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ERRATA

Page 162, Table 1. Should read: Upper Palaeocene *G. velascoensis* Zone, Rock Unit I, samples 1 and 2. Lower Eocene *G. aequa* Zone to *G. aragonensis* Zone, Rock Units II and III, samples 3–48.

Page 196. Caption to Plate 36. Fig. 1 is *Cadomites* (*C.*) *deslongchampsi*, Fig. 3 is *Teloceras banksi*, and Fig. 4 is *Leptosphinctes* (*L.*) aff. *davidsoni*. Figs. 2 and 5 are correct.

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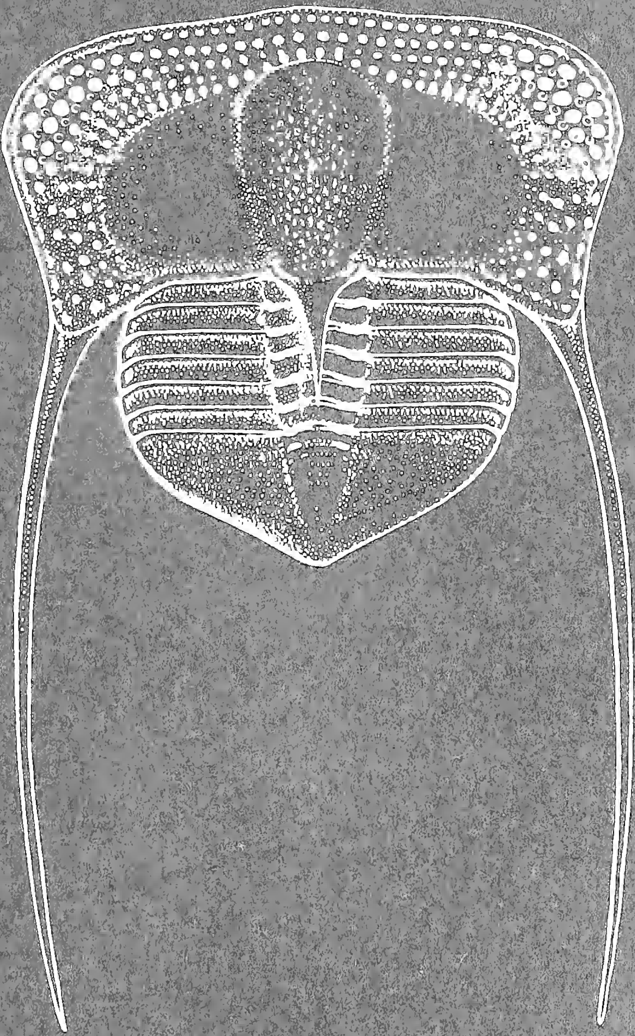

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Cover: *Marrolithus favus* (Salter).

Reconstruction of Ordovician trinucleid trilobite, prepared by Dr. J. K. Ingham as the symbol for the Symposium on the Ordovician System, Birmingham, 1974. Based on silicified material collected by Dr. R. Addison from limestones of Upper Llandeilo age from Wales.

The Palaeontological Association regrets that the details of the paper by Fürsich and Hurst, published in *Palaeontology* Volume 17, Part 4, pp. 879–900, were inadvertently omitted from the Contents lists of both the Part and the Volume.

The following entry should be made in the Contents list for the Volume:

THE PHYLOGENETIC AFFINITIES OF FENESTELLOID BRYOZOANS

by R. TAVENER-SMITH

ABSTRACT. In this paper suggestions are made as to the affinities and derivation of the cryptostomatous sub-Order Fenestelloidea. Diagnostic features of the group are held to be the presence of zooecial apertures on the obverse of a colony only and 'longitudinal striae' on the reverse; also the presence of a primary axial complex within branches. Longitudinal striae are recognized as a fundamental and significant part of the skeletal structure. In *Pseudohornera* it can be seen that the striae are vestiges of formerly existing interzooecial walls which are homologous with range partitions in the Ptilodictyoidea. If longitudinal striae are vestigeal interzooecial walls then their presence on the reverse of fenestelloid fronds suggests that this group was originally bifoliate. If, in bifoliate ancestral forms, zooecia grew back-to-back against a medial lamina, this must be represented in fenestelloid branches by the flattened primary axial skeleton on which zooecial bases rest.

Fenestelloid skeletal rods are structurally identical with acanthopores in the Trepostomata and in view of their size must be considered micracanthopores. The carina of biserial fenestellids represents a preferentially developed interzooecial wall, and carinal nodes are megacanthopores of outstanding stature. The latter structures must have exercised a protective function but it is probable that micracanthopores were concerned with the stabilization of the outer, soft colonial layers.

There is a strong body of evidence linking the Fenestelloidea with the Ptilodictyoidea and a complete morphological series bridging the gap between these sub-Orders can be assembled without difficulty. The structure of the medial lamina in *Pseudohornera* is closely linked on the one hand with the primary branch skeleton of the Fenestellidae and on the other with the mesotheca of the Ptilodictyoidea. Other lines of evidence provide further reasons for believing that the fenestelloids were derived from the ptilodictyoids, with the phylloporinids representing an intermediate stock.

CURRENT problems posed by Palaeozoic bryozoans include the need to understand the relationships of the subdivisions of the Order Cryptostomata to one another, and to the Trepostomata with which all show undoubted affinities.

From many points of view it is not an easy matter to differentiate satisfactorily between the Trepostomata and the Cryptostomata and thorough investigation shows that there is, in fact, no clear-cut means of distinguishing between them. The differences which undoubtedly do exist are essentially matters of degree. Features such as monticules, acanthopores, mesopores or diaphragm-bearing, tubular zooecia with endozones and exozones which are typically associated with the Trepostomata are also found in cryptostomatous forms. But they are not universal among the Cryptostomata and, where present, are developed only to a limited extent. All the signs indicate, therefore, that these two Orders accommodate different but fairly closely related stocks.

Within the Cryptostomata a three-fold division into the sub-Orders Rhabdomesoidea, Ptilodictyoidea, and Fenestelloidea, as suggested by Astrova and Morozova (1956, p. 661), is not only acceptable but is also eminently defensible on grounds both of external morphology and internal structure. Reasons have been given elsewhere (Tavener-Smith 1974) for believing that the rhabdomesoids are a primitive branch of the Cryptostomata and for considering that this sub-Order and the Ptilodictyoidea were independently derived from the Trepostomata, to which both show strong

[Palaeontology, Vol. 18, Part 1, 1975, pp. 1–17, pls. 1–2.]

structural similarities. In this paper attention is focused on the phylogenetic affinities of the remaining sub-Order, the Fenestelloidea, and suggestions are made regarding its derivation and relationships.

STRUCTURAL CONSIDERATIONS

General

Bassler (1953, pp. G120–G147) included within the Cryptostomata a number of diverse groups and it was these (together with the Phylloporinidae) that Astrova and Morozova placed in the three sub-Orders already mentioned. Before proceeding further it is advisable to inquire into those characteristics which may be considered to circumscribe the Fenestelloidea and to distinguish them from other cryptostomatous groups. In this connection the following might commonly be cited:

(i) An upright, fenestrate colonial skeleton with cup-like, fan-like, or foliaceous habit.
(ii) The common presence of compact, box-like zooecia.
(iii) The presence of zooecial apertures on one side of the skeletal meshwork only, the reverse showing parallel, longitudinal striations.
(iv) The presence of a primary skeletal layer forming a ramifying axial component in all branches and an envelope around individual zooecia.

The first consideration, though at first sight fundamental, does not apply throughout the sub-Order; *Penniretepora*, *Diploporaria*, and *Thamniscus* are obvious exceptions. On the other hand, members of other groups undoubtedly do manifest this aspect: some ptilodictyoids have a fenestrate structure (e.g. *Clathropora*, *Coscinella*) and the same growth habit is also known among the Cyclostomata (e.g. *Coscinotrypa*) and Cheilostomata (the Reteporidae). Nor is the presence of compact, box- or sac-shaped zooecia truly diagnostic, for this is common among the Cheilostomata. Also this characteristic is not shown by most phylloporinids which the writer, in agreement with the Russian authors, would include in the Fenestelloidea. Furthermore, some species of *Fenestella* itself have short tubular zooecia.

Items (iii) and (iv) are, however, found to varying extents in all fenestelloids and seem to represent the fundamental attributes of the group, being peculiar to it. Both therefore merit further attention.

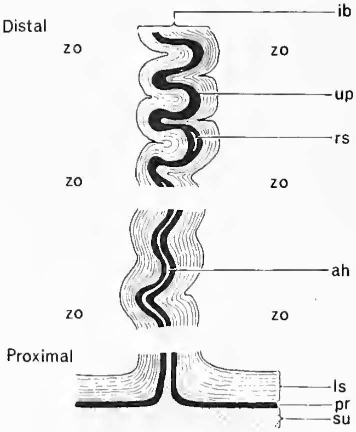
Emplacement of the primary layer

By 'primary layer' in this context is meant the first-formed component of the mineralized skeleton at any point in the colony, whether beneath the initial attachment disc or at the tips of growing branches. This first-formed component is designated *primary* to distinguish it from the differently constructed *secondary* skeleton which was subsequently added and is commonly much thicker. The primary layer has distinctive and characteristic features under either the light or electron microscope. Examination with the light microscope shows primary tissue as an apparently structureless layer of clear calcite, while the much higher magnification in the electron microscope reveals a disorganized granular structure with either vestigial organic investments around the grains, or a complete absence of organic matrix (Tavener-Smith and Williams 1972). These features contrast with the well-organized arrangement of mineral fibres in the secondary layer, which show marked laminar structure and an organic envelope around each crystallite. It seems probable that the poor organization of the primary layer reflects relatively rapid and ill-concerted deposition of an initial mineral investment to secure the immediate support and protection of the newly formed soft parts. The primary layer is, therefore, the first-formed part of the colonial skeleton, and the peculiar circumstances of its formation impressed upon it a distinctive structure which commonly permits differentiation from subsequently added skeletal components. Though in themselves distinct the junction between primary and secondary skeleton is commonly of a gradational nature.

The primary skeletal layer is identifiable not only in the fenestelloids but also in other cryptostomotous groups. It is also regularly to be found in members of the Trepostomata and Cyclostomata and must be regarded as a fundamental skeletal constituent of all Palaeozoic bryozoans, and in some of later date (Tavener-Smith and Williams 1972). But whereas in other groups the primary skeleton has in most cases a strictly localized distribution, being mainly confined to the basal areas of attachment, in the Fenestelloidea the situation is quite different. In that group the primary layer is not only present in the basal disc but also forms a ramifying axial plexus extending throughout all structural components of a complexly branching skeleton (Elias and Condra 1957, p. 26).

A transverse section of any fenestelloid branch examined under the microscope shows the primary skeleton forming a basal platform on which the zooecial chambers rest. The lower limit of the primary layer in such a section commonly exhibits a number of projections, giving it a toothed appearance, while on its upper surface thin extensions of primary material extend upward to form the medial elements of walls between zooecia (Pl. 1, fig. 1). In three dimensions it will readily be appreciated that such medial elements form a cup or envelope around each zooecial chamber that is complete except in the apertural region. The immediate question then is: by what developmental sequence did a primary skeletal component, which must have originated as the basal layer of an attachment disc in fenestelloid ancestors, come to form the axial component of branches in ramifying fenestrate colonies?

The beginnings of an answer seem to lie in certain stocks in which the primary skeletal layer shows a tendency to rise from the substrate on which it originated. This is seen in specimens of early stage rhabdomesoid colonies studied by the author (1974) in which the basal primary layer rises to form an insulating sheath around foreign axial supports. It is also clearly seen in many ptilodictyoid colonies as the medial element of the mesotheca which rose from an encrusting base as a centrally placed lamina within the erect, bifoliate frond. It is true that transverse sections of the mesotheca commonly show the primary layer to be represented only by a system of closely spaced rods (Pl. 2, fig. 2). These are the *median tubules* of earlier authors (e.g. Karklins 1969, p. 7). In some cases these structures show a distinct tendency to lateral flattening, being lenticular in the plane of the mesotheca (Pl. 2, fig. 6), while in others they are united into a continuous medial sheet, shown as a black line in Karklins (1969, p. 23, fig. 6) (see also Pl. 2, fig. 3). The main point, however, is not whether the primary tissue forms tubules or sheets, but that it is demonstrably rising from its original prone position adjacent to the substrate. An excellent illustration of the power of a flat-lying, primary layer to rise locally from the substrate to form a potential medial lamina within an upright frond is shown in a thin section of *Alveolaria semiovata* Wood (lectotype in B.M. (N.H.) Collection) of Pliocene age. In this case the basal lamina clearly consists of primary and secondary components. Both of these are doubled in the 'mesotheca' which is essentially an erect invagination of the basal lamina (text-fig. 1). There can be no doubt, therefore, of the potential ability of a basal primary



TEXT-FIG. 1. Transverse section of *Alveolaria semiovata* Wood showing three stages in the formation of a doubled wall which rises from the basal plate to form an erect medial lamina within the sub-globular colony. Drawn from thin section of lectotype D6905 in the B.M. (N.H.) Collection.

ah: axial slit within doubled 'basal wall'; ib: invaginated basal wall forming medial lamina; ls: laminated secondary wall component; pr: primary basal layer (stained yellow to brown in the section); rs: residual slit in distal part of invagination; up: united primary layers forming a single unit; zo: positions of zooecia flanking the medial lamina.

EXPLANATION OF PLATE 1

All figures are scanning electron micrographs of whole mounts or polished sections.

Fig. 1. *Polypora dendroides* McCoy. Tournaisian, Hook Head, Ireland. Part of transverse section of a branch. The bases of zooecial chambers rest on a primary skeletal layer which shows a digitate lower surface, ×310.

Fig. 2. *Fenestella polyporata* (Phillips). Visean, Black Lion, Ireland. Detail of transverse section of a branch. Primary layer beneath zooecium showing digitate process encased by laminar secondary tissue. The process gives rise to two incipient skeletal rods, ×2700.

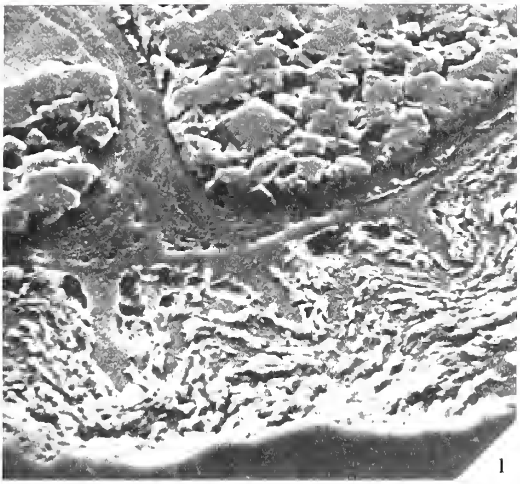
Fig. 3. *Ptylopora pluma* McCoy. Tournaisian, Hook Head, Ireland. Reverse of colony midrib showing longitudinal striae which extend on to dissepiments, where skeletal rods are clearly visible, ×64.

Fig. 4. *Ptylopora pluma* McCoy. Tournaisian, Hook Head, Ireland. Detail of fig. 3 showing ends of skeletal rods as pits (result of differential weathering) aligned along crests of longitudinal striae, ×275.

Fig. 5. *Fenestella cf. albida* Hall. Visean, Florence Court, Ireland. Transverse section of carinal node showing granular primary core surrounded by closely spaced secondary laminae. Obliquely directed off-shoots from the core penetrate secondary layers, giving a stellate pattern, ×1300.

Fig. 6. *Penniretepora pluma* McCoy. Visean, Florence Court, Ireland. Detail of transverse section of colony midrib. Primary tissue in the core of a skeletal rod is flanked by cone-in-cone secondary laminae. Base of a zooecial chamber is top left and branch periphery to bottom right, ×2400.

PLATE 1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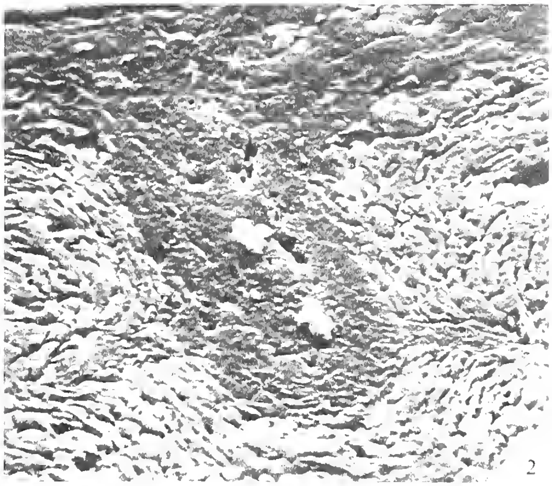
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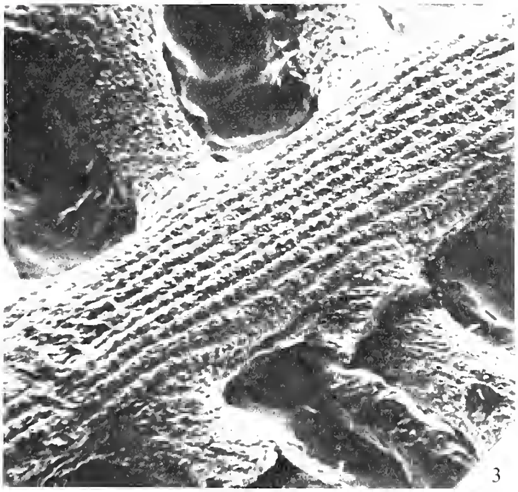
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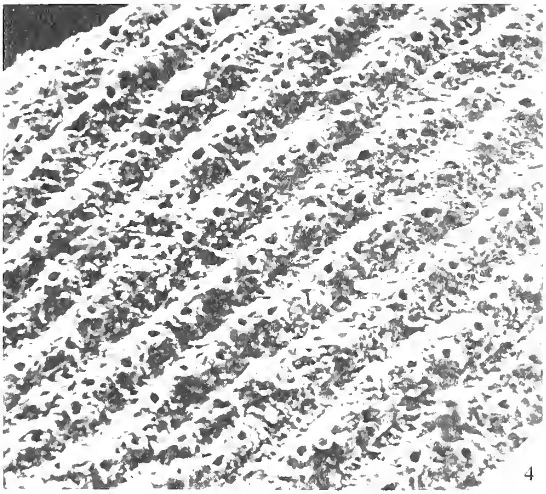
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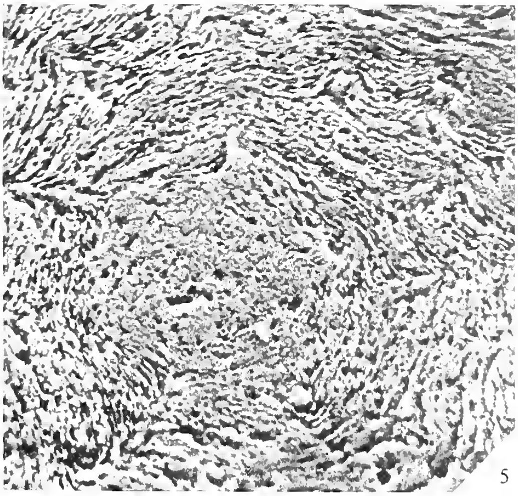
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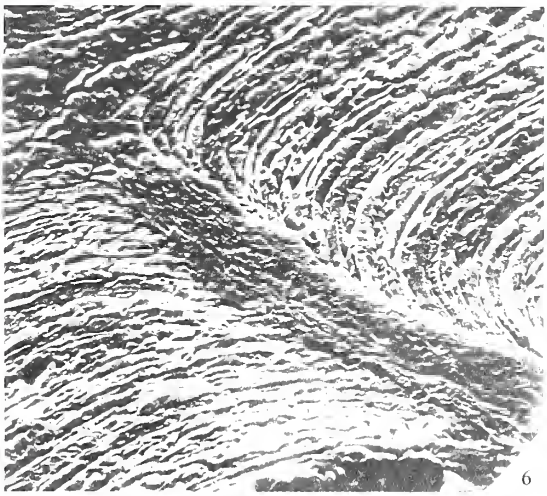
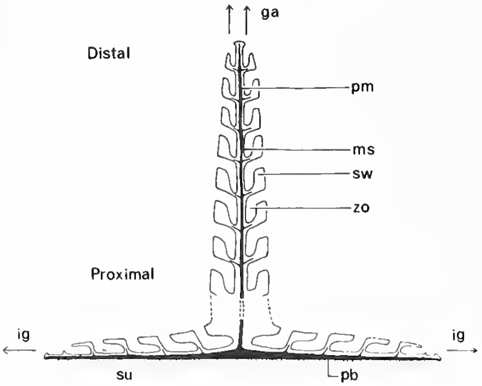

6

TAVENER-SMITH, fenestelloid bryozoa

layer to enter into the axial structure of subsequently formed parts of a bryozoan colony which may adopt an erect posture. It must be pointed out, however, that the structure of primary components of mesothecae in ptilodictyoids does not support the idea that such structures were formed as simple invaginations of the type described above. In these forms (text-fig. 2) the *basal* part of the primary layer is continuous and only the *upper* section was drawn upward into the mesotheca, the primary component of which shows no ultrastructural evidence of having been formed by the union of originally separate layers. In the ptilodictyoids, therefore, the initiation of the mesotheca by upward invagination from the primary basal plate took place only during the later stages of the formation of the primary skeleton (Tavener-Smith 1974). A final point to be made in connection with ptilodictyoid mesothecae is that in some sections examined it was clearly evident that primary tissue of the median lamina extended laterally for short distances on both sides into the walls between adjacent zooecia (Pl. 2, fig. 4). In other words, there are shown the beginnings of a tendency for the primary layer of the mesotheca to extend into the axes of interzooecial walls as cup-shaped bases supporting zooecial chambers.



TEXT-FIG. 2. Diagram of a typical erect bifoliate ptilodictyoid frond growing from a small basal encrustation. Width of primary skeleton greatly exaggerated.

ga: main growth axis; ig: direction of initial growth to form encrusting basal plate; ms: mesotheca; pb: primary layer of basal plate; pm: primary medial layer of mesotheca; su: substrate; sw: secondary wall tissue; zo: zooecium.

Most ptilodictyoid colonies consist of one or more broad, flattened bifoliate fronds and in a few genera growth at the frond margin was differential. In *Clathropora* this gave rise to an initially dentate pattern, the prominences of which grew onward and reunited, leaving behind rounded fenestrules. Repetition of this process led to the formation of a fenestrate frond. In *Taeniodictya* the initial projections grew onward independently of one another and formed ribbon-like branches. In both instances the broad, flattened branches which resulted contain a mesothecal element incorporating a median lamina of primary tissue, the latter in some cases showing the beginnings of extension into interzooecial walls.

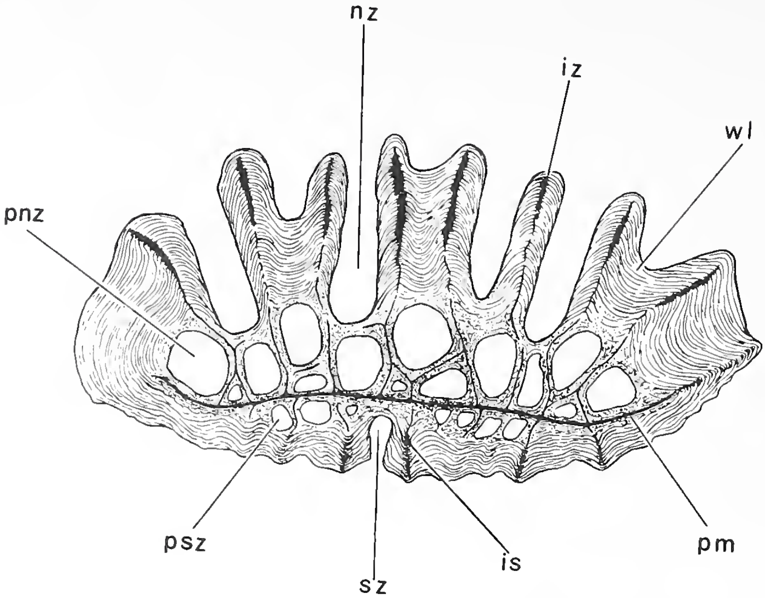
It has been stated that in the Fenestelloidea primary tissue forms a continuous axial complex within all branches of a colony. It constitutes a blade-like base beneath zooecial chambers from which upwardly growing flanges encase the chambers to a varying degree. This primary axial structure ('colonial plexus' of Elias and Condra 1957, p. 26) persists to the distal extremities of growing branches, and the means of its propagation has already been discussed by the writer (1969*a*, pp. 294–299; 1973, pp. 356–357). A clear parallel exists between the situation of primary tissue forming the broad axial plate beneath zooecia in the Fenestelloidea and that within the mesotheca of those ptilodictyoids which develop a fenestrate frond or flattened, ribbon-like branches. The main differences are that whereas the fenestelloids bear zooecia on only one side of a frond the ptilodictyoids are bifoliate, and that whereas the fenestelloid zooecium is invested by a primary envelope the ptilodictyoids show only the beginnings of such structures.

The structure and significance of longitudinal 'striae'

The presence of longitudinal 'striae' on the reverse of branches is a unique feature of the Fenestelloidea, not being evident in other bryozoan groups. Its presence has been remarked on by earlier writers going back to the time of Phillips and McCoy, but no serious inquiry has been made into its origin or significance. The 'striae' are a series of closely spaced, parallel, linear ridges which are always most prominent on the reverse surface of a frond (Pl. 1, fig. 3). But they are not confined to that side, for careful examination commonly reveals them on the obverse also (Tavener-Smith 1969*a*, pl. 53, fig. 5) though in *Fenestella*, the best-known genus of the group, they tend to be obscured by more strongly developed features such as zooecial apertures and carinal nodes. The same is true of all other fenestellid genera having biserial apertures. Striae also tend to be clearly developed on colonial structures not associated with zooecia and their apertures, such as dissepiments and the larger spinose developments. Striae on such structures are always continuous with ones on branches and they must be regarded as fundamental skeletal characteristics.

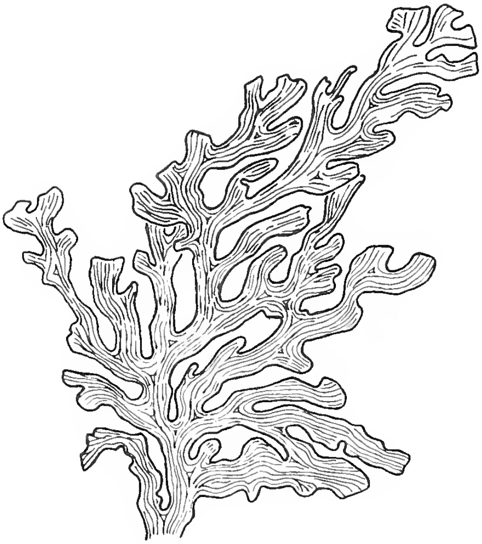
The occurrence of striae as longitudinal lines paralleling the axes of branches means that they cannot have originated as growth lines. This being so, the most natural structures with which they may be associated are the longitudinal dividing walls separating adjacent rows of zooecia. Such walls are also parallel with branch axes and examination of many groups of bryozoa, both ancient and modern, consistently shows that walls between adjacent linear *rows* of zooecia are more strongly developed and of greater morphological significance than those between successive zooecia in the same row (Levinsen 1909, p. 11; Karklins 1969, pp. 12–16).

Proof that longitudinal striae do indeed represent relics of formerly existing interzooecial walls is provided by the structure of the phylloporinid *Pseudohornera*. This genus, together with the rest of the family to which it belongs, was assigned to the Trepostomata by Bassler (1953, p. G115) but other writers have preferred to regard these forms as a primitive fenestelloid stock (Larwood, Medd, Owen and Tavener-Smith 1967, p. 384; Brood 1970, p. 196). Transverse sections across branches of *Pseudohornera diffusa* Hall, the type species, show a unique arrangement. Bisecting the lenticular branch along its major axis is a feature identical in position and structure with a ptilodictyoid mesotheca. This is flanked on one side (the obverse) by a number of short tubular zooecia with well-developed separating walls showing strongly laminar characteristics. On the opposite side of the mesotheca (reverse) the structure is fundamentally the same, but the zooecia are stunted and obsolete (text-fig. 3). Views of the reverse surface of a colony (text-fig. 4; see also Bassler 1953, p. G188, fig. 26) show that the branches bear marked longitudinal striae, and close examination indicates that these correspond in number and position with the vestigial interzooecial walls seen in transverse section. It is therefore clear that in this instance the striae on the reverse are relics of what were originally interzooecial walls, and there seems no reason to doubt that the same is true of fenestelloids in general. *Pseudohornera* therefore illustrates an important intermediate instance in which some



TEXT-FIG. 3. *Pseudohornera*: transverse section of a branch, approximately ×44. Drawn from an acetate peel of *P. diffusa* (Hall) in the U.S.N.M. Collection.

is: obsolete interzooecial wall forming a stria on reverse side; iz: interzooecial wall; nz: normal zooecium; pm: primary medial layer of mesotheca (extensions from this ramify into interzooecial walls); pnz: proximal tubular part of normal zooecium; psz: proximal part of suppressed zooecium; sz: suppressed zooecium; wl: secondary wall laminae.



TEXT-FIG. 4. Reverse of *Pseudohornera* colony showing ribbon-like branches and well-developed longitudinal striae. Drawn from a specimen of *P. diffusa* (Hall) in the A.M.N.H., New York, Collection. Approximately ×2.

essentially ptilodictyoid characters, for example, the tendency towards a flattened, potentially bifoliate branch with mesotheca, are combined with others peculiar to the fenestelloids, for example, zooecial apertures confined to one surface and longitudinal striae on the other.

Study of the ultrastructure of longitudinal striae in fenestelloids and range partitions in ptilodictyoids like *Stictopora* (Pl. 2, fig. 1) shows that the arrangement is fundamentally the same in both cases. (Range partition was defined by Karklins (1969, p. 7) as 'A linear segment of laminated calcite in the exozone of a zoarium between the adjacent ranges of zooecia'.) In transverse sections the primary plate enveloping fenestelloid zooecia shows on its outer side a dentate margin which is most strongly marked on the reverse: the side on which longitudinal striae are most marked. It is important to realize that the tooth-like projections seen in such sections are not spine-like but are thin flanges running the length of the undersurface of each branch. Each flange-like projection from the outer surface of the primary plate is encased by numerous laminae of the secondary skeleton, all of which faithfully follow its outline (Pl. 1, fig. 2). The image of the projection is therefore transmitted through the thick, outer, laminar tissue until the periphery of the branch is reached, where each convexity receives positive expression as a rib-like longitudinal 'stria'. The structure of range partitions in stictoporid ptilodictyoids is virtually the same, for they also consist of numerous superimposed, secondary laminae which are strongly convex outward from a primary origin in the form of a projection from the medial mesothecal layer.

The fundamental importance of longitudinal striae in fenestelloid wall structure is particularly evident in cases where normal branches degenerate at their tips into long, spinose structures devoid of zooecia. In that part of the branch bearing zooecia the striae are virtually restricted to the reverse surface, but beyond the point at which the zooecia terminate striae are strongly developed on *all sides* of the spinose tip. Transverse sections of such spiny branch terminations show a scalloped pattern similar to that seen in a section across a strictoporid stipe, except for the absence of zooecia. The inference to be drawn from this seems to be that although longitudinal striae are closely related to the presence of zooecial chambers they are in a sense even more fundamental to the colony than the zooecia. The axial, primary branch continuation in the above example, together with its outer casing of secondary laminae, are clearly colonial rather than zooecial structures. This is exactly the state of affairs on the reverse side of a normal fenestellid branch where, in spite of the absence of zooecia, primary and secondary tissue of *colonial origin* have combined to form longitudinal striae (Pl. 1, fig. 3). It would appear perfectly logical to deduce from this that, just as the striae on the obverse side of the spiny branch termination are clearly related to the zooecial walls which lie proximal to them, so the striae on the reverse of fenestelloid branches are indicative of the former presence of zooecia on that surface.

The obscure development of striae on the obverse of normal fenestelloid branches is also interesting. In *Polypora* and other multiserial forms such striae may be evident as low ridges, straight or sinuous, separating adjacent rows of zooecial apertures (Miller 1963, p. 169). They are the surface expression of longitudinal interzooecial walls. In *Fenestella* and other biserial forms, however, vestigial striae may be seen either in association with the median keel (carina) or towards the lateral margins of the obverse surface in cases where zooecial apertures are placed close to the keel. Such striae commonly show a sinuous pattern, following the outline of the apertures, and are seen to be continuous with striae on dissepiments. If striae represent the surface expression of former interzooecial walls, and the presence of such striae immediately adjacent to one another reflects the suppression of the zooecia which formerly separated them, then two conclusions must be drawn:

> That biserial forms such as *Fenestella* and its allies evolved from multiserial fenestelloids by the suppression of one or more rows of zooecia.
>
> That in some cases it was the inner rows which were suppressed (leaving, for example, three longitudinal striae associated with the keel, as in *Levifenestella* Miller), while in others it was the outer rows, leaving closely spaced, parallel striae at the branch margins. It may therefore be that biserial fenestelloid genera are of polyphyletic derivation.

For the reasons stated it would seem that the features known as longitudinal striae, which characterize fenestelloid bryozoans and are particularly evident on the reverse side of branches, are relict structures. They appear to represent longitudinal walls which originally separated adjacent rows of zooecia that were at some phylogenetic stage suppressed. If this is so it must be concluded that such rows of zooids occupied the reverse side of branches in ancestral fenestelloids. It is therefore probable that the ancestral forms were bifoliate, the opposed sets of zooecia backing on to a medial platform-like structure or lamina, now represented by the flattened part of the primary skeletal component occurring beneath zooecial chambers. There appears to be a substantial body of evidence suggesting that the fenestelloid basal plate and the ptilodictyoid mesotheca are homologous structures.

Skeletal rods, carinal nodes, and allied structures

Skeletal rods are structures which are considered to be an integral part of the mineralized colonial wall of those bryozoan groups in which they occur (Tavener-Smith 1969*a*, p. 290; Tavener-Smith and Williams 1972, p. 135, etc.). In fenestelloid genera they are almost invariably situated along the crests of longitudinal striae where they commonly form well-defined single or multiple rows (Pl. 1, fig. 4). Likewise, in ptilodictyoids most skeletal rods are situated along the range partitions, though the arrangement is less regular than in fenestelloids (Pl. 2, fig. 5). If fenestelloid longitudinal striae represent vestiges of formerly existing interzooecial walls then the position of acanthopores (structurally identical with skeletal rods) in many genera of the Trepostomata is the same, for these also occur as minute prominences along the distal extremities of interzooecial walls. In terms of the range of acanthopore size, fenestelloid skeletal rods (Pl. 1, fig. 6) with diameters of 10 μm–20 μm, must be considered micracanthopores.

The carinal nodes in *Fenestella*, *Fenestralia*, *Moorephylloporina*, and other genera have posed problems as to their origin and affinities for many years. Likharev (1926, p. 1032) observed that carinal nodes showed the same basic microstructure as the rest of the branch skeleton around zooecial chambers, and Elias and Condra (1957, p. 19) concluded that 'carinal spines are part of the primary skeleton or colonial plexus in Fenestellidae'. Miller (1961, p. 223) suggested that carinal nodes might possibly be homologous with acanthopores in the Trepostomata. The writer is in general agreement with all these observations. Carinal nodes in the Fenestellidae are situated along the medial keel or carina on the obverse of branches. Consideration of its position and internal structure leaves no doubt that the keel corresponds in all respects except size with interzooecial walls separating rows of zooecia in multiserial genera such as *Polypora*. In other words, it is a preferentially developed interzooecial wall—the *only* longitudinal wall of this kind present in biserial fenestellids—and as such it is homologous with longitudinal striae on the reverse of branches, and with range partitions in the Ptilodictyoidea. In *Polypora* and associated genera corresponding structures are seen on some specimens as low, commonly sinuous ridges between zooecial rows. Such ridges may also bear nodes along their length, but these are always less prominent than in biserial forms with a single median keel.

Carinal nodes in biserial fenestellids are of similar structure to skeletal rods in that they consist of a roughly tubular core of granular tissue buttressed by a peripheral zone of closely spaced secondary laminae. The primary material of the core is in direct continuity with that of the axial branch skeleton and the secondary laminae are deflected distally to constitute a clear cone-in-cone structure around the core. One minor difference between the structure of carinal nodes and skeletal rods is that in the former the primary axial core may show slender off-shoots directed distally at oblique angles. These off-shoots penetrate the enveloping secondary laminae (Pl. 1, fig. 5). As a result of this arrangement medial longitudinal sections of carinal nodes may present an appearance reminiscent of a Christmas tree. The relationship between the primary core and flanking laminae is always gradational (Tavener-Smith 1969*b*, p. 94).

Carinal nodes therefore correspond structurally with skeletal rods and also with acanthopores. They must, however, in terms of size, rank as megacanthopores of outstanding stature. Smaller nodes, which may be present on interzooecial ridges in *Polypora* and other multiserial fenestellids, must also be considered to be megacanthopores and homologous structures are found in the Ptilodictyoidea and Rhabdomesoidea. To summarize: it may be said that the carina and its nodes in biserial fenestellids represent the strongly preferred development of a longitudinal interzooecial wall, together with its skeletal rods.

The development of diversified structures from the distal ends of carinal nodes represents a sophisticated trend in biserial fenestellid stocks and several variations of this kind appeared at a relatively early stage in the evolution of the group. They include the geometrically patterned superstructures of *Hemitrypa*, *Loculipora*, and *Isotrypa* which undoubtedly fulfilled a protective function, preserving the delicate extruded tentacles of the lophophore from the attentions of predatory organisms. Structures such as these provide impressive illustrations of the capacity for evolutionary experiment and diversification in the vigorously developing fenestellid stock. The case of *Cervella*, a later genus of Permian age, is different. Here it is possible that the exotic appearance, due to the multiple branching of the distal ends of carinal nodes, is a gerontic feature indicating the senescence of this branch of the stock.

Whereas the function of megacanthopores and their ramifications must have been essentially protective (and this applies equally to the Trepostomata: see, for example, the strong apertural spines in *Tabulipora*) the same cannot be said of micracanthopores. It has been suggested elsewhere (Williams 1956, p. 252; Tavener-Smith 1969*a*, p. 292) that skeletal rods may represent surfaces of attachment for tendons which served to anchor and stabilize the external mantle, a possibility that receives support from the common occurrence of those structures as circlets around the rims of zooecial apertures (Miller 1963, pl. 23, fig. 3). Due to the repeated extrusion and retraction of the lophophore it is in precisely this position that stabilization of the outer mantle tissue would be most necessary, and indeed within the Trepostomata this is the only situation in which micracanthopores occur. The more general distribution and much more numerous occurrence of skeletal rods in the Fenestelloidea may well be associated with the presence of far more extensive areas of branch surface between zooecial apertures. Over these areas it would be essential for the external mantle to be held firmly in position. Finally, it is perhaps relevant to add that the only cases of the occurrence of skeletal rods in bryozoa outside the Trepostomata and Cryptostomata known to the writer occur in the cyclostomatous families Lichenoporidae and Horneridae, in both of which an external mantle of soft tissue is known to exist (Borg 1926, pp. 195–197).

INTERPRETATION OF RELATIONSHIPS

The thesis adopted in this paper is that the origins of the Cryptostomata are to be found within the Trepostomata, or else that both stocks sprang from a common ancestry. There are too many morphological and structural similarities for it to have been otherwise. The common presence of acanthopores and mesopores; the occurrence of tubular zooecia showing endozonal and exozonal regions and bearing diaphragms; these and other features point clearly to a common origin. On the other hand, the general absence of ovicells and of mural pores set these two stocks apart from the other great Palaeozoic group, the Cyclostomata.

EXPLANATION OF PLATE 2

All figures are scanning electron micrographs of whole mounts or polished sections.

Fig. 1. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale) St. Paul, Minnesota. Part of colony showing prominent range partitions separating longitudinal rows of zooecial apertures, ×30.

Fig. 2. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale), St. Paul, Minnesota. Part of transverse section of a frond showing zooecia and mesotheca. The latter has a medial layer of more or less discrete primary rods, ×260.

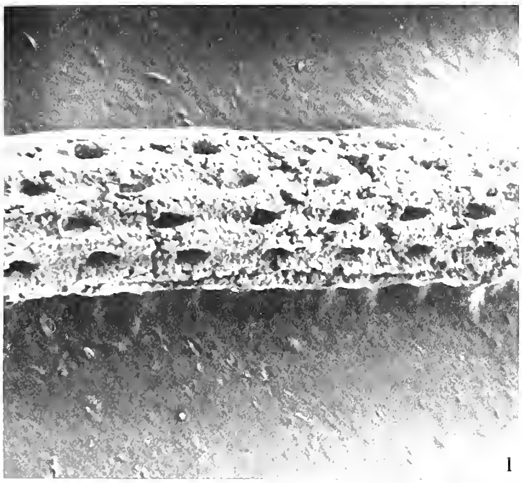
Fig. 3. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale), St. Paul, Minnesota. Detail of fig. 2 showing that primary mesothecal rods locally coalesce to form a continuous medial layer, ×650.

Fig. 4. *Astreptodictya fimbriata* (Ulrich). Ordovician (Decorah Shale), St. Paul, Minnesota. Transverse section showing a primary rod of the mesotheca with an extension which enters medially into an adjacent interzooecial wall, ×2850.

Fig. 5. *Stictopora mutabilis* Ulrich. Ordovician (Decorah Shale), St. Paul, Minnesota. Near-surface tangential section of a branch showing distribution of skeletal rods along a longitudinal range boundary wall between zooecia, ×600.

Fig. 6. *Astreptodictya acuta* (Hall). Ordovician (Decorah Shale), St. Paul, Minnesota. Transverse section showing a lenticular primary medial rod with long axis in the mesothecal plane and a lateral prominence directed towards an adjacent interzooecial wall, ×1325.

PLATE 2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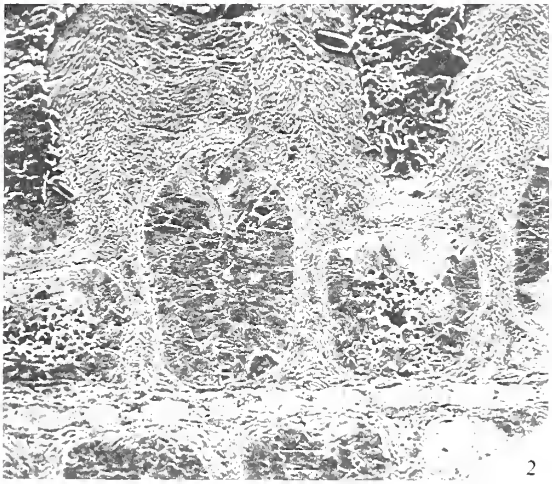
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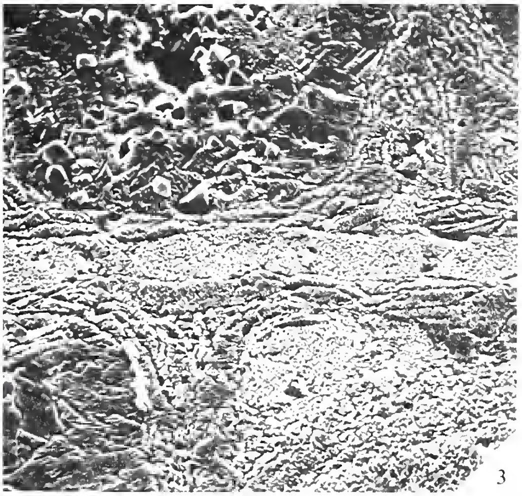
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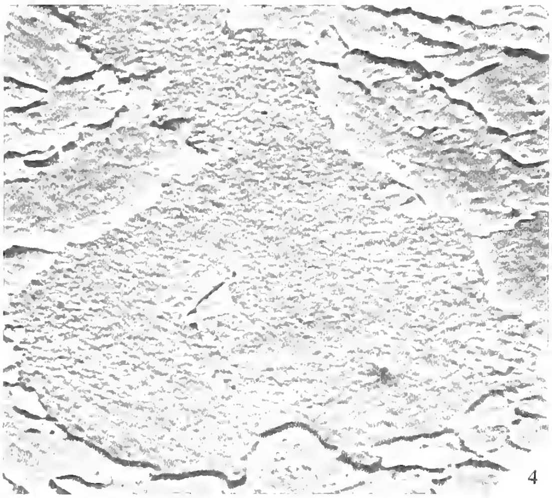
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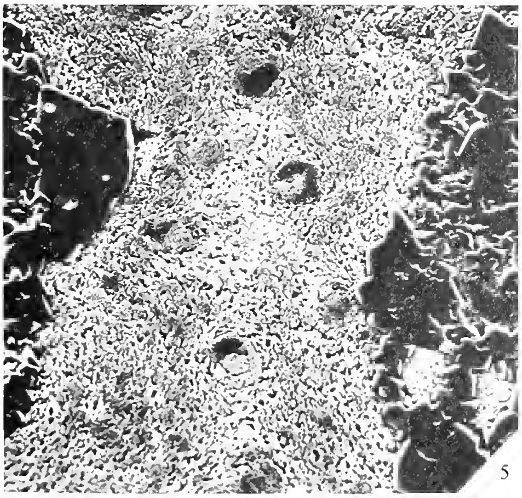
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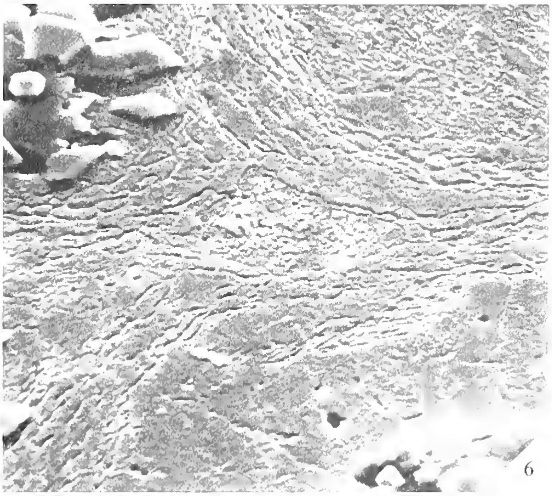
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TAVENER-SMITH, fenestelloid bryozoa

Within the Cryptostomata it has been maintained (Tavener-Smith 1974) that the Rhabdomesoidea and Ptilodictyoidea represent separate lines derived from trepostomatous forebears. If this is so then the Order Cryptostomata is at least biphyletic. The origin of the Fenestelloidea remains to be accounted for and although Bassler (1953), by placing the Phylloporinidae within the Trepostomata, implied that fenestelloid ancestors were in direct relationship with that Order, his contention is not accepted here. Nor does it seem likely that fenestelloids were derived from the Rhabdomesoidea for the long, tubular, diaphragm-bearing zooecia of that group with their well-defined endozonal and exozonal regions are primitive in comparison even with relatively early fenestelloid chambers. In addition, the colonial architecture of the Rhabdomesoidea, with its strongly ramose habit of cylindrical branches and zooecial apertures opening over the whole surface, suggests no affinity with the fenestelloids. Finally, the organization of proliferation fronts, involving in the rhabdomesoids a single 'common bud' at the distal apex of each branch, is difficult to reconcile with that of the Fenestelloidea (Tavener-Smith 1973, p. 356). Another significant difference is the fact that basal attachment discs are unknown in the Rhabdomesoidea though they are the rule among fenestelloids (Cumings 1905, p. 171).

On the other hand, there is a strong body of evidence suggesting a close link between the Fenestelloidea and Ptilodictyoidea. At superficial level, considering only gross morphology, it is not difficult to assemble a continuum of forms which bridge the gap between the two sub-Orders. Typical members of the Ptilodictyoidea form colonies consisting of erect, broadly flattened bifoliate fronds. In a few genera (e.g. *Clathropora*) the frond margin, which in typical ptilodictyoids is smoothly curving, underwent differential growth resulting in a number of stubby prominences which gave rise to a dentate pattern. In *Clathropora* these prominences subsequently reunited to form a crudely fenestrate frond. In other cases, such as *Taeniodictya*, the prominences grew onward without uniting and resulted in a number of flattened, ribbon-like branches. In both genera the branches are bifoliate, with zooecia arranged back to back against a localized and restricted mesotheca.

The phylloporinid genus *Pseudohornera* shows a similar colonial form and internal structure to that described for *Taeniodictya*, with the important modification that zooecia are stunted and obsolescent on one side of the medial lamina. On that surface, however, the interzooecial walls persist as clearly defined linear ridges identical in structure and situation with the longitudinal striae of other fenestelloids. The persistence of vestiges of zooecial structures is also seen on the reverse side of branches in other fenestelloid genera, for example *Fenestrapora* and species of *Septopora*, in the form of scattered pits or 'accessory apertures' which open into blindly ending tubes.

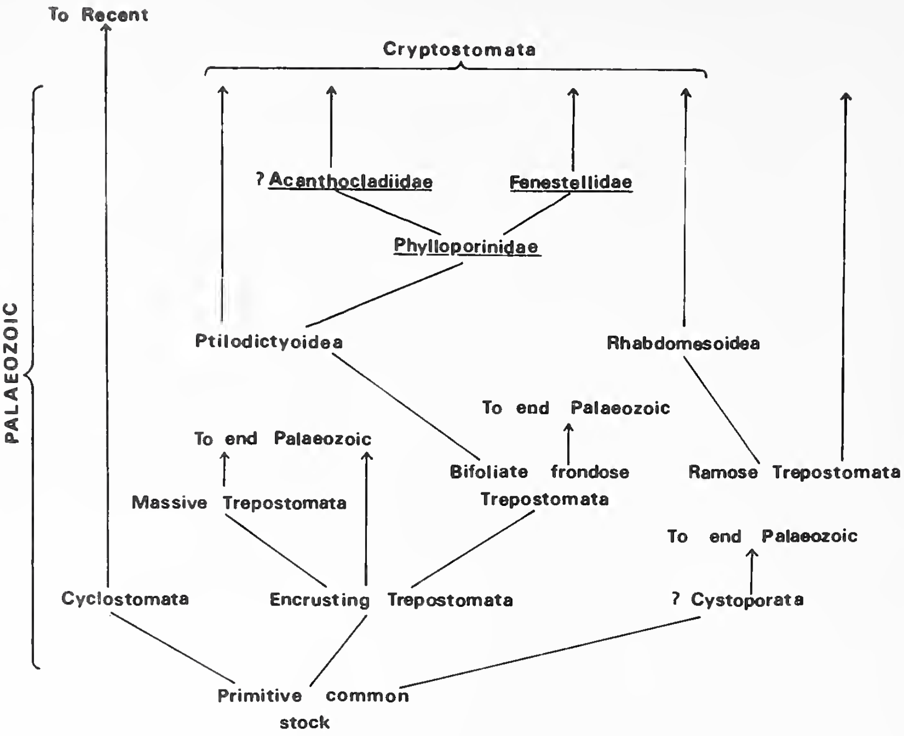
From a form such as *Pseudohornera* it is a short step to the generalized fenestelloid form. This was achieved by the loss of remaining zooecial elements on the reverse side, the consolidation of tubular zooecia into more compact shapes (with the concomitant loss of diaphragms), and the organization of branches into a sub-parallel pattern. At first sinuous branches were connected laterally by anastomoses but, as evolution proceeded and branches straightened, the points of anastomosis were drawn out to form specialized, bar-like dissepiments. This enabled branches and the zooecial apertures upon them to be more widely spaced, which probably conferred an ecological advantage. Dissepiments within the Fenestellidae are invariably sterile, that is, they do not bear zooecial apertures. Connecting struts which do carry apertures were a later development and are confined to the Acanthocladiidae. They appear to have originated quite independently as a result of the union of opposed lateral branches in pinnate forms where the main branches grew in close proximity and parallelism.

The objection that a morphological series such as that outlined above cannot be shown to be a stratigraphic one and therefore has no evolutionary significance does not destroy the argument, for what *has* been demonstrated is that the *potential* for such a series undoubtedly existed. This is important, for the emergence of the earliest fenestelloid stocks with their distinctive characteristics probably took place before the bryozoa formed mineralized skeletons and is therefore not documented in the fossil record. It is commonplace, however, that evolutionary patterns may be repeated through time and in this case the pattern of later events contributes to an understanding of earlier ones.

The structure of the medial lamina of *Pseudohornera* appears identical with that of the ptilodictyoid mesotheca, with which it corresponds in situation and function. It seems logical to believe that such a structure was the forerunner of the primary skeletal layer beneath zooecia in fenestelloid branches, to which it gave rise by the loss of zooecia on one surface. The interzooecial walls on that side have persisted as vestiges, giving rise to the longitudinal striae on the reverse of fenestelloid meshworks. There is, therefore, also a distinct and strong case resting, not on any morphological series, but upon the generalities of skeletal structure, for believing that the sub-Order Fenestelloidea (including the Phylloporinidae) was derived not from the Trepostomata but from early ptilodictyoid stocks. Accordances of zooecial shape and structure support this contention, for fenestelloid chambers have notably stronger affinities with those of the Ptilodictyoidea (many of which show a tendency towards a consolidation in length and reduction or loss of diaphragms) than with chambers of the Rhabdomesoidea or Trepostomata. Zooecia of the Phylloporinidae, with their tubular shapes, diaphragms, and the presence of mesopores in some forms, provide all necessary morphological intermediates between ptilodictyoids on the one hand and the Fenestellidae and Acanthocladiidae on the other.

There can be little doubt that phylloporinid cryptostomes represent an early fenestelloid stock (text-fig. 5) for they manifest an amalgam of primitive and advanced characteristics. That they are themselves true fenestelloids is made plain by their possession of the two critical diagnostic features, namely, a unifoliate frond with longitudinal striae on the reverse side and the presence within branches of a primary axial complex which also forms an investment around zooecial chambers.

The loss of zooecia from one surface of branches was of crucial importance in the emergence of the distinctive fenestelloid growth habit, and contributed significantly to the success of the group. It permitted the increased secretion of skeletal substance on the reverse side of branches which, in conjunction with the longitudinal ribbing of the striae, resulted in greater mechanical strength. This in turn permitted an increase in the size of fronds which was, in the most successful forms, accompanied by a straightening of branches and reduction in branch width (following a reduction of



TEXT-FIG. 5. Suggested phyletic relationships between bryozoan groups during the Palaeozoic era. The three families comprising the Fenestelloidea are underlined.

the number of zooecial rows on a branch). Larger fronds extending higher above the substrate and composed of slender branches bearing more widely spaced zooecial apertures represented ecological advantages which must have contributed powerfully to the immense success of the biserial fenestellids. *Fenestella*, in its shear numerical abundance, reflects the acme of success among fenestelloids in responding to the demands of environment.

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PROTOSTIGMARIA, A NEW PLANT ORGAN FROM THE LOWER MISSISSIPPIAN OF VIRGINIA

by JAMES R. JENNINGS

ABSTRACT. A lycopod underground system from the Price Formation (Lower Mississippian) of Virginia is described as *Protostigmaria eggertiana*. The material consists of impressions that occur in shale and clay underneath a coal in the upper part of the Price Formation. The zone containing the fossil plants resembles the stigmarian underclays that underlie coals of Upper Mississippian and Pennsylvanian age. The plant organ is corm-like, and has short downward extensions to which rootlets are attached. The point of attachment is marked by a circular scar. The remainder of the surface is coarsely rugose. Comparison is made with other lycopod underground parts.

THE abundance of stigmarian remains in the Upper Mississippian and Pennsylvanian is not paralleled by a similar abundance of remains of the underground portions of the arborescent lycopods of the Devonian and Lower Mississippian. The voluminous literature on aerial stems from the Devonian and Lower Mississippian, particularly casts and impressions, contrasts with the current dearth of information concerning the underground parts of these lycopods. In the Devonian lycopod *Lepidosigillaria*, rootlets were borne directly on the rounded base of the plant (White 1907). Another Devonian lycopod, *Cyclostigma*, divided into two short axes at the base and the rootlets were borne on the blunt ends of these. The position of attachment of the rootlets is marked by a circular scar in both of these genera. Neither of these genera had any elongate structure at the base that might resemble a stigmarian axis. This paper describes a lycopod underground system from the Price Formation (Lower Mississippian) of Virginia which adds to the diversity of such structures. Some of the specimens described as *Stigmaria* by Dawson (1873) from the Lower Carboniferous of Canada may represent the same or similar plants.

The material occurs in a roadcut along U.S. 460 at Coal Bank Hollow north of Blacksburg, Virginia, in clay and shale underneath a coal in the upper part of the Price Formation. Because of the abundance of rootlets in this bed, it resembles a stigmarian underclay. A careful search shows, however, that there are no remains of the genus *Stigmaria* in this bed, but instead the material described in this paper. The bed is believed to have formed, like stigmarian underclays, by the disturbance of existing sediment from the penetration of invading rootlets of the lycopods growing in the coal swamp. The evidence for this is: the remains are all oriented in life position rather than inverted, the rootlets are preserved at very high angles to the bedding, the remains of this underground system occur almost exclusively in the strata immediately underneath the coal, and the abundance of the rootlets decreases with increasing depth below the coal.

[Palaeontology, Vol. 18, Part 1, 1975, pp. 19–24, pl. 3.]

SYSTEMATIC DESCRIPTION

Division LYCOPHYTA

Genus PROTOSTIGMARIA gen. nov.

Diagnosis. Form genus for large lycopod underground systems that are corm-like with several short downward extensions to which rootlets are attached, surface rugose, attachment of rootlets marked by circular scar.

Type species. Protostigmaria eggertiana sp. nov.

Protostigmaria eggertiana sp. nov.

Plate 3; text-fig. 1

Diagnosis. Characters of the species as those of the genus; diameter of structure 10–15 cm, downward extensions 1–5 cm, tapering rapidly, rootlet scars 1–7 mm in diameter, furrows present between the extensions with rootlets.

Holotype. Specimen UMMP 60793, in the collections of the University of Michigan Museum of Paleontology (Pl. 3, fig. 1).

Locality. Roadcut along U.S. 460 between the junction with 648 and Coal Bank Hollow about 4·2 km north of Blacksburg, Virginia (Newport $7\frac{1}{2}'$ Quadrangle).

Stratigraphic position. Upper part of the Price Formation.

Age. Lower Mississippian.

Description. The specimens represent the corm-like base and attached rootlets of an arborescent Paleozoic lycopod. This corm-like structure has a coarsely rugose surface (Pl. 3, figs. 1, 2, 4, 5). The ridges and furrows are oriented toward downward extensions to which rootlets are attached. Between these extensions is a somewhat irregular furrow (Pl. 3, figs. 1, 4, 5). It is difficult to determine the exact number of the extensions on any one specimen, since they are preserved as impressions and are, in most cases, incomplete. There are at least three and perhaps four. The diameter of the corm-like structure is approximately 12–15 cm. The downward extensions are approximately 1–5 cm long, tapering rapidly, and bear numerous attached rootlets (Pl. 3, figs. 1, 3) or circular scars that mark their position (Pl. 3, fig. 2). The rootlets are 3–9 mm in diameter. On most specimens it is possible to find some rootlet scars that have been obscured by a rugose surface suggestive of cell proliferation in the

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EXPLANATION OF PLATE 3

Figs. 1–5. *Protostigmaria eggertiana* gen. et sp. nov. 1, holotype showing rugose cortex and downward extensions with attached rootlets. UMMP 60793, ×0·8. 2, specimen with detached rootlets which shows the circular rootlet scars. Arrow indicates a rootlet scar that has been nearly obscured by tissue proliferation. UMMP 60794, ×1. 3, specimen showing the rootlets radiating in several directions. UMMP 60795, ×0·35. 4, 5, part and counterpart of a specimen representing the 'corm' which shows its surface and the furrow between the areas where the rootlets are attached (arrow). UMMP 60796*a*, *b*, ×0·75 and 0·7 respectively. UMMP: University of Michigan Museum of Paleontology.


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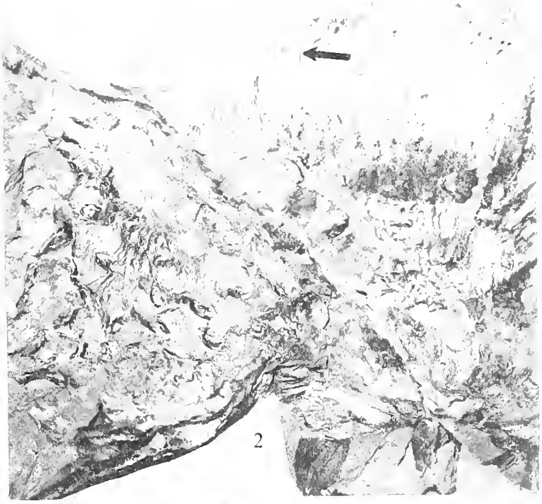
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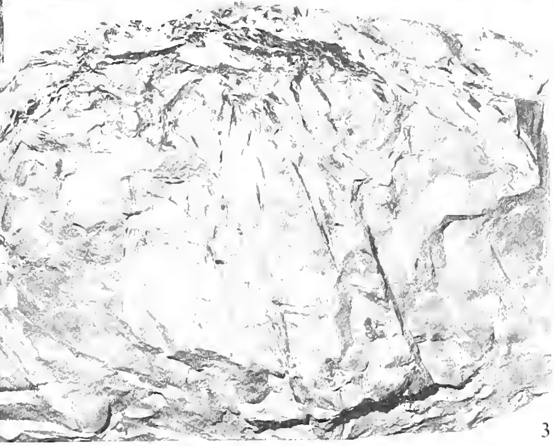
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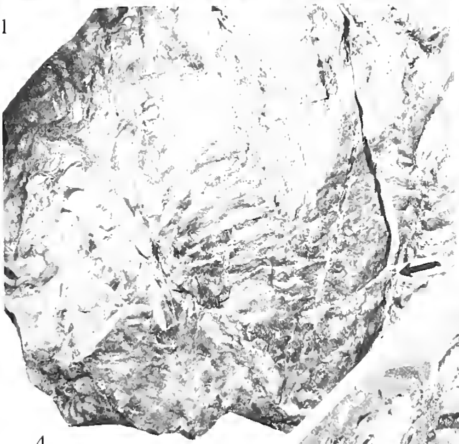
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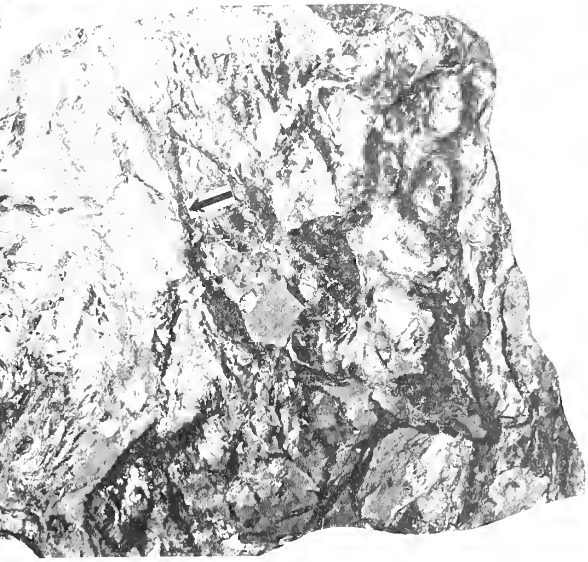
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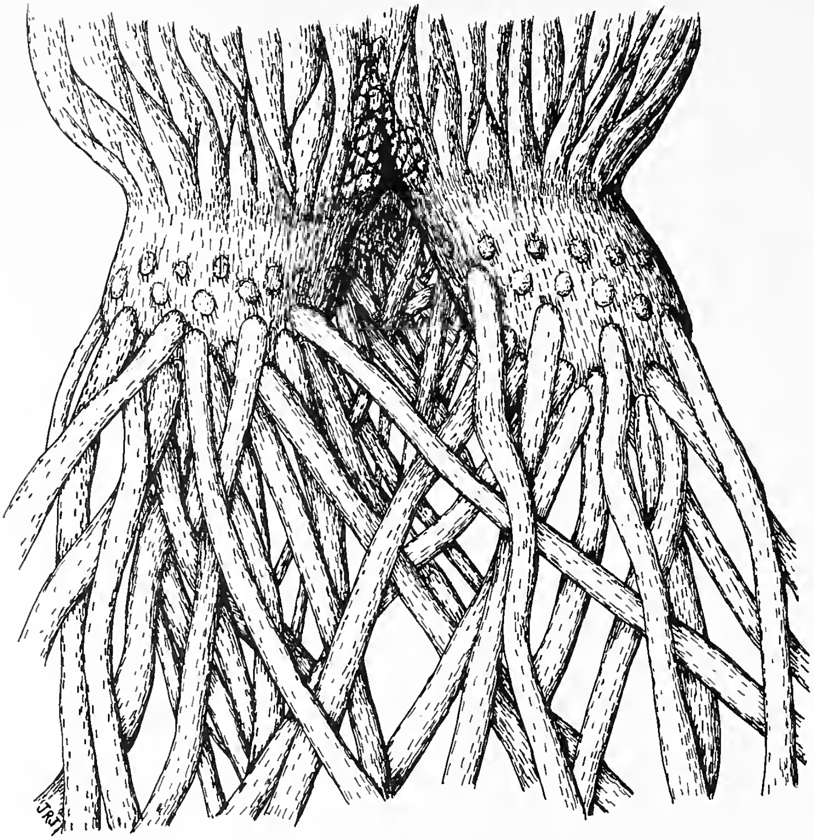
JENNINGS, *Protostigmaria*



TEXT-FIG. 1. Reconstruction of *Protostigmaria eggertiana*. ×0·5 approximately.

cortex (Pl. 3, fig. 2). The longest attached rootlet is 13 cm long, but is not complete. Text-fig. 1 is a reconstruction showing the various features of this plant.

DISCUSSION

A comparison of *Protostigmaria* with the underground parts of *Cyclostigma* and *Lepidosigillaria*, and with *Stigmaria*, indicates clear lycopodiaceous affinities. It shares with the others the circular scars that mark the position of the attachment of the rootlets and, like the base of *Cyclostigma* and *Lepidosigillaria*, was apparently corm-like. The size of the underground system described here suggests that the parent plant had an arborescent habit. It has not been possible, in the absence of physical attachment, to assign *Protostigmaria* to any of the lycopod genera based on aerial stems; however, abundant remains of *Lepidodendropsis* are found in association with it and may have produced this type of underground system. *Protostigmaria* is clearly distinguishable from *Stigmaria*, because in *Stigmaria* rootlets are borne on elongate, dichotomously ramifying axes, while in *Protostigmaria* the rootlets are borne on short downward extensions. *Lepidosigillaria* differs in bearing the rootlets directly on the rounded base of the stem. In *Cyclostigma* the rootlets are borne on each of two derivatives that result from a bifurcation of the aerial stem. These are much larger in relation to the over-all size of the organ than the structures that bear the rootlets in *Protostigmaria*, and there are only two of them, compared to at least three in *Protostigmaria*. The genus *Stigmariopsis*, known from the late Upper Carboniferous of Europe, differs from *Protostigmaria* in consisting of elongate axes that resemble *Stigmaria* except for their branching pattern.

In various species of *Stigmaria* the circular rootlet scars have been shown to represent an abscission layer present at the base of the rootlets (Frankenberg and Eggert 1969; Eggert 1972; Jennings 1973). That *Protostigmaria*, *Cyclostigma*, and *Lepidosigillaria* show similar rootlet scars may indicate a similarity in structure. The fact that some of the scars are partly obscured by a rugose surface that is suggestive of proliferation in the cortex is evidence in favour of this interpretation.

Although *Protostigmaria* increases knowledge of the diversity of lycopodiaceous underground systems, its evolutionary significance is not established. One possible interpretation is that it represents an evolutionary intermediate between a Devonian lycopod such as *Lepidosigillaria*, and *Stigmaria* which became abundant in the Upper Mississippian. *Protostigmaria* bears rootlets on short extensions. This is a condition that is intermediate between the situation in *Lepidosigillaria*, which bears rootlets directly on a rounded base, and *Stigmaria*, which bears the rootlets on elongate, branched axes that extend from the base of the aerial stem.

The resemblance between *Protostigmaria* and *Isoetes* is interesting. Potonié (1894) and Mägdefrau (1931, 1932) have suggested that *Isoetes* is the end product of a reduction series that began with *Sigillaria*, through *Pleuromeia*, through *Nathorstiana* to *Isoetes*. Structural comparisons of stigmarian rootlets with the roots of *Isoetes* (Stewart 1947) have been used in support of this idea. This is definitely not, however, the only possible evolutionary sequence. There are *Isoetes*-like plants known from the Triassic (Brown 1958; Bock 1962). These are clearly not derived from *Nathorstiana* or *Pleuromeia*. *Paurodendron* from the Pennsylvanian has underground parts (Phillips and Leisman 1966) that are corm-like and resemble a diminutive stigmarian axis, particularly in such features as the presence of appendage (rootlet) gaps and the production of secondary xylem. It is certainly possible to postulate an evolutionary line leading from *Protostigmaria*, through a Pennsylvanian lycopod resembling *Paurodendron*, to the *Isoetes*-like plants that are known from the Triassic onward, rather than regarding the very large and complex organ called *Stigmaria* as the direct precursor of the corm of *Isoetes*. Nevertheless, despite the numerous lycopod genera and species that have been based on stem impressions, there are comparatively few underground systems known, and this is especially true for petrifactions. For this reason it is difficult to delineate evolutionary pathways among either Paleozoic or later lycopods. It is hoped that a recognition of the problems involved in attempting to interpret the fossil record of the lycopods will stimulate field work that will uncover evidence leading to the resolution of existing uncertainties.

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THE CRANIAL MORPHOLOGY OF A NEW LOWER CRETACEOUS TURTLE FROM SOUTHERN ENGLAND

by JEANNE EVANS *and* T. S. KEMP

ABSTRACT. A new turtle *Mesochelys durlstonensis* gen. et sp. nov. is described from an almost complete skull and partial postcranial skeleton found at Durlston Bay, Dorset (Purbeckian, basal Cretaceous). Its closest relative is *Glyptops plicatulus* from the Morrison Formation of North America and, together, these two constitute the most primitive cryptodire family Glyptopidae. The structure of the basicranial axis, the pterygoid, and the roofing bones indicate that *Mesochelys* is the most primitive post-Triassic chelonian yet described.

IN December of 1971 Mr. John Evans collected an extremely well-preserved skull and partial postcranial skeleton of a turtle, contained in a large block of limestone on the foreshore of Durlston Bay, Swanage, Dorset. The matrix, a hard, dark limestone possibly from the Upper Building Stone, responded well to the acetic-acid method of preparation. A 10% solution of acid was used and the exposed bone was strengthened by 'Vinalak' (polybutyl methacrylate) in methylethyl ketone. The matrix has been completely removed.

The skull is slightly crushed dorso-ventrally, just separating the sutures sufficiently for them to be clearly determined. The palatines, basioccipital, and exoccipitals are missing, as are the squamosal and quadratojugal of the left side. There is no lower jaw, and the postcranial bones preserved are one cervical vertebra, several caudal vertebrae, the left ilium, pubis and femur, several foot bones, and a very incomplete shell.

SYSTEMATIC POSITION

The great majority of Mesozoic turtles are known only from their shells and it is upon this feature, therefore, that the taxonomy is primarily based (Delair 1958). Even then, several genera have been established on very incomplete specimens, while such phenomena as the degree of individual variation and possible sexual dimorphism have never been investigated. The remains of the shell of the present specimen are insufficient for a positive identification to be made, although enough is known to remove certain genera from consideration, particularly those with distinctive types of shell ornamentation. The general nature of the shell points towards the genera *Pleurosternon* Owen and *Hylaeochelys* Lydekker. The notched xiphiplastral bone is suggestive of the former genus whilst the presence of an emarginate marginal bone suggests the latter.

Skull structure is well known for three Upper Jurassic turtles, of which *Glyptops plicatulus* of the Morrison Formation of North America is the only one with associated postcranial skeleton. The other two were described in detail by Parsons and Williams

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(1961), one from Portland (possibly the same as *Stegochelys planiceps* Owen) and the other from Solnhofen. A fourth kind of chelonian skull, from the Purbeck of Swanage, is currently being described by ourselves. Of these four kinds, the present specimen is very like *Glyptops plicatulus* (Baur 1891; Gaffney 1972*a* and pers. comm.) and must be placed in the same family as that form. Shells referred to *Glyptops ruetimeyeri* are known from the Purbeckian (Watson 1910) although, as indicated above, the shell of our specimen is inadequate for comparison. We have elected to create a new genus for our Dorset form on the basis of several marked differences from *Glyptops*, despite the possibility that it belongs to an existing genus known only from the shell. It seems to us likely that skull structure is eventually going to provide a far more reliable guide than the shell to the taxonomic and phyletic relationships of early turtles, and it is important therefore that one of the most primitive and best known of the Mesozoic kinds should be appropriately named and diagnosed.

Suborder CRYPTODIRA
Family GLYPTOPIDAE

Diagnosis. Primitive cryptodiran turtles with the basisphenoid completely separating the pterygoids; foramen posterior canalis carotici interni lying half-way along the basisphenoid-pterygoid suture. Pterygoid not completely flooring the cavum acustico-jugulare. Epipterygoid present. Prefrontals with moderate dorsal exposures but not meeting one another. Triturating surfaces narrow and not expanding posteriorly.

Genus MESOCHELYS gen. nov.

Diagnosis. Glyptopid turtles with the skull only moderately elongated. Frontal making a long, oblique suture with the nasal. Maxillae well separated from one another. Jugal just entering the orbital margin. Triturating surfaces relatively wide. Carapace with at least one emarginate marginal bone. Xiphiplastron bone notched.

Mesochelys durlstonensis sp. nov.

Diagnosis. As for genus.

Holotype. Cambridge University Museum of Zoology. T 1041. Skull and partial postcranial skeleton.

Locality. Durlston Bay, Dorset.

Horizon. Purbeckian, possibly Durlston Formation (Lower Cretaceous, Casey 1973).

Nomenclature of cranial structures used throughout this paper is that of Gaffney (1972*b*) as developed from Parsons and Williams (1961).

Abbreviations used in text-figures

ad. can. stap-temp.—aditus canalis stapedio-temporalis
ant. postot.—antrum postoticum
bpt. art.—basipterygoid articulation
bpt. pr.—basipterygoid process
BSP—basisphenoid
can. cav.—canalis cavernosus
cond.—condyle
dor. sel.—dorsum sellae
EPT—epipterygoid
F—frontal
for. alv. sup.—foramen alveolare superius
for. car. post.—foramen posterior canalis carotici interni
for. n. abd.—foramen nervi abducentis
for. n. trig.—foramen nervi trigemini

for. pal. post.—foramen palatinum posterius
for. prepal.—foramen praepalatinum
for. stap-temp.—foramen stapedio-temporale
for. supramx.—foramen supramaxillare
fossa acust-fac.—fossa acustico-facialis
hiatus acust.—hiatus acusticus
IL—ilium
in. col. aur.—incisura columellae auris
ISCH—ischium
J—jugal
MX—maxilla
N—nasal
OPIS—opisthotic
opis. sut.—sutural surface for the opisthotic
P—parietal
PMX—premaxilla
PO—postorbital
PRO—prootic
pro. sut.—sutural surface for the prootic
PRF—prefrontal
PT—pterygoid
pt. sut.—sutural surface for the pterygoid
pt. w. q.—pterygoid wing of the quadrate
PUB—pubis
Q—quadrate
QJ—quadratojugal
qj. sut.—sutural surface for the quadratojugal
Q (*opis*)—sutural surface of quadrate for the opisthotic
rec. lab. pro.—recessus labyrinthicus prooticus
rec. lab. so.—recessus labyrinthicus supraoccipitalis
rost. bsp.—rostrum basisphenoidale
sel. tur.—sella turcica
SO—supraoccipital
SQ—squamosal
sq. sut.—sutural surface for the squamosal
V—vomer

Description: skull

General features

The skull is wedge-shaped when seen from above, and low in lateral view. The face is short with circular dorso-laterally directed orbits, and a small, narrow snout. The external nares are confluent. There is only slight emargination of the posterior edge of the skull roof and the crista supraoccipitalis is not well developed. The ventro-lateral margin of the skull in the region of the jugal and quadratojugal bones is distinctly emarginated.

The palatal surface lacks all trace of a secondary palate and the triturating surfaces of the maxillae are only slightly expanded posteriorly and bear sharp labial ridges but no tomial ridges. The paired premaxillae project downwards as a small serrated beak. The posterior surface of the palate is flat and the processus pterygoideus externus of each pterygoid is relatively well developed. The quadrate is stout and curved, and the cavum tympani is developed just as in typical modern turtles. The incisura columellae auris is barely open posteriorly and the antrum postoticum is prominently developed.

In posterior view there is a large fenestra postotica.

The external surfaces of the skull are lightly sculptured and pitted with small nutritive foramina.

Bones of the skull roof

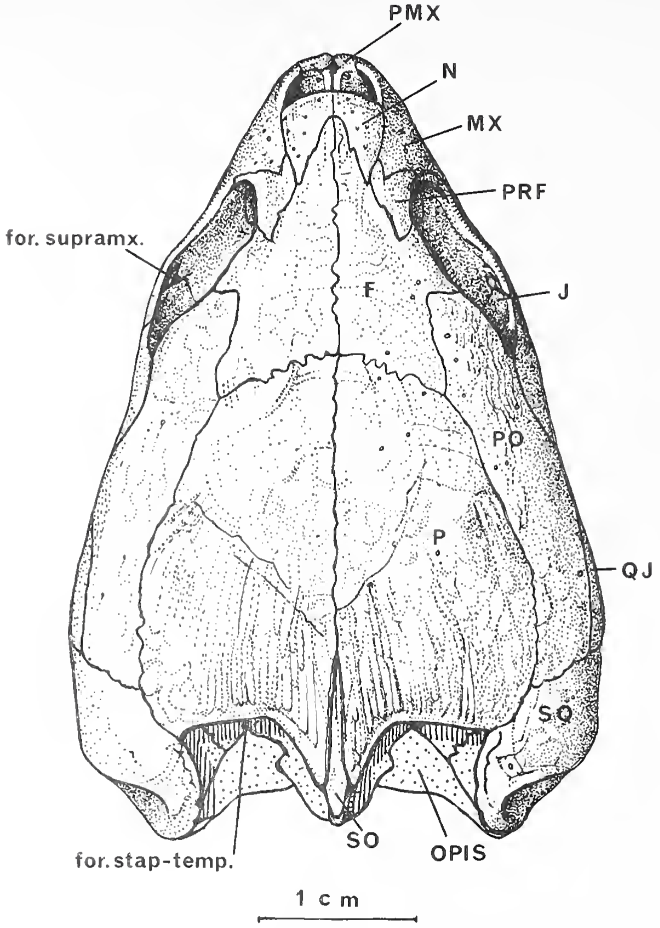
Parietal. The form and large size of the parietal is clear from the figures. The posterior edge is somewhat emarginated between the posteriorly directed spur which runs alongside the supraoccipital and the short contact with the squamosal bone laterally. The processus inferior parietalis (text-fig. 3*b*) is large and descends in a parasagittal plane to contact the small epipterygoid antero-ventrally and the prootic postero-ventrally, these three bones forming the foramen nervi trigeminalis (although in the specimen slight distortion on both sides has rather obscured the foramen). Above the level of the prootic, the parietal forms a very extensive overlapping contact with the external surface of the supraoccipital.

Frontal. The shape of the frontal is rather unusual in being triangular with a pointed anterior process extending, in contact with its fellow, between the nasals. A distinct lateral lappet of the frontal forms a small part of the dorsal margin of the orbit.

A well-developed ventral ridge just lateral to and parallel with the mid-line marks the limit of the sulcus olfactorius.

Nasal. A pair of small nasals are present which contact the frontals and also the prefrontals externally. From side to side the nasals are slightly convex.

Prefrontal. The dorsal exposure of the prefrontal is limited to a small rectangle forming the antero-dorsal corner of the orbital margin. A descending process curves down from the anterior end, medial to and in



TEXT-FIG. 1. *Mesochelys durlstonensis.* Skull, slightly restored, in dorsal view.

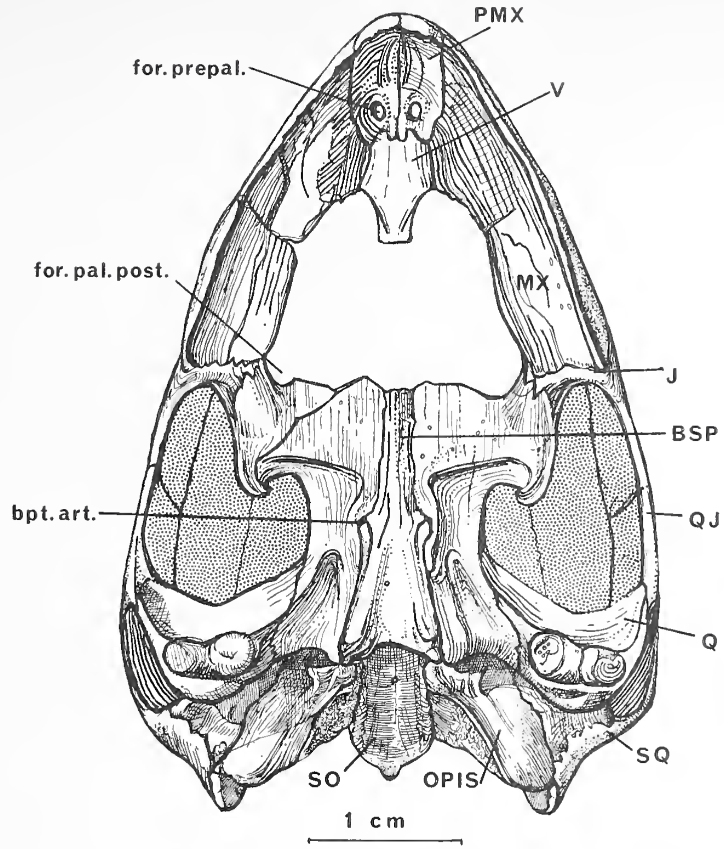
sutural contact with the dorsal process of the maxilla, and so forms the anterior wall of the orbit. The ventral end of the process contacts the vomer.

Postorbital. The anterior end of the postorbital is thickened to form the hind wall of the orbit, but otherwise the bone is thin and makes simple sutures with the adjacent bones.

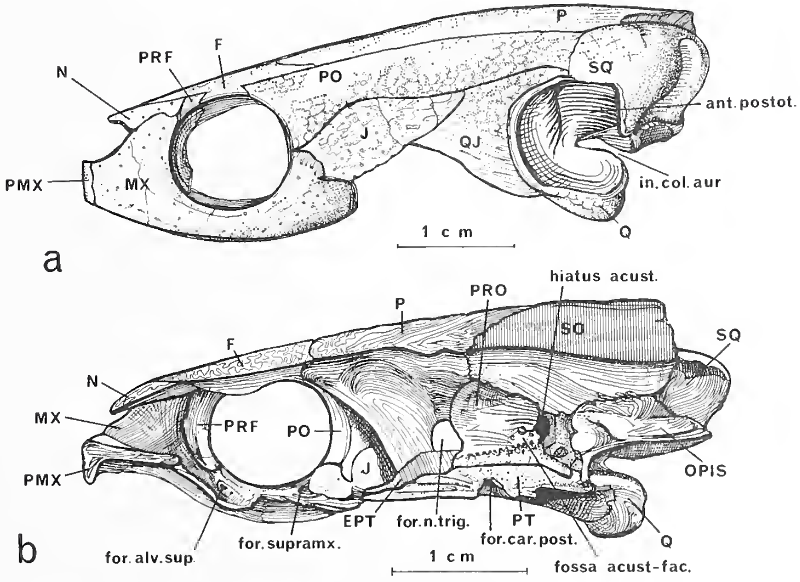
Jugal. The small jugal is greatly thickened anteriorly, where it forms a short portion of the posterior wall of the orbit (text-fig. 3*b*) between the postorbital and the maxilla. However, it barely enters the orbital margin as seen in lateral view (text-fig. 3*a*) because of a superficial extension of the maxilla towards the postorbital. It has a short, stout postero-medial process contacting the pterygoid and behind this region it forms a thin sheet.

Quadratojugal. The quadratojugal is a thin, simple bone of characteristic chelonian form, curving postero-dorsally in contact with the lateral edge of the quadrate.

Squamosal. As in typical advanced chelonians, the squamosal has a ventral extension behind the quadrate forming the posterior wall of the antrum postoticum, and bearing a broad, shallow groove on its posterior face for the depressor mandibuli muscle. The medial part of the squamosal extends inwards a short way, capping the medial extension of the quadrate, and it also makes an edge-to-edge contact with the opisthotic along the dorso-lateral part of that bone.



TEXT-FIG. 2. *Mesochelys durlstonensis.* Skull, slightly restored, in ventral view.



TEXT-FIG. 3. *Mesochelys durlstonensis. a*, skull, slightly restored, in lateral view. *b*, internal view of skull from mid-sagittal view.

Bones of the palate

Premaxilla. The premaxillae are small, paired bones completely lacking an internarial process and together forming a serrated continuation of the labial ridges of the maxillae. The foramen praepalatinum in the palatal surface is towards the posterior edge of the premaxilla, and on the dorsal surface at the anterior edge there is a single, median pit.

Maxilla. The facial exposure of the maxilla is extensive and forms some two-thirds of the external orbital margin, although this bone contributes only the floor of the fossa orbitonasalis. The foramen supramaxillare opens into the posterior part of the floor of the fossa just in front of the suture of the maxilla with the jugal, while the foramen alveolare superius opens into the anterior end of the floor immediately below the descending process of the prefrontal.

The triturating surface of the maxilla is narrow and is only slightly expanded posteriorly. The labial ridge is sharp and well developed along the lateral edge but medially the tomial ridge is negligible.

Vomer. Only the anterior part of the vomer is preserved, as a small median bone with a concave ventral surface and a dorsal surface divided by the medial sulcus vomeri on either side of which is a small boss for contact with the descending process of the prefrontal.

Palatine. Both palatines are missing. However, the position of the apertura narium interna between the palatine, maxilla, and vomer can be inferred from the edges of it on the latter two bones; and similarly, part of the margin of the foramen palatinum posterius between the palatine and the pterygoid remains preserved on the latter. The sizes of these two respective apertures cannot, however, be ascertained with any accuracy.

Pterygoid. The basisphenoid completely separates the paired pterygoids from one another. Each pterygoid is in sutural contact with the full length of the basisphenoid and the sutural faces are oblique, so that the dorsal surface of the basisphenoid is wider than the ventral surface (text-fig. 5). Two points are of particular interest. First, the anterior part of the contact is very much narrower dorso-ventrally than the posterior part, and indeed is no more than an edge-to-edge contact at the very front. Second, the remnant of the primitive basipterygoid articulation can be discerned at about mid-length along the ventral surface of the basisphenoid, where a small lateral spur, the basipterygoid process, fits into a distinct pit (text-fig. 3) in the ventro-medial edge of the pterygoid.

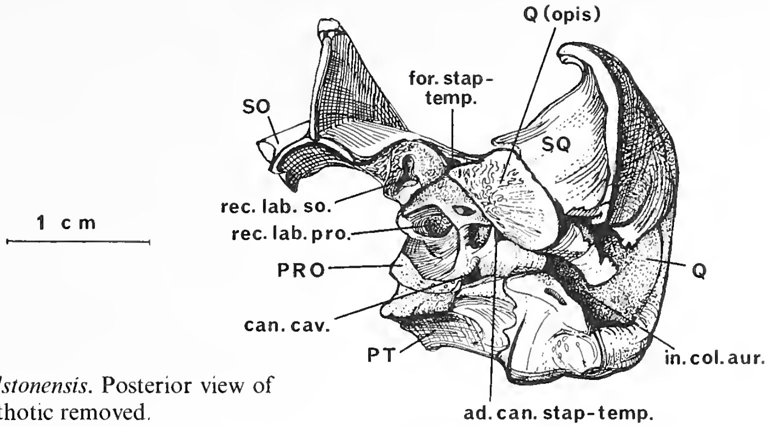
The processus pterygoideus externus is well developed and bears a slight ridge (text-fig. 2) parallel to its posterior edge, presumably marking the anterior limit of origin of pterygoideus muscle fibres. The ridge turns posteriorly alongside the medial edge of the pterygoid and terminates at the level of the basipterygoid articulation.

The antero-lateral part of the pterygoid bears a large, antero-laterally facing pit into which fits the palatal process of the jugal. The maxilla also contacts the pterygoid in this region. The dorsal surface of the pterygoid meets the small, thin epipterygoid anteriorly and has a long horizontal suture with the prootic posteriorly (text-fig. 3*b*). Posteriorly the pterygoid rises up slightly to overlap the outer face of the prootic a little.

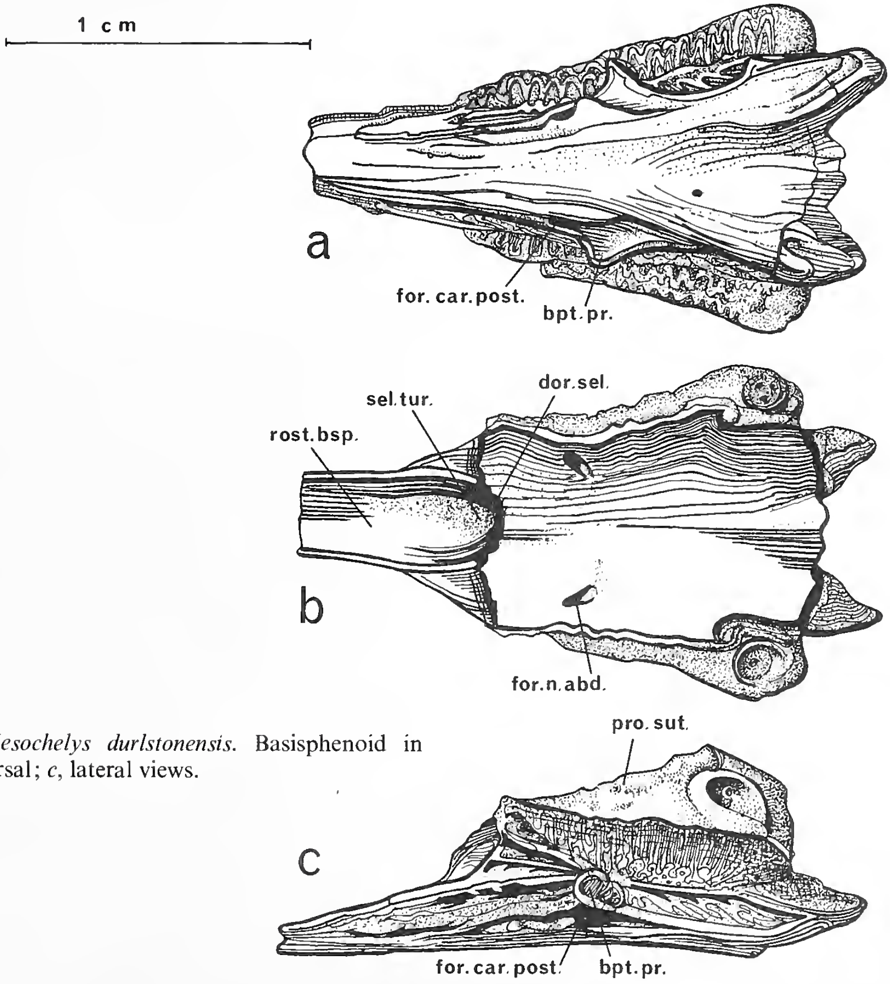
The quadrate ramus of the pterygoid expands ventro-medially to form a horizontal process which partially floors the cavum acustico-jugularis, although much less extensively than in typical modern chelonians. The lateral side of the quadrate ramus is deeper and is completely overlapped by the lower part of the antero-medial wing of the quadrate.

The dorsal surface of the pterygoid shows the typical chelonian form. It has a broad sulcus cavernosus running backwards just lateral to the basisphenoid and becoming the canalis cavernosus where it is roofed over by the prootic. The canal emerges posteriorly into the cavum acustico-jugulare (text-fig. 4). A small ventral foramen lies just behind and lateral to the basipterygoid articulation, and is presumably the foramen pro ramo nervi vidiani which would lead through the pterygoid into the canalis cavernosus, although this cannot be positively confirmed in the specimen. A second foramen opens into the pit for reception of the basipterygoid process. It leads anteriorly and is probably therefore the posterior opening of the canalis nervi vidiani; the anterior opening of this canal lies on the dorsal surface of the pterygoid, lateral to the sulcus cavernosus and towards the anterior end.

Epipterygoid. Both the epipterygoids are damaged slightly. Each is a low, thin plate lying immediately lateral to the sulcus cavernosus of the pterygoid and connecting that bone to the parietal, as noted earlier (text-fig. 3*b*).



TEXT-FIG. 4. *Mesochelys durlstonensis*. Posterior view of right side of skull, with opisthotic removed.

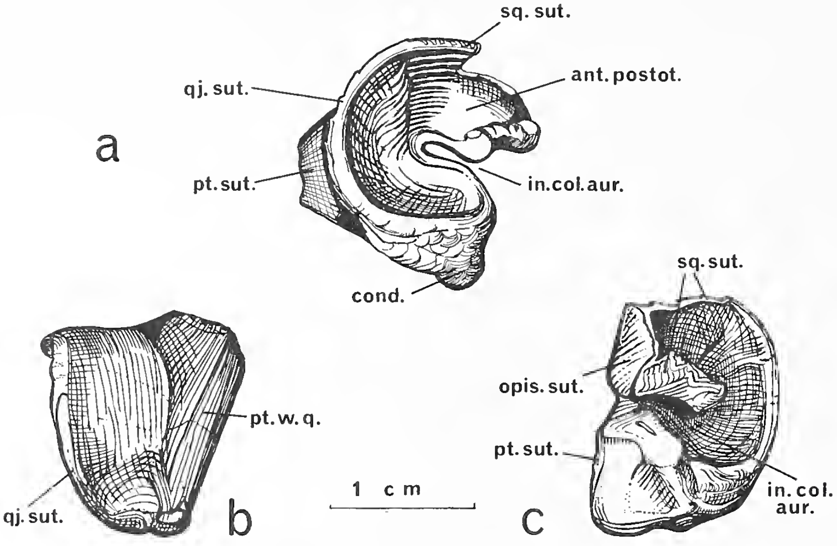


TEXT-FIG. 5. *Mesochelys durlstonensis*. Basisphenoid in *a*, ventral; *b*, dorsal; *c*, lateral views.

Quadrate. The quadrate (text-fig. 6) resembles that of typical modern chelonians. It is very stout and strongly curved to form a deeply concave cavum tympani. The dorsal part continues the curve backwards and downwards to make a prominent antrum postoticum and to reduce the incisura columellae auris to a narrow slit. The articulating condyle is short from front to back and is double, the convex medial part being slightly better developed than the almost flat lateral part.

The curved antero-lateral edge sutures with the thin quadratojugal while the whole width of the dorsal part is capped by the squamosal. Again as in modern forms, the medial part of the quadrate forms a high vertical wing sutured to the pterygoid below, to the prootic antero-dorsally, and by a postero-laterally running suture to the opisthotic behind.

Two canals leading into the cavum acustico-jugulare are formed in part by the quadrate. The canalis stapedio-temporalis runs between the quadrate and the prootic from the roof of the braincase in the temporal fossa into the dorso-lateral part of the cavum; and quadrate forms the dorso-lateral wall of the canalis cavernosis where it emerges into the ventro-lateral region of the cavum.



TEXT-FIG. 6. *Mesochelys durlstonensis.* Left quadrate in *a*, lateral; *b*, anterior; *c*, posterior views.

Bones of the braincase

Basioccipital and exoccipital. These are completely missing. The existing sutural surfaces indicate that the basioccipital met the basisphenoid in a more or less transverse suture, and furthermore that it barely made contact with the pterygoid or otic bones. The exoccipital met the opisthotic by an extensive postero-laterally inclined suture and it also made a much more limited attachment to the supraoccipital.

Supraoccipital. The supraoccipital has a high but thin median keel which abruptly flares out below as the broad braincase roof (text-fig. 4). The crista supraoccipitalis is not developed posterior to the parietal although this could be a result of breakage during preservation. The paired parietals completely cover the anterior one-third of the supraoccipital. The normal series of lateral sutures between the supraoccipital and the prootic, opisthotic, and exoccipital respectively are present.

The middle region of the lateral edge forms the dorsal edge of the unossified hiatus acusticus and the notch which represents the foramen aquaducti vestibuli is perfectly preserved on the left side of the specimen (text-fig. 3*b*). There is a well-developed recessus labyrinthicus supraoccipitalis (text-fig. 4) showing the union of the anterior semicircular canal, most of which is in the prootic, with the posterior semicircular canal of the opisthotic.

Basisphenoid (text-fig. 5). In this account no attempt to distinguish a parasphenoid from a basisphenoid is made since the two are in fact indistinguishable.

The important relationship between the basisphenoid and the pterygoids has been described earlier. There is a transverse suture face extended posteriorly by a pair of ventral spurs for attachment of the (missing) basioccipital. The prootic contacts the basisphenoid along a horizontal line in the postero-dorsal region, behind which is a short facet for contact with the opisthotic.

The dorsal surface is quite strongly concave from side to side and is in two distinct parts. The broader posterior part terminates as the feebly developed dorsum sellae in front of which is the sella turcica at a lower level. The side walls of the sella peter out anteriorly leaving the rostrum of the basisphenoid as a thin process, slightly concave from side to side.

The foramen posterior canalis carotici interni is on the ventro-lateral margin of the basisphenoid at about mid-length, alongside the basipterygoid process. The corresponding anterior foramen lies at the base of the sella turcica. A pair of small anterior foramina nervi abducens enter the dorsal surface of the basisphenoid a little behind the dorsum sellae and the canals emerge alongside the sella turcica.

Prootic. The prootic rises more or less vertically from its horizontal suture with the dorsal surface of the pterygoid to its contacts with the parietal, which overlaps it laterally, and with the supraoccipital (text-fig. 3*b*). The free anterior edge of the prootic is smoothly rounded, forming the posterior margin of the foramen nervi trigemini, and a depression in the lower part of the medial face is the fossa acustico-facialis bearing three foramina, a large anterior one for the facial nerve and a large dorsal one plus a small ventral one for two branches of the acustic nerve.

The posterior part of the prootic is expanded and houses the recessus labyrinthicus prooticus in typical chelonian fashion, freely confluent with the more lateral cavum acustico-jugulare (text-fig. 4).

The dorsal and lateral surfaces of the prootic suture with the quadrate; the contact with the opisthotic is restricted to the upper part of the posterior face of the prootic, the fenestra ovalis laterally and the hiatus acusticus medially separating these two bones.

Opisthotic. The stout paroccipital process runs postero-laterally in broad contact with the quadrate anteriorly, and also just touching the free medial edge of the squamosal. The dorsal surface is in the form of a deep trough and the medial surface bears an extensive sutural facet for the (missing) exoccipital.

The medial part of the opisthotic is expanded, sutures with the supraoccipital above, the prootic anteriorly and just with the pterygoid ventrally, and it carries the recessus labyrinthicus opisthoticus of normal chelonian form. The position of the foramen jugulare anterius is indicated by a smooth groove just in front of the facet for the exoccipital and thus the foramen must have lain between these two bones.

Postcranial skeleton

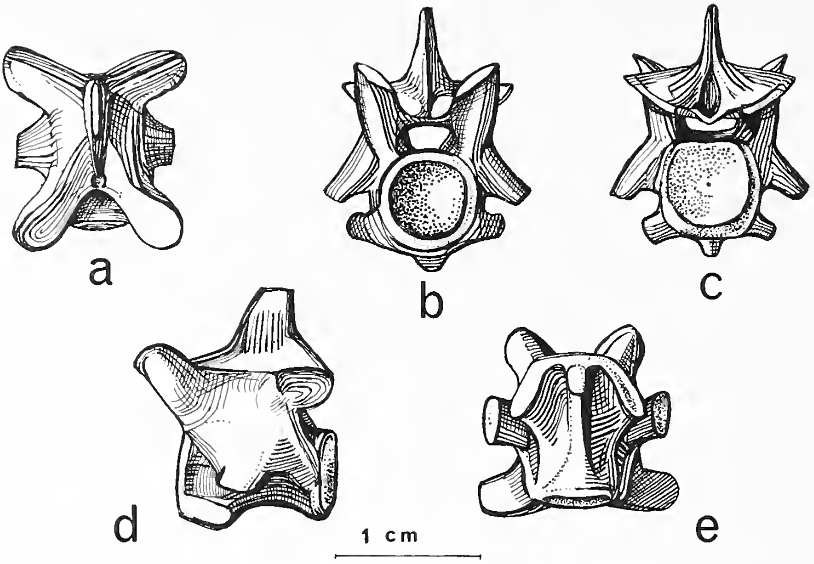
A very incomplete postcranial skeleton is associated with the skull, consisting of parts of the shell, one cervical and a few caudal vertebrae, a radius, an ulna, the left ilium and pubis, the left femur and tibia, and a number of indeterminate phalanges.

Shell (Pl. 5). The over-all form of the shell is flattened. Both the carapace and the plastron are very incomplete but, nevertheless, a number of useful features are to be seen. Of the carapace, a fairly substantial piece remains showing part of the margin including a more or less complete marginal bone. This is important because it shows a characteristic emargination of the edge of the bone itself, a character not present in many Upper Jurassic and Purbeck turtles. The ornamentation of the dorsal surface is very fine, consisting of very small pits at the centre of the scutes and more elongated, almost imperceptible markings towards the edges. The lines indicating the positions of the horny scutes are narrow, very shallow grooves.

Of the plastron, only the incomplete left xiphiplastron bone is recognizable. It does, however, show a characteristic form. The lateral margin is almost straight to the posterior corner, where it turns sharply medially. The posterior edge is markedly concave. The ornamentation of this region of the plastron is very similar to that of the carapace bones.

For the rest, the shell consists of broken, indeterminate fragments of both carapace and plastron, which add no further details of taxonomic value.

Vertebrae. A single cervical vertebra (text-fig. 7) is preserved. The neural arch is broad and rather flat and the respective pre- and postzygapophyses are widely spaced. The neural spine is small and posteriorly placed and the transverse process, also short, points ventro-laterally. The whole of the neural arch is attached to the centrum by an unfused suture. The centrum is circular in section with a mid-ventral keel developed along the anterior half. The anterior face of the centrum is concave, but not notochordal, while



TEXT-FIG. 7. *Mesochelys durlstonensis*. Cervical vertebra in *a*, dorsal; *b*, anterior; *c*, posterior; *d*, lateral; *e*, ventral views.

the posterior face is almost flat. The lower lateral part of the anterior face is produced postero-laterally as a smooth facet presumably for the reception of a free cervical rib.

About five caudal vertebrae remain but all are badly damaged. In general they are small and elongated.

A single very small haemal arch is present.

Forelimb. The only identifiable remains are the right radius and the left ulna. The radius has a strongly flattened head which expands medially. The lower end is only slightly expanded.

The ulna is of about the same thickness as the radius. Its head is less expanded and it bears a small olecranon process. Its distal end is a convex roller shape.

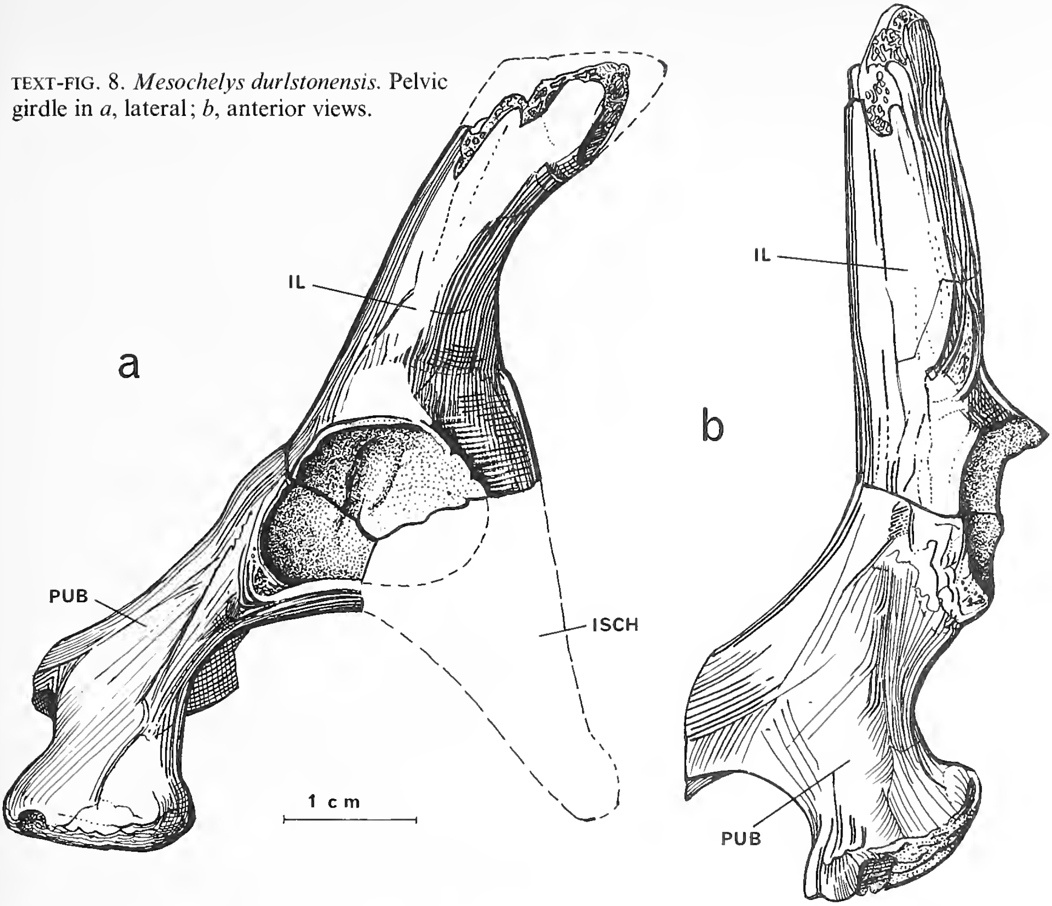
Pelvic girdle. The ilium and the pubis of the left side are almost complete but the ischium is absent except for a possible fragment (text-fig. 8). The general structure is very like that described by Hay (1908) for *Glyptops plicatulus*. The ilium is a narrow process inclined strongly postero-dorsally and more or less circular in cross-section. The distal tip is damaged. The ventral end expands to form the dorsal part of the acetabulum and to make broad buttressing sutures with the ventral pelvic bones.

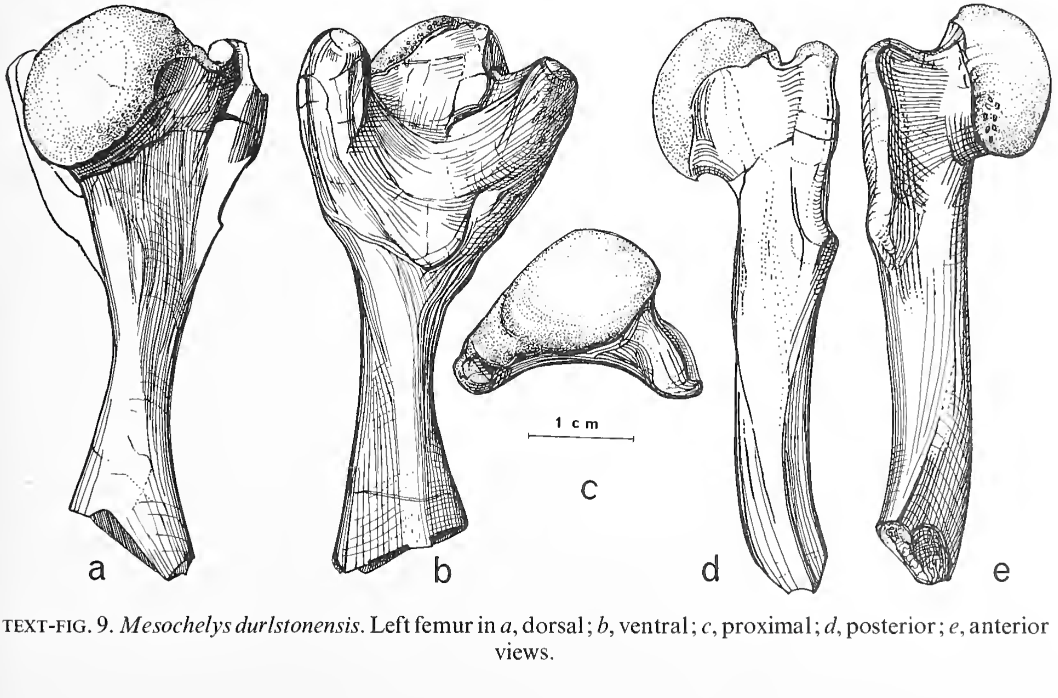
The pubis is stout and consists of a thick dorsal part, triangular in section, forming the anterior part of the acetabulum and carrying a stout, plate-like lateral process ending in a rugose cap that presumably made a ligamentous connection with the plastron. The medially directed process of the pubis is a thin, flat plate which lies at an approximate right angle to the lateral process. The medial part of the process is damaged but presumably formed a pubic symphysis with its fellow, and the posterior edge is finished in a manner indicating the presence of a large thyroid fenestra.

Hindlimb. Only the femur (text-fig. 9) and tibia of the left side are preserved. The femur has the very characteristic chelonian form of a large hemispherical head set to face dorsally. The anterior and posterior trochanters are also very large and developed to about the same extent as one another. Between them, on the ventral surface, is a broad fossa. The shaft narrows rather abruptly distal to the trochanters and then starts to widen again towards the distal end.

The tibia is not well preserved. Its head is expanded and flattened, and bears a well-developed cnemial crest on its mid-dorsal surface. The distal end is an incipiently double convex roller surface.

TEXT-FIG. 8. *Mesochelys durlstonensis.* Pelvic girdle in *a*, lateral; *b*, anterior views.





TEXT-FIG. 9. *Mesochelys durlstonensis.* Left femur in *a*, dorsal; *b*, ventral; *c*, proximal; *d*, posterior; *e*, anterior views.

DISCUSSION

In 1889 Lydekker erected a suborder Amphichelydia for those turtles which had not developed the distinctive features of either of the two living suborders, Cryptodira and Pleurodira. In more recent years it has become widely accepted that the Amphichelydia is an artificial taxon for generally primitive, mainly Mesozoic turtles which cannot as yet be allotted to their true respective phylogenetic places as primitive cryptodires, primitive pleurodires, or short-lived sidelines of chelonian evolution. The work of interpreting the amphichelydians in a more sophisticated way, work which must involve increasing knowledge of skull structure, has commenced largely as a result of two papers. Parsons and Williams (1961) studied the cranial anatomy of two Upper Jurassic forms from Portland and Solnhofen respectively and compared them with the extremely primitive Upper Triassic turtle *Proganochelys*. They concluded that the Upper Jurassic forms were essentially modern in skull structure and indeed they were unable to demonstrate a single character that was not represented in at least some of the extant turtles. This contrasted with the very primitive nature of the skull of *Proganochelys* and illustrated the imbalance of associating the Upper Jurassic forms with *Proganochelys* in a single sub-Order Amphichelydia to the exclusion of all the modern species. Parsons and Williams also noted that, to judge from the differences between their two forms, the Chelonia had already undergone a significant radiation by Upper Jurassic times.

The second important contribution to amphichelydian study was that of Gaffney (1972*a*) on the baenids, a group appearing in the Lower Cretaceous and hitherto regarded as relatively advanced amphichelydians. Quoting from his unpublished thesis (Gaffney, E. S. 1969, 'The North American Baenoidea and the cryptodire–pleurodire dichotomy', Ph.D. thesis, Columbia University, New York) Gaffney concluded that the Cryptodira can be distinguished from the Pleurodira on a number of very marked skull characters which appear to indicate a fundamental and presumably early dichotomy between the two groups, and that on these criteria the baenids must be regarded as members of the Cryptodira, despite their lack of the specializations of the postcranial skeleton found in living cryptodires. Furthermore, Gaffney showed that the Upper Jurassic form *Glyptops plicatulus* has a cryptodiran skull too. His taxonomic conclusion was that *Glyptops* and the baenids should be removed from the Amphichelydia and placed as the most primitive superfamily of the Cryptodira viz.

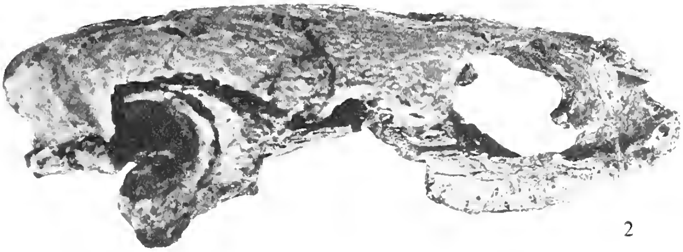
Suborder: CRYPTODIRA
  Superfamily: BAENOIDEA
    Families: GLYPTOPIDAE
      BAENIDAE.

Glyptops is seen as the direct ancestor of the baenids.

EXPLANATION OF PLATE 4

Figs. 1–4. *Mesochelys durlstonensis* gen. et sp. nov. Skull of holotype. Cambridge University, Museum of Zoology, T 1041. 1, left lateral view. 2, right lateral view. 3, dorsal view. 4, ventral view, × 1·5.

1



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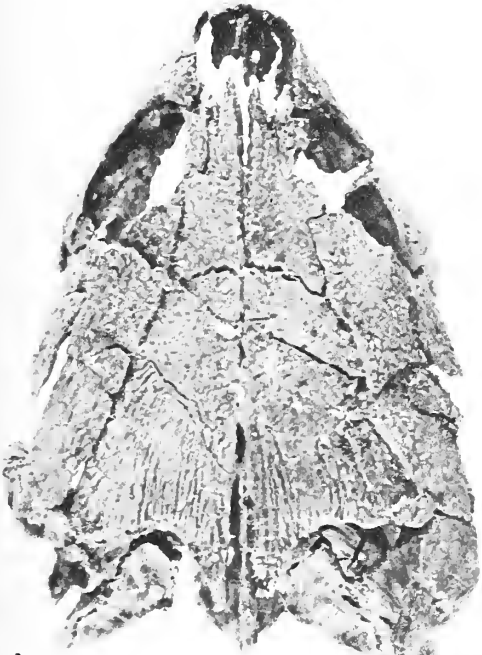

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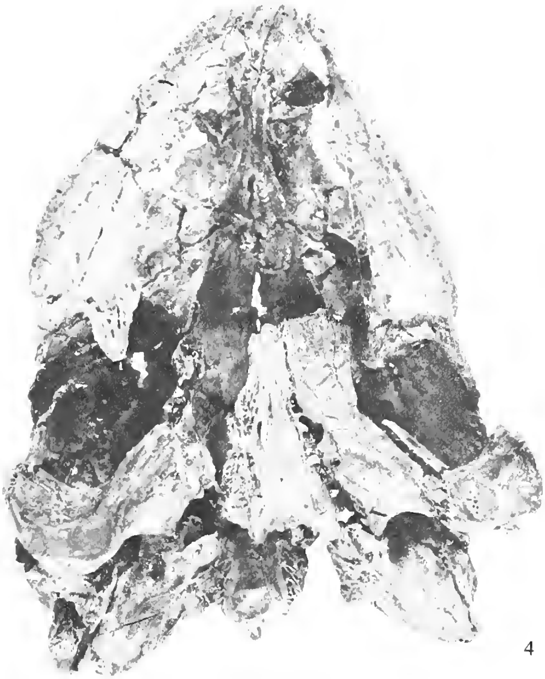

4

EVANS and KEMP, *Mesochelys*

The skull structure of *Mesochelys durlstonensis* indicates that it, too, is a cryptodire, that it is closely related to *Glyptops* and can thus be accommodated in the family Glyptopidae, and that it is, in fact, the most primitive turtle known subsequent to *Proganochelys*.

Of the diagnostic characters of the Cryptodira used by Gaffney (1972*a*), the following can be positively demonstrated in *Mesochelys*.

1. The position of the trochlea for the cartlago transiliens (sliding cartilage of the adductor tendon) is on the anterior edge of the otic chamber and not on a process of the pterygoid.
2. The pterygoid extends posteriorly between the quadrate and the braincase.
3. There is no canal separate from the canalis cavernosus whereby the hyomandibular branch of the facial nerve crosses the equivalent of the cranio-quadrate space. (In Gaffney (1972*a*, p. 249) this character is mis-stated. 'Hyomandibular nerve in its own canal . . .' should presumably read 'Hyomandibular nerve *not* in its own canal . . .' (Gaffney, pers. comm.).
4. Ossified epipterygoid present.
5. Foramen palatinus posterius is in the floor of the fossa orbitalis.
6. Canal for the vidian nerve ends just behind the foramen palatinum posterius.
7. Foramen supramaxillare present.
8. Descending process of the prefrontal meeting the vomer ventro-medially present.
9. Only the position of the mandibular artery and features of the lower jaw are indeterminate in the skull of *Mesochelys*.

The features of the skull of *Mesochelys* which are probably primitive include particularly the organization of the basicranial axis. The basisphenoid completely separates the two pterygoids. At about mid-length along the suture, the basipterygoid articulation can be recognized in the form of a small spur of the lateral face of the basisphenoid fitting into a distinct pit in the medial face of the pterygoid. Anterior to this, the connection between the basisphenoid and each pterygoid is a very thin contact suggesting the relatively recent closure of an interpterygoid vacuity of the basic reptilian type noted in *Proganochelys* by Parsons and Williams (1961). The position of the foramen posterior canalis carotici interni at the level of the basipterygoid articulation is also a primitive reptilian character. Thus, although the nature of the suturing of the basicranial axis to the pterygoid is unquestionably chelonian in nature, the structure of this region in *Mesochelys* shows a greater similarity to the reptilian condition than in other turtles apart from *Proganochelys*. *Glyptops plicatulus*, however, appears to have a similar condition because although not known in detail yet, the basisphenoid does separate the pterygoids completely, and the position of the foramen posterior canalis carotic interni is about half-way down the length of that bone (Gaffney 1972*a* and pers. comm.).

A second primitive feature of *Mesochelys* which is shared by *Glyptops* is the failure of the pterygoid completely to floor the cavum acustico-jugularis, correlated with an extremely limited contact between the pterygoid and the basioccipital bone.

Thirdly, the pattern of roofing bones of the skull of *Mesochelys* is primitive in so far as it has certain basic reptilian features not found in combination in other turtles.

EXPLANATION OF PLATE 5

Figs. 1–4. *Mesochelys durlstonensis* gen. et sp. nov. Shell fragments of holotype. 1, fragment of carapace in external view. 2, same in internal view. 3, left xiphisternal region of plastron in external view. 4, same in internal view, × 0·8.

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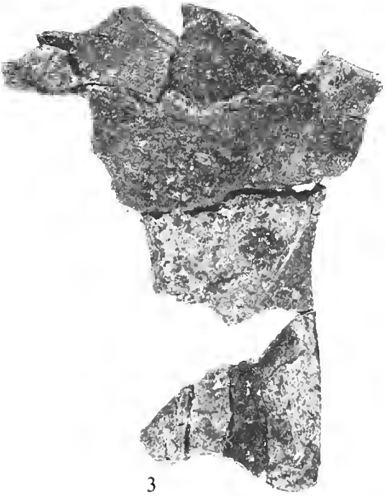

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2

4

EVANS and KEMP, *Mesochelys*

A pair of nasal bones are present which make extensive contact with the frontals, and the dorsal exposure of each prefrontal is moderate, neither expanding to meet its fellow in the mid-line as in Parsons and Williams's Portland skull, nor being reduced as in typical baenids (Gaffney 1972*a*). The skull of *Glyptops* is slightly more specialized in that its maxillae meet medially and thus prevent the nasals from meeting the frontals (Gaffney manuscript). The prefrontal of *Glyptops*, however, is similar to that of *Mesochelys*.

These three primitive characters are not yet known in Jurassic or later turtles outside *Mesochelys* and *Glyptops* and, together with ossified epipterygoids, the narrow triturating surfaces (both probably primitive chelonian characters but which can be found in members of some later groups) relate the two genera in a family, Glyptopidae which is the most archaic family within the Cryptodira. Of the two, *Glyptops* is the more specialized, with a rather longer, narrower skull than *Mesochelys* and with the maxillae meeting in a brief contact mid-dorsally. The jugal is excluded from the orbital margin by a substantial contact between the postorbital and maxilla bones on the side of the skull. The most significant difference from *Mesochelys*, however, according to Gaffney's (manuscript and pers. comm.) account, is the shape of the quadrate bone. *Glyptops* is shown as lacking a postero-ventral extension of its quadrate so that an antrum postoticum is not developed. This is in marked contrast to the typical chelonian type of quadrate of *Mesochelys*. However, Gaffney notes that this region of his *Glyptops* material is badly damaged and so, in the light of the close correspondence of skull structure in these two forms in all other respects, it does seem likely that the appearance of the *Glyptops* quadrate is a result of this damage.

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BAJOCIAN SONNINIIDAE AND OTHER AMMONITES FROM WESTERN SCOTLAND

by NICOL MORTON

ABSTRACT. The sequence of Bajocian ammonites in the Bearreraig Sandstone of Skye is summarized in terms of a modified scheme of zones or subzones: Discites, Ovalis, Laeviuscula, Sauzei (with subzone Sauzei and a new upper subzone Hebridica), and Humphriesianum (with subzones Cycloides, Humphriesianum, and Blagdeni). The first three are used informally to replace Sowerbyi, but Sauzei and Humphriesianum, with subzones as above, can be regarded as part of a formal Lower Bajocian zonal scheme. Upper Bajocian zones cannot yet be distinguished in Skye. Part of the family Sonniniidae is modified and discussed, and the species of *Euhoploceras* (with subgenera *Euhoploceras* and *Fissilobiceras*), *Shirbuirnia*, *Witchellia*, *Pelekodites*, *Sonninia* (with subgenera *Sonninia* and *Papilliceras*), and *Dorsetensia* which are present in western Scotland are described, together with some other ammonites. There is clear dimorphism in some of the faunas, for example *Witchellia* (M) and *Pelekodites* (m), but *Pelekodites* (m) also occurs with *Sonninia* (M+?m), and pairing of dimorphs is obscure and so not attempted. Some species in Scotland are slightly dwarfed in comparison with other parts of Europe.

BAJOCIAN ammonites occur in western Scotland mainly in the Bearreraig Sandstone in the Trotternish peninsula of the Isle of Skye, although they have also been recorded in Mull (Lee and Bailey 1925). The fauna is dominated by species of stephanoceratids (Morton 1971*a*) and sonniniids (Morton 1972, 1973), and the purpose of this paper is to describe the Sonniniidae and some other Bajocian ammonites.

The specimens described are mainly in the collections of the Hunterian Museum, University of Glasgow (HM), but some are from the collections of the Institute of Geological Sciences, Edinburgh (GSE), Dr. J. H. Callomon, London (Call.) and the Department of Geology, Birkbeck College, London (BkC).

STRATIGRAPHY

The lithostratigraphy is based on Morton (1965, 1969) (see also Lee 1920 and Anderson and Dunham 1966). The sequence of faunas and their zonal or subzonal position (see Table 1) are:

1. Bearreraig Burn section; 17 m above base of Shaly Sandstones: *Euhoploceras* (*E.*) ?*dominans* (Buckman), *E.* (*E.*) *marginata* (Buckman)—top of Concavum Zone (Aalenian) or base of Discites Zone (*Hyperlioceras* sp. occurs 1–2 m higher).

2. Bearreraig Burn section; 26 m, 27 m, and 29 m below top of Shaly Sandstones (44 m above base): *Euhoploceras* (*E.*) spp. (? cf. *modestum* (Buckman) and ? cf. *costatum* (Buckman))—Discites Zone.

3. Bearreraig Burn section and foot of high cliff 400 m south of Bearreraig; top 2–3 m of Shaly Sandstones: *Euhoploceras* (*Fissilobiceras*) *fissilobatum* (Waagen), *E.* (*E.*) sp. (? cf. *adicrum* (Waagen)), *Shirbuirnia trigonalis* Buckman—Ovalis Zone.

4. Bearreraig Burn section; 18 m below top of Massive Sandstones: *Witchellia* aff. *rubra* (Buckman), *W.* aff. *laeviuscula* (Sowerby), *W.* aff. *romanoides* (Douvillé), *Pelekodites zurcheri* (Douvillé), *P. macer* (Buckman), *P. minimus* (Hiltermann), *Sonninia* (*S.*) *corrugata* (Sowerby), *Emileia* (*Otoites*) sp. nov.—Laeviuscula Zone (also loose *Sonninia* (*Papilliceras*) *arenata* (Quenstedt) from Sauzei Zone).

5. Rudha Sughar, Bearreraig; loose blocks from top 10–12 m of Massive Sandstones: *Sonninia* (*S.*)

[Palaeontology, Vol. 18, Part 1, 1975, pp. 41–91, pls. 6–17.]

cf. *sowerbyi* (Sowerby), *S.* (*S.*) cf. *propinquans* (Bayle), *S.* (*S.*) *corrugata* (Sowerby), *S.* (*Papilliceras*) *arenata* (Quenstedt), *S.* (*P.*) *mesacantha* (Waagen), *Pelekodites macer* (Buckman), *Strigoceras bessinum* Brasil, *Emileia* (*E.*) sp.—Sauzei Zone and Subzone. A single specimen of *Witchellia* aff. *rubra* (Buckman) suggests that some Laeviuscula Zone may also be present.

6. Torvaig, near Portree; basal bed of Upper Sandstones: *Stephanoceras* (*St.*) *nodosum* (Quenstedt), *St.* (*St.*) aff. *nodosum* and aff. *macrum* (Quenstedt), ?*Chondroceras evolvescens* (Waagen), *Lissoceras oolithicum* (d'Orbigny), *Dorsetensia pinguis* (Roemer), *D. hannoverana* (Hiltermann), *D. hebridica* Morton, '*Sonninia*' aff. *furticarinata* (Quenstedt)—Hebridica Subzone, Sauzei Zone. Formerly placed (Morton 1971*a*, 1972) in the lower part of the Humphriesianum Zone, the basal part of the Upper Sandstones containing this fauna is now excluded from the Humphriesianum Zone and placed in the Sauzei Zone as a new subzone. It can be correlated with the Pinguis-Schichten of northern Germany (see Huf 1968; Westermann 1967, p. 123).

7. Rigg shore; lower part of Upper Sandstones:

(*a*) Near waterfall and southwards along shore: *Oppelia* (*O.*) ?*subradiata* (Sowerby), *Stephanoceras* (*St.*) *mutabile* (Quenstedt), *St.* (*St.*) *nodosum* (Quenstedt), *St.* (*St.*) sp., *St.* (*Normannites*) ?*orbignyi* (Buckman), *St.* (*N.*) ?*densum* (Buckman), *Chondroceras evolvescens* (Waagen), *Dorsetensia liostraca* Buckman, *D. romani* (Oppel), '*Sonninia*' aff. *furticarinata* (Quenstedt), *Poecilomorphus cycloides* (d'Orbigny)—Cycloides Subzone, Humphriesianum Zone.

(*b*) North of waterfall, stratigraphically higher than (*a*): *Stephanoceras* (*St.*) *mutabile* (Quenstedt), *St.* (*St.*) aff. *triplex* Weisert, *St.* (*Normannites*) ?*orbignyi* (Buckman), *St.* (*N.*) ?*densum* (Buckman)—Humphriesianum Subzone, Humphriesianum Zone.

8. Rudha Sughar, Bearreraig; loose blocks from basal 30 m of Upper Sandstones: *Oppelia* (*O.*) ?*subradiata* (Sowerby), *Stephanoceras* (*St.*) *mutabile* (Quenstedt), *St.* (*St.*) aff. *brodiaei* (Sowerby), *St.* (*St.*) aff. *nodosum* and aff. *macrum* (Quenstedt), *St.* (*St.*) aff. *triplex* Weisert, *St.* (*St.*) *pyritosum* (Quenstedt), *St.* (*Normannites*) ?*orbignyi* (Buckman), *Dorsetensia liostraca* Buckman, *D. romani* (Oppel), *D. pinguis* (Roemer), '*Sonninia*' aff. *furticarinata* (Quenstedt)—Hebridica Subzone, Sauzei Zone and Cycloides and Humphriesianum Subzones, Humphriesianum Zone.

9. Pipe-line cutting at Bearreraig; 30 m above base of Upper Sandstones: *Stephanoceras* (*St.*) *pyritosum* (Quenstedt), *St.* (*St.*) aff. *triplex* Weisert, *St.* (*Normannites*) sp.—Humphriesianum Zone and Subzone.

10. Pipe-line cutting at Bearreraig; 4 m above fauna 9, 34 m above base of Upper Sandstones: *Teloceras* (*T.*) *blagdeni* (Sowerby)—Blagdeni Subzone, Humphriesianum Zone.

Apparent ranges of species occurring in the Upper Sandstones (excluding fauna 8) are:

	Hebridica	Cycloides	Humphriesianum	Blagdeni
Oppelia (*O.*) ?*subradiata*		×		
Lissoceras oolithicum	×			
Stephanoceras (*St.*) *nodosum*	×	×		
St. (*St.*) aff. *nodosum* and aff. *macrum*	×	×		
St. (*St.*) *mutabile*		×	×	
St. (*St.*) aff. *triplex*			×	
St. (*St.*) *pyritosum*			×	
St. (*N.*) ?*orbignyi*		×	×	
St. (*N.*) ?*densum*		×		
Teloceras (*T.*) *blagdeni*				×
Chondroceras evolvescens	?	×		
Dorsetensia liostraca		×		
D. romani		×		
D. pinguis	×			
D. hannoverana	×			
D. hebridica	×			
'*Sonninia*' aff. *furticarinata*	×	×		
Poecilomorphus cycloides		×		

11. Bearreraig; loose block presumably from upper part of Upper Sandstones, found by Dr. J. K. Wright: *Garantiana* (*G.*) ?*baculata* (Quenstedt) (i.e. = Morton 1971*a*, p. 287)—Subfurcatum or lower part of Garantiana Zone. (HMS 26429—pl. 16, figs. 9–10.)

12. Prince Charles's Cave; Garantiana Clay: *Garantiana* (*G.*) ?*baculata* (Quenstedt) (Morton 1971*a*, p. 287) or *Pseudogarantiana dichotoma* (Bentz) (Pavia 1973, p. 110)—Subfurcatum or lower part of Garantiana Zone.

TABLE 1. Divisions of the Bajocian Stage recognized in western Scotland

SUBSTAGES	ZONES OR SUBZONES	
Upper Bajocian	Garantiana or Subfurcatum	
Lower Bajocian	Humphriesianum	Blagdeni
		Humphriesianum
		Cycloides
	Sauzei	Hebridica
		Sauzei
	Laeviuscula	
	Ovalis	
	Discites	

DIMENSIONS

Below is a full list of the dimensions given, though not all are appropriate for every species described (all lengths are in mm):

D	Diameter of specimen.
Wh	Whorl height $\left(H = \frac{Wh \times 100}{D}\right)$.
Wb	Whorl breadth $\left(B = \frac{Wb \times 100}{D}\right)$.
W	A measure of whorl shape $= \frac{Wb \times 100}{Wh}$.
Ud	Diameter of umbilicus $\left(U = \frac{Ud \times 100}{D}\right)$.
Vw	Width of venter, in round brackets where the edges of the venter are not distinct $\left(V = \frac{Vw \times 100}{D};\ Vb = \frac{Vw \times 100}{Wb}\right)$.
Rd	Average distance between ribs where Wh was measured $\left(R = \frac{Rd \times 100}{D}\right)$, using prefixes ${}^{p}R$ and ${}^{s}R$ where appropriate to indicate primary or secondary ribs respectively.
Rn	Number of ribs per whorl or part of whorl as specified, counting from the point where Wh was measured towards the apex.
Td	Average distance between tubercles where Wh was measured $\left(T = \frac{Td \times 100}{D}\right)$. A 'd' for Td, Tn, and Tc indicates that the tubercles decline within the distance normally measured.
Tn	Number of tubercles per whorl or part of whorl as specified, counted as for Rn.
Tc	Number of tubercles in the part of the whorl between where Wh was measured and 5 cm adapically along the whorl sides (only on larger specimens).
C	Length of body chamber, measured as the angle subtended about the protoconch by the umbilical end of the aperture and the tips of the saddles of the last septum, in square brackets if the body chamber is incomplete.

S A measure of sutural complexity, based on the amount of indentation of the sides of the lateral lobe compared with the length of the lobe. The amount of indentation is derived by subtracting from the maximum width (SLo) of the lobe the minimum distance (SLi) between the sides of the adapertural part of the lobe (before subdivision). Both are measured in a direction at right angles to the tangent to the venter where the suture crosses the venter. The length of the lobe (SLl) is the orthogonal distance from a line joining the tips of the neighbouring saddles to the tip of the lobe. This may not be at right angles to SLo and SLi. Thus

$$S = \frac{(SLo - SLi) \times 100}{SLl}.$$

This is a measure of the complexity of the suture rather than the size of the lobe, and gives high values of S for complex deeply indented lobes.

'A' or 'P' before the measurements for the diameter indicate that the measurements were made at the aperture or at the end of the phragmocone respectively, while 'c' before any measurement indicates that it is approximate.

Original data for species represented by two or more specimens are not published here, but are deposited with the British Library, Boston Spa, Yorkshire, as supplementary Publication No. SUP 14005 (twenty pages). For these species mean and standard deviation (in round brackets) have been calculated for those dimensions which show little or no variation with growth. Dimensional relationships which are growth variant are expressed by means of regression equations, with the mean square deviation about the regression in square brackets. These are intended partly for comparison of species, but mainly to provide population data for eventual comparison with populations from other areas. The number of observations (cf. number of specimens) is indicated, since most specimens have been measured at at least two or three stages of growth.

Most of the specimens have not been significantly affected by post-burial distortion, but dimensions affected by distortion are indicated by an asterisk.

SYSTEMATIC DESCRIPTIONS

Superfamily HILDOCERATACEAE Hyatt, 1867

Family SONNINIIDAE Buckman, 1892

The generic classification used is modified from Arkell (1957). The basis for the recognition of the genera is as follows (see also Table 2).

Euhoploceras. Distinguished from *Sonninia* (s.s.) by having broader more quadrate whorls, distinct subtabulate (or even bisulcate) venter (V = 9·3 and 8·4, not measurable in *Sonninia*), and low keel. *Fissilobiceras* is included here because of similarities in whorl shape, distinct flattened venter, and low keel, but recognized as subgenus because it is smoother, more involute (U = 26·8 cf. 40·0), and has a more complex suture (S = 67·6 cf. 60·0).

Shirbuirnia. Distinguished from *Euhoploceras* by trigonal rather than subquadrate whorl shape, with fastigate venter not distinct from whorl sides (V not measurable); from *Sonninia* by different whorl shape (with maximum whorl breadth lower in whorl cross-section), low keel, and simpler suture; from *Witchellia* in lacking a tabulate venter; and from large specimens of *Dorsetensia* by broader whorls.

Witchellia. Distinguished from *Euhoploceras* in being more involute (U = 29·8 cf. 40·0 for *Euhoploceras* excluding *Fissilobiceras*) and more compressed, by broader more distinctly tabulate venter (V = 12·5 cf. 8·7) and simpler suture (S = 35·0); from *Sonninia* in having tabulate venter and simpler suture; from *Dorsetensia* see Morton (1972, p. 505).

TABLE 2. Mean and standard deviation of selected characters of sonniniid genera based on specimens from Skye. N indicates the number of measurements available rather than number of specimens—for most specimens sets of measurements at more than one diameter are available.

	N[1]	H		U		V		N[1]	S	
		$\bar{X}$	σ	$\bar{X}$	σ	$\bar{X}$	σ		$\bar{X}$	σ
Euhoploceras (*Euhoploceras*)	6	36·0	2·6	40·0	4·1	9·3	1·5	1	60·0	—
Euhoploceras (*Fissilobiceras*)	12	43·4	6·0	26·8	5·6	8·4	1·2	5	67·6	10·1
Witchellia	135	43·4	3·3	29·8	4·5	12·5	3·6	21	35·0	6·5
Pelekodites	137	39·5	2·9	34·3	3·2	12·9	2·5	14	35·5	6·1
Sonninia	138	41·4	3·1	32·5	3·4	0†	—	33	64·1	7·7
Dorsetensia	100	43·7	3·9	28·2	5·3	11·5*	4·2*	23	39·4	9·2
'*S.*' aff. *furticarinata*	12	46·2	2·6	24·3	4·2	10·6	1·5	2	62·5	—

* Excluding *D. liostraca* which has an acutely fastigate venter.

† Venter of *Sonninia* acutely fastigate, not distinct from whorl sides.

[1] Number of measurements, *not* number of specimens.

Pelekodites. As defined at present includes the great majority of known sonniniid microconchs from the old Sowerbyi Zone, but may disappear if constituent species can be paired with macroconch synonyms, e.g. *Witchellia* (Westermann 1969*a*, pp. 115–116), or *Sonninia* (Westermann and Riccardi 1972, pl. 10, fig. 3). Reasons for retention are discussed below. Distinguished from most by small size and simpler sutures (S = 35·5); from *Witchellia* and *Dorsetensia* by being more evolute (U = 34·3 cf. 29·8 and 28·2) and having squarer whorl cross-section.

Sonninia. Characterized by being more compressed with acutely fastigate venter not distinct from whorl sides, high keel, and complex suture (S = 64·1 cf. 39·4 in *Dorsetensia* which may be otherwise similar except in details of radial line and style of ornamentation). *Papilliceras* is recognized as subgenus distinguished by the development of mid-lateral tubercles (or papillae) on body chamber (cf. Arkell 1957, p. L268, who stated merely that tubercles persist on to body chamber in some). Some species of *Sonninia* (*Sonninia*), including the type of *S.* (*S.*) *propinquans* (Bayle), may have developed tubercles on the body chamber if they were more complete and fully grown, and the subgenera may not be as distinct as apparent at present (see also Westermann and Riccardi 1972, pp. 47, 73–77, and Imlay 1973, p. 5).

'*Sonninia.*' The precise systematic position of '*Sonninia*' aff. *furticarinata* (Quenstedt) is not clear (see p. 80).

Dorsetensia. See Morton (1972, p. 505).

The family ranges from Concavum Zone (Aalenian) (if the base of the Discites Zone is defined by the appearance of *Hyperlioceras* (Morton 1971*b*)) to Lower Bathonian (Arkell 1951), with acme in Lower Bajocian. Important monographs include Buckman 1887–1907, 1909–1930, Haug 1893, Dorn 1935, Spath 1936, Gillet 1937, Hiltermann 1939, Roché 1939, Maubeuge 1951, 1955, Oechsle 1958, Imlay 1964, 1973, Westermann 1969*a*, Westermann and Riccardi 1972.

Dimorphism is very marked in some sonniniid faunas from Skye, for example in the concurrence of *Witchellia* as macroconch and *Pelekodites* as microconch, but in other faunas, for example *Euhoploceras*, it is not at all clear and there is a distinct 'shortage' of microconchs (see also Westermann 1966, 1969*a*). It is possible that the microconchs have been 'lumped' into the one genus *Pelekodites*, but if my earlier interpretation (Morton 1972) of *Dorsetensia* is correct then there may also be unrecognized dimorphism within some sonniniid genera as currently defined. Westermann and Riccardi (1972) describe and figure male and female of some species. In some cases the association seems highly likely, though hardly proved conclusively, and 'marriage' into one species may be appropriate. However, in most cases the association is somewhat tenuous and does not provide a sound basis for revision of sonniniid taxonomy into bisexual biospecies (and this is not considered desirable by some authors—see discussions in Westermann 1969*b*). This should be based on more than one local fauna. Therefore no attempt is made to deal with sonniniid dimorphism other than as separate taxonomic categories, as has Imlay (1973).

Genus EUHOPLOCERAS Buckman, 1913

Subgenus EUHOPLOCERAS (EUHOPLOCERAS) Buckman, 1913

Type species. Sonninia acanthodes Buckman, 1889, original designation by Buckman (1913, p. 4).

Includes. Sherbornites and *Stiphromorphites* Buckman, 1923.

Discussion. The many species of *Euhoploceras*, mainly from Bradford Abbas (Dorset), described by Buckman were referred by Westermann (1966) to a single species *adicra* (Waagen) on the basis of semi-quantitative work on Buckman's plates. There are undoubtedly too many specific names, but Westermann's 'sample' can hardly be said to be adequate to establish the continuity or otherwise of the variation in such a morphologically diverse group. Furthermore, the 0·18 m of the Discites Zone at Bradford Abbas is equivalent to some 35–40 m of strata at Bearreraig, so that it is simply not true to say (cf. Westermann 1966, p. 291) that the Bradford Abbas 'discites bed' is not condensed. Also the assumption that Buckman's specimens all came from one zone or subzone is not justified (see Barker and Torrens 1971, p. 55). Until a revision of the Dorset sonniniids, the specimens from Skye will be compared with Buckman's 'species' rather than lumped into Westermann's enlarged species *adicra*. Similar conclusions were arrived at by Imlay (1973, pp. 4–6).

Euhoploceras (*Euhoploceras*) *marginata* (Buckman)

Plate 6, figs. 2–3

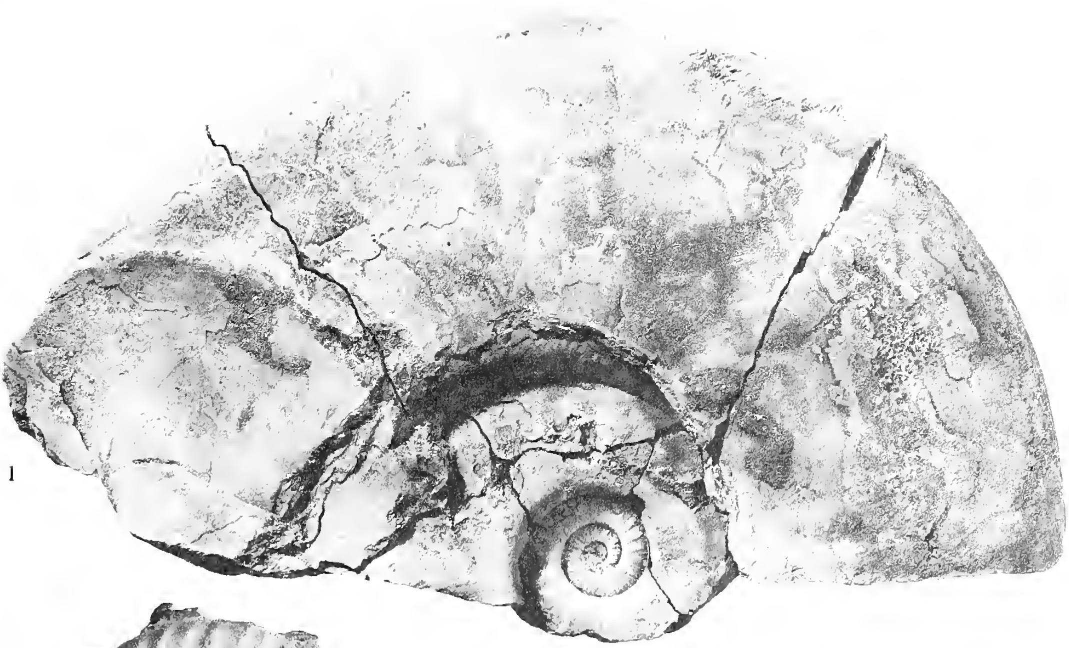
1892 *Sonninia marginata* S. Buckman, pp. 321–322, pl. 62; pl. 63, fig. 2; pl. 65, figs. 1–2.
1894 *Sonninia marginata* S. Buckman, pp. 387, 407, pl. 94, fig. 6.
1937 *Sonninia marginata* Buckman, Gillet, p. 53.

EXPLANATION OF PLATE 6

Fig. 1. *Euhoploceras* (*Fissilobiceras*) *fissilobatum* (Waagen); HMS 26399/1; Ovalis Zone; top 2–3 m of Shaly Sandstones, foot of high cliff 300 m north of Holm, Trotternish, Skye, ×0·63.

Figs. 2, 3. *Euhoploceras* (*Euhoploceras*) *marginata* (Buckman); HMS 26398; top of Concavum Zone or base of Discites Zone; 17 m above base of Shaly Sandstones, lowest exposure in Bearreraig Burn, Trotternish, Skye, ×1.

Fig. 4. *Shirbuirnia trigonalis* Buckman; HMS 15342/1; Ovalis Zone; horizon and locality as fig. 1, ×0·44.



1

2

3

4

MORTON, Scottish Bajocian ammonites

Material. One medium-sized specimen, HMS 26398.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U	Vw	V	Vb	Rd	R	Rn	C
c. 55·0	19·8	36	18·0	33	91	23·9	43	(6·5)	(12)	(36)	3·2	6	24/½wh	[200]

Description. Evolute, thick whorls; large spines, broad distant ribs, and striae replaced at D *c.* 40 mm by close, not quite regular ribs, slightly curved and rursiradiate, but strongly projected ventrally; whorl section subquadrate, with umbilical edge smooth, rounded, becoming steep; venter broad, tabulate, with prominent keel; last suture only partly visible; aperture broken.

Discussion. The specimen is similar to several species which show change in ornamentation from spines or tubercles to ribs, but *ptycta* has more strongly curved ribs, *spinicostata* has the ribs more confined to the whorl sides, *crassa* has more distant ribs which do not show ventral projection, *euromphalica* shows earlier decline of the tubercles, *regularis* has a relatively narrower venter, and *submarginata* has slightly less well-developed ribs and narrower venter. It is most similar (though smaller) to some specimens of *marginata* figured by Buckman and to some described by him as intermediate between *marginata* and *dominans.*

Buckman (1892, p. 322) recorded *S. marginata* from the '*Concavum*-zone' of Bradford Abbas and other localities in Dorset, but this was later changed to Discites Zone (see also Barker and Torrens 1971, pp. 54–55).

Locality. Top of Concavum Zone or base of Discites Zone; approximately 17 m above base of Shaly Sandstones; lowest exposure in Bearreraig Burn, Trotternish, Isle of Skye.

Euhoploceras (*Euhoploceras*) ?*dominans* (Buckman)

Plate 7, figs. 1–2

1892 *Sonninia dominans* S. Buckman, pp. 322–324, pl. 66; pl. 67, figs. 1–2, ?3–4; pl. 69.
1894 *Sonninia dominans* S. Buckman, pp. 435–437, pl. 94, figs. 1–2; pl. 95, fig. 1; pl. 97, fig. 4.
1923 *Sonninia dominans* Buckman, Fallot and Blanchet, pp. 100–101.
1937 *Sonninia dominans* Buckman, Gillet, p. 53.
1966 *Sonninia* (*Euhoploceras*) *adicra* (Waagen) 'forma dominans', Westermann, p. 310.
1973 *Sonninia* (*Euhoploceras*) *dominans* Buckman, Imlay, pp. 63–64, pls. 11–12.

Material. One large fragment, HMS 15337.

Dimensions.

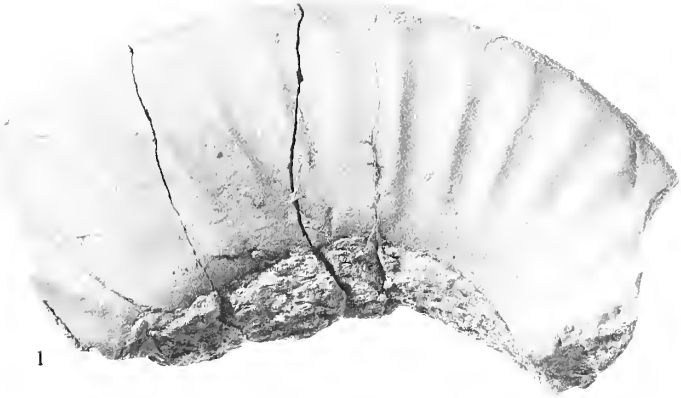
	D	Wh	H	Wb	B	W	Ud	U	Vw	V	Vb	Rd	R	Rn	C
	c. 150	54·5	36	37·1	25	68	*c.* 62·0	41	15·0	10	40	12·1	8	13/¼wh	[*c.* 150]
P	—	43·0	—	32·8	—	76	—	—	12·3	—	38	8·9	—	—	—

EXPLANATION OF PLATE 7

Figs. 1, 2. *Euhoploceras* (*Euhoploceras*) ?*dominans* (Buckman); HMS 15337; top of Concavum Zone or base of Discites Zone; 17 m above base of Shaly Sandstones, lowest exposure in Bearreraig Burn, Trotternish, Skye, ×0·72.

Figs. 3, 4. *Euhoploceras* (*Euhoploceras*) sp. (?cf. *modesta* Buckman); HMS 26403; Discites Zone; 29 m below top of Shaly Sandstones, Bearreraig Burn, Trotternish, Skye, ×0·35.

Figs. 5, 6. *Euhoploceras* (*Euhoploceras*) sp. (?cf. *costatum* Buckman); HMS 26402; Discites Zone; 26 m below top of Shaly Sandstones, Bearreraig Burn, Trotternish, Skye, ×0·33.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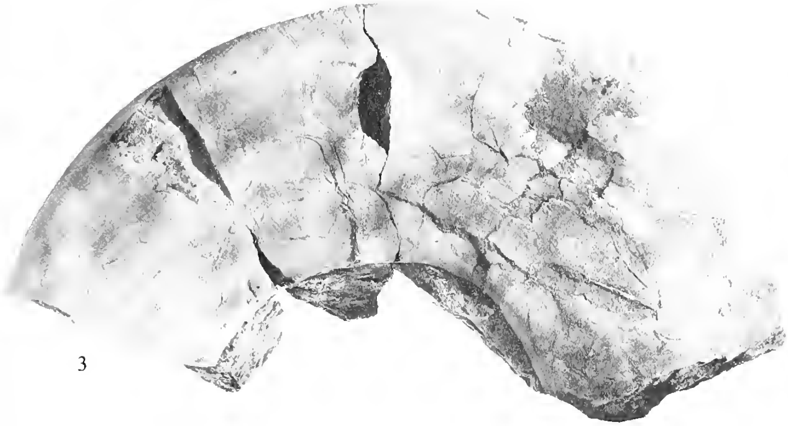
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5


6

MORTON, Scottish Bajocian ammonites

Description. Evolute, mainly body chamber; regular moderately widely spaced straight ribs approximately rectiradiate with slight ventral projection, confined to whorl sides; umbilical edge smooth and rounded; venter broad, smooth, tabulate (almost bisulcate), with keel; last suture partly visible.

Discussion. The ribbing on this specimen is more regular and relatively more widely spaced (R = 8 cf. 6) than in *marginata* described above. Of other similarly ribbed species *dominata* has more closely spaced ribs and *crassa* has broader whorl cross-section. The specimen is most similar to *dominans*, which Buckman (1892, pp. 323–324) recorded from the '*Concavum*-zone' of Bradford Abbas and other localities in Dorset. This may be either Concavum Zone or Discites Zone (Barker and Torrens 1971, pp. 54–55) (see also Imlay 1973, p. 5, etc.).

Locality. Top of Concavum Zone or base of Discites Zone; approximately 17 m above base of Shaly Sandstones; lowest exposure in Bearreraig Burn, Trotternish, Isle of Skye.

Euhoploceras (*Euhoploceras*) spp.

Plate 7, figs. 3–6

Material. Four very large fragments, HMS 15336, HMS 26401, HMS 26402, HMS 26403.

Dimensions.

	D	Wh	H	Wb	B	W	Ud	U	Vw	V
HMS 15336	*c.* 340·0	120·0	35	81·4	24	68	*c.* 145·0	43	(30·6)	(9)
	Vb	Rd	R	Rn	C	SLo	SLi	SLl	S	
	(38)	48·1	14	*c.* 8/$\frac{1}{2}$wh	—	—	—	—	—	
	D	Wh	H	Wb	B	W	Ud	U	Vw	V
HMS 26401	*c.* 305·0	126·0*	41*	—	—	—	*c.* 98·0	32	*c.* 27·5	9
	Vb	Rd	R	Rn	C	SLo	SLi	SLl	S	
	—	—	—	—	[130]	27·0	4·1	38·1	60	
	D	Wh	H	Wb	B	W	Ud	U	Vw	V
HMS 26402	*c.* 300·0	102·0	34	*c.* 68·0	23	67	*c.* 120·0	40	24·0	8
	Vb	Rd	R	Rn	C	SLo	SLi	SLl	S	
	35	29·2	10	*c.* 7/$\frac{1}{4}$wh	[145]	—	—	—	—	
	D	Wh	H	Wb	B	W	Ud	U	Vw	V
HMS 26403	*c.* 310·0	*c.* 105·0*	34*	*c.* 53·0*	17*	50*	*c.* 128·0	41	23·7	8
	Vb	Rd	R	Rn	C	SLo	SLi	SLl	S	
	45	*c.* 35·0	11	*c.* 6/$\frac{1}{4}$wh	[160]	—	—	—	—	
	D	Wh	H	Wb	B	W	Ud	U	Vw	V
	—	84·0	—	50·0	—	60	—	—	22·4	—
	Vb	Rd	R	Rn	C	SLo	SLi	SLl	S	
	45	—	—	—	—	—	—	—	—	

Description. Mostly body chamber; evolute with more or less subquadrate whorls; HMS 26402 has broad irregularly developed straight ribs, slightly rursiradiate, fading on to umbilical shoulder and upper part of whorl sides; HMS 15336 has very broad more distant blunt ribs than HMS 26402 (R = 14 cf. 10); there are a few broad undulations on HMS 26401 and HMS 26403, which is also striate; venters broad, tabulate or subtabulate and almost bisulcate in HMS 26402, with a broad low keel; HMS 26401 shows complex suture with long lateral lobe.

Discussion. HMS 15336 is similar to typical *adicrum* (Waagen), while HMS 26402 resembles *costatum* (Buckman) and related species. HMS 26401 and HMS 26403 have more quadrate whorl section than *parvicostatum* and *nudum* (Buckman), more prominent keel than *contusum*, *simplex*, and *substriatum* (Buckman), but are most similar to *modesta* (Buckman). The specimens are not well enough preserved for definite identification. According to Westermann (1966, p. 289), *Euhoploceras* (*E.*) *adicra* (Waagen) and the related species referred to above are mainly from the Discites Zone. The exact range of most species has not been established (see also Imlay 1973).

Localities. (*a*) Discites Zone; Shaly Sandstones—(i) HMS 26402 from 26 m below the top, (ii) HMS 26401 from 27 m below the top, (iii) HMS 26403 from 29 m below the top—all in the Bearreraig Burn section below the main waterfall. (*b*) Ovalis Zone; top 2–3 m of the Shaly Sandstones; foot of high cliff 300 m north of Holm. Both localities are in Trotternish, Isle of Skye.

Subgenus EUHOPLOCERAS (FISSILOBICERAS) Buckman, 1919

Type species. Ammonites fissilobatus Waagen, 1867, original designation by Buckman (1919, p. 15).

Discussion. Fissilobiceras was regarded as a subgenus of *Sonninia* by Westermann and Riccardi (1972, p. 59) who commented on the differences between it and *Shirbuirnia* (cf. Arkell 1957) and noted the possibility of derivation from the hammatoceratid *Eudmetoceras* (*Euaptetoceras*) *amplectens* (Buckman).

Euhoploceras (*Fissilobiceras*) *fissilobatum* (Waagen)

Plate 6, fig. 1; Plate 8, figs. 1–3

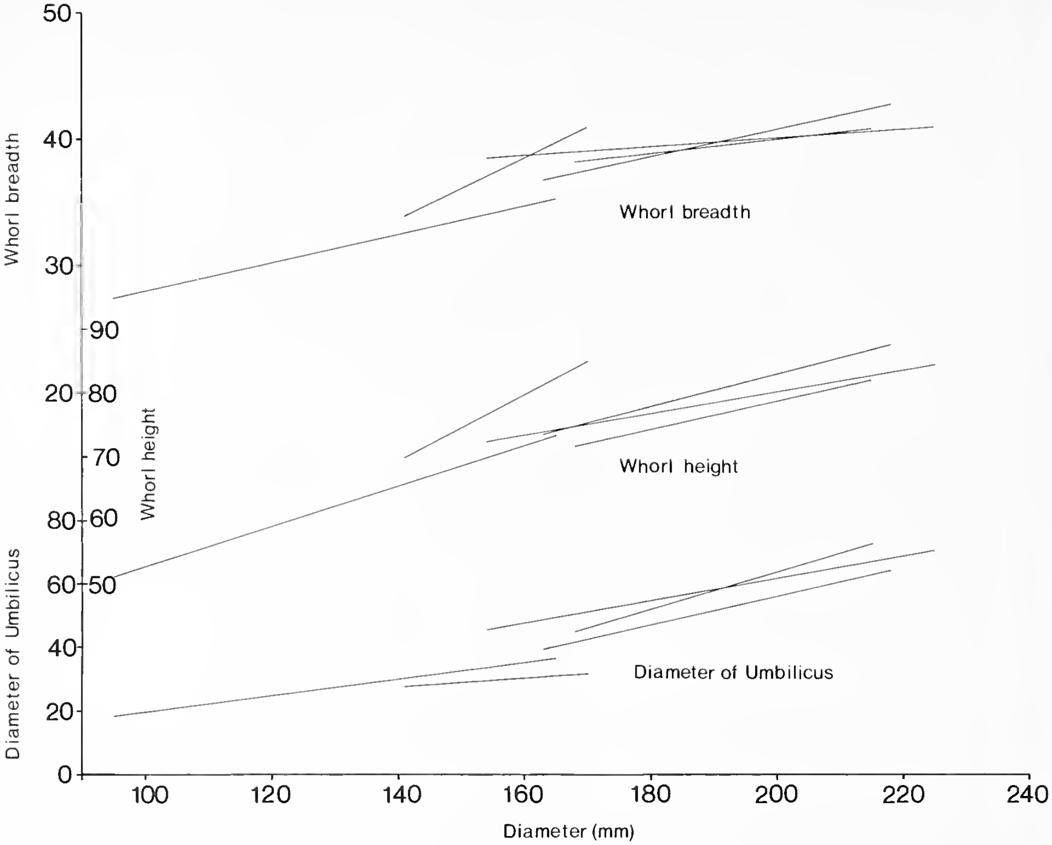
1867 *Ammonites fissilobatus* Waagen, p. 599, pl. 27, fig. 1*a*, *b*.
1886 *Ammonites fissilobatus* Quenstedt, pp. 501–502, pl. 63, fig. 1.
1920 *Fissilobiceras fissilobatum* Waagen sp., Buckman, pl. 181A, B.
1935 *Sonninia fissilobata* Waagen, Dorn, pp. 56–57, pl. 13, fig. 1; pl. 15, fig. 4; pl. 5, figs. 8–9.
1958 *Sonninia fissilobata* (Waagen), Oechsle, pp. 96–98, pl. 11, figs. 11–12; pl. 12, figs. 7–8; pl. 19, fig. 4.
1972 *Sonninia* (*Fissilobiceras*) *fissilobata* (Waagen), Westermann and Riccardi, p. 59, text-fig. 22.

Material. Eight large specimens and two fragments, HMS 15343/1–4, HMS 26397, HMS 26399/1–3, HMS 26400/1–2.

Dimensions. For the full list of dimensions see deposited data.

Mean and standard deviation for characters which show little variation with growth are (twelve observations): H = 43·4 (6·0); U = 26·8 (5·6); V = 8·4 (1·2); Vb = 36·9 (3·9); C = 217·5 (two specimens only); S = 67·6 (10·1). Maximum measured diameter is *c.* 370 mm in HMS 26400/1, *c.* 225 mm in HMS 15343/1.

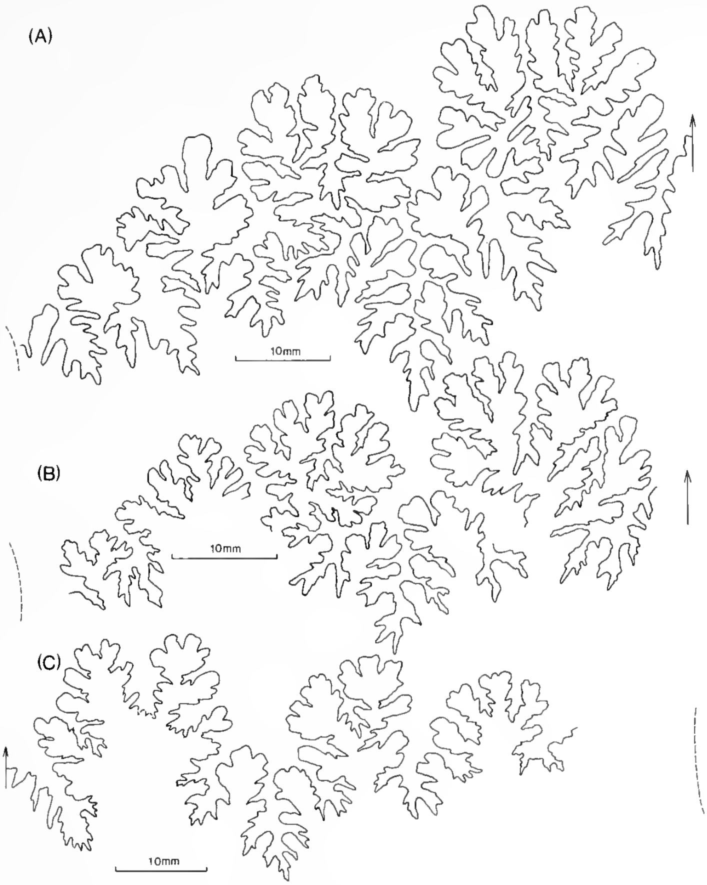
Description. Moderately involute becoming more evolute (see text-fig. 1); innermost whorls ribbed, but ribs become irregular and fade by D approx. 40 mm, or earlier; intermediate and outer whorls smooth or striate; radial line very slightly curved but strongly projected; whorl cross-section elongate sub-oval, maximum thickness just below mid-whorl; umbilical edge rounded, steep but not vertical; venter broad, obtusely fastigate with blunt low keel; sutures complex with long deeply divided



TEXT-FIG. 1. Umbilical diameter, whorl height, and whorl breadth plotted against diameter for specimens of *Euhoploceras* (*Fissilobiceras*) *fissilobatum* (Waagen) from Skye.

lateral lobe and umbilical lobes slightly retracted (text-fig. 2A, B); aperture curved with large ventral projection; body chamber, just under two-thirds of a whorl, shows eccentric coiling with widening umbilicus (see text-fig. 1). Specimen HMS 26397 has the bivalved aptychus preserved inside the body chamber (Morton 1973 and Pl. 8, figs. 2–3).

Discussion. The specimens are smoother, more involute, and have a more distinctly fastigate venter, and a more complex suture than the great majority of species of *Euhoploceras*. They are similar to *nuda* Buckman, but the maximum whorl thickness in this species is lower on the whorl sides giving a more triangular whorl cross-section, while *stephani* Buckman also has a different whorl shape and a simpler suture line. They are similar to *ovalis* Quenstedt but the cross-sections of this species figured by Quenstedt (1886) and Oechsle (1958) show a more rounded venter even on the inner whorls, and a less complex suture with shorter lateral lobe. The whorl cross-section of the Skye specimens, especially the shape of the venter, and the complex suture, especially the long lateral lobe, are most like *fissilobatus* Waagen, although most



TEXT-FIG. 2. Suture lines of A, *Euhoploceras* (*Fissilobiceras*) *fissilobatum* (Waagen), HMS 15343/3 at Wh 69·3 mm (× 1·3); B, *Euhoploceras* (*Fissilobiceras*) *fissilobatum* (Waagen), HMS 15343/4 at Wh 60·9 mm (× 1·4); C, *Shirbuirnia trigonalis* Buckman, HMS 15342/1 at Wh 75·2 mm (× 1·2).

would be larger if complete. At first sight the Skye specimens seem more evolute, but this is because the figured specimens mostly lack a body chamber. The specimen of *fissilobatum* figured by Buckman (1920, pl. 131A) has the trace of the umbilical seam for a further two-thirds of a whorl and this shows that the umbilicus widens in the same way as in the Skye specimens. A minor difference is that the ribbing on the inner whorls of the Skye specimens fades at a slightly earlier stage than on figured specimens of *fissilobatum* from Germany.

In Germany the species *fissilobatum* is recorded from the Sowerbyi Zone by Waagen (1867), the Sowerbyi-Bank by Oechsle (1958, p. 124), and the Brauner Jura γ by Quenstedt (1886, p. 501). Dorn (1935, p. 120) records it as from 'mittleres Gamma', which Westermann (1967, table 6) shows as being in the Sowerbyi Zone, above the Discites Subzone and below the Sauzei Zone. Buckman (1920) records the species from the lower part of the Sandford Lane fossil bed, the '*Shirbuirnia* hemera', of Dorset.

Localities. Ovalis Zone; top 2–3 m of Shaly Sandstones: (*a*) most specimens are from the foot of the high cliff 300 m north of Holm; (*b*) HMS 26400/1–2 are from the foot of the main waterfall in the Bearreraig Burn; both localities in Trotternish, Isle of Skye.

Genus SHIRBUIRNIA Buckman, 1910

Type species. Shirbuirnia trigonalis Buckman, 1910, subsequent designation by Arkell (1954, p. 561).

Discussion. Shirbuirnia has been discussed recently by Westermann and Riccardi (1972, p. 59) who classified it as a subgenus of *Sonninia*, disagreeing with the relationship between *Shirbuirnia* and *Fissilobiceras* suggested by Arkell (1957, pp. L268, 270).

Shirbuirnia trigonalis Buckman

Plate 6, fig. 4

1910 *Shirbuirnia trigonalis* Buckman, p. 92, pl. 10, figs. 2–3.
1924 *Shirbuirnia trigonalis* Buckman, pl. 517A, B.

Material. One large specimen, HMS 15342/1.

Dimensions.

	D	Wh	H	Wb	B	W	Ud	U	
A	*c.* 266·0	*c.* 86·0	32	*c.* 58·0	22	67	103·4	39	
	Rd	R	Rn		C	SLo	SLi	SLl	S
	c. 42·5	16	*c.* 6/½wh		210	—	—	—	—
	D	Wh	H	Wb	B	W	Ud	U	
	253·0	83·1	33	*c.* 52·8	21	64	95·3	38	
	Rd	R	Rn		C	SLo	SLi	SLl	S
	—	—	—		—	—	—	—	—
	D	Wh	H	Wb	B	W	Ud	U	
	c. 198·0	75·9	38	*c.* 51·5	26	68	66·9	34	
	Rd	R	Rn		C	SLo	SLi	SLl	S
	—	—	—		—	—	—	—	—
	D	Wh	H	Wb	B	W	Ud	U	
P	*c.* 180·0	75·2	42	*c.* 47·2	26	63	56·8	32	
	Rd	R	Rn		C	SLo	SLi	SLl	S
	—	—	—		—	25·2	7·4	29·7	60

Description. Increasingly evolute in final whorl; maximum breadth low on whorl sides; inner whorls with broad irregular ribbing; intermediate whorls smooth; outer whorl has very broad low undulations on lower half of whorl sides; whorl section subtrigonal, umbilical edge rounded becoming vertical into deep umbilicus; venter

EXPLANATION OF PLATE 8

Figs. 1–3. *Euhoploceras* (*Fissilobiceras*) *fissilobatum* (Waagen); HMS 26397; Ovalis Zone; top 2–3 m of Shaly Sandstones, foot of high cliff 300 m north of Holm, Trotternish, Skye. 1, side view, ×0·50. 2, 3, aptychus and ventral view, stereopair (separation 65 mm), ×1.

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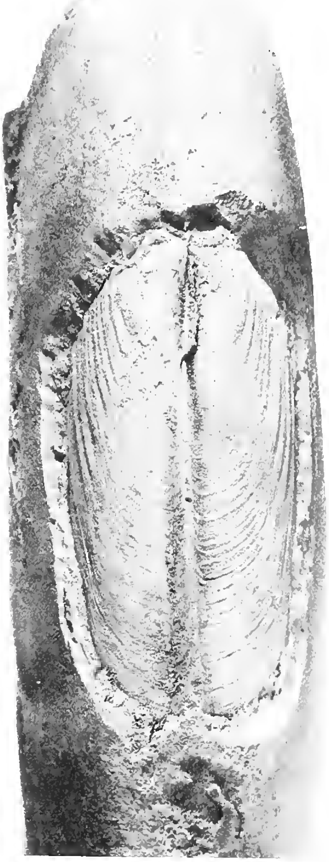

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MORTON, Scottish Bajocian ammonites

fastigate, not distinct from whorl sides, with low blunt keel; suture (text-fig. 2C) less complex than typical of large sonniniids; body chamber over half a whorl in length.

Discussion. This specimen is more evolute, has a different whorl shape and a simpler suture than the specimens of *fissilobatum* (Waagen) with which it occurs. The subtrigonal whorl shape and relatively simple suture are characteristic of *Shirbuirnia*. Of four species described, *stephani* (Buckman, 1882) and *fastigata* Buckman, 1924 are more involute and have sharper venter; *pseudotrigonalis* Maubeuge, 1951 is more involute but otherwise similar. The specimen is most similar to *trigonalis* Buckman, 1910, although this is slightly more involute and larger ($D = 328$ mm cf. c266 mm). *Sh. trigonalis* is listed by Buckman (1924, pl. 517; 1930, p. 36) as coming from the *Shirbuirnia* hemera of Sandford Lane, Dorset.

Locality. Ovalis Zone; top 2–3 m of the Shaly Sandstones; foot of high cliff 300 m north of Holm, Trotternish, Skye.

Genus WITCHELLIA Buckman, 1889

Type species. Ammonites laeviusculus J. de C. Sowerby, original designation by Buckman (1889, p. 82).

Includes. Zugophorites Buckman, 1923, *Gelasinites* Buckman, 1925, *Rubrileiites* Buckman, 1926, *Zugella* Buckman, 1927, ?*Dundryites* and *Anolkoleiites* Buckman, 1926.

Witchellia aff. *rubra* (Buckman)

Plate 9, figs. 1–34

aff. 1926 *Rubrileiites ruber* S. Buckman, pl. 642.
aff. 1939 *Sonninia stephani ruber* (Buckman), Hiltermann, p. 180, pl. 12, fig. 10; pl. 13, figs. 8–9.

Material. Fifty-four specimens, HMS 15344/1–2, HMS 15346/1–3, HMS 26404/1–45, HMS 26405/1–3, HMS 26406, GSE 2968.

Dimensions. For the full list of dimensions see deposited data.

Mean and standard deviation for characters which show little variation with growth are (140 observations): $H = 43{\cdot}4$ (3·4); $U = 29{\cdot}8$ (4·6); $V = 12{\cdot}6$ (3·6); $Vb = 40{\cdot}2$ (4·8); $^{s}R = 6{\cdot}6$ (1·5), but ribs fade on some specimens; $^{s}Rn = 21{\cdot}2/\frac{1}{2}wh$ (3·7); $C = 208{\cdot}6$ (9·0); $S = 35{\cdot}0$ (6·5). Maximum measured diameter is 62·0 mm in HMS 15346/1. Regression equations (see also text-fig. 3) are:

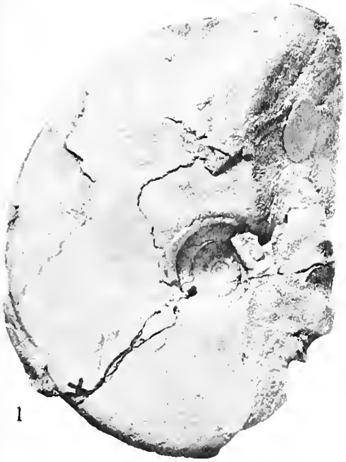
$$\begin{aligned} Wh &= 0{\cdot}50\,D - 1{\cdot}18\ [0{\cdot}44] \\ Wb &= 0{\cdot}19\,D + 2{\cdot}22\ [0{\cdot}28] \\ Ud &= 0{\cdot}18\,D + 2{\cdot}25\ [0{\cdot}68] \end{aligned}$$

EXPLANATION OF PLATE 9

All figures natural size.

Figs. 1–34. *Witchellia* aff. *rubra* (Buckman); Laeviuscula Zone; approximately 18 m below top of Massive Sandstones, ledge behind main waterfall in Bearreraig Burn, Trotternish, Skye. 1, 2, HMS 15346/1; 3, 4, HMS 26404/2; 5, 6, HMS 26404/5; 7, 8, HMS 26404/6; 9, 10, HMS 26404/7; 11, 12, HMS 15344/1; 13, 14, HMS 26404/9; 15, 16, HMS 26404/8; 17, 18, HMS 26404/14; 19, 20, HMS 26404/18; 21, 22, GSE 2968; 23, 24, HMS 26404/21; 25, 26, HMS 26404/22; 27, 28, HMS 26404/23; 29, 30, HMS 26404/24; 31, 32, HMS 26404/37; 33, 34, HMS 26404/38.

PLATE 9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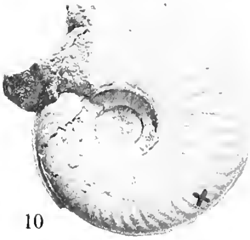
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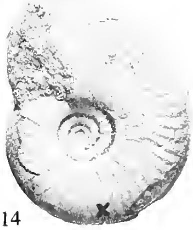
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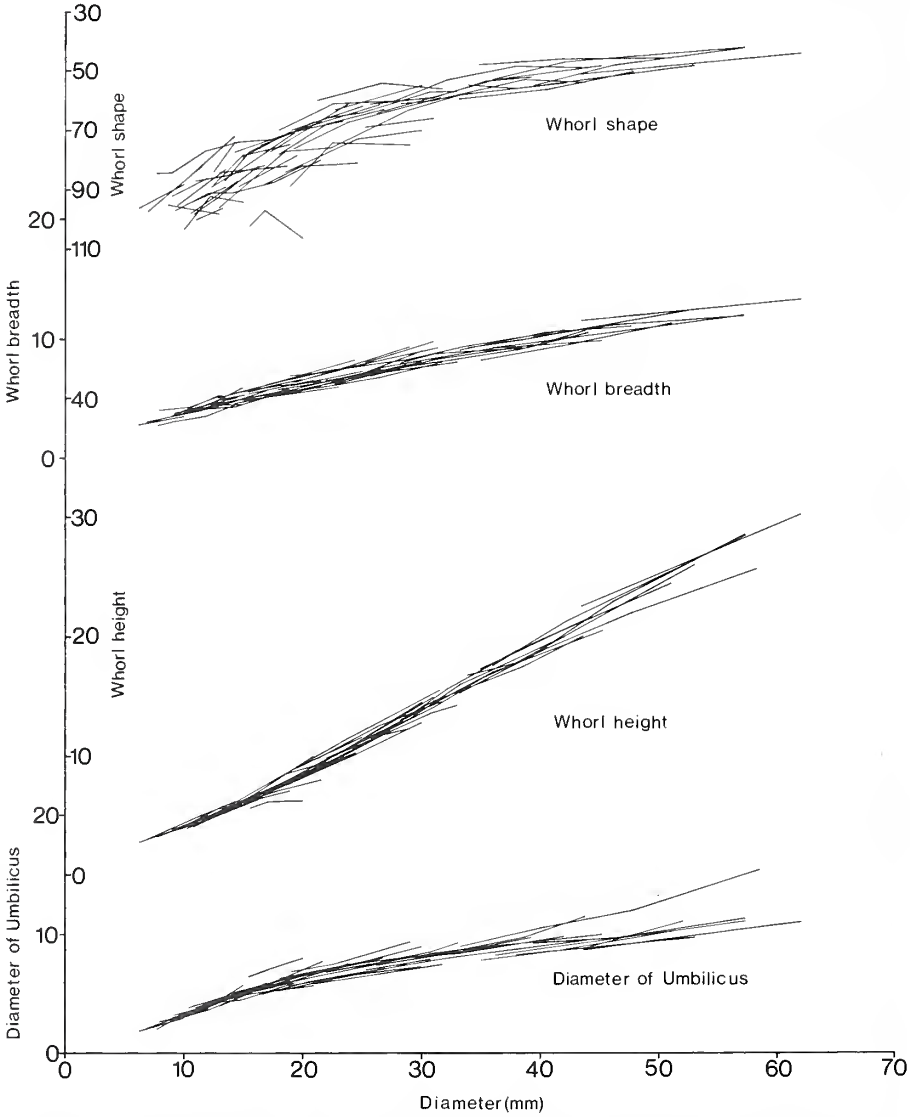
MORTON, Scottish Bajocian ammonites

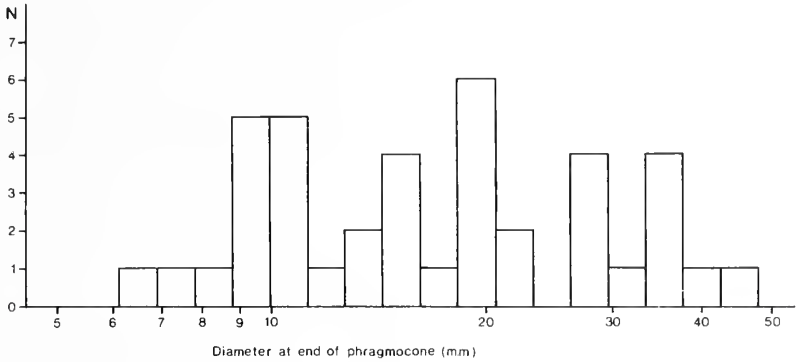
Description. Involute compressed (see text-fig. 3); protoconch bulbous and very broad; first whorls broader than high, smooth then developing broad faint undulations, with rounded venter lacking keel; the broad undulations develop gradually into distinct primary ribs which branch near umbilical shoulder into more prominent secondary ribs; a keel and flattened venter developed (by D 3·5 mm on HMS 26404/27); on outer whorls whorl height greater than breadth, venter more defined, tabulate or even bisulcate with prominent keel; ribbing more pronounced and closer, curved and projected ventrally (sometimes more strongly developed on outer half of whorl sides),



TEXT-FIG. 3. Umbilical diameter, whorl height, whorl breadth, and whorl shape plotted against diameter for specimens of *Witchellia* aff. *rubra* (Buckman) from Skye.

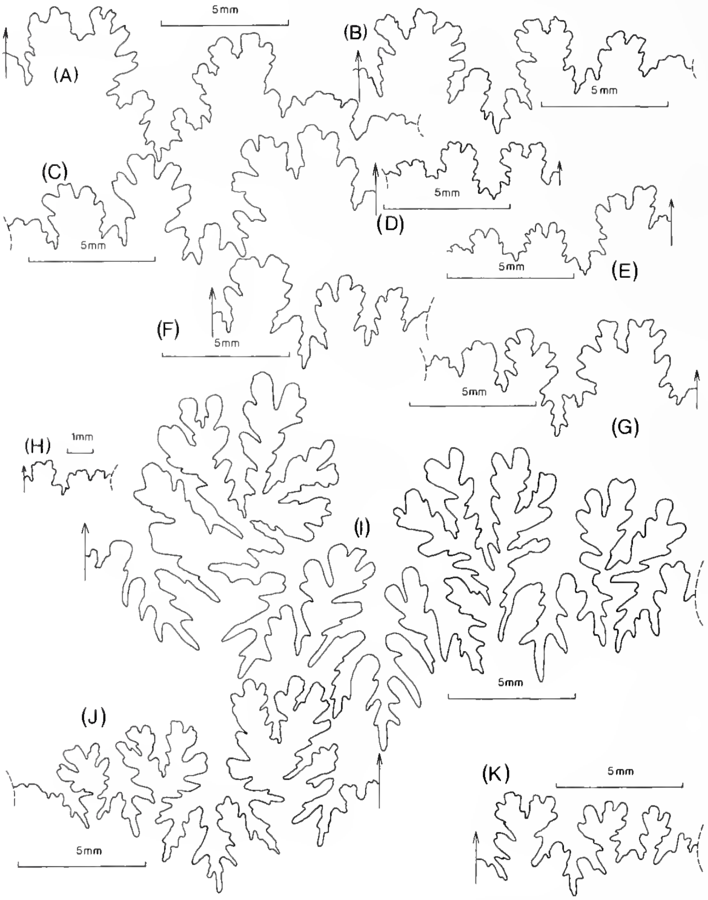
then fainter, many specimens passing from costate to striate, others strongly ribbed at the same diameter; umbilical edge rounded but sharper on outer whorls of larger specimens, with umbilical face vertical in some; aperture curved; body chambers approximately five-eighths of a whorl; few specimens show evidence of maturity; sutures not complex, lateral lobe broad open showing trifid structure (text-fig. 5A, B).

Discussion. The specimens show continuous variation between extremes such as HMS 15346/1 (smooth) and HMS 15344/1 (ribbed). A size-frequency distribution (diameter at end of phragmocone) suggests (text-fig. 4) that there may be three or four groups, with thirteen specimens having diameter 6–11 mm at the end of the phragmocone (Pl. 9, figs. 31–34), seven specimens between 12 mm and 15 mm (Pl. 9, figs. 23–30), nine specimens between 17 mm and 22 mm (Pl. 9, figs. 7–8, 13–14, 17–20), and eleven specimens above 25 mm (Pl. 9, figs. 1–6, 9–12). Of the measured specimens five from loose blocks (e.g. Pl. 9, figs. 21–22) and two lacking body chamber (e.g. Pl. 9, figs. 15–16) are excluded from the above figures. In the absence of evidence of maturity it must be assumed that the majority of the specimens were juveniles, and it is possible that the different size groups represent successive generations. Some of the larger specimens may be adults, but the maximum size reached in the Skye population (62 mm in HMS 15346/1) is less than that of comparable *Witchellia* specimens (especially *rubra*) from Dorset (107 mm in Buckman 1926, pl. 642), and Germany (111 mm in Hiltermann 1939, pl. 12, fig. 10) but may be comparable with some of the specimens from northern Germany figured by Hiltermann (1939). Similar variation was described in *Witchellia* from Alaska by Westermann (1969, pp. 116–126) who also concluded that only one species was represented, and suggested (pp. 108–116) that many north-west European species were variants of one species. The Skye population is more homogeneous, and accuracy in taxonomic labelling would be better served by using the best fit specific name. Of described species (Buckman's unless otherwise stated): *actinophora*, *falcata*, *glauca*, *platymorpha*, *sutneri* (Branco), and *crassifalcata* Dorn are all too strongly ribbed and/or too evolute; *spinifera* and *laeviuscula* (Sowerby) have similar outer whorls but spinous inner whorls (the latter



TEXT-FIG. 4. Size-frequency distribution (using diameter at end of phragmocone) of specimens of *Witchellia* aff. *rubra* (Buckman) from the Laeviuscula Zone, ledge behind main waterfall in Bearreraig Burn, Trotternish, Skye.

according to Westermann 1969*a*, text-fig. 35, p. 111); *gelasina* is too evolute and has too thick whorls; *helvetica* Maubeuge is not easily recognizable; *sayni* Haug is similar to the smaller specimens. The best fit, showing ribbing on the inner whorls, fading on the outer whorl, is *rubra*. The holotype of *rubra* (GSM 47839) is larger than any of the Skye specimens (D = 106·4 mm cf. maximum of 62·0 mm), and has higher whorls (H = 47), narrower umbilicus (U = 21), and narrower venter (V = 9) than the



TEXT-FIG. 5. Suture lines (all × 3·4) of A, *Witchellia* aff. *rubra* (Buckman), HMS 15346/2 at Wh 16·1 mm; B, *Witchellia* aff. *rubra* (Buckman), HMS 26404/8 at Wh 13·8 mm; C, *Witchellia* aff. *romanoides* (Douvillé), HMS 26408 at Wh 13·6 mm; D, *Pelekodites zurcheri* (Douvillé), HMS 26409/1 at Wh 6·0 mm; E, *Pelekodites zurcheri* (Douvillé), HMS 26410/1 at Wh 7·9 mm; F, *Pelekodites macer* (Buckman), HMS 15340/14 at Wh 7·6 mm; G, *Pelekodites macer* (Buckman), HMS 26412/14 at Wh 8·1 mm; H, *Pelekodites minimus* (Hiltermann), HMS 26413/2 at Wh 3·2 mm; I, *Sonninia* (*Sonninia*) cf. *propinquans* (Bayle), GSE 3060 at Wh 21·2 mm; J, *Sonninia* (*Sonninia*) *corrugata* (Sowerby), HMS 15345/1 at Wh 13·0 mm; K, *Sonninia* (*Sonninia*) *corrugata* (Sowerby), HMS 15345/2 at Wh 8·2 mm.

means of the Skye population, but these values are within the ranges of variation. The ribbing and suture (S = 34) are similar. It differs mainly in having a slightly lower, less sharp keel, and less distinct edges to the venter. The holotype is therefore towards one end of the range of variation of the Skye population, but the differences may not be significant. No topotype population data are available so an open (aff.) determination is used here. If Westermann is correct *rubra* would be a junior synonym of *Witchellia laeviuscula* (Sowerby), but the European species of *Witchellia* come from more than one horizon and from several localities, so cannot be regarded as a single population.

According to Buckman (1926) the holotype of *rubra* comes from Frogden Quarry, Dorset—*ruber* hemera. This would be equivalent to the Laeviuscula Zone in modern terminology. In Germany (Hiltermann 1939) the species comes from bed 20 at Bethel and beds 15–22 at Hellern, both in the 'Sowerbyi Zone' according to Huf (1968, pp. 14–15).

Localities. Laeviuscula Zone; approximately 18 m below the top of the Massive Sandstones (cf. Morton 1965, p. 198); ledge behind main waterfall in Bearreraig Burn, Trotternish, Skye. A few specimens (HMS 26405/1-3 and GSE 2968) were found in loose blocks of the Massive Sandstones on the shore just south of Bearreraig, and one specimen (HMS 26406) is from a loose block of the Massive Sandstones at Rudha Sughar, Bearreraig.

Witchellia aff. *laeviuscula* (J. de C. Sowerby)

Plate 10, figs. 1–2

1824 *Ammonites laeviusculus* J. de C. Sowerby, p. 73, pl. 451, figs. 1–2.
1908 *Ammonites laeviusculus* J. de C. Sowerby, Buckman and Secretary, pl. 6, figs. 1–2.
1927 *Witchellia laeviuscula* Sow. sp., Buckman, pl. 745.
1935 *Witchellia laeviuscula* Sow., Dorn, pp. 106–107, pl. 6, fig. 3; pl. 14, fig. 2; pl. 15, fig. 3.
1937 *Witchellia laeviuscula* Sow., Gillet, pp. 61–63, pl. 1, fig. 8; pl. 2, fig. 6; pl. 3, fig. 1.
1969 *Witchellia laeviuscula* (Sowerby), Westermann, p. 111, text-fig. 35.

Material. One specimen, HMS 26407.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U	Vw	V	Vb	C
61·6	26·6	43	*c.* 14·4	23	54	14·6	24	*c.* 5·4	9	38	[185]
P42·5	19·2	45	*c.* 11·0	26	57	10·8	25	3·8	9	35	—
27·2	12·4	46	8·3	31	67	*c.* 7·8	29	—	—	—	—

Description. Moderately involute, compressed; inner whorls as broad as high, with broad not very strong primary ribs and occasional tubercles; outer whorls higher than broad; venter smooth, subtabulate, distinct from whorl sides with prominent keel; body chamber with very close faint ribs, slightly stronger on outer part of whorl sides, fasciculate to very broad folds on inner part of whorl sides; radial line slightly flexed, strongly projected ventrally; end of phragmocone broken; aperture largely obscured, body chamber just over half a whorl in length.

Discussion. This specimen is distinguished from other *Witchellia* because at comparable size broad folds are developed as well as the fasciculate fine ribbing. In this and tuberculate inner whorls, it is comparable with the lectotype of *laeviuscula* (Westermann 1969*a*), but the ornamentation is much stronger on the Skye specimen, *falcata* Buckman (1926, pl. 688) lacks the finer ribbing and is more evolute.

Locality. Laeviuscula Zone; approximately 18 m below the top of the Massive Sandstone; ledge behind main waterfall in the Bearreraig Burn, Trotternish, Skye.

Witchellia aff. *romanoides* (Douvillé)

Plate 10, figs. 3–4

aff. 1885 *Ludwigia romanoides* Douvillé, pp. 28–30, pl. 3, figs. 3–4.
aff. 1885 *Harpoceras romanoides* Douvillé, Haug, p. 677.
aff. 1893 *Witchellia romanoides* (Douvillé), Haug, p. 309.
?non 1935 *Witchellia romanoides* Douvillé, Dorn, pp. 118–119, pl. 20, fig. 3; pl. 9, fig. 20.

Material. One specimen, HMS 26408.

Dimensions.

	D	Wh	H	Wb	B	W	Ud	U	Vw	V	Vb	^{s}Rd	^{s}R	^{s}Rn	C
	52·9	22·3	42	—	—	—	16·1	30	—	—	—	—	—	—	[225]
	49·0	20·5	42	11·6	24	57	15·3	31	4·7	10	41	—	—	—	—
	40·6	17·1	42	10·3	25	60	12·9	32	4·4	11	43	—	—	32/$\frac{1}{2}$wh	—
P	*c*. 33·3	13·7	41	9·5	29	69	10·9	33	3·7	11	39	*c*. 2·9	9	16/$\frac{1}{4}$wh	—
	—	11·5	—	8·9	—	77	9·4	—	3·2	—	36	—	—	—	—

Description. Moderately involute, compressed; inner whorls strongly ribbed, with faint primary ribs branching near umbilical edge and some prominent tubercles; on outer whorls tubercles disappear and ribbing becomes fainter and closer, body chamber striate with faint irregular ribbing; radial line flexed, strongly projected ventrally; venter smooth, broad, tabulate to slightly bisulcate, with prominent hollow keel; umbilical edge sharply rounded, becoming vertical. Suture (text-fig. 5C) simple with lateral lobe broad and open; last sutures approximated; aperture not preserved but body chamber at least five-eighths of a whorl.

Discussion. This specimen is distinguished from other *Witchellia* because it is more evolute and has tuberculate inner whorls although the style of ribbing is similar. It is similar only to *romanoides* (Douvillé), but differs in having a slightly broader more distinct venter.

Locality. Laeviuscula Zone; approximately 18 m below the top of the Massive Sandstones; ledge behind main waterfall in the Bearreraig Burn, Trotternish, Skye.

EXPLANATION OF PLATE 10

All figures natural size.

Figs. 1, 2. *Witchellia* aff. *laeviuscula* (J. de C. Sowerby); HMS 26407.

Figs. 3, 4. *Witchellia* aff. *romanoides* (Douvillé); HMS 26408.

Figs. 5, 6, 11, 12, 17–22, 25–30. *Pelekodites macer* (Buckman); 5, 6, HMS 15350/2; 11, 12, HMS 15350/4; 17, 18, HMS 15350/14; 19, 20, HMS 15350/15; 21, 22, HMS 15351/3; 25, 26, HMS 26412/13; 27, 28, HMS 26412/14; 29, 30, HMS 26412/17.

Figs. 7–10, 13–16. *Pelekodites zurcheri* (Douvillé); 7, 8, HMS 26410/1; 9, 10, HMS 26409/1; 13, 14, HMS 26410/3; 15, 16, HMS 26410/2.

Figs. 23, 24, 31–34. *Pelekodites minimus* (Hiltermann); 23, 24, HMS 26413/3; 31, 32, HMS 26413/2; 33, 34, HMS 26413/1.

Figs. 1–20, 23, 24, 31–34. Laeviuscula Zone; approximately 18 m below top of Massive Sandstones, ledge behind main waterfall in Bearreraig Burn.

Figs. 21, 22, 25–30. Sauzei Zone and Subzone; loose blocks from upper part of Massive Sandstones, Rudha Sughar, Bearreraig. Both localities in Trotternish, Skye.

PLATE 10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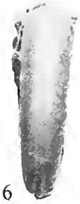
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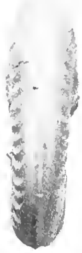
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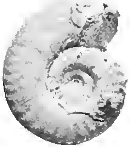
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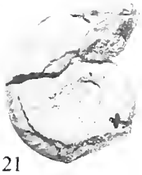
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MORTON, Scottish Bajocian ammonites

Genus PELEKODITES Buckman, 1923

Type species. Pelekodites pelekus Buckman, original designation by Buckman (1923, pl. 399).

Includes. Nannoceras Buckman, 1923, *Maceratites*, *Spatulites* Buckman, 1928.

Pelekodites zurcheri (Douvillé)

Plate 10, figs. 7–10, 13–16

1885 *Sonninia zurcheri* H. Douvillé, pp. 22–24, pl. 1, figs. 5–7.
?1889 *Poecilomorphus macer* S. Buckman, pl. 22, figs. 25–26 only.
1895 *Poecilomorphus moisyi* Brasil, pp. 36–37, pl. 3, figs. 6–7.
?1923 *Pelekodites pelekus* S. Buckman, pl. 399.
?1928 *Maceratites costulatus* S. Buckman, p. 11.
1937 *Sonninia zurcheri* Douvillé, Gillet, p. 48.
1968 *Sonninia* (*Poecilomorphus*) *boweri boweri* Buckman, Huf, pp. 36–44, pl. 1, figs. 6–7; pl. 2, figs. 1–5 (*pars*).

Material. Thirteen specimens, HMS 26409/1–5, HMS 26410/1–10.

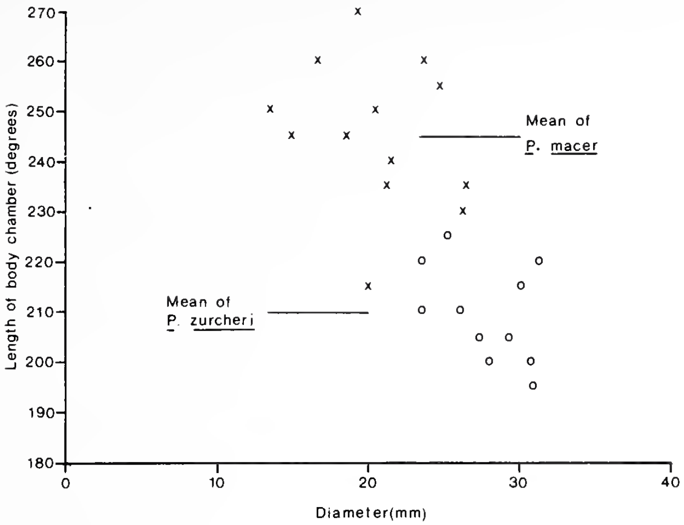
Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (forty-one observations): $H = 38{\cdot}5$ (1·8); $U = 36{\cdot}5$ (1·9); $V = 12{\cdot}1$ (1·7); $Vb = 42{\cdot}0$ (5·5); $^{s}R = 8{\cdot}3$ (1·4); $^{s}Rn = 16{\cdot}5/\frac{1}{2}wh$ (2·1); $C = 209{\cdot}6$ (9·6); $S = 33{\cdot}6$ (3·1). Maximum measured diameter is 31·1 mm in HMS 26410/3; lappets present on HMS 26409/1 at D 26·0 mm, on HMS 26410/1 at D 33·7 mm, and on HMS 26410/2 at D 30·7 mm. Regression equations are:

$$Wh = 0{\cdot}33\,D + 1{\cdot}07\ [0{\cdot}12]$$
$$Wb = 0{\cdot}16\,D + 2{\cdot}59\ [0{\cdot}17]$$
$$Ud = 0{\cdot}38\,D - 0{\cdot}32\ [0{\cdot}17]$$

Description. Moderately evolute, compressed; innermost whorls broader than high, smooth, with broad rounded venter lacking keel; during growth whorl height becomes greater than breadth, a keel develops, and a distinct smooth venter becomes tabulate; broad undulations on whorl sides develop into very short faint primary ribs (which disappear in later whorls) branching near umbilical edge into secondary ribs (still present in the body chamber) slightly stronger on outer part of whorl sides; development of ribbing at variable diameter; radial line flexed, strongly projected ventrally; umbilicus large and shallow with rounded edge; sutures simple with broad open lateral lobe (text-fig. 5D, E); several specimens mature (crowding of the last sutures, increase in relative umbilical diameter) with body chamber usually about seven-twelfths of a whorl and lappets up to 8·5 mm in length.

Discussion. The specimens are adult microconchs and differ from *macer* (see below) in having regularly ribbed shorter body chamber (see text-fig. 6). From specimens of *Witchellia* of similar size they differ in being more evolute, having a squarer whorl section, slightly different style of ribbing, and lappets.

The Skye specimens differ from *macer* Buckman in being more costate, from *aurifer* Buckman in having more regular ribbing, from *spatians* Buckman in being smaller, having more distant ribbing, a less complex suture, and a shorter body chamber, from *hansenbodensis* Maubeuge in having more curved ribbing. They are similar in style of ribbing to several described species, including *zurcheri* Douvillé, 1885, *moisyi* Brasil, 1895, *pelekus* Buckman, 1923, and *costulatus* Buckman, 1928, which probably belong to the one species. The oldest name, *zurcheri*, is used here. Several specimens of



TEXT-FIG. 6. Length of body chamber plotted against diameter for complete specimens only of *Pelekodites macer* (Buckman) (crosses) and *Pelekodites zurcheri* (Douvillé) (circles) from Skye.

Sonninia (*Poecilomorphus*) *boweri boweri* Huf (1968) non Buckman are very similar and almost certainly conspecific.

The specimens described by Buckman and Huf come from the Sowerbyi Zone, as does the lectotype of *zurcheri* (Douvillé 1885, pl. 1, fig. 6, designated by Buckman 1923), while Gillet (1937, p. 48) records the species from the Laeviuscula Zone in Lorraine.

Locality. Laeviuscula Zone; approximately 18 m below the top of the Massive Sandstone; ledge behind the main waterfall in the Bearreraig Burn, Trotternish, Skye.

Pelekodites macer (Buckman)

Plate 10, figs. 5–6, 11–12, 17–22, 25–30

1889 *Poecilomorphus macer* S. Buckman, pp. 116–117, pl. 22, figs. 23–24 only.
1895 *Poècilomorphus macer* Buckman, Brasil, p. 36.
1928 *Maceratites macer* S. Buckman, pp. 11–12.

Material. Forty-two specimens, HMS 15350/1–8, 14–16, 20, HMS 15351/1–9, HMS 26411/1–2, HMS 26412/1–19.

Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (eighty-six observations): H = 40·2 (3·1); U = 33·0 (2·8); V = 13·2 (2·5); Vb = 38·9 (11·4); ^{s}R = 6·8 (1·2); ^{s}Rn = 22·7/½wh (3·5) (^{s}R and ^{s}Rn are based on only a few measurements, most specimens show decline of the ribbing); C = 245·4 (14·6); S = 37·4 (7·9). Maximum measured diameter is 28·0 mm in HMS 15350/3 and HMS 26412/12; lappets present on HMS 15350/2 at D 26·5 mm, HMS 26412/17 at 23·7 mm:

$$\mathrm{Wh} = 0{\cdot}39\,\mathrm{D}+0{\cdot}24\ [0{\cdot}23]$$
$$\mathrm{Wb} = 0{\cdot}19\,\mathrm{D}+2{\cdot}09\ [0{\cdot}16]$$
$$\mathrm{Ud} = 0{\cdot}35\,\mathrm{D}-0{\cdot}26\ [0{\cdot}19]$$

Description. Moderately evolute, compressed; protoconch large and bulbous; innermost whorls broader than high, smooth, with broad rounded venter lacking keel; faint broad undulations develop into variable primary ribs and a keel develops; outer whorls higher than broad with primary ribs branching just above umbilical edge into secondary ribs, but ribbing irregular, sometimes fasciculate and fainter on middle of whorl sides; on outer whorls venter with keel, tabulate or slightly bisulcate; radial line flexed laterally, strongly projected ventrally; umbilicus large and shallow, with umbilical edge rounded not usually steep; sutures simple with broad open lateral lobe (text-fig. 5F, G); in some specimens crowding of sutures, relative widening of umbilicus and spatulate lappets up to 8·8 mm long (Pl. 9, figs. 29–30); body chamber about two-thirds of a whorl; HMS 26412/12 pathological, with keel and venter displaced to one side for at least the outer whorl which is visible.

Discussion. The specimens differ from *zurcheri* in having less regular ribbing and longer body chambers (see text-fig. 6), and from other specimens of similar size from the same localities in being more evolute, having more quadrate whorl section, a different style of ribbing, and lappets. Of described species of *Pelekodites*, Buckman's species *pelekus*, *nannomorphum*, *spatians*, *aurifer*, and *costulatus* are more strongly and more regularly ribbed, but *macer* is very similar. According to Buckman (1928, p. 12) the holotype of *macer* comes from the 'marl with green grains', Frogden Quarry, Dorset (Sonninian, *Witchellia* hemera), that is from the Laeviuscula Zone. The similar specimens described by Huf (1968) as *Sonninia* (*Poecilomorphus*) *boweri boweri* (Buckman) or *S.* (*P.*) *boweri buckmani* (Haug) are from the Sowerbyi and Sauzei Zones.

Localities. (*a*) HMS 15350/1–8, 14–16, 20, HMS 26411/1–2 are from the Laeviuscula Zone; approximately 18 m below the top of the Massive Sandstone; ledge behind main waterfall in the Bearreraig Burn; (*b*) HMS 15351/1–9, HMS 26412/1–19 are from the Sauzei Zone and Subzone; loose blocks from the uppermost part of the Massive Sandstone; Rudha Sughar. Both localities are at Bearreraig, Trotternish, Skye.

Pelekodites minimus (Hiltermann)

Plate 10, figs. 23–24, 31–34

1939 *Sonninia deltafalcata minima* Hiltermann, pp. 174–175, pl. 12, figs. 4, 6.
1968 *Sonninia* (*Poecilomorphus*) *boweri minima* (Hiltermann), Huf, pp. 50–53, pl. 4, figs. 4–6.

Material. Three specimens, HMS 26413/1–3.

Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (ten observations): H = 37·5 (3·3); U = 35·5 (4·6); V = 15·0 (4·3); Vb = 45·0 (7·3); C = 235; S = 18 (on HMS 26413/2 only). Diameters at apertures are 12·5 mm, 13·6 mm, and 17·3 mm; lappets present on HMS 26413/2 at D 13·6 mm and on HMS 26413/3 at 17·3 mm. Regression equations are:

$$\mathrm{Wh} = 0{\cdot}33\,\mathrm{D} + 0{\cdot}41\ [0{\cdot}11]$$
$$\mathrm{Wb} = 0{\cdot}15\,\mathrm{D} + 2{\cdot}13\ [0{\cdot}18]$$
$$\mathrm{Ud} = 0{\cdot}41\,\mathrm{D} - 0{\cdot}50\ [0{\cdot}05]$$

Description. Small, evolute; protoconch large bulbous, and smooth; first whorls smooth, broader than high, with broad smooth venter lacking keel; by second whorl broad blunt undulations on whorl sides; by D 4·0 mm a faint keel bordered by two shallow sulci appears, and whorls become higher than broad; on outer whorls and body chamber faint irregular fasciculate ribbing strongly curved backwards on upper part of whorl curving forwards on to venter; umbilical edge rounded not steep; there is slight increase in relative size of umbilicus in HMS 26413/1 and 2 while HMS 26413/2 and 3 have lappets, up to 3·7 mm in length; sutures simple (text-fig. 5H); in HMS 26413/2 the last two sutures are closer; body chamber about two-thirds of a whorl.

Discussion. The specimens are adult microconchs, reaching maturity at a much smaller size than others from the same bed—the end of the phragmocone being at diameter 8·6 mm in HMS 26413/2 and approximately 10 mm in HMS 26413/3. They are similar to specimens from Bethel, northern Germany, figured by Hiltermann (1939) and Huf (1968). This species (*minima*) is now transferred to *Pelekodites.* According to Huf (1968, p. 53) *P. minimus* occurs in the Sowerbyi Zone of northern Germany.

Locality. Laeviuscula Zone; approximately 18 m below the top of the Massive Sandstone; ledge behind main waterfall in the Bearreraig Burn, Trotternish, Skye.

Genus SONNINIA Bayle, 1879

Subgenus SONNINIA (SONNINIA) Bayle, 1879

Type species. Waagenia propinquans Bayle, 1878, original designation by Bayle in Douvillé's presentation of the Atlas (see *Bull. Soc. géol. Fr.* sér. 3, vol. 7, p. 92).

Includes. Sonninites Buckman, 1925 (not *Sonnites* as given by Arkell 1957, p. L267).

Sonninia (*Sonninia*) cf. *sowerbyi* (J. Sowerby)

Plate 11, figs. 3, 10

cf. 1818 *Ammonites Sowerbyi* Miller (MS.), J. Sowerby, p. 235, pl. 213.
cf. 1908 *Ammonites Sowerbii* J. Sowerby, Buckman and Secretary, text-fig. with explanation of pl. 3.

Material. One medium-sized specimen, HMS 26414.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U	^{s}Rn	Td	T	Tn	Tc	C
c. 89·0	31·2	35	—	—	—	34·7	39	15/$\frac{1}{4}$wh	var.	—	6/$\frac{1}{4}$wh	5	[180]
P 73·2	25·1	34	16·0	22	64	28·4	39	—	var.	—	—	—	—
52·8	21·5	41	*c.* 13·3	25	62	18·2	34	34/$\frac{1}{2}$wh	6·7	13	10/$\frac{1}{2}$wh	—	—
40·5	15·6	39	15·5	38	99	13·7	34	19/$\frac{1}{4}$wh	7·0	17	8/$\frac{1}{2}$wh	—	—

Description. Evolute, compressed; inner whorls with moderately strong distant ribbing and large tubercles, approximately six per whorl; on intermediate whorls ribbing stronger and tubercles larger and closer (approximately fourteen per whorl); last part of phragmocone missing; on body chamber more distant, less regularly developed tubercles remain with more pronounced curved ribbing branching at tubercles, and strongly projected ventrally; on intermediate and outer whorls whorl breadth (between tubercles) less than height; umbilicus large, shallow with rounded indistinct edge; venter acutely fastigate, also not distinct, with high prominent keel; body chamber incomplete at 180° (with trace of umbilical seam for a further 45°).

Discussion. This specimen differs from others from the same locality and from most described species in having the tubercles typical of the inner whorls still present on the body chamber along with well-developing ribbing. The type and distribution of tubercles on the body chamber are not comparable with those found on specimens of *Sonninia* (*Papilliceras*), especially in being less regular. The end of the phragmocone and of the body chamber are missing on the specimen so that it is impossible to establish whether it was mature. It cannot be matched exactly with any complete figured species. The inner whorls are very similar to the holotype of *sowerbyi* which lacks the outer whorls, so it is impossible to be certain of the exact nature of this species. Westermann and Riccardi (1972, p. 47) suggest that it may be the inner whorls of a *Sonninia* (*Papilliceras*). In the past *Sonninia sowerbyi* has been recorded from most parts of the Lower Bajocian, but it seems likely that the holotype and really typical *S. sowerbyi* as distinct from *Euhoploceras* spp. come from the Sauzei Zone.

Locality. Sauzei Zone and Subzone; loose block from the upper part of the Massive Sandstones; Rudha Sughar, Bearreraig, Trotternish, Skye.

Sonninia (*Sonninia*) cf. *propinquans* (Bayle)

Plate 12, figs. 5, 8; Plate 14, figs. 1–6

cf. 1878 *Waagenia propinquans* Bayle, pl. 84, figs. 1–6(?)
cf. 1922 *Sonninia propinquans* Bayle sp., Buckman, pl. 298.

Material. Eleven medium-sized to small specimens, HMS 15339, HMS 26415, HMS 26416, GSE 2972–2974, GSE 2976–2978, GSE 3020, GSE 3060.

Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (twenty observations): H = 41·6 (2·9); U = 34·0 (3·2); ^{s}Rn = 27·7/½wh (3·7); T = 25·6 (5·9); S = 74·6 (7·6). Maximum measured diameter is 73·1 mm in GSE 3060. Regression equations are:

$$\begin{aligned} Wh &= 0{\cdot}39\,D + 1{\cdot}08\ [0{\cdot}99] \\ Wb &= 0{\cdot}18\,D + 4{\cdot}11\ [0{\cdot}70] \\ Ud &= 0{\cdot}34\,D - 0{\cdot}06\ [1{\cdot}37] \end{aligned}$$

Description. Moderately evolute and compressed; innermost whorls smooth or ribbed, but by D 10 mm large distant blunt tubercles dominant; on intermediate whorls tubercles larger, sharper, and more regular, with more or less irregular strong

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EXPLANATION OF PLATE 11

All figures natural size.

Figs. 1, 2. *Sonninia* (*Papilliceras*) *arenata* (Quenstedt); HMS 15341/1.
Figs. 3, 10. *Sonninia* (*Sonninia*) cf. *sowerbyi* (Sowerby); HMS 26414.
Figs. 4–9. *Sonninia* (*Sonninia*) *corrugata* (Sowerby); 4, 5, HMS 15345/3; 6, 7, HMS 26417/16; 8, 9, HMS 26417/20.

All specimens (except figs. 4, 5) from Sauzei Zone and Subzone; loose blocks from upper part of Massive Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye.
Figs. 4, 5. Laeviuscula Zone; approximately 18 m below top of Massive Sandstones; ledge behind main waterfall in Bearreraig Burn, Trotternish, Skye.


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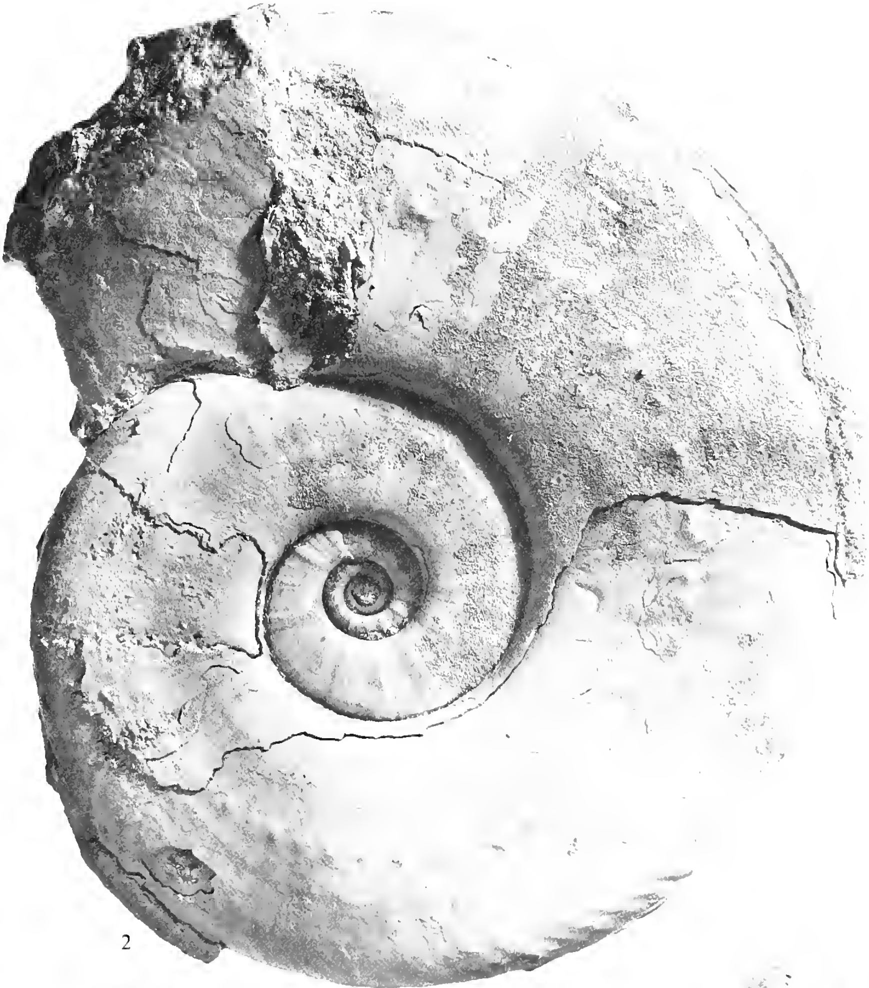
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MORTON, Scottish Bajocian ammonites

ribbing; on outer whorls tubercles more distant or less regular and outermost whorls only ribbed; last tubercle at varying diameter, up to 53 mm on GSE 3060; on outer whorls ribbing more regular, branching just below mid-whorl with secondary ribbing on upper part of whorl more prominent, but strength varies; ribs slightly curved on whorl sides, strongly projected ventrally; umbilical edge rounded, venter rounded—fastigate with prominent high keel; sutures complex, with long deeply divided lateral lobe (text-fig. 5I); body chamber mostly not preserved.

Discussion. These specimens differ from *sowerbyi* in that all show disappearance of the tubercles on the phragmocone, and in being slightly less compressed. Most lack body chamber so that it is not possible to predict the ornamentation of the adult whorls. It is possible that they are the inner whorls of *S.* (*Papilliceras*) *mesacantha* (Buckman) described below, but this does not seem likely because of the better-developed ribbing than typical of the inner whorls of *mesacantha*. They are closely comparable with *propinquans* (especially text-figs. 2–4), although Bayle's specimens show more pronounced ribbing. The problem of the lectotype of *propinquans* is discussed by Huf (1968, p. 26) and Westermann and Riccardi (1972, p. 47), with lectotype designation (of Bayle 1878, p. 84, figs. 3–4) attributed to Roman (1938). However, there is an earlier lectotype designation (of Bayle 1878, pl. 84, fig. 1) by Gillet (1937, pp. 30, 32). *Sonninia propinquans* is recorded from Dorset by Buckman (1922), from France by Mouterde *et al.* (1971, p. 11) and from the Basses Alpes by Pavia and Sturani (1968, p. 311), and in other areas from the Sauzei Zone (see also Gillet 1937, p. 29).

Locality. Sauzei Zone and Subzone; loose blocks from the upper part of the Massive Sandstones (identified from the matrix); Rudha Sughar, Bearreraig (except GSE 3060 from south of Bearreraig), Trotternish, Skye.

Sonninia (*Sonninia*) *corrugata* (Sowerby)

Plate 11, figs. 4–9; Plate 12, figs. 6–7; Plate 13, figs. 4–7

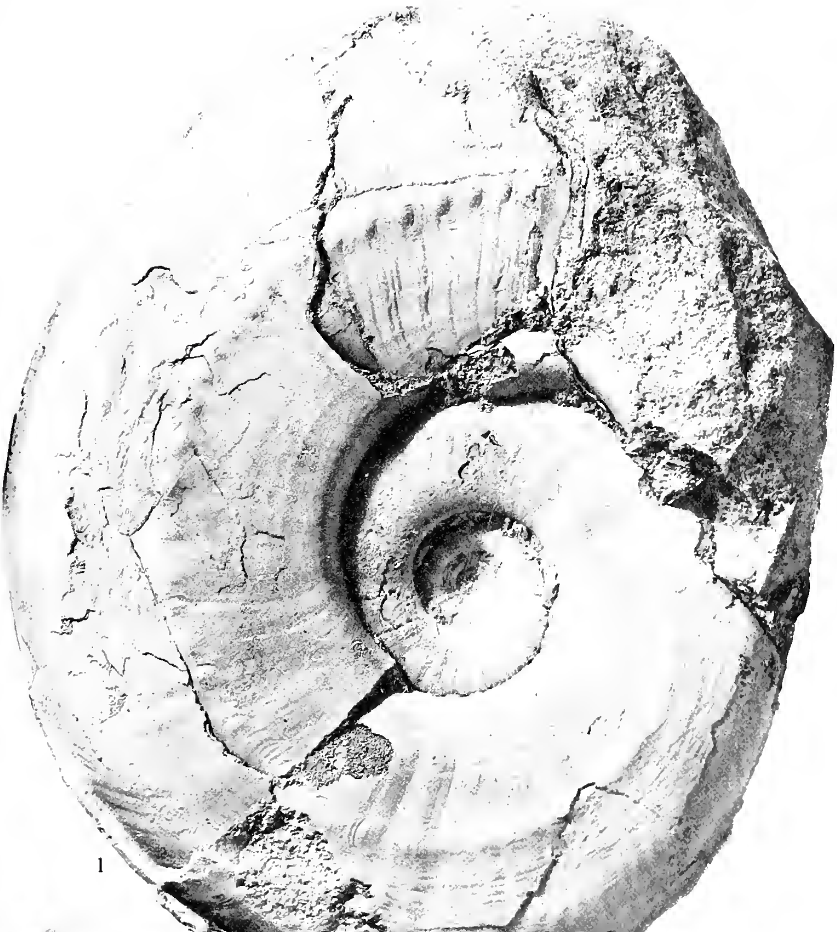
1824	*Ammonites corrugatus* J. de C. Sowerby, p. 74, pl. 451, fig. 3.
non 1885	*Ludwigia corrugata* Sowerby sp., Douvillé, pp. 26–28, pl. 2, figs. 1–5; pl. 3, figs. 1–2 (= *Witchellia sayni* Haug, 1893, p. 308).
1893	*Sonninia corrugata* (Sow.), Haug, p. 283, pl. 8, figs. 1–2.
1908	*Ammonites corrugatus* J. de C. Sowerby, Buckman and Secretary, pl. 4, fig. 4*a*, *b*.
1923	*Sonninia corrugata* J. de C. Sowerby sp., Buckman, pl. 412.
non 1926	*Sonninia corrugata* J. de C. Sowerby sp., Buckman, pl. 412A.
1935	*Witchellia corrugata* Sow., Dorn, pp. 107–108, pl. 5, fig. 4; pl. 9, fig. 2; text-fig. pl. 9, fig. 6.
1937	*Sonninia corrugata* Sowerby, Gillet, pp. 34–35, fig. 24.

EXPLANATION OF PLATE 12

All figures natural size.

Figs. 1, 2. *Sonninia* (*Papilliceras*) *arenata* (Quenstedt); GSE 2912.
Figs. 3, 4, 6, 7. *Sonninia* (*Sonninia*) *corrugata* (Sowerby); 3, 4, HMS 26417/1; 6, 7, HMS 26417/8.
Figs. 5, 8. *Sonninia* (*Sonninia*) cf. *propinquans* (Bayle); GSE 3060.

All specimens from Sauzei Zone and Subzone; loose blocks from upper part of Massive Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye, figs. 5, 8 from south of Bearreraig.



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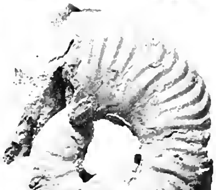

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MORTON, Scottish Bajocian ammonites

1939 *Sonninia corrugata* (Sow.) emend. Dorn, Hiltermann, pp. 163–164, pl. 11, fig. 7; text-figs. 38–39.

1958 *Sonninia corrugata* (Sow.), Oechsle, pp. 117–118.

Material. Thirty-two small specimens, HMS 15340/1–3, HMS 15345/1–5, HMS 26417/1–24, plus small nuclei.

Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (thirty observations): H = 42·7 (2·2); U = 32·4 (2·2); ^{s}R = 5·9 (1·5); ^{s}Rn = 24·4/$\frac{1}{2}$wh (2·7); C = 230 (one specimen only); S = 62·8 (4·8). Maximum measured diameter is 36·9 mm in HMS 15345/1. Regression equations are:

$$\begin{aligned} Wh &= 0{\cdot}46\ D - 0{\cdot}54\ [0{\cdot}24] \\ Wb &= 0{\cdot}28\ D + 1{\cdot}22\ [0{\cdot}30] \\ Ud &= 0{\cdot}27\ D + 1{\cdot}11\ [0{\cdot}17] \end{aligned}$$

Description. Moderately evolute, not very compressed, small; protoconch large and bulbous; innermost whorls smooth, broader than high, with broad rounded venter and keel by D = 2·0 mm; on intermediate and outer whorls keel more prominent; by D 10·0 mm whorl height greater than breadth; faint broad folds (at D = 3·5 mm) becoming more definite (by D = 7·3 mm) developing into close ribbing at varying diameters (generally greater than 10 mm); ribbing fasciculate from broad blunt folds on lowermost part of whorl sides, usually three ribs developed, sometimes with an extra rib intercalated; ribs slightly curved on whorl sides but projected ventrally, fading on to obtusely fastigate venter without distinct edges; umbilicus moderately broad, edge rounded, vertical, and overhanging in some; suture complex, with long deeply divided lateral lobe and slightly retracted umbilical lobe (text-fig. 5J, K); some have last sutures closer together; body chambers incomplete (except HMS 26417/16 with C = 230°) or not preserved.

Discussion. The specimens are smaller than some others from the same localities. Some are nuclei, others are presumably juveniles, but a few may be adults as suggested by crowding of the last few sutures. They differ from *Witchellia* and *Pelekodites* in whorl shape (less quadrate), fastigate rather than tabulate venter, different style of ribbing, and a much more complex suture line (this last is notable in view of the similarities in size). They differ from inner whorls of *Sonninia* (*Sonninia*) and *Sonninia* (*Papilliceras*) in having body chamber present and well-developed fasciculate ribbing but no tubercles, but shape of venter and complexity of suture are similar. The specimens do not resemble the inner whorls of any of the species of *Sonninia* (either subgenus), but must belong to a distinct small species, possibly of microconchs. They differ from most described species of *Sonninia* in size, and from figured specimens of comparable size in lacking tubercles and having fasciculate ribbing. In these features, and in the shape of the venter, they are similar to *Ammonites corrugatus* Sowerby (1824). The holotype of *corrugata* is wholly septate, while Buckman's specimen (pl. 412 only) has only the beginning of the body chamber preserved, so that the type material cannot be established as microconch. According to Buckman (1923) *S. corrugata* (Sowerby) comes from the *sauzei* hemera (i.e. Sauzei Zone) of Dundry, Somerset.

Localities. (i) HMS 15345/1–5 from Laeviuscula Zone; 18 m below the top of the Massive Sandstones; ledge behind main waterfall in the Bearreraig Burn. (ii) Other specimens from Sauzei Zone and Subzone; upper part of Massive Sandstones; Rudha Sughar, Bearreraig. Both localities are in Trotternish, Skye.

Subgenus SONNINIA (PAPILLICERAS) Buckman, 1920

Type species. Papilliceras papillatum Buckman, 1920, original designation by Buckman (1920, pl. 150).

Includes. Prepapillites Buckman, 1927.

Sonninia (*Papilliceras*) *arenata* (Quenstedt)

Plate 11, figs. 1–2; Plate 12, figs. 1–2

1886 *Ammonites arenatus* Quenstedt, pp. 482–484, pl. 60, fig. 10.
?1927 *Prepapillites arenatus* Quenstedt sp., Buckman, pl. 709.
1935 *Sonninia arenata* Quenstedt, Dorn, pp. 38–39, pl. 7, fig. 1; text-fig. pl. 3, figs. 3–4.
1951 *Papilliceras arenatum* Quenstedt sp., Maubeuge, pp. 49–50, pl. 3, fig. 2.
1958 *Sonninia patella arenata* (Quenstedt), Oechsle, p. 102, pl. 12, fig. 10.
?1964 *Sonninia* (*Papilliceras*) cf. *S. arenata* (Quenstedt), Imlay, p. B34, pl. 6, figs. 1–3.
?1973 *Sonninia* (*Papilliceras*) cf. *S.* (*P.*) *arenata* (Quenstedt), Imlay, p. 68, pl. 26, fig. 11.

Material. Seventeen specimens, HMS 15341/1–3, 6–8, HMS 26394, HMS 26396, HMS 26418/1–3, BkC F329, GSE 2911–2912, GSE 7102, Call. J460.

Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (sixty-three observations): H = 41·1 (3·4); U = 32·0 (3·8); ^{s}Rn = 34·9/$\frac{1}{2}$wh (5·1); T = 7·3 (2·3); Tn = 18·6/$\frac{1}{2}$wh (4·4) (on outer whorls only); C = 236·4 (19·1); S = 61·7 (7·9). Maximum measured diameter is 186·4 mm on HMS 26394. H and U vary slightly with growth (see text-fig. 7).

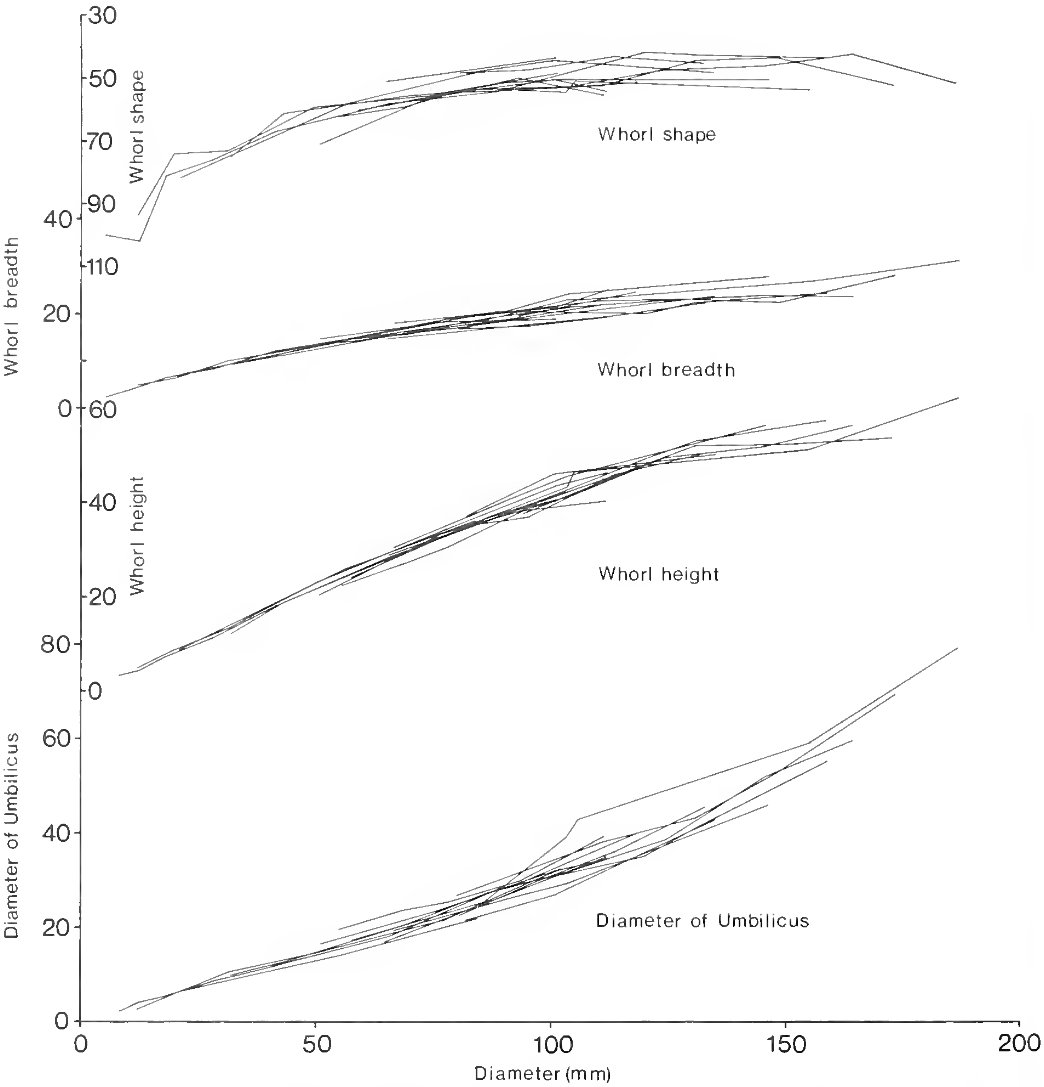
	Aperture	Body chamber	Phragmocone
H	35·0	38·1 (3·5)	42·5 (2·1)
U	37·3	33·9 (3·6)	31·4 (3·4)

Regression equations (see also text-fig. 7) are:

$$Wh = 0{\cdot}34\ D + 5{\cdot}22\ [5{\cdot}65]$$
$$Wb = 0{\cdot}14\ D + 6{\cdot}11\ [4{\cdot}04]$$
$$Ud = 0{\cdot}38\ D - 4{\cdot}26\ [13{\cdot}30]$$

Description. Evolute and compressed, becoming more so with growth; inner whorls as broad as high, with broad rounded venter developing a distinct keel by D 3·5 mm, and with distant blunt tubercles; by D 8·5 mm whorl height exceeds breadth (text-fig. 7) and specimens become suboxyconic when fully grown with whorl sides subparallel; inner whorls with broad blunt ribbing which remains on intermediate whorls where striae may also be developed; ribbing fainter on outer whorls, penultimate whorl of most almost smooth but faintly ribbed on others; at about same stage in growth a faint longitudinal ridge appears on middle of whorl sides and develops on outer whorl into progressively more distinct small tubercles (papillae); on some specimens distinct secondary ribbing develops on upper part of whorl sides; umbilical edge rounded, steep but never vertical; venter not distinct from whorl sides, fastigate with a very high keel, hollow on body chamber but floored on phragmocone; suture extremely complex with long, deeply divided lobes, especially lateral lobe, and very slightly retracted umbilical lobe (text-fig. 8A, B); several specimens with last two or three sutures closer together, complete body chamber and pronounced relative widening of the umbilicus; aperture curved with pronounced ventral projection; three specimens with aptychus preserved inside body chamber (Morton 1973).

Discussion. The specimens are adult macroconchs and the development of the



TEXT-FIG. 7. Umbilical diameter, whorl height, whorl breadth, and whorl shape plotted against diameter for specimens of *Sonninia* (*Papilliceras*) *arenata* (Quenstedt) from Skye.

EXPLANATION OF PLATE 13

All figures natural size.

Figs. 1, 2. *Sonninia* (*Papilliceras*) *mesacantha* (Waagen); HMS 26419.

Fig. 3. *Sonninia* (*Papilliceras*) *mesacantha* (Waagen) with aptychus; HMS 26395.

Figs. 4–7. *Sonninia* (*Sonninia*) *corrugata* (Sowerby); 4, 5, HMS 26417/5; 6, 7, HMS 15345/2.

All specimens (except figs. 6, 7) from Sauzei Zone and Subzone; loose blocks from upper part of Massive Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye.

Figs. 6, 7, from Laeviuscula Zone; approximately 18 m below top of Massive Sandstones, ledge behind main waterfall in Bearreraig Burn, Trotternish, Skye.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MORTON, Scottish Bajocian ammonites

tubercles on the body chamber is characteristic of *Papilliceras*, though most of the species figured by Buckman (1909–1930) are more strongly ornamented, especially on the inner whorls. They are almost identical in ornamentation, etc., with the holotype of *arenata*, although this specimen is much larger (D = 285 mm according to Dorn 1935, p. 38, cf. 186 mm in HMS 26394). The specimens figured by Buckman (1927) and Imlay (1964), and GSE 2911 have much larger tubercles on the body chamber, and may not belong in this species (see also discussion of *mesacantha* below). *S.* (*P.*) *arenata* was recorded by Quenstedt (1886, p. 482) from Brauner Jura γ and by Dorn (1935, p. 120) from 'unteres Gamma', which is in the Sowerbyi Zone according to Westermann (1967, p. 50). Oechsle (1958, p. 102) states that the type specimen comes from the Blaukalk (i.e. Sauzei Zone) and not the '*sowerbyi*-Zone'. Buckman's specimen comes from the '*Shirbuirnia* hemera', while Mouterde *et al.* (1971, p. 11) record the species from the Laeviuscula Zone. In Skye the species was found in loose blocks from the upper part of the Massive Sandstones, thought to be in the Sauzei Zone.

Locality. Sauzei Zone and Subzone; loose blocks from the upper part of the Massive Sandstones; Rudha Sughar, Bearreraig, Trotternish, Skye. One specimen (Call. J460) was found at the waterfall in the Bearreraig Burn.

Sonninia (*Papilliceras*) *mesacantha* (Waagen)

Plate 13, figs. 1–3; Plate 14, figs. 7–9; Plate 15, fig. 1

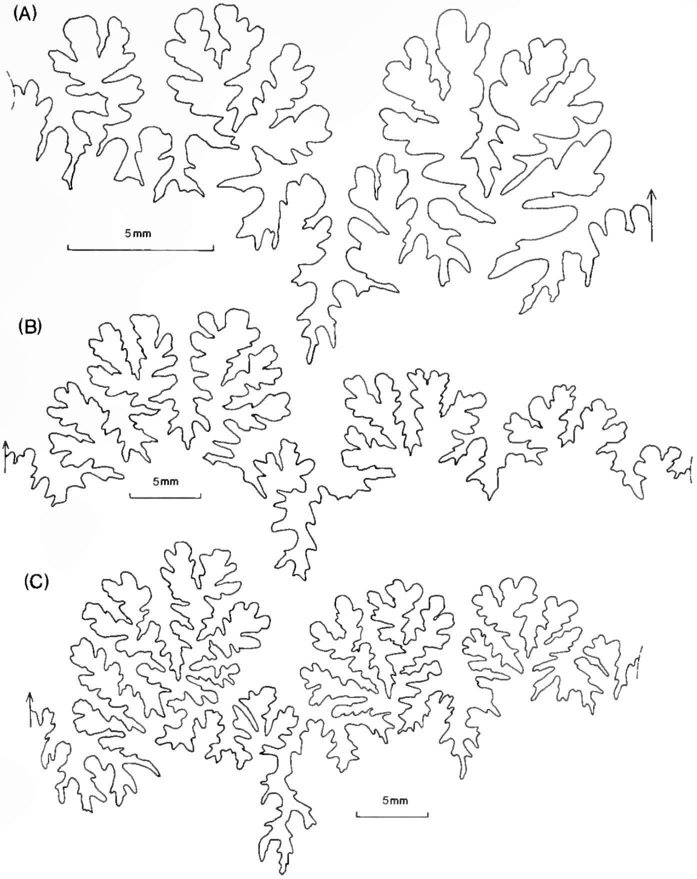
1867 *Ammonites mesacanthus* Waagen, pp. 594–595, pl. 28, fig. 1*a*, *b*.
1885 *Hammatoceras mesacanthum* Waag., Haug, pp. 654–655.
1925 *Papilliceras mesacanthum* Waagen sp., Buckman, pls. 557A, B.
1925 *Papilliceras micracanthicum* Buckman, pl. 611.
1935 *Sonninia mesacantha* Waagen, Dorn, pp. 43–44, pl. 8, figs. 1, 4; text-fig. pl. 4, fig. 1.
1937 *Sonninia mesacantha* Waagen, Gillet, pp. 16–18, fig. 8.
1958 *Sonninia mesacantha* (Waagen), Oechsle, pp. 83–84, pl. 10, fig. 3.

Material. Seven specimens, HMS 26395, HMS 26419, HMS 26420/1–3, GSE 2913, GSE 2971.

Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (twenty observations): H = 41·1 (2·7); U = 32·1 (2·9); ^{s}Rn = 31·3/$\frac{1}{2}$wh (0·9) (on two specimens only); T = 9·1 (5·2); Tn = 16·8/$\frac{1}{2}$wh (7·4); C = 240 and 280; S = 62·0 and 63·0 (both C and S measurable only on two specimens). Maximum measured diameter is 165·0 mm on HMS 26419. Regression equations are:

$$\mathrm{Wh} = 0{\cdot}34\,\mathrm{D} + 5{\cdot}52\ [5{\cdot}65]$$
$$\mathrm{Wb} = 0{\cdot}14\,\mathrm{D} + 7{\cdot}29\ [2{\cdot}61]$$
$$\mathrm{Ud} = 0{\cdot}36\,\mathrm{D} - 3{\cdot}64\ [8{\cdot}78]$$

Description. Evolute compressed, but less than *arenata*; inner whorls broader than high with broad rounded venter and high distinct keel by D 8·5 mm; by D 19 mm whorl height exceeds breadth and with growth whorl section becomes more compressed, venter narrower and more acute, and keel more prominent; innermost whorls almost smooth but by D about 8 mm broad, blunt undulations present developing into distinct ribbing and very large tubercles; on middle whorls large tubercles but ribbing less pronounced; on outer whorls tubercles disappear more or less abruptly at varying diameters and generally penultimate whorl (well before end of phragmocone on larger specimens) smooth or striate, sometimes with very faint



TEXT-FIG. 8. Suture lines of A, *Sonninia* (*Papilliceras*) *arenta* (Quenstedt), HMS 15341/2 at Wh 22·3 mm (× 3·8); B, *Sonninia* (*Papilliceras*) *arenata* (Quenstedt), HMS 15341/3 at Wh 40·2 mm (Quenstedt), HMS 15341/3 at Wh 40·2 mm (× 1·8); C, *Sonninia* (*Papilliceras*) *mesacantha* (Waagen), HMS 26420/1 at Wh 38·5 mm (× 1·8).

ribbing; a faint longitudinal ridge (approximately at mid-whorl) develops into distinct small tubercles; outer whorls with whorl sides slightly convex, umbilical edge sharply rounded with umbilical face steep but not vertical; venter fastigate, with very high keel hollow on body chamber but floored on phragmocone; suture highly complex (text-fig. 8C), with long, deeply divided lateral lobe and one other prominent lobe, slightly retracted; body chamber preserved on several specimens, complete on two with part of aperture preserved, and relative widening of umbilicus but no crowding of sutures. One specimen has the aptychus preserved inside the body chamber (see Morton 1973, and Pl. 13, fig. 3).

Discussion. The specimens are mostly adult macroconchs and differ from *arenata* in the presence of prominent tubercles on the inner whorls. The development of the tubercles on the body chamber is very similar in the two species and is characterstic of *Papilliceras*. Of the species referred to *Papilliceras*: *papillata* and *acanthera* have stronger ornamentation and lack the almost smooth stage, as does *pseudoarenata* (Maubeuge); *arenata* (both Quenstedt's and Buckman's) does not have the tuberculate inner whorls. They are very similar to *mesacantha* and *micracanthica*, although these are almost twice the size. All show tuberculate inner whorls followed by smooth intermediate whorls and then papillate outer whorls. The variation in the Skye specimens, especially in the diameter at which the tubercles on the inner whorls fade, suggests that all belong to the same species, although the holotype of *mesacantha* shows a very short smooth stage between the tuberculate inner whorls and the papillate outer whorls. No data illustrating variation in populations of *mesacantha* are available so that it seems best to group all the specimens discussed above in one species.

Westermann and Riccardi (1972, p. 75) comment on a specimen from Skye which they consider as intermediate between *mesacantha* and *arenata* and suggest that both should be in one species. Similar arguments have been used by Westermann for other sonniniids, and if individual specimens are considered in isolation, or if all European specimens regardless of locality and precise stratigraphical horizon are lumped together then there may be some justification for this view. However, the fact that in the Skye fauna at least there are two distinct types (one with smooth inner whorls, the other with tuberculate inner whorls to varying diameters) suggests that the taxonomic situation is more complex than Westermann's suggestion indicates.

The stratigraphical position of Dorn's specimen (Pl. 8, fig. 1) is doubtful, but Buckman (1925) records his *mesacantha* from the '*sauzei* hemera' and *micracanthica* from the '*propinquans* hemera', both of which would now be regarded as equivalent to the Sauzei Zone. This is the same as given by Waagen (1867, p. 595), confirmed by Oechsle (1958, p. 84), Pavia and Sturani (1968, p. 311), Westermann and Riccardi (1972, pp. 74–75), and most other authors (but cf. Gillet 1937, p. 16).

Locality. Sauzei Zone and Subzone; loose blocks from the upper part of the Massive Sandstones; Rudha Sughar, Bearreraig, Trotternish, Skye.

'*Sonninia*' aff. *furticarinata* (Quenstedt)

Plate 15, fig. 2; Plate 16, figs. 1–2; Plate 17, figs. 3–4

aff. 1858 *Ammonites furticarinatus* Quenstedt, p. 120, pl. 14, fig. 6.
aff. 1886 *Ammonites furticarinatus* Quenstedt, pp. 553–559, pl. 68, figs. 5–8.
aff. 1893 *Sonninia furticarinata* (Quenst.), Haug, pp. 286–287, pl. 8, figs. 3–4.
aff. 1935 *Sonninia furticarinata* Quenstedt, Dorn, pp. 49–50, pl. 20, figs. 1–2; pl. 4, figs. 8–10.
aff. 1958 *Sonninia furticarinata* (Quenstedt), Oechsle, pp. 98–100, pl. 11, figs. 3, 6; pl. 20, fig. 2.

EXPLANATION OF PLATE 14

All figures natural size.

Figs. 1–6. *Sonninia* (*Sonninia*) cf. *propinquans* (Bayle); 1, 2, GSE 2973; 3, 4, GSE 2972.

Figs. 7–9. *Sonninia* (*Papilliceras*) *mesacantha* (Waagen); 7, 8, HMS 26420/2; 9, HMS 26420/1, ventral view of Plate 15, fig. 1.

All specimens from Sauzei Zone and Subzone; loose blocks from upper part of Massive Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye.

PLATE 14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MORTON, Scottish Bajocian ammonites

Material. Three large specimens and five fragments, HMS 15338, HMS 26421/1-2, HMS 26422/1-2, HMS 26423/1-2, HMS 26424.

Dimensions. For the full list of dimensions see deposited data. Mean and standard deviation for characters which show little variation with growth are (twelve observations): H = 46·2 (2·6); U = 24·3 (4·2); V = 10·6 (1·5); Vb = 39·1 (2·9); S = 58·0 and 67·0 (two specimens only). Maximum measured diameter is c316·0 mm in HMS 15338. Regression equations are:

$$\begin{aligned} Wh &= 0{\cdot}48\ D - 2{\cdot}66\ [14{\cdot}98] \\ Wb &= 0{\cdot}19\ D + 9{\cdot}36\ [14{\cdot}06] \\ Ud &= 0{\cdot}18\ D + 7{\cdot}84\ [2{\cdot}34] \end{aligned}$$

Description. Large, moderately involute, compressed; by D 4 mm whorl broader than high, distant large blunt tubercles present, and venter broad and carinate-bisulcate; on later whorls height greater than breadth, tubercles develop into broad blunt distant ribs (which sometimes branch low on the whorl sides); on intermediate whorls ribbing gradually fades (by D c60 mm on HMS 15338, by D c85 mm on HMS 26421/1); outer whorls smooth or striate; at about same stage whorl sides almost parallel and venter less well defined, subtabulate and eventually fastigate; high prominent keel throughout; umbilical shoulder sharply rounded, umbilical face approximately vertical; suture complex, with long deeply divided lateral lobe (Pl. 15, fig. 2); body chambers incomplete.

Discussion. The specimens are larger and smoother than most species of sonniniid and seem to be similar only to *furticarinata* (Quenstedt). They are very close to Quenstedt's species in proportions and in ornamentation—with ribbed inner whorls and striate outer whorls, but differ in the bisulcate rather than rounded venter on the inner whorls.

The precise systematic position of these specimens is uncertain. They differ from typical *Sonninia* in ornamentation and the bisulcate becoming obtusely fastigate venter, though they do have a similar complex suture line. The suture is much more complex than that typical of *Dorsetensia*, though the whorl shape and ornamentation of the inner whorls (especially the carinate-bisulcate venter) suggest that they may be related to *Dorsetensia pinguis*, *hannoverana*, and *hebridica* (Morton 1972) with which they occur in part (see also Table 2).

According to Quenstedt (1886, pp. 553–559), Dorn (1935, p. 120), Oechsle (1958, p. 124), and others, '*Sonninia*' *furticarinata* comes from the lower part of Dogger δ in southern Germany, that is, the lower part of the Humphriesianum Zone.

EXPLANATION OF PLATE 15

All figures natural size unless otherwise stated.

Fig. 1. *Sonninia* (*Papilliceras*) *mesacantha* (Waagen); HMS 26420/1; Sauzei Zone and Subzone; loose block from upper part of Massive Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye.

Fig. 2. '*Sonninia*' aff. *furticarinata* (Quenstedt); HMS 26423/2; fragment of phragmocone showing suture; ?Hebridica Subzone, Sauzei Zone; loose block from lower 30 m of Upper Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye, ×0·75.

Figs. 3, 4. *Emileia* (*Emileia*) sp.; Call. J468; ?Sauzei Zone; loose block from Massive Sandstones, Bearreraig, Trotternish, Skye.

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MORTON, Scottish Bajocian ammonites

Localities. (i) Hebridica Subzone, Sauzei Zone; basal bed of the Upper Sandstones; foot of cliff east of Torvaig, near Portree (HMS 15358, HMS 26421/1–2). (ii) Sauzei Zone (Hebridica Subzone) or Humphriesianum Zone; loose blocks from the lower 30 m of the Upper Sandstones; Rudha Sughar, Bearreraig (HMS 26422/1–2, HMS 26423/1–2). (iii) Cycloides Subzone, Humphriesianum Zone; lower part of the Upper Sandstones; shore south of Rigg waterfall (HMS 26424). All localities are in Trotternish, Skye.

Genus DORSETENSIA Buckman, 1892

Type species. Ammonites edouardianus d'Orbigny, 1844, original designation by Buckman (1892, p. 302).

Discussion. The genus *Dorsetensia* has been discussed earlier by me (Morton 1972) and by Westermann and Riccardi (1972, pp. 96–105) and Imlay (1973, p. 7) (see also Table 2). The only further comments are that poorly preserved specimens of *D. pinguis* (Roemer) (HMS 26425/1–4) occur in loose blocks from the lower part of the Upper Sandstones at Bearreraig (Pl. 16, fig. 7), and that the maximum size of Skye *Dorsetensia* is less than that of the same species in other areas. Buckman (*in* Lee and Bailey 1925, pp. 105–106) identified four species of *Dorsetensia* from Port nam Marbh, Isle of Mull. These specimens (GSE 2835–2836, 2876–2877) are small and not very well preserved, so that the specific identifications must be treated with reserve, but they are enough to confirm the occurrence of the genus in Mull.

Superfamily STEPHANOCERATACEAE Neumayr, 1875
Family STEPHANOCERATIDAE Neumayr, 1875
Subfamily STEPHANOCERATINAE Neumayr, 1875
Genus EMILEIA Buckman, 1898

Using the same taxonomic procedure for the stephanoceratids as before (Morton 1971*a*, following Westermann 1964), macroconch and microconch subgenera *E.* (*Emileia*) and *E.* (*Otoites*) respectively are recognized.

EXPLANATION OF PLATE 16

All figures natural size unless otherwise stated.

Figs. 1, 2. '*Sonninia*' aff. *furticarinata* (Quenstedt); HMS 26421/1; Hebridica Subzone, Sauzei Zone; basal bed of Upper Sandstones, Torvaig, Trotternish, Skye. 1, ×0·9; 2, ×1.

Figs. 3, 4. *Strigoceras bessinum* Brasil; HMS 26428; Sauzei Zone and Subzone; loose block from upper part of Massive Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye.

Figs. 5, 6. *Emileia* (*Otoites*) sp. nov.; HMS 26426; Laeviuscula Zone; approximately 18 m below top of Massive Sandstones, ledge behind main waterfall in Bearreraig Burn, Trotternish, Skye.

Fig. 7. *Dorsetensia pinguis* (Roemer); HMS 26425/2; Hebridica Subzone, Sauzei Zone; loose block from lower part of Upper Sandstones, Rudha Sughar, Bearreraig, Trotternish, Skye.

Fig. 8. *Poecilomorphus cycloides* (d'Orbigny); HMS 26427; Cycloides Subzone, Humphriesianum Zone; lower part of Upper Sandstones, shore just north of Rigg waterfall, Trotternish, Skye.

Figs. 9, 10. *Garantiana* (*Garantiana*) ?*baculata* (Quenstedt) Morton, 1971 = *Pseudogarantiana dichotoma* (Bentz) teste. Pavia, 1973; Subfurcatum or Garantiana Zone; loose block probably from upper part of Upper Sandstones, Bearreraig, Trotternish, Skye.

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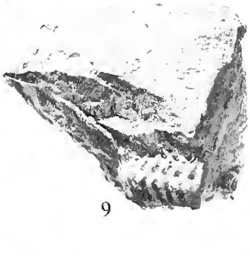

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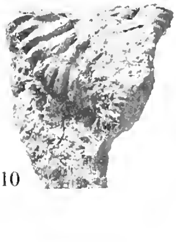

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MORTON, Scottish Bajocian ammonites

Macroconch subgenus EMILEIA (EMILEIA) Buckman, 1898

Type species. Ammonites brocchii J. Sowerby, 1818, original designation by Buckman 1898.

Emileia (*Emileia*) sp.

Plate 15, figs. 3–4

Material. One specimen, Call. J468.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U	^{p}Rd	^{p}R	^{p}Rn	^{s}Rn	C
52·0	25·0	48	*c.* 31·0	60	124	*c.* 14·0	27	3·0	6	8/$\frac{1}{4}$wh	30/$\frac{1}{2}$wh	[*c.* 240]

Description. Involute, cadicone; venter very broad, rounded not distinct from whorl sides; umbilical edge rounded, overhanging, umbilicus deep; fairly strong primary ribs branch into close faint secondary ribs which are uninterrupted across venter; just under three-quarters of a whorl of body chamber present; aperture not preserved.

Discussion. The specimen is not sufficiently well preserved for definite identification, but the width of the whorls and the strength of the ribbing suggests that it is an *Emileia* rather than an *Otoites*, and it is similar to *subcadiconica* Buckman. *Emileia* occurs mainly in the Sowerbyi and Sauzei Zones (e.g. see Westerman 1964, p. 52).

Locality. ?Sauzei Zone and Subzone; loose block from the Massive Sandstones (judging from the matrix); Bearreraig, Trotternish, Skye.

Microconch subgenus EMILEIA (OTOITES) Mascke, 1907

Type species. Ammonites sauzei d'Orbigny, 1846, original designation by Mascke (1907, p. 23).

Emileia (*Otoites*) sp. nov.

Plate 16, figs. 5–6

Material. One small specimen, HMS 26426.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U	Td	T	Tn	^{s}Rn	C
12·0	5·7	48	9·5	79	167	3·4	28	1·4	12	11/$\frac{1}{2}$wh	29/$\frac{1}{2}$wh	[170]

Description. Involute, cadicone; very broad rounded venter separated from lower part of whorl sides by sharply rounded shoulder on which prominent small closely spaced tubercles present; on lower part of whorl sides primary ribs strongly prorsiradiate slightly curved, each terminating in a tubercle; from each tubercle two rectiradiate almost straight secondary ribs branch almost immediately, uninterrupted across venter; suture moderately complex, with second lateral saddle almost as large as first lateral saddle, and umbilical lobe retracted; last four septa approximated; just under half a whorl of body chamber preserved; aperture broken, part of peristome, including lappets, displaced.

Discussion. The specimen seems to be an adult microconch. The style of the ornamentation and the relative size of the umbilicus are typical of *Otoites*. The specimen is much smaller and the ornamentation is closer and finer than the species of *Otoites* figured by Buckman, Westermann (1954), and other authors, although the closest would be *delicatus* Buckman 1913. It may belong to a new miniature species.

Locality. Laeviuscula Zone; approximately 18 m below the top of the Massive Sandstones; ledge behind main waterfall in Bearreraig Burn, Trotternish, Skye.

Superfamily HAPLOCERATACEAE Zittel, 1884
Family HAPLOCERATIDAE Zittel, 1884
Genus POECILOMORPHUS Buckman, 1889

Type species. Ammonites cycloides d'Orbigny, 1845, original designation by Buckman (1889, p. 115).

Discussion. According to Sturani (1971, p. 99) *Poecilomorphus*, with microconch subgenus *Micropoecilomorphus*, evolved from *Toxamblyites* (Buckman 1924) (misspelt *Toxalambites* by Sturani) and should therefore be placed in the superfamily Haplocerataceae, family Haploceratidae (cf. Arkell 1957). *Poecilormorphus* was also discussed by Huf (1968), although none of the species described by him belong in this genus but rather to *Pelekodites* or *Dorsetensia* (see also Morton 1972), and by Imlay (1973, pp. 7–8, 75).

Poecilomorphus cycloides (d'Orbigny)

Plate 16, fig. 8

1844 *Ammonites cadomensis* (non Defrance) d'Orbigny, pl. 121, figs. 1–6.
1845 *Ammonites cycloides* d'Orbigny, p. 370.
1889 *Poecilomorphus cycloides* (d'Orbigny), Buckman, pp. 117–121, pl. 22.
1971 *Poecilomorphus cycloides* (d'Orbigny), Sturani, pp. 100–110, pl. 8, figs. 1–21; pl. 9, figs. 12–16.

Material. One specimen, HMS 26427.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U	Vw	V	Vb	Rd	R	Rn
27·4*	15·5*	60*	9·0*	33*	58*	4·4*	16*	5·0*	18*	56*	3·0	11	13/½wh

Description. Involute; subquadrate whorls (but distorted during compaction); large blunt ribs, strongly rursiradiate but curving forwards on to venter, confined to upper part of whorl sides, fading just below mid-whorl; venter broad, carinate-bisulcate.

Discussion. In spite of the crushing the specimen can be seen to fall within the range of variation of *P. cycloides* as described by Sturani, near typical *cycloides* of Buckman (1927, pp. 9–11). According to Sturani and others, *P. cycloides* is typical of the lower part of the Humphriesianum Zone (Cycloides Subzone).

Locality. Cycloides Subzone, Humphriesianum Zone; lower part of the Upper Sandstones; shore just north of Rigg waterfall, Trotternish, Skye.

Superfamily OPPELIACEAE Bonarelli, 1894
Family STRIGOCERATIDAE Buckman, 1924
Genus STRIGOCERAS Quenstedt, 1886

Type species. Ammonites truellei d'Orbigny, 1845, original designation by Quenstedt (1886, pp. 565–566).

Strigoceras bessinum Brasil

Plate 16, figs. 3–4

1895 *Strigoceras bessinum* Brasil, pp. 43–44, pl. 4, figs. 6–7.
1971 *Strigoceras bessinum* Brasil, Sturani, pp. 118–119, pl. 4, figs. 16–19.

Material. One small specimen, HMS 26428.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U	C
12·6	7·1	56	3·8	30	54	1·6	13	[*c.* 60]

Description. Involute, oxyconic, maximum thickness below mid-whorl; venter acutely fastigate with low keel; smooth or very faint close ribbing; body chamber partly preserved.

Discussion. The specimen is smaller than, but otherwise similar to, *Strigoceras bessinum* Brasil, from the Humphriesianum Zone.

Locality. Sauzei Zone and Subzone; loose block from the uppermost part of the Massive Sandstone, Rudha Sughar, Bearreraig, Trotternish, Skye.

Superfamily PERISPHINCTACEAE Steinmann, 1890
Family PERISPHINCTIDAE Steinmann, 1890
Subfamily ZIGZAGICERATINAE Buckman, 1920
Genus PROCERITES Siemiradzki, 1898

Procerites sp.

Plate 17, figs. 1–2

Material. One specimen, Call. J467.

Dimensions.

D	Wh	H	Wb	B	W	Ud	U
c. 140·0	51·4*	37*	—	—	—	42·8*	31*
122·0*	49·1*	40*	24·2*	20*	49*	*c.* 35·5*	29*

Description. Poorly preserved internal mould of body chamber and part of phragmocone and one inner whorl; broad blunt primary ribs branch near mid-whorl into closer and fainter secondary ribs; ribbing straight, approximately rectiradiate, uninterrupted over venter. On one inside wall of body chamber are several serpulids.

Discussion. The ornamentation is typical of *Procerites*, but the preservation is too poor to allow more precise identification. The presence of the serpulids suggests that the empty shell may have drifted.

EXPLANATION OF PLATE 17

All figures natural size.

Figs. 1, 2. *Procerites* sp.; Call. J467; ?Upper Bajocian; loose block possibly from White Sandstone (Great Estuarine Series), Rudha Sughar, Bearreraig, Trotternish, Skye.

Figs. 3, 4. '*Sonninia*' aff. *furticarinata* (Quenstedt); HMS 26421/1; inner whorls of Plate 16, figs. 1, 2; Hebridica Subzone; Sauzei Zone; basal bed of Upper Sandstones, Torvaig, Trotternish, Skye.

PLATE 17

MORTON, Scottish Bajocian ammonites

Locality. The specimen was found by Dr. J. H. Callomon at Rudha Sughar, Bearreraig. The matrix, a medium grey calcareous sandstone with a few dark grey carbonaceous streaks, indicates that it is certainly not derived from the Upper Sandstones, and probably not from the Massive Sandstones. More likely is derivation from the White Sandstone in the Great Estuarine Series, because *Procerites*, though mainly Lower–Middle Bathonian (Arkell 1957, p. L315), does range down into Upper Bajocian but not to Sauzei Zone.

DISCUSSION AND SUMMARY

A modified scheme of Lower Bajocian zones or subzones is used in Skye: Discites, Ovalis, Laeviuscula, Sauzei (with subzones Sauzei and Hebridica), and Humphriesianum (with subzones Cycloides, Humphriesianum, and Blagdeni). The first three are used informally at present to replace Sowerbyi, but Sauzei and Humphriesianum, with these subzones, can be regarded as part of a formal scheme. Revisions of earlier biostratigraphy include: (*a*) redefinition of the base of the Humphriesianum Zone to exclude the newly defined Hebridica Subzone means that the base of the Humphriesianum Zone in Trotternish lies a short distance above the base rather than coinciding with the base of the Upper Sandstones; (*b*) discovery of *Garantiana* in a loose block of the Upper Sandstones means that the base of the Upper Bajocian must lie an unknown distance below the top of the Upper Sandstones.

A modified generic classification of part of the family Sonniniidae is used and discussed: *Euhoploceras* (with subgenera *Euhoploceras* and *Fissilobiceras*), *Shirbuirnia*, *Witchellia*, *Pelekodites*, *Sonninia* (with subgenera *Sonninia* and *Papilliceras*), and *Dorsetensia*. The species represented are described and discussed, as are species of some non-sonniniid genera including *Emileia* (with subgenera *Emileia* and *Otoites*), *Poecilomorphus*, *Strigoceras*, and *Procerites*. The specimen of *Procerites* is possibly from the lower part of the Great Estuarine Series.

There is clearly dimorphism in at least some of the sonniniid faunas from Skye, with proven microconchs and macroconchs in the Laeviuscula Zone and Sauzei Subzone. Possible dimorphism in the Hebridica and Cycloides Subzones has been discussed earlier (Morton 1972). No attempt is made here to deal taxonomically with sonniniid dimorphism other than as separate taxonomic categories; the approach to the problem used by Westermann and Riccardi (1972) could not be used on the Skye faunas because there is no clear indication of which macroconch and microconch 'species' belong together. Even macroconch: microconch subgenera such as used for Skye stephanoceratids (Morton 1971) could not be used, because for example *Pelekodites* (m) occurs with *Witchellia* (M) in the Laeviuscula Zone and with *Sonninia* (M+?m) in the Sauzei Zone. Analysis of the Skye sonniniids in terms of possible dimorphism is summarized in Table 3.

Bajocian Sonniniidae have been extensively monographed in Europe, and one result of this is an excess of available names. Hiltermann (1939, pp. 136–137) listed over 200, and a rough estimate obtained by adding names he missed and new ones since then, even allowing for non-European species and species transferred to other families, would suggest that there must be some 250 specific names available in the family. There are undoubtedly too many names at present and extensive 'lumping' has been taking place, notably by Westermann (e.g. 1966). Westermann's 'lumping' has been discussed in various places in this paper (e.g. discussion of *Euhoploceras*,

TABLE 3. Possible dimorphism of sonniniids from Skye. The numbers in square brackets refer to the sequence of faunas, the numbers in the round brackets refer to the number of specimens of each species.

	Macroconchs	Microconchs
CYCLOIDES SUBZONE [7, 8]	*D. liostraca* (10) '*S.*' aff. *furticarinata* (1)	?*D. romani* (16)
HEBRIDICA SUBZONE [6]	?*D. hebridica* (5) ?*D. hannoverana* (7) '*S.*' aff. *furticarinata* (3)	?*D. pinguis* (15)
SAUZEI SUBZONE [5]	?*S.* (*S.*) cf. *sowerbyi* (1) ?*S.* (*S.*) cf. *propinquans* (11) *S.* (*P.*) *arenata* (17) *S.* (*P.*) *mesacantha* (7)	?*S.* (*S.*) *corrugata* (27) *P. macer* (28)
LAEVIUSCULA ZONE [4]	*W.* aff. *rubra* (54) *W.* aff. *laeviuscula* (1) *W.* aff. *romanoides* (1)	?*S.* (*S.*) *corrugata* (5) *P. macer* (14) *P. zurcheri* (13)
OVALIS ZONE [3]	*E.* (*F.*) *fissilobatum* (10) *E.* (*E.*) sp. (1) *Sh. trigonalis* (1)	?
DISCITES ZONE [1, 2]	*E.* (*E.*) ?*marginata* (1) *E.* (*E.*) ?*dominans* (1) *E.* (*E.*) spp. (3)	?

Witchellia aff. *rubra*, *Sonninia* (*Papilliceras*) *arenata* and *mesacantha*) and has had to be rejected. It is clear that taxonomic revision of European Sonniniidae will have to be based on populations which are carefully controlled stratigraphically and geographically, rather than on a study of individual specimens.

In the discussions of several species (e.g. *Euhoploceras* (*F.*) *fissilobatum*) it was noted that the specimens from Skye were smaller than figured specimens from other localities with which they were being compared. It seems that the Skye sonniniids are slightly dwarfed, with ontogenetic changes tending to appear earlier (i.e. at a smaller diameter).

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BRITISH LOWER GREENSAND SERPULIDAE

by S. WARE

ABSTRACT. The Lower Greensand serpulids of southern England are revised and the faunas from Faringdon, Oxfordshire, Upware, Cambridgeshire, Brickhill, Buckinghamshire, the Wealden region, and the Isle of Wight are compared. A new genus, *Propomatoceros*, is proposed for Cretaceous tubes hitherto assigned to *Pomatoceros* Philippi and the following new species are described: *Propomatoceros sulcicarinata*, *P. keepingi*, *P. gracilis*, *P. dentata*, *Mucroserpula nitida*, *Proliserpula faringdonensis*, *Flucticularia sharpei*, *Parsimonia upwarensis*, and *Genicularia* (*Glandifera*) *inornata*. The classification of the Serpulidae is discussed.

IN 1829 J. de C. Sowerby described and figured two serpulid species in his *Mineral Conchology of Great Britain*, *Vermetus polygonalis* from the Lower Greensand of Seabrooke, Kent, and *Serpula articulata* from Folkestone, Kent, in beds recorded as Upper Greensand but which are now regarded as Lower Greensand. Since then very little attention has been given to the serpulid fauna occurring in the Lower Greensand deposits of this country and only a few workers appear to have considered the tubes important enough to collect. Keeping (1883) figured four specimens from the Lower Greensand at Upware, Cambridgeshire, and Brickhill, Buckinghamshire, and recorded a total of ten species. Sharpe (1854) recorded four species from the Sponge Gravel at Faringdon, Oxfordshire, and Price (1874), Topley (1875), and Gregory (1895) published lists of serpulids from the Hythe and Sandgate Beds of Kent and Sussex. In Casey (1961) the recorded fauna is listed with the zonal range of each species.

The present study based mainly on the collection at the British Museum (Natural History) and the Keeping Collection housed at the Sedgwick Museum, Cambridge, has shown that the Sponge Gravel at Faringdon contains a much larger serpulid fauna than that listed by Sharpe. The purpose of this paper is to describe this fauna and revise the records from the other areas which include species ranging from the Jurassic to the Upper Chalk.

STRATIGRAPHY

The main outcrops of Lower Greensand deposits are situated in the south-east of England and the Isle of Wight. Elsewhere they occur in a series of outcrops extending from Dilton in Wiltshire north-eastwards to Lincolnshire. In the south-east region serpulids are recorded from the Hythe Beds at several localities but chiefly in the region of Hythe, the Sandgate Beds at Folkestone and Parham, near Arundel, Sussex, the Folkestone Beds at Folkestone, Kent, and the Bargate Beds in the region of Guildford and Godalming, Surrey. In the Isle of Wight they are quite common in fossiliferous horizons of the Atherfield Clay and the Ferruginous Sands. Much of the material examined from the Wealden localities and the Isle of Wight is poorly preserved. In comparison the better preservation of the tubes obtained from the Sponge

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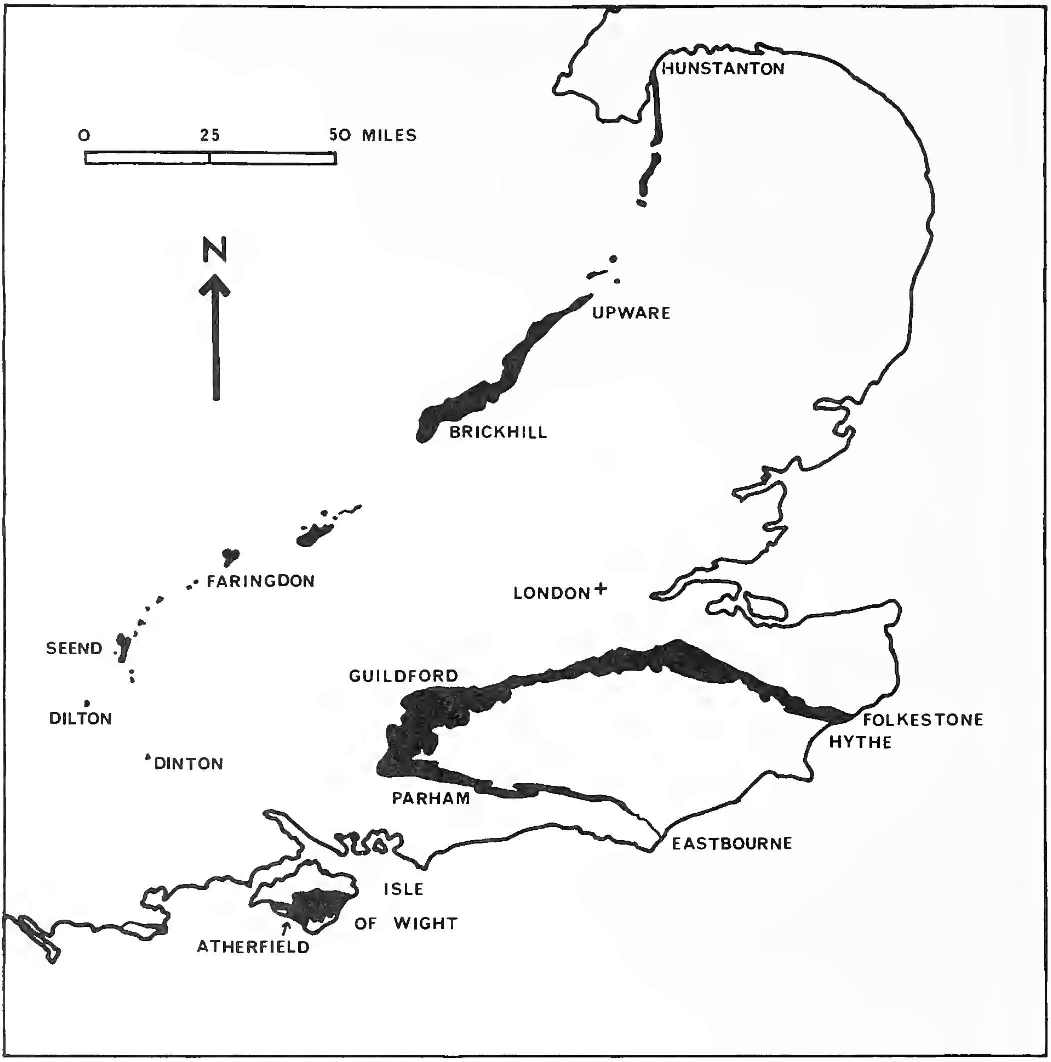
Gravels at Faringdon and the Lower Greensand at Brickhill and Upware may be attributed partly to the protected anchorages provided on the inner walls of large Calcareous sponges abundant at these localities.

A detailed account of Lower Greensand stratigraphy is given by Casey (1961) from whom the distribution map (text-fig. 1) is reproduced.



TEXT-FIG. 1. Distribution of the Lower Greensand.

THE FARINGDON SPONGE GRAVEL FAUNA

Despite the considerable interest the fossils of the Faringdon Sponge Gravel have attracted during the last century or so, only four serpulid species have been recorded from it. Sharpe (1854) noted the abundance of 'serpulae' and listed *Serpula gordialis*

(Schlotheim), *S. plexus* Sowerby, *S. obtusa* Sowerby, and *S. quinquangulata* Roemer (1840) and Keeping (1883) recorded only *S. gordialis* (Schlotheim). *S. obtusa* Sowerby and *S. plexus* Sowerby (non *S. filiformis* Sowerby) are Chalk species reflecting Sharpe's opinion that the Gravel was Upper Cretaceous in age. *S. gordialis* (Schlotheim) ranges throughout the Mesozoic leaving *S. quinquangulata* Roemer the only species limited to the Lower Cretaceous.

The present study has shown *Glomerula gordialis* (Schlotheim) to be very abundant in the Faringdon Sponge Gravel and variable in tube size from the delicate, coiled, attached section to the dense contorted masses of free tube. It is probable that the specimens recorded by Sharpe as *Serpula plexus* Sowerby belong to *G. gordialis* (Schlotheim). The five-sided tubes similar to *S. quinquangulata* Roemer have been placed in two species of *Mucroserpula* Regenhardt and the triangular carinate tubes assigned to a new genus, *Propomatoceros*.

The revised fauna is as follows:

Glomerula gordialis (Schlotheim)
Mucroserpula sp. cf. *mucroserpula* Regenhardt
Mucroserpula nitida sp. nov.
Propomatoceros sulcicarinata gen. et sp. nov.
Propomatoceros keepingi sp. nov.
Propomatoceros gracilis sp. nov.
Flucticularia sharpei sp. nov.
Proliserpula faringdonensis sp. nov.
Genicularia (*Glandifera*) *inornata* sp. nov.

The vast majority of serpulid tubes from this locality have been found encrusting the calcareous sponge, *Raphidonema*, and only rarely attached to bivalves, brachiopods, and bryozoan colonies. Moreover, they are most frequently attached to the inner walls of the sponge where protection from a turbulent environment would be greater. The external ornament of tubes situated deep inside the sponge cup is generally well preserved, whereas in those nearer the rim the ornament is more often blurred or completely eroded. With the exception of *Glomerula gordialis* and *Genicularia* (*Glandifera*) *inornata*, all of the species listed above are attached by a strong basal layer for the greater part of their length. Many of the tubes are pitted with small perforations made by an unknown organism (Pl. 19, figs. 2, 6–7; Pl. 20, figs. 2–3).

The predominance of firmly attached tubes, their location on the inner walls of sponges, and variable preservation suggests that conditions were too turbulent for species with a weak initial attachment to obtain an anchorage or these were later broken off and swept away. This may explain the presence of numerous detached masses of *Glomerula gordialis* (Schlotheim) and the apparent absence of *Rotularia* in the Sponge Gravel. The environmental conditions indicated by the serpulids is consistent with those envisaged by Elliott (1947) of shallow, rapidly moving waters in an irregularity of the sea floor, though the fossil bed itself is a current-bedded deposit of moved materials (Arkell 1947; Elliott 1956).

A single specimen of *Glomerula gordialis* (Schlotheim), BMNH. A. 10287, is attached to a worn plesiosaur vertebra probably derived from the Jurassic strata underlying the Sponge Gravel.

THE LOWER GREENSAND FAUNA AT UPWARE AND BRICKHILL

The ten species listed by Keeping (1883) are the only serpulids recorded from the Lower Greensand at Upware, Cambridgeshire, and Brickhill, Buckinghamshire. Examination of the Keeping Collection comprising sixty-one specimens (SM. B. 25951–B. 26010) loaned to me through the kindness of Dr. R. B. Rickards of the Sedgwick Museum, Cambridge, together with the collection at the British Museum (Natural History) has revealed the need for a complete revision of the existing record from these deposits.

The large tube referred by Keeping to *Serpula lophioda* Goldfuss, an Upper Cretaceous species, has been redescribed under *Propomatoceros dentata* gen. et sp. nov., and those referred to *Serpula rustica* Sowerby under *Parsimonia upwarensis* sp. nov. Some tubes identified as *Serpula antiquata* Sowerby and one as *S. ampullacea* Sowerby are also included in that species. Several identifiable specimens recorded as *S. ampullacea* have been referred to *Mucroserpula* cf. *mucroserpula* Regenhardt. The tube fragment described by Keeping as *Serpula* sp.? is too poorly preserved for generic determination and of eight other tubes so labelled in his collection, two belong to *Mucroserpula* and the remainder are indeterminate.

The revised fauna is as follows:

Propomatoceros dentata gen. et sp. nov.
Mucroserpula sp. cf. *mucroserpula* Regenhardt
Parsimonia upwarensis sp. nov.
Glomerula gordialis (Schlotheim)
Sarcinella plexus (Sowerby)
Genicularia (*Glandifera*) *articulata* (Sowerby)
Rotularia phillipsii (Roemer)
Rotularia polygonalis (Sowerby)

A single tube bearing no resemblance to the indigenous species is comparable with *Serpula sulcata* Sowerby and probably derived from the Upper Jurassic (Pl. 20, fig. 7).

The serpulid fauna of the Lower Greensand at these localities (mainly Upware) has much in common with that of the Sponge Gravel at Faringdon, the most significant difference being the occurrence of *Rotularia* spp. not yet found at Faringdon. *Parsimonia upwarensis* sp. nov. which develops large free sections of tube at Upware is also unrepresented at Faringdon but it occurs in the Bargate Stone of the Guildford region, the tubes being much smaller. Apart from these indications of less-turbulent conditions than those envisaged for the Faringdon serpulids, a much larger percentage of tubes are attached to phosphatic nodules compared with only six specimens encrusting Calcareous sponges. There was no lack of sponges at Upware for providing a protected anchorage; as Keeping (1883, p. 28) commented, sponges were 'nobly represented' and 'Beautiful cup sponges' flourished around the Upware Coral Bank.

It is unfortunate that the volume of material collected from these deposits is so limited and that most of it is so eroded that the external ornament is often barely discernible.

THE FAUNA OF THE WEALDEN REGION AND THE ISLE OF WIGHT

Casey (1961) listed eight species from the Lower Greensand and gave their zonal ranges: *Serpula antiquata* Sowerby, *S. filiformis* Sowerby, *S. articulata* Sowerby, *S. plexus* Sowerby, *S.* cf. *adnata* Wade, *S. gordialis* (Schlotheim), *Rotularia polygonalis* Sowerby, and *R. concava* Sowerby. With the exception of *S. filiformis* [= *Sarcinella plexus* (Sowerby)] and *S.* cf. *adnata* Wade which appears to be the attached portion of *Glomerula gordialis* (Schlotheim), all of the species in this list occur in the deposits of this region. Previous records by Sowerby (1829), Price (1874), and Topley (1875) show that most of the species recorded from this region were obtained from the Hythe Beds at localities in the vicinity of Hythe and the Folkestone Beds at Folkestone, Kent. From the western part of the region, Keeping (1883) recorded *Serpula rustica* Sowerby in the Lower Greensand of Godalming, Surrey, and Topley (1875) listed *Serpula*? sp. from the Bargate Stone at the same locality.

In the collections at the British Museum (Natural History) a sample comprising thirty-one specimens from the Bargate Stone at Littleton and Shackleford, SW. of Guildford, Surrey has yielded four species:

Parsimonia upwarensis sp. nov.
Flucticularia sharpei sp. nov.
Sarcinella plexus (Sowerby)
Rotularia polygonalis (Sowerby)

It is probable that the tubes from Godalming recorded by Keeping as *Serpula rustica* Sowerby were obtained from the Bargate Stone and may be referred to *Parsimonia upwarensis*. Most of the tubes from this horizon are quite well preserved and, excluding the *Rotularia* specimens, they are attached to phosphatic nodules.

The list of species is revised as follows:

Parsimonia antiquata (Sowerby)
Parsimonia upwarensis sp. nov.
Flucticularia sharpei sp. nov.
Glomerula gordialis (Schlotheim)
Sarcinella plexus (Sowerby)
Genicularia (*Glandifera*) *articulata* (Sowerby)
Rotularia concava (Sowerby)
Rotularia polygonalis (Sowerby)

In contrast with the serpulid fauna of the Faringdon Sponge Gravel and to a lesser extent the Lower Greensand at Upware and Brickhill where most of the species have a firm basal attachment, the species which predominate in the Hythe and Folkestone Beds have a weak initial attachment, *Parsimonia antiquata* (Sowerby) being the only firmly fixed species. The restricted fauna of the Bargate Stone includes *Flucticularia sharpei* and *Parsimonia upwarensis* in common with the beds at Faringdon and Upware, and although *Sarcinella plexus* and *Rotularia polygonalis* are recorded from Upware, they are more abundant and representative of the Hythe Beds of this region.

In the Lower Greensand deposits of the Isle of Wight, the serpulid fauna comprising four species is typical of the Wealden region.

Parsimonia antiquata (J. de C. Sowerby)
Glomerula gordialis (Schlotheim)
Sarcinella plexus (J. de C. Sowerby)
Rotularia polygonalis (J. de C. Sowerby)

Whereas *Parsimonia antiquata* (J. de C. Sowerby) occurs only in the *Perna* Bed of the Atherfield Clay, the other species listed are quite common in that bed and also occur in the Crackers near the base of the Ferruginous Sands.

CLASSIFICATION

In the works of Parsch (1956), Regenhardt (1961, 1964), and Schmidt (1955, 1969) distinct classifications with some overlapping have been erected for Jurassic, Cretaceous, and Tertiary serpulid tubes respectively. Parsch classified the Jurassic serpulids of south-west Germany and established species described by Goldfuss, Quenstedt, and others by arranging them within five sub-genera of *Serpula*, each sub-genus being indicated by a prefix (e.g. *Dorsoserpula*). In this respect, and also in being based entirely on tube morphology, his classification is comparable with that proposed by Nielsen (1931) for the Senonian and Danian serpulids of Denmark in which *Ditrupa* was modified to *Ditrupula* and *Serpula* to *Serpentula* to produce a separate parallel classification for the fossil tubes. In the classification adopted by Regenhardt for the Chalk serpulids of Mid-Europe the generic characters are based on the cross-section of the tube and changes in its development, while differences in external ornamentation were the main specific criteria. It comprises thirty-two genera, fourteen of which are new, supercedes almost entirely the work of Nielsen and by including many Jurassic species within its scope it overlaps the classification erected by Parsch. Except for several fossil genera ranging from the Cretaceous to the Eocene, Schmidt has used Recent genera in his classification of Tertiary serpulid tubes.

The existence of separate classifications for Jurassic, Cretaceous, and Tertiary serpulid tubes is unsatisfactory and as Bignot (1968) remarked 'a synthesized complete regrouping of Jurassic, Cretaceous, Tertiary and Recent tubes is desirable'. A revision such as this would possibly help to resolve the problem whether Recent serpulids, where the tube is of minor importance in identification, should be classified separately from fossil tubes. At present a study of the microstructure of the tubes of fossil and Recent genera under the Scanning Electron Microscope is in progress which may provide data for a unified classification.

In this paper the classification is based mainly on the works of Regenhardt (1961, 1964). A new genus, *Propomatoceros*, is proposed for triangular Cretaceous species hitherto included in *Pomatoceros* Philippi.

SYSTEMATIC DESCRIPTIONS

Specimens prefixed A are deposited in the Palaeontology Department, British Museum (Natural History); those prefixed B in the Sedgwick Museum, Cambridge.

Phylum ANNELIDA Lamarck
Class POLYCHAETA Grube, 1850
Family SERPULIDAE Burmeister, 1837
Subfamily SERPULINAE Rioja, 1925
Genus PROPOMATOCEROS nov.

Type species. Propomatoceros sulcicarinata sp. nov.

Derivation of name. Pro—in place of—*Pomatoceros.*

Diagnosis. Serpulinae having a carinate tube, initially triangular, becoming increasingly convex to sub-cylindrical in cross-section. Completely attached or with a free cylindrical anterior segment. Lateral surfaces have fine growth lines arched forward from the basal layer of attachment to the dorsal carina which forms a tooth-like projection over the aperture.

Remarks. Propomatoceros is proposed for Cretaceous serpulid tubes which resemble *Pomatoceros* Philippi in the initial triangular growth stage (Pl. 18, figs. 3–4) but differ in having a further convex and sometimes a free cylindrical stage of variable length (Pl. 18, figs. 1–2, 10).

Regenhardt (1961) erected a new tribe, Mucroserpulae for angular serpulids, placing 4–5 sided tubes in *Mucroserpula* and triangular tubes in *Pomatoceros.* He assigned five Cretaceous species to the genus and extended its range to 'Jurassic, Zechstein'. These Cretaceous species, together with the miscellaneous triangular tubes in the Jurassic, introduce a range of variation too great for their inclusion in *Pomatoceros*; the Cretaceous species are accordingly placed in *Propomatoceros.* They include *Serpula lophioda* Goldfuss and *S. trachinus* Goldfuss from the Cenomanian of Germany, *S. triangularis* Goldfuss (Santonian–Maestrichtian) and *S. biplicatus* Reuss (Turonian) of Germany, and *P. semicostatus* Regenhardt from the Barremian of Hildesheim. In *S. lophioda* the anterior part of the tube becomes strongly rounded and in *S. trachinus* the anterior convexity is even greater. The holotype of *P. semicostatus* loaned to me through the generous assistance of Dr. Hans Lafrenz of the Geologisches-Palaontologisches Institut, Hamburg, is a slender tube comparable in size and external ornament with *Propomatoceros gracilis* sp. nov. from the Faringdon Sponge Gravel. *S. triangularis* and *S. biplicatus* like *S. avita* J. de C. Sowerby from the Turonian of England are triangular throughout their length and lacking evidence of further development, they can only be included tentatively.

Propomatoceros sulcicarinata sp. nov.

Plate 18, figs. 1–4

Holotype. A. 1037.

Paratypes. A. 10233, A. 10297, A. 10812.

Distribution. Yellow Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire.

Diagnosis. A species with a strong square dorsal carina which becomes furrowed in the later stage of growth.

Description. The tube is attached for most of its length and may vary in development from a tight coil to almost straight. Those forming a tight initial coil may be sinuous or curved thereafter. In the early stage of development (Pl. 18, figs. 3–4) the tube has a triangular cross-section which becomes more and more convex as it increases in size and in the final stage it is cylindrical in outline with longitudinal sulci at the junction of the walls and the expanded base. The thick dorsal carina is more or less square and continuous in the early triangular part; in the convex stage it becomes furrowed. This is generally shallow but may be deep enough to produce two parallel carinae before passing to the coarse cylindrical stage where it is rather obscure and irregular. The lateral surfaces have growth lines reflected forward in an arc so that they meet at the dorsal carina. The tooth-like projection formed by the carina over the aperture is very clear in the triangular stage but much less so where the carina is furrowed or obscure.

Remarks. *P. sulcicarinata* can be distinguished from all of the other species by its large partially furrowed dorsal carina. *P. keepingi* sp. nov. is closest to it but has a blade-like carina.

In the Sponge Gravel at Faringdon this species has been found only on the inner wall of *Raphidonema* spp.

Propomatoceros keepingi sp. nov.

Plate 18, figs. 5–6

Holotype. A. 10229.

Paratype. A. 10765.

Derivation of name. After W. Keeping.

Distribution. Yellow Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire.

Diagnosis. A smooth, thin-shelled species with a strong blade-like dorsal carina and convex lateral walls.

Description. The tube is almost completely attached and may be coiled back on to itself or sinuous. On the convex lateral walls a weak ridge extends along the tube approximately midway between the base and the dorsal carina and vertical growth

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EXPLANATION OF PLATE 18

Figs. 1–8. Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire. 1–4, *Propomatoceros sulcicarinata* gen. et sp. nov. 1, holotype, A. 1037, ×2; 2, paratype, A. 10233, ×2; 3–4, initial growth stage; 3, dorsal view, A. 10297, 4, view of aperture, A. 10812, both ×5. 5–6, *Propomatoceros keepingi* sp. nov. 5, holotype, A. 10229, ×2; 6, paratype, A. 10765, ×2. 7–8, *Propomatoceros gracilis* sp. nov. 7, holotype, A. 10814, ×3; 8, view of arched ribs, A. 10813, ×5.

Figs. 9–10. *Propomatoceros dentata* sp. nov. Two adjacent tubes on *Raphidonema* sp. Lower Greensand (Aptian), Upware, Cambridgeshire. 9, holotype, B. 25951a, ×2; 10, tube figured by Keeping, pl. 7, fig. 5, as *Serpula lophioda* Goldfuss, B. 25951b, ×1.

PLATE 18


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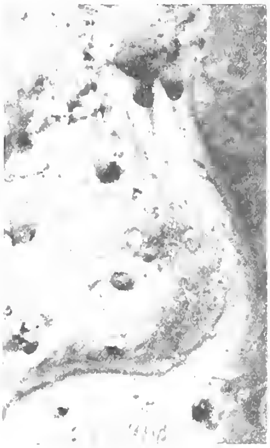
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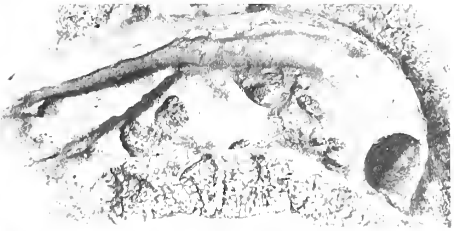
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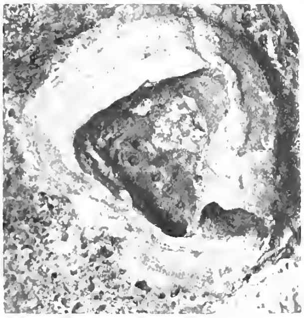
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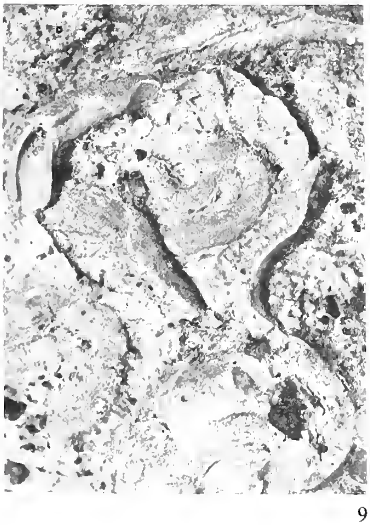
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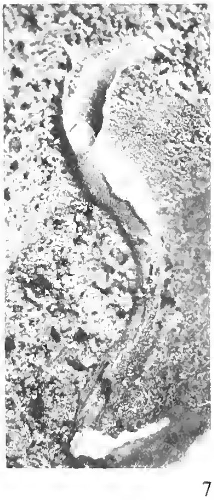
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WARE, Lower Greensand Serpulidae

lines from the base to the ridge arch forward into the carina. In the holotype a transverse swelling marks a pause in growth and a second rib-like swelling marks the beginning of the enlarged anterior tube segment. A prominent blade-like dorsal carina extends unbroken to within 4 mm of the aperture, at which point the tube increases in size and convexity and the carina is less prominent. The aperture is large, sub-cylindrical in outline, and notched at the apex of the tube. The tube is smooth and has very thin lateral walls.

Remarks. P. lophioda (Goldfuss) and *P. trachinus* (Goldfuss) are comparable in the convexity of their cross-section with this species but in the former the carina is much thinner and in the latter it is plicate and gives way to a furrow in the anterior part of the tube. The upper Cretaceous species, *P. avita* (J. de C. Sowerby) and *P. triangularis* (Goldfuss) have sharper carinae and a less convex cross-section.

Propomatoceros gracilis sp. nov.

Plate 18, figs. 7-8

Holotype. A. 10814.

Paratypes. A. 10768-10769, A. 10813.

Distribution. Red Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire.

Diagnosis. A slender, convexly triangular tube with finely striated lateral walls ribbed at intervals and a thin dorsal carina.

Description. The tube is straight or slightly curved, slender with an almost imperceptible increase in size. It increases in convexity gradually from a rather triangular beginning. A thin dorsal carina is continuous along the tube and the lateral walls are marked by fine striae which arch forward from the base to the carina. At intervals these striae may be replaced by ribs similarly arched (Pl. 18, fig. 8). The specimens figured here are incomplete and details of the aperture cannot be given. In A. 10768, a specimen donated recently to the British Museum (Natural History) Collection, the beginning of a cylindrical, possibly free stage of development can be seen.

Remarks. This small slender species is easily distinguishable from all except *P. semicostatus* Regenhardt from the Barremian of Hildesheim, Germany, which resembles it very closely. It is equally slender but rather more triangular initially than *P. gracilis* and the transverse ribbing is confined to the upper part of the lateral walls.

Propomatoceros dentata sp. nov.

Plate 18, figs. 9-10

1883 *Serpula lophioda* Goldfuss; Keeping, p. 131, pl. 7, fig. 5*a*-*b*.

Holotype. B. 25951*a*.

Paratype. B. 25951*b*.

Distribution. Lower Greensand (Lower Aptian), Upware, Cambridgeshire.

Diagnosis. A species with a dentate dorsal carina.

Description. This species is represented by two adjacent tubes attached to the inner wall of a Calcareous sponge, *Raphidonema porcatum* Hinde. The holotype (Pl. 18, fig. 9) is approximately 5 cm long, sinuous, obtusely triangular in cross-section, and attached by a slightly expanded base. A notched, plicate, fin-shaped dorsal carina extends along the tube which lacks the anterior terminal section. The sides are ornamented by transverse striae and at irregular intervals, swellings which bend forward to meet in dentate projections at the carina mark a series of growth pauses. The paratype (Pl. 18, fig. 10) figured by Keeping (see synonymy) is curved, approximately 13 cm in length, obtusely triangular for the first 6 cm and thereafter becomes increasingly convex. In the early part of this tube the dorsal carina is less prominent than in the holotype and becomes both irregular and progressively weaker in the more convex later stage of development.

Remarks. The strong dentate carina distinguishes this species from *P. lophioda* (Goldfuss) and in *P. trachinus* (Goldfuss) which is closest to it, the plicate carina gives way to a furrow in the anterior part of the tube.

Genus MUCROSERPULA Regenhardt, 1961
Mucroserpula nitida sp. nov.

Plate 19, figs. 1–2

Holotype. A. 5669.

Paratype. A. 10772.

Distribution. Yellow Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire.

Diagnosis. A species of *Mucroserpula* with a thin, smooth, angular, non-carinate tube almost entirely attached. Free portion short and cylindrical.

Description. The tube is coiled in a circle or may form a loop, attached for most of its length and pentagonal in cross-section. In the attached stage the sides slope steeply from the base to lateral ridges and become more upright as the tube enlarges. From the lateral ridges to the median ridge the dorsal surface forms a high V-shaped arch which flattens out anteriorly. In the holotype a transverse swelling marks the beginning of the free cylindrical stage of the tube. In this stage the tube increases in size rapidly to the large, dorsally projecting aperture. The tube is very thin and smooth and lacks any external ornament, probably due to its rather weathered state.

Remarks. This species is easily distinguishable from *M. arcuata* (Munster), *M. quinquangulata* (Roemer), and *M. versabunda* Regenhardt by its lack of carinae, and it differs from *M. mucroserpula* Regenhardt in having sharper angulation, and a thin tube which is much smoother in texture.

Mucroserpula sp. cf. *mucroserpula* Regenhardt

Plate 19, figs. 3–5

cf. 1961 *Mucroserpula mucroserpula* Regenhardt, p. 47, pl. 4, fig. 2.

Material. A. 10289, A. 10256 and four other specimens (Faringdon); B. 25989 and six other specimens (Upware).

Distribution. Yellow Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire; Lower Greensand (Lower Aptian), Upware, Cambridgeshire.

Description. These tubes may form a tight coil or a wide curve in their development and are entirely attached. Initially the cross-section of the tube is triangular with very convex sides which meet in a low dorsal ridge. With the increase in size the tube becomes quadrangular as the dorsal surface flattens out and the dorsal ridge weakens and may disappear completely. Transverse growth lines clearly visible only in the later stage of the tube arch forward on the dorsal surface to form projections along the ridge. At the aperture of A. 10289 the tube is 4 mm in width and the thickness of the tube is approximately 1 mm.

Remarks. Although no differences can be discerned between the tubes described here and *M. mucroserpula* Regenhardt from the Hauterivian deposits of Schandelah, Niedersachsen, Germany, their poor preservation does not allow more than a comparison with that species.

Genus FLUCTICULARIA Regenhardt, 1961
Flucticularia sharpei sp. nov.

Plate 20, figs. 1–4

Holotype. A. 10261.

Paratypes. A. 10305, A. 10298.

Derivation of name. The species is named in honour of Daniel Sharpe who first recorded serpulids from the Sponge Gravel at Faringdon, Oxfordshire.

Distribution. Yellow Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire (type locality); Bargate Stone (Aptian, Nutfieldiensis Zone), Shackleford, SW. of Guildford, Surrey.

Diagnosis. An attached species with irregular transverse swellings and three plicate dorsal carinae.

Description. The tube is entirely attached and uniform in its gradual increase in size. It is pentagonal in cross-section and may be sinuous, curved, or loosely coiled in development. At irregular intervals along the tube earlier apertures are indicated by transverse swellings from the inner surfaces of which successive tube segments are secreted. The vertical or slightly diagonal side walls are capped by plicate carinae from which the dorsal surfaces slope upwards very slightly to a stronger median

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EXPLANATION OF PLATE 19

Figs. 1–2. *Mucroserpula nitida* sp. nov. Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire. 1, holotype, A. 5669, ×5; 2, paratype, A. 10772, ×3.

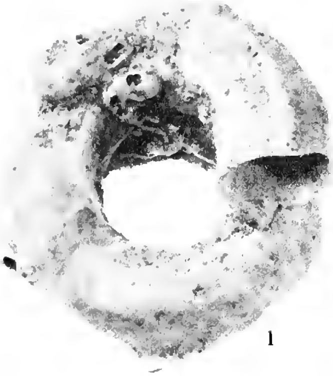
Figs. 3–5. *Mucroserpula* sp. cf. *mucroserpula* Regenhardt. 3–4, Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire. 3, A. 10289, ×5; 4, A. 10256, ×5; 5, B. 25989, ×2; Lower Greensand (Aptian), Upware, Cambridgeshire.

Figs. 6–7. *Proliserpula faringdonensis* sp. nov. Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire. 6, holotype, A. 10766, ×5; 7, paratype, A. 10257, ×5.

Figs. 8–9. *Genicularia* (*Glandifera*) *inornata* sp. nov. Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire. 8, holotype, A. 10222, ×5; 9, paratype, A. 8854, ×5.

Fig. 10. *Genicularia* (*Glandifera*) *articulata* (J. de C. Sowerby). B. 25967, ×5. Figured by Keeping, pl. 7, fig. 7. Lower Greensand (Aptian), Upware, Cambridgeshire.

PLATE 19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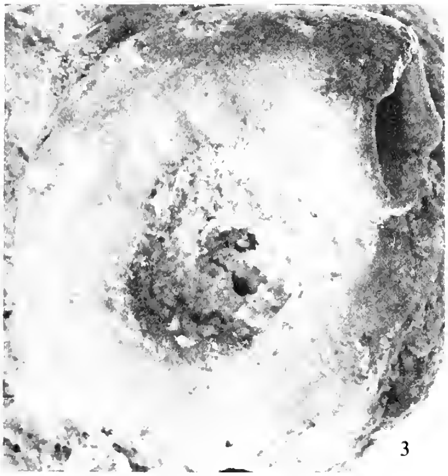
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WARE, Lower Greensand Serpulidae

plicate carina. In the holotype the lumen has a diameter of 2 mm and the carinae form lobes over the aperture.

Dimensions.

	Length	Width (at aperture)
A. 10261	40 mm	3·5 mm
A. 10305	16 mm	2·0 mm
A. 10298	14 mm	—

Remarks. Regenhardt (1961) erected *Flucticularia* for tubes with plicate carinae. Among the Upper Cretaceous species that he included in the genus, *F. fluctuata* (J. de C. Sowerby) and *F. cincta* (Goldfuss) occur in the Chalk of this country, the earliest record for each being Turonian (Rowe 1903, 1908). *F. fluctuata* (J. de C. Sowerby) is easily distinguished from *F. sharpei* by its smaller tube, its regular pentagonal cross-section, and five distinct carinae. *F. cincta* (Goldfuss) is smaller also but almost identical in cross-section. Apart from its size it differs from *F. sharpei* only in the greater thickness of the apertural swellings which occur at intervals along the tube.

Previously unrecorded tubes from the Upper Albian, Red Chalk of Hunstanton, Norfolk, are closely comparable with *F. sharpei*, differing only in a more pronounced plication of the lateral carinae. However, as this may be attributable to their better preservation, they are provisionally included in this species.

Genus PROLISERPULA Regenhardt, 1961

Proliserpula faringdonensis sp. nov.

Plate 19, figs. 6–7

Holotype. A. 10766.

Paratype. A. 10257.

Distribution. Yellow Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire.

Diagnosis. A small sub-cylindrical species with a thick tube segmented by quadrate annular swellings.

Description. The tube is completely attached by an expanded basal layer above which it has a cylindrical cross-section. It may develop in a tight coil or loosely in the form of a loop. The dorsal surface may be rather flattened in one part and lumpy

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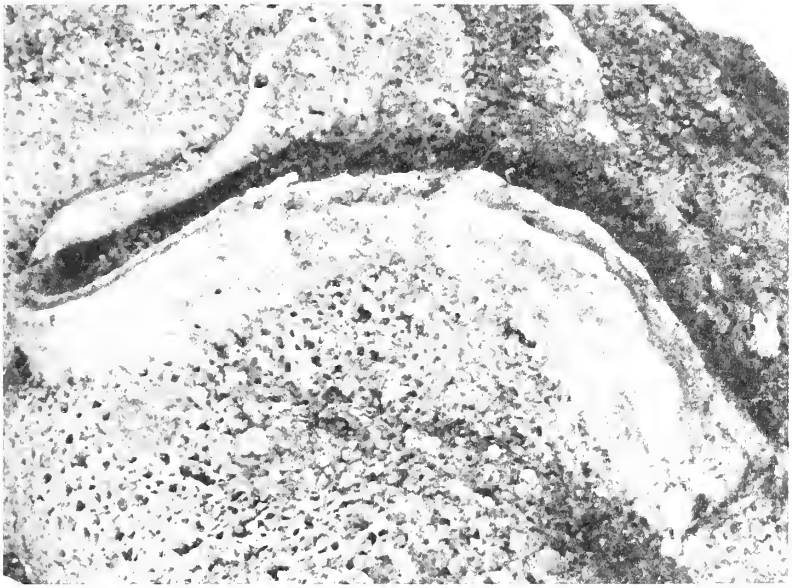
EXPLANATION OF PLATE 20

Figs. 1–4. *Flucticularia sharpei* sp. nov. 1–3, Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire. 1, holotype, A. 10261, ×5; 2–3, paratypes, A. 10305, ×5; A. 10298, ×10; 4, Bargate Stone (Aptian, Nutfieldiensis Zone), Shackleford, SW. of Guildford, Surrey, A. 2648, ×5.

Fig. 5. *Glomerula gordialis* (Schlotheim). Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire. Initial attached stage, A. 10300, ×10.

Fig. 6. *Sarcinella plexus* (J. de C. Sowerby). Ferruginous Sands (Aptian), Shanklin, Isle of Wight, A. 10789, ×2.

Fig. 7. *Serpula* cf. *sulcata* J. de C. Sowerby. Lower Greensand (Aptian), Upware, Cambridgeshire, B. 25973, ×2 (?derived from Jurassic).



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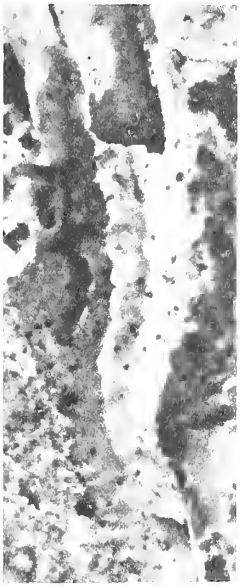

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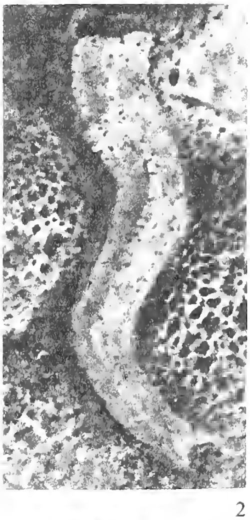

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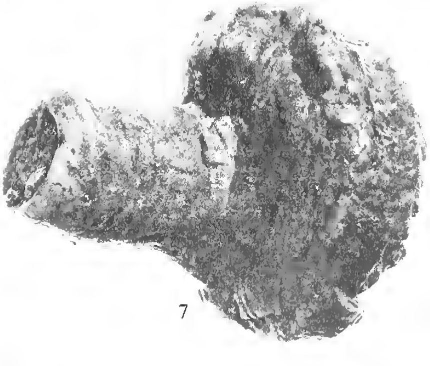

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WARE, Lower Greensand Serpulidae

in another giving the tube an undulating appearance. Transverse striation visible only on the inner surface of the holotype has been obliterated by minute perforations and weathering on the dorsal and outer surfaces. At irregular intervals following a gradual enlargement of the tube, the outer layer thickens to form rounded quadrate swellings from which new segments are secreted. The small circular lumen is enclosed by a thick inner layer and an exceptionally thick outer layer.

Remarks. In his new genus, *Proliserpula*, Regenhardt (1961) described seven species from Upper Cretaceous and one species from Barremian deposits in Germany. He also included *Serpula ampullacea* J. de C. Sowerby and *S. obtusa* J. de C. Sowerby from the British Chalk in this genus. It has not been recorded previously from beds of Aptian age.

P. faringdonensis does not possess any marked differences from some of the coiled Upper Cretaceous species. *P. dithyrambica* Regenhardt is comparable in size, smoothness, and has similar transverse angular swellings; its faint dorsal carina being the only apparent difference. The common Chalk species, *P. ampullacea* (J. de C. Sowerby) and *P.* (*Parricidula*) *parricidula* Regenhardt (= *Serpula ampullacea* J. de C. Sowerby, 1829, pl. 597, fig. 5) are generally much larger, with globose swellings and faintly carinate on the dorsal surface. *P. obtusa* (J. de C. Sowerby), a sinuous, initially triangular species with a thick dorsal carina is not characteristic of this genus and is here considered to belong to *Propomatoceros*.

Genus PARSIMONIA Regenhardt, 1961

Parsimonia upwarensis sp. nov.

Plate 21, figs. 1–7

1883 *Serpula rustica* J. de C. Sowerby; Keeping, p. 131, pl. 7, fig. 6*a–b*.
1883 *Serpula antiquata* J. de C. Sowerby; Keeping, p. 132.

Holotype. The larger overlapping tube on B. 25952.

Additional material. B. 25953, B. 25954–24966, B. 25970–25971, B. 25974, B. 25990; A. 192, A. 10174–10178, A. 10720–10724, A. 2632–2635, A. 2656.

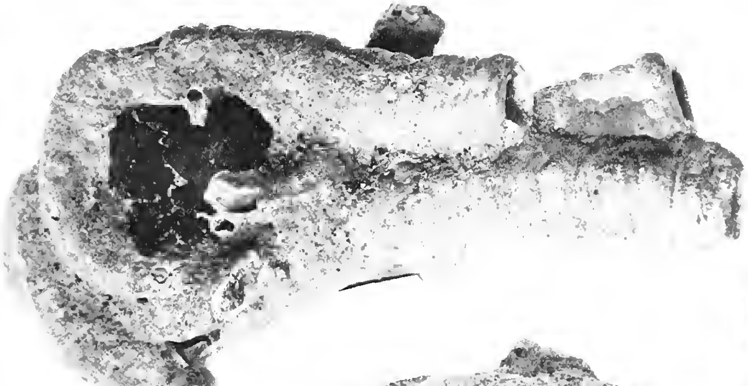
Distribution. Lower Greensand (Lower Aptian), Upware, Cambridgeshire (type locality), Brickhill, Buckinghamshire; Bargate Stone (Aptian, Nutfieldiensis Zone), Littleton and Shackleford, SW. of Guildford, Surrey.

EXPLANATION OF PLATE 21

Figs. 1–7. *Parsimonia upwarensis* sp. nov. 1–5, Lower Greensand (Aptian), Upware, Cambridgeshire. 1, holotype, B. 25952, ×2. Figured by Keeping, pl. 7, fig. 6*a* as *Serpula rustica* J. de C. Sowerby; 2–3, paratypes; 2, B. 25953, ×2; 3, A. 10720, ×2; 4, B. 25970, ×1. Recorded by Keeping, p. 131, as *Serpula antiquata* J. de C. Sowerby; 5, B. 25990, ×2. Recorded by Keeping as *Serpula ampullacea* J. de C. Sowerby; 6–7, Bargate Stone (Aptian, Nutfieldiensis Zone); 6, free tube fragment, Shackleford, A. 2632, ×2; 7, attached stage, Littleton, SW. of Guildford, Surrey, A. 2656, ×5.

Fig. 8. *Parsimonia antiquata* (J. de C. Sowerby), Atherfield Clay, *Perna* Bed (Aptian, Fissicostatus Zone), Atherfield, Isle of Wight, A. 197, ×2.

Figs. 9–10. *Rotularia polygonalis* (J. de C. Sowerby). 9, Ferruginous Sands Crackers (Aptian, Forbesi Zone), Atherfield, Isle of Wight, A. 10761; 10, Hythe Beds (Aptian), Maidstone, Kent, A. 1049. Both ×5.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WARE, Lower Greensand Serpulidae

Diagnosis. A species with a convex, triangular, attached tube, dorsally ridged and an obtusely four-sided free stage of growth.

Description. The tube is attached by an expanded base for a variable length before it becomes elevated and free. In the initial attached stage it may be curved or form a loop and increases gradually in size. It has a triangular cross-section which becomes increasingly convex and a weak ridge extends along the whole of this stage. The free stage of development begins on a platform formed by a thickening of the basal layer which raises the aperture and brings about an upward direction of growth. The free stage of the tube may also vary considerably in length, the longest free segment measuring 60 mm (B. 25958), but the diameter appears to remain constant regardless of the length of the tube. It is almost square in cross-section with rounded edges in well-preserved specimens but roughly cylindrical in weathered specimens. Irregular transverse folds encircle the tube and represent the contracted margins of successive apertures. The short intervening segments have nodular swellings placed unevenly at each edge which produce the obtusely square outline of the free tube in this species. Each side has a wavy median longitudinal furrow well defined in the square parts of the tube but obscure where it is more cylindrical. Transverse growth lines bend forward into the dorsal ridge in the attached stage and into each of the four median furrows in the free stage.

In the holotype the aperture is 8 mm wide with a lumen 5 mm in diameter and the tube on which it has grown has a width of 6 mm and a lumen 4 mm in diameter.

Dimensions of Holotype.

Length	Free segment
50 mm	9 mm

Remarks. Serpula rustica, to which species Keeping referred these tubes was described by J. de C. Sowerby (1829, p. 203, pl. 597, fig. 3) as follows:

> 'Tube externally four angled, angles obtuse; as the tube increases the angles are variously bent and interrupted, at length becoming irregular convexities arranged about a cylindrical tube. Nearly two lines in diameter and almost straight. The aperture is circular with a sharp edge. Found in a light-coloured marl belonging to the Upper Greensand, at East Weare Bay.'

Unfortunately, the specimen that he figured is an incomplete fragment lacking the initial stage of growth which appears to be rather poorly preserved and distorted. Regenhardt (1961) referred the species to his new sub-genus *Genicularia* (*Glandifera*). Well preserved, free, entirely quadrangular nodose tubes from the Gault Clay at Folkestone and the Cenomanian Chalk at Dover, Kent, clearly belonging to this subgenus, are comparable with *G.* (*Glandifera*) *rustica* (J. de C. Sowerby).

The tubes redescribed here resemble *G.* (*Glandifera*) *rustica* (J. de C. Sowerby) only in the quadrangular outline of the free segments; they differ from that species in their development from an attached, triangular stage to a free quadrangular stage, the transverse growth lines and folds, and the aperture which is not constricted as in species of *G.* (*Glandifera*). On the other hand, their development is characteristic of *Parsimonia* Regenhardt and for that reason they are assigned to that genus. *P. upwarensis* is distinguishable from *P. antiquata* (J. de C. Sowerby) by the more triangular outline of the attached stage and the quadrangular free tube. Specimens recorded by Keeping as *Serpula antiquata* J. de C. Sowerby (Pl. 21, fig. 4) differ from the quadrangular tubes only in their more weathered condition which has obscured the angulation and are therefore included in this species.

Parsimonia antiquata (J. de C. Sowerby)

Plate 21, fig. 8

Material. A. 197 and five other specimens.

Distribution. Atherfield Clay, *Perna* Bed (Aptian, Fissicostatus Zone), Atherfield, Isle of Wight.

Diagnosis. Sowerby (1829): 'Cylindrical, partly attached by an expanded surface; surface uneven, with transverse irregular rings.'

Description. The attached, convexly triangular portion of the tube gradually increases in size and convexity to become cylindrical and free. Transverse growth lines on the lateral surfaces of the attached part bend forward to meet in the form of a chevron at the low dorsal ridge. On the cylindrical part of the tube the ridge is absent and the growth lines are circular and coarse, making the surface uneven.

Remarks. Parsimonia antiquata (J. de C. Sowerby) is common in the Lower Cenomanian and Upper Albian deposits of this country but few records exist of its occurrence in the Aptian. Topley (1875) recorded it from the Hythe Beds at Hythe and the Lower Greensand, Isle of Wight. The only other record I have been able to find is that of Casey (1961) where the range is given as *deshayesi* Zone–*mammillatum* Zone. Unless other records exist, it has not been recorded from the *Perna* Beds in the Atherfield Clay previously.

These tubes are referred to *P. antiquata* (J. de C. Sowerby) because they possess no significant differences from the type specimen but better preserved material might indicate the need for placing them in a new species.

Subfamily DITRUPINAE Regenhardt, 1961
Genus GENICULARIA Quenstedt, 1858
Subgenus GLANDIFERA Regenhardt, 1961
Genicularia (*Glandifera*) *inornata* sp. nov.

Plate 19, figs. 8–9

Holotype. A. 10222.

Paratypes. A. 8854, A. 10129, A. 10284.

Distribution. Yellow Sponge Gravel (Aptian, Nutfieldiensis Zone), Faringdon, Oxfordshire.

Diagnosis. A species with four rounded keels, weak obtuse swellings, and shallow median furrows on each of the four sides.

Description. The tube is free, straight or slightly curved, with four rounded keels giving it a quadrangular cross-section with rather concave sides. The keels are composed of short compact segments secreted in the form of weak obtuse swellings. In the holotype (Pl. 19, fig. 8) the swellings are so poorly developed that the keels have a continuous undulating profile but in the somewhat larger paratype (Pl. 19, fig. 9) they are more prominent. On the lateral surfaces shallow longitudinal median furrows forming the margins of the keels are slightly deeper on three of the sides than on the other one. Very faint transverse growth lines which bend away from the aperture at each of the furrows are barely visible on the holotype but quite clearly marked on A. 10284. The aperture is circular, constricted and unbroken in the holotype; in other specimens, e.g. A. 10284, it has indentations coinciding with the longitudinal furrows.

Dimensions.

	Length	Width	
		Minimum	Maximum
A. 10222	13 mm	2·0 mm	2·5 mm
A. 8854	10 mm	3·0 mm	4·0 mm
A. 10129	22 mm	2·5 mm	3·0 mm
A. 10284	6 mm	2·0 mm	2·5 mm

Remarks. The obscure external ornamentation of these tubes can be attributed to a large extent to their weathered condition. Lacking the well-defined nodosity characteristic of *Genicularia* (*Glandifera*) Regenhardt, they have an outline quite similar to species of *Ditrupa* (*Tetraditrupa*) Regenhardt. However, they are more closely comparable with *G.* (*Glandifera*) *vultuosa* Regenhardt from the Aptian of Germany and tubes from the Cenomanian of Dover, Kent, and Hunstanton, Norfolk, and the Gault Clay of Folkestone, Kent, provisionally referred to *G.* (*Glandifera*) *rustica* (J. de C. Sowerby). Both of these species have stronger nodose swellings than *G.* (*Glandifera*) *inornata* and in the latter the longitudinal furrows are narrower and deeper.

Subfamily FILOGRANINAE Rioja, 1923

Genus GLOMERULA Nielsen, 1931

Glomerula gordialis (Schlotheim)

Plate 20, fig. 5

1820 *Serpulites gordialis* Schlotheim, p. 96.
1831 *Serpula gordialis* Goldfuss, p. 234, pl. 60, fig. 8.
1854 *Serpula gordialis* Sharpe, p. 193.
1883 *Serpula gordialis* Keeping, p. 132.
1931 *Glomerula gordialis* Nielsen, p. 88, pl. 1, figs. 9–10.
1961 *Glomerula gordialis* Regenhardt, p. 26, pl. 1, fig. 2.
1964 *Glomerula gordialis* Muller, p. 620, text-figs. 5–6.
1967 *Glomerula gordialis* Pugaczewska, p. 180, pl. 1, figs. 5–10.
1968 *Glomerula gordialis* Bignot, p. 18, pl. 1, fig. 1; pl. 2, figs. 1–4.

Material. 108 specimens mainly from Faringdon, Oxfordshire.

Distribution (Aptian). Sponge Gravel, Faringdon, Oxfordshire; Lower Greensand, Upware, Cambridgeshire and Brickhill, Buckinghamshire; Hythe Beds, Hythe and Broughton Mount, Kent; Ferruginous Sands, Crackers, Blackgang Chine, Shanklin, Isle of Wight; Atherfield Clay (*Perna* Bed), Atherfield, Isle of Wight.

Diagnosis. Tube smooth, undulating; initial stage attached, subcylindrical, coiled; adult stage free, cylindrical, trochospiral or contorted. Diameter of tube: 0·5 mm–2·0 mm.

Remarks. The development of *Glomerula gordialis* (Schlotheim) from a fixed, initially coiled stage to one in which the free adult tube is at first straight and finally spiral or contorted was described by Müller (1964). This concept of the species has since been adopted by Pugaczewska (1967) and Bignot (1968) for Upper Cretaceous tubes from Boryszew, Poland, and the Dieppe region of France.

A collection comprising seventy-four specimens of this species obtained from the Sponge Gravel at Faringdon includes free spiral and contorted tubes and attached coiled initial tubes (Pl. 20, fig. 5) as envisaged by Müller (1964). In diameter the attached tubes have a maximum of 0·5 mm and the free tubes 2·0 mm. The attached tubes occur on shells of various types and phosphatic nodules but mainly on Calcareous sponges, especially *Raphidonema*. In some cases the tube itself is encrusted by bryozoa.

Genus SARCINELLA Regenhardt, 1961

Sarcinella plexus (J. de C. Sowerby)

Plate 20, fig. 6

1829 *Serpula plexus* J. de C. Sowerby, p. 201, pl. 598, fig. 1.
1831 *Serpula socialis* Goldfuss, p. 235, pl. 69, fig. 12.
1836 *Serpula filiformis* Sowerby *in* Fitton, p. 346, pl. 16, fig. 2.
1961 *Sarcinella sarcinella* Regenhardt, p. 29, pl. 1, fig. 6.
1961 *Sarcinella socialis* Regenhardt, p. 29, pl. 1, fig. 5.
1968 *Sarcinella plexus* Bignot, p. 19, pl. 1, figs. 2–4.

Material. Eleven specimens in the British Museum (Natural History) collections and six specimens in the Keeping Collection at Sedgwick Museum, Cambridge.

Distribution (Aptian). Lower Greensand, Upware, Cambridgeshire; Bargate Stone, Littleton and Shackleford, SW. of Guildford, Surrey; Hythe Beds, Hythe and Great Chart, Kent, and Sevenoaks, Kent, and Godstone, Surrey; Folkestone and Sandgate Beds, Folkestone, Kent; Ferruginous Sands, Crackers, Shanklin, Isle of Wight; Atherfield Clay, Atherfield, Isle of Wight.

Emended diagnosis. Smooth, cylindrical tubes occurring in compact, twisted masses or in bunches of slightly curved, more or less parallel tubes. The diameter of the tube which does not vary in individuals ranges from 0·8 mm in slender tubes to *c.* 1·6 mm in the largest ones.

Remarks. Whereas the tubes form twisted masses in *Serpula plexus* J. de C. Sowerby, in *Serpula socialis* Goldfuss, *S. filiformis* J. de C. Sowerby, and *Sarcinella sarcinella* Regenhardt the individual tubes forming the aggregate are almost parallel to each other. No significant difference apart from this exists between these species and for this reason the author agrees with Bignot (1964) in placing them in *Sarcinella plexus* (J. de C. Sowerby). As he pointed out, Regenhardt (1961) overlooked this species which has priority over *S. socialis* Goldfuss.

S. plexus is most frequently found in the form of parallel bunches in the British Lower Greensand beds.

Subfamily SPIRORBINAE Chamberlin, 1919

Rotularia polygonalis (J. de C. Sowerby)

Plate 21, figs. 9–10

Material. Thirty specimens in the British Museum (Natural History) collection and five specimens in the Keeping Collection at the Sedgwick Museum, Cambridge.

Distribution (Aptian). Lower Greensand, Upware, Cambridgeshire; Bargate Stone, Shackleford, SW. of Guildford, Surrey; Hythe Beds, Hythe, Seabrooke and Maidstone, Kent; Ferruginous Sands, Crackers and Upper Lobster Bed, Atherfield, Isle of Wight; Atherfield Clay, Sevenoaks, Kent, and Atherfield, Isle of Wight.

Original description. Spiral portion a short cone, with one involute ridge running up to the apex, and two ridges round the margin; produced part trumpet-formed, with seven acute angles.

Remarks. Although this species is generally found in the form of small discoid tubes (Pl. 21, figs. 9–10) with the characteristic trumpet-shaped free portion missing, it is easily recognized by the three ridges which distinguish it from the other species. Most of the tubes are dextrally coiled and in shape they vary from flat discs to slightly conical. The species is fairly common in the Hythe Beds and Atherfield Clay in Kent and the Crackers in the Isle of Wight, but elsewhere it appears to be comparatively rare.

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CEPHALOPODA FROM THE CARBONIFEROUS OF ARGENTINA

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ABSTRACT. Orthoconic nautiloid Cephalopoda from the Carboniferous of west central Patagonia are described, including a new genus *Sueroceras*. Species described from the Carboniferous of Alaska, U.S.A., Ireland, U.S.S.R., Uruguay, and the Permian of Australia are included in the genus. Other specimens are doubtfully referred to *Reticycloceras* Gordon and *Cycloceras* M'Coy. *Pseudorthoceras* Girty is recorded for the first time from western Argentina. The goniatitid *Glaphyrites* Ruzhencev is also recorded. It is also noted that the goniatitid *Tornoceras* Hyatt seems to be restricted to the Middle Devonian of Argentina.

THE marine Carboniferous of western and southern Argentina has yielded representatives of most invertebrate phyla, but there are few records, particularly descriptions, of cephalopods. This paper describes new cephalopod material from both areas, but principally from Patagonia.

Southern Argentina. Suero (1948, 1952, 1953, 1958, 1961) described a succession of Upper Palaeozoic fossiliferous sediments in central-western Patagonia (Province of Chubut), which he included in his 'Sistema de Tepuel', and which were concentrated at seven levels. A Carboniferous age was assigned to the 'Sistema de Tepuel', although the possible presence of Devonian and Permian strata was not excluded. Suero's original material, together with some subsequent collections have been described by Sabattini and Noirat 1967; Mariñelarena 1970 (Cnidaria); Sabattini 1972 (Bryozoa); Amos 1958*b*, 1961*a*, *b* (Brachiopoda); Gonzalez and Sabattini 1972 (Calyptoptomatida); Sabattini and Noirat 1969 (Gastropoda); Gonzalez 1969, 1972 (Bivalvia); Rossi de García 1972 (Ostracoda); Amos, Campbell and Goldring 1960 (Trilobita).

Cephalopods from this region have been described by Miller and Garner (1953), who identified *Anthracoceras argentinense* and *Eoasianites* sp. Closs (1967) described three fragmentary nautiloids as *Dolorthoceras chubutense*.

Further laboratory and field studies have brought to light additional and better preserved cephalopod material. This includes a goniatite fragment, nine fragmentary phragmocones, and some twenty external moulds of nautiloids, most of which exhibit relatively well-preserved external and internal features.

Western Argentina. The Carboniferous sediments from western Argentina are known from a series of outcrops located from south to north in the Provinces of Mendoza, San Juan, and La Rioja. These sediments have been studied since the end of the last century by a number of authors including Amos (1964) and Polanski (1970) who reported various fossiliferous localities and levels. The invertebrate material has been described as follows: Sabattini 1972 (bryozoa); Reed (*in* Du Toit 1927); Keidel and Harrington 1938; Leanza 1945, 1948; Amos 1957, 1958*a*, 1961*b*; Amos, Baldis and Csaky 1963 (Brachiopoda); Reed (*in* Du Toit 1927); Sabattini and Noirat 1969 (Gastropoda); Reed (*in* Du Toit 1927); Keidel and Harrington 1938; Leanza 1948 (Bivalvia).

[Palaeontology, Vol. 18, Part 1, 1975, pp. 117–136, pls. 22–24.]

Antelo (1969, 1970) described *Protocanites scalabrinii*, from the Maliman Formation in the Province of San Juan. Recently, three fragmentary specimens of orthoconic nautiloid material, from the same locality and level, have become available.

STRATIGRAPHY AND LOCALITIES

1. Province of Chubut (central Patagonia)

The material described was collected from various localities in a region of approximately 5600 sq. km located in the north-western part of the province of Chubut, central Patagonia (43–44° S., 70–71° W.) (text-fig. 1B). The Upper Palaeozoic sediments outcrop in two north–south oriented mountain ranges; the known fossiliferous outcrops being located in the south-west (Sierra de Tepuel) and north-east (Sierra de Languiñeo).

In Arroyo Pescado (Rolleri 1970) the base of the Upper Palaeozoic unconformably overlies metamorphosed sediments of possible Lower to Middle Palaeozoic? age. The 'Sistema de Tepuel' is in turn overlain unconformably by a sequence of Liassic sediments.

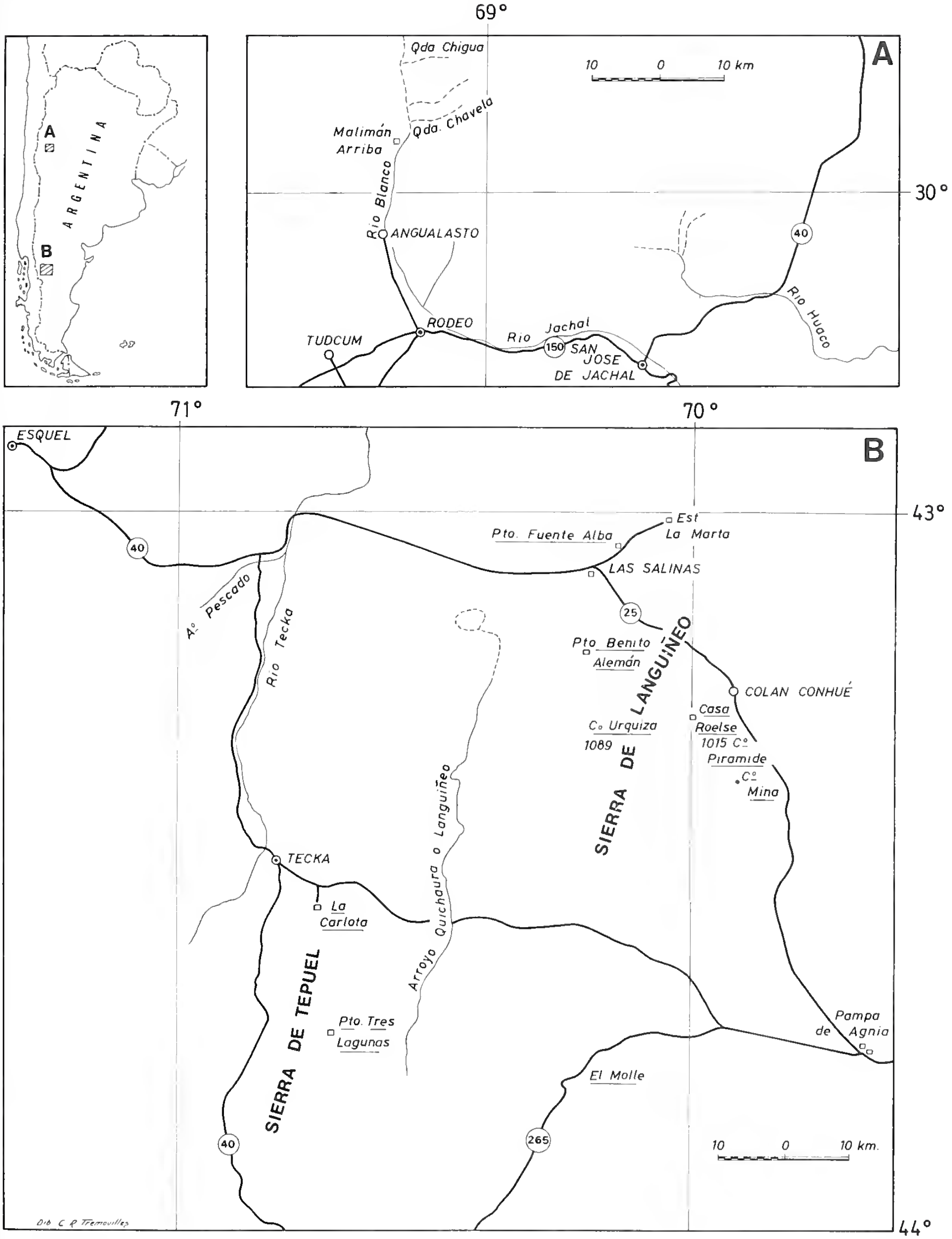
The Upper Palaeozoic sediments included by Suero (1948, p. 11) in the 'Sistema de Tepuel' are almost 5500 m thick. The lower part, 3200 m thick, comprises greywackes, sandstones, and shales intercalated with at least four diamictite and three fossiliferous levels (see also Frakes, Amos and Crowell 1969). The upper part, approximately 2000 m thick, comprises shales and sandstones with four fossiliferous levels. Greywackes and diamictites are absent.

In Suero's (1948) section of Sierra de Tepuel, made about 20 km south of La Carlota (near Puesto Tres Lagunas), there are only two levels with cephalopods. The lowest is almost at the top of the lower part of the 'Sistema de Tepuel' and contains a fauna of trilobites, gastropods, brachiopods, cnidarids, bryozoans, fish bones, and scales. This level, with a similar fauna, is present also in La Carlota (Suero 1948, p. 9) and due to its extensive areal distribution has been used as a marker for the division of the lower and upper parts of the 'Tepuel System' in Sierra de Tepuel and Sierra de Languiñeo (Suero 1948, p. 15; 1958, p. 25; Gonzalez 1972, p. 105).

According to Suero (1948, 1953, 1958; see also Amos *et al.* 1960, p. 229; Closs 1967, p. 124), specimens described under '*Anthracoceras*? *argentinense*' Miller and Garner, 1953 (now *Wiedeyoceras argentinense*, see Miller and Furnish 1958, p. 684; Gordon 1964, p. 245; Furnish and Spinosa 1968, p. 255), *Dolorthoceras chubutense* Closs (1967), and *Australosutura gardneri* Mitchell (*in* Amos *et al.* 1960) come from this level.

The second level with cephalopods recorded by Suero (1948, p. 9, under '21') is near the base of the upper part of the 'Sistema de Tepuel', about 600–700 m above the lower level, and has yielded only nautiloids. However, a goniatitid (*Eoasianites* sp., in Miller and Garner 1953) has been reported also from Sierra de Languiñeo (Puesto Urquiza), close to the base of the upper part of the 'Sistema de Tepuel' but only 200–250 m above the first level with cephalopods (Suero 1958, p. 25).

From Suero's geological map (1948, fig. 5) the presence of both fossiliferous levels can be inferred; the lower one, below and to the west of the diabase sill (Cresta de los Bosques) and the upper one above and to the east in the neighbourhood of Puesto



TEXT-FIG. 1. Index map for the regions with fossiliferous localities in Provinces of San Juan (A) and Chubut (B).

Tres Lagunas. The presence of *Sueroceras irregulare* gen. et sp. nov. at both localities suggests a large vertical distribution within this sequence for this species.

Although only the locality data are known for Suero's specimens described herein, from the stratigraphic information recorded above it is possible to infer that the material from La Carlota and that below the diabase sill to the west of Puesto Tres Lagunas came from the level located near the top of the lower part of the 'Sistema de Tepuel', whereas that from the neighbourhood of Puesto Tres Lagunas belongs to the level close to the base of the upper part.

No information is available about the stratigraphic position of the orthoconic nautiloids found by Suero in other localities, and although from the extensive areal distribution of the lower level with cephalopods it could be assumed that they belong to that part of the section, it is better to give them a general assignation to the middle part of the 'Sistema de Tepuel'.

2. *Province of San Juan* (*western Argentina*)

The fragmentary specimens here described as *Pseudorthoceras* sp. were collected from a locality 75 km north-west of Jachal in the north-western part of the Province of San Juan (30° S., 69° W.). The fossiliferous outcrop is in the Quebrada Chigua, about 30 km north of Angualasto (text-fig. 1A; Antelo 1969, p. 71, fig. 1).

In this area the Carboniferous sequence, described by Furque (1963, p. 52) has been revised recently by Scalabrini Ortiz (1970, 1973). The latter has divided the Carboniferous sediments into two formations: the Lower Carboniferous Maliman Formation, which consists of marine sandstones, and siltstones, and the Upper Carboniferous Cortaderas Formation which consists of continental conglomerates, sandstones, and siltstones, with a thickness of 1188 m and 1160 m respectively in the type sections. The two formations are separated by an unconformity.

The Carboniferous sequence, in this area, overlies with angular unconformity the marine Middle Devonian Chavela Formation (Scalabrini Ortiz 1973). An Upper Devonian age suggested for this unit (Leanza 1968; Antelo 1969; Scalabrini Ortiz 1970, 1973; Furque 1972) is based on *Tornoceras baldisi* Leanza, 1968, described from Quebrada Chavela, about 10 km south of Quebrada Chigua (text-fig. 1A).

The evidence given by Leanza to support an Upper Devonian age was that *Tornoceras* in its world-wide distribution is, with the exception of the subgenus *Protornoceras* restricted to the Upper Devonian. However, from the literature it is evident that *Tornoceras* is Middle-Upper Devonian (Miller 1938; Miller, Furnish and Schindewolf 1957; House 1965), a range exhibited by the type species *T. uniangularis* (Conrad), which is fairly common in the Hamilton Group of New York and its equivalents, and which has been used for naming a biostratigraphical zone in the Middle Devonian (Oliver, de Witt, Dennison, Hoskins and Huddle 1968).

It is interesting to point out that Leanza compared his material with *T. discoideum* (Hall), type species of *Parodiceras* Hyatt, which is considered as a synonym or a subgenus of *Tornoceras*, and that *Parodiceras* is present in the lower part of the Hamilton Group (Marcellus Formation) (House 1965). *Parodiceras* Wedekind, to which Leanza compared some of his material, is synonymous with the Middle Devonian genus *Parodicerellum* Strand, and not with *Tornoceras* as indicated by Leanza (see Miller *et al.* 1957).

T. baldisi is associated with Middle Devonian trilobites (Baldis 1968; Padula, Rolleri, Mingramm, Criado Roque, Flores and Baldis 1968; Cuerda and Baldis 1971). The top of the Upper Carboniferous Cortaderas Formation is unknown in this area.

The orthoconic nautiloid material described below came from a fossiliferous level, with cnidarids, brachiopods, gastropods, bivalves, and crinoids, located in the middle part of the Maliman Formation, about 196 m (440 m if ten andesitic sills are included) above the contact with the marine Chavela Formation (Antelo 1969, p. 69; Scalabrini Ortiz 1970). From the same level came two specimens of goniatitids described as *Protocanites scalabrinii* Antelo (1969, 1970).

CARBONIFEROUS CEPHALOPODS IN THE SOUTHERN HEMISPHERE

As pointed out by Closs (1967, p. 123; 1969, p. 200) orthoconic nautiloids and goniatitids seem to be rare in the Upper Palaeozoic of South America (see also Closs and Kullman *in press*). Apart from some goniatitids from Peru (Berry 1928; Thomas 1928; Newell, Chronic and Roberts 1953), the only other Carboniferous goniatitids and orthoconic nautiloids seem to be those described from Argentina and Uruguay by Closs (1967, 1969) and Antelo (1969, 1970).

Indeed, in the southern hemisphere as a whole this class seems to be of uncommon occurrence in Carboniferous sediments (Hodson and Ramsbottom 1973). A goniatitid has been described from South West Africa (Martin, Walliser and Wilczewski 1970) and some orthoconic nautiloids and goniatitids from Australia (Delépine 1941; Cvancara 1958; Campbell 1962; Campbell and Engel 1963; Brown, Campbell and Roberts 1964; Roberts 1965; Campbell and McKellar 1969).

Brown *et al.* (1964, p. 682) have indicated that in Australia nautiloids seem to be more abundant and widespread than goniatitids, although the latter have been more often described and illustrated. This general statement can be applied to the whole southern hemisphere. Carboniferous orthoconic nautiloids in the southern hemisphere are known only from some specimens described and illustrated in a few papers (de Koninck 1876–1877, and Brown *et al.* 1964, for Australia; and Closs 1967, for Uruguay and Argentina).

It is interesting that there is almost no affinity at the generic level between the Carboniferous cephalopod fauna of Australia and the African and South American faunas.

In the Lower Carboniferous the cephalopod fauna of Argentina is represented only by *Protocanites* Schmidt and *Pseudorthoceras* Girty, whilst in Australia there are at least nine other genera besides *Protocanites*. No Upper Carboniferous cephalopods are known from Australia.

Bearing in mind the differences in the number of taxa involved in these intercontinental comparisons, it could be said that the cephalopod affinities conflict with the conclusions of Campbell and McKellar (1969) who postulated a closer affinity between Australia and Argentina in the Westphalian, and also with the results of Amos and Sabattini (1969) who postulate an affinity in the Westphalian in some cases at the specific level.

One would expect the cephalopods, being nektobenthonic, to be the one group with representatives in the two areas. However, this discrepancy may be due to a difference in age of the strata in the two regions, or to differences in facies or in ecological conditions between the two areas.

Depository. The material is deposited in the collections of the División de Paleozoología Invertebrados, Museo de Ciencias Naturales, La Plata, Argentina, the numbers prefixed MLP.

SYSTEMATIC DESCRIPTIONS

Subclass NAUTILOIDEA Agassiz, 1847
Order ORTHOCERIDA Kuhn, 1940
Superfamily PSEUDORTHOCERATACEAE Flower and Caster, 1935
Family PSEUDORTHOCERATIDAE Flower and Caster, 1935
Genus SUEROCERAS gen. nov.

Type species. Sueroceras irregulare sp. nov.

Derivatio nominis. For the late Dr. T. Suero, who studied the Upper Palaeozoic outcrops from NW. Chubut and collected most of the known fossil material from this region.

Range. Carboniferous–?Permian.

Diagnosis. Orthoconic nautiloids with gently and irregularly expanding conch; circular or subcircular in cross-section; surface ornamented by transverse and longitudinal lirae which form a reticulate pattern. Siphuncle central, with suborthochoanitic to subcyrtochoanitic septal necks; connecting rings subcylindrical to fusiform, contracted at the septal necks; siphuncular deposits continuous on both sides, or on the ventral side, or vestigial (?); cameral deposits of the mural and epi-hyposeptal type.

Other species included in the genus: *Sueroceras* sp., and doubtfully: *Orthoceras striata* J. Sowerby, 1814; '*Orthoceras striatum* J. Sowerby' de Koninck, 1876–1877; *Kionoceras*? sp. C, Gordon 1957; ?*Dolorthoceras reticulatum* Shimansky, 1968; *Dolorthoceras chubutense* Closs, 1967; *Dolorthoceras oklahomense* Smith, 1938.

Remarks. The distinctive reticulate pattern of the ornament, the morphology of the siphuncle and its related structures are sufficient to differentiate this material from all other Orthocerida genera.

The most similar material previously described is that from Alaska included under '*Kionoceras*? sp. C' by Gordon (1957, p. 23). However, *Kionoceras* Hyatt, 1884, a genus whose acme was in the Silurian (Troedsson 1932), has species with relatively more prominent longitudinal ribs (Sweet 1964, p. K229, fig. 159, 1*a–c*; Demanet 1941, p. 119, pl. 4, fig. 6; Shimansky 1968, p. 56, pl. 1, fig. 5; Foerste 1924, p. 29, pl. 14, fig. 1; Troedsson 1932; Grabau and Shimer 1910, p. 61). *Protokionoceras* Grabau and Shimer (1910), a Middle Ordovician–Middle Devonian genus, also has stronger longitudinal ribs, and in the concave interspaces there are finer ribs (Troedsson 1932, p. 14, pl. 7, fig. 7, text-fig. 3; Strand 1934, p. 23, pl. 3, fig. 4; Foerste 1924, p. 30). Furthermore, it has an orthochoanitic to suborthochoanitic siphuncle. *Palmeroceras* Flower has a siphuncular structure with features in common with *Adnatoceras* Flower and *Dolorthoceras* Miller (Flower 1939, p. 119), and 'the very fine, minutely undulating irregular, lamellose lines of growth', exhibited by the type species *P. fustis* (Hall 1879, p. 281, pl. 83, fig. 11 and pl. 113, figs. 16, 17), differ from the transverse lirae of *Sueroceras*.

The specimens described below are similar, in the structure of the siphuncle, to *Dolorthoceras* Miller, but differ mainly in the presence of a reticulate ornament. *Dolorthoceras* Miller, the type species of which, *D. circulare* Miller, is represented by a badly preserved specimen (Miller 1931, p. 419), has been characterized as possessing a smooth surface with only growth lines, and rare fine longitudinal lirae (Flower 1939, p. 93; Gordon 1964, p. 119). Some species, however, with a reticulate ornamentation have been included in it, i.e. *D. oklahomense* Smith (1938, p. 6, pl. 1, figs. 15, 16) and ?*D. reticulatum* Shimansky (1968, p. 77, pl. 5, fig. 2).

Closs (1967, p. 125), when studying the Chubut and Uruguayan material, pointed out that even if the internal features are coincident with those given in the original diagnosis of *Dolorthoceras* the ornament is different, and closer to that of *Mitorthoceras* Gordon, which is characterized by 'raised transverse lirae'. Closs, however, considered 'the morphology of the siphuncle and related structures basic for generic classification whereas the ornament only for specific level', and therefore emended the diagnosis of *Dolorthoceras*, including *Mitorthoceras*, implicitly, as a junior subjective synonym.

This criterion is debatable. Many nautiloid genera differ only in ornament (see Flower 1939), and this has been used in general as a diagnostic feature within the cephalopoda.

The incompletness of our knowledge of the orthoconic nautiloids (Sweet 1964, p. K220) is plainly evident when studying the siphuncular and cameral deposits of fragmentary specimens such as those herein described, due to the fact that the observed features will vary according to the part of the shell and the growth stage of the specimen to which they belong (Flower 1955, pp. 92, 93, 96–98; Fischer and Teichert 1969, p. 7).

For these reasons, and because the ornament in the specimens described by Closs (op. cit.) is similar to that present in the material herein described it is not considered taxonomically significant, at the present state of our knowledge, that the specimens included in *Sueroceras* cf. *S.*? *chubutense* (Closs) have siphuncular deposits lying along both sides while in *S. irregulare* sp. nov. they occur only on one side. More and better material, representing different growth stages, is necessary for a definitive statement about the generic status of Closs's species.

A similar reticulate ornament is present also in *Dolorthoceras oklahomense* Smith (1938, pl. 1, figs. 15–16), a feature which led him to consider the possibility that 'this form represents a new genus'. Although other known internal features seem to be similar to those in *Sueroceras*, because Smith did not give a detailed description the inclusion of this species within *Sueroceras* gen. nov. remains questionable.

A similar case is found with ?*Dolorthoceras reticulatum* Shimansky (1968, p. 77, pl. 5, fig. 2), which has a fairly regular ornament, but whose internal features are unknown.

Besides the Alaskan material described by Gordon (1957), the most similar to the present one is that described from Australia by de Koninck (1876-1877, p. 271, pl. 24, fig. 2) under '*Orthoceras striatum* J. Sowerby', although here also the internal features are virtually unknown. Furthermore, the Australian original material has been destroyed by fire (Dun 1898) and no new material has been recorded. The status of this species is unclear, especially when we consider that the type specimen from Ireland figured by J. Sowerby (1814) and the species diagnosis has been differently understood, in relation to the ornament, by M'Coy (1844, p. 8), Foord (1888, p. 190), and Etheridge (*in* Jack and Etheridge 1892, p. 293). However, it seems that Sowerby's specimen has the same reticulate ornament as the Australian and Patagonian specimens, while this feature is not present in the material described by the other named authors.

According to our definition of *Sueroceras* it should be restricted to the Carboniferous, with a possible extension into the Permian.

The material from Alaska described by Gordon (1957) under '*Kionoceras*? sp. C', which has the closest affinity with the specimen from Patagonia occurs together with *Goniatites crenistria* Phillips, a species which characterizes the lower part of the Upper Viséan.

'*Dolorthoceras*' *reticulatum* Shimansky (1968) occurs in the Lower Carboniferous of the Dombar in the southern Urals.

'*Dolorthoceras*' *oklahomense* Smith was reported from the Buckhorn Asphalt, Boggy Formation of the Pennsylvanian (Desmoinesian) (Smith 1938, p. 3; Fischer and Teichert 1969, p. 7).

The Australian '*Orthoceras striatum* J. Sowerby' (de Koninck 1876–1877) was reported from Wollongang, an area where only Permian sediments occur (David 1950), and the specimen could have come from the 'Shoalhaven Group or even higher, i.e. well up in the Australian Permian marine sequence' (written communication, Campbell 1973).

Sowerby's species was based on one Irish specimen 'found in the Black Rock near Cork' (Sowerby 1814, p. 129), and according to Dr. W. E. Nevill (written communication 1973) 'the locality is at or near the base of . . . (the) . . . Waulsortian Reef', whose range 'elsewhere in W. Europe is given as C_1 and C_2', i.e. on the Viséan–Tournaisian boundary.

Most of the Patagonian material is, apparently, from the top of the lower part of the 'Sistema de Tepuel', where also *Wiedeyoceras argentinense* (Miller and Garner), *Australosutura gardneri* Mitchell, and other invertebrates, have been recorded. The age of this part of the section has been considered, on different grounds, as Westphalian (Amos 1964, p. 62).

An Upper Carboniferous age for *Sueroceras* gen. nov. is supported by the possible association in Uruguay of *S.*? cf. *S.*? *chubutense* (Closs) with a species of *Eoasianites* (*Glaphyrites*) considered to be related to Upper Carboniferous species from North America (Closs 1967, p. 124; 1969, p. 204).

Sueroceras irregulare gen. et sp. nov.

Plate 22, figs. 1–12

Holotype. Incomplete phragmocone (Pl. 22, figs. 1–5) (MLP 11865).

Locus typicus. Puesto Benito Aleman, Sierra de Languiñeo, Province of Chubut.

Stratum typicum. ?Level 17, top of the lower part of the 'Sistema de Tepuel' (Suero 1948).

Derivatio nominis. Latin—from the irregular transverse lirae.

Diagnosis. Orthoconic nautiloids with gently expanding conch, circular in cross-section; surface ornamented by transverse and longitudinal lirae forming a reticulate pattern; transverse lirae irregularly elevated. Siphuncle central with sub-orthochoanitic to subcyrtochoanitic septal necks. Connecting rings subcylindrical, flat to slightly convex in the middle and abruptly contracted at the septal necks; siphuncular deposits continuous on the ventral side or (?)vestigial; cameral deposits ventral and dorsal, of the mural and epi-hyposeptal types, thickest on the ventral side.

Material. Sierra de Languiñeo, Province of Chubut: *a*, Point N255 from Cerro Pirámide, somewhat north of Cresta Baja, two incomplete phragmocones (MLP 11862–11863), internal mould (MLP 11866); *b*, concretions to the west of Puesto Benito Aleman, incomplete phragmocone and holotype (MLP 11864–11865); *c*, Cerro Mina, fragmentary external mould (MLP 11867); *d*, in neighbourhood of Puesto Fuente Alba, on right side of road to Estancia La Marta, three fragmentary external moulds (MLP 11868a, b, c), (?) crushed internal mould (MLP 11869); *e*, N260 from Casa Roelse, fragment of external mould (MLP 11870), fragment of body chamber (MLP 11871); *f*, El Molle, nivel Cañulef, three fragments of external moulds (MLP 11888).

Sierra de Tepuel, Province of Chubut: *a*, La Carlota, 9 km to south-east of Tecka, partially preserved internal mould of phragmocone (MLP 11872); *b*, west of Puesto Tres Lagunas, below diabase sill, three fragmentary external moulds (MLP 11873–11875); *c*, north of Puesto Tres Lagunas, five external moulds of phragmocones (MLP 11876); *d*, N35 from Cerro Playo, about 600 m east of Puesto Tres Lagunas, internal mould of fragmentary phragmocone (MLP 11877).

Description. The holotype (MLP 11865, Pl. 22, figs. 1–5) is part of a phragmocone with circular cross-section, 22 mm long, 12·6 mm in diameter at its oral end, 11·5 mm at the apical end, and with an expansion rate of 1 mm in 19 mm. Septa are straight and shallowly saucer shaped (Pl. 22, fig. 1). There are three chambers preserved, averaging 1·6 in a length equal to the diameter. The surface of the conch is ornamented

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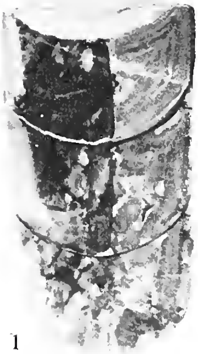
EXPLANATION OF PLATE 22

All figures × 2, unless otherwise stated.

Figs. 1–12. *Sueroceras irregulare* sp. nov., Province of Chubut. 1–5, MLP 11865, holotype, Puesto Benito Aleman, Sa. de Languiñeo; 1, ventrodorsal longitudinal section; 2, enlarged view of fig. 1, × 5; 3, lateral view; 4, enlarged view of fig. 3, × 6; 5, transverse section. 6, MLP 11862, paratype, N255 from Co. Pirámide, Sa. de Languiñeo, ventrodorsal longitudinal section. 7–8, MLP 11863, paratype, N255 from Co. Pirámide, Sa. de Languiñeo; 7, ventrodorsal longitudinal section; 8, enlarged view of fig. 7, × 6. 9, MLP 11872, paratype, La Carlota, Sa. de Tepuel, internal mould showing septa spacing. 10, MLP 11864, paratype, west of Puesto Benito Aleman, Sa. de Languiñeo, fragment of a ventrodorsal longitudinal section. 11–12, MLP 11867, paratype, Co. Mina, Sa. de Languiñeo; 11, side view of a latex cast; 12, enlarged view of fig. 11, × 6.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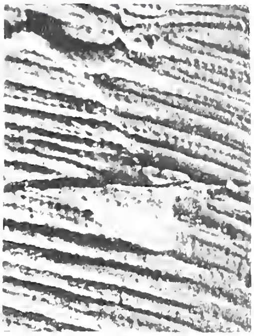
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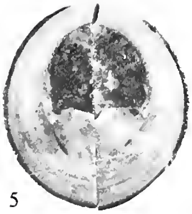
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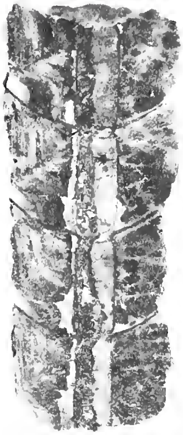
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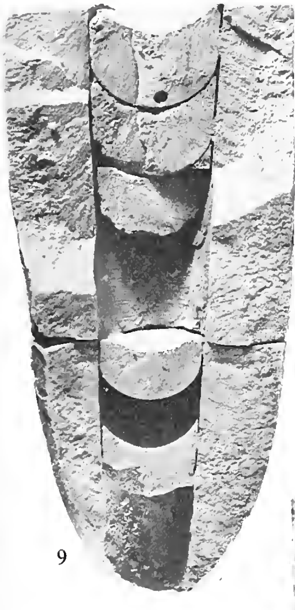
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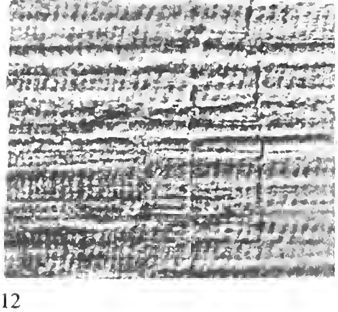
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RICCARDI and SABATTINI, *Suerocas*

with transverse and longitudinal lirae. The transverse sharp rounded lirae are irregularly elevated and are slightly (12°) inclined curving adapically on the ventral side. There are about five lirae per 1 mm. The longitudinal lirae are more regular, relatively less elevated and, therefore, less visible and being interrupted by the transverse lirae, they are more dense, seven per mm.

The siphuncle is central, 20·6% of the shell diameter. The connecting rings are subcylindrical, with the greatest diameter in the middle, and slowly decreasing towards both ends where they are abruptly constricted at the septal necks. The latter are suborthochoanitic to subcyrtochoanitic and have a length of 0·8 mm. The area of adnation is very small (0·5 mm) and equal to the brim.

Endosiphuncular deposits are almost non-existent or vestigial and irregularly distributed. Cameral deposits are of the plano mural, plano episeptal, and plano hyposeptal types. On the ventral side these three types fill the chambers almost completely (Pl. 22, figs. 1, 5), but on the dorsal side the deposits are relatively less thick.

Two specimens (MLP 11862–11863, Pl. 22, figs. 6 and 7–8), with the same type of ornament, 34·2 mm and 27·7 mm long respectively, exhibit four camerae also averaging 1·6 in a length equal to the shell diameter. In both specimens, however, the diameter of the connecting ring is larger than in the holotype, being 24% and 23% respectively of the conch diameter (Pl. 22, figs. 6–8). Furthermore, here the siphuncular deposits are continuous and restricted to one side of the siphuncle where they occupy about half the width of the siphuncle on the ventral side.

Another paratype (MLP 11864, Pl. 22, fig. 10) consists of a fragment of a phragmocone 20·5 mm long. It has a siphuncular diameter amounting to 18% of that of the conch, and continuous siphuncular deposits on the ventral side only. In this specimen, however, the camerae average two in a length equal to the conch diameter.

Only other two paratypes (MLP 11872 and MLP 11871) are preserved as internal moulds. The first (Pl. 22, fig. 9) is a phragmocone 62 mm long with a growth rate of 1 mm in 15 mm. The camerae average 1·8 in a length equal to the diameter and the siphuncle width amounts to 12% of the conch diameter. Due to poor preservation neither camerae nor siphuncular deposits are visible. The longitudinal lirae amount to eight per mm. The other paratype consists of a body chamber 77 mm long with an adoral width of 32 mm and an adapical of 26 mm, and a growth rate of 1 mm in 12·8 mm. The ornament is weaker than in the smaller specimens and the longitudinal lirae are only feebly developed.

Remarks. Some external moulds exhibiting the same type of ornament are also referred to this species, although the transverse lirae are less elevated and the longitudinal lirae less visible. It is possible that these moulds belong in *S.* cf. *S.*? *chubutense* (Closs). However, due to the uncertain status of the latter, they are included tentatively in *S. irregulare* nov. sp.

Sueroceras cf. *S.*? *chubutense* (Closs)

Plate 23, figs. 1–3, 7

v 1967 *Dolorthoceras chubutense* Closs, p. 125, pl. 1, figs. 1–5; ?*non* pl. 1, fig. 6 and pl. 2, figs. 1–3.

Material. Sierra de Languiñeo, Province of Chubut; *a*, west of Puesto Benito Aleman, incomplete phragmocone (MLP 11878); *b*, west of Puesto Benito Aleman, left bank of the Cañadon Aguada Champoza, (?) incomplete phragmocone (MLP 11879).

EXPLANATION OF PLATE 23

All figures ×2, unless otherwise stated.

Figs. 1–3, 7. *Sueroceras* cf. *S.*? *chubutense* (Closs), Sa. de Languiñeo, Province of Chubut. 1, 7, MLP 11878, west of Puesto Benito Aleman; 1, ventrodorsal longitudinal section; 7, enlarged view of fig. 1, × *c.* 6. 2–3, MLP 11879, west of Puesto Benito Aleman, left bank of Cañadon Aguada Champoza; 2, ventrodorsal longitudinal section; 3, enlarged view of fig. 2, × *c.* 9.

Figs. 4–5. *Sueroceras* sp., MLP 11881, La Carlota, Sa. de Tepuel, Province of Chubut. 4, side view of a latex cast; 5, enlarged view of fig. 4, ×6.

Figs. 6, 8, 9. *Pseudorthoceras* sp., MLP 11189a, Quebrada Chigua, Province of San Juan. 6, lateral view; 8, ventrodorsal longitudinal section; 9, enlarged view of fig. 8, ×*c.* 6.

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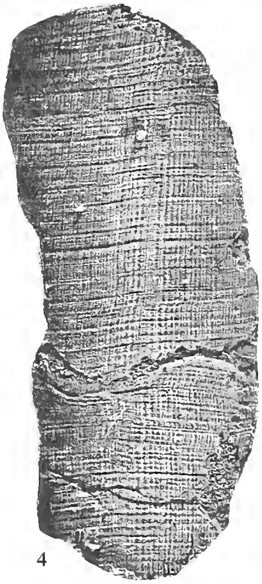

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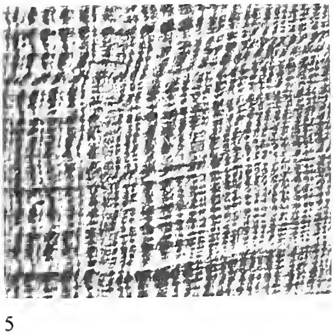

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RICCARDI and SABATTINI, *Sueroceras*

Sierra de Tepuel, Province of Chubut: *a*, west of Puesto Tres Lagunas, below diabase sill, external mould (MLP 11880).

Description. One fragment (MLP 11878, Pl. 23, figs. 1, 7) of a phragmocone about 55 mm long, partially crushed adorally, shows the same external reticulate ornament as *S. irregulare* nov. sp., with sharp rounded irregularly raised transverse lirae and a more regular, and relatively less raised longitudinal component. With six camerae averaging 2·6 in a length equal to the conch diameter. Siphuncle central with subcyrtochoanitic septal necks. Connecting rings fusiform, slightly inflated in the middle and constricted at the septal necks. Siphuncular deposits continuous lying on both sides. Cameral deposits of the mural and epi-hyposeptal types.

Another phragmocone (MLP 11879, Pl. 23, figs. 2–3), tentatively included in this species, shows two camerae in a length equal to the shell diameter. The reticulate ornament is hardly visible, principally the longitudinal lirae.

Remarks. Justification for the inclusion of this species in *Sueroceras* gen. nov. is to be found in the discussion of the genus.

The ornament shows the same transverse and longitudinal lirae as in *S. irregulare* nov. sp. The first are irregular but are more numerous than in the previously described species averaging nine per mm in specimen MLP 11878. In the other specimen (MLP 11879) the lirae cannot be counted exactly due to the preservation, but they seem to be similarly numerous.

As we do not have specimens of a similarly small growth stage as specimen MLP 11879, that can be assigned without doubts to *S. irregulare* nov. sp., it is impossible to know if this specimen could belong to this species or not, especially taking into account that it has an increase in the spacing of the septa with age. Meanwhile it is tentatively included in *S.* cf. *S.*? *chubutense* (Closs).

Only one external mould (MLP 11880) with the reticulate ornament typical of this new genus is included in *S.* cf. *S.*? *chubutense* (Closs) because it also shows the sutures, which indicate a similar spacing of the septa (2·5 camerae in a length equal to the shell diameter) as shown by the other specimens referred to that species.

Although the specimens here described have the same features described by Closs (1967) for the species, his material from Patagonia is so poor that it is difficult to be sure about their identity with our specimens. Particularly if we consider that the specimens from Chubut described by Closs were placed together with some Uruguayan specimens which show relatively more prominent longitudinal lirae (Closs 1967, pl. 1, fig. 6).

The differences between *S. irregulare* nov. sp. and *S.* cf. *S.*? *chubutense* (Closs) lie in the spacing of the septa (2–2·6 and 1·6–1·8 respectively in a length equal to the shell diameter) and perhaps in the presence of siphuncular deposits lying one side and both sides respectively.

Sueroceras sp.

Plate 23, figs. 4–5; Plate 24, figs. 2–4

Material. Sierra de Tepuel, Province of Chubut, La Carlota, 9 km to the south-east of Tecka, three fragmentary external moulds (MLP 11881–11882).

Description. The only observable feature is the ornament, which is reticulate as in *Sueroceras* (above). However, here the transverse and longitudinal lirae are similar in size and regularity, with a close-web fabric. The longitudinal, as well as the transverse lirae amount to about 6–8 per mm, and although some lirae are more raised than others and the longitudinal components occur in pairs, the general aspect is fairly regular.

Remarks. Even if no other features are known, the reticulate ornament is clearly different from that exhibited by *S. irregulare* nov. sp. and *S.* cf. *S.*? *chubutense* (Closs). However, it is possible that these specimens could be extreme variants, in ornament, of any of the other two species, although there are no specimens with a clear intermediate ornament.

Genus *Pseudorthoceras* Girty, 1911

Remarks. The diagnosis of this genus given by Miller, Dunbar and Condra (1933), Flower (1939), Miller and Youngquist (1949), and Gordon (1964) is essentially coincident with that in the Treatise (Sweet 1964, p. K244), although there are some useful additions such as that of Gordon (op. cit., p. 109) pointing out that the 'surface is smooth, ornamented by faint slightly sinuous growth striae', and that the siphuncule in the early stages has subcylindrical connecting rings and is located ventral of centre, 'but rapidly migrate to center of conch . . . commonly with subspherical connecting rings in later stages'.

Concerning differences with the related genus *Mooreoceras* Miller *et al.* (1933), Miller and Youngquist (1949, p. 18), considered that in *Mooreoceras* the 'siphuncule is not quite central in position, and in so far as is known adapical portion of the conch is not curved', there are not 'indigenous cameral deposits' (p. 23), and the cross-section is 'very broadly elliptical (due to a slight dorsoventral depression)' whereas in *Pseudorthoceras* it is circular (p. 23) (see also Miller *et al.* 1933, p. 85).

The alleged absence of endosiphuncular and cameral deposits in *Mooreoceras* has been dismissed by Gordon (1964, p. 112).

Pseudorthoceras sp.

Plate 23, figs. 6, 8–9

Material. Quebrada Chigua, Province of San Juan, two fragments of phragmocones and a body chamber (MLP 11189).

Description. The best-preserved specimen (MLP 11189a) is a fragment 19·5 mm long with a diameter of about 12 mm and circular–subcircular cross-section. The sutures are straight and transverse. There are about three camerae in a length equal to the shell diameter. The siphuncule is central and the septal necks are suborthochoanitic to subcyrtochoanitic. Connecting rings slightly pyriform with the maximum diameter in the adoral part. Brim smaller than neck. Endosiphuncular deposits on the ventral side, with an incomplete development in the adoral direction (Pl. 23, figs. 8–9). Camerae lined with mural and episeptal deposits, thicker on the ventral side where also hyposeptal deposits are present. The shell surface is almost smooth, only with faint slightly sinuous transverse growth lines, and a few irregular wrinkles.

The fragment of another phragmocone (MLP 11189b) 17·5 mm long and with a diameter of about 13 mm has similar external features. A polished longitudinal ventrodorsal section revealed the presence of four camerae, averaging three in a length equal to the shell diameter. The siphuncule is central and the septal necks are suborthochoanitic to subcyrtochoanitic. No other internal structures are visible and the camerae are completely filled with sediment.

Remarks. No specific identification has been attempted. The presence of this genus in West Argentina has been questionably recorded before by Reed (*in* Du Toit 1927, p. 145), who described two fragments of orthoconic nautiloids from the Upper Carboniferous of Quebrada del Salto, Barreal, Province of San Juan, and compared one of them with '*P. knoxense* Girty' from the Pennsylvanian of U.S.A. (see Miller and Youngquist 1949, pp. 18, 21).

The present specimens can be dated as Lower Carboniferous because *Protocanites scalabrinii* Antelo (1969) occurs at the same stratigraphic level.

Genus *Reticycloceras* Gordon, 1960

?*Reticycloceras* sp. 1

Plate 24, figs. 1, 6

Material. Sierra de Languiñeo, Province of Chubut, Puesto Benito Aleman, fragmentary external mould (MLP 11883).

Description. The fragment is 50 mm long, with circular-subcircular cross-section. Surface ornamented with transverse annulations which are rounded, regular, and slightly inclined, bending adapically on the ventral side. There are about two annulations per mm, and on their surface and also on the spaces between them are lirae amounting to eight per mm.

Remarks. The specimen does not allow confidence as to taxonomic status. It bears some superficial resemblance to *Reticycloceras* Gordon and *Criptocycloceras* Shimansky in the presence of annulations and lirae, although in the present material the annulations are more closely spaced.

?*Reticycloceras* sp. 2

Plate 24, figs. 10–11

Material. Sierra de Languiñeo, Province of Chubut, Puesto Benito Aleman, fragmentary external mould (MLP 11884).

Description. The specimen is an orthoconic external mould about 17 mm long, with a circular cross-section, 12·8 mm in diameter at its oral end and 11·3 mm at the apical end, and an expansion rate of 1 mm in about 11 mm. The surface is ornamented with transverse annulations which are rounded, regular, and slightly inclined, bending adapically on the ventral side. There are about three annulations per mm. On the annulations and intervening conch surface are minute lirae amounting to 21 per mm, parallel to the annulations.

Superfamily and Family uncertain

Genus CYCLOCERAS M'Coy, 1844

Remarks. The type species of the genus *Cycloceras* M'Coy 'is based on an internal mould of a body chamber on which even position of siphuncle is indiscernible' (Sweet 1964, p. K259). The status of this and related genera, such as *Perigrammoceras* Foerste, is unclear. According to Sweet 'no species other than the type species should be referred to *Cycloceras* until its type is better known' (see also Miller *et al.* 1933, p. 45; Demanet 1941, p. 97).

EXPLANATION OF PLATE 24

All figures ×2, unless otherwise stated.

Figs. 1, 6. ?*Reticycloceras* sp. 1, MLP 11883, Puesto Benito Aleman, Province of Chubut. 1, side view of latex cast; 6, enlarged view of fig. 1, ×10.

Figs. 2–4. *Sueroceras* sp., La Carlota, Sa. de Tepuel, Province of Chubut. 2–3, MLP 11882a; 2, side view of latex cast; 3, enlarged view of fig. 2, ×6. 4, MLP 11882b, side view of a latex cast.

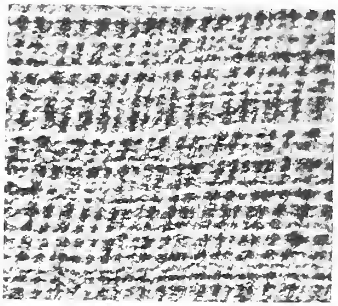
Figs. 5, 7. ?'*Cycloceras*' sp., MLP 11885–11886, Benito Aleman farm, Sa. de Languiñeo, Province of Chubut, side views of latex casts.

Figs. 8–9. *Glaphyrites* sp., MLP 11887, La Carlota, Sa. de Tepuel, Province of Chubut. 8, ventral view; 9, latex cast of the umbilical area.

Figs. 10–11. ?*Reticycloceras* sp. 2, MLP 11884, west of Puesto Benito Aleman, Sa. de Tepuel, Province of Chubut. 10, side view of latex cast; 11, enlarged view of fig. 10, ×10.

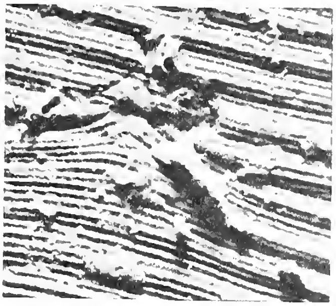

1


2


3


4


5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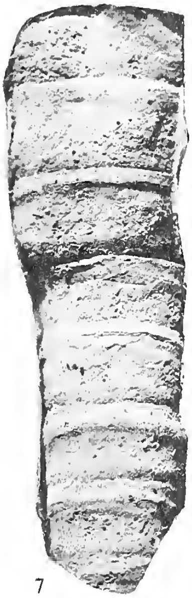
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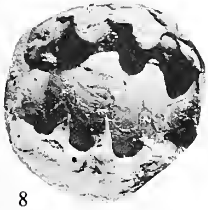
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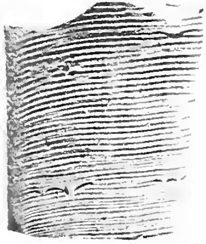
9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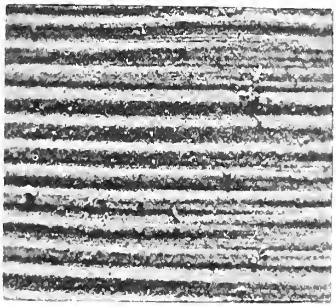

11

RICCARDI and SABATTINI, Cephalopoda

?'*Cycloceras*' sp.

Plate 24, figs. 5, 7

Material. Sierra de Languiñeo, Province of Chubut, right side of road to Colán Conhué, in property of Benito Aleman, in front of gate to Roelse farm, two fragmentary external moulds (MLP 11885–11886).

Description. The two fragments are 39 and 19 mm long with circular to subcircular cross-section. The sutures are straight and there are about two camerae in a length equal to the shell diameter. The surface is smooth with the exception of annulations parallel to the sutures. These annulations are rounded, amount to two per camera, are close to the sutures, and the adoral ones are more prominent than the adapical.

Remarks. It is impossible at the present time to give a more precise identification of this material. The Patagonian specimens show some superficial resemblances to material from the Late Mississippian of South Oklahoma described by Elias (1958, p. 30, pl. 3, fig. 7) under *Cycloceras randolphensis*, and to that from the Lower Carboniferous of Belgium described by de Koninck (1880, p. 71, pl. 41, fig. 3) under '*Orthoceras annuloso-lineatum*, L. G. de Koninck', although in both of these cases there are specimens with fine transverse striae between the annulations, similar to those in the specimens referred to different species of *Cycloceras* by Shimansky (1968, pl. 2). These striae were not recorded by M'Coy (1844, p. 10) in *C. annulare* and '*C.*' *laevigatum* M'Coy.

Subclass AMMONOIDEA Zittel, 1884
Order GONIATITIDA Hyatt, 1884
Superfamily GONIATITACEAE de Haan, 1825
Family NEOICOCERATIDAE Hyatt, 1900
Genus GLAPHYRITES Ruzhencev, 1936

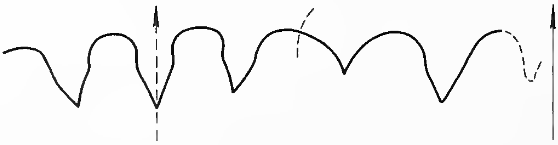
Remarks. Glaphyrites Ruzhencev has been considered as a synonym of *Eoasianites* Ruzhencev by some authors (Miller and Furnish 1940, p. 77; Miller *et al.* 1957, p. L61) whilst others considered it to be a valid genus (Gordon 1964, p. 219) or subgenus of *Eoasianites* (see Closs 1969, p. 201). For the present we follow Gordon (op. cit.) in regarding *Glaphyrites* as a valid genus.

Glaphyrites sp.

Plate 24, figs. 8–9; text-fig. 2

Material. Sierra de Tepuel, Province of Chubut, La Carlota, 9 km south-east of Tecka, fragment of phragmocone (MLP 11887).

Description. The fragment available belongs to a phragmocone about 25 mm maximum diameter. The conch is depressed, globose, and moderately involute with a total of six whorls. The ventral and ventrolateral shoulders are rounded, whilst the umbilical shoulders are subangular and the umbilical wall is gently convex. The surface is ornamented with fairly thick transverse threads, which ventrally are bent slightly adorally. The suture has eight pointed lobes and spatulate saddles. The ventral lobe is shorter than the lanceolate and slightly curved first lateral lobe, while the umbilical lobe is shorter and sharply pointed. The dorsal and internal lateral lobes are lanceolate.



TEXT-FIG. 2. Suture of *Glaphyrites* sp., MLP 11887.

Remarks. A specimen belonging to this genus (Gordon 1964, p. 221) has been described as '*Eoasianites* sp.' by Miller and Garner (1953). It came from Puesto Urquiza, Sierra de Languiñeo (see Suero 1958, p. 25). *Wiedeyoceras argentinense* (Miller and Garner 1953) came from the same locality as the specimen described here.

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EARLY LLANDOVERY TRILOBITES FROM WALES WITH NOTES ON BRITISH LLANDOVERY CALYMENIDS

by J. T. TEMPLE

ABSTRACT. Some early Llandovery (Silurian) trilobites from Wales are described. The calymenids are compared with described British Llandovery species, including two samples from Girvan, Scotland. Principal components analysis is used to demonstrate both the variation in profile of the preglabellar area and the independent and dimorphic (thus probably sexual) variation in relative glabellar width of Llandovery calymenids. *Diacalymene crassa* Shirley and *D. marginata* Shirley differ considerably from *D. diademata* (Barrande) in the profile of the preglabellar area and form the end of a spectrum of variation among British Llandovery calymenids: they are provisionally referred to *Calymene* s.l. Characterization of the genus *Diacalymene* in terms of 'ridging' of the preglabellar area is considered to be vitiated (at least for internal moulds) by the intraspecific variability of this feature and the subjectivity of its recognition. Two species are tentatively distinguished among Welsh early Llandovery calymenids, *C. crassa* and another species similar to a sample from Newlands, Girvan. Seven other species of trilobites are briefly described.

THE present work forms part of a larger study of the early Llandovery shelly faunas of Wales. The term 'early Llandovery' is employed here in the sense of 'pre-Upper Llandovery' or 'pre-Fronian', since it is not yet possible on the basis of their shelly faunas alone to distinguish the Lower from the Middle Llandovery (Rhuddanian and Idwian). This paper describes trilobites unknown or poorly known in the fauna described from near Meifod, Montgomeryshire (Temple 1970). A complete listing of trilobites and brachiopods and an analysis of their distribution in the early Llandovery of Wales will be made when the brachiopod faunas have been fully described.

Trilobites form a numerically insubstantial part of Welsh early Llandovery shelly faunas. In fifty-six samples the number of trilobite cranidia and pygidia is only 2·6% of the number of brachiopod dorsal valves and ventral valves, and this low figure includes one locality unusually rich in trilobites (loc. 7132, with 19·5%). The most abundant trilobites are the calymenids, poorly represented at Meifod but more common in the Haverfordwest area of Pembrokeshire. Description of the Welsh early Llandovery calymenids, to which the major part of this report is devoted, has involved comparison with other British Llandovery members of the family.

LOCALITIES

Specimens described here are from the localities listed below. In the list each locality code number, by which the locality is referred to subsequently in the text (e.g. loc. 6701), is followed by the National Grid reference.

6701:	SJ 1135 1013. 5·2 km SW. of Meifod, Montgomeryshire. This is the locality from which the fauna described earlier was collected (Temple 1970).
7001a:	SJ 2358 1936. 3·5 km WNW. of Llandysilio, Montgomeryshire.
7004b:	SJ 1957 1786. 6·2 km NE. of Meifod, Montgomeryshire.
7021b, c:	SN 7622 3247. 1·8 km SSW. of Llandovery, Carmarthenshire.
7022a:	SN 9531 5116. 1·5 km N. of Garth, Brecknockshire.

[Palaeontology, Vol. 18, Part 1, 1975, pp. 137–159, pls. 25–27.]

7029a: SN 9719 5324. 2·5 km S. of Llanafan-fawr, Brecknockshire.

7121: SM 9643 1473. 450 m SE. of Higgon's Well, Haverfordwest, Pembrokeshire.

7122, 7123, 7126, 7127, 7132, 7140, 7142c, 7148: SM 9573 1547 to SM 9582 1537. Lane leading to Gasworks, Haverfordwest, Pembrokeshire. 7122, 7123, 7140, and 7142c are in the lowest exposed 25 m of the Gasworks Mudstone; 7126, 7127, 7132, and 7148 are in the topmost 25 m of the Gasworks Mudstone.

PRESERVATION AND TECHNIQUES

Nearly all the material is preserved as internal and external moulds. For most trilobite families this preservation is excellent, but for the calymenids it gives rise to a particular problem. The rachial and preglabellar furrows are deep and often undercut, so that the deepest parts of the furrow fillings of external moulds break off and remain at the bottoms of the internal mould furrows. These furrow fillings can be removed by needle to produce excellent internal moulds, but the external moulds, which would normally provide evidence for the exterior surface of the cephalon, are always imperfect and lack the bases of the furrows. Detailed study of cranidia of Llandovery calymenids must therefore be based on internal moulds and, especially in the study of the preglabellar area, the methods used and the results obtained are not directly comparable with those based on exteriors.

Measurements have been made on a microscope with eye-piece graticule. Of the measurements made on calymenid cranidia, variates x_2, x_3, and x_4, which relate to the profile of the preglabellar area, have been measured on silicone rubber casts made from internal moulds and sectioned in the sagittal plane. This method of measurement is essential for those specimens in which the base of the preglabellar furrow is obscured in profile view of the internal mould by the bulging of the preglabellar area backwards opposite the rachial furrows, but even when this is not the case it has been found difficult to measure the profile of the preglabellar area sufficiently accurately from internal moulds.

The original data of the calymenid cranidial measurements x_1 to x_5 have been deposited in the British Library, Boston Spa, Yorkshire, as supplementary Publication No. SUP 14004 (2 pages).

Principal components analysis, the technique used in analysing the calymenid cranidial measurements, is now so widely used for multivariate data in biology and palaeontology that a detailed explanation is not considered necessary here, the reader being referred to Seal's book (1964, p. 101) for an exposition of the technique. It should be noted that, even when not used as a basis for formal statistical tests, principal components analysis is a powerful pictorial technique for displaying the mutual relations of multivariate samples, and it is largely in this latter capacity that it is used here. In this respect, by depicting the simultaneous variation in several characters (before or after abstraction of a size factor represented by the first eigenvector), its superiority to bivariate plotting, which can deal only with characters taken in subjectively selected pairs, is indisputable. Furthermore, the mutual orthogonality of the eigenvectors in principal components analysis allows conclusions to be drawn about the independence of the variation represented by these eigenvectors (each of which involves several characters), as in the variation of relative glabellar width and of preglabellar profile. Principal components analysis of the correlation matrix is used in preference to that of the covariance matrix so as to remove the effects of the disparate sizes of the original variates, i.e. so that small variates (those relating to the preglabellar area) may contribute equally with large variates (glabellar length and width) to the total variance that is partitioned into the eigenvalues. As previously (e.g. Temple 1970, p. 6), the convention is continued of using x for the original variates and y for the variates transformed along the eigenvectors.

The plates which illustrate this paper were made up before agreement had been reached at the 1973 Oslo conference on a standard orientation of trilobites for illustration (Temple, in press). The 'dorsal' view of calymenid cephala and cranidia employed on the plates is obtained by setting horizontal the plane tangent to the crest of the pre-occipital glabella and the occipital ring. 'Normal projection', as used in the description of measurements, is projection at right angles to the line joining the ends of the measured structure.

Registration numbers of specimens prefixed by A are those of the Sedgwick Museum, Cambridge; those prefixed by HMA, of the Hunterian Museum, Glasgow; those prefixed by In or It, of the British Museum (Natural History), London; those prefixed by GSM, OTJ, TCC, or Zs, of the Institute of Geological Sciences, London.

Superfamily CALYMENACEA Milne Edwards, 1840

Family CALYMENIDAE Milne Edwards, 1840

Calymenid remains are most abundant at a high horizon in the Gasworks Mudstone at Haverfordwest (loc. 7132), although occasional specimens are known from other horizons in the Gasworks Mudstone, as well as from other areas.

The following calymenid species have been described from the Llandovery of Britain:

(1) *Diacalymene crassa* Shirley, 1936 (p. 416, pl. 29, figs. 21–23). The only available topotypic specimen is the holotype (GSM 54910—figured here on Pl. 25, figs. 3–4), an internal mould of a cranidium, well preserved except that the occipital ring and fixed cheeks are broken and the preglabellar area is slightly abraded. The type locality is in the Gasworks Mudstone of the Haverfordwest area, but the precise horizon is unknown, and further collecting has not yielded more topotypic material. The paratype of *crassa* (GSM 54911) is not topotypic.

(2) *Calymene replicata* Shirley, 1936 (p. 411, pl. 30, figs. 2–5). The holotype (A 14922a) consists of the internal mould of a cephalon, lacking the dorsal preglabellar area, with three thoracic segments attached; the counterpart external mould, of which a cast was figured by Shirley (pl. 30, fig. 2), is now missing from the Sedgwick Museum collections, so that the preglabellar area of the holotype cannot now be reconstructed. The type locality is near the base of the Upper Llandovery at Lletty'r-hyddod in the Llandovery area. Other topotypic specimens in the Sedgwick Museum (A 14923–14927) show the preglabellar area and also the thorax and pygidium (revealed by preparation of A 14923—Pl. 26, fig. 1) but not the hypostome. Some of the topotypes (although not the holotype) are distorted.

(3) *Calymene planicurvata* Shirley, 1936 (p. 412, pl. 30, figs. 6–7). The holotype (GSM 19624) is an internal mould of a large cranidium, well preserved except for slight breakage of the preglabellar area and lack of the right fixed cheek. The type locality is Bog Mine, Shelve inlier, Shropshire (?Middle Llandovery). Additional topotypic specimens (cranidia and a pygidium) are available in the Institute of Geological Sciences and the British Museum (Natural History).

In addition to topotypic material of these species, the following calymenids have been used for comparative purposes:

(1) Newlands Formation (Middle Llandovery), Newlands, Girvan, Ayrshire, Scotland (Gray Collection, British Museum (Natural History)). Material from this locality was referred by Shirley (1936, p. 411) to *C. replicata*. This collection

is extensive and well preserved, all parts of the exoskeleton being represented (Pl. 26, figs. 5–6, 9–10).

(2) Mulloch Hill Formation (Lower Llandovery), Mulloch Hill, Girvan, Ayrshire (Gray Collection, British Museum (Natural History)). This material is not so extensive as that from Newlands but is well preserved (Pl. 26, figs. 2–4, 7–8).

(3) Bank outlier, Round Hill, Shropshire (British Museum (Natural History)). Equivalent horizon to Bog Mine. A few small specimens.

(4) Gasworks Mudstone, Haverfordwest, Pembrokeshire (Institute of Geological Sciences).

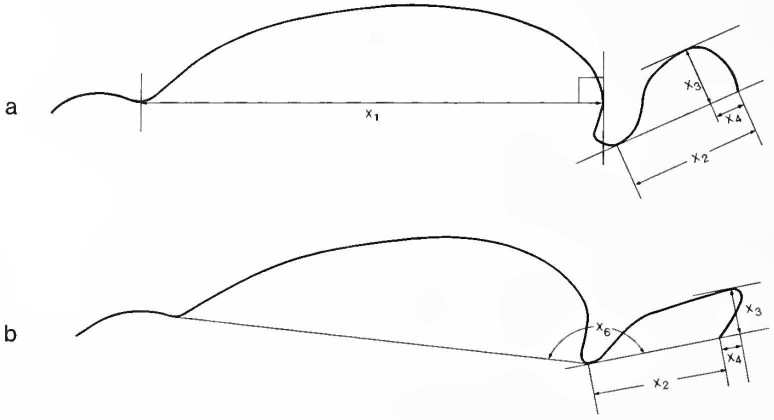
Measurements. The following measurements have been made (x_1, x_5 to x_8 on internal moulds; x_2 to x_4 on sagittally sectioned silicone rubber casts of internal moulds):

Cranidia (text-fig. 1)

x_1 = sagittal length of pre-occipital glabella (from deepest part of occipital furrow to plane tangential to steepest slope of anterior margin of glabella, normal projection);
x_2 = sagittal length of preglabellar area (length of tangent in sagittal plane from rostral suture to surface of internal mould at or in front of preglabellar furrow, normal projection);
x_3 = perpendicular distance between tangent of x_2 and parallel line in sagittal plane tangential to crest of preglabellar area;
x_4 = sagittal distance (projected as x_2) between crest of preglabellar area (as defined by tangent in x_3) and rostral suture (positive if measured forwards as text-fig. 1*a*, negative if measured backwards as text-fig. 1*b*);
x_5 = maximum transverse width of glabella across L_1 lobes (measured between parallel exsagittal vertical planes tangential to outsides of lobes, not at bases of rachial furrows);
x_6 = angle subtended at base of preglabellar furrow by lines in sagittal plane to the base of the occipital furrow and to the rostral suture.

Pygidia

x_7 = sagittal length (measured from deepest point of articulating furrow in front), normal projection;
x_8 = transverse separation of bases of rachial furrows at abaxial ends of articulating furrow.



TEXT-FIG. 1*a*, *b*. Sagittal profiles (schematic) of internal moulds of calymenid cranidia showing measurements. Note (i) that x_4 is positive in the upper profile but negative in the lower one, (ii) that the points in the preglabellar furrow from which x_2 and x_6 are measured will not necessarily coincide, although they happen to do so in the lower profile.

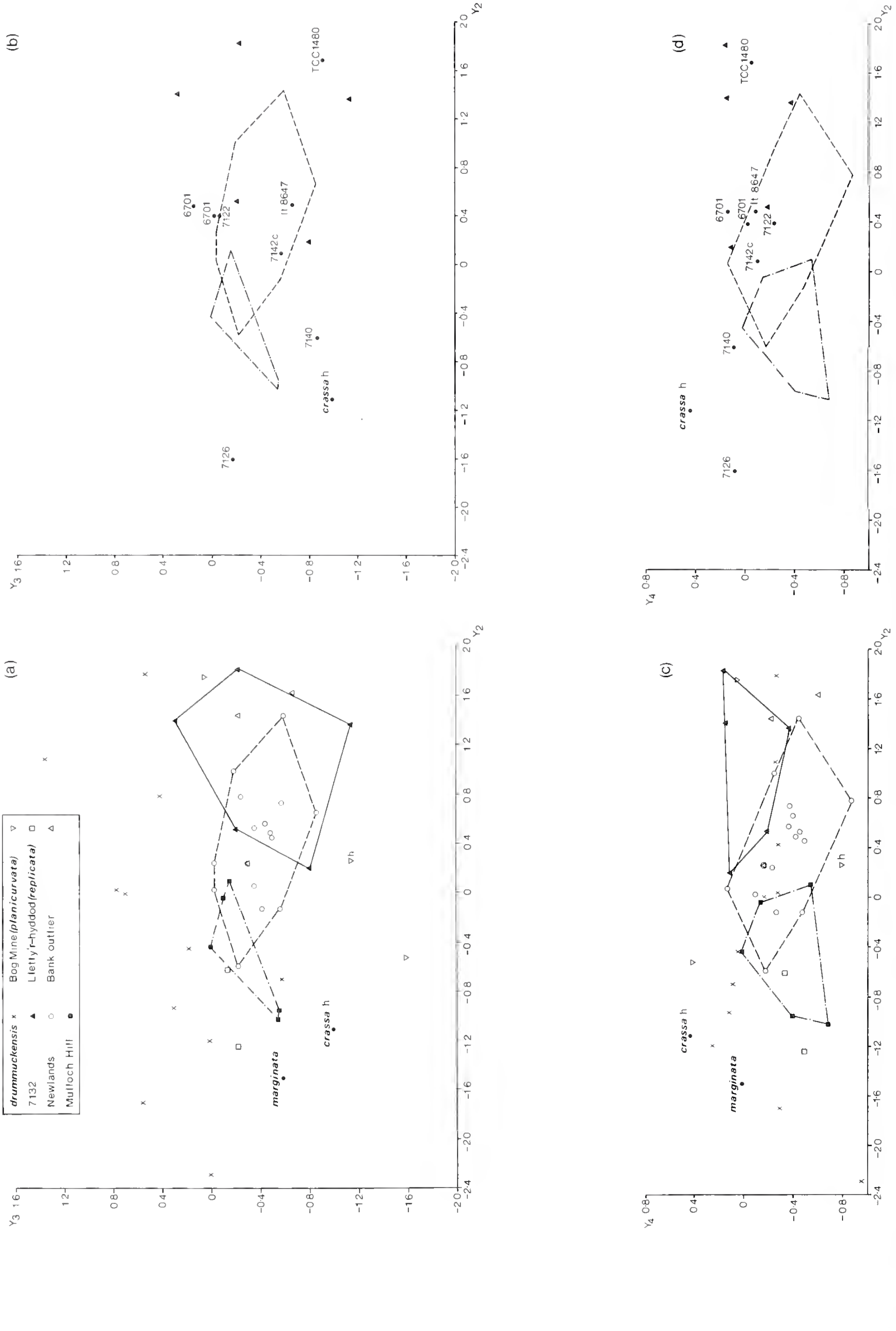
Length and profile of preglabellar area. Variation in the length and profile of the preglabellar area in relation to glabellar length has been investigated by means of a principal components analysis of variates x_1, x_2, x_3, and x_4. The original data have been transformed to scores on the eigenvectors of the correlation matrix (Table 1*a*) based on the collections listed in text-fig. 2. The direction cosines of the eigenvector (y_1) corresponding to the first principal component (i.e. the largest eigenvalue) are all positive and this eigenvector is taken to be a measure of size. The mutual relations of the samples in the space defined by the remaining three eigenvectors are taken to represent the size-independent shape differences between the samples. Two-dimensional plotting on pairs of eigenvectors can be used to depict these three-dimensional relationships (text-fig. 2*a–d*). It will be seen from the direction cosines that the second eigenvector (y_2) is a measure of degree of overhang of the preglabellar area (decreasing scores corresponding to increasing overhang), while the third eigenvector (y_3) contrasts height of preglabellar area (increasing scores) with length of preglabellar area (decreasing scores), and the fourth eigenvector (y_4) is a measure of length (and partly of height) of the preglabellar area relative to glabellar length.

TABLE 1. Column eigenvectors y and eigenvalues λ (as percentages) of correlation matrices based on (*a*) four variates (x_1 to x_4) representing glabellar length and profile of the preglabellar area, and (*b*) the same four variates with the addition of x_5 (maximum glabellar width). The same data, based on the collections listed in text-fig. 2, are used in both analyses. In the last column of (*a*) are shown the standard deviations σ of x_1 to x_4, by means of which additional specimens could if required be plotted on text-fig. 2.

(*a*)	y_1	y_2	y_3	y_4	σ
x_1	0·570	−0·228	−0·128	−0·779	3·0866
x_2	0·555	0·031	−0·660	0·506	0·6773
x_3	0·525	−0·315	0·704	0·361	0·4096
x_4	0·302	0·921	0·231	−0·086	0·1995
λ	69·0	21·6	7·2	2·2	

(*b*)	y_1	y_2	y_3	y_4	y_5
x_1	0·505	−0·146	−0·090	−0·531	−0·659
x_2	0·479	0·107	−0·604	0·623	−0·076
x_3	0·459	−0·220	0·755	0·412	−0·035
x_4	0·224	0·943	0·209	−0·127	0·037
x_5	0·505	−0·174	−0·116	−0·380	0·747
λ	73·4	18·0	5·8	2·1	0·7

Discrimination between the three main early Llandovery samples (Mulloch Hill, Newlands, loc. 7132) is seen from text-fig. 2 to be due almost entirely to the second eigenvector, and the slightly overlapping fields of these samples form a belt almost parallel to the y_2 axis along which there is a progressive increase in degree of overhang of the preglabellar area from loc. 7132 through Newlands to Mulloch Hill. The holotype of *Diacalymene crassa* lies beyond Mulloch Hill on y_2 and is displaced somewhat upwards on y_4. The Upper Llandovery *C. replicata* specimens plot at or slightly beyond the Mulloch Hill end of the early Llandovery belt, while the Bog Mine (*planicurvata*) and Bank outlier specimens partly overlap Newlands and loc. 7132. When the Welsh early Llandovery specimens including loc. 7132 are plotted (text-fig. 2*b*, *d*) they form a belt elongated along y_2 and slightly displaced upwards on y_4 relative to Mulloch


(a)
(b)
(c)
(d)
drummuckensis ×
7132 ▲
Newlands ○
Mulloch Hill ■
Bog Mine (planicurvata) ▽
Llety'r-hyddod (replicata) □
Bank outlier △
Y3
Y4
Y2
1·6
1·2
0·8
0·4
0
-0·4
-0·8
-1·2
-1·6
-2·0
-2·4
2·0
marginata
crassa h
h
6701
6701
7122
It 8647
7142c
7140
7126
TCC1480

Hill and Newlands. Several of the Welsh early Llandovery specimens (locs. 6701, 7122, 7142c, specimens It 8647, TCC 1480) cluster at the loc. 7132 end of this belt, but there is no clearly defined hiatus between these specimens and the isolated specimens (from locs. 7126, 7140) plotting near *D. crassa.*

The y_4 axis of the correlation matrix has an appreciable loading on x_3 as well as on x_2, and in order to determine how much these two variables contribute separately to the upward displacement of the Welsh specimens on y_4 it is necessary to turn to a principal components analysis of the covariance matrix derived from the same data as the correlation matrix. The second and third eigenvectors of the covariance matrix have direction cosines of (−0·165, 0·936, −0·166, 0·264) and (−0·132, 0·110, 0·975, 0·141) and can thus serve as indices of variation in x_2 and x_3 separately. The mean scores of the Mulloch Hill, Newlands, and combined Welsh samples on these two eigenvectors are respectively (−0·11, −0·17), (0·14, −0·19), (0·47, −0·02). There are significant differences on covariance y_2 between all three samples ($p < 0{\cdot}005$ in both cases on rank sum tests), but on covariance y_3 only the Welsh specimens differ significantly ($0{\cdot}005 < p < 0{\cdot}010$). Welsh specimens thus have both longer and higher preglabellar areas than Scottish specimens, while among the latter Newlands specimens have longer preglabellar areas than do specimens from Mulloch Hill. Also included in the principal components analysis were two Upper Ordovician species *Diacalymene marginata* Shirley and *Calymene drummuckensis* Reed which are plotted on text-fig. 2 and are discussed further below. Another aspect of the variation in profile of the preglabellar area is the presence or absence of a 'ridge'. As considerable taxonomic significance has been attached to this feature discussion of it is deferred until the taxonomy of the samples is considered (see p. 147).

Inclination of preglabellar area. The only objective measure of this feature is that given by x_6 and even this is not entirely satisfactory because of the difficulty of measuring it accurately, particularly on large specimens: it shows considerable variation, the extreme range of x_6 over all samples being 138° to 173°, although only three out of twenty-four specimens lie beyond the range 150° to 165°. The range of Newlands values (134° to 165°) includes the holotypes of *crassa* and *planicurvata*, the two measurable topotypes of *replicata*, all the Mulloch Hill specimens, and all except one specimen from loc. 7132. There is no evidence that the collections can be satisfactorily differentiated on the basis of this feature.

Relative width of glabella. A plot of width across L_1 (x_5) against preoccipital glabellar length (x_1) shows much scatter with an apparent tendency to group on either side of

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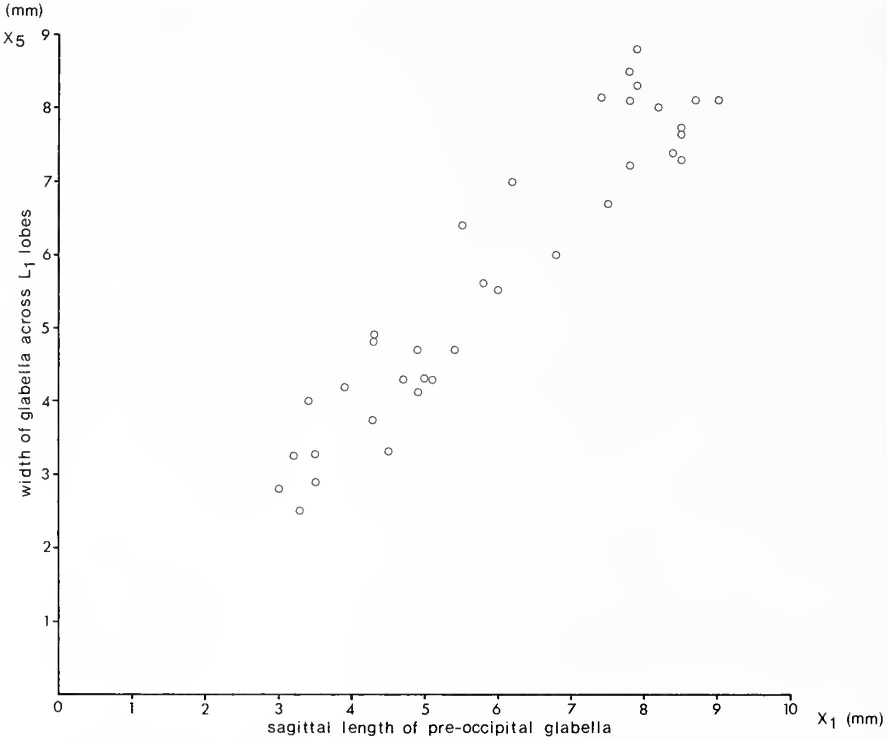
TEXT-FIG. 2*a–d*. Calymenid cranidia plotted on the second and third (figs. *a*, *b*) and second and fourth (figs. *c*, *d*) eigenvectors of the correlation matrix for x_1, x_2, x_3, and x_4 based on collections from Newlands, Mulloch Hill, Thraive Glen (*drummuckensis*), Bog Mine (*planicurvata*), Bank outlier, Lletty'r-hyddod (*replicata*), locs. 6701, 7122, 7132, 7140, 7142c, and specimens GSM 54910 (*crassa* holotype), TCC 1480, It 8647. A topotype of *marginata* (HMA 7334) and a specimen from loc. 7126, although plotted, were not included in the data from which the correlation matrix was calculated. For purposes of clarity the Welsh early Llandovery specimens (except *crassa* holotype and the loc. 7132 sample) have been omitted from figs. *a* and *c*, and are shown in figs. *b* and *d* together with the perimeters of the Newlands and Mulloch Hill spreads. Holotypes are marked *h*.

the line representing equality—at least up to a preoccipital glabellar length of about 9 mm beyond which there is insufficient evidence. The phenomenon is also seen when the Newlands sample, in which complications due to tectonic and compaction distortion are slight, is plotted alone (text-fig. 3). The distribution of the ratio x_5/x_1 for the combined Llandovery samples (excluding distorted specimens), grouped at intervals of 0·05 between 0·7 and 1·2 (lower limits of classes) is 1, 1, 4, 11, 12, 6, 7, 9, 6, 2, 2, with a suggestion of a crude bimodality around equality of length and width.



TEXT-FIG. 3. Maximum transverse width of glabella across L_1 (x_5) plotted against sagittal length of pre-occipital glabella (x_1) for the Newlands sample.

Variation in this character can, however, be more elegantly analysed by principal components analysis, which demonstrates both the bimodality of relative glabellar width and the fact that variation in this character is independent of the previously analysed variation in the profile of the preglabellar area. On rerunning the principal components analysis with the same data but with x_5 added to the four variates (x_1 to x_4) used earlier, there are now five eigenvectors of a 5-variate correlation matrix (Table 1*b*). It will be seen that, relative to the x_{1-4} axes, the first four 5-variate eigenvectors are orientated very close to the four 4-variate eigenvectors: they clearly correspond to these four eigenvectors, and if the data of text-fig. 2 are replotted on 5-variate (instead of 4-variate) y_2, y_3, and y_4 axes the mutual relations of the points are only negligibly altered. The fifth 5-variate eigenvector, on the other hand, is seen from its direction cosines to be concerned almost exclusively with relative glabellar width, its loadings on x_2, x_3, and x_4 which measure the preglabellar profile being very small. Furthermore, the scores of the pooled samples on the fifth eigenvector are bimodally distributed, the frequencies of scores grouped at intervals of 0·05 between −0·5 and +0·3 (lower limits of classes) being 1, 0, 1, 8, 5, 6, 4, 0, 2, 10, 8, 2, 1, 2, 1, 1, 1: the zero near the middle corresponds to the interval from −0·15 to −0·10, the gap being adjacent scores being from −0·1709 to −0·0668. The fifth eigenvector produces therefore a clustering into wide and narrow glabellas more convincing than the clustering based on the x_5/x_1 ratio but corresponding very closely to it: of fifty-three cranidia used in the principal components analysis, only three are classified (into wide or narrow) differently by the two criteria. The fifth eigenvector is by definition at right angles to the other four eigenvectors, in particular to y_2, y_3, and y_4. Variation in relative width of the glabella is thus independent of variation in the profile of the preglabellar area.

Wide and narrow forms are found in all the samples examined, with the exception of the small samples from Bog Mine and Bank where only wide forms occur. The pattern of variation in glabellar width is apparently a simple dimorphism cutting right across the samples, whereas the pattern of variation in profile of the preglabellar area is quite different in that individual samples are homogeneous but differ slightly but consistently from each other. The conclusion seems inescapable that variation in profile of the preglabellar area represents variation between samples in each of which the same two morphs (presumably sexual dimorphs) occur. It is interesting to note that, although the dimorphism is visually very striking (compare for instance the two Newlands cranidia illustrated on Pl. 26, figs. 5 and 9), when the different characters are standardized to unit variance (as in the correlation matrix) variation in this character is considerably less than that of the preglabellar profile (see the percentage eigenvalues in Table 1*b*). The likelihood of dimorphism in glabellar width complicates comparisons between the samples based on this character, as differences between samples may be due to different proportions of the two morphs in the populations rather than (or as well as) to different length–width growth relations. The distribution of the two morphs is shown in Table 2, and although the numbers involved are small there is a preponderance of narrow forms at Newlands and of wide forms elsewhere ($p = 0·024$, single-tailed, for the contrast between Newlands and the rest).

TABLE 2. Numbers of wide and narrow glabellas at different localities, based on scores on y_5 (see Table 1*b*).

	Narrow	Wide
Newlands	12	4
Mulloch Hill	2	3
Loc. 7132	2	3
Lletty'r-hyddod	1	1
Bog Mine	0	3

Free cheek, hypostome, and rostral plate. Free cheeks from Newlands and probably those from loc. 7132 and Mulloch Hill are like the cheek illustrated from Meifod (Temple 1970, pl. 18, fig. 15), that is with a rounded obtuse angle in the outer margin shortly in front of the posterior extremity of the cheek and with a corresponding angle towards the posterior end of the facial suture. No topotype free cheeks of *crassa* are available but a specimen from the Gasworks Mudstone (TCC 1364), which is probably referable to *crassa* on the basis of its preglabellar area, also shows a free cheek of this kind (Pl. 25, fig. 8). In the holotype of *replicata* the angles in the cheek margin and facial suture appear to be less pronounced, although the cheek margin is slightly imperfect hereabouts. The free cheek of *planicurvata* is unknown.

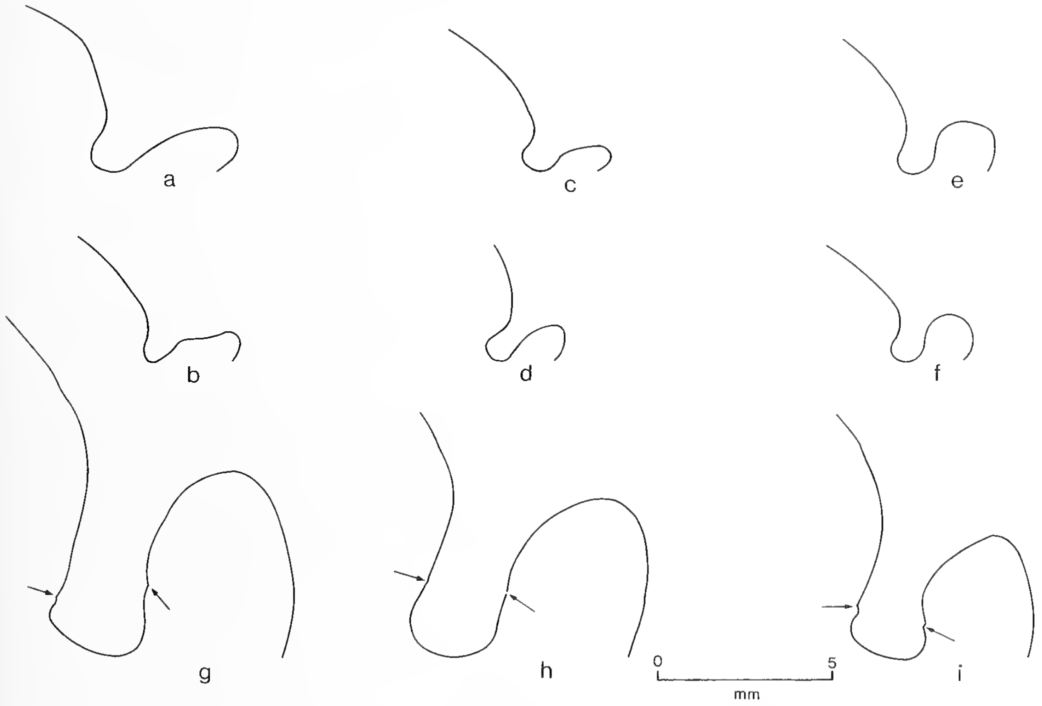
Except for a fragment from loc. 7132 the hypostome is known only from Newlands. The rostral plate also is known from Newlands and Mulloch Hill and in the holotype and another topotype of *replicata* (Pl. 26, fig. 1): in all these forms it consists of an anterior part, moderately concave (sag. and exsag.) in dorsal view, and a posterior flange directed steeply upwards so that its upper edge lies close beneath the preglabellar furrow. The probable *crassa* specimen mentioned above (TCC 1364—Pl. 25, fig. 6) shows the anterior part of the plate somewhat elongated (sag. and exsag.), but the posterior flange is not visible, presumably as a preservational defect.

Thorax. Specimens showing the thorax are available for *replicata* (topotype) and probably *crassa* (TCC 1364), and from Newlands and Mulloch Hill: all show the presence of thirteen segments, although TCC 1364 lacks a pygidium to make the count definitive. The thoracic segments are similar in all these forms.

Pygidia. Topotype pygidia are known for *replicata* (Pl. 26, fig. 1) and *planicurvata*, and a pygidium (TCC 1363—Pl. 25, fig. 7) which may belong to *crassa* is found at the same locality as TCC 1364. Pygidia are also found at Newlands and Mulloch Hill. All these pygidia are of the same general type as that described and illustrated from Meifod (Temple 1970, p. 64, pl. 18, figs. 18–20), although the interpleural furrows are usually not as strongly marked on internal moulds or on exteriors as in the relatively small Meifod specimens. The most characteristic feature of all these pygidia is the pair of strong ridges, more or less exsagittally directed, between the fifth pleural furrows and the posterior end of the rachis. Despite the over-all resemblances of all these pygidia there are slight differences in shape between localities: for instance, at Newlands the rachis has a more pointed posterior termination than at loc. 7132 where it is somewhat transversely truncated. Doubtless, detailed biometrical analysis would reveal further differences between samples, although the situation is likely to be complicated (as in cranidia) by the existence of dimorphism of rachial width, as is suggested by the positively skew distribution of the x_8/x_7 ratio in the Newlands sample (compare also the two pygidia illustrated from Meifod—Temple 1970, pl. 18, figs. 18, 20).

Discussion. All the samples of Llandovery age have a number of features in common—the buttressing of L_2, the outline of the free cheek (doubtful in *replicata*), and the pygidium with strong ridges behind the fifth pleural furrows. Some variation within samples (as in glabellar and rachial width) may be attributable to dimorphism, but the greatest variation between samples concerns the length and profile of the preglabellar area. The latter feature has been used in particular by Shirley (1936) in his important work on calymenid systematics as the distinguishing feature between *Calymene*, to which he referred *replicata*, *planicurvata* and the Newlands sample, and *Diacalymene*, to which he referred *crassa*, *Diacalymene* being considered to differ from *Calymene* in the possession of a 'ridge' on the preglabellar area (Shirley 1936, p. 396). The type species of *Diacalymene* is *Calymene diademata* Barrande 1846 from the Silurian of Bohemia. A small sample of *C. diademata* from one of the original localities, St. Iwan, Bohemia, preserved largely as internal moulds, has been studied in the British Museum (Natural History). Collections of two Upper Ordovician species, referred to *Diacalymene* by Shirley, have also been studied, firstly a sample (mainly internal moulds) of *Calymene drummuckensis* Reed (1906, p. 135, pl. 17, fig. 14; pl. 18, figs. 1–4) from the Upper Drummuck Beds (Ashgill), Thraive Glen, Girvan (British Museum (Natural History)), and secondly a topotype cranidium (internal and external moulds (HMA 7334)) of the slightly earlier *Diacalymene marginata* Shirley 1936 (p. 415, pl. 29, figs. 19–20) from the Lower Drummuck Beds, Quarrel Hill, Girvan.

The preglabellar area of *diademata* is relatively steeply inclined, with values of 140°, 148°, 150° for x_6 in three cranidia: it culminates in a transverse keel (text-fig. 4*g*, *h*, *i*), variably subangular to rounded in section, in front of which its anterior slope is steep but not strongly overturned in front (in the orientation of text-fig. 4).



TEXT-FIG. 4. Right sagittal profiles of preglabellar areas of calymenid species which have been referred to *Diacalymene*. The profiles are orientated so that the tangent from the rostral suture to the base of the preglabellar furrow is horizontal. Profiles are drawn from sagittally sectioned silicone rubber casts of internal moulds; integument about 0·2 mm thick is present in the bases of the pre-glabellar furrows below the small arrows in profiles (*g*)–(*i*). (*a*) *crassa* holotype, GSM 54910, (*b*) *crassa*, Zs 960, from loc. 7140, (*c*) *marginata* topotype, HMA 7334, (*d*)–(*f*) *drummuckensis* from Thraive Glen, respectively In 23372, In 46668, In 41344; (*g*)–(*i*) *diademata* from St. Iwan, Bohemia, respectively In 42354, In 19894, In 59826.

The keel is developed only rarely in *drummuckensis* (text-fig. 4*d*), the preglabellar area in this species being commonly rounded in section (text-fig. 4*e*, *f*) and overhanging in front. In *crassa* (text-fig. 4*a*, *b*) and *marginata* (text-fig. 4*c*) the keel appears to be represented by the overhanging anterior margin of the cranidium, and it is thus more acute and more forwardly directed than in *diademata*.

As the term is interpreted here, the 'ridge' mentioned by Shirley as diagnostic of *Diacalymene* is a different structure from the keel, being situated further back than the keel and just in front of the preglabellar furrow. It is best developed in the topotype *marginata* (text-fig. 4*c*), in the paratype of *crassa* (GSM 54911), and in a loc. 7140 specimen referred to *crassa* (Pl. 25, fig. 2; text-fig. 4*b*), although in the holotype of *crassa* (Pl. 25, figs. 3–4) the ridge is less clearly marked and is not unequivocally discernible in sagittal section—perhaps because of slight abrasion (text-fig. 4*a*). In all these specimens in which the ridge is well developed the anterior part of the preglabellar area is flattened in profile, and the ridge represents the break in slope that delimits the flattened part posteriorly and separates it from the preglabellar furrow. For this reason a slight ridge is developed in one specimen from loc. 7132 in which there is incipient flattening of the anterior part of the preglabellar area. Of three Bohemian specimens of *diademata* in which the preglabellar furrow has been cleared of matrix, one shows a ridge as a broad rounded angulation slightly more than halfway down the convex backward-facing slope of the preglabellar area (text-fig. 4*i*), but in the other two specimens this backward slope is more evenly convex throughout its profile and there is little indication of a ridge. (The presence of integument at the bases of the preglabellar furrows of these two specimens may also help to obscure the ridges, but even if allowance is made for this factor the ridges must be very diffuse.) In specimens of *drummuckensis* (text-fig. 4*d*–*f*) the back slope of the preglabellar area is also convex in profile, either evenly so throughout the profile, or occasionally with sharper curvature locally to produce a slight ridge. It is clear that the preglabellar areas of both *diademata* and *drummuckensis* are very variable in profile (see also below for quantitative assessment of this variability in *drummuckensis*). This variability, taken together with the subjectivity involved in judging whether a particular specimen is ridged or not, apparently vitiates the use of ridging as a diagnostic character of *Diacalymene*, at least for the discrimination of internal moulds.

The three measured specimens of *diademata* are very large compared with most of the Llandovery specimens measured, so that projection of them on to the shape eigenvectors of the correlation matrix (text-fig. 2) involves error due to size extrapolation. They plot, however, so far off the top of the diagrams, with scores (y_2, y_3, y_4) of respectively (−2·62, 2·70, 2·30), (1·89, 5·18, 2·81), (0·65, 2·90, 2·11), as to indicate a fundamental shape difference from the Llandovery samples: their high scores on y_3 reflect the relative shortness and height of the preglabellar area of *diademata*. The *drummuckensis* sample is closer to the Llandovery samples, forming a belt displaced upwards on y_3 and with wide but apparently continuous variation in y_2 scores. This great variation in y_2 can be partly explained by the fact that the size eigenvector of the *drummuckensis* sample (direction cosines 0·580, 0·575, 0·576, 0·014) is differently orientated from that of the pooled samples. Nevertheless, although the range of *drummuckensis* scores on the *drummuckensis* y_2 (direction cosines −0·049, −0·112, 0·136, 0·983) is much less than on the pooled y_2, it is still greater than that of, for instance, Newlands scores on the pooled y_2: *drummuckensis* shows considerable variability in degree of overhang of the preglabellar area. The topotype of *marginata* plots near to *crassa* as a continuation of the Mulloch Hill–Newlands–loc. 7132 spread.

It is hazardous to attempt phylogenetic interpretation on the basis of the present limited studies, but the principal components analysis suggests that it is more plausible to link *marginata* and *crassa* with the Llandovery belt of variation covering Mulloch Hill–Newlands–loc. 7132, than via the Upper Ordovician *drummuckensis* with the morphologically distant *diademata*. Both *crassa* and *marginata* are therefore removed from *Diacalymene* and referred to *Calymene* s.l., although the assignment is provisional until the profile of *C. blumenbachi* has been analysed.

The stratigraphical sequence of the four Girvan samples investigated is (from bottom to top) *marginata*–*drummuckensis*–Mulloch Hill–Newlands. The relations in text-fig. 2 suggests the possibility of evolution at Girvan from *marginata* (with *drummuckensis* as a temporary offshoot) through Mulloch Hill to Newlands. Furthermore, since *marginata* has been widely reported from the Ashgill of England and Wales (Shirley 1936, p. 416; Ingham 1966, p. 498) it is possible to envisage a link by migration between *marginata* and *crassa* from the early Llandovery of Wales. At Haverfordwest the loc. 7132 sample, which appears to be morphologically more advanced even than Newlands on an evolutionary interpretation of the y_2 changes, occurs high in the Gasworks Mudstone. In this case, though, there is no evidence of an evolutionary sequence leading up to it, for the stratigraphical succession of the other Gasworks Mudstone localities (compare text-fig. 2) is (from bottom to top) 7122–7142c–7140–TCC 1480–7126–7132, with an apparently haphazard sequence of y_2 scores. In any case there can be no long-term evolutionary sequence along y_2 in Wales because the Upper Llandovery *replicata* specimens come at the wrong end of the belt of variation. The slightly higher Welsh than Scottish scores on y_4 in early Llandovery forms presumably represent geographical variation in the length and height of the preglabellar area.

Formal taxonomic treatment of the early Llandovery calymenids at specific level is hindered by the inadequacy of the type collections of *crassa*, *replicata*, and *planicurvata*. Indeed, of the collections studied, only the Newlands material, which ironically bears no formal name, is adequate to form the basis of a species, and it is beyond the scope of the present work to establish a taxon for this sample. In the absence of knowledge of variation at most of the Welsh early Llandovery localities neither the statistical nor the biological relations of the samples can be inferred with confidence and any taxonomic decision must be arbitrary.

The grouping of the Welsh specimens adopted here is into two subjectively delimited species, namely *Calymene crassa* based upon the holotype of that species, and *Calymene* sp. A based upon the loc. 7132 sample.

Genus CALYMENE Brongniart, 1822

Calymene crassa (Shirley, 1936)

Plate 25, figs. 1–8; text-fig. 4*a*

1936 *Diacalymene crassa* sp. nov. Shirley, p. 416, pl. 29, figs. 21–23.
non 1970 *Diacalymene* sp. [?*crassa* Shirley, 1936]; Temple, p. 64, pl. 18, figs. 13–20 [= *Calymene* sp. A—see below].

Holotype. Internal mould of cranidium, GSM 54910 (ex Pg. 2364), from Gasworks Mudstone, side of Frolic Path, 383–390 yd SE. of Higgon's Well, Haverfordwest, Pembrokeshire.

Paratype. Internal mould of cranidium, GSM 54911 (ex TCC 1776), from brook 400 yd SE. of Cotts Park, 1½ miles E. of Haverfordwest, Pembrokeshire.

Localities and material. Locs. 7004b (cranidium), 7022a (cranidium, ? free cheek), ?7029a (cranidium), 7126 (cranidium), 7140 (two cranidia, ? free cheek, ? thoracic segment); TCC 1363 (pygidium), TCC 1364 (cephalon and thorax) from Gasworks Mudstone, lane leading to Gasworks, Haverfordwest, Pembrokeshire, at 93 yd from [gas lamp at] junction with New Road.

Measurements (mm)

		x_1	x_2	x_3	x_4	x_5	x_6
Holotype	GSM 54910	10·6	2·8	1·2	0·1	10·7	162°

Remarks. In the absence of a topotype sample from which to assess variation, the limits of this species must be entirely subjective. As interpreted here, the features distinguishing internal moulds of *crassa* from those of *Calymene* sp. A are the flattened profile of the anterior part of the preglabellar area, the resulting accentuation of the ridge which delimits the flattened part posteriorly, and the tendency of the preglabellar area to overhang in front. These qualitative differences from sp. A show up quantitatively primarily by low scores on y_2, but neither qualitatively nor quantitatively is there a clear division between the two species—the loc. 7132 specimen of sp. A which most closely approaches *crassa* in text-fig. 2 also shows incipient flattening of the anterior part of the preglabellar area. Only four specimens other than the holotype are referred to *crassa* with some confidence, namely the paratype GSM 54911 (Shirley 1936, pl. 29, fig. 23), the cranidia illustrated on Pl. 25, figs. 1 and 2 from locs. 7004b and 7140, and a cranidium from loc. 7126. Specimen TCC 1364 (Pl. 25, figs. 5, 6, 8) and a cranidium from loc. 7022a also have the *crassa* type of preglabellar

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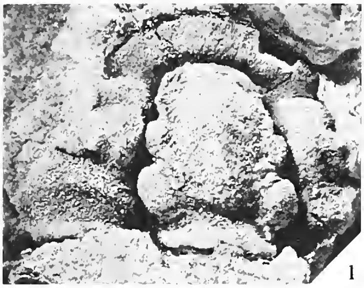
EXPLANATION OF PLATE 25

All specimens are internal moulds except the original of Fig. 8, and all are from early Llandovery.

Figs. 1–8. *Calymene crassa* (Shirley). 1, cranidium with doublure excavated on right side, Zs 953, ×4, NE. of Meifod (loc. 7004b). 2, cranidium, Zs 960, ×2·5, Haverfordwest (loc. 7140). 3–4, cranidium in dorsal and profile views, holotype, GSM 54910, ×2·5, Haverfordwest. 5, 6, 8, cephalon and thorax in profile view (×2·5), cephalon in ventral view after excavation of doublure (×2·5), latex cast of exterior of cheek region (×5), TCC 1364, Haverfordwest. 7, fragmentary pygidium, TCC 1363, ×4, Haverfordwest.

Figs. 9–13, 15, 16. *Calymene* sp. A. 9–10, cephalon in profile and dorsal views, TCC 1480, ×2·5, Haverfordwest. 11, cranidium, Zs 954, ×3, Haverfordwest (loc. 7132). 12, cranidium, Zs 955, ×2·5, Haverfordwest (loc. 7132). 13, cranidium, Zs 961, ×5, Haverfordwest (loc. 7122). 15, 16, pygidia, Zs 958 and Zs 956, ×2·5, Haverfordwest (loc. 7132).

Fig. 14. *Calymene* sp. indet. Pygidium, Zs 959, ×2·5, Haverfordwest (loc. 7121).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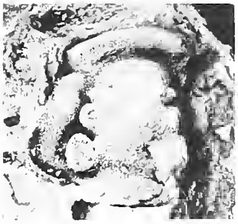
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TEMPLE, British Llandovery trilobites

area, but both are crushed in front and the sharpness and overhang of their cranidial margins have been accentuated by crushing: it is unlikely, though, that their condition could have been produced from a profile that was initially not overhanging to some extent. Specimen TCC 1364 and the pygidium from the same locality (TCC 1363) are important because they provide the only available information on free cheeks, rostral plate, thorax, and pygidium of *crassa*. There is no evidence that in any of these features *crassa* differs from *Calymene* sp. A.

Calymene sp. A

Plate 25, figs. 9–13, 15, 16; Plate 26, figs. 5–6, 9–10

1906 *Calymene blumenbachi* Brongniart, 1822 [partim]; Reed, p. 133, pl. 17, fig. 13.
1936 *Calymene replicata* sp. nov. [partim—Newlands material], Shirley, p. 411.
1970 *Diacalymene* sp. [?*crassa* Shirley, 1936]; Temple, p. 64, pl. 18, figs. 13–20.

Localities and material. Locs. 6701, 7021b, 7122, 7132 (abundant but fragmentary), 7142c, 7148; TCC 1480 (cephalon) from Gasworks Mudstone, lane leading to Gasworks, Haverfordwest, Pembrokeshire, at 138 yd from [gas lamp at] junction with New Road; Newlands Formation, Newlands, Girvan.

Remarks. This species differs from *C. crassa* in having a preglabellar area which, although variable, is not as overhanging in front, and of which the anterior part often develops into a roll-like border. The description of the Meifod material (Temple 1970) may be taken as applying to all the Welsh collections with the proviso noted above about the indistinctness in most specimens of the interpleural furrows of the pygidium.

The type locality is loc. 7132 at Haverfordwest, but even here, the most prolific Welsh locality, the material is not adequate to justify formal establishment of a species. The Newlands sample is arbitrarily referred to sp. A on the basis of its overlap with the Welsh sample on the principal components plots, but it differs slightly from sp. A on both y_2 and y_4 scores. The Mulloch Hill sample, which itself overlaps with Newlands, is equally arbitrarily excluded from sp. A. Collection of an adequate topotype sample of *Calymene planicurvata* Shirley may show that this species is close to or identical with sp. A, but *C. replicata* Shirley differs considerably from sp. A in y_2 scores.

EXPLANATION OF PLATE 26

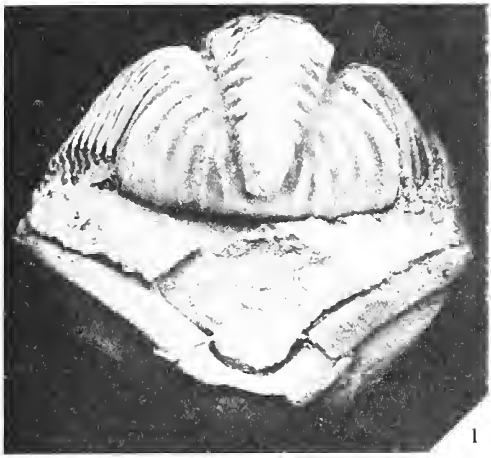
All specimens are internal moulds except the original of Fig. 7, and all are from early Llandovery unless stated otherwise.

Fig. 1. *Calymene replicata* Shirley. Pygidium and ventral view of cephalon of enrolled specimen, topotype A 14923, ×2·5, Lletty'r-hyddod, Llandovery area (Upper Llandovery).

Figs. 2–4, 7–8. *Calymene* sp. Mulloch Hill Beds, Mulloch Hill, Girvan. 2–3, cranidium in dorsal and profile views, In 47724, ×2·5. 4, 7, cephalon and thorax in profile view, latex cast of exterior of cheek region, In 23332, ×2·5. 8, pygidium, In 47696, ×2·5.

Figs. 5–6, 9–10. *Calymene* sp. A. Saugh Hill Beds (Middle Llandovery), Newlands, Girvan. 5, cranidium with narrow glabella, In 43631, ×2·5. 6, free cheek, In 43655, ×3. 9, cranidium with wide glabella, In 43662, ×2·5. 10, pygidium, In 43669, ×3.

Figs. 11–14. *Dalmanites* sp. 11, cranidium, Zs 949, ×3, Haverfordwest (loc. 7127). 12, cranidium, Zs 951, ×2, Haverfordwest (loc. 7126). 13, fixed cheek, Zs 952, ×2, Haverfordwest (loc. 7127). 14, pygidium, Zs 950, ×4, Haverfordwest (loc. 7127).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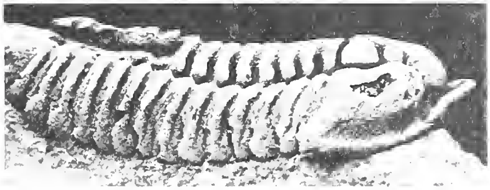
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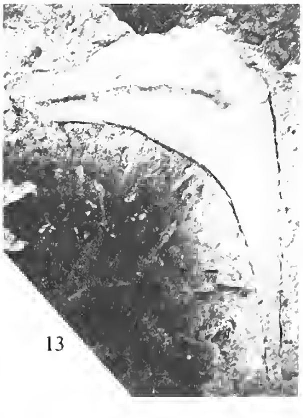
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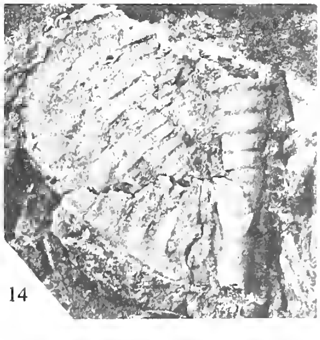
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TEMPLE, British Llandovery trilobites

Calymene sp. indet.

Plate 25, fig. 14

Remarks. Cranidia too poorly preserved for identification, and other parts of the exoskeleton (e.g. pygidia) not diagnostic of either calymenid species recognized, occur at many localities in the early Llandovery of Wales. The figured pygidium, although listed here, may in fact belong to *C. crassa*. It comes from loc. 7121 which is characterized by the occurrence of numerous valves of *Katastrophomena*. The only other locality in the Haverfordwest area (or indeed anywhere in Wales) where abundant *Katastrophomena* are found is a short distance upstream from loc. 7121 at what is probably the type locality of *C. crassa*: the latter may therefore be at the same stratigraphical horizon as loc. 7121, and the calymenids at the two localities may be the same species.

Family HOMALONOTIDAE Chapman, 1890
Genus BRONGNIARTELLA Reed, 1918
Brongniartella sp.

Plate 27, fig. 9

1914 *Homalonotus* sp.; Strahan *et al.*, p. 95.

Remarks. A single damaged pygidium is known from the Gasworks Mudstone at Haverfordwest in the collections of the Institute of Geological Sciences (OTJ 493). The shape and proportions of the rachis and the probable presence of seven pleural furrows are suggestive of *B. platynotus* (Dalman), a species widely spread in Upper Ashgillian strata (Kielan 1960, p. 116, pl. 19, figs. 1–3).

Superfamily CHEIRURACEA Hawle and Corda, 1847
Family CHEIRURIDAE Hawle and Corda, 1847
Genus HADROMEROS Lane, 1971
Hadromeros elongatus (Reed, 1931)

Plate 27, figs. 5, 6, 8

?1851 *Ceraurus Williamsi* (M'Coy); M'Coy, p. 155, pl. 1F, figs. 13, 13*a–b*.

EXPLANATION OF PLATE 27

All specimens except the original of Fig. 11 are internal moulds, and all except the original of Fig. 10 are from the early Llandovery of the Haverfordwest area.

Figs. 1–4. *Acernaspis* sp. 1, cheek and eye, A 32364, × 5, Gasworks Sandstone, Gasworks. 4, eye of same specimen enlarged, × 10. 2, cranidium, TCC 1533, × 6, Gasworks Road, 161 yd S. of gas lamp at junction of New Road and Gasworks Road. 3, thorax and pygidium, OTJ 278, × 4, 20 yd S. of stream, 480 yd W. of Black Backs Bridge.

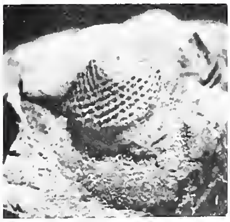
Figs. 5, 6, 8. *Hadromeros elongatus* (Reed). Priory Mill railway cutting, 80 yd S. from level crossing. 5, 8, cranidium in dorsal and profile views, OTJ 612, × 2. 6, cranidium, OTJ 611, × 2.

Fig. 7. *Stenopareia* sp. Right free cheek, Zs 962, × 2. Haverfordwest (loc. 7126).

Fig. 9. *Brongniartella* sp. Pygidium, OTJ 493, × 1·1. Riverside, 235 yd SE. of gate at Higgon's Well.

Fig. 10. Ceratarginae indet. Hypostome, Zs 963, × 12·5. WNW. of Llandysilio (loc. 7001a).

Figs. 11, 12. Odontopleurinae indet. 11, external mould of pygidium, Zs 957, × 6, Haverfordwest (loc. 7132). 12, cephalon, A 32356, × 2, opposite entrance to Gasworks (Turnbull Collection).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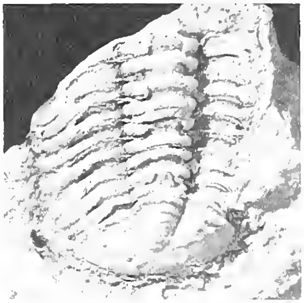
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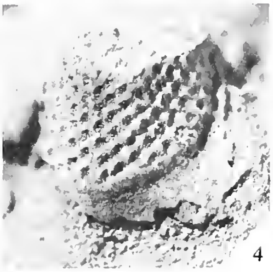
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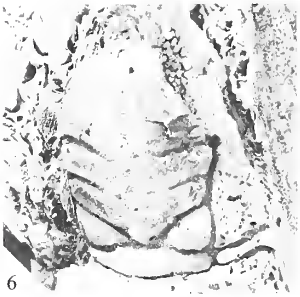
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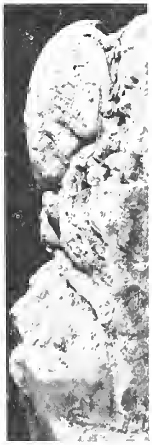
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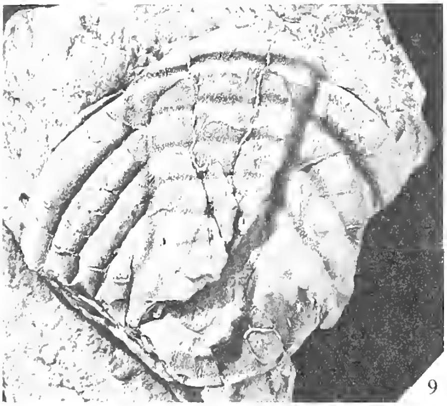
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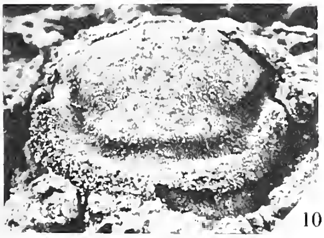
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11


12

TEMPLE, British Llandovery trilobites

1914 *Cheirurus* sp.; Strahan *et al.*, p. 95.
1914 *Lichas* sp.; Strahan *et al.*, p. 95.
1931 *Cheirurus elongatus* sp. n. Reed, p. 103, pl. 4, figs. 5–7; pl. 5, fig. 4.
1935 *Cheirurus conjunctus* sp. nov. Reed, p. 55, pl. 4, fig. 1.
1970 *Cheirurus* sp.; Temple, p. 65, pl. 19, figs. 11–12.
1971 *Hadromeros elongatus* (Reed, 1931); Lane, p. 28, pl. 5, figs. 1–14, 16, 17.

Remarks. No additional cheirurid specimens have been obtained, but there are two fairly good cranidia from Haverfordwest in the collections of the Institute of Geological Sciences. These specimens and those illustrated earlier from Meifod are referred to Reed's species from Newlands, Girvan, on the basis of the backward position (opposite S_1) of the posterior end of the eye. In this respect the specimens from the Lower Llandovery of Skelgill, Westmorland, referred by Lane (1971, p. 30, pl. 4, figs. 5–12) to *H.* aff. *elongatus*, in which the eye reaches less far back, are closer to *H. keisleyensis* (Reed). Unfortunately no pygidia are known from the Welsh early Llandovery except for M'Coy's poor specimen from the Llandovery area which is only tentatively included in the synonymy.

Superfamily PHACOPACEA Hawle and Corda, 1847
Family PHACOPIDAE Hawle and Corda, 1847
Genus ACERNASPIS Campbell, 1967
Acernaspis sp.

Plate 27, figs. 1–4

1970 *Acernaspis* sp.; Temple, p. 68, pl. 18, figs. 10–12, 21.

Remarks. In addition to the material described from Meifod, specimens of *Acernaspis* are known from Llandysilio (loc. 7001a) and Haverfordwest (locs. 7123, 7128, 7147; collections of the Institute of Geological Sciences and the Sedgwick Museum). The material, however, is inadequate either for an assessment of the conspecificity of the different samples, or for comparisons to be made with the finely distinguished species recently described by Männil (1970) from the Lower and Middle Llandovery of Estonia and with the older established *A. elliptifrons* Esmark from the Lower Llandovery of the Oslo region. A specimen from loc. 7123 gave a lens count in vertical files of 4556666.... The illustrated specimen from Haverfordwest (Pl. 27, figs. 1, 4) has seventeen files, of which only the anterior three (567 lenses respectively) are preserved complete, the remaining files showing minimal lens counts of 76676566554332.

Family DALMANITIDAE Vogdes, 1890
Genus DALMANITES Barrande, 1852
Dalmanites sp.

Plate 26, figs. 11–14

Localities and material. Loc. 7126 (cranidium, hypostome), loc. 7127 (cranidium, fixed cheek, pygidium).

Description. The loc. 7127 cranidium (Pl. 26, fig. 11) is an estimated 12 mm long and slightly obliquely distorted. Its palpebral lobe, well preserved on the left side, reaches back to opposite the S_1 furrow, and there is a narrow limb around the glabella behind the facial suture. The glabellar lobation is better seen on the larger cranidium (length approx. 22 mm) from loc. 7126 (Pl. 26, fig. 12). The fixed cheek bears a strong, tapering genal spine. The poorly preserved pygidium is incomplete but originally about 10 mm long, with apparently nine (possibly ten) pleurae. The rachis terminates roundedly approximately 2 mm from the posterior margin, and behind it there is a raised, axially ridged, posteriorly declining post-rachis which apparently continues to the posterior margin and probably slightly beyond into a small mucro.

Remarks. These specimens from Haverfordwest, which are assumed to be conspecific, are the only dalmanitids known in the present collections. The species they represent shows affinity with the Upper Llandovery *Dalmanites vulgaris* (Salter) var. Whittard (1938, p. 133, pl. 5, figs. 15–16). The pygidium of the latter, which is larger than the loc. 7127 specimen, has ten pleurae in contrast to a probable nine, but agrees in showing the rachis terminating well within the margin, a ridged post-rachis, and a small mucro. The Haverfordwest specimens are referred to *Dalmanites* on the basis of the well-defined posterior termination of the pygidial rachis. This is a feature that is found in *Dalmanites* but is developed only incipiently in *Dalmanitina*, where the rachis continues with little interruption into the posterior spine. In some *Dalmanitina mucronata* (Brongniart), as in the pygidium from the St. Martin's Cemetery Beds (?basal Llandovery) of Haverfordwest (Temple 1952, pl. 2, fig. 4), the rachis is posteriorly terminated, although at a point closer to the margin than in the loc. 7127 specimen. It seems likely that there is a gradation within the early Llandovery from *Dalmanitina* to *Dalmanites*.

Superfamily ILLAENACEA Hawle and Corda, 1847
Family ILLAENIDAE Hawle and Corda, 1847
Genus STENOPAREIA Holm, 1886
Stenopareia sp.

Plate 27, fig. 7

1970 *Stenopareia* sp.; Temple, p. 63, pl. 18, figs. 2–6.

Remarks. Two free cheeks from loc. 7126, where also occurs a pygidium of *Stenopareia* sp., are presumably referable to this species and are larger and better preserved than the single cheek known from Meifod. They show the doublure widening rapidly in front, at the same time becoming concave in dorsal view and developing strong terraced lines such as are found on the rostral plate (Temple 1970, pl. 18, fig. 4).

Superfamily ODONTOPLEURACEA Burmeister, 1843
Family ODONTOPLEURIDAE Burmeister, 1843
Subfamily ODONTOPLEURINAE Burmeister, 1843
Odontopleurinae indet.

Plate 27, figs. 11, 12

Remarks. Two pygidia, from Cefn Rhyddan (loc. 7021c) and the Gasworks Mudstone (loc. 7132), show well-differentiated major spines with two pairs of secondary spines adaxially to them and three pairs abaxially; the Gasworks specimen also shows a further small spine or process at the antero-lateral corner of the pygidium. A similar pattern of pygidial spines, the anteriormost being more or less distinctly developed, is found in several Ordovician and Silurian members of the Odontopleurinae. The closest stratigraphically to the present occurrences are '*Acidaspis*' *shanensis* Reed (1915, p. 80, pl. 12, figs. 1-11) from the Lower Llandovery of Burma, an undescribed form related to *Leonaspis girvanensis* (Reed) from the Basal Silurian of Watley Gill, Cautley, Yorkshire, and ?*Acidaspis* sp. indet. Bruton (1967, p. 235, pl. 35, fig. 13) from the Upper Llandovery of Estonia. The Welsh specimens are too imperfect for detailed comparison, but appear to be less coarsely granulated than the Yorkshire form; the external surface of the Estonian pygidium is not known.

A very large cephalon in the Sedgwick Museum (A 32356—sagittal length about 15 mm) from opposite the Gasworks entrance at Haverfordwest (Pl. 27, fig. 12) is tentatively associated with the pygidia described above on the basis of its resemblance to the cephalon of the Burmese form. The disparity in size, however, with other odontopleurid cranidia in the collections is such that meaningful comparisons cannot be made with, for instance, the cranidia from Meifod referred to *Leonaspis marklini varbolensis* Bruton (Temple 1970, p. 69, pl. 19, fig. 17). The pygidia of the Meifod form (loc. cit., fig. 13) are clearly different from those described here, so that two forms of Odontopleurinae occur in the Welsh early Llandovery, but the distinguishing characters of the corresponding cephala are not known.

Superfamily LICHACEA Hawle and Corda, 1847
Family LICHIDAE Hawle and Corda, 1847
Subfamily CERATARGINAE Tripp, 1957
Ceratarginae indet.

Plate 27, fig. 10

Remarks. A small fragmentary cranidium, too poor to illustrate, and a small hypostome are known from loc. 7001a. The hypostome is 2·0 mm in sagittal length and 2·8 mm in maximum width, and has a somewhat asymmetrical posterior margin which is very slightly indented. The subfamily attribution is suggested by Mr. R. P. Tripp who has kindly examined these specimens.

Acknowledgements. I am grateful to the following for access to specimens in their care: Dr. R. A. Fortey and Mr. S. F. Morris (British Museum (Natural History)), Dr. J. K. Ingham (Hunterian Museum, Glasgow), Dr. R. B. Rickards (Sedgwick Museum, Cambridge), Dr. A. W. A. Rushton (Institute of Geological Sciences). Dr. Rushton and Mr. R. P. Tripp have read the text in draft form and their perceptive criticisms have greatly improved it. I am indebted to Mr. C. P. Chalmers for discussion on some statistical questions. Additional programming has been carried out by Mr. M. R. Farmer. The photographs have been taken by Mr. M. S. Hobbs and Mr. E. Cory and the illustrations drawn by Mr. J. L. Richards. Field work has been assisted by the Central Research Fund of the University of London.

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LARGER FORAMINIFERA FROM THE LOWER EOCENE OF THE GEBEL GURNAH LUXOR, EGYPT

by KHALED A. HAMAM

ABSTRACT. Five species of *Nummulites* and four forms of *Operculina* are described and illustrated from the Lower Eocene Thebes Limestone Member of the Thebes Formation, Gebel Gurnah, Luxor, Egypt. *Operculina aegyptiaca*, *O. jiwani gebelensis*, and *O. libyca thebensis* are described as new.

THE Gebel Gurnah lies opposite Luxor on the western side of the Nile Valley at approximately latitude 25° 44′ North and longitude 32° 36′ East, and includes the well-known Valley of Kings. A hundred and twenty-five samples from the succession, which is about 450 m thick, have been thoroughly examined for planktonic and larger Foraminifera (Hamam 1971). The planktonic Foraminifera are in another paper, and the stratigraphic details are not repeated here; the relationships of the samples yielding larger Foraminifera are shown in Table 1; see also Said (1960).

STRATIGRAPHY AND PREVIOUS RECORDS

The lower shaley part of the Gebel Gurnah Section (sample Nos. 1–20) contains a rich and well-preserved planktonic foraminiferal fauna, but has not yielded any larger Foraminifera, nor does the lowermost part of the Thebes Limestone Member, Rock Unit III (sample Nos. 21–48) which is made of chalky limestone. However, in the overlying Rock Unit IV, which is mainly marly and dolomitic limestone, there are numerous and well-preserved larger Foraminifera. Of the twenty samples collected from this Unit IV, only seven (Nos. 57, 59, 62, 64, 65, 67, and 68) contain larger Foraminifera which are always associated with ostracods. Of the twenty-four samples collected from Rock Unit V, a white chalky and nodular limestone, only three (Nos. 84, 87, and 89) yielded larger Foraminifera, which are well preserved but occasionally coated with rock matrix. The uppermost part of the Thebes Limestone, Rock Unit VI, which includes relatively thinner beds of different limestones, contains, in general, an extremely poor fauna: none of the thirty-two samples collected from this unit yielded any matrix-free larger Foraminifera, but a few specimens were observed in thin section. Sample No. 93 contains many well-preserved ostracods, while sample No. 119 yielded poorly preserved and scarcely determinable planktonic Foraminifera.

Delanoue (1868) recorded four species of larger Foraminifera from the Gebel Gurnah section: *Nummulites distans* Deshayes var. *b* d'Archiac, *N. planulata* d'Orbigny, *N. guettardi* d'Archiac and Haime, *Operculina ammonea* Leymerie; while Cuvillier (1930) recorded: *N. atacicus* Leymerie, *N. globulus* Leymerie, *N. guettardi* d'Archiac and Haime, *O. libyca* Schwager, *O. ammonea* Leymerie. Said (1960, 1962)

[Palaeontology, Vol. 18, Part 1, 1975, pp. 161–178, pls. 28–31.]

TABLE 1. Stratigraphical distribution of larger fossil Foraminifera in Gebel Gurnah Section, Luxor, Egypt.

Upper Palaeocene		Lower Eocene											
Gr. velascoensis Zone	Gr. aragonensis Zone	Gr. 'palmerae' Zone											Planktonic zonation
	I–III	IV							V			VI	Rock unit
	1–48	57	59	62	64	65	67	68	84	87	89	93–125	Sample numbers
					×	×	×	×					*Nummulites burdigalensis*
				×	×								*Nummulites globulus*
		×			×	×	×	×	×				*Nummulites silvanus*
						×							*Nummulites* aff. *solitarius*
									×	×	×		*Nummulites subramondi*
				×	×	×	×						*Operculina aegyptiaca*
										×	×		*Operculina jiwani gebelensis*
				×	×	×	×	×					*Operculina libyca libyca*
		×	×										*Operculina libyca thebensis*

recorded: *N. praecursor* (de la Harpe), *N. subramondi* de la Harpe, *O. libyca* Schwager, *Operculina* spp., also from the same section.

Nine larger fossil Foraminifera belonging to the genera *Nummulites* and *Operculina* have been identified in this study, both externally and in equatorial and axial section; 150 oriented thin sections were prepared. The relative proportions of the different species range from horizon to horizon: *O. libyca thebensis* dominates in sample No. 57; *N. globulus* and *O. aegyptiaca* dominate in sample No. 62; *N. burdigalensis* and *O. libyca* dominate in sample No. 64. The former species only is dominant in sample No. 65, while *N.* aff. *solitarius* also occurs rarely. *N. silvanus* commonly occurs in sample No. 68. All the above species have been found in Rock Unit IV. *O. jiwani gebelensis* subsp. nov. and *N. subramondi* are dominant in sample No. 89 of Rock Unit V. All nine taxa described in this paper are represented by megalospheric forms. Two of them, namely *N. burdigalensis* and *O. libyca*, are represented by both microspheric and megalospheric forms.

The species of *Nummulites* which occur in the Gebel Gurnah Section show strong similarity to the European forms, and three species of the five identified were originally described from Europe; *N. burdigalensis*, *N. globulus* and *N. silvanus*. The other two species, *N. subramondi* and *N.* aff. *solitarius*, are Egyptian forms. Among the important planktonic species found in Rock Unit III is *Globorotalia aragonensis* Nuttall, the highest appearance of which coincides with the top of this unit, which is therefore considered to represent Bolli's *Globorotalia aragonensis* Zone. Rock Units IV and V contain *Nummulites* and *Operculina* species of definite Lower Eocene age. From a study of synonyms in the literature, it is concluded that the ranges of the described species are as follows:

Nummulites burdigalensis	Lower Eocene–Eocene
Nummulites globulus	Lower Eocene–Middle Eocene
Nummulites silvanus	Upper Palaeocene–Lower Eocene
Nummulites aff. *solitarius*	Lower Eocene
Nummulites subramondi	Lower Eocene

Operculina aegyptiaca	upper Lower Eocene
Operculina jiwani gebelensis	middle–upper Lower Eocene
Operculina libyca	Lower Eocene
Operculina libyca thebensis	upper Lower Eocene

Rock Units IV and V, which overlie strata containing the *Globorotalia aragonensis* Zone faunas, and which themselves yield faunas with a Lower Eocene aspect, are considered to be upper Lower Eocene and are therefore correlated with Bolli's *Globorotalia palmerae* Zone of Trinidad. Rock Unit VI, which contains few planktonic or larger Foraminifera, is provisionally considered as the topmost part of the Lower Eocene in Egypt. The stratigraphical distribution of the *Nummulites* and *Operculina* species described in this paper are shown in Table 1.

SYSTEMATIC PALAEONTOLOGY

All the figured material is deposited in the British Museum (Natural History), London. The classification followed here is that proposed by Glaessner (1945) and modified by Pokorny (1958). The following terms are used to indicate relative size: less than 2·5 mm = small; 2·5 mm–5·0 mm = medium; above 5·0 mm = large.

Family NUMMULITIDAE de Blainville, 1825
Subfamily NUMMULITINAE de Blainville, 1825
Genus NUMMULITES Lamarck, 1801
Nummulites burdigalensis (de la Harpe)

Plate 28, figs. 1–8

1911 *Nummulites lucasanus* Defrance; Boussac, p. 52, pl. 2, figs. 41, 15.
1919 *Nummulites lucasi* d'Archiac; Douvillé (*pars*), p. 59, pl. 1, figs. 24–27, 37–38; non figs. 28–31.
1926 *Nummulina burdigalensis* de la Harpe, p. 71.
1929 *Nummulina lucasi* (d'Archiac); Rozlozsnik (*pars*), p. 113, pl. 2, figs. 4, 7; non p. 188, pl. 3, fig. 21.
1951 *Nummulites burdigalensis* (de la Harpe); Schaub, p. 113, pl. 1, figs. 13–17*b*; pl. 2, figs. 1–3, 5–8; pl. 3, figs. 1, 3–5; text-figs. 13, 74–81, 83–88*c*, 92*a*–95*c*.
1959 *Nummulites burdigalensis* (de la Harpe); Bieda, p. 21, pl. 1, figs. 1, 3, 4, 8.
1962 *Nummulites burdigalensis* (de la Harpe); Schaub, pp. 532, 534, text-figs. 1*a*, 2.
1967 *Nummulites burdigalensis* (de la Harpe); Nemkov, p. 168, pl. 19, figs. 4–16.

Description. Megalospheric form. External features. Test small, lenticular with raised polar region; equatorial periphery circular and occasionally partly serrate; axial periphery acute; 3–10 small pustules mainly in the polar region and also on the spiral filaments; diameter from 0·05 to 0·15 mm (average 0·12 mm); spiral filaments clearly visible, slightly curved, and radiate; from 19 to 28 in number, usually about 22. The diameter from 1·3 to 2·5 mm, thickness from 0·7 to 1·4 mm, and diameter/thickness ratio from 1·9/1 to 2·4/1.

Internal features. In axial section, protoconch circular from 0·10 to 0·15 mm in diameter; chamber cavity delta-shaped with straight lateral sides; alar prolongations distinct, well marked, relatively wide open, and becoming thinner towards the polar plugs; polar plugs conspicuous, striking, and flaring laterally towards the surface; plugs composed of a group of pillars mainly on the polar region and occasionally on the septal filaments; the base of the polar plug from 0·25 to 0·40 mm in diameter; lateral walls relatively thick, becoming slightly thinner in the last whorl, their thickness varying from 0·05 to 0·12 mm. In equatorial section the bilocular nucleoconch consists of circular to subcircular protoconch and smaller to subequal, hemicircular to reniform deuteroconch; the protoconch from 0·10 to 0·15 mm in diameter; the deuteroconch from 0·16 to 0·24 mm; the spire of three to five closely coiled, regular, and gradually opening whorls; the rate of opening varying from 1/1 to 1·3/1; spiral lamina of moderate thickness almost throughout the spire; height of spiral cavity about 2·5 to 5 times the thickness of the spiral lamina; septa slightly curved in the early whorls, less curved in the later ones; 8–10 septa occur in the first whorl, 16–20 in the second, 17–21 in the third, and 21–24 in the fourth; chambers alar to rectangular in shape; chamber indices vary from 1/1 to 3/1.

Microspheric form. Internal features. Only one specimen (3·6 mm in diameter) found. In equatorial section, the initial chamber(s) indistinct; the slightly irregular spire is composed of about nine, gradually opening whorls.

No. of whorls	2	3	4	5	6	7	8	9
Opening rate	4·00	1·50	1·41	1·23	1·43	1·17	1·14	1·17

Spiral lamina moderate in thickness, which increases gradually from the initial part to the distal part; height of spiral cavity about 3·4–4·3 times thickness of spiral lamina; septa slightly curved to almost straight, slightly inclined on the spiral lamina, and sharply curved backward near the distal end; seven septa occur in the first whorl, 11 in the second, 17 in the third, 20 in the fourth; 21 in the fifth, 20 in the sixth, 25 in the seventh, 25 in the eighth, and 28 in the ninth; chambers rhomboid or rectangular in shape; chamber indices vary from 1/1 to 1·6/1.

Material. The megalospheric form of this species is common at some horizons of Rock Unit IV. Only one specimen of the microspheric form was found.

Remarks. The megalospheric form of *N. burdigalensis* is distinguished in the present material from associated species in having a larger test; raised polar region; acute axial periphery; circular and occasionally partly serrate equatorial periphery; in the occurrence of pustules and granulations; in having relatively large bilocular nucleoconch; delta-shaped chamber cavities with straight lateral sides and well-marked alar prolongations, conspicuous polar plugs; regularly coiled spire and almost straight, slightly curved septa. It is mainly distinguished from *N. globulus* Leymerie in having surface pustules and granulations, serrate equatorial periphery, thinner lateral laminae, delta-shaped chamber cavities with straight lateral sides, and thinner spiral lamina.

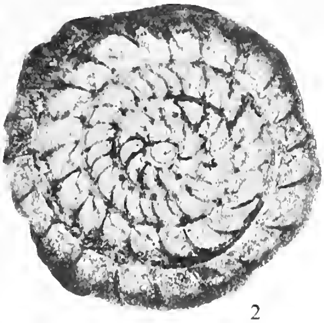
Distribution. A type locality for *N. burdigalensis* was not designated, the present species only mentioned as occurring in the Eocene of France, Italy, U.S.S.R., and Switzerland. Later, it was described from the Lower Eocene (Lower–Upper Ypresian) of Switzerland by Schaub (1951), from the Eocene of Poland by Bieda (1959), and from the Eocene of the Soviet Union by Nemkov (1967). In the Gebel Gurnah Section, *N. burdigalensis* occurs in the upper Lower Eocene.

EXPLANATION OF PLATE 28

Figs. 1–8. *Nummulites burdigalensis* (de la Harpe). 1 (P 49793), 2 (P 49794), equatorial sections of megalospheric specimens, ×24. 3 (P 49795), 4 (49796), external views of megalospheric specimens, ×19. 5 (P 49797, 6 (P 49798), axial sections of megalospheric specimens, ×24. 7 (P 49799), equatorial section of microspheric specimen, ×12. 8, part of the equatorial section of fig. 7 enlarged, ×24. 1, 2, 7, 8 from sample 64; 3, 4, 5, 6 from sample 65, Rock Unit IV, Thebes Limestone Member.

Figs. 9–14. *Nummulites subramondi* de la Harpe. 9 (P 49818), 10 (P 49819), equatorial sections of megalospheric specimens, ×24. 11 (P 49820), 12 (P 49821), axial sections of megalospheric specimens, ×24. 13 (P 49822), 14 (P 49823), external views of megalospheric specimens, fig. 13 ×16, fig. 14 ×19. 9–14 from sample 89, Rock Unit V, Thebes Limestone Member.


1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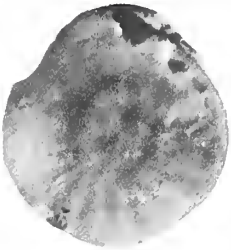
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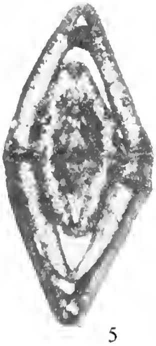
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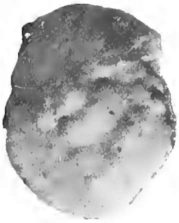
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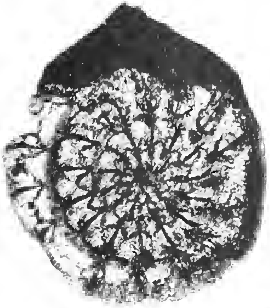
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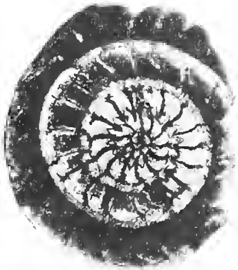
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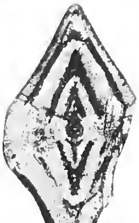
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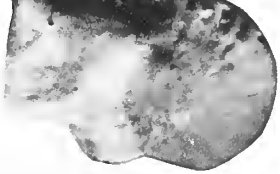
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14

HAMAM, Eocene Foraminifera from Egypt

Nummulites globulus Leymerie

Plate 29, figs. 1-7

1846 *Nummulites globulus* Leymerie; p. 359, pl. 13, fig. 14*a–d*.
1919 *Nummulites globulus* Leymerie; Douvillé, p. 54, pl. 1, figs. 12–17.
1926 *Nummulites globulus* d'Archiac; Doncieux, p. 37, pl. 5, figs. 1–7.
1926 *Nummulites globulus* Leymerie; Nuttall, p. 116.
1927 *Nummulites globulus* Leymerie var. *indicus* Davies, p. 271, pl. 10, figs. 6–10.
1929 *Nummulites globulus* Leymerie; Gomez Llueca, p. 105, pl. 5, figs. 6–10.
1930 *Nummulites globulus* Leymerie; Cuvillier (*pars*), p. 72, non p. 140.
1931 *Nummulites globulus* Leymerie; de Cizancourt, p. 209, pl. 22, fig. 5.
1937 *Nummulites globulus* Leymerie; Davies and Pinfold, p. 22, pl. 3, fig. 3.
1938 *Nummulites globulus* Leymerie; Flandrin, p. 39, pl. 3, figs. 21–23.
1951 *Nummulites globulus* Leymerie; Schaub, p. 103, pl. 1, fig. 1; text-figs. 42*a*–49*b*, 51*a*, *b*.
1952 *Nummulites globula* Leymerie; Azzaroli, p. 120, pl. 9, figs. 4, 5.
1954 *Nummulites globulus* Leymerie; Smout, p. 79, pl. 15, figs. 5, 6.
1959 *Nummulites globulus* Leymerie; Papp, p. 167, text-figs. 3 (4, 5*a*, *b*).
1967 *Nummulites globulus* Leymerie; Nemkov, p. 202, pl. 26, figs. 1–8.

Description. Megalospheric form. External features. Test small to medium-sized, lenticular to subglobular; equatorial periphery circular; axial periphery subacute to acute in well-preserved specimens; polar boss or postules not seen; septal filaments numerous, weakly curved, regular, radiate, and flush; occasionally weakly raised; surface rather smooth. The diameter varies from 1·0 to 2·8 mm, thickness from 0·6 to 1·6 mm, and diameter/thickness ratio from 1·4/1 to 1·7/1.

Internal Features. In axial section, protoconch circular and varies from 0·12 to 0·17 mm in diameter; chamber cavity narrow, wedge- to delta-shaped, sometimes with slightly concave lateral sides; alar prolongation distinct, well marked, wide open, and becoming thinner towards the conspicuous polar plugs, which flare towards the surface, where they vary from 0·25 to 0·5 mm diameter; these plugs are not visible externally because they are concealed by the overlapping of the lateral laminae of the last whorls; lateral walls layered, thick, and maintaining their thickness from the polar region to the equatorial periphery, its thickness varies from 0·07 to 0·17 mm; marginal cord most often indistinct. In equatorial section, bilocular nucleoconch comprises a circular protoconch and reniform deuteroconch; the protoconch varies from 0·10 to 0·20 mm, the average is about 0·17 mm; the deuteroconch from 0·07 × 0·15 to 0·10 × 0·17 mm, the average is about 0·10 × 0·15 mm; the maximum height of nucleoconch varies from 0·20 to 0·25 mm with a spire of three to four closely coiled, usually regular, and gradually opening whorls; the rate of spire opening varies from 1/1 to 2·1/1, the average is 1·1/1 to 1·5/1; spiral lamina relatively thick, thickness varying; height of spiral cavity about one to five times thickness of spiral lamina (average is three times); septa slightly curved in the early whorls, less so in the later ones, relatively thick with marked curvature near distal end; about 8–10 septa occur in the first whorl, 13–18 in the second, 19–24 in the third, and about 21 in the fourth, chambers alar to rectangular in shape; chamber indices vary from 1/1 to 2/1, the average is 1/1 to 1·5/1.

EXPLANATION OF PLATE 29

Figs. 1–7. *Nummulites globulus* Leymerie. 1 (P 49802), 2 (P 49803), equatorial sections of megalospheric specimens, × 24. 3 (P 49804), 4 (P 49805), external views of metalospheric specimens, × 19. 5–7 (P 49806–49808), axial sections of megalospheric specimens, × 24. Sample 62, Rock Unit IV, Thebes Limestone Member.

Figs. 8–13. *Nummulites silvanus* Schaub. 8 (P 49811), 9 (P 49812), equatorial sections of megalospheric specimens, × 24. 10 (P 49813), 11 (P 49814), axial sections of megalospheric specimens, × 24. 12 (P 49815), 13 (P 49816), external views of megalospheric specimens, × 16. Sample 68, Rock Unit IV, Thebes Limestone Member.

Fig. 14. *Nummulites* aff. *solitarius* de la Harpe. P 49817, equatorial section of megalospheric specimen, × 24. Sample 65, Rock Unit IV, Thebes Limestone Member.

PLATE 29


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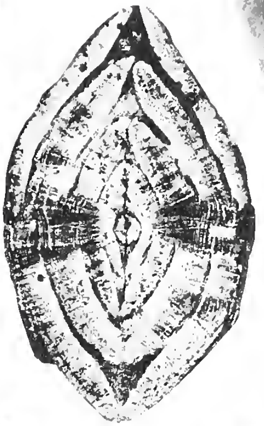
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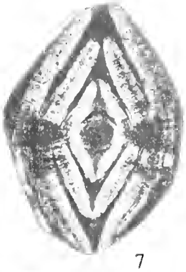
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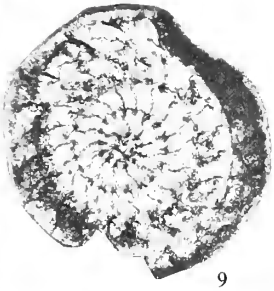
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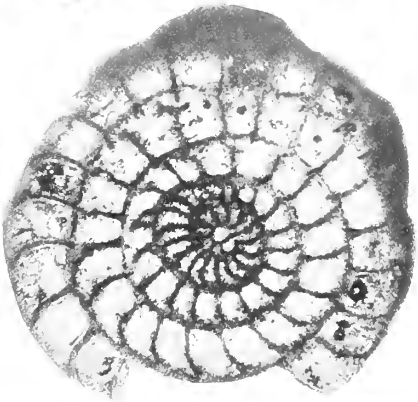
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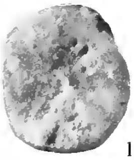
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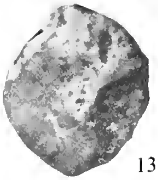
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11

HAMAM, Eocene Foraminifera from Egypt

Material. No microspheric form found. Megalospheric forms are abundant at some horizons in Rock Unit IV.

Remarks. N. globulus is distinguished from other *Nummulites* in having a larger and subglobular test; a rather smooth surface; thick lateral laminae; wedge-shaped chamber cavities; well-marked alar prolongations; distinct and well-developed polar plugs; large nucleoconch with larger and circular protoconch and smaller and reniform deuteroconch; closely coiled spire; thick spiral lamina and almost straight, slightly curved septa. Schaub (1951) described *N. pernotus* from the Palaeocene to Lower Eocene of Switzerland, a form very close to the present species. Earlier, Davies (1927) described both *N. globulus* var. *indicus* and *N. wadiai* from the Ranikot Beds of Thal in Pakistan. Bayliss (1961, unpublished thesis) treated Davies's variety as synonymous with the typical species, a view shared by the present author. In the Gebel Gurnah Section, some individuals in the population of the present species show strong affinities to *N. wadiai* Davies, and further study may prove these species conspecific.

Distribution. Leymerie described *N. globulus* from the Tertiary of France. It was also described from the Lower Eocene of the Pyrénées, France, by Douvillé (1919); from the Middle Eocene of Spain by Gomez Llueca (1929); from the Lower to Middle Eocene of Albania by Cizancourt (1931); from the Lower to Middle Eocene of Algeria by Flandrin (1938); from the Palaeocene to Lower Eocene of Switzerland by Schaub (1951); from the Middle Eocene of Somaliland by Azzaroli (1952); from the Lower Eocene of Qatar by Smout (1954); from the Lower Eocene of Austria by Papp (1959); from Lower to Middle Eocene in the Rakhi Nala Section of Pakistan by Bayliss (1961), and from the Eocene of the Soviet Union by Nemkov (1967). In the Gebel Gurnah Section, *N. globulus* occurs in the upper Lower Eocene.

Nummulites silvanus Schaub

Plate 29, figs. 8–13

1951 *Nummulites silvanus* Schaub, p. 153, text-figs. 189*a*–194*c*.

Description. Megalospheric form. External features. Test small, laterally compressed and flatly lenticular usually without any markedly developed structures in the polar region such as pustules, granules, or bosses; equatorial periphery circular to subcircular; axial periphery acute to subacute; spiral filaments occasionally well visible, thin, slightly curved, and rarely ramified. The diameter varies from 1·1 to 2 mm, thickness varies from 0·3 to 0·8 mm, and diameter/thickness ratio from 2·2/1 to 3·7/1.

Internal features. In axial section the chamber cavity appears as a high, narrow triangle, with straight lateral sides and distinct alar prolongations; polar plugs indistinct or absent; lateral walls thin, delicate, and maintaining their thickness throughout; marginal cord indistinct. In equatorial section, the bilocular nucleoconch is composed of a subcircular to ovoid protoconch and a smaller or subequal, ovoid deuteroconch with straight separating wall; the protoconch varies from 0·05 to 0·10 mm in diameter; the deuteroconch from 0·04 × 0·07 to 0·05 × 0·10 mm; the maximum height of nucleoconch varies from 0·11 to 0·15 mm; the spire is composed of 2·5 to 4 regular to irregular, narrow, and gradually opening whorls; the rate of spire opening varies from 1/1 to 1·6/1; spiral lamina thin and almost regular; height of spiral cavity about four to six times thickness of spiral lamina; septa thin, simply curved to irregular in shape, occasionally the distal part of some gently curving septa suddenly bends forwards to join the spiral lamina; about 9–11 septa occur in the first whorl, 16–20 in the second, 18–22 in the third, and 22–24 in the fourth; chambers variable in shape, rectangular, crescentic, or nearly rhomboid; chamber indices vary from 1/1 to 3·3/1.

Material. Megalospheric forms are rare to common in Rock Unit IV. No microspheric forms found.

Remarks. Nummulites silvanus is distinguished from other *Nummulites* in having a laterally compressed, flatly lenticular test; thin, slightly curved, and rarely ramified spiral filaments; high chamber cavities; thin and delicate lateral walls; straight separating wall between protoconch and deuteroconch; thin spiral lamina; simply curved to irregular septa which sometimes bend forwards to join spiral lamina and rectangular, crescentic, or nearly rhomboid chambers. It lacks pustules, granules, or polar bosses and polar plugs. It is similar to *N. praecursor* (de la Harpe) (= *N. biarritzensis* d'Archaic var. *praecursor* de la Harpe) but has a narrower spire, a smaller nucleoconch, a thinner spiral lamina, and a more compressed test.

Distribution. The present species was originally described from the Upper Palaeocene and from Upper Palaeocene–Lower Eocene transition beds of the Schlierenflysch, Switzerland, by Schaub (1951). In the Gebel Gurnah Section, *N. silvanus* occurs in the upper part of the Lower Eocene.

Nummulites aff. *solitarius* de la Harpe

Plate 29, fig. 14

Description. Megalospheric form. Internal features. Only two specimens found, 1·67 mm and 2·25 mm in diameter. The bilocular nucleoconch comprises a circular protoconch and subequal, subcircular deuteroconch; the protoconch varies from 0·05 to 0·06 mm in diameter; the deuteroconch varies from 0·02 × 0·04 to 0·05 × 0·05 mm; the maximum height of nucleoconch varies from 0·10 to 0·12 mm; the spire is composed of four to five moderately coiled, regular to slightly irregular whorls; three whorls to a radius of 0·7–0·8 mm; the rate of spire opening varies from 1·1/1 to 1·6/1; spiral lamina relatively thin; height of spiral cavity about 3 to 6·5 times thickness of spiral lamina; septa irregular in general, small, closely arranged, and curved in the earlier whorls, becoming larger, irregular, and almost straight or more curved; 12 septa occur in the first whorl, 17–19 in the second, 17–19 in the third, 20–22 in the fourth, and 23 in the fifth; chambers rhomboid or crescentic to rectangular; chamber indices vary from 1·5/1 to 5·5/1.

Material. Two specimens only.

Remarks. Nummulites solitarius de la Harpe was originally described from 'Libysche Stufe' of El-Guss-Abu-Said, Farafrah Oasis, Egypt. Later, Schaub (1951) studied the topotypes and also material from Switzerland, and considered its range to be Paleocene–Lower Eocene. Gebel Gurnah specimens slightly differ from the typical in having a slightly lower rate of spire opening and slightly longer earlier sutures.

Distribution. In the Gebel Gurnah Section, *N.* aff. *N. solitarius* occurs in the upper Lower Eocene.

Nummulites subramondi de la Harpe

Plate 28, figs. 9–14

1883 *Nummulites ramondi* Defrance; de la Harpe, p. 173, pl. 31 (2), figs. 5–12*a* (as figs.).
1883 *Nummulites subramondi* de la Harpe, p. 175, pl. 31 (2), figs. 13–17 (10 figs.).
1951 *Nummulites subramondi* de la Harpe; Schaub, p. 128, text-figs. 119–127*c*.
1959 *Nummulites subramondi* de la Harpe; Papp, p. 167, text-figs. 4 (1*a*, *b*).
1967 *Nummulites subramondi* de la Harpe; Nemkov, p. 249, pl. 38, figs. 1–3.

Description. Megalospheric form. External features. Test small, lenticular with conspicuous strongly raised polar boss which may be flat- or convex-topped, the diameter of which varies from 0·15 to 0·30 mm and height from 0·05 to 0·12 mm, mean 0·07 to 0·12 mm; equatorial periphery circular to subcircular; axial periphery acute; spiral filaments present, radiate and almost straight, from 17 to 24 in number (average about 20). The diameter varies from 0·75 to 1·65 mm, thickness from 0·37 to 1·00 mm, and diameter/thickness ratio from 1·5/1 to 3/1.

Internal features. In axial section, protoconch circular from 0·05 to 0·07 mm in diameter; chamber cavity appears as a narrow isosceles triangle with straight lateral sides and distinct alar prolongations which maintain their width to the conspicuous polar plugs, striking and flaring laterally from near the nucleoconch towards the surface and protruding externally to constitute well-developed and strongly raised polar bosses; the bases of plugs have the same diameter as the bosses; lateral walls layered, of moderate (0·04–0·10 mm) thickness throughout; those of the last whorl are slightly thinner; marginal cord occasionally distinct in the last whorl. In equatorial section, bilocular nucleoconch comprises a circular to subcircular protoconch and a smaller or subequal, ovoid deuteroconch; the protoconch varies from 0·05 to 0·07 mm in diameter; the deuteroconch varies from 0·02 × 0·06 to 0·05 × 0·06 mm; the diameter of nucleoconch varies from 0·08 to 0·12 mm; the spire is composed of three to four regular and gradually opening whorls; first whorl hardly open, followed by moderately open ones; the rate of opening varies from 1/1 to 1·6/1; spiral lamina rather thin and more or less regular; height of spiral cavity about four times thickness of spiral lamina; septa mostly straight, thickened, and very weakly inclined to the spiral lamina; about 8–9 septa occur in the first whorl, 14–15 in the second, 16–19 in the third, and about 22 in the fourth; chambers similar in outline, subquadrate or rectangular; chamber indices vary from 1·1/1 to 2/1.

Material. The megalospheric form is common at some horizons in Rock Unit V. No microspheric form found.

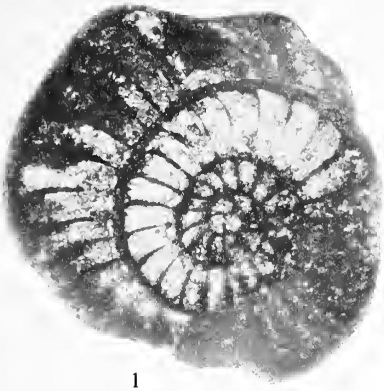
Remarks. Nummulites subramondi is distinguished from associated species in having conspicuous and strongly raised polar bosses; even equatorial periphery; almost straight septal filaments; narrow isosceles triangular chamber cavity in axial section, well-marked, open alar prolongations which maintain their width throughout; rather thin spiral lamina; straight, thickened, and iron-oxidized septa which are almost upright situated on spiral lamina and isometric, subquadrate, or rectangular chambers. Although Gebel Gurnah specimens show slight differences from the type material described by de la Harpe (1883) and Schaub (1951) from the Lower Eocene of Egypt, they are considered to be conspecific. They show all the important diagnostic characters of this species.

Distribution. De la Harpe described *N. subramondi* from the Lower Eocene of Gebel Ter, Nile Valley, Egypt. Later, it was described from the Lower Eocene of Switzerland by Schaub (1951), from the Lower Eocene of Austria by Papp (1959), and from the Lower Eocene of the Soviet Union by Nemkov (1967). In the Gebel Gurnah Section, *N. subramondi* occurs in the upper Lower Eocene.

EXPLANATION OF PLATE 30

Figs. 1–8. *Operculina libyca* Schwager. 1 (P 49842), 2 (P 49843), equatorial sections of megalospheric specimens, fig. 1 × 19, fig. 2 × 10. 3 (P 49844), 4 (P 49845), axial sections of megalospheric specimens, fig. 3 × 24, fig. 4 × 19. 5 (P 49846), external view of megalospheric specimen, × 19. 6 (P 49848), external view of microspheric specimen, × 19. 7 (P 49849), equatorial section of microspheric specimen, × 9·3. 8, part of the equatorial section of fig. 7 enlarged, × 24. 1, 2, 7, 8 from sample 64; 3–6 from sample 65, Rock Unit IV, Thebes Limestone Member.

Figs. 9–14. *Operculina jiwani gebelensis* subsp. nov. 9 (P 49834), 10 (P 49835), equatorial sections of megalospheric paratypes, × 24. 11 (P 49836), external view of megalospheric paratype, × 19. 12 (P 49837), external view of holotype (megalospheric form), × 19. 13 (P 49838), 14 (P 49839), axial sections of megalospheric paratypes, × 24. Sample 89, Rock Unit V, Thebes Limestone Member.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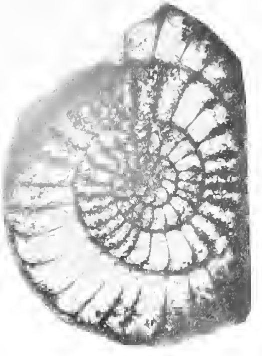
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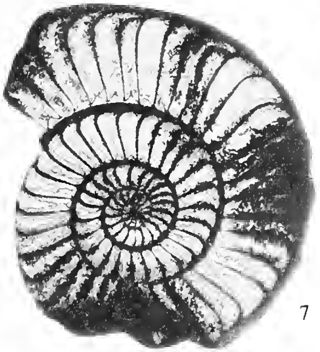
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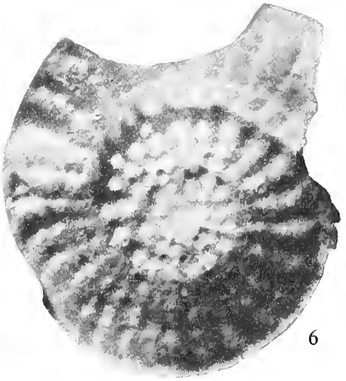
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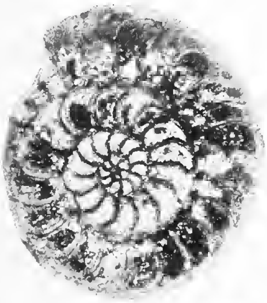
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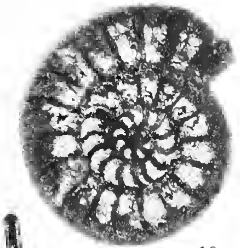
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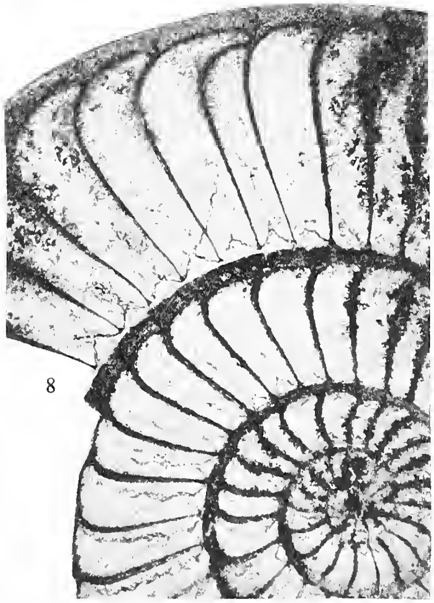
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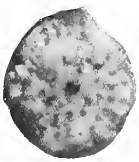
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HAMAM, Eocene Foraminifera from Egypt

Genus OPERCULINA d'Orbigny, 1826

Operculina aegyptiaca sp. nov.

Plate 31, figs. 1–6

Diagnosis. An *Operculina* with small to medium-sized test, a subcircular equatorial periphery, radiate and slightly raised surface ridges running along the sutures, rather wide and isosceles triangular chamber cavities with perfectly straight sides, and curved to slightly irregular and thickened septa.

Description. Megalospheric form. External features. Test small to medium sized, strongly bilaterally compressed; equatorial periphery subcircular; axial periphery acute; surface ornamented with narrow, slightly raised ridge-like structures running along the sutures; intercameral sutures distinct, weakly curved, radial; from 21 to 26 in the last whorl; spiral suture distinct and slightly depressed. The diameter varies from 1·75 to 3·55 mm, thickness from 0·25 to 0·45 mm, and diameter/thickness ratio from 7/1 to 8/1.

Internal features. In axial section, the protoconch varies from 0·05 to 0·10 mm in diameter; chamber cavity rather wide, open, long isosceles triangular in shape with perfectly straight lateral sides, gradually attenuated in thickness towards the equatorial periphery and with inwards convex base; lateral wall rather thick, layered, and varies from 0·10 to 0·125 mm in thickness near the nucleoconch, becoming much thinner in the last whorl where it varies from 0·0375 to 0·075 mm. In equatorial section, bilocular, fairly large nucleoconch comprising a circular to subcircular protoconch and subequal reniform deuteroconch; separating wall slightly convex outwards; the protoconch varies from 0·05 to 0·125 mm in diameter; the deuteroconch from 0·0625 × 0·0875 to 0·10 × 0·125 mm; the maximum diameter of nucleoconch from 0·20 to 0·22 mm; the spire has two to three regular to slightly irregular and rapidly opening whorls; the rate of spire opening varies from 1·4/1 to 2/1; spiral lamina rather thin, regular, and increasing in thickness distally; height of spiral cavity about 2 to 6·25 times thickness of spiral lamina; septa long, thickened, slightly to moderately curved, occasionally irregular, almost regularly spaced, and maintaining their thickness throughout; at the distal end they are sharply curved backwards to join the spiral lamina; about 8–9 septa occur in the first whorl, 16–18 in the second, and 22–26 in the third; chambers higher than long and alar to crescentic in shape; chamber indices vary from 1·5/1 to 3·25/1.

Material. The microspheric form has not been found. Megalospheric forms are common in some horizons of Rock Unit IV.

Remarks. Operculina aegyptiaca sp. nov. is distinguished from *O. gigantea* Mayer and *O. ammonea* Leymerie, mainly in being much smaller, in having a subcircular equatorial periphery, slightly raised ridges running over weakly curved sutures, rather wide triangular chamber cavities with perfectly straight sides in axial section, curved and slightly irregular and thickened septa, and alar to crescentic chambers. *O. alpina* Douvillé, from the Eocene of France, has a larger test, a higher rate of spire opening, and almost straight septa. *O. libyca* Schwager mainly differs in having a complanate to roughly polygonal test; granulated surface; narrower, higher, weakly attenuated, and almost parallel-sided chamber cavities in axial section; thinner septa and spiral lamina; a lax spire and crescentic to rectangular chambers in equatorial section. *O. libyca thebensis* subsp. nov. differs in having rather smooth complanate and much thinner test with raised polar knob; very thin chamber cavities with slightly convex sides inwards in axial section; much thinner septa and spiral lamina; almost straight and regularly spaced septa which give rise to almost rectangular chambers; a lax spire in equatorial section.

Distribution. In the Gebel Gurnah Section, *O. aegyptiaca* sp. nov. occurs in the upper Lower Eocene.

Operculina jiwani Davies *gebelensis* subsp. nov.

Plate 30, figs. 9–14

Diagnosis. An *Operculina* with a small test, slightly raised polar region, subcircular equatorial periphery, granulated and/or raised intercameral sutures, strongly depressed and groove-like spiral suture, conspicuous polar pustule, very thin and high chamber cavity in axial section, thick lateral wall, thin last whorl, very small nucleoconch, and rather thick and slightly curved septa in equatorial section.

Description. Megalospheric form. External features. Test small, bilaterally compressed, and with slightly raised polar region; equatorial periphery subcircular to ovoid with high apertural faces; axial periphery acute; surface coarsely ornamented with pustules and granules which are situated on sutures; granules from 24 to 41 in number and from 0·025 to 0·10 mm in diameter; they increase in number in the later whorls and usually fuse in ridge-like structures along the sutures; in the polar region there is a single conspicuous polar pustule, varying from 0·075 to 0·175 mm in diameter; intercameral sutures almost straight, slightly curved, radial, and granulated or covered with ridges; 20 to 26 sutures in the last whorl; spiral sutures depressed and groove-like as a result of coarse surface ornamentation. The diameter varies from 1·20 to 2·20 mm, thickness from 0·20 to 0·55 mm, and diameter/thickness ratio from 3·4/1 to 6/1.

Internal features. In axial section, protoconch circular and varies from 0·025 to 0·0625 mm in diameter; chamber cavity very narrow, high, and its base convex inwards; polar pustule conspicuous, about 0·15 mm in diameter; polar pustule and surface granules do not express any internal features such as internal pillars and are thickenings of lateral walls; lateral wall thick (about 0·15 mm in the middle of the test), becoming straight, very thin, and delicate in the last whorl where it does not exceed 0·025 mm in thickness. In equatorial section, the very small bilocular nucleoconch is composed of circular protoconch and smaller reniform deuteroconch; the protoconch from 0·025 to 0·06 mm in diameter; the deuteroconch from 0·02 × 0·022 to 0·032 × 0·05 mm; the maximum height of nucleoconch from 0·062 to 0·09 mm; the spire has 3 to 3½, regularly and rapidly opening whorls; the rate of spire opening varies from 1·3/1 to 1·8/1, spiral lamina rather thin increasing in thickness distally; height of spiral cavity about five to eight times thickness of spiral lamina; septa slightly to moderately curved, rather thick, regularly spaced and at their distal end curved backwards to join the spiral lamina; 8–10 septa occur in the first whorl, 14–15 in the second, and 18–21 in the third; chambers higher than long, alar or crescentic in shape; chamber indices vary from 2/1 to 2·7/1.

Material. The microspheric form has not been found. The megalospheric form is common in some horizons of Rock Unit V.

Remarks. This subspecies differs from *Operculina jiwani* Davies s.s. mainly in having smaller test, more lax spire, thinner last whorl, and the presence of a conspicuous single polar pustule. *O. semiivoluta* Nemkov and Barkhatova is similar but differs in being slightly involute, in having a roughly polygonal outline to the equatorial periphery, a ridged rather than a granulated surface, and more septa per whorl.

Distribution. In the Gebel Gurnah Section, *O. jiwani gebelensis* occurs in the upper Lower Eocene; the subspecies also occurs in the Lower Eocene Ghazij Formation of Pakistan (Bayliss 1961, unpublished Ph.D. thesis).

Operculina libyca libyca Schwager

Plate 30, figs. 1–8; Plate 31, fig. 7

1883 *Operculina libyca* Schwager, p. 142, pl. 29 (6), fig. 2*a*–*b*.
1930 *Operculina libyca* Schwager; Cuvillier, p. 71.
1953 *Operculina libyca* Schwager; Le Roy, p. 42, pl. 11, figs. 14, 15.

Description. Megalospheric form. External features. Test small to medium in size, thin, strongly bilaterally compressed, and coarsely roughened at the middle; equatorial periphery complanate to roughly polygonal;

axial periphery acute; coarsely ornamented with granulations at the middle and along the sutures of early whorls; granules variable, sometimes subequal in size, becoming much smaller and fused together, constituting low ridge-like structures on later sutures; granules from 28 to 60 in number and from 0·025 to 0·125 mm in diameter; intercameral sutures indistinct in the early part, becoming distinct, granulated, or covered with low ridge-like structures, almost straight, radiate, and raised later; from 19 to 26 in the last whorl; spiral suture indistinct proximally, becoming distinct, slightly depressed later. The diameter from 1·65 to 3·2 mm, thickness from 0·40 to 0·45 mm, and diameter/thickness ratio from 4·1/1 to 7·1/1.

Internal features. In axial section, protoconch circular and varies from 0·05 to 0·10 mm in diameter; chamber cavity narrow, high, weakly attenuated in thickness towards the equatorial periphery, giving a parallel-sided impression, and with its base slightly convex inwards; the last whorl shows marked decrease in thickness from 0·15 to 0·225 mm, surface granules appear merely as thickenings of lateral walls, which are rather thick (0·125 to 0·175 mm) near the nucleoconch, becoming thinner in the last whorl (0·05 to 0·10 mm). In equatorial section, large bilocular nucleoconch of circular to subcircular protoconch and subequal to slightly larger reniform deuteroconch; separating wall either straight or convex outwards; the protoconch from 0·075 to 0·12 mm in diameter; the deuteroconch from 0·05×0·075 to 0·10×0·137 mm, the maximum height of nucleoconch from 0·15 to 0·22 mm; the spire of $2\frac{1}{2}$ to $3\frac{3}{4}$ regular and rapidly opening whorls; the distal part of last whorl is sometimes narrower than the proximal part and wavy, giving the roughly polygonal outline of the equatorial periphery; the rate of spire opening from 1·6/1 to 2·5/1; spiral lamina thin, regular, increasing in thickness distally; height of spiral cavity about 4 to 12·5 times thickness of spiral lamina; septa long, almost straight, very weakly curved, of even thickness, and regularly spaced; distally they sharply curve backwards to join the spiral lamina; very few septa do not reach the spiral lamina and curve backwards to meet previous ones; about 9–11 septa occur in the first whorl, 15–19 in the second, and 23–26 in the third; chambers higher than long and almost rectangular to crescentic in shape; chamber indices vary from 1·75/1 to 3·8/1.

Microspheric form. External features. Test similar to that of megalospheric form in shape and surface ornamentation; however, those of the microspheric form are larger with their diameter reaching 5·0 mm.

Internal features. Two specimens of the microspheric form were studied in equatorial section. The spire of 5 to $5\frac{1}{2}$ regular and rapidly opening whorls; the rate of spire opening slightly less than megalospheric form, from 1·75/1 to 1·9/1; spiral lamina rather thin, regular, and increasing in thickness distally; height of spiral cavity about four to nine times thickness of spiral lamina; septa long almost straight, very weakly curved, maintaining their thickness throughout, and regularly spaced; at distal end they sharply curve backwards to join the spiral lamina; a few septa only do not reach spiral lamina and curve backwards to meet previous ones; about 9 septa in the first whorl, 13 in the second, 17–21 in the third, 24–26 in the fourth, and 31–36 in the fifth; chamber indices vary from 2/1 to 5·5/1.

Material. The megalospheric form is abundant at some horizons of Rock Unit IV, while microspheric forms are rare.

Remarks. Operculina libyca libyca mainly differs from *O. aegyptiaca* sp. nov. in having a granulated surface, a higher rate of spire opening, higher chambers and thinner spiral lamina and septa. It also differs from *O. libyca thebensis* in having a larger and granulated test; slightly fewer chambers; a relatively thicker lateral wall, spiral

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EXPLANATION OF PLATE 31

Figs. 1–6. *Operculina aegyptiaca* sp. nov. 1 (P 49824), external view of holotype (megalospheric form), ×19. 2 (P 49825), external view of megalospheric paratype, ×19. 3 (P 49826), 4 (P 49827), axial sections of megalospheric paratypes, ×24. 5 (P 49828), 6 (P 49829), equatorial sections of megalospheric paratypes, fig. 5 ×24, fig. 6 ×19. Sample 62, Rock Unit IV, Thebes Limestone Member.

Fig. 7. *Operculina libyca* Schwager. 7 (P 49847), external view of megalospheric specimen, ×19. Sample 65, Rock Unit IV, Thebes Limestone Member.

Figs. 8–13. *Operculina libyca thebensis* subsp. nov. 8 (P 49852), external view of holotype (megalospheric form), ×28. 9 (P 49853), 10 (P 49854), equatorial sections of megalospheric paratypes, ×24. 11, 12 (P 49855), axial section of megalospheric paratype, fig. 11 ×24, fig. 12 ×48. 13 (P 49856), axial section of megalospheric paratype, ×48. Sample 57, Rock Unit IV, Thebes Limestone Member.

PLATE 31


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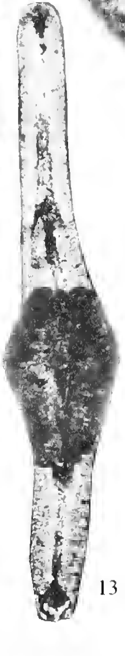
13


10

HAMAM, Eocene Foraminifera from Egypt

lamina, and septa; a larger protoconch, deuteroconch, and nucleoconch, and in lacking the inflated polar region. The form described by Le Roy (1953) from the Maqfi Section shows fewer whorls, otherwise it agrees well with Schwager's species. Nemkov (1967, p. 271) recorded *O. libyca* from the south of the Soviet Union, but provided no illustrations, which makes comment difficult.

Distribution. O. libyca was originally described from Eocene Libysche Stufe of El-Guss-Abu-Said, Farafra Oasis, and from Remihma, Egypt. Cuvillier (1930) recorded it from many Lower Eocene sections in Egypt. Le Roy (1953) described it from the Lower Eocene of Maqfi Section, Farafra Oasis, Egypt. In the Gebel Gurnah Section, *O. libyca libyca* occurs in the upper Lower Eocene.

Operculina libyca thebensis subsp. nov.

Plate 31, figs. 8–13

Diagnosis. An *Operculina* with a thin test, swollen polar knob, smooth surface, very thin septa and spiral lamina, very high and narrow chamber cavity but markedly wider at the base, and slightly inwards convex lateral sides.

Description. Megalospheric form. External features. Test small to medium, thin, strongly bilaterally compressed, occasionally wavy, and with swollen polar knob; equatorial periphery regular and complanate to subcircular; axial periphery acute; surface rather smooth with a swollen polar knob; intercameral suture indistinct in the early whorl, becoming scarcely visible as being slightly raised, almost straight and radial in later whorls; sutures are visible if the specimen is submerged in water, and vary from 23 to 26 in the last whorl; spiral suture indistinct in early whorls, becoming distinct, thin, and flush to slightly depressed; the diameter of swollen polar knob varies from 0·075 to 0·20 mm. The diameter varies from 1·05 to 2·6 mm, thickness from 0·15 to 0·32 mm, and diameter/thickness ratio from 5·1/1 to 9·9/1.

Internal features. In axial section, protoconch circular from 0·025 to 0·05 mm in diameter; chamber cavity narrow and high, weakly attenuated towards the equatorial periphery and with almost parallel to inwards slightly convex lateral sides and markedly wide lower part with internally convex base; lateral wall rather thick in the polar region (0·10 to 0·15 mm), becoming thin in the last whorl (0·025 to 0·05 mm); surface polar knobs are merely thickenings of lateral walls. In equatorial section, the bilocular medium nucleoconch has a circular protoconch and subequal reniform deuteroconch; separating wall convex outwards; the protoconch from 0·025 to 0·075 mm in diameter; the deuteroconch from 0·025 × 0·05 to 0·0375 to 0·075 mm; the maximum width of nucleoconch from 0·075 to 0·10 mm; the spire of about three regular and rapidly opening whorls; the rate of spire opening from 1·85/1 to 2·5/1; spiral lamina very thin, regular, and increases in thickness distally; height of spiral cavity about seven to eighteen times thickness of spiral lamina; septa very thin, long, regularly spaced, maintaining their thickness throughout, and almost straight except distally which is strongly curved backwards to join spiral lamina; a few septa do not reach the spiral lamina and curve backwards to meet previous ones; about 8–9 septa occur in the first whorl, 16–19 in the second, and 22–29 in the third; chambers higher than long and almost crescentic in shape; chamber indices vary from 2/1 to 6/1.

Material. Microspheric form has not been found. Megalospheric forms are common at some horizons in Rock Unit IV.

Remarks. O. libyca thebensis subsp. nov. mainly differs from *O. libyca libyca* in having a rather smooth surface, a swollen polar knob, very thin spiral lamina and septa, a much thinner test, and in lacking surface granules and high ridges.

Distribution. In the Gebel Gurnah Section, *O. libyca thebensis* occurs in the upper Lower Eocene.

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SECONDARY CHANGES IN MICRO-ORNAMENTATION OF SOME DEVONIAN AMBOCOELIID BRACHIOPODS

by ANDRZEJ BALIŃSKI

ABSTRACT. Studies on some species of the Ambocoeliidae from the Devonian of Poland have shown that their micro-ornamentation may be completely changed by secondary factors such as weathering, which leads to the separation of initially invisible coarse-crystalline structures, known as microspines, from the primary shell layer. Thus, secondary microspinosity appears on the surface of originally smooth or radially ornamented specimens. The recognition of primary and secondary micro-ornamentation is shown to be important in taxonomic studies. Comparative studies show that the microspines in the Ambocoeliidae are probably homologous to the microspines *sensu stricto* in other representatives of the Spiriferida.

ON the basis of data drawn from the literature, representatives of the Ambocoeliidae may be divided in regard to micro-ornamentation into forms with (*a*) radial ornamentation, (*b*) microspines, and (*c*) quite smooth. All three types of micro-ornamentation are considered as primary and considerable specific and generic taxonomic importance is ascribed to them.

As shown by observations on some ambocoeliid species from the Devonian of Poland, e.g. *Ambothyris infima* (Whidborne), *Crurithyris inflata* (Schnur), *C. jurkowicensis* Baliński, and *Ilmenia hians* (Buch), the character of the micro-ornamentation may be completely changed by secondary factors (e.g. weathering) even in a single specimen. The progressive process of weathering leads to a gradual separation, from the primary shell layer, of originally invisible, coarse-crystalline structures called microspines, which form a characteristic micro-ornamentation on the surface of weathered specimens known as microspinosity. Complying with the accepted taxonomic principles, one could, therefore, assign the weathered (with microspines) and unweathered (with the primary micro-ornamentation preserved in the form of capillae, or quite smooth) specimens of the same species to different genera.

Since the problem of the microspines in the ambocoeliids has not so far been explained conclusively, the term microspines, as applied to the ambocoeliids, will be used herein in quotation-marks ('microspines'), so as to distinguish them from the true microspines, which occur in other forms, e.g. *Nucleospira lens* (Schnur) or *Reticulariina spinosa* (Norwood and Pratten).

Material and techniques

A major part of this study was based on the specimens of the following four Middle Devonian (Givetian) species from the Holy Cross Mountains, Poland: *Ambothyris infima* (Whidborne), *Crurithyris jurkowicensis* Baliński and *Ilmenia hians* (Buch) from the Jurkowice-Budy (Baliński 1973), and *Crurithyris inflata* (Schnur) from the Skały (Biernat 1966). Specimens of *Nucleospira lens* (Schnur) and *Proreticularia dorsoplana* Gürich from the Middle Devonian of Swietomarz-Sniadka, Holy Cross Mountains (Gürich 1896), were used for comparative studies.

[Palaeontology, Vol. 18, Part 1, 1975, pp. 179–189, pls. 32–35.]

All specimens studied were obtained from the shales or weathered marly limestones by washing and studied with a JSM-2 scanning electron microscope. All specimens were cleaned ultrasonically and coated in two stages with carbon and gold.

SECONDARY CHANGES IN MICRO-ORNAMENTATION OF SOME AMBOCOELIIDS

Ilmenia hians (Buch)

A distinct micro-ornamentation in the form of radial capillae covering the entire shell from beak to the anterior margin (Pl. 32, figs. 1 (bottom part of the figure), 4; text-fig. 1A) is visible on the specimens with a well-preserved primary shell layer. These capillae (five–nine per mm) are limited to the primary shell layer though a few specimens show slight indication of them on the secondary shell layer (Pl. 32, fig. 1 (top part of the figure)).

Specimens from scree or a porous rock are generally etched to a varying degree as a result of the action of water containing various acid residues (e.g. HCO_3^-, humic acids, etc.), and progressive weathering sometimes leads to a complete change in primary micro-ornamentation. In the first stage the characteristic, elongate corrosion pits, which on enlargement reveal a fibrous secondary shell layer, appear on the ridges of capillae (Pl. 32, fig. 1 (bottom part of the figure); text-fig. 1B). Further weathering causes a corrosion of capillae over their entire length as deep as the secondary shell layer. Only the streaks of the primary shell layer, which form furrows between capillae in the uncorroded part, remain intact. Thus, a complete inversion of the primary micro-ornamentation occurs and the primary prominent elements (capillae) become replaced by grooves and vice versa, the ridges formed of the primary shell layer correspond to the primary grooves between capillae (Pl. 32, fig. 1 (central part of the figure); Pl. 33, fig. 1; text-fig. 1C).

The resistance to solution of the primary shell layer in intercapillary grooves should be ascribed to the coarsely crystalline structures arranged in precise radial rows between capillae. With progressive weathering the coarsely crystalline structures separate more and more from the primary shell layer, forming a characteristic micro-ornamentation described in some ambocoeliids as a microspinosity (Pl. 32, fig. 5). Thus, a single specimen may have two completely different types of micro-ornamentation, namely, capillae (primary) and 'microspines' (secondary) (Pl. 32, fig. 1 (the lower- and uppermost parts of the figure)). The character of 'microspinosity' in *Ilmenia hians* (Buch) is particularly like that in *Ilmenispina hanaica* Havlíček

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EXPLANATION OF PLATE 32

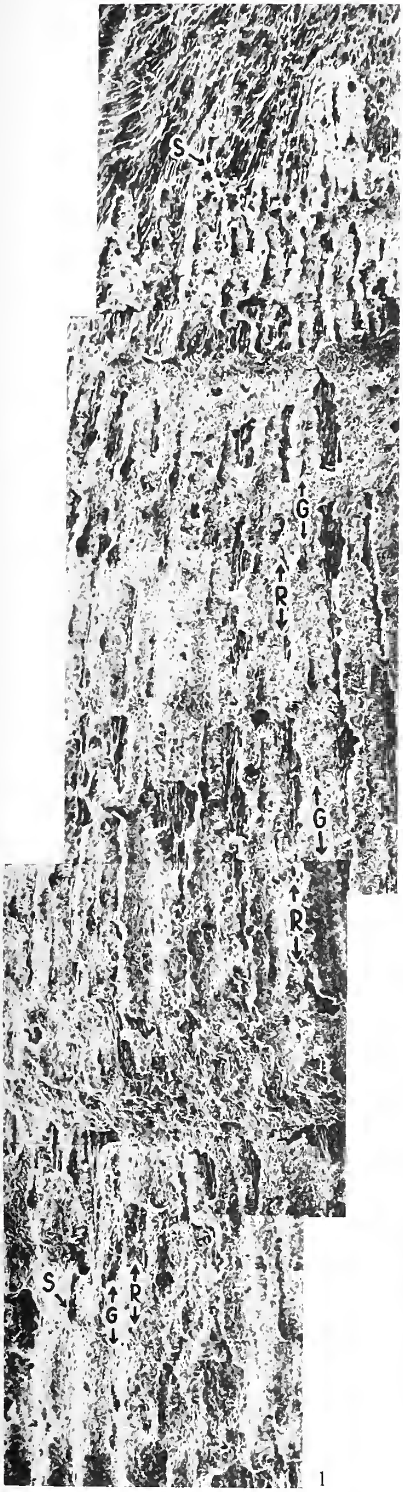
Fig. 1. Scanning electron micrograph. Consecutive stages of changes in micro-ornamentation on the brachial valve of *Ilmenia hians* (Buch), umbonal part at the top of figure (see also fig. 4), ×50.

Fig. 2. Dorsal and lateral views of shell of *Proreticularia dorsoplana* Gürich, ×4.

Fig. 3. Dorsal and lateral views of shell of *Nucleospira lens* (Schnur), ×4.

Figs. 4, 5. Two brachial valves of *I. hians* (Buch). 4, showing primary. 5, showing secondary micro-ornamentation; ×7, ×6 respectively.

Abbreviations on all plates: C—trace of central canal; G—intercapillary grooves; PL—primary shell layer; R—ridges of capillae; S—'microspines'; SL—secondary shell layer.



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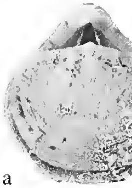

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3a

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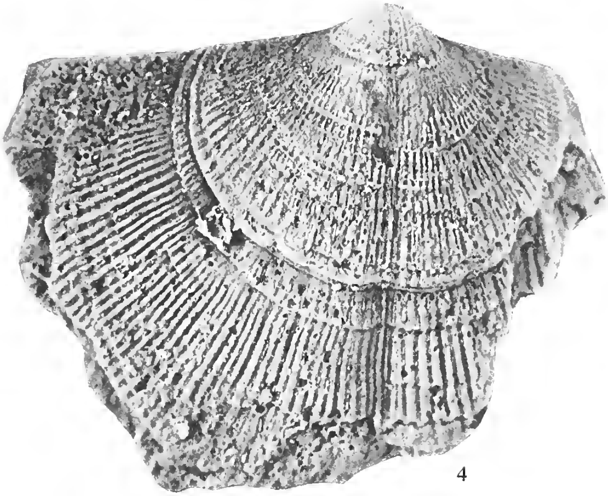

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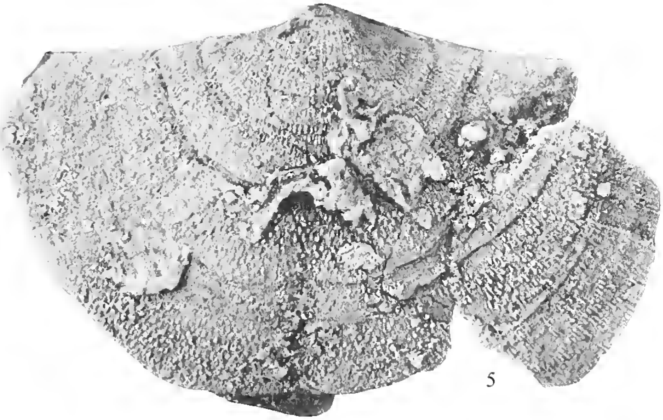

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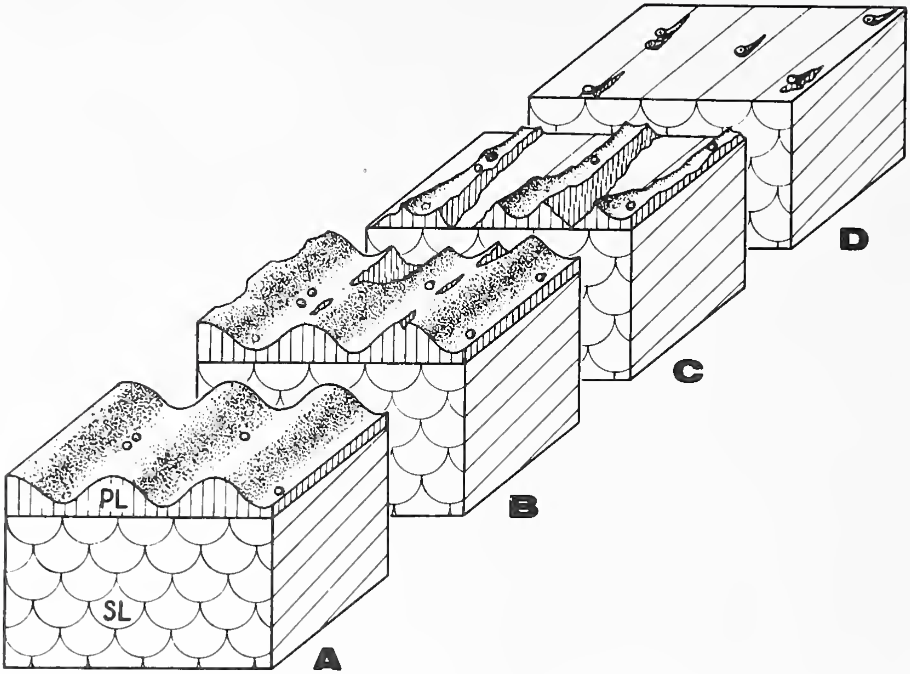
BALIŃSKI, Spiriferid brachiopods



TEXT-FIG. 1. Diagram of secondary changes in micro-ornamentation of *Ilmenia hians* (Buch) (not in scale); PL—primary shell layer; SL—secondary shell layer.

from the Givetian of Moravia (Havlíček 1959, p. 182, pl. XXVII, figs. 15, 17). It is very likely that the genesis of the 'microspinosity' is identical in the two forms.

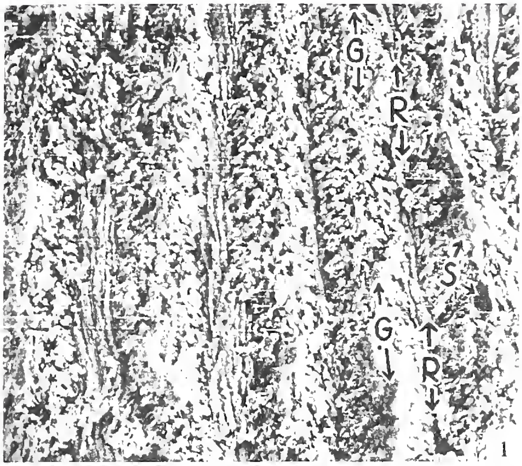
A general pattern of the distribution of 'microspines' in *I. hians* sometimes resembles a chequerboard. Commonly, however, they are fairly irregularly arranged in radial streaks between capillae, with closely spaced 'microspines' distributed along several different radial lines.

Ambothyris George and *Crurithyris* George

Most species of the genus *Crurithyris* George and a representative of a related genus, *Ambothyris infima* (Whidborne) (Baliński 1973), are marked by a presence of 'microspines', which make up an important diagnostic character, interpreted as a primary ornamental feature. The present studies indicate, however, that this type of ornamentation was developed secondarily in a similar way as in *I. hians.*

EXPLANATION OF PLATE 33

Figs. 1–6. Scanning electron micrographs. 1, an inversion of the primary micro-ornamentation on the pedicle valve of *Ilmenia hians* (Buch). Ridges, formed of the primary shell layer originally corresponding to intercapillary grooves, are visible. The secondary shell layer observed in depressions (primary-capillae), ×130. 2, 5, various morphological types of 'microspines' in *I. hians* (Buch), ×800. 3, 4, 6, various morphological types of 'microspines' in *Ambothyris infima* (Whidborne). The primary shell layer observed in all specimens; ×800, ×2400, ×800 respectively.



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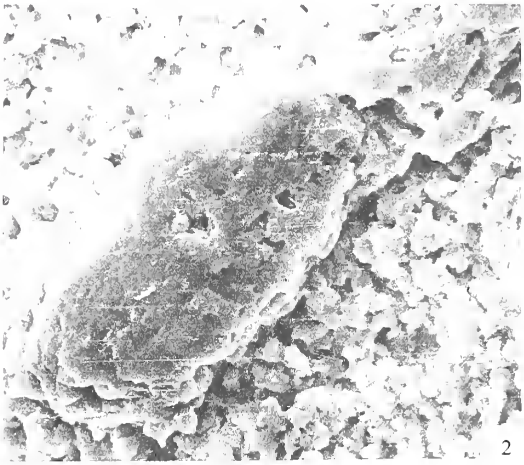

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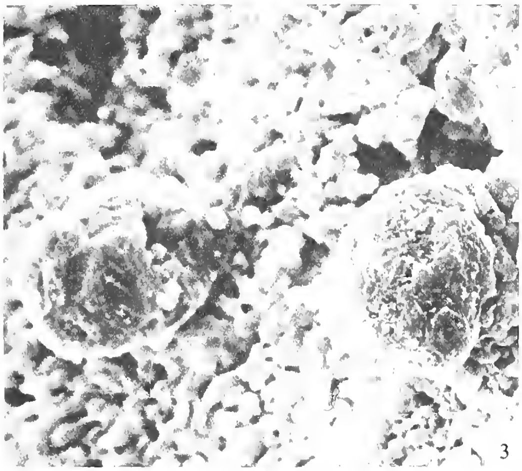

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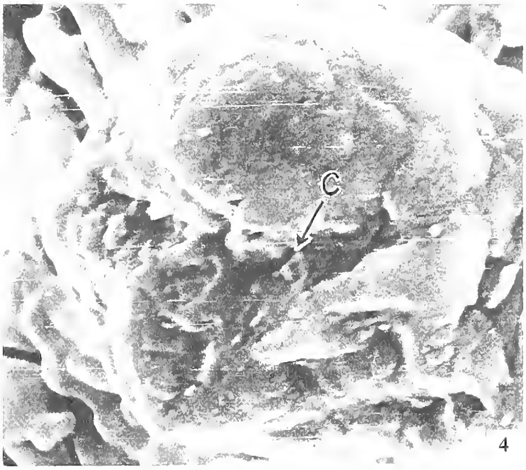

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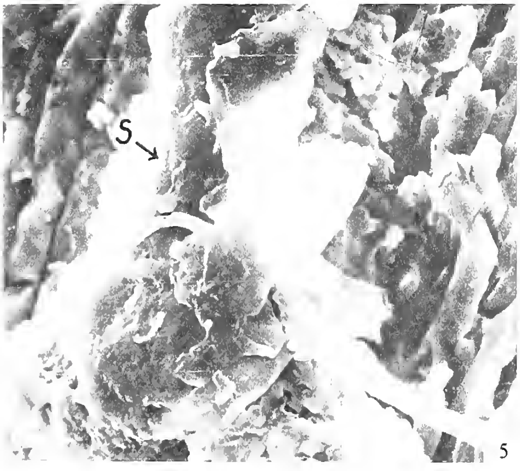

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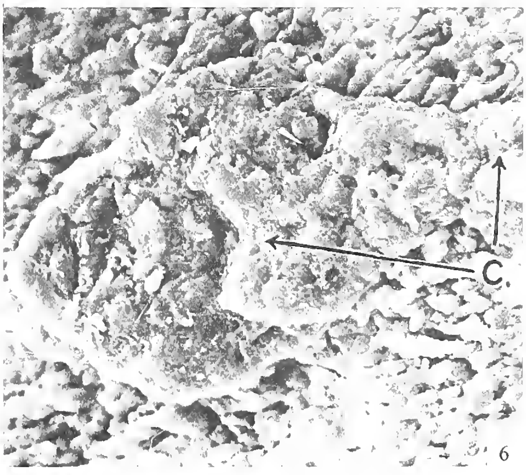

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BALIŃSKI, Ambocoeliid brachiopods

In some specimens of *Crurithyris inflata* (Schnur) with a well-preserved primary shell layer, no 'microspines' are visible (Pl. 34, fig. 2 (bottom half of the micrograph)). Upon weathering a fibrous, secondary shell layer is exposed, with the simultaneous separation of initially invisible, coarsely crystalline structures embedded in the primary shell layer (Pl. 34, fig. 1).

The distribution of 'microspines' in *Ambothyris* and *Crurithyris* is not identical. In *C. inflata* a concentric distribution, conformable with growth layers, is the predominant type of distribution (Biernat 1966, p. 123, pl. XXIX, fig. 9), while in *A. infima* and *C. jurkowicensis* a radial distribution predominates, as in *I. hians*. The concentric distribution of 'microspines' in *C. inflata* was probably emphasized by an exfoliation of concentric growth layers overlapping each other.

MORPHOLOGY OF 'MICROSPINES'

In the ambocoeliids studied, the 'microspines' display a considerable differentiation resulting from the morphogenetic variability and differences in the state of preservation.

In *A. infima* (Whidborne) and *C. inflata* (Schnur) the 'microspines' are somewhat pipe-like in general outline. In their basal part they are elongate and fusiform, but anteriorly they greatly increase in size and rise (Pl. 33, figs. 3, 4, 6; Pl. 34, figs. 4, 6; Pl. 35, figs. 1-4). They are generally devoid of a distinct trace of central canal; its presumed traces only very rarely being observed (Pl. 33, figs. 4, 6; Pl. 35, fig. 2).

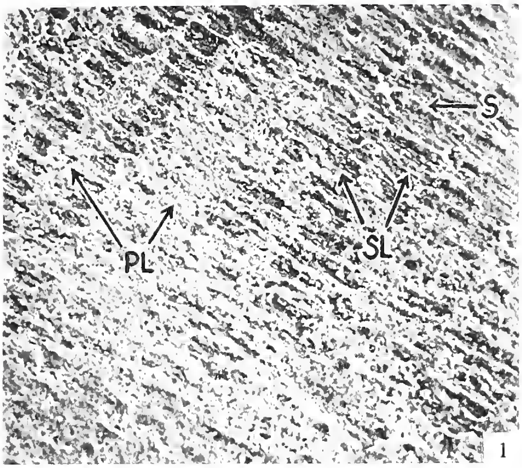
In *I. hians*, much as in *Crurithyris*, the 'microspines' consist of a prostrate basal part and an erect anterior portion (Pl. 33, fig. 5). 'Microspines' (probably strongly corroded), differing considerably morphologically from those described above, are also observed in all the ambocoeliids studied. They are elongate, fusiform, and extended anteriorly. When viewed highly magnified, they display a coarsely crystalline structure and a lack of any traces of central canal (Pl. 33, fig. 2; Pl. 34, figs. 3, 5).

DISCUSSION

In the ambocoeliids, like in other spiriferids, the 'microspines' occur only in the primary shell layer. According to many authors (George 1931; Williams 1956; Vandercammen 1959), all these elements are spines *sensu stricto*, since they had to contain the appendices of the mantle epithelium in their cavities. They might function for a relatively short time and only along the anterolateral margins of the mantle.

EXPLANATION OF PLATE 34

Figs. 1-6. Scanning electron micrographs. 1, 2, a primary (fig. 2—bottom half of the micrograph) and secondary (fig. 1—upper part of the micrograph) micro-ornamentation in *Crurithyris inflata* (Schnur), ×50. 3, 4, various morphological types of 'microspines' in *C. inflata*. Primary shell layer not preserved, only the crystals of the secondary shell layer visible, ×800. 5, 'microspines' of *C. jurkowicensis* Baliński, ×800. 6, 'microspines' of *Ambothyris infima* (Whidborne). A weathered primary shell layer visible, ×240.



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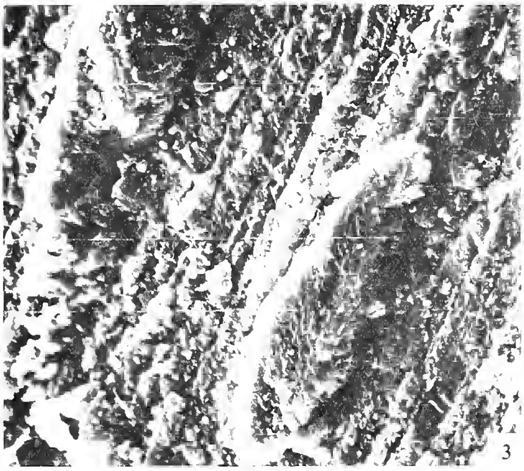

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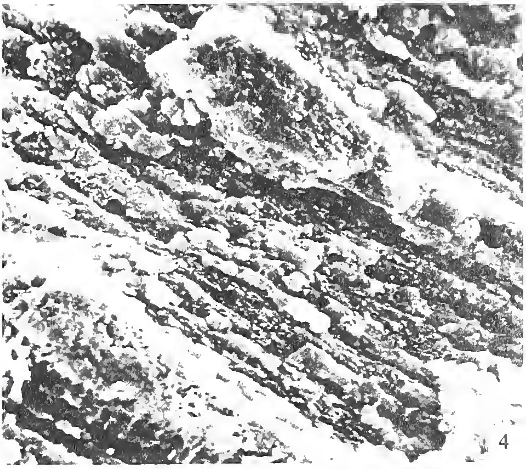

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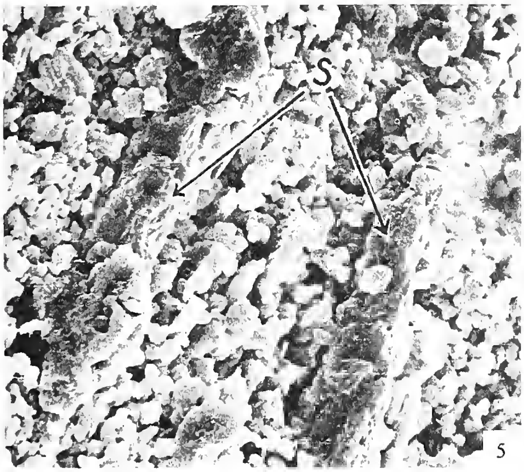

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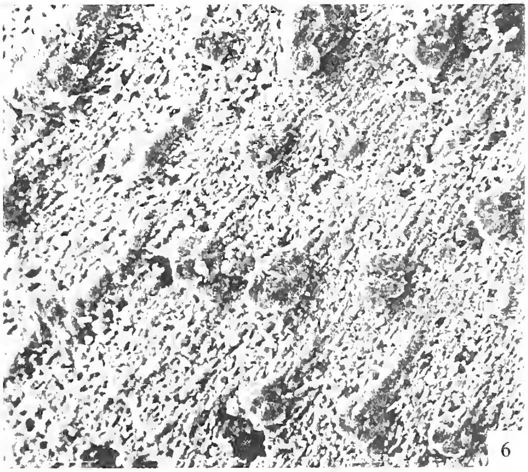

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BALIŃSKI, Ambocoeliid brachiopods

During the shell secretion, these appendices were retracted and the cavities of spines lost their contact with the shell interior (George 1931).

However, the 'microspines' of the ambocoeliids are distinctly different morphologically from analogous structures of many other representatives of the Spiriferida. In *Proreticularia dorsoplana* Gürich (Pl. 32, fig. 2) and *Nucleospira lens* (Schnur) (Pl. 32, fig. 3) they are very long, some of them reaching 0·5 mm, and bear a very distinct trace of central canal (Pl. 35, figs. 5–7). Also long tube-like spines are observed in *Reticulariina spinosa* (Norwood and Pratten) (Campbell 1959, pp. 356–358, pl. 59, figs. 10–14; pl. 60, figs. 4, 6), *Altiplectus*(?) sp. (Ivanova 1971, p. 32, text-fig. 14), and *Spiriferina* d'Orbigny (Ivanova 1971, p. 32, text-fig. 12).

The lack of unequivocal traces of the central canal in 'microspines' in the ambocoeliids studied may be explained by their filling with shell substance by the retracting appendices of mantle epithelium and by the state of preservation. In *Ambothyris infima*, however, the 'microspines' are quite distinct and some of them even display traces of a presumed central canal (Pl. 33, fig. 4; Pl. 35, figs. 2–4).

Despite the lack of unequivocal evidence, it seems that the 'microspines' in the ambocoeliids may be spines *sensu stricto* and not just structures comparable with the pustules of the terebratellacean *Kingena* Davidson (Owen 1970, pp. 41–42, pl. 13, figs. 3–5). The 'microspines' of the ambocoeliids seem to be specialized structures, homologous with true spines of other spiriferids (e.g. *N. lens* (Schnur) and *R. spinosa* (Norwood and Pratten)).

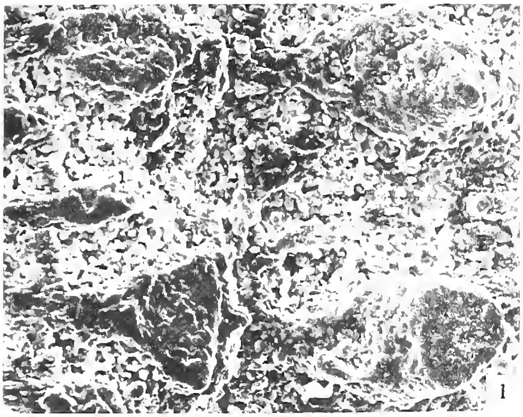
The question occurs whether the 'microspines' of the ambocoeliids were originally embedded completely in the primary shell layer or projected above its surface. The size of the 'microspines' in *Crurithyris* suggests that they did not project above this layer (Pl. 34, figs. 3–5), but in *A. infima* some of them are long, reaching 0·15 mm (Pl. 35, figs. 1–4), and it seems unlikely that the primary shell layer would have been thick enough for the 'microspines' to be completely embedded in it.

In some specimens of *I. hians* with a well-preserved primary ornamentation (capillae), distal parts of the 'microspines' are seen in intercapillary grooves (Pl. 32, figs. 1, 4), while in the remaining specimens they are invisible. This might indicate that the length of 'microspines' was subject to considerable variability within one and the same species.

Spinous elements, somewhat similar to the 'microspines' of the ambocoeliids are observed in some representatives of the Spiriferida. Such structures occur in *Phricodothyris* (Kozłowski 1914, pp. 73–74, text-fig. 18*d*), *Hysterolites*, *Paraspirifer*, *Spinocyrtia*, *Emanuella*, *Gurichiella*, and *Elytha* (see Vandercammen 1959), as well as in *Cyrtina* and *Squamularia* (see Ivanova 1962). The lack of data on the structure of microspines of these genera makes any detailed comparisons with the 'microspines'

EXPLANATION OF PLATE 35

Figs. 1–7. Scanning electron micrographs. 1, 2, 'microspines' of *Ambothyris infima* (Whidborne), ×240, ×800 respectively. 3, 4, lateral and oblique-lateral views of 'microspines' of *A. infima*; ×480, ×800 respectively. 5, 6, microspines of *Nucleospira lens* (Schnur); ×50, ×150 respectively. 7, microspines of *Proreticularia dorsoplana* Gürich, ×800.



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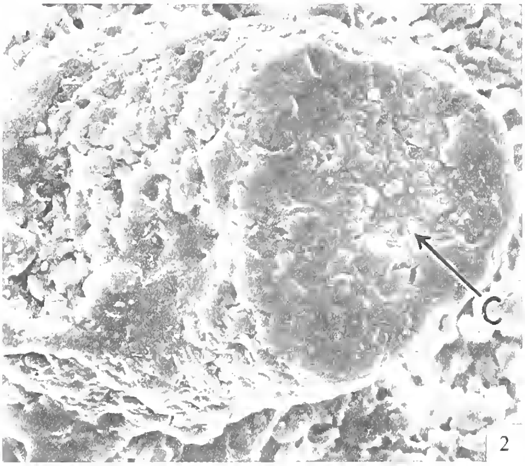

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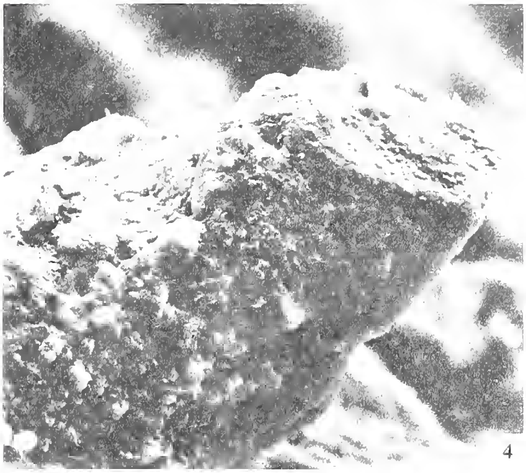

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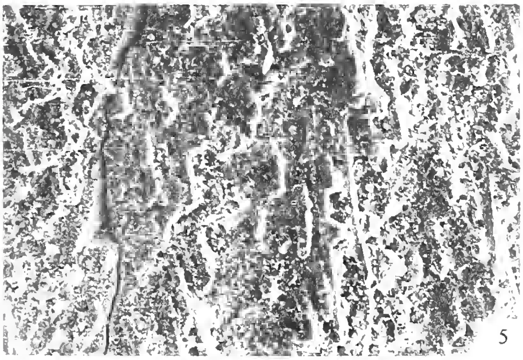

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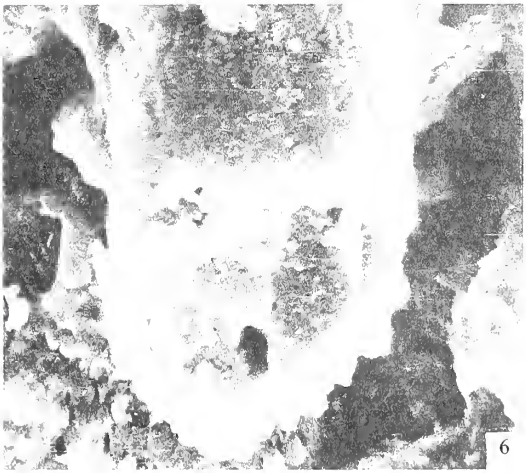

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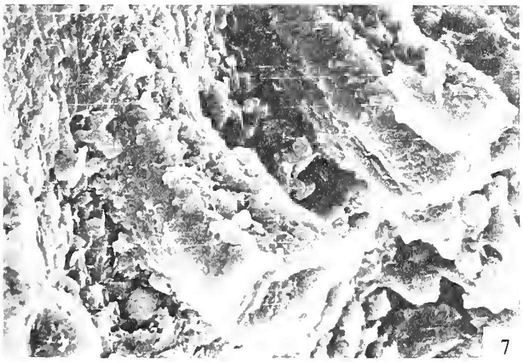

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of the ambocoeliids on the one hand and with the microspines *sensu stricto* on the other impossible for the time being.

Despite considerable morphological differences between the spines in various spiriferids they might perform a very similar function. It is very likely that the spinosity in the Spiriferida is much more common than believed so far. Along with the advancing studies on a better-preserved material, further examples of several varieties of spinosity may be found within this group of brachiopods, but specimens are necessary with a very well-preserved primary shell layer susceptible to exfoliation.

TAXONOMIC IMPORTANCE OF MICRO-ORNAMENTATION

The examples of secondary changes in micro-ornamentation, described herein, may have important consequences to the taxonomy of this group. The occurrence of micro-ornamentation of various types in one and the same specimen, previously interpreted as a primary character, commonly taken as important at the generic level, compels investigators of the Spiriferida to be extremely cautious. The interpretation of micro-ornamentation accepted so far might cause the erection of synonymic taxa based only on the differences in micro-ornamentation, such as, for example, *Ilmenia* Nalivkin and *Ilmenispina* Havliček. Nevertheless, it seems that both the primary and secondary micro-ornamentation might be of a considerable taxonomic importance. However, in each case, equivalent analogous elements should be compared, with the consideration of their genesis and state of preservation.

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AMMONITES FROM THE DOULTING CONGLOMERATE BED (UPPER BAJOCIAN, JURASSIC) OF SOMERSET

by C. F. PARSONS

ABSTRACT. An examination of ammonites from the Doulting Conglomerate Bed (Doulting, Somerset, England) has shown that this bed is Subfurcatum rather than Garantiana Zone in age. This is only the second fully authenticated area of outcrop of this Upper Bajocian Zone in England. The ammonites are described, and their bearing on the correlation of the Upper Inferior Oolite from the Mendips north to the Cotswolds is discussed.

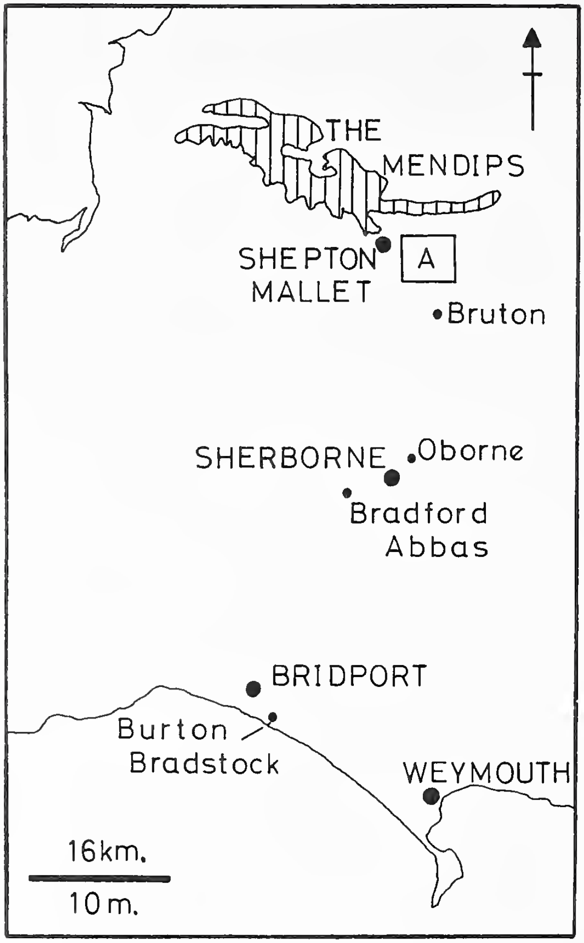
THE Subfurcatum Zone of the Upper Bajocian is probably the most poorly represented of any British Jurassic Zone. The area of outcrop of rocks of this age is so small that it has been suggested that *Strenoceras subfurcatum* (Zieten) was restricted by ecological rather than stratigraphic factors (Stamp 1925). However, the limited lateral range of the Subfurcatum Zone in Britain is merely due to erosion and non-deposition, since beds of this age are widespread elsewhere in Europe. Until recently the only fully authenticated occurrence of the Subfurcatum Zone in England was in the Cadomensis Bed to the east of Sherborne, Dorset (Hudleston and Woodward 1885, p. 193; Buckman 1893, p. 501), and its lateral equivalent to the west, the Irony Bed, which is well seen at Half-Way House and Bradford Abbas, Dorset (Torrens 1969*a*, p. A28; Buckman 1893, p. 487); see text-figs. 1 and 2. It has now been possible to confirm the occurrence of Subfurcatum Zone ammonites in the Red Conglomerate Bed of south Dorset (Gatrall, Jenkyns and Parsons 1972) and it would seem likely that much of the highly condensed Red Conglomerate–Irony Bed horizon found over Dorset and south Somerset is of this age—see Table 1 for Zonal scheme used here.

TABLE 1. Zones and Subzones of the Upper Bajocian Substage in England.

Zones	*Subzones*
Parkinsoni	Bomfordi Truellei
Garantiana	Acris Dichotoma
Subfurcatum	Baculata Polygyralis Banksi

The only other record of Subfurcatum Zone ammonites in the British Isles is from the Garantiana Clay of the Inner Hebrides. Buckman attributed this bed to both the Subfurcatum and Garantiana Zones (Lee 1920). A recent revision of the ammonites

[Palaeontology, Vol. 18, Part 1, 1975, pp. 191–205, pl. 36.]

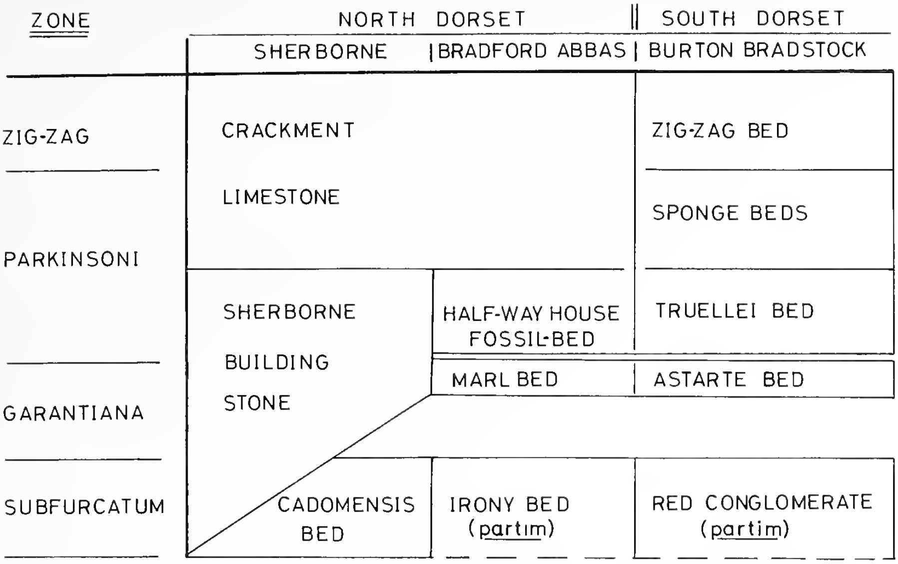


TEXT-FIG. 1. An outline map of part of southern England, showing the main localities mentioned in the text. The square A marks the area shown in text-fig. 3.

has suggested that the Garantiana Clay is solely Subfurcatum Zone in age (Morton 1971). However, the great similarity between the Garantiana Zone *Strenoceras* (*Garantiana*)/*Strenoceras* (*Pseudogarantiana*) dimorphic group and the *S.* (*Baculatoceras*)/*S.* (*Strenoceras*) group of the Subfurcatum Zone would preclude their separation on the basis of the present fragmentary and poorly preserved specimens. I remain unconvinced of the Subfurcatum Zone age of the Garantiana Clay.

A NEW OCCURRENCE OF THE SUBFURCATUM ZONE

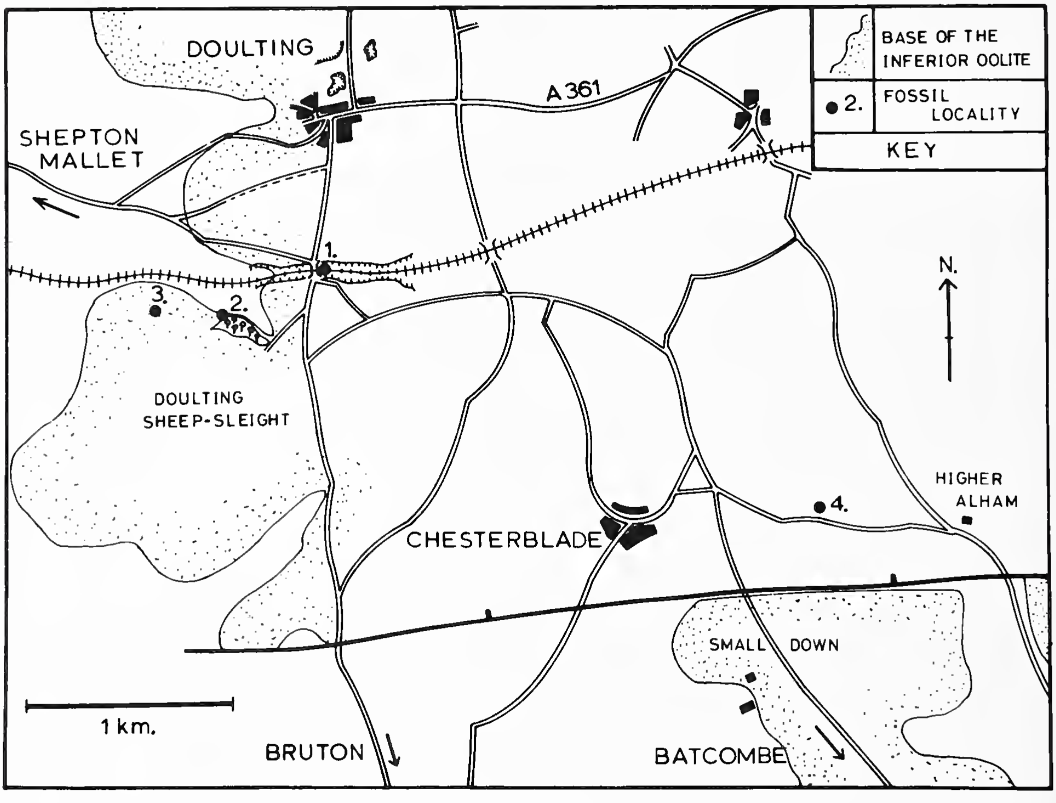
Ammonites recently collected, together with those from existing museum collections, have proved that the Doulting Conglomerate Bed (Richardson 1907) is Subfurcatum rather than Garantiana Zone in age. The Conglomerate Bed at Doulting (near Shepton Mallet, Somerset) is a highly fossiliferous, bioclastic limestone, containing



TEXT-FIG. 2. The lithostratigraphic subdivisions of the Upper Inferior Oolite as seen in Dorset, taken from S. Buckman (1893 and 1910), Richardson (1930), and Torrens (1969*a*).

serpulid- and limonite-encrusted lithoclasts (cf. the 'Snuff-boxes' described by Gatrall *et al.* 1972). It is some 0·35 m thick and is now only poorly exposed. When described by Richardson (1907, 1916) it was still to be seen at the base of the Inferior Oolite at Doulting railway cutting (National Grid Reference ST 645 425—Locality 1, text-fig. 3), where it rests unconformably on the Upper Lias (Bed VI, Richardson 1907, p. 390). In both of his papers Richardson correlated the Conglomerate Bed with the Upper Trigonia Grit of the Cotswolds, which is Garantiana Zone in age (Arkell 1956, p. 31). The only ammonite recorded by Richardson (1907, p. 300) in his two accounts of this bed was a single specimen of *Leptosphinctes* ('*Perisphinctes*') cf. *davidsoni* (S. Buckman), which is now in the Reading University Collections (LRS 3094). However, subsequent to his 1907 publication, Richardson produced a critical catalogue of the John Phyllis Collection, housed in the Shepton Mallet Museum (Richardson 1908, pp. 516–517). Here he listed several ammonites of Sauzei, Humphriesianum, Subfurcatum, and Garantiana Zone age, supposedly from the Doulting area, which he considered to have come from the Conglomerate Bed. The Shepton Mallet geological material has since been stored in a basement. Many labels have been destroyed or lost, making much of the material valueless. However, several ammonites do still exist which can be identified from their labels as coming from the Phyllis Collection. One, *Otoites* cf. *sauzei* (d'Orb.), possibly that recorded by Richardson, still has an original label claiming its locality as the Doulting district. The matrix suggests that this specimen came from either the Pecten Bed of the Cole Syncline, Bruton, Somerset (Richardson 1916), or from further south in the Sherborne district of north Dorset. Two other ammonites, both septate nuclei, and showing the characteristic Conglomerate Bed matrix, are undoubtedly amongst those listed by Richardson. These, *Stephanoceras* sp. and *Leptosphinctes* aff. *davidsoni*, are discussed in greater detail below. On the available evidence from museum material there thus seemed little reason to doubt Richardson's Garantiana Zone correlation for the Conglomerate Bed, provided that one considered the *Stephanoceras* sp. as reworked. However, a unique collection of ammonites made subsequently by C. Cornfield during the course of an undergraduate mapping exercise has changed this interpretation. Specimens of the following were collected from localities 2 and 3 (see text-fig. 3): *Teloceras banksi* (J. Sow.), *Cadomites deslongchampsi* (d'Orb.), *Strenoceras* (*Strenoceras*) cf. *subfurcatum* (Zieten), and *Orthogarantiana* sp. As will be shown below, the total fauna of the Conglomerate Bed can only be reconciled with the basal Banksi Subzone of the Subfurcatum Zone. This then is the first English record of the Subfurcatum Zone, outside of Dorset.

Unfortunately exposures of the Conglomerate Bed are now very poor, thus locality 2 (text-fig. 3) is nothing more than material excavated by badgers, whilst locality 3 is a small natural exposure along the edge of the scarp of Doulting Sheepsleight. However, all the ammonites described below have the highly characteristic matrix of the Conglomerate Bed within their body chambers and there thus can be no question as to their correct horizon. Similarly they cannot be considered reworked, although their fragmentary and serpulid encrusted state does suggest that they were lying on the sea floor for some time before being incorporated in any sediment.



TEXT-FIG. 3. A sketch map of the area south of Doulting, showing the localities mentioned in the text.

SYSTEMATIC DESCRIPTIONS

Abbreviations. Numbers preceded by the following letters refer to specimens in these Institutions and collections:

BMNH	British Museum (N.H.), London.
IGS	Institute of Geological Sciences, London.
L	Manchester City Museum.
LR	Richardson Collection, Reading University.
CP	The author's collection, Liverpool University.

Superfamily STEPHANOCERATACEAE Neumayr, 1875
Family STEPHANOCERATIDAE Neumayr, 1875
Genus CADOMITES Munier-Chalmas, 1892
Cadomites (*Cadomites*) *deslongchampsi* (d'Orbigny)

Plate 36, fig. 4*a* and 4*b*; text-fig. 4

1846 *Ammonites deslongchampsi* Defrance; d'Orbigny, p. 405, pl. 138, figs. 1 and 2.
1909 *Ammonites* (*Coeloceras*) *deslongchampsi* (d'Orb.); Douvillé, pl. 132.
1952 *Cadomites deslongchampsi* (d'Orb.); Arkell (1951–1958), p. 80, text-fig. 21.

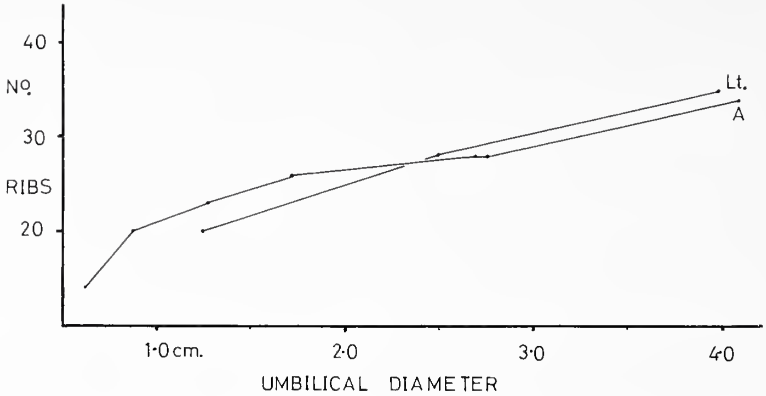
Material. One specimen, BMNH C 77767, collected by C. Cornfield from loc. 3.

Dimensions.

Diameter (D)	Whorl height (Wh)	Whorl width (Wb)	Umbilical diameter (Ud)	Number of primary ribs per whorl (Np)
10·4 cm	3·32 (32%)	3·94 (38%)	4·1 (39%)	44
8·8	3·4 (39%)	4·3 (49%)	2·76 (31%)	38

Description. A complete ammonite, showing the remains of a flared mouth border. The specimen has lost all the shell from its body chamber, but is well preserved on its inner whorls. A moderately coronate ammonite, it shows a distinct uncoiling and retraction of the body chamber, which extends for two-thirds of a whorl. The broadly arched venter is marked on the umbilical edge by sharp tubercules on the internal cast, and where shell is still preserved, spines. The long, sinuous primary ribs divide at the tubercules into three to five fine, slightly prorsiradiate secondaries. The primary rib density per whorl is only moderate for the genus, but it is strictly comparable with that of the lectotype of this species (see text-fig. 4).

Remarks. Allowing for the loss of shell, this specimen is very close to the lectotype of *C. deslongchampsi* figured in Palaeontologia Universalis (Douvillé 1909, No. 132) and later refigured by Arkell (1951–1958, p. 80). The lectotype from the Bayeux Oolite of Normandy is more likely to be Subfurcatum/Garantiana Zones in age than Parkinsoni Zone as suggested by Arkell (1951–1958, p. 79). The matrix, a densely 'iron-shot' oolitic limestone, corresponds more closely with this former horizon than with the Parkinsoni Zone, Truellei Subzone, which is represented in Normandy by a more sporadic 'iron-shot', the limonite ooliths being concentrated in clusters (Rioult 1964). This species is relatively common at the middle of the Subfurcatum Zone in the Sherborne area. Specimens very close to that figured here have been found recently at Oborne Wood, Sherborne (ST 648 188—see Whicher and Palmer 1971), in an horizon equivalent to bed 4, Frogden Quarry, Sherborne (Buckman, 1893,



TEXT-FIG. 4. Number of primary ribs per whorl, plotted against umbilical diameter, for *Cadomites deslongchampsi* (d'Orb.).
Lt. = lectotype, A = figured specimen, BMNH C 77767.

p. 500). This horizon falls within the Polygyralis Subzone of the Subfurcatum Zone (Parsons *in* Sturani 1971, p. 49). I have found no trace of the specimen recorded by Richardson as *Cadomites* aff. *deslongchampsi* from the Conglomerate Bed, in the Shepton Mallet Collections (Richardson 1908, p. 516) and it must be assumed lost.

Genus STEPHANOCERAS Waagen, 1869
Stephanoceras (*Stephanoceras*) sp.

Plate 36, fig. 2

1908 *Stepheoceras* aff. *umbilicus* (Quenstedt); Richardson, p. 517.

Material. One unnumbered specimen in the Shepton Mallet Museum.

Dimensions. Maximum diameter (wholly septate) = 5·8 cm. Due to distortion, whorl width and height measurements are not given.

D	Ud	Np
5·0 cm	1·8 (36%)	21
4·6	1·7 (37%)	22
—	0·8	20
	0·35	18

EXPLANATION OF PLATE 36

All specimens, except 1*a* and 1*b*, are coated with ammonium chloride.

Fig. 1*a*, 1*b*. *Teloceras banksi* (J. Sowerby), BMNH C 7768. Doulting Conglomerate, Doulting Sheep-sleight, ×0·5.

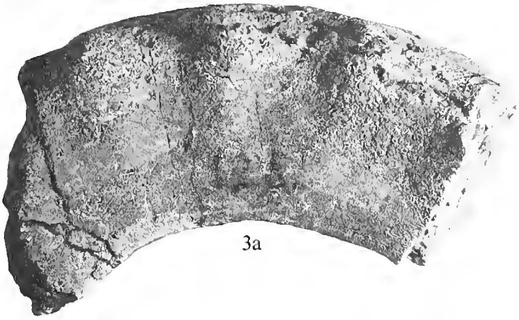
Fig. 2. *Stephanoceras* (*Stephanoceras*) sp. Shepton Mallet Museum (Doulting Conglomerate), ×1·0.

Fig. 3. *Leptosphinctes* (*Leptosphinctes*) aff. *davidsoni* (S. Buckman), Shepton Mallet Museum (Doulting Conglomerate), ×1·0.

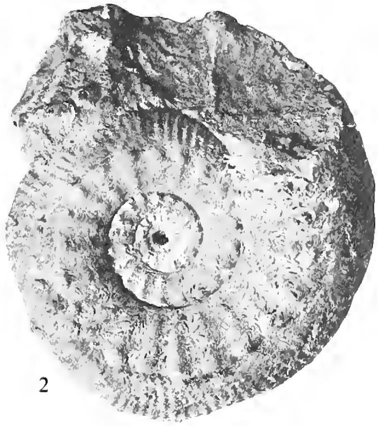
Fig. 4*a*, 4*b*. *Cadomites* (*Cadomites*) *deslongchampsi* (d'Orb.), BMNH C 77767, Doulting Conglomerate, Doulting Sheep-sleight, ×0·5.

Fig. 5. *Strenoceras* (*Strenoceras*) cf. *subfurcatum* (Zieten), BMNH C 77769, Doulting Conglomerate, Doulting Sheep-sleight, oblique view, ×1·0.

PLATE 36

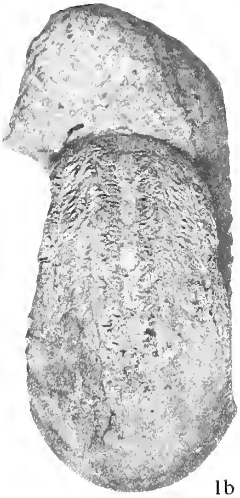

3a

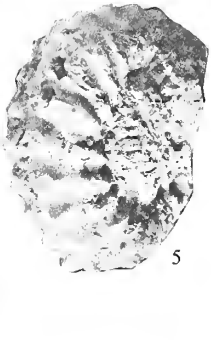

3b


2


4


1a


1b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PARSONS, English Bajocian ammonites

Description. A slightly distorted, coronate, stephanoceratid nucleus, which is totally septate. All the shell has been lost, there is thus no indication, in the form of 'continuation marks' as to its original maximum size. The primary ribs are fairly short, straight, and branch from a strong tubercule into three to four prorsiradiate secondaries.

Remarks. The primary rib density per whorl is low for this size of stephanoceratid nucleus. The closest match is with '*Stephanoceras*' *calix* (W. Smith), an uninterpretable lectotype of which has been figured by Cox (1930, pl. xii, fig. 10). However, the small size and poor state of preservation of the figured specimen, taken together with the high degree of variability found within the Stephanoceratidae, precludes anything other than the most open nomenclature being used here.

This specimen is probably the same as that recorded by Richardson as *S.* aff. *umbilicus* (Quenst.) (Richardson 1908, p. 517). The type specimen of the latter species is an uninterpretable nucleus and is in any case very different. The exact horizon and locality of this specimen are not recorded, but the characteristic matrix of the Conglomerate Bed is unmistakable.

Genus TELOCERAS Mascke, 1907

Teloceras (*Teloceras*) *banksi* (J. Sowerby)

Plate 36, fig. 1*a* and 1*b*; text-fig. 5

1818 *Ammonites banksi* n. sp. J. Sowerby, p. 229, pl. 200.
1909 *Ammonites banksi* (J. Sow.); S. Buckman and 'Secretary', pl. 1.
1926 *Teloceras banksi* (J. Sow.); S. Buckman, pl. 660, A and B.

Material. One large fragment of body chamber BMNH C 77768, a small fragment of an internal whorl, C 78542, and a specimen of a third of a septate whorl, C 78541.

Dimensions. The larger, figured specimen is part of the body chamber of an individual which when complete was greater than 23·0 cm in diameter. It is 12·0 cm long and has primary ribs 5·0–5·5 cm long, with a whorl height of 7·7 cm (*c.* 33%) and a whorl width estimated as 16·0 cm (*c.* 68%).

The second largest specimen (C 78541) has an estimated original diameter in the order of 14·0 cm with a whorl width of 12·1 cm (*c.* 86%) and a whorl height of 6·0 cm (*c.* 43%).

Description. The fragment figured here (C 77768—Pl. 36, fig. 1*a*, *b*) represents the first quarter of the body chamber of a large species of the genus *Teloceras.* It was found by C. Cornfield on Doulting Sheep-sleight (ST 642 422, Locality 2, text-fig. 3) along with another smaller fragment of an inner whorl (BMNH C 78542), which is less easily identified. The three surviving primary ribs of the larger specimen are weak and are terminated by large blunt tubercules or nodes. There is no evidence of secondary ribs on the outer part of the whorl, but the impression of the venter of the preceding whorl shows numerous fairly coarse secondaries. There is an 80° angle between the umbilical wall and the venter, on the line of the tubercules, which together with the very flat curves of both walls gives an almost square cross-section. The matrix of the figured specimen is well 'iron-shot' and contains numerous small limonite stained oncolites (average length 0·9 cm) as well as numerous macro-fossils; *Sphaeroidothyris sphaeroidalis* (J. de C. Sow.), *Pleuromya* sp. etc. The smaller fragment (C 78542) has stronger, coarser primary ribs, distinct secondaries, and a sharper angle between the umbilical wall and the venter, which is also more arched. This

TEXT-FIG. 5. A tracing of the suture of a specimen of *Teloceras banksi* (J. Sow.), BMNH C 78542.

specimen also shows a nearly complete suture (text-fig. 5), which is comparable to that of other species of *Teloceras* (see Weisert 1932, text-figs. 30, 35, 37).

The third specimen (C 78541) comes from an old collection in the Department of Geology, University of Liverpool, and has now been donated to the British Museum. It has an original label attached claiming Doulting as its source and this is confirmed by its matrix, which is characteristic of the Conglomerate Bed. This specimen, although wholly septate, is well preserved and represents approximately one-third of the penultimate whorl of a specimen of *Teloceras*. It has virtually obsolescent primary ribs and prominent tubercules, from which branch four to five secondaries.

Remarks. All the specimens discussed here are comparable with the holotype of *Teloceras banksi* (BMNH 43910) and also to numerous topotypes of this species, which it has recently been possible to collect from a temporary section near Sherborne, Dorset (Whicher and Palmer 1971), from beds equivalent to Buckman's bed 5 at Frogden Quarry (Buckman 1893). The identification of these fragments is beyond doubt since no other species of *Teloceras* shows such a pronounced retraction of the body chamber to give the square cross-section, nor such coarse primary ribs fading to nodes on the outer whorls.

Superfamily PERISPHINCTACEAE Steinmann, 1890
Family PARKINSONIIDAE Buckman, 1920
Genus STRENOCERAS Hyatt, 1900
Strenoceras (*Strenoceras*) cf. *subfurcatum* (Zieten)

Plate 36, fig. 5

1830 *Ammonites subfurcatus* Schlotheim, E. F. von, m.s.; Zieten, p. 10, pl. VII, fig. 6*a–c*.
1928 *Strenoceras* (*Strenoceras*) *subfurcatum* (Schloth.); Bentz, pl. 14, fig. 1.
1956 *Strenoceras subfurcatum* (Schl.); Arkell, pl. 35, fig. 6—selects lectotype.

Material. One specimen (BMNH C 77769) from the Conglomerate Bed of Doulting (ex. C. Cornfield Collection).

Dimensions.

D	Wh	Wb	Ud	Np
3·7 cm	1·16 (31%)	1·4 (38%)	*c*. 1·65 (*c*. 45%)	24

Description. This important specimen was found by C. Cornfield at the same locality as the preceding specimens (Locality 2, text-fig. 3). This ammonite, with a third of a whorl of body chamber, of which an oblique view is shown here (Pl. 36, fig. 5), is unfortunately lacking its inner whorls. Enough, however, remains to show that it is typical of the *Strenoceras* microconch group. The sharp primary ribs (there are no signs of secondaries) are slightly prorsiradiate and are surmounted by two tubercules, one two-thirds of the way up the whorl flank and the other, a stronger tubercule or spine, on the venter. The two rows of ventral tubercules are separated by a shallow sulcus, whilst the lateral tubercules tend to be linked by a spiral ridge similar to that seen in the type of *S. bajocense* (Defrance)—see Arkell, Kummel and Wright 1957, fig. 381. The rib density although only estimated for one whorl is slightly low, with coarser ribs than are seen in most species of this genus.

Remarks. This specimen is close in gross morphology to the type of *S. bajocense* (see above); it is, however, here included in *S. subfurcatum* since this is the oldest available specific name. It would seem likely that most of the subsequently described species of this genus, such as *S. niortensis* (d'Orb.), are junior synonyms of this latter species. The corresponding macroconch to this microconch group is *S.* (*Garantiana*) *baculata* (Quenstedt), both of these two dimorphs being common in the Subfurcatum Zone beds east of Sherborne, Dorset.

Subgenus ORTHOGARANTIANA Bentz, 1928

Strenoceras (?*Orthogarantiana*) sp.

Material. One specimen collected by C. Cornfield from the Doulting Conglomerate of Locality 2 (BMNH C 78543).

Dimensions.

D	Wh	Wb	Ud
5·8 cm	2·37 (41%)	2·25 (39%)	1·95 (34%)

Description. A poorly preserved, heavily weathered specimen, consisting of two-thirds of a whorl of body chamber, the inner whorls being missing. This ammonite is moderately involute and has flat whorl sides and a well-arched venter. There are long, slightly sinuous, prorsiradiate, primary ribs, which divide into two to three fine secondaries. Due to the weathered state of the specimen it is now impossible to tell whether these secondary ribs cross the venter, or if there was once a ventral smooth band present.

Remarks. This specimen is very badly preserved and it is difficult to determine whether it is an example of *Orthogarantiana* or *Garantiana*; the weight of evidence points to the former. This subgenus is common throughout most of the Subfurcatum Zone and ranges up to the very top of the Garantiana Zone.

Family PERISPHINCTIDAE Steinmann, 1890

Genus LEPTOSPHINCTES Buckman, 1920

Leptosphinctes (*Leptosphinctes*) aff. *davidsoni* (S. Buckman)

Plate 36, fig. 3; text-fig. 6

1881 *Perisphinctes davidsoni nov.*; S. Buckman, p. 602.
1883 *Perisphinctes davidsoni* S. Buck.; S. Buckman, pp. 144–145, pl. IV, figs. 1*ab*, *non* 2*ab*.
1921 *Leptosphinctes davidsoni* S. Buckman; Buckman (1909–1930), pl. 201.

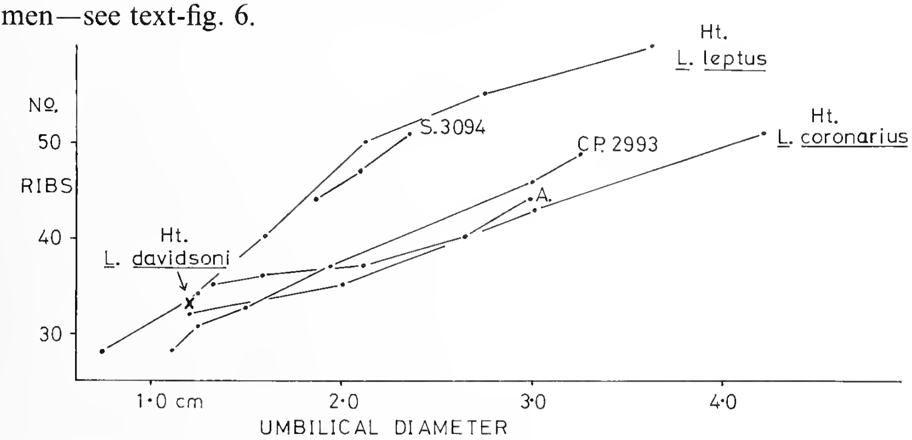
Material. One unnumbered specimen *ex.* J. Phyllis Collection, Shepton Mallet Museum, and one specimen from the Richardson Collection, University of Reading (LRS 3094).

Dimensions.

LRS 3094

D	Wh	Wb	Ud	Np
6·6 cm	2·0 (30%)	1·5 (23%)	3·4 (52%)	—
—	1·4	1·3	2·34	51
4·25	1·3 (31%)	1·24 (29%)	2·1 (49%)	47
—	—	—	1·87	44
Shepton Mallet Museum specimen				
6·7 cm	—	—	2·99 (43%)	44
5·26	—	—	2·65 (50%)	40
			2·11	37
			1·59	36
			1·34	35

Description. Both of these specimens are wholly septate and rather poorly preserved; the Reading specimen has lost both its inner whorls and a third of its outer whorl, whilst the Shepton Mallet specimen is slightly crushed. The latter specimen is on the whole the best preserved and it is figured here (Pl. 36, fig. 3). Both of these specimens are finely ribbed, evolute, serpenticone ammonites, with flattened whorl sides and smoothly rounded venters. The primary ribs are sharp, long, and slightly prorsiradiate and branch on the inner whorls into two short secondary ribs, whilst on the outer whorls the secondaries are merely intercalated. The suture line is well shown on the figured specimen, which, however, shows no sign of any constrictions. The Reading specimen has one strong constriction on the last eighth of the last preserved whorl and it is also more finely ribbed, with a higher primary rib density than the figured specimen—see text-fig. 6.



TEXT-FIG. 6. Number of primary ribs plotted against umbilical diameter, for various species of *Leptosphinctes*.

Ht. = holotype, A = figured specimen in Shepton Mallet Museum.

Remarks. Both of these ammonites are really too small and poorly preserved for accurate identification. *Leptosphinctes davidsoni* (S. Buckman) is very close in style of ribbing, coiling, and whorl cross-section at equivalent diameters, hence this specific name is used in 'open' nomenclature. The Shepton Mallet specimen has a similar primary rib density to that of the holotype of *L. davidsoni* (Manchester, L 11359), a recently collected topotype of the same species (CP 2993), and the holotype of *L. coronarius* S. Buckman (see text-fig. 6). The latter specimen is nothing but a smaller and less weathered specimen of *L. davidsoni*. The Reading specimen on the other hand is more finely ribbed and is a closer match to the holotype of *L. leptus* S. Buckman (IGS 32014—see text-fig. 6). However, until more is known of the variation within these species of *Leptosphinctes*, both the described specimens are here included in *L. davidsoni*. This species has recently been collected from beds equivalent to bed 5, Frogden Quarry (Buckman 1893) at Oborne Wood, Sherborne, Dorset; that is from the Banksi Subzone of the Subfurcatum Zone.

CORRELATION OF THE DOULTING CONGLOMERATE BED AND ITS FAUNA

The ammonite fauna recorded here from the Doulting Conglomerate Bed can only be correlated with the basal Banksi Subzone of the Subfurcatum Zone (see Table 1). Recent work has shown that there is a considerable overlap of Stephanoceratid ammonites, such as *Teloceras*, with Perisphinctids at the base of the Subfurcatum Zone in both the French Basses Alps (Pavia 1969, p. 447, text-fig. 2) and in Dorset (Parsons 1970). The coexistence of *Stephanoceras*, *Teloceras*, *Leptosphinctes*, and *Strenoceras* in the same bed is thus by no means unusual; it is typical of the Banksi Subzone and it mirrors a similar occurrence at Chaudon, near Digne, south-east France (Pavia 1969, p. 447). The Banksi hemera as erected by Buckman (1910, 1909–1930) was based on the 'iron-shot' limestones exposed at Frogden Quarry, near Sherborne (ST 642 185), although he never clearly stated this (Morley Davies *in* Richardson 1930, p. 48). This hemera thus has precedence over the Aplous Subzone of the Subfurcatum Zone (Pavia and Sturani 1968), which is a junior synonym (Parsons *in* Sturani 1971). Banksi Subzone faunas can still be collected from Frogden and they prove to be very similar to both those collected from equivalent beds at Oborne Wood, Sherborne, Dorset (Whicher and Palmer 1971), and to the fauna described here.

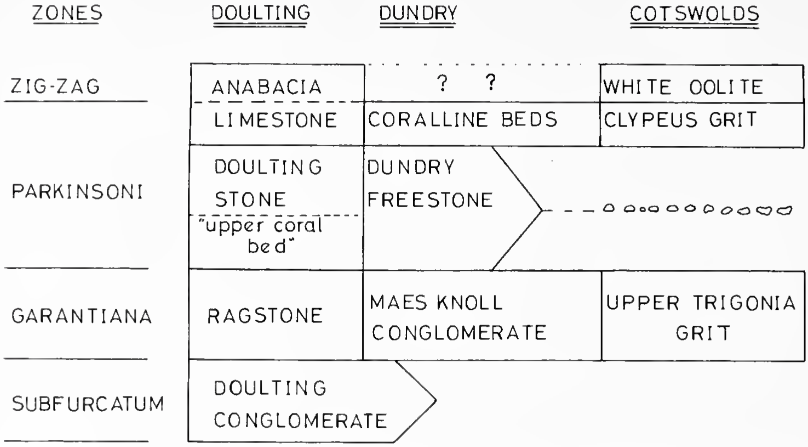
The 'iron-shot' matrix of the Conglomerate Bed, together with the common yellow stained oncolites, is highly distinctive and it enables one to trace it in field rubble. The most northerly point at which the Conglomerate Bed appears to be preserved is in the valley to the west of Doulting. To the south, 'iron-shot' field rubble is present for some distance past locality 3 (see text-fig. 3). Whilst sparsely 'iron-shot' limestones are present at the base of the Inferior Oolite in the valley near Higher Alham (at the far south-east corner of text-fig. 3), it is impossible to be certain of their age as no diagnostic ammonites have been found *in situ*. In this connection it is interesting to note that a single, large specimen of *Teloceras banksi* (at least 30 cm in diameter) has been found in loose material from a dry stone wall near Chesterblade (Locality 4, text-fig. 3). This ammonite has a sandy, slightly 'iron-shot' matrix, very like that of the basal Inferior Oolite at Higher Alham and further south at Batcombe (Richardson 1916). It is thus a distinct possibility that the basal members of the Inferior Oolite south of Chesterblade are also Subfurcatum rather than Garantiana Zone in age. Additional evidence for this correlation is given by the occurrence of

Subfurcatum Zone ammonites in the base of the Sherborne Building Stone Series (see text-fig. 2), at Oborne Lane section (ST 656 186; Buckman 1893, p. 502) and Milborne Port (Kellaway and Wilson 1941, p. 154). The Sherborne Building Stone is mainly Garantiana Zone in age and at Frogden and Oborne Wood it rests unconformably on 'iron-shot' and highly condensed Subfurcatum Zone beds. It thus seems that to the east the Subfurcatum Zone beds become sandier and thicker and are thus indistinguishable from the overlying Garantiana Zone beds (see text-fig. 2). This may well be what has occurred in the Batcombe district.

CORRELATION OF THE UPPER INFERIOR OOLITE NORTH OF THE MENDIPS

There can be little doubt that the extensive transgression at the base of the Upper Bajocian, which is marked by prominent 'hard-grounds' and unconformities over much of southern England, commenced prior to the Subfurcatum Zone rather than the Garantiana Zone. The occurrence of Subfurcatum Zone rocks well to the north of the Sherborne area discredits Morley Davies's concept of a north-westerly overlap of the Sherborne rocks by subsequent strata (Morley Davies 1930, p. 232) and confirms Buckman's concept of the existing outcrops of Subfurcatum Zone rocks being the remnant of once more extensive areas of deposition (Buckman 1923, *in* 1909–1930, p. 54). Since Doulting is so close to the Mendips there is no reason to doubt that the major inundation of this latter area, which is marked by the transgressive nature of the Upper Inferior Oolite, commenced also prior to the Subfurcatum rather than the Garantiana Zone.

The traditional correlation of the Doulting Conglomerate with the Cotswold Upper Trigonia Grit has now proved to be untenable. The rock at Doulting which in fact belongs to the Garantiana Zone is the Ragstone or Rag Bed. This bed has yielded sufficient fragmentary ammonites to enable a provisional correlation to be made with the upper Garantiana Zone. The Ragstone is exposed at the very base of the quarry near Cheylinch (ST 649 435), where it has produced ?*Spiroceras* sp. and *Prorsisphinctes* sp. This bed is the reputed type horizon for *Prorsisphinctes* ('*Glyphosphinctes*') *glyphus* (S. Buckman 1925, *in* 1909–1930, pl. 544), which is very close to, if not conspecific with *Prorsisphinctes* ('*Stomphosphinctes*') *stomphus* (S. Buckman 1921, *in* 1909–1930, pl. 247), which as a species is characteristic of the Astarte Bed of south Dorset and which is upper Garantiana Zone in age. The dating of the Conglomerate Bed is of considerable interest, since it rules out the possibility of the basal unconformity beneath the Ragstone being on the horizon of the supposedly missing Dundry Freestone and Coralline beds of Dundry Hill near Bristol, a correlation suggested by Richardson (1907, p. 386). Taking into account the restrictions placed on any correlations by the Parkinsoni/Zig-Zag Zonal boundary falling within the Anabacia Limestones (Torrens 1969*b*), there seems no alternative but to assume that the Dundry Freestone is the lateral equivalent of the Doulting Freestone; there thus is very little missing at Doulting. A possible recorrelation of the Upper Inferior Oolite north of the Mendips is given here in diagrammatic form (text-fig. 7). The discussion of the detailed ammonite evidence for the changes suggested here is on the whole beyond the scope of this work. However, what must be mentioned is that the ammonite



TEXT-FIG. 7. A revised correlation of the Upper Inferior Oolite from the Mendips north to the Cotswolds.

faunas from the Upper Trigonia Grit of the Cotswolds, mainly *Garantiana s. str.* (e.g. *Strenoceras* (*Garantiana*) cf. *garantiana* (d'Orb.), BMNH C 8839, Rodborough Hill, near Stroud) and early Parkinsonids (e.g. *Parkinsonia* (*P.*) *rarecostata* (S. Buckman), BMNH C 9171, Long Wood, near Stroud), would point to a correlation with the upper Garantiana Zone, Acris Subzone (Pavia 1973, p. 88, text-fig. 2). This might suggest that the Upper Bajocian transgression north of the Mendips occurred at a slightly later date than the pre-Subfurcatum Zone transgression to the south.

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JURASSIC FRESHWATER OSTRACODS FROM THE KOTA LIMESTONE OF INDIA

by A. GOVINDAN

ABSTRACT. Three species of Jurassic freshwater ostracods representing the genera *Timiriasevia*, *Darwinula*, and (?)*Limnocythere* are described from the limestone of the Kota Formation of the Pranhita-Godavari Valley, India. Of these *Timiriasevia digitalis* sp. nov. is new, (?)*Limnocythere* sp. A is left under open nomenclature, and *Darwinula* cf. *D. sarytirmenensis* compared with the Middle Jurassic species of that name recorded from the Mangishlaka Peninsula, U.S.S.R.

A SMALL, well-preserved, ostracod faunule occurring in the limestone of the Kota Formation, a member of the continental Gondwana Group, in the Pranhita-Godavari Valley, provides our first knowledge of definite occurrence of non-marine Jurassic ostracods in India. The purpose of this paper is to describe and illustrate these ostracods and to interpret the palaeoecology of the fauna.

The Gondwana Group of rocks exposed in the Pranhita-Godavari Valley were first described by King in 1881. Since 1960 the geological and geophysical field parties of the Oil and Natural Gas Commission have been carrying out systematic surveys in this area as part of a programme of exploration for oil and gas in the Gondwana sediments. In recent years the Geological Studies Unit of the Indian Statistical Institute have also initiated a programme of study of the geology and palaeontology of this area (Sengupta 1966, 1970; Chatterjee 1967; Kutty 1969; Rudra 1973).

The Kota Formation of Upper Gondwana comprises a sequence of sandstones with conglomerates, red and green clays, and limestones. It overlies unconformably the Maleris. The basal member of the Kota Formation is made up of grey, coarse-grained, friable, poorly sorted, pebbly sandstone, grading in places to conglomerate. These are succeeded by a sequence of red and green clays interbedded with fine-grained sandstones. These, in turn, are followed by a band of grey to cream-coloured, hard, argillaceous, micritic, dolomitic limestone, with thin chert lenses, interstratified with soft clays. The limestone can be traced from south of Bobaram (79° 52′ 35″ N.; 18° 59′ 40″ E.) to north of Kadamba (79° 39′ 20″ N.; 19° 22′ 50″ E.). It is nearly 30–35 m thick and dips 5–10° NE. to ENE. It is dislocated by faults at many places and is overlain by a sequence of red clays and sandstones.

The Kota limestone is widely known for its rich and well-preserved fish remains. Sykes (1851), Bell (1853), and Egerton (1851, 1854, 1878) were the first ichthyologists to describe fossil fishes from it. Three genera are known, namely *Dapedium*, *Tetragonolepis*, and *Lepidotes*. Recently, Jain (1973), who carried out a detailed restudy of the Kota fish remains, has described a new genus *Paradepidium*. Tasch, Sastry, Shah, Rao, Rao and Ghosh (1973) have reported conchostracans, namely *Cyzicus* and *Paleolimnadia*, in these limestones and they have pointed out the close similarity of this fauna with the Antarctic non-marine Jurassic estheriids.

This paper, however, describes ostracod assemblages which were obtained from

[Palaeontology, Vol. 18, Part 1, 1975, pp. 207–216, pl. 37.]

Daroghapalli, Potepalli, Aklapalli, Kanchelli, and Metpalli in the Kota limestone at the north-eastern part of the Pranhita-Godavari Valley (text-fig. 1).

To the author's knowledge, the only known previous record of ostracods from the Kota limestone of the Pranhita-Godavari Valley was a species identified by Jones as *Candona* (*in* King 1881, p. 273). The present study deals with the ostracod assemblage which has not been previously reported from this area.

LOCALITIES AND SAMPLES

The localities from which samples were collected for this report are shown in text-fig. 1. The samples were collected from limestone and from interbedded clays and their details are given below.

Metpalli. A nearly complete section of the Kota limestone, probably the best-exposed in this area, 1 km south-west of Metpalli (79° 44′ 00″ N.; 19° 11′ 00″ E.) on the south side of the lake near the overflow spill. Five samples were studied from the exposed thickness of 34·5 m. The limestone is underlain by calcareous silts and silty clays and overlain by red clays.

Kanchelli. Three samples were collected from the section 1·5 km north of Kanchelli (79° 49′ 55″ N.; 19° 11′ 18″ E.). The exposed thickness of the limestone is 11·7 m. The limestone is overlain by red clays but the base could not be observed.

Daroghapalli. A comparatively well-exposed section north-east of Daroghapalli (79° 41′ 14″ N.; 19° 19′ 40″ E.). Six samples were studied from the exposed thickness of 12·65 m. The limestone is underlain by crimson red clays.

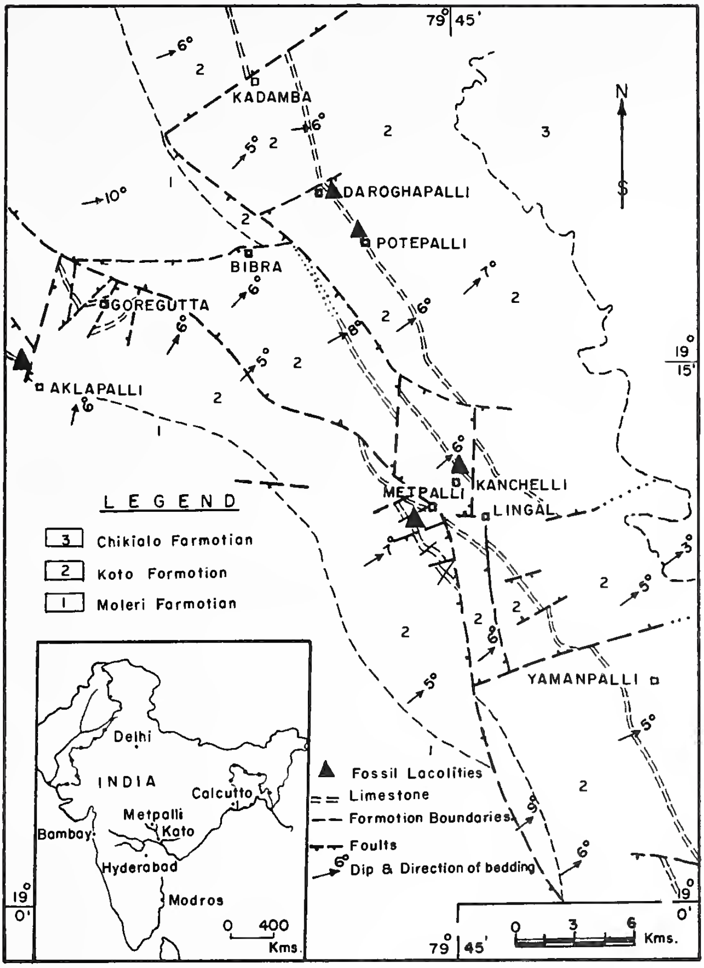
Aklapalli. Three samples were examined from the section exposed 1 km north of Aklapalli (79° 32′ 40″ N.; 19° 14′ 20″ E.). The measured thickness of this band is 18 m.

Potepalli. The nearly 5 m thick limestone band is exposed 1 km NNW. of Potepalli (79° 42′ 25″ N.; 19° 18′ 10″ E.). Two samples were collected.

In the laboratory, the limestone samples were treated with one part of glacial acetic acid in seven parts of water for three to four hours. The procedure was repeated several times to obtain matrix-free specimens. The clays were processed by treating them with hydrogen peroxide. The richest, well-preserved, material was obtained mainly from clays.

THE OSTRACOD FAUNA

The ostracods of the Kota limestone are moderately well preserved and some are silicified. They are abundant in some samples, mostly thin shelled, smooth, moderately large, and commonly filled with material making observation of internal features impossible. Separated valves are rare. Three genera were identified, each represented by a single species. Of these, one is now reported as a new species. One species is left under open nomenclature for want of sufficient study material. The genera identified are *Darwinula*, *Timiriasevia*, and (?)*Limnocythere*. *Darwinula* is well represented in most of the samples.



TEXT-FIG. 1. Map showing the fossil localities. Inset: outline map of India showing the villages Kota and Metpalli.

Perusal of the literature concerning the stratigraphic ranges of these ostracod genera shows that *Darwinula* ranges from Carboniferous to Recent, while *Limnocythere* extends from early Jurassic to Recent (*vide* Moore 1961). *Timiriasevia* is known to range from Middle Jurassic to Lower Cretaceous (*vide* Moore 1961, Q. 358). *Timiriasevia epidermiformis*, the type species of the genus *Timiriasevia*, was originally reported from the Middle Jurassic of U.S.S.R. Recently, Szczechura (1971) has recorded a few *Timiriasevia* species from the Palaeocene of Mongolia. The genus was also recorded earlier from the Bathonian beds of the Paris Basin (Oertli 1958) and from Oxfordshire (Bate 1965).

Darwinula cf. *D. sarytirmenensis*, a species comparable with the Middle Jurassic species of that name reported by Mandelstam (1947) from the Mangishlaka Peninsula, U.S.S.R., is represented abundantly in the Kota limestone. The occurrence of *Darwinula* cf. *D. sarytirmenensis* Sharapova together with *Timiriasevia digitalis* sp. nov. and (?)*Limnocythere* species in the assemblage suggests that the Kota limestone is Middle Jurassic in age. In this context, it is pertinent to point out that the age of the Kota limestone has been determined as Liassic, based on the restudy of the fish fauna by Jain (1973).

ENVIRONMENT

The usefulness of ostracods for palaeoecological interpretations has long been recognized. Curtis (1960), Sandberg (1964), and others have used generic assemblages for precise determination of the various environments. The most striking feature of the Kota limestone ostracod assemblages is their complete domination by freshwater forms, of which the smooth-shelled *Darwinula* constitutes the largest part. *Darwinula* is essentially a freshwater form and occasionally is also encountered in oligo-mesohaline waters (*vide* Morkhoven 1963, p. 29). According to Bate (1967) at present day, *D. stephensoni* (Brady and Robertson), the type species of the genus *Darwinula*, lives in rivers and lakes in East Anglia, from where it was originally described. Moore (1961, Q. 358) gives the ecologic habitat of the genus *Timiriasevia* as freshwater.

In general, the freshwater Jurassic ostracod faunas are often dominated by the species of a small number of characteristic freshwater genera, particularly *Theriosynoecum*, *Darwinula*, *Cypridea*, *Bisulcocypris*, *Limnocythere*. Bate (1965) and Ljubimova (1956) reported on freshwater ostracods from Jurassic sediments in the U.K. and U.S.S.R. From the Kirtlington Quarry section of Oxfordshire, eight species of freshwater ostracod belonging to the genera *Theriosynoecum*, *Timiriasevia*, *Bisulcocypris*, *Darwinula*, and *Limnocythere* were described by Bate (1965). The fauna described by Ljubimova (1956) from the U.S.S.R. included species of *Darwinula*, *Timiriasevia*, *Theriosynoecum*, and other genera. These two freshwater Jurassic faunas correspond very closely to the Kota limestone ostracod fauna. Thus the limestone represents a freshwater facies deposited under lacustrine conditions.

Depository of types. The primary types are deposited at the Oil and Natural Gas Commission Regional Geological Laboratory, Baroda, and are designated here by the prefix ONGC:RGLB. A set of secondary types will be deposited at the British Museum (Natural History), London. Some types are in the author's collection, O.N.G.C. Geological Laboratory at Madras.

The photographic illustrations for this paper were taken by Dr. H. J. Oertli on a Stereoscan Scanning Electron Microscope while text-fig. 2 was drawn by the author using a Carl Zeiss camera lucida.

SYSTEMATIC PALAEONTOLOGY

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Muller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily DARWINULACEA Brady and Norman, 1889
Family DARWINULIDAE Brady and Norman, 1889
Genus DARWINULA Brady and Robertson, 1885

Type species. Polycheles stevensoni Brady and Robertson, 1870, by original designation.

Darwinula cf. *D. sarytirmenensis* Sharapova, 1947

Plate 37, figs. 1–3; text-fig. 2*a–h*

1947 *Darwinula sarytirmenensis* Sharapova; Mandelstam, pl. 2, fig. 8.

Material. More than 200 carapaces and valves.

Occurrence. Metpalli, Daroghapalli, Potepalli, Kanchelli, and Aklapalli, Kota Formation, Pranhita-Godavari Valley, India.

Description. The carapace is elongate-oval in lateral view. The shell material is thin and the surface completely smooth. The greatest height of the carapace is situated in the posterior third and greatest length passing through or slightly below the mid-point. The anterior margin is narrowly rounded; the posterior margin is broadly and regularly rounded. The dorsal margin is nearly straight with convex anterodorsal and posterodorsal slopes. The ventral margin is broadly incurved anteromedially. The left valve is larger than the right which it overlaps along the entire margin and most strongly along the ventral margin. The hinge is adont, consisting in the right valve of a straight shallow groove.

Dimensions (in mm).

Specimen	Length	Height	Width
ONGC:RGLB 380 (entire)	0·890	0·450	0·395
ONGC:RGLB 381 (entire)	0·915	0·408	0·370
ONGC:RGLB 382 (entire)	0·925	0·407	0·370
BMNH:IO 6016 (entire)	0·915	0·408	0·335

Remarks. The Indian material closely resembles *Darwinula sarytirmenensis* Sharapova, described and illustrated by Mandelstam (1947, p. 254, pl. 2, fig. 8) from the Middle Jurassic of the Mangishlaka Peninsula. The specimens studied agree well with *D. sarytirmenensis* Sharapova figured by Mandelstam (op. cit.) and differ only by being slightly smaller in size. The Russian specimens attain a length of up to 1·14 mm and height up to 0·83 mm. The Indian material ranges in length from 0·80 to 0·90 mm and in height from 0·40 to 0·45 mm.

Superfamily CYTHERACEA Baird, 1850
Family LIMNOCYTHERIDAE Klie, 1938
Genus LIMNOCYTHERE Brady, 1868

Type species. Cythere inopinata Baird, 1843, by subsequent designation Brady and Norman, 1889.

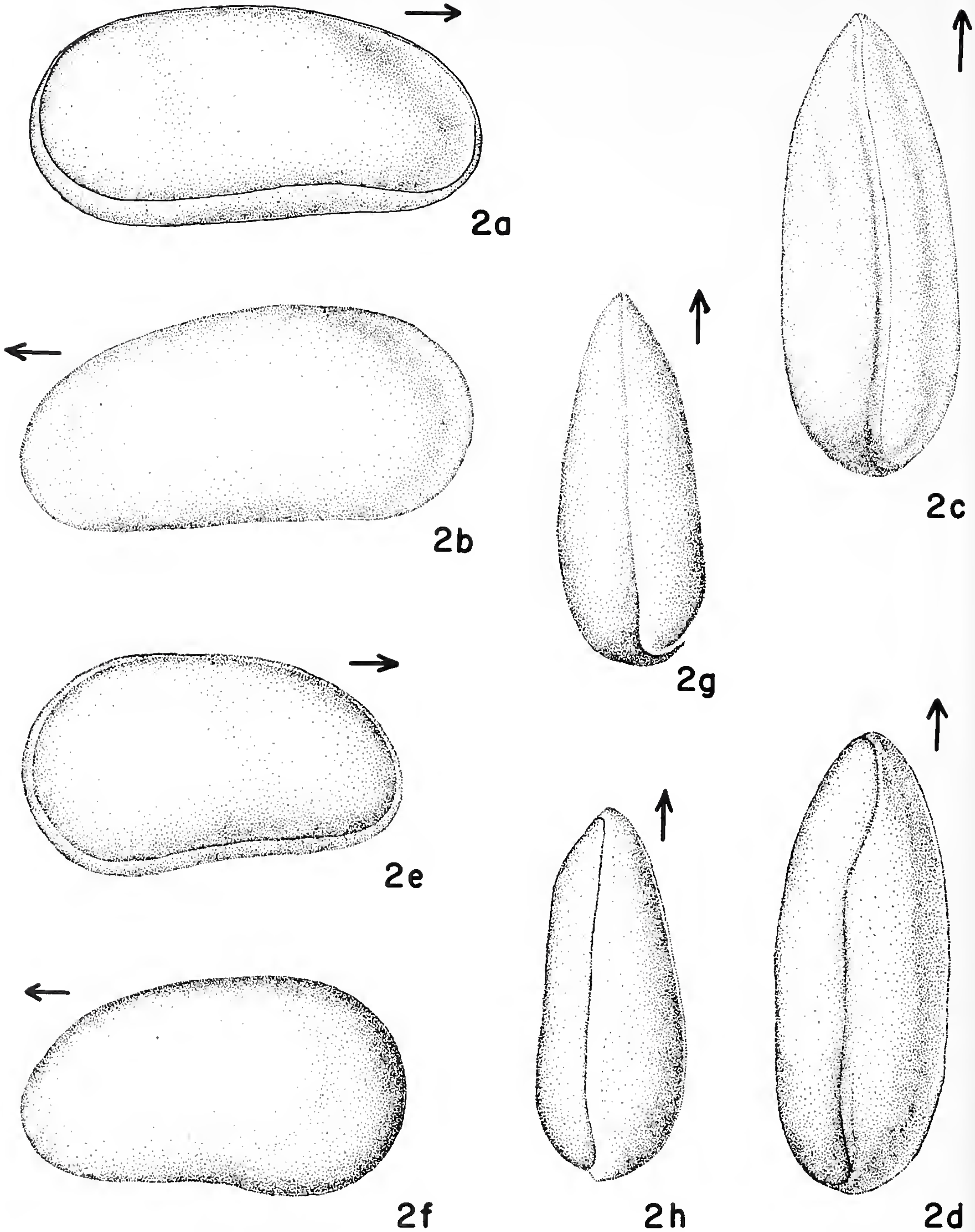
(?)LIMNOCYTHERE sp. A

Plate 37, fig. 6

Material. Three complete carapaces.

Occurrence. Daroghapalli, Kota Formation, Pranhita-Godavari Valley, India.

Description. The carapace is subrectangular in lateral view with the greatest height in the anterior third. The dorsal margin is nearly straight with prominent cardinal angles. The ventral margin is incurved medially. The anterior and posterior margins are regularly and broadly rounded, the posterior end being slightly more narrowly so. Anterior and posterior peripheral margins are compressed to form distinct marginal borders. A deep narrow sulcus is seen just anterior of mid-point. The greatest length of the carapace passes through the mid-point. The shell surface is faintly reticulated, the reticulae arranged in concentric rows close to and paralleling



TEXT-FIG. 2*a–h*, *Darwinula* cf. *D. sarytirmenensis* Sharapova. 2*a–d*, right, left, dorsal, and ventral views complete carapace, specimen ONGC:RGLB 382. 2*e–h*, right, left, dorsal, and ventral views, complete carapace, specimen BMNH:IO 6016 (all figures ×60).

the margins. The internal characters could not be studied as the material yielded only carapaces.

Dimensions (in mm).

Specimen	Length	Height	Width
ONGC:RGLB 383 ♀	0·520	0·340	0·295
ONGC:RGLB 384 ♀	0·595	0·300	0·320
BMNH:IO 6017 ♀	0·590	0·370	0·330

Remarks. Three poorly preserved forms in the material studied could belong to the genus *Limnocythere*. The characteristic deep anteromedian sulcus, the sinuate ventral margin, the broadly rounded ends, the compressed peripheral margins, and the reticulate surface ornamentation seem to fit well. Because there is insufficient material available, it is preferred to record it questionably under the genus *Limnocythere* until additional material becomes available for confirmation.

Genus TIMIRIASEVIA Mandelstam, 1947

Type species. Timiriasevia epidermiformis Mandelstam, 1947, by original designation.

Timiriasevia digitalis sp. nov.

Plate 37, figs. 4, 5, 7–11

Derivation of name. With reference to surface ornamentation of the carapace.

Material. Twenty complete carapaces and thirty-six partly broken carapaces.

Holotype. A complete female carapace, Plate 37, figs. 4–5.

Paratypes. Two complete female carapaces, Plate 37, figs. 9, 10, and 11 and a male carapace, Plate 37, figs. 7, 8.

Type locality. Daroghapalli, Kota Formation, Pranhita-Godavari Valley, India.

Diagnosis. A species of *Timiriasevia* with the following characteristics; carapace large, subrectangular in lateral view, slightly constricted mid-dorsally, greatly expanded posteriorly. Sexual dimorphism strongly evident, female dimorph heart-shaped in dorsal view with tapering anterior end, male lacks the posterior swellings of the female when viewed dorsally. Ornamentation consists of fine reticulations arranged somewhat concentrically in the middle of the posterior half and fine longitudinal ridges aligned roughly parallel to the outer margin; individual longitudinal ridges bifurcate and unite, forming a network pattern when viewed dorsally. Ventrolateral margin thickened with a ridge. Left valve slightly larger than the right.

Description. The carapace is large, subrectangular in lateral view, slightly constricted mid-dorsally, just anterior of mid-point, and with the posterior highly inflated. In dorsal aspect, the carapace is heart-shaped tapering to the anterior with the greatest inflation at about the posterior third of the length. The dorsal margin is nearly straight to gently convex and the ventral margin is straight. The ventro-lateral margin is projected as a thinly developed ridge, particularly around the posterior margin. The anterior margin is broadly and evenly rounded. The anterior marginal zone is compressed to form a flattened marginal border. The posterior margin is broadly rounded. The ventral side of the carapace is flattened to produce a broad surface. The greatest length of the carapace passes through the mid-point and the width is greatest at the posterior third. The lateral surface is ornamented with fine reticulations arranged somewhat concentrically in the middle of the posterior half of the shell. In addition, the ventral ornament consists of fine, closely spaced longitudinal ridges aligned roughly parallel to the outer margins. Individual longitudinal ridges bifurcate and coalesce resulting in a network pattern of ridges in dorsal view (Pl. 37, fig. 11). The left valve overlaps the right slightly along the ventral margin. The absence of single valves in the studied material precludes the possibility of ascertaining the details of the internal structures.

Dimensions (in mm).

Specimen	Length	Height	Width
Holotype, ONGC:RGLB 385 ♀	0·962	0·444	0·592
Paratype, ONGC:RGLB 386 ♀	0·814	0·440	0·518
Paratype, ONGC:RGLB 387 ♀	0·888	0·445	0·520
Paratype, BMNH:IO 6018 ♀	0·960	0·445	0·519
Paratype, BMNH:IO 6019 ♀	0·888	0·485	0·592

Remarks. Timiriasevia digitalis sp. nov. bears no affinities with known Russian Jurassic *Timiriasevia* species, differing from all by the larger, more elongate outline of the carapace, the presence of thickened postero-ventral marginal ridge, the flattened antero-marginal zone, and the distinct surface ornamentation. *T. mackerrowi* Bate, 1965, described from the Bathonian of Oxfordshire, differs considerably in the outline of the carapace and in the ornamentation. In the elongate outline of the carapace and in the type of the ridge pattern the present species also differs from *T. ulanbulakensis* Szczechura, 1971, and *T. naranbulakensis* Szczechura, 1971, described from the Palaeocene of Mongolia.

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EXPLANATION OF PLATE 37

All figures are scanning micrographs.

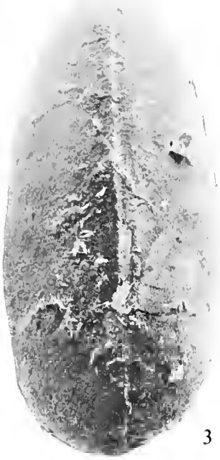
Figs. 1–3. *Darwinula* cf. *D. sarytirmenensis* Sharapova. 1, right side of a complete carapace; ONGC:RGLB 380, ×66. 2–3, right and dorsal views; complete carapace; ONGC:RGLB 381, 2, ×66; 3, ×70.

Figs. 4, 5. *Timiriasevia digitalis* sp. nov. 4, external view of right side of complete female carapace; holotype ONGC:RGLB 385, ×62. 5, dorsal view of the same specimen, ×72.

Fig. 6. (?)*Limnocythere* sp. A. External view of right side of complete carapace; holotype ONGC:RGLB 383, ×72.

Figs. 7–11. *Timiriasevia digitalis* sp. nov. 7, external view of right side of complete male carapace; paratype ONGC:RGLB 386, ×78. 8, dorsal view of the same specimen to show the absence of posterior swellings; ×58. 9, external view of right side of complete female carapace showing characteristic surface ornamentation; paratype ONGC:RGLB 387, ×87. 10, dorsal view of the same specimen showing prominent posterior swellings, ×74. 11, dorsal view of another complete female carapace; paratype BMNH:IO 6018, ×60.

PLATE 37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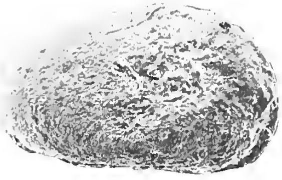
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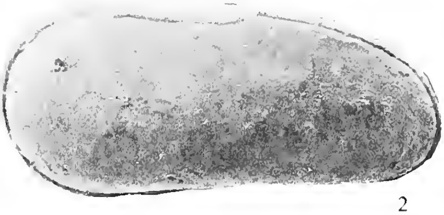
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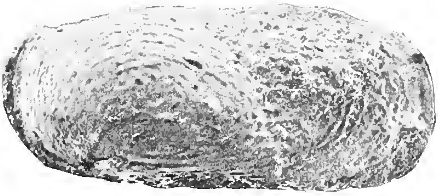
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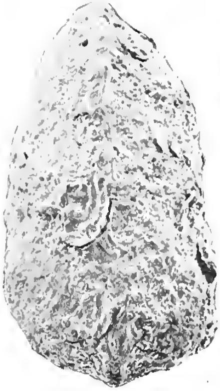
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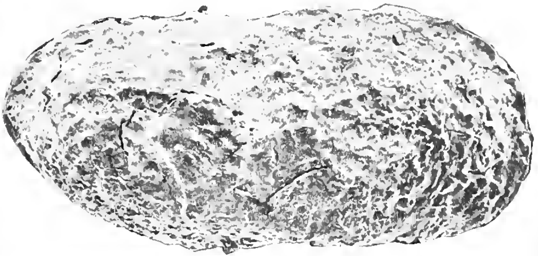
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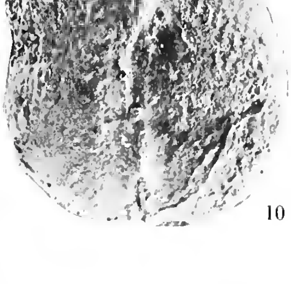
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9

GOVINDAN, Jurassic ostracods

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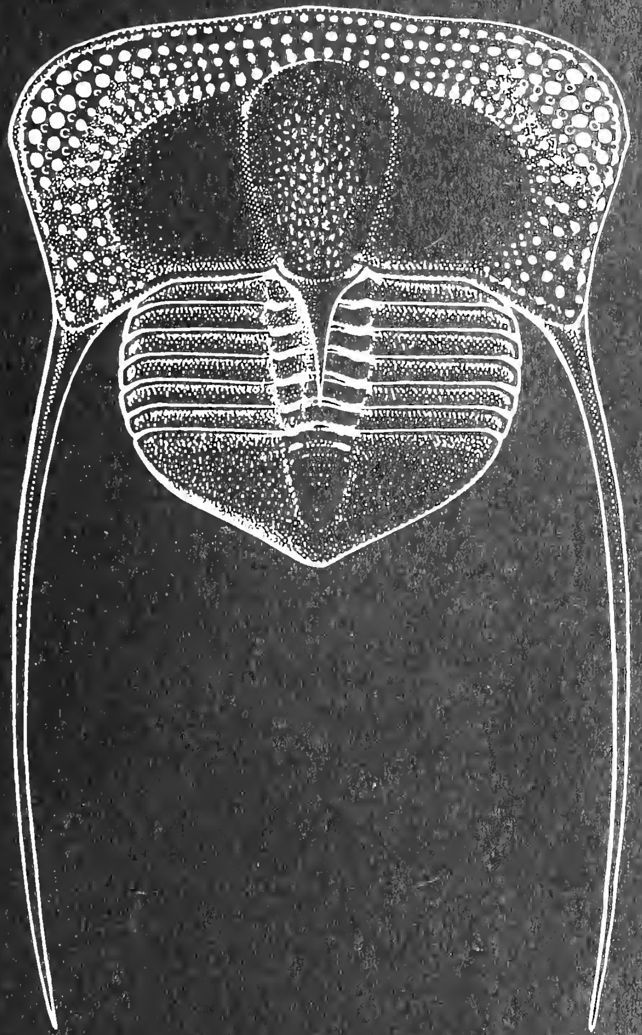

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Cover: *Marrolithus favus* (Salter).

Reconstruction of Ordovician trinucleid trilobite, prepared by Dr. J. K. Ingham as the symbol for the Symposium on the Ordovician System, Birmingham, 1974. Based on silicified material collected by Dr. R. Addison from limestones of Upper Llandeilo age from Wales.

FUNCTIONAL MORPHOLOGY, ECOLOGY, AND EVOLUTIONARY CONSERVATISM IN THE GLYCYMERIDIDAE (BIVALVIA)

by R. D. K. THOMAS

Abstract. Since its appearance near the beginning of the Cretaceous, the family Glycymerididae has retained the same simple shell form. Variation among species is largely restricted to differences in size and external sculpture. This evolutionary conservatism can be explained in terms of the morphology and ecology of *Glycymeris*. Bivariate and multivariate studies of interactions among shell characters show that individual parameters of the shell are closely interrelated; there are rigid geometrical and mechanical constraints on deviations from the simple form. Relative growth of most characters is not strongly allometric; where marked allometry does occur, notably in the growth of the ligament, it is directly related to the over-all size of the animal. Thus the potential for evolutionary change in shell form by heterochrony is limited. Glycymerid soft-part anatomy is unspecialized and the animal is functionally less efficient in several respects than more advanced bivalves. Glycymerids have apparently always occupied the same current-swept marine environments. They evolved as functional generalists, adapted to a physically rigorous environment. The compromises that were essential to this adaptation left the group with insufficient flexibility of form to radiate into a wide variety of environments, whence its conservatism.

Evolution in the Glycymerididae has given rise to a group of species which is particularly conservative in its morphological diversity. These bivalves have always been adapted to the same narrow range of physically rigorous environments. The purpose of this paper is: (1) to document these assertions; (2) to review the soft-part anatomy of *Glycymeris* in relation to its functions; (3) to determine interrelationships among shell characters, and to develop an analysis of the geometrical constraints on glycymerid shell form; (4) to demonstrate relationships between shell form and mode of life; and (5) to argue that morphological compromises required by geometry and functional adaptation have made a significant contribution to the evolutionary conservatism of this group of bivalves.

The generic name *Glycymeris* is used in a broad sense here, to refer to all the species that properly belong to the Glycymerididae. Many other generic names are available but generally unsatisfactory, since they are not based on evolutionary relationships, which are largely unknown. *Glycymeris* is a generalized, free-burrowing descendant of the Arcoida, which was established as a distinct group early in the radiation of the Bivalvia. The animal has filibranch gills, subequal adductor muscles, unfused mantle margins, and a large axe-shaped foot. Its shell is subcircular or somewhat trigonal, usually symmetrical about the umbones, with a chevron ligament and an arched series of taxodont hinge teeth. The shell bears flat ribs and a heavy periostracum, or much more prominent ribs.

This paper is based on a detailed investigation of the Miocene–Recent glycymerids of eastern North America (Thomas 1970), and on the accumulated knowledge of the group as a whole. It presumes to be a synthesis, and sets out to provide a conceptual and methodological framework for future studies of evolution in the Glycymerididae. At the same time, many of its conclusions apply in varying degrees to other groups of bivalves.

[Palaeontology, Vol. 18, Part 2, 1975, pp. 217–254, pl. 38.]

EVOLUTION AND ENVIRONMENT

The purpose of this section is primarily to document the evolutionary conservatism of the Glycymerididae. This group has developed a narrow range of morphologies in its 130 million year history. Furthermore, the environments preferred by fossil glycymerids are essentially identical with those occupied by the group in present-day seas. This ecological information is important in the functional interpretation of glycymerid shell morphology.

Evolution of the shell. It has been convincingly shown, on the basis of shell morphology and stratigraphic ranges, that the glycymerids evolved from another arcoid family, the Cucullaeidae (Nicol 1950). The oldest known glycymerids occur in early Cretaceous sediments of northern France (Gillet 1924) and northern California (Stanton 1895). In both cases these rocks are now thought to be of latest Valanginian age (Corroy 1925; Debrenne 1954; Imlay 1959; Jones, Bailey and Imlay 1969). Well-documented Aptian and Albian glycymerids have been described from Europe and Japan. During the Upper Cretaceous the group achieved a world-wide distribution, but glycymerids of this age are only common in local areas.

The earliest glycymerid shells already have all the essential characteristics of the family (Pl. 38, figs. 11, 12). They are strongly convex, the shell material is relatively

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EXPLANATION OF PLATE 38

Figs. 1–5. *Glycymeris subovata waltonensis* Gardner, all × 1·5. Series showing allometric growth of the ligamental area and increasing posterior elongation of the shell during ontogeny. Allometric growth of the ligament is required by function in all large glycymerids; posterior elongation is a burrowing adaptation developed only in some populations and species. Note isometric growth of the adductor scars, and progressive overgrowth of the hinge plate by the ligamental area. MCZ 17850. Shell Bluff, Walton County, Florida (loc. 10, Thomas 1970). Shoal River Formation, Miocene.

Fig. 6. *Glycymeris pulvinata* (Lamarck), × 1. A typical Eocene species. Note preservation of partially calcified ligament. BMNH LL 90512. Bracklesham Bay, Hampshire, England. Bracklesham Beds.

Fig. 7. *Glycymeris subovata* (Say), × 1. A large shell from its population, showing well-buttressed adductor scars and extensive disruption of hinge teeth by the ventrally expanding ligamental area. MCZ 17852. Colerain Landing, Bertie County, North Carolina (loc. 21, Thomas 1970). Yorktown Formation, Miocene.

Fig. 8. *Glycymeris americana* (Defrance), × 1. MCZ 17877. Dredged in 25 m of water off Cape Fear, North Carolina (loc. 49, Thomas 1970). Living.

Fig. 9. Periostracum of *G. americana*, × 45. Concentric rows of recurved barbs parallel the growth lines of the shell (vertical here). Radial rows of the same barbs are inserted in fine striations on the shell ribs (horizontal here). Barbs catch sand grains, helping to stabilize the shell in burrowing. Geol. Paläont. Inst. Tübingen, Scanning Electron Micrograph 40889/3029/1. Specimen from same population as fig. 8.

Fig. 10. *Glycymeris americana* (Defrance), × 1. Note striations, in which periostracum was inserted, on the low ribs. MCZ 17878. Winnabow, Brunswick County, North Carolina (loc. 39, Thomas 1970). Waccamaw Formation, Pliocene.

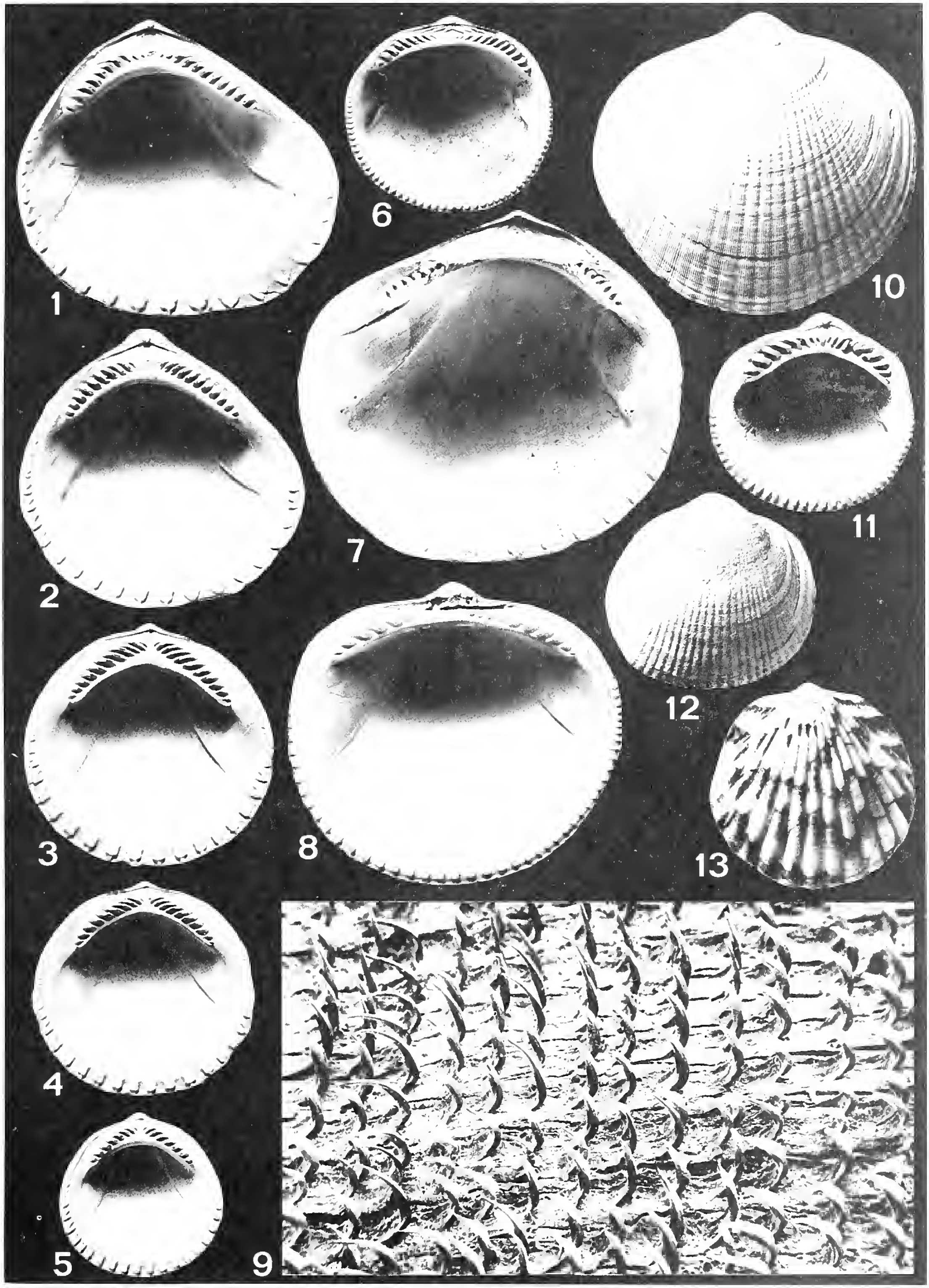
Figs. 11, 12. *Glycymeris umbonata* (Sowerby), × 1·5. Early glycymerids already had all the shell characters of later forms with low striated ribs. BMNH LL 27664, 27665. Blackdown, Dorset, England. Blackdown Sand, Albian, Cretaceous.

Fig. 13. *Glycymeris pectunculus* (Linné), × 1. A typical tropical species, with prominent unstriated ribs. BMNH 197445. Ceylon. Living.

All specimens are right valves, except fig. 7.

All coated with ammonium chloride, except figs. 9 and 13.

Specimens are lodged in the collections of the Museum of Comparative Zoology, Harvard (Invertebrate Paleontology) and the British Museum (Natural History; Mollusca and Invertebrate Palaeontology).



THOMAS, *Glycymeris*

thick, and they are more or less subcircular in shape. The adductor muscle scars are subequal, and the interior margins of the shell interlock by means of strong crenulations. The arched hinge plate bears similar anterior and posterior series of simple teeth, which may be straight, curved, or chevron-shaped, depending largely on the shape of the hinge plate and their positions on it. The large triangular ligamental area is symmetrical, and bears alternating chevron-shaped ridges and grooves, to which the duplivincular ligament was attached. The Cretaceous glycymerids are more particularly characterized by their modest size, a slight posterior truncation of the shell in several species, and their external sculptures. Apart from one or two uppermost Cretaceous species, their heights, or lengths, rarely exceed 25 mm. The posterior truncation may be compared with the flattened posterior margin of the ancestral cucullaeids; in contrast, several later glycymerid species tend to become slightly elongated postero-ventrally. The sculptures of the Cretaceous glycymerids are very subdued; they have low, rounded or flat radial ribs, generally bearing fine striations in which rows of periostracal hairs were inserted. In short, the Cretaceous glycymerids exhibit very little morphological diversity, and they can be assigned to relatively few species, although, like later members of the family, they frequently show considerable intraspecific variation.

During the Cenozoic the diversity of glycymerid species increased substantially, first in the Eocene, and then to a greater extent in the Miocene. The principal morphological modifications involved in this radiation were changes in size and shell sculpture. Species considerably larger and very much smaller than those of the Cretaceous appeared. Radial shell sculptures diversified in several different ways, the most notable development being the advent of forms with smaller numbers of prominent, unstriated ribs. As Nicol (1956) has shown, nearly all living glycymerids can be assigned to one of two broad groups of species. The group with subdued, striated ribs and well-developed periostracum (e.g. *G. glycymeris* and *G. americana*, Pl. 38, fig. 10) ranges from the tropics to the cool-temperate waters of Alaska and southern Chile. In contrast, the group with prominent unstriated ribs and little or no periostracum (e.g. *G. pectunculus*, Pl. 38, fig. 13, and *G. pectinata*) is confined to the tropics. The systematic relationships between species of the two groups have not been worked out, but it is clear that the Cenozoic radiation of glycymerid species occurred largely in tropical and subtropical waters.

Evolution within the Glycymerididae has led to considerable elaboration of the radial sculpture and large differences in size. Rotation of the plane of spiral growth has given rise, in a few species, to umbones facing anteriorly or posteriorly over asymmetric ligamental areas. Other variations are limited to minor, but functionally significant, differences in the convexity and shape of the shell. The fact remains that the fundamental characteristics of the shell, the hinge plate, ligament and muscle scars, have remained very stable.

Evolution of the soft parts. The most striking feature of glycymerid anatomy is that it is so little different from those of other arcoids, which are themselves remarkably undifferentiated. The Glycymerididae have not been shown to have any anatomical characteristics that are unique to the group, apart from the over-all shape of the animal. The similarities extend to quite minor morphological details. For instance, Purchon (1957) found only minor differences between the stomachs of *Glycymeris* and *Anadara granosa*, while the gills and ciliation of the gill filaments are extremely similar in *G. glycymeris* and *Arca tetragona*, as shown by Atkins (1936). Likewise, variations in the size and number of folds of the labial palps among glycymerid species parallel similar variations among species of both *Arca* and *Anadara*.

The anatomy of *Cucullaea* has not been studied in detail, but the brief accounts of Pelseneer (1911) and Heath (1941) suggest that it is at least as similar to that of *Glycymeris* as those of any of the other arcoids, if not more so. The most apparent difference is that the adult *Cucullaea* retains a byssal cavity, although the animal is not known to secrete a byssus; adult glycymerids all appear to lose the byssal cavity. It is notable that in both *Glycymeris* and *Cucullaea* the ventricle surrounds the rectum. This character is shared with *Lunarca pexata* and *Trisidos* (see Heath 1941), neither of which appeared before the Cenozoic, while in all the other arcoids the rectum passes below the heart. This is not a character of high taxonomic significance, but it does corroborate Nicol's (1950) inference that the Glycymerididae evolved from the Cucullaeidae.

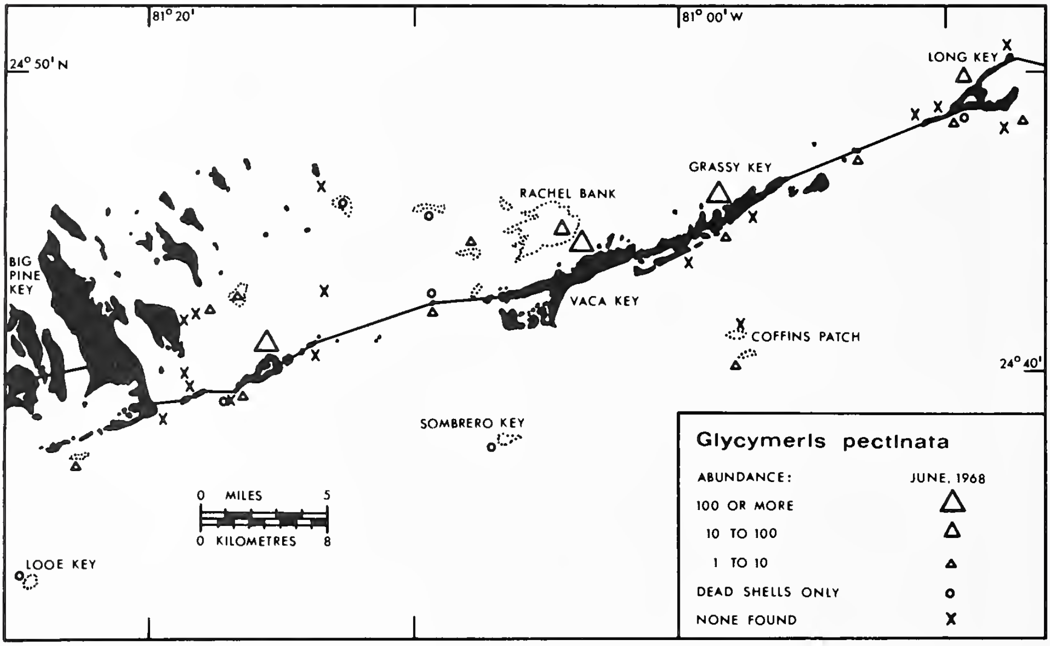
There is very little variation among the soft-part anatomies of even the most widely separated living glycymerid species. Minor variations in the thickness of the gill filaments and the development of the labial palps are apparent. In different species, the shape of the foot may be more or less elongated, and the eyes of the posterior mantle margin may be more or less numerous. These variations have yet to be systematically related either to adaptation to slightly different habitats, or to evolutionary relationships within the group. It is clear that very little diversification of the soft parts has occurred in the Glycymerididae.

Ecology of living species. Living glycymerids occur in normal marine, subtidal environments of the continental shelves. Although isolated individuals may be quite widely distributed, large populations occur sporadically in a narrow range of habitats. These environments are physically rigorous, and harbour faunas of low diversity, including few bivalve species at any one time and place.

The habitats of glycymerids with flat striated ribs and a hairy periostracum are quite well known. The geographic distribution of *G. glycymeris* in the English Channel has been mapped by Holme (1966, p. 409), who observed: 'In much of the western Channel the offshore areas consist largely of shelly sands or shell gravels, with many dead *Glycymeris* shells. The fauna is rather sparse. . . .' He goes on to note (p. 411) that this species prefers hard or gravel bottoms, where there is much water movement, and that 'they are common in tide-swept areas of the central Channel where little else occurs. They are absent from samples in the calmer waters with associated finer sediments. . . .' Holme's station data indicate that *G. glycymeris* is abundant on 'clean shell gravel', 'coarse silty sand and stones', and 'muddy fine gravel and shells', at depths between 16 and 100 m. Many earlier authors have recorded similar observations. Cabioch (1968) also found this species to be common on shell gravel bottoms, in what he calls 'le facies appauvrissement' on account of its limited fauna. *G. glycymeris* is sometimes common on firm sand bottoms, but the species does not occur today off the Dutch coast (Eisma 1966), where, although strong tidal currents occur, the bottom sediments are mostly fine and muddy sands.

Similar unstable sand and gravel habitats are preferred by *G. undata* in the Caribbean, *G. americana* off the eastern United States, and *G. modesta* around New Zealand. Data on these and other species have been compiled elsewhere (Thomas 1970). The environmental distribution of glycymerids with flat striated ribs is quite consistent from one region to another, and we may make the following generalizations. These species occur in both tropical and temperate waters, at depths between 3 and 130 m, although they are not usually common in water shallower than 10 m. They are found on clean sand, clean shell gravel, or muddy gravel bottoms. They favour turbulent waters and strong currents, but are intolerant of turbidity. They are typically associated with bottom communities of low faunal diversity. These factors will be related to the mode of life of *Glycymeris* in later sections.

Much less is known about the habitats of the tropical glycymerids with prominent unstriated ribs and little or no periostracum, so the distribution of *G. pectinata* around the Florida Keys may or may not be typical for these species. Stanley (1970) notes that: '*G. pectinata* prefers coarse, often grass-covered substrata in subtidal environments.' My own more extensive observations (Thomas 1970) indicate that this species occurs in three different situations. Occasional individuals are very widely distributed on off-shore, unstable, poorly sorted skeletal sands, in 2–5 m of water. The species is more common on very shallow subtidal gravel banks. These banks consist largely of broken branches of the coral *Porites*, together with mollusc shells and coarse skeletal sand; they are usually partially overgrown by *Thalassia* 'grass', and are often swept by strong tidal currents. However, *G. pectinata* was found to be most abundant in three sheltered bays, on the north sides of islands (text-fig. 1).



TEXT-FIG. 1. Distribution of *Glycymeris pectinata* (Gmelin) along the middle Florida Keys.

Here the animals were living, in the absence of other bivalve species, in very quiet water at depths of 1–4 m. The bottom sediment consisted of a thin, irregular veneer of poorly sorted coarse skeletal sand, and occasional shell gravel, overlying an eroded limestone platform. This environment is rather different from others in which glycymerids are known to occur, particularly in the absence of strong currents. However, like the current-swept shell gravels, it is an environment which is physically inhospitable to more specialized bivalves. The thin layer of sand provides insufficient cover for infaunal burrowers, but it is enough to inhibit those epifaunal forms which would attach to bare rock. The mobile shallow-burrowing glycymerid is able to take advantage of an otherwise empty habitat.

The environmental range of *G. pectinata* appears to be wider than those of other glycymerid species that have been studied. A similar Japanese species has been reported from coarse sand and shell gravel bottoms at 100–200 m (Okutani 1963). *G. laticostata* also has raised ribs, although they are not very prominent; this is a common species on hard, clean, shell gravel substrates in channels, off New Zealand (Powell 1936). Clearly, there are not enough data for generalizations to be made about the habitat preferences of the glycymerids with prominent unstriated ribs. The limited data suggest that they are not greatly different from those of the glycymerids with flat ribs, their different shell forms notwithstanding. The ecological differentiation of broadly sympatric glycymerid species has yet to be investigated, but it might be expected to shed some light on this problem.

Palaeoecology. It can be shown that glycymerid species have flourished, at least throughout the Cenozoic, and probably since they first evolved, in physical environments essentially identical with those enjoyed by their living descendants. This conclusion is based on lithological and palaeoecological observations; it specifically does not depend on analogy with the habitat of the living animals, or on arguments based on shell form.

I have made a detailed study of the occurrence of *G. americana* and *G. subovata* in the Neogene sediments of the Atlantic coastal plain of the United States (Thomas 1970). These species are abundant in shell beds, consisting of mixtures of broken, worn, and fresh molluscan shells, with a matrix of sand or muddy sand. The assemblages include species derived from a variety of environments, but the predominant species have usually not been transported very far (see Warme 1969; Hallam 1967; but cf. Fagerstrom 1964). Three main lines of evidence confirm that the glycymerids lived on these shell gravels and on unstable sandy bottoms. (1) The glycymerids are abundant in the shell beds, but they are only occasionally found in associated fossiliferous sands and clays. (2) Although the smallest shells have sometimes been winnowed or leached out of the assemblages, frequently complete size ranges, above about 5 mm, are represented. (3) Articulated valves are common in many of the shell beds. Where these are found with the valves gaping, limited transport might have occurred, but these shells are easily disarticulated (Craig 1967). More often, the shells occur with the valves closed, indicating that the animals were buried alive. Since these shells do not often appear to be in life position, it seems likely that the animals were washed out of their shallow burrows and suddenly buried during the last major reworking of the shell gravel in which they are entombed.

These observations confirm that, at least since the early Miocene, species in the *G. americana* and *G. subovata* lineages have lived on subtidal sand and shell gravel bottoms, often swept by fairly strong currents. Palaeogeographic considerations and palaeoecological studies of several authors (reviewed in Thomas 1970) further indicate that these sediments accumulated in inner-shelf environments at depths of up to 50 m.

Similar palaeoecological conclusions have been reached by Báldi (1973), with regard to *G. latiradiata*. This species is locally very abundant in shell gravels and medium- or coarse-grained sands of the Hungarian Oligocene. These sediments accumulated in turbulent, shallow subtidal environments. In the Paris Basin, *G. obovata* is a characteristic species of the shallow-water sediments of the type Stampian. Alimen (1936) describes this species as being very common, often with the valves articulated, in fine shelly sands and fine gravels. One of the commonest species in the Gosport Sand (Eocene) of Alabama is *G. staminea*. This glycymerid occurs in a coquina of shells and shell fragments, with a matrix of clean sand, which is often highly glauconitic. Gardner (1957) concludes that these sediments were laid down on a firm, current-swept bottom, at a depth of less than 38 m. *Glycymeris* is also abundant in sandy sediments of Palaeogene age on the Russian Platform (Semenova 1969).

Less information is available on the habitats of the Cretaceous glycymerids. In the Nacatoch Sand (Maastrichtian) of Texas, *G. rotundata* occurs in indurated lenses of shelly and glauconitic sand; it has not been found in the associated argillaceous sediments. One of the earliest records of abundant, well-preserved glycymerids is from the Upper Greensand (Albian) of south-western England (see Pl. 38, figs. 11, 12). At the classic Blackdown locality, which has never been well exposed, *G. umbonata* is the predominant fossil in Bed 7 of Downes (1882), who observes that the shells occur in clusters, with the valves almost always attached. Downes was of the opinion that the sandy sediment was deposited in still water, on account of the articulated shells, and the lack of breakage and rolling of the fossils. However, the thickness of the shells of several species, the abundance of glauconite (Tresise 1960), and the grain size of the sediment suggest considerable water movement. Higher up in the section, *Glycymeris* is again common, in lenticular bands of mostly broken and water-worn shells.

Fossil glycymerids do occur in sediments other than those described above. Nevertheless, these examples are representative of the situations in which they are most abundant, and apparently in or near their preferred habitats. The physical habitats have been emphasized here, since much less is known of the biological interactions of *Glycymeris*, living or fossil, with other organisms. Off the east coast of the United States a coherent group of species, which I have referred to as the *Eucrassatella*–*Glycymeris* community (Thomas 1970), has existed at least from the early Miocene to the present day. The Upper Oligocene *G. latiradiata* community, recognized in Hungary by Báldi (1973), has much in common with the former community, including the abundance of *Eucrassatella* and the presence of the deep-burrowing *Panopea*. These communities, as well as those in which *Glycymeris* thrives today, belong to the group of '*Venus* communities' recognized by Thorson (1957). *Glycymeris* has apparently always been associated with communities of this type. Some more specific interactions can also be recognized. Throughout the Neogene, the American glycymerids *G. americana* and *G. subovata* were subject to similar, albeit very variable, rates of predation by gastropods, principally naticids. Over the same period, their liability to infestation by the shell-boring polychaete *Polydora* showed no directional change (Thomas 1970).

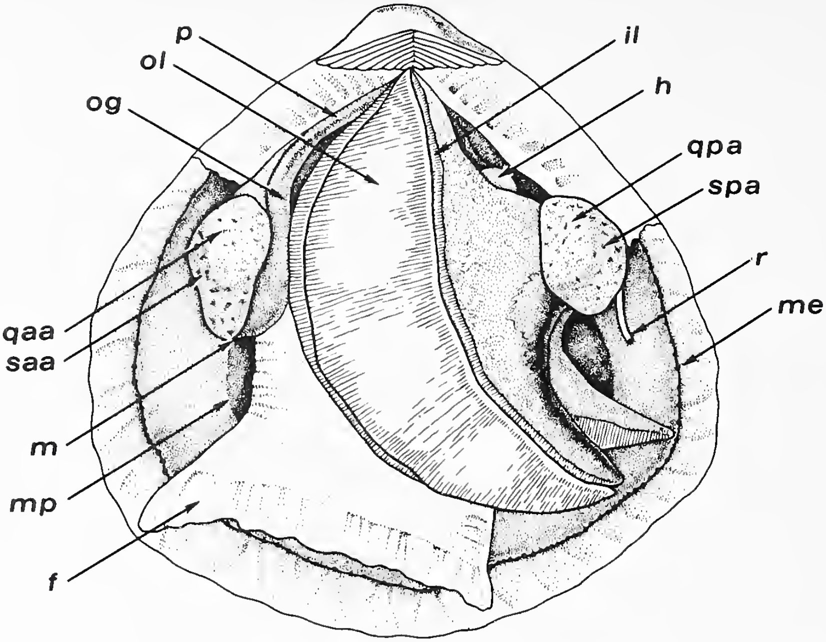
Synthesis. Glycymeris is a mobile shallow-burrowing bivalve. It lies at shallow to intermediate depths on the continental shelf, and no glycymerid is known to have ventured either into brackish water or the deep oceans. Large populations of glycymerids occur in patches on clean sandy or coarse bottoms, often swept by strong currents. These are physically rigorous environments which support biocoenoses of low diversity. Glycymerids are in every respect typical opportunistic species (MacArther 1960; Levinton 1970). The distributions of their populations in time and space, within the environmental ranges of the species, are determined by variable and unpredictable factors. The establishment and extirpation of these local populations are presumably largely controlled by random spatfalls (cf. *Mulinia lateralis*, Levinton 1970) and the stability of the substrate. Salinity and the availability of sufficient dissolved oxygen are essentially invariant in the environments preferred by glycymerids, while temperature variations should rarely exceed the tolerances of the species. The fact that most opportunistic bivalves are suspension feeders implies that fluctuations in food supply may also limit their distribution. The availability of suitable phytoplankton is likely to be particularly critical for glycymerid veligers and spat, primarily limiting recruitment and the establishment of new populations.

The fossil record of glycymerid shells and the soft-part anatomies of the living animals, expressions of the limited morphological diversity of the Glycymerididae, confirm the evolutionary conservatism of this family. Palaeoecological observations show that these animals have lived as opportunistic species in similar environments for most, if not all, of their history. In the following sections the morphology and physiology of *Glycymeris* will be considered in terms of environmental adaptation, and related to this evolutionary conservatism.

GENERALIZED ANATOMY AND PHYSIOLOGY

The soft parts of *Glycymeris* are quite unspecialized, and there is little differentiation among the living species that have been studied. This lack of specialization reflects both its derivation from the ancient arcoid lineage and its own secondary adaptations. The following discussion of some functionally significant points is based on many detailed studies of *G. glycymeris*, several accounts of other species, and my own observations of *G. americana*, *G. pectinata* (text-fig. 2), and *G. glycymeris*.

Glycymeris is a mobile burrower in resistant sands and gravels. As such, it has a massive muscular foot, which is suspended from the shell by four large pedal retractor muscles. The pedal retractors, together with the pedal protractor muscles, form a muscular sheath which encloses the foot and viscera. The interior of the foot and the visceral cavity are crossed by bundles of transverse muscle fibres, which with the muscles of the sheath control the hydrostatic dilation and retraction of the foot (Heath 1941). The haemocoele extends ventrally into the foot, and the blood constitutes the fluid of this fluid/muscle system (Ansell and Trueman 1967). The base



TEXT-FIG. 2. Gross anatomy of *Glycymeris pectinata* (Gmelin), ×4·5. *f*, foot; *mp*, inner mantle surface; *m*, mouth; *saa*, *qaa*, slow and quick anterior adductor muscle; *og*, oral groove; *ol*, ascending lamella of outer demibranch; *p*, labial palps; *il*, descending lamella of outer demibranch; *h*, heart; *qpa*, *spa*, quick and slow posterior adductor muscle; *r*, anus; *me*, eyes on the second fold of the (retracted) mantle margin. Drawing by Laszlo Meszoly.

of the foot is divided by a deep longitudinal cleft into left and right lobes, which are spread sideways to form the pedal anchor in burrowing (see p. 242). There is no byssus or byssal gland in the foot of the adult glycymerid.

Notwithstanding its impressive foot, *Glycymeris* is a slow burrower (Ansell and Trueman 1967; Stanley 1970). The foot takes a long time to probe the substrate, largely because the ligament is weak and unable to brace the shell firmly against the sediment. When *G. glycymeris* is more than one-third buried the ligament is not strong enough even to open the valves against the sand, and they have to be forced apart by the foot (Trueman 1968). Unlike bivalves in which the viscera lie up against the shell, *Glycymeris* is unable to use its adductor muscles in the extension and dilation of its foot, since the mantle cavity extends dorsally almost to the umbones (Ansell and Trueman 1967). Moreover, since the mantle margins are entirely unfused, closure of the shell by the adductors cannot be used to raise the hydrostatic pressure in the mantle cavity; in many bivalves such pressure also helps to force blood from the viscera into the expanding foot (Trueman, Brand and Davis 1966). In *Glycymeris* the highly developed muscular sheath and transverse muscles of the foot and visceral cavity partly compensate for the lack of these special adaptations.

Although the burrowing of *Glycymeris* is slow and mechanically inefficient, compared with that of more specialized bivalves, the animal does move around a good deal, principally at night. When washed out of their shallow burrows, or otherwise disturbed, glycymerids plough considerable distances along the sediment surface in search of a suitable new substrate, leaving meandering furrows behind them (Thomas 1970; Stanley 1970). Lacking siphons, glycymerids are normally just covered by the sediment, with their posterior-ventral mantle margins exposed at the sediment surface. In gravel they may burrow deeper, and can apparently obtain adequate feeding and respiratory currents through the sediment (Ansell and Trueman 1967). The attachment of several epifaunal species to the posterior-ventral margins of many living glycymerids (Thomas 1970) and the presence of well-developed mantle eyes in this region confirm that they are normally exposed at the surface. In the case of fossil glycymerids, the same conclusion can be drawn from the frequent abundance of polychaete shell-borings with their openings along this part of the shell margin.

Glycymeris is a suspension feeder, with large filibranch gills that have been described in great detail by Ridewood (1903) and Atkins (1936). The gill axes are attached dorsally to the mantle, very high up, under the hinge plate (text-fig. 2). They extend steeply downwards to the posterior-ventral margin, reaching it at the point where the two mantle lobes remain in contact during feeding, and thereby separating the posterior inhalant and exhalant currents. The individual gill filaments are attached to one another by interlocking cilia, but their distal ends are not attached to either the mantle or the wall of the visceral cavity. As a result, the inhalant and exhalant chambers of *Glycymeris*, like those of other arcoids, are not as effectively separated as they are in more advanced bivalves.

In addition to the posterior inhalant current, *G. glycymeris* has a subsidiary anterior inhalant current (Atkins 1936). This anterior current, which is thought to represent the primitive bivalve condition (Yonge 1953, 1955), is typical of byssally attached arcoids such as *Arca tetragona* and *Anadara antiquata*, but it is lost in many burrowing forms (Lim 1966). It is not known whether most or only some *Glycymeris* species have such an anterior inhalant current, but those which do must be restricted to coarse, clean, permeable substrates, as noted by Stanley (1970). *Glycymeris* and the other arcoids are also unusual in that they have rejection currents which run posteriorly along the lower margins of the demibranchs, carrying denser particles to the mantle margin, where they are discarded as pseudofaeces (Atkins 1936). The direction and function of these currents may be related to the ancestral anterior-to-posterior direction of the feeding currents; in almost all other living bivalves these currents run anteriorly, carrying food to the labial palps.

All the glycymerid species so far described have very simple palps, with only three or four weakly developed folds. This condition is primarily responsible for their intolerance of fine-grained substrates and turbid water. Furthermore, the Caribbean species *G. pectinata*, which does live in rather more turbid water (see p. 223), has more substantial palps, with a dozen or more clearly defined folds. A similar relationship between the development of the palps and turbidity is seen in other arcoids, and has been well demonstrated among species of *Anadara* by Lim (1966).

Food particles collected by *Glycymeris* travel a roundabout route in order to reach the stomach. They are collected and carried postero-dorsally on the gill filaments, and then dorsally up the gill axis to the labial palps, at the very top of the animal. They must then return ventrally down the long oral groove to the mouth, whence they are carried dorsally again by the oesophagus and into the stomach. In many more advanced bivalves the oral groove is shortened or lost, bringing the palps and the ends of the gills much closer to the mouth. In most bivalves food is carried towards the mouth along both the top and the bottom of each gill lamella, but in *Glycymeris* the ventral margins are occupied with the removal of rejected particles, as noted above.

The structure and function of the glycymerid stomach have been exhaustively described, most recently by Reid (1965). Authors agree that this stomach, which does not differ greatly from those of other arcoids, is simple and unspecialized compared with those of most other bivalves. It is likely that easily digested naked phytoplankton, as opposed to forms with thick cell walls, are the principal source of food for suspension-feeding bivalves such as *Glycymeris* (Jørgenson 1966).

Most bivalve tissues have low oxygen requirements, and it has been generally assumed that the gills are potentially more efficient as respiratory organs than is necessary for the life of the animals (e.g. Ghiretti 1966). Food gathering is certainly the primary purpose of their hypertrophy and specialization. On the other hand, great improvements in the pattern of blood circulation through the gills have been made in the more advanced bivalves, suggesting that the more primitive gills were not in every circumstance more than adequate to fulfil their respiratory function. In *Glycymeris*, as in all arcoids, both the afferent and the efferent blood vessels are located in the gill axis. As a result, blood flowing into each filament must travel down the descending limb and up the ascending limb of the filament, and then all the way back, the two streams being separated by a median septum. Clearly this is an inefficient system compared with those of *Mytilus* and the eulamellibranch bivalves, where the oxygenated blood flows into efferent vessels which run along the distal margins of the demibranchs.

Haemoglobin has been found in the blood of some species of *Glycymeris*, but in others it appears to be absent (Manwell 1963). In a single population of *G. violacescens*, some animals were found to have dark-red blood, others had less haemoglobin, and some had none at all (Kruger 1958; his *G. nummaria*). On the basis of its haphazard distribution among closely related molluscs, and because its occurrence is not correlated with life in oxygen-poor habitats, Read (1966) infers that haemoglobin is of minor importance to these animals. However, in view of the limitations of the respiratory circulation discussed above, it is surely significant that the occurrence of haemoglobin is far more widespread in the Arcoida than in other bivalve groups (data in Read 1966).

Little is known about the reproduction of *Glycymeris*. In common with most other bivalves, these animals show no sign of sexual dimorphism in their shells, and they have been assumed to be truly dioecious. However, Lucas (1964, 1965) has presented evidence that is suggestive of protandry in *G. glycymeris*.

Although the Glycymerididae did not appear until the Cretaceous, *Glycymeris* can nevertheless be regarded as a primitive bivalve in the sense that it is an anatomically and functionally generalized descendant of an ancient and very conservative stock. As such, its potential for evolutionary radiation into new environments has been severely limited by its unspecialized burrowing, feeding, and respiratory mechanisms. On the other hand, the particular combination of adaptations acquired by *Glycymeris* evidently serves it well in the limited range of habitats it prefers. *Glycymeris* is at least as well adapted for life in these physically rigorous environments as any other bivalve.

FORM AND FUNCTION OF THE *GLYCYMERIS* SHELL

The glycymerid shell is a geometrically very simple structure. Nevertheless, it must fulfil three different functions simultaneously: it is at once a protective armour, a skeletal support for the soft tissues, and a burrowing plough. As in other molluscs, the morphology of this shell is determined both by functional requirements and by the constraints of accretionary growth (Stasek 1963; Raup 1966). Growth of the shell is largely isometric, the adult proportions being established in most cases by the time it is about 5 mm high. Relative growth in the early shell has not been studied, but two kinds of allometry, with consequent changes in shape, occur in later ontogeny.

The size of the ligamental area increases exponentially relative to that of the shell as a whole, during ontogeny. This allometry is a functional necessity, as will be shown below, so it occurs in all glycymerid shells except perhaps for very small species. Exponential growth of this kind has its greatest effect when the animal is large, and it places strict limits on potential size increase, as long as the rates of relative growth are unchanged. In contrast, the posterior-ventral margin of the shell may become relatively elongated with increasing size, as a result of differential, but linearly related, growth rates. This allometry is not required by the basic mechanics of the shell, so the adaptation only appears in some species and populations. Here the greatest change in proportion occurs when the shell is small, and no limitation is placed on size increase.

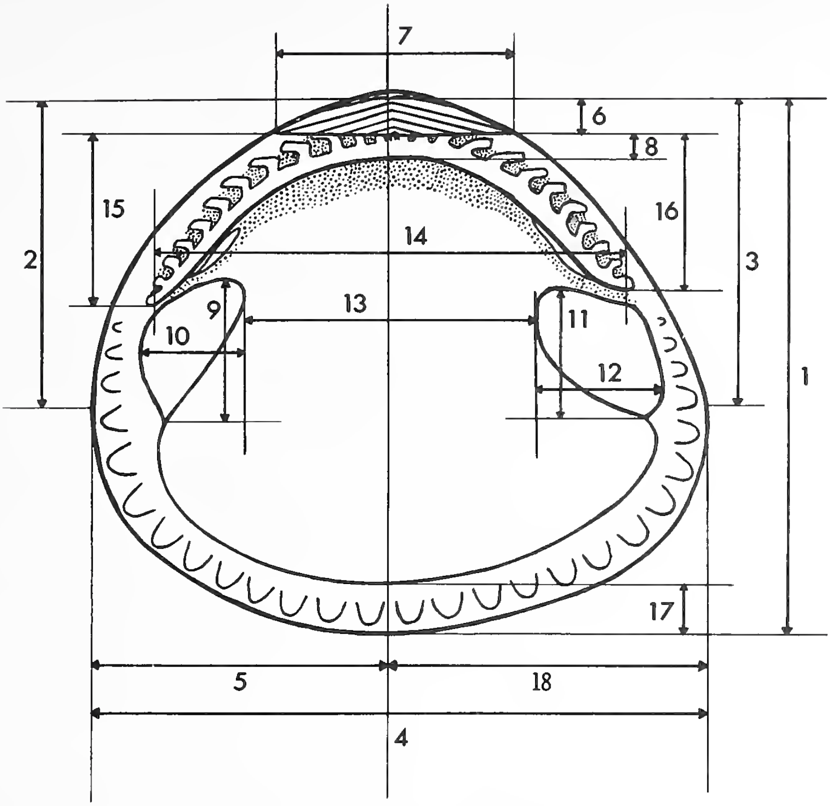
The forms of individual elements of the glycymerid shell will be considered here in relation to their functions. Much of what follows is based on detailed studies of about fifty samples from populations in the *G. americana* and *G. subovata* lineages, from the Neogene sediments of the eastern United States. Parameters measured and referred to here are shown in text-fig. 3 and Table 1. More of the statistical data of this study is given in Thomas (1970). A similar study of one of these populations, of *G. parilis*, has been made by Brower (1973). The following analysis is based on these studies, and on more general observations of a wide range of living and fossil glycymerids. It will become clear that different functions make conflicting demands upon the shell, and that its simple geometry results from a series of compromises among these requirements. Such compromises have left *Glycymeris* well adapted to its particular habitat, but with little evolutionary flexibility, due to the high degree of morphological integration of its shell characters.

Adductor muscle scars. Glycymeris is the archetypical dimyarian. Its subequal adductor muscles are symmetrically disposed behind and in front of the umbones, and are essentially equidistant from the hinge axis. Quick and slow muscle are present in both adductors. As in most dimyarians, the quick muscle constitutes the more dorsal portions of the adductors, where a smaller contraction is necessary to close the valves completely, and hence quickly (cf. the position of the adductors in *Ensis* (Trueman 1967) and the quick muscle in scallops (Gould 1971)). At the same time,

TABLE 1. Definitions of terms and measured parameters, shown in text-fig. 3 (numbers in column A) and referred to in the text. Computer codes in column B, used in multivariate studies, identify the variables of Tables 2 and 3. Variables were measured in the following units, with the precisions given: shell thickness (measured with caliper), 0·1 mm; all other linear variables (measured on a rectangular vernier stage), 0·1 mm; compound variables are ratios and products of these measurements; internal volume (measured by displacement weighing), 1 mm^3; shell weight, 0·001 g.

A	CHARACTER	B
1	Height of shell (measured from umbo)	HTLGSP
2	Height of anterior extremity	HANTEX
3	Height of posterior extremity	HPOSEX
4	Length of shell	LENGTH
	Linear measure of size, square root (height × length)	RTHXL
5	Anterior length	A LEN
18	Posterior length	P LEN
	Asymmetry = A LEN/P LEN (text-fig. 12)	
6	Height of ligamental area	HTLIG
7	Length of ligamental area	LENLIG
8	Median height of hinge plate (directly below umbo)	HTHING
	Height of ligamental area/height of hinge plate	LIGHIN
15	Height of anterior tooth row	HT ATO
16	Height of posterior tooth row	HT PTO
14	Distance between last anterior and posterior teeth	DISTET
9	Height of anterior adductor scar	HT AAD
10	Length of anterior adductor scar	LENAAD
	Area of anterior adductor scar	HXLAAD
11	Height of posterior adductor scar	HT PAD
12	Length of posterior adductor scar	LENPAD
	Area of posterior adductor scar	HXLPAD
13	Distance between inner margins of adductor scars	DISTAD
	Adductor moment = sum of adductor scar areas × mean distance from hinge axis	MOMENT
17	Height of crenulated, extra-pallial, margin	HTCREN
	Width of margin outside anterior adductor	EX AAD
	Width of margin outside posterior adductor	EX PAD
	Shell thickness (between tops of adductor scars)	THICK
	Convexity = maximum perpendicular distance, plane of commissure to exterior surface of shell	CONVEX
	Internal volume (of single valve)	INTVOL
	Approximation for volume = height × length × convexity of shell	HXLXC
	Weight of shell (excellent preservation only)	WEIGHT
	Displacement of mid-point of ligamental area from umbo	UMBO
	Number of crenulations between inner adductor margins	CRENS
	Number of anterior hinge teeth	ATEETH
	Number of posterior hinge teeth	PTEETH
	Number of anterior ligamental chevrons	ACHEV
	Number of posterior ligamental chevrons	PCHEV

the more ventral position of the slow muscle gives it a greater mechanical advantage about the hinge axis, enabling it to hold the valves the more tightly closed against opening forces exerted by the physical environment or potential predators. Glycymerid adductors are extremely strong, absolutely and for their sizes. Plateau (1883) found that *G. glycymeris* took a weight of 2·7 kg, hung at the shell margin, before the valves would open 1 mm. Among the species he studied, Plateau found

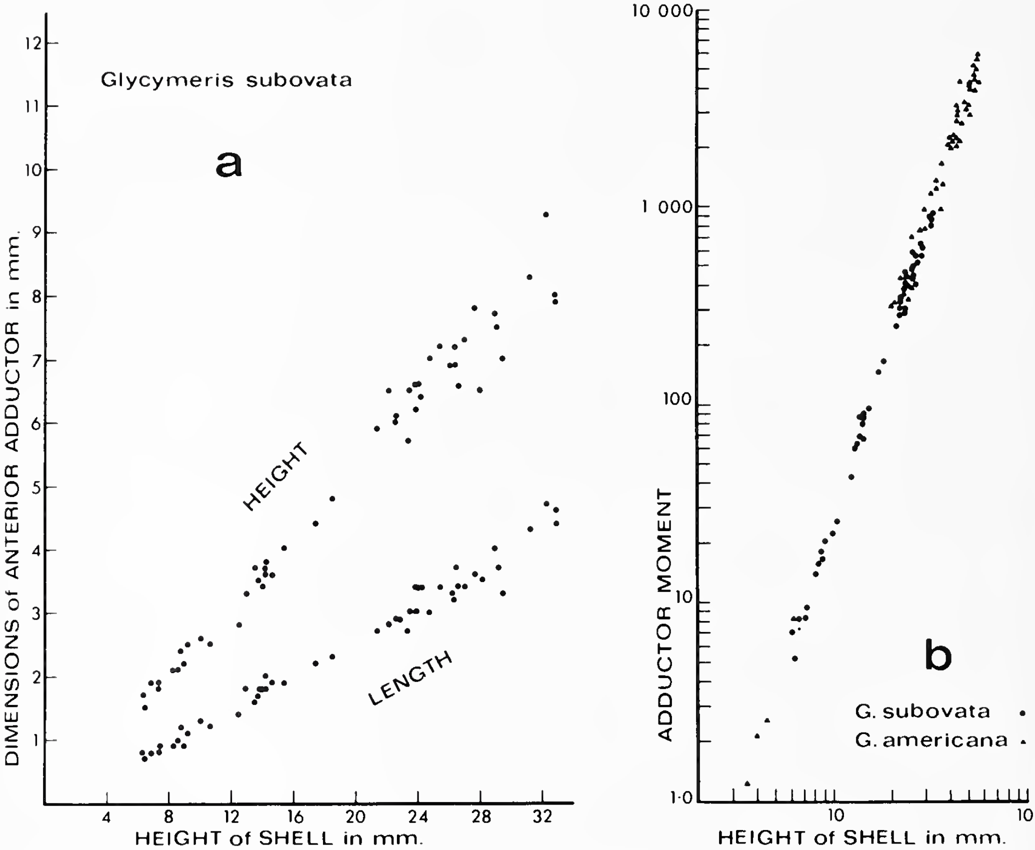


TEXT-FIG. 3. Parameters of the *Glycymeris* shell measured in quantitative studies and referred to in the text. Terms applied to these characters are given in Table 1.

that the strength per unit cross-sectional area of the adductors of *G. glycymeris* was exceeded only by that of *Venus verrucosa*.

In most glycymerids the muscle scars are situated on low buttresses, which are produced by the secretion of thick wedges of adductor myostracum. Kauffman (1969) has suggested that these buttresses serve to strengthen the shell against the stresses developed by the adductor muscles. Buttressed adductor scars are also more nearly perpendicular to the lengths of the adductor muscles than scars flush with the curved surface of the shell. This may improve the effective adhesion of the muscles to the shell by reducing the shear component of adductor stress acting on their attachments. The posterior buttress, like that of *Cucullaea*, often forms a distinct flange, overlapping a groove along the inner margin of the adductor scar (Pl. 38, fig. 7). This groove, which extends back towards the umbo, tracing the line of growth of the adductor margin, appears to have yet another function. Atkins (1936, p. 237) shows a subsidiary ciliary rejection current on the mantle of *G. glycymeris* in this position. The groove forms a distinct channel for this current, away from the food-bearing stream that runs dorsally along the extremity of the outer demibranch of the gill.

The forces exerted by the adductor muscles of fossil glycymerids can be estimated from projections of the areas of their adductor scars on to the commissural plane; these projections represent the cross-sectional areas of the muscles. The estimates do not take account of ontogenetic changes in the proportions of quick and slow muscle, which are not seen on the undifferentiated muscle scars, and which have not been investigated in the living animals. Although one would expect the strength of the adductor muscles to increase in proportion to the weight of the animal, the relative sizes of the adductor scars of *Glycymeris* remain essentially constant during ontogeny (text-fig. 4*a*). The area of the anterior adductor was plotted against a linear measure of shell size ($^2\sqrt{}$ (height × length)) for forty-eight samples from the *G. subovata* and *G. americana* lineages, and log–log reduced major axis regressions were calculated.



TEXT-FIG. 4. Isometric growth of adductor muscles. A, growth of the anterior adductor of *Glycymeris subovata* (Shoal River Formation, Miocene, Florida). Linear dimensions of the muscle cross-section, measured as parameters of a projection of the muscle scar on to the plane of the commissure, increase as linear dimensions of shell size. B, growth of the adductor moment of *G. subovata* (same population as above) and *G. americana* (Duplin Formation, Miocene, North Carolina). The closing moment exerted by the adductors is taken to be proportional to the sum of their cross-sectional areas (mm^2) multiplied by their mean distance from the hinge axis (mm), which is here plotted against shell height. Regressions for these samples are $\log y = 3{\cdot}016 \log x - 1{\cdot}632$ and $\log y = 2{\cdot}915 \log x - 1{\cdot}499$ respectively. The adductor moment increases as the cube of shell height, as does the weight of the animal, so growth is almost isometric.

The mean of the slopes of these lines is 2·017 (standard deviation, 0·099), where a value of 2 represents no allometry between an area and a linear parameter. However, the adductors do not simply hold two independent valves together. Rather, they operate a lever system, in which they exert a moment about the hinge axis (Thomas 1970; Gould 1971; Brower 1973). The closing moment developed by the adductors depends on their distances from the hinge axis as well as on the forces they exert. Relative to a linear dimension X, since the cross-sectional areas of the muscles increase as X^2, and since their distances from the hinge axis increase as X, the total moment increases as X^3, keeping pace with weight, and no allometry is required to maintain functional similarity.

The sum of the areas of the two adductor scars, multiplied by their mean distance from the hinge axis, was plotted against the linear measure of size for the same forty-eight samples (text-fig. 4*b*). In this case, the mean of the slopes of the log-log regression lines is 2·915 (standard deviation, 0·091), compared with a theoretical value of 3 for isometry. The moment exerted by the adductor muscles increases almost linearly with the volume or weight of the animal, implying that there is no major change in adductor function during ontogeny.

It is significant that the magnitude of the total moment does not quite keep up with weight, although the sizes of the muscles themselves do, as shown by the slopes of the regressions. This is largely the result of a negative interaction between two size-correlated shell parameters. The distance between the adductors and the umbo increases linearly with size, but the height of the ligamental area has to increase allometrically (see below). As a result, the hinge axis moves ventrally with increasing size. This displacement is fairly small compared with the distance from the hinge axis to the adductors, but it slightly reduces what would otherwise be the linear increase of that distance. The moment is thus somewhat reduced in larger shells by this ventral movement of the hinge axis; the needed increase in the relative size of the ligament impinges on the volume-related growth of the adductor moment.

Brower (1973) has suggested that the adductors of *G. parilis* exhibit preparatory growth, being larger than necessary to perform their required function in the young animals. He observed that small shells in his sample have relatively large adductor scars, the areas of which grow at significantly less than the rate needed to maintain isometry with respect to shell height (exponent$=$1·79 as opposed to 2; my results for the same population are rather higher). In this case it is the rate of growth of the adductors themselves, and not the relatively modest allometric growth of the ligament, that reduces the rate of increase of the adductor moment below that needed to maintain isometry (Brower's exponent$=$2·84; my data for the same population, 2·81). Clearly these samples are not exceptional, for their parameters lie well within the range of variation among my populations.

The inference that the size of the juvenile adductors is preparatory, rather than immediately functional, is implicitly based on the assumption that the function of the adductors is primarily to close the shell against the ligament, which is small in the early stages of its allometric growth. In fact, the adductors are much stronger than the ligament at all growth stages. *Glycymeris* needs strong adductor muscles to articulate its thick, heavy shell in burrowing. They also serve to keep the valves tightly closed when the animal is washed out and rolled around under turbulent conditions.

Their importance in resisting predators is unknown, although experiments of Hancock (1965) suggest that rates of starfish predation vary with the strength of bivalve adductor muscles. The nearly isometric growth of the glycymerid adductor moment, with only small variations among populations and species, shows that in ontogeny its strength is critically related to shell size, and restrained from deviating far from it.

Ligamental area. The accretionary growth of bivalve ligaments, together with the need to separate the umbones so that the valves may open, constitutes a fundamental limitation on their form and function (Stasek 1963; Raup 1966). As Trueman and Ansell (1969) have observed, bivalves such as *Tellina* with opisthodetic, parivincular ligaments have solved this problem most effectively, although even this type of ligament may be relatively weak in forms such as *Glossus* where the umbones curve sharply away from one another (Owen 1953). For a bivalve of its size and shell thickness, *Glycymeris* has a particularly weak ligament (Trueman 1964).

In common with most arcoids, *Glycymeris* has a 'chevron-type' or duplivincular (Newell 1942) ligament. This ligament is all but entirely external, the valves being articulated about an axis just within its ventral margin. In most species it is symmetrically distributed, before and behind the umbones (amphidetic). It consists of parallel layers of lamellar conchiolin and partly calcified fibrous material. The fibrous layers, which typically lie in chevron-shaped grooves on the ligamental areas of the valves, are elastic only under compressional stress. The lamellar layers, which exert the opening moment of the ligament, are elastic under both tensional and compressional stress (Newell 1937). A ligament consisting of such alternating layers is unspecialized in the sense that the materials of which it is composed are not set apart in positions where they can best perform their different mechanical functions.

The ontogeny of the ligamental area of *G. obovata* (Oligocene, France) has been described by Bernard (1896). In the early post-larval shell the ligament, which is set in a small triangular fossette at the centre of the hinge, is entirely internal (text-fig. 8). As the cardinal platform develops, the hinge axis moves ventrally, and the ligament divides into the first anterior and posterior grooves. Subsequent chevron-sheets of lamellar and fibrous ligament are added alternately beneath the umbones, growing ventrally and outwards from the centre along the hinge axis. At the same time the ligamental area expands ventrally over the upper part of the hinge plate, and the earlier hinge teeth are overridden by a thin wedge of crossed-lamellar shell material, to the surface of which the ligament is attached.

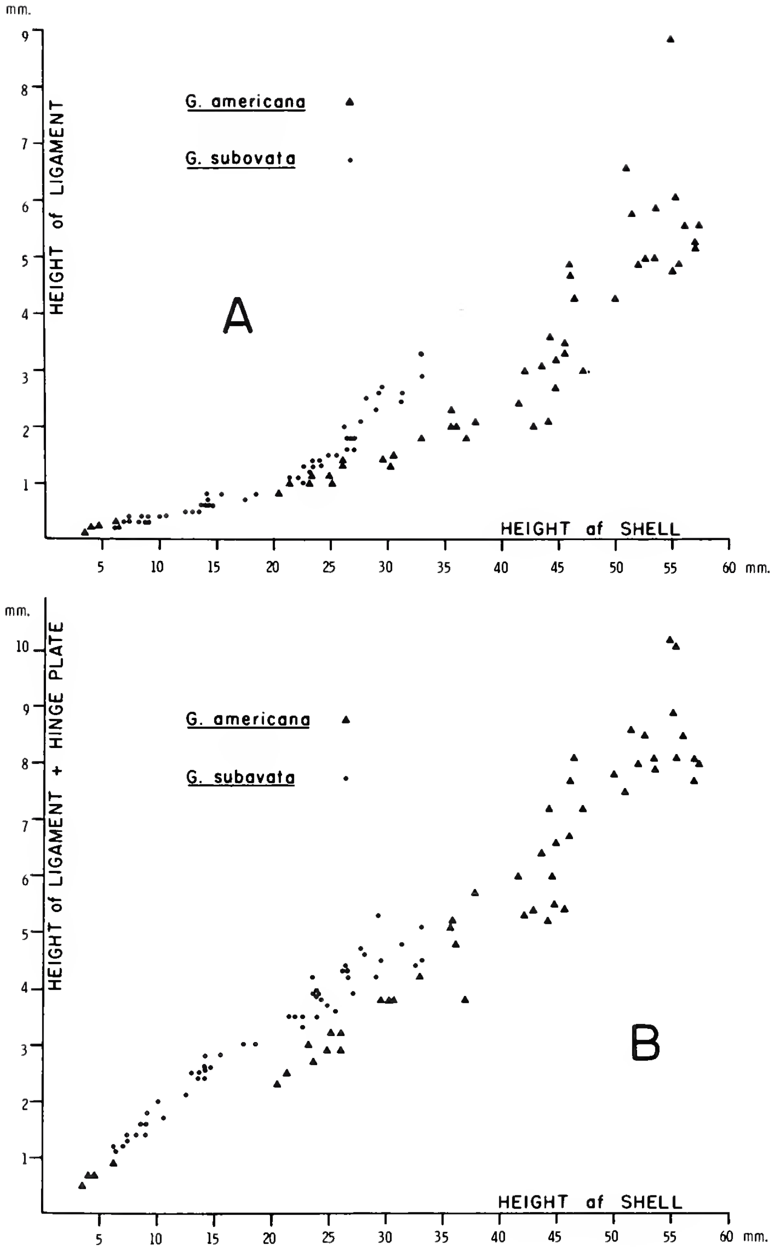
As a result of the considerable inter-umbonal growth of *Glycymeris* the earlier, more dorsal sheets of lamellar ligament are stretched across a wider and wider gap during ontogeny. Up to a point this increases the tension they exert, but finally they break below the umbones. Thus in the larger shells of many species only the latest chevrons and the anterior and posterior ends of the earlier ones are functional, as in other arcoids (Newell 1937; Stasek 1963). In most glycymerids the successive chevron-sheets are added parallel to one another, and are of a similar thickness. Thus, after the earlier stages of growth, the relative proportions of lamellar and fibrous ligament do not change. The number of such ligamental chevrons has nothing to do with the age of the animal, as suggested by Hayasaka (1962), but rather is linearly related to the size of the ligamental area. In a few species the individual sheets thicken ventrally, and new chevrons are added less frequently.

The size and shape of the ligamental area of *Glycymeris* change allometrically with the growth of the shell to a far greater extent than any other character (text-figs. 5*a*, 6; Pl. 38, figs. 1–5). This allometry is necessitated by the dorsal breakage of the ligament. It is not explained by the fact that the ligament moment is inadequate to open the valves, or by any geometrical constraint on the relative size of the ligament in small shells, as supposed by Brower (1973, pp. 83, 89) in his study of the ontogeny of *G. parilis*. The ligament opens the shell by exerting a moment about the hinge axis, opposite to the closing moment exerted by the adductors when they contract. As long as the ligament remains unbroken, the tension it exerts must increase at least as its cross-sectional area (the detailed mechanics are more complicated; Thomas, in preparation), while the moment arm increases as a linear dimension in the absence of allometry. Like the adductor moment, the ligament moment would scale as X^3, maintaining its relationship with the weight of the shell it must articulate, without any allometry, but for the fact that the ligament breaks dorsally. The allometric growth of the internal ligament of *Argopecten*, described by Waller (1969), is required by the changing demands of swimming with increasing size (cf. Gould 1971). In contrast, the allometry of the glycymerid ligament is required by its inability to maintain functional similarity, due to its mode of growth.

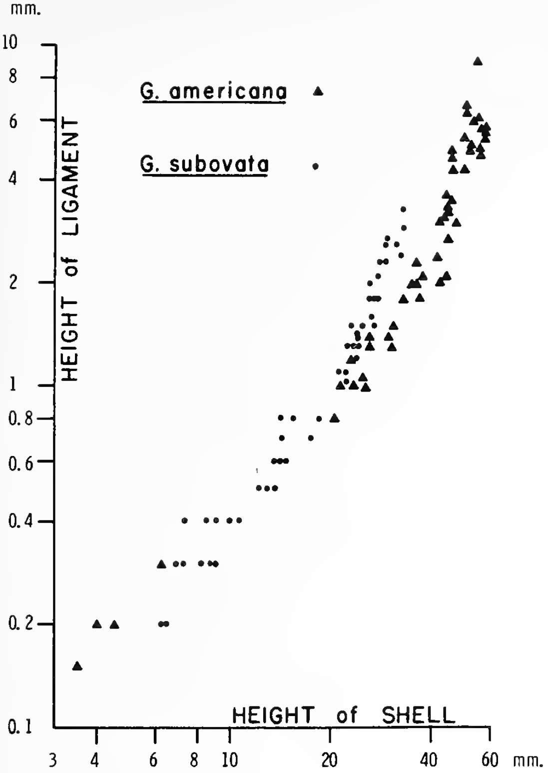
The area of the ligamental attachment was plotted against a linear measure of shell size ($\sqrt[2]{}$ (height × length)) for forty-eight samples of the *G. americana* and *G. subovata* lineages, and log–log reduced major axis regressions were calculated. The average slope of these regressions is 2·641 (standard deviation, 0·279), compared with a value of 2 for isometric growth. The slope for a collection of *G. parilis* is 2·499, in close agreement with the slope of 2·45 obtained by Brower (1973) for a least-squares regression on the same characters of a collection from the same locality. It is not possible to estimate ligament moments, because of the partial breakage of the ligament. However, it is clear that the size of the ligamental area increases allometrically to compensate for this breakage.

Since the dorsal part of the ligament breaks in larger shells, a more efficient ligament would be produced by increasing its length rather than its height. In fact, the shape of the ligamental area usually changes little during growth; its length increases allometrically with shell size, but slightly less rapidly than its height. There is a functional compromise here, in that a longer ligament can be produced only by ventral displacement of the hinge axis, or by increasing the length of the shell at the hinge axis. However, a dorsally longer shell would be less well adapted for the rocking locomotion of *Glycymeris* (see p. 242).

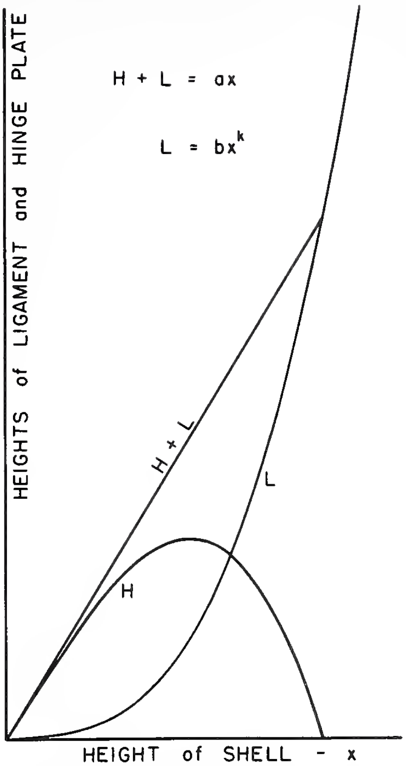
The height of the ligamental area, L, increases logarithmically relative to the height of the shell, but the distance from the umbo to the base of the hinge plate immediately below it, $L+H$, increases linearly with size (text-fig. 5). As a result, the height of the median part of the hinge plate, H, increases at first, stops, and then decreases absolutely during growth, as the hinge plate is overgrown by the rapidly expanding ligament (text-fig. 7). In large shells of some populations the ligamental area may actually extend to the base of the median hinge plate, separating the anterior and posterior series of hinge teeth completely (Pl. 38, fig. 7). This relative growth of the



TEXT-FIG. 5. Growth of the ligament and hinge plate. A, strongly allometric growth of the ligament, shown by the relationship between the height of the ligamental area and the height of the shell. B, isometric growth of the total space between the umbo and the median base of the hinge plate. Same populations as in text-fig. 4.



TEXT-FIG. 6. Double logarithmic plot of the height of the ligamental area against the height of the shell. The curves show that the exponent in this logarithmic relationship itself increases with size in later ontogeny. Same populations as in text-fig. 4.



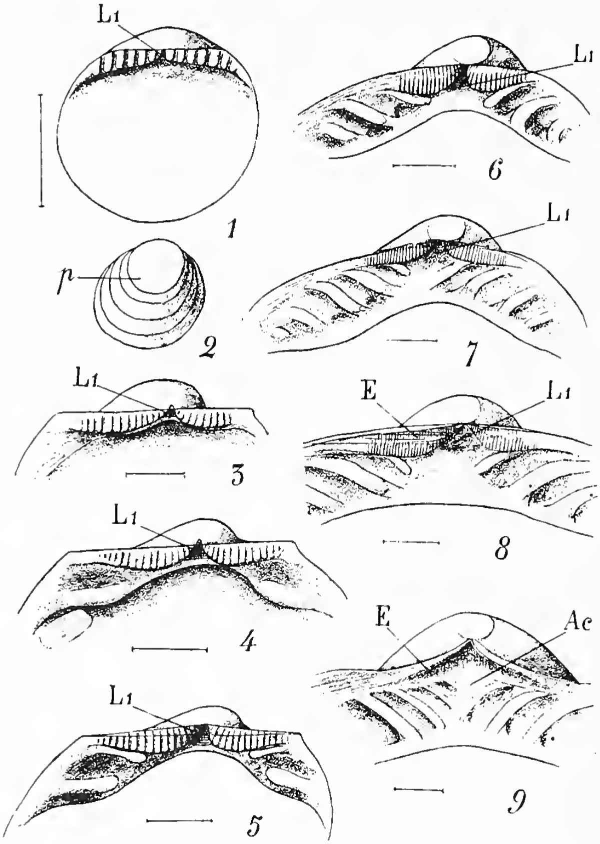
TEXT-FIG. 7. Idealized relationship between the growth of the height of the ligamental area (L), the height of the median hinge plate (H), and their sum, against the height of the shell (x).

ligament considerably reduces the number and effectiveness of the hinge teeth; Brower (1973) gives a simple parabola as the equation of best fit for the number of teeth versus shell height in *G. parilis*. Evidently the strength of the ligament is more critical than the precise alignment of the valves in large glycymerids. The larger ligament could be accommodated without interfering with the hinge if the entire hinge plate were to be displaced ventrally during ontogeny. This would reduce the size of the mantle cavity, increase the weight of the shell, and move the centre of gravity of the animal dorsally. These disadvantages evidently outweigh the need for a complete series of teeth in larger shells.

The ligament of *Glycymeris* is poorly designed for its purpose, especially compared with those of more advanced bivalves. New organic material must continually be secreted to replace that which has lost its function. Yet, despite its allometric growth, the ligament is still one of the weakest among the bivalves. It serves adequately to articulate the valves and to open them during feeding, but is relatively ineffective in bracing the shell against the sediment during the probing phase of burrowing (Ansell and Trueman 1967).

Hinge teeth. The hinge teeth of most bivalves serve two functions. One is to guide the gaping valves into perfect apposition as they close. The other is to prevent the disarticulation of the closed valves by any shearing stress in the commissural plane which might be exerted upon them. The variety of types of bivalve hinge teeth, even amongst animals with a similar mode of life, indicates that these functions can be fulfilled, perhaps equally well, in several different ways. The more advanced heterodonts have developed specialized teeth to perform each function, while in the taxodonts both purposes are served by a large number of similar teeth.

The ontogeny of the hinge teeth of *G. obovata* has been minutely described by Bernard (1896). As the cardinal platform begins to develop, the first true teeth are formed, *parallel* to the hinge axis (text-fig. 8). Subsequent teeth are added ventrally



TEXT-FIG. 8. Ontogeny of the hinge and ligamental area of *Glycymeris obovata* (Lamarck) from the Oligocene of the Paris Basin. 1, prodissoconch, right valve. 2, early dissoconch, exterior right valve. 3–9, growth of the left valve. Scale-bars all represent 0·1 mm. Key: *p*, prodissoconch; Li, primary internal ligament; E, first chevron of lamellar ligament; Ac, region where tooth rows meet, and are subsequently overgrown by the ventrally expanding ligamental area. (From Bernard 1896, p. 60.)

to the expanding cardinal platform by successive bifurcations of the terminal teeth. The new teeth are always subparallel to the hinge axis, but as the shell grows and they occupy progressively more dorsal positions on the hinge plate, they swing around, becoming oblique or chevron-shaped. The earliest teeth ultimately grow perpendicular to the hinge axis, along which they are gradually overgrown by the ventrally expanding ligamental area. In some cases their dorsal margins are cut off sharply against the base of the ligamental area, and shell resorption definitely takes place during growth. As noted above, and by Brower (1973), the number of hinge teeth changes in a complex manner during ontogeny, first increasing with size, and later decreasing due to the overgrowth of the ligamental area.

The hinge teeth of large or very thick *Glycymeris* shells commonly become irregular, much reduced, and sometimes fused together (Pl. 38, fig. 7). This led Jeffreys (1863, p. 168) to the amusing observation that 'The teeth occasionally decay and become carious in living specimens'. In a few cases the hinge teeth even obtrude into the lower part of the ligament, indicating that the animals were unable to resorb their summits completely. These observations suggest either that the form of the hinge teeth is no longer critical in securing the apposition of the valves in such large individuals, or, more likely, that this irregularity is an undesirable but unavoidable consequence of the interaction between the growth of the ligament and that of the hinge plate.

The larger teeth of *Glycymeris* are always more or less bicuspate. Their crests are divided by an oblique longitudinal furrow, which is not reflected by a ridge in the corresponding pit. This furrow may provide a passage for the diffusion of materials for shell secretion in the extrapallial fluid, for the two mantle lobes occupy a very narrow space between the interlocking teeth. The sides of the hinge teeth have distinct vertical ridges and grooves, which further promote the perfect interlocking of the valves.

The shape of the hinge teeth depends both on the arching of the hinge plate, and on its width, which is highly correlated with shell thickness. Shells with longer, straighter hinges, like *G. glycymeris* and *G. americana*, have chevron-shaped teeth with most of their lengths parallel to the hinge axis. Shells with shorter, more strongly arched hinges, like *G. pectinata* and *G. subovata*, have chevron teeth with longer vertical components, the two branches of each tooth being more nearly equal in length. This distinction is complicated by the fact that thinner shells have more parallel teeth, while thick shells tend to have equibranched chevron teeth.

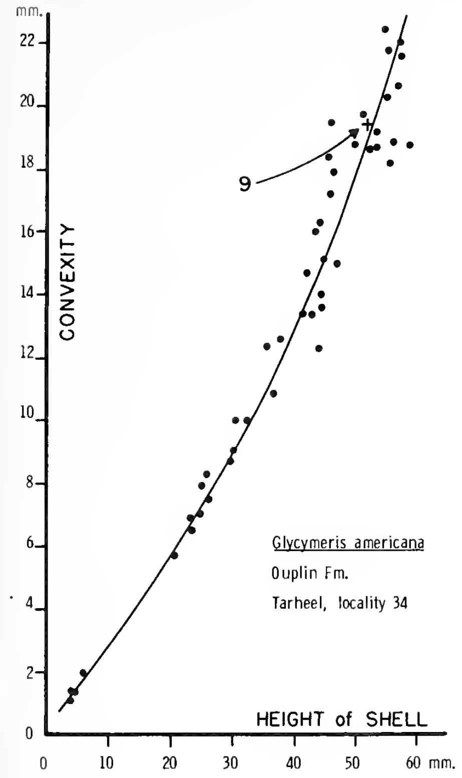
While the shapes of the teeth depend on the shape of the hinge plate itself, they are also directly related to function. Teeth parallel to the hinge axis must be particularly important in aligning the closing valves where the position of the hinge axis, in the lower part of the ligament, is not well defined. However, straight teeth parallel to the hinge axis would provide little protection against disarticulation by anterior-posterior shearing stresses between the valves. Likewise, teeth perpendicular to the hinge axis would provide little resistance to dorsal-ventral shearing stresses. Straight teeth perpendicular to the inner margin of the hinge plate would be rather better, where the hinge plate is strongly arched. Clearly, chevron-shaped teeth are superior to all of these in resisting shearing stresses in the plane of the commissure in all directions.

Spiral curvature. Growth of the exterior of the glycymerid shell occurs along one plane spiral and an infinite number of anterior and posterior turbinate spirals, all originating at or near the umbo (see Lison 1949). In most populations and species these spirals are more or less truly logarithmic, and the convexity of the shell changes little during ontogeny, although it varies considerably from one species to another. In two Miocene samples of *G. americana* the convexity of the shell does increase substantially relative to its height, as shown in text-fig. 9. The change in spiral angle involved in this allometry, calculated for an individual specimen by the formula of Lison (1949, p. 20), is shown in text-fig. 10. The significance of this allometry is not clear. In terms of the model of shell growth proposed by Carter (1967) this kind of change would occur if the rate of shell secretion was maintained while the rate of proliferation of new mantle cells decreased. The shells in these two collections are relatively thick, and their later growth lines are very closely spaced. Increased convexity and shell weight would be quite disadvantageous in terms of burrowing, but they may have a stabilizing function in current-swept environments, as suggested by Stanley (1970, p. 69).

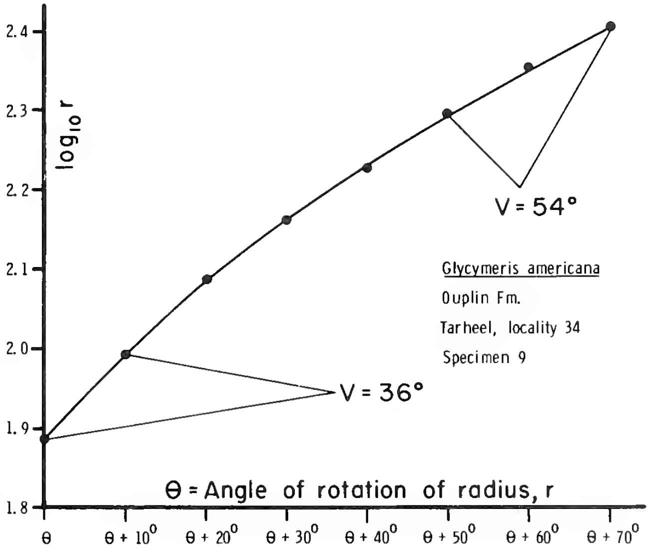
As in other arcoids, considerable shell secretion occurs right up to the glycymerid hinge line, and the growth of the ligamental area also describes a spiral transverse section (Stasek 1963). The curvature of this spiral in *Arca noae* is much stronger than that of the shell exterior, as the umbones of the two valves grow very far apart. In contrast, the allometric growth of the ligament is directed ventrally in *Glycymeris*, and its attachment area shows a shallower curvature than the shell exterior. Paradoxically, the interumbonal growth which ultimately leads to the breakage of the ligament is in the first instance necessary, to stretch the passive elastic ligament between the valves, so that it can exert tension between them. Interumbonal growth is also necessary to separate the opposing umbones, which would otherwise grow together and prevent the valves from opening (Stasek 1963). This problem is evidently not completely solved for *Glycymeris*, in that the umbones frequently exhibit abraded facets at the point where they meet when the valves gape widely.

Shape of the shell margin. It has been suggested that 'The rounded form exemplified by *Glycymeris* is suited to a relatively inactive bivalve . . .' (Purchon 1968, p. 157), but this view is inconsistent with both the form and habits of the animal. The symmetrical shape of the *Glycymeris* shell is in fact related to its mode of locomotion, as will be shown here.

Glycymeris is not a quick or mechanically efficient burrower. However, the animal is able to burrow into firm substrates and to move around a great deal on the surface by means of its exceptionally muscular foot. The movements of *G. glycymeris* have been described by Deshayes (1858), Vlès (1906), and Ansell and Trueman (1967); recently Stanley (1970) and Thomas (1970) have observed the locomotion of *G. pectinata.* At the surface, the animal supports itself in a furrow, with its commissure vertical. From this position the foot probes anteriorly down into the sediment. When fully extended it is dilated, and two ventral lobes, which had been held tightly together during probing, are spread sideways, at right angles to the axis of the foot. The foot thus forms a stable anchor, with the shape of an inverted mushroom. The valves are then sharply closed to about half their previous gape, forcing water out of the mantle



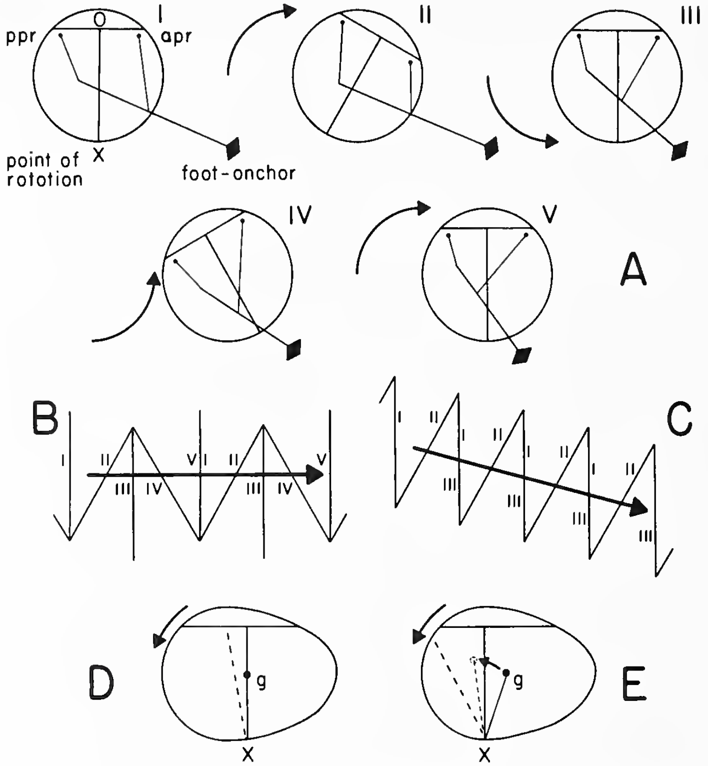
TEXT-FIG. 9. Allometric change in the spiral curvature of a *Glycymeris americana* population during ontogeny, shown by the changing relation of height and convexity of the shell. Curvature of specimen 9 is illustrated in text-fig. 10.



TEXT-FIG. 10. Allometry of the spiral angle, shown by the changing value of log r with increasing θ. Values of V calculated, for increments shown, by the formula of Lison (1949, p. 20). Radii were measured from the pole of the spiral, by the projection method described in Maclennan and Trueman (1942).

cavity into the surrounding sediment, loosening it and making it more easily penetrable.

The action of the pedal retractor muscles in moving *Glycymeris* forward against its pedal anchor is shown diagrammatically in text-fig. 11*a*. From position I to II the bivalve simply rocks forward about its centre of gravity by the contraction of its anterior pedal retractor. From II to III the contraction of the posterior retractor draws the shell forward and down; the median axis is now back in the vertical position. If the animal is to bury itself in the sediment probing now begins again, and these steps are repeated serially (see text-fig. 11*c*). Alternatively, if the animal is to move along the surface, a further contraction of the posterior retractor serves to rock the shell backwards and upward (III–IV). Finally, the anterior retractor and the release of the pedal anchor bring the animal back into a vertical position at the same horizontal level as it began (V). The effect of serial repetition of these movements is shown in text-fig. 11*b*. Such rocking locomotion is characteristic of both *G. glycymeris* and



TEXT-FIG. 11. Burrowing movements and shell form. A, rocking locomotion of *Glycymeris*. *apr*, *ppr*, anterior and posterior pedal retractor muscles. B, locomotion on the surface, diagrammed as changes in the position of the line *OX*. C, similar diagram of downward locomotion, leading to burial in the sediment. D and E, rocking locomotion and the asymmetric shell. D, the animal rocks about its centre of gravity, *g*. E, the animal rocks about a point anterior of its centre of gravity. These diagrams are more completely explained in the text.

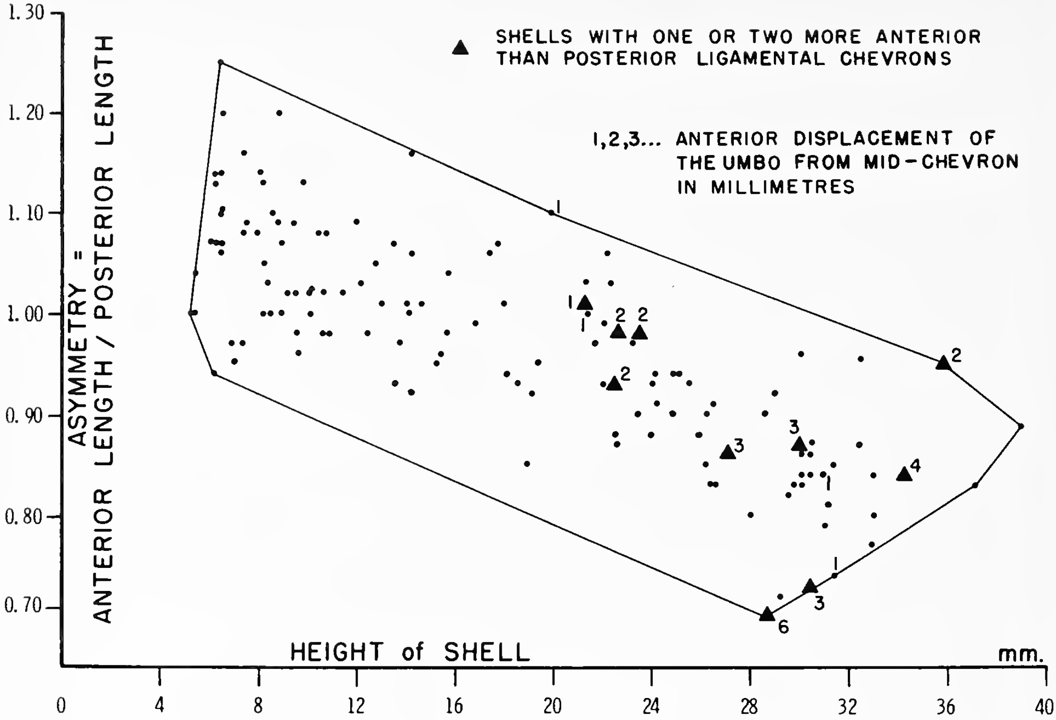
G. pectinata, although Stanley (1970) has stated that the latter species burrows with its hinge line horizontal. The pedal retractors are assisted in these manipulations by transverse muscles in the foot and visceral cavity, and pedal protractor muscles which extend across the foot from beneath the anterior adductor (see also p. 225). The pedal retractors themselves are securely attached to buttressed scars at the ends of the relatively thick hinge plate.

The rocking locomotion of *Glycymeris* provides a functional explanation for the anterior-posterior symmetry of its shell, and for its nearly circular shape. If the animal were posteriorly elongated it might rock about a point below its centre of gravity, which would be behind the median axis, but it could not rock through a very large angle (text-fig. 11*d*). Alternatively, it could rock through a larger angle about a more anterior fulcrum (text-fig. 11*e*) but now it would have to do additional work to lift its centre of gravity, which would be behind the fulcrum. An anteriorly elongated animal would suffer even more acutely from these mechanical problems. Hence the paradigm for an animal with the rocking locomotion of *Glycymeris* (or *Divaricella*, which moves vertically down into the sediment, Stanley 1970) is a symmetrical, circular form, which allows a maximum of rotation while keeping the centre of gravity always directly over the rotational fulcrum.

Since more rocking is involved in moving about on the sediment surface than in burrowing into it, we may infer that the maintenance of a symmetrical, circular shape over a long period of evolution by *Glycymeris* represents a continued need for mobility. Such mobility may be required in searching for suitable new burrowing sites, since the animals are surely often washed out in turbulent environments. However, it is also clear that they move about considerably of their own accord.

In some species, and populations within species, the glycymerid shell does become somewhat elongated posteriorly during ontogeny. This allometric growth is particularly well seen in *G. subovata* from the Shoal River Formation (Miocene) of Florida (Pl. 38, figs. 1–5). In this population the smallest individuals have slightly more of their lengths in front of the umbo than behind it, but posterior length increases more rapidly during ontogeny, and many of the larger shells are quite posteriorly elongated. This asymmetry is a very variable character, as can be seen in text-fig. 12, but the linear increase in posterior elongation is quite clear. In contrast with the growth of the ligamental area, the shape of the juvenile shell is here progressively modified by the difference between two linear growth rates, and not by any relative change in the rates themselves. Where allometric changes are required by linear–surface–volume relationships, as in the case of the glycymerid ligament, linear parameters may be related exponentially; changes in bivalve shell shape required by other kinds of problems seem most often to be achieved by differential linear growth (Thomas 1970). The anterior shape of the juvenile *G. subovata* may be related to the accommodation of the large foot, while the posterior elongation of the adult allows deeper burial, with the posterior margin still in contact with the sediment surface.

The degree of posterior elongation varies greatly among populations of some glycymerid species, and is probably correlated with environmental factors. Purchon (1939) found populations of *Cardium edule* from quieter water to be, on average, more elongated than those from wave-swept marine sand. Holme (1961) found the



TEXT-FIG. 12. Asymmetry of *Glycymeris subovata* from the Shoal River Formation (Miocene, Florida). Plot shows that: (1) asymmetry increases linearly with size, in ontogeny; (2) individual variation in the degree of asymmetry is very great; (3) this asymmetry is not produced by pseudo-turbinate spiral growth; more orthogyrate shells, with additional anterior ligamental chevrons, are not necessarily the most asymmetric shells.

shells of *Venerupis rhomboides* from deeper water to be more elongated than those from shallower water. In the case of *Glycymeris*, the orbicular shells are well adapted for locomotion and reburial, following frequent rolling on coarse gravel bottoms. Elongation of the shell allows slightly deeper burial, with the posterior-ventral margin still at the sediment surface, in more stable sand substrates. Moreover, contact with the sediment surface may not always be necessary in open-framework gravels (see p. 227), whereas it is certainly essential in sand. Available ecological and palaeoecological data are suggestive of such a relationship between shell shape and turbulence or sediment type, but by no means conclusive. The functional arguments for it are more compelling.

Intraspecific variation in the posterior shell shape of *Glycymeris* does not affect the whole shell; that is, the elongated shell is not a simple transformation (Thompson 1942, p. 1026) of the orbicular form. Only the posterior radial ribs are modified in elongated shells; they broaden and swing postero-dorsally during ontogeny, while the anterior and median ribs remain simply radial, like those of orbicular shells. The posterior adductor muscle scar also rotates postero-dorsally with these ribs. Elongation is not produced here by changes in the spiral curvature of the whole shell, as further shown in text-fig. 12. Some specimens of *G. subovata* in this population are planispirally coiled, while others are slightly pseudoturbinate (Carter 1967), the umbones pointing just posteriorly. Pseudoturbinate coiling leads to the development of one or two more anterior than posterior ligamental grooves, and to the posterior displacement of the latest chevrons relative to the umbo. It is clear that the pseudoturbinate shells are not significantly more asymmetric than the planispirally coiled shells.

Differences in shell shape among glycymerid species do often take the form of transformations of the whole shell, and may involve changes in the spiral curvature. It appears that the direction of spiral coiling is relatively invariable and under close genetic control, while changes in the spiral angle and local modifications of the shape of the shell margin may occur within species under the influence of environmental factors.

Ribs, periostracum, and crenulations. The shells of different species of *Glycymeris* bear variously developed radial ribs. Most have either very low, flat ribs bearing fine striations and a heavy periostracum, or prominent, usually rounded, ribs lacking striations, with little or no periostracum. It appears that the periostracum is functionally important to the first group, while raised ribs are of some utility to the second.

Bivalve ribs have generally been considered as corrugations whose primary function is to strengthen the shell. The radial patterns of glycymerid ribs are not obviously related to the stresses developed by the ligament and adductors, but they are simple to program and generate in the accretionary growth of the shell. Bivalve shell is a composite material, and much stronger than has been recognized until recently (Taylor and Layman 1972). On the other hand, some bivalves are capable of breaking their own shells by adduction, if they are artificially prevented from closing (Wainwright 1969). Ribs may also increase the shell's resistance to external stresses, exerted on it by predators or the physical environment. Kauffman (1969) has suggested that the prominent ribs of *G. pectinata* enable it to withstand considerable rolling by waves and currents; they may also deter predators, such as crustaceans and some fishes, which crush their bivalve prey. Raised ribs, particularly the steeper, sharper ones, must also make it more difficult for starfishes and boring snails to grasp potential prey; naticids are said to bore relatively smooth-shelled bivalves (Carriker and Yochelson 1968). The ribs of shallow infaunal bivalves help to stabilize the shell in the substrate (Kauffman 1969), and aid in burrowing even where they are not optimally designed for this purpose (Stanley 1970). In *G. pectinata* the ribs assist the weak ligament in bracing the shell against the sediment, which more than offsets the disadvantage of their resistance to the downward pull of the securely anchored foot. It is clear that glycymerid ribs are not specialized for any one function; they have several different roles, and their simple pattern is governed largely by the process of accretionary growth.

The interior shell margin of all species of *Glycymeris* is lined with distinct crenulations, which alternate with the exterior ribs and are formed by the same microstructural elements of the outer shell layer. These crenulations serve, in conjunction with the hinge teeth, to align and interlock the valves. Carter (1968) has postulated another possible function for such crenulations: they may make it more difficult for a starfish to intrude its stomach into the bivalve by sliding it around the shell margins after entry has been gained at one point.

The periostracum is variably developed in the flat-ribbed glycymerids. It usually extends around most of the shell margin, being progressively worn off towards the umbones. This periostracum has often been described as 'hairy' or 'velvety' on account of the numerous tiny barbs which stand up from its surface. These are arranged in a regular pattern, as radial rows set in the striations on the ribs, and as concentric rows corresponding to growth lines (Pl. 38, fig. 9). In *G. americana* the barbs are apparently secreted in a horizontal position, as blades pointing away from the umbo. Once complete the blades spring up, normal to the surface of the shell. They are not straight, but rather curve back towards the umbo. In this position the tiny barbs catch against sand grains and help to prevent the shell from slipping upwards and backwards as the foot probes the sediment during burrowing. This is presumably a valuable adaptation to a burrowing bivalve with a weak ligament, and hence an otherwise poor shell anchor. Here then is a function both for the periostracum itself, and for the striations in which the rows of barbs are set. The presence of a barb-bearing periostracum in fossil glycymerids can be inferred from the presence of fine radial striations on the ribs.

Multivariate analyses. A principal components analysis of the growth of *G. parilis* by Brower (1973) and several R-mode factor analyses of samples of *G. americana* and *G. subovata* (Thomas 1970) have yielded very similar results. These techniques distinguish clusters of closely related variables (see review by Gould 1970, and references therein) on the basis of linear correlations. Logarithmic transformation of the measured parameters facilitates the recognition of simple allometric as well as rectilinear relationships. The parameters used in my studies are shown in text-fig. 3 and Table 1.

The most striking result of these analyses is the extremely high intercorrelation of all the variables. In Brower's study the first principal component accounts for 93% of the correlation matrix variance, while the first component in some of my analyses explains as much as 97% of the data. Certainly these correlations result partly from the large amount of redundancy among the parameters used. Nevertheless, the intercorrelation among the variables with increasing size is so strong that correlations independent of size are largely swamped, even in the oblique factor matrix. As a result, groups of characters differentiated by R-mode analyses of different samples are not always consistent, being sometimes rather arbitrary divisions of a single tight cluster of vectors.

Certain patterns do recur, and these are accentuated in an analysis of a sample of twenty-two specimens of *G. subovata*, all between 30 and 33 mm in height (compare Tables 2 and 3). With the much-reduced influence of size, the first principal component for this sample explains only 46% of the data. Measurements of the ligamental area form a cohesive group, together with the length of the posterior half of the shell, which also increases allometrically with size (Axis 4). The characters affected by the overgrowth of the hinge plate by the ligamental area, and ventral movement of the hinge axis, form a group which naturally tends to be negatively correlated with the former one (Axis 2). The convexity, thickness, and internal volume of the shell are

TABLE 2. Factor analysis. Reordered oblique projection matrix of 28 variables in 6 axes. Variables were measured on 72 right valves of *Glycymeris subovata* representing a complete growth series. Shoal River Formation, Miocene, Florida. For explanation of character codes, see Table 1.

CODE	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
HTHING	1.000	0.000	0.000	0.000	0.000	0.000
THICK	0.911	0.652	-0.038	0.082	-0.532	0.077
HT ATO	0.543	0.164	-0.043	0.101	0.298	0.004
HT PTO	0.490	0.103	0.022	-0.012	0.401	0.054
CONVEX	0.423	0.353	-0.015	0.129	0.044	0.166
WEIGHT	0.363	0.321	0.010	0.168	0.132	0.100
LENLIG	0.353	0.350	0.089	0.077	0.214	0.009
LIGHIN	0.000	1.000	0.000	0.000	0.000	0.000
HTLIG	0.427	0.674	0.001	-0.002	0.011	0.004
AR LIG	0.395	0.527	0.041	0.036	0.105	0.006
OISTAO	0.000	0.000	1.000	0.000	0.000	0.000
EX AAO	0.000	0.000	0.000	1.000	0.000	0.000
EX PAO	0.167	0.340	0.125	0.894	-0.781	0.346
HTCREN	0.169	0.114	-0.012	0.576	0.393	-0.221
HT AAO	0.000	0.000	0.000	0.000	1.000	0.000
HXLAAO	0.047	0.008	-0.010	0.028	0.944	-0.005
LENAAO	0.091	0.015	-0.019	0.054	0.884	-0.010
HT PAO	0.155	0.133	0.023	0.013	0.778	-0.065
HXLPAO	0.145	0.123	0.018	0.023	0.724	0.007
LENPAO	0.136	0.114	0.013	0.031	0.673	0.071
A LEN	0.104	0.074	0.035	0.258	0.560	0.008
HTLGSP	0.216	0.203	0.012	0.156	0.427	0.049
INTVOL	0.217	0.232	0.018	0.144	0.381	0.076
LENGTH	0.156	0.159	0.041	0.252	0.379	0.072
HXLXC	0.259	0.232	0.013	0.181	0.294	0.095
P LEN	0.192	0.217	0.043	0.250	0.251	0.117
PCHEV	0.000	0.000	0.000	0.000	0.000	1.000
ACHEV	0.075	0.078	0.026	-0.134	0.073	0.896

highly intercorrelated (Axis 3). The parameters of the adductor scars form distinct groups (Axes 1 and 5), their lengths not being highly correlated; however, it is notable that their heights are strongly correlated, directly with one another and inversely with the size of the ligamental area. Clearly the allometric growth of the ligament does impinge on the space available inside the shell. Measures of the extra-pallial margin fall together (Axis 7) and are correlated with the shell-thickness group. The numbers of anterior and posterior ligamental chevrons form a separate group (Axis 6) largely because they are discrete variables, but would otherwise join the parameters of the ligamental area. The main linear measures of shell size, such as height, length, anterior length, and distance between the adductors, are similarly correlated with several groups in which their appearance has no particular significance (Axis 8 and others).

Aside from the relationship of all variables with size, two groups of characters

TABLE 3. Factor analysis. Reordered oblique projection matrix of 28 variables in 8 axes. Variables were measured on 22 specimens of *Glycymeris subovata*, all between 30 and 33 mm high. Shoal River Formation, Miocene, Florida. For explanation of character codes, see Table 1.

CODE	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8
HXLAAO	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LENAAO	0.915	0.171	0.270	0.483	-0.611	0.066	0.368	0.193
HTLGSP	0.467	0.100	0.323	0.143	0.082	0.356	0.465	0.137
HTHING	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
HT ATO	-0.009	0.810	0.229	-0.219	-0.169	-0.091	-0.245	0.206
HT PTO	-0.238	0.713	-0.099	-0.234	-0.061	-0.022	-0.174	0.468
LIGHIN	0.093	-0.746	0.057	0.398	-0.094	0.068	0.023	-0.133
CONVEX	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
THICK	-0.358	0.248	0.857	0.180	-0.205	0.123	0.022	-0.162
WEIGHT	-0.012	0.233	0.836	0.244	0.003	0.104	0.346	0.081
HXLXC	0.221	-0.022	0.592	0.190	0.092	0.189	0.353	0.183
INTVOL	0.256	-0.177	0.555	0.115	0.091	0.077	0.181	0.270
AR LIG	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
LENLIG	-0.278	0.342	-0.117	0.853	0.362	-0.193	-0.069	0.395
HTLIG	0.195	-0.197	0.116	0.818	-0.191	0.138	0.046	-0.270
P LEN	0.086	0.057	0.283	0.552	0.192	0.186	0.429	-0.014
HXLPAO	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
HT PAO	-0.075	-0.330	0.269	-0.378	0.910	-0.219	-0.127	0.169
LENPAO	0.066	0.293	-0.234	0.334	0.906	0.194	0.114	-0.147
HT AAO	0.582	-0.170	-0.240	-0.418	0.725	-0.273	-0.244	0.083
PCHEV	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
ACHEV	-0.117	0.313	-0.287	0.473	0.334	0.755	-0.179	-0.304
HTCREN	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
EX AAO	-0.008	-0.502	0.476	-0.099	-0.248	-0.035	0.805	0.290
EX PAO	-0.265	-0.043	0.296	0.576	-0.101	0.129	0.771	-0.077
LENGTH	0.191	-0.104	0.235	0.311	0.141	0.184	0.461	0.296
DISTAO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
A LEN	0.273	-0.283	0.122	-0.078	0.026	0.135	0.382	0.595

are most cohesive: those related to a larger or smaller ligamental area; and those related to a more or less massive hinge plate, together with shell thickness and convexity. The parameters of the ligament group interact negatively with those of the hinge plate, and parameters of both of these groups interact negatively with characters of the shell interior. Shells with larger ligaments have shorter adductor moment arms, and the heights of the adductors themselves are reduced. Likewise, thicker shells with massive hinge plates and broad extra-pallial margins have smaller adductor scars and less internal volume, despite the fact that more work must be done by the adductors to manipulate a heavier shell. Evidently the advantages of a more massive shell in resisting stresses generated by predators or the physical environment must be offset against disadvantages in locomotion and the need for a mantle cavity large enough to accommodate both large gills and a massive foot.

Factor analysis shows that metric characters of a single structure or functional complex of the *Glycymeris* shell are in general more closely interrelated than characters of different complexes. The same conclusion has been reached by Gould (1967, 1969) for pelycosaurian reptiles and pulmonate snails, and by Olson and Miller (1958) for the blastoid *Pentremites* and a variety of vertebrates. In his study of *G. parilis*, Brower (1973) has suggested that 'the animals might have genetically programmed their growth with two genetic complexes, one devoted to overall size ontogeny and the other assigned to development of the teeth'. However, it is clear that the growth pattern of the hinge plate is the result of interaction between more or less isometric growth typical of the shell as a whole, and the allometric growth of the ligament. The interaction of these two growth patterns is determined by functional considerations and the constraints of shell geometry, as we have seen. Genetic complexes surely control morphology by means of growth gradients and patterns, rather than by direct determination of unit characters, which are often arbitrarily defined in any case. It does not necessarily follow from this that intercorrelated parameters of morphology are controlled by corresponding groups of genes.

With respect to bivalve shell form, the most significant feature of the relationships among parameters of the glycymerid shell is that the same associations occur in ontogeny, in variation within and between populations, and among species. An R-mode factor analysis of specimens of *G. subovata* and *G. americana* treated as one sample reveals much the same character groups as the two species analysed separately. Analyses using ratios of variables also yield similar groupings, indicating that allometric changes in the variables during ontogeny are interrelated in the same way as the variables themselves. The constancy of these interrelationships is a function of the geometric simplicity of the glycymerid shell, and the fact that any considerable change in one character impinges more or less directly on several others. The glycymerid shell as a whole shows a very high degree of morphological integration.

Synthesis. These observations on the form and function of the *Glycymeris* shell lead to two general conclusions. (1) This shell is a geometrically very simple structure; as such its various characters are closely interrelated, and are not free to change independently of one another, in either ontogeny or phylogeny. The size and shape of the ligament affect the disposition of the hinge teeth and the closing moment that the adductors can exert. The shapes of the hinge teeth depend largely on the shape of the hinge plate, which also interacts with the size of the adductors and the volume of the mantle cavity. Both the length of the ligament and the shape of the hinge plate affect the position of the animal's centre of gravity, and hence its locomotion. The evolution of the shell is limited in that any substantial change in one character has a major effect on the shell as a whole. (2) The growth of the *Glycymeris* shell, apart from its ligament and the posterior elongation of some forms, is largely isometric. This limits size in ontogeny and phylogeny, and reduces the opportunity for new adaptations to evolve by heterochrony, a process which Stanley (1972) has shown to be a major factor in bivalve evolution.

The survival of *Glycymeris* for over 100 million years attests that it is well adapted to its particular ecological niche. However, in a number of mechanical respects the animal is less efficient than more specialized bivalves. The ligament is weak and unable to brace the shell firmly against the sediment in which the animal burrows. Radial ribs strengthen the shell, but are not well designed for burrowing. Their mutual abrasion shows that the apposed umbones limit the opening of the valves. The soft parts are functionally inefficient in a variety of ways. In short, *Glycymeris* is a much compromised organism. The compromises which have adapted it to its restricted niche have been made at the expense of the flexibility, or range of possible variations on the theme, necessary for an evolutionary radiation into diverse environments.

CONCLUSIONS

Evolution in the family Glycymerididae has given rise to a modest diversity of species with a very narrow range of morphologies. This conservatism is not exceptional, although certainly greater than average, compared with other bivalves. It is the result of both extrinsic ecological factors and intrinsic morphological factors discussed in this paper. Glycymerids have always been opportunistic species, members of unstable, low-diversity communities inhabiting physically rigorous environments. They are morphologically unspecialized, and the characters of their shells are constrained to be highly intercorrelated by the requirements of function and accretionary growth.

Conservatism in the evolution of a group of species lineages implies survival as well as the absence of change. *Glycymeris* is clearly very well adapted to its particular habitat, from which more specialized forms are excluded by the vagaries of the physical environment. It occupies an ecological niche which is narrow with respect to substrate preference, but broad in terms of the animal's ethology and tolerance of physical instability. This pattern is typical of slowly evolving groups, which tend to be 'adapted to some ecological position or zone with broad but rather rigid selective limits' (Simpson 1944, p. 140; see also Stebbins 1949).

Most authors consider ecological factors to be of primary importance in determining rates of evolution. Stanley (1973) has recently argued most convincingly that differences in the intensity of competition are primarily responsible for the difference in evolutionary rates between bivalves and mammals in general. Low levels of interspecific competition, and consequently low selection pressures, among bivalves have permitted extensive overlap of ecological niches, and the radiation of advanced groups without the extinction of more primitive forms. Population levels are limited by the physical instability of the environment and often by intense predation, rather than by competition. *Glycymeris* could well be taken as the type, perhaps extreme, example for these generalizations. There is no clear evidence of niche partitioning among glycymerid species, and they are subject to variable, sometimes very heavy, predation by naticid gastropods (Thomas 1970). The physical factors which largely define the glycymerid niche are frequently random rather than selective in their effects on populations. Perhaps more important, this physically determined niche has remained constant throughout the evolution of the group. *Glycymeris* did not have to evolve in order to 'keep up with the Joneses', as must organisms whose adaptive zones involve more specific biological interactions with evolving neighbours (Simpson 1944, p. 190; Van Valen 1973). Where an organism is primarily adapted to a constant physical environment, selection tends to be centripetal (Simpson 1944) and is a positive factor in conservatism. As the environment fluctuates, glycymerid lineages change back and forth with it, within the limits set by morphology and behaviour (Thomas 1970).

The principal purpose of this paper has been to determine these limitations. Although extrinsic factors have been stressed in most discussions of evolutionary conservatism, Simpson (1949) clearly recognized the significance of morphological complexity for rates of evolution, again contrasting bivalves and mammals.

The more differentiated an animal is, the more ways there are in which it can evolve without fundamental modifications of its organization, particularly if its organ systems or skeletal parts can change independently of one another. While organisms with complex skeletons such as *Limulus* and *Latimeria* may evolve slowly for other reasons, organisms with very simple skeletons must be conservative, unless they can make large, rapid changes in morphology and adaptive zone, such as occur in the origin of higher taxa. The rudistids are exceptional among bivalves in that they made such an adaptive shift, and were able to maintain high rates of morphological change in their uniquely complex shells, in the course of rapid speciation. In contrast, the high degree of morphological, essentially functional, integration of the simple glycymerid shell does not allow the independent modification of individual characters. Eldredge and Gould (1972) have drawn attention to the importance of homeostatic mechanisms (Lerner 1954) in maintaining the morphological stability of individual species in time as well as space. These mechanisms must be most effective where morphological integration does not allow independent variation or change of characters. While genetic homeostasis can only act directly to stabilize individual species, similar systems of canalized development must be shared by the species of conservative genera and families, such as the Glycymerididae.

Glycymeris is a generalized descendant of the ancient arcoid lineage, which is itself very conservative in its fundamental anatomy, but remarkably diverse in the range of its adaptations. Evidently the glycymerid adaptation is not necessarily an evolutionary dead-end, for the parallelodontids, and hence all later arcoids, are thought to have evolved from Palaeozoic cyrtodontids very much like *Glycymeris* in form and inferred mode of life (Pojeta 1971, and earlier authors cited therein). Thus *Glycymeris* has secondarily reverted to an ancestral free-burrowing adaptation, a phenomenon which Stanley (1972) has recognized in both the Arcoida and the Carditacea. The adaptation and pattern of evolution of the Glycymerididae are in many respects comparable with those of other shallow-burrowing bivalves, to which many of the conclusions of this study should also apply.

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HYDROID-SERPULID SYMBIOSIS IN THE MESOZOIC AND TERTIARY

by COLIN T. SCRUTTON

ABSTRACT. Several species of Mesozoic and Tertiary serpulids from Europe and the Middle East were infested by a colonial organism which is preserved as the mould of a stolonal network with polyp chambers buried in the peripheral zone of the calcareous tube. The polyp chambers open to the outer surface of the tube through small, usually semicircular apertures. The mould is the result of incorporation of the organism into the worm tube during calcification by the serpulid: it is not a boring. The organism is interpreted as a hydroid or group of related hydroids which lived commensally or possibly mutualistically with the serpulids. This hydroid-serpulid symbiosis is compared with the living symbiosis between the hydroids of *Proboscidactyla* and certain species of sabellid polychaetes.

The name of the fossil symbiont is *Protulophila gestroi* Rovereto.

THE strikingly patterned outer surface of a specimen of the serpulid *Parsimonia* sp. from the Gault Clay (Lower Cretaceous) of Kent (Pl. 42, figs. 1–2; text-fig. 2) originally prompted this investigation. The pyritic system of stolons and 'thecae' was at first thought to represent a colonial organism growing on the surface of the tube, but further intensive collecting at the same locality yielded abundant material indicating that this appearance was the result of the exfoliation of the tube. Unworn tubes showed only a series of small apertures scattered over the outer surface (see text-fig. 1). Specimens were recovered showing all stages from this perfectly preserved condition to tubes in which exfoliation revealed the internal network, usually infilled by pyrite.

A subsequent search of the extensive collection of fossil serpulid tubes in the Department of Palaeontology, British Museum (Natural History) yielded much additional material. Signs of the association were found on specimens ranging in age from Middle Jurassic to Pliocene and collected from various localities in Europe and the Middle East.

Few references to this association have been made in the literature. The earliest appears to be that of Sowerby (1829, p. 226, pl. 608, fig. 3) who recorded 'minute pores or short tubes' on the exterior of the Jurassic *Serpula tricarinata*. He was in doubt as to whether they were formed by the worm or some other organism. Wrigley (1951, p. 187), however, erected a new species of *Sclerostyla*, *S. perforata* from the Eocene, for specimens showing perforations in the walls of the tube (Pl. 41, fig. 9). He thus implied the perforations to be formed by the worm although he did not state this explicitly. He did stress, however, that because of their raised and rounded rim, they could not be the work of a parasitic borer.

The system of stolons and 'thecae' exposed by the exfoliation of an infested serpulid tube was first described and named by Rovereto (1901, p. 223, pl. 28, fig. 7*a–c*). He interpreted this pattern as the remains of a new genus and species of ctenostomatous bryozoan, *Protulophila gestroi*, which he considered to be adherent to the outer surface of tubes of *Protula firma* from the Pliocene of Italy (Pl. 42, figs. 3–4). In his discussion of the affinities of *Protulophila*, he noted that it had been considered by

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some specialists to be a hydroid and that its identification as a bryozoan was not entirely certain. His conclusions, however, were based on comparisons with other stoloniferous bryozoans such as *Hypophorella* which is also found associated with polychaete tubes. Finally, Walter (1965, p. 286), working with material from the Upper Jurassic of France in which the relationship between the internal system of stolons and chambers and the external apertures could be recognized, described the organism responsible as a new species of perforant ctenostome bryozoan *Immergentia*? *lissajousi*.

None of these records fully explores the nature of the relationship between the two organisms and none, in my opinion (except in the doubt expressed by Rovereto), correctly identifies the organism infesting the serpulid tubes. This organism is considered here to be a species (or possibly members of a group of closely related species) of colonial hydroid and reasons for this opinion are discussed more fully below. The earliest available name for the moulds left by the hydroids is *Protulophila gestroi* Rovereto.

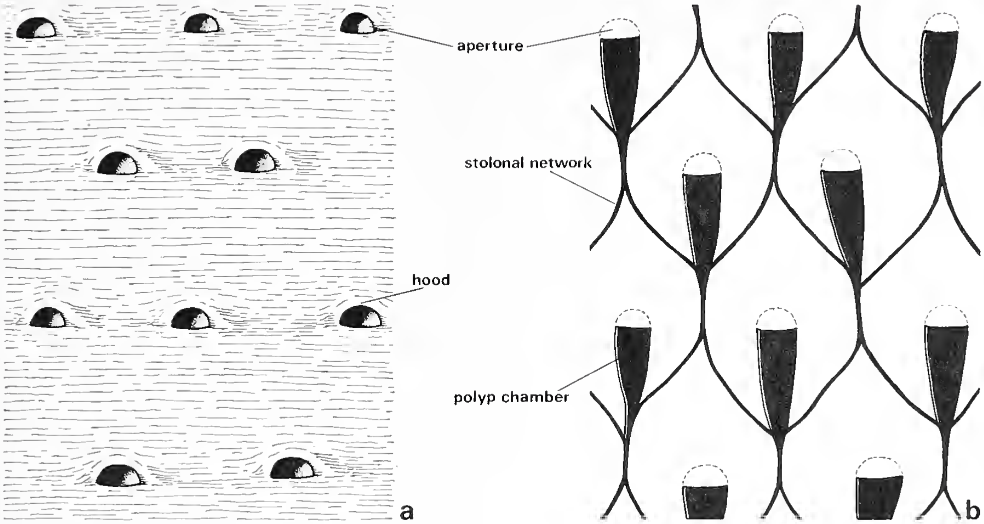
This report is based on the study of approximately 300 specimens, including those described by Walter (1965), Wrigley (1951), and some of those described by Rovereto (1901). Cross- and longitudinal sections have been made of some unabraded serpulid tubes to establish the shape and location of the internal chambers. In addition, two specimens have been serially sectioned for more precise information on the form of the apertures and internal chambers and the structure of the serpulid tube adjacent to them. Because of the small section interval required, between 10 and 30 μm, first attempts were made using acetate peels but since the peripheral layers of the tubes are much less compact than the inner layers plucking tended to destroy the area of maximum interest. Good results were eventually obtained by photographing successive polished surfaces through a polarizing reflected light microscope. The serpulid tubes were mounted with their long axes horizontal in bakelite blocks and prepared using standard techniques. This orientation gives tangential sections when the tube is first exposed and longitudinal sections when approximately half the tube has been removed. The microstructure in the serpulid tubes showed most clearly when viewed through partially crossed polars.

The material figured and listed in this paper is in the collections of the Department of Palaeontology, British Museum (Natural History) unless otherwise indicated.

DESCRIPTION OF THE SYMBIOSIS

External appearance

The external indication of this association is the presence of small pores or apertures scattered over the outer surface of a serpulid tube (text-fig. 1*a*). The apertures are subcircular to semicircular in outline with considerable variation in detailed shape. In semicircular apertures, the long axis is at right angles to the direction of growth of the serpulid tube, usually with the distal lip of the aperture curved and the proximal lip more or less flattened. Aperture size is also variable both within and between specimens. Over the collection as a whole, size varies from 0·10 × 0·22 mm and 0·12 × 0·18 mm to 0·16 × 0·40 mm and 0·20 × 0·36 mm depending on the height-width ratio. Subcircular apertures are *c.* 0·20 mm in diameter. The mean aperture



TEXT-FIG. 1. Morphological terms used in the description of *Protulophila gestroi*. *a*, external appearance. *b*, internal appearance with the serpulid tube exfoliated.

size is 0·15 × 0·28 mm. Within specimens, variation is much lower and the height–width ratio tends to be fairly constant.

The shape and appearance of the apertures vary from species to species of host serpulid. The most important factors influencing aperture morphology appear to be the rugosity of the serpulid tube and the depth to which the internal system of stolons and chambers is buried in the tube wall. Where the internal system is shallowly buried in smooth-walled tubes such as those of the Cretaceous serpulids *Parsimonia* sp. (Pl. 39, figs. 1–5) and *Rotularia* sp. A (Pl. 39, figs. 9–11), the apertural margin is more or less entire and a delicate cowl or hood is formed around the distal lip. The apertures on *Sclerostyla perforata* from the Eocene are similar (Pl. 41, fig. 9). With increasing tube rugosity and depth of burial of the stolons and chambers, the hoods become more massive and tend to overhang the aperture. In *Parsimonia antiquata* from the Lower Cretaceous (Pl. 39, figs. 6–8) the tube is quite smooth but deeper burial of the stolons and chambers is reflected in the development of strongly projecting hoods and associated shallow lateral pits, cut off by the growth of the flanks of the hood. *Rotularia phillipsi* from the Lower Cretaceous (Pl. 39, figs. 12–14) is slightly more rugate but has apertures similarly developed.

More strongly rugate tubes in which the stolons and chambers are deeply buried show correspondingly more elaborately developed apertures: for example, *Serpula sulcata* from the Upper Jurassic (Pl. 40, figs. 3–5). On some specimens of *S. sulcata* the apertures may be produced as short, thin-walled pipes, projecting beneath strongly arched and massive hoods (Pl. 40, figs. 6–10). This structure is also seen in serial section (Pl. 41, figs. 1–3). The most unusual appearance is presented by a specimen of *S. tricarinata* from the Jurassic (Pl. 40, figs. 11–12) on which some apertures project strongly as thick-walled pipes from the relatively smooth surface of the serpulid tube. Elsewhere on this tube, apertures similar to those on *S. sulcata* are present, although in this case the internal chambers and stolons are only very shallowly buried and in places the symbiont may have been exposed.

At their most regular, the apertures are arranged in a quincuncial pattern with a longer axis along the tube length. The most crowded and regularly spaced apertures have a repeat pattern with axes of 0·58 × 0·83 mm (A10924 *Parsimonia* sp., Lower Cretaceous). Spacing is quite variable, however, and on many specimens may be much wider than this. On some Jurassic serpulids apertures may only appear very spasmodically on the surface of the tube (Pl. 40, fig. 6).

Most of the available specimens lack the proximal and distal ends of the serpulid tube and usually apertures are present over their entire length. In some, however, where the tube is more or less complete, apertures may be lacking proximally whilst they are well developed distally. It is very rare for apertures to disappear towards the distal end of a tube. On occasional specimens with the distal extremity of the tube well preserved, small circumferentially elongated pits may be seen on or near the tube rim representing partially formed examples of the normally internal polyp chambers (Pl. 40, fig. 2).

Internal appearance

The apertures are the surface manifestation of small, compressed, subconical internal cavities which for most of their length lie parallel to the external wall of the serpulid tube but bend sharply outwards at their flared end to open at the surface (Pl. 41, figs. 4, 6; Pl. 42, figs. 8, 10). These cavities are here termed polyp chambers (text-fig. 1*b*). Their appearance is best seen in specimens in which exfoliation reveals the stolonal network from which the polyp chambers arise (Pl. 42, figs. 1–10). Stolons and chambers always lie more or less in a single plane at an approximately constant depth below the surface of the tube. In different serpulid species this depth varies and corresponds to a location either at, just outside, or just within the crest on the growing margin of the tube (compare Pl. 40, fig. 2 with Pl. 41, fig. 6; see also Pl. 41, fig. 4).

In tangential aspect the polyp chambers are sub-triangular and elongated along the long axis of the tube. They vary considerably in size and proportions from 0·24 × 0·84 mm and 0·30 × 0·76 mm to 0·28 × 1·10 mm and 0·40 × 1·20 mm even on the relatively few tubes that show them clearly. Variation within a single population is also high, however, and measurements of the chambers on the collection of *Parsimonia* sp. from the Gault Clay (Lower Cretaceous) of Ford Place in Kent range from 0·28 × 1·10 mm to 0·34 × 0·86 mm. In cross-section the polyp chambers tend to be

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EXPLANATION OF PLATE 39

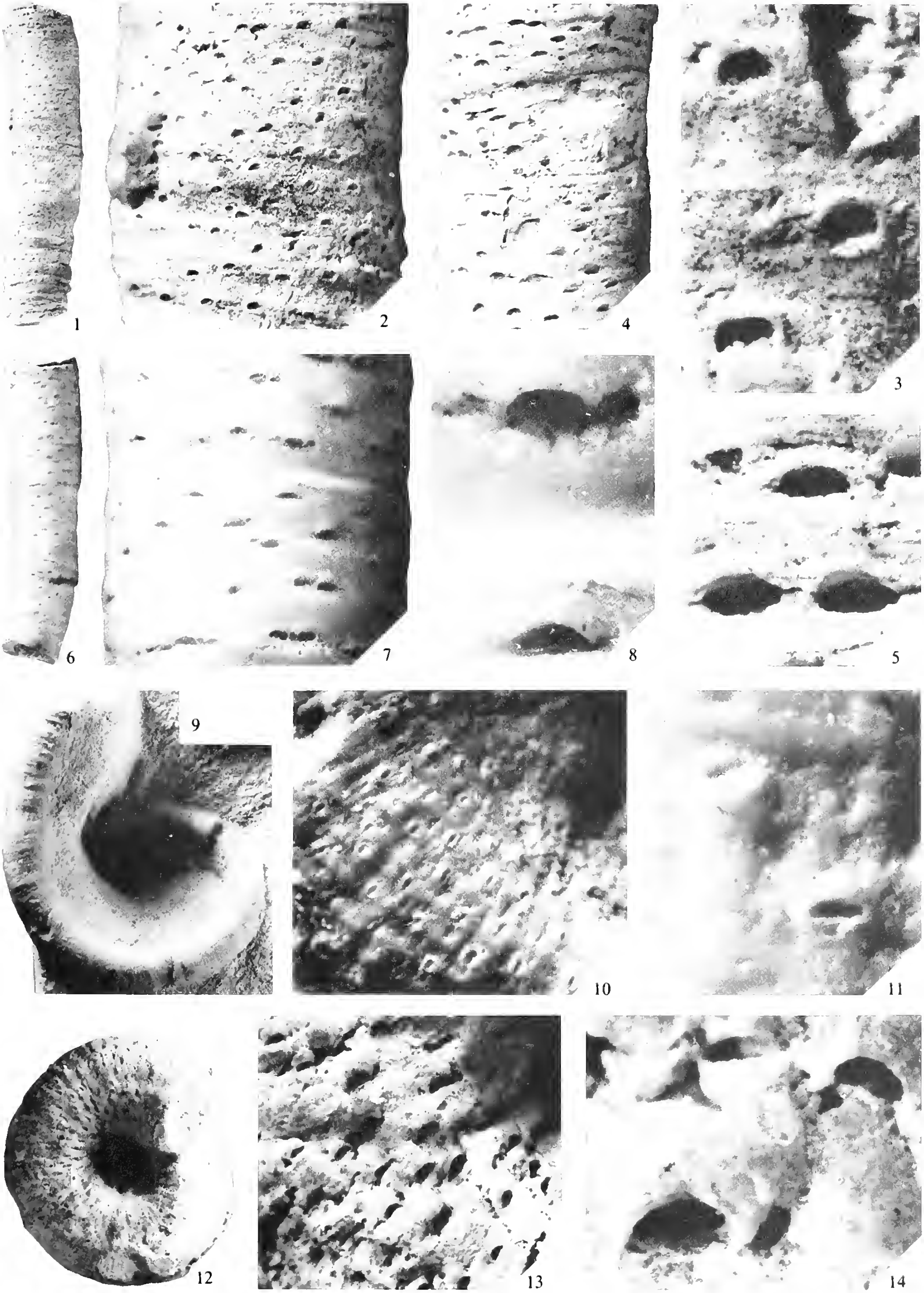
Variation in the distribution and appearance of apertures of *Protulophila gestroi* Rovereto on species of serpulid tubes from the Cretaceous.

Figs. 1–5. *Parsimonia* sp. *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Figs. 1–3, A10889a; 1, × 2; 2, × 8; 3, × 35. Figs. 4–5, A10886; 4, × 8; 5, × 35.

Figs. 6–8. *Parsimonia antiquata* (Sowerby). A7625, Red Chalk, Albian; Hunstanton, Norfolk. 6, × 2; 7, × 8; 8, × 35.

Figs. 9–11. *Rotularia* sp. A. A10429, Grey Chalk, Cenomanian; Dover, Kent. 9, × 1·5; 10, × 8; 11, × 35.

Figs. 12–14. *Rotularia phillipsi* (Roemer). A5039, Speeton Clay, Neocomian; Speeton, Yorkshire. 12, × 2; 13, × 8; 14, × 35.



SCRUTTON, *Protulophila gestroi*

compressed in the plane of the growth-lines of the serpulid tube (Pl. 41, fig. 7). Few measurements are available of chamber compression but it appears to be greater in *Parsimonia* sp., in which the chambers are shallowly buried (0·05 mm wide), than in *S. sulcata* (0·12 mm wide), in which the chambers are more deeply buried.

The stolonal network, consisting of filaments 0·04–0·05 mm diameter, has a diamond to hexagonal pattern when it is most regularly developed and the chambers arise at or close to the base point of each polygon in the network (text-fig. 1*b*). Network size measured transversely and longitudinally to the serpulid tube has minimum dimensions of 0·58 × 0·83 mm and several specimens have average dimensions of about 1·10 × 1·65 mm. The network pattern is strikingly clear and regularly developed in a specimen of *Parsimonia* sp. (Pl. 42, figs. 1, 2; text-fig. 2). In most cases, however, the network is much more irregular in pattern and density (Pl. 42, figs. 5–10) and some polygons may lack chambers (Pl. 42, figs. 3, 4). Examples can also be seen where the network re-establishes itself around the full circumference of a tube after partial disruption (Pl. 42, fig. 8; text-fig. 2).

Most specimens on which the polyp chambers and stolonal network can be seen are tubes of Cretaceous or Tertiary age. Jurassic serpulid tubes on which at least the general outline of stolons and chambers can be seen, appear to be rare (Pl. 41, fig. 8). The available evidence, however, suggests that there is no significant difference, except in depth of burial, between the development of stolons and chambers in Jurassic and post-Jurassic material.

The chambers and stolonal network are frequently infilled by pyrite and sometimes by limonite presumably after pyrite. No surface features are evident on the walls of the stolons and chambers which might reflect morphological details of the symbiont although slight crenulations can occur parallel to the growth-lines of the serpulid tube.

Tube structure of infested serpulids

Serpulid tubes normally possess clearly defined internal growth-lines reflecting the deposition of successive layers of calcium carbonate on the growing margin of the tube. In longitudinal section through the tube wall the growth-lines are asymmetrically arched with the crest of the curve usually strongly displaced towards the exterior surface; in tangential section the lines are parallel and straight, at right angles to the direction of tube growth.

EXPLANATION OF PLATE 40

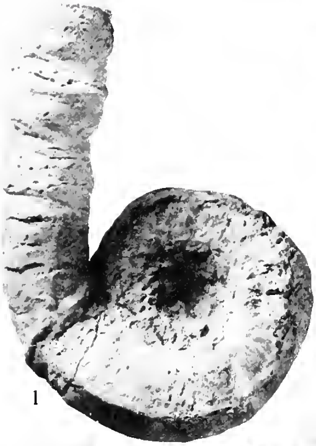
Variation in the distribution and appearance of apertures of *Protulophila gestroi* Rovereto on species of serpulid tubes from the Jurassic.

Figs. 1–2. *Serpula lituiformis* Munster. A630, Oxfordian; Vaches Noires, Normandy, France. 1, × 1·5; 2, part of tube rim, × 8.

Figs. 3–5. *Serpula sulcata* Sowerby. A8367, Ampthill Clay, Corallian; Ampthill, Bedfordshire. 3, × 2·5; 4, × 8; 5, × 35.

Figs. 6–10. *Serpula sulcata* Sowerby. *Rhactorhynchia inconstans* Bed, Kimmeridge Clay; Osmington Bay, Dorset. Figs. 6–7, A10851; 6, × 2; 7, × 35. Figs. 8–10, A10850; 8, × 2; 9, × 8; 10, × 35.

Figs. 11–12. *Serpula tricarinata* Sowerby. A6641, Cornbrash; ?Callovian; Steeple Ashton, near Trowbridge, Wiltshire. 11, × 2; 12, × 8.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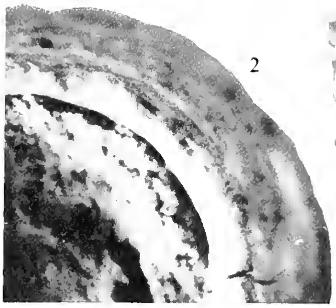
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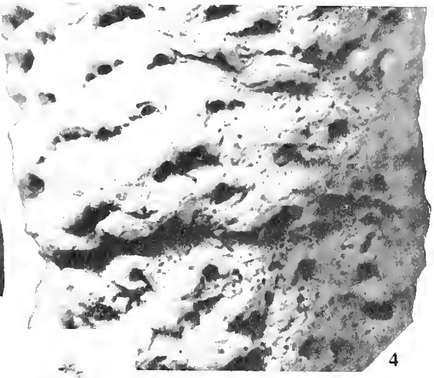
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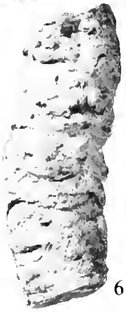
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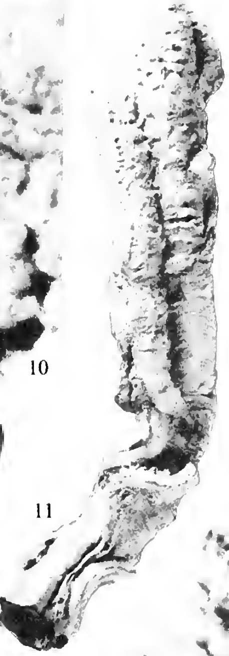
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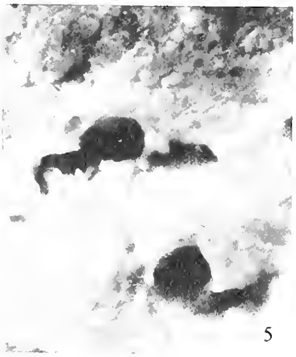
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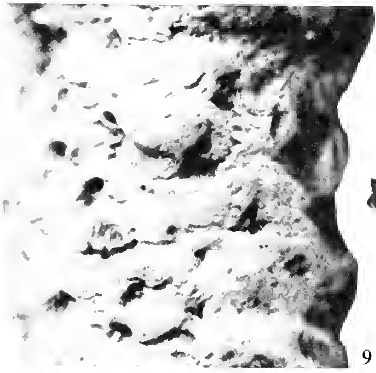
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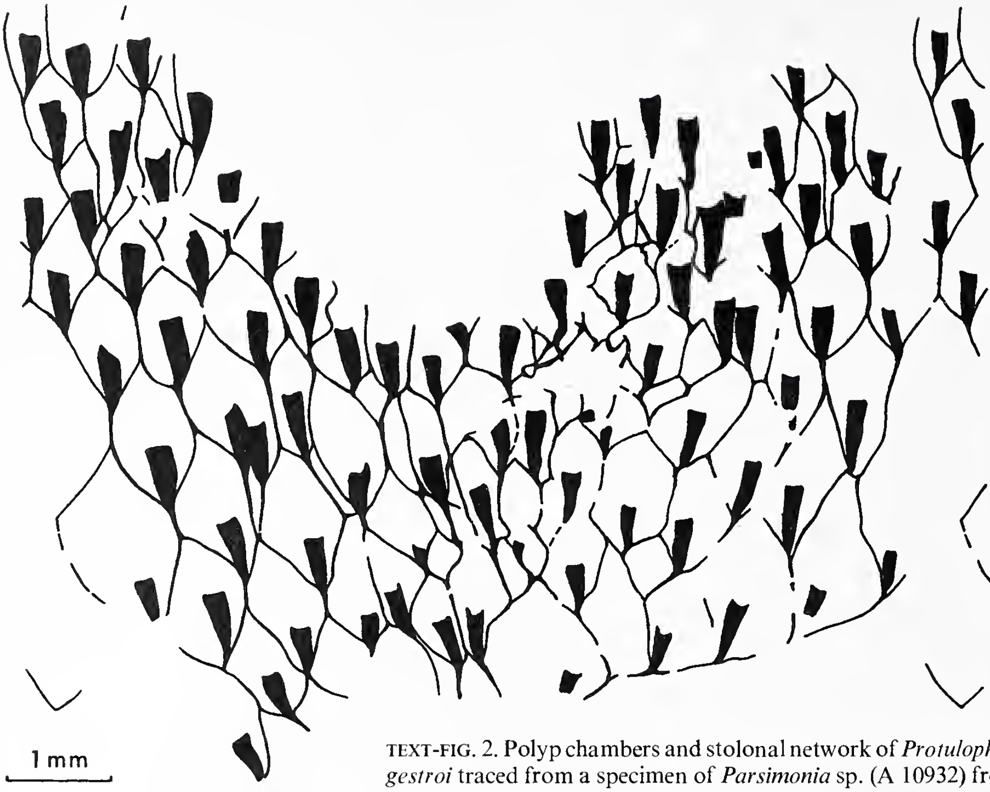
SCRUTTON, *Protulophila gestroi*



TEXT-FIG. 2. Polyp chambers and stolonal network of *Protulophila gestroi* traced from a specimen of *Parsimonia* sp. (A 10932) from the Gault Clay, Albian of Ford Place, Kent.

Thin sections and serial sections show that the growth-lines of infested serpulid tubes are deflected around both stolons and polyp chambers (Pl. 41, figs. 1–7). This is most clearly seen in serial sections of a tube of the strongly ornamented species *S. sulcata* (Pl. 41, figs. 1–4). In this specimen, tangential sections of the massive hood developed over an aperture show very clear growth-lines parallel to the margin of the

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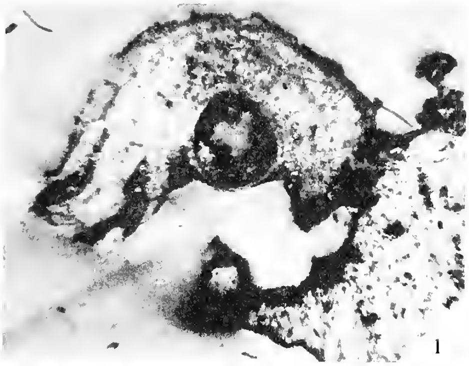
EXPLANATION OF PLATE 41

Figs. 1–4. *Serpula sulcata* Sowerby. A10853, *Rhactorhynchia inconstans* Bed, Kimmeridge Clay, Kimmeridgian; Osmington Bay, Dorset. 1–3, serial sections tangential to the tube surface through an aperture of *Protulophila gestroi*. Spacing of polished surfaces from exterior (fig. 1) of tube inwards, fig. 2 at 0·19 mm, fig. 3 at 0·33 mm, ×45. 4, longitudinal section through polyp chamber. The strong black line passing diagonally upwards from the tube exterior to the base of the polyp chamber is a crack in the tube and is not part of the stolonal network, ×45.

Figs. 5–7. *Parsimonia* sp. *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Figs. 5–6, A10920; 5, tangential polished section through apertures of *Protulophila gestroi*, ×45. 6, longitudinal section through polyp chamber, ×45. 7, A10915, cross-section through peripheral part of serpulid tube with stolons and polyp chambers. The pyrite filled tube sectioned at upper right centre and within the peripheral ring of stolons and chambers is a boring and is not part of *Protulophila*, ×70.

Fig. 8. *Immergentia*? *lissajousi* Walter on *Serpula* sp. cf. *S. lituiformis* Munster. Colln. Dep. Sci. Terre, Fac. Sci. Lyon 28970 (holotype), Oxfordian; Hurigny, Saone-et-Loire, France, ×8.

Fig. 9. *Sclerostyla perforata* Wrigley. A6983 (holotype), London Clay, Eocene; Wokingham, Berkshire, ×8.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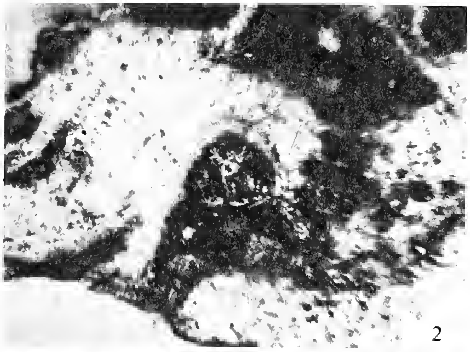
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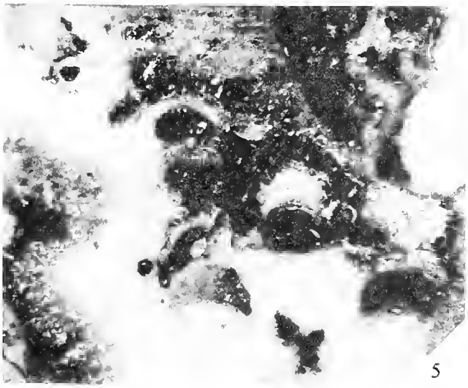
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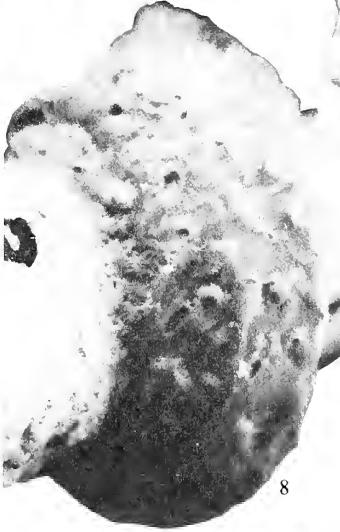
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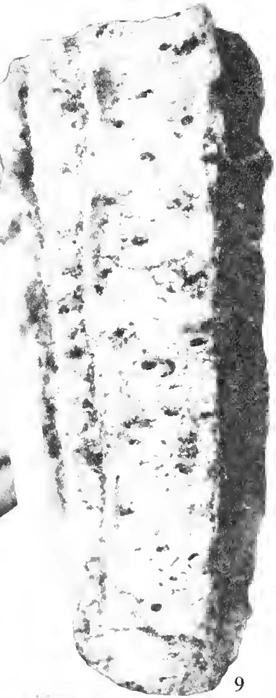
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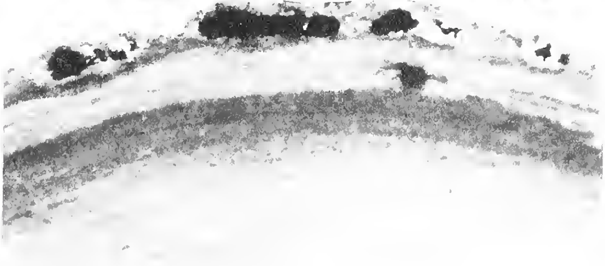
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SCRUTTON, *Protulophila gestroi*

polyp chamber, confirming the impression given by the external appearance of the hoods in this species (Pl. 40, figs. 3-10). In longitudinal section (Pl. 41, fig. 4) the growth-lines are particularly strongly deflected in the hood and can be clearly seen to overlap against the walls of the polyp chamber. The same relationship can be seen, though less clearly, in the serial sections of a tube of *Parsimonia* sp. in which the stolons and polyp chambers are less deeply buried (Pl. 41, figs. 5-6). The cross-section of another tube of this species shows that the growth-lines in the tube interior to the network are somewhat less distorted around the stolons and chambers than those in the external part of the tube (Pl. 41, fig. 7).

In serpulids such as *S. sulcata*, in which a discrete pipe may be secreted at the aperture, the substance and structure of the pipe appear to be continuous with that of the associated hood (Pl. 41, figs. 1, 2).

DISCUSSION

The evidence strongly suggests that the polyp chambers and stolonal network were formed by the incorporation of the symbiont into the host tube during calcification and were not primarily the result of boring activity. Externally, the manner in which the outer tube wall is moulded over shallowly buried chambers and stolons clearly indicates that calcification took place around the body of the symbiont (see particularly Pl. 39, fig. 10; Pl. 41, fig. 8; Pl. 42, upper part of fig. 8). The morphology of the apertures and hoods as well as the deflection of growth-lines in the serpulid tube and the manner in which they overlap against the walls of the polyp chamber all support this conclusion. The symbiont occupied a position in life encircling the serpulid at or very close to the rim of its tube (see text-fig. 5). During calcification, polyps and stolons were gradually incorporated into the host tube and the stolonal system extended and new polyps differentiated to maintain the colonization of the advancing tube rim. Presumably calcification did not take place over the advancing ends of the stolons, perhaps because they were able to inhibit precipitation at the point where their tips appeared at the rim of the tube. Well-preserved tube rims are rare, however, and even on the best of these (Pl. 40, fig. 2) the surface is sufficiently irregular to make the identification of the tiny stolonal orifices uncertain.

EXPLANATION OF PLATE 42

Figs. 1-10. Variation in the polyp chambers and stolonal network of *Protulophila gestroi* on some exfoliated Cretaceous and Tertiary serpulid tubes.

Figs. 1-2. *Parsimonia* sp. A10932, *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Both ×8.

Figs. 3-4. *Protula firma* Seguenza. SV.-I-LF/805-806 Pal. Colln., Univ. Genoa (lectotype of *Protulophila gestroi*), Pliocene; Albenga, Liguria, Italy. 3, ×2; 4, ×8.

Figs. 5-6. *Protula protensa* (Lamarck). A229, ?Miocene; Latakia, Syria. 5, ×2; 6, ×8.

Figs. 7-10. *Parsimonia* sp. *H. orbignyi* Subzone, Gault Clay, Albian; Ford Place Clay pit, Wrotham, Kent. Figs. 7-8, A10923; 7, ×2; 8, ×8. Figs. 9-10, A10892; 9, ×2·5; 10, ×8.

Figs. 11-12. Two infested tubes of *Serpula conformis* Goldfuss growing commensally on the pedicle valve of *Cererithyris intermedia*. A10450, Jurassic; Wiltshire. 11, ×1·5; 12, close up of apertures of *Protulophila gestroi* on one of the serpulids, ×8.


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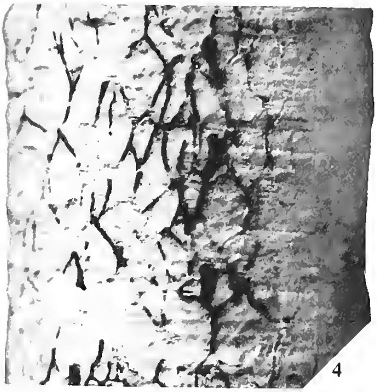
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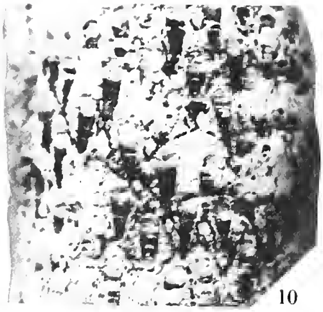
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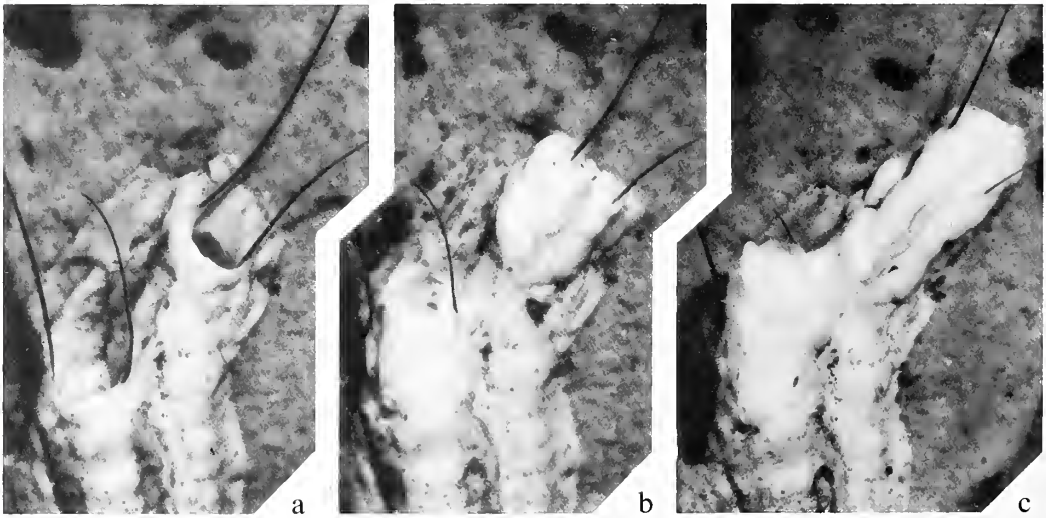
SCRUTTON, *Protulophila gestroi*

An experiment was set up to determine if the peristomial collar of a living serpulid, which acts as a template for the addition of calcium carbonate layers to the tube rim, is sufficiently flexible to envelop polypoid individuals orientated vertically on the tube rim in the manner envisaged here. Thin hairs to represent the polypoid form (eyelashes were found to be of appropriate size) were cemented to the rims of tubes of the adnate serpulid *Pomatoceros triqueter* collected from mean low-tide level in Cullercoats Bay, south-east Northumberland (text-fig. 3). Two tubes on the same small boulder were kept in the laboratory in standing sea water, changed twice weekly, at a temperature of 15–20° C. The new tube growth, after a moderately strong discontinuity, had a sharper, more pronounced keel and remained much whiter than the tube formed prior to collection. Observations made when the serpulids were expanded showed that their peristomial collars were able to fold round the base of each hair. The hairs were thus incorporated into the newly formed tubes, in one case with the formation of a small keel over the buried part of the hair but in the three other cases with perfectly smooth exterior tube surfaces over the hairs. The growing edges of the tubes formed small projections along the hairs and where they diverged outwards from the plane of the tube wall small calcareous cones formed around the bases of the projecting hairs (text-fig. 3*c*, see particularly the right-hand hair).

During the experiment the tubes were extended by 1·8 to 2·0 mm in the first 12 days, and by 1·7 mm in one case and 2·9 mm in the other in the following 76 days during which the experimental conditions were much less rigorously maintained. Neither of these sets of figures may reflect very accurately the growth rates under natural



TEXT-FIG. 3. Tubes of *Pomatoceros triqueter* mounted with hairs (*a*) which are progressively incorporated into the tubes during subsequent growth (*b*, *c*). *a*, hairs on the left-hand tube were fixed using Bostik quick-set epoxy adhesive and those on the right-hand tube with paraffin wax. *b*, appearance after 12 days during which tubes were constantly covered with sea water, changed twice weekly. *c*, appearance after a further 76 days during which the tubes were uncovered for part of the time and the sea water less regularly changed. All × 6.

conditions which vary significantly in several respects, particularly temperature, water movement, and tidal exposure, from the laboratory conditions.

No attempt was made to modify the orientation of the hairs during the experiment. In the fossil material described here, however, it appears that during the later stages of investment of an individual polyp, it changed its orientation relatively suddenly from a vertical to a more or less lateral aspect. This presumably represents a response to the calcifying activity of the serpulid, triggered by the stimulation of the tentacular crown of the polyp by the serpulid's peristomial collar, through which the polyp avoided complete incorporation into the host tube. Thus it seems likely that the chamber length bears a direct relationship to the length of the polyp. The formation of apertures suggests that the polyp was active until at least this stage of tube growth and the hood represents a callus formed by the serpulid in response to the presence of the symbiont.

Variation in aperture and hood morphology seems to reflect differences in the calcifying activity of the various species of serpulid hosts. This would tend to mask any changes in the character of these structures which might reflect slight morphological differences in the symbiont itself and in fact no such changes have been detected within the material studied.

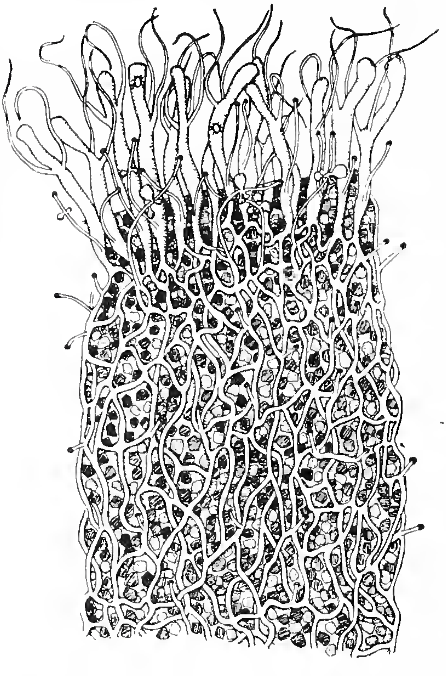
Affinities of the symbiont

Having established the morphology and the mode of origin of the polyp chambers and stolonal system, the identity of the symbiont can be discussed. Previous workers have considered the symbiont to be a ctenostomatous bryozoan, either adherent (Rovereto 1901) or boring (Walter 1965). The stolonal network described here, however, has no really close comparative among the stolon systems developed by living or fossil stoloniferous ctenostomes (see, for example, Prenant and Bobin 1956, pp. 176–335; Brien 1960, pp. 1177–1189; and Bassler 1953, pp. 32–37) and the only similar relationship with a tube worm is that shown by *Hypophorella*. In this case, *Hypophorella* initially ramifies over the inside of the tube of the polychaete *Chaetopterus*. As the worm continues to line its tube, the bryozoan colony becomes embedded and the zooids regain access to the tube lumen by rasping through the lining (Ryland 1970, p. 80). In the case of the present symbiosis, however, the apertures face outwards from the tube and are clearly not the result of burrowing through from within. *Hypophorella* itself does not closely resemble the symbiont described here (see Prenant and Bobin 1956, p. 273).

A closer comparison can be drawn between the present symbiosis and that between the hydroid stage of *Proboscidactyla* (formerly *Lar*) and various sabellid polychaetes (text-fig. 4). This symbiosis is well known and aspects of it have been described by several workers (Uchida and Okuda 1941; Hand and Hendrickson 1950; Hand 1954; Hirai 1960; and Campbell 1968*a* and *b*). Species of *Proboscidactyla* have a reticulated stolonal hydrorhiza which is adherent on the outside of the tubes of particular sabellid species. Gastrozooids are present in a ring around the rim of the tube whilst gonozooids occur in a whorl behind them and sparsely scattered over the immediately subjacent area.

Although the life style of *Proboscidactyla* can be usefully compared with that of the fossil symbiont, colony development in this hydroid appears to be unusual and is inconsistent with the pattern preserved in the fossil material. Campbell (1968*b*) has described how in *Proboscidactyla flavicirrata* the gastrozooids themselves migrate up the growing sabellid tube to maintain their position at the tube rim; the stolon system is developed behind them. This pattern of development is only known so far in *Proboscidactyla* and other hydroids extend the colony by stolon growth followed by the differentiation of new hydranths in peripheral areas. For example, the growth of *Tubularia* in culture reported by Mackie (1966) matches the pattern of growth preserved in the fossil material very closely. He described how new hydranths differentiate at stolon tips with the formation usually of two new diverging stolons at the base of the hydranth (Mackie 1966, fig. 2). This mode of growth on a suitable surface, with anastomosis of the stolons, would produce a hexagonal stolon network as pointed out by Braverman (Mackie 1966 discussion, p. 411) and although Mackie did not record anastomosis in his experiment both Thiel and Rees (Mackie 1966 discussion, p. 411) considered it a common phenomenon in hydroid cultures. It is also illustrated in natural material of *Tubularia* and other hydroids (for example *Proboscidactyla*, see text-fig. 4).

Mackie considered the regular pattern of colonial growth obtained in his glass-slide culture to be rare in nature because of the ease with which growing hydroid stolons are deflected by surface irregularities. The 'substrate' offered by the lip of a growing calcareous serpulid tube, however, with stolon growth keeping pace with tube elongation, is probably sufficiently uniform to explain the relative regularity of the stolonal network in the fossil material.



TEXT-FIG. 4. The hydroid *Proboscidactyla flavicirrata* Brandt growing on the sabellid polychaete *Potamilla myriops* (after a text-figure by Uchida and Okuda (1941) based on living material from Akkeshi Bay, Hokkaido, Japan), approximately × 15.

Although no direct comparison can be drawn between a particular living hydroid and the fossil symbiont there seem to be sufficient points of general similarity to favour its identification as a hydrozoan colony. The polyp chambers are interpreted as formed around the proximal (subtentacular) parts of hydranths rising directly from the stolonal network and the dimensions of the stolons and polyp chambers preserved in the serpulid tubes are of the same order as those of comparable structures in living hydroids. There are no structures in the fossil material which can be specifically identified as occupied in life by reproductive individuals. Gonophores may have been carried on the hydranths, however, or blastostyles developed from hydranths to occupy already formed polyp chambers. In either case the appearance of the polyp chamber would be unmodified.

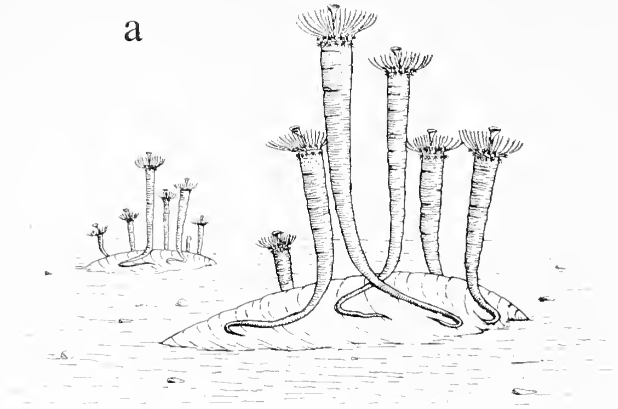
Character and history of the association

The hydroid-serpulid symbiosis seems to have enjoyed considerable success to judge by its geological history. The fossil material spans the period Middle Jurassic (Bajocian) to Pliocene, approximately 170 m.y., with several different genera and species of serpulids involved, including straight and coiled, adherent, and free living tubes. Only limited data are available on the status of the symbiosis at any particular time and place. For example, from the *Rhactorhynchia inconstans* Bed in the Kimmeridge Clay of Osmington Bay, Dorset, seventeen out of thirty-six tubes of *Serpula sulcata* show signs of the infestation and on some of these (for example, the specimen figured on Pl. 40, fig. 6) apertures are sparse and irregularly distributed. Two other common serpulids from the same bed (*S. variabilis* and *S. tricarinata*) show no signs of the symbiosis at all, suggesting that the hydroid was host specific in that assemblage. A much higher percentage infestation was found in a large sample of the tubes of *Parsimonia* sp. from the *H. orbignyi* Subzone of the Gault Clay (Lower Cretaceous) of Ford Place, Kent, in which 174 out of 183 specimens were infested. Several hundred additional tubes from the same horizon were judged to be too worn to retain any trace of the symbiosis.

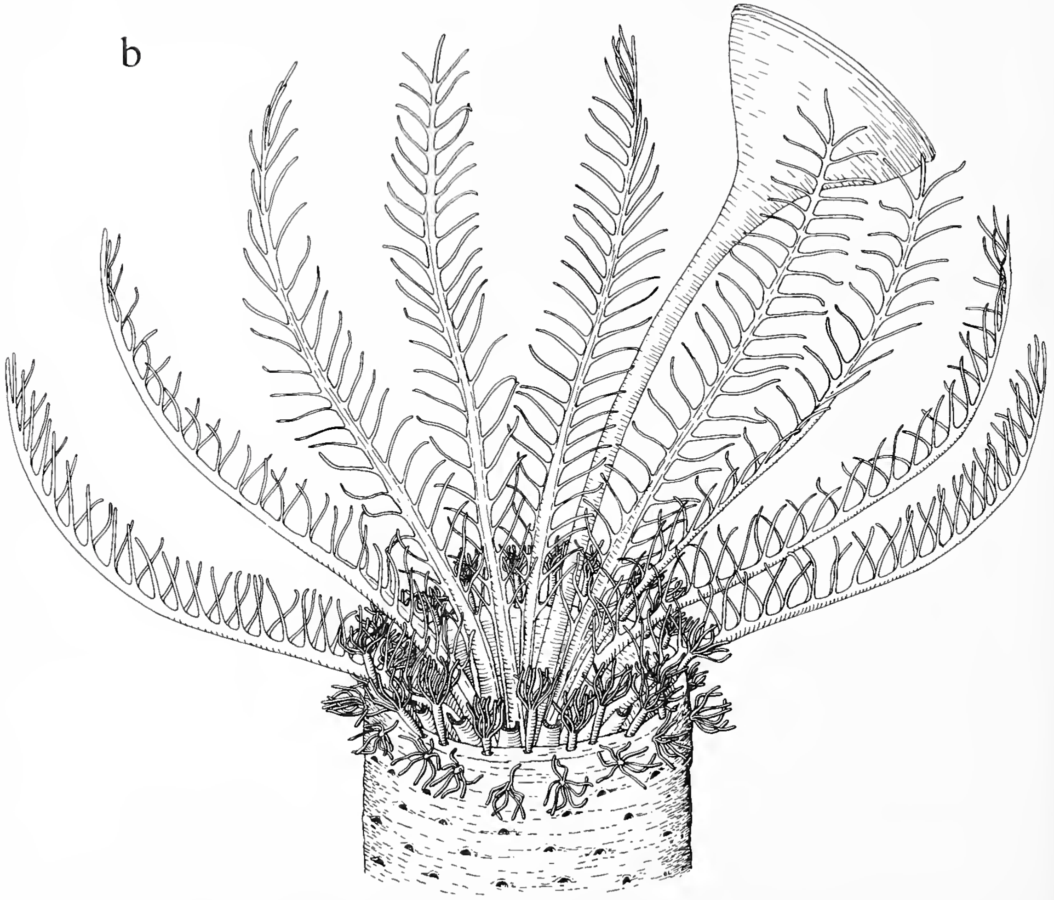
In the early stages of the fossil association it is likely that the calcareous tube of the serpulid was little more than a favourable substrate for growth. Hydranths closer to the worm's crown of brachial filaments, however, would have enjoyed a feeding advantage by poaching from the worm's feeding currents and this may have encouraged growth of the colony towards this source of nutrients. Once hydranths had established themselves on the growing margin of the serpulid tube, they would tend to become incorporated into the tube during calcification, giving rise to the system of stolons and polyp chambers described here.

Once this pattern of growth was established, all new hydranths would have differentiated at the growing margin of the serpulid tube. There is little direct evidence to suggest how dependent the hydranth may have become on its site at the serpulid tube rim, or indeed whether the hydrozoan colony was eventually unable to develop other than in association with a serpulid host. The living *Proboscidactyla*-sabellid symbiosis is probably sufficiently similar, however, to give an indication of the likely character of the relationship. The hydrozoan colonies of *Proboscidactyla* are known only on the tubes of sabellid worms (Campbell 1968*a*). Hand and Hendrickson (1950, p. 83) have described in some detail from their observations of living material how the gastrozooids use their tentacles to capture food particles from the sabellid's feeding currents and to take particles from the brachial groove, or the lips and palps of the worm. Furthermore, Hirai (1960) has shown experimentally that the removal of the sabellid from its tube causes the degeneration of the gastrozooids and gonozooids even though an adequate diet is maintained. Thus the dependence of *Proboscidactyla* on its sabellid host seems to be complete. If a similar degree of dependence evolved in the fossil symbiosis, there is a possibility that active gastrozooids may have been confined to the upper parts of the serpulid tube, close to the crown of the worm, in the manner shown in text-fig. 5.

The existence of a commensal relationship in the fossil material seems clear, but the advantages may not have been all one way. Batteries of nematocysts on the



TEXT-FIG. 5. Reconstruction of the possible appearance of *Parsimonia* sp. in the Lower Cretaceous Gault Sea. *a*, general appearance of serpulids. *b*, head of a tube with serpulid expanded showing relationship with hydroid gastrozooids. The peristomial collar of the serpulid has been omitted and the brachial filaments on the near side of the worm are not shown in full, approximately × 8.



hydranths of the hydrozoan colony may well have conferred protection on the serpulid host although there is little evidence in the fossil record to suggest that such a mutualistic relationship was particularly advantageous. The 95% infestation of *Parsimonia* sp. may or may not prove to be significant; otherwise infested and non-infested serpulids, both of the same and different species, could apparently exist equally successfully in the same environment. The possibility that the *Proboscidactyla*-sabellid symbiosis might be mutualistic does not seem to have been investigated.

Two examples are known where infested serpulids themselves enjoyed a commensal relationship. In both cases the serpulids' hosts were specimens of the Jurassic terebratulid *Cererithyris intermedia*. In the better example two specimens of *Serpula conformis* originate on either side of the umbo of the pedicle valve. They both grow anteriorly close to the commissure, following the left and right flanks of the valve respectively until they meet at the median sulcus (Pl. 42, figs. 11, 12). On the other brachiopod, only one serpulid belonging to the same species is present, following the commissure to the median sulcus on the left lateral side of the pedicle valve. From the orientation of the serpulid tubes on the brachiopods there can be no doubt that this was a living rather than a post-mortem relationship, with the serpulids tapping at first the inhalant currents and later the exhalant current of the brachiopods and the hydroids in turn poaching from the serpulids.

The question naturally arises as to whether several different species of hydroids were involved in the fossil symbiosis as 170 m.y. seems a long time for a single species to survive associated with different serpulids at various times and places. At least five species of *Proboscidactyla* are known as symbionts with sabellid worms at the present day. These living hydroids are clearly selective in their choice of hosts but species that are host specific in one area may have two different host species in another (see, for example, Uchida and Okuda 1941, p. 431 and Hand 1954, p. 56). Thus, the existence of a range of host serpulid species in the past does not in itself prove the presence of more than one hydroid species. In fact the basic morphology of the symbiont is so similar over its known range that even if several hydroids were involved the evidence would suggest that they were congeneric, or at least members of closely related genera. The effects of interspecific differences in serpulid tube calcification on the appearance of hoods and apertures, however, would tend to mask any slight modifications of these structures induced by different but related hydroid symbionts. At the present time, therefore, there appears to be no way in which the fossil material can be reasonably subdivided and all the known examples of this symbiont are placed in a single species here.

It is tempting to speculate that the fossil symbiont could be ancestral to *Proboscidactyla*. Subtentacular hydranth length, shape, and stolon thickness in species of the latter match the dimensions of the polyp chambers, and stolonal network very closely. The life-styles of the two organisms are considered very similar and *Proboscidactyla* appears to be unique among living hydroids in its highly developed symbiosis with sabellid polychaetes. The major difference between the two is in the manner of colony development in *Proboscidactyla*. This appears to be specifically adapted to the continuously elongating tubiform substrate provided by its hosts and these highly specialized hydroids presumably evolved from an ancestor with a more basic pattern of colonial growth. The fossil symbiont would seem to be a reasonable candidate. Whether or not the fossil symbiont infested sabellids as well as serpulids in the past will almost certainly never be established from the fossil record but it is possible that the symbiosis with serpulids is still continuing at the present day, although as yet unrecorded.

SYSTEMATIC PALAEONTOLOGY

Class HYDROZOA Owen, 1843
Order HYDROIDA Johnston, 1836
Genus PROTULOPHILA Rovereto, 1901

1901 *Protulophila* Rovereto, p. 223.

Diagnosis. As for species.

Protulophila gestroi Rovereto, 1901

1901 *Protulophila gestroi* Rovereto, p. 223, pl. 28, fig. 7*a–c*.
1965 *Immergentia*? *lissajousi* Walter, p. 286, figs. *a–c*.

Diagnosis. A system of stolons and polyp chambers preserved by overgrowth of a hydrozoan colony in the outer layers of the calcareous tubes of certain serpulid worms. The stolonal network, consisting of tubes 0·04–0·05 mm diameter, is diamond- to hexagonal-shaped when regularly developed but is often less well ordered. Polyp chambers, compressed, conical, 0·24–0·40 mm broad by 0·76–1·20 mm long, arise at or close to the base points of polygons in the stolonal network. At their densest they are spaced 0·58 mm apart laterally and 0·83 mm apart vertically. The polyp chambers have access to the exterior of the serpulid tube through semicircular to sub-circular apertures, 0·10–0·20 mm high and 0·18–0·40 mm broad. Hoods of variable prominence are developed above the apertures which may be produced in some cases as short pipes.

Lectotype (here chosen). SV.-I-LF/805–806, Palaeontological Collections, University of Genoa. Pliocene; Albenga, Liguria, Italy.

Distribution. Middle Jurassic (Bajocian) to Pliocene of Europe; ?Miocene of Syria.

Discussion. Unfortunately Rovereto's figured material of *Protulophila gestroi* was lost in the floods of 7–9 October 1970 which severely damaged the palaeontological collections of the Department of Geology, University of Genoa (Mastrorilli 1970). By good chance, I had three of Rovereto's unfigured syntypes on loan from Genoa at that time and it is one of these which is here designated lectotype for the species.

There is no doubt that Walter's material should be placed in *P. gestroi*. Although Walter (1965, p. 286) described his examples as lacking stolons, they are present but partly obscured by the density of the polyp chambers and their very shallow burial in the tube wall which has diffused the outline of the stolon and chamber system (Pl. 41, fig. 8).

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Mr. S. Ware (British Museum, Natural History) has facilitated the loan of numerous serpulid tubes from the Museum's collections and has helped me on some points of serpulid taxonomy. Dr. V. I. Mastrorilli (University of Genoa) kindly arranged the loan of some of Rovereto's original material of *Protulophila gestroi* and I am grateful to Dr. D. D. Bayliss (Robertson Research Laboratory) who translated the relevant parts of Rovereto (1901) into English for me. I would also like to thank the friends and colleagues to whom I have shown this material for their valuable comments and discussion.

Text-figs. 1 and 5 were drafted by Mr. E. Lawson (University of Newcastle upon Tyne).

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APPENDIX

This list of the serpulid species acting as hosts to *Protulophila gestroi* is arranged in ascending stratigraphic sequence. Only material deposited with museums and examined by the author is included here. Register numbers refer to specimens in the Department of Palaeontology, British Museum (Natural History) unless otherwise stated.

JURASSIC

Serpula sp. Bajocian. A541 Inferior Oolite; locality unknown.

Serpula intestinalis Phillips. Bathonian. A8769 White Limestone, Honeycombe Leaze, near Fairford, Gloucestershire; A1380–1381, Forest Marble, Fairford, Gloucestershire.

Serpula conformis Goldfuss on *Cererithyris intermedia.* A10407 Bathonian, Lower Cornbrash, Sutton, Wiltshire; A10450 Jurassic, Wiltshire.

Serpula tricarinata Sowerby. A6641 ?Callovian, Cornbrash, Steeple Ashton, Wiltshire.

Serpula lituiformis Munster. A618, A630, A693, A696 Oxfordian, Vaches Noires, Normandy, France.

Serpula sp. cf. *S. lituiformis* Munster (material described by Walter 1965). Colln. Dep. Sci. Terre, Fac. Sci. Lyon 28970 (holotype of *Immergentia*? *lissajousi* Walter), 28971–28975 Oxfordian, localities in Ain, Jura, Saone-et-Loire, and Calvados, France.

Serpula sulcata Sowerby. Oxford Clay. A520 St. Ives, Huntingdonshire; A6738, A6741 Ludgershall, Wiltshire; A6147 Jordan Hill, near Weymouth, Dorset.

Corallian. A6644 Coral Rag, Shotover Hill, near Oxford; A6743 Oakley Beds, Ashenden Junction, Buckinghamshire; A8352 Headington, Oxfordshire; A8367–8369 Ampthill Clay, Ampthill, Bedfordshire; A5107 Nattheim, Germany.

Kimmeridgian. A8529 Weymouth, Dorset; A10850–10866 *Rhactorhynchia inconstans* Bed, Osmington Bay, Dorset.

CRETACEOUS

Rotularia phillipsi (Roemer). Neocomian. A402, A2528, A5039, A5042, A5448–5449, A5051, A10410–10419, A10425 Speeton Clay, Speeton, Yorkshire; A196 Guerum, near Brunswick, Germany.

?*Rotularia* sp. Albian. A100, A446, A934, A1481–1482, A10443, A10445–10449 Gault Clay, Folkestone, Kent.

Parsimonia sp. Albian. A10886–10984 Gault Clay, Ford Place, Kent.

Parsimonia antiquata (Sowerby). Albian. A604, A5194, A7625, A10084 Red Chalk, Hunstanton, Norfolk; A2525 Red Chalk, Speeton, Yorkshire.

Rotularia umbonata (Sowerby). Albian. A271, A1390, A10349–10351, A10386–10387 Red Chalk, Hunstanton, Norfolk; A10394 Upper Greensand, Devizes, Wiltshire.

Cenomanian. A512 Cambridge Greensand, Cambridge.

Glomerula gordialis (Schlotheim). Albian. A10398 Upper Greensand, Blackdown, Devon.

Rotularia sp. A. Cenomanian. A31, A116, A119, A7486–7487, A10429, A10438 Grey Chalk, Dover; A2605 *S. varians* Zone, Burham, Kent; A8387 North Buxbury pit, Wiltshire.

Coniacian. A10391 East Cliffs, Dover.

Upper Cretaceous. A10399 Chalk, Dorking, Surrey.

Proliserpula ampullacea (Sowerby). A10393 Chalk, near Weymouth, Dorset.

Serpula macropus (Sowerby). Senonian. A7425 *M. coranguinum* Zone, Northfleet, Kent.

Serpula sp. Cenomanian. A1673 Chalk Marl, Cambridge.

Coniacian. A10390 East Cliffs, Dover.

EOCENE

Sclerostyla perforata Wrigley. London Clay. A6983 (holotype), A9512–9513 Wokingham, Berkshire; A9141–9143, A9146 London Clay, Amen Corner, Berkshire.

MIOCENE

Protula protensa (Lamarck). A358, A10622 Tortona, Italy; 52346, A10657–10658 Piedmont, Italy; A229, A10664–10665 ?Miocene, Latakia, Syria.

PLIOCENE

Protula protensa (Lamarck). Plaisancian. A44, A10641, A10645 Bordighera, NW. Italy.

Protula firma Seguenza. Pliocene. SV.-I-LF/805–806 Pal. Colln., Univ. Genoa (lectotype of *Protulophila gestroi*), Albenga, Liguria, Italy.

THE INTERPRETATION OF THE LOWER CRETACEOUS HETEROMORPH AMMONITE GENERA *PARACRIOCERAS* AND *HOPLOCRIOCERAS* SPATH, 1924

by P. F. RAWSON

ABSTRACT. *Ammonites* (*Crioceras*) *occultum* Seeley and *Hamites phillipsi* Phillips, the type species of *Paracrioceras* and *Hoplocrioceras* Spath, 1924, are redescribed and the original concept of the genera is reviewed. The 'Tethyan' forms *Emericiceras* and *Aspinoceras* are regarded as junior subjective synonyms of *Paracrioceras* and *Hoplocrioceras* respectively. As defined by Spath, *Hoplocrioceras* embraces small forms with weakly aspinoceratid coiling together with larger, crioceratitid species; this definition cuts completely across existing generic classification of related Tethyan forms. The significance of shell coiling in the classification of some Lower Cretaceous heteromorphs is discussed briefly, and it is suggested that forms with aspinoceratid/ancyloceratid coiling may be dimorphs of larger, crioceratitid forms.

THE Lower Cretaceous heteromorphs *Ammonites* (*Crioceras*) *occultum* Seeley (1865) from the Snettisham Clay (Norfolk) and *Hamites phillipsi* Phillips (1829) from the Speeton Clay (Yorkshire) were designated type species of Spath's (1924) new genera *Paracrioceras* and *Hoplocrioceras* respectively. The generic names have subsequently been applied to a variety of late Hauterivian and Barremian species in north-west Europe, and occasionally further afield, but ignored by most recent workers on the Tethyan, especially French, faunas. Hence an impression is gained that both genera have a 'boreal' distribution when, in fact, their type species are remarkably close to some 'Tethyan' forms. However, the type species are poorly known since both were based on single, incomplete specimens and neither has been revised, though the holotype of *Hoplocrioceras phillipsi* has been described and refigured (Howarth 1962). A limited number of additional specimens allows the ontogeny of both to be outlined for the first time. Spath's (1924) concept of the genera is reviewed in the light of these descriptions.

DESCRIPTION OF THE TYPE SPECIES

Superfamily ANCYLOCERATACEAE Meek, 1876
Family ANCYLOCERATIDAE Meek, 1876
Subfamily CRIOCERATITINAE Wright, 1952
Genus PARACRIOCERAS Spath, 1924
Paracrioceras occultum (Seeley)

Plate 43, figs. 1–6; text-fig. 1*a–b*

v* 1865 *Ammonites* (*Crioceras*) *occultus* Seeley, p. 246, pl. 10, fig. 1.
v 1924 *Paracrioceras occultum* (Seeley); Spath, p. 79.

Holotype. Cookson Collection, Sedgwick Museum, Cambridge, B. 11129.

[Palaeontology, Vol. 18, Part 2, 1975, pp. 275–283, pl. 43.]

Type locality. 'Near Hunstanton' (Seeley 1865, p. 246). The specimen bears a later label claiming, possibly erroneously, that it is from the Heacham Brick Pit, near Snettisham.

Horizon. Snettisham Clay (mid Barremian). The holotype may have been obtained from the local boulder clay (Pleistocene), according to Seeley.

Other described material. Two specimens: Sedgwick Museum B. 11131 and B. 11797, from the Snettisham Clay at Heacham Brick Pit, near Snettisham.

Description. Although the holotype (text-fig. 1*a*–*b*) is a body chamber only, the other two specimens show earlier growth-stages; one (B. 11797) is a well-preserved body chamber and adjacent fragment of phragmocone, closely matching the holotype but with a crushed impression of earlier whorls, while the other (B. 11131) is a smaller individual of 86·5 mm diameter. Both were apparently examined by Spath during the preparation of his 1924 paper.

Coiling is regularly crioceratitid throughout; the first solidly preserved whorl starts at about 40 mm diameter (B. 11131) but rubber casts have been made from external moulds of earlier growth stages (B. 11131, B. 11797). These show that trituberculate ribs have already developed by about 12 mm diameter (B. 11797). From about 15 mm to about 70 mm diameter these ribs are swollen and bear long, sharp umbilical, mid-lateral, and ventro-lateral spines (bluntly rounded on internal moulds). The ventro-lateral spines touch the dorsum of the succeeding whorl. Between each trituberculate rib there are normally two or three (up to five in the early whorls of B. 11797) finer ribs which arise at the umbilical edge and remain non-tuberculate, or bear a small mid-lateral or ventro-lateral tubercle. Occasionally, the posterior rib of a group is associated with the preceding trituberculate rib, looping from the umbilical to mid-lateral tubercle of this stronger rib, then from the mid-lateral or ventro-lateral tubercle, and finally across the venter to the opposing ventro-lateral tubercle. Above about 70 mm diameter the strength of the trituberculate rib gradually diminishes, the mid-lateral tubercle reduces, and the whorl flank consequently becomes flatter (B. 11131, B. 11797), so that by about 85 mm diameter the ribs are almost equal in strength and mid-lateral tubercles have disappeared. This final, presumably adult, growth stage is well seen on both the body chamber of B. 11797 and the holotype (B. 11129).

Changes in the whorl section accompany the changes in sculpture. In the inner whorls the section is rounded, slightly higher than wide, and angular at umbilical and ventro-lateral edges. Sections across the trituberculate ribs are distinctly hexagonal. As the tuberculation diminishes, the whorl flanks flatten and height correspondingly increases, so that the whorl section of the holotype and body chamber of B. 11797 is subquadrate, the flanks almost flat but converging slightly towards the ventral region. The ventro-lateral shoulder and dorsal edge are angular. The dorsum is concave and crossed by forwardly curving rib-folds and finer growth lines. It bears an impression of the tip of the ventro-lateral tubercles of the preceding whorl, and slight indentations on the holotype apparently correspond with the ventro-lateral angle of the preceding whorl. These are absent on specimen B. 11797 and it is unlikely that the body chamber of the holotype was in contact with the penultimate whorl.

The flanks of the holotype are crossed by slightly flexuous ribs, some of which arise singly or in pairs from a radial umbilical swelling while others are intercalated at the angular umbilical edge or higher on the whorl flank. Prominent ventro-lateral

TEXT-FIG. 1. Holotypes. *a*, *b*, *Paracrioceras occultum* (Seeley), Sedgwick Museum B. 11129 (Cookson Collection), a slightly worn body chamber steinkern from the drift (or Snettisham Clay?) near Hunstanton, Norfolk; photograph by Mr. B. J. Samuels. *c*, *d*, *Hoplocrioceras phillipsi* (Phillips), Yorkshire Museum, tablet 424 (Bean Collection), from the Speeton Clay of Speeton, Yorkshire. Photograph kindly given by Dr. M. K. Howarth, who photographically illustrated the specimen for the first time in this journal, vol. 5 for 1962. All photographs × 1.

tubercles occur, sometimes common to two adjacent ribs, at other times limited to a single rib. Normally there are two non-tuberculate ribs between each of the tuberculate ones. The body chamber of B. 11797 has a very similar rib-pattern, but nearly every rib arises at the umbilical edge and most are single.

The suture-line is not adequately preserved on any of the specimens, but the septum has only four lobes, indicating a characteristic crioceratitid suture.

Genus HOPLOCRIOCERAS Spath, 1924

Hoplocrioceras phillipsi (Phillips)

Plate 43, figs. 7–8; text-figs. 1*c–d*, 2

v* 1829 *Hamites phillipsi* (Bean MS.) Phillips, p. 124, pl. 1, fig. 30 (2nd edn. 1835; 3rd edn. 1875).
v* 1924 *Hoplocrioceras phillipsi* (Phillips); Spath, p. 78.
v* 1962 *Hoplocrioceras phillipsi* (Phillips); Howarth, p. 130, pl. 18, fig. 3.

Holotype. William Bean Collection, Yorkshire Museum, York, tablet 424.

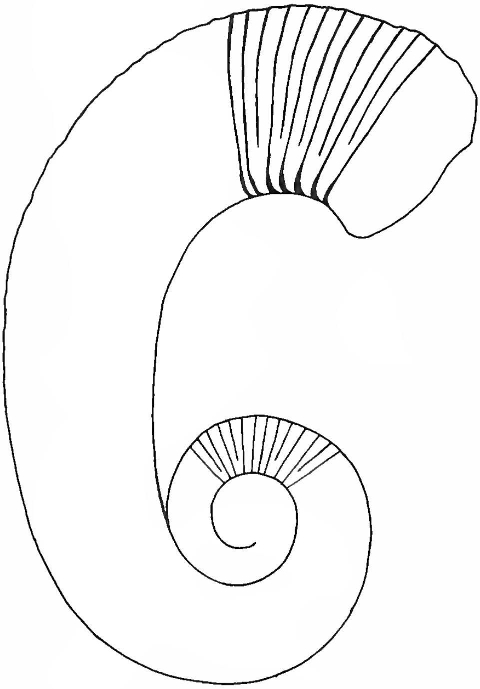
Type locality. Speeton, Filey Bay, Yorkshire.

Horizon. Speeton Clay. The exact horizon is not known, but the specimen is probably from the upper part of the Lower B Beds, of Lower Barremian age (see below).

Other material. One crozier: BM. C. 73594, from an unrecorded horizon in the Speeton Clay of Speeton.

Description. The holotype (text-fig. 1*c–d*) was described and refigured by Howarth (1962). It consists of about one and one-quarter septate whorls coiled so that the venter of one is just about in contact with the dorsum of the next, followed by a slightly crushed, incomplete body chamber which immediately (starting at 46 mm diameter) uncoils, though it remains slightly curved. The dorsum is not clearly visible, but the ventral region is rounded. The ribs are straight and single, with a few intercalated ribs appearing low on the whorl flank. Sutures are visible on the flanks and venter, and are clearly crioceratitid.

BM. C. 73594, the only other known example of the species, is a hooked body chamber (Pl. 43, figs. 7–8) with the last septum preserved. It represents a more advanced growth-stage than the holotype, but at a comparable stage the rib-pattern of both specimens is identical and the general shell proportions appear very similar when allowance is made for the slight crushing in the holotype. The dorsum is flat, crossed only by forwardly curving rib-folds and growth striae, the dorso-lateral edge slightly rounded and the ventro-lateral region well rounded, merging smoothly into the venter. The whorl section is almost elliptical, widest near the dorsum. The ribs are single and straight; primaries are raised slightly at the umbilical edge, exactly as on the body chamber of the holotype, and other ribs are intercalated low on the flank. On average, there is one intercalated rib between each primary, but the pattern is slightly irregular.



TEXT-FIG. 2. *Hoplocrioceras phillipsi* (Phillips). Reconstruction (based on the holotype and BM. C. 73594) to show the aspinoceratid mode of coiling, × 1.

Discussion. Text-fig. 2 is a reconstruction of an adult *H. phillipsi* based on the two specimens described here. The reconstruction supports Spath's (1924, p. 78) view that *H. phillipsi* is close to '*Ancyloceras*' *laeviusculum* Koenen (1902, p. 350, pl. 28, figs. 4–6) with aspinoceratid coiling.

The horizon of *H. phillipsi* is not known, but the German *H. laeviusculum* came from the Lower Barremian *fissicostatum* Zone, the index species of which is known from Bed LB3 at Speeton (Rawson 1971, p. 72).

SPATH'S CONCEPT OF THE GENERA

Spath's definition of *Hoplocrioceras* and *Paracrioceras* was brief, and subsequent interpretation has necessarily relied mainly on some north German species, described by Koenen (1902) and earlier authors, which Spath (1924) also assigned to his new genera. These include forms very distinct from the type species. A full reappraisal of the scope of the genera must await a much-needed revision of the English and north German Barremian crioceratitid faunas; the following notes are limited to a discussion of Spath's concept of the genera in the light of his notes and faunal lists, coupled with the present revision of the type species.

Paracrioceras

No formal diagnosis was published, but Spath (1924, p. 84) noted that *Paracrioceras* is 'characterised by highly tuberculate ornamentation' and that it includes 'the Mediterranean *emerici* group', which resemble (p. 82) the *Paracrioceras* of the north German *roeveri* and *elegans* Zones. It also embraces (p. 85) the 'degenerate' forms of the *robustum* and *denckmanni* type. The faunal list from the Speeton Clay (pp. 77–78) and Snettisham Clay (p. 79) includes *P. statheri* Spath, *P.* aff. *varicosum* (Koenen), *P.* aff. *tuba* (Koenen), *P.* aff. *denckmanni* (Müller), *P.* cf. *woeckeneri* (Koenen), *P.* cf. *elegans* (Koenen), and the type species *P. occultum* (Seeley).

Some of the north German crioceratitids figured by Koenen (1902) have inner whorls close to those of *P. occultum* but with a body chamber ornamented only by well-spaced, strong, trituberculate ribs (e.g. *P. elegans*; Koenen 1902, pl. 24, fig. 2). The later forms which Spath regarded as 'degenerate' *Paracrioceras*, such as *P. denckmanni* (Müller), *P. stadtlaenderi* (Müller), and *P. tuba* (Koenen), are more distinct from *P. occultum*. They are closely coiled with the whorls almost in contact, have strongly tuberculate inner whorls with few, widely spaced ribs, and by diameters of 65–70 mm have lost their tubercles and retain strong, distant, simple ribs only.

The earlier trituberculate whorls of *P. occultum* are very close to those of species of the Tethyan *emerici* group, which (as noted above) Spath also included in *Paracrioceras*. Sarkar's (1954) genus *Emericiceras* was proposed for these Tethyan forms and has been generally accepted by French authors (*Paracrioceras* being ignored), though it is often relegated to a subgenus of *Crioceratites* Leveille. *Emericiceras* is here regarded as a junior subjective synonym of *Paracrioceras*. In turn, *Paracrioceras* of the *occultum* group may be better regarded as a subgenus of *Crioceratites*. Typical *Crioceratites* of the *duvali* group differ from the trituberculate whorls of *P. occultum* only in having more numerous, finer, non-tuberculate ribs between the tuberculate ones, and in sometimes losing the mid-lateral tubercles. In both northern and southern Europe there is a gradation from *Crioceratites* of the *duvali* group in the mid-Hauterivian to more coarsely trituberculate *Paracrioceras/Emericiceras* types in the Lower Barremian.

Wright (1957, p. L208) provisionally included *Hemicrioceras* Spath, 1924 (type species: *Crioceras rude* Koenen, 1902, from north Germany) and *Peltocrioceras* Spath, 1924 (type species: *Crioceras deeckei* Favre, 1908, from Patagonia) in synonomy with *Paracrioceras*. The type species of both genera lack trituberculate ribs in the earlier growth stages and the genera should be kept distinct.

Hoplocrioceras

Again no formal diagnosis of the genus was published, but Spath (1924, p. 78) gave an idea of its intended scope by noting that the type species is 'a form close to *Crioceras laeviusculum* v. Koenen', while defining the genus 'to include also *Crioceras fissicostatum* (Roemer) Neum. & Uhlig, non v. Koenen?, and allied forms'. Thus he linked small aspinoceratid forms with larger species showing crioceratitid coiling throughout growth. This was in agreement with his belief (p. 85) that the nature of the coiling is not of generic importance.

It is not absolutely clear what features Spath regarded as diagnostic of the genus. Subsequent authors (e.g. Anderson 1938; Wright 1957) have stressed the 'bundling of the ribs at the umbilical tubercle', though in its original context (Spath 1924, p. 84) this statement may have referred to the *fissicostatum* group only. Certainly neither *H. phillipsi* nor *H. laeviusculum* have bundled ribs or umbilical tubercles, though the ribs swell slightly at the umbilical edge on the body chamber. On the other hand, two factors indicate a close relationship between the two groups. Firstly, the specimen with bundled ribs on the outer whorl which Neumayr and Uhlig (1881, pl. 56, fig. 1) figured as *H. fissicostatum* (Roemer) can be matched by fragmentary individuals from the Speeton Clay in which the ribs in early growth stages are close to those of *H. phillipsi*. Secondly, *H. laeviusculum* occurs at the same horizon as members of the *fissicostatum* group in the north German Lower Barremian (Koenen 1902).

Some members of the *fissicostatum* group attain an adult growth stage in which the body chamber is ornamented only with strong, simple, tuberculate ribs; these include Koenen's (1902, pl. 22, figs. 1, 2) figured *H. fissicostatum*.

Aspinoceras Anderson, 1938 (type species *A. hamlini* Anderson) is here regarded as a junior subjective synonym of *Hoplocrioceras*. *A. hamlini* was based on a partly distorted specimen with non-tuberculate ribs 'often dividing near the dorsal border and on the upper part of the side' (Anderson 1938, p. 207). The illustrations suggest intercalation rather than division of the shorter ribs, and both rib pattern and coiling appear similar to *H. phillipsi*.

EXPLANATION OF PLATE 43

Figs. 1–6. *Paracrioceras occultum* (Seeley). Snettisham Clay, Heacham Brick Pit, Norfolk. Sedgwick Museum Collection, presented 1904. 1–3, SM. B. 11797; 4–6, SM. B. 11131. Figs. 1 and 6 are rubber casts from the natural external moulds visible on figs. 2 and 5; figs. 2–5 are natural moulds.

Figs. 7, 8. *Hoplocrioceras phillipsi* (Phillips). British Museum (Nat. Hist.) C. 73594 (pres. Dr. R. Francis, 1965). A crozier with shell preserved from the Speeton Clay of Speeton.

All photographs × 1, by Mr. B. J. Samuels of Queen Mary College.

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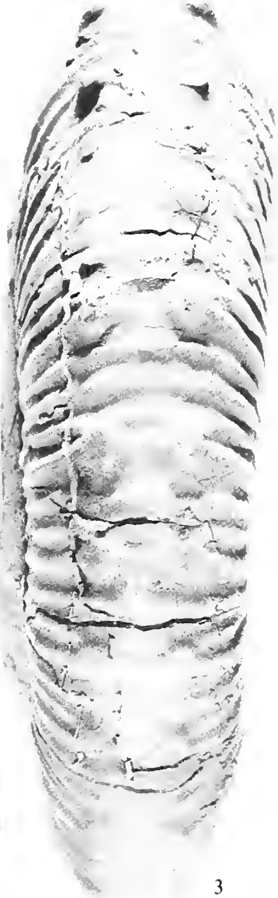

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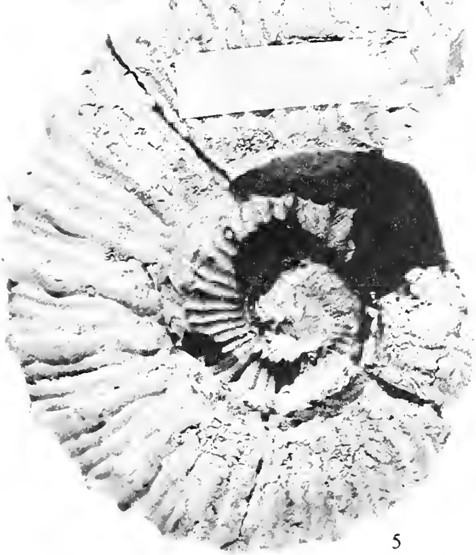

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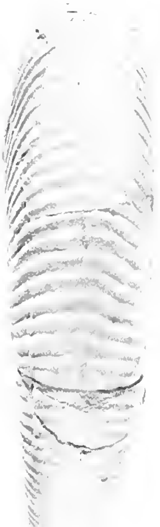

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RAWSON, *Paracrioceras* and *Hoplocrioceras*

DISCUSSION: SHELL SHAPE, SUPRA-SPECIFIC CLASSIFICATION, AND DIMORPHISM

In most studies of the Hauterivian/Barremian heteromorphs of southern Europe, forms with ancyloceratid/aspinoceratid coiling are separated from crioceratitid types at generic and subfamily level (e.g. Sarkar 1955; Thomel 1964; Wiedmann 1962). On the basis of their type species alone, *Paracrioceras* would thus be a typical member of the Crioceratitinae whereas *Hoplocrioceras* would be an early member of the Ancyloceratinae close to *Acrioceras*.

Spath's (1924) grouping of large crioceratitid with smaller aspinoceratid forms in one genus (*Hoplocrioceras*) cuts completely across this procedure. An assessment of the relative merits of these differing schemes of classification is needed, but there is already some evidence to suggest that generic distinction on coiling alone may be unsound. Firstly, there are some other north-west European forms which show differing shell shapes but identical (and highly distinctive) sculpture. These are the species which Spath (1924) grouped into another new genus, *Parancyloceras*, of late Barremian age. The type species, *P. bidentatum* (Koenen), is one of several crioceratitid species, but Spath also included in the same genus some small forms with initial coiled whorls and a straight shaft (with final hook?), such as *P. scalare* (Koenen). Both species groups have simple ribs which are often noticeably flattened on the venter and bear small ventro-lateral tubercles, and both occur at the same stratigraphical horizon.

Secondly, Thomel (1964) pointed out the remarkable similarity between the development and changes in sculpture of the Tethyan *Crioceratites* (subgenera *Crioceratites* and *Emericiceras*) and *Acrioceras* (subgenera *Acrioceras*, *Protacrioceras*, *Aspinoceras*, and *Paraspinoceras*) lineages. Referring to *Acrioceras* sensu lato, Thomel (1964, p. 72) noted 'this branch is incontestably connected to that of *C. duvali*. In fact, some species . . . show great similarities in ornamentation to *C. duvali* Lev., *C. nolani* (Kil.) and related forms from which they differ by their coiling. . . . The order of appearance of representatives of this race presents a curious parallelism with the succession of the sub-genera *Crioceratites* and *Emericiceras* in the course of the Hauterivian and Barremian' (author's translation from the French).

Thirdly, although all the species currently included in *Paracrioceras* are crioceratitids, the type species is accompanied in the Snettisham Clay by body chambers of *Acrioceras* (recorded by Spath 1924 as *A.* cf. *tabarelli* Astier sp. and *A.* cf. *silesiacum* Uhlig sp.), one of which (SM. B. 11130) shows an impression of the inner whorls. These are very close to the comparable growth stage of *P. occultum*. This is exactly the relationship seen between *Emericiceras* (= *Paracrioceras*) and certain *Acrioceras* in the Tethyan faunas discussed above.

Thorough reassessment of the relative importance of coiling and sculpture in the supra-specific classification of these heteromorph forms must await more work on the stratigraphical distribution of the abundant Tethyan faunas. However, the evidence outlined here suggests that far from indicating differences that should be accommodated at subfamily level, the type of coiling may be unimportant even at generic level. The old idea that it may reflect sexual dimorphism is well worth examining in view of the increasing evidence that aspinoceratid/ancyloceratid forms occur at the same horizon as larger crioceratitids with similar sculpture in the early whorls.

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LOOP DEVELOPMENT AND THE CLASSIFICATION OF TEREBRATELLACEAN BRACHIOPODS

by JOYCE R. RICHARDSON

ABSTRACT. The classical separation of Cainozoic long-looped brachiopods into two groups of genera, dallinid and terebratellid, according to certain early developmental features of the loop, does not withstand critical examination. These studies confirm the high taxonomic value of developing loop patterns but consider features of the developing loop, used previously to separate families, to be invalid. The dallinid sequence as defined previously is shown herein to include two groups of genera differing in the loop patterns exhibited during intermediate phases of development. These two groups of genera differ from each other and from terebratellid genera in the manner of resorption of parts of the ring and the stage at which it is freed from the septum. These factors govern the presence in one group (Dallinidae) of descending branches with double anterior limbs and in the other group (Laqueidae) of vertical connecting bands, neither of these structures occurring in the development of the Terebratellidae. The growth phases of the loop are identified by a simpler terminology using descriptive in place of generic adjectives. Two subfamilies, the Dallininae and Nipponithyrinae, are retained in the Dallinidae and four subfamilies, the Kingeninae, Pictothyrinae, Macandreviinae, and Terebrataliinae (nov.), are included in the Laqueidae.

THE form of the loop is of prime importance in brachiopod classification. The dominant brachiopod faunas of the Cainozoic possess long loops and they are noted for the complex ontogenetic sequences from which adult loop patterns derive. The development of long-looped brachiopods from any geological age culminates in a loop possessing the same elements, descending branches and a transverse band uniting ascending branches; crura attach the loop to the cardinalia (the collection of structures in the dorsal valve concerned with articulation). This loop form is achieved by a series of metamorphoses of structures derived from the crura and a median septal pillar in most Mesozoic and Cainozoic genera and from the crura alone in Palaeozoic genera. In the Cainozoic genera reviewed here the crura give rise to the posterior segments of the descending branches and a ring gives rise to the ascending branches and the transverse band. The development of a long loop ultimately free of the septum may include the formation of three pairs of connecting bands linking the loop and the septum, one pair of horizontal bands (lateral connecting bands), and two pairs of vertical bands (medio-vertical and latero-vertical connecting bands).

Developmental features of the loop have long been used to differentiate two ontogenetic sequences, dallinid and terebratellid, within the superfamily Terebratellacea. Three families, namely the Dallinidae, Laqueidae, and Macandreviidae, are alleged to show dallinid development while the terebratellid sequence characterizes the Terebratellidae. The remaining terebratellacean families possess loops thought to be neotenous derivatives of the more complex structures seen in dallinid and terebratellid families.

Different authors have proposed a number of features to distinguish the loop development of dallinid and terebratellid genera. Fischer and Oehlert (1892) and Beecher (1895) claimed that during dallinid development lacunae appear in the

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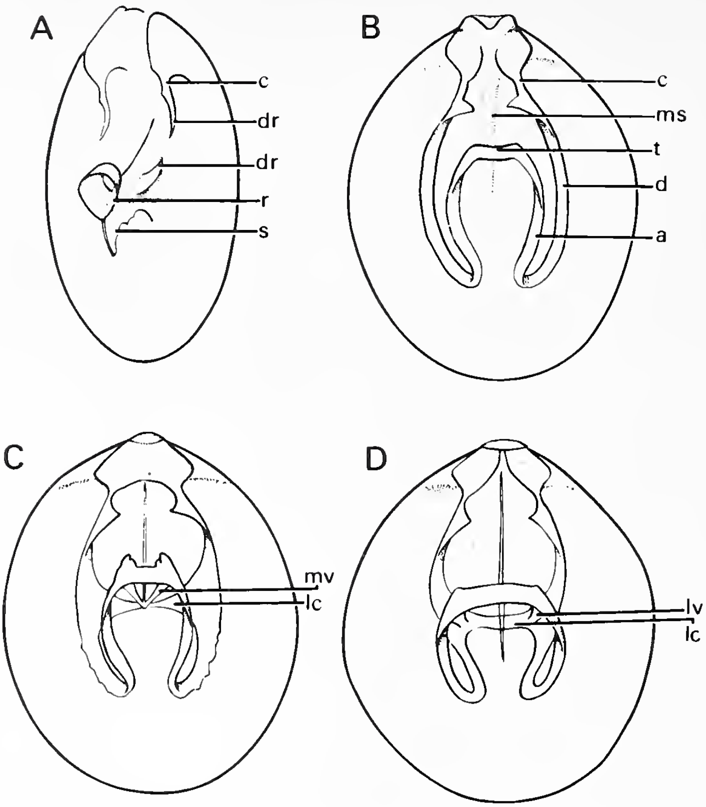


TEXT-FIG. 1. Semi-diagrammatic views of interiors of dorsal valves of four long-looped brachiopods to show: A, the loop rudiments; B, a loop free of the septum as in *Magellania insolita* (Tate); C, a loop with lateral and medio-vertical connecting bands as in *Paraldingia woodsii* (Tate); D, a loop with lateral and latero-vertical connecting bands as in *Frenulina pumila* (Tate).

Abbreviations: a = ascending branches; c = crura; d = descending branches; dr = descending branch rudiments; lc = lateral connecting bands; lv = latero-vertical connecting bands; ms = median septum; mv = medio-vertical connecting bands; r = ring; s = septal pillar; t = transverse band.

anterior regions of the ring which is freed from the septum at an earlier stage than in terebratellid genera. In 1927 Thomson extended these differences stating that early dallinid development is characterized by a hood enveloping the crest of the septum and descending branches arising from the crura only while in terebratellids the septum bears a lamellar ring and descending branches arise from both the crura and the septum. With further reference to early developmental phases, Konjoukova (1948, 1957) states that anterior division of the septum is characteristic of dallinid development. Elliott (1953, 1965) did not include this distinguishing feature in his review of methods of loop development in which he reaffirms the differences previously summarized by Thomson. In addition, Elliott states that since early loop calcification is more extensive in dallinids, the greater resorption necessary to produce the final loop pattern results in different intermediate loop patterns (with lacunae perforating segments of the ring) from those seen in terebratellid genera.

None of these reviews incorporates or comments upon the observation of Friele (1877) that there is a pronounced difference in the loop development of, on the one hand, *Macandrevia* and *Frenulina* and on the other *Dallina* and *Glaciarcula*. Following Beecher's review (1895) these genera have been grouped together as displaying typically dallinid development and ironically there has been extensive use of Friele's illustrations to support such a claim. The position of lacunae in determining different intermediate loop patterns in these two groups of genera has not been included in any classification based on loop development. What has happened is that the presence of lacunae *ipso facto* has become one of the chief differentiating factors in methods of loop development. Any genera displaying lacunae during intermediate phases of loop development are regarded as dallinid while lacunae have not been described in any stage in the development of any terebratellid.

Studies on the development of a number of species (Richardson 1973*a*, in press) have led the author to the conclusion that lacunae may be present in the developing loop of all genera (which in their ontogenies reach intermediate loop patterns) including those attributed to the Terebratellidae. These studies have also led to the conclusion that the pattern described previously as dallinid is a confusing conglomerate of two different patterns of development. Hence an unnecessarily complex picture of the supposed dallinid sequence has evolved and with it a most formidable terminology. All accounts of loop development in different species indicate that three developmental patterns are evident in terebratellacean genera and that the key factors differentiating these are the stage at which the ring is freed from the septum and the manner in which the ring is resorbed. The origin of the descending branches and the presence of lacunae, a hood, a ring, or of a bifurcating septum are not factors which separate types of loop development.

THE DIFFERENTIATION OF DALLINID AND TEREBRATELLID LOOP PATTERNS

Origin of the descending branches

The first author to introduce the method of origin of the descending branches as a differentiating factor in terebratellid and dallinid growth patterns was Thomson in 1927. At that time growth stages prior to the completion of the descending branches had been figured for only two species. Fischer and Oehlert in 1892 described the development of *Terebratella dorsata*, Thomson in 1915 that of *Waltonia inconspicua*. In both species the descending branches arise from both the crura and the septum. Since the publication of Thomson's monograph, developmental stages incorporating the method of growth of the descending branches have been described for four dallinid species *Macandrevia cranium* by Atkins (1959*a*), *Frenulina sanguinolenta* by Richardson (1973*a*), *Gemmarcula humboldtii* (Hagenow), and *Trigonosemus pulchellus* (Nilsson) by Steinich (1965), and for five terebratellid species. *Magellania flavescens* (Lamarck), *Neothyris lenticularis* (Deshayes), *Pirothyris vercoi* (Blochmann), *Jaffaia jaffaensis* (Blochmann) by Richardson (in press), and *Magas chitoniformis*

(Schlotheim) by Steinich (1965). These species are characterized by the double origin of the descending branches with the single exception of *Macandrevia cranium* in which the descending branches arise from the crura only and therefore is the only species known in which this phenomenon occurs. *Macandrevia* is also characterized by pocket-shaped hinge plates and by the loss of the median septum in adult forms, features which distinguish it (together with *Notorgymia* recently described by Cooper 1972) from the large group of other genera referred to the Dallinidae. It does not seem advisable to use the mode of origin of the descending branches as a differentiator in the loop development of families when this is known from only one species which is somewhat aberrant in other morphological features.

Hood and ring

The case of the hood versus the ring is difficult to clarify because these terms and their application do not seem to have been defined, with respect to loop development, by any author. In describing the earliest growth stage observed by him of *M. cranium*, Friele refers to the septum as bearing 'a tube, the posterior end of which is enclosed' and later that 'the first visible change occurs by an opening in the closed end of the tube' (1877, p. 381). In the same paper Friele describes the development of *Dallina septigera* stating that, apart from the shape of the septum, the early appearance of the loop accords with that of *M. cranium*. Fischer and Oehlert refer to the earliest structure on the crest of the septum of *Terebratella dorsata* as 'une petite boucle' (1892, p. 289) and in both *M. cranium* and *D. septigera* as 'une très petite boucle comprimée latéralement' (p. 306). Beecher in describing the development of *Dallinella obsoleta* refers to a 'small cylinder' (1895, p. 393) arching over the septum and, in a general account of loop development, states that in both terebratellid and dallinid genera the appearance of a small ring on the septum is the precursor to the ascending branches. Neither Douvillé (1879) for *Neothyris lenticularis* nor Deslongchamps (1884) for *Frenulina sanguinolenta* refer to the hood/ring before it fuses anteriorly with the descending branches.

In 1927 Thomson introduced the possibility of differences in the hood/ring in differing types of loop development. 'A hood, instead of a ring, is only rarely developed in the Magellaniinae and its lower sides do not project so far forward as in the Dallininae' (1927, p..234). However, when discussing the development of *Waltonia inconspicua* (with *Terebratella dorsata* then the only terebratellid species whose loop development was known) he states that in the earliest stage observed a small hood lies on the back of the septum and 'this hood passes into a ring by absorption of its posterior dorsal portion, but it may persist as a hood in shells up to a length of 6 mm' (p. 262).

To quote such statements would seem to be labouring the point in minor matters of semantics had not Elliott stated that 'apart from the major difference of dalliniform hood and terebratellid ring, the development of the two families differs in the early growth of the descending branches' (1953, p. 269). These differences are reaffirmed in the Treatise by both Elliott and Hatai.

In the absence of specialized knowledge one would expect the hood to be a tube with one closed end and the ring one with both ends open. It seems clear that this is how Thomson interpreted the terms. If these definitions are acceptable then, in all examples known of early development, the first structure to arise on the septum is a hood which by the resorption of its posterior end gives rise to a ring. That is, both a hood and a ring are characteristic of dallinid and terebratellid development and, since one structure is translated into the other, the hood always precedes the ring. There are differences in the shape and extent of these structures in different species as observed and noted above by Fischer and Oehlert and by Thomson. In general, the hood/ring occupies a greater part or length of the crest of the septum at a comparable growth stage in some of the genera attributed to the Dallinidae (*Dallina*, *Campages*) than in terebratellid genera, and this seems to be the feature which Elliott wishes to emphasize. However, the Dallinidae (as defined in the Treatise) also includes genera such as *Frenulina* in which the dimensions of the band making up the ring are similar to those seen in most terebratellid genera. In addition both *F. sanguinolenta* and those terebratellid species studied show variation in the width of the band in different specimens at comparable growth stages.

Lacunae

Since Fischer and Oehlert published a comparative account of loop development in 1892 all authors have grouped together those genera in which lacunae perforate the ring during development. It is claimed that these genera show a dallinid pattern of loop development while genera not demonstrated to possess lacunae in the developing loop display a terebratellid pattern. Elliott (1953) accounts for the presence of lacunae by claiming that the developing loop of dallinid genera shows a greater degree of calcification thus requiring more extensive resorption to achieve the adult pattern.

These differences are not apparent in studies made by me (Richardson, in press) in which lacunae perforate parts of the loop in most species studied. Species in which lacunae are shown to occur are *Magellania flavescens*, *Neothyris lenticularis*, and *Waltonia inconspicua* all of which have been said to show a characteristic terebratellid pattern. Species which do not display lacunae during development, *Jaffaia jaffaensis* and *Pirothyris vercoi*, are characterized by adult loops which do not progress beyond the magelliform stage as defined on page H147 in the Treatise. Differences do exist in the number of lacunae present, in their position, the stage of development at which they occur, and in their duration, differences in this last factor probably accounting for the fact that they have not been described hitherto in any genus attributed to the Terebratellidae.

The median septum

Bifurcation. Konjoukova (1948, 1957) has suggested that one of the principal factors distinguishing dallinid and terebratellid loop patterns is the anterior division or splitting of the median septum during early growth stages in dallinid genera. This method of differentiating the two groups has not been incorporated in any other review of loop development. However, Atkins (1959*b*) in an account of the development of *Terebratalia transversa* states:

> It would seem therefore that *T. transversa* cannot remain in the Dallininae, although it agrees with those of the sub-family in which a number of growth stages are known, *Macandrevia cranium* (Müller) (Friele, 1877; Elliott, '48; Atkins, '59*b*), *Dallinella obsoleta* (Dall) (Beecher, 1895), *Frenulina sanguinolenta* (Gmelin)

> (Eudes-Deslongchamps, 1884, as *Terebratella sanguinea* (Chemnitz)), *Dallina septigera* (Lovén), (Friele, 1877), *Fallax dalliniformis* Atkins '60, and also with *Laqueus californicus* (Koch) (Konjoukova, '57) a member of the Laqueidae, in the anterior splitting or bifurcation of the septum. In *Terebratalia transversa*, however, this occurs later than in the other species mentioned, and the forks are peculiarly heavy and clumsy. *T. transversa* also possesses the dallinid character of anterior spinous projections of the septum (pp. 422–423).

Atkins statement is quoted in full because it is important that it be examined carefully as it is felt that there is confusion in understanding the relationship between the septum and the fused attachments of the ring and the descending branches; if the septum splits there is an implication that the septum itself is a contributor to the bands making up the loop. In the first place the development of those species cited by Atkins must be reviewed.

Beecher describing an early growth stage of *Dallinella obsoleta* (1895, pl. 3, fig. 10) states that 'The ascending lamellae from the septum already have begun to divide or separate anteriorly' (p. 394) and makes no reference to the condition of the septum. Friele describing a 4·5 mm growth stage in *Macandrevia cranium* states that 'The united lamellae then begin to split apart at the anterior end' (1877, p. 381). In the same paper Friele describes the development of *Dallina septigera* which in the early growth stages is similar to *M. cranium* 'The only essential differences are in the form of the septum and the size' (p. 383). At this growth stage the ventral valve of *D. septigera* is 5·5 mm in length and the median septum has a much longer attachment to the valve floor than is the case in *M. cranium*. Both Beecher and Friele give lateral views of the developing loop in addition to ventral views, a factor of great assistance in assessing the relationship of different parts of the loop. This practice would have helped to clarify Konjoukova's figures (1957) of *Laqueus californianus* in which she states there is anterior bifurcation of the septum but her illustrations could just as easily represent the anterior fusion and separation of descending branch and ring attachments with the simultaneous resorption of anterior portions of the septum.

In her account of the development of *Fallax dalliniformis* Atkins states that at a growth stage of 5·4 mm 'The hood, or ascending branches of the loop, had widened greatly: slight anterior bifurcation was evident with short spines bordering it (Text-fig. 10)' (1960*a*, p. 84). Text-fig. 10 is a ventral view of the loop at this growth stage (no lateral view provided) and shows the septum extending well beyond the anterior limits of the loop, consequently the anterior bifurcation described by Atkins refers to the ascending branches. Of the dallinid species cited above by Atkins only the development of *Frenulina sanguinolenta* has been studied by me (Richardson 1973*a*). These growth stages have been compared with those observed by Deslongchamps who does not refer to the bifurcation of the septum nor was this observed by me in any growth stage of *F. sanguinolenta*.

In all cases of loop development observed by the present and previous authors the attachments to the septum of the ring and of the descending branches lie parallel to each other (text-fig. 3). The first step in the formation of the adult loop from these separate structures is their anterior fusion so that the descending branches and the anterior segments of the ring (future ascending branches) become continuous. This fusion follows the gradual approximation of their lines of attachment to the septum and proceeds in an anterior to posterior direction until the full lengths of the attachments of the ring are fused with the descending branches. While these processes of fusion and consequent medial separation are going on the anterior border of the median septum undergoes gradual resorption. As noted in accounts of the development of *F. sanguinolenta* and of *Magellania flavescens*, *Waltonia inconspicua*, *Neothyris lenticularis* (Richardson 1973*a*, in press) it is difficult to assess from isolated growth stages whether the fusion and separation of the anterior segments of the loop involves the septum. In many specimens observed the anterior fusion of the attachments occurs simultaneously with the resorption of those parts of the septum adjacent to the fused lines of attachment of ring and descending branches. Therefore it may appear that a component derived from the septum contributes to the regions of fusion of the ring and the descending branches, a process of inclusion which would be aided by a previously split septum. However, in all species studied other growth stages were observed in which the fusion of the attachments occurred while the septum extends beyond the anterior and ventral limits of these attachments, i.e. while the septum partition-like separates the two sides of the loop. Therefore it appears that in some species at least, the septum does not contribute to the bands of the loop and that one of the variables to be considered in loop development is the stage of fusion of the attachments relative to the degree of resorption of the septum.

By means of whatever agency, splitting or fusion, the anterior division of the loop occurs, it should not be confused with the appearance of the septum in *Terebratalia transversa*. Atkins describes two specimens, 6·1 mm and 6·4 mm in length, in both the septum projects anteriorly beyond the separate attachments of the former and the fused attachments of the latter. As Atkins remarks 'There is evidently some variation in the way in which the anterior ends of the ascending branches free themselves from the septum' (1959*b*, p. 413) but does not expand this statement. Furthermore, she states that the bifurcation of the septum in *T. transversa* is 'peculiarly heavy and clumsy' (p. 422) and this appearance of the septum in *T. transversa* is comparable with the same structure in some growth stages of *Magellania flavescens* (Richardson, in press), i.e. thick ventrally with a jagged anterior edge.

The septum may split anteriorly in some species. It seems clear that this is the case in *Macandrevia cranium*. In *M. cranium* Atkins (1959*a*) describes the occurrence of an anterior split in the septum before the development of the hood. In this species the hood emerges at a late stage, relative to other structures, it rapidly becomes converted to a ring and its attachments fuse with the descending branches almost simultaneously. In *M. cranium* anterior septal splitting could be an aid to compensate for lost time in the development of the hood. The septum does not split in any of the species observed by me and whether it splits in *Dallinella obsoleta*, *Fallax dalliniformis*, *Dallina septigera*, and *Laqueus californianus* is doubtful, in these species the appearance of splitting could be confused with the anterior fusion of attachments of the ring and the descending branches.

The anterior split in the septum of *M. cranium* is preceded in ontogeny by a groove running the full length of the crest of the septum. This groove is also linked with the hood, Atkins commenting for *M. cranium* that 'grooving precedes formation of the hood' (1959*a*, p. 341). The precursor of the hood of *Frenulina sanguinolenta*, *Magellania flavescens*, *Waltonia inconspicua*, *Neothyris lenticularis*, *Pirothyris vercoi*, and *Jaffaia jaffaensis* is a groove which is restricted to the posterior section of the septal crest.

It seems reasonable to assume that these grooves are comparable and that they differ in the extent to which they occupy the crest of the septum. This assumption is supported by the fact that the groove defines the area to be occupied by its successor, the hood. That the groove is the precursor of the hood is also supported by the change in position of the early septal flanges (see p. 293) after the formation of the hood. These flanges, seen first as plates on the posterior border of the septum, become extensions of the posterior corners of the hood. In *M. cranium* the septum develops late in ontogeny and is short in length so that the hood even in occupying its full length is not appreciably wider than any of the species cited above in which the hood does not occupy more than the posterior half of the crest of the septum. A number of Mesozoic species indicate that full grooving of the septal crest with anterior bifurcation may be a more primitive condition than that seen in most Recent species in which the groove is restricted to the posterior segment of the septum. Elliott (1947, 1950) has described such a septum in the early loop phases of *Gemmarcula aurea* and of *Hamptonina buckmani* (Moore), Cooper (1955) in *Gemmarcula arizonensis* Cooper, Baker (1972) in *Zeilleria leckenbyi* (Davidson), and Steinich (1965) in *Gemmarcula humboldtii* (Hagenow) and *Trigonosemus pulchellus* (Nilsson).

Shape and spinosity. Other septal features upon which comment has been made in the above discussion are shape and spinosity. Friele (1877) noted that the median septum had a much longer attachment to the dorsal valve in *Dallina septigera* than in *M. cranium* while Beecher claimed that the septum is generally low in dallinid genera and projecting above the loop in terebratellid genera. Atkins (1959*a*) also drew attention to the dallinid character of anterior spinous projections.

The use of septal shape as a distinguishing feature would be very unsatisfactory. The shape changes so rapidly in early developmental phases in almost every species examined that the chances of matching the same growth phase in even two different species would be remote. However, there are differences in groups of genera in the extent of the septum. These differences are associated with growth or resorption during intermediate growth stages and are referred to below (p. 308). In all loop developmental series observed by me the anterior border of the septum is spinous during resorptive phases in this area.

Origin. In a recent study of the loop development of the Jurassic brachiopod *Zeilleria leckenbyi*, Baker (1972) describes the microstructure and derivation of the median septum. He states that the median septum of the adult plays no part in the development of the ascending elements of the loop. Baker refers to the earlier studies of Muir-Wood (1934) and shows that the median septum of adult shells is a bicomponent valve element resulting from the fusion of a septal pillar and septalial plates. The septal pillar comprises the anterior section and bears the future ascending elements of the loop, the septalial plates arise posteriorly as extensions of parts of the cardinalia. The septalial plates post-date and engulf the remnants of the septal pillar after the resorption of the last connections with the loop.

Studies on Recent terebratellid species (Richardson, in press) indicate that those axial structures culminating in the adult loop and septum arise in the same manner as described by Baker for the Jurassic zeilleriid brachiopods. The microstructure of the developing loop in these species has not been examined but even in the absence of such a study it is clear that the adult median septum is a composite structure. The median septum of *Frenulina sanguinolenta* has also been shown (Richardson 1973*a*) to be derived from twin sources. Baker states that he has taken great care to avoid the use of the term median septum in the description of ontogenetic stages. He uses the term septal pillar to describe the earliest axial structure bearing the ascending elements of the loop and reserves the term median septum for the adult structure arising from the fusion of the septal pillar and septalial plates and which is also free of the loop. Although I am in complete accord with Baker's findings there are difficulties in applying these definitions at this stage. In the first place there are genera such as *Frenulina*, *Jaffaia*, *Pirothyris*, *Waltonia*, in which the adult loop is not free of the septum and in which it is not yet clear whether parts of the early septal pillar are engulfed by septalial plates. Secondly, the descending branches in all species studied also arise from both the cardinalia and the septal pillar; whether or not there are similar differences in microstructure as are evident in the septum is not known. Thirdly, there seems to be some confusion in the use of the terms, septalium, septalial plates, cruralium and their relationship to each other and to septal structures in brachiopods from different geological eras. Finally, the term median septum permeates the literature pertaining to Cainozoic brachiopods to such an extent that until a thorough morphological and ontogenetic study can be made of these structures it is preferable, for sheer convenience, to retain the term median septum to be used in the general sense in which it has been employed in the past. However, in the description of new material the terms septal pillar and median septum should be used where they can be clearly differentiated.

Septal flanges. Atkins (1959*b*) has provided a comprehensive and critical review of the occurrence of septal flanges in different species. These flanges arise on the posterior border of the median septum, they then become lateral expansions of the hood and finally are seen as postero-lateral horns on the transverse band. This sequence has been shown to occur in *Gemmarcula aurea* Elliott by Elliott (1947), *Gemmarcula humboldtii* (Steinich 1965), and in *Frenulina sanguinolenta* (Richardson 1973*a*). These flanges occur during development but are lost in the more advanced loop stages of the Recent species *Terebratalia transversa* (Sowerby) and of *Dallinella obsoleta* as described by Atkins (1959*b*) and Beecher (1895) respectively. They also occur in the Cretaceous species *Trigonosemus pulchellus* as described by Steinich (1965). Atkins noted that horns present on the transverse band of *Macandrevia cranium* are not preceded by flanges on the septum or the hood during the development of this species. Atkins states that their presence in *M. cranium* is due to the narrowing of a wide, transverse band by resorption of its mid-posterior margin. Horns are present also on the transverse bands of two genera, *Paraldingia* and *Jolonica*, whose loop development is unknown but is presumed to be similar to that of *Frenulina* (Richardson 1973*a*). In describing the hood of the Lower Cretaceous genus *Belothyris*, Smirnova (1960) compares the lateral flanges seen with those of *Gemmarcula aurea*. Owen (1970) also noted horns on the transverse bands of species of *Kingena* but does not consider them to be analogous with those seen in *G. aurea* because they show a different angle of deflection.

Thus the occurrence of flanges is described, in even doubtful cases, only in dallinid genera. Although the development of eight terebratellid species has been described none has included a description of septal flanges or of the structures derived from them. These structures are termed 'pre-campagiform flanges' in the Treatise Glossary (Williams *et al.* 1965, p. H150).

Their presence has not been shown in any species of *Campages* nor in the development of *Fallax dalliniformis* Atkins which exhibits the same adult loop pattern as *Campages*. Consequently it is preferable to refer to these structures as septal flanges which in later developmental stages become lateral flanges on the hood then horns or ears on the transverse band whether or not they are ultimately resorbed. However, the presence of horns on the transverse band does not necessarily indicate that they have been preceded in development by septal flanges.

AN ACCOUNT OF FRIELE'S OBSERVATIONS AND THEIR SUBSEQUENT MISINTERPRETATION

Friele (1877) stated that the developing loop of *Macandrevia cranium* displayed a method of ring resorption different from that of *Dallina septigera*. Friele maintained that the early stages of loop development were similar in both species but that during the '*megerlia*' stage of *M. cranium* 'the lateral walls of the ring were broken down by an aperture appearing in the middle of each and widening backwards'; in *D. septigera* 'the breach occurs to the contrary on the posterior end of the walls and extends in a forward direction' (Friele 1877, p. 383).

Friele also noted that young adult loops of *Frenulina sanguinolenta* were comparable with the megerliiform loop pattern of *M. cranium* and that developmental stages of *Glaciarcula spitzbergensis* (Davidson) were allied with those of *D. septigera*. Deslongchamps (1884) also noted these differences in methods of loop development after a study of *F. sanguinolenta* and noted certain similarities apparent in the adult loops of *Frenulina* and of *Laqueus*.

Contrary to the statements of Friele and Deslongchamps, Fischer and Oehlert (1892) claimed that *M. cranium* and *D. septigera* followed the same pattern of loop development and that each species passed through a series of stages termed centronelliform, ismeniiform (= megerliiform of Friele), terebratelliform, and magellaniiform. Fischer and Oehlert did not study the loop development of either *M. cranium* or *D. septigera* and they employed Friele's figures to demonstrate their theories. An examination of those figures from Friele, reproduced by Fischer and Oehlert, of *M. cranium* and *D. septigera* at the so-called ismeniiform stage reveals the apparent cause of error (text-fig. 2).

In the figures of these species lacunae are depicted in parts of the developing loop. However, the presence of these lacunae is not comparable in *M. cranium* and *D. septigera*. In *M. cranium* the lacunae appear in the dorsal bands of the ring while it is still attached (at least posteriorly) to the septum resulting in the delimitation of vertical connecting bands posteriorly; in *D. septigera* the lacunae appear after the dorsal segments of the ring are freed from the septum. A comparative study of Friele's figures of the developing loop of *M. cranium* and of *D. septigera* clearly demonstrates the differences both in the position of the lacunae and in the relative position and stage at which they appear in these two species.

Fischer and Oehlert's assertion that *M. cranium* and *D. septigera* display the same

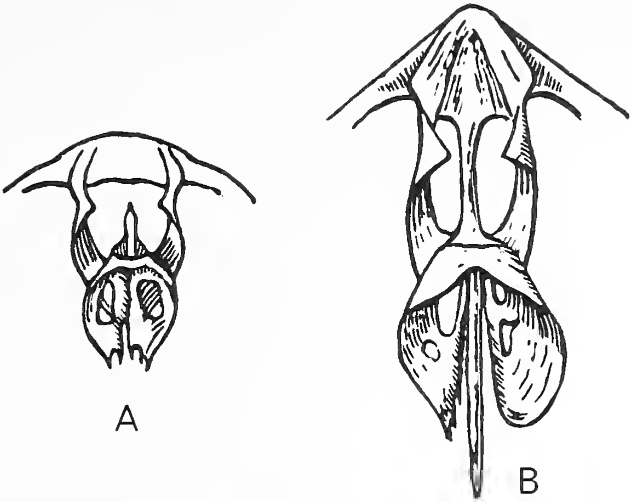
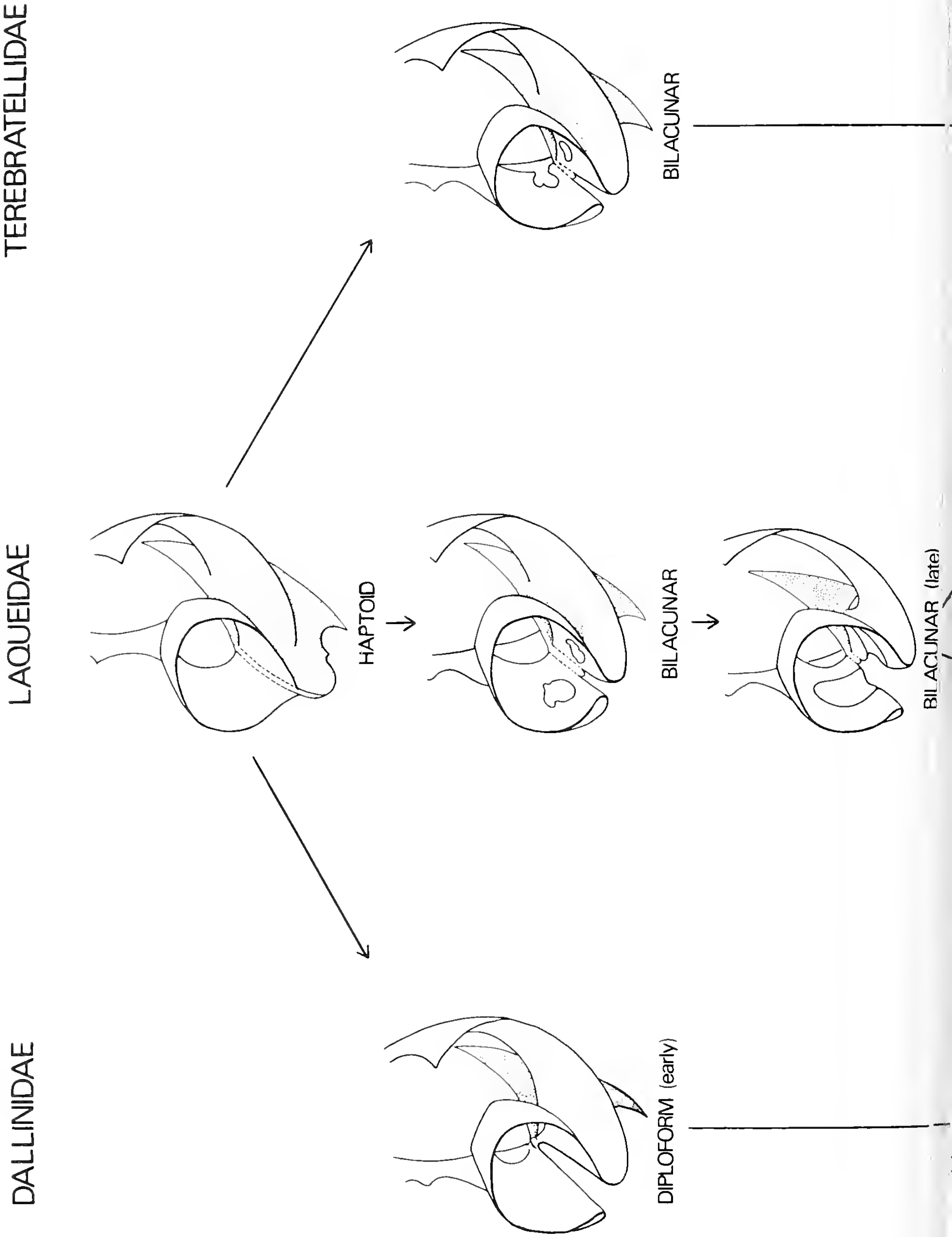


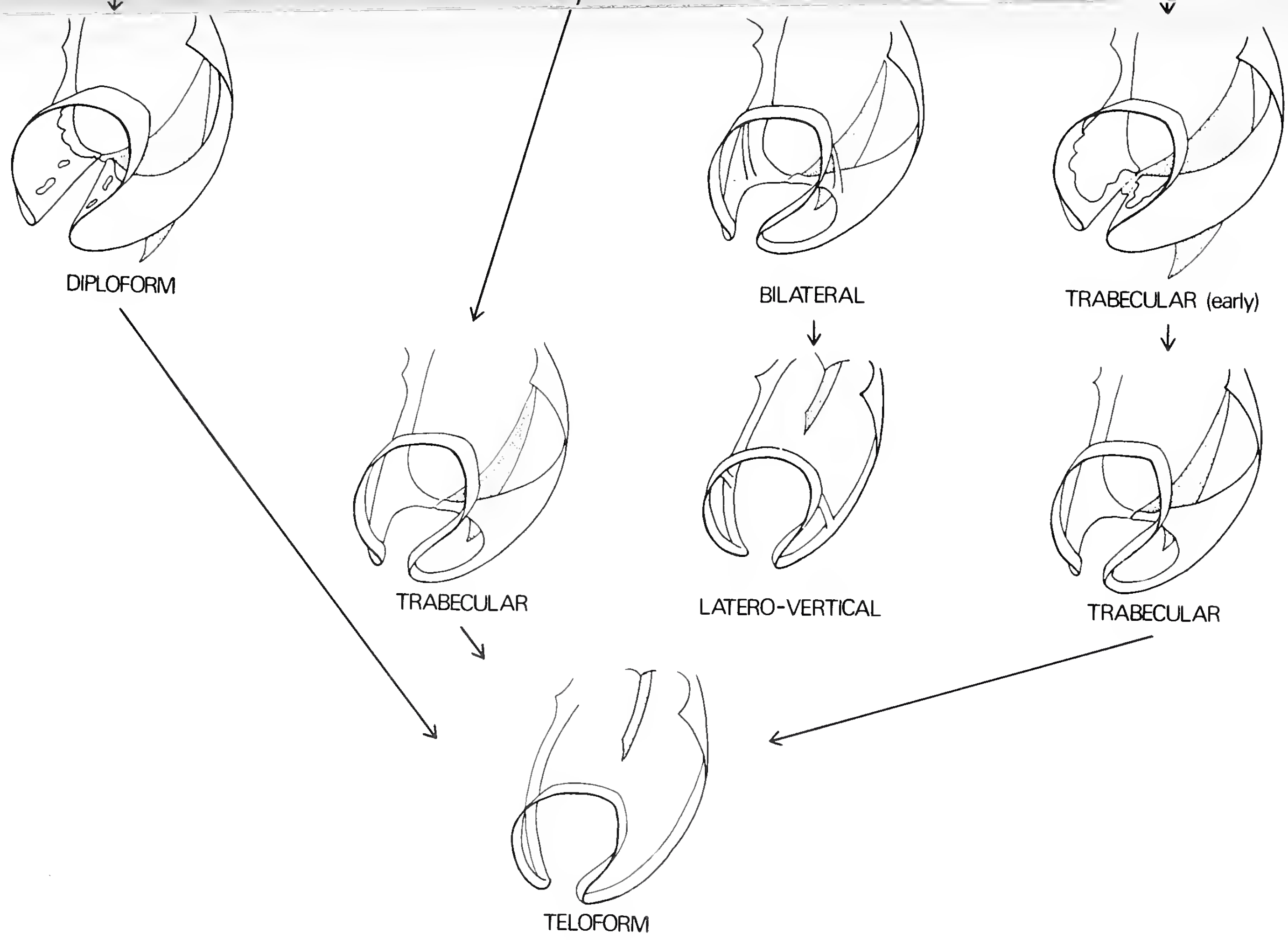
Fig. 20 a. *Macandrevia cranium*, Müller.—b. *Magellania septigera*, Lovén. Appareils au stade *Ismenia* montant la soudure annulaire de l'appareil ascendant avec le septum.

TEXT-FIG. 2. Reproductions of the text and figures of Fischer and Oehlert (1892), p. 308, fig. 20*a*, *b*.

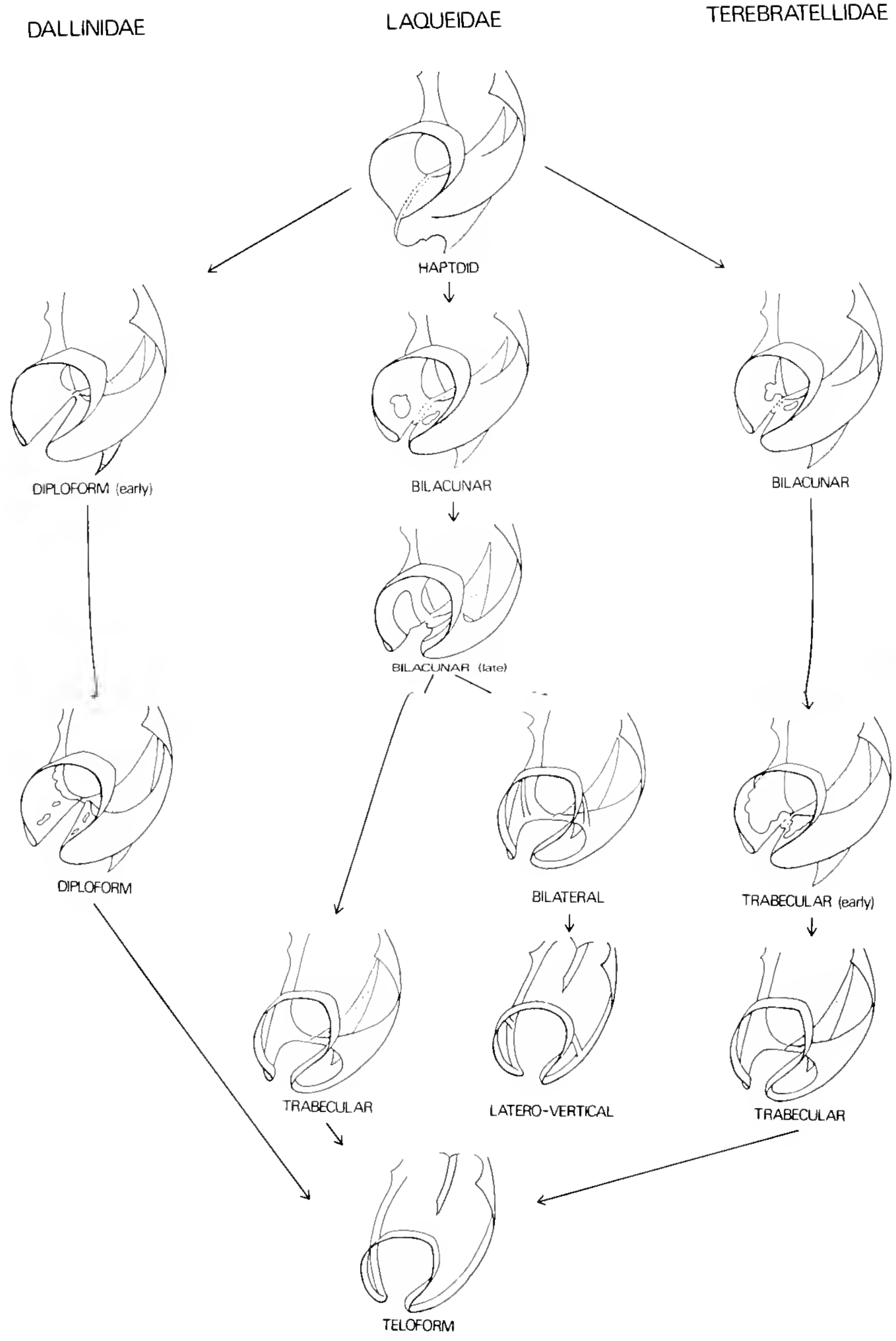
pattern of loop development has remained unquestioned by subsequent authors, Beecher (1895) using their supposedly uniform pattern of development as one of the principal factors differentiating these dallinid genera from terebratellid genera. Thus Fischer and Oehlert followed by Beecher formulated the basic classification of the terebratellacean brachiopods which has resulted in the present confused picture of loop development and generic relationships.

Since the publication of the Treatise the need for a reappraisal of the existing family boundaries has been indicated by some authors. Owen (1970) elevated the Cretaceous dallinid subfamily Kingeninae to family status and showed that relationships in loop structure existed between the members of this family, the Cainozoic genus *Frenulina*, and the laqueid genera *Laqueus* (Recent) and *Waconella* (Cretaceous). In 1973 both Cooper and I transferred the subfamily Frenulininae to the Laqueidae. Cooper's transference of this subfamily to the Laqueidae was based upon the study of growth phases of *Frenulina sanguinolenta* and upon a study of a new genus *Compsoria* with an adult loop pattern intermediate to that of *Frenulina* and *Laqueus*. The concurrent study of species of *Nipponithyris* indicated to Cooper that differences in loop development existed between the Frenulininae and the Nipponithyridinae stating that '*Frenulina* on the other hand in its final or frenuliniform stage has the hood so resorbed as to produce a window in the ascending elements, which is a trend towards the *Laqueus* loop. . . . In *Nipponithyris* the campagiform loop is resorbed anteriorly along the junction of the ascending and descending branches, thus trending towards the terebrataliiform loop stage which is its adult aspect' (Cooper 1973*a*, p. 20). My transfer of the Frenulininae (and the Kingenidae) to the Laqueidae was based also on an examination of the growth phases of the loop of *F. sanguinolenta* which showed


TEREBRATELLIDAE
BILACUNAR
LAQUEIDAE
HAPTOID
BILACUNAR
BILACUNAR (late)
DALLINIDAE
DIPLOFORM (early)



TEXT-FIG. 3. Schematic representation of loop development in the families Dallinidae, Laqueidae, and Terebratellidae commencing with the haptoid loop pattern common to all and which precedes the intermediate loop patterns differentiating each family. This figure may be referred to in conjunction with Table 1.



TEXT-FIG. 3. Schematic representation of loop development in the families Dallinidae, Laqueidae, and Terebratellidae commencing with the haptoid loop pattern common to all and which precedes the intermediate loop patterns differentiating each family. This figure may be referred to in conjunction with Table 1.

relationships with the Tertiary genera *Aldingia* (previously attributed to the Kraussinidae) and *Paraldingia* and to *Kingena mesembrina* (Etheridge) from Australian Cretaceous beds. Cooper (1973*b*) created a new family the Macandreviidae for *Macandrevia* and *Notorygmia* on the basis of great differences in the cardinalia from other genera with supposed dallinid loop development.

The studies referred to above, either directly or indirectly, confirm the differences in loop development noted by Friele (1877) and thus emphasize the need to clarify and redefine patterns of loop development. This review has led to the redistribution of genera attributed previously to the Dallinidae, Laqueidae, and Macandreviidae. The bulk of the genera formerly included in the Dallinidae are transferred to the Laqueidae now regarded as synonymous with the Macandreviidae. With respect to attribution of genera the Terebratellidae remains unchanged but the diagnosis of the family together with the diagnoses of the Dallinidae and Laqueidae has been changed.

LOOP PATTERNS

General. The study of accounts of development of long-looped Mesozoic and Cainozoic brachiopods indicates that many similarities exist. The loop develops as the result of the growth and fusion of two structures, the descending branches and the ring. A median septum functions as a support until these processes of growth and fusion are completed when a loop independent of the septum is formed. In the earliest growth phases known the first structure to appear is the septum, the free border of which becomes grooved as a precursor to the development of a hood then a ring which envelops the crest of the septum. From the lateral walls of the septum lamellar structures arise, lengthen posteriorly, and meet extensions of the crura to form the descending branches (the descending branches arise from the crura alone in *Macandrevia cranium*). The attachments to the septum of the descending branches and the ring run parallel to each other. The fusion of these lines of attachment together with the resorption of parts of both the ring and the septum results in the adult loop pattern. The anterior and dorsal segments of the ring recurve from the descending branches to become the ascending branches which are united by the ventral segment of the ring now termed the transverse band.

Major differences existing between the families occur during intermediate stages of development (text-fig. 3). These differences arise as a result of the pattern and timing of resorption of portions of the ring and the stage at which it is freed from the septum. These factors, in turn, govern the distribution of segments of the ring to form portions of the loop (text-fig. 4). In each family the ventral segment of the ring forms the transverse band and the anterior sections of the lateral and dorsal segments form the ascending branches. The fate of the remaining segments of the ring (the dorsal and dorso-lateral segments posterior to the anterior sections forming the ascending branches) differs in each family. In the Dallinidae they provide ventral components to the anterior limbs of the descending branches; in the Terebratellidae these segments are resorbed; in the Laqueidae there is partial resorption only of the central areas, the posterior rim remaining as the vertical connecting bands.

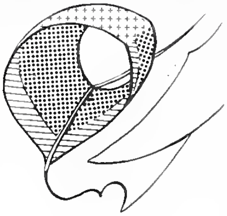
Since early differences in patterns of dallinid and terebratellid loop development

TEXT-FIG. 4. Diagrammatic representation of the haptoid loop phase showing the septum with the ring and part of the descending branch of one side. The shading of the ring differentiates the areas giving rise to parts of the loop.

The ventral segment (+shaded) becomes the transverse band in each family.

The anterior sections of the dorsal and lateral segments (hatched) become the ascending branches in each family.

The dorsal and dorso-lateral segments (dotted) provide ventral components to the descending branches in the Dallinidae; in the Laqueidae the central areas are resorbed, the posterior rim becoming the vertical connecting bands; in the Terebratellidae these segments are resorbed.



have been reviewed in previous sections only intermediate and later patterns of development are reviewed below for each family. Early phases of development cover the formation of the descending branches and of a ring, each structure being separately attached to the median septum. Intermediate loop patterns are defined as those patterns which commence with the anterior fusion of the attachments of the descending branches and the ring, and which incorporate those patterns developed before their complete detachment from the septum. Prior to the fusion of the attachments of the descending branches and the ring, the gross pattern of loop development is similar in each family. The intermediate patterns which differentiate the three families are described below.

At the end of each of the following three sections the studies on loop development appropriate to each family are recorded. These lists of studies include both comprehensive accounts and those which describe only isolated growth phases.

Dallinid. The final stage of early development in members of the Dallinidae shows that the attachments of the ring extend along the full length of the crest of the septum. Fusion of these attachments with the descending branches proceeds in an anterior to posterior direction until the full lengths of the attachments are fused and freed from the septum except for a short posterior section. These posterior segments of the fused attachments remaining connected to the septum are the lateral connecting bands. As a result of this fusion of attachments both the anterior limbs of the descending branches and the lateral connecting bands consist of doubled gutter-like structures, i.e. each has two components, a dorsal component derived from the anterior limbs of the descending branches and a ventral component from the dorsal segments of the ring. The remaining segments of the ring form the ascending branches and the transverse band.

Simultaneously with or shortly after fusion of the attachments lacunae perforate the ventral segments of the anterior limbs of the descending branches, i.e. the segments derived from the ring. This is the adult condition of the loop in *Campages*, in *Nipponithyris* (Pl. 44, figs. 5, 6), and in *Fallax*. This is also the stage represented in pl. 3, fig. 4 in Friele's (1877) account of the development of *Dallina septigera*. Atkins has commented upon the nature of the descending branches in the development of *Fallax dalliniformis* 'the gutter is formed not by the descending branch alone, but by the fused descending and ascending branches as in *Campages furcifera*' (1960*a*, p. 86). Cooper also states that in '*Nipponithyris* the campagiform loop is resorbed anteriorly along the junction of the ascending and descending branches, thus trending toward the terebrataliiform loop stage which is its adult aspect' (1973*a*, p. 20).

During the growth phases outlined above Friele and Atkins both noted spinosity in parts of the developing loop, namely the anterior border of the septum and the anterior and medial borders of the descending branches. In addition to resorption of areas of the septum anterior growth must also occur for, in most species of this family figured, the septum extends at least as far anteriorly as the loop.

The enlargement of the lacunae perforating the anterior limbs of the descending branches results in the resorption of their ventral components, i.e. the segments derived from the ring. The simultaneous resorption of the lateral connecting bands extending between the septum and the descending branches results in a loop entirely free of the septum and seen in adult specimens of *D. septigera*.

Studies of dallinid loop development: *D. septigera* by Friele 1877, Deslongchamps 1884, Fischer and Oehlert 1892, and Atkins 1960*b*. *F. dalliniformis* by Atkins 1960*a*. *Nipponothyris afra* by Cooper 1973*a*.

Laqueid. Early stages of development in the Laqueidae result in the formation of descending branches and of a ring enveloping the crest of the septum. As noted in *Frenulina sanguinolenta* (Richardson 1973*a*) there may be variation in the extent to which the ring envelops the crest of the septum, in other words the width of the band forming the ring may differ in comparable growth phases. Anterior fusion of the attachments of the ring and of the descending branches is either simultaneous with or is rapidly succeeded by the resorption of the anterior crest and border of the septum. While the attachments to the septum of the ring and the descending branches are still separated posteriorly, lacunae perforate the dorsal segments of the ring (text-fig. 3). The enlargement of these lacunae results in the separation of segments of the ring to form different parts of the loop. Those segments anterior to the lacunar borders (their attachments now fused with the descending branch attachments) form the ascending branches and the transverse band, those segments posterior to the lacunae form vertical bands, termed the medio-vertical connecting bands, extending from the septum to the transverse band. As noted above, those segments of the ring

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EXPLANATION OF PLATE 44

Photographs of the loop of three species from three different families illustrating the different patterns evident during intermediate loop phases.

Figs. 1, 2. *Frenulina sanguinolenta* (Gmelin) from Masthead Island, Queensland. Bilateral loop phase. Shell length 8 mm, hypotype NMV H 184. 1, ventral view. 2, laterally tilted view to show vertical connecting band running from the transverse band to the septum and its descending branch attachment.

Figs. 3, 4. *Magellania flavescens* (Lamarck) from Kangaroo Island, South Australia. Early trabecular loop phase showing the appearance of the loop immediately after resorption of dorsal segments of the ring and before resorption of the anterior and medial regions of the descending branches. Parts of the ring remain as jagged edges on the anterior portions of the descending branches and the septum. Shell length 6 mm, hypotype NMV H 202. 3, ventral view. 4, laterally tilted view.

Figs. 5, 6. *Nipponithyris nipponensis*, Yabe and Hatai from Sôyô-maru Strait, Japan Sea. Diploform loop phase. Shell length 12 mm. Specimen from the collection of the late R. S. Allan in the Geology Department, University of Canterbury, Christchurch, New Zealand. 5, ventral view showing lateral connecting bands and descending branches both doubled, their ventral components being derived from the dorsal segments of the ring. Two lacunae may be seen in the ventral components of the descending branches, the enlargements of these lacunae leading to the resorption of these components. 6, laterally tilted view.


1


2


3


4


5


6

RICHARDSON, *terebratellacean loops*

(= ascending branches and transverse band) anterior to the lacunae are fused with the descending branch attachments. Posterior to the lacunae the attachments of the ring and of the descending branches do not fuse, the descending branch attachments forming the lateral connecting bands, the ring attachments forming the dorsal attachments (to the septum) of the vertical connecting bands. This pattern of loop is seen in adult members of *Aldingia*, *Paraldingia*, *Jolonica*, and *Kingena*. These genera all display a loop with two pairs of connecting bands (lateral and medio-vertical) although there are differences in the relative width of the bands going to make up the loop. This pattern is also seen in the developing loop of *Frenulina sanguinolenta* (Pl. 44, figs. 1, 2), *Macandrevia cranium*, *Laqueus californianus*, *Compsoria suffusa* Cooper, *Gemmarcula aurea*, *Dallinella obsoleta*, *Trigonosemus pulchellus*, and fleetingly in *Terebratalia transversa*. This pattern is commonly referred to as frenuliniform which, as Cooper (1973*a*) points out, is not the final stage of the loop of adult members of *Frenulina*.

During the next phases of development the processes of growth involved (simultaneous enlargement and resorption) change the position of the vertical bands relative to the septum so that they shift from medial to lateral regions of the loop. The ventral attachments of the vertical connecting bands remain fused to the transverse band but their dorsal attachments shift away from the septum to the areas of union of the descending branches and the lateral connecting bands. These bands are now called the latero-vertical connecting bands. This type of loop with the two pairs of connecting bands, lateral and latero-vertical, is seen in adult members of *Frenulina*, *Compsoria*, *Laqueus*, and *Waconella*. In the final loop pattern characteristic of *Pictothyris* the lateral connecting bands are resorbed so that only one pair of connecting bands, the latero-vertical bands, are retained. The two loop patterns described above are not characteristic of other genera referred to this family. The adult loops of *Gemmarcula*, *Terebratalia*, and *Dallinella* possess lateral connecting bands only, those of *Macandrevia* and *Notorygmia* are entirely free of the septum which is completely resorbed. These genera display the same pattern of development as other members of the family up to the formation of the lacunae and the delimitation of the medio-vertical connecting bands. From this loop phase two different lines of development may take place; in one the medio-vertical bands are not retained, in the other they are translated into latero-vertical connecting bands (*Frenulina*) which ultimately are retained rather than the lateral connecting bands (*Laqueus*). It is not absolutely clear in accounts of the development of *Macandrevia cranium* and of *Gemmarcula aurea* whether there is any shift in position of the vertical connecting bands prior to their resorption. However, it does seem likely that they skip the stage in which the vertical bands shift from a medial to a lateral position, so that these genera lose the vertical connecting bands before the lateral connecting bands.

The pattern of development outlined above is embellished by additional structures, the septal flanges, in some members of the Laqueidae. As noted on page 293 these flanges, originating as plates on the early septum, ultimately become transformed into horns projecting from the postero-lateral corners of the transverse band. This sequence of development has been described for *Frenulina sanguinolenta*, *Dallinella obsoleta*, *Gemmarcula aurea*, *Trigonosemus pulchellus*, and *Terebratalia transversa*.

Other modifications of the general pattern of development and seen only in some members of the Laqueidae are the origin of the descending branches and the splitting of the septum, both topics being examined in detail in earlier sections. In *Macandrevia cranium* the descending branches arise from the crura alone, the only case known in which the descending branches do not have a double origin. *M. cranium* and *Laqueus californianus* are also described as possessing a median septum which is split anteriorly in early development. The crest of the septum in *Gemmarcula aurea* is described as being grooved with anterior divergences of the two sides.

The degree of spinosity displayed in the developing and adult loops of the Laqueidae is variable and seems to bear no simple relation to any other structure or condition of the loop. All members of the Terebratellacea display spinosity of the anterior border of the median septum during development. The developing loops of *M. cranium* and of *G. aurea* are described as showing spinosity not evident in the adult loops of these species. Apart from the anterior border of the septum neither the developing nor the adult loop of *Frenulina sanguinolenta* shows any spinosity. The adult loop of *Aldingia* is free of spines while spinous bands and branches characterize the adult loops of *Paraldingia woodsii* (Tate) and *Kingena mesembrina*, all with loops of the same pattern.

The loop development of *Terebratalia transversa* tends towards the pattern seen in members of the Terebratellidae in the brief duration of the identity of the lacunae so that vertical connecting bands are present only fleetingly. However, the rapidity with which the lacunae enlarge and breach the posterior walls of the ring is probably much greater in the Terebratellidae than in *T. transversa.* Atkins (1959*b*) in her study of the development of this species did not comment on any particular difficulty in finding this loop phase whereas hundreds of specimens of *Magellania flavescens* were opened before several examples suitable for the illustration of this phase were found.

Studies of laqueid loop development: *Compsoria suffusa* by Cooper 1973*a*. *Coptothyris grayi* by Hatai 1939. *Dallinella obsoleta* by Beecher 1895. *Frenulina cruenta* by Cooper 1973*a*. *Frenulina sanguinolenta* by Deslongchamps 1884; Cooper 1973*a*; and Richardson 1973*a*. *Gemmarcula arizonensis* by Cooper 1955. *Gemmarcula aurea* by Elliott 1947. *Gemmarcula humboldtii* by Steinich 1965. *Kingena mesembrina* by Elliott 1952. *Laqueus californianus* by Konjoukova 1948 and 1957. *Macandrevia cranium* by Friele 1877; Deslongchamps 1884; Fischer and Oehlert 1892; Elliott 1948; and Atkins 1959*a*. *Psilothyris occidentalis* by Cooper 1955. *Terebratalia transversa* by Atkins 1959*b*. *Trigonosemus pulchellus* by Steinich 1965.

Terebratellid. Members of the Terebratellidae follow a similar pattern in early intermediate growth phases to that described for the Laqueidae. In the first place the extent to which the ring occupies the crest of the septum may vary in a single species (Richardson, in press). Secondly, the anterior fusion of the attachments of the ring and of the descending branches may occur simultaneously with the anterior resorption of the septum or this fusion may occur while the septum, partition-like, separates each side of the loop. Finally, lacunae may arise in the dorsal segments of the ring at the same relative phase of development as they do in the Laqueidae, i.e. after the anterior fusion but before the posterior fusion of the ring and descending branch attachments. However, from this stage there are differences in development. In the terebratellid species examined there is a rapid enlargement of the lacunae so that the posterior borders of the ring are breached (Pl. 44, figs. 3, 4). The rapidity with which these lacunae enlarge and break the borders of the ring probably accounts for the fact that they have not been described hitherto in terebratellid development (loc. cit.). It is also possible, as suggested in this paper, that lacunae may perforate the ring in some but not all terebratellid species or even individuals of one species. The width of the band forming the ring, a feature in which variation is apparent, may be such that the greater resorption required is aided by lacunae which perforate the ring and which enlarge rapidly to resorb its posterior segments. It is presumed that, in species with ring bands of narrower diameter, the gradual excavation of the posterior border is sufficient to reduce the width of the band. This is a process which is apparently continuous in all species, particularly later in development when the loop grows by the accretion of lamellae on its anterior borders as simultaneous resorption occurs of its posterior borders. In any case, whatever the amount of resorption required in different individuals the resulting loop pattern displays descending branches (still attached posteriorly to the septum) recurving into ascending branches united by a transverse band. Those portions of the descending branches remaining attached to the septum (and which are analogous with the resorbed dorsal segments of the ring) represent the lateral connecting bands. The resorption of these bands gives the adult loop free of any connection with the septum. Either of the two final loop patterns described above, i.e. with or without lateral connecting bands, are seen in the majority of terebratellid genera.

Studies of terebratellid loop development: *Aneboconcha obscura* by Cooper 1973*b*. *Diestothyris frontalis* by Konjoukova 1948. *Jaffaia jaffaensis* by Thomson 1916 and Richardson, in press. *Magas chitoniformis* by Steinich 1965. *Magellania flavescens* by Richardson, in press. *Magellania venosa* by Fischer and Oehlert 1892 and Cooper 1973*b*. *Neothyris lenticularis* by Douvillé 1879 and Richardson, in press. *Pirothyris vercoi* by Richardson, in press. *Terebratella dorsata* by Fischer and Oehlert 1892. *Waltonia inconspicua* by Thomson 1915 and Richardson, in press.

TERMINOLOGY

When Beecher (1895) established the subfamilies Dallininae and Magellaniinae on the basis of loop development he summarized and extended the practice of naming each different growth phase from the adult loop showing that particular pattern. Thus the Dallininae displayed platidiiform, ismeniiform, mühlfeldtiiform, terebrataliiform, and dalliniform loop patterns and the Magellaniinae bouchardiiform, megerliniform, magadiform, magaselliform, terebratelliform, and magellaniiform patterns. As an inevitable result of the discovery of new genera and of increasing knowledge of brachiopod development, this nomenclature has had to be changed a great deal, a process which would be expected to continue. Like Atkins (1959*a*) it is felt that this type of nomenclature is confusing and that it would be more appropriate to use descriptive in place of generic adjectives to indicate different loop patterns. However, before extending this concept there are some changes made since the publication of the Treatise which should be noted and which are indirectly concerned with the terminology of loop patterns. Atkins (1959*b*) revised the existing state of knowledge of septal flanges (see p. 293) which were referred to later in the

Treatise as pre-campagiform flanges (p. H150). These flanges are not known to occur in *Campages* or its relatives and it is preferable to retain Atkins's term, septal flanges, for these structures. The use of the term vertical connecting bands, which may occupy either a medial or a lateral position, in place of the pre-frenuliniform, frenuliniform, laqueiform, or kingeniform connecting bands has also been recommended (Richardson 1973*a*). Baker suggested that succeeding loop patterns be termed phases rather than stages 'as this suggests the more real, cumulative growth pattern of the loop' (1972, p. 457). This recommendation is adopted but another suggestion of Baker's referring to the use of the term median septum presents difficulties which are discussed on page 293.

The Treatise describes the developing loops of members of the Terebratellidae as being characterized by a series of patterns labelled pre-magadiniform, magelliform, terebratelliform, and magellaniiform. This series of patterns conform with the various terebratellid growth series described in this and previous papers. However, the names applied to the series of patterns found in the Dallinidae (pre-campagiform, campagiform, frenuliniform, terebrataliiform, dalliniform) and the Laqueidae (pre-campagiform, campagiform, frenuliniform, laqueiform) are invalid for a variety of reasons. The use of the term frenuliniform with reference to one of the loop phases seen in the Dallinidae is the result of a misinterpretation, by various authors, of the growth series described by Friele (1877) for *Dallina septigera* (see p. 294). The frenuliniform loop phase is recognized as that stage which displays two pairs of connecting bands, the lateral and the latero-vertical bands. As noted previously vertical bands are delimited as the result of the presence, in the dorsal band of the ring, of two lacunae while the ring is attached posteriorly to the septum. In the Dallinidae resorption of segments of the ring occurs after the ring has lost any connection with the septum thus precluding the formation of vertical connecting bands.

Elliott (1947) proposed the terms pre-campagiform and campagiform to describe the early growth phases of the loop in the Dallinidae and the Laqueidae. Cooper has described the loop structure of adult members of *Campages* (1970) and immature and adult loops of the related genus *Nipponithyris* (1973*a*). The adult loop of *Campages* displays descending branches with double anterior limbs (the ventral components derived from the dorsal segments of the ring) a feature not observed in the developing or adult loop of any member of the Laqueidae or Terebratellidae. This loop pattern corresponds with that described by Friele (1877) for an intermediate loop phase of *D. septigera* and is the same as the adult pattern of *Fallax dalliniformis* described by Atkins (1960*a*). Succeeding developmental phases of *D. septigera* do not display vertical connecting bands and, as noted above, the fusion of the full lengths of the ring attachments with those of the descending branches precludes their formation. The loop pattern displayed by *Campages* is not followed by a frenuliniform phase but in ontogeny this pattern occurs at a comparable stage in the loop development of the Dallinidae to the frenuliniform stage in the Laqueidae. In addition as Cooper (1973*a*) has pointed out the form of the loop of *Frenulina* usually called the frenuliniform phase is not the final phase of the loop in this genus.

If we continue to follow the method of nomenclature used in the past, i.e. naming the loop patterns of a family from the adult genus showing that pattern, the only terms at present valid for each family are dalliniform for the Dallinidae and terebrataliiform for the Laqueidae. Therefore new sets of terms are required for each of the two families, Dallinidae and Laqueidae. The need to provide new names for the loop patterns found in these families is questionable. In the first place no Cainozoic genus of the Dallinidae displays an adult loop pattern earlier than the so-called terebrataliiform phase, and in the Laqueidae no adult loop pattern is known prior to the pre-frenuliniform phase. The second and more significant point is the wisdom of giving different names to similar structures which may follow a similar developmental pattern. Early loop patterns of all three families are similar; any differences which exist in these loop patterns at this stage seem to be differences in the width of the bands forming the descending branches and the ring. To adopt three different series of descriptive names for the loop patterns found in these families tends to give an entirely unjustified impression of separateness. It is desirable to attempt to indicate in their right perspective any similarities and differences which exist. For these reasons it is proposed that the former generic adjectives be replaced with purely descriptive terms some of which can be applied to each family. That such a change is needed is emphasized by Baker's (1972) work on the development of the Jurassic species *Zeilleria leckenbyi* which shows characteristics of both the dallinid and terebratellid loop patterns as then defined. In attempting to indicate these similarities Baker called the loop phases seen in this species pre-paramagadiniform, syncampagiform, frenuliniform, terebrataliiform, dalliniform, zeilleriiform. The existing system could lead to even more formidable assemblages of names. However, Baker has had to base his interpretations of difficult material upon known patterns of development in Cainozoic brachiopods and to cope with such current misinterpretations as the belief that the campagiform precedes the frenuliniform phases in ontogeny. Therefore the following terms are proposed to describe the loop phases which embrace:

1. The formation of the septum, the hood, and the rudiments of the descending branches—the *axial* phase.
2. The presence of a hood in place of a ring and complete descending branches, each structure being separately attached to the septum—*annular* phase.
3. The anterior fusion of the attachments of the ring and the descending branches—*haptoid* phase.
4. The presence of two lacunae in the dorsal segments of the band forming the ring—*bilacunar* phase.
5. The fusion of the attachments of the ring (completely free of the septum) with the descending branch attachments to form descending branches with doubled anterior limbs—*diploform* phase.
6. The presence of two pairs of connecting bands, lateral and latero-vertical—*bilateral* phase.
7. The presence of latero-vertical connecting bands only—*latero-vertical* phase.
8. The presence of lateral connecting bands only—*trabecular* phase.
9. The absence of any connecting bands so that the loop is free of the septum—*teloform* phase.

Thus to employ the proposed terminology terebratellid loop development is characterized by the following patterns: axial, annular, haptoid, bilacunar (thought to be optional), trabecular, teloform; laqueid loop development by axial, annular, haptoid, bilacunar succeeded either by bilateral and latero-vertical or by trabecular and teloform phases; dallinid development by annular, haptoid, diploform, teloform. These terms are used for the principal morphological patterns evident and are employed without consideration of differences in dimensions of the bands in different genera. For example, the bilateral phase in laqueid development applies to the structure of the loop in *Frenulina*, *Compsoria*, and *Laqueus* although the bands forming the loop tend to be wider in *Frenulina* than in the other two genera. Also Baker (1972) refers to dalliniform and zeilleriiform phases both of which are regarded as teloform patterns since they differ only in the slender ribbon-like bands which replace the heavier structures of the earlier loop.

The following table sets out the new and old terminology together with the adult genera displaying the patterns named. In some cases one cannot provide exact equivalents, e.g. the adult loop of *Australiarcula* displays complete descending

TABLE 1. The adult genera of each family displaying the loop patterns defined with the new and the old (in parentheses) terminology.

Phase name	Genus with adult loop pattern
DALLINIDAE	
Axial (precampagiform)	Unknown
Annular (precampagiform)	Unknown
Haptoid (campagiform)	Unknown
Diploform	*Campages*, *Chathamithyris*, *Fallax*, *Nipponithyris*, ?*Glaciarcula*
Teloform (dalliniform)	*Dallina*
LAQUEIDAE	
Axial (precampagiform)	Unknown
Annular (precampagiform)	Unknown
Haptoid (campagiform)	Unknown
Bilacunar (frenuliniform)	*Aldingia*, *Jolonica*, *Kingena*, *Paraldingia*
Followed by either:	
1. Bilateral (laqueiform) and	*Compsoria*, *Frenulina*, *Laqueus*, *Waconella*
Latero-vertical (pictothyridiform)	*Pictothyris*
or	
2. Trabecular (terebrataliform)	*Dallinella*, *Diestothyris*, *Gemmarcula*, *Pacifithyris*, *Terebratalia*, *Trigonosemus*
Teloform (dalliniform)	*Coptothyris*, *Macandrevia*, *Notorygmia*
TEREBRATELLIDAE	
Axial (premagadiniform)	*Neobouchardia*, *Australiarcula*, *Bouchardia*, *Bouchardiella*, *Malleia*
Annular (magadiniform)	*Magadina*, *Magas*
Haptoid (magelliform)	*Jaffaia*, *Magella*, *Pirothyris*
Bilacunar (or equivalent)	Unknown
Trabecular (terebratelliform)	*Aneboconcha*, *Gyrothyris*, *Magadinella*, *Magasella*, *Pachymagas*, *Terebratella*, *Waiparia*, *Waltonia*
Teloform (magellaniiform)	*Aerothyris*, *Austrothyris*, *Cudmorella*, *Iheringithyris*, *Magellania*, *Neothyris*, *Rhizothyris*, *Stethothyris*, *Victorithyris*

branches but no hood or ring while *Bouchardia* possesses a septal ring but no descending branches. In the list of terebratellid loop patterns the phase labelled bilacunar or equivalent means that a bilacunar phase is known in the development of some species but that it is presumed but not proven that there may be other methods of reducing the width of the band forming the ring in other species.

FAMILY AND SUBFAMILY DIAGNOSES

Discussion. The separation of terebratellacean genera according to patterns of ring resorption gives a more credible classification of the Dallinidae, Laqueidae, and Terebratellidae and one in which the relationships between the families are more explicit. The features used to distinguish the members of different families are either the presence of descending branches with double anterior limbs (Dallinidae), of vertical connecting bands (Laqueidae) or the absence of either of these structures in any loop phase (Terebratellidae). Supporting but less decisive distinguishing characters are dental plates, septal length, the width of the bands forming the loop, and cardinalia pattern. Dental plates are present in all members of the Laqueidae, in two of the eleven genera referred to the Dallinidae, and are not present in any member of the Terebratellidae. In general the septum of the Dallinidae is long (as long or longer than the adult loop) and of moderate length (approximately half the length of the loop) in the Terebratellidae; in the Laqueidae the septum appears to occupy the minimum area required to support the developing loop and may be entirely resorbed as soon as all connecting bands are resorbed. Before resorption occurs the descending branches and the ring are formed of bands of greater width in the Dallinidae than they are in the Laqueidae and the Terebratellidae. All members of the Dallinidae possess hinge plates which may be excavate or fused with the valve floor and they are always associated with the septum; the majority of terebratellid genera are similarly equipped (the exceptions being members of the Bouchardiinae in which hinge plates do not form parts of the swollen cardinalia) while the Laqueidae show a wide variation even within species in the condition of the hinge plates and their association or lack of it with the septum. The cardinal process is always prominent in the Terebratellidae; in most members of the Laqueidae and the Dallinidae it is small or absent although one subfamily in each family (each of which includes only Japanese genera) shows a well-developed cardinal process.

Two genera, *Terebratalia* and *Jaffaia*, give some picture of the relationships which may exist between members of different families. The pattern of ring resorption in *Terebratalia transversa* (p. 303) is intermediate in type to that described as characteristic of the Terebratellidae and the Laqueidae. *Terebratalia* is also noted for the variability of the cardinalia and some of its external characters (Atkins 1959*b* and Paine 1969) however the presence of dental plates together with the absence of hinge plates anchor the genus in the Laqueidae. *Jaffaia* has no such determinant characters and remains a linking form between the Dallinidae and the Terebratellidae. In its ontogeny *Jaffaia* does not proceed to the intermediate developmental loop phases considered to be of diagnostic value and the adult loop is of late haptoid pattern. However, the bands forming the ring and the descending branches are as wide as these structures in comparable growth phases of members of the Dallinidae. Further development of the loop in *Jaffaia* could follow either a dallinid or a terebratellid pattern. The absence of dental plates and the nature of the cardinalia form no bar to inclusion in the Dallinidae as it is constituted at present.

Family DALLINIDAE Beecher, 1893. Emend. nov.

Diagnosis. Loop passing through all or part of axial, annular, haptoid, diploform, and teloform growth phases.

Comments. The existing subfamilies Dallininae and Nipponithyrinae are retained for two groups of genera differing in cardinalia pattern. The erection of a third subfamily to embrace those genera with dental plates, namely *Fallax* and *Glaciarcula*, would be quite unwarranted at this stage of our knowledge of these and related genera. *Fallax*, apart from the presence of dental plates, is closely allied with *Dallina* and *Campages*. However, the affinities of *Glaciarcula* are less clear. *Glaciarcula* is allied with *Fallax* in the presence of dental plates and its type of cardinalia and with *Aneboconcha* (subfamily Terebratellinae) in its external features. Friele (1877) commented on the resemblances apparent in the developing loop of *Dallina septigera* and of *Glaciarcula spitzbergensis* and figured two specimens of the latter species in which the anterior limbs of the descending branches appear to be doubled, i.e. at the diploform phase. However, Elliott (1956) states that the loop is terebratelliform while Cooper describes it as 'terebrataliform, much stouter than that of the austral shell *Aneboconcha* and with short, thick attachments to the median septum' (1973*b*, p. 28).

The allocation of Cainozoic genera to dallinid subfamilies and their diagnoses is as follows:

Subfamily DALLININAE Beecher, 1893. Emend. nov.

Dallinidae with adult diploform or teloform loop patterns; without dental plates; with excavate hinge plates fused medially with septum, a small cardinal process if present.

Genera included: *Dallina*, *Campages*, *Pegmathyris*, *Chathamithyris*.

Subfamily NIPPONITHYRINAE Hatai, 1938. Emend. nov.

Dallinidae with adult diploform loop pattern; without dental plates; with hinge plates thickened and fused with valve floor, cardinal process well defined.

Genera included: *Nipponithyris*, *Isumithyris*, *Miyakothyris*, *Yabeithyris*, *Tanakura*.

Subfamily uncertain: *Fallax*, *Glaciarcula*.

Family LAQUEIDAE Thomson, 1927. Emend. nov.

Diagnosis. Loop passing through axial, annular, and haptoid phases to a bilacunar loop pattern; bilacunar pattern may be the adult loop pattern or be followed either by bilateral and latero-vertical phases or by trabecular and teloform phases; dental plates present.

Comments. The simplest method of classifying this family would be to adopt the twofold division evident when only loop developmental patterns are taken into account. The members of this family would then be differentiated on whether vertical connecting bands are retained through later development stages (*Laqueus*, *Waconella*, *Kingena*, *Zittelina*, *Belothyris*, *Frenulina*, *Compsoria*, *Aldingia*, *Paraldingia*, *Jolonica*, *Pictothyris*) or whether the vertical bands are lost before the lateral (horizontal) connecting bands (*Terebratalia*, *Dallinella*, *Trigonosemus*, *Macandrevia*). The features used, other than adult loop patterns, to distinguish the subfamilies (cardinalia type and the presence of septal flanges during development) may prove to be of little diagnostic value within the family Laqueidae. However, further studies of loop development and in particular the study of Mesozoic genera should indicate if such a division would be a better method of classification than that outlined below.

In the previous section on the Dallinidae only Cainozoic genera were redistributed amongst the two subfamilies retained. A number of Mesozoic genera are included in this family. The relationships between *Kingena mesembrina* (Australian Cretaceous) and the Australian Cainozoic genera *Aldingia*, *Paraldingia*, and *Frenulina* have been described previously (Richardson 1973*b*). The European members of *Kingena* and its relatives were reviewed by Owen (1970) who commented also on similarities between these genera and the Recent *Frenulina* and *Laqueus*. The Mesozoic genera discussed in these two papers are included in this reallocation of genera. Steinich (1965) in describing faunas from the Lower Maastricht Chalk of Rügen recorded the loop development of *Trigonosemus pulchellus*. The clarity of Steinich's illustrations and descriptions of this developmental sequence leave little doubt that *T. pulchellus* should be included in the Laqueidae and it appears to be related to members of the Terebrataliinae.

Subfamily KINGENINAE Elliott, 1948. Emend. nov.

Laqueidae with adult bilacunar or bilateral loop patterns, with septal flanges in early loop phases; hinge plates excavate or solid, fused medially or discrete or fused with valve floor, cardinal process small if present.

Genera included: *Laqueus*, *Waconella*, *Kingena*, *Zittelina*, *Belothyris*, *Frenulina*, *Compsoria*, *Aldingia*, *Paraldingia*, *Jolonica*.

Subfamily PICTOTHYRINAE Yabe and Hatai, 1941. Emend. nov.

Laqueidae with adult latero-vertical loop pattern; cardinalia thick, heavy, with prominent cardinal process.

Genera included: *Pictothyris*, *Kikaithyris*, ?*Kamoica*.

Subfamily MACANDREVIINAE Cooper, 1973. Nom. transl. Emend. nov.

Laqueidae with adult trabecular or teloform loop patterns with median septum not associated with cardinalia in trabecular patterns and lost in teloform patterns; hinge plates excavate and fused medially and separately with valve floor, cardinal process small if present.

Genera included: *Macandrevia*, *Notorgymia*, *Diestothyris*.

Subfamily TEREBRATALIINAE n. subf.

Laqueidae with adult trabecular or teloform loop paterns, with septal flanges in early loop phases; hinge plates commonly absent, cardinal process variable in size.

Genera included: *Terebratalia*, *Dallinella*, *Coptothyris*, *Pacifithyris*.
Subfamily uncertain: *Kurakithyris*.

Family TEREBRATELLIDAE King, 1850. Emend. nov.

Diagnosis. Loop passing through all or part of axial, annular, haptoid, bilacunar (fleeting and never represented in adult genera), trabecular, and teloform growth phases; dental plates and spicules absent.

Comments. Since the publication of the Treatise the only change made in this family is the emendation of the diagnosis of the subfamily Bouchardiinae to include *Malleia* (Richardson 1973*c*).

GENERAL DISCUSSION

In place of the two patterns (dallinid and terebratellid) previously described this study indicates that three patterns of loop development are evident in the long-looped brachiopods of the Cainozoic. The key factors determining differences in loop development are not the presence of lacunae, hoods, rings, divided septa, or the origin of the descending branches but are the manner of resorption of parts of the ring (a factor noted by Friele in 1877 but subsequently ignored) and the stage at which the ring is freed from the septum. As a direct result of these factors the developing loop of the Laqueidae displays vertical connecting bands while that of the Dallinidae displays descending branches with double anterior limbs; neither of these structures are present in the developing loop of the Terebratellidae.

Thus the presence either of vertical connecting bands or of doubled descending branches, in intermediate or adult loop phases, provide the key to the type of development characteristic of the Dallinidae or of the Laqueidae. Subsequent resorption of these structures in these two families results in the formation of an adult loop similar to that of the Terebratellidae.

Such an adult loop pattern is also seen as the teloform phase in the development of some Palaeozoic and Mesozoic genera. Differences in the development of these comparable adult structures seem to be centred around the emergence of a septal pillar to carry the future ascending elements. In Palaeozoic genera (Cooper 1955) all parts of the loop develop from the crura, i.e. the descending elements grow forward and fuse medially thus forming a structure which gives rise to the ascending elements. In Mesozoic and Cainozoic genera the descending and ascending elements arise concurrently, the posterior segments of the descending branches from the crura, the ascending elements and the anterior segments of the descending branches from the septal pillar.

The development of a septal pillar may be one device to achieve an adult loop and therefore an adult lophophore more rapidly, a factor which Elliott (1948, 1953, 1957) considers to be of paramount importance in the evolution of brachiopods. I can make no comment on this theory or upon Baker's suggestion (1972) that the presence of spinose branches of the loop may be of greater significance than the absence of a median septum. However, these studies have clarified a number of areas which complement Baker's recent studies on the loop development of the Jurassic species *Zeilleria leckenbyi*. Baker noted that early phases of development are terebratellid in aspect while later phases are dallinid but that, in the possession of spines, the greater part of the development of the zeilleriid loop resembles dallinid development. Baker also showed that the median septum *sensu lato* is derived from two sources, an early septal pillar and a later downgrowth from the cardinalia. In those Cainozoic brachiopods studied by the author the adult septum is also the result of the fusion of two components, and as is the case for *Z. leckenbyi*, the future ascending elements of the loop arise only from the septal pillar. It has also been shown that the early and late developmental phases of the Terebratellidae, Dallinidae, and Laqueidae are similar and that they differ in intermediate phases only in methods of ring resorption. Consequently there is no need to divide the development of *Z. leckenbyi* into dallinid and terebratellid aspects. There are differences in the form of the septal pillar and in the formation of the hood in this Jurassic species and in the Cainozoic genera studied which show a similar but apparently simplified developmental process. If the patterns of loop development in Cainozoic genera have been interpreted correctly then *Zeilleria* is allied to the Laqueidae in the presence of a bilacunar loop phase and of dental plates, the cardinalia being similar to these structures in some members of the laqueid subfamily Kingeninae. The spines so characteristic of *Zeilleria* seem to be vanishing features in the Cainozoic members of the Terebratellacea. Spines appear only sporadically although they tend to be associated more frequently with the loops of the Laqueidae than with those of the other families. The Laqueidae is characterized by much greater fluidity in many morphological characters than are the other families and it is possible that in the Laqueidae one sees the type of archaic reservoir from which diverse groups may spring. Many morphological overlaps can be seen in this family. For example the development of *Terebratalia* leads directly to the terebratellid pattern although other features of this genus anchor it in the Laqueidae. The members of the family also display most of the types of cardinalia which may develop in the other two families. The anterior bifurcation of the septal pillar of *Macandrevia* while not characteristic of Cainozoic genera appears to be present in all Mesozoic genera whose development is known.

It is doubtful whether the families reviewed here should be regarded as of equal taxonomic status with the other four families attributed to the Terebratellacea. The development of the loop, if any, in these families is different in many respects from that of the Dallinidae, Laqueidae, and Terebratellidae so that by comparison these three families appear as a closely related group. The Thaumatosiidae (Cooper 1973*b*), Megathyrididae, Platidiidae, and Kraussinidae vary according to whether ascending or descending elements take precedence in loop development, in addition other factors related to the cardinalia and foramen separate them from the Dallinidae, Laqueidae, and Terebratellidae. Whether the similarities between the former families are sufficient to associate them together as a group distinct from the dallinid–laqueid–terebratellid group is a matter requiring further study.

At present the suborder Terebratellidina contains two superfamilies, the Zeilleriacea and the Terebratellacea. As Baker (1972) has pointed out, his own work on *Zeilleria* and that of Babanova (1965) on another Jurassic genus *Aulacothyris* suggests that typical zeilleriids may need to be removed from the Zeilleriacea to the Terebratellacea. The studies together with those of Owen (1970) on Cretaceous genera also suggest that a closer relationship exists between some Mesozoic and Cainozoic genera than the present classification would indicate. These relationships should become clearer when the development of Mesozoic genera is examined with the evidence now available on the growth patterns of Cainozoic forms. At least workers on Mesozoic genera will no longer have to attempt to force dallinid and laqueid genera into one developmental sequence.

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TANCHINTONGIA GEN. NOV., A BIZARRE PERMIAN MYALINID BIVALVE FROM WEST MALAYSIA AND JAPAN

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ABSTRACT. Broken pieces of a huge thick-shelled myalinid forming a calcirudite in the Kinta Valley, West Malaysia, show that the live shells rested on spectacular flanges formed by acute bends in the lateral flanks of the valves. Consequently the shells had a large permanent posterior gape, and must therefore have lived below low-tide level. The flanges may have acted like snowshoes to support the animals on the surface of a fine carbonate substrate, or they may have acted as outriggers to prevent overturning. Prominent grooves, formed by the ontogenetic shift in the position of the byssal gape, show that the shells were byssally attached throughout life. Associated ammonoids and fusulines provide an early Permian age for the Malaysian shells; similar fragments occur with Permian fusulines in Japan. *Tanchintongia* was at least as large and as thick-shelled as its cool temperate analogue *Eurydesma*, indicating that these features were not simply temperature controlled in Permian bivalves.

THE opencut tin mines of the Kinta Valley near Kampar, Perak, West Malaysia, have yielded a diverse suite of late Palaeozoic invertebrates (Jones, Gobbett and Kobayashi 1966; Batten 1972). One of the most impressive finds was the discovery of a 3–5 m thick calcirudite (Pl. 45, fig. 8; Pl. 46, fig. 9) formed of the fragmentary remains of a huge Permian bivalve at the H. S. Lee No. 8 Mine (lat. 4° 17′ N., long. 101° 06′ E., topographic map of Malaya, sheet 2N/9, old series; grid reference 909356). Forty-nine pieces of the bivalve were collected from this bed during 1964–1966, and were kindly made available for this study by the Department of Geology, University of Malaya. Type material has been placed in the Sedgwick Museum, Cambridge (SM). Since none of the pieces is a complete shell or even a complete valve, the shell had to be reconstructed from the available fragments.

SYSTEMATIC PALAEONTOLOGY

Class BIVALVIA
Family MYALINIDAE Frech, 1891
Genus TANCHINTONGIA gen. nov.

Type species. Tanchintongia perakensis gen. et sp. nov.

Derivation of name. Named for Tan Chin Tong who collected from the fossil bed.

Diagnosis. Huge, massively thickened, equivalved shell with umbonal carina that bends through about 350° to separate the flattened anterior faces of the valves from their concave postero-lateral flanks. These paired carinae appear to have produced a large triangular posterior shell gape. Beaks widely separated by growth of large triangular cardinal areas; ligament duplivincular, lamellar layers inserted in deep grooves confined to anterior half of cardinal areas. Body cavity ventrally elongated, well separated from beaks by massive umbonal thickening; small byssal opening in

[Palaeontology, Vol. 18, Part 2, 1975, pp. 315–322, pls. 45–46.]

valve edges at anterior end of body cavity generates symmetrically disposed byssal grooves through growth of shell.

Discussion. The massive shell, terminal beaks, and duplivincular ligament area (Pl. 45, fig. 1; Pl. 46, figs. 4, 8) relate *Tanchintongia* to the Palaeozoic families Myalinidae and Ambonychiidae. The significant morphologic difference between these families is that ambonychiids are equivalved whereas myalinids have a slightly smaller right valve (Pojeta 1966; Newell 1942). The other difference is stratigraphic—ambonychiids dominate in the Early and Middle Palaeozoic to be replaced by myalinids in the Late Palaeozoic. *Tanchintongia* is problematical because it is equivalved (Pl. 45, figs. 2, 5) yet of Late Palaeozoic age. We speculate that it is secondarily equivalved and therefore a myalinid, because stratigraphically suitable ancestors belong to that family. The secondary valve equality would be necessary to maintain equilibrium in the assumed life position. Other myalinids are believed to have rested on their right valves (Newell 1942, p. 21).

Tanchintongia perakensis sp. nov.

Plate 45, figs. 1–8; Plate 46, figs. 1–9; text-figs. 1–2

Holotype. SM G1874 (Pl. 45, figs. 2–5).

Paratypes. SM G1875–1882.

Description. The few articulated fragments in the collection show that the shell was equivalved (Pl. 45, fig. 5; Pl. 46, fig. 7) with large cardinal areas displaying straight (Pl. 45, fig. 1) or sinuous (Pl. 46, figs. 4, 8) duplivincular ligament grooves on their anterior half (text-fig. 1). Well-preserved umbonal fragments have a sharp lateral carina originating at the beak (Pl. 45, fig. 7) and a deep byssal groove on the anteroventral face (Pl. 45, fig. 6). A small umbonal septum is present in one fragment (Pl. 45, fig. 6); there are no hinge teeth. Larger fragments show that the byssal groove extended posteriorly in each valve (Pl. 45, fig. 1; Pl. 46, fig. 4) to the anterior end of the mantle cavity. In large shells this lay as much as 11 cm in a direct line from the beak (Pl. 46, fig. 4). Thus the early formed parts of the valves are secondarily filled by massive deposits of the inner shell layers in an analogous way to the umbonal region of *Eurydesma* (Runnegar 1970). The space occupied by the anterior end of the mantle cavity is well shown by one articulated fragment (Pl. 46, fig. 7).

Behind the posterior ends of the cardinal areas the lateral carinae splayed outwards to produce the impressive flanges on which the shell rested (Pl. 45, figs. 5, 8; Pl. 46,

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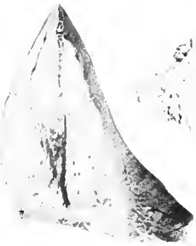
EXPLANATION OF PLATE 45

Figs. 1–8. *Tanchintongia perakensis* gen. et sp. nov., Early Permian, H. S. Lee Beds, H. S. Lee No. 8 Mine, Perak, West Malaysia. 1, hinge of left valve, arrow indicates byssal groove, SM G1875, ×0·5. 2–5, antero-dorsal, left lateral, oblique, and posterior views of holotype, SM G1874, ×0·33. 6–7, internal and external views of umbonal fragment, SM G1876, ×1. 8, exposure of shell bed in mine; the hammer is 36 cm long; note articulated valves (arrowed).

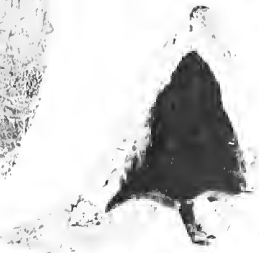

1


4


6


2


3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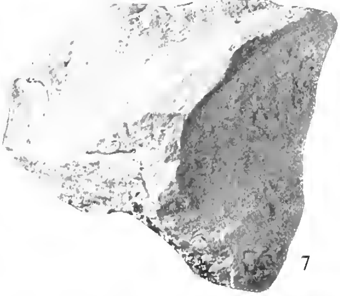
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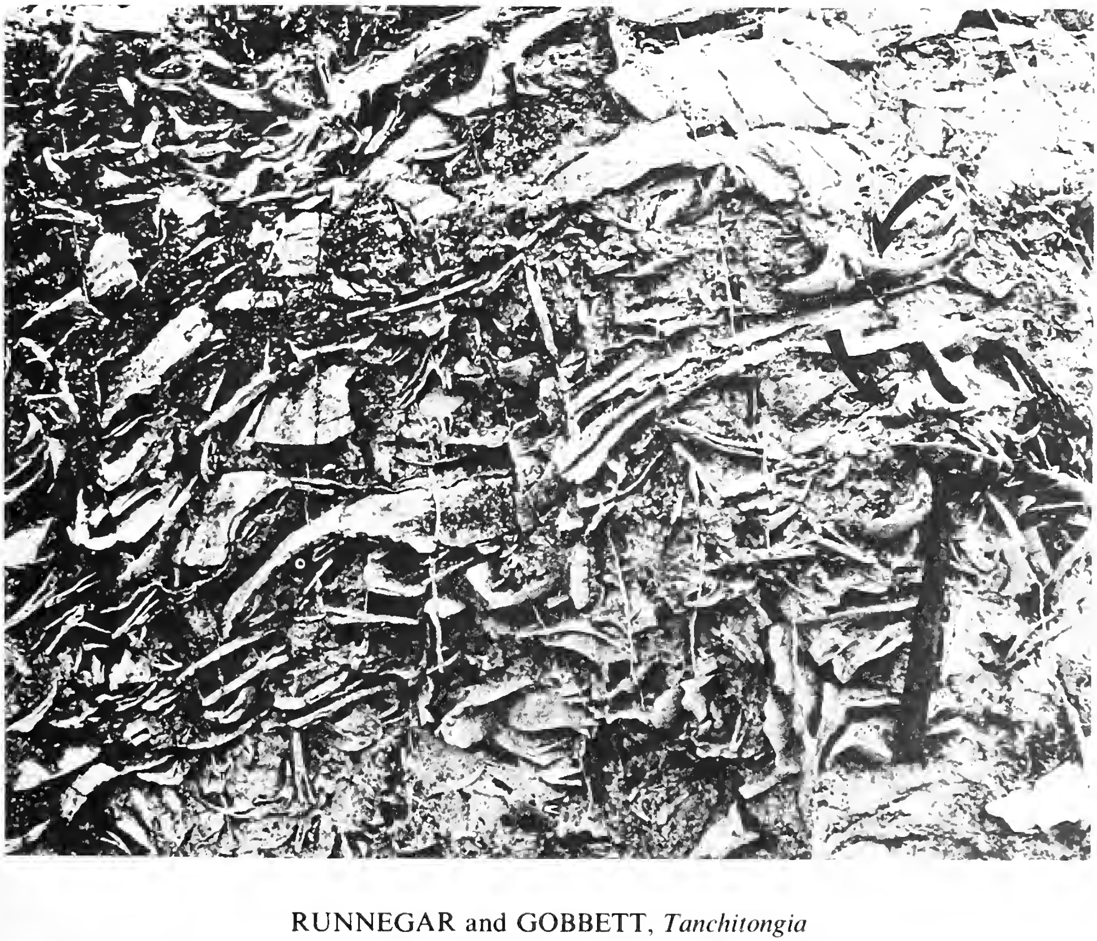
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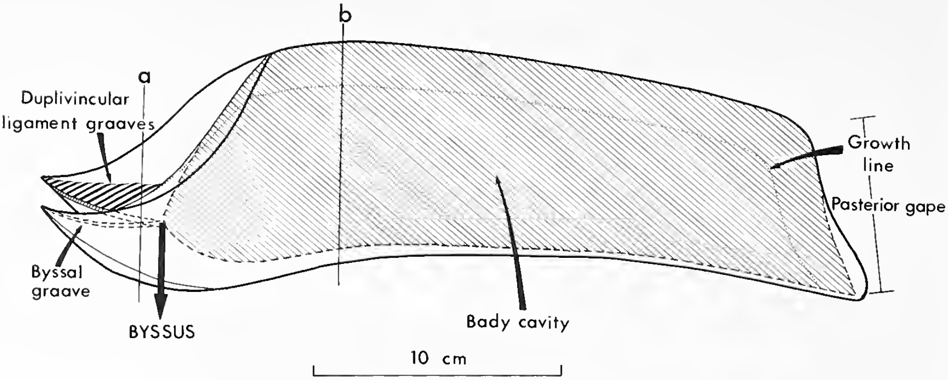
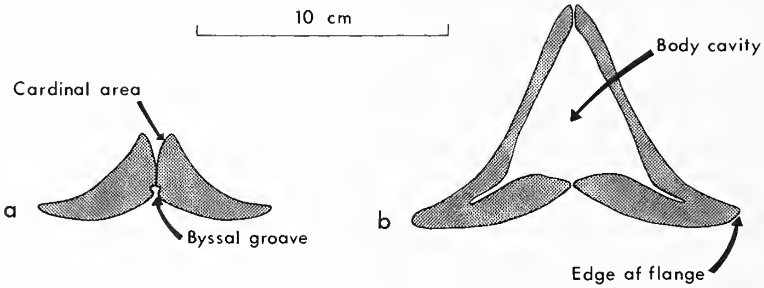
RUNNEGAR and GOBBETT, *Tanchitongia*



TEXT-FIG. 1. Reconstruction of *Tanchintongia perakensis*. a, b, show lines of sections shown in text-fig. 2.

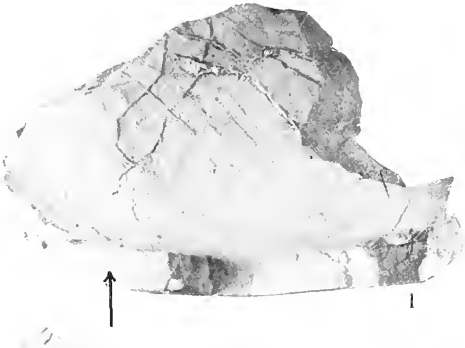
figs. 1–2; text-fig. 2). It is not clear how these structures terminated posteriorly, but one fragment (Pl. 46, figs. 5–6) shows a cross-section near the posterior end of the mantle cavity. Unless the growth pattern changed abruptly with the onset of sexual maturity, it would be geometrically impossible for the posterior end of the shell to be closed. We assume there was a large permanent triangular gape at the posterior end of the shell (text-fig. 1; Pl. 45, fig. 5). Figures 4 and 5 of Plate 46 are juxtaposed to show how the interior of the right valve may have looked. In this reconstruction the cardinal area disappears in the space between the two figures, and the mantle cavity is largest near the left side of Fig. 5.



TEXT-FIG. 2. Diagrammatic cross-sections of *Tanchintongia perakensis* along the lines a and b in text-fig. 1.

EXPLANATION OF PLATE 46

Figs. 1–9. *Tanchintongia perakensis* gen. et sp. nov., Early Permian, H. S. Lee Beds, H. S. Lee No. 8 Mine, Perak, West Malaysia. 1–2, left lateral and anterior views of fragment of left valve, arrows indicate edge of flange in both figures, SM G1877, ×0·33. 3, oblique view of umbonal fragment of left valve, SM G1878, ×0·33. 4, umbonal fragment of right valve showing duplivincular ligament area, byssal groove, and beginning of mantle cavity, SM G1879, ×0·33. 5–6, fragment of posterior of right valve, flange broken off lower right of fig. 6, SM G1880, ×0·5. 7, shell fractured across anterior end of mantle cavity (shaded) looking anteriorly, SM G1881, ×0·5. 8, hinge of umbonal fragment of left valve, SM G1882, ×0·5. 9, exposure of shell bed in mine showing large unbroken valves near top of face.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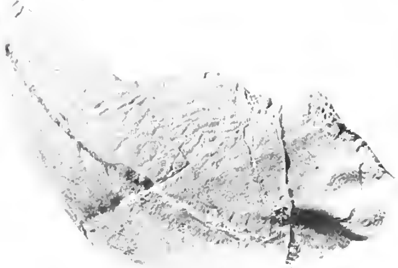
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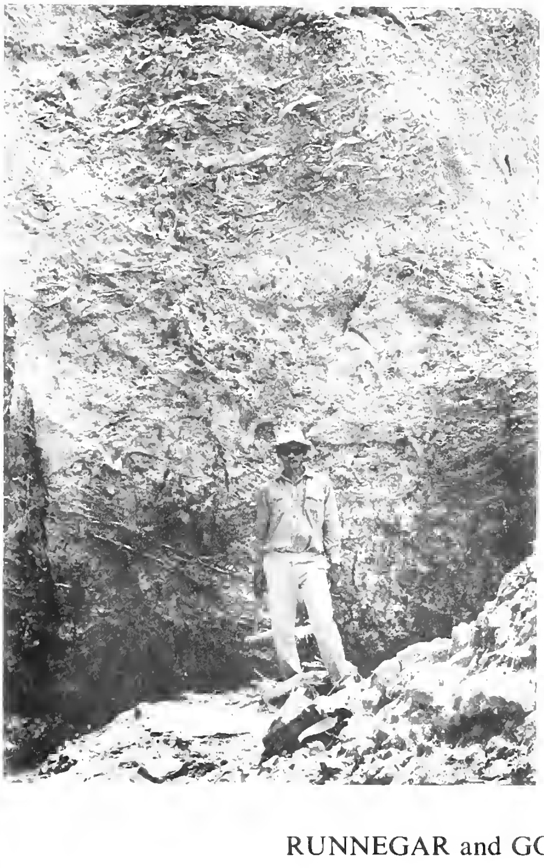
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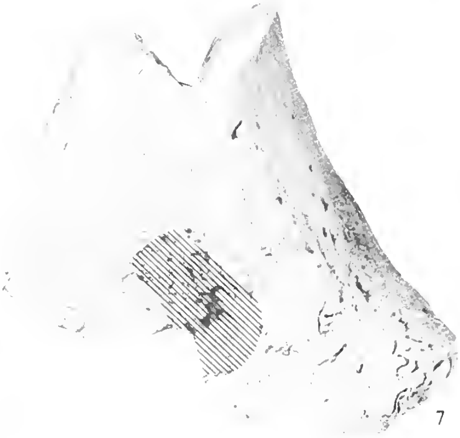
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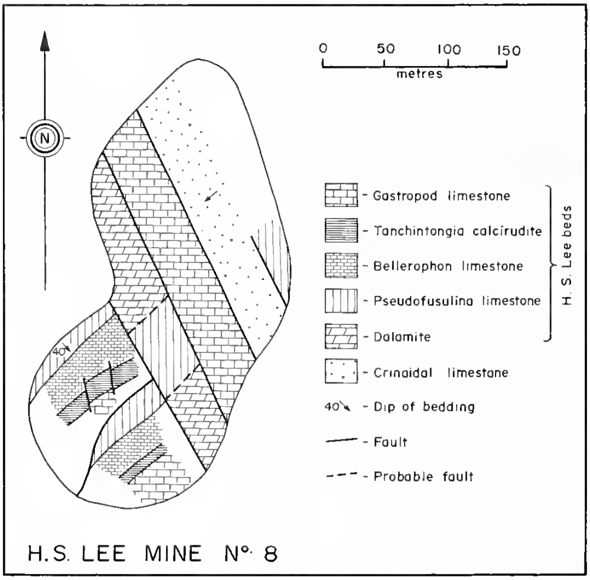
RUNNEGAR and GOBBETT, *Tanchitongia*

Dimensions. No measurements were taken at the field exposures but estimates from photographs (Pl. 45, fig. 8) suggest that some individuals must have exceeded 35 cm in length. This makes *Tanchintongia* one of the largest Palaeozoic bivalves known (Nicol 1964), being comparable in size to specimens of *Atomodesma* (40 cm), *Megadesmus* (20 cm), *Myonia* (19 cm), and *Eurydesma* (16 cm) from the Permian of eastern Australia. The cardinal area of one specimen (Pl. 46, fig. 4) has a height of 8 cm, and the degree of umbonal thickening is comparable with that seen in *Eurydesma* (5·8 cm, Runnegar 1970) and *Myonia corrugata* (5·5 cm, Runnegar 1967), though it is more difficult to measure. Judging from the field photographs (arrowed shells, Pl. 45, fig. 8), the flanges projected laterally up to 8 or 9 cm from the mantle cavity.

Stratigraphic information. All specimens were collected from a 3–5 m thick calcirudite formed from the valves of *Tanchintongia* (Pl. 45, fig. 8; Pl. 46, fig. 9; text-fig. 3).



TEXT-FIG. 3. Sketch map of H. S. Lee No. 8 Mine, Kinta Valley, Perak, West Malaysia, lat. 4° 17′ N., long. 101° 06′ E.

Scattered fragments occur in the limestone under the calcirudite and are there associated with *Pseudofusulina kraffti* (Schellwien). The few other fossils found with *Tanchintongia* resemble those found in overlying and underlying limestones. These limestones contain a diverse invertebrate fauna including goniatites and gastropods (Jones *et al.* 1966; Batten 1972). *P. kraffti* abounds as detrital grains in limestone about 10 m below the *Tanchintongia* calcirudite. This sequence is called the H. S. Lee Beds (Suntharalingam 1968) and can be correlated with the *Pseudofusulina ambigua* Zone of the Japanese Permian, approximately equivalent to the early Leonardian of North America.

In the latter part of 1966 the H. S. Lee No. 8 Mine was flooded and the exposures are no longer accessible.

Occurrence in Japan. One of us (D. J. G.) noticed worn fragments of *Tanchintongia* in a limestone containing *Pseudofusulina* and *Pseudodoliolina* in the large quarries at Akasaka, Japan. No specimens were available for illustration.

DISCUSSION

The persistence of the byssal gape through all growth stages indicates that *Tanchintongia* lived byssally attached throughout its life. It obviously rested on the large lateral flanges, which together form a virtually flat ventral surface to the shell (arrowed shells, Pl. 45, fig. 8). The most obvious functional explanation of these flanges is that they acted like snowshoes to stop the heavy shell sinking into a soft substrate. This may not be the correct explanation, as they could also have functioned as outriggers to prevent the shell from being overturned. In fact a byssally attached shell of this form could easily have withstood a rigorous high-energy environment. The impressive shell thickening may also have served to weight the shell against turbulent currents.

Tanchintongia must have lived subtidally. It is difficult to believe that an animal with a posteriorly gaping shell could have survived exposure and desiccation at low tide. We conclude that *Tanchintongia* lived gregariously in a sublittoral, probably high-energy environment, attached by a byssus, and weighted and perhaps stabilized by its extraordinary shell construction.

Haile and McElhinny (1972) have palaeomagnetic evidence that the Malay Peninsula lay at a relatively low palaeolatitude in the northern hemisphere in Permo-Carboniferous time. The fusulines and gastropods associated with *Tanchintongia* have definite Tethyan affinities (Batten 1972), as do the remaining bivalves in the collection. The existence of a large thick-shelled bivalve in this fauna indicates that it is unlikely that temperature was the controlling factor in the development of shells of this size and thickness, as comparable shells also occur in the cool-temperate assemblages of Australia.

Acknowledgement. This study was supported in part by a grant (E69/17168) from the Australian Research Grants Committee.

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THE SILURIAN CONODONT *OZARKODINA SAGITTA* AND ITS VALUE IN CORRELATION

by R. J. ALDRIDGE

ABSTRACT. A reconstruction of the apparatus of *Ozarkodina sagitta* (Walliser) is proposed, consistent with the composition of other apparatuses of the genus *Ozarkodina* and based on collections of disjunct conodont elements from Bohemia, Britain, Ireland, and the Carnic Alps of Austria. Descriptions of the apparatuses of the three subspecies of *O. sagitta* include details of the previously undescribed hindeodellan, plectospathodontan, and trichonodellan elements.

The stratigraphical distribution of *O. sagitta* in Britain and Bohemia is consistent with a range for the *sagitta* Zone from the lower Wenlock into the lower Ludlow and indicates a possible chronological sequence within the zone from *O. sagitta rhenana* to *O. sagitta bohemica*.

THE conodont form-species *Spathognathodus sagitta* was first described by Walliser (1964) in his comprehensive account of Silurian conodonts from Europe. Walliser (1964, pp. 82–84) recognized three subspecies, which he named *S. sagitta sagitta*, *S. sagitta rhenanus*, and *S. sagitta bohemicus*. *S. sagitta sagitta* was found by Walliser only in the Carnic Alps of Austria, *S. sagitta rhenanus* was recovered only from the Rheinisches Schiefergebirge of Germany, and *S. sagitta bohemicus* occurred only in Bohemia. The geographical separation of these forms indicated that they were possibly geographical subspecies, but Walliser appreciated that the differences may also be due to stratigraphic age and that the forms possibly represented chronological subspecies. The restricted stratigraphic range of the *sagitta* group rendered it useful for correlation, and in the provisional conodont zonal scheme for the Silurian proposed by Walliser (1964, fig. 10) a *sagitta* Zone was distinguished. The complete sequence of Walliser's conodont zones is displayed at the Cellon section in the Carnic Alps, where it is unfortunately impossible to relate the *sagitta* Zone directly to the graptolite zonal scheme or to the Silurian Series defined in the Welsh Borderland. In Bohemia, however, *S. sagitta bohemicus* occurs with *Monograptus testis* at Loděnice and in the lower part of the *M. nilssoni* Zone at Jinonice (Walliser 1964, p. 97) and from this Walliser inferred a range for the *sagitta* Zone from the uppermost Wenlock into the lower Ludlow. An extension of this range was suggested by Fåhraeus (1969, p. 9), who reported the occurrence of *S. sagitta* in the Högklint Beds of Gotland, which were correlated by Martinsson (1967) with the graptolite zone of *Monograptus riccartonensis*, of upper lower Wenlock age. This correlation is confirmed by the recovery of a *riccartonensis* Zone graptolite fauna from the Högklint Beds by Bassett and Cocks (1974).

In addition to *S. sagitta* itself, the *sagitta* Zone is characterized by the form-species *Ozarkodina edithae* Walliser and *Neoprioniodus bicurvatoides* Walliser (Walliser 1964, pl. 7, figs. 3–8). The consistent association of *S. sagitta* with *O. edithae* suggests that they belonged to the same conodont apparatus, and Walliser (1972, p. 77) grouped them together as a partial reconstruction of the multi-element species *O. sagitta*. *N. bicurvatoides* shows a less consistent association, being absent from

[Palaeontology, Vol. 18, Part 2, 1975, pp. 323–332, pl. 47.]

several large collections (Walliser 1964, table 2), and was not included in this reconstructed apparatus. *N. bicurvatoides*, however, occurs with *O. sagitta* in faunas listed from the Carnic Alps by Manzoni (1965) and from Podolia by Drygant (1968), and a possible derivation from the same apparatus is indicated. The fragile nature of this neoprioniodontan element may explain its absence from several reported faunas containing the spathognathodontan and ozarkodinan elements of *O. sagitta*.

Conodont faunas recovered recently from Bohemia (Walmsley, Aldridge and Austin 1974), Wales, and Ireland provide new evidence for the reconstruction of the *O. sagitta* apparatus and enable further comment on the stratigraphic range and value of the *sagitta* Zone.

The conodont fauna recovered from a sample (No. B.W. 12) from the upper Liteň Formation of Svatý Jan pod Skalou, Bohemia, was listed by Walmsley *et al.* (1974). In addition to simple cones and elements of the multi-element species *O. excavata* (Branson and Mehl), the following form-species were recorded:

Spathognathodus sagitta rhenanus Walliser	131
Ozarkodina edithae Walliser	78
Neoprioniodus bicurvatoides Walliser	36
Hindeodella n. sp.	41
Plectospathodus n. sp.	26
Trichonodella n. sp.	13
Lonchodina walliseri Ziegler	1
Ligonodina cf. *L. kentuckyensis* Branson and Branson	5
Trichonodella inconstans Walliser	1

A 20 kg sample collected by the author from the Nash Scar Limestone of Nash Scar Quarry, Presteigne, Radnorshire, Wales (SO 302 623), has yielded the following conodonts:

Ozarkodina excavata (Branson and Mehl)	
ozarkodinan element	10
neoprioniodontan element	2
hindeodellan element	3
plectospathodontan element	2
Spathognathodus sagitta rhenanus Walliser	30
Ozarkodina edithae Walliser	9
Neoprioniodus bicurvatoides Walliser	6
Hindeodella n. sp.	10
Plectospathodus n. sp.	1
Trichonodella n. sp.	2
Lonchodina walliseri Ziegler	2
Lonchodina sp.	1
Lonchodina? sp.	1
Ligonodina cf. *L. kentuckyensis* Branson and Branson	15
Hindeodella sp.	7
Neoprioniodus sp.	1
Ozarkodina cf. *O. typica*	3
Ozarkodina ziegleri aequalis Walliser	1
Trichonodella inconstans Walliser	34
Drepanodus aduncus Nicoll and Rexroad	2

A 1·5 kg coral limestone sample collected by Mr. J. Parkin from Caherconree mountain in the Anascaul inlier, Dingle Peninsula, Ireland, has yielded a small conodont collection, comprising the following form-species:

Spathognathodus sagitta cf. *sagitta* Walliser	11
Ozarkodina edithae Walliser	6
Neoprioniodus bicurvatoides Walliser	2
Hindeodella n. sp.	2

Plectospathodus n. sp.	1
Trichonodella n. sp.	1
Trichonodella inconstans Walliser	1

The reconstruction of conodont apparatuses from large collections of disjunct elements was pioneered by Walliser (1964), and subsequently many such reconstructions have been proposed. Klapper and Philip (1971) recognized that these reconstructed apparatuses, together with those apparatuses known from natural occurrences on bedding planes, conformed to a limited number of basic plans. After testing the validity of these plans on a number of faunas of disjunct elements they accepted them as models for the analysis of complex faunas. Rexroad and Nicoll (1972) and Pollock and Rexroad (1973) applied numerical techniques of reconstruction to some rather small collections of Silurian conodonts and failed to recognize groupings of the types proposed by Klapper and Philip, but many workers, dealing with larger collections, have substantiated the validity of the basic plans (Bergström *et al.* 1974; Druce, Rhodes and Austin 1974; Jeppsson 1969, 1972; Sweet and Bergström 1972; Walliser 1964, 1972; Ziegler 1972).

Klapper and Philip's 'type 1' apparatuses are perhaps the most widely recognized, and they include the genus *Ozarkodina*, which bears the following elements: P = platform (commonly spathognathodontan), O = ozarkodinan, N = neoprioniodontan, A_1 = hindeodellan, A_2 = angulodontan or plectospathodontan, A_3 = symmetrical element, e.g. trichonodellan. If it is assumed that the apparatus of *O. sagitta* is of this type, then the spathognathodontan element has been recognized in *S. sagitta* and the ozarkodinan in *O. edithae*. The faunas listed above all contain *Neoprioniodus bicurvatoides* and it seems reasonable to propose that this is the neoprioniodontan elements of the apparatus. Elements that represent the hindeodellan–plectospathodontan–trichonodellan transition series have not previously been recognized, but the three collections listed above all include similar undescribed elements of these types. The denticulation of these elements is closely comparable with that of *N. bicurvatoides* and their very fragile nature may explain why they have not been previously recorded. It is suggested that these are the remaining elements of the *O. sagitta* apparatus.

In order to test this reconstruction, a sample from a horizon (14D of Walliser 1964) in the *sagitta* Zone of the Cellon section in the Carnic Alps has been processed and picked with care. In addition to simple cones, the sample yielded 268 specimens of the spathognathodontan element of *O. sagitta* and 108 specimens of the ozarkodinan element. Also recovered were *N. bicurvatoides* (13 specimens) and very fragile hindeodellan (25 specimens), plectospathodontan (11 specimens), and trichonodellan (5 specimens) elements morphologically similar to those recovered from Bohemia, Wales, and Ireland. This association of specimens is consistent with the proposed reconstruction of the apparatus of the multi-element species *O. sagitta*.

The record of *O. sagitta rhenana* by Walmsley *et al.* (1974) is the first record of this subspecies in Bohemia and it is significant that it occurs at an older horizon than that at which Walliser found elements of *O. sagitta bohemica*. The horizon containing *O. sagitta rhenana* is referred to the *Monograptus flexilis* Zone, which is approximately equivalent to the British zone of *Cyrtograptus linnarssoni*, both zones succeeding the *rigidus* Zone in the separate areas. The *linnarssoni* Zone is of upper middle

Wenlock age, and this occurrence supports a downward extension of the range of the *sagitta* Zone, as suggested by Fåhraeus (1969, p. 9). A greater extension may be indicated by the recognition of the zone in the Nash Scar Limestone. Although the precise age of this formation has not been determined, Cocks *et al.* (1971, fig. 2) drew a very tentative upper boundary for the unit at the base of the *riccartonensis* Zone. If this is approximately correct, a lower Wenlock age is indicated and the evidence from Gotland for a range of the *sagitta* Zone from within the lower Wenlock is thus corroborated. The total range of the *sagitta* Zone now appears to be from the lower Wenlock into the lower Ludlow.

The recognition of the *sagitta* Zone in strata of lower and middle Wenlock age raises the question of the position of the *patula* Zone, which underlies the *sagitta* Zone and was tentatively placed by Walliser (1964, fig. 10) in the middle Wenlock. The *patula* Zone has not, as yet, been recognized in Britain, Gotland, or Bohemia, so a direct answer is not available. In Britain, the *amorphognathoides* Zone, which underlies the *patula* Zone, is present in the lowermost Wenlock of the Wenlock Edge area (Aldridge 1972, p. 141) and in Bohemia characteristic species of the *amorphognathoides* and *sagitta* Zones occur in association in the Liteň Formation (Walmsley *et al.* 1974). It is thus possible that the characteristic species of the *patula* Zone are somewhat limited in their geographical distribution and that the *patula* Zone of Austria is equivalent to part of the *amorphognathoides* Zone and/or part of the *sagitta* Zone of other areas. It is also possible that the *patula* Zone is widespread but occupies a short stratigraphic interval in the lower Wenlock between the *amorphognathoides* and *sagitta* Zones.

The relationships between the three subspecies of *O. sagitta* remain obscure, but there is now some evidence that *O. sagitta rhenana* and *O. sagitta bohemica* may be chronological subspecies. As noted above, the Bohemian fauna with *O. sagitta rhenana* is of middle Wenlock age, whereas the Bohemian faunas with *O. sagitta bohemica* are of uppermost Wenlock and lower Ludlow age. In Britain, *O. sagitta rhenana* occurs in the Nash Scar Limestone, which may be of lower Wenlock age. The presence of *lundgreni* Zone graptolites in the overlying shale (Bassett, 1974) puts an absolute upper limit of a low upper Wenlock age on the limestone. *O. sagitta rhenana* also occurs in the Dolyhir Limestone of Radnorshire, which is generally regarded as a correlative of the Nash Scar Limestone on the grounds of lithological and faunal similarity and geographical proximity. The spathognathodontan element of *O. sagitta bohemica* is common in the Wenlock Limestone, of uppermost Wenlock age, in Shropshire and the Malvern Hills, and was reported by Austin and Bassett (1967) from a horizon of high upper Wenlock age in the Usk Inlier. Austin and Bassett (1967, p. 278, pl. 14, fig. 15) also reported the spathognathodontan element of *O. sagitta rhenana* in the Usk fauna, but their single specimen does not show the characteristic arrow-shaped basal cavity of this subspecies and their assignment must be considered doubtful. Thus in Britain and Bohemia *O. sagitta rhenana* occurs in older strata than *O. sagitta bohemica*, although this distribution might be influenced by environmental rather than chronological controls. If further evidence supports a chronological sequence from *O. sagitta rhenana* into *O. sagitta bohemica*, it may prove possible to subdivide the *sagitta* Zone, at least over part of its geographical range.

There is little evidence of the relationship of *O. sagitta sagitta* to the other subspecies. Walmsley *et al.* (1974) noted that some of the spathognathodontan elements in the population of *O. sagitta rhenana* from Bohemia were morphologically similar to specimens of *O. sagitta sagitta* from the Carnic Alps. Similarly, the spathognathodontan elements in the Irish fauna are close to *sagitta*, but in some characteristics tend towards *rhenana*.

Although a greater span than that ascribed by Walliser is now recognized for the *sagitta* Zone, it has proved valuable in biostratigraphy. The usefulness of the zone in correlation on an international scale is indicated by its wide recognition throughout Europe and North America. Occurrences in Europe have been summarized by Walliser (1971) and North American records were discussed by Rexroad and Nicoll (1971). Further evidence on the relationships between the subspecies of *O. sagitta* should serve to increase the value of the zone.

SYSTEMATIC PALAEONTOLOGY

Genus OZARKODINA Branson and Mehl, 1933

Ozarkodina sagitta (Walliser, 1964)

1964 *Spathognathodus sagitta* Walliser, pp. 82–84, pl. 18, figs. 8–24.
1964 *Ozarkodina edithae* Walliser, pp. 55–56, pl. 26, figs. 12–18.
1964 *Neoprioniodus bicurvatoides* Walliser, p. 46, pl. 29, figs. 36, 37.

Ozarkodina sagitta bohemica (Walliser, 1964)

Plate 47, fig. 21

1964 *Spathognathodus sagitta bohemicus* Walliser, p. 83, pl. 18, figs. 23, 24.
p1964 *Ozarkodina edithae* Walliser, pp. 55–56, pl. 26, figs. 13, 15, 16 (only).

Remarks. The material to hand, from Britain, Bohemia, and Gotland, is insufficient for expansion of the descriptions given by Walliser (1964). The spathognathodontan elements display a characteristic subcircular flaring of the basal cavity and there is a tendency for fusion of the denticles above the anterior half of the cavity. The few specimens of the ozarkodinan element are indistinguishable from the same element in the other subspecies. The neoprioniodontan, hindeodellan, plectospathodontan, and trichonodellan elements are unknown.

Material. Fifty discrete conodont elements.

Ozarkodina sagitta rhenana (Walliser, 1964)

Plate 47, figs. 1–12, 22, 23

1964 *Spathognathodus sagitta rhenanus* Walliser, pp. 83–84, pl. 18, figs. 12–22.
p1964 *Ozarkodina edithae* Walliser, pp. 55–56, pl. 26, fig. 17 (only).
p1964 *Neoprioniodus bicurvatoides* Walliser, p. 46, pl. 29, fig. 36 (only).

Description. Spathognathodontan element—the blade is straight or slightly curved and higher at the anterior end than at the posterior. The denticles are erect and number from 11 to 17, with most specimens bearing 12–14. The basal cavity flares laterally from about midlength of the blade, tapering posteriorly and giving the unit an arrow-shaped outline in oral view. The denticles over the posterior two-thirds of the cavity are broader, lower, and more widely spaced than the remainder, which are often fused nearly to the apices. The denticles in the central portion of the blade are occasionally totally fused and the three or four denticles at the anterior end are commonly higher and a little less crowded. Specimens are generally robust.

Ozarkodinan element—the blade is flat or very slightly curved and bears posteriorly inclined, slender, sharp denticles, which are fused nearly to their apices. The posteriorly inclined cusp is situated a little posterior of midlength. The denticles increase in height gradually from the anterior end so that their apices form a straight line terminating with the tip of the cusp. The denticles of the posterior part of the blade are lower and increase a little in height anteriorly. The aboral edge of the unit is straight or slightly arched. The subcircular basal cavity is situated beneath the cusp.

Neoprioniodontan element—the cusp is tall, slender, and inwardly curved. The cross-section of the cusp is lenticular, with sharp anterior and posterior edges. The posterior bar is long, straight or somewhat bowed, and directed aborally. The denticles on the posterior bar are closely packed, slender, and of subequal size; they are often fused so that only the apices are free. Anterior to the cusp may be up to four small denticles, which decrease in size anteriorly. The basal cavity is small, rounded, and situated beneath the cusp.

Hindeodellan element—the cusp is tall and elliptical in cross-section with sharp to rounded anterior and posterior margins. The posterior bar is long and straight with tall, slightly posteriorly inclined denticles of subequal size. The anterior bar is much shorter, inwardly curved, and directed a little aborally, with very slender, crowded denticles that tend to be taller at the anterior end. The basal cavity is very small and is situated beneath the cusp.

Plectospathodontan element—the cusp is tall, slightly twisted, and inclined towards the shorter bar. The cross-section of the cusp is elliptical. The denticles on both bars are slender, of subequal size, closely packed, and inclined away from the tip of the longer bar. The shorter bar bears one or two much taller and broader denticles at the end. The basal cavity is very small and restricted beneath the cusp.

EXPLANATION OF PLATE 47

All specimens ×80, and are in the conodont reference collection, Department of Geology, Nottingham University.

Figs. 1-12, 22, 23. *Ozarkodina sagitta rhenana* (Walliser). 1-10 from sample B.W. 12, Bohemia; 11-12 from sample N.S. 3, Nash Scar Limestone; 22, 23 from sample V.G.W. 1, Dolyhir Limestone. Spathognathodontan element—1, oral view of SZ1; 4, lateral view of SZ4; 22, oral view of SZ22. Ozarkodinan element—2, lateral view of SZ2. Neoprioniodontan element—3, lateral view of SZ3; 9, lateral view of SZ9; 11, lateral view of SZ11. Hindeodellan element—5, lateral view of SZ5; 8, lateral view of SZ8. Plectospathodontan element—6, posterior view of SZ6; 10, posterior view of SZ10. Trichonodellan element—7, posterior view of SZ7; 12, posterior view of SZ12; 23, posterior view of SZ23.

Figs. 13-20. *Ozarkodina sagitta sagitta* (Walliser). From sample Cellon 14D, Carnic Alps. Spathognathodontan element—13, oral view of SZ13; 16, lateral view of SZ16. Ozarkodinan element—14, lateral view of SZ14. Neoprioniodontan element—19, lateral view of SZ19. Hindeodellan element—15, lateral view of SZ15; 18, lateral view of SZ18. Plectospathodontan element—17, posterior view of SZ17. Trichonodellan element—20, posterior view of SZ20.

Fig. 21. *Ozarkodina sagitta bohemica* (Walliser). From the Wenlock Limestone of the Ridgeway, Malvern Hills. Oral view of spathognathodontan element, SZ21.


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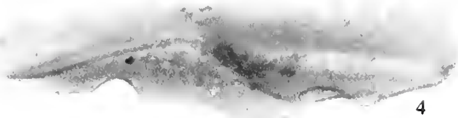
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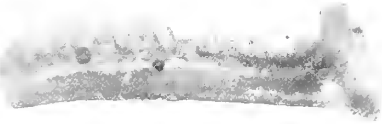
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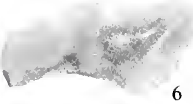
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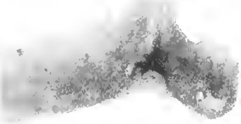
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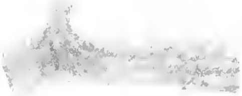
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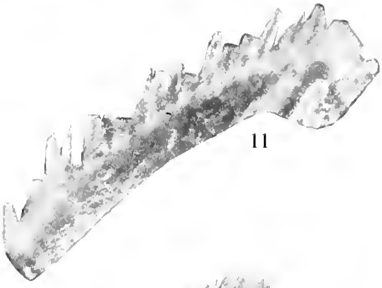
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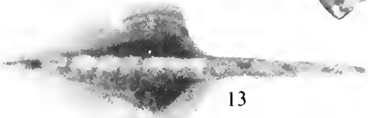
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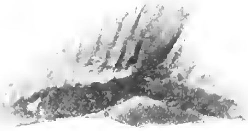
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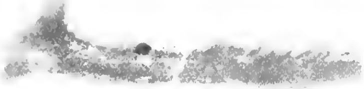
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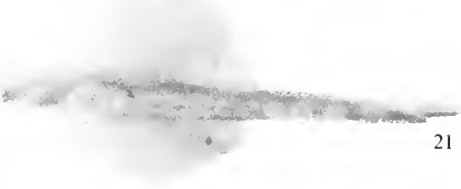
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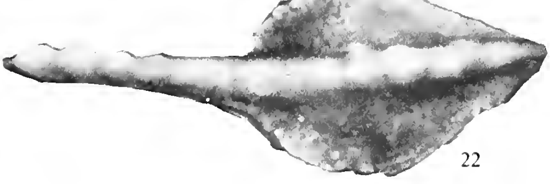
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ALDRIDGE, Silurian conodont *Ozarkodina*

Trichonodellan element—the cusp is erect and subcircular in cross-section. The lateral bars diverge at an angle of 120–150 degrees and bear slender, closely packed, erect denticles of subequal size. The cavity below the cusp is small and is commonly a little expanded posteriorly.

Remarks. Morphological variation is most marked in the spathognathodontan element, with specimens in some collections showing transition towards the spathognathodontan element of the two other subspecies. The collection from Bohemia shows a complete transition between *O. sagitta rhenana* and *O. sagitta sagitta*, with specimens at the *rhenana* end of the spectrum dominating. A small collection of twelve spathognathodontans from the Dolyhir Limestone of Radnorshire is dominated by typical *rhenana* forms, but three of the specimens display a subcircular flaring of the cavity that is more characteristic of *O. sagitta bohemica*.

Material. c. 400 discrete conodont elements.

Ozarkodina sagitta sagitta (Walliser, 1964)

Plate 47, figs. 13–20

1964 *Spathognathodus sagitta sagitta* Walliser, p. 84, pl. 18, figs. 8–11.
p1964 *Ozarkodina edithae* Walliser, pp. 55–56, pl. 26, figs. 12, 14, 18 (only).
p1964 *Neoprioniodus bicurvatoides* Walliser, p. 46, pl. 29, fig. 37 (only).

Description. Spathognathodontan element—the blade is straight or very slightly curved and higher at the anterior end than the posterior. The denticles are slender, erect, and closely packed, numbering from 14 to 20, with most specimens bearing 16–19. The flared basal cavity is situated beneath the posterior half of the blade, giving the unit a characteristic arrow-shape in oral view. The cavity extends as a very narrow groove to the anterior tip of the blade. The denticles over the posterior portion of the cavity are broader, lower, and less closely packed than the remainder. The denticle at the anterior tip of the unit is also generally smaller than its neighbours.

Ozarkodinan element—the unit consists of a flat blade with a straight or very slightly arched aboral edge. The blade bears slender denticles that are inclined posteriorly and fused nearly to their apices. The laterally compressed cusp is situated a little to the posterior of midlength. The denticles of the anterior part of the blade increase regularly in height posteriorly so that their apices form a straight line, terminating at the tip of the cusp. The posterior part of the blade bears lower denticles that increase slightly in height anteriorly. The slightly flared, subcircular basal cavity is situated beneath the cusp.

Neoprioniodontan element—the cusp is tall, very slender, and inwardly curved. The cross-section of the cusp is lenticular, with sharp to slightly rounded anterior and posterior margins. The posterior bar is long, straight or slightly curved, and directed aborally. The denticles of the posterior bar are slender, closely packed, and of subequal size. Anterior to the cusp may be one or two small denticles. The basal cavity is small, rounded, and situated beneath the cusp.

Hindeodellan element—the tall cusp is elliptical in cross-section with rounded anterior and posterior margins. The posterior bar has been broken away from most of the specimens, but on those on which it is retained it is long and straight with posteriorly inclined denticles of varying size. The denticles nearest the cusp, at the anterior end of the bar, tend to be smaller than the rest, which are mostly fairly small and of subequal size, but are regularly interspersed with somewhat larger denticles. The anterior bar is much shorter, curved inwardly, and directed a little aborally, with slender denticles. The denticles at the end of the bar tend to be broader and taller than the remainder and are inclined inwardly. The basal cavity is very small and situated beneath the cusp.

Plectospathodontan element—the slender cusp is twisted and inclined inwardly and towards the shorter bar. The cross-section of the cusp is elliptical. The denticles on both bars are slender, of subequal size, closely packed, and inclined towards the shorter bar. The denticles at the end of the shorter bar are more strongly inclined than the remainder and are also a little taller and broader. The two bars are not greatly different in length. The small basal cavity is situated beneath the cusp.

Trichonodellan element—the cusp is erect and subcircular to elliptical in transverse section. The lateral bars diverge at an angle of 100–150 degrees and bear very slender, erect denticles of subequal size. The small basal cavity is situated beneath the cusp and may be extended slightly posteriorly.

Remarks. The elements of *O. sagitta sagitta* broadly resemble the corresponding elements in *O. sagitta rhenana*, the most apparent difference being the consistently more delicate nature of the *O. sagitta sagitta* specimens. Other morphological differences, however, occur in all elements, and this is particularly marked in the spathognathodontan components. The spathognathodontans from the Carnic Alps show a greater number of more slender, closely packed denticles on the blade than do those of *O. sagitta rhenana* from Bohemia and Britain, these differences being most marked in the larger, presumably mature, specimens. The ozarkodinan element of *O. sagitta sagitta* tends to be shorter and the cusp is more slender. The denticulation of the neoprioniodontan, hindeodellan, plectospathodontan, and trichonodellan elements of *O. sagitta sagitta* is a little less regular than that of the same elements in *O. sagitta rhenana* and the cusp is generally more slender. From the specimens available, it appears that the two bars of the plectospathodontan element differ in their proportionate lengths in the two subspecies. In *O. sagitta sagitta* the two bars are of almost equal length, whereas in *O. sagitta rhenana* one is markedly shorter than the other.

Material. Four hundred and thirty discrete conodont elements.

Acknowledgements. The collection of material from the Carnic Alps was financed by a Royal Society Grant. Samples from Bohemia, Gotland, and Radnorshire were provided by Dr. V. G. Walmsley. Samples from the Dingle Peninsula, Ireland, were provided by Mr. J. Parkin. The author is also grateful to Dr. M. G. Bassett for information on Wenlock stratigraphy. The conodont specimens were photographed by Mr. D. Jones and the manuscript was typed by Miss A. C. Pyle.

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NEW EVIDENCE ON THE NATURE OF THE JAW SUSPENSION IN PALAEOZOIC ANACANTHOUS SHARKS

by RAINER ZANGERL *and* MICHAEL E. WILLIAMS

ABSTRACT. Gegenbaur's classic and almost universally accepted view of the primitive visceral skeleton of vertebrates, envisioning gill, hyoid, and mandibular arches as uniform, serially homologous (homonomous) structures separated by gill clefts, has not been actually demonstrated among either recent or fossil forms. In all cases the mandibular and hyoid arches are specialized in various ways to meet the functional requirements of the mandibular arch that frames the mouth opening. Apparently correlated with these modifications of the first two arches is the loss of a fully developed gill slit between them. Search for a visceral skeleton in which a prehyoidean gill cleft is present (aphetohyoidean condition) has hitherto been conducted unsuccessfully among the acanthodians and placoderms. Such a structure is here reported to be present in certain sharks of Upper Carboniferous age, in which the visceral skeleton is intermediate between Gegenbaur's theoretical scheme and the most generalized condition hitherto recorded among fossil and modern vertebrates. These Palaeozoic elasmobranchs are hence the most primitive gnathostomes presently known.

NEW evidence on the morphology of the head region of elasmobranchs of the Pennsylvanian Mecca fauna of the U.S.A. calls for a re-evaluation of the structure of the visceral skeleton and the nature of the jaw suspension in primitive sharks.

THE PROBLEM OF THE ORIGIN OF GNATHOSTOMES

In the basic plan of the visceral skeleton of gnathostomes, upper and lower jaws (palatoquadrate and Meckel's cartilage respectively) form an arch that is thought to be serially homologous with the hyoid and branchial arches that follow. Between these arches are openings (gill slits) connecting the pharynx with the outside.

In the presumed ancestral condition a series of complete gill arches functioned in support of an uncertain number of gills (usually thought to be 7–9). The gills, in all probability, functioned largely as filter-feeding devices, the respiratory function having been secondary. 'It appears that in the development of jaws, a pair of gill bars lying adjacent to the expanding mouth cavity became armed with teeth and enlarged to function in a new capacity as biting jaws' (Romer 1962). This modification, apparently brought about by a change from microphagous to macrophagous habit, resulted in the transformation of an epibranchial element into the palatoquadrate and a ceratobranchial element into Meckel's cartilage. There is some suggestion that one or two premandibular arches have been obliterated in the process of jaw formation but the evidence is not fully convincing.

The primitive condition, in which a free mandibular arch has evolved while the hyoid arch remains unmodified and is preceded by a fully developed gill slit, does not occur in any of the extant gnathostomes, nor has it previously been reported in any of their fossil relatives. However, in living elasmobranchs and the embryos of modern chimaeroids there exists a spiracle between the mandibular and hyoid arches which is

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thought to be a dorsal remnant of such a gill slit and in certain sharks a hemibranch is present on the posterior wall of the hyoid arch associated with the ceratohyal (text-fig. 5).

Gill slits, of course, are not demonstrable in the fossil record (except in extremely unusual cases) and the postulation of their presence or absence rests on indirect evidence. It is generally thought that the reduction of the prehyoidean gill slit (assuming that there was, indeed, such a stage in gnathostome evolution) came about by the morphological and functional reassignment of the epihyal element to serve as a suspensorium for the mandibular arch, a hyomandibular.

Watson (1937) believed he had found evidence for a prehyoidean gill slit among the earliest of gnathostomes, the acanthodians, and by 'analysis and comparisons' also among the placoderms. He proposed to include these fishes in a new group, the Aphetohyoidea, and placed it on equal rank with the Pisces.

Since the publication of Watson's monograph, the question has been critically re-examined by a number of students resulting in serious doubts concerning Watson's interpretation of the evidence of a prehyoidean gill slit in acanthodians and placoderms. The possibility is currently favoured that the gnathostomes may never have passed through an aphetohyoidean stage in their evolutionary history (Holmgren 1942; Stensiö 1947, 1963; Denison 1961; Jarvik 1963; Miles 1964, 1965, 1968; Moy-Thomas and Miles 1971).

Among the chondrichthyans an unmodified hyoid arch occurs only in the modern holocephalians, the chimaeroids. However, the members of this group are specialized in that the palatoquadrate has become fused to the neurocranium at an early stage in the history of the group (Zangerl and Case 1973) and in the ephemeral appearance of the prehyoid gill cleft (Stahl 1967). In members of the sister group, the elasmobranchs, the hyoid arch is topographically closely aligned to the mandibular arch, and a spiracular tube is present in most forms, including the notidanids where the hyomandibular element is said to have no suspensory function (Daniel 1922).

Hotton (1952) has elaborated on this idea and suggested that the hyomandibular of xenacanths, likewise, might not have served as a jaw suspensory (although in this group as in the notidanids, the hyoid arch is closely aligned with the mandibular arch—being situated directly medial to it—and was probably attached to it by ligaments). Schaeffer (1967) has suggested the same situation may apply to the other cladodont-level forms.

The argument, however, as to whether the hyomandibular is or is not suspensory involves a semantic confusion. In most modern sharks the mandibular arch is protrusal and attached to the neurocranium by means of the hyomandibular. In the Notidanidae the jaws are not protrusal; however, dissection of a young specimen of *Heptranchias perlo* (FMNH 74120) reveals that the hyomandibular is nevertheless suspensory in the sense that it is tightly bound by ligamentous connections to the articular region of the mandibular arch in a manner resembling that of *Chlamydoselachus* (Allis 1923).

The situation in elasmobranchs may thus be summarized as follows: in all forms in which the visceral skeleton has been studied, the epihyal element of the hyoid arch has become morphologically and functionally related to the mandibular arch and thus has become a hyomandibular.

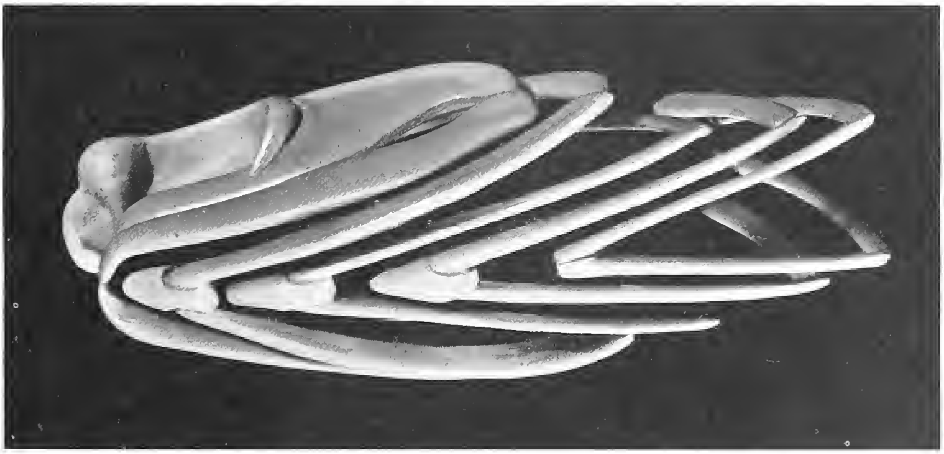
Evidence presented below suggests that in a number of Palaeozoic sharks, the relationship of the mandibular and hyoid arches is considerably more primitive and resembles the (theoretical) basic plan of organization of the visceral skeleton much more closely than in any other jawed vertebrate presently known.

NEW OBSERVATIONS

The new observations were made particularly in one species of anacanthous sharks of the Pennsylvanian Mecca fauna of the North American mid-continent (Zangerl and Richardson 1963, p. 122 and 1975), *Cobelodus aculeatus* (Cope) = *Styptobasis aculeata* Cope (Zangerl 1973). But there are reasons to believe that they also apply to *Denaea* cf. *fournieri* Pruvost and *Symmorium reniforme* Cope. These three genera are fairly closely related and are currently being studied by the writers. Large numbers of partially articulated and slightly disarticulated skeletons of these species are at hand, and the over-all descriptions will be published elsewhere.

The morphology of the neurocranium and most of the visceral skeleton can be determined by using stereological X-ray techniques described earlier (Zangerl 1966) combined with the construction of scale models (text-fig. 1). This technique enables one to study the elements in three dimensions and permits observations that are not readily apparent in the essentially two-dimensional state in which the fossils are preserved (for example, see text-fig. 2). Measurements were taken on disarticulated skeletons where the distortion of individual cartilages is minimal. Measurements on paired elements seldom vary more than a millimetre or two. The precise techniques used will be described more fully in connection with the species descriptions.

The observations shed new light on the morphology of the brain-case and the visceral skeleton of these primitive sharks. Firstly, in the three species mentioned, the typical postorbital process of the elasmobranch neurocranium is not a solid process, but a vertical arcade formed by a thin cartilage band that extends in an arc from the dorsal to the ventral platform of the neurocranium and encloses a large



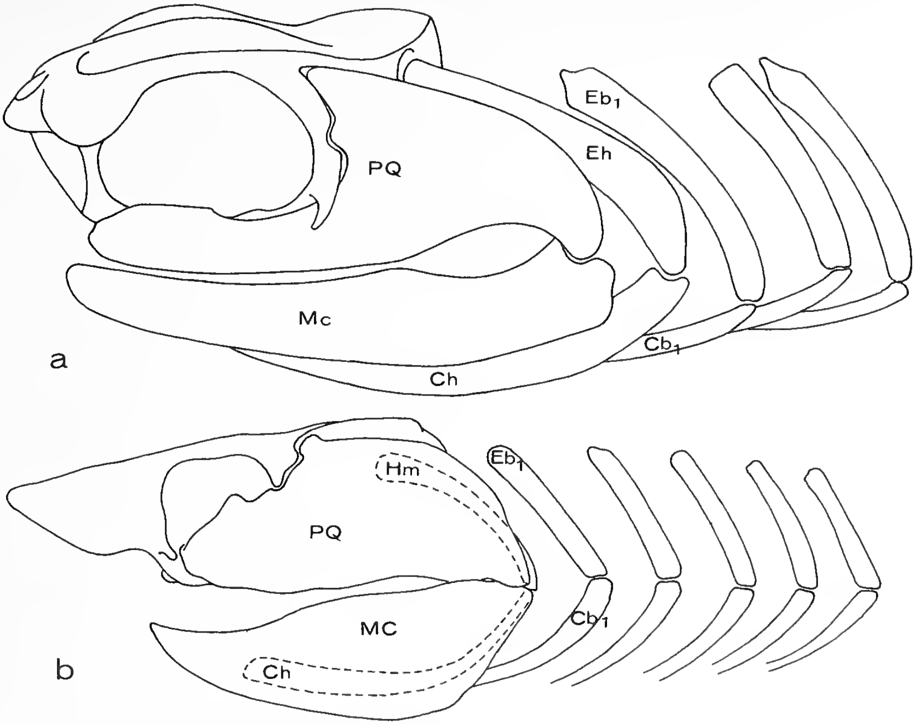
TEXT-FIG. 1. Ventro-lateral view of the model of the head skeleton of *Cobelodus aculeatus* (Cope) based primarily on FMNH PF 7347. About 0·6 × natural size.

TEXT-FIG. 2. Tracing of the skeleton of *Cobelodus aculeatus* (PF 7347) from radiographs. This is the specimen primarily used for the construction of the model. n, neurocranium; pq, palatoquadrate; Mc, Meckel's cartilage; eh, epihyal; ch, ceratohyal; cb, ceratobranchial; oc, orbital cartilage.

space between it and the lateral wall of the brain-case. Moreover, a cartilaginous prong points downward from the described arcade. In life this process embraced the palatoquadrate laterally (text-figs. 1 and 3), thus severely limiting lateral movements of the upper jaw. Each prong also provides a third direct attachment area of the palatoquadrate to the neurocranium in addition to the two seen in the typical amphistylic suspension.

Secondly, the hyoid arch appears to be entirely free of the mandibular arch; in *Cobelodus*, in particular, the upper element (epihyal) articulates with the lower element (ceratohyal) far behind the joint between the palatoquadrate and the mandible (text-fig. 1).

This relationship is determined by the dimensions of the hyoid arch elements relative to those of the mandibular arch (Table 1, text-fig. 2). The ceratohyals of *Cobelodus* are very long compared to Meckel's cartilages so that even if these elements are placed far forward toward the apex of the angle between the mandibles, as far forward



TEXT-FIG. 3. Head skeletons of elasmobranchs in lateral view; *a*, *Cobelodus aculeatus*; *b*, *Heptranchias*; redrawn from Daniel (1934) and Vetter (1874). Cb_1, ceratobranchial 1; Ch, ceratohyal; Eb_1, epibranchial 1; eh, epihyal; Hm, hyomandibular; Mc, Meckel's cartilage; PQ, palatoquadrate.

as it is reasonably possible to place them, they still extend well beyond the posterior ends of the mandibles (text-figs. 1 and 3). The epihyal equals (or nearly equals) in length the distance on the palatoquadrate from the dorsal tip of the otic process to the mandibular joint. Proximally it has a rounded articular surface and was probably anchored (by ligaments, we suppose) to the wall of the otic region of the brain-case in much the same fashion as in the modern *Heptranchias*. A more anterior attachment of the epihyal seems most unlikely in view of the peculiar postorbital arcade described above which provides no appropriate buttress for such an articulation. Furthermore, the otic capsule attachment is the typical condition in sharks, and the assumption of an uncharacteristic forward position of this attachment in the genera at issue would place the epihyal–ceratohyal joint far out of line with the mandibular joint (text-fig. 4), another atypical condition. But even if one were to admit the possibility of such exotic morphology, it would still remain evident that the hyoid arch could have had no ligamentous ties to the mandibular arch in the hexanchid fashion.

In *Denaea* the ceratohyal is relatively shorter than in *Cobelodus* but the epihyal–palatoquadrate relationship (see Table 1) is the same as in *Cobelodus*. The postorbital region of the neurocranium of *Symmorium* appears to be similar as in *Cobelodus* and *Denaea*, but the differentiation of the visceral arches remains to be determined.

In the specimen of *Cobelodus* that served mainly for the construction of the model, three pairs of branchial arches are preserved (text-figs. 2 and 3). The ceratobranchials are long, slender rods much as in *Chlamydoselachus* and the epibranchials are similar to the epihyal except that their dorsal ends appear 'unfinished' on radiographs and hence were not entirely calcified. Pharyngobranchials have not been identified with certainty and may not have been calcified.

The fact that the epihyal cartilage apparently was attached to the wall of the neurocranium and thus probably did not bear a pharyngohyal, suggests that the hyoid arch in these sharks is not quite as unmodified as it is in modern chimaeroids. But in all other respects it satisfies the requirements of the basic organizational scheme of the gnathostome visceral skeleton, as it has been envisioned and universally accepted in principle ever since Gegenbaur (see, for example, Romer 1966, fig. 6). Hence it is highly probable that these anacanthous sharks possessed a full-sized gill slit in front of the hyoid arch instead of a mere spiracle (text-fig. 5).

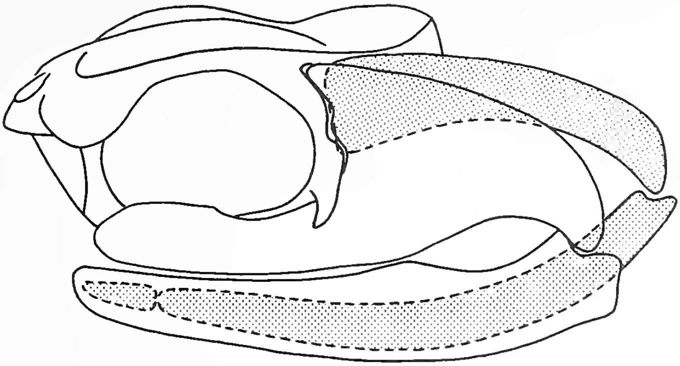
TABLE 1. Indices of dimensions of visceral skeletal elements in anacanthous and some other sharks.

		Index A	Index B
Cobelodus aculeatus	FMNH PF 2618	100	
	PF 7346	99	83
	PF 7347	99	91
	PF 8006	96	
	PF 7342	88	82
Denaea (Mecca fauna)	FMNH PF 2621	88	78
	PF 6767	90	
	PF 2539	90	78
	PF 8014	95	
	PF 2534		77
	PF 2527		79
	PF 2561		77
Denaea fournieri (Fournier and Pruvost 1928, pl. 2, fig. 1)		87	
Denaea fournieri (ibid. p. 4, fig. 3)		93	75
Xenacanthus platypternus (Hotten 1952, fig. 1)	FMNH UF 113	78	68
Heptranchias cinereus (Vetter 1874, pl. 15)		76	±59
Chlamydoselachus (Allis 1923, pls. 7 and 11)			58

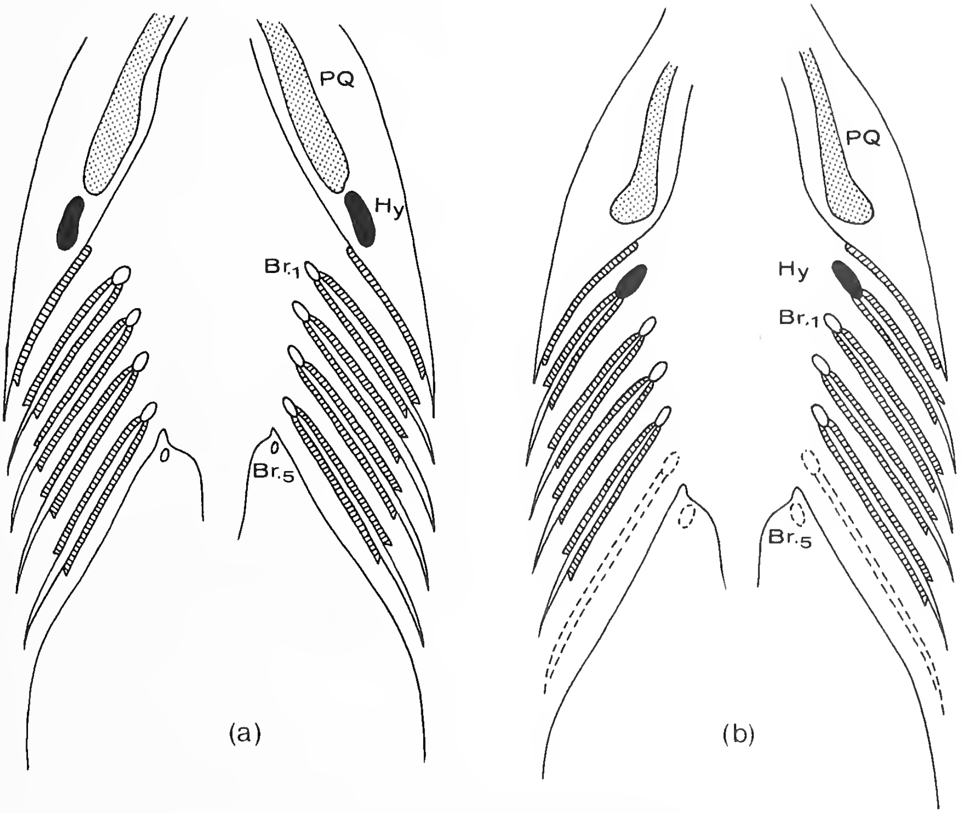
$$\text{Index A} = \frac{\text{length of epihyal (or hyomandibular)} \times 100}{\text{distance from tip of otic process of palatoquadrate to mandibular joint}}$$

$$\text{Index B} = \frac{\text{length of ceratohyal} \times 100}{\text{length of Meckel's cartilage}}$$

FMNH = Field Museum of Natural History, Chicago.



TEXT-FIG. 4. Drawing of the neurocranium and anterior visceral skeleton of *Cobelodus* on the assumption that the epihyal was attached to the brain-case just medial to the otic process attachment of the palatoquadrate. This is clearly an improbable condition.



TEXT-FIG. 5. Diagrammatic horizontal sections through the head region of *a*, an unspecified, modern shark, modified from Schimkewitsch (1910), after Boas; *b*, *Cobelodus–Denaea* showing the unmodified hyoid arch with a gill slit in front of it. Br_1, Br_5, branchial arches 1 and 5; Hy, hyoid arch; PQ, palatoquadrate.

The question as to whether the direct triple attachment of the palatoquadrate to the brain-case is a primitive or derived feature, would appear to be answered by both the phylogenetic and temporal trends in the jaw suspension of elasmobranchs, which progressed in the direction of ever greater mobility and freedom from direct contact with the neurocranium. The condition in *Cobelodus*, *Denaea*, and *Symmorium* clearly belongs at the primitive end of this progression.

The significance of the postorbital arcades is more difficult to assess. The space provided by these arches may have housed muscles or glands, but if so, there are no readily recognizable homologues for either in modern forms. More reasonable seems the thought that the prehyoidean gill pouch extended into this space.

CONCLUSIONS

Observations on many specimens show that the postorbital process of the neurocranium in such anacanthous sharks as *Cobelodus*, *Denaea*, and most probably *Symmorium* consists of a vertical arcade enclosing a rather large space between it and the brain-case. It sends a prong ventrad over the outer face of the palatoquadrate, which is hence directly attached to the neurocranium by three points of contact. This is a more rigid, and thus more primitive, condition of jaw suspension than has hitherto been observed in elasmobranchs.

The hyoid arch had no close topographic relation to, or ligamentous connection with, the mandibular arch. It is as separate from the mandibular arch as is the first branchial arch from it. This strongly suggests that in these sharks the prehyoidean gill slit had not been restricted to a spiracle; *they* are, indeed, aphetohyoideans, not the acanthodians or the placoderms. Being aphetohyoideans these anacanthous sharks represent the most primitive gnathostome condition presently known.

Acknowledgement. The present paper contains part of the results of a broader study of elasmobranchs of the Mecca fauna. Support by National Science Foundation grant GB-35593 is gratefully acknowledged.

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PALAEOGEOGRAPHICAL IMPLICATIONS OF TWO SILURIAN SHELLY FAUNAS FROM THE ARRA MOUNTAINS AND CRATLOE HILLS, IRELAND

by J. A. WEIR

ABSTRACT. A shelly fauna occurring in the Arra Mountains near Ballina, Co. Tipperary, is correlated with a fauna from Ballycar in the Cratloe Hills inlier, South Clare, and assigned to the upper Wenlock. The faunas are considered to have been derived from a shelf area situated to the south-east, and to have been transported north-westwards towards a basin limited south-eastwards and southwards by the Nenagh–Navan Line and by the Gallowshill–Silvermines Fault.

TWO shelly faunas, occurring in the vicinity of Limerick, reinforce Harper and Brenchley's diagnosis (1972) of an area of shelf deposition incorporating certain Lower Palaeozoic inliers of the Central Plain of Ireland. Harper and Brenchley consider that the shelf, which may conveniently be designated the Limerick–Tipperary shelf, is bounded to the north-west by a line, referred to herein as the Nenagh–Navan Line, related to a probable pre-Carboniferous fault with a north-westerly downthrow. This approaches, and may join, the Gallowshill–Silvermines Fault, which throws down to the north and forms the northward limit of the Cratloe Hills and Silvermines inliers, which are situated on the shelf (Harper and Brenchley 1972).

Mixed shelly and graptolitic faunas dominate the Limerick–Tipperary shelf. Orthocone nautiloids intimately associated with thin-shelled brachiopods (*Glassia*) occur, along with thin-shelled bivalves and phyllocarids (Cope 1954, 1959; Weir 1962, p. 251). They indicate tranquil conditions and considerable depths of deposition, and are considered to be autochthonous. The sediments are chiefly siltstone-banded argillites with a small proportion of arenaceous and conglomeratic horizons, some of which are probably fluxoturbidites. The succession in the Cratloe Hills inlier is incomplete due to strike faulting, and no meaningful estimate of thickness can be given.

One such sandstone bed, cropping out in Ballycar South townland in the Cratloe Hills inlier (Baily *in* Foot and Kinahan 1862; Weir 1962, p. 249) yields a shelly fauna. Five metres of sandstone are exposed in a prominent scrub-covered knoll at the edge of a field 100 m west of the Oatfield–Limerick road, and 400 m south of the summit of the road (Irish Grid reference R 565636). The rock is strongly calcified and contains sporadic fossils, mostly brachiopods, and occasional rounded quartz pebbles up to 1 cm long. Though most of the brachiopod valves are preserved unbroken they are always disarticulated, indicating that (unlike those of the associated banded argillites, etc.) the fauna is allochthonous. The fauna cannot, however, have been far transported, as there is little evidence of preferential concentration of flat or convex valves

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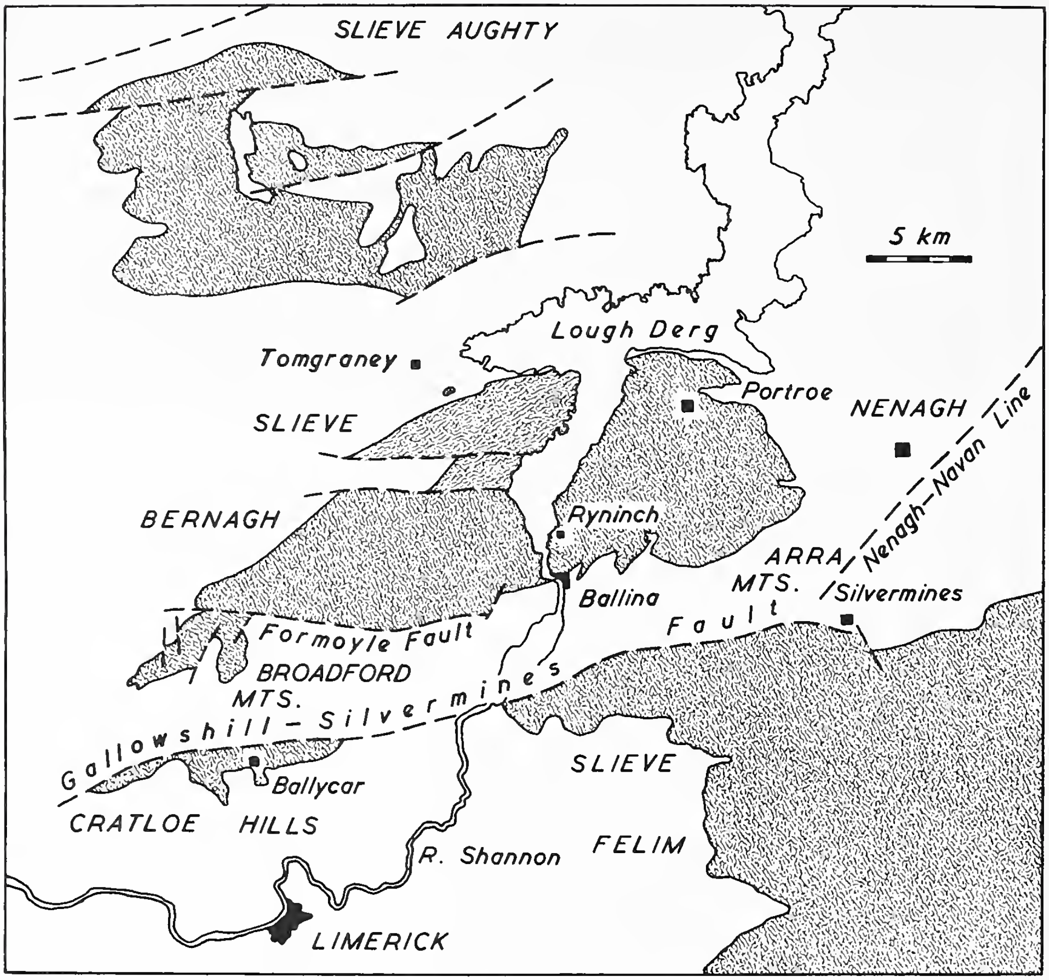


TEXT-FIG. 1. Locality map of the Limerick area. Lower Palaeozoic inliers shaded. Broken lines, faults; complete lines, stratigraphical contacts. Fossil localities of Ballycar (Cratloe Hills) and Ryninch (Arra Mountains) indicated.

(cf. Boucot, Brace and deMar 1958; Martin-Kaye 1951). The locality lies about 1 km south of the Gallowshill Fault.

The basin facies, occurring in the Slieve Bernagh–Arra Mountains and Slieve Aughty inliers, has virtually no autochthonous fauna. In Slieve Bernagh the sediments (Weir 1962) constitute a major 'fining-upwards' cycle, with a basal development of arenite-bearing argillites more sparsely banded but containing occasional thick and coarse conglomerate horizons again probably to be interpreted as fluxoturbidites. Two shelly faunas have been located within the basin; corals have been recorded from one locality in the north-east of the Slieve Bernagh inlier (Baily *in* Foot and Kinahan 1862, p. 17), and a shelly conglomerate (discussed herein) occurs in Ryninch Upper townland in the Arra Mountains. The bed is less than 1 m thick, and is exposed in a small quarry (R 706747) in a field 2 km due north of Killaloe

Bridge, Ballina, and 200 m west of the Ballina–Portroe road. The locality is not reported specifically in the sheet memoir (Foot 1861). The conglomerate (or pebbly sandstone) resembles that at Ballycar, though it is more feldspathic. The fossils occur mostly in thin lenses of rottenstone distributed irregularly through the bed, though occasional isolated shells occur. The rottenstone consists essentially of weathered and comminuted shell debris and crinoid ossicles, together with less fragmentary shells, mostly brachiopods. In general, only the umbonal ends are preserved. There is a very strong selective concentration in favour of convex valves, resulting in a bias towards preservation of dalmanellid pedicle valves. This selective concentration and the fragmentary state of the material again point to allochthonous origin, but contrast with the Cratloe locality, denoting a considerably greater distance of transport.

The following faunas have been collected from the two localities (Ballycar, Geological Survey of Ireland collection and author's collection; Ryninch Upper, author's collection):

TABLE 1

(1 = number of specimens; 2 = percentage of total collection)

	Ballycar		Ryninch Upper	
	1	2	1	2
rugose corals	33	14·7	—	—
favositids	5	2·2	—	—
heliolitids	2	0·9	—	—
Halysites	10	4·5	—	—
Aulopora	1	0·4	—	—
?*Aulopora*	1	0·4	—	—
tabulate corals indet.	3	1·3	—	—
bryozoa	8	3·6	1	0·9
Craniops	4	1·8	1	0·9
orthids indet.	2	0·9	2	1·7
?orthids	—	—	1	0·9
?*Dolerorthis*	5	2·2	3	2·6
Salopina	4	1·8	3	2·6
?*Isorthis*	1	0·4	11	9·6
Resserella	14	6·3	21	18·3
?*Resserella*	1	0·4	4	3·5
Dicoelosia biloba (Linnaeus)	4	1·8	—	—
enteletaceids indet.	5	2·2	1	0·9
Leptostrophia	—	—	1	0·9
?*Leptostrophia*	1	0·4	—	—
Leangella segmentum (Angelin)	16	7·1	—	—
Eoplectodonta duvalii (Davidson)	2	0·9	3	2·6
?*Eoplectodonta*	1	0·4	—	—
Pentlandina	2	0·9	—	—
?*Pentlandina*	1	0·4	—	—
Leptaena	5	2·2	—	—
Strophonella	5	2·2	4	3·5
stropheodontids indet.	3	1·3	—	—
strophomenaceids indet.	4	1·8	—	—
Coolinia	3	1·3	—	—
orthotetids indet.	1	0·4	—	—
?orthotetids	—	—	2	1·7
Anastrophia	2	0·9	—	—

TABLE 1 (*cont.*)

(1 = number of specimens; 2 = percentage of total collection)

	Ballycar		Ryninch Upper	
	1	2	1	2
Clorinda	8	3·6	—	—
pentamerids indet.	3	1·3	—	—
Sphaerirhynchia	1	0·4	—	—
rhynchonellids indet.	8	3·6	11	9·6
Atrypa reticularis (Linnaeus)	5	2·2	2	1·7
?*Atrypina*	1	0·4	—	—
atrypaceids indet.	2	0·9	1	0·9
Meristina obtusa (J. Sowerby)	9	4·0	3	2·6
?*Meristina*	—	—	1	0·9
athyridaceids indet.	3	1·3	1	0·9
Eospirifer	1	0·4	—	—
Cyrtina	1	0·4	—	—
Howellella	6	2·7	—	—
Lophospira	1	0·4	—	—
Liospira	1	0·4	—	—
?*Liospira*	1	0·4	—	—
gastropods indet.	4	1·8	1	0·9
cephalopods indet.	1	0·4	1	0·9
Palaeoneilo	—	—	1	0·9
palaeotaxodontids indet.	—	—	4	3·5
?*Orthonota*	—	—	3	2·6
bivalves indet.	—	—	5	4·3
Tentaculites	—	—	2	1·7
Encrinurus	11*	4·9	5†	4·3
Eophacops	1	0·4	—	—
phacopinids indet.	3	1·3	6	5·2
trilobites indet.*	—	—	3	2·6
Kloedenia	—	—	2	1·7
Beyrichia	—	—	2	1·7
beyrichicopinids indet.	—	—	1	0·9
crinoid calyces	3	1·3	—	—

* cranidia only.
† 5 cranidia + 3 pygidia = 5 individuals.

Though not identical, the faunas have sufficient components in common to justify correlation. Particularly significant features are the abundance of enteletaceids (13% in the Ballycar fauna, 35% in the Ryninch assemblage), the prominence of rhynchonellids, and the occurrence of *Eoplectodonta duvalii* and *Meristina obtuse*. Encrinurids and phacopinids are also noteworthy components. Petrographic characters suggest that both deposits are turbidites.

The Ballycar fauna is associated with siltstone-banded argillites having numerous coarser sandstone horizons averaging around 0·3 m in thickness. Though exposure is unfavourable to the preservation of sole-marks, the sandstones have the composition of lithic greywackes, and are also interpreted as turbidites. It was originally suggested (Weir 1962, p. 249) that the fossil horizon is the lowest level exposed in the Cratloe Hills inlier. The associated succession is identical in facies to the Broadford Group, diagnosed as the lowest stratigraphical unit present in the Slieve Bernagh

Syncline (op. cit., p. 246), and was correlated with the latter on that account. Due to scarcity of associated exposure the stratigraphical context of the Ryninch fauna is less clear, though it lies along the strike of the main outcrop of the Broadford Group in the Slieve Bernagh inlier, and close to that of its inferred contact with the succeeding Craglea Group. Reference of the Ryninch fauna to the Broadford Group would support correlation of the Ballycar succession with the latter.

Following re-examination of the Ballycar fauna, the author's original diagnosis of a Llandovery age (op. cit., p. 249) can no longer be sustained. *Salopina*, *Eoplectodonta duvalii*, and *Eophacops* have been recognized, and *Eocoelia biloba* s.s., *Leangella segmentum*, and *Meristina obtusa* specified. Together these denote a late Wenlock age, and rule out the Llandovery diagnosis. Moreover, no form specific to the Llandovery occurs (L. R. M. Cocks, pers. comm.).

This new interpretation accords well with recent amplification of the knowledge of the regional stratigraphy. Recent discoveries of dark and mottled graptolitic shales in the Slieve Bernagh inlier yield a *crispus* fauna (A. M. Flegg, pers. comm.), and continuity of the graptolitic facies from the Belvoir and Ballyvorgal Groups of the Broadford Mountains (Glenkiln–Upper Hartfell; Weir 1962, 1973) through the Llandovery of the Raheen Bridge inlier (Rickards and Archer 1969; Weir 1973) to this level may be inferred. The geographically isolated and unfossiliferous redbed facies of the Cloontra Group, which crops out within the faulted core of the Broadford Mountains Anticline and on its southern limb, probably succeeds the graptolitic facies. The group may represent a diachronous southward extension of the redbed development within the Lough Mask Formation of Connemara (Piper 1972, p. 37). The latter group is assigned to the *crispus* Zone (Cocks, Holland, Rickards and Strachan 1971, text-fig. 8), i.e. roughly contemporary with the top of the Slieve Bernagh graptolitic facies and inferentially earlier than the Cloontra Group. The latter group is probably of uppermost Telychian (?*griestoniensis*) age, leaving the Broadford Group—interpreted as succeeding the Cloontra Group conformably—to span the greater part of the Wenlock. On this basis there is an impressive acceleration in rate of deposition during the uppermost Wenlock. The Broadford Group has a thickness of some 2000 m, whereas the succeeding Craglea and Moylussa Groups, which, together with the Ballycar–Ryninch fossil horizon are assigned to the late Wenlock (cf. Harper and Brenchley 1972, pp. 259–260), have a thickness aggregating around 6000 m (Weir 1962, p. 235).

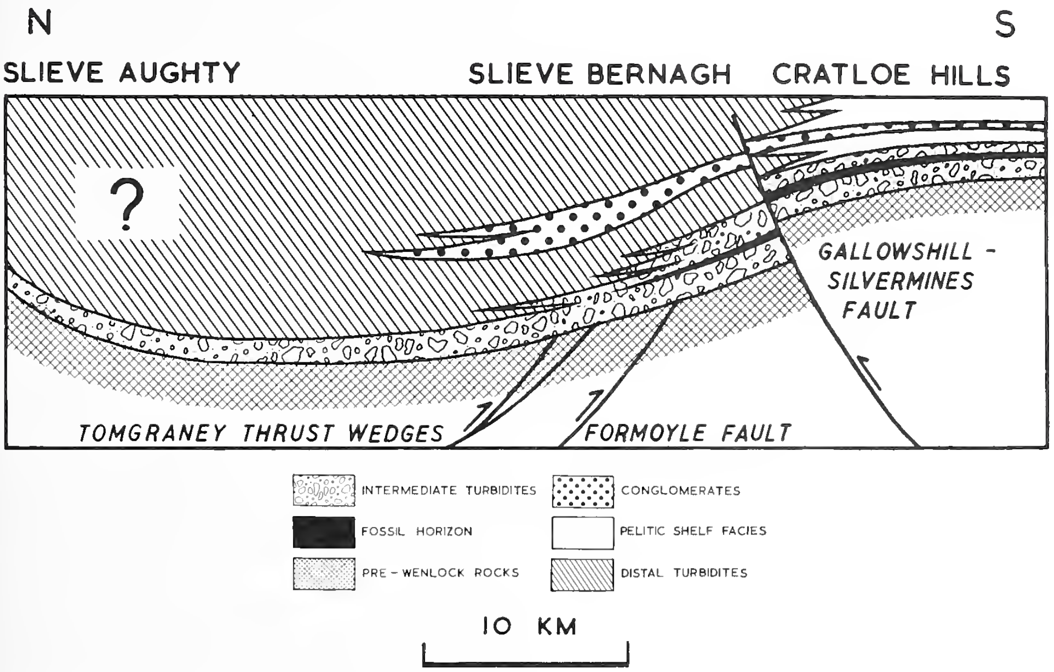
On the knowledge then available, the author suggested (1973) that the south-westward continuation of the axial rise of the Moffat geosyncline may pass close to the Tomgraney inlier. The horizon of the turbidite incursion being obliterated there by faulting, the axial rise could equally be located within Slieve Bernagh. In any event the turbidite influx took place substantially later in Clare than in the Southern Uplands, wherein it took place around *maximus* times (cf. Toghill 1970).

Significant contrasts exist between the two faunas under discussion. A proportion of these must relate to the strong selective concentration of convex valves at Ryninch, accounting for instance for the high return of *Resserella* and other enteletacean pedicle valves. This factor does not, however, account for the scarcity of plectambonitaceids, the lack of pentameraceids, and above all of corals, nor for the appearance of bivalves which are not recorded from Ballycar. These contrasts are more reasonably to be ascribed to community differences in the source areas. The most obvious cause of contrast would be the drawing of the two faunas from different depth-zones. Since, however, the deposits are allochthonous, nothing can be directly deduced concerning bottom conditions in the original habitats, and in particular of the substrates colonized. Caution must therefore be exercised against over-rigorous reference to the depth-controlled Wenlock communities of Hancock, Hurst and Fürsich (1974). The Ballycar assemblage is, however, dominated by small enteletaceids and *Leangella*, appropriate to the *Dicoelosia* community (op. cit., p. 152). This is a deep-water facies corresponding to the *Clorinda* community of the Llandovery (Ziegler 1965; Ziegler, Cocks and Bambach 1968). Larger shells, including the stropheodontids, suggest incorporation of elements of the shallower *Isorthis*, *Homeospira*, and *Salopina* communities, which equate respectively with the *Pentamerus*, *Costistricklandia*, and *Lingula* communities of the Llandovery. This admixture may denote the sampling of more than one source. The preponderance of small enteletaceids at Ryninch suggests a source mainly within the deeper communities, though even here the occasional large stropheodontid hints at a composite origin. The contrasts may equally be related to local environmental factors including nature of substrate, bottom-current intensity, salinity, and oxygenation, none of which can be assessed directly.

Palaeogeographically the *Dicoelosia* community represents the second-outermost shelly community of the Upper Silurian, being separated from the graptolitic facies by the *Visbyella* community. This has no Llandovery counterpart, as the *Clorinda* community gives way to graptolitic assemblages. Depths of up to 1500 m are deduced (Hancock, Hurst and Fürsich 1974, p. 152). *Cardiola* and graptolites, which characterize the autochthonous assemblage of the Cratloe Hills and Devilsbit inliers, are also prominent members of this community, and indicate that this assemblage may have been laid down at around this depth.

The Broadford Group has no precise counterpart in the Southern Uplands turbidite successions. Walton's 'Kirkcolm' facies (1963, p. 84) shows points of resemblance in consisting of medium-grained turbidites of moderate thickness interspersed with argillites, many of them laminated. The turbidite beds are, however, characteristically much thicker than the intervening argillites, which is in direct contrast to the 'Broadford' facies. Walton diagnoses the 'Kirkcolm' facies as the deposit of an offshore environment. The much lower return of arenites, etc., in the 'Broadford' facies suggests deposition even further offshore. No autochthonous fauna has yet been recorded from the 'Broadford' facies, though the occurrence of graptolites in facies of 'Kirkcolm' type (cf. for instance Craig and Walton 1959; Rust 1965, p. 104), suggests that these might also be expected to occur in the 'Broadford' facies.

Other than one diagnosis of northerly or north-westerly current flow, from a Wenlock conglomerate of the succeeding Craglea Group of the Slieve Bernagh inlier (Weir 1960), no reliable palaeocurrent data are as yet available for the Slieve Bernagh area, though the westward and northward thinning of this conglomerate does support north-westward transport, and is of importance in Harper and Brenchley's diagnosis of a north-westward palaeoslope during the Wenlock (1972, p. 262). The Ryninch horizon contrasts with the Ballycar fossil bed in its finer grain size, its lesser thickness, and the highly abraded state of its fossils, all of which point to a greater distance of transport and again support a general northerly descent of the palaeoslope. The Gallowshill–Silvermines Fault defined a break-of-slope, inferentially a submarine fault-scarp, the upthrow side of which housed a *Visbyella* community and thus lay at a depth of around 1500 m. The south-eastward rise of the palaeoslope would be sustained beyond the fault-scarp through successive depth-communities, at an angle sufficient to sustain the flow of the turbidity current which sampled them. Eventual emergence is suggested by the coarseness of certain of the fluxoturbidite-conglomerates. The location of any such landmass is not yet clear, but was probably some kilometres to the south-east.



TEXT-FIG. 2. Diagrammatic section across the Slieve Aughty basin and the Munster shelf, at the close of Silurian deposition. Vertical dimension exaggerated. The succession in Slieve Aughty is as yet largely hypothetical and is queried.

Triggering of the turbidity current was probably related to movement along the Gallowshill/Silvermines–Nenagh/Navan fault-complex. Tectonic conditions earlier in the Wenlock had been markedly unstable, as testified by the numerous turbidite beds (of which the Ballycar–Ryninch horizon is probably the thickest and coarsest). Deposition of the latter ushered in a period during which active differential subsidence of the Slieve Bernagh–Slieve Aughty basin took place. A contrast in sedimentary facies also developed, thin and predominantly pelitic sedimentation taking place on the margin of the Limerick–Tipperary Shelf, and banded argillites with thick fluxoturbidite-conglomerate horizons being laid down in the basin.

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TRANSPORTED ALGAE AS INDICATORS OF DIFFERENT MARINE HABITATS IN THE ENGLISH MIDDLE JURASSIC

by G. F. ELLIOTT

ABSTRACT. A microflora of red, green, and blue-green algae is recorded from the Middle Jurassic Great Oolite (Bathonian) White Limestone Division, near Cirencester, Gloucestershire. New genera described are *Apophoretella* (Myxophyceae) and *Dobunniella* (Chlorophyceae, Dasycladaceae). The fossils are not found where they grew: their probable original environments are discussed, and these suggest conditions like those of the present-day Great Bahama Bank.

QUARRIES in what is now known as the White Limestone Division of the Middle Jurassic Great Oolite (Bathonian) at Daglingworth (or Dagham) Downs, east of Ermine Street to the north of Cirencester, are recorded from the beginning of the nineteenth century or earlier. The present large excavations there of Messrs. W. H. Iles and Sons (Stratton) Ltd. (Nat. Grid SP 001 061), are a rapidly extending complex which includes sections earlier described by Richardson (1930, 1933), Channon (1950), and Torrens (1967); the last gave a detailed section including much deeper levels than seen by the earlier workers.

The algae now described occur in the upper beds, of which the section seen (May 1974) was:

3. Subsurface bed at top of quarry; rubbly limestone, the pieces often showing discoloration within 0·90 mm
2. Bedded intrasparites: numerous irregular sparry seams and lenses of coarser material, including small oncolites, occasionally in regular alternation a few centimetres apart. Also occasional irregular occurrences of seams of pseudoolites with much calcareous debris of invertebrates. Macrofossils seen: *Epithyris* sp., *Protocardia* sp., *Lucina bellona* Morris and Lycett, and *Cossmannia* (*Eunerinea*) *eudesii* (Morris and Lycett). Junction with bed below obscured by talus 3·50 m
1. Pavement of waterworn limestone surface with rounded cavities and attached flat oyster-valves: 'Dagham Stone', forming the floor of the Upper Quarry workings.

Bed 1 above is Bed 6 of Torrens (1967, p. 87). Bed 2, as exposed above the talus, is Torrens's Bed 8. The dasycladacean algae now described occurred *in situ* about the middle of this bed, though the best specimens came from a loose block. The other algae came from the lower half of this bed.

The only previous record of an alga here is of *Solenopora* (Richardson 1930, 1933).

There are some ammonite records, notably of the Middle Bathonian *Morrisiceras comma* S. Buckman, from the *Lucina*-beds of Richardson (1911, 1933) in this part of Gloucestershire. These beds, terminating above at a stratigraphic break, underlie the levels exposed at Daglingworth, and it seems likely that the latter are Upper Bathonian in age (Torrens, *in litt.*, and Torrens 1967).

[Palaeontology, Vol. 18, Part 2, 1975, pp. 351–366, pls. 48–50.]

SYSTEMATIC DESCRIPTIONS

Myxophyceae (*Blue-green algae*). The Myxophyceae are frequently represented in the fossil state by calcareous crusts, nodules, and stromatolites; the associated algae originating these, if preserved, are not usually generically determinable by comparison with Recent genera. In thin-section, however, certain characteristic and consistent types of myxophyte growth are recognizable. Those recognized in the present work are given generic rank and compared with Recent taxa, but it is not claimed that the fossil genera are other than mutually distinguishable lithified myxophyte thread-structures. By reason of the nature and usual preservation of these primitive algae, the exact correspondence legitimately to be inferred between fossil and living analogues is less exact than in many other organisms, and no attempt is made to fit the fossils into the sub-ordinal classification of the living microflora.

Branching of threads, formed of serial cells, in living myxophyceae is by means of 'false-branching', where the new thread, initiated at the side of the old, continues more or less along the original line of growth. Small separate adjacent rounded cells known as heterocysts occur. These phenomena are very rarely clearly to be seen in fossils, though this has been claimed under exceptional circumstances of preservation (e.g. Elliott 1964). In the present Jurassic material little of this kind is clearly visible.

Genus ZONOTRICHITES Bornemann, emend. Elliott

Type species. Z. lissaviensis Bornemann, Triassic.

Diagnosis. Calcified radiate growths of slightly wavy threads, threads spaced apart, branching, and subparallel after commencement of new members, with repeated branching giving an obscure zoned effect. Thread-diameter of 0·020–0·030 mm, growths or crusts up to several centimetres across.

Bornemann's material was from the freshwater Triassic of Silesia; he referred his genus to the Recent family Rivulariaceae (Bornemann 1887). From his illustration, the thread-diameter appears to be about 0·030 mm. Algal material from the marine Upper Triassic of Oman, Arabia, with thread-diameter of 0·025 mm, was referred to *Z. lissaviensis* (Elliott 1964); the comments on preservation in this latter paper are applicable to fossil myxophyceae in general. Living myxophyceae as a group are tolerant of freshwater, brackish, marine, and supersaline environments, and are frequently abundant in the different belts of the littoral.

Zonotrichites sp.

Plate 48, fig. 3

Description. A growth of about 1·6 mm diameter showing a radiate or fan-like

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EXPLANATION OF PLATE 48

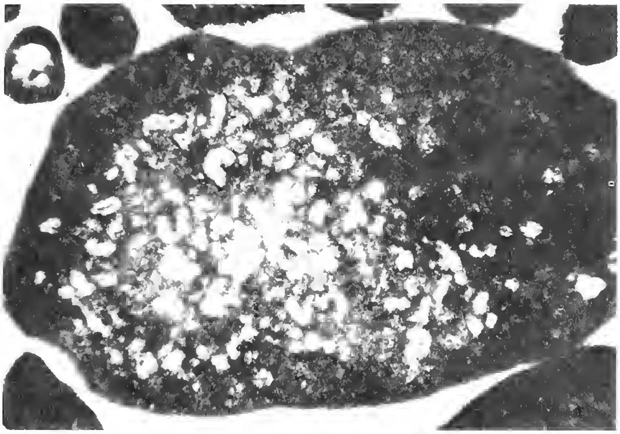
Fig. 1. *Pycnoporidium* cf. *liasicum* Elliott. Random section of rounded piece of growth, ×24. V.57650.

Fig. 2. *Pseudocodium convolvens* Praturlon. Tangential section, ×30. V.57651.

Fig. 3. *Zonotrichites* sp. Vertical section, ×40. V.57651.

Figs. 4, 5. *Dobunniella coriniensis* gen. et sp. nov., syntypes nos. V.57652, V.57653. Transverse section of a large individual, and oblique-transverse of a smaller, ×40.

All specimens from Great Oolite, Upper White Limestone (Middle Jurassic, Bathonian); Daglingworth, Cirencester, Glos.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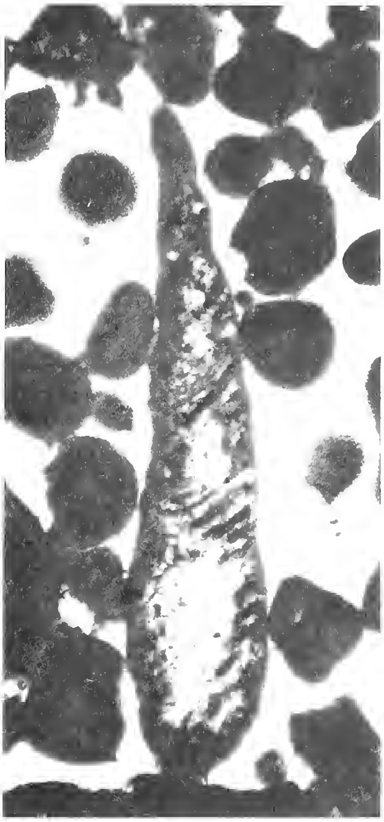
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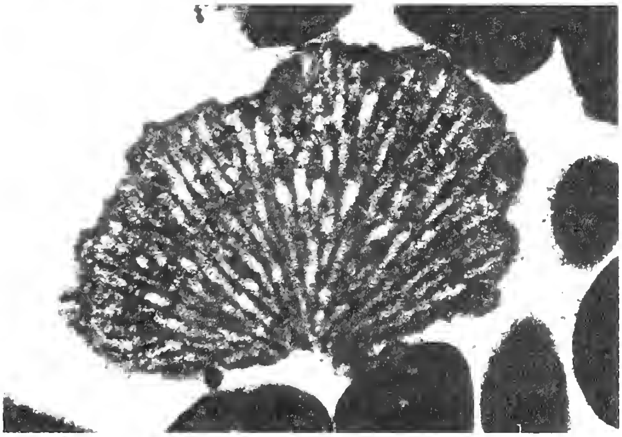
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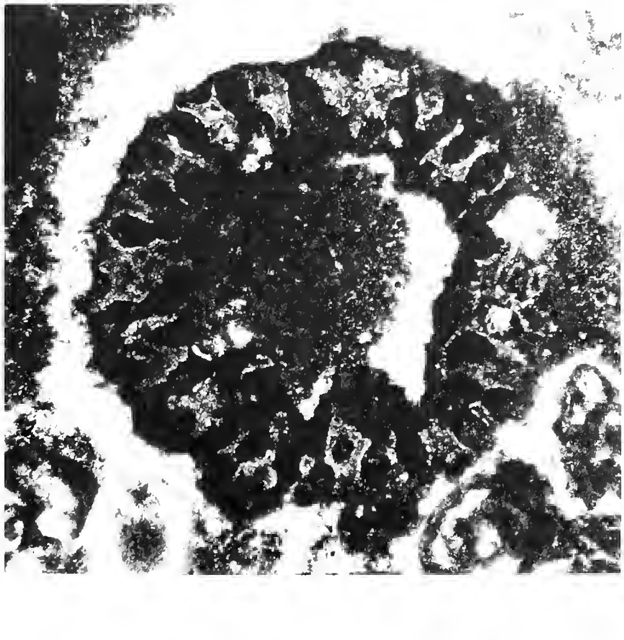
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ELLIOTT, Jurassic Algae

arrangement of dividing divergent threads of about 0·020 mm (0·018–0·023 mm) diameter. The preservation does not show the cellular structure of the threads, nor heterocysts. Initiation of new threads at the side of earlier ones (?false-branching) can be distinguished; at the points of initiation the older threads are about 0·036 mm apart, and about three such branchings can be seen in a length of 0·90 mm.

This growth is referable to *Zonotrichites* as defined above, but is insufficient for reference to a species.

Genus APOPHORETELLA gen. nov.

Type species. A. dobunnorum sp. nov.; Middle Jurassic of England and Italy.

Diagnosis. Calcified radiate growths of flexuous wavy branching threads, threads spaced apart and parallel, with branching tending to occur simultaneously in adjacent threads, so giving a banded appearance in section. Thread-diameter 0·010 mm or less.

Remarks. This alga shows longer, thinner, closer, and more gracefully flexuous threads than *Zonotrichites*, from which it is easily distinguishable.

The distinction between various types of fossil algae, red, green and blue-green, showing more or less radiate threads, or tubules, is not always easy. Thread-diameter is important. The visibility of cell-division within the thread, and whether the threads or tubules are touching or fused, as opposed to separate, is also diagnostic under conditions of good preservation. In *Solenopora* and its allies the partitions separating cells are usually visible, the cell rows are closely packed, curved-radiate outwards in growth, and appear as calcite-filled tubules, representing a former rigid growth. In the Myxophyceae, more variously preserved, the threads are usually separate, often dark in colour, serial cells are not normally visible, and there is a characteristic irregularity suggesting original flexibility.

Doubtful species are known. *Solenopora texana* from the Permian (Johnson 1951) is described with 'No cross partitions visible' (of cell-rows) and 'Cells rather widely spaced with thick coating of algal dust between'; this is not a solenoporoid character. The author compares it to a *Lithothamnium*, whose cells are usually characteristically different from those of *Solenopora*. I have not examined specimens of this; Johnson's illustrations suggest similarity to the Mesozoic myxophyte *Marinella* (Pfender 1939), but not to *Apophoretella*.

The new generic name is from Apophoreta, the morsels of the Roman dinner which convention permitted a guest to take away.

Apophoretella dobunnorum sp. nov.

Plate 49, fig. 3

Holotype. The specimen figured in Plate 49, fig. 3 (thin-section); Middle Jurassic (Bathonian), Great Oolite, Upper White Limestone, Daglingworth Quarry, Gloucester Road, N. of Cirencester, Glos. Reg. No. Brit. Mus. (Nat. Hist.) Dept. Palaeontology, V.57656.

Diagnosis. Characters as given for the genus.

Description. The growth is about 2·6 mm in maximum diameter. In section it shows fine parallel threads radiating from a basal centre seen to one side of the section. Due to poor preservation it is difficult to decide on exact thread-diameters, but they are much less (0·010 mm or less) than in *Zonotrichites*. The threads are long, sinuous, and parallel, the interstices being a little more than thread-diameter. Branching tends to occur simultaneously in adjacent threads, so giving a banded effect to the growth. Heterocysts are not distinguishable.

In comparison with *Zonotrichites* this alga shows longer, thinner, closer, and more gracefully flexuous threads, and is easily distinguishable.

The 'radially-orientated *Schizothrix*-like organic tubes' of Hudson (1970, fig. 8A), from the Scottish Middle Jurassic, are similar to the threads of *Apophoretella*.

The trivial name commemorates the Dobunni, the British tribe in whose former territory the fossil is found. Daglingworth Quarry is near Bagendon, the site of their pre-Roman tribal centre.

Altered Myxophyte Threads

Plate 50, fig. 5

Hudson (1970, fig. 8C, caption B) has also figured 'fine algal tubes, comparable to *Schizothrix*' from the Scottish Middle Jurassic, comparing his material with an illustration of Monty (1967, pl. 11, fig. 2). Monty's figure shows 'Filaments of *Scytonema* and *Schizothrix* . . . reduced to small black streaks within or between crystals of the new mosaic' and is to illustrate the 'formation of crusty flakes built by *Schizothrix*', a post-mortem change in the top intertidal zone and mangrove fringes of the present-day Bahamas. This indication of a Bahaman-type littoral was considered significant in Hudson's study of certain algal beds in the Scottish Great Estuarine Series.

A very similar piece is now figured from Daglingworth; its significance is considered below.

Oncolite

Plate 50, fig. 3

Oncolites are calcareous nodules formed by consecutive growths, predominantly algal, around a nucleus. Typical oncolites, while often irregular in form and very variable, are more or less rounded, and must have been water-moved during growth. A summary account of certain Recent intertidal and subtidal forms and their environments from Florida and the Bahamas was given by Ginsburg (1960).

The Daglingworth example now figured is about 7 mm across, and in section shows many concentric layers of probable myxophyte origin with included detritus. The outer margins are undamaged apart from post-mortem pressure-solution against adjacent ooliths.

These fossils are probably the origin of the record of 'many little "pellets", regular and irregular, of pure white limestone' (Richardson 1933), from the oldest part of the quarry.

CHLOROPHYCEAE (Green Algae)
Order SIPHONOCLADALES (Blackman & Tansley) Oltmanns, 1904
Family SIPHONOCLADACEAE Schmitz, 1879
Genus PYCNOPORIDIUM Yabe and Toyama, 1928
Pycnoporidium cf. *liasicum* Elliott, 1965

Plate 48, fig. 1

Description. Rounded remains of a *Pycnoporidium* sp. occur, but are not well preserved. *P. lobatum* Yabe and Toyama is abundant in the Tethyan Upper Jurassic and Lower Cretaceous, and *P.* cf. *lobatum* was determined from the Scottish Middle Jurassic (Hudson 1970). From the dimensions of the internal structures of the present specimens, it appears closest to the very similar but larger *P. liasicum* described from the Lower Jurassic of Greece (Elliott 1965).

Order SIPHONALES Blackman & Tansley, 1902
Family CODIACEAE Kützing orth. mut. Hauck, 1884
Genus ARABICODIUM Elliott, 1957
Arabicodium sp.

Plate 49, fig. 4

Description. A broken segment, with length (incomplete) of 1·95 mm and diameter of 1·04 mm. The medullary zone of irregular longitudinal threads is missing and replaced by clear calcite, but typical subcortical zones of fine irregular tangled and outwardly directed threads (the area of original plant calcification) are distinguishable.

Arabicodium is common as a facies-fossil in the Upper Jurassic and Lower Cretaceous of the Middle East and elsewhere. In England, a small piece of codiacid probably referable to this genus has been seen by me in the Kemble Beds (Great Oolite) elsewhere in the Cirencester area (Elliott 1973). The relegation of *Arabicodium* (and of *Boueina*) to subgenera of *Halimeda* (Elliott 1965) is not now considered correct.

Order DASYCLADALES Pascher, 1931

Records of dasycladacean algae (family Dasycladaceae) from the limestones of the English Jurassic are extremely rare by comparison with those from equivalent rocks in alpine Europe and Asia. One English example is *Stichoporella stutterdi* (Carruthers) Edwards. This was collected from the Stonesfield Slate and elsewhere in the nineteenth century, and recognized as dasycladacean by Edwards (1928). What

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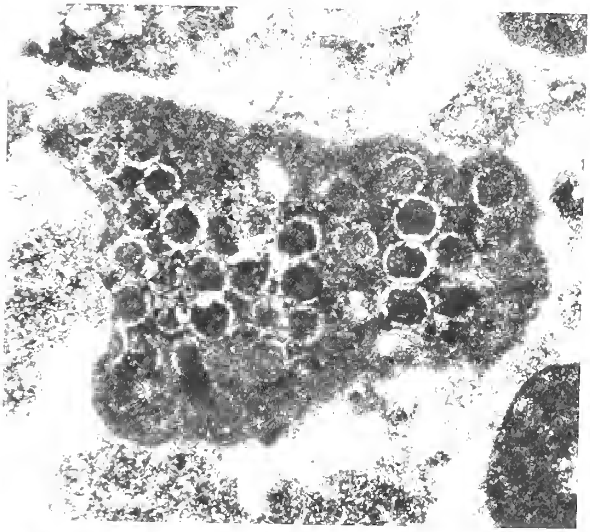
EXPLANATION OF PLATE 49

Figs. 1, 2. *Dobunniella coriniensis* gen. et sp. nov.; syntypes nos. V.57654, V.57655. Tangential and vertical sections, × 55 and × 35 respectively.

Fig. 3. *Apophoretella dobunnorum* gen. et sp. nov.; holotype no. V.57656. Vertical section, × 40.

Fig. 4. *Arabicodium* sp. Vertical section of broken segment, × 40, V.57657.

All specimens from Great Oolite, Upper White Limestone (Middle Jurassic, Bathonian); Daglingworth, Cirencester, Glos.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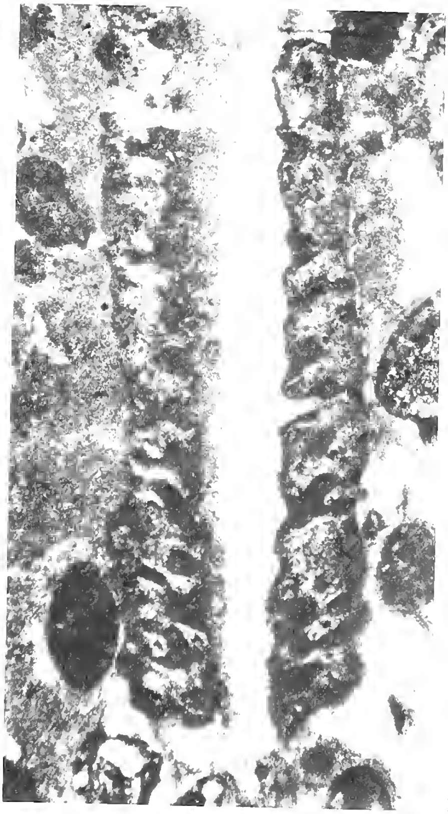
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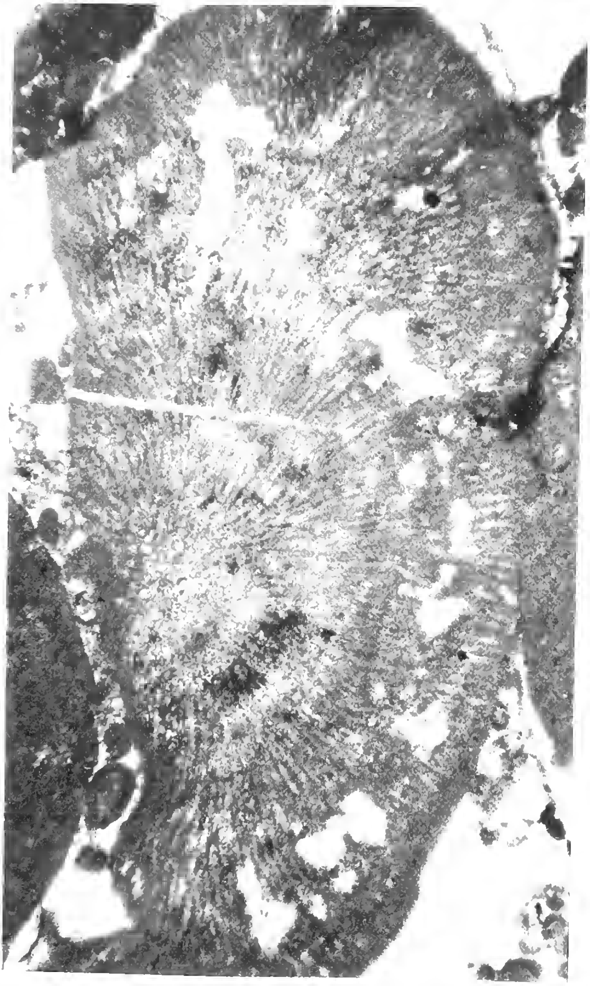
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ELLIOTT, Jurassic Algae

is surmised of the conditions of deposition of English marine carbonate Middle Jurassic rocks, and of their estimated palaeolatitude, suggests that their original littoral would have included suitable areas for dasycladacean growth, by comparison with the present-day occurrences of living members of the family. It is possible that for some reason opportunities for the migration of these plants to what is now the English area were limited. Alternatively, it may be that the dasycladaceans of the Jurassic had not achieved temperature tolerances equal to those shown by present-day representatives, which occur as far north as the Mediterranean. Thus the present addition of two more English records is of special interest. As they are not usually conspicuous fossils after the Triassic, it is possible that others remain to be discovered.

Family DASYCLADACEAE Kützing orth. mut. Hauck, 1884
Tribe THYRSOPORELLEAE Pia, 1927
Genus DOBUNNIELLA gen. nov.

Type species. Dobunniella coriniensis sp. nov. Middle Jurassic of England.

Diagnosis. Cylindrical calcareous dasycladacean tube showing verticils of branches somewhat like those of *Thyrsoporella*; each branch with a very wide primary, two swollen secondaries, and four swollen tertiaries.

Remarks. Dobunniella shows the thickened, swollen, presumed cladospore branches characteristic of the Thyrsoporelleae. In this character it is more like *Thyrsoporella* itself and the related *Belzungia*, both Palaeocene-Eocene, than like *Trinocladus* of the Cretaceous and Palaeocene. The branch-system is, however, much more simple than that of the genera quoted. Massieux (1966) gives the branch-plan of *Thyrsoporella* as 1:2:8:32, and that of *Belzungia* as 1:2:4:8:16:32. *Dobunniella* shows only 1:2:4. A further difference is that unlike the Tertiary genera, the branches of *Dobunniella* are not horizontal (i.e. not at right angles to the long axis of the stem-cell) but are inclined distally. The extent to which the thick and crowded tertiaries protruded outside the zone of calcification in life, and whether possibly they were there further divided or not, is not known, but *Dobunniella* seems to be a primitive genus of its tribe.

There are two other Jurassic records of alleged Thyrsoporelleae, and one Triassic record. *Thyrsoporella* n. sp. was recorded from the Lower Lias of Yugoslavia (Nikler and Sokač 1968, p. 171, pl. 2, fig. 5). *Thyrsoporella* (?) *hatigamoriensis* was described and figured from the Upper Jurassic of Japan (Yabe and Toyama 1949, p. 42, fig. 2).

EXPLANATION OF PLATE 50

Fig. 1. *Dobunniella coriniensis* gen. et sp. nov.; syntype no. V.57658. Outer surface of solid specimen in matrix, × 30.

Figs. 2, 4. *Cylindroporella* cf. *arabica* Elliott. Oblique-longitudinal and oblique-transverse sections, × 100. V.57659, V.57661.

Fig. 3. Oncolite, section × 12. V.57660.

Fig. 5. Intrasparite peloid showing altered myxophyte threads, × 300. V.57661.

All specimens from Great Oolite, Upper White Limestone (Middle Jurassic, Bathonian); Daglingworth, Cirencester, Glos.

PLATE 50


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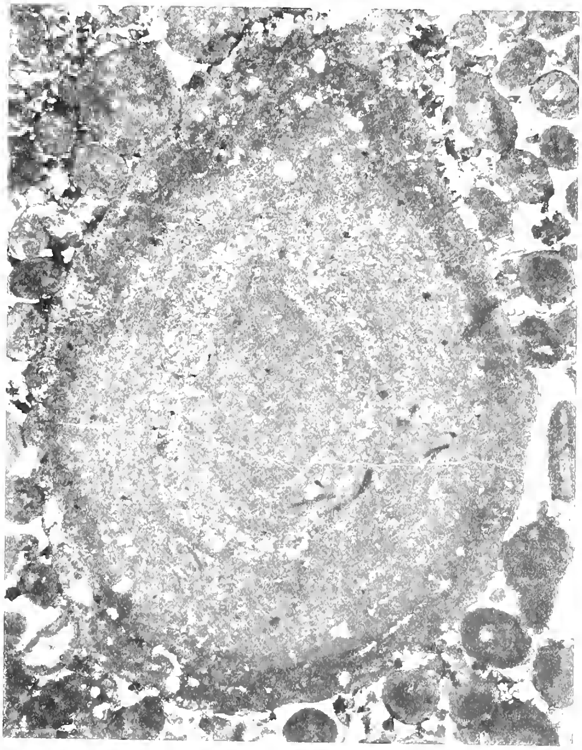
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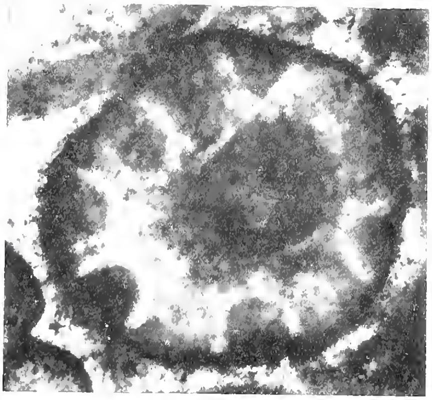
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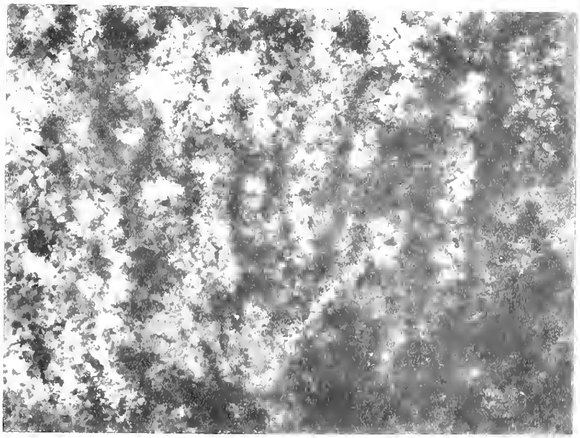
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ELLIOTT, Jurassic Algae

Neither of the figures permits a critical comparison with *Dobunniella*, though a reference to 'branching of the fourth branches from the third ones' in the Japanese account, and the regular banded appearance of branchlets in tangential section, show that this species is certainly not referable to *Dobunniella*. Like *Dobunniella*, it seems from the authors' account to have been poorly calcified near the stem-cell; also, its branchlets seem to have been fewer than in Eocene *Thyrsoporella*. However, *Placklesia multipora* Bilgütay, from the Upper Triassic of Austria (Bilgütay 1968) is earliest of all and shows thickened branches dividing to branchlets of the fifth degree (1:2:8:32:128) very clearly, being thus much more advanced in this character than *Dobunniella*. Another member of the Thyrsoporelleae, *Dissocladella*, whose species are mostly Cretaceous–Eocene, is known also by an older Mesozoic species (?Upper Triassic–?Upper Liassic of Greece): *D. cretica* (Ott 1965). It seems that, although best known from the Cretaceous–Eocene, the Thyrsoporelleae existed from the Triassic onwards.

The name of the new genus commemorates the Dobunni, the tribe inhabiting the Cotswold area in Roman times.

Dobunniella coriniensis sp. nov.

Plate 48, figs. 4, 5; Plate 49, figs. 1, 2; Plate 50, fig. 1, text-fig. 1

Syntypes. The specimens figured in Plate 48, figs. 4, 5; Plate 49, figs. 1, 2; Plate 50, fig. 1; Nos. V.57652, V.57653, V.57654, V.57655, V.57658; from the Middle Jurassic (Bathonian), Great Oolite, Upper White Limestone, Daglingworth Quarry, Gloucester Road, Cirencester, Glos.

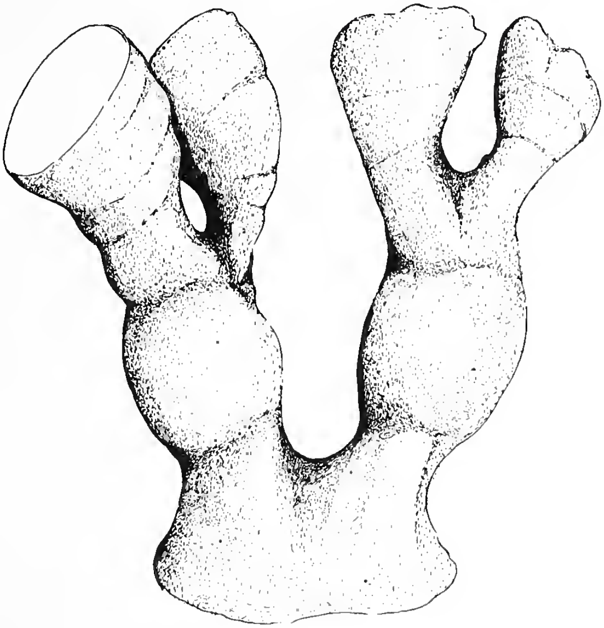
Diagnosis. *Dobunniella* of estimated 8 mm length or more, external diameter up to 1·7 mm, d/D ratio 36–41%; inner calcification weak.

Description. The species is represented by numerous broken pieces of the tubular calcareous encrustation of the plant. The longest fragment seen measured 6·5 mm; the actual plant would be longer, giving an original 'length' (height) of 8·0 mm or more. A normal external diameter is about 1·25 mm; two such specimens (1·25, 1·24 mm) have internal diameters of 0·45 mm giving a d/D ratio of 36%. Specimens of smaller external diameters 0·86 and 0·96 mm give d/D ratios of 41% and 40% respectively. However, a diameter of 1·7 mm has been measured on a large but ill-preserved specimen.

Consecutive verticils are set about 0·22 mm apart. Each verticil usually contains six branches, the inner portions set at an angle of 40–45° distally from the horizontal. These branches are thick and swollen, so that the intervening primary plant calcification is much less than in many dasycladaceans. The calcification appears to have been weak immediately adjacent to the stem-cell. Where a clear delimitation of the junction of a primary branch with the stem-cell is to be seen, with the complete calcified interstice between this and the next primary visible, the measurements usually indicate six branches per verticil. The larger example mentioned, however, contained eight.

In transverse section each branch is seen to begin with a wide and short primary, diameter 0·180 mm. This quickly divides into two divergent secondaries, waisted (diameter 0·063 mm) on leaving the primary but swelling out to diameters of 0·108 mm. Each secondary then divides into two tertiaries, also waisted (0·054 mm diameter) and then expanding to a flared termination of 0·108 mm or more at the outer surface.

These tertiaries, as thick as the secondaries, are accommodated within the wall-thickness (text-fig. 1) by irregular orientation vertically or at an angle to the plane of the secondaries, so that the full terminal thickness of the tertiaries is at the outer surface in all cases. Because of this, sections give a more confused appearance than, say, in *Thyrsoporella* itself. Occasionally a secondary appears to produce only one, or three, tertiaries, but this is probably due to the section cutting adjacent tertiaries from separate consecutive verticils. The appearance of a tertiary divided into adpressed incipient quaternaries (cf. *Dinarella*; Sokač and Nikler 1969) has also been seen, but seems likely to be due to a 'streaky' calcification of the dark infilling of the branches, since this preservation occasionally occurs in the inner portion of branches also. A vertical–tangential section near the outer surface shows numerous undivided tertiaries with diameters of 0·089–0·117 mm, reflecting levels at or just below the terminal expansions at the curved outer surface. On exposed outer surfaces the close-set pores show no clear pattern of arrangement.



TEXT-FIG. 1. Reconstruction of a single living radial branch, freed from the aragonitic surround, in a verticil of a full-grown *Dobunniella coriniensis* Elliott. The drawing shows the morphology and relationship of the primary, secondary, and tertiary portions of the branch; the central stem-cell would have been at the base of the illustration, the exterior of the plant at the top.

Remarks. The trivial name commemorates the Dobunnian capital city of Corinium, the modern Cirencester, 4·5 km from Daglingworth.

Tribe DIPLOPOREAE Pia, 1920

Genus CYLINDROPORELLA Johnson, 1954

Cylindroporella cf. *arabica* Elliott, 1957

Plate 50, figs. 2, 4

Description. Superficial ooliths show cores of fragmentary *Cylindroporella*, a genus with many species, mostly from the Upper Jurassic–Lower Cretaceous of the southern U.S.A., circum-Mediterranean, Middle East, and Madagascar. Dimensions are: outer diameter 0·405–0·455 mm, inner diameter 0·163–0·180 mm, sporangial diameter 0·081–0·117 mm, and distance between verticils 0·162 mm. There are probably six to eight sporangia per fertile verticil, set at right angles to the longitudinal axis of the stem-cell. Most of this is compatible with detail for the small species *C. arabica* Elliott (Upper Jurassic; Middle East, etc.) though the distance between verticils is greater in the English fossil. Although what are believed to be traces of sterile branches have been seen, better material is needed to confirm this distinction from *Sarfatiella* (Conrad and Peybernès 1974); *S. dubari* (Bajocian) and *C. arabica* have close similarities in size and structure. The material is insufficient for full description as a species.

Comparison-tables of *Cylindroporella* spp. are given by Fourcade *et al.* (1972) and Bernier (1971). The only species given by them as older than the Upper Jurassic is *C. ellenbergeri* (Lebouché and Lemoine 1963) from the Lower Lias of southern France. Fourcade *et al.* comment that if the emendation of the genus *Heteroporella* Praturlon by Ott (1968) is accepted, then *C. ellenbergeri* should be transferred to *Heteroporella*. Provisionally, therefore, the English *C.* cf. *arabica* may be the oldest known *Cylindroporella*, or share this distinction with the *Cylindroporella* sp. recorded from the late Bathonian of Israel by Derin and Reiss (1966, p. 29).

INCERTAE SEDIS

Pseudocodium convolvens Praturlon, 1964

Plate 48, fig. 2

Description. A near-vertical tangential section of an elongate fusiform or subcylindrical calcareous body with rounded ends, about 3·0 mm long. The outer surface shows a continuous spiral, with about fifteen turns in 1·08 mm length. Diameter of the spiral thread is 0·036–0·045 mm. The interior is recrystallized but there are traces of irregular subcortical thread-structure.

This fossil is referred to *P. convolvens* Praturlon, described from Middle or Upper Jurassic limestone in Italy (Praturlon 1964). These are elongate, subcylindrical, calcareous bodies showing an outer spiral tube, giving a surface reminiscent of certain structures in the Charophyta, and an inner structure of longitudinal medullary threads, dividing into smaller subcortical threads, reminiscent of the Codiaceae. From these resemblances it seems likely that this organism was a calcareous green alga, but its exact systematic allocation is obscure. The characters and dimensions of the English fossil are compatible with those given in Praturlon's type-description.

From the Scottish Middle Jurassic Hudson (1970, fig. 8B) has figured a similar but not identical organism, in which the internal structure is well developed, but the spiral is not well shown. This again is a single thin-section, but did not seem to be of *P. con-*

volvens itself, when Dr. Hudson kindly sent it to me for examination. It is listed by him as 'Calcareous alga of uncertain affinities, cf. *Pseudocodium convolvens* Praturlon' (Hudson 1970, p. 25, caption C).

RHODOPHYCEAE (Red Algae)
Subclass FLORIDEAE
Order CRYPTONEMIALES Schmitz, 1892
Family SOLENOPORACEAE Pia, 1927
Genus SOLENOPORA Dybowski, 1878
Solenopora jurassica Brown, 1894

Description. Rounded fragments of growths of this alga are found, sections showing the characteristic radial septate-tubular cell-rows of this species. It has already been recorded from the older part of the same quarry-complex by Richardson (1933) as a hand-specimen, and the locality is 6 km south-west of the well-known 'beetroot-stone' locality for the species at Aldgrove (Richardson 1911).

Solenopora sp.

Description. A small fragment shows in section a *Solenopora* with decisively smaller cell-diameter than that of *S. jurassica* (0·018–0·027 mm as compared with 0·036–0·045 mm). The material is insufficient for full description.

ORIGINAL ENVIRONMENTS OF THE ALGAE

Zonotrichites, *Apophoretella*, *Pycnoporidium*, *Pseudocodium*, *Solenopora*, and the oncolites occur in the intrasparite rock. This rock is largely made up of rounded pieces of carbonate sediment (over 99% soluble carbonate on analysis). They are very variable in size, mostly unfossiliferous, occasionally show contact deformation due to original slight plasticity, and are set in clear sparry cement. They are interpreted as penecontemporaneous sediment, broken up, rounded, and rapidly redeposited. The algae occur within a minority of the pieces, with the exception of the oncolites, which could have grown on the site of re-sedimentation, perhaps during slight pauses in deposition.

Of these transported algae, the myxophyceae, *Zonotrichites* and *Apophoretella*, are considered indicative of tidal calcareous mudflat or adjacent marsh conditions, with possible wide salinity fluctuations, and the '*Schizothrix*-flake preservation' is a further pointer to this kind of Bahaman calcareous mud-littoral (Monty 1967). *Pycnoporidium* is compared by Johnson and Konishi (1960) to the living *Cladophoropsis*, a shallow marine warm-water alga. *Pseudocodium* is wholly extinct, and its original habitat not known. *Solenopora* was open-marine; heavily calcified in life, its rounded remains could survive considerable transport, and it is represented by a well-rounded fragment.

The Dasycladaceae and Codiacean occur in the oosparite beds. These contrast with the intrasparites in containing much more organic debris; molluscan, echinoderm, serpulid, brachiopod, and bryozoan. Remains of the dasycladacean *Dobunniella* are numerically abundant; also a lesser quantity of fragments of *Cylindroporella*, and very rare segments of *Arabicodium*. The pieces of *Dobunniella* are broken and often worn; they occur most abundantly in concentrates of coarser materials, apparently due to size-sorting. The *Cylindroporella* remains form the cores of a small number of the superficial oolites. Like the algae of the intrasparite rock, these algal remains have been transported from their original sites of growth.

Both of the dasycladaceans grew originally in clear, shallow, warm coastal waters. Some of the *Dobunniella* remains as now preserved have a 'corroded' appearance, in which the dark infillings of the branch-cavities have resisted erosion better than the calcification. Since the original plant calcification would have been aragonitic and very fragile, some post-mortem lithification must have taken place before transport and final burial. The algae would have grown upright in patches and thickets; after death, the fragile fallen tubes would have undergone carbonate changes, infilling, and possibly other mineralization. This material, with much else, then became available for transport, and after varying wear and tear, was buried in a superficial-oolite shoal, with other skeletal debris.

The rare *Arabicodium* segments had a similar history.

The present occurrence of *Cylindroporella* is also a post-mortem phenomenon. Rey (1973) estimates the original ecology of the Lower Cretaceous *Cylindroporella* of Portugal as between tides and below low-tide level, and this is likely to have been true for the English Jurassic. In the present case a history is indicated of lithification and fragmentation of the calcareous crust from dead plants, subsequent rolling in a suitable environment to become nuclei of superficial ooliths, and final entombment. These superficial oolite developments probably indicate less rapid sedimentation than the intrasparite beds, with much more sorting of cleaner, harder materials.

Taken as a whole, the algae are indicative of warm-climate marine shallow waters. Some are characteristic of intertidal calcareous mud-flats and adjacent marsh of varying salinities like those of the present-day Bahamas, as already indicated for certain algal beds in the Scottish Great Estuarine Series of the same Middle Jurassic age by Hudson (1970). Others indicate shallow, clear, shelf waters, including both sheltered and more open environments. Their final resting-places suggest shallow-water calcareous sedimentation perhaps comparable with that of the present-day Great Bahama Bank (cf. Newell *et al.* 1959). Here living algae of types comparable to those described above grow in various habitats adjacent to or on a very extensive shallow shelf of calcareous sedimentation. This kind of marine environment is compatible with what is surmised from other evidence for the deposition of the Cotswold Great Oolite deposits.

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Note added in proof. A very similar algal microflora to that described above, and at the same stratigraphical level, was found in temporary excavations (Autumn 1974) at Fowlers Hill, Quenington (Nat. Grid SP 147045), 14·5 km from Daglingworth Quarry.

ECOLOGY AND FUNCTIONAL MORPHOLOGY OF AN UNCINULID BRACHIOPOD FROM THE DEVONIAN OF SPAIN

by PETER WESTBROEK, FERRY NEIJNDORFF *and* JAN H. STEL

ABSTRACT. The orientations, with respect to the bedding-planes, of 145 specimens of *Uncinulus pila* (Schnur, 1851) were plotted. From the results it is concluded that this species lived with its beak downwards and that the posterior region, in the sediment, was sealed by squamae and glottae. This interpretation is supported by the mesothyridid to permesothyridid pedicle opening. This life position would have been advantageous in helping the separation of inward and outward currents of sea-water, especially if the animal could rotate on its pedicle in response to changes in the marine flow. Geniculation, at the end of the brephic stage of ontogeny, involved important alterations in the life habits of *U. pila*; in particular its orientation changed from resting on its dorsal valve to the adult vertical position. The ecology of related species is compared and the convergence of habit of the Permian tetracamerid *Septacamera* is noted.

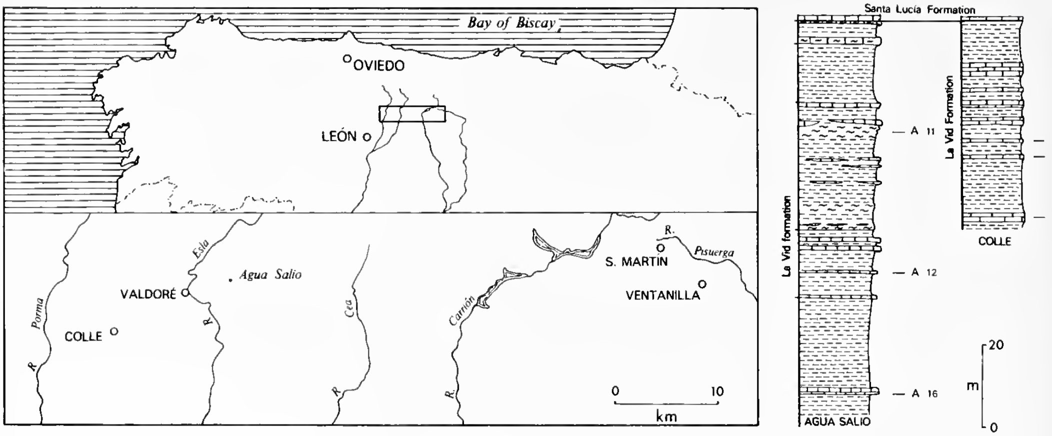
UNCINULIDAE are a group of rhynchonellid brachiopods which are a characteristic constituent of many Silurian and Devonian rocks. Their morphology is eminently suitable for functional, ontogenetic, and phylogenetic analysis and has already been the subject of a number of more or less detailed investigations (Schmidt 1937; Schumann 1965; Westbroek 1967). Fieldwork in the Cantabrian Mountains in Spain has allowed us to study the position of shells of one species of this family, *Uncinulus pila* (Schnur, 1851) in the surrounding rock. These observations, together with some new morphological data, led to reconstruction of the life habits of this species. Moreover, the ecological interpretation allows a better understanding of its morphology and, to a lesser extent, of its ontogeny. On morphological grounds it is suggested that the life habits of *U. pila* were operative in a major part of the family.

MATERIALS AND TECHNIQUES

In total 145 specimens of *U. pila* were collected at four different localities (text-fig. 1) in the Lavid Formation of the Southern Cantabrian Mountains (Emsian, province of León, Spain). On each specimen the orientation relative to the bedding-plane was marked. The angles between both the plane of symmetry of the shell and the interpolated 'horizontal plane' (between both valves) and the bedding-plane were then determined with the Ingerson apparatus (Ingerson 1941). The intersection of the plane of symmetry and the horizontal plane is called here the *longitudinal axis*. The orientation of the shell relative to the bedding-plane could now be plotted on a Wulff's net. With the aid of a counting net (Kalsbeek 1963) a representation of the distribution of the projections on the Wulff's net could be obtained. Plots of the few shells where the antero-posterior direction of the longitudinal axis (and thus the umbo) pointed upwards were not taken into consideration.

For morphological studies of the internal structure of *U. pila*, internal moulds

[Palaeontology, Vol. 18, Part 2, 1975, pp. 367–375, pl. 51.]



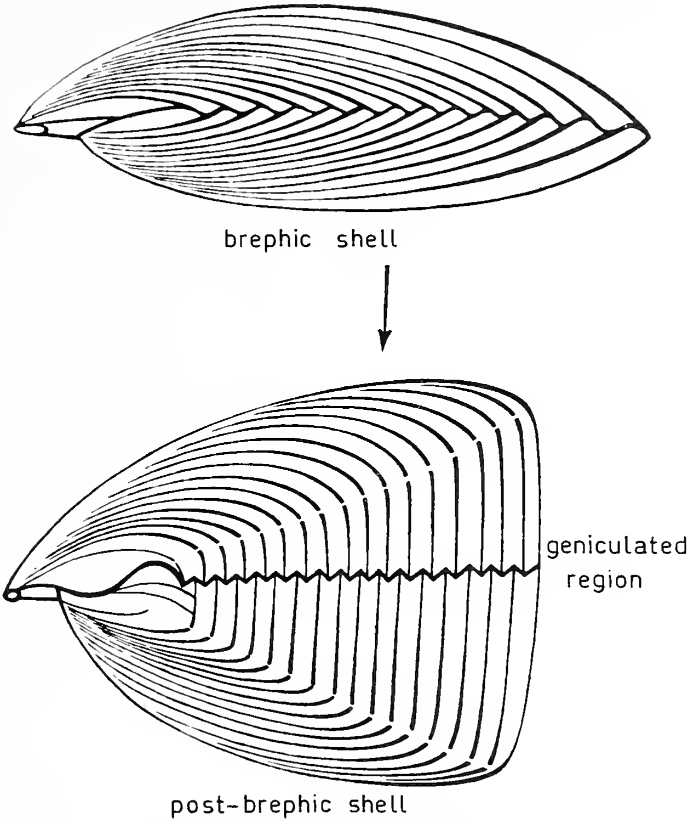
TEXT-FIG. 1. Collection localities for *Uncinulus pila*; 84 specimens from Colle; 61 specimens from Aguasalio. The internal mould figured (Pl. 51, fig. 3) is from between S. Martín and Ventanilla.

were used which were collected at a locality between Ventanilla and San Martín de los Herreros, described by Kanis (1956, pp. 390 and 392, fig. 10 and appendix 3, section II) (see text-fig. 1).

OBSERVATIONS

The ontogeny of all uncinulids characteristically proceeds in two stages (text-fig. 2): brephic shells are flat and grow mainly in length and width. By the end of the brephic stage both valves suddenly start growing in opposite directions so that they make an angle of 180° or even slightly more all along the commissure. As a result of this geniculation a vertical wall is formed and the shell grows in thickness. Geniculation is functionally related with the development of marginal spines—elongated outgrowths of the grooves between the costae—along both valve margins, forming a highly protective grill when the shell is opened. Since the spines project inside the mantle cavity just behind the opposite valve they can only be formed in a geniculated shell. Hence, this protective device can only develop in the post-brephic stage; it is absent in the brephic shell. No spines are formed in the most posterior parts of the geniculated region. In the more evolved uncinulids, like *U. pila*, a squama and a glotta are formed which close off the gape at these sites when the shell is opened (text-fig. 4; Pl. 51, figs. 1*b*, 2*b*).

Uncinulids are uniplicate, i.e. the commissure displays a broad median deflection in the dorsal direction. By analogy with the recent rhynchonellide *Notosaria* it is suggested that this deflection served to separate lateral inward streams of sea-water into the mantle cavity from the median outward stream of filtered water into the sea. Thus the commissure can be divided into five functionally different parts: postero-laterally the shell is sealed off by a pair of squamae and glottae; the inhalant apertures are situated (antero)laterally and the exhalant aperture anteriorly and medially. In most uncinulids, especially in *U. pila*, this functional five-fold subdivision of the commissure is further accentuated by the subpentagonal outline of the shell in dorsal



TEXT-FIG. 2. Geniculation in uncinulid brachiopods and explanation of terminology.

and ventral view (Pl. 51, fig. 1*a*, *b*, *c*). The postero-lateral sides make an obtuse angle, thus giving the shell a stumpy appearance. Along this part of the commissure the gape was closed off by the squamae and glottae which extend precisely from the hinge to the junction with the lateral sides. The lateral sides are subparallel; anteriorly they bend in median direction. Their transition with the postero-lateral sides is not sharply defined but their passage towards the median side which corresponds with the median deflection of the commissure and thus with the exhalant part of the gape, is marked by a sharp vertical ridge. In most of the specimens of *U. pila* the median deflection of the commissure has also a marked posteriorly directed component throughout the ontogeny. As a result the sulcus extends smoothly from near the ventral umbo to the dorsal geniculation. This combination of factors must have provided a neat separation of the inward stream of sea-water (in postero-median direction) from the outward stream (antero-medially). Later on it will be shown how the median trough may have funnelled currents in the surrounding sea-water, so that a maximum separation of inwardly and outwardly streaming water was achieved.

The delthyrium is largely sealed off by a deltidium and the position of the pedicle opening is mesothyridid to permesothyridid, i.e. the very tip of the ventral valve is dissolved between the dental plates, leaving an elongate slot through which the pedicle could protrude (Pl. 51, fig. 2*a*, *b*). This tiny slot and the deltidium is only visible in very few specimens due to abrasion of the fragile umbo. In an earlier study it was tacitly assumed that no such foramen and deltidial plates would occur in species related to *U. pila* (e.g. Westbroek 1967, fig. 53). But at that time these structures were only considered from a static and not from a dynamical and functional point of view. A dynamical approach to fossils sharpens the eye for structural observation. Plate 51, fig. 3*a*, *b* shows a typical internal mould of *U. pila* in ventral view. The position of the ventral adjustor scars could not be determined with certainty on the available moulds. The posterior end of the shell, especially of the ventral valve, is very massive, as suggested by the deep excavations of the mould. But the mould shows a strongly jutting knob in the very umbonal part of the ventral valve, between the dental plates. Here, a well-developed pedicle capsule has been accommodated. A sharp transverse line across the knob probably belongs to a scar of the 'median adjustor'. The location of the pedicle capsule and of the foramen suggests that the preferential direction of the pedicle was antero-posterior.

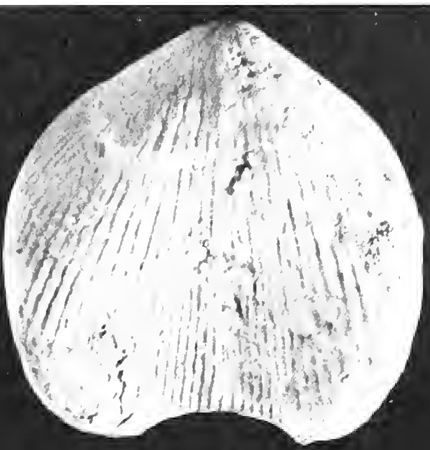
Text-fig. 3 shows the distribution of the orientation of the shells relative to the bedding-plane in the different localities where samples were taken. Also, the distribution of the total number of specimens from Aguasalio and Colle together are given (text-fig. 3*d*). From these graphs it is evident that a large percentage is lying on the pedicle valve (53 specimens, i.e. 37% of the total), and a somewhat lesser percentage on the brachial (20 specimens, 14% of the total). Only 13 shells out of the total of 145 (9%) were lying upside down, i.e. the antero-posteriorly directed 'longitudinal axis' (see above), and thus the umbo, pointed upwards. These shells were not considered in the interpretation of the life position of the animals. Of the 145 shells 54 (37%) were oriented otherwise, and in 26 out of these (18%), the longitudinal axis made an angle of 60° or more with the bedding-plane. The distribution charts display a rather narrow elongated zone from a dorsal, via a vertical, towards a ventral orientation with a marked maximum round a vertical position and minima close to the ventral and dorsal orientations.

In the localities where the sampling was carried out *U. pila* occurs in shaly marls containing abundant fossils and fragments of fossils. At the moment of deposition the sediment must have been a soft mud with many poorly sorted bioclasts. *U. pila* could well be partly buried in the mud and also could adhere with its pedicle to the bioclasts, so that its position was stabilized.

EXPLANATION OF PLATE 51

Figs. 1–3. *Uncinulus pila*. 1*a–c*, ventral, lateral, and frontal views of specimen from Colle, ×4. *a*, shows the subpentagonal outline of the shell; *b*, *c*, relate the uniplicate nature of the commissure with the shape of the shell. A squama is visible in *b*. 2*a*, *b*, morphology of the umbo in two specimens from Aguasalio. The meso- to permesothyridid foramina, the deltidial plates, and a squama are visible. *a*, ×9; *b*, ×7. 3*a*, *b*, internal mould of a ventral valve, collected between San Martín and Ventanilla. Note the jutting knob in the very umbonal part of the valve, very probably corresponding with a well-developed pedicle capsule. ×4·5.

All specimens in Department of Stratigraphy and Palaeontology, Geological Institute, State University, Leiden. Fig. 1*a–c*, W 001; fig. 2*a*, W 002; fig. 2*b*, W 003; fig. 3*a*, *b*, W 004.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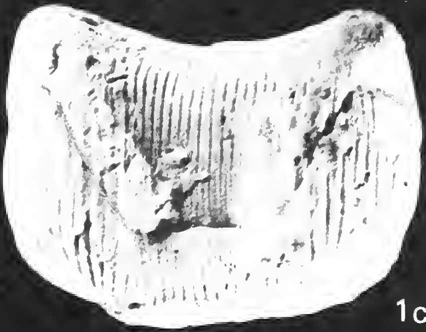
1b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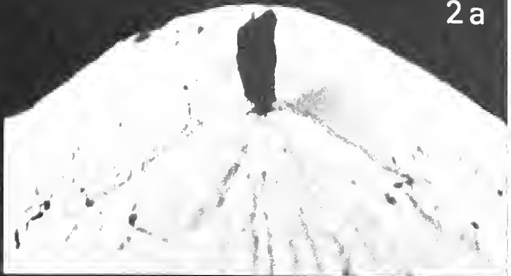
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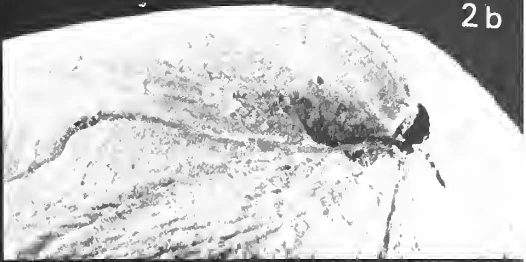
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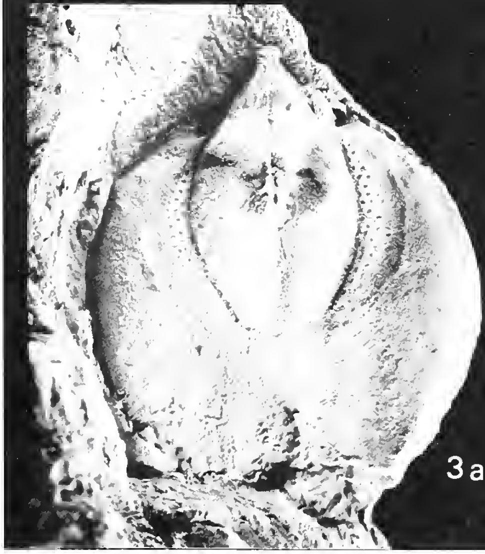
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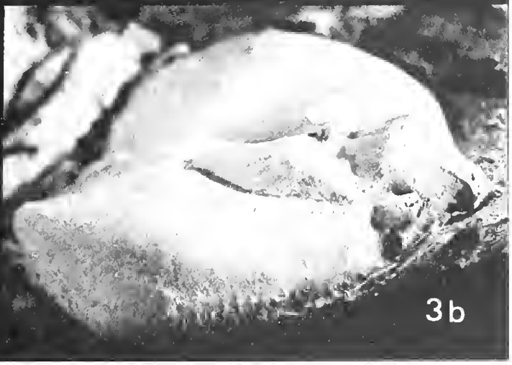
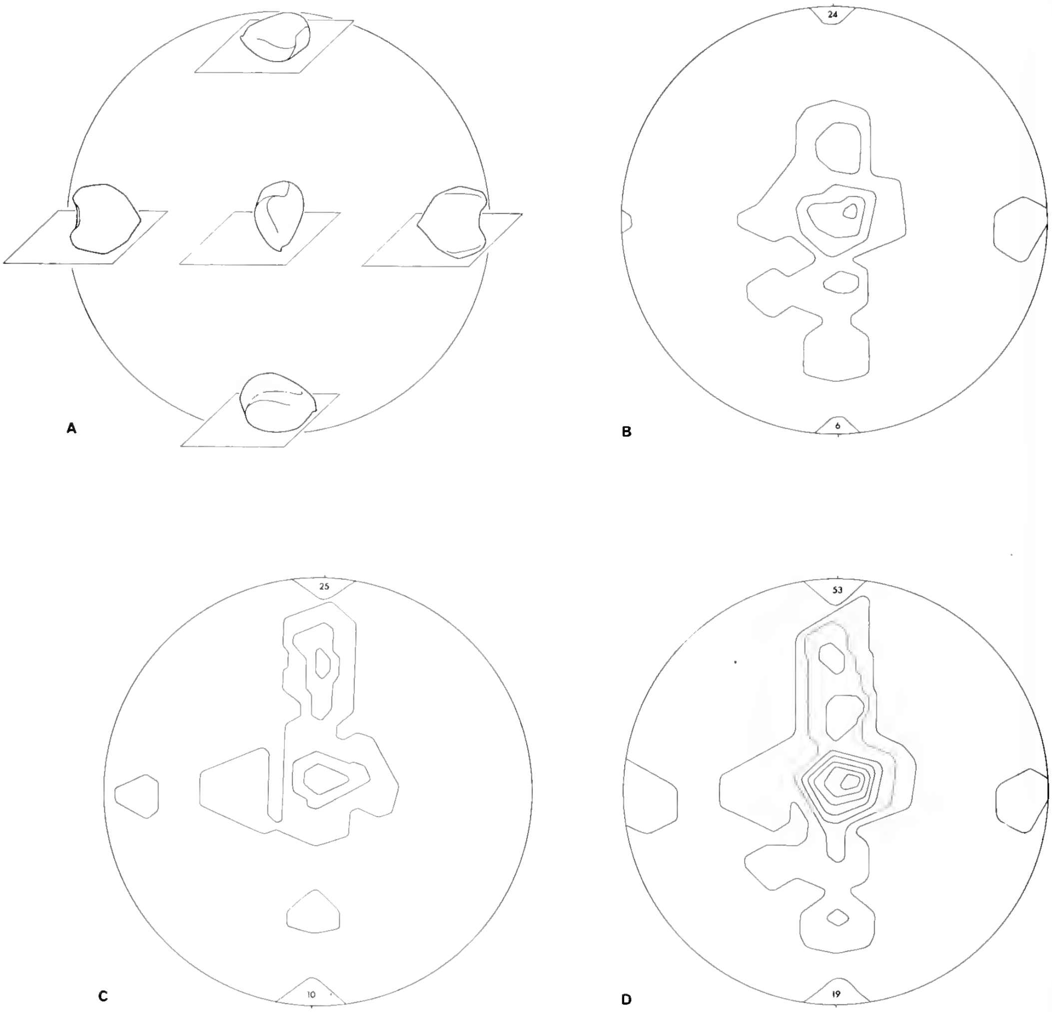

3b

WESTBROEK, NEIJNDORFF and STEL, *Uncinulus pila*



TEXT-FIG. 3. Orientation of shells with respect to the bedding-plane. The lines on the charts connect points where the number of specimens exceeds the values of 1, 3, 5, 7, 9, 11, and 13 per 1% of the total area per chart. For plotting procedure see 'Materials and Techniques'.

A, shows with five examples how the location on the charts must be interpreted with respect to shell orientation.

B, distribution of the orientations of the 61 specimens collected in Aguasalio.

C, distribution of the orientations of the 84 specimens collected in Colle.

D, distribution of the orientations of the 145 specimens collected in Aguasalio and Colle together.

CONCLUSIONS

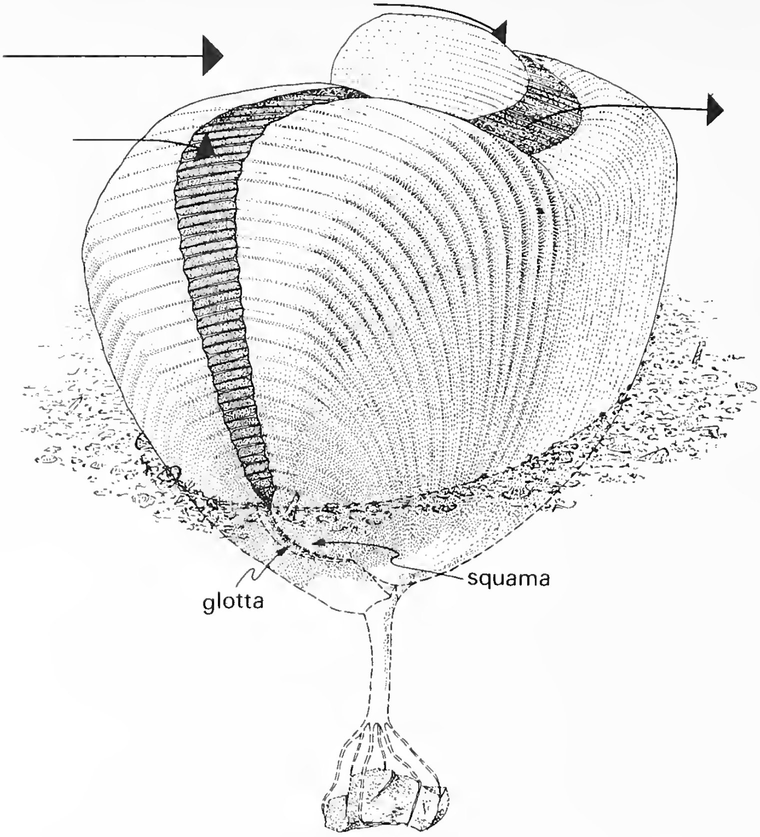
To judge from the shell shape most transported shells will have ended up lying either on the dorsal or on the ventral valve. The most unlikely position would be with the beak downwards. This would be like a top standing on its sharp point without spinning. The pronounced maximum for shells in exactly this position (text-fig. 3) is, therefore, taken to represent specimens in life position. The shells which lie on the valve surfaces are assumed to be transported by streaming water or otherwise. The elongation of the maximum towards the ventral and dorsal positions may be due to incipient post-mortem transport, but it is also possible that this represents *in vivo* deviations from the normal vertical position. Possibly the animals were able to tilt their shells and so to adapt themselves to water currents and other conditions. The fact that so many shells have been preserved in so unlikely a position is considered here as an indication that after death they were kept in place by the surrounding sediment: they must have been partly buried in the mud. Most probably the posterior part of the shell, including the strongly diverging postero-lateral sides of the geniculated region, was stuck in the sediment. This part of the commissure was permanently sealed off from the surrounding medium by the squamae and glottae; the subparallel lateral parts of the commissure could then accommodate the inward stream of seawater. The posterior part of the shell is often strongly thickened and the corresponding shift of the centre of gravity towards the umbo will have helped to keep the shell in this position.

The aforementioned antero-posterior orientation of the pedicle fits in this interpretation remarkably well. Probably the slender pedicle was root-like and adhered to relatively large particles in the sediment, or, in their absence, protruded deep enough into the soft mud to maintain the animal's position and to allow organized reorientations.

By adjusting its position with respect to water currents the animal would have been able to separate the inward and outward water streams most efficiently, as is evident from text-fig. 4. Moreover, the smooth and trough-like sulcus would have smartly funnelled the water stream, thus removing the waste water as efficiently as possible.

The process of geniculation which marks the end of the brephic stage, must have been a complete and sudden reversal in the entire organization of the animal. Apart from a radical change in the direction of shell growth along the valve margins it involved the formation of the marginal spines as a highly effective protective device and a sudden increase in height instead of in width of the spiroloph (Westbroek 1967, p. 36). Weak postero-lateral costae which die out against the squamae and glottae (Westbroek 1967, p. 50) indicate that in brephic individuals the posterior parts of the commissure were not sealed off, so that these young animals cannot have been buried in the sediment with their posterior ends; they must have lived on the dorsal valve instead. So, together with geniculation, a drastic alteration of the animal's orientation must have taken place. It is likely that the orientation of the pedicle was changed accordingly and that the pedicle opening was modified from hypothyridid to submesothyridid by resorption of the tip of the ventral valve between the dental plates.

If our interpretation concerning the life position of *Uncinulus pila* and the correlation with the morphology of the shell is correct, then the presence of squamae and



TEXT-FIG. 4. Interpretation of the life-habits of *Uncinulus pila*.

glottae and a posteriorly directed pedicle opening in other related species may indicate in themselves a similar ecology. In the framework of this publication it was not possible to inspect these characters in more than a few related species. Both *U. subwilsoni* (d'Orbigny, 1850) from the Siegenian Lebanza Formation (Binnekamp 1965), and *U. orbignyanus* (de Verneuil, 1850) from the Eifelian Santalucía Formation are very much like *U. pila* in so far as these relevant characters are concerned. Thus, very probably all three species have behaved similarly with respect to the substratum. The upper Wenlock to Ludlow *Sphaerirhynchia wilsoni* (Sowerby, 1816) which may be regarded as the ancestor of *Uncinulus* (Westbroek, 1967) is remarkably different. Here the posterior part of the gape was not sealed off by squamae and glottae and the position of the pedicle opening was hypothyridid to submesothyridid. Consequently, the shell was probably lying on the dorsal valve and the umbonal part was not buried in the substratum. Thus, this primitive uncinulid behaved like a brephic *Uncinulus* in so far as the orientation of its shell is concerned.

The Permian tetracamerid *Septacamera* Stepanov is a remarkable case of convergence. Grant (1971) described the morphology and the ecology of representatives of this genus. The shell is geniculated and pronounced marginal spines are developed.

The posterior part of the gape was permanently sealed off. The orientation of the shell was vertical and it was maintained in this position by a stout pedicle which protruded through a permesothyridid opening. Unlike *U. pila* the umbo was buried only occasionally. Those widely unrelated taxa must have produced the same morphology and life habits through independent processes of mutation and selection.

The orientation of the fossils in the bedding-plane has been used here as an argument in the ecological interpretation. However, once the vertical life-position of *Uncinulus* is accepted, measurements of the orientation of shells of this genus can be used to estimate post-mortem disturbances of the environment. We estimate, however, that more information must be gathered from other localities and from other species, before the argument can be reversed in this sense into a reliable palaeoecological tool.

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A NEW JURASSIC SCAPHOPOD FROM THE OXFORD CLAY OF BUCKINGHAMSHIRE

by CHARLES PHILIP PALMER

ABSTRACT. A new fossil scaphopod *Prodentalium calvertensis* from the middle Callovian, *Coronatum* Zone, of Calvert, Buckinghamshire, is described and assigned to the genus *Prodentalium*. It is suggested that this essentially Palaeozoic genus ranged into the Mesozoic and was there replaced by *Fissidentalium*, and that the two genera formed an evolutionary sequence.

The association, with *P. calvertensis*, of the foraminiferan *Epistomina* is taken to indicate that these probably formed part of the diet of the scaphopods. Arguments, based on comparative shell morphology of *Prodentalium* and *Fissidentalium*, suggest that *P. calvertensis* lived at a depth in excess of 200 m in the Oxford Clay sea.

STRATIGRAPHY AND LOCATION

The material forming the subject of this report was collected by Mr. Keith Duff (Department of Geology, University of Leicester) from Bed 6 (Callomon 1968, p. 286) in the Lower Oxford Clay at Calvert Pit in Buckinghamshire (G.R. SP 6723).

The bed consists of a light fawny-grey shale lying between two pyritic '*Nucula*' beds and includes ellipsoidal septarian nodules at the top. Callomon (1968) placed this bed in the *Obductum* Subzone of the *Coronatum* Zone, Callovian Stage, and records from it the ammonites *Kosmoceras obductum*, *K. castor*, and *K. gulielmi*. Other fossils occurring in the bed with the scaphopods are: the nuculoid *Mesosacella morrisi* (Deshayes), *Inoceramus* sp., fragments of *Bositra buchi* (Roemer), a small axially ribbed rissoid gastropod, and fish scales. Scattered throughout the bed, and sometimes concentrated into dense patches, are abundant tests of the foraminiferan *Epistomina*.

GENERIC ASSIGNMENT

The small (<15 mm) scaphopods are longitudinally sculptured with numerous unequal, and unsymmetrically placed, riblets. This character relates them to the *Prodentalium–Fissidentalium* group, and distinguishes them from the *Dentalium–Paradentalium–Tesseracme* group which have a symmetrical arrangement of primary ribs, and secondary riblets. None were seen to have an apical notch or fissure, the absence of which indicates a closer affinity with the palaeozoic genus *Prodentalium* with its simple apex, than with the essentially Cainozoic genus *Fissidentalium*, the apex of which is fissured.

These scaphopods are, however, considerably smaller than the average Palaeozoic *Prodentalium*, barely reaching a length of 15 mm; Emerson (1961, p. 467) records some species of *Prodentalium* which reach a length of 200 mm. Nevertheless, in all other respects, these small scaphopods are related by their shell characters to *Prodentalium* rather than to *Dentalium*.

[Palaeontology, Vol. 18, Part 2, 1975, pp. 377–383, pl. 52.]

SYSTEMATIC DESCRIPTION

Genus *Prodentalium* Young, 1942

Type species. Prodentalium reynardi Young, 1942.

Prodentalium calvertensis n. sp.

Plate 52, figs. 1-11

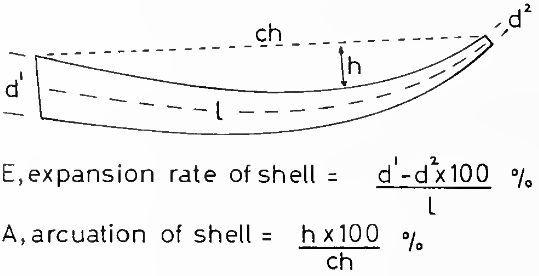
Diagnosis. Small, <15 mm, dentaliid with numerous unequal and unsymmetrically placed riblets, and a simple apex. Differing from palaeozoic species of *Prodentalium* in its smaller size and sharper ribs, and from the Lower Jurassic *Prodentalium*? *liassicum* (Moore) in having about forty-four riblets at the aperture (compared with 'twenty-four longitudinal ridges at rather irregular distances' (Moore 1867, p. 202)).

Material. Eleven moderately well-preserved, but crushed, shells from the Lower Oxford Clay (Callovian) of Calvert, Buckinghamshire.

Holotype. B.M. (N.H.) GG 13330 (Pl. 52, fig. 11). *Paratypes.* B.M. (N.H.) GG 13331-13339 (Pl. 52, figs. 1-10).

Description. The shells, being more or less crushed at the aperture, required that the original diameter be reconstructed from $2W/\pi$ where $W=$ width of crushed shell. It is probable that some of the shells were crushed in a dorso-ventral position so that figures indicating arcuation (text-fig. 1) under column h below are probably more diverse than they would be in an uncrushed sample.

It should be noted that arcuation, as used in this report, is only a rough measure of 'curvature' and not the Curvature of mathematicians; and also the statistics on text-fig. 1 are not identical to those of Henderson (1920) or Fantinet (1959).



TEXT-FIG. 1. Explanation of the terms Expansion (E), and Arcuation (A), as used in this report.

E is the difference between the apertural diameter d^1 and the apical diameter d^2, expressed as a percentage of the length of the tube (l).

A represents the maximum distance from the dorsal surface of the shell to the chord connecting d^1 and d^2, expressed as a percentage of the length of the chord.

EXPLANATION OF PLATE 52

Figs. 1-11. *Prodentalium calvertensis* sp. nov., from Bed 6, Lower Oxford Clay, Calvert Pit, Buckinghamshire. G.R. SP 6723. 1-10, paratypes, B.M. (N.H.) GG 13331-13339; 11, holotype, B.M. (N.H.) GG 13330. Magnifications: 1, 3, 6, *c.* ×5·3; 4, 5, 7-10, *c.* ×6·6; 2, enlarged section of specimen in 1, *c.* ×31.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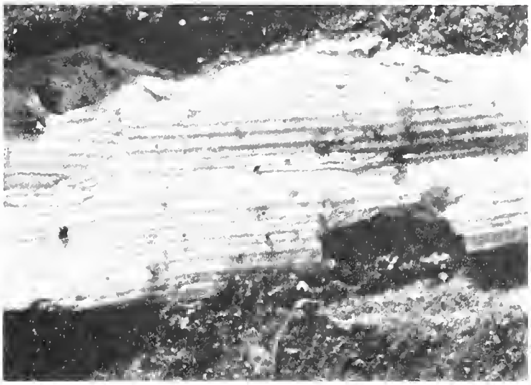
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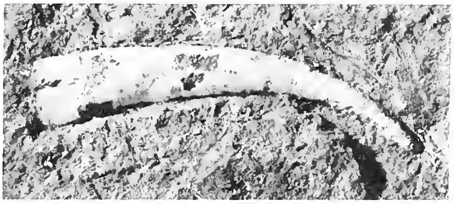
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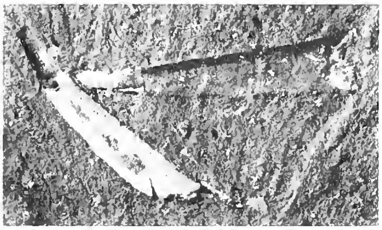
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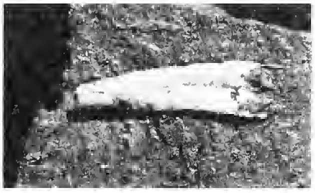
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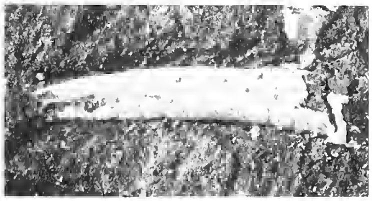
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10


11

PALMER, *Prodentalium calvertensis*

The following table of dimensions in millimetres represents the best readings possible. Key to notation in text-fig. 1.

ch	h	l	d^1	d^2	ribs, increasing to		
7·0	0·7	7·5	0·7	0·4	18	,,	44
6·5	0·5	7·0	0·7	0·4	18	,,	44
8·0	1·0	9·0	0·83	0·4	20	,,	48
7·5	0·4	8·0	0·76	0·3	20	,,	40
7·5	0·3	8·0	0·76	0·3	20	,,	40
8·5	0·8	9·0	0·96	0·4	24	,,	40
5·8	0·3	6·1	0·76	0·4	16	,,	38
14·8	0·3	15·1	0·96	0·3	18	,,	56
7·6	0·5	8·0	0·7	0·3	16	,,	44

Calculations of arcuation yielded a mean figure of A = 7·9%, and the mean of expansion rates was E = 5·1%. The apices were, in all observed cases, simple.

The very fine riblets increase by intercalation so that the density of ribbing remains more or less constant along the length of the tube. The riblets are crossed by lines of growth, about twelve to the millimetre at about 0·7 mm diameter, which run obliquely backward dorso-ventrally. In some specimens these growth lines give the shells a slightly cancellated appearance.

PALAEOECOLOGY

Diet

The scaphopods are randomly distributed, sometimes two to three close together, but usually lying 2–7 cm apart. Associated with them are tests of the foraminiferan *Epistomina* sp. (cf. Barnard 1953, p. 193, fig. A, 7*a–c*) which are more or less evenly distributed except for scattered patches of concentrated tests. These concentrations are often associated with the shells of *P. calvertensis* (Pl. 52, figs. 1, 4, 6, 10) but not always so. The suggestion that these foraminiferans formed the major part of the diet of *P. calvertensis* is supported by the following records.

More than a century ago Clark (1849, p. 323) recorded six forms of foraminiferan from the 'stomach' of *Antalis vulgare* (da Costa) together with the small bivalve *Kellia suborbicularis* (Montagu) and juvenile *Goodalia triangularis* (Montagu). Jeffreys (1882, p. 658) stated that the 'stomach' of *Antalis vulgare* was a 'repertory of littoral Foraminifera' but did not specify which species they were. Pilsbry (*in* Pilsbry and Sharp 1897, p. vi) described the captaculae as '-prehensile, catching foraminifera, etc., upon which the Scaphopod feeds'. Morton (1959, p. 232) recorded four genera of Foraminifera from the proboscis of *Antalis entalis* (Linné), these being *Elphidium*, *Quinqueloculina*, ?*Discorbis*, and the empty test of *Globigerina*. These records alone confirm that scaphopods are basically carnivorous and will take Foraminifera when they are available.

Dinamani (1954) observed the feeding habits of *Dentalium conspicuum* Melville, and described how the animals used their captaculae to carry organic matter to the proboscis. Although he reported no foraminiferans from the stomach and intestines of the animals he studied he did observe 'large diatoms, single algal cells, and unidentifiable particles of detritus'. He described in detail how the captaculae transport, along ciliated tracts, deposit-particles which accumulate just inside the mantle fringe in a longitudinal furrow on the dorsal side of the foot. Some selection takes place here, probably by the frilly lips of the proboscis, and acceptable food particles pass into the proboscis and thence into the stomach. Dinamani's final observation may also explain the patches of concentrated foraminiferan tests associated with *P. calvertensis* in the Oxford Clay. 'Periodically the foot is withdrawn completely, the mantle fringe is drawn across the aperture and a small mass of rejected matter is found to accumulate near the anterior pallial pore, which is pushed out by the foot during its next emergence' (Dinamani 1954, pp. 3–4).

In collecting Foraminifera it seems probable that the 'conveyor-belt' system described by Dinamani is not very selective and that some empty tests must accumulate on the foot of the scaphopod, together with live material. Selection then results in transference of live specimens, or acceptable material, into the proboscis; but as Morton recorded an empty test of *Globigerina* in the proboscis of one of his animals it is clear that the selection is not infallible. However, Dinamani's observations seem sufficient to support the suggestion that the concentrated accumulations of foraminiferans associated with *P. calvertensis* are simply those empty tests of *Epistomina* collected by the captaculae and finally ejected by the foot.

Depth

A hint as to the depth at which these scaphopods lived in the Oxford Clay sea is offered by comparative shell morphology. The argument is tenuous and the conclusion no more than a low probability.

Modern ribbed dentaliid scaphopods (excluding *Antalis* and *Graptacme*) may be divided into two categories; *Dentalium* (s.s.), *Tesseracme*, and *Paradentalium* which have a symmetrical arrangement of primary and secondary ribs and riblets; in contrast *Fissidentalium*, *Compressidentalium*, and *Compressidens* have an unsymmetrical arrangement of many unequal riblets. The first group is usually found at depths which, in round figures, range between 20 m and 2000 m (Pilsbry and Sharp 1897, pp. 1–30). The second group, with which the fossil *Prodentalium* must be associated, is generally found between 200 m and 2000 m (Ludbrook 1954, pp. 99–102). These figures suggest that *P. calvertensis* may have lived in the Oxford Clay sea at depths of at least 200 m.

EVOLUTION

According to Emerson (1961, p. 466, and fig. 2) the genus *Prodentalium* ranges from the Devonian to the Permian, while *Fissidentalium* ranges from the Cretaceous to Recent; today some forty-four species of the latter are found in relatively deep waters in the Atlantic and Indo-Pacific provinces. Both genera are characterized by having numerous unsymmetrically placed riblets; *Fissidentalium* is distinguished by the development of a long apical fissure. Study of these two genera strongly suggests that they are more closely related to each other than to, say, *Dentalium* (s.s.), *Tesseracme*, or *Paradentalium*; and that *Prodentalium* was probably ancestral to *Fissidentalium*.

Adoption of this view is frustrated by a gap during the Triassic and Jurassic periods. Of the sixteen described species of Triassic scaphopod known to me none have the characteristic ribbing of the *Prodentalium*–*Fissidentalium* group. However, in the

Jurassic two forms have it and these are '*Dentalium*' *liassicum* Moore and *Prodentalium calvertensis*; the former is from the lower and the latter from the upper Jurassic. These two examples indicate that a *Prodentalium–Fissidentalium* sequence is possible and might be given equal consideration with Emerson's *Prodentalium–Dentalium* sequence which is outlined below.

Emerson (1961, p. 463) expressed the view that 'the available data indicates the development of two major lines of descent, namely *Plagioglypta–Fustiaria* and *Prodentalium–Dentalium* sequences'; he also suggests that the latter sequence may be linked by the genus *Antalis*. No quarrel is offered against a *Plagioglypta–Fustiaria* sequence except that the present writer has expressed the view (1974) that Emerson's taxon '*Fustiaria* sensu lato' is better regarded as of the family Laevidentaliidae. On the other hand, the sequence *Prodentalium–Dentalium* presents many difficulties since the type species of *Prodentalium* has about 80 irregular and unsymmetrically placed riblets, while the type species of *Dentalium* has about 10 symmetrically placed ribs with concave interspaces. These differences, not only in the number of ribs but also in their character, are considerable and consequently a *Prodentalium–Fissidentalium* sequence is here suggested as an alternative. The type species of *Fissidentalium* has about 26 riblets at the apex increasing to about 75 irregular riblets at the aperture. It seems to differ from *Prodentalium* only in the presence of an apical fissure and appears a more likely direct descendant than *Dentalium*.

If this view is correct then it is relatively easy to derive the symmetrically ribbed scaphopods, centered on *Dentalium*, from the *Prodentalium–Fissidentalium* sequence somewhere in the late Cretaceous or early Palaeogene without the embarrassment of *Antalis* acting as an intermediate between *Prodentalium* and *Dentalium* during the Mesozoic. The type species of *Antalis* is *Dentalium entalis* Linné (Emerson 1961, p. 470), a Recent, virtually smooth, species with an apical notch and living in northern British waters. It is not easy to apply the genus *Antalis* to fossil scaphopods earlier than the Cainozoic. Below the Palaeocene partly or faintly ribbed scaphopods resemble *Antalis* only very remotely and reference of these to that genus is probably incorrect.

CONCLUSIONS

The genus *Prodentalium* ranges beyond the Palaeozoic and at least into the Jurassic. The probability that a *Prodentalium–Fissidentalium* sequence gave rise to *Dentalium* and allied forms in the late Cretaceous is here offered as an alternative to Emerson's postulated *Prodentalium–Dentalium* sequence.

Prodentalium calvertensis probably had the foraminiferan-eating habit of many living scaphopods and it is suggested that it may have lived at a depth in excess of 200 m in the Oxford Clay sea.

Acknowledgements. I thank Mr. Keith Duff for bringing this interesting material to my notice and allowing me to describe it, and also to Dr. C. G. Adams of the B.M. (N.H.) for determining the foraminiferan associated with the scaphopods.

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ARJAMANNIA, A NEW UPPER ORDOVICIAN-SILURIAN PLEUROTOMARIACEAN GASTROPOD FROM BRITAIN AND NORTH AMERICA

by JOHN S. PEEL

ABSTRACT. A new genus, *Arjamannia*, is proposed to accommodate five pleurotomariacean gastropod species from the Upper Ordovician–Silurian of Britain and North America. *A. aulangonensis* sp. nov. is described.

PLEUROTOMARIACEAN gastropods of the extinct family Lophospiridae Wenz, 1938 commonly form a conspicuous element in Lower Palaeozoic gastropod faunas. The occurrence of three lophospirid species with a distinctive reticulate ornamentation, in the Arisaig Group of Nova Scotia, has prompted the description of a new genus, *Arjamannia*, to include these, and other species from the Upper Ordovician and Silurian of Britain and North America.

The type species, *Arjamannia cancellatula* (M'Coy *in* Sedgwick and M'Coy 1852), was originally described from the Lower Llandovery Mulloch Sandstone of Girvan, Ayrshire, but Longstaff (1924) subsequently reported the species also from the Middle Llandovery of near by Newlands. In addition, *A. cancellatula* is currently recorded from the Lower Llandovery Beechhill Cove Formation of Arisaig, Nova Scotia.

Arjamannia thraivensis (Longstaff, 1924) from the Upper Ordovician (Ashgill) Drummock Group of Girvan appears to be the earliest species of *Arjamannia*. In the Silurian (Llandovery), *Arjamannia* is represented by *A. cancellatula*, *A. woodlandi* (Longstaff, 1924) from Britain and Nova Scotia, and *A. inexpectans* (Hall and Whitfield, 1875) from the Brassfield Limestone of Ohio, U.S.A. *A. aulangonensis* sp. nov., from the Doctors Brook Formation (Wenlock) of Arisaig, Nova Scotia, is the youngest known representative of the genus.

SYSTEMATIC PALAEONTOLOGY

The following abbreviations are used in the text: Sedgwick Museum, Cambridge (SM); U.S. National Museum of Natural History, Washington D.C., U.S.A. (USNM).

Class GASTROPODA Cuvier, 1797
Superfamily PLEUROTOMARIACEA Swainson, 1840
Family LOPHOSPIRIDAE Wenz, 1938
Subfamily RUEDEMANNIINAE Knight, 1956
Genus ARJAMANNIA gen. nov.

Type species. Murchisonia cancellatula M'Coy *in* Sedgwick and M'Coy 1852.

Derivation of name. For Arja, arbitrarily combined in the style of the related *Ruedemannia* Foerste, 1914. Feminine.

[Palaeontology, Vol. 18, Part 2, 1975, pp. 385–390, pl. 53.]

Diagnosis. Ruedemanniinid gastropods with reticulate ornamentation and a tendency to develop a conical or subconical spire.

Description. The shell is turbiniform, commonly with a conical spire and adpressed whorls. The base is convex and globose such that the apertural height in many species may constitute more than half of the total height, though in the type species it is rather less. There is no umbilicus but the curvature of the base may produce a shallow pseudo-umbilicus. A true slit is present generating a convex selenizone which typically carries a strong median cord. Ornamentation is reticulate with many sharply defined, closely spaced, spiral lirae and transverse growth lines. A prominent spiral cord is commonly developed on the upper whorl surface but is often reduced or absent in late growth stages. The shell is usually thick, its structure unknown.

Discussion. *Arjamannia* most closely resembles *Ruedemannia* Foerste, 1914 from which, however, it is readily distinguished by its reticulate ornamentation. *Lophospira* Whitfield, 1886 similarly lacks reticulate ornamentation and is further delimited by the absence of a well-developed selenizone of the type seen in *Arjamannia* and *Ruedemannia*.

Arjamannia cancellatula (M'Coy *in* Sedgwick and M'Coy 1852)

Plate 53, figs. 1–5, 7

1852 *Murchisonia cancellatula* M'Coy *in* Sedgwick and M'Coy, pp. 292–293, pl. 1L, fig. 20, 20*a*.
1924 *Lophospira cancellatula*; Longstaff, pp. 419–420, pl. XXXIII, figs. 1, 2.

Holotype. SM A34829, Mulloch Sandstone, Lower Llandovery (Silurian), Mulloch Quarry, Dalquorhan, Girvan, Ayrshire.

Other figured material. SM A34830, same locality as holotype. USNM 169484, Beechhill Cove Formation, Lower Llandovery, from USNM Collection 10114, shore 2050 ft north-east of McGillivray Brook, Arisaig, Nova Scotia (Boucot, *et al*. 1974, pl. 3). USNM 169480, USNM 169483, and USNM 188523, Beechhill Cove Formation, Lower Llandovery, from USNM Collection 10115, McGillivray Brook, 50 ft upstream of contact with underlying Bears Brook Volcanic Group, Arisaig, Nova Scotia (Boucot *et al*., 1974, pl. 3).

Description. Type species of *Arjamannia* gen. nov. with about five whorls. Spire

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EXPLANATION OF PLATE 53

Figs. 1–5, 7. *Arjamannia cancellatula* (M'Coy *in* Sedgwick and M'Coy 1852). 1–4, Beechhill Cove Formation, Arisaig, Nova Scotia, silicon rubber impressions. 5, 7, Mulloch Sandstone, Girvan. 1, USNM 169480, upper whorl surface of gerontic adult, ×2. 2, USNM 169483, ×2. 3, USNM 169484, lateral view showing selenizone, ×3. 4, USNM 188523, juvenile, ×2·5. 5, SM A34830, paratype, ×1·5. 7, SM A34829, holotype, ×1·5.

Figs. 6, 8. *Arjamannia thraivensis* (Longstaff, 1924). USNM 208893, Drummock Group, Girvan, silicon rubber impression, ×1.

Figs. 9–11, 16. *Arjamannia inexpectans* (Hall and Whitfield, 1875). USNM 85063, Brassfield Limestone, Ohio, ×1·5.

Figs. 12, 13. *Arjamannia aulangonensis* sp. nov. USNM 169469, holotype, Doctors Brook Formation, Arisaig, Nova Scotia, ×2. 12, silicon rubber impression showing selenizone. 13, internal mould.

Figs. 14, 15. *Arjamannia woodlandi* (Longstaff, 1924). USNM 188521, Beechhill Cove Formation, Arisaig, Nova Scotia, silicon rubber impression, ×1·5.

Specimens coated with ammonium chloride.


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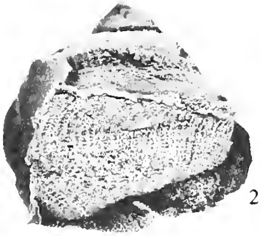
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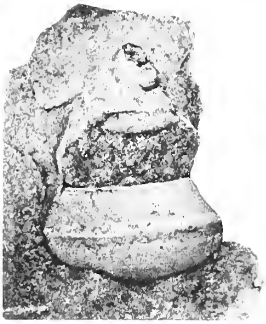
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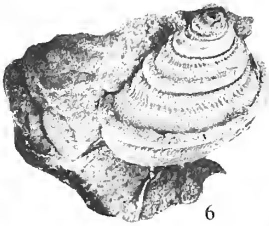
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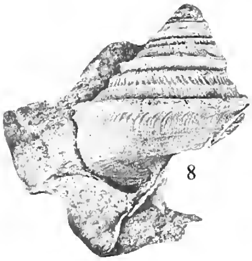
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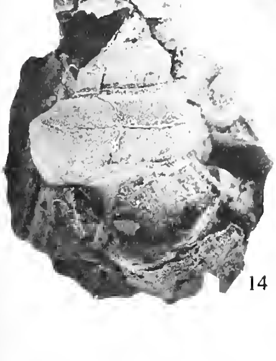
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PEEL, *Arjamannia*

conical with adpressed whorls; whorl embracement at periphery of previous whorl, commonly covering the peripheral selenizone. Peripheral angulation at midwhorl dividing whorl profile into upper whorl surface, above, and convex base, below. Upper whorl surface steeply inclined; divided into two shallowly concave surfaces in early growth stages by a prominent spiral cord half-way between selenizone and suture; reduction in relief of cord in later growth stages producing a flattening of the surface as a whole. Whorl initially vertical below selenizone but increasing in curvature to form inflated base; pseudo-umbilicus shallow. Aperture subquadrate; growth lines prosocline on upper whorl surface at about sixty degrees to the suture before curving backwards into the slit of unknown depth; growth lines curving forwards on vertical whorl surface below selenizone prior to passing radially, with slight forward concavity, across base and into pseudo-umbilicus. Selenizone convex between bordering cords; ornamentation of numerous concave lunulae crossed by a median spiral cord. Shell ornamentation of spiral lirae and growth elements of equal size intersecting to form a fine reticulation with small nodes at the intersections; a prominent spiral cord is commonly present on the upper whorl surface. Shell seemingly thick; structure unknown.

Discussion. The holotype of *A. cancellatula* (Pl. 53, fig. 7) is a rather poor internal mould with parts of four whorls preserved. The earlier whorls have a rounded profile but a strong peripheral angulation at midheight of the final whorl delimits the convex base from the flat, inclined, upper whorl surface. A paratype (SM A34830, Pl. 53, fig. 5) preserves the reticulate ornamentation. No stronger spiral element is seen on the final whorl in this paratype but at least one stronger cord is present on the upper surface of the penultimate whorl.

One of the major sources of variation in *A. cancellatula* is the exact position of whorl embracement. This may vary from below, to just above, the whorl periphery. In the former case the perfection of the conical spire is lost but all details of the selenizone in early whorls may be seen. In the latter, linear sutures and a conical spire are produced and the selenizone may be partly or completely covered by the following whorl.

A fragment from the Lower Llandovery Gasworks Mudstone of Pembrokeshire, SM A32393, can possibly be referred to *A. cancellatula*.

Arjamannia thraivensis (Longstaff, 1924)

Plate 53, figs. 6, 8

1924 *Lophospira thraivensis* Longstaff, pp. 420–421, pl. XXXIII, figs. 5, 6.

Figured material. USNM 208893 from the Drummock Group, 'Starfish Bed', Ashgill (Ordovician), South Threave, Girvan, Ayrshire.

Discussion. This species, figured and described by Longstaff (1924), is characterized by the presence of well-developed reticulate ornamentation only on the base of the whorls. Longstaff (1924) noted that the upper whorl surface has only two strong, and one fine, spiral elements. Other species of *Arjamannia* develop many fine spiral threads on the upper whorl surface although a strong spiral element is also typically present.

A. thraivensis is apparently the earliest species of the genus but the poorly known

Pleurotomaria turrita Portlock, 1843, from the Ordovician of Tyrone, N. Ireland, may belong here.

Arjamannia inexpectaus (Hall and Whitfield, 1875)

Plate 53, figs. 9–11, 16

1875 *Pleurotomaria inexpectans* Hall and Whitfield, p. 117, pl. 5, fig. 12.
1923 *Lophospira* (*Ruedemannia*?) *inexpectans*; Foerste, pp. 96–99.

Figured material. USNM 85063 from the Brassfield Limestone, Middle–Upper Llandovery (Silurian), Whippoorwill Church, north-east of West Union, Ohio, U.S.A.

Discussion. A full description of this species was given by Foerste (1923) but the only published figure is the inadequate original illustration of Hall and Whitfield (1875). The figure and accompanying description were based on two specimens in the collection of U. P. James of Cincinnati. Dr. K. E. Caster (University of Cincinnati; written communication, 1970) believes that this collection was probably donated to the Cincinnati Society of Natural History, whose collections are now located at the University of Cincinnati. However, the specimens have not been found in the relevant collection and are apparently lost. The figured specimen is from collections made by A. F. Foerste, now located in the U.S. National Museum, and is labelled 'typical'.

Arjamannia inexpectans is distinguished from *A. cancellatula* by its greater incremental angle of eighty degrees, compared to the sixty degrees of the latter species, and by its shorter spire and more inflated base.

Arjamannia aulangonensis sp. nov.

Plate 53, figs. 12, 13

Holotype. USNM 169469 from the Doctors Brook Formation, Wenlock (Silurian), in USNM Collection 10919, Doctors Brook, Arisaig, Nova Scotia (Station U64 of Boucot *et al.* 1974, pl. 5).

Description. Species of *Arjamannia* gen. nov. with at least four whorls. Spire conical with adpressed whorls covering the peripheral selenizone of earlier whorls and the lower margin of the selenizone of the penultimate whorl. Upper whorl surface steeply inclined with strong spiral cord at just above midheight. Lower whorl surface uniformly convex, external features unknown. Aperture subquadrate; inner and basal lips unknown; growth lines prosocline on upper whorl surface before curving backwards into a slit of unknown depth. Selenizone relatively wide, shallowly convex between two bordering threads; ornamentation of regularly spaced concave lunulae crossed by a median groove, the edges of which are marked by fine spiral striae. Shell ornamentation composed of a reticulation of equally developed spiral lirae and growth elements with small nodes at intersections. Shell seemingly thin but thickened at the sutures due to the whorl adpression; structure unknown.

Discussion. *Arjamannia aulangonensis* is distinguished from *A. cancellatula* and *A. inexpectans* by its wider selenizone with a median groove. In the latter two species, from the Llandovery, the selenizone is narrow with a strong spiral cord. *A. thraivensis*, from the Upper Ordovician, lacks the well-developed reticulate ornamentation on the upper whorl surface, characteristic of all the Silurian species of *Arjamannia*, and also has a strong spiral cord on the selenizone. The subsutural thickening of the shell associated with the adpressed whorls in *A. aulangonensis* is well illustrated by comparing the silicon rubber impression of the external mould of the holotype (Pl. 53, fig. 12) with the natural internal mould of the same specimen (Pl. 53, fig. 13). The angulation at midwhorl height in the internal mould indicates the position of the selenizone which occurs at just above the suture with the following whorl in the rubber impression.

In addition to the holotype, *A. aulangonensis* is known only from a few poor fragments in the same collection.

Arjamannia woodlandi (Longstaff, 1924)

Plate 53, figs. 14, 15

1924 *Lophospira woodlandi* Longstaff, p. 418, pl. XXXIII, fig. 7*a*, *b*.
1939 *Lophospira woodlandi*; Pitcher, pp. 88–89, pl. II, figs. 1–4.

Figured material. USNM 188521, from the Beechhill Cove Formation, Lower Llandovery (Silurian), in USNM Collection 10819 from Wallace Brook, Pictou County, Nova Scotia (Geological Survey of Canada 'open file' locality map after Harper 1973).

Discussion. Arjamannia woodlandi is distinguished from other species of *Arjamannia* by its greater sutural indentation and lack of adpressed whorls. In this respect, there is similarity in form with many species of *Lophospira* Whitfield, 1886 but the well-developed selenizone and reticulate ornamentation justify placement within *Arjamannia*. The figured specimen from Nova Scotia (Pl. 53, figs. 14, 15) has a more shallowly inclined upper surface than specimens illustrated by Pitcher (1939) from the Upper Llandovery of Shropshire, and is a little taller than wide. The Shropshire specimens, and the original specimens of Longstaff (1924) from the Middle Llandovery of Girvan, are reportedly slightly wider than tall. Ornamentation is poorly preserved in the figured specimen from Nova Scotia due to abrasion.

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INTERRELATIONSHIPS OF EARLY TERRESTRIAL ARTHROPODS AND PLANTS

by P. G. KEVAN, W. G. CHALONER *and* D. B. O. SAVILE

ABSTRACT. At the dawn of terrestrial life some remarkably close interrelationships between arthropods, vascular plants, and fungi existed and promoted co-evolutionary developments which, in the same or analogous forms, have since remained fundamental in the functioning of ecosystems. The fossil record and hypotheses on phylogenies are examined in terms of functional morphology. Spore-eating and disseminating arthropods existed at the same time as the spores of terrestrial plants and fungi became more diverse and obtained characters indicative of protection from and/or dissemination by arthropods. An appendix discusses other aspects of the functional morphology of spores. Arborescence and structures on the stems of plants precede the arrival of alate arthropods, and may have been initially protective. Subsequent events indicate a dispersal role of those features for the insects and the spores they carried. Further evidence suggests that the first terrestrial arthropods were the cause of lesions described from Devonian plants. Such lesions could then have become sites for fungal and other infections. The parasitic, first terrestrial fungi show similar protective and dispersal relations with arthropods as those shown by vascular plants.

'IT would seem probable that the first step in the evolution of true insects from some marine form of Arthropod was taken through an ecological association with the special group of plants which first made good their footing on the dry earth; most probably the Arthropods fed on the plants, and evolved with them, changing their mode of life and their forms as their food plants changed theirs' (Tillyard 1928). And, in reference to the earliest known fossil arthropods of the Devonian, 'one can conceive of forms like *Peripatus* living under rocks . . ., one can admit that scorpions may have lurked in the crevices, Thysanura may have run or jumped about there, and Collembola and Acarina may have worked amongst the debris as they do today' (Tillyard 1931, p. 82).

These two quotations were chosen as they point out the speculative nature of endeavours such as this work, suggest a possible close interrelationship of the terrestrial arthropods and the plants on which they lived (1928), and, paradoxically a non-specific dependence of these arthropods on detritus (1931), while at the same time suggesting that ecological connections of arthropods and plants were established as soon as the former started colonizing dry land.

Other workers, notably Bekker (1947), Taugourdeau Lantz (1971), Smart and Hughes (1973), have indicated similar relationships of early terrestrial arthropods, particularly Collembola, with detritus and with spore feeding. It is even suggested that those arthropods had an important role in spore dispersal, not only for vascular plants (Taugourdeau Lantz 1971) but also for fungi (Bekker 1947).

This paper explores in greater detail the possible interrelationships of arthropods, vascular plants, and fungi at the time when the process of the colonization of the land was just beginning, about 400×10^6 years ago. Evidence to suggest some complex interactions at the advent of co-evolution in terrestrial organisms is drawn from functional interpretations of structure found in Devonian fossils, from analogous modern phenomena, and from assessments of proposed phylogenies.

[Palaeontology, Vol. 18, Part 2, 1975, pp. 391-417, pls. 54-56.]

ARTHROPODA

Ghilyarov (1956, 1959, and earlier) and Manton (1973) propose that the origins of terrestrial Atelocerata (myriapod–insect line) was through minute skin-breathing annelids, or possibly Onychophora which left the water to inhabit damp soil litter. An onychophoran, *Aysheaia pedunculata* Walcott, which grew to about 50 mm is known from marine deposits of the middle Cambrian (Walcott 1911; Hutchinson 1930), and the possibility of even earlier Onychophora exists (cf. Moore 1959). In the soil, increased abrasion and friction necessitated the development of a tougher integument and strong locomotory appendages. This led to the myriapod condition, which was modified by the reduction in the number of legs in accordance with the greater importance of the forelimbs in crawling through narrow passages in the soil. No matter whether the origins of the terrestrial Atelocerata was through Crustacea (Sharov 1966, p. 60) or as described above through Annelida and Onychophora (Tiegs and Manton 1958; Manton 1964, 1969, 1973; Mackerras 1970), myriapods are considered closely related to the hexapods.

Evolution of Chelicerata to the terrestrial habit presumably took place independently of that of Atelocerata. They first appear to have been marine scorpion-like creatures (Aglaspida) which seem closely related to the Eurypterida (sea scorpions) known from Cambrian time. The origins of terrestrial Chelicerata (Arachnida) seem equally ancient (Størmer 1955).

The early arrival of apparently predatory chelicerates on land in the Devonian (see p. 393) indicates that there was probably terrestrial prey at that time. Presumably there were numerous subterranean annelids, other metazoa, and protozoa on which early air-breathing arthropods preyed, and of which we have no fossil record. Another possibility is that at least some early air-breathing arthropods were amphibious, or that at least some were not predators. More will be said of this later.

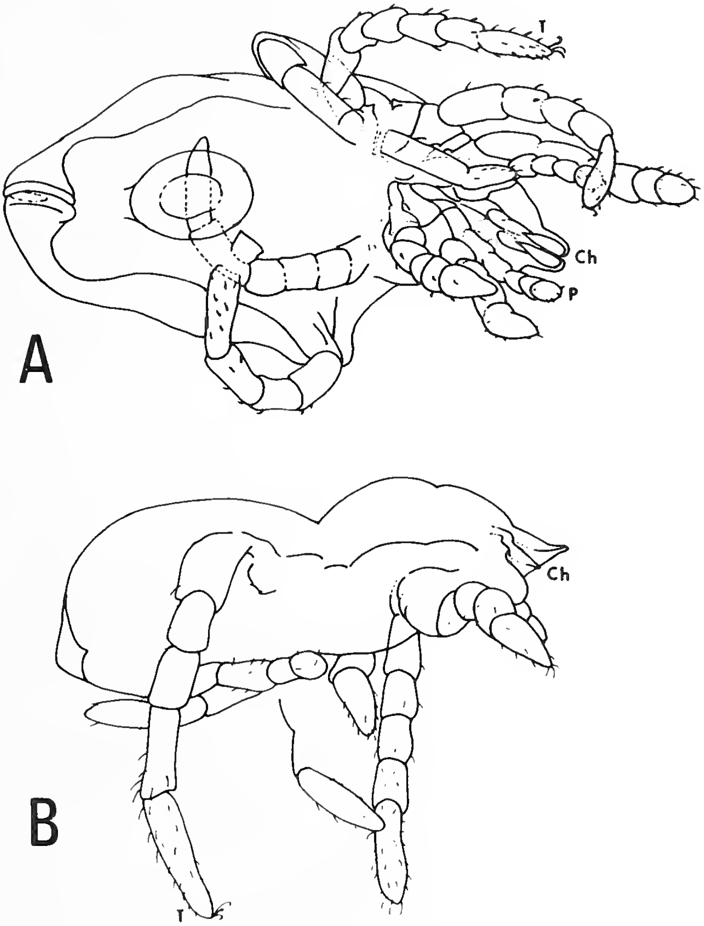
Fossil record and plant relationships

Unfortunately, the fossil record for terrestrial animals in the Devonian and earlier is very sparse. The earliest record is that of myriapods: *Archidesmus loganensis* from the Llandovery/Wenlock (Silurian) and *A. macnicoli* and *Kampecaris* spp. from the Lower Devonian Old Red Sandstone (Peach 1882, 1898; Crowson *et al.* 1967) (text-fig. 4*m*). Hoffman (1969) suggests that there is reason to suspect that some Palaeozoic myriapods were aquatic or semi-aquatic. On the basis of fragmented specimens it is known that the first genus grew in excess of 5 cm and the second 2 cm. Sharov (1966, p. 61) and Hoffman (1969) indicate that these animals (Archipolypoda) are close to Diplopoda, Pauropoda, and Chilopoda, but they provide no additional clue to their relationships with the Hexapoda. Most myriapods (Symphyla, Pauropoda, and Diplopoda) feed on plant debris; only the Chilopoda (centipedes) are carnivorous, and almost exclusively so, being equipped with poison fangs. It is logical to suppose that the fangs developed by specialization of a pair of segmental appendages of the ancestral group to which the above-mentioned fossils seem to belong (Sharov 1966, pp. 61–67; Manton 1969; Hoffman 1969).

What little we know of other Devonian terrestrial arthropods is mainly derived from the Rhynie Chert of early Old Red Sandstone age in Aberdeenshire, Scotland.

The age of this important occurrence is probably Siegenian/Emsian (see discussion in Chaloner 1970). Arthropod fossils have been described by Hirst (1923), Hirst and Maulik (1926), Tillyard (1928, 1931), Scourfield (1940*a*, *b*), Petrunkevitch (1953, 1955), Crowson *et al.* (1967), and others. Tasch (1957) has discussed aspects of the palaeoecology of the aquatic arthropods.

Hirst (1923) describes an assemblage of Chelicerata of which *Palaeocteniza crassipes* (Araneae?) and *Palaeocharinus* spp. and *Palaeocharinoides hornei* (now referred to Trigonotarbida: Palaeocharinidae) are all small (less than 3 mm), apparently predatory terrestrial animals (see also Petrunkevitch 1953, 1955). Hirst also described a mite (text-fig. 1), *Protacarus crani*, which was thought to resemble



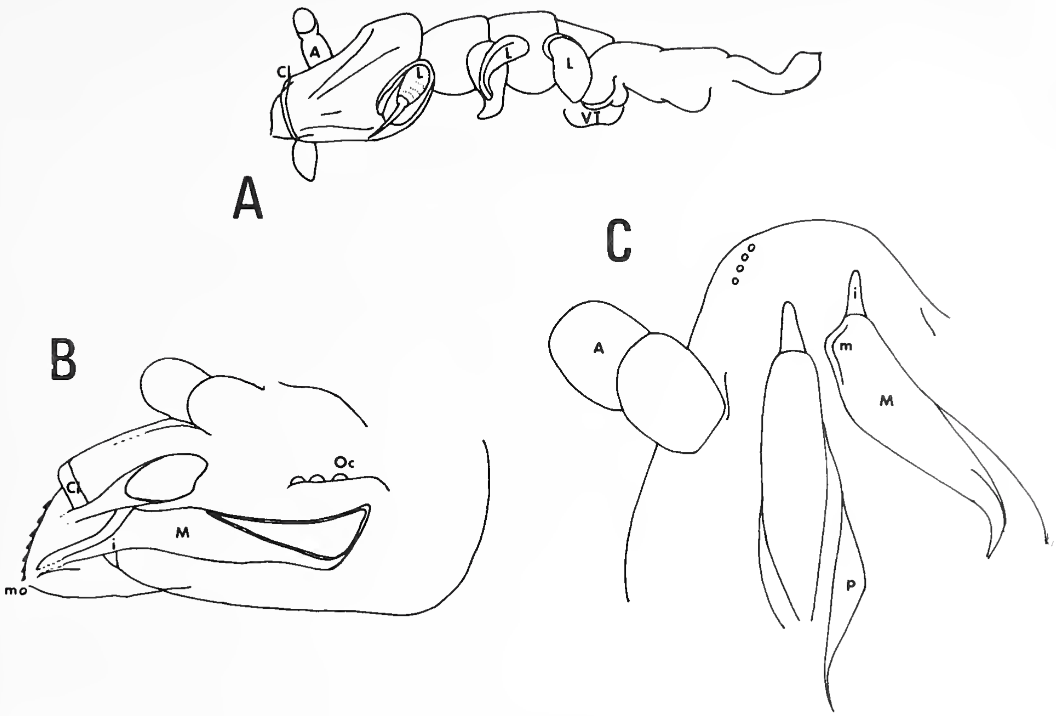
TEXT-FIG. 1. *Protacarus crani* Hirst. A, ventral aspect of *P. crani* (?) (from Hirst 1923) body length 448 μm. B, lateral aspect (from Hirst 1923) body length 310 μm. (By permission of the *Journal of Natural History*, Taylor and Francis, Ltd., London.) Explanation of lettering: *Ch*, chelicerae; *P*, pedipalp; *T*, tarsus showing the three well-developed claw-like setae.

modern running mites (Eupodidae) (Petrunkevitch 1955), but which is now regarded as being most closely attributable to the Pachygnathidae (cf. Krantz 1970, p. 144; Zakhvatkhin 1952), primitive mites which commonly live in forest litter. The fossils of *P. crani* range from 290 μm to 400 μm and apparently had strongly cutinized and pointed tips to their two-segmented chelicerae (see text-fig. 1A). Their pedipalpi were slender. These stylet-like mouthparts suggest that the animals fed on small particulate matter, or perhaps more likely pierced plant or animal tissue to imbibe liquid through the wound (see below). It is almost impossible to say more about their possible diet because of the lack of preservation of internal organs, and almost nothing is known of the diets of modern Pachygnathidae (Krantz 1970, p. 144). The body of *P. crani* may have been covered with fan-shaped setae and the legs had short, curved spines (text-fig. 1).

Hirst and Maulik (1926) described some other animals from the same formation, the first being a minute chelicerate, '*Crania*' *rhyniensis*. (It should be noted that '*Crania*' as used here requires a new name, and is not the inarticulate brachiopod genus.) The second description is of the collembolan, *Rhyniella praecursor* (text-fig. 2), which excited much interest as the oldest known fossil insect (although modern works separate Collembola from Insecta). *R. praecursor* was 1–2 mm long. Its mandibles are reminiscent of those of the Machilidae (Thysanura *s. l.*) in having well-separated molar and incisor regions. Text-figure 2B and C show the weakly developed molar region and the well-developed incisor region, which Scourfield (1940*b*) shows as more elongate than Tillyard (1928) indicates. Massoud (1967) shows some finer details of the mouthparts. Collembola are generally herbivorous or saprophagous (Christiansen 1964). The lack of a well-developed molar area indicates that *R. praecursor* did not eat material needing mastication. Possible foodstuffs include soil micro-organisms, spores, and plant juices obtained through puncture wounds (cf. *P. crani*) (see p. 400 below), although for the latter habit the mandibles do not resemble the piercing type of modern collembolan mandibles.

The affinities of *R. praecursor* are discussed by Tillyard (1928) on the basis of heads only. His conclusions are amended by Scourfield (1940*a*, *b*) on the basis of additional more complete specimens. *R. praecursor* has traits of both Hypogasturidae and Entomobryiidae, so Scourfield suggests that it be placed in the family Protentomobryiidae erected by Folsom (1937) for fossil Collembola from Cretaceous amber. Massoud (1967) and Delamare Deboutteville and Massoud (1967) remark on the similarity of *R. praecursor* to a modern family of Collembola, Neanuridae, which is sometimes considered as part of the Hypogasturidae. Crowson (1970) found this similarity so striking that he suggested that these 'Devonian' fossils of terrestrial animals could be 'modern contaminants'. Both Hypogasturidae and Entomobryiidae are well-known pollen (Kevan and Kevan 1970) and spore (Christiansen 1964) eaters.

Hirst and Maulik (1926) also illustrate some mandibles, which they do not name. Tillyard (1928) describes them under the name *Rhyniognatha hirsti*. Illustrations in both works are similar, but not identical. The mandibles are reminiscent of the sharp bladed and toothed jaws of a carnivore. Tillyard (1931) hints that they may be thysanuran and Hirst and Maulik suggest they may be larval. The former suggestion does not seem probable and the latter is unlikely as it would require the existence of holometabolous insects in the Devonian.



TEXT-FIG. 2. *Rhyiella praecursor* Hirst and Maulik. A, head, thorax with legs (L) and three abdominal segments; 'probably a cast skin' (from Scourfield 1940*a*, *b*). Length of entire animal probably about 1·5–2·0 mm. B, head capsule showing mandibles (M) and other features (from Scourfield 1940*a*, *b*). C, head capsule showing mandibles (M) with well-developed incisor region (i) and less-developed molar region (m). Length of head capsule from apex to end of the pedical of hypopharynx (p) is 314 μm (from Tillyard 1928). (A, B, by permission of *Nature*, Macmillan Journals Ltd., London and the *Proceedings of the Linnean Society*, London, Academic Press Inc., London. C, by permission of the Royal Entomology Society of London.) Explanation of lettering: A, antenna; Cl, clypeus; i, incisor region of mandible; L, leg; m, molar region of mandible; M, mandible; mo, mouth; Oc, oceilli; p, pedical of hypopharynx; VT, ventral tube.

It is curious that the preponderant fossil arthropods from the Rhynie Chert are apparently carnivores. These carnivores are also very small and presumably would be unable to tackle an animal as large as the myriapods which must have existed contemporaneously, if not in the same habitat (cf. Calman *in* Horne *et al.* 1920). It is unlikely that the assemblage of predators subsisted on Collembola and mites alone. Presumably a soil fauna of soft-bodied protozoa and small metazoans would have evolved in association with algae, fungi, and bacteria which must have preceded vascular plant colonization of the land. No fossil record of such fauna could be expected. It is reasonable to suppose that these perishable organisms may be the missing element in the food web (as it is represented in the fossil assemblage) on which the carnivorous arthropods were predators. If this is so, the arthropods preserved in the Rhynie Chert could be quite unrepresentative of the fauna which actually lived there at the time, in both numbers and species diversity. Possibly, at least some of the supposed predators were also facultative herbivores; presumably they could have fed on plant saps and possibly spore protoplasts. Dr. W. D. I. Rolfe (pers. comm. May 1974) has discovered that 'a significant number of Rhynie trigonotarbid arachnids are preserved as fragments within empty sporangia of *Rhynia major* [see Pl. 56, fig. 3]. Another assemblage occurs within a stem fragment [Pl. 56, figs. 1, 2]. Whether such arthropods actively selected this micro-environment for feeding, as a temperature, humidity, or windspeed control, or whether they were swept in by post-mortem winnowing is unknown.' From the relatively unsorted state of the Rhynie plant material the latter mechanism seems the least plausible. We prefer to regard these arthropods within the sporangia and stem fragments as occupying a site into which they had moved in life, perhaps following spore-eating. This is of some interest, particularly because pollen and spore feeding is associated with the predatory habit, and evolution herefrom, in a large number of insect groups and in some mites. Another possibility is that some of the predators were amphibious, feeding in water and returning to land to evade the larger aquatic predators, i.e. the reverse of what happens now in most cases. In circumspection, it is reasonable to assume any combination of the above possibilities in considering the development of a diversity of ecological niches.

It appeared that the next stage of insectan evolution was exemplified by Rodendorf's (1961) finding of a fossil fragment from the late Devonian as a somewhat movable wing of an insect, which he called *Eopterum devonicum* (Eopteridae). The same author (Rodendorf 1970) described another Devonian fossil, *Eopteridium*, also in the Eopteridae, but later (Rodendorf 1972) he writes that eopterids are not insects but are eumalacostracan Crustacea. Despite this setback to a convenient theory it can be presumed that such primitive insects must have arisen at about the time indicated (text-fig. 4*p*) and that they were herbivores which climbed on to vegetation to feed (cf. Sharov 1966, pp. 117 *et seq.*; Crowson *et al.* 1967; Smart 1963, 1971; Smart and Hughes 1973). By the end of the Devonian, arborescent plants had become common (text-fig. 4*l*). Hocking (1957) writes that almost immediately, geologically speaking, following the development of tall plants the first winged insects appeared. Certainly increased humidity in the forests would have provided conditions more tolerable and more stable for evolution of above-ground dwelling arthropods. However, there is a gap of 50 million years from the upper Devonian until the base of the upper Carboniferous when 'winged' insects appear in the fossil record (cf. Riek 1970; Crowson *et al.* 1967). Those 'wings' or paranotal lobes could have functioned as gliding planes for descending insects (Hinton 1963; Flower 1964) either in escape or after feeding. Regarding the latter, Smart (1971) notes that a feature of plants of that time is stems with small up-pointed scale-like leaves or non-vascularized spines: such stems were probably easily ascended, but not easily descended. It is possible that spines and other enations which characterize several early land plant genera served to offer a readily climbed pathway for spore-gathering arthropods which would give such spines an adaptive significance beyond the mere increase in photosynthetic area, which is usually invoked. In contrast Chaloner (1970) suggests that spines on stems of some Devonian plants (e.g. *Psilophyton* spp.: Siegenian) may have been glandular, possibly with a secretion making them unpalatable to terrestrial invertebrates. These spines would afford protection for elevated sporangia from arthropods. The apparent paradox in the above reflects only that similar structures could have different functions on different species or even in different stages of the same species. Other authors have suggested that such spines might have been an adaptation to a scrambling habit of growth. Spines generally are characteristic of at least two distinct groups of early Devonian plants, and they disappeared before the end of the Devonian (although glandular hairs with swollen tips are present in some Carboniferous pteridosperms); whereas scale-like leaves continue to modern times (text-fig. 4*j*). In the Carboniferous insect fossils become diverse, and their relationships with each other and with plants are beyond the scope of this paper (but see Hughes and Smart 1967; Smart and Hughes 1973).

TRACHEOPHYTA

The colonization of the land by plants is usually construed in terms of the rise of vascular plants. Although diversification of these tracheophytes must have affected the first major modification of the land as an environment for animal life, relatively simple plants (algae, fungi, bacteria) must have long preceded vascular plants at least in certain restricted habitats. All three of these groups have a long Pre-Cambrian history (Schopf 1970) and by the Devonian, as now, they must have constituted a significant microflora in suitable sites such as the intertidal zone, the sides of streams, and any terrestrial environments with impeded drainage. Presumably a soft-bodied microfauna of which we have no fossil record would have developed in such habitats. Early land-adapted arthropods might have been foragers on such a terrestrial fauna. The hypothesis of the existence of a pre-vascular land flora gains support from the diversity of early non-vascular land plants. The existence of stiff, upright plants apparently lacking vascular tissue is established for the early Silurian (Schopf *et al.* 1966) and possibly earlier (e.g. Fleming and Rigby 1972). There is a considerable diversity of non-vascular thalloid plants with a cuticle-like covering and resistant spores within the Devonian (*Foerstia*, *Parka*, *Spongiophyton*—see Lang 1945; Kräusel 1960). They are mentioned here merely to suggest that comparable non-vascular plants may have preceded the earliest tracheophytes, and that the pre-Devonian land surface was perhaps not as barren of plant life as the lack of fossil vascular plants might suggest.

Although some authors have claimed to recognize vascular plants in pre-Silurian rocks (e.g. Axelrod 1959) none of these show the criteria which are highly correlated with vascular plants (viz. xylem elements, cuticle with stomata, or spores with a triradiate suture) and as such, they are not generally accepted as vascular plants. It is still fair to say that no pre-Downtonian (pre-late Silurian) fossils are generally accepted as unequivocal vascular plants. None the less, it is clear that a number of Devonian plants showed adaption to life on land (a cuticle, resistant spores) although lacking xylem, so that there was a sizeable element of non-vascular land plants accompanying the early tracheophytes.

In this review we are not concerned with all morphological features in which evolutionary changes can be traced in early terrestrial plants, but only with those which have a direct bearing on other organisms. These may be thought of in general terms as the production of erect vegetative organs, culminating in the arborescent habit; production of leaves or comparable organs in which phloem is accessible to suitably adapted sap-feeding arthropods; and finally, spore-bearing organs and adaptations of spore size and sculpture in connection with arthropod feeding and transport of spores.

Vegetative organs, arthropods, and pathology

One of the earliest land floras of which we have detailed anatomical knowledge is still the Rhynie Chert flora, first described by Kidston and Lang (1917, *et seq.*). Recent additions to our knowledge of this flora, notably from the work of Lyon (1964) are reviewed in Høeg (1967) and Banks (1970). The probable age of this flora is now regarded as late lower Devonian (see discussion in Chaloner 1970) rather than the middle Devonian usually attributed to it. This flora shows at least two distinct lines of vascular plants (Psilopsida, and a Lycopsid forerunner) in addition to some non-vascular land plants (Lyon 1962) and both green and blue-green algae (Kidston and Lang 1921*b*; Croft and George 1959).

Foodstuffs synthesized in the subaerial chlorophyllous tissues of plants, and transported in the form of sap, represent a nutritive (and vulnerable) plant product from the standpoint of arthropod life. Recent work of Satterthwaite and Schopf (1972) has shown that tissue surrounding the xylem in *Rhynia* has features suggestive of sieve areas, thus supporting the supposition of Kidston and Lang and later authors that this tissue represents the site of phloem-equivalent (see text-fig. 4*k*). The relative proximity of this tissue to the plant surface and hence to sap-sucking arthropods (as discussed above) is evident. The Rhynie plants significantly show a number of lesions of the surface, evidently inflicted while they were alive (Pl. 54, figs. 1–4), since in some cases surrounding tissue shows growth response. Most show associated fungal activity (Pl. 54, figs. 5, 6), which seems more likely to have followed than to have caused the lesion, and which could well have been initiated by sap-sucking animals disseminating the spores (cf. modern examples in Leach 1940; Stakman and Harrar 1957).

Kidston and Lang (1921*a*, p. 834) noted these injuries to the axes, and commented: '. . . another feature which is clearly pathological must be briefly described. A considerable number of the stems show dark necrosed areas extending more or less deeply from the epidermis, in other specimens the dark necrosed mass is wanting or has more or less completely disappeared leaving a larger or smaller cavity. . . . The feature of special interest is the behaviour of the cells abutting on the necrosed area

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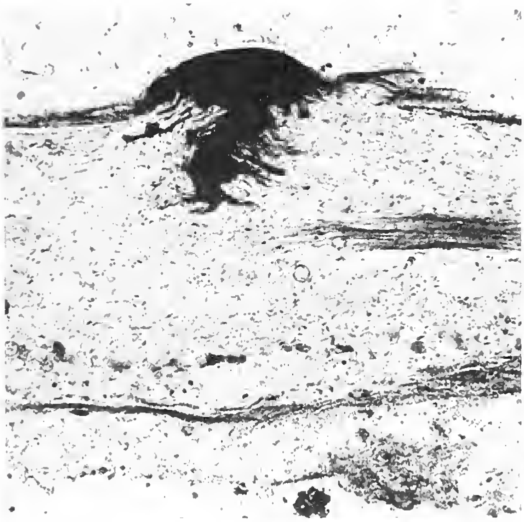
EXPLANATION OF PLATE 54

Figs. 1–6. Axes of *Rhynia* showing various types of ?injury (lower Devonian, Scotland). 1, oblique longitudinal section of axis showing lesion extending to level of vascular tissue, more or less plugged with opaque organic matter, ×50. 2, transverse section of axis showing more extensive damage extending to vascular strand, ×30. 3, axis with enlarged (?traumatic) cortical cells, and associated opaque substance in the intercellular spaces, ×30. 4, transverse section of axis showing peripheral ?lesion with plug of opaque matter, ×40. 5, 6, cavity seen in longitudinal section of an axis, associated with growth of fungal hyphae and ?reproductive structures, 5×120; 6×40.

All slides in the Palaeontology Department, British Museum (Natural History), London. Fig. 1, slide no. V.57834; figs. 2, 3, V.57833; fig. 4, V.57838; figs. 5, 6, V.57832.

PLATE 54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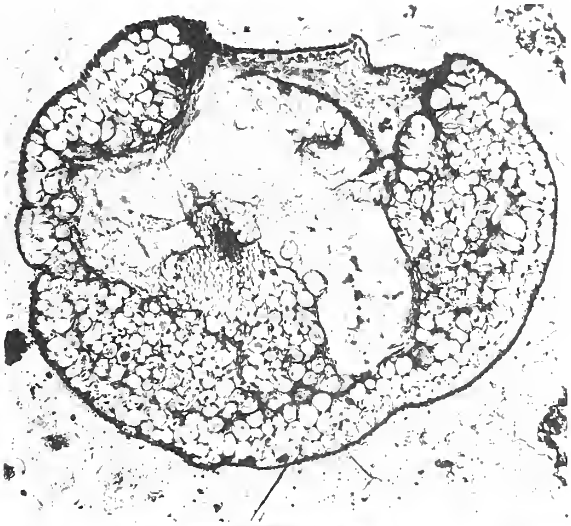
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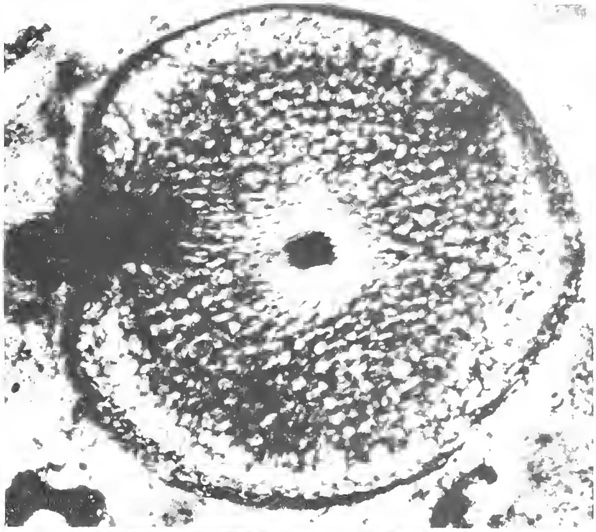
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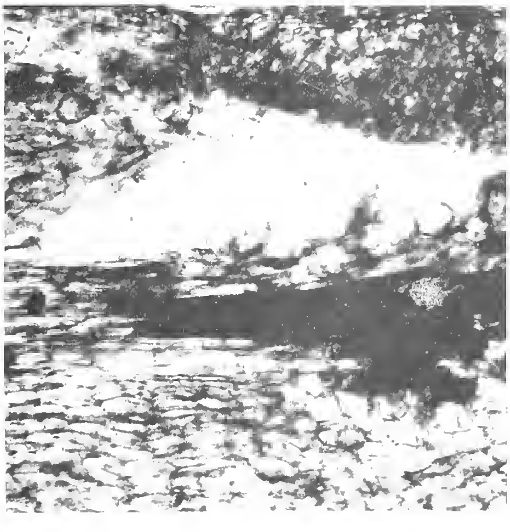
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KEVAN, CHALONER and SAVILE, *Rhynia*

or bounding the cavity; . . . the cells . . . frequently show evidence . . . of an active cell division that can without doubt be interpreted as a wound reaction.'

They speculate (1921*b*, p. 895) that these wounds may be 'a reaction to some prolonged external stimulus' and invoke 'the volcanic conditions that accompanied the supply of siliceous water'. Tasch's work (1957) casts doubt on this speculation. An alternative possibility is that the injury to the plant axes had an organic cause (attack by some animal—arthropod or otherwise).

Three rather different types of injury may be distinguished in *Rhynia* axes, which have no evident causal relationship with invasion by fungi (whether saprophytic, parasitic, or symbiotic—see Kidston and Lang 1921*b*; Boullard and Lemoigne 1971). Firstly, there are areas of disturbed tissue, in which some cells show abnormal enlargement associated with in-filling of intercellular spaces with opaque organic material (Pl. 54, fig. 3). This situation suggests a traumatic response by the plant to physical injury, which must, then, have occurred while the plant was still alive. Penetration of the plant tissue by an arthropod or other metazoan is one way in which this could have occurred.

The possibility that such injury could have been caused by toxic gases or other volcanic products, invoked by Kidston and Lang, seems inappropriate in this case, since damage is both internal (as seen in a single plane of section) and very local.

Rather different injuries (Pl. 54, figs. 1, 3) appear to represent plugs of opaque organic matter in fissures or lesions extending from the outer surface to the region of the phloem-like tissue at the periphery of the stele. In each of the two cases figured, black plugging material seems to be derived from (*Rhynia*) plant tissue, suggesting its formation while the axis was still alive. However, a fungal (or other, pathogenic) origin cannot be ruled out. Here again, however, the possibility of these lesions representing sites of attack by sap-feeding arthropods can reasonably be sustained.

Finally, there are cases of more extensive injury to axes which are hard to visualize as having been caused by any volcanic phenomenon. That shown in Plate 54, fig. 2 suggests injury possibly caused by some organism; at least, it is hard to reconcile such structure with some kind of physical event.

Whereas none of these three types of injury can be regarded as unambiguous evidence of damage by arthropods or other animal agency, all three could be more readily explained in these terms rather than as a result of any purely physical cause.

Smart and Hughes (1973) emphasize the role of bark thickness in controlling accessibility of sap to insects. 'Phloem close to the outer surface of plant stems suited to the hemipteran proboscis appeared only with the Cordaitales' (Carboniferous). it seems more likely that arthropods were able to gain access to phloem strands in leaves of Lycopsids and soft (barkless and fibreless) stems of leafless psilosids as early as the Lower Devonian, as is suggested by the damaged Rhynie axes.

Spore structure and arthropods

Spores showing a clear triradiate germinal suture appear as fossils early in the Silurian period (Llandovery: see Owens and Richardson 1972). The triradiate mark on such Silurian spores (see Pl. 55, fig. 2; text-fig. 4*a*) can be regarded as evidence of spore formation in a tetrad, presumably following a meiosis; as such it indicates spore formation as part of a life cycle involving alternation of haploid and diploid phases. It does not, of course, prove the existence of vascular plants, since bryophytes and certain extinct supposedly land-adapted algal groups (e.g. *Protosalvinia*, *Foerstia*) produced resistant triradiate spores. Even so, the diversification of spore types in the Silurian and Devonian closely parallels that of vascular plants (see Chaloner 1970) and the latter may reasonably be assumed to be the source of most triradiate spores of that period. Putative triradiate spores, showing this tetrad marking with varying degrees of clarity, have been claimed from pre-Silurian strata (see Chaloner 1960; Schopf 1969; Gray and Boucot 1971, 1972; and Boureau and Moreau-Benoit 1972). Late Silurian diversification of spore wall structure was fairly restricted, only eleven 'spore genera' being recognizable by the close of the Silurian (Chaloner 1970; Owens and Richardson 1972; Richardson and Ioannides 1973). Silurian spores show relatively simple development of exine ornament (text-fig. 4*e*, *f*, g), being either smooth with an equatorial thickening (Pl. 55, fig. 2) or having a papillate or ribbed ornament (see Silurian and early Devonian examples in Pl. 55, figs. 2, 4, and 9). Presumably these exine features are related to spore dispersal by physical forces such as wind or water, or to protection from harmful radiation or drying, or both dispersal and protection (see appendix).

Within the early Devonian spore morphology and sculpture types show increasing diversity so that by the end of the early Devonian (Emsian) fifty-five 'spore genera' are recognized (text-fig. 4). Within this period, mean spore size shows a steady increase so that the Silurian spores typically less than 50 μm diameter are succeeded by assemblages with individual spores rising to 100 μm by the Siegenian and to 200 μm by the end of the early Devonian (text-fig. 4*b*, *c*, *d*). This appears to represent the inception of heterospory, as a clear segregation of larger megaspores from smaller miospores follows in the middle and late Devonian (Chaloner 1967). Later Devonian spore exines show increasing elaborations in developing separation of exine layers (perinate, cavate, saccate, or pseudosaccate of various authors' usages: Pl. 55, figs. 1, 3, and 8) and sculpture types ranging from apiculate to reticulate ornamentation of various types (Pl. 55, figs. 5 and 8) and spines (Pl. 55, fig. 3) including forms with grapnel-like terminal hooks (Pl. 55, fig. 7; text-fig. 4*e*–*i*).

It is unlikely that such developments in spore structure were without function. Much energy is involved in the formation of a highly ornamented spore wall, at least in fungi where this has been studied by Savile (1954). Certainly all wall ornamentations increase the surface:volume ratio, and if close together, reduce over-all density by causing the formation of a thicker boundary-layer of air than in smooth spores, so increasing the buoyancy of the spore in air (Stokes's Law). Savile (1954) says that decoration on rust spores is clearly an aid to dispersal, and is often, at least, an advanced character (p. 705), and 'sculpturing serves both to give the spore added buoyancy when it is airborne and to increase its chances of being transported by insects or other small animals' (p. 738). He also points out that small spore-feeding animals must contend with nearly nutritively valueless wall material to assimilate nutritive protoplasm. Hence spines, wall thickening, etc., can function as protective structures against attack. Wall decoration can also be correlated with other features concerning dispersal (see appendix).

Many of the same arguments can be employed in ascribing function to exine sculpturing on pollen. Muller (1970) suggests evolutionary trends in angiosperm pollen, starting from simple gymnosperm types as exemplified by *Cycas* and *Ginkgo* and retained in a few angiosperm (*Magnolia* and *Degeneria*) and proceeding to more and more complex types of grains. Although Muller does not consider the functional significance of ornamentation, the scheme he presents can be thought of as broadly paralleling those of Chaloner (1970) and Savile (1954). Anemophilous plants tend to have small, rounded, smooth, rather thin-walled, dry pollen grains with furrows shallow or absent; whereas pollen of zoophilous plants tends to have thicker, ornamented walls with associated oil or wax (Eames 1961). It is clear that elaborations of angiosperm pollen exines are also associated with their carrying highly labile substances, involved in the stigma reaction on arrival of the pollen at its destination (Mattson *et al.* 1974). These substances may have an incidental or derived role as attractants or 'reward' for insect vectors, as distinct from that of the flower bearing them, or the cytoplasmic contents of the grain. Compositae show the greatest amount of exine sculpturing, and in this group Wodehouse (1935) shows a series of retrograde simplifications of exine sculpturing correlated with the reversion to anemophily.

Spines on pollen grains can also be considered as protective as they make eating the pollen grain or its protoplast more difficult for small animals. Also decorations add structural support which would be more appropriate on a spore being manipulated and transported by animals.

On a larger scale, similar adaptions can be seen on seeds: protective spiny sheaths, retrorse hooks, barbs, and spines for dispersal by animals; wings for wind dispersal, etc. (Stebbins 1971).

Returning to similar features of Devonian spores: long spines appeared on lower Devonian spores (Gedinnian) such as those of *Grandispora* and *Spinozonotriletes* (text-fig. 4*h*). Other processes and verrucosity may have functioned similarly and aided in dispersal. Of particular interest are the grapnel-hooked spores such as those of *Ancyrospora*, *Hystricosporites*, *Nikitinsporites*, and *Densosporites* (e.g. *D. devonicus* and *D. lysii*). It is noteworthy that these middle and upper Devonian spore genera, divergent in other aspects, all show these grapnel-shaped spines (cf. Pl. 55, fig. 7;

EXPLANATION OF PLATE 55

Figs. 1–9. Devonian and Silurian spores, illustrating various types of morphology and sculpture. 1, *Rhabdosporites langi* Richardson (middle Devonian, Russian platform). Saccate, with fine sculpture on the saccus surface, ×500. 2, *Ambitisporites avitus* Hoffmeister (Silurian (?Downtonian), North Africa). Smooth, with an equatorial thickening, ×1000. 3, cf. *Grandispora* sp. (middle Devonian, southern England). Spiny ornament on outer layer of a cavate exine, ×500. 4, *Streelispora newportensis* (Chaloner and Streel) Richardson and Lister (early Devonian, South Wales). Papillate sculpture, ×1350. 5, *Dictyotriletes perlotus* Naumova (upper Devonian, Turnford Borehole, southern England). Reticulate ornament, ×650. 6, *Hymenozonotriletes* sp. (middle Devonian, Russian platform). Broad equatorial flange ('zona'), with ornament, ×250. 7, scanning micrograph of grapnel-shaped spine of *Hystricosporites* (upper Devonian, Wyboston, England), ×1500. 8, *Geminospora* sp. (middle Devonian, Russian platform). Minute conical spines on outer layer of cavate exine, ×1000. 9, *Emphanisporites pseudoerraticus* Richardson and Ioannides (Silurian (?Downtonian), North Africa). Proximal annular thickening and radiating ribs, ×1260.

Figs. 1, 2, 6, 8, 9, slides in Palaeontology Department, British Museum (Natural History), London. 1, 6, 8, V.57835; 2, V.57836; 9, V.57837. 4, 5, slides in the Palynological Collection of the Institute of Geological Sciences, Leeds. 4, PF3239; 5, MPK 521. 3, slide in the Mortimer Collection (Geology Department, University College, London) RE 276/4. 7, specimen stub not preserved.


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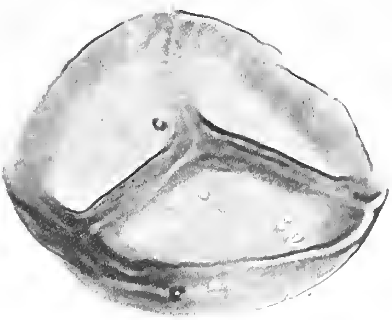
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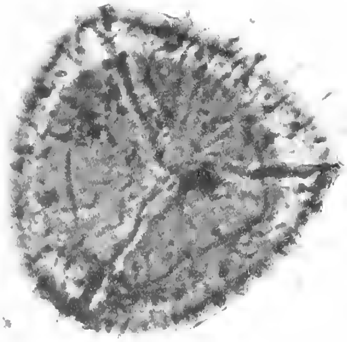
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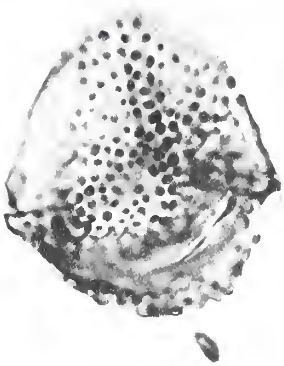
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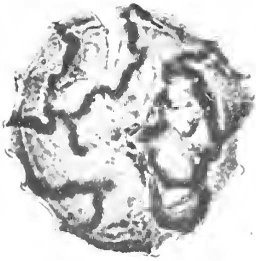
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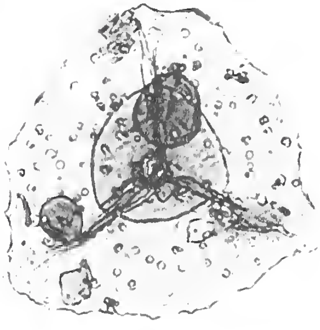
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KEVAN, CHALONER and SAVILE, Devonian and Silurian spores text-fig. 4*i*). This strongly suggests some common selective pressure. The processes are quite far apart in proportion to the (relatively large) diameter of the spores. Such processes could afford protection but would seem to add little buoyancy. The most evident explanation is that these spores were dispersed by arthropods by becoming attached to the setae by the retrorse hooked processes. As has been shown, arthropods likely to have effected such dispersal are known from considerably earlier formations. In fact, Taugourdeau Lantz (1971) writes on the role of insects in Devonian spore dispersal saying: '. . . Ils (Les Collemboles) trouvaient donc leur pâture dans le sous-bois dévoniens et leur rôle pour la dispersion de spores et la colonisation d'espaces vierges est probable, et a dû s'exercer dans des régions variées puisque à l'heure actuelle, ils supportent des températures extremes de −13° à +38° C et qu'ils vivent aussi bien dans la zone de balancement des marées qu'à plus de 5000 m d'altitude . . .' (p. 63). Taugourdeau Lantz shows that spores with grapnel spines show a maximum diversity (in species number) at about the Frasnian stage (late Devonian).

Modern Collembola have been shown to carry spores (Collinge 1910), and to defecate undigested and viable fungal spores (Bekker 1947) similarly as have mites (Griffiths *et al.* 1959; Mignolet 1971) and other soil animals (Talbot 1952) (see p. 395). Occasionally Devonian spores are found showing globules of tapetal residue adhering to the exine, and not apparently forming part of the regularly arranged sculptural elements (cf. Chaloner 1963). It is possible that these represent tapetal material analogous to the 'pollen kit' of entomophilous angiosperms and having some role in relation to insect transport. Normally one might not expect to find spores so freshly preserved as to display such droplets.

Heterospory and arthropods

Megaspores (i.e. those over 200 μm, Chaloner 1967) start appearing in the Emsian, and by the upper Devonian there are clearly defined occurrences of mega- and microspores (text-fig. 4*d*). By the Carboniferous insects were already diverse and Hughes and Smart (1967) and Smart and Hughes (1973) suggest some relationships arthropods may have had in evolution of protected ovules, and pollen and spore dispersal. Faegri and van der Pijl (1970) hint at and document the importance of insects in pollinating of modern Cycadales and Gnetales respectively (see also Leppik 1960).

Thus it seems that some relationship between the evolution of insects and heterospory might be postulated for some groups of plants even in the Devonian. Indeed, if arthropods visited the sporangia (either microsporangia, megasporangia, or clusters of both, as in *Archaeopteris*) to feed on spores or secretions, then spore dispersal

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EXPLANATION OF PLATE 56

Figs. 1–3. Fragments of trigonotarbid arachnids within cavities of plants in thin sections of Rhynie chert. 1, 2, arachnids within stem fragments, cf. *Rhynia* sp. Note chalcedonic 'spirit-level infill' of arachnid in fig. 1, 1×11; 2×16. 3, arachnids inside empty sporangium of *Rhynia major* Kidston and Lang. Note fragments of characteristic prismatic sporangium wall structure at the top centre, and top right, ×19.

All slides in the Kidston Collection, Hunterian Museum, Glasgow University. 1, slide no. 2497; 2, no. 2488; 3, no. 2446.

Plate by Dr. W. D. Ian Rolfe.

KEVAN, CHALONER and SAVILE, Rhynie chert would be encouraged. Any adaptation by the spores to make them attractive to arthropods, to adhere to them, or to enable them to retain viability while passing through the gut, would increase the efficacy of the spore-dispersal process. Heavy, large spores with hooks or other processes could be carried by arthropods on the ground further than by air currents, which are naturally reduced close to the ground and in forest.

As the degree of heterospory progressed through later Devonian time, the number of megaspores per sporangium decreased, and the size of individual megaspores increased. They must have accordingly come to represent an increasingly worthwhile prize of food reserve for attacking insects. The selective advantage of enclosure of the megaspore within an ovule, achieved at the end of the Devonian, may have been protection from insect attack, much as it is postulated that the Cretaceous enclosure of the ovule in an ovary was primarily protection from pollinating-cum-attacking insects (Grant 1950).

Arborescence and arthropods

The evolution of trees has been partly attributed to the upward struggle for light. Although the appearance of fossils of winged insects in the Carboniferous is substantially later than the appearance of trees (e.g. Lepidodendraceae, Cyclostigmataceae, and *Archaeopteris*) in the late Devonian (text-fig. 4*l*), perhaps spore-feeding arthropods had some role in stimulating the elevation of sporangia out of their reach. Desiccation is a problem to soft-bodied insects, and the long ascent to terminal sporangia would subject them to harsh conditions, quite unlike the more stable and humid conditions of the forest floor. The protection of height must have been short-lived as insects took to the air, and acquired waterproof cuticles and closing spiracles (cf. Hocking 1957; Hughes and Smart 1967). Indeed, it is conceivable that in some plants stem and spore structures subsequently correlate in regard to spore dispersal by arthropods (see p. 404). The purpose of this short paragraph is not to suggest that the struggle for light was not important in the development of trees, but that other benefits could also have accrued from that habit.

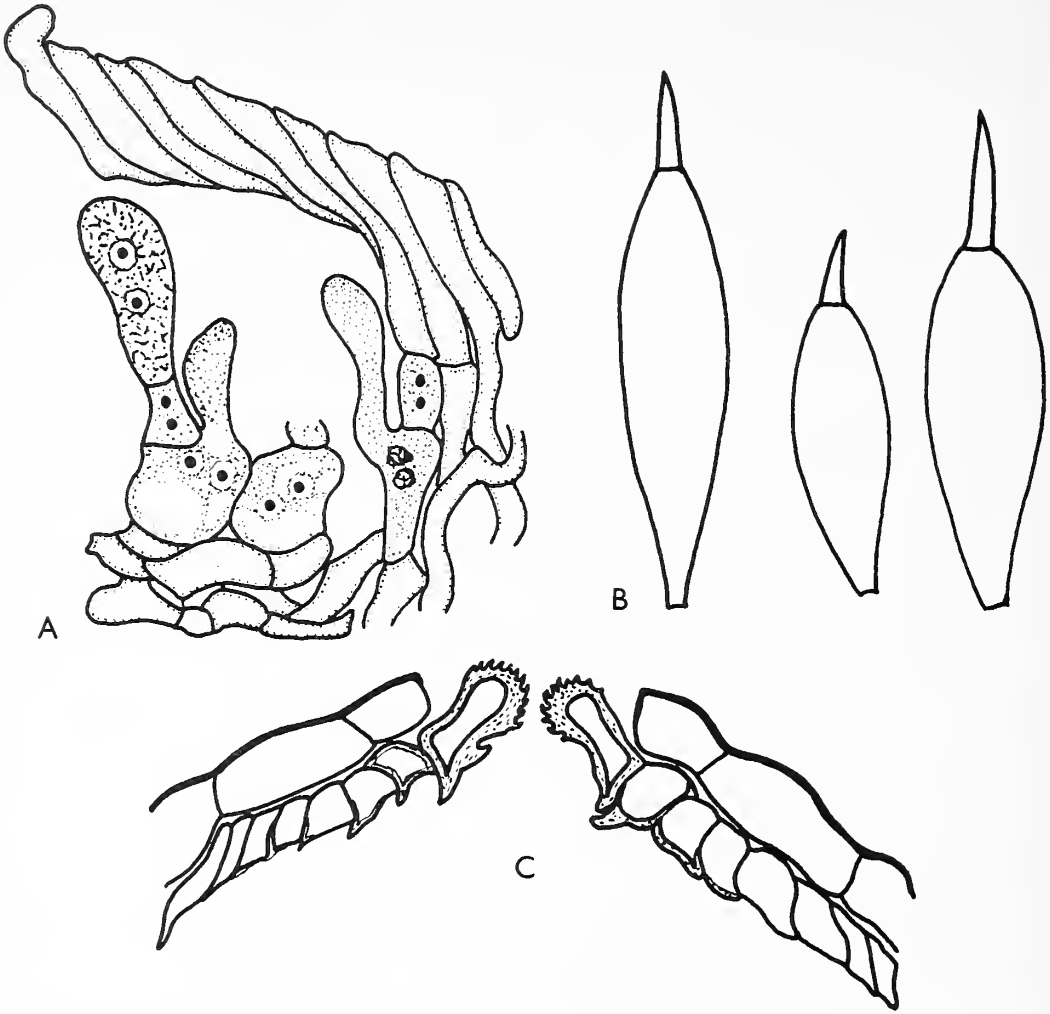
FUNGI

Our understanding of the early fungi is still extremely fragmentary, and is strongly dependent on host relationships of some of the more primitive parasitic genera. The remains of Devonian land plants contain abundant fungal mycelium (Pl. 54, figs. 5 and 6; text-fig. 4*q*) but these seem to have been nearly all phycomycetes or ascomycete-like fungi: some appear to have been associated with living tissue, notably of *Asteroxylon* (Kidston and Lang 1921*b*; Martin 1968). By the upper Carboniferous we have well-authenticated records of Ascomycetes (e.g. *Protoascon*, Batra, Segal and Baxter 1964) and Basidiomycetes (*Palaeancistrus*, Dennis 1970) (text-fig. 4*t*). Growth as internal parasites must have been the main, if not only, method by which fungi were able to leave wholly aquatic habitats and start a subaerial existence (Savile 1968). By growing within host tissues and fruiting on the surface (text-fig. 4*q*) (at first in a saturated atmosphere only) fungi were subjected to selection for mutations favouring protection from desiccation.

Fungi, arthropods, plant pathology, and dispersal

In regard to relationships of fungi to arthropods in the Devonian, there is considerable circumstantial indication of their importance. As discussed above, some Devonian fossil plants show lesions attributable to animal wounds and subsequent infections. Leach (1940), Stakman and Harrar (1957), Carter (1962), Ingold (1971) and others discuss the roles of animals, illustrating the particular importance of arthropods, in transmitting plant diseases, including viral, bacterial, and fungal pathogens. Of particular interest is the conclusion of Kevan (1965) that animals favouring plant pathogens as food would be more likely to spread them than control them (p. 45). Presumably this conclusion could be extended to the thesis that almost any spore feeding will lead to a scattering of spores helpful to the parent plant. In many cases such zootic dispersal has resulted in adaptive modifications. This is seen most strikingly in insect-pollinated angiosperms, in some fungi (Ingold 1971 and p. 409) and, apparently, in Devonian vascular plants. A variety of animals whose close ancestors may have made up part of the Devonian fauna have been implicated in fungus transmission: e.g. nematode worms (Solov'eva 1965; Jensen 1967), molluscs (slugs, Pulmonata) (Johnson 1920; Talbot 1952), worms (unspecified, Talbot 1952; enchytraeid, Kevan 1965), isopods (woodlice) (Talbot 1952), chilopods (Talbot 1952), diplopods (Kevan 1965), Protura (Kevan 1965), Collembola (Theobald 1910; Collinge 1910; Talbot 1952; Hinson *in* Burges 1958; Stainer and Kevan 1973) and mites (Talbot 1952; Griffiths, Hodson and Christenson 1959; Mignolet 1971).

In considering the evolution of fungi and likely events during the Devonian, among fern parasites there is a revealing series. On *Osmunda* is found *Mixia osmundae*, which bridges the gap between Phycomycetes and the primitive ascomycetous genus *Taphrina*. *Taphrina* occurs on ten genera of polypodiaceous ferns, as well as on various predominantly woody and ancient dicotyledons; and in structure it is among the simplest of unequivocal Ascomycetes (Savile 1955, 1968). *Uredinopsis*, the largest of the genera of fern rusts, has telia that are little more than rounded-up mycelial cells and has several conspicuous resemblances to *Taphrina*; its species occur on *Osmunda* as well as many Polypodiaceae. However, *Uredinopsis*, and its companion genera *Milesia* and *Hyalopsora*, have the full life cycle, with pycnia and aecia on *Abies* and uredinia and telia on ferns. Thus a substantial evolutionary period must have been interposed between the extant genera and the first *Taphrina*-like fern rust. Savile (1955) has suggested that this early development occurred on marattiaceous ferns in the Carboniferous, but it may possibly have started in the Devonian. Uredinia of all three rust genera are small and produce a limited number of spores, but all have a simple peridium with an irregular central opening through which spores are thrust at maturity (text-fig. 4*r*). This peridium (text-fig. 3A) is composed of relatively thin-walled cells and could effectively protect unshed spores and sporogenous cells only against small animals without powerful jaws. The spores are borne on short pedicels and converge toward the central opening under the shallow peridium. In *Uredinopsis*, each spore bears a slender apical spine (text-figs. 3B, 4*s*), which plainly must serve to repel small animals attempting to penetrate the ostiole. In the related but more advanced genus *Pucciniastrum*, generally on woody dicotyledons, the peridium is more firmly constructed and the ostiole is ringed by specialized cells bearing upwardly



TEXT-FIG. 3. A, part of uredinium of *Milesia marginalis* after Moss (1926). B, urediniospores of *Uredinopsis osmundae*. Apical mucro is 6–18 μm long. C, uredinial peridium of *Pucciniastrum arcticum*, showing strongly modified ostiolar cells, after Moss (1926). (A, C, by permission of the Annals of Botany Company, Virginia Water, Surrey, England.)

pointing spines (text-fig. 3C) (Moss 1926). These ostiolar cells also clearly serve to discourage entrance to the sorus by very small animals, while not interfering with outward movement of mature spores.

The realization that *Rhyniella praecursor* belonged to a spore- and pollen-eating assemblage strongly suggests that these protective devices in early rusts operated against Collembola, and probably also mites, at a time before the appearance of true insects.

Protective devices, often consisting of massive and variously fused paraphyses, are seen in more modern rusts, in which they perhaps evolved as protection against true insects; but it is noteworthy that they have gradually been eliminated in several lineages. It is suspected that, as improved nutritional balance with the host allowed markedly increased spore production, these far from perfect protective devices were no longer adaptive.

Pycnia of the rusts are analogous to entomophilous flowers, in that they are composed of spermatial cells (pycniospores), receptive hyphae, and a nectary. The nectary attracts insects, which spread pycniospores to compatible receptive hyphae. The small volume of nectar generally makes study of its scent difficult. However, the scent is strong in a few systemic species. It is significant that in the relatively primitive rusts *Melampsorella caryophyllacearum* on *Abies*, and *Chrysomyxa arctostaphyli* on *Picea*, the nectar is weakly carrion-scented; whereas in the much more modern *Aecidium physalidis* on *Physalis*, and *Puccinia punctiformis* on *Cirsium*, the nectar is sweet-scented. These differences probably reflect the times of origin of groups of blossom-visiting insects.

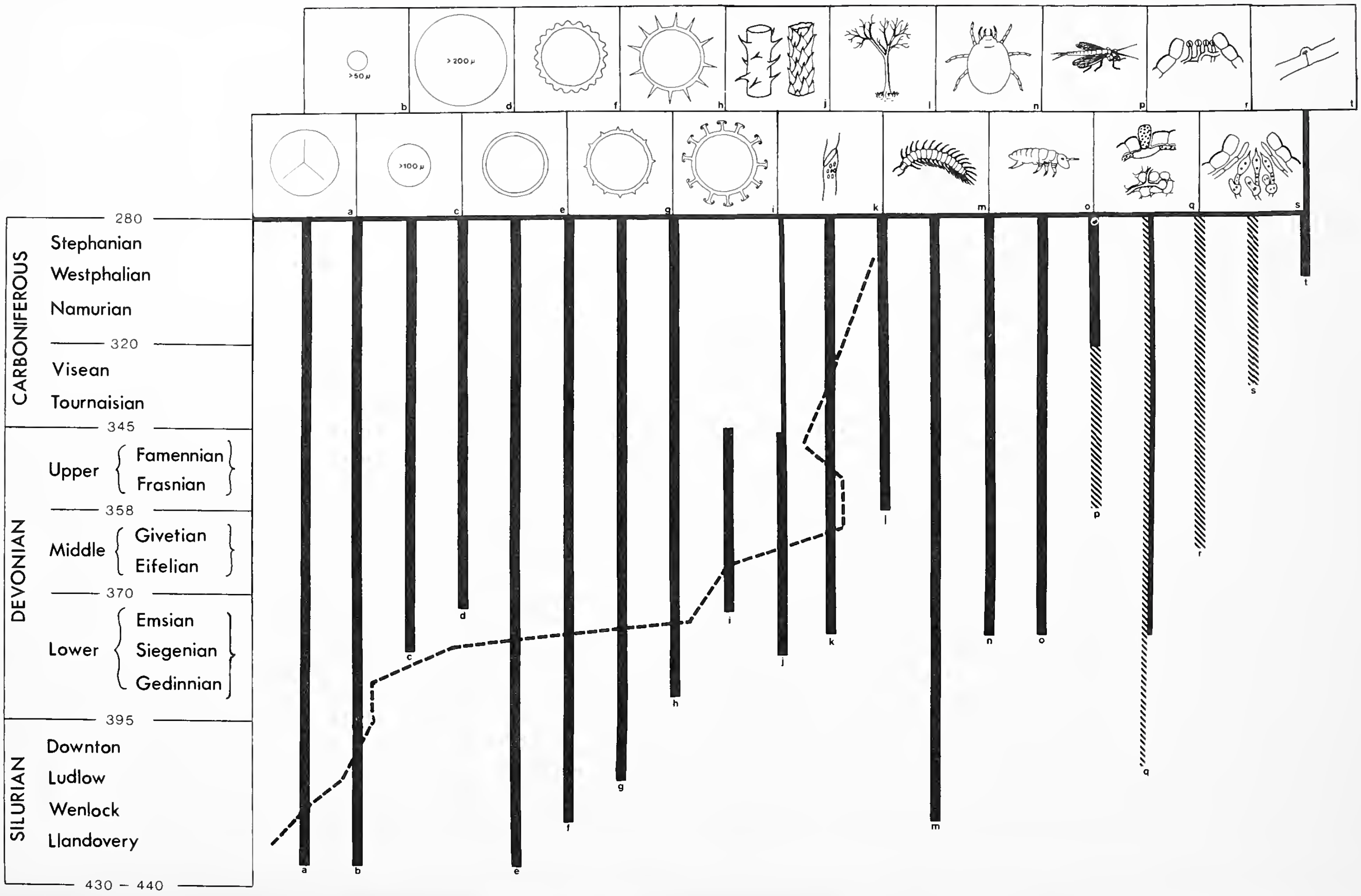
Most rust spores are strongly adapted for dispersal by wind, although some casual dispersal by arthropods must occur as has been suggested for Collembola by Theobald (1910). However, some teliospores of *Nyssopsora* and a few unrelated species of *Puccinia* have very coarse spines, grapnel-hook appendages, or elaborate pedicel decorations, which clearly serve to promote dispersal by arthropods.

CONCLUSIONS

As early as the Devonian co-evolution of arthropods, tracheophytes, and fungi is evident (text-fig. 4).

A variety of soil-inhabiting arthropods are preserved as fossils. Some were predators, some were probably mainly detritus feeders (e.g. myriapods), and others (e.g. mites, Trigonotarbida, and springtails) may have fed extensively on spores, spore protoplasts, and plant sap. Presumably other animals, protozoa, and soft-bodied metazoa, which were not preserved, also flourished in the soil and were an integral part of ecosystems. Mites, trigonotarbids, and springtails, and the hitherto undiscovered progenitors of the true insects could have had considerable influence on the evolution of early vascular plants and their diseases.

Particularly remarkable is the simultaneous increase in complexity of spore structures with arthropod diversity. This is especially interesting considering the likelihood of spore-feeding arthropods acting as spore dispersers; the ensuing adaptation being reflected in spore structure and other modifications, such as are seen in some fungi, vascular cryptogams, and most strikingly in angiosperms. Complexity of spore structure may be related to dispersal by wind and water, to protection from a variety of physical factors, and equally, protection from destruction by those arthropods involved in spore eating and dispersal. Indeed, living arthropods, related to those involved, are known to disperse spores and to eat them. The elaborate spines and other ornamentations seen on Devonian spores seem clearly related to arthropod dispersal and protection, as with modern pollen grains. Heterospory has its origins in the Devonian and we suggest a possible early relation between this and arthropod mediated fertilization. Arborescence precedes the arrival of alate arthropods. It is suggested that the elevation of the sporangia may have been advantageous in reducing the effectiveness of attacking arthropods which were relatively sensitive to desiccation.


CARBONIFEROUS
DEVONIAN
SILURIAN
280
Stephanian
Westphalian
Namurian
320
Visean
Tournaisian
345
Upper
Famennian
Frasnian
358
Middle
Givetian
Eifelian
370
Lower
Emsian
Siegenian
Gedinnian
395
Downton
Ludlow
Wenlock
Llandovery
430 – 440
>50 μ
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Subsequent events indicate relationships between the existence of trees and the development of wings in the true insects.

Fungi appear as parasites of land plants as soon as the terrestrial habit develops. Arthropods, notably insects, mites, and springtails, are known vectors of plants diseases: thus the possibility exists that they had the same roles in the Devonian, or even before. Some primitive fungi show some of the characteristics for arthropod dispersal, and protection from attack by arthropods.

Although we have interpreted some features of early terrestrial plants (e.g. spiny stems, arborescence) as having had possible protective value against arthropod attack, lesions found in fossils of Devonian plants are strongly indicative of damage caused by animals. In some wounds there are clear signs of traumatic responses of living tissue in which cases attacks by mites, springtails, or other animals known from the same habitat seems a more plausible explanation than vulcanism.

Most of the remarks in this paper have concerned the concept of short-distance spore dispersal, and local spreading of propagules. However, the role of arthropods, and especially those capable of becoming aerially planktonic, in long-distance dispersal, not just of themselves, but also of the spores they no doubt carried, could have had great significance to the Devonian ecosystem. Wigglesworth (1973), in discussing origins of insect flight, suggests that the first significance to becoming airborne was to disperse from areas which were becoming unfavourable (drying up), to new favourable areas. This would appear to broadly parallel events leading to the adaptiveness of amphibian progenitors. In the case of arthropods, the likelihood of their carrying spores ready to colonize the potentially favourable destination, could have had considerable significance.

In terms of food sources and an environment less hostile to arthropods than the

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TEXT-FIG. 4. The contemporaneous appearance of a variety of phenomena discussed in the text indicative of co-evolutionary processes in and around the Devonian period.

a, simple triradiate sutures; *b*, spore diameters exceed 50 μm; *c*, spore diameters exceed 100 μm; *d*, spore diameters exceed 200 μm indicating heterospory; *e*, exine smooth; *f*, exine verrucate; *g*, exine with small conical spines; *h*, exine with long spines; *i*, exine with grapnel-like ornamentation; *j*, stem structures: *left*, spiny stems which disappear entirely before the Carboniferous; *right*, leafy stems; *k*, phloem evident in vascular strand; *l*, arborescence; *m*, Myriapoda; *n*, Acarina; *o*, Collembola; *p*, Pterygota; *q*, first terrestrial fungus: *above*, conjectural phycomycete ancestor with multi-nucleate mycelia and spore sacs sheltering in tissues of early emergent aquatic or terrestrial plant; *below*, branching, aseptate hyphae in host tissue; *r*, first rust uredinial state (conjectural); *s*, first *Uredinopsis*-type uredina (conjectural); *t*, mycelium with clamp connection indicative of Basidiomycetes. *Dashed line*: number of genera of spores (each box width is ten genera, each bar five genera).

It is worth noting that it was towards the end of the Silurian that the oxygen level in the atmosphere began to increase more rapidly than before, and that resulted in greater filtering of short-wave ultra-violet radiation, so reducing these biotically harmful rays near the surface of the earth (Berkner and Marshall 1965). The Devonian was a period of high incidence of geomagnetic reversals (McElhinny 1971) yet shows a relatively low extinction rate (Simpson 1966). This appears to contradict the theories of the direct or indirect causal relation between geomagnetic reversals and extinctions proposed by Crain (1971) and Uffen (1963) respectively. Perhaps the circumstance of the unprecedented opportunity of terrestrialization presenting itself as providing marginal environments and the subsequent catastrophic selection in speciation (Lewis 1962) is enough to have delayed the expected decline in diversity until the end of the Devonian when indeed the occurrence of new genera, at least as exemplified by spores, declines (dashed line).

bare mineral soil, algae, fungi, and bacteria must have been as important to soil-dwelling arthropods as the early vascular plants. The latter presumably appeared only after an extensive non-vascular flora had pioneered dry land. During that time, as today, fungi and bacteria must have been important as pathogens and decomposers and, with detritus feeders, were an integral link in the formation of organic soils and humus. The increase in soils and humus creates additional habitats for soil animals, allowing for evolution of a more diverse, more widespread, and more vagile fauna. This in turn, has its effects on the diversity and development of the flora, and so the process continued.

APPENDIX

The function of many spore structures has received little attention. It is therefore worthwhile making a short aside on the possible significance of structures seen in Devonian spores, which may not be directly related to the subject of this paper.

Of course, not all spore structures need be related directly to dispersal or protection from animals. Double ('cavate') spore walls (e.g. *Geminospora*, Pl. 55, fig. 8) could be effective against animal attack, against dehydration, or have a protective function against infection by pathogens prior to germination. Darkly pigmented areas (the so-called dark areas in Devonian and other fossil spore walls are a post-preservation feature; there is no evidence that they represent pigment) could be effective in protection from the adverse effects of ultraviolet light, as is suggested for darkly pigmented fungal spores which remain exposed for long periods (Rabinovitz-Sereni 1932; Buller 1924, p. 541); or dark pigmentation could be effective in absorbing solar radiation, as hastening the mechanisms of spore discharge as has been demonstrated in *Morchella esculenta* by Falck (1916) (Buller 1934, pp. 166, 300, 321). Pigmentation in spores or rust fungi is markedly correlated with aridity (Savile 1970, 1972) and, indeed, the common brown pigment found in various fungal groups offers extreme impermeability to water and other fluids when in high concentration. Pigmentation has been lost in several lines of rusts that have invaded tropical rain forest from less equable climes (Savile, unpub.). Preventing dehydration is probably the most important of the three functions of fungal spore pigments. Pigmentation in fungal spores tends to correlate with wall thickness too, and in coprophilous fungi, whose spores are usually shot from dung to adjacent herbage where they are eaten, the frequently very dark pigment must protect against digestion in passing through the gut of an animal which may be required by some fungal spores for germination (cf. Johnson 1920; Bekker 1947; Talbot 1952; Ingold 1971). In this way, the process broadly parallels that of seeds which require scarification, naturally often by passage through a gut, to germinate (Ridley 1930; Stebbins 1971).

Thickened radiating ribs (e.g. *Emphanisporites*, Pl. 55, fig. 9) and equatorial thickenings (e.g. *Ambitisporites*, Pl. 55, fig. 2) both seen in late Silurian/early Devonian spores may confer rigidity, equipping the spore to survive some water loss without collapse, or physical stress associated with passage through the gut of an animal.

Minor ornamentation (e.g. *Streelispora*, Pl. 55, fig. 4; *Dictyotriletes*, Pl. 55, fig. 5; *Spinozotriletes*, Pl. 55, fig. 3), seen generally in aerially dispersed spores, serves to hold a thicker than usual boundary layer of air, so increasing the buoyancy of the spores by reducing the density of the airborne unit (Stokes's Law as mentioned in the main text). This is especially true of the small and sparse echinulations of most rust urediniospores. Although Buller (1924, p. 542) attributes this to host-attachment function in some rust fungi, the reverse can be said of spores of two large groups of *Puccinia* in which the urediniospores have two flattened cheeks from which echinulation is missing in a circle of diameter about 8–16 μm, which are related to host attachment. Large, smooth, flat pigmented spores of *Pleospora* and related genera with smooth walls can be seen under the microscope to adhere readily and strongly to foliage.

Air sacs are borne on many present-day conifer pollen, and comparable features are recognizable from the middle Devonian onwards (e.g. *Rhabdosporites*, Pl. 55, fig. 1). In conifers, this feature has been regarded as an adaptation to wind pollination, but researchers have differed in their detailed interpretation of their actual role. The broad wing-like flange seen on some living lycopod spores is another feature recognizable from the middle Devonian (e.g. *Hymenozonotriletes*, Pl. 55, fig. 6). Enhanced aerodynamic properties are usually invoked as the adaptive significance of such a feature, as with the saccus. But so many wind-pollinated conifers (including some Pinaceae) have non-saccate pollen that the selective advantage in these terms seems to be questionable. Doyle (1945) advanced the suggestion that they were associated with orienting the pollen during flotation through the liquid-filled micropyle of inverted ovules. The subsequent work of McWilliam (1958) has shown that ovules of *Pinus* became fertilized just as effectively if artificially turned upright immediately after pollination. The sacci may function to protect the large germination area against moisture loss during wind transport—they certainly 'close' across this area when the grain is dry, as Wodehouse (1935) pointed out. The difficulty of attributing function (and hence adaptive *raison d'être*) to pine pollen sacci well illustrates the general problem of interpreting functionally all spore exine morphology.

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OSTRACODS, LAND PLANTS, AND CHARALES FROM THE BASAL PURBECK BEDS OF PORTESHAM QUARRY, DORSET

by D. BARKER, C. E. BROWN, S. C. BUGG *and* J. COSTIN

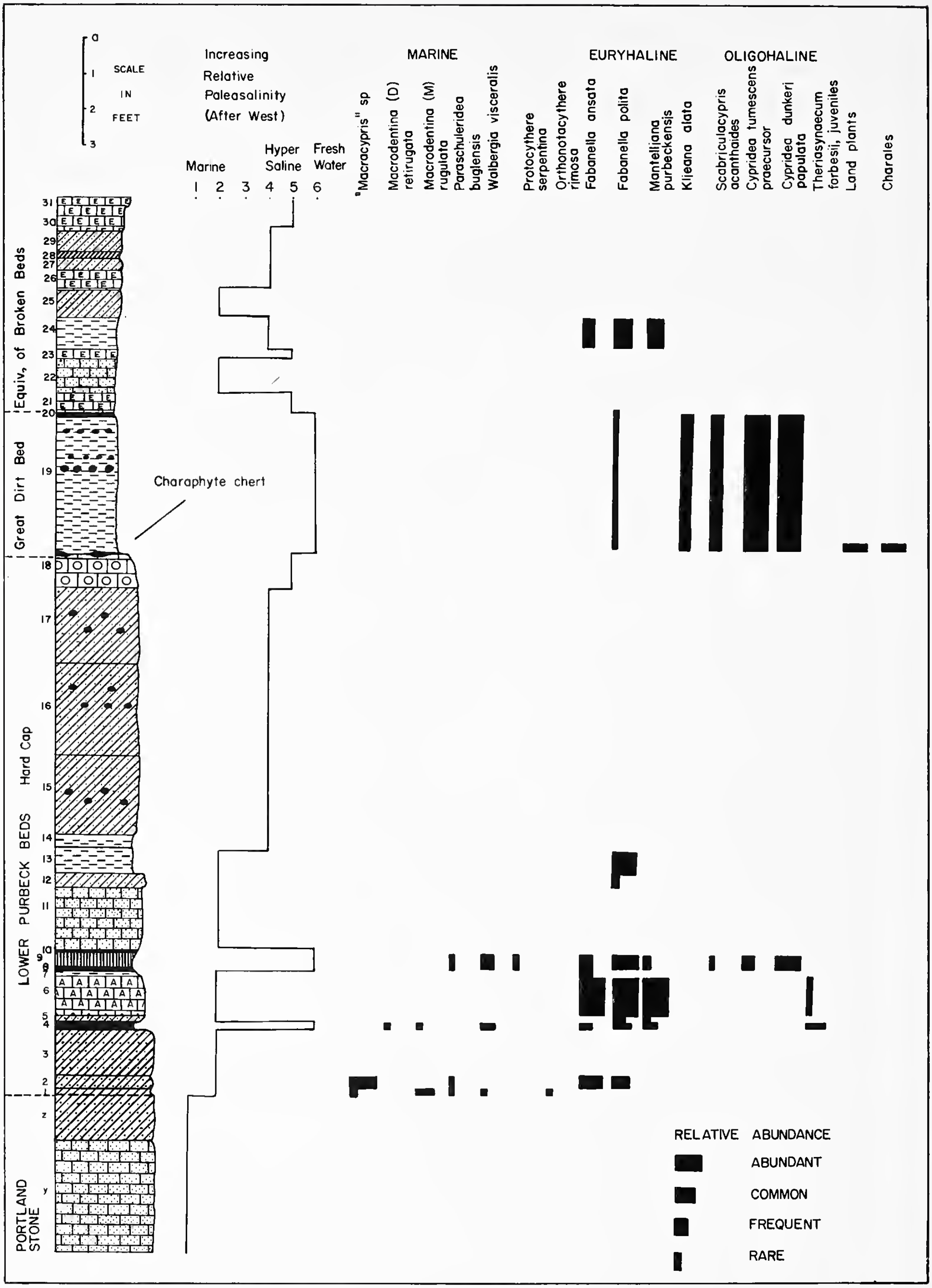
ABSTRACT. A thin cherty layer near the base of the Purbeck Beds in Dorset has yielded a flora of land plants (including stems of *Equisetum mobergii*, isolated seeds referred to *Carpolithes rubeola*, *C. glans*, *C. rhabdotus*, *C. cocos*, *C. gibbus*, *C. acinus*, and *C. westi* spp. nov., and cones of *Araucarites sizerae* sp. nov.) and freshwater Charales (*Clavator westi* sp. nov.) as well as freshwater ostracods. The discovery of *Clavator westi* in Lower Purbeck deposits opens up the possibility of separating the Lower Purbeck from the Middle Purbeck using the Charales. Among the ostracods *Cypridea dunkeri* Jones is shown to have stratigraphical value. Correlation of these basal Purbeck Beds in Dorset with the Swindon Series further north indicates that at Swindon either Purbeck conditions were established earlier than in Dorset, or that Portland conditions recurred later.

THE basal Purbeck Beds are famous for their preservation of a fossil forest with 'tufaceous envelopes', 'dirt beds' with the remains of cycads, ostracod limestones, fossil insects, and freshwater limestones crowded with gastropods. Thus we have a vivid picture of a luxuriant coastal swamp, thickly forested and teeming with life. This paper shows how an examination of the fossils in a quarry in Dorset (map ref. SY 611859) can add to this broad picture. The basal Purbeck Beds are not wholly freshwater. They record cycles, ranging from freshwater to super-saline. This is borne out by text-fig. 1 in which West has kindly provided a graph of relative palaeosalinity based on a detailed petrological study of the section (see West 1975).

The basal Purbeck Beds of Dorset include the Dirt Beds, which are thought to be fossil soils. The soils usually consist of dark calcareous shale with numerous carbonaceous wood fragments and in which fossil coniferous trees are often found (Woodward 1895; Strahan 1898). The most westerly exposure of these Dirt Beds is to be found in an ancient quarry (map. ref. SY 611859) at Portesham in Dorset. The quarry is well known for a 15-ft long tufa-coated tree trunk which was believed to be a fossil elephant. The section exposed is shown in text-fig. 1 and commences in the Portland Beds. These are massive limestones with large marine lamellibranchs which grade upwards to poorly fossiliferous, thinly bedded limestones of the Purbeck. Thus a facies change occurs between the Portland and Purbeck beds which is transitional; the limestones become laminated, there is an increasing abundance of ostracods, and the large marine bivalve molluscs disappear.

In 1961 West reported that Charales and other well-preserved freshwater fossils such as ostracods had been found in chert from one of the Dirt Beds in this small quarry. Subsequently the material was sent to the University of Reading, where Professor Harris supervised the work of Misses Brown, Bugg, and Costin. The ostracods in the section are described separately by Barker. The chert lies in hollows on the eroded surface of rounded, slightly distorted, limestone pebbles. It is a white-weathering rock, rather friable with pseudomorphs after gypsum often separated

[Palaeontology, Vol. 18, Part 2, 1975, pp. 419–436, pls. 57–58.]


0
1
2
3
SCALE IN FEET
Increasing Relative Paleasalinity (After West)
Marine
Hyper Saline
Fresh Water
1 2 3 4 5 6
MARINE
EURYHALINE
OLIGOHALINE
"Macracypris" sp
Macrodentina (D) retirugata
Macrodentina (M) rugulata
Paraschuleridea buglensis
Wolbergia visceralis
Protocythere serpentina
Orthonotacythere rimosa
Fabanella ansata
Fabanella polita
Mantelliana purbeckensis
Klieana alata
Scabriculacypris acanthoides
Cypridea tumescens praecursor
Cypridea dunkeri papulata
Theriosynaecum forbesii, juveniles
Land plants
Charales
Equiv. of Broken Beds
Great Dirt Bed
Hard Cap
LOWER PURBECK BEDS
PORTLAND STONE
31
30
29
28
27
26
25
24
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3
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z
y
Charaphyte chert
RELATIVE ABUNDANCE
ABUNDANT
COMMON
FREQUENT
RARE

by marl. According to West (1975) it is surprising to find the remains of freshwater fossils together with evidence of evaporites in the same bed. In this, the Charophyte Chert of West (1961), siliceous replacements of Charales, freshwater ostracods, and gastropods are to be found in association with silicified and carbonaceous plant remains. The chert easily disintegrates with the addition of dilute hydrochloric acid.

West 1975 suggests that the formation of the Charophyte Chert required dramatic changes in palaeosalinity during its formation. He also suggests there is evidence for fluctuation in the depth of water. Hence one can envisage coastal lagoons, similar to those in South Australia, which are fresh or brackish during the winter with abundant water-plants and molluscs, and in the summer high temperatures produce evaporites. Charales are normally freshwater but can tolerate salinities up to 10‰ (Groves and Bullock-Webster 1924). Carbonaceous dirt beds with plant remains probably originated as marshy soils. The famous 'Mammal Bed' of Durlston Bay is similar and contains freshwater molluscs (Arkell 1941). Thus the Dirt Beds probably indicate sub-aerial exposure. Fragments of Charales are by far the most common plant fossils in the Charophyte Chert, representing a whole suite of organs, stems, vegetative leaves, reproductive leaves, oogonia, and gyrogonites, all of which probably belong to a single *Clavator* species. The land plants are the first to be described from the British Purbeck since *Cycadeoidea gigantea* Seward, 1897.

STRATIGRAPHICAL AND PALAEOGEOGRAPHICAL CONCLUSIONS

A comparison of the Portesham section with sections of similar age at Swindon (Wiltshire) and Aylesbury (Buckinghamshire) has been made. At Swindon the freshwater beds alternate with marine limestones of Portland facies. An analysis of the ostracods showed that these beds are correctly correlated with the basal Purbeck

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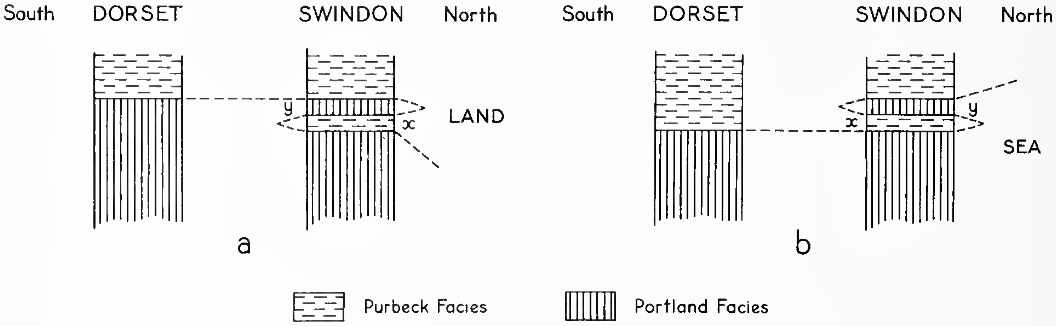
TEXT-FIG. 1. Vertical section of part of the Portesham Quarry exposure, including most of the Lower Purbeck Caps and part of the Portland Stone. The construction of the Palaeosalinity Curve is based on petrographical evidence provided by West, though West (1975) has since made minor revisions. Six groups of faunal and mineralogical features have been used as indices of Paleosalinity from fresh or slightly brackish to evaporitic conditions. The petrographical rock types are represented as follows:

▦	Micrite
E	Secondary limestone, a replacement of calcium sulphate
A	Algal limestone
O	Gypsum conglomerate replaced by limestone
▨	Pelsparite or pelmicrite
▩	Intrasparite
▤	Marl
▥	Carbonaceous shales or dirt beds
■	Chert

Beds and Upper Portland Beds but not with the Middle Purbeck as before seemed possible (Barker 1966). It seems unlikely that the transition from Portland Beds to Purbeck Beds was synchronous in England. The presence of *C. dunkeri papulata* suggests that the Purbeck Beds of Swindon can be correlated with the basal Purbeck Beds of Dorset. As Purbeck Beds at Swindon interdigitate with marine beds of Portland facies, we must conclude that the basal Purbeck Beds in some places were being laid down at the same time as the upper Portland Beds in others. Thus the basal Purbeck Beds are alternative facies of the upper Portland Beds in England.

There are two possibilities (text-fig. 2), firstly the Purbeck intercalation (*x* in text-fig. 2*a*) below the Portland facies (*y* in text-fig. 2*a*) represents a terrestrial influence from a northerly landmass. The Purbeck intercalation at Swindon would therefore be older than the earliest Purbeck Beds in Dorset. The second possibility is that the intercalation of the Portland facies (*y* in text-fig. 2*b*) represents a later marine incursion from a northerly lying sea. If the latter alternative were true, the Portland Beds of Swindon should have a more complete fauna than those of Dorset. In fact they are less complete since no ammonites of the uppermost zone (*Titanites giganteus*) are known, though the Swindon Roach may well be of this age.



TEXT-FIG. 2. Diagram to illustrate the two interpretations of the interdigitation of the Purbeck Beds with the Portland Beds at Swindon (see text for explanation).

In addition to the ostracod and ammonite evidence an additional item sheds further light on the Portland–Purbeck transition. Amongst the silicified fossils recovered from the Charophyte Chert was a single tooth of a *Trigonia*. According to Dr. L. R. Cox it matches the teeth of *Trigonia* so abundant in the Portland 'Roach' of Portland Island (*Laevitrigonia gibbosa*). This indicates that in Charophyte Chert times, the topmost Portland Beds were being eroded not far away from Dorset. This erosion must have taken place before the shells of the Roach had been dissolved away to leave the vacuolar limestone that is now such a familiar feature at this horizon.

THE OSTRACODS (D. B.)

The most abundant ostracod in the Charophyte Chert of Portesham Quarry was identified by West (1961) as *Ulwellia papulata* Anderson, and it was claimed by him as evidence for correlating the Swindon Series with these lowermost Purbeck Beds of Dorset. Earlier Arkell and Sylvester-Bradley (1942) had discussed the age of the Swindon Purbeck Beds and came to no definite conclusions, though Arkell favoured a Middle Purbeck age and Sylvester-Bradley a Lower Purbeck or Portlandian age.

In addition to *Cypridea dunkeri papulata* fourteen species of ostracod have been recognized from the Purbeck Beds shown in text-fig. 1. These can be divided into three groups on the basis of salinity preference: (see text-fig. 1; for systematics see Barker 1966*a*, *b*).

(*a*) Marine including '*Macrocypris*' sp., *Macrodentina* (*D*) *retirugata*, *M.* (*D*) *rugulata*, *Paraschuleridea buglensis*, *Wolbergia visceralis*, *Protocythere serpentina*, and *Orthonotacythere rimosa.*

(*b*) Euryhaline (brackish to hypersaline) with *Fabanella ansata*, *F. polita*, and *Mantelliana purbeckensis.*

(*c*) Oligohaline with *Klieana alata*, *Scabriculocypris acanthoides*, *Cypridea tumescens praecursor*, *Cypridea dunkeri papulata*, and *Theriosynoecum forbesii.*

All the beds of the section ascribed to the Purbeck (i.e. all except Beds y and z) were searched for ostracods, but none were found in those not listed. Euryhaline forms were found in all beds containing ostracods except Bed 1, in which only marine forms occur, and Bed 19 (the Charophyte Chert) in which *C. dunkeri papulata* was the only species found. Beds 4 and 8 are interesting in that they show a mixture of oligohaline, euryhaline, and marine forms. These are 'dirt beds', and contain pebbles of the pene-contemporaneous marine Portland Beds. The marine ostracods in them are therefore likely to have been derived.

THE CHARALES (J. C.)

Fragments of Charales are the commonest plant fossils in the Charophyte Chert. Some 20 kg of the Cherty Limestone was treated with hydrochloric acid and yielded secondarily silicified rock pieces of various sizes and also some hundred grams of sand. Charalean fragments occur with moderate frequency in this sand, at between ten and a hundred per gram. The fragments are small and study of the surface of large cherty lumps, where the silicified fossils project on its surface, shows that even these charalean remains are in small pieces. Evidently the original calcified material was broken up before it was finally deposited, though no doubt further damage happened when the fossils were extracted. Many were very fragile.

The fossils represent a whole suite of organs, stems, vegetative leaves, reproductive leaves, oogonia, and gyrogonites which could well belong to a single *Clavator* species and they are so regarded here. As, however, the fragments are small, the evidence of continuity between the different parts is not as complete as it was for *C. reidi*. It proved impossible to fit the specimens into one of the three species described by Harris (1939) without modifying the concept of those species and accordingly a new species is described, using Harris's descriptive terms.

Apart from very slight traces of a cutinized membrane in the oogonium, the fossils represent the calcified parts alone. There are specimens in the limestone which have escaped secondary silicification but these were not studied. I have assumed that in the silicified specimens the silicification does full justice to the original calcification, and that apparent defects are due to original slight calcification. Sometimes the hollow fossils have been filled up with silica, making them solid.

SYSTEMATIC DESCRIPTIONS

CHAROPHYTA (CHARALES)

Family CLAVATORACEAE Harris, 1939

Genus CLAVATOR Reid and Groves, 1916 emend. Harris, 1939

Clavator westi sp. nov.

Plate 57, figs. 1–10

Diagnosis. Internodes normally attaining a diameter of 0·6 mm, nodes of 1·2 mm. Leaves up to 0·4 mm thick. Calcified parts of spine cells covering leaves and stem, short and weakly developed; often missing on internodes.

Utricle of oogonium weakly developed, sometimes absent; rarely concealing more than two-thirds of oogonial surface. Oogonium ovoid with broad apical beak (which is easily broken). Length with beak about 650 μm, most common length (with partly broken beak) about 600 μm. Breadth about 450 μm, extremes 370 μm and 550 μm. Surface shows large flattened tubercles. Gyrogonite of oogonium ovoid and beaked, typically 385 μm broad and 545 μm long including the apical beak. Length of apical beak 45–75 μm. Gyrogonite lateral view crossed by 6, 7, or 8 spiral cell ridges.

Holotype. British Museum V.44893. Figured on Plate 57, fig. 5. *Material.* British Museum V.44883–44905.

Description. The stem internodes are only fragments ranging in width from 0·4 to 0·8 mm. The length is unknown but may be 1 cm. The internode has a central tube surrounded by twelve cortical tubes which may be inclined spirally. The coating of spine cells is incomplete, so the cortical tubes are clearly seen. Where there are no spine cells preserved, the short cells of the cortical tubes have a hole in their calcified surface where an uncalcified spine cell may have arisen. A well-developed spine cell is surrounded by 6–8 small cells and these by an outer circle of small cells making a rosette of about 20 cells.

The nodes are about twice as broad as the internode. The swelling below is gradual but the contraction above is sudden. Each node has the stumps of six leaves. One shows a small branch stem and at its side a 'nodal hole'. This branch has a sheath of small spine cells. The swelling of the node is caused by the enlargement of six of the cortical tubes and these bear the leaves. The other six cortical tubes diminish and disappear below the leaves. Most nodes have no calcified spine cells but one has a well-developed crust of them. In all these and some other details the node agrees with that of *Clavator reidi* Harris.

EXPLANATION OF PLATE 57

Clavator westi sp. nov.

Fig. 1. Node seen from above showing six leaf bases. V.44898, × 4·5.

Fig. 2. Antheridial leaf. The antheridial holes are in the centre of spine cell rosettes. V.44900, × 4·5.

Fig. 3. Stem internode with longitudinal cortical cells showing small uncalcified regions where it is presumed spine cell rosettes were attached. V.44899, × 4·5.

Fig. 4. Oogonium showing the apical beak and more or less clear traces of nine utricle cells, three of which project basally. V.44888, × 75.

Fig. 5. An unusually well-preserved oogonium still attached to a leaf. V.44893, × 45.

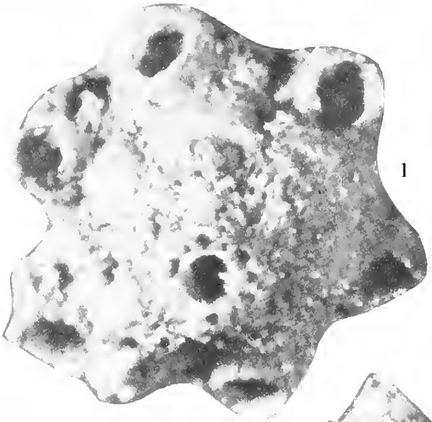
Fig. 6. Node with peculiar spine cells around the leaf bases. V.44905, × 2·5.

Fig. 7. Gyrogonite. V.44892, × 70.

Fig. 8. Stem internode with unusually well-developed spine cells covering the cortical cells. British Museum V.44894, × 4·5.

Fig. 9. Typical stem internode. V.44902, × 4·5.

Fig. 10. Stem internode. The cortical cells are spirally inclined and the spine cell rosettes are well preserved. V.44901, × 4·5.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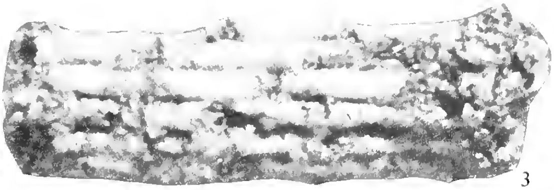
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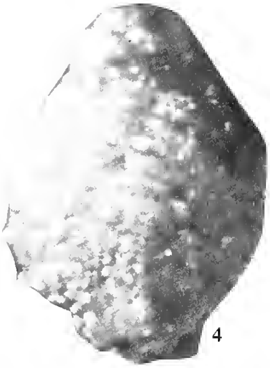
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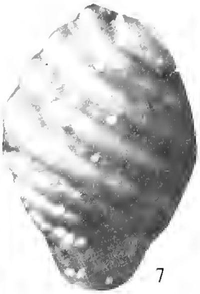
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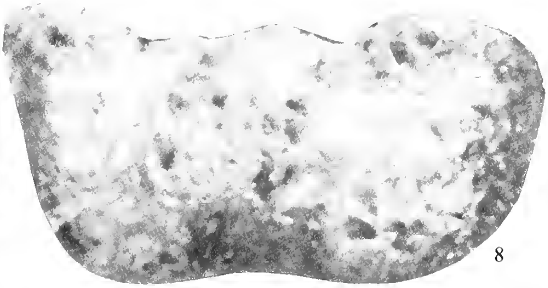
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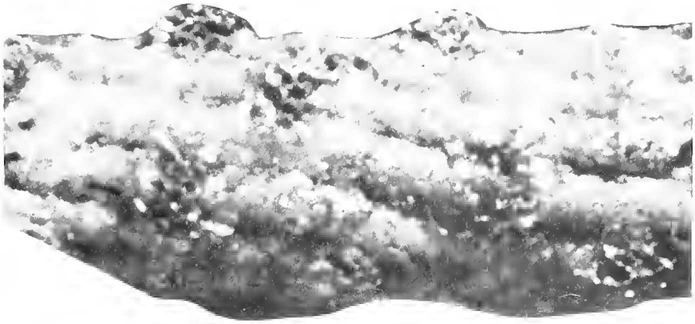
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BARKER *et al.*, Purbeck Charophyta

The leaves are represented by broken stumps on the nodes and by leaf fragments which are strongly curved. Some of these fragments evidently come from wider stumps than any of those seen on nodes. A large leaf had a central cell 380 μm wide and with the crust of spines reached 650 μm but most are much narrower. Leaves have nodes at intervals of 0·3–0·85 mm. Each node has a circle of six 'head' cells and from each of these 6–9 spine cells radiate and sometimes there are smaller cells as well. A few leaves have a regular round or oval hole at each node, considered to be the uncalcified base of an antheridium. One specimen bears on a node a stump considered to be the base of the utricle cells of an oogonium and another has a stump thought to be an oogonial stalk. Only one complete oogonium has been seen attached to a node and this one is abnormal being of very small size. Thus the reproductive leaves though less well known agree with those of the other species in bearing a single antheridium or a single oogonium at each fertile node.

Oogonium. Over 100 detached oogonia were studied. The most perfect are 600–700 μm long but many have lost their apices, and the width (with utricle) is 370–500 μm, most being about 450 μm. There is no obvious correlation between length and breadth. Usually something of the utricle is seen round the base of the oogonium, but sometimes nothing at all and at its best it extends to two-thirds of the length. Of course, this only refers to the calcified parts of the utricle cells, we do not know about any original uncalcified parts. At the base of an oogonium with a well-developed utricle the 6–8 utricle cells leave a gap which was presumably next to the leaf. The oogonial wall beyond the utricle usually shows flattened, almost square, tubercles situated along the mid-line of the spiral cells. As they are regularly spaced they make a pattern often of almost longitudinal files.

Gyrogonite. Only five isolated gyrogonites were seen but when oogonia were cleared by mounting in Canada balsam they were often seen plainly as opaque bodies. A few contain a collapsed brown membrane, the organic inner wall of the oogonium. The lateral face is crossed by 6, 7, or 8 ridges of spiral cells.

Comparison. The material forms a suite of organs, fragments of internodes, nodes, sterile leaves, antheridial leaves, oogonial leaves, and oogonia with more or less developed utricles and isolated gyrogonites. These were attributed to a single species after considering the possibility that there might be more than one. This species agrees fully in essentials with *Clavator reidi*, the type and best-known species of the genus. Harris (1939) described three species of *Clavator*, *C. reidi*, *C. grovesi*, each with a full suite of organs, and *C. bradleyi*, oogonia only. The stems and leaves of *C. westi* are easily distinguished from those of *C. reidi* and *C. grovesi* by their generally smaller size and much feebler development of spine cells, but there are small and perhaps poorly calcified specimens of the other two which look like *C. westi*. The main distinction is in the oogonia.

TABLE 1. A comparison of the Oogonia and Gyrogonites of *Clavator bradleyi* and *C. westi*.

The average dimensions of the oogonia of four species of *Clavator* are as follows:

C. reidi	700 μm long × 450 μm broad
C. grovesi	650 μm long × 450 μm broad
C. bradleyi	550 μm long × 360 μm broad
C. westi	600 μm long × 450 μm broad

	C. bradleyi (Correct to ±10 μm after Harris)	*C. westi* (Correct to ±15 μm)
Gyrogonites, perfect specimens with intact beaks	Lengths 430 μm, 450 μm, 470 μm, 480 μm	Lengths 520 μm, 535 μm, 535 μm, 565 μm, 565 μm
	Thirty-one specimens without apical beaks: Length typically 360 μm, extremes 270 μm and 470 μm	The above five specimens excluding apical beaks from 445 μm to 520 μm
	Breadth about 280 μm, extremes 250 μm and 360 μm	Breadth about 385 μm, extremes 375 μm and 435 μm
Oogonia	Typically 550 μm long × 360 μm broad	Typically 600 μm long × 450 μm broad

The average sizes do not differ much (see Table 1) but there are considerable differences in the utricles: the flat sides of *C. grovesi* distinguishes it at once and so does the usually strong development of *C. reidi. C. bradleyi* and *C. westi* are the most similar and the possibility was considered that they might be the same, but the differences in gyrogonite size are considerable. The selection of good specimens may have caused the apparent differences, though this is unlikely. It will be seen that *C. westi* is usually 50 or 100 μm longer and broader.

Species of other regions. Clavator pecki Mädler 1952 from the NW. German Kimmeridgian differs in its longitudinal, and highly calcified utricle cells. Its gyrogonite is 600–770 μm long, 370–630 μm broad, and the lateral view is crossed by 11–13 spiral cell ridges. The internode is highly calcified and doubly corticated, the cortical cells being remarkably oblique. It is thus very different in all its known parts from *C. westi*.

Carozzi (1948) described a series of gyrogonites from the Purbeck of Switzerland which he was able to identify with *C. reidi*, *C. grovesi*, and *C. bradleyi*. The specimens were studied in rock sections and thus however reliable their identifications may be, they are in a very different form from the present specimens and do not much assist their determination. Nodes and internodes agreeing with those of *C. reidi* are associated with the fructifications.

Clavator harrisi Peck, 1941 from the Lower Cretaceous of Western U.S.A. is known from a series of utricles, gyrogonites, and stem fragments. The oogonium is given as 700 μm × 570 μm; the utricle is usually very well developed (rarely feeble or absent) and usually bilaterally symmetrical rather as in *C. grovesi*. The associated nodes and internodes are very strongly calcified. This species then is very different from *C. westi*.

THE LAND PLANTS (C. E. B. AND S. C. B.)

The species described are the first land plants described since *Cycadeoidea gigantea* Seward, 1897 from the British Purbeck. The material examined was collected by Mr. West and by Professor Sylvester-Bradley from the Charophyte Chert (Bed 18). The plant remains were first noticed by Mrs. Valerie Sizer while treating the material at the University of Leicester.

The specimens studied are thought to have been first calcified and then secondarily silicified. They were extracted from the partly silicified rock with hydrochloric acid. There is an abundance of wood of conifer type, both from small twigs and fragments of larger branches. Unfortunately fine details of pitting were not preserved in the specimens we examined. Some bits of fusainized wood were also present and these are black but all other specimens have lost their original organic material. The seeds and other organs are rare, there were fewer than one per kilogram. Besides the seeds figured and described there are a good many less characterized specimens which are omitted and also obscure bodies of uncertain nature. Since some of the species described are only represented by one or two specimens it seems likely that search of further material would add considerably to the flora.

The fossils are uncompressed and white in colour except for the fusain. Some of them were sectioned by grinding and for this purpose the specimens were enclosed in plaster of Paris hardened in 'Lakeside 700 cement'.

SYSTEMATIC DESCRIPTIONS

EQUISETALES

Genus EQUISETUM Linnaeus

Equisetum mobergii (Halle ex. Möller)

Plate 58, fig. 5; text-fig. 3, figs. 1–6

1908 *Equisetites mobergii* Möller & Halle, p. 26, pl. 4, figs. 29–37.
1913 *Equisetites mobergii* Möller & Halle, p. 21, pl. 2, figs. 21–23; pl. 3, figs. 1–8.

Material. British Museum V.44926–V.44929.

Description. The three small specimens figured, agree with Halle's species though they are preserved differently. The width of the internodes is 2–4 mm, which is slightly narrower than those of Möller and Halle. The tops of the leaf sheaths are damaged and the apices of the teeth are broken, but what remains looks similar to their pl. 3, figs. 5, 6, 7. The specimens show stomata as pits, both on the internode and on the leaf sheath; the pits are scattered and occur at a concentration of up to twenty per sq. mm. As the specimens are solid and uncompressed they show the contour of the leaf sheath segments. The leaf segment forms a raised and rounded ridge with no midrib but two slight furrows separating the middle half from the two lateral quarters. The stem internode shows epidermal cells in vertical rows.

One specimen is hollow and shows some of its structure, there are cortical cavities opposite the leaves, and there is a ring of nodal tubercles probably equalling the leaves in number. These features agree with those of modern *Equisetum* stems.

Remarks. Neither of the two isolated nodes (which are very different from one another) figured by Möller and Halle is like this material: one is far bigger, and the other shows radiating spokes. The identification of this material with the differently preserved originals of *E. mobergii* is inevitably uncertain but there is close general agreement. The age of *E. mobergii* may be rather similar, Upper Jurassic or possibly Wealden (Möller and Halle 1913, p. 41).

Very few Mesozoic species of *Equisetum* have stems as narrow as 2–4 mm. The following are, however, comparable in size:

E. naktongensis Tateiwa including var. *tenuicaulis* see Oishi 1940, p. 189; the internodes differ in having longitudinal ribs.

E. ushimarensis (Yokoyama) may be the rhizomes of the same plant.

E. sp. A. Harris 1961; the stomata differ from our specimens in being in longitudinal lines.

EXPLANATION OF PLATE 58

Figs. 1, 2, 17, 18. Lateral views of *Carpolithes westi*, ×6. 1, is the Type Specimen V.44914. 2, V.44915 is sectioned in text-fig. 4, fig. 10. 17, is V.44914. 18, is V.44916.

Figs. 3, 10, 11, 19. *Carpolithes rhabdotus*, ×6. 3, a lateral view of V.44921 has the hilum downwards. See also text-fig. 4, figs. 2, 3. 10, 11, 19, are of the Type Specimen V.44920.

Fig. 4. *Carpolithes acinus*, Type Specimen, V.44919, ×6.

Fig. 5. *Equisetum mobergii* V.44928, ×6. See also text-fig. 3, figs. 1–3, 5, 6.

Figs. 6, 7. *Carpolithites* sp. V.44925, ×6.

Figs. 8, 9. *Carpolithes gibbus*, Type Specimen, V.44924, ×6. Fig. 9 is the micropylar end.

Figs. 12, 13. *Carpolithes glans*, Type Specimen, V.44911, ×6. Fig. 13 is the micropylar end.

Figs. 14, 15. *Carpolithes rubeola*, Type Specimen, V.44908, ×6. Fig. 15 is the micropylar end.

Fig. 16. *Carpolithes cocos*, Type Specimen, V.44922, ×6. Micropyle is on the left.

Fig. 20. *Brachyphyllum* sp. V.44933, ×6.

Figs. 21, 22. *Araucarites sizerae*, ×6. 21, fragment A is the Type Specimen V.44931. 22, fragment B, V.44932 is the origin of the isolated seed V.44930 in text-fig. 4, figs. 4, 7, 8.

PLATE 58


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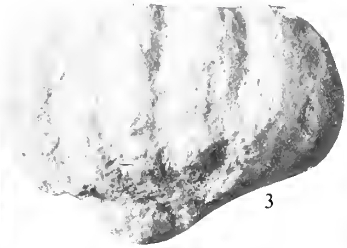
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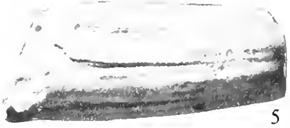
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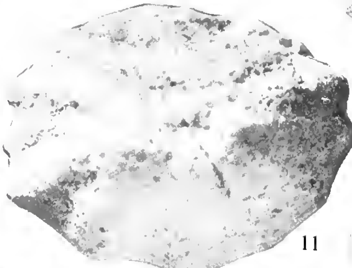
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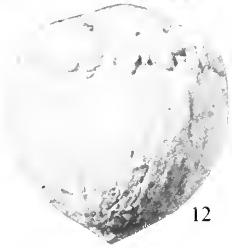
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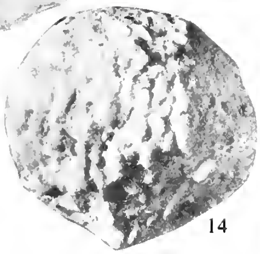
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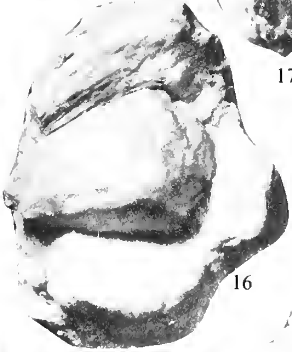
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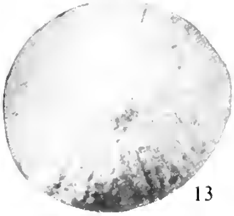
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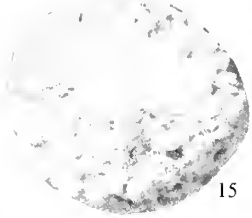
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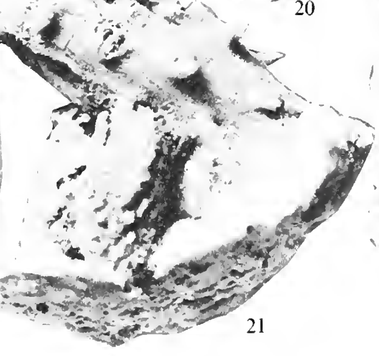
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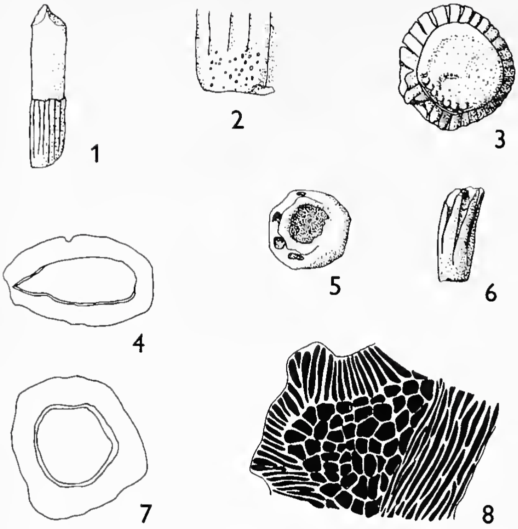
BARKER *et al.*, Purbeck land plants



TEXT-FIG. 3. Figs. 1, 2, 3, 5, and 6. *Equisetum mobergii* (Halle). 1, leaf sheath and part of internode, V.44927, ×8. 2, lower-left corner of V.44927 to show stomata, ×40. 3, end view of leaf sheath, just above nodal level, V.44926, ×8. 5, end view just above nodal level, V.44928, ×29. 6, lateral view of V.44928, ×8. Figs. 4, 7, 8. *Carpolithes rubeola*. 4, longitudinal section, V.44906, ×18. 7, transverse section, V.44907, ×18. 8, L.S. integument, V.44906, ×140.

E. renaulti Raciborski 1894, p. 231; the leaf teeth are shown as having midribs and a stem of comparable size has fewer leaf teeth than ours.

E. gracilis (Nathorst) see Halle 1908, p. 15, has fewer leaves and probably a shorter sheath.

E. quindecimdentata Menendez 1958, p. 6, has rather wider stems with distinct ribs.

Cf. *E. bunburyanus* of Salfeld 1909, p. 7, looks fairly similar but there is rather little information. The leaf teeth perhaps end more abruptly.

CONIFERALES

Brachyphyllum sp.

Plate 58, fig. 20

One small specimen was found, its preservation is poor but examination of the back shows convincingly that the leaves are borne spirally. As the photograph shows the leaves are longitudinally ridged. Between the ridges there are some small and irregular pits (not visible in the photograph) which might represent stomata but no cellular details can be seen. There seems to be no median keel along the leaf, nor median resin body as in some species. Identification of such a twig is difficult but it is noteworthy that similar twigs occur in the Corallian of France (Saporta 1889), in particular *Brachyphyllum jauberti*, *B. moreauanum*, and *B. gracile*, though other specimens of these species are much thicker.

Unclassified seeds

The name *Carpolithes* Schlotheim is used in preference to any of the more recently proposed names. Although these seeds are partly petrified they yield far less information than the well-known Palaeozoic petrified seeds and are not comparable with them. Some Mesozoic seeds have been described by Chandler (1966) from America.

Carpolithes rubeola sp. nov.

Plate 58, figs. 14, 15; text-fig. 3, figs. 4, 7, 8

Derivation of name. From Rubeola, meaning measles, suggested by the lumpy surface.

Diagnosis. Seed orthotropous, stone broadly oval, rounded in section, apex abtusely pointed, base rounded: length 6 mm, width (major axis) 6 mm, depth (minor axis) 5 mm. Surface of stone shows both ridges and lumps. Ridges indefinite in number and unequal in size but running from above the base up to the apex. Three of the ridges stronger than others but not inclined at 120° to one another. Lumps often conspicuous but of very varied size, somewhat elongated but rounded near base of seed. Hilum rounded, indefinite, hilum end rough but much less coarsely rough than sides of seed. Stony layer of integument about 0·7 mm thick composed of three layers of stone cells. Outer layer palisade-like, forming the greater part of the lumps on the seed surface; middle layer of isodiametric cells which form a narrow core in the surface lumps; cells isodiametric both in transverse and longitudinal sections. Inner layer thin, even, composed of narrow elongated cells. Layer regarded as nucellus thin, forming a point near seed apex, closely adherent to integument.

Holotype. British Museum V.44908.

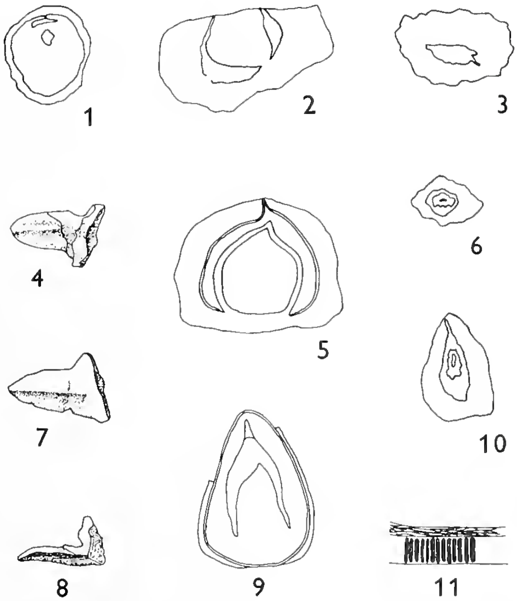
Remarks. The pointed end of the seed which contains the pointed end of the nucellus is regarded as micropylar. No tissues remain inside the nucellus.

Carpolithes glans sp. nov.

Plate 58, figs. 12, 13; text-fig. 4, fig. 5

Derivation of name. From the Latin *glans* meaning 'acorn'.

Diagnosis. Seed rounded in section, 5 mm long, 4 mm wide. Apex protruding as a short micropylar point. Base flattened with raised circular ridge 1 mm tall separated from rest of seed by a groove. Surface rather obscurely marked with longitudinal grooves, length varied, some extending from basal ridge to near micropylar point, others dying away. Grooves approx. 0·25 mm apart, becoming more faint towards apex. Surface



TEXT-FIG. 4. Fig. 1. *Carpolithes acinus.* Longitudinal section, V.44918, ×15. Figs. 2, 3. *Carpolithes rhabdotus*, V.44921; (see also Pl. 57, fig. 3). 2, longitudinal section of hilum end, ×12. 3, transverse section, ×10. Figs. 4, 7, 8. *Auracarites sizerae*, cone-scale bearing seed, V.44930 broken from V.44932, all ×10. 4, from above, 7, from below, ×10. 8, lateral view, ×10. Fig. 5. *Carpolithes glans.* Longitudinal section, V.44910, ×10. Figs. 6, 10. *Carpolithes westi*, ×10. 6, transverse section, V.44912. 10, longitudinal section, V.44915. Figs. 9, 11. *Carpolithes gibbus*, V.44923. 9, longitudinal section, ×18. 11, two thin outer layers of integument, ×180.

of basal ridge covered with irregular lumps, flattened area within this 3·5 mm across. Integument 0·7 mm thick; composed of four layers of cells; the cells of the outer one palisade-like; the cells of the inner layers of approximately isodiametric cells.

Holotype. British Museum V.44911.

Remarks. *C. glans* is represented by two specimens both photographed. One of these was sectioned. *C. glans* resembles *C. rubeola* in size and general shape; integument of *C. glans* is also quite similar except that *C. glans* has four layers of cells and *C. rubeola* has three. The surface of *C. glans* is faintly ridged whereas *C. rubeola* is lumpy and *C. glans* has a wider base.

Carpolithes rhabdotus sp. nov.

Plate 58, figs. 3, 10, 11, 19; text-fig. 4, figs. 2, 3

Derivation of name. From the Greek *rhabdotus* meaning 'fluted'.

Diagnosis. Seed ovoid, slightly flattened, tapering towards apex, basal part flattened but region of hilum raised. Length 9 mm, width in major axis 7 mm, in minor axis 5 mm, surface covered with prominent longitudinal ridges converging towards both ends but ending about 2 mm from base and about 1 mm from the apex. Ridges 12–16 in number, some of them less marked than others. Ridges about 0·5 mm high, edge rounded and furrow rounded. Basal end forming a broad cone, 2–3 mm wide. Micropylar region nearly round, about 1·5 mm wide, consisting of a ring-shaped depression round a central raised area. Stone of integument 1·5–1 mm thick (measured to tip of rib) composed of large isodiametric cells 0·88 mm in diameter, walls 0·01 mm thick. Cavity inside stone showing collapsed membranes about 3 mm × 1 mm.

Holotype. British Museum V.44920.

Description. *C. rhabdotus* is represented by two specimens both photographed, the one which had been broken before study was sectioned. This gave evidence that the micropyle is at the narrower end. The integument was separated from the inner tissue, perhaps the nucellus, by a space at the lower end.

Remarks. Saporta (1875), p. 244 described and figured a similar seed from the Oxfordian of France as *Cycadeospermum schlumbergeri*. It is, however, about three times larger than these seeds and it differs also in not being flattened around the hilum.

Carpolithes cocos sp. nov.

Plate 58, fig. 16

Derivation of name. From the seed's resemblance to a coconut in its husk.

Diagnosis. Seed with two coats. Outer coat fibrous, irregular in shape 1–2·5 mm thick composed largely of longitudinal fibres, base more or less rounded with broad hilum (apex missing). Inner coat a stone 4 mm long forming a three-sided pyramid with a rather flattened base 2·5 mm across. Surface of stone with faint, fine longitudinal striations.

Holotype. British Museum V.44922.

Description. The unique specimen had been broken before it was studied and no sections were attempted. The region of the micropyle had been damaged. The outer coat had here been broken away completely and the stone itself seems to have been slightly damaged. The three flat sides instead of meeting leave a small circular area 0·5 mm wide. This area looks as though it originally had a central canal.

Carpolithes gibbus sp. nov.

Plate 58, figs. 8, 9; text-fig. 4, figs. 9–11

Derivation of name. From the Latin *gibbus* meaning a 'hump back'.

Diagnosis. Seed 3 mm long, 1·5 mm wide (major axis), 1 mm wide (minor axis); one surface markedly convex, slightly keeled, the other slightly concave; hilum end rounded and micropylar end pointed. Surface smooth.

Integument of three layers, outer narrow 0·2 mm wide of palisade-like cells, middle 0·08 mm thick and fibrous, inner much wider, varying between 0·3–0·6 mm and showing no visible cells. Embryo sac 1·9 mm long, 1·5 mm wide at base, tapering to a point. Nucellus represented by nucellar plug 0·5 mm long at narrow end of seed.

Holotype. British Museum V.44924.

Description. C. gibbus is represented by two specimens one of which was sectioned. The nucellar plug was in the apex of the seed at the anterior end of the space left by the shrinkage of the embryo sac. The nucellar plug appears to fill the micropyle.

Carpolithes acinus sp. nov.

Plate 58, fig. 4; text-fig. 4, fig. 1

Derivation of name. From the Latin *acinus* meaning a 'pip'.

Diagnosis. Seed oval, flattened, 3 mm long, 2 mm wide in major axis and 0·4 mm in minor axis. One surface flat, the other convex. Micropyle forming a projection at the broader end, hilum flat. Surface of seed showing fine longitudinal striations. Integument about 0·3 mm thick enclosing nucellus.

Holotype. British Museum V.44919.

Description. C. acinus is represented by two specimens, one photographed and the other sectioned. In the nucellus at the micropylar end was a structure which may have been the pollen chamber, and a small round body which was possibly the embryo [text-fig. 4, fig. 1].

Carpolithes sp. indet.

Plate 58, figs. 6, 7

Material. British Museum V.44925.

This species is represented by two specimens, both with one end missing so both ends of the seed may not have been seen. In one specimen the three ridges meet to form a point, but in the corresponding position on the larger specimen there is a small depression, which may mark the hilum end. The smaller specimen is about 2 mm long and 1·5 mm across the widest part, and the larger is about 4 mm × 3 mm. Both show some structure of the stone where broken. It is about 0·3 mm thick and made up of two layers. The outer layer consists of radiating elongated cells about 0·1 mm × 0·02 mm, and the inner layer is fibrous. The cells are longitudinally arranged and about 0·01 mm wide.

Carpolithes westi sp. nov.

Plate 58, figs. 1, 2, 17, 18; text-fig. 4, figs. 6, 10

Derivation of name. After Mr. I. M. West.

Diagnosis. Seed flattened, wedge-shaped typically 5 mm long, 3 mm wide at basal end, in major transverse axis, 2 mm thick in minor transverse axis.

Flat surface on one side marked with about four longitudinal ridges; other side with a thickened median longitudinal region about 2 mm wide. Surface rather obscurely fibrous. Pointed end sometimes showing a micropyle. Wall of stone of seed approximately 1 mm thick with micropylar canal 1 mm in length, composed of small stone cells, somewhat elongated in a radial direction. Nucellus pointed, 4 mm long, 1·5 mm in major and 0·5 mm in minor transverse axis.

Holotype. British Museum V.44913.

Description. C. westi is represented by a number of specimens showing a range of size 4 mm–8 mm long and 2 mm–5 mm wide at broadest end (basal). Several seeds were sectioned and showed similar structure. In the one figured the inner body regarded as nucellus is a uniform whitish tissue and encloses a brown membrane marked with cells which may form the edge of the megaspore membrane cavity. Inside this is a tiny shrivelled body of unknown nature; but visible in a number of seeds.

Remarks. These seeds look like those figured by Seward 1904, pl. 12, fig. 6 as 'Araucarites' from the English Inferior Oolite and *Carpolithus Lindleyanus* by Phillips 1871, Diag. 32, fig. 1. *C. westi* might be the remains of an *Araucarites* seed, perhaps somewhat water-worn.

CONIFERALES, *ARAUCARIACEAE*

Araucarites sizerae sp. nov.

Plate 58, figs. 21, 22; text-fig. 4, figs. 4, 7, 8

Derivation of name. After Mrs. V. Sizer, who isolated the specimens.

Diagnosis. Cone presumed to be spherical, about 2 cm in diameter. Axis of uniform width, 3 mm in diameter for most of length, tapering at upper end. Cone scales in a spiral, parastichies possibly 3+5. Stalks of cone scales round in section, those at the lower end bent slightly downwards. Outer surface of scales rhomboidal 3–4 mm from corner to corner, with a low, rounded median boss 1–2 mm wide. Seeds embedded singly in cone scale with pointed end towards the axis; seed about 4 mm long (including cone scale boss), 3 mm at wider end, and 1 mm thick.

Holotype. British Museum V.44931.

Description. A. sizerae is represented by two fragments, both illustrated. In both, the solid tissue has been replaced by silica and the gaps between the scales are empty or filled with powdery matter. It is possible that both are parts of the same cone but this could not be proved. The size of the cone and the parastichies were estimated from the two fragments.

Fragment A, the Type—regarded as from the apex, shows the axis bearing cone-scale stalks and some complete cone scales. The outer surface shows some of the cone-scale outlines, though obscurely.

Fragment B—this has lost its cone axis. The outer surface is almost featureless and forms part of an apparently spherical body. The inner side shows cone scales and seeds and in one place pits where cone-scale stalks have been pulled out. A single cone scale with its seed was pulled off and is illustrated in text-fig. 4, figs. 4, 7, 8.

Remarks. This cone is similar to that of a modern Araucaria, though there are no long pointed extensions of scales projecting outside the cone. These may have been rubbed off. No ligule was seen but this is easily missed in such a fossil.

The possibility was considered that the isolated seed called *Carpolithes westi* might be the basal seed-bearing part of the cone scale of the present cone. This still remains a possibility, but it was decided not to make them one species, because they do differ. It may be that the cone fragments are immature while the isolated *C. westi* seeds are mature but there is no evidence of this.

The smallest of the isolated seeds included in *C. westi* is as large as the typical *A. sizerae* seed and most are considerably larger (6–7 mm long). Their shape is also different, they are less flattened.

Since *C. westi* seeds have probably been somewhat worn and smoothed whereas the seeds in the cone have been protected, the actual difference in size may be even greater. Most specimens of *C. westi* have about four longitudinal ridges in one surface and one very rounded ridge on the other; seeds from *A. sizerae*, however, have a smooth upper surface and one marked longitudinal ridge on the lower. As far as is known, recent Araucaria species have much larger cones, and this is also true of the fossil cones described under the name of *Araucarites*. The least different are small specimens of *A. mirabilis* figured by Calder 1953 from Patagonia (Upper Cretaceous or younger). The exposed surface shows that the ends of the scales are broader than those of *A. sizerae* and they are arranged in more numerous parastichies.

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SHORT COMMUNICATIONS

REMARKS ON MUTVEI AND REYMENT'S HYPOTHESIS REGARDING AMMONOID PHRAGMOCONES

by G. E. G. WESTERMANN

In their recent discussion of buoyancy control and function of the siphuncle in ammonoids, Mutvei and Reyment (1973, p. 628) have concluded (for shells of the ceratitid type) that 'more than half of the chambers of the last whorl, and probably all the lower chambers of the second last whorl, must have been entirely filled with cameral liquid if the shell functioned hydrostatically'. The siphuncle is supposed to have functioned only in the chambers of lowermost position in the whorls where it was always fully submerged; the liquid completely filling the last half whorl would have prevented the weak terminal siphuncle from exploding under hydrostatic pressure. This would imply that my calculations of depth limits based on the strength of the ectosiphuncle (Westermann 1971) are inappropriate for the adult growth stage for which I inferred migration to shallower water.

Their evidence is (1) the positive buoyancy of several ceratitid models which (p. 625) 'would require weight increases of from 35% to 45% in order to sink' (this corresponds to 26–31% of the camerae filled with liquid, according to the equation $x:(1-x) = 0{\cdot}35$ to $0{\cdot}45$ where x is the proportion of liquid, (2) the general thinning, often leading to non-preservation, of the siphuncle in the last half to one whorl as reported by earlier authors, (3) the slow growth in thickness of the siphuncular wall in ammonoids as opposed to nautiloids, and (4) the absence of the calcareous 'blotting-paper-lining' of *Nautilus*, which is believed to make extraction of liquid impossible in decoupled position.

Simple calculations of the volume increments in phragmocones comprising logarithmic spirals, however, invalidate this model. Linear dimensions increase with the logarithm of the angle of rotation and volume increases with the cube of linear dimensions, as confirmed by measurements on real shells. The ceratitid phragmocone has an expansion rate of about 2·2; with each whorl (360°) the volume will therefore increase at the rate of $2{\cdot}2^3$ so that the volume increment of the last whorl is $(2{\cdot}2^3 - 1):1 = 9{\cdot}6:1$. For one-half whorl (180°) the increment is $(2{\cdot}2^{\frac{3}{2}} - 1):1 = 2{\cdot}3:1$. Therefore the last half whorl contains more than twice as much cameral volume as all previous camerae, i.e. 70% of the total; thus, liquid filling the last half whorl would reduce the uplift of the ceratitid phragmocone by 70%—not 26–31% as indicated by Mutvei and Reyment's experiments. The increment corresponding to their experimental data is only one-eighth to one-sixth whorl (45–60°), if all earlier

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chambers were empty. If high ontogenetic and/or infraspecific variation is assumed, with the expansion rate ranging from 2·0 to 2·4, the respective values for the half whorl increment would lie between 1·8:1 and 2·8:1. Consequently, the assumption of Mutvei and Reyment that more than the last half whorl and probably parts of the inner whorls, are filled with liquid is incompatible with their experimental data. Their model is internally inconsistent. I believe that, for reasons of economy of shell construction, the actual liquid contained in ammonoid phragmocones rarely exceeded 10–15% of the total volume (i.e. the one to three last camerae).

Furthermore, most recently Dr. R. Cowen (oral communication at the Palaeontological Association's 'Phylogeny of Mollusca' colloquium in London, April 1974) has proposed that decoupling of the connecting rings of the siphuncle from the cameral liquid, *not* immersion in it, was required. Cowen suggests that this would prevent significant passive liquid exchange resulting from pressure differentials during the relatively rapid vertical movement powered by the hyponome; while the osmotic liquid exchange would be for buoyancy adjustment and more persistent (e.g. diurnal) vertical movements requiring only relatively slow exchange of liquid. Thus he regards the surface transport of liquid along the cameral walls towards the ventro-marginal siphuncle in uppermost position as a built-in braking system.

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REPLY TO WESTERMANN

MUTVEI: The osmotic regulation mechanism of the volumes of the cameral liquid in recent and fossil cephalopods has been reviewed by Denton (1974) who arrived at the conclusion that in ammonoids this mechanism cannot yet be interpreted in detail. This topic was only briefly touched on in our paper. The main stress was placed with the fact that in prosiphonate ammonoids, the formation of connecting rings has been delayed, which can only mean that several of the last-formed chambers must have been full of liquid. This condition is fundamentally different from that in all other fossil and recent shell-bearing cephalopods. According to Denton (1974), most recent squids are held neutrally buoyant by an ammonium compound in their tissues. It is significant here that the muscular tissue is greatly reduced and that these squids are not actively swimming animals. Their mode of life would appear to be similar to that of the ammonoids which had feebly developed retractor muscles and which for this and other reasons, discussed in our paper, do not seem to have been actively swimming animals. Contrary to our interpretation, Westermann quotes an opinion that ammonoids were capable of 'relatively rapid vertical movements' by means of the hyponome.

REYMENT: Our results in fact support Westermann's adult migration hypothesis (cf. our paper, p. 635). The inaccurately worded and intuitive remark of mine, quoted in Westermann's first paragraph, needs qualification. This was not based on experiments and cannot be used for calculations. Even so, Westermann's note is well taken, although a better estimate for ceratites can be made by using results on variability (Reyment 1973, pp. 27–28). Computer simulation work I have done recently, using stochastic control theory in which the stochastic element was obtained from empirical information from a set of known variations, indicated for simulated ceratites a possible volume of cameral liquid of some 25–40% of the chambered volume for a range of shell types.

As regards the other comments made in Westermann's note, I beg to differ.

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GLAESSNERELLA (CRUSTACEA DECAPODA, CYMONOMIDAE), A REPLACEMENT NAME FOR *GLAESSNERIA* WRIGHT & COLLINS, 1972 *NON* TAKEDA & MIYAKE, 1969

by C. W. WRIGHT *and* J. S. H. COLLINS

IN a recent monograph on the British Cretaceous Crabs (Wright and Collins 1972) we established a genus *Glaessneria* (type species *Homolopsis spinosa* Van Straelen, 1936, p. 33) for a group of Hauterivian to Cenomanian crabs belonging to the family Cymonomidae. Professor Glaessner has kindly pointed out to us (*in litt.*) that this generic name is preoccupied by *Glaessneria* Takeda & Miyake, 1969, p. 175, set up for a Recent crab from New Zealand.

To replace the homonym *Glaessneria* Wright & Collins, 1972 we propose *Glaessnerella* nom. nov. (type species by original designation *Homolopsis spinosa* Van Straelen).

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