corallites would have been prone to fragmentation. They were, however, well adapted to life in relatively quiet, low energy environments, where the degree of turbulence and sedimentation rates were, for much of the time, very low.

A common characteristic of the group is that corallites are often sinuous (Pl. 1, fig. 1). In an earlier work the author argued that sinuosity developed as corallites re-oriented themselves by settling unevenly in soft sediment (Cossey 1983). More rarely, corallites occur in which sharp changes in the growth direction are apparent (Pl. 1, fig. 3). These geniculated or kinked corallites were probably produced as corallites re-oriented themselves after having been toppled or fragmented on the sea floor. A benthic mode of life may also account for the subtle differences in



TEXT-FIG. 12. Reconstruction of the *Hexaphyllia* community from the fore-reef (locality A). A, *Hexaphyllia marginata*; B, *Streblochondria elliptica*; C, buxtoniids; D, *Fenestella*; E, *Penniretepora*; F, assorted bryozoa including encrusting forms; G, spirorbid; H, gastropod; I, *Aviculopecten*; J, *Leiopteria*; K, *Pinna*; L, *Bollandoceras*; M, orthoconic nautiloid; N, *Cummingella*; O, *Entomoconchus*; P, *Cyclus radialis*; Q, pelmatozoan fragments; R, *Claviradix*.



TEXT-FIG. 13. Reconstruction of the *Hexaphyllia* community from the algal reef (locality B). A, *Hexaphyllia marginata*; B, *Heterophyllia ornata*; C, heterocoral spines; D, *Siphonodendron*; E, *Fenestella*; F, *Fistulipora*; G, *Acanthoplecta mesoloba*; H, *Linoprotonia*; I, *Dielasma*; J, rhynchonellids; K, *Parallelodon*; L, pelmatozoan ossicles. Note that both of the reconstructions illustrated (Text-figs 12–13) are based on the assumption that the fauna recorded from each locality was transported only a short distance from its place of origin.

morphology between the two heterocoral populations described in this account, in which corallites from the algal reef are more cylindrical, have thicker walls, fewer spines and more abundant tabulae than those of the fore-reef. These differences reflect the adaptational responses of the two coeval populations living at different positions within the reef where the degree of water circulation, turbulence and sedimentation rates may have varied considerably. The stouter, cylindrical corallites of the algal reef were stronger and better able to withstand the more turbulent conditions close to the reef crest than those thinner-walled, prismatic and stellate corallites living farther down the reef slope where conditions were much quieter (Text-figs 12–13).

A benthic mode of life is further confirmed by the occurrence of branching forms and weakly colonial coralla. Examples include *Anomalophyllia* from the Namurian Ardengost Limestone, in the Hautes-Pyrénées (Tourneur *et al.* in press), *Stellaphyllia* from the Eifelian Santa Lucia Formation, in northern Spain (Tourneur and Herrmann in press) and most notably in *Oligophylloides* from the Famennian of the Anti-Atlas, Morocco (Weyer 1995*b*). The development of a dense heavy colony is clearly typical of a benthic organism rather than a planktic one.

Attachment structures

Spines. In this account it has been suggested that the primary function of heterocoral spines was to afford protection to the exposed polyp at the growing end of the corallite. The suggestion that the spines could have been used for clinging on to floating seaweed (Schindewolf 1941) cannot be supported as they are non-articulating (see Young 1868, 1869), open arc-shaped structures of regular geometry. This situation appears in striking contrast to the epiplanktic *Cyathaxonia tantilla* where attachment to algae in the plankton is facilitated by development of planispirally coiled protocoralla during early growth (Sando 1977). The spines of heterocorals were therefore quite clearly inappropriate for clinging on to any floating object. Furthermore, there is no direct evidence to support the view of Sugiyama (1984, 1989) that the heterocorals were attached to various objects on the sea floor by the 'cementing tips' of their spines. If the spines were used for attachment in this way, modified spine shapes and attachment scars would be expected, but so far features of this kind have not been described.

Talons. To date, the only positive evidence of heterocoral attachment structures comes in the form of basal and lateral talons. Basal talons formed early in the ontogeny of juvenile corallites following the settlement of larvae on a variety of hard substrates. Although originally described by Rózkowska (1969) in *Oligophylloides* from the Upper Devonian of Poland, these structures have since been documented in both *Mariaephyllia* and *Oligophylloides* attached to an assortment of 'dead' shelly material (including the remains of ammonoids, orthoconic nautiloids, bivalves and pelmatozoan stems) from strata of a similar age in Germany (Weyer 1995*a*, 1995*b*). Further examples, in *Hexaphyllia*, have been illustrated herein.

So far it has been assumed that basal talons were formed initially on hard, non-living substrates and primarily on shell debris that had been deposited on the sea floor. Whilst this certainly appears to be true in the majority of circumstances, it has to be questioned whether such initial attachments could have been made to substrates that were either: hard or soft, alive or dead, floating as part of the plankton, or swimming as part of the nekton. If, with further work, this latter circumstance proves to be the case, then it could help to explain not only the widespread distribution of the group, but also their occurrence in such a wide variety of different sedimentary facies. Rich heterocoral assemblages in pockets within reefs could then be regarded as originating from epiplanktic juveniles attached to drifted material washed into reef cavities, either as a single event in the case of an aggregate of drifted material, or over a period of time in the case of isolated associations. A somewhat similar explanation for the occurrence of rich goniatite assemblages in the Castleton Reef Belt was given by Ford (1965). If, however, as Weyer (1995*a*, 1995*b*) suggested, heterocorals occur only rarely in aphotic environments, this would preclude their membership as part of the plankton (whether attached or not) during adult life. It is therefore clear that heterocorals inhabited areas of deep water on the ocean floor as well as protected areas within shallow water reef systems and that their occurrence in reefs may be linked to the distribution of sheltered reef cavities.

Regardless of where their basal talons were formed, it is clear from the earlier discussion that the heterocorals were benthic during their adult life and that corallites grew upwards, away from the sediment-water interface at a high angle. Confirmation of this is provided in the form of rhodophyte encrustations. For example, Termier *et al*. (1975, fig. 17) illustrated *Aoujgalia variabilis* encrusting a *Hexaphyllia* corallite on all six sides, and Brady (1876, text-fig. 9) illustrated an encrustation of *Stacheia* which appears to encircle completely a corallite resembling *Heterophyllia*. Such circum-corallite encrustations are unlikely to have occurred unless the corallites were protruding from the sediment at a considerable angle.

Besides 'basal talons', the only other convincing attachment structures to be described in heterocorals are those referred to as 'lateral talons', described by Weyer (1995*b*, but see also 1995*a*) in *Oligophylloides tenuicinctus* and *Mariaephyllia* aff. *famenniana* from the Upper Devonian of Germany. These structures developed in corallites which grew beyond the juvenile stage and consist of bulbous projections from the corallite wall which terminate distally with distinctive flat surfaces. Weyer noted the association of these heterocorals with dysphotic cephalopod-rich limestones and suggested that lateral talons represented outgrowths of the corallite wall that were attached to the flat surfaces of benthic rhodophyte thalli growing in deep-water meadows. Although such structures have not so far been recorded in *Hexaphyllia*, Weyer's view confirms the idea that heterocorals were benthic forms that grew upright on the sea floor. Corallites would then have been supported by the slow accumulation of sediment around their base, by subsiding gradually into the sediment (which may explain the sinuous shape of many corallites), or by thickets of algae to which they may have been attached by lateral talons. In connection with the last of these, it is interesting to note that in a reconstruction of Viséan upper reef slope communities from Yorkshire, Mundy (*in* Ramsbottom 1978) illustrated *Hexaphyllia* supported on the sea floor by conjectured vegetation, despite orientating the corallites incorrectly.

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LATE ORDOVICIAN BRACHIOPODS FROM TAIMYR, ARCTIC RUSSIA, AND THEIR PALAEOGEOGRAPHICAL SIGNIFICANCE

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Abstract. Diverse brachiopod faunas are recorded and partly described from the Korotkinskaya Formation of the central Taimyr Peninsula, northern Siberia, Russia. The lowest fauna (Beds 2 and 3) includes eight species of indeterminate late Ordovician age, the main fauna (Bed 4) consists of 39 species of mid Ashgill age, and the highest fauna (Beds 8 and 9), four species of late mid Ashgill age. The new species *Amphiplecia bondarevi*, *Cyclospira orbus*, *Eospirigerina vetusta* and *Plectatrypa laticostata* are described. Close links are drawn with the brachiopod fauna of the Boda Limestone (middle Ashgill) of Dalarna, Sweden, including the identification from Taimyr of forms hitherto considered typical of Dalarna. There are no comparable faunas from rocks of the same age on the now adjacent Siberian Platform. These data strengthen the case for the Taimyr Peninsula forming part of the palaeocontinent of Baltica during the late Ordovician.

The Taimyr Peninsula, in northern Siberia, has been identified for some years as containing late Ordovician and early Silurian rocks and fossils (e.g. Bondarev *et al.* 1968). However, the brachiopod faunas which occur at various places and horizons are not well known. In particular, although a few parts of a key collection made from rocks of Ashgill age by V. I. Bondarev in 1959 have been described previously (Nikiforova 1982, 1985, 1989; Nikiforova *et al.* 1982), the assemblage as a whole has not, and we feel that it is important enough to be reviewed as a complete fauna in this paper, and its biogeographical position evaluated against other contemporary late Ordovician faunas.

LOCALITY AND AGE

The material comes from the Lower Taimyr River Basin (Text-fig. 1) in central Taimyr, from a continuous section along the left bank of the Pryamaya River, about 10 km south of its mouth (localities 542 and 569) at longitude 99° 54′ E and latitude 75° 15′ N, and from Locality 1141 on the right bank of the same river 3 km away, at the same stratigraphical level and on the opposing flank of an anticline. The brachiopods occur chiefly at three levels within the Korotkinskaya Formation (Text-fig. 2): the lower one from the 38 m thick Bed 3, the middle one from the 22 m thick Bed 4, and forming the bulk of the material mentioned in this paper, and the higher one in the 30 m thick Bed 9.

The age of the whole Korotkinskaya Formation is probably Ashgill, although this dating is more secure in its upper half. Bed 9, containing the pentamerids *Tcherskidium* and *Holorhynchus*, is clearly of mid Ashgill age. The only graptolites recovered from the locality were *Climacograptus sensu stricto* sp., determined by Dr R. F. Sobolevskaya, who also considers that Bed 4a, in which they occur, therefore represents the *supernus* Biozone and certainly antedates the highest Ordovician *persculptus* Biozone. The brachiopods described here and bryozoans determined by Nekhorosheva (1968) from Bed 4 are also of mid Ashgill age. The age of the beds below Bed 4 is less well constrained; the *Anoptambonites* illustrated here from Bed 3 could be of latest Caradoc or early Ashgill age.

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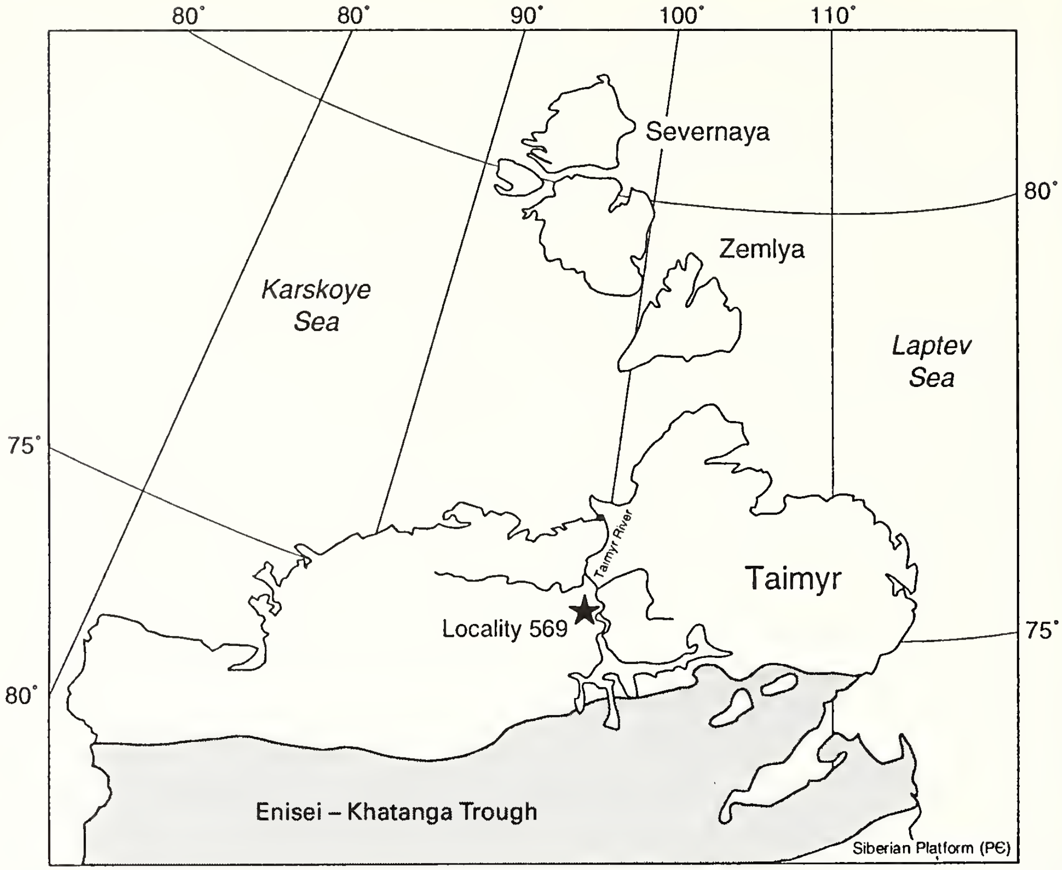


TEXT-FIG. 1. The Taimyr Peninsula, northern Siberia, showing locality 569 from which the fossils described in this paper were collected.

FAUNAL AFFINITIES OF TAIMYR IN THE LATE ORDOVICIAN

The preservation of the brachiopods in the limestones makes identification of this relatively small collection often difficult since some of the taxa are represented by only one or two valves. Nikiforova (1989) identified and illustrated the pentamerides *Holorhynchus* ex gr. *giganteus*, *Tcherskidium unicum* and *Tcherskidium*? sp. nov. from Bed 9 and *Parastrophina lindstroemi pentagonalis* from Bed 4. The fauna from Bed 4 (including localities 4, 4a, 562 and 1141) has been the subject of some disparate papers: Nikiforova (1982) recorded and illustrated the inarticulates *Ectenoglossa?* sp., her new species *Multispinula bondarevi* and in addition elkaniid gen. et sp. indet. from Bed 6b and *Paracraniops*? sp. from Bed 3b. The orthides formed the subject of a further paper by Nikiforova (1985), in which *Hesperorthis* sp., the new species *Ptychopleurella alata*, *Plectorthis* ex gr. *ponderosa*, *Skenidioides* sp., *Dalmanella* sp., the new subspecies *Howellites wesenbergensis aenignus*, and *Dicoelosia* sp. were all described from Bed 4. In addition, the new atrypid genus and species *Euroatrypa tajmyrica* were recognized from Bed 4 by Nikiforova *et al.* (1982). We have briefly reviewed, and in part amended, these attributions in the section on systematic palaeontology below. We also deal with the remainder and majority of the collection from these localities, principally including triplesioids, strophomenides and further atrypoids. The following fauna is now known, from the various horizons (Text-fig. 2):

Bed 9. *Tcherskidium unicum*, *Holorhynchus giganteus*, indet. strophomenoid.

Bed 8. *Eoplectodonta* sp.

Bed 6. elkaniid gen. et sp. indet., *Eospirigerina vetusta.*

Bed 4 (including Bed 4a and Localities 562 and 1141). *Ectenoglossa*? sp., *Multispinula bondarevi, Paracraniops* sp., acrotretid gen. et sp. indet., *Hesperorthis*? sp., *Plectorthis* sp., *Ptychopleurella alata, Skenidioides* sp., gen. nov. aff. *Cyrtonotella, Dalmanella* sp., *Howellites aenigmus, Laticrura*? sp., *Dicoelosia* sp., *Epitomyonia* sp., *Ogmoplecia* aff. *plicata, Amphiplecia bondarevi, Triplesia* sp., *Leangella* sp., *Sowerbyella* (*Sowerbyella*)? sp., *Sowerbyella* (*Rugosowerbyella*) sp., *Eoplectodonta* aff. *rhombica, Eoplectodonta* sp., *Drummuckina*? sp., *Geniculina* sp., *Holtedahlina* sp., indet. strophomenoid, leptaenine spp., *Fardenia*? sp., *Parastrophina pentagonalis, Parastrophinella*? sp., *Tcherskidium* sp., *Holorhynchus* aff. *giganteus, Catazyga* sp., *Cyclospira orbus, Plectatrypa*? *laticostata, Qilianotryma tajmyrica, Eospirigerina vetusta,* indet. cyrtiinid.

Bed 3 (including Bed 3b). *Paracraniops* sp., *Plectorthis* sp., *Dalmanella* sp., *Sowerbyella* (*Rugosowerbyella*) sp., *Eoplectodonta* sp., *Anoptambonites* sp., *Geniculina* sp.

Bed 2 (including Bed 2a). *Sowerbyella* (*Rugosowerbyella*) sp., *Christiania* sp.

Although the fauna of Bed 9 (*Tcherskidium* and *Holorhynchus*) is of use in determining an accurate mid Ashgill (late Rawtheyan) age, these large pentamerides are now known to occur in many places in the late Ordovician tropical areas (apart from *Tcherskidium* in Laurentia). The chief interest of the Taimyr fauna lies in the 39 different species identified from Bed 4, a most diverse fauna, and also distinctive in the rather surprising complete absence of rhynchonellides. The assemblage is dominated by atrypides, with more than 60 specimens of *Qilianotryma tajmyrica*, 37 of *Plectatrypa? laticostata* and 43 of *Eospirigerina vetusta*, totalling 140 of the 304 brachiopod specimens known from that level. The assemblage most similar to that from Taimyr is that from the Boda Limestone of Dalarna, Sweden. Unfortunately, that fauna has never been completely assessed and described; in addition, there are certainly different assemblages present in the varied and complex Boda carbonate mounds and flank deposits. Nevertheless we have been able to examine the large collection from the Boda Limestone in the Riksmuseum, Stockholm, and a smaller one in The Natural History Museum, London. The presence in Taimyr of the triplesiid *Amphiplecia*, hitherto known only from Sweden and Norway (Wright and Jaanusson 1993), and *Ptychopleurella alata* and *Fardenia*? sp., which seem identical to those known only otherwise from Dalarna, indicates close faunal connections between the two areas. Other forms from Taimyr, such as *Eoplectodonta rhombica, Ogmoplecia* aff. *plicata, Geniculina* and *Parastrophina*, also reinforce the Baltic affinities of the fauna, although many other genera, such as *Dicoelosia, Howellites, Cyclospira, Qilianotrema* and *Eospirigerina*, are of much more cosmopolitan distribution in the upper Ordovician. Thus the Taimyr fauna is identified here as of undoubted Baltic affinity.

These faunas from Taimyr and elsewhere in Baltica are in marked contrast with the Ashgill faunas known from the main Siberian palaeocontinent (Andreeva and Nikiforova 1955; Nikiforova and Andreeva 1961; Rozman 1977; Yadrenkina 1984), and most of the rest of Asia, for example north-east Asia (Rozman *et al.* 1970), Gornoi Altai and Salair (Severgina 1978), Kazakhstan (Nikitin *et al.* 1996) and Mongolia (Rozman 1981), which have abundant rhynchonellides, and different plectambonitoid and strophomenoid genera.

PALAEOGEOGRAPHY OF TAIMYR

The Ordovician facies in the Taimyr belt are themselves divided into two distinct groups: to the north-west deeper-water deposits with graptolite shales, and to the south-east shelf deposits with predominantly dolomites, limestones and marls. The limestones in which the Bed 4 faunas are found, as well as the pentamerides including *Holorhynchus* and *Tcherskidium* of Bed 9, suggest a warm shelf environment for the south-eastern belt. However, rocks of latest Ashgill (Hirnantian) age are not yet known from Taimyr. Elsewhere, such Hirnantian rocks have yielded variable *Hirnantia* assemblages which are often indicative of cooler water. To the north of the Ordovician deposits considered here in Taimyr is the substantial Kara Massif, of Precambrian age, with a core of Archaean metamorphic rocks, more than 2000 Ma, overlain by a Riphean complex of about 1000 Ma. Relatively unmetamorphosed Vendian and Early Palaeozoic deposits overlie this complex both to the north in Severnaya Zemlya and to the south in Taimyr. To the south of the Lower Palaeozoic belt in Taimyr there is the east–west trending Enisei-Khatanga Trough (Text-fig. 1) of Mesozoic and Tertiary age which itself abuts southwards on to the Precambrian rocks of the main Siberian plate.

There is general agreement that the Siberian plate, which stretched from the Ural Mountains in the west to the Verkhoyansk Mountains in the east and from the Arctic Ocean in the north to the Kazakhstan and North China plates in the south, was a single entity during the late Ordovician (Zonenshain *et al.* 1990) and that it was inverted north to south by comparison with the present day. However, the maps of Zonenshain *et al.* and some other authors show that the Taimyr Peninsula was not part of the same continental plate as the bulk of Siberia in the Early Palaeozoic. Thus the Kara Massif, with the adjacent Early Palaeozoic deposits described here, was apparently a separate entity from Siberia during the Ordovician, with the suture between it and the Siberian plate presumably now hidden beneath the Mesozoic and Tertiary Enisei-Khatanga Trough. Zonenshain *et al.* (1990, e.g. p. 215) show the Taimyr Peninsula, Severnaya Zemlya and adjacent rocks as a separate palaeocontinent termed Arctida, but we believe from the faunal results presented here that these areas most probably formed part of the Baltica palaeocontinent, or were at most small terranes adjacent to and in direct faunal contact with it, and were faunally distinct, and presumably separate, from Siberia. It is also uncertain whether or not the three tectonically distinct blocks of the Taimyr area today were comparably close in the Ordovician, and only two of the three have Ordovician fossils recorded from them.

Since Ordovician rocks from Taimyr older than those considered here contain substantial evaporite deposits, and the faunas described in this paper are diverse and in limestones, it seems probable that the Taimyr part of the Baltic palaeocontinent was at an equatorial palaeolatitude in the Ordovician. Comparably, Bachtadse *et al.* (1995) have placed the northern margin of Baltica near the palaeoequator in the late Ordovician. Palaeomagnetic work on the Siberian Platform (Torsvik *et al.* 1995, fig. 10) has also placed the plate squarely across the palaeoequator in the late Ordovician but with the orientation inverted by comparison with the present. Thus, both the Baltic and Siberian palaeocontinents were equatorial. However, although Taimyr and Siberia were probably joined before the end of the Palaeozoic, the different Ordovician faunas suggest that the two continents may not have occupied adjacent palaeolongitudes during the Ordovician.

SYSTEMATIC PALAEONTOLOGY

All the following taxa come from Locality 569 in Taimyr (including locality 542-1, which is the same as 569-4), but from various numbered beds (Text-fig. 2). The material previously described and figured by Nikiforova (1982, 1985, 1989) and Nikiforova *et al.* (1982) is all in CNIGR Museum, St Petersburg, Russia: the material from this paper is in The Natural History Museum, London (BC). Comparable material from Boda, Sweden, is deposited in the Riksmuseum, Stockholm (RMS).

Superfamily LINGULOIDEA Menke, 1828

Genus ECTENOGLOSSA Sinclair, 1945

Ectenoglossa? sp.

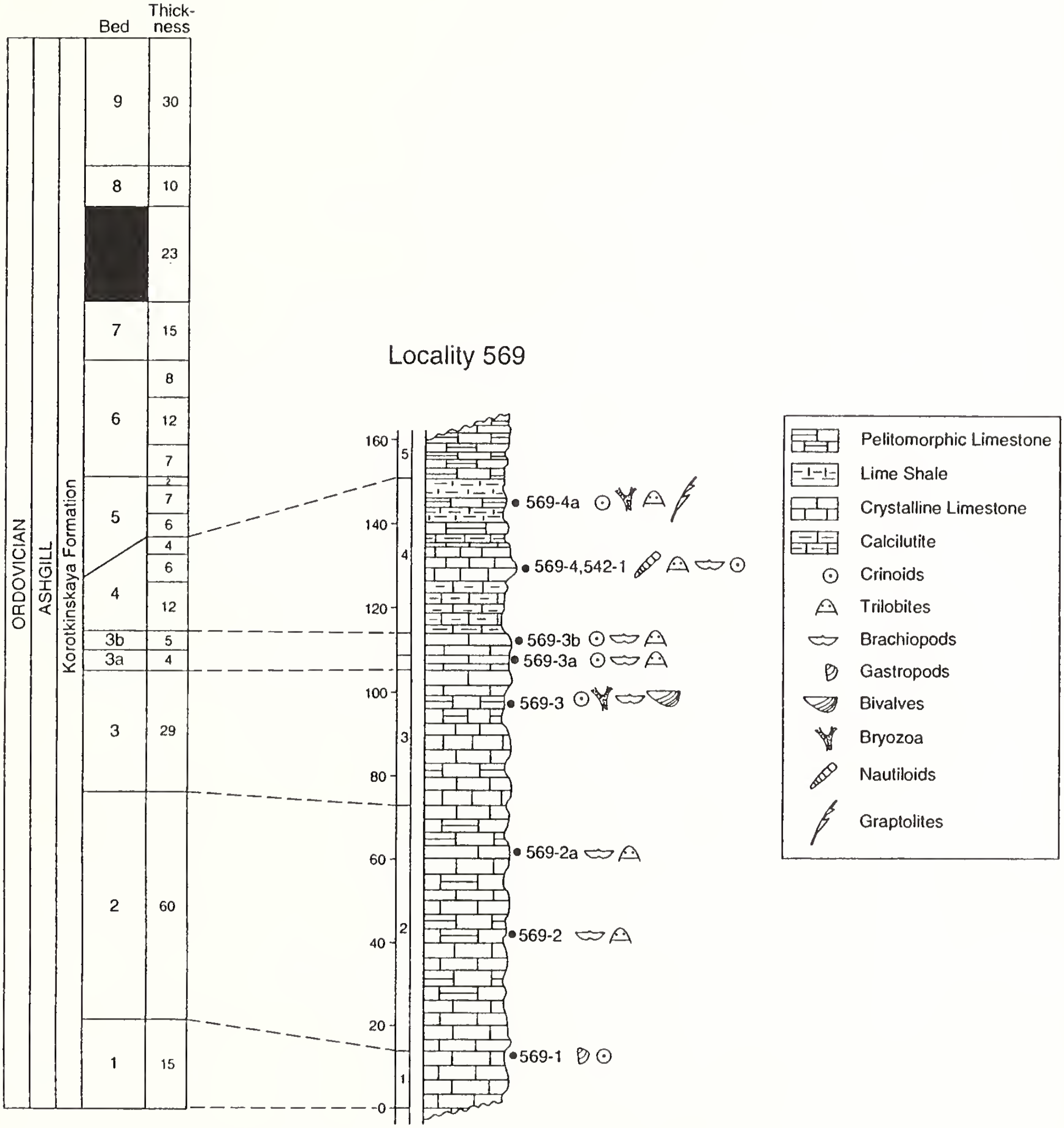
1982 *Ectenoglossa* (?) sp. Nikiforova, p. 254, pl. 1, figs 1–2.

Remarks. The two specimens described and figured by Nikiforova from Bed 4 are undoubtedly obolids but the generic attribution is uncertain. No further material has been found.

elkaniid gen. et sp. indet.

1982 Elkaniidae gen. et sp. indet. Nikiforova, p. 255, pl. 1, figs 3–5.

Remarks. Three valves were recovered from Bed 6b and Nikiforova compared one in detail with *Broeggeria*. No further material is known.



TEXT-FIG. 2. The extent and divisions of the Korotkinskaya Formation in Taimyr (left) and stratigraphical section of the rocks at Locality 569 (right), together showing the levels and beds from which the successive faunas were collected by V. I. Bondarev in 1959 and with their lithologies and faunal constituents. The black area between Beds 7 and 8 represents a gap in exposure.

Superfamily CRANIOPSOIDEA Williams, 1963

Genus PARACRANIOPS Williams, 1963

Paracraniops sp.

1982 *Paracraniops* (?) sp. Nikiforova, p. 256, pl. 1, figs 7–9.

Remarks. Nikiforova's figured specimens came from Bed 3. We have seen three further specimens (on BC 51015 and BC 51052) from Bed 4, and a further two specimens (on BC 51023) from Bed 4a. Our material compares closely with other late Ordovician *Paracraniops* material and there is no doubt as to the generic identity of the Taimyr material.

Superfamily ACROTRETOIDEA Schuchert, 1893

acrotretid gen. et sp. indet.

Remarks. Two characteristic conical valves, which may be certainly identified as acrotretids, were found in Bed 4 (on BC 51037 and BC 51052).

Superfamily SIPHONOTRETOIDEA Kutorga, 1848

Genus MULTISPINULA Rowell, 1962

Multispinula bondarevi Nikiforova, 1982

1982 *Multispinula bondarevi* Nikiforova, p. 257, pl. 1, fig. 6.

Remarks. Only the single type specimen is known, from Bed 4a.

Superfamily ORTHOIDEA Schuchert and Cooper, 1932

Genus HESPERORTHIS Schuchert and Cooper, 1931

Hesperorthis? sp.

1985 *Hesperorthis* sp. Nikiforova, p. 70, pl. 1, fig. 1.

EXPLANATION OF PLATE 1

Figs 1–3. *Plectorthis* sp.; BC 51095; dorsal, lateral and posterior views of a dorsal valve; Bed 4a; ×2.

Fig. 4. gen. nov. aff. *Cyrtonotella*; BC 51067; dorsal interior; Bed 4a; ×4.

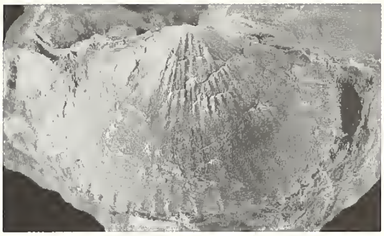
Fig. 5. *Laticrura*? sp.; BC 51066; dorsal interior, Bed 4a, ×3.

Fig. 6. *Howellites aenigmus* Nikiforova, 1985; BC 51375; incomplete dorsal interior; Bed 4; ×4.

Figs. 7–9. *Holorhynchus* aff. *giganteus* Kiær, 1902; BC 51075; dorsal, lateral and anterior views of conjoined valves; Bed 4; ×2.

Figs 10–18. *Ampliplecia bondarevi* sp. nov.; Bed 4; 10, 13, BC 51068; ventral and anterior views of a ventral valve. 11–12, 14, BC 51070; holotype, dorsal, ventral and anterior views of conjoined valves. 15–18, BC 51069; dorsal, ventral, anterior and lateral views of conjoined valves. All ×2.

Figs 19–21. *Fardenia*? sp. 19–20, BC 51081; ventral and posterior views of a ventral exterior; Bed 4. 21, BC 51377; an exfoliated ventral exterior; Bed 4a. All ×4.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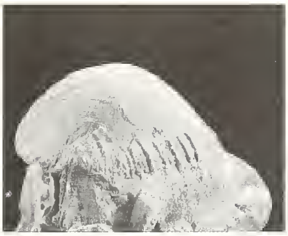
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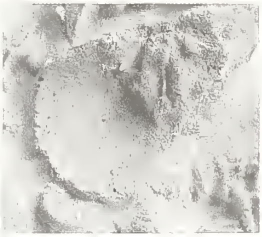
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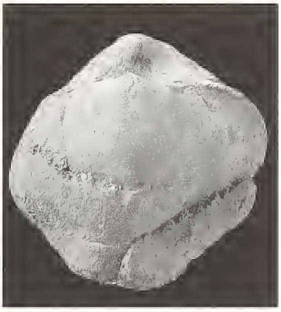
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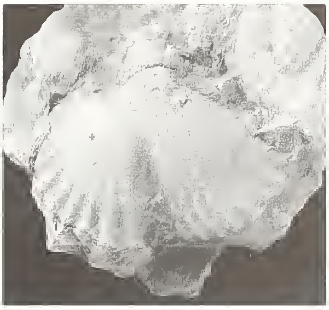
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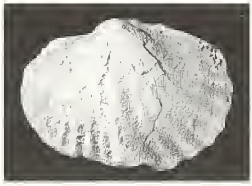
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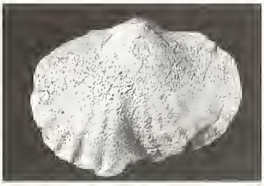
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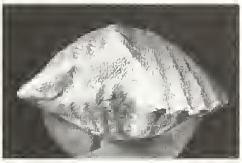
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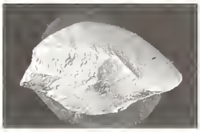
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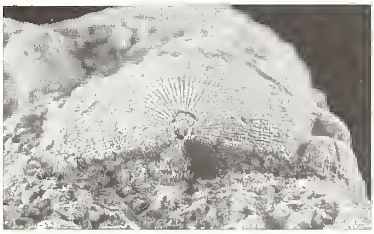
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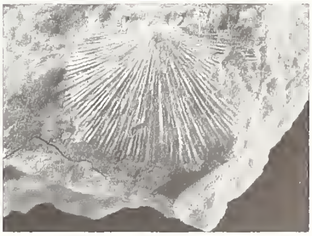
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COCKS and MODZALEVSKAYA, late Ordovician brachiopods

Remarks. Only one external of a ventral valve is known, from Bed 4, the specimen figured by Nikiforova, and the generic attribution is uncertain. Two further dorsal valves, BC 51066 and BC 51095 from Bed 4a, are also doubtfully attributed to the genus.

Genus PTYCHOPLEURELLA Schuchert and Cooper, 1931

Ptychopleurella alata Nikiforova, 1985

1985 *Ptychopleurella alata* Nikiforova, p. 71, pl. 1, figs 2–4.

Remarks. Four ventral valves and two dorsal valves are known, from Beds 4 and 4a. Nikiforova's figures show that *P. alata* is similar in many respects to the two named species of *Ptychopleurella* from the Boda Limestone of Sweden described by Wright (1982), but differs from *P. emarginata* in its shape and less robust cardinalia and from *P. twenhofeli*, originally described from the Cautleyan Portrane Limestone of Ireland, also in its shape and in its ribbing. However, Wright also distinguished a third species from Boda, based only on two pairs of conjoined valves, which he termed *Ptychopleurella* sp., and that form shows considerable similarity to Nikiforova's figures of *P. alata*, and is probably conspecific with it.

Genus PLECTORTHIS Hall and Clarke, 1892

Plectorthis sp.

Plate 1, figures 1–3

non 1956 *Plectorthis ponderosa* Cooper, p. 451, pl. 83, figs 22–32; pl. 84, figs 24–32.
1985 *Plectorthis* ex gr. *ponderosa* Cooper; Nikiforova, p. 72, pl. 1, figs 5–6.

Remarks. Nikiforova recorded one complete shell, three dorsal valves and one ventral valve from both Bed 3 and Bed 4 in Taimyr which she compared with Cooper's species. All Cooper's (1956) figured material of *ponderosa* came from the Martinsburg Formation of Virginia, which is of late Caradoc age. However, it is doubtful whether the Taimyr form is closely related to the North American species. The single very globose dorsal valve illustrated here, BC 51095 from Bed 4a, is probably also congeneric, although whether conspecific with the material illustrated by Nikiforova (1985) is difficult to say since the shell is badly exfoliated.

gen. nov. aff. *Cyrtonotella*

Plate 1, figure 4

Remarks. A single incomplete dorsal interior, BC 51067 from Bed 4a, is tentatively identified here as a new genus perhaps related to *Cyrtonotella*. The shell is certainly impunctate (punctate dalmanelloids and pseudopunctate strophomenoids are preserved on the same block), and it is flat posteriorly becoming slightly concave anteriorly. There is no means of telling whether or not ribbing is present and if so, of what type. The specimen is in some respects similar to *Cyrtonotella kukersiana* from the lower Caradoc of Estonia (Öpik 1934, pl. 47) in the form of its cardinal process, sockets and broad myophragm. However, it differs at least generically from *Cyrtonotella* in the presence of distinctive plates running anterolaterally from the anterior edge of the sockets.

Genus SKENIDIOIDES Schuchert and Cooper, 1931

Skenidioides sp.

1985 *Skenidioides* sp. Nikiforova, p. 73, pl. 1, fig. 7.

Remarks. A single broken ventral valve was recovered from Bed 4, which was described and figured by Nikiforova. A further ventral valve has been identified by us from the same bed on BC 51012.

Both show the characteristic pyramidal shape and form of *Skenidioides*, but without dorsal valves specific identification is impossible.

Superfamily DALMANELLOIDEA Schuchert, 1913

Genus DALMANELLA Hall and Clarke, 1892

Dalmanella sp.

1985 *Dalmanella* sp. Nikiforova, p. 74, pl. 1, figs 8–11.

Remarks. One pair of conjoined valves, five ventral valves and four dorsal valves were recorded by Nikiforova from Beds 3 and 4.

Genus HOWELLITES Bancroft, 1945

Howellites aenigmus Nikiforova, 1985

Plate 1, figure 6

1985 *Howellites wesenbergensis aenigmus* Nikiforova, p. 75, pl. 1, figs 12–15.

Remarks. Two articulated specimens and several others were described by Nikiforova from Bed 4. An additional dorsal valve interior, BC 51375, is figured here from Bed 4a and two further dalmanelloid ventral valve exteriors from Bed 4 (on BC 51039 and BC 51043) and four from Bed 4a (on BC 51016, BC 51022, BC 51045 and BC 51067) are identified tentatively as belonging to the same species. Although Nikiforova identified the form as a subspecies of *H. wesenbergensis*, the excellent revision of that species by Hints (1975, p. 33, pls 6–8) showed that the Taimyr form has a much thinner dorsal myophragm and a more elevated dorsal muscle platform, enabling *aenigmus* to be considered as specifically separate from *wesenbergensis*.

Genus LATICRURA Cooper, 1956

Laticrura? sp.

Plate 1, figure 5

Remarks. A single dorsal interior, BC 51066 from Bed 4a, is referred to *Laticrura* with some caution. The cardinal process is very elongate, projecting for some way posteriorly to the hinge line. The myophragm is very thin posteriorly before thickening to a prominent globosity and then becomes thin again anteriorly before merging with the valve floor at about 60 per cent. valve length. The differentiated setal sources may reflect sharper ribs externally, as shown, for example, in *Laticrura*.

Genus DICOELOSIA King, 1850

Dicoelosia sp.

1985 *Dicoelosia* sp. Nikiforova, p. 76, pl. 1, fig. 16.

Remarks. Three ventral valves with the distinctive bilobed outline of *Dicoelosia* were recovered by Nikiforova from Bed 4. No further material has been identified by us.

Genus EPITOMYONIA Wright, 1968

Epitomyonia sp.

Remarks. A single ventral valve, only showing the exterior, BC 51038 from Bed 4, has the distinctive slightly bilobed outline and curved profile of *Epitomyonia*.

Superfamily TRIPLESIOIDEA Schuchert, 1913

Genus OGMOPLECIA Wright and Jaanusson, 1993

Ogmoplecia aff. *plicata* (Wiman, 1907)

Plate 2, figures 1–7; Text-figure 3

aff. 1907 *Triplesia plicata* Wiman, p. 12, pl. 2, figs 13–17b.
aff. 1993 *Ogmoplecia plicata* (Wiman) Wright and Jaanusson, p. 96, figs 1A–K, 2A–N, 3.

Material. Twenty specimens, many poorly preserved, all from Bed 4 or 4a (including Locality 542-1). All are dorsal valves, except BC 51114 (Pl. 2, figs 5–7), in which both valves are conjoined.

Remarks. Wright and Jaanusson (1993) erected *Ogmoplecia* based on material from the Hulterstad Limestone of Sweden, with the type species, *O. plicata*, as the sole firmly attributed species, together with forms identified as cf. *plicata* from the Portrane Limestone (Ashgill: Cautleyan) and Kildare Limestone (Ashgill: Rawtheyan) of Ireland, the Dolhir Formation (Ashgill: Rawtheyan) of Glyn Ceiriog, North Wales, the Fosse Formation (Ashgill: Cautleyan–Rawtheyan) of Belgium, and the Ashgill Vormsi, Pirgu and Porkuni stages of Estonia. All these occur in Baltica or the neighbouring continent of Avalonia which was in faunal contact if not actually physically joined by the Ashgill (Cocks and Fortey 1990). In addition, Wright and Jaanusson provisionally attributed with a query two of the four species, *insolita* and *shallockiensis*, which were attributed to *Oxoplecia* by Harper (1989) from the upper Ordovician of the Girvan district, Scotland, which then lay on the opposite side of the closing Iapetus Ocean to Baltica and Avalonia.

The dorsal valves, which form a substantial part of the Taimyr Bed 4 and Bed 4a fauna, are very similar to the specimens of *O. plicata* illustrated by Wright and Jaanusson (1993) and the Taimyr material is identified here as *Ogmoplecia* aff. *plicata*. The Taimyr material is attributed to *Ogmoplecia* rather than its near homoeomorph *Oxoplecia* because it lacks a proximal pseudodeltidial fold and the section (Text-fig. 3) shows the absence of the keeled cardinal process, both considered key features by Wright and Jaanusson (1993).

Genus AMPHIPLECIA Wright and Jaanusson, 1993

Amphiplecia bondarevi sp. nov.

Plate 1, figures 10–18

Derivation of name. After V. I. Bondarev, who collected the material.

Holotype. BC 51070, Plate 1, figures 11–12, 14; conjoined valves, Locality 569, Bed 4.

EXPLANATION OF PLATE 2

Figs 1–7. *Ogmoplecia* aff. *plicata* (Wiman, 1907). 1, 4, BC 51115, dorsal and lateral views of a dorsal valve; Bed 542-1. 2, BC 51109; dorsal exterior; Bed 4a. 3, BC 51110; anterior view of a dorsal valve; Bed 4a. 5–7, BC 51114; dorsal, anterior and lateral views of conjoined valves; Bed 542-1. All × 1·5.

Figs 8–9. *Anoptambonites* sp; Bed 3. 8, BC 51053; dorsal interior; × 2·5. 9, BC 51054; dorsal interior; × 4.

Fig. 10. leptaenine gen. et sp. indet.; BC 51376; ventral external mould; Bed 4; × 3.

Figs 11–12. *Sowerbyella* (*Rugosowerbyella*) sp. 11, BC 51037; ventral exterior; Bed 4; × 3. 12, BC 51040; partly exfoliated ventral exterior; Bed 2; × 4.

Figs 13–15. *Geniculina* sp. 13, BC 51055; ventral exterior; Bed 4a. 14–15, BC 51004; dorsal and lateral views of a dorsal interior; Bed 3b. All × 2.

Fig. 16. *Fardenia*? sp.; BC 51052; ventral exterior; Bed 4; × 3.

PLATE 2


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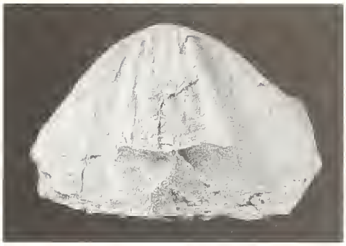
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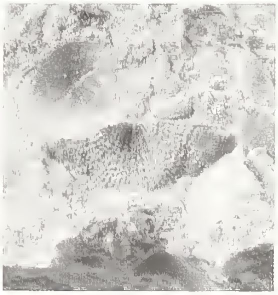
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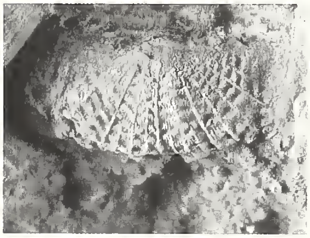
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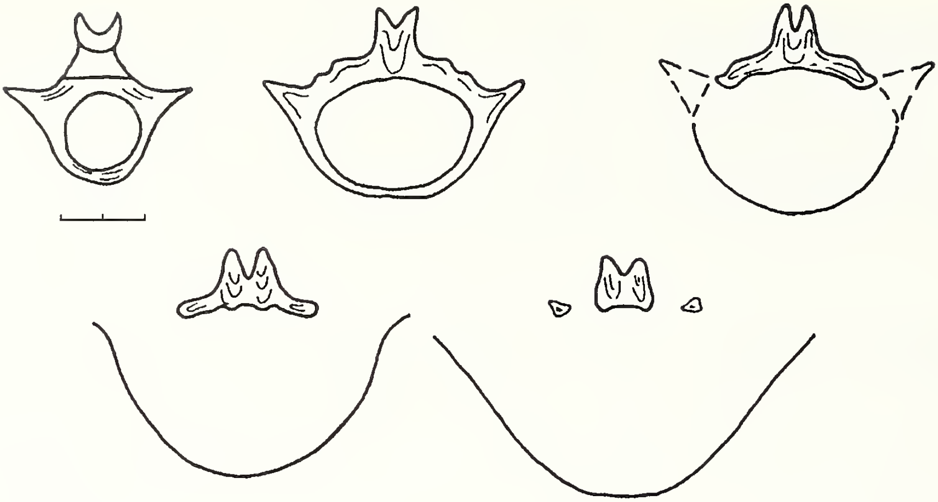
COCKS and MODZALEVSKAYA, late Ordovician brachiopods



TEXT-FIG. 3. Transverse serial sections illustrating the development of the dorsal internal structures in *Ogmoplecia* aff. *plicata* (Wiman). Scale bar represents 2 mm.

Material. Two pairs of conjoined valves, BC 51069–70, and two ventral valves, BC 51068 and BC 51616, and two dorsal valves, BC 51076 and BC 51118, all from Bed 4, and one dorsal valve, BC 51117, from Bed 4a.

Description. Sub-oval outline with width greater than length. Biconvex profile. Asymmetrical shell shape anteriorly. Ribs variably developed, absent posteriorly, between five and seven present in each valve half. Incurved beak and small interarea. Interior not known.

Dimensions. Holotype BC 51070, length 11·6 mm, width 14·2 mm, thickness 7·8 mm; paratype BC 51069, length 9·1 mm, width 11·0 mm, thickness 6·2 mm.

Remarks. The new species differs from the two species hitherto assigned (Wright and Jaanusson 1993), the type species *A. tardicostata* from the Ashgill of Boda, Sweden, and *A. depressa* from the Caradoc of Ringerike, Norway, in its more tightly incurved beak and smaller interarea. The Taimyr specimens illustrated are also smaller than those from the Baltic, but the isolated ventral valve, although not illustrated, is somewhat larger (length 14·3 mm, estimated width 20 mm). There is variation in that the ribbing is much more strongly developed in the holotype and in the isolated ventral valve than in the second articulated specimen. The genus is distinctive in its asymmetrical shell shape, the only triplesioid, apart from *Streptis*, to have one. *Amphiplecia* is known so far only from the Caradoc and Ashgill.

Genus TRIPLESIA Hall, 1859

Triplesia sp.

Plate 4, figures 1–3

Remarks. A single ventral valve, BC 51074 from Locality 1141, is a large smooth triplesioid attributable to *Triplesia*, although the preservation is relatively poor. Its width is preserved to 28 mm.

Superfamily PLECTAMBONITOIDEA Jones, 1928
Family LEPTESTIIDAE Öpik, 1933

Genus LEANGELLA Öpik, 1933

Leangella sp.

Plate 3, figures 5–7

Remarks. The distinctive lateral profile, with incurved beak and relatively large orthocline ventral interarea, and the outline with the globose umbo, form the distinctive shape identifiable as *Leangella* which is common and cosmopolitan in the Caradoc to Upper Silurian (Cocks and Rong 1989). The quinquecostate ornament is also prevalent in many species of the genus. From Taimyr, one pair of articulated valves, BC 51058 (Pl. 3, figs 5–7), and three ventral valves, BC 51059, BC 51061 and BC 51062 are known from Bed 4, and a further pair of conjoined valves, BC 51060, from Locality 1141.

Family HESPEROMENIDAE Cooper, 1956

Genus ANOPTAMBONITES Williams, 1962

Anoptambonites sp.

Plate 2, figures 8–9

Remarks. Two well-preserved dorsal valves, BC 51053–51054, and two poorer dorsal valves, BC 51794 and on BC 51793, and four poorly preserved ventral valves (BC 51793 and BC 51795) have been recovered from Bed 3 at Taimyr, at an horizon extremely rich in stick bryozoans. *Anoptambonites*, with its flaring socket ridges, strong dorsal median septum and prominent elevated and bilobed platform and muscle field is known from the upper Caradoc of Girvan, Scotland, from which Williams (1962) described the type species, but also from the Caradoc of Alaska, and Kazakhstan (Popov 1980) and the Ashgill of Ireland (Mitchell 1977). Bed 3b is less securely dated than the beds above, although it is probably of early Ashgill age.

Family SOWERBYELLIDAE Öpik, 1930

Genus EOPLECTODONTA Kozłowski, 1929

Eoplectodonta aff. *rhombica* (M'Coy, *in* Sedgwick and M'Coy, 1852)

Plate 3, figures 1–4, 8–10

aff. 1852 *Leptaena sericea* var. *rhombica* M'Coy, *in* Sedgwick and M'Coy, p. 239.
aff. 1982 *Eoplectodonta rhombica* (M'Coy) Cocks, p. 769, pl. 81, figs 5–6.

Remarks. Eoplectodonta is a common and cosmopolitan genus from the Caradoc to the middle Silurian, with its type species from the Lower Llandovery of Wales (Cocks and Rong 1989, pp. 133–137). The only two named species from the Ashgill are *E. rhombica*, whose type specimens come from the early Ashgill Crag Hill Beds of northern England, but which has also been recorded from the middle Ashgill of the Oslo region, Norway (Cocks 1982); and *E. oscitanda* Cocks, 1982 from the mid Ashgill Langåra Formation of the Oslo region. From Taimyr, *Eoplectodonta* is a common fossil in Beds 4 and 4a, from which three pairs of conjoined valves, 19 ventral valves and three dorsal valves have been recovered, and five ventral valves from Locality 1141 have been found at a similar stratigraphical level. The largest of these is 26·5 mm wide, which, although not matching the 35 mm achieved by some specimens from Norway, is nevertheless substantially greater than the average size for the genus and has determined the provisional specific attribution. The nine specimens sufficiently well preserved to enable counting of the parvicostellae between the coarser costellae have counts of 5(1), 7(1), 9(3) and 12(4), also putting the species closer to *E. rhombica* than *E. oscitanda*. In addition, there is a number of smaller *Eoplectodonta* specimens in Beds 4 and 4a; whether these are merely young specimens of *E.* aff. *rhombica* or represent a different and smaller species remains uncertain; they are listed here as *Eoplectodonta* spp.

Eoplectodonta spp.

Remarks. The two pairs of conjoined valves, BC 51020 and BC 51035, and one ventral valve, BC 51036, from Bed 3, and the two pairs of conjoined valves, BC 51027 and BC 51030, and three dorsal valves, BC 51018 and BC 51623–51624, from Bed 8 represent less incurved and smaller and different species or at least subspecies of *Eoplectodonta* from *E. rhombica* or *E. oscitanda*; however, the Taimyr material is not adequate to characterize a new taxon effectively, particularly since no interiors are available.

Genus SOWERBYELLA Jones, 1928

Subgenus SOWERBYELLA (SOWERBYELLA) Jones, 1928

Sowerbyella (*Sowerbyella*)? sp.

Remarks. One dorsal valve, BC 51015 from Bed 4, and one ventral valve, BC 51016 from Bed 4a, have a less incurved profile, different from that of *Eoplectodonta* in the same beds. Although the presence of denticles on the hingelines of these specimens cannot be determined, they are attributed provisionally to *S.* (*Sowerbyella*).

Subgenus SOWERBYELLA (RUGOSOWERBYELLA) Mitchell, 1977

Sowerbyella (*Rugosowerbyella*) sp.

Plate 2, figures 11–12

Remarks. Several plectambonitoid exteriors (five pairs of conjoined valves, including BC 51063–51065, and five ventral valves from Bed 4, one pair of conjoined valves, BC 51014, and two ventral valves from Bed 4a, BC 51011 and BC 51023, a ventral exterior, BC 51010, from Bed 3b and BC 51040 from Bed 2) exhibit the characteristic ornament of small rugae interrupted by costellae of the subgenus *Rugosowerbyella*, whose type species (Mitchell 1977) is from the Cautleyan Killey Bridge Formation of Northern Ireland; the subgenus also occurs in the upper Caradoc and lower Ashgill of Girvan, Scotland. Plectambonitoids of uncertain generic affinity, but which display the characteristic ornament and valve profile of *Rugosowerbyella* are also recorded from the Caradoc of the Pre-Chinghiz Mountains, Kazakhstan (Klenina *et al.* 1984, p. 83, pl. 8) and from the lower Ashgill of Västergötland, Sweden (Henningsmoen 1948).

EXPLANATION OF PLATE 3

Figs 1–4, 8–10. *Eoplectodonta* aff. *rhombica* (M'Coy, *in* Sedgwick and M'Coy, 1852). 1, BC 51044; ventral exterior; Bed 4a; × 2·5. 2, BC 51022; ventral exterior; Bed 4a; × 2. 3, BC 51043; dorsal interior; Bed 4; × 3. 4, BC 51034; partially exfoliated ventral valve showing part of the interior; Bed 4a; × 3. 8–10, BC 51051; ventral, lateral and dorsal views of conjoined valves; Bed 4a; × 5.

Figs 5–7. *Leangella* sp.; BC 51058; ventral, lateral and dorsal views of conjoined valves; Bed 4; × 5.

Figs 11–12. *Geniculina* sp.; BC 51007; dorsal and lateral views of a largely exfoliated dorsal valve; Bed 4; × 1·5.

Figs 13–14. *Drummuckina*? sp.; BC 51057; lateral and dorsal views of partly exfoliated conjoined valves; Bed 4a; × 2.

Figs 15–17. *Holtedahlina* sp.; Bed 4. 15, BC 51003; dorsal interior. 16–17, BC 51005; lateral and ventral views of conjoined valves. All × 3.

PLATE 3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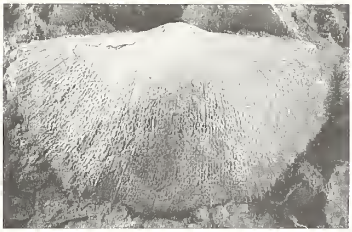
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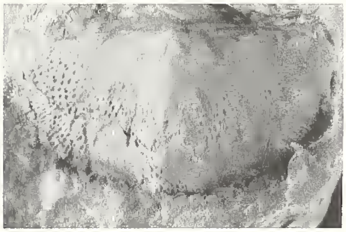
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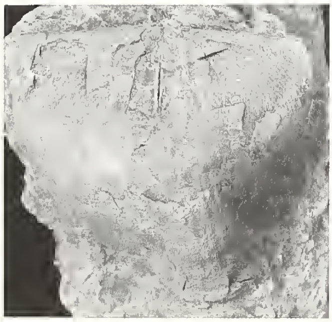
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COCKS and MODZALEVSKAYA, late Ordovician brachiopods

Superfamily STROPHOMENOIDEA King, 1846

Remarks. This superfamily has been the most difficult to identify, since in 14 specimens there appear to be at least seven different taxa, and because many of the specimens are fragmentary, these cannot all be attributed firmly to genera. Two of the specimens, a ventral valve, BC 51002 from Bed 4, and a dorsal valve, BC 51006 from Bed 9, are different from the other forms described here, but can be identified only as a indeterminate strophomenoids.

Family STROPHOMENIDAE King, 1846
Subfamily STROPHOMENINAE King, 1846

Genus HOLTEDAHLINA Foerste, 1924

Holtedahlina sp.

Plate 3, figures 15–17

Remarks. Two specimens, a dorsal interior, BC 51003, and a pair of conjoined valves, BC 51005, both from Bed 4, can be identified together as *Holtedahlina* since they have a dorsibiconvex profile with a ventral sulcus and dorsal fold anteriorly, unequally costellate ornament, a large pesudodeltidium with small chilidial plates and an interior like the true *Strophomena* (Rong and Cocks 1994, pl. 1, figs 7, 9) but with dorsal trans-muscle ridges weakly developed. They are not conspecific with the type species, *H. sulcata* (Verneuil) from the middle Ashgill Whitewater Formation of Ohio, USA, in that the socket ridges are less elongate and the cardinal process less robust in the Taimyr specimens.

Genus DRUMMUCKINA Bancroft, 1949

Drummuckina? sp.

Plate 3, figures 13–14

Remarks. Five specimens, a pair of conjoined valves, BC 51057, and four ventral exteriors, including BC 51056–51057, all from Bed 4a, may be attributable to *Drummuckina*, whose type species *D. donax* (Reed) comes from the Ladyburn Starfish Bed (Ashgill: Rawtheyan) of the Drummuck Group, Girvan, Scotland. The Taimyr form possesses the concavo–convex profile, large chilidium, short dental plates, ventral myophragm and the trapezoidal ventral muscle field characteristic of the genus, but the ornament is unequally rather than equally costellate and the dorsal interior features are difficult to discern; hence the uncertain attribution.

Subfamily FURCITELLINAE Williams, 1965

Genus GENICULINA Rõõmusoks, 1993

Geniculina sp.

Plate 2, figures 13–15; Plate 3, figures 11–12

Remarks. Two dorsal interiors, BC 51004 from Bed 3b and BC 51007 from Bed 4, are known from Taimyr. It is possible that a ventral exterior, BC 51055 from Bed 4a, may be the same species. The dorsal valve from the lower horizon is more sharply geniculate, but both dorsal valves have substantial trails preserved (Pl. 3, fig. 12). All three specimens show unequally parvicostellate ornament, and the dorsal valves show the thin median septum and pair of side septa characteristic of *Geniculina*, although the irregular oblique wrinkles present in *G. pseudoalternata*, the type species from the mid Ashgill Pirgu Stage of Estonia (Rõõmusoks 1993), are missing. Furcitellines such as this are widespread in the Ashgill, although since they are often represented by a small number of specimens, like these from Taimyr, they are as yet relatively poorly documented internationally.

Such specimens often appear in faunal lists as *Oepikina*, although that genus, whose type species *O. septata* is from the Caradoc Lebanon Formation of Tennessee, USA, has a distinctive dorsal subperipheral rim and two or more pairs of dorsal side septa (Rong and Cocks 1994, pl. 3), in contrast with *Geniculina*, *Katastrophomena*, *Panderites*, *Trigrammaria* and other closely related genera.

Family RAFINESQUINIDAE Schuchert, 1893
Subfamily LEPTAENINAE Hall and Clarke, 1894

leptaenine spp.

Plate 2, figure 10

Remarks. Two specimens, the external mould of a ventral valve, BC 51376 from Bed 4, and a broken dorsal valve whose umbo is missing, BC 51017 from Bed 4a, belong to two different leptaenine genera. The ventral valve (Pl. 2, fig. 10) has a square outline comparable to that of *Glossoleptaena* and *Rugoleptaena*, which both occur only in the Upper Silurian and Devonian, and may represent a new genus. The geniculate dorsal valve is morphologically close to *Leptaena sensu stricto*, which ranges from the Caradoc to the Devonian. However, neither specimen can be generically determined with confidence.

Superfamily CHILIDIOPSOIDEA Boucot, 1959
Family CHILIDIOPSIDAE Boucot, 1959

Genus FARDENIA Lamont, 1935

Fardenia? sp.

Plate 1, figures 19–21; Plate 2, figure 16

Remarks. Two ventral valves, BC 51081 and BC 51052, and a possible dorsal valve on BC 51015 from Bed 4, of which only the convex exteriors are visible, probably represent a chilidiopsid. One specimen is relatively small for the group (length 6·4 mm); the other is also below medium size (length 12·2 mm). The shell, as can be seen near the umbo where the specimen is abraded, lacks pseudopunctae, but is laminar rather than fibrous. The pseudodeltidium is very prominent, making assignment to the contemporary Ashgill *Fardenia* questionable, since in that genus it is usually relatively small. The only closely related genus with a large pseudodeltidium (even larger than in the Taimyr specimen) is *Morinorhynchus*, which is only known from the Upper Silurian. A further specimen, BC 51377 from Bed 4a, also showing only the ventral exterior (Pl. 1, fig. 21) which is somewhat exfoliated, is referred provisionally to the same taxon as the form from Bed 4. There is a ventral valve, also showing only the exterior, which is virtually identical to that of the Taimyr specimens, in the Stockholm collections, RMS Br 9017, from the Boda Limestone of Arvet, Dalarna, but again, no firmly attributable interiors of either valve have yet been found from that area.

Superfamily CAMERELLOIDEA Hall and Clarke, 1894
Family PARASTROPHINIDAE Ulrich and Cooper, 1938

Genus PARASTROPHINA Schuchert and Le Vene, 1929

Parastrophina pentagonalis Nikiforova, 1989

Plate 4, figures 12–14

1989 *Parastrophina lindströmi pentagonalis* Nikiforova, p. 78, pl. 1, figs 1–4.

Remarks. Nikiforova recorded 14 specimens from Bed 4 of her new subspecies which she attributed to *P. lindstroemi* described from the Boda Limestone of Sweden (Wright 1974). A further ventral valve, BC 51077, is illustrated here from the same bed, and a small pair of conjoined valves from

Bed 4a, from which two specimens are now known. Nikiforova (1989, p. 80) suggested that the pentagonal (rather than triangular) outline, the more acute apical angle and beak, more prominent fold, and the greater number of lateral plicae are the characteristic features which led her to consider the Taimyr *Parastrophina* to be a separate subspecies of *P. lindstroemi*. However, the number of incipient costae in the fold and sulcus varies, and in some specimens they seem to be scarcely developed. Some specimens from Boda, e.g. RMS Br 6989, also tend towards a pentagonal shape, and hence a different subspecies for the Taimyr and Boda forms may not be valid. However, Nikiforova's section of the Taimyr form (1989, figure 1) does not show any alae developing from the crural plates, which is one of the characteristics of true *Parastrophina*, and until the Boda material has been worked on in more detail, her species name is retained for the Taimyr material. Nikitin *et al.* (1996) have described from Kazakhstan a new subspecies of *Parastrophina angulosa*, another species revised by Wright (1974) and also originally from the Boda Limestone. However, both in ornament and particularly also in internal section these supposed subspecies seem very different from each other and appear to warrant specific separation. Nikitin *et al.* (1996) also described a further new species, *P. tersa*, from the Kazakhstan carbonate mounds, of Ashgill age.

Genus PARASTROPHINELLA Schuchert and Cooper, 1931

Parastrophinella? sp. A

Plate 4, figures 8–11; Text-figure 4

Five specimens from Bed 4 (BC 51078, BC 51080, BC 51090–91 and BC 51112) and three specimens from Bed 4a (BC 51092–3 and BC 51119), all *c.* 10 mm wide, can be attributed tentatively to *Parastrophinella*. All lack ornament apart from three undulose ribs in the antero-central region, commencing at about half valve length or later. A newly sectioned specimen, BC 51080, although very similar externally to the lectotype of *Parastrophina angulosa* as figured by Wright (1974, fig. 3), possesses one ventral rib and has a distinctive interior (Text-fig. 5). The ventral interior is the same as that of *Parastrophina*, with a short median septum, spondylium and teeth, but the dorsal interior has features intermediate between those of *Parastrophina* and *Parastrophinella* from the Anderken Horizon (middle to upper Caradoc) of Kazakhstan, which has a similar septalium, although the exterior has a narrower fold and sulcus and more ribs. However, the Taimyr form is attributed to *Parastrophinella* because the section (Text-fig. 4) reveals that there is a pair of divergent outer plates extending directly to the floor of the valve instead of uniting on to a median septum as in *Parastrophina*. From *Parastrophina orloviensis* from the Orlov Horizon (Ashgill) of the north-western Altai region (Severgina 1978, p. 28, pl. 3, fig. 14) it differs in possessing a narrower

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EXPLANATION OF PLATE 4

Figs 1–3. *Triplesia* sp.; BC 51074; ventral, lateral and posterior views of a ventral valve; Locality 1141; × 1·5.

Figs 4–7. *Tcherskidium* sp.; Bed 4. 4, 7, BC 51072; anterior and posterior views of conjoined valves, the latter sectioned to reveal spondylium; × 1·5 and × 3. 5–6, BC 51071; lateral and ventral views of a ventral valve; × 2.

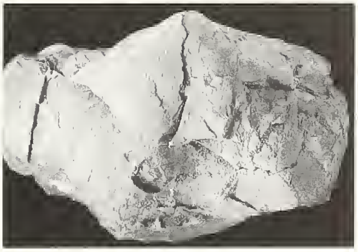
Figs 8–11. *Parastrophinella?* sp. A. 8–9, BC 51092; dorsal and anterior views of a dorsal valve; Bed 4a. 10, BC 51091; ventral exterior; Bed 4. 11, BC 51093; dorsal exterior; Bed 4a. All × 1·5.

Figs 12–14. *Parastrophina pentagonalis* Nikiforova, 1989. 12, BC 51089; ventral view of conjoined valves; Bed 4a; × 3. 13–14, BC 51077; ventral and anterior views of a ventral valve; Bed 4; × 1·5.

Figs 15–16. indeterminate cyrtiinid; BC 51113; lateral and ventral views of a ventral valve; Bed 4; × 1·5.

Figs 17–20. *Catazyga* sp.; BC 51101; ventral, dorsal, anterior and lateral views of conjoined valves; Bed 4; × 2.

PLATE 4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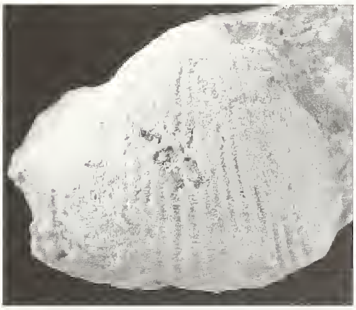
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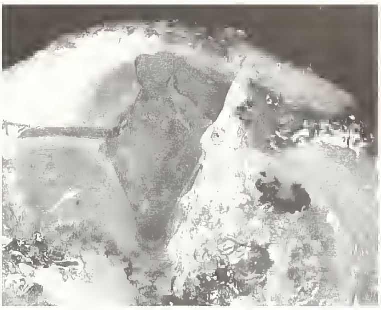
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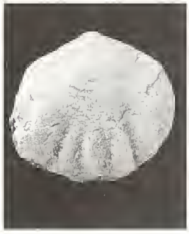
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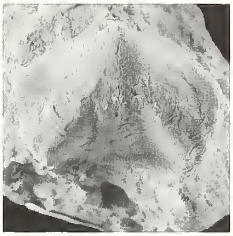
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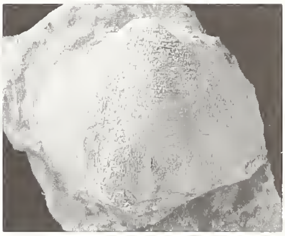
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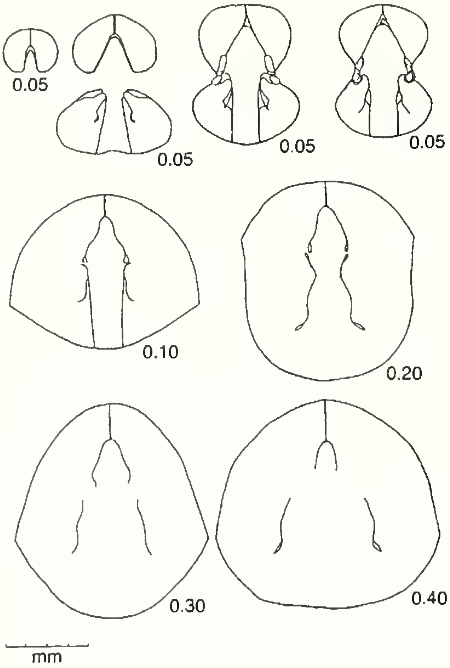
COCKS and MODZALEVSKAYA, late Ordovician brachiopods



TEXT-FIG. 4. Transverse serial sections illustrating the development of internal structures in *Parastrophinella*? sp., BC 51080, from Locality 569, Bed 4. Distances given are those between successive sections. Scale bar represents 4 mm.

ventral sulcus and a flatter ventral valve. The Taimyr form also differs from *Parastrophinella portentosa* from Kazakhstan (Nikitin *et al.* 1996) in its ribs being confined to the valve centre and also being consistent in possessing them (the Kazakhstan specimens vary from having ribs round nearly all the anterior commissure to lacking them entirely).

Superfamily PENTAMEROIDEA M'Coy, 1844
Family VIRGIANIDAE Boucot and Amsden, 1963

Genus HOLORHYNCHUS Kiær, 1902

Holorhynchus giganteus Kiær, 1902

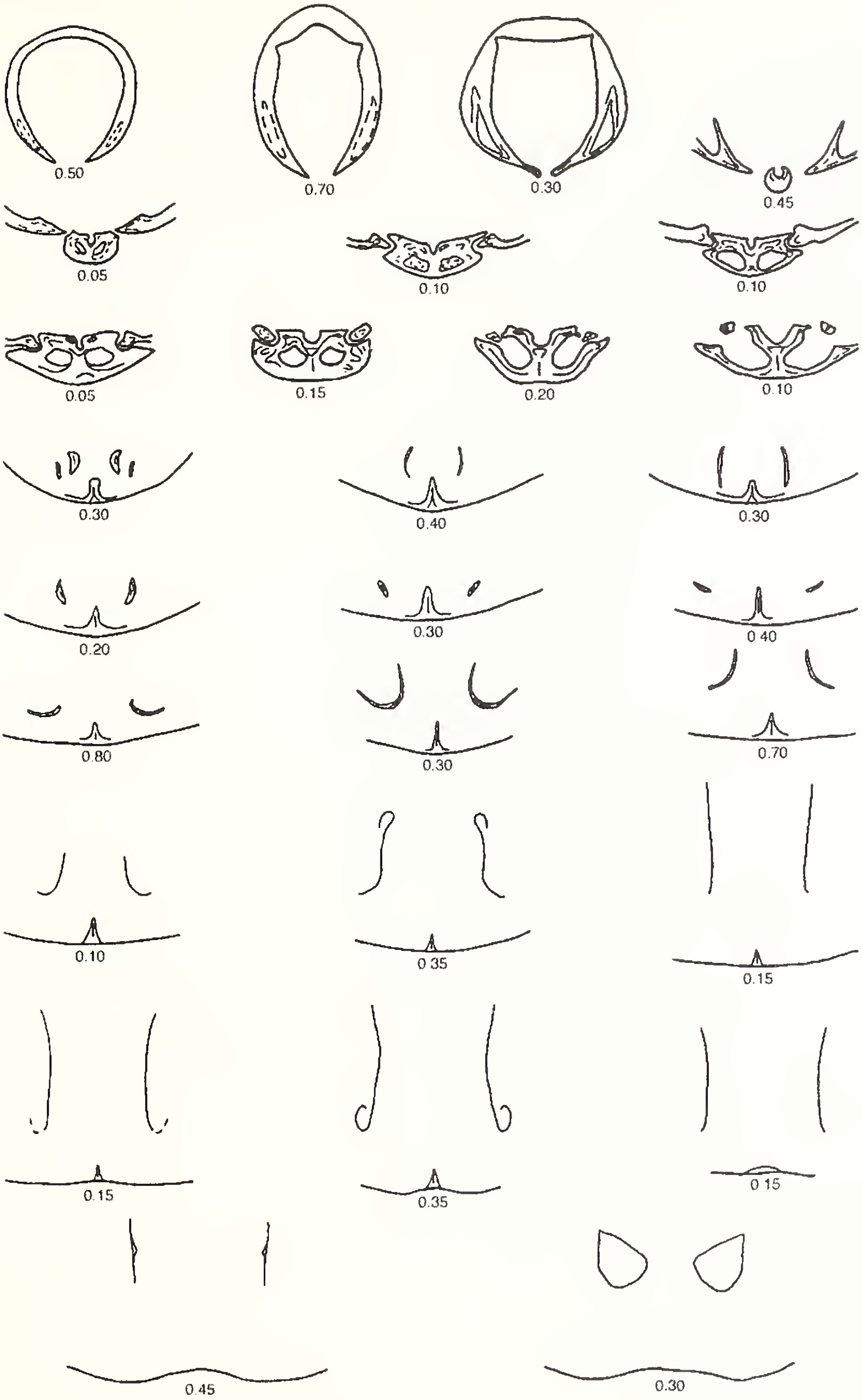
1902	*Holorhynchus giganteus* Kiær, p. 68, figs 1–7.
1982	*Holorhynchus giganteus* Kiær; Cocks, p. 774, pl. 83, figs 12–17.
1989	*Holorhynchus* ex gr. *giganteus* Kiær; Nikiforova, p. 80, pl. 2, figs 1–3.

Remarks. Nikiforova recorded seven ventral valves and one dorsal valve, all from Bed 9, which, although only identified by her as 'ex gr. *giganteus*', we consider conspecific with Kiær's species from the middle Ashgill of Norway.

Holorhynchus aff. *giganteus* Kiær, 1902

Plate 1, figures 7–9

Remarks. In addition to the record of *Holorhynchus giganteus* from Bed 9, we figure a so far unique specimen, BC 51075, as probably attributable to the genus. This comes from Bed 4, which makes this specimen substantially older in the Ashgill than the specimens recorded by Nikiforova and probably older also than the Norwegian types. The specimen is a well-preserved pair of conjoined valves, and, although it is relatively small for the genus (length 18·2 mm), the external features compare well with juvenile specimens of *Holorhynchus giganteus* from the Oslo District (Cocks 1982). However, since no interiors are visible, we identify the specimen here as *H.* aff. *giganteus*.



TEXT-FIG. 5. Selected transverse serial sections illustrating the development of internal structures in *Cyclospira orbus* sp. nov.; BC 51125, length, 11·5 mm; width, 10·7 mm; thickness, 8 mm. Figures are distances in mm between individual sections.

Genus TCHERSKIDIUM Nikolaev and Sapelnikov, 1969

Tcherskidium unicum (Nikolaev, 1968)

1968 *Conchidium unicum* Nikolaev, p. 47, pl. 2, figs 1–3.
1969 *Tcherskidium unicum* (Nikolaev) Nikolaev and Sapelnikov, p. 11, pl. 1, figs 1–4.
1989 *Tcherskidium unicum* (Nikolaev); Nikiforova, p. 81, pl. 2, figs 4–12.

Remarks. Nikiforova recorded 63 articulated specimens and five dorsal valves all from Bed 9. In addition, she figured a further specimen from Bed 9 which she termed *Tcherskidium*? sp. nov. and which we consider to be within the specific variability of *T. unicum*, and thus it is not included separately in our list.

Tcherskidium sp.

Plate 4, figures 4–7

Remarks. There are two specimens, a pair of articulated valves BC 51072 and a ventral valve BC 51071, from Bed 4. A cross section of BC 51072 (Pl. 4, fig. 7) reveals a clear ventral spondylium and there is a pair of dorsal septa. There are well-defined and regular costae of medium size over the whole exterior. In contrast to the higher Bed 9 fauna, where *T. unicum* is a major component, these two specimens represent a minor constituent of the Bed 4 fauna. They are somewhat smaller than typical *T. unicum* and are thus identified here as *Tcherskidium* sp., and may represent an ancestral form of the type species.

Superfamily ANAZYGOIDEA Davidson, 1882
Family ANAZYGIDAE Davidson, 1882

Genus CATAZYGA Hall and Clarke, 1893

Catazyga sp.

Plate 4, figures 17–20

Remarks. A single articulated specimen, BC 51101, with the distinctive fine radial ornament, shape and outline of *Catazyga*, has been found in Bed 4.

Superfamily LISSATRYPOIDEA Twenhofel, 1914
Family CYCLOSPIRIDAE Schuchert, 1913

Genus CYCLOSPIRA Hall and Clarke, 1893

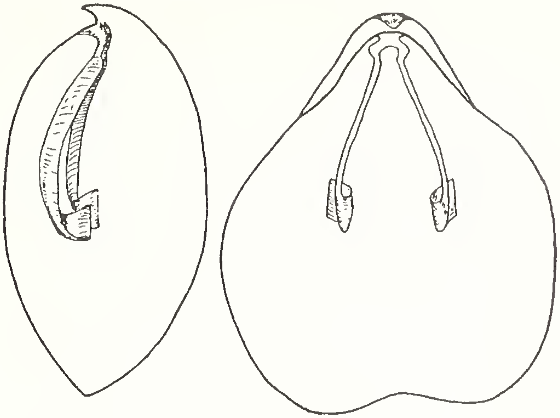
Remarks. The type species of *Cyclospira*, *C. bisulcata*, is from the middle Ordovician of New York State and the genus is widespread in the middle but mainly in the upper Ordovician of North America, Europe and Eurasia. The common species *Protozeuga anticostiana* Twenhofel (1928, p. 213, pl. 21, figs 15–17), was assigned by Schuchert and Cooper (1930, p. 280) to *Cyclospira* on the basis of muscle impressions in the moulds. Cloud (1942, p. 146) revised this species and also assigned it to *Cyclospira* because there is no jugum; however, Dr P. Copper informs us that a jugum is present. *C.*? *anticostiana* occurs in the Vaureal Formation of Anticosti Island, which is of late Ashgill age; and Copper (1995) now assigns it to *Xysila*, rather than to *Cyclospira*.

Cyclospira orbus sp. nov.

Plate 5, figures 1, 3–6; Text-figures 5–6

Derivation of name. From the Latin, *orbus* = orphaned.

Holotype. BC 51087 (Plate 5, figs 6a–e), conjoined valves, Locality 569, Bed 4.



TEXT-FIG. 6. Lateral view of a reconstruction of the spiralia of *Cyclospira orbus* sp. nov., based on the serial sections shown in Text-fig. 5.

Material. Eight conjoined and slightly damaged valves (BC 51082–51087) and one ventral valve all from Bed 4, and three pairs of conjoined valves on BC 51028 from Bed 4a.

Description. Ventri-biconvex shell with oval to rhomboidal outline, large for the genus, lacking radial ornament. The greatest thickness is at the middle valve length. A slight sulcus in both valves, leading to a dorsal sulcus and ventral fold at the anterior commissure. Beak small, incurved, very close to dorsal valve. Ventral interior with teeth supported by thin and rather short dental plates. Discrete cardinal plates joined to the thick median septum, the track of which may be visible on the external surface. Jugum absent; spiralia consisting of thin plates which turn about their axis ventrally and dorsally and continue towards the shell centre (Text-fig. 6).

Measurements (mm). Length, 6·0–9·9 mm; width, 5·5–9·3 mm; thickness, 3·8–6·0 mm.

Remarks. Among the several described middle and upper Ordovician species of *Cyclospira*, the Taimyr shells are comparatively large. The distinctive characters are the relatively low ventral elevation, visible only anteriorly, and the wide dorsal sulcus with no ventral fold. The discrete cardinal plate and the thick and rather long median septum and septarium are similar to those of *Cyclospira globosa* Rozman, 1964 (p. 189, pl. 23, figs 1–3; Rozman *et al.* 1970, p. 113, pl. 18, figs 16–20) from the upper Ordovician of north-east Russia, but the Taimyr shells are distinguished by their oval to rhomboidal outline and by the absence of a median fold in the sulcus. From *Cyclospira glansfagea* Cooper and Kindle, 1936 (pl. 52, figs 1, 4, 7) *C. orbus* is distinguished by a less convex dorsal valve and shallow sulcus without a median fold. The Taimyr shells are larger than *Cyclospira*? *scanica* described by Sheehan (1973) and *C.* ?*minuscula* Cooper (*in* Schuchert and Cooper, 1930, p. 280, pl. 2, figs 9–12).

Superfamily ATRYPOIDEA Gill, 1871
Family ATRYPINIDAE McEwan, 1939

Genus PLECTATRYPA Schuchert and Cooper, 1930

Plectatrypa? *laticostata* sp. nov.

Plate 5, figures 7a–e; Plate 6, figure 19; Text-figure 7

Derivation of name. From the Latin, *laticostatus* = wide ribbed.

Material. Holotype: BC 50991 (Plate 5, figure 7a–e), conjoined valves, Locality 569, Bed 4a; 36 other specimens from Bed 4a, including BC 50986–51101, and three from Bed 4, including BC 51106–51107.

Description. Biconvex and slightly transverse outline, ventral umbo moderately curved, delthyrium covered laterally by deltidial plates fusing at their base, foramen submesothyridid. Shallow ventral sulcus originating near beak, widening anteriorly and extending into a moderately high, semi-elliptical tongue. Dorsal fold variably present in the anterior half of the valve. Ornament costellate with six to nine wide ribs on the shell flanks and from one to five (usually four) ribs in the sulcus. The costae increase by bifurcation and intercalation. Concentric ornament present overall. Dorsal interior with discrete cardinal plates, supported by very short and thickened median septa (Text-fig. 7).

Remarks. This species is the most abundant brachiopod in the Bed 4a collection and also occurs in Bed 4, although there is less common than *Qilianotryma tajmyrica*. The main feature of the new species is the concentric filae which are spaced almost equally over the whole surface of the shell. Since *laticostata* is relatively coarsely ribbed and with short concentric growth interruptions and lamellae, its generic assignment is difficult. The young specimens of *laticostata* are similar to *Plectatrypa sulevi* Jaanusson and *Plectatrypa* n. sp. A of Jaanusson (1956) from the Pirgu Formation of Estonia in having one bifurcating rib in the ventral sulcus and the primary costae limited to the sulcus. The Taimyr shells are distinguished, however, by a pentagonal outline and concentric ornament from *Eospirigerina sulevi* (Jaanusson, 1956, p. 397, pl. 1, fig. 7). From *Eospirigerina porkuniana* and *E. hillistensis* from the Lower Silurian of Estonia (Rubel 1970, p. 30, pl. 14, figs 16–27; pl. 15, figs 1–10) *P.*? *laticostata* is distinguished by a more transverse outline, with the maximum width near the cardinal margin in adult specimens. From '*Plectatrypa*' sp. (Oradovskaya 1983, p. 66, pl. 17, figs 5–6), which may or may not be attributed to that atrypid genus, from the upper Ordovician of north-east Russia, it is distinguished by internal structure and greater numbers of ribs. The type species of *Plectatrypa* is *P. imbricata* (J. de C. Sowerby *in* Murchison, 1839) from the late Wenlock Much Wenlock Limestone Formation of England, and the species has not been properly revised, although Bassett and Cocks (1974) selected a lectotype and refigured the contemporary *P. lamellosa* from Gotland on which regular concentric frills are seen, in contrast to the true *Eospirigerina* (see below) on which concentric frills are rarely seen, and then only in fully mature specimens and near the anterior margin. It seems probable that the Silurian species of both *Plectatrypa* and *Eospirigerina* were derived from a single genus in the late Ordovician. However, the Wenlock forms of *Plectatrypa* differ quite substantially from those of the upper Ordovician, which is why we have attributed *laticostata* to the genus with a query. It is possible that, with more analysis of this multi-specific plexus through space and time, a new genus or subgenus would be appropriate which would include such Ashgill forms as *laticostata*.

Genus QILIANOTRYMA Xu, 1979

Qilianotryma tajmyrica (Nikiforova, *in* Nikiforova *et al.*, 1982)

Plate 5, figure 2a–b

1982 *Euroatrypa tajmyrica* Nikiforova, *in* Nikiforova *et al.*, p. 65, pl. 6, figs 1–7.

Remarks. Recent work by P. Copper (pers. comm.) has synonymized the genera *Euroatrypa* Oradovskaya, *in* Nikiforova *et al.* (1982) and the *nomen nudum Xenatrypa*, with type species *X. sulevi*

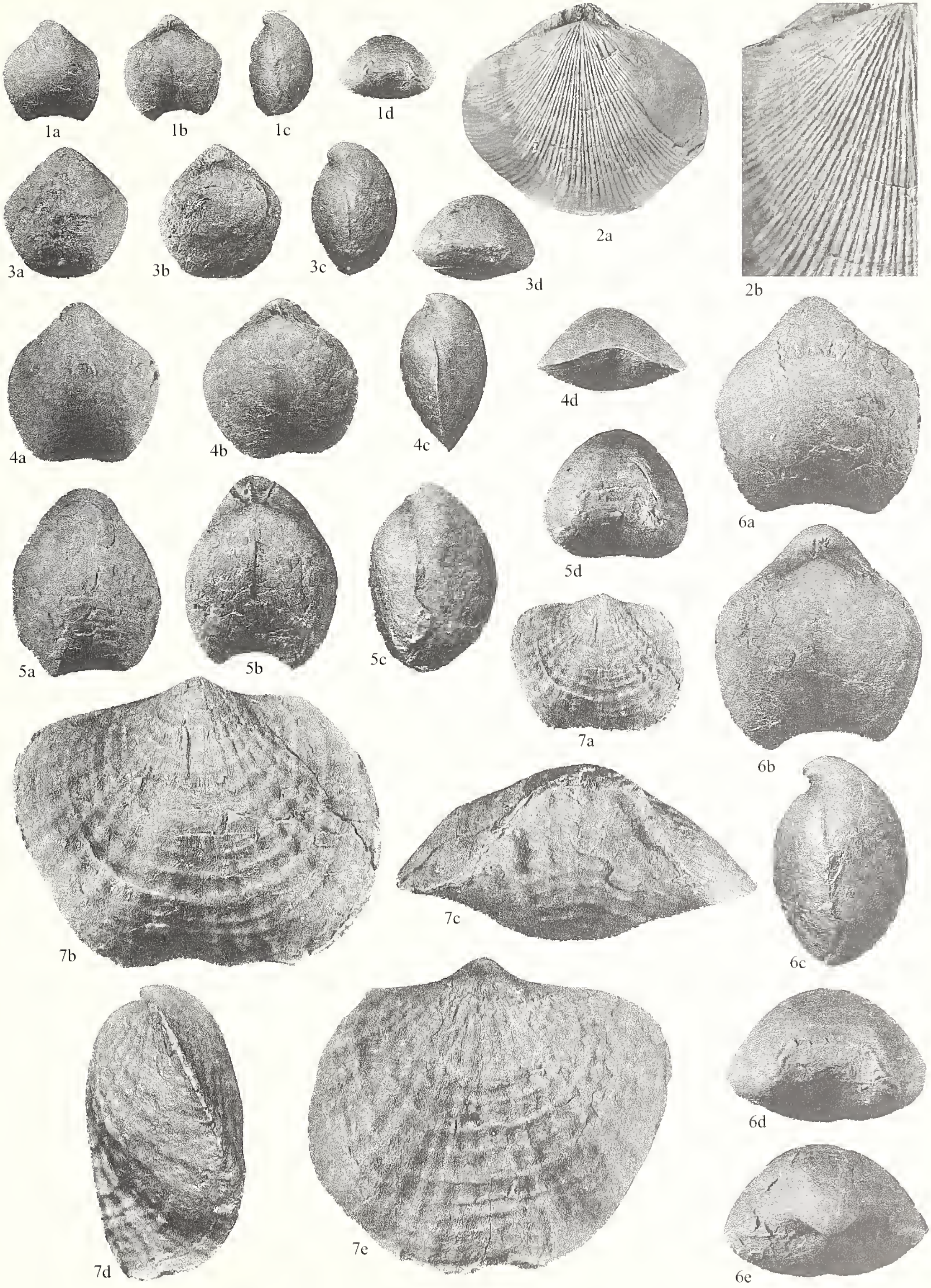
EXPLANATION OF PLATE 5

Figs 1, 3–6. *Cyclospira orbus* sp. nov.; Bed 4; ventral, dorsal, lateral and anterior views of five pairs of conjoined valves. 1, BC 51081. 3, BC 51082. 4, BC 51083. 5, BC 51085. 6, BC 51087, holotype, including (6e) posterior view. All ×3.

Fig. 2. *Qilianotryma tajmyrica* (Nikiforova, 1982); CNIGR Museum 18/11943; Locality 542-1. 2a, dorsal view; ×2. 2b, detail of ornament; ×5.

Fig. 7. *Plectatrypa*? *laticostata* sp. nov.; BC 50991, holotype; Bed 4a. 7a–b ventral; 7c, anterior; 7d, lateral; and 7e, dorsal views of conjoined valves; 7a, ×1·5; 7b–e, ×3.

PLATE 5



COCKS and MODZALEVSKAYA, *Cyclospira*, *Qilianotryma*, *Plectatrypa*?

from the Boda Limestone, Sweden, with *Qilianotryma* Xu (1979) from north-west China. Nikiforova recorded over 60 conjoined valves from Bed 4 and its equivalents, including specimens from locality 542-1 (Pl. 5, fig. 2a–b).

Genus EOSPIRIGERINA Boucot and Johnson, 1967

Eospirigerina vetusta sp. nov.

Plate 6, figures 1–18; Text-figure 8

Derivation of name. From the Latin, *vetustus* = old.

Material. Holotype, BC 50976, conjoined valves from Locality 569, Bed 4a. Other material: 42 conjoined and two ventral valves from localities 542-1 and 569, Beds 4, 4a and 6b, including BC 50969–50984 and BC 51012.

Description. Biconvex shell with sub-circular to slightly transverse outline, sometimes with extended alae, fine ribs and closely spaced uniform concentric growth filae. Maximum width near the cardinal margin. Ventral valve more convex centrally; without well-developed sulcus, but with a gently plicate anterior commissure. Beak straight or slightly incurved with submesothyridid foramen confined by small deltidial plates. Dorsal valve with uniform convexity without fold but sometimes with a shallow furrow posteriorly. The rounded to rectangular tongue is well represented on adult shells. Surface ornament of fine rounded ribs (38–48 along the anterior and lateral margins) which are increased mainly by bifurcations. Fine, closely spaced uniform concentric growth lines well preserved anteriorly. Ventral interior characterized by short, thin dental plates and stout massive teeth. Dorsal high stout myophragm elevated above the discrete cardinal plate for a short distance (Text-fig. 8). Muscle field weakly impressed.

Remarks. The type species of *Eospirigerina* is *Atrypa praemarginalis* from the late Ordovician Edgewood Limestone of Missouri, USA, which was put into the synonymy of *Zygospirella putilla* Hall and Clarke (1894) by Amsden (1974). However, *E. putilla* differs from the Taimyr material in its more closely spaced ribbing and less prominent concentric growth lines from which lamellae are only developed near the valve margin in adult shells (e.g. Amsden 1974, pl. 18, fig. 8J). The equally biconvex shells of our new species with a sub-circular outline, nearly straight cardinal lines and straight to slightly incurved pedicle beak, are similar to those of *Protatrypa malmoeyensis* Boucot, Johnson and Staton, 1964 (p. 810, pl. 126, fig. 11; Copper 1995, p. 858, figs 13–15) from the Lower Llandovery of Norway. The interiors are very different, however (compare Text-fig. 8 with Copper

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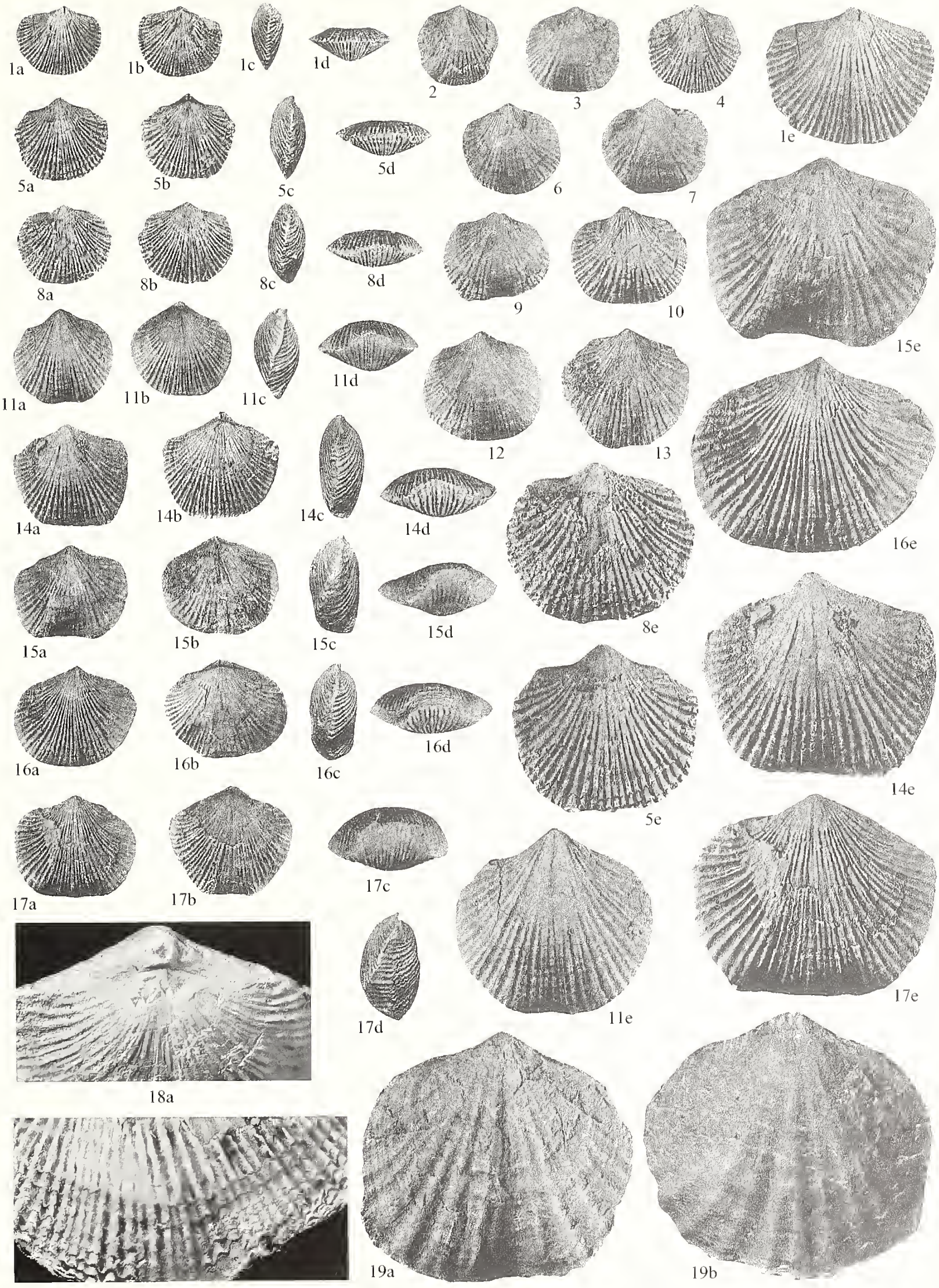
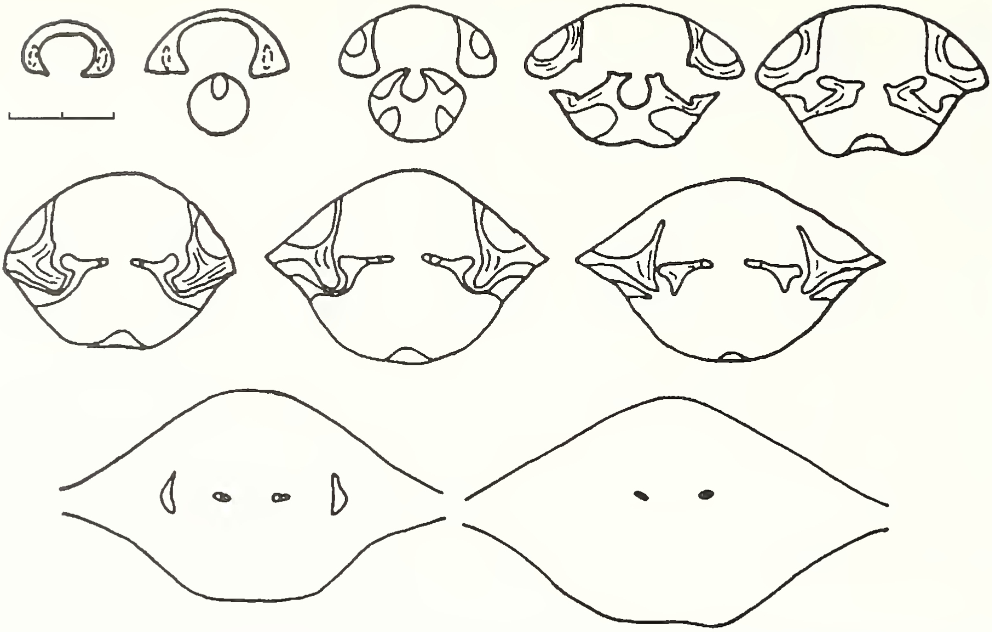
EXPLANATION OF PLATE 6

Figs 1–18. *Eospirigerina vetusta* sp. nov.; 2–4, 6–7, 9–10, 12–13, 18, Bed 4; others, Bed 4a; ventral, dorsal, lateral and anterior views of conjoined valves. All × 1·25; except 1e, 5e, 8e, 11e, 14e, 15e, 16e, 17e, × 2·5, and 18a–b, × 5. 1, BC 50969; 2, BC 50977; 3, BC 50984; 4, BC 50979; 5, BC 50970; 6, BC 50981; 7, BC 50982; 8, BC 50971; 9, BC 50983; 10, BC 50985; 11, BC 50973; 12, BC 50980; 13, BC 50978; 14, BC 50972; 15, BC 50975; 16, BC 50974; 17, BC 50976, holotype; 18, BC 52143.

Fig. 19. *Plectatrypa*? *laticostata* sp. nov.; BC 50998; ventral and dorsal views of conjoined valves; Bed 4a; × 3.



COCKS and MODZALEVSKAYA, *Eospirigerina*, *Plectatrypa*?



TEXT-FIG. 7. Selected transverse serial sections illustrating the development of internal structures in *Plectatrypa*? *laticostata* sp. nov.; length, 12·7 mm; width, 12·6 mm, thickness, 6·4 mm. Scale bar represents 2 mm.

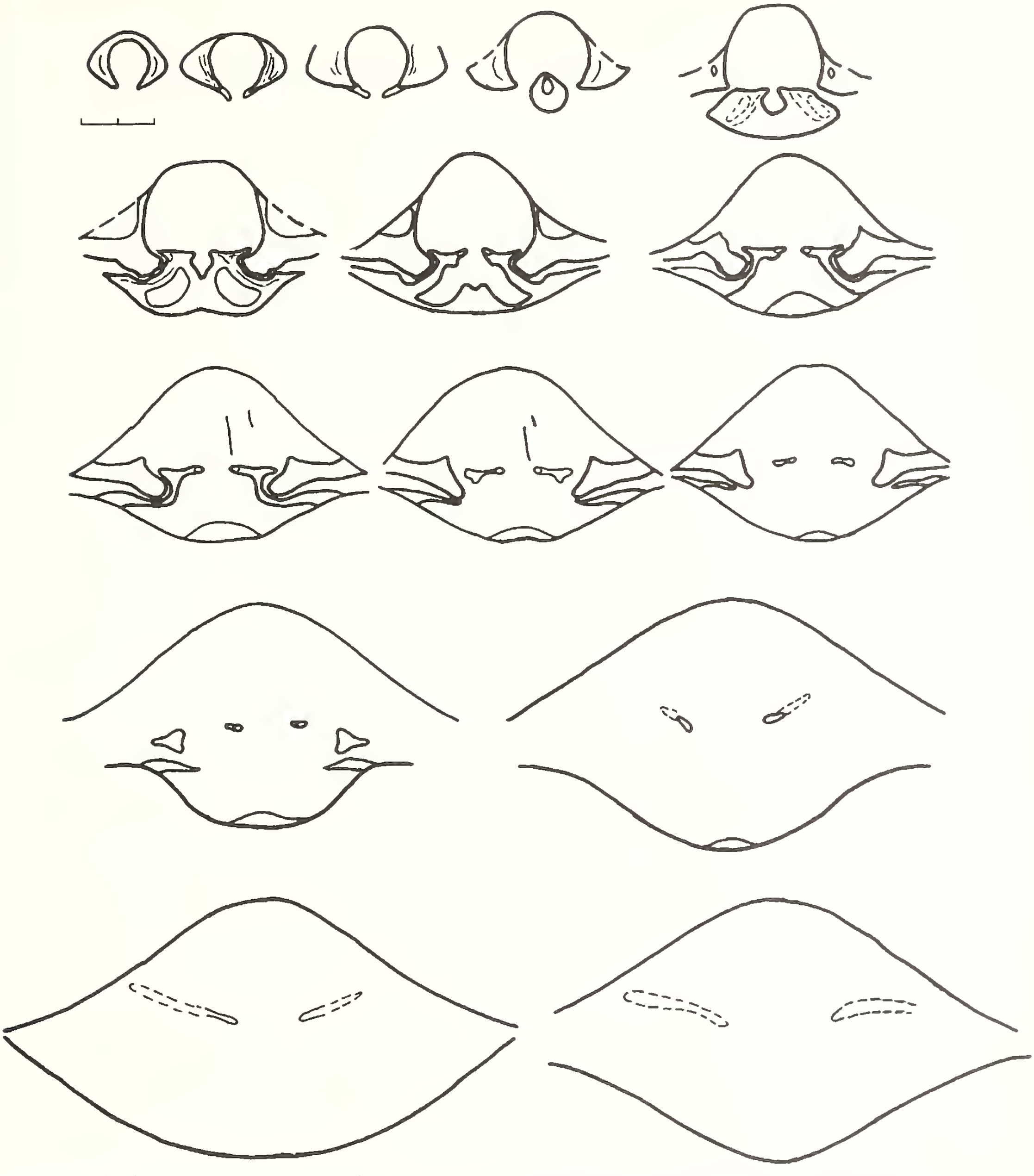
1995, fig. 14). The regularly spaced concentric growth lines are very similar to those of *P. septentrionalis* (Nikiforova and Andreeva 1961, pl. 47, fig. 3) from the Llandovery of eastern Siberia. From *Qilianotryma taimyrica* the new species differs in the absence of a clearly defined fold and sulcus, the less incurved ventral beak, the many fewer ribs, and in the presence of concentric filae.

Superfamily CYRTIOIDEA Frederiks, 1919 (1924)
Family CYRTIIDAE Frederiks, 1919 (1924)

indet. cyrtiinid

Plate 4, figures 15–16

Remarks. The illustrated specimen, BC 51113 from Bed 4, showing only the exterior of a ventral valve, displays the characteristic fine radial ornament of Cyrtiidae and has an anterior median fold comparable to that of *Eospirifer*. Three less complete specimens, BC 51111 also from Bed 4, and BC 51122 and BC 51623 from Bed 4a, are also probably conspecific. Although considered for many years to be no older than late Llandovery, the family is now known from the Ashgill of Tasmania and China.



TEXT-FIG. 8. Selected transverse serial sections, illustrating the development of internal structures in *Eospirigerina vetusta* sp. nov.; length, 14·3 mm; width, 16·3 mm; thickness, 7·75 mm. Scale bar represents 2 mm.

Acknowledgements. We thank Dr V. I. Bondarev, VNII Okeangeologia, St Petersburg, for presenting the collection which he made in Taimyr. We are most grateful to Dr P. Copper, Sudbury, Dr L. E. Popov, St Petersburg, and Professor A. D. Wright, Belfast, for very helpful comments on the fauna, and to Professor J. Bergström for providing access to the Boda material in the Riksmuseum, Stockholm. TLM acknowledges Grant 96-05-65762 from the Russian Foundation for Fundamental Investigations.

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CLASSOPOLLIS IN THE GUTS OF JURASSIC INSECTS

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Abstract. The gut contents of two specimens of fossil insects from the Upper Jurassic of the Karatau Range, Kazakhstan include clumps of *Classopollis* pollen grains. The insects are assigned to different species of *Aboilus* (Hagloidea, Ensifera, Orthoptera) resembling the larger extant grasshoppers. The pollen grains show the conventional *Classopollis* external features, columellate–regulate infrastructure and exinal filaments of the proximal Y-mark as well as a microporous membrane of the distal pore-like structure. Pollinivory may explain excessive *Classopollis* pollen production, while the intricate harmomegathic structures are compatible with the pollen transfer being by large, short distance fliers.

Pollen in the guts of fossil insects was first reported by Krassilov and Rasnitsyn (1982). They described well-preserved bisaccate and monosaccate grains extracted from two early Cretaceous Xyelidae species found in the fossil plant-insect locality Baisa, Vitim River Valley, Trans-Baikal Region. Later, a third species from the same locality yielded a different type of bissacate grain. Subsequently, we scanned a rich collection of fossil insects deposited in the Palaeontological Institute of the Russian Academy of Science, Moscow, in search of appropriately preserved material. Our recent findings include striate pollen grains obtained from three species of Permian Hypoperlidae and Grylloblatidae (Krassilov and Rasnitsyn 1997), and *Classopollis* from two species of Jurassic hagloids (Hagloidea), a semi-extinct superfamily of orthopterid insects related to extant grasshoppers and katydids (Tettigonoidea). The latter finding is of interest not only for the reconstruction of insect feeding habits but also for palynology and plant palaeoecology. *Classopollis* is a characteristic type of Mesozoic pollen showing some angiospermoid (although not necessarily related to angiosperm ancestry) characters (Hughes 1994) and having some palaeoclimatological significance (Vakhrameev 1981; Alvin 1982; Francis 1983; Pocock *et al.* 1990).

MATERIALS AND METHODS

The material came from the Late Jurassic lacustrine marls of Mikhailovka in the Karatau Range, Southern Kazakhstan. The Mikhailovka locality is well-known for its exceptionally rich flora and fauna, the latter including insects, fish and pterosaurs. Its stratigraphy and palaeoecology are described by Hecker (1948) in his monographic study of the Jurassic Karatau Lake. The flora consists of diverse ferns, bennettites and conifers (Doludenko and Orlovskaya 1976) and a few peculiar, achene-like diaspores with pappus (Krassilov 1973). The insect fauna includes abundant orthopterans, of which the genus *Aboilus* Martynov (Prophalangopsidae, Hagloidea, Ensifera) with 12 described, and additional unnamed, species forms a conspicuous element. These large insects are preserved as light brown to yellowish ferruginous impressions with a species-specific pattern of darker bands and spots on the wings, and with the guts often filled with a coaly organic matter.

The gut contents were sampled on several occasions. Small pieces of organic matter were detached with entomological needles, cleaned successively in hydrochloric and hydrofluoric acids, and processed through the Schulze's mixture and potassium hydroxide (strong oxidation was found

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necessary for separating the pollen grains from the amorphous organic matter; more gentle treatment gave less satisfactory results). Pollen clumps and other resistent residues were then mounted for SEM examination.

The material is deposited in the Palaeontological Institute, Russian Academy of Sciences.

INSECTS

Pollen was extracted from two female specimens of *Aboilus*, evidently belonging to different species. In the Karatau material large insects are represented mostly by isolated wings, but there is also a few intact specimens with the intestines well preserved and conspicuous by their coaly infilling.

Since the taxonomy of fossil Hagloidea is based mainly on male stridulatory organs (Gorochov 1995), there are some problems in the taxonomic assignment of females at the specific and even generic level. However, *Aboilus* from the Mikhailovka locality often show well preserved species-specific patterns of dark spots and transverse bands on the forewings, that allow conspecific female and male specimens to be recognized.

Specimen No 2997/317 (Pl. 1, fig. 1) can be assigned provisionally to *A. amplus* Gorochov, one of the largest representatives of the genus, on the basis of its dimensions (forewing about 75 mm long) and the presence of six irregularly arched moderately broad and occasionally interrupted transverse bands, as well as the fairly large additional spots along both costal and anal margins of the forewings. The field between the radial and the median veins near the point of the anterior median vein second branch departure is narrowed, as is also characteristic of *A. amplus* (Gorochov 1995).

The second specimen, No 2904/1675 (Pl. 1, fig. 2) is similar to *A. dilutus* Gorochov in the forewing pattern, with only three incomplete dark bands in the apical half of the wing near the costal margin and numerous irregular spots behind the radial anterior vein. However, our specimen is much larger than the type and only known specimens of *A. dilutus* (with forewing length 65 mm against 48·5 mm in the latter) and may represent a new species. A more precise assignment has to await the discovery of a male specimen with a similar wing pattern.

In both specimens the organic infilling of the guts contained abundant *Classopollis* grains in large clumps (Pl. 1, fig. 5). No other types of pollen or any other distinctive plant remains were found.

POLLEN GRAINS

Pollen grains found in the intestines of *Aboilus amplus* and *A.* cf. *dilutus* do not show any consistent differences and are assumed to belong in a single species of *Classopollis*. The grains are disc-shaped with a central body bordered by an annular equatorial girdle distally marked off with subequatorial groove, or rimula (Pl. 1, figs 3–4) and showing the proximal Y-mark and the distal pore-like depression (pseudopore in Reyre 1970; cryptopore in Taylor and Alvin 1984) typical of the genus (see Couper 1958; Boltenhagen 1968; Reyre 1970; Traverse *et al.* 1975; Pocock *et al.* 1990 for a discussion of the diagnostic features and related nomenclatural problems).

EXPLANATION OF PLATE 1

Fig. 1. *Aboilus amplus* Gorochov; PINRAN 2997/317; insect compression with organically preserved gut content (arrow); × 1.

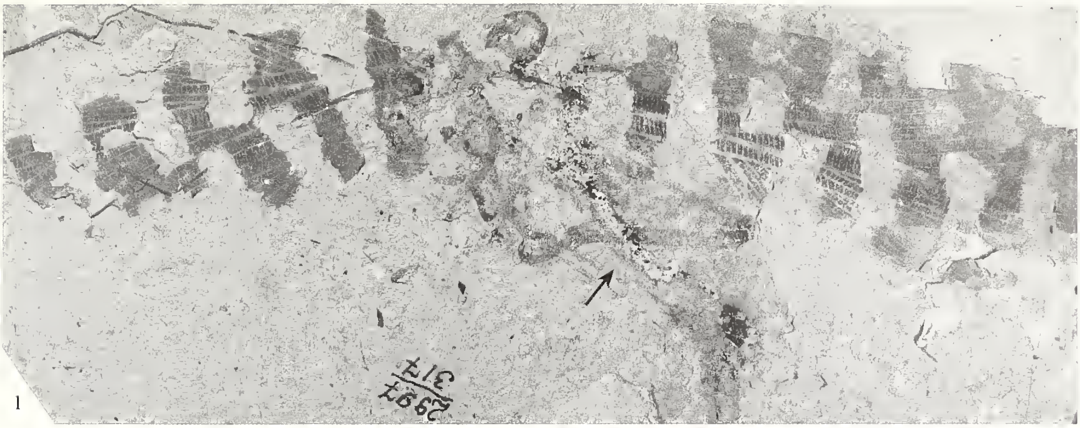
Fig. 2. *Aboilus* cf. *dilutus* Gorochov; PINRAN 2904/1675; insect compression with organically preserved gut content (arrow); × 1.

Fig. 3. *Classopollis* grain from gut of *A. amplus* (fig. 1); distal view (SEM); × 3000.

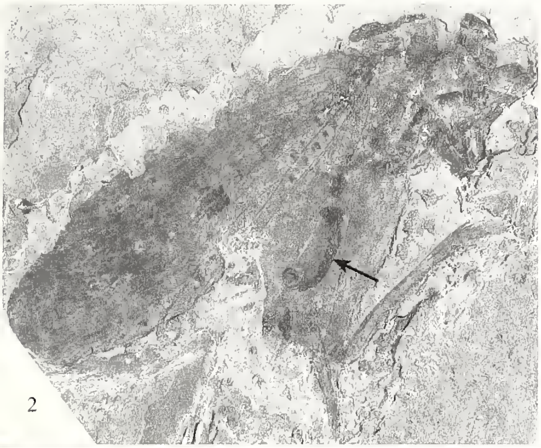
Figs 4–5. *Classopollis* grains from gut of *A.* cf. dilutus (fig. 2); SEMs. 4, distal view; × 3000. 5, clumped grains; × 1700.

All specimens from Mikhailovka, Karatau range, Kazakhstan; Upper Jurassic.

PLATE 1



1



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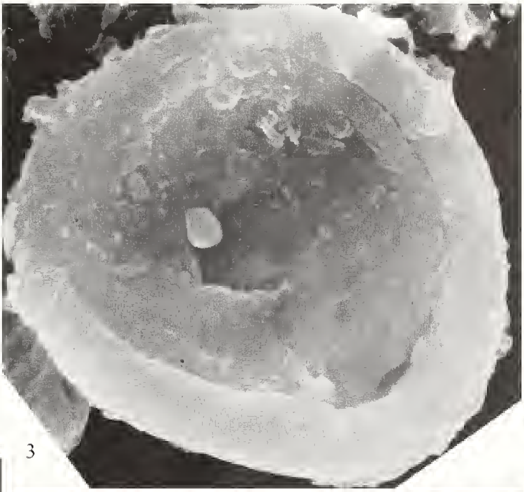


3

4

5

KRASSILOV *et al.*, *Aboilus*, *Classopollis*

The fully developed grains are of a rather uniform size, with the long equatorial axis ranging from 22 μm to 25·5 μm (30 specimens). The smaller grains, 15–20 μm, with a less distinct rimula and distal pore, are considered immature. The equatorial outline is irregular–elliptical, with one end of the ellipse broader than the other, occasionally almost triangular. The girdle is of uniform width, about 3·5 μm. Endostriation normally does not show up on the surface but is occasionally visible in the partly digested grains. The proximal triradiate mark is a triangular area of variable width, 5–9·5 μm. As a rule, a plexus of interconnecting exinal filaments or their remnants protrudes from the Y-mark (Pl. 2, fig. 2). However, in a few specimens the triangular area shows an apparently delicate membrane with small scattered granules (Pl. 2, fig. 3). The rimula is a narrow, occasionally gaping, slit between the central body and equatorial girdle. The distal pore-like structure is a somewhat irregular ellipsoidal depression about 4–5 μm wide, occasionally showing a porous membrane perforated by the dense hexagonal microtubes or micropores (Pl. 2, fig. 1). The grain surface is smooth or minutely scabrate, occasionally showing a rugulate–verrucate pattern, here interpreted as a reflection of infrastructure.

The infrastructure, as seen in fractures of the tectum, consists of conical or clavate columellae, about 1 μm high, distinct or fused and forming a rugulate pattern (Pl. 2, fig. 5). In the grains eroded by intestinal exudates one can see transitions from fully exposed infrastructure to infrastructural elements protruding through the worn-out tectum. The infrastructure is uniformly developed over the central body and the girdle, vanishing in the rimula. Infrastructure of the girdle is traversed by subparallel ridges seen in fractured grains (Pl. 2, fig. 4).

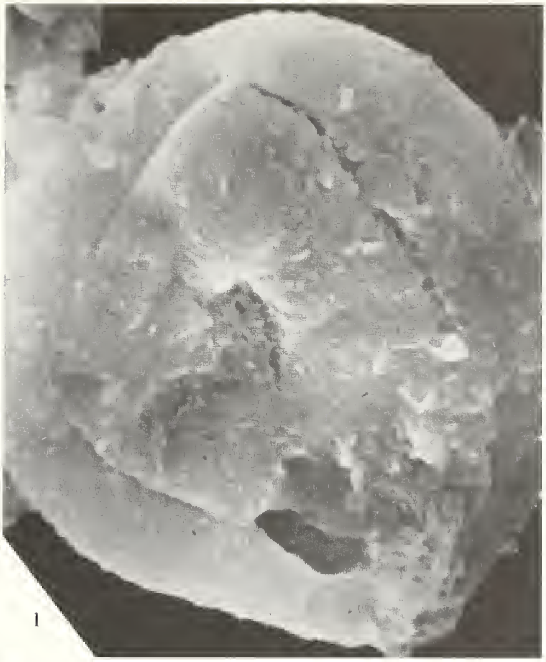
COMMENTS ON THE POLLEN GRAIN MORPHOLOGY

In our material, infrastructure is essentially the same as seen in sectioned *Classopollis* grains (Pettitt and Chaloner 1964; Medus 1977; Taylor and Alvin 1984; Rowley and Srivastava 1986) showing gradations from distinct columellae to a irregular rugulate pattern. Exinal filaments protruding from the proximal Y-mark are a constant feature related to dispersal of intact tetrads or diads (Trevisan 1973; Scheuring 1976; Courtinat 1980). However, neither of these aggregate structures are preserved in the guts. The granular Y-mark membrane is a feature not hitherto reported in *Classopollis*, whereas the microporate membrane of the distal pore favours its interpretation as a germinal aperture.

In contrast with the diverse vegetative morphology of *Classopollis*-producing plants (Watson 1982; Clement-Westerhof and van Konijnenburg-van Cittert 1991; Srinivasan 1995; Zhou 1995), the pollen morphology itself is fairly constant, the variations in the prominence of rimula, distal pore and striation of the girdle being related to the maturity of the grains. Reyre (1970) used surface ornamentation for distinguishing species of dispersed *Classopollis* grains, defining three major structural types as rugulate-verrucate, spinulate (echinulate) and mixed. A comparison of our specimens which show infrastructure with Reyre's examples of rugulate-verrucate and mixed sculptures suggests that the latter might actually reflect infrastructure protruding through the tectum. Our species is comparable to *C. chateaunovii* Reyre, *C. bussonii* Reyre and *C. noeli* Reyre as well as the pollen grains from the cones associated with *Cupressinocladus valdensis* (Seward) Seward (Francis 1983).

EXPLANATION OF PLATE 2

Figs 1–5. *Classopollis* grains from gut of *A. amplus* (Pl. 1, fig. 1); SEMs; Mikhailovka, Karatau Range, Kazakhstan; Upper Jurassic. 1, microporous membrane of distal pore; ×3700. 2, exinal filaments in the proximal Y-mark area; ×3300. 3, proximal view showing Y-mark membrane with granules; ×3000. 4, fractured grain showing endostriation of girdle; ×4000. 5, fractured grain showing infrastructure; ×5300.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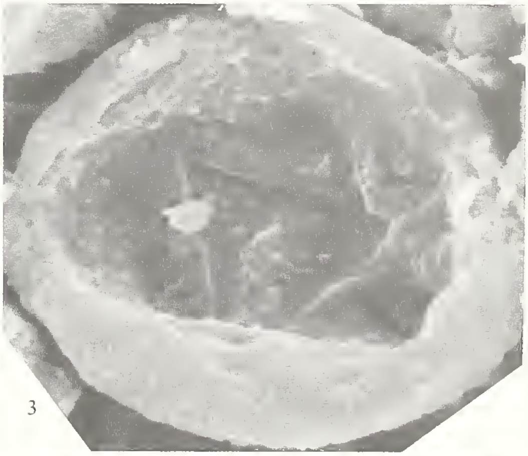
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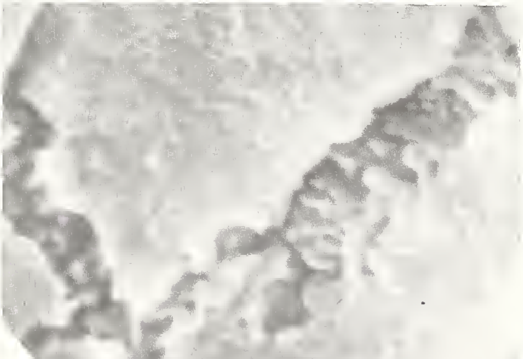
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KRASSILOV *et al.*, *Classopollis*

DISCUSSION

Our findings cast some light on the trophic adaptations of *Aboilus*, the type genus of the extinct subfamily Aboilinae which was widespread in the Jurassic and early Cretaceous. Aboilinae is considered as ancestral to grasshoppers, with the Tettigonioidea (Gorochov 1995) first appearing in the early Cretaceous but remaining rare until the Paleogene. *Aboilus* is similar to the larger extant grasshoppers of the subfamily Cyphoderrinae living in trees or shrubs. However, representatives of the latter are mostly nocturnal whilst *Aboilus* shows a variegated wing pattern more typical of species active in the daylight. Grinfeld (1962), in his extensive studies of insect feeding habits, found that in grasshoppers pollinivory is fairly common. He suggested that pollinivorous adaptations are primary for the family, already appearing in ancestral forms, and that Ensifera, rather than beetles, could have been the most ancient unspecialized pollinators. These suggestions are now receiving some factual support.

That these large insects fed exclusively on *Classopollis* pollen can be taken as evidence of *Classopollis*-producing plants being if not the only then the most abundant pollen source in their habitats. There is little doubt that these habitats were close to the site of deposition, for insects of this size can hardly be transported intact over a considerable distance, either by wind or by water. There is ample evidence (discussed in Francis 1983) of *Classopollis* producers growing in littoral environments. We suggest that the xeromorphic vegetative characters of the *Classopollis*-producing plants are due to littoral adaptations rather than to an arid regional climate. *Classopollis* occurs in both finely laminated marly sediments with gypsum, indicative of seasonal droughts, and coal-bearing polymictic deposits typical of a humid climate (e.g. in the paralic coal basins of Far East Russia and the adjacent Sea of Japan Basin, where these pollen grains constitute up to 80 per cent. of the Lower Cretaceous spore-pollen assemblages). The equatorial girdle and rimula have been interpreted as harmomegathic structures developed in an arid climate (Pocock *et al.* 1990). Alternatively they may have mitigated the effects of long exposure of the pollen when being transferred in larger masses by the slow short distance fliers such as *Aboilus*.

Although pollinivory does not necessarily associate with entomophily, our evidence may strengthen the idea of an animal pollen vector, which has been suggested previously because of the distinctive *Classopollis* morphology (e.g. Pocock *et al.* 1990). Abundance of dispersed *Classopollis* grains may seem more consistent with anemophily than entomophily (Taylor and Alvin 1984). However, entomophilous plants pollinated by pollinivorous insects are known to produce extra pollen for attraction (Faegri and van der Pijl 1966). The same factor might favour the inclosure of ovules and extraovular germination of pollen grains (Krassilov 1982).

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ERRATA

In the article 'Brachidia of late Ordovician and Silurian eospiriferines (Brachiopoda) and the origin of the spiriferides' by Rong Jia-yu and Zhan Ren-bin (*Palaeontology*, **39**, 941–977), the types species of *Eospirifer* was stated (p. 974) to be *Eospirifer praecursor* Rong, Zhan and Han, 1994. The type species of this genus is in fact *Spirifer radiatus* J. de C. Sowerby, 1834.

In the same paper, on p. 970, explanation of Plate 4, details of figure 14 were omitted. These details are as follows: *Eospirifer praecursor* Rong, Zhan and Han, 1994; NIGP124755, the same specimen as illustrated in Pl. 1, figs 1–2, 9, 17; anterior view of conjoined valves; × 8.

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