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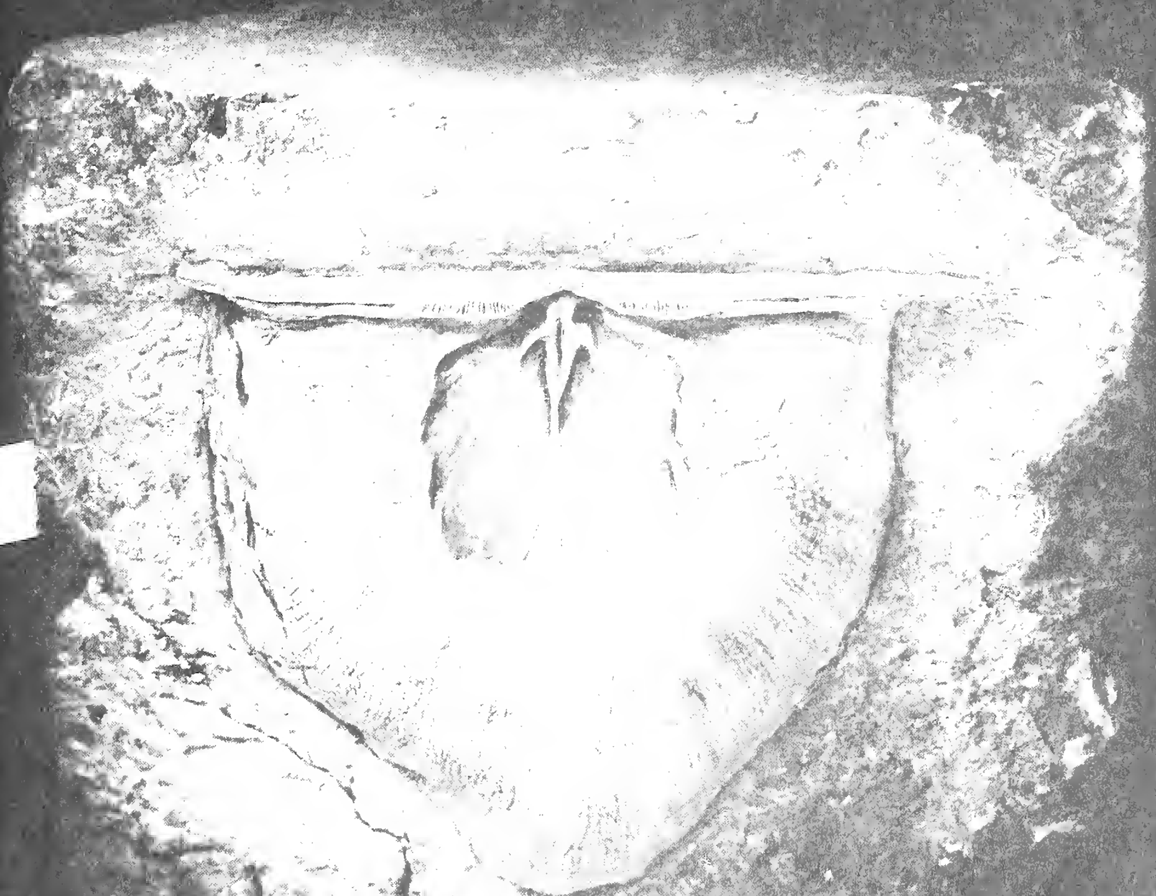

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Cover: Pedicle valve of the brachiopod *Strophonella euglypha* (Dalman, 1828) from the Wenlock Limestone of Dudley, West Midlands; × 2. Photography by Harry Taylor of the British Museum (Natural History) Photographic Studio. One of the specimens illustrated in the *Atlas of Invertebrate Macrofossils* published by the Association.

PROTOCYSTITES MENEVENSIS— A STEM-GROUP CHORDATE (CORNUTA) FROM THE MIDDLE CAMBRIAN OF SOUTH WALES

by R. P. S. JEFFERIES, M. LEWIS *and* S. K. DONOVAN

ABSTRACT. *Protocystites menevensis* Hicks, 1872, from the *Hypagnostus parvifrons* Zone of the Middle Cambrian, near St David's, Dyfed, South Wales, is reconstructed and redescribed. It proves to be a cornute, and therefore a stem-group chordate, representing a plesion intermediate between that of *Ceratocystis perneri* (the most primitive known chordate) and that of *Nevadaecystis americana*. For purposes of reconstruction, tectonic distortion of the fossils was corrected by means of a computer program. The positions of oesophagus, stomach, and intestine are suggested in *P. menevensis* on the basis of skeletal evidence. The locomotory cycle of the animal, which probably crept rearwards over the sea floor pulled by its tail, is deduced.

It is argued that, on a practical definition, every plesion is fundamentally paraphyletic. The term 'more crownward' is used to signify that a plesion is more closely related to the relevant crown group than is some other plesion. The term 'nodal group' is proposed for all those members of a group which possessed all the autapomorphies of the crown group but none of the autapomorphies of any of the subgroups of the crown group.

A comparison between stem chordates and the echinoderms shows that echinoderm 'dorsal' is homologous with chordate ventral and vice versa, so in echinoderms the use of the terms 'dorsal' and 'ventral' should be abandoned.

THE aims of this paper are to redescribe *Protocystites menevensis* Hicks, 1872, from the Middle Cambrian near St David's, Dyfed, Wales; to locate it stratigraphically; to reconstruct its skeletal anatomy, soft parts, and functional morphology; and to determine its systematic position. The species proves to be a stem-group chordate of the group Cornuta. It is the second most primitive cornute known and, at present, the oldest chordate known from Britain. Other interpretations regard *P. menevensis*, and all other cornutes, as echinoderms, e.g. Ubaghs (1967, 1981) and Philip (1979). One of us has argued elsewhere why these various views are mistaken and the arguments will not be repeated here (see Jefferies 1981*a*, *b*, 1986).

The present study of *P. menevensis* began in 1981 when the two junior authors independently examined the lectotype A.1021 in the Sedgwick Museum, Cambridge, and E432 in the British Museum (Natural History). They immediately recognized them as belonging to a species of cornute and several small expeditions to Porth-y-rhaw in 1982 to 1984 yielded much more material. The senior author devoted most of 1984 to reconstructing the animal in detail. The stratigraphical part of this paper results from the work of M. Lewis.

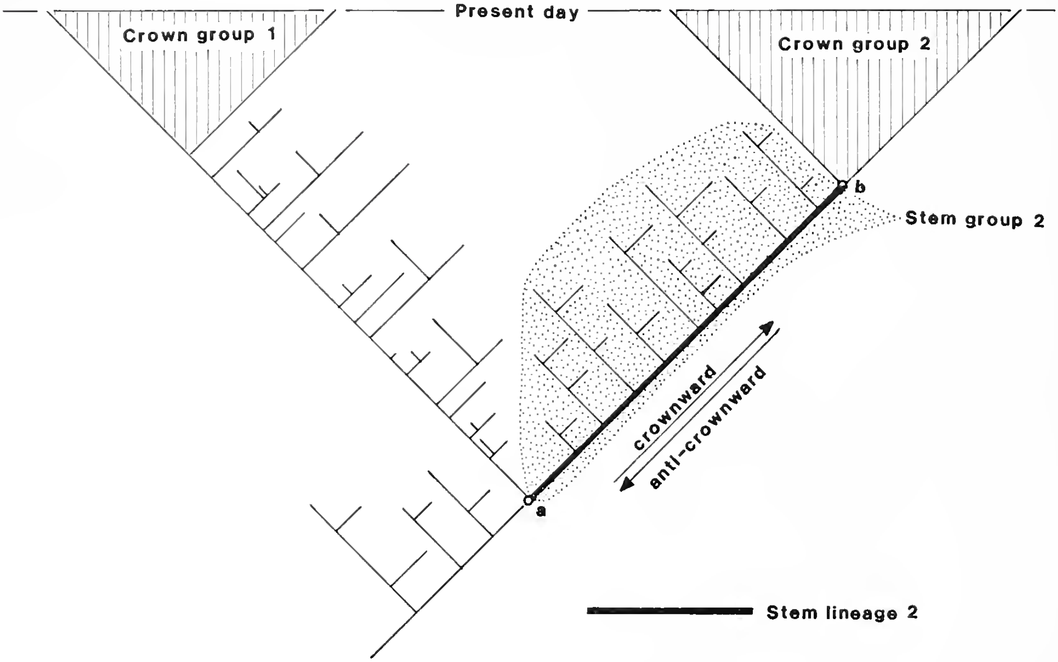
PHYLOGENETIC METHODOLOGY

The terms 'stem group' and 'crown group' as applied in this paper still require explanation (although their use seems to be spreading: Jefferies 1979; Patterson 1981; Smith 1984*a*; Paul and Smith 1984; Thulborn 1984). Given two sister groups (1 and 2) with still extant members (text-fig. 1), there are two obvious ways of delimiting both groups when extinct forms are taken into account. The narrower delimitation of group 2, for example, would include the latest common ancestor of all the living members, *plus* all its descendants, whether living or dead. This delimitation can be called the crown group as proposed in Jefferies (1979)—a term that corresponds to the *group of Hennig

[Palaeontology, Vol. 30, Part 3, 1987, pp. 429–484, pls. 54–60.]

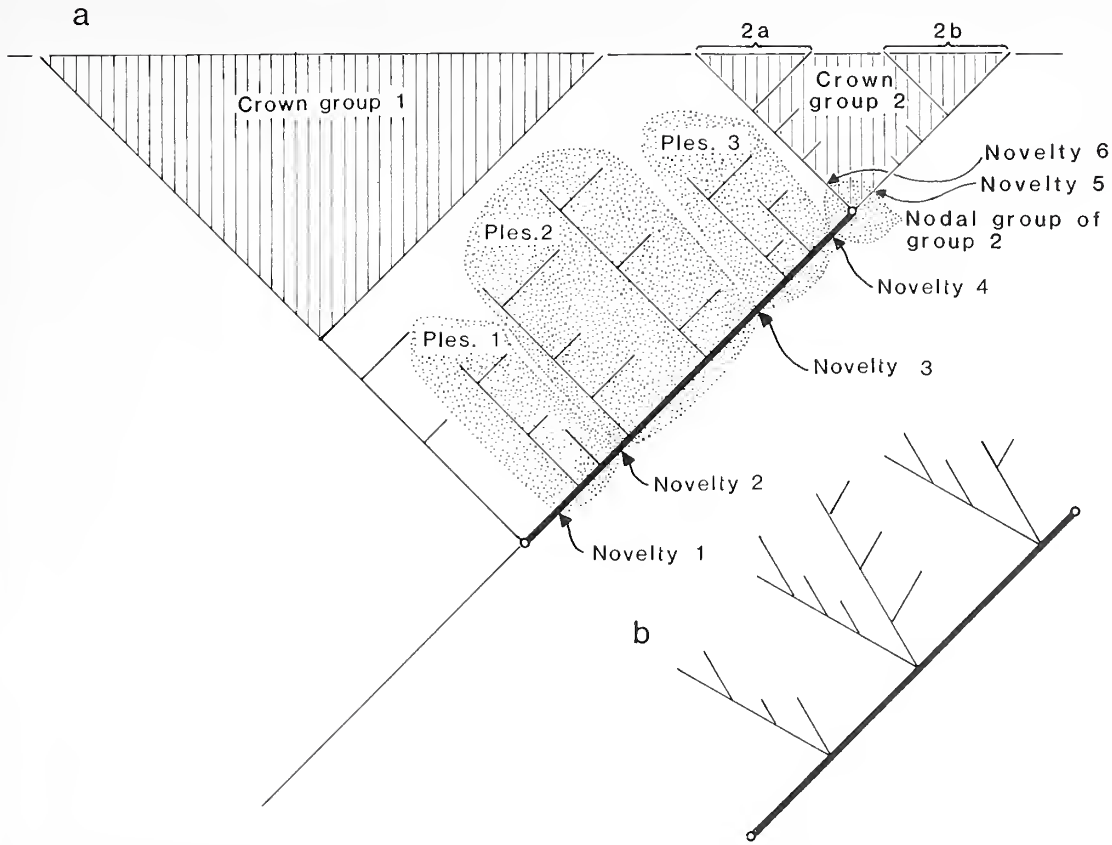
(1969, 1981). The wider delimitation of group 2 would include all descendants of the latest common ancestor of groups 1 and 2 except members of group 1. This delimitation can be called the total group ('Gesamtgruppe' of Hennig). Now, if the crown group of 2 is subtracted from the total group of 2, a paraphyletic ancestral grouping remains which can be called the stem group of 2.

Within this stem group, it is theoretically important to distinguish the stem lineage of 2 (Ax, in press; 'Stammlinie' of Ax 1984)—this, for us, is the lineal sequence of ancestors and descendants which led from the latest common ancestor of [1+2] up to, but not including, the first member of crown group 2, which latter was the latest common ancestor of all living members of 2. (Our usage differs slightly from that of Ax, who includes the latest common ancestor of the living forms in the stem lineage as he defines it.) However, the stem group does not include the stem lineage alone: it also contains the 'side branches'—all descendants of the stem lineage which do not belong to the crown group. Within the stem group, it is possible to conceive of different degrees of relationship to the crown group, and Patterson and Rosen (1977, p. 165) proposed the term 'plesion' for 'fossil groups of species sequenced in a classification according to the convention that each such group is the plesiomorph sister-group of all those, living and fossil, that succeed it . . .'. By thus arranging plesions within the stem group in order of increasing relationship with the crown group, it is possible to reconstruct the sequence of origin of the autapomorphies of the crown group as these evolved within the stem lineage.



TEXT-FIG. 1. Stem group, crown group, and stem lineage. Crown groups 1 and 2 are sister groups with some members still living.

Patterson and Rosen implied, by using the term 'sister-group' in the definition quoted, that plesions are monophyletic. We should like to redefine the word 'plesion', however, to accord more with practical realities, as follows: a plesion includes all, and only, those members of a stem group which, so far as can be discerned, are equally closely related to the crown group. As discussed below, a plesion so defined, if fully known, is necessarily paraphyletic.



TEXT-FIG. 2. The paraphyletic nature of plesions and the position of the nodal group. *a*, the phylogeny of stem group 2 as it actually happened. *b*, cladograms of plesions 1, 2, and 3 so far as reconstructable.

The term 'crownward' has been proposed by Jefferies (1986, p. 13) to mean 'more closely related to the crown group'. Thus, within the stem group of group 2, plesion 3 (of text-fig. 2) is crownward of plesion 2. It is less ambiguous than 'higher', which may indicate stratigraphy, increase in complexity in any direction, or even moral approval; it is also clearer than 'more advanced' since it implies advance towards the crown group along the stem lineage only; and it is better than 'later' which ought to refer only to time. As opposite to crownward, we use 'less crownward' to signify position, or 'anti-crownward' to indicate direction.

To split a stem group into plesions we usually search for a feature shared with the crown group by some members of the stem group, but not by others. However, the feature sought need not be shared with all members of the crown group, since some may secondarily have lost it. And, indeed, a feature shared with more crownward plesions may be used, even when it was later lost within the stem lineage and is therefore primitively absent in the crown group itself. Thus the cornute *Nevadaecystis americana* (Ubaghs, 1963) possesses a strut, in common with more crownward plesions of the chordate stem group such as those of *Cothurnocystis elizae* Bather, 1913 and *Galliaecystis lignieresi* Ubaghs, 1969 (text-fig. 26), but unlike less crownward plesions such as those of *P. menevensis* and *Ceratocystis perneri* Jaeckel, 1900. The strut is a legitimate reason for putting the plesion of *N. americana* more crownward than that of *P. menevensis*. The strut is absent, however, from all mitrates, which are primitive members of the chordate crown group, and is secondarily incomplete in the crownmost members of the chordate stem group, such as the cornute *Reticulocarpos hanusi* Jefferies and Prokop, 1972.

The plesion concept has some difficulties. When a palaeontologist begins to divide a stem group into plesions, each plesion will probably be monospecific, and therefore monophyletic as regards its only known constituent, and this monophyly accords with Patterson's and Rosen's concept of the term plesion. As study proceeds, however, this early false clarity will be lost, because more than one species will come to be assigned to each plesion, and often these species will not share synapomorphies with each other such as would show them to form, on their own, a monophyletic group. Indeed, the stem group can be divided into plesions only to the extent which changes in the stem lineage will allow. The smallest theoretically recognizable segment of a stem lineage will be the sequence of ancestors and descendants lying between one evolutionary novelty and the next more crownward one evolved in the stem lineage, e.g. the segment of the stem lineage within plesion 1, between novelties 1 and 2 in text-fig. 2. All side branches from this segment, together with the segment itself, will necessarily be members of the same plesion, in so far as this term is usable in practice. If, therefore, all members of such a plesion (all its constituent individuals) had come to be known, the plesion would include part of the stem lineage as well as any side branches. And this segment of the stem lineage would be ancestral to forms which did not belong to the plesion, i.e. to more crownward plesions and to the crown group itself. But such a fully known plesion would be paraphyletic by Hennig's definition of paraphyly since, being in part ancestral to non-members, it would have no ancestor common to it alone (Hennig 1966, p. 146). This would remain true, even if the relevant part of the stem lineage was only a single generation. As knowledge advances, therefore, a plesion will change from being monophyletic as regards its single known member species, to being possibly paraphyletic as regards all its known members. On the other hand, as soon as a formerly recognized plesion can be shown to be paraphyletic by demonstrating that an evolutionary novelty evolved within it in the stem lineage, then it will be split into two plesions, one of which will be more crownward than the other. The paradox is therefore reached that a plesion is by its nature paraphyletic, but as soon as it can be *shown* to be so in the particular case, it splits. Also it is possible to show that a particular fossil is *not* a member of the stem lineage if it possesses features which never existed in that lineage. But it is never, or almost never, possible to show that a fossil *was* a member of the stem lineage.

We use the term 'intermediate category' (Hennig's 'Zwischenkategorie') for an overtly paraphyletic grouping of two or more adjacent plesions within a stem group. Such provable paraphyletic groupings may sometimes be convenient to recognize. An example is the group Cornuta for the crownward part of the chordate stem group. (It is still unknown what fossils should be placed less crownward than the cornutes in the chordate stem group.)

We propose the term 'nodal group' for all those members of a monophyletic group which possess all the autapomorphies of the crown group, but are primarily lacking any of the autapomorphies of any of the subgroups of the crown group. Thus, with reference to group 2 in text-fig. 2, the nodal group will show novelty 4 (the last one evolved in the stem lineage of group 2) but will lack novelties 5 and 6 (the first ones evolved in the respective stem lineages of the major subgroups of 2, i.e. 2a and 2b). Thus the nodal group will include the latest common ancestor of the extant members of group 2, and this gives it particular importance, but it will also contain the most crownward parts of the stem group of 2 and the least crownward parts of the stem groups of subgroups 2a and 2b.

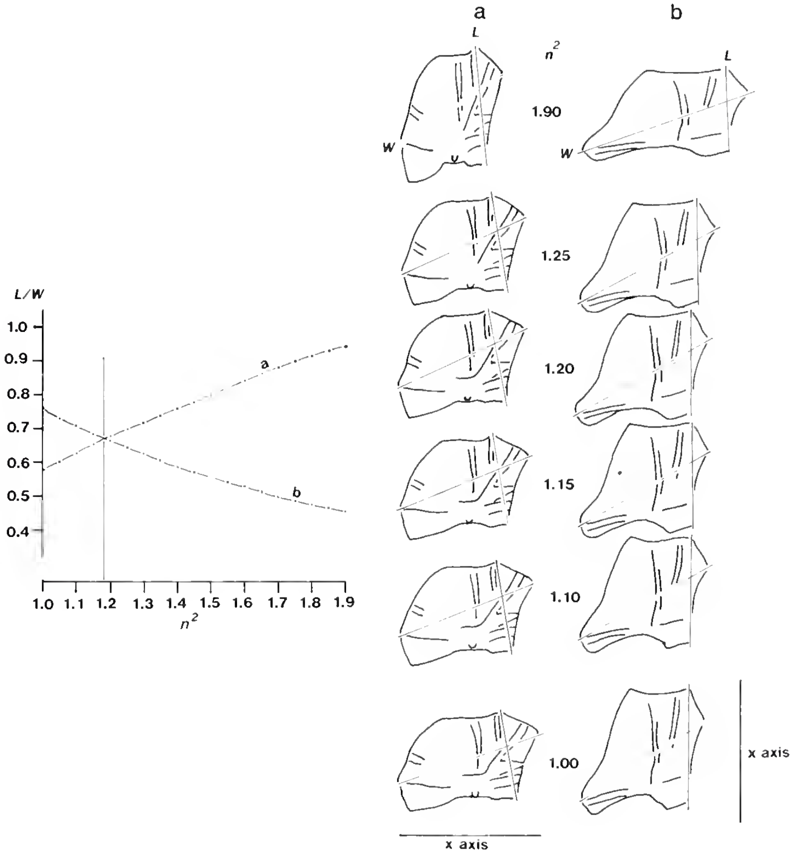
The word 'calcichordate' was proposed by one of us (Jefferies 1967) for any chordate with a calcite skeleton of echinoderm type, and in particular for the cornutes and the mitrates. On these definitions, *P. menevensis* is a calcichordate. However, in the light of Hennig's work (1969, 1981) the 'Calcichordata' form an 'invalid stem group' since the cornutes are stem-group chordates while the mitrates are primitive crown-group chordates (Jefferies 1979, 1986). Consequently, the word 'calcichordate' is best abandoned or, at most, used informally. The word 'Stylophora' (Gill and Caster 1960) is coextensive in meaning with Calcichordata. It should be abandoned for the same reasons, and also because the workers who use it mistakenly regard the cornutes and mitrates as echinoderms and it wrongly implies that the cornute stylocone is homologous with the mitrate styloid.

METHODS OF STUDY

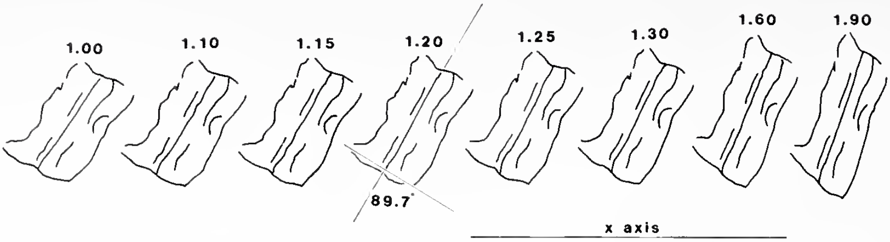
P. menevensis was reconstructed by one of us (R.P.S.J.) on a drawing board, several projections being plotted simultaneously as with previous such studies (e.g. Jefferies 1968, 1969). The specimens were examined by means of latex casts to reconstruct the skeleton, and by direct observation of internal moulds to reconstruct the soft parts. Sometimes pyrite and limonite were removed from the fossils by soaking them overnight in 10% thioglycollic acid; this cleaning allowed much better latex casts to be made.

Correction of distortion

Tectonic distortion made great difficulties. These were partly overcome by means of a computer-graphical method based on suggestions by Appleby and Jones (1976) and Ramsay (1967). The bedding planes of the shale in which the specimens occur are crossed by stretching lineations which give the rock a slight graininess like that of wood. All these lineations run parallel to tight parallel folds in the thinner shelled trilobites and represent the long axis (x-axis) of the strain ellipse for the bedding plane; the direction at right angles to them (y-axis) is the direction of greatest compression in the bedding plane. The original outline of a plate would therefore correspond to the observed outline expanded by some definite factor along the y-axis, perpendicular to the lineations.



TEXT-FIG. 3. Correction of distortion on the basis of two specimens of *P. menevensis* Hicks plate g (see text-fig. 10) compressed approximately perpendicular to each other. The x-axis is the presumed major axis of the strain ellipse. Specimen *a*, BM(NH) E62952; specimen *b*, BM(NH) E62930; n^2, proportionate increase of unit length along the y-axis, relative to the x-axis (further explanation in text).



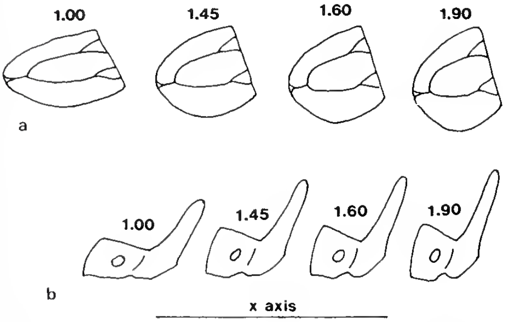
TEXT-FIG. 4. Correction of distortion of a hind-tail ossicle of *P. menevensis* Hicks, BM(NH) E432. The numbers show n^2 (see text).

A computer program was devised by Mr A. J. Paterson of the Biometrics Section, British Museum (Natural History), to modify the observed outlines in the manner required. To use this program, camera-lucida drawings of the specimen were placed on a digitizer with the x-axis (assumed to be parallel to the stretching lineations) arranged parallel to the x-axis of the digitizer. The shape in the drawing was transformed into x–y coordinates by tracing the outline with the cross-wires on the 'puck' (follower) of the digitizer. The y coordinates were then multiplied by a factor n, while the corresponding x coordinates were multiplied by $1/n$. The results of these multiplications were displayed on a visual display unit and simultaneously drawn, as needed, on a plotter. It was also possible to multiply both sets of coordinates by a uniform factor M so that the visual output was magnified to a convenient size. The proportionate increase of the y coordinate relative to the x coordinate was n^2 (since $n \div (1/n) = n^2$).

To decide the appropriate value of n^2, and therefore n, was not easy. With initially symmetrical structures, such as the obliquely distorted heads or tails of trilobites or the tail ossicles of *Protocystites*, the presumed correct value restored the initial symmetry. With asymmetrical structures, such as the head plates of *Protocystites*, it was necessary to find two specimens of the same plate compressed in different directions, preferably at right angles. The appropriate value of n^2 would then be the one that gave the same shape to the two specimens. In fact, this ideal agreement was never achieved, and it was therefore necessary to use some index of shape, such as the ratio of the length of two chosen lines on the plates or the angle of some prominent corner. The appropriate value of n^2 was then the one that gave identical values for the index.

When comparing two specimens of corresponding plates compressed in different directions, a series of computer plots was made for both plates with n^2 increasing at increments of 0·05 from 1·05 to 1·70. Graphs were then drawn of n^2 against the measured value for the chosen index for both plates. The appropriate value of n^2 was that at which the indexes of both plates were equal, i.e. where the lines for the two plates crossed each other on the graph. At this value, the computer plot was presumed to show the original shape of the plate.

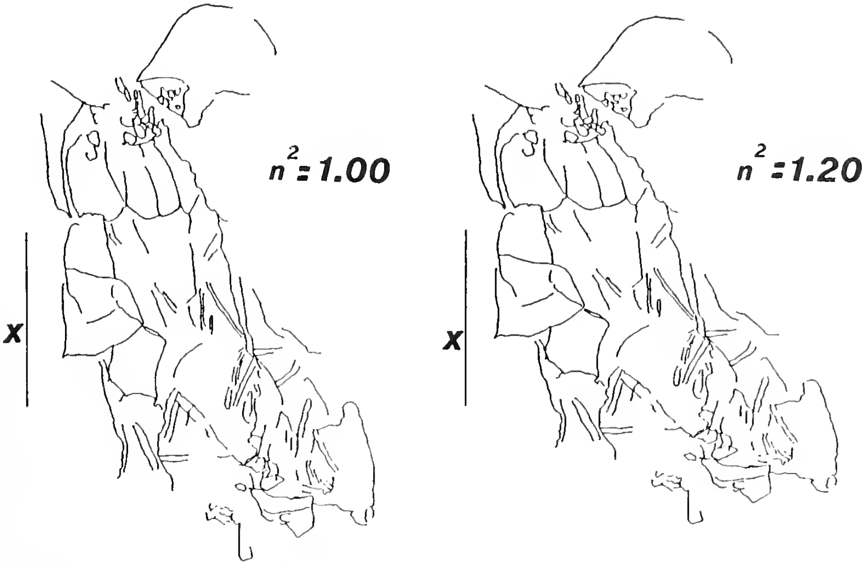
The deduced values for n^2 are not uniform. Three head plates (e, g, and k on text-fig. 10) gave values of n^2 close to 1·20 (text-fig. 3). The same value was found to hold for an isolated hind-tail ossicle (text-fig. 4) and for the hind-tail ossicles of the lectotype (designated below). On the other hand, two specimens of the left



TEXT-FIG. 5. Correction of distortion for two trilobite cephalons. *a*, *Ptychagnostus*. *b*, *Eodiscus*. The numbers show n^2 (see text).

process (the process on plate 1), which was thin and is sometimes visibly crumpled, required a higher value of n^2 at about 1·60. The same value was required to restore symmetry to the trilobite *Eodiscus* (text-fig. 5*b*) whereas a specimen of the cephalon of *Ptychagnostus* (text-fig. 5*a*) became symmetrical at about $n^2 = 1{\cdot}15$. The highest values of n^2, as shown by the trilobite *Eodiscus*, probably approach the distortion of the matrix itself, whereas the lower values usually shown by the skeleton of *Protocystites menevensis* suggest that stereom calcite or its pyritic replacement was, because of its strength, less distorted than the surrounding rock. Indeed many specimens of *P. menevensis* seem to have responded to tectonic pressure by the plates sliding over or against each other, as well as by changing their outline. Sometimes adjacent tail ossicles have been pushed against each other, causing very high local pressures and non-homogeneous distortion, as testified by highly asymmetrical outlines. It is impossible to make proper allowance for these variations.

The reconstructions are therefore based on computer plots with $n^2 = 1{\cdot}20$ ($n = 1{\cdot}095$) which seems to be correct for the tougher parts of the head and tail skeleton of *P. menevensis* (cf. text-fig. 6). The results are probably better than those that would be obtained using uncorrected drawings of the specimens. Nevertheless, there is uncertainty about the shapes of the plates and the relative sizes of different parts of the animal, and this must be remembered in considering the reconstructions.



TEXT-FIG. 6. *Protocystites menevensis* Hicks; uncorrected and corrected drawings of BM(NH) E62963 (ventral aspect). The numbers show n^2 (see text).

Distortion perpendicular to the bedding planes is an even bigger problem than distortion in the plane of bedding. Thin parts of the skeleton, which originally stood almost vertical, and thus perpendicular to the bedding plane, have sometimes been squashed flat on to the bedding plane. This is particularly true of the posterior wall of the head in plates f, g, j, and k (see text-fig. 10). To obtain some idea of the original shape of these plates, replicas based on computer plots with $n^2 = 1{\cdot}20$ were cut in aluminium sheet and bent to the likely original shape in three dimensions. Once again, the results are uncertain, so that the vertical dimension of the reconstructions is not reliable.

Tectonic distortion can thus be partly, but not totally, corrected; better reconstructions will require undistorted material (which may never be found). It is remarkable that tectonic distortion has not destroyed the histology of the plates, for the superficial features of different types of stereom can readily be recognized. (The three-dimensional structure of the stereom is not usually deducible.)

SYSTEMATIC PALAEONTOLOGY

Superphylum DEUTEROSTOMIA Grobben, 1908
Subsuperphylum DEXIOTHETICA Jefferies, 1979
Phylum CHORDATA Bateson, 1886
[Stem group of the Chordata]
Intermediate category CORNUTA Jaekel, 1901
Plesion of *Protocystites menevensis* herein
Genus PROTOCYSTITES Hicks, 1872

Type species. *P. menevensis* Hicks, 1872, by monotypy.

Systematic position. The above statement of systematic position is unorthodox. We deliberately have not placed *P. menevensis* in a family because it is at present alone in its plesion. Any family which included it, therefore, would either be: 1, coextensive with the species *P. menevensis* and therefore redundant; or 2, it would include one or more of the adjacent plesions of the chordate stem group—it would thus be overtly paraphyletic and (unlike the overtly paraphyletic grouping Cornuta, for example) would, in our opinion, never be a useful grouping in practice. Another unorthodoxy is that the intermediate category Cornuta is here given no conventional Linnaean rank. This omission is likewise deliberate and is based on the fact that nobody has yet explained how Linnaean rank can objectively be assigned, particularly to paraphyletic groupings of fossils (Ax, 1984, Ch. K; Ax, in press). Those ranks which are assigned above are either hallowed, though not validated, by long usage (superphylum, phylum) or else are obtained by interpolation (subsuperphylum).

Protocystites menevensis Hicks, 1872

Plates 54–60; text-figs. 6, 10, 15–19, 23–25

1866 *Protocystites* Salter *in* Hicks and Salter, p. 285 (*nom. nud.*).
1871 *Protocystites menevensis* Hicks *in* Harkness and Hicks, p. 396 (*nom. nud.*).
1872 *Protocystites menevensis* Hicks, pl. 5, fig. 19; p. 180 (lower illustration only).
1873 *Protocystites menevensis* Hicks; Salter, p. 3.
1887 *Protocystites meneviensis* Hicks; Barrande, p. 10.
1900 *Protocystis* Hicks; Bather, p. 48.
1943 *Protocystites meneviensis* Hicks; Bassler and Moody, p. 184.
1967 *Protocystites* Hicks; Ubaghs, p. S493.
1967 *Protocystites meneviensis* Hicks; Paul *in* Jefferies *et al.*, p. 567.
1979 *Protocystites meneviensis* Hicks; Paul, p. 453.

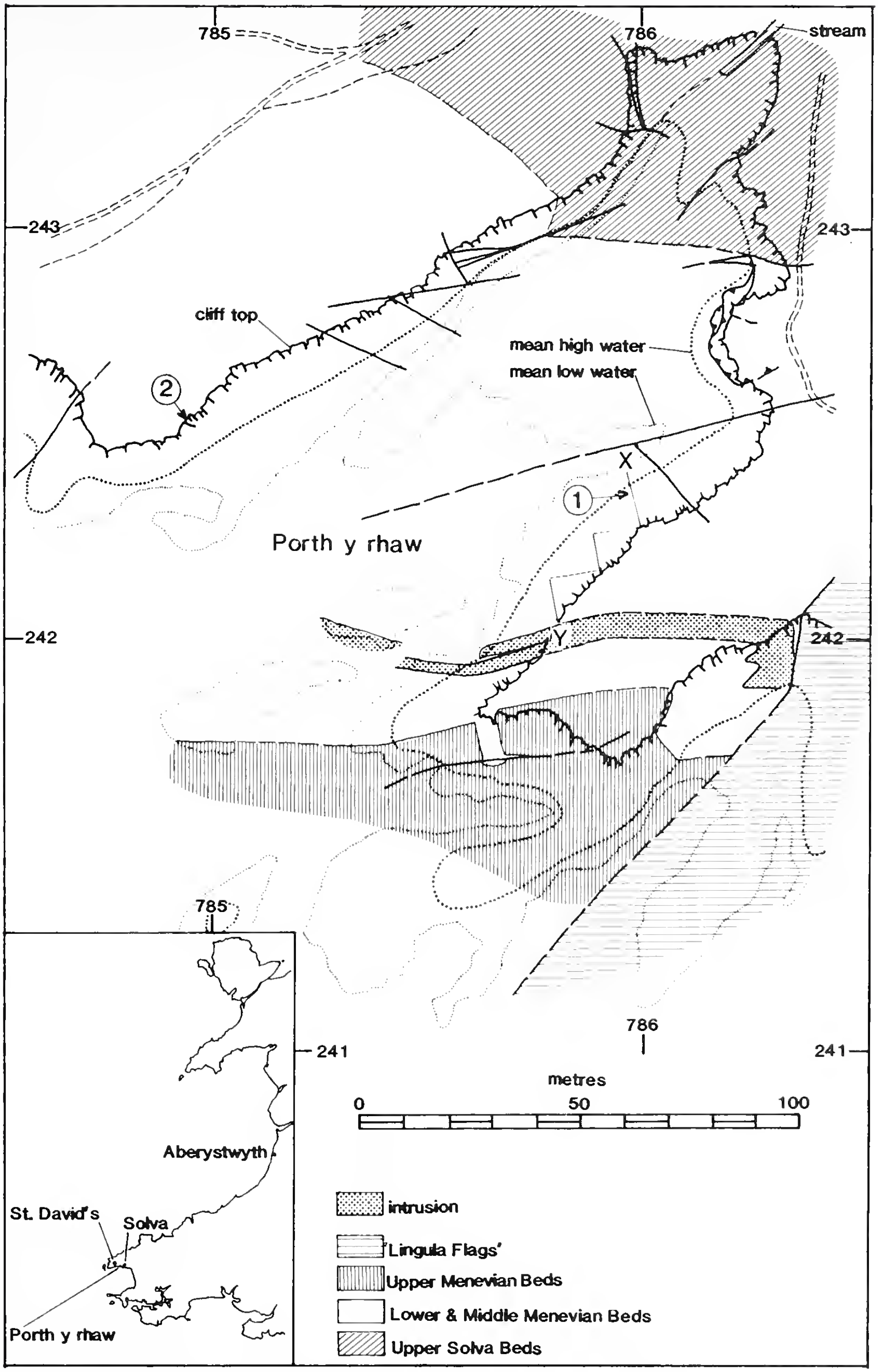
Comments on synonymy. The only previous figure and description of *Protocystites menevensis* was that of Hicks (1872). His illustration shows two specimens which can be identified with specimens A.1021 and A.1022 now held in the Sedgwick Museum, Cambridge. Of these, A.1022 is the operculum of a hyolithid, whereas A.1021 is a fairly good specimen of the species described in this paper and is here designated as lectotype (text-figs. 17 and 18; Pl. 56, figs. 1–3; Pl. 57, figs. 1 and 2). Hicks's figure is very poor and the species is not recognizable from it. Subsequent references to the species or genus, therefore, add nothing to knowledge and are of purely bibliographic interest.

The name *Protocystites* must not be confused with *Proteocystites* Barrande, 1887 which is a diplorite cystoid (see e.g. Kesling 1967, p. S248) and an echinoderm.

Material, horizon, and locality. The material examined is as follows:

(*a*) Sedgwick Museum, Cambridge: A.1021 (here chosen as lectotype) *ex* Hicks Collection, locality Porth-y-rhaw near St David's, Dyfed, horizon Menevian. Figured by Hicks (1872, pl. 5, fig. 19, lower figured specimen only) (text-figs. 17 and 18; Pl. 56, figs. 1–3; Pl. 57, figs. 1 and 2).

(*b*) British Museum (Natural History), London: i, old material, E432 *ex* Hicks Collection, locality St David's, horizon Menevian (text-fig. 19; Pl. 58, fig. 1); ii, new material, E62912–E62921, E62923–E62925, all from loc. 1, Porth-y-rhaw (text-figs. 7 and 8), horizon middle part of *Hypagnostus parvifrons* Zone, Middle Menevian; iii, also new material, E62926–E62934, E62937–E62939, E62942–E62945, E62950, E62952, E62955–E62966, E62968–E62981, E63006–E63056, all from loc. 2, Porth-y-rhaw (text-fig. 7), horizon nearly or exactly the same as for loc. 1.



TEXT-FIG. 7. Geology and topography of Porth-y-rhaw, Dyfed, Wales. 1 and 2 are the localities that produced the new material of *Protocystites menevensis* Hicks. X and Y are respectively the lower and upper ends of the composite profile shown in text-fig. 8.

(*c*) National Museum of Wales, Cardiff: NMW.80.34G.948–958, all from loc. 1, Porth-y-rhaw, same horizon as BM(NH) material from that locality.

Most of the material consists of dissociated plates. All of it is tectonically distorted. Articulated specimens include SM A.1021 (lectotype) and BM(NH) E432, E62950, E62952, E62963 (the most instructive specimen; text-figs. 6, 15, 16; Pl. 54, figs. 1–3; Pl. 55, figs. 1 and 2), E62977, E62979.

Porth-y-rhaw, from which all the recently found material came (our locs. 1 and 2; text-figs. 7 and 8) (as also did one, or perhaps both, of the two nineteenth-century specimens), is a small inlet situated on the coast of Dyfed, Wales, about 3·6 km east-south-east of the cathedral of St David's and about 1·5 km west of Solva Harbour (text-fig. 7). The east side of Porth-y-rhaw (including our loc. 1) is the type section (text-fig. 8) of the Menevian Group of Hicks and Salter (1866). It was on this eastern side that Salter discovered *Paradoxides davidis* Salter, 1863 and its associated fauna in 1862, by chance, as a result of misnavigation. Text-fig. 9 shows the now accepted stratigraphical divisions for the Middle Cambrian near St David's.

Loc. 1 is on the eastern cliff section, Porth-y-rhaw (NGR SM 78596 24235), middle part of *H. parvifrons* Zone, at shore level, stratigraphically *c.* 22–24 m below the basal contact of two, almost vertical, 4 m thick sills and approximately 10–12 m stratigraphically below the local base of the *Ptychagnostus punctuosus* Zone (text-figs. 7 and 8). The nature and distribution of the fauna is shown in text-fig. 8.

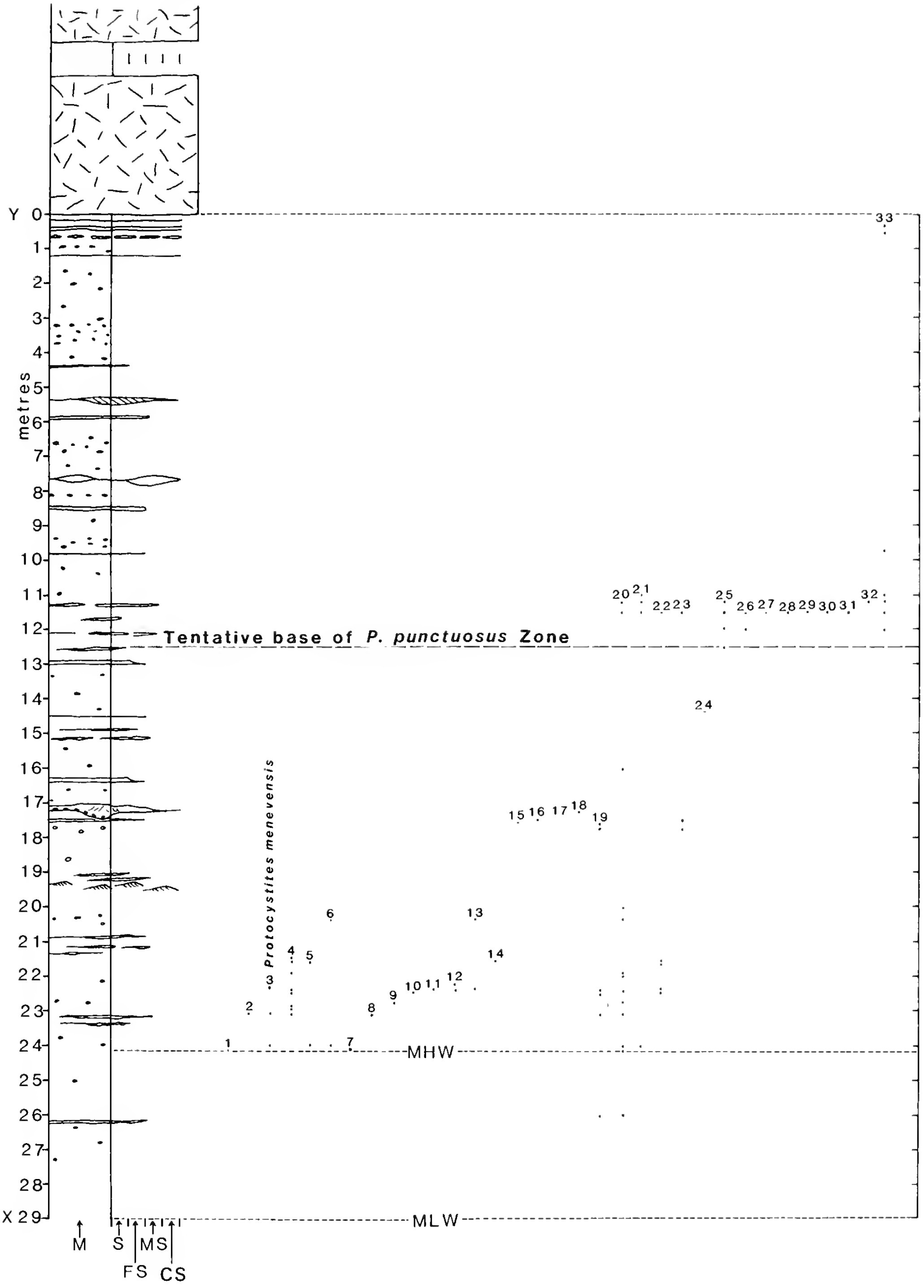
Loc. 2 (text-fig. 7) is on the western cliff section, also in the *H. parvifrons* Zone at or near the same horizon as loc. 1, just above the cliff top near the southern end of Porth-y-rhaw (NGR SM 78492 24252). Here the beds are less cleaved and more suitably weathered for yielding fossils than at loc. 1. In addition to *Protocystites menevensis*, the fauna here comprises the trilobites *Ptychagnostus ciceroides* (Matthew, 1896), *P. davidis* (Hicks, 1872), *P. punctuosus affinis* (Brögger, 1878), *P. punctuosus* s.l. (Angelin, 1851), *Cotalagnostus lens* (Grönwall, 1902), *Phalacroma bibullatum* (Barrande, 1846), *Peronopsis scutalis scutalis* (Hicks, 1872), *P. fallax depressa* Westergård, 1946, *Phalagnostus* cf. *nudus* (Beyrich, 1845), *Eodiscus punctatus punctatus* (Salter, 1864), *Agraulos longicephalus* (Hicks, 1872), *Jincella applanata* (Hicks, 1872), *Hartshillina spinata* (Illing, 1916), *Clarella salteri* (Hicks *in* Salter, 1865), *Acontheus* n. sp. aff. *A. inarmatus* Hutchinson, 1962, and a pagetiid (new genus); and the non-trilobite fossils *Linnarssonia sagittalis* (Davidson, 1871), *Lingulella* sp., *Hyolithes corrugatus* (Salter, 1864), *Stenotheca cornucopia* Hicks, 1872, *Protospongia fenestrata* Salter, 1864, and *Ctenocystis* sp. The record of *Ctenocystis* sp. is of interest as being the only known occurrence of the genus in Britain.

In the western cliff section, where loc. 2 is situated, the stratigraphically overlying *punctuosus* Zone seems to be unrepresented and the base of the *parvifrons* Zone could not be located exactly. However, evidence of the underlying *Tomagnostus fissus–Ptychagnostus atavus* Zone was found 40 m stratigraphically below loc. 2. As already stated, some 12 m of the *parvifrons* Zone exists in the eastern cliff section above the horizon of loc. 1 (text-fig. 8). If the horizons of locs. 1 and 2 are identical, therefore, the greatest possible thickness of the *parvifrons* Zone at Porth-y-rhaw is $12+40 = c.\ 52$ m.

In biostratigraphic terms, 'Menevian' (text-fig. 9) conventionally refers to the traditional zones of *Paradoxides hicksii* and *P. davidis* and possibly other zones. References covering the most important faunas in the Menevian Group include Salter (1863, 1864, 1865), Salter and Hicks (1867, 1869), Hicks *in* Harkness and Hicks (1871), and Hicks and Jones (1872). Most of the trilobites were redescribed by Lake (1906–1946) and they indicate the presence of the *fissus*, *parvifrons*, and *punctuosus* zones of Scandinavian terminology.

The term 'Lower Menevian' is equivalent to the *hicksii* Zone of authors, which can be equated approximately with the *fissus–atavus* Zone of Sweden. *P. hicksii* is here considered a probable senior subjective synonym of

TEXT-FIG. 8. Stratigraphic log of the beds exposed on the foreshore on the eastern side of Porth-y-rhaw, between points X and Y of text-fig. 7, and a complete list of the fossils found in that section. The profile is a composite, built up from three separate sections as shown in text-fig. 7. Locality 1 is at 22–24 m below the lower dolerite sill and is just above mean high-water mark. Abbreviations: M, mud; S, silt; FS, fine sand; MS, medium sand; CS, coarse sand; MHW, mean high water; MLW, mean low water; 1, *Hyolithes* sp.; 2, *Ptychagnostus punctuosus affinis*; 3, *Protocystites menevensis*; 4, pagetiid gen. et sp. nov.; 5, *Linnarssonia sagittalis*; 6, centropleurine fragments; 7, *Meneviella* sp. indet.; 8, *Ptychagnostus punctuosus* s.l.; 9, *Acontheus* sp. nov.; 10, *P. davidis*; 11, *H. corrugatus*; 12, *Jincella applanata*; 13, *Peronopsis fallax depressa*; 14, *Protospongia* sp.; 15, conocoryphid gen. et sp. indet.; 16, *Peronopsis* sp.; 17, *M.* cf. *venulosa*; 18, '*Leperditia*' *hicksi*; 19, *P. scutalis scutalis*; 20, *Eodiscus punctatus punctatus*; 21, *Cotalagnostus lens* (s.l.); 22, *Ptychagnostus ciceroides*; 23, *M. venulosa*; 24, *Clarella* sp.; 25, *P. punctuosus punctuosus*; 26, *Anopolenus henrici*; 27, *Peronopsis* ex gr. *fallax*; 28, *Pleuroctenium* cf. *bifurcatum*; 29, *Holocephalina* cf. *primordialis*; 30, *Phalagnostus* cf. *nudus*; 31, *Solenopleurina variolaris*; 32, *Pseudoperonopsis* sp.; 33, *Paradoxides davidis*.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Tentative base of P. punctuosus Zone
Protocystites menevensis
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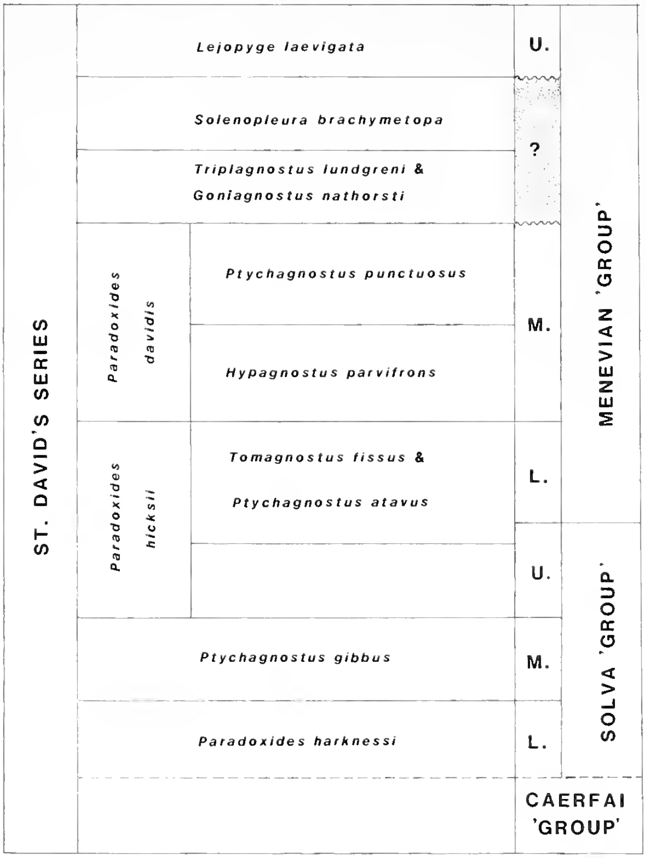


TEXT-FIG. 9. Stratigraphical subdivisions of the Middle Cambrian of St David's (modified after Cowie *et al.* 1972). The zones of *Paradoxides hicksii* and *P. davidis* are traditional for the South Welsh area; those shown to their right are the equivalent zones of the Scandinavian succession. The traditional zones are shown here with their traditional extent, although *P. davidis* at Porth-y-rhaw is in fact unknown outside the *Ptychagnostus punctuosus* Zone.

P. aurora Salter *in* Salter and Hicks (1869), and its range is extended downwards to the base of the Upper Solva Beds. The Lower Menevian Beds, estimated by Hicks (1881, p. 299) to be 300 ft (91 m) thick, consist of light-grey and dark-grey laminated mudstones which suffered soft sediment deformation in the lower part. Towards the top of the division are some greenish mudstone units, lithologically similar to the Upper Caered Mudstones (Nicholas 1916) of St Tudwal's Peninsula, North Wales.

The Middle Menevian Beds were estimated by Hicks (1881, p. 299) and by Stead and Williams (1971, p. 181) to be 350 ft (107 m) thick, although a precise boundary between these and the Lower Menevian Beds was not defined by these authors. The Middle Menevian Beds are darker and more uniform in colour than the Lower Menevian Beds and consist of cleaved pyritic mudstones with occasional thin, sometimes lenticular, sandy horizons and several thin (< 10 cm) pale beds which, according to Nicholas (1916, p. 99) are composed of ashy material. Certain beds contain numerous small flattened phosphatic nodules, and these and the Lower Menevian strata appear to have been deposited in a euxinic environment (Rushton 1974, p. 90). In biostratigraphic terms 'Middle Menevian' is equivalent to the *davidis* Zone of certain authors, which corresponds approximately to the *parvifrons* and *punctuosus* zones of Scandinavian nomenclature (text-fig. 9). The species *P. davidis*, however, seems at Porth-y-rhaw to be confined to the *punctuosus* Zone.

The Upper Menevian Beds at Porth-y-rhaw abruptly succeed the Middle Menevian beds and comprise coarse, dark-grey sandstones with shaly interbeds. These sandstones, exposed at the tip of the eastern headland of Porth-y-rhaw (text-fig. 7), are massive. They form beds up to 1 m thick at the base of the unit and seem to mark the initiation of deposition from current-agitated water or from turbidity currents. This style of deposition continued into '*Lingula* Flags' times (Rushton 1974, p. 90).

The Upper Menevian Beds of Porth-y-rhaw were said to be 100 ft (30 m) thick by Hicks (1881, p. 299) and Stead and Williams (1971, p. 81) but these authors did not define an upper limit. The sandstones contain '*Billingsella*' *hicksi* (Davidson) and other brachiopods and are commonly referred to as '*Orthis*' *hicksi* Beds.

Hicks (1892, p. 22) collected *Paradoxides* and a new species of '*Conocoryphe*' from them. These identifications suggest that the Upper Menevian of this locality may partly correspond to the *P. forchhammeri* 'Stage' of the Scandinavian sequence.

Stead and Williams (1971, p. 188) believed that the junction between Middle and Upper Menevian beds was conformable. However, Taylor and Rushton (1972, p. 9) suggested a widespread non-sequence at this level in England, Wales, and south-eastern Newfoundland caused by a regression during the time of the *Solenopleura brachymetopa* Zone.

As to correlation, the beds of the *parvifrons* Zone are correlated with: the upper part of the Nant-pig Mudstones of St Tudwal's Peninsula, North Wales (Rushton 1974, p. 72; after Nicholas 1916); Illing's (1916) horizons F1–F3, representing the *parvifrons* Zone in the Abbey Shales of Warwickshire (Rushton 1979, p. 43); beds in the lower part of the Clogau Formation in the Harlech Dome, North Wales (Allen *et al.* 1981, p. 303); the lower part of the *davidis* Zone in the Manuels River Formation, south-eastern Newfoundland (Hutchinson 1962); and the *parvifrons* Zone of Scandinavia (summarized by Martinsson 1974). Thomas *et al.* (1984, p. 888) discussed the distribution of the various trilobite species in these rocks.

The lithostratigraphical terminology used for the rocks of Porth-y-rhaw in this paper is in need of revision, but it is not appropriate to make this revision here.

Thus the total stratigraphical range of *Protocystites menevensis* is not known, although all of the abundant new material comes from the middle part of the *parvifrons* Zone of the Middle Menevian. The horizon of the lectotype cannot be ascertained exactly, beyond the fact that it came from the Menevian of Porth-y-rhaw. Harkness and Hicks (1871, p. 396) recorded the species from both Lower and Middle Menevian Beds but this does not tally with our experience.

Preservation and conditions of deposition. The plates of *P. menevensis* and *Ctenocystis* have been completely replaced by pyrite (often converted to limonite), or are represented by air-filled holes. No trace of calcite remains. The superficial histological detail is well preserved so that it is possible to recognize the surface features of different types of stereom. On the other hand, all the plates have been distorted tectonically and are often squashed on to the bedding planes.

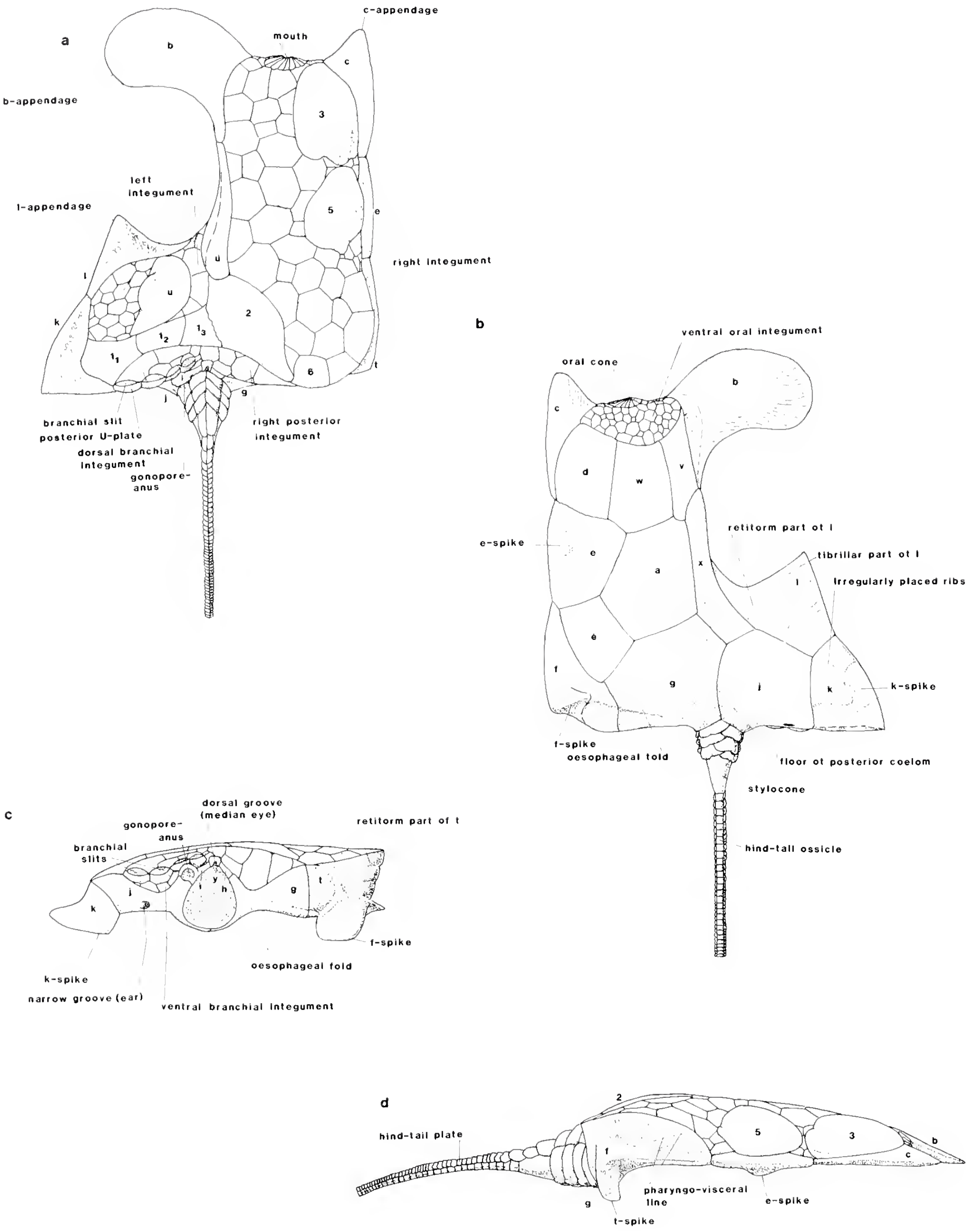
On the sea-floor, the black shale matrix was probably a stinking black mud. However, there is abundant benthos which indicates that the bottom water was usually oxygenated. Conditions may have resembled those of the German Lower Devonian Hunsrückschiefer, which are similarly black with abundant pyritized benthic fossils. Seilacher and Hemleben (1966) have argued, on the basis mainly of trace fossils, that the Hunsrückschiefer were normally laid down in oxygenated bottom water, but that sometimes the bottom water lost its oxygen, asphyxiating the benthos. The same may have been true of the sea in which *P. menevensis* lived. As we show later, the species is adapted to staying up on extremely soft mud.

Anatomical description

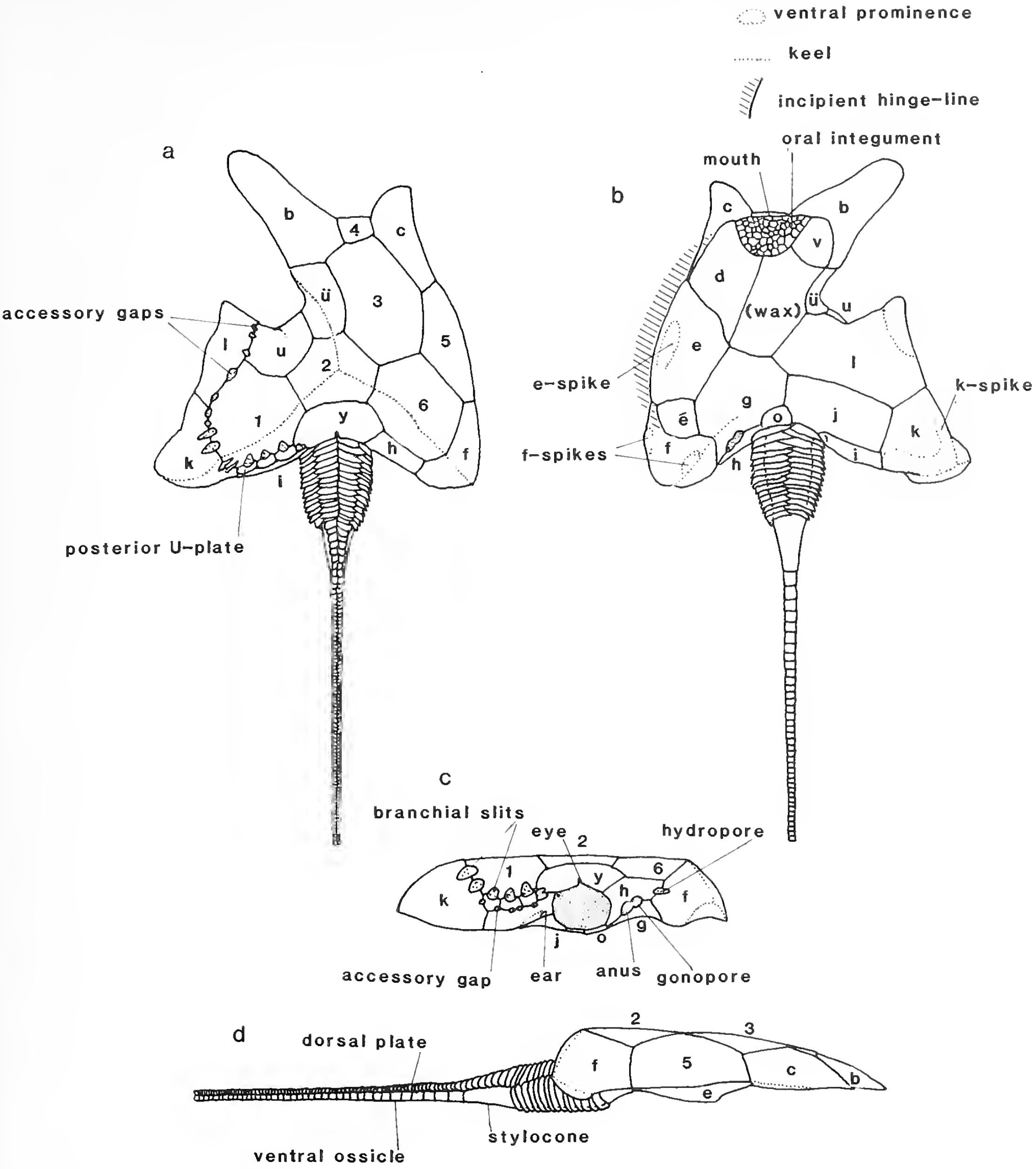
Introduction. In describing the anatomy of *P. menevensis* we frequently refer, in passing, to related species, since without comparison morphological features have little significance. The particular species compared are: *Ceratocystis perneri* Jaekel from the Middle Cambrian of Bohemia, Czechoslovakia (text-fig. 11); *Nevadaecystis americana* (Ubaghs) from the Upper Cambrian of Nevada (text-fig. 12); *Cothurnocystis elizae* Bather from the Upper Ordovician of Scotland (text-fig. 14); and '*C.*' *fellinensis* Ubaghs, 1969 from the Lower Ordovician of the South of France (text-fig. 13).

To anticipate the arguments given below under 'Systematic Position', *Ceratocystis perneri* is less crownward (less closely related to the chordate crown group) than *P. menevensis*, and in many respects shows the most primitive condition among known cornutes; *N. americana* is more crownward than *P. menevensis*; '*Cothurnocystis*' *fellinensis* is more crownward than *N. americana*; and *C. elizae* is more crownward than '*C.*' *fellinensis* (text-fig. 26). These conclusions are mentioned early so that the anatomical description, which is comparative, will be easier to understand. It is unfortunate that *N. americana* is known only from one specimen and that the floor of the head is not visible from beneath, though partly visible from above.

As regards plate notation, one of us used to employ an objective system (Jefferies 1968) in which marginal plates were numbered from the anterior end of the tail and were given suffixes for left and right, dorsal and ventral (e.g. M_{1LD} was the first left dorsal marginal plate). This system was explicitly intended not to imply homology, so that marginal M_{3L} of *C. elizae*, for example, was not homologous with M_{3L} of *N. americana*—they correspond, respectively, to plates t and l of the comparative notation. In earlier studies of cornutes and mitrates, such an objective system was necessary. However, comparative anatomy depends on recognizing and naming homologies, accepting the risk of thereby making mistakes. Accordingly, a comparative, non-objective plate notation was proposed by Jefferies and Prokop (1972) when describing the crownward cornute

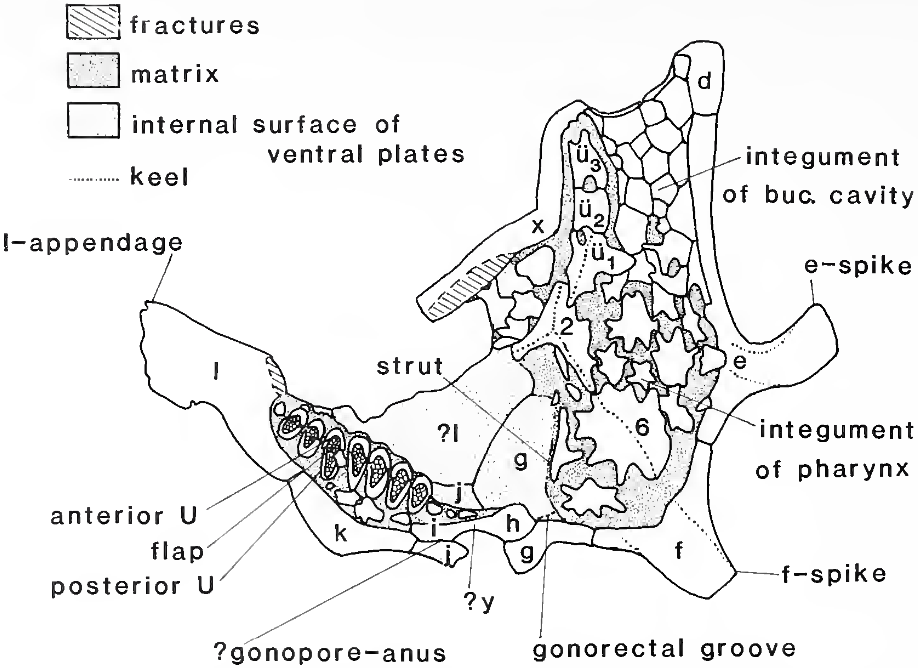


TEXT-FIG. 10. *Protocystites menevensis* Hicks; reconstructed external morphology. *a*, dorsal; *b*, ventral; *c*, posterior; and *d*, right lateral aspects. Letters a–w, é, ü, and numbers 1, 2, 3, 5, 6 indicate plate homologies as explained in text. The exact number of branchial slits is not known.



TEXT-FIG. 11. *Ceratocystis perneri* Jaekel; reconstructed external morphology. *a*, dorsal; *b*, ventral; *c*, posterior; and *d*, right lateral aspects.

Reticulocarpos hanusi. In this notation, marginal plates are given lower-case letters of the roman alphabet. The series starts at plate a, which occupies a position near, but not at, the anterior left part of the head, and is followed by plate b just left of the mouth, and so forth in clockwise order in dorsal aspect around the head to finish at plate l in *R. hanusi*. In applying this scheme to species other than *R. hanusi*, additional letters are interpolated as necessary and, since the number of homologous series of marginal plates in cornutes and



TEXT-FIG. 12. *Nevadaecystis americana* (Ubaghs); Upper Cambrian, Nevada, United States National Museum 143237; diagrammatic drawing of the dorsal aspect of the only known specimen and holotype (redrawn after Jefferies 1969, text-fig. 4).

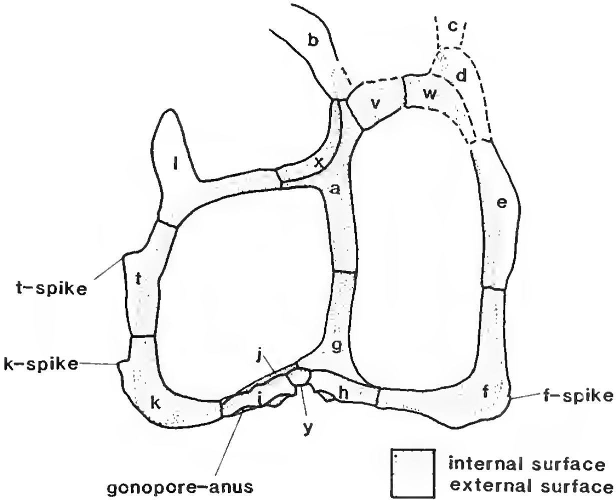
mitrates now exceeds twenty-six, the English roman alphabet is supplemented by letters from German and French (ü, é, etc). (We do not imply that plate ü has any special relation to plate u, nor plate é to plate e; nor do the U-plates of the branchial slits form part of this notation, for with them the U is upper case and describes the shape of the plates.) For centrodorsal plates, in which homologies can be recognized between *Ceratocystis perneri*, *P. menevensis*, and *N. americana*, the numbers 1 to 6 are employed, starting from the situation in *C. perneri* where the sequence is once again clockwise in dorsal aspect. Suffixes are used when several plates correspond to a single dorsal plate in *C. perneri*. This comparative notation is difficult to memorize, but becomes clear in the text-figures.

Various protuberances were borne on the heads of cornutes and, like the plates, these can now be homologized from species to species. Such processes were of two main types—appendages and ventral spikes—though the distinction between the two is not precise. Appendages made up parts of the anterior margin of the head and projected horizontally, or horizontally and downwards; spikes, by contrast, projected downwards from the ventral surface. Jefferies (1968) used an objective notation for the spikes (S_{1R}, S_{2R}, etc.) much like the notation used for the plates, whereas the appendages were referred to as 'left', 'left oral', and 'right oral'. In this paper, we replace these terms by a new notation which refers to the plate on which the process was carried, e.g. e-spike, l-appendage. As with the plates, the new notation is not objective but implies homology. It is convenient, because a plate in cornutes seldom bears more than one individualized process (though that process is often complicated in shape) and such a process is never constituted from more than one plate.

The nomenclature of different types of stereom follows Smith (1984*b*, fig. 3.2).

General external features and the plates of the head. P. menevensis (text-fig. 10) consisted of a head and a tail, like every other cornute and mitrate. The outline of the head was boot-shaped, as was common among primitive cornutes and it particularly resembled that of *C. perneri* in that plate k extended further leftward than plate l. The right margin of the head, as reconstructed, was almost straight and at right angles to the posterior margin. This could be a mistake in the reconstruction caused by tectonic distortion, but if there is no mistake the right margin of the head was different in shape to that of *C. perneri* in which it ran leftwards and forwards. In *P. menevensis* it was in this respect probably more like *N. americana*, '*Cothurnocystis*' *fellinensis*, and *C. elizae*.

The ventral surface of the head of *P. menevensis* was made up, except for a small oral integument, of large plates and would have been rigid (Pl. 55, fig. 1). The dorsal surface also contained some large plates, but was mainly covered with plated integument (Pl. 54, fig. 1). This combination of rigid floor and flexible roof is otherwise known in cornutes only in *N. americana*. It was morphologically intermediate between *Ceratocystis perneri*, where the floor and roof were both rigid, and *Cothurnocystis elizae*, for example, where the floor and roof were both flexible though the floor was crossed by a strut. The large plates forming the floor of *P. menevensis* can be called a ventral shield. We shall describe this shield first, before discussing the skeleton attached to it dorsally.

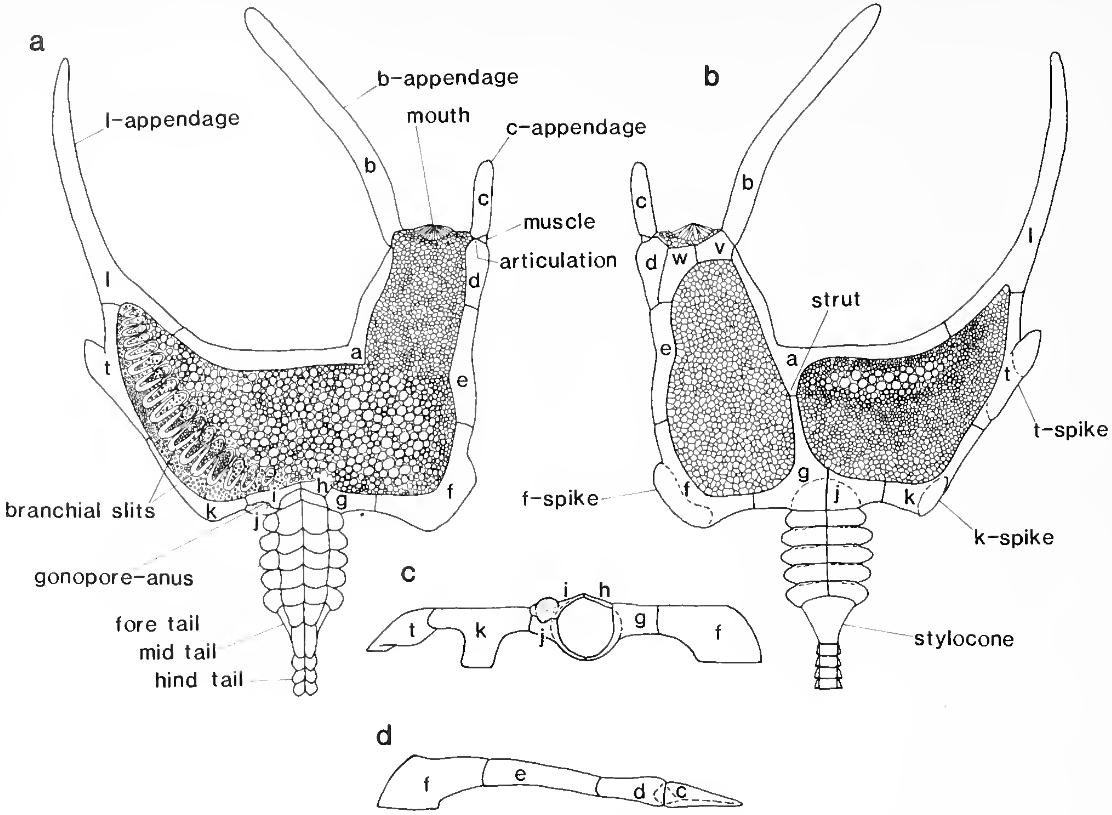


TEXT-FIG. 13. '*Cothurnocystis*' *fellinensis* Ubaghs; Lower Ordovician (probably Lower Arenig), Montagne Noire, France; dorsal aspect of marginal skeleton of head (redrawn after Ubaghs 1969, fig. 19).

The right edge of the ventral shield, and of the head, of *P. menevensis* was made up of plates g, f, e, and c. Plate g (Pl. 55, figs. 1 and 3; Pl. 58, fig. 1; Pl. 60, figs. 3, 4, 9, 10) was the first right ventral marginal (M_{1RV} in the old notation) and included the right half of the tail attachment. Much of its posterior part was almost vertical, forming part of the posterior wall of the head. Its anterior part was horizontal, however, forming part of the rigid floor. Where ventral and horizontal portions joined, there was a distinct fold (oesophageal fold), concave dorsally and convex ventrally, which ran rightwards into plate f. Another fold, similarly convex downwards but wider and resembling half of a crescent in plan view, was situated just anterior to the tail attachment and underlay the right half of the posterior coelom (see below, under 'The chambers and soft anatomy of the head').

Plate f (Pl. 54, figs. 1 and 3; Pl. 55, figs. 1, 4, 5; Pl. 56, fig. 1; Pl. 57, figs. 1 and 4; Pl. 58, figs. 1; Pl. 60, figs. 5, 6, 7) formed the posterior right corner of of the ventral shield, i.e. the 'heel' part of the 'boot'. Like plate g, it was divided into a horizontal portion, which was part of the floor, and a vertical portion, which formed part of the posterior and right lateral walls of the head. Plate f was drawn out horizontally into a sharp-edged peripheral flange and the posterior end of this flange was turned downwards to form the f-spike. Plate f carried the right end of the oesophageal fold, the rest of which was on plate g.

Plate e (pl. 54, figs. 1–3; Pl. 55, fig. 1; Pl. 56, fig. 1; Pl. 57, fig. 3; Pl. 58, fig. 4) formed the middle part of the right edge of the ventral shield. It had a sharp-edged peripheral flange which was continuous with that of plate f and which ran forward into that of plate c. In dorsal aspect it showed, on the right, a distinct marginal frame, the middle part of which articulated with dorsocentral plate 5. On the ventral surface of plate e there was an e-spike, homologous with that of other cornutes. We use the term 'spike' for consistency with other cornutes, though the word is not totally appropriate in *P. menevensis* since the process was rounded in shape and, in particular, had the same slope in all directions, whereas most spikes in cornutes have the anterior slope steeper and sharper than the posterior one. The e-spike of *P. menevensis* was hollow, corresponding to a circular concavity in the internal dorsal face of plate e.



TEXT-FIG. 14. *Cothurnocystis elizae* Bather; Upper Ordovician (Ashgill), Girvan, Scotland (redrawn after Jefferies 1968, text-fig. 1), with most of the hind tail omitted. *a*, dorsal; *b*, ventral; *c*, posterior; and *d*, right lateral aspect of right side of frame only.

Plate c (Pl. 54, figs. 1 and 3; Pl. 55, fig. 1; Pl. 58, fig. 1), which included the c-appendage (right oral appendage), was the most anterior plate on the right side of the ventral shield. It had a sharp-edged keel which was a forward continuation of the peripheral flange of plate e. It was ventrally convex and dorsally plane. Dorsally it articulated with, or was lightly sutured to, dorsocentral plate 3.

The left edge of the ventral shield was formed of plates j, k, l, x, and b. Plate j, which is not well shown in any specimen (but see Pl. 54, fig. 4; Pl. 55, fig. 1; Pl. 56, fig. 3; Pl. 57, fig. 1) was the first left marginal (M_{ILV} of the old notation). It had a vertical portion, forming part of the posterior wall of the head, and a horizontal portion included in the floor. Plate j carried the left half of the tail insertion. A ventrally convex portion of it, resembling half a crescent in plan view, lay just anterior to the tail and was the floor of the left half of the posterior coelom. In the leftward portion of the plate the junction between the horizontal and the vertical parts was abrupt and presented an almost rectangular keel on the external surface. Just dorsal to this keel was an opening (Pl. 55, figs. 1 and 2) which corresponded in general position to the narrow groove of *Ceratocystis perneri*, though it penetrates plate j and not plate i as in *C. perneri*. The opening probably represented an ear, functioning as lateral line, and was thus a primitive representation of the acustico-lateralis system (Jefferies 1969, p. 522; 1986, Ch. 7). Dorsally and towards the median line, plate j of *P. menevensis* would have articulated with plate i and was notched by the ventral margin of the gonopore-anus.

Plate k (Pl. 54, figs. 1, 2, 4; Pl. 55, fig. 1; Pl. 56, fig. 1; Pl. 57, fig. 1; Pl. 58, fig. 1; Pl. 60, fig. 1) of the ventral shield of *P. menevensis* was triangular in plan view and was the leftmost plate in the head. Its horizontal portion made part of the floor and was sharply distinct from the vertical portion which formed part of the posterior and left lateral walls of the head. There was a ventral k-spike (Pl. 60, fig. 1) which was V-shaped, with the limbs of the V running respectively along the left boundary and posterior boundary of plate k. The smooth, outward-facing surfaces of the spike were continuous, respectively, with the posterior and left lateral walls of the plate and were almost vertical. The inward-facing surfaces of the spike were rough and made an angle of *c*. 45° to the horizontal. (The corresponding k-spike of *C. perneri* (text-fig. 11) was similarly V-shaped, though much less well marked than that of *P. menevensis*.) In dorsal aspect, plate k of *P. menevensis* showed a keel which ran forward and rightward from the left corner of the head up towards the dorsal surface. The dorsal edge of plate k (Pl. 60, fig. 2), unlike that of *C. perneri*, was entire and not notched for branchial slits.

Plate l (Pl. 55, fig. 1; Pl. 57, fig. 1; Pl. 58, figs. 1 and 3) lay anterior to plate k and consisted of two portions abruptly separated from each other—the marginal frame and the horizontal lamina. The frame made part of the left wall of the head while the lamina formed part of the floor. The frame extended into a sort of wing—the l-appendage (left appendage)—which was approximately horizontal in disposition, or possibly sloped downwards and forwards to judge by the situation in *C. perneri*. The edge of the l-appendage was continuous posteriorly with the keel that separated the horizontal portion from the left vertical portion of plate k. Anteriorly the edge of the l-appendage passed into a keel which became less and less distinct, to disappear approximately at the anterior border of the plate.

Plate x (Pl. 55, fig. 1; Pl. 58, fig. 1) was elongate and only its anterior third contributed to the left margin of the head and ventral shield and to the left lateral wall. Posteriorly it was horizontal and ran rearward to abut against plates g and j.

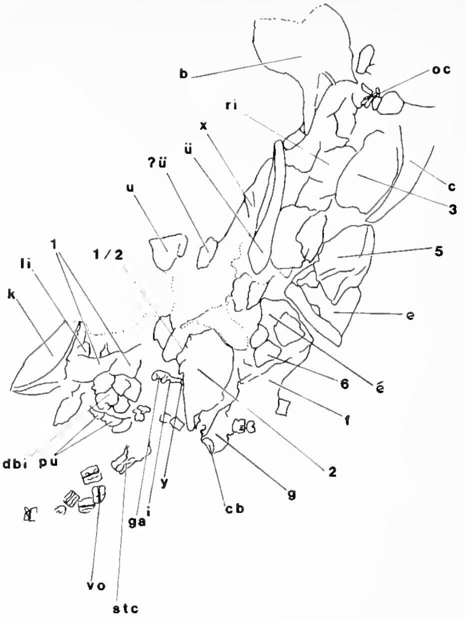
Plate b (Pl. 54, fig. 1; Pl. 55, fig. 1; Pl. 58, fig. 1; Pl 59, figs. 2–4) included the b-appendage (left oral appendage) and was the most anterior plate of the left side. Like plate c on the other side of the mouth, it was convex ventrally and flat dorsally. Unlike plate c, however, there was a thin laminar portion of plate b which extended rightwards to form part of the floor.

Other plates made part of the ventral shield but did not contribute to its right and left edges in ventral aspect. These were plates d, w, and v (Pl. 55, fig. 1; Pl. 58, fig. 1) behind the oral integument, and plates a and é whose positions were more central. Plates d, w, and v made a post-oral series and their anterior outlines were concave where they abutted against the oral integument. The position of plate d thus resembled that of the same plate in *C. perneri* (text-fig. 11*b*), while in *Nevadaecystis* and all cornutes more crownward than it, plate d had become a marginal plate inserted between plates e and c (text-figs. 12–14). Plate a was a large polygonal plate of central position in *P. menevensis*, whereas plate é was a smaller plate situated between plates a and f. (*C. perneri* likewise had a plate é, but also a single large plate corresponding to plates w + a + x of *P. menevensis*.) In '*Cothurnocystis*' *fellinensis* (text-fig. 13) and many more crownward cornutes, on the other hand, plate a was a marginal plate forming the anterior part of the strut and the adjacent parts of the frame. In many crownward cornutes, including *C. elizae* (text-fig. 14), plate x did not exist, whereas in *C. fellinensis* it was a marginal plate overlying parts of plate a.

Concerning the strut, which crosses the head from front to rear in most cornutes, the situation in *P. menevensis* is complicated. The strut of *C. elizae* (text-fig. 14), for instance, was formed of parts of plates g and a and it divided the ventral integument into two parts. Such was the usual situation in cornutes, as seen also in '*C.*' *fellinensis* (text-fig. 13), for example. In *Nevadaecystis*, which so far as can be seen had a rigid floor, the strut was represented by a thickening of plate g which ran forward and presumably continued on to plate a (though that plate is not visible on the only known specimen). There was no trace of such a single thickening on plates g or a of *P. menevensis*. Ribs existed and ran more or less radially out from the growth centres on the thinner parts of plates g, a, j, k, l, x, and b (the laminar part of this plate). However, the ribs were irregular in position and numerous, and none of them can certainly be identified with portions of the strut of other cornutes. Perhaps they represented a primitive, unfixated condition, two apposed ribs of which alone survived to give the strut of more crownward cornutes.

An alternative possible evolutionary beginning for the strut is represented in *P. menevensis* by an internal process on plate g (cleft on the internal mould, text-fig. 23*a*; Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10) situated between the posterior coelom and the right anterior coelom (see below, under 'The chambers and soft anatomy of the head'). If it grew forward during evolution, this process would produce a thickening in the same position as the strut of *N. americana*. In broad terms, however, it is true to say that *P. menevensis* had no strut, or at least, no strut that can certainly be homologized with the strut of cornutes more crownward than *P. menevensis*. The absence of such a strut is probably primitive and likely to be homologous with its absence in *Ceratocystis perneri*. Mechanically speaking, the strut of cornutes would have served mainly to prevent the head being crushed under anteroposterior compression. This function would have been carried out in *P. menevensis* by the triple arch of the dorsal surface (see below), in collaboration with the rigid floor of the head. This also is probably primitive, since the head of *P. menevensis* to this extent retained the box-like construction of the head of *C. perneri*.

TEXT-FIG. 15. Half-scale, outline drawing of Plate 54, fig. 1. For single letters or numbers, see plate notation shown in text-fig. 10. Other labels: 1/2, surface on plate 2 representing articulating junction with plate series 1; cb, cerebral basin; dbi, dorsal branchial integument; ga, gonopore-anus; li, left anterior integument; pu, posterior U-plate; oc, oral cone; stc, stylocone; ri, right integument; vo, ventral ossicle of hind tail.



As to the stereom of the ventral shield, the central part, which was stiffened by ribs, consisted of extremely thin, retiform stereom, except for the ribs themselves which were of labyrinthic stereom and were more convex externally than internally. This type of structure, consisting of a web with struts, would be described by architects as a space frame. It would have combined lightness with stiffness and suggests that *P. menevensis* was adapted for low weight. More peripherally, the ventral shield tended to be thicker. Sometimes it was of perforate stereom externally, but smooth and almost imperforate internally, as in the posterior right-hand part of the floor (plate é and the adjacent parts of plates e, a, and g) where it underlay the cavity of the right anterior coelom (see below, under 'The chambers and soft anatomy of the head'), and also in plates g and j beneath the posterior coelom. The peripheral parts of the ventral shield tended to be formed of labyrinthic stereom, though the sharp edges were sometimes of fibrillar stereom. Thus the oral appendages of plates b and c were covered on their convex ventral surfaces with a sheet of fibrillar stereom (Pl. 55, fig. 1; Pl. 59, figs. 3 and 4), the fibrils being more or less radial in arrangement. But the flat dorsal surfaces of these plates (Pl. 54, fig. 1; Pl. 59, fig. 2) were formed of labyrinthic stereom, except peripherally; this labyrinthic stereom filled, so to speak, the dorsal concavity of the ventral fibrillar layer. Again, in plate l, the posterior parts of the plate, forming part of the floor, were of space-frame type (Pl. 55, fig. 1; Pl. 57, fig. 1; Pl. 58, fig. 3; Pl. 60,

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EXPLANATION OF PLATE 54

Figs. 1–4. *Protocystites menevensis* Hicks. 1–3, BM(NH) E62963 from loc. 2, Porth-y-rhaw (see text-fig. 7); *Hypagnostus parvifrons* Zone, Middle Cambrian. This is the best specimen known. Plate e has been dislocated and rotated approximately 90° from its original position. 1, general dorsal aspect of latex cast (see text-fig. 15 on facing page), ×6·9. 2, latex of posterior left part of head at an earlier stage of dissection than in fig. 1; note the series of plates 1, ×11·9. 3, plate 3 at a higher magnification than in fig. 1 and oriented as in the reconstruction in text-fig. 10, ×12·8; is, imperforate stereom of plate e; rs, retiform stereom of plate e; pbbc, callus marking posterior boundary of buccal cavity. 4, BM(NH) E62979, also from loc. 2, Porth-y-rhaw. Latex in dorsal aspect; note posterior coelom (pc) clearly defined by an arcuate ridge on the dorsal surface of plates g and j; note also the vertical wall (vw) which represented the posterior limit of the posterior coelom and which formed the front wall of the cerebral basin, ×4·2.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

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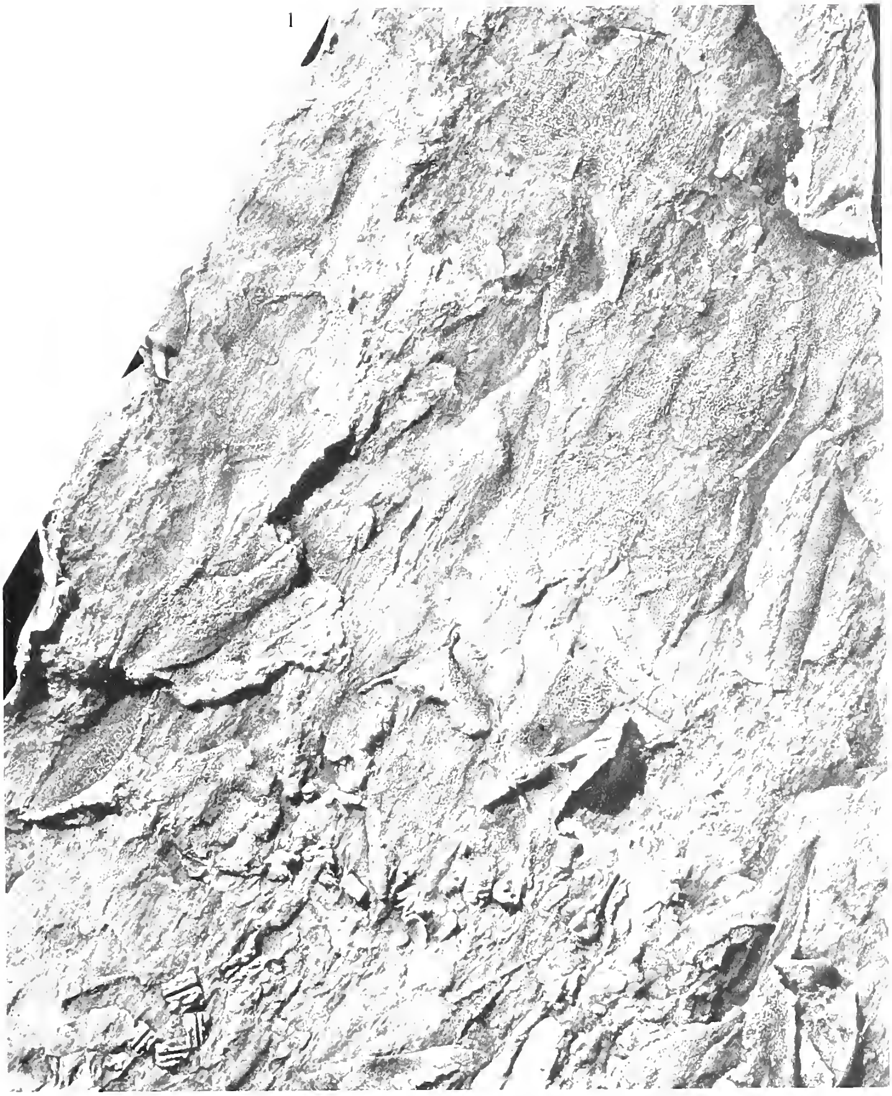

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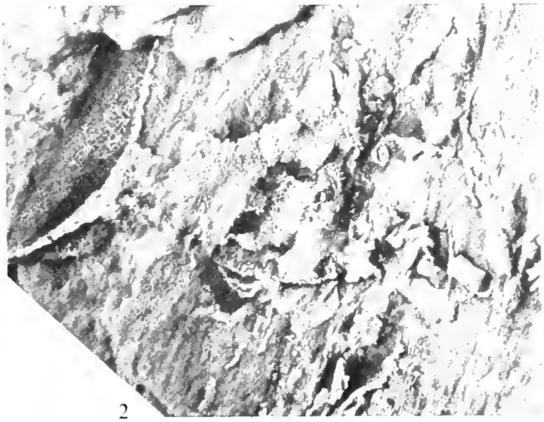

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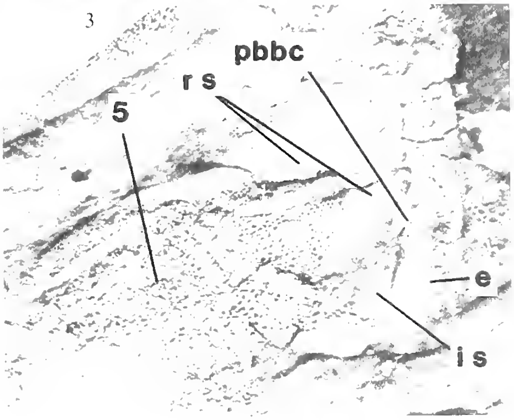
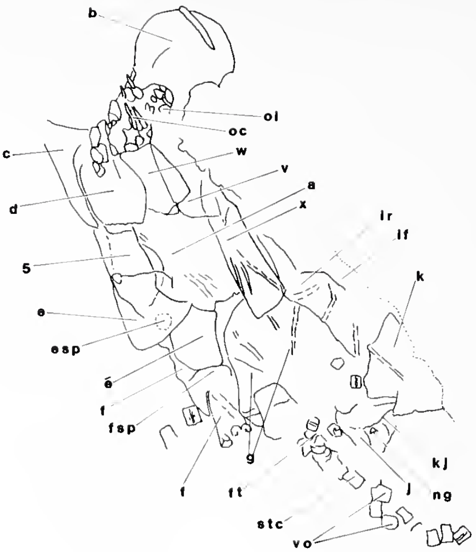


JEFFERIES, LEWIS and DONOVAN, *Protocystites*



TEXT-FIG. 16. Half-scale, outline drawing of Plate 55, fig. 1. For single letters or numbers, see plate notation shown in text-fig. 10. Other labels: esp, e-spike; fsp, f-spike; ft, fore tail; kj, keel on plate j; lf, fibrillar part of l; lr, retiform part of l; ng, narrow groove (ear) in plate j; oc, oral cone; oi, oral integument; stc, stylocone; vo, ventral ossicle of hind tail.

fig. 8), but the vertical wall was of labyrinthic stereom and the l-appendage was fibrillar stereom, with the fibrillae running parallel to the anterior edge of the appendage. The stereom of plate f was particularly complicated. The spike and peripheral flange seem to have been built of labyrinthic stereom which was particularly dense at the sharp edges. Most of the lateral wall of plate f, however, was of very thin retiform stereom crossed by horizontal folds (pw in Pl. 57, fig. 4; Pl. 60, figs. 5–7). This thin part of the wall corresponds to the presence of a pharynx inside the head, as argued below.

The dorsal surface of the head, as already mentioned, contained some regular, individualized plates separated by plated integuments. The first group of individualized plates to be described is the dorsal arch of the tail insertion, consisting of plates h, y, and i (M_{IRD}, M_{PD}, and M_{ILD} of the old notation). Of these, plate y (Pl. 58, fig. 2) formed the keystone of the arch, being median and dorsal in position; its posterior, external surface was notched from below by a groove (the dorsal groove) which in life probably carried a median eye that arose from the dorsal surface of the brain. Plate i (Pl. 54, fig. 1), forming the left part of the arch, ran between plates y and j; at its ventral end it had a large, almost circular embayment which in life carried the gonopore-anus. Plate h (Pl. 54, fig. 4) ran between plates g and y and formed the right part of the dorsal arch.

A comparison of the plates and openings near the tail attachment with those of other cornutes is of interest. Compared with *C. perneri* (text-fig. 11), in *P. menevensis*: 1, the gonopore-anus was left of the tail, not right of it; 2, there was no plate o (M_{PV} of the old notation); 3, plate g formed part of the tail attachment, had a much larger ventral posterior portion, and did not abut against the gonopore-anus; 4, plate j formed a larger part of the tail attachment, had a larger vertical wall, included the narrow groove (ear) (which in *C. perneri* was in i), and formed the lower boundary of the gonopore-anus; 5, plate i was much smaller, contained the

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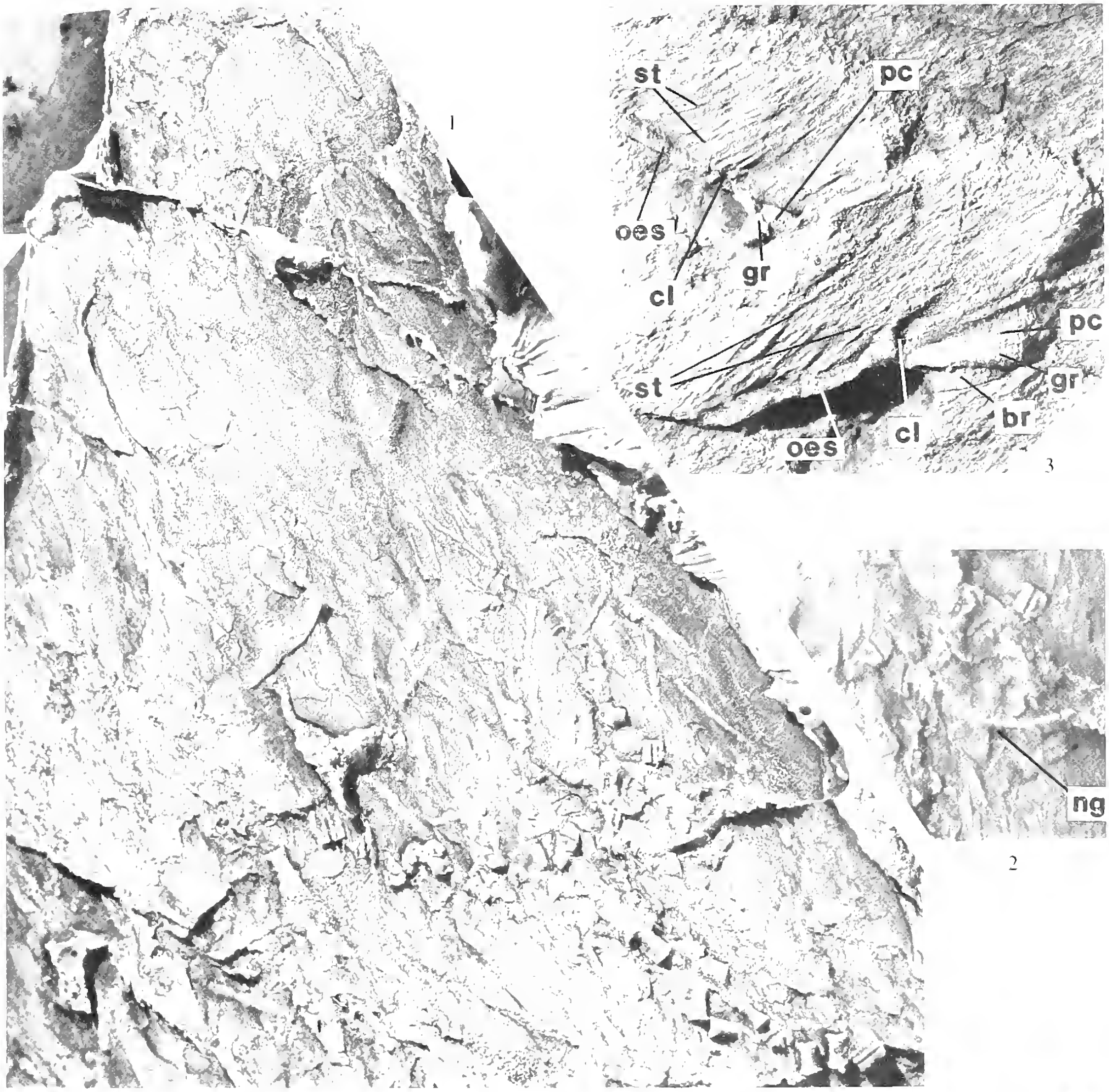
EXPLANATION OF PLATE 55

Figs. 1–5. *Protocystites menevensis* Hicks. All specimens from loc. 2, Porth-y-rhaw. 1, BM(NH) E62963, latex of ventral aspect of best specimen (see text-fig. 16 on facing page), ×6·9. 2, detail of same to show plate j with ear (ng, narrow groove), ×8·8. 3, BM(NH) E62958, natural moulds of internal surfaces of two specimens of plate g, in ventral aspect, suggesting the soft parts (cf. text-fig. 22*a*), ×8·4; br, brain; cl, cleft between posterior coelom and right anterior coelom; gr, gonoduct-rectum; oes, oesophagus; pc, posterior coelom; st, change in nature of stereom from almost imperforate at right posterior to thin and retiform at left anterior (retiform stereom has a granular appearance). 4, 5, BM(NH) E63034, latexes of plate f in ventral and dorsal aspect; oesf, oesophageal fold; fsp, f-spike; 4, ×10·3; 5, ×11·8.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.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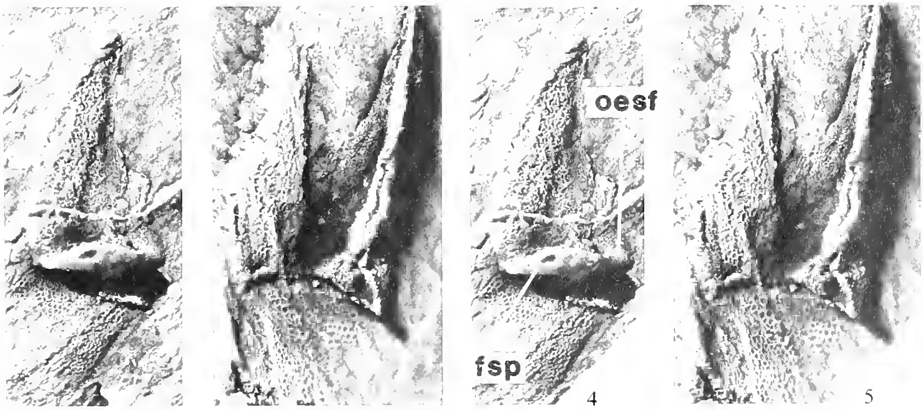
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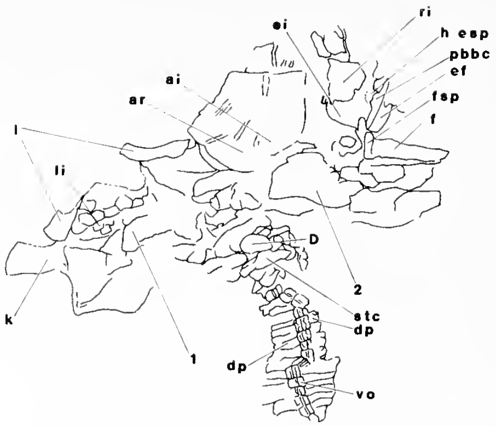
TEXT-FIG. 17. Half-scale, outline drawing of Plate 56, fig. 1. For single letters or numbers, see plate notation shown in text-fig. 10. Other labels; ai, almost imperforate stereom in plate a; D, dorsal plate of fore tail; ar, reticulate stereom in plate a; dp, dorsal plate of hind tail; ef, frame part of plate e; ei, almost imperforate stereom in plate e; fsp, f-spike; h esp, hollow in interior of plate e, corresponding to e-spike; li, left anterior integument; pbbc, callus marking posterior boundary of buccal cavity; ri, right integument; stc, stylocone; vo, ventral ossicle of hind tail.



dorsal boundary of the gonopore-anus, and was dorsolateral in position with respect to the tail attachment, instead of lateral—indeed, much of plate i as seen in *C. perneri* seems to be replaced by integument in *P. menevensis*; 6, plate y was much smaller and bounded anteriorly by integument; 7, plate h was likewise much smaller and bounded anteriorly by integument, was perhaps partly replaced by integument, and did not abut against the gonopore-anus nor the hydropore (which in *P. menevensis* was absent, see below). These differences are in some cases interrelated: thus, the fact that plate g in *P. menevensis* made no contact with the gonopore-anus is due to the position of the latter left of the tail. With one exception, however, all these differences from *C. perneri* are resemblances to '*Cothurnocystis*' *fellinensis* (text-fig. 13) and probably to *N. americana* also (text-fig. 12), whose morphology is less well known. The exception relates to the ear, whose position penetrating plate j (text-fig. 11*b*, *c*; Pl. 55, fig. 2) could be a specialization of *P. menevensis*, though the fact that it was not conflated with the gonopore-anus was a resemblance to *Ceratocystis perneri*. These differences from *C. perneri* are also resemblances to *Cothurnocystis elizae* (text-fig. 14)—the best studied *Cothurnocystis*—except that *C. elizae* lacked plate y, the median eye, and plate x.

A three-legged arch occupied the central part of the dorsal surface of the head. The largest plate in this arch was dorsocentral 2 (Pl. 54, figs. 1 and 4) which lay to the right of the mid-line of the tail and probably

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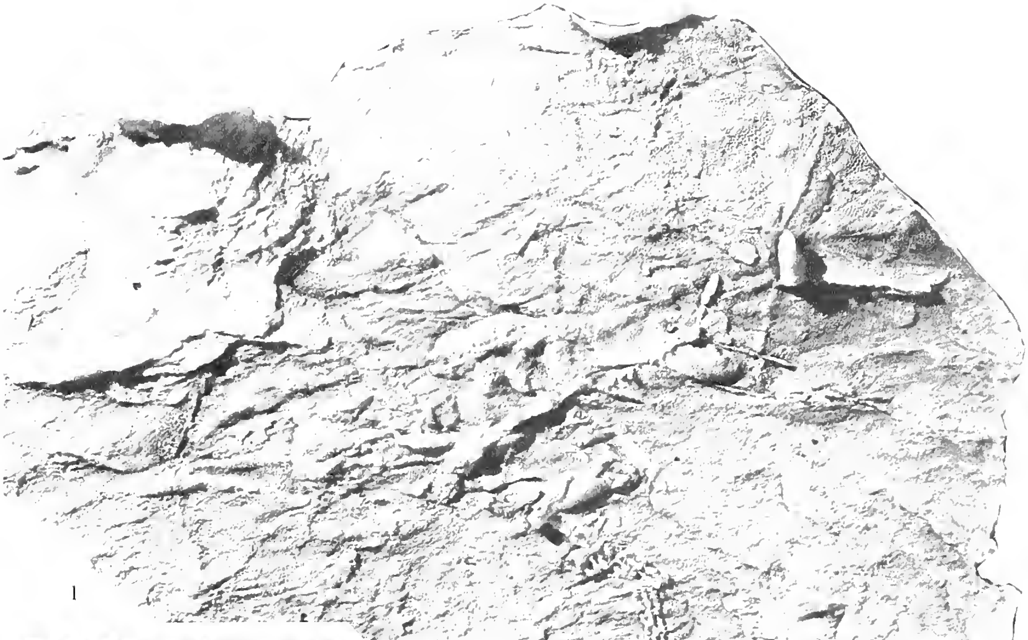
EXPLANATION OF PLATE 56

Figs. 1–5. *Protocystites menevensis* Hicks. 1–3, SM A.1021, lectotype (see also Pl. 57, figs. 1 and 2), *ex* Hicks's Collection; Menevian, Porth-y-rhaw, Dyfed. [The specimen was cleaned in thioglycollic acid which had the unintended effect of removing all pyrite. The gonorectal groove, which was filled with pyrite and showed clearly when the specimen was first seen, is no longer preserved in the cleaned specimen.] 1, latex of dorsal surface of cleaned specimen (general view), showing that it is dislocated; in particular, plate e is pushed against plate f, and plate f has been inverted so that it here shows the ventral aspect with its f-spike (see text-fig. 17 on facing page), × 5·8. 2, portion of hind tail, at higher magnification, to show features of the dorsal plates; the left dorsal plates have rotated outwards and show their internal surfaces, whereas the right plates show their external surfaces (cf. text-fig. 25), × 18·9; ap, articular process; crf, crescentic facet; fp, fibrillar part of dorsal plate; if, inter-plate facet; ms, median suture (i.e. edge of the dorsal plate where it met the median suture); pol, posterior lobe of dorsal plate; tg, transverse groove. 3, plaster cast of a latex made before the specimen was cleaned with thioglycollic acid and which represents the original shape of the natural mould; ventral aspect of region of the posterior coelom (pc) and of the infilling of the gonorectal groove (gr), i.e. mould of the dorsal surfaces of plates g and j; note that the infilling of the gonorectal groove crosses the posterior coelom and ends at the gonopore-anus (ga) to the left of the tail, towards the bottom right of the figure, × 7·5; g/j, suture between plates g and j. 4 and 5, BM(NH) E62920, latexes of left and right aspects of a specimen consisting of ossicles of the mid and hind tail, still articulated with each other but separated from all other plates, both × 7·0.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.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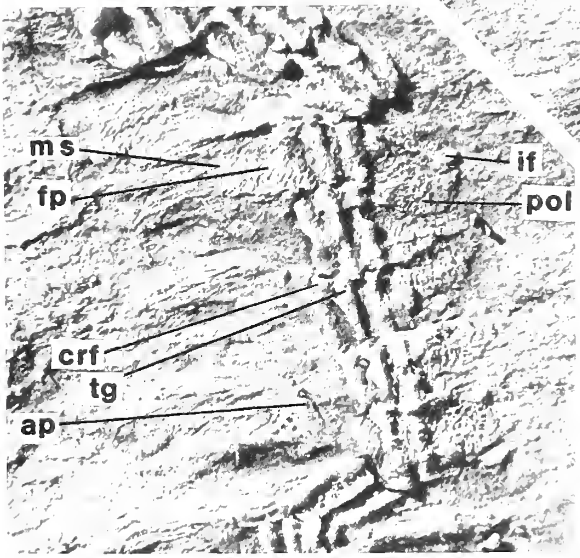

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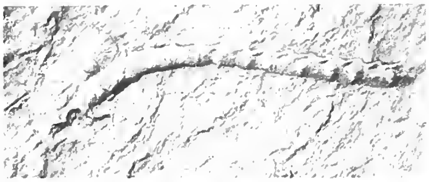
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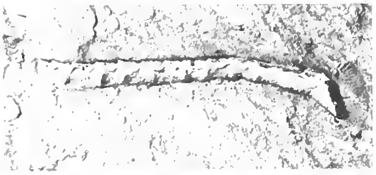
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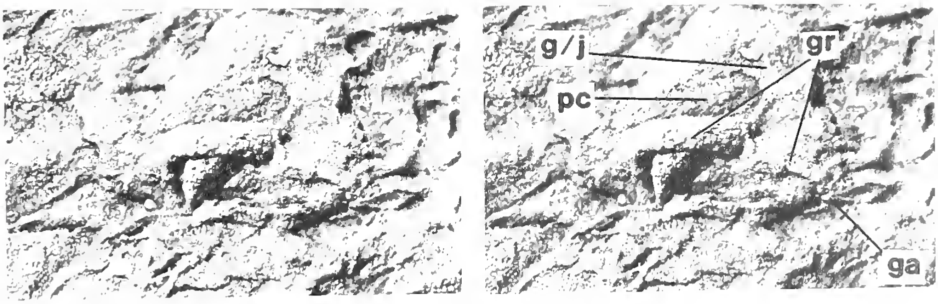

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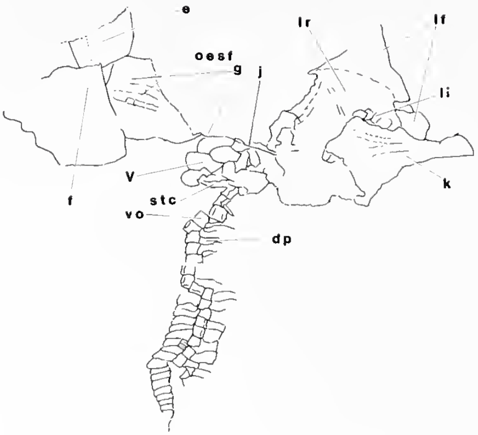
JEFFERIES, LEWIS and DONOVAN, *Protocystites*

TEXT-FIG. 18. Half-scale, outline drawing of Plate 57, fig. 1. For single letters or numbers, see plate notation shown in text-fig. 10. Other labels: dp, dorsal plate of hind tail; lf, fibrillar part of l; li, left anterior integument (ventral surface exposed); lr, retiform part of l; oesf, oesophageal fold; stc, stylocone; vo, ventral ossicle of hind tail; V, ventral plate of fore tail.



contained the summit of the triple arch. A blunt curved ridge on plate 2 followed its left posterior edge. The posterior articulation of plate 2 is uncertain; it may have made direct contact with the marginal frame near the suture of plates f and g; on the other hand, it may have linked with dorsocentral plate 6, which itself made contact with the frame at plate f. The uncertainty is caused by the fact that the plate identified as dorsocentral 6 may in fact have been only an integument plate thickened along its posterior margin (Pl. 54, fig. 1). Plate 2 made contact on its left with a series of plates (1_1, 1_2, 1_3, etc.; Pl. 54, figs. 1, 2, 4; Pl. 56, fig. 1) perhaps variable in number, which passed leftwards to meet the vertical keel on the dorsal surface of plate k. The plates of this series were convex upwards and formed the crest of a gentle ridge which stretched between plates 2 and k. The third leg of the triple arch was plate ü (Pl. 54, fig. 1): this had a distinct keel, being inverted L-shaped in section. It contacted plate b anteriorly and plate x ventrally, and it probably articulated directly with plate 2. On the other hand, an additional plate ($\ddot{u}_2$; ?ü in text-fig. 15) may have been interpolated between plates ü and 2 in life (although, if so, it has been considerably displaced after death in the one specimen where it was seen). The same triple arch can be recognized in *Ceratocystis perneri*, where it was made up of plates 1, 2, ü, and 6, and formed most of the rather solid roof of the head. It also existed in *N. americana*, though plate ü was divided there into at least three plates and the equivalents of plate 1, which may have existed in life, are not preserved in the only known specimen.

Three other individualized plates existed on the dorsal surface: plates u, 3, and 5. Plate u (Pl. 54, fig. 1) lay anterior to plates 1_1, 1_2, and 1_3 and has only been seen on one specimen. It carried an elongated ridge, as also did plate u of *C. perneri*, but the orientation and outline of the plate are uncertain. Plates 3 and 5, likewise only known in the specimen shown in Pl. 54, fig. 1, have already been mentioned as making contact respectively with plates c and e of the ventral shield.

Plated integument formed the rest of the dorsal surface. The largest such stretch of integument lay to the right of the triple arch, ran forward to the mouth and over the front margin of the head into the oral integument of the ventral surface, and was limited on the right and posteriorly by the plates of the ventral

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EXPLANATION OF PLATE 57

Figs 1–4. *Protocystites menevensis* Hicks. 1 and 2, SM A.1021, latex of the lectotype, *ex* Hicks's Collection; Menevian, Porth-y-rhaw, Dyfed (see also Pl. 56, figs. 1–3). 1, general view of ventral aspect (see text-fig. 18 on facing page), × 5·8. 2, portion of hind tail, × 18·9; fp, fibrillar portion of dorsal plate; vp, thick ventral portion of dorsal plate; if, inter-plate facet. 3, BM(NH) E62958, from loc. 2, Porth-y-rhaw (see text-fig. 7); latex of plate e in ventral aspect with boss-like e-spike (same plate as in Pl. 58, fig. 4), × 5·0. 4, BM(NH) E62965, also from loc. 2, Porth-y-rhaw; natural mould of inside of plate f in right posterior aspect (cf. Pl. 60, fig. 8), × 6·3; fsp, f-spike; int, intestine; pw, pharyngeal wall; pvl, pharyngo-visceral line; sto, stomach.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

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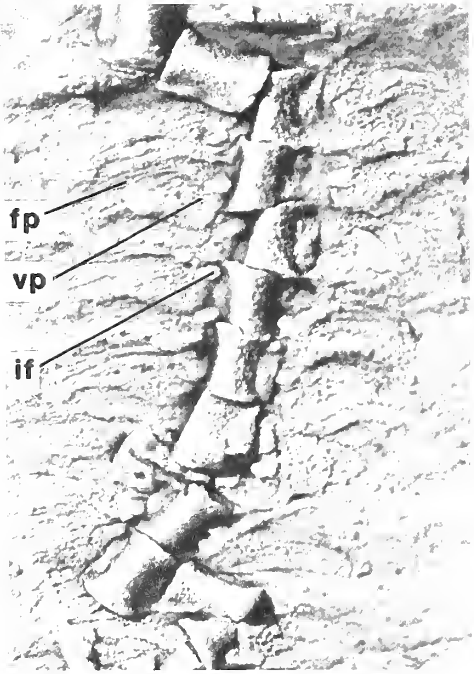

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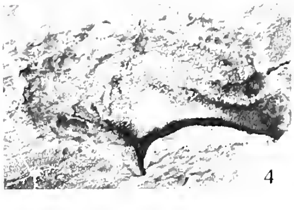

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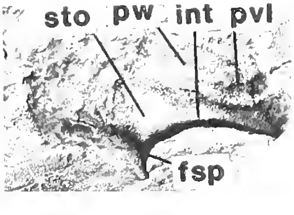
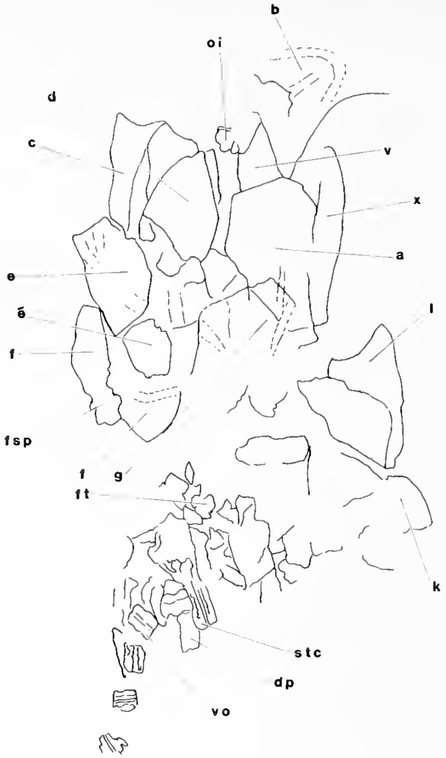


JEFFERIES, LEWIS and DONOVAN, *Protocystites*



TEXT-FIG. 19. Half-scale, outline drawing of Plate 58, fig. 1. For single letters, see plate notation in text-fig. 10. Other labels: dp, dorsal plate of hind tail; fsp, f-spike; ft, fore tail; oi, oral integument; stc, stylocone; vo, ventral ossicle of hind tail.

shield (Pl. 54, fig. 1); we refer to it, including the oral integument behind the mouth on the ventral surface, as the right integument. The second largest patch of integument lay to the left of, and anterior to, the triple arch and surrounded, or almost surrounded, plate u (Pl. 54, figs. 1 and 2; Pl. 56, fig. 1); we call it the left anterior integument. The third largest patch of integument lay behind the triple arch, between it and the posterior wall of the ventral shield and dorsal arch of the tail attachment; we call it the posterior integument. To the left of the tail, the posterior integument was presumably penetrated by branchial slits and consisted of rather thick plates, some of which were half-moon shaped and probably homologous with posterior U-plates (pu in text-fig. 15). Well differentiated anterior and posterior U-plates surrounding *elizae*-type slits ('cothurnopores') did not exist in *P. menevensis*, unlike *N. americana*.

As to their stereom, the plates of the right integument were very thin near the posterior part of the head and made up of a single layer of retiform stereom (Pl. 54, fig. 1). Other integument plates were thicker and made up of at least two layers of retiform stereom. The stereom of the dorsocentral plates, and also plates u and ü, was thicker again and tended to be labyrinthic.

EXPLANATION OF PLATE 58

Figs. 1–4. *Protocystites menevensis* Hicks. 1, BM(NH) E432, *ex* Hicks's Collection; Menevian, from near St. David's; latex of ventral surface (see text-fig. 19 on facing page), × 12·8. 2, BM(NH) E63011, from loc. 2, Porth-y-rhaw (see text-fig. 7); latex of plate y in external aspect to show dorsal groove (dg) for median eye, × 19·2. 3, BM(NH) E63008, from loc. 2, Porth-y-rhaw; latex of plate l in dorsal aspect (same plate as in Pl. 60, fig. 7), × 4·6. 4, BM(NH) E62958, from loc. 2, Porth-y-rhaw; latex of plate e, dorsal surface (same plate as in Pl. 57, fig. 3), × 8·3; is, imperforate stereom; pbbc, posterior boundary of buccal cavity; rs, retiform stereom.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

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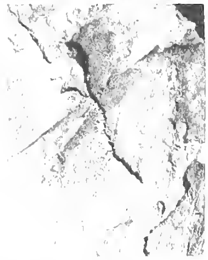

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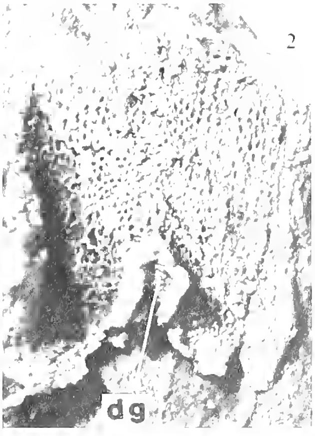


JEFFERIES, LEWIS and DONOVAN, *Protocystites*

The openings of the head. All of these have already been mentioned in describing the external features of the head skeleton. They are crucial in understanding the anatomy, but we shall identify them without giving reasons—the arguments for these identifications are to be found in Jefferies (1986, Chs. 7 and 8).

The mouth was near the anterior end of the head, between the oral-appendage plates (b and c) and anterior to the approximately semicircular oral integument of the ventral surface. It seems to have been guarded by an oral cone (oc of text-fig. 15, cf. Pl. 54, fig. 1; text-fig. 16, cf. Pl. 55, fig. 1) of radially disposed elongated plates. This mouth would therefore be like that of *Cothurnocystis elizae* in position and in having an oral cone. It differed from the mouth of *Ceratocystis perneri* in having an oral cone and in having flexible integument posterodorsal to it, rather than a rigid upper lip. The mouth of *N. americana* is unfortunately not known.

The gonopore-anus was to the left of the tail in *P. menevensis*, between plates i and j. This was very similar to the situation in *Cothurnocystis elizae* and '*C.*' *fellinensis* and differed strikingly from that in *Ceratocystis perneri* where the gonopore and anus were right of the tail and sometimes, though not always, slightly separated from each other. As discussed below, *C. perneri* probably represented the primitive condition in these respects. When the gonopore-anus was to the left of the tail it lay in the outwash from the branchial slits, so that faeces and gametes would have been flushed away (Jefferies 1986, Ch. 7). This was presumably advantageous. As in most cornutes, a gonorectal groove in *P. menevensis* ran inside the head (Pl. 54, fig. 4; Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10) across the floor of the posterior coelom from the gonopore-anus to right of the tail, i.e. to the place where these openings were situated in *C. perneri*. In *N. americana* the gonopore-anus was probably to the left of the tail, for the right part of a gonorectal groove can be seen in the only known specimen and is disposed as in *Cothurnocystis elizae* and most other cornutes. However, the specimen is too damaged to prove the existence of a gonopore-anus between plates i and j.

There was almost certainly no hydropore in *P. menevensis*. This opening existed in *Ceratocystis perneri* where it was a slit crossing the suture of plates f and h. In *P. menevensis* there was no such suture, for plate f did not contact plate h, but the suture of plates f and g had a corresponding position in the head and had no such notch (Pl. 57, fig. 4). It is theoretically possible that a hydropore existed and emerged in the dorsal integument, but this is unlikely since some sort of special organization for it would, in that case, be expected. *C. perneri* is the only cornute known to have had a hydropore, and by outgroup comparison with echinoderms, this is a primitive condition. The absence of a hydropore is an advanced condition and a synapomorphy of *P. menevensis* with all cornutes other than *C. perneri*, with mitrates, and with all other crown-group chordates (including those still extant).

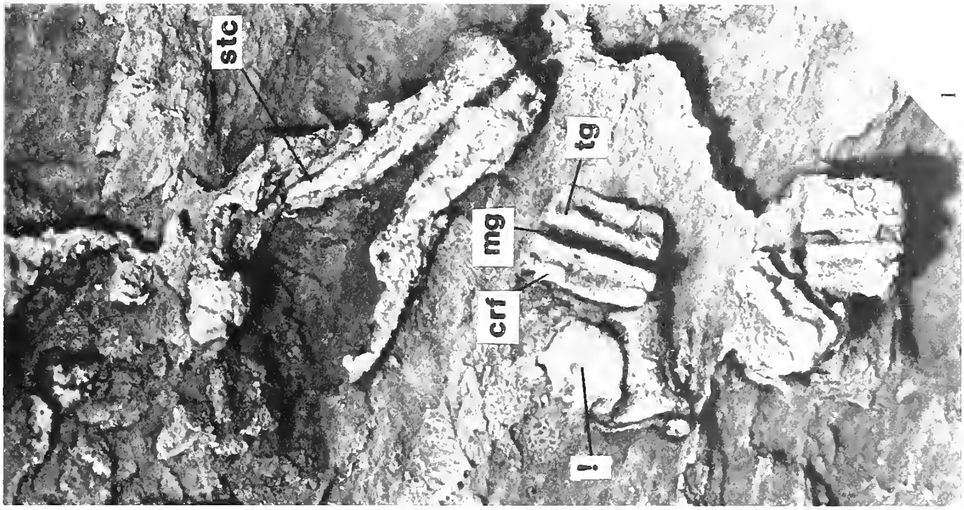
The branchial slits of *P. menevensis* were almost certainly situated just to the left of the tail, in the posterior patch of plated integument, but were not well-defined skeletally. Indeed, the most obvious signs of them are half-moon shaped plates, at least three in number, each of which probably represents the posterior U-plate of a slit (pu in text-fig. 15, cf. Pl. 54, fig. 1). There is space, however, for several other such plates in the specimens. Unlike *N. americana*, there is no definite sign in *P. menevensis* of U-plates framing the slits anteriorly and it may be, as shown in the reconstruction (text-fig. 10), that each slit merely slightly notched the integument anterodorsal to it (this integument is shown in Pl. 54, fig. 1). Comparison with *C. perneri* suggests that the integument anterodorsal to the slits was evolved by the breakup of plate 1, which formed the dorsal margin of all seven slits in *C. perneri*. It is no surprise that the posterior U-plates of *P. menevensis* were differentiated while anterior U-plates were not (or not clearly), since three of the seven gill slits of *C. perneri* had posterior U-plates while none had anterior U-plates. The presumed position of the gill slits of *P. menevensis* is of interest—they would all be posterior to the gentle ridge which ran from plate 2, along plates l_1, l_2, and l_3 to the keel on plate k. This was different from *C. perneri* where two of the slits were anterior to the ridge and only five lay behind it.

EXPLANATION OF PLATE 59

Figs. 1–4. *Protocystites menevensis* Hicks. Latexes, all from loc. 2, Porth-y-rhaw (see text-fig. 7). 1, BM(NH) E63022, stylocone and hind-tail ossicles in dorsal aspect; the ossicle marked ! is seen in anterior or posterior aspect and indicates the original shape in transverse section, × 10·8; crf, crescentic facet; mg, median groove; stc, stylocone; tg, transverse groove. 2 and 3, BM(NH) E62958, a single plate b in dorsal and ventral aspects, × 5·2 and × 8·2 respectively. 4, BM(NH) E62958, a different plate b in ventral aspect, × 4·3.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

PLATE 59



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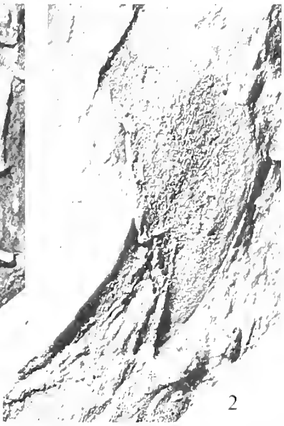

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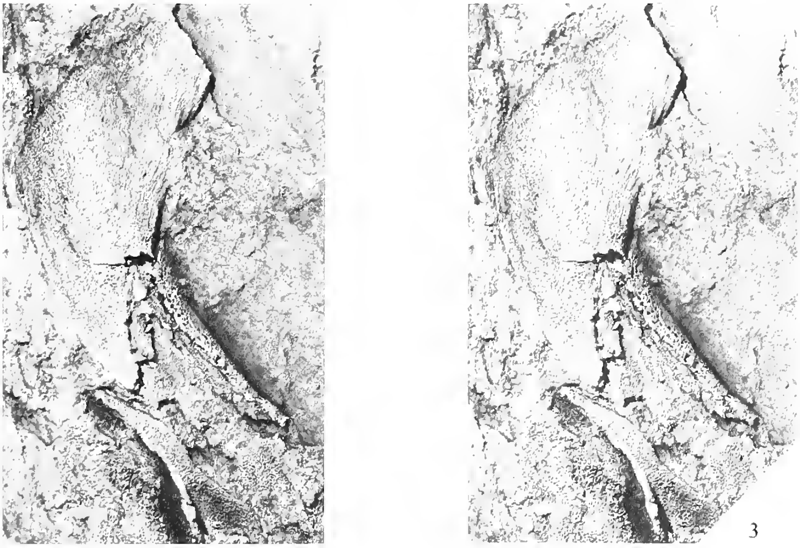

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JEFFERIES, LEWIS and DONOVAN, *Protocystites*

The dorsal groove, which in life probably contained a median eye, was situated in plate y (dg in Pl. 58, fig. 2), at the summit of the dorsal arch of the tail insertion. It is identified as having contained a median eye by comparison with *C. perneri* where it arose in the mid-line from the dorsal face of the brain (i.e. from a region identified as optic by comparison with mitrates and through them with fish; see Jefferies 1986, Chs. 7 and 8) and went up to the dorsal surface of the head where it could readily receive light (Jefferies 1969, p. 521). This eye cannot be homologous with either of the median eyes of modern vertebrates (epiphysis, paraphysis). For these occur only within the monophyletic group of the myopterygians (lampreys + gnathostomes) whereas no median eye exists in: 1, crownward cornutes, e.g. *Cothurnocystis elizae*, *Scotiaecystis curvata* Bather, 1913, and the series of plesions leading crownward of these forms to the mitrates, i.e. *Galliaecystis*, *Amygdalotheca*, *Reticulocarpos hanusi*, and *R. pissotensis* Chauvel and Nion, 1977; 2, the mitrates which were primitive crown chordates and therefore included the latest common ancestor of living chordates; and 3, the myxinoids, which are the living sister group of the myopterygians. The situation of the dorsal groove of *P. menevensis*, notching the ventral edge of plate y, is fundamentally like that of *Ceratocystis perneri* and even more similar, in the small size of plate y, to '*Cothurnocystis*' *fellinensis* and some other cornutes such as *Phyllocystis blayaci* Thoral, 1935, *P. crassimarginata* (Thoral, 1935), and *Chauvelicystis ubaghsi* (Chauvel, 1966) (see Ubaghs 1969). Among known cornutes the presence of plate y with a dorsal groove is certainly a primitive feature.

The narrow groove (ear) of *Protocystites menevensis* is anomalous in some ways. In the one specimen where it has been seen (text-fig. 16; Pl. 55, figs. 1 and 2), it is grossly in the same position as that of *Ceratocystis perneri*, penetrating the posterior wall of the head to the left of the tail. These two cornutes are the only species known to possess such an opening. It seems highly probable that the openings are homologous in both species and, for reasons explained by Jefferies (1986, Ch. 7) with reference to *C. perneri*, that they represent the primitive beginnings of the acustico-lateralis system—or, more precisely, they contained an ear functioning as lateral line. The exact position of the ear of *P. menevensis* is remarkable, however, for it penetrates plate j dorsal to the keel of this plate (Pl. 55, figs. 1 and 2), whereas in *C. perneri* it penetrates plate i ventral to the equivalent keel (which is on plate i) and just dorsal to plate j (text-fig. 11*c*; Jefferies 1969, pl. 95, fig. 1; pl. 96, fig. 10). Although *C. perneri* and *P. menevensis* were the only known cornutes with a narrow groove, it is likely that all cornutes had an ear, for there is evidence of a homologous ear in mitrates (Jefferies 1969, p. 521; 1986, Ch. 8). Probably the ear in most cornutes had become undetectable in the fossils by being conflated with the gonopore-anus. If the gonopore-anus in *C. perneri* is imagined to move from left of the tail to right of the tail, to take up a position between plates i and j as in other cornutes, then the narrow groove would come to be situated in the ventral part of the gonopore-anus. But the narrow groove in *P. menevensis* was separated from the gonopore-anus and is therefore different, not only from that of *C. perneri*, but probably also from that of the ear in all other known cornutes. The fact that the ear is not conflated with the gonopore-anus is therefore a primitive resemblance to *C. perneri*, but its exact position is likely to be a specialization of *P. menevensis* alone.

Flexibility in the heads of Protocystites menevensis, Ceratocystis perneri, *and* Nevadaecystis americana. *C. perneri* (text-fig. 11) shows some signs of flexibility between some of the plates of the head. These signs are of two types: accessory gaps and transversely rounded plate contacts. The accessory gaps are small irregular

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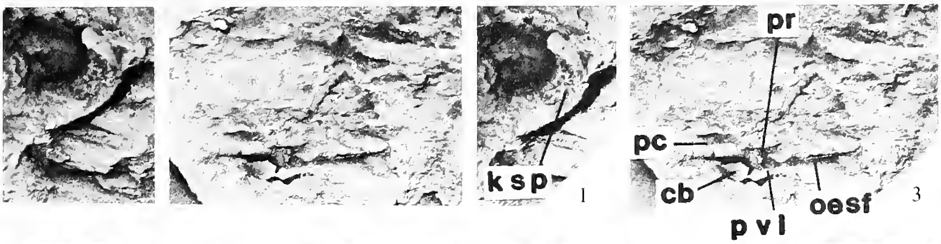
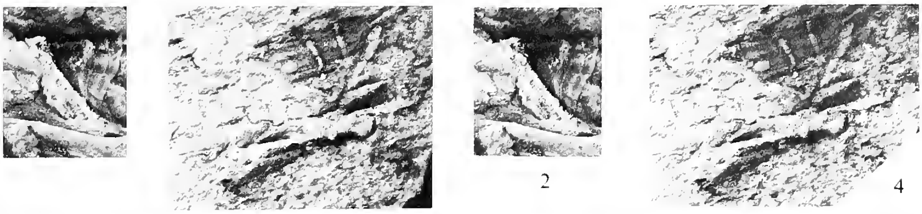
EXPLANATION OF PLATE 60

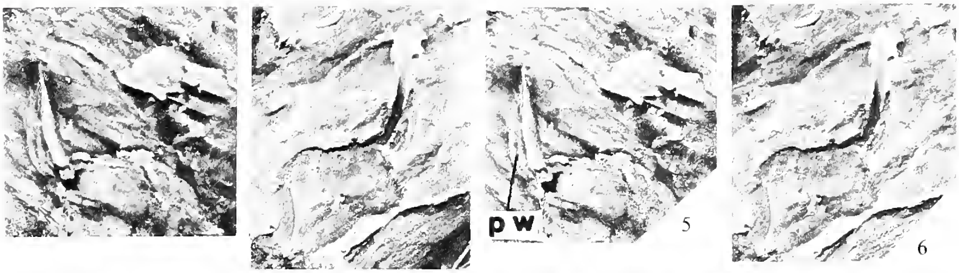
Figs. 1–10. *Protocystites menevensis* Hicks. Isolated plates, all from loc. 2, Porth-y-rhaw (see text-fig. 7). 1 and 2, BM(NH) E63013, latexes of plate k in posteroventral and posterodorsal aspect respectively, both ×4·1; ksp, k-spike. 3 and 4, BM(NH) E62952, latexes of a plate g in dorsal and ventral aspects to show the irregularly disposed ribs in the anterior part of the plate, ×3·9; cb, cerebral basin; oesf, oesophageal fold; pc, posterior coelom; pr, process separating right anterior coelom from posterior coelom (equivalent to cleft in fig. 9, etc.); pvl, pharyngo-visceral line. 5–7, BM(NH) E62958, all showing the same plate; 5 and 6, latexes in ventral and dorsal aspect; 7, natural mould in ventral aspect (cf. Pl. 57, fig. 4), all ×8·7; int, intestine; sto, stomach; pw, pharyngeal wall; pvl, pharyngo-visceral line. 8, BM(NH) E62958, latex of plate l in ventral aspect (same plate as Pl. 58, fig. 3), ×4·6; lsp, l-spike; rs, retiform stereom. 9 and 10, BM(NH) E63034, a plate g as natural mould in ventral aspect and as corresponding latex in dorsal aspect, both ×5·6; br, brain; cl, cleft between posterior coelom and right anterior coelom; gr, gonoduct-rectum; oes, oesophagus; pc, posterior coelom; st, change in stereom from almost imperforate at right posterior to thin and retiform at left anterior.

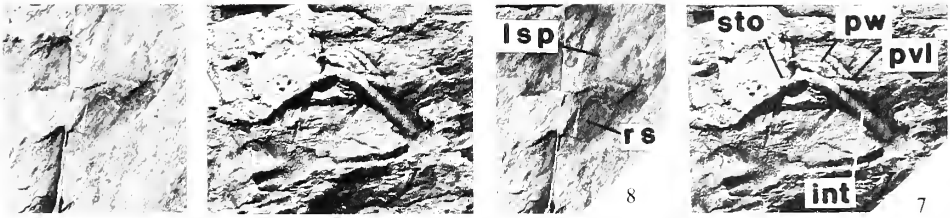
When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

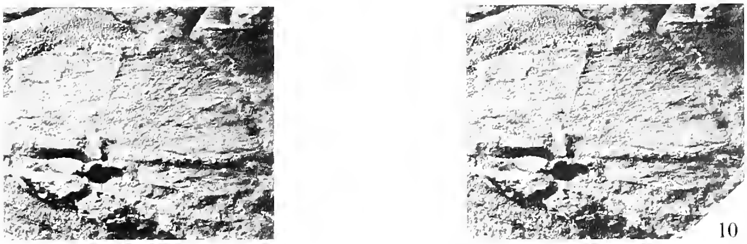
PLATE 60











JEFFERIES, LEWIS and DONOVAN, *Protocystites*

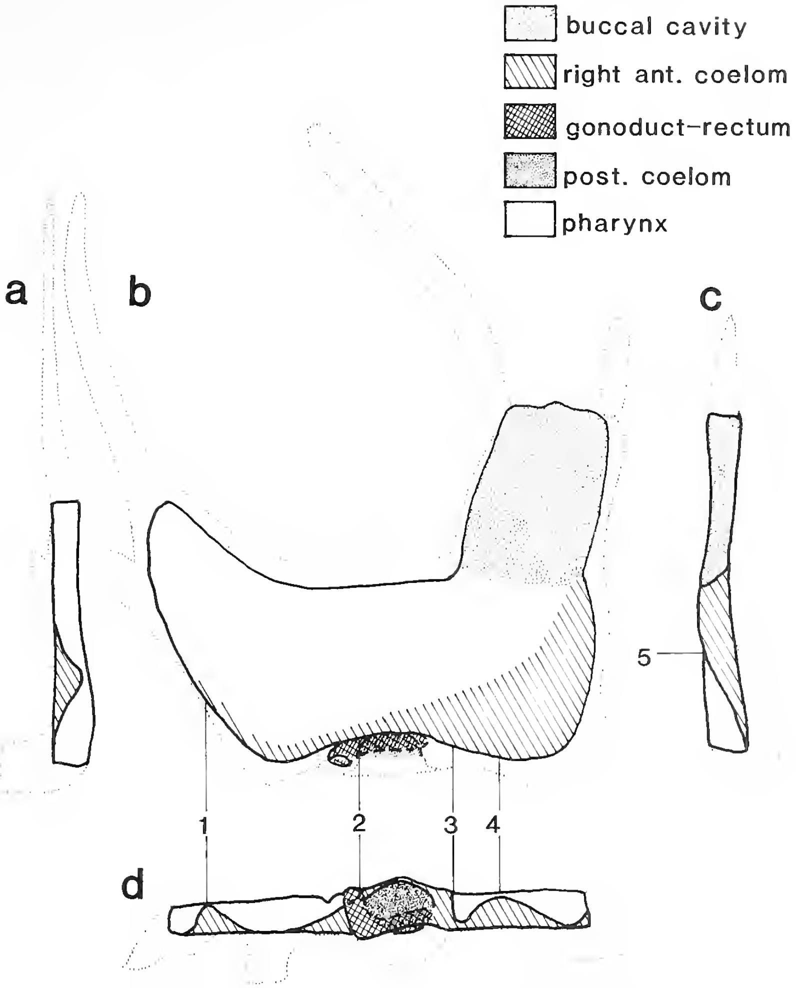
voids situated along the dorsal margins of plates k and l (at their junctions with plates u and 1) and along the ventral (or posterior) margins of the three posterior branchial U-plates, where these joined plates k, i, and y. The accessory gaps were therefore situated at the edges of areas which in *P. menevensis* were flexible, i.e. the left anterior integument and the integument posteroventral to the gill slits. This in turn suggests that the accessory gaps in *C. perneri* represented the beginnings of flexibility in the head—meaning, in this species, the ability slightly to raise and lower the roof.

Transversely rounded plate contacts in *C. perneri* occurred near the right side of the head, along the contacts of plates e and f, plates 5 and e, and plates c and d (text-fig. 11*b*). The most striking was that between plate 5, whose ventral edge was convexly cylindrical, and plate e, whose dorsal edge was concave to receive the opposed cylindrical edge of plate 5. These cylindrically rounded plate contacts were almost continuous with each other in *C. perneri* and would have formed a sort of hinge line near the right side of the head—a line along which minimal rotation would have allowed the roof to be raised or depressed slightly. In *P. menevensis* the dorsal border of plate e made contact partly with integument and partly with centrodorsal plate 5 (text-fig. 15; Pl. 54, figs. 1 and 3). The right integument of *P. menevensis*, being flexible, could presumably inflate and deflate; in this motion, plate 5 would rotate about its contact with plate e, exactly as deduced for *C. perneri* but probably to a greater extent. This situation in *P. menevensis* therefore tends to confirm that the supposed right hinge line of *C. perneri* indeed acted as such. The rest of the right hinge line of *C. perneri*, however, does not seem to have been specially flexible in *P. menevensis*, so far as can be deduced from the ill-preserved fossils. Rather the line of flexibility between plates 5 and e would have passed forward between plates 3 and c and rearward between the dorsal integument and the dorsal edge of plate f. To sum up, signs of slight flexibility between the head plates of *C. perneri* largely correspond to signs of greater flexibility in *P. menevensis*, but there are exceptions where the correspondence does not hold.

The dorsal surface of *N. americana* (text-fig. 12), though not completely known, seems to have been more flexible than that of *P. menevensis*. Thus neither plate 3 nor plate 5 is definitely recognizable, presumably being represented by plates of the dorsal integument of the right side of the head. Plate ü is represented by three adjacent plates, not by one, or perhaps two, as in *P. menevensis*. On the other hand, plate 6 of *N. americana* is larger and more recognizable than that of *P. menevensis*. Indeed, it is possible that the plate labelled 2 in *P. menevensis* is in fact equivalent to 2+6 of *C. perneri* and *N. americana*. Concerning the dorsal integument in the left part of the head in *N. americana*, there is little direct evidence. However, there is a three-rayed keel on plate 2 and the left posterior ray of this keel points towards the left extremity of the head. Perhaps this ray, as in *P. menevensis*, was continued leftward by a line of keeled plates disposed anterior to the gill slits (though no such plates are preserved in the only known specimen). Unlike *P. menevensis*, such a crest cannot have led to plate k, which is entirely posterior to the gill slits in *N. americana* and carries no crest. To sum up, *N. americana* has the same three dorsal integuments as in *P. menevensis* (1, right; 2, posterior; 3, left anterior), and these three integuments are larger relative to the individualized dorsal plates. It is possible that the left anterior integument of *N. americana*, unlike *P. menevensis*, was not entirely separate from the posterior integument.

The chambers and soft anatomy of the head. Considering cornutes as a whole, there is direct evidence for four chambers in the head, and presumptive comparative evidence for a fifth (Jefferies 1986, Ch. 7). The chambers for which there is direct evidence were the buccal cavity, the right anterior coelom, the posterior coelom, and the pharynx (left or primary pharynx) (text-figs. 20–22). The chamber for which the evidence is purely comparative is the left anterior coelom. The evidence for these chambers is different in different cornutes but they probably all existed in all of them. A modification of the cornute arrangement occurred in mitrates, but differed in several ways, chiefly in the existence of a right pharynx, with right gill slits, as well as a left pharynx.

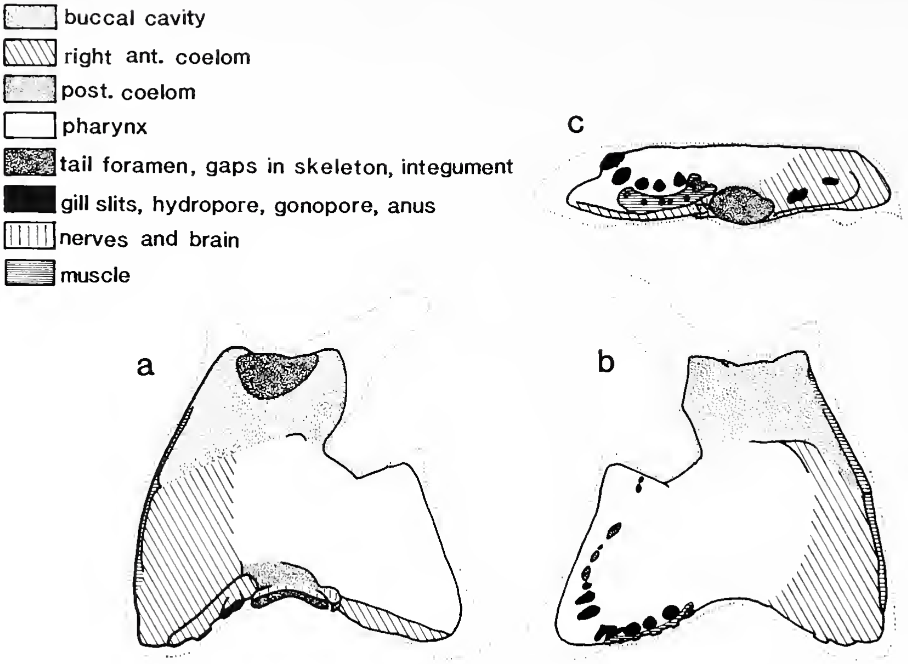
The evidence for these head chambers in cornutes can be exemplified from *Cothurnocystis elizae* (text-fig. 20). (For a complete discussion, see Jefferies 1986, Ch. 7.) In this species the buccal cavity filled the 'ankle' part (buccal lobe) of the boot-shaped head, immediately behind the mouth. It is defined posteriorly on the right by a vertical ridge on the inside face of plate e and posteriorly on the left by the right-angle bend in plate a which delimits the buccal lobe or, in one specimen, by a vertical ridge on the inside face of plate a just anterior to that bend. In middle-sized specimens of *C. elizae* there is also a difference in the plates of the dorsal integument as between the buccal cavity and regions posterior to it: over the buccal cavity, the plates are polygonal without gaps between them, whereas behind the buccal cavity, over the pharynx, the plates are circular and separated by gaps—perhaps suggesting, if there were muscles in the gaps, that the dorsal wall of the pharynx was more muscular than that of the buccal cavity. The posterior coelom in *C. elizae* was a small, approximately hemispherical chamber just anterior to the tail and convex anteriorly. It was defined



TEXT-FIG. 20. *Cothurnocystis elizae* Bather; the chambers of the head (redrawn after Jefferies 1968, text-fig. 4). 1–5 are the high points of the pharyngo-visceral line. *a*, left lateral; *b*, dorsal; *c*, right; and *d*, posterior aspects.

anteroventrally by an anteriorly convex ridge on the upper, interior surface of plates g and j and would have made contact anterodorsally with the concave posteroventral surfaces of plates h and i. A gonorectal groove, indicating the position of gonoduct and rectum, traversed the floor of the posterior coelom from right to left and climbed vertically upwards near its end to finish at the gonopore-anus to the left of the tail. The posterior coelom was homologous with the left epicardium of tunicates (Jefferies, in press, Ch. 7 and 8).

In the 'foot' part of the boot in *C. elizae*, there is direct evidence for two further chambers, one overlying the other. The upper chamber is characterized in the larger specimens by a special ornament on the internal surfaces of the marginal plates: a decussate ornament of strong horizontal lines crossed by weak vertical ones. The branchial slits opened through the roof of this chamber, so it can be identified as the pharynx. The lower chamber was mainly situated in the posterior right corner of the head and is characterized by the smooth surface of the stereom where the chamber made contact with the inside faces of the marginal plates. A sharp but undulating line (the pharyngo-visceral line) separated the smooth areas from the overlying ones of decussate pharyngeal sculpture. The undulations of the pharyngo-visceral line are the same in different specimens, and there are five high points where it made contact, or almost so, with the upper edge of the



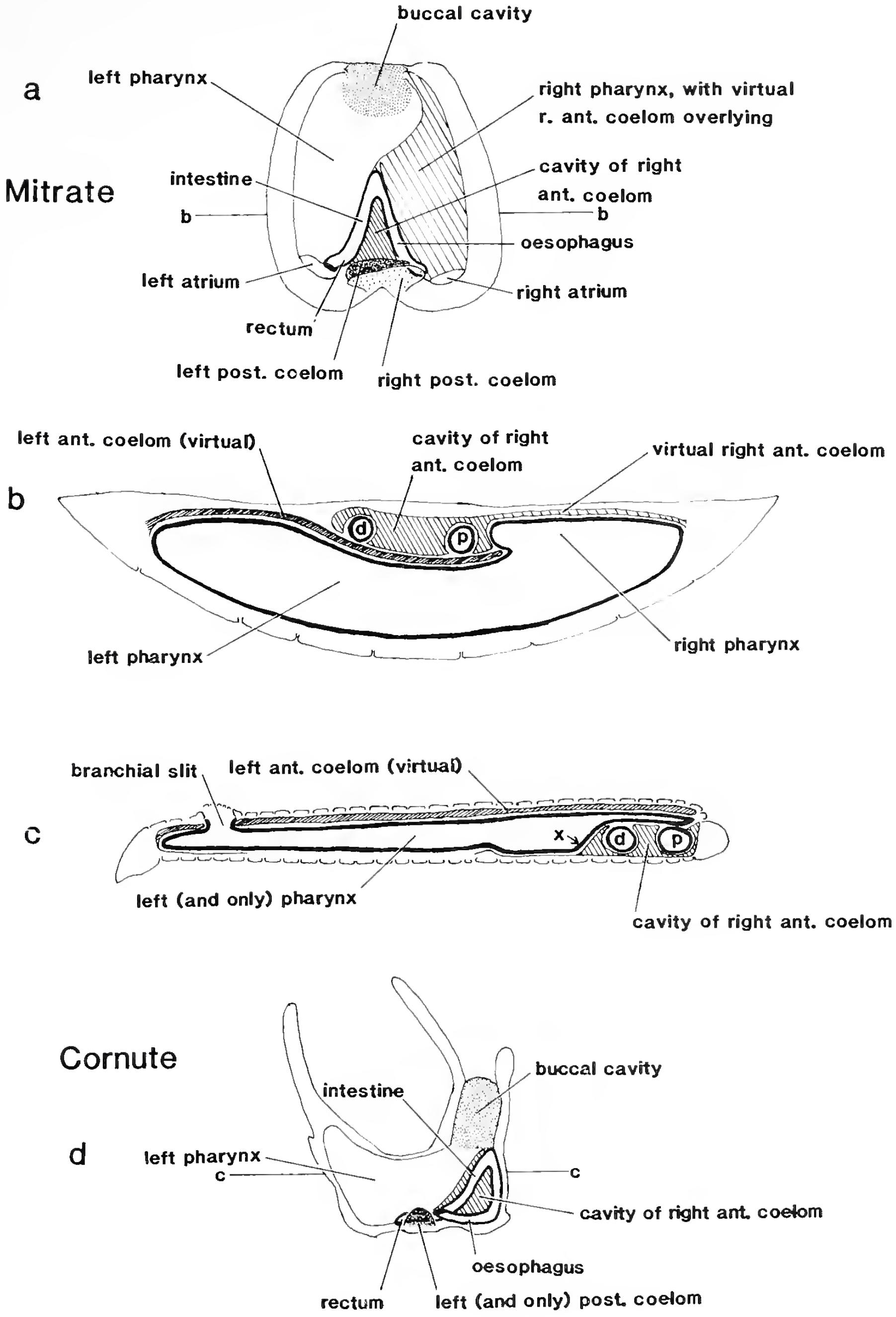
TEXT-FIG. 21. *Ceratocystis perneri* Jaekel; the chambers and other soft parts of the head (redrawn after Jefferies 1969, text-fig. 10). *a*, ventral; *b*, dorsal; and *c*, posterior aspects.

marginal plates. These points are numbered 1 to 5 from left to right. The gonorectal groove, which passes under the posterior coelom, emerges on the right from the lower chamber and approaches the posterior coelom from anterior right. If the groove indeed carried the gonoduct and rectum, then the non-pharyngeal gut (except the rectum) and the gonad were situated in this lower chamber, which therefore functioned as coelom; we call it the right anterior coelom.

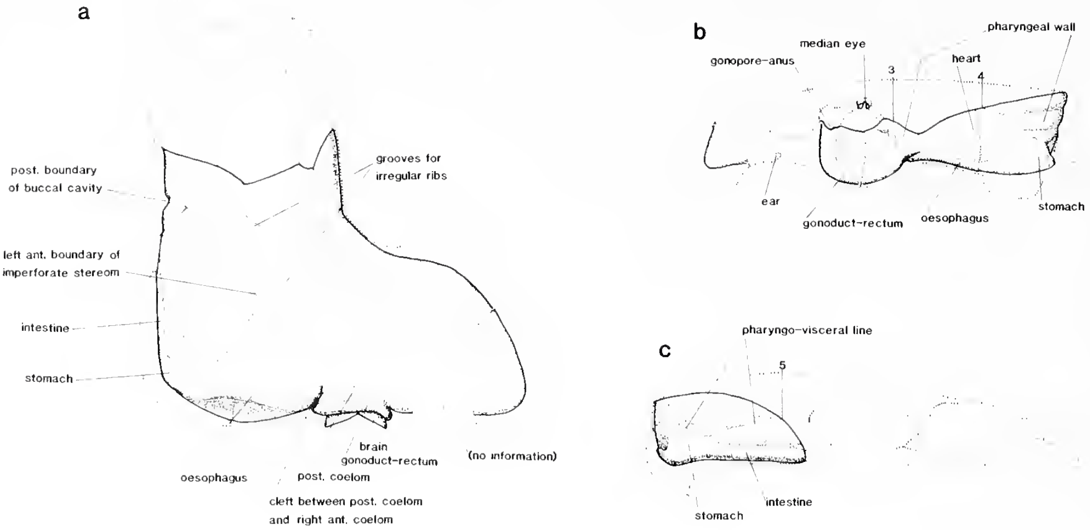
The fifth chamber in *C. elizae*, for which there is only comparative evidence, can be called the left anterior coelom. It probably overlay the pharynx and buccal cavity and would probably have been virtual (i.e. with no open cavity). It corresponds to the left somatocoel of echinoderms (which faces upwards in crinoids), the left mandibular somite of vertebrates and acraniates, and the left metacoel of hemichordates. Once again, the arguments for its existence can be found in Jefferies (1986, Chs. 7 and 8).

The same chambers probably also existed in *Ceratocystis perneri* (text-fig. 21). Here again, there is direct evidence for buccal cavity, right anterior coelom, posterior coelom, and pharynx; and the left anterior coelom is presumed to have existed. The main differences in the head chambers between *C. perneri* and *Cothurnocystis elizae* were: 1, in *Ceratocystis perneri* the right anterior coelom was extensively in contact with the right side of the head, whereas in *Cothurnocystis elizae*, so far as is determinable, it made contact only with the right and posterior faces of the marginals; 2, in *Ceratocystis perneri* the hydropore, gonopore, and anus opened direct from the cavity of the right anterior coelom, passing through the posterior wall of the head to the right of the tail, whereas in *Cothurnocystis elizae* there was no hydropore and the gonopore-anus was to the left of the tail, connected with the right anterior coelom by gonoduct and rectum which traversed the floor of the posterior coelom (as indicated by the gonorectal groove).

In *P. menevensis* the same chambers probably existed as in other cornutes. The buccal cavity presumably occupied the 'ankle' part of the boot-shaped head, i.e. the buccal lobe. Its probable right posterior margin was defined by a triangular wedge of callus on the internal face of plate e (pbbc in text-fig. 15, cf. Pl. 54, figs. 1 and 3; text-fig. 17 and Pl. 54, fig. 1; Pl. 56, fig. 1; Pl. 58, fig. 4), this wedge being comparable in position to the ridge on the internal face of plate e in *C. elizae* and many other cornutes. The posterior coelom was well defined ventrally by a crescentic area on the floor of the head just to the left of the tail. This crescent was concave upwards (pc in Pl. 54, fig. 4; Pl. 55, fig. 3; Pl. 56, fig. 3; Pl. 57, fig. 4; Pl. 58, fig. 4) and floored by



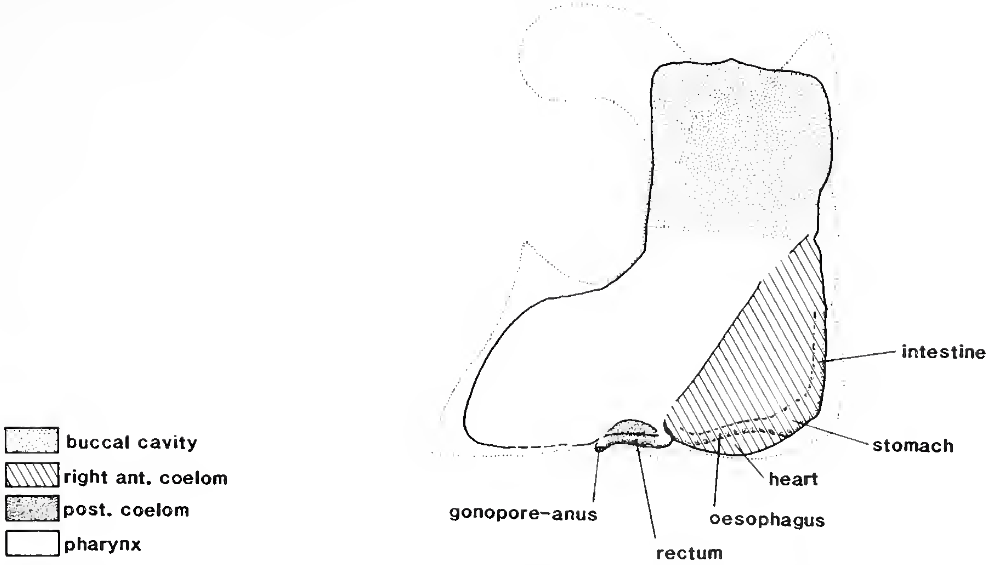
TEXT-FIG. 22. The soft parts of the head in: *a*, *b*, a mitrate (*Mitrocystites*); and *c*, *d*, a cornute (*Cothurnocystis*) (redrawn after Jefferies 1981*a*, fig. 5). *a*, dorsal aspect; *b*, section through b–b of *a*; *c*, section through c–c of *d*; *d*, dorsal aspect. The mitrate condition can be derived from the cornute condition mainly by origination of a right pharynx, which would have appeared at the point x of *c*.



TEXT-FIG. 23. *Protocystites menevensis* Hicks; reconstructed internal natural mould (i.e. soft parts). *a*, ventral; *b*, posterior; and *c*, right lateral aspects. The reconstruction stops arbitrarily at the anterior margins of plates a, e, and x.

almost imperforate stereom (text-fig. 23*a*; Pl. 55, fig. 3), by contrast with the floor anterior to it, which is made of thin, retiform stereom stiffened with ribs. A distinct gonorectal groove crosses the floor of the posterior coelom transversely and climbs upwards to the left of the tail to end at the gonopore-anus (Pl. 56, fig. 3). Thus the gonoduct and rectum would have crossed the floor of the posterior coelom, as in *C. elizae* and all known cornutes except *Ceratocystis perneri* where, as already stated, the gonopore-anus was to the right of the tail. A high wall rising from the floor of the head in plates g and j formed the posterior limit of the posterior coelom (vw in Pl. 54, fig. 4) and separated that chamber from the deduced position of the brain. The latter was situated in a distinct cerebral basin (Pl. 54, figs. 1 and 4; Pl. 60, fig. 3) excavated in plates g and j and faced with almost imperforate stereom. In having such a basin, with a high wall in front of it, *P. menevensis* once again differed from *C. perneri* and resembled more crownward cornutes such as *Cothurnocystis elizae*. Anterodorsally, the limit of the posterior coelom presumably coincided with the posteroventral surfaces of plates h, y, and i, but these surfaces have not been seen in the available specimens.

Regarding the chambers in the remainder of the head—behind the buccal cavity but in front of the posterior coelom—*P. menevensis*, like other cornutes, probably had a pharynx overlying a right anterior coelom, with the latter lying mainly in the posterior right portion of the head. As to the evidence, in the posterior wall and right wall of the head, on the inside faces of plates g and f, a clear pharyngo-visceral line is visible (text-fig. 23*c*; pvl in Pl. 57, fig. 4; Pl. 60, figs. 3, 6, 7). This line separates a smooth, almost imperforate, surface below, with a thick wall of stereom, from retiform stereom above, forming a very thin wall. Indeed, in the anterior part of plate f the stereom above the line is not merely retiform but thrown into horizontal folds, like those in the pharyngeal ornament of *C. elizae*. Moreover, the wall of plate f is so thin above the line in this region that the folds are visible from outside, and thus the pharyngo-visceral line can be detected externally (text-fig. 10*d*; pw in Pl. 60, fig. 5). Also, the undulations of the line in the right part of the head are the same as in *C. elizae* with high points 3, 4, and 5 clearly recognizable. It is reasonable to suppose that, as with *C. elizae*, the marginal plates were in contact with the pharynx above the pharyngo-visceral line (or rather with virtual left anterior coelom embracing the pharynx) and with right anterior coelom beneath it. Moreover, the left boundary of the right anterior coelom, or at least the cavity of that coelom, is indicated in *P. menevensis* by a change in the stereom in the floor of the head. Thus, in the right posterior portion of the head, in plates f and é (Pl. 54, fig. 1), in the posterior right parts of plates g (Pl. 55, fig. 3; Pl. 60, fig. 9) and a (Pl. 56, fig. 1, for the internal surface of the plate; Pl. 55, fig. 1 for the external surface), and in the right posterior part of plate e,



TEXT-FIG. 24. *Protocystites menevensis* Hicks; the chambers and other soft parts of the head in dorsal aspect.

the upper surface of the floor of the head is constructed of almost imperforate stereom, continuous with that below the pharyngo-visceral line in the right and right posterior wall of the head. The left anterior limit of such stereom is a line running forwards and rightwards from near the right side of the tail insertion (text-fig. 23*a*); and to the anterior left of this line, the floor stereom is of different nature being thin and retiform, except where it is thickened by ribs (space-frame construction). The region of almost imperforate stereom, whether in the floor or in the posterior faces of the posterior and right walls below the pharyngo-visceral line, was probably in contact with the right anterior coelom and indicates the extent of that chamber. The rest of the floor of the head, left of the area of almost imperforate stereom, was presumably overlain by pharynx, though perhaps there was, beneath the pharynx but above the stereom, a purely virtual extension of right or left anterior coeloms in this region. The pharynx would also have made contact with the posterior and right walls of the head dorsal to the pharyngo-visceral line (though again it would probably have been clothed with virtual left anterior coelom). As in other cornutes, the branchial slits, just to the left of the tail insertion, would penetrate the roof of the pharynx.

The pharyngo-visceral line cannot be traced to the left of the tail insertion. This is because no known specimens show the internal face of the left part of plate j.

A process on the internal surface of plate g, and a corresponding cleft in the natural mould (text-fig. 23*a*; Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10), is situated between the deduced positions of the posterior coelom and the right anterior coelom. It varies in shape, but tends to be anteroposteriorly elongate. Probably this process was intercameral and represented the stereomic infilling of a gap between the limiting epithelia of the posterior and right anterior coeloms. As already mentioned, this process is situated in a position corresponding to the posterior end of the strut in cornutes more crownward than *P. menevensis*. It may represent the evolutionary beginnings of the strut.

The left anterior coelom probably covered the whole of the dorsal surface of the pharynx in *P. menevensis* but had no cavity, being solely virtual. As with other cornutes, and also with mitrates, the arguments for its existence are purely comparative.

As to the contents of the right anterior coelom, the most direct evidence comes from *Ceratocystis perneri*, where the hydropore, gonopore, and anus opened directly out of it. In that species, therefore, the right anterior coelom is likely to have contained the non-pharyngeal gut, the gonad, and whatever organs were associated with the hydropore. Among the latter, the heart and pericardium were probably included for the pulsatile madreporic vesicle (pericardium) and the contained head process of the axial organ (heart) are situated near the hydropore in living echinoderms. Important evidence as to the contents of the right anterior coelom comes also from mitrates such as *Placocystites forbesianus* (Jefferies and Lewis, 1978) (Jefferies 1986, Ch. 8). In mitrates, however, the position of the right anterior coelom, hanging from the ceiling of the head near the mid-line, is governed by the right pharynx which in cornutes did not exist. Clear signs indicate that the oesophagus of mitrates opened from the right posterior coelom into the pharynx to the right of the mid-line, near the posterior right corner of the cavity of the right anterior coelom (as shown in text-fig. 22*a*). From here, the non-pharyngeal gut ran forward to an unknown extent, along the right margin of the cavity of the right anterior coelom, turned through an angle, and ran rearwards along the left margin of this cavity to join the rectum, which debouched into the left atrium. The gonad was probably situated in this loop of the gut, partly because the gonoduct seems to arise from this position in the mitrate *Mitrocystella*, and partly because the gonad is situated in the loop of the gut in enterogonous tunicates. The contents of the right anterior coelom of mitrates is further discussed by Jefferies (1986, Ch. 8).

The cornute condition of the right anterior coelom can partly be deduced by mentally subtracting the right pharynx from the mitrate condition, reversing what happened in evolutionary history. This would allow the cavity and contents of the right anterior coelom to fall to the floor of the head and to occupy the posterior right portion of the head, as seems to have been true in *C. perneri*, *Cothurnocystis elizae*, *Protocystites menevensis*, and other cornutes. In that case, the non-pharyngeal gut would follow the periphery of the cavity of the right anterior coelom (as suggested in text-fig. 22*d*). Part of the intestine would run leftwards and rearwards along the left margin of the cavity to join the rectum in the posterior coelom. (There is direct evidence in *C. elizae* that the intestine approached the rectum by running leftwards and posteriorly, but in *P. menevensis* the internal moulds indicate that it probably joined the rectum by running almost vertically downwards.) And the oesophagus of cornutes would run rightwards, from a position to the right of the tail insertion, just in contact with the right posterior wall of the head.

Some direct indication of the non-pharyngeal gut inside the right anterior coelom of *P. menevensis* is probably given by the internal sculpture of plates g and f. As already mentioned, a distinct fold in plate g, concave upwards and convex downwards (Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10) and corresponding to a horizontal hemicylinder on the surface of the natural mould, runs rightwards into plate f (Pl. 55, fig. 4) and coincides with the position of the oesophagus as reconstructed above for cornutes in general; we assume that the fold carried the oesophagus and therefore call it the oesophageal fold. This fold is ventral to high point 4 of the pharyngo-visceral line but makes up only a small portion of the internal surface beneath that high point. Some other organ, as discussed later, presumably filled the area between the oesophageal fold and the pharyngo-visceral line. More anteriorly, in the right wall of plate f (Pl. 57, fig. 4; Pl. 60, figs. 6 and 7), the pharyngo-visceral line ascends towards high point 5. On the internal natural moulds, however, the surface beneath this line is complex in this region. Ventrally the natural mould formed a horizontal hemicylinder whose upper edge was distinct from, and much more ventral than, the pharyngo-visceral line and whose radius was about the same as that suggested for the oesophagus by the oesophageal fold. This hemicylinder corresponds to a groove on the inner face of plate f and presumably it too carried a portion of the gut. More posteriorly, just anterior to the right posterior angle of the head, the hemicylinder expands into something more inflated. This inflation may represent the stomach (Pl. 57, fig. 4; Pl. 60, fig. 7), in which case the gut anterior to it would be part of the intestine.

The organ beneath high point 4 but dorsal to the presumed oesophagus may have been the pericardium and heart. This conclusion, which is highly tentative, is based on two opposite approaches. First, the position roughly coincides with that of the hydropore in *Ceratocystis perneri*; and the heart and pericardium of echinoderms (head process of axial gland and madreporic vesicle) are located just internal to the hydropore. Secondly, the heart of tunicates is located on the right side of the gut, as may have been true of mitrates also. If so, then mental subtraction of the right pharynx to yield the cornute condition would bring the heart against the right posterior wall of the head, next to the oesophagus, to occupy the observed space above the oesophageal fold but beneath high point 4. We believe that the grounds for placing the heart, gonad, and non-pharyngeal gut somewhere inside the right anterior coelom are reasonably strong. The reasons for putting them in particular grooves and depressions in the inner face of the skeleton are necessarily weaker.

Not much can be said about the brain and cranial nerves of *P. menevensis*. The brain, as already mentioned, would have occupied a well-defined cerebral basin excavated in plates g and j (Pl. 54, fig. 1; Pl. 55, fig. 3; Pl. 60, figs. 9 and 10) and faced with almost imperforate stereom. This basin formed part of the posterior surface of the wall that stood behind the posterior coelom. The brain would have extended upwards into the median eye (occupying the dorsal groove) in the posterior surface of plate y (Pl. 58, fig. 2). The left and right pyriform bodies (trigeminal ganglia), which were present in all other cornutes just anterior to the brain, could not be located in *P. menevensis*. If they existed, they either made no contact with the skeleton or else the specimens are too crumpled to show them.

The tail. The tail of *P. menevensis*, like that of all other cornutes, is divided into fore, mid, and hind regions. In text-fig. 10 it is shown as small and slender relative to the head, when compared with *Cothurnocystis elizae* or *Ceratocystis perneri*, for instance. This may be correct but, because of tectonic distortion, it is impossible to be sure. The abrupt end of the tail is usual, or perhaps universal, in cornutes and mitrates, and in general probably means that more distal segments were regularly lost by autotomy, perhaps several times in the life of the animal. In *P. menevensis*, however, none of the observed tails is well enough preserved to show how it terminated. The reconstruction of the fore tail was particularly difficult, for its dorsal surface is not shown adequately by any specimen.

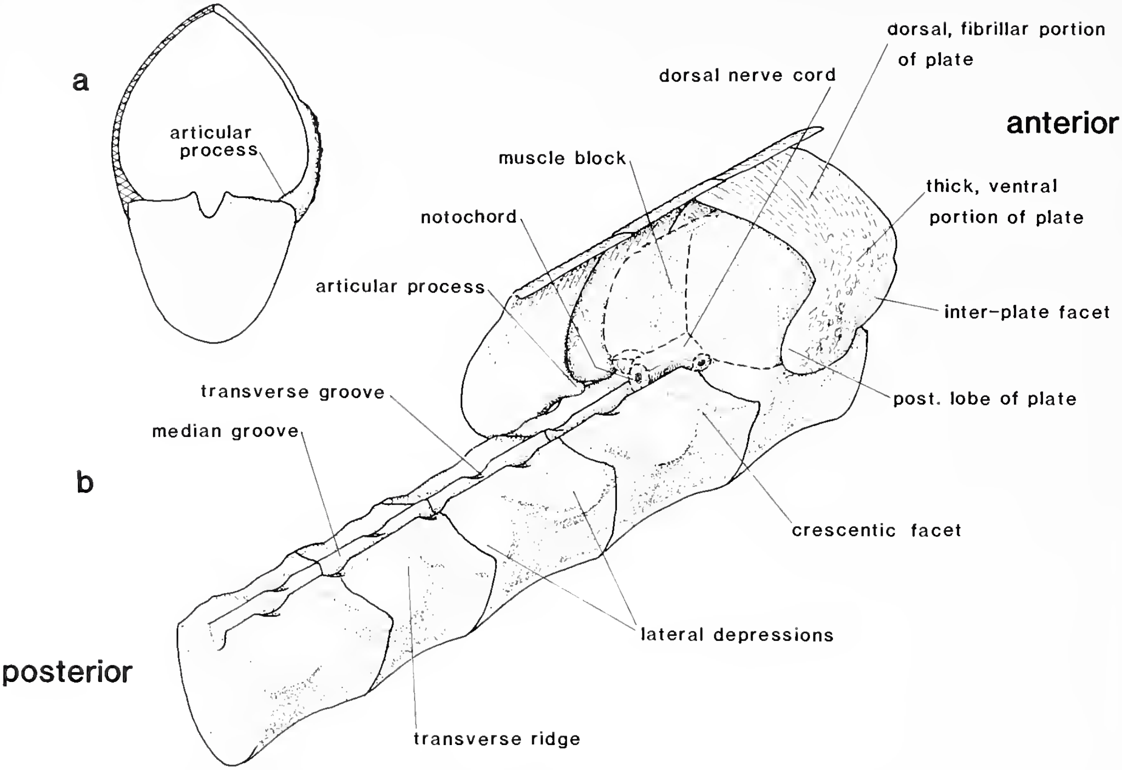
The skeleton of the hind tail consisted of a median series of ventral ossicles, approximately hemicylindrical in shape, and dorsal plates arranged in right and left series (Pl. 56, figs. 1, 2, 4, 5; Pl. 57, figs. 1 and 2; Pl. 59, fig. 1). So far as can be judged, the plates were not opposite each other on the right and left. Neither were they uniformly related to the ventral ossicles beneath them: the number of plates in the left and the right series, as indicated in particular by the repetition of segmental structures on the dorsal surface of the ossicles, is greater than the number of ossicles, i.e. there is somewhat more than one plate per ossicle on each side proximally, and about two plates per ossicle on each side distally.

The ossicles in life were probably about as wide as deep, as suggested by a specimen whose longitudinal axis lies perpendicular to the bedding plane (Pl. 59, fig. 1). The dorsal, interior surface of the series of ossicles (Pl. 56, fig. 2; Pl. 59, fig. 1) bore a deep median groove which was rounded V-shaped in transverse section. The walls which formed the right and left sides of the groove were intermittently notched by semicircular transverse grooves, but the notches, like the plates, were not opposite each other, nor uniformly related to the ossicles that bore them. Lateral to each notch was a depression in the dorsal surface of each ossicle, each depression being separated from those more proximal and more distal by a transverse ridge. (Each notch is located near the anterior end of the corresponding depression.) The dorsal surface of the ossicles varied in width, being narrowest at the ridges and widest at the depressions. At the lateral end of each ridge there was a flat crescentic facet, concave outwards, which received the articular process of the corresponding dorsal plate.

The dorsal plates, as seen in the specimens, are usually spread out on the bedding plane on either side of the ossicles, being slightly concave on the original internal surface and slightly convex on the original external surface (Pl. 56, fig. 2; Pl. 57, fig. 2). In our view, the outward spread of the plates is preservational and caused by the explosive release of the gases of putrefaction from the soft tissues of the hind tail after death; and the slightness of curvature of the plates probably results from post-mortem compaction perpendicular to the bedding plane. (Ubaghs, who believes that the plates of cornutes could open outwards in life (1981), would probably dispute both these views.) The plates in text-fig. 25 are reconstructed with greater curvature than observed, on the assumption that the median groove of the ossicles contained the notochord and this, being anti-compressional, would lie in the mechanical neutral axis of the hind tail, and therefore near the centre of the hind tail in transverse section. The deduced curvature of the plates is similar to that seen in *C. perneri*, *N. americana*, or *Cothurnocystis elizae*, for example.

Each dorsal plate consisted of a thick-shelled ventral portion and a thin-shelled dorsal portion. The thin-shelled portions presumably met those of the opposite side of the tail at a median dorsal suture, and the edge of such a plate where it would have met the suture is visible in Plate 56, fig. 2 (ms). However, such a median dorsal contact between the dorsal hind-tail plates of the left and right sides has never been seen in the fossils. As already mentioned, it is unlikely that a plate of the left side was ever exactly opposite one of the right, and vice versa. The thick-shelled part of the plate was formed of labyrinthic stereom externally, and of smooth, almost imperforate, stereom internally. The thin-shelled part of the plate consisted of fibrillar stereom, with the fibres directed approximately parallel to the posterior and anterior edges. The thick-shelled part had a convex posterior outline which formed a ventral lobe, and this lobe overlapped the posterior part of the next plate behind. The external surface of the anterior part of the thick-shelled portion of the plate bore a smooth facet (inter-plate facet) which would have slid against the inside face of the next plate in front. The thin-shelled part of each plate probably slightly overlapped the corresponding part of the next plate behind. The anteroventral angle of each plate was produced medianward into an articular process which made contact in life with the crescentic facet on the ventral ossicle.

Three segmentation series, therefore, seem to have existed in the hind tail: 1, that of the ossicles mid-ventrally; 2, the left series of dorsal half-segments; and 3, the right series of dorsal half-segments. The skeleton of each half-segment contained: 1, a plate with its thin- and thick-shelled portions, ventral lobe, articular process, and inter-plate facet; 2, a depression on the dorsal surface of the ossicles, between two successive transverse ridges; and 3, a transverse groove (notch) leading into that depression from the median groove. Each half-segment would have had corresponding soft parts whose nature will be discussed later. Left and right half-segments were about equal in number, but not opposite each other and had no one-to-one



TEXT-FIG. 25. *Protocystites menevensis* Hicks; anatomy of the hind tail. *a*, anterior aspect of a hind-tail ossicle with attached dorsal plates; *b*, posterodorsal aspect of several ossicles and plates. The dorsal nerve cord is shown as overlying the notochord by analogy with the mitrates.

relationship with the ventral ossicles. One specimen suggests that, when the dorsal plates and corresponding soft parts had been lost, the column of ventral ossicles would curve downwards under its own elasticity so as to be concave ventrally (Pl. 56, figs. 4 and 5). This specimen suggests that such would be the relaxed condition of the hind tail during life.

The fore tail would have had a large lumen. The skeleton of the ventral surface of the fore tail can be restored with some confidence (cf. text-fig. 18 and Pl. 57, fig. 1). There were about three ventral plates on the left and right, and these overlapped each other in the ventral mid-line and alternated. A similar alternation occurred in *Ceratocystis perneri* (text-fig. 11*b*) where, however, there were many more half-segments on each side (about seventeen instead of about three). The dorsal surface of the fore tail is much harder to reconstruct. In text-fig. 10 the left and right dorsal series of plates, three plates in each series, are shown and the plates of left and right sides are shown as alternating. All this may have been true, partly by analogy with *C. perneri*, but the relevant specimens are smashed to pieces in this region. One specimen (the lectotype, text-fig. 17 and Pl. 56, fig. 1), however, shows a single reasonably complete dorsal plate, so the reconstruction is plausible. It is clear that, as in other cornutes, the skeleton of the fore tail was looser than that of the mid and hind tails and would have allowed much movement. The mid-ventral alternation of left and right plates suggests that most of the movement was flexion from side to side.

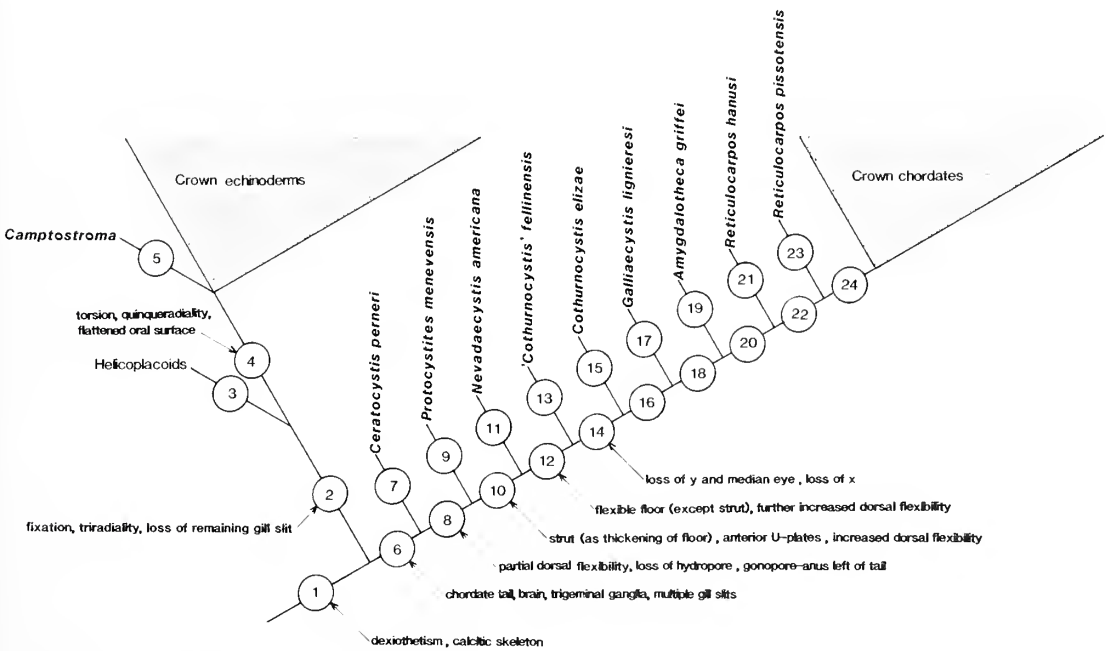
The skeleton of the mid tail consisted of a massive stylocone ventrally (text-fig. 15 and Pl. 56, fig. 1; text-fig. 17 and Pl. 57, fig. 1; Pl. 58, fig. 1; Pl. 59, fig. 1) and presumably there were left and right series of plates dorsally. The stylocone was an approximately conical ossicle with a deep anterior excavation. It was probably serially homologous to several ventral hind-tail ossicles. The dorsal surface of the stylocone has a sculpture much like that of the hind-tail ossicles and there are indications of about three half-segments on each side.

As to soft parts, the lumen of the fore tail was probably largely filled with muscle which, to judge by the mid-ventral alternation of left and right plates, probably served mainly to swing the tail from side to side. Concentration of muscle in the proximal part of an appendage is efficient because, for a given angle of bending, the muscles require a smaller percentage contraction than if attached more distally, and muscles work most efficiently at small percentage contractions (Gray 1957). To prevent telescoping, some anti-compressional structure in the soft parts of the fore tail would have been required, which suggests that a notochord was present. This notochord would have continued rearwards from the fore tail into the mid and hind tail where it would have occupied the median groove. In the hind tail, however, the notochord would have had no anti-compressional function; rather it would have served, like the string in a bead necklace, to keep the ossicles in alignment. By analogy with mitrates, where there is direct evidence in the fossils, and with all living chordates, the notochord was presumably overlain by a dorsal nerve cord. The transverse grooves (notches) probably represent places where nerves went off from the dorsal nerve cord, and perhaps blood vessels from a longitudinal vessel in the notochord, to more lateral parts of the tail. The imbrication of successive dorsal plates in the hind tail indicates that the tail could have curled upwards. Such curling implies the presence of muscles in the lumen of the hind tail which, on contraction, would have shortened the dorsal side of the tail and so caused flexion. These muscles would have required an antagonist, and this was probably supplied by the elasticity in the ligaments of the column of ventral ossicles which, as already noted, seems to have flexed downwards when relaxed. The presence of serial depressions in the dorsal surface of the ossicles, separated by transverse ridges and supplied by whatever filled the transverse grooves, suggest that these muscles were divided into blocks (somites), each muscle block occupying a depression.

SYSTEMATIC POSITION

Some methodological remarks

Text-fig. 26 is a cladogram of the dexiothetes which lays particular stress on the less crownward cornutes near *P. menevensis*. We regard a cladogram as a phylogeny conventionalized by placing all the known forms under consideration at the ends of branches. The terminal branches of a



TEXT-FIG. 26. A cladogram of the Dexiothetica to show the position of *Protocystites menevensis* Hicks within the chordate stem group and the origin of some important evolutionary novelties. For fuller explanation see text.

cladogram are therefore in the first place conventional. They can sometimes be shown to have existed, when they did exist, by two types of argument—morphological and stratigraphical. The morphological argument requires that some feature has arisen within the terminal branch, as an autapomorphy of the single species or the species group at the end of the branch. The stratigraphical argument requires, in the present case, that the animal or animals at the end of the branch be contemporaneous with, or preferably later than, their more crownward neighbour. To show that a terminal branch did *not* exist is difficult or impossible. In the present instance this means that, even if the morphological and stratigraphical arguments for the existence of a terminal segment failed, it would be impossible to prove that any known form lay exactly in the chordate stem lineage, in the sequence of even-numbered segments 6–24. Text-fig. 26 is not comprehensive crownward of *N. americana* (segments 12–24) nor anti-crownward of *C. perneri* (segment 6), in the sense that known fossils other than those named belong, or can be suspected of belonging, in those regions. Moreover, the parts of the diagram crownward of *Cothurnocystis elizae* are not discussed in this paper, since they are treated by Jefferies (1986, Chs. 7 and 9).

Particular difficulties arise in establishing the primitiveness of some features of *Ceratocystis perneri*—the least crownward cornute known. When a feature is found in *C. perneri* and also in some related forms, then there is no dilemma. For example, *C. perneri* had a hydropore, uniquely among cornutes; but this feature also occurs in crown echinoderms and in hemichordates (left mesocoel pore), which indicates that it existed in segments 1, 2, 4, 6, and 7 of text-fig. 26 and disappeared within segment 8. Again, *C. perneri* had a rigid floor to the head, and this also existed in *P. menevensis* and *N. americana*; this indicates that a rigid floor existed throughout segments 7–11, in the crownward part of 6, and in the anti-crownward part of 12, and that it disappeared in segment 12. Features unique to *C. perneri* among known forms, however, present difficulties: for prima facie, they could either have arisen in segment 7, as autapomorphies of *C. perneri*, or they could be primitive features of cornutes present throughout segment 7, in the crownward part of segment 6, and in the anti-crownward part of segment 8.

The stratigraphical criterion of primitiveness is of no help in resolving such dilemmas, for the Cambrian record of cornutes it too incomplete, on several grounds. First, only four cornutes have been described from the Cambrian, i.e. *C. perneri*, *P. menevensis*, and the 'stylophoran' of Sprinkle (1976, pl. 1, fig. 1), all of which are approximately contemporaneous and Middle Cambrian in age, and *N. americana* which is Upper Cambrian in age. Secondly, these four forms are considerably different from each other, while *N. americana* from the Upper Cambrian is in most ways intermediate between *P. menevensis* and Sprinkle's 'stylophoran' (which broadly belongs to *Cothurnocystis*) from the Middle Cambrian. Thirdly, new forms are being discovered in the Cambrian (four new species of Cambrian cornute came to our attention in the years 1981 to 1985, one of which is *P. menevensis*). In deciding what features are primitive among Cambrian cornutes, therefore, stratigraphy is useless. (We do not deny that stratigraphy can indicate primitiveness in other groups of fossils (Fortey and Jefferies 1982).)

Functional analysis can sometimes suggest which of two alternative feature states is the more primitive. Thus, in having its gonopore-anus to the right of the tail, *Ceratocystis perneri* was less efficiently laid out than other cornutes, whose gonopore-anus was to the left of the tail and therefore in the branchial outwash, so that faeces and gametes could be flushed away. This suggests: that having the gonopore-anus to the right of the tail was more primitive than the alternative; that this primitive state existed in the crownward part of segment 6 of text-fig. 26, the anti-crownward part of segment 8, and throughout segment 7; and that the change to the location left of the tail happened in segment 8. Such arguments are risky, in as much as functional interpretations are always uncertain.

Anti-crownward extrapolation of an evolutionary trend can also be invoked to indicate that a unique feature of *C. perneri* was primitive. The anti-crownward sequence *Cothurnocystis elizae*, '*C.*' *fellinensis*, *N. americana*, *P. menevensis*, *Ceratocystis perneri* is one of decreasing relationship to the chordate crown group on several grounds. It is also one of decreasing flexibility of the dorsal surface. This suggests that the rigid, or almost rigid, roof to the head seen in *C. perneri*, and only in it among known cornutes, is the evolutionary starting point from which the flexible roof, seen in increasing degree crownward among other cornutes, developed—essentially in segments 8, 10, 12, and 14 of the chordate stem lineage. However, this argument lacks logical rigour, to the extent that evolution may reverse in direction. It can partly, but not completely, be subsumed as a series of more rigorous sub-arguments in which *C. perneri* is not unique among known forms. For example, *C. perneri* and its crownward neighbour *P. menevensis* are the only known cornutes showing individualized plates 3 and 5 in the roof of the head. If *C. perneri*, because of its hydropore, is the least crownward cornute known, then *P. menevensis* is its crownward neighbour because it retains plates 3 and 5 (among other arguments) and all other cornutes lack these plates as distinguishable elements, presumably having lost them. But sub-arguments of this sort can show only that a condition seen in *P. menevensis* is primitive with respect to all cornutes except *C. perneri*. They cannot show that a condition known uniquely in *C. perneri* is primitive. Anti-crownward extrapolation of evolutionary trends goes further than these sub-arguments, but is less logically rigorous. It can be expressed, in this instance, as a working rule: when *P. menevensis* shows some feature state intermediate between that of *C. perneri* on the one hand, and *N. americana* on the other, then the feature state in *C. perneri* is likely to represent the primitive condition from which the others were derived.

The primitiveness, or otherwise, of a feature known uniquely in *C. perneri* therefore remains undecided if its primitiveness for cornutes cannot be established in one of the following ways: 1, by outgroup comparison with echinoderms (such a comparison, if successful, would imply its existence in the crownward part of segment 1, and at least throughout segments 2, 4, 6, and 7 of text-fig. 26); 2, by its presence, perhaps in less marked form, in the least crownward of other cornutes; 3, by functional arguments. Such unique features of *C. perneri* could be primitive for cornutes (present at the junction of segments 6, 7, and 8) or could be autapomorphies of *C. perneri* evolved within segment 7. Only the recognition of stem chordates less crownward than *C. perneri*, or of nodal-group dexiothetes, will favour one or other of these alternatives. To assume that all features of *C. perneri*, even those known uniquely in it, were primitive for cornutes and existed in the chordate stem lineage, is not legitimate and leads into an intellectual trap. For it is like assuming, in view of *Ornithorhynchus*, that all other mammals evolved from a toothless ancestor, with a duck-like beak; or, in view of modern amphioxus, that the latest common ancestor of vertebrates and acraniates was brainless, which cannot be true (Jefferies 1973).

The above methodological discussion assumes the relationships which will be discussed in the rest of this section. This is legitimate, since the assignment of different cornutes to their places in the cornute cladogram does not start from a blank (see Jefferies 1979; in press, Ch. 9). Our task is to fit *P. menevensis* into a phylogenetic framework which is already partly known.

The cladogram of the dexiothetes and the position of Protocystites menevensis *within the chordate stem group*

The cladogram shown in text-fig. 26 is, in our view, the most parsimonious and probable arrangement of the Dexiothetica, so far as the facts at present available indicate. The evolutionary novelties assignable to the various segments are as follows.

Segment 1. In this segment, which was the dexiothete stem lineage, a form like the pterobranch *Cephalodiscus* lay down on its originally right side and lost the openings and tentacles of the right side and probably also the pterobranch stalk. This process of lying on the right side, with all its consequences, can be called dexiothetism. Henceforth, in the dexiothete stem lineage, the primitive and hemichordate right became ventral in chordate terms and hemichordate left became dorsal. Also a calcite skeleton of stereom mesh was acquired (Jefferies 1986, Chs. 2 and 7). No known fossil forms have yet been assigned to the dexiothete stem group through which segment 1 would have passed.

Segment 2. This is the least crownward part of the echinoderm stem lineage. The evolutionary novelties acquired in the echinoderm stem lineage as a whole (segments 2 and 4) can now be discussed much more fully than before because of two stimulating and perspicacious recent papers (Paul and Smith 1984; Smith 1984*a*). In segment 2 fixation occurred, probably by extending the lower surface of the animal (corresponding to the hemichordate right side and the chordate ventral surface) down into the sea-floor. As seen from above, the mouth remained peripheral in position as in a cornute. The ambulacra leading into the mouth (presumably connected with the water vascular system and thus with the left mesocoel = left hydrocoel) became triradiate. Any gill slits on the upper surface were lost—those on the lower surface would already have disappeared as a result of dexiothetism. Thus segment 2 gave rise to the helicoplacoids as a plesion.

Segment 3. This is purely conventional, and perhaps did not exist. Three genera of helicoplacoid are known.

Segment 4. In this segment the mouth moved into the centre of the upper surface by the process known in crinoid embryology as torsion. The triradiate ambulacra became pentaradiate but retained a distinct 2+1+2 pattern reflecting the primitive triradiality. The upper surface became flat. This produced the form *Camptostroma* which may actually lie on the echinoderm stem lineage or even be the latest common ancestor of living echinoderms (the first crown echinoderm). It thus belongs, in the present state of knowledge, to the nodal group of the echinoderms.

Segment 5 is conventional and perhaps did not exist.

All known echinoderms, apart from helicoplacoids and perhaps *Camptostroma*, are probably crown-group echinoderms, being assignable to one or other of the two primary echinoderm subgroups (Pelmatozoa and Eleutherozoa).

The meanings of the words 'dorsal' and 'ventral' require discussion. The upper surface of pelmatozoans and stem-group echinoderms is homologous, if the above account is correct, with the left side of hemichordates and with the upper (i.e. dorsal) surface of chordates. Unfortunately, however, the use of the terms 'dorsal' and 'ventral' in echinoderm literature is based on eleutherozoans such as starfishes and sea-urchins which have inverted in evolution so that the primitive upper surface faces downwards. Hence 'dorsal' and 'ventral' in echinoderms mean the exact opposite to what they do in chordates. The chordate usage clearly has priority (Latin *dorsum* = back; *venter* = belly) and is habitual to far more people than the echinoderm usage. The best solution to this nomenclatorial difficulty would be to eliminate the words 'dorsal' and 'ventral', henceforth, from echinoderm terminology. The words 'aboral' and 'oral' have respectively the same meaning as the conventional 'dorsal' and 'ventral' in all echinoderm groups except helicoplacoids, for which the words 'upper' and 'lower' can fittingly be used with their obvious meanings.

Segments 6 and 7. A large number of important changes occurred in segment 6: the locomotory tail was acquired and reached roughly the condition seen in *Ceratocystis perneri* with fore, mid, and hind portions, while the soft parts of the tail probably included muscle blocks, notochord, and dorsal nerve cord; the brain was developed at the anterior end of the tail; the plates of the head evolved, probably to an almost rigid condition as seen in *C. perneri*; the water vascular system was lost, but the hydropore was retained as outlet for the axial sinus (which in the early embryology of crinoids it still is); the gill slits increased to seven in number (assuming that the single gill slit on the left side of *Cephalodiscus* represents the primitive complement in Dexiothetica), and probably an endostylar mucous filter developed inside the enlarged pharynx; the ear, paired trigeminal ganglia, and median eye developed; and the layout of the head chambers seen in *Ceratocystis perneri* evolved, with the viscera concentrated in the right anterior coelom to the right of the tail, and with a large pharynx, a large buccal cavity, and a posterior coelom. A virtual left anterior coelom lay dorsal to the other chambers.

Features known uniquely in *C. perneri* create special methodological problems, as already argued. Many of them were probably primitive for cornutes, i.e. were present in the crownward part of segment 6. Such include: the almost rigid surface of the head (by anti-crownward extrapolation); the presence of a single plate (w+a+x) (by anti-crownward extrapolation since plates w, a, and x are less differentiated from each other in *P. menevensis* than in '*Cothurnocystis*' *fellinensis* for example); the large number (> 2 on either side) of dorsal segments per ventral ossicle in the hind tail (by anti-crownward extrapolation); the presence of a hydropore (by outgroup comparison with echinoderms); the position of the gonopore-anus to the right of the tail (by functional argument); the absence of a high wall in front of the brain (by functional argument since this wall is associated with the presence of the rectum in the posterior coelom, and this in turn depends on the gonopore-anus being left of the tail).

Many features known uniquely in *Ceratocystis perneri*, however, are of indeterminate status. They may have been primitive for cornutes and present in the crownward part of segment 6, or they may be autapomorphies of *C. perneri* among known forms, and in that case evolved in segment 7. Such include: the absence of an oral pyramid; the position of two of the gill slits (nos. 1 + 2) anterior to the left posterior dorsal crest; the ear penetrating plate i (it penetrates plate j in *P. menevensis*); the presence of plate o; the separation, in some specimens, of gonopore from anus; the large number of segments in the fore tail (about seventeen rings of successive plates on each side). The allocation of these features as evolutionary novelties to their correct segment must await the recognition of plesions less crownward than *C. perneri*, or perhaps between *C. perneri* and *P. menevensis*.

Segment 8. Most of the differences between *C. perneri* and *P. menevensis* probably arose as evolutionary novelties in this segment. The exceptions are features that arose in segment 7, none of which is certainly identifiable, and those that arose in segment 9 as autapomorphies of *P. menevensis*. Evolutionary novelties that probably arose in segment 8 include: loss of hydropore; migration of gonopore and anus to the left of the tail and perhaps their unification to a single opening (if this latter had not already happened in segment 6); acquisition of a high wall behind the posterior coelom, in plates g and j, forming the cerebral basin; increase in the angle between the posterior and right margins of the head (if correctly reconstructed in *P. menevensis*); reduction in the number of segments in dorsal parts of the hind tail to only slightly more than one per ossicle on either side proximally; acquisition of an oral cone (if this did not already exist in segment 6); better development of f-spike and k-spike; reduction in size of plate y.

Segment 9. Features found exclusively in *P. menevensis*, but not in *C. perneri* nor in *N. americana*, and which do not represent morphological intermediates between these two species, were probably autapomorphies of *P. menevensis*, i.e. were evolved in segment 9. Such features are minor but do seem to exist. They include: the very light build of the skeleton with two-dimensional retiform stereom in large parts of the dorsal integument and ventral floor, strengthened in the floor by irregularly placed struts to give a 'space-frame'; the roundness of the e-spike; the bluntness of the ridge on plates 1 and 2; perhaps the small number of segments in the foretail (only three, as compared with about seventeen in *C. perneri* and five in *N. americana*). The lightly built stereom strengthened by ribs, and the rounded dorsal ridges would have reduced weight and can probably be seen as adaptations to life on a very soft sea-bottom. The small number of segments in the fore tail perhaps suggests that *P. menevensis* was less motile than *C. perneri* or *N. americana*. The autapomorphies of *P. menevensis* show that segment 9 was not purely conventional but really existed.

Segment 10. Most of the differences between *N. americana* and *P. menevensis* are shared by *N. americana* with more crownward plesions and therefore arose as evolutionary novelties in segment 10. They include: the strut as a thickening of plate g in *N. americana*—as already mentioned, the strut may have begun from the internal process of plate g as seen in *P. menevensis* or by the stabilization of apposed ribs in plates g and a in the 'space-frame' structure as seen in *P. menevensis* (but in that case the space-frame type of construction would not be an autapomorphy of *P. menevensis*); the clear differentiation of anterior U-plates in the branchial slits; the breakup of plate ü into three pieces (though perhaps it was already in two pieces in *P. menevensis*); the disappearance of plates 3 and 5 as recognizable entities and the smaller size of plate 2; the fact that plate d is part of the frame instead of merely forming part of the floor of the head behind the mouth; the fact that plate 1 extends more leftwards than plate k; the accurately opposite position of left and right hind-tail plates. As already said several times, the only available specimen of *N. americana* is poor.

Segment 11. Two features of *N. americana* are unique to it and are thus likely to be autapomorphies of the species and evolved in segment 11. These are the rightward spread of the e-spike and f-spike so that both are clearly visible in dorsal aspect. These autapomorphies show that segment 11 actually existed. This is also evident on stratigraphical grounds, for *N. americana* is less crownward than the *Cothurnocystis*-like species of Sprinkle (1976), particularly in having a rigid floor to the head, but is stratigraphically later (Upper Cambrian rather than Middle Cambrian).

Segment 12. For purposes of text-fig. 26 we choose '*C.*' *fellinensis* to represent its particular plesion, mainly because Ubaghs (1969) has described this species with his usual thoroughness (text-fig. 13). Many other species of cornute belong near this position but cannot yet be accurately placed—among them the undescribed Middle Cambrian 'stylophoran' of Sprinkle (1976). Evolutionary novelties which can be ascribed to segment 12 are as follows: flexibility of the floor of the head (apart from the strut); plate t and the t-spike; and breakdown of the triple-arch of the dorsal surface so that only a line of spines anterior to the gill slits remains as a vestige. In '*C.*' *fellinensis* plate k extends somewhat further leftwards than plate l. This could be a primitive feature, in which case *N. americana* acquired the opposite condition in segment 11, or could be a secondary reversion simulating a primitive condition.

Segment 13. The only evidence for this segment is stratigraphical: '*C.*' *fellinensis* is contemporaneous with *Galliaecystis lignieresi* and *Amygdalotheca griffei* (both from the Lower Arenig of the Montagne Noire) and these two species are more crownward.

Segment 14. The chief changes in this segment are: the loss of plate y and the median eye; the loss of plate x; and the loss of the spines which in '*C.*' *fellinensis* form a curved row anterior to the gill slits. So far as can at present be determined, the family Scotiaecystidae (*Scotiaecystis*, *Thoralicystis*, and *Bohemiaecystis*) belongs to the plesion of *C. elizae*.

Segment 15. This must have existed for stratigraphical reasons. *C. elizae*, from the uppermost Ordovician (Ashgill) of Scotland is younger than all the cornute plesions crownward of it, i.e. *G. lignieresi* and *A. griffei*, both from the Lower Arenig, *Reticulocarpos hanusi* from the Llanvirn, and *R. pissotensis* from the Llandeilo. It is also younger than the earliest known members of the chordate crown group (the mitrates *Peltocystis cornuta* and *Chinianocarpos thorali* from the Lower Arenig of the Montagne Noire).

Segments 16 to 24. We shall not discuss these here since there is nothing to add to the account given by Jefferies (1986).

Thus *Protocystites menevensis* fits into a plesion between those of *Ceratocystis perneri* and *N. americana.* It increases our knowledge of the evolution of the chordate stem lineage within the less crownward cornutes.

LOCOMOTION IN *PROTOCYSTITES MENEVENSIS*

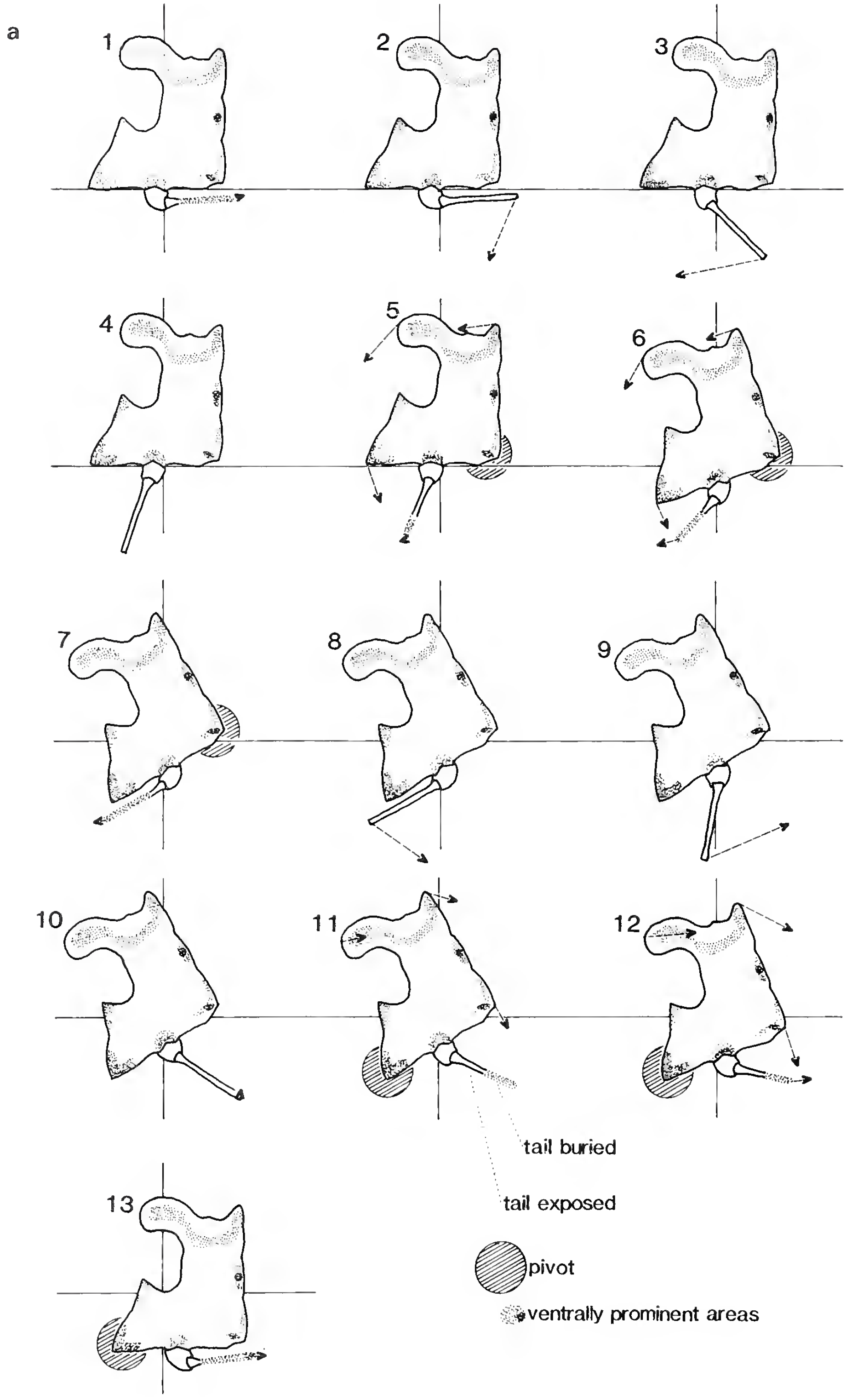
The strange shape of cornutes such as *P. menevensis* demands a functional explanation. Details of their morphology suggest that they could move rearwards, at least occasionally, pulled by the tail. Thus in *Cothurnocystis elizae* or *S. curvata* (Jefferies, in press, Ch. 7) the ventral spikes of the head have points or sharp edges anteriorly but blunt terminations posteriorly, while the anterior appendages would have sloped forwards and downwards into the mud. Both of these types of anteroposterior asymmetry would tend to prevent forward movement and to facilitate rearward movement. Also there is evidence that the tail was highly flexible in all cornutes, as is appropriate to a locomotory organ. Neither the anteroposterior asymmetry of the spikes and appendages, nor the flexibility of the tail, can be explained if the animal always rested immobile on the sea-bottom. The tail of *C. elizae* would mainly have moved from side to side, as indicated by the existence of gaps between the major plates of the fore tail on right and left but not in the vental mid-line. Also the end part of the hind tail of *C. elizae* seems to be specially adapted for bending downwards. The external morphology of this species therefore suggests that the animal pulled itself across the sea-floor by side-to-side wagging of the tail, gripping the sea-floor intermittently during the locomotory cycle by pushing the distal part of the hind tail downwards into the mud. The fore-tail plates of *Ceratocystis perneri* and *P. menevensis* probably likewise flexed from side to side, in view of the overlap of the fore-tail plates across the ventral mid-line. Similarly, there is evidence that the mitrates moved rearwards pulled by the tail, as suggested in particular by the presence of cuesta-shaped ribs with the steep slope of the cuestas always morphologically anterior (Jefferies 1984, 1986). An asymmetrical shape, such as the head of a boot-shaped cornute, is easier to pull across a surface than to push, since it is directionally stable when pulled but directionally unstable when pushed. This is probably the fundamental reason why cornutes and mitrates moved rearwards. With these thoughts in mind, we now reconstruct the locomotory cycle of *P. menevensis* in detail. In what follows, we use the word 'yaw' in the standard sense for rotation about a vertical axis and 'roll' for rotation about a horizontal, anteroposterior axis.

The two largest ventral spikes of *P. menevensis* are situated near the left and right ends of the head on plates k and f respectively. This suggests that movement involved yaw, with left spike and right spike acting alternately as pivots; and such a yawing motion agrees with the presumed side-to-side flexion of the tail as suggested by the ventral overlap of the fore-tail plates. The motion would have been somewhat like one way of moving a heavy cupboard across a floor, by pivoting it alternately about its left and right leading corners. The muscles moving the head of *P. menevensis* would have been mainly those filling the large lumen of the fore tail; these would have represented the motor of the animal. An adequate reconstruction of the locomoty cycle must, therefore, explain how pressure was placed alternately on left and right spikes during crawling (on the k-spike and then the f-spike, and then the k-spike again).

Our reconstruction of the locomotory cycle of *P. menevensis* is given in text-fig. 27. Text-fig. 27*a* shows successive stages of the cycle in dorsal aspect and in absolute space, whereas text-fig. 27*b* shows the head and respective positions of the tail, always in exact posterior aspect. The drawings in text-fig. 27 are based on an adjustable model where the notochord in the fore tail is represented by a flexible ruler which allows side-to-side flexion, while the head and mid and hind tail are represented by their outlines drawn on stiff white card, as described by Jefferies (1984). The dorsal projections of the mid and hind tail in text-fig. 27*a* have been modified according to the reconstructed inclinations of these parts in text-fig. 27*b*. The outline of the head is shown in dorsal aspect, neglecting the effects of inclination during roll. Ventrally prominent structures (ventral spikes, etc.) are indicated by concentrations of dots, whose density suggests the degree of ventral prominence.

Each arrow in text-fig. 27 connects a particular anatomical point in one stage with its new position in the next stage. An arrow thus indicates approximately the direction of travel, at the stage shown, of the point in question. The lengths of the arrows for the different points of a given stage also suggest their velocities relative to each other. However, successive stages shown are not supposed to be separated by equal intervals of time. The relative lengths of arrows for the same point at different stages therefore have no meaning. We have assumed that mud had strength and could resist motion, whereas water did not. The force produced by the mud on the moving tail would have been equal and opposite to the force exerted by the tail on the mud. Thus the arrows of movement are opposite in direction to the forces that the movement provoked.

At stage 1 of text-fig. 27*a*, *b* the hind tail was buried in the sea-floor and curved ventrally (by the relaxation of its dorsal muscles). This position represented the close of the previous locomotory cycle. By stage 2 the hind tail had been raised out of the mud and straightened. Between stages 1 and 2, therefore, the tip of the tail had moved upwards and a resultant downward force would have acted on the hind tail, tending to rotate the head in roll and to drive the right spike (f) into the sea-bed while lifting the left spike (k) out of the sea-bed. The actual axis of rotation of the head would have been approximately anteroposterior and probably located near the mid-ventral line of the tail attachment, which protrudes ventrally below the general ventral surface of the head. This ventral protrusion would have allowed the head to rock, see-saw fashion, alternately to right and left, resting on the protrusion and on the mid-ventral line of the fore tail.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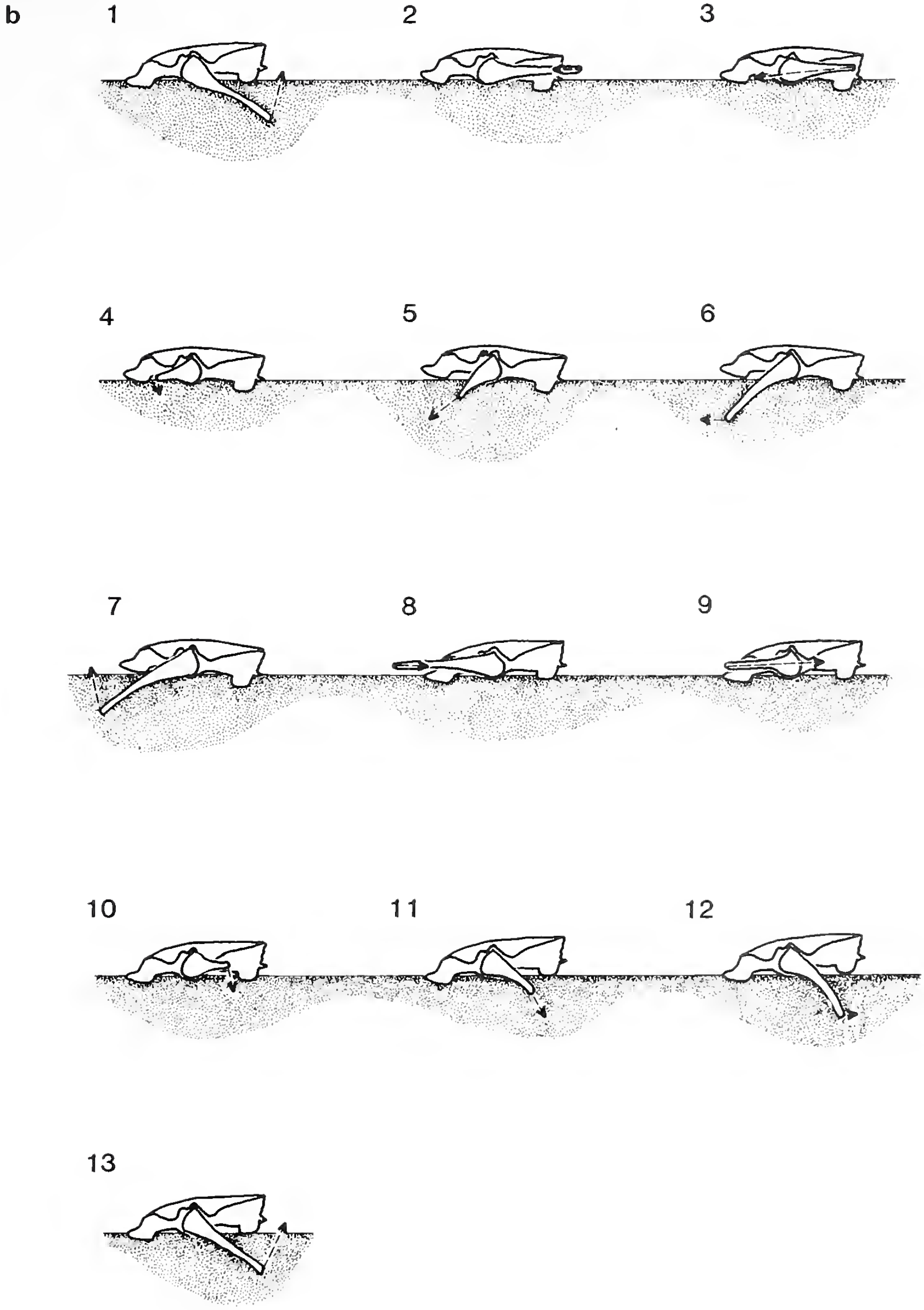

TEXT-FIG. 27. *Protocystites menevensis* Hicks; reconstructed locomotory cycle. *a*, dorsal aspect; *b*, posterior aspect (note that, unlike *a*, the viewpoint of successive diagrams is fixed relative to the animal but not in absolute space). Locomotion probably involved yaw, with the f-spike (on the right) and the k-spike (on the left) being used alternately as pivots. The head was pulled rearward by the tail when this penetrated the sea-bottom on the side farthest from the pivot. The movements of the tail in the vertical dimension, as seen in *b*, would automatically throw the weight of the head on to the intended pivot and lift the side of the head that was to be moved.

Through stages 2 to 5 the tail swung leftwards in the sea water to a position just left of the mid-line of the tail attachment. This movement, being in water, would have met little resistance and had no effect on the position of the head.

By stage 5 the hind tail had moved down into the sea-floor. This would have tended to rotate the head in roll with the same sense as previously and thus to lift the left spike further and throw the weight of the head more on to the right spike (f). At stage 6, further movement of the tail leftwards towards the head had the effect of rotating the head in yaw about the right spike as pivot. As a consequence the left side of the head moved rearwards in space. This yaw continued until stage 7.

At stage 8 the hind tail had been lifted out of the sea-floor. This movement was opposed by a force exerted by the mud downward on the hind tail which rotated the head in roll, driving the left spike down into the sea-floor and lifting the right spike. This rotation in roll was therefore opposite in sense to that between stages 1 and 2. Once again, the axis of rotation would probably have been approximately in the mid-line of the tail insertion, rocking on the ventral protrusion of the tail insertion and of the ventral mid-line of the fore tail.

Through stages 8, 9, and 10 the tail moved rightward, but in the water. The movement would therefore have met with little resistance and would have had no effect on the position of the head.

At stage 11 the mid and hind parts of the tail moved down into the sea-floor. Since these parts were right of the mid-line of the tail insertion and their movement was opposed by an upward force in the mud, the head would have tended to rotate in roll in the same sense as between stages 7 and 8, i.e. the left spike would have been driven further into the mud and the right spike lifted higher. The same rolling rotation would have tended to push the left oral appendage (b-appendage) downwards into the mud.

Through stages 11 to 13 the tail flexed rightwards and rotated the head in yaw about the left (or k-) spike as pivot. Thus the right side of the head was moved rearwards. In this yawing rotation the parts of the head furthest from the pivot would have been supported on the b-appendage (left oral appendage). This was curved approximately, though not accurately, concentric to the k-spike and therefore would scarcely have resisted the yawing rotation about that spike. At stage 13 a position was reached exactly like stage 1, except that the head had moved rearwards and rightwards. Thus the locomotory cycle was complete.

Locomotion, therefore, would probably have involved yaw alternately about the left and right spikes, combined with roll so that left and right spikes were alternately pushed into the mud and lifted clear of it. These motions of the head would have resulted automatically from the movements of the tail from side-to-side and up-and-down into the mud. The rolling movement would have been facilitated by the ventral protrusion of the head near the tail insertion. All boot-shaped cornutes, since they have spikes and appendages concentrated at left and right of the head and the same ventral protrusion of the head near the tail, probably crept rearwards somewhat in this manner.

CONCLUSIONS

P. menevensis Hicks, 1872, from the Middle Cambrian of South Wales, is a cornute and therefore a stem-group chordate. In the present paper it is described in detail for the first time and reconstructed. It shared with *N. americana* the remarkable condition that the roof of the head was flexible but the floor rigid.

Within the chordate stem group, *P. menevensis* belongs to a plesion between that of *C. perneri* and that of *N. americana*. It is crownward of *C. perneri* (i.e. more closely related to the chordate crown group) especially in lacking a hydropore, in having the gonopore-anus to the left of the tail, and in the flexible, or partly flexible, roof to the head. It is less crownward than *N. americana* especially in lacking the strut, in retaining a greater number of individualized plates in the roof of the head, and in the absence of specialized U-plates framing each gill slit anteriorly.

Specialized features (autapomorphies) of *P. menevensis* included the very lightly built stereom (particularly of the dorsal integument, of the right posterior wall of the head, and of parts of the floor of the head) and the presence of irregularly placed ribs in the lightly built parts of the floor. These autapomorphies were probably weight-saving adaptations favouring a life on very soft mud.

As to soft parts, details of the superficial internal anatomy of *P. menevensis* suggest the positions of the oesophagus, stomach, and intestine in the right anterior coelom. The left boundary of that coelom, or at least of its patent cavity, is indicated by a change in the stereom structure from retiform to almost imperforate along a line in the floor of the head.

The locomotory cycle of *P. menevensis* is reconstructed above. The animal probably crept rearwards by pivoting alternately around spikes near the left and right posterior corners of the head. This movement was produced by waving the tail alternately to the left and right while lowering it into, or raising it out of, the mud in particular parts of the cycle. This same locomotory cycle was probably usual in boot-shaped cornutes and was therefore probably primitive for stem-group chordates, so far as these are at present known.

Concerning morphological terminology, we have abandoned the objective notation of plates which was formerly used for cornutes and mitrates (e.g. Jefferies 1968). Instead we apply the comparative terminology proposed by Jefferies and Prokop (1972); this uses the same lower-case letter (a, b, é, ü, etc.) for all plates believed to be homologous in cornutes and mitrates. The terms dorsal and ventral, as conventionally used in echinoderms, should be abandoned, since in that phylum they signify the exact opposite to what they mean in chordates.

As to phylogenetic terminology, we argue that the plesion, though a useful concept in subdividing a stem group, is inherently paraphyletic when completely known, i.e. when all its constituent species are known. We use the term ‘crownward’ to mean ‘more closely related to the crown group’, with its opposites ‘less crownward’ to indicate phylogenetic position and ‘anti-crownward’ to indicate direction away from the crown group along the stem lineage. ‘Crownward’ is more restricted in meaning than ‘advanced’, for it means ‘advanced along the stem lineage only’. Hennig’s term ‘intermediate category’ is used for a paraphyletic group which provably comprises two or more adjacent plesions within a stem group. We propose the term ‘nodal group’ to comprise those forms which could, on the basis of synapomorphies, be crownward members of the stem group of some extant group, or could be primitive members of the crown group.

Tectonic distortion of the material made *P. menevensis* difficult to reconstruct. This distortion was corrected, to some extent, with the help of a computer program and a plotter. This correction was a necessary preliminary to the normal process of reconstructing the animal in three dimensions on a drawing board.

Thus *P. menevensis*, a strange boot-shaped animal, throws light on the evolution of our early ancestors and marks the oldest occurrence known of the chordate phylum in Britain.

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A REVIEW OF FAVOSITID AFFINITIES

by COLIN T. SCRUTTON

ABSTRACT. Although the favositids have been traditionally interpreted as a group of Palaeozoic tabulate corals, there has been persistent speculation, particularly over the last decade, that they could be the massive basal skeletons of sponges and should be transferred to the Porifera. Two recent papers, claiming respectively the preservation of spicules and the fossilization of soft polyps, strongly focus the dispute. Here, all the evidence relating to the affinities of favositids, including these recent claims, is reviewed. It is concluded that this evidence strongly favours retention of the favositids within the Tabulata and assignment of the Tabulata to the Cnidaria Anthozoa.

THE favositids are an important group of extinct organisms with a massive or branched calcareous coralline skeleton and are conventionally assigned to the Palaeozoic subclass Tabulata. Almost all specialists classify the Tabulata as corals in the anthozoan Cnidaria (Hill 1981). That the favositids might be sponges was first seriously suggested when the sclerosponges were discovered early this century (Kirkpatrick 1912), an observation largely overlooked and ignored at the time. During the last twelve years, however, the rediscovery of the sclerosponges has promoted a long-running debate concerning the affinities of favositids and even of the Tabulata as a whole (Hartman and Goreau 1975; Flügel 1976; Stel 1978; Oliver 1979, 1986; Scrutton 1979; Oekentorp and Stel 1985). Two recent papers appear to polarize the argument: the claimed discovery of spicules in the favositid *Thamnopora* (Kazmierczak 1984), and the report of fossilized polyps in *Favosites* itself (Copper 1985). All specialists regard *Favosites* and *Thamnopora* as closely related so both presumably cannot be right. This paper sets these recent conflicting claims in context by reviewing all the evidence relating to the problem of affinity of these structurally simple fossils.

Some supposed tabulate corals variously homoeomorphic with favositids have been reclassified in the light of sclerosponge work. The Chaetetida, in whole or in part, are now widely considered to be sponges (Hartman and Goreau 1972; Fischer 1977; West and Clark 1984; Vacelet 1985; but see also Hill 1981) and some have yielded unquestionable spicules (Dieci *et al.* 1977; Gray 1981). However, Sokolov (1962) had already argued strongly against the inclusion of this group in the Tabulata before the new sclerosponge discoveries. In addition, a reassessment of *Nodulipora* and *Desmidopora*, formerly classified as Favositidae (Hill and Stumm 1956), has established a good case for their transfer to the sclerosponges (Hartman and Goreau 1975; Stel and Oekentorp 1981). It is possible that some further tabulate taxa may also eventually require reassignment, but generally it is considered less likely that tabulates other than favositids could be sponges (Hartman and Goreau 1975; Scrutton 1979), although transfer of the whole group to the Porifera has been proposed (Stel and de Coo 1977). The definition of the Tabulata taken here is that outlined by Scrutton (1984), who argued that the subclass essentially constitutes a monophyletic grouping. In this paper, discussion is limited to *Favosites* and its close relatives, collectively and informally termed favositids and equivalent in general terms to the Favositina of Hill (1981).

The sclerosponges are now considered to be a polyphyletic collection of various demosponges (Vacelet 1977, 1985). They are united only by the possession of a massive 'coralline' basal skeleton which in itself seems to be of little phylogenetic significance. Indeed, the basal skeleton in different sponges shows a wide range in macroscopic form, microstructure, and mineralogy. The term sclerosponge is retained here informally, as the group collectively represents the most coral-like representatives of the sponges. It includes the Tabulospongida of Hartman and Goreau (1975)

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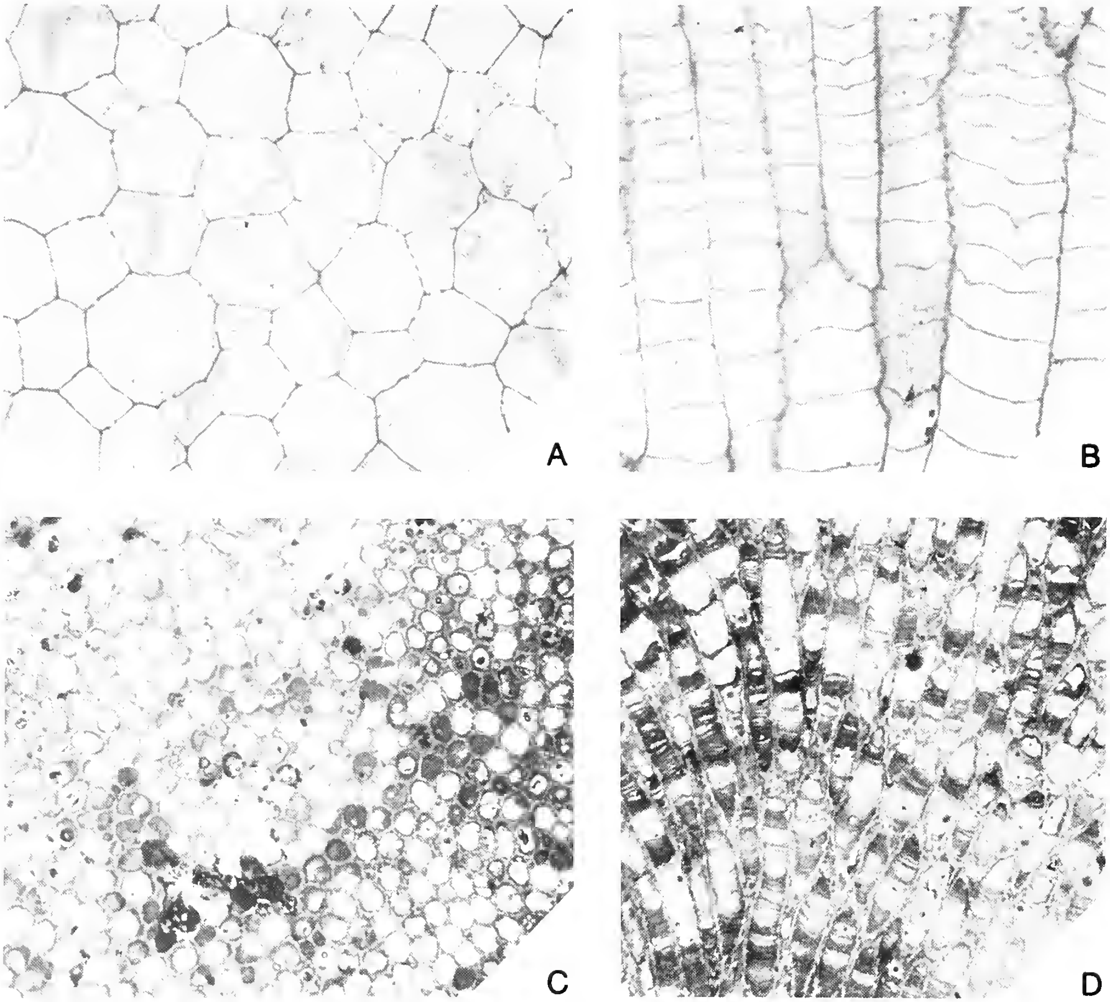
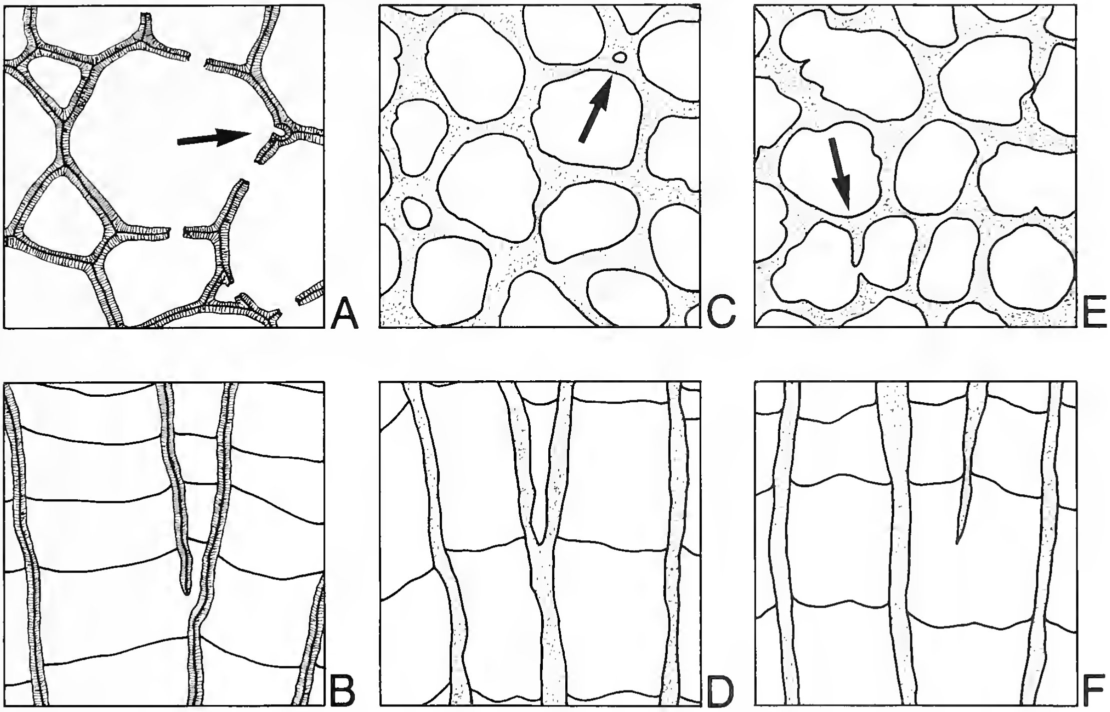


TEXT-FIG. 1. Comparison of basic morphology and characteristic corallite/calicle size in a favositid and a sclerosponge, in transverse and longitudinal sections. A, B, *Favosites multipora* Lonsdale, BM(NH) R51936; Silurian, Wenlock Series, Much Wenlock Limestone; road cut on B4378, 2·5 km north-north-east of Much Wenlock, Shropshire. C, D, *Tabulospongia japonica* Mori, BM(NH) 1986:7:7:1A; Recent; Ishigaki-shima, Ryukyu Islands, Japan. All ×8.

as well as the morphologically very similar Chaetetida and these two orders together represent the sclerosponges most closely homoeomorphic with favositids (text-fig. 1).

ANALYSIS OF FAVOSITID STRUCTURE

Favosites is a colonial organism consisting of closely appressed polygonal tubes interconnected by mural pores (text-fig. 1A, B). Conventionally, the skeletal tubes in favositids are called corallites (as in corals generally) whilst those in sclerosponges are calicles; it will be convenient to use these terms here although I do so without prejudice. In favositids, corallite 'diameters' vary from *c.* 0·5–5·0 mm, comparable to corallite size in many other tabulate corals and some scleractinian corals, although



TEXT-FIG. 2. Three different methods of origin of new units within a colony. A, B, lateral increase in favositids; the point of communication with the parent corallite is so small that the critical stage is seldom seen in random sections; for this reason, increase in favositids was earlier thought to be intermural increase. C, D, intramural increase in sclerosponges; the new calicle arises within the wall with no communication with surrounding calicles. E, F, longitudinal fission in sclerosponges; an existing calicle is subdivided subequally by the growth and fusion of pseudosepta from opposite walls; occasionally, subdivision may be effected by a single pseudoseptum growing from one wall across the calicle. A, C, E are cross-sections, with an arrow indicating the critical stage of increase; B, D, F are 'perfect' longitudinal sections through the corresponding critical stages.

to few rugose corals (most of which have larger corallites). Of the living sclerosponges so far known, none has calicle diameters in excess of 0·6 mm (text-fig. 1C, D), and those with the larger diameters have a functional relationship between the calicles and ostia in which the tissue enclosed by each calicle is the unit supported by a single ostium (Hartman and Goreau 1975). *Merlia*, however, with very small calicles (0·12–0·15 mm), has no such relationship. The fossil tabulosponges and the chaetetids have calicle diameters not exceeding *c.* 1·2 mm, with most in the range 0·15–0·50 mm, significantly smaller than the corallites in the majority of favositids.

New corallites in *Favosites* are now known always to arise by lateral increase (Oliver 1968; Stel 1978; Scrutton 1979), equivalent to the peripheral intracalicular increase of Hill (1981) (text-fig. 2A, B). The process is structurally comparable with lateral increase in other corals. In sclerosponges, however, new calicles arise either by longitudinal fission or by apparently true intramural increase (Hartman and Goreau 1972, 1975) (text-fig. 2C–F). There appears to be no overlap between the two groups.

The determination of original composition and microstructure in fossil material is a more debatable area but the favositid skeleton was most probably originally calcitic (Richter 1972; Sandberg 1975). Corallite walls are considered to have had a fibronormal microstructure, although some argue that lamellar microstructure was primary in certain genera (Lafuste 1962). More critically, there is no doubt that this fabric is based on an epithecal surface bounding individual corallites which is expressed as a median dense band when corallite walls are fused back to back (Oekentorp and Sorauf 1970; Schouppé and Oekentorp 1974; Stel 1978; Hill 1981) (text-fig. 3A–C). Precisely similar walls are known in cerioid rugose corals such as *Actinocyathus*, *Hexagonaria*, *Lithostrotion*, and many others (Hill 1981), as well as in other tabulate corals (Flower 1961). This indication of the individuality of the component corallites within the favositid colony is buttressed by two additional features. First, by the occurrence of subcerioid growth, in which irregular intercorallite cavities are formed within an otherwise cerioid morphology (Philip 1960). Secondly, by the manner of formation of pseudoperculae, plates with concentric growth lines, often with an excentric origin, that individually close off abandoned calices in some specimens (Dunbar 1927; Swann 1947). The presence of intermural spaces (Swann 1947; Ross 1953) would represent further evidence, although some structures so described are due to commensal organisms and others are at least enhanced diagenetically if not wholly of diagenetic origin (Oekentorp 1969). Even so, the distribution of the commensal structures themselves often follows a pattern related to the corallite walls which suggests that the latter defined individual units of soft tissue.

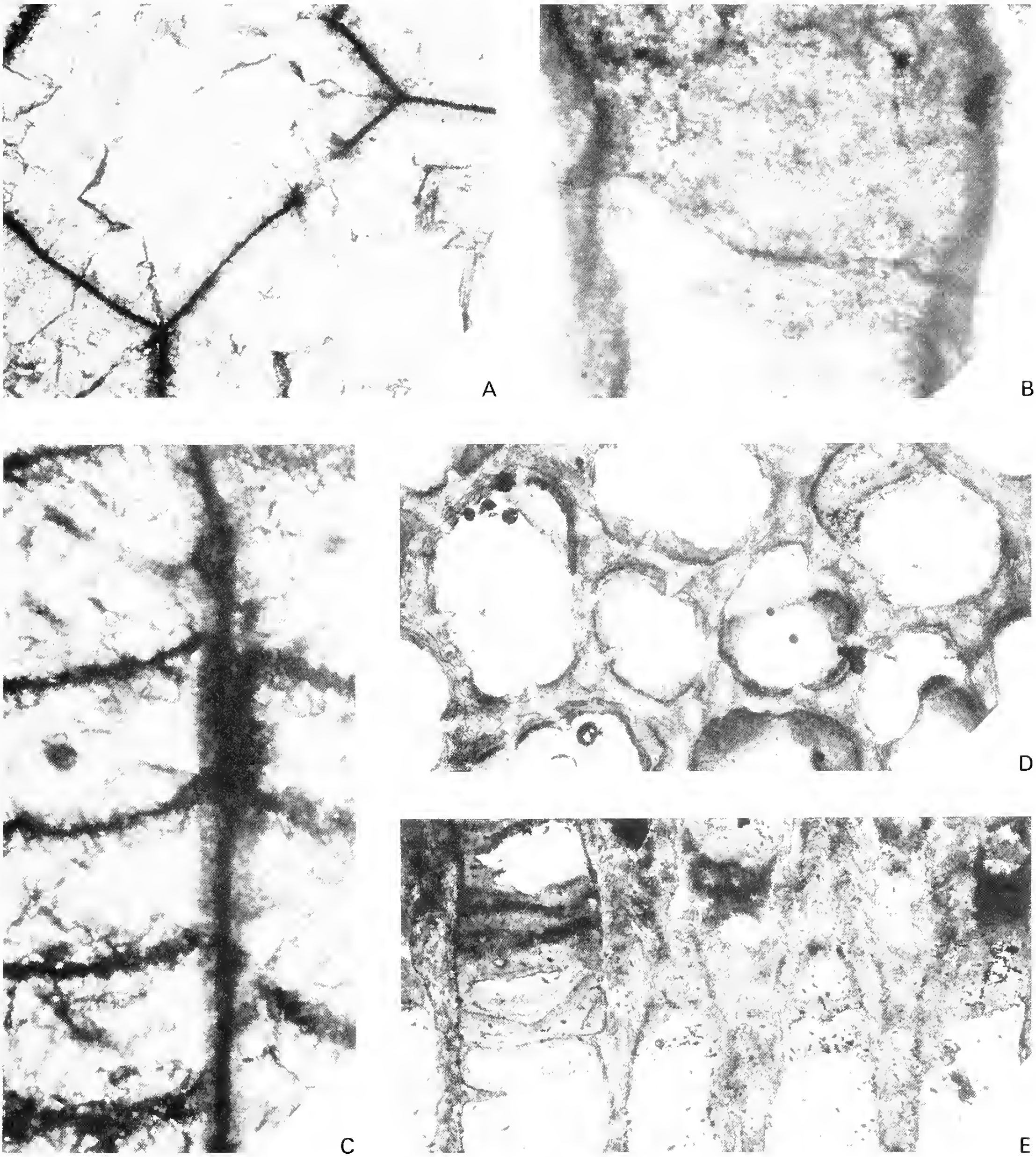
Sclerosponges are mainly aragonitic with spherulitic or trabecular structure, although calcitic lamellar skeletons are known in tabulosponges (Hartman and Goreau 1972, 1975; Vacelet 1985) (text-fig. 3D, E). In neither, however, is there any indication of an axial zone in the wall representing fused epitheca, or of any individuality of the component calicles (Hartman and Goreau 1975). Intercalicular walls have a unitary microstructure. The 'epitheca' of sclerosponges (Hartman and Goreau 1972, 1975) is equivalent to the holotheca of non-cerioid tabulate and massive rugose corals (Hill 1981). In most, if not all, cerioid tabulates and rugosans the outer wall of the colony is the sum of the free epithecal walls of adjacent, peripheral corallites.

The septal spines and tabulae of *Favosites* can be matched by both other corals and some sclerosponges in gross morphology and possibly microstructure, although if favositid septal spines are trabecular, as Hill (1981) speculated, then they are uniquely cnidarian (text-fig. 3C, E). Although favositid spines may be arranged in regular vertical rows and there may be twelve such rows, other configurations may occur and their distribution may also be irregular (Schouppé and Oekentorp 1974; Oekentorp 1976; Oekentorp and Stel 1985). A very similar range of variation appears to be possible in some sclerosponges. However, some favositids, the Agetolitidae, have unusually well-developed septa for which rugosan septal insertion has been claimed (Kim 1974), thus strongly supporting anthozoan affinities.

The mural pores of favositids (text-figs. 2A, B, 3A, B) are structurally comparable with, and were presumably identical in function to, the horizontal tubules of syringoporoids. There is no difference between the appearance of syringoporoid intercommunication when the corallites become compressed and contiguous and the mural pores of favositids (see, for example, Hill 1981). Some other tabulate coral groups also possess mural pores of supposed similar function to those of favositids, if of different structure in detail, but pores are not present in all tabulate corals. No similar structures are known in living sclerosponges and the chaetetids, although they are present in the probable fossil sclerosponges *Nodulipora* and *Desmidopora*. Stel and Oekentorp (1981) suggested a relationship between the presence of pores and larger calicle size in sclerosponges, although they noted an exception to this themselves. Flügel's (1976) suggested analogy between mural pores in favositids and astrorhizal systems in sclerosponges is ingenious but unconvincing (Scrutton 1979; Stel and Oekentorp 1981).

Mural pores are as equally unknown among rugose and scleractinian corals as among the bulk of sclerosponges. However, in favositids they can be interpreted most convincingly as a device allowing interpolypal communication and thus a higher level of integration of the colony than in unmodified cerioid morphologies (Coates and Oliver 1973). In other corals this is achieved by the wholesale loss of the epithecal barrier to integration, or by pervasively and finely perforate walls in some Scleractinia. It is clear, however, that the presence or absence of mural pores cannot be taken as a criterion of great significance in determining the affinity of the favositids.

Neither favositids nor any other tabulate corals show any sign of astrorhizal structures like those



TEXT-FIG. 3. Microstructural characteristics of a favositid and a sclerosponge. A–C, *Favosites multipora* Lonsdale (specimen details as for text-fig. 1A, B). The dark mid-line of the wall, representing fused epithecae of adjacent corallites, and its fibro-normal coating is clear in A and C, and growth lines on the epithecal surface in section can be distinguished in B; mural pores are present in A and B and septal spines are sectioned (particularly top left) in C. D, E, *Tabulospongia japonica* Mori (specimen details as for text-fig. 1C, D). The skeleton is high-Mg calcite with lamellar microstructure, clearly seen in E; the undulose surfaces of the lamellae are responsible for the concentric patterns in the wall in cross-section D; calical spines are well developed, formed of sharply peaked extensions of lamellar tissue, but spicules are not incorporated into the calcitic skeleton. All × 50.

of sclerosponges and stromatoporoids. As many sponges do not reflect the system of exhalant canals in their skeletons, this may not be particularly significant. However, the individuality of favositid corallites strongly argues against the former presence of continuously integrated tissue across the colony surface as in sponges. Under these circumstances, some skeletal reflection would be expected of a sponge-scale exhalant current system—hence Flügel's interpretation of mural pores (Flügel 1976). Mural pore distribution, however, seems to have no pattern to it that would support such an interpretation. Indeed, *Nodulipora* may possess both astrorhizae and mural pores with no specific relationship between them (Stel and Oekentorp 1981).

Turning now to recent developments: first, Kazmierczak (1984) has claimed the preservation of desma-like spicules in a Devonian *Thamnopora*. These are rare, approximately parallel-sided, irregularly branched structures preserved in the peripheral part of the skeleton in microgranular low-Mg calcite and lined with micrite. They do not have a convincing spicular morphology. Their appearance, location, and mode of occurrence, however, strongly suggests that they are endolithic borings (Oekentorp 1985; Finks 1986). No convincing records of spicules in favositids are known. On the other hand, this is not a strong argument in itself *against* sponge affinites as several sclerosponges, particularly tabulosponges (Hartman and Goreau 1975; Mori 1976, 1977), do not incorporate spicules into their calcareous skeletons (text-fig. 3D, E).

The second recent development is the report by Copper (1985) of presumed polyps of cnidarian character preserved in Silurian *Favosites* from Anticosti Island. Six well-preserved colonies show small dome-like structures in the centres of calices, with axial pits surrounded by normally twelve concentrically wrinkled radiating segments. In the specimen figured, their development is strikingly wide and uniform. A possible diagenetic origin for the structures has been suggested by Oekentorp and Stel (1985); their reference to a *Protrochiscolithus* figured by Flower (1961, pls. 14 and 16) is misleading, however, as the polypoid appearance of the silicified surface in that case is a direct reflection of the septal structure of the genus. No such interpretation seems possible with Copper's *Favosites*. Oliver (1986) tentatively suggested an origin related to pseudoperculae; this may be important in understanding how calcification might have occurred, but the 'polyps' are most unlike known pseudoperculae in detailed form and regularity. It is a remarkable case of preservation and one not easy to explain, but it is difficult to avoid the conclusion that the structures seen are indeed the remains of polyps. The twelve tentacles of Copper's favositid polyps are intriguing in view of the frequency with which twelvefold septal distributions occur in tabulates (taken here to include the heliolitids: Hill 1981; Scrutton 1979, 1984). However, septal layouts and patterns of insertion in tabulates require further study (Oliver 1986) and it is premature at the moment to set aside the Tabulata as a group characterized by dodecal symmetry (Copper 1985; Oekentorp and Stel 1985).

CONCLUSIONS

There appears to be no single item of evidence in favour of the favositids being sponges, other than a very gross morphological similarity with the tabulosponges. Mural pores and septal structures in favositids both show features more strongly related to other tabulates and to the Rugosa respectively, whilst neither in the broadest sense is exclusively cnidarian. On the other hand, corallite size, and particularly mode of increase and evidence of corallite individuality are all positive cnidarian features. The polyps described by Copper (1985) appear to represent one additional, if spectacular, item on the cnidarian side. The weight of evidence is strongly in favour of favositids being cnidarians and a subgroup of the monophyletic subclass Tabulata (as defined by Scrutton 1984). To maintain any claim for sponge affinities for these extinct organisms, not only must Copper's polyps be explained away, but some new and convincing positive evidence must be forthcoming.

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A STAURIKOSAURID DINOSAUR FROM THE UPPER TRIASSIC ISCHIGUALASTO FORMATION OF ARGENTINA AND THE RELATIONSHIPS OF THE STAURIKOSAURIDAE

by D. B. BRINKMAN *and* H.-D. SUES

ABSTRACT. A partial skeleton of a staurikosaurid, cf. *Staurikosaurus* sp. is described from the Ischigualasto Formation of Argentina. This specimen provides additional anatomical data for an evaluation of the phylogenetic affinities of the Staurikosauridae. Colbert's (1970) assignment of *Staurikosaurus* to the Dinosauria is supported. No synapomorphies exist to support close relationships between *Herrerasaurus* and *Staurikosaurus*. It is concluded that *Staurikosaurus* and *Herrerasaurus* form successive sister taxa to an assemblage composed of Ornithischia and Saurischia, with the latter only including Sauropodomorpha and Theropoda.

THE early diversification of the Dinosauria is documented virtually exclusively by skeletal remains from a sequence of Late Triassic continental strata in South America (Bonaparte 1978). The oldest known dinosaurs occur in the Santa Maria Formation of Rio Grande do Sul, Brazil, which is most likely Carnian in age (Colbert 1970). *Staurikosaurus* Colbert, 1970 is the best known of these forms (Colbert 1970; Galton 1977) and is documented by lower jaws and a fairly complete postcranial skeleton (MCZ 1669). *Spondylosoma* Huene, 1942 from the same formation is very poorly known but has also been classified as dinosaurian (Huene 1942; Bonaparte 1978). The holotype material consists of vertebrae, parts of both scapulae, the proximal end of a left humerus, the proximal end of a right femur, and a partial right pubis and is currently being redescribed by Galton (pers. comm.). The Ischigualasto Formation of north-western Argentina, which is probably slightly younger than the Santa Maria Formation, has yielded material referable to three genera of dinosaurs (Bonaparte 1978). Of these, *Herrerasaurus* and *Ischisaurus*, first described by Reig (1963), are generally classified as primitive saurischians, and *Pisanosaurus* Casamiquela, 1967 is referred to the Ornithischia. Reig (1963) also described '*Triassolestes*' (*Trialestes* Bonaparte, 1982) as a podokesaurid theropod but Bonaparte (1978, 1982) has reinterpreted this taxon as a crocodylomorph archosaur. The material referable to *Herrerasaurus* and *Ischisaurus* has only been described in a most preliminary fashion. *Pisanosaurus* is based on an extremely poorly preserved specimen, and Bonaparte's (1976) assignment of this genus to the Heterodontosauridae (which are otherwise only definitely known from the Lower Jurassic of southern Africa) is indeed questionable.

In this paper we describe a single fragmentary skeleton of a primitive dinosaur, which we interpret as the first record of a staurikosaurid from the Ischigualasto Formation. This specimen provides much additional information on the structure of these dinosaurs, and, based on these new data, the phylogenetic position of *Staurikosaurus* and related forms will be reconsidered.

The occurrence of a staurikosaurid in the Ischigualasto Formation is documented by a single specimen in the collections of the Museum of Comparative Zoology at Harvard University, MCZ 7064. It consists of a partial postcranial skeleton including the atlas-axis complex, parts of at least five dorsal vertebrae, fragments of both scapulocoracoids, proximal and distal ends of both humeri, a partial left ilium, the proximal ends of both ischia, the distal end of a right femur, the proximal and distal ends of a right tibia, the proximal end of a right fibula, and some pedal phalanges. The

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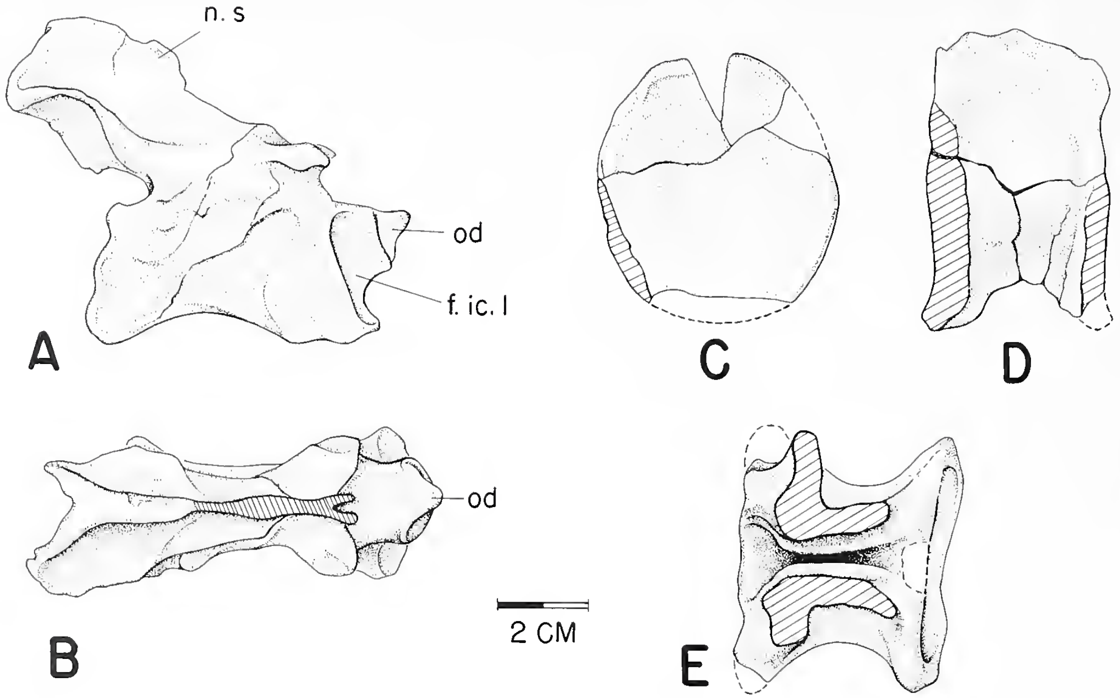


TEXT-FIG. 1. Cf. *Staurikosaurus* sp., MCZ 7064. A, B, atlas centrum, atlas intercentrum, and axis, in A, right lateral and B, dorsal view. C–E, centrum of a posterior dorsal vertebra, in C, anterior, D, lateral, and E, dorsal view. Abbreviations: f.ic.1—facet for atlas intercentrum, n.s—neural spine of axis, od—odontoid process.

material was collected by A. S. Romer in 1958 from a site 1 km north-west of Arroyo de Agua, San Juan province, Argentina. In the field-notes, the specimen (field-number 295-58M) is recorded as much of an indeterminate skeleton. Some of the preserved pieces still show evidence of articular context: the tibia and fibula are preserved in articulation and the left humerus is in contact with the left scapulocoracoid. Thus the material probably represents the remains of a single skeleton. A nearly complete skull of a large archosaur, MCZ 7063, was possibly originally part of the same specimen but regrettably all direct information bearing on this appears to have been lost. The skull is definitely not referable to the rauisuchid *Saurosuchus* from the same formation (Bonaparte 1978), but determination of its affinities must await further preparation. Many of the bones were covered by hematite, the removal of which is extremely laborious.

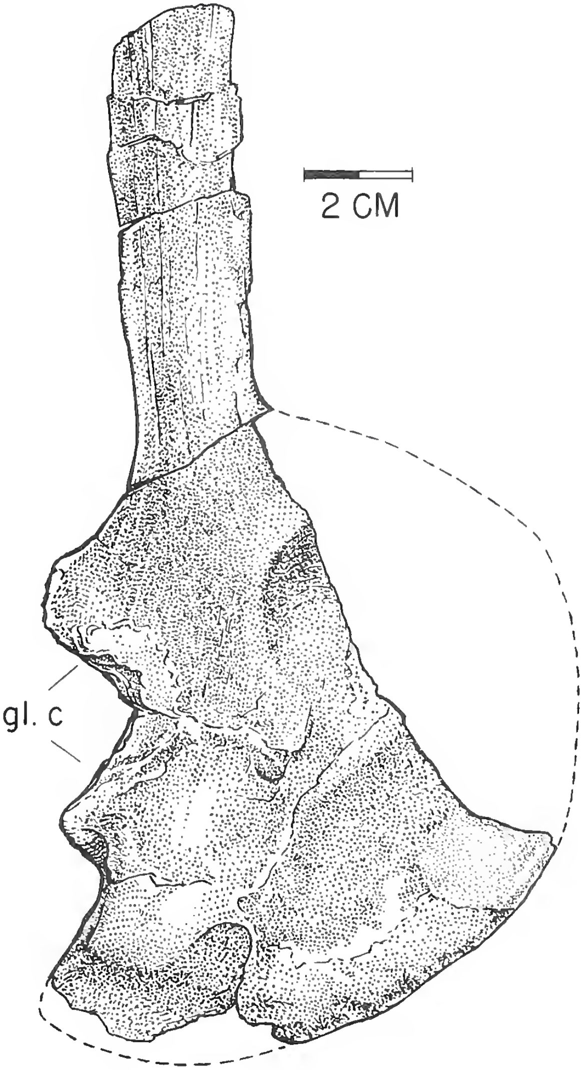
DESCRIPTION

Subdivision ARCHOSAURIA
DINOSAURIA
Family STAURIKOSAURIDAE
cf. *Staurikosaurus* sp.

Postcranial axial skeleton. The postcranial axial skeleton is documented by the atlas-axis complex and parts of at least five dorsal vertebrae. The atlas centrum, axis intercentrum, and axis are preserved in association (text-fig. 1) but it is uncertain whether they are fused or whether their contacts are merely obscured by adhering hematite.

The atlas centrum bears a prominent odontoid process (od, text-fig. 1A, B). Its height is about half that of the axis centrum. Below the atlas centrum, the anterior face of the axis intercentrum forms a crescent-shaped surface for the atlas intercentrum (f.ic.1). The axis is elongate, the length of its centrum being about twice its height. The neural arch bears a large posteriorly directed spine (n.s). The neural spine is bifurcated at its apex, with each branch extending to the posterior extremity of a postzygapophysis. Transverse processes are absent. The sides of the axis centrum are pinched in at a point just about mid-height; the ventral edge of the centrum is rounded. The posterior articular face of the centrum is concave.

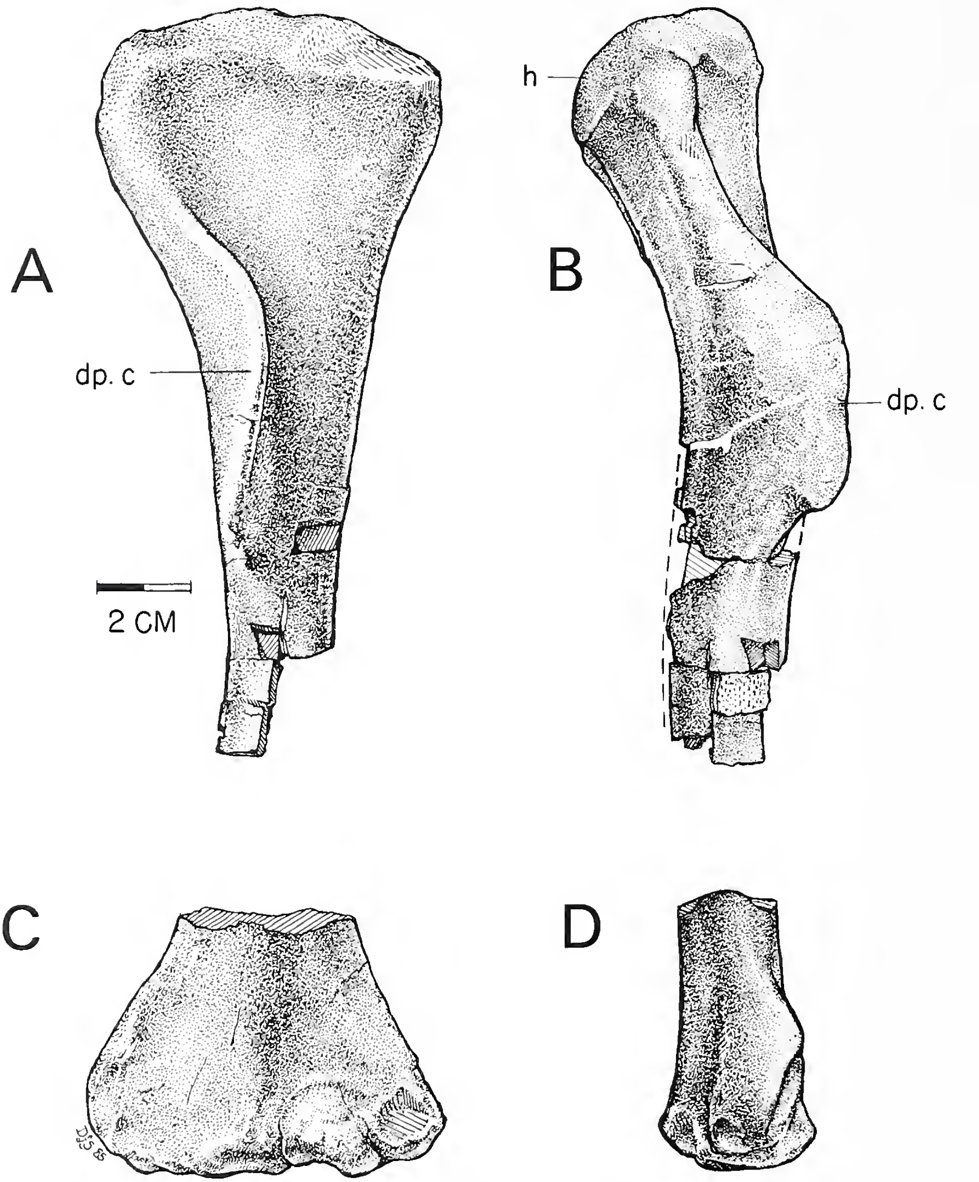
One dorsal centrum is nearly complete (text-fig. 1C–E). It is short, slightly more than half as long as it is high (text.-fig. 1D), and probably represents a posterior dorsal. Its articular ends are nearly flat, although the posterior face shows a slight central depression. The floor of the neural canal on broken centra narrows toward the centre where it sinks deeply into the centrum (text-fig. 1E), rather than extending continuously on level with the pedicles of the neural arch. A similar inward extension



TEXT-FIG. 2. Cf. *Staurikosaurus* sp., MCZ 7064. Conjoined right scapula and coracoid in lateral view. Abbreviation: gl.c—glenoid cavity.

of the floor has elsewhere only been reported in dorsal vertebrae of the theropod *Dilophosaurus* (Welles 1984); the distribution of this peculiar feature among other archosaurian groups remains to be determined.

Appendicular skeleton. The scapula and coracoid form a single element but the line of fusion between the two bones remains apparent. The scapulocoracoids are documented by the left scapula and



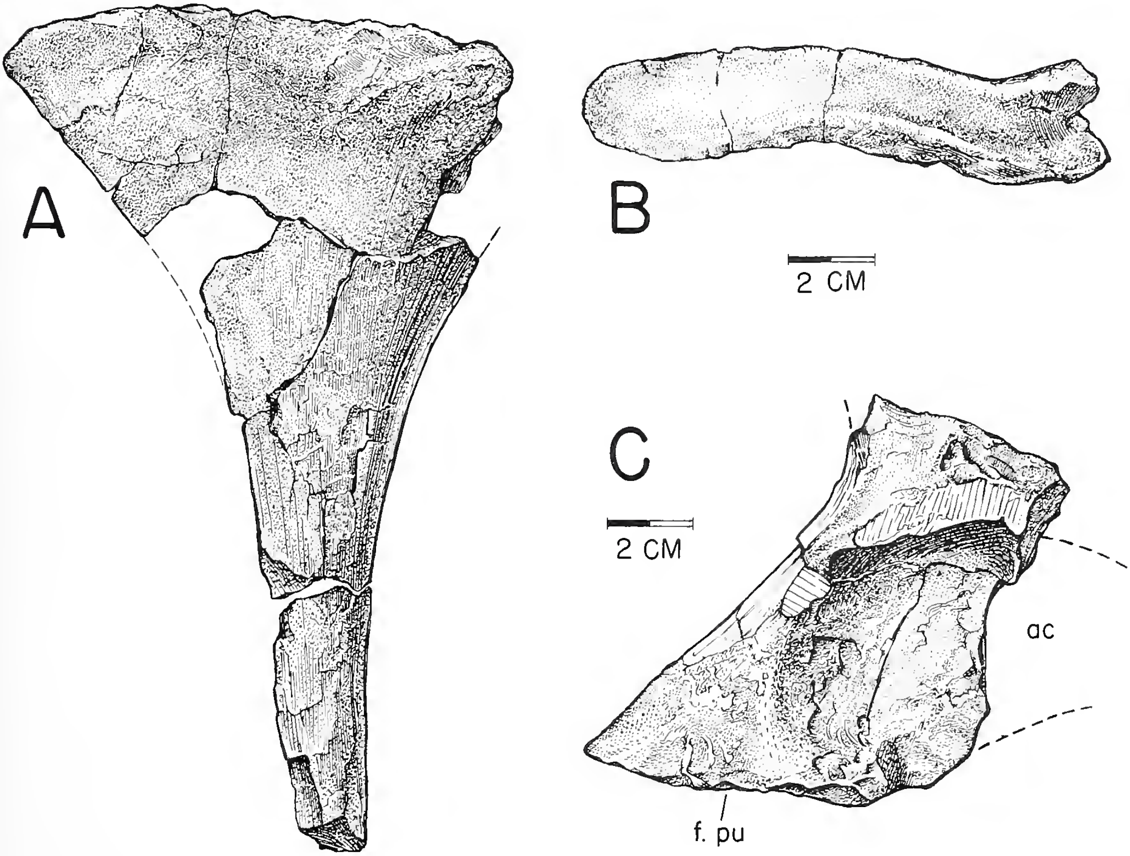
TEXT-FIG. 3. Cf. *Staurikosaurus* sp., MCZ 7064. A, B, proximal end of right humerus in A, medial and B, anterior views; C, D, distal end of left humerus in C, medial and D, anterior views. Abbreviations: dp.c—delto-pectoral crest, h—proximal articular head.

anterior half of the conjoined coracoid and a nearly complete right coracoid, and the base of the attached scapula.

The scapulocoracoid is characterized by a very slender scapular blade and a large, plate-like coracoid (text-fig. 2). The basal portion of the scapulocoracoid is rectangular in outline and bears the glenoid posteriorly. The scapular blade is narrow anteroposteriorly and is oval in transverse section. Although its dorsal margin is not preserved there are no indications for an expansion of the dorsal (vertebral) end.

The humerus (text-fig. 3) is represented by the proximal and distal ends of both elements. Its overall length cannot be determined. The articular ends are two-and-a-half times as wide as the humeral shaft. The humeral head (h, text-fig. 3A) is hemispherical and is restricted to the centre of the proximal end of the bone. The deltopectoral crest (dp.c) is prominent and arises slightly distal to the proximal articular end. It extends more or less perpendicular to the long axis of the proximal portion of the humerus (text-fig. 3B). The humeral shaft is circular in transverse section distal to the deltopectoral crest. The distal articular end of the humerus bears distinct radial and ulnar condyles. The radial condyle faces distinctly ventrally. The ulnar condyle is situated distal to it and faces primarily distally. The ectepicondyle has a notch of uncertain significance in its lateral margin.

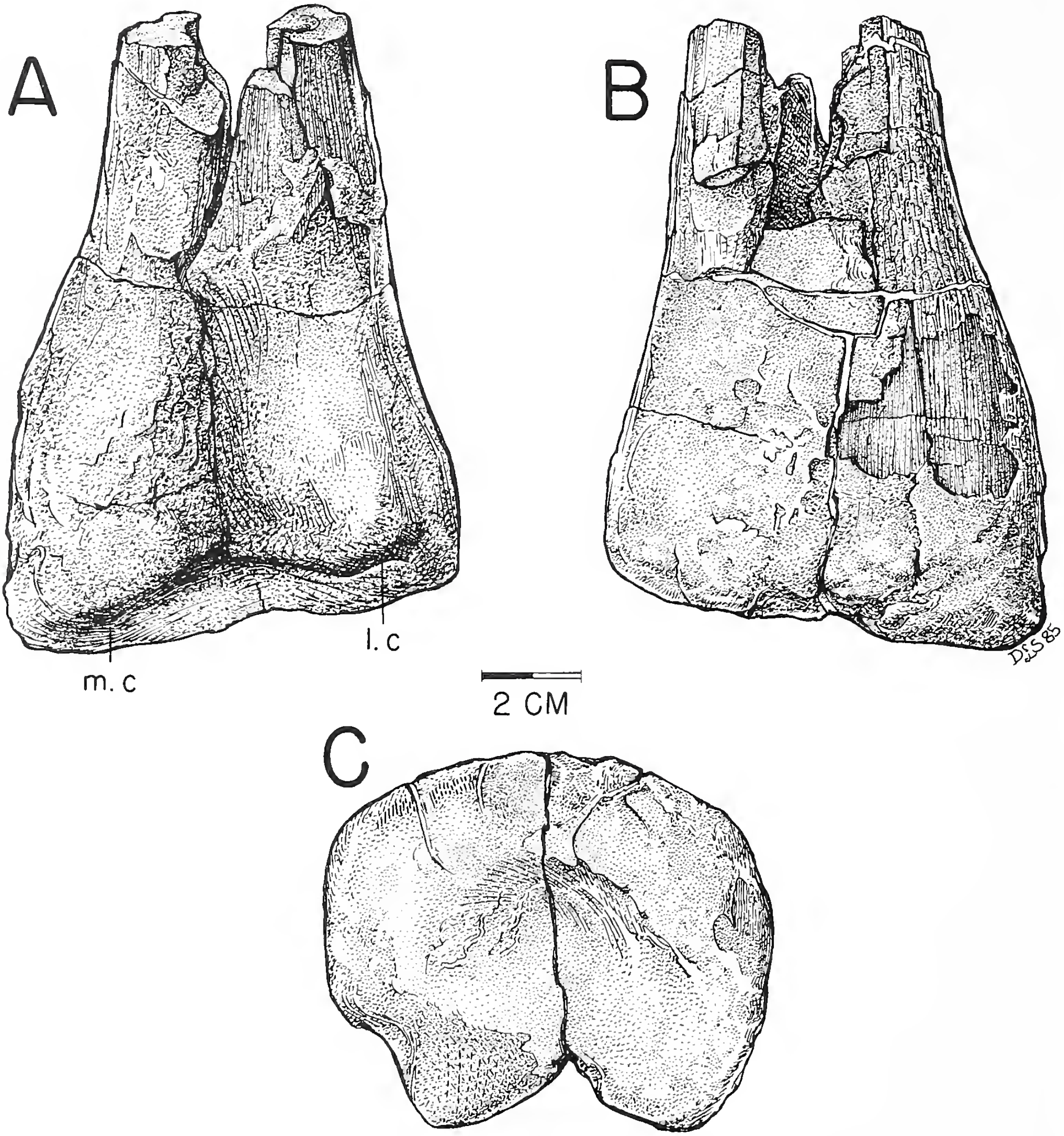
The partial left ilium (text-fig. 4C) includes the supra-acetabular rim and the pubic ramus. The



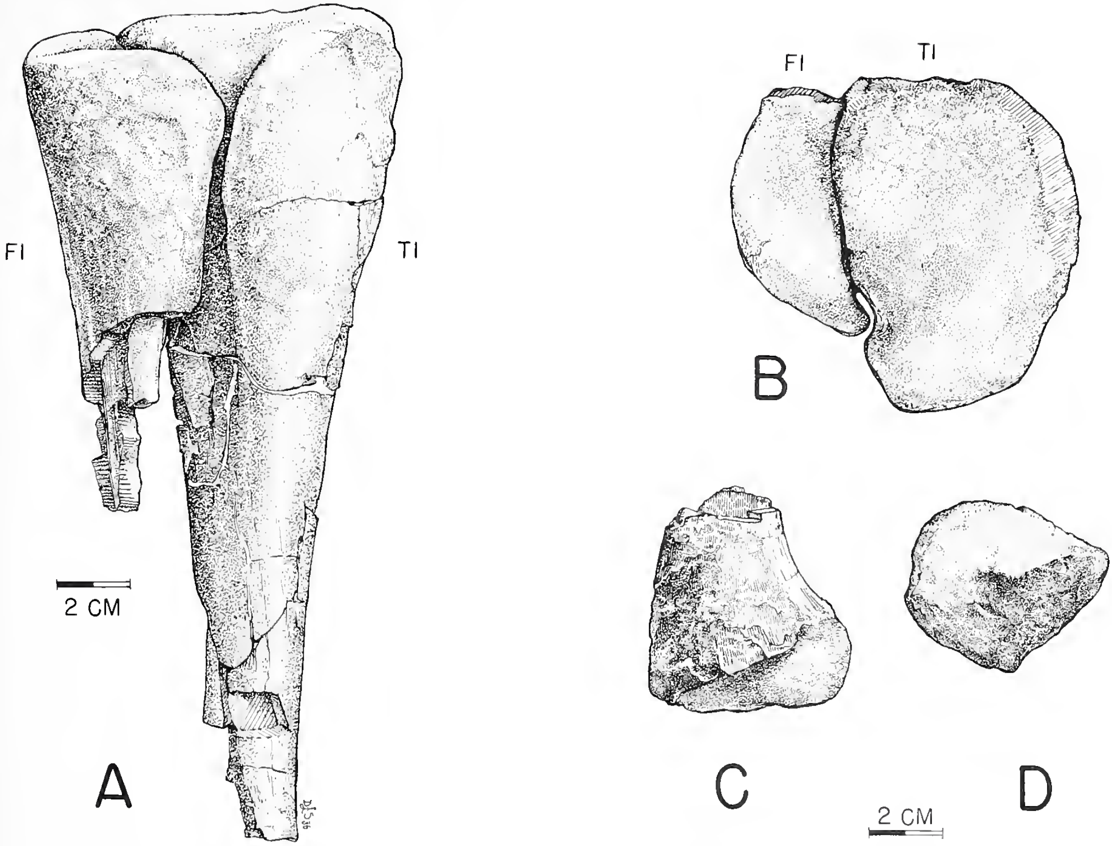
TEXT-FIG. 4. Cf. *Staurikosaurus* sp., MCZ 7064. A, B, partial right ischium in A, lateral and B, proximal end view. C, partial left ilium in lateral view. Abbreviations: ac—acetabular wall, f.pu—articular facet for pubis.

supra-acetabular rim is prominent. It is concave ventrally, forming a socket for the reception of the proximal head of the femur. The lateral aspect of the iliac blade lacks the strong vertical buttress extending dorsally from the supraacetabular rim present in certain rauisuchians (Chatterjee 1985). The well-developed medial wall of the acetabulum (ac) extends far ventrally and forms a knife-like edge at about the level of the articular contact for the pubis (f.pu). While the acetabulum probably was perforated, the opening was quite small. The pubic peduncle of the ilium is robust and large.

The proximal ends of both ischia are preserved. The ischium has a broad, triangular proximal



TEXT-FIG. 5. Cf. *Staurikosaurus* sp., MCZ 7064. Distal end of right femur in A, posterior, B, anterior, and C, distal end view. Abbreviations: l.c—lateral condyle, m.c—medial condyle.



TEXT-FIG. 6. Cf. *Staurikosaurus* sp., MCZ 7064. Partial right tibia and fibula. A, B, articulated proximal portions of tibia and fibula in A, anterior and B, proximal end view. C, D, distal end of tibia in C, anteromedial and D, distal end view.

portion and a rod-like distal region (text-fig. 4A, B). The articular surfaces for the ilium and pubis are separated only by a slight narrowing of the bone, with that for the former being larger and situated at a low angle relative to the latter.

The femur is documented by the distal end of the right bone (text-fig. 5). The diameter of the femoral shaft increases toward the distal articular end. At the proximal end of the preserved fragment, the diameter of the shaft is slightly more than half the width across the distal end. This increase in width is developed asymmetrically so that the medial portion of the distal end is more prominent than the lateral one (text-fig. 5A, B). The distal end of the femur is rounded in outline. It bears a central depression, which is surrounded in front and on either side by a low, broad ridge (text-fig. 5C). A smaller depression is developed anterior to the central one. The distal condyles (l.c, m.c, text-fig. 5A) occupy subterminal positions on the posterior (ventral) aspect of the femur.

Both the proximal and distal ends of the right tibia are preserved. It has an expanded proximal portion that rapidly becomes narrow distally (text-fig. 6A). A distinct cnemial crest, laterally bordered by a groove, is developed. The proximal portion of the right fibula (text-fig. 6A, B) is preserved in its original articular context. It has a broad semilunate proximal end, which fits tightly against the lateral aspect of the tibia. Together the two bones form a rounded articular surface. The distal end of the tibia (text-fig. 6C, D) is rounded in articular view and is much smaller in diameter than the proximal end. Its articular surface has a helical shape with the two ends of the spiral joined by a flat surface. The difference in the relative position of the two ends of the spiral produces a notch for the reception of the ascending process of the astragalus.

No tarsal bones are preserved. The pedal digits are only documented by a few non-diagnostic articular ends of phalanges.

TAXONOMIC AFFINITIES OF MCZ 7064

MCZ 7064 is identified as a staurikosaurid, rather than as a herrerasaurid, based on the structure of the ischium and of the distal end of the tibia. The triangular proximal end of the ischium matches that of *Staurikosaurus pricei* (MCZ 1669) closely and differs from that of *Herrerasaurus*, which shows a distinct angulation between the posterior margin of the ischiadic shaft and the posterior edge of the acetabular portion (Reig 1963, fig. 2). The outline of the distal end of the tibia is again closely similar to that of *S. pricei* (Galton 1977, fig. 2M) and different from that in *Herrerasaurus* where the distal end is more expanded (Reig 1963, fig. 3B, C). The distal ends of both tibiae in the holotype of *S. pricei* have a deep groove extending proximally from the notch formed by the helical articular surface but this feature has been exaggerated by overpreparation; the distal end of the right tibia in MCZ 7064 has no comparable distal groove.

Direct comparison of MCZ 7064 with the type specimens of *Spondylosoma absconditum* and *I. cattoi* was not possible. The former differs from *Staurikosaurus pricei* in the development of the pubic apron (Galton, pers. comm.) as well as in the structure of the vertebrae (Colbert 1970). *Staurikosaurus* differs from *I. cattoi*, currently being restudied by F. Novas, in the presence of a low lesser trochanter on the proximolateral aspect of the femur (Galton 1977). In both *Ischisaurus* and *Herrerasaurus* the lesser trochanter forms a small but very prominent ridge in a more distal position on the proximolateral aspect of the femur (Novas, pers. comm.).

Considering its slightly later occurrence in time and the possible structural differences to the holotype of *S. pricei*, specimen MCZ 7064 is tentatively identified as cf. *Staurikosaurus* sp.

DISCUSSION

The new data on skeletal structure provided by MCZ 7064 invite examination of the phylogenetic position of the Staurikosauridae relative to dinosaurs and other archosaurs. Outgroups used in determining the polarity of character states displayed by *Staurikosaurus* were Lagosuchidae (Bonaparte 1975*a*), Ornithosuchidae (Walker 1964; Bonaparte 1975*b*), and Rauisuchia (= Rauisuchidae + Poposauridae; Chatterjee 1985). These extensive comparisons with non-dinosaurian archosaurs were undertaken because of the current debate about which group of archosaurs is most closely related to the Dinosauria. We regard Dinosauria as a monophyletic assemblage, following the recent discussions by Benton (1984) and Gauthier and Padian (1985), rather than as an artificial grouping comprising two distinct orders Ornithischia and Saurischia, which supposedly have independent, possibly multiple origins among 'thecodontian' archosaurs (Charig 1982).

The first problem to be considered is the placement of *Staurikosaurus* in the taxon Dinosauria. Colbert (1970) listed seven characters in support of his assignment of this genus to the Dinosauria:

(1) transverse processes supported by a pair of strong ventral buttresses;
(2) acetabulum perforated;
(3) ischium rod-like;
(4) ilium as deep as long and truncated posteriorly;
(5) femur shorter than tibia;
(6) proximal head of femur set off from shaft;
(7) fourth trochanter on femur strongly developed.

Since the publication of Colbert's original description of *Staurikosaurus* much new material of early Mesozoic non-dinosaurian archosaurs has been described, including forms that share some of the character-states enumerated by Colbert. Characters (1) and (3) are also developed in the poposaurid rauisuchian *Postosuchus* (Chatterjee 1985). *Lagosuchus* shares characters (5) and (7) with dinosaurs

(Bonaparte 1975*a*). Characters (5) and (6) are present in pterosaurs (Wellnhofer 1978; Padian 1983). The size of the acetabular opening is uncertain in MCZ 7064, and the opening (2) may not have been much larger than that in certain Ornithosuchidae (Walker 1964; Bonaparte 1975*b*) and in *Postosuchus* (Chatterjee 1985). Character (4) is possibly autapomorphous for *Staurikosaurus*, particularly the marked posterior truncation of the iliac blade. None of the above characters are unique to dinosaurs.

In the asymmetrical development of the distal articular end of the femur, *Staurikosaurus* resembles both other dinosaurs and *Lagosuchus*. In most more primitive archosaurs the distal end is also asymmetrical but the *lateral* portion is more prominent. This structural difference can be related to a difference in the function of the femur; the femur extends laterally during femoral retraction in primitive archosaurs (Brinkman 1980).

Gauthier and Padian (1985, p. 189) hypothesized the following set of synapomorphies in a common ancestor of Dinosauria (= Sauropodomorpha + Theropoda and Ornithischia):

(1) Manus with phalangeal formula 2–3–4–3–2 (reduction in outer digits);
(2) semiperforate acetabulum;
(3) prominent supraacetabular buttress {supraacetabular rim in our usage};
(4) fossa on ventral margin of postacetabular portion of ilium (for origin of M. caudifemoralis brevis);
(5) prominent anterior (or lesser) trochanter of femur;
(6) prominent cnemial crest on tibia, projecting beyond femoral condyles and curving anterolaterally;
(7) tibia in which proximal end is expanded anteroposteriorly and in which distal end is broadened transversely ('twisted' tibia), with notch in distal end for reception of ascending process.

In addition, Gauthier and Padian note the existence of 'several other synapomorphies' but these were not specified in their paper and cannot be critically evaluated. Of these features, *Staurikosaurus* shares (2) to (4) and (6). The presence of character (1) cannot be determined. Character (5) is found in *Herrerasaurus* but the feature is apparently developed in a rather different fashion in *Staurikosaurus*. *Staurikosaurus* lacks tibial twisting, representing the plesiomorphous condition, but has a notch in the distal end of the tibia for the reception of the ascending process of the astragalus. Thus character (7) actually consists of two independently acquired features and should be modified accordingly.

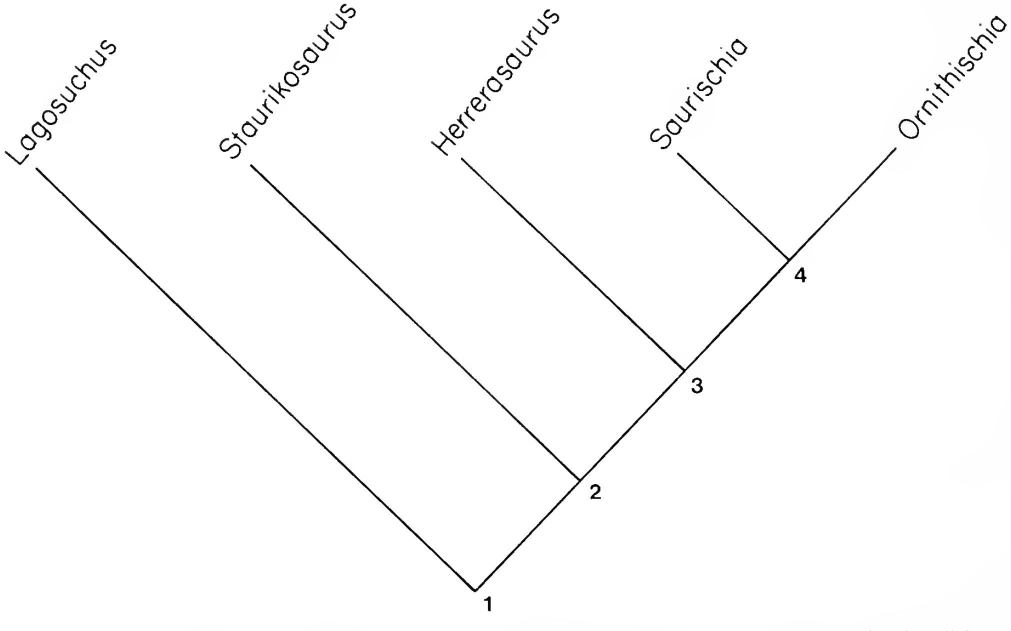
Benton (1984, pp. 13–14) has presented a list of possible synapomorphies for a monophyletic assemblage Dinosauria, which, in addition to characters (5) and (7) listed by Gauthier and Padian, includes the following features:

(1) Absence of postfrontal;
(2) deltopectoral crest extending far down along humeral shaft;
(3) forelimb about half as long as hindlimb;
(4) reduced contact between pubis and ischium;
(5) fourth trochanter prominent and positioned low on femur;
(6) proximal head of femur set off from shaft;
(7) reduced, roller-like astragalus with ascending process;
(8) calcaneum reduced or absent;
(9) advanced mesotarsal ankle joint;
(10) pedal digits II to IV bundled, elongate, and subequal in length;
(11) pedal digits I and V reduced and divergent;
(12) foot with digitigrade pose.

Characters (8), (10), and (11) of this list are also found in *Lagosuchus* (Bonaparte 1975*a*); metatarsal II in *Lagosuchus* is but slightly shorter than are metatarsals III and IV. characters (1), (3), (6), part of (7), (8), (9), part of (10) and (12) are shared by pterosaurs (Wellnhofer 1978; Padian 1983). Characters (1), (3), and (7) to (12) cannot be determined in the presently available staurikosaurid material but characters (2), (4), (5), and (6) are developed in *Staurikosaurus*.

We support Colbert's assignment of *Staurikosaurus* to the Dinosauria. Like *Herrerasaurus*, *Staurikosaurus* occupies a basal position within this group as defined by recent authors and is more primitive than other dinosaurs in the outline of the distal end of the tibia. *Herrerasaurus* also has a semiperforate acetabulum with a strongly developed medial wall but is more derived in the transverse expansion of the distal end of the tibia (Reig 1963; Benedetto 1973). The markedly anteroposteriorly expanded distal end of the pubis is probably an autapomorphy for this genus. This feature is also developed, to a lesser extent, in *S. pricei*; in the podokesaurid theropod *Coelophysis* the pubis terminates distally in a knob-like thickening (Colbert 1970).

Staurikosaurus and *Herrerasaurus* were placed in a single family Herrerasauridae by Benedetto (1973) who noted numerous similarities between them. Galton (1977), emphasizing certain differences between these two genera, proposed a separate family Staurikosauridae for the reception of *Staurikosaurus* but left the question of their interrelationships unresolved. With the possible exception of the anteroposterior expansion of the distal end of the pubis, we find no synapomorphies in support of a sister-group relationship between *Herrerasaurus* and *Staurikosaurus* and regard the similarities between the two taxa as plesiomorphous. Only one feature of *Staurikosaurus*, the presence of a narrow scapular blade, is an apparent autapomorphy for this genus. Judging from outgroup comparisons (particularly with *Lagosuchus*; Bonaparte 1975*a*) and the condition in most early dinosaurs including prosauropods and *Coelophysis*, a wide scapular blade is primitive for Dinosauria. According to Reig's (1963, pp. 6–8) list of skeletal material for *Herrerasaurus*, the scapula in this form is unknown. We hypothesize *Staurikosaurus* and *Herrerasaurus* as successive



TEXT-FIG. 7. Hypothesis of interrelationships for *Staurikosaurus*, *Herrerasaurus*, and other Dinosauria (Saurischia only including Theropoda and Sauropodomorpha). *Lagosuchus* is included in the cladogram as an outgroup, following Bonaparte (1975*a*) and Gauthier and Padian (1985). Selected synapomorphies are: (1) neck sigmoidally curved, 'three-regionalized' vertebral column, femur with moderately developed lateral condyle, astragalus with ascending process, mesotarsal joint (Gauthier and Padian 1985); (2) semiperforate acetabulum with prominent supraacetabular rim, distinct lesser (anterior) trochanter on femur, distal end of tibia with fossa for reception of ascending process of astragalus (see text); (3) distal end of tibia transversely expanded ('twisted' tibia); (4) medial wall to acetabulum less well developed, pedal digit V small.

sister taxa to a clade Saurischia + Ornithischia as defined by Gauthier and Padian (1985) (text-fig. 7). *Staurikosaurus* is clearly the most primitive known representative of the Dinosauria. Galton (1977) classified both *Herrerasaurus* and *Staurikosaurus* as Saurischia *incertae sedis*. We accept Gauthier and Padian's more restrictive use of the term 'Saurischia' to include only Theropoda and Sauropodomorpha (which, in fact, agrees with the traditional usage of that name) and suggest placement of the two primitive South American dinosaurs in separate and distinct higher taxa to reflect their respective phylogenetic positions.

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A CARIBBEAN RUDIST BIVALVE IN OMAN: ISLAND-HOPPING ACROSS THE PACIFIC IN THE LATE CRETACEOUS

by P. W. SKELTON *and* V. P. WRIGHT

ABSTRACT. The hippuritid rudist bivalve *Torreites* is described from the Maastrichtian of Oman and the United Arab Emirates. Together with the single fragment from the region on which *T. milovanovici* Grubić, 1979 was based, the specimens are placed in a newly recognized geographical subspecies of *T. sanchezi* (Douvillé, 1927), a species previously considered endemic to the Caribbean Province. The Arabian *T. s. milovanovici* Grubić differs from its Caribbean parent, *T. s. sanchezi* (Douvillé) (incorporating all previously recognized *T. sanchezi*, as well as *T. coxi* Grubić, 1979) only in the angle (α) between the *arête cardinale* and the ventralmost pillar: α is 12°–75° in the former and 50°–126° in the latter.

The loss of the normal hippuritid pore and canal system in *Torreites* is confirmed and shown to have been associated with exposure of the mantle margins, which may have contained symbiotic algae, as in the living *Tridacna*.

Homeomorphy and plate tectonic drifting are rejected as explanations for the apparent disjunct endemism of *Torreites*. Rather, larval dispersal along a corridor of shallow staging posts is favoured. A Mediterranean Tethys/Atlantic route is considered unlikely, because of barriers. There is good evidence, in contrast, for such staging posts across the Pacific and eastern Tethys in Campanian–Maastrichtian times.

ALTHOUGH the distinctive Late Cretaceous rudist bivalve *Torreites* has generally been considered endemic to the Caribbean Province (Kauffman 1973), a single worn fragment of a right valve from Sheikdom Sharjah, in the United Arab Emirates (UAE), was assigned to the genus by Grubić, in 1979. Such a strikingly disjunct distribution for a sessile benthic inhabitant of shallow equatorial seas demands a palaeobiogeographical explanation. Yet this and other purported cases of apparent disjunct endemism between the eastern Tethyan and Caribbean regions (e.g. Chubb 1956; Elliott 1981) have attracted surprisingly little comment in the literature. Possibly there has been a tacit (though uninformed) assumption that such distantly separated forms are more likely to have been mere homeomorphs than true congeners, or that the currently known localities are but preservational relics of an originally cosmopolitan range.

During geological reconnaissance work in Oman (by V.P.W. in 1983) and in the UAE (by P.W.S. in 1984), we found several further, well-preserved specimens of *Torreites*. The purpose of this paper is to establish recognition of the genus in the region beyond any doubt, on the basis of a suite of characters, the replication of which by homeomorphy would have been exceedingly unlikely. The quality of our material also prompts a systematic re-evaluation of the new species of the genus erected for the Middle Eastern form by Grubić, and allows the reconstruction of some previously unrecognized aspects of the original soft part anatomy and life habits of the animal.

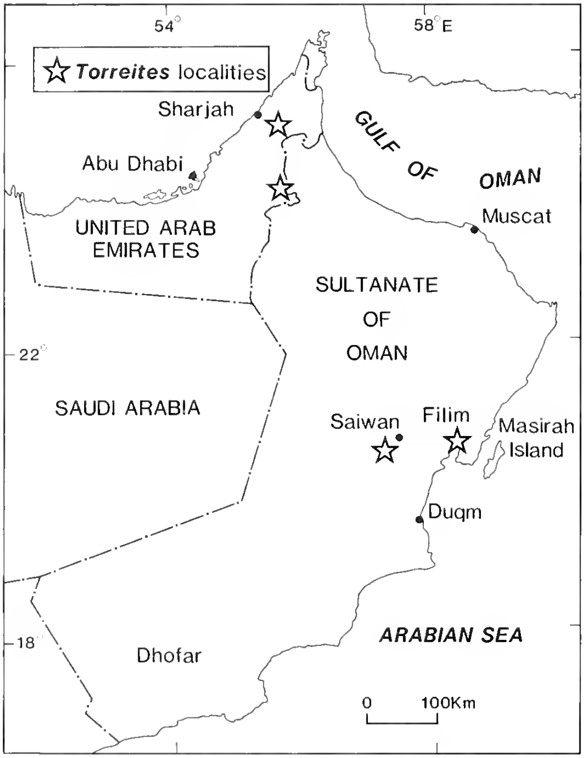
Grubić (1979) inferred that the disjunct distribution of the genus implied closer proximity of Oman to the Caribbean in Late Cretaceous times. However, recent Deep Sea Drilling Project work in the Pacific (Schlanger *et al.* 1981) has shown that, in the Late Cretaceous, shallow-water benthos with Caribbean affinities extended far across the Pacific, exploiting shallow-water 'stepping stones' formed by numerous volcanic seamounts and islands. We argue here that the disjunct distribution of *Torreites* was more probably the product of larval dispersal via such staging posts than of the drifting apart of Oman and the Caribbean implied by the hypothesis of Grubić.

[Palaeontology, Vol. 30, Part 3, 1987, pp. 505–529, pls. 61–62.]

GEOLOGICAL SETTING

The main suite of specimens described here was collected from the foot of a small escarpment of Cretaceous strata east of the main Tertiary escarpment, some 30 km south-south-west of the Saiwan airfield, in eastern central Oman, at latitude 20° 39′ N. and longitude 57° 31′ E. (text-fig. 1). The area is remote, with no previous published account of its Mesozoic geology, although a generalized geological map of the region is given by Gorin *et al.* (1982). The scarcity of landmarks and settlements makes it impossible to provide more precise locality details. The rudists were loose specimens from the talus at the foot of the escarpment. They are associated with a yellow-weathering bioclastic calcarenite. The Upper Cretaceous of the area comprises a basal clastic member overlain by a limestone member, which yields the rudists. Both members fall within the Aruma Group of Glennie (1977), of Santonian–Maastrichtian age. It is unclear as to whether the rudist-bearing limestone is high in the Fiqa Formation (a predominantly marly formation of Santonian–Maastrichtian age) or if it corresponds to the Simsima Formation (Late Maastrichtian, according to Harris *et al.* 1984, though work in progress on this formation in the UAE by P.W.S. with S. C. Nolan, indicates, rather, an early to medial Maastrichtian age). The age of the *Torreites*-bearing units, however, must be considered tentative because of the lack of earlier work in the area. One further specimen was collected in Oman, at Filim in northern Masirah Bay (lat. 20° 36′ N. and long. 58° 12′ E.) (text-fig. 1).

The specimens from the United Arab Emirates were found at two localities (text-fig. 1). A small hillock, Qarn Murrah, projecting through the desert sands some 8 km west of Jebel Faiyah, in eastern Sharjah (lat. 25° 07′ N. and long. 55° 46′ E.), has several specimens in life position, in a sequence of reddish bioclastic packstones to grainstones. To the south the basal chert conglomerate exposed around the core of an anticline at Jebel Huwayyah, some 10 km north-east of Buraimi/Al Ayn (lat. 24° 16′ N. and long. 55° 48′ E.), yielded a single worn right valve. In both cases, a



TEXT-FIG. 1. Localities in Oman and the United Arab Emirates where the specimens of *Torreites* described in this paper have been collected and/or observed.

Maastrichtian age is indicated, by the accompanying large foraminifera, *Orbitoides media* (d'Archiac) and *Omphalocyclus macroporus* Lamarck, as well as by the hippuritid rudist *Pironaea praeslavonica* Milovanović, Sladić and Grubić, at Qarn Murrah, and by the large foraminifer, *Loftusia* sp. in conformably overlying beds at Jebel Huwayyah. Work in progress by P.W.S., with S. C. Nolan, suggests that both occurrences may indeed be confined to the Lower Maastrichtian.

Grubić (1979, p. 85) stated that his specimen came from 'Guru Mileih, Sheikdom Sharjah', and he assigned it a Maastrichtian age from its association with *Orbitoides media* and *Omphalocyclus macroporus*. The lithology of the matrix on this specimen is very similar to that observed at Qarn Murrah, however, and the specimen may indeed come from there (enquiries about the names of small hills in deserts often provokes confusing responses).

SYSTEMATIC PALAEONTOLOGY

Superfamily HIPPURITACEA Gray, 1848
Family HIPPURITIDAE Gray, 1848
Genus TORREITES Palmer, 1933

Type Species. Hippurites (*Vaccinites*) *Sanchezi* Douvillé, 1927.

Emended diagnosis. Medium to large-sized hippuritid, with a conical right valve (RV), and an operculiform left valve (LV) with a ventrally biased apex. The outer shell layer of the LV is externally smooth and devoid of pores and canals. It is also much thinner than that of the RV, the internal margin of which is thus exposed. Apically blind radial canals penetrate the inner shell layer of the LV. The RV exterior is radially ribbed, with three solid radial infoldings (text-fig. 2) comprising a dorsal '*arête cardinale*' (P_0) and two posterior pillars (P_1 and P_2). The former has a rounded inner tip and extends much further inwards than either of the subequal pillars. The three infoldings tend to be uniformly thick, though the *arête cardinale* may taper inwards. Their crests project through sinuses indented from the LV margin. They are positioned around an angle of arc of between 12 and 126°. The two teeth and posterior myophore of the LV are strongly projecting, and are arrayed at between 25 and 50° across the inner end of the *arête cardinale*.

Remarks. The original description of the type species (Douvillé 1927) drew attention to the unusually elongate *arête cardinale* and to the even thicknesses of the pillars. Palmer's (1933) original diagnosis for the genus noted most of the other key features: the imperforate outer layer of the LV; the radiating canals in the inner shell layer of the LV; and the sinuses in the LV for the RV infoldings. Rutten (1936) demonstrated that the canals in the inner shell layer of the LV open directly over the body cavity (in contrast to those in the outer shell layer of the LV in other hippuritids: see Skelton, 1976). He, MacGillavry (1937), Jung (1970), and Van Dommelen (1971) provided many quantitative data, including a higher range of values (75–120°) for the angle of arc formed by the RV infoldings in *T. sanchezi* than that observed (45–70°) in a smaller species, *T. tschoppi* MacGillavry. Grubić (1979) erected three new species, two based on previously described Caribbean specimens (*T. coxi*, based on specimen G.14066 of Jung, 1970, and *T. chubbi*, based on that described by Chubb, 1971) and the third, *T. milovanovici*, on the single RV fragment from Sharjah. This latter was distinguished by the very low angle of arc between P_0 and P_2—only 'about 10°'. Our specimens from Oman and the UAE share the latter feature, but are otherwise so similar to *T. sanchezi* that we would judge them merely to represent a subspecific variant of that species (see the synonymy below).

Stratigraphical ranges. In the Caribbean region the genus *Torreites* ranges from the Santonian or lowest Campanian to the Lower Maastrichtian. *T. sanchezi* is characteristically found in the '*Barrettia* Beds', in Cuba, Puerto Rico, and Jamaica, with either or both of *Barrettia monilifera* Woodward and *B. gigas* Chubb (Van Dommelen, 1971, p. 34; though N. F. Sohl, pers. comm. of August 1983, refers more specifically to a consistent co-occurrence with the latter species). MacGillavry and his co-workers (summarized in MacGillavry 1937) favoured a Maastrichtian age for the *Barrettia* Beds, based largely on orbitoid foraminifera in those of the Cuban Habana Formation. In contrast, Hawkins (1924), working on Jamaican echinoids, and Muellerried

(1936), extrapolating from ammonite-bearing sequences in Chiapas, Mexico, postulated a Turonian age. Subsequent work has refuted the conclusions of Hawkins and Muellerried (N. F. Sohl, pers. comm.), and largely vindicated those of MacGillavry and his co-workers. *B. monilifera* is now judged to be of Late Campanian, and *B. gigas*, of latest Campanian/earliest Maastrichtian age (Sohl and Kollmann 1985, fig. 19). De la Torre *et al.* (1978) referred the *Barrettia* fauna of Cuba to the upper part of the Lower Maastrichtian. So the inferred range of *T. sanchezi* in the Caribbean is best bracketed within the Upper Campanian to Lower Maastrichtian interval.

The specimen described by Chubb (1971) as '*T.* cf. *sanchezi*' (= *T. chubbi* Grubić, 1979), however, comes from the Peter's Hill Limestone of Jamaica, now considered of latest Santonian to earliest Campanian age (N. F. Sohl, pers. comm.).

T. tschoppi was considered 'probably Upper Campanian' by MacGillavry (1937, p. 20), though Van Dommelen (1971, text-fig. 18) extended its range into the Santonian, albeit with uncertainty. It is certainly older than *T. sanchezi* (Van Dommelen, 1971; N. F. Sohl, pers. comm.).

The specimens from the UAE are all considered Maastrichtian, while those from Oman can probably be assigned to that stage, too, though with less certainty (see. p. 506).

Characters of systematic value. Text-fig. 2 shows the characters measured and the abbreviations used for them in the description of specimens that follows.

The five main characters of systematic value are:

1. the overall size of the shell (L, D_1 and D_2);
2. the angle of arc between the *arête cardinale* and the ventralmost pillar (α);
3. the lengths (l) and widths (w) of the *arête cardinale* (P_0) and pillars (P_1 and P_2);
4. the angle made by the myocardinal array with the inner tip of the *arête cardinale* (β);
5. the character of the RV outer shell layer (its thickness, rib-width, and depth of intervening grooves between ribs).

The symbols used alongside the synonymy list are as explained in Matthews (1973).

Torreites sanchezi (Douvillé)

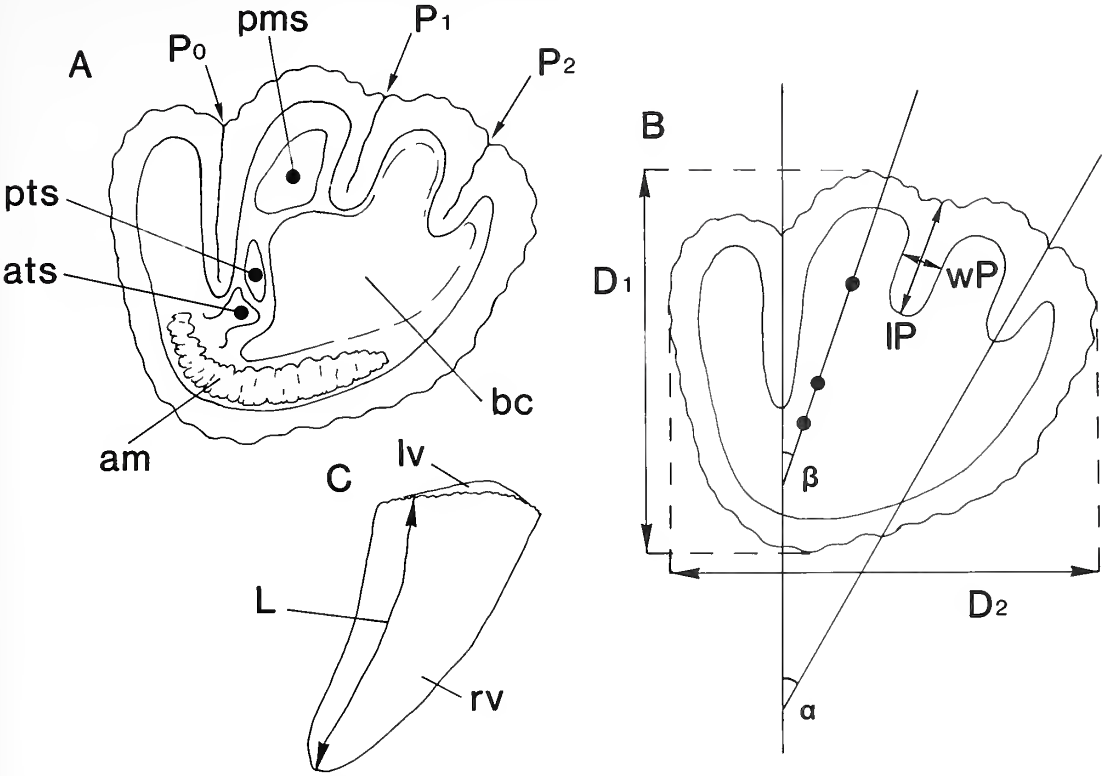
Plate 61, figs. 1–5; Plate 62, figs. 1–4

*1927 *Hippurites* (*Vaccinites*) *Sanchezi* Douvillé, p. 54, pl. 4, fig. 1.
1933 *Torreites sanchezi* Douvillé; Palmer, p. 100, pl. 7, figs. 1 and 2; pl. 8, figs. 1 and 2.
1936 *Torreites sanchezi* (Douvillé); Rutten, p. 135, text-fig. 4*g*.
1937 *Torreites sanchezi* (Douvillé); Vermunt, p. 269 (description only).
1937 *Torreites sanchezi* (Douvillé); MacGillavry, p. 128, pl. 5, fig. 4*e–h*.
1970 *Torreites sanchezi* (H. Douvillé); Jung, p. 5, pls. 1–3, text-figs. 1 and 2.
1971 *Torreites sanchezi* (Douvillé); Van Dommelen, p. 34, table 5.
v. 1979 *Torreites milovanovici* Grubić, p. 84, pls. 1 and 2; text-fig. 4.
. 1979 *Torreites coxi* Grubić, p. 86, text-figs. 5 and 6 [text-fig. 5 = *T. sanchezi* (H. Douvillé); Jung, 1970, pl. 3].

Emended diagnosis. Large species of *Torreites*: D may exceed 100 mm and L, 200 mm. Ventral flank of RV flattened, even embayed, and separated from somewhat flattened anterior part by a blunt carina. Outer shell layer of RV very thick (5–10 mm), and marked externally by deeply indented radial grooves separated by broad rounded ribs usually over 5 mm wide. These indentations correspond to salient ridges on the inner margin of the valve, and are present along the three infoldings of the RV wall, as well as around its periphery. The outer shell layer of the LV is only about 1 mm thick, and its marginal growth laminations are recurved over at least the peripheral parts of the valve's outer surface. The *arête cardinale* and pillars are spaced around an arc (α) of 12–126°. *Arête cardinale* much longer than the subequal pillars (of which P_1 tends to be the longer).

Holotype. Hippurites (*Vaccinites*) *Sanchezi* Douvillé, 1927, p. 54, pl. 4, fig. 1.

Material studied. Five full-sized specimens were collected by V.P.W. some 30 km south-south-west of the Saiwan airfield, eastern central Oman, in 1983 (see p. 506), and have been deposited in the British Museum (Natural History) (nos. BMNH LL 28000–28004). One further specimen (P.W.S. Collection, no. 84/x.1) was collected by V.P.W. from Filim (north Masirah Bay), in 1983. All are well preserved, though with some patchy



TEXT-FIG. 2. Diagrams showing the morphology and measured characters of *Torreites sanchezi*. A, RV interior. Abbreviations are: am, anterior adductor muscle scar; ats, anterior tooth socket; bc, body cavity; P_0 *arête cardinale*; P_1 and P_2, the two pillars (infoldings of the RV outer shell layer); pms, socket for the LV posterior myophore; pts, posterior tooth socket. B, as in A, showing measured characters. Abbreviations are: α, angle of arc described by lines drawn through the middles of P_0 and P_2; β, angle of arc described by lines drawn through P_0 and the myocardinal array (using the black dots centred on the sockets shown in A); D_1, commissural diameter parallel to P_0; D_2, commissural diameter normal to P_0; lP, pillar length; wP, pillar width. C, outline of both valves. Abbreviations are: L, RV length, measured along the external trace of P_0; lv, left valve; rv, right valve.

silicification of the outer (calcitic) shell layer, and with the inner shell layers (originally aragonitic) now replaced by calcite spar. Four the the specimens have all or part of both valves preserved, while the remaining two (BMNH LL 28003 and 28004) are RVs only, though the latter also has a fragment of another, juvenile RV attached to its flank. A slightly worn RV was recovered by P.W.S., in 1984, from the basal chert pebble and shell rubble conglomerate underlying the Simsima Formation at Jebel Huwayyah, near Al Ayn, UAE (see p. 506) (P.W.S. Collection, no. 84/32.1). Other specimens, in life position, were studied in the field (but not collected) by P.W.S., in 1984, at Qarn Murrah, Sharjah (see p. 506).

Description. Measurements of the specimens are shown in Table 1, and plots of their overall dimensions, and of changes in shape of the *arête cardinale* and pillars, as well as in their arrangment (α), with respect to commissural diameter (D_1), are shown in text-figs. 3, 4, and 5, respectively.

The RVs in BMNH LL 28000–28004 are of gently curved elongate conical form, reaching over 230 mm in length in LL 28001. The other two specimens have RVs of more obtusely conical form. The LVs are operculiform and only very gently convex towards the strongly ventrally biased apex. The commissure is of rounded trigonal form, with the anterior and ventral margins slightly flattened, and the posterodorsal margin, with the infoldings, somewhat bulging (Pl. 61, fig. 1; text-fig. 6E–G).

TABLE 1. Measurements on specimens of *Torreites sanchezi milovanovici* Grubić from the Maastrichtian of Oman and the United Arab Emirates, described in this paper. Specimen numbers beginning with LL are housed in the British Museum (Natural History), and those with P.W.S., in the collection of the senior author. Locality data are given in the text (p. 506), and the abbreviations for the measurements explained in text-fig. 2.

	Shell size (mm)			Hinge Angle (°)	Pillar Angle (°)	Pillar dimensions (mm)					
Specimen	L	D_1	D_2	β	α	lP_0	lP_1	lP_2	wP_0	wP_1	wP_2
(*a*) LL 28000	190	103	89	—	39	32	29	26	8	10	9
(*b*) LL 28001	234	96	110	—	31	46	40	34	6	13	10
		80	91		37	31	21	25	6	10	9
		> 48	56		49	18	13	14	7	6	6
		35	42		70	11	> 9	> 7	5	5	6
(*c*) LL 28002	226	104	113	—	28	36	29	42	14	11	7
(*d*) LL 28003	164	93	89	—	42	36	29	23	8	10	10
(*e*) LL 28004	> 127	100	98	25	15	45	36	33	10	12	11
		70	78		31	27	19	19	8	10	8
		44	57		61	15	12	11	8	7	7
(*f*) LL 28004 (small RV)	—	> 48	> 52	—	50	16	> 11	> 10	5	7	7
(*g*) P.W.S. 84/x.1	160	108	113	—	40	45	33	23	8	~ 10	~ 10
(*h*) P.W.S. 84/32.1	> 42	116	> 93	—	20	> 50	> 35	20	16	12	9
		38	45		75	22	20	16	6	6	5

The pale brown, calcitic outer shell layer of the RV is more than 5 mm thick in all the adult specimens, with a highly distinctive ornament (Pl. 61, fig. 4): broad ribs, 5–8 mm wide, with coarse growth rugae, are separated by deeply indented grooves. The latter are expressed on the inner valve margin as salient spurs (Pl. 62, fig. 3). The spurs continue along the infolded shell wall of the *arête cardinale* and pillars, giving them the distinctively branched medial structure, when seen in section (Pl. 61, figs. 2 and 3), noted by Grubić (1979).

The calcitic outer layer of the LV is only about 1 mm thick, and, apart from faint growth indulations, is smooth (Pl. 62, fig. 1); no vestiges of any pores or canals are seen in it. Sections across the margins of this outer shell layer (Pl. 62, fig. 4; text-fig. 7) show the growth lines to be recurved on to at least the periphery of its upper surface. The subdued character of its growth undulations contrast markedly with the coarse rugae of the RV.

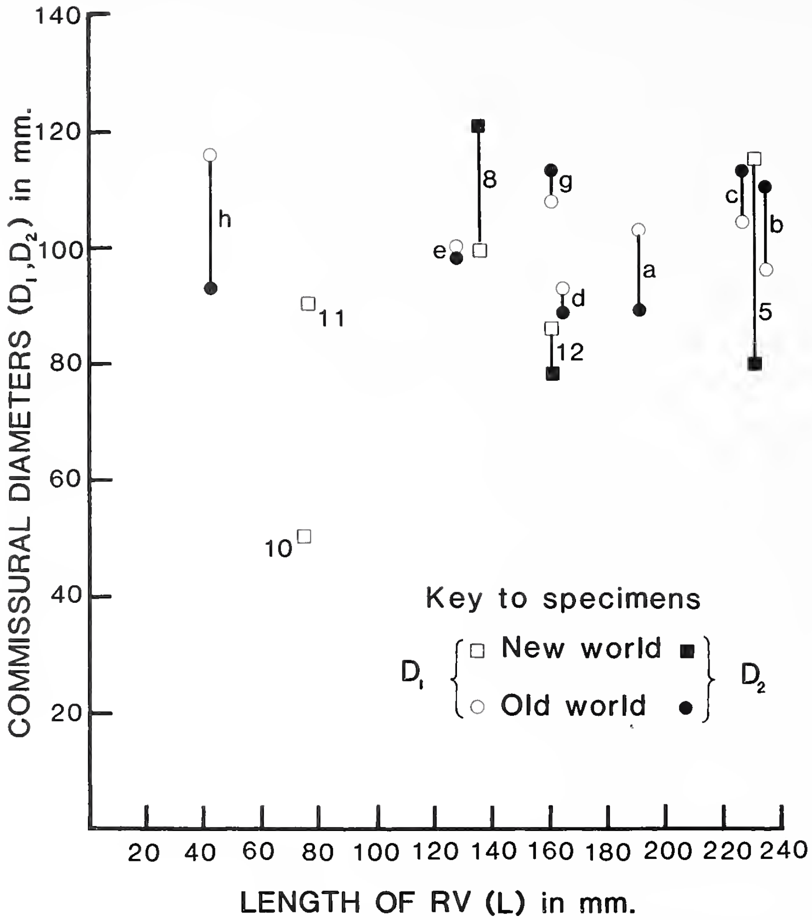
The discrepancy in thickness between the outer shell layers of the two valves means that most of the inner margin of the RV extends out beyond the rim of the LV (Pl. 62, figs. 1 and 3).

Although the inner shell layers, which would originally have been aragonitic (Skelton, 1976), are now replaced by calcite spar, evidence for the blind canals that penetrate the LV inner shell can be seen in one of the specimens (Pl. 61, fig. 5).

EXPLANATION OF PLATE 61

Figs. 1–5. *Torreites sanchezi milovanovici* Grubić, 1979. 1–3, BMNH LL 28004, unnamed limestone member in Aruma Group (probably Maastrichtian), 30 km south-south-west of the Saiwan airfield (lat. 20° 39′ N. and long. 57° 31′ E.), eastern central Oman. 1, RV interior (see text-fig. 2 for explanation); 2, 3, sections across successively younger ontogenetic stages of the RV, which is attached to the RV of another juvenile individual (*lower right*), all × 1. 4, BMNH LL 28002, locality and age details as in 1–3; ventral flank of RV, × 0·5. 5, P.W.S. 84/x.1, unnamed limestone member of Aruma Group (probably Maastrichtian), Filim, northern Masirah Bay (lat. 20° 36′ N. and long. 58° 12′ E.), Oman; detail of broken section across posteroventral part of LV, showing the (dark) thin calcitic outer shell layer above, and the canaliferous recrystallized inner layer (originally aragonite), below, forming a descending prominence, × 3.

SKELTON and WRIGHT, *Torreites*



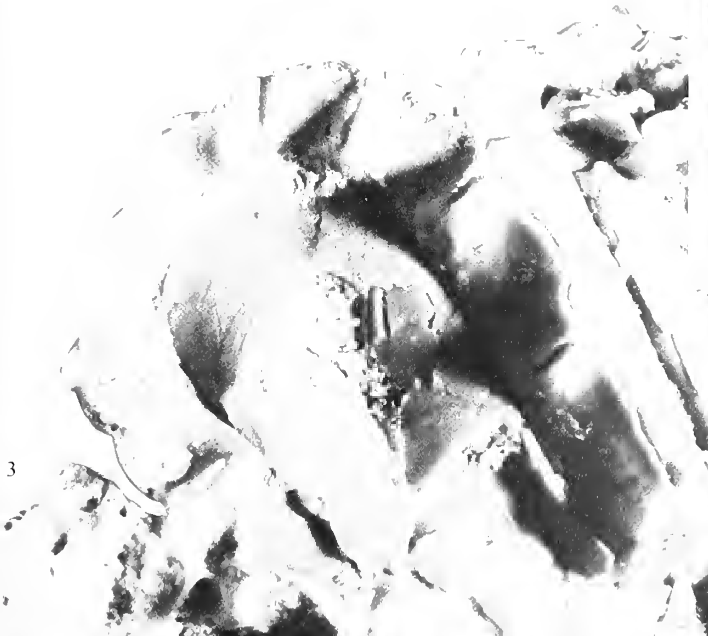
TEXT-FIG. 3. Graph of D_1 and D_2 against L for the specimens of *Torreites sanchezi* listed in Tables 1 and 2. The measurements are explained in text-fig. 2.

EXPLANATION OF PLATE 62

Figs. 1–4. *Torreites sanchezi milovanovici* Grubić, 1979. 1, BMNH LL 28002, unnamed limestone member in Aruma Group (probably Maastrichtian), 30 km south-south-west of the Saiwan airfield (lat. 20° 39′ N. and long. 57° 31′ E.), eastern central Oman; bivalved specimen, viewed from the LV side, showing the (incomplete) operculiform LV fitting in the RV, the inner margins of which are thus exposed around the LV periphery, × 0.75. 2, BMNH LL 28001, locality and age details as in 1; detail showing blade-like posterior myophore of LV (*centre*), seen in section from dorsal side, projecting down between the *arête cardinale* (P_0, *right*) and P_1 (*left*) of the RV, × 1·25. 3, 4, BMNH LL 28003, locality and age details as in 1. 3, posterodorsal region of bivalved shell, viewed from the LV side, showing the somewhat crushed operculiform LV, with subdued external growth undulations, as well as the exposed RV inner margin, with salient ridges, running around the LV periphery and projecting up through sinuses in the latter, above the *arête cardinale* (P_0, *left*) and pillars (P_1 and P_2), × 2·5; 4, close-up of broken section across a chip of the LV margin, indicated by an arrow in 3, showing the recurved growth lines in the outer shell layer (see text-fig. 7 for explanation), × 10.

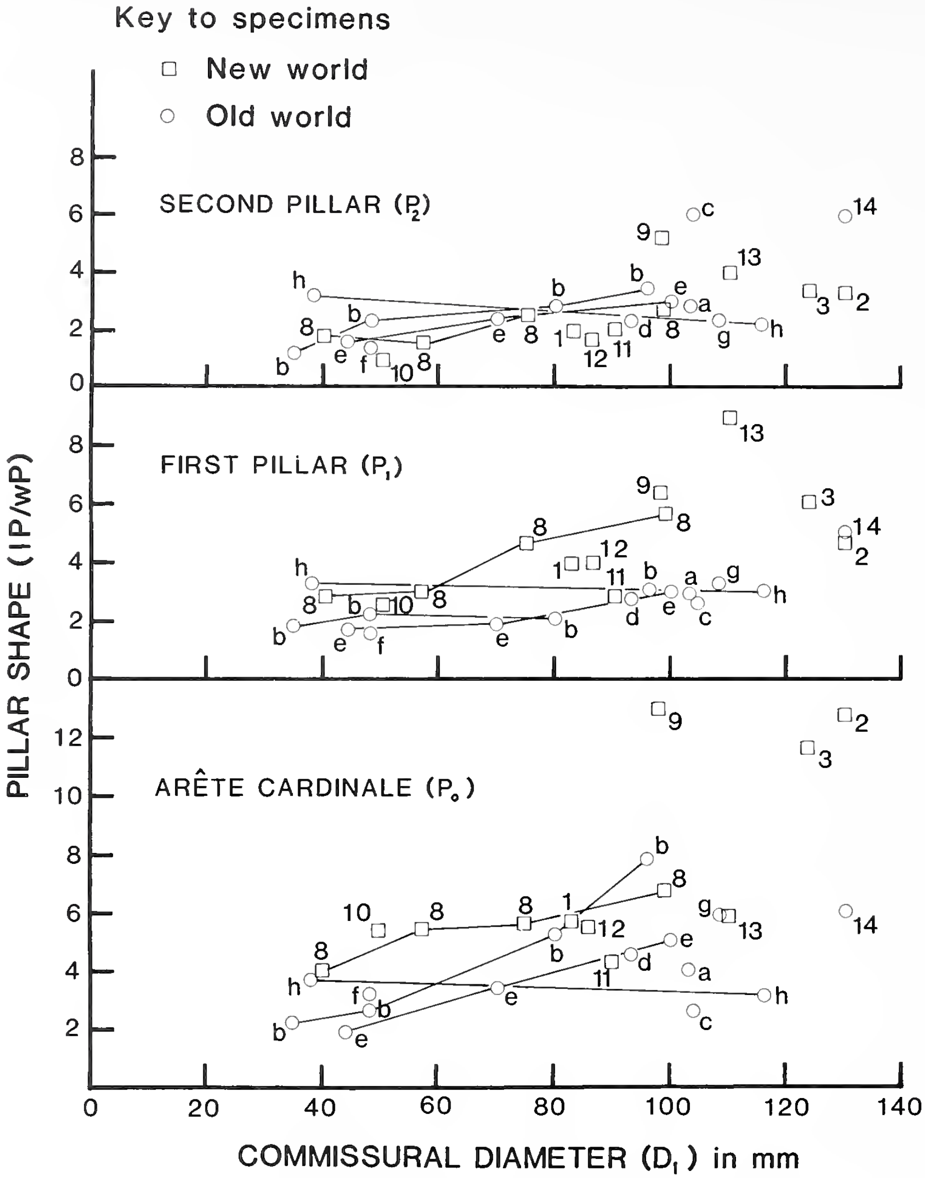

1


2


3


4

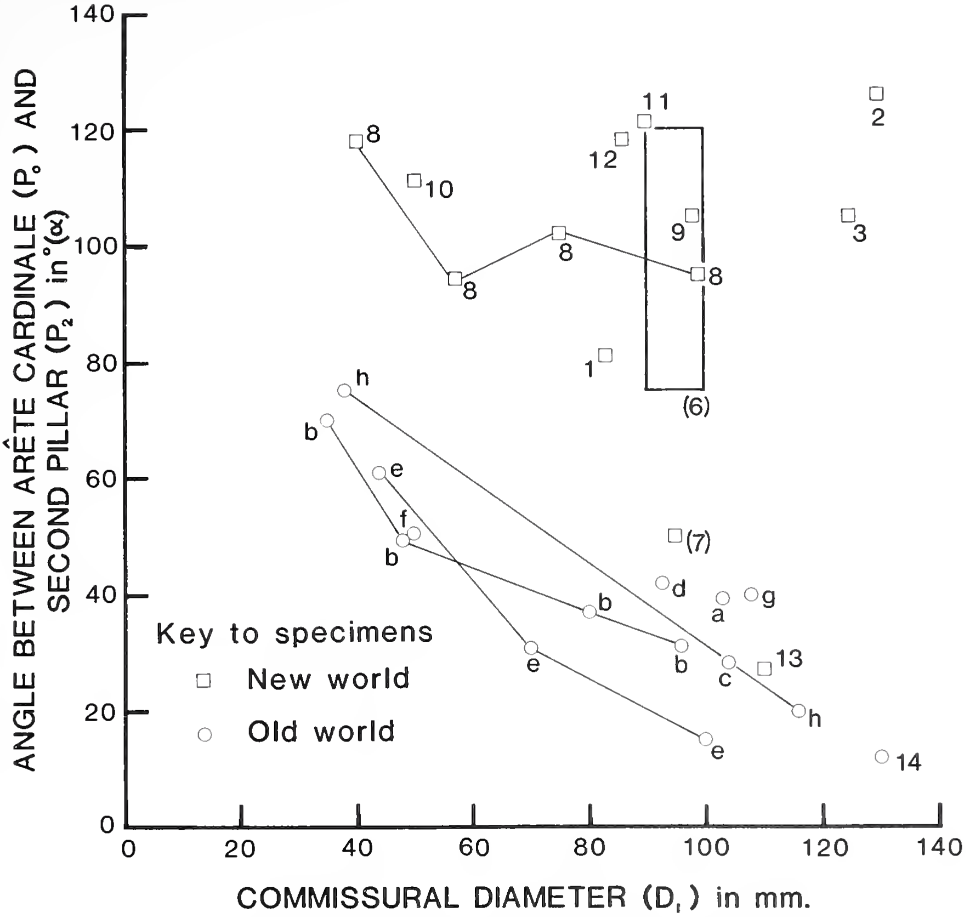
SKELTON and WRIGHT, *Torreites*



TEXT-FIG. 4. Graphs of lP/wP against D_1 for P_0, P_1, and P_2 of the specimens of *Torreites sanchezi* listed in Tables 1 and 2. The measurements are explained in text-fig. 2.

Three deep radial grooves on the posterodorsal flank of the RV correspond with the infolded *arête cardinale* and pillars. The crests of these project through wide sinuses embayed from the margin of the LV (Pl. 62, fig. 1).

The elongate *arête cardinale* and the shorter, subequal pillars are wide and finger-like in section. P_1 is usually, but not invariably longer than P_2 (see Table 1). In some specimens the *arête cardinale* tapers inwards slightly, so becoming narrower than the pillars (Pl. 62, fig. 1). The strikingly low values of α are achieved ontogenetically: sections across the RV show the angle to reach 75° in the juvenile shell (Pl. 61, figs. 1–3; text-figs. 5 and 6E–G).



TEXT-FIG. 5. Graph of α against D_1 for the specimens of *Torreites sanchezi* listed in Tables 1 and 2. The measurements are explained in text-fig. 2.

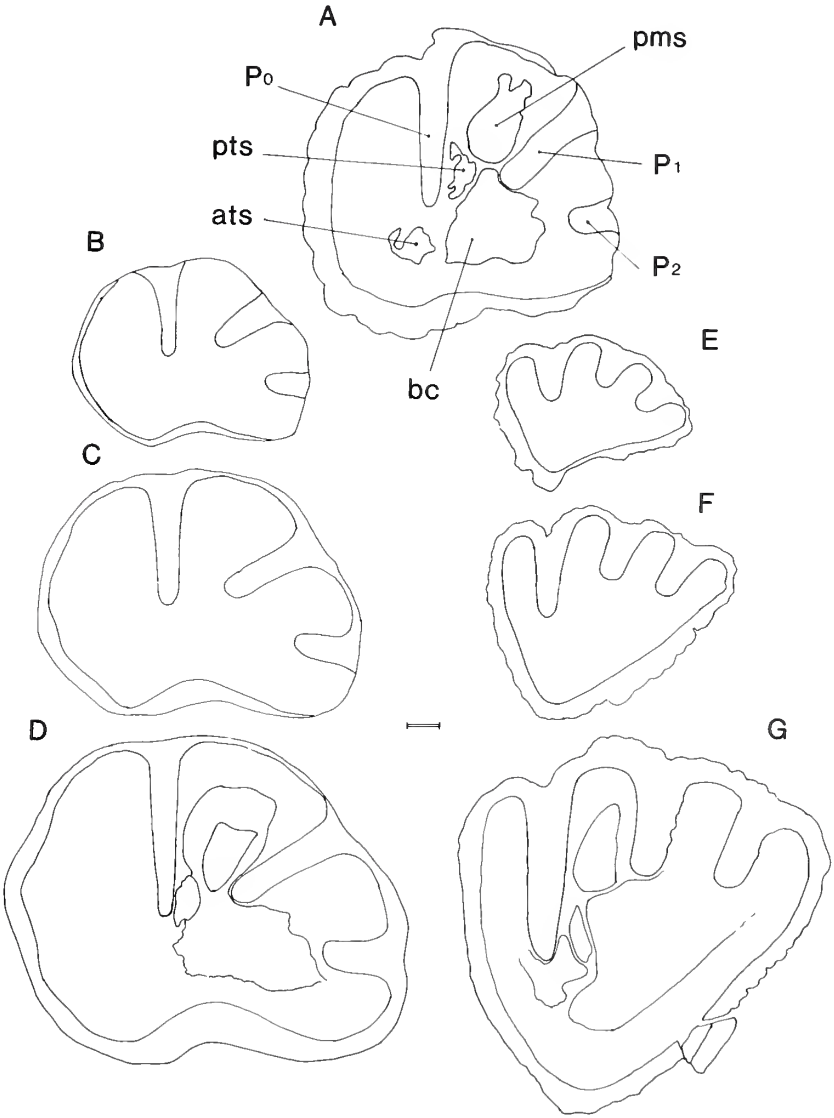
The dentition (Pl. 61, fig. 1), shows β to be about 25°. The narrow sockets for the LV teeth are separated by a pinched, wall-like RV tooth lying posteriorly to the inner tip of the *arête cardinale*. The latter has a rounded inner termination indicating complete absence of a ligament. The tooth-like posterior adductor myophore of the LV is situated dorsally behind the teeth, projecting down between P_1 and the *arête cardinale* (Pl. 62, fig. 2), where it is received in the RV by a large socket (Pl. 61, fig. 1; text-fig. 2A). The anterior adductor myophore of the LV forms an arcuate ledge extending some way around the anterior and ventral margins, where it faces on to a broad inclined shelf in the RV, supporting a distinctively reticulate muscle scar (Pl. 61, fig. 1; text-fig. 2A).

The body cavity is very shallow, and its volume further reduced by the large, downwardly projecting myocardinal elements of the LV. Much of the apical 'limb' of the RV is filled by tabulae, though these are largely obscured by recrystallization.

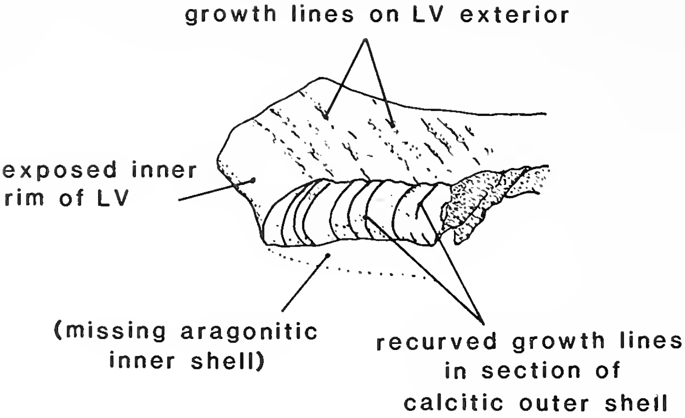
Palaeoecology. Though found close together, specimens BMNH LL 28000–28004 were recovered as loose blocks, and so their original life position remains uncertain. Evidence for attachment of one individual to another is shown by specimens LL 28001 and LL 28004 (Pl. 61, fig. 3). Otherwise they represent solitary individuals. The elongated and curved horn shape of specimens LL 28000, LL 28001, and LL 28002 suggests a reclining, boat-like habit, with the convex flank of the RV shallowly embedded in the sediment and the commissure raised up, away from it (text-fig. 8). The evidence of associated borings and epibionts lends some

TABLE 2. Measurements on specimens of *Torreites sanchezi sanchezi* (Douvillé) (1–12) from the Upper Campanian to Lower Maastrichtian of the Caribbean, '*T.* cf. *sanchezi*' (13) from the topmost Santonian to basal Campanian of Jamaica, and *T. s. milovanovici* Grubić (14) from the Maastrichtian of Sharjah (UAE), taken from the literature. The original species designations and references thereto (where locality details may be found) are recorded for each specimen cited. The abbreviations for the measurements are explained in text-fig. 2.

	Shell size (mm)			Hinge Angle (°)	Pillar Angle (°)	Pillar dimensions (mm)					
Specimen	L	D_1	D_2	β	α	lP_0	lP_1	lP_2	wP_0	wP_1	wP_2
T. sanchezi											
1. Douvillé (1927) (holotype)	—	83	>83	34	81	40	>32	>14	7	8	7
2. Palmer (1933), pl. 7, fig. 2	—	130	>120	—	126	90	20	52	7	11	6
3. Palmer (1933), pl. 8, fig. 2	—	124	120	50	105	70	49	27	6	8	8
4. Rutten (1936) (description)	—	—	—	20–30	—	—	—	—	—	—	—
5. Vermunt (1937), (description)	230	115	80	—	—	—	—	—	—	—	—
6. MacGillavry (1937)	—	'90–100'		—	'75–120'	—	—	—	—	—	—
7. MacGillavry (1937), exceptional specimen	—	—	—	—	50	—	—	—	—	—	—
8. Jung (1970), G.14065 on pl. 2	135	99 75 >57 >40	122 98 >72 >43	—	95 102 94 118	54 39 27 >16	40 33 >21 >11	25 >20 >13 >9	8 7 5 4	7 7 7 4	9 8 7 5
9. Jung (1970), G.14066 on pl. 3	—	98	104	34	105	65	45	26	5	7	5
10. Van Dommelen (1971), J.3702*a* (table 5)	74	(50)		—	111	27	15	5	5	6	5
11. Van Dommelen (1971), J.3702*b* (table 5)	76	(90)		49	121	>30	26	14	7	9	7
12. Van Dommelen (1971), J.3676 (table 5)	>160	86	78	32	118	33	24	14	6	6	8
'*T.* cf. *sanchezi*'											
13. Chubb (1971)	—	>110	—	—	27	65	45	28	11	5	7
'*T. milovanovici*'											
14. Grubić (1979)	—	>130	100	—	12	>60	50	60	10	11	10



TEXT-FIG. 6. Drawings of sections across the RVs of *Torreites sanchezi* showing the ontogenetic divergence in pillar arrangement between the Caribbean (A–D) and the Arabian (E–G) subspecies. The drawings show the outlines of the outer shell layer, as well as some of the internal features in A, D, and G, and are all the same scale (scale bar = 1 cm). A is from the holotype (Douvillé 1927, pl. 4, fig. 1). Abbreviations are as in text-fig. 2A. B–D are from a specimen (G.14065) illustrated by Jung (1970, pl. 2, fig. 1*b*, *c*, and *d* respectively). E–G are from specimen BMNH LL 28004, illustrated here in Plate 61, figs. 3–1 respectively.



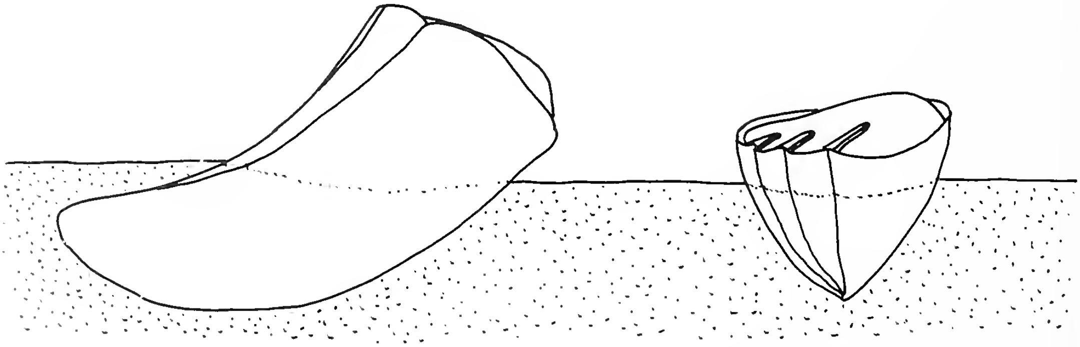
TEXT-FIG. 7. Explanatory drawing of the marginal fragment of LV outer shell layer of *Torreites sanchezi* (specimen BMNH LL 28003), shown in Plate 62, fig. 4. A radial section across the valve rim, adjacent to the inner tip of P_1, is shown facing the observer.

support. In LL 28001 there is a slight preponderance of borings on the concave dorsal flank of the RV, where the fragment of another individual is also attached: the convex ventral flank would here seem likely to have been lowermost, and such a position is further substantiated by the orientation of some fine geopetal sediment inside the shell. LL 28002 is of similar shape, but has borings and rare encrusters scattered around all its flanks: possibly it suffered post-mortem displacement. However, it clearly shows xenomorphic overgrowth on to another rudist fragment high up on its convex ventral flank, again hinting at this surface having lain against the seafloor in life. In LL 28000 the anterodorsal face is convex and the posteroventral face is concave. A slight preponderance of borings on the latter face, as well as a couple of compactional indentations on to that surface hint at it having been uppermost.

LL 28003 and LL 28004 have more or less straight RVs, with borings scattered around all their flanks. These would seem to have lived in an essentially upright position (text-fig. 8). Burial in such a position is indicated in specimen LL 28003 by compaction along the central axis of the RV.

The matrix associated with these specimens is a pale yellow (weathered), medium-grained bioclastic packstone with subangular to subrounded bioclasts: it is presumably of shallow marine origin, as suggested by the grain-supported texture and rounding of the bioclasts.

Specimens PWS 84/x.1 and PWS 84/32.1 have obtusely conical RVs, and are likely to have been shallowly embedded, barrel-like elevators (text-fig. 8). Specimens of similar form were observed *in situ* at Qarn Murrah, Sharjah, with such an upright habit (text-fig. 9). Again, these are associated with medium-grained to fine-grained biomicrite packstones of presumed shallow marine origin.



TEXT-FIG. 8. Diagram showing the two kinds of life position apparently exhibited by *Torreites sanchezi milovanovici*—a reclining, boat-like habit (left) and an upright habit (right). Note that elevation of the commissure from the substratum (dotted ornament) is achieved in both cases. The difference between them probably only reflects variability in the orientations established during larval settlement and early growth.

TEXT-FIG. 9. Two RVs of *Torreites sanchezi milovanovici* shown in section in upright life position (cf. text-fig. 8, right), on the upper surface of a bedding plane of Maastrichtian limestone (Simsima Formation) at Qarn Murrah, Sharjah (UAE) (see text-fig. 1 and p. 506 for locality details). The lens cap is 5·5 cm across.

Discussion. The possibility of our specimens merely being Old World homeomorphs of *Terreites* can be immediately rejected: they share with the New World forms too many constructionally independent, specialized features for coincidental convergence to be plausible. The features in question comprise: (1) the smooth upper surface of the left valve; (2) the apically blind canals in the LV inner shell; (3) the unusual relative sizes and shapes of the RV pillars and *arête cardinale*, and their exposure through broad sinuses in the LV; and (4) the distinctive radially indented ornament of the RV outer shell.

Plots of the overall dimensions (text-fig. 3), and of the shapes (text-fig. 4), and relative positions of the pillars and the *arête cardinale* (text-fig. 5) of our specimens, drawn from Table 1, form compact, well-defined clusters; they clearly all belong to one species population. The fragmentary RV holotype of '*T. milovanovici* Grubić' represents a slightly larger individual than any of ours (see Table 2, specimen 14), but all its measured features plot comfortably as extrapolations from the cluster of data points for our specimens. In fact the obliquity of the section across the valve figured by Grubić (1979, pl. 1) is slightly misleading in making the pillars look more extended than they are. Our measurements are taken directly from the specimen itself, with allowances being made for this 'cut effect'.

All the Old World specimens, then, may satisfactorily be grouped in a single species. It is the relation of this to the New World species that is more problematical.

Prior to Grubić (1979) only two species of *Torreites* had been recognized, the type species *T. sanchezi* (Douvillé) and *T. tschoppi* MacGillavry. The latter is typically much smaller than the Old World form (rarely > 40 mm in commissural diameter), with simple costulate ribs about 1–2 mm wide, and is found in dense clusters of individuals, rather than in ones or twos (MacGillavry 1937, p. 129). Besides, it also appears to be older than the Old World specimens (see p. 506). It is thus clearly distinct from the Old World species. However, it approaches the latter in having a relatively low α, of about 45–70°, according to MacGillavry (1937).

Measurements reported for, or taken directly from the published figures of all described specimens referred to *T. sanchezi* are shown in Table 2, and are also plotted on text-figs. 3–5. Grubić (1979) erected two new species from among these, *T. coxi* and *T. chubbi*. The former was founded on two specimens, the holotype being one of those described by Jung (1970) (specimen 9, Table 2). It has the same size, ornament, and basic pillar arrangements as in the other *T. sanchezi*, but was considered to differ in possessing a relatively longer and thinner *arête cardinale*, and pillars with slightly bulging inner tips. With such small samples available, these subtle distinctions do not carry conviction. The holotype simply lies at the edge of a rather broad cluster of points for *arête cardinale* shape in the New World *T. sanchezi* (text-fig. 4). Moreover, the swelling of the pillar tips shown in Jung's Plate 3 is only very slight. The species cannot be upheld and we here suppress it as a junior subjective synonym of *T. sanchezi*.

T. chubbi is based on a single poorly preserved specimen described as *T.* cf. *sanchezi* by Chubb (1971) (specimen 13, Table 2). Again, its independent status is dubious, though the specimen is intriguing in possessing a relatively low value of α (27°, rather than the 40° reported by Grubić). It is also older than the other specimens considered here (probably latest Santonian to earliest Campanian; see p. 506). Further material is needed to clarify its position, particularly in relation to the coeval *T. tschoppi*.

The final comparison left to be made, then, is with *T. sanchezi* itself. Plots of the shapes and relative positions of the pillars and *arête cardinale* (text-figs. 4 and 5) for all the specimens included here in the New World *T. sanchezi* (specimens 1-12 in Table 2) form coherent, if somewhat broadly spread clusters of data points, supporting their inclusion within one species population. Their commissural diameters (text-fig. 3) also plot together reasonably well, with the exception of the small specimen 10 on Table 2; the variation in shell length can readily be attributed to ecophenotypic variation in relation to life position (text-fig. 8).

The Old World specimens share with the New World *T. sanchezi* the same adult size range (text-fig. 3) as well as precisely the same distinctive external ornament: the broad radial ribs of the Old World specimens have widths varying from about 5 to 8 mm, exactly as in those of the New World specimens (e.g. Jung 1970, pl. 1, figs. 2 and 3). The one value of β from the Old World specimens (from BMNH LL 28004) is at the lower end of the range exhibited by those from the New World (compare Tables 1 and 2). Pillar form in the two populations (text-fig. 4) is closely similar in smaller (younger) individuals, though in the largest individuals P_1 tends to become relatively longer and more slender in the New World specimens. A similar trend in the *arête cardinale* (P_0) is even more pronounced. There is thus some slight ontogenetic divergence between the two populations from a more or less similar juvenile condition. This divergence may be linked constructionally with the rather more marked separation of the two populations on the basis of α values (text-fig. 5): those in the Old World specimens are notably smaller than those of the others. Again, there appears to have been ontogenetic divergence, involving reduction in α throughout growth in the Old World forms, but with little change in the New World forms. Yet the existence of some specimens among the New World population with low values of α (e.g. specimen 7 on Table 2, cited by MacGillavry 1937, p. 129) gives support for close linkage between the two populations.

Although these few differences between the adults of the Old and New World populations are sufficient to render each distinctly recognizable, it is the close similarity of the two populations in all other respects that is the more striking. Given the small samples involved and our relative ignorance of many aspects of rudist functional morphology, it is really a matter of subjective judgement as to whether the Old World population should still be recognized as a distinct species ('*T. milovanovici*'), or whether it should be treated, as we propose here, as a geographical subspecies of *T. sanchezi*, which we label *T. s. milovanovici* Grubić, 1979, in contrast with the New World stock of *T. s. sanchezi* (Douvillé, 1927), in which we include all the New World records of *T. sanchezi* recognized here. We favour this latter option because of the existence of exceptional specimens in the New World with α values close to those of specimens from the Old World. These suggest that the one significant diagnostic feature of the Old World population may already have existed within the range of morphological variability of the New World population.

The paradox of the extraordinarily wide geographical separation of the two subspecies will be considered in a later section (p. 522).

PALAEOBIOLOGY AND EVOLUTIONARY RELATIONSHIPS OF *TORREITES*

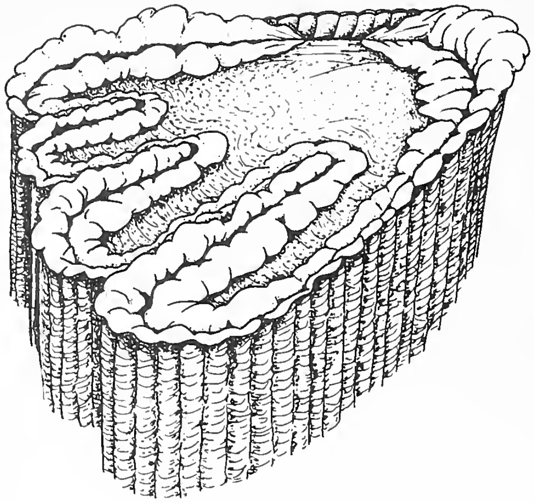
Torreites is rare in the Caribbean Province; Grubić (1979, p. 94) noted that the then published record of the genus was founded on only about twenty specimens (which have nevertheless fuelled at least nine systematic papers alone!). Our material, as well as expanding the recorded total of specimens by at least a third, is also significant for its good state of preservation. Placement of the genus in the Hippuritidae can be confirmed, while the reason for its aberrant lack of pores in the LV can now be explained from investigation of the growth lines in that valve.

Though generally considered a hippuritid because of its pillars (Douvillé, 1927), *Torreites* differs from all other hippuritids in its lack of pores. Van Dommelen (1971, p. 65) commented: 'In reality, however, all we know about the VS [= LV] of *Torreites* is, that the outer shell layer is imperforate in the parts between L, S and E [= P_0, P_1 and P_2]. But what about the slit-like openings over these infoldings of the available eroded specimens? Have they been covered or not covered, and if covered, was this cover a reticulum or something different?' MacGillavry (1937, p. 128) too, queried whether or not the pillars really had been exposed through open sinuses in the LV. It is unambiguously clear from our specimens (e.g. Pl. 61, fig. 5 and Pl. 62, figs. 1, 3, 4) both that, no roof of any kind existed over the crests of the *arête cardinale* and the pillars, and that the LV outer shell layer is indeed imperforate. Is *Torreites* thus a hippuritid that has lost its pores, or one descended from a primitive form that never had them, or not a hippuritid at all? The latter option is the least likely. Not only does *Torreites* possess the pillars so characteristic of the family, albeit of unusual form, it also has a typically hippuritid myocardinal apparatus with its markedly tooth-like posterior myophore in the LV, received in a socket in the RV. Its overall shell form, with an elongate-conical RV and operculiform LV, is also typical of, though not exclusive to the family.

If *Torreites* is accepted as a hippuritid, the lack of pores is unlikely to be a primitive trait. Pores are already well established in the earliest hippuritids, which predate the oldest *Torreites* by about two stages. *Torreites* is further characterized by such specializations as the extreme elongation of the *arête cardinale*, despite loss of the ligament itself, and the blind canals in the LV interior.

Two features in our specimens together suggest that the lack of pores is secondary: (1) the thinness of the outer shell layer in the LV relative to that in the RV, with the margin of the latter projecting well beyond that of the former (Pl. 62, fig. 3); and (2) the recurvature of the growth lines in the outer shell layer of the LV on to its outer surface (Pl. 62, fig. 4; text-fig. 7), indicating that mantle tissue reached out on to at least the peripheral parts of the outer surface of the valve. Mantle tissue would thus have been freely exposed both around the inner margin of the RV and around the periphery, if not more, of the outer surface of the LV. In normal hippuritids, no mantle tissue was directly exposed in this manner. Rather, extensions of it lined the pore and canal system in the LV outer shell layer, where its cilia are interpreted as having driven water currents, drawn from above the shell, over the covered inner rim of the RV, enabling the entrapment there of food particles, without the need of valve gaping (Skelton 1976). The free exposure of mantle tissue in *Torreites* would have made redundant the canal and pore system of its ancestors. Its atrophy would then have been hastened by the lowering and retreat of the LV outer shell layer to allow maximum exposure of the RV inner rim. A reconstruction of *Torreites* in life, with its corona of exposed mantle tissue is shown in text-fig. 10.

What was the adaptive significance of this exposure of mantle tissue? One possibility is that the externalization of food entrapment (Skelton 1976) was taken a stage further than in the ancestral hippuritids, with direct trapping of food particles on the exposed mantle projections, as has been proposed for radiolitids (Skelton 1979*a*). But such a trivial modification of function seems an unsatisfactory explanation for so considerable a morphological change; it is hard to conceive of any obvious benefit to feeding efficiency that might have been won thereby, and the increased exposure would seem in any case to have carried an increased risk of physical or biological damage to the mantle rims. One significant effect of the exposure, however, would have been the emergence of mantle tissue from the darkened confines of the ancestral pore/canal and covered rim system, into the light. This immediately calls to mind the possibility of symbiotic zooxanthellae, by analogy



TEXT-FIG. 10. Reconstruction of the appearance in life of *Torreites sanchezi milovanovici*. The upper part of the shell is shown, with thick extensions of mantle margin projecting out between the valve rims, in the manner of the living Giant Clam, *Tridacna*. It may be surmised that, as in the latter, these mantle extensions were vividly and variably coloured.

with the Giant Clam, *Tridacna*. The possibility of algal symbiosis in rudists has frequently been raised in the literature (e.g. Kühn 1937; Philip 1972; Coates 1973; Kauffman and Sohl 1974; Vogel 1975; and Skelton 1979*a*) and has recently been ably reviewed by Cowen (1983). The consensus of most of these works is that such symbiosis was widespread in the group—a conclusion supported by Cowen himself. Skelton (1979*a*), in contrast, argued that positive evidence for possession of zooxanthellate tissue, in the form of clear adaptation of the shell to allow maximum exposure of mantle tissue to the light, is only seen in certain broad-rimmed radiolitid genera. Their symbiosis is considered to have arisen as a secondary adaptation of the enlarged mantle margins associated originally with food particle entrapment. The layout of the pore and canal system in normal hippuritids, in particular, was well suited for supplying the RV mantle rim with feeding currents, and is most satisfactorily explained thus. Cowen nevertheless felt that the tissue within the canal and pore system could have been exposed to light through the shelly cover over the radiating canals. Yet in some hippuritids this cover is actually quite thick (often over 3 mm), and, moreover, the canals show no tendency to flatten out in such a way as to maximize exposure to light. Many hippuritids seem, in any case, to have lived in somewhat turbid, poorly lit waters (Skelton 1979*b*). It thus remains unlikely that any of the normal hippuritids, at least, possessed zooxanthellae. With *Torreites*, however, we may have an exception; its clear morphological adaptation for free exposure of mantle tissue suggests a hippuritid 'redesigned' as a photophile. The scarce palaeoecological information on *Torreites*—implying a basically upward growth form and occupation of shallow, clear waters—is consistent with the algal symbiosis hypothesis.

SIGNIFICANCE OF THE PRESENCE OF *T. SANCHEZI* IN OMAN AND THE UAE

Torreites is not alone among Campanian-Maastrichtian shallow marine benthos in showing disjunct endemism between the Caribbean Province of Kauffman (1973) and various sites in the eastern part of the Tethyan Realm, ranging from the Middle East to the East Indies. Chubb (1956), recognized such a distribution in the radiolitid rudist genus, *Thyrastylon*, remarking (p. 39): 'It is indeed interesting that in the same epoch, the Maestrichtian [*sic*], a form closely resembling *T. coryi* [a Caribbean species] was living in Persian seas, so that the geographic range of *Thyrastylon* extended from Guatemala to Persia, a distance of nearly 10,000 miles.' Kollmann and Sohl (1980) stated that the itieriid gastropod, *Vernedia friesi* Kollmann and Sohl, from the Upper Cenomanian or Lower Turonian of Colima Province, Mexico, had a closer affinity with a southern Indian form, *V.*

globoides (Stoliczka), from the Campanian to Maastrichtian Arrialoor Group of the Trichinopoly District, than with the European and Transcaucasian species of the genus. Another gastropod, *Actaeonella borneensis* Nuttall and Leong, is known both from an uncertain Cenomanian to Campanian level in Borneo and from Campanian to Maastrichtian strata in Mexico and Cuba (Sohl and Kollmann 1985). The codiacean alga *Ovulites* occurs in the Upper Cretaceous of the Caribbean and in northern Iraq, Afghanistan, and Tibet, though not from the Mediterranean Tethys (Elliott 1981). These are but a few examples that complement the clear-cut case of *Torreites* to establish this form of disjunct endemism as a palaeobiogeographical problem in need of a solution.

There are three possible explanations for such a highly disjunct distribution of shallow-water benthic taxa: (1) false synonymy of coeval homeomorphs; (2) plate tectonic drifting apart of formerly united shallow-water provinces; and (3) temporary range extension between the two regions brought about by the development of a continuous intervening chain of shallow-water 'staging posts' for planktonic larval dispersal.

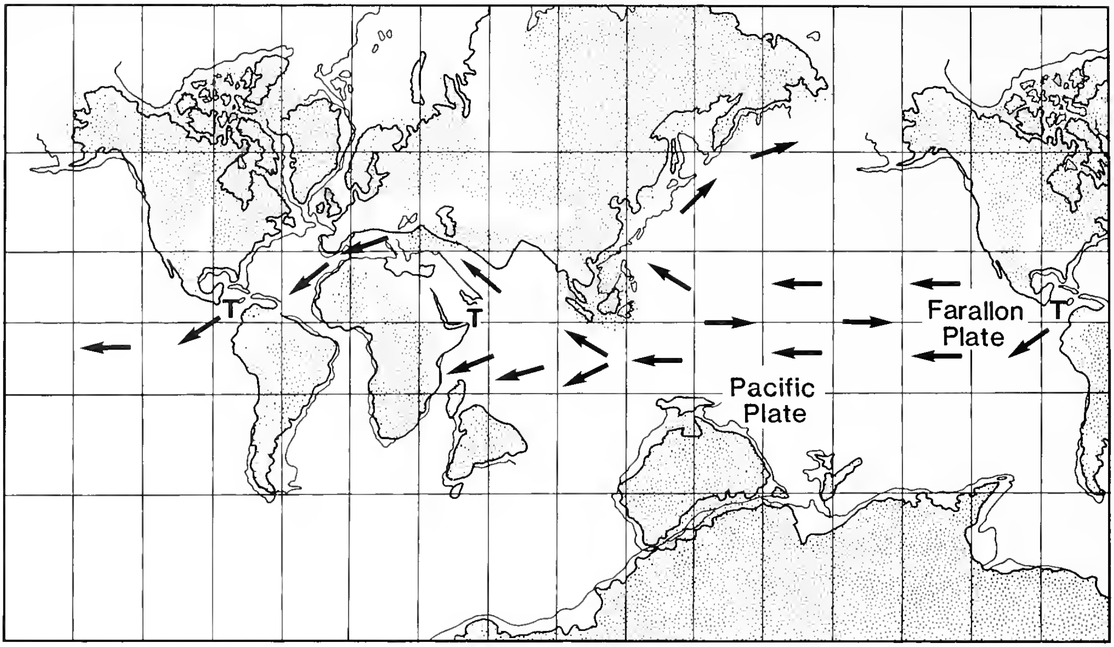
The first option, of coeval evolution of not one, but several pairs of homeomorphs in the two regions, over the same limited time interval, is in itself improbable, and becomes yet more so with every new example of the disjunct distribution that is added to the list. The importance of *Torreites* is that its several constructionally independent diagnostic features allow us expressly to reject homeomorphy as a reasonable hypothesis in its case; any argument for homeomorphy in the other examples cited must now be relegated to special pleading for particular examples.

The second explanation, based on drifting apart of the two regions was evidently that favoured by Grubić (1979, p. 94), who concluded: 'The presence of a specific Caribbean Upper Cretaceous rudist from in the eastern Mediterranean can by no means be interpreted other than by assuming that both Americas, Antilles and the Mediterranean were much closer in the Upper Cretaceous.' Such an explanation would be reasonable if there were matching geotectonic evidence. However, there is none for Oman having been anywhere near the Caribbean in Late Cretaceous times. The strata containing *Torreites* in Oman and the UAE represent the first marine autochthonous deposits upon the Semail Nappe, itself already obducted on to the Arabian foreland (see Glennie 1977 and Murris 1980 for details). So the area in question was then, as it is today, firmly part of the Arabian continent. Likewise, the Caribbean sites with *Torreites* (Cuba, Jamaica, and Puerto Rico) were unambiguously associated with the central American region in the Late Cretaceous (Mattson and Lewis 1980).

We are then left with the third possibility, of planktonic larval dispersal along a chain of staging posts. In the absence of recorded fossils of rudist prodissoconchs, the character of rudist larvae can only be surmised from circumstantial evidence. The geologically almost simultaneous appearance in the Late Turonian of the primitive hippuritid species, *Hippurites resectus* Defrance in Europe and North Africa (Douvillé 1890–1897, 1910) and of the almost certainly synonymous '*H. mexicanus* Barcena' in Mexico (Muellerried 1930), for example, favours a readily dispersed planktonic larval stage (incidentally, this is against the notion of a larval brood pouch speculated upon by Skelton (1976)). So it is not unreasonable to suppose that such a larval stage existed in *Torreites*.

The two possible oceanic routes for dispersal between the Old and New World sites of *Torreites* are: (1) via the Mediterranean Tethys and Atlantic; and (2) across the Pacific and eastern Tethys (text-fig. 11).

The Mediterranean/Atlantic route is considered unlikely for two reasons. First, the bivalve endemism data of Kauffman (1973) suggest that the 'north Indian Ocean sub-province' (incorporating Oman and the UAE) and neighbouring 'eastern Mediterranean sub-province' became significantly distinct from the 'western Mediterranean sub-province' in Campanian–Maastrichtian times, implying the presence between them of barriers to dispersal. In a recent study of Campanian/Maastrichtian rudist distributions in the Mediterranean region, Philip (1985) similarly establishes a clear distinction between an 'Aquitano-Pyrenean palaeobiogeographic unit' and an 'eastern and central Mediterranean' one, with continental barriers lying between them. A few central Mediterranean forms are preserved in southern Spain, however, presumably derived via a North African



TEXT-FIG. 11. Inferred Campanian–Maastrichtian palaeogeography of the World, showing oceanic surface currents (arrows). The Americas are duplicated at each end of the map to allow direct comparison between the Mediterranean Tethys/Atlantic and Pacific marine connections between the two sites from which *Torreites* has been recovered (indicated by T). It is argued in the text that a chain of shallow staging posts, spread across the Pacific and eastern Tethys, was the most likely means by which the range of *Torreites* was extended, by larval dispersal, from the Caribbean, across to the Arabian region. Continental positions derived from Smith and Briden (1977), land (dotted ornament) and sea (white) distributions from Zeigler *et al.* (1983), and ocean currents from various sources cited in the text.

route (Philip 1983). In any case, there are no records, as yet, either of *Torreites* or *Thyrastylon*—both very distinctive fossils—anywhere in the Mediterranean region.

The second objection to the Mediterranean/Atlantic route is the increasingly impassable width of the Atlantic in Campanian–Maastrichtian times, as reflected in the rising generic dissimilarity between its two sides with respect to bivalves (Kauffman 1973) and, in particular, to rudists (Coates 1973).

The alternative explanation is that *Torreites*, *Thyrastylon*, and the other disjunct endemics discussed earlier were somehow able to cross the Late Cretaceous Pacific Ocean. In which direction might such dispersal have taken place? Many authors have argued for a circum-global East to West equatorial current during the Cretaceous, passing through Tethys, and across the Pacific Ocean (text-fig. 11; Luyendyk *et al.* 1972; Gordon 1973; Berggren and Hollister 1974, 1977; and Lloyd 1982). The Tethyan Realm was thus extended for several thousand kilometres into the eastern Pacific (Gordon 1973) and many Pacific seamounts have now been found to have been capped by rudist-bearing atolls in Aptian to Cenomanian times (recently reviewed, with references therein, by Winterer and Metzler 1984 and Konishi 1985). From mid-Aptian times onwards, the opening Atlantic promoted the growth of endemism in the Caribbean, with respect to the rest of Tethys (Coates 1973; Skelton 1982), to provincial levels by Late Santonian times (Kauffman 1973). This suggests that the Late Cretaceous *Torreites* is most likely to have originated in the Caribbean, and then dispersed westwards towards eastern Tethys (text-fig. 11). Such a model is consistent with MacGillavry's (1937) identification of the older Caribbean species *T. tschoppi* as an ancestral form.

Evidence for staging posts that would have facilitated the trans-Pacific dispersal of *Torreites* and other forms is now well documented from DSDP work. Beckmann (1976), for example, has described redeposited Campanian–Maastrichtian shallow-water foraminifera from the Line Islands seamount chain. Two of the genera, *Asterorbis* and *Sulcoperculina*, had previously only been recorded from the Caribbean and surrounding areas. A third, typical Caribbean form, *Pseudorbitoides israelskyi* Vaughan and Cole, was also known from eastern Tethyan sites (details in Dilley 1973). Other findings, reviewed by Schlanger *et al.* (1981), have extended the evidence for such staging posts as far across the ocean as the Nauru Basin (Marshall Islands). These records indicate that the Pacific Plate was studded with islands and/or seamounts which served as stepping stones for some Caribbean shallow-water benthos in Campanian–Maastrichtian times. Evidence that the Farallon Plate, which at that time separated the Pacific Plate from the Americas by some 6000 km, was similarly endowed was also provided by Schlanger *et al.* (1981). This survives in the form of ophiolite complexes with exotic limestones, plastered on to the western flanks of the Americas during subduction of the plate.

There is thus direct evidence for former staging posts, carrying a Caribbean-derived shallow marine benthic fauna of Campanian–Maastrichtian age, for over half the distance between the Caribbean and Oman. Documentation of suitable staging posts along the remaining (eastern Tethyan) part of the route is very much more difficult, because the available evidence is now caught up in the various Tethyan suture zones running from the East Indies to the Middle East (Audley-Charles *et al.*, 1980). It seems, however, that some shallow or even emergent physiographical prominences, such as island arcs and small continental blocks may then still have lain in the oceanic gap between India and Eurasia, although most of these had already been accreted on to Eurasia by mid-Cretaceous times (Tapponnier *et al.* 1981). Moreover, Maastrichtian orbitoid and rudist-bearing facies are known from the southern edge of the Lhasa Block, in Tibet (Herm *et al.* 1985 and pers. comm.), which was by then accreted on to the southern flank of Eurasia.

From the evidence given above, it is therefore not unreasonable to postulate that *Torreites* spread from the Caribbean to Oman, exploiting a continuous chain of shallow-water staging posts that stretched across the Pacific and eastern Tethys during Campanian–Maastrichtian times.

As a test for this hypothesis, we predict that *Torreites*, or other forms with the same disjunct distribution, such as *Thyrastylon*, will eventually be recovered either from DSDP material from the Pacific, or from shallow-water Tethyan carbonates of Campanian–Maastrichtian age caught up in Himalayan and other eastern Tethyan suture zones. Conversely, the discovery of such faunal elements in the western Mediterranean (e.g. north-western Africa or southern Spain) would militate against our hypothesis.

Two palaeobiogeographical corollaries to this model are worth noting. First, the repeated population-sampling effect that would have accompanied the successive westward dispersals of spat from staging post to staging post ought, surely, to have resulted in a pronounced 'founder' effect in the population that eventually became established in Oman and the UAE (see Mayr 1970, for explanation of the founder principle). It is thus remarkable that the only significant modal deviation of the Old World population from the Caribbean population is in the ontogenetic reduction of α (p. 520), which, in our view, only merits distinction at the subspecific level.

Our model for the historical biogeography of *Torreites* and its 'fellow travellers' also bears on the current debate about the relative roles of vicariance and dispersal in explanations for the geographical distributions of taxa (concisely reviewed by Forey 1981). In identifying the Caribbean as the centre of origin for *Torreites*, and treating its appearance in eastern Tethys as a result of dispersal along staging posts between the two areas, we have clearly adopted a 'dispersalist' explanation for the disjunct distribution of the genus. In our view the appearance of the staging posts caused the decline of the Pacific Ocean as a barrier to dispersal of Caribbean shallow-water benthos during the Campanian–Maastrichtian. The Pacific, then, became a 'filter' for biogeographical range expansion (Simpson 1962) at that time, because selected taxa appear to have made the full crossing. Forey's (1981) characterization of such accounts as emphasizing processes supposed from *ad hoc* considerations to have brought about distributional patterns, and as lacking in any general principles of pattern analysis—an advantage reserved for vicariance studies—is a misleading criticism, suggesting, as it does, that the accounts are difficult, if not impossible, to test. The hypothesis of the appearance of a trans-Pacific filter for the westward dispersal of Caribbean shallow marine benthos in the Late Cretaceous, could readily be tested by an analysis of fossil distributions. If our model is correct, then among the taxa showing apparent disjunct endemism on either side of the Pacific there should be an overwhelming preponderance of stratigraphically older records, for each of the taxa considered, on the Caribbean side. The test should be workable, because the purported sequence of events was spread over a 'geological' time scale of millions of years, and so ought to have left a realistically detectable imprint on the fossil record. In the case of *Torreites*, for example, there is a generous stratigraphical spread between (1) the first record of *Torreites* in the Santonian or earliest Campanian, (2) the establishment of the full chain of staging posts in the Campanian-Maastrichtian, and (3) the first record of *Torreites* in the Old World (Early Maastrichtian). It should be noted, however, that what is being discussed here is a biogeographical range expansion provoked by changes in the geological context for dispersal. The process of larval dispersal itself is admittedly beyond geological analysis, because such events on the 'ecological' time scale would be, to all intents and purposes, geologically instantaneous.

Since we are dealing with the effect on the distribution of taxa of the disappearance of a former barrier (the Pacific Ocean prior to the completion of the chain of staging posts), we could not, indeed, employ any vicariance method of analysis, simply because these are all irrelevant to such a phenomenon. As Forey (1981) makes clear, the aim of vicariance analysis is to unravel the history of progressive fragmentation of an already widespread ancestral biota. Were we investigating, say, the partitioning of the Tethyan Realm in the Late Cretaceous as a result of the *appearance* of barriers, then some form of vicariance analysis might be both appropriate and effective. Our point, then, is that barriers come and go on a geological time scale, and so the two methods of analysis both have roles to play in palaeobiogeography: vicariance analysis where developing barriers fragmented an ancestral biota; and 'dispersal' analysis where the demise of barriers has allowed range extensions to take place. Both methods, we believe, can yield hypotheses about historical biogeography that can be further tested from fossil distributions.

SUMMARY OF CONCLUSIONS

Systematics. The hippuritid rudist bivalve species, *T. sanchezi* (Douvillé, 1927), is here considered to comprise two geographical subspecies. The nominotypical subspecies, *T. s. sanchezi* (Douvillé) is known from the Upper Campanian to Lower Maastrichtian of the Caribbean Province of Kauffman (1973), and is considered, by subjective synonymy, to include *T. coxi* Grubić, 1979, as well as the other unquestionable records of *T. sanchezi* in the faunal province. An Arabian subspecies, *T. s. milovanovici* Grubić, 1979, is recognized from new specimens collected by ourselves from the Maastrichtian of eastern central Oman and the United Arab Emirates together with the single specimen from Sharjah Emirate, which constitutes the holotype for the former '*T. milovanovici* Grubić'. The only essential morphological difference between the two subspecies is in the angle (α) between the *arête cardinale* and the ventralmost pillar in adult shells: that in *T. s. sanchezi* ranges from 50 to 126°, while, in *T. s. milovanovici*, this angle is from 12 to 75°.

Palaeobiology. The extension of the inner margin of the RV beyond that of the LV and the recurvature of the shell growth laminations in the LV on to its smooth upper surface, in *Torreites*, indicates that marginal mantle tissue was freely exposed in life (text-fig. 10). It is considered likely that the mantle tissue, thus exposed, contained symbiotic zooxanthellae, as in the living Giant Clam, *Tridacna*. The externalization of the mantle tissue accounts for the atrophy of the (redundant) canal and pore system in the LV, diagnostic of other hippuritids. The upward growth tendency, and preference for shallow, well-lit marine settings, of *Torreites*, as indicated by sedimentological data, are consistent with the zooxanthellate hypothesis.

Palaeobiogeography. Three possible explanations for the apparent disjunct endemism of *Torreites* (along with certain other shallow marine benthic taxa) in the Caribbean and in Oman and the UAE are considered: (1) homeomorphy is rejected due to the negligible probability of several distinctive and constructionally independent diagnostic features arising in two coeval populations; (2) the plate tectonic drifting apart of originally neighbouring areas (as favoured by Grubić 1979) is rejected since all the available geotectonic evidence is against any possibility of the two regions having been conjoined in the Late Cretaceous; and (3) an episode of range extension between the regions, brought about by larval drift along a continuous but temporary chain of staging posts between them, is favoured by us. Of the two possible routes thus implicated, we prefer the trans-Pacific option to that via the Mediterranean Tethys and across the Atlantic. First, palaeobiogeographical data from the Mediterranean suggest that significant barriers to dispersal existed there by Campanian/Maastrichtian times (Kauffman 1973; Philip 1985). Secondly, the Atlantic is also known to have become a major barrier by this time (Kauffman 1973). In contrast, the equatorial Pacific Ocean floor is known to have been studded with shallow seamounts and islands, stocked by shallow marine benthos derived from the Caribbean, at this time (Schlanger *et al*. 1981). These, combined with the shores and/or other shallow marine promontories of eastern Tethys could have served as staging posts for the trans-Pacific dispersal of *Torreites* and the other taxa sharing its strikingly disjunct distribution.

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A REINTERPRETATION OF ICHTHYOSAUR SWIMMING AND BUOYANCY

by MICHAEL ALAN TAYLOR

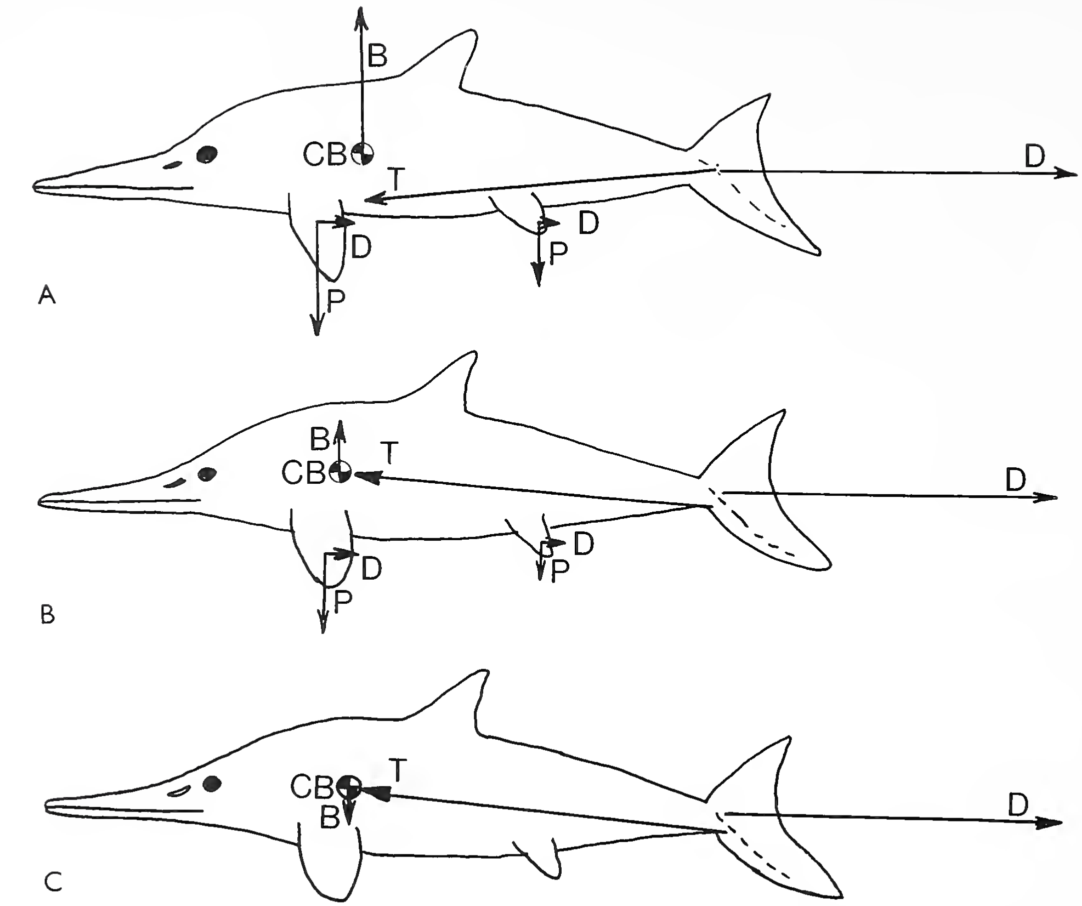
ABSTRACT. A new functional analysis of the reversed heterocercal caudal fin of ichthyosaurs suggests that its function, other than propulsion, was not control of buoyancy, but to produce powerful downwards pitching moments. These moments were used to initiate manœuvres, to dive after breathing at the surface, and, in one form, to feed. This model is of potential value in analysing the palaeobiology and evolution of ichthyosaurs and other marine reptiles with similar caudal fins.

THE caudal fin of ichthyosaurs is usually assumed to have had the primary function of propelling the animal, but this does not explain why many ichthyosaurs had a caudal fin of the reversed heterocercal type, with a fleshy dorsal lobe, and a ventral lobe containing the terminal vertebral column. Previous studies have inverted existing analyses of the unreversed heterocercal caudal fin of sharks (e.g. Alexander 1974) to conclude that the secondary role of the ichthyosaurian caudal fin was to neutralize positive buoyancy (McGowan 1973). I here apply a new analysis of the shark caudal fin by Thomson (1976) and Thomson and Simanek (1977) to conclude that the secondary role of the ichthyosaurian caudal fin was, rather, to initiate manœuvres. Furthermore, this new analysis indicates potential new evidence for the palaeobiology of different ichthyosaurs and for the reasons behind the evolution of the reversed heterocercal caudal fin in ichthyosaurs and other marine reptiles.

FUNCTIONAL ANALYSIS

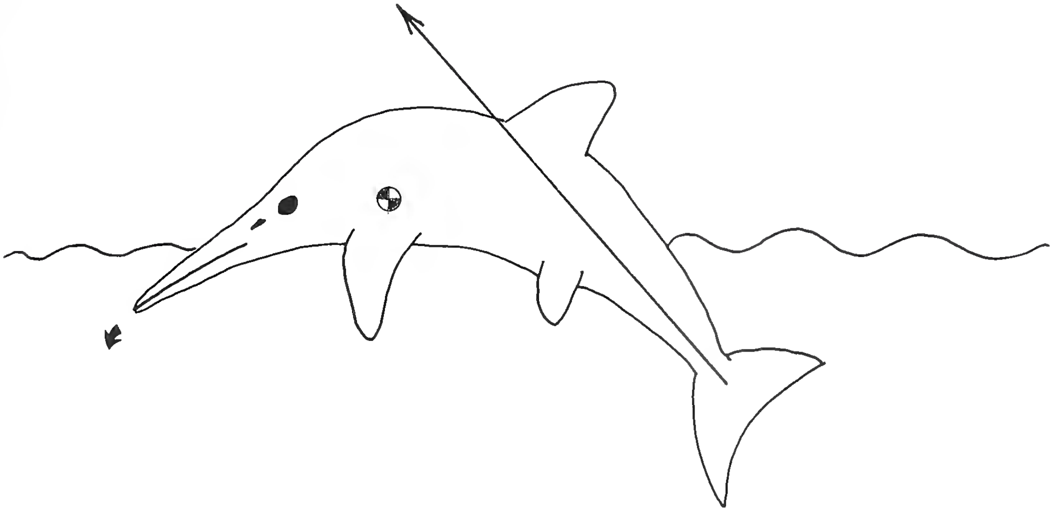
Previous analyses of the swimming and buoyancy of ichthyosaurs (McGowan 1973; Wade 1984) assume that each ichthyosaur was lighter than water and reconstruct the caudal fin as producing a forwards and slightly downwards directed thrust (text-fig. 1A). The downwards component of this thrust has the function of neutralizing part of the upthrust from the negative buoyancy; the remainder of this upthrust is neutralized by lift forces produced by the pectoral fins. The pectoral fins are assumed to be anterior to the centre of balance so that the moment which they produce about the centre of balance is in the opposite sense to, and therefore balances, that produced by the caudal fin. However, by inversion, this analysis is subject to some of the criticisms directed at the original analysis of the shark caudal fin (Alexander 1974; Thomson 1976; Thomson and Simanek 1977). The lift and drag forces vary with speed while the weight and buoyancy remain constant, leading to shifts in the overall balance of forces. In many sharks, and possibly in ichthyosaurs, the pectoral fins are so close to the centre of balance that they have disproportionately short lever arms about the centre of balance and so have to produce large lift and correspondingly large drag forces to counter the moment produced by the caudal fin, with its much longer lever arm (although this could have been alleviated by the use of the pelvic fins). Most importantly, ichthyosaurs were not necessarily lighter than water, and their buoyancy varied with factors such as fatness, repletion or starvation, pregnancy, and above all, the depth of water above the immersed animal (Wade 1984). During a dive, the increase of pressure with depth would compress the air in the lungs and lead to rapid increases in overall density and loss of positive buoyancy and gain of negative buoyancy, as in modern reptiles (Seymour 1982). The ichthyosaur would have had to cope with rapid changes in the magnitude and polarity of its buoyancy.

[Palaeontology, Vol. 30, Part 3, 1987, pp. 531-535.]



TEXT-FIG. 1. Old and new models of forces acting on a swimming ichthyosaur. B, upthrust or downthrust due to buoyancy; CB, centre of balance; D, drag; P, hydrodynamic downthrust from pectoral and perhaps pelvic fins; T, propulsive thrust from caudal fin. A, old model, assuming positive buoyancy. The caudal fin's thrust is directed forwards and downwards and has the role of partially counteracting the positive buoyancy. The lift from the pectoral fins counteracts the remaining buoyancy and its moment about the centre of balance counters that from the caudal fin. B, new model, showing how the caudal fin's thrust is forwardly and upwardly directed so as to pass close to or through the centre of balance in normal swimming. The lift from the pectoral (and perhaps pelvic) fins serves only to neutralize upwards or downwards forces remaining from the addition of the upwards component of the caudal fin's thrust to any positive or negative buoyancy. This is the worst case, when the animal is at the surface and positive buoyancy is greatest, and the pectoral and pelvic fins produce lift and therefore drag. C, new model, when the animal has dived to just below neutral depth and it has slight negative buoyancy. The upwards component of the caudal fin's thrust cancels out the negative buoyancy, and the pectoral and pelvic fins need to produce no lift. This is the most efficient situation. Hunting or cruising ichthyosaurs would probably swim in this efficient manner.

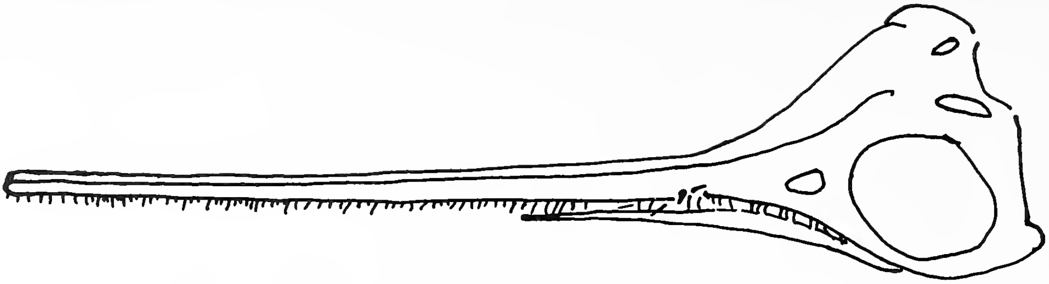
The new analysis of the shark caudal fin by Thomson (1976) and Thomson and Simanek (1977) can be inverted to reinterpret the ichthyosaurian caudal fin (text-fig. 1B). The propulsive force from the caudal fin is directed forwards and slightly upwards. Its angle with the horizontal can be varied by controlling the beat of the dorsal and ventral lobes, as in sharks. In an ichthyosaur swimming straight and level, the line of thrust passes through the centre of balance, and the pectoral fins need produce only enough lift to compensate for residual up- or down-thrust remaining when the tail's downthrust is added to any positive or negative buoyancy. The lines of thrust from the caudal and pectoral fins pass through, or close to, the centre of balance, so that little or no moments are produced about it and correspondingly little lift and drag are wasted on balancing these moments. The ichthyosaur can now control its buoyancy of whatever magnitude or direction.



TEXT-FIG. 2. The use of the caudal fin in manœuvre. The line of action of the caudal fin can be raised above the centre of balance by modifying the beating of the tail or by flexing the body or both. This produces a strong downwards pitching action which can be used (as here) when starting diving during breathing at the surface, or can be turned into any other manœuvre by use of the pectoral and pelvic fins.

The secondary role of the caudal fin is in manœuvring, as in sharks (Thomson 1976; Thomson and Simanek 1977). The ichthyosaur would initiate a turn by raising the line of thrust of the tail above the centre of balance, producing a strong downwards pitching moment which could be converted by the pectoral and pelvic fins into a turn in any required direction (text-fig. 2). Flexion of the body and tail would contribute to this pitching effect (Appleby 1979). In sharks the positively heterocercal caudal fin produces an upwards pitching action which brings the ventrally located but protrusible mouth into action against prey. By contrast, ichthyosaurs had terminally located narrow rostra. The inverted heterocercal caudal fin would, however, have allowed these air-breathing animals to breathe at the surface. Swimming at, or just below, the water surface is energetically costly because of drag caused by surface turbulence and the production of bow waves (Goldspink 1977). The ichthyosaur could swim up to the surface, start pitching downwards at the surface, and already be diving while it breathed through the nostrils placed high on the sides of the snout just in front of the eyes (text-fig. 2). A strong diving action is particularly important since the animal is most buoyant at the surface.

On the face of it the new analysis of ichthyosaur swimming incorporates an apparent inefficiency (text-fig. 1B). Any positive buoyancy adds to the upwards component of the caudal fin thrust to produce an upthrust which must be neutralized by the production of lift, and therefore drag, by the pectoral and pelvic fins. However, this would be worst at the surface or at shallow depths, when swimming is in any case energetically costly. When the animal dived again, and especially if it exhaled, it would reach neutral depth and then, below that, a point where it became slightly negatively buoyant. At this point the buoyancy and the upthrust from the caudal fin would balance and there



TEXT-FIG. 3. The head of *Eurhinosaurus* showing the greatly undershot lower jaw (after McGowan 1979, pl. 5, fig. 2). Original *c.* 110 cm long.

would be no need for the pectoral and pelvic fins to produce any lift, and associated drag (text-fig. 1C). The relative magnitude of the upwards component of the caudal fin thrust would depend upon the trade-off between efficient swimming and manœuvrability, as has been suggested for sharks (Thomson 1976; Thomson and Simanek 1977). A relatively small upwards component, and thus a nearly horizontal line of thrust, would promote minimal drag and therefore high speed, or efficient cruising; a more sharply inclined line of thrust would produce greater manœuvrability at the expense of efficiency.

PALAEOBIOLOGICAL INFERENCES

The aberrant ichthyosaur *Eurhinosaurus* may provide evidence for this hypothesis. It had a long, tooth-armed upper jaw overhanging a much shorter lower jaw (text-fig. 3), and is reconstructed as having slashed downwards through shoals of small fish and cephalopods (McGowan 1979). The ability to pitch downwards strongly is implied by this habit.

Further testing of the hypothesis may come from analysis of variation within ichthyosaurs. In sharks the variation of the caudal fin, especially in the degree of asymmetry about the horizontal axis, the angle of the terminal vertebral column with the horizontal, and the aspect ratio, has been correlated with the ecology of different forms, as this variation controls the angle with the horizontal made by the caudal fin thrust and therefore the balance between manœuvrability and the energetic efficiency in terms of drag (Thomson 1976; Thomson and Simanek 1977). The existence of exceptional cases of soft part preservation of ichthyosaurs (McGowan 1973, 1979; Martin *et al.*, 1986) provides evidence for the outline of the caudal fin (so long as it is authentic, Riess 1985). This is an opportunity to correlate palaeobiological inferences from caudal fin form with independent evidence from overall body form, paired fin structure, and feeding adaptations, so as to reconstruct the palaeobiology of different ichthyosaurs and different age-classes within species, and test the present hypothesis of caudal fin function.

The hypothesis of caudal fin function will also be relevant to studies of the origin and evolution of the ichthyosaurian reversed heterocercal caudal fin during evolution from terrestrial ancestors, and of the independently evolved reversed heterocercal caudal fin of other marine reptiles such as the thalattosuchian crocodilians (Buffetaut 1979).

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A NEW SILURIAN XIPHOSURAN FROM PODOLIA, UKRAINE, USSR

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ABSTRACT. A single incomplete specimen of a xiphosuran, *Pasternakevia podolica* gen. et sp. nov., from the Ludlow Series of Podolia, Ukraine, USSR, is described. It has a smooth, spatulate carapace and rounded genal cornua. The opisthosoma bears nine free tergites (second to tenth); the first tergite is reduced and hidden beneath the carapace. The tergites have a broad axial region and small pleurae; the second tergite is hypertrophic. Telson and appendages are not preserved. *P. podolica* resembles *Pseudoniscus* Nieszkowski, 1859 and *Cyamocephalus* Currie, 1927; it is thus placed in the infraorder Pseudoniscina Eldredge, 1974, but certain characters are shared with the synziphosurines. It comes from the lagoonal deposits of the upper part of the Ustye Suite (Bagovytsa Horizon) where it occurred together with *Baltoeurypterus tetragonophthalmus* (Fischer, 1839).

АНОТАЦІЯ. Описується єдиний неповний екземпляр мечохвоста *Pasternakevia podolica* gen. et sp. nov. із лудловського ярусу Поділля (УРСР). Представлений він гладким лопатовидним карапаксом із закругленими щічними шипами і опістосомою. Опістосома складається з дев’яти видимих тергітів; перший тергіт редукований, схований під карапаксом. Тергіти мають широкі осьові частини та малі плеври; другий тергіт гіпертрофований. Тельсон і придатки не збереглися. Мечохвіст подібний до *Pseudoniscus* Nieszkowski, 1859 та *Cyamocephalus* Currie, 1927, у зв’язку з чим віднесений до інфразагону Pseudoniscina Eldredge, 1974, хоч має також і деякі ознаки синцифозур. Походить він із лагунних відкладів верхньої частини устівської світи баговицького горизонту, де знайдений разом із *Baltoeurypterus tetragonophthalmus* (Fischer, 1839).

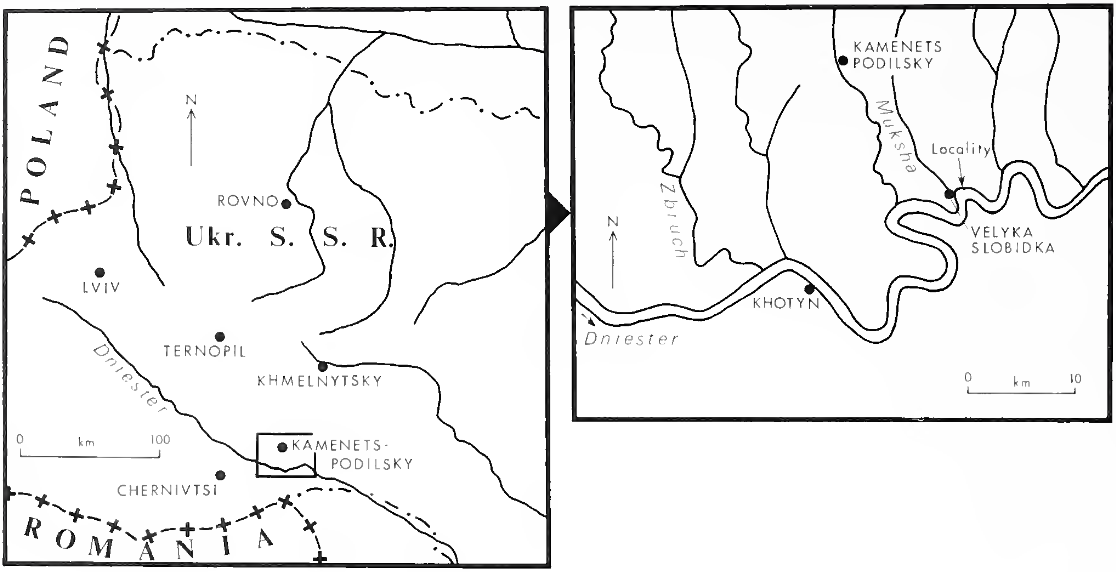
THE late Silurian saw the climax of the first phase of evolution of the Xiphosura. In the *Treatise* (Størmer 1955) these middle Palaeozoic xiphosurans were united in the suborder Synziphosurina Packard, 1886, but some are now considered to belong to the sister group, the suborder Limulina Richter, 1929 (Eldredge 1974; Bergström 1975), and the infraorder Pseudoniscina Eldredge, 1974 was erected for them and some primitive bellinuroids. Xiphosuran phylogeny is founded to a large extent on scattered records of genera based on few, or commonly single, specimens; new finds often seem to confound rather than confirm established conceptions. The new genus described below follows this pattern since, while it undoubtedly lies within the Pseudoniscina, it also shares at least one character with some synziphosurines. For this and other reasons outlined below—and particularly if some bellinuroids are included in the Pseudoniscina (Eldredge 1974; cf. Fisher 1982, fig 1; 1984, fig. 2)—the monophyletic status of the infraorder must be considered suspect.

Eldredge (1974) convincingly argued that the most anterior opisthosomal tergite in synziphosurines and pseudoniscines belongs to the second opisthosomal somite. The tergite corresponding to the first opisthosomal somite is reduced to the form of an articulating half-ring and can only be seen in dorsally flexed specimens. Our identification of the opisthosomal tergites follows that of Eldredge (1974), so that the nine visible tergites are numbered second to tenth (II–X).

Stratigraphy and geological setting. The described specimen comes from dolomite marl (domerite) of the upper part (*c*. 22–23 m above the base) of the Ustye Suite of the Bagovytsa Horizon, which crops out on the left bank of the Dniester River *c*.1·5 km downstream of the village of Velyka Slobidka (Podolia, Ukraine, USSR; text-fig. 1). Subsequent extensive searches failed to reveal any more specimens of the genus.

The section consists of light-grey, vesicular, granular and platy, pelitomorphic, and rarely stromatolitic dolomites alternating with fine, platy domerites (text-fig. 2). Bed thicknesses are 0·15–

[Palaeontology, Vol. 30, Part 3, 1987, pp. 537–542.]



TEXT-FIG. 1. Location map.

1·50 m, and suite thickness as a whole is 30 m. These rocks are lagoonal in origin and contain only rare remains of chelicerates, of which the best known is *Baltoeurypterus tetragonophthalmus* (Fischer, 1839); shrinkage cracks commonly occur on the surfaces of domerite beds (Nikiforova *et al.* 1972).

In the lower part of the suite, rare, thick beds of limestones occur with abundant faunal remains which allow their correlation with Eltonian to lowermost Leintwardinian (Ludlow) strata of Britain (Tsegelnjuk *et al.* 1983; Drygant 1984); the layer with *Pasternakevia* correlates with the lowermost Leintwardinian.

Preservation. The fossil consists of a single piece: the cast and internal mould of the whole carapace and slightly damaged opisthosoma of nine tergites. Since the animal is not flexed dorsally, the half-ring belonging to the first opisthosomal somite cannot be seen and is presumed to be hidden beneath the carapace. The cuticle is rather thin, consisting of dark-grey matter which is clearly distinguished on the pale rock background. Though originally chitinous, the cuticle has almost certainly been replaced by material whose nature has not been determined.

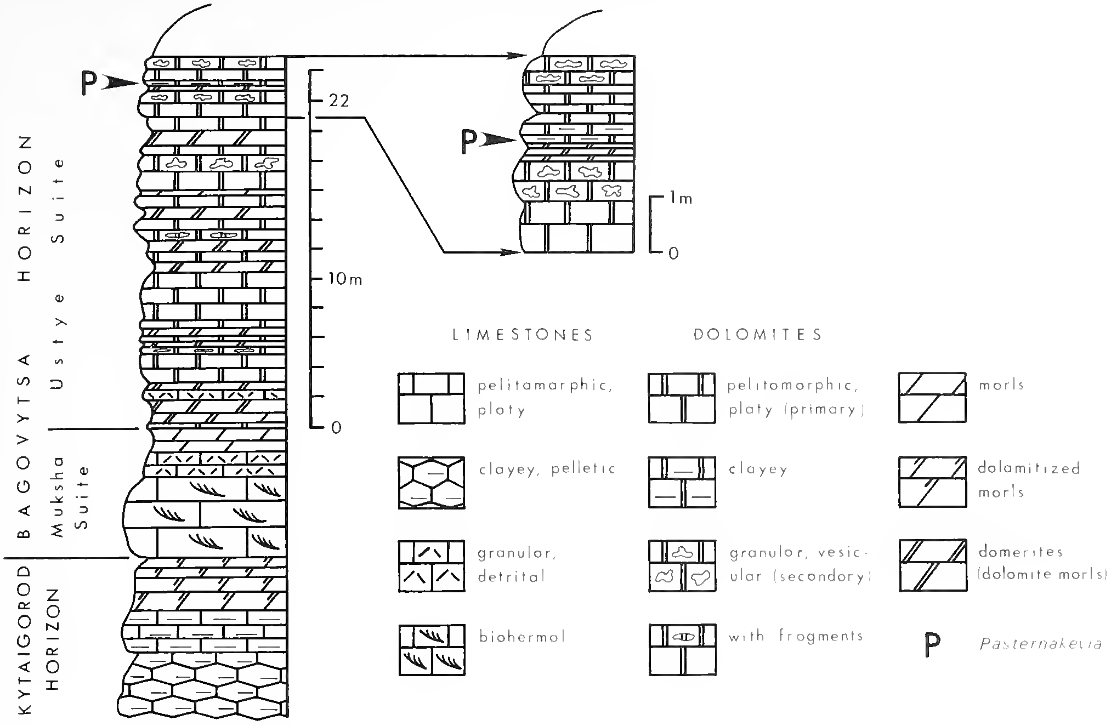
SYSTEMATIC PALAEONTOLOGY

Phylum CHELICERATA Heymons, 1901
Class XIPHOSURA Latreille, 1802
Order XIPHOSURIDA Latreille, 1802
Suborder LIMULINA Richter and Richter, 1929
Infraorder PSEUDONISCINA Eldredge, 1974 (emended)
Genus PASTERNAKEVIA gen. nov.

Type and only known species. Pasternakevia podolica sp. nov.

Derivation of name. In honour of Professor S. I. Pasternak, a prominent researcher of the Cretaceous fauna of the Ukraine.

Diagnosis. Carapace spatulate, nearly as long as opisthosoma (excluding telson); cardiac and ophthalmic morphology obscure; genal cornua broad and rounded, lacking anterior median projection.



TEXT-FIG. 2. Columnar section of the outcrop located on text-fig. 1 showing occurrence of *Pasternakevia* gen. nov.

Nine opisthosomal tergites with broad axial region and small pleurae; tergite of first opisthosomal somite greatly reduced, that of second hypertrophied. No fused tergites.

Pasternakevia podolica sp. nov.

Text-fig. 3*a*, *b*, *d*

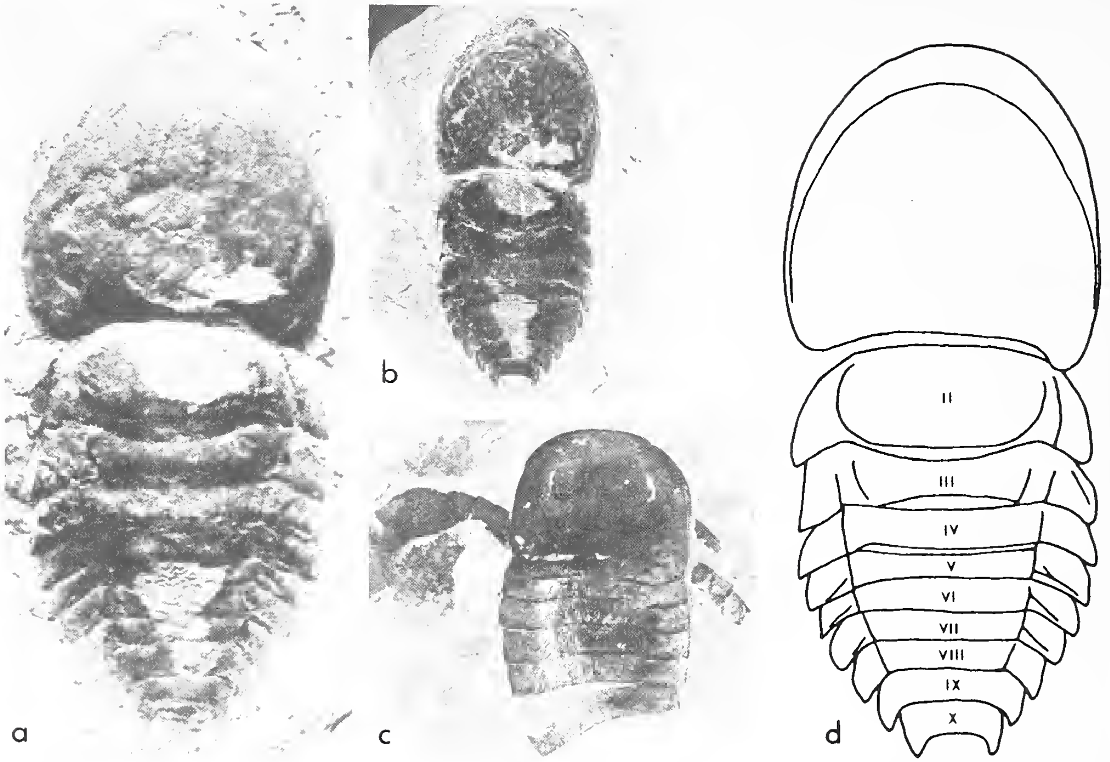
Holotype. Lviv State Natural Museum of the Ukrainian Academy of Sciences (Monographical Funds), No. 35611; single dorsal piece (only known specimen) consisting of the carapace and opisthosomal tergites; from the upper part (*c*. 22–23 m above the base) of the Ustye Suite (Bagovytsa Horizon, middle Ludlow) on the left bank of the Dniester River *c*. 1·5 km downstream of the village of Velyka Slobidka (Podolia, Ukraine, USSR).

Derivation of name. After Podolia, the region in which the locality lies.

Diagnosis. As for the genus.

Description. *Pasternakevia* is nearly half as wide as it is long (excluding the telson which is not preserved), with the carapace occupying 0·44 of its length. The three largest opisthosomal tergites are nearly as wide as the carapace and thus the body appears parallel-sided for much of its length.

The carapace is spatulate, nearly as long sagitally (sag.) as it is wide; the sides are parallel in the posterior half, and the anterior rim of the carapace forms a semicircle. The posterior border of the carapace is gently procurved, meeting the lateral borders in blunt genal cornua. A long, crescentic feature on the carapace, widest anteriorly and tapering gradually to merge with the lateral borders near the genal angles, may represent the impression of the prosomal doublure or ventral marginal plate(s) adpressed against the carapace. The carapace is convex dorsally, the highest part being a broad circular area forming the posterior two-thirds; the surface slopes steeply away from this area to the crescentic feature and the genal areas. The posterior border is



TEXT-FIG. 3. *a*, *b*, *d*, *Pasternakevia podolica* gen. et sp. nov., No. 35611, holotype and only known specimen; upper part of Ustye Suite, Bagovytsa Horizon (middle Ludlow), near Velyka Slobidka, Ukraine, USSR; *a*, dorsal view in low-angle light, × 3·0; *b*, dorsal view in high-angle light, × 1·5; *d*, outline drawing of specimen showing main features and tergite numbers, × 3·0. *c*, *Baltoeurypterus tetragonophthalmus* (Fischer, 1839), No. 35612, from same horizon and locality as *Pasternakevia*, × 1.

gently arched. Typical xiphosuran carapace features cannot be discerned, except for a faint parabolic ridge situated centrally at the anterior side of the circular area; this could represent the anterior part of the cardiac lobe. Though obscured by a general wrinkling of the carapace surface, any original features must have been faintly expressed in life.

Nine dorsal tergites are readily apparent on the opisthosoma (belonging to the second to tenth opisthosomal somites); the first tergite is presumed to be concealed beneath the carapace (see above). Since the telson is not preserved attached, we cannot be certain that the most posterior tergite is the last, but its small size suggests that it is. The second tergite is the largest and is obviously hypertrophied. The third is only half the length (sag.) of the second, but is as wide. The fourth is three-quarters the length (sag.) of the third, and is also as wide as the second and third. Thereafter the tergites are roughly the same length but become increasingly narrower (exsag.). Each tergite consists of a wide, raised axial part, occupying about two-thirds of the total width, and narrower (exsag.) pleurae. The axial part of the second tergite is greatly swollen. On the third to tenth tergites the axial part has straight anterior and posterior borders. The anterior and posterior borders of the axial region of the third and more posterior tergites are depressed to accommodate adjacent tergites during flexure of the opisthosoma; that anteriorly on the third tergite is recurved on its posterior side to accommodate the hypertrophied second tergite. The pleurae are separated from the axis by dark coloured depressions, possibly indicating the presence of muscle attachments beneath. Together, these depressions line up as a pair of axial furrows which run nearly straight and converge from the genal angles of the carapace to the presumed anterolateral corners of the telson. As the outline of the opisthosoma is broadly curved, the pleurae are widest on the middle tergites. The pleurae curve gently backwards as spatulate lobes, with the posterior more strongly curved than the anterior. At least the third to the eighth pleurae bear furrows running from the anteromedial to posterolateral corners, becoming shallower posterolaterally. The opisthosoma lacks ornamentation.

Dimensions (*in mm*). Lengths (sag.): total (excluding telson), 30·7; carapace, 13·5; opisthosoma (excluding telson), 17·2; tergites II, 4·8; III, 2·4; IV, 1·8; V, 1·6; VI, 1·1; VII, 1·4; VIII, 1·0; IX, 1·6; X, 1·5. Widths: carapace, 14·0; tergites II, 13·2; III, 13·2; IV, 13·2; V, 12·5; VI, 11·5; VII, 10·6; VIII, 8·1; IX, 7·0; X, 4·7.

Discussion. *Pasternakevia* resembles *Pseudoniscus*, known from Saaremaa, Estonia (*P. clarkei* Ruedemann, 1916), Lesmahagow, Scotland, and Ludlow, England (*Pseudoniscus* spp., Eldredge 1974), all of which are Ludlow in age. Similarities include: overall dimensions, spatulate carapace, number of opisthosomal tergites, no fused tergites, and lack of opisthosomal tagmosis (see Eldredge 1974, table 3). *Pasternakevia* differs from *Pseudoniscus* in lacking an anterior median carapace projection, its broad opisthosomal axial region, and hypertrophied second tergite. Another pseudoniscine, *Cyamocephalus* Currie, 1927, resembles *Pasternakevia*. *Cyamocephalus* is known from rocks of Ludlow age at Lesmahagow, Scotland (*C. loganensis* Currie, 1927), and Ludlow, England (*C.* cf. *loganensis* Eldredge and Plotnick, 1974).

Both *Pasternakevia* and *Cyamocephalus* lack the median anterior carapace projection found in *Pseudoniscus*. *Cyamocephalus* has a long opisthosoma with fused sixth and seventh opisthosomal tergites and the seventh hypertrophied, features absent from *Pseudoniscus* and *Pasternakevia*. These dissimilarities warrant the separation of all three animals at the generic level. To include *Pasternakevia* within the infraorder Pseudoniscina Eldredge, 1974, this taxon requires emendation to remove the character 'second segment not hypertrophic'. At present, it seems appropriate to include the genus within Pseudoniscina with this emendation.

The presence of a hypertrophic second opisthosomal tergite is a character which *Pasternakevia* shares with the synziphosurines *Bunodes* Eichwald, 1854 and *Limuloides* Salter *in* Woodward, 1865 (Eldredge 1974). The question arises: is this character homoplasous, i.e. derived independently in two separate clades? Eldredge (1974), Bergström (1975), and Stürmer and Bergström (1981) agree that the synziphosurines (*Bunodes*, *Weinbergina*, *Legrandella*, and *Limuloides*) are separate from other Xiphosura at high taxonomic rank. However, the distinguishing characters (carapace morphology and opisthosomal tagmosis) are not always strictly definable. In the Pseudoniscidae, for example, the carapace morphology is typically obscure, and in a reconstruction of *Weinbergina* by Stürmer and Bergström (1981, e.g. fig. 5) the separation of pre- and postabdomen is indistinct. The Ordovician genus *Lemoneites* Flower, 1968 also shares characters in common with both synziphosurines and limulines (Eldredge 1974). Consequently, the current phylogeny of these lower and middle Palaeozoic Xiphosura must be considered speculative; as more new taxa are described, character matrix analyses (e.g. Eldredge 1974) will help to answer the homoplasy question and produce new phylogenetic schemes.

As mentioned above, in the dolomite rocks of Ustye Suite of Podolia a normal marine fauna is absent. *Pasternakevia* is accompanied only by relatively few fossils of the eurypterid *B. tetragonophthalmus* (Fischer, 1839) (mainly as isolated parts but occasionally as almost whole animals; text-fig. 3*c*), fragments of *Pterygotus* sp., and some unidentifiable arthropods. No *Baltoeurypterus* specimen exceeds 10 cm in length; the fragments of *Pterygotus* indicate that the complete animals were much bigger. These chelicerates lived in a shallow lagoon, separated from an open basin to the west by a chain of bioherms (Drygant 1984). Sedimentary conditions in the lagoon were not stable, hence the deposition of thin, rhythmical, magnesial sediments which were periodically enriched with clayey material. Common desiccation cracks indicate frequent subaerial exposure in some places. The bed with *Pasternakevia* is a thin-bedded, clayey dolomite formed during a regressive phase, but before its maximum.

The mode of life of *Pasternakevia* cannot be determined with certainty. Sphaeroidal enrolment was almost certainly possible, since it is known in *Pseudoniscus* (Bergström 1975) which has a similar gross morphology. Flexure of the opisthosoma into a dorsally concave shape was also possible, as evidenced by the topography of the axial region of the tergites. Enrollment was undoubtedly a defence strategy, while flexure in the opposite direction was used in righting the overturned animal and may also have been a help in burrowing. The spatulate carapace, effaced features, and broad axial region of the opisthosoma give *Pasternakevia* a streamlined shape similar to that of burrowing illaenid trilobites; it might also have been advantageous to a swimming form, but at small size and slow swimming speeds (low Reynolds numbers) effacement confers little advantage, so burrowing seems a more likely explanation. The hypertrophic second tergite suggests enlarged ventral organs: genitalia or, more likely, gills. It could be that enhanced gas- or ion-exchange abilities enabled *Pasternakevia* to inhabit a hypersaline environment. *Bunodes lunula* Eichwald, 1854 also has a hypertrophic second tergite and is found in similar dolomitic limestones in Estonia, but it is there accompanied by *Pseudoniscus aculeatus* Nieszkowski, 1859, which has a normal second tergite, so this hypothesis remains speculative.

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A TAPHONOMIC AND DIAGENETIC CASE STUDY OF A PARTIALLY ARTICULATED ICHTHYOSAUR

by DAVID M. MARTILL

ABSTRACT. A single carcase of the large Middle Jurassic ichthyosaurian *Ophthalmosaurus* sp. was rapidly decomposed in well-oxygenated bottom water of the Lower Oxford Clay Midlands basin. Parts of the soft tissues lying within anoxic sediments were subjected to slower rates of decay and portions of the integument are now preserved as replacements by bacterial and possibly fungal mats. Elements of the skeleton were encrusted with epibionts on their upper surfaces. Burial diagenesis has significantly affected some skeleton elements, with the infilling of voids with calcite, pyrite, and sphalerite. Rarely, bone phosphate has been replaced by pyrite. Compaction of bones and septarian cracking of surrounding concretionary mudstone has caused crushing and brecciation of trabecular bones. More massive bones with cross-sections capable of transmitting overburden pressures have resisted compaction.

THE partial skeletal remains of an ichthyosaur, *Ophthalmosaurus* sp. were discovered (by Mr Lez Fitchett, an employee of French Kier Construction) in the autumn of 1982 at Milton Keynes, Buckinghamshire, during the construction of Caldecotte Lake. The specimen has been examined in detail whilst still *in situ* and has formed the basis of a case-study on the preservation of marine vertebrates in bituminous shales. The skeleton is now a mounted specimen in Milton Keynes Public Library, BCM 1983/1008.

A systematic excavation of the specimen was undertaken between 12 October 1982 and 15 October 1982. Samples of the surrounding sediment were collected with the specimen for micro-palaeontological and sedimentological analysis.

The specimen is that of a mature adult, approximately 5 m long (text-fig. 1). Some skeletal elements do not appear on the diagram as they were disturbed by the excavating machinery, and cannot be accurately positioned. Misplaced elements include part of the coracoid, the right? ulna, part of the rostrum, and numerous digits. Part of the right side of the rib cage was also slightly disturbed.

Horizon. The stratigraphic distribution and preservation of fossil vertebrates in the Lower Oxford Clay has been discussed by Martill (1985, 1986). The skeleton was found in the Lower Oxford Clay (Middle Callovian, Middle Jurassic), lying partly within greenish bituminous shale and enclosed by a large septarian concretion. Two thoracic vertebrae detatched from the main part of the skeleton were enclosed in a pyrite concretion. There is no published lithological section for the site, but a section for the nearby brick pits at Bletchley is given by Callomon (1968) and probably differs only in minor details.

Beds 17 and 9 of Callomon's section can be identified in the site at Milton Keynes, and from a comparison of the concretion with those occurring at Bletchley it appears that this specimen is from bed 9. Thus the skeleton is from the obductum Subzone of the coronatum Zone.

Locality. Caldecotte Lake is situated on the South side of Milton Keynes at National Grid Reference SP 892 352. Excavation of the site is now complete and all exposures of the Oxford Clay have disappeared due to flooding and landscaping of the site.

Taxonomy. The skeleton is that of an associated, partially articulated *Ophthalmosaurus* sp. Specific identification cannot be determined as the diagnostic coracoids (Appleby 1956) are not sufficiently well preserved to show the anterior and posterior notches. Two species of *Ophthalmosaurus* are

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TEXT-FIG. 1. Outline skeletal plan of *Ophthalmosaurus* sp. BCM 1983/1008 as found *in situ* at Caldecotte Lake, Milton Keynes, Buckinghamshire. Certain elements of the skull and shoulder girdle are omitted from the plan as they were disturbed by earth-moving machinery.

recorded from the Lower Oxford Clay; *O. icenicus* Seeley 1874, and *O. monocharactus* Appleby 1956. The differences between the two are small, and considering the degree of variability seen within *Ophthalmosaurus*, the differences may be sexual (Andrews 1910).

MATERIAL AND METHODS

The specimen consists of a partially articulated skeleton wanting only a few elements. Due to intense brecciation it is not clear which elements are present in the concretion. Those parts of the skeleton known to be preserved include all of the posterior portion of the vertebral column from about the ?20th vertebrae to the tip of the tail. A few of the neural arches, especially the more posterior ones are present. Of the skull there is a right quadrate, left and right lachrymals, right coronoid, right dentary, angular and surangular, and portions of the left and right premaxillae. There are also a few plates from the sclerotic ring. The rib cage is almost complete, although the right side is very disarticulated. The fore limbs are represented by left and right radii, left and right ulna, and numerous carpals and metacarpals. A highly brecciated humerous was found within the concretion. The left ischio-pubis, left femur, and fused left tibia and fibula were found with numerous digits.

The skeleton was found lying in clay, grey/green, rather tenacious and slightly bituminous, and was partly enclosed by a large septarian concretion. Two detached vertebrae were found enclosed in a flat pyrite concretion. The following excavation procedure was carried out so that the skeleton could be removed to the laboratories of the Geology Department of the University of Leicester for cleaning, preparing, and subsequent mounting.

1. The skeleton was completely exposed *in situ* by careful digging with knives, forks, spoons, and small trowels. Where the overburden exceeded more than a few centimetres a spade was employed.

2. The exposed skeleton was overlain with clear acetate sheeting and the position of all the bones was mapped out using an indelible ink marker pen. Each bone received a unique number on the plan and was placed in a sealable polythene bag bearing the same number. Where the bone was broken into two or more pieces, all of the pieces were placed in the same bag.

3. Fractured elongate bones of the lower jaws were collected in their entirety by excavating around them until they were left lying on an elevated plinth of clay. The clay plinth was undercut using a 'cheese wire' technique and a length of square section guttering slid underneath. This was then lifted and individually wrapped to protect the fragile bones during transit.

4. The specimen was removed to the laboratory for cleaning. During this stage a black and buff coloured surface coating was discovered on the surfaces of some of the bones. Cleaning of the bones was achieved by soaking in warm water using only mild detergents to assist break down of the clay.

5. Removal of hard rock (mainly fibrous calcite) adhering to bones found in the clay was achieved by use of a pneumatic chisel (*Vibrotool*) and steel needles.

6. Bones in the concretion were considered unsuitable for use in the reconstruction of the skeleton, but were used for diagenetic studies. The large calcareous concretion was cut up with a rock saw. Thin sections were made from the remaining fragments. Bone used for scanning electron microscopy was extracted from the matrix using 10% acetic acid.

7. Prepared bone was examined by light and scanning electron microscopy. Bone coatings were examined by both scanning and transmission electron microscopy. Mineral phases were identified using normal petrographic thin sections.

TAPHONOMY

The remains constitute an associated skeleton of a single individual. Much of the skeleton is disarticulated, but a few elements, notably the left side of the thoracic ribs are articulated, and show true bone to bone relationships, as in the living animal. Some skull elements enclosed within the concretion, and the anterior part of the rostrum disturbed by the excavator, are also articulated. The remainder of the skeleton is disarticulated, but most of the individual bones have not been moved from their original positions by more than a few centimetres. Thus the overall shape of an ichthyosaur skeleton is retained.

The cause of death of the animal cannot be satisfactorily determined. Advanced ossification, indicated by irregular expansions to the ends of the ribs, and by fusing of the ?left tibia and fibula suggest it was an old animal. There is little disruption of the skeleton to suggest the animal was the prey of a large carnivore such as a pliosaur, so it is likely that it died of old age or disease.

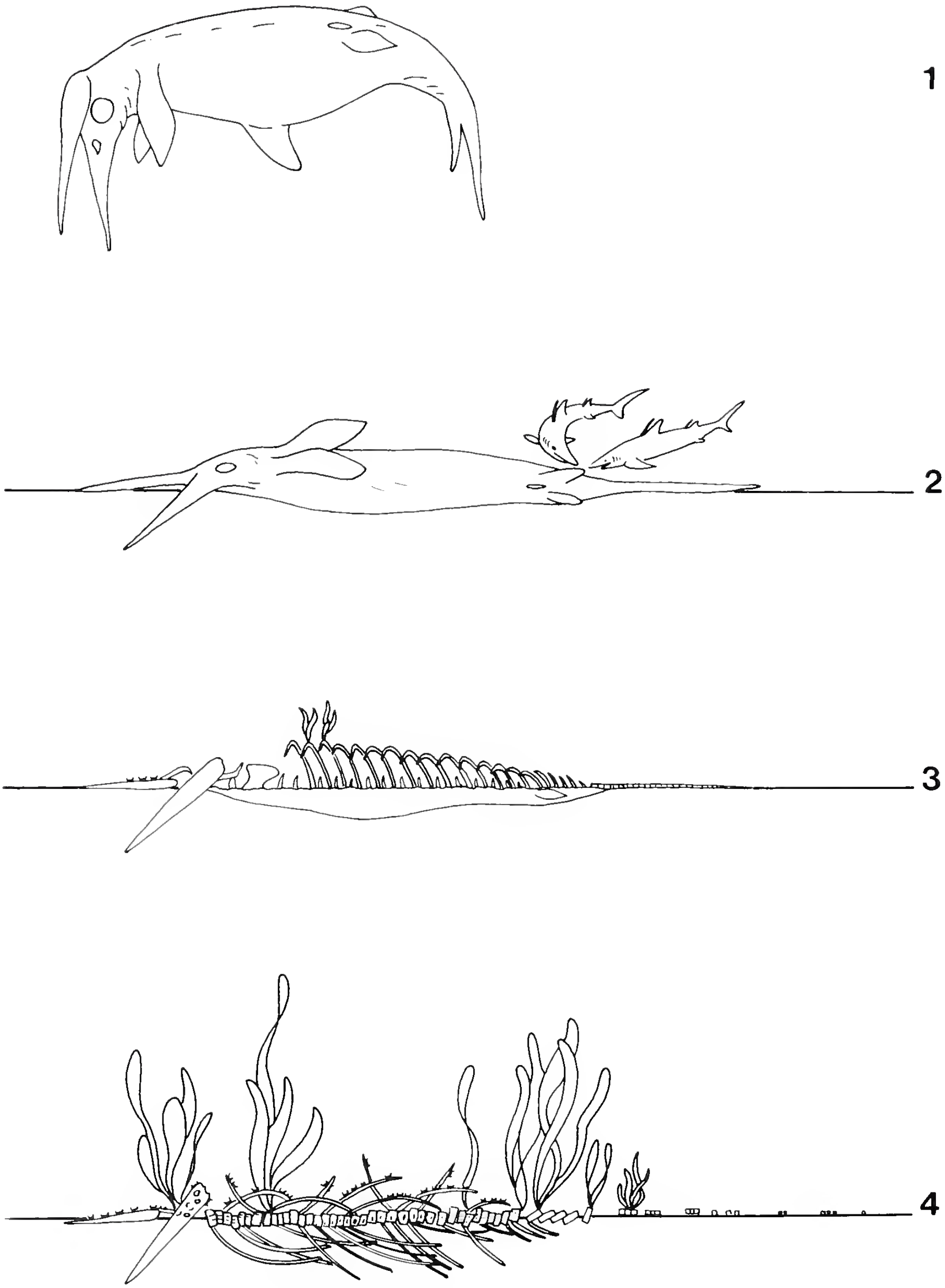
Apart from the right hind limb, all appendages are present, including the extreme tip of the tail. This indicates that very little scavenging took place during post-mortem drifting, with only the right rear paddle possibly missing due to scavenger activity. The carcass arrived on the sea-floor intact, with most of the soft tissue present, serving to hold the skeleton together.

The position of the skeleton, lying on its left side suggests that it landed on the sea-floor ventrally, and as the flesh decomposed the skeleton collapsed forwards and on to its left side.

The carcass descended to the sea-floor with a velocity sufficient to allow the tip of the rostrum to penetrate the sediment. Penetration of the rostrum tip into the sediment indicates that the skull arrived on the sea-floor first, and may have been suspended below the main body of the carcass. Presumably the sediment was soft, possibly even soupy, and the sinking velocity of the carcass need not have been great.

Decomposition of the soft tissue in the water column took place rapidly and left the right side of the rib cage exposed to sea water. Soft tissues in contact with the sediment decomposed more slowly, and in the case of some of the tissues which had sank into the sediment, decomposition was not completed. Text-fig. 2 summarizes the taphonomic history of the specimen.

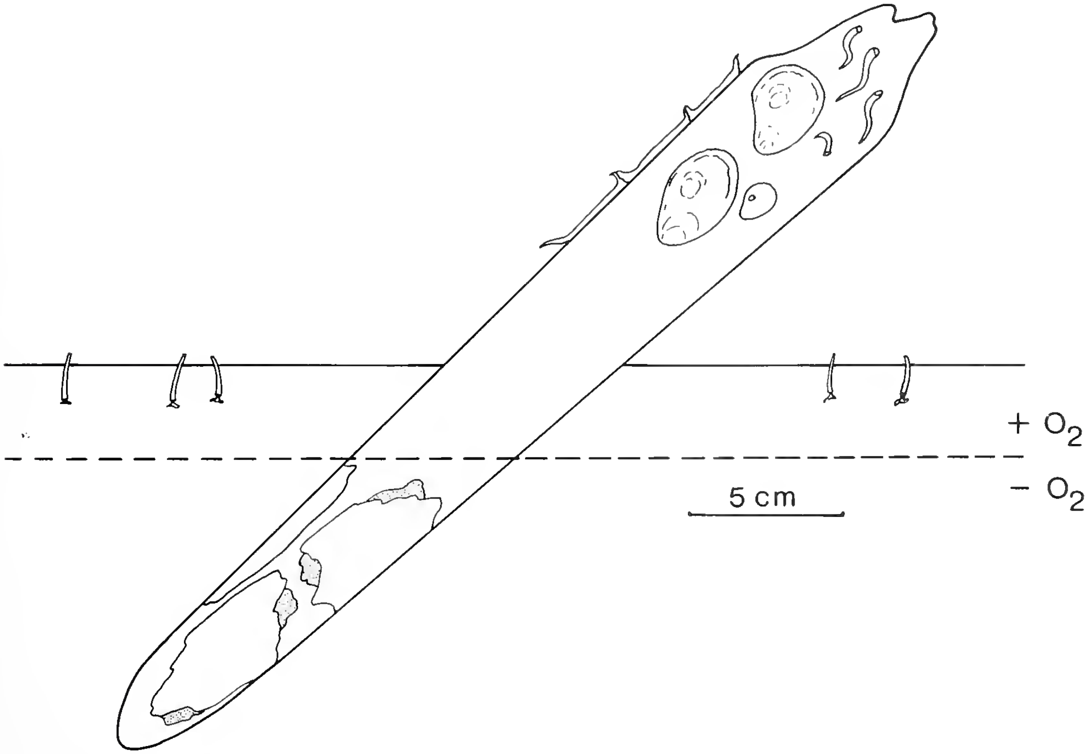
The bottom waters of the Lower Oxford Clay Midland basin were in general well oxygenated and capable of supporting a diverse benthos (Duff 1975). The clays around the specimen, however,



TEXT-FIG. 2. Summary of taphonomic history of BCM 1983/1008 based on observations made from position of skeleton and state of preservation of skeletal elements. 1, carcass drifts in water column with skull suspended below main body of carcass. 2, carcass descends to sea-floor and part of rostrum penetrates sediment. Light scavenging may take place. 3, rapid decomposition of soft tissues in well oxygenated bottom water. 4, collapse of skeleton and encrustation by epibionts.

yielded only a restricted benthos of nuculacean bivalves, scaphopods, and foraminifera; although the latter cannot be definitely considered benthic. Oysters and serpulid worms were found encrusting the skeleton but were not found in the surrounding sediment (see below). This suggests that the skeleton acted as a benthic island. Sea water in contact with the sediment may have been slightly depleted in oxygen, and the oysters and serpulids encrusting the skeleton survived due to their elevated position in more oxygenated water. If this is the case then current activity must have been at a minimum to prevent mixing of the oxygen-depleted water with the oxygen-rich water. However, this is not the only mechanism for producing the restricted infauna; the soft substrate may also have been a contributing factor. The restriction of the benthos limited scavenging of the carcass while on the sea-floor, but the movement of a few bones, notably the two vertebrae in the pyrite concretion, is not due to current activity, and can almost certainly be attributed to scavenging. Current activity is ruled out on the grounds that the two vertebrae are large and a current strong enough to move them would have also moved the smaller elements of the skeleton. If seaweed grew on the surface of the bones, it is possible that added bouyancy might assist movement during storm activity. It is, however, difficult to establish if the skeleton lay within the photic zone.

Epibionts. Many of the disarticulated elements of the skelton are pale buff in colour. These bones are frequently encrusted with epibionts, including oysters and serpulid worms. The oysters are only found encrusting the buff coloured bones, and are restricted to the upper surfaces (text-fig. 3). No micro-epibionts have been found on the underside of the skeleton, or on the dark brown bones of the articulated portions of the skeleton. The oysters are preserved in dark grey calcite. They frequently reach a length of 4 cm, and on flat bones they remain attached continuously during



TEXT-FIG. 3. Portion of rostrum having penetrated soft sediment. Soft tissues are preserved below oxygen minimum zone. Epibionts encrust bone in well oxygenated water.

ontogeny. Oysters encrusting bones with strongly curving surfaces, i.e. ribs, are only attached during early ontogeny, later stages of shell growth migrate away from the bone surface and the oyster shell becomes curved. On very smooth bone surfaces the oyster may not secrete shell material, but lie in direct contact with the bone.

Serpulid worms are less common then oysters, and are usually small, being generally less than 1 cm long. They are preserved as white calcareous conical tubes, approximately 2–3 mm diameter anteriorly. No geotropism or phototropism has been established, but the distribution pattern on the skeleton follows that of the oysters.

Soft tissues. The undersides of the articulated parts of the skeleton are dark brown, and devoid of epibionts. A black coating adheres to the underside of the articulated vertebrae that lie within the shale, and also to the underside of some of the ribs from the left side of the rib cage. (In life this would be the outer surface of the left side of the rib cage.) The black coating, overlain by a slightly reflective white/buff coating was also found on a portion of the premaxilla.

These coatings are restricted to the dark brown coloured bones. No oyster encrustations are found on the dark brown bones which suggests that these bones were in contact with, and partly buried in the sediment. The black and white coatings may be by-products of a decomposing integument (Pl. 63, figs. 1 and 2). The abundance of pyrite within the sediment and encrusting some of the bones shows that reducing conditions were present within the sediment. If the oxic/anoxic boundary was close to the sediment water interface, the penetration of the ichthyosaur carcass into the sediment may have introduced some of the soft tissues to reducing conditions, thus reducing the rate of decay.

Scanning electron microscopy of the black coating from the underside of the vertebral column shows it to be composed of an amorphous mass of carbonaceous material, underneath which are numerous ovoids approximately 1 μm long, and about 0·5 μm diameter (Pl. 63, figs. 3 and 4). These ovids are interpreted as lithified bacteria, similar to those reported from soft-part outlines of Eocene frogs and bats (Wuttke 1983). The bacteria represent a replacement of some of the original soft tissues. In the case of the ichthyosaur *Stenopterygius* spp. from the Posidonia Shale (Toarcian, Lower Jurassic) of Holzmaden, West Germany, these black coatings may extend into the sediment to produce an outline of the entire animal (McGowan 1979). In the Lower Oxford Clay the micro-environment in which this process can occur was restricted to the undersides of bones lying within anoxic sediment, and has prevented complete outlines from being preserved.

DIAGENESIS

Apart from compaction and mineralization effects the skeletal elements are preserved in two distinct ways: as dark brown bones with a smooth surface; or, as light buff bones with a soft powdery surface. The powdery surface is considered to be an effect of prolonged exposure to sea water, but might also be attributable to the encrusting of the bone surface by marine algae. Internally, the light buff bones are indistinguishable from the dark brown bones. Parts of the rib cage of the right side of the skeleton were freshly fractured due to the weight of the earth-moving machinery. It can be seen that in some of the ribs no mineralization of the voids in the bone has taken place. This has

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EXPLANATION OF PLATE 63

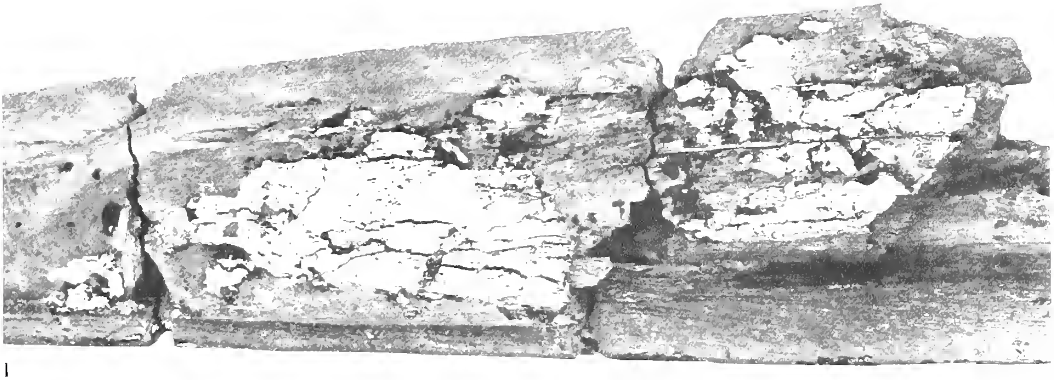
Preserved bacterial mats on surface of ichthyosaur bones.

Fig. 1. Rostrum of *Ophthalmosaurus* sp. BCM 1983/1008, showing black film overlain by buff coloured reflective coating. × 1.

Fig. 2. Underside of thoracic centrum of *Ophthalmosaurus* sp. BCM 1983/1008 showing black film only. × 1.

Fig. 3. SEM of lithified bacteria composing black film. × 10 000.

Fig. 4. Transmission electron micrograph of ultra thin section from black film taken from below thoracic vertebrae showing electron dense bacterial bodies. Osmium stained. × 30 000.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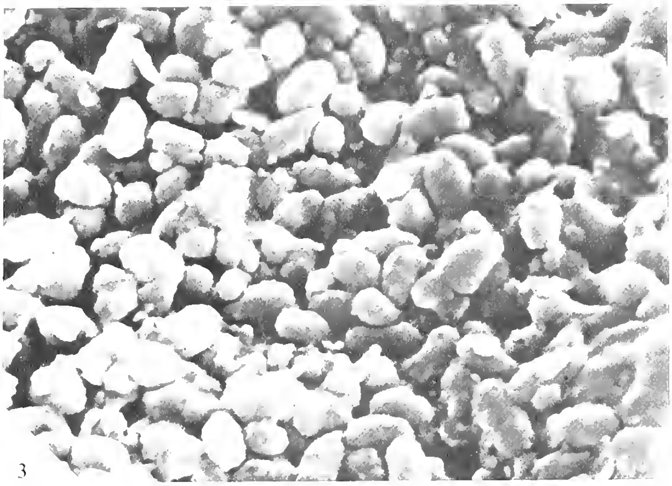
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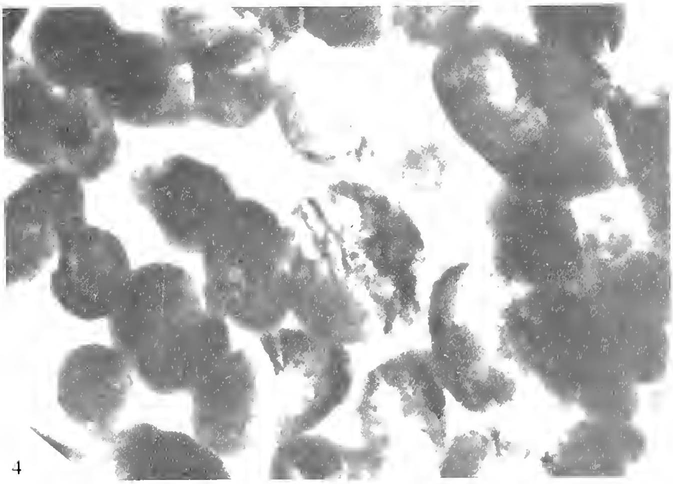
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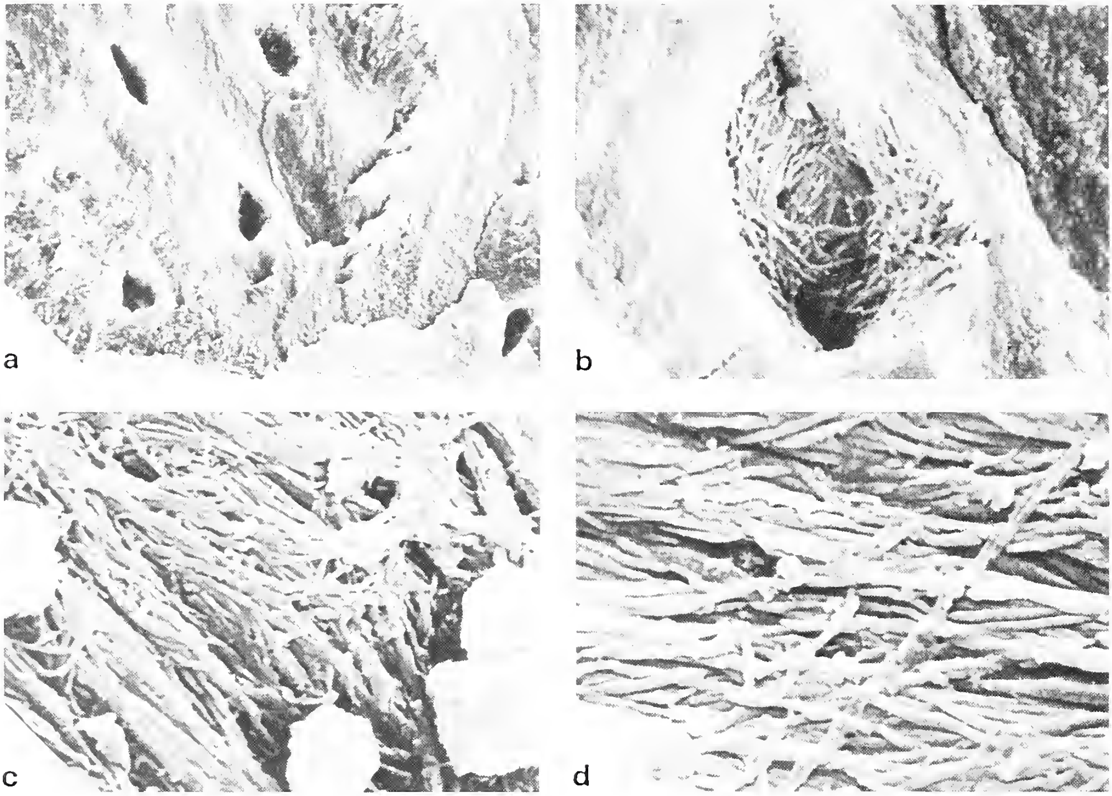
MARTILL, *ichthyosaur taphonomy*



TEXT-FIG. 4. Ultra structure of bone from *Ophthalmosaurus* sp. revealed by SEM after preparation in 10 % acetic acid. *a*, portion of jaw showing lacunae. × 100. *b*, detail of single lacuna with lining of newly mineralized collagen fibrils. × 400. *c*, tangled webs of mineralized collagen fibrils from vertebral centrum overgrown by small euhedral pyrite crystallites. × 520. *d*, bundles of collagen fibrils twisted in rope-like fashion from highly trabecular vertebral centrum. × 900.

made the bones very fragile. In other bones, however, the void spaces have been filled with a variety of mineral phases (see below), and are more robust. Scanning electron microscopy of both the bone surface and fractures of bone trabeculae etched in acetic acid show that no alteration of the phosphatic bone matrix has taken place during burial diagenesis.

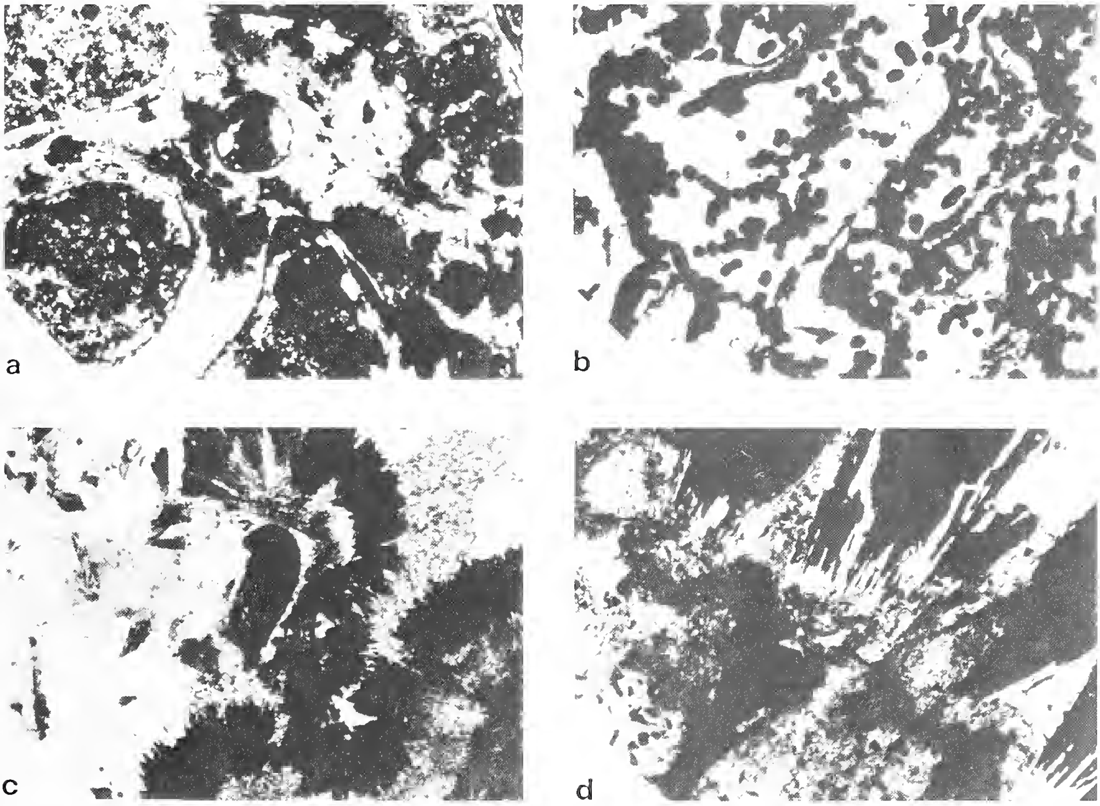
Bone ultra-structure. Thin sections and acetic acid etched samples of the bone show that the phosphatic matrix of the bones from this specimen have remained relatively unaltered since the death of the animal, and that the structures observed in thin sections, and with the electron microscope, are primary features. In thin section the trabecular bone of vertebrae and ribs is seen to be rich in lacunae and canaliculae, most of which have remained as voids within the bone; only in a few sections have these been filled with diagenetic minerals, notably pyrite. High power scanning electron microscopy of the internal surface of lacunae (text-fig. 4*a*, *b*) shows an irregular mass of phosphatized collagen fibres, which at ultra high-power show evidence of banding. The surface of the bony trabeculae is likewise unaltered, even after the effects of mineralization. Parts of a vertebral centrum filled with late ferroan calcite were etched in 10% acetic acid until all the carbonate phase had been removed. An examination of the prepared surface showed bundles of phosphatized collagen fibrils lying roughly parallel to the surface of the trabeculae. These are occasionally transgressed by isolated fibrils of phosphatized collagen. In some parts of the bone the parallel fibrils become tangled masses, and single bundles may bifurcate (text-fig. 4*c*, *d*). Each bundle of phosphatized collagen consists of nine or more individual fibrils, all of which are entwined like rope. The bundles are approximately 3 μm diameter, with individual strands less than 200 nm diameter. The longest individual strands are over 9 μm long, but the bundles are several times longer than this.

Good resolution work at high power is difficult to achieve, but when possible, the banding on the phosphatized collagen fibres appeared to be due to spaces 15 nm across, between individual crystallites of apatite approximately 100 nm across. The organic matrix of the bone was not present.

Diagenetic minerals

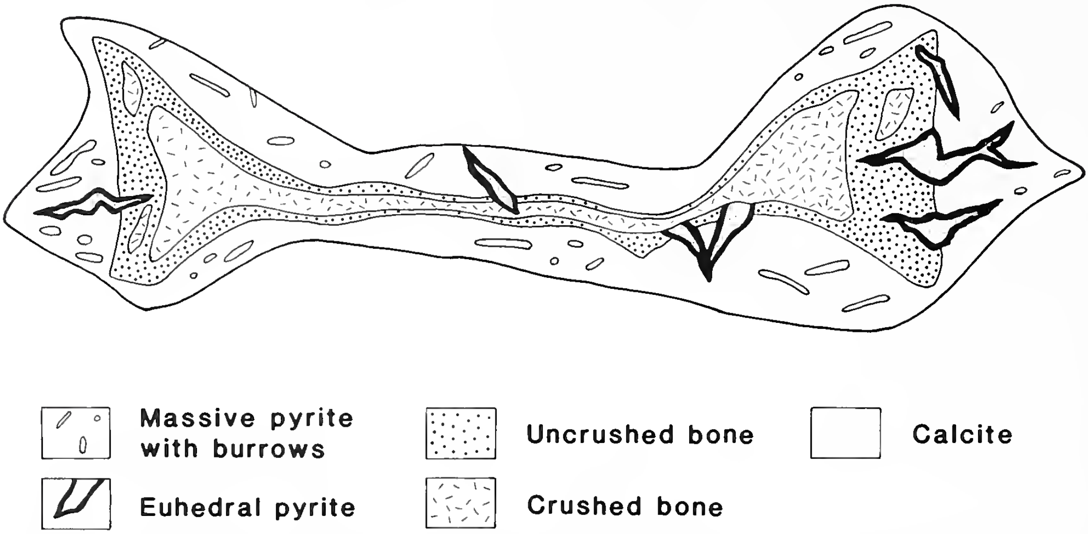
Pyrite. No alteration of the original mineral matrix of bone has taken place in those elements found within the shales or the large calcareous concretion, but there has been some replacement of phosphatic material in the two thoracic vertebral centra preserved in the pyrite concretion. Thin sections of the pyrite concretion show that lacunae and canaliculae, and void spaces in the trabecular parts of the bone are filled with pyrite. In some parts of the concretion the pyrite appears to have spread outwards from lacunae and pyrite filled voids to replace the bone material itself (text-fig. 5*a*).

Pyrite is also abundant in the trabecular bone as aggregates of pyrite octahedra. The aggregates



TEXT-FIG. 5. Thin section through over pyritized trabecular bone. *a*, pyrite (black) filling lacunae, void spaces, and partially replacing bone. ×20. *b*, chains of pyrite framboids on surface of bone. ×20. *c*, blade-like pyrite possibly pseudomorphing marcasite growing tangential to bone surface. ×20. *d*, detail of blade-like pyrite. ×20.

may completely fill voids in the bone, but frequently aggregates are less than 1 μm diameter and pyrite crystallites may represent the activity of a single sulphate reducing bacterium. These aggregates are seen in thin section as rounded bodies, isolated or in chains (text-fig. 5*b*). Individual octahedra are less than 3 μm diameter, but are well-formed crystallites, whereas the aggregates are up to 20 μm diameter, but the crystallites are less distinct, giving the aggregates a granular appearance.



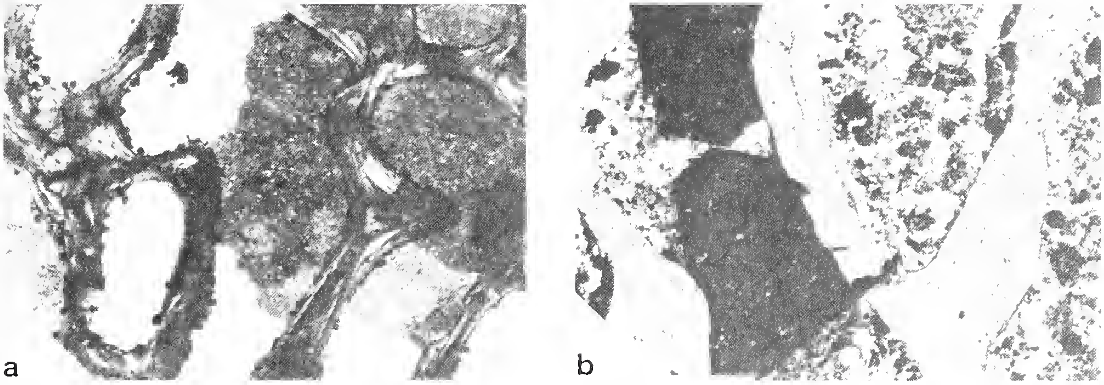
TEXT-FIG. 6. Disc-shaped pyrite concretion overgrowing thoracic centrum. Pyrite formation has preserved burrows in the sediment and prevented the centrum from suffering severe compaction damage, but some crushing has still taken place. Septarian cracking of the concretion has also affected the bone.

Concretionary pyrite is abundant in parts of the Lower Oxford Clay where it can be found overgrowing ammonites and fossil wood. It commonly forms flat disc-like concretions in the plane of the bedding. The concretionary pyrite on the two vertebral centra of this specimen is of a similar habit (text-fig. 6). Each vertebra is totally overgrown, and extensions of the pyrite extend horizontally, uniting the two centra. Two forms of pyrite are present, an amorphous pyrite mudstone found on the outside of the centra, and a micro-crystalline pyrite found lining void spaces in the bone, and lining later fractures in the amorphous pyrite.

The bone within the pyrite concretion has a few microfractures, and has been subjected to slight compaction, but it is apparent that the bones in the pyrite concretion have resisted compaction more than the bones in the shales.

Sphalerite. Small quantities of euhedral sphalerite are found in early fractures between bones, in large voids in trabecular bone, and in the tooth groove of the premaxilla and dentary. Occasionally sphalerite is found on the surface of the bone, but it appears to be most common in areas that have not been subjected to compaction. Sphalerite post dates in part the main compaction phase, as it can be found filling cracks in brecciated bone and surrounding bone shards (text-fig. 7*b*), but it is not found in fractures in the large calcareous concretion. It is considered to be of a later origin than the pyrite, post compaction of the bone, but pre-brecciation of the concretion.

Calcite. Late ferroan calcite is abundant, and found filling voids in bones, small fractures in the pyrite concretion, and large fractures in the calcareous concretion. In uncompacted trabecular bones it is found as coarse crystals completely filling cavities (text-fig. 7*a*). Crystal boundaries are irregular, suggesting some pressure solution at the boundaries. No fringing cements have been observed.



TEXT-FIG. 7. Void filling minerals in trabecular bone. *a*, trabecular bone with coarse-grained ferroan calcite filling void spaces. Crossed nicols. × 20. *b*, euhedral sphalerite (dark grey) filling void and fracture in trabecular bone (light grey) with later ferroan calcite (mottled). Transmitted light. × 20.

Many of the bones in the bituminous mudstone are coated with fibrous ferroan calcite (beef) up to 2 mm thick, with a thin film of clay sandwiched in between. This fibrous coating causes problems for the preparator as it requires removal with a vibrotool.

COMPACTION

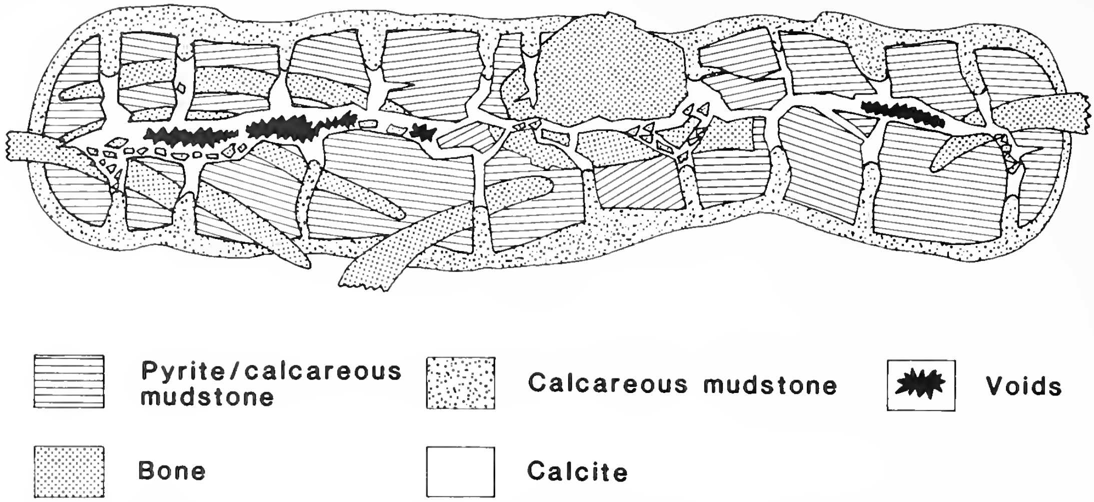
Compaction has had a deleterious affect on the specimen, and has resulted in differential preservation of the skeleton. Many of the elements of the skeleton that were lying within the bituminous mudstone have been uniaxially flattened by compaction. Failure of the bones is of a brittle nature, often with the complete shattering of all the inner trabeculae. The more solid margins of bones have resisted compaction, as have those bones with shapes that can transmit overburden pressures around their surface.

Compaction of some of the vertebrae has been greater than 50 % and has been unaffected by the position of the bone in the sediment. Vertebrae lying flat on the bedding planes have been flattened anteroposteriorly, while those lying vertically are flattened dorsoventrally. Confining pressure of the sediment has kept the brecciated bone together, and later cementation by ferroan calcite has allowed individual bones to be collected entire, although severely crushed. During acetic acid preparation the compacted elements of the skeleton fall into thousands of bone shards most of which are less than 1 mm long.

Early formation of the calcareous concretion has prevented bones enclosed by the concretion from being compacted, but compaction has caused the concretion to brecciate (Hudson 1978). Wide cracks have developed in the concretion which have penetrated the bones. Geopetal fabrics can be observed where shards of bone have fallen to the bottom of the cracks (text-fig. 8). Uncompacted clay has been squeezed into the cracks, and has penetrated cavities in the bone. Differential movement of the brecciated concretion and re-cementation of the fragments by coarsely crystalline ferroan calcite has resulted in a bone breccia.

Formation of the pyrite concretion appears to have post-dated the formation of the calcareous concretion, as the two vertebral centra preserved within the concretion show a slight degree of compaction, but this is not as severe as that which affected the bones in the shale.

Compaction has not affected the microstructure of the most highly compacted vertebrae, where lacunae and canaliculae can still be observed. Thus failure due to compaction is entirely of a brittle nature, with no observable alteration due to pressure solution or recrystallization. All fractures are clean and sharp and some appear to be controlled by the cleavage of void filling calcites.



TEXT-FIG. 8. A composite section through mudstone concretion illustrating diagenetic and compactional features affecting the preservation of enclosed skeletal elements of *Ophthalmosaurus* sp. Part of BCM 1983/1008.

CONCLUSION

The Milton Keynes specimen of *Ophthalmosaurus* died as a large adult, with disease possibly being a contributing factor to its death. The carcass sank rapidly to the sea-floor and was almost unaffected by scavengers. It lay partly buried in the sediment, where parts of the soft tissue underwent a long slow period of incomplete degredation by sulphate-reducing bacteria. The upper part of the carcass underwent rapid decomposition, and the exposed skeleton was encrusted by a restricted, but abundant epifauna. Parts of the skeleton became detached due to a combination of benthic scavenging, drifting due to adhering seaweed and perhaps storm activity. After burial, early formation of a calcareous concretion occurred around the anterior part of the post cranial skeleton. Compaction due to burial crushed many of the more trabecular, and flat bones, and also caused brecciation of the concretion, but later compaction caused some septarian cracking of the pyrite concretion also. Small quantities of sphalerite formed in lower pressure areas after an initial compaction phase. The three broad preservational styles in which this specimen occurs; in compacted shale, calcareous concretion, and pyrite concretion, are typical of vertebrates in the Lower Oxford Clay of the South Midlands, but at Peterborough pyrite is less abundant and normally only found as thin films on the surface of bones. At Peterborough septarian concretions occur around vertebrates in the Jason Zone (Martill 1985), although septarian, brecciation is generally less severe than in concretions from the Milton Keynes district.

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THE ARMOURED DINOSAUR *POLACANTHUS FOXI* FROM THE LOWER CRETACEOUS OF THE ISLE OF WIGHT

by WILLIAM T. BLOWS

ABSTRACT. A new specimen of the Lower Cretaceous nodosaurid ankylosaur *Polacanthus foxi* was found in the Wealden formation of the Isle of Wight in 1979. Three types of presacral spine are now recognized and new dermal elements of unknown position were found. Cranial and cervical fragments are described for the first time, including an axis formerly identified by Seeley, 1876, as ?*Iguanodon*. The sacrum shows a widening of the neural canal, as in *Stegosaurus* and others, and the tail plates differ from those of the holotype. The systematic status of *P. foxi* is reviewed, and comparisons are made with other contemporary nodosaurid taxa as far as possible. The genus *Polacanthus* appears to be valid despite suggested synonymy with *Hylaeosaurus*, it may, however, have closer affinities with comtemporary taxa of the New World, notably *Hoplitosaurus*. *Polacanthus* appears to have a greater geological range than *Hylaeosaurus*.

LEE (1843) described and illustrated three pieces of saurian dermal plates which, at the time, were unknown to science. These specimens can now be identified as fragments of sacral dermal plate of *Polacanthus*. The site of these pieces is recorded as the 'Hastings Sands' of Sandown Bay, Isle of Wight. According to Rawson *et al.* (1978) the Hastings Beds do not outcrop on the Isle of Wight, and the specimens probably came from the Wealden Marls (Wessex Formation), the usual horizon for *Polacanthus*. Not only is this possibly one of the earliest descriptions of *Polacanthus* material (without using the name), but Lee's manuscript has a footnote telling of the loss of these specimens in a hackney coach.

In 1865 William Fox excavated a partial skeleton of an armoured dinosaur from Barnes High, near Atherfield, Isle of Wight (Blows 1983). Much of the pelvis, hind limbs, and verterbral column were collected together with considerable dermal armour, which was made the type of *P. foxi*. A journal (Anon. 1865) described this discovery in a brief notice accompanied by a drawing of a collection of these bones. This account also included the name *Polacanthus* for the first time, and attributed this name to Owen. Huxley (1867) mentioned the name during an account of *Acanthopholis*, and again attributed it to Owen. However, Huxley is the earliest known author of the name. Hulke (1881, 1887) made a full description of the remains when they arrived in London in 1881. Again he attributed the name to Owen.

Since this time, only one other important specimen of *Polacanthus* has been described (Lydekker 1891) also from the Isle of Wight. It is a portion of the pelvis with some overlying dermal armour. This armour was thought to be smooth rather than patterned (as in *P. foxi*) and this lead to the suggestion that it could be a new species (Seeley 1891), later called *P. becklesi* Hennig 1924, after the collector Mr Beckles. However, this species is here synonymized with *P. foxi*. Other genera of contemporary age are *Hylaeosaurus* Mantell 1833, *Polacanthoides* Nopcsa 1928, and *Hoplitosaurus* Lucas 1902, all based on inadequate material, and their affinities with *Polacanthus* are poorly understood.

The object of this paper is to describe the most recent discovery of *Polacanthus* (Blows 1982) which was collected by the author from Compton Bay beach, Isle of Wight from 1979 to 1984.

Abbreviations. AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); BYU, Brigham Young University; GM, Gosport Museum; KU, Kansas University; MIWG, Museum of Isle

[Palaeontology, Vol. 30, Part 3, 1987, pp. 557–580.]

of Wight, Geology; CAMSM, Sedgwick Museum Cambridge; USNM, United States National Museum; YPM, Yale Peabody Museum.

SYSTEMATIC PALAEONTOLOGY

Order ORNITHISCHIA
Suborder ANKYLOSAURIA
Family NODOSAURIDAE
Genus *Polacanthus* Huxley 1867

Type species. P. foxi Hulke 1881.

Holotype. BMNH R175, partial skeleton with dermal armour (Fox Collection).

Type locality. Barnes High, West of Cowleaze Chine, Atherfield, Isle of Wight (NGR SZ 443 806).

Type horizon. Wealden Marls (Wessex Formation), Lower Cretaceous (Barremian).

Range. Wealden Marls (Wessex Formation) to Ferruginous Sands (?) (Aptian).

Diagnosis. Moderate to large size nodosaurid (Coombs 1978); presacral series of five fused vertebrae; sacrum of five fused vertebrae; maximum sacral canal expansion at S2 level; five sacral ribs; long posterior dorsal ribs supporting overlying dermal armour and adjoining anterior ilium; ribs flat dorsally, supported by a ventral ridge giving a T-shaped cross-section; anterior caudal vertebrae with long lateral processes, thickened neural process with a supraspinous notch; caudal series terminating in a vertebral–dermal mass with ossified tendons (?primitive club); presacral dorsal spines attain maximum heights over the shoulder region, reducing in height both anteriorly and posteriorly; the spines have flattened bases, the dorsal keel in large specimens twist through nearly 90° from base to apex, presacral spines mounted in a double row laterally to the spinal column; presacral 'lumbar', sacrum, and both ilia covered by a large, flat dermal plate of armour, approximately 1 m square, ornamented on the dorsal surface by ossifications; caudal armour of tall upright or short roof-like plates in double row, descending in height posteriorly and having narrow, hollow bases; rounded, oval, or subtriangular ossicles of sizes up to 110 mm across.

Referred specimens. BMNH R9293, three skull fragments (?nasal, supraoccipital, angular); left neural arch of atlas; CAMSM B53371, axis vertebra; BMNH R9293, (?)fourth cervical vertebra, four dorsal vertebrae and vertebral processes; sacrum with part neural arch; two caudal vertebrae (?first and second); two fragments of ilium; ?portion of ischium; two ribs complete; parts of three more ribs; rib head and fragments; terminal phalanx; ossified tendons; numerous endoskeletal fragments; five dermal plates (caudal series); four dermal spines (presacral series), two dermal spines (presacral series), one spiked plate (?caudal); ten large pieces of sacroiliac shield; fifteen smaller pieces of sacro-iliac shield; thirty-six dermal ossicles; CAMSM B53353, dermal ossicle; CAMSM B53354–53358, five dermal ossicles; CAMSM B53588–53591, four ossicles; CAMSM B53594–53597, four dermal ossicles; BMNH R9293, numerous dermal fragments; small complete bone (one side of bilateral pair) of unknown origin; CAMSM B53372, small complete bone (the other side of bilateral pair) of unknown origin.

Locality. The remains lay scattered within a confined pocket exposed at very low tide on Compton Beach, Isle of Wight (NGR SZ 374 845).

Horizon. The site occurs in the lowest beds of the Wealden Shales (Vectis Formation) and represents the first recorded find of *Polacanthus* from this stratigraphic unit (Dr A. Insole, pers. comm.). The bed is a pale grey, non-fissile, massive clay generally devoid of fossils. The strata dip strongly to the west and can be traced in the corresponding cliff section.

DESCRIPTIVE ANATOMY

The skeleton was disarticulated with bones at different depths. They may have been eroding out for some time. The axis vertebra (described Seeley 1876) and fourteen pieces of dermal armour were registered at Cambridge Sedgwick Museum between 1860 and the 1940s, and are considered to be the same skeleton as R9293. The (?)fourth cervical vertebra was registered with the British Museum (Natural History) (R9293) in the 1960s, and the main pocket of bones was found and excavated by the author from 1979 to 1984. Other elements may have washed out over this time span to be destroyed by sea action, or be held by private collectors.

The area containing the remains was about 4 square metres. The lack of duplicated bones, beyond that found within one skeleton, plus the rarity of nodosaurid finds in the Weald, suggests the presence of a single animal. Large bones were smashed (e.g. pelvis and overlying armour), and scattered with some loss.

Skull. The holotype of *Polacanthus* is without a skull. A referred specimen, a basisphenoid (BMNH R4951) from the Isle of Wight, is suggestive of nodosaurids but cannot be assigned to a genus with any certainty. A 'lower jaw' (BMNH R175X) has been identified as a fragment of an *Iguanodon* ilium (D. Norman, pers. comm. 1976). The new skeleton has two skull fragments and one possible jaw fragment.

Nasal. This is a flat bone with only one edge and one corner intact. One surface is rounded with grooves, the other is gently depressed with flat dermal ossifications. The preserved edge appears to be part of the medial suture across the skull roof.

Supraoccipital. This is a fragment of bone found loose on the site. It is massive compared to *Stegosaurus* and *Silvisaurus*, with a deeply roughened sutural surface for articulation with the paraoccipital bone, and a smoother articulation surface for the parietal bone. The ventral surface is grooved, the roof of the brain case, and together with the opposite smooth dorsoposterior surface, wedges towards the foramen magnum.

Lower jaw. The jaw fragment is probably the left angular (Galton, pers. comm. 1983). It is a boat-shaped bone with a deeply concave inner surface, and a convex outer surface bearing a dermal ossification. One edge is smooth and sharp, the other is irregular and gently curved.

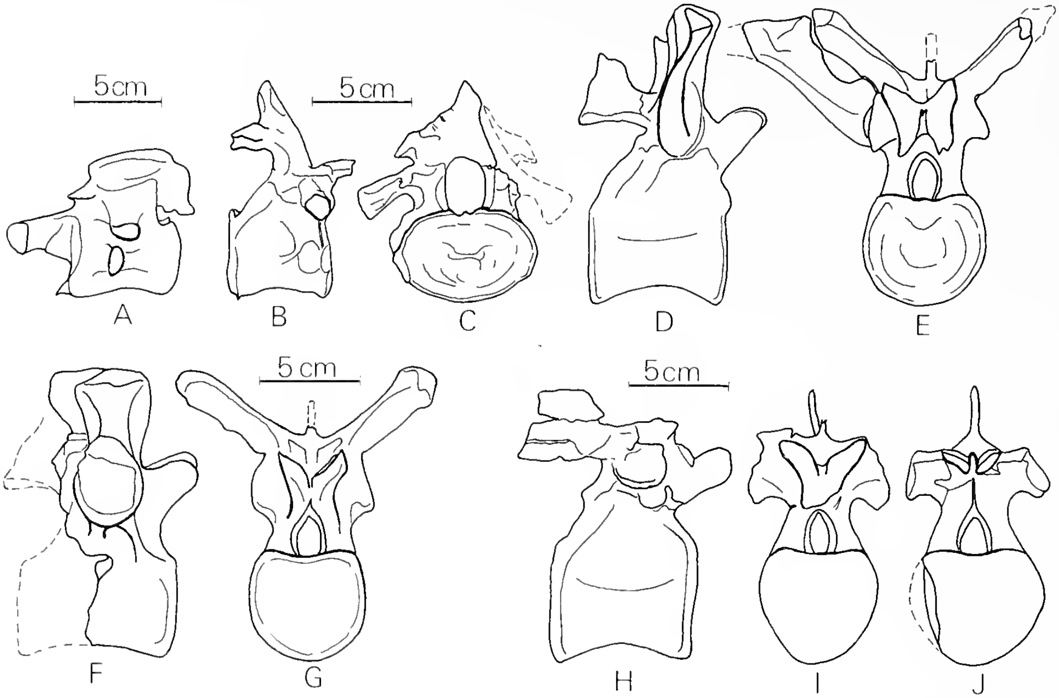
The dentition of *Polacanthus* is unknown.

Post-cranial skeleton

Cervical vertebrae. The entire cervical series is missing in the holotype. A single cervical vertebra, considered as part of the type (BMNH R175) is referable to an ornithopod, probably *Iguanodon*. In the new specimen, one cervical element (from the atlas vertebra) is known from the site. However, an axis vertebra (SMES B53371) and a (?)fourth cervical (BMNH R9293) are from the same locality and probably from the same skeleton (test-fig. 1). The atlas as preserved, consists of only the left neural arch. The right neural arch and intercentrum are missing. The atlas and axis vertebrae were not fused in *Polacanthus*. The atlas corresponds well with *Stegosaurus* as described by Gilmore (1914) except the narrowing below the processes, being more constricted anteriorly and overlain by a pronounced prezygapophysis. The neural arch was not fused to either the intercentrum or the neural arch of the other side along the mid-line, which corresponds with a sub-adult status. The posterior process is missing.

The axis vertebra. Seeley (1876) first described this bone (CAMSM B53371) and regarded it as 'probably *Iguanodon*'. The characteristics are those of general ornithischian dinosaurs and are well described by Seeley (text-fig. 1A). The presence of both diapophysis and parapophysis indicate the double-headed nature of the cervical rib.

(?)*Fourth cervical vertebra.* Parts of the neural process, the left pre- and postzygapophysis and left lateral process only are missing in this specimen (BMNH R9293) (text-fig. 1B, C). The centrum is amphiplatyan, the articular surfaces being nearly a third greater in width than height and centrally depressed. The large neural canal is ovoid, being greater in height than width. The floor of the neural canal dips downwards to create a central cavity within the centrum. The

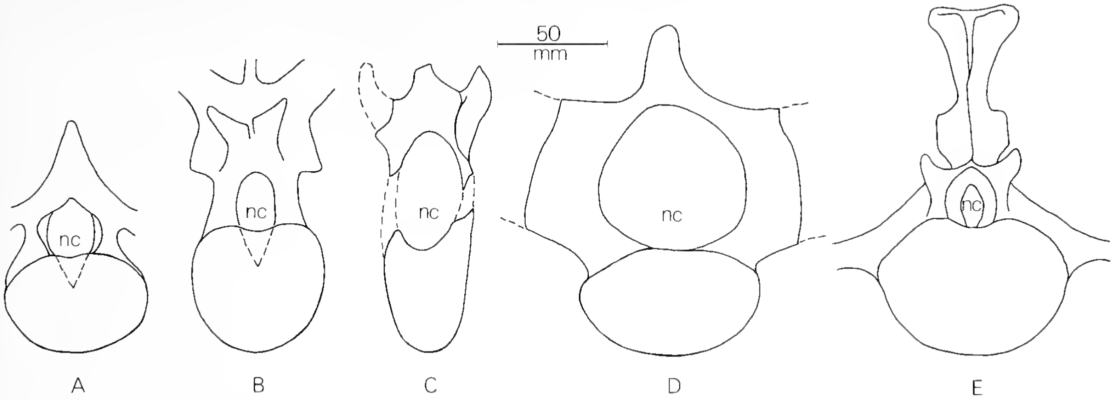


TEXT-FIG. 1. *Polacanthus foxi.* Lower Cretaceous, Isle of Wight. A, SMES B53371, axis vertebra, left lateral view. B, C, BMNH R9293, (?)fourth cervical vertebra. B, right lateral view; C, anterior view. D, E, BMNH R9293, dorsal vertebra. D, right lateral view; E, anterior view. F, G, BMNH R9293, dorsal vertebra. F, right lateral view; G, anterior view. H–J, BMNH R9293, dorsal vertebra. H, right lateral view; I, anterior view; J, posterior view.

pre- and post-zygapophyseal articular surfaces lay approximately on the same horizontal level, the prezygapophysis only extending beyond the limits of the centrum. The neural process is inclined posteriorly.

Dorsal vertebrae. Four free dorsal vertebrae exist in both the holotype and the new specimen. These latter are better preserved than the type, but in both, the vertebrae consist of two almost complete (R175 numbered C12, C14 and R9293 numbered 3, 4); one with only half a centrum (R175 numbered C16, R9293 numbered 2); one being a centrum only (R175 numbered C19, R9293 numbered 1). Other isolated dorsal vertebrae (BMNH 2527; MIWG 5188; CAMSM B53587) are worthy of description. Hulke (1881) and Nopcsa (1905) described the main features of the dorsal vertebrae, but in the new specimen the floor of the neural canal dips into the centrum in a V-shaped manner, with a maximum depth half-way along the vertebral length, similar to the cervicals previously described (text-fig. 2A, B). It occurs in all four vertebrae but is obscured by matrix in the holotype, although fractures across the centra indicate this feature.

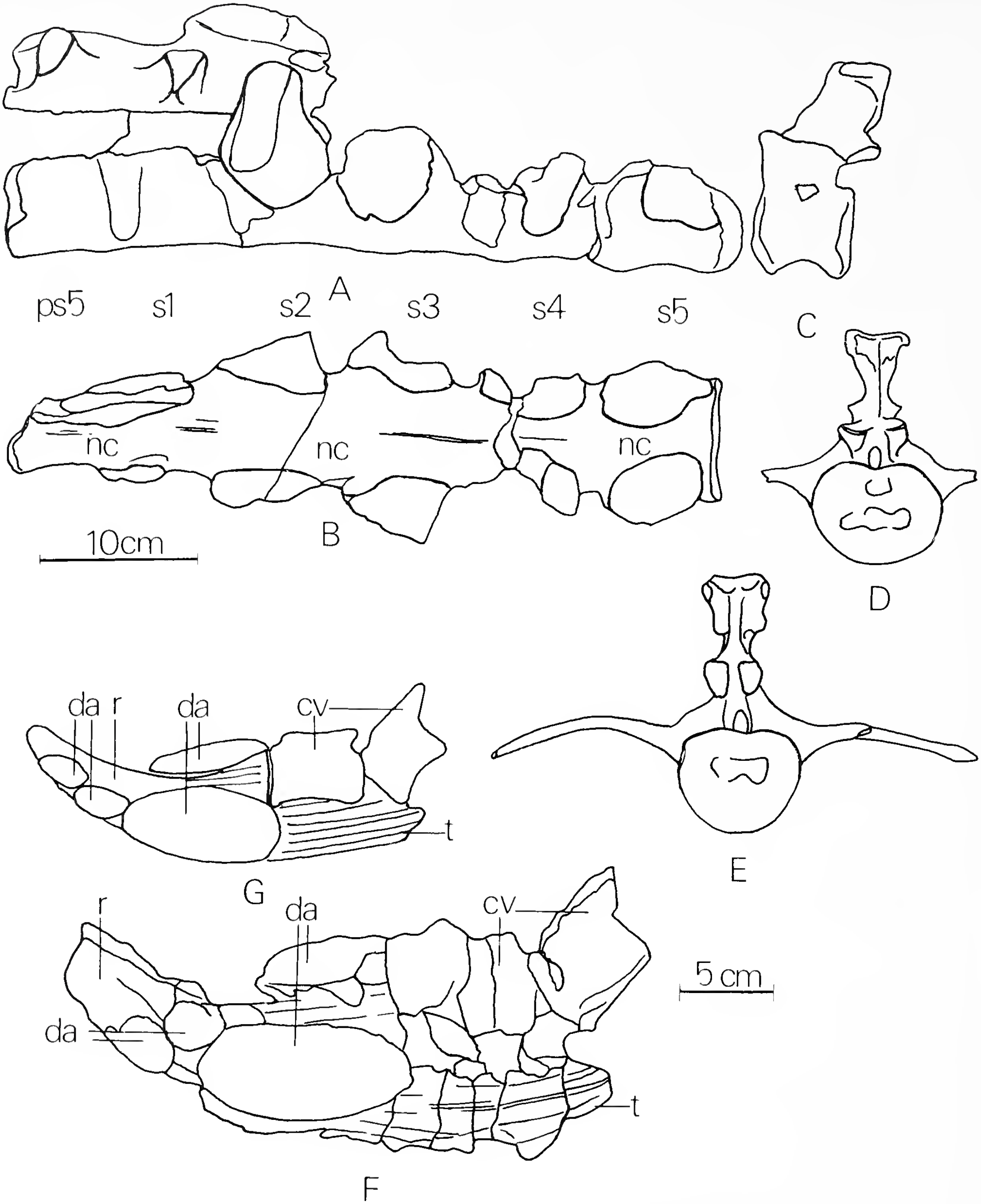
An isolated dorsal vertebra (BMNH 2527) from Barnes High, Isle of Wight (Hulke Collection) is much larger than the other *Polacanthus* Vertebrae (see table of measurements). Another dorsal vertebra from Atherfield, Isle of Wight (SMES B53587), is almost complete. It has transverse processes angled at 60° rather than the usual 90°. A dorsal centrum (MIWG 5188) is complete and unworn. Sutural grooves on each side of the neural canal suggests a juvenile nature. The neural canal floor dips as previously described although partly filled with matrix.



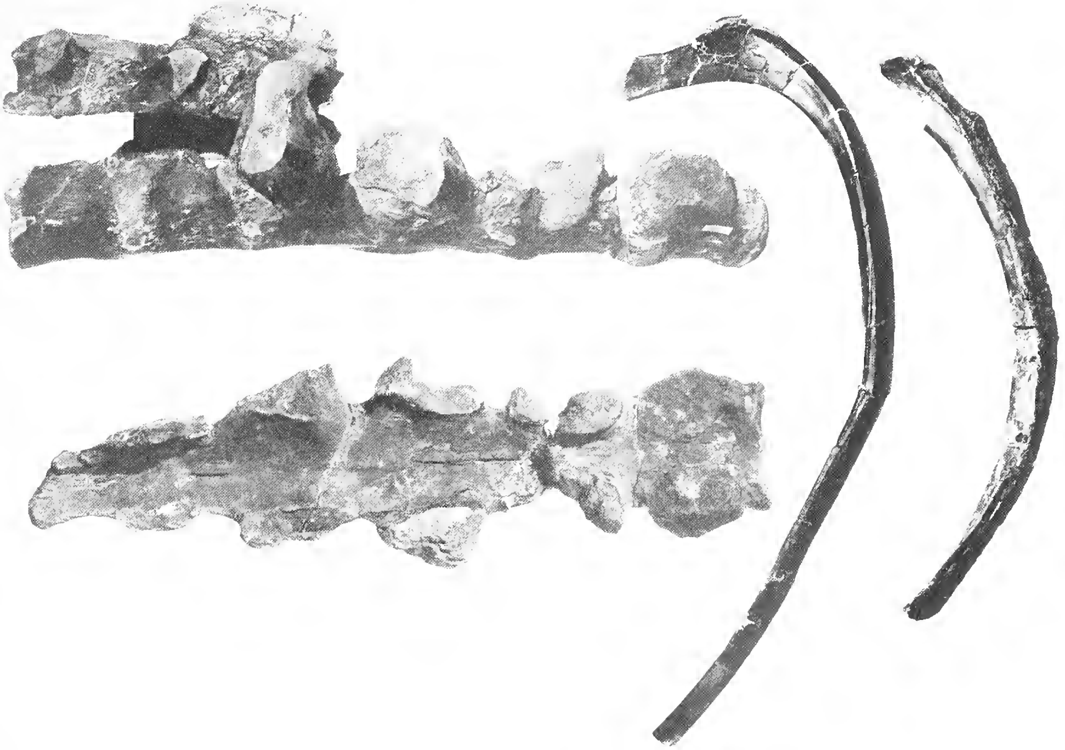
TEXT-FIG. 2. *Polacanthus foxi.* Lower Cretaceous, Isle of Wight. A–E, BMNH R9293, vertebrae showing neural canal (nc). A, cervical vertebra; B, dorsal vertebra; C, anterior sacral vertebra; D, sacral vertebra at S2 level; E, caudal vertebra.

Sacrum. The sacrum (text-fig. 3A, B) is well understood from the holotype which has five vertebrae, with a further five presacral ('lumbar') vertebrae fused into a presacral rod. The holotype has part of the overlying dermal plate and ossified tendons attached. The new specimen of five sacral centra and one presacral centrum is free from attachments, and the neural canal is fully exposed. Nopcsa (1905) stated 'There does not seem to exist any especial widening out of the neural canal in the sacral region, as recorded for *Stegoceras* (*sic- Stegosaurus*) and also visible in *Dacentrurus* (*Omosaurus*)'. However, sacral neural canal expansions are reported in other nodosaurids: *Sauropelta* (Ostrom 1970), *Nodosaurus* (Lull 1921), *Panoplosaurus* (Sternberg 1921), and *Silvisaurus* (Eaton 1960), and some ankylosaurids (Maryanska 1977). In BMNH R9293 an extensive broadening of the canal reaches a maximum width and height at the level of the second and third sacral vertebrae, confirming this feature in *Polacanthus.* In this respect *Polacanthus* resembles *Stegosaurus*, where a neural expansion occurs over the anterior half of the sacral canal (Gilmore 1914). The holotype sacrum bears five pairs of sacral ribs, the first pair are least robust, arising between the centre of the posterior presacral and first sacral vertebrae. The following three pairs are the most stout, and the posterior ribs arise from the centrum of sacral 5. The sacral ribs and posterior neural arch of the new specimen are missing. A third sacrum from the beach near Whale Chine, Isle of Wight, in a block of sandstone (BMNH no number) bears all the sacral ribs which unite distally prior to the iliosacral joints, as in the holotype. The ventral surface only is exposed, the first two anterior presacrals are missing and two sacral centra are eroded. This is the first recorded discovery of *Polacanthus* in the (?)Ferruginous Sands (F. A. Middlemiss, pers. comm.).

Caudal vertebrae. Nopcsa (1905) noted a discrepancy in the holotype tail vertebral count; there are in fact twenty-one preserved. A tail-end mass consisting of two verterbrae, dermal armour, and ossified tendons are included in this number (text-fig. 3F–G). Also the first caudal vertebra is attached to the posterior sacrum at an angle by matrix and may have been regarded as sacrum, or sacrocaudal, and remained uncounted. Both Hulke (1881) and Nopsca (1905) missed this vertebra in their text, regarding the first free vertebra as caudal 1, although Hulke (1887) figures and labels this vertebra (c.v., caudal vertebra). The tail-end mass has a rod-like bone tapering to almost a point representing the termination of the vertebral column. This curves dorsally towards the tip and is hidden mostly by overlying dermal ossifications. It must be a fusion of terminal vertebrae. Two larger dermal plates attached to the mass represent the termination of a tail long bilateral row of plates. Only one surface of the right plate is exposed, the left plate shows two surfaces with a sharp keel-edge. Irregular dermal ossicles are scattered over the vertebral rod between and beyond the plates up to the tail



TEXT-FIG. 3. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. A–E, BMNH R9293, vertebrae. A, sacrum and anterior neural arch in left lateral view, ps—presacral, s—sacral vertebrae; B, sacrum in superior view showing neural canal (nc); C, first caudal vertebra, left lateral view; D, first caudal vertebra, anterior view; E, second caudal vertebra, posterior view. F–G. BMNH R175, caudal end mass. F, right lateral view, cv—caudal vertebra, da—dermal armour, r—rod of bone, t—tendons; G, restored caudal end mass, right lateral view (see F for abbreviations).



TEXT-FIG. 4. *Polacanthus foxi* Lower Cretaceous, Isle of Wight. BMNH R9293 sacrum and ribs. *Left*: Sacrum, lateral and superior views. *Right*: Ribs.

tip. A group of tendons run throughout the length of the mass along the ventral surface to end at the tail tip. The two caudals found with R9293 are most likely to be the first and second. The second caudal has lateral processes which are thin and long, and both have stegosaur-like expansions of the neural process with a supraspinous notch. A small proximal vertebra (BMNH R4952) from Grange Chine, Isle of Wight, may be the first caudal of a junior individual. A caudal vertebra (MIWG 5144) from Brook Bay, Isle of Wight, is a heavily pyritized, water worn centrum.

Ribs. The holotype has ten free anterior dorsal ribs (labelled left: L4, 5, 7, 8, 9, 10; and right: R3, 6; with two unlabelled) and ten posterior dorsal ribs, five each side attached to the overlying sacral armour. The new specimen has one complete anterior dorsal rib (text-fig. 4), fragments of three others, a rib head attached to a dorsal vertebra, one almost complete posterior rib with evidence of sacral shield attachment, and a few rib fragments. Hulke (1881) describes the ribs sufficiently to establish their major features, including those of the type that are found on the ventral sacral shield (Hulke 1887). These arise from the presacral 'lumbar' vertebrae, although their attachment to the vertebrae is now missing in the holotype. The broad dorsal surfaces of these ribs, in contact with the sacral shield above, are supported by a narrow ventral ridge throughout much of their length. The most anterior of these ribs are the longest, extending flat, bilaterally to beyond the medial edge of the ilia, the posterior three appear to fuse with the ilia. A similar situation, without the sacral shield, occurs in *Euoplocephalus* (Coombs 1978, text-fig. 13). These ribs would not have needed to curve very much proximally in order to unite with the presacral vertebrae in the holotype. However, ribs of a similar nature (new specimen R9293 and R4134) show considerable curvature, suggesting that the vertebral column was deeper set than the holotype shows. This is further supported by the steep angle of the lateral process on the sacral neural arch of the new specimen. Nopcsa (1905) draws attention to evidence that shows a space existed between the ribs and sacral shield. There is evidence that suggest the pelvic region at least, in the holotype, has been crushed (see pelvis below).

It is possible that the dorsal ribs anterior to the sacro-lumbar unit was deep set below the maximum height curvature of the ribs, and this is supported by the steep angles of the vertebral lateral processes found in dorsal vertebrae (Nopcsa 1905). This feature is seen in *Palaeoscincus* (Gilmore 1930, fig. 11) where the neural process hardly reaches the maximum rib height. Presacral ribs differ from anterior dorsal ribs by a strong 'T' cross-section, the dorsal platform roughened by fibrous tissue compared to the smooth ventral surfaces.

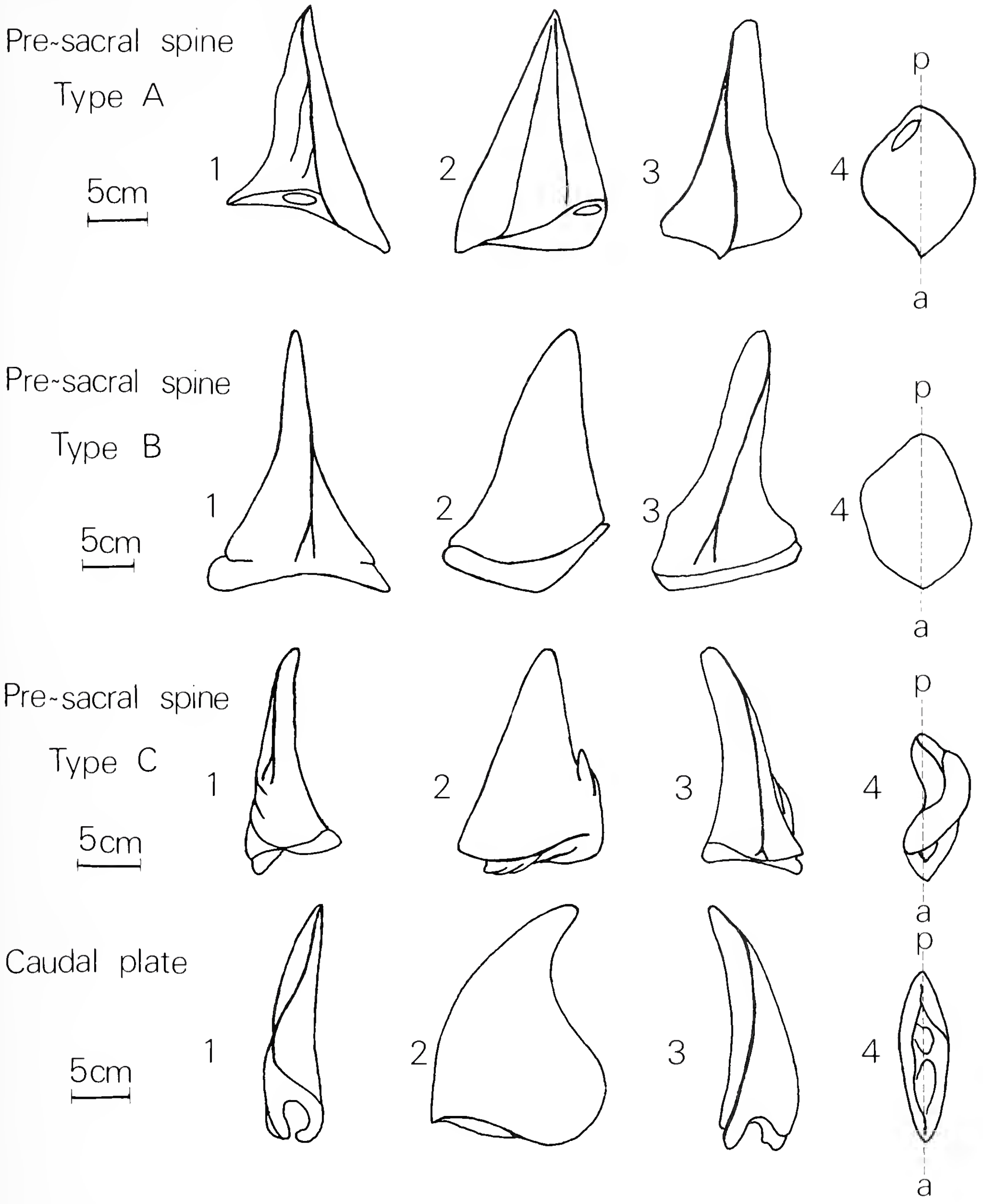
Pelvis. The pelvis is well understood from the holotype (Hulke 1887). Two fragments of ilium found with the new specimen are poorly preverved and offer little new information. An acetabulum with proximal end of the ischium was badly worn before burial. An anterior fragment of ilium shows the dorsal surface not seen in the holotype because of the overlying sacral shield. This surface is generally flat but roughened, especially along the lateral border. A portion of pelvis (BMNH R1926, Beckles Collection) was considered to be a different species of *Polacanthus* (*P. becklesi* Hennig 1924) because of smooth dermal armour and greater thickness of ilium than the holotype (Seeley 1891). It is the medial aspect of the acetabulum with attached eroded sacral ribs and proximal end of ischium, apparently uncrushed but water worn. The fragment of ilium from R9293 is broken but undistorted, and demonstrates varying thicknesses approaching that of the Beckles specimen. Possibly, the holotype may have been subject to earth pressure causing an artificial thinning of the ilia (Lydekker 1891). This is not a factor on which to found a new species (the question of smooth dermal armour will be taken up later).

Seeley (1891) described a bone suggested by him to be the pubis of *Polacanthus* (removed by Nopcsa 1905, to an *Iguanodon*-like genus), the pubis of nodosaurs being much reduced to a ridge on the anterior border of the acetabulum (Coombs 1978).

Limbs. No elements of the limbs have been recovered from the new specimen site except a single terminal phalanx. Hulke (1881) briefly described some bones, considered as 'unguals' by William Fox, as 'broad, depressed and blunt'. The number is not stated, and now I can only define one terminal phalanx among the isolated parts of the holotype. This specimen measures 82 mm long by 63 mm at the widest point, but it is distorted by compression, and this may have caused the articulating surface to appear on the ventral side. The bone has a rounded termination, and no narrow 'neck' between the articulating surface and the body of the phalanx, possibly an adult feature. The terminal phalanx from the site, considered part of the same skeleton, is smaller than the holotype, more pointed and has a flatter base. A slightly narrowed neck gives rise to expanded lateral boarders over the anterior two-thirds of the bone. These are separated from the raised body by grooves anteriorly. The neck of the bone is possibly a juvenile feature compared to the holotype ungual, suggesting further the sub-adult status of the new specimen.

Bones of undefined origin. The new specimen includes a small, complete bone of unknown origin. Its appearance is suggestive of a dermal scute, and this was the label attached to its counterpart in Cambridge (SMES B53372). The two are a bilateral pair and originate from the same lacality. Each has a sharp-edged ridge across the superior surface with a low peak set at one end. The base inclined to the ridge at an angle of about 45°, and is gently concaved and roughened to suggest a sutural surface with another bone. The shape of the base is oval, but broader at one end than the other. The surface features are unlike other dermal elements, and the existence of an exact bilateral pair is suggestive of possible endoskeletal origin. However, microscopic examination of the surface is suggestive of dermal origin (D. Cooper, pers, comm.). The two do not in themselves unite, but appear to form mirror images some distance apart. Until more complete material is available the origin, orientation, and symmetrical designation of these bones will be in doubt.

Armour. The dermal elements of *Polacanthus* were interpreted by Nopcsa (1905) for the holotype, and the new specimen falls broadly within this scheme. The animal had a bilateral row of dorsolateral



TEXT-FIG. 5. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, presacral and caudal spines. 1, posterior view; 2, medial view; 3, anterior view; 4, inferior (basal) view, a—anterior, p—posterior.

spines of varying height and broad bases along the neck and thorax. The caudal region had a double row of narrow plates set dorsolaterally in decreasing size from tail root to tip. The pelvis and sacrum are covered by a large sacral shield, and numerous smaller ossicles were distributed across the trunk and tail between the larger elements. This arrangement is well understood from description of the holotype, but each of the components are worthy of reassessment in the light of the new specimen. In addition, new dermal elements, unknown in the holotype (Blows 1982), are described.

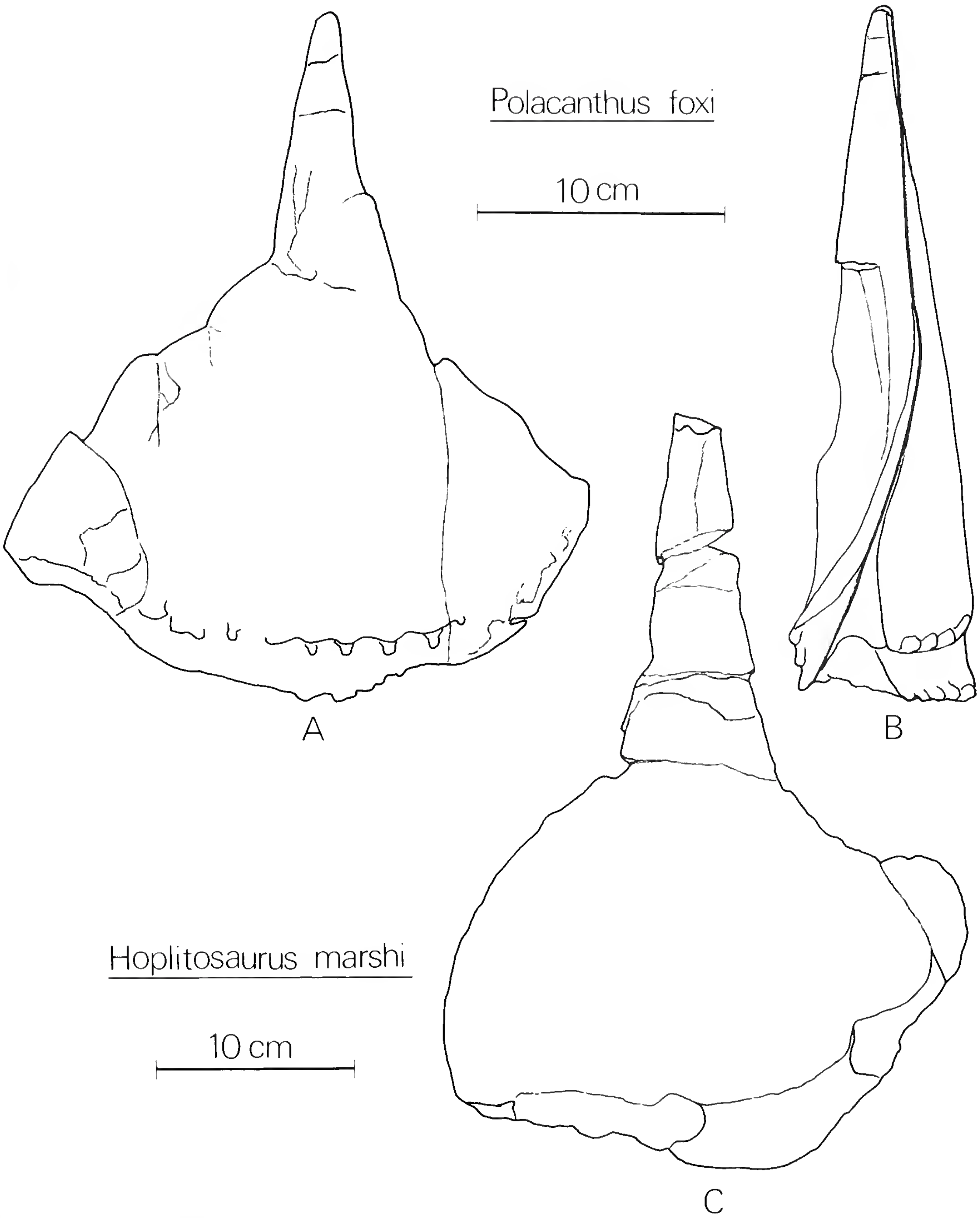
Presacral dorsal spines. The holotype has seven preserved spines (Type A, text-fig. 5), five more are plaster replicas for display purposes. Nopcsa quotes eight spines and distributes them as three left and five right. His illustration (Nopcsa 1905, pl. xii) of the skeleton indicates seven spines as preserved, five right and two left. The new specimen has four recognizable spines (Type A) of various sizes.

Each Type A spine has two distinct edges to the keel which unite at a sharp summit. In the largest spine (text-fig. 8) the two keel edges twist through nearly 90° towards the summit. The bases are solid, broad, flat, and generally asymmetrical; only the smallest spine showing some degree of concavity and symmetry in the base. The base has a hook-like feature produced by an extension of one keel edge below the base margin. Opposite this the larger spines have a groove just inside the base margin. Following Nopcsa in the orientation of the larger spines, the lateral face of the keel is smooth and slightly concave, the medial face is angled into three planes. All the faces of the keel are irregularly grooved, often thought to be of vascular origin, and the base has a crossing fibrous texture.

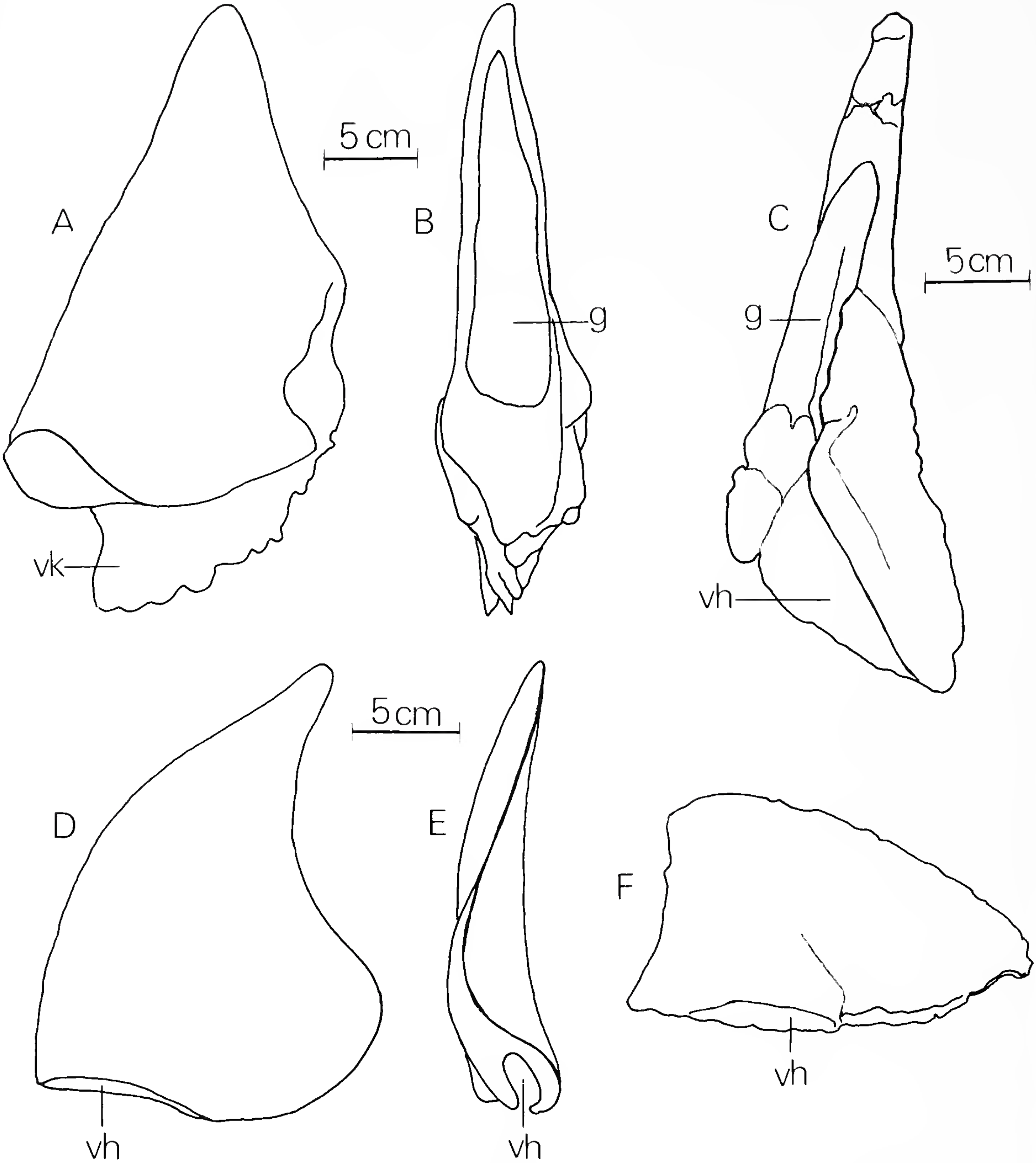
Several of these spines of the holotype are unusually flat and broad, possibly further evidence of general post-mortem crushing. Nopcsa's orientation of these spines shows a consistent pattern. The anterior keel edge is curved outwards, the posterior edge being shorter. This makes the basal hook-like feature anterior, the opposite groove in larger spines being posterior. Other spines are of a slightly different nature (Type B, text-fig. 5). They are MIWG 1191*a*, a large dorsal spine missing the top, from Sedmore Point, Isle of Wight; and MIWG 5307, a large complete dorsal spine from grey marls several hundred metres east of Chilton Chine, Isle of Wight, about 11 ft. above beach level. They are both presacral in origin because they have solid, broad bases, but they vary from Type A by the following points: the dorsal keel is flat on both sides and the edges are straight, or very gently curved, twisting slightly or not at all. The base has two distinct areas of dermal attachment, a prominent medial anterior process and lateral posterior process. Both areas are separated from the dorsal keel by a step in the bone. There is no hook-like feature in Type B spines. These spines could reach the size of Type A (see MIWG 1191*a*). Two spines from the new specimen are of the same general variety as Type B, one larger and one smaller, but differ by having narrower, smooth and gently arched bases. These do not reach the full extent of the dorsal keel edges which extend beyond the anterior limit of the base into a V-shape similar to caudal plates. Type C is designated to these spines.

Postsacral caudal plates. The other free standing elements are tail plates extending along the tail in descending size and shape (text-figs. 5 and 7). The holotype has fifteen tail plates set in two rows, seven right and eight left. Nopcsa's skeletal restoration illustrates twenty-two caudal plates in eleven pairs (including the tail tip plates as a pair). The new specimen has five plates referable to the tail, with a number of fragments of others. Three plates are left side and two right, with four fragments referable to the right. The dorsal keel is flat on both sides and tapers to a round peak. The base is narrow and hollowed throughout the posterior two-thirds, the cavity created extending as much as 40 mm into the plate. The base edges are asymmetrical and sinusoidal and are heavily roughened with notches and grooves for dermal attachment. The caudal plates of the holotype differ considerably, the above base shape appears in only one anterior plate (numbered BR1). The others have symmetrical bases with a V-shaped cavity throughout the base length, and a similar hook-like feature to that of Type A spines.

Two caudal plates show variation from this. The first is part of the new specimen (R9293;



TEXT-FIG. 6. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, ?anterior caudal dermal plate, A, ?medial view, B, lateral view. C, *Hoplitosaurus marshi*. Lower Cretaceous, USA. USNM 4752, ?medial view (redrawn from Gilmore 1914).



TEXT-FIG. 7. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. A, B, GM 981.45, dermal plate; A, ?medial view, B, posterior view. C, *Hoplitosaurus marshi*. Lower Cretaceous, USA. USNM 4752, dermal plate, posterior view (redrawn from Gilmore 1914). D–F, *P. foxi*. Lower Cretaceous, Isle of Wight. D, E, BMNH R9293, caudal plate; D, ?medial view, E, posterior view. F, BMNH R175, caudal plate, ?medial view, g—groove, vh—ventral hollow, vk—ventral keel.

text-figs. 6 and 8) and is distinguished by a long, solid base, the keel narrowing sharply to a peak supporting a straight, narrow cylindrical spine. This spine is nearly half the overall height of the plate, and is similar to the peaks of Type A spines. The length and asymmetry of the plate base suggests early caudal positioning on the left side, possibly the first postsacral plate. The second plate of unusual nature was described previously (Delair 1982) (GM 981.45; text-fig. 7) and is from the Barnes High area of the Isle of Wight (Kemp Collection, 1974). The anterior and posterior edges are straight and the peak is posteriorly inclined. The dorsal keel thickens from the anterior edge to create two posterior edges separated by a groove from base to apex. The solid base supports a rugosed, deep ventral keel for dermal attachment. These plates are discussed later.

Sacral shield. The dermal plate which covered the sacrum and ilium is well known and described by Hulke (1887). This holotype shield is slightly flattened by crushing. It is a complete unit, averaging 8 mm thick, and is not fused to the underlying bone. The dorsal surface is patterned with round, subtriangular or oval bosses bearing various degrees of raised peaks, separated by multiple tubercles and covered with fine grooves. The ventral surface, nor seen in the holotype, has a surface pattern of cross fibrous tissue, like coarse textile (e.g. sackcloth), and is pock-marked by multiple blood vessel openings. Ten large fragments and many smaller pieces exist of this shield in the new specimen (text-fig. 9). The central pieces are thicker, the shield thins towards the lateral and posterior borders. The portion of *Polacanthus* ilium, referred to under 'pelvis' as *P. becklesi* (R1926) was thought to have a fragment of smooth sacral shield attached; this diagnostic feature suggested the new species (Hennig 1924). Close examination of the surface of the armour reveals the bases of at least three bosses and surrounding tubercles; the armour was patterned. This specimen is referred to *P. foxi*, the name *P. becklesi* is obsolete. The holotype shows a very shallow, almost flat patterning to the armour over the same region of ilium as R1926, and the Beckles specimen is clearly badly water worn, being impregnated with calcareous deposits from the sea.

Ossicles. The isolated elements of armour, which were not incorporated within the shield, and which probably covered the dorsum, flanks and tail between the free standing armour were ossicles. They range in size from 9 mm to 70 mm across and number thirty-six from the new skeleton. The larger are subtriangular to nearly round and peaked to one edge, with flat or slightly convex bases. The dorsal surface has vascular grooving. The smaller ossicles are rounded with flat bases. Two ossicles are notched, they have a small rounded piece of one border missing; an incomplete border development and not a fracture. In Sedgwick Museum, Cambridge, about thirteen ossicles exist, all from the Isle of Wight and possibly from this new skeleton. In Sandown Museum, Isle of Wight, a group of dermal pieces (MIWG 37) from Brook contains ossicles of larger size than the maximum collected with the new specimen. One ossicle measures 93 mm by 75 mm, another 60 mm by 100 mm. The British Museum (Natural History), London, has six ossicles plus thirty-nine of the holotype (twenty-eight small, eleven large). Some of the holotype ossicles are the largest known for this genus (e.g. 105 mm by 93 mm).

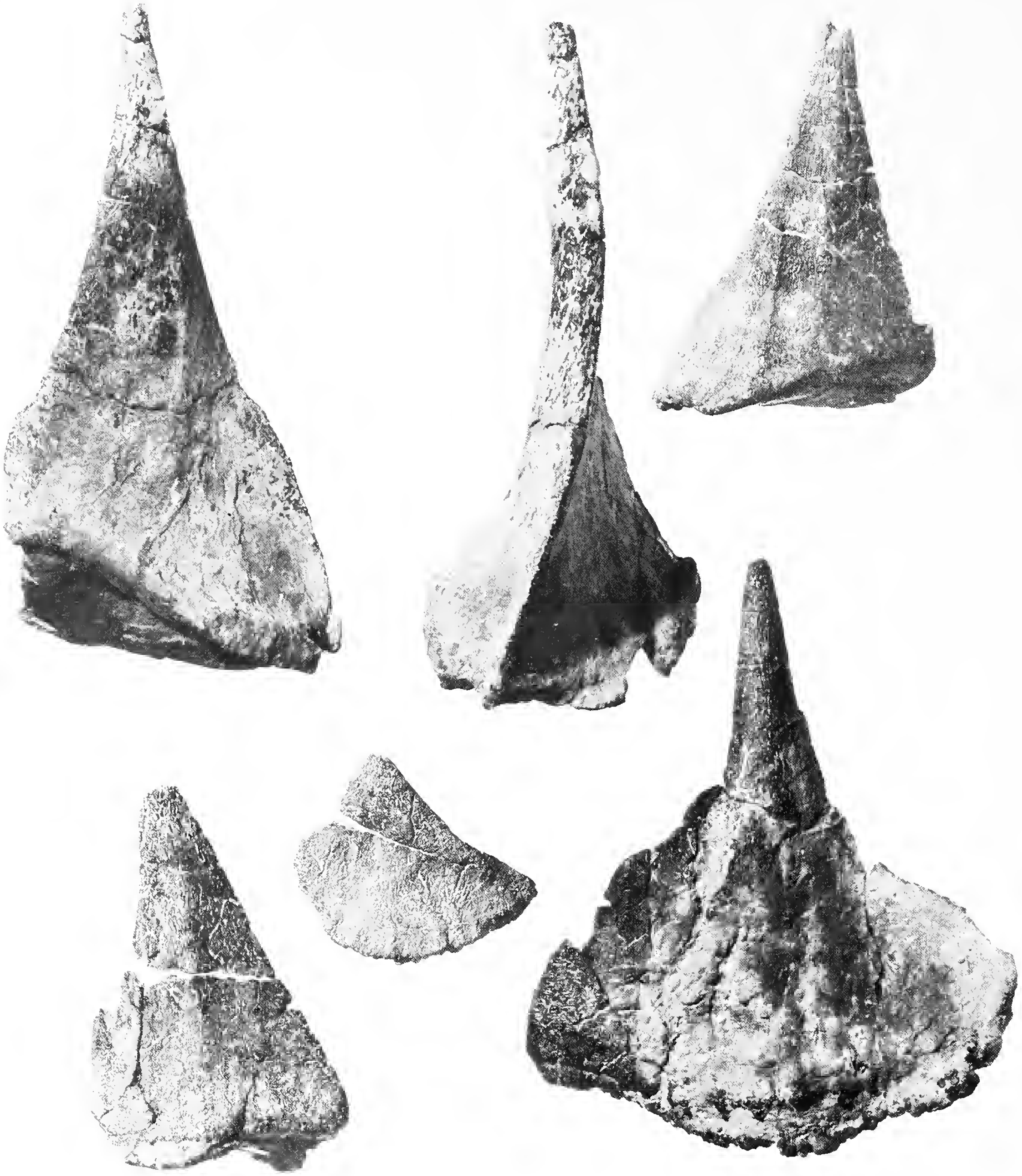
Summary of dermal armour in *Polacanthus* (text-fig. 10):

1. Presacral spines; Type A (both holotype and R9293), a bilateral row; Type B (isolated specimens, MIWG), a bilateral row(?); Type C (R9293), a bilateral fringe (?).
2. Sacral shield (both holotype and R9293) covering pelvis and sacrum.
3. Caudal plates; roof-like (holotype) or tall (R9293) both descending in size in a bilateral row down the tail; Hoplitosaur-like (R9293) (?)anterior plate only.
4. Ossicles; subtriangular or round between other elements (both specimens).

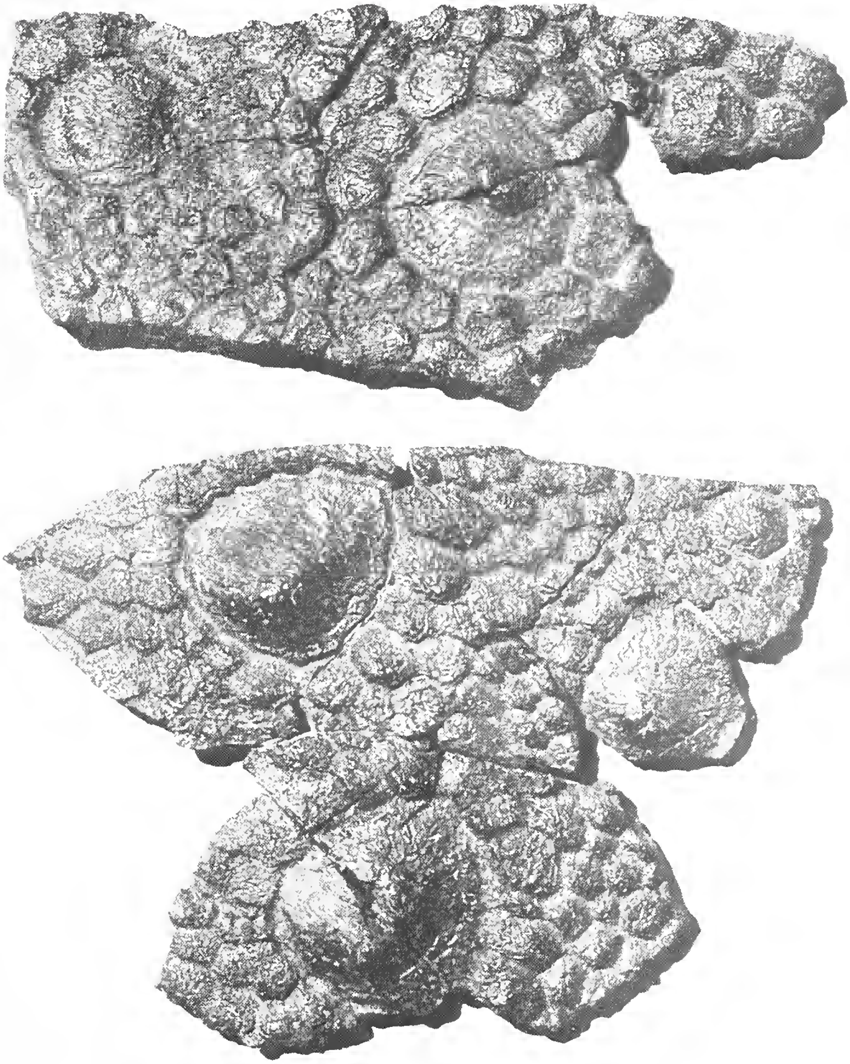
DISCUSSION

Preservation

The new specimen is considerably less complete and more disarticulated than the holotype, yet better preserved. The holotype is distorted by crushing throughout various sections, but crushing in the new specimen is limited.



TEXT-FIG. 8. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, dermal spines and plates. Top row: Type A presacral spines. Bottom row: Type C presacral spine, posterior spine and *Hoplitosaurus*-like caudal plate.



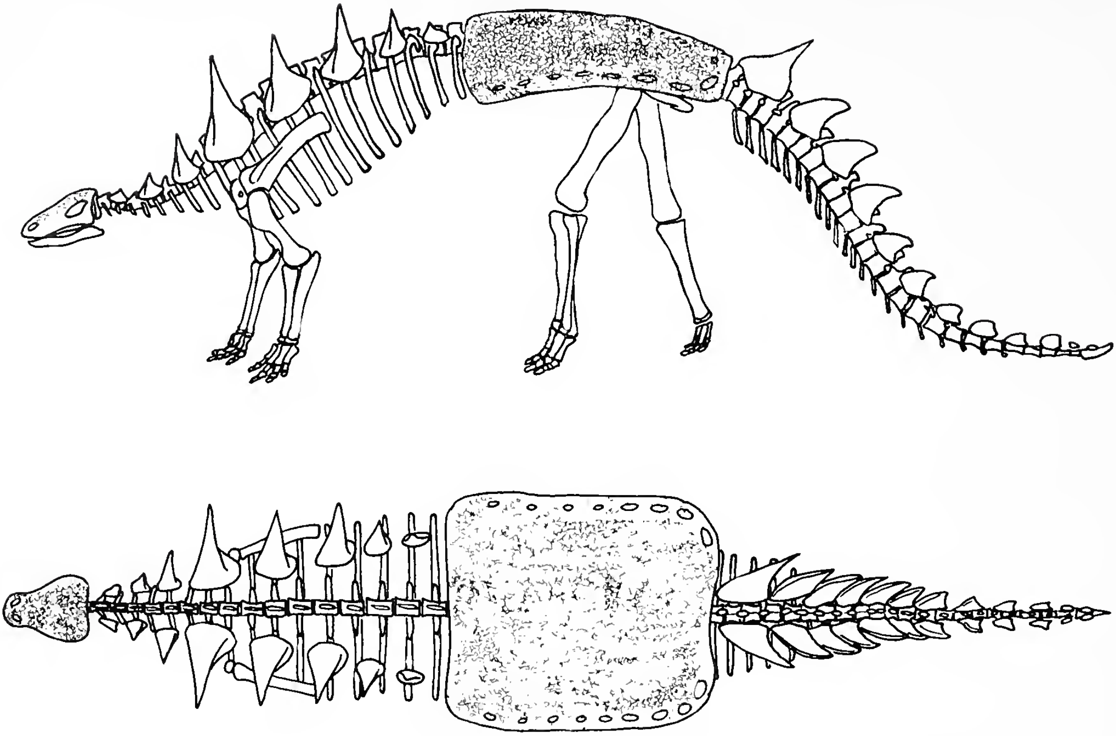
TEXT-FIG. 9. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, dermal armour, two sacral shield fragments, superior (dorsal) view.

Age

The sub-adult status of the new specimen is indicated by separated sutures within the skull fragments, the elements of the atlas vertebra are separated and the characteristic shape of the terminal phalanx.

Post-cranial skeleton

The skeleton of *Polacanthus* is very similar to *Stegosaurus* in many detailed and overall structures, suggesting a possible parallel evolution from a single source; the nodosaurs expanded more rapidly after the decline of the stegosaurs. The osteology of stegosaurs is now well known (Gilmore 1914; Ostrom and McIntosh 1966).



TEXT-FIG. 10. *Polacanthus foxi.* Lower Cretaceous, Isle of Wight. Restoration of skeleton, lateral and superior views. Based on BMNH R175 and R9293.

Post-cranial armour

The structure of Lower Cretaceous nodosaur dermal anatomy is always difficult because the material is usually isolated or disarticulated from endoskeletal remains. Nopcsa's interpretation (1905) of the arrangement of presacral spines remains valid. The angle between the spine base and dorsal keel suggests a position on the animal approximately 40° from the mid-line; a dorsolateral position. The presence of Type C spines in association with the new specimen possibly suggests a lateral fringe over the shoulder region (as in *Palaeoscincus* Matthew 1922) or perhaps a similar arrangement at the tail base. The lateral position of these spines is suggested by the unusual base shape and deep dermal insertions; the weight of the spine would not be directly above the body, creating a need to withstand gravitational forces.

The existence of Type B spines as purely isolated elements causes problems. They strongly suggest a similar position as Type A spines, but their absence in skeletons remains unexplained. No Type B spine can therefore be directly attributed to *Polacanthus* on the basis of known material. However, with absence of other nodosaurs identified from the Isle of Wight Wealden strata, tentative assignation of Type B spines to *Polacanthus* is made on the grounds of possible sexual diamorphism. The discovery of Type B spines in association with other skeletal material will resolve this.

Variation within the caudal plates occurs between the holotype and the new specimen. In the former, only the most anterior plate is of the type described in the new specimen, the others create diminishing roof-like structures along the tail, and flat rounded elements at the tail end. The most anterior plate of the new specimen is probably the Hoplitosaur-like plate with the central spine, unlike any other seen in the holotype. The significance of these two tail armours may be sexual or suggestive of species variation. If sexual diamorphism could be demonstrated in dermal structures, the caudal plate variation and robust (R9293) or slender (R175) presacral spines could be suspected as such in *Polacanthus*.

The Hoplitosaur-like plate may be indicative of closer affinities with the American Lakota genus *Hoplitosaurus* (USNM 4752). The caudal plate described by Delair (1982) (GM 981.45) enhances the *Polacanthus–Hoplitosaurus* link. The assignment of this specimen to *Polacanthus* is tentative on the grounds that a wider range of armour existed within this genus than previously known, and there is no evidence of another genus within the Lower Cretaceous of the Isle of Wight. The structure of the plate is similar to those of an early caudal position and the deep ventral keel is indicative of a lateral projection where deep dermal insertion is needed to overcome gravitational forces.

Histological examination of *Polacanthus* dermal armour has been carried out by Dr Cooper of Worthing. He sectioned both small presacral spines and sacral shield. He writes 'They show the same features of ossified collagen bundles which pass at random in all directions. This armour has clearly formed by transformation of dermal collagen directly into bone, i.e. by metaplasia of collagen as in a tendinous insertion into a long bone. There has then been subsequent formation of marrow spaces and a few Haversian systems in the armour. There is no evidence that any of the dermal elements formed from cartilage or had any form of muscle attachments. The fine channels on the surface of the armour could well be vascular but could also be to increase the surface area of the bone-keratin interface to provide a very rigid attachment for the keratin horn' (D. Cooper, pers. comm.).

The accepted function of dermal elements has always been their protective value against predators. Recently, some work has been conducted on heat dispersal properties of dermal plates in *Stegosaurus* which is well endowed with these elements (Farlow *et al.* 1976).

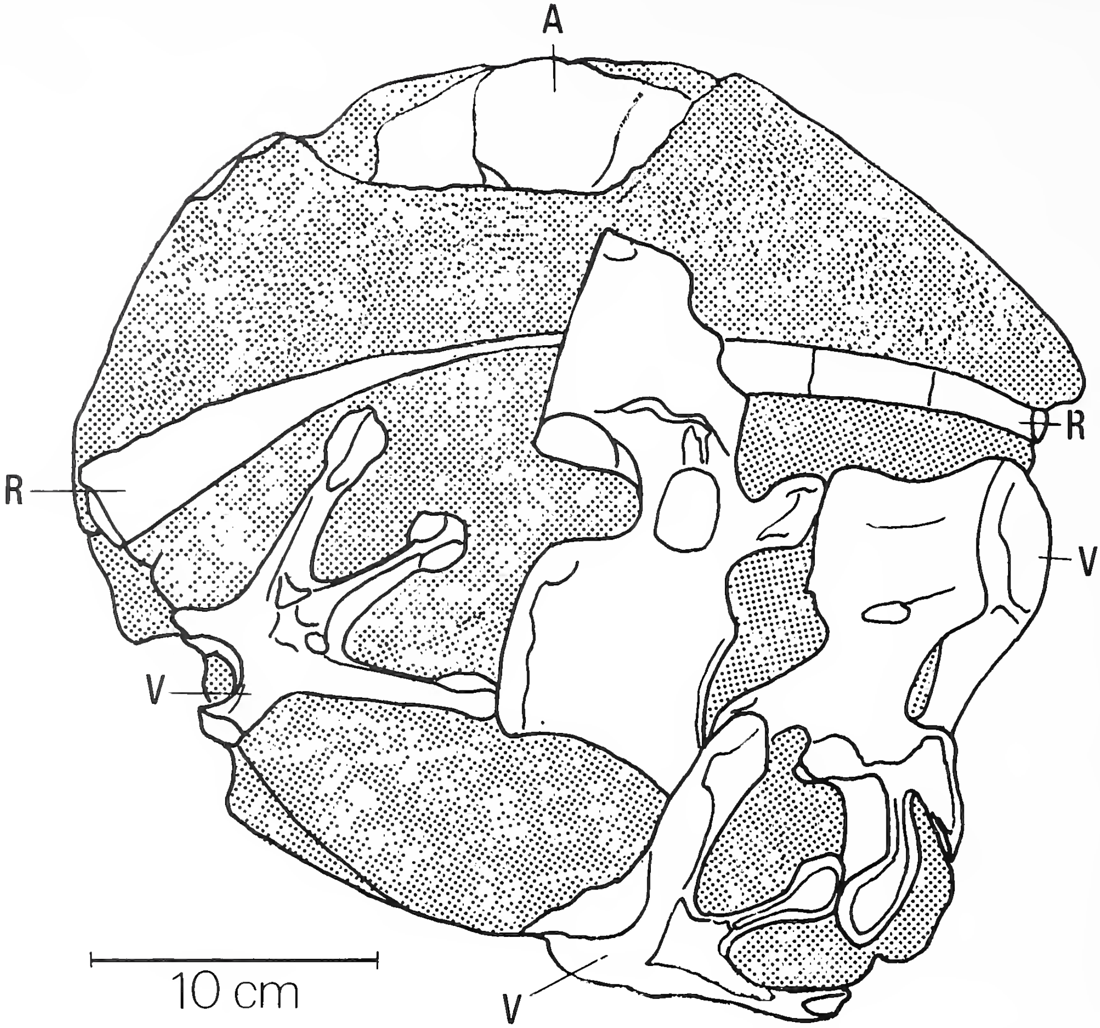
Dr Cooper writes 'I do not think now that one can compare *Polacanthus* armour with the plates of *Stegosaurus* which appear to have a heat radiating function, though similar heat exchange might incidentally occur in the larger lateral spines. However, their primary function is obviously armour protection' (D. Cooper, pers. comm.). A dual purpose may seem incompatible. Should such elements become damaged in a predator confrontation a high vascularity necessary for heat dispersal could predispose to severe blood loss. Selective and well-controlled vasoconstriction would be essential, as postulated for *Stegosaurus* (Farlow *et al.* 1976).

THE RELATIONSHIPS OF *POLACANTHUS*

1. Polacanthus *with* Hylaeosaurus

Coombs (1971) and others suggest that *Polacanthus* and *Hylaeosaurus* are possibly synonymous. *Hylaeosaurus* appears limited to the South East English mainland geology, which occupies most of the Wealden Series from Ryazanian to Barremian (Rawson *et al.* 1978). *Hylaeosaurus* has occurred in the 'Tilgate Forest' (Mantell 1841; Owen 1856) which probably refers to the Tilgate Stone (Gallois 1965), extensively quarried in Mantell's day, and the stata from which he obtained *Iguanodon*. It is also known as Cuckfield Stone (Rawson *et. al.* 1978), and divides the Grinstead Clay into Upper and Lower components (Hastings Beds). The palaeontological record is grossly incomplete, but the current evidence restricts *Hylaeosaurus* to the Upper Valanginian (Tunbridge Wells Sand/Grinstead Clay), which is unexposed on the Isle of Wight.

Polacanthus ranges from Wealden Marls to (?)Ferruginous Sands (Barremian to Lower Aptian) mostly from the Isle of Wight with one specimen from the mainland. This is a slab of grey matrix from the Greensands overlying the Lias at Charmouth, Dorset, and containing parts of four disarticulated but associated dorsal vertebrae, a rib section, and portions of flat dermal armour (sacral shield) (text-fig. 11). Between the ranges of the two genera a gap occurs in the Lower Weald Clay (Hauterivian). This may well be a collecting anomaly, or may have evolutionary significance. Currently it suggests a geological separation between the two genera, with *Hylaeosaurus* being considerably the older. The *Polacanthus* range correlation on the mainland (Upper Weald Clay to



TEXT-FIG. 11. *Polacanthus foxi*. Middle Cretaceous, Charmouth, Dorset. Dorsal vertebrae, rib and sacral shield armour in matrix.

Hythe Beds) does not seem to yield this genus. It is important to realize that the rarity of nodosaurids and the inadequacy of Wealden collecting (especially of the mainland) constitutes a vestige of material from which positive conclusions are difficult.

In *Hylaeosaurus* the series of long pointed spines appear to take a lateral fringe position over the shoulder region, similar to the arrangement in *Palaeoscincus* (Matthew 1922; Gilmore 1930). Post-mortem displacement is limited, as indicated by the largely articulated nature of the endoskeleton. The presacral spines of *Polacanthus* appear to be positioned more dorsolateral, and Types A or B are not found in the holotype or referred specimens of *Hylaeosaurus*. The shield of armour in *Polacanthus* is found as fragments on the Isle of Wight. No evidence exists of this shield in *Hylaeosaurus*, and no fragments of sacral shield are known from the mainland Wealden formation or referred to *Hylaeosaurus*. A similar situation occurs with ossicles, which are numerous, variable in shape, both large and small in *Polacanthus*, but remain rare in *Hylaeosaurus*, being round, small and button-like. Caudal plates also are scarce in *Hylaeosaurus*, a nearly complete tail (BMNH 3789) has the bases only preserved of what could be two caudal plates, whilst both *Polacanthus* discoveries are dominated with caudal armour. The current evidence suggests that *Hylaeosaurus* was a primitive nodosaurid existing earlier than *Polacanthus*, and having a different armour arrangement. At present, these two genera should be considered completely separate.

2. Polacanthus *with* Polacanthoides

Nopcsa's (1928) *Polacanthoides* can be dismissed on the grounds that:

a, two bones (BMNH R1106 and R1107) are from the Isle of Wight and not from 'Bolney, Sussex' as stated by Nopcsa (1928); *b*, they are casts, the originals returned to the Isle of Wight and are now lost, and therefore should not have been designated as holotypes; *c*, the scapula (BMNH 2584) from Bolney, Sussex is clearly associated with a tibia (BMNH 2615) (Mantell 1841, p. 143; Lydekker 1888), but Nopcsa (1928) does not mention this tibia.

The difference between the scapula of *Hylaeosaurus* and *Polacanthoides* is the acromion process; large and flange-like in *Polacanthoides*, thumb-like in *Hylaeosaurus* (Nopcsa 1928; Ostrom 1970). Ostrom upheld the distinction of *Polacanthoides* from *Hylaeosaurus*, but Coombs (1978) synonymizes the two genera, and finds the acromion size to be no grounds for the foundation of a genus. The name *Polacanthoides* (and thus *P. ponderosus*) is *nomen dubium*. The tibia and humerus (BMNH R1106, R1107) (Hulke 1874) are from the Isle of Wight, and may be *Polacanthus*. The tibia is very similar to *Polacanthus* (Ostrom 1970, p. 135), but no humerus is known of *Polacanthus* for comparison. On geological grounds these two bones may be referable to *Polacanthus* rather than *Hylaeosaurus*.

3. Polacanthus *with* Hoplitosaurus

The new *Polacanthus* has suggested close affinities with the American genus *Hoplitosaurus marshi* (Lucas 1902; USNM 4752). Both genera have flat and standing dermal elements. *Hoplitosaurus* armour is described by Gilmore (1914, pp. 118–121), and I refer to his numbering:

1, simple flattened, which correspond to variations within the ossicles of *Polacanthus*;
2, rounded ossicle-like, which correspond to ossicles of *Polacanthus*;
3, keeled, which correspond to ossicle variation within *Polacanthus*;
4, triangular, plate-like, which correspond to caudal plates of *Polacanthus*, in particular R9293;
5, spined, of which he recognizes the following sub-types:

a, 'scutes', which correspond with the Hoplitosaur-like plate of R9293 (Gilmore 1914, pl. 28). Gilmore misinterpreted Nopcsa (1905) by thinking such elements were placed anterior to the sacral shield. In fact, no elements of this kind exist in the holotype (R175), the first European plate of this type occurs in R9293. Some presacral spines of R175 have a similar central spine, but differ in having broader, plain bases. It is easy to see how this plate type has developed from the presacral spines but has caudal plate qualities. The position is therefore most likely to be the first plate, immediately behind the sacral shield. It would seem that R175 never did possess such a plate, whilst R9293 and USNM 4752 did. Whether this is an indication of sexual variation, along with the difference in caudal plates between R175 and R9293, is unknown.

b, dermal elements with grooved posterior borders, of which only one English example exists, GM 981.45 from the Weald of the Isle of Wight (Delair 1982). The presence of grooved plates in *Hoplitosaurus* (Gilmore 1914) suggests the possible inclusion of the English plate within the genus *Polacanthus*. The deep ventral keel is its only unique character, suggestive of deep dermal insertion to overcome gravity.

c, compressed spines with heavy, massive, expanded bases, comparable to the presacral (Type A) spines of *Polacanthus*.

Hoplitosaurus and *Polacanthus* dermal armour compares well. The absence of a sacral shield in *Hoplitosaurus* may be the only objection, although reference is made to this under (2) above (in Gilmore 1914, p. 118). The two could be found synonymous, in which case *Polacanthus* (Huxley

1867) takes priority over *Hoplitosaurus* (Lucas 1902). If the sacral shield was considered sufficient grounds to allow species differentiation then *Polacanthus marshi*, new combination, could be reserved for USNM 4752. This synonymy would extend the geographical range of *Polacanthus* outside England to the American Lakota Formation as suggested for other Isle of Wight genera, e.g. *Hypsilophodon wielandi* (Galton and Jensen 1979).

CONCLUSIONS

Polacanthoides ponderosus is not valid. *Polacanthus* and *Hylaeosaurus* are separate genera. *Hoplitosaurus* is probably a subjective junior synonym of *Polacanthus*, possibly extending the range of *Polacanthus* into America. If species differentiation was shown between the two holotypes, *P. marshi*, new combination is proposed for USNM 4752.

Acknowledgements. I thank the following for allowing me to examine specimens in their care; Dr Angela Milner and Sandra Chapman, British Museum (Natural History); Mr Steven Hutt (Museum of Isle of Wight, Geology); Dr David Price (Sedgwick Museum); Mr David Kemp (Gosport Museum). My gratitude is also extended to those persons who have helped and advised on the new specimen; Dr Peter Galton (Bridgeport University); Dr David Norman (Oxford University); Dr Beverly Halstead (Reading University); Dr Alan Insole (Museum of Isle of Wight, Geology); Dr Dale Russell (National Museums of Canada); Mr Richard Ford (Yarmouth, Isle of Wight); Dr David Cooper (Worthing, Sussex). Finally, my gratitude goes to all those persons who have helped with the site excavation, preparation of the fossils, and production of this paper; Mr Terence Hunter; Mrs Jessica Blows.

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APPENDIX I

Specimens of Polacanthus foxi *Hulke 1881*

Holotype: BMNH R175, partial skeleton; Referred specimens: MIWG 37, seven ossicles, one tail plate base; MIWG 4222, one ossicle (Poole Collection); MIWG 1983, one ossicle, one sacral shield fragment; MIWG 5144, caudal vertebra; MIWG 5307, dorsal spine (collected April 1983); MIWG 5145, caudal plate fragment; MIWG 5186, six plate fragments, one ossicle; MIWG 5187, two ossicles; MIWG 1191*a*, dorsal spine; MIWG 5188, dorsal centrum; CAMSM B53595, dermal ossicle; CAMSM B53594, small dermal ossicle; CAMSM B53590, dermal ossicle; CAMSM B53588, dermal ossicle; CAMSM B53589, dermal ossicle; CAMSM B53591, dermal ossicle; CAMSM 53597, dermal ossicle; CAMSM B53371, axis vertebra; CAMSM B53372, unidentified bone; CAMSM B53353, large dermal ossicle; CAMSM B53354, flat ossicle; CAMSM B53358, flat ossicle, CAMSM B53357, ossicle; CAMSM B53355, ossicle; CAMSM B53356, ossicle; CAMSM B53596, dermal ossicle; CAMSM B53587, dorsal vertebra; CAMSM B53593, dermal ossicle; BMNH R4952, caudal vertebra (Gunyon Collection 1923); BMNH 36515–36517, two dermal spines (Mantell Collection); BMNH 40458, dermal ossicle; BMNH 37713–37714, two dermal ossicles (Saul Collection 1863); BMNH R643, dermal ossicle (Lee Collection 1885); BMNH R1876, dermal plate (Beckles Collection); BMNH 34533, dermal ossicle (Backhouse Collection); BMNH R1875, dermal spine (Beckles Collection); BMNH R2527, dorsal vertebra (Hulke Collection 1869); BMNH 39556, rib head; BMNH R202, two ossicles; BMNH R202–R202(A), four dermal spines (Fox Collection); BMNH R203, two dermal spines (Fox Collection); BMNH R1926, ilium fragment with sacral armour (type of *P. becklesi*) (Beckles Collection); BMNH R4134, vertebral process and rib head; BMNH R9905, sacrum; BMNH R9293, partial skeleton with dermal armour (Blows Collection 1979) and cervical vertebra; GM 981.45, dermal plate (Kemp Collection); block containing dorsal vertebrae, rib, and dermal armour (private collection); spine and caudal vertebra (Ford Collection).

APPENDIX II

Table of measurements in millimetres:

i. Cervical vertebrae

	SMES B53371	BMNH R9293
Length of centrum	54	50
Width of anterior surface	64	65
Height of anterior surface	40	43
Total height of vertebra	80	107
Greatest width of neural canal	25	23
Greatest height of neural canal	25	30

ii. Dorsal vertebrae

		Length of centrum	Height of centrum	Width of centrum		Height of neural canal		Overall height
				Anterior	Posterior	Anterior	Posterior	
Holotype R175	C12	62	50	—	61	30	25	130+
	C14	77	51	53	52	23	25	110+
	C16	—	—	—	—	—	—	—
	C18	—	—	—	58	—	48	—
	C19	80	50	56	52	—	—	—
BMNH R9293	1	70	53	61	61	25	30	—
	2	—	56	63	—	25	—	130+
	3	75	59	63	56+	22	27	150+
	4	73	57	63	65	22	31	135+
BMNH 2527		84	73	82	—	23	—	212+
SMES B53587		78	60	68	69	23	24	144+
MIWG 5188		70	60	71	70	—	—	—
Charmouth specimen		70	65	—	—	—	—	170

iii. Sacral vertebrae

	R175	R9293	BMNH R9905
Length of five sacral centra	350	365	360
Length of five presacral centra	410	—	—
Width of posterior articular surface (S5)	—	78	—
Height of posterior articular surface (S5)	—	50	—
Maximum width of neural canal (S2–S3 level)	—	78	—
Maximum height of neural canal (S2–S3 level)	—	60	—
Maximum width between (R) and (L) sacro-iliac joints	418	—	425

iv. Caudal vertebrae

	R175		R9293		R9252	MIWG 5144
	1st	2nd	1st	2nd		
Overall height	—	165	146	155	107+	—
Length of centrum	60	50	60	55	40	45
Width of centrum	85	90	83	82	52	55
Height of centrum	40	60	58	60	52	60

v. Terminal phalanges

	R175	R9293
Total length	82	60+
Greatest width	60	35
Height of articular surface	20	19
Width of articular surface	50	29

vi. Measurements of spines (Type A)

	Total height	Length of base	Width of base
Holotype, BMNH R127			
R2 (f6), large spine	325+	205	100
R4 (f4)	305+	230	90
L1 (g7), medium spine	322	198	115
L2 (g6), large spine	392+	210	110
R3 (f5)	340+	215	111
R5 (f3), medium spine	175+	190	110
R4 (f1), smallest spine	90	140	80
BMNH R9293			
Largest spine, left side, shoulder	322 approx.	190	148
Large spine base, left side	—	197	95
Medium spine, right side	215 approx.	140	95
Smallest spine, anterior to pelvis	90	117	74

vii. Measurements of spines (Type B)

	MIWG 1191*a*	MIWG 5307
Overall height	—	260
Length of base (along keel)	—	170
Width of base (opposite keel)	—	130

viii. Measurements of spines (Type C)

	BMNH R9293	
Overall height	207+	195+
Length of base (along keel)	200	120
Width of base (opposite keel)	130	50

ix. Measurements of plates

	Overall height	Length of base	Greatest width of base
Holotype, R175			
Early caudal, BR1	200+	—	—
Middle caudal, BL3	110	192	—
Late caudal, BR6	70	126	—
BMNH R9293			
Spined plate, left	280	238	58
Early caudal, left	245+	218	42
Early caudal, left	230	—	45
Early caudal, left	210	160	40
Early caudal, right	200+	200	45
Late caudal, right			
GM 981.45			
Early caudal(?)	330	160	60

x. Measurements of modified ossicles

	SMES	MIWG
Maximum width across base	87	77
Length of base parallel to keel	70	67
Height of ossicle	38	37

xi. Bilateral bones of unknown origin

	B53372	R9293
Length (overall)	40	39
Height (overall)	30	29
Length of base	35	34
Width of base	20	20

ENGLISH EOCENE CRUSTACEA (LOBSTERS AND STOMATOPOD)

by W. J. QUAYLE

ABSTRACT. The Eocene lobsters from the London Clay, Bracklesham and Barton Beds are revised. Nine species of lobster are represented, three new, *Homarus morrisi*, *Hoploparia wardi*, and *H. victoriae*, belonging to six genera. *Trachysoma scabrum* Bell is placed in *Glyphea*. The remaining species, *H. gammaroides* M'Coy, *Archaeocarabus bowerbanki* M'Coy, *Linuparus eocenicus* Woods, *L. scyllariformis* (Bell), and *Scyllarides tuberculatus* (König), are redescribed with further information. The stomatopod *Squilla wetherelli* Woodward is redescribed and placed in *Bathysquilla*.

IN 1849 M'Coy described three new species of lobster from the London Clay, *Hoploparia gammaroides*, *H. belli*, and *Archaeocarabus bowerbanki*. In 1858 Bell described *Trachysoma scabrum*, new genus and species, and *Thenops scyllariformis*, new species, and redescribed *Scyllaridia koenigii*, first described by König (1825), as *Cancer* (*Scyllarus*?) *tuberculatus*; he also made additions to M'Coy's descriptions of *H. gammaroides*, *H. belli*, and *A. bowerbanki*. All of Bell's specimens came from the London Clay. Woods in his monograph of the Fossil Macrurous Crustacea of England (1925–1931) described *Linuparus eocenicus*, a new species from the London Clay, and redescribed *H. gammaroides*, *A. bowerbanki*, *L. scyllariformis*, and *Scyllarides koenigii*; *H. belli* was relegated to synonymy. In a footnote on p. 94 he mentioned a large specimen of *Homarus* sp. from the Barton Beds of Hampshire, first mentioned by Gardner *et al.* (1888). On p. 73 he mentioned but did not describe the only known specimen of *Trachysoma scabrum* and figured it on pl. 22, fig. 1. Cooper (1974) listed the known records of the English Palaeogene decapod Crustacea up to that time.

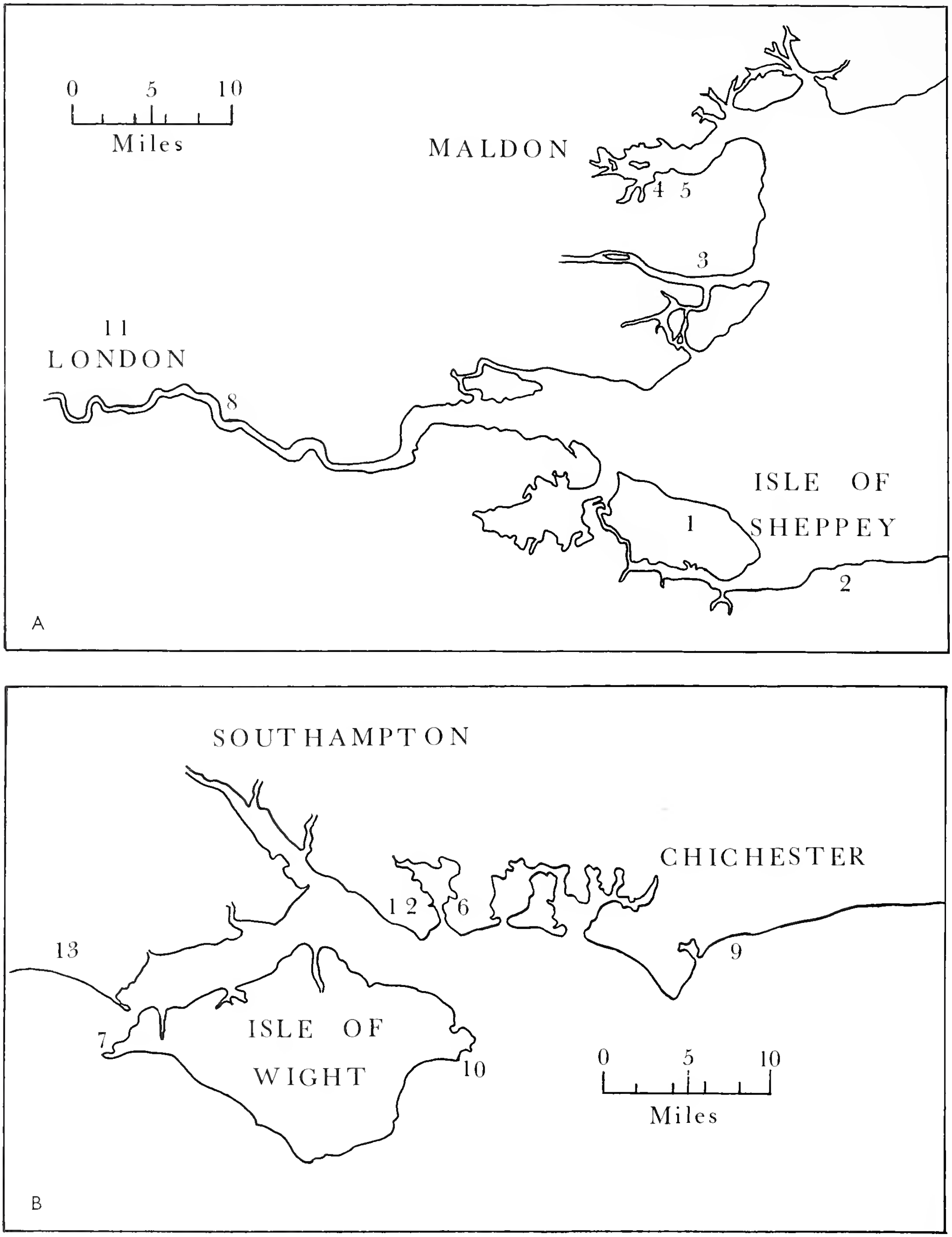
Further collecting from some of the older sites, with some new ones, has added considerably to our knowledge of the English Eocene macrurous Crustacea.

STRATIGRAPHY

Some of the localities mentioned by the earlier authors are no longer available, though on rare occasions temporary exposures occur through road works and building. The following is a list of localities from which the specimens used in this work were obtained, either by the old collectors such as Bowerbank, Wetherell, Meyer, and Caleb Evans, or in recent years.

1. Isle of Sheppey, Kent; cliff and foreshore exposures, London Clay, Divisions C, D, and E (King 1981, 1984). Grid reference TQ 955 738–TR 024 717.
2. Herne Bay, Kent; Beltinge cliff, London Clay, Divisions A2, A3, and lower half of B (King 1981), TR 195 685. Cliffs are now landscaped, leaving a foreshore exposure of A2. Thanet Beds, TR 2051 6881 and TR 2046 6875, Units E and G (Ward 1979).
3. Burnham on Crouch, Essex; tidal river, with foreshore exposures, London Clay, Division D (King 1981), TQ 920 968–922 966.
4. Maylandsea, Essex (George and Vincent 1982, pp. 39–41); tidal river with foreshore exposures, London Clay, lower part of Division B (King 1981), TL 908 034–908 037.
5. Steeple, Essex (George and Vincent 1977, pp. 105–107); tidal river with foreshore exposures, London Clay, lower part of Division B (King 1981), TL 916 043.

[Palaeontology, Vol. 30, Part 3, 1987, pp. 581–612, pls. 64–67.]



TEXT-FIG. 1. Localities in A, the London Basin and B, the Hampshire Basin (see text for key to numbers).

6. Portsmouth Docks, Hampshire; former temporary exposure, 'Dockyard Extension Works'. The crustacean fauna (Woodward 1871, 1873) is similar to that of Whitecliff Bay. All the Crustacea came from the London Clay, the Dentalium Bed of Meyer (1871), in the upper part of Division B2 (King 1981).

7. Alum Bay, Isle of Wight, Hampshire; cliff exposure, London Clay, Divisions A, B, C, and D (King 1981), SZ 306 853.

8. Aveley, large quarries south-west of Aveley, Essex; London Clay, Divisions A, B, and C (King 1981), TQ 557 805 and 555 809. Working has now ceased. Material collected by R. J. Kirby is in the Oxford University Museum.

9. Bognor Regis, Sussex; foreshore exposure, London Clay, Divisions A to C, SZ 942 990–895 970.

10. Whitecliff Bay, Isle of Wight, Hampshire; cliff and foreshore exposures, Bracklesham Group, SZ 640 861. Crustacea found in a line of iron stained phosphatic nodules in the Wittering Division (Fishers Bed 1), approximately 7·5 m above the base of the Bracklesham Group. Some 75 % of the nodules collected *in situ* and others collected loose from the beach (probably from this horizon) had pieces or specimens of crustaceans. *Linuparus* is common, in association with *H. morrisi* sp. nov. A nodule in the Sedgwick Museum, C69620, collected by H. Keeping in 1887, and labelled Lower Bagshot Beds, is thought to have come from this horizon.

11. Various London Clay localities around London, now no longer available, i.e. Whetstone; Chalk Farm, Divisions B and C; Highgate, Division E (King 1981), and various motorway construction sites around London.

12. Lee-on-the-Solent, Hampshire; foreshore exposure, Elmore Formation (Kemp *et al.* 1979), Huntingbridge Division, Bracklesham Group, SU 569 500.

13. Barton Beds, Christchurch Bay; cliff with occasional foreshore exposures; stratigraphic horizons as in Burton (1929), SZ 199 928–261 923.

Repositories. Specimens prefixed BM are in the Palaeontological Department, British Museum (Natural History); SM, Sedgwick Museum, Cambridge; OUM, Oxford University Museum, Oxford; PE, Passmore Edwards Museum, London; JSQ, W. J. and S. Quayle Collection; JC, John Cooper Collection.

SYSTEMATIC PALAEONTOLOGY

Infraorder ASTACIDEA Latreille, 1803
Family NEPHROPIDAE Dana, 1852
Subfamily HOMARINAE Huxley, 1879
Genus HOMARUS Weber, 1795

Type species. Cancer gammarus Linné, 1758, Recent, European, by subsequent designation (Rathbun 1904, p. 170).

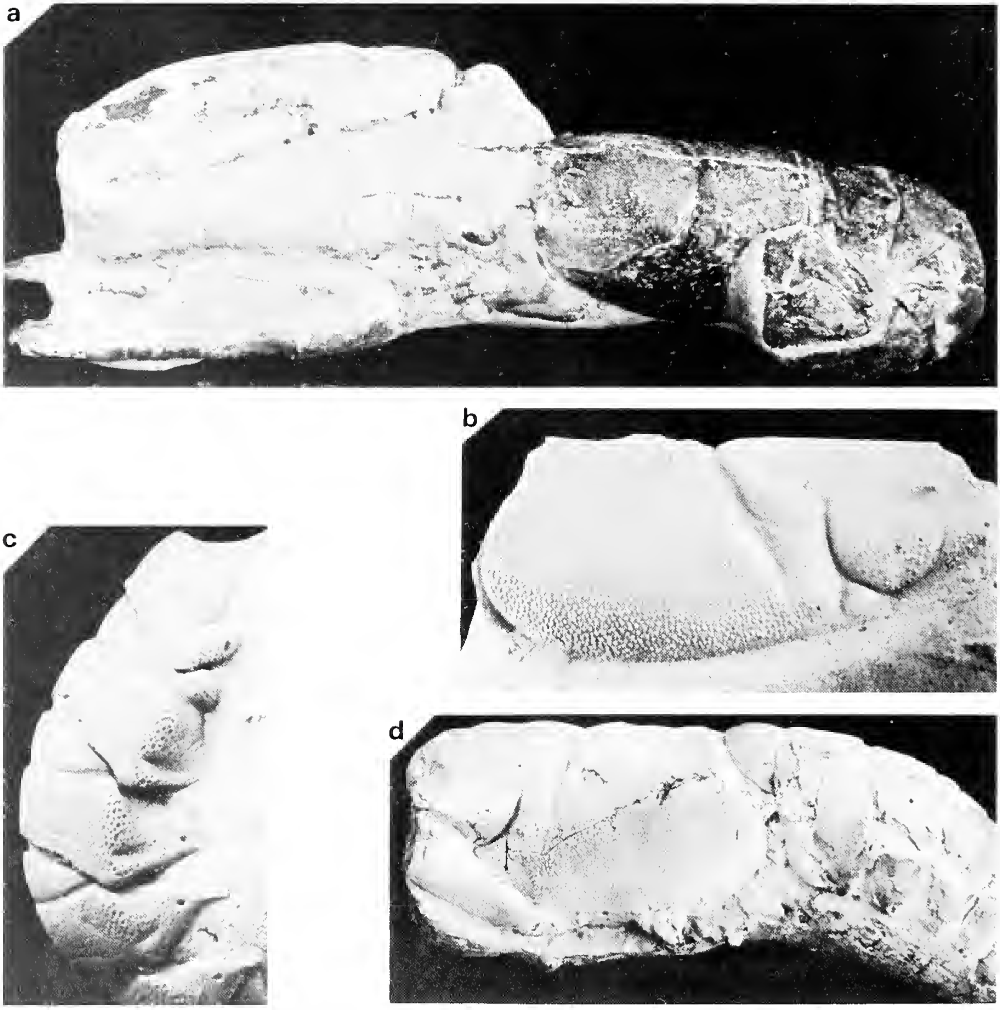
Diagnosis. Rostrum rather short and spiny, carapace without ridges or spines behind the suborbital spine, cervical groove clearly developed only below gastro-orbital groove, postcervical groove long and smoothly curved, connecting lowest part of cervical with posterior part of branchiocardiac groove; chelae stout, heterochelous.

Range. Cretaceous–Recent.

Discussion. Woods (1931) could find no generic distinction between the fossil forms of *Hoploparia* and the living species of *Homarus*. Stenzel (1945, p. 427) stated that eleven species of *Homarus* had been described from the Cretaceous of the United States east of the Rockies. These eleven are largely made up of specimens identified by Rathbun (1926*b*, 1935) as *Hoploparia*. Stenzel also described two new species, *Homarus brittonestris* and *H. davisi*. These are similar to the living species of *Homarus* in the nature of the carapace grooves.

Glaessner (1969) whilst noting that 'the distinction between some of these species is difficult and disputed' maintained that a number of characters show that the genera are distinct. In *Homarus*: cervical groove clearly developed only below the gastro-orbital groove; postcervical groove long and curved, connecting the lowest part of the cervical groove with the posterior part of the branchio-cardiac groove; carapace without ridges or spines behind the suborbital spine. In *Hoploparia*: cervical groove developed above and below the gastro-orbital groove; postcervical distinct and connected with the cervical groove through a semicircle; carapace can have ridges or spines behind the suborbital spine.

There appear to be two distinct patterns of grooves. The first compares with the living forms of *Homarus* as depicted by Glaessner (1969, R461, fig. 1*b*) and Holthuis (1974, p. 816, fig. 24). The second is as for the fossil species of *Hoploparia* (text-fig. 4A).



TEXT-FIG. 2. *a*, *Homarus morrisi* sp. nov., London Clay, Soft Rock, Bognor Regis, holotype, BM In.63392, ×0·8. *b*, *c*, *Hoploparia gammaroides* M'Coy, London Clay, Isle of Sheppey, lectotype, BM 46366. *b*, carapace, ×2. *c*, somites one to five, ×2. *d*, *H. wardi* sp. nov., London Clay, Isle of Sheppey, holotype, SM C19314, ×1·1.

Homarus morrisi sp. nov.

Plate 64, figs. 5 and 7; text-figs. 2*a* and 3

1849 *Hoploparia gammaroides* M'Coy, p. 177.
1850 *Astacus belli* (M'Coy); Dixon, pp. 114, 222, pl. 15, figs. 3 and 4.
1858 *Hoploparia gammaroides* M'Coy; Bell, p. 38, pl. 8, figs. 5 and 6?; pl. 9.
1980 *Hoploparia gammaroides* M'Coy; Morris, p. 9.

Derivation of name. After Mr S. F. Morris, Department of Palaeontology, British Museum (Natural History).

Types. Holotype: BM In.63392 (text-fig. 2*a*), collected by B. A. Williams (Venables 1971), London Clay, Soft Rock, Bognor Regis. Paratypes: BM In.35299, In.48223, In.48226, and In.48227 collected by E. M. Venables; BM In.63364 (Pl. 64, fig. 5), In.63365 (Pl. 64, fig. 7), collected by D. Bone; all from Soft Rock, London Clay, Bognor Regis, Sussex.

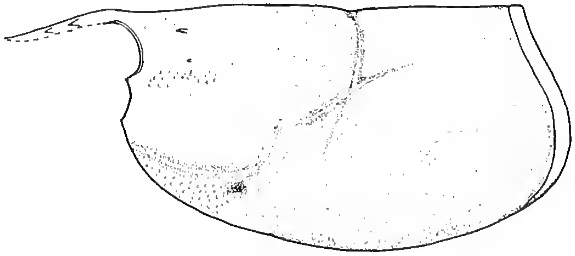
Diagnosis. A *Homarus* with fine grooves, with two rows of spines on the inner edge of the palm and a single spine on the outer margin at the base of the dactylus; carapace with fine pits.

Horizon and locality. London Clay: Soft Rock and the Beetle Bed, Bognor Regis; Isle of Sheppey: near Copenhagen House, London; Bracklesham Group, Bracklesham Bay, Selsey and Whitecliff Bay, Isle of Wight; Barton Beds, Christchurch Bay.

Description. Cephalothorax. Rostrum dentate, slightly less than half the length of the carapace; carapace with a postorbital spine and directly below this, a suborbital spine. The cervical groove starts almost level with the antennal base and drops down, curving to join the antennal groove. This runs almost straight to the front margin. The postcervical groove starts on the median line, slightly more than half the carapace length from the base of the rostrum. It drops almost straight down, then curves towards the front at a slight downwards angle and dies out. The postcervical is joined at the bend by the faint branchiocardiac groove running away towards the rear, another fine groove drops away at this point and runs parallel with the cervical groove for a short distance before dying out. Carapace with fine pitting. (Refer to text-fig. 4A for position of carapace grooves.)

Abdomen. On the second abdominal somite the pleuron is quadrate, the anterior angle rounded, and the posterior angle with a posterior pointing spine. Surfaces are smooth with fine pores; there is a large pit between the lateral and posterior margins before they join. Somites three to five have a transverse groove on the anterior third, extending to the boundary of the tergum at the anterior margin; pleura are triangular, falcate, with an acute posterior pointed spine, their surfaces smooth with fine pits. The telson is approximately as broad as long, its longitudinal margins with a fine beading; on the inner edge of the beading there is a smooth groove, then a ridge.

Appendages. On the large first cheliped the width of the palm is from three quarters to equal to the length; the inside face of the palm is flatly convex, the outer face half round; the inner edge is flattened along its length and the margin is armed with two rows of alternating teeth, five on the outer, four on the inner, the last on the joint margin; the outer margin is half round; the palm is smooth with fine pits of various sizes. A flat surface develops on the outer edge, extending to the full width at the base of the fixed finger, continuing parallel with the margin and becoming more noticeable on the outer face; it is about a third or more of the width of the fixed finger. The inner margin of the fixed finger is wide, almost flat, and armed with depressed oval teeth of varying size that lie close together. From the base of the fixed finger are three or four transverse



TEXT-FIG. 3. *Homarus morrisi* sp. nov., reconstruction of carapace (× 1·2).

oval teeth of approximately the same size though their height gradually increases. These are followed by a larger oval raised tooth (greater length along the median line) and two much smaller oval teeth. The dactylus is about as long as the palm, its outer margin half round with a spine on the outer edge by the base. The outer surface is lightly rounded with a spine by the joint, paired to one on the palm. The inner surface is nearly flat with a similar spine to that on the outer surface. The prehensile edge is armed with one large oval tooth followed by three others diminishing in size towards the front, then a large rounded one followed by several smaller rounded ones.

On the small claw the palm is nearly as wide as long, the top and bottom surfaces convex. The inner margin has nine spines in two rows, the last on the margin of the joint with the dactylus. The outer margin is slightly flattened. The surfaces are smooth with fine pores, except for a spine on each surface at the joint with the dactylus. Only the base of the dactylus was preserved, oval in cross-section with a single spine on the outer margin at the joint, armed with fine spiniform teeth on the prehensile edge.

Discussion. Bell (1858, p. 39) comparing BM 59136 (pl. 9) with *H. belli* remarked 'that it more nearly approximates the common lobster and would probably be a distinct species'. It is now considered that this specimen and a large majority of the lobsters from the Isle of Sheppey are *Homarus*. The larger lobsters from this locality though well preserved are usually found in a crushed or flattened state, leading to distortion of the grooves. This makes identification difficult; where claws are preserved a spine can usually be found at the base, on the outer edge of the dactylus.

As well as the London Clay sites, the Barton Beds of Christchurch Bay have produced several large specimens of *Homarus* since the first recorded specimen (SM C7742) was collected by H. Keeping (Gardner *et al.* 1888). These specimens are thought to have originated from Horizons A3 and F. Due to the crushed state of the carapace where present, identification is difficult; so far only small pieces of the prehensile edges of the claws have been preserved; the pieces that do exist, though much larger, are apparently *H. morrisi.*

The Thanet Beds of Herne Bay have also produced specimens of *Homarus*, though only one has the remains of the prehensile edge and parts of the claws. These, together with the specimens from the Bracklesham Group of Bracklesham and Whitecliff Bay, are also apparently *H. morrisi.* It is appropriate to include these specimens with *H. morrisi* until better preserved material can be found to prove or disprove this statement. The Barton material known to date is: SM C7742; BM In.60905; piece of limb, JC Collection; BA/103–106, JSQ Collection. Herne Bay material: specimen collected D. Kemp, JC Collection. Bracklesham Bay material: BM In.29208 collected E. Williams. Whitecliff Bay material: W88, 117, and 123, JSQ Collection.

H. morrisi is similar to *H. gammarus* (Linné) and *H. americanus* Milne-Edwards, living members of the genus from Europe and America. It has a similar flattened edge on the outer margin of the propodus; the rostrum is dentate and downturned and the carapace grooves and spines are in

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EXPLANATION OF PLATE 64

Figs. 1 and 2. A small specimen of the Recent lobster *Homarus gammarus* (Linnaeus). 1, lateral view of the carapace, × 1·5. 2, claw showing spines on the outer margin of the dactylus and palm, × 1·75.

Figs. 5 and 7. *H. morrisi* sp. nov., London Clay, Bognor Regis. 5, crusher claw, BM In.63364, × 1·3. 7, fine claw, showing arrangement of spines on the outer margin of the dactylus and palm, BM In.63365, × 1·2.

Figs. 3, 4, 6, 10. *Hoploparia gammaroides* M'Coy, London Clay. 3, crusher claw, OUM L558, Aveley, × 1. 4, third maxilliped, BM In.63356, Maylandsea, × 2·2. 6, lateral view of carapace, BM In.63354, Aveley, × 1·5. 10, arrangement of spines (only one of the two rows is visible) on the palm; the base of the dactylus is smooth, OUM L563, Aveley, × 1·7.

Figs. 8 and 9. *H. victoriae* sp. nov., Bracklesham Group, Lee-on-the-Solent. 8, lateral view of carapace, BM In.63357, × 1·8. 9, prehensile edge of fixed finger crusher claw, showing the arrangement of the teeth (base only preserved), BM In.63363, × 2·5.

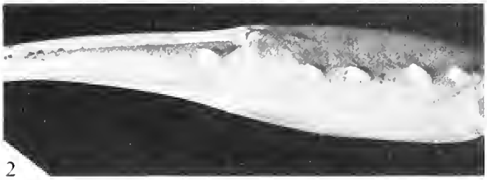
Fig. 11. *H. wardi* sp. nov., London Clay, Chalk Farm, lateral view, SM C19318, × 1·25.

Figs. 12–14. *Glyphea scabra* (Bell), London Clay. 12, lateral view of the holotype, BM 59146, Chalk Farm, × 2. 13 and 14, left and right lateral views of BM In.63366, Aveley, × 2·3.

Specimens in figs. 3, 5–8, 11, 13, and 14 have been whitened with ammonium chloride.

PLATE 64


1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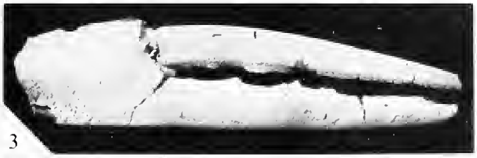
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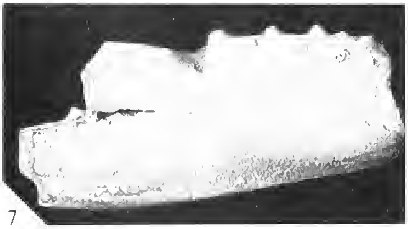
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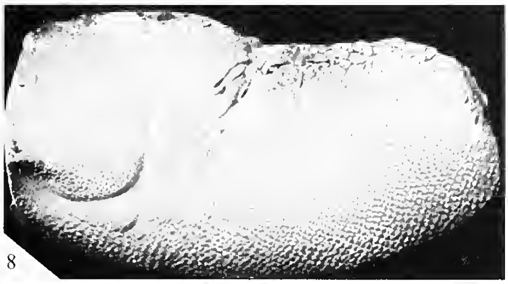
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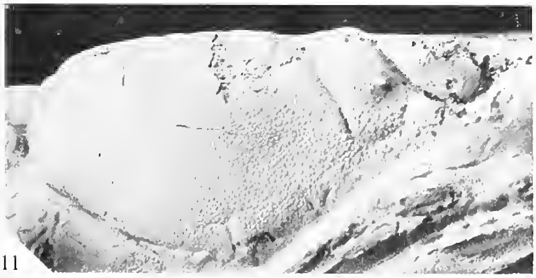
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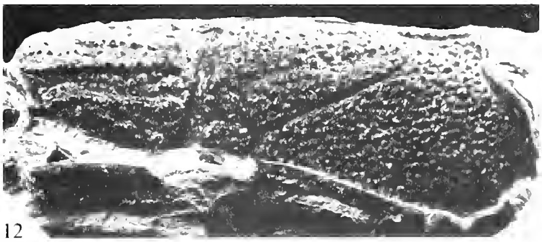
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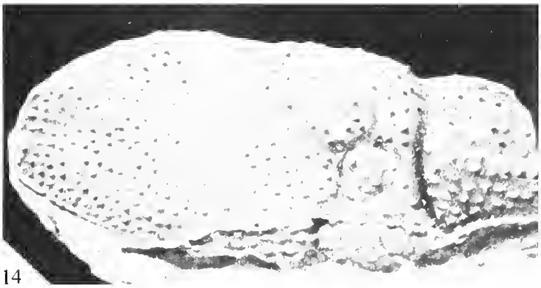
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QUAYLE, *Homarus*, *Hoploparia*, *Glyphea* similar positions. It differs in that the inner margin of the palm has a double row of spines with the last at the joint margin. *H. gammarus* and *H. americanus* have a single row with the last spine before the joint margin.

H. davisi Stenzel, 1945 from the Cretaceous, Dallas Co., Texas, has a dentate carina running back from the antennal spine and a line of tubercles on the posterior edge of the postcervical groove; *H. morrisi* has neither of these characters. *H. brittonestris* Stenzel, 1945, also from the Cretaceous, Dallas Co., Texas, has a dentate rostrum and an antennal ridge followed by a small spine. The carapace is covered with tubercles, the largest over the gastric region and on top of the ridges in the vicinity of the rostrum. *H. morrisi* differs from *H. brittonestris* in having fewer rostral spines, no antennal ridge, and a finely pitted carapace.

H. hakelensis (Fraas) from the Cenomanian shale, Mount Lebanon, Syria, was provisionally placed in this genus by Glaessner (1945, p. 702). Due to the crushed state of these specimens it is difficult to make any valid comparison.

Genus HOPLOPARIA M‘Coy, 1849

Type species. Hoploparia longimana (Sowerby), 1826, Upper Greensand, Lyme Regis, by subsequent designation (Rathbun 1926*a*, p. 129).

Diagnosis. Rostrum dentate, cervical groove clearly developed above and below the gastro-orbital groove, postcervical groove distinct, connecting with cervical groove through a semicircle; chelae strong, long, heterochelous.

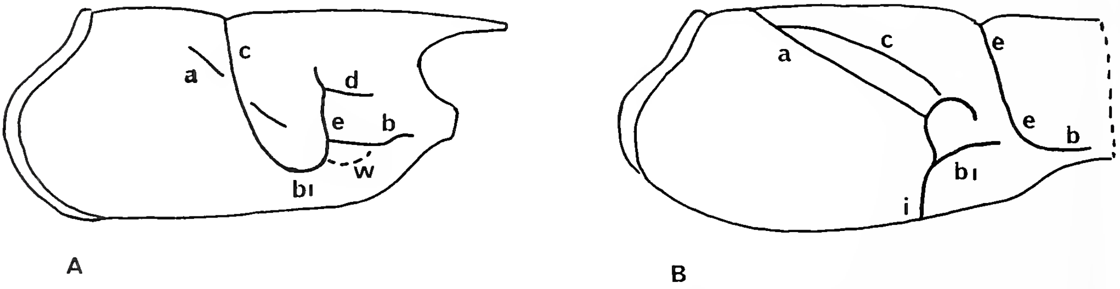
Range. Lower Cretaceous–Middle Eocene.

Hoploparia gammaroides M‘Coy, 1849

Plate 64, figs. 3, 4, 6, 10; text-fig. 2*b*, *c*

1849 *Hoploparia gammaroides* M‘Coy, p. 177.
1849 *Hoploparia belli* M‘Coy, p. 178.
1858 *Hoploparia gammaroides* M‘Coy; Bell, p. 38.
1858 *Hoploparia belli* M‘Coy; Bell, p. 39, pl. 10, figs. 1–3, 5–8.
1929 *Hoploparia gammaroides* M‘Coy; Glaessner, p. 219 (see for intermediate synonymy).
1931 *Homarus gammaroides* (M‘Coy); Woods, p. 93, pl. 26, figs. 5 and 6; pl. 27, figs. 1, 2, 4.
1974 *Hoploparia gammaroides* M‘Coy; Cooper, p. 85.
1980 *Hoploparia gammaroides* M‘Coy; Morris, p. 9.

Types. M‘Coy based his description on specimens at the University of Cambridge and the Bowerbank Collection, which should now be in the Sedgwick Museum and the British Museum (Natural History). No figure was given or reference made to identifiable specimens. In order to select a type for *H. gammaroides*



TEXT-FIG. 4. Carapace grooves. A, *Hoploparia* sp. (× 1·3). B, *Glyphea scabra* (Bell) (× 2·0). Identification of grooves: a, branchiocardiac; b1, hepatic; b, antennal; c, postcervical; d, gastro-orbital; e, cervical; ω, prominence omega; i, inferior.

both of these collections were carefully examined for a specimen that M'Coy could have used in his original description. It is almost certain that this description was based on material of more than one genus, i.e. *Homarus* and *Hoploparia*. No suitable specimen was found in the Sedgwick Museum and only one possible specimen in the British Museum (Nat. Hist.). This specimen, BM 46366 (Bowerbank Collection), has the characters of the species and was collected from the London Clay, Isle of Sheppey. Due to the uncertainty that M'Coy used BM 46366 (text-fig. 2*b*, *c*) for his original description of *H. gammaroides*, however, it is here designated the neotype.

Other material. The following specimens have been used as a basis for the description. OUM L461, L558 (Pl. 64, fig. 3), L559, L560, L563 (Pl. 64, fig. 10), L564, all *ex* Kirby Collection; BM In.63354 (Pl. 64, fig. 6), *ex* King Collection; BM In.63355–In.63356 (Pl. 64, fig. 4), *ex* JSQ Collection.

Diagnosis. A *Hoploparia* with the cervical joining the antennal groove at an obtuse angle; the antennal region prominent but without spines; posterior edge of the postcervical groove bordered with a line of fine granules; prominence omega, small and obscure, surface with fine tubercles.

Horizon and locality. London Clay, Lower Eocene of Aveley, Chalk Farm, Copenhagen House, Isle of Sheppey, Maylandsea, and Steeple.

Description. Cephalothorax. The median line on the rostrum is flanked by carinae, with a shallow depression between. The postorbital spine is below but almost level transversely with the start of these carinae. The rostrum is half the length of the carapace; its outer edges converge towards the tip. Approximately half-way along the rostrum a large, anterodorsally pointing spine projects on either side of the margin. A similar but larger spine projects on either side at about three quarters the length of the rostrum which then continues almost straight and parallel sided. At the second pair of spines the shallow depression has almost died out.

The cervical groove is deep, starting almost level with the suborbital spine and dropping nearly straight down with a very slight forward angle to join the antennal groove at an obtuse angle, turning towards the front and continuing straight until below the antennal region where it turns sharply anteriorly. At the junction of these grooves and the hepatic groove is a small obscure area known as the prominence omega. The distinctive broad postcervical groove runs from the median line slightly more than half the distance from the base of the rostrum to the posterior margin of the carapace. It slopes forward to the level of the antennal groove to join the hepatic groove. This is semicircular and joins the cervical groove. The hepatic groove starts strong, weakens towards mid length, then becomes stronger. At the top of the cervical groove a faint gastro-orbital groove runs towards the front. The branchiocardiac groove is evident faintly on some specimens, running backwards and upwards from the cervical groove at the level of the suborbital spine. A further faint furrow extends downwards from the postcervical groove at the level of the base of the orbit. The frontal and orbital regions are finely punctate; the antennal has fine tubercles and the odd pit; the branchial has regular spaced, fine and larger tubercles with some fine pitting towards the posterior margin; the gastric has scale-like pits on the top half, and tubercles on the bottom half; the cardiac is strongly pitted. (Refer to text-fig. 4 for position of grooves.)

Abdomen. The first abdominal somite is the smallest, the tergum with a transverse smooth groove, the raised portion pitted. The lateral margin of the pleuron is straight and finishes in a forward pointing, flat, blunt, tooth which overlaps the posterior edge of the carapace. The second somite has a transverse groove on the anterior third of the tergum, extending down to form a semicircle on the pleuron; the surfaces are smooth in front of the groove on the tergum, variably pitted behind. The pleuron is broadly quadrate, the anterior angle rounded, the posterior angle extended into a spine; between the lateral and the posterior margins is a large deep pit; surfaces are ornamented with fine pits, with some areas nearly smooth. The third and fourth somites have a transverse groove on the anterior third which extends to the boundary of the tergum at the anterior margin; surfaces are smooth in front of the groove, pitted behind. The pleuron is triangular, falcate, with an acute posteriorly directed spine. A weak semicircular groove starts and finishes at the pleuron boundary; below this groove and on the median line is a large pit; surfaces are variably pitted. The fifth somite is slightly smaller. The sixth is almost as deep as the second, with a groove crossing the tergum, which is pitted, near the anterior edge. The pleuron is triangular with an acute spine. A weak semicircular groove, which is a continuation of the tergum groove, finishes at a small spine on the posterior edge at the pleural boundary.

Telson. The telson is longer than broad, the outer margins converging slightly towards the rear. On each side of the median line a rounded ridge extends posterolaterally from near the front to a posteriorly pointing spine at slightly over three quarters distance along the margin. Beyond this the margin is semicircular, the surfaces finely pitted. The endopodite is nearly as broad as long, the posterior margin well rounded, the sides converging towards the front to form a well-rounded margin. A longitudinal ridge diverges slightly from the median line on the inner side of the endopodite; there are fine tubercles on the ridge and the outer side; the inner side away from the ridge is smooth; the posterior quarter is finely ribbed at right angles to the margin. The exopodite is elliptical, nearly twice as long as broad and divided transversely by a suture at approximately two thirds of its length. The posterior margin of the anterior section is armed with a series of spines, the largest on the outer angle; the surface is finely punctate. The bottom third is finely ribbed, parallel with the median line, its surface finely punctate.

Appendages. Antennae long, reaching nearly as far forward as the outstretched first pair of pereiopods. Antennal peduncle slightly more than one third the carapace in length, the three segments round to oval in cross-section and more or less equal in length to one another. On the first section of the peduncle the outer edge is flattened to form a sharp ridge which develops into a forward pointing spine. Jutting out in front of this first section and above the spine can be seen the remains of the antennal scale on some specimens. Pieces of the antennule peduncle can be seen on BM In.63354, length approximately to the end of the second section of the antennal peduncle.

The third maxilliped is approximately two thirds the length of the carapace. The merus is triangular in cross-section, its outer margin rounded; the lower margin has small evenly spaced pores; surfaces are finely punctate. The propodus is slightly longer than the carpus, both more or less oval in cross-section. The dactylus is spear shaped, flattened, approximately the same length as the carpus.

On the right-hand cheliped, the crusher, the outer margin of the propodus is rounded, with a faint suggestion of a lateral groove immediately inside the margin on either surface. The margin is smooth with lines of variable sized pits running along the fixed finger on the outer and inner surfaces. The fixed finger is oval in cross-section near the tip, changing to half round by the base of the finger, the inner surface nearly flat; a median triangular ridge runs along the length of the fixed finger. At the base of the ridge and running parallel to it is a line of pits; the remainder of the surface is ornamented with fine pitting. The ridge of the finger is armed with various sized teeth; from the base there are three oval blunt teeth of similar size, then a large blunt oval one (greater diameter along the median line); these are followed by groups of fine teeth divided by a slightly larger tooth. The palm is slightly shorter than the finger, and half as wide as long, nearly oval in cross-section; it thins rapidly near the inner margin to form a lateral groove on either surface. The inner margin of the palm has three large triangular spines on the outer edge, with a smaller spine behind the posterior tooth. Slightly away from the lateral line of spines but parallel with it are two similar spines on the under surface. These alternate with the previous spines. The dactylus is oval in cross-section, slightly flattened on both surfaces, the outer margin rounded. The prehensile edge is armed with a large oval tooth (the greater diameter along the median line), a smaller tooth separated by a gap from a large round tooth, then an assortment of large, fine and slightly larger teeth.

On the fine or left-hand claw, the outer margin of the propodus is smooth and round, straight for most of the length with a slight curve inwards at the tip, the surfaces with fine pitting. The fixed finger is nearly oval in cross-section towards the tip, half round in cross-section at the base; a triangular ridge on the median line runs along the prehensile edge, with fine spines or teeth in groups of three or four with a slightly larger spine in between. This sequence is repeated until approximately one third the length from base where there is a large, slightly offset spine followed by groups of fine and slightly larger spines. A line of pits runs parallel to the ridge; surfaces have variable pits. The finger is at least one and a half times the length of the palm, which is approximately half as wide as long. The outer surface of the palm is deeply convex, starting to flatten out near the inner margin. The inner surface is not as strongly curved. The inner margin is armed with three similar sized triangular spines with a smaller spine behind; parallel with these is another line of two or three similar spines on the under surface, alternating with the previous spines. The dactylus is almost oval in cross-section, flattened slightly on both surfaces, the outer margin rounded, the prehensile edge with a triangular median ridge on the top of which are groups of three or four spiniform teeth, with a slightly larger one in between. The carpus is nearly as broad as long with various anteriorly directed spines on the top and the margins, the underside with an anteriorly directed spine at the front, the surfaces variably pitted. The merus is half the length of the large claw, flattened to oval in cross-section, the front outer margin drawn out into a long sharp point with a smaller spine on the inner margin. Only pieces of the ambulatory legs are preserved; these are rounded to oval in cross-section, smooth with fine lines of pores or isolated pits; the second pair is chelate.

Discussion. When M'Coy (1849) established *Hoploparia* he included two new species from the London Clay, *H. gammaroides* and *H. belli*. Bell (1858) maintained both species but Woods (1931) found that the smaller specimens (*H. belli*) differed in no significant respect from the larger (*H. gammaroides*) and united the two. A study of the original material confirms the view of Woods.

Bell (1858, p. 40) noted that *H. belli* (= *H. gammaroides*) appears to resemble *H. longimanus* (Sowerby) of the Lower Greensand. The latter has a line of tubercles behind and parallel with the postcervical groove, which in *H. gammaroides* are finer (Pl. 64, fig. 6). The junction of the antennal and the cervical groove is at an obtuse angle in both. The ornamentation of the carapace is quite different. *H. longimanus* has spines or tubercles on the carinae and a dentate carina runs back from the antennal spine towards the cervical groove. In *H. gammaroides* this area is prominent but without tubercles; it can vary in individuals as do some of the other surface decorations. *H. stokesi* (Weller, 1903) from the Lower to Middle Campanian, James Ross Island, is similar to *H. longimanus*, the main differences being in the carapace grooves, greater spinosity, and the proportions of the cephalothorax (Ball 1960, p. 12). The American species *H. tennesseensis* Rathbun, 1926*b* from the Upper Cretaceous, Ripley Formation, has a deep groove along the outer margin of the propodus and a row of three spines on the inner side of the inner margin, with one spine at the proximal end of the outer side of this margin. *H. gammaroides* has a double row of spines but arranged differently and no groove along the outer margin of the propodus. *H. gammaroides* differs from the above mentioned Cretaceous species in that the prehensile edge of the claw is armed differently.

Several Eocene species of *Hoploparia* are known, some only from pieces of claw. *H. klebsi* Noetling, 1885 from Germany has a row of spines running back from the antennal spine; the rostrum carinae running back on to the carapace are dentate. The inner margin of the palm of *H. klebsi* is armed with forward pointing teeth as well as the outer margin of the dactylus (Förster and Mundlos 1982, fig. 2). *H. gammaroides* differs from this species by having a prominent antennal region without spines; the prehensile edge of the claw and the inner margin of the palm are armed differently. *H. groenlandica* Ravn, 1903 from the Eocene of Kap Dalton, East Greenland has the cervical joining the antennal groove at an obtuse angle as in *H. gammaroides*. The hepatic groove is distinct throughout its length, and two dentate carinae run from the base of the rostrum nearly to the cervical groove. The chelae of *H. groenlandica* appear to differ from those of *H. gammaroides* in having a flat area on the inner and outer margins, but this may be preservational. Ravn (1903, p. 119) noted that this species has a greater resemblance to *H. gammaroides* though he relied on Bell's (1858) description and figures to come to this conclusion. The specimens are now assigned to *Homarus* and *Hoploparia wardi* sp. nov. The hepatic groove of *H. gammaroides* is not distinct throughout its length; the rostral carinae are not armed and finish almost level transversely with the postorbital spine. These characters make *H. gammaroides* different from *H. groenlandica*. *H. corneti* van Straelen, 1921 from the Eocene of Belgium is too poorly illustrated (van Straelen 1921, p. 136) for any detailed comparison with other species.

Hoploparia wardi sp. nov.

Plate 64, fig. 11; text-fig. 2*d*

1849 *Hoploparia gammaroides* M'Coy, p. 177.
1858 *Hoploparia gammaroides* M'Coy; Bell, p. 38, pl. 8, fig. 4.
1858 *Hoploparia belli* M'Coy; Bell, p. 40, pl. 10, fig. 9.
1931 *Homarus gammaroides* M'Coy; Woods, p. 93, pl. 27, fig. 3.
1980 *Hoploparia gammaroides* M'Coy; Morris, p. 9.

Derivation of name. Named after Mr David Ward.

Types. Holotype: SM C19314 (text-fig. 2*d*), Forbes Young Collection, London Clay, Isle of Sheppey. Paratypes: SM C19318 (Pl. 64, fig. 11), Walton Collection, and BM 59132B, Wetherell Collection (Bell 1858, pl. 10, fig. 9), London Clay, Chalk Farm; BM 46356, Bowerbank Collection (Bell 1858, pl. 8, fig. 4; Woods 1931, pl. 27, fig. 3), London Clay, Isle of Sheppey.

Diagnosis. A *Hoploparia* with a prominent carina running back from the antennal spine with two, possibly three tubercles and a further one between the nearly parallel postcervical and the cervical grooves; distinct hepatic groove throughout its length; prominence omega triangular with fine tubercles; carapace ornamented with well-spaced fine tubercles, more closely spaced ventrally.

Description. Cervical groove deep, runs anteroventrally to join the antennal groove which curves gently anteriorly (rest of groove not seen). The distinct postcervical groove starts on the median line and runs anteroventrally to join the semicircular hepatic groove which joins up with the cervical groove. The hepatic groove is distinct throughout its length. Between the postcervical and the cervical grooves and in line with the cheek, is a swollen area capped with a prominent tubercle. Antennal region elevated into a strong keel with two, possibly three, tubercles. Carapace ornamented with variably sized fine tubercles, rear margin with a smooth flange. First abdominal somite traversed by a smooth groove, surface anterior of groove smooth with fine pitting behind. Somites two to four have a transverse groove on the anterior third which extends to the boundary of the tergum at the anterior margin; surfaces are smooth in front of the groove, with fine pitting behind which appears to increase in size and quantity from the tergum boundary downwards.

Discussion. In Bell's (1858) redescription of *H. gammaroides*, he quoted a sentence from M'Coy's original description: 'the cheek is elevated into a strong keel with about three large spinose tubercles; cheeks prolonged as a semi-cylindrical sheath to the outer antennae half the length of the rostrum.' Bell noted that he had not observed this structure, yet his figure 4 on plate 8 clearly shows a tubercle above the hepatic groove. The specimen (BM 46356, Bowerbank Collection) plainly shows a tubercle above the hepatic groove, with the cheek elevated into a strong keel, with two, possibly three, spinose tubercles. As regards the cheeks, it is quite possible that on the specimens available the antennal peduncle was fragmentary; it could then be mistaken as a continuation of the cheek. Bell also noted p. 41 that BM 59132B (pl. 10, fig. 9) differed in some respects from *H. belli.*

Rathbun (1935, p. 61) used four incomplete specimens to describe *H. johnsoni* from the Lower Eocene, Sucarnoochee Bed, Midway, Alabama. It has at least one spine on the lateral ridge leading to the rostrum and the antennal ridge is weakly defined (Rathbun 1935, pl. 14, figs. 27 and 28). *H. wardi*, though similar to *H. johnsoni*, is different in that it has a pronounced antennal ridge, smooth carinae from the rostrum, and a different arrangement of the larger carapace tubercles. *H. wardi* differs from its near neighbour *H. gammaroides* by the arrangement of the spines leading towards the antennal spine, the deep and clearly defined hepatic groove, and the postcervical and cervical grooves which run parallel and closer together. The prominence omega is triangular and ornamented with fine tubercles on both of these species. In *H. klebsi* the postcervical and cervical grooves appear to be parallel similar to *H. wardi* (Förster and Mundlos 1982, pl. 33, fig. 3) but in *H. wardi* the carina from the rostrum is smooth and the large carapace tubercles are different. In *H. groenlandica* the postcervical and cervical grooves are not parallel but diverge dorsally as for *H. gammaroides*, whereas in *H. wardi*, the postcervical and cervical grooves run parallel and the carapace is ornamented with several large tubercles.

Hoploparia victoriae sp. nov.

Plate 64, figs. 8 and 9

1979 *Hoploparia gammaroides* M'Coy; Quayle and Collins *in* Kemp *et al.*, p. 102.
1981 *Hoploparia gammaroides* M'Coy; Quayle and Collins, p. 735.

Derivation of name. After my daughter, Miss Victoria Quayle.

Types. Holotype: BM In.63357 (Pl. 64, fig. 8). Paratypes: BM In.63358–In.63363 (Pl. 64, fig. 9), all *ex* JSQ Collection, from Unit 7, Elmore Formation, Bracklesham Group, Middle Eocene, Lee-on-the-Solent, Hampshire.

Diagnosis. A *Hoploparia* with the cervical joining the antennal groove in a curve; prominence omega well rounded and conspicuous, plain or pitted surface; antennal region rounded but not prominent; posterior border of postcervical groove plain or pitted.

Description. Cephalothorax. The rostrum is half the carapace in length, with a median depression bounded on each side by a carina; at approximately the mid length is the base of a spine and at the end a further spine (the arrangement of the spines is possibly as for *H. gammaroides*). The cervical groove is deep, extending ventrally from the level of the suborbital spine, forming a smooth curve to join the deep antennal groove. The antennal groove becomes finer towards the anterior margin of the carapace, where it almost disappears. At the junction of these grooves and the weak hepatic groove is a small, prominent well-rounded area, the prominence omega. The hepatic groove alongside this area is smooth, wide, and deep, but elsewhere, even on well-preserved specimens, is very indistinct. A weak furrow extends anteriorly from the top of the cervical groove, passing under the suborbital spine. The postcervical groove is deep, situated at over half the carapace length from the base of the rostrum. The dorsal part cuts the median line at right angles and runs anteroventrally approximately 30° to the vertical to join up with the hepatic groove. A further deep furrow extends ventrally from the postcervical groove at the level of the base of the orbits. The branchiocardiac groove curves posterodorsally from the cervical groove, at the level of the suborbital spine. The marginal furrow is well marked and the posterior margin bears a smooth, finely punctate flange. Surface ornamentation on the carapace is as follows: frontal and orbital area, smooth with well-spaced pits; antennal area, pitting with small tubercles; branchial area, blunt tubercles with pits; gastric and cardiac areas, surface rough with pitting.

Abdomen. The tergum of the first abdominal somite is crossed by a deep groove two thirds the distance from the front; raised portions are pitted. A groove crosses the tergum of the second somite in the anterior third and extends down to form a semicircle on the pleuron. The pleuron is quadrate, the anterior angle rounded, the posterior angle with a posterior pointing spine. Between the bottom of the semicircle and the posterior spine is a large clear pit; the rest of the surface is ornamented with variable pitting. The third somite is likewise traversed by a groove which extends to the pleuron, where it forms a weakly defined semicircle. The pleuron is falcate, with an acute posteriorly pointed spine, its surface ornamented with variable pits, the area in front of the tergum groove smooth. Somite four is similar to three; the groove on the pleuron is very weak, the pleura having a solitary pit similar to that on somite two. The fifth somite is like three and four but narrower, its surfaces variably pitted.

Ventral surfaces. There is a median tubercle on the abdominal sterna of the first to third somite. Mandibles are almost rectangular, smooth and transversely convex with other surfaces and margins rounded.

Appendages. On the right-hand first cheliped, the crusher, the palm is approximately twice as long as wide, oval in cross-section, thinning rapidly towards the inner margin which has two rows of alternating, anteriorly directed spines (six in all?). The palm is coarsely pitted. The fixed finger is nearly oval in cross-section, its outer margin rounded with a slight groove on the upper surface, its inner margin wide, almost flat. From the base of the fixed finger the prehensile edge is armed with depressed oval teeth that lie close together with their greater length at right angles to the median line. The first tooth is the smallest with a marked increase in size to the third; then the teeth remain almost the same size up to the tenth (rest not seen). The dactylus (of which only fragments are known) is oval in cross-section, its outer margin wide and flat, the prehensile edge armed with close, round to oval, flattened teeth, smallest at the joint. On the upper and lower surfaces a spine is evident by the joint. On the left-hand first cheliped, the small claw, the palm is approximately twice as long as wide and oval in cross-section. It thins rapidly towards the inner margin which is dentate with a double row of alternating spines. The fixed finger has a rounded outer margin, the inner margin almost flat for its entire width, the prehensile edge armed with small spiniform teeth for most of its length. The carpus is approximately two thirds the length of the merus, triangular in cross-section, its inner and outer margins tapering towards the merus. The lower surface has a row of three or four anteriorly directed spines. The upper surface is slightly rounded with an anteriorly directed spine towards the rear. Ornamentation on the upper surface is scale-like. There are small blunt tubercles on the lower surface. The merus is over twice as long as wide, oval in cross-section, its inner and outer margins tapering from the front towards the ischium. There are one or two blunt spines on the anteroventral margin; surfaces are smooth, finely punctate. The ischium is smooth and finely punctate. On the second and third pereiopods the merus and ischium are round and smooth with surfaces finely punctate; the merus is approximately three times the length of the ischium.

Discussion. H. victoriae differs from *H. gammaroides* in that the antennal and cervical grooves join in a curve; the posterior edge of the postcervical groove is plain or with pits; the antennal region is rounded on the surface and only prominent at the front; prominence omega rounded with plain or pitted surface; the prehensile edge of the propodus of the crusher claw is armed with oval teeth increasing in size away from the joint and transverse to the median line. *H. victoriae* differs from *H. wardi* and *H. klebsi* in that the cervical and postcervical grooves are further apart and diverge dorsally, and in the carapace ornamentation, small tubercles with fine pitting. It differs from *H. groenlandica* in that the rostral carinae are smooth.

Infraorder PALINURA Latreille, 1803
Superfamily GLYPHEOIDEA Winckler, 1883
Family GLYPHEIDAE Winckler, 1883
Genus GLYPHEA von Meyer, 1835

Type species. Palinurus regleyanus Desmarest, 1822, by original designation.

Diagnosis. Carapace with short pointed rostrum; tuberculate longitudinal carinae on anterior part. Cervical groove deep and steeply inclined in lateral view. Postcervical and banchiocardiac grooves very oblique, joined medially and laterally and in some species at additional points. Anterior portion of carapace rectangular in dorsal and lateral views. Branchiostegite with long narrow anterior extension. Abdominal terga smooth, telson rounded, exopods of uropods with diaeresis. Antennal scale pointed; first pereiopod subchelate.

Range. Upper Trias–Lower Eocene.

Glyphea scabra (Bell, 1858)

Plate 64, figs. 12–14; text-fig. 5*b*

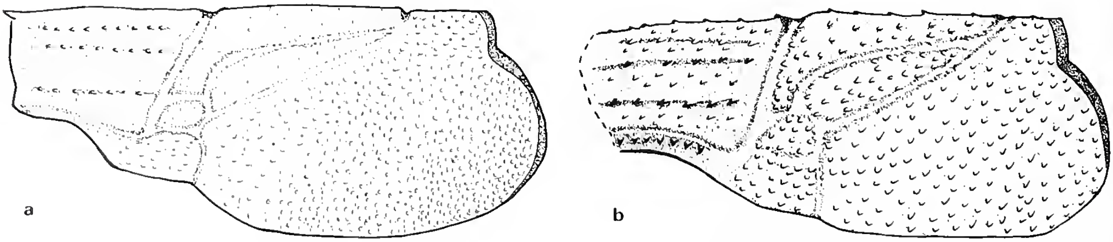
1858 *Trachysoma scabrum* Bell, p. 41, pl. 10, fig. 11.
1929 *Trachysoma scabrum* Bell; Glaessner, p. 387.
1930 *Trachysoma scabrum* Bell; Woods, p. 73, pl. 22, fig. 1*a*, *b*.
1969 *Trachysoma scabrum* Bell; Glaessner, R464.
1974 *Trachysoma scabrum* Bell; Cooper, p. 85.
1980 *Trachysoma scabrum* Bell; Morris, p. 17.

Holotype: BM 59146 (Pl. 64, fig. 12), by monotypy, London Clay, Chalk Farm, Camden Town, London.

Other material. BM In.63366 (Pl. 64, figs. 13 and 14), collected by D. Ward, London Clay, Aveley, Essex; PE 80/454, collected S. W. Vincent, A127 (roadworks) at Folkes Lane, Cranham (TQ 580 884).

Diagnosis. A *Glyphea* with the carapace covered in different size sharp pointed tubercles.

Description. Cervical groove deep, starting at a point about two fifths the distance from the front to the posterior margin of the carapace. It runs nearly straight, until half-way across the carapace where it bends slightly forward and continues to the antennal groove. In front of the cervical and above the antennal groove are three longitudinal carinae armed on the top with sharp anteriorly directed tubercles; the surfaces between the carinae are ornamented with further sharp tubercles. The antennal groove is deep, nearly straight with a slight upwards angle. The branchiocardiac groove is clearly marked. It starts at approximately four-fifths the distance from the front with a slight forward curve, then runs almost straight across the carapace at an angle of 45° to meet the small lobe above the hepatic lobe. The indistinct postcervical groove forms an acute angle with the branchiocardiac groove near the dorsal margin; anteriorly the grooves are joined by a semicircle and a triangular area is formed between them. The hepatic groove starts at the junction of the branchiocardiac



TEXT-FIG. 5. *a*, *Glyphea* sp. (× 1·5). *b*, Reconstruction of *Glyphea scabrum* (Bell) (× 2·2).

and inferior grooves, runs slightly anterodorsally from this junction, then ventrally before joining the cervical groove above the antennal groove. The area bounded by the hepatic, inferior groove and the lower margin is roughly rectangular and decorated with sharp tubercles. The remainder of the surface of the carapace is also ornamented with tubercles.

What may be part of the propodus is evident on BM In.63366 (Pl. 64, fig. 13). It is oval in cross-section, the top margin with anteriorly directed equally spaced teeth, the outer surface with a smooth groove running parallel with the top margin; all surfaces with tubercles. (Refer to text-fig. 4B for position of carapace grooves.)

Discussion. Bell (1858) described the new genus *Trachysoma* from one specimen collected by Wetherell, to which he gave the trivial name *scabrum*. The holotype consists of an incomplete carapace with limb fragments and part of the antennal peduncle. Bell (p. 42) was not certain of the affinities of this species. Woods (1930) figured this unique specimen (pl. 22, fig. 1*a*, *b*) but gave no description or remarks. Cooper (1974) mentioned a specimen collected by D. Ward, BM In.63366. This consists of an imperfect carapace with a limb fragment. The only other known specimen (PE 80/454), part of a carapace, was collected by S. Vincent. Glaessner's (1969) diagnosis of *Trachysoma* refers to a long, low and narrow carapace with deep straight cervical grooves, and straight postcervical and branchiocardiac grooves. He also included *Glypheopsis* Beurlen in this genus, the type of which is *Orphea ornata* Quenstedt, 1858. This appears to have straight postcervical and branchiocardiac grooves (R465, fig. 269.2*a*, *b*). BM 59146 and BM In.63366 have had little or no preparation since being collected. What appears to be the rounded ventral margin of the carapace on BM 59146 is in fact a limb lying across the carapace. Likewise what appears to be a dentate ventral margin forward of the cervical groove is in fact a line of sharp tubercles. Both of these specimens were masked by matrix in a similar position which concealed the true shape of the carapace, which preparation of BM In.63366 has subsequently revealed, though details of the rostrum and anterior are still not known. A new reconstruction based on these specimens (text-fig. 5*b*) shows that the carapace compares in its proportions and grooves to *Glyphea* (text-fig. 5*a*) to which it is here assigned.

Superfamily PALINUROIDEA Latreille, 1803
Family PALINURIDAE Latreille, 1802
Genus ARCHAEOCARABUS M'Coy, 1849

Type species. Archaeocarabus bowerbanki M'Coy, 1849, London Clay, Isle of Sheppey, by original designation.

Diagnosis. Rostrum of moderate size made up of three spines, centre one gripped by two processes of the ophthalmic somite; supraorbital spines widely separated. Sternal plate with four pairs of tubercles.

Range. Lower Eocene, England.

Discussion. Woods (1931) diagnosed *Archaeocarabus* as like *Palinurus* but with the rostrum similar to that of *Jasus* Parker, 1883, particularly in that it is gripped by two processes of the ophthalmic somite. He distinguished it from *Jasus* by the more widely separated supraorbital spines and the presence of a row of tubercles on the plastron. The differences in the rostral area between *Jasus* and *Archaeocarabus* can be seen by comparing text-fig. 6C with text-fig. 6D. In *Archaeocarabus* there are three spines; in *Jasus* a single central spine. The rostrum or central spine in each case is gripped by two processes of the ophthalmic somite. These two processes in *Archaeocarabus* tend to lie alongside the spine with a slight upwards curve, rather than come straight up from the ventral side as in *Jasus*.

Archaeocarabus bowerbanki M'Coy, 1849

Plate 65, figs. 1–9; text-fig. 6

1849 *Archaeocarabus bowerbanki* M'Coy, p. 174.
1854 *Archaeocarabus bowerbanki* M'Coy; Pictet, p. 443, pl. 42, fig. 3.
1858 *Archaeocarabus bowerbanki* M'Coy; Bell, p. 42, pl. 11, figs. 1–5.

1925 *Archaeocarabus bowerbanki* M'Coy; Woods, p. 36, pl. 8, fig. 5; pl. 9, fig. 6; pl. 10, figs. 1–3.
1929 *Archaeocarabus bowerbanki* M'Coy; Glaessner, p. 57.
1962 *Archaeocarabus bowerbanki* M'Coy; Roberts, p. 176.
1969 *Archaeocarabus bowerbanki* M'Coy; Glaessner, R473, fig. 277.2*a*, *b*.
1974 *Archaeocarabus bowerbanki* M'Coy; Cooper, p. 85.
1980 *Archaeocarabus bowerbanki* M'Coy; Morris, p. 1.

Types. M'Coy's syntypes are SM C7737, C7738, C19074, BM 46358, 46359, and 59764, all from the London Clay, Isle of Sheppey. SM C7737 (Woods 1926, pl. 9, fig. 6) is here designated lectotype.

Other material. BM 38388 (Pl. 65, fig. 6) and 59140 (Pl. 65, fig. 8); BM In.63378 (Pl. 65, fig. 5), In.63379 (Pl. 65, fig. 4), In.63380 (Pl. 65, figs. 1 and 3), In.63381 (Pl. 65, fig. 2), In.63382 (Pl. 65, fig. 9), In.63383–In.63386 (Pl. 65, fig. 7), *ex* JSQ Collection; all from the London Clay, Isle of Sheppey.

Diagnosis. As for genus.

Description. Cephalothorax. The front is straight and occupies nearly half the carapace width; it is armed with several anteriorly directed spines. Length of the rostrum is two thirds of its width and occupies approximately a quarter of the width of the frontal margin; it consists of a thin median spine with a slightly shorter stout lateral spine either side. The median spine is armed dorsally with one anteriorly directed spine at approximately half the length, with a further spine at the base; lateral spines, broad at the base, are flat and triangular; the median spine is gripped on either side by two slightly upturned rounded cone-shaped processes of the ophthalmic somite. The somite is slightly wider than the rostrum; its outer margins are angled inwards; the top surface is concave and the sides drop steeply away; surfaces are smooth with a few small pits. The remainder of the front is made up of three short spines on either side of the rostral spines, followed by the supraorbital spines. These are large, anteriorly directed, laterally compressed and triangular in shape and lean slightly outwards; they are approximately half the carapace width in length and are situated at the anterolateral angle. Behind each runs the postorbital carina; this is cut by the cervical groove and continues behind with a slight inwards angle, gradually dying out and ending three quarters of the length of the carapace from the front. On the carina there are two smaller, anteriorly directed spines behind the supraorbital spine and behind these, large spiny tubercles are interspersed with smaller ones. Between the supraorbital spines the carapace is almost flat with a few small tubercles. Half the distance from the front to the postcervical groove there is a transverse row of three small tubercles. Behind this and on either side of the mid-line are two longitudinal rows of three larger, anteriorly directed spines; from the second tubercle to the postcervical groove the general ornamentation of the carapace changes to a greater number of tubercles.

The postcervical groove is deep and broad, straight for half the width of the carapace, then joining the cervical groove which curves in front of the fourth spine on the continuation of the postorbital carina; it continues to run straight to cut the lateral margin at right angles, drops vertically down the side as a deep groove, then develops a slight forward curve which continues as the antennal groove. Behind the postcervical groove a slight median carina with large and small tubercles runs almost to the posterior margin where it is cut by a deep transverse groove, parallel to and just inside the flanged edge of the posterior margin. The lateral margins behind the cervical groove are parallel and start with a large forward pointing spiny tubercle, followed by four or five smaller spiny tubercles to half-way along the margin; a more general ornamentation then develops of small and large tubercles. The rest of the carapace is ornamented with a variety of medium and small tubercles. The large and small tubercles have on their front sides rows or groups of fine pores at the base. Below the supraorbital spine the orbital margin finishes in a large triangular infraorbital spine similar to but not as large as the supraorbital. Here starts the antennal carina which runs parallel to the postorbital carina and finishes at the antennal groove; it is armed with three flattened anteriorly directed triangular spines. At a point half-way between the carinae and alongside the cervical groove is the start of another carina that

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EXPLANATION OF PLATE 65

Figs. 1–9. *Archaeocarabus bowerbanki* M'Coy, London Clay, Isle of Sheppey. 1 and 3, BM In.63380. 1, lateral view, × 1·1. 3, dorsal view, × 1·1. 2, eye and orbit, BM In.63381, × 2. 4, basal segments of antenna, BM In.63379, × 1·7. 5, ophthalmic somite, BM In.63378, × 4. 6, anterior of BM 38388, × 2. 7, lateral view, BM In.63386, × 0·8. 8, sternum, BM In.59140, × 1. 9, claw, BM In.63382, × 1·8.

Specimens in figs. 3, 5, and 9 have been whitened with ammonium chloride.

PLATE 65

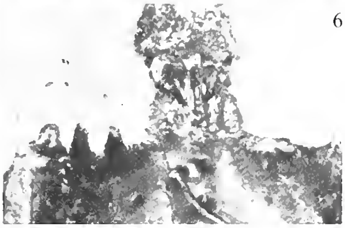

1


2


3


4


5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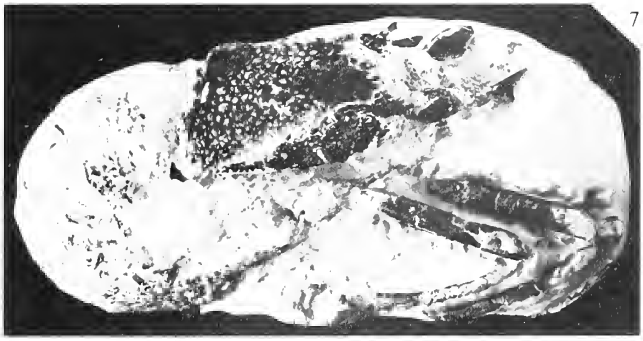
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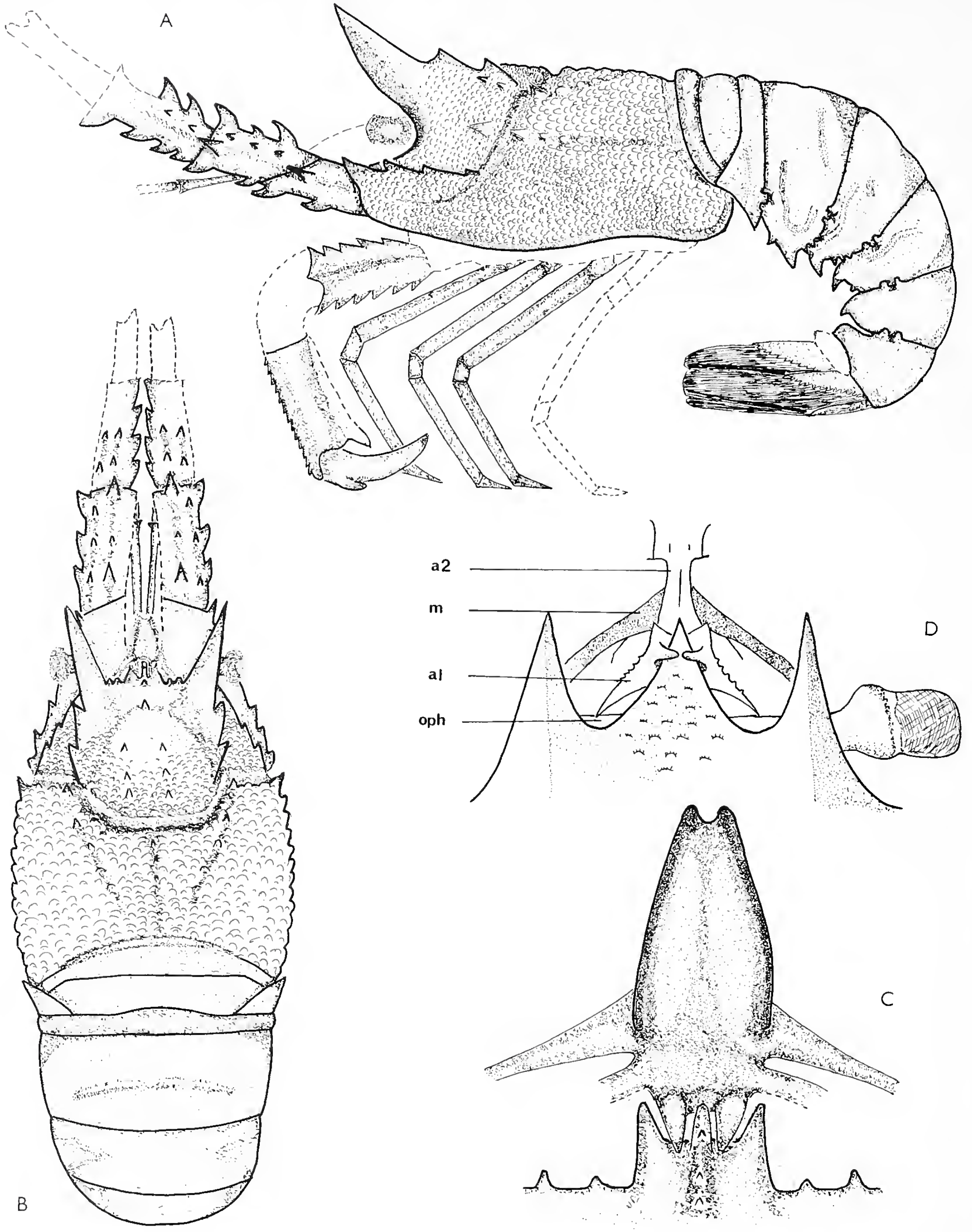
8


9

QUAYLE, *Archaeocarabus*



TEXT-FIG. 6. *Archaeocarabus bowerbanki* M'Coy, diagrammatic reconstruction. A, B, lateral and dorsal view (× 1·1). C, details of the ophthalmic somite and rostrum (× 3·6). D, *Jasus lalandii* (Milne-Edwards), Recent, South Africa, frontal area (after Glaessner 1969) (× 1·25): a2, base of antenna; m, articulating membrane; a1, antennular base; oph, eye stalk.

forms the continuation of the lateral margin posterior to the cervical groove, which dies out before the orbital margin and is armed with two or three blunt spines. There are a further two, anteriorly directed triangular spines between this carina and the postorbital carina at the forward edge of the cervical groove.

Abdomen. On the abdominal somites the tergum is more or less semicircular in cross-section, with a grooved and flanged posterior margin. The pleura have one to three flat spines on each margin and end in a large recurved central spine. On the first somite the flange develops a triangular flap on each side, which accommodates the posterolateral angles of the carapace when the abdomen is rolled up. The surfaces are variably pitted.

Telson. The calcified part of the telson is parallel sided, with the posterior margin concave; there are a few tubercles towards the centre. Approximately the first half of the outer margin of the exopodite and endopodite is calcified. This area is elliptical, approximately three times longer than wide, smooth on the outer edge, strongly serrate on the inner and terminates in a ventrally directed spine. Only fragments of the remainder of the tail are known.

Ventral structures. The anterior margin of the epistome is concave on each side of the median spine and reached by the median furrow. The anterior part of the sternum is a small rectangular area, a fifth of the total length; the outer margins then diverge to give the maximum width at the second sternite, which remains almost constant as far as the concave rear margin. Along the median line and on the rear margin of each sternite behind the rectangular area are pairs of tubercles. The first and last pair are smaller than the intermediate pairs. The surface of the sternum is finely granulated and decorated with tubercles on the outer margins.

Appendages. The long slender basal podomere of the antennule reaches as far forward as the end of the second podomere of the antenna. The basal podomere expands distally to accommodate the second slender podomere, only small pieces of which are preserved. The first three podomeres of the antenna are round to oval in cross-section and armed with various sized spines. The dorsal and ventral margins of the second and third podomeres are flattened slightly longitudinally, and armed with large flattened anteriorly directed triangular spines. The flagellum is unknown but was probably similar to Recent *Palinurus*. The eye is very large and the peduncle short, about one third the width of the eye.

The first pereiopod is chelate, the propodus three to four times the width of that on limbs two to five, but approximately the same length; in cross-section it is round to oval, becoming broadly dilated towards the dactylus; the width of this flattened end is two thirds the length of the rounded, slightly curving, outer margin of the pointed dactylus. On the outer margin, opposite the joint, is a large posteriorly directed spine. There are two or three longitudinal rows of uniform pits on the outer and inner surfaces, with the odd larger pit. On the second, third, and fourth pereiopods the merus is slightly longer than the propodus. Both are oval to triangular in cross-section. The merus is smooth and finely punctate; the propodus has longitudinal lines of small evenly spaced pores; the rest of the surface is finely punctate. The dactylus is slightly less than half the length of the propodus, round in cross-section, with a pointed end.

Discussion. Due to the very fragile nature of the carapace of *Archaeocarabus*, it is rarely found complete; BM In.63380 (Pl. 65, figs. 1 and 3), though small, is possibly the best preserved. The carapace of the larger specimens appears to be more rounded, with the carinae becoming indistinct.

Rathbun 1935 described two new species of *Archaeocarabus*? and in 1945, a further one. Roberts (1962, p. 176) was doubtful whether these three species should have been placed in *Archaeocarabus*.

Genus LINUPARUS White, 1847

Type species. Palinurus trigonus von Siebold, 1824, by original designation.

Diagnosis. Cephalothorax depressed, carapace with three longitudinal keels, no rostrum; supraorbital spines close to the median line, fused to form plate or separated by indentation.

Range. Lower Cretaceous–Recent.

Discussion. Three species of Recent *Linuparus* were recognized by Berry and George (1972): *L. trigonus* (von Siebold), 1824, western Pacific, Japan, South China Sea, Philippines, and eastern Australia, *L. sordidus* Bruce, 1965, from the South China Sea to north-western Australia, and *L.*

somniosus Berry and George, 1972, from the western Indian Ocean, Mozambique, and Natal, living in depths from 81 to 328 m. There were variations in the type series of each, small specimens having better developed spines than large ones. As pointed out by Woods (1925) there are also variations in the fossil species.

Linuparus eocenicus Woods, 1925

Plate 66, figs. 1–5; text-fig. 7*a*, *b*

1858 *Thenops scyllariformis* Bell, p. 33, pl. 7, figs. 5?, 6, 7?, 8?
1925 *Linuparus eocenicus* Woods, p. 31, figs. 3–5; pl. 7, figs. 4–6; pl. 8, fig. 1.
1929 *Linuparus eocenicus* Woods; Glaessner, p. 233.
1974 *Linuparus eocenicus* Woods; Cooper, p. 85.
1980 *Linuparus eocenicus* Woods; Morris, p. 10.
1980 *Linuparus scyllariformis* (Bell); Morris, p. 10.

Types. Woods's syntypes are SM C7732, C7733 (Pl. 66, fig. 3)–C7736, Meyer and Carter collections, from the London Clay, Portsmouth Docks, Hampshire; BM 59145, London Clay, Highgate tunnel, London. SM C7735 (Pl. 66, figs. 1 and 2) is here designated lectotype.

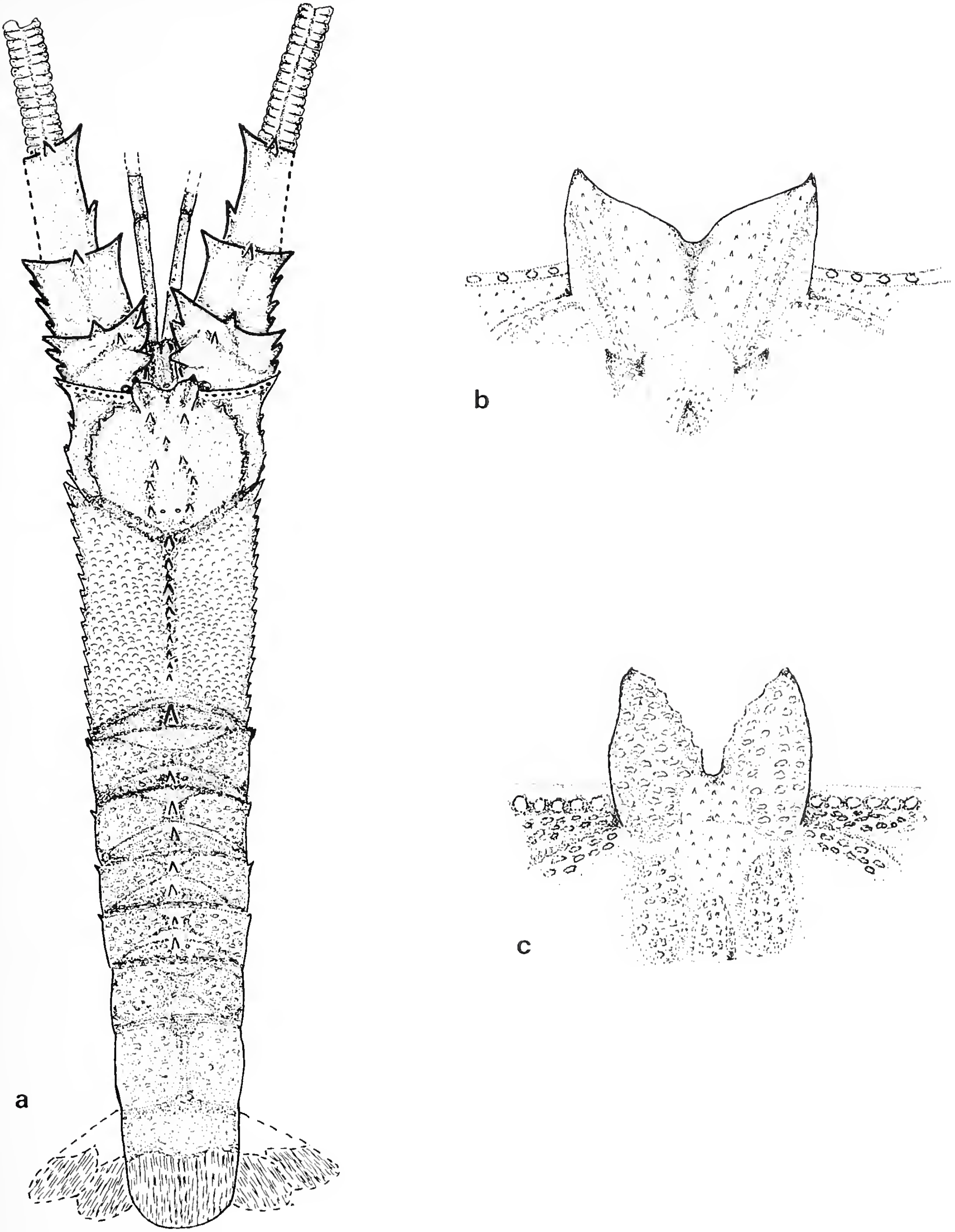
Other material. SM X1357–1362; OUM L552–L554, L568–L570; BM In.63370, In.63371 (Pl. 66, fig. 4)–In.63374 (Pl. 66, fig. 5)–In.63377; all *ex* JSQ Collection, Whitecliff Bay, Isle of Wight. The following of Bell's syntypes of *L. scyllariformis*: BM 59012, 59107–59109, 59111, 59141 certainly, and 46365, 46367, 59765, 59114, and 59110*b* probably, belong to *L. eocenicus*.

Horizon and locality. The London Clay of: Portsmouth Docks; Isle of Sheppey; Burnham on Crouch; Highgate and Chalk Farm, London; Frinton on Sea; Base of Division E, Barwell Court, Surrey; and the Wittering Division, Bracklesham Group, Whitecliff Bay.

Diagnosis. A *Linuparus* with the supraorbital spines united for half their length; carinae with spiny tubercles, raised areas decorated with fine tubercles.

Description. *Cephalothorax*. The supraorbital spines take up approximately one quarter the width of the frontal margin. They are ridged longitudinally, the outer margin sloping steeply away from the ridge. The inner margins, from the tip of the spine to the centre line where they meet, form a shallow U. They are united for approximately half their length. The frontal margin outside the supraorbital spines is concave, with well-spaced tubercles running along the top surface, and terminates in an anteriorly directed anterolateral spine. A short distance behind each supraorbital spine is a postorbital spine, which continues posteriorly as a ridge as far as a median spine. Behind this the median line is flanked by carinae, which diverge slightly and then converge meeting just anterior of the cervical groove; these carinae bear small anteriorly directed spines. In between these carinae almost at the cervical groove is a pair of small, deep, round pores, flanking the median line. From near the base of the supraorbital spines, rounded carinae extend outwards in a curve to the cervical groove and bear several forward pointing spines; the area bounded by these is concave. The raised surfaces are covered with fine tubercles; other areas are nearly smooth. External to the curved carina the carapace at first slopes sharply ventrally and then becomes nearly horizontal; surfaces are tuberculate. The lateral margin in front of the cervical groove is angular and bears several small anteriorly directed spines and usually one or two larger spines along its length; it is nearly parallel to the axis of the body. The cervical groove is deep and in the form of a shallow V. At the lateral margin the deep groove runs directly ventrally and then bends sharply anteriorly. Behind the cervical groove are three nearly parallel longitudinal carinae, the median prominent, the outer angular. Between the median and lateral carinae the carapace is flattened or concave and ornamented with regularly spaced uniform tubercles. Carinae are ornamented with numerous spines, usually decreasing in size towards the posterior. External to the lateral carina the carapace is vertical except near the cervical groove, where the upper part is concave and the lower convex. Just in front of the posterior margin of the carapace is a broad smooth groove which interrupts the median carina and curves backward on each side, becoming narrower towards the lateral margins. This part of the carina is produced into an anteriorly directed spine.

Abdomen. The abdomen is similar in length to the carapace, tapering slightly posteriorly. The carinae on the carapace are continued as slight ridges on each tergum. The first somite bears one anteriorly directed spine on



TEXT-FIG. 7. *a*, *b*, *Linuparus eocenicus* Woods. *a*, diagrammatic reconstruction (×0·7); *b*, supraorbital spines (×2·1). *c*, *L. scyllariformis* (Bell), supraorbital spines (×1·7).

the median ridge at the posterior margin. In front of this a smooth groove runs almost parallel to the posterior margin for approximately half the width of the somite, where it divides. One arm runs to the posterior margin at the outer edge, the other to the outer edge near the front of the somite; the two triangular areas enclosed are ornamented with some fine tubercles and pits; the area in front is smooth. Somites two, three, and four have a median carina, which is interrupted in the middle of each tergum by a broad transverse groove, sloping posteriorly on each side, narrowing and nearly reaching the posterior margin. The tergum surface is ornamented with a mixture of pits and fine tubercles. Each tergum has two anteriorly directed spines on the median carina, one in front and one behind the groove; on the outer margins there is a suggestion of a longitudinal ridge with a spine at the front. On the fifth somite the spines on the median ridge have disappeared, but the outer spine is still evident with the transverse groove becoming indistinct. The sixth somite, which is almost twice the length of the others, has a smooth median groove with a longitudinal row of tubercles on each side; the rest of the surface is ornamented with fine tubercles. The pleura on somites four and five bear two spines on the forward margin followed by a central ventrally directed strong spine. The posterior margin is smooth laterally becoming serrate, the size of teeth increasing adaxially; a concave area flanks the central spine. Only parts of the pleura of somites two and three are known but they are presumably as for four and five.

Ventral structures. The epistome has a strong median groove between prominent ridges which diverge anteriorly. The anterior margin is concave with a tubercle either side of the median groove. The anterolateral margins are directed at approximately 45° to where they turn posteriorly and become almost parallel. Between the margins and the two median ridges are two large depressions, one alongside each ridge.

The sternum between the third maxilliped and the first pair of pereiopods is triangular and bears two flat, rounded bosses anteriorly, one behind the other; surfaces are pitted. The coxae of the third maxillipeds fit between these bosses. Each sternite has ridged sides tapering towards the front, decorated with pits and tubercles. The lateral and posterior margins join in a triangular, laterally directed spine. The sternite for the first pereiopod is ridged along the median line; the second, third, and fourth have a large tubercle either side of this line. The fifth has two pairs of small tubercles, one pair either side of the median line; the outer ridge is smooth except for some tubercles towards the front. Between the tubercles on the sternite for the fourth limb is a groove along the median line. There is a single central tubercle on the first abdominal somite. On the second there are three tubercles, the two anterior approximately half the size of the posterior one. On the third somite the three tubercles are in a similar position to the second but are all the same size with a smaller tubercle in between the pair. The fourth and fifth have a pair of tubercles, one either side of the median line.

Appendages. The antennular somite is longitudinally rectangular with a broad median furrow and it extends forward between the basal podomere of the antennae. The basal podomere of the antennule is round and thin, extending past the second podomere of the antenna. The first podomere of the antenna is broad and one third wider than the second. The outer and inner margins are sharp and armed with two or three forward pointing spines. The second podomere is similar in length to the first; the third is the longest, but also the narrowest.

The coxa of the third maxilliped is triangular, its surfaces pitted. The merus is approximately half the size of that on the second pereiopod; surfaces nearly smooth with very shallow pits. The first pereiopod is larger than the rest, the coxa nearly as long as the ischium and basis, surfaces with shallow pitting. The merus, three times as long as the carpus, is flattened and forked at the carpus articulation with sharp spines on the ventral margins by the fork; the propodus is half the length of the merus. Other limbs are similar but the fifth appears to be smaller.

Discussion. Of the three Recent species of this genus *L. trigonus* is the nearest to *L. eocenicus.* On *L. trigonus* the supraorbital spines have a dentate inner margin; the frontal margin has a prominent spine half-way between the supraorbital and the anterolateral spine. On *L. eocenicus* the supraorbital spines have a smooth inner margin and there is no prominent spine on the frontal margin. Possibly the arrangement of the spines on the pleura is different.

The fossil species are known from the Cretaceous and the Eocene. *L. canadensis* (Whiteaves, 1885), Northwest Territory, Highwood River, Alberta, has two spines on the tergum boundary whereas *L. eocenicus* has one. *L. vancouverensis* (Whiteaves, 1895) from the Nanaimo Group, Vancouver and Hornby Islands, British Columbia, has a double row of tubercles on the carapace carinae (Rathbun 1935, pl. 10, figs. 1–3); the carapace carinae continue back on to the tergum as ridges armed with a single row of tubercles. In *L. adkinsi* Rathbun, 1935 (pl. 10, figs. 4–10) from the Denton Clay, Texas, the three carinae behind the cervical groove are granulated, the median one with a double row of tubercles. The tergum has a pronounced median carina with a series of tubercles. *L. eocenicus* bears a single row of tubercles on the carapace carinae which continue back on to the tergum as a ridge with a single or double spine.

The English Cretaceous has produced *L. carteri* (Reed, 1911) from the Lower Greensand, Atherfield, Isle of Wight. The cervical groove starts as in other species of the genus but forms an obtuse angle where it becomes transverse just before it crosses the median line; from this obtuse angle a further groove runs backwards. In addition the arrangement of the tubercles on the carinae and the general ornamentation of the carapace (Woods 1925, pl. 7, figs. 2 and 3) differentiate this species from other members of the genus.

The Eocene members of the genus include *L. texanus* Rathbun, 1935 (pl. 16, figs. 9 and 10) from the Midway of Dimmit County, Texas. It is possible that this species, which was described from one specimen, is not distinct. Rathbun (1935) described the abdomen as lacking the first and second segments: it is suggested that these are really segments one to five and not three to seven. The median spine on all the specimens of species examined is lost on the fifth segment with a groove appearing on the sixth, which does not appear to happen in this case. *L. wilcoxensis* Rathbun, 1935 (pl. 16, figs. 11–14) from the Sucarnoochee Beds, Wilcox County, Alabama, appears to be very similar to *L. eocenicus*. The abdomen has two spines on the median carina on segments two to four with possible differences on the outer carinae of these segments.

Woods (1925, p. 32, pl. 7, fig. 6*b*) described the antennular somite of *L. eocenicus* as triangular. On closer examination the sides of the 'triangle' are seen to be chipped or broken and in recently collected specimens it is evident that this somite is long and parallel sided, with a deep median furrow (Pl. 66, fig. 5).

Linuparus scyllariformis (Bell, 1858)

Plate 66, figs. 6–8; text-fig. 7*c*

1858 *Thenops scyllariformis* Bell, p. 33, pl. 7, figs. 1–4.
1925 *Linuparus scyllariformis* (Bell); Woods, p. 29, pl. 8, fig. 2*a*, *b*.
1929 *Linuparus scyllariformis* (Bell); Glaessner, p. 233.
1974 *Linuparus scyllariformis* (Bell); Cooper, p. 85.
1980 *Linuparus scyllariformis* (Bell); Morris, p. 10.

Types. Bell's syntype BM 59106, figured Woods (1925, pl. 8, fig. 2), London Clay, Whetstone, London is here designated lectotype. Of the paralectotypes BM In.43325, BM 59110*a*, 59113, 59142, 59143 certainly and 59144 probably belong to *L. scyllariformis*.

Other material. OUM L265, L460, L462 (Pl. 66, fig. 8), L555 (Pl. 66, fig. 6), Kirby Collection; BM In.63367–In.63369, *ex* JSQ Collection; PE 82/395 collected C. King.

Horizon and locality. The London Clay of: Herne Bay, Aveley, Maylandsea, Steeple, Whetstone, Felixstowe, and roadworks on the M25, Ockendon Road, approximate grid reference TQ 565 926.

Diagnosis. A *Linuparus* with large separate pyriform supraorbital spines, with prominent pits as surface decoration on ridges and spines.

Description. *Cephalothorax*. Large separate pyriform supraorbital spines on either side of the median line are divided by a deep U-shaped depression. The frontal margin runs slightly concave outwards from near the base of these spines to end in a prominent anteriorly directed anterolateral spine. The dorsal surface along the frontal margin bears evenly spaced blunt tubercles; the front edge of the margin is at right angles to the dorsal surface and is smooth except for rare fine tubercles, which tend to increase in number towards the anterolateral angle.

Directly behind and in line with the supraorbital spines are blunt postorbital spines, which continue back in the form of rounded ridges; between and parallel to these is a small rounded median ridge, separated by a small gap from a rounded tubercle at the front. Posterior to this, there is on each side a rounded carina. These diverge slightly almost as far as the cervical groove where they converge enclosing a flat area. From near the base of the supraorbital spines rounded carinae extend outwards in a curve to the cervical groove. These carinae are ornamented with two or three blunt tubercles. External to these carinae the carapace slopes vertically, then becomes nearly horizontal as far as the lateral margin where it slopes steeply again and begins to curve inwards. The lateral margin is slightly concave for one third the length from the anterolateral spine to where it erupts into another prominent forward pointing spine, beyond which it curves inwards to the cervical groove. The carapace in front of the cervical groove is ornamented with numerous pits on the spines, ridges, tubercles, and carinae, whilst the flat or concave areas are nearly smooth with fine tubercles. The cervical groove is deep. Behind it are three parallel longitudinal carinae, of which the median one is prominent; the carapace between the median and the lateral carinae slopes steeply away from the centre with a slight concavity until it reaches the outer margin. Just in front of the posterior margin of the carapace is a broad, smooth transverse groove, which interrupts the median carina and curves back on either side, becoming narrower towards the outer margins. The carapace behind the cervical groove is ornamented with fine equal-sized tubercles except for the carinae which are covered with pits.

Abdomen. The abdomen tapers slightly towards the tail. The carinae on the carapace continue as ridges on each tergum. The first somite has one anteriorly directed spine on the central ridge at the posterior margin. In front of this a groove runs almost parallel to the posterior margin for approximately half the width of the somite where it forks, one branch to the posterior margin at the outer edge, the other forward to the outer edge near the front of the somite. The two triangular areas enclosed by these branches are deeply pitted, whilst the area in front is smooth with very fine punctae. Somites two, three and four have two anteriorly directed spines on the central ridge of the tergum, separated midway by a deep transverse groove; this slopes back on either side to cut the outer ridge just in front of the posterior margin. On each of the outer ridges are two forward pointing spines, one in front, the other behind the groove. The tergum surface is deeply pitted, except the grooves which are smooth. The fifth somite lacks spines, and the posterior groove has almost disappeared. The sixth has a deep median groove with a prominent longitudinal line of pits on either side. The tergum of each somite is triangular in transverse section with a slight flattening towards the outer ridge.

Ventral surfaces. The epistome has a deep median furrow; anteriorly running parallel to this furrow is a large forward pointing blunt tubercle, the top surface of which has a line of several deep pits. The front edge of the epistome is concave with steeply sloping sides, ornamented with variably sized fine tubercles with some shallow pits.

Appendages. The antennular somite is longitudinally rectangular, with a deep, broad, median furrow extending forward between the basal segments of the antennae. The first podomere of the antennal peduncle has two forward-pointing spines on the outer edge; the top surface is coarsely pitted, the underside smooth, with fine well-spaced pits. The second podomere is nearly half the width of the first and has small spines on the outer edge. The third is smaller than the second with two spines on the inner margin. The flagellum is longitudinally grooved on the upper and lower surfaces.

On the third maxilliped the merus is two thirds the length of that on the first pereiopod, its outer side flat, inner edge flattened, margin tuberculate, surfaces deeply pitted. The first pereiopod is larger than the remainder. The merus is equal in length to the total length of the carpus, propodus, and dactylus, roughly oval in cross-section, flattening on the underside towards the front, the surface becoming concave; the inner margin is tuberculate, the surfaces decorated with small tubercles. The carpus is rectangular, flattened at the merus and increasing in depth towards the front (i.e. triangular in side view) and decorated with various sized tubercles. The propodus is slightly longer than the carpus, approximately oval in cross-section but slightly flattened, the surfaces with tubercles and pits. The dactylus, one third the length of the merus, is pointed distally; fragments of the inner margin show a line of large shallow pits with very fine pits inside these. Merus, carpus, and propodus of the second pereiopod are similar to the first but smaller.

EXPLANATION OF PLATE 66

Figs. 1–5. *Linuparus eocenicus* Woods. 1–3, London Clay, Portsmouth Docks. 1 and 2, dorsal and ventral view of lectotype, SM C7735, ×1. 3, lateral view, SM C7733, ×0·65. 4 and 5, Bracklesham Group, Whitecliff Bay. 4, anterior, showing supraorbital spines, BM In.63371, ×0·7. 5, antennular somite, BM In.63374, ×0·6.

Figs. 6–8. *Linuparus scyllariformis* (Bell), London Clay. 6, dorsal view, OUM L555, Aveley, ×1. 7, ventral view, BM 59106, Whetstone, ×0·8. 8, supraorbital spines, OUM L462, Aveley, ×1.

Specimens in figs. 1, 2, and 6 have been whitened with ammonium chloride.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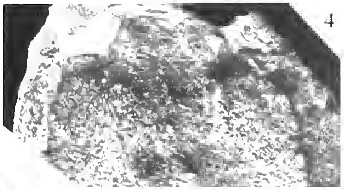
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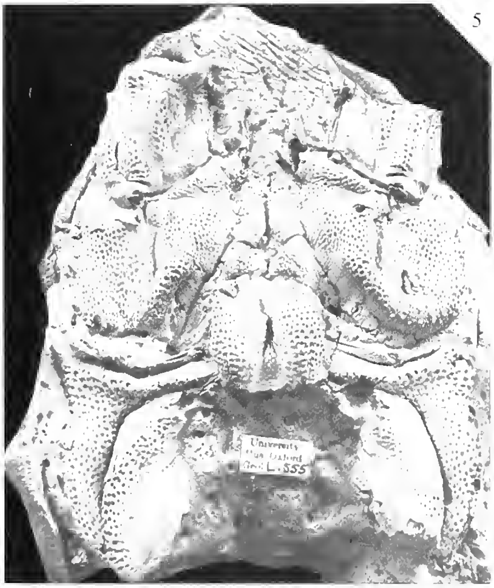
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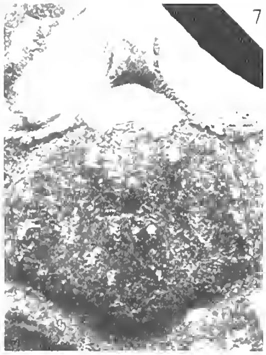
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QUAYLE, *Linuparus*

Discussion. On the other species of this genus the carinae and ridges are usually dentate or tuberculate. *L. scyllariformis* differs in that the area in front of the cervical groove is ornamented with numerous pits on the spines, ridges, tubercles, and carinae, and behind this groove the carinae are covered with pits.

Family SCYLLARIDAE Latreille, 1825
Genus SCYLLARIDES Gill, 1898

Type species. Scyllarus aequinoctialis Lund, 1793, by original designation, Recent.

Diagnosis. Eyes near anterolateral angles; lateral margins of carapace without deep fissures, rostrum salient.

Range. Lower Cretaceous–Recent.

Discussion. Woods (1926, p. 41) says of *S. koenigi* (= *S. tuberculatus*) 'This species agrees so closely with living forms of *Scyllarides* and differs from that of *Scyllarus* that there seems no reason for retaining Bell's genus *Scyllaridia*' (1858, p. 35). Holthuis (1954) proposed use of the Plenary Powers to render the name '*Scyllarides*' Gill, 1898 the oldest available for this species; *Scyllaridia* was suppressed by the International Commission (1954, Opinion 293, pp. 134–136). Glaessner (1969, R475) stated that 'if the fossil is not congeneric with the recent genus as claimed by Woods (1926), it must be given a new name'. However, the present author agrees with Woods that the fossil belongs to the Recent genus.

Scyllarides tuberculatus (König, 1825)

Plate 67, figs. 1–6

1825 *Cancer* (*Scyllarus*?) *tuberculatus* König, p. 3, pl. 4, fig. 54.
1843 *Cancer tuberculatus* König; Morris, p. 72.
1854 *Zanthopsis tuberculatus* König; Morris, p. 116.
1858 *Scyllaridia Koenigii* Bell, p. 35, pl. 8, figs. 1–3.
1870 *Scyllaridia Bellii* Woodward, p. 493, pl. 22, figs. 1 and 2.
1925 *Scyllarides koenigi* (Bell); Woods, p. 39, pl. 10, figs. 7–10.
1929 *Scyllarides koenigi* (Bell); Glaessner, p. 376.
1969 *Scyllarides*? *koenigi* (Bell); Glaessner, R475, fig. 281.3.
1974 *Scyllarides koenigi* (Bell); Cooper, p. 85.
1980 *Scyllarides tuberculatus* (König); Morris, p. 16.

Types. The holotype, by monotypy, is BM 42228 (Pl. 67, figs. 4 and 5), London Clay, Isle of Sheppey. Of Bell's figured specimens, syntypes of *S. Koenigii*, the original of pl. 8, fig. 1, is missing; pl. 8, fig. 2 is BM 59115 (Pl. 67, fig. 6) and fig. 3 is BM 46364, both from the London Clay, Isle of Sheppey.

Other material. OUM L566 (Pl. 67, figs. 2 and 3); BM In.63387–In.63389 (Pl. 67, fig. 1), *ex* JSQ Collection; all from the London Clay, Isle of Sheppey.

EXPLANATION OF PLATE 67

Figs. 1–6. *Scylarides tuberculatus* (König), London Clay, Isle of Sheppey, Kent. 1, ventral view, BM In.63389, × 2·5. 2 and 3, OUM L566. 2, somites four to six with calcified part of telson, × 1·4. 3, lateral view, × 2·4. 4 and 5, dorsal and lateral view of the holotype, BM 42228, × 1·2 and 1·1. 6, dorsal view, BM 59115, × 1·45.

Figs. 7–9. *Bathysquilla wetherelli* (Woodward), London Clay, Isle of Sheppey, Kent. 7 and 8, BM In.63390. 7, fragments of carapace, thoracic somites six to eight, abdominal somites one to four, × 1. 8, part of the raptorial claw, × 5. 9, abdominal somites one to five, BM In.63391, × 2·3.

Specimens in figs. 1–6 and 9 have been whitened with ammonium chloride.

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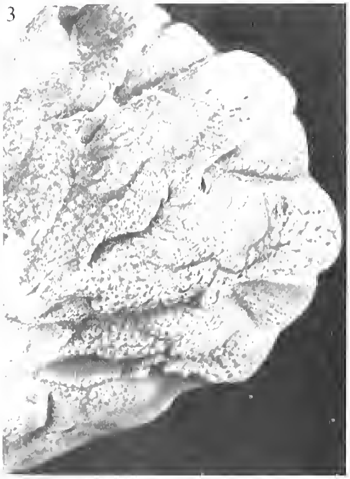

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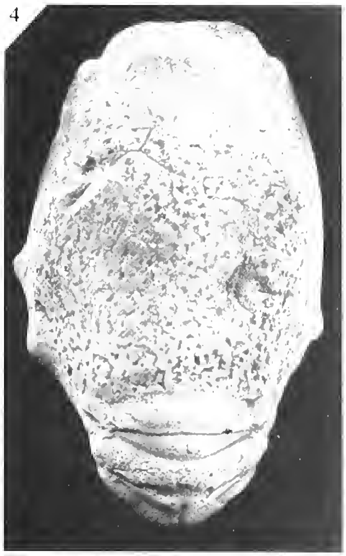

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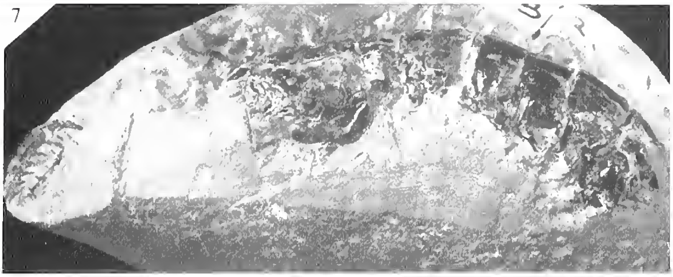

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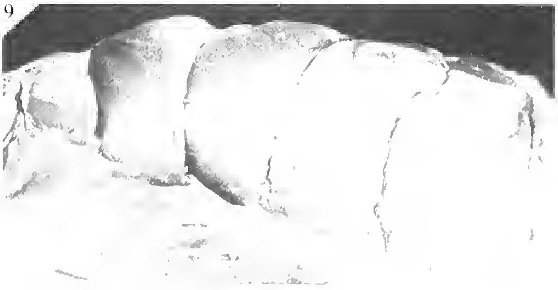

QUAYLE, *Scyllarides*, *Bathysquilla*

Horizon and locality. The London Clay, Isle of Sheppey and Whetstone, London; derived material from the London Clay, Red Crag, Felixstowe, and Walton-on-the-Naze.

Diagnosis. A *Scyllarides* with carapace and ridges covered with various sized tubercles, a large spiny tubercle on the median carina and another between this and the cardiac carina.

Description. The following is not a full description but consists of additions or changes to that of Woods (1925).

Cephalothorax. The margin between the rostrum and the preorbital spine is concave and occupies one quarter the anterior width. The strong anterodorsally directed preorbital spine is the continuation of a longitudinal carina which runs parallel to the median line, broken by the branchiocardiac groove, and continuing nearly to the posterior margin. Between the preorbital spine and the branchiocardiac groove lies a small blunt tubercle. The orbit is well rounded and terminates on the anterior margin; its lower margin bears an anteriorly directed spine on the outer side; the orbits occupy approximately one quarter of the anterior margin. The remainder of the margin to the anterolateral angle is slightly concave. There is a strong forward pointing lateral spine at the anterolateral angle reaching slightly further forward than the rostrum. The postcervical groove cuts the median line at right angles at a point approximately half the distance from the rostrum to the rear of the carapace; it forms an obtuse angle with the cervical groove, which is directed anterolaterally.

Some of the carapace tubercles have groups or lines of fine pores, possibly for setae. Larger pores lie in front of the tubercles on the elevated gastric region and lateral margins. There are other small round holes or pits at various places on the carapace. The outer margin runs slightly inwards from the anterolateral angle to the niche for the cervical groove. There are several forward pointing small blunt spines on this margin. The remainder of the lateral margin runs almost parallel, with several anteriorly directed blunt spines.

Abdomen. On the tergum of abdominal somites two to five a deep transverse groove cuts the median line at one third the distance from the front and runs forward until it reaches the anterior margin, just above the tergum boundary. A carina is formed on the median line behind this groove. Approximately half-way down the tergum a slight groove starts at right angles to the main groove and continues roughly in a semicircle to the posterior margin at the tergum boundary. This groove encloses a raised area which continues on to the pleura. The anterior margin slopes from the median line vertically to the tergum boundary, where a hollow boss accommodates the cone-shaped tubercle on the posterior margin of the previous somite. The margin then curves gently towards the rear and forms a scythe-like ventral spine with the posterior margin. The posterior margin ventral to the cone-shaped tubercle is slightly convex with a serrate edge of five or six downward pointing blunt spines. At the last of these spines the margin becomes strongly concave to form the posterior edge of the ventral spine. The posterior margins of the terga of somites five and six bear posteriorly directed blunt tubercles or spines. On the tergum of the sixth somite there is an additional groove, with a rear margin with blunt tubercles, instead of a median carina. On the pleuron of the sixth somite the posterior margin is slightly more concave, almost semicircular, to accommodate the tail members. The surfaces of somites one to six have irregular sized pits, both deep and shallow.

Telson. The calcified part of the telson has blunt tubercles of various sizes with groups or rows of fine pores towards the rear; towards the lateral margins the ornament changes to small irregular pits.

Ventral surfaces. The sternum, which is triangular with a median groove, is evident between the first and fifth pair of pereiopods. There is a pair of small tubercles at the front, flanking the median line, opposite the coxa of the first pereiopod. This is followed by four pairs of large tubercles, flanking the median line and opposite the coxae of the succeeding pereiopods. Between the last two pairs of tubercles on the median line is a round cavity. The posterior margin of the sternum is straight, the surfaces tuberculate on raised portions, smooth at the bottom of grooves.

Appendages. The coxae of the first to fifth pereiopods are triangular. The basis and ischium have a combined length similar to that of the coxa. The merus is oval in cross-section with a longitudinal ridge and pitted surfaces.

Discussion. König (1825) described and figured a unique specimen (BM 42228, Pl. 67, figs. 4 and 5) from the London Clay of the Isle of Sheppey, to which he gave the name *Cancer* (*Scyllarus*?) *tuberculatus*. Bell (1858, p. 36) considered that 'the whole surface of the carapace is fictitious, and the very tubercles on which the name was found exist only in obedience to the skill and trickery of the artist', an opinion with which Woods (1925) largely agreed. As a result of his misinterpretation, Bell disregarded König's name *tuberculatus* and substituted the honorific *Koenigi*. On examination by the present author, however, it became clear that this specimen consists of a normally preserved (i.e. with surface detail) abdomen of *Scyllarides* and an internal cast of the carapace. The general shape of the two tubercles on either side of the body as depicted by König (1825, pl. 4, fig. 54) is evident on the specimen. Bell's argument for changing the name of this species rested on the fact that he considered that the carapace surface and the tubercles were fictitious. König's original name is retained here, as advocated by Morris (1980).

Order STOMATOPODA Latreille, 1817
Family SQUILLIDAE Latreille, 1803
Genus BATHYSQUILLA Manning, 1963

Type species. *Lysiosquilla microps* Manning, 1961, by original designation, Recent.

Diagnosis. Telson with blunt median carina and all four pairs of marginal teeth with movable apices.

Range. Lower Eocene–Recent.

Bathysquilla wetherelli (Woodward, 1879)

Plate 67, figs. 7–9

1879 *Squilla wetherelli* Woodward, p. 549, pl. 26, fig. 1.
1969 *Squilla*? *wetherelli* Woodward; Holthuis and Manning, R541.
1974 *Squilla wetherelli* Woodward; Cooper, p. 85.
1980 *Squilla wetherelli* Woodward; Morris, p. 17.

Type. The holotype, by monotypy, is BM 59780 (Woodward 1879, pl. 26, fig. 1), London Clay, Highgate, Wetherell Collection.

Other material. BM 38399 collected W. Griffith; BM In.38262 collected D. J. Jenkins; In.63390 (Pl. 67, figs. 7 and 8) and In. 63391 (Pl. 67, fig. 9), both *ex* JSQ Collection.

Horizon and locality. All from the London Clay: BM In.38262, Beltinge, East Cliff, Herne Bay; BM 38399, BM In.63390, and In.63391, Isle of Sheppey.

Diagnosis. A stomatopod with a marginal carina on the abdominal somites and a fine transverse groove on the tergum of the second abdominal somite; the propodus of the raptorial claw is armed with spiniform teeth.

Description. The posterolateral angle of the carapace is well rounded, and the posterior margin straight. The surface of the thoracic tergites curves steeply ventrally on either side of the median line in a regular curve to the lateral margin of the tergum where there is a slight ridge. The pleura of somites seven and eight have a deep U-shaped indentation in the lateral margin. The width of the somites increases slightly towards the telson, eight being the widest at approximately half the width of the first abdominal somite. Abdominal somites one to four curve steeply ventrally on either side of the median line in a regular curve to the lateral margin where there is a slight ridge which turns slightly inwards to form a semicircular depression on the pleuron. This depression varies in width and depth; on the second somite it is nearly the full width and half the depth of the pleuron but it decreases in size on successively posterior pleura. The remaining surface of the pleuron is almost flat. The posterolateral angle of each pleuron is produced backwards into a small acute tooth and the posterior margin is straight. Each somite (one to four) has an oblong punctum on either side near the lateral margin of the terga; somites two to four bear two small sub-central puncta on the anterior border; three and four have a single central punctum on the posterior border. A fine groove, approximately two thirds the width of the tergum in length, runs parallel to the posterior margin and cuts the median line of the second somite at mid-point. Part of the tergum of the fifth somite is preserved with a single central punctum near the posterior margin. The sixth somite has a scabrous surface ornamentation.

The remains of the raptorial claw are evident on BM In.63390 (Pl. 67, fig. 8). Part of the inner margin of the propodus is preserved showing four equally spaced spiniform teeth. The dactylus is almost complete; the inner margin bears at least seven strong triangular teeth increasing in size to the terminal one.

Discussion. The Recent members of this group are abundant but are mainly restricted to tropical and subtropical seas. The type species *Lysiosquilla microps* was described by Manning (1961, p. 693) from two Recent specimens taken from 732 and 916–952 m off the east and west coasts of Florida.

Fossil stomatopods are rare and usually imperfectly preserved. The oldest known, *Sculda* Münster, 1840 (Holthuis and Manning 1969, R541), occurs in the Jurassic lithographic limestones of Solenhofen, Bavaria. New material from the Eocene of the Isle of Sheppey shows that the species described here cannot be included in the genus *Squilla*. Some of the diagnostic characters are not preserved but the longitudinal carinae on the abdomen and the upper margin of the propodus, and the even pectination of closely placed short blunt spinules are absent. This species shows similarities to both *Harpiosquilla* Holthuis, 1964 and *Bathysquilla*. The first closely resembles *Squilla* and has spaced spiniform teeth on the upper margin of the propodus of the raptorial claw but in all species the abdomen is strongly carinate. *Bathysquilla* lacks carinae on the abdomen and the propodus of the raptorial claw is armed with spiniform teeth. The affinities of this species therefore lie with *Bathysquilla*.

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ORDOVICIAN ACRITARCHS FROM THE MEITAN FORMATION OF GUIZHOU PROVINCE, SOUTH-WEST CHINA

by LI JUN

ABSTRACT. An early Arenig acritarch assemblage is described from the Meitan Formation of Tongzi, Guizhou Province, south-west China. Twenty-four species belonging to twenty genera are included. One new genus, *Tongzia*, and four new species, *Rhopaliophora membrana*, *Pirea sinensis*, *Schizodiacrodium*? *multiramiferum*, and *Tongzia meitana* are proposed. The assemblage belongs to the Mediterranean Province and shows that a homogeneous Arenig assemblage extended from east Newfoundland through the Mediterranean to south-west China.

COMPARED with other areas, notably Europe, Palaeozoic acritarchs have been neglected in China apart from some pioneering work. Cambrian sphaeromorphs from south-west China were described by Ouyang Shu *et al.* (1974). Xing Yusheng (1980, 1982) reported on seven genera from the Dachengsi Formation (Arenig) of Sichuan and on Lower Cambrian acritarchs from near Kunming of Yunnan, both in south-west China. Zhong Guofang (1981) described an assemblage from the Dawan Formation (late Arenig) from Hubei Province recording six genera of non-sphaeromorph acritarchs. Seven genera were recorded (Li Zaiping 1982) from the Machiakou Formation (late Arenig/Llanvirn) of Hebei Province, northern China.

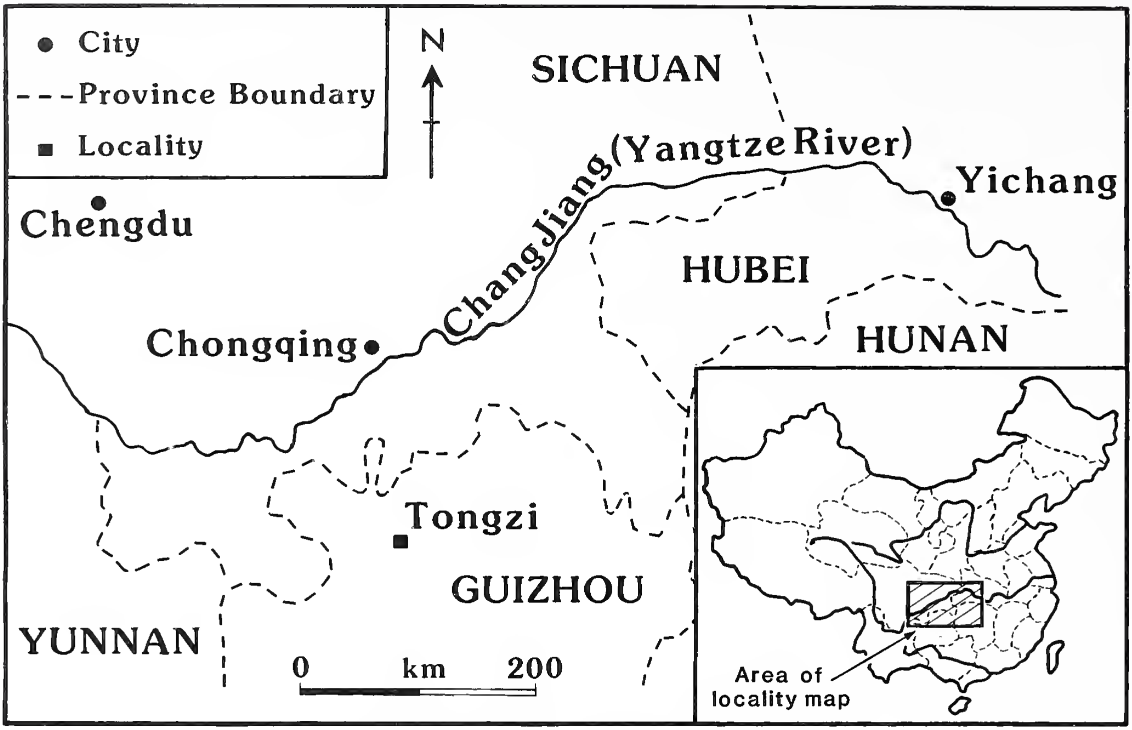
The present paper describes acritarchs from the Meitan Formation of Guizhou Province (text-fig. 1). In Arenig times this locality lay towards the centre of the Upper Yangtse Paraplatform about 350 km south-east of Xing Yusheng's locality on the Mount Emei Shan and about 550 km south-west of Zhong Guofang's locality in Yichang also in the same paraplatform. Li Zaiping's material came from north China about 1500 km to the north-east.

MATERIAL

Two samples of yellow-grey shale from the Meitan Formation from the Honghuayuan section at Tongzi were provided by Dr Geng Liangyu of the Nanjing Institute of Geology and Palaeontology. The section is at Honghuayuan (106° 51′ E., 28° 4′ N.), about 7 km south of Tongzi County, on the west slope of a hill: the beds dip at 7° to the north-east (bearing about 50°). The Ordovician consists of, in descending order, the Wufeng, Jiantsaokou, Pagoda, Shihtzupu, Meitan, Hunghuayuan, and Tungtzu formations. According to the description of the section by Zhang and Chen (1964), the Meitan Formation is 180 m thick and comprises a 92 m thick lower part, consisting of yellow-grey shales, and an 88 m thick upper part, consisting of yellow-grey sandy shales, both with thin-bedded limestone intercalations. Four graptolite biozones were set up within the lower part of the Meitan Formation, i.e. from base to top, *Didymograptus filiformis* Biozone, *D. protobifidus* Biozone, *D. deflexus* Biozone, and *Azygograptus suecicus* Biozone. These represent 15·5 m, 48 m, 23·5 m and 5·0 m respectively in terms of thickness. Sample MDZ, from the *D. deflexus* Biozone, is located 70 m above the base of the formation; sample MAZ from the *A. suecicus* Biozone is located 85 m above the base.

The material was prepared in the Department of Geology, University of Sheffield using standard palynological techniques. Organic residues were then sieved through a 20 μm mesh screen and mounted on slides. Acritarchs are well preserved, abundant, and yellow-brown in colour. Some dark-brown to black Chitinozoa were also seen. Specimens on strew slides are located by sample, slide, and co-ordinate code, for example, MAZ 44, T22/4 is sample MAZ, slide number 44, England Finder reference co-ordinate T22/4. The

[Palaeontology, Vol. 30, Part 3, 1987, pp. 613–634, pls. 68–72.]



TEXT-FIG. 1. Map of China showing the Tongzi locality.

types and illustrated material are housed in the collections of Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China.

SYSTEMATIC PALAEONTOLOGY

For brevity, only name changes are listed in synonomies

Group ACRITARCHA Evitt, 1963

Genus ACANTHODIACRODIUM Timofeev, 1958 emend. Deflandre and Deflandre-Rigaud, 1962

Type species. Acanthodiacrodium dentiferum Timofeev, 1958.

Acanthodiacrodium? *tasselii* Martin, 1969

Plate 71, figs. 5, 7, 8

Description. The vesicle is hollow and elongate oval in outline; the wall is single-layered and bears eight to fifteen processes at each pole. These may either be solid or hollow with their interior communicating with the inner cavity. The surface of the vesicle is ornamented by longitudinal ribs. No opening was observed.

Dimensions (five specimens). Length of vesicle 20–42 μm, breadth of vesicle 17–26 μm, ratio of vesicle length to breadth 1:0·8, rib spacing 1–3 μm, length of processes 3–8 μm.

Remarks. Actinotodissus Loeblich and Tappan (1978) differs from *Acanthodiacrodium* by having processes that communicate freely with the vesicle interior. When Martin (1969) established the species *A. tasselii* she did not mention whether or not the processes communicate with the vesicle interior. The present specimens, which resemble those described by Martin (1969) and Vavrdová (1972), are thus assigned to the genus *Acanthodiacrodium* with reservation.

Genus ADORFIA Burmann, 1970

Type species. Adorfia firma Burmann, 1970.

Adorfia cf. *firma* Burmann, 1970

Plate 70, fig. 7

Description. The vesicle is polygonal in outline; the wall is single-layered and carries irregularly distributed processes. These are short, plump, and communicate freely with the inner cavity. Distally they are manate with capitate pinnae mainly at the distal portion of the processes. No opening was observed.

Dimensions (two specimens). Diameter of vesicle 20–50 μm, process length 5–12 μm, process breadth 1·5–3·0 μm, process number peripherally about fourteen, length of pinnae 1–2 μm.

Remarks. The specimens here differ from type material of *Adorfia firma* Burmann 1970 from later Arenig of GDR by having more processes. They are distinguished from *Vogtlandia multiradialis* Burmann, 1970 (Arenig, GDR) and *Evittia flosmaris* Deunff, 1977 (Llanvirn, Morocco) by the presence of capitate pinnae.

Genus ARBUSCULIDIUM Deunff, 1968

Type species. Arbusculidium destombesii Deunff, 1968.

Arbusculidium filamentosum (Vavrdová) Vavrdová, 1972

Plate 68, figs. 1, 3, 5

1965 *Dasydiacrodium filamentosum* Vavrdová, pp. 355–356, pl. 3, fig. 3; pl. 4, fig. 1; text-fig. 4*a–c*.
1972 *Arbusculidium filamentosum* (Vavrdová); Vavrdová, p. 81, pl. 1, fig. 3.
1980 *Dasydiacrodium filamentosum* Vavrdová; Xing, p. 438.

Description. The vesicle is hollow, ellipsoidal to subcylindrical in outline. The processes are restricted to the polar areas; one pole carries three to five simple processes which are broad-based, hollow, communicating freely with the vesicle cavity. They taper gradually towards closed, pointed tips. The opposite pole bears a set of branching, anastomosing filose processes which are arranged in a circle around the pole, forming a collar-shaped net. The vesicle wall is about 0·5 μm and decorated by longitudinal ribs. No opening was observed.

Dimensions (eleven specimens). Length of vesicle 35–40 μm, breadth 25–32 μm, rib spacing 2–5 μm, process length 15–20 μm, length of the collar 10–20 μm.

Previous records. Arenig, Czechoslovakia (Vavrdová 1965); Arenig, GDR (Burmann 1968); ?Upper Arenig or lower Llanvirn, Morocco (Cramer, Allam *et al.* 1974); Wenlock (reworked?), Belgium (Martin 1969); Arenig, France (Rauscher 1974); Arenig–Llanvirn, East Newfoundland (Martin, in Dean and Martin 1978); Arenig, China (Xing 1980).

Genus BALTISPHAERIDIUM (Eisenack 1958) emend. Eisenack, 1969

Type species. Baltisphaeridium (as *Ovum hispidum*) *longispinosum* Eisenack, 1931. Holotype lost. Neotype: *B. l.* (as *filifera*) *longispinosum* Eisenack, 1959.

Baltisphaeridium longispinosum longispinosum (Eisenack 1931) Staplin *et al.*, 1965

Plate 72, fig. 2

1931 *Ovum hispidum longispinosum* Eisenack, p. 110, pl. 5, figs. 6–12, 14–17.
1938 *Hystrichosphaeridium longispinosum* (Eisenack) Eisenack, p. 12, pl. 1, figs. 4, 6, 7.
1959 *Baltisphaeridium longispinosum filifera* Eisenack, p. 195, pl. 15, fig. 1.

1965 *Baltisphaeridium longispinosum* Eisenack; Eisenack, p. 134, pl. 13, figs. 1 and 2.
1965 *Baltisphaeridium longispinosum longispinosum* (Eisenack) Staplin *et al.*, p. 190, pl. 20, figs. 11 and 15; text-fig. 11.

Description. The vesicle is hollow, circular to subcircular in outline. The wall is single-layered, bearing regularly arranged processes. These are hollow, shut off from the inner cavity, and closed distally. The length of processes is variable, usually equal to or exceeding the vesicle diameter. No opening was observed.

Dimensions (five specimens). Vesicle diameter 48–56 μm, length of process 35–60 μm, breadth of process 1·0–2·5 μm.

Remarks. This taxon, although characteristic of the Baltic Province, appears to have a world-wide distribution.

Previous records. Upper Arenig to upper Llandovery, Baltic (Eisenack 1931); Upper Llanvirn to Llandeilo, Sweden (Eisenack 1965; Staplin *et al.* 1965); Upper Arenig and Caradoc, Poland (Gorka 1969); Caradoc to Ashgill, Belgium (Martin 1974); Llanvirn, France (Rauscher 1974).

Genus CORYPHIDIUM Vavrdová, 1972

Type species. Coryphidium bohemicum Vavrdová, 1972.

Coryphidium bohemicum Vavrdová, 1972

Plate 72, figs. 5 and 9

1972 *Coryphidium bohemicum* Vavrdová, pp. 84–85, pl. 1, figs. 1 and 2; text-fig. 4.

Description. The vesicle is hollow, subquadrate in outline, with round corners. The wall is single-layered, about 0·5 μm thick and is ornamented by striate ribs, densely spaced (approximately 1–2 μm) and parallel to the edges. Numerous processes decorate the surface; they are proximally opened, truncated or bifurcate distally. The process distribution is more or less regular over the surface, with some concentration at the corners. On some specimens, a round to oval opening occurs.

Dimensions (more than thirty specimens). Length of vesicle edge 24–34 μm, rib spacing 0·5–1·0 μm, process length 3–9 μm, process number at each corner eight to fifteen.

Previous records. Arenig, Llanvirn, Czechoslovakia (Vavrdová 1972); Arenig, France (Rauscher 1974; Cocchio 1982); Upper Arenig to lower Llanvirn, Morocco (Cramer, Allam *et al.* 1974); Arenig to Llanvirn, Belgium (Martin and Rickards 1979); Arenig, east Newfoundland (Martin, in Dean and Martin 1978); Arenig, China (Xing 1980); Arenig to lower Llanvirn, Britain (Downie 1984); Arenig, Sardinia (Albani, Di Milia *et al.* 1985).

Genus CRISTALLINIUM Vanguestaine, 1978

Type species. Cristallinium cambriense (Slavikova) Vanguestaine, 1978.

EXPLANATION OF PLATE 68

All figures × 1000.

Figs. 1, 3, 5. *Arbusculidium filamentosum* (Vavrdová) Vavrdová, 1972. 1, MAZ 46, M40/1; 3, MDZ 1, N27; 5, MDZ 1, F22/2.
Fig. 2. *Veryhachium trispinosum* (Eisenack 1935) Deunff, 1954 ex. Downie, 1959. MAZ 46, M24/3.
Fig. 4. *Leiosphaeridia tenuissima* Eisenack, 1958. MDZ 1, K43/1.
Fig. 6. *Cristallinium dentatum* (Vavrdová) Martin, 1982. MDZ 35, P33/4.

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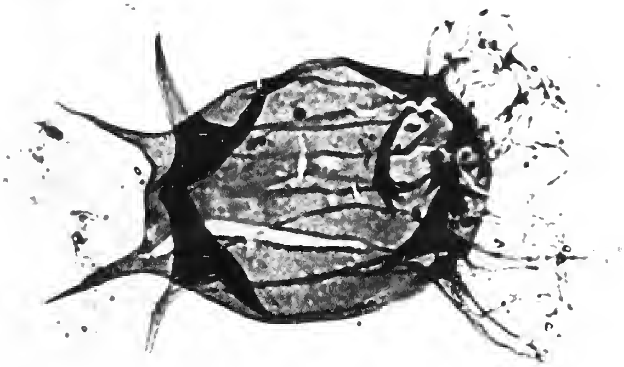

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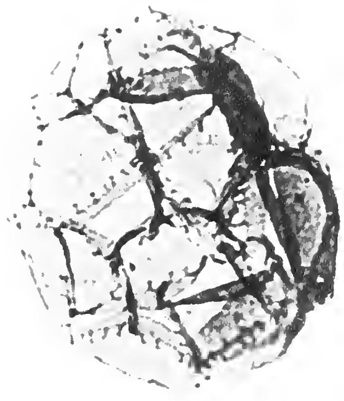

6

LI JUN, *Ordovician acritarchs*

Cristallinium dentatum (Vavrdová) Martin, 1982

Plate 68, fig. 6

1976 *Staplinia dentata* Vavrdová, p. 58, pl. 2, figs. 5 and 6; text-fig. 5.
1978 *Dictyotidium*? *dentatum* (Vavrdová) Martin, in Dean and Martin, p. 8, pl. 3, figs. 14 and 28.
1982 *Cristallinium dentatum* (Vavrdová) Martin, p. 36.

Description (based on a single specimen). The vesicle is subcircular to polygonal in outline. The wall is thin and divided into numerous polygonal fields. The edges of the polygonal fields bear several short, solid and capitate processes.

Dimensions. Diameter of vesicle 40–45 μm, height of processes about 1 μm, process number at each edge six to nine.

Previous records. Upper Arenig, Czechoslovakia (Vavrdová 1976); Arenig, east Newfoundland (Martin 1982).

Genus CYMATIOGALEA (Deunff 1961) Deunff, Gorka and Rauscher, 1974

Type species. Cymatiogalea margaritata Deunff, 1961.

Cymatiogalea cf. *cristata* (Downie 1958) Deunff, Gorka and Rauscher, 1974

Plate 72, figs. 3 and 4

Description. The vesicle is hollow, circular or hemicircular in outline; wall is usually divided into polygonal areas by low sutural ridges. Four to six processes are arranged along each side, they are decorated with lateral spines which branch into two to four pinnae distally; in some cases second-order branching can be seen. Excystment is by a large subpolygonal to round opening.

Dimensions (eighteen specimens). Diameter of vesicle 24–45 μm, size of opening 14–38 μm, length of processes 5–12 μm, length of branching 1–3 μm.

Remarks. The specimens here differ from the Tremadoc type material of *Cymatiogalea cristata* from England by the presence of lateral processes and second-order branching and the lack of flanges on the vesicle wall.

Cymatiogalea cuvillieri? (Deunff 1961) Deunff, 1964

Plate 72, fig. 8

Description. The single specimen recorded has a vesicle with subcircular outline, the surface of the vesicle is divided into polygonal fields, the boundaries of which are formed by short spines, 2–3 μm in height, and about three to five spines can be seen on each boundary. The wall is simple and *c.* 0·5 μm thick, decorated by small verrucae. At one pole of the vesicle an opening occurs, the diameter of which is *c.* 18 μm, approximately three-quarters the size of the vesicle.

Remarks. The single poorly preserved specimen is questionably assigned to *Cymatiogalea cuvillieri*, a species usually recorded from the Tremadoc.

Genus LEIOSPHAERIDIA (Eisenack 1958) Downie and Sarjeant, 1963

Type species. Leiosphaeridia baltica Eisenack, 1958*a*.

Leiosphaeridia tenuissima Eisenack, 1958*b*

Plate 68, fig. 4

1958*b* *Leiosphaeridia tenuissima* Eisenack, pp. 391–392, pl. 2, figs. 1 and 2.

Description. The vesicle is hollow and circular in outline, the wall is single-layered, very thin (*c.* 0·2 μm thick), without process and ornamentation, although some compressional folds occur. No opening was observed.

Remarks. Sphaeromorphs are not common and are represented in the present study only by this species and *Synsphaeridium* cf. *gotlandicum* Eisenack, 1965.

Previous records. Tremadoc, USSR (Eisenack 1958*a*); undivided Palaeozoic, North Africa (Combaz 1966); Caradoc, England (Turner 1984).

Genus MULTIPLICISPHAERIDIUM (Staplin 1961) Lister, 1970

Type species. *Multiplicisphaeridium ramispinosum* Staplin, 1961.

Multiplicisphaeridium cf. *irregulare* Staplin, Jansonius and Pocock, 1965

Plate 70, figs. 9 and 10

Description. The vesicle is subcircular in outline; the wall is thin, about 0·5 μm thick, and carrying numerous processes. These are conical, hollow, and communicate freely with the inner cavity. Distally they are simple or branching. Branching occurs in an irregular manner at any distance from the process base. No opening was observed.

Dimensions (seven specimens). Diameter of vesicle 12 μm, process length 11–13 μm, number of processes peripherally fourteen to twenty-two.

Remarks. The specimens here are considerably smaller than the typical ones from Anticosti Islands (vesicle diameter 25–35 μm, Staplin *et al*. 1965). Jacobson and Aïcha (1985) argued that the depth of 3005 ft from which *Multiplicisphaeridium irregulare* was recorded, was not the Middle Ordovician Trenton Formation as originally reported, but the Upper Ordovician (lower–middle Ashgillian) Vaureal Formation.

Genus PETALOFERIDIUM Jacobson, 1978

Type species. *Petaloferidium stigii* Jacobson, 1978.

Petaloferidium florigerum (Vavrdová 1977) Jacobson, 1978

Plate 72, fig. 7

1977 *Evittia florigera* Vavrdová, p. 116, pl. 4, figs. 1–10; text-fig. 6*a*, *b*.
1978 *Petaloferidium florigerum* (Vavrdová) Jacobson, p. 296.

Description (based on single specimen). The vesicle is hollow and subcircular to polygonal in outline. The wall is single-layered, laevigate, and carries processes which are open to the inner cavity but are closed distally, where there is a pronounced swelling and a darker spot.

Dimensions. Vesicle diameter 20 μm, process length 3–5 μm, process number fourteen.

Remarks. This species may need to be subdivided since specimens from early Llanvirn of Czechoslovakia (Vavrdová 1977, 1982) included both laevigate and striate forms, multi-process and two-process forms. Single specimen here fits Vavrdová's multi-horn but has no striations.

Previous records. Early Llanvirn, Czechoslovakia (Vavrdová 1977, 1982).

Genus PETEINOSPHAERIDIUM Staplin, Jansonius and Pocock, 1965

Type species. *Peteinosphaeridium trifurcatum trifurcatum* ex *P. bergstromii* Staplin, Jansonius and Pocock, 1965.

Peteinosphaeridium trifurcatum intermedium Eisenack, 1976

Plate 72, fig. 9

1976 *Peteinosphaeridium trifurcatum intermedium* Eisenack, p. 195, pl. 4, figs. 8–11.
1976 *Peteinosphaeridium trifurcatum* Eisenack; Kjellstrom, p. 36, fig. 29.
1984 *Peteinosphaeridium trifurcatum intermedium* Eisenack; Turner, pp. 132–133, pl. 9, figs. 1, 4–6.

Description. The vesicle is circular in outline, the wall is firm, single-layered, *c.* 1 μm thick, carrying numerous processes; these are solid, distally trifurcate or quadrifurcate and bear delicate, more or less transparent longitudinal membranes. The vesicle wall is granulate. Excystment is by means of a pylome.

Dimensions (eighteen specimens). Diameter of vesicle 32–46 μm, process length 6–12 μm, branch length 1–4 μm, number of processes peripherally twenty-five to thirty-eight.

Remarks. Eisenack (1976) attributed two infraspecific taxa to the species *Peteinosphaeridium trifurcatum*, i.e. *P. trifurcatum intermedium* and *P. trifurcatum hypertrophicum*. Only the former was found in the present study.

Previous Records. Arenig, Baltic (Eisenack 1976); Llanvirn–Llandeilo, Sweden (Kjellstrom 1976); Caradoc, Kentucky, USA (Jacobson 1978); Caradoc, England (Turner 1984).

Genus PIREA Vavrdová, 1972

Type species. Pirea colliformis (Burmann) Vavrdová, 1977.

Pirea sinensis sp. nov.

Plate 70, figs. 1–4

Derivation of name. Sinae (Latin), Chinese.

Holotype. Plate 70, fig. 1 (MAZ 44, X49).

Isotypes. Plate 70, fig. 2 (MAZ 44, Q23); fig. 3 (MAZ 46, D23); fig. 4 (MAZ 44, E23/4).

Locality and horizon. West slope of Honghuayuan Hill in Tongzi County, Guizhou, China; 85 m above the base of Meitan Formation, Arenig, Ordovician.

Diagnosis. Vesicle pear-shaped with a single process drawn out from apical end, wall decorated by solid spines, randomly distributed in the antapical part but apically forming longitudinal rows. Excystment by a pylome at the antapical end.

Dimensions (eleven specimens). Vesicle length 62–78 μm, vesicle breadth 36–45 μm, process length 11–15 μm, process breadth 7–10 μm, spine length 0·5–1·0 μm, spine spacing *c.* 1 μm, spacing of longitudinal rows 1·0–1·5 μm. Diameter of pylome 8–12 μm.

Description. The vesicle is hollow, thin walled, and ovate in outline. A single process is drawn out from the apical end. This is hollow, communicating with the vesicle, and is distally closed and slightly expanded. The wall of the test in the lower three-quarters is densely covered with uniform, small, solid, often capitate spines distributed randomly. At the apical end they form longitudinal rows. Excystment is by a pylome at the antapical end, with or without operculum.

Comparison. The new species resembles *Pirea ornatissima* Cramer and Diez, 1977, but can be distinguished by the ornamentation. *P. ornatissima* is also decorated with solid sculptural elements on the lower part of the vesicle; but apically the wall is smooth, with about a dozen longitudinal folds. *P. sinensis* is ornamented by capitate spines randomly distributed in the lower part of the vesicle, and the spines are arranged in longitudinal rows that extend onto the process at the apical end.

Genus POLYGONIUM Vavrdová, 1966

Type species. Polygonium gracilis Vavrdová, 1966.

Polygonium gracile Vavrdová, 1966

Plate 72, fig. 1

1966 *Polygonium gracilis* Vavrdová, p. 413, pl. 1, fig. 3; pl. 3, fig. 1; text-fig. 4*a*, *b*.
1972 *Polygonium gracile* Vavrdová, p. 80.

Description. The vesicle is hollow, polygonal or subpolygonal in outline, with sides more or less equal in length and slightly concave. The wall is single-layered, with long, simple processes drawn out at corners. They number twelve to fifteen, communicate freely with inner cavity and are closed distally, with wide bases and pointed tips. No opening was observed.

Dimensions (thirty-two specimens). Diameter of vesicle 24–31 μm, length of process 10–18 μm.

Remarks. The commonest species in the present study, with related species of *Tectitheca* which may integrate with *Polygonium*, it makes up more than 30% of the total assemblage.

Previous records. Arenig, Czechoslovakia (Vavrdová 1966, 1972); Arenig, France (Rauscher 1974); Later Arenig to early Llanvirn, Morocco (Cramer, Allam *et al.* 1974); Upper Cambrian to lower Llanvirn, Britain (Downie 1984).

Genus RHOPALIOPHORA Tappan and Loeblich, 1971

Type species. Rhopaliophora foliatilis Tappan and Loeblich, 1971.

Rhopaliophora membrana sp. nov.

Plate 71, figs. 1 and 3

Derivation of name. Referring to the membrane-like processes.

Holotype. Plate 71, fig. 1 (MAZ 45, N32/1).

Isotype. Plate 71, fig. 3 (MDZ 3, P33/3).

Locality and horizon. West slope of Honghuayuan Hill in Tongzi County, Guizhou, China; 70 and 85 m above the base of the Meitan Formation, Arenig, Ordovician.

Diagnosis. Vesicle circular to subcircular in outline, with membrane-like processes appearing as irregular extension; excystment by means of pylome.

Description. The vesicle is *c.* 1 μm thick, with membrane-like processes of varying shape, width, number, and extension; the vesicle surface is ornamented by microgranules. Excystment is by a round pylome with an elevated rim. Double pylome occurs on some specimens, and free opercula have been seen in some cases.

Dimensions (twelve specimens). Vesicle diameter 28–46 μm, process length 3–16 μm, pylome diameter 13–16 μm.

Remarks. This species differs from other species of *Rhopaliophora* by the membrane-like processes.

Rhopaliophora palmata (Combaz and Peniguel) Playford and Martin, 1984

Plate 71, figs. 4 and 6

1972 *Peteinosphaeridium palmatum* Combaz and Peniguel, p. 136, pl. 2, figs. 4, 9–12.
1984 *Rhopaliophora palmata* (Combaz and Peniguel) Playford and Martin, pp. 210–212, fig. 9A–N.

Description. The vesicle is hollow and circular to subcircular in outline. The wall is single-layered, carrying numerous short, stout processes. The processes may be variable in shape and length, separated from inner cavity. The body surface is psilate. Excystment is by a circular pylome with elevated rim.

Dimensions (eight specimens). Vesicle diameter 27–32 μm, length of process 2–5 μm, process spacing 5–8 μm, pylome diameter 5–9 μm.

Previous records. Arenig to Llanvirn, Canning Basin, Australia (Combaz and Peniguel 1972; Playford and Martin 1984).

Genus SCHIZODIACRODIUM Burmann, 1968

Type species. Schizodiacrodium ramiferum Burmann, 1968.

Schizodiacrodium? *multiramiferum* sp. nov.

Plate 69, figs. 4–6

Derivation of name. multi (Latin), numerous; *ramiferum* (Latin), branched. Referring to presence of numerous processes.

Holotype. Plate 69, fig. 4 (MAZ 46, T22/4).

Isotype. Plate 69, fig. 6 (MAZ 47, F43).

Locality and horizon. West slope of Honghuayuan Hill in Tongzi County, Guizhou, China; 85 m above the base of the Meitan Formation, Arenig, Ordovician.

Diagnosis. Vesicle polyhedral, slightly elongated, with numerous processes arranged on polar areas; processes bifurcate, trifurcate, or multifurcate, all branches recurved.

Description. The vesicle is slightly elongate, polyhedral in outline and somewhat centrally constricted. The wall is thin, *c.* 0·3 μm thick and carries numerous processes on polar areas. These are arranged in a circle, are broadly based, communicating freely with the inner cavity, and branched distally. The branching angle varies from 80 to 150°. Branching is bifurcate, trifurcate, or multifurcate. All branches are slender, characteristically recurved, with closed tips. Occasionally second-order branches occur. No opening was observed.

Dimensions (nine specimens). Vesicle length 32–38 μm, breadth 20–25 μm, process breadth 2–5 μm, process number at each pole nine to eleven, branch length 5–7 μm, branch breadth 0·2–0·5 μm.

Remarks. In some cases polar differentiation is weak (see Pl. 70, fig. 5) and therefore this taxon is questionably assigned to genus *Schizodiacrodium*. The present species differs from others of *Schizodiacrodium* in having strikingly recurved branches. *Multiplicisphaeridium maroquense* Cramer, Allam *et al*., 1974 and *Vogtlandia flos* Martin, 1978 also have similarly recurved branches, the former may differ from the new species by having fewer processes (four to seven) and the latter by radial symmetry instead of axial symmetry.

Genus STRIATOTHECA Burmann, 1970

Type species. Striatotheca principalis Burmann, 1970.

Striatotheca principalis parva Burmann, 1970

Plate 70, fig. 5

1970 *Striatotheca principalis parva* Burmann, p. 300, pl. 8, fig. 6.

Description. The vesicle is quadrate to rectangular in outline, with approximately straight sides, each corner passes into a gradually tapering process. The processes communicate freely with the inner cavity and are closed distally. The body surface is decorated by subparallel ribs, which extend on to the proximal quarter of the processes. No opening was observed.

Dimensions (twenty-four specimens). Vesicle length 25–34 μm, rib spacing 1 μm, rib breadth 0·5–0·8 μm, process length 16–20 μm.

Previous records. Arenig, GDR (Burmann 1970); Arenig, France (Rauscher 1974); Upper Arenig, Italy (Tongiorgi and Di Milia 1984); Upper Arenig, Hungary (Albani, Lelkes-Felváry *et al.* 1985).

EXPLANATION OF PLATE 69

All figures × 1000.

Figs. 1–3. *Tongzia meitana* gen. et sp. nov. 1, holotype, MAZ 45, L48; 2, MAZ 44, T52/4; 3, MAZ 45, X54.

Figs. 4–6. *Schizodiacrodium*? *multiramiferum* sp. nov. 4, holotype, MAZ 46, T22/4; 5, MAZ 46, M12; 6, MAZ 47, F43.

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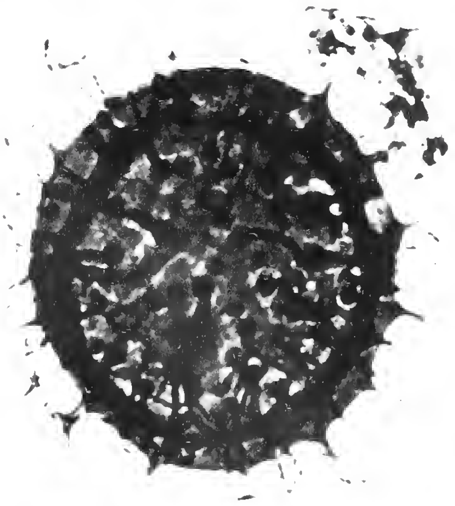

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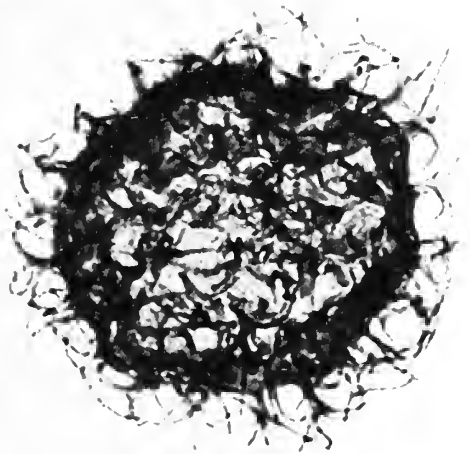

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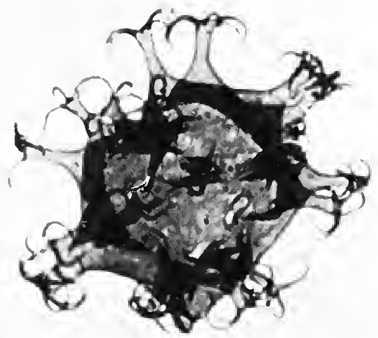

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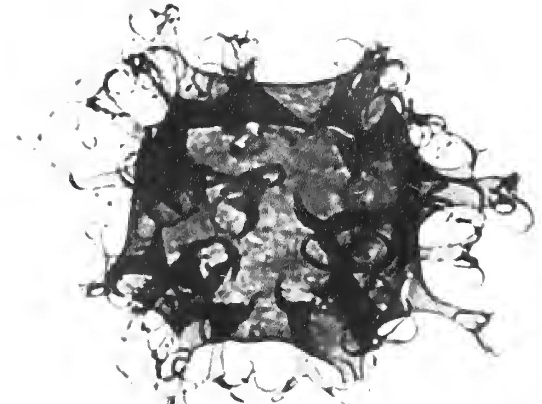

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LI JUN, *Tongzia*, *Schizodiacrodium?*

Striatotheca quieta (Martin 1969) Rauscher, 1974

Plate 70, fig. 6

1969 *Veryhachium quietum* Martin, pp. 101–102, pl. 5, fig. 225; pl. 6, fig. 293; text-fig. 48.
1970 *Striatotheca acutiuscula* Burmann, p. 303, pl. 8, figs. 3 and 4.
1974 *Rugulidium quietum* (Martin) Cramer, Allam *et al.*, p. 60, pl. 25, fig. 12; pl. 26, figs. 15–17.
1974 *Striatotheca quieta* (Martin) Rauscher; p. 76, pl. 3, fig. 10.

Description. The vesicle is quadrate on outline, with slightly bulging sides. The processes, which are short, conical, hollow, and with obtuse tips, extend from each corner. The surface of the vesicle is ornamented by subparallel, fine, closely spaced ribs.

Dimensions (four specimens). Length of vesicle 26–30 μm, rib breadth 0·5 μm, rib spacing 1 μm, length of process 2–5 μm.

Previous records. Late Arenig or early Llanvirn, Morocco (Cramer, Kanes *et al.* 1974); Arenig, France (Rauscher 1974); Upper Arenig, Italy (Tongiorgi and Di Milia 1984); Late Llanvirn, GDR (Burmann 1970); Caradoc (reworked), England (Turner 1982); Wenlock (reworked?), Belgium (Martin 1969).

Striatotheca cf. *transformata* Burmann, 1970

Plate 70, fig. 8

Description. The vesicle is pentagonal in outline. The wall is single-layered, *c.* 0·3 μm thick. Five processes are drawn out at corners; they communicate with the inner cavity and are closed distally, with pointed tips. Surface of vesicle is decorated by ribs, which cover the entire surface of the body and extend to the base of the processes. They are subparallel to the edges, forming incomplete pentagons. No opening was observed.

Dimensions (two specimens). Height of the pentagon 20–30 μm, breadth of rib 0·3 μm, rib spacing 1·0–1·5 μm, length of edge 17–23 μm, length of process 10–15 μm.

Remarks. Like *Striatotheca transformata* from GDR, which is also Arenig in age, the specimens here have five processes, but differ in having pentagonal outlines instead of a quadrate one.

Genus SYNSPHAERIDIUM Eisenack, 1965

Type species. Synsphaeridium gotlandicum Eisenack, 1965.

Synsphaeridium cf. *gotlandicum* Eisenack, 1965

Plate 71, fig. 2

Description. The individual bodies are subcircular to ellipsoidal in outline, and form irregularly shaped clusters. The wall is single-layered, decorated with hairs. No opening was observed.

Dimensions (two clusters). Individual body diameter 19–30 μm, number of individuals on each cluster fifteen to thirty, cluster diameter 60–100 μm, length of hairs 0·5–1·0 μm.

EXPLANATION OF PLATE 70

Unless otherwise specified, all figures × 1000.

Figs. 1–4. *Pirea sinensis* sp. nov. 1, holotype, MAZ 44, X49; 2, MAZ 44, Q23; 3, MAZ 46, D23; 4, MAZ 44, E23/4.

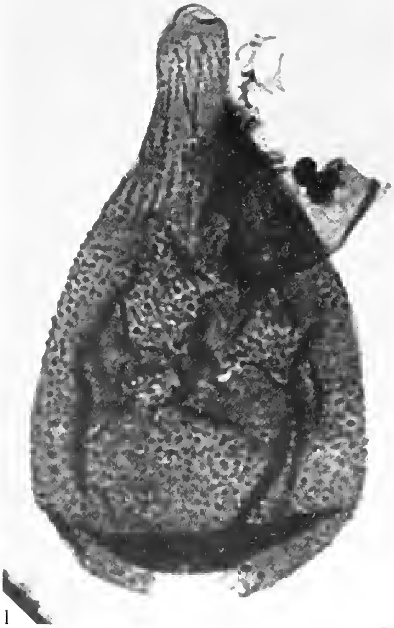
Fig. 5. *Striatotheca principalis parva* Burmann, 1970. MAZ 44, B34, ×900.

Fig. 6. *S. quieta* (Martin) Rauscher, 1974. MAZ 44, G44.

Fig. 7. *Adorfia* cf. *firma* Burmann. MAZ 46, L26/3.

Fig. 8. *S.* cf. *transformata* Burmann. MAZ 44, R39, ×900.

Figs. 9 and 10. *Multiplicisphaeridium* cf. *irregulare* Staplin *et al.* 1965. 9, MAZ 44, Q43; 10, MAZ 45, C42/2.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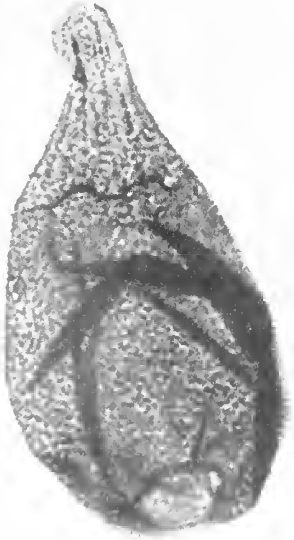
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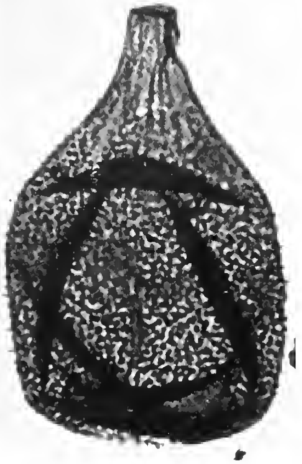
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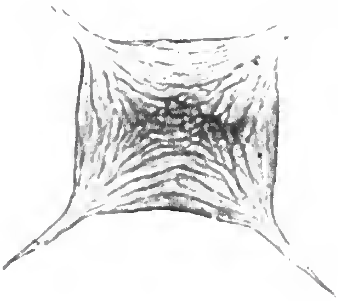
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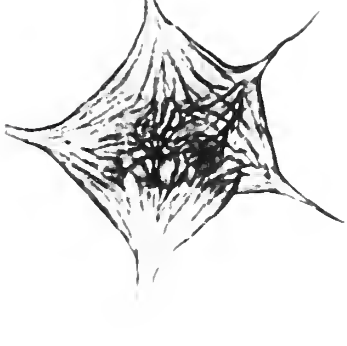
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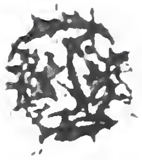
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10

LI JUN, *Ordovician acritarchs*

Remarks. The individual bodies here correspond to those of *Synsphaeridium gotlandicum* in shape and ornamentation but are smaller than the type material. The type material is Silurian, but the genus has also been reported from the Arenig of Bohemia (Vavrdová 1973, p. 286).

Genus TECTITHECA Burmann, 1968

Type species. Tectitheca valida Burmann, 1968.

Tectitheca cf. *additionalis* Burmann, 1968

Plate 72, fig. 6

Description. The vesicle is hollow and subpentagonal in outline, comprising a shortened upper part extending into a long, rapidly tapering apical process with a conically expanded base. In the middle part are four processes with six to seven similar processes around the basal line. The processes are closed distally and communicate freely with the inner cavity. Both vesicle and process surface are thin and faintly granulose. No opening was present.

Dimensions (six specimens). Diameter of vesicle 23–27 μm, length of process 20–25 μm.

Comparison. The specimens here differ from the type material from upper Arenig or lower Llanvirn of GDR in the more broadly based processes.

Genus TONGZIA gen. nov.

Derivation of name. From Tongzi County.

Type species. Tongzia meitana sp. nov.

Diagnosis. Vesicle circular to subcircular in outline, bearing radiating processes that are hollow, and plugged at the base. All processes bifurcate in a similar fashion. No second-order branching was seen. Surface of vesicle and processes decorated with granules.

Remarks. The method of opening is not known. This new genus is distinguished from *Baltisphaeridium* by always having bifurcate processes. *Ordovicidium* Tappan and Loeblich, 1971 differs from the new genus by having multifurcate processes. *Skiagia* Downie, 1982 has processes with funnel-shaped ends.

Tongzia meitana sp. nov.

Plate 69, figs. 1–3

Derivation of name. After the Meitan Formation.

Holotype. Plate 69, fig. 1 (MAZ 45, L48).

Isotypes. Plate 69, fig. 2 (MAZ 44, T52/4); fig. 3 (MAZ 45, X54).

Locality and horizon. West slope of Honghuayuan Hill in Tongzi County, Guizhou, China; 85 m above the base of the Meitan Formation, Arenig, Ordovician.

EXPLANATION OF PLATE 71

Unless otherwise specified, all figures × 1000.

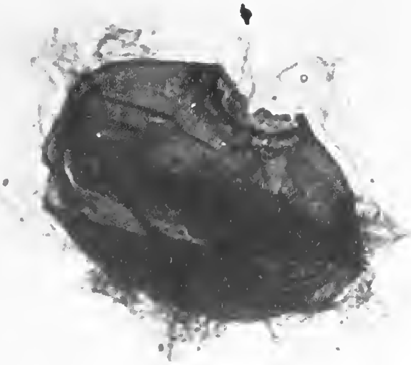
Figs. 1 and 3. *Rhopaliophora memdrana* sp. nov. 1, holotype, MAZ 45, N32/1; 3, MDZ 3, P33/3.

Fig. 2. *Synsphaeridium* cf. *gotlandicum* Eisenack, 1965. MDZ 1, Q31/4.

Figs. 4 and 6. *R. palmata* (Combaz and Peniguel) Playford and Martin, 1984. 4, scanning electron micrograph, × 1800; 6, MAZ 45, C36.

Figs. 5, 7, 8. *Acanthodiacrodium*? *tasselii* Martin, 1969. 5, MAZ 48, F32; 7, MAZ 46, H11/2; 8, MAZ 44, H51.

Fig. 9. *Peteinosphaeridium trifurcatum intermedium* Eisenack, 1976. MAZ 44, Q35.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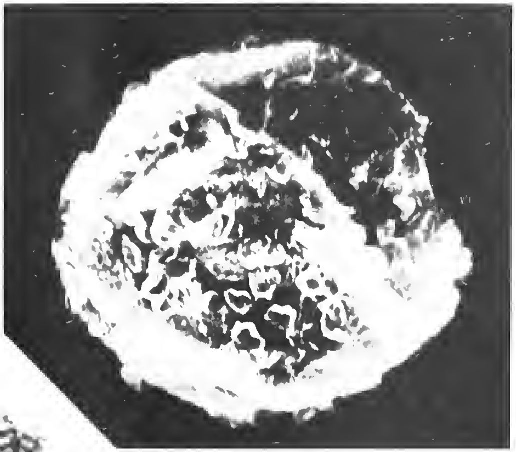
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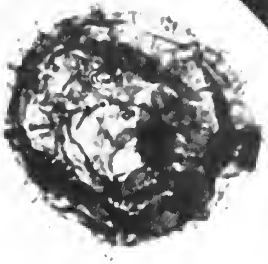
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LI JUN, *Ordovician acritarchs*

Diagnosis. As for genus.

Dimensions (twelve specimens). Diameter of vesicle 44–56 μm, process spacing 3–8 μm, granule spacing 0·5–1·0 μm, process length 4–7 μm, occasionally 14 μm, branch length 4–10 μm, ratio of process to vesicle diameter *c*. 0·1:1.

Description. The vesicle is hollow, circular to subcircular in outline. The wall is firm, single-layered, and carries numerous hollow, evenly distributed processes. These do not communicate with the cavity and bifurcate distally, with pointed and closed tips. The branching angles varied from 60 to 160°, usually 110°. Surface of vesicle, process, and branches are ornamented by densely arranged granules. No second-order branching nor opening were observed.

Genus VERYHACHIUM (Deunff 1951) Deunff, 1954 ex. Downie, 1959

Type species. *Veryhachium trisulcum* (Deunff) Deunff, 1954.

Veryhachium trispinosum (Eisenack 1935) Deunff, 1954 ex. Downie, 1959

Plate 68, fig. 2

1938 *Hystrichosphaeridium trispinosum* Eisenack, p. 16, fig. 2.
1959 *Veryhachium trispinosum* (Eisenack) Downie, pp. 68–69, pl. 12, fig. 7.

Description. The vesicle is triangular in outline, with three long, hollow processes drawn out at corners. The wall is single-layered, 0·5 μm thick, without ornamentation. The processes are simple and closed distally with pointed tips. Some specimens show excystment by epityche.

Dimensions (twenty-two specimens). Vesicle diameter 25–32 μm, process length 17–29 μm.

Remarks. This is a common species from late Arenig to the Carboniferous. It first appears in the early Arenig where it is rare; it is common in the present study.

DISCUSSION

Composition of assemblages. The overall composition of the two assemblages is shown in Table 1. Although they are from different graptolite biozones *Didymograptus deflexus* (sample MDZ) and *Azygograptus suecicus* (sample MAZ), they are remarkably similar. The commonest species is *Polygonium gracile* which, with the closely related *Tectitheca* cf. *additionalis*, makes up 36 and 29% of the total. Also common are the genera *Striatotheca* (13 and 18%), *Veryhachium* (9 and 15%), and *Coryphidium* (6 and 8%). Total number of identified species is 24, 23 from MAZ and 21 from MDZ; 20 are common to both.

Age. As mentioned above, the samples came from the *D. deflexus* and the *A. suecicus* Biozones respectively. The *D. deflexus* Biozone occurs in Britain, and the *A. suecicus* Biozone, which is just above the former, was correlated with the *Isograptus gibberulus* and *D. nitidus* Biozones of Britain

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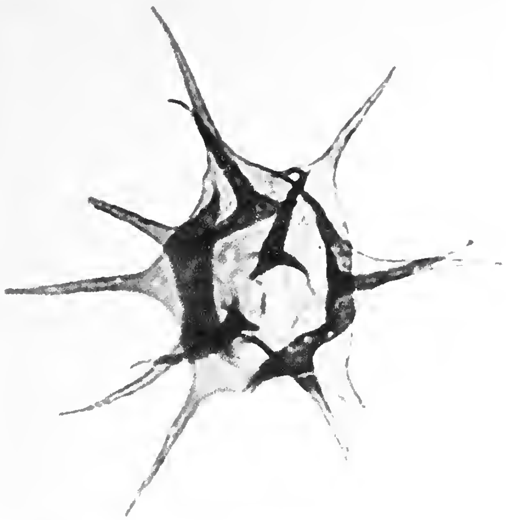
EXPLANATION OF PLATE 72

Unless otherwise specified, all figures × 1000.

Fig. 1. *Polygonium gracile* Vavrdová, 1966. MAZ 44, C49/2.
Fig. 2. *Baltisphaeridium longispinosum longispinosum* (Eisenack) Staplin *et al*. 1965. MAZ 44, B34, × 600.
Figs. 3 and 4. *Cymatiogalea* cf. *cristata* (Downie) Deunff *et al*., 1974. 3, MDZ 3, H21/4; 4, MAZ 44, H46/2.
Figs. 5 and 9. *Coryphidium bohemicum* Vavrdová, 1972. 5, MDZ 1, P49/3; 9, MDZ 1, R35/3.
Fig. 6. *Tectitheca* cf. *additionalis* Burmann, 1968. MAZ 45, C52/4.
Fig. 7. *Petaloferidium florigerum* (Vavrdová) Jacobson, 1978. MAZ 44, E38/3.
Fig. 8. *Cymatiogalea cuvillieri*? (Deunff) Deunff, 1964. MAZ 44, C51.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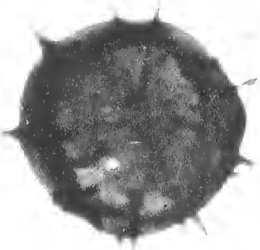
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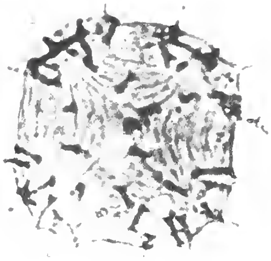
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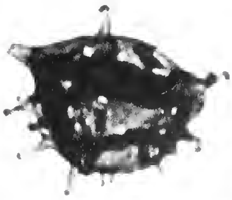
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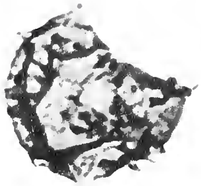
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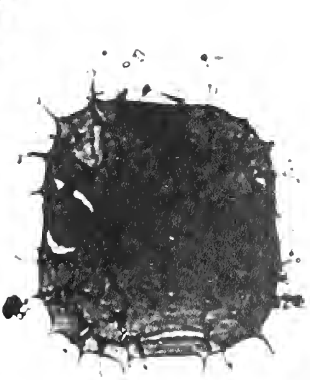
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LI JUN, *Ordovician acritarchs*

TABLE 1. Composition of assemblages from two horizons in the Meitan Formation, Tongzi, Guizhou Province, south-west China.

Species present	Composition of assemblages (%) MAZ	MDZ
Acanthodiacrodium? tasselii	2	1
Adorfia cf. *firma*	5	—
Arbusculidium filamentosum	3	2
Baltisphaeridium longispinosum longispinosum	1	1
Coryphidium bohemicum	6	8
Cristallinium dentatum	—	1
Cymatiogalea cf. *cristata*	1	1
C. cuvillieri?	4	—
Leiosphaeridia tenuissima	2	2
Multiplicisphaeridium cf. *irregulare*	1	2
Petaloferidium florigerum	3	—
Peteinosphaeridium trifurcatum intermedium	3	1
Pirea sinensis	3	2
Polygonium gracile	32	24
Rhopaliophora membrana	1	3
R. palmata	1	4
Schizodiacrodium? multiramiferum	1	7
Striatotheca principalis parva	8	11
S. quieta	2	2
S. cf. *transformata*	3	5
Synsphaeridium cf. *gotlandicum*	2	1
Tectitheca cf. *additionalis*	4	5
Tongzia meitana	3	2
Veryhachium trispinosum	9	15

(Mu Enzhi *et al.* 1979; Zhang Wentang *et al.* 1982). Graptolites from the section indicate an early Arenig age (Harland *et al.* 1982, p. 14). The acritarchs support the age determination. The assemblages characterized by diagnostic acritarch genera such as *Coryphidium*, *Striatotheca*, and Pirea are clearly from the Arenig/Llanvirn (Burmann 1968, 1970; Cramer, Allam *et al.* 1974; Cramer, Kanes *et al.* 1974; Cramer and Diez 1977; Vavrdová 1972). Some species, e.g. *Arbusculidium filamentosum*, *Cristallinium dentatum*, and *S. principalis parva*, are not known from the Llanvirn thus confirming an Arenig age. The abundance of *V. trispinosum* is unusual in the early Arenig since it is generally very rare until the late Arenig (Downie, *pers. comm.*).

Environment. This was marine and the richness and variety of the assemblage suggest a continental shelf site of deposition.

Provincialism. Comparison within China is limited to three localities. The Tongzi locality is some 350 to 550 km from the nearest of these. The two localities, however, are still in the Upper Yangtse Paraplatform of deposition. Xing Yusheng (1980) listed *Coryphidium bohemicum* and *A. filamentosum*, two very characteristic species in an assemblage apparently similar to that of Tongzi. Zhong Guofang (1981) described an assemblage which is more difficult to compare due to poor preservation. *Coryphidium* and *Arbusculidium* were not recorded by Zhong. The assemblage described from northern China consists largely of sphaeromorphs and *Baltisphaeridium* and *Micrhystridium* (Li Zaiping 1982). It is in the North China Platform and has none of the distinctive species characteristic of the Tongzi assemblage.

In making comparison with other regions of the world, most of the data come from Europe and North Africa. Vavrdová (1974) divided the European Arenig/Llanvirn assemblages into a Baltic Province and a Mediterranean Province. According to her division, the Baltic Province comprising the northern part of the Soviet Union, Sweden, Poland, northern Germany, and probably part of the British Isles is characterized by the dominance of acanthomorphs with many species of *Baltisphaeridium*, *Peteinosphaeridium*, and *Goniosphaeridium*. Representatives of diacromorphs are apparently absent. The Mediterranean Province extending from Belgium, France, Spain, northern Africa to southern Germany, central Bohemia, and Bulgaria is characterized by the prevalence of diacrodians such as *Arbusculidium*, *Coryphidium*, and *Striatotheca*.

Elements of the Mediterranean flora have been described from GDR (Burmann 1968, 1970), Czechoslovakia (Vavrdová 1965, 1966, 1972, 1977), Hungary (Albani, Lelkes-Felvary and Tongiorgi 1985), Sardinia (Albani, Di Milia *et al.* 1985), Bulgaria (Kalvacheva 1982), Ireland (Smith 1981), Britain (Turner 1982; Downie 1984), France (Rauscher 1974), Belgium (Martin 1977), and Spain (Cramer and Diez 1976). That described from Czechoslovakia by Vavrdová is the richest, comprising some forty-two Arenig species and fifty-eight from the Llanvirn. A rich Arenig to Llanvirn assemblages of more than fifty species is reported from Morocco (Cramer, Allam *et al.* 1974; Cramer, Kanes *et al.* 1974; Cramer and Diez 1977). This includes many characteristic Mediterranean genera listed by Vavrdová (1974) with a number of new species. The occurrence of *Coryphidium* species in Libya and Saudi Arabia (Cramer and Diez 1976) indicates that the two localities should be included in the Mediterranean Province. Martin (*in* Dean and Martin 1978) lists forty-one species belonging to twenty-one genera from east Newfoundland. The presence of the genera *Arbusculidium*, *Coryphidium*, and *Striatotheca* shows a clear affinity with the Mediterranean Province.

This assemblage from the Upper Yangtze Paraplatform clearly has a greater affinity with the Mediterranean Province than with the Baltic. It has fewer species than Czechoslovakia and Morocco. Of twenty genera recognized in Tongzi only two, *Tongzia* gen. nov. and *Rhopaliophora*, have not been found in the Mediterranean Province. Comparison with the Baltic Arenig shows that only *B. longispinosum*, *P. trifurcatum intermedium*, and *Leiosphaeridia tenuissima* are in common and they occur rarely. The assemblage from the North China Platform (Li Zaiping 1982) appears more similar to the Baltic one but the data are not good enough to make a satisfactory comparison.

Little can be said about the rest of the world. Arenig to Llanvirn assemblages from the Canning Basin, north-west Australia (Combaz and Peniguel 1972; Playford and Martin 1984) contain mostly new species not known elsewhere. The acritarchs are thus difficult to compare with Baltic and Mediterranean assemblages although similar assemblages are recorded from the western part of North America (K. J. Dorning, *pers. comm.*). Of the species with widespread records, *P. trifurcatum* and *B. longispinosum* are characteristic of the Baltic Province, but appear to have a world-wide distribution. *Veryhachium trispinosum* and *V. lairdii* are widespread across the Mediterranean belt. *V.* cf. *oklahomense*, similar to *V. lairdii*, is stated to have an ornament of fine ribs (Playford and Martin 1984, p. 215) and so resembles *Striatotheca* species. *Pirea*, a species recorded previously only in the Mediterranean Province, was also described. *Rhopaliophora*, a genus originally described from the late Ordovician of Indiana and not recorded in Europe and Africa, was recognized both in the Canning Basin and in the present study.

With the exception of east Newfoundland there are few detailed published accounts of Arenig assemblages from North America. However, *Rhopaliophora* (Tappan and Loeblich 1971) and *Petaloferidium* (Jacobson 1978) from the central United States are two genera also recorded in the present study.

The significance of this assemblage from south-west China, in terms of palaeogeography, cannot be definitely ascertained because of the absence of adequate knowledge of Arenig acritarchs from large areas of the world, but it seems to indicate the presence of a fairly homogeneous Arenig assemblage extending from east Newfoundland through the Mediterranean area and the Middle East to south-west China (the Mediterranean Province of Vavrdová).

The primary factor controlling acritarch provincialism was thought to be palaeotemperature which is mainly determined by palaeolatitude (Cramer and Diez 1974). The Mediterranean Province was believed to represent a cold belt (Vavrdová 1982). Based on trilobites, a Lower Ordovician *Selenopeltis* Province characteristic of cool waters is recognized (Whittington and Hughes 1972). The extent of the *Selenopeltis* Province is roughly the same as that of the Mediterranean Province. The Chinese trilobite fauna is classified as of 'uncertain affinity' because it appears to belong in the *Selenopeltis* Province at the family level but not so at the generic level (Whittington and Hughes 1972). Plotting the distribution of *Neseuretus*, a trilobite genus considered to be a good indicator of epicontinental seas at relatively high latitudes, rather than comparing whole faunas at the generic level, the existence of a broadly united Gondwanan continent in the early Ordovician, including southern Europe attached to North Africa, and including also the southern part of China, has been proposed (Fortey and Morris 1982). The present study supports this to some extent. Lu Yanhao *et al.* (1976) argued that no Ordovician latitudinal and climatic differentiation could be derived from the distribution of Chinese faunas because they, both shelly and graptolitic, showed a mixture of elements belonging to different provinces. The Ordovician graptolite fauna of south-west China is believed to link up with those of Europe, North Africa, and South America, and the climate of the Ningkuoan (equivalent of Arenig and Llanvirn) might have been warm and arid (Mu Enzhi *et al.* 1979). We should take these arguments into account and need more data for a better understanding of bioprovincialism and differentiation of climatic zones.

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THE BELEMNITE *ACROTEUTHIS* IN THE *HIBOLITES* BEDS (HAUTERIVIAN–BARREMIAN) OF NORTH-WEST EUROPE

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ABSTRACT. *Hibolites*, a Tethyan-derived genus, was the dominant belemnite in north-west Europe for most of Hauterivian to earliest Barremian (Early Cretaceous) time, while the Boreal genus *Acroteuthis* continued to thrive in more northerly latitudes. Rare *Acroteuthis* occur in the *Hibolites* beds and are easily confused with the slightly younger *Aulacoteuthis*. Two new *Acroteuthis* species belonging to the subgenus *Boreioteuthis* are described here by Pinckney: *A.* (*B*). *rawsoni* and *A.* (*B.*) *stolleyi*.

THE latest Jurassic–early Cretaceous belemnite genus *Acroteuthis* is a member of the boreal subfamily Cylindroteuthinae, occurring mainly in Siberia, the Russian Platform, north-west Europe, East Greenland, and Arctic Canada. In north-west Europe it first appeared in mid-Volgian (late-Tithonian) times and died out early in the Barremian; over that interval, seven discrete assemblages are distinguished (Pinckney and Rawson 1974). However, while the genus was the dominant belemnite in late Volgian to earliest Hauterivian sediments, it was almost completely replaced early in the Hauterivian by the immigration of *Hibolites* from Tethys (Rawson 1973; Mutterlose *et al.* 1983). In England the faunal change was taken as one of the main boundaries in the Speeton Clay (D/C beds boundary: Lamplugh 1889), though here the abruptness of the change is exaggerated by condensed sedimentation. *Hibolites* was almost completely replaced by a new boreal immigrant, *Praeoxyteuthis*, early in the Barremian (C/B beds boundary at Speeton) though *H. minutus* continued through the Barremian.

While *Hibolites* was flourishing in north-west Europe during Hauterivian and earliest Barremian times, *Acroteuthis* continued to evolve in other boreal areas. A few examples have been found in the *Hibolites* beds of England and north Germany (text-fig. 1) and their occurrence is reviewed here. They include two new species (assigned to the subgenus *Boreioteuthis*) described here by G. Pinckney. The described specimens are from the following collections: BGS, British Geological Survey, Keyworth; BM, British Museum (Natural History), London; GM, Geological Museum, Copenhagen; GPIG, Geologisches-Paläontologisches Institut, Göttingen University; GPIH, Geologisches-Paläontologisches Institut, Hannover University; NLfB, Niedersächsisches Landesamt für Bodenforschung, Hannover; SC, Stühmer collection, Heligoland; WC, C. W. and E. V. Wright Collection, London; UC, University College London.

ACROTEUTHIS ASSEMBLAGES IN THE *HIBOLITES* BEDS

Acroteuthis assemblages 6 and 7 of Pinckney and Rawson (1974) are represented in the *Hibolites* beds. Assemblage 6 includes four species, *A.* (*A.*) *subquadratus* (Roemer), *A.* (*A.*) *explanatoides* (Pavlow), *A.* (*A.*) *acmonoides* Swinnerton, and *A.* (*A.*) *paracmonoides* (Swinnerton), all of which also occur in the underlying assemblage 5. It is characterized by greater numbers of the more slender species *A. acmonoides* and *A. explanatoides*. Assemblage 6 occurs in the highest part of the *Acroteuthis* beds and, at Speeton, as a relic fauna in the lower part of the *Hibolites* beds (text-fig. 2). The constituent species are well known from Swinnerton's (1937, 1948) monograph and are not redescribed here.

Assemblage 7 is completely distinct from the underlying ones. It is characterized by forms with an apical groove. Three species occur, *A.* (*A*?) *conoides* Swinnerton and two previously undescribed

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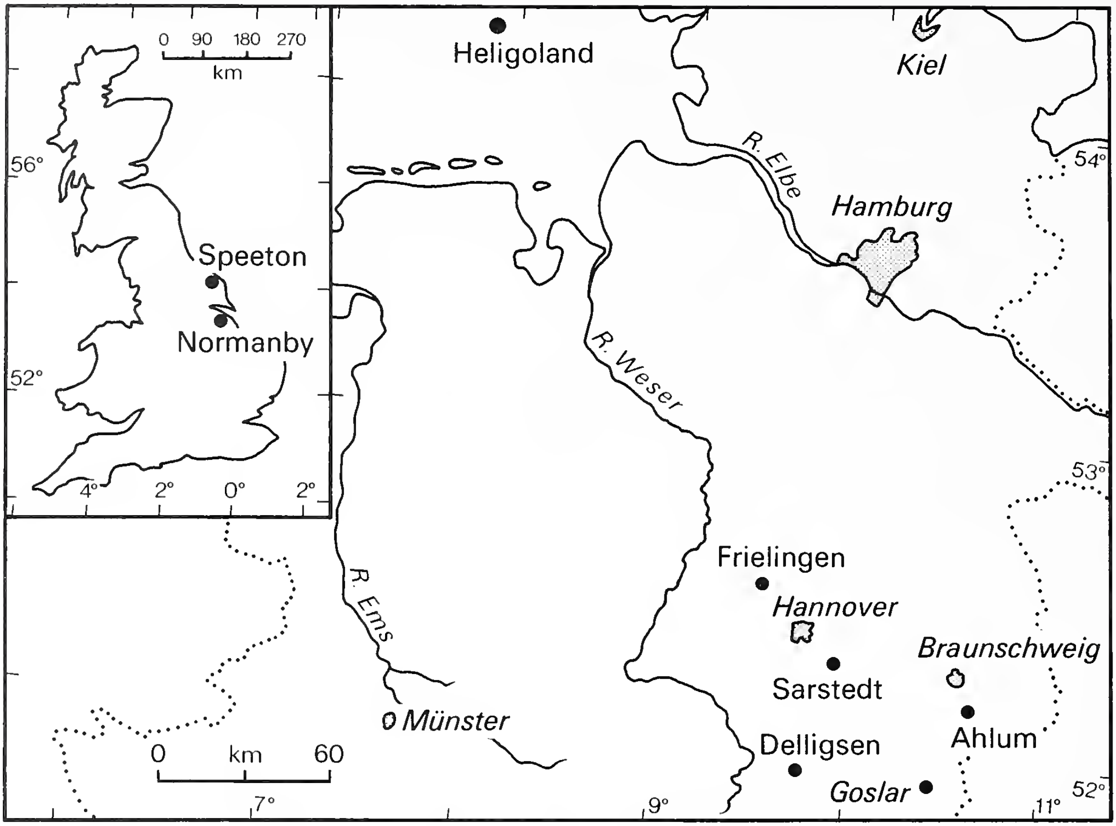


TEXT-FIG. 1. Map showing localities at which *Acroteuthis* occurs in the *Hibolites* beds.

ones, A. (*Boreioteuthis*) *rawsoni* Pinckney sp. nov. and A. (*B. stolleyi*) Pinckney sp. nov. All three species are described and their phylogenetic significance discussed below. The assemblage 7 fauna occurs in the middle to upper part of the *Hibolites* beds in both England and north Germany.

LOCALITIES

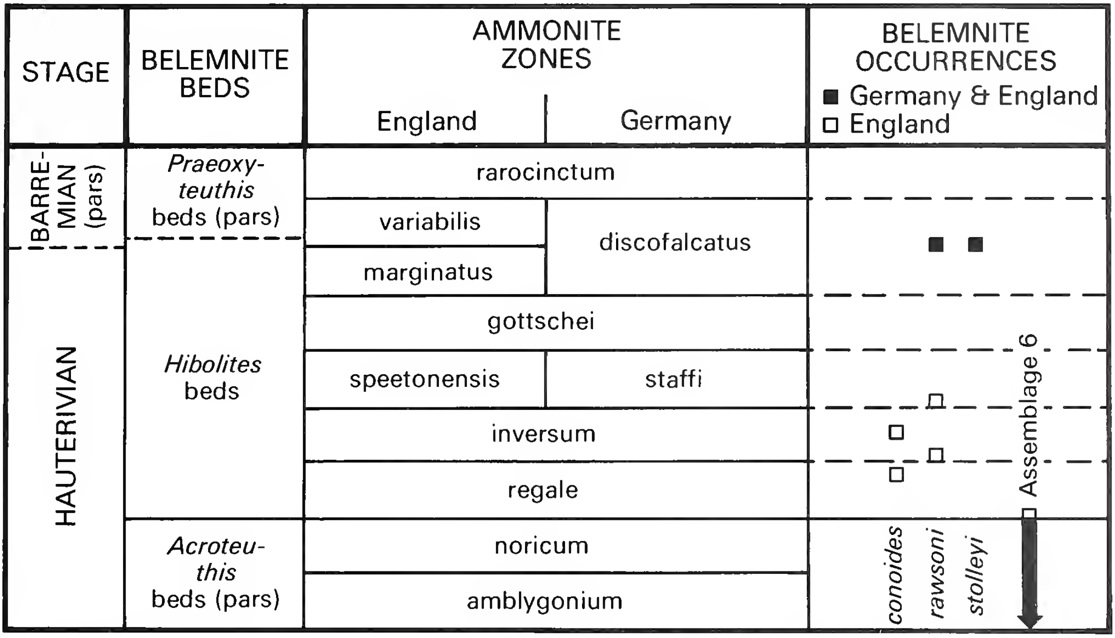
Seven localities in the *Hibolites* beds have yielded *Acroteuthis*: Speeton and Lincolnshire in eastern England, the North Sea island of Heligoland, and four sections in Lower Saxony (text-fig. 1).

Speeton. The lithostratigraphy of the C beds (*Hibolites* beds) has been described in detail by Fletcher (1969) and a lithic log published by Rawson (1971). *Acroteuthis* representing assemblages 6 and 7 have been found in the mid C beds (*regale* to *speetonensis* Zones) and bed C1 (*variabilis* Zone).

Lincolnshire. A single *A*. (*B*). *rawsoni* was collected from the Tealby Limestone of Normanby during the last century by the Revd J. Lee. The limestone is of earliest Barremian (*variabilis*–*rarocinctum* Zones) age.

Heligoland. Lower Cretaceous rocks are exposed on the sea-floor east of Heligoland in the 'Skit Gatt'. In recent years skin divers have collected rich cephalopod faunas from these outcrops. The ammonite faunas indicate that the lower part of the Hauterivian (*amblygonium*, *noricum*, and possibly *regale* Zones) is condensed or missing but the remainder of the Hauterivian and Barremian are well represented (Kemper *et al.* 1974; Rawson 1975). The belemnites include several hundred *H. jaculoides* and one specimen each of *A*. (*B*.) *rawsoni* and *A*. (*B*.) *stolleyi*.

Ahlum. This old section is no longer visible: it was situated south of Ahlum, about 4 km east of Wolfenbuttel (TK 25 Wolfenbüttel, Nr. 3829, re: 36 44 048, h: 57 82 550). Stolley (1906) described the sequence; from the lowest beds he recorded *Simbirskites* (*Craspedodiscus*) of the *phillipsi* group which indicates the *discofalcatus* Zone. Two large *Belemnites* aff. *subquadratus* were noted and later Stolley (1925) included them (with additional material) in *A. ahlumensis* Stolley *nom. nud.* He also recorded some much more slender forms. Stolley's records apparently represent *A.* (*B.*) *stolleyi* and *A.* (*B.*) *rawsoni*, several examples of which are still preserved in old collections from Ahlum.



TEXT-FIG. 2. Stratigraphical occurrence of *Acroteuthis* in the *Hibolites* beds of north-west Europe.

Delligsen (*Hils*). During recent excavations for the foundations of a sports hall in Delligsen (TK 25 Alfeld, Nr 4024, re: 35 54 900, h: 57 56 460), dark clays were exposed from which a single *A.* (*B.*) *stolleyi* and a fragment of *S.* (*C.*) *discofalcatus* were collected.

Frielingen. In 1979 a new clay pit, Ziegelei Oltman, was opened near Frielingen, about 20 km north-west of Hannover (TK 25 Garbsen, Nr. 3523, re: 35 34 275, h: 58 17 125). It exposes about 14 m of clay, forming a rhythmic sequence of pale and dark beds, occasionally intensively bioturbated. A rich *discofalcatus* Zone ammonite fauna occurs: *S.* (*C.*) *discofalcatus* (Lahusen), *S.* (*C.*) *juddi* Rawson, *S.* (*C.*) *phillipsi* group, *S.* (*S.*) *toensbergensis* (Weerth), and *Paracrioceras spathi* Kemper, Rawson and Thieuloy. These occur with abundant *H. jaculoides* and hence the total assemblage indicates the middle part of the *discofalcatus* Zone: it correlates with the lower part of the English *variabilis* Zone of earliest Barremian age.

The top two metres of the section have yielded sixteen specimens of *Acroteuthis* (*Boreioteuthis*), an unusually large number: both *A.* (*B.*) *rawsoni* and *A.* (*B.*) *stolleyi* occur.

Sarstedt. The clay pit of Ziegelei Gott lies on the outskirts of Sarstedt, about 30 km south-east of Hannover (TK 25 Sarstedt, Nr. 3725, re: 35 60 400, h: 57 90 650). It is one of the key sections in north Germany, exposing about 70 m of shallow-water Upper Hauterivian, Barremian and Upper Aptian clays deposited on the flank of a salt stock. (For section details see Mutterlose 1983, fig. 4). The section has yielded two loose specimens of *A.* (*B.*) *stolleyi*, probably from the *discofalcatus* Zone.

TEXT-FIG. 3. *a–h*, *Acroteuthis* (*Boreioteuthis*) *rawsoni* Pinckney sp. nov. *a–d*, Paratypes, *discofalcatus* Zone, Frielingen (GPIH 1985-I-1, 1985-I-2); *e*, *f*, Paratype, bed C6 base (*speetonensis* Zone), Speeton (BM.C.59522); *g–h*, Holotype, mid C Beds, Speeton (BGS 24454). *i*, *j*, *A*. (*A*.?) *conoides* Swinnerton. Bed 'C7 or above', Speeton (WC 18350). *k*, *l*, *A*. (*B*.) *stolleyi* Pinckney sp. nov., Paratype, *discofalcatus* Zone, Frielingen (GPIH 1985-I-11). *a*, *c*, *e*, *g*, *i*, *k*, ventral views; *b*, *d*, *f*, *h*, *j*, *l*, lateral views; × 1.

SYSTEMATIC PALAEONTOLOGY

(by G. Pinckney)

Order BELEMNITIDA Zittel, 1895
Suborder BELEMNITINA Zittel, 1895
Family BELEMNITIDAE d'Orbigny, 1845
Subfamily CYLINDROTEUTHINAE Stolley, 1919

Genus ACROTEUTHIS Stolley, 1911

Diagnosis. Rostrum depressed, generally wedge-like in profile; apical line markedly displaced towards the venter; alveolus excentric and moderately deep.

Subgenus ACROTEUTHIS Stolley, 1911

Type species. *Belemnites subquadratus* Roemer, 1836.

Diagnosis. *Acroteuthis* with relatively large rostra that are wedge-like in profile, with only a weakly-developed ventral groove. Juvenile rostra moderately slender, spindle-shaped.

Acroteuthis (*Acroteuthis?*) *conoides* Swinnerton, 1937

Text-figs. 3*i*, *j*, 4*a*, *b*

v* 1937 *Acrouteuthis conoides* Swinnerton; p.17, pl. 6, fig. 2
?1964 *Acroteuthis* cf. *conoides* Swinnerton; Jeletzky, p. 56, pl. 14, fig. 3.
?1964 *Acroteuthis* aff. *conoides* Swinnerton; Jeletzky, p. 58, pl. 15, fig. 3.

Type. Holotype, BGS 17298 (Danford Collection), Beds C7–C8, Speeton Clay, Speeton, Yorkshire.

Material. 6 specimens from the C beds of the Speeton Clay: BM.C.59521 (Rawson Collection) from C7E; WC 21284 from C8 and 18350 from 'C7 or above'; BGS (Danford Collection) 17299, 17318, and 17319 from 'mid C'.

Diagnosis. Rostrum slender and conical; ventral apical groove well developed; apical angle acute in both outline and profile; transverse sections slightly depressed in alveolar and stem regions, becoming compressed posteriorly. Alveolus occupies about half length of guard and is weakly excentric.

Discussion. *A*. (*A.?*) *conoides* was described in detail by Swinnerton (1937). It is only tentatively referred to the subgenus *Acroteuthis* because it appears to be a transitional form towards *Boreioteuthis*. It resembles the latter in the weakly depressed condition of the rostrum and in the slight excentricity of the alveolus, but differs in the more feeble development of the ventral groove. Its stratigraphical horizon is also transitional between the ranges of the two subgenera in north-west Europe.

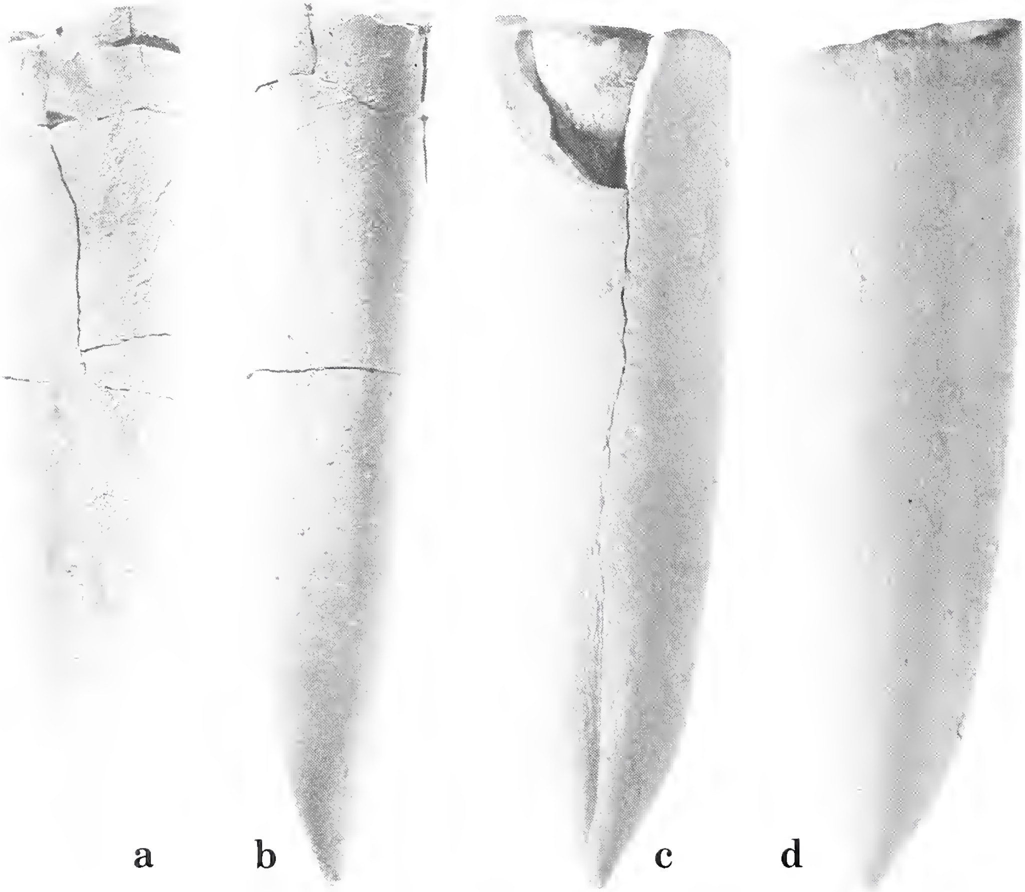
A. (*A.?*) *conoides* most closely approaches conical variants of *A*. (*A*.) *explanatoides* (Pavlow), but has a more compressed rostrum, better developed ventral groove and more acute apex in both outline and profile.

Geographic distribution: *A*. (*A.?*) *conoides* is known only from England, though very similar, possibly identical, forms have been figured from Northern Canada (Jeletzky 1964).

Subgenus BOREIOTEUTHIS Saks and Nalnyaeva, 1966

Type species. *Acroteuthis* (*Boreioteuthis*) *niiga* Saks and Nalnyaeva, 1966. Lower Volgian, northern Siberia.

Diagnosis. *Acroteuthis* with relatively large, moderately elongate, weakly depressed rostra; with a well-developed ventral groove extending into the stem region; and with markedly slender, clavate juvenile rostra.



TEXT-FIG. 4. *a*, *b*, *Acroteuthis* (*A.*?) *conoides* Swinnerton, bed C8 (*regale* Zone), Speeton (WC 21284); *c*, *d*, *A.* (*Boreioteuthis*) *stolleyi* Pinckney sp. nov., holotype, *discofalcatus* Zone, Ahlum (NLf B Kv56). *a*, *c*, ventral views; *b*, *d* lateral views; × 1.

Discussion. The subgenus *Boreioteuthis* is distinguished from *Acroteuthis s.s.* by its better-developed median ventral groove, which extends beyond the apical region, and by its more slender juvenile rostrum. It differs from the subgenus *Microbelus* in the possession of a larger 'adult' rostrum, and in the better development of the median ventral groove.

Our concept of *Boreioteuthis* is broader than that of Saks and Nalnyaeva (1966). Here, all *Acroteuthis* species with a median ventral groove that extends beyond the apical region are included, whereas Saks and Nalnyaeva (1966) only placed species possessing a ventral groove that extended into the alveolar region in this subgenus.

Stratigraphical distribution. According to Saks and Nalnyaeva (1966), *Boreioteuthis* ranges in age from Oxfordian to Barremian. However, in western Europe it is known only from strata of late Volgian and late Hauterivian to earliest Barremian age.

Acroteuthis (*Boreioteuthis*) *rawsoni* sp. nov.

Text-fig. 3*a–h*

?1901 *Belemnites speetonensis* Pavlow and Lamplugh; Pavlow, p. 82 pl. 8, fig. 7.
vp. 1937 *Acroteuthis festucalis* Swinnerton, pl. 9, fig. 2, *non* pl. 9, figs. 1 and 3.

v. *1974* *Acroteuthis* (*Boreioteuthis*) sp. nov. b, Pinckney and Rawson, p. 202.
v. 1982 *Acroteuthis* (*Boreioteuthis*) cf. *festucalis* Swinnerton; Stuhmer, Spaeth and Schmid, pl. 20, fig. 2.
v. *1983* *Acroteuthis* (*Boreioteuthis*) *rawsoni* Pinckney [MS]: Mutterlose, p. 15 (*nomen nudum*).
v. *1983* *Acroteuthis* (*Boreioteuthis*) *rawsoni* Pinckney [MS]: Mutterlose, Schmid and Spaeth, p. 299 (*nomen nudum*).

Type series. Holotype: BGS 24454 (Danford Collection), mid C beds, Speeton Clay, Speeton. Paratypes: 1 specimen from the Tealby Limestone of Lincolnshire (BM. C.59519); 2 from the Speeton Clay of Speeton (UC Pinckney Collection 366 from C7H, BM.C.59522 [Rawson collection] from the base of C6); 8 from the middle of the *discofalcatus* Zone at Frielingen (GPIH 1985-I-1–1985-I-8); 4 from Ahlum, probably *discofalcatus* Zone (GM 1923.599 [1 of 3 specimens], GPIG 3 uncatalogued specimens); 1 from Heligoland (SC 1503, figured Stuhmer *et al.* 1982).

Diagnosis. Rostrum slender and weakly depressed; apex very acute and only slightly depressed; median ventral groove quite well developed, extending into stem region; alveolus shallow.

Description. Rostra quite short, subconical to subcylindrical, very slender; actual length of rostrum up to 6·5 times the maximum width. In outline the sides of the alveolar and stem regions are usually quite straight and subparallel, but may converge slightly adapically. Rostral sides are weakly curved in the apical region and converge with moderate rapidity to form a long, acute to very acute apex, varying from about 32° to 40°. In profile the sides of the rostrum are almost straight in alveolar and stem regions. They are subparallel in front but converge gently adapically, so that the point of maximum thickness of the rostrum is near the alveolar rim. Convergence of rostral margins in apical region is quite gentle. Dorsal surface only slightly more curved than ventral, producing a feebly depressed, weakly asymmetrical apex, ranging from about 30° to 36°.

Transverse sections are weakly depressed and strongly quadrate through most of length of rostrum, except in apical region where they approach an oval form. Dorsal surface almost semicircular. Ventral surface, which is about same width as dorsal, is also semicircular in the alveolar region but flattens adapically. Flattening is accompanied by the development of a distinct, long, median ventral groove which is deep and narrow in the apical region but shallow and often excavate in the stem region, where it disappears. Rostral flanks markedly flattened.

Lateral lines are generally poorly visible. On well-preserved rostra, the upper main lateral line is represented by a relatively broad, flattened belt, and the lower by an indistinct, narrow, flattened belt. The minor lateral line has not been seen.

Alveolus shallow, occupying about one third of the actual length of the rostrum. It consists of a ventrally curved, conical depression, the apex of which is weakly excentric. The apical line is also excentric and curves gently towards the venter throughout its course.

No juvenile specimens are known. Evidence from dorsoventral longitudinal sections indicates that the juvenile rostrum is clavate and very slender, the maximum thickness being up to eight times the total rostral length.

Discussion. Swinnerton (1937) included specimens here regarded as *A*. (*B*.) *rawsoni* in his new species *A*. *festucalis*. However, the holotype of the latter differs from *A*. (*B*.) *rawsoni* in its greater size, more weakly developed median ventral groove, and in the possession of a feebly clavate rostrum. Moreover, the species are well separated stratigraphically, *A*. (*A*.) *festucalis* being of Volgian age and *A*. (*B*.) *rawsoni* of mid to late Hauterivian age.

A. (*B*.) *rawsoni* superficially resembles *Aulacoteuthis descendens* (Stolley) but differs principally in its slightly stouter form, less strongly developed ventral groove, and in the occurrence of cylindroteuthid lateral lines.

Acroteuthis (*Boreioteuthis*) *stolleyi* sp. nov.

Text-figs. 3*k*, *l*, 4*c*, *d*, 5*a*, *b*

v ?1906 *Belemnites* aff. *pseudopanderi* Sinzov; Danford, p.7, pl. 3, fig. 16; pl. 6, fig. 16.
? *1925* *Acroteuthis ahlumensis* Stolley, p. 117 (*Nomen nudum*).
v. *1974* *Acroteuthis* (*Boreioteuthis*) sp. nov. c, Pinckney and Rawson, p. 202
v. *1980* *Acroteuthis* (*Boreioteuthis*) *stolleyi* Pinckney [MS]; Mutterlose, pp. 239, 240 (*nomen nudum*).
v. *1983* *Acroteuthis* (*Boreioteuthis*) *stolleyi* Pinckney [MS]; Mutterlose, Schmid and Spaeth, p. 299 (*nomen nudum*).

TEXT-FIG. 5. *Acroteuthis* (*Boreioteuthis*) *stolleyi* Pinckney sp. nov., paratype, *discofalcatus* Zone, Frielingen (GPIH 1985-I-10). *a*, ventral view; *b*, lateral view; × 1.

Type series. Holotype: NLfB Kv56, Simbirskiten Schichten, Ziegelei Ahlum, Wolfenbuttel, near Braunschweig. Paratypes: 8 specimens from Frielingen (GPIH 1985-I-9–1985-I-16); 6 from Ahlum (GM 1923·599 [2 of 3 specimens], 1923.600 [2 specimens], GPIG 2 uncatalogued specimens); 2 from Sarstedt (GPIH); 1 from Heligoland (SC), 1 from Delligsen (Strohmeyer private collection: cast in GPIH).

Diagnosis. Rostrum quite stout and weakly depressed; apex obtuse and inflated; median ventral groove quite well developed, extending into stem region; alveolus quite deep.

Description. Rostra large, subcylindrical to subconical and moderately stout, actual length of rostrum being about 3·5 times the maximum width. In outline the sides of alveolar and stem regions are almost straight and subparallel, but they converge slightly adapically. Rostral sides converge more rapidly and curve quite strongly in apical region to form a moderately obtuse apex, ranging from about 55° to 65°. In profile, sides of rostrum almost straight and subparallel in alveolar region, but they curve gently and converge in stem region. Convergence of rostral margins in apical region is strong. Ventral surface quite weakly curved, but dorsal surface markedly inflated, producing an obtuse, asymmetrical apex, varying from about 50° to 60°.

Transverse sections are weakly depressed and quadrate in alveolar region, but become more compressed and oval adapically. Dorsal surface is subsemicircular in front and closely approaches a semicircular condition in the apical region. The ventral surface, which is about the same width as the dorsal, is subsemicircular in the alveolar region but becomes flatter and weakly concave in apical and stem regions, where the median groove is developed. The groove is quite deep in the apical region but shallows adorally, eventually disappearing in the stem region. It does not extend quite to the apical tip, where the venter is feebly swollen. Rostral flanks quite strongly flattened.

Evidence of lateral lines is poor. The upper main lateral line is best developed and forms a broad, indistinct belt in the alveolar and stem regions that disappears adapically. The nature of the other lateral lines is unclear.

The alveolus is deep and occupies almost two thirds of the total length of the rostrum. It comprises a ventrally curved conical depression, the apex of which is moderately excentric. The apical line is also excentric and curves gently towards the venter throughout its course.

No juvenile specimens of *A.* (*B.*) *stolleyi* have been seen. However, smaller individuals are more slender with a more acute, less inflated apex and a shallower alveolus.

Discussion. A. (*B.*) *stolleyi* very closely resembles *A.* (*A.*) *pseudopanderi* (Sinzov emend. Pavlov) but has a better-developed median ventral groove and a shallower alveolus. It can be distinguished from *A.* (*A.*) *acrei* Swinnerton, *A.* (*A.*) *partneyi* Swinnerton, *A.* (*A.*) *bojarkae* Saks and Nalnjaeva, and *A.* (*A.*) *chetae* Saks and Nalnjaeva chiefly in the stronger development of the ventral groove, which extends into the stem region.

A. (*B.*) *stolleyi* apparently embraces *A. ahlumensis* Stolley. The latter was neither figured nor described and is therefore a *nomen nudum*. However, specimens of *A.* (*B.*) *stolleyi* from Ahlum were purchased from Stolley by the Mineralogisk Museum, Copenhagen (now Geologisk Museum), and bears his labels '*A. ahlumensis*'.

A. (*B.*) *stolleyi* probably occurs in bed C1 (*variabilis* Zone) at Speeton. Two specimens are known, though both are too corroded for firm identification. One, Danford's (1906) figured *Belemnites* aff. *pseudopanderi*, came from 'the lower of the two mottled beds at the upper limit of the C division' (= C1B), while a fragment with the apical region missing has been collected recently from bed C1A (BM.C.59523: Rawson Collection).

PHYLOGENETIC PROBLEMS

The Acroteuthis *subgenera*

The origin and phylogeny of the *Acroteuthis* subgenera is relevant to our interpretation of the late forms described here and is therefore discussed briefly.

Acroteuthis is divided into three subgenera: *Microbelus* (Callovian–Hauterivian in the USSR, Middle and Upper Volgian in north-west Europe), *Boreioteuthis* (Oxfordian–Barremian in the USSR, Upper Volgian–Early Barremian in north-west Europe), and *Acroteuthis s.s.* (Middle Volgian–Upper Hauterivian in USSR and north-west Europe, ?Aptian in USSR).

Microbelus is characterized by a relatively small, quite slender, depressed guard, with a median ventral groove confined to the apical region. According to Saks and Nalnyaeva (1966, p. 172) it evolved from *Pachyteuthis* (*P.*) *parens* Saks and Nalnjaeva in the Callovian. Saks and Nalnyaeva (1966, p. 174) also suggested that *Boreioteuthis* and *Acroteuthis s.s.* both evolved from *A.* (*Microbelus*) *pseudolateralis* Gustomesov, the former in the Oxfordian and the latter during the Volgian. Both *Boreioteuthis* and *Acroteuthis s.s.* are larger than *Microbelus: Boreioteuthis* has a well-developed ventral groove extending on to the stem region while *Acroteuthis s.s.* has a weakly developed one.

Saks and Nalnyaeva (1966, p. 173) suggested that from the Volgian onward each subgenus represented an independently evolving lineage.

While we agree that *Boreioteuthis* is probably derived from *M. pseudolateralis* by an increase in the length of the ventral groove, the evolution of *Acroteuthis s.s.* is more problematic for two reasons:

1. There is a long time gap between the extinction of *M. pseudolateralis* in the Late Oxfordian and the first appearance of true *Acroteuthis* in the Middle Volgian, and no transitional forms are known.

2. Many of the earliest *Acroteuthis s.s.* (e.g. *A.* (*A.*) *lindseyensis* Swinnerton) closely resemble *Pachyteuthis* species. These resemblances may be homeomorphic, but if not then *Acroteuthis s.s.*

may have evolved directly from *Pachyteuthis* (Callovian–Kimmeridgian) and the genus *Acroteuthis* as currently defined would be polyphyletic in origin.

Origin and evolution of the conoides–rawsoni–stolleyi *group*

A. (*A.*) *explanatoides* (Pavlow) is a long-ranging form (earliest Ryazanian to early Hauterivian) which apparently gave rise to several shorter-lived species. The last of these was *A.* (*A.*?) *conoides*, an interpretation on which we concur with Saks and Nalnyaeva (1966, p. 175). The species occur in stratigraphic succession at Speeton (text-fig. 2) with only a small gap between them which may well reflect simply their rarity in the *Hibolites* beds.

Stratigraphic occurrences (text-fig. 2) suggest that there may be an evolutionary lineage from *A.* (*A.*?) *conoides* through *A.* (*B.*) *rawsoni* to *A.* (*B.*) *stolleyi*. Early *A.* (*B.*) *rawsoni* slightly overlap with *A.* (*A.*?) *conoides* in the *inversum* Zone while younger examples occur with *A.* (*B.*) *stolleyi* in the *discofalcatus* Zone. Three main evolutionary trends are identified in this apparent lineage:

1. an increase in the length and depth of the ventral groove;
2. a decrease in the degree of depression of the rostrum in transverse section;
3. a progressive change from an essentially conical to a cylindrical rostrum.

If this lineage is confirmed by further finds, then the species *rawsoni* and *stolleyi* will need to be placed in a new subgenus which bears only a homeomorphic relationship to *Boreioteuthis*.

HOMEOMORPHY WITH *AULACOTEUTHIS*

The development of an apical groove characterizes not only *Boreioteuthis* and some *Acroteuthis* but also the oxyteuthinid genus *Aulacoteuthis*. The subfamily Oxyteuthinae characterizes strata immediately overlying the *Hibolites* beds in north-west Europe (Mutterlose 1983) and exhibits an evolutionary lineage: *Praeoxyteuthis*, a slender, ungrooved genus gave rise to *Aulacoteuthis*, characterized by an apical groove, which in turn evolved into the ungrooved *Oxyteuthis*.

Most *Aulacoteuthis* are readily distinguished from the north-west European *Boreioteuthis* by a longer groove and a slimmer guard. However, *A. descendens*, the youngest (mid-Barremian) form, has a short, stout guard with a groove that is sometimes short. Such forms closely resemble *A.* (*B.*) *rawsoni* and can only be differentiated by the lateral lines. While the latter possesses cylindroteuthid lateral lines, *A. descendens* has oxyteuthid ones (Mutterlose 1983, fig. 57). The close homeomorphy of the two species has caused confusion in the literature. From Simbirsk (now Ulyanovsk) on the Volga, Pavlow (1901, p. 82, pl. 8, fig. 7) described a short-grooved, stout belemnite from the mid-Hauterivian *versicolor* Zone and identified it as *Belemnites speetonensis* (i.e. *Aulacoteuthis*). It is here tentatively placed in *A.* (*B.*) *rawsoni*, though Swinnerton (1948, p. 48) identified the same specimen as *A. descendens*. This may be one of the reasons why Swinnerton regarded *Aulacoteuthis* and *Oxyteuthis* (including *Praeoxyteuthis*) as two forms derived from a common stock rather than agreeing with Stolley (1925, 1927) that the former was a grooved stage interposed in the evolution of the latter two genera. The proven stratigraphic separation of the late Hauterivian to earliest Barremian *Boreioteuthis* from the mid-Barremian *Aulacoteuthis* supports the morphological evidence that they are homeomorphs.

CONCLUSIONS

While the rare *Acroteuthis* in the lower part of the north-west European *Hibolites* beds are simply relics of an earlier fauna, later examples of the *Acroteuthis* (*A.*?) *conoides*–*Boreioteuthis* group are a new, more strongly grooved group that can be confused with slightly younger *Aulacoteuthis*. Material is insufficient to prove whether the *conoides*–*rawsoni*–*stolleyi* succession evolved in the area or whether the species migrated individually from other boreal areas, but *in situ* evolution is our preferred model. It is striking that while *Hibolites* is abundant in both shallow and deep water clays, *Boreioteuthis* is unusually common in the one section (Frielingen) where deeper water clays are exposed, so it may have adapted to an offshore environment.

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Cover: Pedicle valve of the brachiopod *Strophonella euglypha* (Dalman, 1828) from the Wenlock Limestone of Dudley, West Midlands; × 2. Photography by Harry Taylor of the British Museum (Natural History) Photographic Studio. One of the specimens illustrated in the *Atlas of Invertebrate Macrofossils* published by the Association.

EDIACARAN BIOTA OF THE WERNECKE MOUNTAINS, YUKON, CANADA

by GUY M. NARBONNE *and* HANS J. HOFMANN

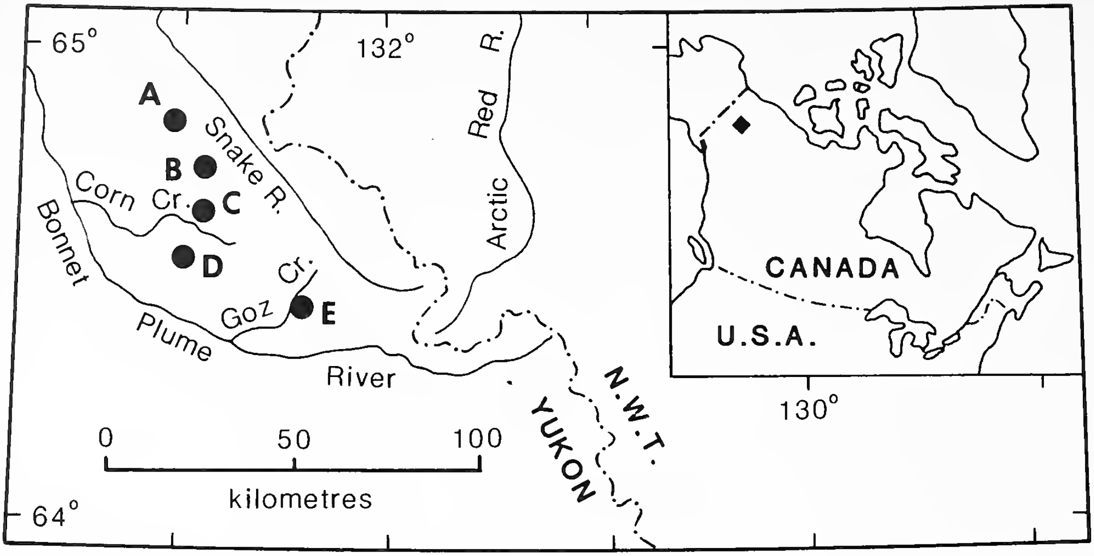
ABSTRACT. Soft-bodied metazoans, trace fossils, and metaphytes occur throughout several hundred metres of post-tillite, pre-Cambrian strata in the Wernecke Mountains, east-central Yukon Territory. The fossils occur in three unnamed units of siltstone deposited under shallow shelf and deeper water conditions. The oldest fossiliferous unit, the 'Goz siltstone', contains *Charniodiscus*? and *Cyclomedusa* sp. Siltstone unit 2 has yielded macrofossils (*Beltanelliformis brunsae*, *Medusinites asteroides*, *Rugoconites*? sp.), trace fossils (*Planolites montanus*), and carbonaceous compressions (*Vendotaenia*? sp.). Siltstone unit 1, the youngest of the three siltstones, exhibits abundant soft-bodied macrofossils (*Beltanella gilesi*, *Beltanelliformis brunsae*, *Charniodiscus* cf. *arboreus*, *Cyclomedusa plana*, *C.* sp., Ediacaria flindersi, Kullingia? sp., *Medusinites asteroides*, *Nadalina yukonenis* gen. et sp. nov., *Spriggia annulata*, *S. wadeae*, *Tirasiana* sp.) and trace fossils (*Gordia marina*, *Neonereites*? sp., *Planolites montanus*, and a backfilled burrow). Overlying Proterozoic carbonates contain only simple trace fossils.

The Wernecke assemblage is similar to other occurrences of the Ediacaran fauna, but is most closely comparable with the Valday assemblage of the Russian Platform and the type assemblage in South Australia. Similarity of the faunal sequence in the Wernecke Mountains with that present in the type Ediacaran and Vendian implies that evolutionary stages previously identified within these systems may be globally significant.

THE Ediacaran fauna is a distinctive assemblage of soft-bodied metazoans and simple trace fossils that occurs above the highest Varangian tillites and below the lowest fossiliferous deposits of the Cambrian (see Glaessner 1984 and references therein). This fossil assemblage has been reported from every continent except Antarctica (Glaessner 1984, Fig. 1/8), and is particularly well developed in Australia, Namibia, Newfoundland, and the Russian Platform. The widespread occurrence of this distinctive assemblage has supported calls for recognition of a formal, sub-Cambrian geological period, variously termed the Vendian (Sokolov 1952; Sokolov and Fedonkin 1984), Ediacaran (Jenkins 1981), Ediacarian (Cloud and Glaessner 1982), or Sinian (Grabau 1922; Xing 1984). While all have 'the base of the Cambrian' as their common upper limit, none of these proposed formal units has the same lower limit. A discussion of the relative merits of each is beyond the scope of the present paper. However, for the purposes of this paper we prefer to use Ediacaran for the shortest interval with soft-bodied fossil assemblages, because the first *diverse* assemblage to be described and used for comparison derives from the Ediacara Hills region in South Australia. The faunally characterized Ediacaran is encompassed chronologically by the longer Vendian interval (and the Vendian by the still longer Sinian).

Elements of the Ediacaran fauna were first discovered in the Wernecke Mountains (text-fig. 1) during a reconnaissance geologic study by Fritz *et al.* (1983). Their collection included the trace fossils *Gordia* sp. and *Palaeophycus tubularis* Hall (Fritz *et al.* 1983; Nowlan *et al.* 1985), and the macrofossils *Cyclomedusa davidi*? Sprigg and *Beltanelliformis brunsae* Menner (Hofmann *et al.* 1983); Hofmann (1984) subsequently described microfossils from these samples. During the summer of 1984, the present authors carried out more detailed geological studies (Narbonne *et al.* 1985), collecting numerous fossil specimens from three unnamed formations. These specimens help to elucidate the taxonomy, palaeoecology, and palaeogeography of early metazoans, and also aid in the regional and global correlation of the fossil-bearing strata.

[Palaeontology, Vol. 30, Part 4, 1987, pp. 647–676, pls. 73–75.]



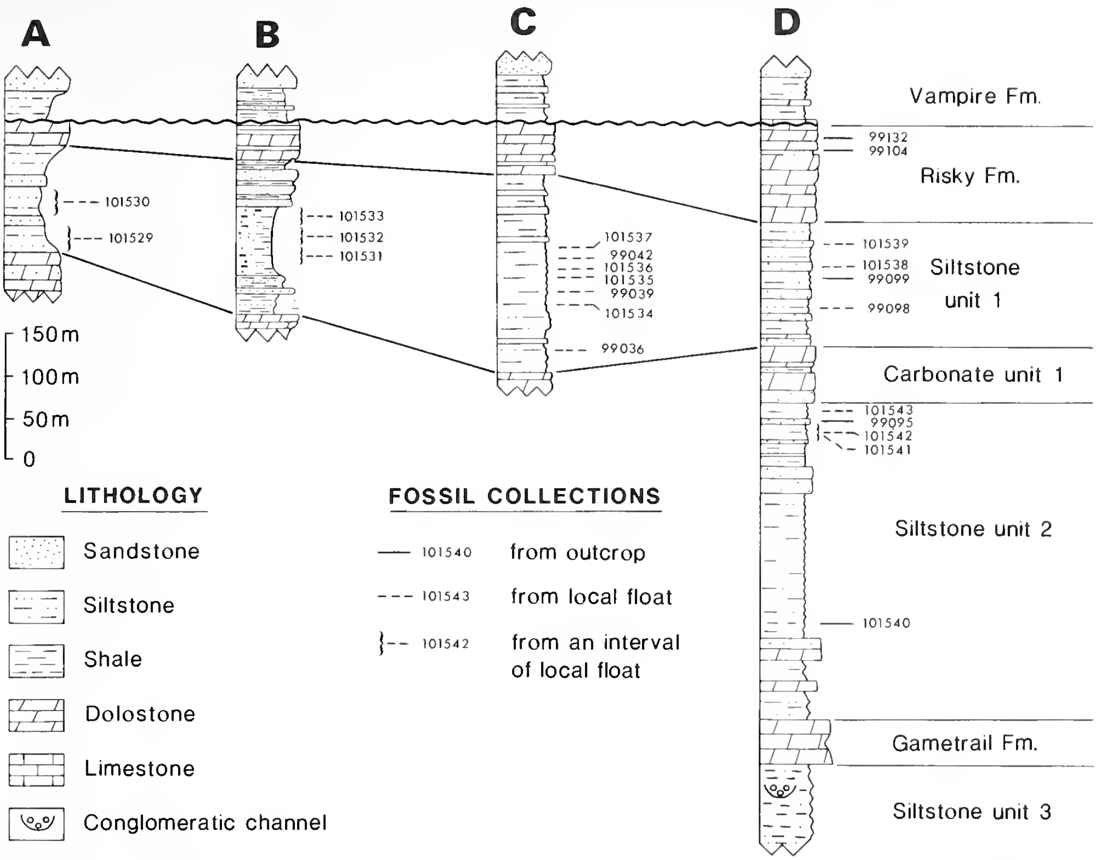
TEXT-FIG. 1. Index map showing location of sections studied in the eastern Wernecke Mountains.

GEOLOGICAL SETTING AND AGE

The Wernecke Mountains lie on the southern edge of the Yukon Stable Block (Lenz 1972), a site of predominantly shallow-water sedimentation throughout most of the late Proterozoic and early Palaeozoic. To the south, the strata pass into deeper-water shales and turbiditic conglomerates (Gordey 1980; Cecile 1982).

The strata considered in this study occur in equivalents to the upper part of the Windermere Supergroup, a predominantly clastic succession that can be traced throughout the Canadian Cordillera (Eisbacher 1981). The base of the Windermere Supergroup is younger than 770 Ma (Park and Aitken 1986) and probably younger than 730 Ma (Evenchick *et al.* 1984); its top is located at the base of the lowest Cambrian unit (Eisbacher 1981). Ediacaran macrofossils occur in the upper part of the Windermere Supergroup in southern British Columbia (Hofmann *et al.* 1985), western Northwest Territories (Hofmann 1981) and eastern Yukon Territory (Hofmann *et al.* 1983; this study). The Windermere Supergroup in the study area is more than 2 km thick, and exhibits glacial and glaciomarine deposits possibly equivalent to the Sturtian and Marinoan glaciations in its lower half (Eisbacher 1985). The Windermere Supergroup is disconformably overlain by the Vampire Formation (text-fig. 2), which contains, in its basal beds, small shelly fossils including *Anabarites trisulcatus* and *Protohertzina anabarica*; Nowlan *et al.* (1985) regarded this fauna as correlative with the *Anabarites-Circotheca-Protohertzina* Assemblage Zone of south-western China and with the Nemakit-Daldyn Horizon of Siberia, both of which would be placed immediately below the base of the Cambrian if the proposed base in Yunnan, China is accepted (Cowie 1985). Trace fossils in the same beds include two genera of arthropod burrows (*Rusophycus* and *Cruziana*) generally regarded as Cambrian or younger in age (Nowlan *et al.* 1985; Narbonne *et al.* 1987). The Vampire Formation is conformably overlain by the Sekwi Formation, a Lower Cambrian carbonate unit containing trilobites of the *Fallotaspis* and *Nevadella* zones near its base (Fritz 1978). Thus, the units bearing the fauna reported here occur stratigraphically between late Proterozoic glacial deposits and fossiliferous Lower Cambrian strata, and can therefore be regarded as Ediacaran in age.

Ediacaran strata in the study area comprise a succession of alternating carbonate and fine siliciclastic units, with soft-bodied macrofossils recognized only in the siliciclastic units (Narbonne *et al.* 1985). Due to the reconnaissance level of geological study, formal stratigraphic names have not yet been proposed for most of these units nor can the palaeoecology be discussed in detail. This paper



TEXT-FIG. 2. Stratigraphic sections with collection localities (Geological Survey of Canada [GSC] numbers). Sections A, D from Narbonne *et al.* (1985), Section B from Aitken (1984), Section C from Fritz *et al.* (1983). Risky Formation (Aitken, in press) = map unit 11 of Blusson (1971).

will use the names suggested by Fritz *et al.* (1983), Fritz (1984), Aitken (1984), Narbonne *et al.* (1985), and Aitken (in press).

The oldest unit containing macrofossils is the 'Goz siltstone', which crops out on Goz Creek at locality 'E' (text-fig. 1). The 'Goz siltstone' occurs as a small, isolated fault block; it cannot be directly correlated with any unit in sections A–D, but is lithologically similar to Siltstone unit 3 at locality 'D' and the Sheepbed Formation of the western Northwest Territories (Narbonne *et al.* 1985). The 'Goz siltstone' consists predominantly of thin- to medium-bedded siltstone. Slump and load structures are common; ripple-marks are very rare. Granule-filled channels averaging 0·5 m deep occur sporadically. Most channels are filled with clast-supported, normally graded material, but some contain matrix-supported, massive fill. These features, combined with the apparent absence of structures typical of shallow-water conditions, suggest that deposition occurred on a slope in a deeper-water setting. Macrofossils occur on bedding surfaces in the siltstone.

Siltstone unit 2 at locality 'D' (text-figs. 1 and 2) consists predominantly of recessive-weathering shale and siltstone with sporadic interbeds of quartzose sandstone and minor dolostone. Individual sandstone beds are very thin and graded, and most likely represent storm deposits. The upper part of the unit has several laterally discontinuous, coarsening-upwards sandstone packages up to 8 m thick; lower parts of the cycles are characterized by planar-tabular and hummocky cross-stratification, and the upper parts of cycles exhibit sporadic desiccation cracks. Deposition probably occurred on a wave- or storm-dominated shelf, with the coarsening-upwards sandstones representing sand bars. Carbonaceous remains of metaphytes occur in dark-grey shale in the lower part of the unit (GSC loc. 101540), whereas metazoans and trace fossils occur as positive features on the soles of very thin to thin, storm-deposited sandstone beds near the top of the unit (text-fig. 2).

Siltstone unit 1 crops out at localities 'A' to 'D' (text-figs. 1 and 2). It is lithologically similar to Siltstone unit 2, differing mainly in that the thick sandstone beds are more continuous laterally. Synaeresis cracks are abundant, but desiccation cracks were not observed. Deposition probably occurred on a wave- or storm-dominated shelf. Macrofossils are found sporadically throughout the lower two-thirds of the unit; trace fossils occur rarely in the lower half of the unit but are common throughout the upper half. Macrofossils and trace fossils are seen chiefly as positive features on the soles of very thin to thin, storm-deposited sandstone beds; only very rarely are they preserved as negative features on the tops of these beds. No slabs exhibiting both macrofossils and trace fossils were observed.

These occurrences suggest that the Ediacaran organisms preserved in Siltstone units 1 and 2 lived in a shallow sublittoral environment, whereas those present in the 'Goz siltstone' lived in a deeper-water environment. This is consistent with other reports of the Ediacaran fauna, which are from both shallow shelf (e.g. Goldring and Curnow 1967; Jenkins *et al.* 1983) and deeper slope (e.g. Anderson and Conway Morris 1982; Gibson *et al.* 1984) settings.

BIOSTRATIGRAPHY

As now known, the Ediacaran macrobiota of the Wernecke Mountains comprises an assemblage of 14 species of metazoan fossils (one of which is new), 1 metaphyte, and 5 trace fossils. In addition, 3 dubiofossils are reported. The greatest taxonomic diversity is exhibited by soft-bodied discoidal structures: 11 of the 14 species can be broadly referred to 9 'medusoid' genera; one species is a pennate coelenterate, and one is a possible organ of attachment to the substrate. The numerically dominant soft-bodied organism in the assemblage is a gregarious species of compressed globular structures assigned to *Beltanelliformis brunsae*. In addition, 5 species of ichnofossils characterize the upper part of the sequence studied. Of these ichnofossils, only *Planolites montanus* is common.

The Ediacaran fauna of the Wernecke Mountains is considerably more diverse than that reported from map-unit 10B of the Mackenzie Mountains of the western Northwest Territories by Hofmann (1981). However, the presence of *B. brunsae* and *Gordia marina* in both areas is consistent with lithostratigraphic evidence (Fritz *et al.* 1983; Aitken, in press) that the strata are equivalent.

The Wernecke assemblage is broadly similar to Ediacaran assemblages reported from other areas, particularly Australia and Eurasia (text-fig. 3). Similarity of the Wernecke assemblage to Ediacaran/Vendian assemblages from Australia, the Russian Platform, Siberia, China, England, Newfoundland, and several other localities supports recent calls (e.g. Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984) for recognition of a formal geological period based on this fauna.

Although many authors believe that several biostratigraphic zones can be recognized within the Ediacaran/Vendian, intercontinental correlation of these macrofossil zones has proved difficult. The Vendian of the Russian Platform can be divided into four zones which Sokolov and Fedonkin (1984) considered to be stages. The global applicability of these 'zones' or 'stages' is currently uncertain (see Jenkins 1981, p. 181 and references therein). Nevertheless, there would appear to be a close correlation between the faunal sequences of the Wernecke Mountains and the Russian Platform (text-fig. 4).

The basal, Volhyn 'Series' contains deposits of the Varangian glaciation, but apparently lacks macrofossils and trace fossils (Sokolov and Fedonkin 1984). This is most likely equivalent to strata below the fossiliferous units discussed in this paper, which contain glacial deposits and apparently lack macrofossils and trace fossils (Eisbacher 1981). Intercontinental correlation of glacial deposits in the Windermere Supergroup has been discussed by Eisbacher (1985), who recognized equivalents of the Sturtian and Marinoan (= Varangian) glaciations in these strata.

The overlying Redkino 'Series', represented by the Mogilev, Yaryshev, and Nagoriany Formations in the Ukraine and by the Pletevev and Ust-Pinega Formations in the Baltic region, contains a diverse

SYNOPSIS OF WERNECKE MOUNTAINS MACROBIOTA

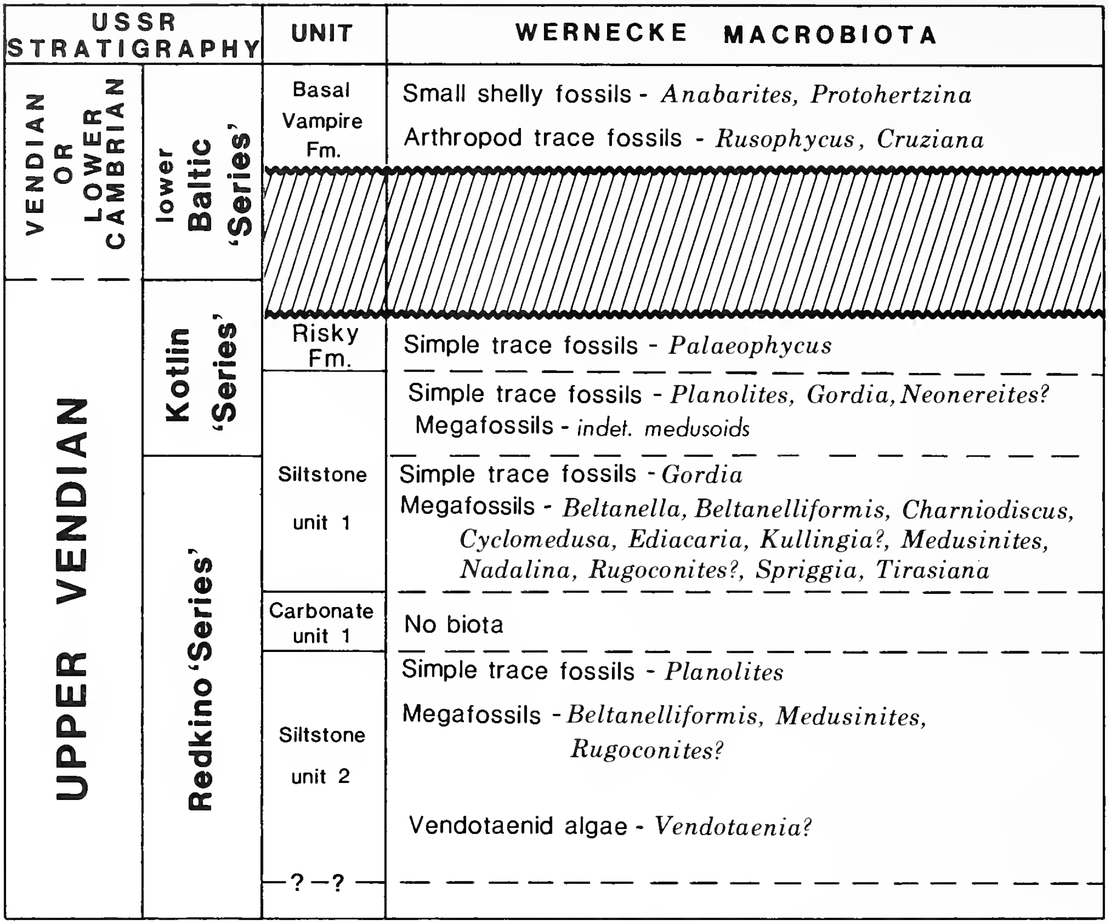
TAXA	OCCURRENCES																											
UNITS	Map unit 11		Siltstone unit 1																Siltstone unit 2					Goz siltstone			Vendian, Eurasia	Ediacaran, Australia
SECTIONS	D		A		B			C							D									E				
GSC localities	99132	99104	101530	101529	101533	101532	101531	101537	99042	101536	101535	99039	101534	99036	101539	101538	99099	99098	101543	99095	101542	101541	101540	101546	101545	101544		
Phylum COELENTERATA																												
Beltanella gilesi Sprigg, 1947							○						○														◇	◇
Charniodiscus cf. *C. arboreus* (Gl. in Gl. & D., 1959)				○																								□
C.? sp.																									○		□	□
Cyclomedusa plana Glaessner & Wade, 1966											○																◇	◇
C. sp.							○	○	○			○												○		○	□	□
Ediacaria flindersi Sprigg, 1947						○																					◇	◇
Kullingia? sp.													○														□	□
Medusinites asteroides (Sprigg) Gl. & W., 1966									○	○										○							◇	◇
Nadalina yukonensis gen. et sp. nov.																○												
Rugoconites? sp.																						○						□
Spriggia annulata (Sprigg) Southcott, 1958			○																								□	◇
S. wadeae Sun, 1986													○														□	◇
Tirasiana sp.							○		○																		◇	□
Phylum uncertain																												
Beltanelliformis brunsae Menner, 1974			○	○		○	○		○			○	○	○					○	○	○	○					◇	□
ICHNOFOSSILS																												
Gordia marina Emmons, 1844					○													○									◇	
Neonereites? sp.					○																						□	
Palaeophycus tubularis Hall, 1847	△	△																										
Planolites montanus Richter, 1937			○		○	○	○		○	○					○		○					○					◇	◇
Backfilled burrow						○																						
Group VENDOTAENIDES Gnilovskaya, 1971																												
Vendotaenia? sp.																							○				□	
DUBIOFOSSILS																												
Dubiofossil A										○																		
Dubiofossil B						○																						
Dubiofossil C																						○						

HJH 86

TEXT-FIG. 3. Synopsis of Ediacaran macrobiota of Wernecke Mountains. Specimens from the present study are shown by circles; triangles identify specimens described by Nowlan *et al.* (1985) from map-unit 11 (= Risky Formation). For comparison, same (rhombs) or similar (squares) forms from Australia and Eurasia are also indicated.

assemblage of soft-bodied metazoans along with vendotaenid algae and simple trace fossils (Palij *et al.* 1979; Sokolov and Fedonkin 1984). This is similar to the 'Goz siltstone', Siltstone unit 2, and the lower two-thirds of Siltstone unit 1, which contain a similar assemblage. Indeed, most of the specific forms found in these three units have also been described from the type Redkino 'Series' (text-fig. 3).

The overlying Kotlin has yielded vendotaenid algae and simple trace fossils, but only sparse 'medusoids' (Palij *et al.* 1979; Sokolov and Fedonkin 1984). This compares with the upper third of Siltstone unit 1 and all of the Risky Formation (= map-unit 11 of Blusson 1971; see Aitken, in



TEXT-FIG. 4. Proposed correlation of the upper part of the Windermere Supergroup with the Vendian of the Russian Platform. Similar correlations can be made with the Ediacaran of Australia.

press), which exhibit simple trace fossils and sparse, predominantly indeterminate 'medusoids'. Both in the Russian Platform and in the Wernecke Mountains, this zone contains relatively few diagnostic taxa, and is recognized primarily by its position between the more distinctive fossil assemblages of the overlying and underlying strata.

Overlying the Kotlin 'Series' on the Russian Platform is the Baltic 'Series'. This 'series' traditionally has been regarded as Lower Cambrian (e.g. Sokolov 1973; Palij *et al.* 1979), but recently some authors (e.g. Sokolov and Fedonkin 1984) have included its basal 'horizon', the Rovno, in the upper Vendian. The small shelly fossil assemblage of the basal Vampire Formation is broadly similar to that of the Nemakit-Daldyn (Nowlan *et al.* 1985), which Sokolov and Fedonkin (1984) regarded as the Siberian equivalent of the Rovno 'Horizon'. However, the abundance of arthropod traces (*Rusophycus*, *Cruziana*) in the basal Vampire suggests that correlation with the Lontova 'Horizon', which immediately overlies the Rovno on the Russian Platform, is more probable. The Lontova 'Horizon' is also part of the lower Baltic 'Series', and is generally regarded as Lower Cambrian (e.g. Fedonkin 1985*b*).

Similar correlations can be made with the Ediacaran of South Australia (Jenkins 1981). Marinoan (= Varangian) glaciomarine deposits occur at the top of the Umberatana Group (Coats 1981), and have been correlated with probable glacial deposits in the middle part of the Windermere Supergroup by Eisbacher (1985). Problematic remains of Ediacaran aspect occur sporadically throughout the lower part of the overlying Wilpena Group (Cloud and Glaessner 1982, fig. 2F; Dyson 1985), and a diverse Ediacaran assemblage is present in the upper part of the Wilpena Group (Pound Subgroup). The macrofossil assemblage of the Pound Subgroup is closely similar to that of the Wernecke Mountains (text-fig. 3) and the Redkino 'Series' of the Russian Platform (Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984), thereby implying that the strata are equivalent. The Pound Subgroup is disconformably overlain by the Uratanna Formation, which contains Cambrian trace fossils near its top (Daily 1972, 1973).

Similarity of the faunal and floral sequence between the Wernecke Mountains, the Russian Platform, and the Adelaide Geosyncline suggests that intercontinental correlation of stages and even zones may be possible within the Ediacaran/Vendian.

SYSTEMATIC PALAEONTOLOGY

The taxonomic affinities of the Ediacaran fauna are currently controversial. Until recently, most authors followed Sprigg (1949), Richter (1955), and Glaessner (1979, 1984) in regarding most discoid and pennate forms as the impressions of fossil coelenterates. Seilacher (1984) and McMenamin (1986) have questioned this interpretation, suggesting that some of these fossils may represent radial or circular burrows, internal sandy skeletons, or representatives of an extinct phylum. A full evaluation of the affinities of the Ediacaran fauna is beyond the scope of this paper and we have tentatively followed the *Treatise* (Glaessner 1979) in referring most of our taxa to the Coelenterata (text-fig. 3).

In the following section, synonymies include only putative pre-Cambrian occurrences. An alphabetical list for each major group of the Ediacaran biota of the Wernecke Mountains, and their stratigraphic and geographic distributions, is shown in text-fig. 3. Terminology regarding preservation follows Frey (1973, table 5).

All figured specimens are in the repository of the National Type Collection of Invertebrate and Plant Fossils (GSC) in Ottawa.

Phylum COELENTERATA

Genus BELTANELLA Sprigg, 1947

Type species. Beltanella gilesi Sprigg, 1947.

Beltanella gilesi

Plate 73, fig. 6

For synonymy up to 1966, see Glaessner and Wade (1966).

1972*a* *Planomedusites grandis* Sokolov, pl. 2, fig. 1.
1973 *Planomedusites grandis* Sokolov, p. 210, fig. 3/1.
1979 *Planomedusites grandis* Glaessner, p. A96, fig. 10/3.

Description. Smooth disc with narrow raised rim; two specimens preserved in convex hyporelief, respectively 36 and 46 mm in diameter and 1·5 mm and 1·7 mm in maximum relief; smaller specimen with central protruberance 3 mm across, partly enclosed by low concentric ridge 9 mm in diameter; larger specimen exfoliated and incomplete; both specimens surrounded by a flange about 2·5 mm wide.

Remarks. Our structures strongly resemble the holotype of *B. gilesi* Sprigg, which, however, has uniformly sized and equidistantly spaced circular markings at two-thirds the distance to the margin, as well as radial grooves. Glaessner and Wade (1966) hypothesized that these features might be accidental, a view supported by undescribed new specimens from Australia (R. J. F. Jenkins, pers. comm. 1986). *Beltanella* is similar in size and morphology to *Ediacaria* Sprigg (Glaessner and Wade 1966; Glaessner 1979), but can be distinguished by the presence of an outer flange.

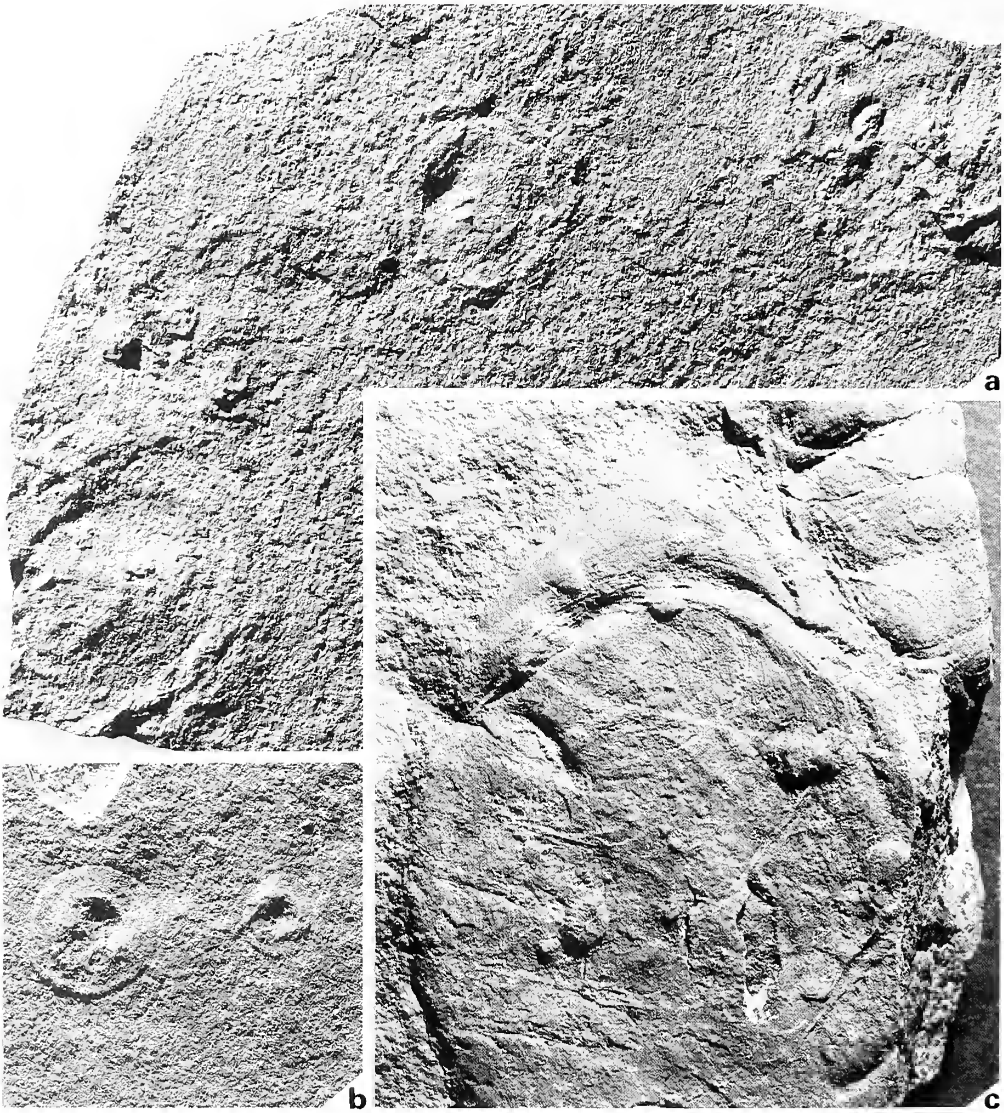
Genus CHARNIODISCUS Ford, 1958

Type species. Charniodiscus concentricus Ford, 1958.

Charniodiscus cf. *arboreus* (Glaessner, 1959)

Text-fig. 5*d*

Description. Two incomplete specimens preserved as large, ovate convex hyporeliefs. Larger specimen 98 × 72 mm, with at least 5·6 mm of relief at margin; roughly bilaterally symmetrical impression of flattened, bag-like



TEXT-FIG. 5. Macrofossils from the 'Goz siltstone' and siltstone unit 1. *a*, *Cyclomedusa* sp., epirelief. GSC loc. 101546. GSC 83016, × 1. *b*, *Charniodiscus*? sp., epirelief. GSC loc. 101545. GSC 83017, × 1. *c*, *Charniodiscus* cf. *arboreus* Glaessner. Two incomplete specimens (middle, GSC 83019; upper right, GSC 83020). Hyporelief. GSC loc. 101529, × 1.

body with parallel-sided, regular segments between 7 and 10 mm wide, extending outwards in apparently alternating series, at angles of about 60° with a poorly defined axial region, opening towards the more pointed end of the specimen (distal apex). Segments separated by straight to very slightly curved 1·0–1·5 mm wide furrows and associated one or two juxtaposed low, parallel, levee-like ridges; suggestion of short, oblique secondary furrows directed inward at angles near 40° from main furrows in wider (lower) part of specimen. Apical region subtriangular, concavo-convex, marked by fine wrinkles parallel with concave side of apical region; region 15 mm across immediately below triangular apex marked by delicate concentric wrinkles. Surface of segmented portion with randomly spaced (and probably accidental) subcircular tubercles 0·5–7·0 mm across and up to 1·0 mm of relief. Transverse section across lower end showing two irregular narrow vertical zones marked by mineralogical and textural contrast.

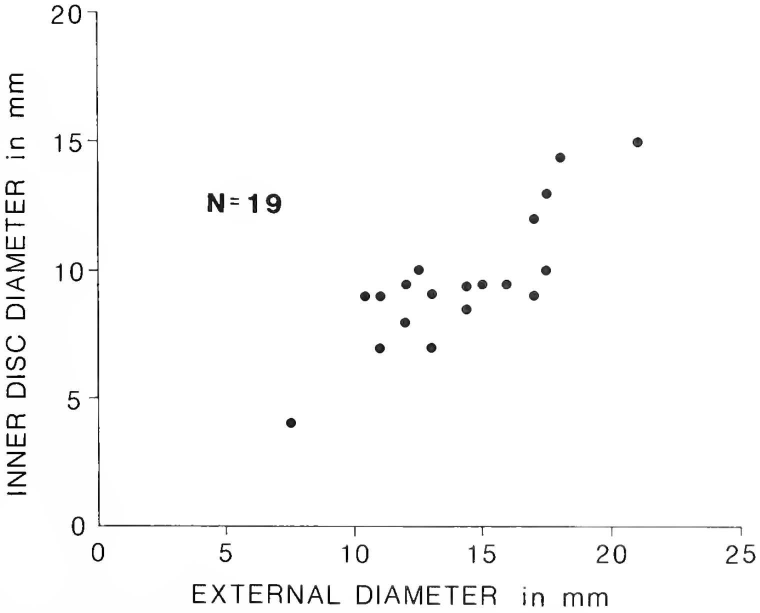
Smaller specimen an ovate hyporelief 50 × 26 mm, 10 mm high; surface bearing transverse convex segments of unequal width, from 6–12 mm wide, separated by pronounced furrows; surface marked by fine, oblique wrinkles continuous across furrows; transverse section showing recurved nature of impression and sedimentary lamination paralleling lower surface of hyporelief.

Remarks. The structures are indicative of the organization and highly flexible nature of genera such as *Charniodiscus* and *Inkrylovia.* The larger specimen somewhat resembles the *Rangea arborea* illustrated by Glaessner *in* Glaessner and Daily (1959, pl. 43, figs. 2 and 3; pl. 44, fig. 3; later assigned to *Arborea arborea* [Glaessner and Wade 1966, p. 619], and finally placed in synonymy with *Charniodiscus* [Glaessner 1979, p. A99]), and may represent a partially decomposed and over-folded specimen of this taxon. The smaller specimen has few distinguishing characteristics; its preservation is similar to a specimen referred to *Inkrylovia* from the correlative map-unit 10B in the Mackenzie Mountains 250 km east-south-east (Hofmann 1981, fig. 3A, B).

Charniodiscus? sp.

Text-figs. 5*b*, *c* and 6

Description. Nineteen specimens occurring as convex epireliefs and concave hyporeliefs at the interface between two very thin beds of siltstone. Bipartite structure, consisting of a rough-textured central disc surrounded by a smooth, flat outer ring with slight (< 0·3 mm) relief. External diameter 7·5–21·0 mm (mean = 14·3 mm); diameter



TEXT-FIG. 6. Size variations in *Charniodiscus*? sp. from the 'Goz Siltstone'.

of the inner disc 4–15 mm (mean = 9·7 mm); diameter of the inner disc 50–90% (average 68%) of the entire fossil (text-fig. 6). Outer margin of the fossil circular to subcircular, with minor indentations (text-fig. 5*c*). Inner disc centrally to slightly eccentrically located. Faint impression of a rod-like stem 2·5–6·0 mm wide attached to the inner disc. Specimens preserved as cleavage reliefs, with no structure visible below or above the bedding surface.

Remarks. The apparent absence of vertical tubes below or above the specimens implies that the structures did not form as a result of water or gas escape. Small pyrite concretions approximately one metre lower stratigraphically exhibit a central core of pyrite and an outer ring of darker (reduced) sediment; these can readily be distinguished from *Charniodiscus*? sp. by the fact that the outer ring has a different mineralogy and colour, but no difference in relief. The faint impression of a stem further serves to distinguish *Charniodiscus*? sp. from inorganic sedimentary structures and from medusiform genera with bipartite organization (e.g. *Medusinites* Glaessner and Wade, 1966; *Nimbia* Fedonkin, 1980).

Ford (1958) originally described *Charniodiscus* solely on the basis of its bipartite disc-like structure, but later (1963) figured the entire specimen with the bipartite disc attached by a stem to a frond-like structure. Subsequent workers (e.g. Jenkins and Gehling 1978; Glaessner 1979) have regarded the frond as the diagnostic portion of the organism. The Wernecke specimens exhibit an incomplete stem but lack the attached frond, and hence can only tentatively be referred to *Charniodiscus*.

Genus CYCLOMEDUSA Sprigg, 1947

Type species. Cyclomedusa davidi Sprigg, 1947.

Cyclomedusa plana Glaessner and Wade, 1966

Plate 73, fig. 3

1966 *Cyclomedusa plana* Glaessner and Wade, p. 607, pl. 98, figs. 1–3.
1968 *Cyclomedusa plana* Zaika-Novatskiy and Palij, pp. 133–134, fig. 1 (English translation, pp. 269–270, fig. 1).
1973 *Cyclomedusa plana* Sokolov, p. 209, fig. 2/1.
1979 *Cyclomedusa plana* Glaessner, p. A94, fig. 9/2*a*.
?1981 *Cyclomedusa* cf. *plana*, Fedonkin, pp. 58–59, pl. 2, fig. 1; pl. 3, fig. 4.
?1983 *Cyclomedusa* cf. *plana*, Fedonkin *in* Velikanov *et al.*, pl. 28, fig. 7.
?1985*a* *Cyclomedusa* cf. *plana* Fedonkin, pp. 71–72, pl. 2, figs. 3 and 5; pl. 5, fig. 7.

Description. One partially preserved circular impression (hyporelief) with bipartite organization; inner disc, 24 mm in diameter, with four coarse, slightly eccentric folds; small, bud-like, concentric pattern superimposed

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EXPLANATION OF PLATE 73

Fig. 1. *Cyclomedusa* sp. Sprigg. GSC loc. 101537. GSC 83021, × 1.
Fig. 2. *Nadalina yukonensis* gen. et sp. nov., epirelief. Holotype. GSC loc. 101535. GSC 83022, × 1.
Fig. 3. *C. plana* Glaessner and Wade, hyporelief. GSC loc. 101535. GSC 83023, × 1.
Fig. 4. *Spriggia wadeae* Sun, hyporelief. GSC loc. 101534. GSC 83024, × 1.
Fig. 5. *Kullingia*? sp., hyporelief. GSC loc. 101534. GSC 83025, × 1.
Fig. 6. *Beltanella gilesi* Sprigg, hyporelief. GSC loc. 101531. GSC 83026, × 1.
Figs. 7–9. *Medusinites asteroides* (Sprigg), hyporelief. 7, GSC loc. 99095. GSC 83027, × 1; 8, GSC loc. 99042. GSC 83028, × 1; 9, GSC loc. 101536. GSC 83029, × 1.
Fig. 10. *S. annulata* (Sprigg). Specimen on shale pebble. GSC loc. 101530. GSC 83030, × 1.
Fig. 11. *Rugoconites*? sp., next to small, unidentified circular structure. Hyporelief. GSC loc. 101541. GSC 83031, × 1.

PLATE 73

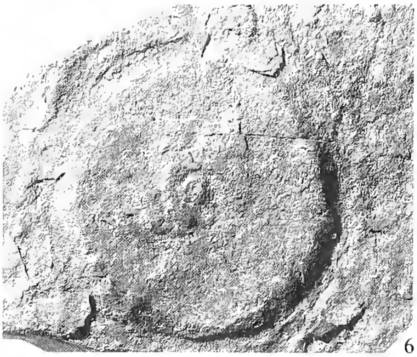

1


2


3


4


5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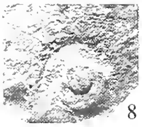
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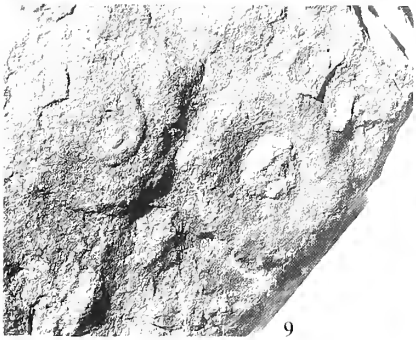
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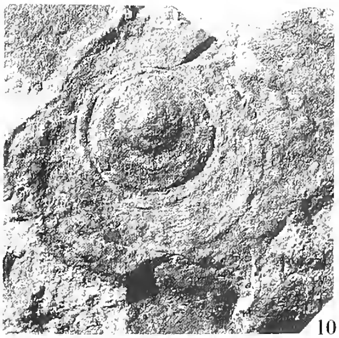
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11

NARBONNE and HOFMANN, Ediacaran biota

on third fold. Outer zone smooth, with 1–2 mm wide annulus of low relief at margin. Diameter of fossil 52 mm; total relief 0·7 mm, maximum in inner disc.

Remarks. C. plana is distinguished by its relatively small, coarsely corrugated central disc and its large, smooth outer ring without rugosities. Unless the small concentric structure on the third ring of the central disc represents the impression of a separate, small specimen of *Cyclomedusa*, this structure could be interpreted as a bud, much like one of the Australian paratypes in which the central cone appears to be twinned. Otherwise, the fossil most closely resembling our specimen is one from the Yaryshev Formation of the Ukraine (Zaika-Novatskiy and Palij 1968, fig. 1; see also re-illustrations in Sokolov 1973, fig. 2/1, and Glaessner 1979, fig. 9/2*a*).

Cyclomedusa sp.

Plate 73, fig. 1; text-fig. 5*a*

1983 *Cyclomedusa davidi?* Hofmann *et al.*, p. 455, fig. 2A, B.

Description. Circular to elliptical structures with numerous coarse, concentric rugae, slightly eccentric in some specimens; preserved as epi- and hyporeliefs; distinct small central tubercle (hyporelief) or pit (epirelief) at or near centre; indistinct radial markings in some specimens (e.g. Hofmann *et al.* 1983, fig. 2B); diameters 17–76 mm (N = 23, mean 38·6 mm), 0·5–3·0 mm in relief.

Remarks. The collection constitutes a heterogeneous lot, with specimens differing widely in quality of preservation. It includes large, flattish specimens as well as small discs with proportionately higher relief. All are characterized by moderately coarse, concentric rugae. The fifteen specimens from the 'Goz siltstone' referred to *C. davidi*? by Hofmann *et al.* (1983, p. 455) have now been determined to be epireliefs. The collection has been supplemented by several additional specimens, which include one showing a more eccentric position of the central depression, somewhat like the *C. serebrina* from the Ukraine (Palij *et al.* 1979, pl. 48, fig. 4); however, the poorly preserved marginal wrinkles do not overlap as in the Ukrainian specimen.

Cyclomedusa is the most cosmopolitan of the Ediacaran macrofossils (see also Wade 1972, p. 205), and most specimens have been referred to *C. davidi* Sprigg. Sun (1986) has reviewed the taxonomy of *Cyclomedusa*, restricting *C. davidi* to forms with numerous fine radial grooves on the oral surface. The scarcity of radial grooves in the specimens from the Wernecke Mountains may be taxonomically significant, or may simply reflect preservation of the aboral surface of *C. davidi.*

Genus EDIACARIA Sprigg, 1947

Type species. Ediacaria flindersi Sprigg, 1947.

Ediacaria flindersi Sprigg, 1947

Text-fig. 7

For synonymy up to 1966, see Glaessner and Wade 1966.

1978 *Tirasiana disciformis* Fedonkin, fig. 3, no. 6.
1979 *Ediacaria flindersi* Glaessner, p. A95, fig. 9/1.
1981 *Tirasiana disciformis* Fedonkin, p. 57, pl. 2, fig. 4.
1985*a* *Ediacaria flindersi* Fedonkin, pp. 74–75, pl. 1, figs. 2 and 5; pl. 2, fig. 4.

Description. Very large circular structures with tripartite organization, composed of three superimposed concentric discs, preserved as convex hyporelief. Two specimens; complete specimen (text-fig. 7) comprising inner disc 36 mm in diameter, with about 2 mm of relief, superimposed on second disc 100 mm across and about 3 mm in relief, attached to third disc 165 mm across, with about 5·5 mm of relief. Surface of innermost disc with one faint concentric circular furrow midway between its centre and its periphery; second disc with at least five distinct, narrow, unevenly spaced concentric ridges which are developed most strongly in its peripheral

TEXT-FIG. 7. *Ediacaria flindersi* Sprigg, hyporelief. GSC loc. 101532. GSC 83014, × 0·5.

portion; largest disc with faint concentric markings midway between inner and outer limits. Very faint radial markings also locally visible. Middle and outer discs with indentations that coincide with an arcuate groove which has large radius and is tangent to central disc. Part of specimen traversed by 1·0 mm-wide shrinkage crack filling. Second, incomplete specimen (GSC 83053) exhibiting inner disc 74 mm in diameter, with about 1 mm of relief, superimposed on second disc 110 mm in diameter with about 1 mm of relief attached to third disc 222 mm in diameter with about 2 mm of relief: middle disc with four concentric ridges near its periphery.

Remarks. E. flindersi is the largest 'medusoid' known from the Ediacara assemblage (Glaessner and Wade 1966), and the two specimens from the Wernecke Mountains are at the upper end of its known size range. Sprigg's (1947, 1949) original specimens are marked by strong radial grooves, but these are not present on the ex-umbrellar surface (Glaessner and Wade 1966; Sun 1986, p. 336). The specimens from the Wernecke Mountains are most similar to a large specimen from the Vendian of the White Sea coast, originally referred to *Tirasiana disciformis* Palij, 1976 by Fedonkin (1978, fig. 3, no. 6; 1981, pl. 2, fig. 4) but now referred to *E. flindersi* (Fedonkin 1985*a*, pl. 1, fig. 5).

Genus KULLINGIA Glaessner *in* Føyn and Glaessner, 1979

Kullingia? sp.

Plate 73, fig. 5

? 1979 *Kullingia concentrica* Glaessner *in* Føyn and Glaessner, pp. 39–40, fig. 8*a*.
? 1985 *Kullingia concentrica* Gureev, pp. 99–100, pl. 39, figs. 1–4.

Description. Two specimens from GSC locality 101543 preserved as convex discoidal hyporeliefs; figured specimen 54 mm in diameter, with about 1 mm of relief; surface smooth, provided with closely spaced, faint, regular concentric wrinkles that are most prominent near periphery; central disc 7 mm across barely noticeable; no radial pattern distinguishable; second specimen juxtaposed to first, partially preserved, about 60 mm across, with 1 mm of relief.

Remarks. The structures have some of the characteristics of *Kullingia*, but folds in the central portion of the discs are poorly preserved making the specimens resemble those of *Beltanelliformis*. Their larger size and more regular concentric ridges and furrows set them apart.

Genus MEDUSINITES Glaessner and Wade, 1966

Type species. Medusinites asteroides (Sprigg) Glaessner and Wade, 1966.

Medusinites asteroides (Sprigg), *emend.* Glaessner and Wade, 1966

Plate 73, figs. 7–9

1949 *Medusina mawsoni* Sprigg, p. 89, pl. 13, fig. 4; text-fig. 7B.
1949 *Medusina asteroides* Sprigg, p. 90, pl. 13, text-fig. 7C.
1956 *Protolyella asteroides* Harrington and Moore, p. F155, fig. 127/1.
1956 *Protolyella mawsoni* Harrington and Moore, p. F155, fig. 127/2.
1966 *Medusinites asteroides* Glaessner and Wade, pp. 605–607, pl. 94, figs. 1–5.
1968 *Medusinites asteroides* Wade, pp. 259, 260, figs. 22 and 24.
? 1973 *Medusinites patellaris* Sokolov, p. 210, fig. 3/2.
1979 *Medusinites asteroides* Glaessner, p. A94, fig. 10/1.
? 1980 *Paliella patelliformis* Fedonkin, p. 10, pl. 2, figs. 1–3.
? 1981 *Paliella patelliformis* Fedonkin, pp. 62–63, pl. 31, figs. 2 and 3; pl. 32, figs. 1 and 2.
? 1983 *Paliella patelliformis* Fedonkin, pl. 28, figs. 1, 2, 4–6.
1983 *Medusinites asteroides* Fedonkin, pl. 28, fig. 10.
? 1983 *Medusinites* sp. Fedonkin, pl. 34, fig. 1.
1985*a* *Medusinites asteroides* Fedonkin, pl. 8, fig. 2.
? 1985*a* *Medusinites* sp. Fedonkin, pl. 8, fig. 3.
? 1985*a* *Paliella patelliformis* Fedonkin, pp. 73–74, pl. 3, fig. 9; pl. 10, fig. 5.

Description. Subcircular convex hyporeliefs, composed of smooth central disc, separated by a subcircular groove from a broad, smooth outer ring, itself surrounded by a groove; disc one-third to one-half of diameter of whole structure. Outer diameters of three specimens 9·0, 20·5, and 25·6 mm; disc diameter respectively 4·3, 10·9, and 8·3 mm; relief respectively 0·8, 1·3, and 1·8 mm.

Remarks. Glaessner and Wade (1966) erected the genus *Medusinites* to include both *Medusina asteroides* Sprigg and, questionably, *M. mawsoni* Sprigg. Our three specimens, none of which shows any radial elements, most closely resemble the holotype of *M. mawsoni*, and two specimens of *Medusinites asteroides* illustrated by Glaessner and Wade (1966, pl. 97, figs. 1 and 2). Similar structures from the USSR were illustrated by Sokolov (1973, p. 210, fig. 3, no. 5) as *M. patellaris*, and as *M. asteroides* by Fedonkin (1983, pl. 28, fig. 10).

The genus *Paliella* (Fedonkin 1980, p. 10) is very close in morphology to *Medusinites*, and is said to be distinguishable from it by the presence of radial grooves in the outer zone. However, such grooves, though not dominant, are present in the type material of *Medusinites* (e.g. Sprigg 1949, text-fig. 7B, C; Glaessner and Wade 1966, pl. 97, figs. 3 and 5). Moreover, Fedonkin (1983, pl. 28, figs. 5 and 6) illustrated under *Paliella* specimens in which radial elements are not distinct. *Paliella* may thus be a junior synonym of *Medusinites*, or, if the radial pattern were considered characteristic and dominant, the structures could be referred to *Protolyella* Torell, in which case *Paliella* may be a junior synonym of *Protolyella*.

Genus NADALINA gen. nov.

Type species. Nadalina yukonensis sp. nov.

Diagnosis. Discoidal structure of centimetric size, with large smooth inner disc separated from surrounding annular field with narrow marginal rim of small relief by a ring of numerous, equally spaced millimetric pits (as seen in epirelief); width of annulus about one-half of radius of inner disc.

Etymology. Named for its occurrence in the Nadaleen River map area (National Topographical Series of Canada Map 106C, 1:250,000).

Nadalina yukonensis sp. nov.

Plate 73, fig. 2

Diagnosis. As for genus.

Holotype. GSC 83022.

Etymology. Named for its occurrence in the Yukon Territory of Canada.

Description. One whole specimen, preserved as elliptical epirelief on medium grey, medium-grained sandstone; 62 × 55 mm in size, with about 1 mm of relief. Disc differentiated into 2 zones, an inner flat disc without distinctive markings, 38 × 33 mm across, and an outer ring about 6–10 mm wide with less smooth surface and a 1–2 mm wide raised rim at the outer margin; between the 2 zones a partially preserved ring marked on one side of specimen by at least 9 pits, 1–3 mm wide and up to 1 mm deep, more or less regularly spaced, 5–9 mm apart. Poorly preserved partial impression of a second specimen (GSC 83015) on the same slab about 75 × 90 mm in size, with outer ring 12 mm wide, marked on inside with at least 7 pits 1–3 mm across, spaced 5–10 mm apart.

Occurrence and type locality. Siltstone unit 1, Section D (GSC locality 101538).

Remarks. The structure is unlike any known to us; we regard it as a new genus and species, and interpret it as the impression of a medusoid. The illustrated specimen is sufficiently well preserved and distinct to serve as a basis for a new taxon.

Genus RUGOCONITES Glaessner and Wade, 1966

Type species. Rugoconites enigmaticus Glaessner and Wade, 1966.

Rugoconites? sp.

Plate 73, fig. 11

Description. Single specimen, poorly preserved as convex hyporelief; subcircular disc 29 × 32 mm in diameter, with 2·7 mm of maximum relief; outer zone on one side of specimen with short radial furrows spaced about 3 mm apart, apparently emanating from points of bifurcation uniformly located about 5 mm from the periphery. Possible presence of ring surrounding specimen beyond margin, suggested by a diffuse, irregularly patterned, 7-9 mm wide zone.

Remarks. The pattern and size of the questionably bifurcating furrows are suggestive of the morphology of *Rugoconites*, of which two species have been described. The coarse furrow pattern would fit *R. enigmaticus* better than *R. tenuirugosus*, but our only specimen is so poorly preserved as to make even the identification of the genus doubtful. The genus has not before been reported from outside Australia.

Genus SPRIGGIA Southcott, 1958

Type species. Madigania annulata Sprigg, 1949.

Spriggia annulata (Sprigg, 1949) Southcott 1958

Plate 73, fig. 10

1949 *Madigania annulata* Sprigg (*partim*), pp. 93-94, pl. 16, fig. 1.
1956 *Madigania annulata* Harrington and Moore, p. F154, fig. 124.

1958 *Spriggia annulata* (Sprigg), Southcott, p. 59, fig. 3.
1979 *Cyclomedusa davidi* Føyn and Glaessner, p. 40, fig. 5*c*.
? 1981 *Cyclomedusa delicata* Fedonkin, pp. 59–60, pl. 2, fig. 2.
1984 *Spriggia annulata* Jenkins, p. 97, pl. 1, fig. 6.
? 1985*a* *Cyclomedusa delicata* Fedonkin, pp. 72–73, pl. 1, fig. 4.
1986 *Spriggia annulata* Sun, pp. 337–339, fig. 2E, fig. 5.

Description: Single, bipartite disc 28 mm in diameter, preserved in convex relief on a shale clast. Inner disc 17 mm in diameter, slightly convex (3 mm relief), with slightly eccentric papilla surrounded by annular rugae. Outer flange flat. Both inner disc and outer flange sculpted with numerous, submillimetric, concentric wrinkles.

Remarks. *Spriggia* has recently been revised by Sun (1986), who discussed its complex nomenclatural history and its distinction from similar genera. Sun regarded *Spriggia* as the impression of a fossil chondrophore.

Spriggia wadeae Sun, 1986

Plate 73, fig. 4

? 1979 *Cyclomedusa minuta* Fedonkin, *in* Palij *et al*., pp. 63–64, pl. 58, fig. 4.
? 1981 *Cyclomedusa minuta* Fedonkin, p. 59, pl. 4, fig. 2.
1986 *Spriggia wadeae* Sun, pp. 339–346, figs. 6A–D and 8A–C.

Description. Single disc preserved as convex hyporelief, 20 mm across, 0·7 mm high, with sharp outer margin and distinctly flat appearance, though sculptured by numerous annular ridges increasing in width outwards to a maximum of 1·0 mm wide. Attached to one side of specimen along about one-half of periphery, is an irregular crescentic marking 1·6 mm high, with maximum width of 10 mm, characterized by poorly defined submillimetric irregularities; shale matrix from underlying layer covering parts of disc and crescent.

Remarks. This structure is broadly similar to *C. minuta* from the White Sea coast (see synonymy), particularly because of the presence of the crescentic projection. However, *C. minuta* is considerably smaller and contains fewer annular ridges. The distinction between *S. wadeae* and *S. annuluta* has been discussed by Sun (1986).

Genus TIRASIANA Palij, 1976

Type species. *Tirasiana disciformis* Palij, 1976.

Tirasiana sp.

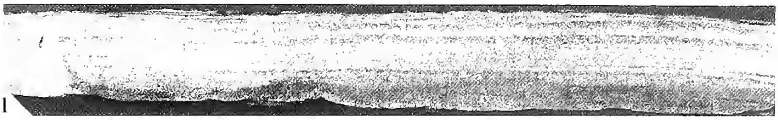
Plate 74, figs. 2 and 4

Description. Small discoidal hyporeliefs 10–18 mm in diameter (N = 4), 0·5–1·0 mm high, with tripartite organization: small central tubercle surrounded by inner disc that extends about halfway to periphery of whole impression; prominent circular groove separating inner disc from broad outer disc. Outer disc of specimen at bottom of Plate 74, fig. 4 bearing indistinct radial markings and narrow concentric circular groove; inner disc of specimen in Plate 74, fig. 2 with at least five circular markings of uniform size equidistant from centre, and incomplete subsidiary concentric wrinkles.

EXPLANATION OF PLATE 74

Figs. 1, 3, 5–7. *Beltanelliformis brunsae* Menner. 1, vertical section along top margin of 3. GSC loc. 101534. GSC 83032, × 1. 3, hyporelief, cluster of large specimens with smooth centres. 5, hyporelief; cluster of specimens with concentric wrinkles in central parts of discs. GSC loc. 99094. GSC 83035, × 1. 6, hyporelief; cluster of small specimens with high relief cast in underlying shale. GSC loc. 101541. GSC 83036, × 1. 7, epirelief; cluster of large specimens with low relief on underlying sandstone. GSC loc. 101532. GSC 83037, × 1.

Figs. 2 and 4. *Tirasiana* sp., hyporeliefs. 2, GSC loc. 99042. GSC 83033, × 1. 4, GSC loc. 101531. GSC 83034, × 1.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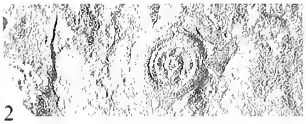
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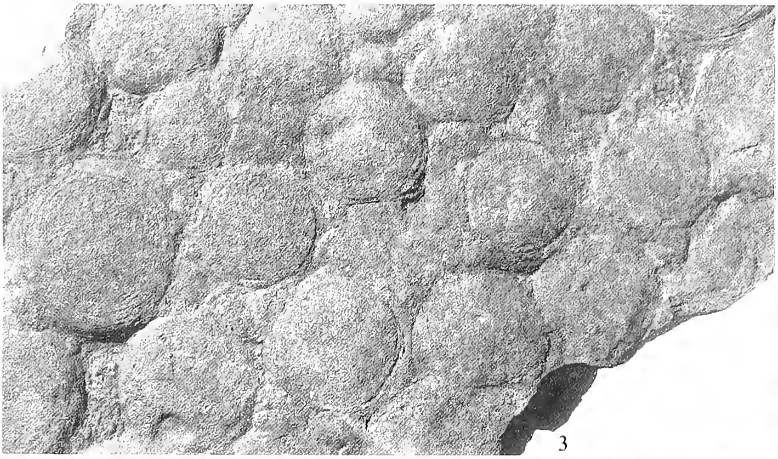
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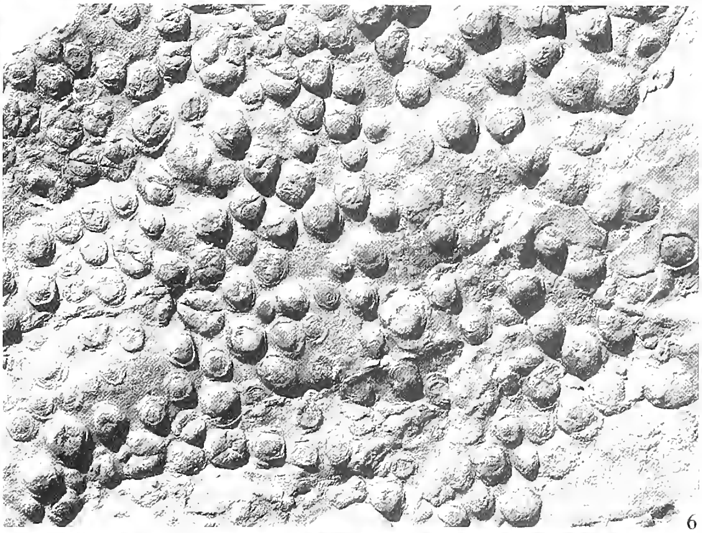
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7

Remarks. The specimens are very similar to a slightly larger specimen of *Tirasiana* sp. from the Yaryshev Formation in the Ukraine illustrated by Palij *et al.* (1979, pl. 49, fig. 7), which also has circular markings in the middle ring surrounding the central tubercle, like the specimen in Plate 74, fig. 4. The specimen in Plate 74, fig. 2 resembles *Protoniobia* Sprigg, 1949 (pl. 9, fig. 1) but lacks the marginal subcircular structures. *Protoniobia* was regarded as a concretion by Cloud (1968), and was treated as a 'rejected and unrecognizable' taxon by Glaessner (1979, pp. A112–A113), but we regard our specimen as organic.

Phylum uncertain

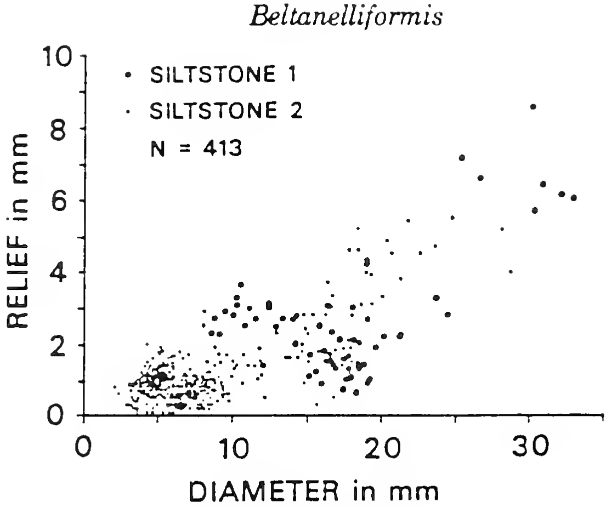
Genus BELTANELLIFORMIS Menner, in Keller *et al.* 1974

Type species. Beltanelliformis brunsae Menner, in Keller *et al.* 1974.

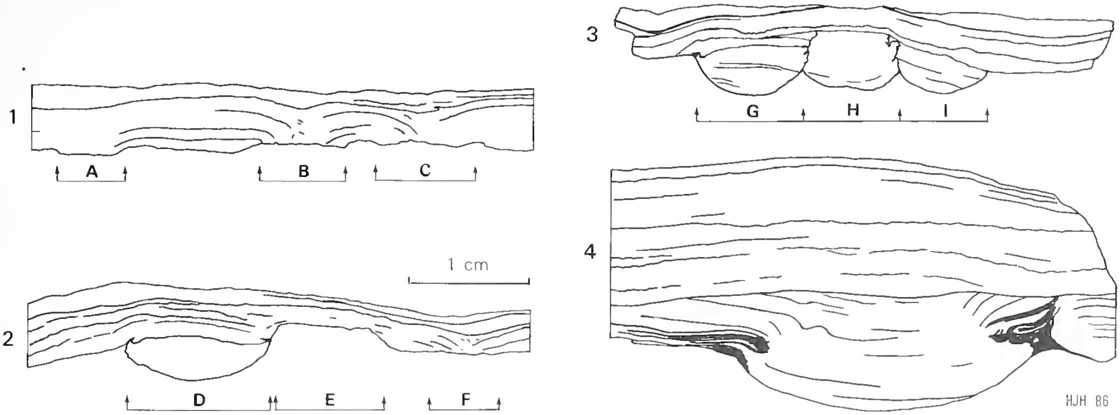
Beltanelliformis brunsae Menner, in Keller *et al.* 1974

Plate 74, figs. 1, 3, 5–7; Plate 75, figs. 1–8; text-figs. 8 and 9

? 1969 'minute fossils' Wade, pl. 69, fig. 7.
1974 *Beltanelliformis brunsae* Menner, *in* Keller *et al.*, p. 132, pl. 1, fig. 10.
1976 *Nemiana simplex* Palij, pp. 70–71, pl. 21, fig. 5; pl. 22, figs. 1–3.
1979 *Nemiana simplex* Palij *et al.*, p. 64, pl. 49, figs. 1, 5, 6.
1981 *Beltanelliformis brunsae* Fedonkin, p. 58, pl. 1, figs. 1–6.
1981 *Nemiana simplex* Fedonkin, p. 57, pl. 3, figs. 2 and 9.
1981 ?*Sekwia excentrica* Hofmann, fig. 4H.
1983 *Beltanelliformis brunsae* Hofmann *et al.*, p. 455, fig. 1C.
1985 *Beltanelloides simplex* (Palij) Gureev, pp. 97–98, pls. 35, 36, 37, figs. 1–4, 7; pl. 38, fig. 1.
1985*a* *Beltanelliformis brunsae* Fedonkin, pp. 70–71, pl. 5, fig. 2.
1985*a* *Nemiana simplex* Fedonkin, p. 70, pl. 5, fig. 3.
1985 *Nemiana simplex* Bekker, pl. 29, fig. 6.



TEXT-FIG. 8. Size variation of *Beltanelliformis brunsae* Menner from the Wernecke Mountains.



TEXT-FIG. 9. Vertical sections of *Beltanelliformis brunsae*. 1 corresponds to Plate 75, fig. 1. 2 to Plate 75, fig. 2. 3 is a tracing from a thin section cut across the three aligned specimens at right margin of Plate 75, fig. 3. 4 is a tracing from a thin section cut parallel to the large specimen illustrated in Plate 75, fig. 4.

Description. Flat to button-shaped, circular to subcircular convex hyporeliefs and concave epireliefs; less commonly, concave hyporeliefs and full reliefs; 2·2–33·1 mm across; (mean diameter = 9·15 mm; s = 5·88 mm; N = 413); 0·1–8·5 mm in relief (mean relief = 1·35 mm; s = 1·21 mm; N = 413); specimens in Siltstone unit 1 generally larger than those in Siltstone unit 2 (text-fig. 8). Individuals typically very closely crowded, with pronounced unimodal size distribution for specimens on individual bedding planes. Specimens with high relief (diameter/relief < 10) smooth, or provided with one or more curvilinear, irregularly linear, bifurcating, or star-shaped furrows or folds. Specimens of low relief (diameter/relief > 10) with narrow concentric peripheral wrinkles or folds, and smooth central field; some vertical sections showing collapsed sediment immediately above disc (e.g. Pl. 75, figs. 1–3; text-figs. 9.1; 9.2, specimen F); all gradations between low- and high-relief specimens present (text-fig. 8). Vertical sections of complete, high-relief specimens exhibiting lenticular nature, with semicircular bottom, deformed upper semicircle, and involuted sides; internal sediment fill laminated, graded, massive, or exhibiting slump structures (text-figs. 9.2, specimen D; 9.3; 9.4). Rare concave hyporeliefs hemispheroidal with central circular marking (e.g. Pl. 75, fig. 5) to relatively flat and wrinkled. Concave epireliefs shallow and relatively smooth, or with irregular, partly concentric wrinkles. Specimens preserved in full relief subspherical, with circular marking on top (Pl. 75, figs 6 and 7).

Remarks. The discs here assigned to *B. brunsae* are the most common fossils in the Wernecke assemblage. They typically are closely crowded, and the size distribution of specimens on individual bedding planes is strongly unimodal, indicating that each sample represents a population of individuals at the same stage of ontogenetic development assembled on a mud substrate, before the arrival of storm-deposited sand.

The Wernecke specimens are similar to forms described from the Russian Platform under a variety of names (see synonymy). The size range of typical '*Nemiana simplex*' from the Ukraine is reported to be 2–60 mm (Palij 1976, p. 70; Gureev 1985, p. 97). Our specimens are mainly at the lower end of the size range for this form, and are more similar to the '*N. simplex*' from the White Sea coast (Fedonkin 1981, p. 57, pl. 3, figs. 2 and 9), for which diameters are between 10 and 30 mm and the relief is 0–3 mm. Specimens from the Soviet Union also exhibit a single circular marking on their upper surface which Fedonkin (1985*a*) interpreted as an oral opening. Taxonomic assignment and interpretation of the discs from the Soviet Union is difficult because, despite an abundance of photographic illustrations of the basal surface, little has been documented of their internal structure.

The Wernecke discs show considerable variation in preservation from one bedding plane to another, ranging from smooth, flat discs with numerous delicate marginal wrinkles (= *B. brunsae* Menner) to more strongly convex forms with fewer and coarser, more irregular wrinkles, some of which extend into the central parts of the disc (= *N. simplex* Palij). This morphological transition indicates to us that *Beltanelliformis* and *Nemiana* are best explained as preservational variants of a single globular biological taxon.

Any interpretation of *Beltanelliformis* must account for: (1) the concentric wrinkling; (2) the variety of sedimentary fills and structures in and above the fossils (text-fig. 9; Pl. 74, fig. 1; Pl. 75, figs. 1, 2, 4); and (3) the complete gradation between *Beltanelliformis*-type and *Nemiana*-type preservation (text-fig. 8). We propose that *Beltanelliformis*-type forms were preserved where globular bodies resting on the mud substrate, either as single spheroidal organisms, or, less likely, as spheroidal colonies comparable to those figured by Glaessner (1969, fig. 3), were buried by storm-deposited sand. If, upon burial, the bodies quickly collapsed, undisturbed lamination would be preserved above the locus of these bodies (e.g. Pl. 74, fig. 1). If the bodies maintained their integrity long enough to allow the accumulation of sand around and above them subsequent decay of the spheroids would have produced the collapse of the sand into the space previously occupied by the bodies, resulting in the disturbed lamination now encountered above some of the specimens (text-figs. 9.1; 9.2, specimen F). In contrast, specimens exhibiting, *Nemiana*-type preservation probably were partially buried in the mud, most likely as a result of slow accumulation of mud around the bases of the spheroidal organisms. As a consequence of rapid, storm-induced burial, some specimens were filled with graded to parallel laminated sand (text-figs. 9.2, specimen D; 9.3). Other specimens remained unfilled, and subsequent collapse of the organism produced disturbed (slumped) lamination (text-fig. 9.4). Folding of the tough outer wall of the organism during rapid burial probably produced the concentric to irregular wrinkles visible on most specimens of *Beltanelliformis* and '*Nemiana*'.

Lithology also appears to have played an important role in determining the mode of preservation. Gureev (1985) has pointed out that, in the Ukraine, *Beltanelloides sorichevae* (*Beltanelliformis*-type preservation) occurs predominantly in shale, whereas '*Beltanelloides simplex*' (*Nemiana*-type preservation) occurs predominantly in siltstone and sandstone. Based on this, Gureev (1985) suggested that the two forms might be synonymous. Our specimens further support this hypothesis. In the Wernecke biota, the best examples of *Beltanelliformis*-type preservation (e.g. Pl. 74, fig. 2) are cast by argillaceous siltstone, whereas the best examples of *Nemiana*-type preservation (e.g. Pl. 75, figs. 5–8) are cast by sandstone.

Some specimens of *Beltanelliformis* exhibiting *Nemiana*-type preservation superficially resemble hemispherical anemone burrows such as *Bergaueria* Prantl, 1945. Palij *et al.* (1979) pointed out that '*Nemiana*' can be distinguished from *Bergaueria* by the presence of numerous wrinkles and folds resulting from deformation of a soft-bodied organism following burial, the consistent absence of an overlying vertical cylinder, and by the fact that adjacent specimens deform but do not cross-cut each other. The sporadic occurrence of specimens preserved in concave hyporelief (Pl. 75, fig. 5) in the Wernecke assemblage further suggests that *Beltanelliformis* represents the impression of a soft-bodied organism rather than a hemispherical burrow-fill. Hemispherical specimens of *Beltanelliformis* also superficially resemble the base of the Cambrian–Ordovician fossil *Protolyella* Torell 1870, which Seilacher (1984) has interpreted as the internal sandy skeleton of an anemone. However, *Protolyella* exhibits concentric hemispherical sediment fill reflecting active packing by the organism, whereas hemispherical *Beltanelliformis* were passively filled with graded, laminated, or massive sediment.

EXPLANATION OF PLATE 75

Figs. 1–8. *Beltanelliformis brunsae* Menner. 1, vertical section along inclined left margin of specimen in fig. 3, showing sagged laminae above specimens of *Beltanelliformis*. 2, vertical section along upper right margin of fig. 3, showing draping of laminae over specimens, × 1. 3, lower surface, showing close association of high relief (GSC 83038) and low relief (GSC 83039) forms. GSC loc. 101532. 4, vertical section showing laminated fill and slight draping of large specimen. GSC loc. 101531. GSC 83040, × 1. 5, cluster with specimens in both convex and concave hyporelief. GSC loc. 99095. GSC 83041, × 0·7. 6, bedding plane view of specimen preserved in full relief. GSC loc. 99036, GSC 83042, × 2. 7, side view of specimen in fig. 6, × 2. 8, largest observed specimens in the Wernecke assemblage. GSC loc. 101531. GSC 83043, × 1.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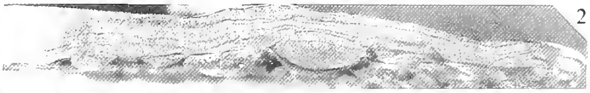
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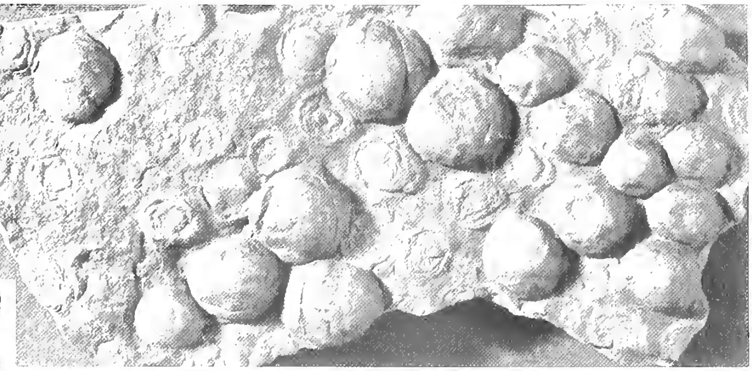
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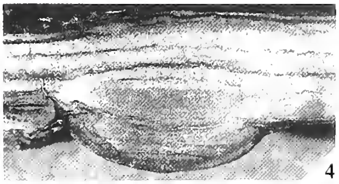
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NARBONNE and HOFMANN, *Beltanelliformis*

Nevertheless, *Beltanelliformis*, *Bergaueria*, and *Protolyella* can be closely similar in plan view, and can only be distinguished through study of their three dimensional form and the nature of their internal sediment.

Beltanelliformis brunsae was originally regarded as a medusoid (e.g. Sokolov 1972*a*, *b*; Menner 1974; Palij *et al.* 1979; Fedonkin 1981). However, Sokolov (1976), Sokolov and Fedonkin (1984, p. 13), and Glaessner (1984, pp. 24–25) who use the designation *Beltanelloides sorichevae* for such structures, later related them to *Chuaria*-like organisms, which are typically preserved as carbonaceous compressions. A lack of associated carbonaceous material, the apparent presence of a circular aperture on the upper surface, and the centimetric size of some specimens, makes the comparison of *Beltanelliformis* with chuariamorphids tenuous. Neither *Beltanelliformis* nor *Beltanelloides* appear in the *Treatise* (Glaessner 1979), and we have not had the opportunity to compare type material of these two taxa. The former may be an objective synonym (ICZN 1964, Art. 61*b*), however, because of the possible distinctness of specimens referred to *B. sorichevae* Sokolov (1972*a*, pl. 4, figs. 4–8), which have no circular impressions in the centre, and to *Beltanelliformis brunsae* Menner (Sokolov 1972*a*, pl. 4, fig. 2), and the apparent questionable nomenclatural status of the former (no holotype designated for species from among two 'forms'; no diagnosis given; ICZN 1964, Art. 13*a* (i), 15, 45*b*, *e*, 72*a*), we have assigned our structures to the validly published taxon *Beltanelliformis*.

ICHNOFOSSILS

Ichnogenus GORDIA Emmons, 1844

Type ichnospecies. *Gordia marina* Emmons, 1844.

Gordia marina Emmons, 1844

Text-fig. 10*a*

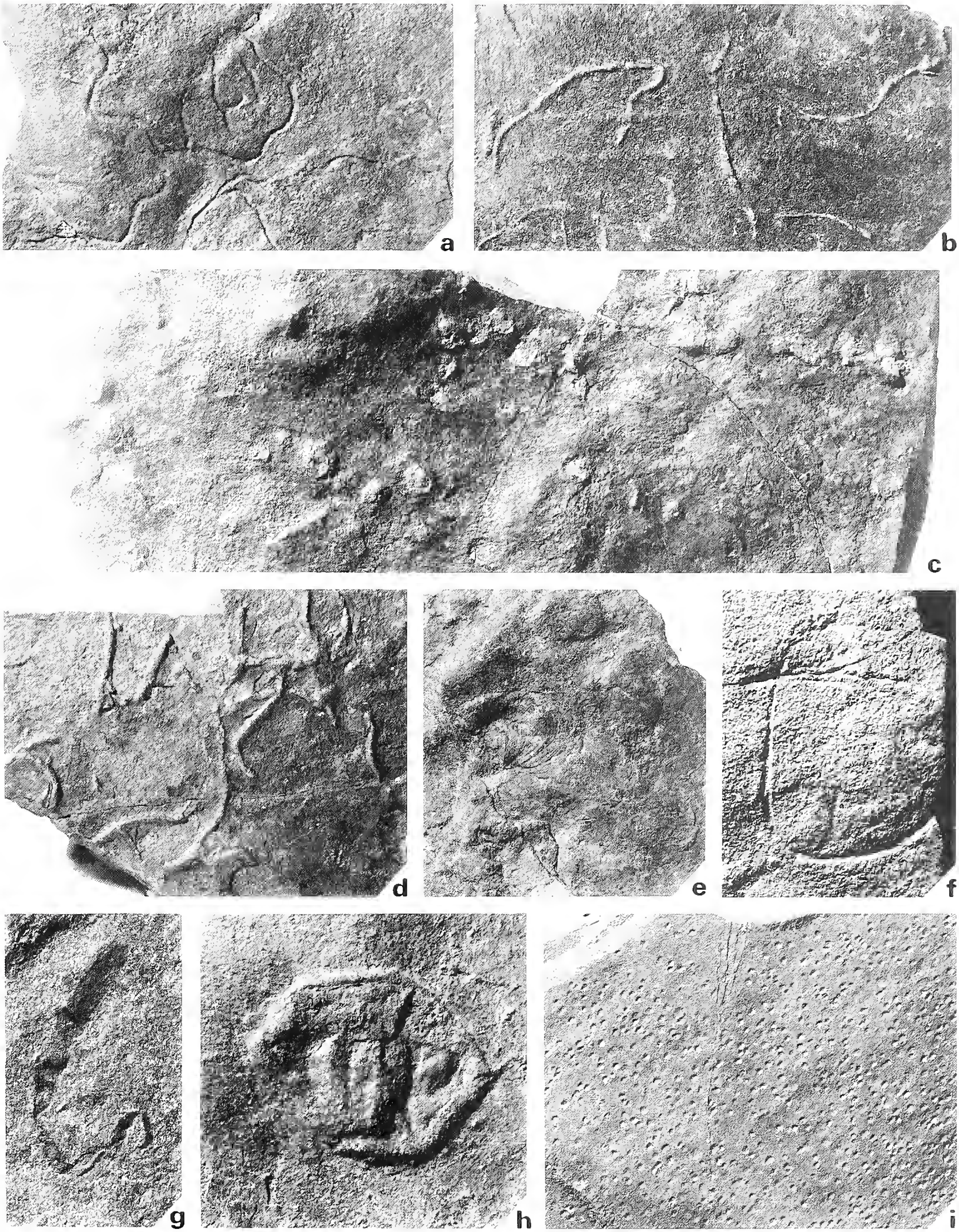
? 1976 'crawling trails', Palij, pl. 26, figs. 1 and 2.
? 1979 'crawling trails, first variety', Palij *et al.*, p. 77, pl. 53, figs. 2 and 4.
? 1981 *Gordia* sp., Hofmann, p. 309, fig. 5*b*.
1983 *Gordia* sp., Fritz *et al.*, pl. 44.1, fig. 3.
? 1985*b* *Gordia* sp., Fedonkin, pl. 23, fig. 1.

Description. Two specimens, preserved as concave epireliefs and convex hyporeliefs on very thin beds of fine-grained sandstone. Burrows horizontal and irregularly meandering; true branching absent, but cross-overs present. Burrows smooth with a diameter of approximately 1 mm. Burrow fill similar to host lithology.

Remarks. The presence of numerous cross-overs is commonly used to distinguish *Gordia* from slender specimens of *Planolites* and *Helminthopsis* (Książiewicz 1977, p. 155). This criterion, based on Phanerozoic specimens, appears to be less significant in the Ediacaran, where forms transitional between *Gordia* and *Planolites* are common (e.g. text-fig. 10*b*; Glaessner 1969, fig. 5B; Palij *et al.* 1979, pl. 53, figs. 2 and 4). Książiewicz (1977) and Crimes and Anderson (1985) recognized three ichnospecies of *Gordia*: *G. marina* Emmons, *G. molassica* (Heer 1865), and *G. arcuata* Książiewicz 1977, but we agree with Pickerill (1981) that *G. molassica* is indistinguishable from *G. marina*.

Gordia occurs widely in Phanerozoic strata and is one of the most commonly reported Ediacaran ichnofossils. *G. marina* occurs on the Russian Platform and in northwestern Canada, *G. arcuata* has

TEXT-FIG. 10. *a*, *Gordia marina* Emmons, concave epirelief. GSC loc. 101533. GSC 83044, × 1. *b*, *Planolites montanus* Richter, hyporelief. GSC loc. 101531. GSC 83045, × 1. *c*, *Neonereites*? sp., hyporelief. GSC loc. 101533. GSC 83046, × 1. *d*, *P. montanus* Richter, hyporelief. GSC loc. 101532. GSC 83047, × 1. *e*, horizontal backfilled burrow, ?epirelief. GSC loc. 101532. GSC 83048, × 1. *f*, Dubiofossil A, probably epirelief. GSC loc. 101536. GSC 83049, × 1. *g*, *Vendotaenia*? sp. GSC loc. 101540. GSC 83050, × 2. *h*, Dubiofossil B. GSC loc. 101532. GSC 83051, × 1. *i*, Dubiofossil C. GSC loc. 101541. GSC 83052, × 1.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been reported from northern British Columbia (Fritz and Crimes 1985), and *Gordia* sp. occurs in the Ediacaran of Australia (Glaessner 1969, fig. 5*b*), the Russian Platform (Palij *et al.* 1979), the Mackenzie Mountains (Hofmann 1981), and Newfoundland (Crimes and Anderson 1985). *Gordia* probably represents the crawling or feeding burrow of a worm-like organism (Chamberlain 1977).

Ichnogenus NEONEREITES Seilacher, 1960

Type ichnospecies. Neonereites biserialis Seilacher, 1960.

Neonereites? sp.

Text-fig. 10*c*

Description. Four specimens occurring in convex hyporelief on thinly bedded, fine-grained sandstone. Burrows slightly to moderately sinuous, up to 90 mm long, each consisting of a uniserial string of spherical to slightly ellipsoidal pellets 3–5 mm in diameter; pellets locally in contact, but typically irregularly spaced up to 5 mm apart; pellets composed of well-sorted sand.

Remarks. Specimens closely resemble those figured by Fritz and Crimes (1985, pl. 3*f*) from the Ediacaran of northern British Columbia. Among described species of *Neonereites*, they most closely resemble *N. uniserialis* Seilacher, but differ in that the pellets are irregularly spaced. *N. uniserialis* has been reported from the Vendian of the Russian Platform (Fedonkin 1977; Palij *et al.* 1979) and is common in Phanerozoic deposits (Häntzschel 1975). *Neonereites* probably represents the feeding burrow of a worm-like organism, most likely an annelid (Hakes 1976).

Ichnogenus PLANOLITES Nicholson, 1873

Type ichnospecies. Planolites vulgaris Nicholson and Hinde, 1875.

Planolites montanus Richter, 1937

Text-fig. 10*b*, *d*

1970	'hypichnial and exichnial casts', Banks, p. 26, pl. 1*b*, *d*.
? 1970	'curved trails', Webby, p. 87, fig. 3*d*.
1970	*Planolites ballandus* Webby, p. 95, fig. 14A–C.
1973	'hypichnial and endichnial burrows', Banks, p. 4, fig. 4*a*.
1977	*Planolites* sp., Fedonkin, p. 184, pl. 2*d*.
1979	'crawling traces, third variety', Palij *et al.*, pp. 77–78, pl. 54, fig. 2.
1979	*Planolites* cf. *serpens*, Palij *et al.*, p. 73, pl. 42, fig. 6.
1984	*Planolites* sp. Glaessner, p. 70, fig. 2/7.
1985*b*	*Planolites* cf. *serpens* Fedonkin, pl. 28, figs. 3, 6.

Description. Specimens occurring in convex hyporelief and concave epirelief on very thin beds of siltstone and fine-grained sandstone. Burrows highly sinuous and undulatory, occurring on bedding surfaces as small knobs and discontinuous, curved, burrow segments. Burrows cylindrical, with diameters ranging from 0·4 to 1·2 mm (N = 100); indistinct, irregularly spaced constrictions giving burrows a faint 'pinch-and-swell' appearance. True branching and cross-overs of adjacent specimens rare. Burrow fill structureless, and differing from host lithology.

Remarks. The taxonomy of *Planolites* has recently been reviewed by Pemberton and Frey (1982), who concluded that *Planolites* can be distinguished from the morphologically similar burrow *Palaeophycus* Hall by the presence of processed burrow-fill and the absence of a burrow lining in *Planolites*. Many specimens of *P. montanus*, including the ones in this study, exhibit a faint 'pinch-and-swell' appearance reminiscent of *Torrowangea* Webby, 1970. However, the swellings in *Torrowangea* are well defined and evidently represent a back-fill structure (Webby 1970), whereas the swellings in *P. montanus* are poorly defined and apparently reflect the undulose nature of the burrow. The typically meandering pattern of *Torrowangea* also differs from the sinuous to undulose pattern of *P. montanus*.

P. montanus is very common in the Wernecke assemblage, a feature typical of many Ediacaran assemblages (see synonymy above). *P. montanus* also occurs commonly throughout the Phanerozoic (Pemberton and Frey 1982). *Planolites* probably represents the feeding burrow of a vermiform organism (Pemberton and Frey 1982).

BACK-FILLED BURROW

Text-fig. 10*e*

Description. Single, fragmentary specimen on the (?)upper surface of a very thin bed of argillaceous, fine-grained sandstone. Specimen a gently curved, partially compressed cylinder 11 mm wide and at least 17 mm long; with well-developed back-fill.

Remarks. Although its fragmentary nature precludes definite identification, the specimen exhibits a back-fill structure similar to *Muensteria* von Sternberg 1833 or *Beaconites* Vialov 1962. Similar traces occur in the Ediacaran of Australia (R. J. F. Jenkins, written comm. 1986).

METAPHYTES

Group VENDOTAENIDES Gnilovskaya, 1971
Genus VENDOTAENIA Gnilovskaya, 1971

Type species. Vendotaenia antiqua Gnilovskaya, 1971.

Vendotaenia? sp.

Text-fig. 10*g*

Description. Isolated, smooth carbonaceous ribbons, curved and bent, 0·4–2·0 mm wide, largest fragment of nine specimens seen 30 mm long; faint, submillimetric longitudinal striae present in portions of filament.

Remarks. The ribbons have an appearance intermediate between those referred to *Vendotaenia* and *Tyrasotaenia* from the Russian Platform. The broad diameter, the curved nature, and the faint microscopic longitudinal striae suggest affinity with *Vendotaenia*, whereas twisted specimens bear more resemblance to *Tyrasotaenia*. However, longitudinal striae have also been reported for the latter genus, though these have been ascribed to folding of the thallus.

DUBIOFOSSILS

Dubiofossil A

Text-fig. 10*f*

Description. Almost complete, flat, gibbous disk, 40 × 29 mm, with marginal groove 0·8 mm deep; margin on one side almost rectilinear for about 17 mm, remainder evenly curved. No further identifiable markings.

Remarks. The specimen has no diagnostic features which would allow it to be classified. Possibly, it represents a severely distorted *Cyclomedusa*, though the absence of concentric wrinkling is against such an interpretation.

Dubiofossil B

Text-fig. 10*h*

Description. Single specimen preserved in convex hyporelief, 39 × 28 mm; subhexagonal, with outer rim 1·2–4·5 mm wide and 0·5–1·2 mm high. Trapezoidal ridge 15 × 12–19 mm and up to 2·0 mm high near centre of specimen. Faint parallel ridges approximately 1·0 mm apart locally preserved on central trapezoid and outer rim.

Remarks. The hexagonal outline and central trapezoid are both features that have not previously been described from Ediacaran macrofossils. The specimen appears to have been flattened, and consequently it is difficult to determine whether these represent primary features. Patterns such as those exhibited by dubiofossil B occur commonly on much smaller compressed leiospherid microfossils (e.g. Timofeev 1969), and it is possible that our specimen represents a large, compressed, spheroidal or sac-shaped organism.

Dubiofossil C

Text-fig. 10*i*

Description. Large number of minute pits, preserved on the upper surface of an olive-grey weathering siltstone lamina; diameters 0·5–1·2 mm, relief about 0·1 mm; specimens scattered, generally not contiguous. Similar, but smaller depressions exposed in one corner of the slab 1·0 mm below the first layer.

Remarks. The pits do not appear to be moulds of sand grains, inasmuch as the overlying sediment of coarse siltstone/very fine sandstone is, within some pits as well as outside them, still attached to the epirelief surface and does not contain coarse sand grains. Because of their small size and the inferred subtidal setting of the sediment, they do not appear to be rainprints. We thus consider it possible that they are fossils; they may represent an assemblage of juvenile forms of *Beltanelliformis* or *Bergaueria*. Alternatively, they resemble small pits associated with some specimens attributed to *Arumberia* (e.g. Bland 1984, figs. 1*b* and 2*b*, *c*), which differ, however, by the presence of superimposed fine, parallel to subparallel narrow ridges and wider grooves.

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CARADOCIAN BIVALVE MOLLUSCS FROM WALES

by S. P. TUNNICLIFF

ABSTRACT. The occurrence of a widespread, distinctive, and sometimes well-preserved bivalve fauna from the Lower Longvillian (Ordovician, Caradoc) rocks of North Wales is recorded, especially from the Allt-Tair-ffynon Beds at Allt y Gadair, south of Llanfyllin, Powys. Six species are described, of which *Cymatonota verisimilis* sp. nov., *Myodakryotus deigryn* gen. et sp. nov., and *Pseudarca celtica* sp. nov. are new. The new family Myodakryotidae is established to accommodate the new genus *Myodakryotus*.

THE Allt-Tair-ffynon Beds (Caradoc, Soudleyan–Longvillian: Williams *et al.* 1972) of Allt y Gadair (SJ 145 175; text-fig. 1), south of Llanfyllin, Powys, Wales, yielded a number of well-preserved and unusual bivalves to early Geological Survey collectors in the late 1840s. These were studied by J. W. Salter, and were referred to by him in his palaeontological contribution to Ramsey's (1866) *Memoir*, 'The Geology of North Wales'.

Some of the specimens listed in BGS records can no longer be accounted for, possibly because, in the past, such collections were often distributed for teaching purposes. However, the significant bivalves have survived and other specimens have been collected since.

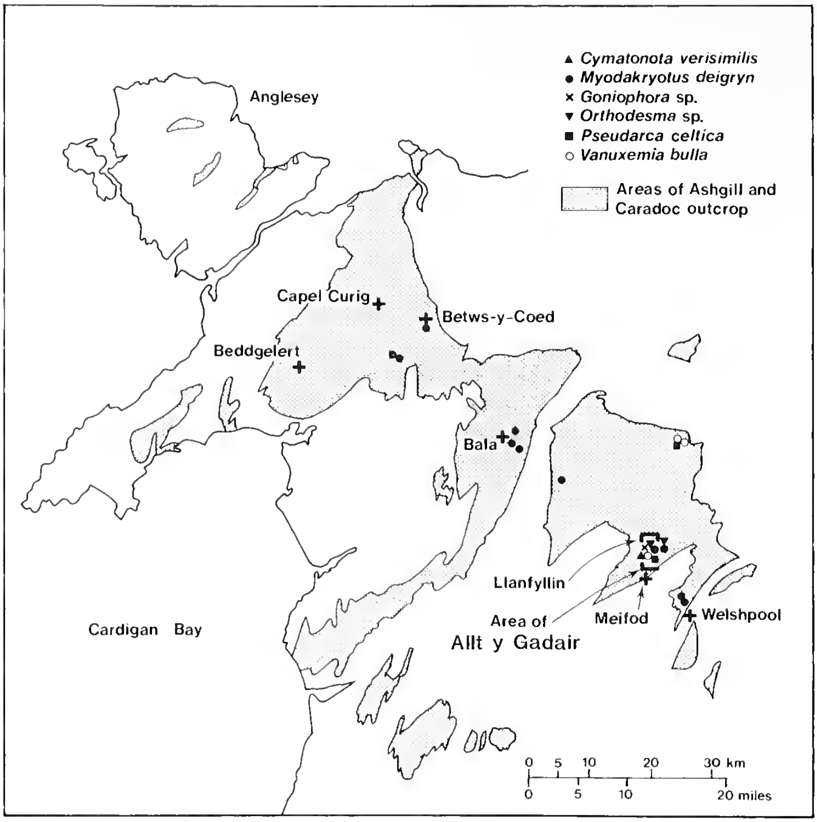
The locality is recorded variously as Galt-y-Gader, Gallt y gader, Alt-y-gader, and Allt-y-Gader and is referred to as near Meifod or near Llanfyllin, both of which were used as field stations by Geological Survey collectors. There is no doubt, however, that these all refer to the same hill, though not necessarily exactly the same localities. On the old series Ordnance Survey maps it was spelt 'Gallt y Gader' but on new 1:50000 series maps it is 'Allt y Gadair', the form adopted herein. A copy of the old series geological map in the Biostratigraphy Research Group, BGS, has MS locality numbers and some notes on the reverse side; for Allt y Gadair, they are as follows, with grid references added:

Llanfyllin (station) 19 Gallt y Gader, Bala Lime? (SJ 1460 1715); 20 N. End of Gallt y Gader, Bala Lime? (SJ 1500 1815); 21 E. Flank of Gallt y Gader, Bala Lime? (SJ 1520 1715).

M'Coy knew of the locality and described *Arca Edmondiaformis* [*sic*] from there in 1851 (p. 52). Subsequently, in Sedgwick and M'Coy (1852, p. 352), he listed *Orthis expansa* (J. de C. Sowerby), *O. porcata* (M'Coy) and *A. Edmondiiformis* [*sic*] (M'Coy) as coming from Allt-y-Gader, near Llanfyllin, and he redescribed *A. Edmondiiformis* (p. 283, pl. 1*k*, figs. 2 and 3).

Wedd *et al.* (1929, pp. 42–45) recorded a single Caradoc bivalve from the area of Geological Survey sheet 137; an ?*Orthonota* (see *Orthodesma* sp. herein) from Bryngwyn Camp, 3 km east of Allt y Gadair. Whittington (1938) recorded no bivalves from the nearby Lluest Quarry but established a lower Longvillian age for the highest Allt-Tair-ffynon Beds. Although Drs Pickerill and Brenchley have collected widely over the area, their collections include no bivalves from Allt y Gadair (Brenchley, pers. comm., Feb. 1981). Dr N. J. Morris (pers. comm.) has also searched in vain for the bivalve-rich horizon. With the help of Dr D. E. White, I have examined exposures on the northern end of Allt y Gadair without finding any weathered rock precisely comparable with the known specimens. I conclude, therefore, that the original specimens came from lenses or beds now obscured.

[Palaeontology, Vol. 30, Part 4, 1987, pp. 677–690, pls. 76–77.]



TEXT-FIG. 1. Distribution of bivalve elements of the Caradocian Allt y Gadair fauna in North Wales.

DISTRIBUTION OF THE BIVALVE FAUNA

The species described here from the Allt-Tair-ffynon Beds at Allt y Gadair are:

Cymatonota verisimilis sp. nov.
Myodakryotus deigryn gen. et sp. nov.
Goniophora sp.
Orthodesma sp.
Pseudarca celtica sp. nov.
Vanuxemia bulla (Salter)

At least two of these species, *Goniophora* sp. and *V. bulla* also occur in the Bryn Siltstone Formation (Longvillian: Brenchley 1978, pp. 146–149) at Nant Iorwerth (SJ 216 364) near Glyn Ceiriog, south of Llangollen, some 20 km NNE of Allt y Gadair. The Nant Iorwerth specimens are associated with single specimens of *Lyrodesma* and ?*Tancrediopsis* and with more numerous dalmanellid and sowerbyellid brachiopods. No *Lyrodesma* has been seen from the Allt y Gadair collections, nor any palaeotaxodont, although the old lists do record *Ctenodonta*. Specimens of *M. deigryn* are recorded from as far to the north-west as Betws-y-Coed and Roman Bridge, and as far south-east as the Welshpool area.

Also present in the collections from Allt y Gadair are the monoplacophoran *Cyrtolites nodosus* (Salter), the gastropod *Cyclonema crebristria* (M'Coy), and a number of other fragmentary unidentified gastropods, as well as the brachiopod *Macrocoelia* and dalmanellid brachiopod and trilobite fragments.

All the bivalve specimens from the Allt-Tair-ffynon Beds at Allt y Gadair are preserved in a highly fossiliferous, fine-grained rotten mudstone which is chocolate brown in colour when weathered. The specimens from Bala, Nant Iorwerth, and the other localities mentioned in this paper are also from fine-grained mudstones which are grey in colour.

All of the occurrences of these distinctive bivalve faunas are from approximately contemporaneous horizons of early Longvillian age. Indeed, the widespread and sudden appearance of these bivalve faunas with such unusual genera as *Myodakryotus* and *Pseudarca*, at lower Longvillian horizons is notable because over much of North Wales the appearance of a number of genera and species is taken as indicative of the onset of Longvillian times (e.g. Whittington 1962). In particular, the trilobites *Kloucekia* and *Estoniops* and brachiopods such as *Howellites antiquior* (M'Coy) are taken as indicators of Longvillian age. Although scant attention has been paid previously to the molluscan faunas, the bivalves have a contribution to make to Caradocian biostratigraphy as well as palaeoecology.

Pseudarca is known principally from France, but the rest of the Allt y Gadair bivalves are of eastern North American aspect. There is, however, a notable lack of taxodont or other smaller infaunal forms such as the actinodontoid *Lyrodesma*. All the specimens available are of similar size and this feature and the fragmentary nature of many of the associated trilobite and brachiopod fragments suggests that they are part of a well-sorted thanatocoenosis in which burrowing forms such as *Cymatonota* and *Orthodesma* are mixed with semi-infaunal *Vanuxemia* and presumably epifaunal *Goniophora* and *Myodakryotus*.

Specimen numbers bearing the prefix BGS are housed in the collections of the British Geological Survey, Keyworth; those with the prefix SM are in the Sedgwick Museum, Cambridge; those with NMW are in the National Museum of Wales, Cardiff; and BM indicates the British Museum (Natural History).

SYSTEMATIC PALAEOTOLOGY

In general, the classification used by Pojeta (1978) is adopted. Synonymies follow the recommendations of Matthews (1973).

Subclass ISOFILIBRANCHIA Iredale, 1939
Family MODIOMORPHIDAE Miller, 1877
Genus *Goniophora* Phillips, 1848

Type species. Goniophora cymbaeformis (J. de C. Sowerby), by original designation of Phillips (1848, p. 264). The genus has been discussed recently by Liljedahl (1984).

Goniophora sp.

Plate 76, figs. 6 and 9

Material. BGS Zv 2018*a* and *b* (internal moulds of two valves, an almost complete left valve, and a fragmentary right valve), from Allt y Gadair, Llanfyllin.

Description. The material available shows the shell to be equivalve, prosogyrate, and apparently rhomboidal with a pronounced sigmoidal carina extending from the umbo towards the posteroventral margin. Dorsal margin straight, anterior margin rounded, posterior margin possibly truncated obliquely. The area dorsal from the carina has one or two coarse but faint radial ribs, and the rest of the shell shows a fairly coarse concentric ornament. Musculature, dentition, and ligament unknown.

Remarks. Of the two specimens of *Goniophora* sp. the right valve, BGS Zv 2018*b*, is fragmentary but the left, Zv 2018*a*, is nearly complete. From Britain, Reed (1905, p. 500, pl. 24, fig. 15) and Hind (1910, p. 539, pl. 4, figs. 24–27) have described and illustrated Ordovician *Goniophora* spp., but both appear more elongate than the present specimens. *G. carinata* (Hall) from the Ottawa

Formation (Black Riveran–Trentonian) from Canada, redescribed by Wilson (1956, p. 76, pl. 9, fig. 20), is closer in size and shape to the Welsh specimens. A single specimen of a *Goniophora* (BGS Zs 2751) from the Killey Bridge Formation (Ashgill, Cautleyan) of the Pomeroy Inlier, Co. Tyrone, was described by Tunnicliff (1982, p. 80, pl. 12, fig. 15), and has proportions similar to the Welsh specimens.

A slab (BGS Zv 2010) from the Bryn Siltstone Formation at Nant Iorwerth (SJ 216 364) bears a fragment of the posterior part of a left valve closely corresponding to the Allt y Gadair fragments and probably represents the same form. The Nant Iorwerth specimen is associated with sowerbyellid and dalmanellid brachiopods and with single specimens of *Lyrodesma* and ?*Tancrediopsis*.

Subclass PTERIOMORPHIA Beurlan, 1944
Family CYRTODONTIDAE Ulrich, 1894
Genus *Vanuxemia* Billings, 1858

Type species. *Cyrtodonta rugosa* Billings, 1858, by subsequent designation of Williams and Breger (1916, p. 149).

Vanuxemia bulla (Salter, 1866)

Plate 76, figs. 11–15; Plate 77, fig. 11; text-fig. 2*a–c*

v* 1866 *Palaearca*? *bulla* Salter, p. 344, woodcut 13, fig. 3 (two views), p. 270 (in list).

Type material. BGS GSM 12397 is here selected as lectotype. This is the specimen figured by Salter (*in* Ramsey 1866), an internal mould of a left valve from the Allt-Tair-ffynon Beds at Allt y Gadair. Paralectotypes are BGS GSM 12398, Zv 2018, internal moulds of right valves from the same horizon and locality. Other material consists of BGS GSM 22190, an internal mould of a left valve, and NMW.27.110.G609, an internal mould of a right valve, from the Bryn Siltstone Formation (Longvillian) at Nant Iorwerth (SJ 216 364), and two specimens, SM 53554–53555, from the same horizon at Bryn Quarry, Glyn Ceiriog, which are internal moulds of left and right valves respectively. There are also three specimens in BM(NH), BM 42791, a right valve, internal mould, recorded as from Meifod; BM L13156, a large right valve, internal mould, from Glyn Ceiriog; BM PL4436 labelled 'W.pool 21m2', left valve, internal mould, probably from Allt y Gadair.

Description. Strongly inflated *Vanuxemia* (maximum inflation of 17 mm in a valve 26 mm long), in which the height is one-tenth to one-fifth greater than the length and the umbo is at about the anterior one-tenth to one-fifth. The hinge line is straight with sets of anterior and posterior teeth separated by an edentulous area. There are three anterior teeth on a hinge plate, the most posterior being hoseshoe shaped in the left valve. There are apparently two ridge-like posterior teeth in the left valve and one in the right. The anterior

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EXPLANATION OF PLATE 76

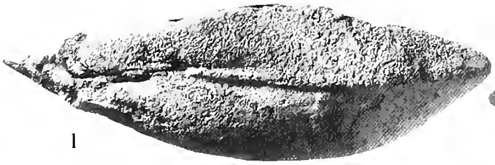
Figs. 1–5. *Orthodesma* sp. 1 and 3, dorsal and left lateral views of internal mould, conjoined valves, BGS GSM 22055. 2 and 4, dorsal and right lateral views, internal mould, conjoined valves, BGS GSM 24287. Both from Allt-Tair-ffynon Beds, Allt y Gadair, Llanfyllin. 5, left lateral external view of gaping conjoined valves, BM 44492, from Meifod.

Figs. 6 and 9. *Goniophora* sp., dorsal and lateral views of internal mould, left valve, BGS Zv 2018, from Allt-Tair-ffynon Beds, Allt y Gadair, Llanfyllin.

Figs. 7, 8, 10. *Pseudarca celtica* sp. nov. Holotype, BGS GSM 24179, internal mould, left valve; 7 and 10, latex cast, 8, lateral view.

Figs. 11–15. *Vanuxemia bulla* (Salter 1866). 11 and 15, lectotype, BGS GSM 12397, anterior and lateral views of internal mould, left valve. Allt-Tair-ffynon Beds, Allt y Gadair, Llanfyllin. 12 and 13, lateral and anterior views, internal mould, right valve, NMW.27.110.G609, from the Bryn Siltstone Formation, Nant Iorwerth, Glyn Ceiriog (NGR SJ 216364). 14, latex of hinge area of internal mould, left valve, BGS GSM 22190, horizon and locality as for 12 and 13.

All ×2 except Fig. 10, which is ×4.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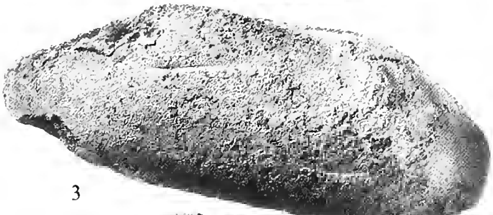
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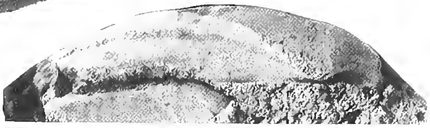
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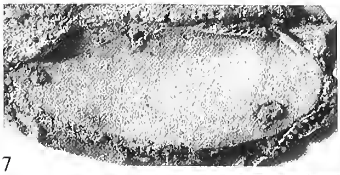
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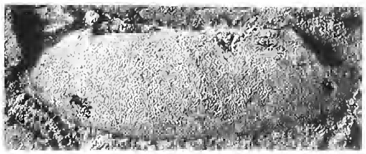
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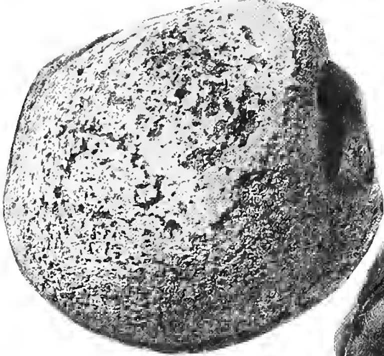
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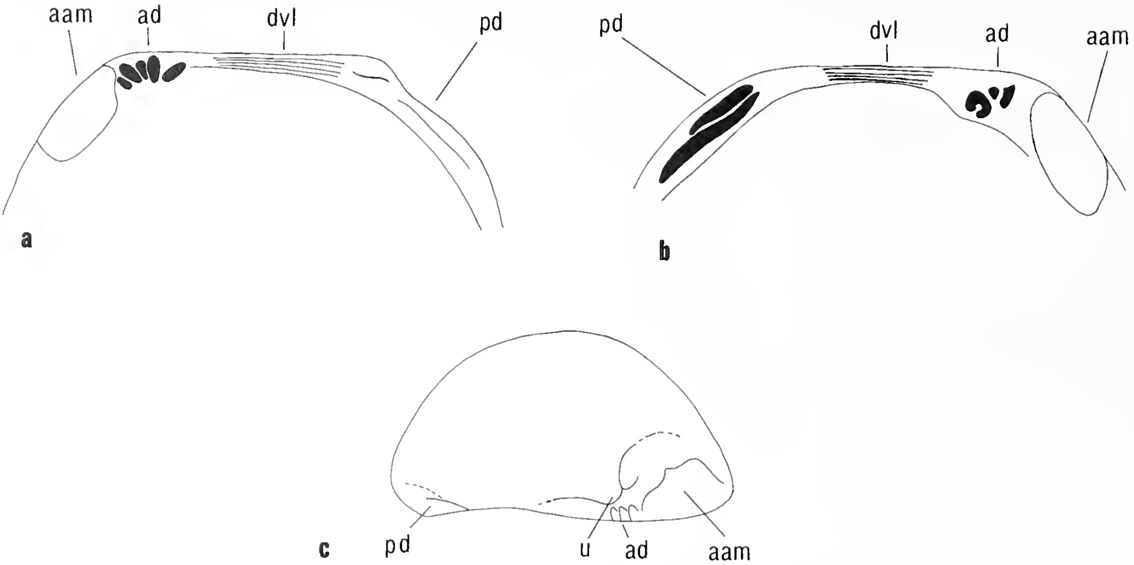
TUNNICLIFF, *Orthodesma*, *Goniophora*, *Pseudarca*, *Vanuxemia*



TEXT-FIG. 2. *Vanuxemia bulla* (Salter), ×2. *a*, NMW 27.110.G609, latex, right valve. *b*, BGS GSM 22190, latex, left valve. *c*, BM (NH) PL4436, dorsal view, internal mould, left valve. u = umbo, aam = anterior adductor muscle scar, ad = anterior dentition, pd = posterior dentition, dvl = duplivincular ligament.

adductor muscle scar is strongly impressed and large, about one-quarter of the height of the shell in height. Posterior adductor muscle scar not discernible. Ornament of coarse concentric undulations only faintly seen on the internal moulds.

Remarks. The lectotype no longer shows the dentition illustrated by Salter (*in* Ramsey 1866, woodcut 13, fig. 3) but this is seen in one specimen from Nant Iorwerth (BGS GSM 22190, Pl. 76, fig. 14; text-fig. 2*b* and NMW.27.110.G609, Pl. 76, figs. 12 and 13; text-fig. 2*a*). A single posterior tooth is seen in a specimen of the right valve (BM 42791).

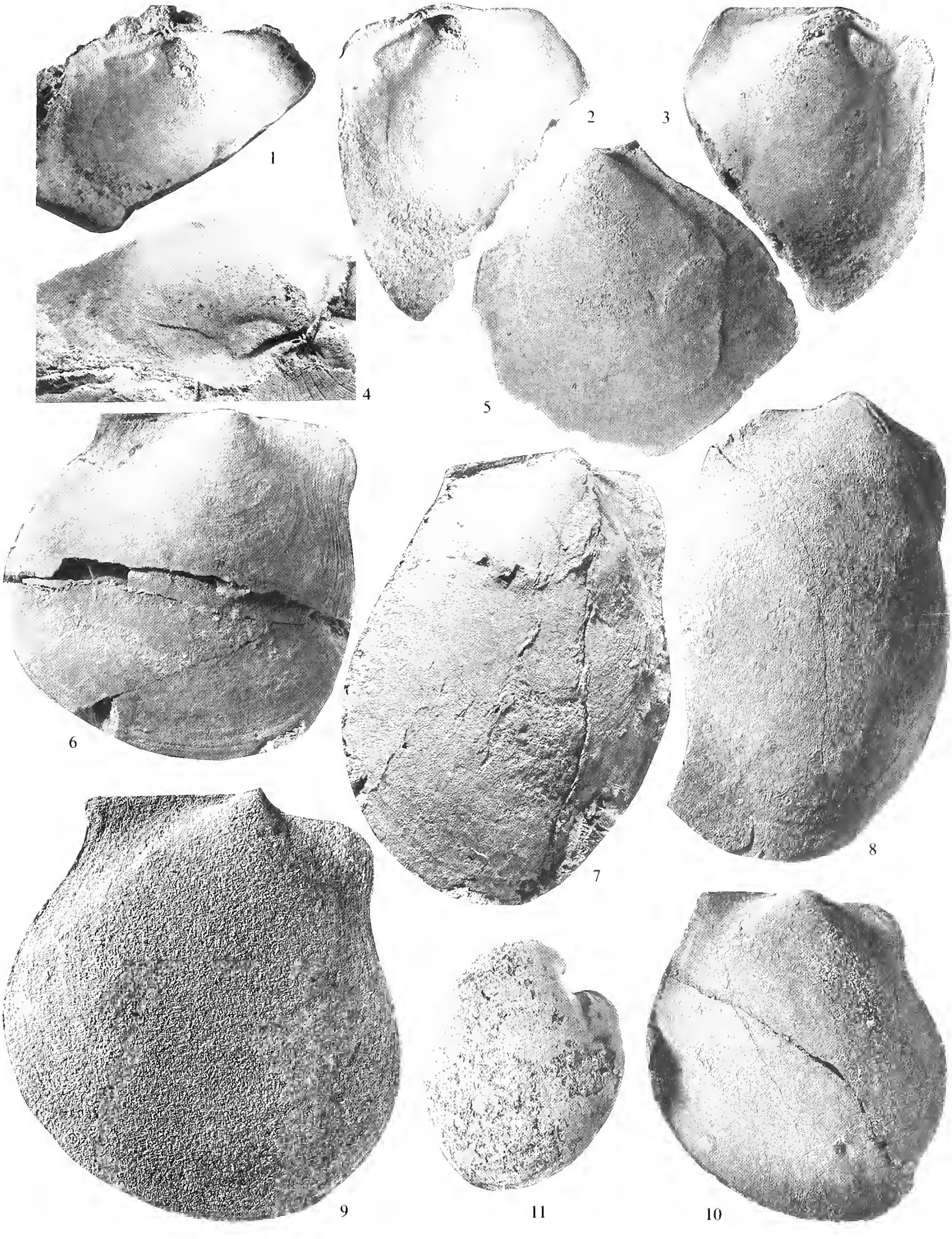
The strongly inflated valve and general appearance of *V. bulla* corresponds well with that generally accepted for *Vanuxemia*. However, its dentition does not readily compare with the better preserved North American material of *Vanuxemia* and *Cyrtodonta* such as that illustrated by Pojeta (1971, pls. 6–9; 1978, pls. 8 and 9).

EXPLANATION OF PLATE 77

Figs. 1–10. *Myodakryotus deigryn* gen. et sp. nov. 1–4, holotype, BGS GSM 22040. 3, internal mould, right valve; 1, 2, 4, oblique ventral, oblique anterodorsal and lateral views of latex cast. 5, internal mould, left valve, BGS GSM 22041. All from the Allt-Tair-ffynon Beds, Allt y Gadair, Llanfyllin. 6, external lateral view of right valve, BGS GSM 22053, from Gelli-Grin Formation, Pont Rhiwedog, Bala, Gwynedd. 7 and 8, external lateral views of two right valves, BGS DJ 3338, 3337 from beds of Longvillian age near Roman Bridge, Gwynedd (NGR SH 7163 5121). 9, external lateral view of right valve, BGS Zv 2032, from Allt-Tair-ffynon Beds, near Cefn Lleyfnog, Llanfyllin. 10, external lateral view of right valve, BGS Zv 1468, from Gelli-Grin Formation, Cwm Chwilfod, Bala (NGR SH 955 400).

Fig. 11. *Vanuxemia bulla* (Salter 1866). Internal mould, right valve, BGS Zv 2018, Allt-Tair-ffynon Beds, Allt y Gadair, Llanfyllin.

All ×2.



TUNNICLIFF, *Myodaktryotus*, *Vanuxemia*

Family MYODAKRYOTIDAE nov.

Type genus. Myodakryotus gen. nov. here designated.

Diagnosis. Heteromyarian, pectiniform pteriomorphs with variable ornament.

Description. Equivalve, pectiniform, heteromyarian, prosogyrate pteriomorphs with small anterior and posterior ears and variable ornament.

Known stratigraphic range. Restricted to Ordovician rocks of Caradoc age in Britain and their approximate equivalents (Black Riveran, Trentonian: see Ross *et al.* 1982) in North America.

Remarks. A new family is established here to accommodate *Myodakryotus* gen. nov., which is considered to be synonymous with New Genus 10 of Pojeta (1978), subsequently referred by Pojeta and Runnegar (1985) to *Prolobella*?, and generically similar to those specimens described by Wilson (1956, p. 56) as *Actinopterella*? *tessellata* Wilson.

The affinitites of *Myodakryotus* are far from clear, but the combination of dimyarian musculature with the pectiniform shape, distinctive, almost cardinal dentition, and apparent lack of a duplivincular ligament precludes its being placed in any of the three families of Pteriomorphia recognized from the Ordovician: Cyrtodontidae, Ambonychiidae, and Pterineidae (Pojeta 1978, p. 235). The shell form is closest to that of a pterineid (if the pectinacean resemblance is discounted) but the dentition is strongly reminiscent of the anterior dentition in some cyrtodontids (e.g. *C. saffordi* (Hall), Pojeta 1978, pl. 8, fig. 11).

Pojeta and Runnegar (1985, p. 327) placed the Ordovician limiform shells which they assigned to *Prolobella* in the Limidae 'for now', and (Pojeta 1985, fig. 2) suggested that the Limacea might be derived from the Cyrtodontidae approximately during Caradoc times. This seems likely as outlined below, but the presence of the distinct anterior adductor muscle in *Myodakryotus* precludes its placement in the strictly monomyarian Limidae and I am obliged to propose the family Myodakryotidae to bridge the gap between the Cyrtodontidae and the Limidae.

I suggest that the Myodakryotidae could be derived from a cyrtodontid form by the acquisition of pectiniform shape, involving a development of the anterior portion of the shell, leaving the anterior teeth and adductor muscle close to the umbo, and the loss of the posterior dentition and reduction of the ligament. This would presumably reflect a change in life-style from the infaunal cyrtodontid type to a byssate epifaunal existance as suggested for the Ambonychiidae and some pterineids (Pojeta 1971, pp. 32–34).

Whether the Myodakryotidae have any direct bearing on the possible origins of the Pectinacea has yet to be fully determined.

Genus *Myodakryotus* nov.

1978 New genus 10 Pojeta, p. 239, pl. 12, figs. 1–8.

Derivation of name. Compounded from Greek *myo-dakrytos*, muscle, tearful, and rendered euphonically in Latin form with masculine gender. The name refers to the teardrop-shaped anterior adductor muscle scar and the shape of some internal moulds (e.g. Pl. 77, fig. 5).

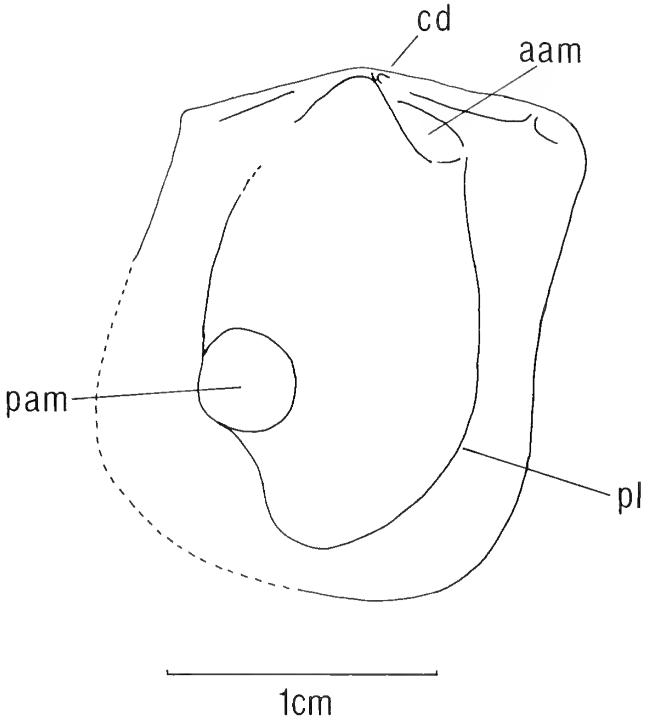
Type species. M. deigryn here designated.

Diagnosis. As for family.

Description. As for family.

Other species. M. hermione (Billings), from the upper Middle Ordovician (Pojeta 1978, p. 239, pl. 12, figs. 1–8; Pojeta and Runnegar 1985, p. 327, fig. 17) and *M. tesselatus* (Wilson) from the Ottawa Formation (Black Riveran–Trentonian age) of eastern Canada. Judging from the published information the three species may be distinguished by their ornaments. The figures by Pojeta and Runnegar (1985, fig. 17A, B) of *M. arctica* (Schuchert) from the Upper Ordovician of Baffin Island, Canada, reveal no ornament.

TEXT-FIG. 3. *Myodakryotus deigryn* gen. and sp. nov., holotype, BGS GSM 22040, internal mould right valve, × 2. cd = cardinal dentition, pl = pallial line, aam = anterior adductor muscle scar, pam = posterior adductor muscle scar.



Myodakryotus deigryn gen. et sp. nov.

Plate 77, figs. 1–10; text-fig. 3

Derivation of name. Welsh *deigryn* (m), a tear; from the teardrop-shaped anterior adductor muscle scar and the shape of some internal moulds (e.g. Pl. 77, fig. 5).

Material. Holotype, BGS GSM 22040, internal mould, right valve (a second, less well-preserved internal mould, right valve, on the same slab is a paratype) and paratype, BGS GSM 22041, internal mould, left valve, all from Allt-Tair-ffynon Beds, Allt y Gadair, Llanfyllin. Other paratypes are BGS GSM 22052, 22053, right valves from the Gelli Grin Formation (Longvillian), Pont Rhiwedog, near Bala, Gwynedd (exact locality uncertain but in the area of SH 947 348) and BGS Zv 2032, 2033, slabs with left and right valves from the Allt-Tair-ffynon Beds near Cefn Lleyfnog, Llanfyllin; BGS DJ 3337, 3338, two right valves from rocks in the Cwm Eigiau Formation of Longvillian age near Roman Bridge, Gwynedd (SH 7163 5121); BGS Zv 1468, external of right valve from the Gelli Grin Formation at Cwm Chwilfod, north-east of Bala (SH 955 400); BGS Zv 913, external of left valve (incomplete) from the Gelli Grin Formation at Bryn Cut, Bala (*c.* SH 951 344); BGS Zv 646 from Waterloo Bridge, Betws-y-Coed; BGS Zv 2557, 2558 and Zv 2541 from the area of Moel y Garth and the Quakers' Burial Ground, north-west of Welshpool; NMW.77.11G.307 (Brenchley Collection) from the Cwm Rhiwarth Siltstone Formation at Cwm Rhiwarth (SJ 020 296). All specimens are from horizons within the Longvillian stage of the Caradoc.

Description. Orthocline, prosogyrate, subcircular, equivalve, equilateral shell of pectiniform appearance, a little higher than long (h:1 1·0 to 1·1), with small anterior and posterior ears. Inflation of a single valve about 5 mm in a shell 30 mm high. Teeth a little anterior from beak and with the form of a single chevron or horseshoe-shaped tooth with a simple tooth posterior to and parallel with the posterior limb of this. Ligament uncertain, but possibly opisthodetic, from the nature of the dorsal margin (but a duplivincular ligament is possible: see remarks below). A shallow groove extends from below the beak towards the posterior ear. Musculature heteromyarian: a subcircular posterior adductor muscle scar, about one-fifth of the height of the shell in diameter and situated well within the body of the shell; the anterior adductor muscle scar is tear-drop shaped, close to the umbo and anterodorsal margin, to which its axis is subparallel. Accessory muscles unknown. Pallial line complete, non-sinuate and co-marginal (generally at a distance of about one-sixth of the width of the shell from the margin) extending from the anterior end of the anterior muscle scar, touching the outer edge of the posterior adductor muscle scar, where it shows a slight embayment, and returning towards the umbo. Ornament of generally fine concentric lines, occasionally coarser especially on or near the ears; some specimens show faint radial ornament. The area dorsal of the anterior muscle scar is separated from it by a strong ridge, a weaker extension of which bisects the area and meets the anterodorsal angle of the shell.

Remarks. It is perhaps surprising that such a distinctive species, collected so widely in North Wales at a particular horizon has not been described before and it is especially remarkable that Salter (1866) made no mention of it. The only forms known to resemble *M. deigryn* are those figured by Pojeta (1978, pl. 12, figs. 1–8) as New genus 10 *hermione* Billings from the upper Middle Ordovician, and specimens described by Wilson (1956, p. 56, pl. 7, figs. 8–11) from the Ottawa Formation (Black Riveran–Trentonian age) of eastern Canada, as *A.*? *tessellata* Wilson. Pojeta subsequently (Pojeta and Runnegar, 1985, p. 327, fig. 17) reassigned New genus 10 *hermione* and another species, *arctica* (Schuchert), from the upper Ordovician of Baffin Island, Canada, to *Prolobella* Ulrich with a qualifying question mark. He stated (1978, p. 239) that the musculature of his New genus 10 was poorly known and that the ligament and dentition were unknown, but that the ornament is of co-marginal growth lines and fine radial ribs. By 1985 (Pojeta and Runnegar 1985, p. 327) he had more internal detail including (pers. comm.) evidence of a duplivincular ligament, but the dentition remained unknown and he referred to a single, posterior adductor muscle suggesting that the anterior adductor muscle was not recognizable in the specimens before him. In some of the Welsh specimens radial ornament is apparent but faint. With the larger, strongly impressed anterior muscle scar, they differ from the American species which in turn seem, from Pojeta's illustrations (1978, pl. 12, fig. 6) to have a more strongly impressed posterior muscle scar. However, the similarities are otherwise so great that one must conclude that the two species are closely allied and place them in the same genus. Wilson's figures show most of the features of the Welsh specimens, but have a tessellated ornament and poorly known musculature and dentition.

Ulrich's original figure of his *P. striatula* (1897, pl. 35, fig. 27) suggests a more prosocline form lacking any posterior auricle. His description (1897, p. 532) as 'very inequilateral' seems contrary to the evidence presented by *Myodakryotus*. In the absence of a revised description of the type material of *Prolobella* I feel the establishment of the new genus is justifiable.

Subclass ORTHONOTIA Pojeta, 1978

This subclass was established by Pojeta (1978, p. 240) to accommodate five genera: *Cymatonota*, *Orthodesma*, *Palaeosolen*, *Psiloconcha*, and an unnamed genus. Taxonomy at the level of order, superfamily and family remains unestablished.

Genus *Cymatonota* Ulrich, 1893

Type species. By original designation *C. typicalis* Ulrich (1893, p. 661).

Cymatonota verisimilis sp. nov.

Text-fig. 4*a*, *b*

v. 1866 *Orthonota verisimilis* MSS Salter, p. 270 (in list only), *nom. nud.*

Type specimens. Holotype designated here, BM 42792, an internal mould of conjoined valves, complete except for the extreme posterior portion, recorded as from Meifod, but possibly from Allt y Gadair (obtained from W. Prosser); paratypes BGS GSM 24292, 24293 from Allt y Gadair, Llanfyllin.

Description. Valves very elongate with parallel dorsal and ventral margins. Height less than a quarter of the length. The inflation of a single valve is about a quarter of the height. The umbo is almost terminal anteriorly,

TEXT-FIG. 4. *Cymatonota verisimilis* sp. nov., ×2. *a*, holotype, BM 42792, left lateral view, internal mould, conjoined valves, recorded as from 'Meifod'. *b*, BGS GSM 24292, lateral view, posterior portion, right valve, Allt-Tair-ffynon Beds, Allt y Gadair, Llanfyllin. The richly fossiliferous nature of the bivalve-bearing rocks at this locality can be seen in this figure; present are trilobite, brachiopod, and gastropod fragments including *Cyrtolites nodosus* (Salter).

and the positions of the muscle scars are uncertain, although an area in the preumbonal region of the shell may represent an anterior adductor muscle scar about half as high as the shell. Details of the ligament and dentition are unknown. The ornament consists of two zones of ornament separated by a line running from the umbo to the posteroventral angle (no carina or ridge is developed) as seen in recent *Ensis* spp. Ventral to this line, the ornament is of parallel, fairly coarse (*c*. 1 per mm) co-marginal lines which undulate gently in section. The posteroventral ornament is of similar co-marginal lines but with a stronger and more irregular undulation. There was a permanent posterior gape.

Remarks. The dimensions of the holotype are: height 12·0 mm, length 54·0 mm, and inflation of a single valve 3·5 mm. Ornament is best seen in the paratypes, both of which are fragmentary. BGS GSM 24293 is an internal mould of a section of the right postumbonal shell about 25 mm long and showing the dorsal margin with a thin fragment of the left valve in place. BGS GSM 24292 also shows the internal mould, postumbonal section (*c*. 50 mm) of a right valve but with the umbo itself missing. Both specimens have a height of about 13 mm and both show the nature of the posterior ornament. The posterior end of the shell in BGS GSM 24292 suggests the presence of a permanent gape.

Although Salter (1866, p. 270) clearly intended to describe this species as *Orthonota verisimilis*, he never did so and his use of that taxon becomes invalid as a *nomen nudum*. It is reintroduced here to retain the association with Salter's work and to avoid future confusion. It was recorded in one of the old Geological Survey lists as '*Orthonota vessimilis* (sic) MSS exactly like *Solen*'. Compared with other species of *Cymatonota* (e.g. Ulrich 1893, pl. 55, figs. 1–14; Pojeta 1978, pl. 15, figs. 9, 11–13), *C. verisimilis* is distinctive in its remarkably parallel dorsal and ventral margins and its almost terminal umbones.

Genus *Orthodesma* Hall and Whitfield, 1875

Type species. By original designation, *Orthodesma rectum* Hall and Whitfield (1875, p. 93).

Orthodesma sp.

Plate 76, figs. 1–5

v. 1866 *Orthonota* sp. Salter, p. 270 (in list).

Material. Three internal moulds of conjoined valves, BGS GSM 22055, 24286, 24287 all from Allt y Gadair, Llanfyllin; BGS WK 339, conjoined valves from Bryngwyn Camp, near Llanfyllin; BM 42793, 44492–44494, BM L13526, 13547, left, right, and conjoined valves all recorded as from Meifod and purchased from W. Prosser.

Description. Elongate, modioliform or soleniform shell with height about half the length, tapering rapidly towards the anterior end, with the highest part of the shell towards the posterior end. The umbones are at about the anterior quarter. Maximum inflation of the two valves coincides with the highest part of the shell and is 14·5 mm in a shell 42·7 mm long (BGS GSM 24287). Posterior dorsal margin straight, anterior dorsal margin drops away from umbo. Posterodorsal margin truncate, posteroventral margin rounded, anterior margin rounded, ventral margin nearly straight or with a sinus a little posterior to the umbo and, in some, anterior to the umbo. Adductor muscle scars of subequal size and round to ovate; anterior adductor scar almost terminal, posterior adductor scar faint, below posterodorsal angle and in the upper half of the shell. Pallial line not distinguishable. Details of ligament and dentition not known. Ornament of concentric undulations about 2 mm apart, faint on the internal moulds, and finer comarginal lines (*c.* 5 per mm).

Remarks. Two of the specimens (BGS GSM 22055, 24287) appear to be inequivalve, but this is probably the result of distortion, for they are inequivalve in opposite senses, and most of the other specimens suggest an equivalve condition. None of the specimens shows a clear gape at either end as is suggested for the genus by Ulrich (1894, p. 516). Pojeta (1971, p. 24) also expressed doubt over this feature.

Subclass ACTINODONTIA Pojeta, 1978
Family LYRODESMATIDAE Ulrich, 1894
Genus *Pseudarca* Tromelin and Lebesconte, 1875

Type species. Pseudarca typa Tromelin and Lebesconte. This genus was treated as a nuculoid by McAlester (1968, p. 47), who redescribed the type species and discussed synonyms.

Pseudarca celtica sp. nov.

Plate 76, figs. 7, 8, 10

? 1866 *Orthonota* sp. Salter, p. 270 (in list).

Material. Holotype, BGS GSM 24179, an internal mould, left valve, from the Allt-Tair-ffynon Beds at Allt y Gadair, Llanfyllin. A slab in the Sedgwick Museum, SM A53554, from the Bryn Formation, Bryn Quarry, Glyn Ceiriog, bears what appears to be the anterior portion of an internal mould of conjoined valves of *P. celtica.* On the same slab is a specimen of *Vanuxemia bulla* (q.v.).

Description. Elongate, with a rounded anterior end and probably a rounded posterior end (the posterodorsal angle is missing). The dorsal margin is straight behind the umbo and curves continuously with the anterior margin before the umbo. The ventral margin is gently curved such that the highest part of the shell is behind the umbo, a little anterior to the midpoint. Dimensions of the holotype: length 22·5 mm, height 7·4 mm, h : l 0·33, maximum inflation of the single valve *c.* 1·5 mm. The umbo is at about the anterior one-fifth, it is small and opisthogyrate. A hinge plate behind the umbo is just over one-tenth of the height of the shell high and 0·13 of the length of the shell in length, and it tapers towards the posterior. It bears eight radiating, possibly striated teeth which are longer towards the posterior. A single tooth lies anterior to the umbo. Immediately behind the umbo is a faint, poorly-developed sulcus extending perpendicularly downwards and fading rapidly. Ligament unknown but probably opisthodetic. An elongate anterior muscle scar lies immediately anterior to the umbo with a strongly impressed dorsal edge and bounded on the anterior edge by a rounded ridge running close to the anterodorsal margin. The posterior adductor muscle scar is unknown. Ornament unknown.

Remarks. I know of no previous record of *Pseudarca* from Britain. Babin (1966, pp. 243–244, pl. 9, figs. 4–6, 8) has described *Siliquarca* [= *Pseudarca*] *typa* Tromelin and Lebesconte, the type species, and has placed several other French species in synonymy with it. However, *P. typa* has almost twice as many posterior teeth as *P. celtica* and appears to taper more towards the posterior. Despite the conventional view of the genus as a nuculoid (McAlester, 1968, p. 47; 1969, p. N234), Babin (1966, p. 237) placed *Siliquarca* in the family Lyrodesmatidae and the features shown in this species tend to corroborate his opinion.

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SKELETAL STRUCTURE, DEVELOPMENT AND ELEMENTAL COMPOSITION OF THE ORDOVICIAN TREPOSTOME BRYOZOAN *PERONOPORA*

by DAVID R. HICKEY

ABSTRACT. ED spectroscopy of Ca and other elemental densities indicate differences in the rates of secretion and growth among crystallite ultrastructures, acanthostyles, the median lamina, zooecial wall, and stages of ontogeny and astogeny in *Peronopora*. Growth rate (inversely proportional to Ca density) was highest within the granular skeleton of the median lamina and 'A-type' acanthostyles (paurostyles). Growth rate decreased exponentially from the median lamina through the recumbent zone, endozone, and exozone. Paurostyle cores were deposited more rapidly than endozonal wall but less rapidly than recumbent zone wall and the median lamina. Zones of disordered irregular crystallites and laminar growth alternate in zooecial wall axes, and were respectively linked with increased secretion rates and increased episodicity during the cystiphragm/mesozooecial tabulae emplacement cycle. Cu and Mn densities support the sequence of relative growth rates inferred from the Ca data. Paurostyles and the median lamina contain more Cu than other structures. Mn is also most abundant in the median lamina and declined monotonically with reduced growth rate. The median lamina is structurally continuous with the basal lamina but was not secreted against cuticle. Formation of the median lamina and paurostyle cores may be explained by differentiation of inner epithelium for high rates of secretion.

BRYOZOAN skeletal ultrastructures, if not diagenetically altered, are most informatively viewed as products of the physiology of growth (Sakagami *et al.* 1984; Sandberg 1977, 1983; Tavener-Smith and Williams 1972). This study seeks to link differences in the skeletal ultrastructure of *Peronopora vera* Nicholson and *P. decipiens* Rominger to the rates and modes of growth of astogenetic sequences and skeletal structures. The ultrastructures of zooecial wall 'flanks' (that region of proximally directed laminae lateral to the wall axis) and axes, acanthostyles (acanthopores), and the median lamina ('mesotheca' of other authors; 'median wall' of Boardman 1983) are described by means of SE microscopy and analyzed for compositional differences by means of ED spectroscopy. Results of this study provide information about the relative growth rates of skeletal structures and astogenetic zones which can be extended to other taxa and used as bases for hypotheses concerning the evolution of skeletal structures.

The term 'granular' has been applied to two similar crystallite morphologies in many studies of skeletal ultrastructure (e.g. Tavener-Smith and Williams 1972). Both types lack regular crystallite surfaces. The term 'granular' is herein applied to large, approximately equidimensional, non-tabular crystallites that appear optically hyaline and homogeneous. The term 'irregular' is applied to smaller, non-tabular crystallites which are optically differentiable, irregular, and variable in dimensions and shape.

Much of the ultrastructure of bifoliate *Peronopora* resembles that of other trepostomes described by Tavener-Smith and Williams (1972), Tavener-Smith (1969*a*), Armstrong (1970), Bigey (1979, 1982), and Bigey and Lafuste (1982). However, the median lamina of bifoliate *Peronopora* is an unusual and distinctive structure among trepostome genera; it is otherwise found only in *Polyteicus* Pocta, *Diplostenopora* Ulrich and Bassler, *Stenocladia* Girty, *Nipponostenopora* Sakagami, *Petalotrypa* Ulrich, rare variants of *Amplexopora thomesi* Ross, and *Araxopora* Morozova. A similar

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structure is an important synapomorphy of bifoliate cryptostomes and many fistuliporines. Trepostome median lamina ultrastructure has been studied only in *Peronopora compressa* Ulrich (Tavener-Smith and Williams 1972) and *Petalotrypa* sp. (Bigey 1979). The astogenetic origin and ultrastructure of the median lamina has an important bearing on the growth mode of trepostomes (Tavener-Smith and Williams 1972) and the evolutionary origin of *Peronopora* (Hickey, in press). Additional observations demonstrate that the median lamina of the primary frond is structurally continuous with the basal lamina ('epitheca' of other authors) but is none the less interior-walled skeleton. The median lamina contains style-like structures (Boardman and Utgaard 1966) which optically resemble acanthostyle cores but differ in ultrastructure. The styles and granular layer of the median lamina exhibit ultrastructural details as yet unreported in the mesothecal skeleton of other taxa.

Few studies of the elemental composition of bryozoan skeletons have been undertaken. Phillips (1922) reported Cu, Zn, Fe, and Mn in one Recent bryozoan. Clark and Wheller (1917) found Si, Al, Fe, Mg, P, and S in a survey of 9 Recent bryozoans. Schopf and Manheim (1967) reviewed the chemical composition literature and reported Ca, Mg, Sr, Ba, Fe, P, Zn, and C in 29 Recent bryozoan species. Soulé and Soulé (1981) analyzed heavy metal uptake in 7 Recent bryozoa and discovered traces of Fe, Cr, Hg, Ni, and Zn in exoskeletons, Fe and Hg in tissues and As, Cd, Cr, Cu, Fe, Hg, Mn, Ni, Pb, and Zn in bulk samples. Morrison and Anstey (1979) provide one of the few studies of the elemental composition of fossil bryozoans. They detected C, Fe, S, Si, Al, and K in the brown bodies of *Heterotrypa* Nicholson and *Peronopora*.

Minor and trace elements, aside from Mg and Sr, have received little attention in biogeochemical studies of bryozoans or other organisms. Most studies have sought correlations between composition and temperature or salinity variation in bivalves (e.g. Dodd 1967; Eisma *et al.* 1976; and others), or links between mineralogy and phylogenetic affinities among bryozoans (Schopf and Manheim 1967). A few studies have focused on ontogenetic variation of elemental abundances in bivalves (Crisp 1975, 1983; Goreau 1977; Rosenberg 1980; Rosenberg and Jones 1975). The latter aspect of skeletal chemistry could provide data pertinent to studies of the physiology of skeletal secretion and growth in bryozoans. No compositional studies of this kind have been undertaken with fossil bryozoans. However, Sakagami *et al.* (1984) have defined categories of skeletal composition indicative of equilibrium and nonequilibrium skeletal formation in some Recent and fossil bryozoans. They concluded that the presence of Mn, Fe, Zn, Co, Cu, and Ni within cheilostome skeletons was a product of physiological control over skeletal composition.

Mg, Cu, Fe, Mn, Si, Yb, and Nb were found in *P. vera* Ulrich. This investigation is concerned with the systematic variations of Ca and trace element concentrations during astogeny and relative element abundances among major skeletal components and different microstructures. The abundance distribution of Ca, usually ignored in compositional analyses (Rosenberg 1980), is of particular interest in this study. Ca abundance could provide a measure of relative rates of skeletal and crystallite growth (Rosenberg, pers. comm. 1984). EDS analyses of Ca indicate that relative skeletal growth rates decreased with increasing age from the median lamina through the exozone. Granular crystallite morphologies typical of the median lamina and acanthostyles are indicative of higher growth rates than crystallites comprising laminar wall. The median lamina was deposited most rapidly. The development of the median lamina may be explained in terms of the differentiation of inner epithelium to produce regions of increased, and relatively continuous crystallite secretion. Acanthostyles were deposited more rapidly than endozonal and exozonal skeleton. Differences in individual crystallite shape, thickness, orientation, and laminae number suggest differential growth rates and episodicity between zooecial wall flanks and axes and cyclical zonation within axes. Exterior-walled skeleton (Boardman *et al.* 1983; 'single-walled' skeleton of many authors) of the basal lamina is inferred to have been deposited more rapidly than most interior-walled (Boardman *et al.* 1983; 'double-walled' skeleton of many authors) skeleton.

Astogenetic trends and differential abundances of trace elements could reflect the effects of growth rates (Rosenberg 1980), or other aspects of physiological change during astogeny. The abundance variations of Mn, Cu, and Fe among skeletal structures and astogenetic zones support the inferences based on Ca abundance. Results support the inferences concerning relationships between skeletal ultrastructures and growth rates proposed by Tavener-Smith (1969*a*, *b*; 1975).

If similar crystallite morphologies in the interior-walled skeleton of other trepostome taxa are not products of alteration, the evolution of differences in zooecial wall structure among astogenetic zones and acanthostyle microstructures among closely related taxa could be interpreted in terms of heterochronic processes. Studies of compositional differences among astogenetic growth zones provide a basis for the construction of growth curves for taxa like *Peronopora* that possessed periodically deposited intrazooecial structures such as cystiphragms. Results also suggest that the evolution of mesothecal structures in other taxa involved a differentiation of inner epithelium crystallite secretion rates along the colony margin.

MATERIALS AND METHODS

Specimens used in this study belong to *P. vera* and *P. decipiens* from the Kope (Eden Shale) and Dillsboro Formations of the Cincinnatian Series (Late Ordovician) from the Ohio Valley region. Several preparation methods were used in the SEM investigation. Specimens were either fractured, or etched in 0·1% formic acid for 60–90 seconds or 1·25% EDTA for 30 minutes. Electron micrographs of acetate peels were also made. Specimens were coated with gold-palladium or carbon. Etched specimens were carbon coated for energy dispersive X-ray (EDS) analysis of elemental composition.

Electron micrographs were taken with an ISI (International Scientific Instruments) S-III SEM and the EDS analyses were made with a JSM-35C SEM, manufactured by Japan Electron Optics Limited. The latter machine is equipped with a dual annular photolithographic disc back-scattered electron detector and a Tracor Northern Energy Dispersive X-ray analysis system. EDS analyses were done at 20 kv, over time intervals of 60 seconds. Beam strength was held constant to prevent systematic bias in the relative abundance measures. Possible biases due to the variable surface topography of etched specimens are believed to have been minimal (Flegler, Director, MSU Electron Optics Center, pers. comm.). Analyses were limited to elements with atomic numbers above that of carbon because specimens were carbon coated.

Two elemental analyses were made. Changes in element abundances were measured with a narrow beam probe in a proximo-distal series of thirty-seven points taken alternately from laminar regions of the zooecial wall axis, and from cystiphragms periodically emplaced along the wall of a single zooecium. This analysis was designed to determine if there exist any elemental abundance periodicities associated with the cycle of cystiphragm emplacement. A second analysis was performed to determine if elemental abundances differed in systematic manners among astogenetic growth zones and among different skeletal structures. Abundances were measured with a line scan at magnifications of 1,000 to 9,000 for the exozone, endozone, acanthostyles, recumbent zone, and median lamina for each of fifteen zooecia of a single specimen. Magnifications that differ by less than an order of magnitude should not have a significant effect on measured abundances (Flegler, pers. comm.). Only the latter analysis provides replicate data amenable to statistical treatment and reliable inference. Mean elemental abundances were statistically compared among skeletal structures and among astogenetic zones. The Student's t-test was used to evaluate differences in the mean abundances; it was preferable to other parametric tests because sample sizes were small ($n \leqslant 15$).

Skeletal structures and different crystallite ultrastructures, as well as matrix, could respond differentially to diagenesis. Trace element distributions may be greatly influenced by the distribution and abundance of organic material in the earliest stages of diagenesis following burial. Mean abundances within skeletal structures were statistically compared with those of the zooecial void cement in order to determine whether diagenetic alteration significantly influenced skeletal composition. Some idea of the effects and extent of diagenesis on the results of this study is indicated by comparisons between element concentrations within the diagenetic zooecial void matrix and individual skeletal elements. Several elements are significantly enriched within and among various skeletal structures in comparison to mean levels found in the void cement.

Distributions of Ca and some of the trace elements are consistent with independent predictions of compositional behaviour which would be expected in the relative absence, or limited influence of diagenesis on skeletal material. Of these, Mn, Fe, and Cu occur in cheilostomes with nonequilibrium growth (Sakagami *et al.* 1984) and are thus inferred to have been little influenced by diagenesis. Yet, a differential response of skeletal materials to diagenesis and/or the effects of early-stage diagenesis could have affected the observed variations and trends. Thus, any conclusions regarding astogenetic trends and structural differences are tentative and subject to confirmation by additional studies and alternative methods.

SKELETAL STRUCTURE

The autozooecia of bifoliate *Peronopora* are subcircular to circular in cross-section, short, and arranged in fairly well defined longitudinal ranges. Recumbent zones are well developed where autozooecia diverge from either side of a median lamina (if present) in bifoliate species (Boardman and Utgaard 1966). The median lamina is a distinctive intracolonial structure, unusual among trepostomes. Cystiphragms form continuous overlapping series throughout the autozooecial tubes. The area subtended by cystiphragms decreases monotonically during autozooecial ontogeny. Cystiphragm overlap increases distally as size and spacing decrease. Acanthostyles are generally abundant, large, and may inflect autozooecial walls. The polygonal mesozooecia (mesopores) may be abundant, large, and closely tabulated.

Zooecial walls

The majority of the interior-walled skeleton is laminar, like that typical of most trepostomes (e.g. Armstrong 1970; Bigey 1979, 1982; Bigey and Lafuste 1982; Tavener-Smith 1969*a*; Tavener-Smith and Williams 1972). Autozooecial and mesozooecial wall laminae are of variable thickness, length, and continuity (Pl. 78, figs. 1 and 2). Exozonal laminae may occasionally extend the length of a wall flank and intercalate with laminae from the adjacent wall in the compound wall axis. Crystallite shape and discontinuity of laminae render it difficult to define discrete, continuous laminations. The location of actual growth surfaces is therefore obscured.

Edgewise crystallite growth can also produce the appearance of a laminated wall without synchroneity of laminae and growth surfaces (Boardman and Cheetham 1969; Boardman and

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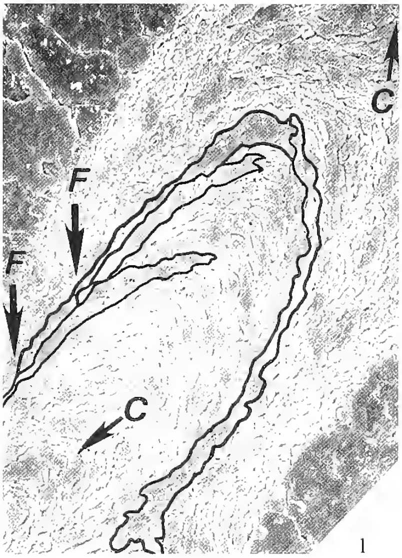
EXPLANATION OF PLATE 78

Figs. 1–8. *Peronopora vera*, Eden Shale, Ohio. 1, exozonal autozooecial wall; wall flank laminae (F) continuous with laminae comprising cystiphragm (distal to outlined laminae) and larger core crystallites (C) proximal and distal (arrows) to cystiphragm (bottom centre). Unusually long laminae and intercalation of laminae are outlined in region of wall axis between zones of larger crystallites. Long., MSU 220335-00245, Eden Shale, Ohio, × 1,000. 2, exozonal autozooecial wall. Large, irregular, disordered wall core crystallites (C) (right) proximal to wall flank laminae (F) continuous with cystiphragm (bottom left, out of field). Long., MSU 220335-00251, Eden Shale, Ohio, × 5,000. 3, pluricupular zooecial wall flank crystallites. Fractured section. Long., MSU 220335-00241, Eden Shale, Ohio, × 2,600. 4, fine ultrastructure of median granular layer. Compare granular-rhombic crystallites of median lamina with pluricupular crystallites of zooecial walls in fig. 3. Fractured section, Transv., MSU 220335-00241, × 1,000. 5, granular acanthostyle core, pluricupular crystallites of thin laminae proximal to core and larger crystallites of laminar zooecial wall to far left, right and top centre. Tang., MSU 220335-00245, Eden Shale, Ohio, × 1,000. 6, granular crystallites of acanthostyle axial core (C) and pluricupular crystallites of sheath laminae (S). Fractured section. Transv., MSU 220335-00241, × 1,500. 7, acanthostyle core and sheath laminae within autozooecial wall. Long., MSU 220335-00245, × 400. 8, acanthostyle axial core (centre) and flanking laminae. Fractured section. Transv., MSU 220335-00241, × 2,400.

Fig. 9. *P. decipiens*, median lamina; outer laminar layer (OLL), median granular layer (MGL), zooecial wall (ZW), and median styles (MS; arrows). Transv., MSU 220314-00415. Dillsboro Fm., Indiana, × 240.



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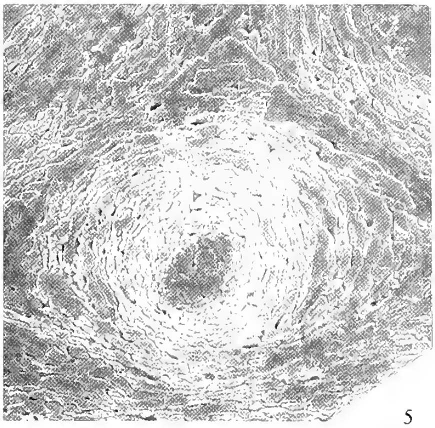
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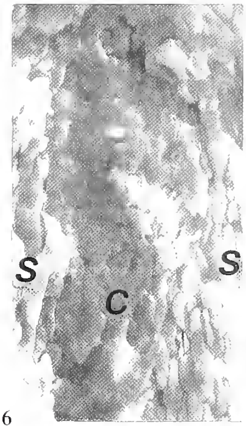

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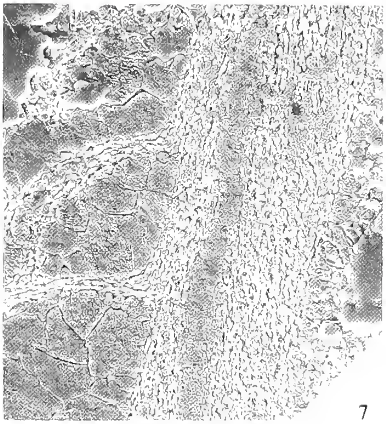
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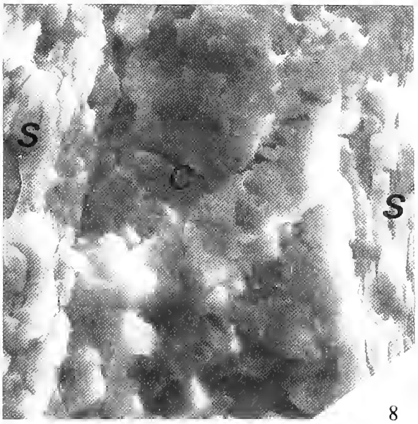

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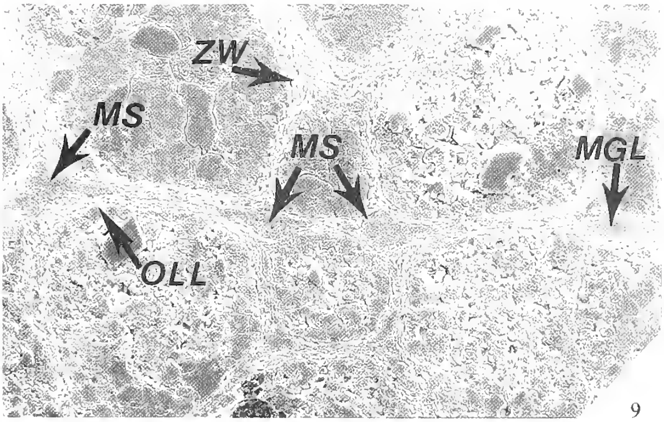

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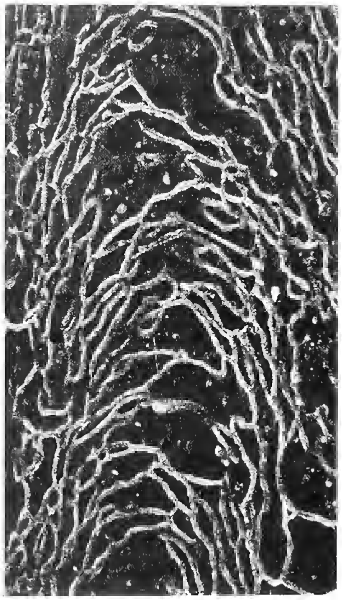
HICKEY, *Peronopora*



TEXT-FIG. 1. *Peronopora vera*, mesozooecial wall (axis parallel to long axis of photo) and adjoining tabula (bottom centre). Note disordered wall core and laminar flanks. Acetate peel (negative) replica. Long., MSU 220335-00239, Eden Shale, Ohio, × 2,000.

Towe 1966). Armstrong (1970) suggested the possibility of edgewise growth in *Stenopora crinita* Lonsdale. Undamaged distal tips of zooecial walls in *Peronopora* reveal continuity of laminae across wall cores with no evidence of concerted edgewise growth. Therefore structural laminae and growth surfaces are considered equivalent, and no evidence suggests non-laminar growth.

Wall laminae of cystiphragms and mesozooecial tabulae intercalate with zooecial walls and often become attenuated and terminate before reaching the wall core (Pl. 78, fig. 1). Zooecial laminae are generally thickest, and crystallites largest and most irregularly shaped within wall axes proximal to zones of laminae continuous with cystiphragms or tabulae (Pl. 78, figs. 1 and 2). Laminae which extend into zooecial walls from the distal surfaces of cystiphragms, and those typical of outer zooecial wall flanks, tend to be thinner and composed of smaller, and thinner 'pluricupular' (Pl. 78, fig. 3; see definition below) crystallites. A more pronounced alternation of axial crystallite size and shape occurs within walls shared by mesozooecia (text-fig. 1).

Wall laminae within the endozone are few in number, steeply to vertically inclined, and arch sharply over an undifferentiated, laminar wall axis (Pl. 78, fig. 9). The laminae and component crystallites throughout most of the endozone are pluricupular and somewhat larger than those of the wall flanks within the exozone. The most proximal portions of the recumbent zone are composed of granular crystallites which are short distal extensions of the median lamina (Pl. 79, fig. 4).

Crystallites

Individual crystallites of zooecial walls do not display the planar surfaces or uniform thickness and size of the tabular crystallites found in many Tubuliporata (formerly cyclostomes; Boardman 1983) and Trepostomata described by Brood (1976), Sandberg (1977), Tavener-Smith and Williams (1972), and others. For example, the laminar wall crystallites of *Stenopora* (Armstrong 1970) and *Leioclema asperum* Hall (Tavener-Smith 1969*a*) are more uniformly tabular than those of *Peronopora*. Fractured sections (Pl. 78, fig. 3) and light formic acid etches reveal that most crystallites of *Peronopora* are pluricupular-shaped like those of *Leptotrypella* Vinassa (Bigey and Lafuste 1982). Pluricupular crystallites are wafer-like tablets with undulating proximal and distal surfaces and attenuated margins (Pl. 78, figs. 1–3). Laterally adjacent crystals often exhibit intercalated, interlocking boundaries. Exozonal axial crystallites are generally larger and more irregularly shaped than those of wall flanks (Pl. 78, figs. 1-3). Wall axes contain large, irregular crystallites which may envelop smaller crystallites. The smallest crystallites could be relicts of differential etching in response to minor compositional differences. Large irregular crystallites disrupt lamina continuity and thickness and give a generally disordered appearance to regions of the wall axis deposited between cystiphragms and tabulae (Pl. 78, figs. 1 and 2). Wall axes shared by mesozooecia appear more disordered than those of autozooecia (text-fig. 1).

Acanthostyles

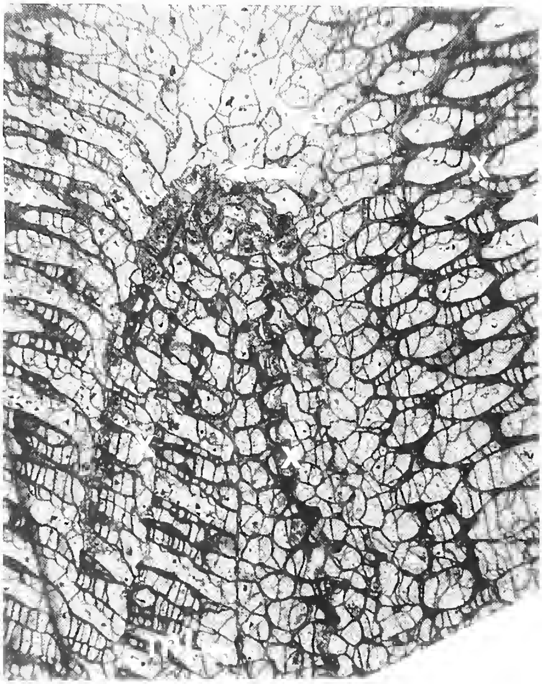
The acanthostyles of *Peronopora* have a paurostyle-like (terminology of Blake (1983) extended to trepostomes) morphology (Pl. 78, figs. 5-8). Sheath laminae (Blake 1983) adjacent to the acanthostyle axial core are composed of nearly tabular crystallites. Crystallites become thicker, longer, and more pluricupular away from the core (Pl. 78, figs. 5 and 7). Crystallites in regions of distally concave laminae between axial cores and zooecial walls are generally larger, longer, and more tabular in shape than those of zooecial walls. Fractured sections reveal large granular crystallites within the axial core (Pl. 78, figs. 6 and 8). The boundary between cores and flanking laminae is irregular yet distinct (Pl. 78, fig. 7). Laminae do not extend across the cores and no growth discontinuities were found within the core.

Median lamina

The median lamina varies in structure and continuity within and, possibly, between species. It consists of one to three components: 1, an outer laminar layer; 2, a median granular layer; and, 3, granular 'tubules' or median styles (median 'tubules' or 'rods' of other authors) (Pl. 78, fig. 9). The outer layer contains a variable number of horizontally disposed laminae composed of small pluricupular crystallites (Pl. 79, figs. 2-6). The distalmost laminae are continuous with the zooecial walls of the recumbent zone (Pl. 79, figs. 4 and 5). These laminae arch over a short distal extension of granular median lamina at the bases of zooecial junctions between adjacent walls. The median lamina may be composed entirely of two outer laminar layers, particularly in very thin walled regions and near the bases of secondary fronds. In the former case the median lamina is optically visible as a parting plane between layers of laminar skeleton separating oppositely oriented zooecia. For this reason the outer laminar layer is considered a component of the median lamina.

The median granular layer is optically hyaline, but granular in etched section (Pl. 78, fig. 7; Pl. 79, figs. 2-7). The granular layer may vary irregularly in thickness or become thin between regular lensoidal swellings (Pl. 78, fig. 9). The median layer is comprised of large, tightly interlocking granular crystallites (Pl. 79, figs. 2-6). The granules are composed of small, rhombic crystallites (Pl. 78, fig. 4; Pl. 79, fig. 1). These crystallites are broadly similar to those of the exterior walls (fixed-wall) of some cheilostomes (Sandberg 1983, figs. 121, 123-125) and the 'secondary layer' of some tubuliporates (Brood 1976; Tavener-Smith and Williams 1972). The major differences between these crystallites in *Peronopora* and those of the 'secondary layer' in tubuliporates are their lack of organization into discrete laminae, poorly defined boundaries between individual crystallites, and variable crystallite size in the former. Comparable ultrastructural detail could not be observed in the 'primary granular layer' of tubuliporates or ptilodictyines figured by Tavener-Smith and Williams (1972) or in the median lamina of the trepostome *Petalotrypa* sp. (Bigey 1979) or the cystoporate *Cystodictya* (Healy and Utgaard 1979).

The granular layer may be either internally continuous (Pl. 78, fig. 9), discontinuous, lensoidal (Pl. 79, fig. 6), or separated into segments by folding of the laminar layer around the distal end of each segment (Pl. 79, fig. 2). Segmentation of the granular layer indicates periods of slowed or interrupted growth at the frond terminus. This segmentation demonstrates the direction of growth of the medial layer and provides evidence about the location of the secretory epithelium. Regions of discontinuity and/or thinning are often associated with unusually wide zones of thin-walled ('endozonal') growth (text-fig. 2) and recumbent zooecia which lack cystiphragms (Boardman and Utgaard 1966). These observations suggest a model to explain local discontinuities in median lamina formation (see discussion). The median laminae of primary and secondary fronds are



TEXT-FIG. 2. *Peronopora vera*, discontinuity of median lamina (ml) in region of prolonged endozonal growth (e). Note endozonal (e)–exozonal (x) growth cycles, growth check at former frond margin (large arrow), absence of median lamina within endozonal region and lack of cystiphragms within recumbent zooecia. Long.–Transv., MSU 220314-00253, Eden Shale, Indiana, × 13.

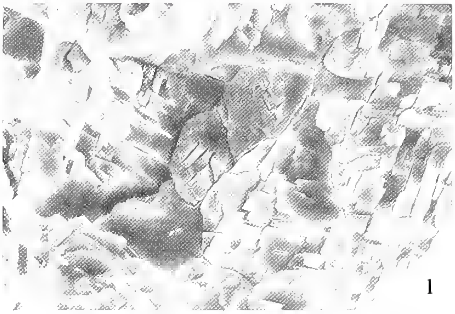
always discontinuous; they are separated by exozonal growth in the parent frond and thin-walled growth at the bases of secondary fronds.

The rounded to elliptical, optically hyaline tubes described by Boardman and Utgaard (1966), and herein termed median styles, display an ultrastructure identical to that of the granular layer (text-fig. 3). The median styles are composed of tightly interlocking granules with an ultrastructure identical to that of the median granular layer. Like acanthostyles and the median rods of ptilodictyines (Karklins 1983), they were not hollow tubes, but continuously deposited, solid structures. Similar structures occur in the mesotheca of the trepostome *P. perforata* Nekhoroshev (Volkova 1974). In *Peronopora* they are generally centered on the junctions between adjacent zooecial ranges and extend the length of one to several zooecial bases in longitudinal section. Oblique sections through the mesostyles could produce the 'mesothecal lenses' (Pl. 79, figs. 3 and 4) described by Tavener-Smith and Williams (1972). Where mesostyles occur within the granular layer, they may be undifferentiated from it or separated by a thin parting. Median styles may occur in the absence of the medial granular layer.

EXPLANATION OF PLATE 79

Fig. 1. *Peronopora vera*. Fine ultrastructure of median granular layer. Fractured section, Transv., MSU 220335-00241, × 1,000.

Figs. 2–6. *P. decipiens*, MSU 220314-00415, Dillsboro Fm., Indiana. 2, Growth check in median lamina showing outer laminar layer (OLL) folded around distal tip of median granular layer (MGL). Long., × 720. 3, lensoidal region (median style (MS)) of median granular layer (MGL) between compound zooecial walls (ZW). Outermost laminae of outer laminar layer (OLL) continuous with recumbent zooecial wall (centre, top, and bottom). Transv., × 940. 4, elliptical median style. Zooecial wall at top right. Labelled as above. Long., × 1,300. 5, median lamina; pluricupular crystallites of outer laminar layer (OLL) and median granular layer (MGL). Transv., × 3,200. 6, median lamina. No medial parting present. Note thinning of median granular layer at right. Labelled as above. Transv., × 660.



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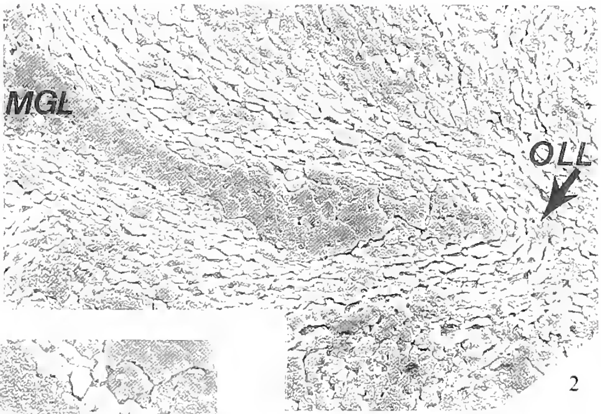

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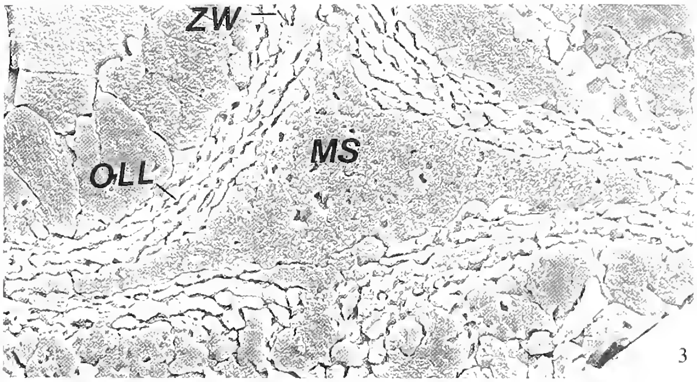

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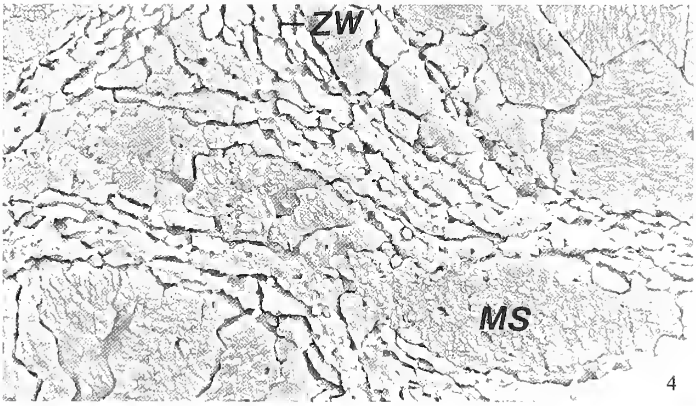

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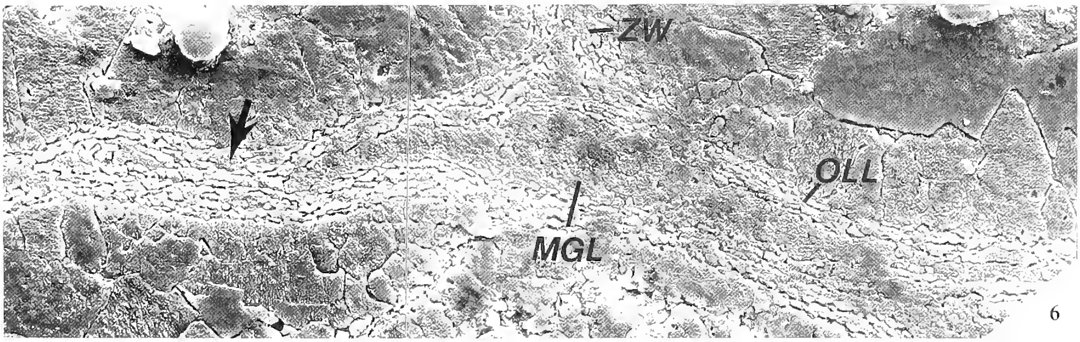

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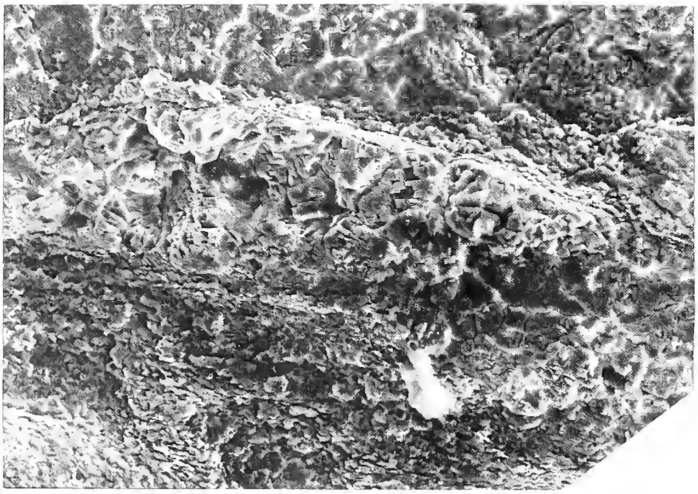
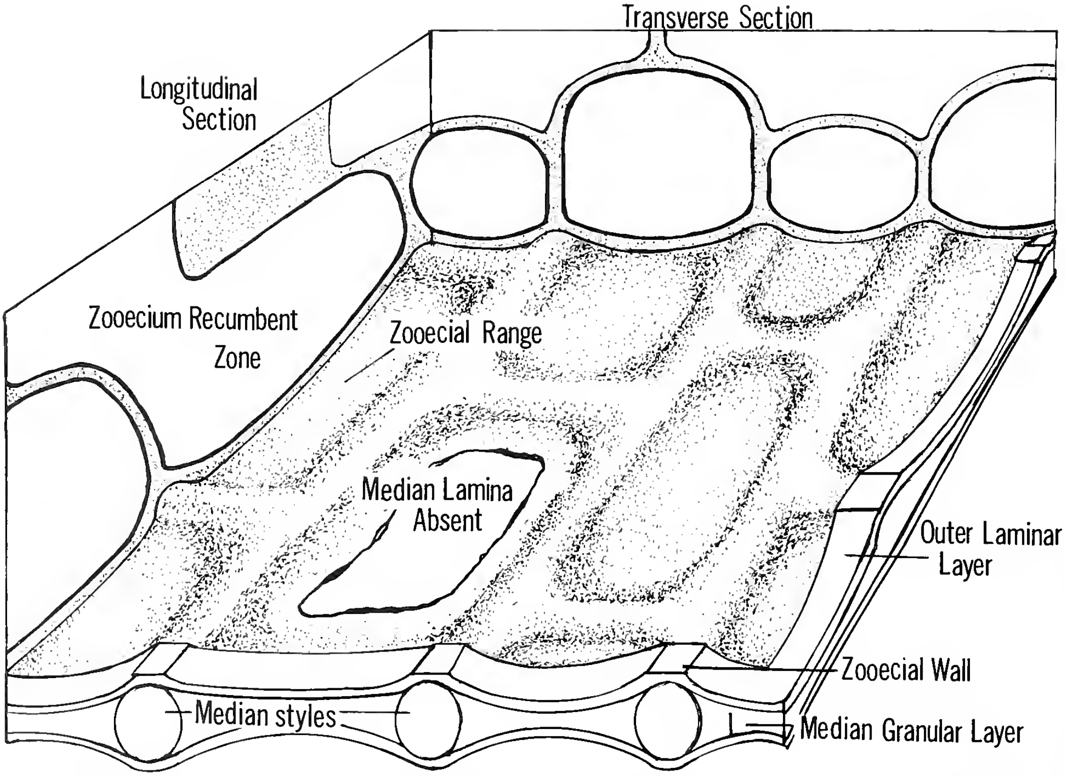
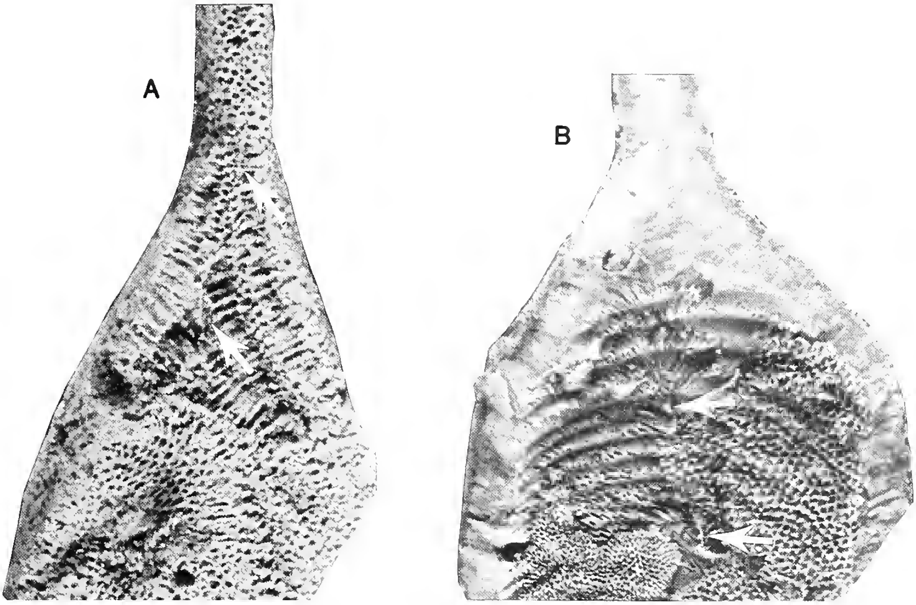


TEXT-FIG. 3. *Peronopora vera*, fine ultrastructure of median style. Fractured section, Transv., MSU 220335-00241, ×200.



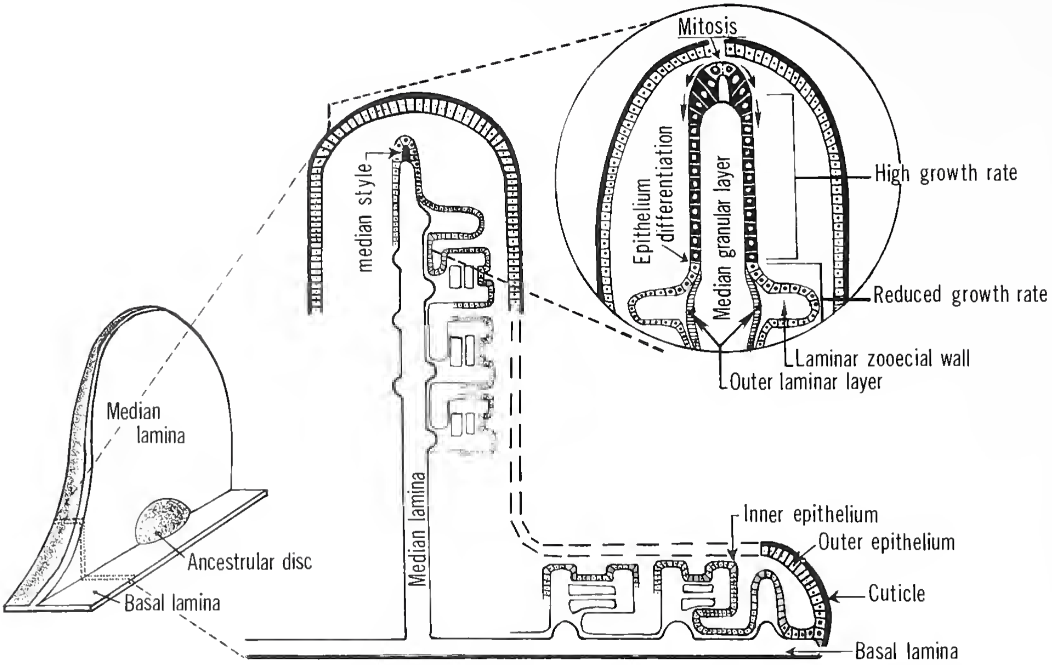
TEXT-FIG. 4. Reconstruction of the median lamina showing distribution of median styles, lensoidal swellings, and local thinning of medial granular layer.

The distribution of mesostyles and thickness variation within the median lamina suggest that the mesostyles and lensoidal regions served as space-filling structural supports between adjacent zooecia (Pl. 78, fig. 9). Tavener-Smith (1969*b*) suggested that median rods in fenestellids may have served to anchor the median lamina skeleton to the outer epithelium or cuticle. The median styles of *Peronopora* could have assumed a similar function, although evidence indicates (see below) that they were secreted by inner, not outer epithelium, and thus not directly associated with outer epithelium or cuticle. Short discontinuities of the median layer may represent local thinning or non-deposition of the median granular layer beneath recumbent zooecial bases rather than an actual discontinuity of the skeletal layer. A three-dimensional reconstruction of the median lamina is illustrated in text-figure 4.



TEXT-FIG. 5. A, *Peronopora decipiens*, colony base showing median lamina (arrows), basal lamina not preserved, MSU 220314-00415, × 5. B, *P. decipiens*, colony base showing junction of median lamina (arrows) and basal lamina. Latter not preserved, but presence indicated by epizoans underlying (on opposite side of) preserved ornamentation of bivalve, upper surface of which was encrusted by young *Peronopora*, MSU 220314-00486, Dillsboro Fm., Indiana, × 5.

An understanding of the skeletal growth of *Peronopora* depends on the relationship between the exterior-walled basal lamina, median lamina, and interior-walled skeleton (Tavener-Smith and Williams 1972). Complete basal portions of early colonies demonstrate that the median lamina was continuous with the basal lamina of the primary frond (text-fig. 5). The median lamina arose after the formation of an elliptical ancestrular disc (Hickey, in press). Completion of the disc was followed by reorientation of the zooecia at the proximal and distal margins of the disc so that the normally basal portions of adjacent zooecial tubes became lateral walls separating oppositely diverging zooecia. The median lamina was formed by vertical extension of the basal lamina following the completion of the recumbent zones of these zooecia. Thus the median lamina was generated at the terminal margins of the primary frond and arched over the ancestrular disc with continued vertical frond growth. Text-figure 6 illustrates the primary features of early astogeny and relationships among the major skeletal structures in bifoliate *Peronopora*.



TEXT-FIG. 6. Growth model for bilaminate species of bifoliate *Peronopora*. *Left*, reconstruction of relations between median and basal laminae and ancestrular disc; *Centre*, relationships between epithelial layers and skeletal layers, median lamina and basal lamina; *Right*, detail of growth model showing region of epithelial differentiation for high and reduced growth rates, granular and laminar skeleton.

Continuity of the median and basal laminae implies, but does not require, deposition in contact with the cuticle. A tendency for fractured specimens to split along separate linear series of zooecia or lamina could be taken as evidence of deposition against a cuticle (Sandberg 1977). Although zoaria of *Peronopora* readily split along the median lamina, the parting tends to be irregular; it usually passes along alternate sides of the central layer rather than through its centre. The inner surface of the median lamina does not exhibit an ultrastructure comparable to the planar spherulitic crystallites of fixed-walled skeleton in cheilostomes (Sandberg 1983).

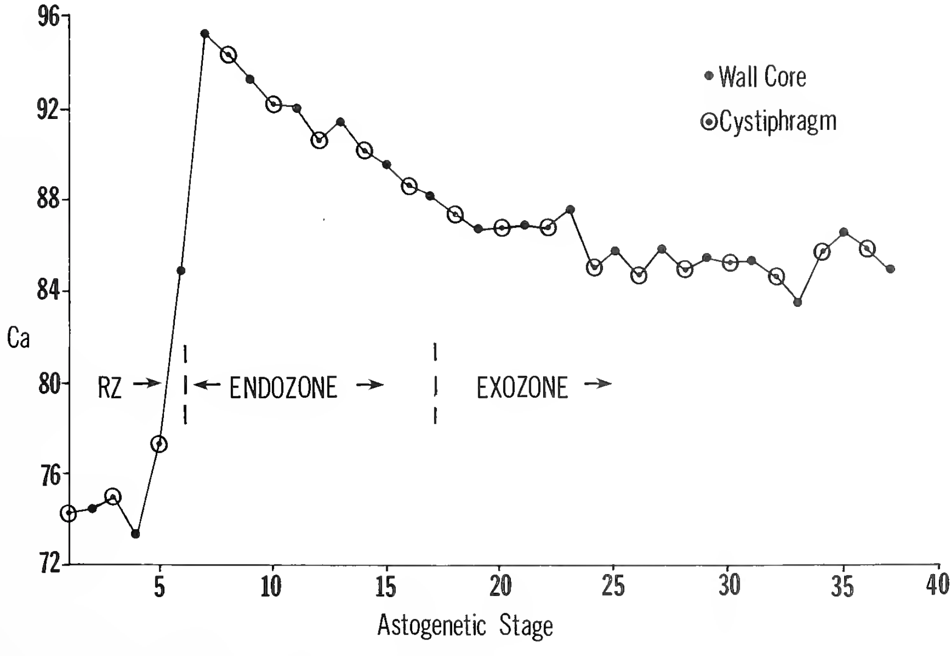
Tavener-Smith and Williams (1972) concluded that the median lamina of *P. milleri* was not deposited against a cuticle because the median lamina consisted of discontinuous 'mesothecal lenses' with no evidence of a medial parting. This study found no ultrastructural evidence of a medial parting within the continuous medial layer (Pl. 78, fig. 9; Pl. 79, figs. 5 and 6) despite the common occurrence of a dark medial line in thin section. Folding of laminar internal-walled skeleton around the distal ends of median granular layer 'segments' (Pl. 79, fig. 2) indicates that a secretory epithelium of the median lamina could not have been located between the median granular layer and the outer laminar layer as suggested by Tavener-Smith and Williams (1972). The discontinuity of the median laminae of primary and secondary fronds of *Peronopora* also shows that median lamina skeleton could not have been deposited against cuticle or within a fold of (basal) epithelium. Thus, the median lamina was continuous with the upper portion of the basal lamina but must have been deposited by inner epithelium at the growing margin of the colony (text-fig. 6). The inner epithelium appears to have been capable of secreting skeleton which was ultrastructurally very similar or identical to exterior-walled skeleton (see discussion).

ELEMENTAL COMPOSITION

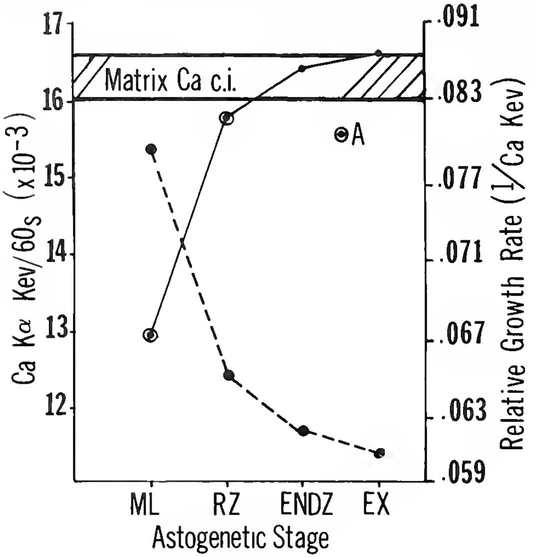
Elemental rhythms and ontogenetic trends

Elemental abundances in some organisms other than bryozoans are known to vary with tidal (Rosenberg and Jones 1975), diurnal (Schmalz and Swanson 1969), or seasonal cycles (Bryan 1973; Goreau 1977; Crisp 1975). If the physiological process of skeletal growth do interact with ambient levels of trace elements in the environment, or if non-equilibrium modifications in elemental composition occurred in conjunction with the periodic formation of structures, such processes could be evinced in abundance cyclicities. Cystiphragms are periodically formed structures which could have been deposited in association with tidal cycles (Bartley and Anstey 1983). A single zooecial wall of *P. vera* was analysed for periodic abundance fluctuations of Ca, Cu, Si, Fe, Mg, Mn, and Nb between the laminae of cystiphragms and intervening regions of laminar zooecial wall deposited between cystiphragms. This analysis was designed to determine whether elemental abundances were distributed in a systematic manner in association with the periodic emplacement of cystiphragms. With the possible exception of Ca, none of the elements displayed periodic structural variations.

There is some indication of a periodic fluctuation of Ca within the endozones and exozones of the autozooecial wall. Ca abundance changed in a systematic manner with ontogeny (text-fig. 7). Minimal values in the thin-walled recumbent zone increased abruptly during transition from the recumbent zone to the lower endozone. Abundance gradually decreased from the endozone through the latest exozone. Within the exozone, Ca levels of cystiphragms and contiguous zooecial wall laminae are generally lower than those of intervening laminae of axial positions in the wall, but the difference is not statistically significant. This structural fluctuation is also present, though weakly developed, within the endozone.



TEXT-FIG. 7. Distribution of Ca in zooecial wall of *Peronopora vera*. MSU 220335-00252. RZ = recumbent zone. 'Astogenetic Stage' approximated by datum points located at equal intervals, alternately within wall axis and on each successive cystiphragm wall.



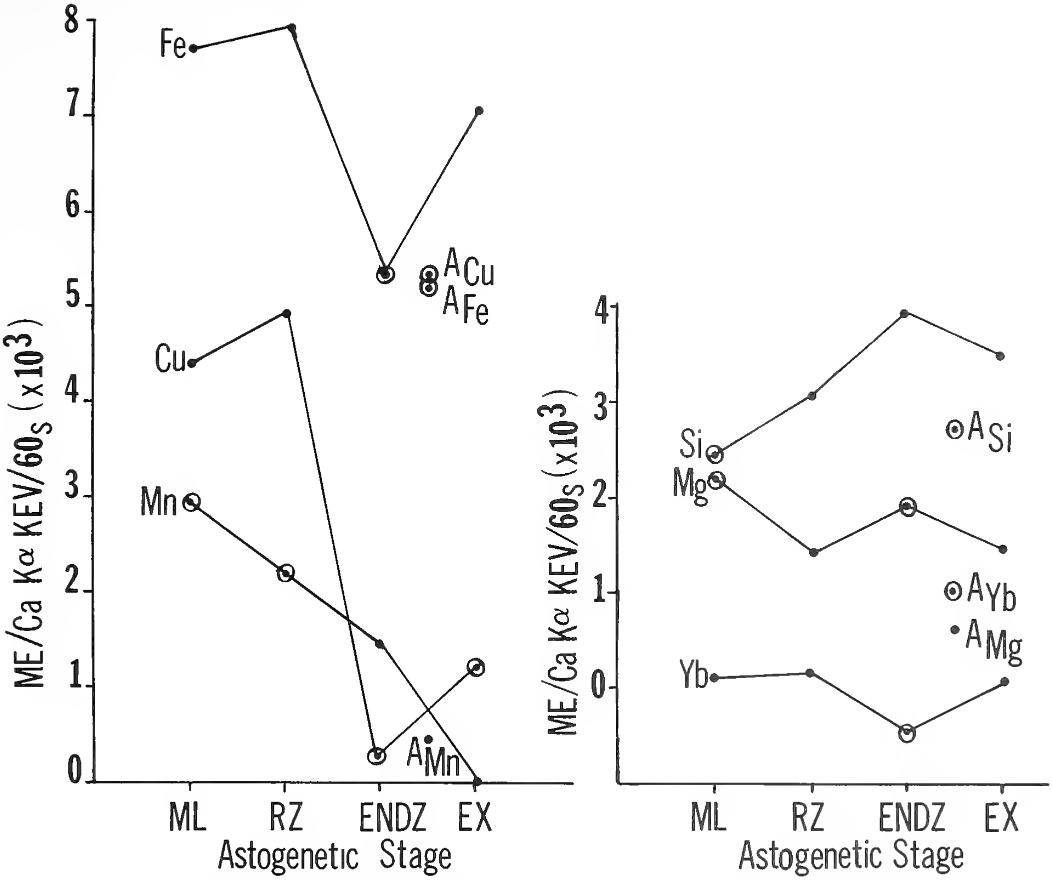
TEXT-FIG. 8. Distribution of Ca among median lamina (ML), recumbent zone (RZ), endozone (ENDZ), exozone (EX), and acanthostyles (A, circled) for fifteen zooecia of *Peronopora vera*. MSU 220335-00252. Circled datum indicates Ca density value differing significantly from void cement. C.I. = confidence interval for Ca density levels of zooecial void cement. Solid line: Ca density distribution. Dashed line: relative growth rates of astogenetic zones and skeletal structures.

Rosenberg (1980) has stressed the need for replicated analyses in studies of this kind. His review of similar studies of bivalves noted that element abundances may vary among planes of cross-section and among individuals, suggesting that allometric analyses of ontogenetic trends may explain much of the variation in compositional trends. Thus, although the above results are interesting, no general inferences should be drawn from them. In contrast, the second analysis is based on the mean values of Ca and trace element abundances from three astogenetic zones, acanthostyles, and the median lamina measured in 15 individual autozooecia of a single colony. Statistical treatment of these data permits inferences about the relationships between compositional change and growth. The difference in exozonal Ca abundance between the former and following analyses were probably due to the absence of replicate data from other zooecia and the collection of data from points of very limited surface area (small beam size) in the former.

Astogenetic trends

Analysis of fifteen zooecial walls revealed a Ca trend that is broadly similar to that of text-figure 7, but differs critically in the relative values of the endozone and exozone. Ca levels are minimal in the median lamina and become progressively greater in the recumbent zone, endozone, and exozone (text-fig. 8). All pair-wise comparisons between astogenetic zones and other structures show significant differences in Ca abundance. Ca abundance within the exozone is significantly greater than that of the endozone at $p = 0{\cdot}10$. Acanthostyle axial cores contain significantly less Ca than the recumbent zone, endozone and exozone ($p < 0{\cdot}05$), but significantly more Ca than the median lamina ($p < 0{\cdot}05$). The median lamina contains significantly less Ca than acanthostyles and astogenetic zones of zooecial wall skeleton ($p < 0{\cdot}05$).

Ca densities of the endozone and exozone do not differ significantly from that of the zooecial void cement. Thus it is possible that Ca abundance within void matrix could have varied in a proximo-distal manner similar to that of the skeleton. However, some aspects of the Ca distribution suggest that the observed trend is not a product of diagenesis. Significant differences ($p < 0{\cdot}05$) do occur among the void cement and acanthostyles, recumbent zone and median lamina. Ca concentration within void cement was measured at approximately the mid-point of each zooecial tube; a position equivalent to that of the inner exozone. Acanthostyle Ca abundance was measured within the exozone, yet is significantly lower than that of the matrix, exozonal, and endozonal wall. In addition, petrologic criteria indicate that the recumbent zone of *Peronopora* and other



TEXT-FIG. 9. Trace element distributions in *Peronopora vera*. MSU 220335-00252. Labelled as for text-fig. 8. Circled points indicate densities significantly different from void cement.

taxa is less-well calcified than endozone or exozone (Boardman and Utgaard 1966). Thus, it appears that the trend in skeletal Ca abundance is not a product of diagenesis. Additional studies of this kind are needed to confirm or reject the results of this study.

Mg abundance declined slightly over the course of astogeny in *P. vera* (text-fig. 9). Because Mg readily substitutes for Ca, it is expected to vary inversely with Ca. The overall trend is toward decreasing Mg concentration, yet Mg is most abundant within the median lamina and endozone, and least abundant in the recumbent zone and exozone. Mg concentrations of the median lamina and endozone are significantly greater than that of the void cement ($p < 0{\cdot}05$).

Mn concentration decreased monotonically with autozooecial age in *P. vera* (text-fig. 9). Mn abundance is inversely proportional to Ca density across astogenetic zones, a relationship which could reflect elemental substitution. Mn concentrations within the median lamina and recumbent zone are significantly greater than that of the void matrix ($p < 0{\cdot}05$).

Cu and Fe exhibit parallel fluctuations over the course of astogeny; both generally decline with increasing age (text-fig. 9). Fe and Cu reach maximal abundance in the recumbent zone and acanthostyles respectively. The minimum values for Fe and Cu occurred in acanthostyles and the endozone respectively. Levels of Fe in the endozone and acanthostyles are significantly less than that of the void cement. Cu abundances in the endozone and exozone are significantly lower than that of the void cement. Cu concentration in acanthostyles is significantly greater than that of the void cement. Si gradually increased with age through the endozone but declined somewhat within the exozone. Si concentration is significantly less abundant in the median lamina than in the void cement. Yb concentration remained essentially constant with increasing age but differed significantly from the void cement in the endozone.

Structural variation

Acanthostyle cores contain significantly more Cu than the median lamina, endozone, or exozone. The concentrations of Fe, Cu, Si, and Yb in acanthostyles differ significantly from that of void cement. The median lamina contains significantly more Mn than the zooecial wall skeleton and void cement. Si and Mg concentration are also significantly greater in the median lamina than in the void cement.

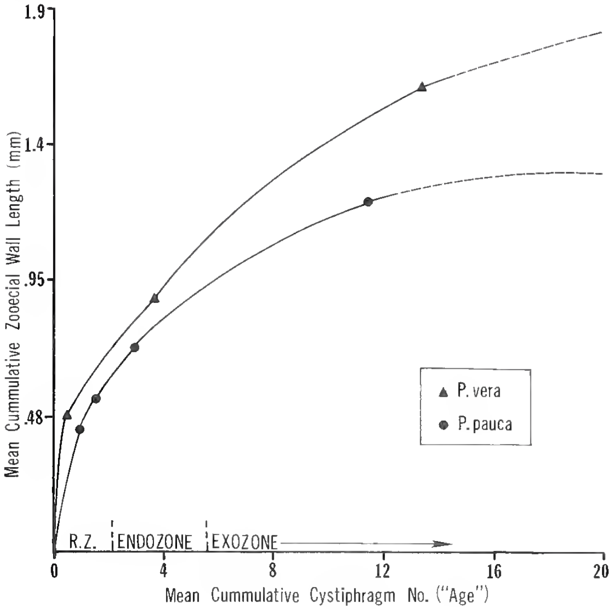
DISCUSSION

Astogenetic growth zones

Tavener-Smith (1969*a*, *b*, 1975) and others have proposed that differences in crystallite morphology reflect differences in the continuity and rates of crystallite and skeletal secretion and growth among astogenetic zones. These inferences were based on consideration of the effects of the thermodynamics of crystallite growth on ultrastructure, the differential response of skeletal structure to episodic *versus* continuous growth, and the astogenetic succession of crystallite/skeletal wall morphologies. These hypotheses of growth rate are important for two reasons. Firstly, they can increase our understanding of growth, development, and skeletal formation. Secondly, knowledge of the relative growth rates of skeletal structures can be used to explain the evolution of zooecial wall and other skeletal structures. The results of elemental analyses (particularly Ca) in *Peronopora* support the inferred associations between crystallite/skeletal morphology and secretion rates. The data also support inferences about the relative rates of growth among astogenetic zones.

If it can be assumed that EDS measurements of Ca abundance reflect the density distribution of calcium within the skeleton (and that this distribution is not a result of diagenesis), relative levels of Ca can be used as a gauge of relative growth rates. It is assumed that the relative abundance values obtained from a given surface area can be extrapolated to proportional values of density when comparing surfaces of approximately equal area. Rosenberg (1983) argued that this assumption was a valid interpretation of the distribution of Ca in fossil brachiopods. This interpretation is based on the thermodynamics of crystal growth which predict an inverse relationship between growth rate and Ca density. Thus zones of continuous and rapid growth should display lower Ca densities than zones of slower, laminar (episodic) growth. An equivalent relationship should exist among Ca densities and astogenetic zones of predominately laminar growth. Less 'densely' laminated recumbent zone and endozone should display lower Ca densities than thicker-walled exozone. In addition, granular and irregular crystallites should contain less Ca than laminar skeleton and tabular crystallites. A corollary of this relationship predicts that trace elements which commonly substitute for Ca should be greater within skeleton with lower Ca densities and by inference, higher rates of crystallite secretion and skeletal growth. Those which easily complex with organic materials could be expected to be more common in more densely laminated wall and/or zones of disordered growth in wall axes.

The thin-walled recumbent zone and endozone are commonly believed to have been faster growing than the thick-walled exozone. The relative densities of Ca in these astogenetic zones are in accord with theoretical predictions of Ca density behaviour with growth rate variation (text-fig. 4). These data also support the petrologic evidence that autozooecial recumbent zones in *Peronopora* were lightly calcified (Boardman and Utgaard 1966). Therefore Ca density data support the hypothesis that growth rate decreased exponentially with increasing age from the recumbent zone through the exozone in *Peronopora*. The recumbent zone formed more rapidly than the endozone



TEXT-FIG. 10. Growth curves based on cystiphragm distribution per unit wall length for *Peronopora vera* (MSU 220314-00508, Eden Shale, Indiana) and *P. pauca* (paratype, IU8252G 160-1170, Indiana University specimen, Whitewater Fm., Indiana).

and the endozone formed more rapidly than the exozone. The results also allow inferences about the relative growth rates of other structures. The median lamina was secreted most rapidly, followed by acanthostyle cores and the recumbent zone. Granular crystallites of optically hyaline skeleton generally reflect higher rates of secretion and growth than tabular crystallites within internal-walled skeleton. Presumably, these results could be extrapolated to other taxa which show various modes of skeletal differentiation within and among recumbent/endo- or exozones, mesothecal, and exterior-walled skeleton. Further EDS analyses on other taxa should provide interesting data on bryozoan growth rates.

If rates of wall growth gradually decrease from the recumbent zone through the exozone, and if cystiphragms or other intrazooecial structures were formed with a regular periodicity (Bartley and Anstey 1983) then it is possible to construct growth curves for bryozoans. The area subtended by cystiphragms and the spacing between cystiphragms decreases (degree of cystiphragm overlap increases) from the recumbent zone through the endozone in bifoliate *Peronopora* (Hickey, in press). Spacing is minimal and appears to remain relatively constant throughout the exozone. The size/spacing distributions are consistent with the assumption that cystiphragms were formed with a regular periodicity while growth rates of zooecial wall decreased with age. Thus, a plot of the cumulative number of cystiphragms per unit length of zooecial wall should reveal changing rates of wall growth. Text-figure 10 illustrates preliminary results of such growth curves for single colonies of *P. vera* and *P. pauca*. That these growth curves are of the same shape as that of the Ca density data (and the inverse of the Ca growth rate curves) lends support to the hypotheses that zooecial wall growth rates generally decreased with increasing age. Knowledge of the actual time lapse (e.g. fortnightly cycles, etc.) between cystiphragm formation is not necessary for such a reconstruction of relative growth rates. The growth curves for *P. pauca* and *P. vera* suggest that the growth rate of the former species declined more rapidly than that of the latter; a conclusion consistent with the thicker exozonal walls of the former species. The ability to construct relative growth curves could add to the understanding of the palaeobiology and systematics of bryozoans. Such growth curves could be used as taxonomic descriptors.

Trace element data may also have a bearing on interpretations of skeletal growth rates. Several studies have found that Mg and Mn concentrations can vary with growth rate. Goreau (1977) found an increase in Mg with decreasing growth rate in the coral *Montastrea annularis*. However, Zolotarev (1974) documented a decline in Mg with reduced growth rate in the bivalve *Mytilus yessoensis*. A gradual increase with age and reduced growth rate is evident in the data of Moberly (1968) for the bivalve *Aequipecten irradians*. Crisp (1983) reported a decreasing Mn concentration with increasing age in freshwater bivalves. However, he also found that Mn concentrations were greatest in the slowest growing portions of the oldest growth increments. Crisp (1975) found an apparent habitat dependence in Mn ontogenetic trends; Mn decreased with increasing age among individuals of the bivalve *Lampsilis* sp. from one habitat, but increased with age among individuals from a different habitat. The bivalve *Anodonta corpulenta* displayed an increase in Mn with increasing age.

The monotonic decrease of Mn density with increasing age in *Peronopora* is consistent with the expected distribution of trace elements with respect to Ca and inferred growth rates (text-fig. 9). The Mn trend could reflect a direct physiological function of skeletal growth rates and/or a function of elemental substitution for Ca. Substitution is expected to have been greater in faster growing zones of lesser Ca density such as the median lamina and recumbent zone. However, simple substitution is probably an inadequate explanation for the Mn trend given that the incorporation of Mn in cheilostome skeletons is under physiological control (Sakagami *et al.* 1984). Mg also shows a slight decrease in density with increasing age and decreasing growth rate; however, these data are much less definitive. Mg concentration is expected to have been a simple equilibrium function of crystallite growth rate (Sakagami *et al.* 1984).

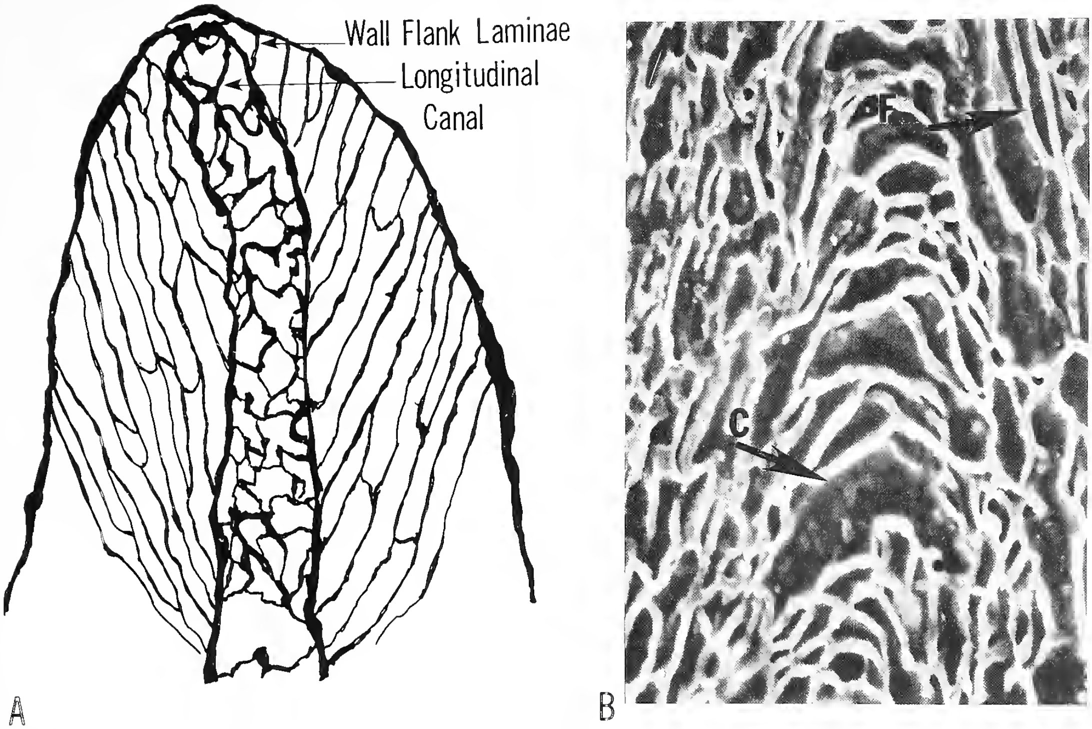
The meaning of the astogenetic trends of other trace elements is not entirely clear. Each of the elements analyzed show significant density differences between one or more astogenetic zones and the void cement. Some of the variation could be attributed to substitution for Ca and thus, could be interpreted as rate related phenomena. The data suggest that some elements could have been preferentially concentrated/excluded at various stages of growth or among skeletal structures. By analogy with the composition of cheilostomes (Sakagami *et al.* 1984), the abundances of Fe, Cu, and Mn could represent products of differential concentration or exclusion through physiological control over ambient levels. Alternatively, the data could indicate that astogenetic stages and skeletal structures were differentially influenced by diagenesis as a function of crystallite type and/or ultrastructural variation within laminated zooecial wall. Additional studies could conceivably determine whether such results reflect ontogenetic variation, differential response to diagenesis, or the influence of environmental factors.

The differences in Ca density among growth zones of laminar skeleton, crystallite types and skeletal structures in *P. vera* are consistent with independent inferences about relative rates of skeletal growth based on observations of microstructural variation in this and other studies. Such compositional variations appear to reflect real differences in the physiology of skeletal growth. The distributions of most trace elements are not as easily interpreted as is that of Ca. However, the distributions of Ca, Cu, and Mn among crystallite types are generally consistent with predictions of thermodynamics and a variety of qualitative observations and may be extended to skeletal growth rates during astogeny.

Zooecial wall growth

Tavener-Smith and Williams (1972) suggested that differences between thicknesses of the laminae of wall axes and flanks within some 'amalgamate' trepostomes are due primarily to oblique orientations of laminae within the axial zones. The 'bimodal' nature of axial crystallite dimensions and lamina frequencies in *Peronopora* produce indistinct zones of laminae which resemble the independent wall units discussed by Boardman (1960). These zonal microstructural variations indicate that axial crystallite shape and thickness differences are not entirely artefacts of lamina orientation. Zonal differences in crystallite morphology and lamina number could be characteristic of taxa with cyclical growth rates.

Some aspects of the central wall structure of the Recent tubuliporate *Heteropora pelliculata* Waters (Ross 1976, 1977) provide a developmental analogue for interpretation of differential wall



TEXT-FIG. 11. A, zooecial wall structure of *Heteropora pelliculata*, decalcified long. sec. Redrawn from photograph in Ross (1976). B, *Peronopora vera*, exozonal autozooecial wall. Disordered central wall structure (C), laminar wall flanks (F). Acetate peel, Long., MSU 220335-00239, Eden Shale, Ohio, × 3,000.

flank/axis ultrastructure in *Peronopora* and similar trepostomes. Distal portions of zooecial walls of *H. pelliculata* display irregularly shaped, disordered crystallites in a relatively dense organic matrix within central longitudinal 'canals' (Ross 1976, text-fig. 1). Ross (1977) suggested that the 'canals' may serve as loci for locally accelerated growth and conduits for the resorption and distribution of skeletal and other materials. Acetate peels (negative replicas) of the axial zone of zooecial walls in *Peronopora* bear a striking textural resemblance to the distribution of the organic matrix in the interior of the longitudinal canals of decalcified specimens of *H. pelliculata* (compare text-fig. 11*a*, *b*). It is not suggested that the axial zones in *Peronopora* contained longitudinal 'canals' as Ross proposed for *H. pelliculata* and it should also be noted that the zooecial wall flanks of *H. pelliculata* are proximally oriented, unlike those of *Peronopora*. However, the textural similarity between the axial zones of the two taxa strongly suggests that the axial zones of *Peronopora* could have been characterized by relatively rapid, disordered crystallite growth and higher organic content similar to *H. pelliculata*. The dynamics of crystallite growth in general suggest that irregularly shaped, disordered crystallites were more rapidly formed than those with uniform shapes (Tavener-Smith 1969*b*). This interpretation is supported by Ca data which indicates that the similar granular crystallite morphologies of the median lamina and acanthostyle cores were a product of increased rates of crystallite secretion.

Large, granular crystallites also occur between the laminar annular thickenings (monilae) of *Stenopora crinita* (Armstrong 1970) and the laminar monilae of *Tabulipora* Young. Evidence of fortnightly tidal cycles has been found within the monilae of *Tabulipora* (Rabbio and Regalbuto 1985). Constricted zones of granular zooecial wall occur between the fortnightly cycles recorded within the monilae of *Tabulipora*. The limited width and granular morphology of the constricted regions suggests that these portions of the wall were formed more rapidly than the laminar monilae. Thus wall growth in *Tabulipora* appear to have varied between slow, laminar (episodic) and rapid, continuous modes in conjunction with tidal cycles.

Microstructural zonation of the crystallite morphology of *Peronopora* is inferred to reflect periodic variations in growth rates and episodicity of laminae formation. Although most individual laminae are difficult to trace for long distances within a wall, the number of laminae intersected by a line drawn parallel to the zooecial wall growth axis can provide rough estimates of laminae frequency. Counts of laminae within a given unit wall length made by independent observers differ significantly from the null hypothesis of no difference in means. However, differences in laminae frequency between axial and flank regions within a given unit length differ significantly ($p < 0{\cdot}05$) despite the variation attributable to observational error. Lamina frequency consistently differ by a factor of two or more between zooecial wall flanks (mean = 19·3) and axes (mean = 27·4) per unit (distal) length. In addition, laminae appear to be at least twice as numerous—per unit wall length—within the laminar zones of wall axes than within zones of irregular axial crystallites. Axial laminae within intervening zones of larger, irregular crystallites are often less distinct than those of wall flanks and laminar zones of the axis. These frequency distributions of laminae reflect a greater degree of intercalation between the laterally discontinuous laminae of axial zones than among laminae in the adjacent wall flank, and an alternation between laminar and irregular crystallite growth within the wall axis. It is inferred that the episodicity of laminae formation was greater (and rate of skeletal formation thus lower) within laminar portions of axial zones than on wall flanks. Irregular crystallite morphology can be attributed to increased rates of crystallite secretion and decreased episodicity by inference from the similarity between irregular and granular crystallite ultrastructures.

The irregular and disordered crystallite morphology and approximate doubling of laminae number within different zones of the zooecial wall axis of *Peronopora* strongly suggests periodic variation of growth rate and episodicity within the axis. Structural differences between wall axes and flanks suggest periodic alternations between increased growth rates and increased episodicity, respectively. Structural zonation is most pronounced within mesozooecial walls. Zones of irregular crystallites within the axial wall occurring proximal to cystiphragm/tabula emplacements could indicate increased rates of crystallite secretion preceding cystiphragm/tabula formation. The increased frequencies of laminae composed of more tabular-shaped crystallites occur in zones which are contiguous with cystiphragm and tabula walls. This structural variation suggests slower rates of crystallite secretion and increased episodicity of lamina formation during periods of cystiphragm formation.

Periodic variation in ultrastructure could be linked to periodicities of element abundances. Rosenberg and Jones (1975) found regular fluctuations in Ca and S abundance in living specimens of the bivalve *Cardium edule* which were correlated with tidal cycles. Individual lamina of bryozoan skeletal walls are presumed to be daily deposits (Tavener-Smith 1969*b*; Rabbio and Regalbuto 1985). Laminae are nested within periodic cystiphragm emplacements; events of a higher temporal order that could be linked with tidal cycles (Bartley and Anstey 1983). Variation in Ca density could be expected in association with the structural variation of zooecial wall which occurred during the cystiphragm formation cycle in *P. vera*. The observed variation of Ca density between periods of cystiphragm emplacements and normal wall growth in *P. vera* could reflect cyclic growth phenomena associated with periodic changes in environmental variables (text-fig. 7). However, the data are equivocal because the difference between mean Ca levels in cystiphragms and zooecial walls is not statistically significant. The results do indicate that further studies of relationships between structural periodicities, Ca variations and growth rhythms are warranted.

Evolution of wall structure

If crystallite morphologies and astogenetic zones of growth can be linked to differential growth rates, the evolution of wall structure among closely related taxa may be described in terms of heterochronic change. Tavener-Smith (1969*a*) and Brood (1976) have noted the presence of short distal extensions of granular exterior-walled skeleton at the base of zooecial walls in free-walled taxa. Larwood and Taylor (1979) proposed that the evolution of free-walled taxa from primitive fixed-walled taxa in the Palaeozoic could be interpreted in terms of paedomorphic heterochronic changes which prevented the coalescence of free-walled skeleton with outer epithelium. The early termination and/or reduced growth rate of the granular external-walls could have been the principal heterochronic change leading to the origin of paedomorphic free-walled taxa. This interpretation of skeletal growth rates supports the hypothesis of Larwood and Taylor (1979). Given either early termination (progenesis) or reduced growth rate (neoteny), the phylogenetic phenomenon would have been reverse recapitulation (terminology of Alberch *et al.* 1979).

Tavener-Smith and Williams (1972) noted that the optical differences between the zooecial wall microstructures of the former trepostome suborders Amalgamata and Integrata reflect the increased 'granularity' (irregularity) and greater dimensions of axial wall crystallites in the latter. These suborders may have grouped together taxa with homogeneous rates of laminar growth, and taxa with locally accelerated rates of axial growth, respectively. Given a hypothetical ancestral taxon with homogeneously laminar growth, accelerated axial growth in a derived taxon could be interpreted as a peramorphic product representing acceleration. The evolution of the 'amalgamate' Atactotoechidae from the 'integrate' Amplexoporidae (Astrova 1965, p. 114) provides a concrete example. In this case, the derivation of uniformly laminar walls from primitive granular walls could be viewed as an example of paedomorphosis representing the process of neoteny in a phylogenetic pattern of reverse recapitulation.

The evolution of wall structure among *Peronopora*, *Prasopora*, and *Atactoporella* has been interpreted in terms of heterochronic processes (Hickey, in press). *Prasopora* can be considered primitive and probably ancestral to *Atactoporella* (Astrova 1978) and *Atactoporella* appears to be the ancestral sister group of *Peronopora* (Hickey, in press). *Prasopora* is characterized by a 'granular' zooecial wall structure, while zooecia of *Atactoporella* and *Peronopora* have predominately laminar walls. The derived laminar wall structures of the latter two genera appear to have evolved through a paedomorphic decrease in the rate of wall growth during astogeny.

Acanthostyle development and evolution

The epithelial origins of acanthostyles are uncertain. The optically hyaline appearance of the axial cores of trepostome acanthostyles and portions of 'heterostyles' (Blake 1983) resembles that of exterior-walled skeleton. This suggests that the axial crystallites of trepostome acanthostyles could have been secreted by outer epithelium as Tavener-Smith (1969*b*) proposed for fenestellid skeletal rods and 'primary skeleton'. However, secretion of core crystallites by outer epithelium in trepostomes appears to be precluded by the lack of any examples in which acanthostyle cores are proximally continuous with exterior-walled skeleton. Overgrowth of the axial core terminus by laminar skeleton in the trepostome *Leptotrypella? praecox* Boardman (Boardman 1983, text-fig. 51-1*c*, p. 104), the complex growth mechanics needed to explain the alternation of hyaline and laminar skeleton in trepostome 'heterostyles' (Boardman 1983, p. 105), and the different ultrastructures of acanthostyles and median lamina in *Peronopora* also argue against secretion of axial core skeleton by outer epithelium. Yet, the microstructural contrasts between axial cores and sheath laminae indicate there were distinct growth differences of some kind.

Armstrong (1970) postulated that acanthostyle axial cores in *Stenopora* could have been deposited by patches of specialized epithelium. This hypothesis is supported by four lines of evidence in *Peronopora* as well: 1, the distinct boundary between cores and sheath laminae; 2, the contrasting morphologies of core and sheath crystallites; 3, laminar versus continuous growth modes; and, 4, differential Ca and trace element concentrations between acanthostyle core crystallites and laminar exozonal skeleton.

Several observations provide clues for an explanation of these microstructural differences. The solid nature of acanthostyle axial cores has been well established (Armstrong 1970; Blake 1973, 1983; Boardman 1983; Tavener-Smith 1969*a*). Infrequent lamination of the axial core skeleton in most taxa indicates that the deposition of granular crystallites was relatively continuous. The topographic prominence of acanthostyles and the relationship between axial cores and sheath laminae indicate that granular crystallite deposition within axial cores was locally accelerated relative to laminae formation (Tavener-Smith 1969*a*, *b*). Occasional preservation of 'brown bodies' and pyrite grains within acanthostyle axial cores (Boardman 1983) suggests a high organic content; organic material could presumably have been more readily incorporated within core skeleton if growth were rapid. Thus axial core ultrastructure appears to be a product of accelerated crystallite secretion.

Armstrong (1970, p. 584) found iron carbonate minerals in the acanthostyles of *Stenopora*. This was interpreted as an additional indication of a specialized epithelial origin for acanthostyles. The results of this investigation can be interpreted in a similar manner. Ca densities are lower, and by inference, growth rates were higher in acanthostyles than within endozone and exozone (text-fig. 8). Substitutional elements such as Cu, Fe, and Mn are generally most abundant in acanthostyle cores (text-fig. 9). Acanthostyles are enriched in Cu, Fe, Si, and Yb relative to the zooecial void cement. High Cu levels in acanthostyle cores satisfy the predicted increase in substitutional element abundances within zones and structures with low Ca densities. The high levels of Cu are consistent with non-equilibrium skeletal formation (Sakagami *et al.* 1984). These data support the hypothesis that paurostyle cores were secreted more rapidly than endozonal and exozonal laminar skeleton. Furthermore, they suggest a more specific explanation for the skeletal differences between acanthostyle cores and laminar skeleton.

Paurostyle morphology could be explained by development of an extreme differentiation of laminar and granular crystallite growth modes. This differentiation could have been accomplished by patches of inner epithelium with particularly high rates of crystallite secretion. The disordered axial growth and irregular crystallites typical of zooecial walls in 'integrate' taxa could be considered a developmental analogue with the early stages of acanthostyle evolution in trepostomes. Paurostyles could have evolved from laminar zooecial wall by a highly localized acceleration of crystallite secretion rates. Irregular crystallites of zooecial wall axes could be invoked as a transitional step in this hypothetical transformation series.

Given the above model of acanthostyle origins, it is possible to describe the evolution of different acanthostyle types among closely related taxa in terms of heterochronic changes in rates of skeletal growth. Paurostyle morphology is assumed to be the primitive state (Tavener-Smith 1969*b*). Heterostyles, and heterostyle-like structures of some trepostomes, are composed of alternating layers of hyaline and laminar skeleton (Blake 1983). Most rhabdomesid aktinotostyles are composed of distally (and laterally) deflected laminar skeleton (Blake 1983). Aktinotostyles could have been derived from paurostyles by a decreased rate of crystallite secretion coupled with an increase in lamination episodicity. Similarly, heterostyle structure could be explained in terms of periodic alternation between the primitive paurostyle growth mode and decreased secretion rates coupled with increased episodicity. Thus both aktinotostyles and heterostyles (in part) could be considered paedomorphic products of neoteny. In this model, heterostyle evolution must have involved temporal signals which induced switching from one growth mode to another. The presumed ease with which such heterochronic modifications could occur suggests that homoplasic evolution of all acanthostyle types may have been common.

The median lamina

The median lamina arose as a distal extension of basal lamina skeleton. However, there is no evidence to indicate that the median granular layer was deposited against cuticle or within a distally directed fold of basal epithelium. The absence of a medial parting argues against the first interpretation. The second interpretation is precluded by occasional growth checks in the median granular layer which were followed by deposition of the outer laminar layer around the distal margin of the median layer, and the fact that the median granular layers of primary and secondary fronds are discontinuous. These factors, in concert with a very low Ca density indicate that the skeletal structure of the median granular layer was a product of very high, relatively continuous, rates of crystallite secretion by inner epithelium at the distal margins of the colony (text-figs. 6–

8). The generally high levels of Fe, Mn, and Cu within the median lamina (text-fig. 9) satisfy the predicted increase in substitutional element abundances and/or the presence of non-equilibrium growth products within zones and structures with low Ca densities. The similarity between granular median and basal lamina skeleton suggest that granular exterior-walled skeleton also grew more rapidly than laminar interior-walled skeleton.

The ultrastructural character of basal lamina skeleton does not appear to have been a consequence of deposition against cuticle *per se*, but rather differentiation of the crystallite secretion rates of inner epithelium (text-fig. 6). Because both granular median lamina and laminar zooecial wall skeleton are products of secretion by inner epithelium, some mechanism for differentiation of cellular processes and skeletal products is required. It is evident from the astogenetic succession of skeletal types and their common epithelial origin that new epithelial cells must have been added at the colony margin in a manner similar to the 'conveyor-belt' model of skeletal formation proposed by Tavener-Smith (1969*b*). Thus, it could be hypothesized that the stimulus for the developmental differentiation of epithelial processes/skeletal products lay in positional and/or temporal regulation of cellular activity and products. As cells produced at the colony margin migrated proximally, or as the colony margin advanced a predetermined distance, the mode and rate of inner epithelial secretion switched from high, continuous rates of growth and production of granular crystallites to slower, episodic growth rates, tabular crystallites and laminar skeleton.

Local discontinuities in the median lamina of *Peronopora* may be explained in terms of a growth rate model. Local discontinuities of the median lamina in *Peronopora* often occur in association with regions in which thin-walled ('endozonal') zooecial growth was prolonged (text-fig. 2). The recumbent zones of zooecia in these regions are also unusually long and lack cystiphragms (Boardman and Utgaard 1966, p. 1096). The periodic interruption of median granular layer formation was followed by relatively wide regions of endozonal growth. These widened endozonal regions occur not only at the base of young secondary fronds, but also periodically throughout frond growth along the margin of young fronds. Periodic prolongation of the relatively high growth rates typical of the recumbent zone and endozone is indicative of a colony-wide increase in growth rate. That a high growth rate was prolonged beyond its normal duration is also supported by the atypical lack of cystiphragms within the recumbent zones of the autozooecia in these regions. In other words, growth rate appears to have been high enough in these instances to have produced a relatively long recumbent region and some degree of endozonal growth before the first period of cystiphragm emplacement.

Rapid growth is energetically more expensive than slow or normal growth rates. Thus, if endozonal growth is indicative of high growth rates, the association of 'endozonal' growth with discontinuities in the median lamina suggests that there could have been a limited availability of energy for skeletal formation. High rates of growth along the colony margin may have precluded formation of the median lamina during limited periods of accelerated growth. The median lamina was formed during periods of normal growth. When growth rates increased, presumably energy that would otherwise have been allocated to median lamina formation was diverted to permit somewhat longer periods of 'endozonal' growth. Such an explanation could be considered a special case of generally poor developmental regulation of median lamina formation.

Diagenesis

The compositional differences between skeletal structures and the diagenetic matrix, coupled with the results of Sakagami *et al.* (1984), and readily interpretable astogenetic trends consistent with inferences based on alternative arguments suggest that elemental data could reflect real differences in the physiology of growth. Significant differences between the matrix and skeletal structures and among skeletal structures do not unequivocally demonstrate the absence of diagenetic alteration. However, the primary results of this study are consistent with independent predictions of compositional behaviour which would be expected in the relative absence, limited or differential influence of diagenesis on skeletal material and are consistent with inferences based on alternative evidence. Further studies of this kind are warranted because they could contribute to knowledge about skeletal diagenesis, the physiology of skeletal growth and growth rates in extinct organisms.

CONCLUSIONS

The skeleton of *P. vera* contains Cu, Si, Fe, Mg, Mn, Yb, and Nb, many of which occur in concentrations significantly different from that of the zooecial void matrix. Ca density is inversely related to rates of skeletal growth and crystallite secretion. The density distributions of Ca and other trace elements among crystallite types, skeletal structures, and astogenetic growth zones support inferences concerning relative rates of crystallite secretion and skeletal growth based on alternative lines of evidence in bifoliate *Peronopora*. EDS data indicate differences in the rates of secretion and growth among crystallite types, acanthostyle cores, the median lamina, zooecial wall, and stages of zooecial ontogeny and colonial astogeny. Growth was most rapid within the granular skeleton of the median lamina and 'A-type' acanthostyles (paurostyles). Growth rate decreased from the median lamina through the recumbent zone, endozone, and exozone. Paurostyle cores were deposited more rapidly than endozonal wall but less rapidly than recumbent zone wall and the median lamina. Cu and Mn abundance distributions also support the succession of relative growth rates based on Ca data. Paurostyles contain more Cu than other structures. Mn is also most abundant in the median lamina and declined monotonically with reduced growth rate. Zones of disordered, irregular crystallites and laminar growth alternate in zooecial wall axes and are linked with increased secretion rates and increased episodicity, respectively during the cystiphragm/tabula emplacement cycle.

Results of this study are preliminary but suggest that compositional studies can provide information about relative rates of skeletal growth. The astogenetic growth rate curve derived from EDS data supports the results of growth curves based on an alternative method presented herein; intrazooecial cystiphragm frequency distribution per unit autozooecial wall length. A combination of these methods permits the reconstruction of astogenetic growth rates and their use as taxonomic descriptors. If differential growth rates can be identified on the basis of ultrastructural morphology, the evolution of skeletal wall microstructure and acanthostyle types may be interpreted in terms of heterochronic change.

The median lamina of bifoliate *Peronopora* is composed of one to three structures: 1, an outer laminar layer; 2, a medial granular layer; and 3, granular mesostyles. The mesostyles and medial layer are composed of smaller rhombic crystallites which have not been described in mesothecae of other stenolaemates. The median lamina is structurally continuous with the basal lamina but was not secreted against cuticle and is therefore interior-walled skeleton. Formation of the median lamina and paurostyle cores may be explained by differentiation of inner epithelium for high rates of secretion and growth. Local discontinuities in the median lamina can be explained by an energy budget-growth rate hypothesis.

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A NEW ENCHODONTID FISH GENUS FROM THE UPPER CENOMANIAN OF JERUSALEM, ISRAEL

by MENAHEM RAAB *and* YAEL CHALIFA

ABSTRACT. *Parenchodus longipterygius* n. g. et sp. belonging to the Enchodontidae is described on the basis of eight specimens. These were found in platy limestones of the late Cenomanian Kefar Shaul Formation, in the vicinity of Jerusalem, Israel. The species is characterized by a short, high body, a fenestra-less premaxilla, and by the long and narrow postcleithrum reaching the ventral margin of the belly. Other characteristics are the axial skeleton with thirty vertebrae, of which only seven are abdominal; dorsal and anal fins with long bases; a ventral, well-developed pectoral fin; a naked body, devoid of scales except for two dorsal postoccipital and three lateral scutes at the base of the tail; and with a reduction and fusion of the endoskeletal elements of the caudal fin. The fish was a small, fast swimming predator. The structure of the head, the absence of scales, and the fusion of the caudal fin elements suggest that this genus is related to *Enchodus*.

FINDS of fossil fish in the vicinity of Jerusalem have been recorded since the beginning of the century (Blanckenhorn 1905; Shalem 1925, 1927), however, they have never been studied in detail. The fossil fish come from the Laminated Limestone Member, which constitutes the upper part of the Kefar Shaul Formation and overlies its Lower Argillaceous Member.

The Laminated Limestone Member consists of buff to yellowish-white, red stained, thin-bedded, laminated to platy (up to 15 cm), fine-grained limestone with argillaceous material between the plates (Arkin *et al.* 1965, p. 20; Braun 1970, p. 33). The formation is overlain by the dolomitic, partly calcareous Weradim Formation, and overlies the dolomitic-calcareous Amminadav Formation. The complex of strata belongs to the Judea Group which is widely extended in Israel.

The distribution of the fish-bearing Laminated Limestone Member around the type locality is very restricted. It extends over less than 10 sq. km, in varying thicknesses up to 15 m, and is confined to the eastern flanks of the Judea anticline, in the western outskirts of Jerusalem.

Another restricted occurrence of fish-bearing strata, of a similar lithology and more or less in a similar stratigraphic position, is exposed near the town Ramallah, some 20 km north of Jerusalem.

The underlying Argillaceous Member is thicker, up to 60 m thick, and though of greater extent than the Laminated Limestone Member, it wedges out in all directions, within a distance of up to a few tens of kilometres.

The overlying Weradim Formation is much more extended than the Kefar Shaul Formation. Its thickness ranges from 25 to 115 m, and where the Kefar Shaul Formation is missing, it directly overlies the Amminadav Formation (Braun 1970). These field relationships may be an indication that the Weradim Formation gradually replaced the Kefar Shaul Formation.

The fish-bearing Laminated Limestone Member is quite poor in fossils of other groups. The fish assemblage comprises several holosteans, and many teleosts, which have not yet been studied. Some pelecypods, echinoids, and especially ammonites, though badly preserved, enable dating the member as of late Cenomanian age (Shalem 1925, 1927; Picard 1938). The fishes are also accompanied by crustacean and terrestrial plant remains (Lewy and Raab 1976).

Thin sections examined microscopically revealed finely laminated micrites, rich in faecal pellets, filamentous algae, and fish teeth and scales. Rare planktonic and benthonic foraminiferids also occur (Hamaoui and Raab, 1965 pp. 34–35).

A low energy, marine environment of restricted, shallow, partly closed basins was suggested (Lewy and Raab 1976, p. 32.5).

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The underlying Argillaceous Limestone Member of the Kefar Shaul Formation is very rich in invertebrate megafossils. Assemblages comprising pelecypods, echinoids, and especially ammonites (e.g. *Turrilites costatus* Passy and *Neolobites vibrayeanus* (d'Orbigny)) assign a late Cenomanian age to the member (Avnimelech and Shoresh 1962; Lewy and Raab 1976).

The overlying Weradim Formation, which partly replaces the Kefar Shaul Formation (see above), is poor in fossils, most probably due to extensive dolomitization. However, in places, especially in quartzolitic lenses, various pelecypods, particularly rudists (known as reef builders) were recorded (Braun 1970, p. 33; Shalem 1927: 'calcari superiori a Radioliti').

METHODS AND TECHNIQUES

The exposed side of the specimens, which were embedded in fine-grained limestone slabs, was mechanically cleaned under a stereoscopic binocular, with the aid of needles and fine brushes. The slabs were then embedded in polyester resin and later soaked in 10% acetic acid to remove the enclosing calcareous matrix of the underside (Rixon 1976).

SYSTEMATIC PALAEONTOLOGY

Suborder ENCHODONTOIDEI Berg, 1940
Family ENCHODONTIDAE Lydekker, 1889

Diagnosis. (Emended, after Goody 1969, p. 71.) Head deepened, especially posteriorly; body may be deepened in thoracic region. Posttemporal fossa unroofed. Lower jaw long and deep behind the constricted symphysis; articular facet visible in lateral view. Opercular convex posteriorly, and deeper than it is broad; preopercular without prominent ventral spine. Pectoral fins larger than pelvic fins and extremely low on body. Pelvic fins abdominal. No posterior extension of the cleithrum. Lateral line scales present or absent, if present they do not overlap; mid-dorsal scutes reduced and not overlapping.

Genus PARENCHODUS n.g.

Diagnosis. A fish with a short, high, and laterally compressed body. The length of the head exceeds one third of the standard length, slightly exceeding also the depth of the head at the occipital region. The maximal depth of the body is half the standard length. The obit is large, its length reaching one third of the length of the head. The premaxilla lacks a fenestra for reception of the end of the large dentary tooth. Postcleithrum well developed, long and narrow, reaching the ventral margin of the belly. Axial skeleton with thirty vertebrae, twenty-three of them caudal. Dorsal fin with a long base, occupying most of the back, reaching the caudal peduncle.

Body naked, except for two unequal, not overlapping scutes on the mid-dorsal, postoccipital region, and three overlapping lateral scutes on each side of the caudal peduncle. The bases of the caudal fin rays deeply embrace the hypural plates.

Etymology. Para (Greek), near—resemblance to *Enchodus.*

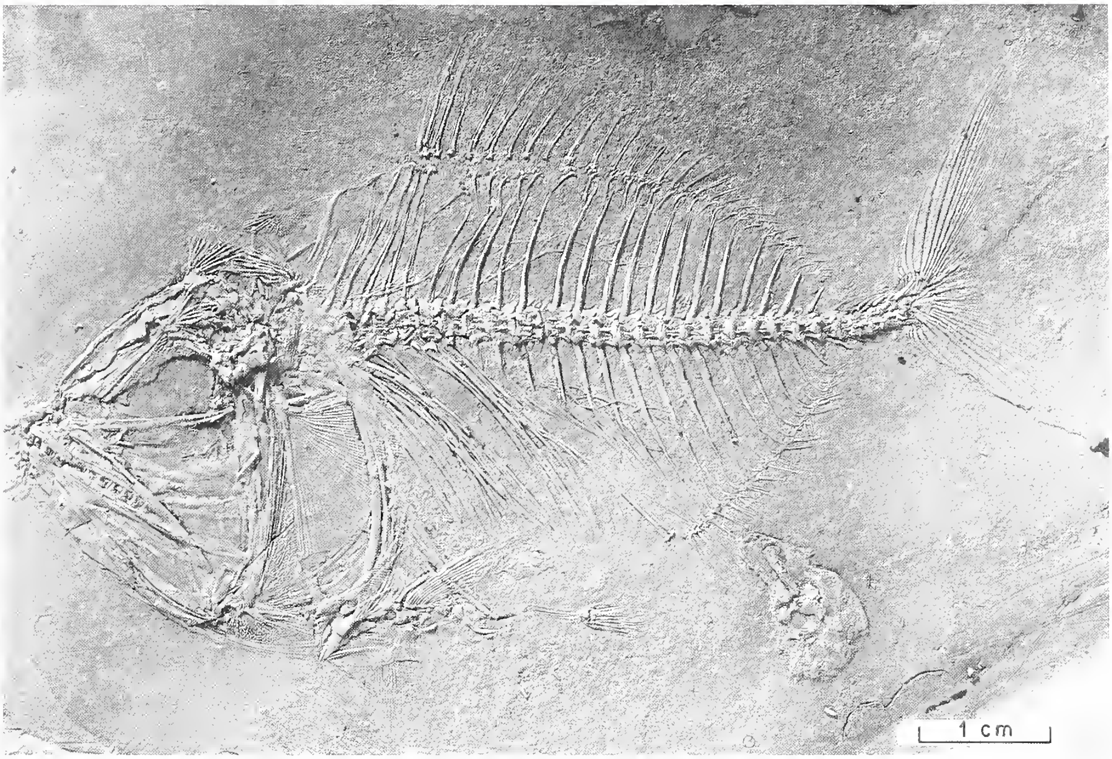
Type species. Parenchodus longipterygius n. sp.

Parenchodus longipterygius n. sp.

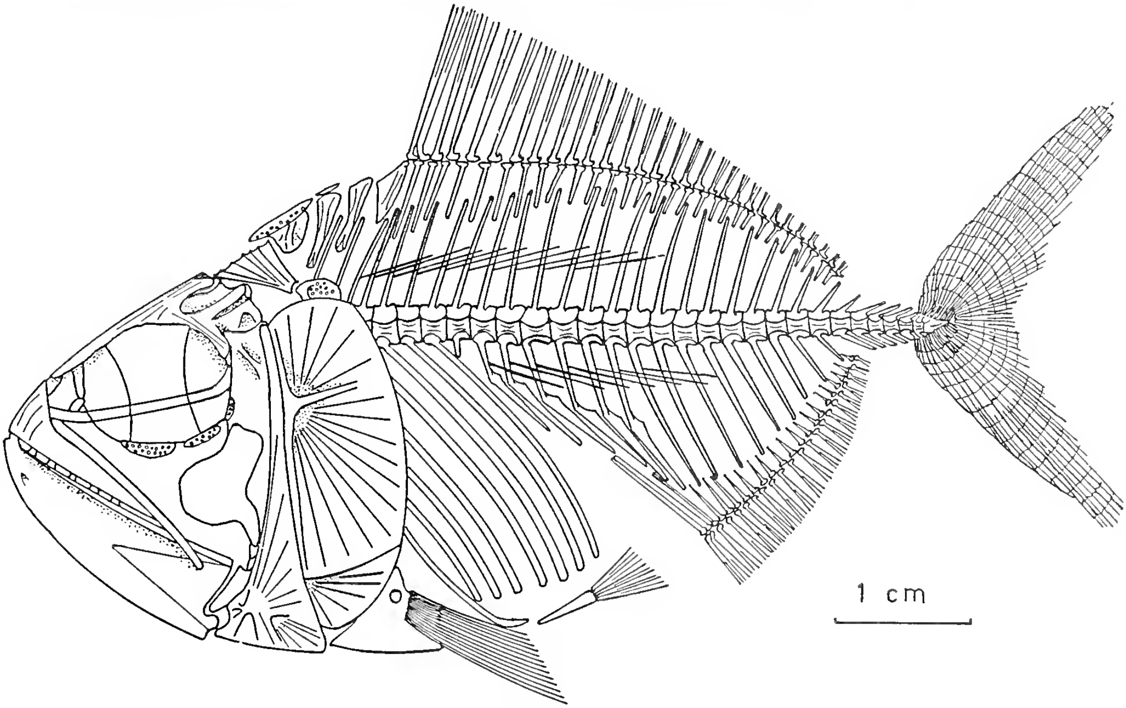
Diagnosis. Parenchodus of up to 75 mm standard length, with fin rays counting as follows: dorsal fin, 30; pectoral fin, 14; pelvic fin, 5; and anal fin, 22.

Holotype. P.163, The Hebrew University of Jerusalem. An almost complete fish embedded in resin (text-figs. 1 and 2).

Referred material. Seven specimens: P.143, P.150, P.1502, P.1503 (text-fig. 3), P. 1504, P.1508 (text-fig. 7), HUJ. DY-15, deposited in The Hebrew University of Jerusalem.



TEXT-FIG. 1. *Parenchodus longipterygius* n. g. et sp. Holotype, P.163, Upper Cenomanian, Kefar Shaul Formation, Jerusalem, Israel. An almost complete specimen. Left side.



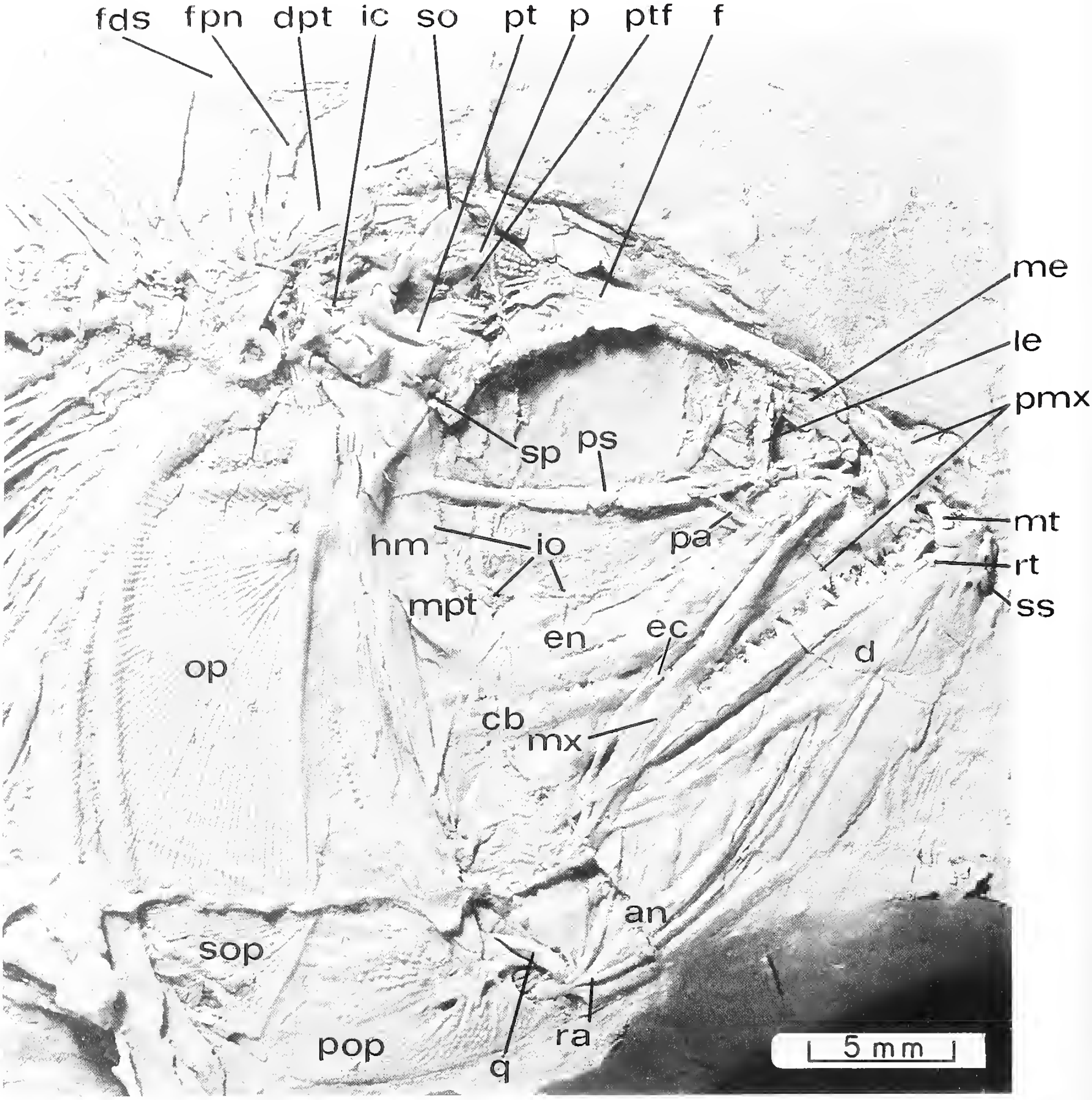
TEXT-FIG. 2. *Parenchodus longipterygius* n. g. et sp. Restoration of the skeleton, lateral view.

Locality and horizon. Givat-Shaul, a western suburb of Jerusalem. The Upper Cenomanian, laminated limestone Member of the Kefar-Shaul Formation.

Etymology. Longipterygius—having a long fin.

DESCRIPTION

General features. The body is short, deep, and laterally compressed. Its maximal standard length is 75 mm, slightly more than twice its maximum depth. The head is short and deep; its length slightly



TEXT-FIG. 3. *Parenchodus longipterygius* n. g. et sp. P.1503, Upper Cenomanian, Kefar Shaul Formation, Jerusalem, Israel. Lateral view of the skull.

TABLE 1. Dimensions (in mm) and ratios of six specimens of *Parenchodus longipterygius* n. g. et sp.

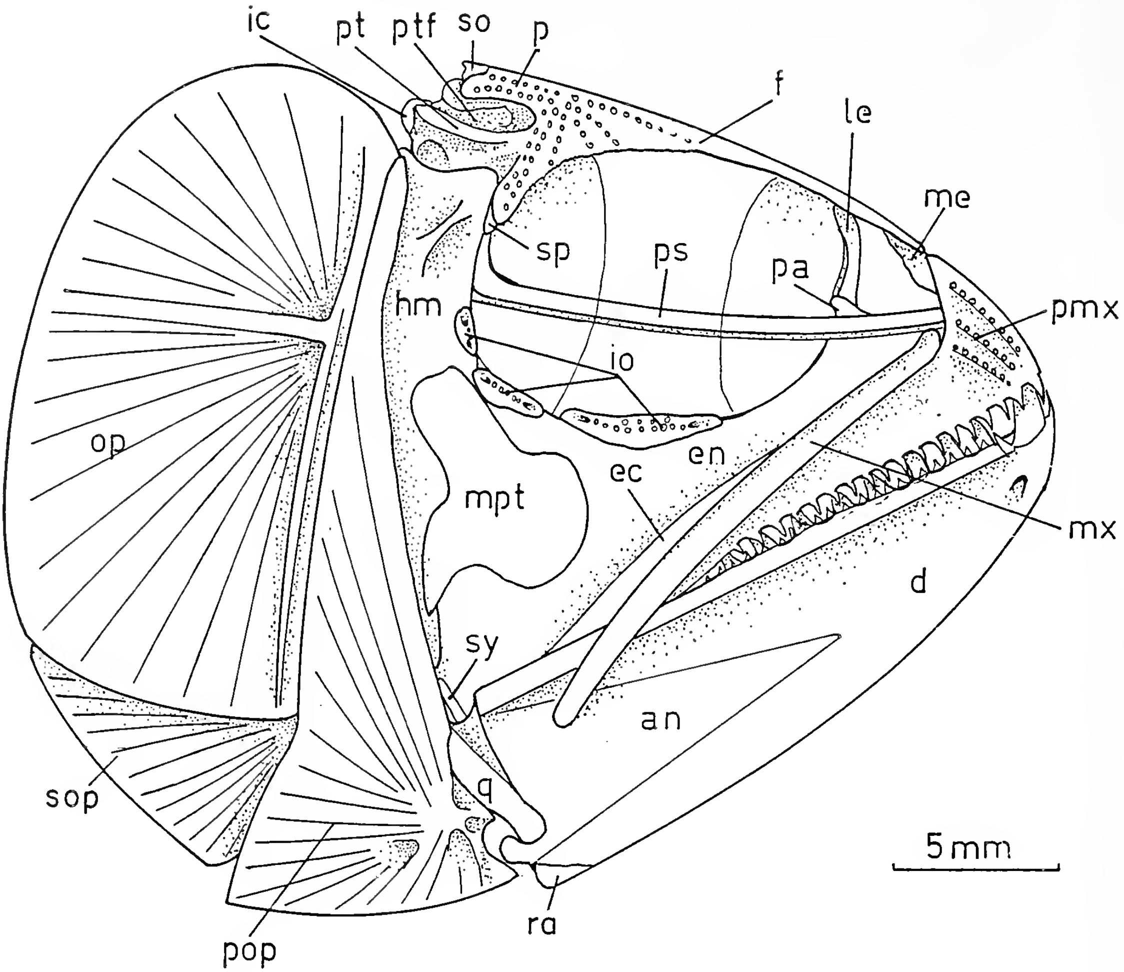
Specimen	P.1502	P.163	P.143	HUJ. DY-15	P.1503	P.1504	Mean
Standard length	61	67	69	74·5			
Maximum depth of trunk	23	35	34	31	34		
Depth of trunk as percentage of standard length	37	52	49	41			44
Length of head	23·5	29	31	29	31	28	
Length of head as percentage of standard length	38	43	44	38			40·75
Depth of head	23	25	28·5	25	27·5	24·5	
Depth of head as percentage of head length	97	86	91	86	88	87	89
Length of orbit		8	8	11·5	9·5	9	
Length of orbit as percentage of the head length		28	26	40	31	32	31·4

exceeds its maximal depth at the occipital region, and is more than one third of the standard length. The oral gape is wide, the length of the lower jaw is about three times its maximum depth. The orbit is large, occupying half the length of the neurocranium. The dimensions of 6 specimens are given in Table 1. The post- and preorbital regions are narrow. Three infraorbitals exist. The postcleithrum is narrow and long, reaching the ventral margin of the belly. There are 30 vertebrae of which 23 are caudal. The dorsal fin is long and consists of 30 fin rays. The pectoral fin is in a ventral position and consists of 14 fin rays. The pelvic fin is smaller than the pectoral fin, in abdominal position, and consists of 5 fin rays. The anal fin has a long base and consists of 22 fin rays. The caudal fin is deep, deeply forked with a very narrow peduncle, carrying flat neural and haemal spines, strongly inclined backwards. The anterior haemal spines have a wide and shallow proximal part. Three supraneurals exist. Dentition well developed. The palatine carries one large, striated conical tooth. The ectopterygoid bears large teeth. The dentary has 2 rows of conical teeth. The typical anterior mandibular tooth is exceptionally large—about a quarter of the total length of the entire lower jaw and longer than the palatine tooth. The maxilla is toothless. One row of narrower and high conical gill-rakers exists on the floor of the anterior part of the gill chamber.

The body is naked, except for two large, not overlapping, unequal scutes, at the mid-predorsal. Three lateral scutes exist at the base of the caudal fin; they are large, overlapping and have crenulated margins.

Neurocranium and the skull roof (text-figs. 3 and 4). The skull roof is flat, anteriorly narrow becoming wider posteriorly, widest above the posterior part of the orbit. Its posterior margin is notched by a wide, unroofed posttemporal fossa. The neurocranium is deep and wide posteriorly, becoming narrower anteriorly. The orbit is large, occupying more than half the length of the neurocranium. The posterior margin of the skull roof extends backwards laterally.

The frontals form most of the skull roof, meeting along the median line in a sinuous suture. At the posterodorsal corner of the orbit, the frontal widens abruptly laterally, forming a wing-like process, inclined ventrally in front of the sphenotic. This process builds the front wall of the posttemporal fossa (text-figs. 3 and 4). The frontals reach the premaxillae anteriorly. Their surface is ornamented by prominent ridges, radiating from the centre of ossification, which is situated above the posterior part of the orbit. The ridges in front of and behind the centre of ossification are tuberculated, whereas laterally they are replaced by closely spaced tubercles. The lateral margins of the frontals are crenulated. A branching point of the supraorbital sensory canal occurs in front and close to the centre of ossification of the frontals. One branch is directed anteriorly along the bone; a second runs



TEXT-FIG. 4. *Parenchodus longipterygius* n. g. et sp. Restoration of the skull. Lateral view.

posterolaterally along the lateral expansion to the pterotic, and a third turns backward, mesial to the posttemporal fossa, passing to the parietal.

The parietals are small and narrow, in close contact with the posterior margin of the frontals. They are located mesial to the posttemporal fossae. The dorsal surface of the bone is tuberculated.

The supraoccipital is small, median, separating the parietals. A low crest extends along the median line of the supraoccipital from the anterior to the posterior end, without protruding posteriorly. The surface of the bone is smooth.

The sphenotic is situated at the posterodorsal corner of the orbit, posteroventral to the wing-like lateral process of the frontal. The lateral surface of the sphenotic is triangular and slightly tuberculated. The exposed part of the pterotic is very thick, forming the posterior continuation of the lateral process of the frontal. A ridge runs along the middle of the bone, bordering the posterolateral side of the posttemporal fossa. The dilatator fossa lies lateral to the ridge.

The parasphenoid is beam-like in lateral view, with a low ventral carina along it. Beyond the orbit the carina expands ventrally and the beam dorsally to meet the prootic. The parasphenoid terminates anteriorly in front of the anterior end of the maxilla.

The features of the prootic, including the arrangement of its foramina, generally fits the enchodontid prootic, as described by Goody (1969, p. 85, fig. 38B).

The mesethmoid is well developed and ossified. Its dorsal side is covered posteriorly by the frontal and anteriorly by the premaxilla.

The lateral ethmoid is a beam-like bone. Its ventral face is grooved to accommodate the dorsal process of the palatine.

The circumorbital bones are represented by only three thin infraorbital plates, which housed the infraorbital sensory canal. They extend from the centre of the posterior margin of the orbit to the centre of its ventral margin, without touching each other. The anterior one is the longest and the posterior one is the shortest.

The intercalar is the only bone that could be identified in the posterior wall of the neurocranium, as a well-developed thickening below the pterotic.

An incomplete interorbital septum forms two wings, penetrating into the anterior and posterior regions of the orbit, but not meeting.

Hyopalatine bones (text-figs. 3 and 4). The hyomandibular is narrow and long, forwardly inclined. The upper half of the bone is flat, carrying a prominent arched ridge, running obliquely from anterodorsal to posteroventral. It is wide, plate-like, with a thick, wedge-like lower part.

The symplectic is small and wedge-like with about half its length inserted in the groove of the quadrate.

The quadrate is a narrow, high triangle. The ventral apex of the triangle is rounded, slightly arched posteriorly. The bone is relatively thick and its surface is striated, except for its anterior and dorsal margins, which are thin and smooth. A deep groove exists in the upper part of the inner side of the bone, for the symplectic.

When the mouth was closed the lower jaw covered the anterior margin of the quadrate and only its thickened part remained exposed in lateral view.

The endopterygoid is thin and large, forming most of the infraorbital region. It carries tubercle-like teeth. Its posterodorsal part is covered by the metapterygoid.

The dorsal margins of the ectopterygoid are exposed dorsal to the maxilla. The ectopterygoid continues forward, covered by the maxilla and the premaxilla. It is long and flat, and bears along its entire margin a row of high conical teeth (similar to the premaxillary teeth).

The metapterygoid is thin with rounded margins, except for the posterior ones which extend into two lobes, a dorsal one, prominently ridged and a ventral one, thin and flat. Both lobes overlap the hyomandibular, below its mid-length.

The palatine is thick and short and bears posteriorly a dorsal process which fits a groove in the ventral side of the lateral ethmoid. In lateral view the palatine is recognized as a thickening behind the premaxilla. It bears at its anterior end a very large, somewhat compressed, striated tooth.

Upper jaw. The premaxilla is triangular, with a posteriorly extended base. The frontal area of the premaxilla is tuberculated and its lateral area is smooth. The premaxilla forms more than three-quarters of the margin of the upper jaw and bears thin, high conical teeth, similar in size to the smaller teeth of the lower jaw (see below p. 724). The foremost tooth is the largest, the others becoming gradually smaller backwards. The fenestra in the premaxilla, so typical of enchodontids (Goody 1969, p. 71) was not observed.

The maxilla is long, rod-like, thick anteriorly, wide and flat posteriorly, toothless. Its anterior part is situated along the dorsal margin of the premaxilla, crossing the gape at an angle of about 45°. The anterior end of the maxilla is slightly bent ventrally, and is situated below the premaxilla, probably in a groove in its inner side. The surface of the maxilla is smooth.

Lower jaw. The lower jaw is relatively high, especially in its posterior part; its maximum height is about one third of its total length (text-fig. 3).

The angulo-articular is well developed, triangular, with ventral margin extending forward almost to the mid-length of the jaw. It is ornamented by strong tuberculated ridges, radiating sparsely from a centre near the articulation of the jaw. It bears a postarticular process, which fits in a notch at the ventroanterior end of the preopercular. The retroarticular is reduced to a small bone situated in the posteroventral corner of the lower jaw.

The dentary is smooth, except for a fine radial striation originating from a centre near the symphysis. The dorsal margin of the dentary thickens into a wide flange, reaching the symphyseal region, and bearing two rows of teeth. The external row contains numerous, closely spaced, high, conical, smooth, sharp teeth, which are somewhat irregular in size, though the anterior ones are larger. A second, internal row, consists of seven to eight high, thick, slightly laterally compressed and striated teeth. The size of these teeth is almost twice that of those of the outer row. The foremost tooth of the inner row is the largest. This large tooth (text-figs. 3 and 5A)—so typical for the genus *Enchodus*—protrudes just beyond the symphysis. It is very high, its height slightly exceeding a quarter of the length of the jaw. Its base is wide and its surface smooth. It is situated on the margin of the jaw, with a slight forward inclination. The tooth has an asymmetric cross-section, with a convex posterior face, and a flat to concave anterior face. It has two cutting edges, one anterolateral and the other posteromedial. A smaller tooth could be observed laterally and behind the foremost fang in specimen P.163. A smaller tooth (relatively to the fang) and in a similar position and direction is illustrated by Woodward (1903, pl. 14, fig. 7). Such teeth, so close to the fangs, do not seem functional and hence might be regarded as replacement teeth. The symphyseal region is relatively high, and its dorsal margin lipless. The symphysis is built of three interlocking finger-like processes on each dentary. A conspicuous foramen of the mandibular sensory canal is situated just behind the symphysis.

Branchial arches and branchiostegal rays. The ceratohyal and the hypohyal (seen on the right side of specimen P.143) constitute one beam-like element, extending backwards from the middle of the lower jaw to the posterior end of the preopercular.

The beam bears eleven posteriorly arched branchiostegal rays. These are long, thin, and have a thickened base. A pair of high and thin beam-like first ceratobranchials (text-fig. 3) carry high, slender, slightly anteriorly inclined gill-rakers.

Operculum. The opercular bones form together a narrow cover, twice as high as its maximum width.

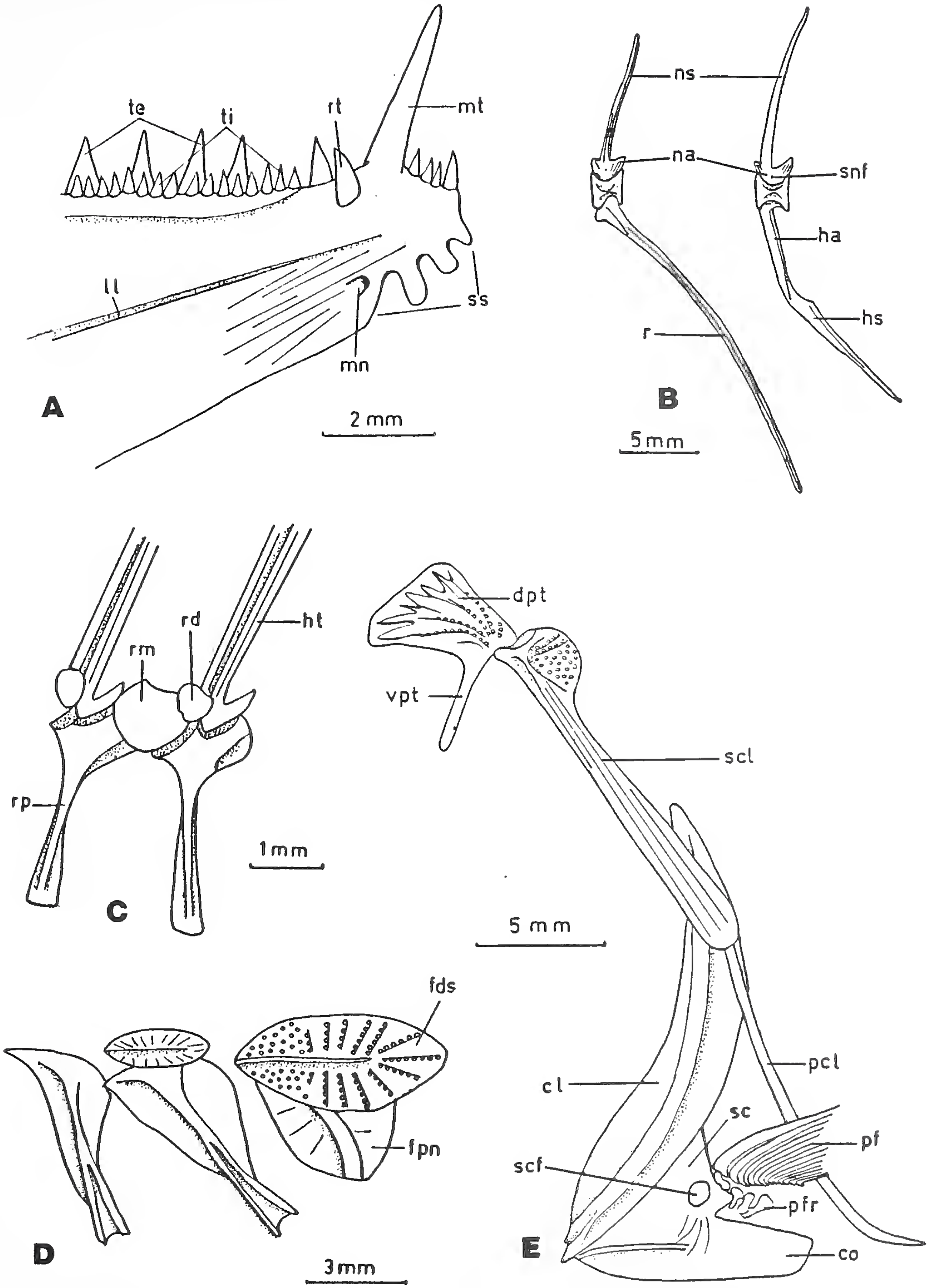
The opercular is narrow and high. Its dorsal, posterior, and ventral margins form a continuous arched line. The anterior margins are almost straight, perpendicular to the body axis. Its articular condyle with the hyomandibular is located at about two-thirds of its height. An inner, supporting beam extends from the condyle backwards, and another along the anterior margins, just beyond the area covered by the preopercular. The surface of the opercular is covered by finely tuberculated prominent ridges, radiating from the centre of ossification, which is situated near the condyle.

The triangular subopercular is slightly overlapping the ventral margins of the opercular. It is ornamented by finely tuberculated ridges, radiating from the anterodorsal corner.

The preopercular is thick, high-triangular, with a posteriorly and anteriorly extended ventral base. In its anteroventral corner there is a socket for the postarticular process of the lower jaw. Tuberculated ridges radiate from a centre beyond the articulation socket, changing dorsally, and especially along the anterior margin, into fine striae. The preopercular sensory canal ran along the preopercular, opening through three large pores in the anteroventral area of the bone. From the anteriormost opening, which is directed forward, the lateral line canal continued to the mandible. Interopercular bone absent.

Axial skeleton. The vertebral column numbers 30 vertebrae, of which only 7 are abdominal and 23 caudal. Eadh centrum is almost quadrangular and strongly constricted in the middle. A finely striated ridge runs along the lateral side of each centrum. The centra are approximately equal in length along most of the body, however an abrupt shortening occurs at the caudal peduncle. A high neural arch extends all along each centrum, not fused with it (text-fig. 5B). The neural arch comprises a narrow prezygapophysis, and a high and wide postzygapophysis, both with a delicately striated surface. The centre of the lateral side of each neural arch is pierced by the foramen for the spinal nerve.

In the abdominal region the neural spines are paired. They originate at the anterior part of the



TEXT-FIG. 5. *Parenchodus longipterygius* n. g. et sp. Restoration of: A, anterior part of right lower jaw. B, abdominal vertebra no. 7 (*left*) and precaudal vertebra no. 7 (*right*). C, pterygiophores and dorsal fin rays. D, supraneurals and dorsal scutes. E, left pectoral girdle in lateral view.

neural arches. Each spine is high, acute, striated along its entire length and is slightly inclined backwards. The highest neural spines occur at about the middle of the dorsal fin, from where they start to shorten gradually, becoming more inclined backwards. Near the base of the caudal fin the spines become short, stout, and much more inclined.

The pleural ribs are very long and longitudinally furrowed. They are inclined backwards and arched forwards. They are carried by enlarged parapophyses, not fused to the centrum. Epineurals occur up to the centre of the dorsal fin. Epipleurals occur along the anterior half of the caudal region (text-figs. 1 and 3).

The haemal arches are relatively long, at least in the anterior part of the caudal region. The first caudal centrum bears only a haemapophysis. The haemal spines increase gradually in length, reaching a maximum in caudal vertebra 7, where the distal end of the haemal spine reaches the base of the anal fin. Hereafter backwards, the spines become shorter. Each of the first six haemal spines is flat and wide at its base, becoming sharp distally.

The caudal peduncle is short. The neural and haemal spines are flat, expanded, and sharp at their distal ends. They are strongly inclined backwards and fit tightly to each other. Three large oval scutes, with indented margins, are situated along the four terminal vertebrae, each overlapping the following scute, and together forming a lateral keel-like structure (text-fig. 7).

Three supraneurals are situated in front of the dorsal fin (text-fig. 5D). The first one is oval, with a wide supporting ridge along it. It supports the first dorsal scute from below. The second is high-triangular. It bears a longitudinal supporting ridge, expanding backwards and forwards at the distal end, and split at its proximal end, at about half its length. This element supports the second dorsal scute. The third supraneural is similar in form to the second, but does not support any scute.

Pectoral fin and girdle. The pectoral fin is ventral, carrying 14 unsegmented, distally branched fin rays. Its length is about that of 6·5 successive vertebrae, and almost twice the length of the pelvic fin. Complete pectoral girdles, including their dermal and endoskeletal elements, can be observed in specimens P.143 and P.163.

The cleithrum is flat and smooth supported all along its midline by a heavy, striated ridge. It is arched forward and terminates somewhat ventral to the posteroventral end of the preopercular. The bone becomes narrower towards its extremities.

The supracleithrum is thick and flat, rod-shaped, ornamented by longitudinal, closely spaced grooves. It touches the outer dorsal surface of the cleithrum, and is directed obliquely from posteroventral to anterodorsal. Its dorsal end is expanded posteriorly. The expansion is flat, rounded, and closely covered by tubercules. It is traversed by the lateral line canal on its way from the body to the head (text-fig. 5E).

The postcleithrum is exceptionally developed. It is thick, long, rod-like slightly arching in the posteroventral direction. The bone is longitudinally striated. Its proximal end is in contact with the posterior inner region of the supracleithrum. Ventrally it terminates at the horizontal level of the posteroventral corner of the mandible. The distal end is sharply bent posteriorly, almost reaching the anterior end of the pelvic girdle. The pair of postcleithra look like very large ribs, and most probably served as a support to the body wall of the very deep belly.

The dorsal arm of the posttemporal is well developed, wide, and triangular. The posterior corner of the triangle articulates with the supracleithrum. The apex of the triangle reaches the dorsal mid-line. The outer surface of the posttemporal is ornamented by prominent tuberculated ridges, scattered over the bone in a fan-like fashion, centred at the posterior corner of the triangle. The ventral arm of the posttemporal has the shape of a flattened rod with an enlarged base and is densely striated. It starts in front of the articulation point of the posttemporal with the supracleithrum. The lateral line canal traversed the posttemporal on its way from the supracleithrum to the head. The pores of the canal are distinct near to the articulation area.

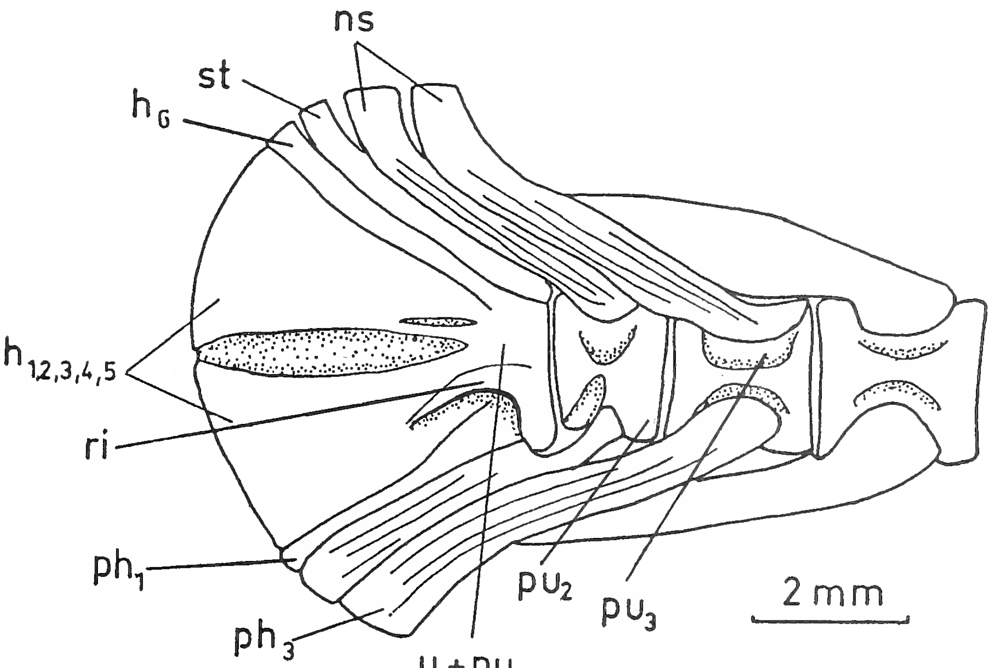
The coracoid is a large thin trapezoidal plate, with a horizontal base extending slightly backwards. Its anterior margins are firmly jointed to the posteroventral margins of the cleithrum. A prominent ridge extends from the centre of the coracoid to its anterior corner. The coracoid thickens near its contact with the scapula.

The scapula is small and thick relative to the coracoid, and has a large and distinct scapular foramen. Four radials can clearly be counted in the pectoral girdle (specimen P.163).

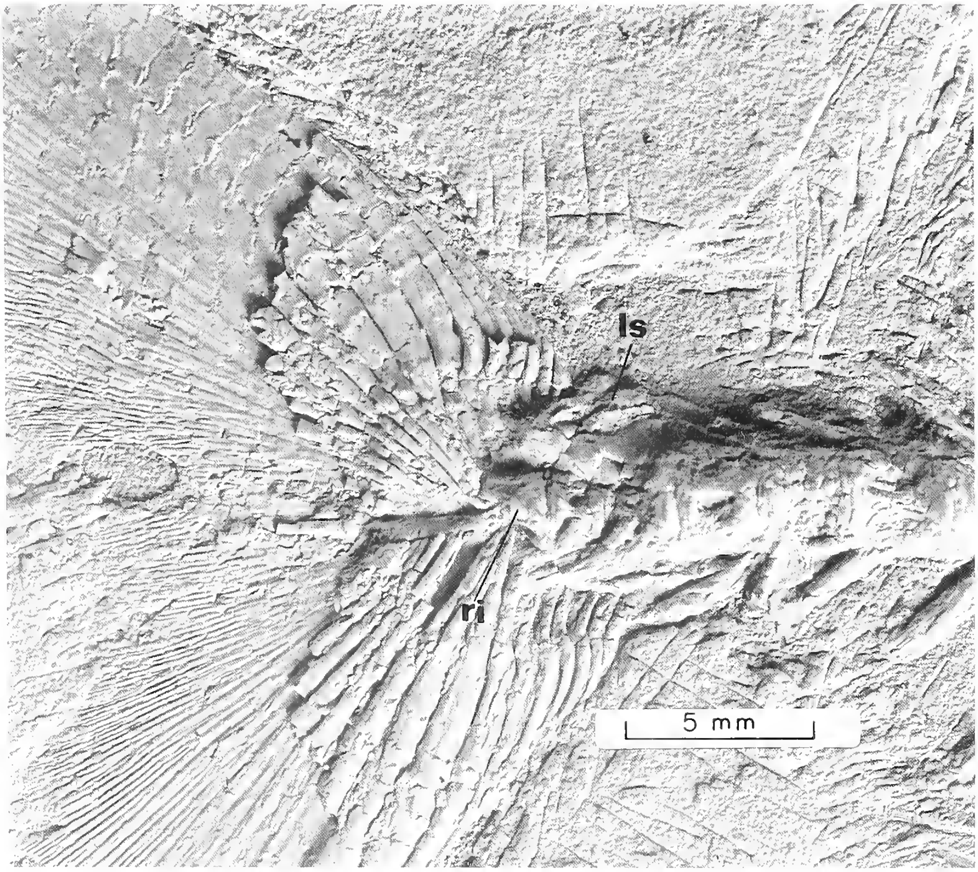
Pelvic fin and girdle. The pelvic fin is abdominal. It originates at the level of the sixth caudal vertebra. It consists of five to six unsegmented fin rays. These are longitudinally grooved and distally branched. The pelvic fin is half the length of the pectoral fin. The pelvic girdle is flat and thin, wedge-like, with a few longitudinal thickenings. Four radials exist.

Dorsal fin. The dorsal fin has a long base, and occupies most of the back. It is as long as nineteen successive vertebrae, and contains thirty fin rays. Its anterior part is high, shortening gradually posteriorly. Each lepidotrich is longitudinally grooved whereas the last two are completely bifurcated. The fin rays are unsegmented. The first pterygiophore is very expanded and forwardly inclined. The proximal segments of the pterygiophores are flat, truncated ventrally, with a longitudinal ridge. Their distal end is expanded in a nail-head form, with two articulation facets. The middle radial is wide and thick. The distal radial is also preserved as a small rounded element, embraced between the bases of the hemitrichia. The fin ray is attached anteriorly by its base to the distal radial of the preceding pterygiophore, and by its ventral side to the proximal radial of the underlying pterygiophore (text-fig. 5C). The head of each proximal radial is anteriorly in close contact with the middle element of the preceding pterygiophore, dorsal to the base of the fin ray and posterior to its middle radial. The middle and distal radials form together a continuous flexible support for the dorsal fin.

Anal fin. The anal fin extends along about eleven vertebrae on the posterior half of the venter. It starts opposite the mid-length of the dorsal fin and contains twenty-two blunt, longitudinally grooved, unsegmented fin rays. The lepidotrichia of the last several rays are split from their bases. The anterior



TEXT-FIG. 6. *Parenchodus longipterygius* n. g. et sp. Restoration of the endoskeleton of the caudal fin.



TEXT-FIG. 7. *Parenchodus longipterygius* n. g. et sp. P.1508, Upper Cenomanian, Kefar Shaul Formation, Jerusalem, Israel. Lateral view of the tail.

part of the anal fin is relatively high (as high as the length of four vertebrae), becoming lower posteriorly. The proximal elements of the pterygiophores have one or two longitudinal grooves and are truncated at their proximal end. The two anterior elements are thick and long, the following ones become gradually shorter. The distal elements of the pterygiophores are small, thin, with an undefined shape.

Caudal fin (text-figs. 6 and 7). The caudal fin is large, deeply forked. The dorsal lobe is somewhat longer than the ventral one. The dorsal and the ventral lobes contain ten and nine principal fin rays, respectively. These are segmented and branched distally. Nine segmented, undivided accessory fin rays precede the principal fin rays of each lobe.

The proximal ends of the principal fin rays, except for the two middle ones, are narrow and sharp. They embrace the hypural plate in such a way that their proximal ends almost meet. The two middle rays have a truncated, thickened base, only touching the posterior edge of the hypural plate, not embracing it.

The endoskeleton of the caudal fin consists of four vertebrae, namely, two separate preurals (pu_2, pu_3) and a ural vertebra fused to the first preural, to form a single triangular centrum. The hypurals are fused into one wide plate, which is divided by a relatively wide longitudinal furrow—the continuation of the vertebral axis—into a ventral and a dorsal part. An additional long and narrow hypural occurs in close contact dorsally to the hypural plate. The terminal centrum ($u_1 + pu_1$) bears a high, narrow stegural. The neural and the haemal spines of pu_2 and pu_3 are thick, wide, their distal ends are truncated, and they are not fused to their centra. The surface of these elements is finely striated. The truncated distal margins of the haemal spines, the parhypurals, the hypurals, the stegural, and the neural spines of pu_2 and pu_3, form a continuous arched line constituting the posterior margin of a wide plate supporting the fin rays. A distinct semilunar ridge, arching ventrally, occurs on the ventrolateral area of the terminal centrum (text-fig. 7). Its ventral position as well as its direction hinders its identification as the uroneural of ural 1. It is probably only a thickening of the centrum of the vertebra, intended to enlarge the adhesion surface of the caudal fin muscles. A functionally similar element was recorded by Nursall (1963, p. 459). However, the two elements are not homologous, since Nursall's hypurapophysis is a lateral process of the anterior hypural whereas the element described here is a part of the terminal centrum. Summarizing the main features of the caudal skeleton, it is characterized by (1) fusion of the hypurals, (2) epaxial and hypaxial elements not fused to the centra—a primitive feature, (3) reduction in elements—epurals and uroneurals missing and, (4) the loss of ural 2.

Scales. The body is naked, without scales except for two dorsal scutes and a row of three lateral scutes at the base of the tail. The dorsal scutes are large, oval, not overlapping. They are situated along the dorsal mid-line, from the occiput to near the anterior end of the dorsal fin. The first scute is more than twice as large as the second. The scutes are supported by the two first supraneurals (text-fig. 5D).

The posterior part of each dorsal scute is ornamented by scattered tubercles whereas the anterior part bears tuberculated ridges, radiating from the centre of the scute. An inner supporting ridge runs along the posterior half of the scute.

Three relatively large scutes occur laterally along the four terminal vertebrae. They are thin, with indented margins, successively overlapping each other, to form a lateral keel-like structure (text-fig. 7).

DISCUSSION

The basic features of *Parenchodus* agree well with those used by Goody (1969) in defining the family Enchodontidae: Head and body high; posttemporal fossa unroofed; lower jaw long and posteriorly high; articular facet exposed laterally; opercular high, with convex posterior margins; preopercular without a ventral spine; pectoral fin ventral, larger than the pelvic fin; pelvic fin abdominal; existence of a few, non-overlapping dorsal scutes. Only one feature, namely the total reduction of the lateral line scales in *Parenchodus*, disagrees with Goody's diagnosis of the family. It seems that this feature is not enough for the erection of a separate family.

The tendency towards a short and deep body, indicated as one of the features defining the genus *Enchodus* (Goody 1976), and characterizing especially the old world species of *Enchodus*, is exhibited in extreme form in *Parenchodus*.

This tendency correlates well with other structural features, so typical of short and deep fish, namely: (1) reduction in number of vertebrae; (2) reduction in number of abdominal vertebrae (in *Parenchodus*, the abdominal vertebrae constitute only 25% of the total number of vertebrae); (3) shortening of the post- and preorbital regions; (4) enlargement of supraneurals, serving as a support to the high epaxial, post-cranial region; (5) long, rib-like postcleithra, supporting the belly; (6) long-based dorsal and anal fins, and a well-developed pectoral fin, providing manoeuvering ability. All of these features can be observed in other deep-body fishes such as *Pharmacichthys* and *Aipichthys* from the Cenomanian of Lebanon (Gayet 1980) or *Exellia* and *Ceratoichthys* from the Middle Eocene of Monte Bolca, Italy (Blot 1969).

Such a body-shape could be the result of a different habitat and mode of life of *Parenchodus* compared to the other genera of the family. *Enchodus* and *Palaeolycus* were active, mid-water, or pelagic predators (Goody 1969, 1976), whereas *Parenchodus* was a predator which probably lived among and in vertical reefal elements. Although the body of *Parenchodus* is not streamlined, the structure of the caudal fin indicates a good swimming ability. These features are as follows: (1) a well-developed and deeply forked caudal fin; (2) a stout peduncle; (3) a reduction in the elements of the caudal skeleton as manifested by the fusion of the hypurals, and the lack of uroneurals and epurals; (4) a large contact area between the bases of the caudal fin rays and the hypurals; (5) a lateral expansion of the centre of the fused terminal vertebrae ($u_1 + pu_1$) enlarging the adhering area of the caudal fin muscles; (6) the lateral keel-like structure formed by the overlapping lateral scutes at the base of the tail (typical of fast-swimming fishes, Hildebrand 1976).

Parenchodus exhibits extremely the tendency of the family Enchodontidae towards a short body. This feature existed, though to a lesser degree, in the Old World *Enchodus*-species.

The short and high body of *Parenchodus* seems to be an adaptation to the special ecological conditions which prevailed in the sea in the area of Givat Shaul during the late Cenomanian.

Since no evidence for a reefal facies is exhibited in the Kefar Shaul Formation, the existence of such an environment should be looked for in the partly contemporaneous, rudist-containing Weradim Formation.

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ABBREVIATIONS USED IN TEXT-FIGURES

an	angular
cb	ceratobranchial
cl	cleithrum
co	coracoid
d	dentary
dpt	dorsal limb of the posttemporal
ec	ectopterygoid
en	endopterygoid
fds	first dorsal scute
fpn	first postneural
f	frontal
h_{1-6}	hypurals 1–6
ha	haemal arch
hm	hyomandibular
hs	haemal spine
ht	hemitrichium
ic	intercalar
io	infraorbital
le	lateral ethmoid
ll	lateral line canal
ls	lateral scute
me	mesethmoid
mn	foramen of the mandibular branch of the lateral line
mpt	metapterygoid
mt	largest mandibular tooth
mx	maxilla
na	neural arch
ns	neural spine
op	opercular
p	parietal
pa	palatine
pcl	postcleithrum
pf	pectoral fin
pfr	pectoral fin radial
ph	parhypural
pmx	premaxilla
pop	preopercular
ps	parasphenoid
pt	pterotic
ptf	posttemporal fossa
pu	preural
q	quadrate
r	pleural rib
ra	retroarticular
rd	distal radial
ri	ridge on the centrum u_1+pu_1
rm	median radial
rp	proximal radial
rt	replacement tooth
sc	scapula
scf	scapular foramen
scl	supracleithrum
snf	spinal nerve foramen
so	supraoccipital
sop	subopercular
sp	sphenotic
ss	symphyseal suture of the mandibular
st	stegural
sy	symplectic
te	external teeth row
ti	internal teeth row
u	ural
vpt	ventral limb of the posttemporal

BIOGEOGRAPHY AND EVOLUTION OF AFRICAN FRESHWATER MOLLUSCS: IMPLICATIONS OF A MIOCENE ASSEMBLAGE FROM RUSINGA ISLAND, KENYA

by P. W. KAT

ABSTRACT. A freshwater mollusc fauna from the Early Miocene Gumba beds of Rusinga Island, Kenya, is re-examined. The fauna consists largely of mutelid bivalves, and two new species of the genus *Pleiodon*, *P. lanceolatum* and *P. rusingae*, are described. The Gumba fauna is compared with those of the contemporary Mohari Formation of the Edward-Albert Rift and the early Miocene Turkana Grits in northwestern Kenya. None of the early Miocene freshwater faunas thus far described contains representatives of the presently widespread and diverse bivalve family Unionidae and gastropod family Viviparidae. Ancestors of the recent African viviparids and some of the unionids are proposed to have been introduced when Africa and Eurasia were joined by closure of the Tethys Sea. The Miocene faunas are also uninformative as to the origins of the distinctive endemic mollusc fauna of Lake Tanganyika. Collectively, however, these faunas provide valuable insight into African freshwater molluscan species diversity during the Miocene, and relationships between Miocene and extant taxa.

THE pre-Pleistocene fossil record of African freshwater mollusc faunas remains little investigated despite their potential to provide information on molluscan biogeography, evolution, and origins of endemic assemblages of the older great lakes such as Tanganyika and Malawi (Fuchs 1936; Dartevelle and Schwetz 1948; Gautier 1965, 1970; Lepersonne 1970). Faunas of the Miocene are perhaps best known, and have been collected from three main areas: the Edward-Albert Rift (the Mohari Formation; early Miocene by mammalian faunal inference; see Gautier and Van Damme 1973), near Lake Turkana (the Turkana Grits, age estimated between 17 and 23 my; see King and Chapman 1972; Van Couvering and Van Couvering 1976), and around the Winam Gulf area of Lake Victoria (especially the Gumba Beds on Rusinga Island, age estimated at 19 my; see below) (Verdcourt 1963; Gautier and Van Damme 1973; Van Damme 1984). These Miocene faunas largely predate the establishment of the major African rift systems, and are thought to be contemporary with taxa ancestral to the distinctive endemic mollusc fauna of Lake Tanganyika (Fuchs 1936; Gautier 1967; Beadle 1974; Andrews and Van Couvering 1975). Also, pre-rift drainage patterns are thought to have linked the Zaire (Congo) River with large areas of eastern Africa (e.g. Cooke 1958; Fryer and Iles 1972; Beadle 1974), and taxa of the Mohari mollusc fauna have been proposed to be conspecific with taxa of the Gumba Beds (Gautier 1967; Gautier and Van Damme 1973).

The Miocene and largely Pleistocene freshwater molluscs of the Edward-Albert Rift have been well described (e.g. Adam 1957, 1959; Gautier 1965, 1966, 1970; Lepersonne 1970; Gautier and Van Damme 1973). In contrast, the Rusinga freshwater fossils were only examined by Verdcourt (1963), and proposed similarities between the two faunas were based largely on incomplete or fragmentary specimens. Since Verdcourt's (1963) initial description of this fauna, several other collections have been made and deposited in the Division of Palaeontology of the National Museums of Kenya. These subsequent collections constitute a marked improvement over the poor material available to Verdcourt, and have both clarified relationships between the two faunas and their levels of diversity.

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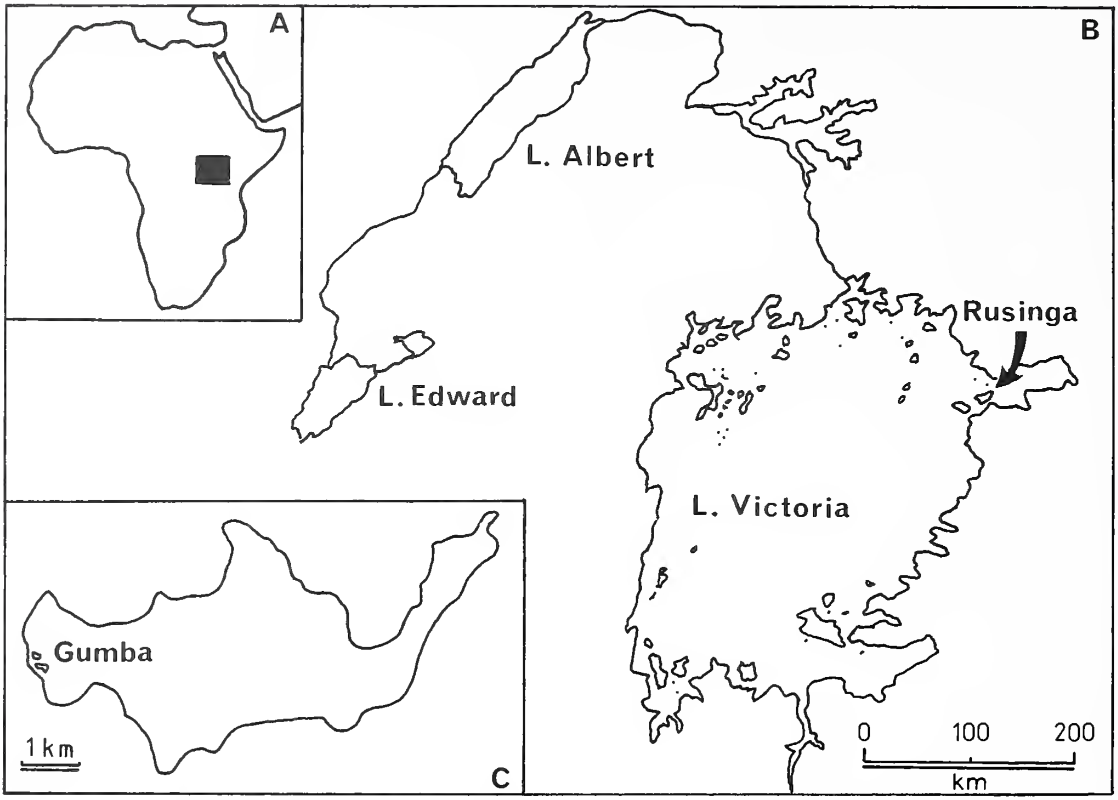


TEXT-FIG. 1. Location of the Gumba Beds on Rusinga Island, Lake Victoria, Kenya.

ENVIRONMENT AND AGE OF THE GUMBA BEDS

The freshwater molluscs examined here occur in the Gumba Beds on the western part of Rusinga Island (text-fig. 1). The fossils occur in lenticles of coarse sand/gravel consisting of very poorly sorted, angular particles indicative of a relatively high-energy depositional environment such as a stream channel. Most of the shells are fragmentary. *In situ* 'reefs' of the freshwater bivalve *Etheria elliptica* occur in the same and underlying deposits, all of which lie between the Rusinga Agglomerate (19·5 my; Basal Agglomerate of Kent 1944) and the Hiwegi Formation (17 to 18·5 my; Tuffaceous Series of Kent 1944), and are contemporary with the 'Unnamed Formation' (19 my; Argillaceous Series of Kent 1944) (dates in Van Couvering and Miller 1969). In addition to the gravels, the beds also contain a variety of other aquatic deposits such as sandstones and deep water greenish siltstones. Kent (1944), Bishop (1963), and Temple (1969) generally agree on the existence of one or a series of lakes in the region formed by volcanic damming of drainages. These Miocene lakes, however, were not ancestral to Lake Victoria, which was formed much later as a result of the development of the African rift systems, uplifting, and the formation of volcanic fields which reversed some of the westward flowing drainages of the region (Bishop 1965; see Kendall 1969 for a general background description of the formation of Lake Victoria).

SYSTEMATIC PALAEONTOLOGY

Superfamily UNIONACEA
Family MUTELIDAE
Genus ETHERIA
Etheria elliptica Lamarck, 1807

Text-fig. 2F

Discussion. This is the most common bivalve species present, occurring in *in situ* 'reefs', and as articulated and fragmentary valves within the gravels. The species is presently widely distributed within Africa, occurring in the Nile, Zaire (Congo), and Niger River basins as well as on Madagascar. It is not known from Lakes Tanganyika and Malawi, but occurs in large numbers in Lake Victoria.

Material. Twenty-two single and three articulated valves.

Genus PLEIODON
Pleiodon moharensis (Gautier, 1965)

Text-fig. 2E

1963 *Iridina* sp., Verdcourt, p. 31, fig. 63*a*, *b*.
1963 *Mutela* sp., Verdcourt, p. 30, fig. 62.
1965 *Iridina* (*Pliodon*) *moharensis* Gautier, pp. 144–146, pl. 6, figs. 5–7; pl. 7, figs. 1, 3, 5.
1965 *Iridina* (*Pliodon*) *subelongata* Gautier, pp. 146–147, pl. 7, figs. 7 and 8; pl. 8, fig. 3.

Discussion. This is the largest *Pleiodon* species present, with an elongate ovate shell. The valves are compressed to subcompressed, and solid in large specimens. The anterior end is regularly rounded, and the posterior end often squared or bluntly rounded. The ventral margin is straight to slightly concave in large specimens; the dorsal margin is generally straight. A broadly rounded posterior ridge is present. The umbos are low and situated in the anterior third of the shell. Shell sculpture consists of concentric striae. The dentition is taxodont and well developed, consisting of straight teeth set at a slight angle to the hinge anterior to the umbo. Anterior adductor and retractor scars are deep, and dorsal retractor scars are set below the umbo. The posterior adductor scar is distinct, and the posterior retractor scar is well separated from that of the adductor. The pallial line is usually distinct.

Material. Sixteen partial valves, one complete valve.

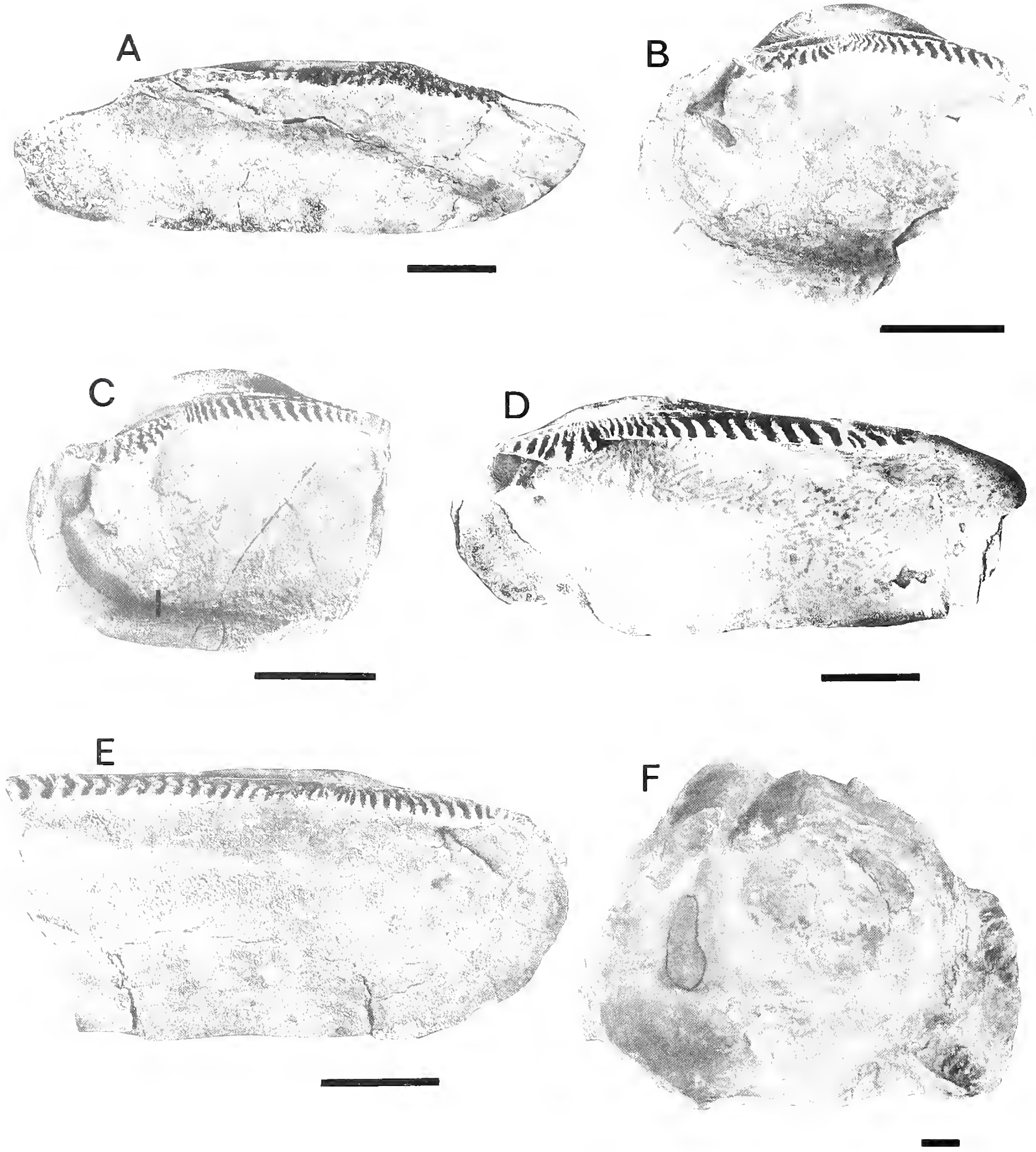
Occurrence. This species is also known from the Mohari Formation in the Edward-Albert Rift (Gautier and Van Damme 1973), and was postulated by Gautier (1966) to be closely related (ancestral?) to recent *P. spekii* from Lake Tanganyika.

Pleiodon tavernieri (Gautier, 1965)

Text-fig. 2B, C

1963 *Caelatura* sp. Verdcourt, p. 30, fig. 61.
1965 *Iridina* (*Pliodon*) *tavernieri* Gautier, pp. 138–140, pl. 4, figs. 5 and 7; pl. 5, figs. 1, 2, 4, 5, 7.
1970 *Pliodon* (*Pliodon*) *tavernieri* Gautier, p. 123, pl. 5, fig. 7.

Discussion. This is the smallest bivalve species represented, and is variable in shape between subtriangular and ovate. Specimens are generally subinflated, with a straight or slightly curved ventral margin and a rounded anterior margin. A posterior ridge is well defined, especially in the subtriangular specimens, where the posterior end is pointed. The umbos are full, project above the hinge line, and are located in the anterior one-third to one-half of the shell. Shell sculpture consists of fine radial lines. The dentition is taxodont, and the hinge plate is relatively straight posteriorly but curved anteriorly. The teeth are irregular anterior to the umbo, and become chevron-shaped posteriorly. The beak cavities are deep, and dorsal muscle scars are visible under the hinge plate. The



TEXT-FIG. 2. The mutelid bivalve species of the Gumba Beds. A, *Pleiodon lanceolatum* (holotype, KNMI-RU-16814). B, C, *P. tavernieri* (KNMI-RU-14840, 14835). D, *P. rusingae* (holotype, KNMI-RU-16815). E, *P. moharensis* (KNMI-RU-16811). F, *Etheria elliptica* (KNMI-RU-16809A). All scale bars = 1 cm.

anterior adductor and retractor muscle scars are deep and the pallial line distinct. The shell can become thick in large specimens.

Material. Fifteen partial and three articulated valves.

Occurrence. This species also occurs in the Mohari Formation (Gautier and Van Damme 1973), where the specimens are apparently less triangular than those from Rusinga.

Pleiodon lanceolatum sp. nov.

Text-fig. 2A

Description. A medium-sized, very elongate ovate shell more than three times as long as high, moderately inflated. The anterior and posterior ends are pointed, and the dorsal and ventral margins are straight. A well-developed posterior ridge is present. The umbos are low and situated in the anterior third of the shell. The hinge plate is very narrow and set with fine taxodont dentition especially anterior to the umbo. Posterior to the umbo, the teeth consist of delicate, rather rounded chevrons. The beak cavities are shallow, and the dorsal retractor muscle scars are located posterior to the umbo. The anterior retractor and adductor muscle scars are distinct, the pallial line is faint, and the posterior adductor and retractor scars not present in the type specimen. The species differs from other known *Pleiodon* by its elongate shape, pointed anterior end, and delicate dentition.

Material. Holotype KNMI-RU-16814 consisting of a single, partial left valve.

Dimensions (in mm).

	Length	Width
KNMI-RU-16814	58	18

Pleiodon rusingae sp. nov.

Text-fig. 2D

Description. A medium-sized, subcompressed, elongate ovate shell more than twice as long as high. The anterior end is regularly rounded, and the posterior end bluntly pointed. The ventral margin is straight or very slightly curved. The dorsal margin is straight and the posterior ridge well defined. The umbos are low, situated in the anterior quarter of the shell. Dentition is taxodont, and the hinge plate short and curved anterior to the umbo. Posterior to the umbo, the hinge plate is straight and set with regular, strong teeth lying at an angle to the hinge line. The beak cavities are shallow, and the dorsal retractor muscle scars are set posterior to the umbo. The anterior adductor and retractor muscle scars are deep and the pallial line is well defined. The posterior adductor scar is well defined, and separated from the posterior retractor scar. The species differs from other *Pleiodon* described mainly by its distinctive short and curved anterior hinge plate.

Material. Holotype KNMI-RU-16815; Paratypes KNMI-RU-16817, 16818, 14818, 14834.

Dimensions (in mm).

	Length	Width
KNMI-RU-16815	70	25

Order MESOGASTROPODA
Family AMPULLARIIDAE
Genus PILA
Pila ovata Olivier, 1804

Discussion. The single gastropod species from the Gumba Beds is only known from opercula. Verdcourt (1963), however, mentions that shells of this species and those of the related ampullariid *Lanistes carinatus* were collected from other localities on Rusinga Island. Both species are also known from the Mohari Formation (Gautier and Van Damme 1973). The present geographic range of *Pila ovata* extends from Egypt to northern Mozambique and westwards to Nigeria (Brown 1980).

Material. Eight opercula.

TABLE 1. Freshwater Molluscan faunas of the Miocene East African sites mentioned in the text

Rusinga Island (*c*. 18–23 my)	Turkana Grits (*c*. 17–23 my)	Edward-Albert Rift (early Miocene)
	BIVALVES	
Etheria elliptica		*Etheria elliptica*
Pleiodon moharensis		*Pleiodon moharensis*
P. tavernieri		*P. tavernieri*
P. rusingae		
P. lanceolatum		
	Pleiodon sp.	
	Mutela sp.	
		Aspatharia triangulata
		Corbicula consobrina
	GASTROPODS	
Pila ovata	*Pila ovata*	*Pila ovata*
Lanistes carinatus	*Lanistes carinatus*	*Lanistes carinatus*
Melanoides tuberculata	*Melanoides tuberculata*	*Melanoides tuberculata*
	Saulea sp.	

Sources: Verdcourt (1963); Gautier and Van Damme (1973); Van Damme (1984).

DISCUSSION

East African Miocene freshwater faunas appear to consist mainly of mutelid bivalve taxa such as *Aspatharia*, *Pleiodon*, and *Etheria*, and prosobranch gastropod taxa such as *Lanistes*, *Pila*, *Gabbiella*, *Cleopatra*, and *Melanoides* (Table 1). All these taxa with the exception of *Pleiodon* remain widely distributed in Africa. Among the bivalves, *Etheria* is an apparently monotypic genus with a wide distribution, although soft part anatomy and molecular genetics of widely separated populations have not been compared. *Aspatharia* has diversified into an as yet unknown number of species (48 according to Pilsbry and Bequaert 1927; 9 according to Haas 1969), some of which are ostensibly widely distributed, while others are endemic to single lakes such as Victoria and Malawi. Among the gastropods, *Pila*, *Lanistes*, and *Melanoides* are also encountered outside Africa (e.g. Brandt 1974; Smith and Kersaw 1979; Brown 1980). *Lanistes* (19 African species) and *Melanoides* (27 African species) are especially diverse (Brown 1980). The 20 species of *Cleopatra* and 22 species of *Gabbiella* listed by Brown (1980) are essentially African; a few species in each genus are widely distributed, but many are confined to particular localities or lakes.

Pleiodon is poorly represented in extant African freshwater faunas. The fossil record of the genus dates back to the Upper Cretaceous, where two taxa are encountered in the Nubian Sandstone near Aswan in Egypt (Cox 1955). With the addition of two new species from the Gumba Beds, the number of *Pleiodon* taxa described from the Miocene has increased to four (an undescribed species from the Turkana Grits could increase this total; see Van Damme 1984). *P. moharensis* and *P. tavernieri* apparently were widely distributed in pre-rift drainages. The more restricted occurrence of *P. lanceolatum* and *P. rusingae* could either be indicative of habitat differences between the sites or the occurrence of endemic taxa in the Miocene Winam Gulf area lakes. *Pleiodon* had further diversified by the Pleistocene: early Pleistocene Edward-Albert rift deposits contain six species, including *P. tavernieri* and *P. moharensis* (Gautier 1970). Elsewhere, *Pleiodon* sp. occurs in the Plio-Pleistocene Koobi Fora formation near Lake Turkana (Williamson 1981). This diverse assemblage declined during the later Pleistocene, and *Pleiodon* is now represented by two species with relictual distributions: *P. spekii* in Lake Tanganyika (previous distribution: Edward-Albert rift (Gautier 1970) and Lake Kivu (Dartevelle 1948)) and *Pila ovata* in West Africa (previous distribution: Edward-Albert rift (Gautier 1970)). Pain and Woodward (1964) describe an additional West African species, *P. waterstoni*, but I agree with Gautier (1966) that this is probably an ecotypic variant of *P. ovata*.

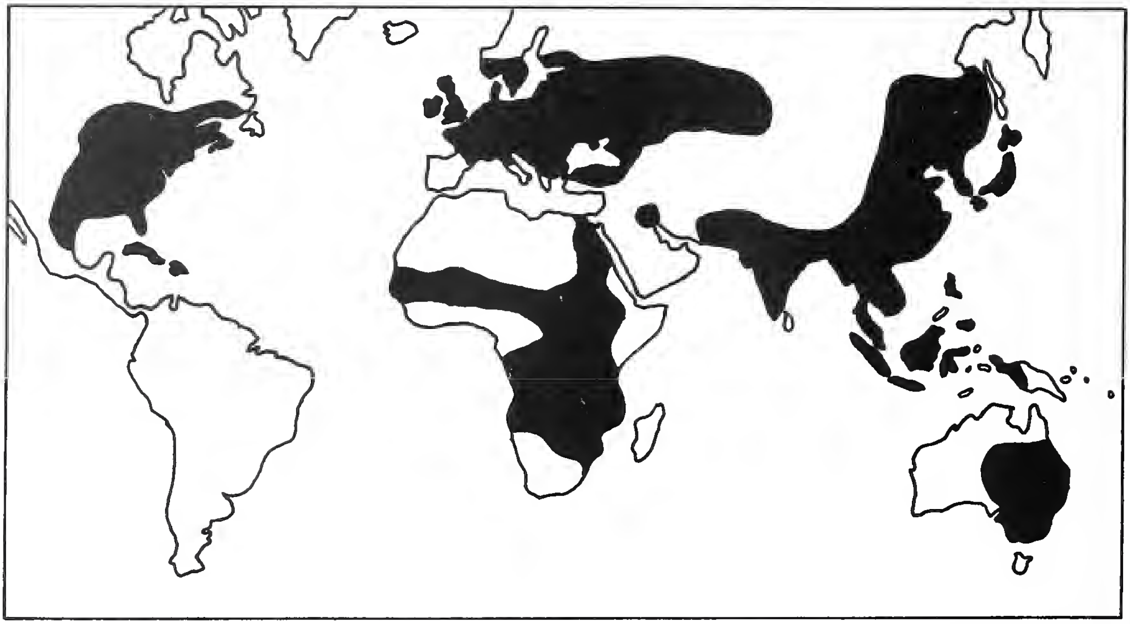
The Rusinga deposits lack representatives of *Aspatharia*, *Gabbiella*, *Cleopatra*, and *Melanoides*, taxa reasonably common in the Edward-Albert rift (Gautier and Van Damme 1973). These differences could be due to dissimilarities in the habitats represented: the Mohari Formation has been hypothesized to represent a marshy environment close to a river (Gautier and Van Damme 1973), and the fauna is dominated numerically by taxa such as *Lanistes* and *Cleopatra*, which presently occur in swamps and slowly flowing rivers (Brown 1980). In contrast, the coarse, poorly sorted sediments and the predominance of *E. elliptica* (which is very rare in the Mohari) indicates a fluviatile and higher energy environment for the Gumba Beds. *Melanoides* occurs in contemporary sediments at Nyakach, about 50 km east of Rusinga (pers. obs.).

Entirely absent from all early Miocene deposits examined to date are representatives of the presently widespread and diverse bivalve family Unionidae and gastropod family Viviparidae. It is possible that ancestors of some of the present African unionids (especially the genus *Caelatura*) and all viviparids were introduced after these deposits were formed, when Africa and Eurasia were joined by the closure of the Tethys Sea (e.g. Dewey and Bird 1970; Andrews and Van Couvering 1975). This event is also thought to have mediated the introduction of several mammal taxa (Cooke 1968), all African cyprinid fishes (Bowmaker *et al.* 1978), a large number of the present Pan-Ethiopian freshwater invertebrates other than molluscs (Harrison 1978), and many flowering plant taxa (Smith 1973).

Newton (1920) and Prashad (1928), however, consider the Viviparidae to have been present on ancient Gondwanaland, based on the occurrence of an upper Cretaceous (Tertiary according to Dartevelle 1948) 'viviparid' in southern Africa, and a high degree of similarity between African and Indian viviparid species. Later, Rennie (1943) described 'viviparid' taxa from the Early Jurassic of Mozambique. All these fossils, however, are poorly preserved, and seem more likely to be representatives of *Cleopatra* (Thiariidae) which Prashad (1928) included in the Viviparidae. *Cleopatra* was widespread in the Miocene, and now occurs throughout Africa and Madagascar. The earliest unambiguous viviparid taxa (*Bellamya* and *Neothauma*) occur in Pliocene deposits (e.g. Gautier 1970; Williamson 1981; Van Damme 1984).

The present distribution (text-fig. 3) and fossil occurrences of the Viviparidae outside Africa also argue against their presence on Gondwanaland. In South America, viviparids are only known from the Palaeocene, and these representatives became extinct a short time later. Parodiz (1969) believes these viviparids, as well as other elements of the South American Palaeocene molluscan fauna, to have been derived from North American ancestors at the end of the Cretaceous. Similarly, viviparids are unknown from Madagascar, and apparently have no fossil record in Australia (Prashad, 1928). Smith and Kersaw (1979) believe the present viviparid fauna, as well as several other Australian freshwater molluscs, to have been derived from Asian ancestors in relatively recent times. The similarity between Recent Indian and African viviparids is more likely to have resulted from shared ancestry with a taxon that invaded Africa relatively recently than shared ancestry with a Gondwanaland taxon. Molecular genetic and karyologic data support a relatively recent divergence among African viviparid taxa.

The taxonomy of the numerous recent *Caelatura* species and their relationships to unionid taxa outside Africa is poorly understood. Unambiguous fossil *Caelatura* are, like viviparids, first encountered in Pliocene and Pleistocene deposits. Recently, Heard and Vail (1976) placed southern African *Cafferia caffra* in the genus *Unio* (Unionidae) based on shell sculpture, some soft-part anatomy, and larval and reproductive characteristics. *Unio* s.s. is otherwise only known from the Palaearctic and Heard and Vail suggest the south African taxon to be a 'biogeographic relict'. Regardless of its generic placement (see Mandahl-Barth 1982), *Cafferia* appears to have a fossil record dating to the Upper Cretaceous in the Transvaal (Modell 1964), which would imply a long-standing presence of some unionid taxa in Africa. Similarly, three endemic and monotypic unionid genera (*Brazzaea*, *Pseudospatha*, and *Moncetia*) occur in Lake Tanganyika, and one monotypic genus (*Prisodontopsis*) is endemic to Lake Mweru (Pain and Woodward 1968; pers. obs.). The Tanganyika unionids exhibit anatomical evidence of shared ancestry (pers. obs.), but their relationship to *Prisodontopsis* and *Cafferia* is unknown. All five taxa, however, clearly represent a distinct and separate group of unionids from *Caelatura*, but much more fossil evidence is necessary to elucidate their origin and past distributions.



TEXT-FIG. 3. Distribution of extant members of the gastropod family Viviparidae (based on Starobogatov 1970).

Also missing from the East African Miocene faunas are gastropods that could elucidate the origin of the thalassoid gastropod assemblage of Lake Tanganyika. This highly distinctive group consists of about twenty-five conchologically diverse species distributed among sixteen largely monotypic endemic genera (no other African lake appears to contain even a single endemic snail genus), and is thought by Brown (1980) to have originated from Miocene thiariid taxa living in central Africa before formation of the lake. Brooks (1950) and subsequent authors such as Boss (1978) believe the thalassoid snails to have evolved entirely within Lake Tanganyika, and thus to represent an ancient endemic radiation in which morphologic differentiation has transcended the species level. While the fossil record indicates that several mollusc taxa now endemic to the lake previously had more extensive geographic ranges (e.g. the viviparid *Neothauma tanganyicense* which is found in Pleistocene deposits of the Edward-Albert rift and Lake Rukwa (Cox 1939; Gautier 1970); species of the thiariid genus *Lavigeria* which are also found near Lake Rukwa (Cox 1939); and *Pleiodon spekii* mentioned above), there is to date no fossil evidence of thalassoid species having occurred outside the Tanganyika basin. The soft-part anatomy of these snails is presently too imperfectly known to determine if there exist shared anatomical characters (e.g. see Davis' (1979) analysis of the conchologically variable Mekong River triculine gastropods) indicative of a truly endemic radiation, and biochemical data which could indicate a possible shared genetic identity are in the early stages of being gathered. The origin and evolution of the thalassoid snails must therefore remain speculative at this point.

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MENISCATE TRACE FOSSILS AND THE *MUENSTERIA–TAENIDIUM* PROBLEM

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ABSTRACT. The systematics of meniscate trace fossils are in need of revision. Most authors follow Seilacher and call unbranched, unlined meniscate burrow fills *Muensteria*. However, Sternberg's original description of *Muensteria* is highly confused, involving true algae, a coprolite, and forms of *Chondrites*, and the name cannot be considered available for trace fossils. Re-examination of the original description of *Taenidium* Heer has revealed that the earliest ichnospecies erected, *T. serpentinum*, corresponds closely to the forms called *Muensteria* in the more recent literature. Subsequent ichnospecies placed in *Taenidium* include septate branched forms that require a new name. It is these branched meniscate burrows that commonly have been referred to *Taenidium*. We designate the branched forms *Cladichnus* ichnogen. nov. on the basis of *T. fischeri* Heer. *T. satanassi* ichnosp. nov. is described from the lower Tertiary of Italy. Other ichnogenera of meniscate trace fossils are briefly discussed, including *Nereites*, *Keckia*, *Scolicia*, *Psammichnites*, *Scoyenia*, *Beaconites*, *Phoebichnus*, and *Ancorichnus*.

TRACE fossils having a cylindrical form and meniscate structure are common in many settings. Generally they represent the active packing of sediment behind animals moving through the loose substrate for food, or vertical escape traces. Although meniscate structures are particularly characteristic of shallower marine deposits, they also occur in continental and deep marine basinal settings. Authors today tend to follow Seilacher (1958, 1962, 1964) in considering that *Muensteria* embraces these 'stuffed linear burrows', but this conflicts with the original diagnosis of Sternberg (1833, p. 31): '*Frons coriacea, fistulosa, cylindracea aut simplex caespitosa aggregata, aut dichotoma, transverse elevato-striata, striis interruptis creberrimis. Sporangia punctiformis, sparsa, creberrima, inter strias laminae frondis immersa*' (Approximate translation: Leathery frond, pustulose, cylindrical, or simply aggregated as a bush, or dichotomous; transversely striated in relief, with dense, interrupted striae. Sporangia punctiform, scattered, very dense, immersed between the laminae of the frond.)

In contrast, '*Taenidium*' is generally used for branched meniscate structures, although this conflicts with Heer's (1877) original diagnosis: '*Frons cylindrica, fistulosa, plerumque simplex, rarius ramosa, annulata, dissepimentis instructa*' (Cylindrical fronds, pustulose, usually simple, rarely branched, annulated, provided with partitions.)

A close inspection of the status of these names is clearly overdue (see e.g. Frey and Howard 1985, p. 378).

STRUCTURE OF MENISCATE TRACE FOSSILS

There are several reasons for the confusion that at present characterizes the systematics of meniscate trace fossils. Among the most important is the heterogeneous nature of the taxobases used. These comprise: (1) a meniscate backfill, together with the presence or absence of (2) discrete wall structure, (3) wall ornament, and (4) true branching. Not all of these features are suitable or easy to use as diagnostic characters. Another cause of taxonomic difficulty is that many of the taxa were introduced as algae and were thus described in non-ichnological terms. These problems, of course, are far from restricted to the meniscate trace fossils, but are of general occurrence in older ichnological systematics (Pemberton and Frey 1982).

[Palaeontology, Vol. 30, Part 4, 1987, pp. 743–763]

Backfill. Meniscate backfill occurs in many morphologically distinctive groups of trace fossils. It is considered an essential feature of such ichnogenera as *Ancorichnus* and *Scolicia*, but also occurs as an accessory feature, albeit rarely, in ichnospecies of *Ophiomorpha* and *Teichichnus* (Frey and Bromley 1985), *Chondrites*, and many others. As a basic result of any tunnelling that involved active stuffing behind an animal, meniscate backfill alone is not particularly suitable as an ichnological taxobase.

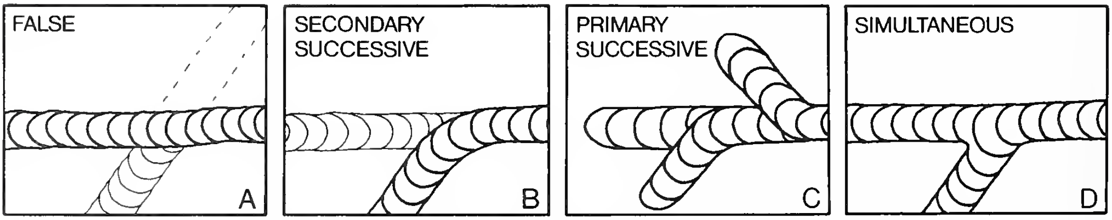
Wall structure. The boundary between burrow fill and undisturbed surrounding sediment may display a host of different features. The boundary may be defined by a clean discontinuity surface caused by a different grain orientation on either side of the junction (e.g. Heinberg 1973, 1974), or by a difference in consistency of the two sediments. Diagenesis may enhance this difference to produce a coloured halo or local concretionary effect. A thin film of clay minerals or carbonaceous material may occur at the boundary, but this is commonly difficult to detect and is lost in weathered material; we do not regard this film as a true 'lining'. Alternatively, the burrowing organism may have actively deposited a true lining on the open wall, as in *Ophiomorpha* ichnospp. (Frey *et al.* 1978), or the animal's burrowing technique may have produced a superficial zone around the periphery of the fill with a special construction, as in *A. ancorichnus* (Heinberg 1974). In these cases, therefore, the boundary is marked by a zone of sediment having a distinctive structure. Finally, local compaction of sediment caused by the construction of the burrow may have produced a preservable boundary feature. In a variable lithology, the characteristics of the burrow boundary may change locally, reflecting the original sediment consistency and consequent changes in burrowing technique. This is also the case for the scratch ornament, which may well be preserved in a firm, fine-grained lithology but is lost in a soft, coarse sand (Fürsich 1974, p. 22).

A corollary of this problem of substrate variation is that of preservation in general. The 'same burrow' may exhibit widely different morphologies in different preservational situations, e.g. in full relief within a sandstone, or epirelief at the sandstone boundaries. In some cases these widely different morphologies have been lumped together as a single ichnotaxon on the basis of their belonging to the 'same burrow' (see the *Scalarituba/Phyllodocites/Nereites/Neonereites* problem: Chamberlain 1971, 1978).

Branching. The main problem here is that of ramification. Burrows may branch in several distinct fashions (Bromley and Frey 1974, fig. 6):

A. On irregular rock surfaces, simple intersection of burrows can be mistaken easily for true branches (text-fig. 1A); this is particularly so where a high degree of compaction has brought burrows that originally lay at different levels in the sediment into close juxtaposition (text-figs. 2 and 3).

B. Commonly a deposit feeder reworks the backfill of a pre-existing burrow and then leaves the earlier course (text-fig. 1B) at an angle to produce a side branch. We suggest calling this type



TEXT-FIG. 1. Diagrammatic representation of four distinct modes of producing branched biogenic structures. A, false branching, where accidental intersections on an irregular surface can give the spurious impression of branching. B, secondary successive branching, where an animal followed the fill of an earlier burrow for some distance, giving the false impression of branched burrows. C, primary successive branching, where the same animal produced a systematically branched structure, actively filled. D, simultaneous branching, where a network of open burrows is produced; the simultaneous stuffing of both branches would produce this pattern, but it is a process that is presumably not possible.

TEXT-FIG. 2. *Taenidium satanassi* ichnosp. nov. Field photograph of material displaying the opposite colour-play to the usual: the pelleted sediment here is the paler. Scale, 1 cm.

'secondary successive branching', as it is produced by two individuals in successive burrowing operations. In many such cases the direction of movement (meniscus orientation) is opposite in the two burrows, which reveals the type of structure immediately (e.g. Brady 1947, pl. 69, fig. 1; herein text-fig. 2). In other cases, however, where the menisci are concordant (e.g. Bromley and Asgaard 1979, fig. 10) it is not easy to distinguish this branching category from the next.

C. In burrow systems where successive probings are made after backfilling previous probes (e.g. *Chondrites*: Seilacher 1957, fig. 2; Ferguson 1965), a single individual produces a branched structure having a characteristic backfill pattern (text-fig. 1C). We call this type of bifurcation 'primary successive branching' (text-fig. 4).

D. Finally, where an open gallery is produced, side branches and dichotomous bifurcations exist simultaneously as empty habitations. This type we call 'simultaneous branching'. The fill might be emplaced either in successive operations, i.e. one branch filled at a time, as in *Ophiomorpha* (Bromley and Frey 1974, fig. 11), or alternatively, the two branches might be filled at more or less the same time. In the latter case, a backfill pattern is produced (text-fig. 1D), but although this structure has been illustrated in sketches (e.g. Seilacher 1955, fig. 5.83) it is not easy to understand the mechanics of the process. Probably 'simultaneous backfill' does not exist. It is easy to envisage this structure arising in a growing alga, however, the menisci representing successive terminations of the thallus (e.g. Fischer-Ooster 1858, pl. 7, fig. 3). We emphasize these difficulties because branching patterns play an important role in understanding the history of the taxonomy of meniscate trace fossils.

Algal origins. Most ichnogenera erected in the nineteenth century were initially described as body fossils of fucoid algae (Häntzschel 1975, p. 14). This fact renders interpretation of the initial descriptions very difficult, owing to the terminology used and the unintentional bias of original authors. 'Sporangia' usually may be interpreted as pellets, 'epithelia' as walling material, etc. A greater

TEXT-FIG. 3. *Taenidium satanassi* ichnosp. nov. showing false branching (cf. text-fig. 1A). Scale, 1 cm.

problem, however, is the tendency to assume that 'fucoid' fossils were branched in the same way as the extant seaweed *Fucus* (text-fig. 3), a tendency that was encouraged by discoveries of truly branched trace fossils (e.g. *Chondrites*). Thus even unbranched trace fossils such as *Cruziana* were described as branched, owing to the misinterpretation of intersections (Osgood 1975, p. 6).

Meniscate ichnotaxa share all these problems. On account of the 'branching bias', authors tended to regard crowded, intersecting trace fossils as more 'complete' than isolated ones, and secondary successive branching and false branching were readily interpreted as true ramifications. In this way, crowded or bunched trace fossils were selected for illustration, and consequently as type material, whereas in trace fossils such material preferably should be avoided. As explained above, branching in trace fossils is a complicated and critical matter; it is not sufficient merely to repeat the original author's statement regarding branching in algal terms when emending the diagnosis of a fucoid taxon in terms of trace fossils.

Taxobases for meniscate trace fossils

Ichnotaxa are based upon morphological features of trace fossils, primarily those that reflect behavioural qualities of the excavating organism. Morphology is also influenced, however, by external factors such as stratinomic conditions and diagenesis. Such morphological features are unsuitable as taxobases and primary features reflecting behaviour should be chosen if possible (Seilacher 1953; Fürsich 1973; Bromley and Frey 1974). For example, as Smith and Crimes (1983) pointed out, *Scolicia* and *Subphyllochorda* represent closely similar if not identical patterns of behaviour. Their preservation, however, is different—*Scolicia* being a concave epirelief and *Subphyllochorda* a full relief expression of the same structure. Häntzschel (1975) suggested, therefore, that *Subphyllochorda* be considered a junior synonym of *Scolicia*. In contrast, the structures *Ophiomorpha*, *Thalassinoides*, *Spongeliomorpha*, and *Gyrolithes* may all be found in mutual connection as a single burrow system (Fürsich 1973; Bromley and Frey 1974; Pemberton and Frey 1982); yet they represent different behavioural responses of the burrowing organism to environmental and biological factors, and so should not be placed in synonymy. In this way, the ichnotaxon unites behavioural patterns of the same type. This is not to question the importance of preservational aspects: taphonomic processes are closely linked to sedimentary facies and the dominance of a particular preservational style in an ichnotaxon in a given occurrence provides useful information on depositional environments.

CONCLUSIONS

The erection of several ichnogenera for the septate or meniscate trace fossils is clearly justified on the basis of their wall details and presence or absence of branching (see below): walled structures include *Phoebichnus*, *Ancorichnus*, and an unnamed branching group; unwalled structures containing longitudinal canals or ridges are distinguished as *Scolicia* and *Psammichnites*; *Nereites* has a unique disturbance zone around it, whereas *Scoyenia* has no wall but is ornamented by longitudinal scratches; *Beaconites* is dubious, having a weak wall or none at all, and it should probably be included in *Taenidium* as defined herein; *Keckia* appears to be a *nomen dubium* and is probably a heterogeneous taxon, including elements resembling several other taxa.

The unwalled meniscate trace fossils pose the greatest problem. *Muensteria*, in spite of the general use of this name today, must be regarded as unavailable for trace fossils. On the basis of its first ichnospecies, *Taenidium* is available for the unbranched ichnospecies of *Muensteria* of authors, and *T. serpentinum* remains its type ichnospecies. However, Heer's *T. fischeri* and *T. lusitanicum* must be transferred to the flabelliformly branched and annulated *Cladichnus* ichnogen. nov.

SYSTEMATIC PALAEONTOLOGY

In our attempt to clarify the meaning of *Muensteria* and *Taenidium*, we reinterpret their original diagnoses in terms of ichnotaxobases and must therefore examine briefly the distinguishing features of related meniscate ichnogenera. We suggest synonyms among these ichnogenera (although we have not examined type material) which are treated below in chronological order.

Muensteria Sternberg, 1833

Discussion. Many authors have used the taxon *Muensteria* in recent years to define simple, unlined, unbranched meniscate structures (e.g. Seilacher 1962, 1964; Fürsich 1974; Chamberlain 1977; Pemberton and Frey 1984; Frey and Howard 1985), despite the fact that Häntzschel (1962, 1975) clearly demonstrated the weakness of the taxon. Thus, although *Muensteria* for these authors is a fairly well-defined concept, *Muensteria* Sternberg remains largely uninterpreted: it is, as Häntzschel (1975) stated, a heterogeneous genus.

Sternberg (1833) based his algal genus *Muensteria* on six species. We have not been able to locate his type material. The generic diagnosis has been given above. The diagnoses and illustrations of the six species are uneven. The first three were based on Jurassic material, from Solnhofen lithographic limestone.

The first species, *M. clavata*, was not illustrated, but reference was made to Brongniart's (1828) *Fucoides encoelioides* (Ekdale *et al.* 1984, fig. 1-1, top left). Sternberg disagreed with Brongniart that the species was closely related to the recent alga *Encoelium bullosum*, and therefore altered its species name. Sternberg's diagnosis for *M. clavata* is a shortened version of Brongniart's (1828, p. 55) for *F. encoelioides*. Brongniart's sample was collected in the Jurassic limestone of Solnhofen and probably comprised poorly preserved plant remains, as did Sternberg's fossils; in fact the trace fossil '*Muensteria*' of authors is unknown in the Solnhofen sediments, which were deposited in largely anoxic environments (F. T. Fürsich, pers. comm. 1984).

Sternberg's second species, *M. vermicularis*, differs from *M. clavata* only in being solitary. The illustration supports the description, showing a particularly unimpressive specimen. The palaeobotanist Andrews (1955, p. 191) chose this to be the type species of the genus, identifying the plant as an 'alga?'.

The third species, *M. lacunosa*, appears to be a coprolite, and was considered as such by Schenk (1864, p. 296). The remaining three species derive from Vienna and are branched. *M. hoessii* (Sternberg, 1833, pl. 6, fig. 4; cf. text-fig. 4) appears to be a *Chondrites*, and its diagnosis describes it as dichotomous. *M. flagellaris* Sternberg, 1833, pl. 8, fig. 3, also strongly resembles *Chondrites*; his diagnosis distinguishes it on the basis of short side branches. Finally, *M. geniculata* has a characteristic spreite and has been designated type ichnospecies of *Hydrancylus*.

TEXT-FIG. 4. *Chondrites hoessii* (Sternberg, 1833), MGUH 17555, from the same horizon as *Taenidium satanassi* ichnosp. nov., showing the faintly meniscate fill and primary successive branching. Scale, 1 cm.

We conclude that Sternberg's genus has no single claim for validity, so *Muensteria* must be considered unavailable as an ichnogenus. As a plant taxon it is probably a *nomen dubium.*

The next author to use *Muensteria* was Schafhäutl (1851) whose *M. annulata* is a clearly branched trace fossil (apparently in a primary successive manner) but extremely poorly defined.

Fischer-Ooster (1858) greatly complicated the issue by erecting three subgenera for *Muensteria.* The only one that concerns us is *M.* (*Keckia*), into which he placed *M. annulata* Schafhäutl and, mysteriously as a synonym, *K. annulata* Glocker, 1841. Also in *M.* (*Keckia*) he placed Sternberg's *M. hoessii.*

Heer (1877) further confused matters by erecting a simple branched species, *M. antiqua*, and by introducing a further genus, *Taenidium*, that mainly differs from *Muensteria* in possessing menisci (Heer 1877, p. 117), although Heer's illustration of *M. hoessii* (1877, pl. 69, fig. 3) clearly shows menisci.

Nereites MacLeay, 1839

[= *Phyllodocites* Geinitz, 1867; *Scalarituba* Weller, 1899; *Neonereites* Seilacher, 1960;
Maldanidopsis Plička, 1973.]

Discussion. The close relationship between *Nereites*, *Neonereites*, and the meniscate burrow *Scalarituba* was demonstrated by Seilacher and Meischner (1964). Although these ichnogenera have highly distinctive morphologies, they appear to be merely preservational variants of the same behavioural expression (Ekdale *et al.* 1984, figs. 2–5). This equivalence was emphasized by Chamberlain (1971) and Seilacher (1983).

Thus, although *Scalarituba* has the appearance of a simple meniscate structure corresponding more or less to the concept of *Muensteria* of authors, in fact it is merely the cylindrical septate axis of a more complex structure, as is demonstrated by the common presence of a more or less visible halo. In Frey *et al.*'s (1984, fig. 1A) illustration of Weller's holotype of *S. missouriensis*, this halo is visible and corresponds to the disturbance zone surrounding the central meniscate fill that is emphasized in *Nereites* preservation. Seilacher (1983) advocated placing *Scalarituba* and *Neonereites* in synonymy with *Nereites*, thus completing the trend started by Chamberlain (1971, 1978). The more important ichnogenera included by Seilacher in this group of synonyms are *Scalarituba*, *Phyllodocites*, *Neonereites*, and *Helminthoida*; however, the last-named has a non-septate central fill and therefore is distinct.

Keckia Glocker, 1841

Discussion. Glocker (1841) erected *Keckia annulata* on the basis of two specimens from Upper Cretaceous sandstone (Germany). Despite his beautiful colour plate (1841, pl. 4), it is not clear what the genus comprises. Described in terms of plants and compared to lycopodiaceans, Glocker (1841, pp. 318–319) considered the crescent-shaped rings visible in parts of his specimens to be atypical of fucoid structures. On this basis, he distinguished his genus from *Muensteria* Sternberg. Furthermore, *K. annulata* was considered to be more densely branched than *M. hoessii.* From his plate the branching pattern appears to be primarily successive in most cases. However, the structure of the fossil varies so extensively from part to part that possibly it is composed of intersections of several distinct taxa. Although one branch of the larger specimen and the small second specimen appear to be unwalled meniscate burrows, we regard this confusingly based ichnotaxon as a *nomen dubium.*

Scolicia de Quatrefages, 1849

[*Bolonia* Meunier, 1886; *Taphrhelminthopsis* Sacco, 1888; *Subphyllochorda* Götzinger and Becker, 1932.]

Discussion. Seilacher (1955, 1983) stated that the morphological differences between the ichnogenera listed above (among many others) represent various preservational expressions of the same fundamental type of burrowing activity. *Bolonia* and *Subphyllochorda* were mentioned by Häntzschel (1962, 1965, 1975), together with other ichnotaxa, as belonging to the '*Scolicia* group' even if not classifiable as true synonyms, but *Taphrhelminthopsis* was described separately. Häntzschel (1975), Książkiewicz (1977), Smith and Crimes (1983), and others have shown by means of sketches the possible relationship between biostratinomic processes and the morphology of the same structures belonging to the *Scolicia* group, to which the effects of preservation must be added (D'Alessandro 1980, fig. 3). Thus the ichnogeneric names under discussion appear to reflect different taphonomic features of the same type of trace, and should therefore be placed in synonymy. Nevertheless, some authors (e.g. Książkiewicz 1977; Crimes 1977; Smith and Crimes 1983) preferred to retain distinct ichnogeneric names even in cases where such names could with reasonable safety be ascribed to taphonomic variation.

Thus we consider the ichnogenus *Scolicia* to include those trace fossils in which the sediment is backfilled to form densely packed lamellae bearing one or two parallel ridges, strings, or grooves lying below or within the lamellar fill. The concave epirelief expression takes the form of a bilaterally symmetrical laminated trail divided into two or three lobes by longitudinal grooves; as a slightly convex epirelief variant, *Scolicia* displays a plait-like pattern (Książkiewicz 1977, fig. 24*f*; Smith and Crimes 1983, fig. 4*d*). *Scolicia* always lacks the median vertical discontinuity plane that is characteristic of *Curvolithus* and the distinctively different *Gyrochorte* (see Heinberg 1973).

Psammichnites Torell, 1870

[= *Olivellites* Fenton and Fenton, 1937*a*; *Aulichnites* Fenton and Fenton, 1937*b*;
?*Laminites* Ghent and Henderson, 1966.]

Discussion. The original material of *Olivellites* was described (Fenton and Fenton 1937*a*) as a meandering trace fossil preserved in convex epirelief. It appears to be bilaterally symmetrical and divided into two zones by a median solid string. The fill is composed of concave thin backfill lamellae; in the string itself, the sediment was described as 'not closely packed' (Fenton and Fenton 1937*a*, p. 453).

The original specimen of *Aulichnites* is a full relief structure that seems to differ from *Olivellites* exclusively in lacking the string; thus it appears to be divided into two lobes by a single median furrow. Hakes (1977) demonstrated that the lower surface of the original specimen of *Aulichnites* is regularly convex. It is reasonable to suppose, therefore, that both ichnogenera represent preservational variants of the same structure. Furthermore, the morphology of *Olivellites* closely corresponds to that of *Psammichnites* (see Häntzschel 1975, fig. 62, 2c), of which we consider it a junior synonym.

In its original diagnosis, *Laminites* was described as a subcylindrical backfilled trace having concave or biconcave laminae alternately dark and light; these laminae were interpreted as having been produced by separate packets of faeces extruded into the burrow (Ghent and Henderson 1966). The trace fossil is preserved as convex epirelief. Further examples of such a structure were given by Chamberlain (1971, 1978). In longitudinal section it is not always possible to distinguish *Scolicia* from *Laminites*. At present, our knowledge of this form is still limited as regards its morphological range and preservational variants; the construction of its under surface, so critical in the *Scolicia* group, is unknown. Therefore, provisionally we consider *Laminites* to be a synonym of *Psammichnites*, until its construction is better understood.

Taenidium Heer, 1877

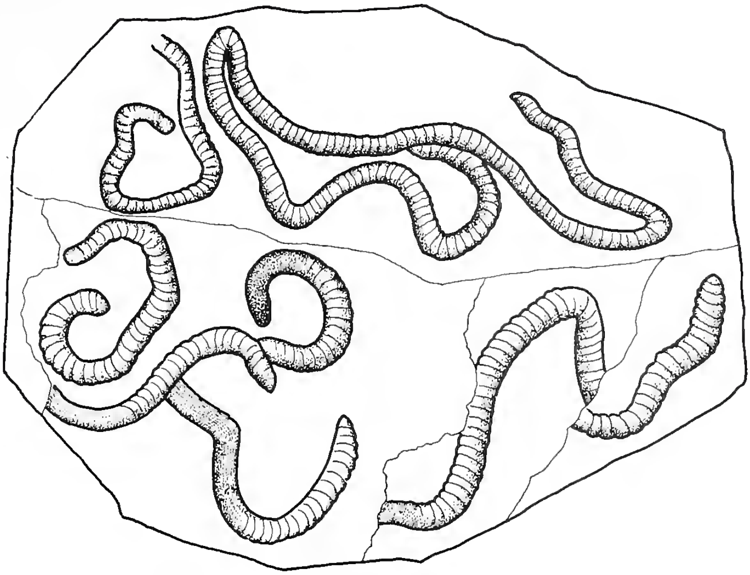
non 1823 *Fucoides encoelioides* Brongniart, p. 55, pl. 6, fig. 4.
non 1833 *Muensteria* Sternberg, pp. 31–32, pl. 6, fig. 4; pl. 7, fig. 3.
1858 *Muensteria hoessii* (*non* Sternberg) Fischer-Ooster (*partim*), p. 62, pl. 16, fig. 4.
1877 *Taenidium* Heer (*partim*), p. 117, pl. 45, figs. 9 and 10*b*; pl. 50, figs. 1 and 2.
? 1877 *Muensteria flagellaris* (*non* Sternberg) Heer, pl. 66, figs. 4 and 5.
1877 *Muensteria hoessii* (*non* Sternberg) Heer, p. 164, pl. 69, fig. 3.
1947 *Scolecocoprus* Brady, p. 471, pl. 69, fig. 1.
1958 *Muensteria* Sternberg; Seilacher, p. 1071, table 2, fig. 28.
1958 *Muensteria hoessii* (*non* Sternberg) Seilacher, p. 1071, table 2, fig. 40.
1962 *Muensteria* Sternberg; Häntzschel (*partim*), p. 205.
1962 *Muensteria hoessii* (*non* Sternberg) Seilacher, p. 229, pl. 2, fig. 6.
1964 *Muensteria* Sternberg; Seilacher, p. 309, fig. 7 (27), table 1 (27).
1971 *Taenidium serpentium* Heer; Chamberlain, p. 241, pl. 32, fig. 10.
1974 *Muensteria* Sternberg; Fürsich (*partim*), p. 34, fig. 29*a*.
1974 *Muensteria* Sternberg; Heinberg, p. 17, figs. 1B and 9C.
? 1977 *Keckia* cf. *hoessii* (Sternberg); Książkiewicz, pl. 3, fig. 12.
1977 *Muensteria* Sternberg; Chamberlain (*partim*), p. 14, figs. 2E and 5F.
1977 *Taenidium serpentium* Heer; Chamberlain, p. 18, figs. 2A, H, 3F, I, 7A.
1983 *Muensteria* Sternberg; Wetzel (*partim*), p. 290, fig. 2.
non 1984 *Muensteria* Sternberg; Bracken and Picard, p. 485, fig. 12.
1984 *Muensteria* Sternberg; Pemberton and Frey, p. 291.
1985 *Muensteria* Sternberg; Frey and Howard, pp. 378–379, figs. 10.12, 16.3(B), 19.6.
1985 *Entradichnus* Ekdale and Picard, p. 8, pl. 2A, B.
1986 *Muensteria* ichnosp. D'Alessandro *et al.*, p. 299, fig. 5B.

Preliminary remarks. Taenidium is generally considered today to be a branched meniscate structure (Häntzschel 1975, fig. 70.1). However, the terms in which the genus was introduced originally (Heer 1877) are very similar to the original diagnosis of *Muensteria* (see introduction above). Its original Latin diagnosis is unsatisfactory owing to the linguistic bias caused by an algal interpretation.

Heer's first species, *T. serpentinum* (text-fig. 5) has been designated subsequently by Andrews (1955, p. 243) as type species of 'alga?'; and by Häntzschel (1975, p. 112) as type species of a branched, root-like system of burrows, even though this species is unbranched. Heer's diagnosis is as follows: '*T. fronde semplici, valde incurvata, serpentina, 3 mm lata, evidenter articulata, articulis 1 mm longis*'. (Simple *Taenidium* frond, strongly bent, serpentine, 3 mm wide, evidently articulated, the joints 1 mm long.)

Heer's second and third species, *T. gillieroni* and *T. convolutum*, are also unbranched and differ only in size from the type species. Their illustrations show no true branching, but indicate superficial wrinkling and evenly spaced menisci (Heer 1877, pl. 45, figs. 9 and 10*b*; pl. 50, figs. 1 and 2). *Taenidium* is thus meniscate and unbranched, and on this basis it would be logical to consider *Taenidium* to be the first valid name for *Muensteria* of authors. These three species were founded on Swiss Jurassic material.

Later in the same work, Heer (1877, p. 162) illogically named a strongly branched, radiating, septate structure *T. fischeri* and he listed *M. annulata* of Schafhäutl (1851) among its synonyms. Afterwards



TEXT-FIG. 5. *Taenidium serpentinum* Heer, 1877. Redrawn from Heer's pl. 45, fig. 9. About natural size.

(Heer 1881) he founded a new species, *T. lusitanicum*, for a palmate form. These later species differ radically from the original ones in possessing ramification. Nevertheless, Häntzschel (1975, p. 112) pronounced *T. fischeri* the 'most typical', and confirmed the general tendency to consider *Taenidium* a much-branched ichnogenus. As pointed out above, however, this is not the original connotation.

Emended diagnosis. Unlined or very thinly lined, unbranched, straight or sinuous cylindrical burrows containing a segmented fill articulated by meniscus-shaped partings.

Type species. T. serpentinum Heer, 1877.

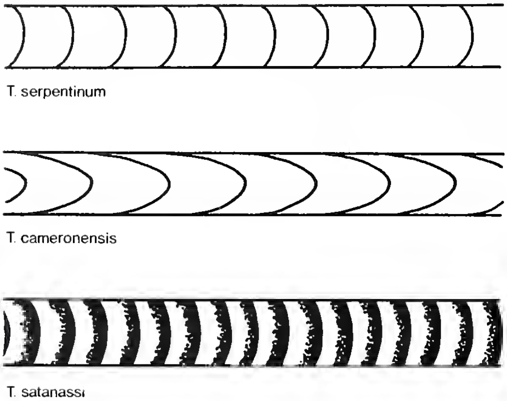
Discussion. Fragments of *Cladichnus* that do not show their characteristic branching may be confused with short lengths of *Taenidium*. However, individual branches of *Cladichnus* commonly are less winding, have stronger annulation or moniliform development, or they may possess cone-in-cone articulations, and consequently have a less linear border than *Taenidium*. Many species in the literature are based on fragments too small to display sufficient characteristics for identification.

Nereites, when only its central axis is preserved, may be mistaken for *Taenidium*; the disturbance zone around *Nereites* is revealed, however, in such cases where two burrows cross (Frey *et al.* 1984, fig. 1A).

Taenidium differs from *Ancorichnus* in lacking a 'distinct mantle' (Heinberg 1974). However, on the basis of illustration, the trace fossils *A. coronus* (Frey *et al.* 1984, figs. 1D, E and 3) and *A. capronus* (Howard and Frey 1984, figs. 2 and 3A, B) appear to be thinly walled and thus less distinct from *Taenidium* than from *A. ancorichnus*. McCarthy's (1979, p. 263, fig. *d*) *Keckia*, a trace fossil having 'poorly defined walls', was compared to Frey and Howard's (1970, fig. 8*a*) 'chevron trails'; but Frey and Howard (1985) placed the latter in synonymy with *A. capronus*.

There is a close resemblance between *Taenidium* and *Beaconites*. When the latter is better known it may be revealed as a junior synonym of *Taenidium*. However, differences such as the irregularity and flattened shape of the menisci, and the large size of the structures, may be used to perpetuate the ichnospecies of *Beaconites*.

The morphology of *Imbrichnus protuberans* in bedding plane view (Marintisch and Finks 1982, pl. 5, fig. 1) resembles *Taenidium* in the same view. Moreover, the vertical structure through the



TEXT-FIG. 6. Essential features of the three valid ichnospecies of *Taenidium*.

mid-line of *I. protuberans* (their pl. 5, fig. 2) shows imbricate structure that may represent the lower half of the simple meniscate fill of *Taenidium*. On the other hand, *I. wattonensis* Hallam has an imbricated structure (Hallam 1970, p. 198) that does not take the form of hemispherical menisci.

Interpretation. Different authors have interpreted active fill of burrows in different ways. Some have assumed that the material packed behind the animal on its way through the sediment is entirely faecal, having passed through the gut (Fürsich 1974, p. 35). Others have emphasized that the sediment is transported around the body during the animal's progress through the substrate (e.g. Heinberg 1974, p. 18; Bromley and Asgaard 1975, p. 276). The alternation of two types of sediment that produces the meniscus structures may arise from physical sorting of the sediment, producing alternate fine-grained and coarse laminae (Stanley and Fagerstrom 1974, p. 74), or from a combination of ingestion and external transport (Bromley and Asgaard 1979; Pemberton and Frey 1984). It seems reasonable in most cases to regard the sediment packages that resemble lithologically the surrounding sediment as non-ingested, and the alternating compressed fine-grained material as coprolitic in origin. The proportions of these two components vary in different types of burrow fills.

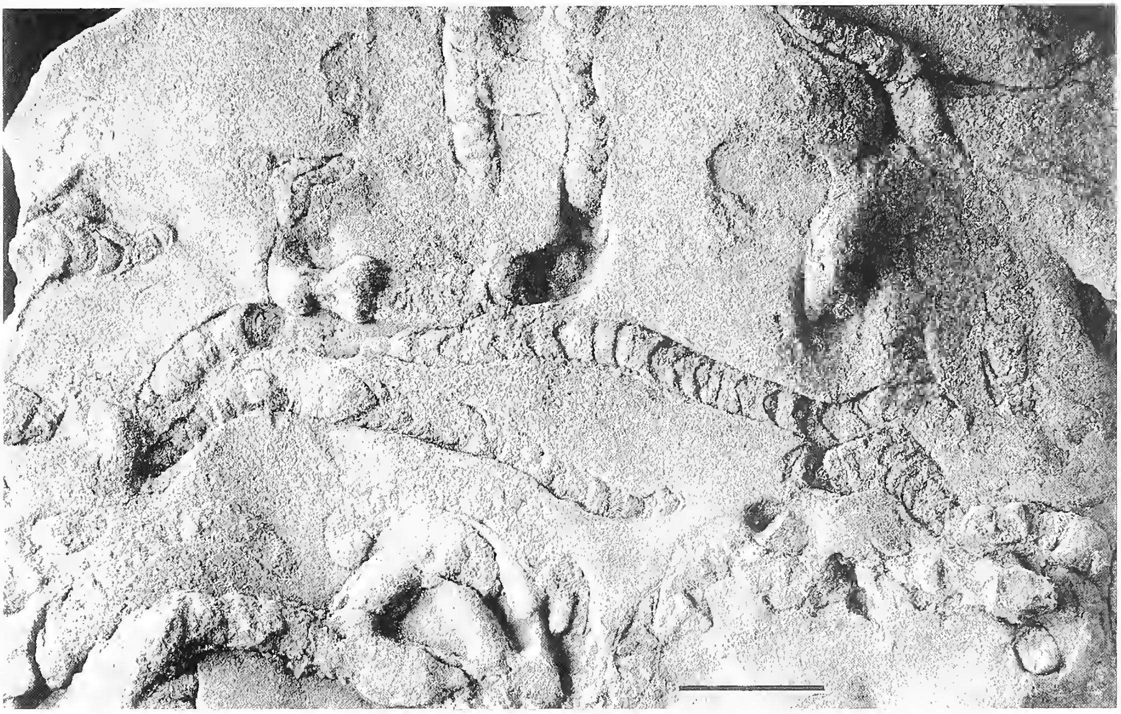
Included species. We recognize three valid ichnospecies (text-fig. 6) while four other ichnospecies must be regarded as dubious: type ichnospecies—*T. serpentinum* Heer, 1877; other ichnospecies—*T. cameronensis* (Brady, 1947) and *T. satanassi* ichnosp. nov.; dubious ichnospecies—*Muensteria cretacea* Heer, 1877, *T. carboniferum* Sacco, 1888, *T.? maeandriformis* Müller, 1966, and *M. planicostata* Książkiewicz, 1977.

Taenidium serpentinum Heer, 1877

Text-figs. 6A and 7

? 1858 *Muensteria hoessii* Fischer-Ooster (*partim*), p. 62, pl. 16, fig. 4 (*non* fig. 5).
1877 *Taenidium serpentinum* Heer, p. 117, pl. 45, figs. 9 and 10B.
1877 *Taenidium gillieroni* Heer, p. 117, pl. 50, fig. 1.
1877 *Taenidium convolutum* Heer, p. 117, pl. 50, fig. 2.
? 1877 *Muensteria flagellaris* Heer (*non* Sternberg), pl. 66, figs. 4 and 5.
+1877 *Muensteria hoessii* Heer (*partim*), p. 164, pl. 69, fig. 3 (*non* pl. 66, fig. 6).
+1958 *Muensteria hoessii* Heer; Seilacher, p. 1071, table 2, fig. 40.
+1962 *Muensteria hoessii* Heer; Seilacher, p. 229, pl. 2, fig. 6.
1971 *Taenidium serpentium* Heer; Chamberlain, p. 241, pl. 32, fig. 10.
+1977 *Muensteria* cf. *hoessii* Sternberg; Chamberlain (*partim*), p. 14, figs. 2E and 5F.

Diagnosis (*emended*). Serpentiform *Taenidium* having well-spaced, arcuate menisci; distance between menisci about equal to or a little less than burrow width. External moulds may show slight annulation corresponding to menisci, or fine transverse wrinkling. Secondary subsequent branching and intersections occur. Boundary sharp, lining lacking or insignificant.



TEXT-FIG. 7. *Taenidium serpentinum* Heer, 1877, MGUH 17552, from the Lower Jurassic Gule Horn member, Neill Klinter Formation of Jameson Land, East Greenland. Scale, 2 cm.

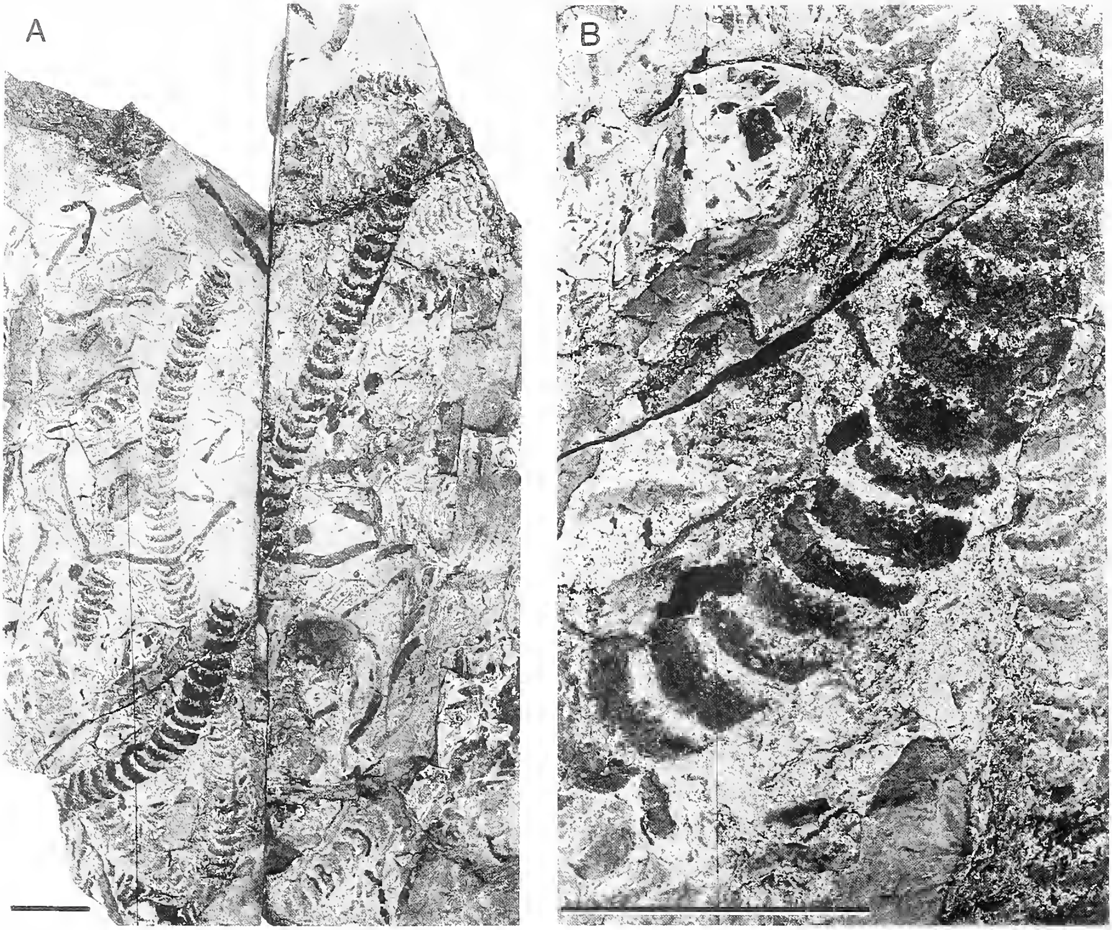
Type area and age. Switzerland, Jurassic.

Discussion. This name is useful for the common form of '*Muensteria*'; for example, in the Lower Jurassic of East Greenland (Surlyk *et al.* 1971, p. 29; Heinberg and Birkelund 1984, *partim*) (text-fig. 7), where the form is generally preserved in full relief in micaceous sandstone. The wall of this trace fossil is sharp and possibly lined by an extremely thin film of clay or mica grains. Similarity with the illustrations of Heer (1877, pl. 50, figs. 1 and 2) is striking.

The citations in the synonymy list prefixed with a cross (+) may represent a distinct ichnospecies. As far as can be judged from illustrations, these burrows are larger and the fill has more densely alternating packets of two types of sediment than the typical *T. serpentinum*. Nevertheless, as we are dealing with incomplete burrows, shown only in longitudinal section, we prefer temporarily to include them in *T. serpentinum*.

If they *are* considered to comprise a separate ichnospecies, the once commonly used specific name '*hoessii*' would not be suitable because it was employed by Sternberg for two different structures: a *Chondrites* (1833, pl. 6, fig. 4) comparable with our text-fig. 4, and an incomplete burrow (1833, pl. 7, fig. 3) of doubtful interpretation. The name, therefore, could be employed in the ichnogenus *Chondrites* as *C. hoessii* (Sternberg). Fischer-Ooster (1858, pl. 16, figs. 4 and 5) applied the name to meniscate traces, one of which cannot be included in *Taenidium*, being bordered by a wide band, and the other being scarcely significant. Heer (1877) determined two different structures as *M. hoessii*: one that could be an incomplete *Spirophycus* (pl. 66, fig. 6) and another that suggests a real *Taenidium*. *M. hoessii* is thus a *nomen catastrophicum*, as is the genus itself.

Häntzschel's (1972) *T. carbonicum* (a *lapsus* by Häntzschel for *T. carboniferum* Sacco) has an indistinct dark zone surrounding a well-preserved meniscate fill. The zone appears to cut other burrow fills, indicating that this structure should be referred instead to *Nereites*.



TEXT-FIG. 8. *Taenidium satanassi* ichnosp. nov. in cleavage relief preservation. A, B, MGUH 17553, specimen containing the holotype (most conspicuous, longest preserved burrow, detailed in B); the other meniscate structures are paratypes. C, D, MGUH 17554, paratypes. Scale, 2 cm.

The non-marine *Entradichnus meniscus* may belong here, although the menisci appear to be closely spaced and rather flat, as in *B. antarcticus* Vialov.

Taenidium cameronensis (Brady, 1947)

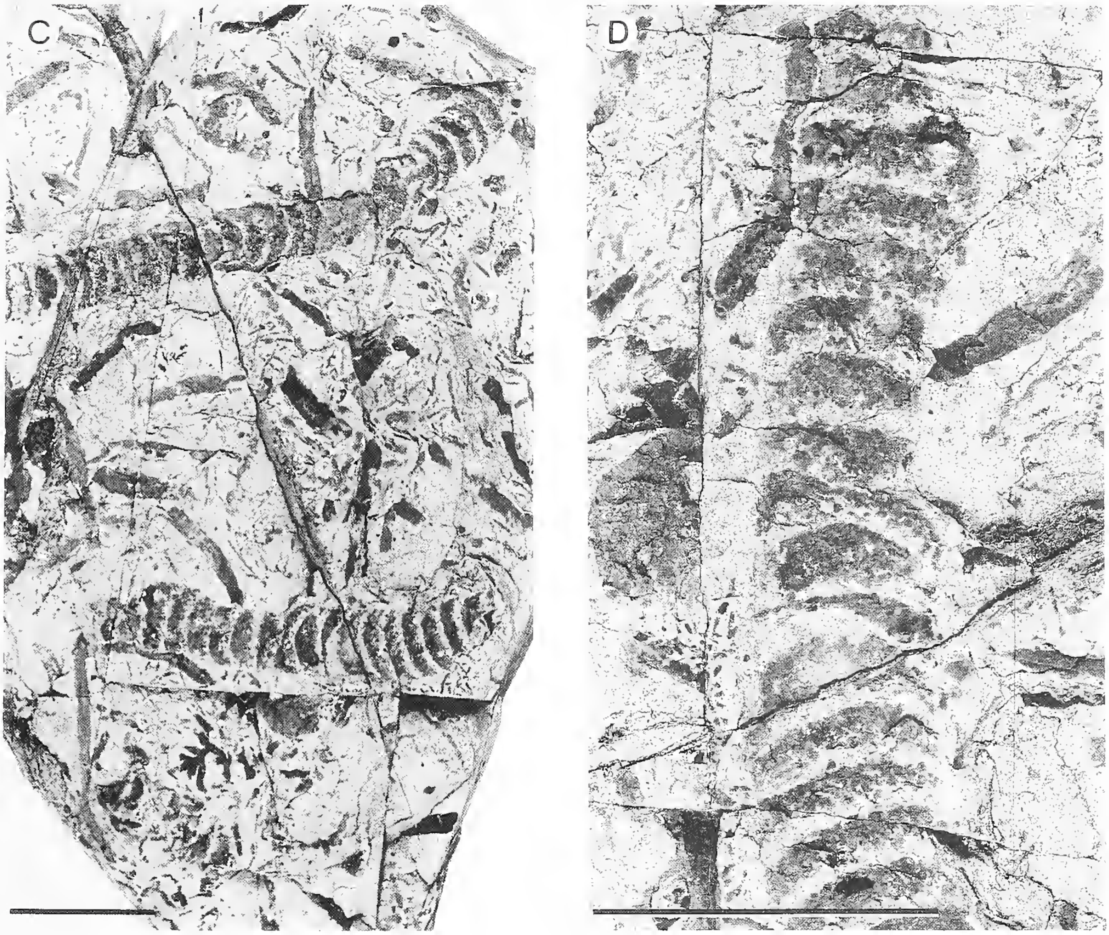
Text-fig. 6B

1947 *Scolecocoprus cameronensis* Brady, p. 471, pl. 69, fig. 1.
? 1979 *Keckia* sp. McCarthy, p. 363, fig. 3*c*.

Diagnosis (emended). Taenidium having intermeniscate segments generally longer than wide, and deeply concave menisci; secondary successive branching and intersection occur.

Type area and age. Arizona, probably Permian.

Discussion. This ichnospecies is separated from *T. serpentinum* on the basis of its distinctly longer packets of sediment between successive menisci in the backfill. The arc of the meniscus is also much



deeper, tending towards parabolic, so that each packet nests around the next. Hitherto, all references to this ichnospecies have been from shallow water settings (e.g. Decourten 1978, p. 491, fig. 1).

Taenidium satanassi ichnosp. nov.

Text-figs. 2, 3, 6C, 8A–D, 9

1958 *Muensteria* Seilacher, p. 1071, table 2, fig. 28.
1986 *Muensteria* ichnosp. D'Alessandro *et al.*, p. 299, fig. 5B.

Derivation of name. Satanassus, Satan, after whom the type locality is named, a river that had disastrously unpredictable floods.

Type material. Holotype, MGUH 17553 (text-fig. 8A, B) and paratypes, MGUH 17553, 17554 (text-fig. 8A, C, D) deposited in the Geological Museum, University of Copenhagen, Denmark; from Fiumara Satanasso, Villapiana, near Sibari, southern Italy; Saraceno Formation, middle-upper Eocene.

Other material. Several specimens from the lower part of the Saraceno Formation, deposited in the Department of Geology and Geophysics, University of Bari, and Department of Earth Science, University of Calabria.

TEXT-FIG. 9. Sketch of an example of *Taenidium satanassi* ichnosp. nov., convex hyporelief, showing the tightest observed curvature.

Diagnosis. Weakly sinuous to nearly straight *Taenidium*, the fill consisting of evenly alternating meniscus-shaped packets of two types of sediment, of more or less equal thickness; sediment packets considerably shorter than wide.

Description. The burrows lie parallel or weakly inclined to bedding. The fill in the type material is very characteristic, the packets of sediment being alternately dark and pale. One of these two types of sediment, usually the dark material, is clearly pelleted and grades on the concave side into the other type of sediment which, in turn, is closely similar to the surrounding sediment. The packets of unpelleted sediment are usually a little thinner than the pelleted segments, or may reach equal size. The curvature of the meniscus is relatively wide, and the sediment packets consequently do not partially enclose or wrap around each other. In thin section the unpelleted sediment packets seem to run continuously into the surrounding sediment without interruption, but on weathered surfaces a very faint colour difference and boundary interface can be detected. There is thus no detectable wall lining or special grain orientation at the junction.

The burrows have an average width of 8·82 ± 0·73 mm (n = 33), showing an observed range of 4–14 mm and a unimodal size-frequency distribution. The type material is highly compacted; it is mainly preserved in (now flattened) cleavage relief on upper surfaces or, more rarely, in semirelief on soles.

Discussion. T. satanassi differs from the other ichnospecies in its weakly arcuate menisci, more or less equally sized packets of alternating sediment type, obviously pelleted form of the fill (text-fig. 8), straight-sided boundary, and little-winding course. Greater affinity exists between *T. satanassi* and the forms prefixed by a cross in the *T. serpentinum* synonymy. The main differences here are in the more or less equal quantities of alternating sediment types in the former, and the more arcuate menisci of the latter so that each packet partially wraps around the next.

T. satanassi resembles *B. antarcticus*. However, the latter's backfill appears to have alternating sediment units of unequal thickness; furthermore, the septa appear flattened at the centre but curve more or less abruptly as they approach the boundary (Vialov 1962; Gevers *et al.* 1971, p. 84; Bradshaw 1981, p. 631), whereas those of *T. satanassi* curve in a regular arc. Moreover, *B. antarcticus* seems to have a wall.

T. satanassi also resembles the meniscate trace fossil of Stanley and Fagerstrom (1974, figs. 6–8), recently included in *Ancorichnus* by Frey *et al.* (1984). However, a clear difference can be observed in the arrangement of the menisci when the direction of the burrow changes. In *Taenidium* the diameter of the structure remains constant and the menisci tend to keep parallel to each other, fanning out slightly where the burrow bends (text-fig. 9); when the traces described by Stanley and Fagerstrom (1974) bend, the menisci are oriented at variable angles and truncate one another. Thus, this character may be the morphological expression of a distinct burrowing pattern. A different form of irregular meniscate development is shown by the form referred to as *Muensteria* ichnosp. by Bromley and Ekdale (1984, figs. 3B and 4A–C) in chalk.

Dubious ichnospecies of *Taenidium*

M. cretacea Heer, 1877, p. 144, is characterized by extremely deeply concave menisci that divide the cylindrical structure into pale and dark densely alternating units; each unit wraps around several of the following. It is not easy to evaluate this fragment; it may represent part of a body fossil.

The original description of *T. carboniferum* Sacco, 1888, p. 162, includes '*Frons . . . moniliformis, subcylindrica, . . . annulosa . . . articulata; articuli crassi, subelliptici, inter se profunde disjuncti . . .*'; Sacco added that the rounded segments are separated by 0·5 mm. This form was included in the algal genus '*Taenidium*', having segments distinctly separated; on this basis, we hesitate to consider it a *Taenidium* and suggest that it could belong rather to the ichnogenus *Hormosiroidea*.

The single specimen *T.? maeandriformis* Müller, 1966, resembles *T. serpentinum* in its winding course and size. The flattened fill consists of segments about as wide as long, separated by fairly flat menisci, distinguishing it from *T. camaronensis*. The meandering course and mode of preservation are reminiscent of *Nereites*, but no lateral zones are visible. Owing to this uncertainty, therefore, we reserve judgement on this ichnospecies. This name was used again by Plička (1973) who described a large example of unquestionable *Nereites*, but considered it to be the body fossil of a worm and assigned it to a new genus, *Maldanidopsis*.

Muensteria planicosta Książkiewicz, 1977, was founded on a winding meniscate trace fossil, preserved as hyporelief; the menisci are regularly arcuate and very dense (Książkiewicz 1977, p. 122, pl. 13, fig. 1). The trace bends abruptly through a right angle, showing changes in width, characters that are atypical of *Taenidium* but reminiscent of '*Laminites*'.

Scoyenia White, 1929

Discussion. The morphology and ethology of this trace fossil and its environmental significance have been analysed recently (Bromley and Asgaard 1979; Frey *et al.* 1984). Straight or gently curved endogenic structures, limited by distinct boundaries and ornamented with external longitudinal striae, are included here. The burrow contains a conspicuously meniscate backfill. *Scoyenia* is an unbranched burrow that commonly exhibits cross-overs, intersections, or secondary successive branching (Bromley and Asgaard 1979, figs. 9A and 10).

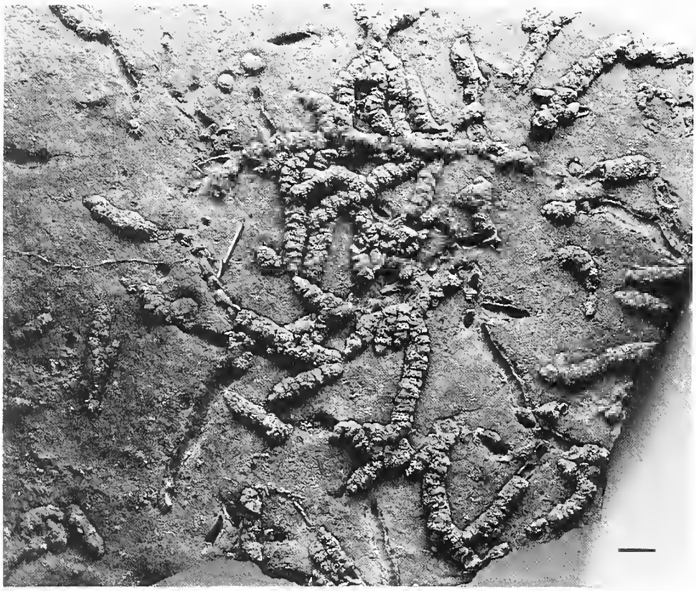
Beaconites Vialov, 1962

Discussion. The original description of *B. antarcticus* Vialov, 1962, was extremely weak. Re-examination of topotypic material by Bradshaw (1981) has improved our understanding of this form but, owing to the high degree of weathering, details of the burrow boundary are unclear. In the type ichnospecies, Bradshaw (1981, p. 630) wrote of 'a poorly developed sand lining' and this is supported by her fig. 15. The illustration by Gevers *et al.* (1971, pl. 18, fig. 3) similarly shows a boundary ridge in cross-section, interpretable as a wall structure. The sediments were apparently deposited in a non-marine environment. Giant meniscate structures have also been assigned to the ichnogenus *Beaconites* (e.g. Gevers *et al.* 1971; Ridgeway 1974; Pollard 1976) and these have been placed in *B. barretti* by Bradshaw (1981). The description of this ichnospecies also implies a weak wall structure (Gevers *et al.* 1971, p. 84; Bradshaw 1981, p. 631) although in the illustrations the wall appears to be composed only of the superposed nested menisci rather than being a discrete structure. This also appears to be the case in the giant burrows illustrated by Allen and Williams (1981). The vertical orientation of many of these continental occurrences (Allen and Williams 1981; Bracken and Picard 1984) may indicate an escape element that would further separate them from normal '*Muensteria*' of authors.

Examination of unweathered material will be necessary to clarify the relationship between *Beaconites*, *Taenidium*, and *Ancorichnus* (as emended by Frey *et al.* 1984).

Phoebichnus Bromley and Asgaard, 1972

Discussion. The strongly walled *Phoebichnus trochoides* is distinguished by its special wall construction and radiating morphology (Bromley and Asgaard 1972; Bromley and Mørk 1984).



TEXT-FIG. 10. MGUH 17556, a branching, annulated, meniscate structure in hyporelief, from the Upper Permian, Domkirken, Scoresby Land, central East Greenland (L. Stemmerik Collection); arrow indicates the meniscate fill where the thick wall is broken away. Scale, 2 cm.

Ancorichnus Heinberg, 1974

Discussion. Among the unbranched meniscate trace fossils, *Ancorichnus* is distinctive in having a well-developed, unornamented wall structure. In *A. coronus* Frey *et al.*, 1984, and *A. capronus* Howard and Frey, 1984, the wall material is far less well developed than in the type ichnospecies *A. ancorichnus*, and their ichnogeneric placing is therefore questionable.

Branched septate burrow having wall structures

Discussion. There is a distinctive group of branched trace fossils that has a resemblance to *M. annulata* Schafhäutl, possessing a complicated and thick wall structure. These walled trace fossils have received heterogeneous taxonomic treatment, and it is not clear to which ichnogenus or ichnogenera they should be referred (but see D'Alessandro, Bromley, and Stemmerik, in prep.).

As in the case of the *Nereites*/*Scalarituba*/*Neonereites* group, the walled, branched, septate burrows have a complicated structure that is capable of producing widely varying morphologies according to the stratinomic position and taphonomic processes. Thus, in semirelief, the annulated or striated external sculpture of the walling material is emphasized (e.g. D'Alessandro 1982, pl. 40), whereas only in axially sectioned material is the septate central backfill visible (text-fig. 10).

Fucusopsis was used by Książkiewicz (1970, 1977) for structures of this kind, and *Radionereites* by D'Alessandro (1982). Neither ichnogenus has been demonstrated to have septate interiors, however. Pemberton and Frey (1982) placed *Fucusopsis* in synonymy with the non-septate *Palaeophycus*. Topotypic material of *Radionereites* (kindly supplied by M. Gregory) confirms that D'Alessandro's form does not belong to this ichnogenus.

Cladichnus ichnogen. nov.

1858 *Muensteria* (*Keckia*) *annulata* Schafhäutl; Fischer-Ooster (*partim*), p. 37, pl. 7, fig. 4 (*non* fig. 3 = *Chondrites*); pl. 12, fig. 8.
1877 *Taenidium fischeri* Heer, p. 162, pl. 67, figs. 1–5, 7.
1881 *Taenidium lusitanicum* Heer, p. 12, pl. 20.
1887 *Muensteria annulata* Squinabol, p. 554, pl. 17, fig. 3.

1947 *Saportia striata* Wilckens (*non* Squinabol), p. 41, pl. 7, fig. 3.
1947 *Taenidium lusitanicum* Heer; Wilckens, pp. 41–45, pl. 6, figs. 1 and 2; pl. 7, fig. 1.
1955 *Taenidium fischeri* Heer; Seilacher, fig. 5.83.
1958 *Taenidium fischeri* Heer; Seilacher, p. 1073, table 3, fig. 48.
1962 *Taenidium* Heer; Häntzschel, fig. 136.2.
non 1971 *Taenidium annulatum* Schafhäutl; Chamberlain, pl. 32, fig. 12.
1975 *Taenidium* Heer; Häntzschel (*partim*), p. 112, fig. 70.1.
1977 *Taenidium fischeri* Heer; Książkiewicz, pl. 5, fig. 3.
1978 *Taenidium* Heer; Kern, p. 249, fig. 8F.
1983 *Taenidium* ichnosp. Pedersen and Surlyk, p. 53, fig. 12.
1986 *Taenidium annulatum* Schafhäutl; D'Alessandro *et al.*, p. 300, fig. 5C.

Derivation of name. Greek *klados*, branch.

Type species. Cladichnus fischeri (Heer, 1877).

Diagnosis. Annulated or monilliform burrow fills composed of meniscus-shaped segments, comprising primary successively branched and radiating systems; wall lining lacking or very thin.

Discussion. These meniscate burrow fills have a smooth outer sculpture and are annulated or monilliform. They show primary successive branching, generally at acute angles, and the menisci are concave towards the proximal direction. Branching may produce a radiating plan (*C. fischeri*; text-fig. 11), or be palmate (*C. lusitanicum*) or dendroid (*Taenidium* ichnosp. of Pedersen and Surlyk 1983). It is uncertain whether or not the type species has a wall structure. If it has, it is no more than a film-like or insignificant skin. In the figure of Heer (1877, pl. 67, fig. 6) in which a wall is indicated, the illustration is said to represent the condition 'in life' (as an alga!) and is therefore a spurious reconstruction. Heer (1881, pl. 20) and Pedersen and Surlyk (1983, fig. 12C) indicated a very thin wall material.

Cladichnus fischeri (Heer, 1877)

Text-fig. 11

? 1858 *Muensteria* (*Keckia*) *annulata* Schafhäutl; Fischer-Ooster (*partim*), p. 37, pl. 7, fig. 4 (*non* fig. 3); pl. 12, fig. 8.
1877 *Taenidium fischeri* Heer, p. 162, pl. 67, figs. 1–5, 7.
1887 *Muensteria annulata* Squinabol, p. 554, pl. 17, fig. 3.
1955 *Taenidium fischeri* Heer; Seilacher, fig. 5.83.
1958 *Taenidium fischeri* Heer; Seilacher, p. 1073, table 3, fig. 48.
1962 *Taenidium* Heer; Häntzschel, fig. 136.2.

TEXT-FIG. 11. Field photograph of *Cladichnus fischeri* (Heer, 1877) from the same horizon as the *Taenidium satanassi* material. Scale, 1 cm.

1975 *Taenidium* Heer; Häntzschel (*partim*), p. 112, fig. 70.1.
1977 *Taenidium fischeri* Heer; Książkiewicz, pl. 5, fig. 3.
1978 *Taenidium* Heer; Kern, p. 249, fig. 8F.
1986 *Taenidium annulatum* Schafhäutl; D'Alessandro *et al.*, p. 300, fig. 5C.

Diagnosis. Radiating and primary successively branched *Cladichnus.*

Discussion. Muensteria annulata Schafhäutl, 1851, is not listed as a synonym because it is a dubious structure. In the illustration it closely resembles the branching, septate, walled burrow, but it is not clear whether or not a wall structure is present. Heer considered *M. annulata* a synonym of his *T. fischeri.*

Most *Cladichnus* show a tendency to radial development. In some examples (text-fig. 11) the radiating burrow fills are generally straight, originate at several levels from a central shaft, and show little or no subsequent branching. In others, branching of the radial elements may occur but to what extent is hard to discern. In early illustrations suggesting algal origin (e.g. Heer 1877, pl. 67, fig. 1), simultaneous filling is suggested, but it is probable that most such branching is in fact intersection, compacted close application of elements, and primary subsequent branching. In lower Tertiary material from Italy (text-fig. 11), extreme compaction has given the impression of true branching in cases where intersection can be demonstrated by careful inspection.

Other ichnospecies of *Cladichnus*

We place *T. lusitanicum* Heer, 1881, temporarily in *Cladichnus* owing to its primary successive branching pattern and meniscate fill. However, its palmate form is highly distinctive and represents a fundamentally different burrowing behaviour from the radiating forms. Pedersen and Surlyk's (1983) *Taenidium* ichnosp. has a root-like branching pattern and appears to be a distinct ichnospecies of *Cladichnus.*

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AMMONITES FROM THE TYPE SANTONIAN AND ADJACENT PARTS OF NORTHERN AQUITAINE, WESTERN FRANCE

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ABSTRACT. The ammonite fauna of the Santonian stage in its type area and adjacent parts of northern Aquitaine is revised, and five species recognized: *Placenticeras polyopsis* (Dujardin, 1837), *P. paraplanum* Wiedmann, 1978, *Texanites* (*Texanites*) *gallicus* Collignon, 1948, *Eulophoceras austriacum* (Summesberger, 1979) and *Boehmoceras loescheri* Riedel, 1931. The Santonian corresponds to the range zone of *P. polyopsis*, the *P. syrtale* of European authors, a view already expressed by A. de Grossouvre in 1901; no finer zonal division based on ammonites is recognizable.

THE Santonian is the middle division of the now redundant Senonian Stage. The latter term was introduced by Alcide d'Orbigny in 1843; the former by Henri Coquand in 1857. Saintes was mentioned by d'Orbigny as a typical area for the Senonian in the *Cours Elementaire* (1852, pp. 669-691); it and its environs—Saintoinge—give the Santonian its name. The original definition of the Santonian was as follows (Coquand 1857*b*, p. 749):

> Deuxième étage.—Santonien.
>
> Craie tendre avec silex (*Pleurotomaria santonesa*, d'Orb., *Rhynchonella vespertilio*, d'Orb., *R. intermedia*, Coquand, *Terebratula Nanclasi*, Coq., *Micraster laxoporus*, d'Orb., *Hemiaster stella*, Desor, *Salenia geometrica*, Agass.).

The stratotypes of the Santonian are localities cited by Coquand in 1856 for his 'Troisième sous-étage' of the 'Prèmiere étage' (which he subsequently named Santonian). They are 'les bords de la Charente jusqu' aux côteaux qui, à partir de Gimeux, Genté, Ségonzac, dessinent une bourrelet saillant parallèle aux dernières rides de la craie inférieur. Ce plain, qui prend le nom de *Petit-Champagne* . . . Une excellent étude de ce système peut se fair dans les environs du Château de Malberchie' (Coquand 1856, pp. 86-87). 'Road-side sections at Javrezac' are not the only locality mentioned specifically by Coquand, as van Hinte (1979) claims.

In 1859, Coquand listed the fauna of his Santonian, recording the following ammonites (p. 978), none of which has been traced: (1) *Ammonites Bourgeoisi* d'Orbigny, 1850; this is a Coniacian *Protexanites* (Kennedy 1984*a* p. 105, pl. 23, figs. 1-4, 7-9; pl. 24, figs. 1-8; pl. 26, figs. 4 and 5; text-figs. 32, 33, 34, 35A-E, 36B, C, E, F). (2) *A. Orbignyi* d'Archiac, 1843; this is unrecognizable. (3) *A. polyopsis* Dujardin, 1837; this is an exclusively Santonian *Placenticeras* (Kennedy and Wright 1983 p. 856, pls. 86-88; text-figs. 1-4; see below). (4) *A. santonensis* D'Orbigny, 1850; this is a *Neoptychites cephalotus* (Courtiller, 1860) of the Turonian (Kennedy and Wright 1979 p. 676, pl. 86, figs. 4 and 5). (5) *A. coniaciensis* Coquand, 1859; this was described as follows:

> 'Hauteur, 65 millim.; diamètre transversal, 55 millim. Coquille comprimée, assez largement ombiliquée, spire formée de tours convexes, ornée de côtes alternativement simples et bifides, chaque tour possède cinq rangées de tubercules; la première disposée autour de l'ombilic, deux médianes et deux près du pourtour externe; celle qui est la plus rapprochée du dos et qui termine les côtes est saillante. Dos caréné, carène tranchante logée entre deux sillons.
>
> Cette espèce à été toujours confondue avec 1' *A. varians.*—Cognac, Malberchie, Épagnac.'

[Palaeontology, Vol. 30, Part 4, 1987, pp. 765-782, pls. 80-82]

COQUAND 1856 "1^{re} nomenclature"	COQUAND 1857, 1858 "2^{e} nomenclature"	COQUAND 1857 "3^{e} nomenclature"	ARNAUD 1877
1^{er} ETAGE 5e horizon de Rudistes 3^{e} sous-étage Craie tendre, à silex	2^{e} ETAGE: SANTONIEN Craie tendre avec silex Pleurotomaria Santonesa, Janira Truellei, Spondylus hippuritorum, Rhynchonella vespertilio, Rhynchonella intermedia, Terebratula Nanclasi, Micraster laxoporús, Hemiaster stella, Salenia geometrica	2^{e} ETAGE: SANTONIEN 7e horizon de Rudistes Micraster brevis, Spondylus truncatus, Rhynchonella vespertilio, Radiolites Arnaudi	Calcaire noduleux, glauconieux Conoclypeus ovum Marnes et grès supérieurs Ostrea acutirostris, Sphaerulites Hoeninghausi Marnes à Ostrea vesicularis et Ostrea proboscidea Marnes et grès inférieurs Rhynchonella deformis, Botriopygus

TABLE 1. Correlation of previous subdivisions of the Santonian in northern Aquitaine.

This is a very clear description of a *Texanites* (*Texanites*) but is insufficiently detailed to determine which species is described. In the absence of type specimens I regard it as a *nomen dubium*. (6) *Baculites incurvatus* Dujardin, 1837; this is a Coniacian-Santonian species (Kennedy 1984*a* p. 143, pl. 32, figs. 12, 15-19; pl. 33, figs. 1-22; text-figs. 41 and 42F-M). (7) *Scaphites constrictus* d'Orbigny, 1842; the correct author is J. Sowerby, 1817; the species is a Maastrichtian *Hoploscaphites* (Kennedy 1986*a* p. 64, pl. 13, figs. 1-13, 16-24; pl. 14, figs. 1-38; pl. 15; text-figs. 9 and 11A-H).

Arnaud (1862-1897) refined the stratigraphy of the Cretaceous of the Aquitaine Basin, and his vast collections form the basis of the present study.

His initial division of the stage (1877*b*, p. 3) was:

2^{e} série: *Santonien*

18. Marnes et grès inférieurs: *Rhynchonella deformis*; *Botriopygus*
19. Marnes à *Ostrea vesicularis* et *O. proboscidea*
20. Marnes et grès supérieurs: *Sphaerulites Hoeninghausi*, *Ostrea acutirostris*;
21. Calcaire noduleux glauconieux; *Conoclypeus ovum*.

A letter system replaced this in the summary diagram at the end of this work, and was the basis of all later modifications, summarized in Table 1 herein.

De Grossouvre (1894) used Arnaud's Collections for his revision of the ammonites of the 'Craie Supérieur', referring specimens to the Arnaud letter divisions and recognizing a Santonien Inférieur and Supérieur in his tabulation of ranges. In 1901 de Grossouvre repeated Arnaud's letter system in his account of the 'Craie de l'Aquitaine' (pp. 351 et seq.). He records *Mortoniceras serratomarginatum* Redtenbacher, *M. texanum* Roemer, *Placenticeras syrtale*, and *Baculites incurvatus* from M^1, *M. texanum* and *P. syrtale* from M^2, the latter extending to N^2. In his summary chapter 22 (Classification des couches supracrétacées, p. 751 *et seq.*), the Santonian is defined as follows (p. 795): 'Le Santonien comprend les couches situées au-dessus du Coniacien et inférieurs à la zone à *Placenticeras bidorsatum*, par laquelle débute le Campanien; *Pl. syrtale* existe sur toute la hauteur de cet étage, on pourrait encore le définir comme constituant l'assize du *Pl. syrtale*.' From his work in the Corbières, de Grossouvre recognised what would now be called

ARNAUD 1877		ARNAUD 1883		DE GROSSOUVRE 1901	
				ZONES	AQUITAINE
Marnes et grès santoniens supérieurs	N^c Calcaire glauconieux à Conoclypeus ovum N^b Banc à Ostrea acutirostris N^a Grès à Sphaerulites Hoeninghausi	N^2	Grès ou calcaire marneux, avec ou sans silex, et géodes de quartz Ammonites polyopsis, etc.	Placenticeras syrtale	Calcaire sableux à Rudistes Marnes à Ostracées
Marnes à Ostrea vesicularis et Ostrea proboscidea		N^1	Calcaire marneux avec silex, passant à des marnes grises ou verdâtres, pétries d'Ostracées O.vesicularis, etc.		
		M^2	Calcaire marneux ou noduleux grès calcarifère Ammonites polyopsis, etc.		
Marnes et grès santoniens inférieurs Botriopygus Toucasanus				Mortoniceras texanum	Banc à Botriopygus Couches à Ammonites texanus
		M^1	Calcaire marneux arénacé Ammonites coniacensis, etc.		

assemblage zones within the Santonian, a lower one characterized by the occurrence of *Mortoniceras texanum*, and an upper one with *P. syrtale* and *Pachydiscus isculensis* as indices (table 35, following p. 830) or with *Placenticeras syrtale* alone as index (tables 36–39, following p. 830). A *texanum* + *syrtale* Zone were recognized by Haug (1911), while the Colloque sur le Crétacé Supérieur held in 1959 (Dalbiez 1960) recognized a *texanus* Zone below and a *syrtale–isculensis* Zone above.

As I have noted elsewhere (Kennedy 1984*b*, 1985) neither *P. syrtale* nor *M. texanum* occur in France, while in Aquitaine it is only possible to define the Santonian in ammonite terms by the appearance of *Texanites* (*Texanites*) and as the range zone of *P. polyopsis* Dujardin, 1837 (= *syrtale* of European authors); I have traced only five surviving texanitids from the Santonian in Aquitaine: they are recorded from M^1, M^2, and N^2. I have seen no specimens referable to *Paratexanites serratomarginatus* (Redtenbacher, 1873), recorded by de Grossouvre and by Gillard (1944) from M^1; elsewhere I have suggested it to be exclusively Upper Coniacian in France (Kennedy 1984*a*, p. 117, pl. 23, figs. 5 and 6; pl. 26, figs. 1–3; pl. 27, figs. 1–7; text-fig. 35F, G), and de Grossouvre (1901) ultimately concluded that Santonian *P. serratomarginatus* were actually *P. emscheris* (Schlüter, 1876), I have equally seen none of these from Aquitaine, nor of the Coniacian *Protexanites bourgeoisi* (d'Orbigny, 1850) noted from the Lower Santonian by de Grossouvre in 1894 (table, p. 86).

The ammonite distributions from the present work can be summarized as follows:

Placenticeras polyopsis (Dujardin, 1837)	M^1	M^2	N^1	N^2
P. paraplanum Wiedmann, 1978	—	—	—	N^2
T. (*Texanites*) *gallicus* Collignon, 1948	M^1	M^2	—	—
Eulophoceras austriacum (Summesberger, 1979)	—	—	—	N^2
Boehmoceras loescheri Riedel, 1931	—	M^2	N^1	—

I see no possibility of subdividing the Santonian in ammonite terms in Aquitaine, a disappointing result when compared with the results from my revision of the Coniacian Kennedy (1984*a*) and Campanian of the region (Kennedy 1986*b*).

Low diversity and small numbers of individuals are an obvious explanation for this. There are striking differences in stratigraphic ranges of taxa common to Aquitaine and the richly ammonitiferous sequences of the Corbières (Aude), as noted by de Grossouvre (1901) and Bilotte and Collignon (1983), so that some environmental limitation on ammonite occurrence might be involved. To this must be added the marked coarsening in resolution of ammonite zones in successive stages of the Upper Cretaceous. Taking the time scales of Odin (1985) and Snelling (1985) and the standard zonations for the Upper Cretaceous stages in north-west Europe proposed by Kennedy (1984*b*), average zonal durations are as follows: Cenomanian (4 Ma) 0·57 Ma; Turonian (4 Ma) 0·75 Ma; Coniacian (2 Ma) 0·5 Ma; Santonian (3 Ma) 3 Ma; Campanian (11 Ma) 2·7 Ma. No zonal division based on ammonites can be recognized in the Maastrichtian (7 Ma) of north-west Europe at this time. A 3 Ma *polyopsis* Zone for all of the Santonian is thus of the same order of duration as the succeeding Campanian zones recognized in Aquitaine.

Location of specimens. The following abbreviations are used to indicate the location of specimens mentioned in the text:

EMP: École des Mines, Collections, now at the Université Claud Bernard, Lyon.
FSL: Université Claude Bernard, Lyon.
GPIB: Geological and Palaeontological Institute, Bonn.
SP: Collections of the Sorbonne, now housed in the Université Pierre et Marie Curie, Paris.

Suture terminology. The system of Wedekind (1916) as revised by Kullmann and Wiedmann (1970) is used here. E = external lobe, L = lateral lobe, U = umbilical lobe, I = internal lobe.

Dimensions. All dimensions are given in millimetres; D = diameter, Wb = whorl breadth, Wh = whorl height, and U = umbilicus; c = costal and ic = intercostal. Figures in parentheses refer to dimensions as a percentage of diameter. The term *rib index* as applied to heteromorphs is the number of ribs in a distance equal to the whorl height at the mid point of the interval counted.

Synonymies. Only citations which include illustrations of material or important systematic, stratigraphic, or geographic information are included.

SYSTEMATIC PALAEONTOLOGY

Order AMMONOIDEA Zittel, 1884, pp. 355, 392
Suborder AMMONITINA Hyatt, 1889, p. 7
Superfamily HOPLITACEAE H. Douvillé, 1890, p. 290

[*Nom. correct.* Wright and Wright, 1951, p. 21 (*pro* Hoplitida Spath, 1922a, p. 95, *nom. transl. ex* Hoplitidae Douvillé, 1890, p. 290)]

Family PLACENTICERATIDAE Hyatt, 1900, p. 585

[= Hypengonoceratinae Chiplonkar and Ghare, 1976, p. 2; Baghiceratinae Chiplonkar and Ghare, 1976, p. 3]

Genus PLACENTICERAS Meek, 1876, p. 462

[see Kennedy and Wright 1983, p. 869 for synonymy]

Type species. Ammonites placenta DeKay, 1828, p. 278, by original designation by Meek, 1876, p. 462.

Placenticeras polyopsis (Dujardin, 1837)

1837 *Ammonites polyopsis* Dujardin, p. 232, pl. 17, fig. 12.
1983 *Placenticeras polyopsis* (Dujardin, 1837); Kennedy and Wright, p. 856, pls. 86–88; text-figs. 1–4 (with full synonymy).
1983 *Placenticeras syrtale* (Morton); Collignon, p. 200, pl. 6, fig. 1.

1983 *Stantonoceras guadaloupae* (Roemer); Collignon, p. 201, pl. 6, fig. 3.
1983 *Stantonoceras guadaloupae* (Roemer) var. *quadrata* de Grossouvre; Collignon, p. 201, pl. 6, fig. 2.
1983 *Stantonoceras depressum* (Hyatt); Collignon, pl. 202, pl. 7, fig. 2.
1985 *Placenticeras polyopsis* Dujardin; Kennedy, pl. 2, figs. 7–10.

Lectotype. The original of Dujardin 1837, pl. 17, fig. 12*a*, a juvenile macroconch from the 'Craie Tufau' of Touraine, France; designated by Kennedy and Wright 1983, p. 856; present whereabouts unknown.

Material. Numerous specimens. SP unregistered *ex* Arnaud Collection, from Assise M^1, Larat; M^2, L'Ombre, Miremont, Colombier du Miremont, Ribérac, Périgueux, route d'Agonac (Périgueux), Beaulieu (Siolac, Souterrain de Beaulieu), St Léon-sur-Vezère, Champagnac-de-Belair, Versannes, Épagnac, Puygaty, Rognac; M^{1-2} at Angoumac, Cognac; N^{1-2}, St Caprais, N^2 at Arcivaux, Saintes, Foquebrune, and Sarlat, route d'Eyzies. EMP *ex* Boucheron Collection, from La Valette. M. Séronie-Vivien Collection: SX62, from Mater (= *Stantonoceras guadaloupae* in Séronie-Vivien 1972, text-fig. 26); 5579*e*, 80*e*, Castelfadézé (= *S. guadaloupae* in Séronie-Vivien 1972, p. 88); SU2B, 2C, from l'Amblardie (= *S. guadaloupae* in Séronie-Vivien 1972, p. 78); J. P. Platel Collection: three specimens from Agonac.

Discussion. The Aquitaine material noted above adds nothing to the detailed description of the species given by Wright and Kennedy (1983).

Occurrence. Widespread in Aquitaine, ranging from low in M^1 to N^2. Also known from Touraine, Corbières, the Beausset Basin (Var) in France, Austria, the Germanies, and the Tombigbee Sand Member of the Eutaw Formation in Alabama. See detailed discussion by Wright and Kennedy (1983).

Placenticeras paraplanum Wiedmann, 1978

Plate 80, figs. 1–3, 8–10

1978 *Placenticeras paraplanum* Wiedmann, p. 666, pl. 1, figs. 3 and 4; text-fig. 2*a*.
1979 *Placenticeras paraplanum* Wiedmann; Summesberger, p. 152, pl. 13, figs. 53–57; text-figs. 38 and 39.
1985 *Placenticeras* aff. *paraplanum* Wiedmann; Amédro and Hancock, p. 24 *et seq*., text-fig. 11*a–c*, *f*, *g*.

Holotype. By original designation, the original of Wiedmann 1978 pl. 1, figs. 3 and 4; text-fig. 2A, from the Upper Santonian Gosau Beds of the Gosau Basin, Austria.

Material. SP unregistered *ex* Arnaud Collection, from Assise N^2, Arcivaux, Saintes (Charente-Maritime); from Assise N^2, Beillant (Charente-Maritime); FSL, six specimens from the autoroute sections west of Saintes (details in Amédro and Hancock 1985).

Dimensions.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
SP, Arcivaux	84·2 (100)	25·5 (30·3)	39·7 (47·1)	0·64	17·0 (20·2)

Description. All specimens are ill-preserved composite moulds. Coiling moderately evolute, with 55 % of previous whorl covered. Whorl section compressed (Wb : Wh ratio 0·64), with greatest breadth at umbilical shoulder. Umbilicus small (20 % of diameter), shallow, conical, with flat, outwards-inclined wall. Umbilical shoulder narrowly rounded; inner flanks broadly rounded, outer flanks flattened, convergent. Venter narrow, concave with sharp shoulders at smallest diameter visible, broad, with shoulders blunter and broadly arched venter on outermost phragmocone whorl. Flank ornament distinctive, with markedly convex distant very broad ribs with steep apical face but apertural face that merges imperceptibly with flank; a strong furrow precedes each rib, and may develop into a marked constriction (Pl. 80, fig. 2), so that the shell surface has the step-like topography of a tiled roof. Flank ornament strengthens progressively through ontogeny, and, on the outer phragmocone whorl, is accompanied by blunt outer ventrolateral clavi, 9–10 per half whorl.

Sutures ill-exposed, typical for genus.

Discussion. The striking convex course of the flank ornament, furrows/constrictions plus late appearance of clavi separate this species from all other European forms referred to the genus. The early whorls show a striking resemblance to those of the much larger species *P. bidorsatum* (Roemer, 1841) (see revision in Kennedy 1986*b*). Indeed, Amédro and Hancock (1985) regarded some of the present specimens as transitional to *P. canaliculatum* (Hyatt, 1903), a synonym of *P. bidorsatum*. The adult ornament of the two is highly distinctive, but the similarity of early growth stages suggests that *bidorsatum* is a hypermorphic giant derivative of *paraplanum*.

Occurrence. Assise N^2 in Aquitaine; high Santonian of the Corbières (Aude); Upper Santonian of the Gosau Basin, Austria.

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894, p. 22

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

Family COLLIGNONICERATIDAE Wright and Wright, 1951, p. 30

[*nom. subst. pro* Prionotropidae Zittel, 1895, p. 530; *Prionotropis* Meek, 1876, p. 453, *non* Fieber, 1853, p. 127; = *Collignoniceras* Breistroffer, 1947; = Prionocyclidae Breistroffer, 1947, *ex Prionocyclus* Meek, 1876, p. 298, ineligible as family type]

Subfamily TEXANITINAE Collignon, 1948, p. 54 (9)

[*nom. transl.* Wright 1957, p. L429 *ex* Texanitinae Collignon, 1948, p. 54(9)]

Genus TEXANITES Spath, 1932, p. 379

Type species. Ammonites texanus Roemer, 1852, p. 31, pl. 3, fig. 1, by original designation.

Subgenus TEXANITES (TEXANITES) Spath, 1932, p. 379

Texanites (*Texanites*) *gallicus* Collignon, 1948

Plate 80, figs. 4–7; Plate 81, figs. 1–6

1894 *Mortoniceras texanum* F. Römer sp.; de Grossouvre, p. 80, pl. 16, figs. 2 and 4; pl. 17, fig. 1.
1948 *Texanites texanus* Roemer var. *gallica* Collignon, p. 75 (30), pl. 8 (2), fig. 1.
1963 *Texanites texanus gallica* Collignon, 1948; Young, p. 81, pl. 38, figs. 3 and 4.
1966 *Texanites gallicus* Collignon; Collignon, p. 78, pl. 487, fig. 1964; pl. 508, fig. 2020; pl. 509, fig. 2020.
1970 *Texanites gallicus* (Collignon); Matsumoto, pp. 267, 270, 272.
1980 *Texanites texanus* s. l. (Roemer, 1852); Klinger and Kennedy, p. 162 (*pars*), text-figs. 124 and 125.
1982 *Texanites gallicus* Collignon; Martinez, p. 121, pl. 20, figs. 1 and 2.
1983 *Texanites gallicus* Collignon, 1948; Collignon, p. 203.
1985 *Texanites* (*Texanites*) *gallicus* Collignon, 1948; Kennedy, pl. 2, figs. 3–6.

Types. Collignon cites French, Venezuelan, Italian, Bulgarian, and Madagascan specimens in his text and synonymy, but failed to select a holotype. Young (1963, p. 81) presumed the original of de Grossouvre (1894,

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EXPLANATION OF PLATE 80

Figs. 1–3, 8–10. *Placenticeras paraplanum* Wiedmann, 1978. 1–3, FSL A362, from the Upper Santonian of Autoroute Cutting S2, west of Saintes (Charente-Maritime). 8–10, SP unregistered *ex* Arnaud Collection, from Assise N^2, Arcivaux, Saintes (Charente-Maritime).

Figs. 4–7. *Texanites* (*Texanites*) *gallicus* Collignon, 1948. SP unregistered *ex* Arnaud Collection, two paralectotypes, figured by de Grossouvre 1894, pl. 16, figs. 2 and 4, from Assise M^2, Nieul-le-Virouil (Charente-Maritime).

All figures are natural size.


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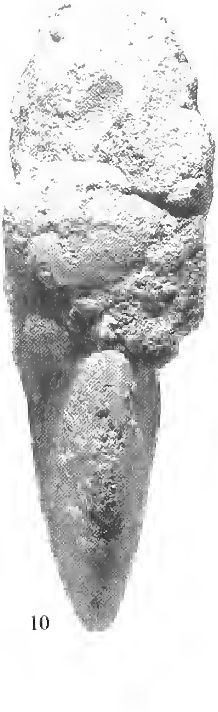
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KENNEDY, *Placenticeras*, *Texanites* (*Texanites*) pl. 17, fig. 1) to be the holotype, as did Martinez (1982, p. 121); in part 2 of his texanitid revision, Collignon (1948, p. 42 (99)) refers to this as the 'type', which I take to be a valid lectotype designation; it is from the Santonian of the Corbières. Two of the three small paralectotypes figured by de Grossouvre (1894, pl. 16, figs. 2 and 4) have been traced and are shown in Pl. 80, figs. 4–7; SP unregistered *ex* Arnaud Collection, from Assise M², Nieul-le-Virouil (Charente-Maritime).

Material. SP unregistered *ex* Arnaud Collection, an unregistered specimen from Assise M¹, Les Rentes, Cognac (Charente) plus a fragment from M¹, Sergéac. EMP unregistered: two specimens labelled Lavalette (Charente), without horizon indicated, *ex* Boucheron Collection.

Description. All specimens are composite moulds. Juveniles to a diameter of 66 mm are very evolute, whorls overlapping only to the extent that the marginal tubercle (4) is just concealed below the umbilical seam of the preceding whorl. Whorl section as wide as high at smallest diameter visible, becoming compressed as size increases, with greatest breadth at lateral (2) tubercle. Umbilicus broad (up to 44 % of diameter) and shallow. There are 32–36 ribs per whorl. They arise, singly or in pairs, at sharp umbilical bullae, of which there are approximately 22 per whorl in the best-preserved specimen, with occasional intercalatories arising low on the flank. Ribs are straight and prorsiradiate across the flanks, and bear a small conical inner lateral (2), rounded to feebly clavate submarginal (3), larger, rounded to feebly clavate marginal (4) and strong clavate external (5) tubercle. There is a sharp siphonal keel, flanked by deep, broad grooves.

A larger specimen (Pl. 8, figs. 5 and 6) is badly crushed, and 123 mm in diameter. At this size, there are 26 straight, prorsiradiate primary ribs per whorl; the umbilical (1), lateral (2), and submarginal tubercles are all markedly rounded, and the specimen closely resembles the lectotype.

Sutures not seen.

Discussion. Collignon (1948) correctly identified the differences between European specimens referred to *Texanites texanus* and the American lectotype, which is shown here in Text-figure 1. He erected two varieties, *gallica* and *hispanica*, later (1966) elevating them to specific rank. *T. gallicus* is certainly very distinct from *T. texanum*, having 50 % more ribs, markedly crowded and arising in pairs on the inner whorl. *T. texanum twiningi* Young, 1963 (p. 82, pl. 38, fig. 5; pl. 39, fig. 1; pl. 41, figs. 2 and 5; pl. 48, fig. 4) differs from the nominate subspecies only in its slightly higher rib density, and is equally distinct from *T. gallicus*. *T. hispanicus* is held to differ from *T. gallicus* by having the ribbing arising on the umbilical wall and a lateral (2) tubercle that migrates outwards to mid-flank during ontogeny. It and *T. gallicus* are probably conspecific, but the present material is inadequate for any firm conclusion on the point. There is also a close similarity to *T.* (*Texanites*) *quinquenodosus* (Redtenbacher, 1873), recently revised by Kennedy, Summesberger and Klinger (1981) (p. 126, figs. 8–16). They differ most obviously in the markedly clavate tubercles of *T. quinquenodosus* compared to the rounded tubercles in *T. gallicus*.

Occurrence. Assise M¹ and M² in Aquitaine, Lower Santonian of the Corbières; also recorded from Spain, Bulgaria, ?Italy, Venezuela and Zululand and from the Lower and Middle Santonian of Madagascar.

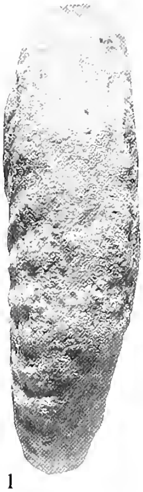
Family SPHENODISCIDAE Hyatt, 1900, p. 585
Subfamily SPHENODISCINAE Hyatt, 1900, p. 585
(= Libycoceratinae Zaborski, 1982, p. 306)
Genus *Eulophoceras* Hyatt, 1903, p. 85

(= *Praelibycoceras* H. Douvillé, 1912, p. 315; *Pelecodiscus* Van Hoepen, 1921, p. 30; *Sphenodiscoceras* Spath, 1921, p. 242; *Skoumalia* Summesberger 1979, p. 141)

Type species. Eulophoceras natalense Hyatt, 1903, p. 86, pl. 11, figs. 2–6.

EXPLANATION OF PLATE 81

Figs. 1–6. *Texanites* (*Texanites*) *gallicus* Collignon, 1948. 1–4, EMP unregistered *ex* Boucheron Collection, from Lavalette (Charente), without indication of precise horizon; 5 and 6, SP unregistered *ex* Arnaud Collection, from Assise M², Les Rentes, Cognac (Charente). All figures are natural size.



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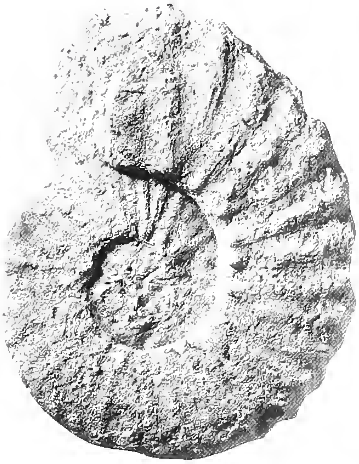

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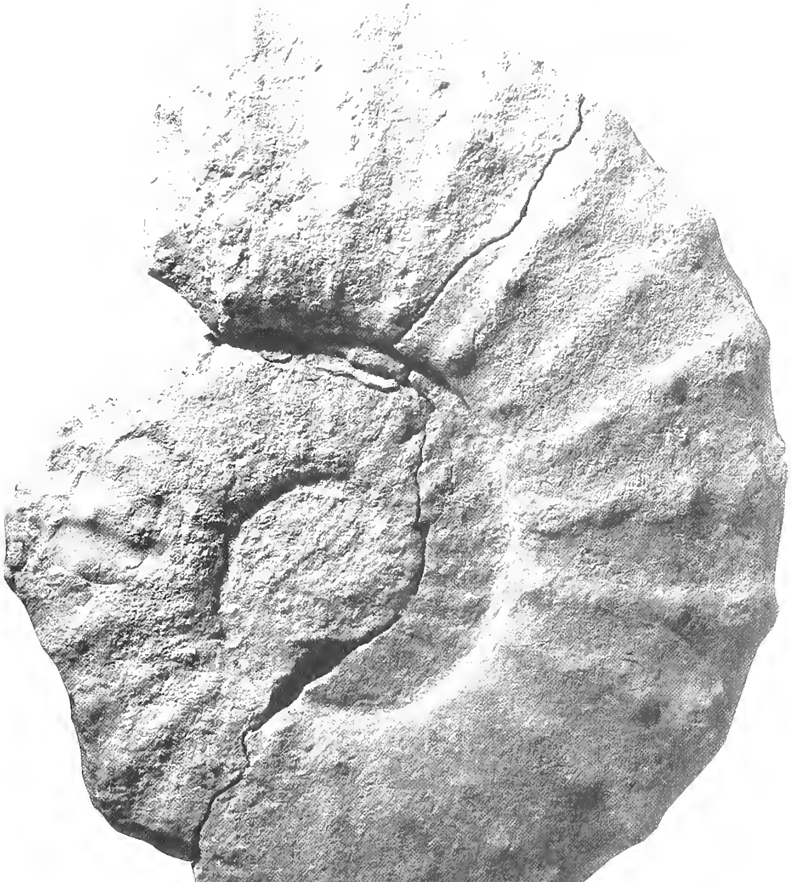

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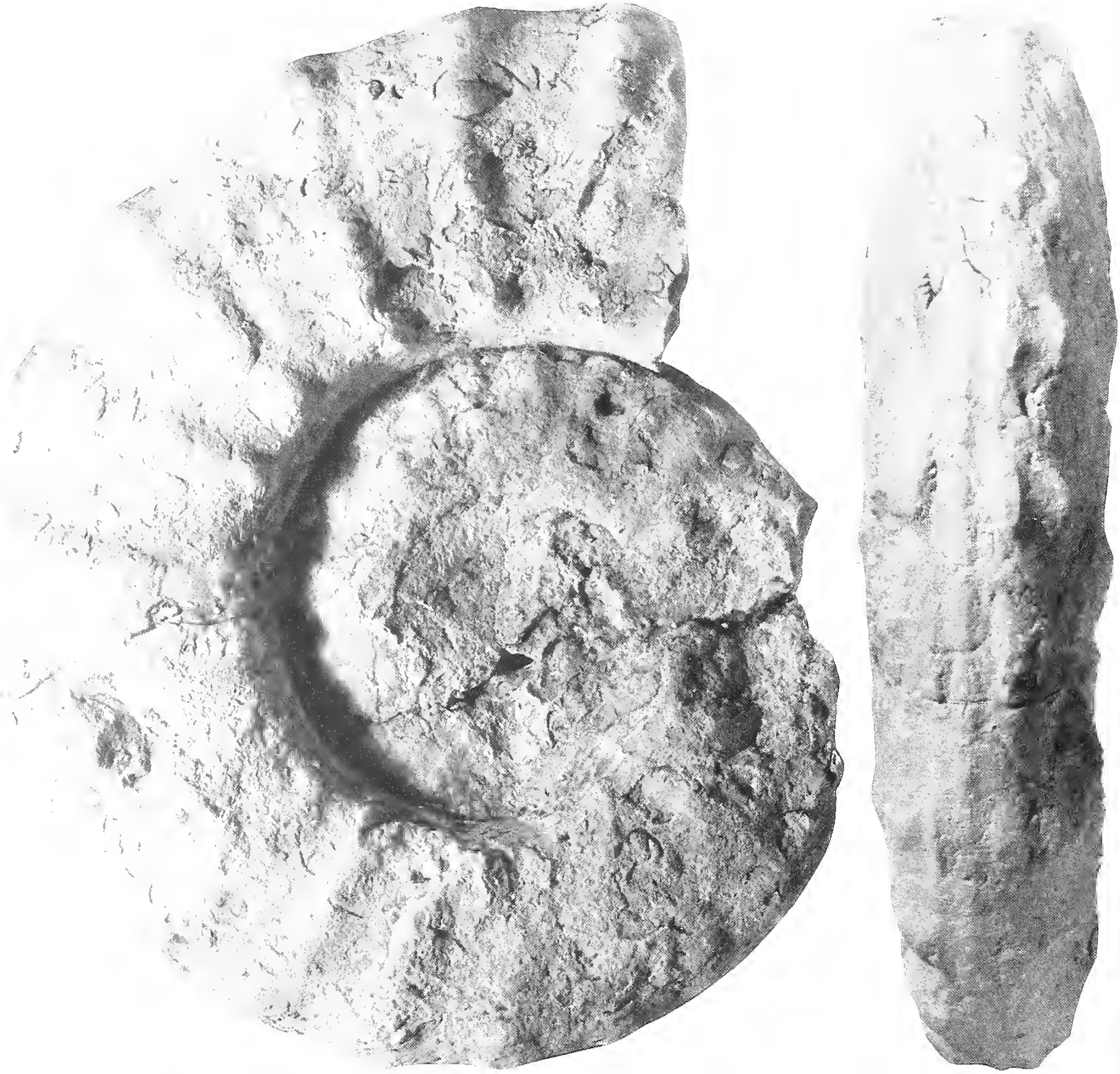
KENNEDY, *Texanites* (*Texanites*)



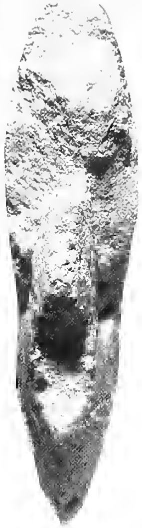
TEXT-FIG. 1. *Texanites* (*Texanites*) *texanus* (Roemer, 1851). The lectotype, GPIB 45*a*, the original of Roemer's pl. 3, fig. 1, from Austin, Texas. The original is 144 mm in diameter.

EXPLANATION OF PLATE 82

Figs. 1–3. *Eulophoceras austriacum* (Summesberger, 1979). FSL A363, from the Upper Santonian of Autoroute Cutting S2, west of Saintes (Charente-Maritime).

Figs. 4–16. *Boehmoceras loescheri* Riedel, 1931. All SP unregistered, *ex* Arnaud Collection; 4–6, 11–13, from Assise N^1, Charmant (Charente); 7–10, 14–16, from M^2, Nieul-le-Virouil (Charente-Maritime).

All figures are natural size.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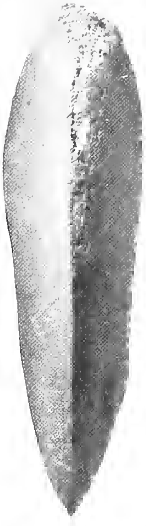
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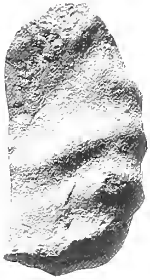
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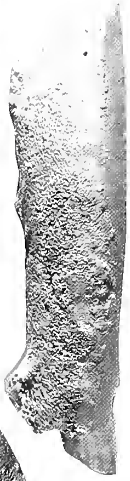
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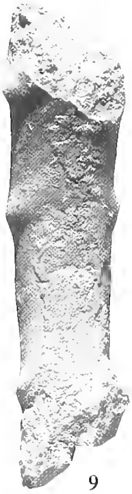
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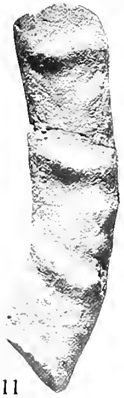
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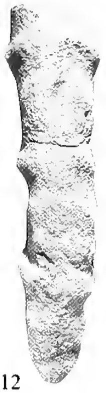
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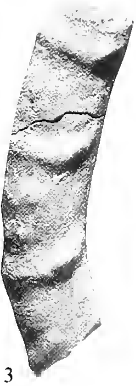
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KENNEDY, *Eulophoceras*, *Boehmoceras*

Eulophoceras austriacum (Summesberger, 1979)

Plate 82, figs. 1–3

1979 *Skoumalia austriaca* Summesberger, p. 141, pl. 9, figs. 37–41; text-figs. 26–30.
1980 *Skoumalia austriaca* Summesberger; Summesberger, p. 280, pl. 2, figs. 5 and 6; pl. 3, figs. 7 and 8; text-figs. 5 and 6.
1985 *Eulophoceras austriaca* (Summesberger); Amédro and Hancock, p. 23, fig. 11*d*, *e*.

Holotype. The original of Summesberger (1979, pl. 9, figs. 37 and 38) from the Upper Santonian of the Gosau Basin (Sandkalk Member, Bibereck, Hofergraben).

Material. A specimen from the autoroute cutting, S2, west of Saintes (Charente-Maritime) (see Amédro and Hancock 1985 for details); FSL collections, no. A363.

Description. The specimen is a composite mould. Oxycone. Umbilicus comprises less than 9 % of diameter. A marked facet separates flank from a more obtuse, sharper venter. Low, faint, broad, prorsiradiate, feebly concave ribs ornament the inner flank but decline by mid-flank, giving rise to low, falcoid, concave riblets and striae which strengthen periodically into small inner ventrolateral tubercles.

Sutures not seen.

Discussion. The single specimen corresponds to the feebly ornamented form B of *Skoumalia austriaca* Summesberger, 1979 (p. 141, text-figs. 29 and 30; pl. 9, figs. 39–41; 1982, p. 280, pl. 2, figs. 5 and 6; pl. 3, figs. 7 and 8; text-figs. 5 and 6). Form A, to which the holotype belongs, is much more strongly ornamented, with umbilical bullae.

Summesberger regarded *Skoumalia* as Diaziceratinae although uncertain as to the position of the subfamily. His illustrations of the suture (1979, text-figs. 27, 28, 30; 1982, text-fig. 6) show what may be the beginnings of an adventive lobe, suggesting Sphenodiscinae, to which I refer it, as a synonym of *Eulophoceras* Hyatt, 1903, because some specimens of the highly variable type species (of which *E. amapondense* (Van Hoepen, 1921), *E. umzambiense* (Van Hoepen, 1921), *E. tenue* (Spath, 1922*b*) and *E. minor* (Spath, 1922*b*) are synonyms) have umbilical bullae and feeble ventral nodes (e.g. Spath 1922*b* pl. 6, fig. 2).

The only other European occurrence of *Eulophoceras* is in the Corbières (Aude), where Collignon (1983, p. 205, pl. 7, figs. 4 and 5) has described two completely smooth specimens from the Upper Santonian as *E.* cf. *miloni* Hourcq, 1949 and *E. grossouvrei* Collignon, 1983, differentiating them on details of whorl section and the sutures, which were not illustrated. It is not possible to compare them usefully with the present material without detailed restudy, although larger specimens from the region (SP unregistered *ex* Toucas Collection) clearly represent a different species.

Occurrence. Upper Santonian of Austria and northern Aquitaine.

Suborder ANCYLOCERATINA Wiedmann, 1966, p. 54
Superfamily TURRILITACEAE Gill, 1871, p. 3
Family BACULITIDAE Gill, 1871, p. 3
[= Eubaculitinae BRUNNSCHWEILER, 1966, p. 24]
Genus BOEHMOCERAS Riedel, 1931, p. 690

Type species. By the subsequent designation of Wright 1957, p. L220: *Ancyloceras krekeleri* Wegner, 1905 p. 210, pl. 8, fig. 2.

Diagnosis. Medium-sized rapidly expanding criocones with compressed oval whorl section, venter flanked by shallow depressions, producing a blunt keel. Ornamented by straight to concave prorsiradiate primary ribs, strengthened into crescentic umbilical bullae or not, shorter intercalated ribs well-developed or not; ribs may split into secondaries on ventrolateral area giving a distinctive corded keel. Aperture with short dorsal and long ventral rostrum. Suture with rectangular bifid lobes and saddles.

Discussion. Recent authors place *Boehmoceras* in the Family Phlycticrioceratidae Spath, 1926 (e.g. Wright 1957, p. L220; Summesberger 1979, p. 117). It appears, rather, to be a recoiled baculitid, as briefly noted elsewhere (Kennedy and Wright 1985, p. 142). The ornament of crescentic ribs, strengthened into dorsolateral bullae in *Boehmoceras loescheri* Riedel, 1931, is a typical *Baculites* feature, as is the rostrate aperture and suture with rectangular bifid elements. Specimens illustrated here (Pl. 82, figs. 7–10, 14–16) show remarkable resemblance to the Coniacian *B. incurvatus* Dujardin, 1837 (p. 232, pl. 17, fig. 13; see Kennedy 1984*a*, p. 143, pl. 32, figs. 12, 15–19; pl. 33, figs. 1–22; text-figs. 41 and 42*f–m*); some body chambers of this species are markedly curved (e.g. Kennedy 1984*a*, pl. 33, figs. 4 and 7) and the genus *Boehmoceras* is yet another example (albeit short-lived) of recoiling in heteromorphs. Resemblance to *Phlycticrioceras* Spath, 1926 is superficial only. That genus has clearly differentiated ventrolateral and siphonal tubercles and a far more intricately subdivided suture (De Grossouvre 1894, text-fig. 88; Kennedy 1984*a*, text-fig. 42*e*). Two species are currently referred to *Boehmoceras*, *B. krekeleri* (Wegner, 1905) known from the Upper Santonian of the Münster Basin, North Germany and the Gosau Basin, Austria, and *B. loescheri* Riedel, 1931 which has the same geographic distribution plus the present records from Arnaud's Assizes M^2 and N^1 at Nieuil-le-Virouil (Charente-Maritime) and Charmant (Charente) respectively. Previous illustrations and the material before me provide too small a sample to determine whether these species actually merit separation.

Occurrence. Mid–Upper Santonian. North Germany, Austria, and northern Aquitaine, France. Santonian of Alabama and Texas in the USA (W. A. Cobban, pers. comm.).

Boehmoceras loescheri Riedel, 1931

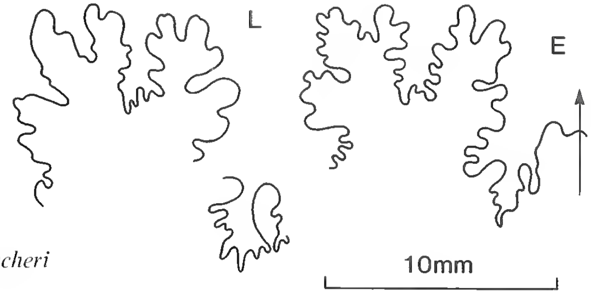
Plate 82, figs. 4–16; text-fig. 2

1931 *Boehmoceras löscheri* Riedel, p. 692, pl. 78, figs. 3–6.
1979 *Boehmoceras loescheri* Riedel; Summesberger, p. 119, pl. 2, figs. 15, 16, 18; text-figs. 9–12.
1983 *Boehmoceras* Kennedy and Wright, p. 866.
1985 *Boehmoceras* sp. Kennedy, pl. 2, fig. 1.

Types. Riedel's syntypes, if they survive, are in the collections of the Zentrales Geologisches Institut, Berlin. They are from the Upper Santonian of the Münster Basin, German Federal Republic.

Material. Five unregistered specimens in the SP Collections, *ex* Arnaud Collection. Two (Pl. 82, figs. 7–10, 14–16) are from Nieul-le-Virouil (Charente-Maritime), one labelled M^2, the other M ?; three specimens (Pl. 82, figs. 4–6, 11–13 plus an unfigured fragment) are from Charmant (Charente), labelled N^1.

Description. The smallest specimen available is from Charmant, and has a maximum preserved whorl height of 12 mm. It is highly distorted and the original whorl section is compressed at the apical end but depressed at the apertural. Coarse primary ribs are separated by interspaces approximately equivalent to the whorl height. They are feeble and convex across the dorsum, strengthening into coarse concave crescentic dorsolateral bullae that give rise to strong primary ribs that sweep across the flank before declining somewhat over the venter.



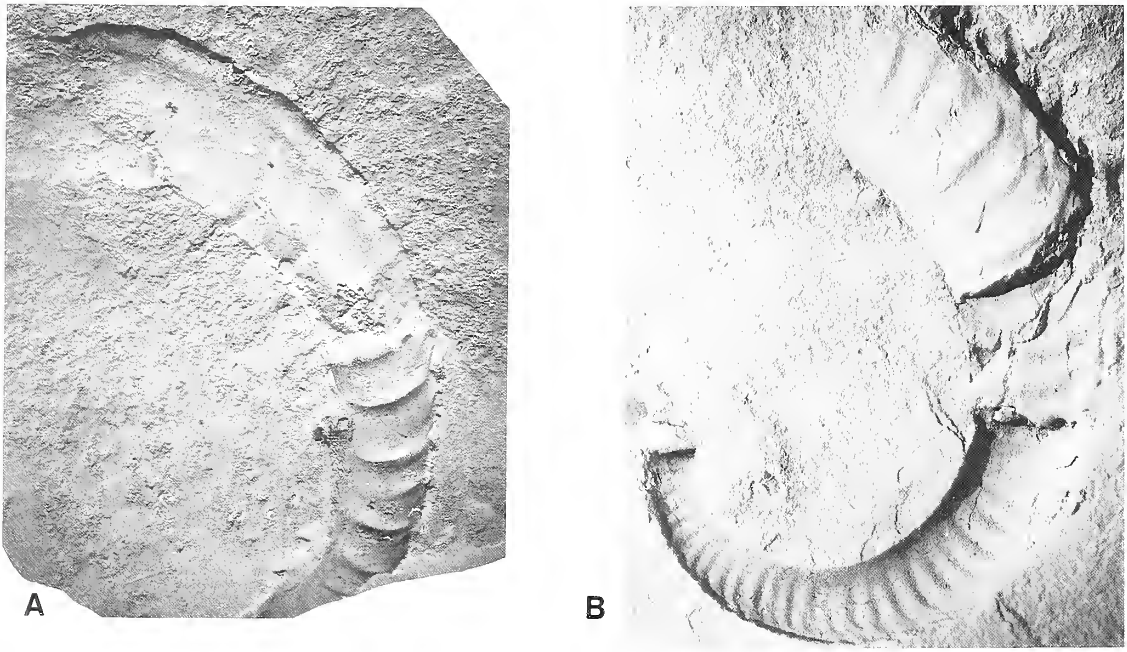
TEXT-FIG. 2. External suture of *Boehmoceras loescheri* Riedel, 1931.

One or two coarse, distant secondary ribs arise around mid-flank and cross the venter, without attaining the strength of the primaries. The unfigured fragment from Charmant is crushed but shows the same style of ribbing but with much weaker secondary ribs. The third fragment appears to be from close to the adult aperture and shows ribs that coarsen markedly over ventrolateral shoulders and venter (Pl. 82, figs. 4–6). The specimens from Nieul-le-Virouil are much better preserved undeformed internal moulds, one wholly the other part body chamber. The whorl section is compressed, with an intercostal whorl breadth to height ratio of 0·67–0·72, the dorsum broadly, the venter more narrowly rounded.

The primaries are very distant, feeble, and convex on the dorsum, sweeping back over the dorsolateral region and strengthening into crescentic dorsolateral bullae. These decline into concave ribs that project strongly forwards and decline over the venter.

Between are much finer secondaries, mere striae on the inner flank but strengthening over the venter. They appear distinctly scale-like in the body chamber fragment.

Suture line (text-fig. 2) with rectangular bifid lobes and saddles; moderately incised.



TEXT-FIG. 3A, B, *Boehmoceras krekeleri* (Wegner) Riedel, 1931, × 1. Specimens are from the Santonian of the Münster Basin, German Federal Republic, and in the Probenarchiv, Bernau (photographs courtesy of Zentrales Geologisches Institut, per H. Summesberger). B is the original of Riedel 1931, pl. 77, fig. 4.

Discussion. Marked differentiation of ribbing in the Aquitaine material indicates it should be referred to *B. loescheri*. The only other species, *B. krekeleri* (Wegner, 1905) (p. 210, pl. 8, fig. 2; Riedel 1931, p. 691, pl. 77, figs. 3–5; pl. 78, figs. 1 and 2; Summesberger 1979, p. 118, pl. 2, fig. 14; text-figs. 7 and 8) presents certain problems of interpretation, as noted by Summesberger (1979), for the type appears to be lost. Specimens subsequently referred to *B. krekeleri* by Riedel (see text-fig. 3) show uniform, rather closely spaced ribs, without the same degree of differentiation into primaries and secondaries. As noted above these differences may be within the limits of intraspecific variation. Without more material, it is impossible to say.

Occurrence. Upper Santonian of the Münster Basin (Recklinghäuser Sandmergel), Gosau Basin, Austria (Sandkalk Member, Bibereck, Hofergraben 1); Assise M^2 and N^1 in northern Aquitaine.

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SILURIAN MYODOCOPID OSTRACODES: THEIR DEPOSITIONAL ENVIRONMENTS AND THE ORIGIN OF THEIR SHELL MICROSTRUCTURES

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ABSTRACT. European Silurian myodocopid ostracodes form part of an almost exclusively pelagic, recurring faunal association. In general, they are facies related to typically laminated mud-silt or carbonate sequences deposited in relatively quiet, low energy, probably outer shelf to shelf slope environments. Their palaeogeographical and facies distributions may in part be due to depth control.

Reticulation, corrugation, and tuberculation are recognized as the true, genetically controlled external shell ornament in Silurian bolbozoid and 'cypridinid' myodocopids. In contrast, enigmatic polygonal and associated radiate shell microstructures, described from a wide variety of Silurian myodocopids, are interpreted as the surface expression of calcium carbonate platelets and possibly the result of *in vivo* shell calcification and post-mortem 'diagenetic' changes; they cannot, therefore, similarly be used in taxonomy.

A model based on analogues in Recent myodocopids and on possible variation in the pattern of nucleation centres in the shell is proposed to explain the mode, variety of styles, intraspecific, and ontogenetic variation of shell calcification in typical Silurian myodocopids. Pore canals may be the nucleation centres of calcium carbonate. If centres are numerous and densely arranged, this may account for the formation of closely packed, polygonal microstructural patterns on (and through) the shell. If nucleation centres are sparser and distant, calcification possibly terminates before all platelets can coalesce, thus accounting for observed patterns of isolated to clustered platelets of various larger sizes. Radiate ('rosette') type platelets are possibly produced when post-mortem acicular recrystallization affects various sized platelets. Smooth valves may represent newly moulted individuals; patches of platelets might indicate poor or an intermediate stage of calcification; specimens with densely packed platelets may have completed cuticle calcification.

THE last thirty years have witnessed substantial research on several major faunas of Silurian ostracodes (e.g. see Siveter 1978, 1980) but no monographic study has encompassed Silurian representatives of the extant order Myodocopida. Though treated in part by Canavari (1900) and Bouček (1936), our primary taxonomic knowledge of the group in the Silurian still relies largely on the work of Barrande (1872) and Jones (1861, 1873, 1884). However, as Siveter (1984) has shown, Silurian myodocopids are important and unique ecologically in possibly representing pioneer pelagic ostracode stock and they have unfulfilled biostratigraphical and biogeographical potential. This paper is our first of an intended series on British, Czechoslovakian, French, and Sardinian Silurian myodocopids (see also Palmer and Gnoli 1985) which will test this potential. We address a problem fundamental to classification within the group: what is the nature of their true external ornament and what is the nature, origin (biological or 'diagenetic'?), and significance of enigmatic microstructures which we have recognized in the shell of many types of Silurian myodocopids? Essentially, which of these characters can, and which cannot, be used taxonomically? In addition, we outline the distribution, depositional setting, and palaeoecology of Silurian myodocopids.

Herein myodocopid refers to Silurian myodocopines of two broad taxonomic groups, bolbozoids and 'cypridinids' (text-fig. 2). Entomozoid ostracodes (Silurian–Carboniferous) have traditionally been placed alongside the bolbozoids (in the Entomozoacea; Sylvester-Bradley *in* Moore 1961), with which they often occur in space and time in the Silurian. However, we would support a notion that the 'entomozoid' group (as currently, but erroneously, understood and used in the literature, e.g. forms such as *Entomis migrans*) is not closely related to typical myodocopines.

Silurian myodocopids are restricted mainly to finely laminated, fine-grained clastic sediments,

[Palaeontology, Vol. 30, Part 4, 1987, pp. 783–813, pls. 83–88.]

where they often occur in substantial numbers, with a recurring association of graptolites, nautiloids, and bivalves. They are typically preserved as mould faunas and partly for that reason have been so neglected.

By examination of our abundant, newly collected Silurian myodocopid material from Wales, France, and Czechoslovakia, and comparison with Recent myodocopids, it is concluded that the microstructures described herein from the Silurian shells are probably manifestations of both the calcification process and, to varying degrees, a diagenetic overprint. Such microstructures cannot, therefore, be used as characters in taxonomy. In order to explain the variety of observed shell microstructures in Silurian myodocopids, a model outlining possible modes of shell calcification in such groups is proposed.

EUROPEAN DISTRIBUTION OF SILURIAN MYODOCOPIDS

Both their morphology and pattern of distribution suggest a pelagic mode of life for typical Silurian myodocopids (Siveter 1984). European Silurian myodocopids are currently known from the Wenlock–Pridoli time interval and occur in the Welsh Basin of Britain, the Armorican Massif and Montagne-Noire of France, the Barrandian basin of Czechoslovakia, Poland, Sardinia, Portugal, and Spain (text-fig. 1). Although the range of facies within which they occur in these areas is somewhat restricted, this is an otherwise widespread geographic distribution, and contrasts with a generally more restricted distribution known from other Silurian ostracode assemblages. For example, Silurian ostracode faunas from Czechoslovakia (Bouček 1936) are dominated by non-palaeocopes and are substantially different in overall composition from contemporaneous, beyrichiacean rich faunas of northern Europe (e.g. Britain, Baltoscandia) and eastern North America (Siveter MS). In this case, though the barrier of the incipient 'mid-European' Rheic Ocean was perhaps hindering the dispersal of some invertebrate groups such as benthic palaeocopes and non-palaeocope ostracodes, the same was certainly not true of myodocopid ostracode species. Moreover, some Silurian myodocopids also occur in North Africa (unpublished information) and, for example, Australia (Jones 1861, 1873, 1884; De Koninck 1876; Strusz, pers. comm.). Because of this 'great extension of this old creature's habitat . . .' Jones (1884, p. 393) suggested a 'truely pelagic nature' for some '*Entomis*' myodocopids.

Localities and material. The material studied amounts to several thousand specimens from the following areas and localities. Information on the localities of all our collections will be given in later papers.

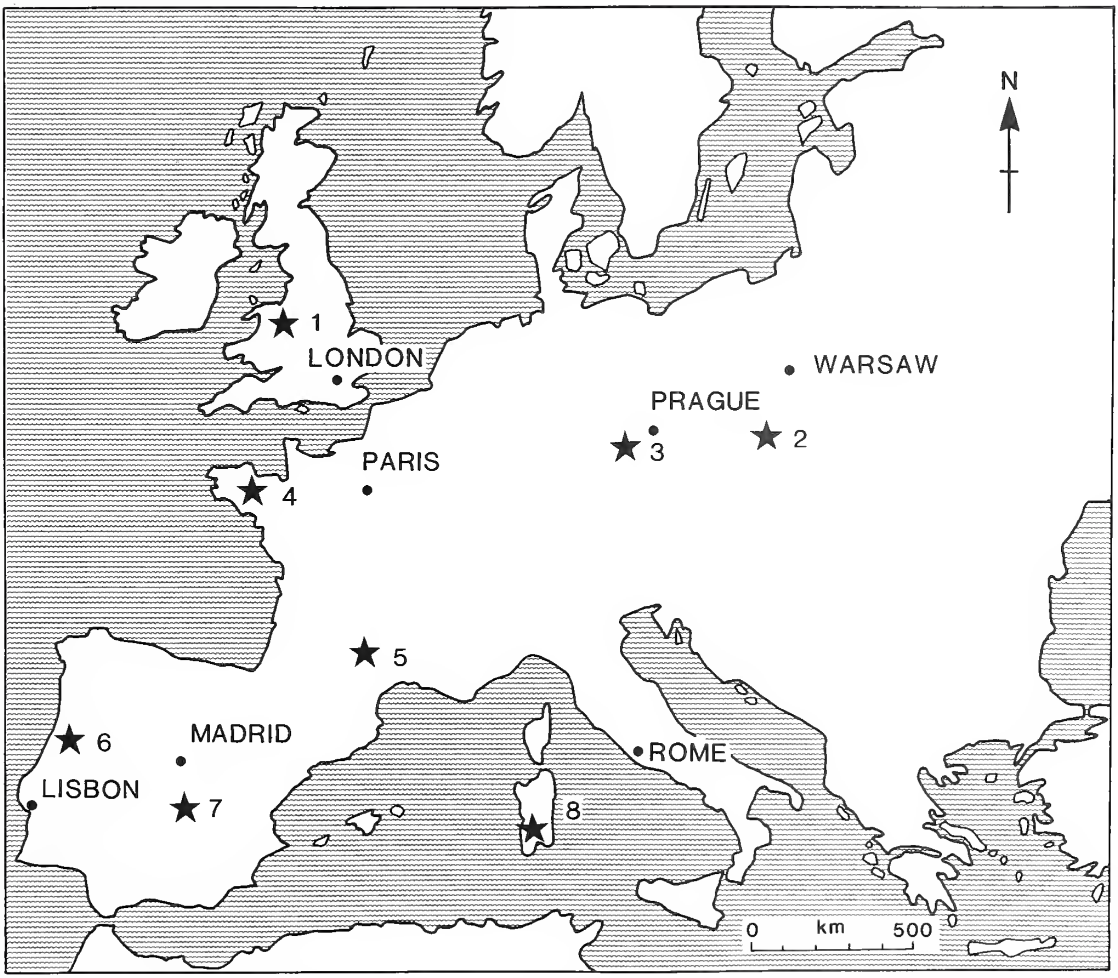
Armorican Massif, France. Localities in Ille-et-Vilaine, Mayenne, Sarthe, and Finistère. Their ages are determined typically using graptolites or chitinozoans, but are generally imprecisely known. Current studies on new graptolite collections may provide more finely resolved age determinations.

1. 'Les Buhardières'; exposure along D104 road between Saint-Germain-le-Fouilloux and Andouillé, Mayenne; Laval Synclinorium.
2. 'La Cultais'; outcrops near 'La Cultais' farm, Vieux-Vy-sur-Couesnon, Ille-et-Vilaine; Menez-Bélair Synclinorium. See Paris 1977, 1981.

Localities 1 and 2 belong to the upper part of La Lande Murée Formation (Paris 1981 and pers. comm.). The sediments ('ampelites') are grey to black, finely laminated shales. Trace and major element geochemical studies show that, as with most Silurian black shales, these sediments are highly organic- and Vanadium-rich (Dabard 1983; Dabard and Paris 1986). The ostracodes occur as abundant, slightly tectonically deformed internal and external moulds. Associated fossils include graptolites, small, thin-shelled bivalves, fragments of orthoconic nautiloids and disarticulated eurypterid, and phyllocarid crustacean ('*Ceratiocaris*') remains.

The cleavage prevents accurate determination of the graptolites at locality 1 but there are clearly numerous pristiograptids of the *P. dubius* type, some *Monoclimacis* cf. *haupti*, and long distal fragments of slender monograptids with simple, straight thecae and unelaborated thecal apertures of the *nilssoni*/*progenitor* type. Until the proximal ends are found, confident identification cannot be made and the possible stratigraphic range of this locality extends through a large part of the Ludlow (D. Palmer). Graptolites of locality 2 indicate an upper Ludlow to lower Pridoli age (Jaeger, *in* Paris 1981).

3. 'Le Moulin de Régereau'; exposure along the road between Origné and l'Huisserie, Mayenne; Laval Synclinorium. See Peneau 1936; Paris 1981. The sediments consist of siltstones and mudstones of assumed



TEXT-FIG. 1. Distribution of the main faunas of Silurian myodocopid ostracodes in Europe. 1, Welsh Basin (Siveter 1984; Siveter and Palmer, in prep.). 2, Poland (Gürich 1896). 3, Bohemia (Barrande 1872; Bouček 1936; Siveter and Palmer, in prep.). 4, Armorican Massif (Siveter, Vannier and Palmer, in prep.). 5, Montagne-Noire (Chaubet 1937). 6, Portugal (unpublished information). 7, Spain (unpublished information). 8, Sardinia (Canavari 1900).

Pridoli age (Paris 1981). Rare ostracodes are associated with bivalves, the crinoid '*Scyphocrinites*', and fragments of '*Ceratiocaris*', all decalcified and preserved as moulds.

4. Chemiré-en-Charnie, Sarthe; Laval Synclioríum. Siliceous nodules collected by Guillier (Guillier and de Tromelin 1874; Guillier 1886) and deposited at the Musée d'Histoire Naturelle de Nantes, Loire-Atlantique.

5. Saint-Denis-d'Orques; outcrop at the intersection of the Laval to Le Mans motorway and the Saint-Denis-d'Orques to Brûlon road, Sarthe; Laval Synclinorium.

Localities 4 and 5 consist of siltstones and mudstones containing numerous, partly pyritized nodules in which the ostracodes (myodocopids and palaeocopes) occur as normally well preserved and undeformed moulds of single valves or closed carapaces. The diverse fauna includes crinoids, fragments of the phyllocarids *Ceratiocaris* and *Schugurocaris* (I. Rolfe, pers. comm.), the rhombiferan echinoderm *Lophotocystis* (J. Chauvel, pers. comm.), and graptolites of Ludlow or Pridoli age (D. Palmer).

Welsh Basin. We have collected Silurian myodocopids from many localities in this region, mainly in the Long Mountain district but also from the 'Radnor' and 'Denbigh' areas. Material studied specifically for the present paper comes from just two localities (1, 2).

1. Cause Castle Farm (SJ 341 077), Long Mountain, Shropshire.

This is one of about 100 localities in the Long Mountain yielding infrequent myodocopid ostracodes, which generally occur scattered throughout the laminated muddy siltstone facies of the Ludlow Long Mountain Siltstone Formation and succeeding Causemountain Formation (Palmer 1970). At this locality (= LMS Formation) some silt laminae are crowded with the moulds of finely comminuted shell debris, plus a few small but entire shells (e.g. lingulids), crinoid columnals, and eurypterid and phyllocarid fragments. Associated are occasional large myodocopid valves and numerous graptolites, *Saetograptus leintwardinensis*, the index for the eponymous, basal Ludfordian zone.

2. Friends Meeting House Quarry (SO 138 641), Llandegley, Powys.

Apart from the Long Mountain, the 'Radnorshire' area (now in Powys) is the only part of the Welsh Basin to have yielded a large number of myodocopid bearing localities, some twenty-two being cited by Kirk in her unpublished thesis (1947). Most occur in her 'Striped Flag Series', which consists of finely laminated and banded or 'striped' admixtures of mud and silt, generally with planar lamination or small scale cross-stratification. The characteristic, autochthonous fauna of the Striped Flags consists of graptolites, orthocones, and bivalves. Minor associates include myodocopids, rare crinoids, phyllocarids, and small brachiopods such as *Aegeria grayi* and *Lingula lata*. Intercalated south to south-east derived slump sheets often introduce an allochthonous, shelf shelly fauna into the area. The Striped Flags encompass the Ludlow *N. nilssoni*, *L. progenitor* (see Palmer 1970), *L. scanicus* s.l., and *P. tumescens*/*S. chimaera* graptolite zones. However, Kirk also records rare myodocopids in strata as old as the '*vulgaris*' (= *ludensis*) Zone and as young as the *S. leintwardinensis* Zone, and immediately above. Thus the total range for myodocopids in 'Radnorshire' is essentially the same as in the Long Mountain. Friends Meeting House Quarry comprises typical 'Striped Flags' lithology and mould fauna, and lower Ludlow, *C. scanicus* Zone, graptolites including *C. scanicus* s.l., *S. varians*, *S. chimaera semispinosus*, *P. dubius*, *P. tumescens*, and *B. bohemicus* (D. Palmer).

The geological survey of the 'Denbigh' area, Clwyd, resulted in finds of a few scattered Silurian myodocopid localities in North Wales (Warren *et al.* 1984). Here, myodocopids appear to be relatively very rare, but their stratigraphic distribution is broadly as in the Long Mountain, specimens being scarce in the upper Wenlock (*C. lundgreni* Zone), somewhat commoner in the Ludlow (*N. nilssoni* to *C. scanicus* zones) and again less common higher in the Ludlow (up to and including the *S. leintwardinensis incipiens* Zone; younger Silurian strata are not preserved). Both their facies and faunal associations are the same as elsewhere in the Welsh Basin. The myodocopids occur mainly in the 'ribbon banded mudstone' (Warren *et al.* 1984, pp. 44–46) of the Nantglyn Flags Group (straddling the Wenlock–Ludlow boundary) and the higher Elwy Group (Ludlow), a facies virtually identical to the 'Striped Flags' of the Radnor area. Its faunas are dominated by graptolites accompanied by orthoconic nautiloids and bivalves (particularly cardiolids) and also include crinoids (especially scyphocrinitids; Warren *et al.* 1984, p. 44) which are sometimes preserved complete and occasionally with orthocone 'substrates'.

Czechoslovakia. Silurian myodocopids in Czechoslovakia are predominantly of Ludlow age. Some of Barrande's original localities were either small and isolated from the main outcrop, and are now unidentifiable, or were poorly localized within thick sections so that they are now also unavailable. However, modern investigations by Czech palaeontologists have resulted in new exposures at the same horizons, yielding faunas similar to those of the 'lost' localities. For example, Barrande's type locality for '*Bolbozoe*' *bohemica* can no longer be located at Vyskočilka, but this species can still be obtained (DJS) from a similar horizon (*C. scanicus* Zone) on Holý Vrch Hill at Lounín near Zdice. Here, as in other Czechoslovakian Ludlow localities, the myodocopids are often abundant as moulds or as degraded carbonate shells in thin, platy, planar laminated, muddy limestones and are accompanied by orthoconic nautiloids, graptolites, and occasional bivalves.

Preservation. The vast majority of myodocopids we have studied are preserved as moulds. This may be as much the result of their occurrence in particular sedimentary environments or lithologies (fine-grained clastics), where virtually all the calcareous-shelled fossils have been dissolved, and/or as a product of the thinness of their shells. Exceptions are found where myodocopids occur in limestones (e.g. Sardinia) and then, although recrystallized, shells can be preserved as carbonate; however, we have not yet studied in detail this important mode of preservation.

Sedimentary matrix. That the types of deposit in which European Silurian myodocopids have so far been found are rather restricted could in part be preservational due to their relative fragility. The curiously impersistent stratigraphic record of the group since Silurian times supports this contention. Nevertheless, the limited facies pattern of occurrence of our Silurian species requires further explanation, especially since the group in general is considered to be pelagic.

The sediments in which our Silurian myodocopids are found are characteristically laminated and lack any indication of bioturbation or hardly any of the contemporaneous representatives of the typical brachiopod-dominated, shelly (shelf) faunas. Sedimentologically, they occur in a three component system of muds, muddy silts, and carbonate. A main feature is the fine (silt or smaller) grain size of the terrigenous material compared with the larger size of much of the carbonate 'clast' material, which is essentially made up of whole fossils and thus derived from within the depositional environment. Most of the myodocopid-bearing deposits consist of closely spaced planar laminations which result from either alternations of 'clean' silt laminae with muddy silts or, muddy silts with dark hemipelagic muds. Less commonly the latter may predominate, as in the dark grey (originally black?; but now chloritized) shales of Brittany. Because of the fine grain size, the moulds of the Brittany myodocopids preserve exquisite details of shell structure. Increase in the bioclastic component of the sediment in the Bohemian and Sardinian myodocopid-bearing strata tends to diminish but not destroy lamination, as the fossils themselves are commonly arranged as parallel orientated, bedding plane assemblages. This results in a coarse 'grain' parting lineation (see Gnoli *et al.* 1979, figs. 2 and 9*a*).

The bioclastic component varies greatly in volume and grain size, sometimes forming only a small proportion of the sediment (1 % volume in some Welsh Borderland localities), especially where muddy silts predominate and there are only very rare macrofossils which are almost invariably preserved as moulds. In the middle of the range are the highly fossiliferous, but now decalcified, hemipelagic muds of Brittany and the similarly fossiliferous, fine grained, laminated, and shaley micrites (microsparites) typical of the Bohemian localities. In contrast, myodocopid-bearing coquinoid 'cephalopod' limestones of Sardinia have a small terrigenous clastic component (5 %; Garuti *in* Gnoli *et al.* 1979) and consist largely of complete shells of all sizes in a micrite matrix.

Certain sedimentary characteristics appear common to almost all the myodocopid-bearing deposits of this study, thus suggesting similar underlying parameters in their mode of deposition. In particular, the fineness of the non-organic clastics and the prevalence of close spaced, planar laminae seem to indicate a relatively 'quiet' but not static depositional environment (except perhaps as represented by the black shales of Brittany) debarred from both the massive turbiditic input of terrigenous material often associated with deep basins and from the rigours of high energy and coarse (tidal) clastics of shallow shelves. Most of the inorganic sediment (muddy silt) was seemingly deposited as turbid flows of low velocity and of no erosive power, which were frequently and intermittently introduced into areas experiencing a low level 'rain' of hemipelagic mud. Gentle bottom traction currents reworked the surface layers of the 'homogenised', structureless muddy silt layers to form winnowed, often micaceous, 'clean' silt laminae. The overall result was to produce the 'Striped Flag' or 'ribbon banded mudstone' type of lithology, with its alternations of muds, muddy silts, and silts. Currents were of the appropriate strength to orientate fossils (e.g. orthocones and graptolites in the Welsh Basin localities) without any size sorting (e.g. of bivalved organisms) or much abrasion or fracture (ostracodes and bivalves may be articulated), and sometimes to produce a parting lineation or small scale, wispy cross-lamination but no other depositional or erosional structures. In Bohemia, for example, it is common for the orthocones and graptolites to show parallel orientation consistently throughout several centimetres of strata, indicating bottom currents of fairly persistent velocity and direction over a considerable timespan (Petránek and Komárkova 1953; Turek 1983).

Although the volume of terrigenous silt and mud is relatively low in Bohemia and virtually absent in Sardinia, there is similar evidence of both having been depositional areas again debarred from both deeper water turbiditic and shallow shelf clastic depositional processes. The carbonate that is present shows no reefal or other shallow water structures. Indeed, the dominant bioclastic components can be diagnosed quite differently (see below) and their presence is possibly the result of both a primary lack of sediment to 'dilute' the accumulating shelly remains and secondary accumulation by currents.

Numerical occurrence and faunal associates of myodocopids. The frequency of occurrence of European Silurian myodocopids is generally very low and is partly why they have received so little attention. Moreover, they tend to occur in comparatively low diversity faunas, which lack the more commonly studied members of the Silurian shelf benthos. Some idea of their frequency can be gained from studies in the Long Mountain, a sequence more thoroughly investigated (by D. P.) in terms of its myodocopid and associated fauna than any other Silurian myodocopid-bearing area. Their distribution throughout the laminated siltstones of some 1500 fossiliferous localities of Ludlow age is diffuse, only about 7% yielding myodocopids, which generally comprise less than 10% of the fauna of each locality. That a previous investigator of the Long Mountain sequence (Das Gupta 1932) did not record any myodocopids, also reflects their relative scarcity.

Whilst the basis for comparing the various localities and areas (text-fig. 1) arises from the presence of myodocopids, we also recognize a number of features in common in the associated faunas, although the taxa may differ even at the family level and different members may dominate in particular localities. We are essentially dealing with a known but little studied and relatively low diversity graptolite–orthocone–bivalve faunal association, whose minor members include various arthropods (ostracodes, phyllocarids, eurypterids, and rare, small trilobites) echinoderms (mainly crinoids, small pisocrinids, and scyphocrinitids), and a few brachiopod species (small lingulids and chonetids).

In Welsh Borderland myodocopid-bearing localities, graptolites and occasional small bivalves tend to dominate the faunas, with orthocones or myodocopids next most abundant. All other associated organisms tend to be very rare. The fauna from Cause Castle Farm, Long Mountain, is graptolite dominated, with the associated myodocopids, lingulids, phyllocarids, and crinoid columnals being current assembled on clean silt laminae. Generally in this area of the Long Mountain, graptolites and occasional small pterineid bivalves (up to 400 individuals/m^2) predominate. Myodocopids are slightly more abundant at Friends Meeting House Quarry, where even so, they comprise only about 10% of a generally sparse, graptolite dominated fauna and are, once more, scattered at very low densities throughout 3–4 m of laminated muddy silts. Here, fossils tend to be more abundant in the hemipelagic muds, especially on certain bedding planes. They are also present, but much less common, scattered throughout the muddy silts, their concentration being 'diluted' by the frequent incursions of sediment. Higher frequencies may again be encountered on the winnowed silt laminae, where they may have been concentrated by the removal of the mud or by current transport.

Compared with these Welsh occurrences, myodocopids can be much more abundant in the few localities in Bohemia and Brittany that have yielded them since the pioneer work of Barrande (1872), Barrois (1886), and Kerforne (1901). In the platy limestones of Bohemia graptolites and orthocones are common but faunas tend to be predominantly myodocopids, with some bedding plane assemblages achieving densities of 400 myodocopid individuals/m^2. Even greater abundances occur in the black shales of Brittany, where densities of 2000/m^2 or more are common and where, at some of the cited localities, ostracodes may dominate in comprising over 90% of individual assemblages. However, myodocopine s.s. valves are not always dominant, since the same bedding planes in Brittany may also have greater numbers of a smaller, thin shelled (and consequently poorly preserved) entomozoid ostracode. In the coquinoid (cephalopod) limestones of Sardinia orthoconic nautiloids tend to be the dominant group. However, some limestone blocks contain graptolite dominated assemblages and/or abundant entomozoid myodocopids (see Palmer and Gnoli 1985 for geological background). The accompanying faunas are slightly more diverse than elsewhere, with taxonomically richer assemblages of bivalves and phyllocarids (Gnoli and Serpagli 1984). Again, the orthocones and graptolites show parallel orientation (Gnoli *et al.* 1979) and the vagaries of faunal composition may reflect fluctuations in bottom traction current strength.

Mode of life. European Silurian myodocopids are clearly part (albeit often a minor one) of a recurring faunal association generally dominated by organisms which are usually considered to be pelagic, either as virtually passive drifters (the planktonic graptolites and scyphocrinitids), or as active swimmers (the nektonic cephalopods, myodocopids, phyllocarids, eurypterids, and small spinose trilobites) at various levels within the water column. Only the bivalves and rare, small brachiopods appear to have been benthic, although doubts have been raised over such an interpretation for the mode of life of representatives of both groups (Watkins 1978, pp. 51–52; Kříž 1969, pp. 111–114; Nye *et al.* 1975). The main bivalve groups present are praecardiaceans *sensu* Newell (1969) and pterineids. The praecardiaceans are largely endobyssate suspension feeders and constitute the only possible (semi-) infaunal representatives. The pterineids are epibyssate suspension feeders (Kříž 1984).

The occasional presence of abundant small pterineids is significant since they may have been the only genuine, flourishing, autochthonous shelled benthos in areas where myodocopids are found. Their abundance in all growth sizes, often with both valves, indicates that their associated bottom conditions were unlikely to have been foul and toxic. Since they also occur in finely laminated muddy silts with no indication of bioturbation, the near surface sediments may have been deficient in oxygen, sufficient to prevent the establishment of an infauna. This possibility is supported by the presence of disseminated, fine-grained, framboidal pyrite within the muddy silts. The few other benthic fossils, found on clean silt laminae, are representatives of some of the most common epibenthic brachiopod species characteristic of the shelf. They are clearly allochthonous, transported individuals.

Epizoans are very rare, consisting mainly of spirorbids, bryozoans, and small crinoids attached to orthoconic nautiloids in the Welsh material, and spirorbids attached to phyllocarids in some of the French material. Since all surfaces of the orthocones tend to be colonized, it seems that colonization happened either *in vivo* or post-mortem, but whilst the shell of the host was still buoyant, rather than after it lay on the substrate.

Environments of deposition. All the evidence suggests that the relevant depositional areas were not within normal epicontinental shelf water zones, but were more likely to have been in either outer shelf to shelf margin or even shelf slope environments. Of the areas considered, the Welsh basin is perhaps best known and understood, with its 'Striped Flag' and 'ribbon banded mudstone' lithologies representing sedimentation against a background deposition of dark laminated hemipelagic mud. This 'tranquil' depositional environment was frequently interrupted by incursions of turbid mud-silt suspension flows, depositing occasionally graded but otherwise structureless thin muddy silt layers (1–5 cm thick). The substrate surface was also reworked by low velocity bottom currents, which winnowed out the fines and left thin, 'clean' silt laminae and shell lags, with the elongate fossils becoming parallel orientated. The thinness and high frequency of repetition of these sediment layers is sufficient for them to be compared with present-day marine, 'varve'-like (non-glacial) deposits. The sedimentation model (Thornton 1984, p. 388 *et seq.*) for the latter has hemipelagic muds settling out during the summers, the organic content being heightened by algal blooms. During winters, increased river run off leads to an increased supply of terrigenous material of which the fines (mud and silt) are carried out across the shelf in turbid suspension by storms. The resulting deposits are the thin, structureless or graded mud-silt layers.

In the Long Mountain area, the frequent colonization of the sea floor only by abundant small pterineid bivalves suggests that here Ludlow water depths were too great for the brachiopod dominated faunas of the shelf. The viability of the bivalve faunas also shows that bottom conditions were at times neither anoxic nor too turbid for suspension feeders to flourish. Yet (see above), oxygen depletion may have occurred within and virtually up to the sediment-water interface. In 'Radnor' and 'Denbigh' the intercalated slumps in the 'Striped Flags' suggest an intermittently unstable slope environment.

Compared with the Welsh area, Brittany includes what almost certainly was a stagnant anoxic basin with only hemipelagic mud deposition and a planktonektonic fauna. The ostracode rich Ludlow limestones of Bohemia are in many ways similar to the Welsh sediments but with a lesser proportion of terrigenously derived silt. This fraction is replaced by fine-grained bioclastic carbonate derived from the organically rich carbonate shelf. Recent work on the implosion of cephalopod shells from this area (Westermann 1985) indicates outer shelf depths (> 300 m) for these deposits. Certainly there is again neither infauna nor shallow shelf epibenthos.

The Sardinian limestones differ in that they are almost wholly bioclastic carbonate (often entire shells, not size-sorted) with a minute proportion of hemipelagic mud and minimal terrigenous material. For the depths of deposition of the limestones Jaeger (1976) suggests deep water within Palaeotethys whilst Gnoli *et al.* (1979) prefer shallower shelf conditions but with anoxic bottom waters. Westermann's criteria have yet to be applied to the orthoconic nautiloids of this area.

Geographical distribution. The apparent contradiction posed by the supposed pelagic mode of life and the somewhat restricted geographical distribution of Silurian myodocopids exists not only in terms of their facies occurrence, but also in a wider palaeogeographical context. Contemporaneous shelf sediments in, for example, the Welsh Borderland of the Welsh Basin have probably been as closely examined as any sediments for their fossil content and yet while almost no myodocopids have been recorded other representatives of the faunal association are known. Furthermore, myodocopids are unknown from the Silurian rocks of Scandinavia, the USSR, or North America. Apart from France, England, Czechoslovakia, and Sardinia, myodocopids are also known (but unstudied) from Poland, Spain, and Portugal (text-fig. 1), Morocco, Australia, and possibly China. Clearly the overall distribution of Silurian myodocopids is enigmatic and needs explanation based on further studies. It is possible, at least in the case of their best-known (narrow) belt of occurrence encompassing western Britain, Brittany, Bohemia, and Sardinia, that myodocopids had some depth control or preferred vertical range (e.g. 200–500 m) that resulted in their remains being restricted to marginal shelf sediments. A variation on this would arise if they were nekto-benthic, as envisaged for longicone nautiloids with strong septa (Westermann 1985, p. 91) and again restricted to substrates at water depths of about 200–500 m.

MORPHOLOGY OF SILURIAN MYODOCOPID OSTRACODES

All of the Silurian myodocopids treated in detail and figured herein, from France and Britain, are based on mould material. Casts of external moulds were prepared with Silicone rubber using the technique described by Siveter (1982).

Pending current studies on their systematics, most of the Silurian myodocopids of this paper are cited under open nomenclature. However, in interpreting the microstructural and sculptural features of their shells it is necessary to outline features of their carapace morphology. The Silurian myodocopids discussed herein fall into two broad taxonomic groups, bolbozoids and 'cypridinids' (text-fig. 2).

EXPLANATION OF PLATE 83

Examples of true ornament in Silurian myodocopid ostracodes.

Figs. 1, 3, 5, 7, 8. Bolbozoid gen. et sp. nov. A. Right valve, IGR 33040, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 1, lateral view, × 18. 3, detail of tubercles with pores, posteroventral part of valve, × 180. 5, single pores and (?) double pore-like structures in the anteroventral part of the valve, × 150. 7, detail of (?) double pore-like structure (from 5), × 505. 8, detail of single pore (from 5), × 505.

Figs. 2, 4, 6. '*Bolbozoe*' sp. nov. A. Left valve, IGR 33048, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 2, lateral view, × 36. 4, detail of corrugated surface on either side of posterior sulcus, × 96. 6, detail of ventral part of the valve showing corrugations surmounted by four tubercles, × 165.

All specimens are silicone rubber casts from external moulds. All SEM except fig. 2. IGR = Institut de Géologie de l'Université de Rennes.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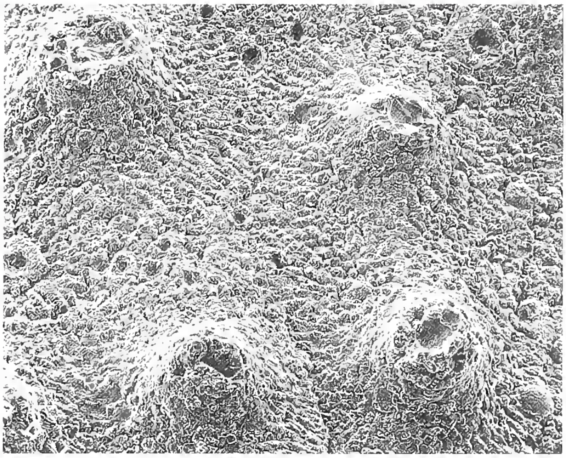
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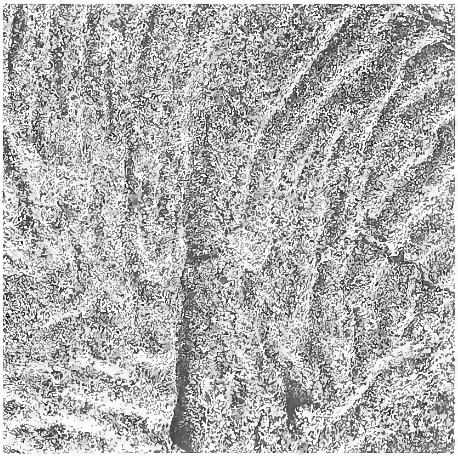
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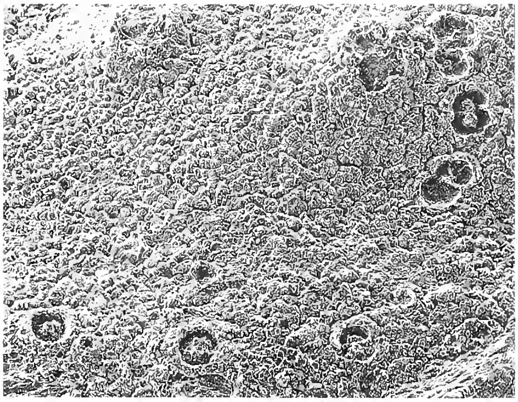
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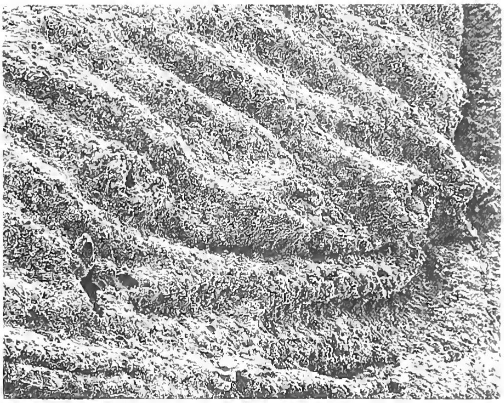
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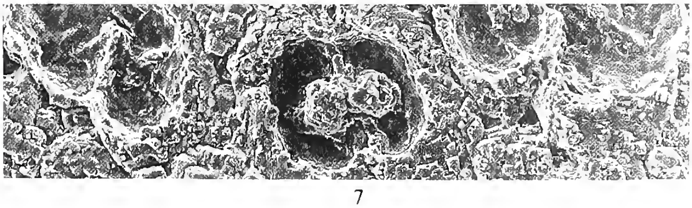
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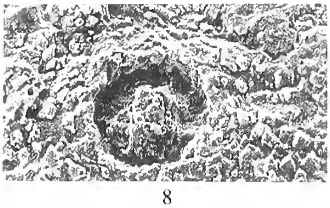
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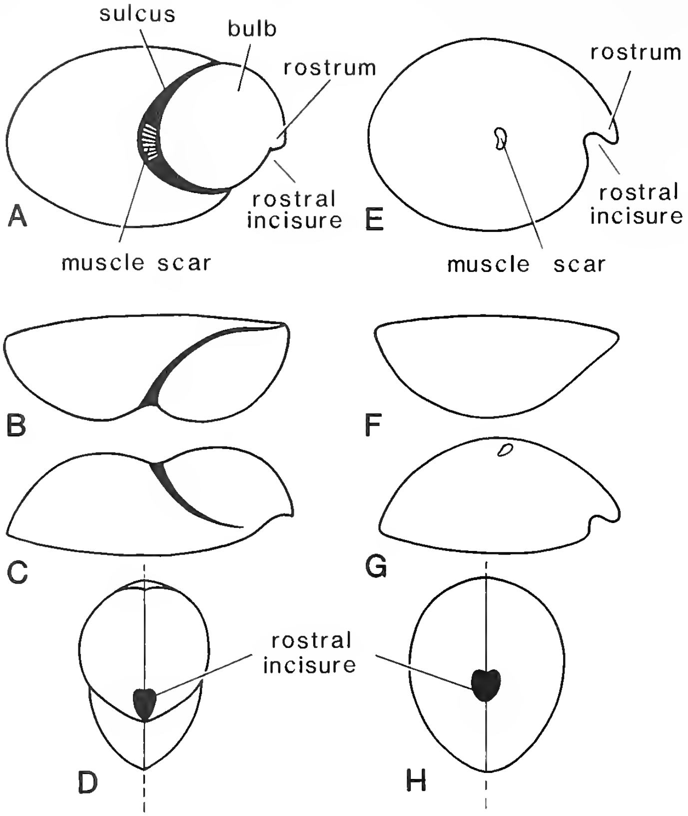


TEXT-FIG. 2. Morphological features of two groups of Silurian myodocopid ostracodes: A–D, a bolbozoid; E–H, a 'cypridinid'. A, E, right lateral views; B, F, dorsal views of right valves; C, G, ventral views of right valves; D, H, anterior views of carapaces.

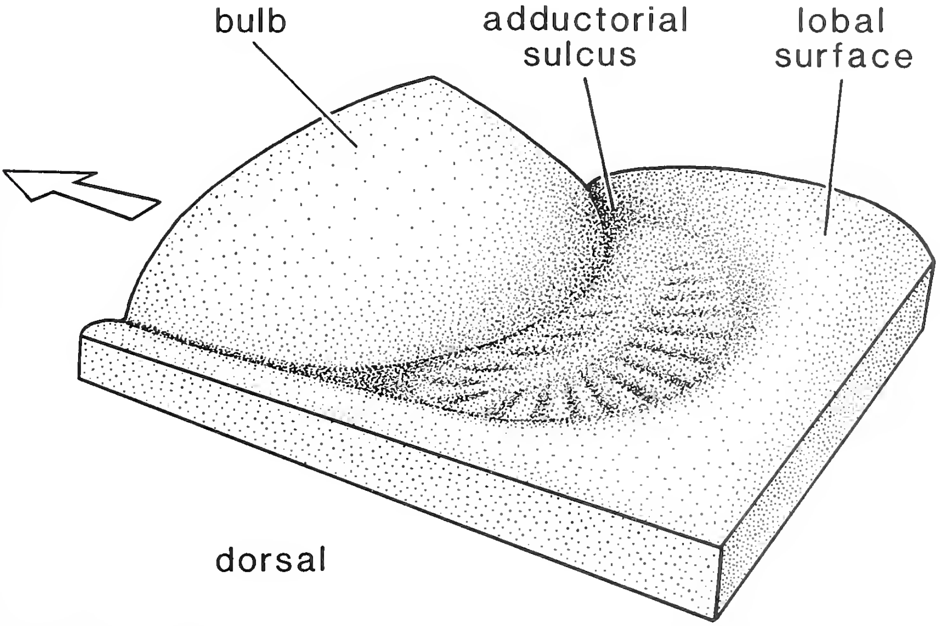
Many of the Silurian myodocopids show plastic deformation of the valves and clear adductor muscle scar impressions externally on their valves, both of which suggest the occurrence of a rather thin, flexible but flimsy shell (Siveter 1984). Taken together with their geographical distribution and the fact that many have an anterior rostrum and rostral incisure (suggesting the presence of protruding, possible swimming appendages, e.g. see Kornicker 1975; fig. 141*a*, *b*), many Silurian myodocopids such as bolbozoids can be reasonably interpreted as pelagic ostracodes (Siveter 1984).

Bolbozoids (text-fig. 2A–D). These unusually large ostracodes are characterized by having a huge anterodorsal bulb delimited posteriorly and ventrally by a deep adductorial sulcus (e.g. Pl. 83, figs. 1 and 2; Pl. 84, figs. 2, 6, 7; Pl. 85, fig. 3; Pl. 86, figs. 1, 2, 5, 6), and are assigned to the Family Bolbozoidae (e.g. Siveter 1984). A sigmoidal, posterior sulcus (e.g. Pl. 84, figs. 2 and 7) and a caudal process (e.g. Pl. 83, fig. 2) occur in some forms. Undeformed, non-flattened material from the Armorican Massif and Bohemia confirms that the lobal surface of most bolbozoids is quite strongly convex. The function of the anterodorsal bulb, which is often larger and more hemispherical in instars, is speculative. Bearing in mind its position, that it often shows plastic deformation which possibly indicates a thin shell, and the fact that except for its ventral-most region it is consistently the only part of the lobal surface to lack ornament in several types of bolbozoids (see text-fig. 5), it is possible that the bulb on each valve was the site of some form of visual organ. Silurian bolbozoid and 'cypridinid' myodocopids clearly exhibit a prominent anterior rostrum and rostral incisure (identified in three-dimensional, closed carapaces; see text-fig. 2) like those of Recent myodocopids (cf. Pl. 84, figs. 1 and 2 with Pl. 88, figs. 1, 3, 5–8).

A radiate adductor muscle scar pattern, consisting of a series of narrow, closely spaced, alternating ridges and grooves near the base of the vertical part of the adductorial sulcus, occurs in many Silurian bolbozoids. In some the pattern is simple, consisting of a few ridges and grooves of equal width, converging toward the bulb (e.g. Pl. 83, fig. 1). Others have a more complex, feather-like arrangement, composed of two unequal series of radiate ridges and grooves converging on a narrow, median (external) ridge curved parallel to the margins of the adductorial sulcus (e.g. Pl. 84, figs. 2 and 8; Pl. 87, fig. 6; text-fig. 3; and Gürich 1896, pl. 15, fig. 12, for *Bolbozoe polonica*). A secondary 'crenulation' of the ridges in some specimens is of possible comparable functional significance (offering increased attachment area/bonding) to that of the intricate pattern of micro-attachment points of the adductor muscle scars in some Recent cylindroleberidid myodocopids (see Kornicker 1975, fig. 265*c*–*e*).

In its biserial arrangement this distinctive muscle scar recalls that of platycopes such as cytherellids (see Van Morkhoven 1962, fig. 40) and, more pertinently, shares strong morphological similarities with Carboniferous entomoconchacean myodocopids (see Van Morkoven 1962, fig. 38; Kornicker and Sohn 1976, fig. 35) and particularly with Recent, oceanic thaumatocypridacean myodocopids (e.g. see *Thaumatoconcha caraionae* and *T. elongata* in Kornicker and Sohn 1976, figs. 35 and 44). In this context it is also taxonomically significant to note that Kornicker and Sohn (1976, p. 4, fig. 2) maintain that, based on cladistic analysis of the soft parts (eye; copulatory organ; appendages) of Recent myodocopids, entomoconchaceans and thaumatocypridaceans are not closely related to cypridinacean myodocopids.

'*Cypridinids*' (text-fig. 2E–H). One group of Silurian myodocopids have simple, oval, dome-like shells and differ considerably from bolbozoids in muscle scar pattern, in being relatively shorter and higher, and in lacking sulci or an anterodorsal bulb (see Pl. 84, fig. 1; Pl. 85, fig. 1; Pl. 87, figs. 1 and 2). The general designation 'cypridinid' is employed herein for these forms. Their shape and outline is comparable with Devonian and Carboniferous cypridinids (Bless 1973; Sohn 1977), Mesozoic myodocopids such as *Triadocypris* (Weitschat 1983), and particularly with the Recent cypridinacean families Cypridinidae, Philomedidae, and Cylindroleberididae (see Pl. 88; Kornicker 1975, 1981; Kornicker and Caraion 1978).



TEXT-FIG. 3. Schematic representation of adductor muscle scar of a Silurian bolbozoid ostracode (see Pl. 84, figs. 6 and 8); dorsal oblique view. Arrow indicates anterior.

TRUE ORNAMENT

Three types of external surface ornament have been recognized in Silurian myodocopids treated herein: reticulation, corrugation, and tuberculation (text-fig. 4). Similar ornament is also known in many fossil and Recent ostracode groups (see Sylvester-Bradley and Benson 1971 for details and terminology).

Reticulation (text-fig. 4A). Reticulation is frequently developed in bolbozoids, often occurring on all surfaces of the valve except for the upper part of the anterodorsal bulb, the rostrum, and the adductorial and posterior sulci (e.g. Pl. 84, fig. 7; text-fig. 5E, F). The reticulation consists of coarsely elliptical, ovoid, polygonal or, more rarely reniform fossae, each 200–600 μm across in adults. The deepest and widest fossae are normally in the ventral part of the valve (Pl. 84, fig. 7); medially, fossae often have an elliptical, elongate, or even sigmoidal shape (Pl. 84, figs. 4 and 7). The reticulum of young instars appears relatively less strongly developed and in some mature instars affects the whole shell thickness and is hence reflected on the internal mould. Reticulation also occurs in some Silurian 'cypridinids'; in 'Cypridinid' gen. et sp. nov. A a regular pattern of shallow, elliptical to polygonal fossae (each 100–300 μm across) covers the posterior half of the valve (Pl. 84, figs. 1 and 3).

Similar external reticulation is known from Ordovician to Recent in a wide variety of ostracode groups such as binodicopes (see Schallreuter 1980, 1983), palaeocopes (see Schallreuter 1982*a*, *b*), podocopes (see Benson 1971, 1973), and Recent myodocopids. The cypridinid *Scleroconcha flexilis* (Brady, 1898) and the philomenid *Anarthron chilensis* (Hartmann, 1965) are just two Recent myodocopids (Kornicker 1975, figs. 196 and 224) which illustrate similar reticulation to those of Silurian bolbozoids such as '*Bolbozoe*' cf. *bohemica* Barrande, 1872 (Pl. 84, fig. 7; Pl. 87, fig. 6).

As observed in podocopids, the pattern and form of external (polygonal) reticulation in ostracodes is closely determined by the arrangement of the underlying layer of individual epidermal cells (Okada 1981, 1982). The 'individual cell: polygon' correlation and the process of cell division were clearly demonstrated using growth series of Recent and fossil ostracodes. From the size and ontogenetic changes of their fossae, it is possible that the development of the reticulum was similarly controlled in Silurian myodocopids.

Corrugation (text-fig. 4B). A series of sigmoidal to sinuous and occasionally bifurcated grooves and ridges occurs in Silurian bolbozoids (e.g. Pl. 83, figs. 2, 4, 6) and 'cypridinids' (unpublished material from Morocco). Corrugation typically occurs throughout the lateral surface except on the sulci, rostrum, and upper part of the bulb (e.g. Pl. 83, figs. 2, 4, 6). Sometimes it seems best developed posteriorly and ventrally (e.g. Pl. 84, figs. 2 and 4). Juvenile bolbozoids have a relatively incomplete pattern of corrugation; ridges are shorter and less densely packed.

EXPLANATION OF PLATE 84

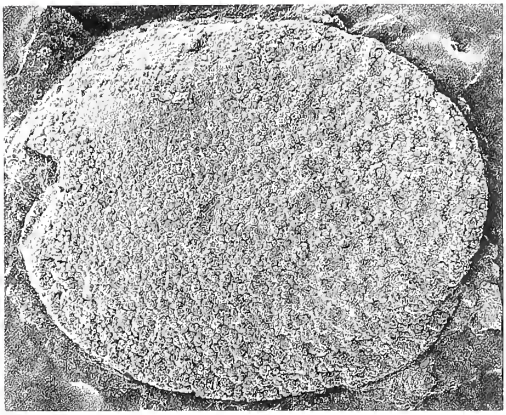
Examples of true ornament and adductor muscle scar patterns in Silurian myodocopid ostracodes.

Figs. 1, 3, 5. 'Cypridinid' gen. et sp. nov. A. Left valve IGR 33035, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 1, lateral view, ×51. 3, detail of posterior surface reticulation, ×105. 5, reniform adductor muscle scar (and pattern of shell microstructures), ×225.

Figs. 2 and 4. '*Bolbozoe*' sp. nov. A. Right valve BM OS 13060. Long Mountain Siltstone Formation, Ludlow Series, Cause Castle Farm, Long Mountain, Powys, Wales. 2, lateral view, ×18. 4, detail of ventral part of the valve showing a combination of tubercles, corrugation, and reticulation, ×45.

Figs. 6–8. '*B.*' cf. *bohemica* Barrande, 1872. 6 and 8, right valve, IGR 33067, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 6, lateral view, ×27. 8, radiate adductor muscle scar, dorsal oblique view, ×105. 7, lateral view of open carapace, IGR 33057, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France, ×27.

All specimens are silicone rubber casts from external moulds. All SEM except fig. 7. BM = British Museum (Natural History), London.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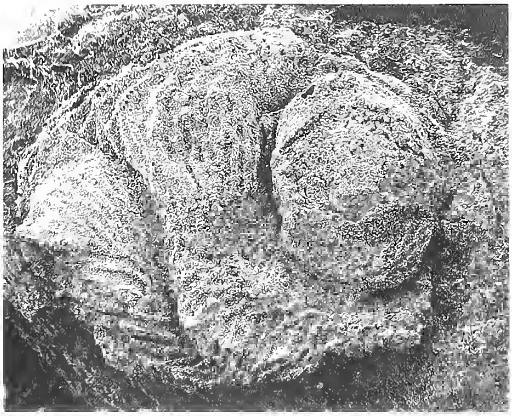
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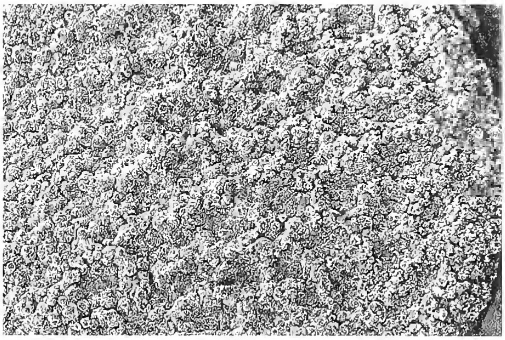
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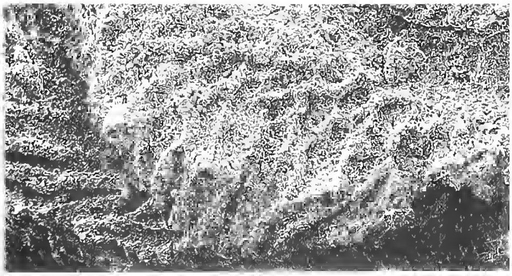
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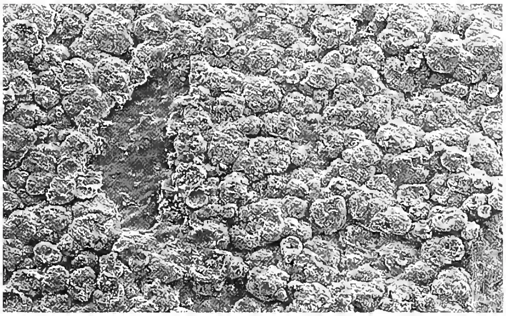
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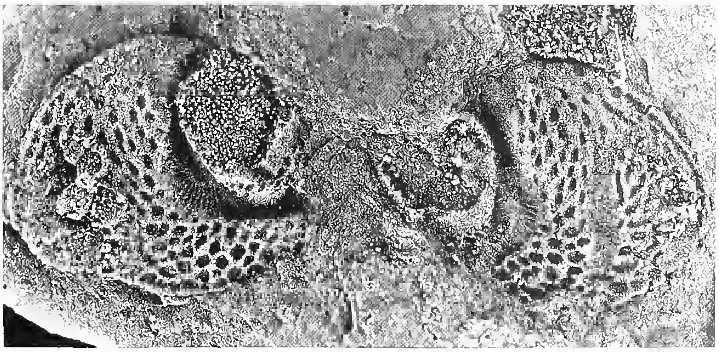
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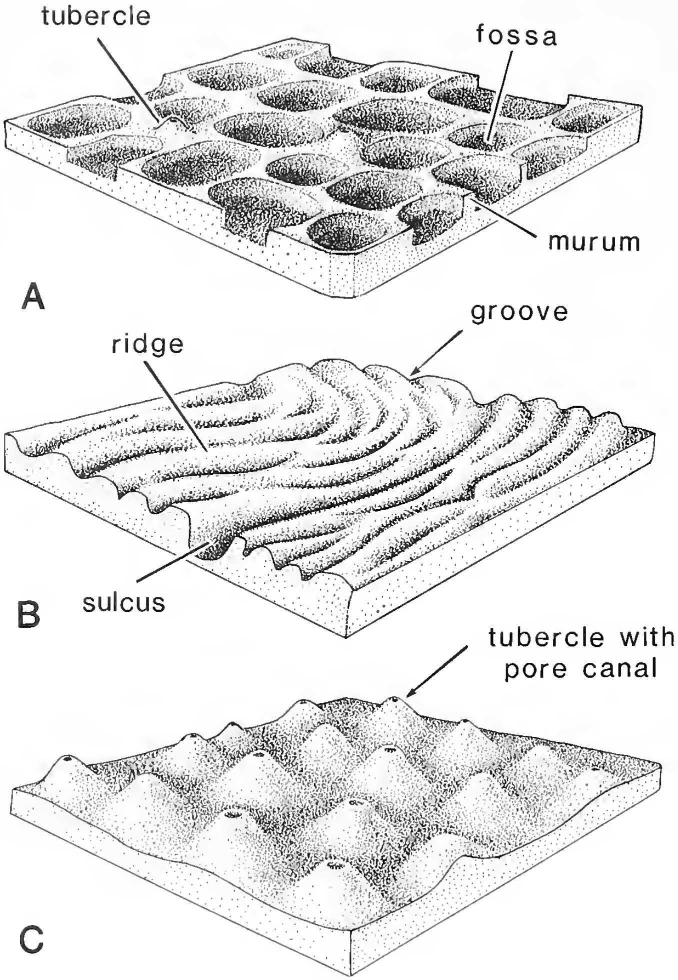
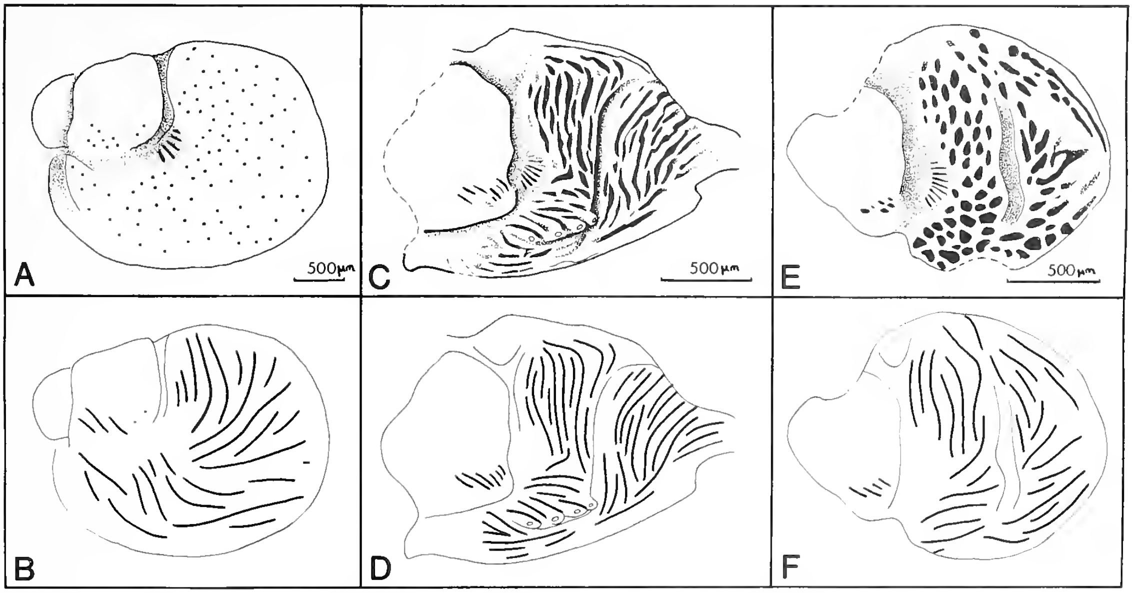
SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes



TEXT-FIG. 4. Schematic representation of individual types of true ornament in Silurian myodocopid ostracodes. A, reticulation; B, corrugation; C, tuberculation.

In '*Bolbozoe*' sp. nov. A most corrugations appear to run parallel to the sulci but ventrally they are aligned parallel to the ventral margin (Pl. 83, fig. 2). This pattern is strikingly comparable to that of the fossae in the dominantly reticulate bolbozoid '*B.*' cf. *bohemica* (cf. Pl. 84, figs. 2 and 7) and also mirrors the alignment of tubercles in other Silurian tuberculate bolbozoids (e.g. Pl. 83, fig. 1). Seemingly the distribution of fossae, corrugations, and possibly tuberculation represent homologous patterns within groups of Silurian bolbozoids (text-fig. 5).

Forms of corrugation are also known, for example, in Palaeozoic platycopes (e.g. Schallreuter 1978), Mesozoic and Tertiary podocopes (e.g. Clements 1974; Doruk 1974), Recent polycope myodocopids (e.g. Hasan 1983), and Carboniferous entomozoids s.s. (e.g. Gooday 1983). Though entomozoids were traditionally classified as myodocopine myodocopids (e.g. Sylvester-Bradley *in* Moore 1961), as restricted to the 'fingerprint' ostracodes of current usage this group of Silurian-Carboniferous ostracodes lack characteristic features (e.g. rostrum and rostral incisure) of typical myodocopines and therefore belong outside that group. The arrangement and spacing of longitudinal and bifurcated primary ribs of several entomozoid taxa (e.g. see ?*Kuzminaella* sp. of Gooday 1983, fig. 10) are like the corrugated surface of Silurian bolbozoids. Gooday (1983) noted that shell ornament may not be reflected on the internal surface in entomozoids from the Carboniferous, a characteristic



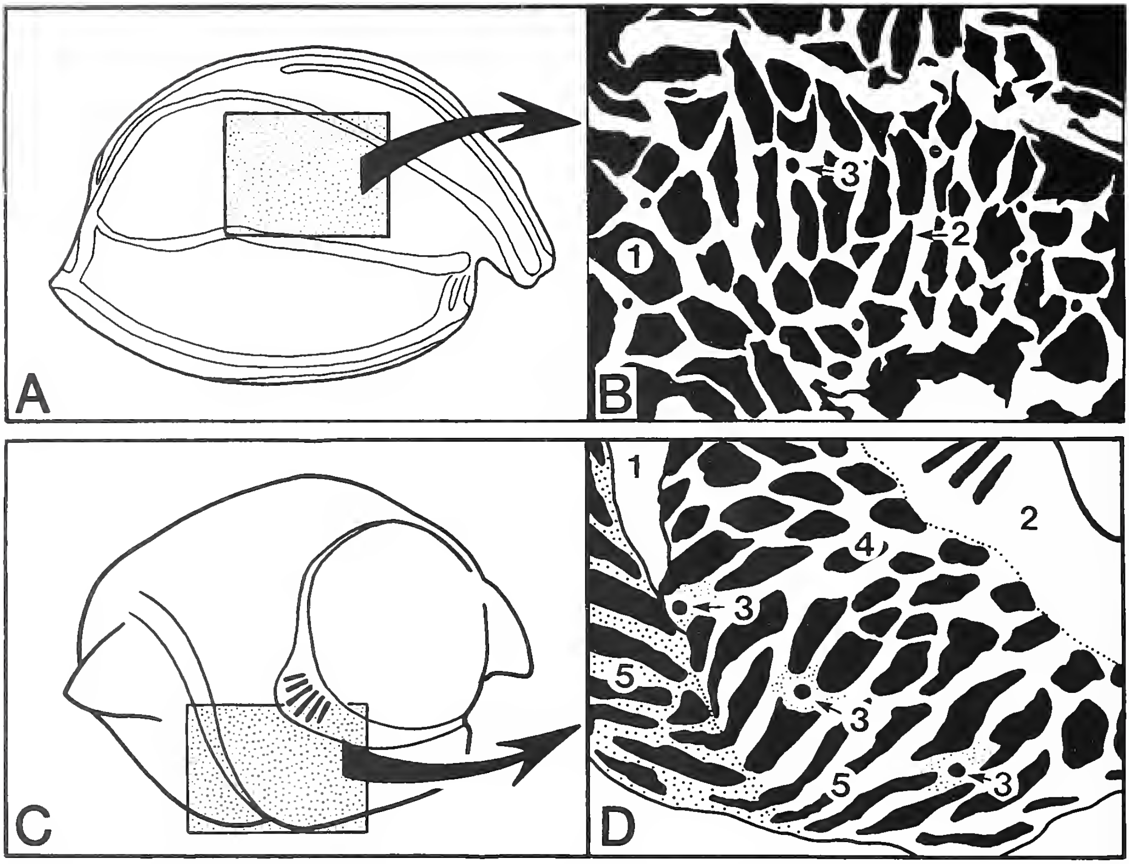
TEXT-FIG. 5. Valves (A, C, E) illustrating similar patterns of alignment (B, D, F) of tuberculation (A, B), corrugation (C, D), and reticulation (E, F) in bolbozoids. A, B, Bolbozoid gen. et sp. nov. A, based on right valve, IGR 33040 (valve reversed). C, D, '*Bolbozoe*' sp. nov. A, based on left valve, IGR 33048. E, F, '*B.*' cf. *bohemica*, based on left valve, IGR 33057.

also observed in many Silurian myodocopids. Ribbing may be an adaptation in entomozoids to a pelagic lifestyle (Gooday 1983; Siveter 1984) and it is possible, but again speculative, that the same may be the case for corrugations.

Tuberculation (text-fig. 4C). Tubercles are common in Silurian bolbozoids, though their number, size, and arrangement vary between taxa (cf. text-fig. 5A, C). In Bolbozoid gen. et sp. nov. A tubercles of *c.* 70–300 μm diameter cover lobes but not the sulci, rostrum, or dorsal part of the bulb (Pl. 83, figs. 1, 3, 5; text-fig. 5A). Most are regularly spaced, have a pore-like central perforation (Pl. 83, fig. 3) and show linear alignment (text-fig. 5A, B). Other bolbozoids such as '*B.*' sp. nov. A (Pl. 83, figs. 2 and 6; text-fig. 5C, D; Pl. 84, figs. 2 and 4) have only a ventral row of three to four tubercles in adults. In '*B.*' *bohemica* tubercles are more numerous and prominent in early instars, but are virtually lacking in adults. Tubercles can have expression on both internal and external shell surfaces in Silurian bolbozoids; the central perforation probably penetrates the shell thickness and may represent a normal pore canal communicating in life with the epidermal cells. Tuberculation is common throughout the Ostracoda as shown, for example, in palaeocopes (Martinsson 1962; Siveter 1976; Schallreuter 1982*c*), podocopes (Sylvester-Bradley and Benson 1971), and Recent myodocopids (Kornicker 1981, pl. 70).

Composite ornament (text-fig. 6C, D). Some Silurian myodocopids exhibit an intricate combination of reticulation, corrugation, and tuberculation (e.g. Pl. 84, figs. 2 and 4; text-fig. 6C, D). In '*B.*' sp. nov. A the reticulum centroventrally is surmounted by tubercles with pores and laterally merges with corrugations. This 'composite' external ornament has counterparts in Recent myodocopids such as *S. frons* (text-fig. 6A, B).

Normal pores. Though not ornament as such, the presence of normal pores in Silurian myodocopids is worth recording. Apart from having pores within tubercles, in one well-preserved specimen of



TEXT-FIG. 6. Comparison of true ornament in a Recent and a Silurian myodocopid ostracode. A, B, *Scleroconcha frons* Kornicker, 1975, philomedid, right valve (redrawn from Kornicker 1975, fig. 209*a–b*). Recent, SW Pacific off Chile; 1190–1263 m depth. A, lateral view, × 50. B, detail of the external surface ornament (reticulation), × 200. B1, fossa; B2, elongate fossa; B3, normal pore canal. C, D, '*Bolbozoe*' sp. nov. A, bolbozoid, right valve. Based on BM OS 13060 (see Pl. 84, figs. 2 and 4), Ludlow Series, Silurian, Long Mountain, Powys, Wales. C, lateral view, × 20. D, detail of external surface ornament, × 75. D1, posterior sulcus; D2, adductorial sulcus and muscle scar; D3, tubercles with pores; D4, reticulation; D5, corrugation.

Bolbozoid gen. et sp. nov. A (Pl. 83, figs. 1, 3, 5, 7, 8), pore-like structures were also observed anteroventrally. They consist of several single, circular and also double, semicircular openings about 30 μm in diameter, often with a central 'boss'. Comparable 'normal pores' occur in many Recent myodocopids: *Polycope choane* has sparsely distributed single and double pores on its lateral surface (Hasan 1983) and there are living cylindroleberidids with various types of minute, sparse, rimmed pores, pore groups, or tubed pores whose number and position can vary within a species (see Kornicker 1975, pls. 310, 320, 321).

In summary, the external sculptures of Silurian myodocopids described above are considered to be true, genetically controlled ornament, similar to that of many Recent myodocopids. Such features develop gradually and to a consistent pattern throughout the ontogeny of both Silurian and Recent myodocopid species. Lastly, patterns of reticulation, corrugation, and tuberculation in groups of Silurian myodocopids seem to be homologous (text-fig. 5) and the result of evolutionary processes rather than the chance factors.

SHELL MICROSTRUCTURES

Silurian myodocopids from the Welsh Basin, Armorican Massif, and Bohemia exhibit enigmatic, surface polygonal and radiate microstructures, each usually with a central perforation (Pls. 85–87).

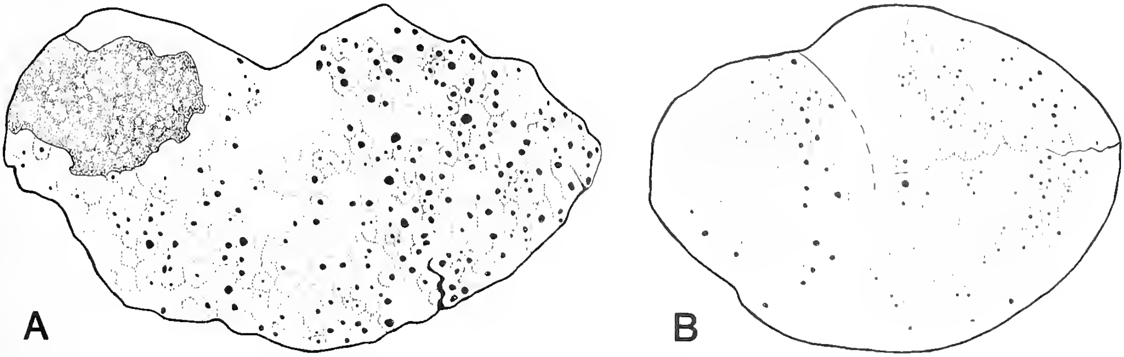
Radiate microstructures. Subcircular radiate microstructures, herein termed rosettes (e.g. Pl. 85, fig. 3, *B.* cf. *anomala*), occur on both internal and external moulds, either individually; as clusters (e.g. Pl. 85, figs. 1, 2, 4, 5, 'Cypridinid' sp.; Pl. 87, figs. 6 and 7, '*B.*' cf. *bohemica*); more rarely as rosettes covering virtually the entire surface of the valve (e.g. Pl. 85, figs. 9–11, *B.* cf. *anomala*); and sometimes as tiny rosettes within a basically polygonal pattern of shell microstructure (see 'composite microstructure' below). Each rosette consists of some ten to thirty acicular radii and (excluding rosettes in composite patterns) is *c.* 100–500 μm across; most have a central perforation.

Polygonal microstructures. On the surfaces of both internal and external moulds of many of our Silurian myodocopids a pattern of relatively small, polygonal microstructures is discernible (e.g. Pls. 86, 87). The polygons vary in size (10–150 μm), shape (degree of elongation), outline (angular to more rounded), and packing (dense to loose) to give different types of patterns on the surfaces of the valves of several taxa. In three dimensions these structures are interpreted as polygonal platelets (text-fig. 9).

Typical polygonal patterns are shown in text-fig. 7. A specimen of *B.* cf. *anomala* (text-fig. 7A; Pl. 86, figs. 2 and 4) shows closely packed, centrally perforated polygons over almost all the external surface except the anterodorsal bulb; they are mostly irregular in shape, size (60–150 μm), and in the diameter of their central perforation. Similar polygons occur in a specimen of 'Cypridinid' gen. et sp. nov. B (Pl. 87, figs. 2–4). In another specimen of *B.* cf. *anomala* (Pl. 86, fig. 5, text-fig. 7B) the packing appears looser and some polygons ill-defined, though most have central perforations. Generally, the upper (outer) part of the central perforations of the polygons is often enlarged, such that each perforation can appear as a tiny concavity housing a minute hole (e.g. Pl. 86, fig. 4; Pl. 87, fig. 4; text-fig. 9).

Another common pattern consists of closely packed but smaller, rounded to polygonal, granule-like microstructures (each *c.* 10–60 μm diameter), some of which have a central perforation (Pl. 84, figs. 1, 3, 5; Pl. 87, figs. 1 and 5).

Composite microstructures. Radiate and polygonal microstructures of various sizes often occur in the same valve (text-fig. 9). For example, tiny radiate microstructures are often found intimately associated within a pattern of perforated polygons (e.g. Pl. 85, fig. 7, Bolbozoid gen. et sp. nov. A; Pl. 87, figs. 6 and 7, '*B.*' cf. *bohemica*). In many cases both the smaller, granule-like elements and the perforated polygonal platelets (combined range: 10–150 μm diameter) occur as a gradational,



TEXT-FIG. 7. Pattern of perforated polygons on lateral surface of *Bolbozoe* cf. *anomala* Barrande, 1872. A, left valve, lateral view, IGR 33023 (see Pl. 86, fig. 2), × 25. B, left valve, lateral view, IGR 33029 (see Pl. 86, fig. 5), × 25.

intermingled pattern on individual valves (e.g. Pl. 87, fig. 4, 'Cypridinid' gen. et sp. nov. B; Pl. 87, fig. 5, 'Cypridinid' gen. et sp. nov. A).

The nature and origin of polygonal and radiate microstructures. The patterns of perforated polygons and radiate microstructures have many, shared characteristics which indicate that such microstructures should not be interpreted as true external ornament.

1. Their general distribution on valves appears to be random, with apparently no consistent trends in individuals or species.

2. In some specimens the microstructures are observed to be 'superimposed' on true ornament such as tubercles (Pl. 85, figs. 6 and 7), as well as on the adductorial sulcus (Pl. 87, figs. 6 and 7) and the rostrum (Pl. 84, fig. 1; Pl. 87, fig. 2), two regions where ornament is either otherwise unknown (adductorial sulcus of '*B.*' cf. *bohemica*) or not expected to occur (rostrum of Silurian myodocopids in general).

3. Critical evidence is found in some well-preserved carapaces which show a different polygonal pattern (Pl. 87, fig. 1) or arrangement of rosettes on the two valves. In one specimen a single radiate structure is developed only on the left valve (Pl. 85, fig. 3).

4. In contrast with the typical ornament of Silurian myodocopids (reticulation, corrugation) perforated polygons and radiate microstructures manifest complimentary patterns on both external and internal moulds.

5. Similar polygonal and radiate microstructures are found in various bolbozoid and 'cypridinid' myodocopid taxa from various localities of probably different ages. Compare, for example, the radiate structures in the specimen of 'Cypridinid' sp. from 'La Cultais' (Pl. 85, figs. 1, 2, 4, 5) with those of the specimen of *B.* cf. *anomala* from 'Les Buhardières' (Pl. 85, figs. 3 and 8); or compare the polygonal structures in the specimens of *B.* cf. *anomala* from 'Les Buhardières' (Pl. 86, figs. 1–6) with those of 'Cypridinid' gen. et sp. nov. B from Saint-Denis-d'Orques (Pl. 87, figs. 2–4).

Accepting this evidence that the shell microstructures are not ornament, they may have originated in one of several possible ways:

1. Microborings associated with endolithic fungi and algae occur in fragments of molluscs, echinoderms, coralline algae, barnacles, serpulids, and foraminiferans from shelf sediments (Perkins and Halsey 1971). Such activity produces different sizes (1–20 μm diameter), shapes, and patterns of perforations which are not dissimilar to those of some of the Silurian myodocopids. However, microborings in Recent material are never associated with complex, three-dimensional radiate or

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EXPLANATION OF PLATE 85

Examples of polygonal and radiate microstructures of the shell of Silurian myodocopid ostracodes.

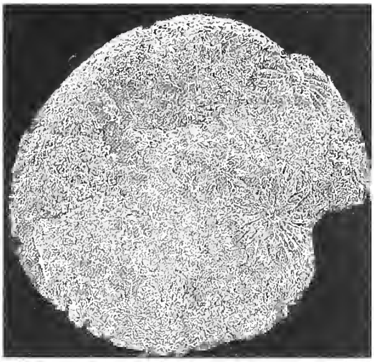
Figs. 1, 2, 4, 5. 'Cypridinid' sp. Right valve, IGR 33054, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 1, lateral view, × 75. 2, anterior oblique view, × 75. 4 and 5, details of acicular radiate structures ('rosettes') in anterior part of the valve (from 1 and 2 respectively; × 205, × 215).

Figs. 3 and 8. *Bolbozoe* cf. *anomala* Barrande, 1872. Open carapace, IGR 33025, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 3, lateral view, × 56. 8, detail of perforated, acicular radiate structure ('rosette') on ventral part of the left valve, stereo-pair, × 380.

Figs. 6 and 7. Bolbozoid gen. et sp. nov. A. Right valve, IGR 33040, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 6, lateral view, × 14. 7, detail of posteroventral part of external surface showing an acicular radiate structure ('rosette') on the side of a tubercle (*top right*) and closely packed perforated polygons (*lower left*), × 245.

Figs. 9–11. *B.* cf. *anomala* Barrande, 1872. Left valve, IGR 3300, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 9, oblique ventral view, × 17. 10 and 11, details of closely packed radiate structures ('rosettes') on the lateral surface of the valve, × 200, × 150.

All specimens are silicone rubber casts from external moulds. All SEM except fig. 3.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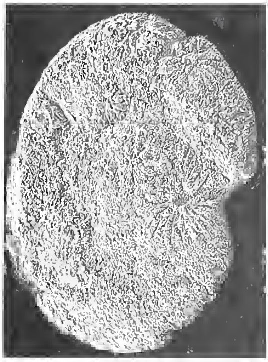
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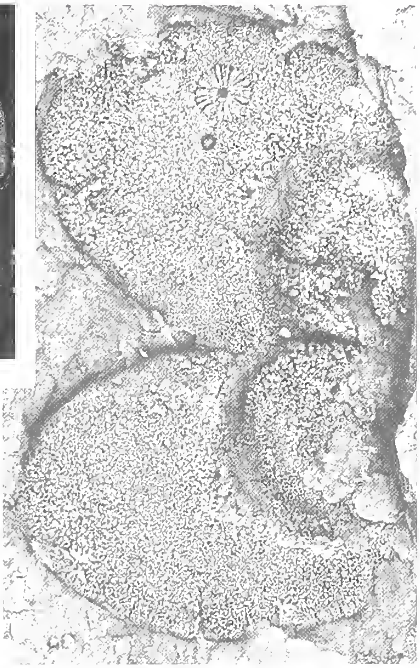
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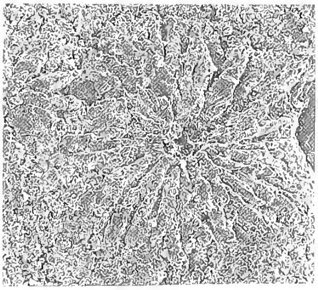
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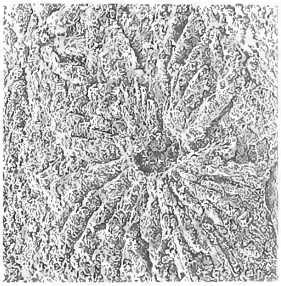
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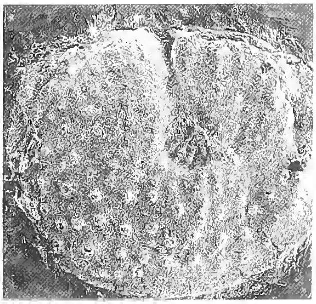
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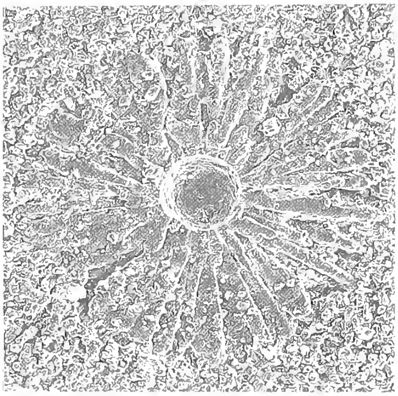
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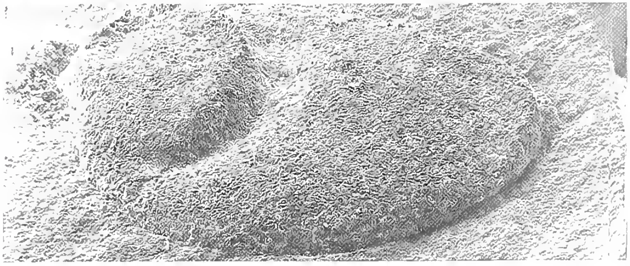
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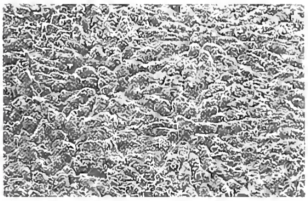
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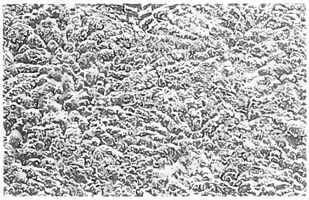
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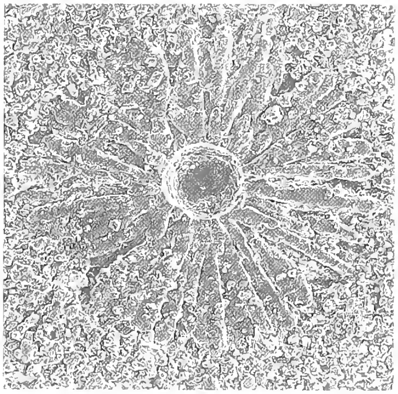
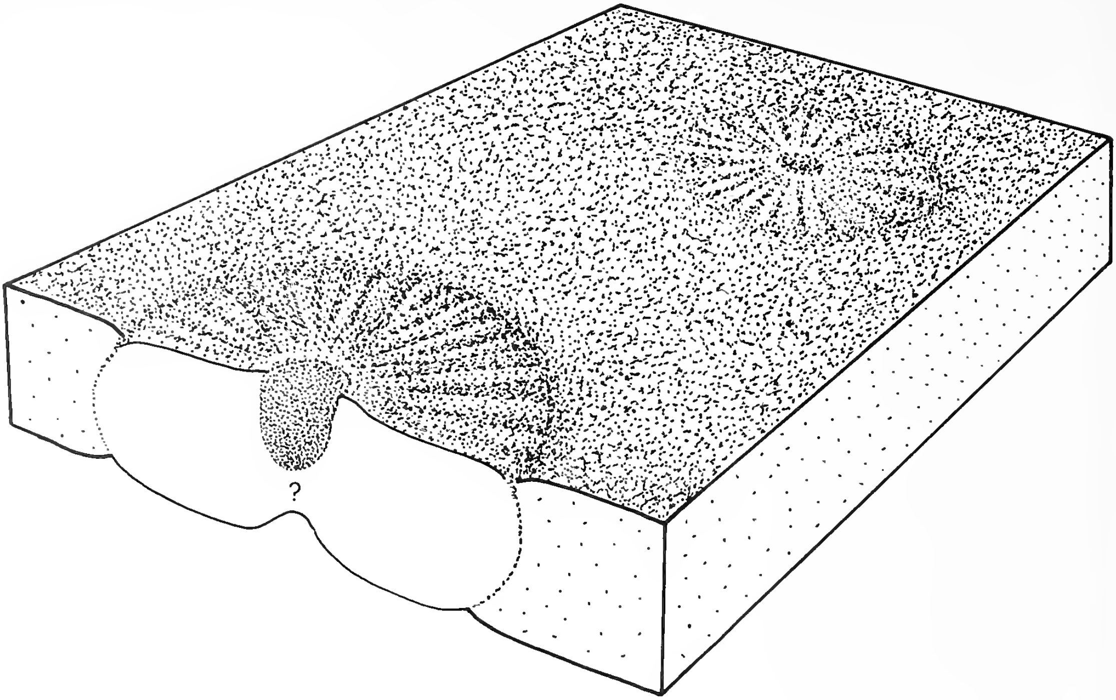


SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes



TEXT-FIG. 8. Reconstruction of acicular radiate structure ('rosette') based in part on observations on internal and external moulds of IGR 33025 (*Bolbozoe* cf. *anomala* Barrande, 1872; see Pl. 85, figs. 3 and 8). Central perforation may or may not completely penetrate shell thickness. True shell thickness unknown.

polygonal structures like those described from the Silurian myodocopids and such an origin is considered untenable.

2. It is possible that some kind of acidic action within the sediment might have produced these randomly distributed perforations and irregular polygonal patterns on the calcareous shells. Such acid erosion is unlikely for several reasons. First, the radiate structures and perforated polygons are lacking from associated faunas of palaeocope ostracodes, bivalves, eurypterids, and phyllocarids. Secondly, delicate external features such as muscle scars and minute pores are remarkably well preserved. Thirdly, the geochemistry of the Silurian black siltstones and mudstones indicates reducing conditions for the substrate (Dabard and Paris 1986).

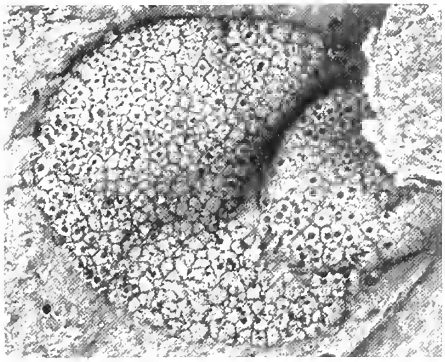
EXPLANATION OF PLATE 86

Examples of polygonal and radiate microstructures of the shell of Silurian myodocopid ostracodes.

Figs. 1–6. *Bolbozoe* cf. *anomala* Barrande, 1872. 1 and 3, right valve, IGR 33027. 1, lateral view, × 22. 3, detail of packed, perforated polygons in ventral part of the anterodorsal bulb, stereo-pair, × 260. 2 and 4, left valve, IGR 33023. 2, lateral view, × 22. 4, detail of packed, perforated polygons in posterodorsal part of the valve, stereo-pair, × 260. 5, left valve, showing perforated polygons, IGR 33029, lateral view, × 22. 6, left valve, IGR 33026, lateral view, × 12, together with two other valves showing different types of external shell surfaces on the same slab (smooth surface; small, closely packed polygons; larger, packed, perforated polygons). All from La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France.

All specimens are Silicone rubber casts from external moulds. Figs. 1, 2, 5, 6 are light photographs; 3 and 4 are SEM.

PLATE 86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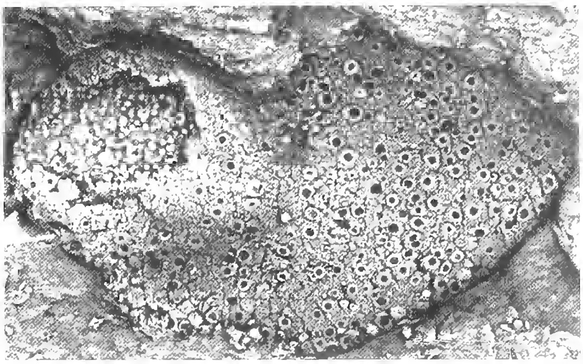
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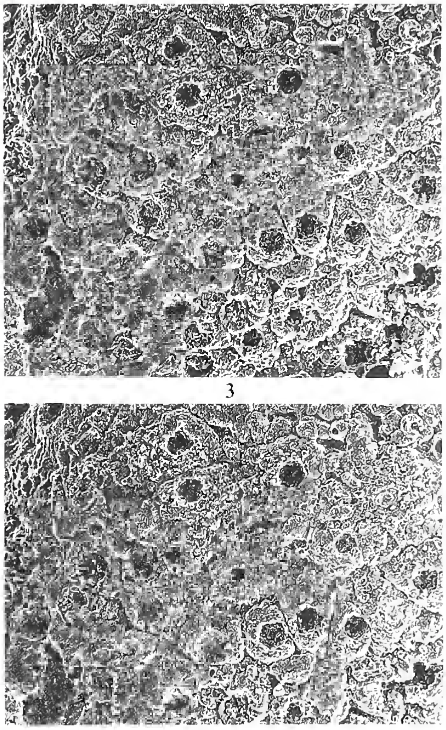
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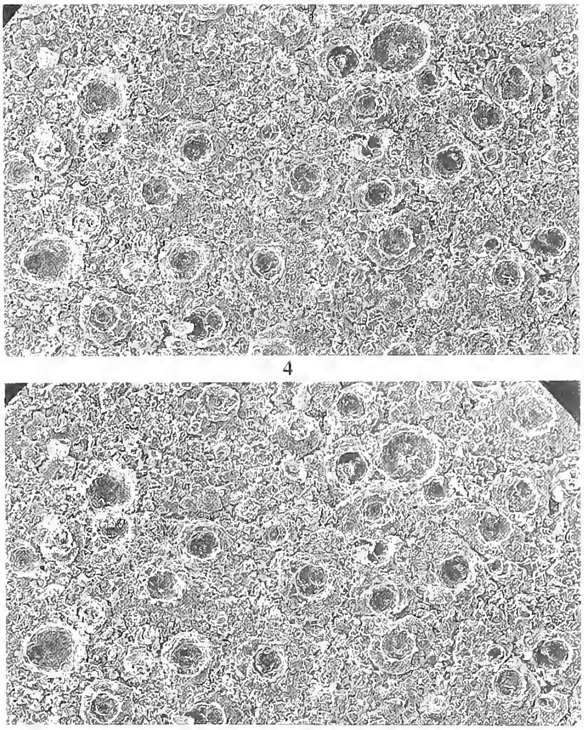
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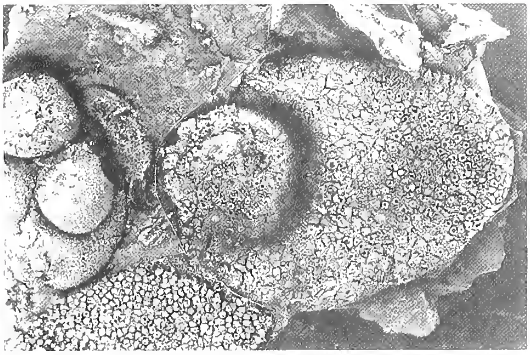
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SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes

3. The origin of the radiate and polygonal microstructures may be directly related to processes concerned with shell calcification and its subsequent alteration. Radiate structures and perforated polygons are generally expressed on both internal and external moulds of individual valves, thus suggesting that the whole shell thickness is usually involved in the formation of these microstructures. Indeed, in one specimen (Pl. 86, fig. 5; text-fig. 7B) fracturing across the valve has clearly occurred in a zig-zag path, indicating boundaries between polygons. Three-dimensional reconstructions (text-figs. 8 and 9) depict individual radiate structures and perforated polygons each as internal and external surface expressions of isolated and coalesced platelets respectively. The central perforations may represent former normal pore canals although there is no firm evidence that they completely penetrate the thickness of the shell.

Bate and Sheppard (1982) have observed isolated and coalesced discs and spherulites of calcium carbonate within the cuticle matrix of Recent myodocopids, structures that they interpret as fundamental products of the *in vivo* calcification process responsible for producing the calcified ('shell') cuticle. According to these authors, growth of these structures appears to take place either by coalescence or by accretion around the disc ('plate') perimeter. The discs lie within and cut across the layers of chitin and observations under plane polarized light clearly show their radiate, crystalline nature (Bate and Sheppard 1982, pl. 2, figs. 1 and 2; herein Pl. 88, fig. 4). Such discs and spherulites, which are clearly present in the shell in many Recent myodocopids (see Pl. 88, figs. 1–8), share striking similarities with the platelets described herein from Silurian myodocopids: e.g. in size, shape (cf. Pl. 86, figs. 1–6 with Pl. 88, figs. 1–3), random distribution, coalescence (cf. Pl. 86, fig. 3 and Pl. 87, fig. 4 with Pl. 88, fig. 2), and the occurrence of central perforations (see Bate and Sheppard 1982). In addition, within their cuticle Recent myodocopids also show loosely packed (Pl. 88, fig. 1) and isolated platelets (Pl. 88, fig. 5). It is, therefore, possible that the radiate structures and perforated polygonal platelets in our Silurian myodocopids were produced by a similar process of shell calcification which may have taken place *in vivo*. Further, presumably post-mortem changes of the calcium carbonate platelets would then consist mainly of *in situ* recrystallization of the calcium carbonate, thus preserving most of their original form and arrangment. Under certain chemical conditions, the calcium carbonate of some platelets may have been rearranged to form acicular radiate structures (rosettes).

There is also, however, evidence based on several observations of Recent material, for an apparently entirely post-mortem crystallization of calcium carbonate matter in myodocopids. Discoidal, spheroidal, and irregular-shaped 'nodules' (up to 300 μm diameter) have been 'produced' within the cuticle of Recent cypridinid valves simply by drying the valves and then soaking them in water (Sohn

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EXPLANATION OF PLATE 87

Examples of polygonal and radiate microstructures of the shell of Silurian myodocopid ostracodes.

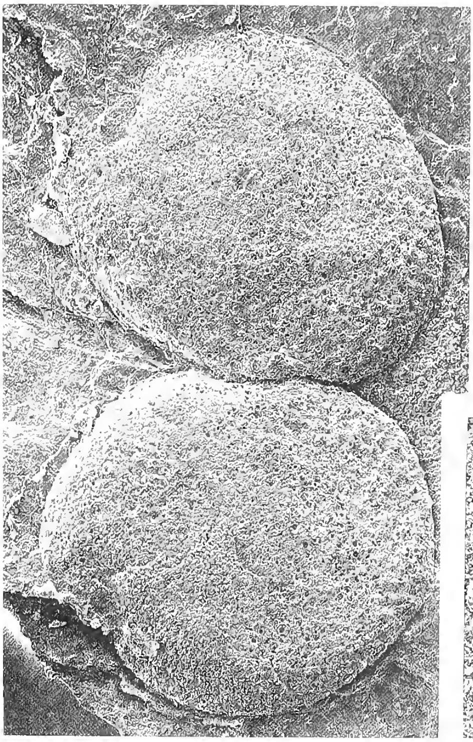
Figs. 1 and 5. 'Cypridinid' gen. et sp. nov. A. Open carapace, IGR 33016, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 1, lateral view, × 15. 5, detail of central area of the left valve showing reniform muscle scar, perforated platelets and closely packed microplatelets, × 150.

Figs. 2–4. 'Cypridinid' gen. et sp. nov. B. Right valve, IGR 33200, siltstones of Ludlow or Pridoli age, Saint-Denis-d'Orques, Sarthe, Armorican Massif, France. 2, lateral view, × 18. 3, detail of adductor muscle scar (from 2), × 52. 4, packed, perforated polygons in anteroventral part of the valve, stereo-pair, × 52.

Figs. 6 and 7. '*Bolbozoe*' cf. *bohemica* Barrande, 1872. Right valve, IGR 33059, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 6, lateral view, × 9; note microstructures on dorsal part of the adductorial sulcus and on ornamented part of adjacent central lobal area. 7, detail of dorsal end of the adductorial sulcus showing radiate microstructures ('rosettes') and perforated polygons, stereo-pair, × 54.

Fig. 8. *B.* cf. *anomala* Barrande, 1872. Left valve, lacking any discernible microstructures, IGR 33018, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France, × 19.

All specimens are Silicone rubber casts from external moulds. All SEM except fig. 6.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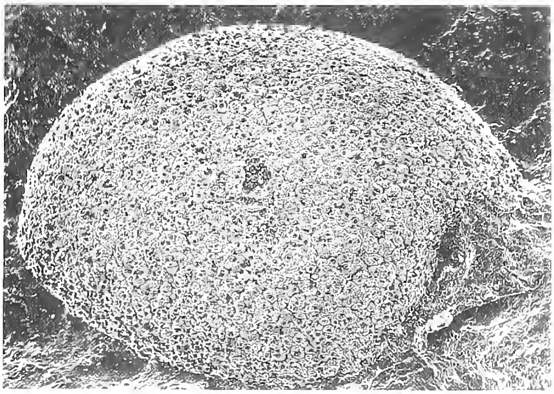
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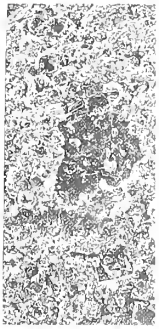
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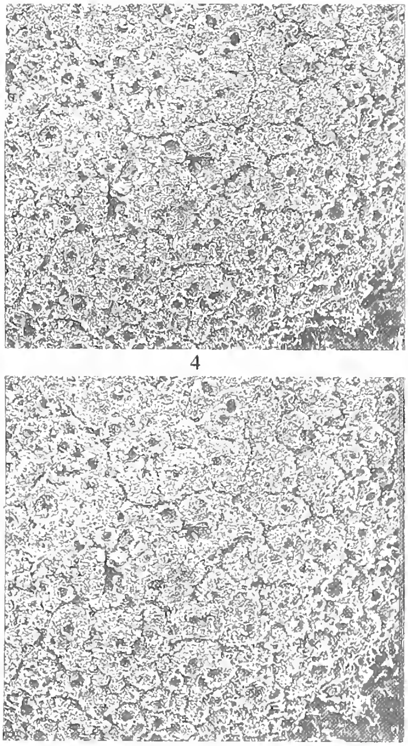
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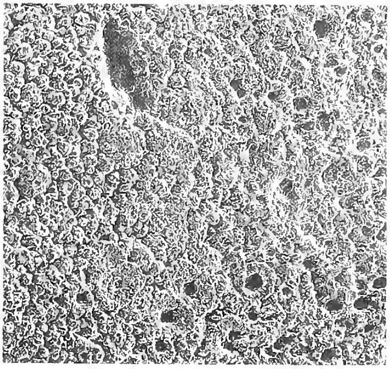
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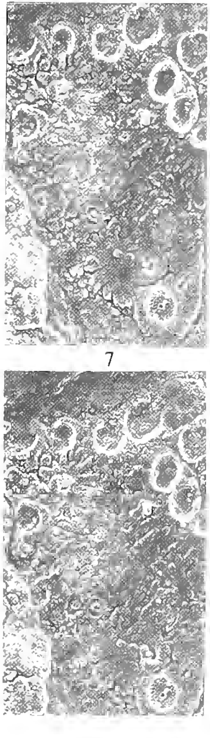
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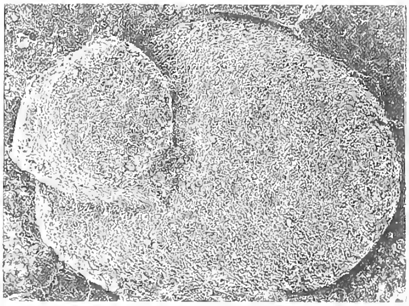
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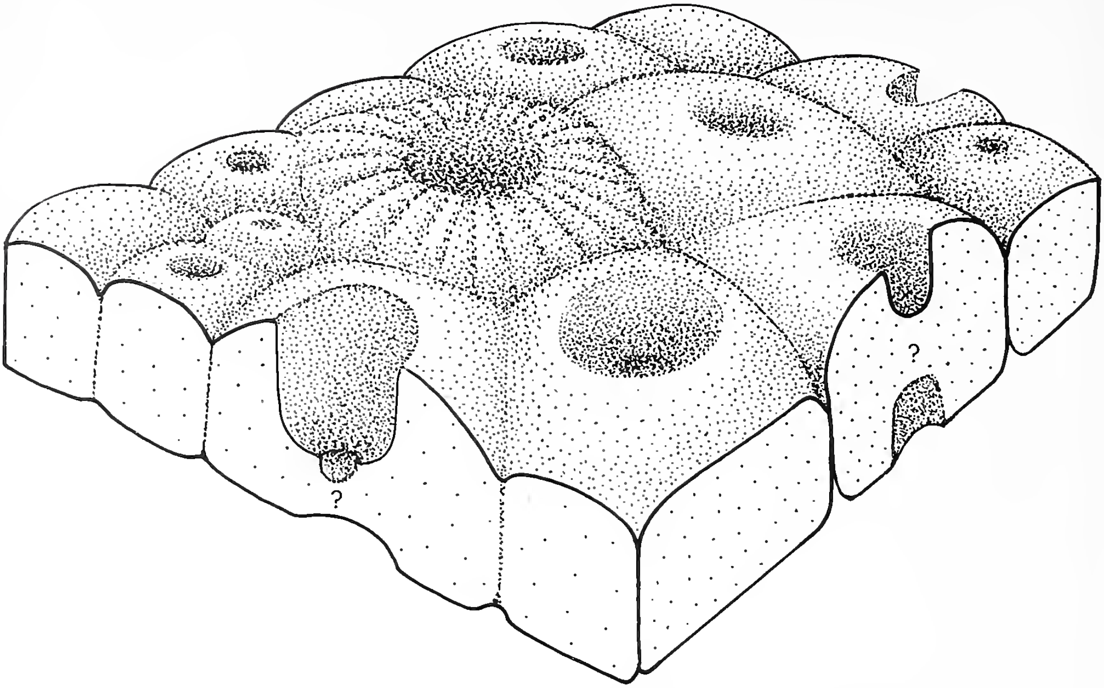
SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes



TEXT-FIG. 9. Reconstruction of packed polygonal platelets, including some showing acicular radiate structures; based on observations on internal and external moulds (e.g. see Pl. 85, figs. 6 and 7; Pl. 86, figs. 1–6). Central perforation may or may not completely penetrate shell thickness. True shell thickness unknown.

and Kornicker 1969). These nodules, of monohydrocalcite ($CaCO_3H_2O$) and calcite, are morphologically comparable to the platelets in our Silurian specimens and, according to the authors, can develop post-mortem in many Recent cypridinacean myodocopids. Sohn and Kornicker (1969, pl. 2, figs. 3 and 4) demonstrated that the initial form of the 'shell' carbonate in such valves is that of an amorphous gel evenly distributed throughout the cuticle; only subsequently is the carbonate redistributed during a change in form to monohydrocalcite, with nucleation leading to 'nodule' production. In addition, Kornicker (1981, herein Pl. 88, fig. 6) illustrated radiate, rosette-like structures produced by post-mortem mineral rearrangement within the cuticle matrix of a Recent myodocopid. Supposed post-mortem recrystallization (of possible platelets) occurs in Carboniferous cypridinacean myodocopids (see Sohn 1977; Bless 1973), where the obvious radiate markings consist of single or coalesced rosettes resembling those in Silurian myodocopids (cf. Pl. 85, figs. 9–11 with Sohn 1977, fig. 1*h*). Sohn (1977, p. 128) considered that the nodule 'artefacts' that Sohn and Kornicker (1969) induced in Recent *Vargula* specimens are not similar to the radiating structures seen in the Carboniferous '*Cypridina*' *radiata* and other species, but we are inclined to take the opposite view.

In summary, the evidence for the role and timing of the calcification process in Recent myodocopids is equivocal. Sohn and Kornicker (1969) emphasize the possibility of a very rapid posthumous production of crystalline nodules. They state, however, that the same process can also occur (though rarely) *in vivo*. Unfortunately they do not elaborate upon, or illustrate evidence for, this crucial statement. By comparison, Bate and Sheppard, in describing the process of cuticular spherulite (= nodule) development, appear to assume uncritically that it occurred *in vivo*, despite the fact that 'some non or poorly calcified individuals were present' (1982, p. 26). Furthermore, they seem to have been unaware of Sohn and Kornicker's earlier work and its fundamental implications for their own study. From this, and also because they do not record the preservational medium or give the post-mortem age of their Recent specimens, it is difficult to assess the possible role that post-mortem processes may have played in the formation of the spherulites in Bate and Sheppard's material.

Ultimately this crucial question of the relative timing and role of the calcification process in the myodocopid cuticle can only be resolved by the study of living or freshly killed specimens. With regard to our fossil material we can say that it contains microstructures like those 'produced' in Recent myodocopid taxa and we therefore conclude that the same calcite depositional processes may well have been operative. Furthermore, the ubiquity of such structures in taxa separated in time by some 400 m.y. emphasizes that they cannot be of use in low level systematics.

There is, however, a further point that may lend weight to the argument for *in vivo* calcification in our fossil material. One of the main conclusions of Sohn and Kornicker's study was that their post-mortem interpretation for the calcification process explains 'the scarcity of fossil Myodocopida', since after 'the nodules formed, the protein and chitin framework of the shell usually disintegrated; consequently, recognisable myodocopid fossils are rare' (1969, pp. 104–105). However, our studies show that at least in certain Silurian environments, myodocopids can occur comparatively often and it could be that their relatively high preservational potential results from an early (*in vivo*) onset of the calcification process.

We suggest that a distinction can be drawn between various possible sequences of the implied calcification process and a model based on these differences is outlined below.

POSSIBLE MODE AND STYLES OF CALCIFICATION IN SILURIAN MYODOCOPIDS

The inferred presence of calcium carbonate platelets, comparable with those of Recent myodocopids (e.g. Bate and Sheppard 1982), within the shell of Silurian bolbozoids and 'cypridinids' implies a particular mode of calcification. However, the occurrence (within and between individuals of the same and different species) of a variety of sizes and styles of radiate and/or polygonal microstructures (Pls. 85–87) attributable to such processes clearly requires explanation. Taking into account the findings and *in vivo* interpretations of Bate and Sheppard (1982), a model to explain the possible mode of calcification and the formation of the various types of radiate and polygonal microstructures of the Silurian myodocopid shells is proposed (text-fig. 10).

Nucleation centres have obvious importance at the beginning of any calcification process. If such centres are numerous and densely packed, the resulting pattern of calcification will be very different than if they were sparse and distant. Thus, based on possible variation in number, density, and distribution of centres, four cases of shell calcification are considered in order to account for the formation of the variety of microstructures observed (text-fig. 10A–D). The central perforations present in most of the platelets of our Silurian myodocopids (text-figs. 7–9)—possibly normal pore-canals (see above)—provide in some cases possible nucleation centres. This has parallels in Recent myodocopids; Bate and Sheppard (1982) concluded that nucleation of calcium carbonate in *Halocypris inflata* might preferentially take place around pores.

Case A (text-fig. 10A, 1–4). Here the nucleation centres for initial calcification would be distributed regularly and densely across the cuticle matrix (Stage A1). Spherulites or discs of calcium carbonate begin to form heterochronously and grow outwards in all directions (Stage A2). Further calcification at new centres and peripheral accretion around existing discs produces a pattern of packed polygonal platelets which then effectively prevents further 'lateral' calcification taking place (Stage A3). At this stage the calcareous platelets are likely to be intimately associated with layers of chitin, as demonstrated by Bate and Sheppard (1982, pls. 5 and 6) in Recent myodocopids. As a result of possible microbiological action with the sediments the exuviae and post-mortem shells (Stage A4) would then probably lose any outer and internal organic (chitin) layers they might have had. At the same time and later some amounts of mineral recrystallization/rearrangement of the calcareous platelets would occur. Such a process would account for the formation of the granule-like, finely packed polygonal patterns (e.g. Pl. 84, fig. 5; Pl. 87, fig. 5).

Case B (text-fig. 10B, 1–4). Here, nucleation centres are less densely distributed and possibly correspond to normal pore canals (Stage B1). The calcification process is essentially similar to that in Case A, but with the possible growth of larger platelets. In Stage B4, a pattern of perforated polygons results, as seen after the degradation of organic matter (including the possible resultant enlargement of pore-canals) and a mineral rearrangement which included the development of a few acicular radiate microstructures (see Pl. 86, figs. 1–6; Pl. 87, figs. 2–4; text-fig. 9).

Case C (text-fig. 10C, 1–4). The number of nucleation centres (Stage C1) is sparser than in Case B. Post-mortem recrystallization produces a pattern of packed, perforated rosettes (Stage C4) (e.g. Pl. 85, figs. 9–11).

Case D (text-fig. 10D, 1–4). Here, centres of nucleation are very sparse and irregularly distributed (Stage D1). As in Cases A–C, spherulites grow outwards in all directions by peripheral accretion (stages D2, D3). The calcification process terminates before all the platelets could coalesce (Stage D3), because of the relatively large distance between nucleation centres. Post-mortem, acicular recrystallization then produces isolated rosettes (e.g. Pl. 85, figs. 3 and 8; text-fig. 8) or clusters of rosettes (e.g. Pl. 85, figs. 1, 2, 4, 5; Pl. 87, fig. 7).

Variation in the distribution and density of nucleation centres could explain the occurrence of various sized, closely packed platelets on the same valve (e.g. Pl. 87, figs. 3–5).

The model proposed (text-fig. 10) can be used to interpret cases where possible conspecific valves, often from the same horizon, locality, and (even) slab, show a variety of microstructures. For example, some specimens of *B.* cf. *anomala* are 'smooth' (Pl. 87, fig. 8), others show extensive patches of polygonal platelets (Pl. 86, fig. 5; text-fig. 7B), and yet others have a complete polygonal pattern developed (Pl. 86, figs. 2 and 4; text-fig. 7A). Most important and revealing as far as the interpretation of their various microstructures is concerned, are those conspecific valves occurring adjacent to each other on a single slab (Pl. 86, fig. 6). In this case the 'smooth' valves might possibly represent newly moulted individuals (text-fig. 10, stages A1, B1, C1, D1) with very small amounts of cuticle

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EXPLANATION OF PLATE 88

Specimens of Recent myodocopid ostracodes showing various degrees of valve calcification.

Figs. 1–3. *Amboleberis antyx* Kornicker, 1981. Cylindroleberidid, right valve, USNM 157625. Recent, Grand Récif, Madagascar, West Indian Ocean; 21 m depth. 1, lateral view showing numerous circular platelets within the shell, × 45. 2, detail of platelets, some coalescing × 125. 3, closely packed platelets in anterior part of the valve, below rostrum, × 245.

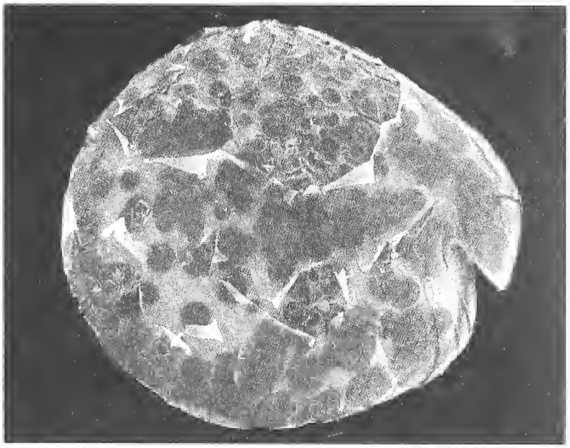
Fig. 4. *Halocypris inflata* (Dana, 1849). Halocypridid, broken shell fragment. Recent, North Atlantic Ocean; 0–10 m depth. Shell surface under plane polarized light showing crystalline nature of circular platelets; growth of platelets is thought (Bate and Sheppard 1982) to take place by coalescence and by accretion around platelet perimeter, × 300.

Fig. 5. *Tetraleberis maddocksae* Kornicker, 1981. Cylindroleberidid, left valve, USNM 157626. Recent, Grand Vasque Lagoon, Madagascar, Western Indian Ocean; 18 m depth. Lateral view, × 24. Juvenile specimen in process of moulting; shows a few large platelets sparsely distributed within the shell.

Figs. 6 and 7. *Leuroleberis sharpei* Kornicker, 1981. Cylindroleberidid. Recent, Monterey Bay, California; 36 m depth. 6, right valve USNM 139286, showing radiating concretionary structure on dorsal part of the valve from which surface layers have peeled (specimen boiled for 15 min. in dilute potassium hydroxide), × 18. 7, anterior part of left valve, USNM 156930, showing abundant oval fossae on external surface and closely packed platelets of various sizes within the shell, × 46.

Fig. 8. *L. mackenziei* Kornicker, 1981. Cylindroleberidid, left valve, USNM 156967. Recent, New South Wales Coast, Australia. Lateral view showing platelets coalescing to form large calcified areas within the shell, × 17.

Figs. 1–3, 5–8 from Kornicker 1981; 4 from Bate and Sheppard 1982. USNM = National Museum of Natural History, Smithsonian Institution, Washington.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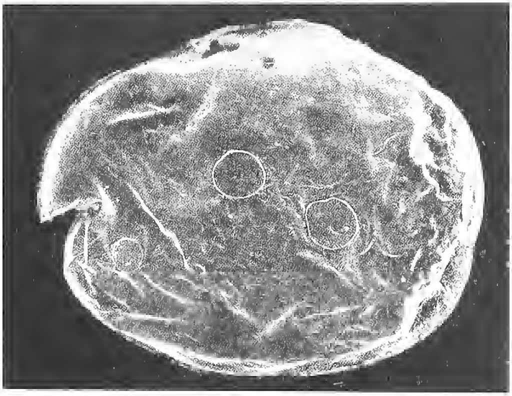
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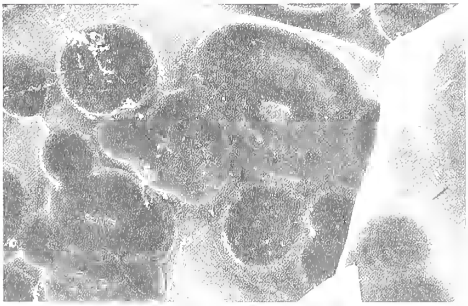
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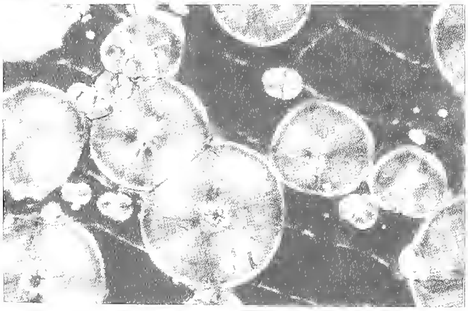
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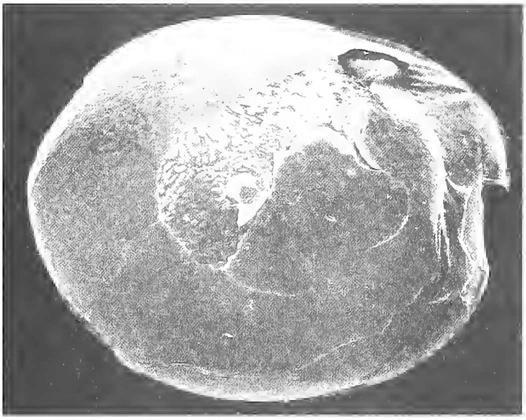
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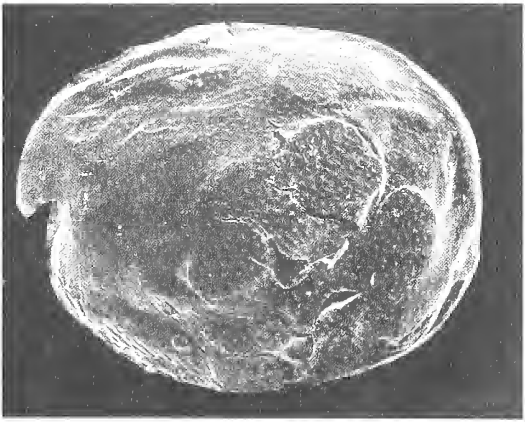
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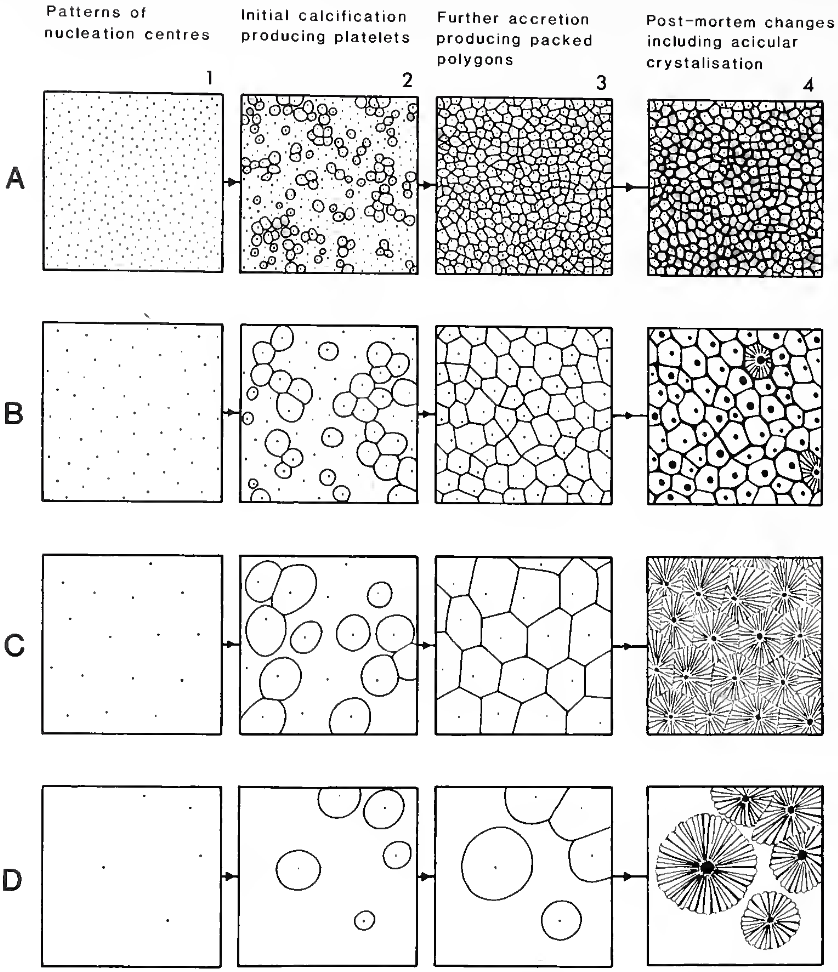
SIVETER, VANNIER and PALMER, Recent myodocopid ostracodes



TEXT-FIG. 10. Model to explain the possible mode of calcification and formation of patterns of shell microstructures in Silurian myodocopid ostracodes. A, regular, densely distributed nucleation centres. B, C, less dense. D, irregular, sparsely distributed nucleation centres.

calcification (for detailed observations on the development of newly formed cuticle in ostracodes, see Rosenfeld 1979; Okada 1982). In the same way, patches of platelets on the valve surface might indicate an intermediate stage of calcification (text-fig. 10, stages A2, B2, C2, D2) or poor calcification, and specimens with relatively closely packed polygonal patterns have possibly completed their cuticle calcification prior to moulting anew (text-fig. 10, stages A3, B3, C3, D3). Such an interpretation is supported by observations (Bate and Sheppard 1982) on sympatric specimens of the Recent myodocopid *H. inflata*: some were fully calcified (having coalesced platelets forming a completely rigid shell), and others were either poorly calcified (patches of platelets) or lacked calcification (no platelets). Although not explicitly stated by Bate and Sheppard, these variations could reflect different states of calcification between moults. Another example, and particularly convincing in this context is the poorly calcified, 'in-moult' specimen of the Recent myodocopid *Tetraleberis maddocksae* figured by Kornicker (1981, pl. 34, fig. *a*; herein Pl. 88, fig. 5).

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A RE-EVALUATION OF THE PLANTS *TINGIA* AND *TINGIOSTACHYA* FROM THE PERMIAN OF TAIYUAN, CHINA

by GAO ZHIFENG *and* B. A. THOMAS

ABSTRACT. The two characteristic Cathaysian Carboniferous–Permian genera *Tingia* and *Tingiostachya* are reviewed and rediagnosed in the light of new specimens from Taiyuan, northern China. Epidermal features of *Tingia* include bands of longitudinally arranged stomata. *Tingiostachya* is shown to have spirally arranged sporophylls with each bearing one spheroidal sporangium, rather than the previously described whorls of four sporophylls and tetralocular sporangia. *Tingiostachya tetralocularis* and *Tingia elegans* are rediagnosed. The morphological and taxonomic relationships between the two genera are discussed, and it is proposed that a new family Tingiostachyaceae includes *Tingiostachya* and the satellite taxon *Tingia*.

FOUR floras can be recognized in Carboniferous and Permian strata: the Euramerian flora, the Angaran or Kusnezk flora, the *Glossopteris* flora, and the Cathaysian flora (Chaloner and Meyen 1973; Li and Yao 1982, 1983). The Cathaysian flora extended over what is now China, Korea, Japan, and as far as Sumatra and New Guinea. The flora started to diversify from the Euramerian flora in the late Carboniferous, reached its greatest diversity in the early Permian, and persisted into the late Permian. The Cathaysian flora can itself be divided roughly by the present latitude of 35° N. into two distinct floras, the Northern Cathaysian flora and the Southern Cathaysian flora (Li and Yao 1983).

In the Northern flora, plant assemblages are found throughout the sequence of strata from the late Carboniferous (Stephanian) to the late Permian (Lee 1963, 1964; Li and Yao 1983). Here the late Carboniferous consists mainly of shales, coal-seams, and limestones with the *Neuropteris ovata–Lepidodendron posthumii* assemblage. The assemblage is recognized as the oldest division of the Cathaysian flora because of the presence of *Tingia* and the abundance of distinctive lycophytes. The early Permian Shanxi (Shansi) Series is mainly of terrestrial origin although it includes several thin marine layers with *Lingula* spp. The *Emplectopteris triangularis–Taeniopteris* spp.–*Emplectopteridium alatum* assemblage characterizes this series. Only thin coal seams are present in the overlying Lower Shihezi (Shihhotse) Series and the plants constitute the *Emplectopteris triangularis–Taeniopteris* spp.–*Cathaysiopteris whitei* assemblage. There are no coal seams in the Upper Shihezi Series except in the southern marginal areas and the plant assemblage has changed to what has been interpreted as the main late Cathaysian flora with the major characteristic elements being *Gigantonoclea hallei*, *Fascipteris* spp., and *Lobatannularia eusifolia*.

The plant assemblage sequence in the Southern flora, unlike that of the Northern flora, is discontinuous and the stratigraphic succession is interrupted by volcanic and marine deposits.

The Lower Permian plants described here are from exposures in Simugedong approximately 5 km north-east of East Hill Mine, Taiyuan, Shanxi province, northern China (text-fig. 1). Here the Permian strata are well exposed and widely used as an index section in China. The assemblages of the Northern flora mentioned above were mainly established from work in the Taiyuan area as the local strata contain one of the best-known Lower Permian floras of the northern hemisphere. The main groups of plants previously described from this flora are pteridophytes, cycadophytes, and the Noeggerathiales (including *Tingia* and *Tingiostachya*) with *Tingia* being one of the characteristic genera of this flora.

[Palaeontology, Vol. 30, Part 4, 1987, pp. 815–828, pls. 89–90.]

TEXT-FIG. 1. Map showing distribution of *Tingia* and *Tingiostachya* in south-east Asia. 1, Halle 1925 and 1927, Konno and Asama 1951, and present specimens. 2, Konno, 1929. 3, Stockmans and Mathieu 1939. 4, Bohlin 1971. 5, Konno *et al.* 1971. 6, Feng *et al.* 1977. (1–3 and 6 both genera; 4 and 5 *Tingia*).

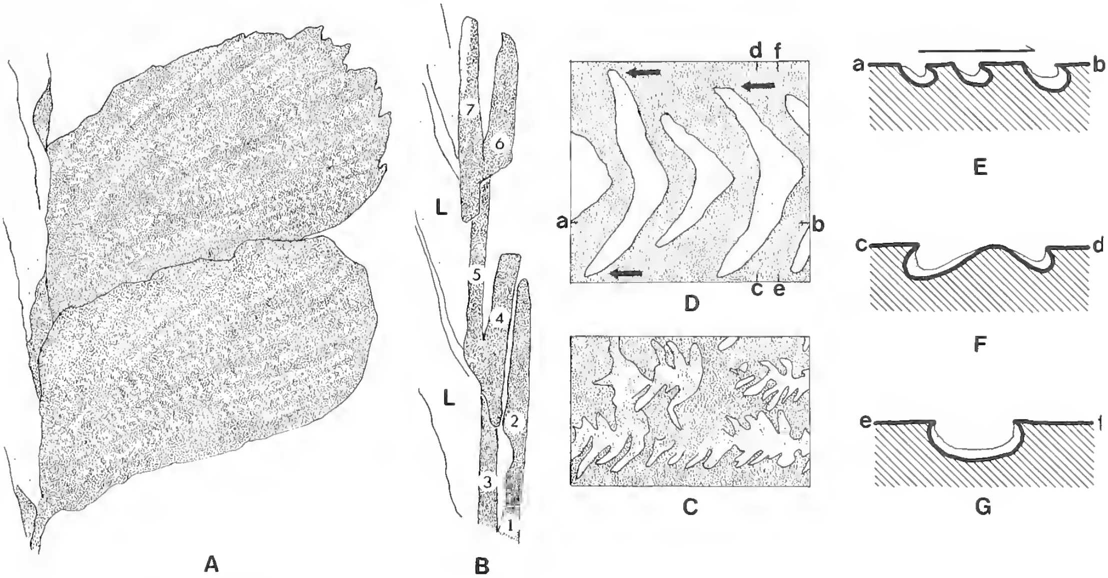
MATERIAL AND METHODS

The specimens described here are preserved as compressions and impressions in a grey shale. The irregular surface produced during the splitting of the shale necessitated some *dégagement* of many of the specimens. This was done with the aid of tungsten needles sharpened by heating and subsequently dipping into molten sodium nitrite. Maceration of portions of leaves, sporophylls and sporangia unfortunately gave neither cuticle nor spore coats, so both fragments of the specimens and their impressions were prepared for high-resolution studies by scanning electron microscope. Both 'Silflo' dental rubber and cellulose acetate (nitrocellulose dissolved in amyl acetate) pulls were used to prepare these impressions. Specimens were coated with gold using an Emscope sputter coater prior to examination with a Cambridge S600 Scanning Electron Microscope.

The specimens will be deposited in the Beijing Graduate School, China Institute of Mining, Beijing, China (numbers prefixed by GP).

HISTORY OF RESEARCH

Tingia. This genus was instituted by Halle (1925) for some Permian leafy shoots from northern China, which had previously been described by Schenk (1883) under *Pterophyllum* Brongniart. Halle placed these specimens in a new genus as they had anisophyllous shoots with four ranks of leaves, unlike the simpler two ranked



TEXT-FIG. 2. *Tingia elegans* Konno. A, two larger leaves showing lines of crescent-shaped depressions in the furrows situated between the veins, GP0089, × 5. B, part of GP0089 showing the smaller leaves; the numbers indicate their acropetal order. L indicates impressions of the larger leaves, × 5. C, part of GP0089 showing the arrangement of the crescent-shaped depressions, × 20. D, schematic drawing of part of figure C showing crescent-shaped depressions within a furrow, each depression being down towards the leaf apex. Arrows indicate the positions where stomata are observed normally, × 5. E–G, schematic sections through the crescent-shaped depressions as indicated in D. The thick line represents the compression; hatched area the underlying rock; dotted areas the portions of the sediment trapped in the depression during the splitting of the shale. The arrow in E is directed towards the leaf apex.

arrangement of leaves in *Pterophyllum*. Halle's original diagnosis of *Tingia* was 'Dorsiventral, frond-like anisophyllous shoots with thick axis. Leaves apparently arranged in four rows, two on the upper and two on the lower side of the axis. Leaves of the two rows on one (the upper?) side smaller, directed forward at narrow angle to the axis, those of the other two rows (on the lower side?) larger, spread out in one plane and forming a more open angle to the axis: each lateral half of the shoot thus provided with two rows of dissimilar leaves. Leaves of the larger (normal) type varying from broadly cuneate-obovate to oblong or linear, with entire lateral margins but more or less deeply lobed at the apex. Several veins entering each leaf, dichotomizing mostly in the lower part of the leaf, all branches continuing to the apex.' Originally Halle diagnosed two species—*Tingia carbonica* (Schenk) and *T. crassinervis* sp. nov. Subsequently Halle (1927) added *T. partita* sp. nov. on revising the genus. Previously he had been unsure of the orientation of the shoots, but in 1927 stated that the two ranks of smaller leaves were on the lower side of the shoot. He also pointed out for the first time that the smaller leaves were often deeply dissected.

Konno (1929) described two further species, *T. hamaguchii* and *T. elegans* together with new specimens of *T. partita* and *T.* (cf.) *carbonica* from the Lower Permian of North Korea. He revised Halle's generic diagnosis by adding several new morphological characters. The foliage shoot was shown to become gradually narrower towards the base, while 'contracted at the top into a pointed or bluntly pointed apex'. The axis was 'straight or slightly falcate, unbranched, gradually thinned at the upper and abruptly thickened at the lower end, with several longitudinal striations'. Larger leaves were described as highly variable in form, generally alternate, although sub-opposite in their lower part, and more crowded in the upper region of the shoot. The smaller leaves were generally of a much more regular form.

Other specimens have been described subsequently from the Permian of northern China, the far north of North Korea, and Malaysia. They are *T. laciniata* Kawasaki (1934), *T. kikkawai* Kawasaki (1934), *T. gerardi* Stockmans and Mathieu (1939), *T. trilobata* Stockmans and Mathieu (1939), *T. minor* Konno and Asama (1951), *T. acuminifissa* (Krasser) Bohlin (1971), *T. subcarbonica* Konno, Asama, and Rajah (1971), *T. oblonga*

(Sze) in Gu and Zhi (1974), and *T. yichuanensis* Feng (in Feng *et al.* 1977). However, it is important to realize that amongst these only *T. subcarbonica*, *T. yichuanensis*, and *T. laciniata* were described as having the characteristic four ranks of anisophyllously arranged leaves. Konno *et al.* (1971) did not describe the smaller leaves on their *T. subcarbonica* nor mention them in their diagnosis. Unfortunately, their illustrations are also not convincing enough to prove that the specimens really do possess these smaller leaves. The other species seem to have been included in *Tingia* on the basis of the apparent similarities of their overall appearance to Halle's specimens; that is on the features of their larger leaves.

Similar specimens found outside Asia were described by Darrah (1938) as belonging to *Tingia*. However, these were later shown by Mamay (1968) to be without the two ranks of smaller leaves and he then removed them to his new genus *Russellites*. They were subsequently moved to *Yuania* by Du and Zhu (1982).

There is clearly a difficulty in identifying specimens as *Tingia* when the main generic character of possessing small leaves may be simply concealed by the alignment of the specimens. This problem is returned to later.

Tingiostachya. *T. tetralocularis* was named by Konno (1929) for some specimens from the Lower Permian of the Jido Series in the far north of North Korea. These specimens, described as reproductive organs, were found associated with either *Tingia hamaguchii* or *T. elegans*. Konno's original diagnosis of the genus was 'Fertile shoot (in the geno-type, *T. tetralocularis*) consists of two parts: a long(?) slender axis and cylindrical terminal cones. Axis slender, forked dichotomously at apex, longitudinally ribbed with small uniform leafy scales. Cone terminal, developed on each of the dichotomized branchlets of the axis, with numerous sporophylls in four vertical series. Sporophylls uniform, more or less elongated, but only slightly modified from the foliage leaf in *Tingia*. A large tetralocular synangium, hemispherical, placed directly on the upper surface of each bract, apart from the cone-axis, receiving one group of bundles from the axis which runs along the median zone of the bract.' Konno described the spore as 'often well preserved, usually of obovate contour, with the larger diameter from 150 μm to 130 μm'.

Another two specimens of *Tingiostachya* have been described by Stockmans and Mathieu (1939) from Kaiping, northern China, although both cones were thought to be specifically indeterminable. The sporophylls of one of these cones (associated with their new foliage species *Tingia trilobata*) seem lobed like the ordinary large leaves of *Tingia*, although they were much smaller and not clearly discernible. Using a pull technique, Stockmans and Mathieu recovered triradiate spores from both cones. These were very similar, about 100 μm in diameter, with smooth surface and said to resemble closely the microspores of *Noeggerathiostrobus* figured by Nemejc (1935).

Examination of the new Taiyuan material has yielded new information that permits a re-evaluation and a rediagnosis of the two genera. Because we have no conclusive evidence that *Tingiostachya* came from the same parent plant as *Tingia* we propose to follow the classification system proposed by Thomas and Brack-Hanes (1984) in their discussion of the lycophytes. They proposed that families should be based on reproductive characters alone, with other organs only included as so-called satellite taxa. This allows a classification system to be constructed to show the most probable relationships between fertile and sterile organs without broadening the family definition to include isolated sterile organs of doubtful affinity. We therefore propose that the family Tingiostachyaceae be used to include the one genus *Tingiostachya*. *Tingia* should be taken as a satellite taxon within the Tingiostachyaceae.

SYSTEMATIC PALAEONTOLOGY

Family TINGIOSTACHYACEAE fam. nov.

Diagnosis. Pedunculate cones with spirally attached sporophylls. Single sporangia attached to proximal part of the adaxial surface of sporophylls with upwardly extended lateral margins (alations).

Genus. *Tingiostachya* Konno.

Satellite taxon. *Tingia* Halle.

Genus TINGIOSTACHYA Konno (1929)

Type species. *Tingiostachya tetralocularis* Konno (1929).

Emended diagnosis. Fertile shoot consisting of a peduncle, with spirally arranged leaves and a terminal cone once dichotomized at its base. Leaves on peduncle ensiform, spirally arranged. Cone axis slender. Sporophylls spirally arranged, pedicels arising at right angles, with upwardly extending lateral margins (alations). Laminae lanceolate, parallel to cone axis. Sporangia spheroidal, attached to proximal part of adaxial surface of pedicel. Sporangia with small spores.

Tingiostachya tetralocularis Konno (1929)

Plate 89, fig. 10; Plate 90, figs. 1–7; text-fig. 3A–E

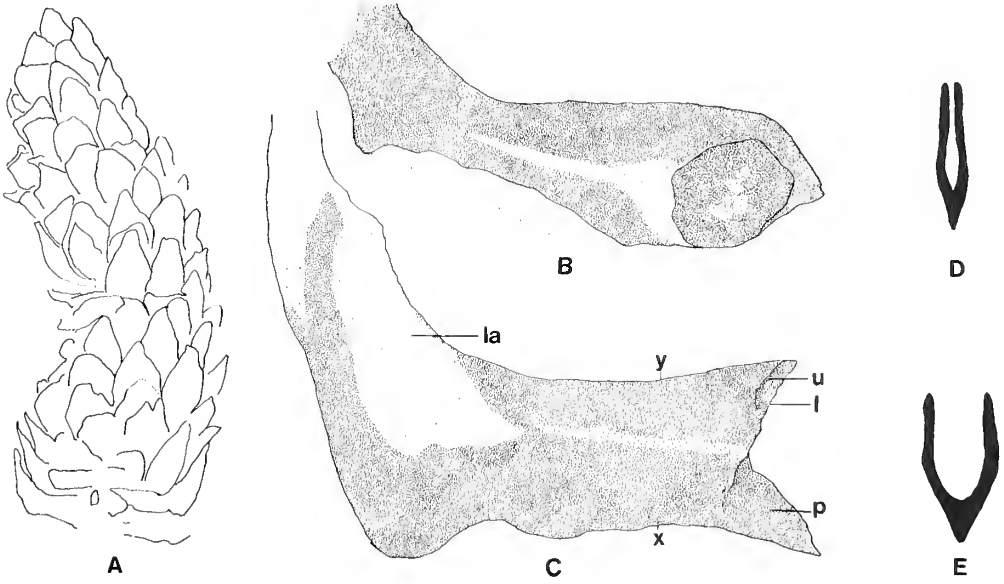
1929 *Tingiostachya tetralocularis* Konno, p. 120; pl. XXIII, fig. 5*c*; pl. XXIV, figs. 4 and 5; pl. XXVII.

Emended diagnosis. Cone about 13·0 cm long, individual cones 8·0–12·0 mm broad. Sporophyll pedicel about 0·5 mm high and 3·0 mm long with upward lateral extensions (alations) about 1·5 mm high. Laminae 5–7·0 mm long, 2–3·0 mm broad. Sporangia 1·0–1·5 mm in diameter. Spores 20 μm in diameter. Peduncle 2–3·0 mm broad; Leaves ensiform about 9·0 mm long and 1·0 mm broad.

Neotype. GP0094, from the Lower Permian, 5 km north-east of East Hill Mine, Taiyuan, Shanxi province, northern China; the whereabouts of the figured specimens of Konno (1929) are unknown (K. Asama, pers. comm.)

Distribution. North Korea: Anji-ri, Daido-gun, S. Heiando (Jido Series and Kobosan Series, Permian). China: East Hill, Taiyuan (Lower Shihezi (Shihhotse) Series, Lower Permian).

Descriptions of new specimens. Those from Taiyuan suggest a rather different morphological interpretation to that proposed by Konno (1929). They are still interpreted as strobili, but their sporophylls are clearly arranged spirally instead of in whorls of four as suggested by Konno. His conclusion that they possessed



TEXT-FIG. 3. *Tingiostachya tetralocularis* Konno. A, outline drawing showing the apical arrangement of the sporophylls. GP0094, ×2. B, single sporophyll from GP0095 showing a sporangium, ×20. C, single sporophyll from GP0095 showing the two alations (u = upper; l = lower; la = lamina; p = pedicel), ×15. D, schematic cross-section (x–y) of lamina in C showing the compression as embedded in the shale. E, schematic cross section of the same sporophyll, as in life.

their leaves in fours was possibly influenced by the fact that *Tingia* shows four ranks of leaves. It is hard to imagine how the fossilization of an organ having the whorled construction shown by Konno (1929, text-fig. 4A) could possibly result in the appearance of the compression shown in his plate XXIV, fig. 4 and plate XXVII, fig. 2. These photographs show strobili with sporophylls appearing to be in spirals.

Among the new specimens of *Tingiostachya* from Taiyuan, the three most complete show a slender axis, with elongated leaves (Pl. 90, fig. 1), bearing a terminal cone that dichotomizes once just above its base (Pl. 90, figs. 1–3). One shows the cone apex (Pl. 89, fig. 10) to be rounded with the terminal sporophylls gently curved around it. No cone is complete; the longest is 6·8 cm. Their widths are all between 8·0 and 12·0 mm. The axis of the cone is slender, 2–3·0 mm broad and longitudinally ribbed. The sporophylls are all regularly arranged in a spiral on the axis (Pl. 90, fig. 3; text-fig. 3A). Their pedicels are at right angles to the axis and about 3·0 mm long. The laminae turn abruptly upwards to be parallel to the axis and there is a very small heel protruding downwards from the distal end of each pedicel. The laminae are lanceolate-triangular in outline with acute apices, about 6·0 mm long and up to 1·8 mm broad in their basal region, and have entire margins.

Those specimens which are split longitudinally and roughly through the middle reveal certain undescribed features of sporophyll construction. In some laterally compressed sporophylls a layer of light coloured sediment can be seen between two layers of compression material (Pl. 90, fig. 5; text-fig. 3C–E). This suggests that the sporophyll pedicel was not flat, but that its sides were extended and curved upwards. These extensions appear to be approximately equal to, or slightly more than the height of the pedicel. The rounded sporangia (Pl. 90, figs. 4, 6, 7; text-fig. 3B) are about 1·1–1·6 mm in diameter, being probably compressed from an originally spheroidal shape. Each appears to be attached individually to the proximal part of the adaxial surface of a sporophyll pedicel. They were probably protected by the sporophyll alations in life but revealed in the fossil by the splitting of the compression. Scanning electron microscope observation of several impressions of sporangia showed many flattened circular structures which were all approximately 30 μm in diameter. These are interpreted as representing casts, or possibly moulds, of spores. Unfortunately no structural details nor features of surface ornamentation could be seen on any of these putative spores. Some sporangia also possess what appear to represent impressions of the sporangial wall cells. These are about 20 μm broad and radially elongated around the edges of the sporangia.

There are small circular marks on the cone axis which are very similar in size to the sporangia, but are flat and rough in appearance unlike the raised and smooth circles, with concave centres, of the sporangia. They are best interpreted as false pedicel scars formed by the forced removal of the sporophylls during the splitting of the matrix. Judging from the appearance of the present specimens, Konno could have mistaken some of these false scars for sporangia, for he described the sporophylls as having four sporangia, or a tetralocular synangium attached to the upper surface.

Comparisons. The main means of identifying reproductive organs as *Tingiostachya* are the way in which the terminal cones dichotomize once at their very base, their spirally arranged sporophylls, and their spheroidal sporangia attached to the proximal part of the adaxial surface of the sporophyll pedicel. There are no other described genera that can be thought to be closely comparable.

EXPLANATION OF PLATE 89

Figs. 1–9. *Tingia elegans* Konno. 1, GP0087, leafy shoot showing acropetal overlapping arrangement of the deeply lobed larger leaves and their reduction in size towards the base of the shoot, ×2. 2, GP0088, leafy shoot showing basipetal overlapping arrangement of leaves and basal part of the shoot, ×1·5. 3, SEM of a rubber peel of a leaf impression from GP0096 showing the furrows between the veins, ×40. 4, SEM of an amyl acetate peel of the lower surface of a larger leaf compression from GP0097 showing the epidermal cells over a vein, ×200. 5, GP0090,the apical part of a leafy shoot showing size reduction towards the apex of the shoot, ×2. 6, GP0089, leafy shoot showing smaller leaves, ×5. 7, GP0098, a larger leaf showing its toothed upper margin and apex and its dichotomous venation, ×8. 8, GP0046, part of a leafy shoot showing the smaller leaves and the overlapping larger leaves, ×2. 9, SEM of a rubber peel of impression showing a putative stoma on the edge of furrow on the lower surface of leaf from GP0096, ×700.

Fig. 10. *Tingiostachya tetralocularis* Konno, GP0091, the apex of a cone with its spirally arranged and incurved sporophylls, ×10.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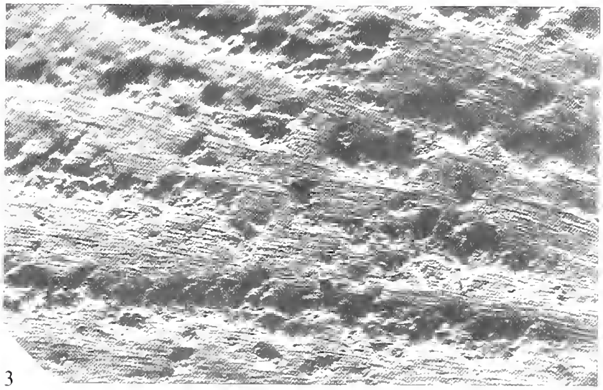
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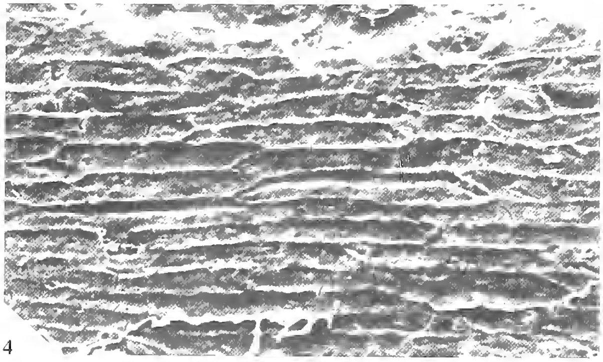
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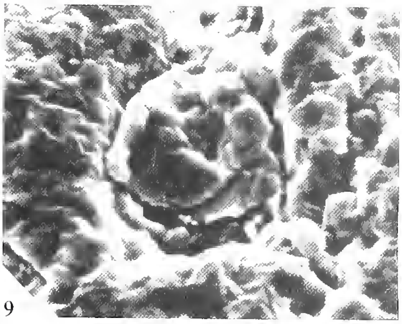
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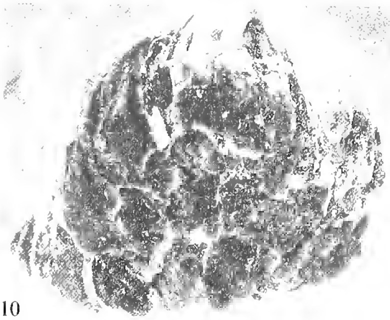
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GAO and THOMAS, *Tingia*, *Tingiostachya*

Noeggerathiostrobus Nemejc (1928) has often been thought to be quite similar but this was through the mistaken interpretation that *Tingiostachya* possessed tetralocular synangia. In fact *Noeggerathiostrobus* has a single terminal cone with its bract-like units arranged in semicircular discs around an axis. The sporangia are located on the upper surface of the discs in rows and have been shown to produce two sizes of spores (Nemejc 1928; Halle 1954).

As mentioned earlier, the only named species of the genus is *T. tetralocularis* Konno (1929). As the Taiyuan specimens appear very closely comparable in size and in sporophyll morphology to Konno's figured specimens, we refer them to his species. The specimens of Stockmans and Mathieu (1939, 1957) are much smaller so we prefer to continue to keep them separate.

Genus TINGIA Halle (1925)

Type species. Tingia carbonica (Schenk) Halle (1925)

Emended diagnosis. Dorsiventral, anisophyllous, unbranched foliage shoots; two rows of larger leaves becoming smaller towards apex and base, two rows of smaller leaves. Larger leaves obovate to linear with toothed apical margins and decurrent bases, alternately arranged on axis, spreading; veins dichotomizing, ending in marginal teeth. Smaller leaves almost parallel to shoot axis.

Tingia elegans Konno (1929)

Plate 89, figs. 1–9; text-fig. 2A–G

Emended diagnosis. Larger leaves obovate, about 10 mm long and 6 mm broad; apex rounded with teeth about 1 mm long; lower margin straight with decurrent base; veins dichotomize twice or more. Epidermal cells longitudinally elongate along the veins and approximately 100 μm long and 15 μm wide. Stomata visible on edges of veins, approximately 25 μm long and 20 μm broad. Smaller leaves about 4 mm long, 1 mm wide.

Neotype. GP0087, from the Lower Permian, 5 km north-east of East Hill Mine, Taiyuan, Shanxi province, northern China. The whereabouts of the figured specimens of Konno (1929) are unknown (K. Asama, pers. comm. 1986).

Distribution. Riajin-ri, Daido-gun, south Heiando, North Korea (Jido Series and Kobosan Series, Permian). East Hill, Taiyuan, China (Lower Shihezi Series, Lower Permian) and all the other localities indicated for the genus on the accompanying map.

Descriptions of new specimens. About forty specimens collected by Gao from the East Hill region of Taiyuan were studied. Most are compressions with many lacking their counterpart impressions. Unfortunately all are fragmentary with only one showing an apex (Pl. 89, fig. 5) and three their basal regions (Pl. 89, figs. 1 and 2). The longest fragment of shoot is 12 cm, although we estimate their original lengths to be in the order of 20 cm or more. The axes are longitudinally striated and vary in width from 1 mm to 3 mm in different specimens. The shoots are dorsiventral and anisophyllous with two ranks of larger leaves and two ranks of much smaller leaves (Pl. 89, figs. 6 and 8).

It is difficult to see the arrangements of both kinds of leaves on most specimens. There are two ways in which the larger leaves overlap each other on the shoot. If the overlapping is directed towards the apex

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EXPLANATION OF PLATE 90

Figs. 1–7. *Tingiostachya tetralocularis* Konno. 1, GP0093, a once dichotomized, longitudinally split cone on its leafy pedicel, ×1·5. 2, GP0093, a once dichotomized cone on its leafy pedicel, ×2. 3, GP0094, a once dichotomized cone showing its spirally arranged lanceolate sporophylls, ×2. 4, GP0093, single sporangium, ×30. 5, GP0095, single isolated sporophyll (drawn as text-fig. 3C), ×10. 6, GP0095, single sporophyll with a sporangium (drawn as text-fig. 3B), ×10. 7, GP0094, part of sporangium hidden under the overlapping compression of the sporophyll alation, ×20.


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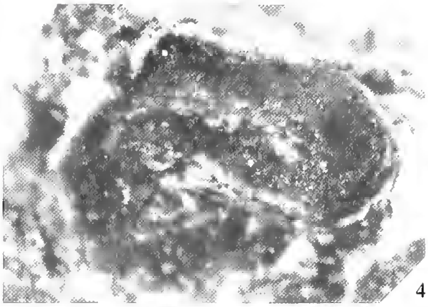
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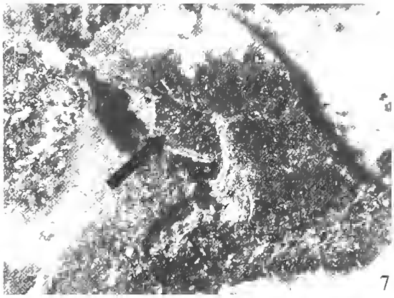
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GAO and THOMAS, *Tingiostachya*

(Pl. 89, fig. 1), that is with the lower margin of each leaf being hidden by the upper margin of the subsequent leaf, the smaller leaves are angled down into the matrix where they are hidden unless uncovered. In those specimens where the overlapping is directed towards the base the smaller leaves are directed upwards. However, only one specimen has been found that shows both types of leaves in this arrangement (Pl. 89, fig. 8). Most have lost their smaller leaves which were ripped off with the counterpart portion of matrix during the splitting of the shale (Pl. 89, fig. 2).

The larger leaves are usually obovate, sometimes slightly elongate in form, with their oblique and decurrent bases attached to the axis by short petioles. The length of the larger leaves varies from 8 to 15 mm and the median width from 4 to 7 mm in different specimens. The angle of the lower leaf margin to the axis varies from 40° to 80°; being constant within a specimen but varying between them. Occasionally the two ranks are attached at different angles, although we attribute this to compression effects during preservation. The lower margin of the leaves are straight and the upper margins somewhat semicircular. The apical portion of the upper margin and the rounded apex are toothed with the longest teeth in the former area (Pl. 89, fig. 7). The veins are usually dichotomizing and terminate either singly, or very occasionally in pairs, in the marginal teeth. There are about ten to eighteen veins in the broadest part of the leaf and about the same number or slightly more reach the margin.

The splitting of the shale has resulted in two basic kinds of specimens. One shows the larger leaves as dark compressions with either discontinuous light furrows and/or more occasionally discontinuous light or dark ridges. The other kind show the larger leaves as impressions with discontinuous light ridges and/or light or dark furrows running along their length. These latter ridges and furrows equate to those visible on those leaves preserved as compressions. These furrows are positioned between the veins and are most obvious in the middle and apical parts of the leaves. (Pl. 89, fig. 3; text-fig. 2A). Distinctive features have been observed in the furrows of some specimens in which the leaves overlap each other towards the apex. These furrows consist of many closely packed but individual depressions; each being crescent-shaped with its convex side directed towards the leaf apex (text-fig. 2A, C, D). These crescent-shaped depressions are also angled down towards the leaf apex (text-fig. 2 E–G) and very occasionally they are joined together in the middle. Scanning electron microscope observations of epoxy and rubber pulls from impressions of the leaves show epidermal cell outlines (Pl. 89, fig. 4) that are longitudinally elongated along the veins and about 50–150 μm long and 8–32 μm wide. Stomata are also visible on the sides of the furrows, that is on the very edges of the well-preserved veins. We suspect that there were many stomata in the crescent-shaped depressions, but the retention of quantities of rock matrix in these depressions prevents us from making the necessary observations. The probable guard cell-like structures (Pl. 89, fig. 9) that can be seen are about 25 μm long and 10 μm broad. Regular hollows, mostly in the furrows, that have similar sizes to the stomata are most probably evidence of stomata in which the guard cells were not preserved.

The smaller leaves are ensiform with tapering margins, 7 mm long, 1–2 mm wide, and directed apically along the axes (Pl. 89, figs. 6 and 8; text-fig. 2B).

The basal part of the shoot shows a rather different arrangement to the main leafy part. The larger leaves become basipetally smaller and are arranged more acutely to the axis. The smallest are 3·0 mm long, 1·5 mm broad, and dissected into three lobes, thereby appearing very similar to the smaller leaves in both size and shape.

Comparisons. The generic identification of *Tingia* is based on the dorsiventral and anisophyllous arrangement of its shoots with two ranks of larger leaves on one side of the shoot and two ranks of much smaller leaves on the other. The toothed apex and apical part of the upper margin of the larger leaves and the numerous dichotomizing veins that terminate in the teeth are also characteristic features. The outwardly similar genera *Noeggerathia* Sternberg, *Russellites* Mamay, and *Plagiozamites* Zeiller with their dorsiventrally flattened large leaves are not anisophyllous as they possess no ranks of smaller leaves. As the new Taiyuan specimens are both dorsiventral and anisophyllous they clearly belong to *Tingia*.

Fifteen species of *Tingia* have been described to date, excluding the two removed by Mamay to *Russellites*. However, only eight are known to have the anisophyllous arrangement of four ranks of leaves. The morphological details of all fourteen species are summarized in Table 1 as described by their authors. The closest comparable species to the new specimens are *T. hamaguchii* Konno (1929), *T. partita* Halle (1927), and *T. elegans* Konno (1929).

T. hamaguchii has similar shaped leaves to the new specimens although they are about twice the size. It also has a looser leaf arrangement (about 1 leaf per cm instead of 1·3–3 leaves per cm as

TABLE 1. Comparison of the species of *Tingia*.

	Characters							
	Shoot		Larger leaves					
	Total width (mm)	Width of axis (mm)	Angle to the axis	Shape	Length (mm)	Width (mm)	Apex	Number of veins in the middle of the leaf
Species described with four ranks of leaves								
T. carbonica (1)	60–75	3–8	40–60	oblong-linear	100	10	truncate	12–24
T. crassinervis (1)	110–130*	10	40–60	oblong-linear	>90*	20*	obtuse	20
T. partita (2)	40–45	5	50–60	obcuneiform	20–25	10	truncate	?
T. hamaguchii (3)	20–30	2	40–50	obtetragonal	15–30	7*	obtuse*	18–24
T. elegans (3)	17–24	1–1·5	30–60	obovate	10–16	10	rounded	13–15
T. laciniata (4)	>120*	4*	45*	lanceolate	50	10	obtuse*	25
T. subcarbonica (5)	>275*	10–15	60	broadly linear	130	25	truncate	60
T. yichuanensis (10)	30*	2	55	obovate	13	7	rounded	18
Species described with no reference to the smaller leaves								
T. kikkawai (4)	?	?	?	elliptical	20–30	10–12	?	?
T. gerardii (6)	17–24	2*	45*	obovate	12–15	14*	rounded*	?
T. trilobata (6)	30–40*	5	45	triangular	25–30	9*	truncate	?
T. minor (7)	5–7	1	30–40	obovate	4–5	2*	rounded	?
T. oblonga (8)	20*	1	60–70	oblong	10	5	obtuse	?
T. multidentata (9)	5–7	3·5	50	triangular	15	8	obtuse*	?
T. acuminifissa (9)	30*	3	40*	triangular	15*	7*	truncate*	?
Present specimens	11–26	1–3	40–80	obovate	8–15	4–7	rounded	10–18

(1) Halle 1925. (2) Halle 1927. (3) Konno 1929. (4) Kawasaki 1934. (5) Konno *et al.* 1971. (6) Stockmans and Mathieu 1939. (7) Konno and Asama 1951. (8) Gu and Zhi 1974. (9) Bohlin 1971. (10) Feng *et al.* 1977.

* Not mentioned in published description, data from photographs.

in the Taiyuan specimens) and the leaves are more closely aligned to the axis (their lower margins being at 25°–50° instead of the 40°–80° in the Taiyuan specimens). *T. partita* differs from the present specimens in having larger and more triangular-shaped leaves with more divergent veins and deeply dissected apices that are most closely comparable to *T. elegans* (which was included as a synonym of *T. hamaguchii* by Lee *et al.* (Gu and Zhi 1974)), and in having similar leaf morphologies and leaf densities (Konno's specimens average 2 leaves per cm). The figures of Konno's earlier specimens seem to show more elongated leaves (Konno 1929, pl. XXV, figs. 1–8), whereas Konno and Asama's later specimens appear virtually identical to ours (Konno and Asama 1951, pl. 9, figs. 5–7). The differences in appearance of the leaf shape of Konno's original specimens can be interpreted as due to the different manner of leaf overlap. Here it is the upper margin which is hidden by the leaf above, thereby producing an elongated appearance to the otherwise obovate leaf.

DISCUSSION

Tingia and *Tingiostachya* have been classified in various ways by different authors. This has resulted from the varied interpretations and preferred emphasis of vegetative or reproductive characters. Furthermore, it has been generally assumed that the two organs came from the same parent plant because of their consistent association at different sites, even though they have never been found in organic attachment to each other or to any other organ. Indeed, as they have never been found other than as isolated organs we have no knowledge of the overall morphology of the parent plant.

Halle (1925) proposed *Tingia* to be an aquatic plant with the two ranks of larger leaves floating on the surface and the two smaller leaves submerged. Konno rejected Halle's proposal, suggesting instead that *Tingia* grew in the same manner as extant *Selaginella* and *Lycopodium* although he did note that it was much larger and never branched. He concluded that *Tingia* shoots were most probably foliage branches given off laterally or almost horizontally on the ground from a creeping stem.

From the morphological characters of the Taiyuan specimens we conclude that they represent long shoots, rather than pinnate frond-like organs, that were shed from woody plants. They were most likely to have been orientated with their smaller leaves uppermost as in the anisophyllous species of *Selaginella*. This we deduce from the fact that it is the surfaces of the larger leaves furthest away from the smaller leaves that have the crescent-shaped grooves. If these really are stomatal grooves then they are virtually certain to have been on the underside of the leaves. The larger leaves also appear to be quite thick and this together with their possession of 'stomatiferous' crescent-shaped depressions suggests that they were quite fleshy. Furthermore, it can be taken to suggest that the plants were growing in a relatively dry environment.

Halle (1927) suggested that there was a close relationship between the genera *Tingia*, *Noeggerathia*, and *Plagiozamites*. He therefore proposed that *Tingia* be used as the basis for the family Tingiaceae that included these three genera. Halle of course had found no reproductive organs. Konno compared *Tingiostachya* with the Sphenophyllales and Lycopodiales before classifying it with the extant Psilotaceae on account of the presumed tetralocular synangia even though he noted several major morphological differences. Nemejc (1931) subsequently rejected Konno's interpretations of the plant's affinity and followed Halle in grouping *Tingia*, *Noeggerathia*, and *Plagiozamites* together on the basis of common foliage organization, but placed them in the Noeggerathiales instead of using the family Tingiaceae.

Browne (1933) suggested the affinities of *Tingia* and *Tingiostachya* should lie with the Sphenophyllales. This was based on the supposed verticillate arrangement of the sporophylls in *Tingiostachya* and that the leaves of *Tingia* were similar to the undivided wedge-shaped leaves of the Euramerian genus *Sphenophyllum*. Browne also suggested that the Psilotales should be included in the Sphenopsida.

Stockmans and Mathieu (1939, 1957) and Lee (1963) did not attempt to put either *Tingia* or *Tingiostachya* into a family but included them both as *incertae sedis*.

Most recent accounts accept some relatively close relationship between *Tingia*, *Tingiostachya*, and *Noeggerathia*, although there is differing opinion on their classifications. Boureau (1964) includes the Tingiales (*Tingia* and *Tingiostachya*) in the Noeggerathiophytina. Bohlin (1971) and Lee *et al.* (*in* Gu and Zhi 1974) both take a wide view of the Noeggerathiales as containing *Tingia* and several other leaf genera including *Plagiozamites*, *Yuania*, and *Concophyllum*. Lee *et al.* (Gu and Zhi 1974) also included the reproductive genus *Discinites* and Bohlin (1971) the other leaf genus *Ginkgophyllum*. Taylor (1981) merely points out the similarity between *Tingia* and *Noeggerathia* and includes them both in the progymnosperms. Beck (1981) suggested a relationship between *Tingia*, *Noeggerathia*, and *Archaeopteris* including the former two in the Noeggerathiopsida.

Both *Tingia* and *Tingiostachya* appear to us to suggest a quite unique plant; assuming of course that they really did belong to the same parent plant. We do not accept that there can be any meaningful classification system established on the basis of rather broad similarities of vegetative organs. Neither do we believe that there is any close relationship between *Noeggerathiostrobus* and *Tingiostachya* as we have reinterpreted it here. Indeed, we cannot even say if the parent plant was a pteridophyte, a gymnosperm, or even a progymnosperm.

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NEW CRETACEOUS FISH FOSSILS FROM SEYMOUR ISLAND, ANTARCTIC PENINSULA

by LANCE GRANDE *and* SANKAR CHATTERJEE

ABSTRACT. Based on Late Cretaceous fossils from Seymour Island, hexanchiform sharks and a beryciform teleost are reported from the Antarctic region for the first time. The hexanchiform is a species of *Notidanodon*, and the beryciform is a new genus and species of Trachichthyidae. Fragmentary orthacodontid teeth (*Sphenodus*? sp.) are also reported. An abundance and variety of indeterminate teleost bone fragments (e.g. isolated teeth and centra) were also found. During the Late Cretaceous and Early Tertiary of the Antarctic region, the diversity of fossil teleosts is much less apparent than that of the fossil sharks; but this is probably only an artefact of preservation, because skeletal fragments (isolated teeth in particular) normally are much more diagnostic (i.e. identifiable) for chondrichthyans than they are for teleosts.

SEYMOUR ISLAND, located on the north-east side of the Antarctic Peninsula, is potentially of great significance to studies on the history and biogeography of the region's fish fauna. Cretaceous and Tertiary deposits there include the only known fossil teleosts, neoselachians ('modern' chondrichthyans), and holocephalans from the Antarctic region. Nearly all of these fossils belong to extant families or higher taxa that do not live in the Antarctic region today (i.e. Odontaspididae, Lamnidae, Squalidae, Pristiophoridae, Squatinidae, Myliobatidae, Chimaeriformes, Siluriformes) (Grande and Eastman 1986). Two of the Cretaceous fossils described here also belong to higher taxa not found in the region today (Hexanchiformes and Beryciformes).

There is relatively little higher taxonomic diversity in the Recent fish fauna of the Antarctic region. The fauna is dominated by the percomorph suborder Notothenioidei, endemic to the region and comprising at least 67% of the species and 90% of the individuals in the Antarctic region (Grande and Eastman 1986; De Witt 1971). The incidence of endemism for notothenioids is 86% at the species level with only a few species found in New Zealand, southern South America, the Falkland Islands, and Australia. The only chondrichthyans reported from the Recent fauna are in the skate family, Rajidae. In the fossil faunas, to date, no rajids have been discovered, and the only report of a notothenioid (Woodward 1908) was found to be probably in error (Grande and Eastman 1986).

Woodward (1908) was the first to describe fossil fishes from Seymour Island, and he described both Cretaceous and Tertiary material, consisting of isolated centra and scales. He referred some of the material to *Ptychodus* sp., but this was later (Welton and Zinsmeister 1980; Grande and Eastman 1986) referred only to Elasmobranchii indeterminate and Teleostei *incertae sedis*. The Tertiary elasmobranchs were later reported by Elliot *et al.* (1975), De Valle *et al.* (1976), Cione *et al.* (1977), Welton and Zinsmeister (1980), and Grande and Eastman (1986). Grande and Eastman also reported a Tertiary holocephalan and siluriform, and reviewed the work of all previous workers; therefore, previous work will not be reviewed in depth here.

The only Cretaceous fish to have previously been described from Seymour Island, other than the Woodward material described here, is the lamnid shark *Isurus* sp. (Grande and Eastman 1986: p. 122). The specimens described below are from the same formation and locality as that specimen.

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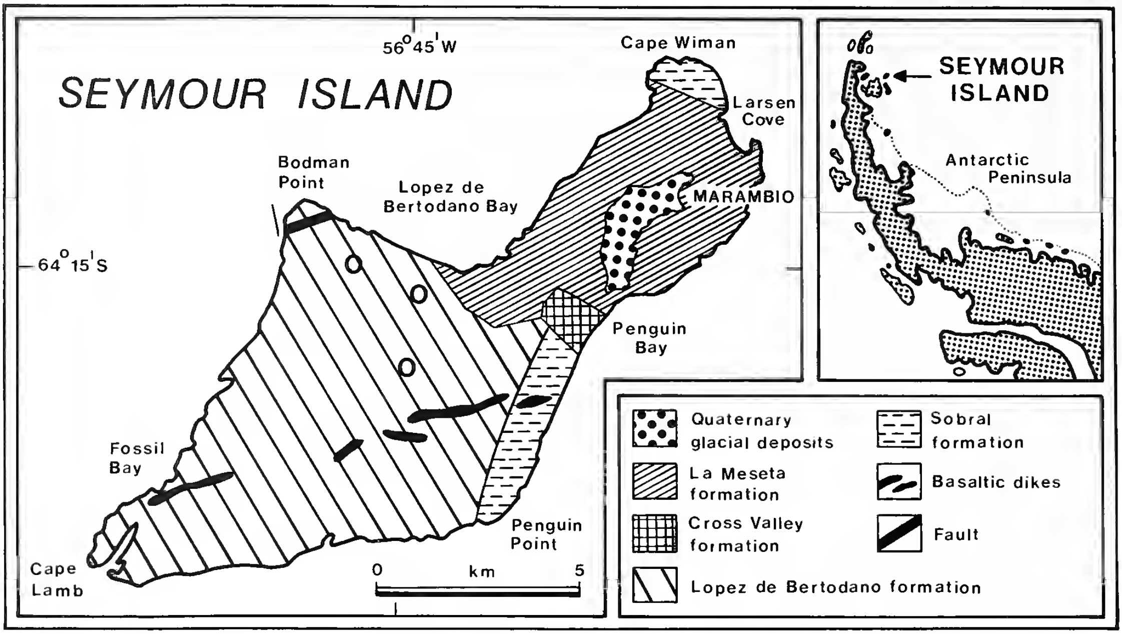


TEXT-FIG. 1. Map showing Seymour Island and Antarctic Peninsula. Circles indicate the Cretaceous fossil fish localities. Ages of rock units: Lopez de Bertodano, Late Cretaceous; Sobral, Late Cretaceous–Palaeocene; Cross Valley, Palaeocene; La Meseta, Eocene; Basaltic dikes, ?Late Tertiary (after Zinsmeister 1982).

GEOLOGICAL SETTING

The thick sequence of fossiliferous marine and non-marine clastics on Seymour Island represent the most complete and well-exposed section of the Upper Cretaceous to Lower Tertiary rocks known in the southern hemisphere. The succession has been divided into two groups: the lower Marambio Group comprised of Lopez de Bertodano and Sobral Formations, and the upper Seymour Island Group consisting of Cross Valley and La Meseta Formations (Bibby 1966; Rinaldi *et al.* 1978; Zinsmeister 1982).

The physical setting of Seymour Island makes it in some ways an ideal place for fossil collection in Antarctica. The island is small—about 20 km long and 9 km wide—and is virtually snow free the year round. The oldest sequence, the Lopez de Bertodano Formation, crops out in the southern two-thirds of Seymour Island (text-fig. 1). It consists of 1200 metres of loosely consolidated greyish sandstones and sandy siltstones, dipping gently eastward. Concretionary horizons occur throughout the sequence. The invertebrate fauna is diverse, consisting of ammonites, echinoids, bivalves, gastropods, arthropods, serpulid worms, and foraminiferans, and suggests Middle Campanian to Maestrichtian age (Howarth 1966; Spath 1953; Macellari and Huber 1982).

Recently a large collection of vertebrate fossils was made from the Lopez de Bertodano Formation. The new material includes the remains of bony fish, sharks, plesiosaurs, mosasaurs, pterosaurs, and possibly birds (Chatterjee and Zinsmeister 1982; Chatterjee *et al.* 1984).

PREPARATION METHODS

The beryciform skull described here was preserved in a hard, calcite-cemented, coase-grained sandstone. The bone is badly fractured and much softer than the matrix, making detailed preparation extremely difficult. Minor preparation was done with needles under a dissecting microscope after immersion in 8% formic acid to soften the matrix.

NEWLY REPORTED CRETACEOUS MATERIAL

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order HEXANCHIFORMES
Family HEXANCHIDAE (*sensu* Ward, 1979)
Genus *NOTIDANODON* Cappetta, 1975
Notidanodon sp.

Referred material. FMNH PF10724 (text-fig. 2A, B), FMNH PF10725 (text-fig. 2C, D), and TTU P9178, 9180, 9182–9185 (all partial isolated tooth fragments). TTU P9182 is in a block of matrix that also has some prismatic cartilage preserved (text-fig. 2E).

Description. The three most complete specimens are FMNH PF10724, 10725, and TTU P9182 (text-fig. 2A–E), and the following description is based on these specimens. Terminology and systematics used for Hexanchidae follow Ward (1979). The teeth are labio-lingually compressed with apically or apico-distally directed principal cusp and distal cusplets. The mesial cusplets are almost as large as the distal cusplets and are mesio-basal to, and distinct and separate from, the principal cusp. Thus, following Ward (1979, p. 122) the tooth fits the diagnosis for the genus *Notidanon* Cappetta 1975. One specimen (TTU P9182: text-fig. 2E) is in a block of matrix that also has some prismatic cartilage preserved, apparently from the same animal. Morphologically, this material most closely resembles *N. lanceolatus*, *N. pectinatus*, and *N. dentatus* (see Ward and Thies 1987) and probably belongs in one of these three very similar looking species. The material differs from *N. loozi* (e.g. Ward 1979, pl. 3, fig. 8) in that the last mesial cusplet points nearly parallel with the principal cusp (text-fig. 2A, B). The species of this genus, known only by isolated teeth, are discussed in Cappetta, 1987.

This is the first report of a hexanchiform from the Antarctic region. The genus is also known from the Palaeocene of Europe, USSR, and from the Upper Cretaceous of North America and New Zealand (Cappetta 1987). Based on available material, monophyly of this 'isolated-tooth genus' seems unsubstantiated.

Order HEXANCHIFORMES? (*sensu* Cappetta, 1987)
Family ORTHACODONTIDAE? (*sensu* Cappetta, 1987)
Genus *SPHENODUS*? Agassiz 1843
Sphenodus? sp.

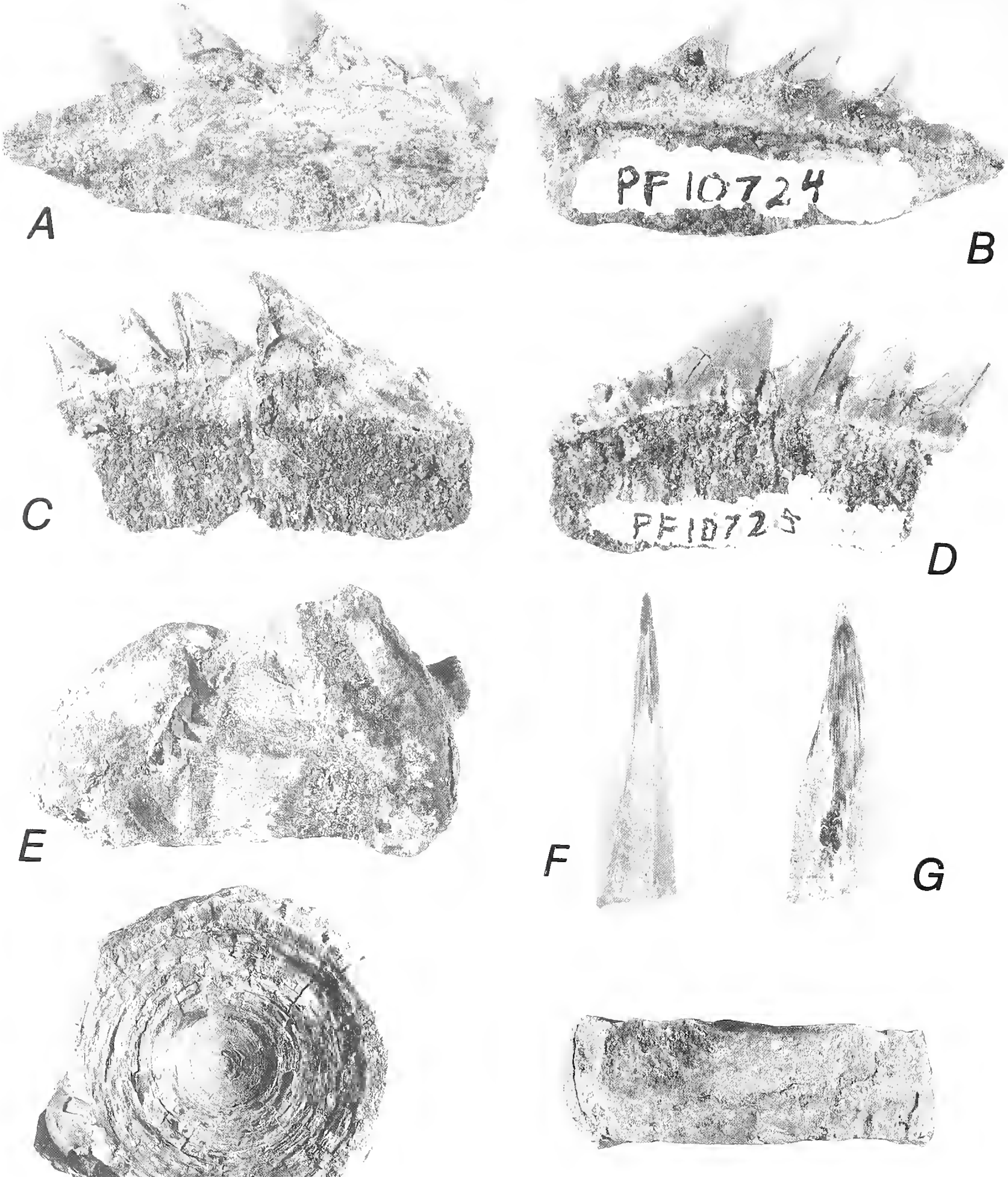
Referred new material. FMNH PF10723 (text-fig. 2F, G) and TTU P9188, 9189, 9191, and 9192 (all partial teeth missing root and base).

Description. Because of incomplete preservation, precise identification of these teeth is not possible. All are somewhat labio-lingually compressed with sharp unserrated mesial and distal cutting edges and sharp points. The teeth were nearly symmetrical in lateral outline, and not curved as in *Isurus*. Their outer surface is smooth, although where the shiny enamel layer is worn off the tooth is striated underneath. They closely resemble fossil species described as *Orthacodus* Woodward, 1889 (e.g. see pl. 1, figs. J, N–P in Uyeno *et al.* 1981 and various figures in a review of the genus by de Beaumont 1960). *Orthacodus* (= *Sphenodus*) is known only by isolated teeth, apart from some skeletal remains from Solnhofen (Cappetta 1977), and the assignment of this poorly known genus to Hexanchiformes is debatable (see Cappetta 1977, p. 50).

Order indeterminate
Family indeterminate
Indeterminate selachian vertebral centra (first reported by Woodward 1908, pp. 1–2)

Referred new material. TTU P9193, 9194, FMNH PF11920, 11921 (two small and two large centra; one of the large illustrated in text-fig. 2H, I).

Description. These centra are identical to those described by Woodward (1908), which he referred to *Ptychodus* [not *Ptychodus* according to Welton and Zinsmeister (1980) and Grande and Eastman (1986)]. One (text-fig. 2H) is so close in size (10 cm diameter) and appearance to a specimen described and illustrated by Woodward that it could possibly be from the same individual. For detailed description see Woodward 1908).



TEXT-FIG. 2. A–E, *Notidanodon antarcti* n. sp., from Upper Cretaceous deposits of Seymour Island. A, B, holotype, nearly complete tooth (FMNH PF10724), ×2·4. A, lateral view (anterior facing right). B, medial view (anterior facing left). C, D, partial tooth (FMNH PF10725), ×2. C, lateral view (anterior facing right). D, medial view (anterior facing left). E, nearly complete tooth in matrix with prismatic cartilage preserved (arrow) (TTU P9182), ×2, anterior facing up. This is the first report of a hexanchiform from the Antarctic region. F, G, *Orthacodus* sp., partial tooth from Upper Cretaceous deposits of Seymour Island (FMNH PF10723), ×2·3. F, anterior view. G, lateral view (anterior facing right). H, indeterminate selachian vertebral centrum (FMNH PF11920), ×2·5. I, dorsal view of FMNH PF11920, ×2·2, from Upper Cretaceous deposits of Seymour Island.

Class OSTEICHTHYES
Subclass ACTINOPTERYGII
Subdivision TELEOSTEI
Order BERYCIFORMES (*sensu* Zehren, 1979)
Superfamily TRACHICHTHYOIDEA (*sensu* Gayet, 1982)
Family TRACHICHTHYIDAE (*sensu* Gayet, 1982)
Subfamily TRACHICHTHYINAE (*sensu* Gayet, 1982)
Genus *ANTARCTIBERYX* gen. nov.
Antarctiberyx seymouri n. sp.

Holotype. TTU P9210. A poorly preserved anterior skull section with partial dentary attached. This is the only known specimen.

Diagnosis. This species differs from all other trachichthyids in the extreme development of the ornamented nasal bridge and in the pattern of radiating spines and serrations on the dorsal surface of the bridge (text-fig. 3D, E).

Etymology. *Antarcti* and *seymouri* refer to type locality; *beryx*—a fish (Latin).

Description. The specimen (text-fig. 3A–E) is poorly preserved and incomplete. It is missing the braincase and gill-cover regions, the postcranial skeleton, and the left side of the skull. Many other bones of the skull are either incomplete, or hidden by overlying rock or bones. Based on the limited information available (described below), the specimen still appears to be identifiable as a trachichthyid of the subfamily Trachichthyinae (*sensu* Gayet 1982).

Bone terminology below is largely after Patterson (1964). The most prominent features of the skull roof (text-fig. 3C, D) are large, well-developed mucus cavities (features derived for 'trachichthyoid beryciforms' according to Rosen 1973, p. 477, and for trachichthyids according to Gayet, 1982, fig. 15).

The frontals (f) are nearly complete, but these are the posteriormost elements of the skull roof that are preserved in the specimen. The frontals are complicated by high crests surrounding part of the mucus cavities. The main (medial) crest of each frontal runs forward beyond the median, posteriormost cavity, and curves medially to meet its counterpart above the anterior edge of the orbit. The crests are highest anteriorly, and they bear small spines along their edges (text-fig. 3D).

The nasals (na) are relatively large bones closely sutured to the frontals. The medial edges of the nasals form a high, spiny crest which is divided anteriorly, forming a V-shaped space which houses the ascending processes of the premaxillae. The wide lateral cavities on the frontal continue anteriorly to the nasals. A bridge over the nasal groove (nabr) is formed anteriorly by a process extending from the lateral and medial edges of the nasal. The lateral edge of the nasal and the dorsal surface of the nasal bridge are highly ornamented with spines and serrations (text-fig. 3E). Of all 'beryciforms' examined here, the form of the nasals in *Antarctiberyx* most closely resemble those of the living trachichthyid, *Paratrachichthys* (e.g. see figs. 49 and 50 in Zehren 1979). The development of the nasal bridge (text-fig. 3D) is more pronounced in *Antarctiberyx* than in any other taxon examined here.

A small, slender unornamented bone (ub1) is present between the nasal and the first antorbital (text-fig. 3B). Although it is possible that it is an antorbital bone (= accessory nasal of Starks 1904, p. 611), it is much deeper in the specimen than the infraorbitals, and positive identification of this bone is not possible.

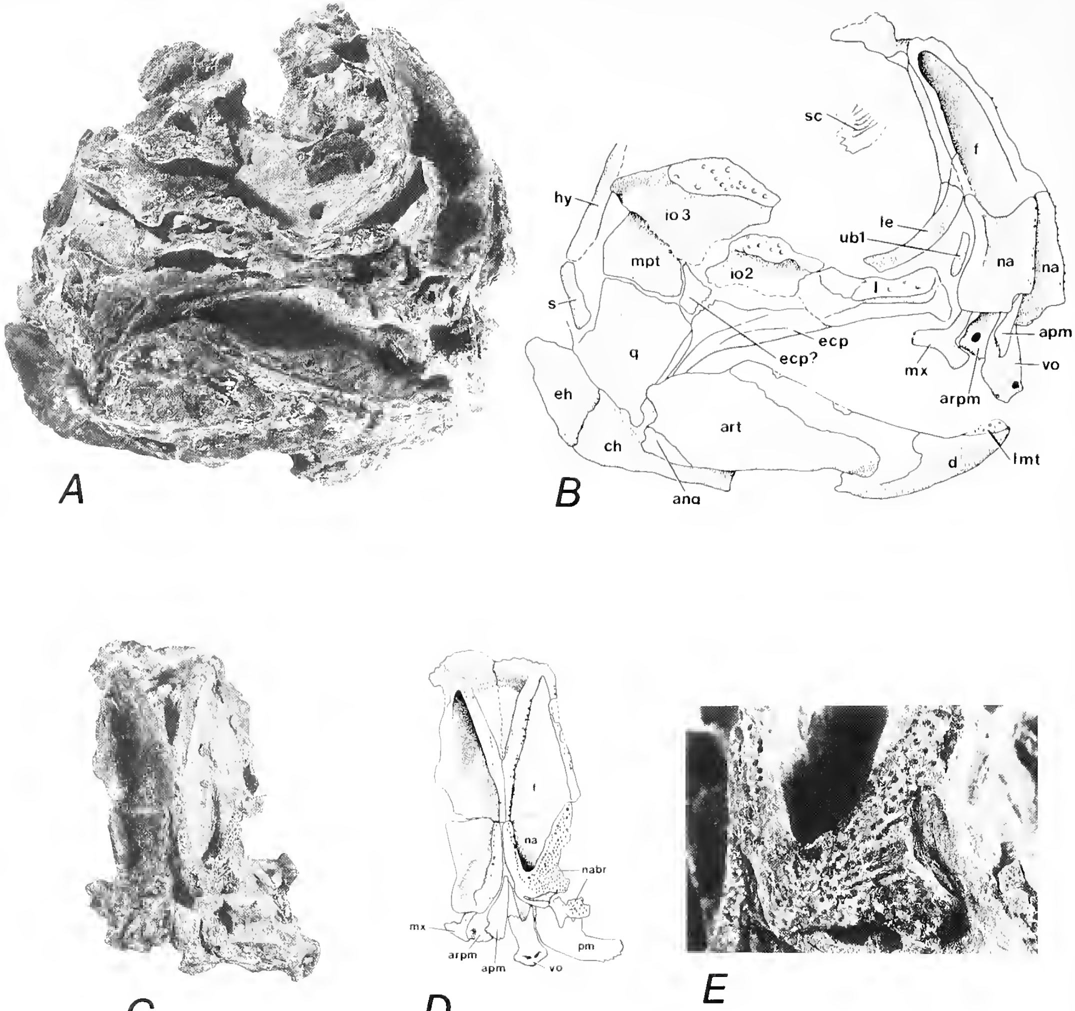
Of the vomer (vo), only the head is visible on the specimen, but the lateral facets for articulation with the maxillae are visible. No teeth are visible on the ventral surface of the vomer, but this could be an artefact of preservation).

The infraorbital bones (io) are not clearly preserved in the specimen, but the first three (or four?) are visible (text-fig. 3A, B). The flanges overhanging the groove for the sensory canal are ornamented. The ventral borders of the infraorbitals are incomplete. The subocular shelf is not visible in the specimen, possibly due to lack of preservation.

Most of the maxilla (mx) is missing, exposing much of the suspensorium. Of the hyomandibula (hy), only a ventral piece is preserved (text-fig. 3B).

The symplectic (s) is a small rod-shaped bone (text-fig. 3B) inclined forward at about forty-five degrees to the ventral limb of the hyomandibula, and articulating with the quadrate. (Due to poor preservation, the details of this articulation are not apparent.)

The quadrate (q) is triangular, with a large condyle for the articular. The ectopterygoid (ecp) joins its



TEXT-FIG. 3. A–E, *Antarctiberyx seymouri* n. sp., holotype, from Upper Cretaceous deposits of Seymour Island (TTU P9210). A, B, right lateral view of skull (photo and drawing), ×1. C, D, dorsal view of skull (photo and drawing), ×0·75. E, enlarged photograph of bridge over nasal groove showing ornamentation pattern, ×2·5.

anterior edge and the metapterygoid (mpt) its dorsal edge. The preopercle (and the rest of the opercular series) is missing.

The ectopterygoid (ecp) is long and curved bone tapering to a point against the quadrate. The anterior edge of the bone is not clear because there are several cracks in the bone, but one could well be a suture with the palatine (as described for other trachichthyids in Patterson 1964).

The metapterygoid (mpt) is a sheet of smooth bone. The anterior and dorsal margins of this bone are hidden (text-fig. 3B).

There is very little left of the upper jaw in the specimen. Only what appears to be the ascending process (apm) and the articular process (arpm) of the premaxilla are preserved on the right side (text-fig. 3A, B), and on the left side there is also part of the body of the premaxilla (text-fig. 3C, D). The ascending process is long and stout, and well separated from the articular process. The maxillary head is too fragmentary to allow detailed description.

The lower jaw, though not well preserved, is nearly complete (text-fig. 3A, B). The dentary (d) tapers from a high coronoid process, and appears to have been toothed to its tip. Near the symphysis, the teeth (indicated primarily by empty sockets in the specimen) extend to the lateral face of the bone (text-fig. 3B). The articular (art) has a large, concave facet for the quadrate posteriorly. This is considered by Gayet (1982) and Stewart (1984) to be a character of trachichthyids.

Two bones of the hyoid arch are also visible on the specimen (text-fig. 3A, B), a triangular posterior ceratohyal (eh) which is closely articulated with the anterior ceratohyal (ch). The dorsal and anterior margins of the anterior ceratohyal are obscured by the lower jaw and the suspensorium.

Scale (sc) fragments are also present in the matrix on the specimen (text-fig. 3B), and are probably from the same individual. They are ornamented and bear spines on their posterior margins.

Taxonomic placement. Following recent revisions of 'beryciforms' by Gayet (1982) and Stewart (1984), *Antarctiberyx* appears to belong in Trachichthyidae based primarily on two characters: the teeth on the labial side of the mandible and the presence of the large mucus cavities on the top of the head. The appearance of the nasal bridge and frontals is also very similar to that in extant trachichthyids (e.g. see illustrations of *Paratrachichthys* sp. in Zehren 1979, figs. 49 and 50).

Order Indeterminate
Indeterminate teleost scraps

Referred new material. About one hunded specimens, mostly isolated centra and bone fragments (deposited at TTU), but including some poorly preserved partial skulls. The presence of such material indicates that more diagnostic material will eventually be found in the Cretaceous deposits of Seymour Island.

DISCUSSION

It seems clear, based on fossil evidence from Seymour Island (Grande and Eastman 1986; and above), that the Antarctic region had a much more diverse chondrichthyan fauna during Cretaceous and Early Tertiary time than it does today. The diversity of fossil teleost fauna is much less apparent, but this may be only an artefact of preservation. The fossils from Seymour Island are mostly isolated teeth, scales, and skull fragments. The most complete teleost found so far (*A. seymouri* n. sp.) is only a partial anterior region of a head (text-fig. 3A–E). The fact that isolated teeth are much more diagnostic for chondrichthyans than they are for teleosts may be the main reason why there appears to be a much larger diversity of fossil chondrichthyans than of fossil teleosts. A wide variety of teleost centra is present in the Tertiary and Cretaceous deposits of Seymour Island (many UCR specimens listed in Grande and Eastman 1986; and many TTU specimens mentioned above), but these appear to be identifiable only as Teleostei indeterminate. It is hoped that with continued collecting on Seymour Island, the Tertiary and Cretaceous teleost faunas will become better known.

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ABBREVIATIONS

In text-figures: ang, angular; apm, ascending process of premaxilla; arpm, articular process of premaxilla; art, articular; ch, anterior ceratohyal; d, dentary; ecp, ectopterygoid; eh, posterior ceratohyal; f, frontal; hy, hyomandibula; io, infraorbital; l, lacrimal (first infraorbital); le, lateral ethmoid; lmt, area on labial side of mandible showing traces of teeth and tooth sockets; mpt, metapterygoid; mx, maxilla; na, nasal; nabr, bridge over nasal groove (see text); pm, premaxilla; q, quadrate; s, symplectic; sc, scale; ub1, unornamented bone; vo, vomer.

Institutional: FMNH PF, Fossil Fish Collection, Department of Geology, Field Museum of Natural History, Chicago, Illinois; TTU, Museum of Texas Tech University, Lubbock, Texas.

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AN UNUSUAL OSTEOLEPIFORM FISH FROM THE LATE DEVONIAN OF VICTORIA, AUSTRALIA

by J. A. LONG

ABSTRACT. A new osteolepiform fish, *Beelarongia patrichae* gen. et sp. nov., is described from the Late Devonian (Frasnian) lacustrine Mount Howitt site, eastern Victoria. *Beelarongia* is cosmine-covered, has a broadly flaired parietal shield with large extratemporal bones, cheek plate with an additional small postorbital bone and broad lateral extrascapulars. The orbits are very small. The scales are rhombic with high dorsal processes. *Beelarongia* is considered closely related to *Canowindra grossi* Thomson because of the shape of the parietal shield, presence of an accessory postorbital bone behind the small orbit, and broad extrascapular series.

UNTIL recently almost our entire knowledge of the osteolepiform fishes was based on studies of material from the Northern Hemisphere which formed part of the Laurasian landmass in mid-Palaeozoic times. New discoveries from Australia and Antarctica, which formed East Gondwana, or the antipodes to Laurasia during the Devonian, reveal a diverse osteolepiform fauna, some elements of which are unexpectedly different from the Northern hemisphere faunas. Aside from fragments attributed to *Strepsodus* by Woodward (1906) the first fossil crossopterygian described from Australia was *Canowindra grossi* Thomson (1973) from the Upper Devonian Mandagery Sandstone of New South Wales. Thomson described the single complete fish from a natural mould, but was uncertain how to classify it. Since then Long (1985*b*) has redescribed *Canowindra* from new preparation of the original specimen, and regards it as an osteolepiform which is representative of a new higher taxon. Young and Gorter (1981) described ?*Gyroptychius* cf. *G. australis* from the Middle Devonian Hatchery Creek fauna, New South Wales, and Long (1985*a*) described a primitive eusthenopterid, *Marsdenichthys longioccipitus*, from the Late Devonian Mount Howitt locality, Victoria. Other osteolepiforms from Australia include *Gogonasus andrewsi* from the Upper Devonian Gogo Formation, Western Australia (Long 1985*c*) and new species of *Megalichthys* from the Lower Carboniferous of Queensland (Long and Turner, 1984). In August 1986 a complete skull of *Gogonasus* was discovered at Gogo and this material is currently under study. The new form described here is significant in that it shares several distinctive characters with *Canowindra*, and together with another undescribed form from the Middle Devonian of Antarctica may represent an endemic Gondwanan group of Osteolepiformes. In this paper the Mount Howitt form is described in detail. The erection of higher taxonomic ranks will be postponed until all the new material is fully described.

The material of *Beelarongia* was collected in the original excavations of the Mount Howitt site over the 1970/1 field seasons by Professor Jim Warren (Monash University, Zoology Dept.). As most of the bone was weathered away the pieces of cranium were recognized as natural impressions in the black shale and assembled together as best possible despite the absence of some pieces. The specimen was then cast with latex. All of the pieces are thought to belong to the one individual, although as they were found separately throughout the collection it cannot be determined exactly when they were found and if they came from the same horizon.

Terminology for dermal bones used herein follows Jarvik (1980) as discussed in Borgen (1983). The words 'breadth, length, and height' are abbreviated as L, B, and H respectively. All measurements were taken across the surface of bones, thus incorporating some degree of flattening where present. Indices are expressed as the product of two linear dimensions multiplied by 100.

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SYSTEMATIC PALAEONTOLOGY

Order OSTEOLEPIFORMES (OSTEOLEPIDIDA)

Remarks. Despite recent arguments that the Osteolepiformes could be a paraphyletic group (Rosen *et al.* 1981; Lauder and Liem 1983; Gardiner 1980), I have presented arguments that the group is probably monophyletic (Long 1985*a*), but admit that the evidence for this hypothesis is scarce. Osteolepiform fishes uniquely possess a pectoral girdle with a large ornamented anocleithrum separating the cleithrum from contact with the supracleithrum. There are large basal scutes present at fin bases (Andrews 1973). The cheek has a bar-like preopercular bone which forms the rear border to the single, large irregularly-shaped squamosal, and is steeply inclined. The squamosal is unique amongst Osteichthyes in occupying most of the cheek plate area and having six sides of which five suture to other cheek bones. This character also applies to some early tetrapods which are here regarded as a subgroup of the Osteolepiformes, probably of close affinity to the Panderichthyidae (Schultze 1970; Schultze and Arsenault 1985) and not immediately related to the Dipnoi as suggested by Rosen *et al.* (1981). The only group of Osteolepiformes in which cheek patterns may be confused with those of tetrapods is the panderichthyids (Schultze and Arsenault 1985). The cheeks of panderichthyids are poorly known. They differ slightly from those of other osteolepiforms in contact margins between the lachrymal and jugal (*Elpistostege*) and in having a slightly smaller lachrymal (*Panderichthys*). In the primitive labyrinthodonts which retain an osteolepiform-like cheek pattern (*Ichthyostega*, *Acanthostega*, *Crassigyrinus*) the preopercular is much reduced and the jugal has become much larger than the squamosal (Jarvik 1980; Panchen 1973, 1985).

Beelarongia gen. nov.

Etymology. From the aboriginal word '*beelarong*' meaning shiny (Reed 1975), an allusion to the cosmine covered dermal bones and scales.

Diagnosis. A presumably cosmine-covered osteolepiform with a fronto-ethmoid shield/parietal shield ratio of approximately 80; index of lengths of frontal/parietal bones about 60. Parietal shield anteriorly narrow but posteriorly broad with a B/L index of 180, posterior margin strongly pointed posteriorly. Extratemporal very large, being almost one third as broad as one side of the parietal shield. Median extrascapular having a short anterior margin, one fifth the extent of that of the broad lateral extrascapulars. Cheek with long postorbital and one small accessory postorbital bone. Orbits very small. Opercular large, rounded. Cleithrum with broad unornamented anterior flange. Scales rhombic with large dorsal processes.

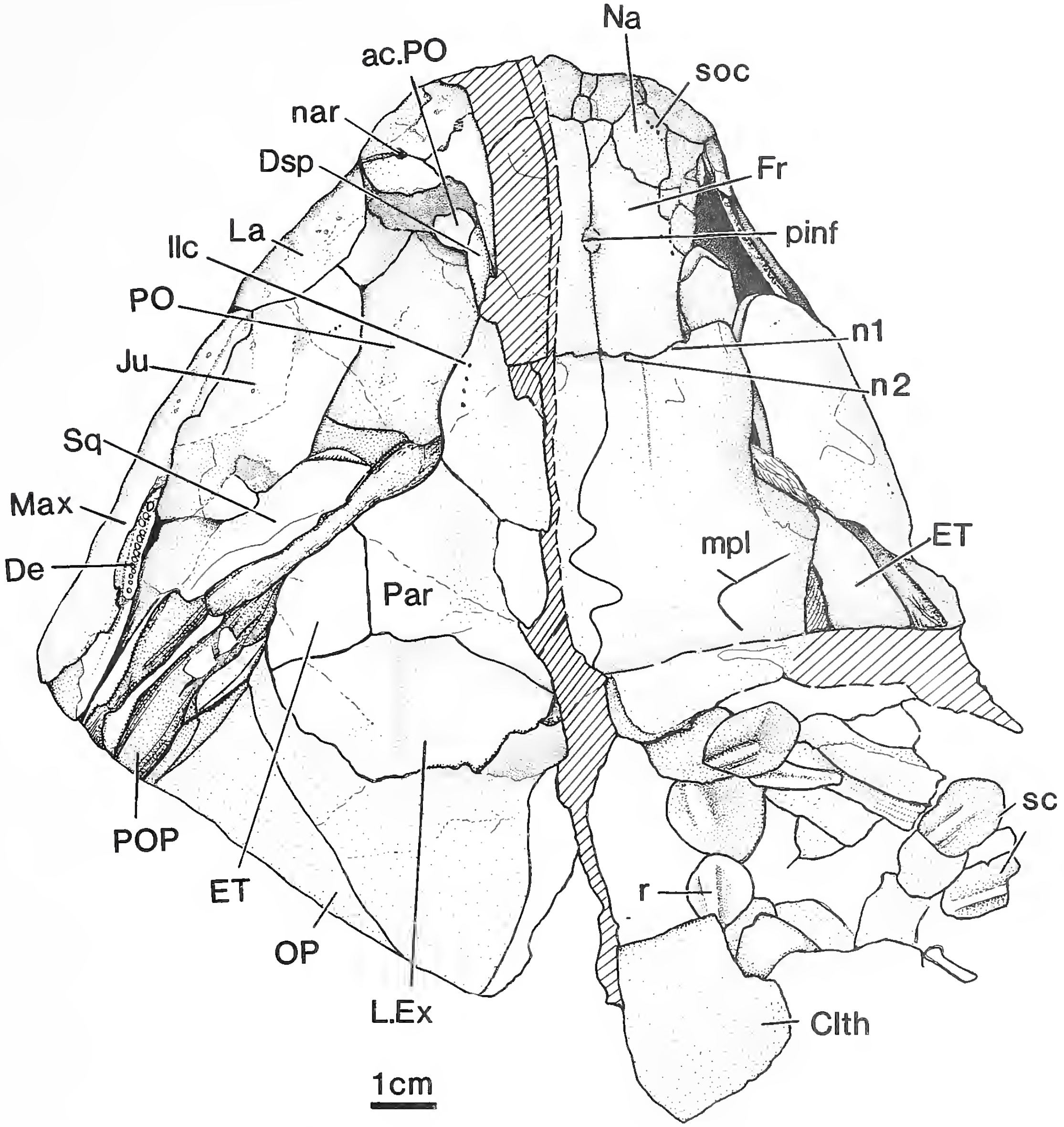
Remarks. Beelarongia is distinguished from all other osteolepiforms, except *Canowindra*, by its very small orbits which have a small accessory postorbital bone behind them, the unusually large extratemporal bones and very broad posterior division on the parietal shield. It is distinguished from *Canowindra*, which also has the above features, by the presumed presence of cosmine, narrower shape of the extratemporal bones, the rhombic scales with high dorsal processes, and the simpler cheek pattern with only one accessory postorbital bone (*Canowindra* has two accessory postorbitals, Long 1985*b*). Cosmine is presumed to be present on *Beelarongia* because of the smooth surface of the bones and scales from the natural mould. The thick rhombic scales of *Beelarongia* are almost identical to those of other cosmine-covered osteolepiforms.

Type species. B. patrichae sp. nov.

Beelarongia patrichae sp. nov.

Plate 91; text-figs. 1–5, 6B

Etymology. After Dr Pat Rich (Monash University, Earth Sciences Dept.) who has given me much assistance and encouragement.



TEXT-FIG. 1. *Beelarongia patrichae* gen. et sp. nov., sketch of holotype NMV P160872, cranium in dorsal view. The rest of the specimen, containing most of the left opercular and pectoral girdle is not shown here. Cross hatching indicates damaged areas filled in by latex. ac.PO, accessory postorbital; Clth, cleithrum; De, dentary; Dsp, dermosphenotic; ET, extratemporal; Fr, frontal; Ju, jugal; La, lachrymal; L.Ex, lateral extrascapular; llc, main lateral line canal pores; Max, maxilla; mpl, middle pit-line groove; Na, nasal; nar, external nostril; n1, n2, notches on posterior margin of frontal; OP, opercular; Par, parietal shield; pinf, pineal foramen or elevation; PO, postorbital; POP, preopercular; r, basal ridge of scales; sc, scales; soc, supraorbital sensory-line pores; Sq, squamosal.

Holotype. NMV P160872 (Pl. 91), an almost complete head preserved as a natural mould in dorsal view, with part of the pectoral girdle and fin attached. Housed in the Museum of Victoria, Melbourne (NMV).

Material. NMV P160873, an isolated section of scales with part of a fin attached; NMV P160874, part of the squamation, and NMV P160875, cleithrum and clavicle.

Occurrence. From the lower mudstone outcropping along the Howqua River at the base of Mount Howitt (Marsden 1976); Avon River Group, Late Devonian (Frasnian, Long 1983).

Diagnosis. As for genus, only species.

Description. Beelarongia was a moderate-sized osteolepiform having an estimated maximum cranial length of 100 mm from the single known skull. The shape of the head can be easily determined from the holotype, being broad posteriorly but rapidly narrowing anteriorly, and quite depressed in cross-section. The sections of body squamation give no indication of the body shape or the disposition of the fins.

Fronto-ethmoid shield. The fronto-ethmoid shield is approximately as broad as long, with the dorsal face being flat posteriorly, arching convexly at the rostral margin (text-figs. 1 and 2). Few bones can be distinguished due to the poor preservation. The large frontals are separate from the other bones forming the shield, with a distinct concave lateral margin on the right frontal for the dermosphenotic. The supraorbital canal is assumed to run off the frontal to the dermosphenotic, indicated on the specimen by a series of fractures where the canal would be expected. Approximately halfway along the median suture between the frontals there is a median rough area on the cast; this is either a pineal thickening or a foramen (pinf).

The frontals (Fr) comprise three quarters of the estimated length of the fronto-ethmoid shield, being about twice as long as broad. In the right frontal a row of pores representing the supraorbital canal (soc) can be seen close to the rostral margin. The posterior margin of the fronto-ethmoid shield has an irregular shape with two notches (n1, n2) present on the margin of the right frontal (text-fig. 1), possibly for ligaments as Jarvik (1972) has suggested for similar notches in the fronto-ethmoid shield of *Glyptolepis*. The dermosphenotic (Dsp) is seen on the left side, displaced from the skull roof table to lie next to the postorbital (text-figs. 1 and 2). It is almost rhombic in form with rounded margins, comprising three quarters the length of the frontals and is half as broad as long. The mesial margin is smoothly convex to fit into the frontal, but the lateral margin is straighter with a long posterior division contacting the postorbital and a short anteromesially directed anterior side for the supraorbital. The dermosphenotic has an extensive overlap surface for the anterior part of the postorbital (oa.Dsp, text-fig. 2B) indicating that the cheek was firmly attached to at least the anterior division of the skull.

An indistinct foramen, possibly the nasal opening (nar), is visible on the left side of the fronto-ethmoid shield (text-figs. 1 and 2A). It is an almost circular opening situated just anterior to the lachrymal as in other osteolepiforms. The orbital notch is not clearly defined on the fronto-ethmoid shield. The close proximity of the bones surrounding the orbit, and the reconstruction of these bones in the articulated cheek indicate that the orbits of *Beelarongia* were very small, similar to those of porolepiforms in being even smaller than those of small-eyed osteolepiforms such as *Glyptopomus* (Jarvik 1950) or *Latvius* (Jessen 1966, 1973).

Parietal shield. The parietal shield is well preserved although only the extratemporal bones (ET) are clearly differentiated from the rest of the cosmine-covered shield (Pl. 91; text-fig. 1). In cosmine-covered osteolepidids the sutures between the parietal, intertemporal, and supratemporal are occasionally not visible (Jarvik 1948, 1985; Jessen 1966) but are distinct in forms which have no cosmine. The absence of such sutures in *Canowindra* is believed to reflect the actual condition of fusion between these bones rather than the sutures being merely masked by the external cosmine layer (Long 1985*b*). As *Beelarongia* is closely related to *Canowindra*, as discussed below, the condition of the partietal shield in *Beelarongia* is also thought to be similar to that of *Canowindra*. The overall shape of the parietal shield is similar to that of *Latvius grewingki* (Gross 1956, pl. 1), but differs in having an even broader posterior region with larger extratemporals. The posterior margin has two clearly defined angular notches, the first being just mesial to the extratemporal, the second being situated about midway along the

EXPLANATION OF PLATE 91

Figs. 1–3. *Beelarongia patrichae* gen. et sp. nov. 1, holotype cranium NMV P160872 in dorsal view. 2, cleithrum in lateral view with clavicle in ventrolateral view, NMV P160875. 3, part of the squamation showing scale with high dorsal process, NMV P160874. Latex casts whitened with ammonium chloride.

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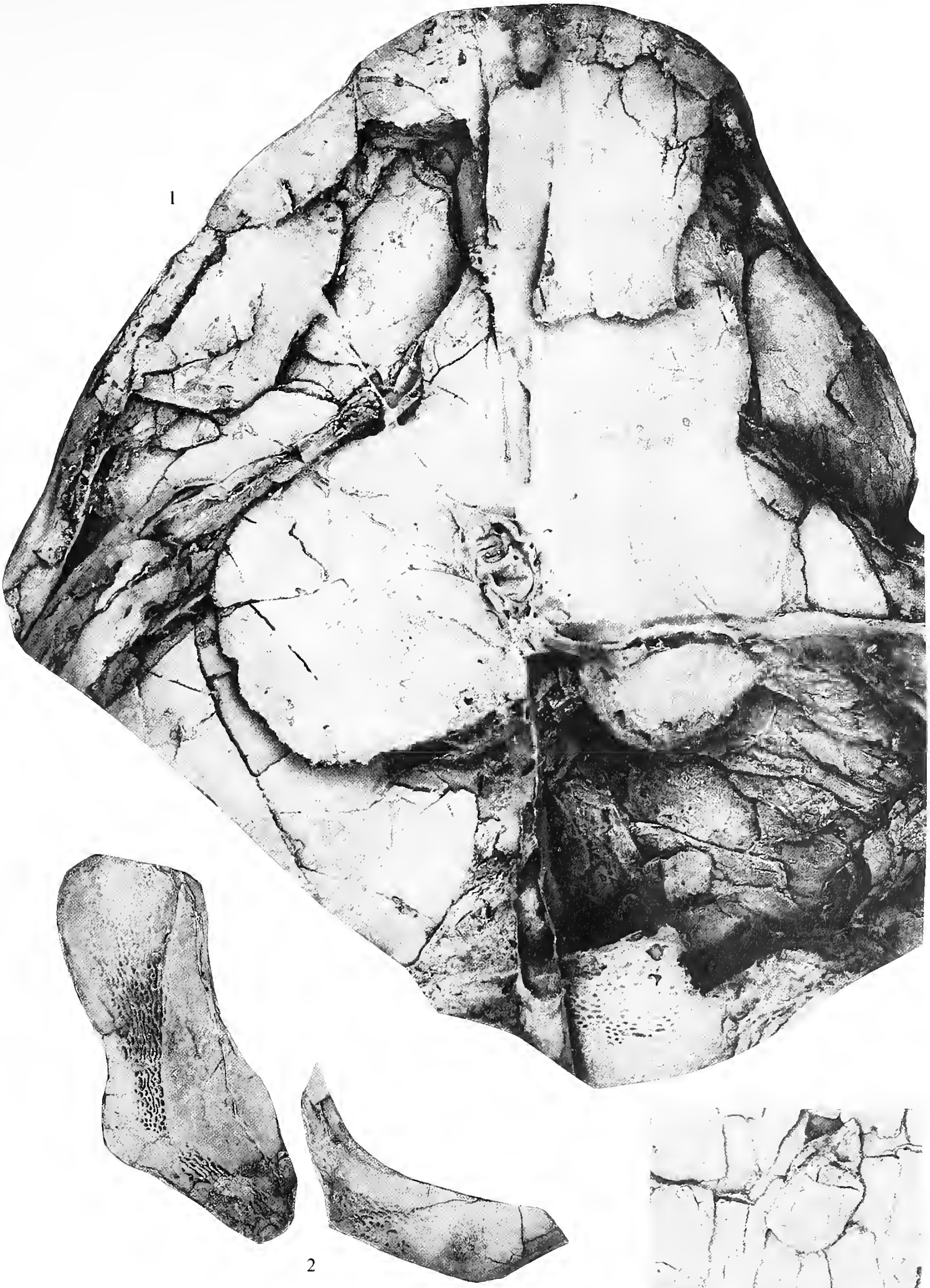

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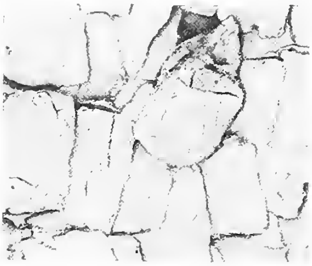
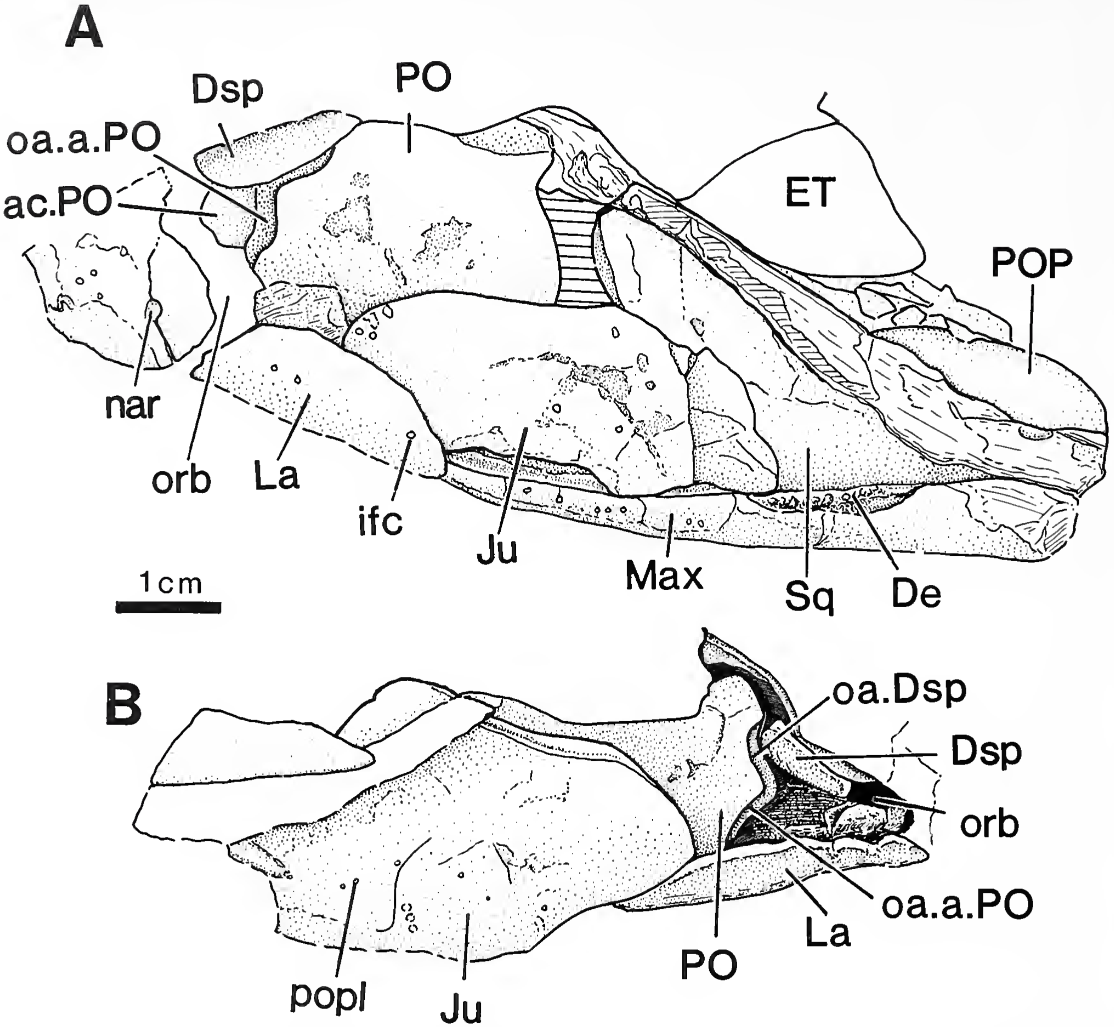


LONG, canowindridoid osteolepiforms



TEXT-FIG. 2. *Beelarongia patrichae* gen. et sp. nov., cheeks in lateral view, from holotype NMV P160875. A, left cheek. B, right cheek. Parts of the dorsal edge of the cheek were not well preserved and did not cast very well. Abbreviations as for text-fig. 1 except for: ifc, infraorbital sensory-line canal pores; oa.a.PO, overlap area for accessory postorbital bone; oa.Dsp, overlap area for dermosphenotic; orb, orbit; popl, preopercular sensory-line canal.

margin. These notches are also seen on *C. grossi* and a few other osteolepiforms (*Thursius moythomasi*, Jarvik 1948, pl. 19; *Gyroptychius dolichotatus*, Jarvik 1985, fig. 12). The anterior margin of the parietal shield is not completely shown in the specimen, but is assumed to have an irregular form to comply with the notches for ligamentous attachments seen on the posterior margin of the fronto-ethmoidal shield. The lateral margins of the parietal shield are smoothly curved with a strong median concavity before splaying out laterally near the contact with the extratemporal. The parietal suture courses in an irregular zig-zag fashion close to the posterior margin. The transverse (middle) and posterior parietal pit-lines are situated close to the posterior margin of the shield, meeting at a point slightly closer to the extratemporal than to the median suture.

The extratemporal (ET) is a large, triangular bone approximately as long as broad. It is a third as long as the parietal shield and almost a third as broad as one half of the shield. The mesial and posterior margins of the extratemporal are almost straight, but the lateral margin is strongly convex. Although the shape of the extratemporal is similar to that of several other osteolepiforms, most of which have a high degree of variation in the shape of that bone (e.g. *G. dolichotatus*, Jarvik 1985, fig. 12) none of the described forms approach *Beelarongia* or *Canowindra* in the proportional size of the extratemporal to the rest of the parietal shield. *Porolepis* has a similarly sized extratemporal but differs in the shape of this bone, which is more elongated (Jarvik 1972).

Extrascapulars. The left lateral extrascapular (L.Ex) is preserved on the holotype. The imperfect bone preserved on the right side which shows an overlap surface is not the right lateral extrascapular but part of the right opercular which has been displaced over the rear of the skull roof. Overlap relationships are not known for the extrascapulars, although it may be noted that in *Canowindra* there is normal osteolepiform overlap of the median bone by the lateral extrascapulars. The lateral extrascapular is a large rounded bone which is about one and a half times as broad as long. The anterior margin is strongly convex with two angular prominences. The lateral margin, considerably shorter than the mesial margin, is gently convex (Pl. 91A). The median extrascapular would have been very narrow at its contact with the parietal shield. There is no indication of the course of the main lateral line canal or the occipital canal on the material.

Cheek. The cheek of *Beelarongia* is well preserved on the left and part of the right side of the holotype (text-figs. 1 and 2). The anterior division is poorly known because of post-mortem collapse of the bones around the orbit. It is clear that the normal pattern of cheek bones was present: squamosal (Sq), jugal (Ju), postorbital (PO), lachrymal (La), preopercular (POP), and probably the quadratojugal although this is not seen in the material. The posterior region of the cheek is not at all well preserved, but part of the preopercular is preserved on the left side of the specimen. The infraorbital series of *Beelarongia* differs from that of most osteolepiforms in that the lachrymal is quite smaller and narrower than the jugal and postorbital elements (text-fig. 6).

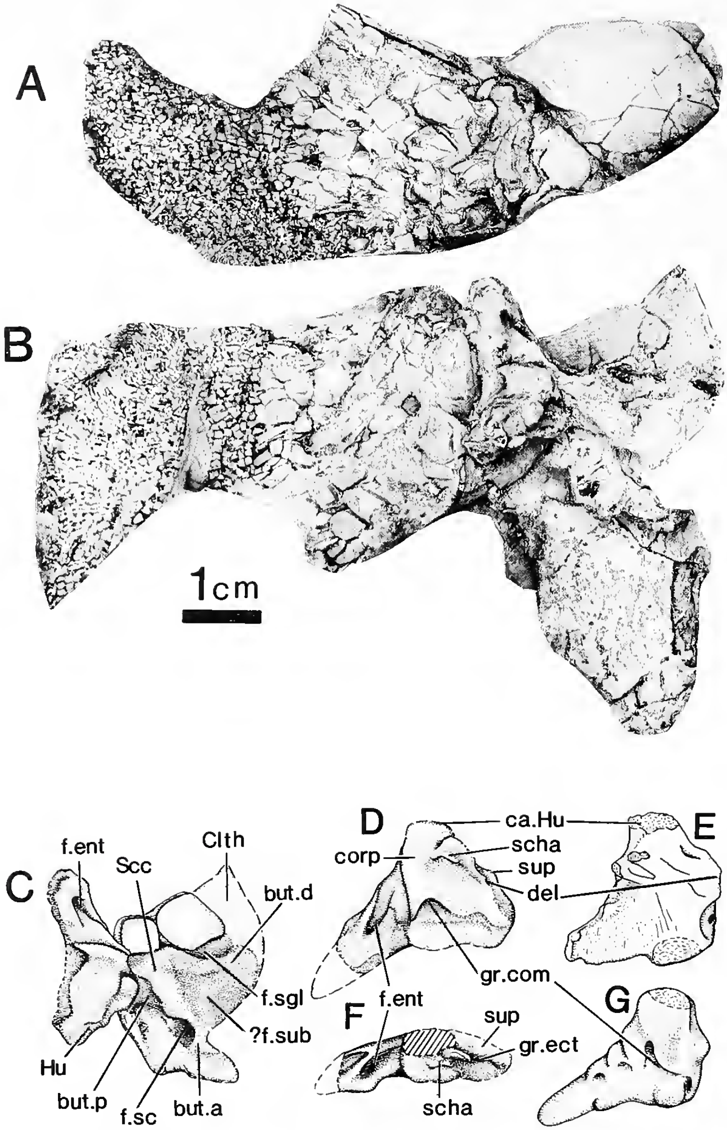
The lachrymal can be seen on both sides of the holotype immediately ventral and posterior to the orbit. It is two thirds the length of the jugal, and slightly more than half as long as the fronto-ethmoid shield. The dorsal margin is not well preserved on either of the two examples, presumably fitting below the orbit, but not necessarily participating in the orbit. Open pores of the infraorbital canal are visible close to the ventral margin of the lachrymal.

The jugal is a large bone contacting the lachrymal anteroventrally, the postorbital dorsally, the squamosal posteriorly and the maxilla ventrally. The anterior contact is obscure, as if the bones are place in approximate juxtaposition there is a space immediately posterior to the orbit for a small accessory postorbital bone. This is further supported by the anterior margin of the postorbital which shows a broad overlap flange for another dermal element (text-fig. 2A). There is a small area of bone preserved anterior to the postorbital which is identified as the accessory postorbital (ac.PO, text-fig. 2A). This bone is a small almost square plate which corresponds in size to the anterior accessory postorbital of *Canowindra*, but differs markedly from that element in *Canowindra* by its shape. However, it is alternatively possible that this small bone in front of the postorbital is part of the supraorbital which has fallen down from the skull roof. In view of the anterior overlap area on the large postorbital and the general fit of the bones around the orbit it is most likely that an additional postorbital element is indeed present, as restored in text-fig. 5. The jugal has an elongate form, being slightly more than twice as long as high. The dorsal margin is gently curved, turning steeply at the anterior margin to form an anterior point. The posterior margin is strongly convex, curving downwards to meet the straight ventral margin. There are numerous pores present indicating the presence of the preopercular sensory line, although its exact course and junction with the infraorbital canal are not clear.

The postorbital (text-figs. 1 and 2) is a large bone dorsal to the jugal, lateral to the dermosphenotic and anterior to the squamosal. It is unusual in having a broad anterior end with two overlap flanges, a dorsal one for the dermosphenotic (oa.Dsp) and a ventral flange for an additional small accessory postorbital bone (oa.a.PO), as also occurs in *Canowindra* in which two accessory postorbitals are found (Long 1985*b*). The anterior part of the dorsal margin is relatively straight, but moderately inclined anteroventrally; the anterior margin being pointed with a concave facet bearing broad overlap surfaces on either side of the point. The posterior margin is indented for overlap of the squamosal. Overall the postorbital is slightly longer than high, and marginally shorter than the jugal.

The anterior region of the squamosal (Sq) is preserved on both sides of the specimen (text-fig. 2). The anterior margin has a dorsal pointed division for contacting the postorbital and a smoothly concave ventral division for the jugal. From the extent of the whole cheek, restored by the relative position of the opercular and fronto-ethmoidal shield, the squamosal was particularly large relative to the other cheek bones, a character typifying the osteolepiforms.

The dorsal region of the preopercular can be seen on the left side of the specimen. All that can be said about this bone is that it was situated right at the rear of the cheek complex with a steeply inclined long axis as in other osteolepiforms.

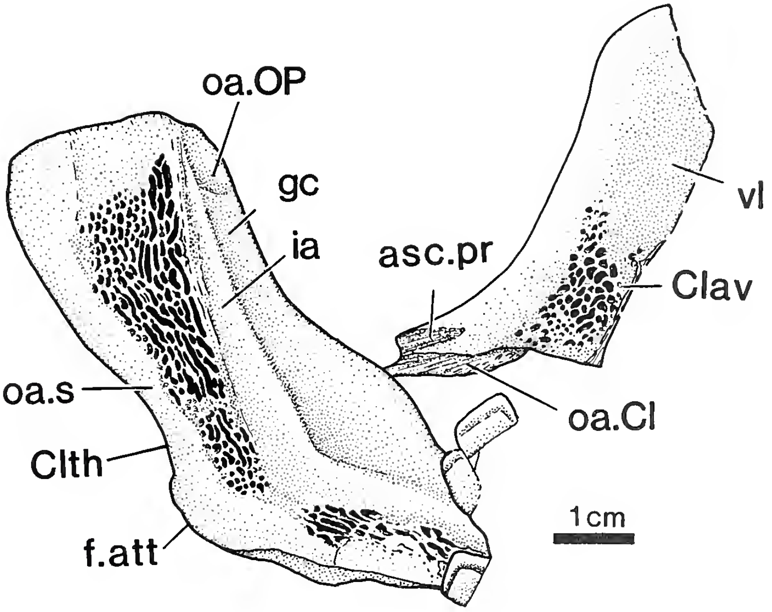


TEXT-FIG. 3. *Beelarongia patrichae* gen. et sp. nov., left pectoral girdle and fin, from the holotype NMV P160875. A, external view of fin, counterpart to B, internal view of cleithrum showing scapulocoracoid and humerus. C, sketch interpretation of scapulocoracoid and humerus as preserved. D, F, attempted restoration of the humerus in (D) ventral and (F) anterior views. E, left humerus of *Sterropterygion* in ventral view (after Rackoff, 1980). G, left humerus of *Eusthenopteron* in ventral view (after Jarvik, 1980). but.a, but.d, but.p, anterior, dorsal and posterior buttress of scapulocoracoid; ca.Hu, caput humeri; Clth, cleithrum; corp, corpus of humerus; del, crest for deltoideus muscle; ent, entepicondyle; f.ent, entepicondylar foramen; f.sc, supracoracoid fossa; f.sgl, supraglenoid foramen; ?f.sub, area of subscapular fossa; gr.com, commissural groove; gr.ect, ectepicondylar groove; scha, shelf for attachment of scapulohumeroideus muscle; sup., ridge for supinator muscle; Scc, medial division of the scapulocoracoid.

Operculogular series. The opercular bone (OP) is the only element of this series preserved on the specimen, being almost completely preserved on the left side. Text-fig. 1, which shows part of the opercular, does not show that part of the specimen which joins onto the opercular as this contains the pectoral girdle and cannot be properly studied if glued back to the block containing the cranium. The opercular is subrectangular in shape with an estimated B/L index around 112 (restoring the dorsal margin). The anterior margin is straight and comprises 54% of the opercular length in its extent. The dorsal margin is not preserved, but can be restored to fit the posterolateral margin of the skull table. This gives a deeply concave dorsal margin. The posterior margin is strongly convex, curving smoothly round to the ventral margin without a marked posteroventral corner developed.

Pectoral girdle and fin. The holotype shows the proximal region of the left pectoral fin and shoulder girdle preserved (text-fig. 3), and NMV P160875 shows the external surfaces of the cleithrum and clavicle well preserved (Pl. 91; text-fig. 4). It should be noted that the left pectoral girdle and fin attach to the side of the skull in text-fig. 1, completing the posterior region of the opercular and showing the humerus and scapulocoracoid resting inside the flattened cleithrum.

The cleithrum (Clth; text-figs. 1, 3, 4) has a large dorsal rectangular division which is slightly more than twice as long as the ventral triangular division (dividing line taken as the line passing through the broadest section of the bone). The externally exposed ornament is restricted to a narrow triangle on the dorsal rectangular division, occupying less than half of the surface area. The dorsal margin is straight, and the anterodorsal corner has a depressed curved area for the overlap of the opercular (oa.OP). The posterior margin has a slightly concave dorsal division with a well rounded bulge for the scapulocoracoid where the pectoral fin inserted (f.att). The inwardly bent smooth area anterior to the ornament has a broad outer region (ia), probably for the membranous cover of the posterior wall of the branchial cavity (Jarvik 1948, p. 98) and a slightly narrower inner strip which was presumably covered by soft tissues at the rear of the gill cover (gc). The visceral surface of the cleithrum is partially



TEXT-FIG. 4. *Beelarongia patrichae* gen. et sp. nov., cleithrum in lateral view with associated clavicle in ventrolateral view, NMV P160875. asc.pr, ascending process of clavicle; Clav, clavicle; Clth, cleithrum; f.att, area where pectoral fin attaches to scapulocoracoid; gc, inner smooth lamina of cleithrum forming part of the gill chamber; ia, inner smooth area of cleithrum; oa.Cl, overlap area for cleithrum; oa.OP, overlap area for opercular; oa.s, overlap area for scales; vl, ventral lamina of clavicle.

preserved on the holotype, being smooth and featureless aside from the endoskeletal attachment area, hidden on the specimen by the scapulocoracoid (Scc). In having a relatively short ventral triangular division the cleithrum of *Beelarongia* is typical of osteolepiforms, although the development of a broad, smooth, inwardly bent area on the external surface is a feature of porolepiform cleithra (Jarvik 1972, p. 125).

The clavicle (Clav) is partially preserved on NMV P160875 (text-fig. 4). It has an ascending process (asc.pr) with a distinct overlap flange for the cleithrum (oa.Cl), and features a broad ventral lamina (vl). In overall length it approaches that of the cleithrum (noting the absence of the tip of the ascending process). The dorsolateral vertical portion of the clavicle is a narrow, smooth region which meets the ventral, ornamented wall along a pronounced lateral ridge.

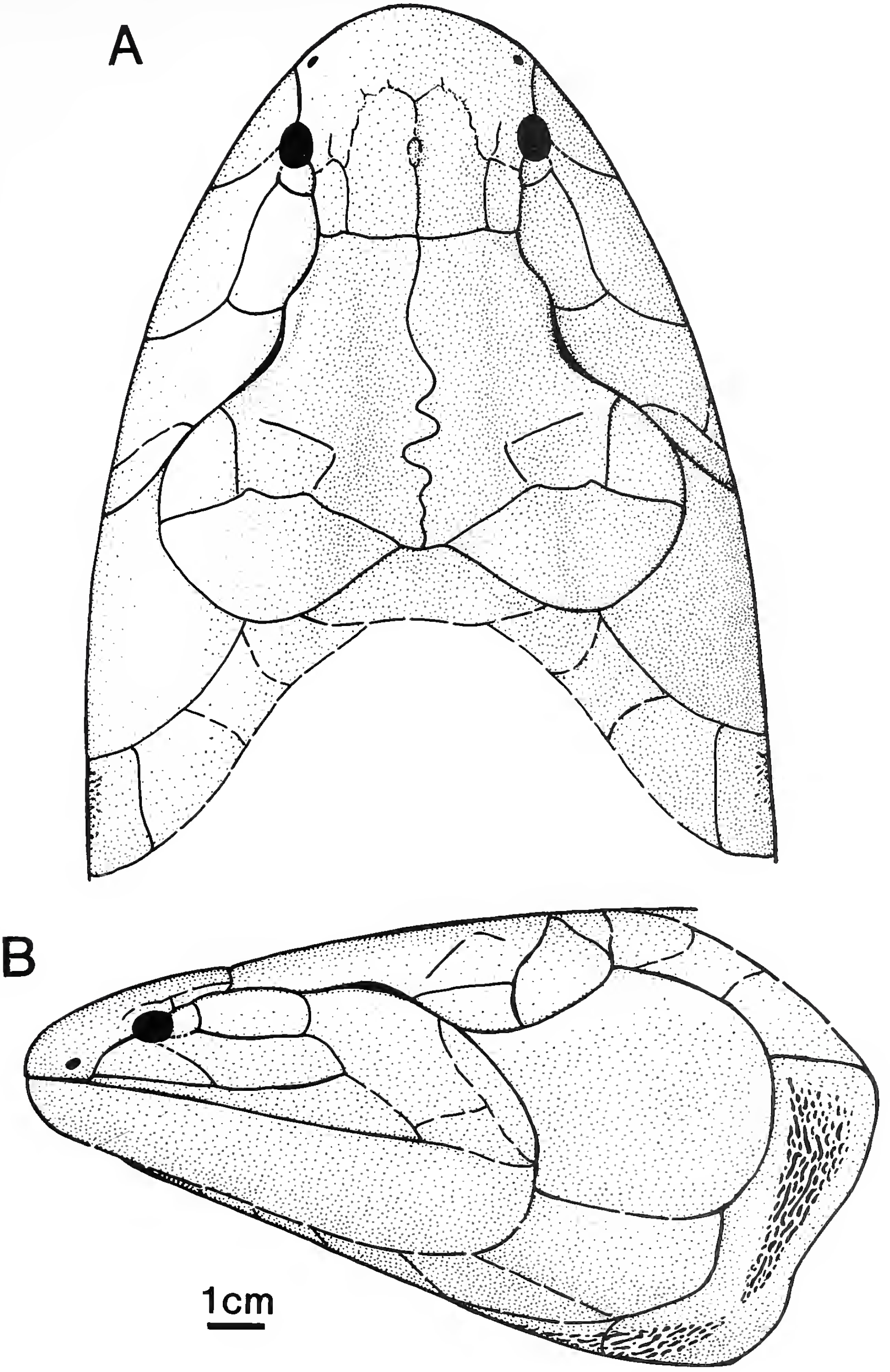
The scapulocoracoid (Scc) and humerus (Hu) are poorly preserved inside of the left cleithrum. In general form the scapulocoracoid (text-fig. 3C) is elongate, being just under half as broad as long, and slightly broader than deep (height relative to mesial wall of cleithrum). The mesial or visceral surface is quite flat, merging smoothly forward to meet the mesial wall of the cleithrum, although as it is studied from a latex cast the exact nature of the subscapular fossa (?f.sub) cannot be determined. There appears to be anterior (but.a) and dorsal buttresses (but.d) supporting the central body of the scapulocoracoid, as in other osteolepiforms (Andrews and Westoll 1970*a*, 1970*b*; Janvier 1980), although the space between the posterior buttress (but.p) and the wall of the cleithrum is not differentiated on the latex cast. At the point where the humerus meets the scapulocoracoid, at the glenoid fossa, the mesial surface of the scapulocoracoid is most furthest from the inner surface of the cleithrum. Both the supracoracoid foramen (f.ssc) and supraglenoid fossa (f.sgl) are seen. Overall the scapulocoracoid of *Beelarongia*, as far as can be described, conforms to the usual osteolepiform type, but may differ in the absence of a well-developed subscapular fossa if this absence is not an artifact of latex casting, as may be the case here.

The humerus (Hu, text-fig. 3C, D, F) can be seen to be a broad bone, more than twice as broad as the long axis of the shaft, as preserved, but probably much broader as the entepicondylar process is incomplete. To facilitate comparisons I have figured the humeri of two other osteolepiforms (text-fig. 3E, G) in which it is well known: the osteolepid, *Sterropterygion* (Rackoff 1980), and the eusthenopterid, *Eusthenopteron* (Andrews and Westoll 1970*a*; Jarvik 1980). The distal surface is not well preserved on the specimen as it is covered by scales of the fin web which reach high up on the fin-lobe. In overall form the humerus is similar to that of *Eusthenopteron* (text-fig. 3G) in the long entepicondyle (ent.) and well defined commissural groove (gr.com). Processes for attachment of the scapulohumeroideus (scha), supinator (sup), and deltoideus (delt.) muscles are present, but the latter two are not as well developed as on the osteolepid *Sterropterygion* (text-fig. 3E). The deltoideus crest is seen as a small bump separated from the dorsal side of the humerus which bears the supinator muscle ridge by a well formed groove (text-fig. 3F). The entepicondylar foramen (f.ent) is a deeply excavated pit seen on the ventral surface of the entepicondyle. This differs from the condition in both *Sterropterygion* and *Eusthenopteron*. In *Eusthenopteron* the entepicondylar foramen or canal runs almost parallel with the corpus of the humerus to open posteriorly near the articulatory facet for the ulna, and in *Sterropterygion* the entepicondylar foramen is either not noticeable or absent (Rackoff 1980, figs. 5 and 6). This major difference in the morphology of the humerus indicates a possible early differentiation of the pectoral fin of *Beelarongia* from that of other osteolepiforms.

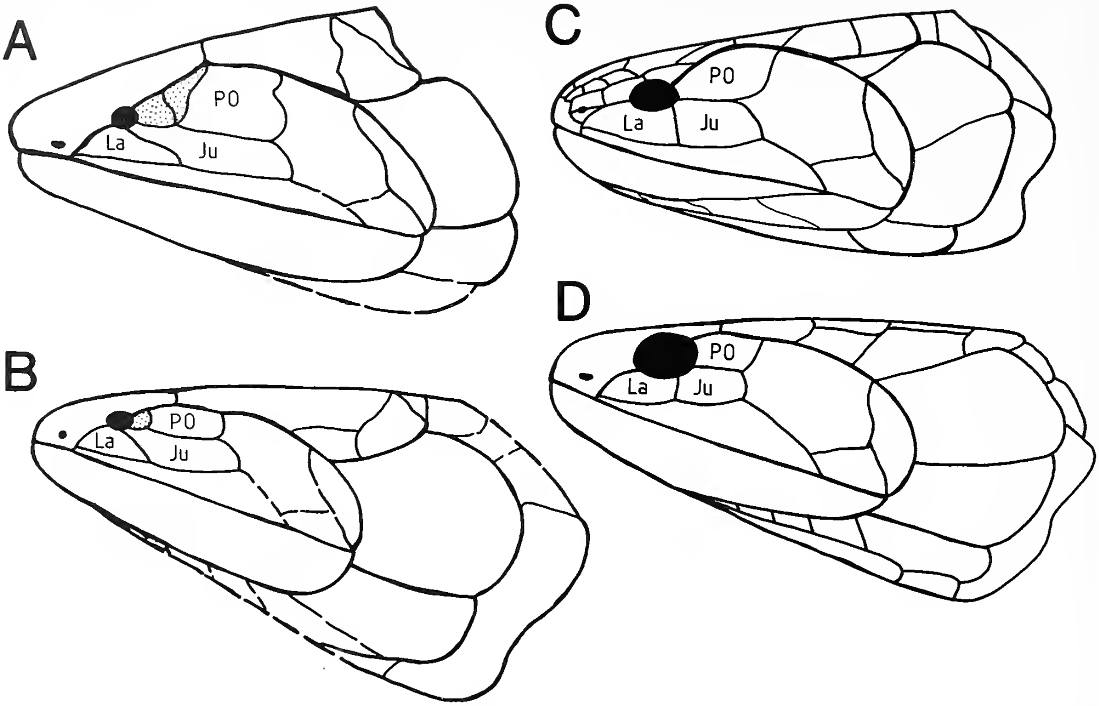
The proximal region of the pectoral fin can be seen on the holotype (text-fig. 3A, B). The scale covered lobe is short, relative to cranial length, as in osteolepiforms (although it should be noted that the length of the pectoral fin is unknown for other primitive 'crossopterygians' such as *Porolepis*, *Powichthys*, or *Youngolepis*; Jarvik 1972; Jessen 1980; Chang 1982). Lepidotrichia (f.r) are segmented and bifurcation occurs only once in the preserved area. Each lepidotrichial segment has a rectangular cosmine face separated from the cylindrical basal bone by a restricted neck.

Scales and squamation. There are a few specimens showing the scale morphology and parts of the intact squamation (holotype, NMV P160873, P160874; Pl. 91, fig. 3; text-fig. 1) but none of these specimens have the bone preserved well enough to show histological structure.

The typical flank scales are rectangular, being about three-quarters as long as deep. The thick cosmine covered external surface has a narrow groove running parallel to the dorsal and anterior margins for an interlocking fit with the overlapping scales. The dorsal end of each scale features a large process which is approximately one third as high as the whole scale, similar to the condition in palaeoniscoid scales. Anterior to the cosmine surface is a smooth overlap area equal to about one fifth of the scale breadth. The basal surface of each scale has a vertical thickening running parallel to the anterior margin and a large depressed area in the ventral half of the scale for receiving the dorsal process of the scale below. Scales covering the pectoral fin are rhombic, decreasing in size distally from the fin base. Along the leading edge of the fin there is an elongated narrow basal fin scute. Minute fin scales close to the junction with lepidotrichial rows are rectangular in form.



TEXT-FIG. 5. *Beelarongia patrichae* gen. et sp. nov. Attempted restoration of the head in A, dorsal view, and B, lateral view, after the holotype, NMV P160875.



TEXT-FIG. 6. Comparison of the heads in lateral view (A–D) of two closely related East Gondwana osteolepiforms (A, B) and two typical osteolepiforms (C, D). Accessory postorbital bones stippled. A, *Canowindra grossi* (after Long 1985*b*). B, *Beelarongia patrichae* gen. et sp. nov. C, the eusthenopterid *Eusthenopteron foordi* (after Jarvik 1980). D, the osteolepidid *Osteolepis macrolepidotus* (after Jarvik 1948). Abbreviations as for text-fig. 1.

The squamation is known from isolated blocks of scale impressions of uncertain position on the body. Scale rows are near-vertically disposed on the body, as seen close to the cranium and indicated by the angles of contact between externally exposed scale surfaces.

DISCUSSION

Within the Osteolepiformes *Beelarongia* shares the following features with *Canowindra grossi*: small orbits, parietal shield with a very broad posterior division, large extratemporal bones, possible fusion between the parietal–intertemporal–supratemporal bones, extrascapulars which are unusually broad and short, and an additional cheek element anterior to the postorbital bone (text-figs. 5 and 6A, B). The taxonomic distribution of these characters within the Osteichthyes has been discussed for *Canowindra* (Long 1985*b*) and this will not be reiterated here, except to say that on the basis of that work *Beelarongia* is here regarded as a sister taxon to *Canowindra*. Both *Beelarongia* and *Canowindra* are regarded as true osteolepiforms because of the nature of the cheek plate (having a single large squamosal, lacking a prespiracular bone behind the postorbital, no preoperculo-submandibular present, and bar-like preopercular which is steeply inclined to form most of the posterior margin of the cheek plate), the overlap relationships of the extrascapulars (median extrascapular overlapped by lateral extrascapulars), the presence of only one pair of external nares (known with certainty only in *Canowindra*), and in the structure of the shoulder girdle (large externally exposed anocleithrum, cleithrum with short ventral division). In addition *Beelarongia* has basal scutes, another characteristic feature of Osteolepiformes (Andrews 1973). The suggestion that *Beelarongia* and *Canowindra* are closely related implies that the transition from rhombic to cycloid scales and the loss of cosmine in *Canowindra* occurred independently of other osteolepiform lineages.

Unfortunately we do not have information on the braincase or palate of these two interesting taxa, and lack of such data inhibits discussion of their relationships within the Osteolepiformes. Current views on osteolepiform interrelationships (e.g. Vorobyeva 1977) require revision in the light of recent discoveries (Long 1985*c*). Further remains of osteolepiforms which share derived characters with *Beelarongia* and *Canowindra* are now known from the Middle Devonian of Antarctica (Mount Crean fauna) and the Late Devonian of Victoria (South Blue Range fauna), supporting the suggestion (Long 1985*b*, 1985*d*) that these species probably belong to a new higher taxon of Osteolepiformes endemic to the East Gondwana Province (*sensu* Young 1981). The new material includes some preservation of the braincase and palate and, when described will enable further discussion of this problem.

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WHY THE RHYNCHONELLID BRACHIOPODS SURVIVED AND THE SPIRIFERIDS DID NOT: A SUGGESTION

by DEREK V. AGER

ABSTRACT. It is suggested that the rhynchonellid brachiopods survived to the present day whilst all other forms with spirolophous lophophores became extinct because the latter were restrained by calcareous spiralia whereas the former were able to extend their lophophores outside their shells.

ALAN HOVERD has shown recently (1985) that the living rhynchonellid brachiopod *Notosaria nigricans* (Sowerby) can uncoil and extend its lophophore or feeding organ beyond its shell. This had only previously been recorded, in *Hemithiris psittacea* (Gmelin), by Morse (1869) and by implication in other rhynchonellid species by Davidson (1887), who noted that the lophophore might extend more than four times the length of the shell. However, this observation appears to have been subsequently overlooked by other brachiopod workers. Such a capability is obviously advantageous for a suspension feeder, since it greatly extends the area for trapping food particles in the water. Hoverd has shown that it is also advantageous in that the lophophore acts as a brood chamber for the larvae and then liberates them into the water when extended. It is possible that brachiopods adopted a different feeding strategy in the juvenile stage, before the development of calcareous brachidia, but we cannot know about this in the extinct spiriferids.

Rhynchonellid brachiopods have a longer history than any other articulate group, since they range from the Ordovician to Recent, whereas their present-day contemporaries, the terebratuloids, only range back to the Devonian. The rhynchonellids are particularly interesting in that they are the only living group with a spirally coiled fleshy lophophore. However, a similar spiral lophophore was clearly present in the past in the hugely diverse group of brachiopods included within the Order Spiriferida. All these other forms, i.e. the Suborders Atrypidina, Retziidina, Athyridina, and Spiriferidina (including the punctate forms), had calcareous supports in the form of spiralia for their lophophores (text-fig. 1). With such rigid supports it would clearly have been impossible for them to extend their lophophores beyond the shell. Only in the rhynchonellids is the lophophore support limited to simple rods or crura. Generally speaking the crura can only have supported the proximal ends of the lophophore and would still have permitted the main spiral part to extend like a spring. Certain groups of rhynchonellids, for example the stenocismatids, which abound in Permian rocks, have more complex structures, but this group soon became extinct as did those such as *Rhynchonellina*, of the Early Mesozoic, with very long crura.

Among the spire-bearers with calcareous spiralia the most interesting in this connection are the atrypids, which are very common in Silurian and Devonian rocks, but suddenly became extinct, all over the world, at the top of the Frasnian stage (Copper 1966). The distinguishing feature of these atrypids was that their spiralia were directed in a dorsal direction, as are the lophophores in modern rhynchonellids, and not laterally as in all other spire-bearers. I have earlier suggested (Ager 1968) that there was a 'take-over' by the rhynchonellids from the atrypids at the end of Frasnian times. I later demonstrated in the Silurian and Devonian rocks of Morocco (Ager *et al.* 1976) how the rhynchonellids of the Famennian Stage, at the end of Devonian times, may have taken over an exactly similar ecological niche to that previously occupied by atrypids, in this case a colonial development on a substrate of algal turf on a local rise within a shallow muddy sea. It

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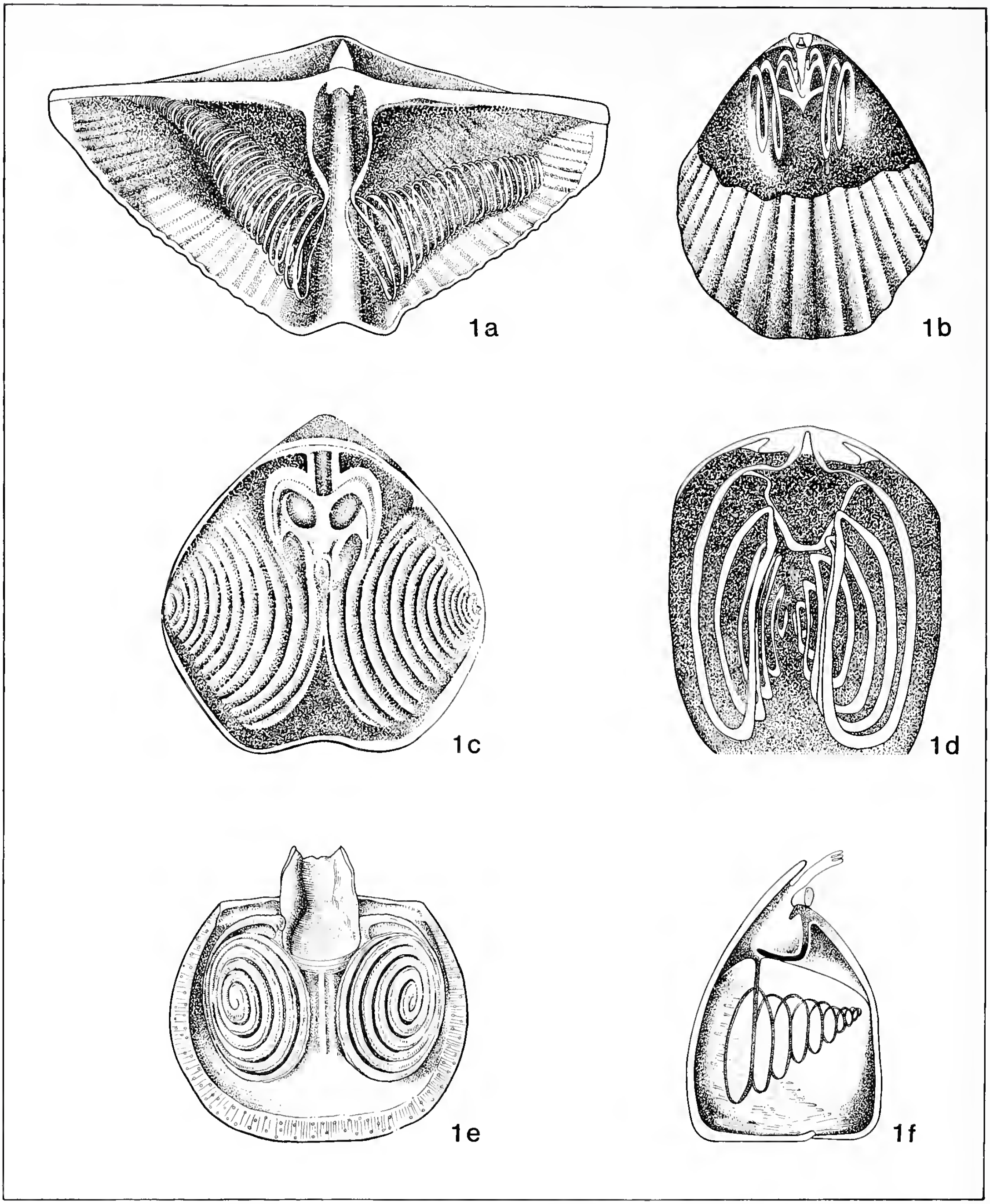


TEXT-FIG. 1. Form of the spiralia in (*a*) the Sub-Order Spiriferidina, (*b*) the Sub-Order Retziidina, (*c*) the Sub-Order Athyridina, (*d*) the Sub-Order Atrypidina, (*e*) the Family Thecospiridae, and (*f*) the *known* form of the lophophore in the Order Rhynchonellida.

is noteworthy that after playing a comparatively minor role in earlier shelf faunas (as far back as the Ordovician), the rhynchonellids suddenly proliferated in the Famennian following the extinction of the atrypids, as illustrated in many papers by Sartenaer (e.g. 1968, 1969) on Famennian rhynchonellids around the world. The only significant difference between the atrypids and the rhynchonellids is the presence in the former of calcareous lophophore supports or spiralia.

The rhynchonellids would have had an obvious advantage over the atrypids if they could then, as now, protrude their lophophores beyond their valves for feeding purposes and as part of the reproductive process. Hoverd also pointed out (1985) that modern rhynchonellids have the further unusual ability of regenerating their lophophores if the ends are snapped off (by the sudden closing of the shell in an emergency when the lophophore is extended).

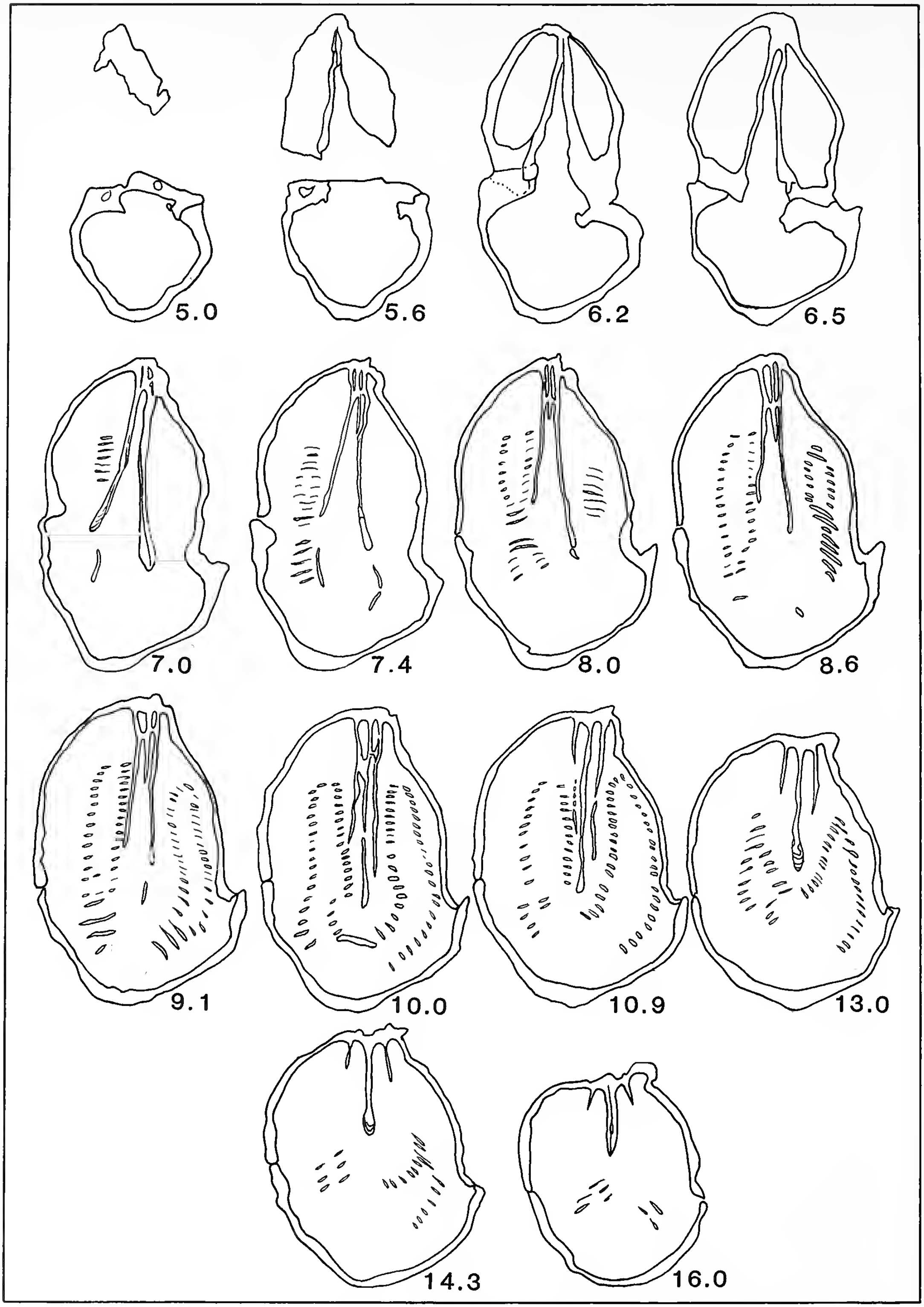
Of course, we know nothing about the lophophores of other important groups such as the orthids and pentamerids, which are long extinct and which have no indication of the lophophore shape in their brachidia. However, it may be significant that just as the atrypids may have been replaced ecologically by the ‘ordinary’ rhynchonellids, so the pentamerids may have been replaced by the stenocismatid rhynchonellids. Both have a spondylium-type structure in one or both valves and both seem to have prospered in the vicinity of reefs. The stenocismatids began just when the pentamerids declined to extinction in the Mid to Late Devonian and they had a final burst of abundance before their own extinction in the Late Permian. They are particularly common, for example in the vicinity of the Magnesian Limestone reefs of Durham (N. Hollingworth, pers. comm. 1985).

After the extinction of the atrypids, the other forms with laterally directed calcareous spiralia continued to flourish through the Carboniferous, Permian, and even Triassic Periods. Athyrids such as *Tetractinella* were locally abundant, for example in the Italian Middle Triassic, and many other forms lasted as late as the Rhaetian (Pearson 1977). There must have been some advantage in laterally directed lophophores, presumably in the separation of inhalant and exhalant feeding currents. Ager and Wallace (1966) suggested that they permitted a more efficient lateral flow of water rather than that conventionally assumed. However, the laterally directed spiral lophophores still had the limitation of a rigid framework supporting the fleshy lophophores and this presumably could not compete with the more flexible lophophores of the increasingly abundant rhynchonellids. In other words most of the spire-bearers opted for strength rather than flexibility.

In Palaeozoic times there was also the hugely successful order of brachiopods the Strophomenida, which ranged from the early Ordovician to the early Jurassic and which included the chonetids and productids that dominated the brachiopod world of the late Palaeozoic. There is clear evidence (from impressions or ridges inside the valves of genera such as *Leptaenisca* and *Davidsonia*) of spiral lophophores directed dorsally but without calcareous supports. Only in one small group the Thecospiriidae are calcareous spiralia preserved, directed ventrolaterally (text-fig. 1*e*). It may be significant that this family is restricted to rocks of Triassic age, the last of all the Strophomenida apart from the very problematical and isolated superfamily, the Cadomellacea of the Toarcian.

With the coming of Jurassic times the rigid spire-bearers were clearly in a decline and after the widespread extinctions at the end of the Triassic, only one genus—*Spiriferina*—survived, in progressively decreasing diversity, in the Early Jurassic. By the end of the Pliensbachian they had all but disappeared and they only lingered on, very locally, into the earliest Toarcian.

The progressive extinction of the last of the spire-bearers was detailed by Thomas (1978). It is noteworthy that the spire-bearers suffered a major eclipse in the widespread sulphurous black mud conditions at the end of the Triassic in the areas where they were still endemic. Then their final extinction came in the similar conditions of the Toarcian when they were even more localized. Of particular interest is one of the last species: *S. adscendens* (Eudes-Deslongchamps) of the late Pliensbachian, in which Thomas found ventrally directed spiralia (text-fig. 2). No other species is known to have this type of internal structure after the extinction of atrypids in the Late Devonian. One can surmise that this was evolutionary convergence with the contemporaneous rhynchonellids and was perhaps an advantage in the special environment of turbid black sulphurous bottom waters. Miguel Mancenido in fact suggested (in Thomas, p. 291) that this species may have opened



TEXT-FIG. 2. Ventrally directed spiralia in the probably unique species *Spiriferina adscendens* (Eudes-Deslongchamps). By kind permission of Dr Alun Thomas.

its valves as wide as possible withdrawing the spiralia and presenting the unprotected lophophore into the surrounding waters for feeding. However, it is not clear how this could be done and it would appear that this rare species also could not escape the calcareous straight-jacket of its own spiralia so that it, and the whole group of spiralia-bearing brachiopods, soon after became extinct.

Acknowledgements. I should like to record my sincere thanks to Alan Hoverd for useful discussions when I was in New Zealand and to Alun Thomas for permission to use unpublished information from his thesis. John Edwards kindly drew the diagrams in text-fig. 1 and Mrs V. Jenkins typed the manuscript.

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THE PALAEONTOLOGICAL ASSOCIATION

ANNUAL REPORT OF COUNCIL FOR 1986

MEMBERSHIP AND SUBSCRIPTIONS. Membership totalled 1,368 on 31 December 1986, a decrease of 10 from the previous year. There were 869 Ordinary Members, a decrease of 6; 70 Retired Members, an increase of 2; 123 Student Members, an increase of 6; and 306 Institutional Members, a decrease of 12. Total individual and institutional subscriptions to *Palaeontology* through Marston's agency numbered 442, an increase of 15.

Subscriptions to *Special Papers in Palaeontology* numbered 116 individuals, an increase of 3; and 122 Institutions, a decrease of 6. Orders through Marston's agency for *Special Papers* numbered 322 volumes.

Sales of back parts of *Palaeontology* via the Membership Treasurer realized £475·15. Sales of back parts of *Palaeontology* under the special offer for clearance of surplus backstock, yielded £7,168·51 gross (less at least £687·23 postage). Sales of back numbers of *Special Papers in Palaeontology* to individuals yielded £1,039·58. Institutions purchased 3 copies of *Palaeontology* and 47 *Special Papers*. Sales of 4 copies of the *Atlas of the Burgess Shale* through the Marketing Manager yielded £60; and sales of *Fossil Plants of the London Clay* through him numbered 57 copies, yielding £341 and $24. Sales of the *Atlas of Invertebrate Macrofossils* under the special offer to members of the Association yielded £442 net. Royalties from Longman, from sales of the latter, amounted to £1,512. A special sale of *Special Paper 22* to members of the Geological Curators' Group yielded £360·74 net.

FINANCE. During 1986 the Association published Volume 29 of *Palaeontology* at an estimated cost of £57,873 (including postage and distribution). *Special Papers 35* and *36* were published at an estimated cost of £9,177 and £7,114 respectively (including postage and distribution). The Association is grateful to all those who made donations to offset the cost of publishing *Palaeontology*.

PUBLICATIONS. Volume 29 of *Palaeontology* for 1986, published in four parts, contained 877 pages and 75 plates. *Special Papers 35* (*Studies in palaeobotany and palynology in honour of N. F. Hughes*, edited by D. J. Batten and D. E. G. Briggs), and *36* (*Campanian and Maastrichtian ammonites from northern Aquitaine, France*, by W. J. Kennedy) were published in December.

MEETINGS. Nine meetings were held in 1986. The Association is indebted to the organizers, hosts, and field leaders of these.

a. *Review Seminar* on 'Palynological approaches to palaeoenvironmental analysis', held on 26 February, at the British Geological Survey, Keyworth, Nottingham. About 70 people attended the meeting, which was convened by Dr Rex Harland.
b. *Joint Seminar with the Malacological Society* on 'The species concept in living and fossil molluscs', held on 12 March at the British Museum (Natural History). Dr G. Oliver and Dr J. D. Taylor convened the meeting, which was atttended by 51 people.
c. *Twenty-Ninth Annual General Meeting*, held in the Lecture Theatre of the Geological Society of London on 19 March. Professor D. M. Raup delivered the Annual Address, on 'Extinction'. The Sylvester-Bradley Award was made to Mr D. K. Loydell.
d. *Workshop* on 'Microcomputers in palaeontology' held at the University of Dundee on 3 April. The meeting was attended by 26 people, and was convened by Dr A. W. Owen. A software package for the treatment of palaeontological data, 'Palstat', written by Dr D. A. T. Harper and Dr P. D. Ryan was introduced at the meeting, and is published by Lochee Publications, on behalf of the Association.
e. *Field Meeting*, organized by the Carboniferous Group, to the Llandudno and Anglesey area, North Wales, on 18–21 April. The meeting was led by Dr I. D. Somerville, and attended by over 60 members.
f. First *Lyell Meeting*, held jointly with the Geological Society of London, on 'Gondwana and Tethys' at the Society's rooms in Piccadilly, on 7–8 May. Over 150 attended the symposium, which was convened by Professor A. Hallam and Professor M. G. Audley Charles. Papers are to be published as a volume by the Geological Society.

g. *'Progressive Palaeontology' Meeting*, held at the Open University, Milton Keynes, on 29 May. The meeting was convened by Rachel Wood, and was attended by 42 people.

h. *Review Seminar* on 'Palaeobiology of benthic molluscs', held on 12 November at the University of Cambridge. More than 60 people attended the meeting, which was convened by Dr J. A. Crame and Dr S. Conway Morris.

i. *The Annual Conference*, held at the University of Leicester, on 18–21 December, comprised an open meeting followed by a field trip to the Jurassic of the district, led by Dr J. D. Hudson and Dr R. G. Clements. The conference was attended by over 180 people, and the Local Secretary was Dr David J. Siveter. The President's Award was made to Mr P. A. Allison

COUNCIL. The following members served on Council following the Annual General Meeting on 19 March 1986. *President*: Dr L. R. M. Cocks; *Vice-Presidents*: Dr M. G. Bassett, Dr D. E. G. Briggs; *Treasurer*: Dr M. Romano; *Membership Treasurer*: Dr A. T. Thomas; *Secretary*: Dr P. W. Skelton; *Marketing Manager*: Dr V. P. Wright; *Institutional Membership Treasurer*: Dr A. W. Owen; *Editors*: Dr D. Edwards, Dr P. A. Selden, Dr P. R. Crowther, Dr L. B. Halstead, Dr T. J. Palmer, and Dr C. R. C. Paul; *Circular Reporter*: Dr Derek J. Siveter; *Public Relations Officer*: Dr M. J. Benton; *other members*: Dr M. E. Collinson, Dr H. A. Armstrong, and (by co-option to vacant positions) Professor B. M. Funnell and Dr P. D. Taylor.

CIRCULARS. Four Circulars, numbers 123–6, were distributed to Ordinary, Student, and Retired Members, and, on request, to over 90 Institutional Members.

COUNCIL ACTIVITIES. There has been much fruitful liaison with other bodies in 1986. Early in the year, the Geological Society of London, together with the Association, the British Micropalaeontological Society, and the Palaeontographical Society formally set up the 'Joint Committee for Palaeontology', with the purpose of strengthening relationships between the sponsoring societies and promoting the subject of palaeontology in general. Like the other constituent bodies, the Association is represented on the J.C.P. by two members of Council. The J.C.P. has already been active, for example, in preparing a general submission concerning palaeontology to the University Grants Committee review on university provision for the Earth Sciences, alongside those made separately by its constituent societies.

A special offer on surplus backparts of *Palaeontology* was made to members of the Association, and subsequently to members of a number of other palaeontological societies, and was a great success. Council is indebted to Dr M. G. Bassett and his staff at the National Museum of Wales for putting the offer into effect.

Council granted financial contributions towards the projected re-launching of the *Cephalopod Newsletter* and the 1987 issue of the *Reef Newsletter*, and also made an award from its Conservation Fund to the work of the West London Wildlife Group in the conservation of some 3,000 tons of tip material of Westphalian age, at Lower Writhlington, Avon, in which much well-preserved arthropod, plant, and some vertebrate material is present.

A new series of annual joint meetings with the Geological Society, the 'Lyell Meetings' was launched in May, with a two-day symposium on Gondwana and Tethys. The next, planned for February 1987, will be on 'Catastrophes and the history of life'. Thereafter the Lyell meetings will be co-ordinated by the J.C.P.

A successful joint symposium with the Malacological Society was held in March, and in 1987 there are to be joint meetings with the Society for Experimental Biology ('Biomechanics in evolution'), the Systematics Association and the Linnean Society ('The phylogeny and classification of the tetrapods'), and the Conservation Committee of the Geological Society and the Geological Curators' Group ('The use and conservation of palaeontological sites'), while a further meeting with the Linnean Society, on the co-evolution of organisms and the atmosphere, is planned for December 1987.

Other plans for 1987 include the publication of the Association's first software package, 'Palstat', which was introduced for experimental testing in April 1986 and displayed in its final form at the Annual Conference in December 1986. The next volume in the 'Fossils of the X Formation' series, that on *Fossils of the Chalk* will be published in mid to late 1987, and further titles are in the pipeline. The Association's 30th anniversary year is also to be marked by a celebratory dinner following the Annual Address in March, and by a 'long weekend' field trip to West Germany, in September, with an exciting programme of visits to several sites with exceptionally preserved biotas.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1986

Balance Sheet as at 31 December 1986

1985				
£	£		£	£
48,521		Investments at Cost (see schedule)		51,917
		Current Assets		
	2,000	Sundry debtors	2,829	
	45,363	Cash at bank	76,330	
	2,029	Sylvester-Bradley Fund	1,974	
		Loans	450	
	49,392		81,583	
		Current Liabilities		
	5,811	Subscriptions received in advance	2,854	
		Provision for cost of:		
	13,500	*Palaeontology*	16,000	
		Special Papers	16,291	
	3,025	Sundry creditors	2,973	
	1,000	Loan from Royal Society		
	23,336		38,118	
26,056				43,465
£74,577				£95,382
		Represented by:		
		Publications Reserve Account		
	45,365	Balance brought forward	69,917	
	24,552	Excess of income over expenditure for the year transferred from Income and Expenditure Account	20,860	
69,917				90,777
		Sylvester-Bradley Fund		
	1,816	Balance brought forward	2,029	
	200	Donation		
	213	Interest	145	
	(200)	Grant awarded	(200)	
2,029				1,974
2,631		Meeting Reserve		2,631
£74,577				£95,382

INCOME

1985 £		£	£
	Subscriptions		
	1986	41,474	
	1985	368	
44,753			41,840
	Palaeontology		
	Sales	34,486	
	Donations	694	
32,041			35,180
	Special Papers		
	Sales	8,319	
	Donations	582	
8,853			8,901
	Burgess Shale Portfolio		
	Sales	169	
483			169
	Fossil Plants of the London Clay		
	Sales	335	
	Postage/Stationery	(29)	
696			306
	Atlas of Invertebrate Macrofossils		
	Sales	2,074	
	Postage/Stationery	(120)	
1,800			1,954
2,554	Offprints		303
62	Profit of Sales of Investments		4,209
11,602	Investment Income (see schedule)		12,180
235	Sundry Income		30
£103,079			£105,072

FOR THE YEAR ENDED 31 DECEMBER 1986

EXPENDITURE

1985 £		£	£
	COST OF PUBLICATION OF *PALAEONTOLOGY*		
	Volume 29—Part 1	13,668	
	Part 2	14,292	
	Part 3	13,913	
	Part 4 (provisional)	16,000	
	Other provision for 28/4	(129)	
53,698			57,744
	COST OF PUBLICATION OF *SPECIAL PAPERS*		
	No. 35	9,177	
	No. 36	7,114	
14,594			16,291
2,093	WAREHOUSING OF PUBLICATIONS		2,280
	GRANTS		200
	COST OF CIRCULARS		
	Preparation	2,917	
	Postage	1,044	
	Credit	(480)	
3,719			3,481
	ADMINISTRATIVE COSTS		
	Postage and stationery	610	
	Editorial expenses	386	
	Meeting expenses	2,910	
	Audit fee	250	
	Membership of Societies	60	
4,423			4,216
£78,527			£84,212
£24,552	EXCESS OF INCOME OVER EXPENDITURE FOR THE YEAR TRANSFERRED TO PUBLICATIONS RESERVE ACCOUNT		£20,860

Schedule of Investments and Investment Income as at 31 December 1986

		Cost £	Gross Income for Year £
£2,000	11% Exchequer Stock 1991	1,991	150
£12,000	13¼% Exchequer Stock 1987	11,520	1,590
£1,000	9% Treasury Stock 1992/1996	992	90
£1,000	9% Treasury Stock 1994	955	90
£4,000	8% Treasury Stock 2002/2006	2,192	320
£5,357	13¼% Treasury Stock 1997	5,000	710
£3,280	13¼% Exchequer Stock 1996	3,000	435
5,270	M. & G. Charifund Units	4,073	1,265
10,000	New Throgmorton Trust (1983) p.l.c. 25p Income Shares	1,706	474
700	Clarke, Nicholls & Coombs p.l.c. 25p Shares	668	62
6,180	M.E.P.C. p.l.c. 6½% Convertible Unsecured Loan Stock 1995/2000 .	4,943	402
374	M.E.P.C. p.l.c. 25p Shares	703	58
1,140	National Westminster Bank p.l.c. £1 Ordinary Shares	3,929	260
10,150	Agricultural Mortgage Corporation Ltd. 7¾% Debenture Stock 1991/1993	8,251	787
1,865	Imperial Group p.l.c. 25p Ordinary Shares—sold March 1986 . .	—	176
1,460	Saatchi & Saatchi 6·3% Convertible Cumulative Redeemable Preference £1 Shares	1,994	129
			6,998
	Bank Interest		5,182
		51,917	12,180
	Market Value at 31 December 1986 (1985—£74,498)	£83,255	

Report of the Auditor to the Members of The Palaeontological Association

In my opinion, the Accounts as set out on pages 861–864 give a true and fair view of the state of the affairs of the Association at 31 December 1986 and of its income and expenditure for the year ended on that date.

March 1987
Market Harborough, Leicestershire

G. R. Powell
Chartered Accountant

INDEX

Pages 1–206 are contained in Part 1; pages 207–428 in Part 2; pages 429–645 in Part 3; pages 646–868 in Part 4. Figures in **Bold Type** indicate plate numbers.

NOTES FOR AUTHORS

The journal *Palaeontology* is devoted to the publication of papers on *all aspects* of palaeontology. Review articles are particularly welcome, and short papers can often be published rapidly. A high standard of illustration is a feature of the journal. Four parts are published each year and are sent free to all members of the Association. *Typescripts* should conform in style to those already published in this journal, and should be sent to **Dr. Dianne Edwards, Department of Plant Science, University College, P.O. Box 78, Cardiff CF1 1XL,** who will supply detailed instructions for authors on request (these are published in *Palaeontology* 1985, **28,** pp. 793–800).

Special Papers in Palaeontology is a series of substantial separate works conforming to the style of *Palaeontology*.

SPECIAL PAPERS IN PALAEONTOLOGY

In addition to publishing *Palaeontology* the Association also publishes *Special Papers in Palaeontology*. Members may subscribe to this by writing to the Membership Treasurer: the subscription rate for 1987 is £33 (U.S. $58) for Institutional Members, and £16·50 (U.S. $30) for Ordinary and Student Members. A single copy of each *Special Paper* is available to Ordinary and Student Members *only*, for their personal use, at a discount of 25% below the listed prices. Non-members may obtain copies, but at the listed prices, from Marston Book Services, P.O. Box 87, Oxford OX4 1LB, England.

RECENT PALAEONTOLOGICAL ASSOCIATION PUBLICATIONS

Special Papers in Palaeontology

Numbers 1–19 are still in print and are available (post free) together with those listed below:

20. (for 1977): Fossil Priapulid Worms, *by* S. CONWAY MORRIS. 155 *pp.*, 99 *text-figs.*, 30 *plates*. Price £16 (U.S. $24).
21. (for 1978): Devonian Ammonoids from the Appalachians and their bearing on International Zonation and Correlation, *by* M. R. HOUSE. 70 *pp.*, 12 *text-figs.*, 10 *plates*. Price £12 (U.S. $18).
22. (for 1978, published 1979): Curation of Palaeontological Collections. A joint Colloquium of the Palaeontological Association and Geological Curators Group. Edited by M. G. BASSETT. 279 *pp.*, 53 *text-figs*. Price £25 (U.S. $38).
23. (for 1979): The Devonian System. A Palaeontological Association International Symposium. Edited by M. R. HOUSE, C. T. SCRUTTON and M. G. BASSETT. 353 *pp.*, 102 *text-figs.*, 1 *plate*. Price £30 (U.S. $45).
24. (for 1980): Dinoflagellate Cysts and Acritarchs from the Eocene of Southern England, *by* J. P. BUJAK, C. DOWNIE, G. L. EATON *and* G. L. WILLIAMS. 100 *pp.*, 24 *text-figs.*, 22 *plates*. Price £15 (U.S. $23).
25. (for 1980): Stereom Microstructure of the Echinoid Test, *by* A. B. SMITH. 81 *pp.*, 20 *text-figs.*, 23 *plates*. Price £15 (U.S. $23).
26. (for 1981): The Fine Structure of Graptolite Periderm, *by* P. R. CROWTHER. 119 *pp.*, 37 *text-figs.*, 20 *plates*. Price £25 (U.S. $38).
27. (for 1981): Late Devonian Acritarchs from the Carnarvon Basin, Western Australia, *by* G. PLAYFORD and R. S. DRING. 78 *pp.*, 10 *text-figs.*, 19 *plates*. Price £15 (U.S. $23).
28. (for 1982): The Mammal Fauna of the Early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset, *by* M. J. BISHOP. 108 *pp.*, 47 *text-figs.*, 6 *plates*. Price £25 (U.S. $38).
29. (for 1982): Fossil Cichlid Fish of Africa, *by* J. A. H. VAN COUVERING. 103 *pp.*, 35 *text-figs.*, 10 *plates*. Price £30 (U.S. $45).
30. (for 1983): Trilobites and other early Arthropods. Edited by D. E. G. BRIGGS and P. D. LANE. 276 *pp.*, 64 *text-figs.*, 38 *plates*. Price £40 (U.S. $60).
31. (for 1984): Systematic palaeontology and stratigraphic distribution of ammonite faunas of the French Coniacian, *by* W. J. KENNEDY. 160 *pp.*, 42 *text-figs.*, 33 *plates*. Price £25 (U.S. $38).
32. (for 1984): Autecology of Silurian organisms. Edited by M. G. BASSETT and J. D. LAWSON. 295 *pp.*, 75 *text-figs.*, 13 *plates*. Price £40 (U.S. $60).
33. (for 1985): Evolutionary Case Histories from the Fossil Record. Edited by J. C. W. COPE and P. W. SKELTON. 202 *pp.*, 80 *text-figs.*, 4 *plates*. Price £30 (U.S. $45).
34. (for 1985): Review of the upper Silurian and lower Devonian articulate brachiopods of Podolia, *by* O. I. NIKIFOROVA, T. L. MODZALEVSKAYA and M. G. BASSETT. 66 *pp.*, 6 *text-figs.*, 16 *plates*. Price £10 (U.S. $15).
35. (for 1986): Studies in palaeobotany and palynology in honour of N. F. Hughes. Edited by D. J. BATTEN and D. E. G. BRIGGS. 178 *pp.*, 29 *plates*. Price £30 (U.S. $50).
36. (for 1986): Campanian and Maastrichtian ammonites from northern Aquitaine, France, *by* W. J. KENNEDY. 145 *pp.*, 43 *text-figs.*, 23 *plates*. Price £20 (U.S. $35).

Field Guides to Fossils

1. (1983): Fossil Plants of the London Clay, *by* M. E. COLLINSON. 121 *pp.*, 242 *text-figs*. Price £7·95 (U.S. $12).

Other Publications

1982. Atlas of the Burgess Shale. Edited by S. CONWAY MORRIS. 31 *pp.*, 24 *plates*. Price £20 (U.S. $30).

1985. Atlas of Invertebrate Macrofossils. Edited by J. W. MURRAY. Published by Longman in collaboration with the Palaeontological Association. xiii+241 *pp.* Price £13·95. Available in the USA from Halsted Press at U.S. $24.95.

Palaeontology

VOLUME 30 · PART 4

CONTENTS

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