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ERRATA

p. 49, line 21: for '*Diagnosis*' read '*Emended diagnosis*'.

p. 107, Text-fig. 3. 'K' is wrongly oriented, the hinge-line being declined anteriorly.

p. 108, line 11: for 'Table 3' read 'Table 1'.

p. 108, line 27: for 'Table 3' read 'Table 1'.

p. 109, line 3 from bottom: for '(Table 4)' read '(table p. 110)'.

p. 112, caption to Table 2: for 'p. 106' read 'p. 110'.

p. 112, left-hand heading to Table 3: for 'Differences of means in Tables 1 and 2' read 'Differences of means in Table 2 and table p. 110'.

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PALAEONTOLOGY

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RESTUDY OF TYPES OF SEVEN ORDOVICIAN BIFOLIATE BRYOZOA

by JUNE R. P. PHILLIPS

ABSTRACT. Restudy of original material and additional specimens for the type species of six bifoliate cryptostome genera indicates the need for revising the current suprageneric classification. The genera involved are regrouped into three informally named taxonomic categories. *Escharopora recta* Hall, *Graptodictya perelegans* (Ulrich), *G. elegantula* (Hall), and *Stictoporella interstincta* Ulrich are placed in the escharoporid group, *Stictopora fenestrata* Hall, *S. nicholsoni* (Ulrich), and *Eurydictya montifera* Ulrich are placed in the stictoporid group, and *Pachydictya robusta* Ulrich and probably *Trigonodictya conciliatrix* (Ulrich) stand in the pachydictyid group. The categories are distinguished from each other by distinctive lamellate zooecial wall structures, mode of growth of the zooecium from the mesothecal plane, and occurrence of mesopores, acanthopores, and transverse structures in the zooecial tube.

Sectioning of the type species of *Stictopora*, *S. fenestrata*, reveals that the genus *Rhinidictya* is a synonym of *Stictopora*.

INTRODUCTION

RECENT work by the author on the bifoliate cryptostomatous Bryozoa of the Ordovician and Silurian of Anticosti Island indicates that the primary types of many species and genera need to be restudied and critically evaluated. This paper is concerned with the interpretation of the type species of six genera—*Eurydictya*, *Pachydictya*, *Escharopora*, *Stictopora* (*Rhinidictya* is a synonym of *Stictopora*), *Graptodictya*, and *Stictoporella*. The original material for the type species was restudied, and additional material was used for understanding the type species of *Eurydictya*, *Escharopora*, *Stictopora*, *Graptodictya*, and *Stictoporella*. In the generally accepted classification (Bassler 1953) the genera discussed are assigned to three families: *Escharopora* and *Graptodictya* to the Ptilodictyidae, *Stictopora* and *Stictoporella* to the Stictoporellidae, and *Rhinidictya*, *Eurydictya*, and *Pachydictya* to the Rhinidictyidae. As a result of the present study, the genera are regrouped into categories informally named stictoporid, pachydictyid, and escharoporid. These groups are distinguished from each other by the type of zooecial wall structure, mode of growth of the zooecium from the mesothecal plane, structure of the mesothecal plane, occurrence of mesopores, and transverse structures in the zooecial tubes.

The bifoliate mode of growth in Bryozoa generally results in so distinctive an external appearance of the zoarium that genera have commonly been erected on this feature alone without consideration for internal structures. As the nine bifoliate species restudied here have delicate zoaria they are invariably fragmented. *Stictopora nicholsoni* (Ulrich) develops a zoarium with long bifurcate ribbon-shaped branches which originate from a circular basal attachment. *Graptodictya perelegans* (Ulrich) and *Eurydictya montifera* Ulrich develop from a pointed proximal tip from which extends a bifurcate ribbon-shaped branch in the former species and a broad explanate frond in the latter. Although *Escharopora recta* Hall develops from a pointed proximal tip and is initially a narrow cylindrical stem, it becomes a flat stem within a short distance and lacks bifurcation. The distal part of the zoarium is not known. Only zoarial fragments of the other species are known. Zoarial fragments of *Pachydictya robusta* Ulrich, *Trigonodictya conciliatrix* (Ulrich), *Stictopora fenestrata* Hall, *Graptodictya elegantula* (Hall), and *Stictoporella*

[Palaeontology, Vol. 3, Part 1, 1960, pp. 1–25, pls. 1–10.]

interstincta Ulrich are bifurcate and ribbon-shaped. In addition to the different growth forms of the zoaria, externally the seven species have surficial differences in the peristomes, monticules and maculae, mesopores, and striate lateral margins. However, it is the internal structures that show that the nine species should be grouped into three categories. *Escharopora recta*, *Graptodictya perelegans*, *G. elegantula*, and *Stictoporella interstincta* constitute the escharoporid group, *Stictopora fenestrata*, *S. nicholsoni*, and *Eurydictya montifera* form the stictoporid group, and *Pachydictya robusta* and probably *Trigonodictya conciliatrix* stand in the pachydictyid group.

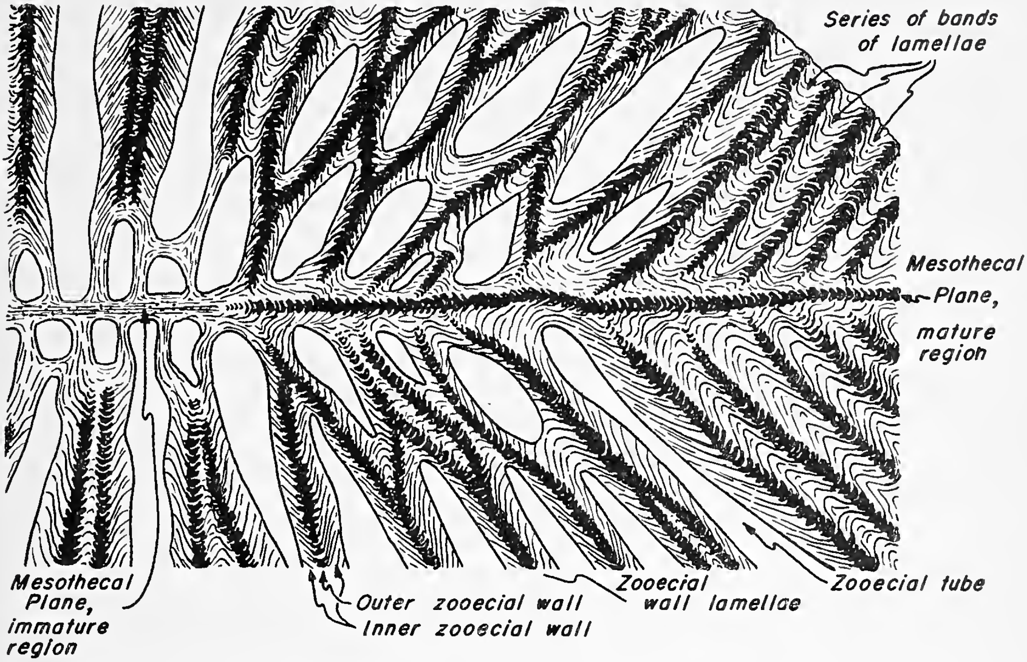
Acknowledgements. I am indebted to the American Association of University Women for the opportunity to undertake this study in the United States. Professor Carl O. Dunbar, Yale University, Drs. G. A. Cooper and R. S. Boardman, U.S. National Museum, Dr. D. W. Fisher, New York State Museum, Dr. D. F. Squires, American Museum of Natural History, and Dr. C. W. Cullison, Geological Survey of Illinois, have aided this study with their kind help. Miss Helen Duncan, U.S. Geological Survey, Dr. R. S. Boardman, and Mr. C. A. Ross, Yale University, kindly read and criticized the manuscript and offered helpful suggestions. The text-figures are the work of Dr. C. A. Ross. Most of the photographs were taken by Dr. J. Scott, U.S. National Museum. Publication of this paper has been aided by a grant from the Schuchert Fund, Peabody Museum.

Abbreviations of repositories: AMNH, American Museum of Natural History. GSI, Geological Survey of Illinois. NYSM, New York State Museum. USNM, United States National Museum.

MORPHOLOGY

Immature and mature regions. In the escharoporid (Pl. 6, fig. 11; Pl. 8, fig. 2) and the stictoporid (Pl. 1, fig. 10; Pl. 3, fig. 6) the line of demarcation between the immature and mature regions is taken at the abrupt change in direction of the zooecial walls. In the pachydictyid group (Pl. 4, fig. 2) the zooecia do not abruptly change direction of growth and the line of demarcation between the immature and mature regions is taken at the initial thickening of the zooecial walls. In this latter group tabulate interspaces develop in the immature region (Pl. 4, fig. 4), whereas in the escharoporid group mesopores are present in the mature region (Pl. 6, fig. 1). In the stictoporid group mesopores and tabulate interspaces are absent.

Mesothecal plane. In all nine bifoliate species the zooecia grow on opposite sides of a mesothecal plane which is a plane of bilateral symmetry through the zoarial branches (Pl. 2, fig. 1; Pl. 4, fig. 1; Pl. 6, fig. 1). This planar structure is formed by the basal zooecial walls where they are laterally contiguous across the zoarial branch (Pl. 1, fig. 7; Pl. 2, fig. 6; Pl. 8, fig. 2; Pl. 9, fig. 7). The basal wall of each zooecium forms a small section of the mesothecal plane and overlaps the preceding basal zooecial wall by as much as one-third its length, thus forming a bilaminate structure. The escharoporid group with zoaria of either bifurcate, ribbon-shaped branches, or non-bifurcate flat stems possesses this simple bilaminate structure of the mesothecal plane in the immature region (Pl. 6, fig. 1; Pl. 9, figs. 4, 5, 6). However, the lateral extension of the mesothecal plane into the mature region at the edges of the zoarial branch causes the mesothecal plane to lose its bilaminate identity although retaining its position in the plane of bilateral symmetry. In the mature region at the edge of the zoarial branch (Pl. 6, figs. 1, 3) the mesothecal plane becomes a band of convex lamellae which continue into the lamellae of the zooecial walls. As the mature region at the edges of the branch widens, new lamellae extend from the mesothecal plane so that the lateral margin consists of a series of bands of lamellae (text-fig. 1).

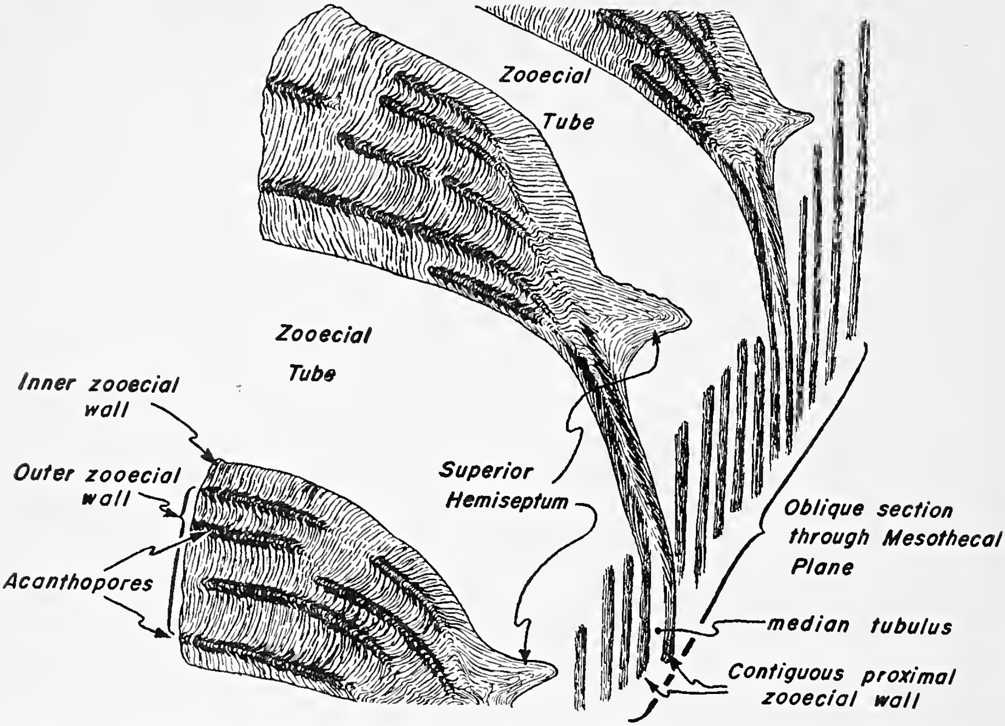


TEXT-FIG. 1. *Escharopora recta* Hall, transverse section, AMNH $\frac{668}{1}$, ×100 approx.; lateral margin on right-hand side.

In the pachydictyid and stictoporid groups the thin mesotheca is pierced by median tubuli (Pl. 2, fig. 1; Pl. 3, fig. 2; Pl. 5, fig. 3; Pl. 7, fig. 4). These tubuli represent the extension of the acanthopores into the basal part of the zooecial walls. In transverse section of *Pachydictya robusta* (Pl. 5, fig. 2) thin young zooecial walls are pierced by dark lamellate acanthopore walls. In *P. robusta* the mesothecal plane with median tubuli extends into the non-zooecial lateral margin (Pl. 4, fig. 3) where acanthopores develop from the mesothecal plane and pass through the lamellae of the walls to the periphery.

Hemisepta and diaphragms. The hemisepta are short shelf-like structures generally developed in the basal mature to submature region and extend into the zooecial tubes from the zooecial wall.

The superior hemiseptum is a short structure projecting from the proximal wall into the zooecial tube. At the base of the mature region in the stictoporid and escharoporid groups, curved lamellae project from the proximal wall into the zooecium (Pl. 1, fig. 7; Pl. 2, fig. 4; Pl. 7, fig. 7) and usually form a hook-shaped hemiseptum as seen in longitudinal section. Subsequent deposition in the later stages of growth may result in addition of lamellae on top of the hemiseptum and these additional lamellae may extend across the zooecial tube (Pl. 1, figs. 7, 10; Pl. 2, fig. 6; Pl. 6, fig. 11). Such a hemiseptum connects either with the mesotheca or the lower part of the distal wall (Pl. 2, fig. 6). *Eurydictya montifera* has two well-developed superior hemisepta which are located in the submature region and basal mature regions (Pl. 3, fig. 6). The pachydictyid group lacks superior hemisepta and the zooecial walls curve gently from the immature to the mature region (Pl. 4, fig. 2).



TEXT-FIG. 2. *Stictopora nicholsoni* (Ulrich), oblique longitudinal section through the mesothecal plane, USNM 137615, ×150 approx.

Inferior hemisepta occur as short spines and project at right angles from the mesotheca or the distal wall and may be present in the stictoporid group (Pl. 2, fig. 4).

In the stictoporid and escharoporid groups transverse structures other than hemisepta are rare. In some specimens in the immature and mature regions a thin laminate diaphragm crosses a zooecial tube, and curves up along the inner walls eventually passing into the lamellae of the zooecial walls (Pl. 9, fig. 7).

In the pachydictyid group diaphragms are sparse in zooecia, and possess a laminate structure. They thicken slightly at their connexion with the inner zooecial wall (Pl. 5, fig. 1). Thus the diaphragms curve distally along the inner zooecial wall for a considerable distance before they pass into the zooecial wall. In the submature region the diaphragms are thin, laminate structures and in the outer mature region they thicken greatly and may amalgamate to fill completely the zooecial tube.

Acanthopores and median tubuli. Acanthopores are present only in the stictoporid and pachydictyid groups. They are of one size and are small in diameter in comparison to similar well-developed structures in trepostomes such as *Leioclema.*

In the stictoporid and pachydictyid groups acanthopores occur in the basal zooecial walls in the mesothecal plane where they have been called median tubuli. From the mesothecal plane they extend outwards through the zooecial walls to the periphery, and maintain growth approximately parallel to the direction of growth of the zooecia (Pl. 5, figs. 2, 3). In the mature region they generally multiply and are very numerous around the zooecial apertures (Pl. 1, fig. 7; Pl. 2, fig. 5; Pl. 3, figs. 3, 7). These tubules possess a clear lumen and lamellate wall structure which intertongues with the zooecial wall structure. In longitudinal section they appear as narrow distinct bands extending through the zooecial walls (Pl. 1, fig. 7). In the stictoporid group the acanthopore walls consist of distally convex lamellae which are more closely spaced than the lamellae of the zooecial walls. Unlike the acanthopore wall structure in such trepostomes as *Bastostoma* and *Trematopora*, in which the lamellae are steeply inclined, the acanthopore wall structure in the stictoporid and pachydictyid groups is smoothly arched. In tangential section (Pl. 2, fig. 5; Pl. 3, fig. 5; Pl. 5, fig. 4) the acanthopores are small tubes outlined by thin dense walls.

Mesopores. In tangential section mesopores appear as small polygonal tubes enclosed in the zooecial walls (Pl. 10, figs. 4, 6). The tubes are smaller than the adjoining zooecia, but the wall structure of the mesopores and zooecia is identical. In the stictoporid group mesopores are absent and in the escharoporid group non-tabulate mesopores occur only in the mature region. In the pachydictyid group tabulate interspaces occur in the immature and submature regions (Pl. 4, figs. 1–4).

Monticules and maculae. The terms monticule and macula describe aggregations of several types of zoarial deposits. Surficially marked either by elevated, or by flat or slightly depressed areas, they are common features in many zoaria, and may represent stages of zoarial growth. The flat or slightly depressed areas apparently occur in the younger part of a zoarium and the elevated areas apparently occur in the older part of a zoarium, e.g. *Pachydictya robusta*.

In *Stictopora nicholsoni* and *Escharopora recta* the zoaria apparently lack monticules and maculae. In *Graptodictya perelegans* and *G. elegantula* in areas of bifurcation the zooecia are enlarged and have thickened walls (Pl. 8, figs. 3, 4). These areas may be regarded as rudimentary maculae. In *Stictoporella interstincta* maculae consist of aggregations of mesopores (Pl. 10, fig. 3) level with the surface of the zoarium. In *Pachydictya robusta* (Pl. 4, fig. 5) both monticules and maculae consist of elevated enlarged zooecia and thickened walls.

In *Euridictya montifera* monticules are well developed across the zoaria (Pl. 3, figs. 3, 4, 7). They also have lamellae over the elevated zooecia, as in *Pachydictya robusta*.

Zooecial aperture. The arrangement and attitude of the zooecial apertures vary across the zoarial branch. Zooecia situated in the middle of the branch generally are aligned parallel to the direction of growth of the branch and open directly to the surface; such zooecia are described as median-direct (Pl. 2, fig. 2). Zooecia situated on the margin of the zoarial branch commonly are directed obliquely to the zoarial surface and also to the axis of growth of the branch; these are termed lateral-oblique zooecia (Pl. 9, figs. 1, 2). A linear series of zooecia parallel with the direction of growth of the zoarial branch is termed a range (Pl. 1, fig. 8).

In the three groups lateral addition of zooecia by budding in the lateral margins widens the zoarial branches. Initially the new zooecia have lateral-oblique zooecial apertures on the margins of the branches, but after bifurcation of a branch these lateral ranges become realigned as median-direct zooecia. In *Escharopora recta* (Pl. 6, figs.1, 3) zooecia bud laterally from the mesothecal plane and extend outwards to appear on the edge of the zoarial branch. The new buds near the lateral margins lack the typical thin basal walls but instead are enclosed by lamellae of the mature region.

Distal growth of the zoarial branches takes place in the mesothecal plane, and zooecia bud distally from the preceding longitudinal zooecia.

SYSTEMATIC DESCRIPTIONS

Stictoporid group

In the stictoporid group (text-fig. 2) the early thin walls of the zooecia grow only a short distance above the mesothecal plane as steeply inclined partitions before abruptly changing direction, curving away from the mesothecal plane (Pl. 1, fig. 10), and thickening greatly. In the mature region lamellae, steeply inclined towards adjacent zooecia, form the inner zooecial wall. These short lamellae curve sharply as broad arches toward adjacent zooecia and are distally convex. Longitudinal sections through the mature region display this lamellate wall structure (Pl. 3, fig. 6), and tangential sections show a narrow concentric band forming the inner wall, and broad lamellae in the outer wall

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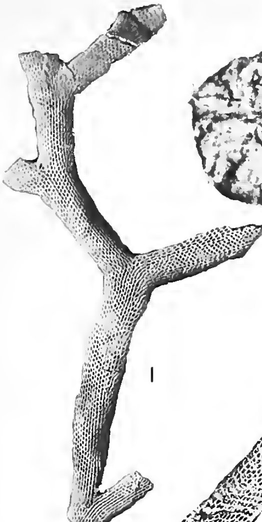
EXPLANATION OF PLATE 1

Figs. 1, 2, 4, 6–8, 10. *Stictopora nicholsoni* (Ulrich). 1, Zoarial fragment, paratype USNM 137620, ×2. 2, External view of lectotype USNM 137622, ×3. 4, Median tubuli in mesothecal plane, transverse section of lectotype USNM 137622, ×100. 6, Deep tangential section near the base of the mature region and passing obliquely through the mesothecal plane; hemisepta project from the zooecial walls; mesothecal plane passes obliquely across the photograph from lower left to upper right hand corner, USNM 137617, ×50. 7. Oblique longitudinal section passing through the mesothecal plane; on the left near the periphery, acanthopores are cut obliquely, USNM 137615, ×50. 8, Deep tangential section of lectotype USNM 137622 having ranges of elongate zooecia and linear series of acanthopores, ×50. 10, Longitudinal section of lectotype USNM 137622 having superior hemisepta, ×50.

Figs. 3, 5, 9, 11. *Stictopora fenestrata* Hall. 3, Transverse section of topotype NYSM 11231 having median tubuli, ×50. 5, Tangential section of lectotype NYSM 915 showing longitudinal series of acanthopores in zooecial walls, ×100. 9, External view of lectotype NYSM 915, ×5, most of the zoarium is split along the mesothecal plane. 11, Oblique longitudinal section of lectotype NYSM 915 cutting obliquely through the mesothecal plane and zooecia, ×100.

EXPLANATION OF PLATE 2

Figs. 1–6. *Stictopora nicholsoni* (Ulrich). 1, Transverse section of paratype USNM 137615 with median tubuli, ×50. 2, Tangential section in older part of zoarium where thickened zooecial walls almost obscure the zooecial apertures; acanthopores are numerous; paratype USNM 137615, ×50. 3, Tangential section in younger part of zoarium having wide zooecial apertures, paratype USNM 137620, ×50. 4, Longitudinal section of paratype USNM 137618 showing superior and inferior hemisepta, ×50. 5, Tangential section of paratype USNM 137615 showing acanthopores in the lamellate zooecial walls, ×100. 6, Oblique longitudinal section through mesotheca and early part of zooecium, paratype USNM 137615, ×100.



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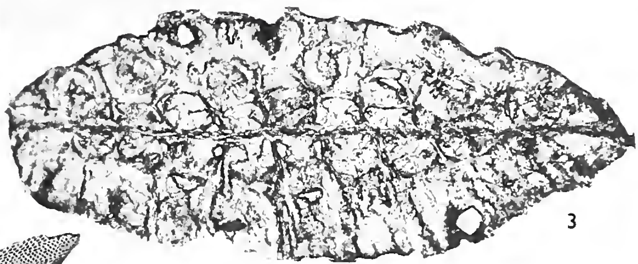

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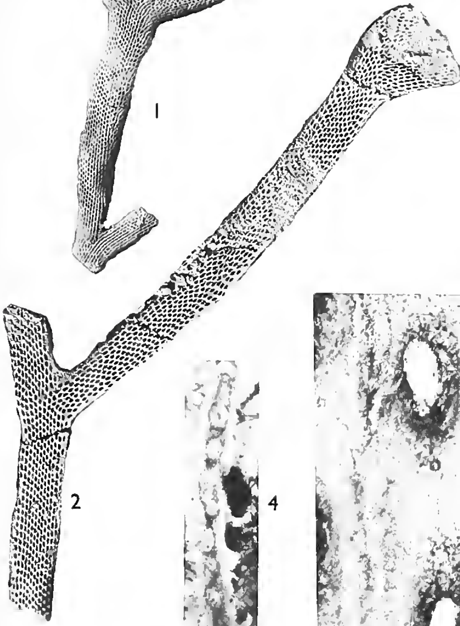

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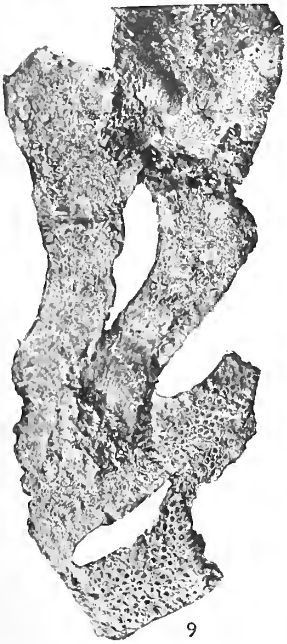

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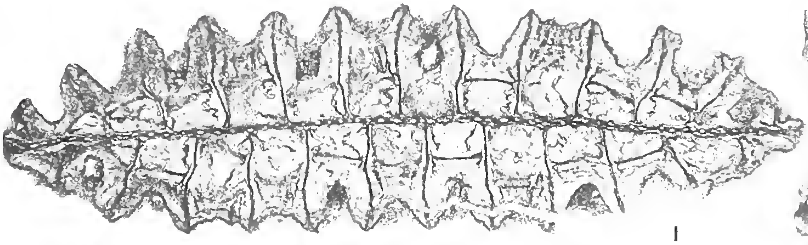
PHILLIPS, *Stictopora*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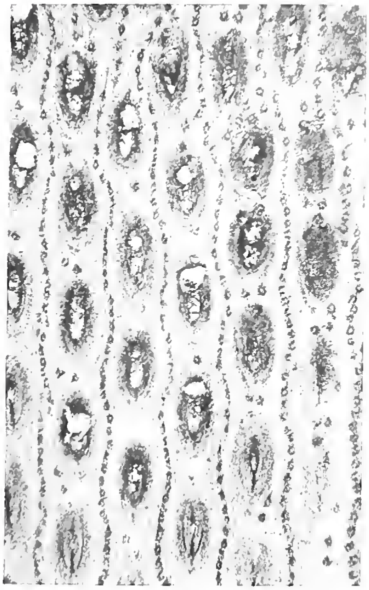
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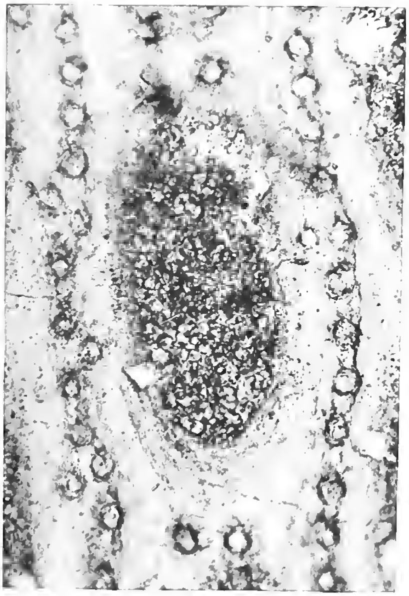
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6

PHILLIPS, *Stictopora*

(Pl. 2, fig. 5; Pl. 3, fig. 5). As in the escharoporid and pachydictyid groups no line of demarcation marks a boundary between adjacent zooecia, there being apparently continuous lamellae from one zooecium to the next. Thickening of the zooecial walls may be so extensive that the zooecial apertures become greatly restricted (Pl. 2, fig. 2). The mesothecal plane is pierced by median tubuli which represent the extension of the acanthopores into the basal part of the zooecial walls. Acanthopores are numerous around the zooecial apertures. They have a clear lumen and lamellate wall structure. Superior hemisepta are developed at the base of the mature region, and the genus *Eurydictya* is characterized by the development of two superior hemisepta at the base of each proximal zooecial wall. Diaphragms are rare and when present they are thin laminate structures. Inferior hemisepta are usually present.

Genus STICTOPORA Hall 1847

Type species *Stictopora fenestrata* Hall (1847, p. 16), designated Ulrich (1886, p. 67)

Stictopora Hall 1847, p. 73.
Sulcopora d'Orbigny 1849, p. 499.
Rhinidictya Ulrich 1882, p. 152.

Emended definition. Bifoliate branching zoarium which grows from a circular basal attachment. Mesothecal plane extends the full width of the zoarium and possesses numerous median tubuli. Zooecia bud from the mesotheca in ranges and they alternate on opposite sides of the mesotheca with overlap of the proximal zooecial walls. Small acanthopores in the zooecial wall extend from the mesotheca to the periphery and the dark lamellate acanthopore walls are very distinct in longitudinal section. Acanthopores multiply at the base of the mature region.

Thin longitudinal laminate zooecial walls in the immature region thicken abruptly into the sub-mature region with a change in direction of zooecial growth, and the walls become curved lamellae in the mature region. The zooecial wall lamellae slope steeply along the inner wall towards adjacent zooecia. This narrow inner band of wall lamellae curves over abruptly to form broad convex lamellae in the outer part of the zooecial wall. The boundary between adjacent zooecial walls is not apparent. Lamellate superior hemisepta are present on the proximal wall. Inferior hemisepta and diaphragms are limited in their development.

Stictopora fenestrata Hall 1847

Plate 1, figs. 3, 5, 9, 11

Stictopora fenestrata Hall 1847, p. 16, pl. 4, figs. 4*a*, 4*b*, 4*c*, 4*d*.
Rhinidictya fenestrata (Hall); Clarke 1903, p. 159.

Type material. Lectotype NYSM 915 ($\frac{6810}{1}$), designated here as specimen figured by Hall (1847, pl. 4, figs. 4*c*, 4*d*); Chazy limestone (Chazy), Clinton County, New York.

Description. Zoaria: zoarial fragment of lectotype 2 cm. in length and topotype material reaches 1 cm. in length. Very slender ribbon-shaped branches with frequent bifurcations which occur about every 4 mm. in the lectotype. The branches have straight and very narrow margins without zooecia, and the zooecial surfaces are slightly convex, apparently lacking monticules and maculae.

Zooecia are oblique to the surface and form ranges in which the zooecia generally alternate (Pl. 1, fig. 9). Longitudinal series of acanthopores demarcate the ranges and surround the zooecial apertures (Pl. 1, fig. 5).

Zooecial structures: the early zooecial walls are thin and extend only a short distance at an inclination of 15–25° to the mesothecal plane before they abruptly change direction and curve outward with an angle of 60° to the mesothecal plane. The walls thicken greatly at the base of the mature region. Lamellae lining the inner zooecial wall in the mature region lie steeply inclined toward adjacent zooecia. Toward the outer wall these steep lamellae curve abruptly toward adjacent zooecia and become broad convex lamellae (Pl. 1, fig. 11). No demarcation line marks a boundary between adjacent zooecia and these lamellae are apparently continuous between zooecia. At the base of the mature region very short superior hemisepta are present.

Thin laminate diaphragms may be present and usually one diaphragm per zooecial tube crosses the tube in the immature or submature region.

Acanthopores (Pl. 1, fig. 5) are 0·002 mm. in diameter and originate as median tubuli in the mesothecal plane. In the mature region the acanthopores multiply and are numerous at the periphery where they may form three or four longitudinal series between adjacent zooecia. The dark laminate acanthopore walls intertongue with the zooecial wall lamellae.

Measurements	*Lectotype*	*Topotype*
Zoarial branch width—mm.	1·8–2·0	. .
Zoarial branch thickness—mm.	0·5–0·6	0·4–0·6
Width of lateral margin—mm.	0·2	. .
Ranges on branch	11–12	11–12
No. of median ranges	7–8	7–8
No. of lateral ranges at each margin	1 or 2	1 or 2
No. of zooecia in 2 mm.		
Longitudinally	6	7
Laterally	10–11	12
Acanthopores per zooecium	At least 16	At least 16
Interspace between zooecia in mm.		
Longitudinally	0·18–0·22	0·11–0·20
Laterally	0·10–0·13	0·10–0·15
Zooecial apertures—mm.	(0·06×0·03) (0·10×0·06)	(0·08×0·06) (0·15×0·10)
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·60–0·75	0·75

Remarks. Stictopora fenestrata is very similar to *S. nicholsoni* in possessing numerous median tubuli, acanthopores, and slender bifurcating ribbon-shaped branches. It differs from this species in poor development of superior hemisepta and more oblique zooecial apertures.

Topotype material for study of this species came from the rock specimen containing the lectotype.

The generic status of the genus *Stictopora* has long been in confusion. The chronological development of the systematics is briefly as follows.

Hall (1847, pp. 73, 74) erected the genus *Stictopora*, describing six species including *S. fenestrata* and *S. glomerata* from the Chazy, New York, and *S. elegantula* and *S.*? *acuta* from the Trenton, New York. Hall, however, did not designate a type species. As *S.*? *acuta* was doubtfully assigned to the genus it is not available for selection as the type of the genus. D'Orbigny (1849, p. 499) erected the genus *Sulcopora*, choosing *Stictopora fenestrata* Hall as the type species. Ulrich (1882, p. 152) erected the genus *Rhinidictya* on a Trenton species, *R. nicholsoni* Ulrich (1882, p. 171), from High Bridge, Kentucky, and he made no diagnostic comparison with other genera. Then in 1886 Ulrich, in his discussion of *Stictopora mutabilis* var. *minor*, stated that *S. fenestrata* which he (1886, p. 67) designated the type of the genus *Stictopora* was more nearly related to *R. nicholsoni* than to *S.*? *acuta*, and that *Rhinidictya* was a synonym of *Stictopora*. With this designation of *S. fenestrata* as the type species of *Stictopora*, *Sulcopora* fell into synonymy with *Stictopora*. Ulrich further stated that when he had proposed the genus *Rhinidictya* he was under the impression that *S. fenestrata* was closely allied to *S.*? *acuta* and that *Rhinidictya* was a distinct genus. As Ulrich was unable to study the type material of *S. fenestrata* he based his interpretation of this species on homeotypes from what he regarded as Chazy limestone in Kentucky and Tennessee. The type material of the species has remained unsectioned until now.

In the succeeding year Hall (1887, p. xx) designated *S. elegantula* as the type species of *Stictopora* and the majority of later workers followed this designation and overlooked Ulrich's earlier designation of *S. fenestrata* as the type species. Consequently species assigned to *Stictopora* require individual assessment of structures in the light of present-day systematics.

In my recent search for the type material for *Stictopora fenestrata* Hall, it was found that the specimen listed by Whitfield and Hovey (1898, p. 21) as the type specimen of *S. fenestrata* Hall does not compare with any of Hall's original figures illustrating three specimens. Hall's two specimens (Hall 1847, pl. 4, figs. 4*c*, 4*e*) have not been located but in the U.S. National Museum there are two very thick thin-sections with tangential sections of three fragments, and these sections are labelled '*Sulcopora fenestrata* (Hall), Chazyan, Chazy, N.Y., no. 114234, section of type'. These sections may have been cut from Hall's original type material.

Examination of these two sections shows that the zooecia are in longitudinal ranges and that they have small circular to elliptical apertures separated by lateral and longitudinal interspaces as wide as the apertures. The zooecial interspaces or walls are finely lamellate and are pierced by numerous acanthopores. As many as four longitudinal series of acanthopores are present in the lateral interspaces. The zooecial apertures are oblique to the plane of section. These features are the same as those seen in *Stictopora fenestrata*.

Stictopora nicholsoni (Ulrich) 1882

Plate 1, figs. 1, 2, 4, 6–8, 10; Plate 2, figs. 1–6

Rhinidictya nicholsoni Ulrich 1882, p. 170, pl. 8, figs. 6, 6*a*, 6*b*.

Type material. Lectotype here designated as USNM 137622, specimen figured by Ulrich (1882, pl. 8, figs. 6, 6*a*); from Tyrone formation (Trenton), High Bridge, central Kentucky. Sectioned paratypes

USNM 137615–21, 137641, 137642; unsectioned paratypes consisting of five very small zoarial fragments, USNM 43706; from Tyrone formation (Trenton), High Bridge, central Kentucky.

Description. Zoaria: narrow ribbon-shaped branches of the zoaria fragment very readily and even the weight of the matrix enclosing the colonies is sufficient to break the branches. Zoarial fragments in the syntypic series range in length from 0·5 cm. to 1·5 cm. Specimen USNM 137615 is a well-preserved colony in which the branches are essentially parallel, except for bifurcations and undulations of the branches through the matrix.

Bifurcation of the branches of the zoaria is frequent. In one zoarial fragment, USNM 137620, the interval of bifurcation gradually decreases from 1·4 cm. to 0·5 cm. in four bifurcations. In USNM 137621 the more distal branches grow back over the earlier proximal branches.

In USNM 137616, which appears to be the more proximal region of a zoarium, the bifurcations are numerous, with fifteen bifurcations in 2·9 cm. Small circular processes, 0·7 to 0·9 mm. diameter, grow from the lateral region of the branches, and may be calcareous supports for the zoarium.

Branches have straight, narrow margins without zooecia, and the surfaces of the zoaria are essentially flat and lack monticules and maculae (Pl. 1, figs. 1, 2).

The elongate zooecia, oblique to the surface, form ranges, and the zooecia usually alternate in adjacent ranges (Pl. 1, fig. 8; Pl. 2, figs. 2, 3). The number of ranges across a branch is exceedingly variable due to the many bifurcations of the branches. The median-direct zooecia are always elongated parallel to the direction of growth of the zoarial branch. However, the two outermost ranges on a lateral margin have lateral-oblique zooecia.

Longitudinal series of acanthopores demarcate the ranges and enclose the zooecia (Pl. 1, fig. 8; Pl. 2, figs. 2, 3, 5). The thickness of the longitudinal and lateral zooecial walls varies considerably, as seen from the table of measurements. Likewise the size of the zooecial apertures is variable. In the older part of the zoarium zooecial walls are wider than in the younger parts of the zoarium (Pl. 2, figs. 2, 3). In USNM 137622 the longitudinal distance between zooecia increases distally along the branch away from the point of bifurcation. The number of zooecia, six, longitudinally located per 2 mm. on a branch is extremely constant.

Zooecial structures: the early zooecial wall is thin and in the mesothecal plane it overlaps the proximal part of the preceding zooecial wall by about one-third its length. In Pl. 2, fig. 6, the mesothecal plane is cut obliquely to display the contiguous basal zooecial walls. The thin zooecial walls extend only a short distance at an inclination of 35° to 45° to the mesothecal plane before they abruptly change direction, curving outward with an angle of 65° to the mesothecal plane. At this change in direction of growth, which marks the transition from the immature region to the mature region, the walls thicken greatly (Pl. 1, fig. 10; Pl. 2, fig. 6). Lamellae lining the inner zooecial wall in the mature region lie steeply inclined toward adjacent zooecia. Toward the outer wall these steep lamellae curve abruptly toward adjacent zooecia and become broad, distally convex lamellae. No demarcation line marks a boundary between adjacent zooecia and these lamellae are apparently continuous structures between zooecia. Additional convex lamellae distally widen the mature region. The zooecial apertures may become greatly restricted with increasing development of lamellae, mainly at the distal surface, but also along the inner zooecial wall (Pl. 2, fig. 2).

At the base of the mature region, curved lamellae from the proximal wall project out into the zooecial tube and usually form a hook-shaped hemiseptum. At later stages of growth additional lamellae may be deposited on top of the hemiseptum and may extend across the zooecial tube. Such an extension of lamellae on top of the hemiseptum connects either with the mesotheca or the lower part of the distal wall (Pl. 2, fig. 6). In some zooecia an inferior hemiseptum occurs on the mesotheca and projects transversely into the zooecial tube (Pl. 1, fig. 6; Pl. 2, fig. 4).

Diaphragms are rare but, when present, these thin, laminate structures cross the zooecial tube and curve distally along the inner walls, eventually passing into the wall lamellae.

Acanthopores (Pl. 1, fig. 7; Pl. 2, fig. 5) are 0·01 to 0·02 mm. in diameter, and originate as median tubuli in the mesothecal plane. These tubuli extend outwards as acanthopores to the periphery of the zoarium, approximately parallel to the direction of zooecial growth. In the mature region the acanthopores commonly multiply and are numerous at the periphery (Pl. 2, figs. 2, 3). Distally convex lamellae of the acanthopore walls are more closely spaced than those of the zooecial walls so that the acanthopore walls which intertongue with the zooecial wall lamellae are distinct bands in longitudinal sections (Pl. 1, fig. 7).

The non-zooecial lateral margins also have distally convex lamellae which are pierced by acanthopores.

Measurements	*USNM 137622*	*USNM 137615*	*USNM 137616*	*USNM 137617*	*USNM 137620*
Zoarial branch width—mm.	1·85–2·0	1·7 incomplete	2·9	1·7	1·1–2·1
Zoarial branch thickness—mm.	0·46	0·6–0·9	indet.	indet.	indet.
Width of lateral margin—mm.	0·20	0·4–0·5	indet.	indet.	indet.
Ranges on branch	8–14	12–14	15	10	12–13
No. of median ranges	6–9	10	12–13	7–8	9–10
No. of lateral ranges on each margin	1–2	2	1–2	1–2	1–2
No. of zooecia per 2 mm.					
Longitudinally	6	6–7	6	6	7
Laterally	12–16	10–14	12–14	12	11–12
Acanthopores per zooecium	22 av.	2 av.	22 av.	22 av.	20–22
Interspace between zooecia—mm.					
Longitudinally	0·08–0·26	0·11–0·20	0·07–0·26	0·13–0·16	0·13–0·16
Laterally	0·04–0·02	0·05–0·10	0·07–0·16	0·08	0·10–0·13
Zooecial apertures—mm.	(0·22 × 0·07)	(0·22 × 0·08) (0·11 × 0·05)	(0·16 × 0·04)	(0·2 × 0·08) (0·12 × 0·05)	. . . .
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·74	0·68	. .	. .	. .

Remarks. *Stictopora nicholsoni* resembles *S. fenestrata* and *Eurydictya montifera* in possessing median tubuli, acanthopores and regularly arranged elongate zooecial apertures but differs from *S. fenestrata* in having more strongly developed superior hemisepta and differs from *E. montifera* in having only one superior hemiseptum per zooecium, more obliquely inclined zooecia in the mature region, and in lacking monticules. The growth of *S. nicholsoni* and *E. montifera* is also different; *S. nicholsoni* has bifurcate ribbon-shaped branches and *E. montifera* has a broad zoarial expansion.

Of the original material figured for *Stictopora nicholsoni*, the tangential section (Ulrich

1882, pl. 8, fig. 6*b*) has not been located. As the lectotype designated here (Pl. 1, fig. 2) was an unsectioned fragment, it seems that the original figured tangential section was made from a specimen other than the lectotype.

Eurydictya montifera Ulrich 1890

Plate 3, figs. 1–7

Eurydictya montifera Ulrich 1890, p. 521, pl. 30, figs. 3–3*d*.

Type material. Fragment of holotype GSI 2668; fragment of holotype USNM 137614; from Cincinnati group (Richmond), Wilmington, Illinois.

Description. Zoaria: these are broad bifoliate expansions with distinct elevated monticules which are distributed across the zooecial surface (Pl. 3, fig. 1). The zoarium develops from a pointed proximal tip and extends as a broad explanate frond. Lateral margins of the zoaria are indistinct. Zooecia are regularly arranged in cross-line pattern between monticules. The monticules are low knobbly elevations rising 0·1 to 0·5 mm. above the zoarial surface. The diameter and elevation of individual monticules vary greatly, some monticules are low undulations and others distinct knobs and on occasions two or more monticules may coalesce. In the mature stage of development of the zoarium the zooecial apertures in the monticules are covered and a circle of larger zooecia surrounds the cones.

Zooecial structures: zooecia leave the mesothecal plane at an angle of 20° to 25°. The exceedingly fine laminae of the mesothecal wall are inclined steeply outwards from the plane. In the immature region the thin early zooecial wall is longitudinal laminate and these laminae are almost parallel to the mesothecal plane.

A sharp change in the direction of growth of the zooecium, considerable thickening of the zooecial walls and development usually of two superior hemisepta mark the beginning of the mature region (Pl. 3, fig. 6). The angle of the zooecial wall in the mature region to the mesothecal plane is 80°. The walls of the mature region possess the same lamellate structure as in *Stictopora nicholsoni*. Lamellae lie steeply inclined toward adjacent zooecia and line the inner zooecial wall. They curve abruptly toward adjacent zooecia as broad, distally convex continuous sheets. The lamellae in the two superior hemisepta in a zooecium are steeply inclined as in the inner zooecial wall. Hemisepta do not extend across the zooecial tube and inferior hemisepta are absent.

Acanthopores, 0·02 mm. in diameter, originate in the mesothecal plane and extend through the zooecial wall to the periphery (Pl. 3, fig. 2). They multiply in the mature

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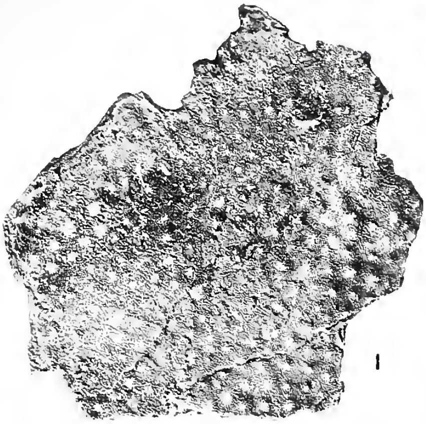
EXPLANATION OF PLATE 3

Figs. 1–7. *Eurydictya montifera* Ulrich. 1, External view of zoarium with prominent monticules, fragment of holotype GSI 2668, ×1. 2, Transverse section showing median tubuli in mesothecal plane, fragment of holotype USNM 137614, ×50. 3, Deep tangential section through monticule, holotype GSI 2668, ×50. 4, Shallow tangential section through monticule, acanthopores pierce the wall lamellae, holotype USNM 137614, ×50. 5, Tangential section of zooecium with sharp apertural outline; zooecial wall lamellae pierced by acanthopores, holotype USNM 137614, ×100. 6, Longitudinal section through holotype GSI 2668 showing well-developed hemisepta, ×50. 7, Longitudinal section through holotype GSI 2668 showing zooecial apertures in monticule filled with transverse lamellae, ×100.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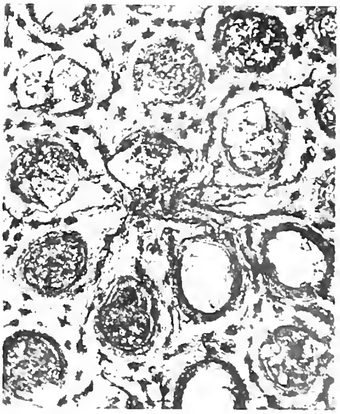
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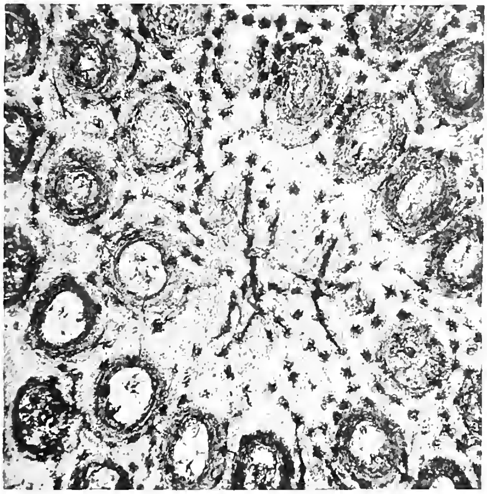
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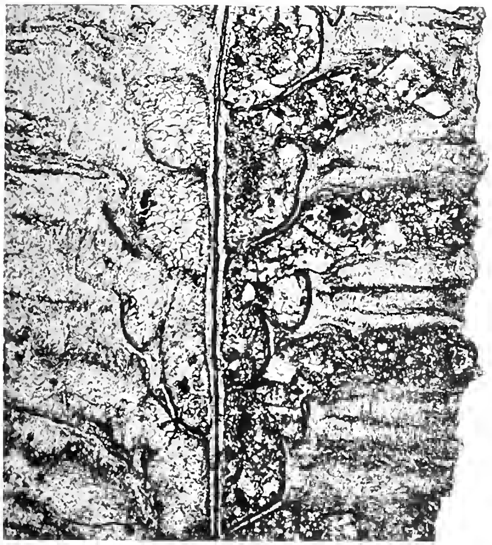
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PHILLIPS, *Eurydictya*

region and are numerous at the surface of the zoarium. The acanthopore walls are composed of distally convex laminae and have structure similar to those in *Stictopora nicholsoni*. Median tubuli are numerous in the mesothecal plane and are easily observed in transverse thin section (Pl. 3, fig. 2).

Diaphragms are not present. Monticules consist of zooecia elevated above the zoarial surface and are covered by lamellae. Longitudinal sections through monticules show variable structures. In some monticules the zooecia are continuous from the mesothecal plane to the periphery and have typical zooecial structures (Pl. 3, fig. 7). But in other monticules the elevation may appear as a greatly disordered number of partitioned zooecia. The zooecial apertures are covered by a lateral extension of the lamellate zooecial wall across the zooecial apertures. Acanthopores enclosing zooecia in the monticules are oblique to the direction of zooecial growth, and radiate outward around the apex of the elevated monticule (Pl. 3, fig. 7).

Measurements	*Holotype*
Zoarial branch thickness—mm.	1·46–1·60
No. of zooecia per 2 mm.	
Longitudinally	7·5
Laterally	10–11
Acanthopores per zooecium	18–21
Interspace between zooecia—mm.	
Longitudinally	0·09–0·13
Laterally	0·13–0·19
Interspace between zooecia near monticule—mm.	
Longitudinally	0·19
Laterally	0·10–0·14
Zooecial aperture—mm.	(0·14×0·12) to (0·16×0·14)
Zooecial aperture in monticule—mm.	(0·16×0·14) to (0·18×0·16)
Area of monticule—sq. mm.	0·8 av.
Distance between monticules—mm.	2·5–3·0
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·72 in proximal region of zoarial fragment 0·62 in distal region of zoarial fragment

Remarks. Eurydictya montifera is compared with *Stictopora nicholsoni* in Remarks on *S. nicholsoni*. The covered monticules and well-developed superior hemisepta, usually two per zooecium, characterize the species. Distinct acanthopores are abundant.

The fragmentary zoarium of the holotype consists of two pieces. One fragment, GSI 2668, was figured by Ulrich 1890, Pl. 30, fig. 3, and measures 6×5 cm. but is partly obscured by matrix. The other fragment is specimen USNM 137614, a small triangular fragment of 1·5 sq. cm. which has been broken from the proximal region of GSI 2668.

The figured tangential, longitudinal and transverse sections of Ulrich (1890, pl. 30, figs. 3*b*, 3*c*, 3*d*, respectively) are in the type collection of the U.S. National Museum.

Pachydictyid group

In the pachydictyid group the zooecia leave the mesothecal plane at about 80° and their thin early walls are pierced by dark lamellate acanthopore walls (Pl. 5, figs. 1, 2). Tabulate interspaces appear between the zooecial walls a short distance above the mesothecal plane in the immature region (Pl. 4, figs. 1, 4). The zooecial walls thicken without change in direction of growth; the base of the mature region is taken at this thickening of the zooecial walls (Pl. 4, fig. 3; Pl. 5, figs. 1, 2). In the mature region the zooecial walls are composed of broad, distally convex lamellae in the outer walls, as in the stictoporid wall structure, but more steeply inclined lamellae form the inner walls of the pachydictyid group (Pl. 5, figs. 1, 2). The inner walls in this group are composed of exceptionally long lamellae aligned parallel to the direction of zooecial growth and form the lining to the broadly arched lamellae of the outer walls. The long lamellae may be traced a considerable distance distally before they pass from the inner wall into the broadly arched lamellae of the outer wall. The distally arched lamellae of the outer wall, curving toward adjacent zooecia intertongue in an irregular, thin, dark zone (Pl. 4, figs. 2, 4; Pl. 5, fig. 2). In tangential section (Pl. 4, fig. 6; Pl. 5, fig. 4) the wall structure is similar to the stictoporid wall but the inner concentric band corresponding to the long lamellae of the inner wall is more distinct.

The mesothecal plane is pierced by median tubuli which represent the extension of the acanthopores into the basal part of the zooecial walls. Acanthopores are numerous around the zooecial apertures and have a clear lumen and lamellate wall structure. Hemisepta are absent. Diaphragms are present in the mature region of zooecia; in the early mature region they are thin laminate structures and in the outer mature region the laminate diaphragms are greatly thickened and they may amalgamate to fill completely the zooecial tube. Tabulate interspaces are present in the immature and submature regions.

Pachydictya robusta Ulrich 1882

Plate 4, figs. 1–6; Plate 5, figs. 1–4

Pachydictya robusta Ulrich 1882, p. 173, pl. 8, figs. 10*a*–c.

Type material. Lectotype here designated USNM 137608, specimen illustrated by Ulrich 1890, pl. 8, fig. 10. Sectioned paratypes USNM 137609 to 137611, 137623 to 127625, and thin sections illustrated

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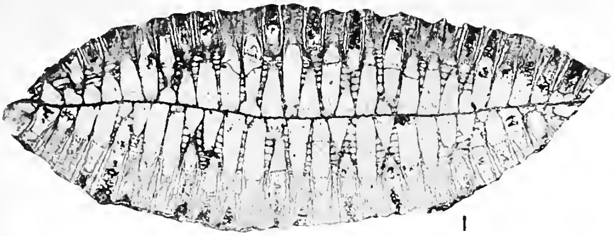
EXPLANATION OF PLATE 4

Figs. 1–6. *Pachydictya robusta* Ulrich. 1, Transverse section of paratype USNM 137609, ×7. 2, Longitudinal section of lectotype USNM 137608 showing narrow immature region with abrupt development of tabulate interspaces, ×50. 3, Transverse section of lectotype USNM 137608 having median tubuli, closely tabulate interspaces, and acanthopores, ×50. 4, Transverse section of lectotype USNM 137608 showing lamellate wall structure, ×100. 5, External view of lectotype USNM 137608 having distinct non-zooecial lateral margins, ×1. 6, Tangential section of lectotype USNM 137608 with small numerous acanthopores in the zooecial walls, ×100.

EXPLANATION OF PLATE 5

Figs. 1–4. *Pachydictya robusta* Ulrich. 1, Longitudinal section through zooecial wall and passing from immature to mature region; thin walls in the immature region, rapid thickening of the walls in the mature region and steeply inclined lamellae of the inner walls curving abruptly into broad convex lamellae. Thin layered diaphragms curve sharply up along the inner zooecial wall for some distance before curving into the outer convex wall lamellae; dense acanthopore walls pierce the zooecial walls, paratype USNM 137609, ×100. 2, Transverse section of USNM 137611 showing median tubuli in the mesothecal plane and median tubuli extending as acanthopores into the mature region where they multiply, ×100. 3, Transverse section of USNM 137611 showing median tubuli in mesothecal plane, ×100. 4, Tangential section of USNM 137609 across zooecia and a monticule, ×50.



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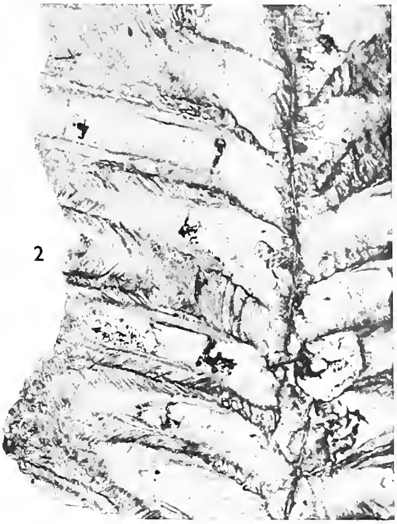

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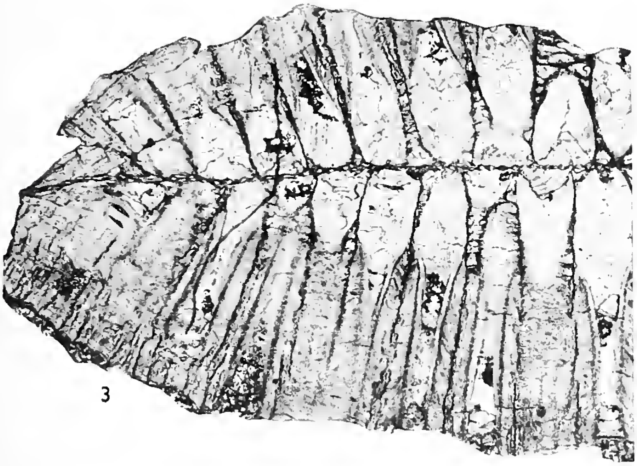

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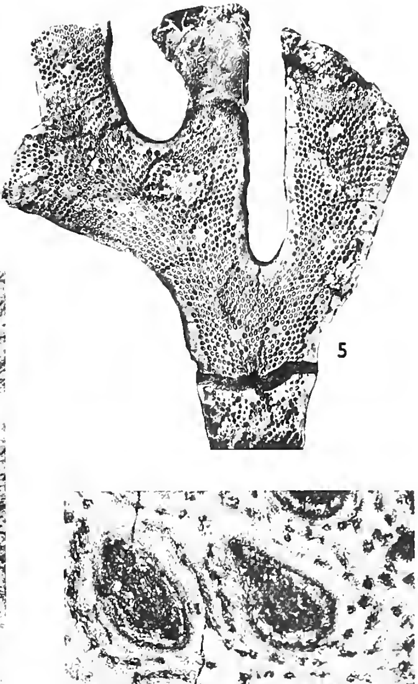

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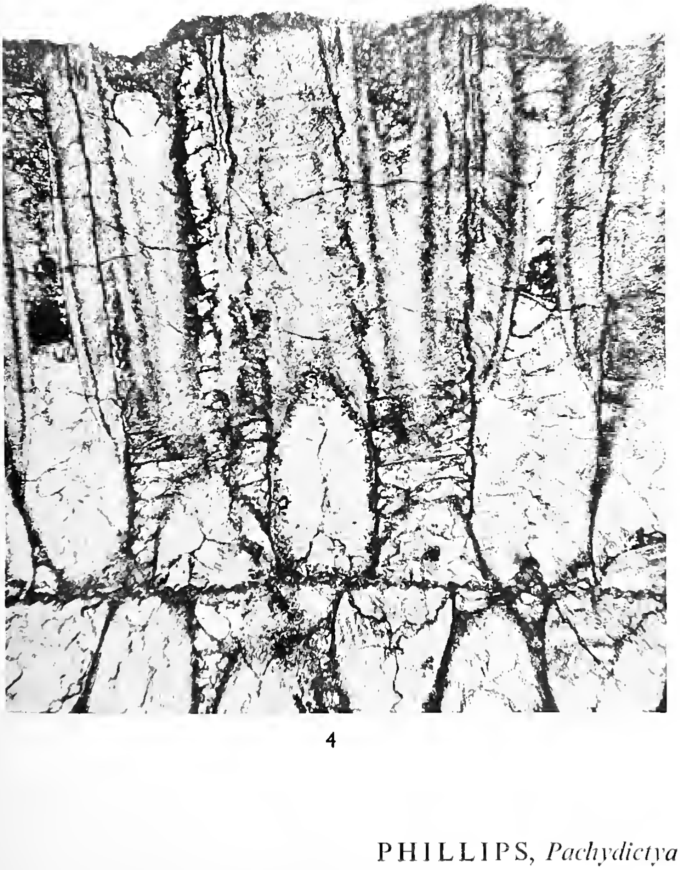

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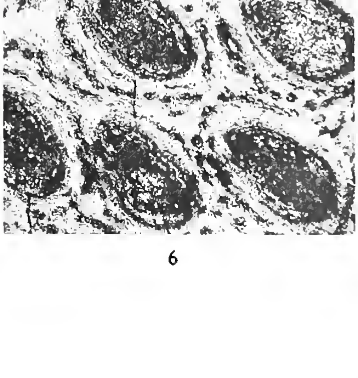

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PHILLIPS, *Pachydictya*


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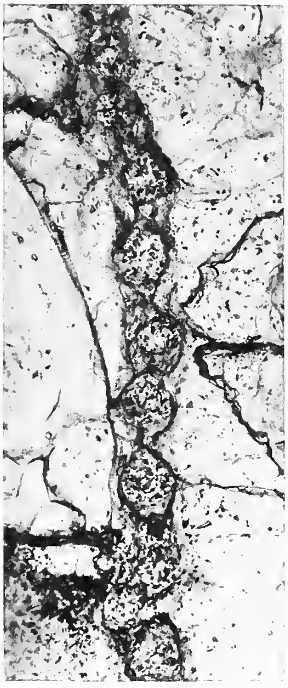
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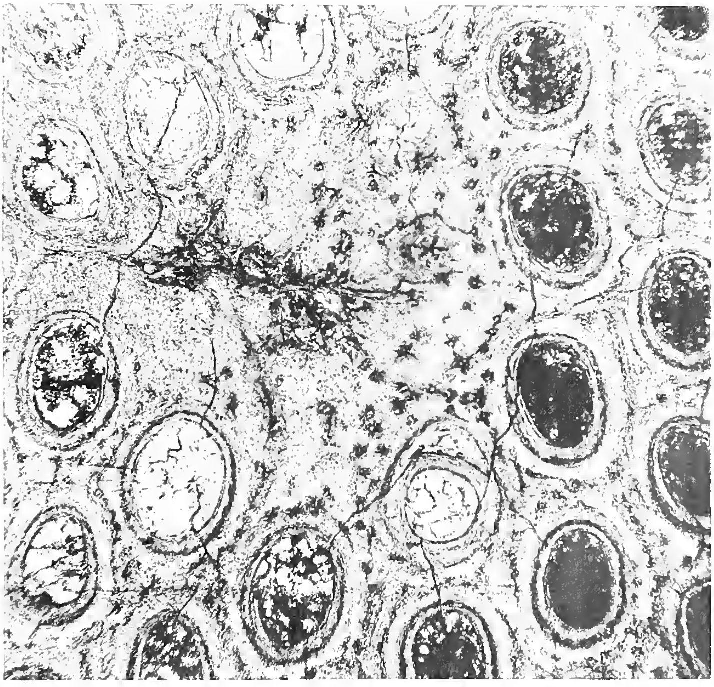
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PHILLIPS, *Pachydictya*

by Ulrich 1882, pl. 8, figs. 10*b*, 10*c*, now in the U.S. National Museum. Unsectioned paratypes consist of nine small zoarial fragments which do show surficial features of the species, USNM 43701. The lectotype and the syntypic series came from 'lower beds of Trenton group, near Knoxville, Tennessee' (Ulrich 1882), the exact location is not known.

Description. Zoaria: zoaria are broad bifurcate branches. The zoarial fragment of the lectotype is 6 cm. in length and 1·1 to 1·3 cm. in width. Bifurcations are frequent and narrow rounded forks develop between the bifurcate branches. The frequency of bifurcation is not determinable on the fragmentary syntypic material. Branches vary from broad, thin bifoliate ribbons with flat zoarial surfaces to more robust, thicker ribbons with convex zoarial surfaces. Smooth, straight, non-zooecial lateral margins border the branches and range in width from 0·6 to 0·9 mm. Weathered lateral margins reveal fine oblique striae corresponding to the acanthopores in this outer region.

The zoarial surface is covered with aggregations of zooecia which occur either as low knobs (monticules), 0·5 mm. above the surface, or flat dense areas regularly distributed across and along the branches. Monticules do not occur in the non-zooecial margin but are present in other parts of the lateral margins. The area of a monticule averages 0·5 sq. mm. and includes one to five zooecia.

Oval zooecia, surrounded by small acanthopores, form an indistinct longitudinal alternating arrangement (Pl. 4, fig. 5), having a suggestion of both median-direct zooecia and oblique-lateral zooecia. Curved growth lines cross the zoarial branch and are asymmetrically arched in a distal, lateral direction. They result from growth of new zooecia on the lateral margins. The number of zooecia across a branch ranges from 24 to 28.

Tabulate interspaces are usually not observed on the zooecial surface, but, when present, in weathered specimens they appear as single series of polygons around, but not isolating, the zooecia.

Zooecial structures: the zooecia grow from the mesothecal plane at a high angle, 55° to 65° (Pl. 4, fig. 2). The thin, longitudinal-lamellate walls are pierced by thin dark lamellate acanthopore walls (Pl. 5, figs. 1, 2). A short distance above the mesotheca, tabulate interspaces appear between the zooecial walls (Pl. 4, figs. 1, 4). Farther out, the zooecial walls thicken without marked change in the direction of growth. The base of the mature region is taken where thickening of the zooecial walls begins (Pl. 5, fig. 1). In the mature region, lamellae lie steeply inclined toward adjacent zooecia and line the inner wall of the zooecium. The steep lamellae extend a considerable distance distally before they curve over toward a dark irregular median line (Pl. 5, fig. 2), which develops from irregular intertonguing of the lamellae in the outer zooecial wall. Steeply inclined lamellae of the inner wall appear to form a separate lining in contrast to the distally arched lamellae of the outer wall, but the steep lamellae of the inner wall may be traced distally into the arched lamellae of the outer zooecial wall.

Acanthopores, 0·1 to 0·2 mm. in diameter, originating as median tubuli, extend from the mesothecal plane to the periphery parallel to the direction of growth of the zooecia (Pl. 4, figs. 3, 4). The acanthopore wall is composed of distally convex dark lamellae. The acanthopores are numerous in the zooecial walls at the surface of the zoaria (Pl. 4, fig. 6; Pl. 5, fig. 4). Median tubuli are abundant in the mesothecal plane (Pl. 5, fig. 3). The mesothecal plane with median tubuli extends out into the non-zooecial lateral margin where acanthopores leave the mesothecal plane as median tubuli and pass through wall lamellae to reach the periphery (Pl. 4, fig. 3).

In the zooecia diaphragms are sparse. An occasional thin layered diaphragm crosses the zooecial tube at the base of the mature region (Pl. 5, fig. 1). It thickens slightly upon meeting the zooecial wall, and continues distally along the inner wall for a considerable distance before curving over into the zooecial wall lamellae. In the outer mature region diaphragms may be more numerous, three to four per zooecium. In the younger part of the zoarium the diaphragms are thin and layered; in the older part of the zoarium they thicken greatly and may completely fill the zooecial tube. Covered monticules develop at this stage. In tangential section the steeply inclined inner wall lamellae appear as a distinct inner concentric band surrounded by lamellae of the outer wall which is pierced by numerous acanthopores.

In the immature and submature regions tabulate interspaces are present between zooecia. Thin laminate diaphragms lie across the interspaces and distally line the inner walls for some distance before curving over into the wall lamellae. Diaphragms are 0·04 to 0·06 mm. apart. These tabulate interspaces are infilled in the submature region by greatly thickened lamellate zooecial walls.

Measurements	*USNM 137608 Lectotype*	*USNM 137624*	*USNM 137625*
Zoarial branch width—cm.	0·55–0·70	Branches incomplete	
Zoarial branch thickness—mm.	1·5	2·0	2·9
Width of lateral margin—mm.	0·6	. .	. .
No. of zooecia per 2 mm.			
Longitudinally	2·5–5	5	4–5
Laterally	3	5	5–6
Acanthopores per zooecium	25	Abundant	Abundant
Interspace between zooecia in mm.			
Longitudinally	0·24–0·40	0·15–0·21	0·15–0·20
Laterally	0·14–0·18	0·15–0·20	0·15–0·20
Zooecial aperture—mm.	(0·30×0·16)	(0·25×0·20)	(0·30×0·15)
	(0·28×0·14)	(0·3×0·2)	(0·35×0·20)
Distance between monticules—mm.	3·5–5·0	. .	. .
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·77	0·64	0·72–0·62

Remarks. Pachydictya robusta differs from *Stictopora fenestrata*, *S. nicholsoni*, and *Eurydictya montifera* in possessing tabulate interspaces in the immature and submature regions and in lacking hemisepta. It is similar to these three species in having median tubuli and acanthopores. The wall structure is in part similar to the stictoporid wall structure but the lamellae of the inner zooecial wall in *P. robusta* are more steeply inclined and the outer wall lamellae intertongue with adjacent wall lamellae in a distinct and irregular median zone.

Tabulate interspaces in the immature and submature regions are a characteristic feature of the species. Their development is suggestive of the vesicular tissue in some ceramoporoid bryozoans.

Trigonodictya conciliatrix (Ulrich) 1886, type species of the genus *Trigonodictya*, was originally described as a species of *Pachydictya*. Transverse sections (Pl. 7, figs. 4, 5) of syntypes USNM 137626 and USNM 137640 show the mesothecal plane with median tubuli. The mesothecal plane may be curved (Pl. 7, fig. 5) or it may be laterally bifurcate

(Pl. 7, fig. 4). Bifurcation of the mesothecal plane in more than one plane produces great diversity in growth form. The branches may be fanshaped fronds with longitudinal ridges, thin and triangular in transverse section, or curved bifoliate ribbons, or thin truncated pyramids. The internal wall structure appears similar to the pachydictyid wall structure but further sectioning of the many syntypes is required before the taxonomic position of this genus is determined.

Escharoporid group

In the escharoporid group thin longitudinally lamellate zooecial walls leave the mesothecal plane at a low angle (Pl. 6, fig. 11; Pl. 9, fig. 7). The walls extend only a short distance outward before they abruptly change direction of growth and pass from the immature region to the greatly thickened mature region (Pl. 9, fig. 7). In the mature region lamellae lie steeply inclined along the inner wall of the zooecium (Pl. 9, fig. 7; Pl. 8, figs. 4, 5) and curve in broad arches into the outer zooecial wall. There is no demarcation line between zooecia and the lamellae are continuous from one zooecium to the next. Layers of dark lamellae occur regularly throughout the wall and in longitudinal section they resemble coarse lines stretched between zooecia (Pl. 6, fig. 11; Pl. 8, fig. 5). This is a distinctive feature of the escharoporid wall structure.

In tangential section inner wall lamellae appear as narrow concentric bands around the apertures, and dark lamellae fleck the outer zooecial wall (Pl. 7, fig. 6; Pl. 8, figs. 1, 3, 4; Pl. 10, fig. 6). The dark layers appear either as dark grains, linear series of dense granules, or short dark lines, depending of the plane of section through the convex lamellae. Dark grains appear when lamellae are cut perpendicular to the plane of section, linear series of dense granules appear when broadly curving lamellae in the outer walls are cut obliquely, and the short dark lines result when the broad upper convex region of the layers is cut.

The mesothecal plane has a thin simple bilaminate structure in the immature region of the zoarium. However, the extension of the mesothecal plane laterally into the mature region at the edges of the zoarial branch loses its bilaminate identity although retaining its position in the plane of bilateral symmetry, and becomes a band of convex lamellae which continue into the lamellae of the zooecial wall. Acanthopores and median tubuli are absent. Superior hemisepta occur at the bases of the zooecial tubes. Diaphragms are rare. Mesopores are non-tabulate.

Escharopora recta Hall 1847

Plate 6, figs. 1–11

Escharopora recta Hall 1847, p. 73, pl. 26, figs. 1*a*–1*d*.

Type material. Syntype NYSM 654 ($\frac{6320}{1}$), specimen figured by Hall (1847, pl. 26, figs. 1*a*, 1*b*); from the Trenton limestone (Trenton), Jacksonburg, Herkimer County, New York. Lectotype AMNH $\frac{668}{1}$, here designated as specimen figured by Hall (1847, pl. 26, figs. 1*c*, 1*d*); from Trenton limestone (Trenton), Middleville, New York.

Description. Zoaria: these solid, subcylindrical bifoliate stems have finely striate nonzooecial lateral margins. Branching has not been observed. The syntype 654 is a large specimen, 10 cm. in length and 7 mm. (average) wide. The stem tapers at its proximal end where it is 4·5 mm. wide. There is also some tapering of the stem at its distal end.

In the lectotype AMNH $\frac{668}{1}$, a considerably smaller specimen, the stem tapers from 3·3 mm. at the distal end to 1·0 mm. at 1·5 cm. above the proximal end. Abrasion has accentuated tapering of the proximal end which is now almost cylindrical. The distal end of this specimen is uniform in width.

Elongate zooecial apertures possess very attentuated rhomboidal peristomes arranged in diagonal pattern across the stem. Smaller zooecial apertures and thicker walls are found in the proximal region and larger zooecial apertures and thinner walls are present in the distal region of the zoarium.

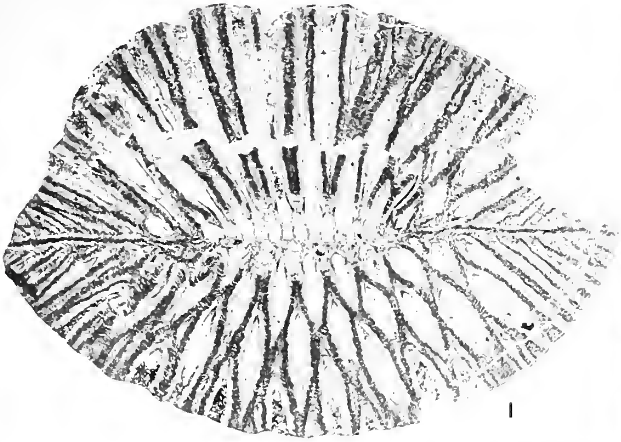
Zooecial structures: zooecia leave the mesotheca and have thin zooecial walls directed at a steep angle, 20° to 40°, to the mesotheca. The walls extend only a short distance outward before they suddenly change direction and pass from the thin immature region to the greatly thickened mature region. Zooecia open obliquely to the zoarial surface. Lamellae lie steeply inclined along the inner walls of the zooecium with the proximal wall projecting into the basal mature region to form a superior hemiseptum (Pl. 6, fig. 11). The lamellae of the inner wall curve sharply toward adjacent zooecia and are broadly arched. There is no demarcation line between zooecia and the lamellate walls are continuous from one zooecium to the next. Dark lamellae occur regularly throughout the walls, and in longitudinal section they resemble coarse bands stretched between zooecia.

In tangential sections (Pl. 6, figs. 5, 6, 10) elongate zooecial apertures have an irregular longitudinal pattern, and a distinct diagonal pattern. The steeply inclined lamellae of the zooecial wall appear as narrow concentric bands around the zooecial apertures and the broadly arched laminae fill the intervening areas of the zooecia. As outlined in the discussion of the escharoporid wall structure the dark laminae fleek the wall as granules or lines, depending on the position of section through the arched lamellae.

Laterally in the mature region the mesothecal plane loses its bilaminate identity although the zoarium retains its bilateral symmetry. Near the margins of the stem the mesothecal plane changes into a band of convex lamellae which are continuous into the zooecial walls (Pl. 6, figs. 1, 3). As the lateral margins widen bands of convex lamellae rather than zooecia form in these areas. Zooecia bud from the lateral portions of the mesothecal plane and thus the new zooecial bud which originates in the lamellae of the mature region lacks the typical thin basal wall.

EXPLANATION OF PLATE 6

Figs. 1–11. *Escharopora recta* Hall. 1, Transverse section of lectotype AMNH $\frac{668}{1}$ cut 2 cm. above the proximal tip. Thin bilaminate mesothecal plane in immature region; mesothecal plane at edge of zoarial branch becomes a band of convex lamellae, ×25. 2, External view of zoarial surface at distal end, AMNH $\frac{668}{1}$, ×5. 3, Transverse section showing portion of the mesothecal plane, wall lamellae and new zooecial bud developing in the mesothecal plane at the edge of the zoarial branch, AMNH $\frac{668}{1}$, ×75. 4, External view of AMNH $\frac{668}{1}$, ×2. 5, Deep tangential section of AMNH $\frac{668}{1}$ having narrow mesopores between zooecial apertures, ×50. 6, Shallow tangential section of AMNH $\frac{668}{1}$ having longitudinal canals between elongate zooecial apertures and escharoporid wall structure, ×50. 7, Oblique longitudinal section of syntype NYSM 654 having narrow immature region and escharoporid wall structure in the mature region, ×100. 8, External view of syntype NYSM 654 showing large non-bifurcate stem, ×1. 9, External view of zooecial apertures on syntype NYSM 654, ×5. 10, Deep tangential section of syntype NYSM 654, ×100. 11, Part of a longitudinal section of AMNH $\frac{668}{1}$; the photograph is cut near the mesothecal plane and on the outer edge of the mature region, ×50.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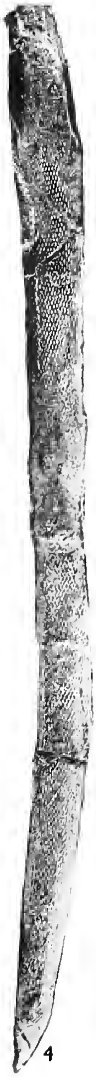
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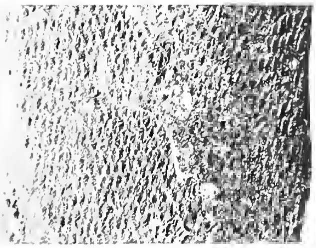
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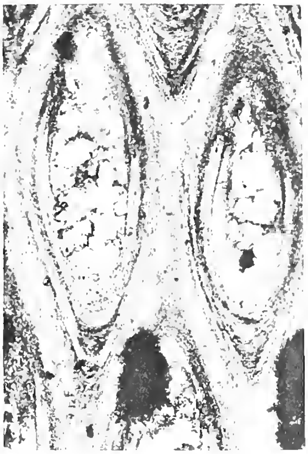
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PHILLIPS, *Escharopora*

In specimen AMNH $\frac{668}{1}$ longitudinal series of small non-tabulate mesopores are interspersed in the outer part of the zooecial wall but do not extend into the wall for any appreciable depth. In the outer 0·2 mm. of the mature region each longitudinal series of mesopores joins to form a canal having an average length of 0·8 mm. Only deep tangential sections reveal the mesopores (Pl. 6, fig. 6). This feature is not well developed in the syntype.

Measurements	*Syntype NYSM 654*	*Lectotype AMNH 668/1*
Zoarial branch width—mm.	4·0 proximally 7·0 distally	3·3 distally
Zoarial branch thickness—mm.	1·7	2·4 at 2 cm. above proximal tip
Width of lateral margin—mm.	indet.	0·5
Zooecia across branch	30 in 6 mm.	9·5–10 in 1·43 mm.
No. of zooecia per 2 mm.		
Longitudinally	4	3·5–4
Laterally	10	6
Interspace between zooecia—mm.		
Longitudinally	0·2–0·4	0·13–0·56
Laterally	0·08–0·12	0·07–0·10
Zooecial aperture—mm.	(0·30 × 0·10) (0·26 × 0·08)	(0·40 × 0·22)
Thickness of mesotheca—mm.	0·02	0·01–0·02
Mesopore opening—mm.	length (0·13–0·09) width (0·01–0·02)	(0·05 × 0·01)
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·85	0·80–0·90

Remarks. Escharopora recta is similar to *Graptodictya pereglans*, *G. elegantula*, and *Stictoporella interstincta* in the mode of growth of the zooecial wall, in zooecial wall structure, and in the development of superior hemisepta on the proximal walls. It is distinguished from these species by its well-developed tapered stem, diagonally arranged zooecia surrounded by rhombic peristomes, wide mature region, and longitudinal series of mesopores which form narrow canals at the zoarial surface.

Both the lectotype and syntype have been crushed and the proximal walls broken near the mesothecal plane. The zooecia are disjointed at the zoarial surface. In Pl. 6, fig. 11, the proximal wall is broken away from the mesothecal plane and this gives a false impression of inferior hemisepta.

Escharopora recta, type species of *Escharopora*, occurs in shale partings in calcarenite in its type area. It is not an abundant form.

Graptodictya perelegans (Ulrich) 1878

Plate 7, figs. 1–3, 6, 7; Plate 8, fig. 4

Ptilodictya perelegans Ulrich 1878, p. 94, pl. 4, figs. 16, 16*a*.
Graptodictya perelegans (Ulrich) Ulrich 1882, p. 165.

Type material. Holotype USNM 137607; from Waynesville formation (Richmond), Clarksville, Ohio.

Description. Zoaria: these zoaria are slender bifurcate ribbon-shaped branches. The delicate well-preserved holotype has frequent bifurcations. The more distal branches overlie the partly crushed more proximal zoarial branches. Striated non-zooecial lateral margins are smooth and evenly curved in the region of bifurcation, where monticules have enlarged zooecial apertures, (0·06–0·08) × (0·12–0·14) mm. diameter, and thickened zooecial walls.

Well-defined peristomes outline the oval zooecial apertures and striae are present on the surface of the zooecial walls (Pl. 7, fig. 2).

Zooecial structures: in the holotype, zooecia leave the mesothecal plane at an angle of 20° (Pl. 7, fig. 1) and have thin lamellate walls in the immature region. An abrupt change in the direction of zooecial growth and conspicuous thickening of the zooecial walls mark the base of the mature region. The immature region is one-third to one-quarter the width of the mature region. Thickened zooecial walls of the mature region have typical escharoporid wall structure (Pl. 8, fig. 4; Pl. 7, figs. 1, 3, 6, 7). The mesothecal plane is thin and lacks median tubuli. The lateral extension of the mesothecal plane into the lateral margins of the zoarial branch is short and lamellate. Superior hemisepta are short and lamellate (Pl. 7, fig. 7). Diaphragms are not observed.

Measurements	*Holotype USNM 137607*
Zoarial branch width—mm.	2·3
Zoarial branch thickness—mm.	0·8
Width of lateral margin—mm.	0·3–0·5
Zooecia across branch	12
No. of zooecia per 2 mm.	
Longitudinally	3–4
Laterally	4
Interspace between zooecia—mm.	
Longitudinally	0·22–0·28
Laterally	0·10–0·14
Zooecial aperture—mm.	Length (0·14–0·10) Width (0·08–0·06)
Ratio: Depth of mature region / Depth of zooecium	0·79

EXPLANATION OF PLATE 7

Figs. 1–3, 6, 7. *Graptodictya perelegans* Ulrich. 1, Longitudinal section of holotype USNM 137607 showing narrow immature region, wide mature region with lamellate zooecial walls, and short superior hemiseptum on the proximal zooecial wall, ×50. 2, External view of holotype USNM 137607 showing distal branches partly overlying earlier proximal branches; striate non-zooecial lateral margins, ×2. 3, Transverse section of holotype USNM 137607 showing lamellate zooecial walls in the mature region, ×100. 6, Tangential section of holotype USNM 137607 in region of bifurcate branch; concentric band lines the inner zooecial walls and dark lamellae fleck the striate outer zooecial wall, ×50. 7, Longitudinal section of holotype USNM 137607 showing lamellate zooecial wall in the mature region and lamellate superior hemiseptum on the proximal wall; the mesotheca is present on the right-hand side of the photograph as a dark vertical line, ×100.

Figs. 4, 5. *Trigonodictya conciliatrix* (Ulrich). 4, Transverse section of paratype USNM 137640 showing bifurcate mesotheca at lateral margins, median tubuli in the mesothecal plane, acanthopores in the zooecial walls, and tabulate interspaces between zooecia, ×25. 5, Transverse section of paratype USNM 137626 showing strongly curved mesothecal plane, ×25.

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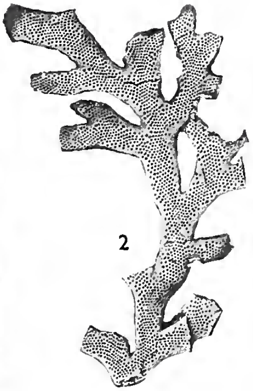

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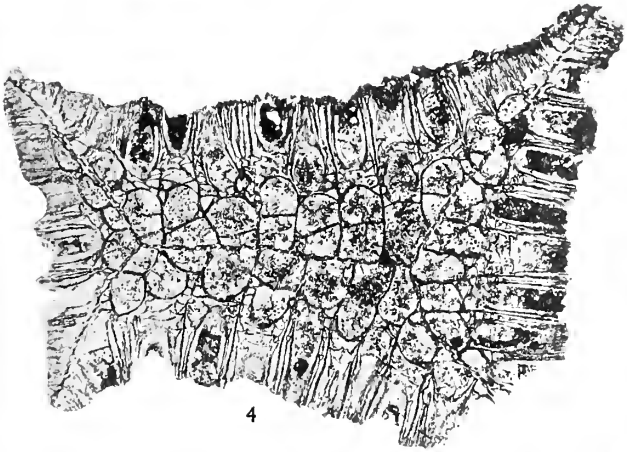

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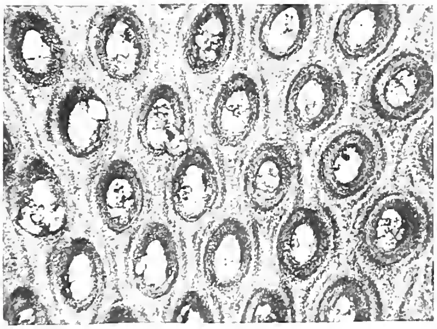

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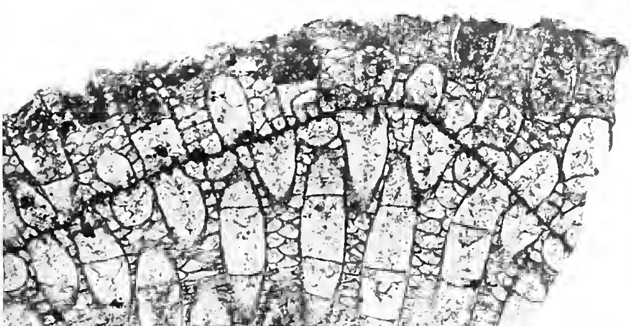

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PHILLIPS, *Graptodictya* and *Trigonodictya*

Remarks. Graptodictya perelegans (type species of *Graptodictya*) differs from *Stictopora fenestrata* and *S. nicholsoni* in the arrangement and outline of the zooecial apertures, in the zooecial wall structure, in the nature of the mesothecal plane, and in the absence of median tubuli and acanthopores. *G. perelegans* is very similar to *G. elegantula* in zooecial wall structure, in the nature of the mesothecal plane, in the mode of growth of the zoarium having bifurcate branches and striate non-zooecial lateral margins and in the peristomes around the zooecial apertures. Monticules in the region of bifurcation are better developed in *G. perelegans* than in *G. elegantula* but this difference may result from the varying stage of development of the zoaria. *G. perelegans* has a greater axial ratio and more restricted zooecial apertures.

Additional material studied came from the Waynesville formation in the type area.

Graptodictya elegantula (Hall) 1847

Plate 8, figs. 1–3, 5; Plate 9, figs. 1–7

Stictopora elegantula Hall 1847, p. 75, pl. 26, figs. 4*a*, 4c.

Type material. Lectotype here designated AMNH $\frac{667}{1}$, specimen figured by Hall (1847, pl. 26, figs. 4*a*, 4*b*); from Trenton limestone (Trenton), Watertown, New York Additional Material: USNM 137671; Trenton limestone (Trenton), Black Creek, Herkimer County, New York. USNM 137673, Trenton limestone (Trenton), Trenton Falls, New York. USNM 137672; 137674, Trenton limestone (Trenton), Rathbone Brook, New York.

Description. Zoaria: the lectotype (Pl. 9, figs. 1, 2) is 2 cm. long. Two bifurcations are present within a short interval, and the lateral margins are smoothly curved in regions of bifurcation where branches diverge at angles of 50° to 60°. The bifoliate stem averages 2·9 mm. in width and has distinct lateral margins with oblique striae. The width of these margins is 0·30 to 0·36 mm., increasing in the region of bifurcation.

Circular to elongate zooecial apertures have well-defined complete peristomes. The zooecial apertures form a diagonally intersecting pattern on the zoarial surface; zooecial apertures are larger near the lateral margins and in the region of bifurcation of the branches. Sinuous striae mark the surface between zooecial apertures. Acanthopores and mesopores are absent.

Zooecial structures: zooecia leave the mesothecal plane at 20° to 30°. The thin walls are steeply curved in the immature region. An abrupt change of direction of zooecial growth and the development of greatly thickened walls mark the base of the mature region. Younger zoarial branches (Pl. 9, figs. 5, 7) have a narrow mature region about equal in width to the immature region, while older parts of the zoarium have a mature region three times as wide as the immature region, which is relatively constant in measurment (Pl. 8, fig. 2). Thickened zooecial walls of the mature region have a typical escharoporid wall structure (Pl. 8, figs. 2, 5; Pl. 9, fig. 7). Longitudinal sections show the strongly lamellate walls and tangential sections (Pl. 8, figs. 1, 3; Pl. 9, fig. 3) display the characteristic pattern of the convex lamellae and concentric band of the steeply inclined lamellae lining the zooecial cavity.

The mesothecal plane is thin and lacks median tubuli. The lateral extension of the mesothecal plane into the mature region at the margins of the zoarial branches is short and lamellate.

Short, lamellate superior hemisepta extend from the walls of zooecia (Pl. 8, figs. 2, 5). Diaphragms are rare, but, when present, they are thin, straight structures crossing the zooecial tube in the submature region.

Measurements	*AMNH 667/1*	*USNM 137674*	*USNM 137671*
Length of zoarial fragment—cm.	2·0	3·5	1·3
Zoarial branch width—mm.	2·9	1·5	2·5
Zoarial branch thickness—mm.	0·75	0·3–0·5	1·3
Width of lateral margin—mm.	0·30–0·36	0·29	0·20
Zooecia across branch	12–14; stem width 2·9 mm.	15	15–16
No. of zooecia per 2 mm.			
Longitudinally	3·5–4·0	3·5–4·0	3·5–4·0
Laterally	4–5	5–6	5–6
Interspace between zooecia—mm.			
Longitudinally	0·07–0·11	0·12	0·11–0·16
Laterally	0·06	..	..
Zooecial aperture—mm.	0·20–0·22	(0·08×0·13)	(0·18×0·25) (0·10×0·13)
Zooecial aperture in region of bifucation	0·37–0·33	..	..
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·60	0·53	0·67

Remarks. Graptodictya elegantula has been compared with *G. perelegans* in Remarks of this latter species.

Hall's paratype AMNH $\frac{667}{2}$ is a bifurcate zoarial fragment split along the mesothecal plane. The brittle nature of the paratype does not permit sectioning so that the internal structures are not known. The paratype is a fragment 2·5 cm. in length and 0·55 cm. in width, and considerably larger than the lectotype which is a younger zoarial fragment.

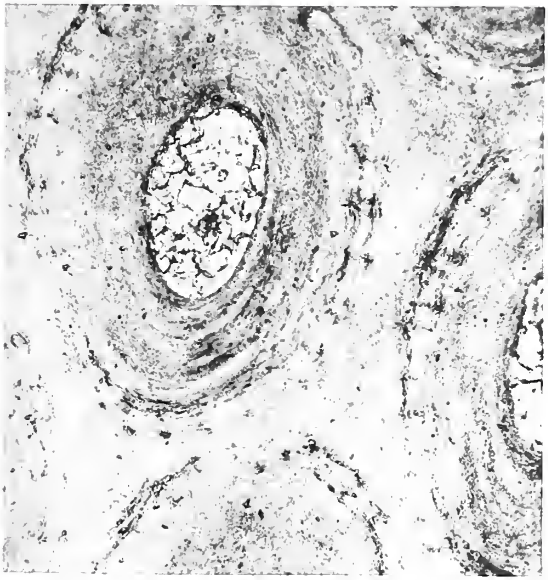
EXPLANATION OF PLATE 8

Figs. 1–3, 5. *Graptodictya elegantula* (Hall). 1, Tangential section of USNM 137673 showing narrow concentric bands lining inner zooecial walls, and dark lamellae flecking the outer zooecial wall, ×100. 2, Longitudinal section of USNM 137671 showing dark wall lamellae in the mature region and short superior hemiseptum on the proximal wall of the zooecium, ×50. 3, Tangential section of USNM 137673; larger zooecia appear as the lateral margin is approached, i.e. right-hand side of photograph, ×50. 5, Longitudinal section of USNM 137671 with dark wall lamellae in the mature region, superior hemiseptum on the proximal wall at the base of the mature region, ×100.

Fig. 4. *Graptodictya perelegans* Ulrich. Tangential section of holotype USNM 137607 cutting zooecial apertures on a lateral margin in the left-hand fork of a bifurcate branch; striate lateral margins are strongly flecked with dark lamellae, ×50.

EXPLANATION OF PLATE 9

Figs. 1–7. *Graptodictya elegantula* (Hall). 1, External view of lectotype AMNH $\frac{667}{1}$, ×2. 2, External view of lectotype AMNH $\frac{667}{1}$ showing distinctive striate lateral margins, ×5. 3, Very deep tangential section of lectotype AMNH $\frac{667}{1}$ showing concentric bands lining inner zooecial walls, ×50. 4, Oblique transverse section of lectotype AMNH $\frac{667}{1}$ showing mesothecal plane without median tubuli, ×50. 5, Transverse section of USNM 137674 with narrow mature region in young part of zoarium, ×25. 6, Transverse section of USNM 137671 with dark wall lamellae in the mature region, ×50. 7, Longitudinal section through USNM 137674 showing escharoporid wall structure and thin diaphragm in the immature region connecting with proximal zooecial wall and mesotheca, ×50.



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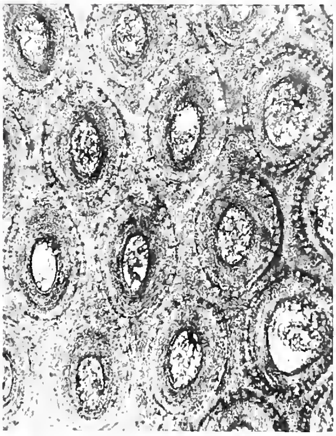

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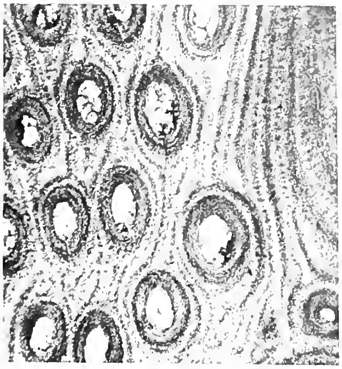

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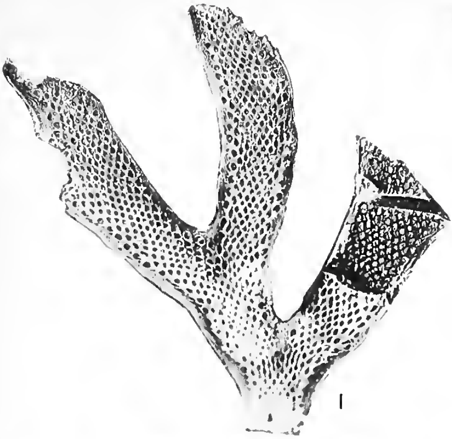
PHILLIPS, *Graptodictya*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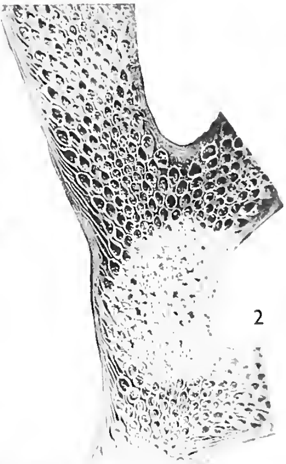
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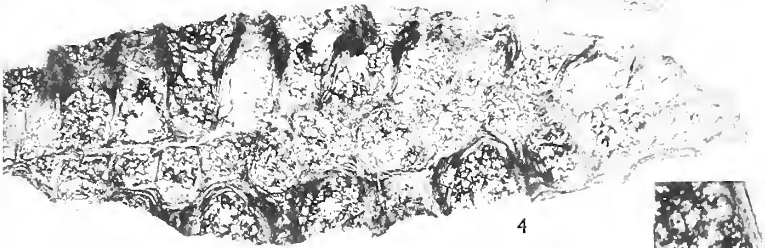
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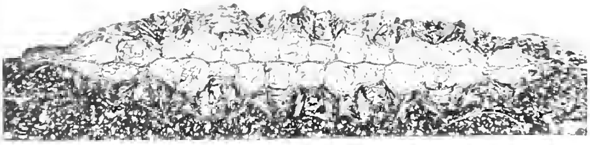
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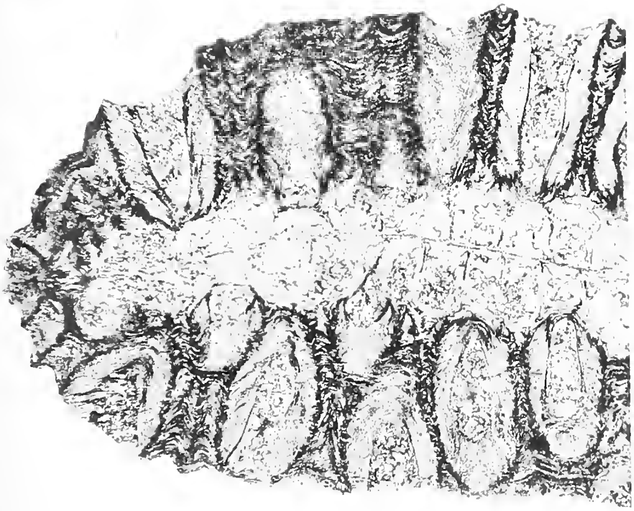
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PHILLIPS, *Graptodictya*

No surficial features are present. The paratype was not included in the present study of *G. elegantula.*

Hall (1887, p. xx) selected *G. elegantula* as the type species of *Stictopora*, but Ulrich's earlier designation in 1886 of *S. fenestrata* as the type species of *Stictopora* invalidated Hall's designation.

Stictoporella interstincta Ulrich 1882

Plate 10, figs. 1–7

Stictoporella interstincta Ulrich 1882, p. 169, pl. 8, figs. 9, 9*a*.

Type material. Holotype USNM 137612, unsectioned. Sectioned topotype USNM 137613 in the rock specimen containing the holotype; from the base of the Economy member (Cincinnatian), River Quarries, West Covington, Kentucky.

Description. Zoaria: the zoaria are slender bifurcate branches; bifurcations are frequent but the interval of bifurcation is not determinable as the delicate zoaria break readily and are preserved as fragments.

The appearance of the zoarial surface is distinctive. Sub-polygonal zooecial apertures are arranged in an alternating longitudinal pattern (Pl. 10, figs. 1–4), and rectangular or polygonal mesopores occur between the zooecial apertures but do not isolate them. Usually mesopores are located at the proximal and distal ends of the zooecial apertures. Maculae, composed of about fourteen mesopores, are level with the zoarial surface (Pl. 10, fig. 3) and have an area of 0·4 sq. mm. They occur in the region of bifurcation of zoarial branches. A single series of mesopores forms the lateral margin of the branches. Five to seven zooecial apertures are exposed laterally across the proximal part of the zoarial branch; the number increases to seven or eight in the more distal part of the zoarial branch.

Zooecial structures: zooecia arise steeply from the mesothecal plane at an angle of 20°. Slender proximal walls curve sharply away from the mesothecal plane at the base of the mature region where they thicken considerably. The inclination of the zooecial walls in the mature region is 55° to the mesothecal plane. A superior hemiseptum may be present at the base of the mature region in each zooecium. The wall structure in the mature region is the same as in the species of *Escharopora* and *Graptodictya.* Steeply inclined lamellae line the zooecia and curve sharply toward adjacent zooecia forming broad convex lamellae. In tangential section dark lamellae fleck the outer zooecial walls and the inner wall lamellae appear as narrow concentric bands around the apertures.

Non-tabulate mesopores develop at the base of the mature region. Mesopore openings may be greatly restricted by the lamellae of the inner walls. Mesopore wall structure is the same as the zooecial wall (Pl. 10, fig. 6). A superior hemiseptum may extend across a zooecium from the proximal wall to connect with the distal wall and may curve distally along the inner walls, eventually passing into the lamellae of the zooecial wall (Pl. 10, fig. 7). Diaphragms are rare. Acanthopores are absent. The mesotheca lacks median tubuli (Pl. 10, fig. 5).

Remarks. Stictoporella interstincta is similar to *Escharopora recta*, *Graptodictya perelegans*, and *G. elegantula* in wall structure, and in having a simple mesothecal plane without median tubuli. It differs from *G. perelegans* and *G. elegantula* in the presence of abundant

Measurements	*Holotype*	*USNM 137613*
Zoarial branch width—mm.	1·5–2·0	1·5
Zoarial branch thickness—mm.	..	0·6
Zooecia across branch	5–6	5–6
No. of zooecia per 2 mm.		
Longitudinally	3–5	3–5
Laterally	8	6–8
Interspace between zooecia—mm.		
Longitudinally	..	0·20–0·22
Laterally	..	0·18–0·20
Zooecial apertures—mm.	Length (0·3–0·14)	(0·26–0·16)
	Width (0·10–0·14)	(0·10)
Mesopore openings—mm.	Length 0·07–0·26	0·16–0·06
	Width 0·02	0·02
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	..	0·67

mesopores in the mature region, and from *Escharopora recta* in possessing polygonal mesopores regularly developed at the distal ends of the zooecial apertures and in having a different growth form.

The holotype is a tiny fragment, too small for sectioning. However, topotype material on the same slab as the holotype was sectioned and the description of the internal structures is based on this topotype material. Additional material for study came from the Economy member, K. C. C. R. Tunnel, Covington, Kentucky. The type locality is no longer exposed and it is not possible to collect further topotype material.

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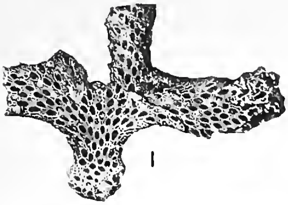
EXPLANATION OF PLATE 10

Figs. 1–7. *Stictoporella interstincta* Ulrich. 1, External view of zoarium showing mesopores between zooecia and along lateral margins, holotype USNM 137612, ×4. 2, External view of holotype USNM 137612, ×1½. 3, External view of holotype USNM 137612 showing macula consisting of mesopores near region of bifurcation, ×16. 4, Tangential section of topotype 137613 with mesopores opening on the distal side of zooecial apertures, ×5. 5, Oblique transverse section of USNM 137613 showing mesotheca without median tubuli, ×50. 6, Tangential section through zooecial apertures and mesopores of USNM 137613; the inner zooecial wall consists of fine concentric lamellae and the outer zooecial wall is flecked by dark lamellae, ×100. 7, Longitudinal section of USNM 137613; broad distally convex lamellae in the mature region, superior hemiseptum on the proximal zooecial wall, and diaphragm across the immature region of the zooecial tube, ×50.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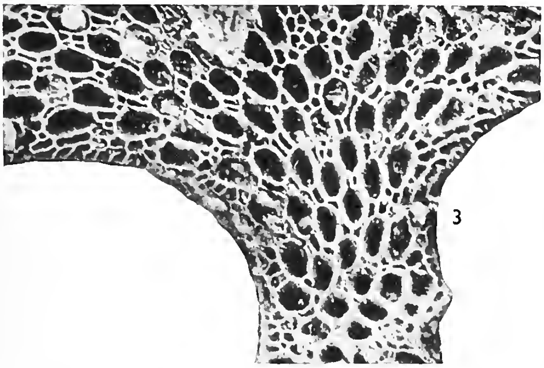
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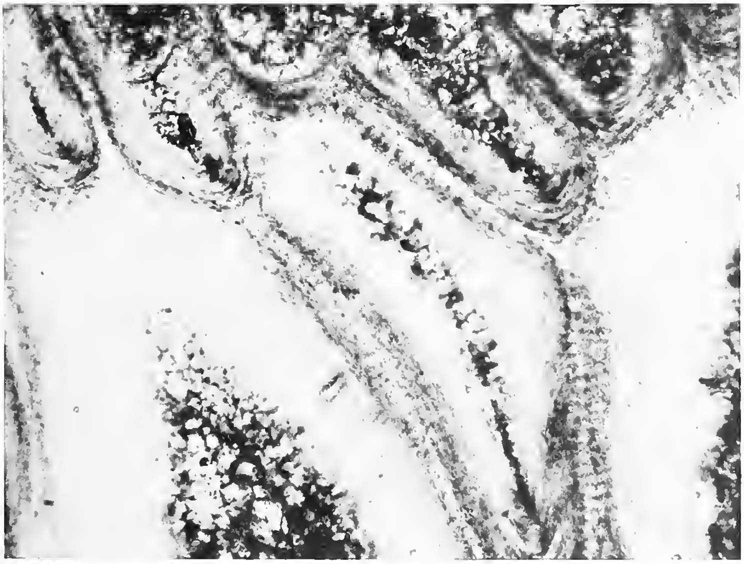
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PHILLIPS, *Stictoporella*

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DEVONIAN SPORES FROM MELVILLE ISLAND CANADIAN ARCTIC ARCHIPELAGO

by D. C. McGREGOR

ABSTRACT. Twenty-four species of spores are described from a bituminous coal of Melville Island. Of these, twenty species of small spores and three species of megaspores are new, and two of the latter represent new genera, *Hystricosporites* and *Circumsporites*. Evidence suggests that lycopsids were dominant constituents in the flora which produced the spores. The assemblage differs distinctly from those described by Naumova (1953) and may contain elements of an uppermost Devonian-Lower Carboniferous flora, related to assemblages detected elsewhere in the Canadian Arctic. The geological significance of the assemblage is indicated.

INTRODUCTION

ONE of the most neglected areas of palaeobotany awaiting exploration concerns spores of Devonian age. Naumova (1953), Chaloner (1959), and others have demonstrated the potential botanical and geological significance of these fossils, and there have been reports of their abundance in certain strata. Even so, detailed investigations of Devonian spore assemblages are rare, and there are no published accounts of small spores of Devonian age from the Canadian Arctic.

During geological reconnaissance in the Canadian Arctic Islands, E. T. Tozer of the Geological Survey of Canada obtained samples from thick sequences of sandstone, siltstone, shale, and coal, containing fragmentary remains of plant megafossils. Preliminary examination of several of these samples, from Melville, Ellesmere, and Prince Patrick Islands, revealed abundant small and large spores, often excellently preserved.

The spores described are from one of these samples, a bituminous coal collected at Stevens Head, on the west coast of Melville Island (Geological Survey of Canada Locality No. 5116). The beds containing the coal conformably overly strata with marine Middle Devonian (Givetian) faunas identified by D. J. McLaren (*in* Tozer 1956, p. 15). The coal is therefore not older than Givetian. More recent geological investigations of Melville Island have shown that at at least one locality marine Upper Devonian fossils lie above coal measures similar to the beds exposed at Stevens Head (E. T. Tozer, personal communication). It thus seems reasonable to dismiss the possibility that the Stevens Head coal is of Mississippian age. According to D. J. McLaren (personal communication) the coal is most probably of Frasnian age or, less likely, Famennian. Available evidence suggests that it is of approximately the same age as coal on Ellesmere Island, 500 miles to the east, from which six species of megaspores were recently obtained and described by Chaloner (1959).

This investigation was begun by the writer at McMaster University as part of a doctorate thesis, under the guidance of Prof. N. W. Radforth, whose continued support and encouragement are gratefully acknowledged. Particular thanks are also extended to Dr. Glenn E. Rouse for much stimulating discussion in the early stages of the work. The Geological Survey of Canada is thanked for provision of the material studied. Dr. E. T. Tozer and Dr. D. J. McLaren offered valuable criticism on matters pertaining to the geology of the area in question. Financial support for the major part of the in-

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vestigation was provided by the National Research Council. This paper is published with permission of the Director, Geological Survey of Canada, Department of Mines and Technical Surveys, Ottawa.

Preparation of spores. Ten cc. of the coal was washed thoroughly and crushed. It was then treated with Schulze's solution, consisting of 1 cc. of crystalline potassium chlorate added to a sufficient quantity of concentrated nitric acid to equal twice the depth of the coal in the beaker. After twenty hours the supernatant liquid was decanted and the remaining sediment washed several times by addition of water and decantation after the sediment had been allowed to settle. A final short treatment with cold 10 per cent. potassium hydroxide solution followed, and the mixture was again washed several times. It was necessary to examine the mixture periodically during both the Schulze's and the alkali treatments in order to be able to stop the process at the point where the microfossils were best defined. Sufficient water was then added to the sediment to allow the use of a pipette for transfer of material to a microscope slide, where it was mixed with a small amount of corn syrup, following the method described by Radforth and Rouse (1954). Some preparations were stained with safranin; others were not stained.

SYSTEMATIC TREATMENT

The classification of Potonié and Kremp (1954) and Potonié (1956) is followed. Unless otherwise noted, the description of each new species is based on examination of at least ten specimens. Types are stored in the palaeobotanical collection of the Geological Survey of Canada, Ottawa.

Anteturma SPORITES H. Potonié
Turma TRILETES Reinsch
Subturma AZONOTRILETES Luber
Infraturma LAEVIGATI (Bennie and Kidston) R. Potonié
LEIOTRILETES (Naumova) Potonié and Kremp

Leiotriletes dissimilis sp. nov.

Plate 11, fig. 1

Diameter: 43–55 μ. Ornamentation: laevigate; punctate in contact areas. Other features: spore radial, trilete, subtriangular, margins convex. Laesurae extend almost to the equator. Commissure slightly open, lips low and distinct. Wall 1–1·5 μ thick.

Holotype. Pl. 11, fig. 1; Geological Survey of Canada (GSC) Plant Type no. 13019, slide no. MI–12; 44·5μ.

Leiotriletes confertus sp. nov.

Plate 11, fig. 2

Diameter: 35–55 μ. Ornamentation: laevigate to very minutely granulate. Other features: spore radial, trilete, broadly subtriangular to circular in outline. Laesurae extend almost to the equator. Lips low, distinct, about 1·5 μ wide. Wall 1–2 μ thick.

Holotype. Pl. 11, fig. 2; GSC Plant Type no. 13020, slide no. MI–22; 41μ.

Leiotriletes marginalis sp. nov.

Plate 11, fig. 3

Diameter: 33–54 μ. Ornamentation: laevigate. Other features: spore radial, trilete, subtriangular with convex interradial margins. Laesurae extend almost to the equator. A concentric margin about 1·5 μ in width encircles the periphery of the spore. This marginal structure is peripheral in all planes of compression, and has no apparent outer wall or folds.

Holotype. Pl. 11, fig. 3: GSC Plant Type no. 13021, slide no. MI–12; 33μ.

Leiotriletes microdeltoidus sp. nov.

Plate 11, fig. 4

Diameter: 33–54 μ. Ornamentation: very minutely scabrate. Other features: spore radial, trilete, broadly subtriangular to circular. Laesurae simple, about one-third the length of the radius of the spore. Tips of rays joined to one another by dark lines which delimit a well-defined triangle.

Holotype. Pl. 11, fig. 4; GSC Plant Type no. 13022, slide no. MI–22; 44μ.

PUNCTATISPORITES (Ibrahim) Potonié and Kremp

Punctatisporites arcticus sp. nov.

Plate 11, fig. 5

Diameter: 60–68 μ. Ornamentation: scabrate. Ornamentation faintly visible at margin. Other features: spore radial, trilete, subtriangular to ovate. Laesurae extend almost to the equator. Commissure distinct, lips low. Wall 1 μ thick.

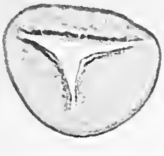
Holotype. Pl. 11, fig. 5; GSC Plant Type no. 13023, slide no. MI–12; 60μ.

EXPLANATION OF PLATE 11

All figs. are ×500, except fig. 13 (×250) and fig. 16 (×1,000).

Fig. 1. *Leiotriletes dissimilis* sp. nov., holotype (GSC 13019).
Fig. 2. *Leiotriletes confertus* sp. nov., holotype (GSC 13020).
Fig. 3. *Leiotriletes marginalis* sp. nov., holotype (GSC 13021).
Fig. 4. *Leiotriletes microdeltoidus* sp. nov., holotype (GSC 13022).
Fig. 5. *Punctatisporites arcticus* sp. nov., holotype (GSC 13023).
Fig. 6. *Punctatisporites scabratus* sp. nov., holotype (GSC 13024).
Fig. 7. *Punctatisporites putaminis* sp. nov., holotype (GSC 13025).
Fig. 8. *Cyclogranisporites amplus* sp. nov., holotype (GSC 13026).
Fig. 9. *Planisporites minimus* sp. nov., holotype (GSC 13027).
Fig. 10. *Planisporites dilucidus* sp. nov., holotype (GSC 13028).
Fig. 11. *Verrucosisporites grandis* sp. nov., holotype (GSC 13031).
Fig. 12. *Apiculatisporis elegans* sp. nov., holotype (GSC 13029).
Figs. 13, 14. *Hystricosporites delectabilis* gen. et sp. nov. 13, Holotype (GSC 13032); 14, Bifurcate appendages of *H. delectabilis*.
Fig. 15. *Verrucosisporites variabilis* sp. nov., holotype (GSC 13030).
Fig. 16. Tubercles with apical spines, on holotype of *Biharisporites submamillarius* sp. nov. (GSC 13033).

PLATE 11



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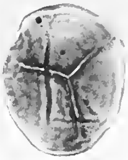

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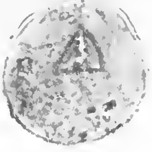

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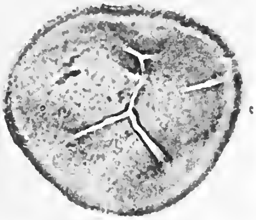

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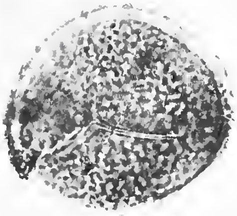

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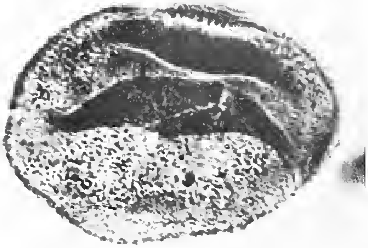

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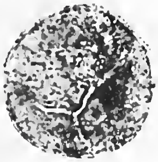

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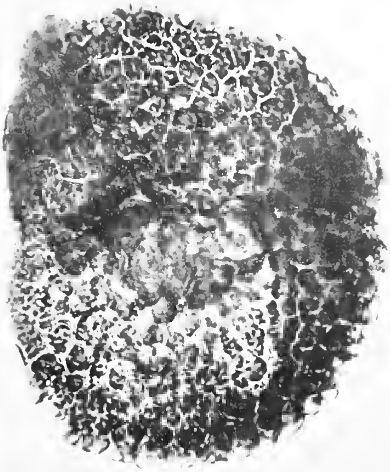

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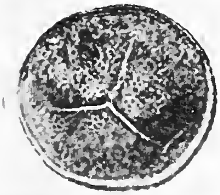

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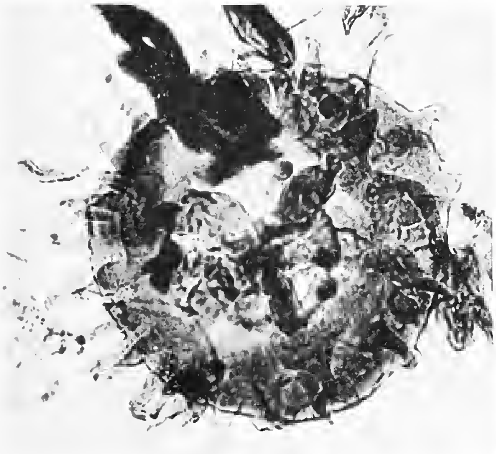

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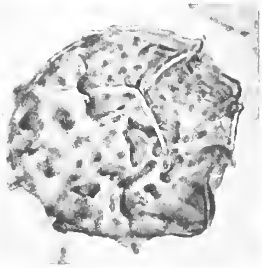

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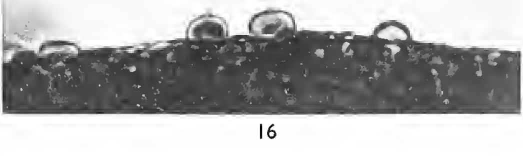

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McGREGOR, Devonian spores from Canadian Arctic

Punctatisporites scabratus sp. nov.

Plate 11, fig. 6

Diameter: 55–66 μ. Ornamentation: scabrate, minute. Other features: spore radial, trilete, broadly subtriangular. Laesurae about two-thirds the length of the radius of the spore. Lips narrow, distinct. Wall 2–3 μ thick.

Holotype. Pl. 11, fig. 6; GSC Plant Type no. 13024, slide no. MI–12; 66μ.

Similar forms. *Punctati-sporites orbicularis* Kosanke (1950) is smaller than *P. scabratus* but otherwise closely resembles it.

Punctatisporites putaminis sp. nov.

Plate 11, fig. 7

Diameter: 55–73 μ. Ornamentation: scabrate; visible at margin under high magnification. Other features: spore radial, trilete, ovate to circular. Laesurae about two-thirds the length of the radius of the spore. Lips low. Wall 2·5–5·5 μ thick, unfolded.

Holotype. Pl. 11, fig. 7, GSC Plant Type no. 13025, slide no. MI–23; 64μ.

Similar forms. *Punctatisporites ambiguus* Leschik (1955) resembles *P. putaminis*, but its two-layered wall is a distinguishing feature.

Infraturma APICULATI (Bennie and Kidston) R. Potonié

CYCLOGRANISPORITES Potonié and Kremp

Cyclogranisporites amplus sp. nov.

Plate 11, fig. 8

Diameter: 77–121 μ. Ornamentation: small, rounded, distinct granules. Other features: spore radial, trilete, broadly subtriangular to circular. Laesurae simple, half to two-thirds the length of the radius of the spore. Wall 1·5–3·5 μ thick.

Holotype. Pl. 11, fig. 8; GSC Plant Type no. 13026, slide no. MI–22; 92μ.

Similar forms. Spores of *Acitheca* (*Pecopteris*) *longifolia* R. and W. Remy (1955) from the Upper Carboniferous are similar but are perhaps slightly smaller and have a thinner wall than *Cyclogranisporites amplus*. *Cyclogranisporites sp.*, figured but not described by Hoffmeister, Staplin, and Malloy (1955*a*) from the Upper Devonian of Alberta, falls within the size range of *C. amplus* (according to their illustration), and appears in other respects to be similar.

Planisporites (Knox) Potonié and Kremp

Planisporites minimus sp. nov.

Plate 11, fig. 9

Diameter: 32–44·5 μ. Ornamentation: minutely echinate. Elevations distinctly conelike, less than 1 μ long, and alike in size. Other features: spore radial, trilete, circular. Laesurae about two-thirds the length of the radius of the spore. Lips low. Wall 1 μ thick, and unfolded.

Holotype. Pl. 11, fig. 9; GSC Plant Type no. 13027, slide no. MI–22; 43 μ.

Similar forms. Naumova's (1953) Middle and Upper Devonian species *Lophotriletes rotundus* may agree in part with *Planisporites minimus*, but the rays vary in length, according to her illustrations, and lips are not present. *Cyclogranisporites parvipunctatus* (Kosanke) Bhardwaj (1957) possess hemispherical granules, while those of *Planisporites minimus* are distinctly conelike. The Upper Carboniferous spore figured by Knox (1939, fig. 41), as nearly as can be determined from her illustration, resembles *P. minimus* rather closely.

Planisporites dilucidus sp. nov.

Plate 11, fig. 10

Diameter: 51–67 μ. Ornamentation: echinate. Elevations conelike, less than 1 μ long, about eighty visible on the equator. Other features: spore radial, trilete, circular. Laesurae two-thirds to three-quarters the length of the radius. Lips low. Wall 1 μ thick, rarely folded.

Holotype. Pl. 11, fig. 10; GSC Plant Type no. 13028, slide no. MI–22; 55 μ.

Similar forms. Lophotriletes subrotundatus Naumova (1953) closely resembles this species, but a critical comparison of the ornamentation of her specimens would be necessary before any conclusions could be reached as to synonymy. Spores of *Crossotheca Hoeninghausi* Brongniart and *C. Hughesiana* Kidston in Kidston (1923) also show similarity to *Planisporites dilucidus.*

APICULATISPORIS Pontonié and Kremp

Apiculatisporis elegans sp. nov.

Plate 11, fig. 12

Diameter: 67–85 μ. Ornamentation: closely spaced, elongate apiculations, up to 1·5 μ long, slightly variable in size. Other features: spore radial, trilete, circular. Laesurae about two-thirds the length of the radius. Commissure simple. Wall thin, rarely folded.

Holotype. Pl. 11, fig. 12; GSC Plant Type no. 13029, slide no. MI–12; 80 μ.

Similar forms. The spore called *Lophotriletes magnus* Naumova by Ishchenko (1956, p. 42) compares well with *A. elegans*, but some confusion exists because Naumova's original description of the species (1953) does not conform with Ishchenko's interpretation. Naumova restricted the species to roundly triangular spores with rays as long as the radius of the spore, which are features not possessed by *A. elegans.*

VERRUCOSISPORITES (Ibrahim) Potonié and Kremp

Verrucosisporites variabilis sp. nov.

Plate 11, fig. 15

Diameter: 43–76 μ. Ornamentation: broad, tapering, pointed spines up to 6 μ long, their basal diameter about equal to their height; occasional sharply pointed papilla-like projections; also occasional rounded projections which may reach 12 μ in diameter at their base and 10 μ in height. The complete range of variation may occur on a single specimen. Other features: spore radial, trilete, circular. Laesurae simple, at least half the length of the radius. Wall up to 3 μ thick.

Holotype. Pl. 11, fig. 15; GSC Plant Type no. 13030, slide no. MI–12; 68 μ.

Similar forms. *Raistrickia rubida* Kosanke (1950) superficially resembles this spore, but its wall is much thicker than that of *V. variabilis*.

Verrucosisporites grandis sp. nov.

Plate 11, fig. 11

Diameter: 98–150 μ. Ornamentation: stout verrucate projections cover the entire spore. On the distal portion, the projections are polygonal or irregular in transverse view, up to 6 μ wide, rounded or somewhat flattened at their apex, or occasionally ending in a small papilla. On the proximal face they are of smaller size but otherwise similar. There is usually a very slight elongation and fusion of verrucae at the outer boundary of the contact faces. Other features: spore radial, trilete, broadly subtriangular to circular in polar view, distinctly anisopolar in lateral view, proximal face flattened, distal portion hemispherical. Laesurae simple, about three-quarters the length of the radius, usually obscured by ornamentation.

Holotype. Pl. 11, fig. 11; GSC Plant Type no. 13031, slide no. MI–22; 128 μ.

Similar forms. *Verrucosisporites ovimammus* Imgrund (1952) possesses similar ornamentation, but is distinguishable from *V. grandis* by its lack of any suggestion of equatorial arcuate structure or anisopolar profile. In general form *V. grandis* shows some similarity to both *Lycospora magnifica* sp. nov. and *Biharisporites ellesmerensis* Chaloner (1959). It was excluded from *Lycospora* because of its large size, its distinctive verrucate ornamentation, and its very weak arcuate zone, and from *Biharisporites* because of the ornamentation of the contact faces and much smaller size.

HYSTRICOSPORITES gen. nov.

Type species *H. delectabilis* gen. et sp. nov.

Diagnosis. Trilete miospore or megaspore bearing discrete appendages which taper throughout their length and bear bifurcate grapnel-like tips. Appendages dispersed on both proximal and distal portions of the spore. Outline of spore subcircular in transverse plane of compression.

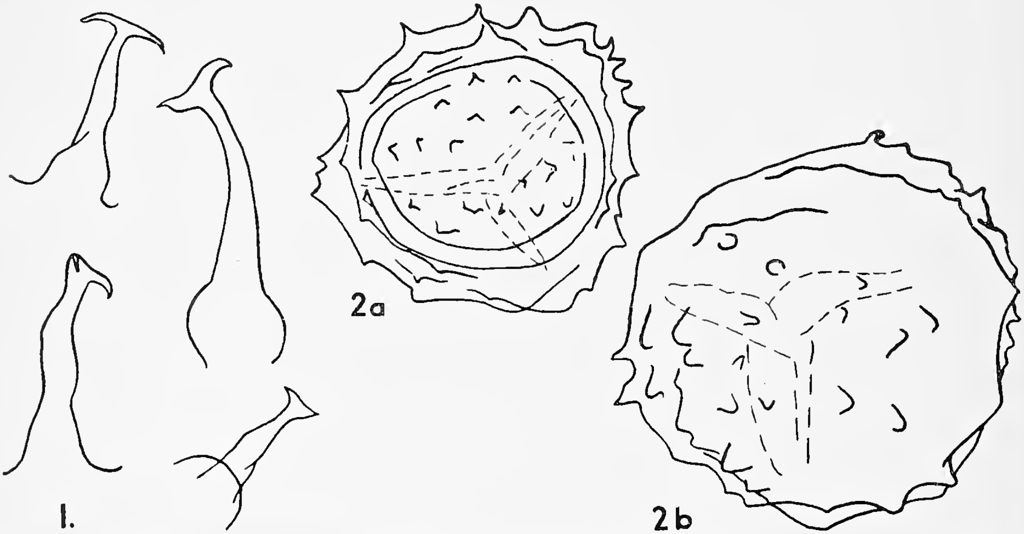
Remarks. *Hystricosporites* differs from *Archaeotriletes* (Naumova) Potonié (1958) in the absence of any equatorial flange or any apparent concentration of the appendages in the equatorial region, and from *Nikitinsporites* Chaloner (1959) in the absence of '. . . greatly elevated triradiate lips forming an apical prominence'. As in *Nikitinsporites*, the appendages of *Hystricosporites* cover the proximal and distal portions of the spore. *Ancyrospora* Richardson (1960) bears bifurcate processes, but is monosaccate.

It may be argued that there is sufficient similarity among these spores in their possession of anchor-like appendages to justify their inclusion in a single genus, and that Naumova's original description of *Archaeotriletes* (1953, p. 51) was valid even though she did not designate a type (see also Funkhouser 1958). Evidently much difference of opinion has existed regarding necessity of type designation for validity of fossil plant names. In this particular case I believe that less confusion would be caused by creation of a new genus (*Hystricosporites*) in conformity with the views of Potonié (1958) and Chaloner (1959) than by retention of Naumova's circumscription of *Archaeotriletes*.

Hystricosporites delectabilis gen. et sp. nov.

Plate 11, figs. 13, 14; text-fig. 1

Diameter: 145–340μ, exclusive of appendages. Ornamentation: scabrate. Body also bears elongate, slightly tapering appendages with grapnel-like bifurcations at their tips (Pl. 11, fig. 14; text-fig. 1). Appendages one-third to two-thirds the length of the radius of the spore body. Base of appendages expanded, often bulbous. Other features: spore radial, trilete, circular. Laesurae almost as long as the radius of the body, with more or less well-defined lips, sometimes raised and convoluted. On some specimens the triradiate structure is poorly defined. Wall thin.



TEXT-FIGS. 1, 2. 1, Appendages of *Hystricosporites delectabilis* sp. nov., ×500, showing variation in form in the holotype (GSC 13032). 2*a*, 2*b*, Specimens of *Hymenozonotriletes inaequus* sp. nov., ×500, showing variation in prominence of ornamentation, distal view; 2*a*, holotype (GSC 13042); 2*b* (GSC slide MI–13).

Holotype. Pl. 11, fig. 13; GSC Plant Type no. 13032, slide no. MI–16; 196μ, exclusive of appendages.

Similar forms. Chaloner (1959) refers to several records of spores with anchor-like spine apices from deposits of Middle or Upper Devonian age. Of these, type 'e' of Høeg (1942) and Type G_1 of Lang (1925) most closely resemble *A. delectabilis* and may be at least in part synonymous with it. *Azonotriletes ancistrophorus* Luber (Luber 1955, p. 70) from the Upper Devonian and Lower Carboniferous of the U.S.S.R. is similar to *Hystricosporites* except for its apparent lack of any triradiate mark. Table 1 gives previously recorded occurrences of spores with anchor-like appendages.

In her description of *Archaeotriletes*, Naumova (1953, pp. 8, 51) noted a similarity between the Devonian spores and 'megaspores' of the present-day *Azolla*. This resemblance, which would presumably apply to spores here named *Hystricosporites* is, however, only superficial. The bifurcate glochidia of *Azolla* have no evident homologue in the Devonian spores. The megaspore of both living and fossil *Azolla* is papillate, and possesses no elaborate bifurcate processes (Arnold, 1955).

BIHARISPORITES R. Potonié

Biharisporites submamillarius sp. nov.

Plate 11, fig. 16; Plate 12, figs. 1–3

Diameter: 280–610 μ. Ornamentation: stout hemispherical tubercles spaced irregularly over all portions of the spore except the contact areas. Tubercles 6–12 μ wide at their base and up to 10 μ high. Each bears at its summit a small, tapering, pointed spine (Pl. 11, fig. 16). Tubercles discrete and typically wider than long, but in some specimens approximately equidimensional. A gradation exists between specimens with the wall thickly set with tubercles and those with very few tubercles (cf. Pl. 12, figs. 1, 2). Considerable variation also exists in the size of the tubercles from one specimen to another; on those with few tubercles they are usually smaller in size. Rarely there is some fusion of the tubercles at the outer boundary of the contact faces. Between the tubercles and on the contact faces the wall is ornamented by small pits and elevations of irregular pattern (similar to 'scabrate' of Harris (1955) but on a larger scale). Other features: spore radial, trilete, broadly subtriangular in polar view. Triradiate ridges prominent, often slightly convoluted, about two-thirds to three-quarters the length of the radius of the spore, up to 55 μ high at the pole, tapering to their extremities. Distinct contact faces extend about two-thirds the distance to the equator. On some spores a membranous, laevigate, centrally located body is apparent in the interior of the spore. Its relation to the surrounding spore wall is obscure; if it were unfolded it would be difficult to discern in an intact specimen, and this may be the case in those specimens in which it was not seen. In a few specimens, the mesosporium-like structure was found projecting from the edges of a broken spore; occasionally similar structures were found completely free (Pl. 12, fig. 3).

Holotype. Pl. 12, fig. 1; GSC Plant Type no. 13033, slide no. MI–12; 372 μ. *Paratype*. Pl. 12, fig. 2, GSC Plant Type no. 13034, slide no. MI–12; 600 μ.

Similar forms. Chaloner (1959) has described *Biharisporites ellesmerensis* which resembles *B. submamillarius* rather closely, although several differences are apparent when specimens of each are compared. *B. submamillarius* is larger (280–610 μ as compared with 204–304 μ); the triradiate ridges of *B. submamillarius* are slightly higher relative to the total size of the spore than those of *B. ellesmerensis*, and slope away from the pole to their extremities while those of the latter species maintain a much more uniform height throughout. A more marked difference lies in their ornamentation. That of *B. submamillarius* consists of tubercles which are rarely fused, even at the outer boundaries of the contact faces, and which are less closely spaced than in *B. ellesmerensis*. In addition, the papilla at the tip of each tubercle is a prevalent feature in *B. submamillarius* rather than only an occasional one as in *B. ellesmerensis*. The tubercles of the former are quite symmetrically rounded both transversely and laterally, which is not true for specimens of *B. ellesmerensis* that I have examined.

A mesosporium-like body is present both in the interior of *B. submamillarius* and in the type specimen of Potonié's (1956) designated genotype, *B. spinosus*, although it has not been stated as a distinguishing criterion of either species, or of the genus. Such internal structures do, of course, occur in other genera than *Biharisporites*. Høeg, Bose, and Manum (1955) list several references from the literature on fossil megaspores in which 'mesosporoid' bodies are mentioned or illustrated.

Infraturma MURORNATI Potonié and Kremp

CONVOLUTISPORA Hoffmeister, Staplin and Malloy

Convolutispora flexuosa forma *minor* Hacquebard 1957

Plate 12, fig. 4

Remarks. The diameter range of this spore is 47–81 μ, which would include the 72 μ measurement given by Hacquebard (1957, p. 312). The only apparent points of difference between the present type and *C. flexuosa* forma *minor* as originally described are the occasional subtriangular shape and greater width of rugulae (up to 13 μ) in the former. However, it is impossible to judge the variation in dimensions that may have existed in the Horton spore on the basis of the two specimens recorded by Hacquebard. The circumscription of the species is consequently regarded here as extended to include the Melville Island spore. Laesurae, observed on a few specimens, extend about three-quarters the distance to the equator. Diameter of figured specimen, 78 μ.

Convolutispora florida Hoffmeister *et al.* (1955*b*) is smaller than *C. flexuosa* forma *minor*, but otherwise resembles it. *Periplectotriletes amplectus* (Luber) Ishchenko forma *kasachstanensis* Luber (*in* Ishchenko 1956, p. 46) has narrower rugulae than *Convolutispora flexuosa* forma *minor*.

Infraturma PERINOTRILITI Erdtman

CIRCUMSPORITES gen. nov.

Type species *C. melvillensis* gen. et sp. nov.

Diagnosis. Trilete megaspore with enveloping perisporium-like wall appressed over its complete area to a more or less thin-walled central body. Perisporium and central body ornamented. Spore subtriangular to circular in polar view.

Circumsporites melvillensis gen. et sp. nov.

Plate 12, figs. 6, 7

Diameter: 203–292 μ, including ornamentation; body 187–270 μ. Ornamentation: perisporium thickly covered by sac-like projections which taper from broad bases to blunt or pointed apices. Projections frequently joined to one another for most of their length, their tips remaining free (Pl. 12, fig. 6). The perisporium, if partly dissociated from the

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EXPLANATION OF PLATE 12

All figs. are ×500, except fig. 1 (×250), fig. 2 (×110), fig. 3 (×200), and fig. 7 (×250).

Figs. 1, 2. *Biharisporites submamillarius* sp. nov. 1, holotype (GSC 13033); 2, paratype (GSC 13034).

Fig. 3. Thin-walled structure similar to those seen in interior of *Biharisporites submamillarius* (GSC Slide MI–12).

Fig. 4. *Convolutispora flexuosa* forma *minor* Hacquebard (GSC Slide MI–16).

Fig. 5. *Lycospora magnifica* sp. nov., holotype (GSC 13036).

Figs. 6, 7. *Circumsporites melvillensis* gen. et sp. nov. 6, ornamentation of perisporium; 7, holotype (GSC 13035).

Fig. 8. *Perotrilites sp.* (GSC Slide MI–14).

Figs. 9, 10. *Lycospora magnifica* forma *endoformis* sp. et f. nov. 9, holotype (GSC 13037); 10, paratype (GSC 13038), internal body apparently close to the proximal wall of the spore.

Fig. 11. *Lycospora pallida* sp. nov., paratype, distal view (GSC 13040).


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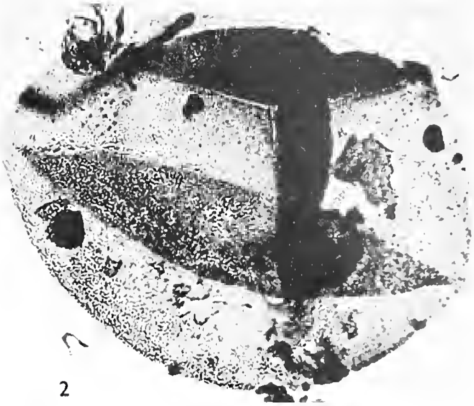
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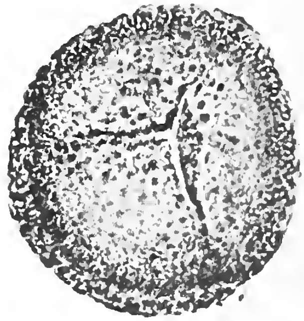
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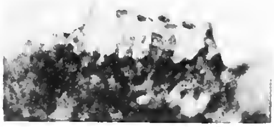
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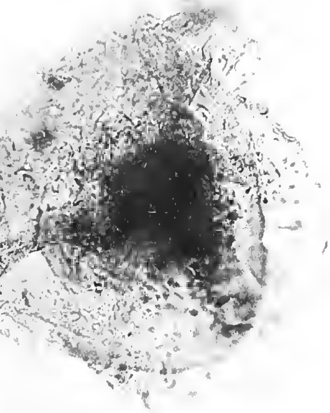
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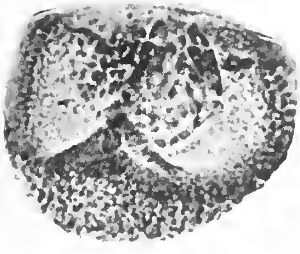
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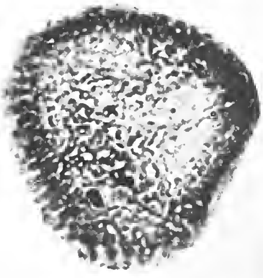
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McGREGOR, Devonian spores from Canadian Arctic

central body (as in the holotype), has a beaded appearance. Central body with small pits and elevations similar in appearance to those on the contact faces of *Biharisporites submamillarius*. Other features: spore radial, trilete, broadly subtriangular to circular. Laesurae usually weakly defined or inevident, but, where visible, almost as long as the radius of the body. Walls of perisporium and body thin.

Holotype. Pl. 12, fig. 7; GSC Plant Type no. 13035, slide no. MI–20; 228 μ, including ornamentation.

PEROTRILITES Couper

Perotrilites sp.

Plate 12, fig. 8

Diameter: 90 μ (one specimen only). Ornamentation: perisporium granulate; granules 3–7 μ apart. Body laevigate. Other features: spore radial, trilete, very broadly subtriangular. Laesurae about two-thirds the length of the radius, consist of three convoluted, fold-like rays, no commissure being visible. Thin-walled perisporium closely envelops body.

Remarks. Only one specimen of this type was found. In the double nature of its wall it resembles a complex of spores which occurs at several localities in the Lower and Middle Devonian of eastern Canada (McGregor 1957), and also resembles Middle and Upper Devonian species which Naumova (1953) has described as *Hymenozonotriletes*. However, *Perotrilites sp.* cannot be placed in *Hymenozonotriletes* as emended by Potonié (1958, p. 29). It also differs from *Endosporites* in several features, the most prominent being the close appression of the perisporium and the body.

Turma ZONALES (Bennie and Kidston) R. Potonié
Subturma ZONOTRILETES Waltz
Infraturma CINGULATI Potonié and Klaus
LYCOSPORA (S. W. and B.) Potonié and Klaus

Lycospora magnifica sp. nov.

Plate 12, fig. 5; Plate 13, figs. 2–4

Diameter: 69–119 μ. Ornamentation: distal portion scabrate, this ornamentation superimposed upon verrucate units of low relief (about 1–2 μ high) and up to about 5 μ in diameter. Proximal portion scabrate. Some specimens possess low verrucate projections up to 4 μ in diameter in the angles of the rays near the proximal pole (Pl. 12, fig. 5). On some specimens the verrucate pattern is less apparent. Verrucate elements tend to be joined laterally on the arcuate thickening, often possess minute papilla-like extensions in this area. Other features: spore radial, trilete, broadly subtriangular to circular. Arcuate thickenings form narrow cingulum at outer boundary of proximal face. Laesurae extend to, or almost to, the cingulum. Lips low and narrow. Proximal face flattened, distal portion hemispherical.

Holotype. Pl. 12, fig. 5; GSC Plant Type no. 13036, slide no. MI–12; 87 μ.

Similar forms. This species and the other species from the Melville Island formation which have been assigned to *Lycospora* are unusually large for the genus. The large size of *L. magnifica* distinguishes it from *L. torulosa* Hacquebard (1957) to which it is superficially similar.

Lycospora magnifica forma *endoformis* sp. et f. nov.

Plate 12, figs. 9, 10

A thin-walled, transparent body is present in the interior of this spore. Its relationship to the outer wall of the spore is not clear; it may be in contact with the inner side of the outer wall at the proximal pole (Pl. 12, fig. 10). In other respects, including size (69–124 μ), this spore is identical with *L. magnifica*.

Holotype. Pl. 12, fig. 9; GSC Plant Type no. 13037, slide no. MI–12; 83μ. *Paratype*. Pl. 12, fig. 10; GSC Plant Type no. 13038, slide no. MI–12; 82μ.

Lycospora pallida sp. nov.

Plate 12, fig. 11; Plate 13, fig. 1

Diameter: 64–82 μ. Ornamentation: granulate; granules on distal side of spore more or less joined at their base to form a rugulate pattern. Ornaments often more elongate at equator, appearing mammillate in transverse view. Ornaments reduced in size on proximal face, granules discrete. Other features: spore radial, trilete, broadly subtriangular to circular. Laesurae extend almost to the equator, are often indistinct. Lips low and narrow. Proximal face flattened, distal portion hemispherical. The degree of elongation and lateral fusion of ornaments at the equator is somewhat variable from specimen to specimen, so that the cingulum so formed varies in prominence.

Holotype. Pl. 13, fig. 1; GSC Plant Type no. 13039, slide no. MI–12; 64μ. *Paratype*. Pl. 12, fig. 11; GSC Plant Type no. 13040, slide no. MI–12; 74μ.

DENSOSPORITES (Berry) Potonié and Kremp

Densosporites crassus sp. nov.

Plate 13, fig. 8

Diameter: 83–96 μ (three specimens). Ornamentation: punctate. Other features: spore radial, trilete, broadly subtriangular to ovate. Laesurae simple, extend to margin of body. Dense equatorial thickening (cingulum), 10–20 μ wide. Wall of body only slightly less opaque than that of cingulum.

Holotype. Pl. 13, fig. 8; GSC Plant Type no. 13041, slide no. MI–12; 83 μ.

EXPLANATION OF PLATE 13

All figs. are ×500, except fig. 4 (×100).

Fig. 1. *Lycospora pallida* sp. nov., holotype (GSC 13039).

Figs. 2–4. *Lycospora magnifica* sp. nov. 2, 3, spores from periphery of mass shown in fig. 4; 4, mass of spores (GSC Slide MI–13).

Fig. 5. *Hymenozonotriletes inaequus* sp. nov., holotype (GSC 13042).

Figs. 6, 7. *Tholisporites densus* sp. nov. 6, holotype (GSC 13043), transverse view; 7, paratype (GSC 13044), lateral view.

Fig. 8. *Densosporites crassus* sp. nov., holotype (GSC 13041).

Fig. 9. *Tholisporites tenuis* sp. nov., holotype (GSC 13045).

Fig. 10. *Tholisporites punctatus* sp. nov., holotype (GSC 13046).

Figs. 11, 12. (?) *Latosporites sp.* (GSC Slide MI–22).


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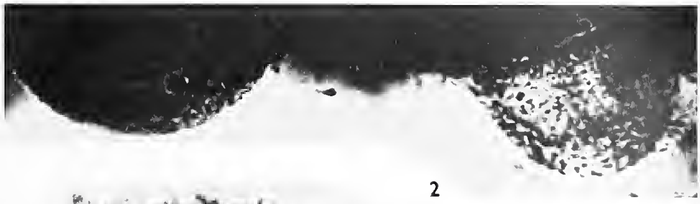
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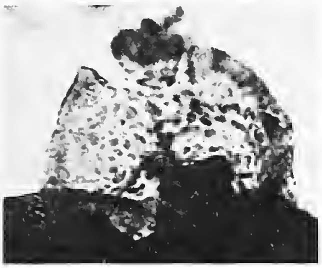
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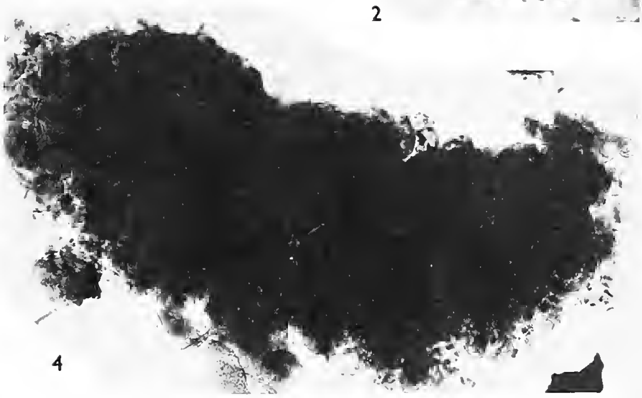
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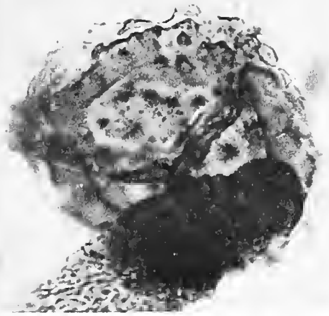
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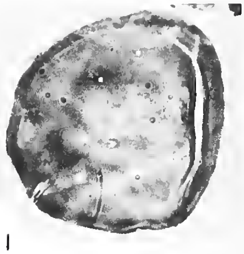
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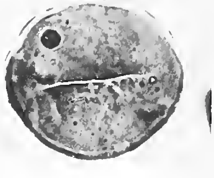
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McGREGOR, Devonian spores from Canadian Arctic

Infraturma ZONATI Potonié and Kremp
HYMENOZONOTRILETES (Naumova) Potonié
Hymenozonotriletes inaequus sp. nov.

Plate 13, fig. 5; Text-fig. 2

Diameter: 93–121 μ. Ornamentation: proximal portion laevigate toward the pole. Distal portion with low, pointed, tapering projections up to 4 μ wide and about 3 μ high. Toward equator, projections increase in size and are joined basally to form sub-concentric flange-like structures, either prominently displayed (text-fig. 2*a*) or of lesser size (text-fig. 2*b*). Equatorial projections with papillate tips. Other features: spore radial, trilete, circular. Laesurae almost as long as body of spore. Commissure obscured by thick folds along rays. A dense ring, similar to that present in species of *Densosporites*, is evident near the equator on some specimens; on other specimens it is discontinuous or inevident.

Holotype. Pl. 13, fig. 5; GSC Plant Type no. 13042, slide no. MI–22; 93 μ.

Similar forms. One of the specimens of *Hymenozonotriletes argutus* illustrated by Naumova (1953, pl. 9, fig. 9) resembles *H. inaequus*, and may be synonymous with it, although Naumova interprets the equatorial portion as a perisporium. *Densosporites aseki* Potonié and Kremp (1956) differs from *Hymenozonotriletes inaequus* in its smaller size and relatively less opaque central portion. *Lepidozonotriletes aculeatus* Hacquebard (1957) has larger ornaments and flange-like rays. *Densosporites devonicus* Richardson (1960) has smaller, bifurcate appendages.

The marginal structure of spores similar to *Hymenozonotriletes inaequus* has been variously interpreted as a perisporium (Naumova 1953; Hacquebard 1957) and a zona (Potonié 1958). *H. inaequus* is here regarded as having a zona in the sense of Potonié and Kremp (1955, p. 15). Its structure is apparently fundamentally similar to that of *Densosporites devonicus* Richardson, but it is placed in *Hymenozonotriletes* rather than in *Densosporites* because of its conformity to the emended diagnosis of *Hymenozonotriletes* by Potonié (1958, p. 29).

Infraturma PATINATI Butterworth and Williams
THOLISPORITES Butterworth and Williams
Tholisporites densus sp. nov.

Plate 13, figs. 6, 7

Diameter: 45–89 μ. Ornamentation: laevigate. Other features: spore radial, trilete, broadly oval to circular in polar view, distal portion hemispherical, proximal portion less convex than the distal. Laesurae simple, about four-fifths the length of the radius. Patina extending over entire distal portion, of equal thickness over all of its area (up to 11 μ thick), except where it becomes thin abruptly at the outer margin of the proximal face. Proximal wall thin. On most specimens a thin, transparent, veil-like structure extends over the proximal face, apparently enveloping the laesurae (Pl. 13, fig. 7). This membranous layer appears to be an extension of the outer part of the thick distal patina. Thickness of patina equals 4–14 per cent. of total spore diameter, and bears no constant relation to the total spore size.

Holotype. Pl. 13, fig. 6; GSC Plant Type no. 13043, slide no. MI–12; 69 μ. *Paratype*. Pl. 13, fig. 7; GSC Plant Type no. 13044, slide no. MI–12; 86 μ.

Similar forms. Tholisporites scoticus Butterworth and Williams (1958) is the only species previously placed in this genus. *T. densus* differs from it in larger size, laevigate wall, and constant thickness of patina (i.e. not thickened at the equator), and the membranous layer over the proximal face. From the Lower Carboniferous and Upper Devonian of the U.S.S.R., Luber (1955, p. 64) reports the occurrence of a spore (*Zonotriletes pelorius* Luber) of variable size and form, which possesses a distal thickening of the wall with 'growth layers'. This laminated nature of the patina of *Z. pelorius* seems to distinguish it from spores of the *Tholisporites* type.

Tholisporites tenuis sp. nov.

Plate 13, fig. 9

Diameter: 54–77 μ. Ornamentation: Laevigate. Other features: spore radial, trilete, ovate to circular in polar view. Laesurae almost as long as radius, simple. Distal wall thickened to a slight patina (up to 3 μ). Proximal wall thin, with a thin membranous layer, often weakly defined, covering the proximal face, as in *T. densus*.

Holotype. Pl. 13, fig. 9; GSC Plant Type no. 13045, slide no. MI–12; 72 μ.

Tholisporites punctatus sp. nov.

Plate 13, fig. 10

Diameter: 57–92 μ. Ornamentation: scabrate. Other features: spore radial, trilete, subcircular. Laesurae simple, almost as long as radius. Distal patina 3–10 μ thick, becoming thin abruptly near the equator, of constant thickness over distal portion. There is a suggestion of a thin proximal membrane similar to that of *T. densus* and *T. tenuis*, but its presence has not been confirmed.

Holotype. Pl. 13, fig. 10; GSC Plant Type no. 13046, slide no. MI–12; 82 μ.

Turma MONOLETES Ibrahim
Subturma AZONOMONOLETES Luber
Infraturma PSILAMONOLETI v. d. Hammen
LATOSPORITES Potonié and Kremp

(?) *Latosporites sp.*

Plate 13, figs. 11, 12

Diameter: 50·5 μ and 66 μ (two specimens only). Ornamentation: minutely punctate. Other features: spores bilateral (?). The tetrad mark resembles a monolete commissure, but possesses a very short, poorly defined Y-like bifurcation. On the larger specimen (Pl. 13, fig. 11) the small arm is at one end of the large aperture, and the arms of the Y are short, without raised margins. On the smaller specimen (Pl. 13, fig. 12) the locus of the division is about two-thirds the distance from the end of the major aperture; one arm continues in line with the major aperture and bears low lips, while the other division is very short and without lips. Wall of large specimen 4·5 μ thick; wall of small specimen 2 μ thick. Outline elliptical to subcircular.

Similar forms. Spores of *Asterotheca meriani* (Brongn.) Stur described by Bhardwaj and Singh (1957) occasionally possess a 'pseudotrilete mark', which is interpreted by these authors as a secondary feature caused by flattening during fossilization. *Leschikisporis* *aduncus* (Leschik) R. Potonié (1958) has an asymmetrical triradiate mark but the one shorter ray stands perpendicular to the locus of the other two rays, which it does not do in either of the specimens from Melville Island.

COMPOSITION OF THE ASSEMBLAGE

Twenty new species and one new forma of miospores and three new species of megaspores are recognized, as well as specifically unnamed specimens of *Perotrilites* and (?) *Latosporites*. One species, *Convolutispora flexuosa* forma *minor* Hacquebard, has been previously reported, from the Horton group (Mississippian) of Nova Scotia.

Lycospora magnifica is the most abundant miospore in the assemblage, comprising 35 per cent. of the total of the small spores. Next in abundance are *Tholisporites densus* (28%), *Lycospora vulgaris* (20%), *Tholisporites punctatus* (5%), *Lycospora pallida* (3%), and *L. magnifica* forma *endoformis* (2%). None of the other small spore species constitutes as much as 2 per cent. of the total.

Biharisporites submamillarius comprises 72 per cent. of the megaspores, with *Hystricosporites delectabilis* 18 per cent., and *Circumsporites melvillensis* 10 per cent. The percentages are based on separate counts of 200 specimens each for the miospores and the megaspores.

In diameter range there is a distinct break between those of 45 μ to 110 μ and those of 200 μ to 600 μ, with only a few specimens lying outside these limits.

COMPARISON WITH OTHER ASSEMBLAGES

Naumova's (1953) Frasnian and Famennian assemblages of the Russian Platform comprise several dozen species, and none, with the exception of some of the weakly ornamented circular forms, offer similarity with those from Melville Island. Evidently the latter represent a flora not reported by Naumova, especially since her dominant sub-groups *Retusotriletes*, *Lophozonotriletes*, and *Hymenozonotriletes* (except for *H. inaequus* and possibly *Perotrilites sp.*) are not present in the arctic assemblage. Spores comparable with those of Naumova do occur in the Gaspé Sandstone (McGregor 1957) but again there are no spores in this assemblage which resemble those from Stevens Head.

'Upper Devonian' spores briefly reported by Hoffmeister, Staplin, and Malloy (1955*a*) from western Canada bear little resemblance to those from Melville Island, except for the form with bifurcate appendages which is comparable with *Hystricosporites delectabilis*. These authors do not give exact geological data, and there is apparently some evidence of contamination in their preparations (1955*a*, p. 10).

Closest agreement with the larger spores from Melville Island is evident in those described by Chaloner (1959) from Okse Bay, Ellesmere Island. There is a general similarity between *Biharisporites submamillarius* and *B. ellesmerensis* Chaloner, and between *Hystricosporites delectabilis* and *Nikitinsporites canadensis* Chaloner. In addition, small spores that I have examined from the Okse Bay locality (unpublished) are of relatively large size, as are those from Stevens Head, and the megaspores, as first pointed out by Chaloner, tend to be relatively small, just as do the megaspores from Stevens Head. In both there is a tendency toward convergence in size between the megaspores and the miospores.

Regarding spores with grapnel-like appendages, resembling in this respect *Hystricosporites*, Table I shows that their known geological range is from the Middle Devonian (Lower Givetian in Richardson 1960) to perhaps as high as the Tournaisian.

Tholisporites, one of the dominant miospore genera in this coal, has been reported from one other source, the lower part of the Limestone Coal (Namurian) of Scotland (Butterworth and Williams 1958). The significance of this comparison is not yet known, since the two assemblages are otherwise quite different, and other Upper Devonian or Lower Carboniferous strata in which *Tholisporites* may occur have not been studied.

One of the species encountered here, *Convolutispora flexuosa* forma *minor*, also occurs in the early Mississippian of Nova Scotia (Hacquebard 1957), but the two floras are otherwise not alike, except that both lack distinctive younger Mississippian genera such as *Tripartites*, *Rotaspora*, and *Reinschospora*, or distinctive Devonian genera such as *Retusotriletes* and *Lophozonotriletes*.

Evidently the spores from the Melville Island coal possess only a suggestion of relationship to known Devonian and early Carboniferous records. Their closest affiliations seem to be with other assemblages from the Arctic, still incompletely known. Evidence concerning Upper Devonian and lowermost Carboniferous spores and relationships to their sporophyte counterparts is still too fragmentary to confirm the presence of a distinct flora of this age, of which this may be a part, or to speculate on the extent of such a flora in the arctic. If the suggested age assignment for the coal (Frasnian or perhaps Famennian) is correct, this new assemblage existed contemporaneously with Naumova's (1953) Givetian–Frasnian–Famennian flora.

BOTANICAL RELATIONSHIPS OF THE SPORES

The spores here assigned to *Lycospora* possess several features in common, which suggests that they were produced by a closely related group of parent plants. They are distinctly anisopolar, have a narrow equatorial zona, a broadly subtriangular outline, and an ornamentation of low projections. *Verrucosisporites grandis* may also belong to this complex, since it too possesses most of these characteristics. These features have also been associated with lycopsid affinity (Potonié and Kremp 1955). Chaloner (1959) suggests that the megaspore *Biharisporites ellesmerensis* is lycopsid, and its similarity to *B. submamillarius* would consequently be tentatively in favour of a lycopsid affinity for the latter as well.

There is some justification for suspecting that species of two of the dominant genera in the assemblage, *Lycospora* and *Biharisporites*, represent the microspores and megaspores of the same complex of plants, and that at least one of the species of *Lycospora*, perhaps *L. magnifica*, was borne by the same parent as *Biharisporites submamillarius*. These two species possess similar ornamentation (granulate-scabrate to verrucate, even with occasional papilla-like extensions on the ornaments of some specimens of *Lycospora magnifica*), both have reduced ornamentation on the proximal face, and both are broadly subtriangular in transverse outline. Furthermore, both possess gradations of similar order in the size and shape of ornaments. If these species do represent the same parent, the presence of the thin 'mesosporoid' body in some specimens of each might be expected.

A spore-mass composed of *Lycospora magnifica* was encountered (Pl. 13, figs. 2–4).

The elongate-oval shape and the dimensions of the mass (0·9mm.×0·4 mm.), and its compactness, suggest that it may represent the original form of a sporangium. No remnant of sporangial wall was seen, or any evidence of synangial or columellate structure. No tetrads were evident, although the spores were definitely trilete. Various palaeozoic plants, both lycopsids and non-lycopsids, bore sporangia of this general size and shape.

Butterworth and Williams (1958) postulated a relationship between *Tholisporites* and *Densosporites*, and more recently Chaloner (1958) established that at least one species of *Densosporites* was produced by a herbaceous lycopod. If Butterworth and Williams are correct, the three species of *Tholisporites* in the Melville Island coal might have had lycopsid origin as well, and would perhaps have been precursors of *Densosporites* species of the Carboniferous.

TABLE 1. *Previous records of spores with grapnel-like appendages*

Reference	*Designation*	*Locality*	*Age*
Lang 1925	Types G_1, G_2	Cromarty, Scotland	Middle Devonian
Kräusel and Weyland 1929	*Aneurophyton germanicum*?	Elberfeld, Germany	Middle Devonian
Arnold 1933; 1935	*Lepidostrobus gallowayi*	Pennsylvania, U.S.A.	Upper Devonian
Nikitin 1934	*Kryshtofovichia africani*	Voronezh district, U.S.S.R.	Middle Devonian
Arnold 1936		Scaumenac Bay, Canada	Upper Devonian
Arnold 1936	'. . . referable to Type G . . .'	Pittston, Penn., U.S.A.	Upper Devonian
Hoeg 1942	Spore types e, f	Spitzbergen	Middle/Upper Devonian
Eisenack 1944	*Triletes ancyreus*	Baltic	Middle and (?) Upper Devonian
Naumova 1953	*Archaeotriletes spp.*	Russian Platform	Middle and Upper Devonian
Luber 1955	*Azonotriletes ancistrophorus*	European and Asiatic U.S.S.R.	Upper Devonian
		Kazachstan	Tournaisian
Hoffmeister *et al.* 1955*a*	'new genus'	Alberta, Canada	Upper Devonian
Kedo 1957	*Archaeotriletes spp.*	Pripiat depression, U.S.S.R.	Upper Devonian
Chaloner 1959	*Nikitinsporites canadensis*	Ellesmere Island, Canada	Upper Devonian
Chaloner 1959		Perry, Maine, U.S.A.	Upper Devonian
Richardson 1960	*Ancyrospora, Cosmosporites, Densosporites spp.*	Cromarty, Scotland	Middle Devonian

Hystricosporites is probably closely allied to the various spore-types with anchor-like appendages that have been reported previously (Table 1), and which are prominent constituents of certain Middle and Upper Devonian floras. Undoubtedly a corresponding prominent megafloral component existed, but to date none has been demonstrated. Whatever the origin of the spores bearing these appendages may have been, their presence here is evidence of a denominator in the Canadian Arctic which is common to

Devonian floras of Quebec, Spitzbergen, Scotland, Germany, eastern United States, and Russia.

It is difficult to assess the affinities of those spores with relatively simple features, here assigned to *Punctatisporites*, *Cyclogranisporites*, *Apiculatisporis*, and *Planisporites*. Spores with granulate or apiculate ornamentation occur in almost all sediments in which dispersed spores have been found. Some of them may be allied to the ferns (Potonié and Kremp 1955; R. and W. Remy 1955) and the pteridosperms (Kidston 1923), but caution is necessary because the role played by homoplasy is not known. Based on present evidence, therefore, it would be unwise to more than suggest a fern or pteridosperm element in the Stevens Head coal.

As previously mentioned, three species of miospores and one of megaspores are exceedingly abundant in the coal. One would perhaps expect a greater degree of similarity among the percentages of the various species if the locale of deposition were accessible to wind-blown spores. Certainly the thick-walled spores so prevalent in the assemblage and the numerous megaspores argue against dispersal by wind. Probably then deposition was autochthonous, from a vegetation possibly dominated by the plants (lycopsids?) which bore the four most abundant spore species. Even if these plants were not dominant in the vegetation, they must have been most prolific in spore production.

Naumova's contention (1953), based on her study of Devonian miospores, that thin wall and reduced sculpture indicate a hydrophytic flora, while thick wall and prominent sculpture point to a mesophytic or xerophytic one is not easy to apply here. There is a definite over-all reduction in wall sculpture, but almost all of the miospores are thick walled.

There is little evidence to indicate the degree of relationship with the megaflora of Nathorst (1904) from the Upper Devonian of Ellesmere Island. Types that could be compared with known spores of *Archaeopteris*, a major constituent of Nathorst's flora, are not present in the spore assemblage. Fry (*in* Tozer 1956) identified *Bothrodendron sp.* L. and H. along with '. . . an axis similar to those associated with *Archaeopteris*' from similar beds on Prince Patrick Island, but again the relationship to the spores is not known.

GEOLOGICAL IMPLICATIONS

Previously, spore assemblages of comparable abundance and variety to this one have been applied profitably in correlation and dating of strata of various ages. So far, this has been particularly effective when groups of species are used (Balme 1957; Naumova 1953). Now, the application of spores from Devonian deposits in the Arctic in a similar way depends only on establishment and analysis of reference collections to which unknown samples can be compared. It may be possible to go even farther, and select single species as zonal guide fossils, since several of the species described here are of unusual construction.

Preliminary work on other Devonian strata in the Arctic has shown that other assemblages exist, not only in coal but also in shale and sandstones. There is thus broad scope for further exploration of these fossils in order to establish their full value to the geology of this area.

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SPORES FROM THE MIDDLE OLD RED SANDSTONE OF CROMARTY, SCOTLAND

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ABSTRACT. Plant spores are described from the Cromarty nodule beds (Middle Old Red Sandstone) of Scotland. The spores include three new genera *Cosmosporites*, *Rhabdosporites*, and *Ancyrospora*. The genus *Auroraspora* Hoffmeister, Staplin, and Malloy is emended to include forms, with a light coloured central body, which closely resemble spores of the species *Endosporites macromanifestus* Hacquebard. In agreement with Bhardwaj 1957 the genus *Cristatisporites* is here placed in the series Cingulati.

INTRODUCTION

THE principal fossils used as stratigraphic indices within the Middle Old Red Sandstone of Scotland are fossil fish; and a correlation based mainly on fish bands exists for this area. Recently, however, T. S. Westoll (1951) has suggested that the fish fauna of the main fish band (Achanarras band) may be a facies fauna because similar faunas are found at several levels on the south side of the Moray Firth. Westoll likewise indicates several anomalies in the fish fauna within the Orcadian basin. There is a need for evidence to supplement that provided by the fish remains and it is hoped that a study of the plant spores may eventually aid in elucidating the stratigraphic succession within the Old Red Sandstone basins.

Collections have been made of the fish bands from Orkney, Caithness, Cromarty, and from the south side of the Moray Firth and spores isolated from representative samples. The preservation of the carbonaceous material varies considerably in the different areas but it is excellent in the beds from the Cromarty area and has yielded an abundance of well-preserved spores some of which are described in this account.

Earlier work (Lang 1925) had drawn attention to the existence of a microflora in this region and contained descriptions and figures of nine types of plant spore identified under an arbitrary classification (A–I). During the present work Lang's earlier types have been recognized, together with a number of new types. The present account identifies and describes the new types of spores and revises some of the previously described spore types, bringing the whole together under a binomial system of classification for the first time in British Devonian microfloras. This will thereby facilitate subsequent identification of the microflora and enable more exact comparison with plant spores known from the Devonian of other areas. As the work proceeds it is hoped that a study of large numbers of these spores will enable limits to be set to specific variation, with the consequent evaluation of their stratigraphic usefulness. The assemblages so far studied correspond closely to assemblages known from the Middle Devonian of other areas particularly those from Europe and the U.S.S.R.

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Previous literature on Devonian plant spores. The earlier literature consists mainly of the incidental description and figures of spores associated with palaeobotanical work on fossil plants. Spores were obtained from sporangia by the use of cellulose film pulls and consequently the figures were often poor, and their descriptions too inadequate to enable comparisons to be made. As early as 1885 Clarke described 'spores' from Devonian deposits but Schopf (1957) commented, 'spore-like fossils may be present but some spherulitic and oolitic inorganic forms are evidently confused with them'.

Later more attention was paid to Devonian spores and they were isolated and described as distinct fossils. Lang (1925) described nine types of spores (A–I) from the Middle Old Red Sandstone of Scotland and later Krausel and Weyland (1929) described forms similar to Lang's types G and H from the Middle Devonian of Eberfield. These authors also described forms similar to, but smaller than, type G (Lang) from sporangia closely associated with the remains of *Aneurophyton germanicum.*

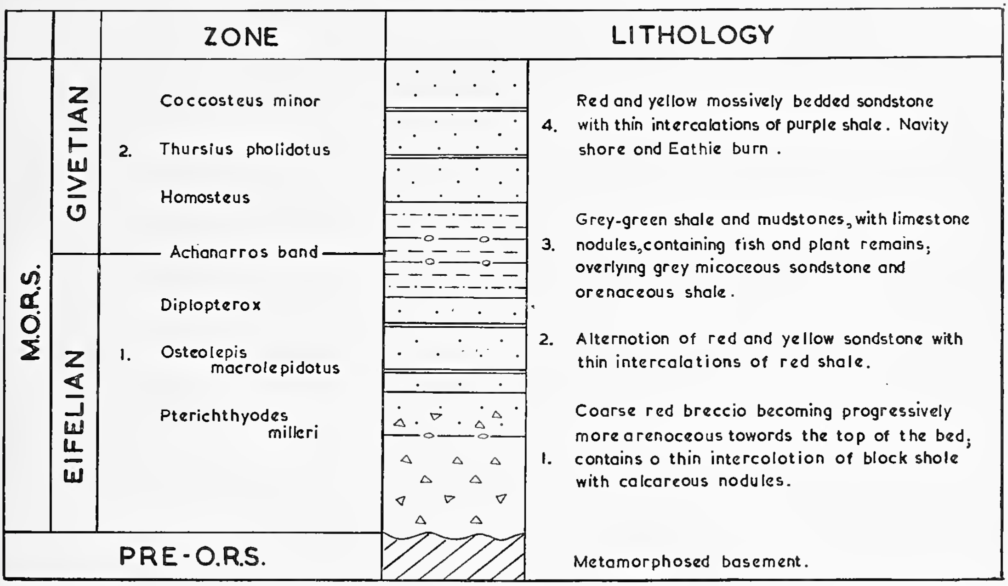
In 1936 Elovskava described seven spore forms from the Barzas coals (Kutznetsk basin, Russia) and classified these into groups and subgroups. In this work two main groups were instituted depending on the absence, or presence of 'wings', and referred to as groups 1 and 2 respectively. The 'wingless' spores of group 1 were further subdivided on the basis of ornamentation, size, and wall thickness, and those of group 2 were subdivided on width of 'wing' and ornamentation. Thomson (1940) used the same criteria to subdivide his Middle Devonian spores into seven groups as follows: 1 Laevigato—Zonales, 2 Apiculato—Zonales, 3 Angusto—Zonales (Magni), 4 Angusto—Zonales (Parvi), 5 Laevigati, 6 Granulati, and 7 Apiculati. Several of his forms resemble spores described by Lang as types A and C although type G, which is common in many Middle and Upper Devonian deposits, was not reported. Høeg (1942) followed Thomson's grouping and placed his seven types into Thomson's groups Granulati and Apiculati. The type F of Høeg (group Apiculati) is indistinguishable from some of Lang's type G and similar spores to type G (Lang) were also described from the *Archaeopteris* beds of Scaumenac bay, Canada (Arnold 1936).

Eisenack (1944) described forms similar to types A, B, ?C, and G of Lang together with several new types, and utilized a system of binomial classification placing his forms into the genus *Triletes* Reinsch. Previously, however, Schopf (1938) had emended and restricted *Triletes* to a group of megaspores and, therefore, Eisenack's use of *Triletes* is not valid.

Recent workers have tended to use a binomial system of nomenclature, for example, Hoffmeister, Staplin, and Malloy (1955); Radforth and McGregor (1954), however, used an arbitrary system.

The most comprehensive work of Devonian spores is that of Naumova (1953) who described spores from the Upper Givetian, Frasnian, and Fammenian deposits of the U.S.S.R. In her classification (first proposed in 1937) Naumova used very wide subgroups and placed together forms which were structurally dissimilar. Further, although the figures are excellent, her descriptions are often inadequate. In view of these facts it is proposed to follow the classification of Potonié and Kremp (1954) which is widely used although not accepted without reserve.

Evidence of stratigraphic horizon. The Middle Old Red Sandstone age of the Orcadian deposits was established at an early date when Traquair, on palaeontological evidence, substantiated the earlier view of Murchison. Traquair pointed out that three distinct fish faunas could be recognized in Scotland corresponding with Lower, Middle, and Upper Devonian. Further, the fossil fish have been used to zone the Middle Old Red Sandstone deposits of this area and, with the plant remains, have been used to equate the Orcadian deposits with Devonian sequences on the continent (Westoll 1951).



TEXT-FIG. 1. Succession of Middle Old Red Sandstone, Cromarty. (Fish zones based on Westoll 1937; 1951.)

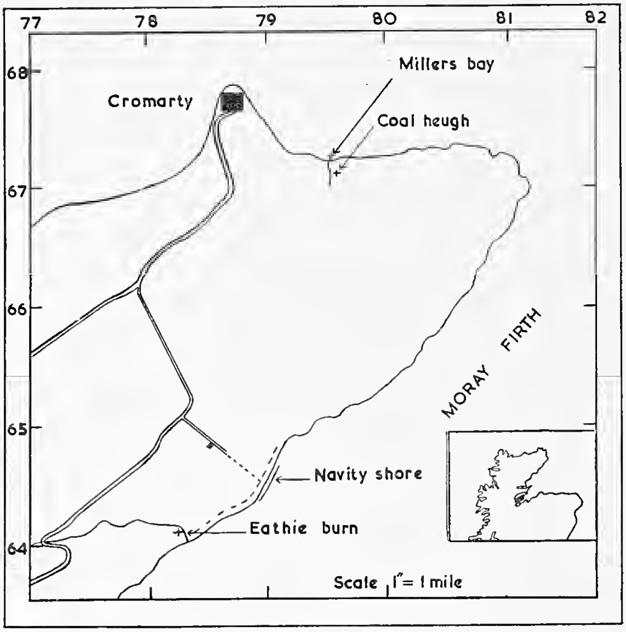
The Achanarras fish band, an important horizon in north-east Scotland, is traceable in Caithness, Orkney, Shetland, Edderton and Cromarty, and the south side of the Moray Firth. Westoll (1951) places the Achanarras horizon at the junction of the Eifelian and Givetian stages but refers to the possibility of the Achanarras fauna being a facies fauna although he says ‘in general . . . this fauna seems to mark a narrow zone’.

The Cromarty fish beds are stated to yield a fauna comparable with that of the Achanarras fish band and are therefore probably Upper Eifelian to Lower Givetian in age.

Middle Old Red Sandstone deposits as developed in the Cromarty area and along the south side of the Moray Firth are much thinner (approximately 150–250 feet thick in the neighbourhood of Cromarty) than those in Caithness and Orkney. Furthermore, the lithology of the deposits is distinct in the two areas. The sequence in the Cromarty area is as seen in text-figure 1. All the Middle Old Red Sandstone strata shown in the section are probably very close to the junction of the Eifelian and Givetian.

Collections were made from the sequences at Miller’s Bay, the Navity shore, and Eathie burn, and also from exposures at Coal Heugh. Spores have been isolated from samples of most of the rocks collected including the thin shale intercalation in the breccia (lithology 1, text-fig. 1) and the arenaceous shales of the Cromarty and Navity shores. The preservation of carbonaceous material is good in most of the beds but is excellent in the calcareous nodules and associated mudstones.

Method of preparation. Each sample was washed in distilled water and broken up into fragments about 5 mm. in diameter. It was then treated in dilute hydrochloric acid (1:5) and after all calcium carbonate had been removed, the acid was decanted and the material washed in distilled water. The residue was placed in a polythene flask and 40 per cent. hydrofluoric acid added. After it had been heated in a water bath for 16 to 24 hours the acid was decanted and the residue washed in distilled water. It was then treated in Schulze's solution for 2 to 3 hours, washed alternately in distilled water and potassium hydroxide, and finally mounted in glycerine jelly or canada balsam. Mounting in canada balsam was preceded by washing the material in successively more concentrated solutions of alcohol.



TEXT-FIG. 2. Index map of localities. Inset shows the Cromarty area (black) in relation to north Scotland.

In the case of the shales bromine was used prior to heating in hydrofluoric acid. The fragments were soaked in bromine for 48 hours which broke the material down into a fine mud. It was then washed in distilled water until all the bromine was removed. The material was halved and subjected to either dilute hydrochloric acid (1:5) or dilute acetic acid (1:5) and then the residue was washed, treated with hydrofluoric acid, oxidized, and mounted as described above. Slides from the same sample treated with and without bromine and with hydrochloric or acetic acid show the spores to be comparable in size and relative abundance.

SYSTEMATIC DESCRIPTIONS

All the slides referred to by serial numbers in the text are in the collection of the Geology Department, University of Sheffield; position on the slide is indicated by the instrument settings of a Cooke, Troughton, and Simms microscope.

Order (Anteturma) POLLENITES R. Potonié 1931
Division (Turma) SACCITES Erdtman 1947
Subdivision (Subturma) MONOSACCITES (Chitaley 1951) Potonié and Kremp 1954
Series (Reihe) INTRORNATI Butterworth and Williams 1958
Genus AURORASPORA Hoffmeister, Staplin, and Malloy 1955

Type species *A. solisortus* H., S., and M. 1955

A group of monosaccate spores, without a limbus, which includes spores of type A (Lang) occurs regularly in all preparations. Besides type A (Lang) the group includes spores which closely resemble the species *Auroraspora solisortus* H., S., and M. In distinguishing *Auroraspora* from *Endosporites*, Hoffmeister, Staplin, and Malloy stated, '*Auroraspora* has a dark, subtriangular to subcircular central body and a delicate transparent bladder. . . . The central body of *Endosporites* approximates the bladder in thickness.' In the preparations studied by the author dark- and light-coloured central bodies occur in spores which are otherwise identical. Further, Hoffmeister, Staplin, and Malloy, in comparing *Auroraspora* and *Endosporites*, do not mention the limbus which is considered by many workers as a diagnostic feature of *Endosporites* and does not occur in *Auroraspora*. Therefore it appears desirable to emend *Auroraspora* so as to include all the spores of the monosaccate group described herein rather than to subdivide the group and erect a new genus for spores resembling type A Lang. It has not been possible to obtain cotypes of *Auroraspora solisortus* for this purpose.

Diagnosis. Radial, trilete, monosaccate spores, central body margin distinct; completely enclosed by a bladder which has no limbus and is unornamented.

Description. Colour, bladder pale to dark yellow, central body yellow to dark brown. Outline subtriangular with convex sides, to subcircular; central body subtriangular to subcircular in proximal view. Bladder completely encloses spore body, width of bladder around the central body (proximal view) equal to subequal; bladder has minute, often radiating, folds, or often strongly folded; may have strong folds along the tetrad rays, these folds usually reach the equatorial margin. Margin without limbus. Bladder externally smooth but infragranular or infrapunctate, infrapunctation often irregular; central body smooth. Length of tetrad rays varies from one-third to equal the radius of the body of the spore.

Comparison. This genus differs from *Endosporites* in the absence of a limbus. The spores of *Cosmosporites* gen. nov. (see p. 52) are very similar to those of *Auroraspora* but the spores of the former have an external ornament of cones or small spines and the presence or absence of ornament on these monosaccate spores is considered to be sufficient justification of generic distinction.

The spores of *Endosporites macromanifestus* Hacquebard have no limbus, and they appear to be identical to spores found in the Middle Old Red Sandstone of Scotland (Hacquebard 1957, p. 17) which are here placed in the genus *Auroraspora*. *E. macromanifestus* has a smaller size range (112–173 μ) than the spores described here (102–254 μ) and, therefore, the species is emended to include all the spores of the latter range.

Auroraspora macromanifestus (Hacquebard) emend.

Plate 14, figs. 1, 2; text-fig. 6A.

Type A Lang 1925, p. 255, pl. 1, figs. 1, 2.
Triletes velatus Eisenack 1944, p. 108 (pars) (not pl. 1, figs. 1–3).
Endosporites macromanifestus Hacquebard 1957, p. 317, pl. 3, figs. 14, 15.

Holotype. Hacquebard 1957, pl. 3, fig. 16; size 150μ, central body diameter, measured from photograph, approximately 100μ. Horton group (Mississippian), Nova Scotia.

Occurrence. Cromarty nodule beds (Achanarras horizon) Miller's Bay, Coal Heugh, Navity shore and Eathie burn; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 102 to 254μ, body diameter 54 to 126μ. Ratio of central body diameter to whole diameter 36 to 82 per cent. Outline dominantly subtriangular; spores have prominent folds along the tetrad mark, the folds reach, or nearly reach, the equatorial margin.

Description. Colour pale yellow to dark yellow, central body dark brown in some specimens. Equatorial outline subtriangular with convex sides and rounded apices. Central body round to subtriangular in proximal view. Bladder often folded and has pronounced folds along the tetrad marks, these folds usually reach the equatorial margin; bladder externally smooth but infragranular, or infrapunctate, infrapunctation irregular. Central body laevigate. Rays of the tetrad mark approximately half the radius of the body of the spore, only seen in a few specimens since commonly obscured by the triradiate folds.

Remarks. The size range of the specimens of *Auroraspora macromanifestus* found in shales associated with nodule beds on the Navity shore is greater than that for the spores isolated from these beds on the northern shore of Cromarty. Individual spores are larger than those found at Miller's Bay and Coal Heugh. The differences between spores from the two areas can be seen from the ratio of the body diameter to the whole diameter of the spore. The ratios for the three main localities are: Miller's Bay 50–73 per cent. (north shore, Cromarty), Coal Heugh 50–72 per cent. (north shore, Cromarty), Navity shore 36–82 per cent. (south shore, Cromarty). The range of the ratio for the spores of *A. macromanifestus* found on the Navity shore includes the range for this

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EXPLANATION OF PLATE 14

All figures magnified ×300 except where stated otherwise.

Figs. 1, 2. *Auroraspora macromanifestus* (Hacquebard). 1, slide CR. 155 reference 051559; 2, slide CR. 94. 184551 showing folding of the bladder.

Fig. 3. *Auroraspora aurora* sp. nov. Holotype, slide CR. 80 reference 188437.

Fig. 4. *Cosmosporites velatus* comb. nov. Slide CR. 170 reference 189631.

Figs. 5, 6. *Cosmosporites microspinosus* gen. et sp. nov. 5, holotype ×200, slide CR. 92 reference 195598. 6, ×600, part of the equatorial margin showing minute spines which bifurcate at their tips.

Fig. 7. *Ancyrospora grandispinosus* gen. et sp. nov. Holotype ×200, slide CR. 162 reference 156619.

Figs. 8–9. *Rhabdosporites langi* comb. nov. 8, slide CR. 61 reference 111465, large specimen showing pronounced folds. 9, slide CR. 47 reference 169624, small specimen showing triradiate mark.

Figs. 10, 11. *Densosporites devonicus* sp. nov. 10, holotype, slide CR. 80 reference 258499, showing folds along the triradiate mark. 11, spore showing triradiate mark, without folds.

Fig. 12. *Cristatisporites orcadensis* sp. nov. Holotype, CR. 81 reference 160471.

Fig. 13. *Cristatisporites conannulatus* sp. nov. Holotype, CR. 87 reference 140440.

Fig. 14. *Cristatisporites mediconus* sp. nov. Holotype, CR. 88 reference 093490.


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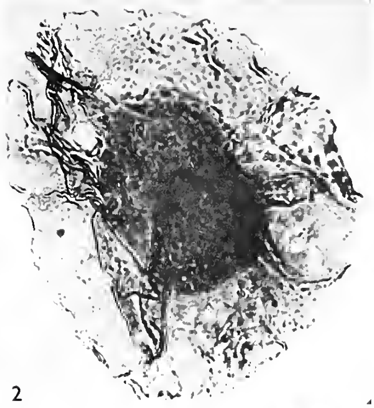
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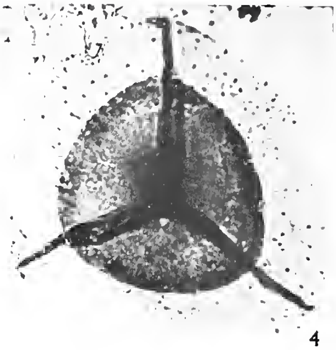
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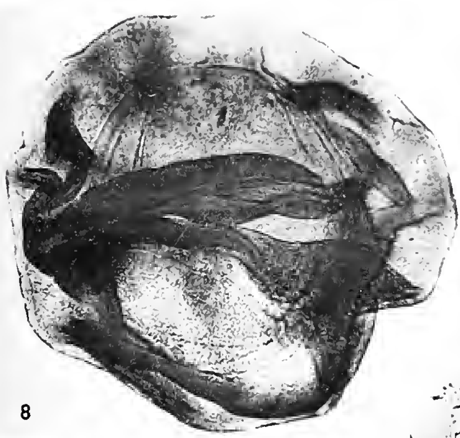
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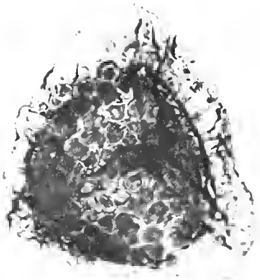
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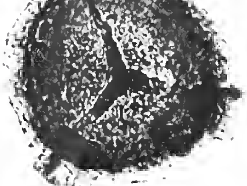
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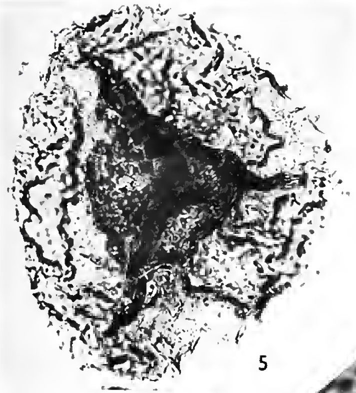
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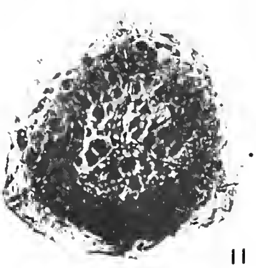
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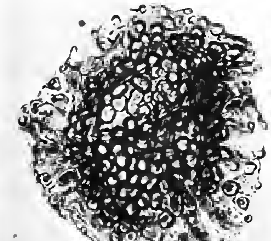
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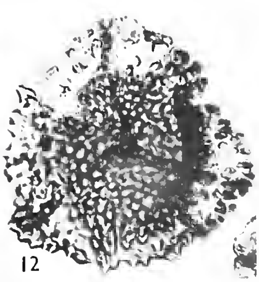

12

RICHARDSON, Middle Old Red Sandstone spores

species at the other two localities and, therefore, it is not considered justifiable separately to identify the larger spores.

These spores were originally described as type A by Lang (1925) and similar spores, from the upper Eifelian, were included in *Triletes velatus* by Eisenack (1944). Eisenack also included in this species forms which have a spinose ornament. In view of the heterogeneous nature of *T. velatus* and the fact that *Triletes* Reinsch was restricted to certain megaspores by Schopf in 1938, the species is not regarded as valid. Hacquebard (1957) described spores which appear to be identical with type A of Lang as *Endosporites macromanifestus*. The name *macromanifestus* is adopted here because, although *Triletes velatus* was erected in a prior publication, the spore chosen by Eisenack as the type of *T. velatus* has ornament (Eisenack 1944, pl. 1, fig. 2) and is referred to *Cosmosporites* (see below).

Auroraspora micromanifestus (Hacquebard) comb. nov.

Endosporites micromanifestus Hacquebard 1957, p. 317, pl. 3, fig. 16.

Holotype. Hacquebard 1957, pl. 3, fig. 16, size 88·6μ, central body measured from photograph approximately 48μ. Horton group (Mississippian), Nova Scotia.

This species is stated by Hacquebard to be identical to *Auroraspora* [*Endosporites*] *macromanifestus* except that it is smaller, and the bladder generally more distinctly infragranulose. It is, therefore, included here in the genus *Auroraspora*.

Auroraspora aurora sp. nov.

Plate 14, fig. 3

Holotype. Size 201μ, body diameter 108μ. Slide CR. 80. Reference 188437. Shales from the Cromarty nodule beds, Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, Coal Heugh, Navity shore and Eathie burn; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 120 to 201μ, body diameter 66 to 108μ. Ratio central body diameter to whole diameter 35 to 60 per cent. Outline rounded to subtriangular, bladder very thin and with minute folds.

Description. Colour yellow to dark yellow, central body brown in some specimens. Equatorial outline subtriangular with convex sides, or rounded. Central body round to subtriangular in proximal view. Width of bladder around the central body equal to subequal. Junction between central body and bladder distinct. Bladder thin, often wrinkled into numerous small folds. Bladder and body laevigate. Folds along the tetrad mark are absent. Triradiate mark usually distinct, rays of the mark vary from one-third to one-half and occasionally equal the radius of the body of the spore.

Comparison. *A. aurora* differs from *A. macromanifestus* in the rounded or rounded triangular outline of the spore and the central body. The bladder in *A. aurora* is often very fine and is wrinkled into numerous small, often radiating, folds. The spores do not possess the prominent folds along the tetrad mark which are typical of *A. macromanifestus*. In *A. aurora* the rays of the tetrad mark vary a great deal, from one-third to equal the radius of the body of the spore.

There is a close resemblance between *A. aurora* and *A. solisortus* H., S., and M., and the difference is one of size. The species *A. solisortus* has a range of 61–78 μ compared with a range of 120–201 μ in the species *A. aurora*.

Series (Reihe) EXTRORNATI Butterworth and Williams 1958

Genus COSMOSPORITES gen. nov.

Type species *Cosmosporites velatus* (Eisenack) comb. nov.

Diagnosis. Radial, trilete, monosaccate spores, completely enclosed in a bladder which has no limbus. Equatorial outline subtriangular with convex sides; central body round to subtriangular. Spores originally elliptical in polar section. Bladder has an external ornament which consists of pointed cones or spines which usually bifurcate at their tips. Folds often present along the rays of the tetrad mark. Derivation of name: G. Cosmos, ornament.

Comparison. This genus is erected for what appears to be a homogeneous group of spores which possess an external ornament of cones or short spines. It is distinguished from *Grandispora* H., S., and M. by its marked subtriangular outline, the possession in some of the spores of small spines which bifurcate at their tips, and by its large size.

Cosmosporites velatus (Eisenack) comb. nov.

Plate 14, fig. 4; text-fig. 3

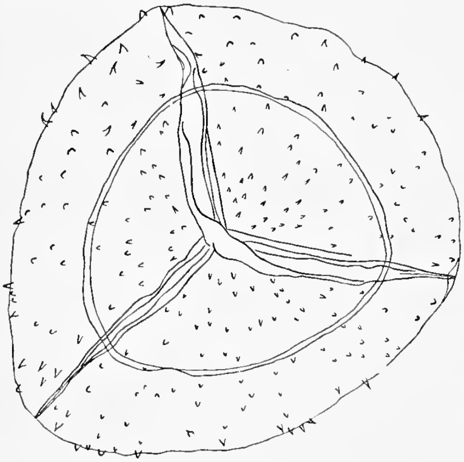
Triletes velatus Eisenack 1944, p. 108 (pars), pl. 1, figs. 1–3.

Holotype. Eisenack 1944, pl. 1, fig. 2; size 208 μ, central body 114 μ, cones 1 μ. Probably Middle Devonian.

Occurrence. Cromarty nodule beds (Achanarras horizon), Coal Heugh, Miller's Bay, Navity shore, Eathie burn; especially abundant at Coal Heugh; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 108 to 208 μ, body 54 to 116 μ; bladder has an external ornament consisting of cones of variable size in different spores, cones 1–4 μ.

Description. Colour of the bladder pale yellow, body dark yellow to brown. Equatorial outline subtriangular with convex sides and rounded apices, body rounded to sub-triangular. Bladder ornamented by pointed cones of variable size on different spores, usually between 1 and 2 μ, occasionally they are 4 μ long. Ornament appears to be confined to the distal surface. Body distinct smooth. Bladder is sometimes strongly folded and there are folds along the triradiate mark which reach the equatorial margin. Triradiate mark, often obscured by folds, two-thirds of the radius of the body.



TEXT-FIG. 3. *Cosmosporites velatus* comb. nov. Camera lucida drawing × 500.

Comparison. Cosmosporites velatus differs from *C. microspinosus* sp. nov. by its ornament of cones, the larger central body in relation to the whole diameter, and by its smaller size.

Cosmosporites microspinosus sp. nov.

Plate 14, figs. 5, 6

Holotype. Size 249μ, central body 100μ. Slide CR. 92. Reference 198598. Cromarty fish band (Achanarras horizon), Navity shore.

Occurrence. Shales at the tops of the Cromarty nodule beds on the Navity shore, shales at Coal Heugh (Achanarras horizon); Lower Givetian, M.O.R.S. Rare.

Diagnosis. Spores radial, trilete; size 186 to 282μ, central body 98 to 156μ; bladder has an external ornament consisting of minute spines which usually bifurcate at their tips and are widely spaced, spines 3 to 9μ long.

Description. Colour yellow to dark yellow, central body brown. Equatorial outline subtriangular with convex sides and rounded apices, body triangular to subtriangular. Width of bladder around central body subequal. Ornament consists of minute spines which usually bifurcate at their tips, are widely spaced, and are borne on the distal surface and the equatorial margin. Central body indistinct, appears smooth. Bladder often folded and corroded. Prominent folds obscure the tetrad mark and usually reach the equatorial margin.

Remarks. Eisenack (1944) in his description of *Triletes velatus* records that he has spores which have small bifurcating spines, and these may be comparable to *C. microspinosus* sp. nov. Eisenack, however, did not figure or name these spores but considered that they were intermediate between his species *Triletes velatus* and *T. paravelatus*. In the material studied, however, the spores which resemble *T. velatus* have a loose exine which is demonstrated by folding which does not affect the central body, whilst spores which resemble *Triletes paravelatus* (probably *Cristatisporites*) are also found, but in these spores the exoexine and the intexine appear to be attached as no folding has been observed which affects only the exoexine (text-fig. 8).

Genus RHABDOSPORITES gen. nov.

Type species *Rhabdosporites langi* (Eisenack) comb. nov.

Diagnosis. Radial, trilete, monosaccate spores completely enclosed in a bladder which has no limbus. Equatorial outline of both bladder and body subcircular to elliptical. Spores originally spherical, or nearly so, with body attached on the proximal side. Bladder possesses an external ornament which covers the whole surface and consists of evenly distributed, closely packed rods which are parallel sided elements and have truncated tips. Body membrane smooth. Derivation of name: G. Rhabdo, rod.

Comparison. The nature of the external ornament distinguishes this genus from *Glomospora* and *Remysporites* Butterworth and Williams which also possess an external ornament. In contrast to the evenly distributed rods of *Rhabdosporites*, *Glomospora* has an external ornament consisting of 'slightly raised spiral or parallel ridges', and in *Remysporites* the bladder is laevigate to microreticulate.

Rhabdosporites langi (Eisenack) comb. nov.

Plate 14, figs. 8–9; text-figs. 4, 6B

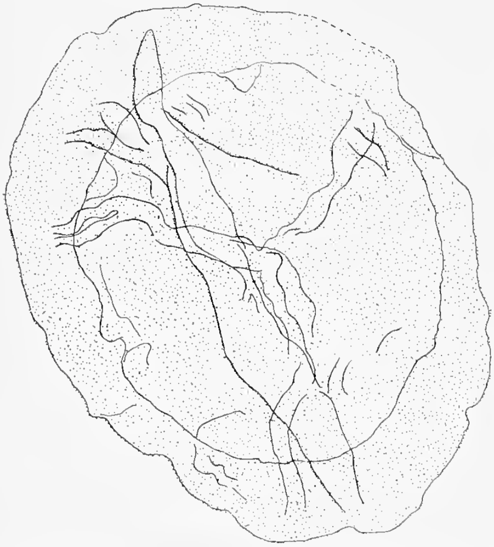
Type B Lang 1925, p. 256, pl. 1, figs. 3–6.
Triletes langi Eisenack 1944, p. 112, pl. 2, fig. 4.

Holotype. Eisenack 1944, pl. 2, fig. 4; size 174μ, central body 132μ. Probably Middle Devonian.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, Coal Heugh, Navity shore, and Eathie burn; especially abundant at Coal Heugh; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 95μ to 190μ, central body 67 to 154μ; bladder covered with fine rods, 0·5 to 1μ long.

Description. Colour of the bladder yellow, central body yellow to brown. Equatorial outline of both the bladder and the central body, subcircular to elliptical; central body often placed eccentrically. Bladder is ornamented, uniformly covered by densely packed rods which are parallel sided and have truncated tips. Central body smooth. Bladder usually strongly folded. Triradiate mark often indistinct, rays one-half to one-third, and occasionally nearly equal to, the radius of the body of the spore; sometimes there are folds on the bladder parallel to the rays of the trilete mark.



TEXT-FIG. 4. *Rhabdosporites langi* comb. nov. Camera lucida drawing × 500.

Remarks. Lang (1925) figured *Rhabdosporites* as type B and later Elovskava (1936) included spores of similar appearance in group 2 form 5. In form 5 Elovskava included spores with and without ornamentation and described them as having a wing which was one or two layered. One of Elovskava's figures (pl. 3, fig. 1), however, is ornamented, has folds, and resembles *Rhabdosporites*.

Naumova (1953) figured spores as *Archaeozonotriletes* which appear to resemble *Rhabdosporites*. *Archaeozonotriletes* as defined by Naumova appears to be a very heterogenous group and probably includes spores which have a bladder and others with a cingulum. Of Naumova's species, *Archaeozonotriletes macromanifestus* most closely resembles *Rhabdosporites* as far as can be determined from Naumova's drawings and descriptions but *A. macromanifestus* has a definite narrow equatorial rim which is not present in *Rhabdosporites*. Further it is not certain whether or not *A. macromanifestus* has a bladder and Naumova did not mention any folding which is a common feature of *Rhabdosporites*. Potonié (1958), in emending *Archaeozonotriletes*, drew attention to its heterogeneous nature as defined by Naumova. He took *A. variabilis* as type species and proposed to include in the genus only forms which are similar to it. Potonié stated that *A. variabilis* has an eccentric cingulum but Naumova's drawings indicate that it may have a bladder. The species *A. variabilis*, in contrast to *Rhabdosporites*, has a smooth surface.

Genus ANCYROSPORA gen. nov.

Type species *Ancyrospora grandispinosa* sp. nov.

Diagnosis. Radial, trilete, monosaccate spores, completely enclosed in a bladder without a limbus. Equatorial outline circular to subcircular, body subcircular to subtriangular. Spores originally elliptical in polar section; central body attached on proximal and distal surfaces. Bladder bears large processes which bifurcate at their tips. Derivation of name: G. Ankyra, anchor.

Comparison. Ancyrospora differs from *Grandispora* H., S., and M. in the presence of large anchor-shaped appendages and in the large size of it spores. It differs from *Cosmosporites* in having circular to subcircular outline in equatorial view, large spines and thick exine. *Hystricosporites* McGregor 1960 also has grapnel-shaped appendages but has no central body.

Remarks. The term bladder is used here because, although in *Ancyrospora* it is a thick membrane which bears large spines, it is in part widely separated from the central body. Naumova used the term perispore, but, since her interpretation of this feature differs from that used by Potonié and Kremp (1955, p. 19), adoption of this term would only lead to confusion. The author regards the outer layer of this spore as the exoexine and the central body as the intexine. Further, the perisporal membrane occurs on the spores of modern plants, it is not usually preserved in the fossil state, and it has a structure which is very different from that of the exoexine and the intexine.

Ancyrospora grandispinosa sp. nov.

Plate 14, fig. 7; text-figs. 5, 6c

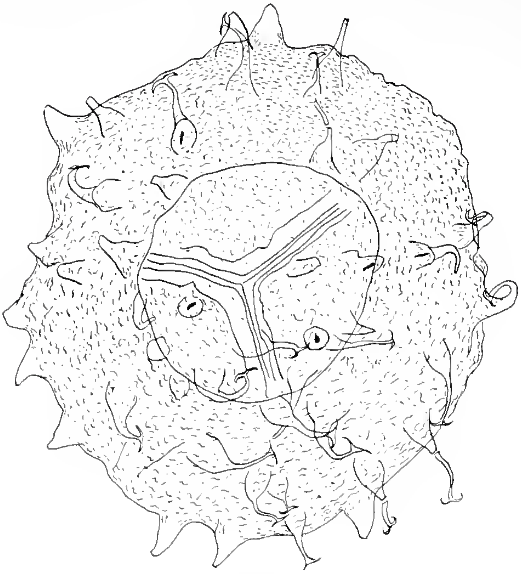
Holotype. Size 237 μ, central body 114 μ; spines 39 to 51 μ. Slide CR. 162. Reference 158617. Cromarty nodule beds. Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Navity shore, Coal Heugh, and Eathie burn; Lower Givetian, M.O.R.S.

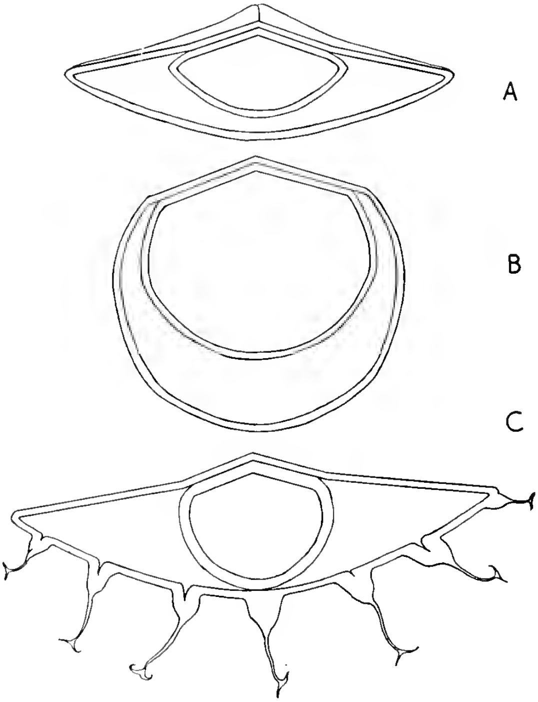
Diagnosis. Radial, trilete, spores; size 174 to 276 μ, body diameter 90 to 210 μ; outline circular to subcircular; bladder bears spines which have wide bases and bifurcate at their tips, 24 to 54 μ long.

Description. Colour dark yellow to dark brown. Equatorial outline of the bladder and body circular to subcircular. Body occasionally subtriangular. Bladder width around the central body equal to subequal in proximal view; surface of the bladder covered by numerous minute wrinkles; infrapunctate; central body smooth. Bladder bears long spines with hollow, wide, conical bases which taper sharply to a more slender stem, the stem tapers more gently to the apex where it swells slightly and bifurcates, the tips of the spines are pointed; spines 24 to 54 μ long, 9 to 54 μ apart. Triradiate mark distinct, with raised lips, equal to the radius of the body of the spore.

Comparison. This species resembles *Archaeotriletes honestus* Naumova 1953 (horizon Fammenian) except that around the central area of Naumova's spores there is a thickened zone and the size is 90 to 100 μ, considerably smaller than the smallest specimen of *Ancyrospora grandispinosa* (174 μ). *Archaeotriletes* has been emended by Potonié (1958) and now includes only spores with a membranous zona. Type G 1 of Lang is identical to some spores included in *A. grandispinosa.*



TEXT-FIG. 5. *Ancyrospora grandispinosa* gen. et sp. nov. Camera lucida drawing ×300.



TEXT-FIG. 6. Diagrammatic reconstructions in polar section. A, *Auroraspora macromanifestus*. B, *Rhabdosporites langi*. C, *Ancyrospora grandispinosa*.

Order (Anteturma) SPORITES H. Potonié 1893
Division (Turma) TRILETES Reinsch 1881
Subdivision (Subturma) ZONOTRILETES Waltz 1935
Series (Infraturma) CINGULATI Potonié and Klaus 1954
Genus DENSOSPORITES (Berry 1937) Potonié and Kremp 1954

Type species *Densosporites covensis* Berry 1937

Densosporites devonicus sp. nov.

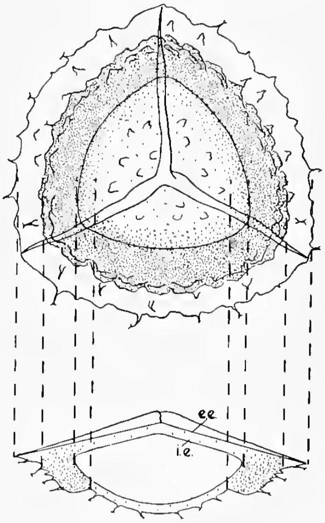
Plate 14, figs. 10, 11; text-fig. 7

Holotype. Size 110μ, cingulum 27–33μ; Slide CR. 80. Reference 127511. Shales at the top of the Cromarty fish band (Achanarras horizon), Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon) only found in samples from the shales associated with the nodule bed, Navity shore; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 87–159μ, cingulum 18–39μ; dark and light zones of the cingulum clearly separated, dark zone greater than, or equal to, width of light zone; distal surface and equatorial margin ornamented with spines which often bifurcate at their tips; rays of tetrad mark one-half to two-thirds and occasionally equal radius, often accompanied by folds to equatorial margin.

Description. Colour pale yellow except for the inner zone of the cingulum which is dark brown and often opaque. Equatorial outline subcircular to subtriangular in proximal view. Dark and light zones of the cingulum distinct, dark (inner) zone overlaps the central area, the outer edge of this zone is more irregular and has the form of a series of overlapping scales; outer light zone is thin membranous often with a scalloped margin. Ornament consists of distinct spines which cover the distal surface and equatorial margin; they vary a great deal in thickness, length, and density, and vary from types in which the bifurcation is barely perceptible to ones in which it is well developed with the extremities considerably splayed. Exine infrapunctate, especially marked on the central area. Rays of the tetrad mark one-half to two-thirds and occasionally equal the radius of the spore, folds often run parallel to them and reach the equatorial margin. The folds are wider in the polar region than at the equatorial border.



TEXT-FIG. 7. *Densosporites devonicus* sp. nov. Diagrammatic reconstruction in plan view and polar section; e.e., exoexine; i.e., intexine.

Comparison. This species is distinguished from other species of *Densosporites* by the large size, and presence of spines which bifurcate at their tips and by the frequent occurrence of prominent folds along the tetrad mark. *Hymenozonotriletes inaequus* McGregor (1960) has more prominent spines which do not bifurcate but have papillate tips.

Remarks. Potonié (1958) has emended *Hymenozonotriletes* Naumova and selected *H. polyacanthus* Naum. as type species. Naumova's figures of this spore (1953, pl. 4, figs. 11–12) show a zone of equatorial thickening, prominent triradiate folds, and also relatively long spines. Structurally *Hymenozonotriletes* (Naum.) Potonié appears to be very similar to *Densosporites* and, in emending *Hymenozonotriletes*, Potonié stated, 'the zona resolves itself more or less into longer rays' (presumably the equatorial spines). 'In this fact appears to exist a distinction to certain forms of the genus *Densosporites*' (Potonié 1958, p. 29). This distinguishes *Densosporites* and *Hymenozonotriletes* on the degree of development of the spinose ornament. In the author's opinion this is an insufficient basis for generic distinction since it would be difficult to name spores with intermediate spinose development. The spores described here have not the prominent spinose development of *Hymenozonotriletes* and therefore are placed in *Densosporites*.

With regard to the structure of *Densosporites* it may be important that in some spores included in the genus there are folds along the triradiate mark which reach the equatorial margin (Potonié and Kremp 1956, text-fig. 51 and pl. 18, figs. 390, 405–7). The prominent folds along the triradiate mark in *Densosporites devonicus* are regarded by the author to indicate a continuous membrane on the proximal surface (see text-fig. 7). Bhardwaj (1957), discussing the same feature in comparing *Lycospora* and *Cirratriradites*, stated that he did not consider it important that in certain species of *Lycospora* the triradiate folds do not cross the equatorial flange, whereas in *Cirratriradiate* the folds extend across the flange to the equatorial margin. He stated: 'If the cingulum is part of the trilete apparatus, i.e. modification of the arcuate ridges, the trilete rays must extend on to it as in *Cirratriradites*.'

In view of the fact that there is doubt as to the importance of the continuous tetrad marks, that species with such marks are included in *Densosporites*, and that the valid publication of *Hymenozonotriletes* is later than that of *Densosporites*, the spores described here are placed in the latter genus.

Genus CRISTATISPORITES Potonié and Kremp 1955

Type species *Cristatisporites indignabundus* (Loose) Potonié and Kremp

Remarks. A group of spores found closely resemble *Cristatisporites* Potonié and Kremp. Three species are recognized in this group as follows, *C. orcadensis*, *C. conannulatus*, and *C. mediconus*. Most of the spores of the three species show a clear differentiation into a central area and an equatorial flange (text-fig. 6) and therefore the genus *Cristatisporites* is here included in the subdivision Zonotriletes. In one of the species described below, *C. conannulatus*, the cones around the margin of the central area are fused giving rise to a thickened band, and in another species, *C. orcadensis*, there are some spores which have a flange completely covered by cones making it a very stout structure. Both these structures are in contrast with the more or less membranous collar or corona of fused hairs, which form the flat strongly spreading structure of series Zonati (Potonié and Kremp 1954); therefore the spores described here are placed in the series Cingulati. This is in agreement with Bhardwaj (1957), who placed *Cristatisporites* in the Cingulati. After studying the diplotype and several species of *Cristatisporites* he concluded that it was closely related in structure and organization to *Densosporites*.

Cristatisporites orcadensis sp. nov.

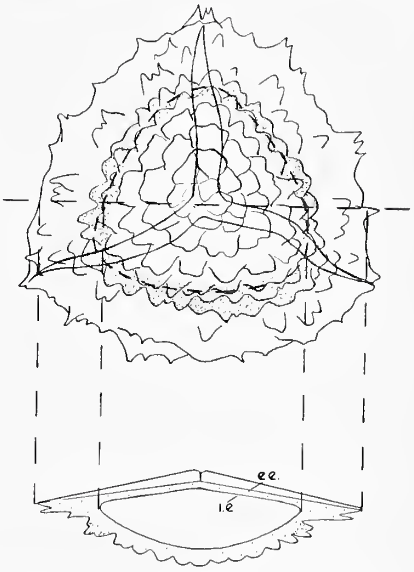
Plate 14, fig. 12; text-fig. 8

Holotype. Size 112μ, central area 72μ. Number of peripheral cones 46. Slide Cr. 81. Reference 160471. Cromarty nodule beds (Achanarras horizon).

Occurrence. Cromarty nodule beds (Achanarras horizon), Coal Heugh, Navity shore, and Eathie burn; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 96–153μ in diameter, central area 63–102μ; ratio of central area diameter to whole diameter 57 to 98 per cent. Cones on central area and flange rounded to pointed, large number of peripheral cones up to 49, sharply pointed giving a dentate margin; cones 3–7μ wide, 4–9μ high.

Description. Colour yellow to dark yellow. Subtriangular in equatorial outline with convex sides and rounded apices. There is a differentiation to form a central area and flange which in some specimens is distinct while in others it is hidden by the ornament. Ornament, distal, consists of cones which occur on the central area and the flange. Cones on the central area vary; in some spores they form concentric patterns and are fused at their bases, whereas in others they are fused in groups and are less regular. Some cones are larger and closely packed and possess polygonal bases. Cones on the central area have pointed or rounded apices whilst those on the flange have mainly pointed apices, are less regularly distributed, and occasionally form groups; cones on the central area width equal to or greater than, height, cones on flange height often greater than the base. Marginal cones sharply pointed, often in groups of two or three cones, give denticulate margin, in some specimens they become very long and form an incised border. Number of cones around equatorial margin twenty to forty-nine. There are prominent triradiate folds which obscure the tetrad mark and which usually reach the equatorial margin.



TEXT-FIG. 8. *Cristatisporites orcadensis* sp. nov. Diagrammatic reconstruction in plan view and polar section; e.e., exoexine; i.e., intexine.

Comparison. Some of the spores included in *C. orcadensis* resemble the figure of *Hymenozonotriletes praetervisus* Naumova 1953 (Upper Givetian, Russian Platform) but the description of the latter is insufficient to allow detailed comparison and further *H. praetervisus* is smaller than *C. orcadensis. Hymenozonotriletes* Naum. is defined to include all forms with a thin filmy margin (Naumova 1937) and appears to include spores with a bladder as well as spores with a flange or cingulum.

Cristatisporites orcadensis differs from both *C. conannulatus* and *C. mediconus* by the presence of numerous pointed cones on the central area and zona, and the large pointed cones on the equatorial margin.

Eisenack (1944) figured and described *Triletes paravelatus* which probably belongs to *Cristatisporites*. Eisenack's photographs are not very clear but they show differences to *C. orcadensis*. The latter has well-marked flanges along the triradiate mark which are not shown in the figures of *T. paravelatus*, the size range is smaller than that of *T. paravelatus*, and the outline is more regular.

Cristatisporites conannulatus sp. nov.

Plate 14, fig. 13

Holotype. Size 112μ, central area 72μ. Number of peripheral cones twenty-four. Slide CR. 87. Reference 140439. Shales at the top of the Cromarty fish band (Achanarras horizon), Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, and Navity shore; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 99 to 120μ, central area 69 to 96μ, ratio of body diameter to whole diameter 57 to 98 per cent. Large rounded cones, fused in groups, on central area and flange, and fused in a ring around the margin of the central area; cones 6–9μ wide, height less than width.

Description. Colour yellow to dark yellow. Spores radial, trilete, subtriangular in equatorial outline. Ornament distal, consists of large rounded cones, height less than width. Near the junction of the central area and the equatorial flange the cones are fused to form a continuous ring which simulates a thickened band. Cones on the centre of this area more scattered, and fused in small groups of two or three; cones on the flange are widely spaced, also rounded and are fused in groups. The equatorial cones vary from ten to thirty-four in number, smaller than the others, are mainly rounded but occasional pointed cones are also present. Prominent triradiate folds obscure the tetrad mark and reach the equatorial margin. These folds are broader at the proximal pole than at the equatorial margin.

Comparison. This species differs from *C. orcadensis* and *C. mediconus* in the rounded nature of the cones on the central area and flange and their fusion around the margin of the central area in the form of a ring.

Cristatisporites mediconus sp. nov.

Plate 14, fig. 14

Holotype. Size 120μ, central area 78μ, flange 12 to 22μ. Peripheral cones small, twelve in number. Slide CR. 88. Reference 092490. Shales at top of the Cromarty nodule beds (Achanarras horizon), Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, and Navity shore; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete, size 90–135μ, central area 70–93μ, ratio of central area diameter to whole diameter 53 to 83 per cent., consists of large rounded cones confined to the central area, width 6–18μ; height 3–6μ, and few small peripheral cones.

Description. Colour yellow with dark yellow to dark brown central area. Outline subtriangular with convex sides and rounded apices. Central area sharply divided from a well defined flange 12 to 27μ wide. Ornament is on the distal surface, consists of large rounded cones restricted to the central area and a few small cones on the equatorial margin. Cones of the central body are rounded, closely packed, and show a polygonal pattern at their bases. The height of the cones is less than, or equal to, the width; equatorial margin bears only a few small pointed cones five to twenty-two in number. There are prominent triradiate folds which obscure the tetrad mark and reach the equatorial margin; the folds are wider at the proximal pole than at the equatorial margin.

Comparison. This species is distinguished from *C. conannulatus* and *C. orcadensis* by the large cones on the central body and the general lack of cones on the flange with few, small and pointed cones on the equatorial margin.

CONCLUSIONS

Two distinctive features of the Middle Old Red Sandstone spores are seen: (*a*) the large size of many of the spores and (*b*) the predominance of spores which have spinose appendages terminated by grapnel-tipped hooks.

With regard to the size, Naumova mentioned that the Givetian spores she studied were represented for the most part by large forms. Of the spores described in this paper five species range over 200 μ as follows: *Auroraspora aurora* (120–210), *A. macromanifestus* (102–254), *Cosmosporites microspinosus* (186–282), *C. velatus* (108–208), *Ancyrospora grandispinosa* (174–274), and *Rhabdosporites langi* nearly reaches 200 μ (95–190).

With regard to the type of spore the entire assemblage is very distinctive, especially so in view of the predominance of Type G of Lang. These spores are characterized by long spinose appendages which bifurcate at their tips. Since Lang described type G in 1925 spores from various parts of the world, with similar spinose appendages, have been referred to it. Although the appendages are similar, however, the group defined on the basis of this specialized ornament is probably heterogeneous, as other features of these spores vary greatly and differ from those originally defined as type G. More work needs to be done before the spores arbitrarily described as type G can be fitted into the binominal classification.

The spores with anchor-shaped processes, as pointed out by Naumova, resemble the massulae of the modern water fern *Azolla*. It is possible that the similar appendages of type G spores served to facilitate attachment and may have helped the spore to float (in *Azolla* the hooks aid the attachment of macrosporangial and microsporangial massulae). Further, the fact that the spores have thick walls also suggests that water was the medium of transport. It is perhaps significant that spores with these two features are so predominant in the Devonian.

Spores with an ornament of grapnel-tipped processes, as seen in type G (Lang), have not been recorded from the Carboniferous and this appears to be a feature peculiar to Devonian spores. However, in addition to this type of organization there are spores with bladders, cingulae, and zonae (e.g. *Auroraspora*, *Rhabdosporites*, *Densosporites*, and *Cristatisporites*), all of which types of organization are well known in the Carboniferous. In the Middle Old Red Sandstone it is notable that the particular spinose ornamentation referred to may be present upon spores which otherwise simulate the organization of Carboniferous spores (e.g. *Densosporites devonicus* and *Cosmosporites microspinosus*).

Finally, the assemblage of plant spores found in north-east Scotland is comparable with those assemblages described from other Middle Devonian deposits by Eisenack, Krausel and Weyland, Naumova, and Thomson. The significance of spores of type G can be judged from the fact that they have been observed in North America, Spitzbergen, Germany, and Russia in deposits of Middle and Upper Devonian age. The assemblage found in the Middle Old Red Sandstone deposits of Scotland corresponds, in general, with that described by Naumova (1953) from the Upper Givetian of U.S.S.R. but since

Naumova has not yet described assemblages from the Lower Givetian any further detailed comparison at this stage is not possible.

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KULINDRICHNUS LANGI
A NEW TRACE-FOSSIL FROM THE LIAS

by A. HALLAM

ABSTRACT. *Kulindrichnus langi* is the name given to a trace-fossil common in the Blue Lias. This is stumpy cylindrical or conical in shape and is formed of a shell aggregate often enveloped by a phosphatic sheath. It is interpreted as a burrow produced possibly by a cerianthid sea anemone.

THE structures produced by organisms in sediments and their geological significance are fields of study which German palaeontologists, most notably Abel and Richter, have almost made their own. Seilacher (1953) placed the systematic study of these structures on a firm and logical basis, and has given cogent reasons for using the Linnaean binomial nomenclature for the classification of trace-fossils. His proposals are adopted in this paper.

I wish to thank Professor C. F. A. Pantin and Dr. A. Seilacher for their helpful suggestions. The work was carried out during the tenure of a D.S.I.R. Research Grant.

DOMICHNIA Seilacher 1953
Kulindrichnus langi ichnogen. et sp. nov.

Plate 15

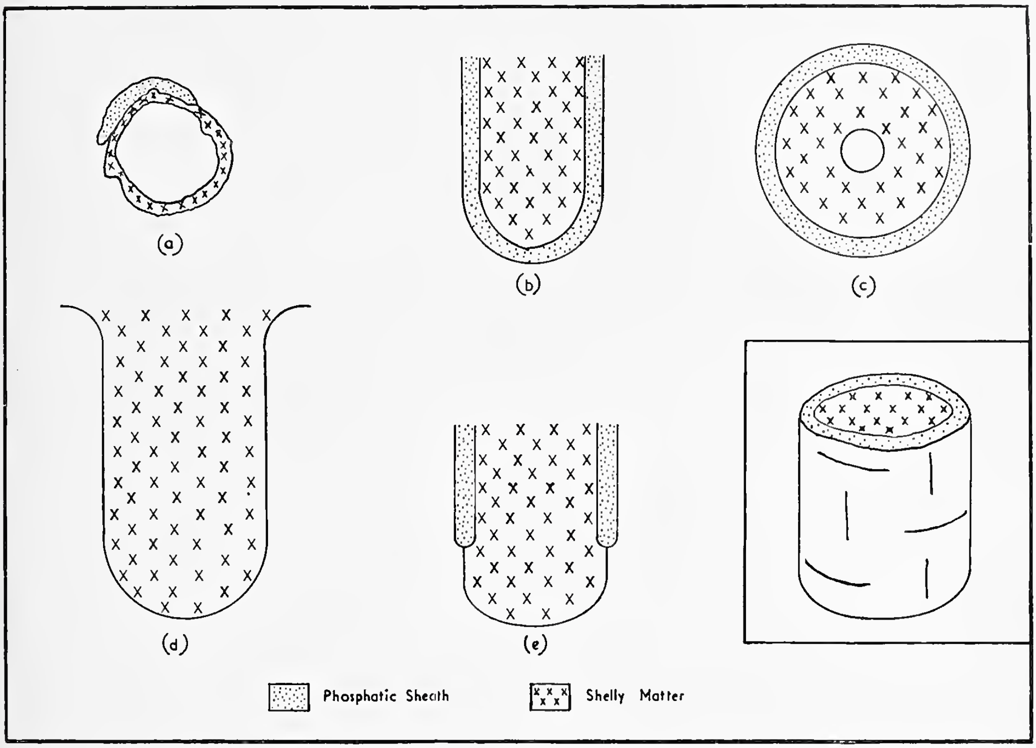
Diagnosis. Structure cylindrical or conical with apex downward; up to 130 mm. long and 75 mm. in diameter. Oriented subvertically in bed. Composed partly or wholly of small shells and shell fragments which may be aligned peripherally to the margin. Matrix sometimes phosphatic. Often bounded by sheath of phosphatic rock up to 10 mm. thick.

Description. The essential structure of *Kulindrichnus* is that of a stumpy cylinder or cone of shelly material. Its long axis in the enclosing bed is always within 20° of the vertical and the structure closes downwards. Although the cylinder is the commoner shape, cones with the apex downward are met with frequently. Whatever the shape there is a tendency to expand at the top (text-fig. 1*d*). The majority of specimens examined during the present investigation have been truncated a little by recent erosion. The few observations made on the upward terminations suggest that they are normally indefinite. Though *Kulindrichnus* extends up to 130 mm. in length and 75 mm. in width it is usually much smaller, the diameter, for example, ranging between 20 and 50 mm. The internal structures can be studied after cutting transverse and longitudinal surfaces which are then polished and varnished; thin sections are also useful.

The shell particles include fragments of pelecypods and echinoderms together with highly variable quantities of ostracods, foraminifera, and minute gastropods. Pelecypod fragments up to 20 mm. long have been observed but in general they are less than 5 mm. The particle distribution varies from complete randomness to a limited degree of order.

[Palaeontology, Vol. 3, Part 1, 1960, pp. 64–68, pl. 15.]

Thus in some specimens there is an axial zone free of shells. This may be of negligible diameter or so conspicuous that the shelly matter forms a mere peripheral ring when viewed in transverse section (text-figs. 1*a*, *c*). Elongate fragments sometimes show a crude alignment with the walls of the structure. The shells may be tightly packed within the cylinders or only patchily distributed. The internal matrix is invariably a calcareous rock, normally a fine-grained limestone, similar to the external matrix. There might be abundant detrital quartz or glauconite, depending on the nature of the depositional environment. Almost invariably, however, the *Kulindrichnus* structures are much richer in shelly matter than the immediate surroundings.



TEXT-FIG. 1. *Kulindrichnus langi*. Diagrams (*a*) to (*e*) based on actual specimens, approximately $\times\frac{1}{2}$. (*a*) and (*c*) transverse sections showing axial zone free of shelly matter. (*b*), (*d*), and (*e*) longitudinal sections. Inset—reconstruction of burrow indicating calcite-infilled cracks in phosphatic sheath.

There is a pronounced association with collophane rock or phosphorite. The limestone of the internal matrix is generally phosphatic to some extent but more characteristically the phosphorite takes the form of a peripheral zone, up to 10 mm. thick, enveloping the cylinder or cone as a sheath (text-fig. 1) which is normally open at the top. This may be due in some instances to Recent weathering, for one specimen from Skye has been seen in which the sheath closed upwards. The sheath usually possesses a sharp inner boundary but its outer boundary is more often than not ill-defined, due to the gradual transition through pale brown rock into normal limestone. An analysis of a sample of the pale brown phosphatic limestone gave a value of 6·2 per cent. P_2O_5, which is greater than that for normal limestones of the Blue Lias by a factor of more than sixty. As might be expected the phosphorite sheath exhibits a high degree of variability. It might be partly or wholly absent (text-figs. 1*a*, *d*). The concentration of phosphate, as indicated by the intensity of the colour, differs a great deal even in the same specimen. Though usually the sheath marks exactly the outer boundary of the shelly core it is not uncommon to find specimens in which a narrow separation of up to 10 mm. exists. Thin radial and tangential calcite-filled cracks are characteristic of the sheaths. There may be indications of more pronounced rupture which has resulted in the 'bursting out' of some shelly material (Pl. 15, fig. 1). Microscopic examination of thin sections reveals an intimate relationship between the phosphorite and small shells. Most significantly, fragments of pelecypod shells convex outwards may be bounded on their inner sides by phosphorite, suggesting that the outward migration of the latter was impeded.

In the Blue Lias of Dorset the relationship of *Kulindrichnus* to other trace-fossils including *Chondrites* and *Rhizocorallium* can be studied with ease, particularly in bed 49 of Lang (1924). The whole fossil, phosphorite sheath included, both transgresses and is transgressed by structures attributable to burrowing organisms (e.g. Pl. 15, figs. 3, 4). These observations prove that the phosphatic part of *Kulindrichnus* developed within the soft sediment.

Occurrence. Although *Kulindrichnus* makes its first appearance in the upper part of the *Planorbis* Zone it occurs most characteristically and abundantly in the Lower Sinemurian. It is common in the *Bucklandi* and *Semicostatum* Zones of Dorset, Glamorgan, the Midlands, and Yorkshire and the *Semicostatum* and *Turneri* Zones of west Scotland. As it is also common in the *Semicostatum* Zone of Württemberg its distribution presumably extends throughout north-west Europe. Whether it occurs at higher horizons in the Lias has not been ascertained.

The typical *K. langi* structures have been discovered only in highly calcareous rocks, usually calcilutites and hard marls but also sandstones (in Scotland). Large exposures of shales on the foreshore at Lyme Regis and Redcar have been closely examined but have yielded only rare, minute phosphatic tubular structures which will be discussed below.

An examination of extensive exposures of limestone surfaces in the British coastal sections reveals that the *Kulindrichnus* structures are, in general, distributed randomly and evenly. There is, however, an occasional suggestion of structures occurring in pairs, separated by less than 50 mm. (e.g. bed 23, Dorset). As they are normally more cal-

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EXPLANATION OF PLATE 15

Figs. 1–4. *Kulindrichnus langi*. 1, Holotype seen in transverse section. × 1. Sedgwick Museum J.47829. This shows up clearly the sharp contrast between the dark phosphatic sheath and the inner shelly part which in one place appears to have burst out of the sheath. 2, Longitudinal section of a paratype. × 1. Sedg. Mus. J.47830. As the base of this specimen was found exposed on a weathered surface it is not certain that the observed downward thinning of the phosphatic sheath is original. 3, Transverse section of a paratype. × 1. Sedg. Mus. J.47831. 4, Longitudinal section of the same specimen. × 1. Both figs. 3 and 4 show clearly (*a*) *Kulindrichnus* transgressing *Chondrites* structures in the matrix and (*b*) a core of comparatively shell-free limestone rimmed by a peripheral zone of shelly material of variable thickness. The phosphatic sheath is developed only in the lower part of the specimen and is therefore only seen in fig. 4.

The holotype and paratypes were all collected by the author from the *Semicostatum* Zone, Dorset (bed 49 of Lang 1924).


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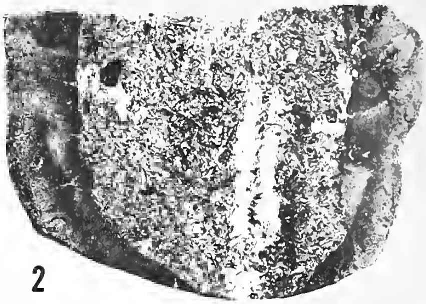
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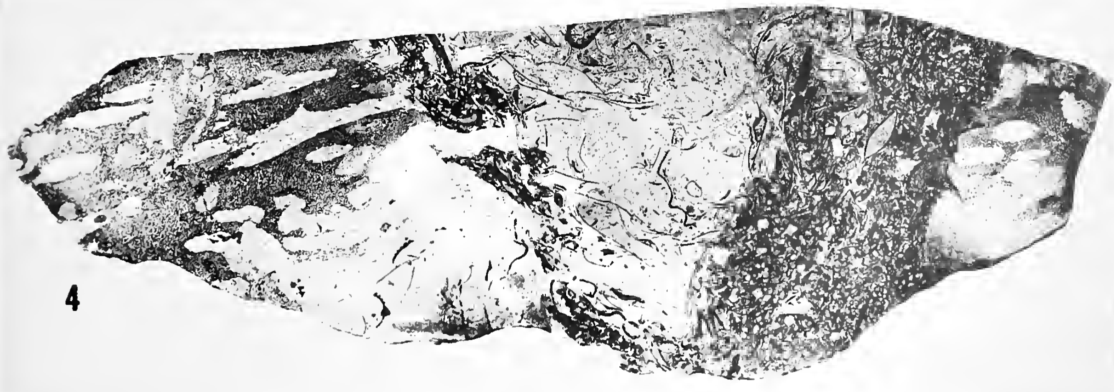
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HALLAM, *Kulindrichnus*

careous than the surroundings they tend to weather out as convex protuberances. Those with a phosphatic sheath tend to weather completely free from the matrix so that a collection of free-lying specimens is likely to be biased.

Interpretation. The shape and orientation of *Kulindrichnus* with respect to the bedding indicate some form of burrow occupied by a sedentary organism (text-fig. 1, inset). There are three main problems. The first concerns the origin of the phosphatic sheath and the variably phosphatic interior. The action of sea water alone on the exposed surface of the burrow can be ruled out because phosphatic limestone surfaces are never found elsewhere. Therefore the organism itself must have been responsible, though whether the phosphate enrichment in the sediment is due to the presence of a faecal lining or to the decay of the organism is not clear. As regards the mechanism of phosphatization the evidence mentioned earlier points strongly to a radial migration outwards from the burrow of phosphorus-rich material and a chemical interaction with and/or surface adsorption on grains in soft calcareous mud. An interesting comparison can be made with the remains of prehistoric men who are sometimes found enveloped in a matrix rich in vivianite. This must owe its origin to an outward migration of phosphate from the bones (T. W. Farrer, personal communication). The mechanism probably involves preferential adsorption on mineral matter in the matrix, a phenomenon utilized in chromatography. No clear relation has been established between the presence of phosphorite and the lithology of the rock.

The second matter relates to the origin of the small shells and shell fragments. Undoubtedly the burrows are greatly enriched with respect to the surrounding rock. The uniformly small size of the shell particles and the traces of organized structure in some specimens point to activity on the part of the animal that inhabited the burrows. The disorganized structure of the majority of specimens could be due partly to the collapse of the shelly walls after the organism had decayed or vacated the burrow. It is impossible to exclude, however, some adventitious filling of the empty burrows by the action of currents operating close to the sea floor, especially in those cases in which they are packed to the top with shells. In any case the limy infilling probably originated in this way. There is no indication that the burrow-inhabiting organisms were selective for anything other than particle size. The evidence suggests that any available material was used to line the burrow. Thus one specimen from Redcar was found to be enriched in grains of glauconite.

Finally there is the problem of the organism itself. At the present time there are only two groups of marine organisms that inhabit subvertical burrows which they line with shells and other resistant materials—terebellid worms and cerianthid sea anemonies. The dimensions of *Kulindrichnus langi* do not suggest terebellids. The ratio of the diameter to the length and the absolute size of the diameter are too high even when allowance is made for the fact that sometimes the shell lining exceeds the core in thickness. One is therefore led to consider the cerianthids. *Cerianthus*, described by Schäfer (1956), is a mud-inhabiting sea anemone that builds a vertical tube, much wider than itself, which is lined with sand grains and shell fragments. Even this genus is probably too wormlike. *Saccanthus*, however, is a more stumpy member of the same family that has about the right proportions. It may be tentatively suggested, then, that *K. langi* represents the burrow of a cerianthid.

Related structures. Thick shale beds in the *Bucklandi* Zone of Redcar, Yorkshire, have yielded a small number of phosphatic tubes up to 13 mm. in diameter. They usually lie close to the plane of the bedding and are squashed parallel to this plane, indicating that the phosphorite did not harden before compaction. If *Kulindrichnus* occurs in the Blue Lias shales it must be represented by these structures, which would suggest dwarfing. Similar phosphatic tubes lying oblique to the bedding have been found in limestones of the *Johnstoni* Subzone in Dorset and Glamorgan. They extend up to 10 mm. in diameter and exceed 30 mm. in length. Throughout the bottom four zones of the Lias small irregular clumps of shell debris can be found. By their size and their occasional association with phosphorite they could represent collapsed *Kulindrichnus* structures.

The only mention known to the writer in the literature of structures like *Kulindrichnus* is that of Klüpfel (1918, p. 183), describing the *Gryphaea* beds of Lias α in Lorraine (*Bucklandi* and *Semicostatum* Zones). 'Nicht selten', he remarks, 'enthält der Kalk harte, faustgroße, walzen- oder tonnenförmige Körper, die mit Muscheldetritus erfüllt und hier und da von einem hellgrauen phosphoritischen Mantel umgeben sind. Andere von Fossildetritus erfüllte sehr zähe Knollen haben eine kegelförmige Gestalt oder zeigen Formen, die an den Hals einer Flasche erinnern. Diese Bildungen, die nicht an einen bestimmten Horizont gebunden zu sein scheinen, sind in aufrechter Stellung mit der oft knolligen Spitze nach oben dem Kalk eingewachsen und lösen sich beim Zerschlagen heraus.'

The species is named after Dr. W. D. Lang, who has done much distinguished work on the Lias of Dorset.

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UPPER SILURIAN BRYOZOA FROM CENTRAL WALES

by D. E. OWEN

ABSTRACT. A thin band of limestone in the *Gypidula* beds of the Lower Ludlow succession of Builth was described by S. H. Straw (1937) as being made up of shells and nodular Bryozoa. The Bryozoa are described and shown to belong to eight species, seven new and one described by R. S. Bassler (1906) from the Rochester Shale. They are *Fistulipora umbrosa* sp. nov., *F. strawi* sp. nov., *Dekayella megacanthopora* sp. nov., *D. ramosa* sp. nov., *Leioclema explanatum* Bassler, *Monotrypa flabellata* sp. nov., *Rhombopora minima* sp. nov., and *Ptilodictya gracile* sp. nov.

S. H. STRAW (1937, pp. 423–4) described a thin band of limestone made up of shells of *Gypidula galeata* (Dalman) and of nodular Bryozoa near the base of the Gypidula beds of his Upper Silurian (Ludlovian) succession. He noted certain genera in his paper and intended to give them a more thorough examination later. He has handed over the material to the author and the Bryozoa are described herewith. All the specimens were collected from the right bank of the river Wye between Aber-Duhonw and the lodge of Glanwye, near Builth Wells, Radnorshire.

The Bryozoa, which make up a large proportion of the limestone, are jumbled in with shells and occasional corals. The weathered surfaces of the rock show the fossils as hollow casts and it is therefore difficult to describe their surface features, but thin sections of unweathered rock have shown that eight species, belonging to six genera, are represented. All but one (*Leioclema explanatum* Bassler) appear to be new, but this is not as surprising as it might seem at first, since the comparable Silurian horizon is represented in the United States by the specialized Cayuga salt-bearing deposits, which are devoid of Bryozoa. Species and individuals all tend to be smaller than the typical Wenlock forms but to compare closely with those in the Aymestry Limestone. In fact, the author has already collected five species, described here, from the Aymestry Limestone.

Order CYCLOSTOMATA Busk 1852
Family FISTULIPORIDAE Ulrich 1882
Genus FISTULIPORA M'Coy 1850

Fistulipora umbrosa sp. nov.

Plate 16, figs. 1, 2; text-fig. 1

Holotype. Section LL 1526A in the Manchester Museum.

Diagnosis. Zoarium massive, nodular, showing marked layering in section as though successive incrustations had built up the nodule. Average diameter of nodules 15–20 mm. Zooecia straight, oval in section, with thick shadowy granular walls, no lunules and very occasional diaphragms. The average size of the zooecia is 0·4 to 0·5 mm. by 0·3 to 0·4 mm. and the zooecia may be in contact or separated by narrow tabulated mesopores or vesicular tissue. Mesopores are 0·1 to 0·2 mm. across and their diaphragms occur at about $1\frac{1}{2}$ times tube width.

[Palaeontology, Vol. 3, Part 1, 1960, pp. 69–74, pl. 16.]

Remarks. It is in the shadowiness of the walls that *Fistulipora umbrosa* differs from all other species of *Fistulipora*, though its method of growth and general characters are typical of the genus. Specimens, either whole or fragmentary, are very common through the bed.

Fistulipora strawi sp. nov.

Plate 16, figs. 3, 4; text-fig. 2

Holotype. Sections LL 1526D, F in the Manchester Museum.

Diagnosis. Zoaria encrusting but thick, average depth 4 to 5 mm., often occurring detached. Average width 8 to 10 mm. Zooecia cylindrical tubes without diaphragms, section nearly circular to polygonal with rounded corners, approximately 0·3 mm. in diameter, with slight lunules. Walls thin and granular. Mesopores 0·2 to 0·3 mm. closely tabulated, diaphragms occur at about one-half to three-quarters tube width.

Remarks. This species is very common and is much more typically fistuliporid than *Fistulipora umbrosa* from which it differs in having flatter encrusting zoaria, much thinner walls and traces of lunules.

In 1885 Nicholson and Foord redefined the genus *Fistulipora* M'Coy, emphasized the importance of the lunule, and described twelve species, four of them new. Three of their new species, and a fourth described by Lonsdale, occur in British Silurian rocks, all from the Wenlock series. They are: (1) *F. crassa* Lonsdale with a massive branching zoarium up to 10 cm. in length. In this, the vesicular tissue separating the zooecia is very simple and nowhere resembles tabulated mesopores. (2) *F. nummulina* Nich. and Foord has discoidal, lenticular zoaria up to 5 cm. across, and zooecia with occasional diaphragms, and lunules more marked than in *F. strawi.* (3) *F. dobunica* Nich. and Foord has exceedingly thin encrusting zoaria, and small zooecia scarcely distinct from the intervening vesicular tissue. (4) *F. cornavica* Nich. and Foord is encrusting hemispherical and layered. The marked lunules and diaphragms distinguish it from *F. umbrosa* and *F. strawi.*

EXPLANATION OF PLATE 16

All specimens from right bank of River Wye, between Aber-Duhonw and Glanwye, near Builth Wells, Radnorshire. Except for fig. 9, all figures are of the holotypes.

Figs. 1, 2. *Fistulipora umbrosa* sp. nov.; vertical section showing zooecia and mesopores; tangential section showing shadowy walls.

Figs. 3, 4. *Fistulipora strawi* sp. nov.; vertical section showing tabulated mesopores; tangential section showing zooecia with traces of lunules.

Figs. 5, 6. *Dekayella megacanthopora* sp. nov.; vertical section showing thickening in mature zone; tangential section showing large acanthopores.

Figs. 7, 8. *Dekayella ramosa* sp. nov.; vertical section showing tabulated mesopores; tangential section showing rounded zooecia, mesopores, and acanthopores.

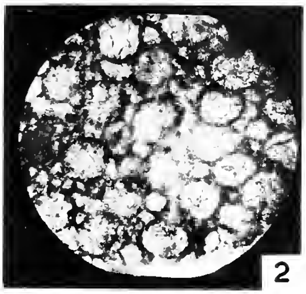
Fig. 9. *Leioclema explanatum* Bassler; vertical section showing intersecting mesopores.

Figs. 10, 11. *Monotrypa flabellata* sp. nov.; vertical section showing crenulated walls; tangential section.

Figs. 12, 13. *Rhombopora minima* sp. nov.; transverse section showing thickened mature zone; vertical section showing vestibule and hemiseptum.

Figs. 14, 15. *Ptilodictya gracile* sp. nov.; transverse section showing mesotheca and thick zooecial walls; vertical section showing rows of rectangular zooecia.

PLATE 16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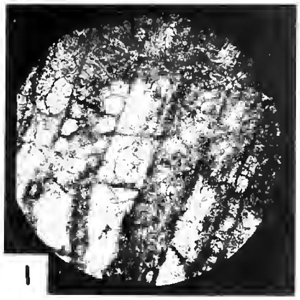
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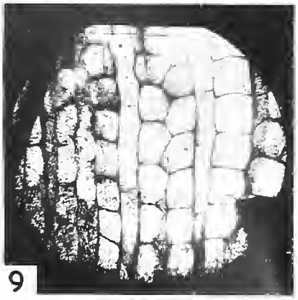
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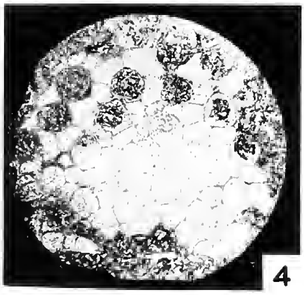
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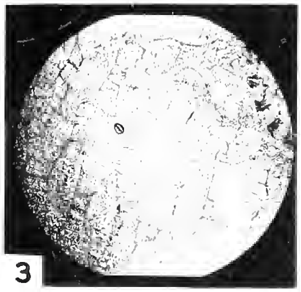
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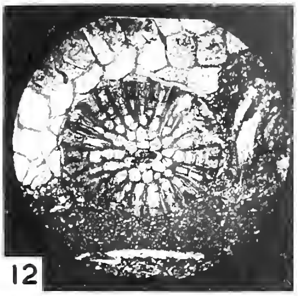
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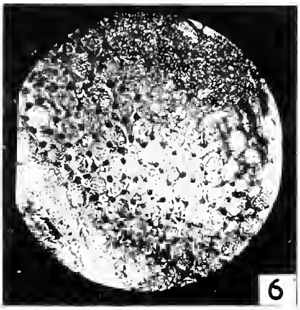
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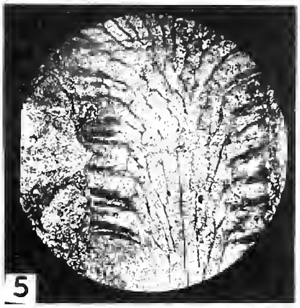
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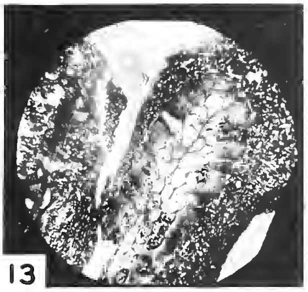
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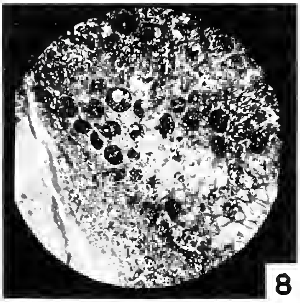
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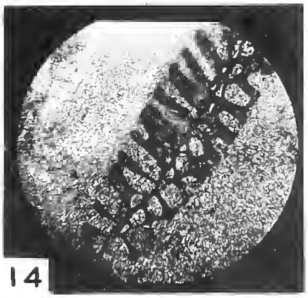
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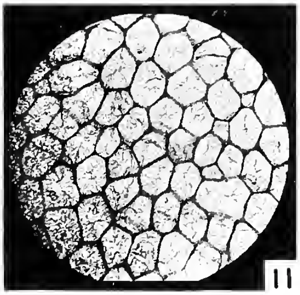
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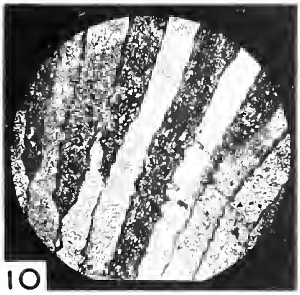
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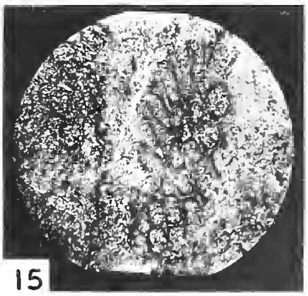
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OWEN, Silurian Bryozoa

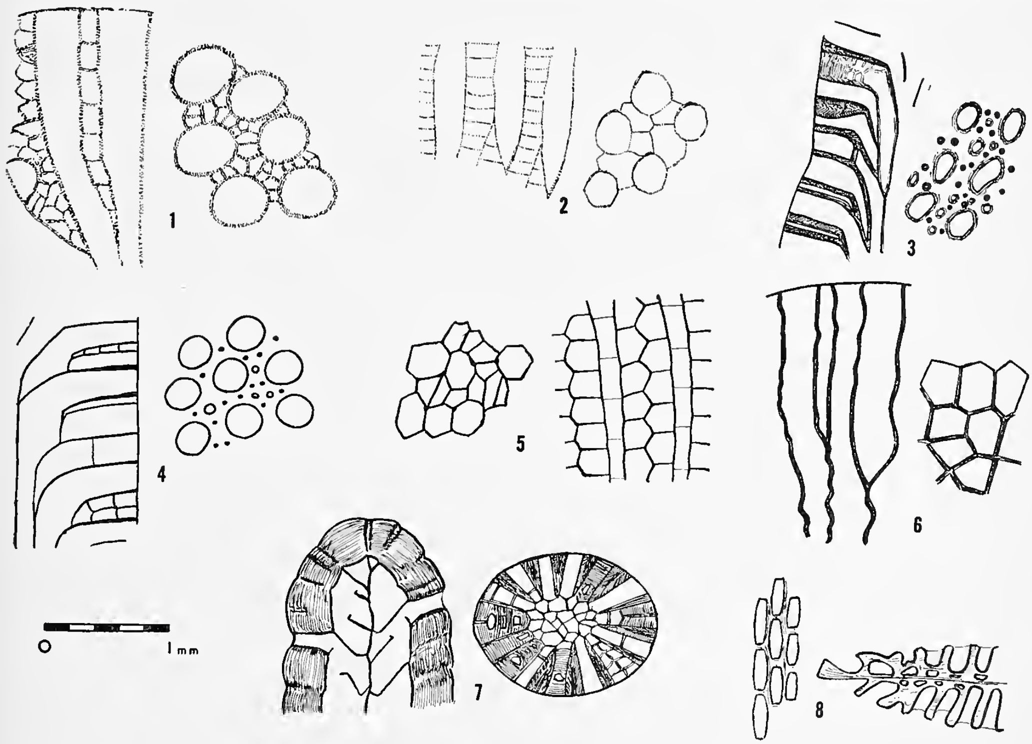
Order TREPOSTOMATA Ulrich 1882
Family HETEROTRYPIDAE Ulrich 1890
Genus DEKAYELLA Ulrich 1882

Dekayella megacanthopora sp. nov.

Plate 16, figs. 5, 6; text-fig. 3

Holotype. Section LL 1526A in the Manchester Museum.

Diagnosis. Zoarium ramose, slender, 1·5 to 2 mm. diameter. Zooecia oval in section, 0·25 mm. along the long axis, 0·15 mm. across, with marked thickening of walls in the mature region. Zooecia start nearly parallel to the surface in the immature region and turn sharply to reach the surface at right angles. Diaphragms few. Many mesopores 0·05 to 0·1 mm. across having few diaphragms. Many acanthopores, some up to 0·1 mm. in diameter and some perhaps a tenth of this size with gradations between the two extremes.



TEXT-FIGS. 1–8. Vertical and tangential sections of Upper Silurian Bryozoa. 1, *Fistulipora umbrosa* sp. nov. 2, *F. strawi* sp. nov. 3, *Dekayella megacanthopora* sp. nov. 4, *D. ramosa* sp. nov. 5, *Leioclema explanatum* Bassler. 6, *Monotrypa flabellata* sp. nov. 7, *Rhombopora minima* sp. nov. 8, *Ptilodictya gracile* sp. nov.

Remarks. This species is very common and is distinctive particularly in tangential section, when the white dots of the mesopores and the dark points, often with a tiny white centre, of the acanthopores are seen.

Dekayella ramosa sp. nov.

Plate 16, figs. 7, 8; text-fig. 4

Holotype. Section LL 1526A in the Manchester Museum.

Diagnosis. Zoarium ramose, about 3 mm. in diameter. Zooecia circular in section, about 0·3 mm. across, thickened only slightly in the mature region. Zooecia parallel to surface in immature region but turn sharply to reach surface nearly at right angles. Occasional diaphragms. Mesopores numerous, often tabulated, 0·05 to 0·1 mm. diameter. Acanthopores slightly variable in size up to 0·05 mm., occurring evenly at the junction of three zooecia even if some of these zooecia are modified as mesopores.

Remarks. This species is less common than *D. megacanthopora* and is distinguished from it by its larger size, thinner walls in the mature region and less distinctive mesopores and acanthopores.

Family STENOPORIDAE Waagen and Wentzel 1886

Genus LEIOCLEMA Ulrich 1882

Leioclema explanatum Bassler

Plate 16, fig. 9; text-fig. 5

Diagnosis. Zoaria forming thick incrustations or laminar expansions of one layer, 5 to 10 mm. thick. Diameter 10 to 15 mm. Zooecia subcircular to polygonal with rounded corners, 0·25 mm. diameter with diaphragms $1\frac{1}{2}$ to 2 tube widths. Mesopores large 0·2 to 0·25 mm. across, numerous and tabulated, the diaphragms a tube width apart and often alternate and the wall between two mesopores often zigzagging. Acanthopores small and inconspicuous at angles in zooecial wall.

Remarks. This species differs from other species of *Leioclema* in having inconspicuous acanthopores which do not distort the zooecial wall. Both free and encrusting examples occur in this deposit and they appear to be identical to those forms described by Bassler (1906) from the Rochester Shale.

Family TREMATOPORIDAE Miller 1889

Genus MONOTRYPA Nicholson 1879

Monotrypa flabellata sp. nov.

Plate 16, figs. 10, 11; text-fig. 6

Holotype. Section LL 1526A in the Manchester Museum.

Diagnosis. Zoarium hemispherical, fanlike in section, sometimes attached at the base to other objects. Average diameter 10–12 mm., average height 7 to 8 mm. Zooecia polygonal with separate walls; thickening from immature to mature region only slight;

average diameter 0·3 mm.; walls with wide crenulations, about four to 1 mm. and with some straight or nearly straight sections. Diaphragms occasional but rare.

Remarks. This is the commonest species in the deposit and its crenulated walls are easily recognizable in the hand specimens with a lens. It is very like *M. benjamini* Bassler from the Rochester Shales but differs in having zooecia of much smaller diameter and fewer and larger crenulations.

Two species of Monotrypa have been described from the British Silurian rocks, *M. crenulata* Nicholson (1884, p. 125) and *M. macropora* Foord (1884, p. 338). The former, which is conspecific with *Favosites fibrilla* Smith, occurs typically in the Wenlock Limestone of Dudley, and is a large hemispherical species 3 to 4 cm. in diameter and height. The zooecial walls have marked crenulations and diaphragms occur at 1–2·5 mm. intervals. *M. macropora* Foord, from the Wenlock Shales, is a wide flat form with straight walls and more numerous diaphragms. Neither would be confused with *M. flabellata*.

Note on *Favosites fibrilla* Smith

Dr. K. P. Oakley drew the author's attention to this species described by Smith (1930, p. 319) from material from Llandovery in the Geological Survey Museum (Geol. Soc. Coll. 6858), and considered by him to be a species of *Monotrypa*. Spjeldnaes (1957) suggested it might be *Amplexopora* but gave no reasons.

Diagnosis. Zoarium hemispherical, fanlike in tangential section, approximately 20 mm. across. Zooecia polygonal, 0·4 to 0·5 mm. diameter with crenulate walls, few diaphragms, crenulations about three to the millimetre. Mesopores and acanthopores absent. Separation of zooecial walls very marked.

Remarks. This form differs from *M. crenulata* Nicholson only in having fewer diaphragms more widely spaced. In the author's experience, the frequency of diaphragms can vary in different parts of a zoarium. Thus *F. fibrilla* Smith would appear to be *M. crenulata* Nicholson. *Amplexopora* differs from *Monotrypa* most obviously in having numerous acanthopores. These are absent in *F. fibrilla* Smith. In older collections there are numerous specimens labelled *Favosites fibrosa* (Goldfuss) and *Alveolites fibrosa* (Goldfuss). Lonsdale (1839) figures the former and M'Coy (1854) the latter. Neither appears to be Goldfuss's original species (1826) which is ramose. According to Spjeldnaes (1957) Lonsdale's figured specimen is *Batostoma murchisoni*.

Order CRYPTOSTOMATA Shrubsole and Vine 1882
Family RHABDOMESIDAE Vine 1883
Genus RHOMBOPORA Meek 1872

Rhombopora minima sp. nov.

Plate 16, figs. 12, 13; text-fig. 7

Holotype. Section LL 1526A in Manchester Museum.

Diagnosis. Zoaria small ramose stick-like 1 to 1·5 mm. in diameter. Zooecia with occasional diaphragms arise from central axis at about 45°; a few reach the surface through well-marked vestibules at right angles to the axis, with inferior hemisepta; between these there is a solid wall of fibrous structure with many acanthopores.

Remarks. This species is fairly common and the thick-walled mature zone and its clearly marked vestibules are distinctive.

Family PTILODICTIDAE Zittel 1880
Genus PTILODICTYA Lonsdale 1839

Ptilodictya gracile sp. nov.

Plate 16, figs. 14, 15; text-fig. 8

Holotype. Section LL 1526C in the Manchester Museum.

Diagnosis. Zoaria consist of thin net-like ribbons, 3 to 4 mm. in diameter. No complete specimen has been preserved in the rock examined and the total length is therefore not known. Zooecia arise from mesotheca and rise slightly to the surface; walls thick, apertures rectangular with rounded corners, 0·25 mm. long, 0·1 mm. wide arranged in parallel, longitudinal rows, 8–16 in width. No mesopores or acanthopores.

Remarks. This species is similar in many respects to *Pachydictya crassa* (Hall) as figured by Bassler (1906, p. 57). There is no evidence from fragments found, however, that the zoaria branched dichotomously, though such junctions would be strongest and therefore most likely to be preserved. More important is the fact that *Ptilodictya gracile* has neither diaphragms nor vesicular tissue between the zooecia, two characteristics of *Pachydictya*. Transverse sections through the smaller tips are extremely common throughout the deposit.

Acknowledgements. I thank Dr. S. H. Straw for his kindness and help and for handing over the material for study; Dr. H. Dighton Thomas for criticizing the manuscript; and Dr. K. P. Oakley for advice and access to his notes and unpublished thesis.

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A REVIEW OF THE CARBONIFEROUS GONIATITE ZONES IN DEVON AND CORNWALL

by N. E. BUTCHER AND F. HODSON

ABSTRACT. A re-examination of existing museum collections of goniatites from the Culm Measures of Devon and Cornwall shows that most of the Carboniferous goniatite zones and subzones are represented in this region. The only zones for which there is at present no evidence are the *Eumorphoceras* and Lower *Gastrioceras* Zones.

ALTHOUGH Carboniferous goniatites have been known from Devon and Cornwall since they were figured and described by J. de C. Sowerby (*in* Sedgwick and Murchison 1840) and J. Phillips (1841), little modern work has been done on these faunas. The present study, largely a re-examination of existing museum specimens, most of which were collected fifty years or more ago, was initiated by N. E. B.; the identifications have been attempted by F. H. Much of the material is poorly preserved and precise identification has proved difficult in some cases. A description is given below of the main elements of the goniatite faunas from the Lower and Upper Carboniferous as they are now known.

Material. All the specimens referred to in this paper, with the exception of those in the collection of Dr. D. E. Owen, Keeper of the Manchester Museum, are deposited in the following museums, abbreviated in the text as indicated: BM—British Museum (Natural History). EM—Exeter Museum. GSM—Geological Survey Museum. NDA—North Devon Athenaeum, Barnstaple. SM—Sedgwick Museum, Cambridge. TM—Museum of the Torquay Natural History Society.

Acknowledgements. Our thanks are due to Mr. E. W. J. Moore and Dr. W. H. C. Ramsbottom for commenting on some of the material examined. We are also grateful to the following museum officials for their assistance: Dr. R. C. Blackie (EM), Mr. A. E. Blackwell (NDA), Mr. A. G. Brighton (SM), Mr. H. L. Douch of the County Museum, Truro, Mr. J. M. Edmonds of the University Museum, Oxford, Mr. W. E. Hall (TM), Mr. A. D. Hallam of the County Museum, Taunton, Dr. M. K. Howarth (BM), Miss M. E. Jenkinson of Bideford Museum, Dr. W. H. C. Ramsbottom (GSM), and Mr. T. Williams of the Royal Geological Society of Cornwall. Dr. D. E. Owen kindly made his collection available. Mr. C. W. Taylor gave valuable assistance with the collections in the North Devon Athenaeum, Barnstaple. N. E. B. acknowledges financial assistance from the Research Board of Reading University. We are grateful to Professor P. Allen for his critical reading of the manuscript.

LOWER CARBONIFEROUS

Strata of Lower Carboniferous age are found in relatively narrow outcrops on and near the northern and southern margins of the great central outcrop of Upper Carboniferous sediments. There are thus two separate east–west belts to be considered.

1. The Northern Belt. The Pilton Beds of north Devon contain a mainly trilobite–brachiopod fauna in which ammonoids are rare. From a study of the trilobites from the Barnstaple area Goldring (1955) proved the presence in these beds of the Upper Famennian *Wocklumeria* Zone (the topmost zone of the Devonian) and the basal Carboniferous

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Gattendorfia Zone. Goldring's discovery of *Gattendorfia* itself near Barnstaple confirms the latter correlation.

J. G. Hamling found several small ammonoids (TM Hamling Coll. 2190–1 and BM C19564–8) in black shales from two wells near Mount Sandford, 2 miles south-east of Barnstaple. These specimens are important in view of the fact that this locality is near the junction between the Pilton Beds and the succeeding Lower Culm Measures (see Hamling and Rogers 1910, pl. 33). Hamling (1908, p. 279) recorded them as *?Clymenia*, with which Paul (1937, p. 436) tentatively agreed, but Goldring (1955, p. 48) suggested they might be *Nomismoceras*. The poor state of preservation of these evolute forms unfortunately does not permit even generic identification. We are, however, indebted to Dr. M. R. House for his opinion that they are not Clymenids. It seems most probable that they are Prolecanitids (Pl. 17, fig. 1), and possibly of Tournaisian age.

Hamling also collected a goniatite (BM C19550) from the railway cutting west of Swimbridge Station. The locality is shown on Hamling's geological map of north Devon (Hamling and Rogers 1910, pl. 33) as occurring at the junction between the Pilton Beds and the Lower Culm Measures near Swimbridge. This specimen (Pl. 17, fig. 2) is identified as *Pericyclus* (*Rotopericyclus*) aff. *homoceratoides* Schindewolf which thus indicates the *Pericyclus* Zone of the German zonal scheme (Schindewolf 1951).

EXPLANATION OF PLATE 17

Fig. 1. Prolecanitid. From a well, 80 yards north of Venn Cross Quarry, near Barnstaple. TM Hamling Coll. 2190, ×2. The label on this specimen states 'south' of Venn Cross Quarry, but this must be an error (see Hamling 1908, p. 279). Goldring (1955, p. 48) has given the locality correctly with map reference SS 57883132.

Fig. 2. *Pericyclus* (*Rotopericyclus*) aff. *homoceratoides* Schindewolf. Railway cutting west of Swimbridge Station. BM C.19550, ×1½.

Fig. 3. *Merocanites* cf. *henslowi* (J. Sowerby). Westleigh, near Burlescombe. GSM 59906, ×1.

Fig. 4. *Bollandoceras micronotum* (Phillips) group. Doddiscombsleigh. BM C.9105, ×2.

Fig. 5. ? *Pericyclus sp.* or *Imitoceras ornatissimus* (de Koninck) group. Quarry east of Bableigh, near Barnstaple. NDA 789, ×1.

Fig. 6. *Sudeticeras* aff. *ordinatum* Moore. Spara Bridge, near Ashton Station. GSM US 1810, ×2.

Fig. 7. *Merocanites* aff. *applanatus* Frech. Codden Hill Quarry, near Barnstaple. NDA 823, ×¾.

Fig. 8. *Entogonites grimmeri* (Kittl). Just north of Canonteign, near Trusham. GSM US 1438, ×4.

Fig. 9. *Goniatites concentricus*/*striatus* group. Hele Quarries, ¾ mile south of Dulverton Station. GSM US 965, ×1½.

EXPLANATION OF PLATE 18

Fig. 1. *Goniatites crenistria* Phillips. Venn, near Barnstaple. TM Hamling Coll. 690, ×2.

Fig. 2. *Goniatites falcatus* Roemer. Hele Quarries, ¾ mile south of Dulverton Station. GSM US 963, ×2.

Fig. 3. *Goniatites sphaericostriatus* Bisat. Bonhay Road, Exeter. BM C.9111, ×3. (*a*) Ventral view, (*b*) lateral view.

Fig. 4. *Girtyoceras burhennei* (H. Schmidt). Fremington. NDA 875c, ×1½.

Fig. 5. *Goniatites bisati* Moore. Bampton. BM C.1641b, ×2.

Fig. 6. *Paragoniatites newsomi* (J. P. Smith) group. ¾ mile south of Ugbrooke House, near Chudleigh. GSM US 436, ×5.

Fig. 7. *Bollandites* of the *castletonense* (Bisat) group. Westleigh, near Burlescombe. BM C.9113, ×2. (*a*) Ventral view, (*b*) lateral view.

Fig. 8. *Goniatites* aff. *granosus* Portlock. Waddon Barton, near Chudleigh. EM Downes Coll., ×2.


1 × 2

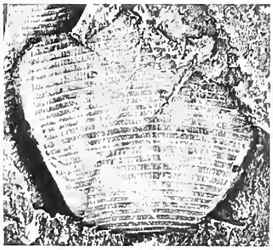

2 × 1½


3 × 1


4 × 2


7 × ¾


5 × 1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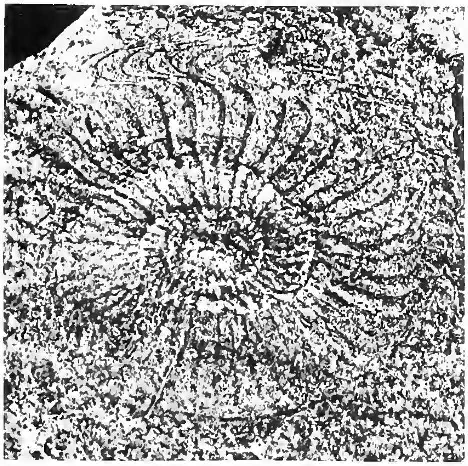
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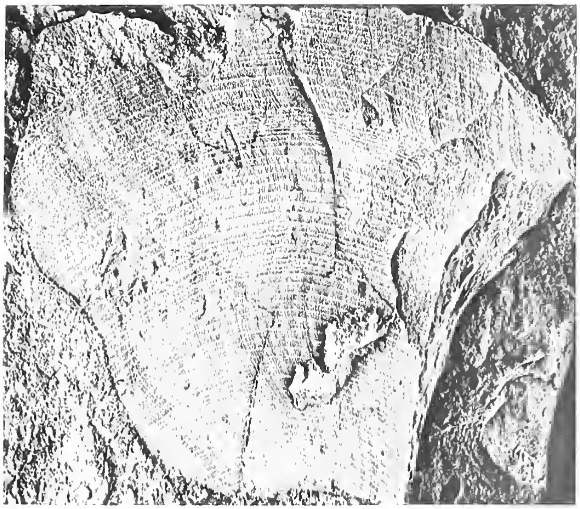
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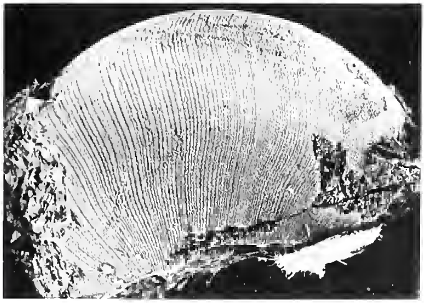
BUTCHER and HODSON, Carboniferous goniatites



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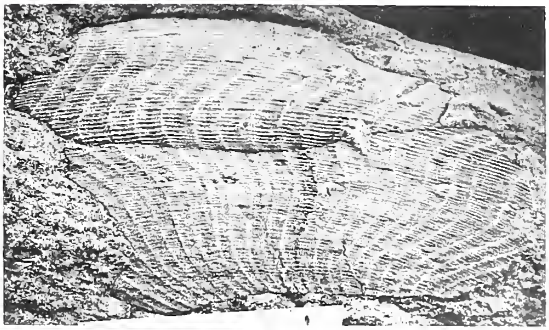

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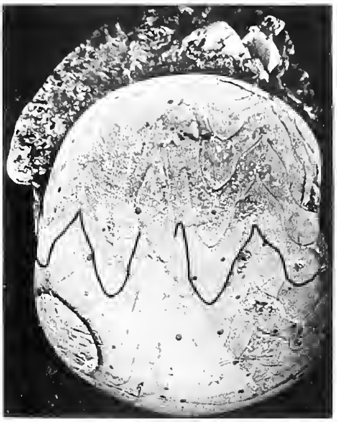

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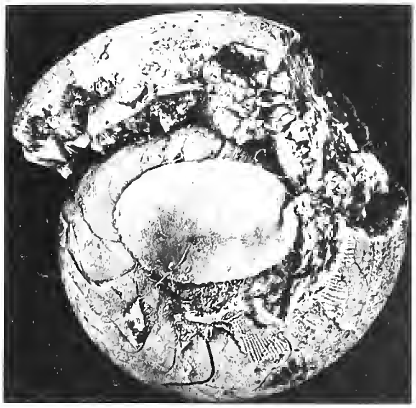


3b × 3

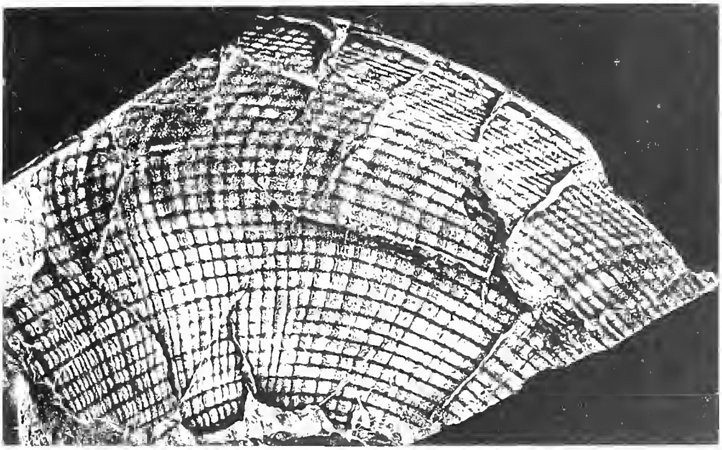
4 × 1½

7a × 2

5 × 2

6 × 5

7b × 2



8 × 2

BUTCHER and HODSON, Carboniferous goniatites

It is possible that the Codden (or Coddon, see Woodward 1902, p. 481, footnote) Hill Chert Beds may in part be of *Pericyclus* Zone age, since several poorly preserved impressions of a coarsely ribbed goniatite referred to *Pericyclus sp.* (Crick, *in* Hinde and Fox 1895, p. 653) have come from these beds. Where the state of preservation allows it is seen that many of these specimens are involute. The best-preserved specimen (NDA 789 Partridge Coll.), from a quarry east of Bableigh, near Barnstaple, is illustrated in Pl. 17, fig. 5. These involute forms do not appear to agree with any of the figured and described species of *Pericyclus*. They may represent a new species of this genus or may even possibly belong to the *Imitoceras ornatissimus* (de Kon.) group, known from the *Pericyclus* reefs of western Ireland (Foord 1897–1903).

This coarsely ribbed goniatite is associated in the Codden Hill Beds with large, poorly preserved prolecanitids, the two forms having been found on the same bedding-plane (e.g. SM E16049). The latter have been referred to '*Prolecanites compressus*' (see Hudson and Turner 1933, p. 478). The specimens in the museum collections are too poorly preserved for specific identification, with the exception of one recently found loose in Codden Hill Quarry by Mr. C. Winzar. This large specimen (NDA 823, Pl. 17, fig. 7) may be referred to *Merocanites* aff. *applanatus* (Frech) which would suggest the B_1 zone.

The B_2 zone is certainly present at the eastern end of this northern belt near Burlescombe because the Westleigh limestones (Owen 1939) have yielded a *Bollandites* of the *castletonense* (Bisat) group (BM C9113 Vicary Coll., Pl. 18, fig. 7). *Merocanites* cf. *henslowi* (Sow.) (GSM 59906 Harding Coll.) also occurs at Westleigh (Pl. 17, fig. 3).

The subdivisions of the P_1 zone can now all be identified in these northern outcrops. The P_{1a} subzone occurs at the old Venn Quarry near Barnstaple where the limestones yielded *Goniatites crenistria* Phillips (TM Hamling Coll. 690, Pl. 18, fig. 1). The P_{1b} index fossil *Goniatites falcatus* Roemer was collected by Ussher from shales in Hele quarries, $\frac{3}{4}$ mile south of Dulverton Station (GSM US 963, Pl. 18, fig. 2). These quarries also yielded him a *Goniatites* of the *concentricus/striatus* group, also indicative of P_{1b} (GSM US 965, Pl. 17, fig. 9). The succeeding P_{1c} subzone is indicated by several specimens, collected from Fremington by T. M. Hall, of *Goniatites sphaericostriatus* Bisat, with which is associated *Girtyoceras burhennei* (Schmidt) (NDA 875c, Pl. 18, fig. 4). Bampton is the type locality of Phillips' (1841) species, *Goniatites spiralis*. Bisat (1955) has redescribed material from this P_{1d} locality under the modern name of *Neoglyphioceras spirale*. J. E. Lee collected from Bampton a form which can be compared with *Goniatites bisati* Moore which would again indicate the P_{1d} subzone (BM C1641b, Pl. 18, fig. 5).

The P_{2a} subzone is suggested by some spirally ornamented goniatites collected by Dr. D. E. Owen from Whipcote Quarry near Burlescombe which approach *Goniatites granosus* Portlock (Owen 1949). This species was also collected by I. Rogers, from a locality near Yelland Farm, near Fremington. Higher Viséan subzones have not yet been recognized in these northern outcrops.

2. The Southern Belt. As in North Devon, the *Wocklumeria* and *Gattendorfia* Zones are now both known from the southern Upper Devonian and Lower Carboniferous outcrops. House and Selwood (1957) record the discovery of *Wocklumeria* near Launceston, and Selwood (1958) has in addition found *Gattendorfia* near this town. The beds containing these ammonoids are, on their lithology, referred to the Transition Series of Dearman and Butcher (1959).

The succeeding Lower Culm Measures stand in contrast to the northern Lower Culm outcrops in that, with the exception of the higher Viséan horizons, they have yielded very few goniatites. Of the Lower Culm goniatites, most have come from the outcrops east of the Dartmoor granite. The Vicary Collection (BM) contains a B_2 goniatite preserved in limestone from Doddiscombsleigh (C9105) which may be referred to the *Bollandoceras micronotum* (Phillips) group (Pl. 17, fig. 4). The top of the B_2 zone is proved in shales just north of Canonteign near Trusham by the occurrence of *Entogonites grimmeri* (Kittl) (GSM US 1438 Ussher Coll., Pl. 17, fig. 8).

The P_{1a} and P_{1b} subzones have not yet been recognized, but the occurrence of P_{1c} limestones is indicated at Bonhay Road, Exeter, by the subzonal index fossil *Goniatites sphaericostriatus* (BM C9111 Vicary Coll., Pl. 18, fig. 3).

Waddon Barton (Dewey 1948) has yielded abundant impressions of the P_{1d} form, *Neoglyphioceras spirale*, preserved in distinctive reddish-coloured shales. A few specimens of *Goniatites* aff. *granosus* (Pl. 18, fig. 8) are also known from here (EM Downes Coll.), so that this locality must lie close to the P_1/P_2 junction.

The P_2 goniatite, *Sudeticeras* aff. *ordinatum* Moore (Pl. 17, fig. 6) was collected by Ussher from black shales by Spara Bridge, near Ashton Station (GSM US 1810). The topmost subzone of the Viséan, P_{2c}, has been identified ¾ mile south of Ugbrooke House, near Chudleigh, by the occurrence in shales (GSM US 436 Ussher Coll.) of a goniatite of the *Paragoniatites newsomi* (J. P. Smith) group (Pl. 18, fig. 6).

UPPER CARBONIFEROUS

Goniatites are so far only known close to the northern and southern margins of the great central outcrop of Upper Carboniferous sandstones and shales, the Upper Culm Measures of Sedgwick and Murchison (1840).

1. North. The lowest Namurian horizon so far dated in north Devon is that of R_{1c}, shown by Moore's (1929) record of *Reticuloceras reticulatum* (Phillips) (Pl. 19, fig. 5) near Fremington Station (NDA 792B). The locality must lie near to the R_1/R_2 junction since Moore also found the R_{2a} form *Reticuloceras gracile* Bisat close by.

Recently, one of us (N. E. B.) has found *Reticuloceras superbilingue* Bisat (Pl. 19, fig. 7) 1¼ miles south of Bampton (GSM 87249). Because *Gastrioceras* has not been found

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EXPLANATION OF PLATE 19

Fig. 1. *Homoceras magistrorum* Hodson. Bonhay Road, Exeter. BM C.9110, ×3.

Fig. 2. *Homoceras undulatum* (Brown). Bonhay Road, Exeter. BM C.9109, ×3.

Fig. 3. *Homoceras beyrichianum* (de Koninck) emend. Haug. Bottom of Idestone Hill, 3 miles south-west of Exeter. EM Collins Coll. 224, ×3.

Fig. 4. *Reticuloceras nodosum* Bisat and Hudson. Pinhoe, Exeter. BM C.9123, ×4. (*a*) Lateral view, (*b*) ventral view.

Fig. 5. *Reticuloceras reticulatum* (Phillips). Fremington (shore). NDA 792B, ×3.

Fig. 6. *Reticuloceras bilingue* Bisat. Ballast from Perridge Tunnel, 3½ miles west-south-west of Exeter. GSM US 1822a, ×2.

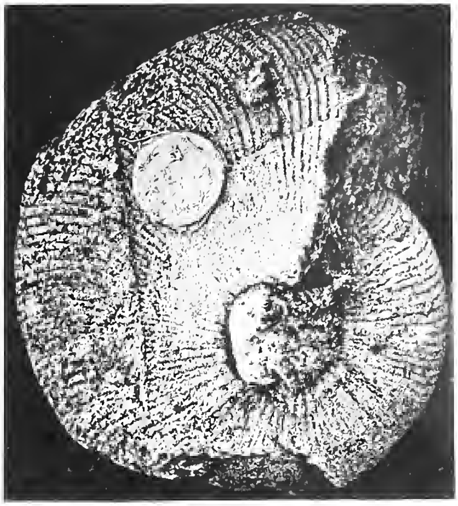
Fig. 7. *Reticuloceras superbilingue* Bisat. Quarry, 1¼ miles south of Bampton, GSM 87249, ×3.

Fig. 8. *Reticuloceras* aff. *gracile* Bisat. Pinhoe brickfield, Exeter. EM Collins Coll. 145, ×1½.

Fig. 9. *Gastrioceras circumnodosum* Foord. North of Shag Rock, near Knap Head, north Cornwall. SM E.14609, ×3.

PLATE 19

1 × 3



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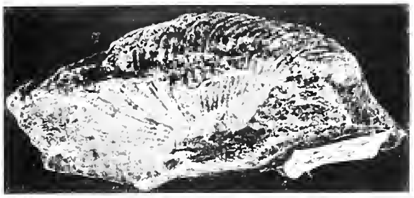

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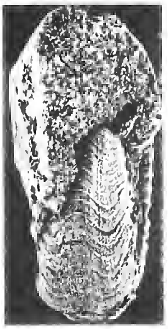
4a × 4



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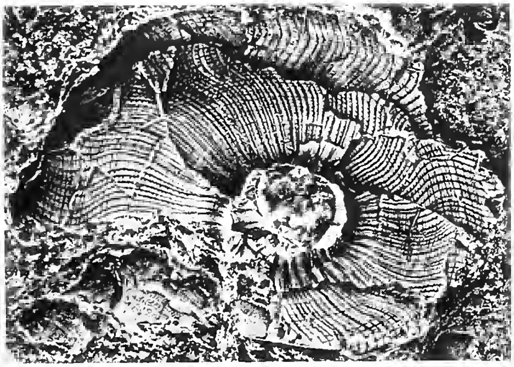
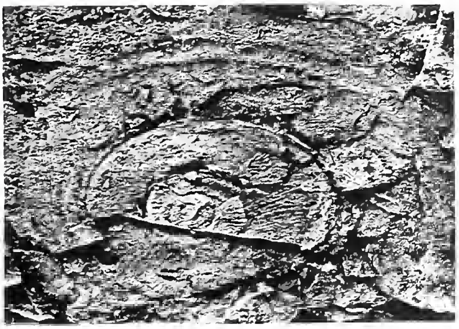


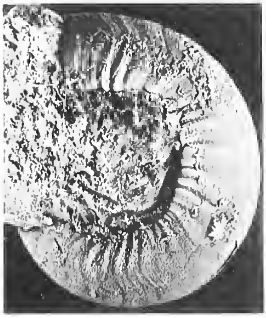
5 × 3

6 × 2



7 × 3

8 × 1½



9 × 3

BUTCHER and HODSON, Carboniferous goniatites

associated with this species, the horizon is R_{2c}. This is the highest Namurian zone yet recognized in Devon.

Gastrioceras has long been known from north Devon but all the records are of the G_2 *Gastrioceras circumnodosum* Foord group of the Lower Westphalian. In addition to the well-known localities near Instow Station, Mouth Mill near Clovelly, and Hescott Quarry near Hartland (Rogers 1910), this horizon also occurs farther south on the coast, north of Shag Rock, near Knap Head, near Welcombe (SM E14609, Pl. 19, fig. 9).

2. *South.* Here, in contrast to the north, the *Homoceras* Zone can be shown to be present, both in the west and in the east. Collins (1911) records many goniatites from the Exeter region. Of these, specimens from the bottom of Idestone Hill, 3 miles south-west of Exeter, are *Homoceras beyrichianum* (de Kon.) emend. Haug, indicating the H_{1b} subzone (EM Collins Coll. 224, Pl. 19, fig. 3). The Vicary Collection (BM C9109) contains the H_{2b} form *Homoceras undulatum* (Brown) (Pl. 19, fig. 2) from Bonhay Road, Exeter, from which locality Vicary also collected *H. magistrorum* Hodson (BM C9110, Pl. 19, fig. 1) which marks the base of the *Reticuloceras* Zone. The *Homoceras* Zone is also tentatively identified on the north Cornish coast at Voter Run, near Crackington Haven, from material collected by Dr. D. E. Owen (Owen 1949), although specific identification is not possible.

Exeter is the type locality of *Reticuloceras inconstans* (Phillips 1841), from which record Bisat (1924, p. 67) inferred the presence of the Lower *Reticuloceras* Zone in Devon. The Pinhoe brick pit, near Exeter, yielded to Collins and Vicary *Homoceras striolatum* (Phillips), *Reticuloceras nodosum* Bisat and Hudson (BM C9123 Vicary Coll., Pl. 19, fig. 4), and *R.* aff. *gracile* (EM Collins Coll. 145, Pl. 19, fig. 8), and Collins also collected *R. nodosum*, *R.* cf. *regularum* Bisat and Hudson, and *R. moorei* Bisat and Hudson from Stoke Road, under Stoke Wood, also near Exeter. Thus the whole of R_1 and the lower levels of R_2 appear to be present in the Exeter area.

The highest zone so far recognized in the south is that of R_{2b}, proved by the occurrence of *R. bilingue* Bisat (Pl. 19, fig. 6) at Perridge Tunnel (GSM US 1822a Ussher Coll.), 3½ miles west-south-west of Exeter.

CONCLUSIONS

The sequence of Carboniferous goniatite zones and subzones now known to be present in Devon and Cornwall is shown in Table 1. This may be linked with the succession of Devonian ammonoid zones shown to be present in south Devon and north Cornwall by House (1958). Together they show that there is an almost continuous succession of strata to which the ammonoid chronology can be applied.

In Table 1 the most notable absentee is the *Eumorphoceras* Zone, the index fossils of which are unrepresented in the museum collections examined. It may be that in Devon and Cornwall strata of *Eumorphoceras* Zone age are really absent. Moreover, it is possible that the *Homoceras* Zone is absent in north Devon. It is perhaps worth emphasizing that no record has yet been obtained of the Lower *Gastrioceras* Zone. Further collecting, however, may well close these gaps in knowledge of this region.

TABLE 1. *The sequence of goniatite zones and subzones recognized in Devon and Cornwall*

		German Zones	*British Zones*	*North*	*South*
Upper Carboniferous	Westphalian		G_2	×	—
	Namurian		G_1	—	—
			R_{2c}	×	—
			R_{2b}	—	×
			R_{2a}	×	×
			R_{1c}	×	—
			R_{1b}	—	×
			R_{1a}	—	×
			H_{2c}	—	—
			H_{2b}	—	×
			H_{2a}	—	—
			H_{1b}	—	×
			H_{1a}	—	—
			E_2	—	—
			E_1	—	—
Lower Carboniferous	Viséan		P_{2c}	—	×
			P_{2b}	—	—
			P_{2a}	×	×
			P_{1d}	×	×
			P_{1c}	×	×
			P_{1b}	×	—
			P_{1a}	×	—
			B_2	×	×
			B_1	×	—
		II Pericyclus		×	—
	Tournaisian	I Gattendorfia		×	×
Upper Devonian	Famennian	VI Wocklumeria		×	×

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STRUCTURE OF THE SPORE WALL IN CERTAIN MIOSPORES BELONGING TO THE SERIES CINGULATI POT. AND KLAUS 1954

by A. H. V. SMITH

Abstract. Miospores of the genera *Densosporites* and *Anulatisporites* are described in which the spore wall consists of two separate membranes. The inner membrane, considered to be the intexine, forms a 'central body' which can be seen in equatorial section of the spore exines in polished surfaces of coal and in specimens isolated from the coal.

The presence of an inner membrane or 'mesosporium' has been demonstrated in the megaspore *Duosporites congoensis* Høeg, Bose, and Manum 1955 from the *Glossopteris* flora of the Belgian Congo. These authors cite several examples from published work to support their view that a so-called mesosporial membrane is of more common occurrence in spores than has been believed hitherto. The examples they quote relate almost entirely to megaspores but the existence of an homologous membrane has recently been observed in certain miospores not previously recorded as possessing such a membrane.

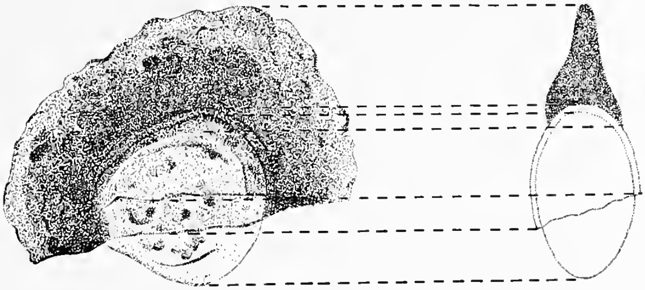
The miospores concerned belong to the genera *Densosporites* (Berry) Potonié and Kremp 1954, and *Anulatisporites* (Loose) Potonié and Kremp 1954, found in British Carboniferous coals. The inner membranes were first seen when a piece of durainous coal cut parallel to the bedding and containing large numbers of *Densosporites* was polished and examined by reflected light using a low-power oil immersion objective. Subsequently a careful examination of spores isolated from the coal by using fuming nitric acid revealed an occasional specimen in which part of the outer membrane had become severed and lost leaving the inner membrane protruding and intact. Examples of *Densosporites* with an inner membrane showing in this way have been observed in separations made from coals of Lower and Upper Carboniferous age. Spores belonging to the genus *Anulatisporites* do not usually occur in such dense accumulations in the coal as certain species of *Densosporites* and the inner membrane in this genus has so far only been observed in isolated specimens.

The specimens of *Densosporites* exposed in the polished surface of durain (Pl. 20, figs. 1, 2) all show the membrane which can be seen as a thin, undulating, or folded line on the inside of the thickened equatorial zone. In most cases it is continuous but in some specimens it shows short breaks. It may lie close to the equatorial thickened zone or may be shrivelled to a greater or lesser extent, in which case it is well separated from the zone of thickening. The majority of specimens in the block were cut more or less in the equatorial plane and in this plane the membrane appears, at least in the fossil state, to be entirely free of the thick outer coat of the spore. Owing to the preferred orientation of the spores in the plane of section, no indication has been found of the attachment of the membrane to the outer coat at any point. An examination of the spores in polar plane, by preparing sections cut vertical to the bedding of the coal, similarly

[Palaeontology, Vol. 3, Part 1, 1960, pp. 82–85, pl. 20.]

failed to show the manner of attachment due to the extremely compressed state in which the spore exines are preserved in this plane.

In the isolated specimens of *Densosporites* (Pl. 20, figs. 3–7) and *Anulatisporites* (Pl. 20, fig. 8) the thickened outer coat of the spore has in each case broken across, but the inner membrane is intact and protrudes as a distinct 'central body'. The specimen photographed in Fig. 5 shows the break in the outer coat taking a different course on proximal and distal sides of the spore.



TEXT-FIG. 1. A diagrammatic reconstruction, × 1,000, of the specimen of *Densosporites* shown in fig. 5, pl. 20, as the unflattened spore might appear in plan view and polar section.

The photographs of the four species of *Densosporites* show the differentiation of the equatorial zone or cingulum into a thicker, darker inner and a thinner lighter outer region. The sculpturing of the cingulum is also apparent. According to Potonié and Kremp 1954 these features distinguish *Densosporites* from *Anulatisporites* in which the cingulum is without structure and sculpturing.

Among the species of *Densosporites* illustrated in Pl. 20 are two, *D. striatus* (Knox) Butt. and Will. 1958 and *D. loricatus* (Loose) S. W. and B. 1944 in which there is a well-marked differentiation of the cingulum into darker and lighter zones. *D. striatus* (fig. 3) differs from *D. loricatus* (fig. 4) in that the plications which characterize the inner part of the cingulum extend into the outer thinner region. In the specimen of *D. loricatus* the cingulum has fractured in such a way as to show clearly its cuneiform shape in section. The remaining species of *Densosporites* are considered to be *D. spongeosus* Butt. and Will. 1958 (fig. 5) in which the cingulum and central area possess a perforate ornamentation, and *D. sphaerotriangularis* Kosanke 1950 (figs. 6, 7) in which the cingulum is composed of a number of small plicating sheets. The species of *Anulatisporites* (fig. 8) is *A. anulatus* (Loose) Pot. and Kr. 1954.

The reconstruction of the structure of *Densosporites* based on the specimen shown in fig. 5 is given in text-fig. 1. The structure of *Anulatisporites* is essentially the same.

The terminology of the structural elements of which the walls of spores and pollens are composed is confused by the variety of names which have been applied to them by different authors. Potonié (1952) has attempted to establish a set of terms which were originally defined for pollen but which for simplicity he applies to both spores and pollens. He considers that those parts of the spore wall, exine or exospore, which are normally preserved in fossil material, comprise an outer membrane, the exoexine, composed of different structural elements and an inner membrane, the intexine. The mesosporium being the inner part of the exine is considered to be equivalent to the intexine. The membrane described in this paper is cutinized and may therefore be regarded as constituting part of the exine. It is accordingly equated with the intexine.

The separation of the intexine from the exoexine is considered by Potonié (1934) to take place in the formation of air sacs in such miospore genera as *Endosporites* Wilson and Coe 1940 and *Florinites* Schopf, Wilson, and Bentall 1944. However, the tenuous nature of the 'central body' wall in *Florinites* led Schopf *et al.* (1944) to suggest that it may not be exosporal in origin.

The separation at maturity of the intexine from the exoexine to a greater or lesser extent and its mode of attachment are features of considerable taxonomic importance. The genus *Duosporites* has been established on the basis of the occurrence of a membrane referred to as a mesosporium by Høeg *et al.* detached from the exoexine except in an area on the proximal side of the megaspore (loc. cit.). In the absence of this feature these spores would be considered as a species of *Laevigatisporites* (Ibr.) Pot. and Kremp 1954. Similarly certain large spores of Lower Cretaceous age possessing a prominent neck have been placed in the genus *Pyrobolospora* Hughes 1955 to distinguish them from spores belonging to the genus *Lagenicula* (Bennie and Kidston) Pot. and Kremp 1954 which they superficially resemble but from which they differ in the separation of the exoexine from the intexine below the neck.

Recently a miospore genus *Vallatisporites* Hacquebard 1957 has been described, which is reported to resemble *Densosporites* in the construction of the equatorial portion but is said to differ from it in possessing a well-defined central body. The latter is separated from the equatorial portion by a distinct groove or rampart-like area from which the name *Vallatisporites* is derived. The existence of a central body would not be sufficient justification for establishing a new genus since it can reasonably be assumed that all species of *Densosporites* possess the structure which has been demonstrated for four species. However, the presence of the groove, which permits the recognition of the central body in the undamaged spore, suggests that the cingulum does not clasp the central body in the manner described by Potonié and Kremp (1954) for *Densosporites*. For this reason the genus *Vallatisporites* may be considered valid for spores in which the body is separated from the cingulum by a groove in the manner described by Hacquebard.

In miospores possessing air sacs, the mode of attachment of the 'central body' to

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EXPLANATION OF PLATE 20

Fig. 1. Durain from Silkstone coal. Section parallel to the bedding, photographed by reflected light using oil immersion objective ×400. The double membrane constituting the spore walls of the miospores of *Densosporites* can be seen in those specimens cut more or less in their equatorial plane.

Fig. 2. Part of the field of fig. 1 ×1,000.

Figs. 3–8. *Densosporites spp.* and *Anulatisporites sp.* in which part of the outer membrane of the spore wall has broken away exposing the inner membrane or 'central body'. Transmitted light ×750.

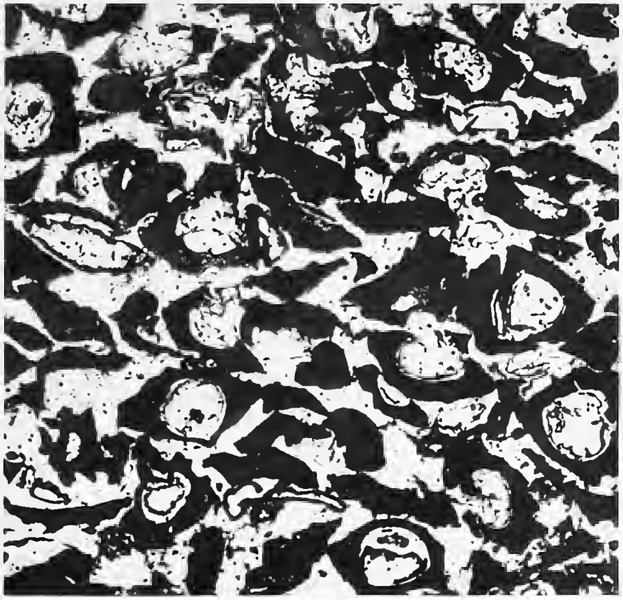
Fig. 3. *D. striatus* (Knox) Butt. and Will. From Silkstone coal (Lower Coal Measures, Yorkshire).

Fig. 4. *D. loricatus* (Loose) S.W. and B. From Upper leaf of Flint coal (Middle Coal Measures, Shropshire).

Fig. 5. *D. spongeosus* Butt. and Will. From Chapelgreen coal (Upper Limestone Group of Scotland).

Figs. 6, 7. *D. sphaerotriangularis* Kos. From 'Branch' band Silkstone coal (Lower Coal Measures, Yorkshire).

Fig. 8. *A. anulatus* (Loose) Pot. and Kr. From Ganister Clay coal (Lower Coal Measures, Durham).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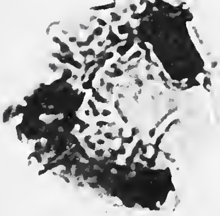
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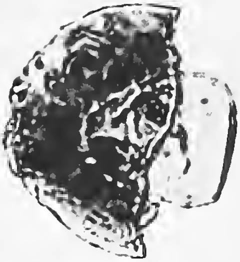
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SMITH, Carboniferous spores

the membrane constituting the air sac has been recognized as a fundamental distinction between genera (Schopf *et al.* 1944). In *Florinites* attachment is distal whereas in *Endosporites* it is proximal and represents a more primitive type of organization (Schopf 1938).

Since the presence of an 'internal body' has for so long been undetected in spore exines which are a frequent constituent of the miospore assemblages of some coal seams it is considered likely that the careful investigation of suitably preserved material may show that some other miospores possess this feature.

Acknowledgements. I should like to express my thanks to Dr. M. A. Butterworth and to a former colleague Dr. R. W. Williams for their patient searches which yielded two of the specimens illustrated in pl. 20.

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FOSSIL OAK WOOD FROM THE BRITISH EOCENE

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ABSTRACT. The circumscription of the organ-genus *Quercinium* Unger is discussed in relation to the wood structure of the Recent oaks and emended so as to include fossil wood conforming to the wood of the living species of *Quercus* L. and *Lithocarpus* Blume, since the wood of these genera is anatomically indistinguishable. *Quercinium quercoides* (Goepp.) Edwards is designated type species, and the name *Quercinium* Unger recommended as a *nomen conservandum* against the earlier valid name *Kloedenia* Goeppert. Two fossil woods, each with a type of structure found today in species of tropical evergreen oaks, are described and figured: *Quercinium porosum* sp. nov. from the Woolwich Beds (Landenian), Herne Bay, Kent; *Quercinium pasanioides* sp. nov. from the London Clay (Ypresian), near Ipswich, Suffolk.

FOSSIL wood resembling that of recent *Quercus spp.* has generally been referred to the genus *Quercinium* Unger (1842). Unger based this genus upon three very briefly described specimens of fossil wood which agreed in gross structure with the wood of oaks of the ring porous type with rays of two distinct sizes: 'Ligni strata concentrica distincta. Radii medullares biformes ("heteromorphi" in Unger 1850) . . . Vasa porosa . . . in uno v. in duobus stratis coacervata, in reliquis multo minora, fasciculatim aggregata.' The diagnosis was emended slightly by Mercklin (1855) who added a description of the wood parenchyma.

Felix was the first to deviate much from the original circumscription of the genus when he described under *Quercinium* a species, *Q. knowltoni*, in which the pores decrease in size gradually through the growth ring (Felix 1896). In this respect it resembled a wood previously described by Conwentz as *Quercites transiens*. Subsequent authors have used *Quercinium* as 'merely a form-genus for fossil wood closely resembling the recent *Quercus*' (Edwards 1931, p. 66), with neither type species nor generic diagnosis. Unfortunately a situation similar to this exists in respect of many genera created for fossil wood of dicotyledons. Furthermore, *Quercinium* is to be regarded as an organ-genus since its affinity with the Recent oaks is undoubted.

It would in fact be impracticable to restrict the genus to Unger's diagnosis since the growth ring in the wood of *Quercus* and allied genera is very variable, and all grades occur between ring porous and diffuse porous types, with and without a seasonal decrease in pore size. It is equally certain that this organ-genus cannot be regarded as comprising fossil wood of *Quercus* alone.

The major trends of specialization in the structure of the wood of the oaks appear to be closely associated with the differentiation of the growth ring with distinct early and late wood, and parallel grades are to be found in each of the large genera *Castanopsis* Spach., *Lithocarpus* Blume, and *Quercus* L.

The boundary of the growth ring is often difficult to trace in species from the humid tropical regions but in many evergreen oaks from temperate regions the ring is clearly marked by a more or less gradual diminution in diameter of the vessels in the late wood. In the truly ring porous types the radial pattern, which is a characteristic feature of transverse sections of wood throughout the oak–chestnut alliance, is often altogether lost

[Palaeontology, Vol. 3, Part 1, 1960, pp. 86–92, pls. 21–22.

from the early wood and the large pores of this zone form a tangentially continuous ring. In many species of *Quercus*, where this is the mature arrangement, the first few rings of secondary wood possess the radial, diffuse porous pattern.

Examination of a large number of ring porous woods led Metcalfe and Chalk (1950) to conclude that 'it would appear unwise . . . to rule out the possibility that ring porousness may represent an ecological specialization, which occurs in wood at very different levels of general specialization and in widely separated taxonomic groups' (op. cit., p. xlviii). The oaks furnish an instructive illustration of a trend to ring porousness within several closely related species groups, which has apparently gone hand in hand with their general adaptive radiation from tropical centres.

The wood rays are basically of two distinct sizes in the Fagaceae but, as in *Castanea* and *Nothofagus*, specialization has led to the elimination of the very broad rays from *Castanopsis*, and a few species of *Lithocarpus*, e.g. *L. fenestratus* (Roxb.) Rehd., *L. pachyphyllus* (Kurz) Rehd. (Gamble 1881), *L. lappaceus* (Roxb.) Rehd. (Gamble 1881; Tippo 1938), and *L. sieboldii* (Makino) Nakai (Metcalfe and Chalk 1950). Broad rays may also be absent from the young stems and branches of several *Quercus spp.*

Wood parenchyma, typically banded in the oaks, may vary between individual species from regular and continuous bands of one to four cells in radial extent to discontinuous and wavy tangential strings of cells, in some forming a sort of reticulate arrangement and in yet others the parenchyma is rare and diffuse. In some *Quercus spp.* at least there is considerable variation between different samples and this appears often to be related to the width of the growth rings.

CIRCUMSCRIPTION OF THE ORGAN-GENUS

Fossil wood ascribable to the recent *Castanea* and *Castanopsis* will be excluded from the organ-genus *Quercinium* if this latter be restricted to wood with rays of two distinct sizes.

The two genera *Lithocarpus* and *Quercus* are not distinguishable on the basis of wood anatomy alone. Types of structure found in one genus grade insensibly into those of the other at all levels of specialization of the growth ring. The evergreens in the genus *Quercus* have wood indistinguishable from that of many species of *Lithocarpus*, and it would hardly be possible to distinguish the ring porous wood of *L. uraianus* (Hay.) Hay., for example, from many other *Q. alba*-type woods.

I propose to emend the organ-genus *Quercinium* to include fossil wood conforming to that of the Recent genera *Quercus* L. and *Lithocarpus* Blume. The two new species described in this paper have a structure found today in species of evergreen oaks from the tropics, and are thus included in the organ-genus as now understood.

Family FAGACEAE
Organ-genus QUERCINIUM Unger

Emended diagnosis. Fossil secondary wood, or stems or roots with some secondary wood. Rays of two distinct sizes; uniseriate rays numerous, multiseriate rays often very broad and high and appearing compound or aggregate. Wood parenchyma commonly in tangential bands or strings, but may be diffuse. Vessels mostly large and solitary except in the late wood of ring porous species, and showing some radial pattern in transverse sections; often accompanied by tracheids (vasicentric); vessel members with simple perforations, exceptionally scalariform when very narrow; intervascular pitting alternate to sub-opposite. Ray to vessel pits large, gash-like, usually vertically or obliquely elongated. Remainder of wood tissue of fibre-tracheids and/or fibres.

Type species. The selection of a type species for *Quercinium* is desirable since one has never been designated. The three species originally included in the genus by Unger (1842) were given such inadequate description that it would be impossible to recognize any of them again, and the specimens do not appear to have been preserved. At that time, however, Unger observed that *Kloedenia quercoides* Goeppert (1839) could probably be included in *Quercinium*, and in 1845 he cited this earlier name as synonymous with *Quercinium sabulosum*, one of his three original species, ignoring the priority of Goeppert's name. Thus, on Unger's own admission, *Q. sabulosum* may be accepted as a synonym of *K. quercoides*. Meanwhile Goeppert had described another specimen apparently identical with his *Kloedenia* material, under a new name *Quercites primaevus* Goeppert (1845), abandoning completely his previous name. Felix (1883) re-examined some of Goeppert's original *Kloedenia* material, provided a full description, and used a new combination, *Quercinium primaevum*, which is invalid, since the earlier name for this material, *K. quercoides* Goepp., was validly published. The valid name for this species remains *Kloedenia quercoides* Goepp. If this be accepted into the organ-genus diagnosed above, the name *Quercinium* should, according to the International Code, be abandoned in favour of *Kloedenia*. This latter name has been used only once and has

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EXPLANATION OF PLATE 21

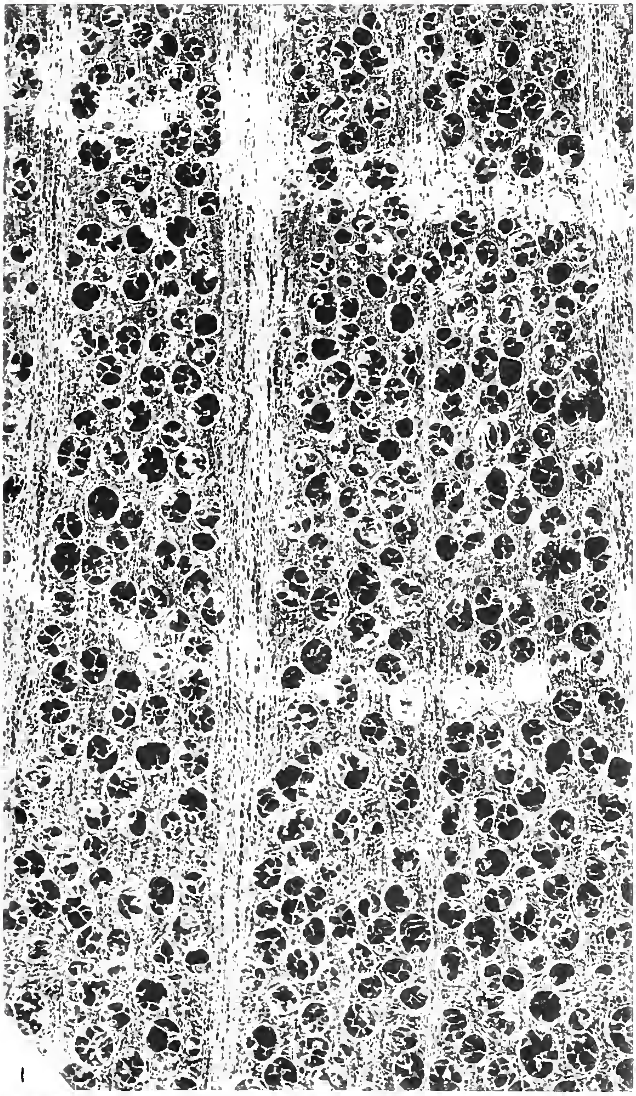
Figs. 1, 2. *Q. porosum*. 1, Transverse section of secondary wood showing the close arrangement of the large vessels, the broad rays, and absence of growth rings. ×16. The two light areas are caused by a dark gum-like infiltration of the tissue. 2, As fig. 1, but showing origin of a broad ray by aggregation of fine rays and elimination of the intervening tracheary tissue. ×37.

Figs. 3, 4. *Q. pasanioides*. 3, Transverse section for comparison with fig. 1. The vessels are arranged in radial strings, and the banded parenchyma shows as light, wavy lines. Tangential compression during fossilization has reduced the tangential diameter of most of the vessels here. ×16. 4, Transverse section of a radial cluster of vessels accompanied by vasicentric tracheids. The tangential bands of parenchyma are visibly differentiated from the fibres of the ground tissue, as are the numerous fine rays. ×37.

EXPLANATION OF PLATE 22

Figs. 5, 6, 11. *Q. porosum*. 5, Radial section. Part of a broad ray is shown on the left, and to the right of centre some intervascular pitting of a vessel. Tyloses fill the vessels and wood parenchyma is abundantly represented. ×50. 6, Tangential section, showing part of a broad vertically compound ray of some twelve cells in width, and uniseriate rays. ×50. 11, Radial section, part of a vessel with tyloses and ray cells showing the simple, elongated pits to the vessel. ×135.

Figs. 7–10. *Q. pasanioides*. 7, Tangential section, showing uniseriate rays and a broad ray with fibrous inclusions. ×50. 8, Radial section to show appearance of the regularly banded wood parenchyma; some chambered crystalliferous cells are visible in the strand to the left of centre. ×50. 9, Radial section, to show ray to vessel pitting of elongated simple pits; small, bordered pits of the fibre-tracheids are also shown. ×135. 10, Radial section, showing the richly pitted walls of the ray cells ×135.



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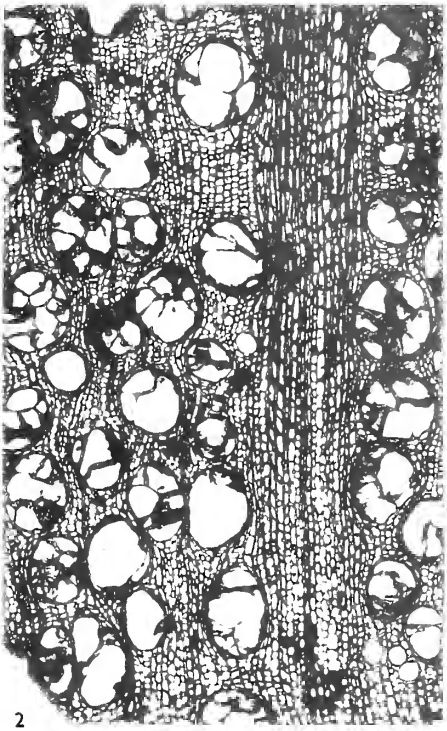

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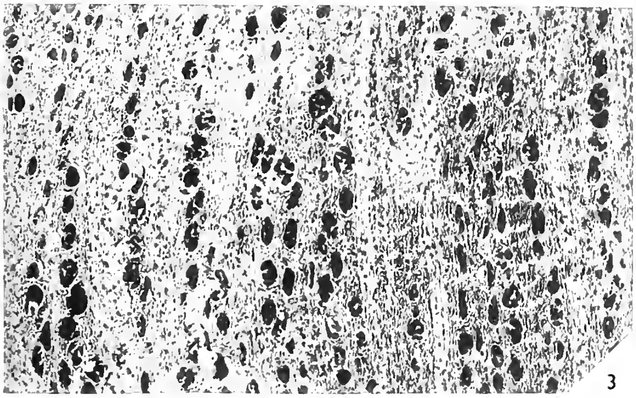

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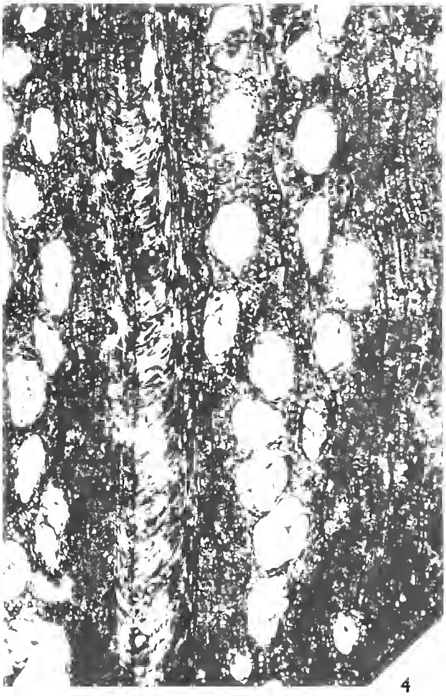

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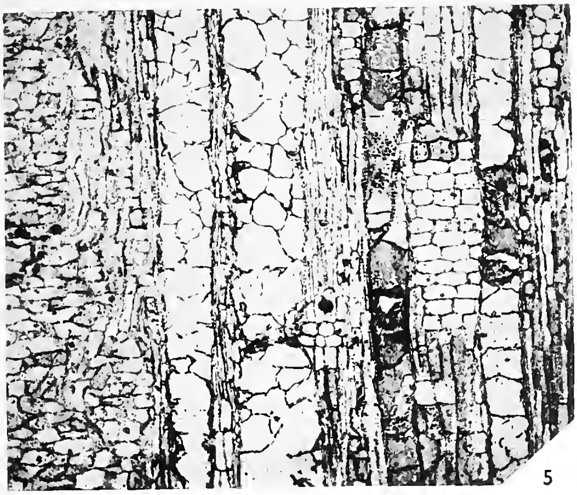
BRETT, *Quercinium*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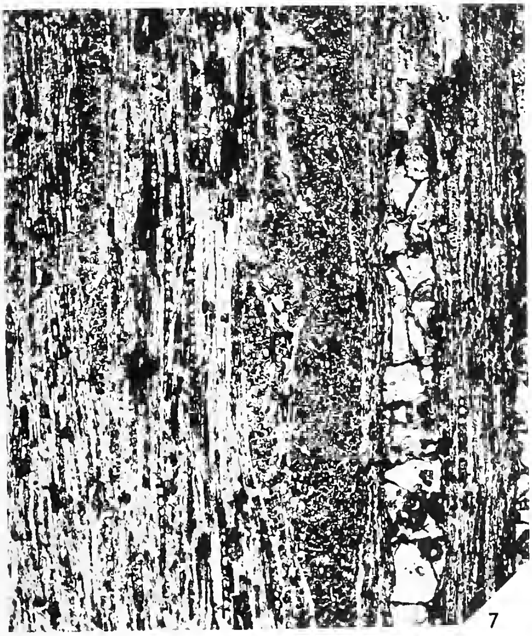
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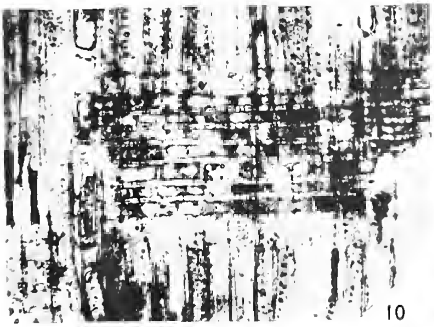
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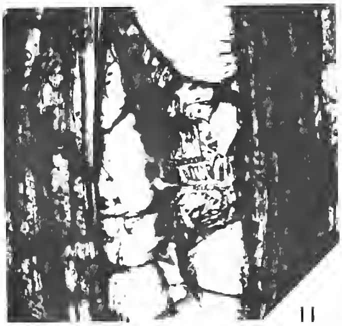
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BRETT, *Quercinium*

since been generally abandoned by authors. I would therefore recommend that *Quercinium* Unger be added to the list of *nomina conservanda*.

Edwards (1931) drew attention to the confusion in the nomenclature of this species and used the combination *Quercinium quercoides* (Goepp.) Edwards. Under this name I designate this species as the type species of the organ-genus *Quercinium* Unger.

Synonymy of type species. *Kloedenia quercoides* Goeppert 1839. *Quercinium sabulosum* Unger 1845. *Quercites primaevus* Goeppert 1845. *Quercinium primaevum* (Goepp.) Felix 1883.

SYSTEMATIC DESCRIPTIONS

Quercinium porosum sp. nov.

Plate 21, figs. 1, 2; Plate 22, figs. 5, 6, 11

Holotype. No. V 26291 and slide preparations in Dept. of Palaeontology, British Museum (Nat. Hist.), London. Silicified wood from the sands of the Woolwich and Reading Series, Herne Bay, Kent. Eocene (Landenian).

In transverse sections the vessels are abundant, almost always solitary, and show no special pattern, 6–10 per sq. mm., tangential diameter 80μ–270μ (average 237μ); members short, around 0·6–0·8 mm., perforations simple, transverse or slightly oblique. Intervascular pitting mostly alternate, of circular bordered pit pairs. Tyloses fill all the vessels. Imperforate tracheary cells with walls of moderate thickness, numerous large, circular bordered pits with crossed, elliptical inner apertures. Parenchyma abundant, diffuse; half-bordered pit pairs from the tracheary cells distinguish the parenchyma in transverse sections. Rays of two distinct sizes; uniseriate rays abundant, deflected by the vessels, eight to twelve per mm., two to thirty cells high in tangential section. In transverse section some very broad rays appear to be formed by aggregation of many uniseriate rays. Broad rays occur every 2–3 mm. and are up to twenty cells in width, and may be over 5 mm. high. Pits from the vessels to the ray cells are large, gash-like, and mostly elongated obliquely to the vertical.

Viewed in radial section the ray cells are mostly slightly elongated radially but more or less square to upright at the margins, they are abundantly pitted. Growth rings are not discernible. There are slight suggestions of periodicity in the ground tissue, often accompanied by occasional very small pores, but there is no obvious overall difference in pore size or distribution here.

The combination of the following characters distinguishes this species from all those previously described: the almost complete absence of periodicity in growth, and the crowded, large pores which show little or none of the radial pattern typical of the oaks in general. These characters were found to be closely matched in a sample of the wood of the living species *Quercus* (*Cyclobalanopsis*) *lamellosa* Sm., although the sample also showed areas with fewer pores in radial/oblique arrangement.

Quercinium pasanioides sp. nov.

Plate 21, figs. 3, 4; Plate 22, figs. 7–10

Holotype. No. V 25808 and slide preparations in Dept. of Palaeontology, British Museum (Nat. Hist.), London. Calcified wood from the London Clay 5 feet below the surface in the valley of the river Finn between Tuddenham and Rushmere, near Ipswich, Suffolk. This is from the lowest portion of the formation. In this region the London Clay has been found to be at the most about 100 feet thick (Boswell 1927). Eocene (Ypresian). Presented to the British Museum by Mr. H. E. P. Spencer in 1938.

In tranverse section the vessels are mostly solitary but occasionally in radial or oblique pairs, about nine per sq. mm. and disposed in a radial flame-like pattern; tangential diameter from 60 μ for the rare small vessels to 200 μ, average about 130 μ (estimated from measurements of apparently undistorted pores in the transverse sections). Average member length around 0·460 mm., perforations simple, horizontal or slightly oblique. Pitting to tracheids is alternate, circular bordered pits with elliptical apertures. Tyloses fill all the vessels. Imperforate tracheary cells are of two kinds: vasicentric tracheids with wide lumen and bordered pitting on all walls in single or alternating longitudinal rows, half-bordered pitting to the parenchyma; fibre-tracheids of smaller diameter and with narrow lumen, bordered pitting rather small and sparse. Parenchyma mostly in regular bands one to four cells in width, about three to four bands per mm., but these are not always tangentially continuous; vertically the strands may consist of up to twelve cells, these cells being three to five times the height of the ray parenchyma. The strands commonly include one or several chambered cells, each containing usually four crystals. Rays of two distinct sizes: uniseriate rays numerous, up to 15 per mm., multiseriate rays mostly not less than 1 mm. apart. The cells are elongated radially in both types of ray, except for the marginal rows in which they are square or even upright. The multiseriate rays may be as much as twenty cells broad, up to 1 cm. in height in tangential section and traversed by fibres, often contorted, thus appearing to be compounded of narrower units. Height of the uniseriate rays is commonly eight to twelve cells but varies from three or four to as many as twenty cells. All the ray cells are richly pitted; the ray to vessel pits are large, usually elliptical with the long axis vertical. Growth rings are barely distinguishable but may be traced in places by a slight difference in character of what is taken as late wood. In such zones, which do not always coincide on opposite sides of the broad rays, the parenchyma bands appear slightly closer and there are more of the smaller, rounder vessels.

In all its general features the fossil is remarkably like the wood of several evergreen oaks but differs from many of the Recent species and from the few similar species of *Quercinium*, chiefly in the characters of the indistinct growth ring and the more or less regular banded parenchyma. Thus it is set apart from the fossils *Quercinium anomalum* Platen, *Q. wardi* Platen (both Platen 1908), and *Q. ricardensis* (Webber) Boeshore and Jump (Webber, 1933), to which it otherwise shows most resemblance. Among the specimens of Recent wood compared with the fossil species, that of *Lithocarpus* (*Pasania*) *hystrix* (Korth) Rehd., in the Kew collection from Malaya, stands out as a very close match in all details: in more general terms this is a type of wood found in the oaks of the rain forests of south-east Asia.

DISCUSSION

The wood of many plants growing in tropical and subtropical regions often shows little or no evidence of periodicity in radial growth. The lack of sharp distinction between growth increments in wood is more particularly a feature of trees, mostly evergreens, growing in the rain forests where the environment is little affected by a seasonal régime, and periodicity in cambial activity is apparently more directly controlled by inherent factors (see Richards 1952, ch. 8).

The presence in the London Clay of a wood of this character, when considered in association with the taxonomic affinities of the fruits and seeds described by Reid and Chandler (1933), lends firm support to these authors' conclusions regarding the living conditions of the 'tropical' element in the flora of the London Clay. I believe there is sufficient evidence to regard the L.C. flora as consisting of more than a single vegetation type. There are several woods and small twigs from the Clay with structural and taxonomic affinities quite different from those of the wood (*Q. pasanioides*) described above; these include both dicotyledonous and coniferous types. It is difficult to escape the conclusion that they grew under quite different conditions. I have described one such wood previously (*Cercidiphyllum*) and at the same time stressed the presence in this flora of a temperate element, which is presumed to be part of an earlier flora in the region under consideration (Brett 1956; Reid and Chandler 1933, p. 60). As such, this element must be regarded as representative of one or more plant associations ecologically distinct from the rain forest and littoral vegetation types which are also represented in the London Clay flora. Disregarding for the present the possibility that the wood and small twigs have drifted in the sea from higher latitudes, the alternative explanation for their occurrence in the London Clay must be that they have been carried down river from some region inland where a more temperate climate prevailed and seasonal differences in rainfall and/or temperature were greater. Thus, together with those fruits and seeds whose taxonomic affinities are with Recent temperate genera, they may represent the vegetation of some cooler upland valleys.

The flora of the Woolwich and Reading Series immediately precedes that of the London Clay but is unfortunately still little known. Miss M. E. J. Chandler, who has recently been working on the Woolwich and Reading fruits and seeds, is of the opinion that conditions during this period were probably very little different from those of London Clay times, i.e. the lowlands had a tropical climate; several of the London Clay genera are in fact represented (Chandler, personal communication). The nature of the wood described above (*Q. porosum*) certainly suggests a tropical environment, and I have another wood from the same locality which also supports this view and is a member of the Anacardiaceae, a family well represented in the London Clay flora. As in the London Clay, however, there are other woods, fruits, &c., the conifers in particular, which suggest the temperate (? montane) element.

A species of *Quercinium* from beds of similar age to the Woolwich and Reading in the Paris Basin has been described by Fritel and Viguier (1911). From their description the wood appears to be of the red-oak type, at any rate distinctly ring porous, and therefore quite different from *Q. porosum*.

The identification of these two woods as belonging to the Fagaceae extends the earliest record of the occurrence of that family in British deposits back from the Brackelsham Beds (Cuisian/Lutetian) to the Ypresian and Landenian. On the continent of Europe and also in North America, oaks and other Fagaceae have been recorded from leaf remains from the early Cretaceous onwards. Some of the leaves from the Lower Eocene (Landenian) of Belgium and France have been referred to the genus *Pasaniopsis* on account of their resemblance to tropical oaks, while others are referred to *Quercus* and *Dryophyllum* (Saporta and Marion 1878; Depape 1925).

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OSTRACODA FROM THE UPPER SILURIAN STONEHOUSE FORMATION, ARISAIG NOVA SCOTIA, CANADA

by M. J. COPELAND

ABSTRACT. Several species of ostracods of the genera *Beyrichia*, *Kloedenia*, *Leperditia*, and *Primitia* have been described from Upper Silurian strata of the Stonehouse formation near Arisaig, Nova Scotia. Previous indentifications of some of these ostracods are considered doubtful due in part to the confusion arising from their original descriptions by James Hall (1860). The present examination gives more detailed information concerning these previously described species and reveals for the first time the presence of several species previously recorded only from northern Europe. On the basis of the contained ostracod fauna, correlation of the Stonehouse formation is made with the *Beyrichia* Limestone of the Baltic region.

INTRODUCTION

NUMEROUS references have been made to ostracods from the upper part of the Silurian Arisaig group since the earliest description of this fauna by James Hall in 1860. Many specimens have been found near the middle and upper parts of the Stonehouse formation (McLearn 1924), the youngest exposed sequence of Silurian rocks in the area. Species of the genera *Beyrichia*, *Leperditia*, and *Primitia* have been reported and figured by Hall (1860), Jones (1881; 1890; 1891), and others. In the present paper previously described ostracod genera and species from this formation are evaluated and several other species are recorded for the first time.

The original description of part of this fauna by James Hall has confused subsequent workers. He described three species, *Beyrichia pustulosa*, *B. eqilatera* (*sic* = *equilatera*), and *Leperditia sinuata*, but gave no figure for *L. sinuata*. The small size of the original woodcuts of the other two species gave no adequate representations of their true morphologies. Indeed, Jones (1891, pp. 73–74) considered Hall's original figures of *B. equilatera* to be 'a small *Beyrichia tuberculata*, or one of its varieties' and he decided 'to accept the published *description* (1860) as belonging to *B. aequilatera* Hall, and to regard the little *woodcut* on the same page as belonging to the other species occurring so abundantly with *B. aequilatera*' (i.e. *B. pustulosa*). It is no wonder, therefore, that a confusing synonymy has arisen concerning these two species.

Subsequent to Hall's work, Jones recorded the presence of several other species of *Beyrichia* from these strata (*B. tuberculata* (Kloeden), *B. bronni* Reuter, *B. tuberculata strictispiralis* Jones, *B. tuberculata noetlingi* (Reuter), *B. tuberculata gibbosa* Reuter, *B. maccoyiana* Jones, and *B. wilckensiana* Jones). One of these, *B. wilckensiana*, has subsequently been referred to the genus *Kloedenia*, but the assignments of the other beyrichiid species have remained relatively unchanged. The multiplicity of these beyrichiids and the indefinite descriptions of *B. equilatera* and *B. pustulosa* have raised the problem of the possible synonymy of certain of these species. Other recorded genera from these beds include *Primitia* (*P. mundula* (Jones), *P. concinna* Jones and Holl, *P. ovata* Jones and Holl, and *P. sp.*) and *Ctenobolbina? sp.* The latter genus is not considered in this

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paper, since the identification is questioned and no specimens have been obtained during the present study.

In attempting to describe these ostracods, an examination of Hall's type specimens in the American Museum of Natural History was considered advisable. Accordingly, type specimens of *B. pustulosa* and *L. sinuata* were obtained (*B. equilatera* not being available) and comparison attempted with material available in collections of the Geological Survey of Canada.

The author gratefully acknowledges the loan of type specimens from the American Museum of Natural History. Dr. R. V. Kesling of the Museum of Paleontology, University of Michigan, kindly read the manuscript and made many helpful comments. Photographs were made by Mr. E. C. Elliot of the Geological Survey of Canada. The paper is published by permission of the Director, Geological Survey of Canada, Department of Mines and Technical Surveys, Ottawa, Ontario.

Mode of Preservation. Most ostracods from the Stonehouse formation are preserved only as internal moulds of individual valves preserved in red and pink sandy limestone or calcareous sandstone. The matrix is composed chiefly of pink calcium carbonate, which, on being weathered, leaves a residual ferruginous stain on the outcrop. This stain coats the specimens, giving them a hematite-red colour. Despite this undesirable type of preservation, sufficient surface details are generally present on most specimens to permit their specific identifications. Specimens also occur in massive grey, sandy, coquinal limestones. They are well preserved for the most part, but the beyrichiids are rarely obtained as complete valves due to the necessity of uncovering and breaking them free from the matrix. The smooth-shelled genera, however, are more easily prepared in this manner. Absence of complete carapaces may indicate the dissociation of valves due to current action prior to burial.

Stratigraphic position. The age of the Stonehouse formation has been variously considered as Middle or Late Silurian. Williams (1914) gave a detailed account of the early history of this problem and considered (p. 133) the Stonehouse as equivalent to the Ludlow of Europe. McLearn (1924, pp. 20 ff.) considered the Stonehouse fauna as equivalent to that of the Pembroke of Maine, the Upper Ludlow of Britain, and étages 9e–9g of Oslo (Christiania). Swartz *et al.* (1942) regarded the Stonehouse as equivalent to the upper part of the Wenlockian, Ludlovian, and Downtonian (emended) Series of Great Britain and equal to the upper part of the Niagaran (Guelph) and Cayugan Series of North America. Flower (1943, p. 251), basing his conclusions on fauna obtained from a drift boulder, considered that the Stonehouse cephalopod fauna 'may not be much younger, if at all, than known Middle Silurian strata of Europe and America'. More recently, Boucot (personal communication, manuscript in press), on the basis of brachiopod affinities, considers the Stonehouse formation as possibly equivalent to the Downtonian Series of Great Britain.

On the basis of ostracod fauna, correlation with rocks of the Downtonian Series is considered most probable for the Stonehouse formation. This is based on the occurrence of similar fauna from Oesel (zone K of Reuter 1885; Obere Oesel-Gruppe of von Bubnoff 1926) and Upper Silurian drift (Obersilurischen Diluvialgeschiebe) from northern Germany (Obere Beyrichien-Kalke of Krause 1891). These European faunas contain specimens of *Beyrichia tuberculata* (Kloeden), *B. salteriana* Jones, *B. buchiana* Jones, *B. maccoyiana* Jones, and *Kloedenia wilckensiana* (Jones) which Kesling and Wagner (1956, p. 36) considered of Downtonian age. Moberg and Grönwall (1909), working in southern Sweden, identified among other ostracods *Primitia mundula*, *Beyrichia kochii*, *B. maccoyiana*, *Kloedenia wilckensiana*, and *Cytherellina siliqua*—species recorded from the *Beyrichia* Limestone and now found in the Stonehouse formation. The beds containing these species in Sweden were correlated with the Downtonian sandstone, Tilestones and Ledbury Shales of Great Britain—all contained within the Downtonian Series. Also, Henningsmoen (personal communication) is of the opinion that the *Beyrichia* Limestone fauna is post-9g in the Oslo region terminology and is probably of Downtonian age. From the foregoing it appears probable that the *Beyrichia* Limestone ostracods occur in beds of Downtonian age in northern Europe and that a similar age should be assigned the Stonehouse fauna. The exact stratigraphic distribution of ostracods throughout the Stonehouse formation is not at present known. This will constitute a separate study to be published at a later date.

Palaeontology. The following ostracod species have been identified from the Stonehouse formation; their distribution in northern Europe is given below.

	N. Germany (*drift*) Beyrichia *Ls.*	*Oesel and and Gotland*	*Southern Sweden*
Aparchites sinuatus (Hall) 1860	×		
B. kochii Boll 1862	×	×	×
B. maccoyiana Jones 1855	×	×	×
B. maccoyiana var. *sulcata* Reuter 1885	×		
B. pustulosa Hall 1860	×		
Bythocypris phillipsiana (Jones and Holl) 1869	×	×	
Kloedenia wilckensiana (Jones) 1855	×	×	×
Primitia mundula (Jones) 1855	×	×	×
Cytherellina siliqua (Jones) 1855	×	×	×

It has been demonstrated by numerous authors that the northern German 'Obersilurischen Diluvialgeschiebe' is the product of Pleistocene glaciation, probably of the Weichsel stage (Kesling and Wagner 1956, p. 39). Flow lines of this glaciation were shown (ibid., fig. 2) indicating derivation of drift boulders of this age from the islands of Gotland and Ostrov Sarema (Oesel). Both Reuter (1885, p. 666) and Kesling and Wagner (1956, p. 37) considered boulders containing an admixed ostracod fauna (*B. maccoyiana* from Gotland and *K. wilckensiana* from Oesel) as being derived from strata intermediate between the two islands cropping out beneath the Baltic Sea. It is with this fauna that the Stonehouse ostracods find their closest affinity.

B. tuberculata (Kloeden), the most representative species of the German 'Beyrichienkalk', is not present in the Stonehouse assemblage. Its place within the fauna was occupied by a somewhat similar species, *B. pustulosa* Hall. As yet, descriptions of specimens of *B. tuberculata* identified by Jones from this formation are considered as being based on specimens of *B. pustulosa*.

Little evidence is available indicating the relationship of this fauna with that of any other area in North America. *Bythocypris phillipsiana* has been reported from the Lower

Cayugan McKenzie formation of Maryland (Ulrich and Bassler 1923) and *Beyrichia equilatera*, *B. tuberculata*, and *B. kloedeni* are recorded from near Lake Temiscouata, Quebec (*Geol. Surv. Canada*, *Ann. Rept.*, 1888, **3**, M; &c.). These latter species may indicate possible equivalence to the Stonehouse fauna, but additional specimens are required to verify these identifications.

SYSTEMATIC DESCRIPTIONS

BEYRICHIA M'Coy

The systematic position of *Beyrichia* M'Coy 1846 has been discussed in detail by Henningsmoen (1954, pp. 18–27) and Kesling and Wagner (1956, pp. 39–43). Henningsmoen erected six sub-genera of *Beyrichia* on the bases of differing velate and surface ornamentations. These were, for the most part, accepted by Kesling, but depend on their validity to a certain extent on the designation of type species (*B. kloedeni* M'Coy 1846 or *Battus tuberculatus* Kloeden 1834). Since this question does not have definite bearing on the present discussion, Henningsmoen's classification is followed in this paper.

The *Beyrichia* species obtained from the Stonehouse formation fall within two of these subgenera—*Nodibeyrichia* and *Neobeyrichia*—the former characterized by divided anterior and posterior lobes and the latter by three simple lobes and a marginal ridge or frill. Unfortunately, the separation of species within these subgenera is somewhat difficult unless well-preserved material is available.

BEYRICHIA (NODIBEYRICHIA) Henningsmoen

Type species *Beyrichia bronni* Reuter

The description of this subgenus is as follows (Henningsmoen 1954, p. 26):

> '*Beyrichia* species with L1 split into two nodes. Lp may also be split into two or more nodes. A secondary fissus may be present. Velate structure developed as a ridge. Surface granulose or smooth.'

Division of the Lp (L3 of Kesling) into two or more parts has been used as a useful criterion for division of the subgenus into species. In some species the nodes comprising L3 are fairly continuous and knoblike as in *B. tuberculata* (Kloeden), whereas in other species this lobe is distinctly disrupted and pustulose as in *B. baueri* Reuter. Numerous variations exist between these extremes, specific differentiation being based on the type, number, and orientation of the resultant nodes. It is understandable that, where specific characteristics are based on such microscopic detail and easily defaced by natural action, duplication and misunderstanding of specific designations could arise.

Beyrichia (*Nodibeyrichia*) *pustulosa* Hall

Plate 23, figs. 2–9

B. pustulosa Hall 1860, pp. 157–8, fig. 19; Dawson 1860, p. 67; Honeyman 1864, p. 344; Dawson 1868, pp. 608–9, fig. 216; Jones, *in* Honeyman 1870, p. 492; Dawson 1878, pp. 608–9, fig. 216; Jones 1881, p. 344; Jones 1881, p. 313; Jones 1890, p. 18; Jones 1891, p. 76; Dawson 1891, pp. 608–9, fig. 216; Ulrich and Bassler 1908, pp. 286, 289; Williams 1914, p. 72; Bassler 1915, p. 123; Bassler and Kellett 1934, pp. 67, 204; Henningsmoen 1954, p. 26; Kesling 1956, p. 45.

B. tuberculata (Kloeden); Jones 1870, p. 492; Jones 1881, p. 344, pl. 10, figs. 8?–10; Jones 1881, p. 313; Jones 1890, p. 552; Jones 1891, pp. 74–75, pl. 11, fig. 3; Ami 1893, p. 191; McLearn 1924, p. 20; Bassler and Kellett 1934, p. 67.

B. noetlingi Reuter 1885, p. 637, pl. 25, figs. 5A–C; Bassler and Kellett 1934, p. 67; (authors).

B. tuberculata pustulosa (Hall); Jones 1890, p. 18, pl. 2, figs. 1*a*–*c*; Jones 1890, p. 552; Jones 1891, p. 76, pl. 11, fig. 2; Ami 1893, p. 191.

?*B. tuberculata bronni* (Reuter); Jones 1890, p. 552.

?*B. tuberculata gibbosa* Jones 1890, p. 552.

?*B. bronni* Reuter; Jones 1890, p. 552.

B. tuberculata noetlingi (Reuter); Jones 1891, p. 78, pl. 11, figs. 4*a*–*b*, 5; Ami 1893, p. 191; Bassler 1915, p. 124.

?*B. tuberculata strictispiralis* Jones 1891, p. 77, pl. 11, fig. 1; Ami 1893, p. 191; Bassler 1915, p. 124; Bassler and Kellett 1934, pp. 67, 210; Henningsmoen 1954, p. 26; Kesling 1956, p. 45.

B. gedanensis pustulosa (Hall); Kiesow 1892, p. 98, pl. 24, figs. 5*a*–*b*, 6*a*–*b*.

The original description of this species is essentially adequate, but it does not appear to entirely agree with the published figures. The woodcut shown by Hall (1860) and reproduced by Dawson (1868; 1878; 1891) is too poor to be of assistance. The figures by Jones (1881; 1890; 1891), however, show additional features. These latter figures vary greatly in details. Figures 9–10 (1881, pl. 10) show the species as bearing a posterior lobe with five or six rounded tubercles aligned variously in two or possibly three rows. Figure 1 (1890, pl. 2) depicts the posterior lobe of this species as having six nodes aligned in two rows, the dorsal one being somewhat enlarged. In this figure there are four nodes in the anterior row and two in the posterior. Figures 1 to 3 (1891, pl. 11) show the posterior lobe of this species as consisting of four (?) tubercles aligned in an arcuate row. These nodes are rounded in figure 2 and elongate-oblique in figures 1 and 3, the latter being reminiscent (except in number) of *B. tuberculata* (Kloeden).

Such variation within this species may easily be explained by the type of preservation of the specimens. They are known mostly from moulds of the interiors of disarticulated valves. The preserved ornamentation of this species shows variations in size and shape that may not entirely reflect the true surface characteristics of the valves. Description must, however, be based on the preserved characteristics of the internal moulds which, it is believed, reflect the true external features of the valves as closely as possible. Such variation is depicted on the accompanying plate. A revised description based on these specimens is as follows:

Valves elongate–ovate, hinge line straight, three-quarters as long as valve, surface ornamentation unknown but presumed to be pustulose as in *B. tuberculata* (Kloeden), free border with entire marginal and velate ridges separated from each other by a smooth channel. Three main lobes are present, L1 divided into two ovate–oblique nodes, situated near and parallel with the dorsal and ventral anterior corners, the dorsal node projecting above the hinge. In the adult female the ventral anterior lobe is greatly enlarged, overhanging the free margin and extending from the mid-anterior to the mid-ventral borders. L2 separated from the other lobate areas by a deep 'U-shaped' sulcus consisting of S1 and S2. These joined sulci continue ventrally to the marginal ridge slightly anterior to L2 in the adult male valve and slightly posterior to L2 in the adult female. L2 egg-shaped, extending from beneath the hinge to the mid height of the valve. L3 large, variously lobed, consisting of six nodes arranged in two arcuate rows, the anterior row with four and the posterior row with two nodes. The nodes of the anterior row are separated by three shallow furrows, the dorsal and ventral nodes largest. The smaller posterior nodes are situated posterior and opposite to the two upper furrows of the anterior row.

Remarks. This species is considered synonymous with *B. noetlingi* Reuter, *B. gedanensis* (Kiesow), and their varieties. The close resemblance of *B. bronni* Reuter and *B. pustulosa* Hall indicate them to be closely allied forms, differing specifically in the shape and number of nodes on the posterior lobe. The division of the posterior lobe into three or four major elements appears to be a feature common to these species and is indicated in a more elemental form by *B. tuberculata* (Kloeden).

BEYRICHIA (NEOBEYRICHIA) Henningsmoen

Type species *Beyrichia buchiana* Jones 1855

The description of this subgenus is as follows (Henningsmoen 1954, p. 25):

> '*Beyrichia* species with L1 isolated from L2 and Lp. L2 and Lp may be united or not. Velate structure developed as a ridge, or a narrow ridge-like frill. Surface granulose or smooth.'

This subgenus is distinguished from others of the genus by the tumid outline of the lobes. In many species (e.g. *B. maccoyiana*) the three lobes are without intermediate furrows, whereas some (e.g. *B. kochii*) have L3 divided variously into nodes or tubercles.

Beyrichia? (Neobeyrichia) equilatera Hall

B. equilatera Hall 1860, p. 158, fig. 20?; Dawson 1860, p. 67; Honeyman 1864, p. 344; Dawson 1868, p. 609, fig. 217; Dawson 1878, p. 609, fig. 217; Jones 1881, p. 344; Jones 1881, p. 313; Jones 1890, p. 18, pl. 2, fig. 6; ibid., p. 552; Jones 1891, p. 72; Dawson 1891, p. 609, fig. 217; Ami 1893, p. 191; Williams 1914, p. 72; McLearn 1924, p. 20; Bassler and Kellett 1934, pp. 67, 191.

This species, if it exists, is very incompletely known. The original woodcut is very indistinct, does not agree with the written description, and may indeed represent an individual of *B. pustulosa* Hall as suggested by Jones. The figure by Jones (1890) only questionably agrees with the original description but may portray a more reliable representation of the species. Unfortunately, no type material is available on which to base an adequate redescription of the species. The original description could equally well apply to a defrilled male specimen of *B. maccoyiana*, *B. salteriana*, or *B. reuteri*, but this should have been immediately evident to Jones and so is not considered probable. It is hoped that further investigation will uncover additional specimens.

Beyrichia (Neobeyrichia) kochii Boll

Plate 23, fig. 23

B. kochii Boll 1862, p. 121, pl. 1, fig. 2; (authors).

This species is distinguished from other species of the subgenus by having a nearly confluent L2–L3, an oblique groove crossing L3 and both dimorphs with a narrow velar frill and a small tubercle in the dorsal part of S2. Only L3 is tuberculate, the remaining parts of the valve are smooth.

Beyrichia (*Neobeyrichia*) *maccoyiana* Jones

Plate 23, figs. 12, 13

B. maccoyiana Jones 1855, p. 88, pl. 5, fig. 14; Jones *in* Honeyman 1870, p. 492; Jones 1881, p. 313; (authors).
B. spp. (part) Honeyman 1864, p. 344; Jones 1881, p. 344; Jones 1881, p. 313.

This species is represented in the Stonehouse collections by several incomplete valves, two of which are figured. They are entirely representative of the species as described from Europe and no new description is necessary. All the valves obtained are of male specimens.

Beyrichia (*Neobeyrichia*) *maccoyiana* var. *sulcata* Reuter 1885

Plate 23, figs. 14–16

B. maccoyiana sulcata Reuter 1885, p. 644, &c., pl. 26, figs. 17*a*, *b*; (authors).

The variety as originally described is entirely representative of the Stonehouse specimens. The diagnostic characteristics of this variety appear to be the division of L3 into two nodes by an angulated furrow and the presence of a notch or furrow on the ventral surface of the adult female brood pouch. The male frill (fig. 14) does not appear to be as striated as that of *B. maccoyiana* but this may be due to preservation.

KLOEDENIA Jones and Holl

Type species *Beyrichia wilckensiana* Jones 1855

A revised description of this genus has been given by Kesling (*in* Kesling and Wagner 1956, p. 63).

Kloedenia wilckensiana (Jones)

Plate 23, figs. 17, 18

Beyrichia wilckensiana Jones 1855, p. 89, pl. 5, figs. 17, 18; Jones *in* Honeyman 1870, p. 492; Jones 1881, p. 313; (authors).
Kloedenia wilckensiana (Jones); Jones and Holl 1886, p. 347; (authors).
Kloedenia sp. McLearn 1924, p. 20.
Beyrichia spp. (part) Honeyman 1864, p. 344; Jones 1881, p. 344; Jones 1881, p. 313.

Kesling (*in* Kesling and Wagner 1956, pp. 61 ff.) is the latest author to discuss fully the relationships of this species. His work has shown the existence of ontogenetic variation and has more clearly defined the characteristics of sexual dimorphism within the species. Most of these characteristics demonstrated in Kesling's work have been observed in the Arisaig specimens. The ontogenetic variation is shown by the relative decrease in size of L2, the forward shift of S2, and the narrowing of the marginal area in progressive instars. Sexual dimorphism is manifest in the 'convexity of the ventral lobe, the number and spacing of crests on the ventral lobe, the prominence of L2, and the presence of a low, humplike ridge behind S2' (Kesling, ibid., p. 64).

Numerous specimens of several instars have been observed during preparation of this material. No attempt has been made to graphically portray the instar variation due to the difficulty of preparation of perfect valves for measurement.

Remarks. Specimens of this species are well preserved in the Stonehouse strata. They occur as single valves of a brown-black colour, mostly in grey coquinal limestones, few specimens being observed in the red sandy limestone strata.

APARCHITES Jones

Type species *A. whiteavesi* Jones 1889

Aparchites sinuatus (Hall)

Plate 23, figs. 19, 20

Leperditia sinuata Hall 1860, p. 158; Dawson 1860, p. 67; Honeyman 1864, p. 344; Dawson 1868, p. 609; Dawson 1878, p. 609; Jones 1881, p. 344; Jones 1881, p. 313; Jones 1890, p. 24, pl. 1, figs. 12*a–c*; McLearn 1924, p. 20; Bassler and Kellett 1934, pp. 67, 400.

Aparchites sinuatus (Hall); Bassler and Kellett 1934, p. 161.

Primitia ovata Jones and Holl 1865, p. 423, pl. 13, figs. 13*a, b, c*; Jones 1881, p. 344; Jones 1881, p. 314; Jones 1890, p. 552; Jones 1891, p. 72; Ami 1893, p. 191; (authors).

Aparchites ovatus (Jones and Holl); Jones 1889, p. 384; (authors).

Revised description. Valves ovate in lateral view, hinge line short, surface punctate. Anterior and posterior ends of the valves thickened, slightly reflexed, flattened, mid area of valves convex, supporting a dorsal ridge parallel to the hinge and elevated above it.

Remarks. This is the most common species observed in the Stonehouse material. The original description mentions the presence of a small tubercle near the anterior end and the sinuous nature of the posterior ventral margin. As is typical of the genus, no tubercle is present on any of the specimens examined. The posteroventral sinuosity is believed to indicate the slight flexure of the valve surface where it contacts the ventral margin rather than a distinct indentation as mentioned by Hall (p. 158).

EXPLANATION OF PLATE 23

Fig. 1. *Primitia mundula* (Jones), lateral view; ×17; hypotype, G.S.C. No. 14497.

Figs. 2–9. *Beyrichia* (*Nodibeyrichia*) *pustulosa* Hall. 2, male right valve; ×9; hypotype, G.S.C. No. 14498. 3, male right valve; ×9; hypotype, G.S.C. No. 14499. 4, male left valve; ×9; hypotype, G.S.C. No. 14500. 5, male left valve; ×9; hypotype, G.S.C. No. 14501. 6, male left valve; ×9; hypotype, G.S.C. No. 14502. 7, female right valve; ×9; hypotype, G.S.C. No. 14503. 8, male left valve; ×9; hypotype, G.S.C. No. 14504. 9*a*, *b*, ventral and dorsal views of male specimen; ×9; hypotype, G.S.C. No. 14504.

Figs. 10, 11. *Cytherellina siliqua* (Jones), lateral views of two specimens; ×17; hypotypes, G.S.C. Nos. 14505–6.

Figs. 12, 13. *Beyrichia* (*Neobeyrichia*) *maccoyiana* Jones. 12, part of male right valve; ×17; hypotype, G.S.C. No. 14508. 13, part of male left valve; ×17; hypotype, G.S.C. No. 14509.

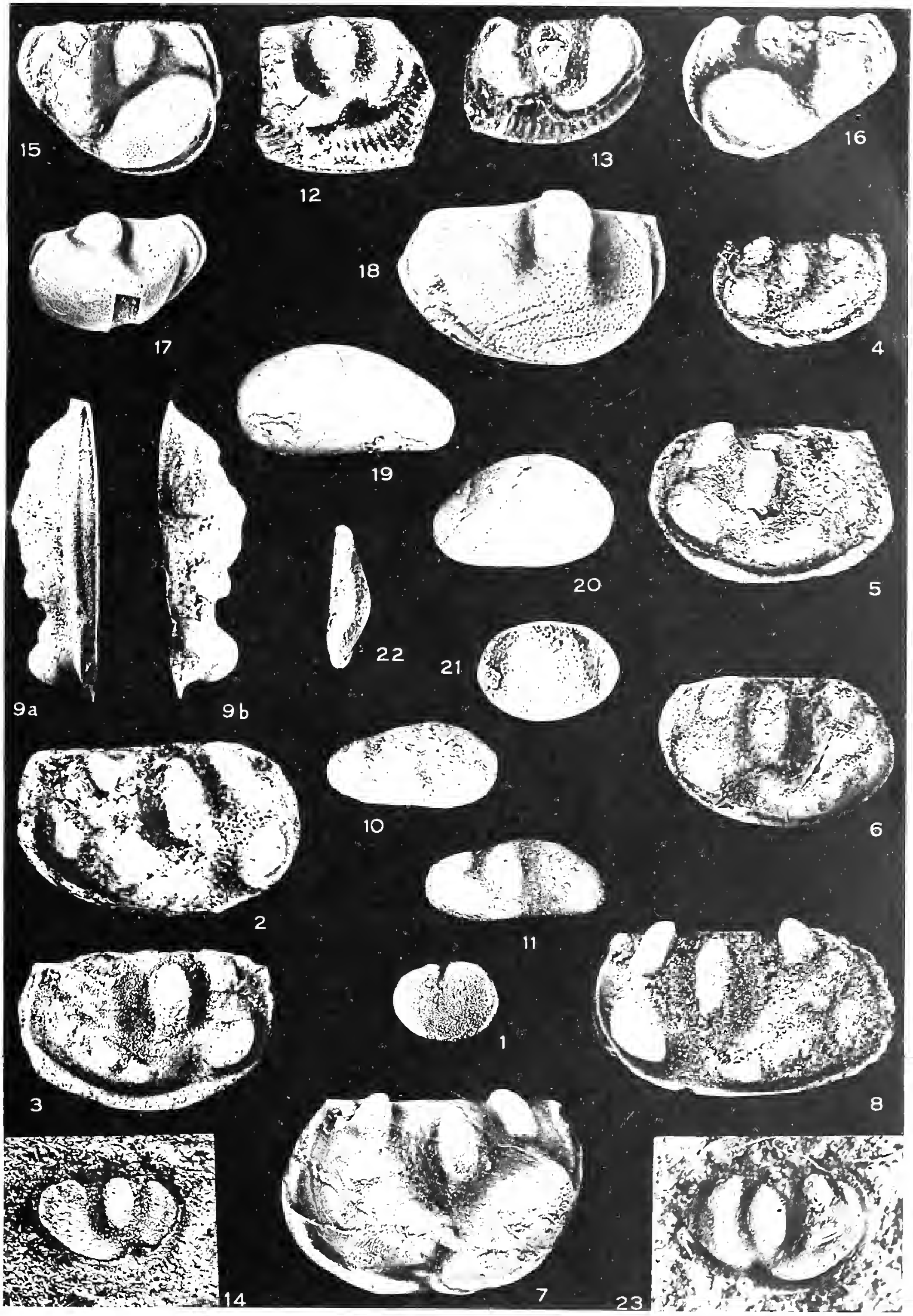
Figs. 14–16. *Beyrichia* (*Neobeyrichia*) *maccoyiana* Jones var. *sulcata* Reuter. 14, male right valve; ×17; hypotype G.S.C. No. 14510. 15, female right valve; ×17; hypotype G.S.C. No. 14511. 16, female left valve; ×17; hypotype G.S.C. No. 14512.

Figs. 17, 18. *Kloedenia wilckensiana* (Jones). 17, lateral view of female left valve; ×9; hypotype, G.S.C. No. 14513. 18, lateral view of male right valve; ×17; hypotype, G.S.C. No. 14514.

Figs. 19, 20. *Aparchites sinuatus* Hall, lateral and dorsal views; ×17; hypotype, G.S.C. No. 14515.

Figs. 21, 22. *Bythocypris phillipsiana* (Jones and Holl), lateral views of two specimens; ×17; hypotypes, G.S.C. Nos. 14516, 14517.

Fig. 23. *Beyrichia kochii* Boll, lateral view of male left valve; ×17; hypotype, G.S.C. No. 14507.



COPELAND, Upper Silurian Ostracods

BYTHOCYPRIS Brady

Type species *Bairdia bosquetiana* Brady 1866 = *Bythocypris reniformis* Brady 1880

Bythocypris phillipsiana (Jones and Holl)

Plate 23, figs. 21, 22

Primitia concinna Jones and Holl 1865, p. 424; Jones *in* Honeyman 1870, p. 492; Jones 1881, p. 313.
?Leperditia minuta (Eichwald); Jones and Holl 1865, p. 424.
Bairdia phillipsiana Jones and Holl 1869, p. 213, pl. 14, figs. 7*a–c*.
?Leperditia sinuata Hall; Jones 1870, p. 492.
Bythocypris phillipsiana (Jones and Holl); Jones and Kirkby 1886, p. 250; Krause 1891, p. 510, pl. 33, figs. 4*a–c*; (authors).

Specimens of this species are common in the Arisaig strata. They are preserved as individual valves showing only the external surface, no hinge structures or muscle scars being visible. They agree with the original description by Jones and Holl.

PRIMITIA Jones and Holl

Type species *see* Warthin 1948, pp. 645–6

Primitia mundula (Jones)

Plate 23, fig. 1

Primitia mundula (Jones); Jones *in* Honeyman 1870, p. 492; Jones 1890, p. 552; Jones 1891, p. 72; Ami 1893, p. 191; (authors).

The revised description of this species by Jones and Holl 1865 (pp. 419–20) agrees very closely with the specimen figured here. The species was emended by Swartz (1936, *J. Paleont.* **10**, p. 565), type figures published at that time differing slightly from the original description. It is not known whether the dorsal angles are present on the specimen figured in this report, because their positions are obscured.

CYTHERELLINA Jones

Type species *Beyrichia siliqua* Jones 1855

Cytherellina siliqua (Jones)

Plate 23, figs. 10, 11

Beyrichia siliqua Jones 1855, p. 90, pl. 5, fig. 22; (authors).
Cytherellina siliqua (Jones); Jones and Holl 1869, p. 216, pl. 14, figs. 2, 5, 6; (authors).
Bythocypris siliqua (Jones); Bassler and Kellett 1934, p. 233.

Specimens similar to those figured here have been reported from northern Europe and Great Britain. Exfoliated specimens are trilobate, the lobes apparently increasing in size anteriorly. According to Jones (1869, pp. 215–16) no external evidence is visible of the internal lobes. This cannot be substantiated since, as yet, no perfect specimens have been obtained from Arisaig.

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NON-MARINE LAMELLIBRANCH ASSEMBLAGES FROM THE COAL MEASURES (UPPER CARBONIFEROUS) OF PEMBROKESHIRE WEST WALES

by T. B. H. JENKINS

ABSTRACT. Assemblages of non-marine lamellibranchs are described from twelve horizons in the Ammanian and four in the Morganian strata of the Pembrokeshire coalfield. In the case of the Ammanian assemblages it is usually possible to indicate the approximate correlative fauna in one or more of the major British coalfields.

INTRODUCTION

THE first records of non-marine lamellibranchs from this part of the South Wales coalfield are contained in two Memoirs of the Geological Survey and refer to the more conspicuous faunal horizons which are low in the Coal Measure succession (Strahan *et al.* 1914, pp. 161, 179; Cantrill *et al.* 1916, p. 116). Davies and Trueman (1923) related these occurrences to similar ones in the Gwendraeth and Amman Valleys of the main coalfield. Further details of the lamellibranch succession in east Pembrokeshire were given by George and Trueman (1925). The fauna from the roof of the Lower Level Vein, at Bonville's Court Colliery, Saundersfoot, received biometric attention from Davies and Trueman (1927). The zonal scheme of these authors was applied by Dixon (1933) to the eastern, or Saundersfoot, district, and subsequently Trueman (1934) diagnosed the presence along the St. Bride's Bay coast in the west of Pembrokeshire of strata belonging to the Modiolaris, Phillipsii, and Tenuis Zones.

Dix (1933; 1934) revised the palaeobotany, previously investigated by Goode (1913) and Kidston (*in* Strahan *et al.* 1914; Cantrill *et al.* 1916), and established the presence in Pembrokeshire of her floral zones C, D, and G. Dix (1942) referred the Monkstone Grit to the Lenisulcata Zone but unfortunately much other detailed work was left unpublished.

This paper describes and illustrates some assemblages of non-marine lamellibranchs from the Pembrokeshire coalfield. The faunas discussed were selected for their palaeontological interest and stratigraphical significance and most are here newly recorded. Correlations of the Pembrokeshire Coal Measures (fig. 1), to be discussed in a later paper, rest in large part on comparisons of the composition and distribution of these non-marine faunas among others.

Measurements of shells were made in the manner introduced by Davies and Trueman (1927) and the tabulation of dimensional data follows the pattern used by Eagar. In many cases, however, the preservation does not allow the thickness measurement (T) to be made and sometimes, as with the *Anthraconauta* faunas, the indefinite nature of the umbo makes inadvisable the measurement of the anterior end (A). The limitations of imperfect preservation and subjective orientation are, however, not such as invalidate

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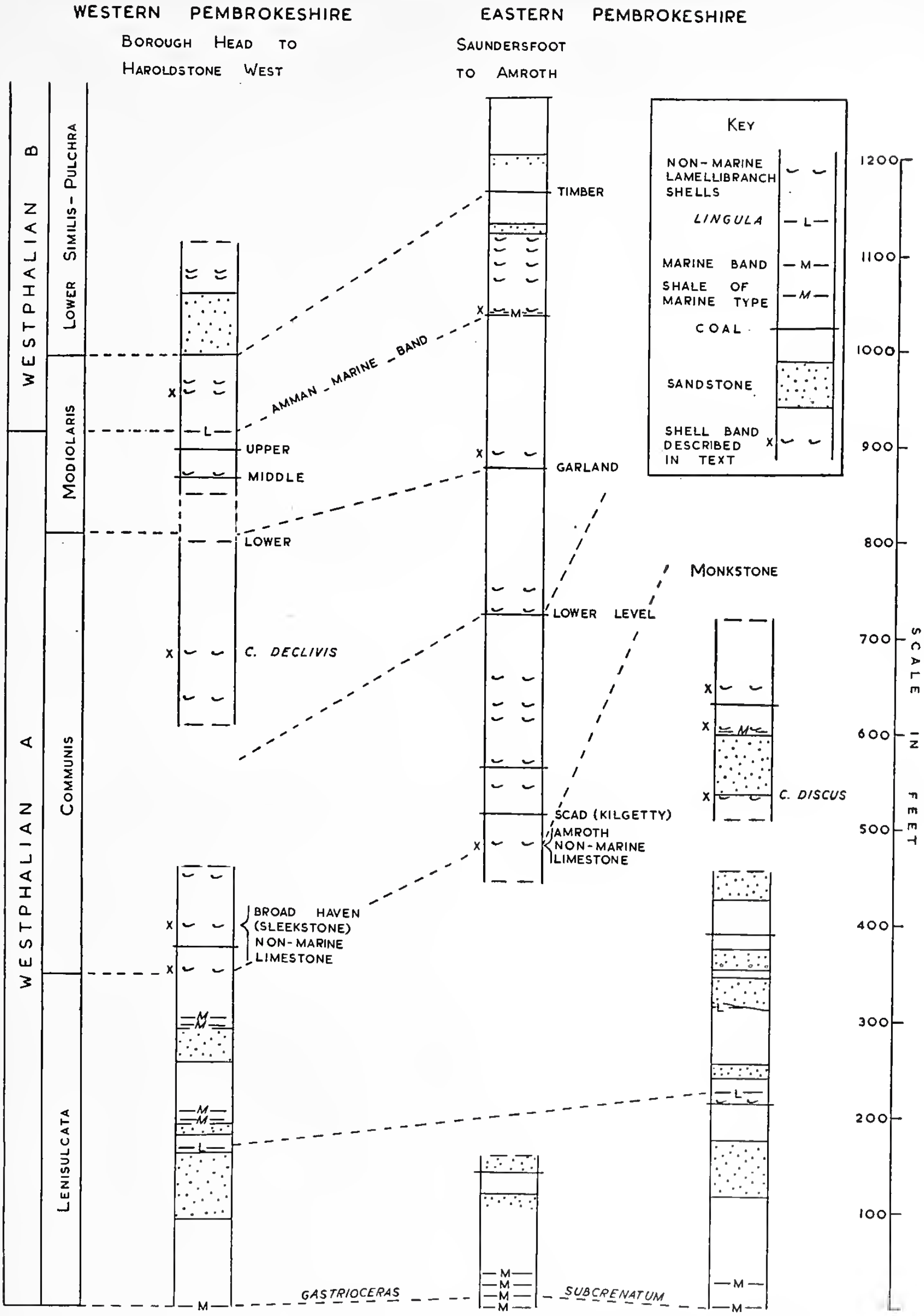

TEXT-FIG. 1. Some natural sections of the Ammanian in Pembrokeshire.

this method of measuring, and certain of the collections are susceptible to more detailed statistical treatment than any here attempted.

The specimens illustrated are in the author's collection at the Department of Geology, University College, Swansea. The figures are natural size.

The authorship of the species mentioned in this paper is as follows: *Anthraconaia bellula* (Bolton), *A. glotae* (Weir and Leitch), *A. lenisulcata* (Trueman), *A. pringlei* (Dix and Trueman), *A. pruvosti* (Chernyshev), *A. pruvosti* (Weir and Leitch *non* Chernyshev), *A. pulchella* Broadhurst, *A. williamsoni* (Brown). *Anthraconauta calcifera* (Hind), *A. minima* (Auctorum), *A. phillipsii* (Williamson), *A. subovata* Dewar, *A. tenuis* (Davies and Trueman), *A. trapeziforma* Dewar. *Anthracosia aquilina* (J. de C. Sowerby), *A. aquilinoides* (Chernyshev), *A. concinna* (Wright), *A. lateralis* (Brown), *A. ovum* Trueman and Weir, *A. phrygiana* (Wright), *A. planitumida* (Trueman), *A. regularis* (Trueman), *A. rectrotracta* (Wright). *Anthracosphaerium affine* (Davies and Trueman), *A. bellum* (Davies and Trueman), *A. turgidum* (Brown). *Carbonicola acuta* (J. Sowerby), *C. bipennis* (Brown), *C. browni* Trueman and Weir, *C. cristagalli* Wright, *C. communis* Davies and Trueman, *C. declivis* Trueman and Weir, *C. discus* Eagar, *C. embletoni* (Brown), *C. fallax* Wright, *C. limax* Wright, *C. martini* Trueman and Weir, *C. obliqua* Wright, *C. obliquissima* Trueman and Weir, *C. oslancis* Wright, *C. pilleolum* Eagar, *C. protea* Wright, *C. pseudorobusta* Trueman, *C. pyramidata* (Brown), *C. rhomboidalis* Hind, *C. similis* (Brown), *C. subconstricta* Wright (*non* J. Sowerby), *C. venusta* Davies and Trueman. *Naiadites carinatus* (J. de C. Sowerby), *N. flexuosus* Dix and Trueman, *N. modiolaris* (J. de C. Sowerby), *N. productus* (Brown) *N. quadratus* (J. de C. Sowerby), *N. triangularis* (J. de C. Sowerby). Where ambiguity exists the authorship is indicated in the text.

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LENISULCATA ZONE

Nine horizons yield non-marine lamellibranchs between Saundersfoot and the Trevane anticline just south of Monkstone and it is likely that they all fall within this zone.

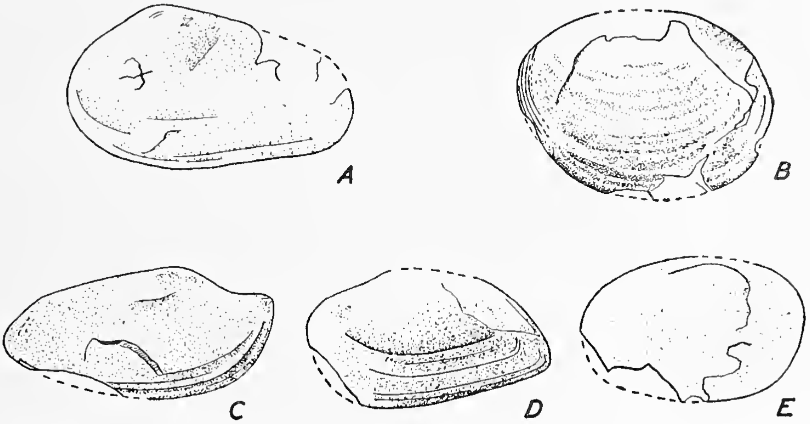
(*a*) *Band with* Carbonicola discus *Eagar* (fig. 2). Crushed shell impressions occur in the uppermost 3 feet of fine, dark platy shale outcropping 200 yards south of Swallowtree stream in the section north of Monkstone Point. The collection of twenty shells consists mainly of posteriorly tapered examples of *Carbonicola* (fig. 2A, C, D) some being referable to *C.* cf. *protea* (fig. 2D), *C.* cf. *obliqua* (fig. 2C), *C.* cf. *browni*, and *C.* cf. *pseudorobusta*. A minority of the shells are orbicular and include *C. discus* sensu stricto (fig. 2B), and *C.* aff. *discus* (fig. 2E). Variation within the sample may be discontinuous but it is impossible to demonstrate this with the small collection available. Dimensions for the *Carbonicola* assemblage are given below. One large specimen of *Naiadites* cf. *flexuosus* was found.

Length (L) *in mm.*	*Height* (H) / *Length* (L)	*Anterior end* (A) / *Length* (L)
Range 28·5–39·6	47·2–75·6[1]	26–43
Mean 33·0 (12)	65·7 (11)	32·5 (10)

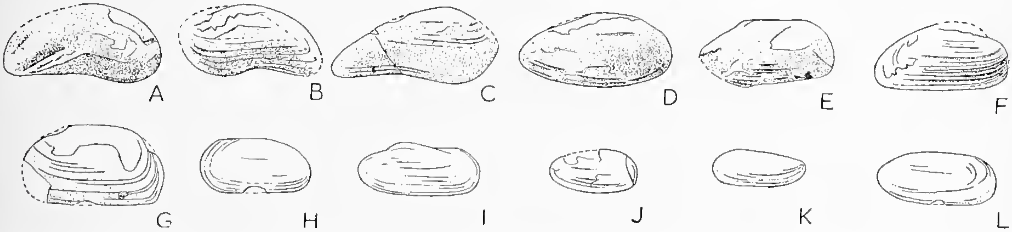
[1] Omitting one shell with H/L ratio of 91 per cent.

The figures in brackets in this and similar subsequent tables refer to the number of shells measured.

These specimens are comparable with shells described by Eagar (1947) from 16 ft. 3 in. to 18 ft. 9 in. above the Soft Bed Coal at Honley, near Huddersfield, and reported by him to occur very widely in the Pennine region at a constant horizon within the middle division of the strata between that coal and the Middle Band Coal (Eagar 1951; 1952, pp. 25–29, 51). At localities between Honley and Halifax successive assemblages in this Soft Bed–Middle Band sequence are respectively characterized by the presence of *C.* cf. *pseudorobusta* and similar forms and by the brief acme of the distinctive *C. discus* fauna. Unfortunately the sparseness of the Swallowtree collection and other factors prevent a comparison of the dimensions of the Pembrokeshire and Yorkshire assemblages. It appears, however, that the known range of variation of the *C. discus* fauna in the Pennine province is comparable with that shown by the Pembrokeshire members of this short-lived species (Eagar 1952, table 8).



TEXT-FIG. 2. Shells from a band with *Carbonicola discus* Eagar, ×1. Lenisulcata Zone, cliffs 200 yards south of Swallowtree Stream, near Saundersfoot. Author's Coll.; *a* A, M2/9; B, M2/10; C, M2/3; D, M2/13; E, M2/18b.



TEXT-FIG. 3. Shells from the Lenisulcata Zone, ×1. A–E, about 116 feet above the band with *Carbonicola discus* Eagar, cliffs between Swallowtree Stream and Monkstone Point, south of Saundersfoot. Author's Coll.; A, M31/1a; B, M32/12; C, M32/6; D, M40/8; E, M40S/1. F–L, from about 65 feet above the band with *C. discus*. Locality as above. F, M42/18; G, M42/33a; H, M42/2; I, M42/15; J, M42/37e; K, M42/37b; L, M42/1.

(*b*) *Shells from about 65 feet above the band with* C. discus (fig. 3F–L). In the Monkstone–Swallowtree section the top of the shale carrying the fauna with *C. discus* is eroded at the base of a partly cross-bedded sandstone approximately 65 feet thick which is capped by 3 ft. 4 in. of dark fine shale. The base of this shale is of marine type and yielded *Planolites*; at 6 to 12 inches above the base lamellibranch impressions occur fairly abundantly and persist less frequently through the upper part of the band.

The lamellibranchs are all small and 68 per cent. are expanded (dorso-ventrally) posterior to the umbo. Such anthraconaioid shells (fig. 3H–L) are elongate or only moderate in relative height and about half have a postero-ventral angulation; this character is more prevalent in the larger specimens (e.g. fig. 3M, the umbonal region of which is probably distorted); in the smaller anthraconaioids (e.g. fig. 3I, K) the angulation is completely suppressed. *C.* aff. *pilleolum* (F), *C.* cf. *protea* (small form) (G), *C.* aff. *fallax*, *C.* cf. *limax* and an elongate–oval form are represented among the minority of shells lacking anthraconaioid character. Dimensions appear in Table 3.

One specimen is referred to *Naiadites*?

(*c*) *Shells from about 116 feet above the band with* C. discus (fig. 3A–E). At this horizon in the cliffs just north of Monkstone small crushed shells (fig. 3A–E) were found, sparsely preserved in hard, grey silty mudstone.

C. cf. *fallax* (fig. 3E) and *C.* cf. *protea* occur together with several shells characterized by recurved ventral margins, some of which may be referred to *C.* cf. *pilleolum* (fig. 3A, B). No anthraconaioid shells were found.

	L in mm.	*H/L %*	*A/L %*
Range .	14·1–20·7	45·0–55·6	22–33
Mean .	18·7 (8)	51·2 (8)	28 (7)

This assemblage is similar to some of the *fallax–pilleolum* faunas described by Eagar (1947; 1951; 1952) from the Bassy Mine succession of the Pennine coalfields.

(*d*) *Shells from the eastern Cleddau.* In this section fine, dark grey-green shale forms the roof of a 4-inch coaly layer and comprises the lowest of five pene-marine bands; its base contains *Planolites* which persists less frequently into the 9 inches of similar shale bearing impressions of small (L<20 mm.) lamellibranchs. Of fifteen almost complete shells one only is posteriorly tapered, the remainder being posteriorly expanded and, mostly, anthraconaioid; they are determined as *A.?* aff. *bellula*. Dimensions are given in Table 3 which shows the correspondence in H/L per cent. values of anthraconaioid phase faunas in and just below the Lenisulcata Zone in Pembrokeshire and the north of England. The Welsh shells are smaller in absolute size.

TABLE 1

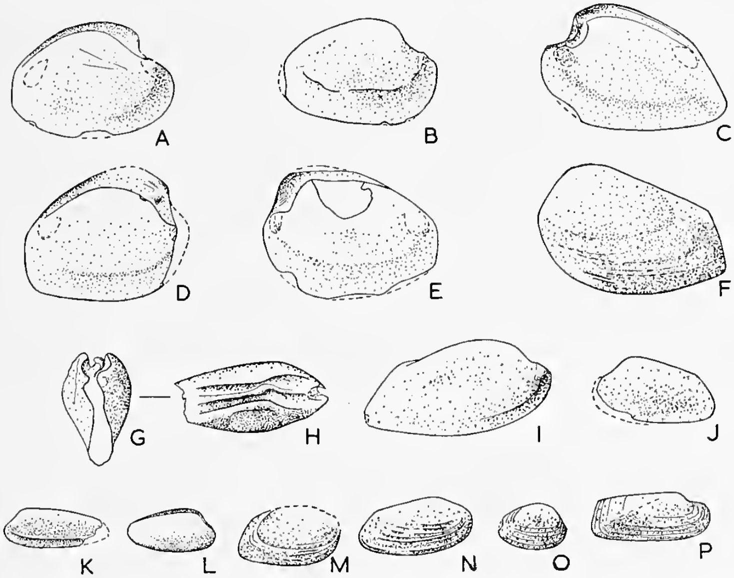
Locality text reference	*Mean length in mm.*	*H/L%*		*Number of shells measured*	*Percentage posteriorly expanded*
		Mean	*Range*		
Monkstone (*b*) . .	17·4	44·5	36·5–65·1	26	68%
Eastern Cleddau (*d*) . .	12·5	44·2	33–51	L 10	93%
Honley, Yorkshire . .	32·1	44·6	37·8–57·2	26	65%
Parbold, Lancashire . .	23·0	42·8	37·3–47·6	15	?66%[1]
Midhopestones, Lancashire .	23·44	40·92	35·3–46·8	71	65%

[1] '. . . *Anthraconaia*-like forms are at least twice as abundant as those referable to *C. limax* and elongate *C.* aff. *fallax*.'

The sources of the data on the north of England faunas are: Honley—shells from 10 ft. 9 in. to 11 ft. 3 in. above the Soft Bed Coal, i.e. base of the Middle Division of Soft Bed Succession (Eagar 1947, table i, p. 21). Parbold—shells from 0 to 3 in. above the base of band marking base of Upper Division of Bassy Mine Succession (Eagar 1951, table iii, p. 32). Midhopestones—shells from just below the *Gastrioceras subcrenatum* marine band (Eagar 1953, p. 173).

COMMUNIS ZONE

At Amroth and Broad Haven the basal beds of this zone contain two almost identical non-marine limestones but their lamellibranch faunas (*a* and *b* below) are dissimilar.

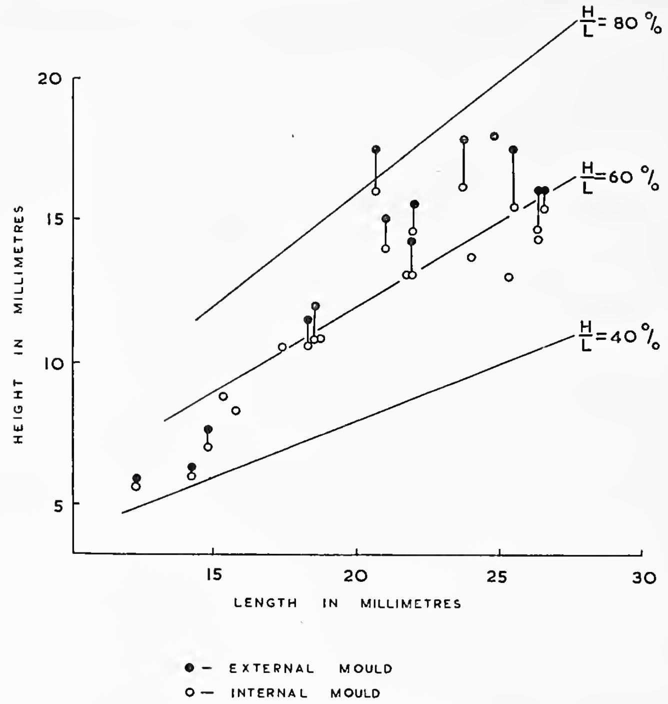


TEXT-FIG. 4. Shells from the basal beds of the Communis Zone, × 1. A–L, Amroth non-marine limestone, 30 feet below Kilgetty (Scad) Vein, cliffs west of Amroth, Pembs. Author's Coll., A, FWL/34b; B, FWL/7b; C, FWL/8; D, FWL/18a; E, FWL/35b; F, FWL/34a; G, H, FWL/40; I, FWL/33; J, FWL/36; K, FWL/18b; L, FWL/22a. M–P, about 47 feet below the non-marine limestone near the Sleek Stone, Broad Haven, Pembs. Author's Coll., M, H2/1a; N, H2/6; O, H2/20; P, H2/10.

The Amroth band is probably represented in St. Bride's Bay by a black, mainly non-calcareous, shale yielding very small shells (*c*). Another assemblage of small *Carbonicola* is described from the upper Communis Zone south of Little Haven.

(*a*) *The Amroth non-marine limestone* (figs. 4A–L; 5). Near Amroth a blue silty limestone, 2½ feet thick, weathering to an ochreous rottenstone, outcrops 30 feet below the Kilgetty (or Scad) Vein. First recorded by Strahan *et al.* (1914, pp. 161–2), it has also been mentioned by Jones (*in* Cantrill *et al.* 1916, p. 117), Trueman and Davies (1923), and by George and Trueman (1925, p. 411) who referred the abundant shells to *C.* cf. *acuta*.

The fauna consist of small shells and exhibits an exceptionally wide range of H/L per cent. values (Table 4). The scatter diagram (fig. 5) shows apparent clustering of (i) the relatively larger shells having high H/L per cent. values, (ii) small shells of low or moderate height; but there are insufficient specimens to prove discontinuity from the measurements of standard parameters. Specimens referable to *C.* aff. *bipennis* (fig. 4J). and *C.* cf. *declivis* (fig. 4K) are included in the (ii) group while *C.* aff. *subconstricta* Wright (*non* J. Sowerby) (fig. 4I), *C.* cf. *obliquissima* (fig. 4F), and *C.* cf. *martini* appear among the larger shells. But the distinguishing character of this fauna derives from the strong representation of shells having H/L ratios over 65 per cent. in external mould measurement and which are referable to cf. *Anthracosia regularis*. Dimensions are as follows:



TEXT-FIG. 5. Height plotted against length of *Carbonicola* shells from the Amroth non-marine limestone.

	External moulds		*Internal moulds*	
	Range	*Mean*	*Range*	*Mean*
L in mm.[1] .	. .	. .	12·3–26·5	20·6 (22)
H/L% . .	44·2–85·3	64·2 (14)	42·0–77·9	58·0 (20)
A/L% . .	9–24	18 (11)	16–39	26 (20)

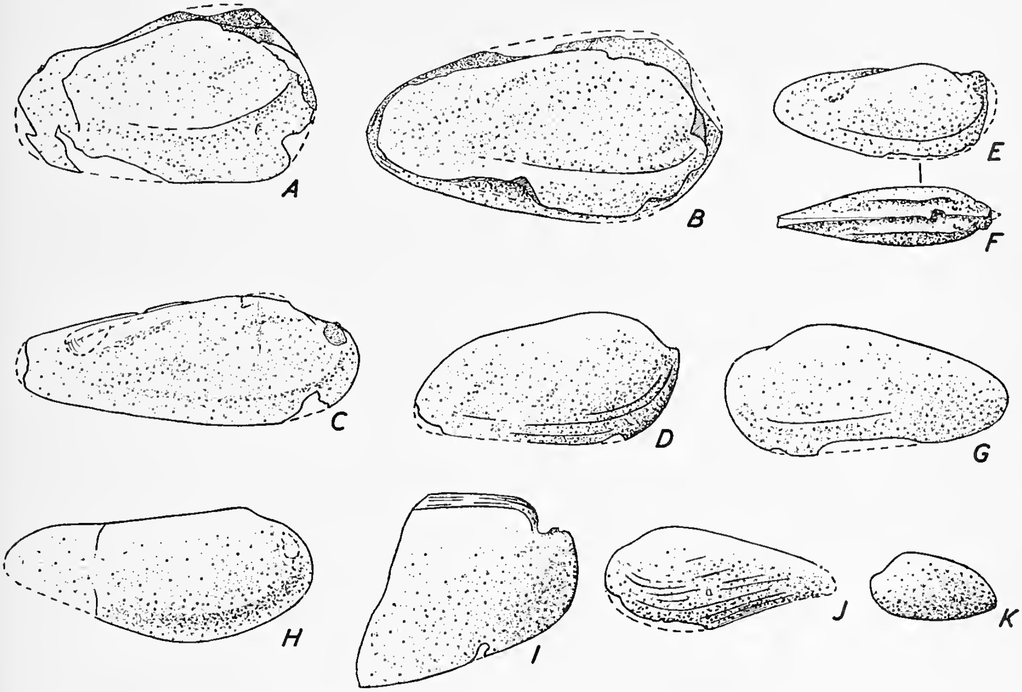
---

[1] Since the shells are marginally very thin at the extremities the internal and external lengths are assumed to be equal and are tabulated under the former heading.

Some of the specimens (fig. 4C, especially) have a deep lunular hollow which suggests that, given restricted umbonal resorption, the early growth-lines were probably inclined appreciably to the mid-ventral commissure.

This fauna resembles in several respects that occurring about 60 feet below the Arley

Mine–Better Bed Coal horizon in the Pennine coalfields (Wright *in* Tonks *et al.* 1931, p. 134; Eagar 1954, p. 56; 1956, pp. 356–60; Calver 1956, p. 32) and is probably an approximate correlative of that band.



TEXT-FIG. 6. Shells from the Broad Haven (or Sleekstone) non-marine limestone, × 1. Communis Zone, just north of the Sleekstone, near Broad Haven. Author's Coll.; A, H3/10; B, H3/14; C, H3/20; D, H3/29; E, F, H3/6; G, H3/13; H, H3/16; I, H3/24a; J, H3/18; K, H3/19.

(*b*) *The Broad Haven* (*or Sleekstone*) *non-marine limestone* (fig. 6). Just north of the Sleekstone fold a non-marine muddy limestone 3 ft. 3 in. thick outcrops at about 20 feet above the lowest worked coal and weathers to a rottenstone from which Jones (*in* Cantrill *et al.* 1916, p. 116) recorded *C. acuta*; Trueman and Davies (1923) have inferred it to be equivalent to the Amroth limestone. The assemblage consists mainly of *Carbonicola* with sparse *Naiadites* and *Anthraconaia*. The possibly homogeneous *Carbonicola* fauna includes a large proportion of *C. browni* (fig. 6C, E–H) and *C.* aff. *bipennis* (K), *C. pseudorobusta* (cf. A), *C.* aff. *cristagalli*, *C.* aff. *rhomboidalis*, and *C.* cf. *martini*. Elongate, posteriorly tapered forms like *C. browni* comprise more than 40 per cent. of the collection; shells with higher H/L ratios, comparable with *C. pseudorobusta* and *C. rhomboidalis*, comprise a further 40 per cent. The latter group is not unexpected here but the occurrence of completely typical *C. browni* extends its known range downwards to a low horizon in the Communis Zone and the abundance of this species renders doubtful the statement that 'the species probably never formed the majority in any assemblage' (Trueman and Weir 1946, p. 12).

Anthraconaia is represented by a part of a large internal mould (fig. 6I) showing an edentulous, striated, posteriorly widening, straight hinge-plate. *N.* cf. *flexuosus* also occurs.

TABLE 2

	External moulds		*Internal moulds*	
	Range	*Mean*	*Range*	*Mean*
L in mm.[1] .	. .	. .	9·8–56·9	31·4 (21)
H/L% . .	39·4–61·4	50·1 (9)	36·0–62·0	49·1 (18)
T/L% . .	. .	16·1 (1)	16·7–40·7	27·8 (10)
A/L% . .	13·4–28·9	20·2 (5)	11·2–31·4	24·1 (17)

[1] See table of dimensions on p. 106.

External and internal measurements. A quantitative statement of the systematically important differences between internal and external measurements of specimens from the limestones appears as Table 3.

TABLE 3

	Differences of means in Tables 1 and 2		*Means of simultaneous differences*[1]	
	Amroth	*Broad Haven*	*Amroth*	*Broad Haven*
H/L% (E–I)	6·2	1·0	4·9 (13)	3·8 (5)
A/L% (I–E) .	8·0	3·9	7·8 (10)	7·5 (2)

[1] 'Simultaneous difference' is that obtained from a specimen which allows the measuring of both internal and external characters: effectively a direct measurement of peri-umbonal relative thickness of shell matter in H and L directions. Figures in brackets refer to the number of such specimens measured. H/L per cent. (E–I) values give excess of external over internal ratios; A/L per cent. (I–E) conversely.

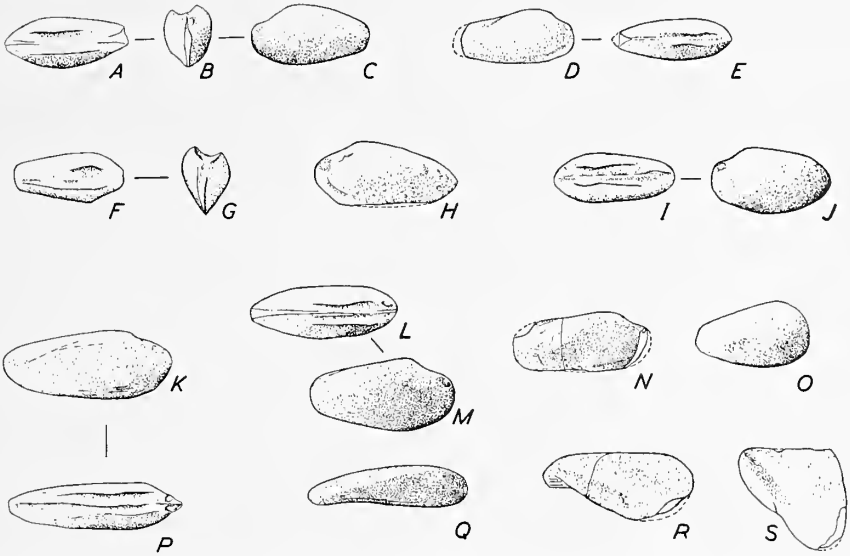
The frequent shells with high H/L ratio having damaged umbones in the Broad Haven limestone cannot be externally measured with any precision and the mean value for external relative height in Table 2 is thus almost certainly too low. Consequently the value of 1 per cent. in Table 3 is probably also much too low and the corresponding means of simultaneous differences may well be nearer the true average for the assemblage. The four comparisons of peri-umbonal shell-thickness shown in Table 3 indicate that the Amroth specimens have relatively stouter shells.

(*c*) *Shells from about 47 feet below the non-marine limestone near the Sleekstone, Broad Haven* (fig. 4M–P). Small shells occur as impressions in dark-grey shale and sandy shale at this horizon. *Anthraconauta* and *Carbonicola* are moderately abundant and there is one specimen of *Anthraconaia* among a total of twenty-five shells.

Carbonicola (fig. 4M–O) exhibits wide variation but the specimens are invariably small or very small, eleven measurable specimens giving the following dimensions:

L in mm.		*H/L%*		*A/L%*	
Mean	*Range*	*Mean*	*Range*	*Mean*	*Range*
14·9	9·4–19·5	52·7	41·9–70·4	27	20–30·4

Elongate, obliquely truncate forms (e.g. fig. 4N) and higher almost orbicular forms (e.g. fig. 4O) occur. There are no closely comparable named species of *Carbonicola* of this diminutive size. It should be noted, however, that the Amroth limestone fauna shows certain resemblances, e.g. in the presence of small high shells and the frequency of oblique posterior truncation. Also, individual specimens can be matched fairly closely: compare I with N, and O with D in fig. 4.



TEXT-FIG. 7. Shells from 116 feet below the Lower (Coal) Vein of Little Haven. Communis Zone, ×1. Author's Coll.; A, B, C, H51/40; D, E, H51/15; F, G, H51/17; H, H51/33; I, J, H51/27; K, P, H51/13; L, M, H51/8; N, H51/41; O, H51/6; Q, H51/1; R, H51/43; S, H51/44.

Badly preserved *Anthraconauta* of the *subovata* group generally lie on bedding planes different from those on which *Carbonicola* are found. *A. subovata*, *A. trapeziforma*, and a form similar to that figured by Dewar (1939, pl. 4, fig. 2A) occur.

The specimen referred to *Anthraconaia* (fig. 4P) appears to be of a new species which Mr. D. G. Jones has also found at about 10 feet below the Cnapiog (or Garw) Coal of Glynneath, Glamorgan. Eagar (1956, fig. 9*k*) has figured a shell from about the same horizon which may well be of the same group.

(*d*) *Shells from 116 feet below the Lower (Coal) Vein of Little Haven* (fig. 7). The specimens, ironstone internal moulds, are enclosed in grey shale which carries much other ironstone. *Carbonicola* is strongly represented by an assemblage of small shells (fig. 7A–Q), mainly elongate and invariably posteriorly tapered, which includes *C. declivis* s.s. (fig. 7K–P, N) in association with *C.* aff. *declivis* (fig. 7D–E, H) and a number of relatively high (H/L>55%) forms (e.g. fig. 7J, *C. martini* juv.?). Umbonal moulds are mainly of a single kind—diminutive, gaping *C. communis*-type (fig. 7B, G). The assemblage is probably homogeneous and the specimen figured at 7Q may be an aberrant variant.

Trueman and Ware (1932) recorded somewhat similar material from the alleged Millstone Grit of Clyne Common, Gower. Dimensions of the present collection are:

	L in mm.	*H/L%*	*T/L%*	*A/L%*
Range	12·3–23·2	34·1–56·7	25·9–47·3	18–41
Mean	16·8	46·3	33·9	28·9
Number of shells measured . . .	15	15	14	15

Naiadites (fig. 7R, S) are variable in outline and are provisionally referred to *N.* cf. *flexuosus.*

MODIOLARIS ZONE

(*a*) *The basal band* (fig. 8A–K). Shells are found abundantly in the roof shales of the Garland Vein at Lloyd's Patch, near Wiseman's Bridge, and identical specimens are found about 18 feet below the base of the thick sandstone near Hean Castle, east Pembrokeshire; very similar shells occur near the south wall of The Settlings (near Little Haven) in St. Bride's Bay. The specimens are preserved as partially crushed impressions in dark, fissile shale. *Carbonicola* predominates and is associated with *Anthraconaia* cf. *williamsoni* and *Naiadites spp. Carbonicola* cf. *pyramidata* and *C.* cf. *rhomboidalis* occur but most of the *Carbonicola* are small (L<20 mm.): in characters other than size, however, many resemble *C. oslancis* s.l.

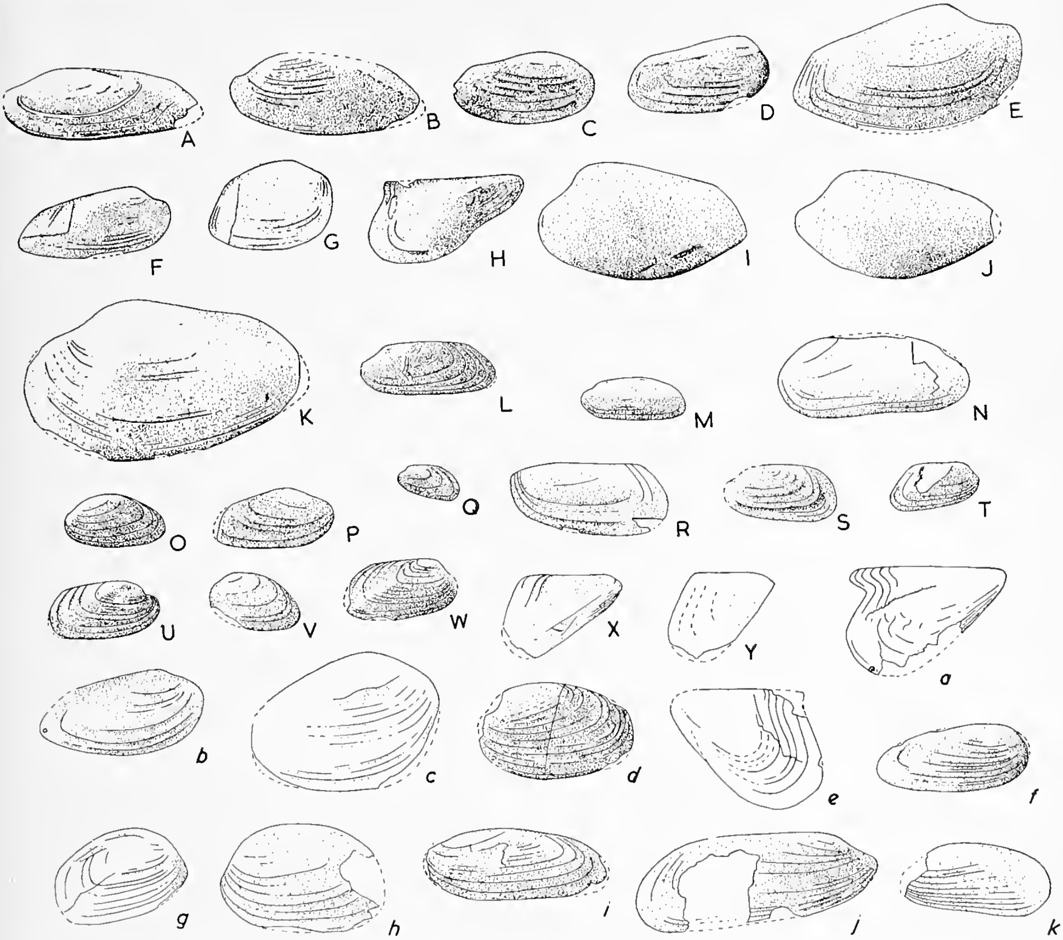
Dimensions of *Carbonicola:*

		Number of shells	*Mean*	*Maximum*	*Minimum*
Lloyd's Patch, near Wiseman's Bridge, east Pembs.	L in mm. .	59	16·1	30·2	7·1
	H/L% . .	49	49·3	73·0	30·8
	A/L% . .	48	24·1	34·8	8·5
The Settlings, Little Haven, west Pembs.	L in mm. .	10	14·3	20·0	10·4
	H/L% . .	9	44·8	51·1	35·7
	A/L% . .	7	20·2	26·4	16·7

Most of the small forms of *Carbonicola* are of moderate relative height. Evenly convex ventral margins, high rounded anterior lobes, inconspicuous umbones, and obliquely truncate posterior ends are common features. A small proportion of the shells are referable to *C. oslancis* s.s. (fig. 8E) and most of the others are comparable with this form. More elongate shells (fig. 8A, B, F) are numerous. *C. similis* (fig. 8G) and *C. embletoni* are rare. *C.* aff. *venusta* occurs *inter alia* in uncrushed internal ironstone moulds (fig. 8I, J, K) from shale closely associated with that yielding the *C. oslancis* fauna at Lloyd's Patch.

Anthraconaia cf. *williamsoni* is represented by two imcomplete specimens. *Naiadites* occurs fairly frequently and *N.* cf. *modiolaris* (fig. 8H), *N.* cf. *productus,* and *N.* cf. *flexuosus* are present.

In the main basin of the South Wales coalfield the fauna most closely resembling this *C. oslancis* fauna is that from the roof of the Stinking Vein of the Gwendraeth Valley (Dix 1928, pp. 460–2). There seems little doubt that the fauna here recorded is a stunted equivalent of that described by W. B. Wright (1931) from the roof of the Trencherbone in Lancashire.



TEXT-FIG. 8. Shells from the Modiolaris Zone, × 1. A–K, the basal band, roof shales of the Garland Vein at Lloyd's Patch, near Wiseman's Bridge. Author's Coll.; A, M9/20a; B, M20/2; C, M20/5; D, M20/6; E, M20/15; F, M20/37a; G, M20/39; H, M20/1a; I, M7/27; J, M7/31; K, M7/13. L–Y, the mussel-band immediately overlying the Amman Marine Band at Lloyd's Patch, near Wiseman's Bridge. L, M12/35; M, M21/11; N, M12/28; O, M21/21c; P, M12/32; Q, M21/13; R, M21/21d; S, M12/16; T, M21/21b; U, M12/24; V, M21/10; W, M21/6; X, M12/18; Y, M21/17. *a–k*, from 42 feet above the Amman Marine Band, Falling Cliff, near Little Haven. *a*, H25/42b; *b*, H25/1a; *c*, H25/24f; *d*, H25/42a; *e*, H25/1e; *f*, H25/35; *g*, H25/33b; *h*, H25/44f; *i*, H25/8; *j*, H25/23a; *k*, H25/33a.

(*b*) *The mussel-band immediately overlying the Amman Marine Band* (fig. 8L–Y). Dark-grey fissile shale directly overlying the Amman Marine Band yields non-marine lamellibranchs abundantly at Lloyd's Patch, near Wiseman's Bridge in east Pembrokeshire, but the equivalent stratum near Little Haven, on St. Bride's Bay, is only very sparsely fossiliferous. At the former locality the mussel-band is 21 inches thick and yielded over a hundred impressions. *Anthracosia* predominates and is accompanied by *Naiadites spp.* and *Belinurus sp.* Of the shells referred here to *Anthracosia* about 90 per cent. are posteriorly expanded and all are of small size. No hinge characters are preserved and the generic assignment is based on the observed grading of anthraconaiiform shells with undoubted specimens of *Anthracosia.*

Anthracosia cf. *aquilinoides* (fig. 8M, N), *A.* aff. *ovum* (fig. 8O), and *A.* sp. nov. cf. *aquilinoides* (fig. 8L) are frequently represented. The assemblage gives the following values:

	L in mm.	*H/L%*	*A/L%*	*V/H%*
Upper limit . . .	24·5	65·4	32	97·0
Lower limit . .	5·5	40·1	15	63·2
Mean	14·0	50·1	22·4	82·0
Number of observations	70	64	50	45

V of the right-hand column is the measurement of subumbonal depth (v of Leitch 1940).

Most of the shells are oblique and some are closely comparable with the indicated species except in size. A frequent character is a flatly curved ventral margin and in some specimens this is straight or even slightly recurved (fig. 8N). Many shells exhibit greater posterior expansion than is seen in the type of *A. aquilinoides* and this expansion is occasionally accompanied by an accentuation of the posterior superior angulation, to give an anthraconaioid outline (compare fig. 8N, M, L). Such forms appear to intergrade with the rest of the assemblage and are referred to *Anthracosia* sp. nov. cf. *aquilinoides*, following Trueman and Weir (1951, p. 129). The minority of shells lacking posterior expansion include forms referable to *A.* cf. *retrotracta* and *A.* cf. *concinna.*

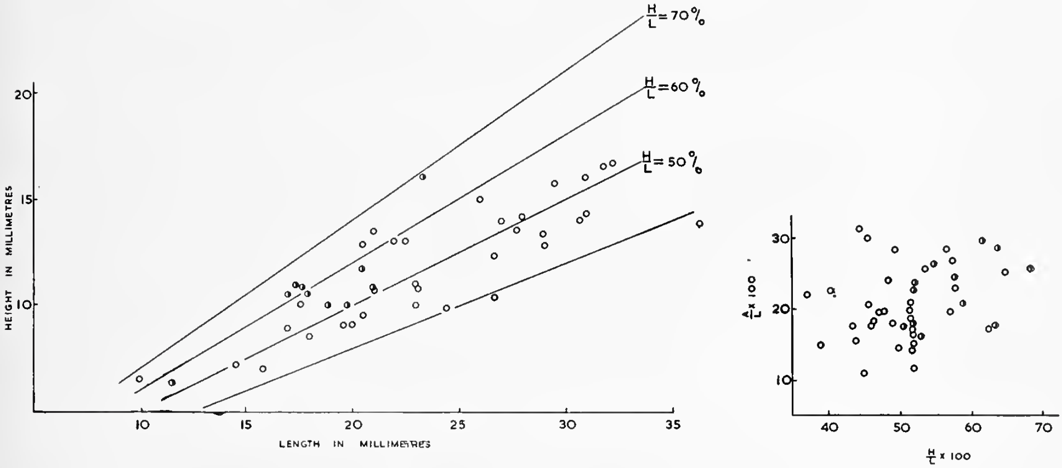
This occurrence of a fauna dominated by small, posteriorly expanded non-marine lamellibranchs (belonging, presumably, to a genus which normally shows no such expansion) in a band which directly overlies a marine stratum recalls the similar phases bearing anthraconaioid faunas in the Lenisulcata Zone and lower. The resemblance doubtless stems from adaptation to similar environments.

Naiadites is characterized by an absence of a distinct 'wing' and forms referable to *N.* cf. *triangularis* (fig. 8Y) and *N.* cf. *modiolaris* occur.

(*c*) *The mussel-band 42 feet above the Amman Marine Band at Falling Cliff near Little Haven* (figs. 8*a–k*, 9A, B). This locality and horizon yielded about eighty specimens, more or less completely crushed in dark fissile shale overlying a thin coal. *Anthracosia* is the dominant genus; *Naiadites* and probably *Anthracosphaerium* also occur; the imperfect preservation sometimes makes it difficult to assign with confidence certain specimens to either *Anthracosphaerium* or to the species of *Anthracosia* having relatively great height. The following table of dimensions, therefore, refers to the entire Anthracosiidae assemblage; the scatter diagrams (fig. 9A, B) illustrate the proportion of generically doubtful shells present and an apparent clustering of such shells is seen from fig. 9A.

L in mm.		*H/L%*		*A/L%*	
Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*
10·0–36·3	23·0 (45)	37·2–68·5	51·9 (45)	11–32	21·0 (43)

Anthracosia exhibits a wide range of variation between representatives of the following species, which are in order of abundance: *A. aquilina*, *A.* aff. *ovum* (fig. 8*d*), *A.* aff. *retrotracta*, *A.* aff. *regularis* (fig. 8*c*), *A. lateralis* (fig. 8*f*), *A.* cf. *phrygiana*, *A.* cf. *planitumida*, *A.* cf. *aquilinoides* (fig. 8*j*), and *A.* cf. *duponti*. Some of the anthracosiids may be cf. *Anthracosphaerium turgidum*, cf. *A. affine*, and cf. *A. bellum*. *Naiadites quadratus*, *N.* cf. *modiolaris*, *N.* cf. *carinatus*, and *N.* cf. *triangularis* (fig. 8*a*, *e*) also occur, but no *Anthraconaia* was seen at this horizon. This assemblage is characterized by the wide variation in the dominant genus *Anthracosia*.



TEXT-FIG. 9. A, Height plotted against length of Anthracosiidae shells from a band 42 feet above the Amman Marine Band, Falling Cliff, near Little Haven. B, relative length of anterior end plotted against relative height. Loc. hor. and symbols as A. The symbol ○ denotes an *Anthracosia* shell; ◑ denotes a specimen which could, on form, be assigned to either *Anthracosphaerium* or *Anthracosia*.

Other mussel-bands in Pembrokeshire near or slightly above the one just described also show wide variation among the many species of *Anthracosia*. *Anthraconaia* is always rare, if present at all, and no homogeneous assemblages of *Anthracosphaerium* are known in Pembrokeshire. *Leaia* occurs at one horizon.

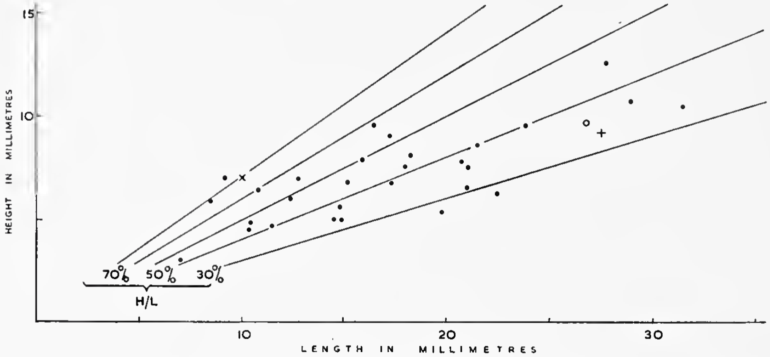
SIMILIS–PULCHRA ZONES

The Upper and Lower Similis–Pulchra Zones are sparsely represented in the collection and only one assemblage merits description.

(*a*) *Band outcropping near Landshipping Quay* (figs. 10, 11). Shell impressions occur in highly disturbed dark shale repeated at 173 and 200 yards south of Landshipping Quay on the eastern bank of the Deugleddyf estuary. *Planolites* occurs nearby in similar sediment but its exact relation to the mussel-band could not be ascertained. The lamellibranchs lie along the bedding-planes and are crushed, usually laterally but some dorsoventrally. *Anthraconaia* is the dominant genus. Badly preserved *Anthraconauta* of the *subovata* group also appears to be present.

Elongate *Anthraconaia* (fig. 10H, J, M, N) referable to *A.* cf. *pruvosti* (Weir and Leitch *non* Chernyshev) are associated with forms of moderate height (fig. 10F, G, L) including *A.* cf. *pulchella* and rather rare small sub-quadrate shells, not illustrated, comparable with *A. glotae.*

TEXT-FIG. 10. Shells from near Landshipping Quay, × 1. Upper? Similis-Pulchra Zone, bed outcropping 173 and 200 yards south of Landshipping Quay. Author's Coll., F, C5/28b; G, C5/19b; H, C5/20; J, C5/19a; K, C5/31a; L, C5/31b; M, C5/30; N, C5/32.



TEXT-FIG. 11. Height plotted against length of *Anthraconaia* shells from near Landshipping Quay. Upper? Similis-Pulchra Zone; 173 and 200 yards south of Landshipping Quay. Symbols show the positions which would be occupied by the holotype of *Anthraconaia glotae* (Weir and Leitch) — ×; by the type of *Anthraconaia pruvosti* (Chernyshev), — o, dimensions of the left valve from Pruvost 1919, pl. 26, fig. 1; and by a specimen illustrated by Weir and Leitch 1936, fig. 15a, — +.

Dimensions of *Anthraconaia* yield the following values:

L in mm.		*H/L%*		*A/L%*	
Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*
7·0–31·5	16·9 (34)	26·8–76·1	44·6 (29)	15–42	28·0 (26)

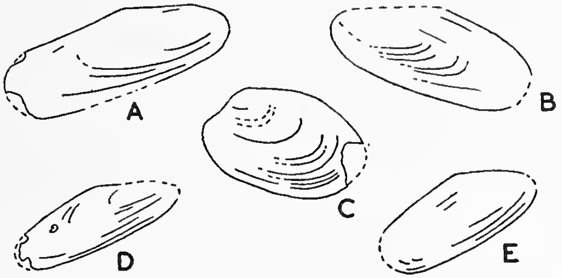
Posterior expansion occurs in only about 17 per cent. of these *Anthraconaia*, sub-parallelism of upper and lower margins being common, especially in the longer specimens. The upper posterior angulation is usually wide (about 140°) and in some shells is replaced by a rounded margin. In many specimens an almost flat area lies dorsal to a low ridge extending postero-ventrally from the umbones. Slight lateral constriction often affects the mid-ventral area but it is possible that this feature is related to the crushing of carinate shells.

The scatter diagram (fig. 11) suggests a marked negative correlation between size (as measured by length) and the H/L ratio.

This association of an extremely elongate species with a sub-quadrate *Anthraconaia* recalls the *A. glotae*–*A.* cf. *pruvosti* fauna described by Weir and Leitch (1936) from Bothwell, Scotland.

PHILLIPSII AND TENUIS ZONES

(*a*) *Between Druidston and Nolton Haven* (figs. 12 and 13). The lowest and topmost of four fossil bands in this section exhibit interesting differences of composition. The lowest band (I) is exposed only in the core of the anticline at North Haven, 6 feet above beach level, but the topmost band (IV), some 300 feet higher in the sequence, is accessible at four points, being repeated by strong folding. The second and third bands lie within 30 feet of the lowest and yielded only indifferent material referable mainly to *Anthraconauta* aff. *phillipsii* and rarely to *A.* cf. *tenuis*.



TEXT-FIG. 12. Shells from between Druidston and Nolton Haven, ×1. Tenuis Zone, band IV, uppermost of four horizons with lamellibranchs, in cliffs between Druidston and Nolton Haven. Author's Coll., A, H45/3b; B, H45/18b; C, H45/18a; D, H45/2a; E, H45/4d.

The lowest band provided over a hundred impressions in grey shale. Forms referable to *A. phillipsii* predominate, while *A.* cf. *tenuis* is rare and *A. tenuis* s.s. is absent. One specimen of *Anthraconaia* cf. *pringlei*, several insect wings and many specimens of *Euestheria* cf. *dawsoni* (Jones) were found.

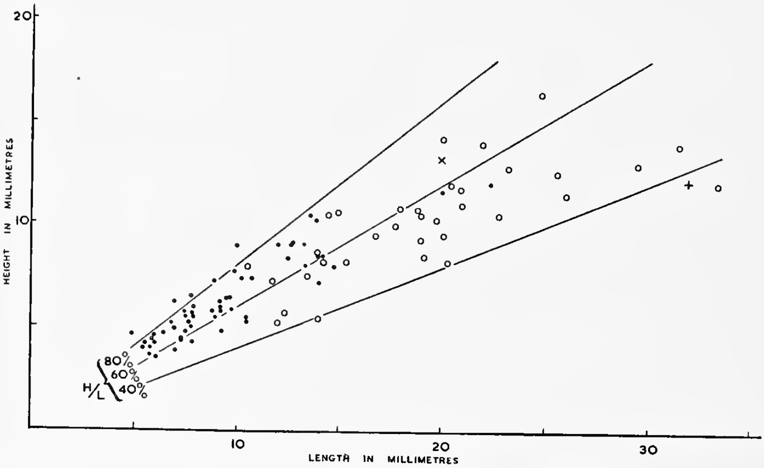
In band IV *Anthraconauta*, *Euestheria*, and *Spirorbis sp.* are found crushed in tough dark shale overlying a thin unnamed coal. *A. tenuis* (fig. 12A, B, D, E) is typically represented and as frequently as *A. phillipsii*. A more ovate form referable to *A.* aff. *phillipsii* also occurs (fig. 12C); similar variants have previously been found high in the Tenuis Zone in Glamorgan (Dix and Trueman 1931, p. 191) and near its base in Monmouthshire (Sullivan and Moore 1956).

The dimensions of the *Anthraconauta* shells yield the following values:

	L in mm.		*H/L%*			
Band	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*
I . . .	4·9–22·4	9·3 (61)	50·4–96·0	67·5 (58)	123°–165°	142° (82)
IV . .	9·8–33·5	19·1 (37)	40·5–76·4	54·2 (34)	140°–170°	153° (46)

The specimens having rounded posterior angles are not suitable for measurement of angle β.

The scatter diagram (fig. 13) illustrates the differences in dimensions exhibited by these faunas and shows that within the region of size overlap ($10<L<23$ mm.) the dimensional characters of the assemblages are discernibly different. This suggests that the differences of proportions are not entirely due to the evident contrast in size distributions. The faunal change is taken to mark the boundary between the Phillipsii and Tenuis Zones.



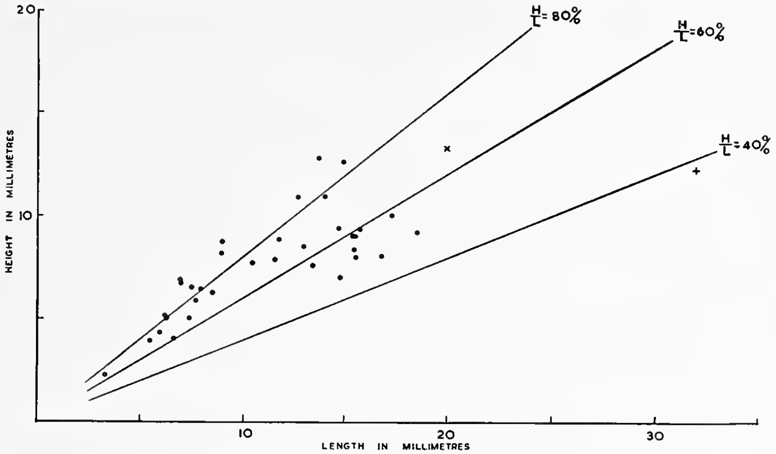
TEXT-FIG. 13. Height plotted against length of *Anthraconauta* shells from the lowest and highest bands between Druidston and Nolton Haven, Phillipsii and Tenuis Zones. Dots represent specimens from the lowest band (I), circles those of the uppermost band (IV). The positions which would be occupied by the holotypes of *Anthraconauta phillipsii* and *A. tenuis* are shown by the symbols × and + respectively.

(*b*) Anthraconauta *from Rickets Head* (fig. 14). Trueman (1934) recorded *Anthraconauta tenuis*, *A. phillipsii*, and some small forms which resemble *A. calcifera* from shales at Rickets Head. Overlying a seat-earth 93 feet below the base of the Rickets Head sandstone is a dark much sheared shale which contains crushed *Anthraconauta*, *Spirorbis*, insect wings, and plant fragments. The lamellibranchs are mainly small *A. phillipsii* and *A.* aff. *phillipsii*; about 15 per cent. are referable to *A.* cf. *tenuis* but only one specimen is *A. tenuis* s.s. (this specimen is incomplete: it is omitted from the table of dimensions and is not shown in fig. 14). The dimensions of the *Anthraconauta* give the following values:

L in mm.		*H/L%*		β	
Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*
3·3–18·5	10·8 (33)	47·7–99·0	70·9 (33)	125°–170°	144° (47)

It will be noted that the mean H/L value exceeds that of the relatively high *A. phillipsii* and the scatter-diagram (fig. 14) shows that the dimensions of *A. tenuis* are not attained. This assemblage cannot be held to indicate the Tenuis Zone and it is preferably assigned to the Phillipsii Zone.

(*c*) Anthraconaia *from Rickets Head* (figs. 15, 16). The upper of two shell bands in the shales associated with the Rickets Head Veins lies 12 feet below the Rickets Head sandstone. The lamellibranchs are preserved as 'solid' ironstone moulds in dark shale. *Anthraconauta phillipsii* occurs rarely with the *Anthraconaia* shells. Some specimens show both growth-lines and muscle-scars; consequently in the following table of *Anthraconaia* dimensions no distinction is made between internal and external measurements.



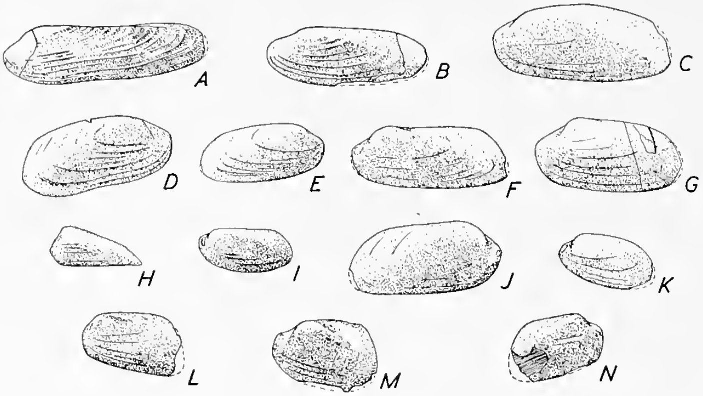
TEXT-FIG. 14. Height plotted against length of *Anthraconauta* from Rickets Head. Phillipsii Zone, 93 feet below the sandstone at Rickets Head, Pembs. The positions which would be occupied by the holotypes of *Anthraconauta phillipsii* and *A. tenuis* are shown by the symbols × and + respectively.

	L in mm.	*H/L%*	*T/L%*	*A/L%*
Upper limit . .	25·0	72·0	51·9	29·2
Lower limit . .	8·7	39·0	27·4	16·4
Mean	16·3	53·8	36·8	23·2
Number of observations	45	43	39	41

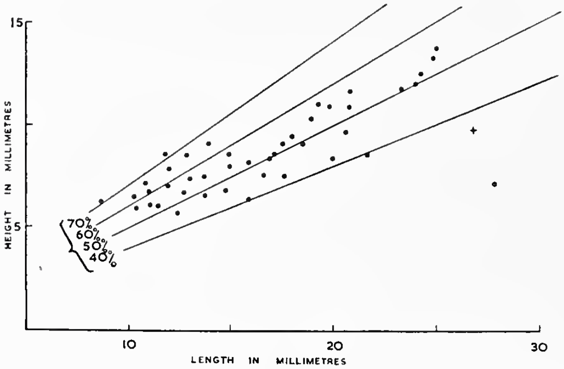
The *Anthraconaia* shells are small and 98 per cent. are posteriorly expanded with respect to both umbonal height and thickness; hinge-lines are long and straight to moderately arched (fig. 15C, D), and a carina of varying definition runs postero-ventrally from inconspicuous umbones.

In other characters the assemblage is extremely variable. The original of fig. 15A is a very long shell, probably slightly crushed dorso-ventrally; its dimensions are omitted from the table. Shells such as those illustrated in fig. 15E, F, J can be regarded as normal representatives and are referable to *Anthraconaia* sp. nov. cf. *pruvosti ?* (Chernyshev); the high shells (H/L$\geqslant$60) are also unlike any named species (fig. 15L, M, N). Sinuation of the ventral margin (fig. 15D) is uncommon; one of the two specimens found lacking posterior expansion is illustrated (fig. 15H). The assemblage exhibits a tendency to diminished H/L values with increasing length (fig. 16). The only closely comparable shells which the writer has seen are derived from the roof of the Gwscwm Vein

(Phillipsii Zone) of Burry Port, Carmarthenshire, and were thought by Dix and Trueman (1931) to be probably related to *A. pringlei.*



TEXT-FIG. 15. *Anthraconaia* from Rickets Head, ×1. Phillipsii Zone, 12 feet below the sandstone at Rickets Head. Author's Coll., A, H34/19; B, H34/32; C, H34/2; D, H34/12; E, H34/3; F, H34/10; G, H34/104; H, H34/6; I, H34/8; J, H34/47; K, H34/34; J, H34/61; M, H34/69; N, H34/48.



TEXT-FIG. 16. Height against length of *Anthraconaia* from Rickets Head, Phillipsii Zone, 12 feet below the sandstone at Rickets Head, Pembs. The symbol + indicates the position which would be occupied by the type of *A. pruvosti* (Chernyshev), dimensions of the valve from Pruvost 1919, pl. 26, fig. 1; the specimen represented by the open circle is incomplete and may be distorted.

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GLASS FIBRE RESIN CASTS OF FOSSILS

by A. E. RIXON AND M. J. MEADE

ALMOST every worker with macrofossils must, at some time, have had cause to regret the vulnerability of plaster casts. After months of negotiation a much-needed cast may arrive broken in transit: or having survived the hazards of modern transport, it is dropped and has to be mended. A repaired cast is never satisfactory, for one is never sure how much of it exists only in the imagination of the person making the repair. Various methods have been devised for strengthening plaster, but none of them seems to be very efficient. In an attempt to overcome this problem the authors, with the assistance of Mr. E. Balog, have been experimenting with glass fibre resin casting. The method evolved is rather more difficult and more costly than plaster casting, but the trouble and expense are justified by the great strength, resistance to abrasion, and lightness of the finished product.

It is well known that glass fibre casts can be taken from suitably treated plaster moulds, and since the technique for doing this with fossils is only a variation of that used in industry it is not discussed here. It is not, however, generally appreciated that such casts can be made using flexible polyvinyl chloride moulds, and it is this method with which we propose to deal.

There are two types of object met with in casting. The fossil which is still partly embedded in the matrix, and that which occurs in the round. Each requires a different moulding technique. The first case being the simpler it is dealt with first.

A mould of the fossil, using polyvinyl chloride or rubber is first prepared in the manner previously described by us (Rixon and Meade 1956). The surface of the mould is now painted over with undiluted Silicone Fluid M.S. 200/350cs, and the excess is carefully wiped off with a fluff-free tissue. Very little silicone need remain, and it is important to see that it does not collect in the depressed ornament of the mould. The resin we have used is Crystic 189, and the formula recommended by the makers is:

Crystic resin 189	60 parts by weight
Crystic Pregel 17	40 ,, ,, ,,
Catalyst paste H	4 ,, ,, ,,
Accelerator E	4 ,, ,, ,,
Titanium dioxode	3 ,, ,, ,,

A rough estimate is made of the amount of resin required to cover the surface of the mould thinly and the ingredients mixed in the following order. Since the Catalyst paste H must be fully dissolved this is added to the Crystic resin first and stirred well. The solution of this substance is accelerated if the resin is now warmed, to about 29° C. This must be done with care as the mixture is inflammable, and if the heating is overdone the resin will set prematurely. When all the catalyst has dissolved the titanium dioxide is added. It is best made into a lump-free paste with a little of the resin before being added to the main mix. Now the Pregel 17, which is a thixotropic paste, is thoroughly stirred in. Finally the accelerator E is poured in while stirring. This must be well dispered through the mixture.

The vessel containing the prepared resin is now tapped to make the air rise to the surface, where the bubbles can be removed. The mixture is painted into the mould until the whole is covered with a thin coat. It will not matter if this is very thin in places. This coat is left to harden for about half an hour. This time varies with local conditions and can be made longer or shorter by varying the accelerator content. Brushes and glassware should be cleaned immediately with acetone followed by hot water, a detergent, and some scouring powder. While the resin is setting chopped stranded glass mat is cut into convenient pieces. If the contours of the mould

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are complicated the pieces should be about half an inch wide and an inch and a half long; for less complex shapes larger pieces can be used. It will readily be seen that if the pieces are too large there is a danger that they will be pulled out of one place by the mere action of pushing them into another.

A further batch of resin is now prepared, but this time the Pregel 17 is left out and the weight of accelerator reduced by half. Some of the strips of glass mat are placed in a flat dish and the resin poured on to them and pressed well in with a palate knife. If large pieces of mat are used the resin will have to be painted on to them and then rolled in between two pieces of cellophane. The resin-soaked glass is lifted with the palate knife and placed in the mould over the pregel coat which by then should have set hard. The whole surface of each piece of glass mat should not come into contact with the mould at once, but should be pressed on gradually to avoid trapping air, and each piece should be slightly overlapped by the next. The mat must be pushed down into the mould with a stiff brush, care being taken to work it into hollows and over ridges, and to see that it is flat to the mould in all places. When the mould is completely covered the casting is left for two hours to set and harden. If greater thickness is required another application can be made provided that it is done within a few hours. A smoother backing can be obtained by finishing with a layer of surgical cellulose soaked in resin. Whole castings can be made using this instead of glass, but they have nothing like the same strength and require much more resin.

Using single-piece moulds we have produced successful glass fibre casts of the antiarchan fish *Bothriolepsis*, a complicated shape with deep relief and a mass of fine detail. One of these was repeatedly walked on by a 14½ stone man and sustained no damage. Simpler subjects are fossils preserved in the flat fissile flags of the Scottish Middle Old Red Sandstone. A glass fibre cast of the osteolepid fish *Thursius* from this formation, measuring 27 × 16 cm., weighs 87 grammes, and is about 3 mm. thick. One is tempted to write an address on the back, stamp it, and send it through the post. Such casts could be stored in a filing cabinet. A coloured cast sometimes shows ornamentation and relief better than a white one. These casts can be painted with ease using dry colours with shellac as a binding medium. Basic colours other than white can be obtained by replacing the titanium dioxide by burnt sienna, burnt umber, and raw umber in powder form.

Making glass fibre casts in the round from a double mould is much more difficult. A visible joint line is hard to avoid, but this is a problem which can be solved by improved technique. Both halves of the mould are treated as described above, but care is taken to avoid building the glass above the edges of the mould halves. This is not easy and it may be necessary to trim the edge with scissors after the resin is set. When the two halves have set some resin mixture is painted on the edges and a little is poured into one half of the mould, and the whole is closed and secured. It is then rotated so that the liquid resin will flow continually round the joint line until it sets. This point is indicated by a control sample of the resin setting on the bench. The mould is left for a further hour after this before it is opened.

It is hoped to improve results by experimenting with different types of glass mat and with synthetic fibre flocks. Since submitting this article we have made very successful casts using Fibreglass Chopped Strands H.P.A. 1 inch long. These are cheaper and easier to use than the mat.

Those who wish to try these methods are recommended to start with glass fibre chopped strand mat Type H.P.A. from Messrs. Fibreglass Ltd., St. Helens, Lancs. Crystic resin 189 is made by Scott Bader Ltd., 109 Kingsway, London, W.C.2, and Silicone Fluid M.S. 200/350cs can be obtained from Messrs. Hopkins and Williams, Chadwell Heath, Essex. The moulds we have used are made from I.C.I.'s Welvic paste from I.C.I. Plastics Division, Welwyn Garden City, Herts.; or from Vinamould H.M.C. 1028 of Vinyl Plastics Ltd., Butterhill, Carshalton, Surrey; or from Revultex rubber latex from Revertex Ltd., Harlow, Essex.

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PALAEONTOLOGY

VOLUME 3 · PART 2

CONTENTS

ABNORMAL GROWTHS IN SOME DEVONIAN GONIATITES

by MICHAEL R. HOUSE

ABSTRACT. Specimens of *Sobolewia* from the Givetian of Cornwall and Algeria are described which show a regular pitting on the internal moulds. The same phenomenon is noted on an Algerian Eifelian goniatite and also on German specimens of *Sellanarcestes* from the Emsian and Eifelian and on an Eifelian *Anarcestes*. The pits, which are commonly arranged in sub-radial rows, are interpreted as formed in life as mound-like growths on the inside of the anterior part of the body chamber shell, but not along the apertural margin. Several hypotheses on their origin are discussed.

THE curious pitting seen on the internal moulds of some Devonian goniatites which is here described was first observed on specimens of *Sobolewia* from the locality described by Fox (1894, p. 637) at Pentonwarra Point, Trevone, north Cornwall. The fauna here was recently shown to belong to the Terebratum Zone of the Middle Devonian Maenioceras Stufe and not to the Upper Devonian as had hitherto been supposed (House 1956). The goniatite genera now known from this locality include *Tornoceras*, *Aulatornoceras*, *Protornoceras*, *Maenioceras*, *Sobolewia*, *Agoniatites*, *Wedekindella*, and *Werneroceras*, but only certain specimens of *Sobolewia* show the pitting.

During April 1957 a period was spent in Paris examining the superb collections of Devonian ammonoids from North Africa at the Sorbonne. Discussion with Madame Germaine Petter of the Centre de Recherches Sahariennes revealed that many Saouran specimens of *Sobolewia* show the pitting as does one Eifelian specimen. In August 1958, whilst studying the ammonoid collections in the Geologisch-Paläontologisches Institut at Göttingen, one Emsian goniatite was noted showing pits. Later, at the Geol.-Pal. Institut at Marburg, Dr. O. H. Walliser was able to show the writer several Middle Devonian specimens which also showed pitting.

Special thanks are due to Madame Petter for discussion in Paris and for reading and commenting on the typescript and to Professor Pierre Pruvost for providing facilities for study at the Sorbonne. Dr. Herman Schmidt and Dr. Otto H. Walliser are also to be thanked for discussion and for making specimens available for study. In an unsuccessful attempt to discover whether such pits occurred on the moulds of ammonoids of other periods the matter was discussed, in person or by correspondence, with most leading specialists. Acknowledgement is due especially to Mr. W. S. Bisat and to the late Dr. W. J. Arkell. Also appreciated are the comments of Dr. Otto Haas, Professor F. Hodson, and Dr. G. A. L. Johnson. The Durham Colleges in the University of Durham have given grants to facilitate travel in Europe in the course of monographic work on the English Devonian ammonoids. Mr. C. Chaplin of the Durham Colleges, Dr. Walliser of Marburg, and Mr. Jack Scott of the U.S. National Museum in Washington have given help in the preparation of the accompanying photographs.

DESCRIPTION

Cornish specimens. The specimens of *Sobolewia* from Trevone are preserved as internal moulds of iron pyrites with occasional pyritic casts of the original shell. Pitting has been

[Palaeontology, Vol. 3, Part 2, 1960, pp. 129–136, pl. 24.]

seen on specimens between 8 mm. and 21 mm. diameter and it occurs on septate portions of the moulds and on at least the posterior portions of the body chamber. Not all specimens of *Sobolewia* show the pitting and some show only occasional development of pits.

The pits range between 0·3 mm. and 0·9 mm. in diameter and their sides slope convexly inward to form a sub-conical depression which may reach 0·5 mm. in depth. Where observed the pit bottom is rounded. The outer margin of the pits grade evenly into the internal mould of the shell. The relation of the pits to the shell has been elucidated in one instance by the dissection of an undisturbed pyritic cast of the shell from above a pit. The outer surface of the shell showed no evidence of disturbance. Pits formed on the moulds of mural areas of the septa show no difference from those found elsewhere. Occasionally two or more pits may partly coalesce.

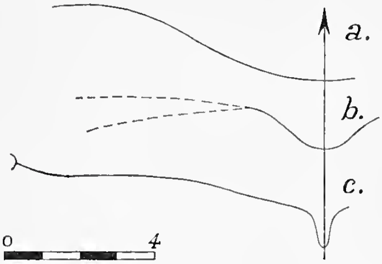

Fig. 1

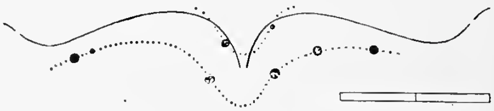

Fig. 2

TEXT-FIG. 1. *Sobolewia* aff. *nuciformis* (Whidborne). *a*, Course of growth lines. *b*, Approximate course of pit rows (variable over the umbilico-lateral areas). *c*, Suture. Scale in millimetres. All based on SM. H7422 collected by the author from the Terebratum Zone, Givetian, at Pentonwarra Point, Trevone, North Cornwall.

TEXT-FIG. 2. *Sellanarcestes* cf. *wenkenbachi* (Kayser). Diagram showing one suture and the distribution of pitting on a specimen in the Göttingen Geologisch-Paläontologisches Institut from the Emsian Mandelner Schichten at Mandeln, Germany. The dotted line shows a hypothetical arrangement of the pits into rows. Each scale division represents approximately 5 millimetres.

In some specimens the pits occur rarely and it is not possible to distinguish any regular arrangement of them. In several specimens, however, the pits are seen to be arranged in rows which pass out from the umbilicus, cross the lateral areas either radially or with a slight forward projection, and on the ventro-lateral slopes pass back to form a shallow and narrow sinus on the venter (text-fig. 1*b*). In some specimens there are five to eight of these rows in a half whorl with about five pits between the umbilicus and the venter. There is approximately an equal development of pits on either side, but the pits are not symmetrically placed. The pit arrangement between successive rows does not show precise agreement. The distance between the rows agrees in general with the distance between the septa. The rows do not agree with the course of the growth lines (text-fig. 1*a*, *b*, Pl. 24, fig. 5) at the same diameter, nor do they correspond with the course of growth lines for one whorl orad of the pit rows.

North African specimens. Specimens of *Sobolewia* in the Sorbonne from the Givetian of the Redjel Imrad collected by J. Fallot show pitting on the internal moulds exactly comparable with that described for Cornish specimens. In no specimen is there any trace of the original shell. Other genera from the same locality show no pitting.

A single specimen from the southern border of the Erg el Djemel (Ougarta) from the Eifelian 'niveau à *Pinacites jugleri*' shows the pitting in a remarkable way (Pl. 24, fig. 6). This specimen is unfortunately not generically determinable since it is crushed laterally and the sutures cannot be seen. The specimen is 20·4 mm. in diameter and at least the last whorl represents the body chamber. Pitting can be observed on the right side of the specimen, but that side is poorly preserved. The figured left side shows no orderly arrangement of pits in the apicad portion of the body chamber, but in the subsequent whorl they become almost invariably arranged into forwardly projecting slightly concave rows with some suggestion of a backward deflexion over the venter. There is a noticeable absence of pits on the umbilical shoulder: between the shoulder and the venter there are usually between eight and ten pits. Ventro-laterally the pit arrangement is disturbed and although there is some indication of a backward deflexion to form a sinus there are many pits which do not follow this regular course. Except in a few cases there is not complete agreement in the position of pits in successive rows. Whilst the pits are usually of the same size they occasionally coalesce and there are some smaller pits. The small particles seen within many of the larger pits are pyritic concretionary structures. Growth-lines are not well shown on the specimen but in the early portion of the last whorl there is evidence that they sweep very slightly back from the umbilicus to form a very shallow sinus on the outer flanks: their course over the venter cannot be discerned.

German specimens. One specimen of *Anarcestes sp*. in the Clausthal Museum (No. L 62) from the Upper Eifelian Goslaren Schiefer (Pl. 24, fig. 7) shows a pattern of pitting which is closely comparable to that seen on the Cornish and Algerian specimens. Again the pits are apparently arranged into sub-radial rows with some evidence of a ventral sinus. The separation between the rows in this case does not agree with the septal separation at the same diameter, but it may agree with the septal separation at earlier diameters which cannot be seen. The pit arrangement is not laterally symmetrical.

There is a specimen in the Geol.-Pal. Museum at Berlin (No. c104) from the Eifelian Ballersbacher Kalk at Blauer Bruch near Wildungen which Dr. O. H. Walliser has determined as *Sellanarcestes* cf. *wenkenbachi* (Kayser) (Pl. 24, figs. 8, 9) which shows pitting with a different arrangement to that so far described. Although there is a radial pattern there are fewer pits and these appear to be spirally arranged and single prominent pits lie in a constant ventro-lateral position throughout the last whorl.

A specimen from the Upper Coblencian (Emsian) of Mandeln which Schmidt (1926, p. 293) figured and referred to '*Anarcestes wenkenbachi*' shows evidence of pitting (text-fig. 2). This specimen is in the Geol. Pal. Institut at Göttingen. In this example the pits are not frequent and are completely without symmetry in their arrangement, but they can be interpreted as arranged into a row which has a salient on the outer flanks and a concavity on the venter.

The most remarkable pitting is exhibited by a single specimen of *Anarcestes* (*A.*) *sp.* in the Clausthal Geol.-Pal. Institut from the Eifelian Wissenbacher Schiefer (text-fig. 3). In this case the pitting is restricted to a broad band low on the flanks. There is no evidence to suggest any radial arrangement of the pits at all. Further, the pits are not of uniform size, and very small pits occur among pits of similar size to those found in the forms already described.

TEXT-FIG. 3. *Anarcestes* (*Anarcestes*) *sp.* Lateral view of a specimen in the Clausthal Museum labelled '*Anarcestes vittatus*' from the Eifelian Wissenbacher Schiefer showing pits on the internal mould. The arrow shows the direction towards the aperture. Each scale division represents 5 millimetres. Based on drawings and a photograph and checked against the original specimen by Dr. O. H. Walliser of Marburg.

INTERPRETATION

The possibility that the pits are post-fossilization features is clearly ruled out in the case of *Sobolewia* by their relation to the shell and mural portions of the septa: these show that the pits were formed during life. In the other cases it is difficult to conceive how such regular pitting could have arisen accidentally. There is therefore no comparison with the pitting which has been described, for example, on the surface of the holotype of *Perisphinctes* (? *P.*) *listeri* (de Haan) from the Jurassic Corallian Beds of Nunnington, Yorkshire, which Dr. Vernon Wilson has suggested may be due to the subsequent action of rootlets and humic acid (*in* Arkell 1950, p. 265). The Cornish specimens described here have been extracted from freshly exposed and unweathered intractable slate.

From the preceding description and observations the following inferences on the origin of the pits may be made.

1. The pits are moulds of mounds which were developed during life on the inner surface of the shell.
2. The mounds were probably solid since mural portions of the septa reflect their shape and iron pyrites subsequently formed around them.

3. The mounds were formed in the body chamber and near to the aperture, but were not formed along the shell-growth margin. Where there is a regular arrangement of the pits into rows the course of the rows does not agree with that of the growth lines.

4. At least in specimens other than the *Anarcestes* (*A.*) *sp.* from the Wissenbacher Schiefer, the arrangement of the pits into rows which agree approximately in their separation with the septal distance suggests that the mounds were formed periodically after each forward movement of the visceral mass associated with septal formation.

The several possible causes of the mounds will, for convenience, be discussed under three heads.

(1) *Functional mounds.* There are at least three known ammonoid structures with which the mounds may have been functionally associated: *a*, small muscle attachment; *b*, incipient false constrictions; *c*, modified conellae.

The evidence appears to tell against the mounds representing the site of small muscles. Were this the case it might be expected that the pit arrangement would be laterally symmetrical and that there would be nearly precise agreement between the position of the pits in successive rows. Further, it might be expected that all specimens of affected genera preserved as internal moulds would show the pitting, but this is not the case. However, a pitting on the interior of the posterior parts of the nautiloid body chamber has been illustrated in *Phragmoceras* by Foerste (1929) and Sweet (1959) has illustrated similar structures in the genera *Parryoceras*, *Beloitoceras*, *Oncoceras*, and *Diestoceras*. But in these cases the pitting is regular and restricted to a band immediately orad of the last septum. The pit rows in the Devonian goniatites are not comparable with the course of the annulus for Crick (1898) has shown that when this structure is shown on ammonoids it is still in the posterior part of the body chamber as in the living *Nautilus*.

The pits show little analogy with constrictions except that the course of the pit rows shows agreement with false constrictions in failing to accord with the growth lines, in being structures on the inside of the body chamber, and in their formation being near the aperture. The frequency of constrictions rarely, if ever, agrees with the septal frequency. No constrictions have been recorded in the Devonian genera affected by the pitting. Pit-like depressions on the lateral areas of the internal moulds of some ammonoids with constrictions do occur, however, and they are shown on *Dunbarites rectilateralis* (Miller) (see Miller and Furnish 1940, p. 532, pl. 63, figs. 1, 4), but there are never rows of pits as shown in some Devonian goniatites.

The mounds are not directly comparable with the conellae described within the shell of certain Jurassic ammonites (Hölder 1952; 1952*a*) for although these structures are conical their apices are directed outwards, whereas the apices of the mounds in the Devonian goniatites are directed inwards. Further, the relative size of conellae is much smaller than the mounds. Also conellae are usually interpreted as formed by diagenic dissolution of the shell, whereas the Devonian structures were clearly formed in life.

(2) *Alien organic growths.* Internal discrete alien organic growths might be expected to leave trace of a distinct boundary on the internal moulds. This is not seen on the Devonian specimens and in all cases the pits are in smooth continuity with the surrounding areas. The pits on the body chamber of *Manticoceras oxy* Clarke, refigured by Miller (1938, Pl. 16), were formed by orbiculoideans growing on the internal surface of the

body chamber and these show the distinct boundary to be expected from organic growths.

Borings through the shell from the outside are common among recent Mollusca and may give rise to internal mounds. Professor F. Hodson informs the writer that borings are not uncommon on the shells of Carboniferous goniatites and they are well shown on the holotype of *Hibernicoceras posthibernicum* Hodson and Moore (1958, pl. 4, fig. 1). Structures have also been figured by Schindewolf (1934, pl. 2, fig. 7*a*, *b*) as borings in the shell of a specimen of *Cymaclymenia striata* (Münster) from the Upper Devonian of Hönnetal, Germany. The pits in *Sobolewia* can hardly be due to borings since the shell above the pits is undisturbed. Whilst no trace of the shell is visible in the affected North African Eifelian specimen (SM. H 7423) the arrangement of the pits into periodic rows could only be explained as due to borings if some soft part structure extended fully one whorl beyond the aperture of the body chamber which is itself at least one whorl in length: it seems unlikely that this could be the case.

(3) *Localized shell thickenings.* The continuity between the pits and adjacent areas suggests that the mounds were tumerous concretions of actual shell material which formed after each advance of the body mass. Such tumerous growths might be due either to organic infection or inorganic irritation which led to the precipitation of actual shell material. In either case the resulting structures could be termed pathological (Moodie 1923, p. 29). Were organic infection the cause it is surprising that the pits are usually so regular for, at times, the infection might be expected to disrupt the soft parts considerably. The possibility that the mounds might be caused by the irritation of permanent cysts or similar structures within the visceral mass is considered unlikely because of the lack of agreement in the position of the pits in successive rows.

An inorganically or organically caused irritation not primarily related to the shell or the soft parts seems a more likely solution. Small particles could conceivably enter between the shell and the visceral mass and lead to structures comparable with the pearl mounds of present-day lamellibranchs. The precise origin of natural pearls has been so disputed that attempts to deduce it for Devonian goniatites are unlikely to be profitable. Magraw (1956) has recently suggested that foreign particles may explain abnormal apertural developments in *Gastrioceras*. If a similar type of interpretation is correct for *Sobolewia* then the rows of mounds must be caused by some structure in the soft parts

EXPLANATION OF PLATE 24

Figs. 1–5. *Sobolewia* aff. *nuciformis* (Whidborne). 1, SM. H7421 collected by the author from the Givetian Terebratum Zone at Pentonwarra Point, Trevone, north Cornwall. ×4. 2–5, SM. H7422 collected by the author from the same locality and horizon. 2, 3 ×4, 4 ×12, 5 ×11.

Fig. 6. Goniatite indet. SM. H7423 from the Eifelian 'niveau à *Pinacites jugleri*', Erg el Djemel (Ougarta), North Africa. ×3.

Fig. 7. *Anarcestes sp.* Clausthal Museum No. L.62 from the Upper Eifelian Goslaren Schiefer. ×4.

Figs. 8, 9. *Sellanarcestes* cf. *wenkenbachi* (Kayser). Berlin Museum No. c104 from the Middle Couvinian (Eifelian) at Blauer Bruch near Wildungen. ×2.

All the specimens are of natural internal moulds, but SM. H7422 retains a portion of the original shell preserved as a pyritic cast. The specimens were lightly coated with a sublimate of ammonium chloride before being photographed. The prefix SM. refers to the Sedgwick Museum collections where some of the figured specimens have been deposited.


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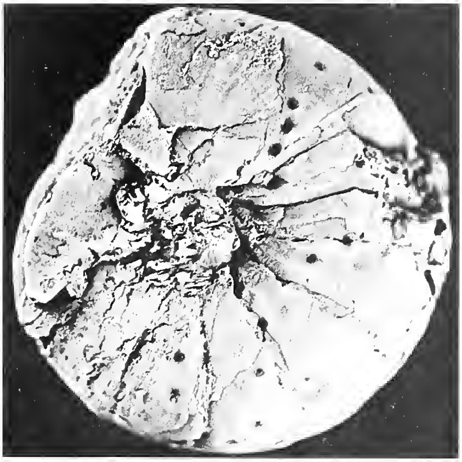
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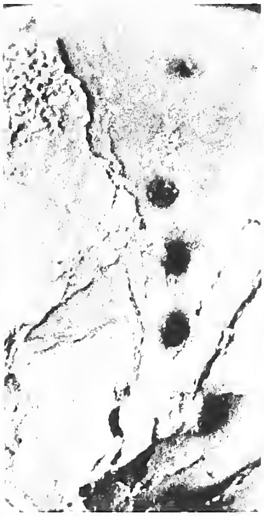
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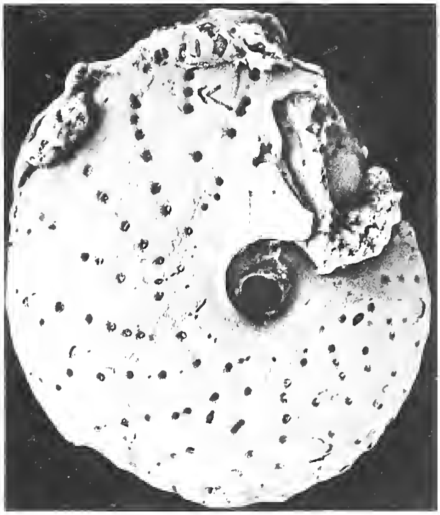
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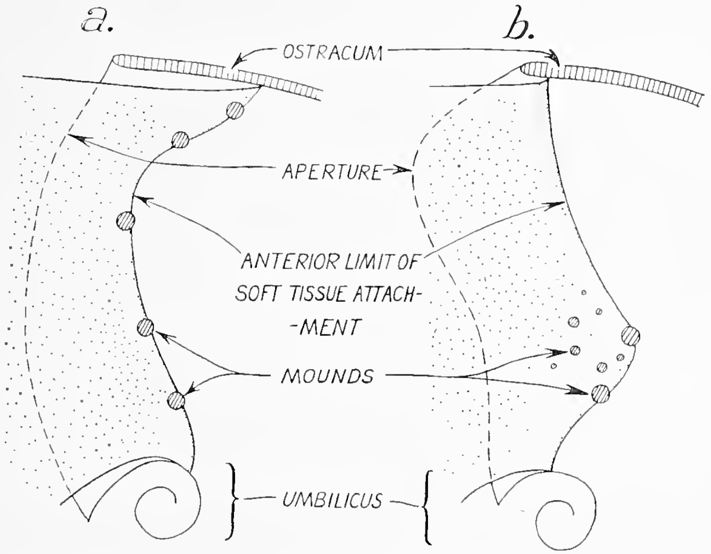
9

HOUSE, Abnormal growths in Devonian goniatites

which limited the backward passage of foreign particles. Perhaps this structure might be the anterior limit of soft part attachment, comparable with the pallial line of the lamellibranch. The restriction of the mounds to a band on the flanks could be explained by a lateral sinus along the 'pallial line' (text-fig. 4). This line, in other forms, might be the site of the precipitation of false constrictions. The wrinkle layer on Devonian goniatites commonly reaches near to the aperture and the striae of it do not follow the course of the growth lines. There is, unfortunately, insufficient evidence on the course of the wrinkle layer in the affected Devonian goniatites to tell whether the pit rows follow the same course.



TEXT-FIG. 4. Diagram showing a hypothetical relation between mounds and soft parts in *a*, *Sobolewia* and *b*, *Anarcestes*. Based on specimens described in the text.

CONCLUSIONS

The evidence at present available is not conclusive as to the origin of the pits seen on some Devonian goniatites, but appears to favour an hypothesis that the pitting is due to pearl-like mounds which were formed in life on the inside of the body chamber and probably caused by the irritation of foreign particles which entered between the body and the shell: the particles were apparently restricted in their passage backward by some unknown structure in the soft parts, possibly the anterior limit of soft part attachment. Periodic forward movement of the visceral mass associated with septal formation during growth then explains the arrangement of the pits into periodic rows the separation of which generally agrees with the septal distance. A sinus formed along the limit of soft part attachment could explain the restriction of the pits into a lateral band in some cases.

The genera in which this phenomenon has been observed are all members of the

Devonian family Anarcestidae with the possible exception of *Sobolewia* which is commonly placed in the Prolobitidae. Affected specimens occur in the Emsian, Eifelian, and Givetian. Occurrences are known in North Africa, Germany, and England.

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LOWER CARBONIFEROUS NON-MARINE LAMELLIBRANCHS FROM EAST FIFE, SCOTLAND

by G. M. BENNISON

ABSTRACT. *Carbonicola antiqua* Hind (*non* Brown) and *C. elegans* (Kirkby) are redescribed from the Calciferous Sandstone Series of East Fife, and *Anthraconaia? kirki* sp. nov. proposed. Variation of the shells at different localities is discussed and the significance of faunal associations is assessed.

THREE species of non-marine lamellibranch have been described from the Calciferous Sandstone Series (Lower Carboniferous) of East Fife. Of these, two were referred to *Carbonicola* and one to *Naiadites* by Hind (1894–6). Detailed work has shown that the two species of *Carbonicola* were correctly referred to that genus by Hind, and that they are morphologically more primitive than other representatives of the genus, as well as occurring at a lower horizon. Examples of *Anthraconaia?* are also described here. The strata from which the shells described are derived are of Viséan age (Currie 1954), and are extremely variable. They thin from about 4,000 feet on the coast of East Fife, to little more than 200 feet in the Lomond Hills 15 miles away. Rapid lateral thinning of individual beds, local unconformities cutting out parts of the succession, slumping of shales, and the lenticular form of the false-bedded, ripple-marked sandstones all show that deposition was in water shallow enough to be affected by currents or wave action. Occasional coal seams indicate temporary emergence. Lack of precise knowledge of the stratigraphy of the beds is a serious limitation to palaeontological study. Text-fig. 1 shows the localities mentioned.

Certain detailed correlations postulated by Kirkby cannot be sustained, though little can be suggested in their place. The Randerstone shore section is low in the Calciferous Sandstone Series—Kirkby equates his Limestone 5 with Bed 618 of the Pittenweem to Anstruther section—but it is doubtful if Limestone 10 is the equivalent of Bed 649. They differ in lithology and in fauna and form part of different successions. Nor can the postulated correlation of the beds with *C. antiqua* at Kilminning and Kilrenny Mill be upheld. Variation in the shells differs at these localities and the beds are lithologically distinct. Summarized detailed successions are as follows:

KILMINNING

10–12 ft. shale
10 in. hard red limestone with abundant *C. antiqua*
3 in. calcareous sandstone
+5 ft. massive sandstone

KILRENNY MILL

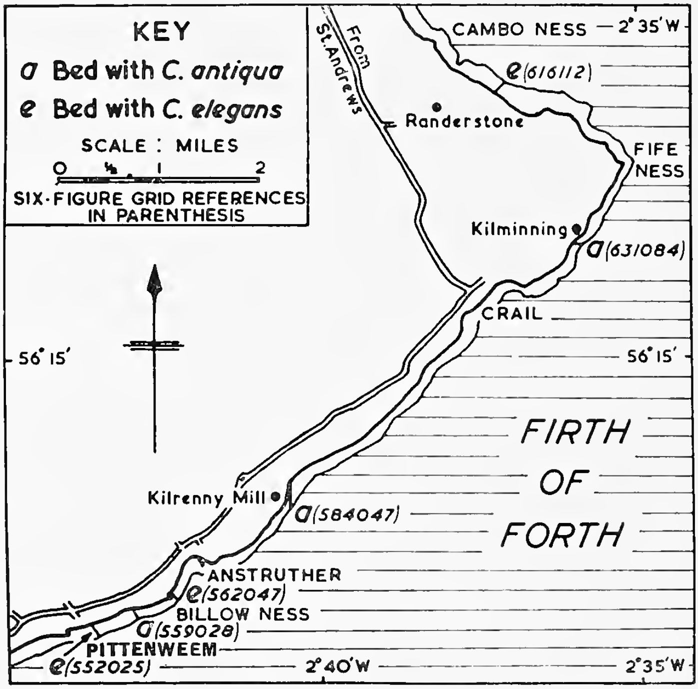
8 ft. shales and sandstones
3 in. cementstone
5 in. mudstone with *C. antiqua*
1 in. clay
6–10 in. hard, yellow, calcareous sandstone with many *C. antiqua*
4 ft. 9 in. sandy shale

CARBONICOLA IN THE LOWER CARBONIFEROUS

Lower Carboniferous *Carbonicola* differ from most Westphalian forms in having tilted growth lines. These reflect a progressive change in the direction of growth and

[Palaeontology, Vol. 3, Part 2, 1960, pp. 137–152, pl. 25.]

result in low umbones directed towards the anterior in the adult shell. In some specimens the umbo is not the highest part of the dorsal margin. The postero-dorsal margin, which is typically arched, becomes strongly arched in some variants. The hinge is edentulous, a condition not typical in *Carbonicola*, although noted in the Namurian species *C. pervetusta* (Bennison 1954, p. 41). Further, Eagar (1946, p. 7), describing small forms from the *Anthraconaia lenisulcata* zone of the Coal Measures, has observed that teeth are ill defined and that dentition is represented mainly by swellings and depressions in the hinge-plate. Trueman and Weir (1951, p. 106) state that the edentulous condition occurs 'not infrequently' in *Carbonicola*: in this case it may be indicative of a primitive condition.



TEXT-FIG. 1. Sketch map to show the location of non-marine lamellibranch beds in east Fife.

Despite a superficial similarity to *Anthracosia*, due to the tilted growth lines and the low umbones, and, despite the vertical anterior umbonal slope of the internal mould, these *Carbonicola* are seen to differ fundamentally from *Anthracosia* in that the internal moulds do not have a robust median dorsal ridge. By implication, the hinge-plates cannot be bevelled as in *Anthracosia*. It is the structure of the dorsum which distinguishes *Anthracosia* from *Carbonicola* (Trueman and Weir 1951, p. 105), although 'the dorsal structure indirectly affects some aspects of external shape—e.g. umbonal tilt and outline of dorsal plan'. Thus in the Lower Carboniferous there are early members of the Anthracosiidae resembling *Carbonicola* in essential characters but bearing a superficial similarity to *Anthracosia*.

Carbonicola antiqua Hind

Plate 25, figs. 1, 2, 6–8

? *Pachyodon nucleus* Brown 1843, p. 394, pl. 16, fig. 1.
Carbonicola antiqua Hind 1894, p. 79, pl. 11, figs. 28–30.
Non *Carbonicola antiqua* (Brown); Trueman and Weir 1947.

Type material. The specimen figured by Brown as *Pachyodon nucleus*, from Woodhall, Water of Leith, near Edinburgh, is lost. I have studied faunas from Brown's type locality collected by Geological Survey officers, but found nothing with which *nucleus* could be identified. As the identity of Brown's species cannot be determined it is impracticable to sustain the name *nucleus*. Brown was correct (1849, p. 178, pl. 23, fig. 31) in renaming his Coal Measures form *Pachyodon antiquus* as *senex* on referring that species to the genus *Unio*, for the name *Unio antiquus* was preoccupied by Sowerby's (1833) species. The correct name for *C. antiqua* Brown, as used by Trueman and Weir (1947), is therefore *C. senex* (Brown). No homonymity occurs, however, in the case of *C. antiqua* Hind. Hind's specimens are syntypes and his first figured specimen (1894, pl. 40, fig. 28, B.M. L.46889) is here selected as lectotype.

Diagnosis. Shell ovate to subtriangular. Umbones low, anterior end short, *c.* 20 per cent. of the length or less. Growth lines tilted. Tumid, thickness over 40 per cent. of the length. Posterior bluntly rounded or obliquely truncated. Lower border gently rounded, or straight for the posterior two-thirds of its length.

Dimensions

	L (*mm.*)	*H* (*mm.*)	*A* (*mm.*)	*T* (*mm.*)
Pl. 25, fig. 1 (L.46889) (Hind, pl. 11, fig. 28) . . .	24·0	14·5 (60·4%)	4·2 (18·3%)	est. 5·9 (single valve) (*c.* 49%)
Pl. 25, fig. 2 (L.46890) (Hind, pl. 11, fig. 29) . . .	25·3	15·4 (60·9%)	4·5 (17·7%)	12·6 (49·6%)

Description and discussion. The syntypes are rather larger than the mean for the topotype material from Kilminning collected by the author, but the values for H/L and A/L are very close to the modes of the community. The lectotype is near the norm of the community and is typical in every way except in the detail of the posterior-umbonal slope, which is less strongly arched than in some variants, and the umbo, which is more pronounced than in the majority of adult specimens. The growth lines are only moderately tilted. The figured syntype represents a common variant with low umbones, highly tilted growth lines and a rather bluntly truncated posterior end. Variation in the community is discussed below. *C. antiqua* is edentulous and in no case have teeth or dental sockets been found; this is in accord with Hind's original description although his figured hinge-plate (1894, pl. 11, fig. 28*a*) does not provide clear evidence of this.

Comparison. C. elegans is the only other species of Lower Carboniferous lamellibranch which resembles *C. antiqua. C. elegans* occurs 250 feet below and 950 feet above *C. antiqua* and their ranges, though not fully known, must overlap. The two species do not occur together. They can be readily distinguished, chiefly on account of a large discrepancy in the value of H/L, and by features fully discussed in the emended description of *C. elegans*.

C. antiqua and *C. elegans* differ from *C. pervetusta*, the earliest form assigned to *Carbonicola* by the writer, in the following features: the umbones are low and directed towards the anterior; the growth lines are tilted; the shells are more tumid; the anterior end is short—A/L = 20 per cent. or less; the shells normally attain a greater size; and the range of variants is different.

Distribution. The syntypes are from red limestone at Kilminning, between Fife Ness and Crail. This species also occurs in two beds at Kilrenny Mill, and sparsely at a higher horizon between Pittenweem and Anstruther. It is restricted, therefore, to the lower part of the Calciferous Sandstone Series. The habitat of *C. antiqua* is discussed below.

Carbonicola elegans (Kirkby)

Plate 25, figs. 3–5, 9–12

Pleurophorus elegans Kirkby 1880, p. 586.
Carbonicola elegans Hind 1895, p. 81, pl. 20, figs. 12–15, 15*a*.

Type material. *C. elegans* was first described without figures from the No. 10 Limestone of Randerstone. Hind subsequently figured three complete specimens and a broken shell showing the hinge-plate, giving the locality as 'East of Pittenweem'. The evidence indicates that Hind was in error as to the locality of these specimens. Hind does not state that they are Kirkby's original material, but he acknowledges (1895, p. 82) the loan of material from Kirkby's collection. *C. elegans* occurs east of Pittenweem in a dwarf fauna from Bed 386 of Kirkby's Pittenweem–Anstruther section, but it seems improbable that the figured shells came from that locality. The writer has not found any specimen there as large as the figured shells, nor have any been observed in Kirkby's material in the Hancock Museum. The red limestone matrix of the figured shells is quite unlike pale grey ironstone of Bed 386, but is indistinguishable from the No. 10 Limestone, Randerstone. *C. elegans* is also found in Bed 649, at Billow Ness, 1 mile east of Pittenweem but much nearer to Anstruther. It is almost impossible to obtain a good specimen from this bed because of the nature of preservation of the fossils and it is unlikely that 'East of Pittenweem' refers to this locality. The writer is of the opinion that the figured shells are from the No. 10 Limestone, Randerstone, but that there is insufficient evidence to show whether they were Kirkby's original material.

EXPLANATION OF PLATE 25

Figs. 1–2. *Carbonicola antiqua* Hind. Calciferous Sandstone Series, red limestone, Kilminning, Crail, Fife, ×2. 1, Lectotype, L.46889, complete shell. 2, Syntype, L.46890, right valve.

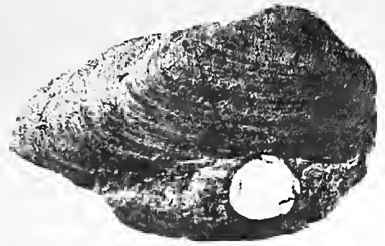
Figs. 3–5. *Carbonicola elegans* (Kirkby). Calciferous Sandstone Series, Limestone 10, Randerstone, Fife. 3, L.47165, left valve, ×2. 4, L.47163, right valve, ×2. 5, L.47164, internal mould, ×2½.

Figs. 6–8. *C. antiqua*. Calciferous Sandstone Series, calcareous sandstone, Kilrenny Mill, Anstruther, Fife. 1001, internal mould, lateral, anterior, and dorsal views, ×2.

Figs. 9–12. *C. elegans*. Topotype material. 9–11, R.10.2, internal mould, anterior, lateral and dorsal views, ×2. 12, In the collection of Dr. A. Wattison, internal mould showing muscle scars and pallial line, ×2½.

Figs. 13–14. *Anthraconaia? kirki* sp. nov. Calciferous Sandstone Series, mudstone, Kilrenny Mill, Anstruther, Fife. ×2½. 13, holotype, S.13440, 14, paratype, S.13442.

(Figs. 1–5 reproduced by permission of the British Museum (Nat. Hist.). Reg. nos.: prefix L denotes British Museum (Nat. Hist.); prefix S denotes Hunterian Museum, Glasgow; prefix R denotes University of St. Andrews collection. Remaining specimen in the author's collection.)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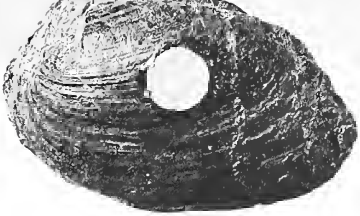
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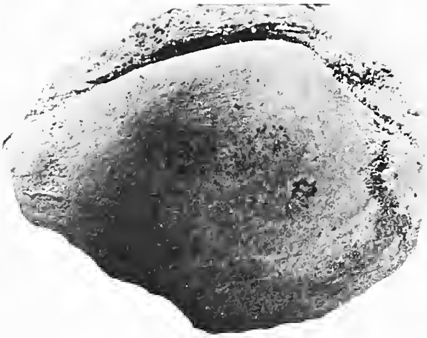
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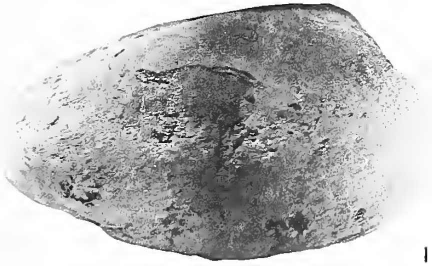
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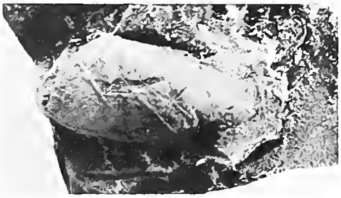
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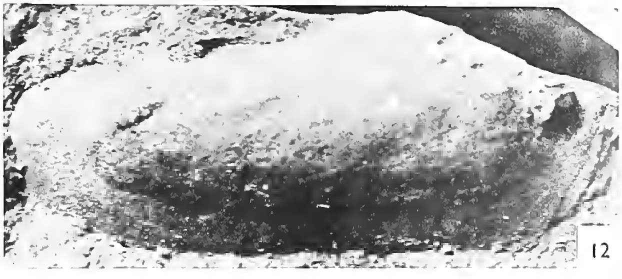
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BENNISON, Lower Carboniferous non-marine lamellibranchs

Dimensions

	L (mm.)	*H (mm.)*	*A (mm.)*	*T (mm.)*
Pl. 25, fig. 3 (L.47165) (Hind, pl. 20, fig. 15)	17·6	8·5 (48·3%)	3·3 (18·7%)	est. 6·2 (35·2%)
Pl. 25, fig. 4 (L.47163) (Hind, pl. 20, fig. 13)	17·8	8·4 (47·2%)	3·7 (20·2%)	est. 6·0 (33·7%)

Description and discussion. Hind's specimens are larger than the mean for the topotype material from Randerstone. Shell ovate, elongate with H/L less than 50 per cent. Anterior end short, *c.* 20 per cent. of the length. Very fine, tilted growth lines. Moderately tumid. Lower border gently curved, posterior end rounded or obliquely truncated. Antero-umbonal slope concave. Slight carinate feature running downwards and backwards from umbo. Umbones low and directed towards the anterior. Edentulous. *C. antiqua* is thick shelled where it occurs in limestone and calcareous sandstone, but it is much thinner shelled where it is found in shale.

Comparison. C. elegans resembles *C. antiqua*, but the modal value of H/L is some 12 per cent. less. Growth lines are finer in *C. elegans* than in most variants of *C. antiqua*, and in no case have variants of the former with very coarse growth lines been observed. *C. elegans* and *C. antiqua* have not been found in the same bed; this mutual exclusion may indicate that they are biospecies. The variation of A/L in *C. antiqua* encompasses the variation of A/L in *C. elegans*, so that length of the anterior end is not a diagnostic character. The shape variation is more restricted in *C. elegans* and no variants with pronounced arching of the dorsal margin, nor variants which are skew ovals (due to the lowest part of the ventral margin being near the posterior end) such as are found in *C. antiqua*, have been observed.

Distribution. C. elegans has been recorded from Beds 386 and 649, separated by 1,200 feet of strata, of the Pittenweem–Anstruther shore, as well as from the No. 10 Limestone, Randerstone. It is clear from the correlation proposed by Kirkby (1880, p. 572), as modified by Kirk (1925, p. 369), that Bed 649 and the No. 10 Limestone must be at nearly the same horizon, but that they are not precise equivalents has been shown above.

Anthraconaia? kirki sp. nov.

Plate 25, figs. 13, 14

Holotype. Hunterian Museum, Glasgow, no. S.13440. *Paratype* no. S.13442.

Diagnosis. Small, elongate with a mean value for H/L approximately 40 per cent. for the four specimens measured. Anterior end short, not exceeding 20 per cent. of the length. Umbones low, anterior-umbonal slope concave. Hinge-line long and extending the greater part of the length of the shell. Posterior end rounded and slightly expanded. Greatest height of shell about one-third of the length from the posterior end. Ventral border gently curved. Growth lines fine, numerous, tilted. No distinct carina, but a swelling runs obliquely backwards and downwards from the umbo towards the posterior-inferior angle.

Dimensions

	L (*mm.*)	*H* (*mm.*)
Pl. 25, fig. 13 (S.13440), holotype .	9·6	3·3 (34·4%)
Pl. 25, fig. 14 (S.13442), paratype .	10·8	4·6 (43%)
S.13441	*c.* 12	6·0 (50%)
1139	14·9	5·7 (38%)

Only four measurable specimens have so far been obtained. Measurements of the length of the anterior end (not given here) are in the region of 1·5–2·5 mm., representing a value of 20 per cent., or less, for A/L.

Description. In two specimens both valves are present with the umbones in contact but they are agape. It is not possible to estimate tumidity as no specimens were obtained showing the original convexity. The angle β appears to be relatively low, just exceeding 100°, but the angle γ cannot be estimated from the limited material available. No evidence is available on the interior of the shell.

Comparison. A.? kirki is similar to the more elongate forms of *Anthraconaia* such as *A. williamsoni* or to *A. bellula* from the Millstone Grit. The following characters suggest the affinity of *A.? kirki* to *Anthraconaia*: the hinge-line and ventral margin are subparallel; the shell is expanded posteriorly; and it possesses an ill-defined carinal feature. Further, it forms a small percentage of a non-marine lamellibranch fauna. It seems preferable to refer this species to the genus *Anthraconaia* with a query, for Dr. J. Weir has pointed out to me that it is far removed in time from the typical *Anthraconaia* of the *adamsi–salteri–modiolaris* group, and that vital knowledge of the internal characters is lacking.

COMMUNITIES OF *CARBONICOLA*

I. *Carbonicola antiqua*

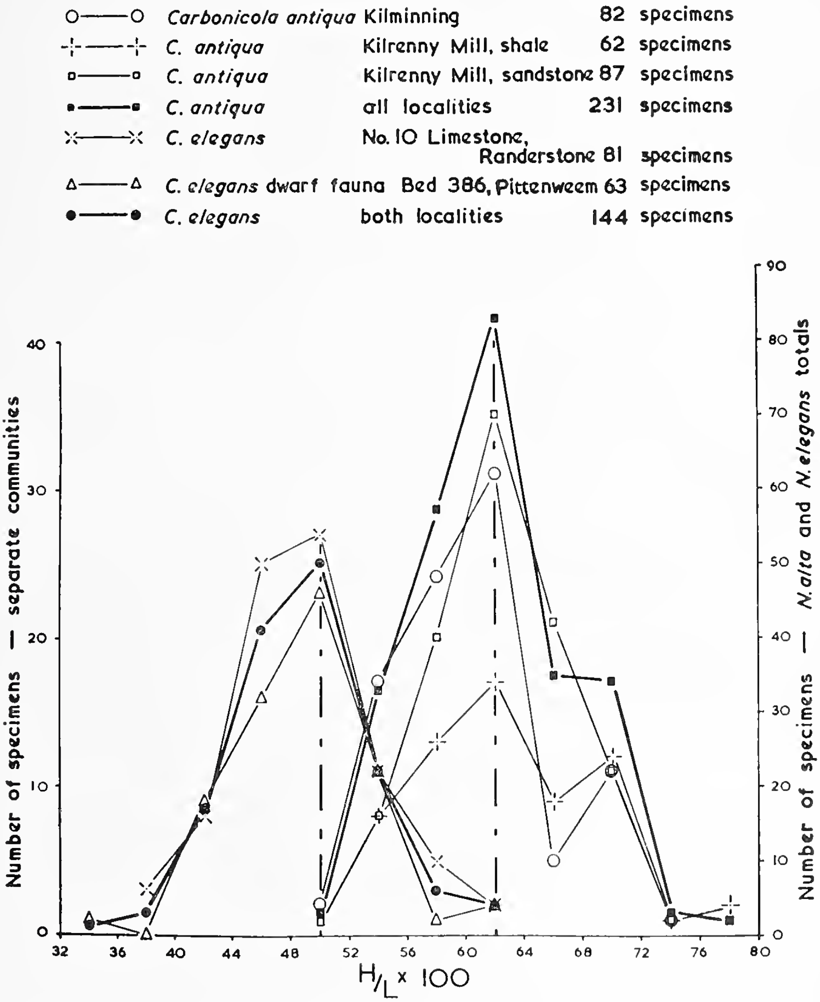
1. *Kilminning. Carbonicola antiqua* is abundant in a 10-inch bed of red limestone at Kilminning, Fife, from which the syntypes were obtained. Specimens are poorly preserved and difficult to extract, but over 100 were examined and over ninety measured. The mean values for length, height, and length of anterior end of the shells from this collection are less than those for the collections from shale and sandstone at Kilrenny Mill.

	L	*H*	*A*	*d*	*No. of specimens*
Kilminning limestone . .	20·6	12·4	3·9	8·6	91
Kilrenny Mill shale . . .	22·0	13·8	5·1	9·7	62
Kilrenny Mill sandstone . .	23·1	13·6	4·7	. .	13

(Measurements in mm., only external measurements have been utilized.)

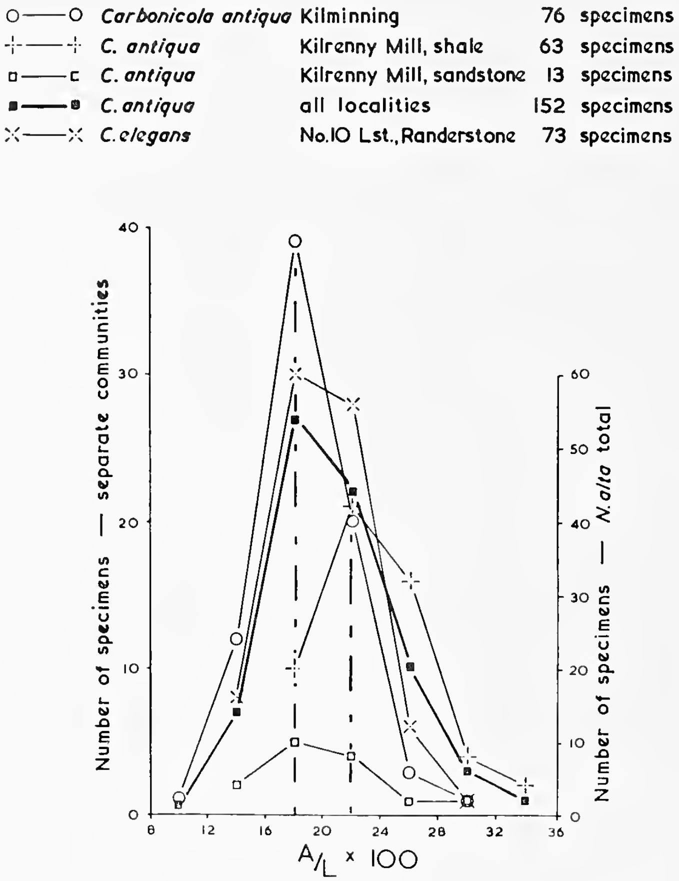
The abundance of shells in the Kilminning limestone and their eroded nature suggests that they have been sorted by wave or current action. The relatively high percentage of small forms (less than 15 mm. in length) may be due to this sorting effect and the small range of variation in size confirms that this is not a life assemblage.

	% of specimens with L less than 15 mm.	*% of specimens with L less than ⅔ mean value*	*Range of value of L (mm.)*
Kilminning Limestone . .	17%	2% (less than 13·7 mm.)	13·4–28·2 (diff. 14·8)
Kilrenny Mill shale. . .	6%	6% (less than 14·5 mm.)	9·3–31·4 (diff. 22·1)
Kilrenny Mill sandstone . .	1%	1% (less than 15·4 mm.)	14·5–25·9 (diff. 11·4)



TEXT-FIG. 2. Graphs to show the ratio of length (L) to height (H) in collections of *Carbonicola antiqua* and *C. elegans* from east Fife.

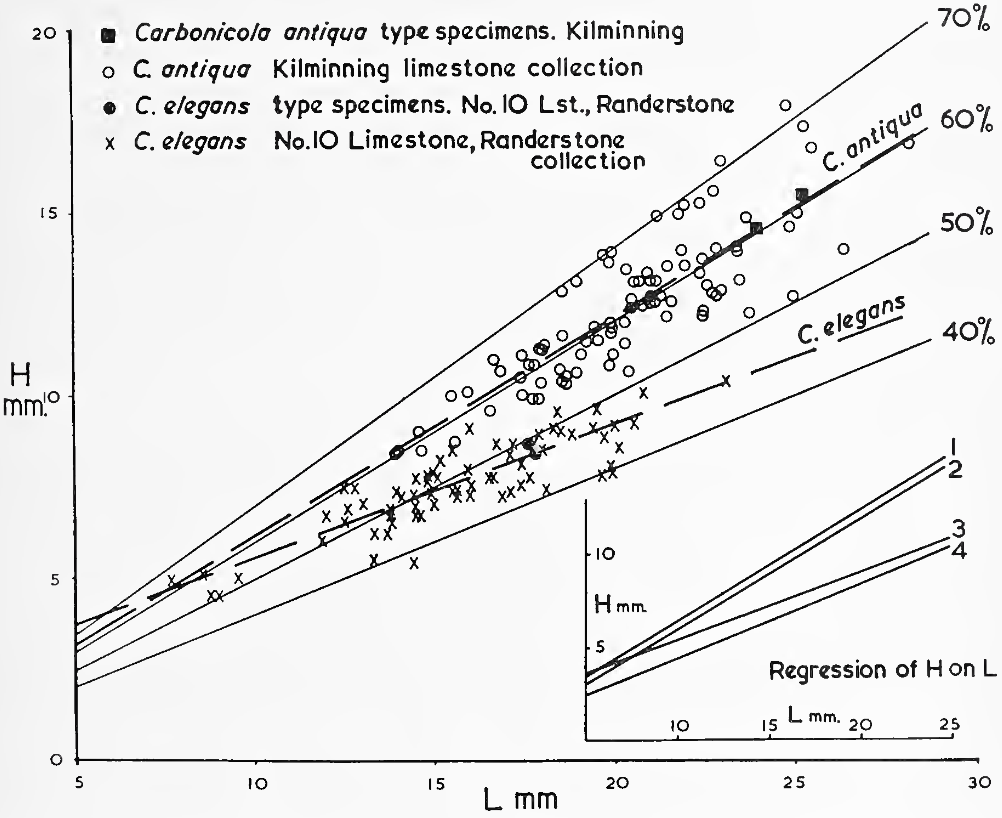
The variation graph for H/L (text-fig. 2) shows a modal value of 62 per cent. for the Kilminning shells, with a variation of 12 per cent. on either side of the mode. The other collections show close agreement, both in mode and range of variation. The variation graph for A/L (text-fig. 3) shows that the Kilminning shells have a different modal value and a different range of variation from the Kilrenny Mill collections; the modal value for A/L is approximately 4 per cent. lower in the case of the Kilminning collection. Two factors might affect the proportions of the shells. The shells are rather small and if growth were allometric then the modal value of this collection would be low. A scatter diagram (text-fig. 5) does not reveal any tendency for length of anterior end to increase relatively with length and, calculating the regression of A on L, we find that the line would pass nearly through the intersection of the axes of the scatter diagram. The other factor affecting the proportions of the shells is the degree of crushing, related to the compaction of the sediment: this is noticeably less in the case of shells from the limestone than in shells from shale. The effects of crushing, if the shells are lying parallel to the bedding planes, as in this case, is to increase A/L; see Dix and Trueman (1931, p. 192) and Eagar (1947, p. 11). The second term, in a calculation of the slope of the



TEXT-FIG. 3. Graphs to show the ratio of length (L) to length of anterior end (A) in collections of *Carbonicola antiqua* and *C. elegans* from east Fife.

regression line of A on L, is a measure of that slope: *C. antiqua*, Kilminning limestone $A = 0{\cdot}25+0{\cdot}176L$. *C. antiqua*, Kilrenny Mill shale $A = 0{\cdot}45+0{\cdot}256L$.

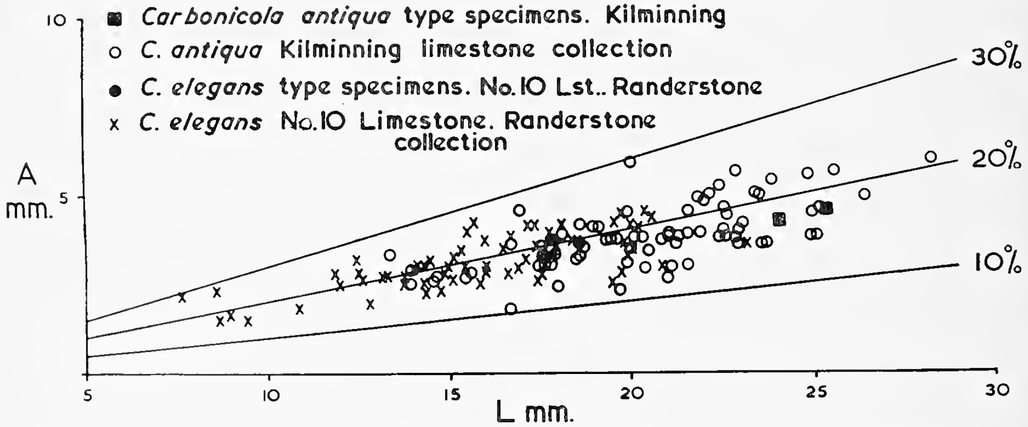
This seems to explain the discrepancy in the values of A/L in *C. antiqua*, and it seems unlikely that such a discrepancy may be attributed to evolutionary change or to a difference of habitat.



TEXT-FIG. 4. The relationship between length (L) and height (H) in *Carbonicola antiqua* and *C. elegans*. Inset: regression lines of H on L. 1 = *C. antiqua*, Kilrenny Mill shale collection, 2 = *C. antiqua*, Kilminning limestone collection, 3 = *C. elegans*, No. 10 Limestone, Randerstone collection, 4 = *C. elegans* dwarfs, Bed 386, Pittenweem collection.

In the collection from Kilminning T/L is high and variants with a bluntly rounded posterior end are relatively common. Variation in shape of shell is shown in text-fig. 6, which shows that some variants have a more pronounced dorsal arch, that some are skew ovals, and that some have an obliquely truncated posterior. The first two kinds of variants have a relatively high value for H/L, but the presence of such variants is inadequately expressed by the simple H/L ratio. A fourth measurement, the distance from the anterior end to the point of maximum downward curvature of the lower border, denoted by d, has been used (see Leitch 1940, p. 15). d/L is typically about 40 per cent., but ranges from 25 to 68 per cent.

2. *Kilrenny Mill shale. C. antiqua* is common in blue-grey shaly mudstone which almost immediately succeeds a highly fossiliferous calcareous sandstone. Many of the shells are excellently preserved, but they are less numerous than in the limestone of Kilminning and fewer measurable specimens were obtained. Individual shells here attain the greatest size. The shells show little evidence of sorting by wave action—although specimens often comprise single valves only—for there is here the greatest range in size and the greatest proportion of young (small, less than two-thirds the mean L) shells. This is, therefore, the most representative collection of *C. antiqua* and may approximate to a life assemblage. The assemblage includes about 8 per cent. of *Anthraconaia? kirki* and *c.* 2 per cent. of *Naiadites obesus* (R. Etheridge, jun.).

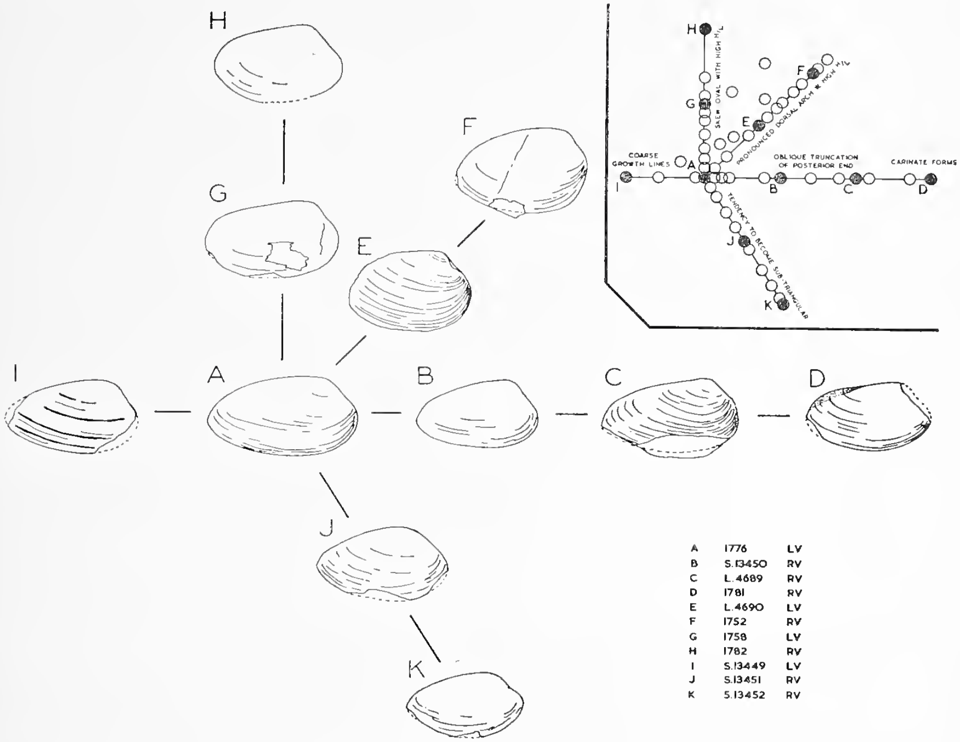


TEXT-FIG. 5. The relationship between length (L) and length of anterior end (A) in *Carbonicola antiqua* and *C. elegans*.

Variation in shape of shell is shown in text-fig. 7. It is apparent that variants with an obliquely truncated posterior end are more common than in the Kilminning collection, and a relatively large *pseudorobusta*-like variant (text-fig. 7L) is found in the Kilrenny Mill shale only. It is impossible to calculate the variation in shape of shell attributable to crushing effects and it is, therefore, questionable whether the shape variations, illustrated in text-figs. 6 and 7, represent true differences arising from adaption to environment or from evolutionary changes (Kirkby's view, that the shell beds of Kilminning and Kilrenny Mill could be correlated, has been discussed, and cannot be sustained).

3. *Kilrenny Mill sandstone.* In a calcareous sandstone of variable thickness (it is seen to thicken from 6 in. to 18 in. in a lateral distance of a few feet) *C. antiqua* is abundant. In most specimens the shell material has been dissolved away leaving excellent moulds and, although these provide information on the internal character of *C. antiqua*, comparison with the other collections is difficult. In a few specimens the shell material is partially eroded and interior and exterior dimensions can be compared. It was observed that a correction made to the measurements of internal moulds, by adding 0·6 mm. to the length and height, was justifiable. The average shell thickness is of the order of 0·3 mm. and a comparison of the mean values of L, H, and H/L for the whole collection

(with the correction applied) and the mean values obtained from the limited number of exteriors showed close similarity. No such correction was applied in the case of the anterior end, chiefly due to the difficulty of estimating the position of the umbo. The mean value of length, for this collection, is high but no very large shells have been found (see table above). Small shells are absent, providing evidence of sorting—as might be expected in a sediment with much detrital quartz.



A	1776	LV
B	S.13450	RV
C	L.4689	RV
D	1781	RV
E	L.4690	LV
F	1752	RV
G	1758	LV
H	1782	RV
I	S.13449	LV
J	S.13451	RV
K	S.13452	RV

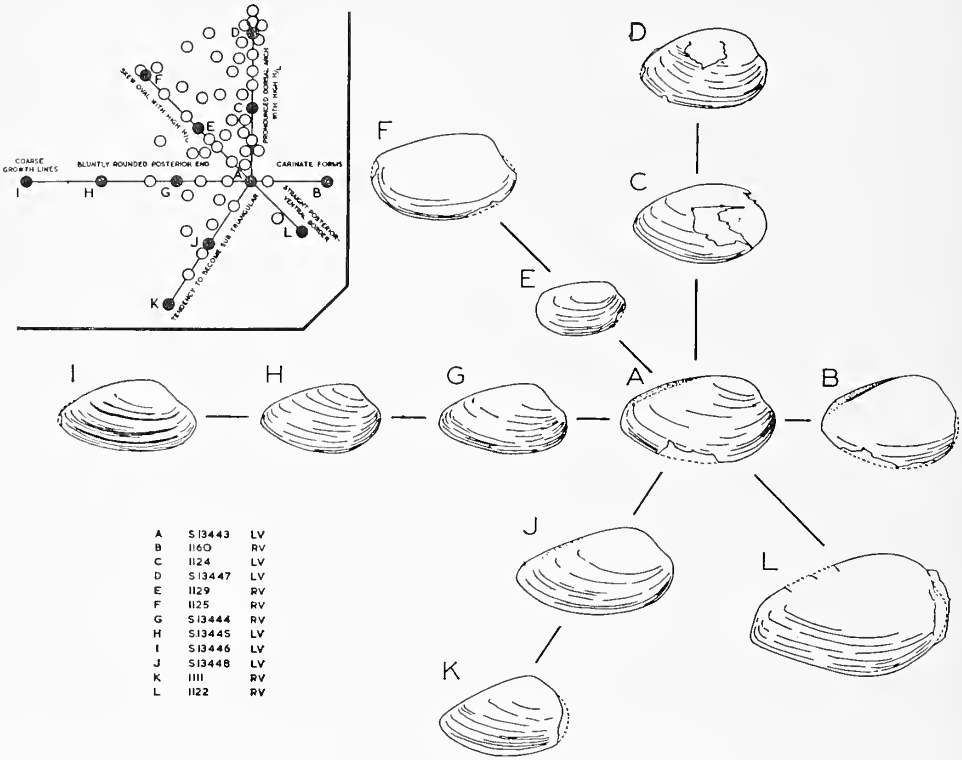
TEXT-FIG. 6. Pictograph showing variation in shape of shell of *Carbonicola antiqua* from Kilminning, Fife. Inset shows distribution of variants relative to the figured specimens, which are represented by lettered black circles. For purposes of comparison all shells have been drawn as right valves. About two-thirds natural size. (Registered numbers with prefix L refer to Brit. Mus. (Nat. Hist.) specimens, with prefix S refer to Hunterian Mus., Glasgow specimens. Other specimens in author's collection.)

4. *Bed 586 of Kirkby's main section, Pittenweem–Anstruther shore.* This exposure is covered by massive fallen blocks of sandstone. Only a few square inches of shale can be examined and, from these, three specimens of *C. antiqua* were obtained. Its presence is thus confirmed but comparison with collections from other localities is not possible.

II. *Carbonicola elegans*

1. *Kirkby's No. 10 Limestone, Randerstone.* This is the only horizon from which *C. elegans* has been obtained in sufficient numbers to permit precise comparison with *C.*

antiqua. It is the probable horizon of Hind's specimens, and the horizon from which the species was first described by Kirkby. The collection shows a wide range of variation in the value of H/L, from *c.* 36 per cent. to 64 per cent., some variants having a value for H/L comparable with the modal value of the *C. antiqua* collections (text-fig. 2). The modal value of the *C. elegans* collection is 12 per cent. lower than that of the *C. antiqua* collections and, since no change in mode with horizon is known in either species, this appears to be a significant difference. Further, there is a tendency for H/L to decrease with increase in size of the individual in *C. elegans* (text-fig. 4); this is shown by calculating the regression of H on L. The regression line (text-fig. 4, inset, line 3) does not, if produced, pass through the origin of the graph. The difference between the slope of this line and the regression lines calculated for the Kilrenny Mill shale and Kilminning limestone collections of *C. antiqua* (lines 1, 2) are significant.



A	S 13443	LV
B	1160	RV
C	1124	LV
D	S 13447	LV
E	1129	RV
F	1125	RV
G	S 13444	RV
H	S.13445	LV
I	S 13446	LV
J	S 13448	LV
K	1111	RV
L	1122	RV

TEXT-FIG. 7. Pictograph showing variation in shape of shell of *Carbonicola antiqua* from shale, Kilrenny Mill, Fife. Inset shows distribution of variants relative to the figured specimens, which are represented by lettered black circles. (For location of specimens see text-fig. 6.)

The modal value of A/L for this collection of *C. elegans*, 18 per cent., is close to that of the *C. antiqua* collections. The more reliable comparison can be made between the two limestone faunas, the Kilminning Limestone and the No. 10, Randerstone, for in both the effects of crushing are at a minimum (text-figs. 4, 5). Calculation of the regression of A on L showed no statistically significant difference for the two species.

2. *Bed 649 of Kirkby's main section, Pittenweem–Anstruther shore.* In this bed at Billow Ness, as Kirkby remarked (*in* Geikie 1902, p. 96), *C. elegans* occurs as a small percentage of a dominantly *Naiadites obesus* fauna. Usually the posterior-dorsal area of *N. obesus* is broken off, so that the shell bears a close resemblance to *C. elegans*. Because of this preservation it is difficult to estimate how commonly *C. elegans* occurs, but prolonged collecting has yielded a few well preserved shells which can be referred to that species without doubt.

3. *Bed 386 of Kirkby's main section, Pittenweem–Anstruther shore.* A 3-inch bed of calcareous iron-rich siltstone includes dwarfed shells of *Carbonicola elegans*. The mean length of shell is less than 7 mm., less than half that of those from No. 10 Limestone, Randerstone. In measuring such small shells the operational error is liable to be high when expressed as a percentage of length or height. For this reason the same reliance cannot be placed on the H/L ratio although the modal value of 50 per cent. for this collection is comparable with that of the Randerstone shells and the regression lines (text-fig. 4 inset) are similar. The shells appear to resemble *C. elegans* in every way except size: they are, however, relatively thick shelled. It is difficult to establish whether the fauna is 'dwarfed' by adverse ecological conditions, or whether only small shells are present as a result of sorting by waves or currents. The former seems probable in view of the lithology (fine angular quartz grains are abundant and may have inhibited growth), and the range of variation in size of shell (L = 3 mm. to 11·5 mm.) does not confirm sorting effects. However, very young individuals (spat) are not present in the assemblage.

The following table shows the similarity of different collections of *C. antiqua*, differences due to relative amounts of crushing being reflected in regression equations of both H on L and A on L. The greater difference between *C. antiqua* and *C. elegans* is indicated in the figures for H/L as well as the regressions.

	C. antiqua			*C. elegans*	
	Kilmining	*K. Mill sh.*	*K. Mill sst.*	*No. 10 Lst.*	*Bed 386*
$\bar{L}$	20·6 mm.	22·0 mm.	23·1 mm.	15·7 mm.	6·9 mm.
$\bar{H}$	12·4 mm.	13·8 mm.	13·6 mm.	7·6 mm.	3·3 mm.
$\bar{A}$	3·9 mm.	5·1 mm.	4·7 mm.	3·1 mm.	..
$\bar{d}$	8·6 mm.	9·7 mm.	..	..	..
Mode H/L	62%	62%	62%	50%	50%
Mode A/L	18%	22%	18%	18%	..
Mode d/L	42%	42%	..	..	..
Correlation:					
^{r}HL	0·854	0·893	..	0·856	..
^{r}AL	0·651	0·793	..	0·729	..
Regression:					
H =	0·25+0·593L	0·41+0·610L	..	1·82+0·368L	0·52+0·405L
A =	0·25+0·176L	0·45+0·256L	..	0·51+0·165L	..

CONDITIONS OF SEDIMENTATION

One of the features of *Carbonicola* from the Lower Carboniferous is its occurrence in rocks of widely differing lithology. It is found in calcareous, arenaceous, and argillaceous rocks. The question whether it could survive under such differing conditions of sedimentation arises. Further, if it lived in such a variety of environments, why should *C. antiqua* and *C. elegans* each occur at so few horizons, as far as is known, and be mutually exclusive of each other? In some cases, for example the No. 10 Limestone, the Kilminning limestone, and probably the Kilrenny Mill sandstone, the shells have been collected together by currents. The specimens are usually single valves and are probably not in their ecological stations. The occurrence of *C. antiqua* in the shaly mudstone of Kilrenny Mill probably provides the only reliable evidence of its ecology. The presence of large numbers of *C. antiqua* in the underlying sandstone is enigmatic, for this sediment comprises angular quartz grains cemented by calcite. The coarse texture of the rock, the variations in thickness of the bed, and the similarity in size of all the shells, together with the presence of macroscopic plant fragments, indicate turbulent conditions (Broadhurst 1959).

The habitat of *C. elegans* is even more difficult to assess. Only in the No. 10 Limestone of Randerstone is *C. elegans* abundant and here there is evidence of sorting. Petrologically, this rock could be classified as a microscopic limestone breccia. Apart from complete shells, the rock is made up largely of shell fragments of about 4 mm. diameter. It is surprising that *C. elegans* is not found in the shales immediately above the No. 10 Limestone in which *Naiadites obesus* is common, the more so since these two species occur together in Bed 649 at Billow Ness. Microscopic examination of the rock which yields the *C. elegans* dwarf fauna, Bed 386, reveals a matrix which includes 40 per cent. of angular quartz grains (0·1 mm. in diameter). This silt may have inhibited the growth of *C. elegans*.

C. antiqua and *C. elegans* are found in beds which occur in a succession which is not dominantly marine, but which includes shales and limestones with varied marine faunas. The absence of contemporaneous marine forms (but see below) from the *C. antiqua* and *C. elegans* shell beds is an indication of their non-marine habitat. Both species are found in association with *Naiadites obesus* which, elsewhere, is found in close proximity to marine forms. The only other faunal associations of these species of *Carbonicola* are with *Spirorbis* (cf. the association of *Spirorbis* with non-marine shells noted by Etheridge (1800, p. 217); see also Trueman (1942) and with ostracods. Kirkby (1880, p. 577) records the presence of numbers of *Littorina scotoburdigalensis* with *Carbonicola elegans*. Hind (1895, p. 82) notes that Etheridge believed this gastropod to be 'nearer to *Paludina*' (= *Viviparis,* a fresh-water form). Unfortunately the author has not found any specimens of it. Kirkby (*in* Geikie 1902) records only three species of ostracod in association with *C. elegans*, namely *Cytherella attenuata*, *C. extuberata*, and *Cythere superba*. Latham (1932) showed that these are among the commonest forms in the Calciferous Sandstone Series, are of long range, and occur in varied faunal associations, frequently with *Naiadites obesus* but also with *Schizodus* and other marine lamellibranchs. The known faunal associations of the two Calciferous Sandstone Series species of *Carbonicola* are summarized:

Carbonicola antiqua
Naiadites obesus
Spirorbis sp.
Anthraconaia? kirki
Cytherella sp.
Fish teeth

Carbonicola elegans
Naiadites obesus
Spirorbis sp.
? Littorina scotoburdigalensis
Cytherella attenuata
Cytherella extuberata
Cythere superba
Fish teeth and spines

The presence of macroscopic drifted plant fragments, occurring on the same bedding planes as the shells, indicates the proximity of land. Little can be said to account for the mutual exclusion of *C. antiqua* and *C. elegans*; the only observed difference in the matrices was the relative abundance of iron in the shell beds including *C. elegans*. The presence of one species rather than the other may well be related to salinity or temperature, environmental characters which are not reflected in the lithology.

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AMMONOIDS AND TRILOBITES FROM THE UPPER DEVONIAN AND LOWEST CARBONIFEROUS OF THE LAUNCESTON AREA OF CORNWALL

by E. B. SELWOOD

ABSTRACT. An ascending sequence of strata, comprising the Petherwin Beds, the Stourscombe Beds, and the Yeolmbridge Beds, is noted at the Devonian–Carboniferous boundary. The ammonoid and trilobite fauna of these beds is described.

The genus *Kenseyoceras* and the contained subgenus *K.* (*Mayneoceras*) are proposed, and *Epiwocklumeria* is redefined. The following species are redescribed or proposed:

Petherwin Beds (*Platyclymenia* and *Clymenia* Zones): *P.* (*Platyclymenia*) *valida* (Phillips), *P.* (*Platyclymenia*) *pattisoni* (M'Coy), *Costaclymenia muensteri* (Ansted). Stourscombe Beds (*Wocklumeria* Zone); *Wocklumeria sphaeroides* (Rh. Richter), *Epiwocklumeria dunhevedensis* sp. nov., *Kosmoclymenia pattisoni* sp. nov., *Cymaclymenia constricta* sp. nov., *C. constricta* var. *globosa* nov., *Parawocklumeria laevigata* sp. nov., *P. laevigata* var. *obesa* nov., *Parawocklumeria sp.*, *K.* (*Kenseyoceras*) *rostrata* gen. and sp. nov., *K.* (*Mayneoceras*) *sinuconstricta* subgen. and sp. nov., *Discoclymenia cornwallensis* sp. nov., *D.* aff. *cornwallensis* sp. nov. Yeolmbridge Beds (*Gattendorfia* Zone): *C.* (*Macrobole*) *drewerensis* Rud. & E. Richter sens nov., *C.* (*Macrobole*) *sp.*

FOR many years it was considered that rocks of highest Devonian and lowest Carboniferous age were unrepresented on the southern limb of the great Culm synclinorium of Devon and Cornwall. Recently ammonoids and trilobites, the subject of this paper, have been collected from a series of beds hitherto undifferentiated in the Launceston district of Cornwall; these fossils show that a complete succession of beds is represented between the Devonian and Carboniferous systems at Launceston.

The Petherwin Beds, the Stourscombe Beds, and Yeolmbridge Beds constitute the ascending sequence of strata at the Devonian–Carboniferous boundary. Faunas from the Petherwin Beds have been known since the area was first surveyed by the Geological Survey (de la Beche 1839). The Stourscombe Beds and the Yeolmbridge Beds are newly identified stratigraphical units recognized within the area mapped as Lower Culm by the Geological Survey (Tavistock and Launceston Sheet—No. 337).

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Specimens which have been described and figured in the palaeontological part of this paper are placed in museums which have been abbreviated in the descriptions as follows: GSM, Geological Survey Museum, London. BM, British Museum (Nat. Hist.), London. SMC, Sedgwick Museum, Cambridge. BU, Geology Museum, University of Bristol. PMC, Penzance Museum, Cornwall.

All localities mentioned in the text are to be found on the Ordnance Survey One Inch Sheet No. 186, and are referred to by their O.S. National Grid Reference.

The terminology used in the descriptions of the ammonoids is similar to that employed in the *Treatise on Invertebrate Paleontology* (*Part L. Mollusca*); foreign specimens, included in tables for comparative purposes, are referred to by the date of the

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paper from which the information was taken. Abbreviations are to be interpreted as follows: W. T.—whorl thickness, W. H.—whorl height, D.—diameter, U.—umbilicus. The trilobite terminology is that of Goldring (1955).

STRATIGRAPHY

The Petherwin Beds

The Geological Survey (Reid *et al.* 1911) applied the name Petherwin Beds to a thick succession of slates containing thin calcareous bands with brachiopods, and also to thicker limestones with abundant ammonoids which are associated with the slates. The stratigraphical relationships of these two lithologies cannot be determined in the field. However, it appears highly probable that the ammonoid-bearing limestones, which represent a very different sedimentary facies from the main bulk of the slates, are not interbedded with them, but constitute an underlying group of strata. The brachiopod slates are here referred to the Upper Petherwin Beds and the ammonoid bearing limestones and associated strata, which include a sandstone, to the Lower Petherwin Beds.

The Lower Petherwin Beds. Only two exposures yield fossils of the Lower Petherwin Beds at the present time. The more complete section is at the locality described (Reid *et al.* 1911) as the Gatepost Quarry (SX 326 821). The fauna, which is largely confined to a rottenstone horizon, includes:

Gonioclymenia (*Kalloclymenia*) *biimpressa* (von Buch 1839)—BU 12876.
Clymenia hoevelensis (Wedekind 1914)—BU 12864.
Kosmoclymenia undulata (Münster 1832)—BU 12868–70.
K. bisulcata (Münster 1840)—BU 12867.
K. sedgwicki (Münster 1840)—BU 12871.
Cymaclymenia striata (Münster 1832)—BU 12872, 12873.
C. camerata Schindewolf 1923—BU 12874, 12875.
Imitoceras cf. *lineare* (Münster 1832)—BU 12878.
Phacops (*Phacops*) *granulatus* (Münster 1840)—BU 12917, 12918.
P. (*Phacops*) *accipitrinus accipitrinus* (Phillips 1841)—BU 12926, 12927.

The second locality is at a neighbouring road section, by Oldwit Farm (SX 319 819), where the following have been identified:

Gonioclymenia (*Kalloclymenia*) *sp.*
Clymenia hoevelensis (Wedekind 1914)—BU 12865, 12866.
Kosmoclymenia sp.
Cymaclymenia sp.

The ammonoids obtained from these two localities show that the fauna of the Lower Petherwin Beds is closely comparable to that of the lower (*Clymenia hoevelensis*) subzone of the German *Clymenia* Zone.

An examination of the available specimens from the Launceston district in the Geological Survey Museum, the British Museum (Nat. Hist.), the Sedgwick Museum, and the Museum at Penzance reveals that a number of species formerly collected from the beds is not present in the fauna from the two localities mentioned above. The species in question are characteristic of the *Platyclymenia* Zone of the continental succession. It thus appears that the strata referable to this zone were formerly exposed in the district. Many of the specimens in the old collections are not properly localized, but most of them certainly come from the old limestone quarry at Landlake (SX 328 823) now completely filled with refuse. Enough specimens are clearly labelled as coming from this quarry to make it certain that the *Platyclymenia* Zone was exposed there. In addition, specimens of the same species as those occurring in the Gatepost Quarry have also been recorded from this quarry; it is thus evident that the lower *Clymenia* Zone was also once exposed. The fauna, with revised identifications, of the Landlake Limestone Quarry is as follows:

Costaclymenia muensteri (Ansted 1838)—SMC H4010.
Gonioclymenia (*Kalloclymenia*) *biimpressa* (von Buch 1839)—GSM 7083.
Platyclymenia (*Platyclymenia*) *walcotti* Wedekind 1914—GSM 57322.
P. (*Platyclymenia*) *richteri* Wedekind 1914—GSM 57323, 57327.
P. (*Platyclymenia*) *annulata* (Münster 1832)—?GSM 57328.
P. (*Platyclymenia*) *valida* (Phillips 1841)—GSM 7176.
P. (*Platyclymenia*) *bicostata* Wedekind 1914—SMC H992.
P. (*Platyclymenia*) *pattisoni* (M'Coy 1851)—SMC H990.
Clymenia hoevelensis (Wedekind 1914)—GSM 57314, 57315, 57324; SMC H989, H4012.
Kosmoclymenia undulata (Münster 1832)—GSM 57317, 57318, 7176; BM 37955; SMC H4011, H4013, H1488; PMC 152.
K. bisulcata (Münster 1840)—SMC H988.
K. sedgwicki (Münster 1840)—GSM 57325, 57326; SMC H1487; BM C51014.
K. linearis (Münster 1832)—?GSM 57316.
Cyrtoclymenia plicata (Münster 1839)—GSM 7174, ?7172.
C. angustiseptata (Münster 1832)—BM 37827.
Imitoceras cf. *disciforme* Schindewolf 1923—GSM 57300.
I. cf. *quadripartitum* (Münster 1839)—GSM 57303.
Sporadoceras rotundum Wedekind 1908—GSM 57301.
Phacops (*Phacops*) *granulatus* (Münster 1840)—PMC 113.
Cyrtosymbole) (?*Waribole*) *dunhevedensis* (Thomas 1909).

The Upper Petherwin Beds. Ammonoids and trilobites are particularly rare in the Upper Petherwin Beds. A single distorted specimen of the genus *Kosmoclymenia*, together with a trilobite cranidium referable to the subgenus *C.* (*Waribole*), has been discovered in the brachiopod slates of the Lower Landlake Slate Quarry (SX 328 824).

The Stourscombe Beds

The name Stourscombe Beds has been used for a group of nodular and thin-bedded cherts and slates which have yielded a rich fauna of ammonoids and trilobites. The ammonoid fauna has largely been collected from the nodular development of the Stourscombe Beds seen in two disused quarries near Stourscombe (SX 344 839). In the westerly quarry it has been possible to divide the beds into two faunal divisions; an upper division characterized by the genus *Wocklumeria* and a lower division in which *Parawocklumeria* is abundant and *Wocklumeria* absent. This faunal division may be compared closely to the subzone of *P. paradoxa* (Wedekind) which forms the upper part of the *Wocklumeria* Zone in Germany. The fauna from Stourscombe includes:

**Gonioclymenia* (*Kalloclymenia*) *frechi* Lange 1929—GSM 87075; BU 12802, 12803.
G. (*Kalloclymenia*) *wocklumensis* Lange 1929—GSM 87076, 87077; BU 12799–801.
†*Wocklumeria sphaeroides* (Rh. Richter 1848)—GSM 87033–7; BU 12824–8.
†*Epiwocklumeria dunhevedensis* sp. nov.—GSM 87038.
Postglatziella carinata Schindewolf 1937—GSM 87039, 87040; BU 12815, 12816.
Kosmoclymenia undulata (Münster 1832)—GSM 87097; BU 12808, 12809.
K. bisulcata (Münster 1840)—GSM 87041; BU 12810, 12811.
K. linearis (Münster 1832)—GSM 87042; BU 12806, 12807.

K. wocklumeri (Wedekind 1914)—GSM 87078; BU 12805.
*_K. serpentina_ (Münster 1832)—BU 12804.
*_K. pattisoni_ sp. nov.—GSM 87043.
Cyrtoclymenia plicata (Münster 1839)—GSM 87080.
C. angustiseptata (Münster 1832)—BU 12813, 12814.
*_C. tetragona_ Schmidt 1924—GSM 87044; BU 12812.
Cymaclymenia striata (Münster 1832)—BU 12836.
*_C. striata_ var. nov.—GSM 87045, 87046.
*_C. cordata_ Wedekind 1914—GSM 87047.
C. camerata Schindewolf 1923—GSM 87048; BU 12843, 12853.
C. constricta sp. nov.—GSM 87049, 87050; BU 12837, 12839–42.
C. constricta sp. nov. var. A nov.—GSM 87052.
*_C. constricta_ sp. nov. var. _globosa_ nov.—GSM 87051.
*_Parawocklumeria laevigata_ sp. nov.—GSM 87053–6; BU 12829–34.
*_P. laevigata_ sp. nov. var. _obesa_ nov.—GSM 87088.
*_Parawocklumeria sp._—GSM 87057.
Kenseyoceras (_Kenseyoceras_) _rostrata_ subgen. et sp. nov.—GSM 87058–63; BU 12844–7.
_K._ (_Mayneoceras_) _sinuconstricta_ subgen. et sp. nov. GSM 87069; BU 12835.
_K._ (_Mayneoceras_) _nucleus_ (Schmidt 1924)—GSM 87064–8; BU 12848–9.
Imitoceras lineare (Münster 1832)—GSM 87083; BU 12819, 12820.
I. substriatum (Münster 1840)—GSM 87084; BU 12882.
I. intermedium Schindewolf 1923—GSM 87085; BU 12821.
I. varicosum Schindewolf 1923—GSM 87086.
*_I. subbilobatum_ (Münster 1839)—GSM 87087.
*_Discoclymenia cucullata_ (von Buch 1839)—GSM 87070.
*_D. cornwallensis_ sp. nov.—GSM 87071, 87072.
*_D._ aff. _cornwallensis_ sp. nov.—GSM 87073.
*_Sporadoceras orbiculare_ (Münster 1832)—BU 12817, 12818.
*_S. orbiculare_ var.—GSM 87074.
Phacops (_Phacops_) _granulatus_ (Münster 1840)—BU 12920, 12921.
_P._ (_Phacops_) _accipitrinus accipitrinus_ (Phillips 1841)—BU 12928.
_P._ (_Phacops_) _wedekindi_ Rud. & E. Richter 1926—BU 12930–2.
_P._ (_Phacops_) _ensae_ Rud. & E. Richter 1926—BU 12935–8.
_P._ (_Cryphops_?) _wocklumeriae_ Rud. & E. Richter 1926—BU 12943–4.
*_P._ (_Dianops_) _sp._—GSM 87091.
*_Chaunoproetus_ aff. _carnicus_ (Rud. Richter 1913)—GSM 87092.

* Lower faunal division only.
† Upper faunal division only.

A few ammonoids have been collected from Overwood Farm (SX 303 873). At this locality there are relatively few siliceous nodules, and the majority of these are unfossiliferous. The slates, on the other hand, have yielded a large number of trilobites. The fauna from this locality includes:

_G._ (_Kalloclymenia_) _sp._
Wocklumeria sp.
Cyrtoclymenia angustiseptata (Münster 1832)—GSM 87081.
Parawocklumeria sp.
Phacops (_Phacops_) _granulatus_ (Münster 1840)—BU 12923–5.
_P._ (_Phacops_) _accipitrinus accipitrinus_ (Phillips 1841)—BU 12929; PMC 100 (labelled 'Near Yeolmbridge').
_P._ (_Cryphops_?) _ensae_ Rud. & E. Richter 1926—BU 12940–2.
Cyrtosymbole (_Waribole_) cf. _warsteinensis_ Rud. & E. Richter 1926—BU 12945–7.
_C._ (_Waribole_) aff. _conifera_ Rud. & E. Richter 1926—GSM 87093; BU 12951.
_C._ (_Waribole_) aff. _italica_ (Gortani 1907)—GSM 87094–5; BU 12956, 12957.
_C._ (_Macrobole_?) aff. _bergica_ Rud. Richter 1913—GSM 87096; BU 12962, 12963.
_C._ cf. _nepia_ Rud. & E. Richter 1926—BU 12958–60.

Similar trilobite-bearing slates occur at three localities in the Devonian inlier at Lifton; Heale Farm (SX 362 862), Smallacombe Farm (SX 375 860), and Coombe Farm (SX 386 858).

The slates with thin cherts, which form the more extensive development of the Stourscombe Beds, are generally unfossiliferous. Formerly these beds were included in the

Lower Carboniferous, but the discovery of a single specimen (GSM 87082) of *Parawockhumeria distorta* (Tietze 1870) from a locality north-north-west of Oldtree Lodge (SX 306 846) and other ammonoids from widely separated localities now enables these slates to be correlated with the upper part of the *Wockhumeria* Zone.

The Yeolmbridge Beds

The name Yeolmbridge Beds has been applied to a series of slates, sandstones, and limestones which conformably succeed the Stourscombe Beds.

The fauna from these beds is largely restricted to two localities; at Penfoot (SX 302 833) and Yeolmbridge (SX 322 875). At Penfoot the bulk of the fauna has been obtained from a nodular limestone and includes:

Gattendorfia subinvoluta (Münster 1839)—BU 12886–90.
G. crassa Schmidt 1924—BU 12882–3.
G. tenuis Schindewolf 1952—BU 12885.
G. occlusa Librovitch 1940—BU 12884, 12915.
Imitoceras lineare (Münster 1832)—BU 12893.
I. cf. *intermedium* Schindewolf 1923—BU 12894, 12895.
I. cf. *substriatum* (Münster 1840)—BU 12896.
C. (*Macrobole*) *drewerensis* Rud. & E. Richter 1951—BU 12904–8.
C. (*Macrobole*) *duodecimae* Rud. & E. Richter 1951—BU 12911, 12912.

At Yeolmbridge the fauna has been obtained from two exposures in the disused Yeolmbridge Slate Quarry; one consisting of a fresh limestone on the north side of the quarry, and the other of decalcified lenticles occurring in a sandy slate on the south side of the quarry. The fauna includes:

Gattendorfia sp.—BU 12892.
Imitoceras sp.
Cyrtosymbole (*Macrobole*) *drewerensis* Rud. & E. Richter 1951—GSM 87098, 87099; BU 12901–3.
C. (*Macrobole*) *duodecimae* Rud. & E. Richter 1951—GSM 87100; BU 12913, 12914.
C. (*Macrobole*) aff. *blax* Rud. & E. Richter 1951—GSM 87101; BU 12910.
C. (*Macrobole*) *sp.*—GSM 87097; BU 12909.

The fauna obtained from these localities in the Yeolmbridge Beds is very similar to that obtained from the *Gattendorfia* Zone of the Continent.

SYSTEMATIC DESCRIPTIONS

Ammonoids

Family GONIOCLYMENIIDAE Hyatt 1884
Genus COSTACLYMENIA Schindewolf 1920
Costaclymenia muensteri (Ansted 1838)

Plate 26, fig. 1

1838 *Endosiphonites münsteri* Ansted, p. 419, pl. 8, fig. 1.
1852 *Clymenia muensteri* M'Coy, p. 402, pl. 2A, fig. 12.
1950 *Costaclymenia binodosa* G. & H. Termier, p. 77, pl. 160, figs. 28–30.

Holotype (by monotypy). SMC H4010. Pl. 26, fig. 1.

Type locality. Landlake Limestone Quarry, nr. Launceston.

Horizon. Lower Petherwin Beds.

Remarks. Gümbel (1863) states that *C. muensteri* is identical to *Clymenia binodosa* which was figured by Münster in 1839 (pl. 2, figs. 3*a*–*c*). On this contention Ansted's name should have had priority, but it was not used because Münster's species was allegedly conspecific with *Goniatites binodosus* Münster 1832 (pl. 6, figs. 5*a*, *b*). However, the two specimens figured by Münster are not obviously conspecific, and since *C. muensteri* is quite distinct from Münster's earlier figures Ansted's species is still valid.

Only a single specimen has been recorded, and although this specimen closely resembles *C. binodosa* (Münster 1839) it is not considered to be identical to it, for the ribs and tubercles are more numerous and less prominent. In addition the whorl flanks in *C. muensteri* converge slightly towards the venter, whereas the whorl cross-section of *C. binodosa* is rectangular.

The whorl cross-section and the rather weak ornament make the specimens figured by G. & H. Termier (1950) closer to *C. muensteri* than to *C. binodosus.*

Mr. A. G. Brighton has drawn the author's attention to a manuscript note with the specimen which reads: 'It appears to have been subsequently to the drawing of Ansted's figure broken, and in that state was refigured by M'Coy. . . . Since then the greater part of the missing piece has been restored.'

Measurements of holotype (in mm.). D. 97, W.H. 36, W.T. 18, U. 41.

Genus GONIOCLYMENIA Hyatt 1884

Subgenus GONIOCLYMENIA (KALLOCLYMENIA) Wedekind 1914

Remarks. The genus *Kalloclymenia* was erected by Wedekind in 1914, and distinguished from *Gonioclymenia* with which its species had previously been included by the following characters: (*a*) the absence of a spiral groove on the venter, (*b*) the nature of the ribs, and (*c*) the lower rectangular whorl cross-section. The suture-line is, by diagnosis, indistinguishable from that of *Gonioclymenia.* Lange (1929) observed that only the first criterion is valid for generic diagnostic purposes and suggested that the name *Kalloclymenia* be reduced to subgeneric status.

In the *Treatise on Invertebrate Paleontology* (1957) the generic status of *Kalloclymenia* is reaffirmed with a note that the ventral sinus and the low rectangular whorl cross-section are diagnostic. The author does not agree with the latter contention, for G. (*K.*) *wocklumensis* Lange 1929 in particular has a whorl section in which the whorl height is considerably in excess of the whorl thickness. It is therefore proposed to continue the usage of Lange, for the important stratigraphical position which has been ascribed to *Kalloclymenia* on the Continent, which might conceivably warrant generic status, is not valid in Cornwall.

On the Continent the incoming of *Kalloclymenia* has proved a useful datum to mark the lower limit of the *Wocklumeria* Zone. In Cornwall, however, *Kalloclymenia* occurs earlier, for it has been found associated with the index fossil of the lower *Clymenia* Zone in the Petherwin Beds. It thus appears that the lower limit of the *Wocklumeria* Zone needs redefinition. This problem will be discussed in a later paper on the stratigraphy of the area.

The reduction of *Kalloclymenia* to a subgenus of *Gonioclymenia* raises the question of the status of *Otoclymenia* Schindewolf 1923, for this genus was reduced (Schindewolf 1937) to a subgenus of *Kalloclymenia.* The distinctive ornament of parabolic ribs and nodes undoubtedly means that it should be distinguished from *Kalloclymenia*; it is suggested that *Otoclymenia* be referred to a new subgenus of *Gonioclymenia.*

Gonioclymenia (*Kalloclymenia*) *biimpressa* (von Buch 1839)

Plate 26, fig. 2

1841 *Goniatites insignis* Phillips, p. 119, pl. 49, fig. 228.
1929 *Gonioclymenia* (*Kalloclymenia*) *biimpressa* Lange, p. 80, pl. 2, fig. 20, text-figs. 16, 17.
1950 *Gonioclymenia insignis* G. & H. Termier, p. 77, pl. 160, figs. 20–22.

Remarks. Goniatites insignis was referred by Gümbel (1863) to *Gonioclymenia subarmata* (Münster), but the specimen figured by Phillips lacks the characteristic, rather noded ornament of Münster's species (1832, pl. 6, fig. 2). The ornament is much closer to that of *G.* (*Kalloclymenia*) *biimpressa* (von Buch), the holotype of which was refigured by Lange (1929). It does seem, however, that the ornament persists in the British specimens on to more mature whorls than on the holotype.

Measurements of figured specimen (GSM 7083) (in mm.). D. 61, W.H. 15·5, U. 34.

Gonioclymenia (*Kalloclymenia*) *frechi* Lange 1929

1929 *Gonioclymenia* (*Kalloclymenia*) *frechi* Lange, p. 81.

Remarks. The specimens occurring in Cornwall are very close to the described species but show a relatively greater whorl height.

Gonioclymenia (*Kalloclymenia*) *wocklumensis* Lange 1929

1929 *Gonioclymenia* (*Kalloclymenia*) *wocklumensis* Lange, p. 79, pl. 2, figs. 18, 18*a*, text-figs. 14, 15.

Remarks. In the Cornish specimens the whorl height is relatively greater, and the convergence of the flattened flanks at the venter is less than that indicated in Lange's original description. It has been observed that the mature suture line does not develop until approximately the fifth or sixth whorl; i.e. a diameter of some 15 mm. The adventitious lobe does not make its appearance until the fourth whorl. The whorl cross-section in the young stages is much squarer than that exhibited in the mature form.

Family WOCKLUMERIIDAE Schindewolf 1937

Genus WOCKLUMERIA Wedekind 1918

Wocklumeria sphaeroides (Rh. Richter 1848)

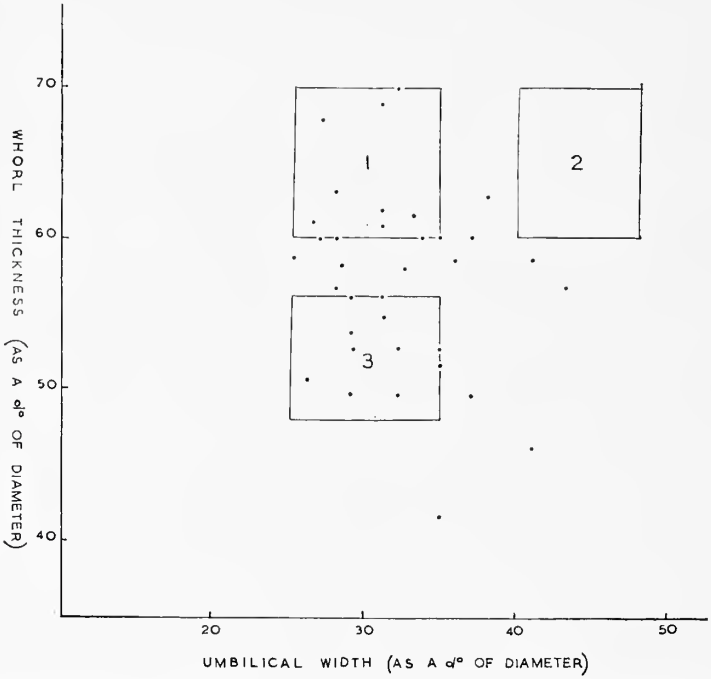
Plate 26, figs. 3–5; text-fig. 1

1937 *Wocklumeria sphaeroides* Schindewolf, p. 69, pl. 1, figs. 12–15; pl. 2, figs. 1–3, text-fig. 12 (with previous synonymy).
1937 *Wocklumeria plana* Schindewolf, p. 70, pl. 2, figs. 4–6.
1937 *Wocklumeria aperta* Schindewolf, p. 71, pl. 2, figs. 7–9, text-fig. 14.
1954 *Wocklumeria sphaeroides* Pfeiffer, p. 58, pl. 8, figs. 5, 6.
1954 *Wocklumeria plana* Pfeiffer, p. 58, pl. 8, fig. 7.

Remarks. The genus *Wocklumeria*, monospecific when erected by Wedekind (1918), was reinvestigated by Schindewolf (1937) who, after a study of many specimens, recognized two additional species *W. plana* and *W. aperta*, closely related to the genotype.

A study of a number of specimens from Cornwall has revealed a much greater variability than was noticed by Schindewolf in his material. A number of gradational forms have been found between *W. plana* and *W. sphaeroides*, and between *W. aperta* and *W.*

sphaeroides. The scatter diagram (text-fig. 1) shows that there is a complete gradation existing between the extreme globose and extreme discoidal forms. The suture-lines of the two species recognized by Schindewolf in this range are, by diagnosis, identical; thus the remaining distinguishing feature is the height of the aperture. Since '*sphaeroides*' forms have been seen with '*plana*' apertures and vice versa there appears no reason to separate the two.



TEXT-FIG. 1. Scatter diagram of specimens of *Wocklumeria* from the Stourscombe Beds. The limits of species defined by Schindewolf are indicated thus: (1) *W. sphaeroides*, (2) *W. aperta*, (3) *W. plana*.

In both German and British specimens there is a preponderance of specimens within the limits formerly defining *W. sphaeroides* and *W. plana*. No Cornish specimen falls within the limits of *W. aperta* as defined by Schindewolf, though several specimens are very close to it. Since Schindewolf defined *W. aperta* on only six specimens there is probably no significance in this fact and nothing to indicate an interruption in the continuous variation of *W. sphaeroides*.

In the light of this evidence, there appears little basis for the division of the range of forms of *W. sphaeroides*; *W. plana* and *W. aperta* are consequently here considered to be synonyms of Richter's species. It has thus become necessary to redefine *W. sphaeroides* in more general terms.

Diagnosis. *Wocklumeria* with discoidal to globose shell, moderately wide umbilicus and low aperture. Young forms triangular in outline impressed by three deep constrictions; adult stage rounded, normally lacking constrictions. Ventral lobe deep, pointed, first lateral saddle rounded passing into a moderately wide and pointed first lateral lobe; this lobe is as deep or deeper than the ventral lobe. Second lateral saddle rounded, umbilical lobe broad, divided at the umbilical seam by a strong saddle; prongs of umbilical lobe pointed. Dorsal lobe pointed, with almost parallel sides. First and second dorso-lateral saddles rounded, separated by pointed dorso-lateral lobe.

Description. Shell discoidal to globose, involute, greatest thickness at the umbilicus. Five to six whorls, involution considerable, umbilicus moderately large to small, deep; revealing the triangular shape of the earlier whorls. Laterally whorls slightly to moderately compressed, strongly rounded ventrally, flanks deeply impressed by the preceding whorl, aperture small. Body chamber one whorl, anterior portion deviating from the normal whorl spiral, thus considerably increasing the size of the umbilicus at this point. Aperture marked posteriorly by a constriction. Suture-line, see Schindewolf (1937, text-figs. 12*a*, *b*). Chamber posterior to body chamber small in mature specimens. Siphuncle dorsal, septal necks retrochoanitic extending to almost half a chamber in length.

Young stages impressed by three deep constrictions, these occupy the same relative positions on each whorl so that a pronounced triangular shape is produced. With age the constrictions weaken and finally disappear.

Ornament has not been seen on the Cornish specimens, but Schindewolf records occasional intensified growth lines which follow a straight course over the flanks and venter. In addition, a slight spiral ornament has been recorded.

Genus EPIWOCKLUMERIA Schindewolf 1937 emend.

1937 *Epiwocklumeria* Schindewolf, p. 72.

Remarks. *Epiwocklumeria* was erected by Schindewolf using *Wocklumeria paradoxa* var. *applanata* Wedekind 1918 as the monogenotype. The affinities of *Epiwocklumeria* to the Gonioclymeniaceae were demonstrated; in the same work *Wocklumeria paradoxa* Wedekind, which was referred to the genus *Parawocklumeria* Schindewolf (1926), was placed in the Parawocklumeriaceae.

On the basis of the suture-line a new Cornish species belongs to the genus *Epiwocklumeria*, but it has several characters of *Parawocklumeria*, including a subglobose shape and straight constrictions; features thought by Schindewolf to be of generic importance. The addition of the new species requires modification of the generic diagnosis.

Emended diagnosis. A genus of the Wocklumeriidae with discoidal to globose form, shell broadly triangular in outline, the sides and venter impressed by three strong constrictions. Umbilicus almost closed. Ventral lobe of suture line deep, pointed; first lateral saddle rounded passing into an open V-shaped first lateral lobe. Second lateral saddle gently rounded, umbilical lobe shallow, divided at the umbilical seam by a small saddle. Dorsal lobe broad, V-shaped. First and second dorso-lateral saddles rounded, separated by a rounded dorso-lateral lobe.

Comparison with other genera. This genus resembles *Wocklumeria* on the basis of the suture-line, but differs in the very small size of the umbilicus, the more compressed form, and the absence of several contrasting stages during development. *Epiwocklumeria* shows a marked superficial similarity to *Parawocklumeria* but it has a fundamentally different suture-line.

Epiwocklumeria dunhevedensis sp. nov.

Plate 26, figs. 6, 7; text-fig. 2

Derivation of name. After Dunheved, the ancient name of Launceston.

Holotype. GSM 87038, Pl. 26, figs. 6, 7, text-fig. 2.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Upper faunal division).

Material. Only a single internal mould known.

Diagnosis. Shell subglobose, triangular in outline, the sides and venter impressed by three pronounced constrictions. Umbilicus almost closed. Suture-line typical of the genus, the ventral lobe being shallow and rounded.

Description. Species of *Epiwocklumeria* with subglobose shell, involute, greatest thickness at the umbilicus; involution almost entire, umbilicus minute, deep, and triangular in outline. Laterally whorls moderately compressed, strongly rounded ventrally; greatly impressed by the preceding whorl. Flanks marked by three constrictions following a straight course from the umbilicus to the periphery, being gently arched forwards over the venter. Body chamber approaches one whorl in length. External suture (text-fig. 2) typical of the genus; ventral lobe small, rounded. First lateral saddle pronounced, passing into a pointed, deep first lateral lobe. Second lateral lobe broadly rounded, passing into rounded umbilical lobe. No ornament has been observed.

TEXT-FIG. 2. *Epiwocklumeria dunhevedensis* sp. nov.; holotype, GSM 87038, suture-line at 16 mm. diameter.

Measurements of holotype (in mm.). D. 17, W.H. 8, W.T. 11, U. 1.

Comparisons. This species differs from *Epiwocklumeria applanata* in the greater whorl thickness, the straight course of the constrictions over the whorl sides, and the size of the ventral lobe. Were it not for the characteristic suture line it would be difficult to distinguish this species from *Parawocklumeria laevigata* sp. nov.

Family GLATZIELLIDAE Schindewolf 1928

Genus POSTGLATZIELLA Schindewolf 1937

Postglatziella carinata Schindewolf 1937

Plate 26, figs. 8, 9

1937 *Postglatziella carinata* Schindewolf, p. 82, pl. 3, figs. 4–7, text-figs. 19*a*, *b*.

Remarks. The few specimens from Stourscombe referable to this species differ from Schindewolf's specimens only in having the ribs more widely spaced.

Family CLYMENIIDAE Edwards 1849
Genus PLATYCLYMENIA Hyatt 1884
Platyclymenia (*Platyclymenia*) *valida* (Phillips 1841)

Plate 26, fig. 10

1841 *Clymenia valida* Phillips, p. 126, pl. 54, fig. 245.
non 1914 *Platyclymenia valida* Wedekind, p. 37, pl. 3, figs. 3, 4.
non 1956 *Platyclymenia* (*Platyclymenia*) *valida* Müller, p. 70, pl. 2, fig. 10.

Holotype (by monotypy). GSM 7176. Pl. 26, fig. 10.

Type locality. Landlake Limestone Quarry, nr. Launceston.

Horizon. Lower Petherwin Beds.

Diagnosis. Platyclymenia with wide umbilicus and strong, closely spaced ribs on the young whorls. Ribs on the later whorls weaken in intensity, broaden, and become widely spaced at the umbilicus; towards the venter these give rise to three to four weak secondary and intercalatory ribs. Whorl cross-section rectangular.

Description. Shell evolute, with only very slightly embracing whorls. Umbilicus large, moderately deep, in complete specimens probably exposing all of the inner whorls. Whorl flanks flattened, particularly in the mature shell; venter broadly rounded to flattened. Whorl cross-section rectangular, considerably higher than wide.

Ornament on the inner whorls comprises distinct, irregularly spaced concave ribs. Frequently two or three ribs apparently arise from an almost common origin, this gives an irregular, noded appearance to the umbilical rim. On the succeeding whorls the ribs weaken and become more regular and closely spaced. On the final part of the last whorl the ribs at the umbilicus become quite widely spaced and broadly rounded. Towards the venter these divide into three to four fine, but weak, sigmoidal ribs. The fine ribs, some of which appear to be intercalatory, arise from a slightly raised area at approximately the mid-point of the flanks; as a result a weak spiral line is produced. Suture-line (Phillips 1841, p. 126, pl. 54, fig. 245*b*) typical of the genus.

Measurements of holotype (in mm.). D. 40, W.H. 13, W.T. 6, U. 18.

Remarks. The specimens figured and described by Wedekind (1914, p. 37, pl. 3, figs. 3, 4) as *Platyclymenia valida* (Phillips) lack the characteristic bifurcating ribs of the holotype, and appear to represent a new species not recorded from the Petherwin Beds. There are other records of the occurrence of the species in Germany which are unaccompanied by figures (Schindewolf 1923, Lange 1929, Matern 1931, Freyer 1957); it seems probable from the descriptions that reference was being made to the descriptions and figures of Wedekind rather than to those of Phillips.

Platyclymenia (*Platyclymenia*) *bicostata* Wedekind 1914

1914 *Platyclymenia bicostata* Wedekind, p. 36, pl. 3, figs. 16–18.
1923 *Platyclymenia bicostata* Schindewolf, p. 450.
1927 *Platyclymenia bicostata* Schlosser, p. 5, fig. 21.
1931 *Platyclymenia bicostata* Matern, p. 100.
1957 *Platyclymenia bicostata* Freyer, p. 56.

Remarks. A single specimen of this species is recorded from the Landlake Limestone Quarry. This specimen shows the characteristic paired ribs of the species. The posterior member of each pair of ribs is normally more strongly developed than the anterior. In the mature whorls the intensity of the ribbing decreases; a fragment of the latest whorl preserved appears to be almost smooth.

Platyclymenia (*Platyclymenia*) *pattisoni* (M'Coy 1851)

Plate 26, fig. 11

1851 *Clymenia pattisoni* M'Coy, p. 488.
1852 *Clymenia pattisoni* M'Coy, p. 403, pl. 2A, fig. 11.
1854 *Clymenia pattisoni* M'Coy, p. 293.
1855 *Clymenia subnautilina* Sandberger, p. 5, pl. 1, figs. 1*a–f*.
1910 *Clymenia pseudoflexuosa* Rzehak, p. 181, pl. 1, fig. 1, pl. 2, figs. 8, 9.
1914 *Platyclymenia quenstedi* Wedekind, p. 45, pl. 3, fig. 10, pl. 2, fig. 5.
1922 *Platyclymenia subnautilina* (= *Platyclymenia quenstedi*) H. Schmidt in Kegel, p. 39.
1923 *Platyclymenia quenstedi* Schindewolf, p. 457, text-fig. 19*a*.
1929 *Platyclymenia* (*Varioclymenia*) *subnautilina* Lange, p. 102.
1931 *Platyclymenia quenstedi quenstedi* Matern, p. 102.
1950 *Platyclymenia quenstedi* G. & H. Termier, p. 74, pl. 154, figs. 8–11; pl. 157, figs. 31–33; pl. 161, figs. 18–20.
1956 *Platyclymenia* (*Platyclymenia*) *subnautilina* Müller, p. 73.

Holotype (by monotypy). SMC H990. Pl. 26, fig. 11.

Type locality. Landlake Limestone Quarry, nr. Launceston.

Horizon. Lower Petherwin Beds.

Remarks. Clymenia pattisoni M'Coy was referred by Gümbel (1863, p. 126) to *Clymenia flexuosa* Münster (1840). However, it is quite distinct from this species, for *C. pattisoni* has a suture-line characteristic of the genus *Platyclymenia*, whereas *C. flexuosa* has a suture-line typical of the genus *Kosmoclymenia*.

M'Coy's species is identical to *P.* (*Platyclymenia*) *subnautilina* (Sandberger) and its junior synonyms *P.* (*Platyclymenia*) *quenstedi* Wedekind, and *Clymenia pseudoflexuosa* Rzehak. Sandberger's original figures are good and Schmidt's synonymy appears quite

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EXPLANATION OF PLATE 26

Fig. 1. *Costaclymenia muensteri* (Ansted), Landlake Limestone Quarry. Holotype, SMC H4010, ×1.

Fig. 2. *Gonioclymenia* (*Kalloclymenia*) *biimpressa* (von Buch), Landlake Limestone Quarry. GSM 7083, ×1.

Figs. 3–5. *Wocklumeria sphaeroides* (Rh. Richter), Stourscombe. 3, 4, Lateral and ventral view of mature individual showing the change in spiral angle of the anterior part of the body chamber and the apertural constriction, GSM 87033, ×1. 5, Young specimen showing constrictions and triangular-shaped umbilicus, GSM 87037, ×2.

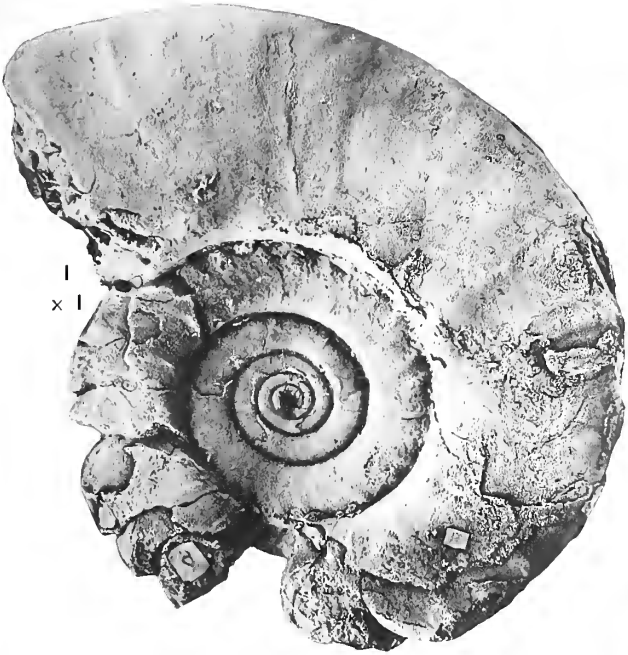
Figs. 6, 7. *Epiwocklumeria dunhevedensis* sp. nov., Stourscombe. Holotype, GSM 87038. 6, Lateral view showing straight constrictions, ×2. 7, Ventral view showing suture-line, ×1½.

Figs. 8, 9. *Postglatziella carinata* Schindewolf, Stourscombe. 8, GSM 87040, ×2. 9, GSM 87039, ×3.

Fig. 10. *Platyclymenia* (*Platyclymenia*) *valida* (Phillips), Landlake Limestone Quarry. Holotype, GSM 7176, ×1.

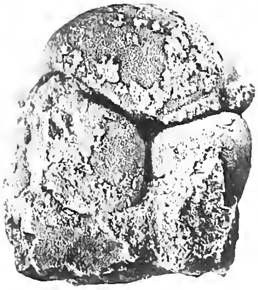
Fig. 11. *Platyclymenia* (*Platyclymenia*) *pattisoni* (M'Coy), Landlake Limestone Quarry. Holotype, SMC H990, ×2.

Fig. 12. *Kosmoclymenia linearis* (Münster), Stourscombe. GSM 87042, ×1.

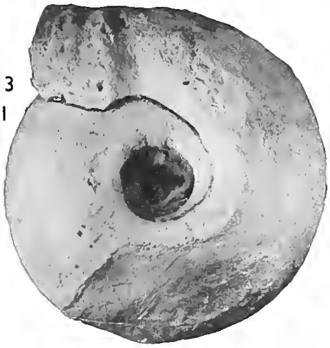

1 × 1


7 × 1½


12 × 1


6 × 2

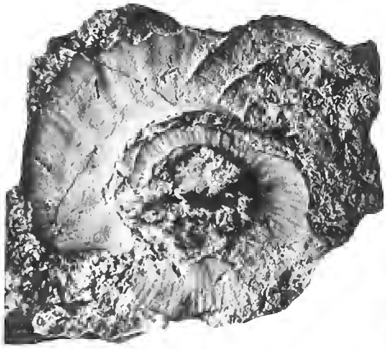

8 × 2


3 × 1

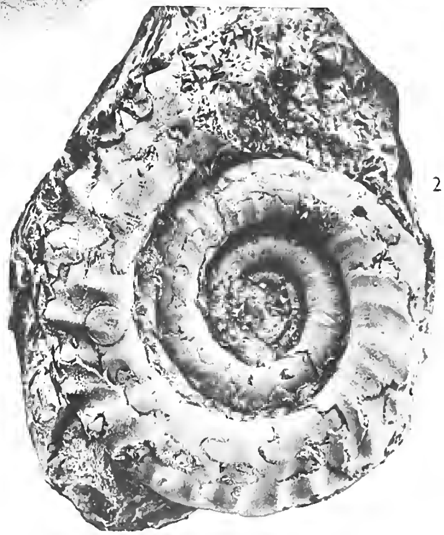

4 × 1


5 × 2


9 × 3


11 × 1


10 × 2


2 × 1

SELWOOD, Ammonoids from Cornwall

valid and was confirmed by Lange (1929) and by Müller (1956). The identity of *Platyclymenia pattisoni* with these species means that *Platyclymenia subnautilina* must now be reduced to a synonym of the Cornish species; the name of which has a priority of several years.

Measurements of holotype (in mm.). D. 20, W.H. 7, W.T. 5, U. 9·5.

Genus KOSMOCLYMENIA Schindewolf 1949

Kosmoclymenia pattisoni sp. nov.

Plate 27, fig. 1

Derivation of name. After Mr. S. R. Pattison, an early pioneer in Launceston geology.

Holotype. GSM 87043. Pl. 27, fig. 1.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Material. A single specimen showing both suture- and growth-lines.

Diagnosis. *Kosmoclymenia* with disk-shaped shell, umbilicus wide, deep for genus. Initially the whorls increase slowly in size, but the last 1½ whorls increase rapidly. Whorl height exceeds whorl thickness. Ornament consists of pronounced, raised growth lines.

Description. Shell evolute, planorbiform, with seven to eight very slightly embracing whorls. Umbilicus large, relatively deep, exposing all of the inner whorls. Up to a diameter of 2–3 mm. whorl thickness may equal whorl height, thereafter whorl height always exceeds whorl thickness. Venter broadly rounded. Initial increase in whorl size slight; last 1½ whorls increasing very rapidly, almost doubling in height in the last whorl. In young stages whorl sides rounded, later whorls broadly rounded to flattened. The rapid increase in size of the final whorl creates a rather deeper umbilicus than is normal for the genus. Ornament composed of biconvex growth lines. Suture-line typical of the genus.

Comparisons. The general appearance of the shell is similar to *K. wocklumeri*, but the flanks are not so flattened and they do not converge to a flattened venter. The ornament is also much stronger than in this species. *K. linearis* is characterized by a slow increase in the size of the whorl, and in consequence the umbilicus is very shallow. *K. sedgwicki* is more compressed and involuted than this species.

Measurements of holotype (in mm.). D. 50, W.H. 18, W.T. 14, U. 22.

Family CYRTOCLYMENIIDAE Hyatt 1884

Genus CYRTOCLYMENIA Hyatt 1884

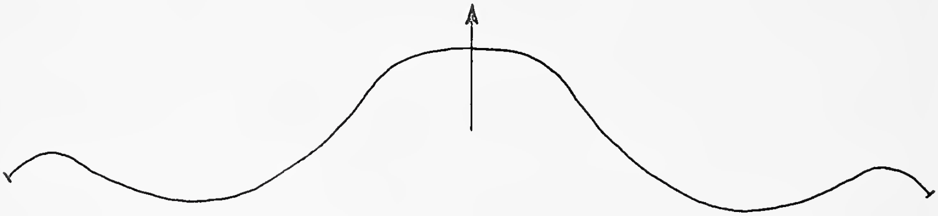
Cyrtoclymenia tetragona Schmidt 1924

Plate 27, fig. 11; text-fig. 3

1924 *Cyrtoclymenia tetragona* Schmidt, p. 127, pl. 6, figs. 22, 23.

Remarks. Specimens from Cornwall agree closely with the original description, and exhibit details of the suture-line not previously recorded. Just posterior to the body chamber the septa are crowded, but they become more widely spaced posteriorly. The suture-line consists of a pronounced, rather flattened, ventral saddle which passes into a broad, shallow lateral lobe. A weak lobe is developed at the umbilicus. A geniculate constriction mid-way along the body chamber is present on one specimen. The specimen figured is less globose than that illustrated by Schmidt.

Measurements of figured specimen (GSM 87044) (in mm.). D. 27·5, W.H. 13·5, W.T. 10·5, U. 4·5.



TEXT-FIG. 3. *Cyrtoclymenia tetragona* Schmidt; GSM 87044, suture-line at 26 mm. diameter.

Genus CYMACLYMENIA Hyatt 1884

Cymaclymenia striata var.

Plate 27, figs. 3, 4

Remarks. A number of specimens differ from *C. striata* (Münster 1832). The whorl thickness of these specimens is greater and the involution is considerable; the umbilicus only amounts to one-seventh of the shell diameter. This variety has only been found in the lower faunal division at Stourscombe.

Cymaclymenia constricta sp. nov.

Plate 27, figs. 8–10

Derivation of name. After the constrictions on the venter.

Holotype. GSM 87050. Pl. 27, figs. 8, 9.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

Material. Internal and external moulds.

Diagnosis. Discoidal *Cymaclymenia* with narrow umbilicus. Flanks and venter rather flattened; venter shows pronounced sinuate constrictions.

Description. Shell discoidal, involute, umbilicus narrow and deep but exposing all of the inner whorls. Whorl section rather compressed, whorl height just exceeding whorl thickness. Venter broadly rounded, becoming flattened in mature specimens; clearly marked by periodic sinuate constrictions which do not continue on to the flanks. Constrictions closely spaced in young specimens but more widely spaced in adult forms. Whorl flanks flattened at maturity, though broadly rounded in youth; tending to converge towards the venter. Final whorl increases rapidly in size, involution of this whorl two-thirds to four-fifths. Suture-line typical of the genus, though the ventral saddle is not well developed; eight to nine chambers per whorl. Preservation of the material is not delicate enough for growth lines to be preserved.

Measurements of holotype (in mm.). D. 17, W.H. 10, W.T. 7·5, U. 4.

Comparisons. The presence of constrictions is not a particularly common feature of this genus. *Clymenia semistriata* Münster (1832) exhibits constrictions over the flanks, but these are absent over the venter. The specimen figured by Münster (1840) as *Clymenia dorsocostata* appears to show constrictions over the venter, but these are much more closely spaced, and weaker, than those shown by the Cornish specimens, and appear to be produced by raised growth-lines.

Cymaclymenia constricta sp. nov. var. A

Plate 27, figs. 12, 13

Holotype. GSM 87052. Pl. 27, figs. 12, 13.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Remarks. This variety shows more widely spaced and decidedly weaker constrictions on the venter at all growth stages. In addition the increase in the size of the final whorl, and the amount of involution is not so great.

Measurements of holotype (in mm.). D. 32, W.H. 16, W.T. 12·5, U. 6·5.

Cymaclymenia constricta sp. nov. var. *globosa* nov.

Plate 27, figs. 14, 15

Holotype. GSM 87051. Pl. 27, figs. 14, 15.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Remarks. This variety, represented by a single specimen, shows a whorl thickness in excess of the whorl height; thus the shell is more globose than is normal for the species. The venter is strongly rounded and the first constrictions do not develop until a diameter of 13·5 mm. is reached.

Measurements of holotype (in mm.). D. 16·5, W.H. 8, W.T. 8·5, U. 4.

Family PARAWOCKLUMERIIDAE Schindewolf 1937

Genus PARAWOCKLUMERIA Schindewolf 1926

Parawocklumeria laevigata sp. nov.

Plate 27, figs. 16–20; text-fig. 4A

Derivation of name. After the smooth shell.

Holotype. GSM 87053. Pl. 27, figs. 18, 19.

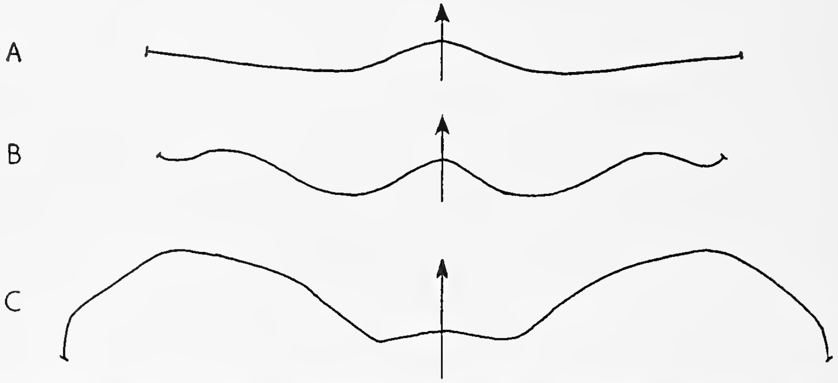
Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Material. Internal and external moulds.

Diagnosis. Parawocklumeria with discoidal to subglobose shell; umbilicus narrow, of triangular shape. Three strong constrictions give a pronounced trilobation to the shell. Ornament absent. Suture-line variable.

Description. Shell discoidal to subglobose, involute, greatest thickness at the umbilicus. Five to six whorls, involution almost complete. Umbilicus minute, deep, and triangular in shape. Whorls laterally compressed, strongly rounded ventrally, greatly impressed by the preceding whorl. Flanks marked by three deep constrictions, occupying the same relative position on each successive whorl. Constriction straight and radial on the flanks, swinging weakly forward over the venter. Shallow secondary constrictions, broader than the main constrictions and present only over the venter, occur anterior to



TEXT-FIG. 4. A, *Parawocklumeria laevigata* sp. nov.; GSM 87054, suture-line at 9 mm. diameter. B, *Parawocklumeria laevigata* sp. nov. var. *obesa* nov.; holotype, GSM 87088, suture-line at 6·5 mm. diameter. C, *Parawocklumeria sp.*; GSM 87057, suture-line at 10 mm. diameter.

EXPLANATION OF PLATE 27

Fig. 1. *Kosmoclymenia pattisoni* sp. nov., Stourscombe. Holotype, GSM 87043, ×1.

Fig. 2. *Kosmoclymenia bisulcata* (Münster), Stourscombe. GSM 87041, ×2.

Figs. 3, 4. *Cymaclymenia striata* var., Stourscombe. 3, specimen showing growth-lines, GSM 87046, ×1. 4, GSM 87045, ×$\frac{1}{2}$.

Fig. 5. *Cymaclymenia cordata* Wedekind, Stourscombe. GSM 87047, ×1.

Figs. 6, 7. *Cymaclymenia camerata* Schindewolf, Stourscombe. Ventral and lateral view, GSM 87048, ×1.

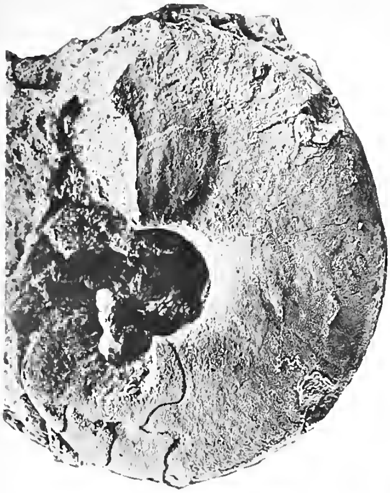
Figs. 8–10. *Cymaclymenia constricta* sp. nov., Stourscombe. 8, Lateral view of holotype, GSM 87050, ×1. 9, Ventral view of holotype showing constrictions on the venter, GSM 87050, ×1. 10, Ventral view of specimen with rather flattened venter, GSM 87049, ×1.

Fig. 11. *Cyrtoclymenia tetragona* Schmidt, Stourscombe, GSM 87044, ×1.

Figs. 12, 13. *Cymaclymenia constricta* var. A, Stourscombe. Ventral and lateral view, GSM 87052, ×1.

Figs. 14, 15. *Cymaclymenia constricta* var. *globosa* var. nov., Stourscombe. Lateral and ventral view, GSM 87051, ×2. The final part of the last whorl has been removed in fig. 14 to show the characteristic whorl cross-section.

Figs. 16–20. *Parawocklumeria laevigata* sp. nov., Stourscombe. 16, Ventral view showing secondary constriction lying just anterior to the main constriction on the venter, GSM 87055, ×2. 17, Ventral view of mature individual showing closely spaced suture-lines just posterior to the body chamber, GSM 87054, ×2. 18, 19, Lateral and ventral view of holotype, GSM 87053, ×2. 20, Specimen showing asymmetrical suture-lines, GSM 87056, ×3.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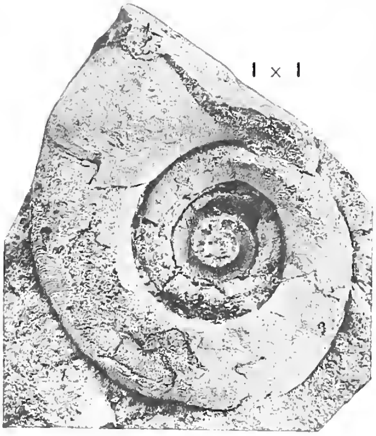
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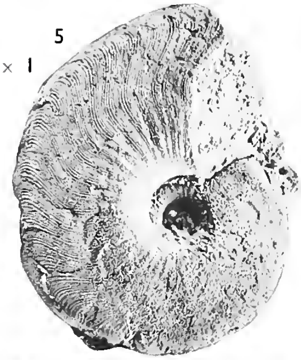
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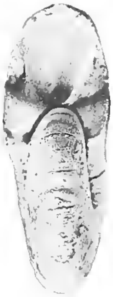
13 × 1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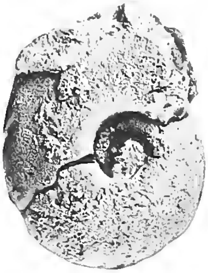
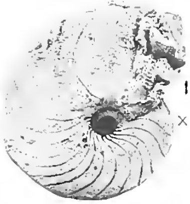

15 × 2


14 × 2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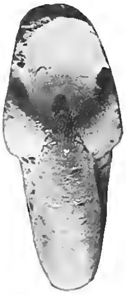
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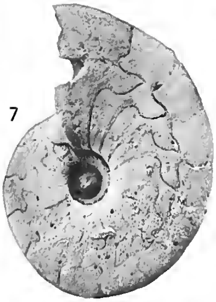
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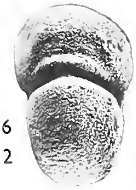
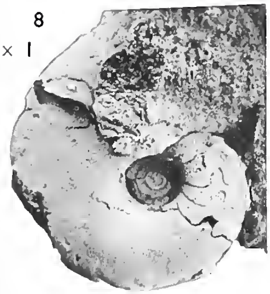

16 × 2


17 × 2

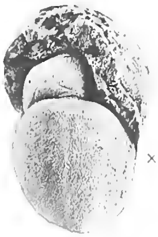

18 × 2


8 × 1


9 × 1


10 × 1


20 × 3


19 × 2

SELWOOD, Ammonoids from Cornwall

the main constrictions in some internal moulds. A median furrow is occasionally preserved extending between the constrictions on the internal mouls of some specimens (Pl. 27, fig. 19). Body chamber 1–1½ whorls. In mature specimens the final suture-lines become progressively more closely spaced. Siphuncle dorsal, septal necks retrochoanitic. External suture-line (text-fig. 4A) variable; ventral saddle broadly rounded passing into a very shallow lateral lobe and saddle. Umbilical lobe frequently not developed. Suture-line often asymmetrical in form (Pl. 27, fig. 20).

Measurements of holotype (in mm.). D. 16, W.H. 7, W.T. 10, U. 2.

Comparisons. Only *P. paradoxa* (Wedekind) bears comparison with the species. The marked ornament on the German species is absent in *P. laevigata*, and in addition the umbilicus of the Cornish species is wider and the ventral saddle of the suture line is less pronounced. Secondary constrictions are not present in *P. paradoxa*.

Parawocklumeria laevigata sp. nov. var. *obesa* nov.

Plate 28, figs. 1, 2; text-fig. 4B

Derivation of name. After globose shell.

Holotype. GSM 87088. Pl. 28, figs. 1, 2.

Type locality and horizon. As for *P. laevigata.*

Material. Internal and external moulds.

Diagnosis. Globose variety of the species possessing a suture-line closely resembling *P. paradoxa* (Wedekind).

Measurements of holotype (in mm.). D. 8, W.H. 4, W.T. 7·5, U. 0·75.

Comparisons. P. laevigata var. *obesa* is very similar to *P. laevigata*, and though it is somewhat more globose, the essential difference lies in the nature of the suture-line (text-fig. 4B) which is much more elaborated both in young and adult forms.

Parawocklumeria sp.

Plate 28, fig. 3; text-fig. 4C

Description. A single specimen of *Parawocklumeria* from the lower faunal horizon in the West Quarry at Stourscombe has a subglobose shell of similar form to *P. laevigata*. The suture-line is, however, distinctive, being characterized by an exceedingly small ventral saddle which follows the anterior arching of the constriction over the venter. The lateral lobe is shallow and passes into a pronounced lateral saddle. The umbilical lobe lies at the umbilical seam. Umbilicus deep, moderately small, and of triangular shape. No ornament has been observed.

Measurements. D. 10·5, W.H. 4·5, W.T. 7, U. 1·5.

Family CHEILOCERATIDAE Frech 1897

Genus KENSEYOCERAS gen. nov.

Derivation of name. After the River Kensey.

Type species. Kenseyoceras (Kenseyoceras) rostrata sp. nov.

Range. Upper Devonian. *Wocklumeria* Zone (V1).

Diagnosis. Shell discoidal to subglobose, completely involute. Flanks marked by deep radial constrictions which swing forwards at the venter to form grooves bounding a median keel. Suture-line consists of a ventral saddle divided by a deep parallel-sided lobe, lateral lobe bell shaped passing into a gently arched lateral saddle.

Comparisons. Two species *K.* (*Kenseyoceras*) *biforme* (Schindewolf 1937) and *K.* (*Mayneoceras*) *nucleus* (Schmidt 1924), now placed in this genus, were referred to the genus *Prionoceras* by Schindewolf (1937). *Prionoceras* is alleged to show a suture-line with a prolobitid development; a feature which would place the above species in the Prolobitidae. However, it has never been conclusively demonstrated that *Prionoceras* has a prolobitid suture-line, and *P. biforme* and *P. nucleus* were referred to the genus without reference to the development of their suture-lines. If *Prionoceras* is found to lack the prolobitid suture then it almost certainly becomes a member of the Cheiloceratidae and indistinguishable from *Imitoceras* (*Treatise on Invertebrate Paleontology*, p. L50). It has not been possible to break the shells of species of *Kenseyoceras* completely down to the protoconchs, but the earliest sutures examined have given no indication of a prolobited suture-line development. The form of the suture-line makes closer reference to the Cheiloceratidae and to the subfamily Imitoceratinae in particular. Of the genera composing the Imitoceratinae *Kenseyoceras* is most closely related to *Imitoceras*, but is distinguished from it by the presence of a raised keel bounded by spiral grooves.

Remarks. Schmidt (1924) figured two new species, *Glatziella nucleus* (p. 119, pl. 6, figs. 10, 10*a*, 11) and *Gattendorfia globularis* (p. 120, pl. 6, figs. 12, 12*a*, 13, 13*a*), from rocks at the Devonian–Carboniferous boundary in the Sauerland. In this work he failed to designate the holotypes of his new species. Lange (1929) observed that, apart from the suture-line, *Gattendorfia globularis* was quite distinct from other species of *Gattendorfia* and included it in a new subgenus, *Gattendorfia* (*Balvia*). No lectotype was designated.

Schindewolf (1937, p. 15, footnote 1) noted that Schmidt had confused three species in the descriptions of *Gattendorfia globularis* and *Glatziella nucleus*, and reinterpreted Schmidt's figures thus:

Glatziella nucleus Schmidt (p. 119, pl. 6, figs. 10, 10*a*).
Gattendorfia globularis Schmidt (p. 120, pl. 6, figs. 13, 13*a*).
Prionoceras biforme n. sp. (pl. 6, figs. 11, 12, 12*a*; holotype figs. 12, 12*a*).

Schindewolf also (1937, p. 24, footnote 3) referred the revised species *Glatziella nucleus* to *Prionoceras*. The revised species *Gattendorfia globularis* becomes, on this new interpretation, a characteristic member of the genus *Gattendorfia*. Since there is no doubt that *G. globularis* represented the subgenotype of *G.* (*Balvia*) Lange, *Balvia* is reduced to a subjective synonym of *Gattendorfia* (not *Imitoceras* as is suggested in the *Treatise of Invertebrate Paleontology*, p. L49). A new genus is therefore proposed to include *P. biforme* and *P. nucleus*.

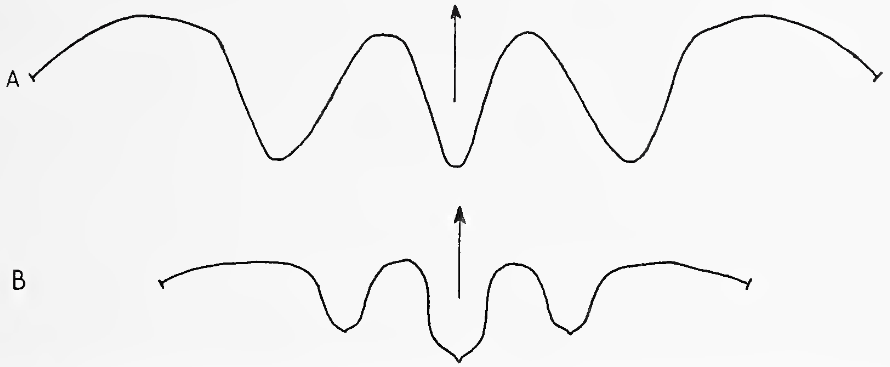
KENSEYOCERAS (KENSEYOCERAS) subgen. nov.

Diagnosis. Discoidal to subglobose. Final third of body chamber characterized by a median keel bounded by furrows. Keel carried forwards to form a pronounced rostrum. Apertural modification terminated posteriorly by constrictions which cross the flanks and reach to the umbilicus.

KENSEYOCERAS (MAYNEOCERAS) subgen. nov.

Derivation of name. After Cuthbert Mayne, a Launceston martyr.

Diagnosis. Discoidal *Kenseyoceras* with pronounced constrictions over the flanks which cross the venter in youth, but later pass into sulci bordering a median keel.



TEXT-FIG. 5. A, *Kenseyoceras* (*Kenseyoceras*) *rostrata* sp. nov.; GSM 87059, suture-line at 9 mm. diameter. B, *Kenseyoceras* (*Mayneoceras*) *nucleus* (Schmidt); GSM 87068, suture-line at 7 mm. diameter.

Kenseyoceras (*Kenseyoceras*) *rostrata* sp. nov.

Plate 28, figs. 4–10; text-fig. 5A

Derivation of name. After the pronounced rostrum.

Holotype. GSM 87058. Pl. 28, fig. 4.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

Material. Internal and external moulds.

Diagnosis. Shell discoidal to subglobose, anterior portion of body chamber with a pronounced keel, terminated posteriorly by a tubercle, and bounded by grooves which posteriorly cross the flanks as constrictions reaching to the umbilicus. Keel and sulci produced anteriorly to form a broad rostrum.

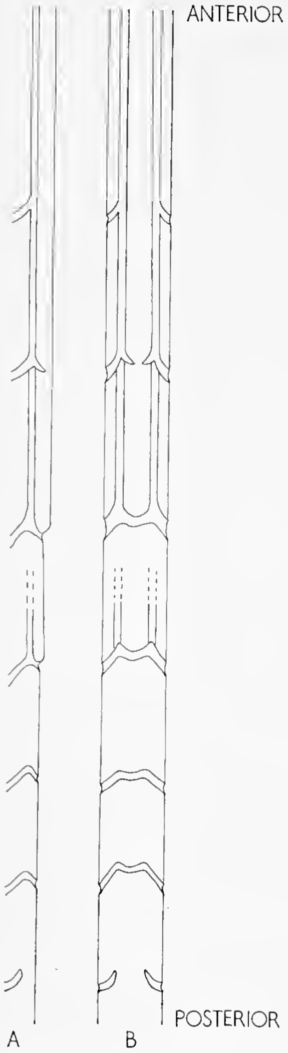
Description. Shell discoidal to subglobose, involute, greatest thickness at the umbilicus. Five to six whorls, inclusion complete; umbilicus closed and depressed. Whorls slightly compressed laterally, strongly rounded ventrally, flanks moderately convex; whorls deeply impressed by the preceding whorl, aperture height small. Body chamber just exceeds one volution. Suture-lines closely spaced just posterior to the body chamber (Pl. 28, fig. 8). External suture-line consisting of deep and pointed ventral lobe. First lateral saddle acutely rounded, passing into a broad V-shaped first lateral lobe; second lateral saddle broadly arched, passing into moderately deep umbilical lobe.

On the last third of the body chamber a pair of constrictions, deeply concave to the anterior, extend from the umbilicus towards the periphery attaining maximum concavity one-third of the distance from the venter. From this point each is carried forward, just off the venter, forming two deep sulci separated by a raised, slightly corded keel. The sulci are continued into a rostrum where the free end of the keel is terminated in a small, hyponomic sinus; the proximal end of the keel is marked by a tubercle. A second less prominent pair of constrictions, similar to, but less concave than the former, occupy a position just posterior to the aperture. Fine ornament is seldom preserved.

Measurements of holotype (in mm.). D. 10·5, W.H. 4·5, W.T. 6·5, U. closed.

Comparisons. This species is comparable to *Prionoceras biforme* Schindewolf (see above); although no description of the species is given, Schindewolf does select a holotype from Schmidt's figures. In the English species the rostrum maintains the whorl spiral, and the keel is more pronounced and terminated posteriorly by a tubercle. In addition, the pattern formed by the sulci at the posterior termination of the apertural modification is not so highly elaborated over the keel as that figured by Schmidt (1924, pl. 6, fig. 12).

Remarks. There appears to be a good deal of variation in the shape of the shell of this species which covers all gradations from discoidal to subglobose. In addition the tubercle at the posterior end of the keel is frequently not fully developed.



TEXT-FIG. 6. *Kenseyoceras* (*Mayneoceras*) *nucleus* Schmidt. Diagrams illustrating the successive stages in the development of the keel. A, Lateral view. B, Ventral view. The diagrams represent the appearance of rather more than two whorls if they were to be uncoiled.

Kenseyoceras (*Mayneoceras*) *nucleus* (Schmidt 1924)

Plate 28, figs. 11–17; text-figs. 5B, 6

1924 *Glatziella nucleus* Schmidt, p. 119, pl. 6, figs. 10, 10*a* (*non* 11).
1929 ? *Prionoceras* or ? *Gattendorfia* (*Balvia*) *nucleus* Lange, p. 61, pars.
1937 *Prionoceras nucleus* Schindewolf, p. 24, footnote 3.

Diagnosis. Shell discoidal. Flanks impressed by three constrictions in youth, increasing to four or rarely five with age. Mature shell bears pronounced keel bounded by spiral grooves.

Description. Shell compressed, discoidal in shape, involute. Seven to eight whorls, inclusion complete; umbilicus closed. Whorls considerably compressed laterally, strongly rounded ventrally; whorls deeply impressed by the preceding volutions. Twelve to thirteen suture-lines per whorl, these are closely spaced anteriorly. External suture-line (text-fig. 5B); ventral lobe deep, parallel sided, first lateral saddle rounded, passing into moderately deep first lateral lobe.

Second lateral saddle gently arched, passing into shallow umbilical lobe. Dorsal lobe deep and narrow.

In young forms whorl sides deeply impressed by three straight constrictions reaching from the umbilicus to the periphery. Initially the constrictions do not unite over the venter but are carried forwards, forming two short spiral grooves. In older specimens these grooves become united through the formation of a posteriorly arched furrow. Subsequently two spiral grooves, separated by a slightly raised keel, develop anteriorly to the constrictions. At first the keel and grooves fail to persist from one constriction to the next, but later become continuous. When this condition is established the constriction pattern over the venter weakens and finally disappears; the lateral constrictions merging into the spiral grooves. No fine ornament has been observed on the Cornish specimens.

In the early stages a suture-line often coincides with a constriction; the ventral lobe of the suture is then much deeper than the constriction sinus.

The adult shell bears four or rarely five constrictions.

Kenseyoceras (*Mayneoceras*) *sinuconstricta* sp. nov.

Plate 28, figs. 18–20

Derivation of name. After the sigmoidally curved constrictions.

Holotype. GSM 87069. Pl. 28, figs. 18–20.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

Material. Internal and external moulds.

Diagnosis. Discoidal to subglobose *K.* (*Mayneoceras*) with flattened venter and parallel-sided flanks. Flanks impressed by three sigmoidally curved constrictions.

Description. Shell discoidal to subglobose, involute; greatest thickness at the umbilicus. Six to seven whorls, inclusion complete; umbilicus closed. Shell considerably compressed laterally, flattened ventrally, flanks parallel-sided. Each whorl considerably impressed by the preceding whorl. Body chamber just exceeds one whorl. Suture-line typical of the genus.

Flanks deeply impressed by three sigmoidally curved constrictions; the intensity of the constrictions increasing towards the venter. Over the venter constrictions show a well-developed median sulcus separating two equally developed lobes. In mature specimens a median keel develops anterior to the last constriction, this keel is bounded by grooves.

Measurements of holotype (in mm.). D. 11, W.H. 6, W.T. 6·5, U. closed.

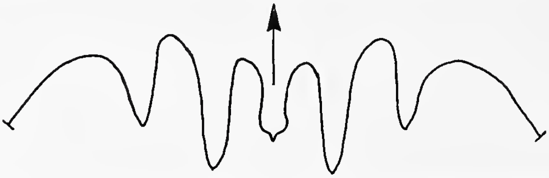
Comparisons. This species may be distinguished from *K.* (*Mayneoceras*) *nucleus* by its thicker whorl cross-section, flattened venter, and by the sinuous pattern of the constrictions over the flanks.

Genus SPORADOCERAS Hyatt 1884

Sporadoceras orbiculare var.

Plate 29, figs. 1, 2; text-fig. 7

Remarks. The suture-line of this variety (text-fig. 7) differs from that described for the species. The lobes are narrow and of unusual depth for the species.



TEXT-FIG. 7. *Sporadoceras orbiculare* var.; GSM 87074, suture-line at 47 mm. diameter.

Genus DISCOCLYMENIA Hyatt 1884

Discoclymenia cornwallensis sp. nov.

Plate 28, figs. 22, 23; text-fig. 8

Derivation of name. After the county of Cornwall.

Holotype. GSM 87071. Pl. 28, fig. 22; text-fig. 8.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

Material. Internal and external moulds.

EXPLANATION OF PLATE 28

Figs. 1, 2. *Parawocklumeria laevigata* sp. nov. var. *obesa* nov. Stourscombe. Ventral and lateral view of holotype, GSM 87088, ×3.

Fig. 3. *Parawocklumeria sp.* Stourscombe. GSM 87057, ×3.

Figs. 4–10. *Kenseyoceras* (*Kenseyoceras*) *rostrata* gen. and sp. nov., Stourscombe. 4, Lateral view of holotype showing apertural modification, GSM 87058, ×3. 5, GSM 87061, ×2, and 6, GSM 87062, ×3, ventral views showing variation in whorl thickness. 7, 8, Specimen viewed from above showing posterior termination of the apertural modification and suture-line, GSM 87059, ×3. 9, Specimen showing tubercle at posterior termination of keel, GSM 87063, ×2. 10, Fragment showing corded keel, GSM 87060, ×2.

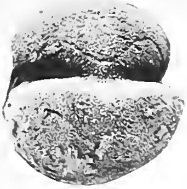
Figs. 11–17. *Kenseyoceras* (*Mayneoceras*) *nucleus* Schmidt, Stourscombe. 11, 12, Lateral and ventral view of young specimen showing suture-line and three constrictions which do not unite over the venter, GSM 87068, ×3. 13, 14, Lateral and ventral view of slightly older specimen showing four constrictions almost uniting over the venter, GSM 87065, ×3. 15, 16, Lateral and ventral view showing the keel developing between two spiral grooves, GSM 87064, ×3. 17, Ventral view showing almost continuous spiral grooves between the constrictions and weakening of the constriction over the venter, GSM 87066, ×3.

Figs. 18–20. *Kenseyoceras* (*Mayneoceras*) *sinuconstricta* sp. nov. Stourscombe. Ventral and lateral view of holotype, GSM 87069, ×3.

Fig. 21. *Discoclymenia cucullata* (von Buch) Stourscombe. GSM 87070, ×2.

Figs. 22, 23. *Discoclymenia cornwallensis* sp. nov. Stourscombe. 22, Lateral view of holotype, showing suture-lines in contact, GSM 87071, ×1. 23, Specimen showing growth-lines, GSM 87072, ×2.

PLATE 28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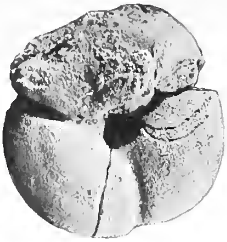
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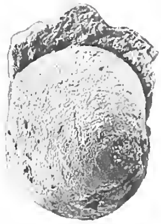
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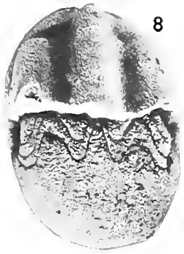
6 × 3


2 × 3


7 × 3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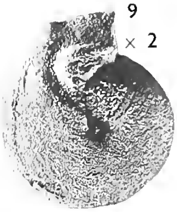
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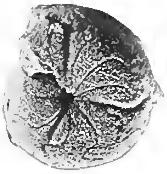
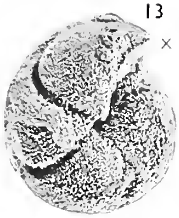
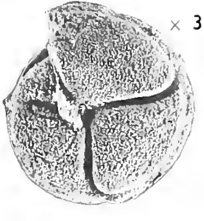
10 × 2


11 × 3


12 × 3


13 × 3


14 × 3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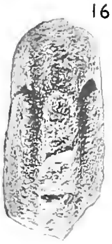
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19 × 3


20 × 3

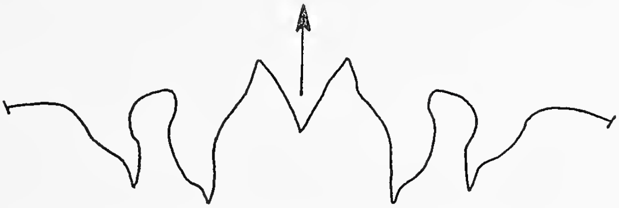

22 × 1


23 × 2

SELWOOD, Ammonoids from Cornwall

Diagnosis. Thickly discoidal *Discoclymenia* with convex growth-lines. The suture-line has a broad V-shaped ventral lobe, and a pointed first lateral saddle bearing on its dorsal side a very flat adventitious lobe.

Description. Shell thickly discoidal; involute with closed umbilicus. Greatest thickness at the umbilicus. Whorl subquadrate in section, whorl height exceeding whorl thickness. Venter broadly convex, flanks flattened, converging slightly towards the venter. Growth-lines convex, fine and closely spaced. Constrictions not seen.



TEXT-FIG. 8. *Discoclymenia cornwallensis* sp. nov.; holotype, GSM 87071, suture-line at a whorl height of 36 mm.

Suture-line (text-fig. 8). Ventral lobe of broad V shape. First lateral saddle pointed, bearing on its dorsal side a very flat, adventitious lobe. First lateral lobe asymmetrical, deep, and pointed. Second lateral saddle rounded, directed upwards towards the venter. Second lateral lobe asymmetrical, broad, and pointed, with almost straight ventral surface; dorsal surface undulatory, passing into a gently arched umbilical saddle.

Measurements of holotype (in mm.). W.H. 36, W.T. 28.

Remarks. A feature of the figured specimen is the closely spaced nature of the suture-lines, and the manner in which the first lateral saddles of each suture are in contact. In one instance the first lateral lobe seems to have been interrupted by the first lateral saddle of the preceding suture.

Comparisons. The suture-line of this species is comparable to *Discoclymenia sp.* of Müller (1956, p. 62), differing only in the size of the ventral lobe; in Müller's species this is narrow and parallel sided. The adventitious lobe in *D. cucullata* (von Buch 1839) is more strongly developed than in *D. cornwallensis*.

Discoclymenia aff. *cornwallensis* sp. nov.

Plate 29, fig. 3

Remarks. This form is similar to *D. cornwallensis*, but it shows a slightly different suture-line. This is not so elaborated and shows the smoother form more generally associated with *Sporadoceras*; in addition the ventral lobe is deep and parallel sided.

Genus GATTENDORFIA Schindewolf 1920

Gattendorfia crassa H. Schmidt 1924

1940 *Gattendorfia crassa* Librovitch, p. 45, pl. 4, figs. 1–4 (with full synonymy).
1952 *Gattendorfia crassa* Schindewolf, p. 296, text-figs. 16, 17.
1954 *Gattendorfia crassa* Pfeiffer, p. 57, pl. 7, fig. 3.
1955 *Gattendorfia crassa* Goldring, p. 48.

Comparison with described forms (measurements in mm.)

Specimen	*D.*	*W.T.*	*W.T. %D.*	*W.H.*	*W.H. %D.*	*U.*	*U. %D.*
1952	46·0	37·0	60	22·0	47	10·5	22
BU 12883 . . .	10·0	7·0	70	5·0	50	2·5	25

Gattendorfia occlusa Librovitch 1940

1940 *Gattendorfia occlusa* Librovitch, p. 237, pl. 6, figs. 5, 6, text-figs. 16, 17.

Comparison with described forms (measurements in mm.)

Specimen	*D.*	*W.T.*	*W.T. %D.*	*W.H.*	*W.H. %D.*	*U.*	*U. %D.*
1940 (holotype) . .	31·0	15·0	46	18·0	58	3·0	9
Range	. .	. .	41–62	. .	46–58	. .	9–17
BU 12884 . . .	12·5	5·5	44	6·0	48	2·0	16
BU 12915 . . .	8·5	3·0	35	3·5	41	1·0	11

Remarks. Two specimens from Penfoot show remarkably small umbilici. The proportions of these specimens are very close to those of *G. occlusa* from Kazakhstan; the specimens are referred to this species in preference to the involute European species *G. involuta* Schindewolf which is inadequately described.

Gattendorfia tenuis Schindewolf 1952

1952 *Gattendorfia tenuis* Schindewolf, p. 298, pl. 3, fig. 1, text-fig. 18.

Comparison with the holotype (measurements in mm.)

Specimen	*D.*	*W.T.*	*W.T. %D.*	*W.H.*	*W.H. %D.*	*U.*	*U. %D.*
BU 12885 . . .	19	7	37	8	42	5	26
1952 (holotype) . .	73	23	31	33	44	18	24

Remarks. The proportions of the Cornish specimen are close to those of the holotype, but the shell has a slightly greater whorl thickness.

Gattendorfia subinvoluta (Münster 1839)

1940 *Gattendorfia* cf. *subinvoluta* Librovitch, p. 40, pl. 3, figs. 6*a*, *b* (with full synonymy).
1952 *Gattendorfia subinvoluta* Schindewolf, p. 295, text-fig. 15.

Comparison with described forms (measurements in mm.)

Specimen	*D.*	*W.T.*	*W.T.* %*D.*	*W.H.*	*W.H.* %*D.*	*U.*	*U.* %*D.*
1940	14·5	6·5	45	4·7	32	7·5	51
1952	52·0	24·0	46	19·0	37	16·0	30
BU 12886 . . .	18·0	6·0	33	6·5	36	7·0	39
BU 12887 . . .	20·5	8·5	41	7·0	33	9·0	43
BU 12888 . . .	13·0	6·5	50	4·5	34	6·0	46
BU 12889 . . .	19·0	6·0	31	5·5	29	7·5	39
BU 12890 . . .	18·0	6·0	33	6·0	33	8·0	44

Remarks. G. subinvoluta is the most commonly occurring Cornish species of this genus. Specimens collected show that the species is variable, particularly in whorl thickness. The Cornish specimens tend to be more evolute than forms described from Germany, for the umbilicus has a size range most comparable to *G.* cf. *subinvoluta* Librovitch, in which the umbilicus is 51–52 per cent. of the diameter.

Trilobites

Family PHACOPIDAE Hawle & Corda 1847

Genus PHACOPS Emmrich 1839

Phacops (*Phacops*) *accipitrinus accipitrinus* (Phillips 1841)

1955 *Phacops* (*Phacops*) *accipitrinus accipitrinus* Goldring, p. 46 (with previous synonymy).

Remarks. P. (*Phacops*) *accipitrinus accipitrinus* occurs commonly in the lower part of the Pilton Beds of north Devon, but it is uncommon in beds of equivalent age in Cornwall.

Although phacopid trilobites occur quite commonly with the rich ammonoid fauna to be found in the siliceous nodules of the Stourscombe Beds, only a single pygidium referable to this species has been recorded. Rare specimens have also been found in the more slaty developments, where they are associated with a rich benthonic fauna. The species has also been collected from the cephalopod limestones of the Lower Petherwin Beds. This represents the oldest horizon from which the fossils have been recorded in this country. However, a comparable range has been observed on the Continent.

Phacops (*Phacops*) *wedekindi* Rud. & E. Richter 1926

1926 *Phacops* (*Phacops*) *wedekindi* Rud. & E. Richter, p. 145, pl. 8, figs. 40–43, text-figs. 17*c*, *d*.
1937 *Phacops* (*Phacops*) *wedekindi* Rud. Richter in Schindewolf, p. 39.

Remarks. Specimens referred to this species are identical to those described from Germany but the eyes have fewer (20–25) facets.

Phacops (*Cryphops*?) *ensae* Rud. & E. Richter 1926

1926 *Phacops* (*Cryphops* ?) *ensae* Rud. & E. Richter, p. 164, pl. 9, figs. 61–64.
1954 *Phacops* (*Cryphops* ?) *ensae* Pfeiffer, p. 40, pl. 2, fig. 4.

Remarks. The granulation of the cephalon of specimens from Cornwall is frequently coarser than that described for the species. This is particularly true of the central part of the glabella; towards the periphery, however, the ornament becomes finer and more closely spaced. In most of the material collected the lateral border of the cephalon is only very weakly ornamented, and in some cases the posterior border appears quite smooth.

Phacops (*Cryphops*?) *wocklumeriae* Rud. & E. Richter 1926

1926 *Phacops* (*Cryphops* ?) *wocklumeriae* Rud. & E. Richter, p. 167, pl. 9, figs. 65–67.
1937 *Phacops* (*Cryphops* ?) *wocklumeriae* Rud. Richter in Schindewolf, p. 39.
1954 *Phacops* (*Cryphops* ?) *wocklumeriae* Pfeiffer, p. 41, pl. 2, figs. 5–8.

Remarks. This species, which seems to be limited to the upper part of the Stourscombe Beds, occurs less frequently than *P.* (*Cryphops* ?) *ensae*. The tubercles on the test, particularly on the cheek areas, are more widely spaced and rather coarser than described by Rud. & E. Richter. Whilst the length of the glabella is normally much less than its maximum breadth, one specimen shows a glabella with a length almost equal to its maximum breadth.

Phacops (*Dianops*) *sp.*

Plate 29, fig. 4

Remarks. Only a single specimen of a species of the subgenus *P.* (*Dianops*) has been discovered in Cornwall. The broad outline of the specimen is similar to *P.* (*Dianops*) *bartzschi* Pfeiffer (1954, p. 46, pl. 2, figs. 6, 7), but it lacks the diagnostic ornament of this species. In addition to the lack of ornament the specimen can be distinguished from *P.* (*Dianops*) *griffithides* (Rud. & E. Richter 1919) by the greater breadth of the cephalon and by the more rounded anterior margin of the glabella.

Family PROETIDAE Salter 1864

Genus CHAUNOPROETUS Rud. Richter 1919

Chaunoproetus aff. *carnicus* (Rud. Richter 1913)

Plate 29, figs. 8, 9

1913 *Drevermannia*? *carnica* Rud. Richter, p. 379, pl. 22, fig. 16.
1926 *Drevermannia*? *carnica* Rud. & E. Richter, p. 85, pl. 6, figs. ?74, ?75, ?76.
1937 *Drevermannia*? (*Carnica*) *carnica* Rud. Richter in Schindewolf, p. 39.
1955 *Drevermannia*? (*Carnica*) *carnica* Maksimova, p. 124, pl. 9, figs. ?7, ?8.

Remarks. A single ill-preserved cranidium has been found in the Stourscombe Beds which appears to be reasonably close to the holotype of the species. However, the anterior border is less strongly incurved and the anterior branch of the facial suture diverges more strongly than is normal for the species; the suture is placed closer to the glabella. The occipital ring does not show the large median measurement described by Richter. Glabellar furrow 1p only has been detected.

Specimens figured later by Rud. & E. Richter (1926) show variation particularly in the shape of the glabella and the distance of the facial suture from the glabella. The figures suggest that several species may be involved.

GENUS CYRTOSYMBOLE Rud. Richter 1913

Cyrtosymbole (*Waribole*) aff. *conifera* Rud. & E. Richter 1926

Plate 29, fig. 7

1926 *Cyrtosymbole* (*Waribole*) *conifera* Rud. & E. Richter, p. 53, pl. 3, figs. 37, 38, 40.

Remarks. Several specimens, including an almost complete exoskeleton, from the Stourscombe Beds appear to be very close to this species apart from certain differences in the facial suture. In particular the anterior branch of the suture is more strongly rounded, and cuts the anterior border closer to the median line than in the specimens figured by Rud. & E. Richter. The palpebral lobes are of comparable size to the holotype but are placed a little more anteriorly; γ, and in some cases δ, are farther from the glabella than is usual in the species. The glabella is irregularly, and slightly more strongly, granulated than in the German specimens. No granulation has been observed on the free cheek or pygidium.

Cyrtosymbole (*Waribole*) aff. *italica* (Gortani 1907)

Plate 29, fig. 6

1907 *Dechenella italica* Gortani, p. 39, pl. 1, fig. 27; pl. 2, fig. 32.
1912 *Cyrtosymbole* (?) *italica* Rud. Richter, pp. 259, 337.
1913 *Cyrtosymbole* (?) *italica* Rud. Richter, p. 398, pl. 23, fig. 2.
1913 *Proetus* (*Cyrtosymbole*) *italicus* Gortani, p. 265, text-fig. 1.
1926 *Cyrtosymbole* (*Waribole*) *italica* Rud. & E. Richter, p. 51.

Remarks. Several Cornish specimens, although not perfectly preserved, are similar to the species described by Gortani from the Carnic Alps. This species has not been recorded elsewhere, though the closely related *Cyrtosymbole* (*Waribole*) *octofera* Rud. & E. Richter occurs in the *Wocklumeria* Zone in Germany.

The posterior branch of the facial suture, hitherto incompletely figured, diverges moderately strongly from the glabella, reaching the posterior margin a distance from the axial furrow almost equal to half the breadth of the occipital ring. The palpebral lobes are not quite as broad as those figured by Gortani.

A single free cheek has been found which is similar to the incomplete specimen figured by Gortani, but on the cheek area it shows a raised line passing around the anterior part of the eye. This is a similar line to that seen in *C.* (*Waribole*) *octofera*, but weaker.

Ornament is not characteristic of the species, but the free cheek described shows a fine granulation and the axial part of the glabella of one cranidium is also granulated.

In the Carnic Alps the species is alleged to occur in the *Clymenia* Zone; however, the clymenid *Postglatziella* is also recorded from the same beds. This is a species generally supposed to be of *Wocklumeria* Zone age. It is thus possible that the Carnic specimens, like those from Cornwall, come from this zone.

Cyrtosymbole (? *Waribole*) *dunhevedensis* Thomas 1909 nom. correct.

1909 *Proetus dunhevidensis* Thomas, p. 197, pl. 7, fig. 6.
1926 *Cyrtosymbole* (? *Waribole*) *dunhevidensis* Rud. & E. Richter, p. 53.

Remarks. The single specimen of this species located, according to Thomas, in the Southgate Museum, Launceston, has not been found. No further specimens have been found during the present investigation. The spelling of the specific name which, due to a slip in the original description, read *dunhevidensis*, is corrected.

Cyrtosymbole (? *Calybole*) cf. *nepia* Rud. & E. Richter 1926

1926 *Cyrtosymbole nepia* Rud. & E. Richter, p. 61, pl. 4, fig. 50.
1954 *Cyrtosymbole nepia* Pfeiffer, p. 35.
1955 *Cyrtosymbole* (? *Calybole*) *nepia* Maksimova, p. 103, pl. 6, fig. 4.

Remarks. Several minute pygidia have been collected. Although not perfectly preserved these specimens appear to be similar to *C. nepia*, a possible larval form.

Cyrtosymbole (? *Macrobole*) aff. *bergica* Rud. Richter 1913

Plate 29, fig. 5

1913 *Cyrtosymbole bergica* Rud. Richter, p. 387, pl. 22, figs. 22, 23.
1926 *Cyrtosymbole bergica* Rud. Richter, p. 59.

Remarks. An almost complete cephalon, from the Stourscombe Beds, shows close affinitics to the specimen figured by Rud. Richter (1913). However, the exoskeleton where it still remains has a fine granulation which is particularly evident on the free cheeks. Ornament has not previously been described in the species.

The facial suture of the figured specimen, although comparable to the holotype, shows certain differences from it. In particular the posterior branch of the suture which runs parallel, and rather nearer, to the axial furrow than in the German species, cuts the posterior border at a slightly greater distance from the genal angle. γ on the anterior branch is slightly farther from the glabella.

The occipital ring, which is not preserved in the holotype, is comparable to that of *Cyrtosymbole* sp. cf. *bergica* (Rud. & E. Richter 1926, p. 60, pl. 4, figs. 48, 49).

The preservation is such that only the glabellar furrow 1p can be detected.

Pygidia referred to the species show nine clear rings on the axis and three (+1) ribs on the flanks.

This specics has not previously been ascribed to any subgenus of *Cyrtosymbole*. The long posterior branch of the facial suture running parallel to the axial furrow suggests that a tentative reference can be made to *C.* (*Macrobole*).

Cyrtosymbole (*Macrobole*) *drewerensis* Rud. & E. Richter 1951, sens nov.

Plate 29, figs. 14–16

1951 *Cyrtosymbole* (*Macrobole*) *drewerensis drewerensis* Rud. & E. Richter, p. 235, pl. 1, figs. 7–11; pl. 5, figs. 47, 48, text-figs. 1M and 3.
1951 *Cyrtosymbole* (*Macrobole*) *drewerensis longisuta* Rud. & E. Richter, p. 238, pl. 1, figs. 12, 13; pl. 5, fig. 48.
1954 *Cyrtosymbole* (*Macrobole*) *drewerensis longisuta* Pfeiffer, p. 51.

Remarks. This species is the most commonly occurring trilobite in the Yeolmbridge Beds. Variation within the species was noted by Rud. & E. Richter, but it has been found difficult to refer many of the Cornish specimens to either of the subspecies recognized by them due to the occurrence of intermediate forms and the variation in other characters.

On the whole the palpebral lobes, which are elongate, are broader and the maximum breadth occurs just anterior to glabellar furrow 1p; this is slightly more posterior than is usual in the species. Glabellar furrow 4p is normally developed.

Granulation is varyingly developed and does not appear to be necessarily limited to specimens with *longisuta* type glabellae. For instance, the specimen figured in Pl. 29, figs. 14, 15, is very close in its general form to *C.* (*Macrobole*) *drewerensis drewerensis*, but it shows a slight tuberculation at the posterior margin of the glabella. The anterior border of the glabella of this specimen is wider than that figured by Rud. & E. Richter.

Another cranidium (Pl. 29, fig. 16) is very close to *C.* (*Macrobole*) *drewerensis longisuta*; the glabella is covered by a fine granulation, but the anterior end of the glabella does not taper so sharply. The palpebral lobes are slightly longer than is usual in the species.

Pygidia referable to this species are not common in the Yeolmbridge Beds. The length of the axis tends to be rather shorter than in the German specimens; in other respects they are closely comparable.

The variation noted in Cornwall in this species with regard to the shape and granulation of the glabella, and in the facial suture, suggests that *C.* (*Macrobole*) *drewerensis longisuta* has no taxonomic significance.

Measurements (in mm.)

Specimen	GSM 87099 Pl. 29, figs. 14, 15	GSM 87098 Pl. 29, fig. 16	BU 12897
Length of cranidium	6·5	4·75	5·5
Breadth of cranidium	5·0	2·25	2·75
Length of glabella	5·0	3·25	4·0
Breadth of glabella	4·0	3·0	3·0

Specimen	BU 12905	BU 12904	BU 12902	BU 12901
Length of pygidium	4·0	3·0	6·5	5·5
Breadth of pygidium	7·5	5·5	11·0	10·0
Length of axis	3·0	2·25	5·0	4·5
Breadth of axis	1·75	1·5	2·5	2·75

Cyrtosymbole (*Macrobole*) *duodecimae* Rud. & E. Richter 1951

Plate 29, fig. 17

1951 *Cyrtosymbole* (*Macrobole*) *duodecimae* Rud. & E. Richter, p. 238, pl. 12, figs. 18–21; pl. 5, fig. 49, text-fig. 4.
1954 *Cyrtosymbole* (*Macrobole*) *duodecimae* Pfeiffer, p. 51, pl. 4, fig. 5.
1955 *Cyrtosymbole* (*Macrobole*) *duodecimae* Goldring, p. 32, pl. 1, fig. 2, text-figs. 5*a*, *b*.

Remarks. Only a few specimens from the Yeolmbridge Beds can be referred to this species and these are very close to the holotype. In the single cranidium the divergence of the facial suture near the posterior border furrow is such that the suture cuts the posterior margin at a distance from the axial furrow equal to half the breadth of the occipital ring. This distance is greater than that noted by Rud. & E. Richter. The glabella of the Cornish specimen is very slightly more slender than in the holotype. Glabellar furrow 4p has not been observed.

Pygidia are fairly common and agree closely with the described form, but as in the specimens from the Pilton Beds (Goldring 1955) a few show a length of pygidium rather greater than half the breadth.

Measurements (in mm.). GSM 87100 (Pl. 29, fig. 17), length of cranidium 4·5; breadth of cranidium 3·0; length of glabella 3·25; breadth of glabella 2·7.

Specimen	BU 12911	BU 12912	BU 12913	BU 12914
Length of pygidium . .	6·0	2·0	3·25	4·0
Breadth of pygidium . .	10·5	4·0	7·5	9·0
Length of axis . . .	5·0	2·0	2·5	3·0
Breadth of axis . . .	3·5	1·5	2·25	2·5

Cyrtosymbole (*Macrobole*) aff. *blax* Rud. & E. Richter 1951

Plate 29, figs. 12, 13

1951 *Cyrtosymbole* (*Macrobole*) *blax* Rud. & E. Richter, p. 240, pl. 2, figs. 14–16, ?17; pl. 5, fig. 50, text-fig. 5.

Remarks. A single cranidium from the Yeolmbridge Beds is very close to *C.* (*Macrobole*) *blax* but shows certain differences from it. The palpebral lobes are broader and placed slightly more posteriorly, the anterior border of the cranidium is situated very slightly farther from the glabella, and the granulation of the glabella is only very sparsely distributed.

EXPLANATION OF PLATE 29

Figs. 1, 2. *Sporadoceras orbiculare* var.; Stourscombe. Lateral and ventral view showing suture-line, GSM 87074, ×1.

Fig. 3. *Discoclymenia* aff. *cornwallensis* sp. nov. Stourscombe. GSM 87073, ×1.

Fig. 4. *Phacops* (*Dianops*) *sp.*; Stourscombe. Plan view, GSM 87091, × 2.

Fig. 5. *Cyrtosymbole* (? *Macrobole*) *bergica* Rud. Richter, Overwood Farm, nr. Yeolmbridge. Plan view, GSM 87096, ×4.

Fig. 6. *Cyrtosymbole* (*Waribole*) aff. *italica* (Gortani), Overwood Farm, nr. Yeolmbridge. Plan view, GSM 87094, ×4.

Fig. 7. *Cyrtosymbole* (*Waribole*) aff. *conifera* Rud. & E. Richter, Overwood Farm, nr. Yeolmbridge. Plan view, GSM 87093, ×4.

Figs. 8, 9. *Chaunoproetus* aff. *carnicus* (Rud. Richter) Stourscombe. Side and plan view, GSM 87092, ×4.

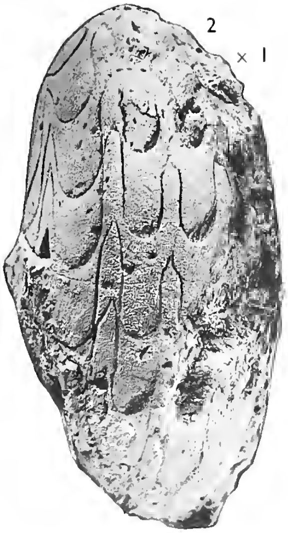
Figs. 10, 11. *Cyrtosymbole* (*Macrobole*) *sp.* Yeolmbridge Slate Quarry. Plan and side view, note elongate glabella, GSM 87097, ×4.

Figs. 12, 13. *Cyrtosymbole* (*Macrobole*) aff. *blax* Rud. & E. Richter, Yeolmbridge Slate Quarry. Plan and side view, GSM 87091, ×4.

Figs. 14–16. *Cyrtosymbole* (*Macrobole*) *drewerensis* Rud. & E. Richter, Yeolmbridge Slate Quarry. 14, 15, Plan and side view of cranidium, GSM 87099, ×4. 16, Plan view of cranidium, GSM 87098, ×4.

Fig. 17. *Cyrtosymbole* (*Macrobole*) *duodecimae* Rud. & E. Richter, Yeolmbridge Slate Quarry. Plan view, GSM 87100, ×4.


1 × 1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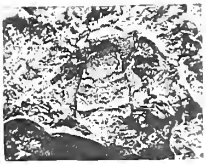
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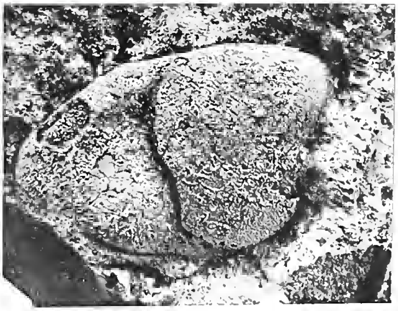
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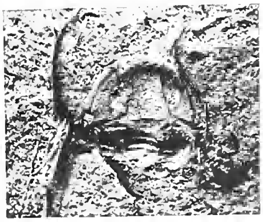
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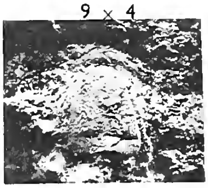
7 × 4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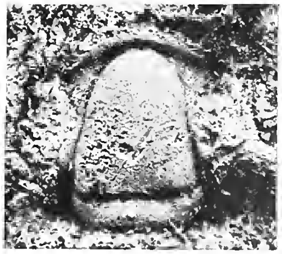
8 × 4


10 × 4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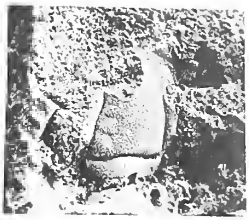
14 × 4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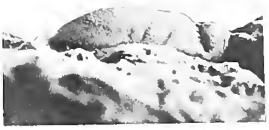
11 × 4


13 × 4


15 × 4


16 × 4

SELWOOD, Ammonoids and trilobites from Cornwall

The palpebral lobes are not as large, and the anterior branch of the facial suture diverges more strongly from the glabella at γ, than in the closely related species *C.* (*Macrobole*) *mulesi* Goldring (1955).

An incomplete pygidium can probably also be referred to this species. No fine granulation has been detected, and, unlike the pygidium described by Rud. & E. Richter, the anterior portions of the ribs are larger than the posterior. Four ribs can be detected, but only the first two are distinct.

Measurements (in mm.). GSM 87101 (Pl. 29, figs. 12, 13), length of cranidium 6·0; breadth of cranidium 4·5; length of glabella 4·5; breadth of glabella 4·0. BU 12910, length of pygidium 4·0; breadth of pygidium 6·0; length of axis 3·0; breadth of axis 2·0.

Cyrtosymbole (*Macrobole*) *sp.*

Plate 29, figs. 10, 11

Description. A species has been noted in the Yeolmbridge Beds which is characterized by a particularly slender cranidium. The glabella is elongate and tapers sharply to the anterior; its length is just over twice its breadth. The preglabellar field is small and the anterior border curved. The occipital furrow is broad and deep, rising posteriorly into the occipital ring which continues the outline of the glabella. At the median line the occipital ring widens slightly and is marked by a mesial tubercle. Four glabellar furrows are present; 1p is a shallow groove curving slightly posteriorly and extending almost to the occipital furrow, 4p is short and indistinct.

The anterior branch of the facial suture diverges moderately from the glabella. β is rounded and lies on a line just posterior to the anterior end of the glabella. The palpebral lobe is small and elongate with γ lying farther from the glabella than δ; γ is placed between 2p and 3p, δ lies one-third of the distance from 1p to the occipital furrow. The posterior branch of the suture is long and straight and runs parallel to the axial furrow. Near the posterior border it diverges strongly to reach the posterior margin at a distance from the axial furrow equal to half the breadth of the axial ring. The posterior border of the cranidium is much narrower than the occipital ring and only very weakly arched.

Measurements (in mm.). GSM 87097 (Pl. 29, figs. 10, 11), length of cranidium 8·5; breadth of cranidium 4·0; length of glabella 6·25; breadth of glabella 3·0.

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THE MIDDLE PALAEOZOIC SQUAMULATE FAVOSITIDS OF VICTORIA

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ABSTRACT. Of the thirteen nominal species of squamulate favositid described from the Middle Palaeozoic of Eastern Australia and New Zealand, two, *Favosites squamuliferus* Etheridge 1899 and *F. grandiporus* Etheridge 1890, are recognized as discrete species, and one closely related non-squamulate species, *F. moonbiensis* Etheridge 1899, is also recognized. *F. squamuliferus* is interpreted as an extremely variable species containing eight arbitrarily separated formae. Eleven European and Russian species are noted which fall within the range of variation of *F. squamuliferus* and *F. grandiporus*. Favositid wall structure and septal apparatus are also discussed.

INTRODUCTION

THIS study arose during the description of a coral fauna from the basal Devonian (?) Limestones outcropping along the Tyers River, Gippsland, Victoria. As work progressed the squamulate favositids of this fauna were found increasingly difficult to classify in terms of existing Australian 'species' until it was realized that the only satisfactory treatment was to regard them as constituting a single species exhibiting remarkably gross intraspecific variation. Attention was then turned to the favositids occurring in some of the higher Devonian limestone horizons of Victoria, those of the Lilydale Limestone (of upper (?) Lower Devonian age) and of the lower Middle Devonian of Buchan and Bindi. Although the favositids of these horizons have not been investigated in the same detail as those of the Tyers River limestone, the same general conclusion is suggested by the material to hand—that the squamulate favositids show such great variation that satisfactory separation into the previously defined 'species' proves impossible in a moderately large collection.

Intraspecific variation in corals. Very little has been done on the variation of tabulate corals. Jones (1936), in studying the three Silurian species *Favosites gothlandicus* Lamarck, *F. forbesi* E. & H., and *F. multiporus* Lonsdale, considered them to be conspecific and recognized them merely as 'formae' within the species *F. gothlandicus*. Jones considered the variation between the forms to be due solely to environment.

More work has been done on variation in rugose corals. Wells (1937) described in detail variation within the Middle Devonian rugose coral *Heliophyllum halli* E. & H. and in place of eight previously described species recognized the single species with one variety and eleven 'formae' between which there was found to be continuous variation. Wells analysed the possible causes of variation and summarized earlier work on variation in corals. Olliver (1958) described the variation in external form of another Devonian rugose coral *Metriophyllum exiguum* (Billings) and recognized six formae 'which form an intergradational system'.

Certainly more examples of variation have been described in scleractinians, particularly Recent forms. The work of Vaughan (1907) on *Porites compressa*, a living hermatypic coral from Hawaii, should be mentioned. Besides the typical form, Vaughan recognized sixteen formae and four sub-formae between which there is continuous

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variation. Further, the difficulty encountered in the definition of species of certain living hermatypic scleractinians is well known. Thus Bernhard (1901) experienced so much difficulty in cataloguing Recent corals in the British Museum (Natural History) that he abandoned the binomial system of nomenclature and substituted a geographical number system.

Nominal species and varieties of squamulate favositids. The following thirteen nominal species and varieties have been proposed for squamulate favositids from various localities from the Lower and Middle Devonian of Eastern Australia and New Zealand:

Favosites grandipora Etheridge 1890.
Favosites squamulifera Etheridge 1899.
Cannapora australis Chapman 1908.
Favosites nitida Chapman 1914.
Chaetetes stelliformis Chapman 1918.
Favosites (*Emmonsia*) *spinigera* Chapman 1921 (*non* Hall 1879).
Alveolites victoriae Chapman 1921.
Alveolites regularis Chapman 1921.
Favosites murrumbidgeensis Jones 1937.
Favosites bryani Jones 1937.
Favosites nitidus var. *medius* Hill and Jones 1940.
Favosites ovatiporus Hill and Jones 1940.
Favosites pluteus Hill 1950.

To these may also be added *Favosites basaltica* var. *salaebrosa* Etheridge 1899, although Hill (1950) considered that this form does not possess squamulae. However, prior to now, squamulae have not been recognized as such in six of the species listed above.

Of the species which have been proposed, *F. grandiporus* and *F. squamuliferus* are retained while the rest are regarded as synonyms of one or the other, although some of the names have been retained in the description of formae within *F. squamuliferus*. *F. moonbiensis* Etheridge 1899, the non-squamulate counterpart of *F. squamuliferus*, is also regarded as a discrete species, mainly, however, for simplicity of nomenclature.

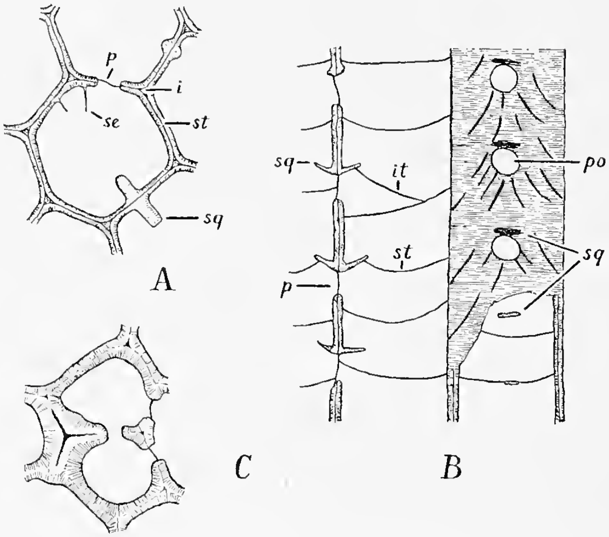
MORPHOLOGY

The main factor common to the above species is that they possess comparatively large mural pores usually in a single row toward the centre of each corallite face. Occasionally they may become widely biserial when the corallite face is wide. In most members of the group squamulae are developed above the mural pores, apparently bearing some relation to them. Thus in these characters most members of the group bear resemblance to *Alveolites battersbyi* E. & H., the type species of the genus *Caliapora* Schlüter 1889. Descriptions of the wall structure and septal apparatus of the members of the group are given in some detail as they have considerable bearing on the question of the generic placement of the group as well as on favositid taxonomy generally.

A. *Wall structure.* Swann (1941; 1947) in his description of the *Favosites alpenensis* lineage recognized the presence of calcareous deposits between the corallite walls of certain favositids. The deposits are distinct from the very thin primary walls and peripheral stereozones of the corallites. They are usually differently stained from the calcite of the peripheral stereozones and so are fairly obvious when they occur. Swann (1947) designated these median wall deposits as the 'intramural coenozone' considering that as such they represented the presence of a coenosarc in favositids.

Deposits between the walls of adjacent corallites in favositids had been noted prior to this. Nicholson (1881, p. 21) in his description of *Favosites inosculans* stated: 'The line of demarcation between the sclerenchyma of any tube and that of its neighbours is in general recognizable by the presence of a clear linear space. . . .' This is well shown in his figures of this species. Etheridge (1899*a*, p. 21) also noted the occurrence of intermural deposits towards the corners of the corallites in *F. moonbiensis* and described them as a 'light clear spot in the wall substance'. Lecompte (1936) also noted such deposits and applied the term 'fissure axiale' to them.

Hill (1950) convincingly rejected Swann's idea that intermural deposits were organic structures, for, as Hill comments, the 'coenozone', as described by Swann, does not possess the fibrous structure which is characteristic of all coral material other than the epitheca. Hill suggested that this coenozone was a phenomenon of fossilization caused by recrystallization along the junction of two sets of fibres. She noted that a similar structure is present along the median line of the septa in specimens of the rugose coral *Pycnactis* from the Silurian of Great Britain.



TEXT-FIG. 1. Generalized morphology of *F. squamuliferus* and *F. grandiporus* ×20 approx. A, *F. squamuliferus* forma *bryani* based on T.S. 891. Transverse section; Tyers River limestone. B, *F. grandiporus* showing well-developed 'stellate' intermural space with thickening and bleaching of the stereome of the neighbouring corallites in its vicinity. (From T.S. 1209.) Transverse section; Lilydale Limestone. C, *F. squamuliferus* forma *bryani* based on T.S. 917. Longitudinal section; Tyers River limestone. *i*, intermural space; *p*, mural pore with pore plate; *po*, mural pore; *se*, septal spine; *sq*, squamula; *it*, incomplete tabula; *st*, suspended tabula.

Ross (1953) substituted the term 'intermural spaces' for Swann's 'intramural coenozone', also considering that Swann's reasons for regarding them organic in origin were unsatisfactory. Ross concluded that, as the spaces were developed between adjacent corallites in particular growth zones, they were produced as a response to adverse environmental conditions.

The author is in agreement with Ross as to the cause of intermural spaces for the same reason (Pl. 34, fig. 3). Furthermore, within the Victorian squamulate favositids they are so consistently developed that it is hard to imagine them as merely due to fossilization, particularly as other species of *Favosites* occurring side by side with *F. squamuliferus* may not show any development of intermural deposits. In *F. squamuliferus* forma *australis*, a form characterized by subcerioid growth of the corallum, all degrees of development of intermural spaces can be found. In places the corallites are widely separated and elsewhere the walls of adjacent corallites are directly in contact so intermural spaces cannot occur (Pl. 33, fig. 5). Again, with the peculiar 'stellate' intermural spaces discussed below, the stereome of corallites in their immediate vicinity is often bleached and thickened (Pl. 33, figs. 6, 9; Pl. 34, figs. 4, 5; text-fig. 1C). This would be unlikely were intermural deposits merely a fossilization phenomenon.

The intermural spaces of *F. grandiporus* and *F. squamuliferus* and of the closely related non-squamulate *F. moonbiensis* are of a peculiar type. These spaces have already been described by Etheridge (1899*a*) in the latter species. In this type of intermural space the zone of usually almost clear calcite at the junction of walls of adjacent corallites may appear as a very thin band sometimes enclosing whole corallites (Pl. 33, fig. 12), but more often is more or less confined to the junctions of three or more corallites (Pl. 33, figs. 2, 6–11; text-fig. 1A) although the spaces may irregularly expand elsewhere. When the spaces are confined to the angles of the corallites, they may give rise to 'stellate' structures within the walls (Pl. 33, figs. 6, 9) which may be accentuated by bleaching and thickening of the stereome in their immediate vicinity (Pl. 33, figs. 6, 9; text-fig. 1C). In poorly preserved specimens which have suffered marked recrystallization the 'stellate' structures are often strongly emphasized.

This type of 'stellate' wall structure has been described before in various species of *Favosites*. Swann (1947) noted intermural spaces 'thickening greatest at the corners of the corallites' in *F. warthini*, a species showing strong rounding of the corallites. Similar 'stellate' swellings within the walls at the junctions of corallites have been referred to by various authors, although no explanation has been given as to their nature. Examples are:

Favosites asteriscus Frech (Frech 1899, p. 234), a squamulate species, Middle Devonian, China; *F. proasteriscus* Charlesworth 1914, Lower Devonian, Eastern Alps; *F. stellaris* Chernyshev 1937, Devonian (?), Novaya Zemlya; *F. interstinctus* Regnéll 1941, Siluro-Devonian, Tien-shan. Regnéll also gave a comprehensive survey of 'stellate structures' and described them in *Thamnopora tubifera*.

Porfiriev (1937) appears to have noted the work of Frech who considered that the possession of such stellate swellings within favositid walls could be regarded as having generic significance. Porfiriev proposed the genus *Asteriophyllum* based on *A. ænigmaticum*, a species differing only in this respect from *Favosites*.

As 'stellate swellings' appear to be caused by the pulling apart of the walls of adjacent corallites particularly at their corners and the thickening of the stereoplasm of the corallites in their vicinity and were probably developed due to adverse environmental conditions, it is doubtful whether their possession should be regarded as being of generic significance in favositids. Naturally, when cylindrical corallites are packed into a cerioid growth habit, the walls at the corners are not so closely in contact as elsewhere (Pl. 33, fig. 5). Some species exhibit this more than others. For this reason the genus *Asteriophyllum* is best regarded as a synonym of *Favosites*.

Even greater taxonomic importance has been placed on the presence of intermural spaces in favositids. Recently Lafuste (1958, p. 412), on the basis of Swann's (1941) description of favositid wall structure, states of his separation of *Thecia* E. & H. from the Favositidae: 'It is convenient to set apart from *Thecia* the forms which possess a wall of the kind which Swann described in *Favosites*, i.e., a median lamella, two thin dark planes on each side, and two borders of perpendicular fibres. Such a microstructure disagrees with the trabecular constitution of *Thecia* chiefly by its continuity along the periphery of the corallites. . . . It is therefore impossible to agree with Hill and Stumm, who put *Thecia* in the family Favositidae.' Thus even family significance has been placed on a character which at the best can be regarded as being developed as a response to environment.

B. *Septal apparatus.* (i) *Septal spines.* The septal apparatus of *F. squamuliferus* is one of the most variable characters of a particularly variable species. Thin discrete septal spines may occur together with squamulae (Pl. 33, figs. 1, 3; text-fig. 1A). The septal spines are remarkably sporadic in their occurrence and are often present only in certain parts of a corallum. Their presence or absence bears little or no relationship with the various formae of *F. squamuliferus* and they have no correlation with the stratigraphic occurrence of the species. That they have not been observed in certain specimens could well be due to poor preservation, but this cannot be argued for most of the material examined. They are apparently absent in some of the formae of *F. squamuliferus*, but this is most likely due to the small number of specimens so far examined belonging to those formae.

(ii) *Squamulae.* The term 'squamula' as used here implies merely a horizontally flattened, usually blunt septal spine (see text-fig. 1). There can be no doubt that squamulae represent modified septal spines. The view of earlier authors (e.g. Nicholson 1879; Smith and Gullich 1925; Jones 1936; Weissermel 1939) that squamulae were a form of 'degenerate' tabulae appears to have been based partly on a misconception as to their nature. Nicholson, for example, considered what are undoubtedly broken tabulae to be squamulae in *F. forbesi.* Swann gave the following observations in support of the septal nature of squamulae: 1, Squamulae, in common with septal spines, are continuous with peripheral stereozones of corallites. 2, Squamulae are arranged in vertical rows similar to septal spines. 3, Squamulae were apparently secreted by the polyp well up from the basal disc. Swann did not mention the trabeculate nature of squamulae which had been earlier established by Kraicz (1937) in *F. hemisphaericus* var. *bohemicus* Počta. It has also been discussed by Hill (1950) in describing some Australian favositids.

Although squamulae had been recognized by Etheridge (1899*a*) in his description of *F. squamuliferus* they had not been recorded as such in any of the other closely related nominal species till Hill (1950) drew attention to their occurrence in *F. stelliformis* (Chapman), *F. bryani* Jones, and *F. murrumbidgeensis* Jones, as well as in a new species *F. pluteus.* Hill distinguished two types of squamulae—'eaves-like' squamulae which occur in the first four of the above species, and 'shelf-type' squamulae typical of *F. pluteus.* The 'eaves-like' squamulae occur back-to-back in adjacent corallites above each mural pore, as they are developed from the fibrous stereome of the upper margin. They are generally upwardly directed and thicken toward their base. The 'shelf-type' squamulae, on the other hand, consist of horizontal plate-like projections of uniform thickness often bearing no relation to the mural pores and so not developed back to back on opposite sides of the walls.

An examination of a collection of specimens from various localities in Victoria in addition to the large collections from the Tyers River limestone suggests that this distinction cannot be maintained. The shape of squamulae and their relation to the mural pores is extremely variable even in different parts of the one corallum. Even a specimen illustrated as *F. pluteus* by Hill (1949, pl. 8, fig. 26*a*, *b*; M.U.G.D.T.S. 649) shows 'shelf' squamulae occurring side by side with 'eaves' squamulae. In this slide the uniform thickness of many of the squamulae is apparently due to the deposition of an uneven layer of secondary calcite (Pl. 31, fig. 5). Further, in some specimens upwardly directed tapering squamulae may bear no relation to the mural pores (Pl. 31, fig. 1) while in still others thin flat squamulae may occur back to back in adjacent corallites (Pl. 31, figs. 6, 8). There is perhaps a trend for the squamulae to lose their relationship with the mural pores and become longer and thinner, as forms showing squamulae of this type are more common in the Middle Devonian of Buchan and Bindi than at the base of the Devonian. Confirmation of this would lie in a detailed examination of our Middle Devonian favositids. It should be pointed out that Hill (1954) was unable to uphold the separation of *F. pluteus* from *F. bryani* in her description of the coral fauna from Waratah Bay.

One specimen showed a further variation in the squamulae. T.S. 892 (Pl. 31, figs. 1, 2) shows the cross-sections of the cut ends of the squamulae where the section passes close to the plane of the corallite wall. In places this section of the squamulae can be seen to be circular, and so they may be regarded as discrete septal spines. It can be seen also that this is not consistent even within the one section; in other places they are flattened in cross-section.

The degree of development of squamulae can be seen to have been related to the rate of growth of the corallum. In zones where the tabulae are closely spaced (i.e. apparently zones of slow growth) the squamulae are usually strong and moderately closely spaced; in zones of rapid growth with distant tabulae the squamulae may be reduced so as to appear absent in parts of the corallum (Pl. 30, fig. 3). The 'species' *F. ovatiporus* Hill and Jones 1940 is based on a corallum showing well-spaced tabulae and a virtual absence of squamulae, together with large, ovate mural pores (Pl. 32, figs. 1, 2) the shape of which again appears to be a function of the rapid growth of the corallum. This, in fact, can be seen in the one section; portions of T.S. 913 and T.S. 1031 (Pl. 34, fig. 1) show well-spaced tabulae and large ovate mural pores and reduced squamulae while other zones of the coralla have the appearance of *F. nitidus* with closely spaced tabulae, moderately strong squamulae, and comparatively small mural pores. The variable development of squamulae can be pointed to in *F. grandiporus* also. This species has typically a subdigitate corallum with a rapidly grown axial zone and a more slowly grown distal region. In the axial part of the corallum the squamulae are small and slender, whereas distally they are thick and large (Pl. 32, figs. 6, 7).

The taxonomic importance of the presence of squamulae should also be discussed. Hill (1950) with reservation placed the species *F. moonbiensis* Etheridge in the synonymy of *F. bryani* (here regarded as a forma of *F. squamuliferus*) as she noted the two were indistinguishable except that *F. bryani* possessed squamulae. If the two species are not very closely related then we have here a remarkable case of virtually isochronous parallelism, particularly in view of the fact that both possess intermural deposits confined to the corallite corners (cf. Pl. 31, fig. 3 and Pl. 33, fig. 2 with Pl. 31, figs. 2, 4, 7 and Pl. 33, fig. 3). Extensive collecting from the limestones and underlying mudstones along the Tyers River showed that *F. moonbiensis* is one of the most common favositids of the mudstone facies, whereas it is completely absent in the overlying limestones. On the other hand, the various formae of *F. squamuliferus* are confined to the limestone facies except for two isolated coralla collected in the upper, more calcareous phases of the mudstone. (For further details of the distribution of these species see Philip 1960.) The few other localities in Eastern Australia from which *F. moonbiensis* has been recorded should be investigated to find whether this facies relationship exists elsewhere. This relationship between *F. squamuliferus* and *F. moonbiensis* suggests that squamulae in the Victorian forms were developed as a response to gross environmental changes. This view is perhaps supported by the fact that in longitudinal sections of *F. moonbiensis* swellings in the stereome of the walls above the mural pores are sometimes encountered. These could well represent 'incipient' squamulae (Pl. 31, fig. 3).

This whole discussion raises the question of the relationship of *Favosites* to *Caliapora* Schlüter and *Emmonsia* E. & H. Hill and Stumm (1956, p. F464) define *Caliapora* to include forms 'like *Emmonsia* but with squamulae with concave upper surfaces'. As has been already stated and is obvious in an examination of the plates, the group dealt with here exhibits such extreme variation in the shape of squamulae that even specific significance cannot be placed on this feature. It seems then that *Caliapora* cannot be separated from *Emmonsia*. Schouppé (1951; 1954*a*) has continued to regard *Caliapora* as a subgenus of *Alveolites*. There appears to be certain justification in regarding *Caliapora*-like forms as being related to *Alveolites* for certain species (e.g. *Alveolites fornicatus* Schlüter) usually placed in that genus are very similar morphologically to the type species of *Caliapora*.

None of the more recent authors who have upheld the generic status of *Emmonsia* has doubted the polyphyletic origin of species placed in this group. Smith and Gullick (1925) explicitly stated that the genus is polyphyletic, 'an assembly of polygerontic forms exhibiting a form of degeneration common in many lineages of *Favosites*'. This view is again expressed by Fenton and Fenton (1936), Swann (1947), and Stumm (1949). Great difficulty has been encountered in the application of the genus. Fenton and Fenton (1936, p. 22) would retain '*Favosites* for forms in which $\frac{2}{3}$ of the tabular structures are complete (tabulae) and introduce *Emmonsia* when squamulae number more than $\frac{1}{3}$ the total . . .', a procedure which appears arbitrary in the extreme. Ross (1953) overcame the difficulty of the polyphyletic origin of the genus by employing *Emmonsia* as a genomorph of *Favosites* in the sense in which the concept was introduced (Smith and Lang 1930) for a morphological stage which occurs in different lineages. In dealing with the present group of favositids it is doubtful whether even this procedure is justified, as squamulae here were apparently developed as a response to gross environmental changes.

It should be noted that Swann (1947) suggested as a new generic character of *Emmonsia* the alternation of squamulae with mural pores, but Ross (1953) has shown (as also did Swann) that this character is developed in different lineages of the North American favositids.

The present conclusion, then, is that *Caliapora* Schlüter and *Emmonsia* E. & H. are best regarded as synonyms of *Favosites*, and the application of *Emmonsia* as a genomorph is not justified in dealing with the Eastern Australian Devonian favositids.

F. grandiporus Etheridge possesses a subdigitate corallum and also shows considerable distal thickening of the corallite walls (Pl. 32, figs. 6, 7). In these characters it approaches species which are generally referred to *Thamnopora*. Swann noted a similar case in his description of *F. alpenensis* lineage. One offshoot from the main lineage, *F. dumosus* Winchell, possesses the same distal thickening and growth habit as *Thamnopora*. This again suggests a possible polyphyletic origin of species included in *Thamnopora*.

The Upper Carboniferous North American genus *Acaciapora* Moore and Jeffords 1945 differs from *Thamnopora* only in the possession of squamulae. Out of the context of its relationship with *F. squamuliferus*, *F. grandiporus* could be placed in this genus, if separation of this genus were considered justified.

METHOD OF STUDY

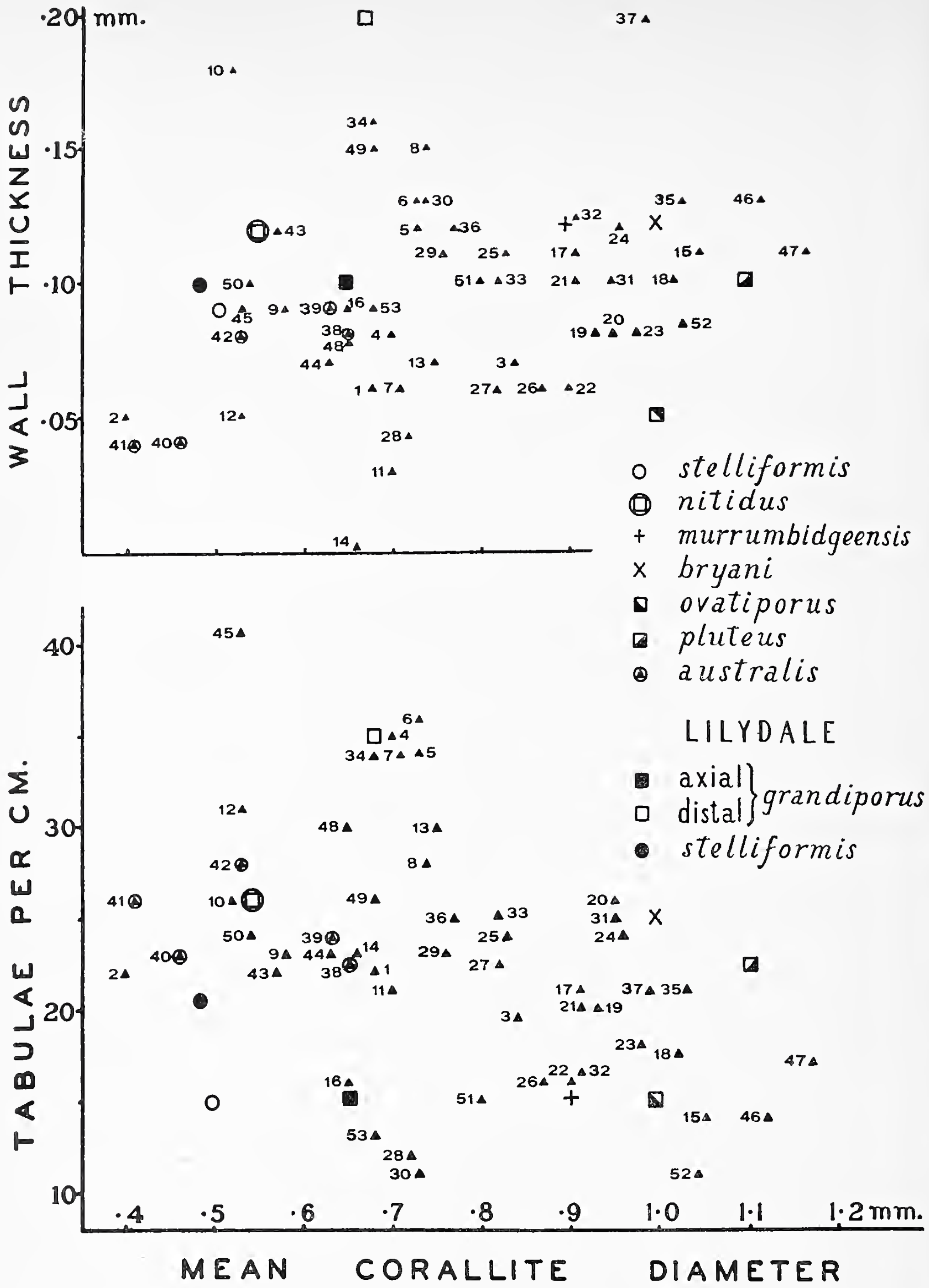
The fauna investigated in detail was taken from the limestone horizon exposed in the valley of the southern part of the Tyers River, Gippsland, Victoria. Precise correlation of this fauna with overseas sections is difficult, but it is best regarded as being of basal Devonian age. Coralla were collected from various localities in the limestone which reaches a maximum thickness of less than 200 feet. In view of the fact that *F. squamuliferus* is a long-ranging species (from Upper Silurian to Middle Devonian) the coralla were treated as being contemporaneous. This is further justified by the fact that there is no faunal differentiation within the limestone horizon apart from that which can be ascribed to facies changes.

In the early stages of the work, when only a few coralla had been examined, many of the squamulate 'species' listed earlier were recognized in the fauna, but as more and more specimens were examined separation into the previously defined 'species' became wellnigh impossible. Differentiation of these 'species' has proved troublesome before, even in small collections (Hill 1954).

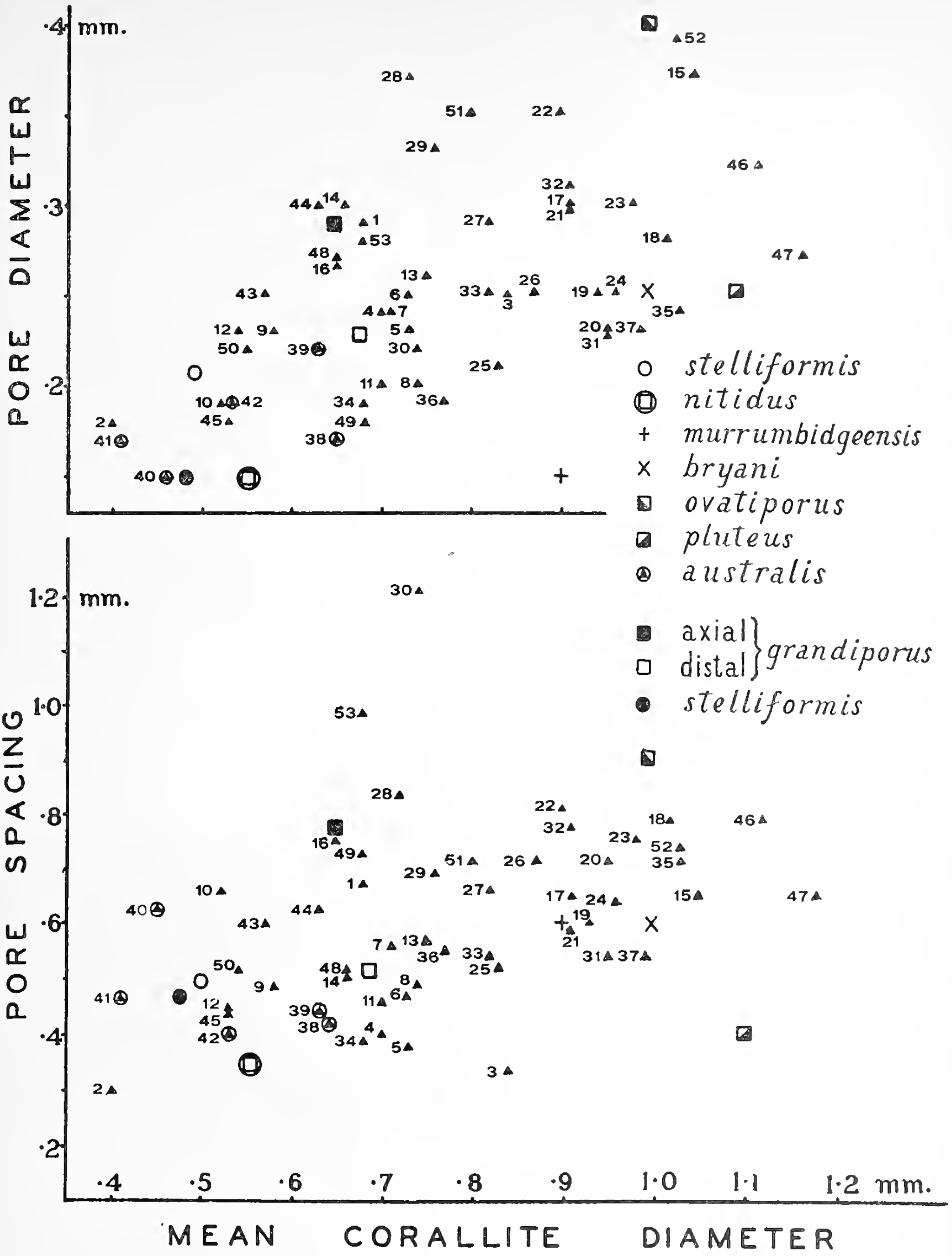
It was found that the only adequate way to characterize the extreme variation of the squamulate favositids within the Tyers fauna, short of illustration of virtually each specimen, was to construct scatter diagrams of the various commensurable characters by which favositid species are defined. A few particularly variable coralla were rejected as it was considered that they could not be defined adequately merely by average measurements.

Of the 135 coralla collected, 53 were considered suitable, after the preparation of sections, for the calculation of average measurements. The features determined were:

1. *Mean corallite diameter.* An endeavour was made to measure the maximum diameter of the corallites in thin sections normal to the direction of growth. The diameter was measured from the boundary of the primary walls of the corallites. At times this measurement was made with polished surfaces.
2. *Mean number of tabulae per centimetre.* The number of tabulæ over a comparatively large length of corallites was measured to include the different spacing of tabulae within the one corallum. At least 10 cm. of corallite length was measured for each corallum, and usually the figure was greatly in excess of this.
3. *Mean diameter of mural pores.* The diameter of all mural pores visible in each section was taken. In one case this was as few as six, but usually many more were used. As the mural pores were often oval, the square root of the height by the width was taken as the diameter.
4. *Average spacing of mural pores.* This measurement is the vertical spacing of the centres of mural pores and was arrived at by the addition of half the vertical diameter of two consecutive mural pores and the length of corallite between them. Measurements 3 and 4 were made simultaneously although



TEXT-FIG. 2. Scatter diagrams of the average wall thickness and average number of tabulae per centimetre against the mean corallite diameter for fifty-three specimens of *F. squamuliferus* from the Tyers River limestone. Superimposed are the approximate positions of six of the more commonly used 'species' of squamulate favositid, the positions of which were arrived at from the descriptions and figures of various authors. Specimens of *F. squamuliferus* forma *australis* from the Tyers River limestone are designated by a different symbol. The two illustrated specimens from the Lilydale Limestone are also included. No morphological separation of the fauna into 'species' is possible.



TEXT-FIG. 3. Scatter diagrams of average mural pore diameter and average mural pore spacing against mean corallite diameter for fifty-three specimens of *F. squamuliferus* from the Tyers River limestone. Superimposed are the approximate positions of the more commonly used 'species' of squamulate favositid, which were arrived at from the descriptions and figures of various authors. Specimens of *F. squamuliferus* forma *australis* from the Tyers River limestone are designated by a different symbol. The two illustrated specimens from the Lilydale Limestone are also included. Only an arbitrary separation is possible.

the spacing of the pores was measured also in well-oriented longitudinal sections normal to the corallite faces where the pores are represented by breaks in the walls.

5. *Mean diameter of corallite walls.* This included the total diameter of the walls of two adjacent corallites and in places included intermural spaces. It was measured half-way between the corners of the corallites so as to avoid measurements through the thickened corners in specimens where the corallites were rounded.

An attempt was also made to characterize the orientation and length of the squamulae, but these proved so variable even in the one corallum that this was abandoned.

The thin sections used in the construction of the scatter diagrams are in Melbourne University Geology Department Thin Section Collection T.S. 849 and 861 to 965 inclusive. The average characters arrived at for each of the fifty-three specimens are entered in the thin-section catalogue.

Examination of the four scatter diagrams reproduced here shows that it is impossible to subdivide morphologically this fauna into components between which there is no intergradation. The same is also true of the six other possible scatter diagrams which were constructed. Certain individual specimens may appear to be isolated from the group in one particular character (14, 37—wall thickness; 30—pore spacing; 45—tabulae spacing), but these individuals represent the extreme development of a feature already shown to a lesser degree by other members of the group. The divergent types are represented as formae within the single species.

The scatter diagrams show a certain degree of correlation between morphological features which could be expected on general grounds. For example, with increasing corallite diameter the mural pores generally become larger and more distant while the wall thickness perhaps tends to increase. Another trend which can be seen from the scatter diagrams which are not reproduced here is an increase of the spacing of the mural pores with increase in spacing of the tabulae. Overall, however, it can be seen that there is no great degree of correlation between the various morphological features.

SYSTEMATIC DESCRIPTIONS

Genus FAVOSITES Lamarck

Favosites grandiporus Etheridge

Plate 32, figs. 6, 7; Plate 33, fig. 9; Plate 34, fig. 4; text-fig. 1c

Favosites grandipora Etheridge 1890, p. 61, 2, pl. 8, figs. 6–9.
Alveolites victoriae Chapman 1921, p. 215, pl. 11, figs. 17, 18.

Diagnosis. Corallum subdigitate, cylindrical, sometimes amalgamated by later overgrowths. Corallites gently expanding in axial region, bending sharply to emerge normal to the surface of the corallum; corallites polygonal in axial region, usually rounded distally, diameter averaging between 0·6 and 1 mm.; distally the mural pores are more closely spaced and smaller, the tabulae more crowded, the walls thicker, and the squamulae more strongly developed.

Observations. The measurements of a typical specimen can be seen in text-figs. 2, 3. It may be that this species, differing from *F. squamuliferus* in the growth habit and distal thickening of the corallites, is transitional morphologically with that species. However, the material so far investigated from the Lilydale Limestone, the only horizon from which *F. grandiporus* is known, suggests that it is a separable species. Distal thickening of corallites in tabulate corals is generally regarded as a character of generic merit.

Reference to Chapman's type slides of *Alveolites victoriae* shows that this species is based on a specimen of *F. grandiporus* with comparatively large corallites. In his original description Chapman noted the distal thickening of the walls of the corallites and his plate shows the characteristic wall structure of *F. grandiporus*. Chapman apparently regarded as 'teeth' the remnants of the walls of corallites on each side of a mural pore, as encountered in transverse sections, and so placed the species in the genus *Alveolites*.

Of the well-developed squamulae in this species Jones (1937, p. 93) has stated: 'The appearance of spines in longitudinal section is caused by the breaking down of the wall where the large mural pores almost meet.'

Favosites squamuliferus Etheridge

Favosites squamulifera Etheridge 1899*a*, pp. 166–7, pl. 38, figs. 4, 5.
Emmonsia squamulifera (Etheridge fil.); Jones 1937, p. 99.

Diagnosis (after Etheridge). Corallum massive, corallites approximately the same size, averaging 1 mm. or less in diameter, mural pores small, in a single column on each corallite face; squamulae horizontal or inclined, tabulae moderately closely spaced.

Observations. Etheridge's meagre description and inadequate figures make the interpretation of this species difficult. The type specimens are reported by Hill (1950) to be missing, and there is even some doubt as to the type locality of the species. Not until the tabulate corals of the Tamworth district of New South Wales are investigated in detail will this species be properly understood. Because of this the use of the species here is undesirable, but as it cannot be questioned that it is the first name employed in the literature to this species it is retained.

It is more than likely that *F. squamuliferus* will prove to be identical with *F. bryani* Jones. As *F. bryani* is much more precisely defined, it is retained in the naming of the forma which most probably includes *F. squamuliferus* s.s.

Favosites squamuliferus forma *bryani* Jones (forma α[1])

Plate 31, figs. 1, 2, 4–6, 8; Plate 33, fig. 3; text-fig. 1A, B

?*Favosites squamulifera* Etheridge 1899*a*, pp. 166–7, pl. 38, figs. 4, 5.
?*Favosites gothlandica* Lamarck; Chapman 1920, p. 186 (*partim*), pl. 23, figs. 18, 19.
Favosites (*Emmonsia*) *spinigera* Chapman 1921, pp. 214–15, pl. 9, fig. 21 (*non* Hall 1879, p. 108, pl. 4, figs. 1–5).
Favosites murrumbidgeensis Jones M. S., *in* Allan 1935, p. 7, pl. 4, figs. 5, 6.

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[1] The formae recognized within *F. squamuliferus* are designated with a Greek letter, a procedure used by Olliver (1958). Although the 'forma', as used by various authors, has no standing as a taxonomic category and so the laws of priority do not apply, later authors are liable to elevate the names employed as formae to the rank of subspecies. Thus Bassler (1950, p. 81) lists Lecompte's (1939) two formae of *F. goldfussi*, *F. goldfussi* forma *regularis*, and *F. goldfussi* forma *pyriformis* as subspecies, thus presumably making the former a further homonym of *Favosites regularis* (Chapman 1920) along with *F. kemilhoenis* var. *regularis* Ozaki 1934, *F. regularis* Jones 1937, and *F. hisingeri* var. *regularis* Ruhkin 1938 and the latter a homonym of *F. pyriformis* (Hall 1852). To avoid such possible contingencies it is best to refrain from applying to new formae names which could be used as trivial appellations.

Favosites bryani Jones 1937, pp. 96–97, pl. 15, figs. 3–6.
Favosites murrumbidgeensis Jones 1937, p. 98, pl. 16, figs. 5, 6.
?*Emmonsia squamulifera* (Eth. fil.); Jones 1937, p. 99.
Favosites bryani Jones; Hill and Jones 1940, pp. 190–1, pl. 5, figs. 2*a*, *b*; Jones 1941, p. 42, pl. 1, fig. 1; Hill 1942, p. 8, pl. 2, fig. 6; Jones 1944, p. 34, pl. 1, figs. 1, 2; Hill 1950, p. 150, pl. 7, figs. 23, 24.
Favosites pluteus Hill 1950, p. 151, pl. 8, figs. 25–26.
Favosites affin. *bryani* Jones; Hill 1954, pp. 113–14, pl. 9, figs. 23, 24.

Material. Specimens 3, 17–21, 23–27, 31–33, 35, 46, 47; figured slides T.S. 891 (18); T.S. 892 (20); T.S. 895 (21); T.S. 917 (31); T.S. 921 (32) and T.S. 649 from Rocky Camp, Murrindal Limestone, Buchan.

Diagnosis. Corallum massive, corallites polyhedral averaging greater than 0·8 mm. diameter and usually less than 1·5 mm.; mural pores uniserial circular to slightly ovate between 0·15 and 0·35 mm. in diameter and between 0·3 and 0·8 mm. apart. Squamulae

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EXPLANATION OF PLATE 30

Longitudinal sections; all figures ×10 and unretouched. The serial number in parentheses refers to the number of the specimen in the scatter diagrams, and the prefix 'T.S.' refers to catalogue numbers in the Melbourne University Geology Department Thin Section Collection of Fossils.

Figs. 1, 2. *Favosites squamuliferus* forma *stelliformis* (γ). 1, T.S. 849 (2). Small corallite diameter, poorly developed squamulae, and well-spaced tabulae developed in places at similar heights in adjacent corallites. Tyers River limestone. 2, T.S. 1211 (also Pl. 33, fig. 6). Well-developed flattened squamulae occurring back to back in neighbouring corallites above mural pores. 'Pore plates', usually present in *F. squamuliferus*, also seen. Lilydale Limestone.

Figs. 3–5, 7. *F. squamuliferus* forma *nitidus* (β). 3, T.S. 875 (9) (also Pl. 33, fig. 7). Variable development of squamulae. 4, T.S. 924 (34) (also Pl. 33, fig. 8). Very closely spaced suspended and 'incomplete' tabulae and thick-based squamulae. 5, T.S. 880 (12). Moderately large mural pores and small squamulae. 7, T.S. 865 (4). Mural pores and small squamulae. All from Tyers River limestone.

Fig. 6. *F. squamuliferus* forma *australis* (δ). T.S. 935 (39) (also Pl. 33, fig. 5). Wide, irregular intermural spaces, well-spaced tabulae, and small squamulae. Tyers River limestone.

Fig. 8. *F. squamuliferus* forma η. T.S. 882 (14) (also Pl. 33, fig. 4). Extremely thin-walled form with small squamulae and well-spaced tabulae. Mural pores also seen. Tyers River limestone.

EXPLANATION OF PLATE 31

Longitudinal sections; all figures ×10 and unretouched.

Figs. 1, 2, 4–6, 8. *F. squamuliferus* forma *bryani* (α). 1, 2, T.S. 892 (20). Strong, upwardly curved squamulae, in places not occurring back to back in adjacent corallites. The cut ends of the squamulae are in places circular rather than flattened. Tyers River limestone. 4, T.S. 917 (31). Short, upwardly directed squamulae, well-spaced tabulae, and a single column of moderately large mural pores. Tyers River limestone. 5, T.S. 649. Slide illustrated as '*F. pluteus*' (Hill 1950, pl. 18, fig. 26*a*, *b*). Note upwardly directed, tapering squamulae above the mural pores. An irregular deposit of secondary calcite can be seen obscuring the taper of the squamulae and giving also the appearance of very thick tabulae. Murrindal Limestone, Rocky Camp, Buchan. 6, T.S. 921 (32). Similar specimen with horizontally directed squamulae, some of which do not occur back to back in neighbouring corallites. Tyers River limestone. 8, T.S. 895 (21). Large, closely spaced mural pores, and thin, delicate squamulae, thus approaching forma *ovatiporus*. Tyers River limestone.

Fig. 3. *F. moonbiensis* Etheridge. T.S. 800 (also Pl. 33, fig. 2), cf. figs. 4, 7. Note similarity between this form and *F. squamuliferus* forma *bryani*. Occasional swellings in the stereome of the walls above mural pores may be encountered (e.g. top right-hand corner of figure). These swellings could represent 'incipient' squamulae. Mudstone beneath the limestone, Tyers River.

Fig. 7. *F. squamuliferus* forma ζ. T.S. 915 (30). Note the small, distantly spaced mural pores, well-separated tabulae, and reduced squamulae. Tyers River limestone.


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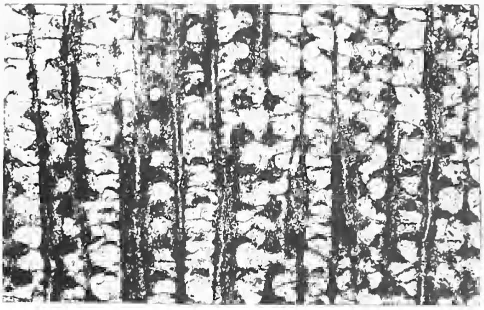
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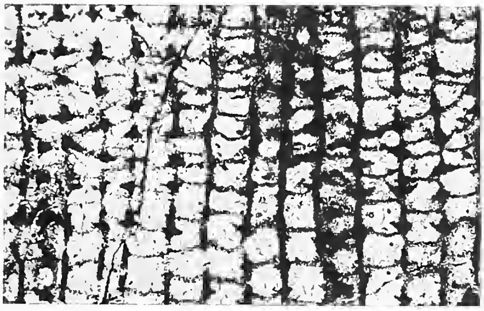
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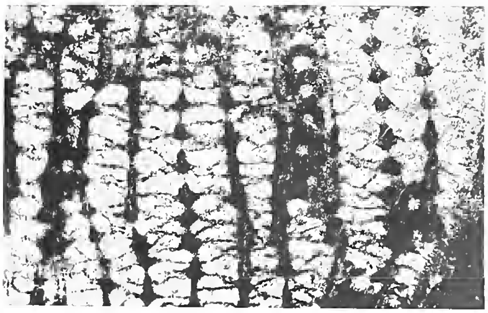
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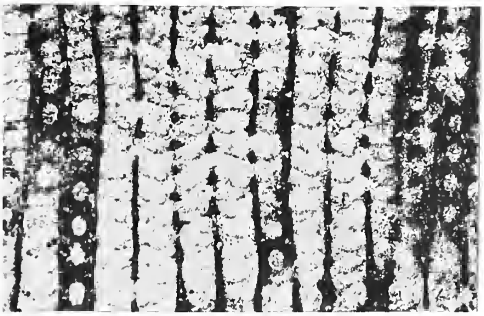
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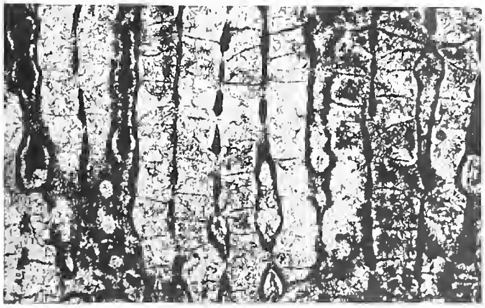
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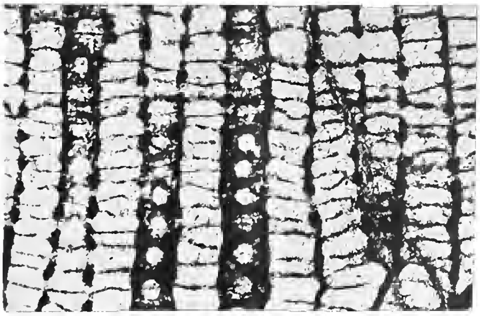
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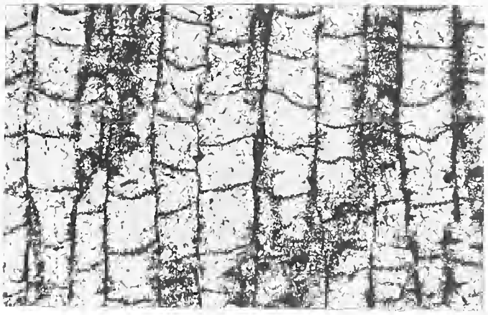
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PHILIP, Australian favositids

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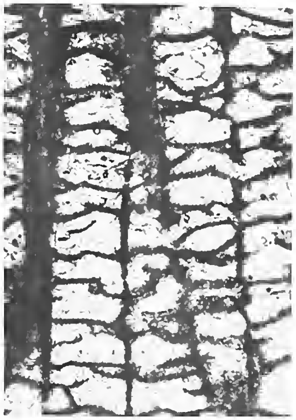

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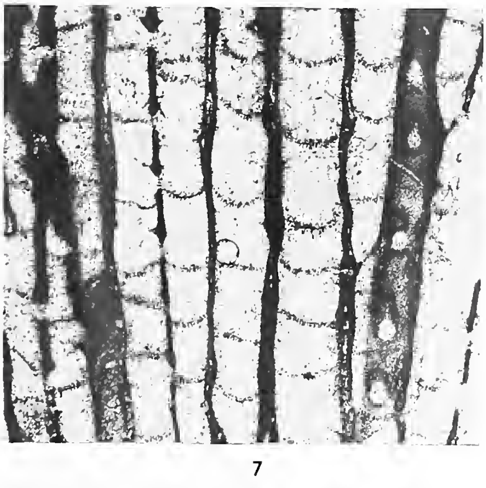

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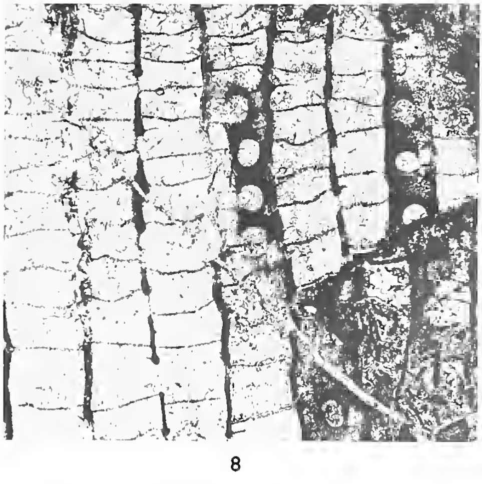

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PHILIP, Australian favositids

highly variable, horizontal or upwardly directed, developed either back to back in adjacent corallites above the mural pores or isolated. Slender septal spines may also be present.

Observations. F. squamuliferus forma *bryani* is arbitrarily separated from forma *nitidus* (β) and forma *stelliformis* (γ) by the corallite diameter. In the forms with smaller corallite diameter the tabulae may be more closely spaced. As can be seen from the synonymy of this species five different specific names have been applied to this forma.

F. squamuliferus forma *nitidus* (β)

Plate 30, figs. 3–5, 7; Plate 34, figs. 1, 7, 8, 10

?*Favosites* sp. indet. Etheridge 1899*b*, p. 33, pl. B, figs. 7–9.
Favosites nitida Chapman 1914, p. 309, pl. 54, figs. 21–23; pl. 55, figs. 24, 25.
Favosites forbesi (*partim*) Chapman 1914, pl. 53, fig. 19 (*non.* pl. 56, fig. 27).
Favosites nitida Chapman; Jones 1937, p. 93, pl. 12, figs. 4, 5.
Favosites nitidus Chapman; Hill and Jones 1940, p. 198, pl. 6, figs. 3*a*–*c*.
Favosites nitidus var. *medius* Hill and Jones 1940, pp. 198–9, pl. 6, figs. 4*a*, *b*; pl. 7, figs. 1*a*, *b*, 2.
Favosites nitidus Chapman; Jones 1941, p. 43, pl. 1, fig. 2; Hill 1950, pp. 148–9, pl. 7, figs. 20*a*, *b*; Hill 1954, p. 113, pl. 9, figs. 25*a*, *b*.

Material. Specimens 1, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 16, 29, 34, 44, 45, 48, 50, 53; figured slides T.S. 865(4); T.S. 870(6); T.S. 875–6(9); T.S. 880(12); T.S. 924–5(34); T.S. 967; T.S. 1031.

Diagnosis. F. squamuliferus with average corallite diameter between 0·5 and 0·8 mm.

Observations. In general, besides the smaller corallite diameter, this forma has smaller mural pores and may also have closer tabulae than is usual in forma *bryani*.

Hill and Jones (1940) note that there is a complete gradation between *F. nitidus* and *F. salaebrosus* Etheridge 1899 and that *F. salaebrosus* should be set aside for forms having a considerable number of reclined corallites which as a result appear alveolitoid in transverse sections. They proposed *F. nitidus* var. *medius* to include forms intermediate between *F. nitidus* and *F. salaebrosus*. If squamulae prove to be present in the type slides of *F. salaebrosus* then this species could be set aside as a further forma of *F. squamuliferus* to include forms with reclined corallites.

F. squamuliferus forma *stelliformis* Chapman (γ)

Plate 30, figs. 1, 3; Plate 33, fig. 6

Chaetetes stelliformis Chapman 1918, p. 393, pl. 42, figs. 1–3.
Alveolites regularis Chapman 1920, p. 216, pl. 11, figs. 19, 20.
Favosites stelliformis (Chapman); Hill, 1950, p. 149, pl. 7, figs. 21, 22.

Material. Specimen 2; figured slides T.S. 849 (2) also T.S. 1210-1 from the Lilydale Limestone.

Diagnosis. F. squamuliferus with the average diameter of corallites less than 0·5 mm.

Observations. Hill (1950, p. 149), although recognizing the relationship to *F. squamuliferus* forma *nitidus*, suggested by this form from Buchan, states: 'Its unusual characters, the numerous oval pores separated by squamular aggregations of trabeculae and the regular tabular floors throughout the corallum, suggest it might be wise to erect a new genus for it.' The similar height of tabulae in adjacent corallites is fairly common in *F. squamuliferus*, particularly in those specimens with small corallites. The holotype of *F. nitidus* var. *medius* (Hill and Jones 1940, pl. 6, fig. 4*a*) shows this character although perhaps not as strikingly as in the specimens illustrated as *F. stelliformis* by Hill. It should be noted that Chapman's original figures of *F. stelliformis* do not show this at all well, nor do other specimens of this forma from Buchan and Bindi.

F. squamuliferus forma *australis* (Chapman) (δ)

Plate 30, fig. 6; Plate 33, fig. 5; Plate 34, fig. 3

Cannapora australis Chapman 1907, p. 76, pl. 3, figs. 6, 7; pl. 8, figs. 17, 18.

Material. Specimens 38–42; figured slides T.S. 934–5 (39); T.S. 985.

Diagnosis. F. squamuliferus with small corallite diameter and sub-cerioid growth allowing separation of the corallites.

Observations. Chapman's type specimens of this species were collected from the Tyers River limestone, but have apparently been lost. The topotype illustrated matches Chapman's figures very closely. Although the corallites may not all be in contact in other formae of this species (a feature which is often difficult to detect even in thin section) extreme cases of this feature appear to be confined to specimens of *F. squamuliferus* with small corallite diameter, well-spaced tabulae, and reduced squamulae.

F. squamuliferus forma *ovatiporus* Hill and Jones (ε)

Plate 32, figs. 1, 2

Favosites ovatiporus Hill and Jones 1940, pp. 199, 200, pl. 7, figs. 3, 4; pl. 8, figs. 1, 2; Hill *in* Thomas 1947, p. 41.

Favosites? *ovatiporus* Hill and Jones 1940 var.; Hill 1954, p. 113, pl. 8, figs. 21, 22.

Material. Specimens 15, 22, 28, 51, 52; figured slides T.S. 912 (28) and T.S. 961(51).

Diagnosis. F. squamuliferus with large, ovate mural pores greater than 0·35 mm. in diameter, and well-spaced tabulae, usually less than 15 per cm.

Observations. As has been mentioned earlier the squamulae are so reduced in this forma that in places in a corallum they are virtually absent.

EXPLANATION OF PLATE 32

Longitudinal sections; all figures × 10 and unretouched.

Figs. 1, 2. *F. squamuliferus* forma *ovatiporus* (ε). 1, T.S. 912 (28). Occasional large ovate mural pores, typically concave distant tabulae, and exceedingly small squamulae. 2, T.S. 961 (51). Stronger squamulae, closer tabulae, and smaller mural pores; i.e. intermediate between forma *bryani* and forma *ovatiporus*. Tyers River limestone.

Figs. 3–5. *F. squamuliferus* forma *θ*. 3, T.S. 944 (43) (also Pl. 33, fig. 11). Irregularly spaced mural pores, small squamulae, and expanding corallites which give rise to a subdigitate corallum which characterizes this forma. Note also comparatively thicker walls. 4, T.S. 930 (36). Intermediate between forma *nitidus* and forma *θ*. 5, T.S. 932 (37), (also Pl. 33, fig. 12). Larger corallite diameter again with small squamulae, thick walls, and irregularly distributed mural pores. Clear zones in the middle of the walls represent intermural spaces. Tyers River limestone.

Figs. 6, 7. *F. grandiporus* Etheridge. 6, T.S. 1208 (also Pl. 33, fig. 9, Pl. 34, fig. 4). Axial portion of a large cylindrical corallum. Note comparatively thin walls, well-spaced tabulae and mural pores, as well as small squamulae. 7, T.S. 1205. Distal portion of same corallum, showing strong thickening of the walls, heavier squamulae, and crowded tabulae. Mural pores are also smaller and more closely spaced. Lilydale Limestone.


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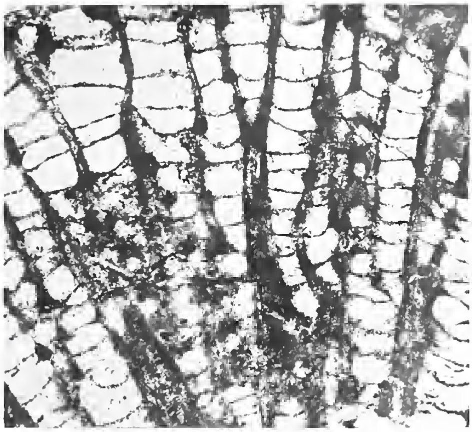
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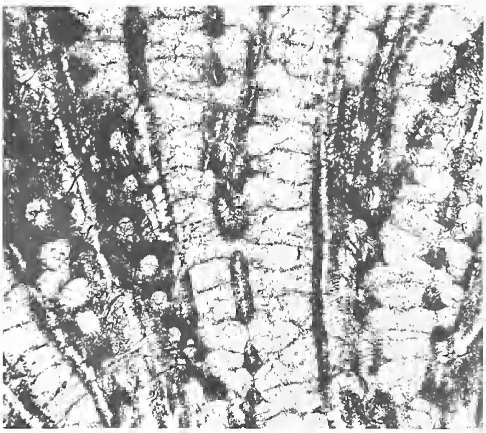
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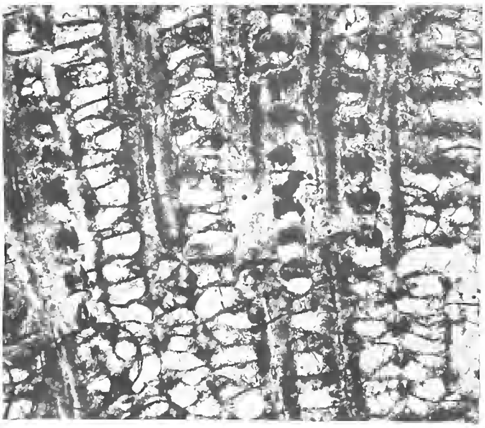
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PHILIP, Australian favositids

F. squamuliferus forma ζ nov.

Plate 31, fig. 7

Diagnosis. F. squamuliferus with widely spaced tabulae and reduced squamulae as in *F. squamuliferus* forma *ovatiporus* but the mural pores are comparatively small and average 1·2 mm. apart.

Material. Specimen 30; figured slide T.S. 915 (30).

F. squamuliferus forma η nov.

Plate 30, fig. 8; Plate 33, fig. 4

Material. Specimen 14; figured slides T.S. 882–3 (14).

Diagnosis. F. squamuliferus with very thin walls averaging less than 0·01 mm. thick.

Observations. The single specimen from the Tyers limestone on which this forma is based shows consistently thin walls with a very narrow sporadic stereozone which may thicken slightly at the corners of the corallites. Other specimens (e.g. T.S. 967; Pl. 33, fig. 1) may show in places similar very thin walls, but this was the only specimen collected in which the feature was constant.

F. squamuliferus forma θ nov.

Plate 32, figs. 3–5; Plate 33, figs. 11, 12; Plate 34, fig. 5

Material. Specimens 36, 37, 43, 49; figured slides T.S. 943–4(43); T.S. 930(36); T.S. 931–2 (37); T.S 1013.

Diagnosis. Subdigitate thick-walled *F. squamuliferus* with irregularly spaced mural pores and reduced squamulae.

Observations. This forma perhaps represents a morphological stage between *F. squamuliferus* and *F. grandiporus* since it possesses the subdigitate growth habit and thick walls of the latter species, although it lacks its characteristic distal thickening of the corallite walls.

Apart from the eight formae of *F. squamuliferus* recognized here, *F. salaebrosus* Etheridge should most probably be set aside as a ninth for forms of *F. squamuliferus* with reclined corallites.

It is considered that it is worth separating the species into the various formae since outside of a large collection one forma may appear to be separated from typical members of other formae by differences of specific merit.

COMPARISON OF *F. GRANDIPORUS* AND *F. SQUAMULIFERUS* WITH NON-AUSTRALIAN SPECIES

Certain species have been described from the Upper Silurian to Middle Devonian limestones in Europe and Russia which fall in the morphological range of the species *F. grandiporus* and *F. squamuliferus* as these variable species must be understood. This list is probably by no means complete as the writer has been unable to trace most of the recent Russian literature and some of the more obscure European publications. It would be of interest to establish whether these overseas species exhibit the same extreme variation as the Australian species. The species which have been found are:

(1) *Favosites brusnitzini* Peetz 1901, p. 177, pl. 3, fig. 11*a*, *b*. Chernyshev 1951, pp. 27–28, pl. 5, figs. 3–5, basal Devonian, Kuznetsk Basin. Chernyshev gives the corallite diameter of this species as between 0·5 and 1 mm., wall thickness 0·05 to 0·06 mm.; tabulae 9–16 in 5 mm., and the mural pores 0·2 mm. in diameter and about 0·5 mm. apart. The backed squamulae above the mural pores are apparent in Chernyshev's pl. 5, fig. 5. In all respects the neotype of this species chosen by Chernyshev cannot be distinguished from *F. squamuliferus* forma *bryani* Jones or forma *nitidus* Chapman.

(2) *Favosites intricatus* Barrande, Počta 1902 (Počta 1902, pp. 233–5, pl. 88, 91, 95, 102), Lower Devonian, Koněprus, Bohemia. The slides on pl. 102, figs. 2, 3 show a form indistinguishable from *F. squamuliferus* forma *bryani* or forma *nitidus* Chapman with well-developed squamulae. Squamulae do not appear to be present in the specimens illustrated on pl. 95; the septa are very much stronger and the mural pores are more often biserial than is usual in *F. squamuliferus*.

EXPLANATION OF PLATE 33

Transverse sections; all figures ×10 and unretouched.

Figs. 1, 7, 8, 10. *F. squamuliferus* forma *nitidus* (β). 1, T.S. 967. Note variable wall thickness. Squamulae can be seen occurring back to back in adjacent corallites and occasional thin septal spines are also apparent. 7, T.S. 876 (9) (also Pl. 30, fig. 3). Poorly developed intermural spaces. 8, T.S. 925 (34) (also Pl. 30, fig. 4). Well-developed intermural spaces in the thickened angles of the corallites. 10, T.S. 870 (6). Constant diameter of walls and no rounding of corallites. Intermural spaces insignificantly developed. Tyers River limestone.

Fig. 2. *F. moonbiensis* Etheridge. T.S. 798 (also Pl. 31, fig. 3). Identical with *F. squamuliferus* forma *bryani* except in the absence of septal apparatus. Note the clear intermural spaces enlarging toward the corners of the corallites. Mudstone beneath the limestone, Tyers River.

Fig. 3. *F. squamuliferus* forma *bryani* (α). T.S. 891 (18). Blunt squamulae occurring back to back with discrete septal spines in some corallites. Tyers River limestone.

Fig. 4. *F. squamuliferus* forma η. T.S. 883 (14) (also Pl. 30, fig. 8). Form characterized by extremely thin walls. Tyers River limestone.

Fig. 5. *F. squamuliferus* forma *australis* (δ). T.S. 934 (39) (also Pl. 30, fig. 6). Form characterized by subcerioid growth. Note wide separation of corallites in places and 'stellate' intermural spaces present in parts of the figure. Tyers River limestone.

Fig. 6. *F. squamuliferus* forma *stelliformis* (γ). T.S. 1210 (also Pl. 30, fig. 2). Well-developed 'stellate' intermural spaces at corners of corallites and thickening of corallite walls in their vicinity. Lilydale Limestone.

Fig. 9. *F. grandiporus* Etheridge. T.S. 1209 (also Pl. 32, figs. 6, 7; Pl. 34, fig. 4). Section cut toward distal region of corallum. Note 'stellate' intermural space in top left of figure showing thickening and bleaching of the stereome of the corallites in its immediate vicinity. Lilydale Limestone.

Figs. 11, 12. *F. squamuliferus* forma θ. 11, T.S. 943 (43) (also Pl. 32, fig. 3). Rounding of corallites and bleaching of stereome in vicinity of intermural spaces. 12, T.S. 931 (37) (also Pl. 32, fig. 5). Thick-walled form showing well-developed intermural spaces and rounding of corallites. Tyers River limestone.

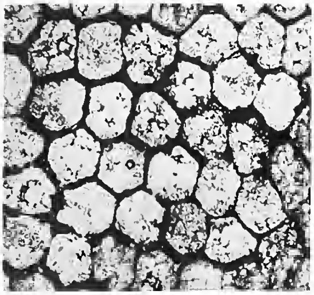
EXPLANATION OF PLATE 34

Figs. 1, 2. *F. squamuliferus* forma *nitidus* (β). 1, T.S. 1031. Corallum showing a growth zone approaching forma *ovatiporus* with increase of spacing of tabulae, reduction of the squamulae and development of large, distant, ovate mural pores. ×5. 2, T.S. 967. Corallum showing variation of corallite diameter and wall thickness. Tyers River limestone. ×5.

Fig. 3. *F. squamuliferus* forma *australis* (δ). T.S. 985. Widely developed intermural spaces occurring at similar heights between adjacent corallites. Tyers River limestone. ×5.

Fig. 4. *F. grandiporus* Etheridge. T.S. 1209. Well-developed 'stellate' intermural spaces. Lilydale Limestone. ×20.

Fig. 5. *F. squamuliferus* forma θ. T.S. 1013. Irregularly developed intermural spaces with bleaching of the stereome of the corallites in their vicinity. Tyers River limestone. ×20.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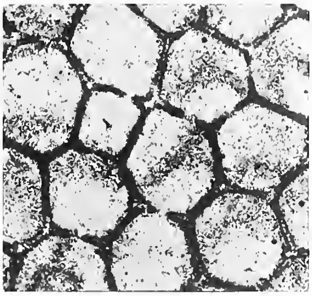
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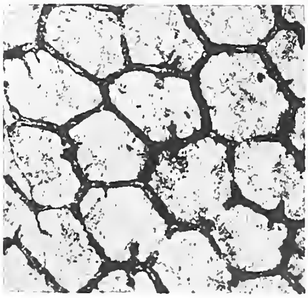
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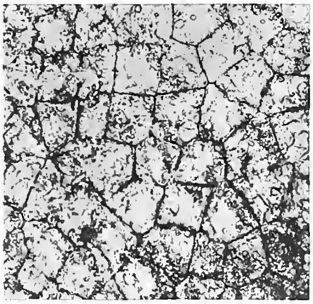
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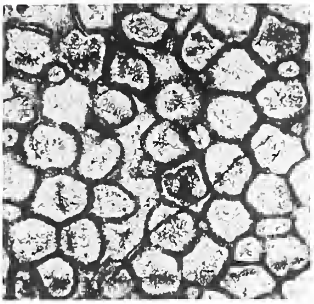
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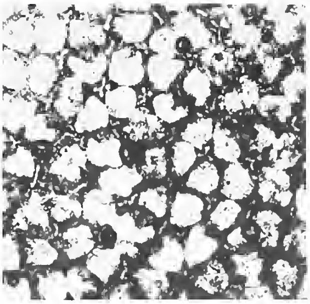
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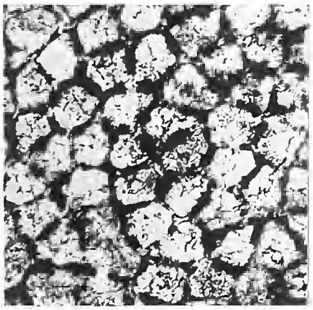
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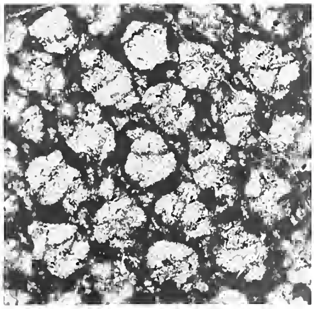
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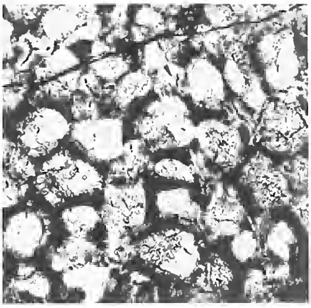
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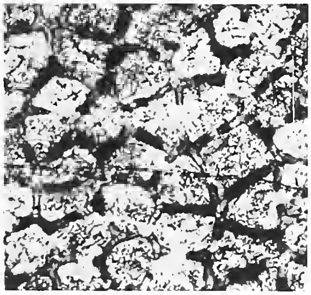
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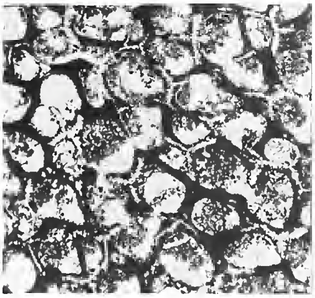
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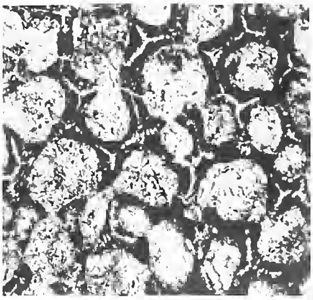
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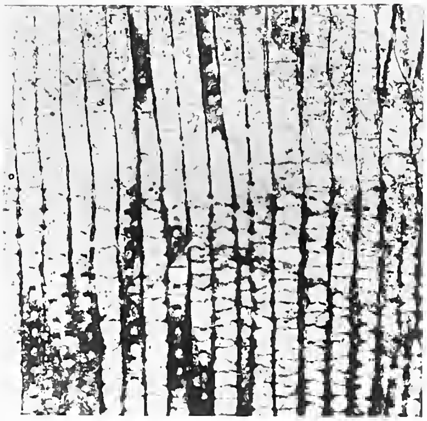
PHILIP, Australian favositids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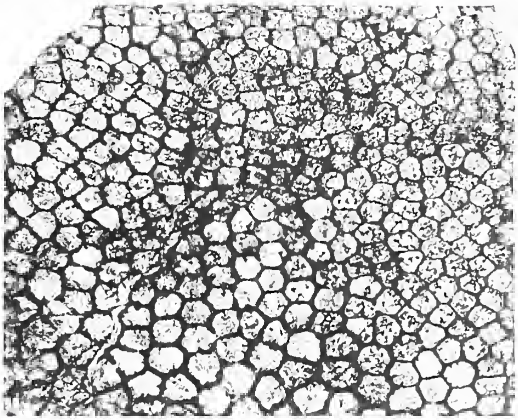
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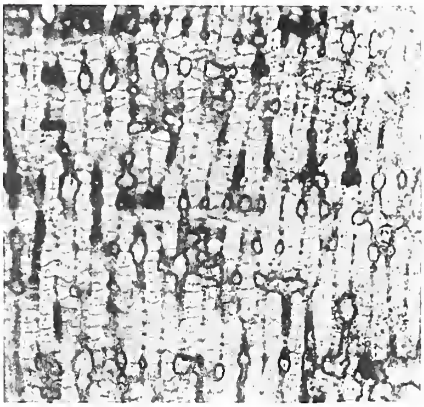
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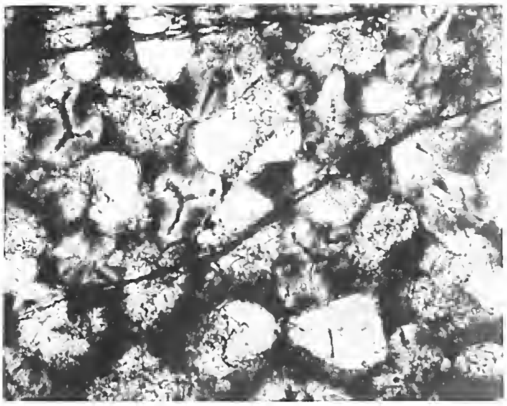
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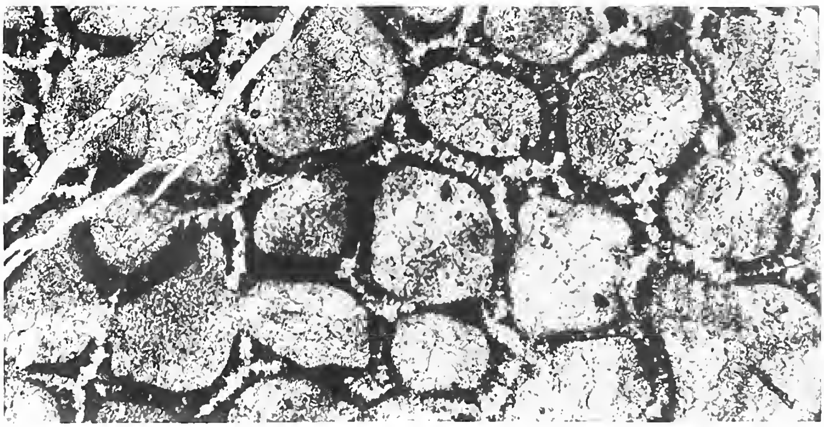
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PHILIP, Australian favositids

(3) *Favosites proasteriscus* Charlesworth 1914, pp. 373–4, pl. 33, fig. 1*a*, *b*; Lower Devonian, Carnic Alps. This species, with corallites 1 mm. in diameter, possesses intermural deposits similar to those of the Australian species. Charlesworth speaks of the 'undulating' character of the corallites in longitudinal sections, stating that in this respect the species is similar to *F. intricatus* Barrande. This suggests that the species may be squamulate, in which case the species shows strong affinities to *F. squamuliferus* forma *bryani*. If it is not, the species bears a close relationship to *F. moonbiensis* although the tabulae are much closer in *F. proasteriscus*. Charlesworth states there are twenty-five tabulae per cm., but his plate shows about fifty. *F. interstinctus* Regnéll 1941 from the Siluro-Devonian of Chöl-tagh, eastern Tien-shan, is also a species close to *F. moonbiensis*.

(4) *Alveolites* (*Caliapora*) *frechi* Charlesworth 1914, p. 381, pl. 34, fig. 1*a*, *b*. Lower Devonian, Carnic Alps. This species, with a corallite diameter of about 0·5 mm., appears very similar to forms included here in *F. squamuliferus* forma *nitidus* although it is impossible to arrive at any real understanding of the species from Charlesworth's description and figures.

(5) *Alveolites* (*Caliapora*) *carnicus* Charlesworth 1914, p. 396, pl. 34, fig. 2. Upper Silurian, Carnic Alps. Again it is very difficult to interpret this species with a corallite diameter of about 1 mm. and strong squamulae. The form figured, however, appears to be closely related to *F. squamuliferus* forma *bryani* or the thick walled subdigitate forma θ.

(6) *Favosites inosculans* Nicholson; Le Maitre 1931, pp. 575–7, pl. 29, figs. 1–4. non *Favosites*? *inosculans* Nicholson 1881, pp. 20–21, pl. 1, figs. 4, 4*a*. Upper Lower Devonian; Bassin d'Ancenis. The form illustrated by Le Maitre is closely comparable with *F. squamuliferus* forma *nitidus* in all respects except perhaps that the form of growth is more reminiscent of *F. squamuliferus* forma θ.

(7) *Favosites alpina* (Hornes) Penecke; Le Maitre 1934, p. 171, pl. 8, figs. 7–9. non *Favosites alpinus* Penecke 1894, *vide* Schouppé 1954*b*, pp. 25–26, pl. 1, figs. 4, 10. Upper Lower Devonian; Bassin d'Ancenis. Although Le Maitre did not describe the mural pores in this form, they appear to be uniserial in her plate. In every other respect this form falls within the range of *Favosites squamuliferus* forma *bryani*.

(8) *Favosites inosculans* Nicholson; Le Maitre 1937, pp. 113–14, pl. 8, figs. 1–3. non *Favosites*? *inosculans* Nicholson 1881. Lower Middle Devonian, Ville-de-d'Ardin. Le Maitre's figures are of a form indistinguishable from *F. grandiporus* Chapman showing distally pronounced thickening of the corallite walls, strongly developed squamulae as well as crowded tabulae. The dimensions of the form illustrated fall within the range of *F. grandiporus*.

(9) *Favosites festivus* Chernyshev 1951, p. 26, pl. 5, figs. 1, 2. Upper Silurian, Kuznetsk Basin. Chernyshev gives the corallite diameter of this species as between 0·4 to 0·5 mm.; tabulae 20 to 25 per 5 mm.; mural pores ovate 0·15 to 0·24 mm. in diameter and less than 0·5 mm. apart. Small squamulae above the mural pores are seen in Chernyshev's figure. This species is very closely comparable to *F. squamuliferus* forma *stelliformis*. In transverse sections the walls of the corallites have a much stronger inosculating appearance in Chernyshev's species, apparently due to pores being developed at the same height in adjacent corallites. Chernyshev compares this species with *Favosites fistulosis* (Chernyshev 1937, p. 76, pl. 4, fig. 1*a*, *b*, a reference unavailable to me in Australia). He notes that *F. festivus* differs from *F. fistulosis* in bigger corallites (0·6 to 0·8), fewer tabulae, and smaller, not so variable mural pores. If these are the only differences, then *F. fistulosis* is identical with *F. squamuliferus* forma *nitidus*.

(10) *Favosites endygashensis* Chernyshev 1951, p. 36, pl. 12, figs. 1, 2. Middle Devonian, Kuznetsk Basin. Chernyshev gives the dimensions of this species as corallites 1 to 1·6 mm. in diameter with thick walls 0·1 to 0·2 mm. apart; 7 to 12 tabulae in 5 mm., the mural pores 0·3 mm. in diameter about 1 mm. apart. Further, the corallum is said to be 'tree-like, with short branches'. Thus this thick-walled subramose form is comparable with *F. squamuliferus* forma θ. Closely comparable squamulae are also to be seen in Chernyshev's figure. *Pachypora crassiramosa* Chernyshev 1951 is a very closely related form with larger corallites between 1·5 and 2 mm. in diameter.

(11) *Alveolites* (*Caliapora*) *heritschi* Schouppé 1954*a*, pp. 422–4, pl. 27, fig. 22. Lower Devonian, Carnic Alps. This species, with its corallite diameter about 0·6 mm. appears to be closely comparable with *F. squamuliferus* forma *nitidus*. However, in the character of the mural pores it may differ from *F. squamuliferus* for Schouppé remarks that the pores, although large, are not frequent.

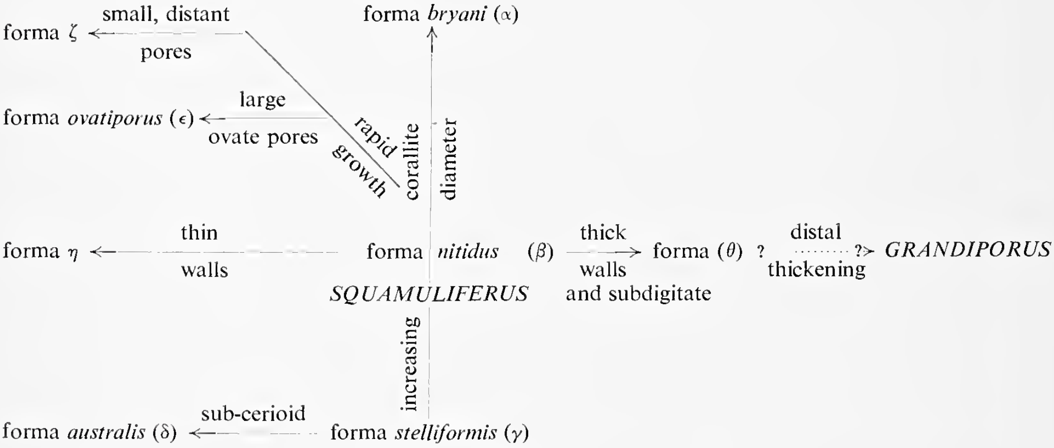
It is noteworthy that the time range of the forms overseas which fall within the morphological range of *F. squamuliferus* is virtually identical with the time range of the species in Australia—from Middle or Upper Silurian to Middle Devonian. The undoubted Silurian occurrences in Victoria are from the Eildon district where Hill recorded the presence of '*F. ovatiporus*' from a limestone lens which occurs beneath the horizon of *Monograptus uncinatus*, and from the Middle (?) Silurian of the Cowombat Creek from which Chapman (1920) illustrated a form as '*Favosites gothlandica*' (pl. 23, figs. 18, 19) which is identical with *Favosites squamuliferus* forma *bryani*. Again with *F. grandiporus*, which in Australia is only known from the Lilydale Limestone, of probable upper Lower Devonian age, Le Maitre (1937) illustrated an identical form from the basal Middle Devonian of France.

REMARKS ON THE VARIATION IN *F. SQUAMULIFERUS*

Discussion of the causes of variation in fossil species must at the best be conjectural. Thus detailed analyses within the framework applicable to modern forms (e.g. Mayr, Linsley, and Usinger 1953) have little value, although such frameworks are interesting inasmuch as they cover all the possible causes of intra-specific variation.

A major point which has arisen from the occurrences of species in the fauna analysed in detail is that it appears that squamulae were developed in this group as a response to major environmental changes; the species *F. moonbiensis* is confined to what was presumably a muddy environment, whereas *F. squamuliferus* and its formae are characteristic of a limestone environment.

Two of the formae appear to have arisen due to differential growth. These are *F. squamuliferus* forma *ovatiporus* (ε) and forma ζ, and presumably include coralla which grew more rapidly than those of the more typical formae. Again the development of wide intermural spaces in *F. squamuliferus* forma *australis* (δ) was probably caused by adverse environmental conditions.



MORPHOLOGICAL RELATIONSHIP OF THE SPECIES AND FORMAE OF AUSTRALIAN SQUAMULATE FAVOSITIDS

However, the extreme variability, for example in corallite diameter, must have stemmed from genetic variability of the species; a certain degree of this variation perhaps could be ascribed to micro-environmental differences, but it is impossible to trace these in a limestone which is basically an accumulation of reworked organic débris. In this respect it should be noted that other species of *Favosites* occurring side by side with *F. squamuliferus* show very little variation.

The possibility cannot be overlooked that there is present in the fauna more than one species of squamulate favositid, the ranges of variation of which overlap, but only an arbitrary subdivision into formae could be achieved. Detailed work on the younger horizons in which *F. squamuliferus* occurs may establish that in those horizons stable groups are present in the species within its presently defined range of variation. Until this is done it is best to divide the species merely into formae.

Acknowledgement. I am indebted to Dr. Dorothy Hill of the University of Queensland who read and criticized the manuscript.

Addendum. Since this manuscript was submitted for publication the writer has had the opportunity to study B. S. Sokolov's (1955) monograph on tabulate corals. Lengthy comment cannot be made here; suffice to say that to co-ordinate this present work with Sokolov's taxonomic level the genus used here should be regarded as a sub-order or family, and the species as families or genera. However, this is not possible in terms of Sokolov's classification as the three species mentioned here, and regarded by the present writer as very closely related, overlap three of Sokolov's 'sub-orders', namely the Favositina (*F. moonbiensis* Eth.), the Thamnoporina (*F. grandiporus* Eth.), and the Alveolitina (*F. squamuliferus* Eth.).

Sokolov, furthermore, holds that the stellate intermural spaces as seen in *Asteriophyllum ænigmaticum* Porfiriev and *Favosites stellaris* Chernyshev were caused by symbiotic worms. Although this can be argued for such forms of *Favosites* as those where definite tubules are present within the corallite walls (as in the 'genera' *Gephuropora*, *Parafavosites*, &c.), this interpretation does not appear to be applicable for the wall structures of the species group described here.

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NEW SPECIES OF BRACHIOPODS FROM THE UPPER DEVONIAN OF HAY RIVER, WESTERN CANADA

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ABSTRACT. *Nervostrophia borealis*, *N. maclareni*, and *Cyrtina lapidea* are described and figured as new species from the Hay River formation of the North West Territories, Canada. *Douvillinella? crickmayi* is described and figured as a new species from the lower Grumbler formation of the same area. All the fossils are of Frasnian age.

THE fossils described were collected by Dr. P. E. Kent of BP Exploration (Canada) Limited and by Dr. E. W. Best, R. L. Pemberton, and A. E. H. Pedder of Triad Oil Co. Ltd. in June 1958. The author is much indebted to these companies for permission to publish the work and to present the type specimens to the Geological Survey of Canada.

Biostratigraphy. Stratigraphical thicknesses in the Hay River area have mostly been obtained from scattered incomplete river sections and various published estimates differ considerably. Warren and Stelck (1950, p. 68) gave the thickness of the type Hay River formation (as later restricted by Crickmay) as about 270 feet; Crickmay's figure for the same interval is 630 feet (1957, p. 6). Farmilo is quoted by Law (1955, p. 1977) as having measured about 900 feet of Hay River shale on Hay River and deWit (unpublished) has obtained for Triad Oil Co. Ltd. a total thickness of 1,250 feet for the Hay River shales. Both of these latter measurements include Crickmay's Simpson formation, but, even so, indicate a thickness in excess of 630 feet for the type Hay River formation (restricted). Bore-hole evidence (Law 1955, fig. 5) also indicates a greater thickness than quoted by Crickmay.

The new species were obtained from three beds. The lowest is a grey argillaceous limestone grading to a pure coquina bed in part, and is exposed on Hay River opposite mile 14 of the Mackenzie Highway (Grimshaw Road). Part of its fauna is: *Eliasopora sp.*, *Hederella sp.*, *Orbiculoidea sp.*, *Productella sp.*, *Nervostrophia borealis* sp. nov., *Monelasmina besti* Pedder, *Schizophoria sp.*, *Atrypa sp.*, *Spinatrypa sp.*, *Eleutherokomma reidfordi* Crickmay, *Cyrtospirifer* [= *Regelia*] *glaucus* Crickmay, *Cyrtina lapidea* sp. nov., *Spirorbis sp.*, *Tentaculites mackenziensis* Kindle, ostracods, and a trilobite. The horizon is the lowest assigned to the Hay River formation as restricted by Crickmay.

The second bed is a limestone exposed just above Louise Falls on Hay River. Stratigraphically it is immediately below the topmost shale and siltstone of the Hay River formation and is currently regarded as being from 30 to 40 feet below the top of that formation. The rock is very fossiliferous, but only those specimens exposed are easily collected and these are generally water worn. Part of the fauna is: *Macgeea proteus* Smith, *Nervostrophia maclareni* sp. nov., *Productella sp.*, *Atrypa sp.*, *Cyrtospirifer sp.*, *Adolfia sp.*, pelecypods, *Tentaculites sp.*, *Devonocidaris sp.*, and *Decadocrinus sp.*

The highest bed is a maroon argillaceous limestone exposed on Hay River opposite mile 38 of the Mackenzie Highway. It is near the base of the Grumbler formation and

[Palaeontology, Vol. 3, Part 2, 1960, pp. 208–216, pls. 35–36.]

the following is part of the bed's fauna: *Clionoides sp.*, *Spongophyllum imperfectum* Smith, *Aulocaulis sp.*, *Thamnopora sp.*, *Vinelloidea sp.*, *Leptotrypella sp.*, *Hederella sp.*, *Hernodia sp.*, *Petrocrania sp.*, *Stropheodonta sp.*, *Douvillinella? crickmayi* sp. nov., *Schuchertella sp.*, *Schizophoria sp.*, *Gypidula sp.*, *Atrypa rubromitra* Crickmay, *A. spp.*, *Cyrtospirifer sp.*, *Tenticospirifer sp.*, *Adolfia spp.*, *Cyrtina sp.*, *Cranaea sp.*, pelecypods, cephalopods, *Cornulites sp.*, *Spirorbis angulosus* Fenton and Fenton, crinoid fragments.

SYSTEMATIC PALAEONTOLOGY

Superfamily STROPHOMENACEA Schuchert 1896

Family STROPHEODONTIDAE Caster 1939

Genus NERVOSTROPHIA Caster 1939 emended Williams 1953

Genoholotype (by author's original designation) *Stropheodonta nervosa* Hall = *Strophomena nervosa* Hall 1843, text-figs. 1, 1*a* on p. 266, Chemung group, Bath and Campbelltown, New York.

Nervostrophia borealis sp. nov.

Plate 35, figs. 1–10

1950 *Douvillinaria variabilis* (Calvin); Warren and Stelck, p. 69.
1956 *Douvillinaria variabilis* (Calvin); Warren and Stelck, pl. 16, fig. 26.
1959 *Nervostrophia sp.* Pedder, p. 472.
Non *Douvillinaria variabilis* Calvin sp.

Name derivation. Latin, *borealis* = northern.

Types. Holotype, specimen originally Triad Oil Co. Ltd. collection no. X46e, now Geological Survey of Canada type no. 14,598. Six paratypes, specimens originally Triad Oil Co. Ltd. collection nos. X46f–k, now Geological Survey of Canada type nos. 14,599 to 14,604.

Type stratum. Hay River formation, coquina bed 630 feet below top (Crickmay 1957, p. 6; not 1953, p. 11); Upper Devonian, Frasnian.

Type locality. Canada, North West Territories, Hay River opposite mile 14 of the Mackenzie Highway measured south-westward, about 80 feet above water-level and 10 feet below bank top. Latitude 60° 41′ N., longitude 115° 54′ W.

Description. Shell small and fragile. Profile plano-convex. Outline semicircular anteriorly, posteriorly just flexed at pedicle beak, cardinal extremities with small mucrones, postero-lateral margins weakly concave. Anterior commissure rectimarginate. Shell substance very thin, calcitic and pseudopunctate.

Pedicle valve weakly convex centrally and postero-centrally, plane near lateral and anterior margins. Umbonal region, small, longer than broad and only slightly elevated. Beak minute and blunt. Beak ridges sharp along entire length. Interarea plane, apsaclinal, very broadly equilaterally triangular with an apical angle of about 168°. Delthyrium open anteriorly, closed posteriorly by a strongly medianly arched pseudodeltidium. Hinge-line straight, denticulate along most of its length in young valves and for about two-thirds of its length in adults. Process pits deep as thin shell permits, slightly posteriorly directed. Ventral process low and narrow. Muscle scars petal-shaped, about one-half as long as the valve, lightly impressed, bounded postero-laterally by heavy ridges, open antero-laterally and anteriorly. Adductor and diductor scars not differentiated in the type specimens. Median septum very fine, about one-half the length of the muscle scars. Interior surface, with the exception of the muscle scars and cardinalia, entirely and finely papillose; postero-lateral muscle bounding ridges less finely papillose.

External surface ornament variable, of more or less continuous, generally straight, rarely sinuous costae, separated by from one to four intercalated costellae; costellae rare in gerontic specimens; costae and costellae number about seven per millimetre near margins of valve. Concentric micro-fila superimposed on entire surface, numbering about fifteen per millimetre. Interarea with growth striae parallel to hinge-line and with clear traces of denticles, especially anteriorly.

Brachial valve plane. Umbo and beak not developed. Interarea linear. Notothyrium displaced by cardinalia. Chilidium degenerate. Hinge-line straight, socketed opposite denticles of pedicle valve. Cardinal process lobes, stout, disjunct, with attachment faces posteriorly directed. Socket plates small, attached to and parallel to cardinal process lobes. Muscle scars subtriangular, lightly impressed, bounded postero-laterally by large hummocks divergent 90° to each other, open anteriorly; each muscle divided anteriorly by low, broad, elongate elevations parallel to postero-lateral muscle ridges. Median septum broad posteriorly, rapidly tapered to a fine ridge anteriorly, three-fourths the length of the valve. Interior surface, with the exception of the cardinalia and deeper parts of muscle scars, finely and irregularly papillose; postero-lateral muscle ridges and elevations in anterior part of muscles less finely papillose; exterior ornament similar to that of pedicle valve, but costae less developed and approaching the size of the costellae. Denticle sockets visible from exterior through a thin shell layer.

Dimensions (partly reconstructed and estimated from the contour of the concentric micro fila). Holotype, paratypes 2, 4 (pedicle valves), and 5 (brachial valve), length 11·4, 5·1, 5·4, and 5·0 mm., width 14·0, 8·0, 8·3, and 6·6 mm., depth 1·3, 1·1?, and 0·1 (not including depth of process lobes) mm.

Remarks. No similar fossil has been named from the Upper Devonian. The species superficially resembles *Douvillinaria variabilis* (Calvin) from the Independence formation of Iowa, but is not congeneric with it.

Nervostrophia maclareni sp. nov.

Plate 36, figs. 1–5

Name derivation. Patronym for Dr. D. J. McLaren, Geological Survey of Canada, Ottawa.

Types. Holotype, specimen originally Triad Oil Co. Ltd. collection no. X38s, now Geological Survey of Canada type no. 14,605. Three paratypes, specimens originally Triad Oil Co. Ltd. collection nos. X38t–v, now Geological Survey of Canada type nos. 14,606 to 14,608.

Type stratum. Hay River formation, upper unnamed siltstone, shale, and limestone unit, 30 to 40 feet below the top of the formation (Crickmay, 1957, p. 6; not 1953, p. 11); Upper Devonian, Frasnian.

Type locality. Canada, North West Territories, a few feet above Louise Falls on Hay River. Latitude 60° 30′ N., longitude 116° 14′ W.

Description. Shell large and thin for genus. Profile plano-convex. Outline variably subsemicircular. Hinge-line straight, cardinal extremities strongly mucronate, postero-lateral margins moderately concave. Anterior margin rectimarginate. Shell substance very thin, calcitic and pseudopunctate.

Pedicle valve very weakly convex, mostly plane, but anterior and lateral margins slightly convex. Umbonal region very slightly inflated. Beak minute and blunt. Beak ridges sharp along entire length. Interarea very broadly equilaterally triangular, plane surfaced. Nature of delthyrium and its cover not revealed in the primary material.

Hinge line denticulate for about 75 per cent. of its length. Process pits shallow. Nature of cardinalia and musculature not revealed in the primary material. Internal ornament centrally finely and closely papillose with traces of the external ornament visible near the margins. External ornament of continuous, straight, or slightly sinuous costae developed from costellae, latter number from two to nine, generally five, between each costae; costae and costellae number about six per millimetre near the margins of the valve. Faint concentric micro-fila superimposed on most, if not all, the surface.

Brachial valve plane. Umbo not developed. Beak represented by a minute projection of the base of the cardinal process. Notothyrium displaced by cardinalia. Chilidium probably degenerate. Hinge-line socketed opposite the denticles of the pedicle valve. Cardinal process lobes not well preserved in type material, disjunct, with attachment faces posteriorly directed. Socket plates larger than average relative size for the genus, attached to and divergent from, the cardinal process lobes. Muscle scars small, petal-shaped, superficial, bounded postero-laterally by large crescent-shaped hummocks, open in other directions. Median septum degenerate. Postero-lateral muscle bounding hummocks strongly papillose, other parts of the interior surface not markedly papillose, external ornament visible from the interior near the valve margins. External ornament similar to that of the pedicle valve. Denticle sockets visible from the exterior through a very thin shell layer.

Dimensions. Holotype and paratype 3, length 20·0 and 13·5 mm., width (less mucrones) 26·8 and 25·0 mm. (with mucrones)? and 36·0 mm. depth (pedicle valve only) 1·5 and 1·2 mm.

Remarks. In several respects this species is not typical of *Nervostrophia*. The shell is exceptionally thin and delicate, a median septum is scarcely developed in the brachial valve; the relatively large, divergent socket plates and unimpressed muscle scars of the brachial valve are also exceptional for the genus.

From *Nervostrophia calvini* Stainbrook, occurring in the Independence formation of Iowa, this species is distinguished by its lack of a strong geniculation near the anterior and antero-lateral commissure and also, perhaps, by internal details, which have not been illustrated for *N. calvini*.

From *N. vestita* Crickmay, occurring lower in the Hay River formation on Hay River, this species is distinguished by its shorter median septum and postero-lateral muscle bounding ridges in the pedicle valve and by its less nervose surface ornament.

Genus DOUVILLINELLA Spriestersbach 1926 emended Williams 1953

Genoholotype (by monotypy) *Douvillina filifer* Schmidt 1913, pp. 313, 314, pl. 23, figs. 1*a*–7. *Cultrijugatus* zone (Couvinian, or lower Middle Devonian), südlich der Attendorn-Elsper Doppelmulde, Germany.

Remarks. Spriestersbach proposed *Douvillinella* as a subgenus of *Stropheodonta*, differing from that genus by possession of brace plates (Stützplatten) and in having concave ventral and convex dorsal valves instead of convex ventral and concave dorsal valves. The species described below is associated with *Douvillinella* only because it is a resupinate *Douvillina*-like stropheodontid. It is possibly not congeneric with *Douvillina filifer* Schmidt.

Douvillinella? crickmayi sp. nov.

Plate 36, figs. 7–11; text-fig. 1*n*

1950 *Strophonella sp.* Warren and Stelck, p. 67.

Name derivation. Patronym for Dr. C. H. Crickmay, Imperial Oil Ltd., Calgary, Alberta.

Types. Holotype, specimen originally Triad Oil Co. Ltd. collection no. X28v, now Geological Survey of Canada type no. 14,609. Four paratypes, specimens originally Triad Oil Co. Ltd. collection nos. X28w–z, now Geological Survey of Canada type nos. 14, 610 to 14,613.

Type stratum. Grumbler formation, maroon argillaceous limestone about 80 feet above the base of the formation; uppermost Frasnian.

Type locality. Canada, North West Territories, Hay River opposite mile 38 of the Mackenzie Highway (Grimshaw Road), measured south-westward. Latitude 60° 29′ N., longitude 116° 19′ W.

Description. Shell small and robust. Profile very gently resupinate, concavo-convex immediately anterior of hinge, convexi-plane or just convexi-concave centrally, biconvex near anterior margin (text-fig. 1*n*). Outline semicircular anteriorly, postero-lateral margins nearly straight, cardinal extremities with small mucrones. Anterior commissure rectimarginate. Shell substance relatively thick, calcitic and pseudopunctate.

Pedicle valve almost plane, very gently convex umbonally, plane or just concave centrally, very gently convex near anterior and lateral margins. Umbonal region feebly developed. Beak minute, projecting only very slightly. Beak ridges sharp along entire length. Inter-area plane, apsaclinal, subrectangular. Delthyrium equilaterally triangular with an

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EXPLANATION OF PLATE 35

All illustrations unretouched, photographed by K. S. Wilson. Specimen numbers refer to Geological Survey of Canada type numbers. All specimens are from the Hay River coquina bed, Hay River opposite mile 14 of the Mackenzie Highway, North West Territories, Canada.

Figs. 1–10. *Nervostrophia borealis* sp. nov. 1, 2, Holotype, 14,598, external and internal pedicle views, ×4 and ×4. 3, 4, Paratype 2, 14,600, internal and external views, ×5 and ×5·6. 5, 6, Paratype 5, 14,603, external and internal brachial views, ×4·3 & ×4. 7, Paratype 3, 14,601, lateral brachial view, ×4. 8, Paratype 4, 14,602, external pedicle view, ×4. 9, Paratype 1, 14,599, internal brachial view, ×4. 10, Paratype 6, 14,604, external brachial view, ×4.

Figs. 11–17. *Cyrtina lapidea* sp. nov. 11–13, Holotype, 14,614, anterior view, ×4, anterior view, ×2, brachial view, ×1. 14, 15, Paratype 1, 14,615, lateral view, ×3·5, posterior view, ×3·6. 16, 17, Paratype 2, 14,616, internal view, ×4, external view, ×2.

EXPLANATION OF PLATE 36

All illustrations unretouched, photographed by K. S. Wilson. Specimen numbers refer to Geological Survey of Canada type numbers.

Figs. 1–5. *Nervostrophia maclareni* sp. nov., 30–40 feet below top of the Hay River formation, a few feet above Louise Falls on Hay River, North West Territories, Canada. 1, 2, Holotype, 14,605, external pedicle views, ×1 and ×2. 3, Paratype 1, 14,606, internal brachial view, ×2. 4, Paratype 2, 14,607, external brachial view (left side of crack) and external pedicle cast (right side of crack), ×2. 5, Paratype 3, 14,608, external pedicle view (partly obscured by matrix), ×1·8.

Fig. 6. *Cyrtina lapidea* sp. nov., Hay River formation coquina bed, Hay River opposite mile 14 of the Mackenzie Highway, North West Territories, Canada, paratype 3, 14,617, external brachial view, ×2·4.

Figs. 7–11. *Douvillinella? crickmayi* sp. nov., about 80 feet above the base of the Grumbler formation, Hay River opposite mile 38 of the Mackenzie Highway, North West Territories, Canada. 7, 8, Holotype, 14,609, external and internal pedicle views, ×2 and ×2. 9, Paratype 4, 14,613, external brachial view, ×2. 10, Paratype 3, 14,612, external pedicle view, ×5. 11, Paratype 1 (right), 14,610, internal brachial view and paratype 2 (left), 14,611, internal pedicle view, ×2.


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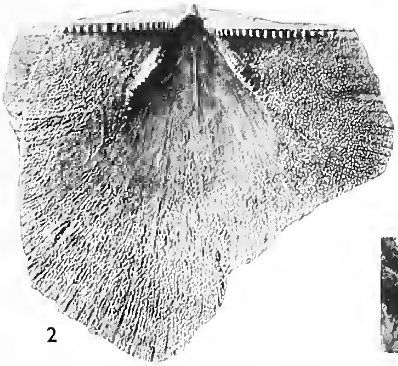
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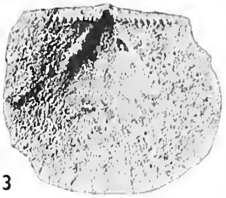
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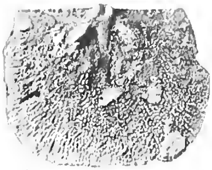
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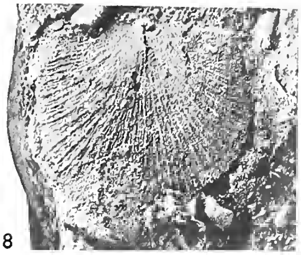
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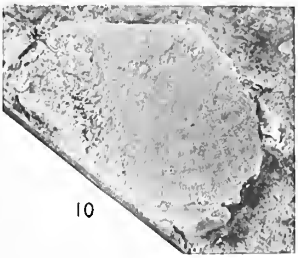
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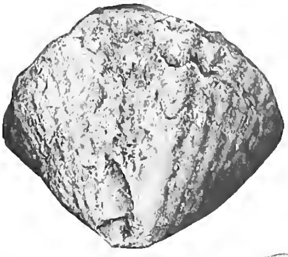
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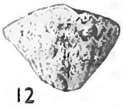
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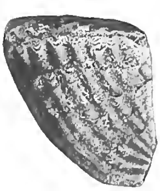
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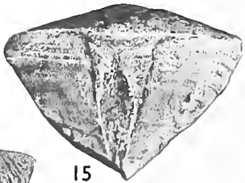
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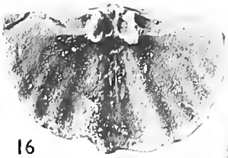
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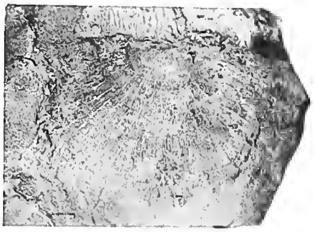
PEDDER, Devonian Brachiopoda from Canada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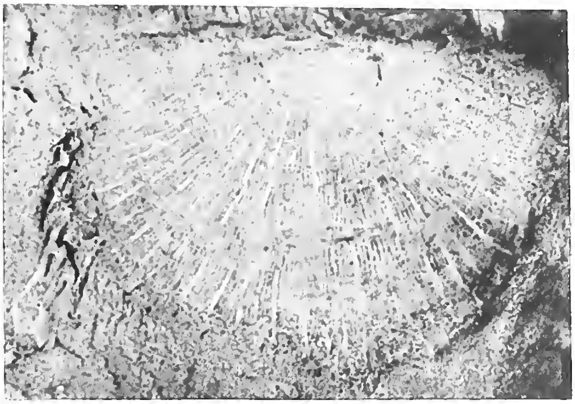
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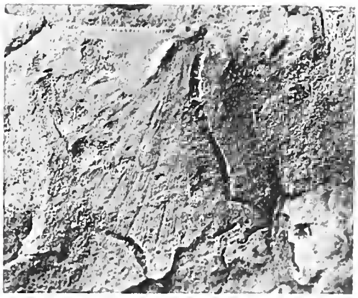
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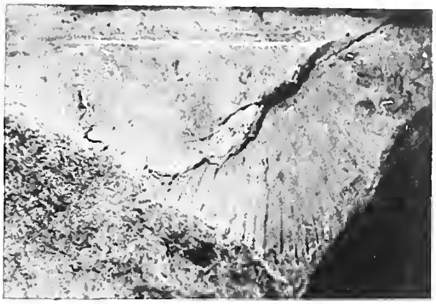
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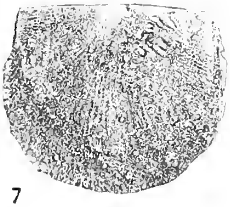
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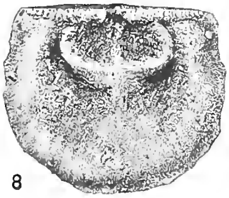
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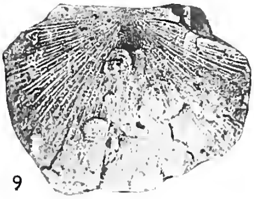
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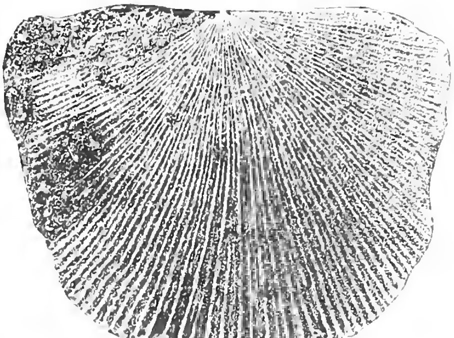
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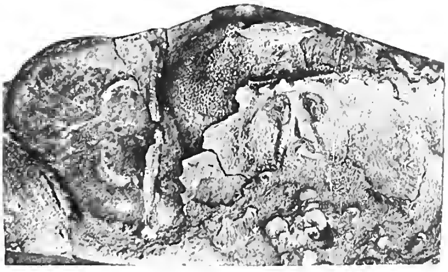
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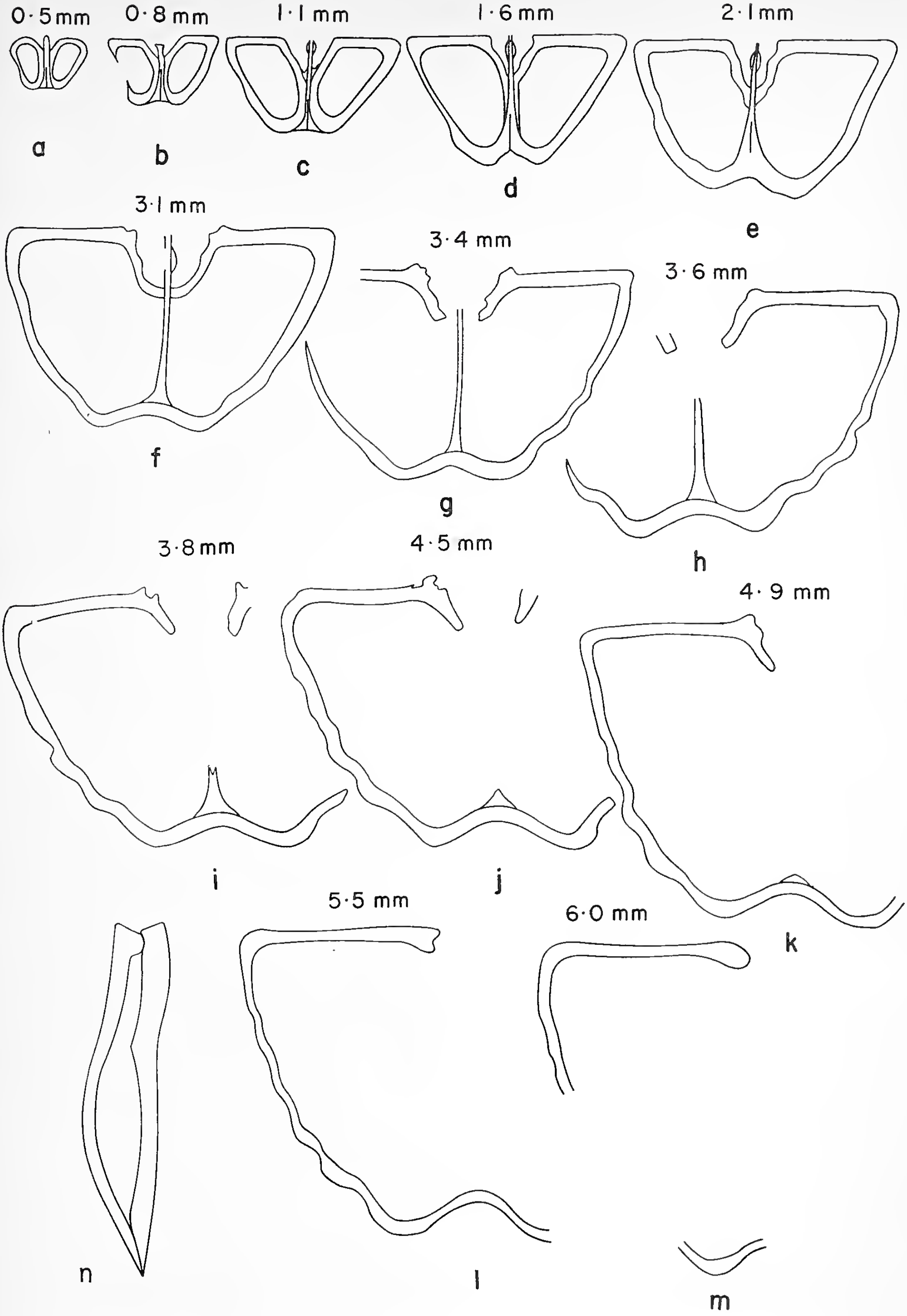
PEDDER, Devonian Brachiopoda from Canada



TEXT-FIG. 1. *a–m*, *Cyrtina lapidea* sp. nov., Hay River formation coquina bed, Hay River opposite mile 14 of the Mackenzie Highway, North West Territories, Canada, paratype 4 (now destroyed), series of sections of pedicle valve, ×10, measurements above each figure indicate distance from beak. *n*, *Douvillinella? crickmayi* sp. nov., diagrammatic but based on holotype and paratypes, longitudinal section, ×5.

apical angle of about 12°, entirely closed by a completely and strongly arched pseudodeltidium. Hinge-line straight, denticulate along entire length. Process pits deep, slightly posteriorly directed. Ventral process robust, anteriorly prolonged to a fine low median ridge, extending to the anterior edge of the muscle scars. Muscle scars prominent, elevated to the form of a saucer, posterior edge at a variable angle of about 20° with the hinge-line, anterior edge parallel with hinge-line, lateral margins rounded, more sharply so laterally than anteriorly. Interior surface, apart from the muscle scars and cardinalia, finely and evenly papillose; cardinalia smooth, muscle scars with faint radial striations. External ornament of fine, variable, primary and intercalated costae of different sizes, numbering about six per millimetre at the poster-lateral margins and about four per millimetre at the anterior margin of adult valves. Growth lines strong, but developed only near the margins of some valves. Interarea smooth with faint traces of denticles visible anteriorly.

Brachial valve generally very slightly concave immediately anterior of the central part of the hinge-line, gently convex elsewhere (text-fig. 1*n*). Outline similar to that of the pedicle valve, but less or not mucronate. Umbo and beak not developed. Interarea apsaclinal and almost linear. Notothyrium displaced by cardinalia. Chilidium vestigial, gently convex. Hinge-line straight, socketed opposite the denticles of the pedicle valve. Cardinal process lobes of average size, disjunct, with attachment faces posteriorly directed. Muscle scars asymmetrically petal-shaped with long narrow extensions parallel to and laterally adjacent posteriorly, to the brace plates, deeply impressed. Median septum broad, relatively low, anteriorly bifurcated, bifurcated parts confluent with the elongated brace plates. Interior surface of cardinalia smooth, muscle scars without papillae, but irregularly pitted, rest of central part of surface finely and evenly papillose, valve borders with clear traces of surface costae. Exterior surface ornament same as that of pedicle valve with denticle sockets visible through a very thin shell layer.

Dimensions. Holotype (dissociated pedicle valve) and paratype 4 (dissociated brachial valve), length 12·1 and 11·8 mm., width 14·1 and 15·5 mm., depth 1·9 and 1·8 mm.

Remarks. Strophonella does not occur in the Grumbler formation. Warren and Stelck (1950, p. 67) were probably referring to this species, since it is common in the lower Grumbler maroon beds, while other resupinate stropheodontids are either rare or absent. No similar species has been named.

Superfamily PUNCTOSPIRACEA Cooper 1944
Family CYRTINIDAE Stehli 1954
Genus CYRTINA Davidson 1858

Genolectotype (by Dall 1877, p. 24). *Cyrtia helteroclita* Defrance 1824, p. 306, pl. 80, figs. 3, 3*a*.

Cyrtina lapidea sp. nov.

Plate 35, figs. 11–17; Plate 36, fig. 6; text-fig. 1*a–m*

1950 *Cyrtina sp.* Warren and Stelck, p. 69.
1959 *Cyrtina sp.* Pedder, p. 472.

Name derivation. Latin, *lapideus* = made of stone.

Types. Holotype, specimen originally Triad Oil Co. Ltd. collection no. X461, now Geological Survey of Canada type no. 14,614. Three preserved paratypes, specimens originally Triad Oil Co. Ltd. collection nos. X46m–0, now Geological Survey of Canada type nos. 14,125 to 14,617. Fourth paratype, specimen originally Triad Oil Co. Ltd. collection no. X46p, subsequently destroyed for serial sectioning.

Type stratum. Hay River formation coquina bed 630 feet below top (Crickmay 1957, p. 6; not 1953 p. 11); Upper Devonian, Frasnian.

Type locality. Canada, North West Territories, Hay River opposite mile 14 of the Mackenzie Highway (Grimshaw Road) measured south-westward, about 80 feet above water-level and 10 feet below bank top. Latitude 60° 41′ N., longitude 115° 54′ W.

Description. Shell small, subpyramidal, generally slightly asymmetrical rarely strongly asymmetrical or symmetrical. Profile subtriangular. Outline nearly semicircular. Hinge-line 95–100 per cent. of total shell width, just flexed centrally. Cardinal extremities abruptly rounded or minutely mucronate. Anterior commissure uniplicate. Shell substance moderately thick, calcitic, finely and closely endopunctate.

Pedicle valve subpyramidal, weakly convex along posterior midline, almost straight, but steeply inclined anteriorly; lateral slopes only very gently convex but steeply inclined. Sulcus with origin at beak, shallow, gently concave transversely, produced to a short semicircular tongue. Umbonal region not differentiated. Beak blunt, just projecting, straight. Beak ridges variable, either sharp or rounded. Interarea equilaterally triangular, orthoclinal, or proclinal and plane surfaced towards hinge, apsaclinal and concave towards beak, apical angle about 90°. Delthyrium with an apical angle of about 26°, closed near hinge by an arched pseudodeltidium. Foramen triangular towards beak, semi-elliptical towards pseudodeltidium, long axis four-fifths of the length of the delthyrium. Hinge teeth tear-shaped in section, of moderate size. Dental plates ankylosed to median septum in posterior 1·5 mm., of valve, withdrawn forming a spondylium from 1·5 to 3·2 mm. from beak tip, gradually reduced anteriorly, disappearing about 5·7 mm. from beak tip. Median septum high and produced to a tichorhinum in posterior 3·2 mm., gradually reduced anteriorly. Muscle scars not seen in primary material.

Brachial valve weakly convex. Fold transversely convex posteriorly, flat-topped anteriorly, low, elevated only in anterior three-fifths of adult valve. Umbonal region and beak not differentiated. Interarea linear. Hinge-plate well developed about the sockets and socket plates, divided by a median ridge. Sockets large, bounded internally by, and partly excavated into, strong socket plates, divergent to each other at 90°. Cardinal process bilobed, smooth. Spiralia not preserved in primary material, attachment confluent with the anterior parts of both the socket and hinge plates. Median septum extremely low and fine, absent in anterior two-fifths of valve.

Ornamented by from 5 to 8, typically 7, costae on the pedicle valve and by from 4 to 7, typically 6, on the brachial valve; costae rounded and progressively diminished laterally. Sulcus smooth. Fold smooth or with very weak anterior median furrow. Interarea with vertical striae. Growth lines irregular, mostly very fine and crowded, especially on the interarea, but gerontic specimens may bear coarser growth lines near the commissure. Abundant fine endopunctae clearly visible on shell surface, except on the interarea.

Dimensions. Holotypes and paratypes 1 to 3, length 4·7, 5·3, 5·2, and 6·4 mm., width 7·7, 7·0, 6·6, and 8·0 mm., depth 5·4, 5·1 (both valves), 1·1 and 1·8 (brachial valves only) mm.

Distinctions. From *C. inulta* Stainbrook, occurring in the Independence formation of Iowa, this species is distinguished by its smaller ($\times\frac{2}{3}$) average size, finer costae, less developed sulcus and tongue and by the absence of a micro-ornament of fine radial granulose ridges described on *C. inulta*. The internal structure of *C. inulta* is undescribed in literature; there may be, therefore, further distinctions between the two species.

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THE DOWNTONIAN OSTRACODERM *CORVASPIS KINGI* WOODWARD, WITH NOTES ON THE DEVELOPMENT OF DERMAL PLATES IN THE HETEROSTRACI

by L. B. TARLO

ABSTRACT. Further specimens of the Downtonian Ostracoderm *Corvaspis kingi* Woodward are described, and the genus is shown to belong to the family Psammosteidae. The variation of ornamentation seen in *Corvaspis* is used to demonstrate the relationship between the three main types of growth of dermal plates known in the Heterostraci.

INTRODUCTION

THE affinities of the ostracoderm *Corvaspis kingi* have been the subject of much debate, but the discovery of new material and a reinterpretation of that already known now make it possible to place the genus in the family Psammosteidae, so that the family Corvaspidae becomes redundant.

A fragment of this ostracoderm, which had been collected by Professor J. Kiaer from the Downtonian of Spitsbergen, was figured although not described, by Jaeckel (1927, p. 925) as a new Palaeaspid (Cyathaspid). Woodward (1934, pp. 566–7) erected *Corvaspis kingi* for similar material from the Downtonian of Corvedale (Shropshire) collected by Mr. W. W. King, and placed the genus in the Cyathaspidae. Stensiö (1944, p. 4) recorded *Corvaspis* from the Czortkow Series of Podolia.

Denison (1953, pp. 304–18) redescribed the unusual ostracoderm *Cardipeltis* and noted that its histological structure and ornamentation closely resembled those of *Corvaspis*, but as little was then known of *Corvaspis* he was unable to suggest the possible relationship between these two genera. A few months after Denison's paper appeared, Dineley (1953) described further remains of *Corvaspis* including median plates, ridge plates, and orbital plates, as well as small irregular plates and scales.

Corvaspis, like most Heterostracans, has a complex carapace of bony plates covering its head and the anterior part of its trunk, the posterior part being covered by small scales. The carapace is made up of a number of different plates, the presence or absence of which is of diagnostic value. Dineley showed that *Corvaspis* must be excluded from the Cyathaspidae since it possesses orbital plates; he also regarded it as having ridge plates, and although he considered that the genus might be 'akin to the Drepanaspidae' (Psammosteidae), an animal having ridge plates clearly did not belong to any known family (1953, p. 166). In consequence, he felt justified in proposing a new family—the Corvaspidae—to receive *Corvaspis kingi* and his new species *C. graticulata*. As is shown below, however, Dineley's so-called 'ridge plates' can better be interpreted as branchial plates, thus equating *Corvaspis* with most other Heterostracans, and removing the necessity for a separate family.

Bystrow (1955, pp. 472–523) figured the microstructure of *Corvaspis kingi* which appears Cyathaspid in nature, but he showed that it was similar in certain respects to

[Palaeontology, Vol. 3, Part 2, 1960, pp. 217–226, pls. 37–38.]

Kallostrakon podura which in turn could be compared with the Psammosteid *Psammolepis paradoxa*. Recently Stensiö (1958, pp. 321–6) reviewed previous work on *Corvaspis*, retaining it in the order Corvaspida (= Corvaspidae of Dineley). At the same time he suggested that the Ludlovian *Strosipherus* and the Dittonian *Penygaspis* might be included in this order. Further specimens of *Corvaspis kingi* collected during 1953–5 by Mr. J. R. L. Allen, Dr. L. G. Love, Dr. T. Orvig, Mr. H. A. Toombs, and myself are described below, and these help to establish the Psammosteid affinities of the genus. The new material comes from the Earnstrey Hall locality in Shropshire, details of which can be found in Wills (1935, p. 427). Most of the specimens come from the '4-foot band of very tough calcareous pellet rock and conglomerate', a large block of which has fallen into the bed of the stream.

DESCRIPTION OF PLATES

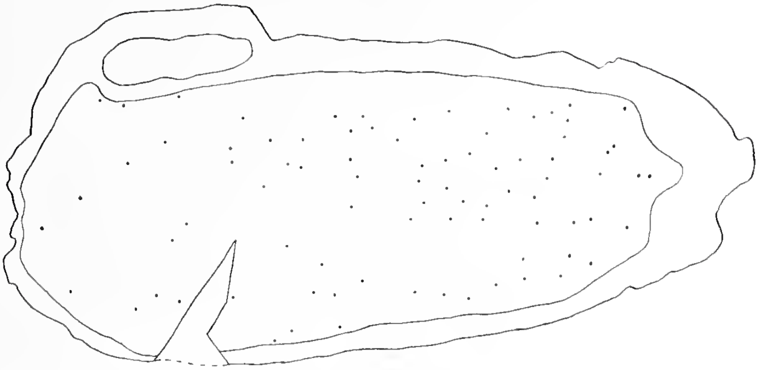
Median plates. Dineley (1953, p. 171) described an almost complete median plate, which Stensiö (1958, p. 324) suggests was on the ventral surface of the body. This plate is somewhat oval in outline, its anterior border being gently curved while the lateral borders are more or less straight. Unfortunately the posterior border is missing. The new material contains a complete median plate which has a similar anterior border, and a posterior border which is almost straight transversely. Its lateral edges are also fairly straight, but they tend to diverge posteriorly, so that, as can be seen from text-fig. 1, the plate is narrower anteriorly. A small plate is incorporated within the median plate on one side of the posterior part, making it asymmetrical.

There are other ventral median plates which seem to be variations on the simple oval one already described. In these the central part of the anterior border is produced, as is shown in text-fig. 2*b*.

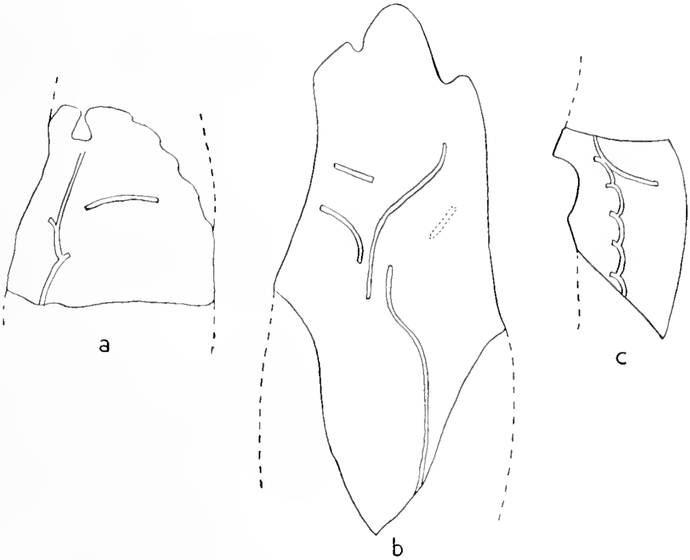
The type specimen described by Woodward is the anterior part of a median plate, the anterior border of which is deeply excavated at the midline. Stensiö interprets this plate as forming part of the dorsal surface of the animal, and the new collection also includes a similar bilobed median plate (see Pl. 38, fig. 3). In the Psammosteids, the Pteraspids, and also the Traquairaspids, the dorsal median plate has an excavated anterior border while the border of the ventral plate is generally convex, thus *Corvaspis* may well be related to one of these groups.

Both Woodward and Dineley noted that the sensory pores were in two irregular lines running longitudinally on either side of the median plates, and in text-fig. 1 the complete median plate is shown with the pores plotted. Though this gives some indication of the pattern of the sensory canal system itself, it can only be fully ascertained by grinding the specimen through to just below the dentine layer where the canal system proper occurs. This has recently been attempted, and from the specimens figured below (text-fig. 2) it appears that the canal system found is roughly comparable to those known in other Heterostracans, although the pattern is not a clear-cut one and cannot be used with any certainty. When more specimens are available to allow the necessary sacrifice, it may be possible to obtain a complete picture of the canal system in *Corvaspis*.

The ornamentation of the dermal plates is quite distinctive and can readily be used to identify the genus. Generally it consists of flat-topped dentine ridges with a faintly crenulate base; these ridges are usually disposed longitudinally and, as noted by Woodward (1934), in the median plates 'an irregular network of fine grooves divides this ridge ornament into small areas which have the false appearance of separate plates'. Woodward also described an ornamentation in which these small polygonal areas were separated by rows of small rounded tubercles instead of faint grooves and, as noted by Dineley, both types of ornament can appear in one plate. Stensiö (1958, p. 324) suggested



TEXT-FIG. 1. *Corvaspis kingi* Woodward. Ventral median plate with sensory pores plotted, wide border of rounded tubercles indicated; isolated area in upper left portion of figure represents incorporated tesserae. ×1, B.M. P.40575.

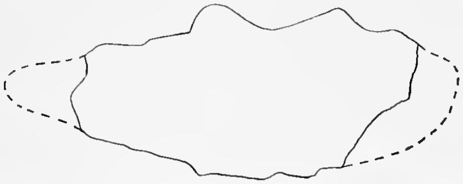


TEXT-FIG. 2. *Corvaspis kingi.* Fragments of median plates showing sensory canals; all horizontal sections taken at junction of cancellor layer and outer dentine layer. *a*, ×1, A–T 225; *b*, Anterior part of ventral median plate. ×1, A–T 238; *c*, ×1, A–T 309.

that the polygonal areas separated by tubercles belonged to the posterior part of the plate, the others being anterior. Some of the median plates recently found show that in *Corvaspis* there is a much greater variety of ornament than was formerly realized. It is in fact possible to trace a gradation from an ornamentation of polygonal areas separated by tubercles to one in which the longitudinal dentine ridges continue almost the whole length of the plate without a break. The significance of this variation is discussed below. In addition all median plates, whatever their form of ornamentation, have a wide border of rounded tubercles.

A specimen is also figured (Pl. 38, fig. 6) which shows the healing of damage in the carapace, the area of new growth consisting of dentine ridges arranged in random fashion.

Branchial plates. Some arched, elongate, asymmetrical plates were termed 'ridge plates' by Dineley (1953, p. 174), since he believed that they might correspond to the 'ridge scales' (fulcral scales) of other Heterostracans. He suggested that their degree of arching indicated that they were placed in the median line of the trunk or tail region rather than in a lateral position. The plate he figured is incomplete along one border, but luckily one of the new specimens is complete in this region and shows that the plate is even more asymmetrical than Dineley suspected; one border, probably the dorsal, having a very distinctive broad notch (see text-fig. 3). The arching and general shape of the plate is similar to that seen in the branchial plates of the Cyathaspids, Pteraspids, and Traquairaspids, and this, coupled with the strong asymmetry, suggests that the plate is in fact a branchial. Moreover, the specimen figured by Dineley shows a sensory canal running obliquely across one corner, which is consistent with its being a branchial plate rather than a ridge plate.



TEXT-FIG. 3. *Corvaspis kingi.* Left branchial plate, showing asymmetry and flange with broad notch on upper part of figure. ×1½, A–T 233.

Along the crest of the branchial plate is a line of small tubercles, around which the adjacent dentine ridges curve, giving a very characteristic pattern. The remainder of the plate is covered with short ridges aligned longitudinally, except where they curve round sensory pores.

Orbital plates. Dineley (1953, p. 173) described and figured orbital plates for the first time, although all his specimens were small with irregular margins. Subsequently a specimen was discovered which shows that the orbitals are large rectangular plates with a circum-orbital sensory canal (Pl. 37, fig. 2). The specimens figured previously would thus seem to have been merely the central portions of the orbital plates, and this new find is of some significance since such a large orbital plate can only be envisaged as belonging to the carapace of a dorso-ventrally compressed animal like a Psammosteid. Previously the orbitals were taken to be small plates, which might well have belonged to any Heterostracan family outside the Cyathaspids.

In the central portion of the orbital plate, the dentine ridges are arranged in concentric rows around the orbital cavity, the rest of the plate being composed of a wide border of small tubercles. In one sector, however, the dentine ridges form a series of concentric rings around sensory pores.

Lateral plates. Dineley's small irregular plates are of two kinds: first those similar to the plate incorporated in the median plate described above, which are here termed tesserae, and second those here regarded as lateral plates. The latter, unlike the tesserae, have their dentine ridges arranged in a haphazard manner; some have a rather intricate outline, whereas others with a more simple outline are traversed by sensory canals (Pl. 37, figs. 5, 6). These lateral plates probably occur in the pre-orbital region of the ventral surface, situated behind and to the side of the mouth.

Tesserae. It was suggested by Dineley that the median plate was surrounded by a mosaic of small plates, and this is confirmed by the fact that they may become incorporated into the median plate around its margin (Pl. 37, fig. 1). Such fields of tesserae between the major plates are characteristic of the Psammosteidae. Unlike the lateral plates the tesserae are fairly simple in outline and in some the ornamentation consists of small tubercles arranged concentrically; others have a pattern of longitudinal ridges with only a narrow border of tubercles (Pl. 37, figs. 3, 4).

Post-orbital plate. A single asymmetrical and somewhat arcuate plate is included in the new collection (Pl. 37, fig. 7). It seems unlikely that this plate could have occupied a median position in the body and it is tentatively suggested that it represents a post-orbital plate, such as is present in the Psammosteids.

Microstructure. The histological structure of the plates and scales of *Corvaspis kingi* has been described and figured by Bystrow (1955, pp. 492–4). However, under high magnification it can be seen that the normal dentine tubules rebranch into innumerable and much finer tubules which continue through the seemingly structureless outermost layer to the exterior, as is shown in Pl. 37, fig. 8*b*.

AFFINITIES OF *CORVASPIS*

As has been demonstrated the possession of orbital plates excludes *Corvaspis* from the Cyathaspidae despite the fact that its plates have a similar histological structure, the cancellar layer possessing large spaces which reach from the basal lamellar layer to the outer dentine one. Moreover, it possesses fields of tesserae which are known only in the Ordovician Astraspids and the Psammosteids, but it is excluded from the former by its histological structure. This suggests Psammosteid affinities for *Corvaspis* but in the Psammosteids the cancellar layer has a spongy appearance. However, a transition from the typical Psammosteid condition to that in *Corvaspis* can be seen in *Kallostrakon podura* Lankester (a form related to *Corvaspis*) where both spongy tissue and large spaces are present.

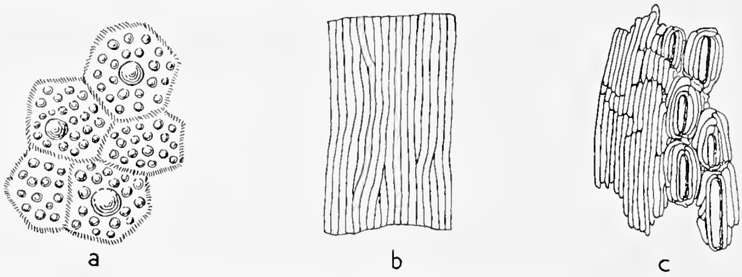
The large flat orbital plates fit best into the structure of a dorso-ventrally compressed animal such as the Psammosteid *Drepanaspis* (Obruchev 1943, pp. 268–71), and the plate interpreted as a post-orbital, if correctly diagnosed, would mean that *Corvaspis* must belong to this family since only in the Psammosteids is such a plate known.

The evidence thus points to the Psammosteid affinities of *Corvaspis* and for this reason it is here included within the family Psammosteidae, making it no longer necessary to retain the family Corvaspidae.

As noted above, the Dittonian *Cardipeltis* is similar to *Corvaspis* in both its histology and ornamentation, and in the possession of tesserae, branchials, and median plates. However, in *Cardipeltis* the median plate extends laterally as far as the branchial openings, whilst *Corvaspis* has a field of tesserae on either side of the median plate. If, in *Corvaspis*, the fields of tesserae around the median plate were to be completely incorporated into it, then a median plate similar to that in *Cardipeltis* could be produced. From the pattern of the sensory canal system in *Cardipeltis* it is clear that the known median plates extend only as far as the pineal region, and it seems reasonable to assume, as Stensiö has done (1958, p. 328), that there were small plates and orbitals anterior to the median plates. If this were so and further fusion of plates took place, one would have the condition where an entire carapace could arise as a single unit. This occurs in the Emsian Amphiaspids described by Obruchev (1938; 1958) from north-west Siberia, and *Cardipeltis* could thus be interpreted as an early offshoot from the Psammosteid stock leading to the Amphiaspids.

DEVELOPMENT OF DERMAL PLATES IN THE HETEROSTRACI

After the discovery by Woodward and White (1938) that primitive Elasmobranch scales are composite in nature, Orvig (1951) and Stensiö (1958) developed a new theory on the growth of scales and dermal bone in the lower vertebrates. Their recognition of the fact that two types of growth occur in dermal plates is here used to assess the significance of the variation in ornamentation within the Heterostraci.

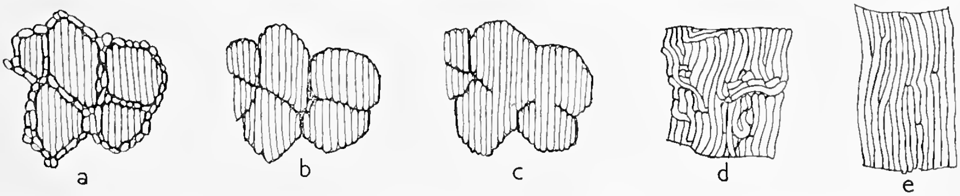


TEXT-FIG. 4. Ornamentation of dermal plates. *a*, *Astraspis sp.*, showing independent polygonal tesserae and zones of tubercles produced by cyclomorial growth. *b*, *Poraspis sp.*, showing longitudinal dentine ridges produced synchronomorially. *c*, *Tolepelepis sp.*, showing individual units produced by cyclomorial growth, with adjacent synchronomorial area.

The most primitive Heterostraci known are the Ordovician Astraspidae, which have a carapace composed of isolated polygonal tesserae. These small plates have an ornamentation consisting of one large tubercle surrounded by concentric rows of smaller tubercles. It is evident that during the early stages of ontogeny, single isolated tubercles were present in the skin which formed primordia around which successive zones of tubercles appeared, until the animal reached its definitive size, when the borders of the small plates thus formed would meet. The growth of these individual units by addition of zones of tubercles is termed cyclomorial growth by Orvig (1951, p. 367) (see text-fig. 4*a*).

In Silurian times the Heterostraci were represented by the Cyathaspids which had a carapace composed of two median plates and two branchials. These plates are ornamented by longitudinal dentine ridges, and in general appeared only when the animal was fully grown. There are no signs of cyclomorial growth, each plate being formed as a complete unit, with the dentine ridges all appearing simultaneously. This type of growth Orvig (1951, p. 367) termed synchronomorial (see text-fig. 4*b*).

A number of Cyathaspids are known from the Ludlovian of Oesel which do not possess this general type of ornamentation, but instead have one which can easily be derived from that seen in the Astraspids. The dorsal plate in *Tolepelepis*, for example, is made up of many cyclomorial elements, in each of which there is a longitudinal primordium, with smaller longitudinal ridges on either side. In the posterior part of the plate these elements take on the appearance of imbricating scales. The lateral region of the dorsal plate of *Tolepelepis*, however, has a similar ornamentation to that of the more normal Cyathaspids, showing synchronomorial growth, the only vestige of the individual elements being the faint grooves which break up the longitudinal dentine ridges (see text-fig. 4*c*). *Corvaspis* from the Downtonian shows further stages in the growth of the dermal plates, its median plates being more advanced than those of *Tolepelepis*. In *Corvaspis* the plates also appear to be formed of numerous polygonal units fused together, but each unit is formed synchronomorially in contrast to the cyclomorial formation in *Tolepelepis*. In the posterior part of the median plates of *Corvaspis*, the synchronomorial units are separated from one another by narrow zones of tubercles formed cyclomorially, giving the units the appearance of scales (Pl. 38, fig. 1; text-fig. 5*a*). It seems likely that, as suggested by Stensiö, the median plates gradually became continuous in this way with the squamation of the scales.



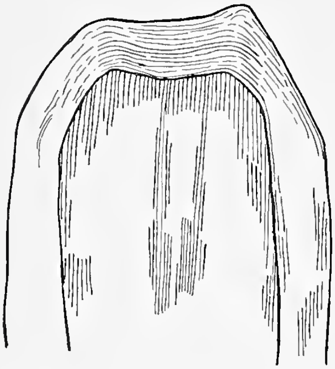
TEXT-FIG. 5. Variation of ornament in *Corvaspis kingi*. *a*, Polygonal synchronomorial units with margins of tubercles produced by cyclomorial growth. *b*, Polygonal synchronomorial units separated by grooves. *c*, Partial fusion of adjoining synchronomorial units. *d*, Complete fusion of original polygonal units giving single large synchronomorial area with occasional random ornamentation. *e*, Final stage showing longitudinal dentine ridges running almost without a break (cf. *Poraspis* fig. 4*b*).

Normally the polygonal units are marked off from one another by faint grooves (Pl. 38, fig. 2; text-fig. 5*b*), but in some cases this division into individual units is incomplete, the dentine ridges of two or three synchronomorial units being continuous, probably due to the units fusing before calcification (Pl. 38, fig. 3; text-fig. 5*c*). A further stage is well seen in Pl. 38, fig. 4, and text-fig. 5*d*, where the only trace of the original polygonal unit is an occasional faint transverse groove and an irregularity in the arrangement of the dentine ridges. This type of ornament is also seen in the Dittonian *Cardipeltis* which seems to suggest that this genus is a direct descendant of *Corvaspis*. The final stage in the trend of ornamentation is seen in a specimen of *Corvaspis* in the collection of Birmingham University (B.U. 717) which shows a median plate ornamented by straight longitudinal ridges, which extend almost the whole length of the plate without interruption (Pl. 38, fig. 5; text-fig. 5*e*).

A similar trend is seen in *Traquairaspis* (Pl. 38, fig. 7) where the primitive Downtonian *T. campbelli* has, in the centre of the ventral median plate, a large synchronomorial unit in which the ornamentation is random as in *Corvaspis* (text-fig. 5*d*), suggesting that it was derived from a number of small individual units. The later Downtonian *Traquairaspis symondsi* possesses a large central synchronomorial unit completely devoid of ornamentation (White 1946). In both cases the central unit has around it concentric zones of cyclomorial growth.

In *Corvaspis* also, whatever the form of ornamentation of the median plates, they are bordered by rows of small rounded tubercles forming a zone of cyclomorial growth. This type of median plate in which there is a large central synchronomorial unit around which there is an area of cyclomorial growth is also seen in the primitive Dittonian Pteraspid *Penygaspis dixoni* (White), although in this case the ornamentation is typically Pteraspid (White 1938; Stensiö 1958) (text-fig. 6).

If the synchronomorial unit were acquired early in the ontogeny instead of when the animal was approaching its definitive size, and the area of its median plates continued to increase by concentric growth, this would give the normal type of growth seen in the Pteraspids, which are an advanced group of the Heterostraci. That this is more likely than the evolution of the Pteraspid type of growth direct from the Astraspid condition is borne out by vestiges of the primitive condition found in some Pteraspids. *Pteraspis althi* Stensiö, for example, has a pre-oral region composed of small polygonal synchronomorial units rather like those seen in *Corvaspis* (Stensiö 1958, p. 277), while in *Rhinopteraspis dunensis* (Roemer) this same region is composed of a single synchronomorial unit in which the dentine ridges run longitudinally without a break (Tarlo 1958). These contrast with *Pseudopteraspis elongata* (Zych), which has the normal Pteraspid cyclomorial growth in its pre-oral region, and as figured below (text-fig. 7) these examples of fundamentally different Pteraspids demonstrate the three main types of ornamentation found in the Heterostraci.



TEXT-FIG. 6. *Penygaspis dixoni* (White), showing large central synchronomorial unit around which concentric growth occurs cyclomorially (after White 1938).

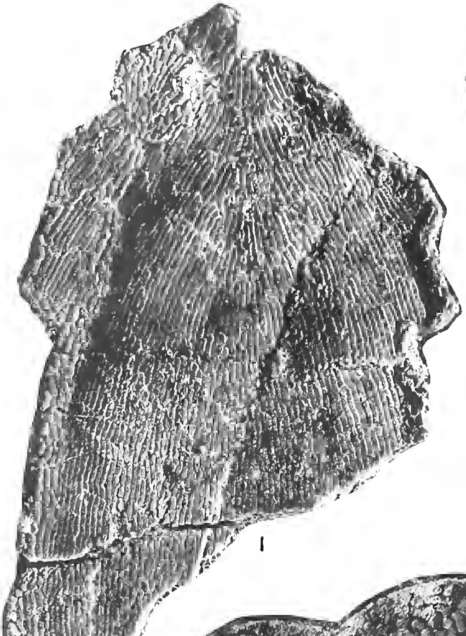
EXPLANATION OF PLATE 37

Figs. 1–8. *Corvaspis kingi* Woodward, Downtonian, Earnstrey Hall, Shropshire. 1, Anterior part of ventral median plate, showing the incorporation of tesserae on one side. ×2, B.M. P.40573. 2, Orbital plate. ×3, A–T 231. 3, Tessera, showing cyclomorial growth. ×3, A–T 308. 4, Tessera, showing synchronomorial growth. ×3, A–T 235. 5, Lateral plate, showing haphazard arrangement of ornament. ×3, A–T 234. 6, Lateral plate, traversed by line of sensory pores. ×3, A–T 226. 7, ? Post-orbital plate. ×2, B.M. P.40574. 8*a–b*, vertical section of scale. A–T 206. 8*a*. Complete scale. ×40. 8*b*. Part of scale, showing fine dentine tubules in outermost layer. ×220.

EXPLANATION OF PLATE 38

Figs. 1–6. *Corvaspis kingi* Woodward, Downtonian, Earnstrey Hall, Shropshire. 1, Fragment of median plate, showing polygonal areas separated by tubercles. ×2, B.U. 718. 2, Ventral median plate, showing polygonal areas separated by faint grooves. ×2, A–T 236. 3, Dorsal median plate, showing fusion of polygonal areas. ×2, A–T 237. 4, Ventral median plate, showing areas of random ornamentation. ×2, A–T 201. 5, Fragment of median plate with little trace of polygonal areas. ×2, B.U. 717. 6, Fragment of median plate showing healed area with random ornamentation. ×3, B.M. P.17038.

Fig. 7. *Traquairaspis campbelli* (Traquair), Downtonian. Natural mould of ventral median plate, showing central synchronomorial unit with random ornamentation, with outer zone of cyclomorial growth. ×2, B.M. P.27380.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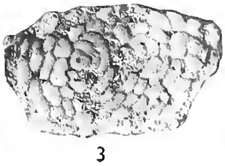
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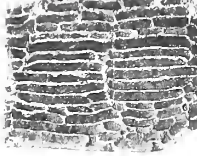
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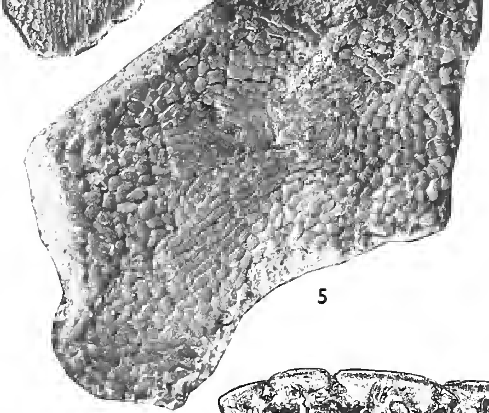
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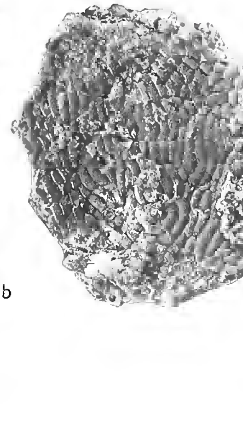
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TARLO, *Corvaspis*


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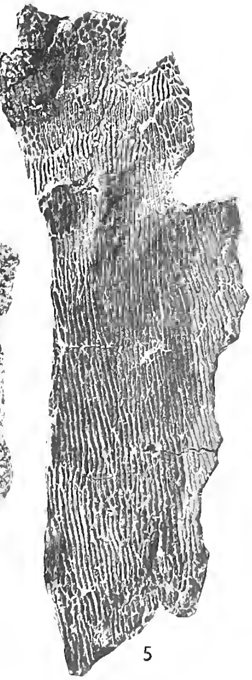
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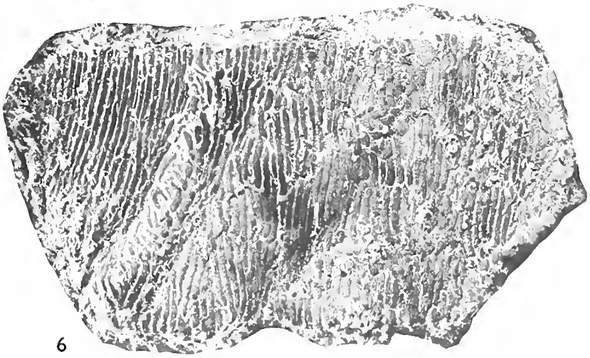
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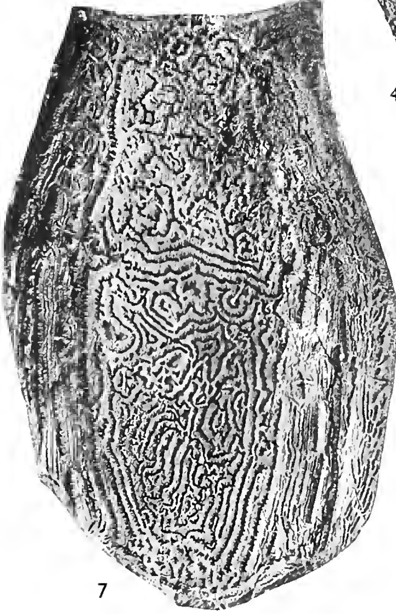
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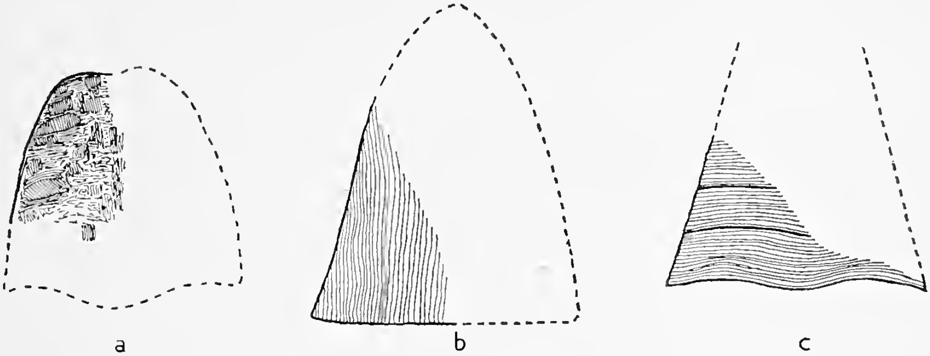
TARLO, *Corvaspis* and *Traquairaspis*

Thus it can be seen that what were formerly considered to be three distinct types of growth of dermal plates in the Heterostraci are all related. The most primitive type is that in which independent cyclomorial plates increase in size until they form a complete carapace; the next major stage is where the complete median plate is a single synchronomorial unit, and finally if this unit is acquired at an early stage of life it can become a primordium around which cyclomorial growth can occur until the animal is fully developed.



TEXT-FIG. 7. Ornamentation of pre-oral regions in the pteraspids. *a*, *Pteraspis althi* Stensiö, showing individual synchronomorial units. *b*, *Rhinopteraspis dunensis* (Roemer), showing large single synchronomorial unit. *c*, *Pseudopteraspis elongata* (Zych), showing zones of cyclomorial growth.

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Repositories. A-T., Allen-Tarlo Collection, Reading University; B.U., Geological Department, Birmingham University; B.M., British Museum (Natural History), London.

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AUSTRALOSUTURA GEN. NOV. (TRILOBITA) FROM THE CARBONIFEROUS OF AUSTRALIA AND ARGENTINA

by A. J. AMOS, K. S. W. CAMPBELL, and R. GOLDRING

ABSTRACT. A revised description of the Carboniferous trilobite *Cordania gardneri* Mitchell 1922 is given, based on some topotype material from Australia, and new material from Argentina. The species is assigned to a new genus *Australosutura* Campbell and Goldring 1960.

LOCATION AND STRATIGRAPHY OF MATERIAL FROM AUSTRALIA

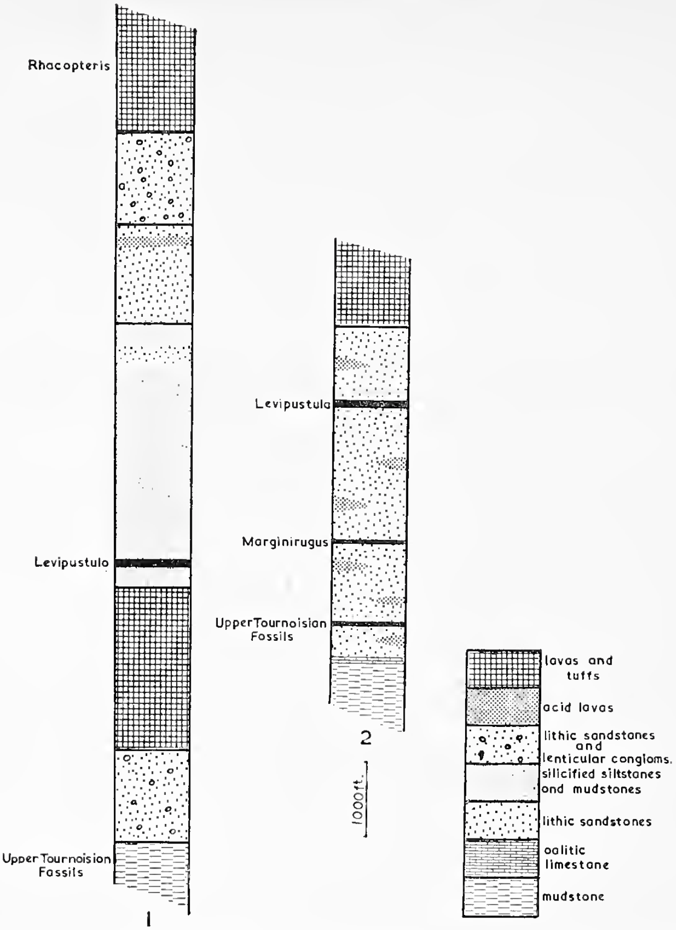
Australosutura gardneri was first described by Mitchell (1922, p. 536) from the shore of Lake Boolambayt, one of the Myall lakes north of Newcastle, New South Wales. The stratigraphy of this area is still poorly known, though it is being studied at the present time. The specimens of *A. gardneri* occur in a richly fossiliferous bed an unknown interval (some hundreds of feet at least) above a very prominent sandstone containing the brachiopod *Marginirugus barringtonensis alatus* Campbell 1956, which is considered to be of Lower Viséan age. Fortunately the species is known from two other New South Wales localities where the stratigraphy has been more adequately studied; the Barrington area (Voisey 1940), and the Booral area (Osborne 1950); the successions in these areas have been re-examined recently, and the results are set out in the accompanying columns (text-fig. 1).

In all three areas *A. gardneri* is associated with a very distinctive fauna dominated by the productid *Levipustula* Maxwell 1957 and an undescribed acrospiriferid. However, though all three faunas have many elements in common and are quite distinct even at the generic level from the earlier Carboniferous faunas, they are not identical, and it is possible that they are only approximately contemporaneous.

The *Levipustula* fauna is also very prominent in Queensland where it occurs extensively in the Neerkol mudstones which overlie the late Viséan limestones of the Rockhampton Series of the Rockhampton area, and the Turner Creek Clastics of the Mt. Morgan area, the upper parts of which are Viséan (Hill 1934; Maxwell 1954). The Neerkol mudstones are generally considered by Queensland geologists to be of Muscovian age. Study of the brachiopods, bryozoa, and molluscs of the *Levipustula* faunas of the three New South Wales localities indicates a Westphalian age and hence broadly confirms the Queensland determination. A systematic study of the fauna is to be published shortly.

The most significant fossils for the determination of age are: Spirifers similar to the Pennsylvanian *Neospirifer triplicatus* (Hall); *Lissochonetes*, which is known only from post-Viséan deposits elsewhere; *Levipustula*, which is common in the Westphalian of western Europe, but is not yet known from elsewhere; *Limipecten*, which, although it is known from the Viséan of western Europe, does not appear until the Upper Carboniferous elsewhere in the world. None of the associated fifteen genera of fossils, many of them endemic, suggests an earlier age. K. S. W. C.

Palaeontology, Vol. 3, Part 2, 1960, pp. 227–236, pls. 39–40.]



TEXT-FIG. 1. (1) Generalized stratigraphic succession east of the township of Booral on the south-eastern side of the Gloucester trough, New South Wales. (2) Generalized stratigraphic succession between Barrington and the Gloucester River, on the north-eastern side of the Gloucester trough, New South Wales.

LOCATION AND STRATIGRAPHY OF MATERIAL FROM ARGENTINA

The specimens from Argentina came from three localities in the west of the Province of Chubut: (1) La Carlota, about 8 km. south-east of Tecka, (2) Cerro Mina, east of Sierra de Languineo and 75 km. east of Tecka, and (3) Sierra de Tepuel, about 25 km. south of Tecka. At these three localities the trilobites were found in silicious nodules at the top of the lower section of the 5,200 m. of Upper Palaeozoic sediments exposed in the Sierra de Tepuel, Sierra de Languineo, and Sierra de Tecka of Suero's (1948, 1953) 'Tepuel System'.

The lower section, 3,200 m. thick, consists of glacimarine conglomerates together with sandstones, quartzites, and greywackes with intercalated shales. The upper section, 2,000 m. thick, differs from the lower by the absence of glacial conglomerates and greywackes, but includes micaceous sandstones and shales with well-preserved plant remains.

The lower section has yielded brachiopods, pelecypods, bryozoans, gastropods, conulariids, corals, and fish scales. The upper section has also yielded brachipods including *Levipustula*, and the brachiopods from both sections are now being studied (Amos, in press). In the upper section goniatites have been found. Miller and Garner (1953, p. 821) described *Anthracoceras? argentinense* Miller and Garner 1953 and *Eoasianites sp. A.? argentinense*, although found at La Carlota together with the trilobites, was not found *in situ* but came from a pebble of dark limestone. Curiously no limestone beds are exposed in the neighbourhood and possibly the pebble came from a bed no longer exposed. Miller and Garner gave the age of the goniatites as Middle Pennsylvanian (Westphalian). Amos considers the age of the lower section to be Viséan on brachiopod evidence.

A. J. A.

DESCRIPTION

Family BRACHYMETOPIDAE Prantl and Přibyl 1950 emended Hupé 1955

AUSTRALOSUTURA gen. nov.

Type species *Cordania gardneri* Mitchell 1922

Derivation of name. From the southern hemisphere, and with facial sutures.

Range. Carboniferous. The age of the beds in which the trilobites occur is not known with certainty either in New South Wales or in Argentina. Although it is suggested that the age of the beds in Argentina is Viséan it is thought that the age of the beds in Australia is Westphalian. Further research may produce more conclusive data for the age determination in both countries.

Distribution. New South Wales, Burindi, and Kuttung Series; Argentina, top of lower section of 'Tepuel System'.

Diagnosis. Cephalon and glabella strongly inflated. Glabella subcylindrical with prominent, subtriangular basal lobes and deep glabellar furrows 1p. Glabellar furrows 2p clear. Preglabellar field short and high. Very broad, concave, and pitted border furrow preceded by short convex border. Sublunate, strongly convex eyes. Long genal spines. Facial suture curves strongly away from eye. β on crest of border and ω just inside genal spines. Surface of cheek area, preglabellar field, glabella and occipital ring with numerous tubercles. Thorax of nine tuberculate segments. Pygidium with fifteen rings and nine (+1–2) ribs. Axis semioctagonal in cross-section, and overhanging postaxial portion, but not border. Rings strongly arched and tuberculate with prominent median row. Ribs with anterior portions twice as strong as posterior portions and both tuberculate.

Comparisons with other genera. Mitchell (1922, p. 537) concluded that *A. gardneri* could not be included in either *Phillipsia* Portlock 1843 or *Griffithides* Portlock 1843. He commented on its very close similarity to species of *Brachymetopus* M'Coy 1847, but decided that the presence of facial sutures prevented its inclusion with this genus. On the suggestion of Vogdes he finally assigned the species to *Cordania* Clarke 1892.

The cephala of *Cordania* and *Australosutura* are similar in each having a highly inflated glabella, faint glabellar furrows 2p, and prominent detached basal lobes. In *Australosutura* the glabella is relatively longer, and the preglabellar field shorter and steeper. Both genera have nine thoracic segments. The pygidia differ considerably. In *Cordania* it is transversely elliptical; in *Australosutura* it is comparatively longer, has a greater number of rings and ribs, fifteen rings and nine (+1–2) ribs as against thirteen rings and eight ribs in *Cordania cyclurus* (Hall and Clarke 1888), and the termination of the axis overhangs the postaxial portion, though not the border. The form and surface of the rings and ribs differ; in *Cordania* the anterior and posterior portions of the ribs are about equally developed and bear granules in addition to the tubercles on the anterior portions. Both portions continue to the margin.

In much of the material from Australia and Argentina the free cheeks are attached to the cranidium, and Mitchell (1922, p. 538) considered that fusion of the cheeks had begun. Whittington (personal communication) regards the facial suture of *Cordania* as normal and functional. Since isolated free cheeks and cranidia of *Australosutura* have been found in Australia the facial suture cannot be regarded as otherwise than functional. *Cordania* may possibly be ancestral to *Australosutura*.

Australosutura differs from the type species of *Brachymetopus* (type species *Phillipsia maccoyi* Portlock 1843, Goldring and Stubblefield 1957, p. 421) in possessing facial sutures, a longer glabella, and shorter preglabellar field. The details of the skeletal surface, in particular, the pair of prominent tubercles between the glabella and the anterior part of the eye, the row of tubercles on the border of the cephalon, and the tubercles on the pygidial axis, are very similar to that present in *B. maccoyi* and in *B. woodwardi* Whidborne 1896 (Goldring 1955). *B. strzeleckii* M'Coy 1847 also has similar features though the glabella is much shorter than in *A. gardneri*. In *B. ouralica* de Verneuil 1845 the anterior border is less arched than in either *A. gardneri* or *B. maccoyi*. The pygidium of *A. gardneri* is close to *B. maccoyi* and *B. ouralica* though the median tubercles of *A. gardneri* are of more even size on successive rings; the ribs of *B. woodwardi* and *B. maccoyi* are very similar to those of *A. gardneri*, but the ribs of *B. ouralicus* bear a greater number of tubercles on both portions.

Australosutura gardneri (Mitchell 1922)

Plates 39, 40

1922 *Cordania gardneri*, n. sp.—Mitchell, p. 536, pl. 54, figs. 1–7.
1924 *Cordania gardneri* Mitchell—Mitchell, p. 53, pl. 10, fig. 15.

Derivation of name. After Frank Gardner who first brought the species to notice.

Lectotype. Broken cephalon figured by Mitchell (1922, pl. 54, fig. 1, Australian Museum, Sydney, F.26974). Of the several specimens figured by Mitchell, those figured as pl. 54, figs. 2–5 and 7 are missing. Figure 6 of the same plate may be a reconstruction of F.27345. The specimen Mitchell figured later (1924, pl. 10, fig. 15) is F.27949.

Type locality. Brambles Farm, Myall Lakes, Eurenderee, Gloucester, New South Wales. Shore of Lake Boolambayt near grid reference 341812, Port Stephens, 1 inch: 1 mile Military Sheet.

Horizon. Upper Burindi Series (Voisey 1940, p. 196; David 1950, p. 290), Upper Kuttung Series (Osborne 1950, p. 24).

Material. Complete dorsal exoskeletons, together with independent cephala, thoracic segments, and pygidia. No hypostomes. The material from Argentina occurs as external and internal moulds in siliceous nodules and shows little or no sign of distortion. The Australian material occurs as internal and external moulds in very fine grained sandstones and siltstones at the type locality. Specimens are mostly distorted. The type of preservation at the other Australian localities is similar, but the sediments are coarser grained.

Diagnosis. As for the genus.

Description of material from Argentina. Cephalon. Side view. Outline of the glabella almost a quadrant, with occipital ring prominently arched, in one specimen (Museo la Plata, Coll. Suero 5024) as high as the glabella, and occipital furrow strongly rounded. Preglabellar furrow broad, shallow, and facing anteriorly. Preglabellar area short (sag.) almost vertical, bearing strong tubercles, which terminate abruptly at commencement of border furrow. The border furrow has irregularly arranged pits, of varying sizes (8–10 per sq. mm.) and is strongly concave, though the side towards the glabella is a straight slope at 45°. Border a moderately convex ridge which bears tubercles near top of posterior slope.

Front view. Occipital ring strongly arched with glabella similarly arched in front. Laterally basal lobes project beyond outline of occipital ring. Palpebral lobes slope upwards from axial furrows to prominent and strongly convex eyes. In outline posterior border of each cheek appears from behind eye and falls steeply towards genal spine. Below eye cheek descends with only slight convex slope to border furrow.

Plan. Excluding genal spines, outline of cephalon, subsemicircular, with length (sag.) rather greater than half breadth. Glabella subcylindrical, tapering anteriorly sharply between basal lobes, less so between lobes 2p and expanding very slightly beyond glabellar furrows 2p before broad, rounded termination. Basal lobes subtriangular and well defined. Glabellar furrow 1p sharp and very deep at axial furrows, becoming broad and shallow at bifurcation. Posterior branch merges into occipital furrow and anterior branch extends shortly on to glabella. Glabellar furrow 2p a broad, smooth knick, and glabellar lobe 2p only slightly inflated. No evidence from tuberculation of any more glabellar furrows. Occipital furrow deep and narrow posterior to basal lobes, expanding towards axial furrow and at junction with furrow 1p where it arches forward and becomes broad and shallow. Posterior to basal lobes, occipital ring very short (exsag.), but expanding where glabellar furrows 1p join the occipital furrow to twice this length (sag.). Small occipital node.

Area of fixed and free cheek broad. Centre of eye opposite junction of glabellar furrow 1p with axial furrow, and surrounded laterally by smooth terrace which extends to opposite glabellar furrow 2p and to half length of basal lobe. Palpebral lobe smooth. At axial furrow length of posterior border less than length of occipital ring, but border widens laterally. It is strongly convex and continues with equal prominence along genal spine. Posterior border furrow broad and smooth though narrower near axial furrow. Lateral border furrow very broad and pitted, joining posterior border furrow and continuing, with pits, down genal spine. Lateral border gently rounded, tapering gradually to base of genal spine, and then more strongly down it. Genal spine extends to fifth thoracic segment. Eye sublunate with minute facets.

Facial suture. Anterior branch curves strongly outwards, crosses border furrow and then turns inwards to margin; β at crest of border. Posterior branch curves sharply outwards and terminates only just inside base of genal spine, and rather farther from the median line than β.

Surface. Cheek area and preglabellar field with numerous close-set tubercles of variable size (3–4 per sq. mm.), many with apical openings; one is particularly prominent on fixed cheek opposite glabellar furrow 2p. A row of slightly enlarged tubercles between palpebral lobe and axial furrow. Posterior part of fixed cheek smoother and with only a few small tubercles. Glabellar and occipital ring with tubercles of about equal size to those on cheek, but less closely spaced, and on crest of glabella very weak (on available material). Tubercles on basal lobe larger on inner part than toward axial furrow. Top of inner slope of border with a single row of tubercles which weaken laterally and are scarcely discernible along genal spine. Outer slope of lateral border and continuation of posterior border along genal spine with fine parallel terrace lines.

On ventral surface doublure, including rostrum, covered with terrace lines, and equal in breadth to border furrow plus border of dorsal surface. Facial suture continues inward course over anterior margin and meets rostral suture (rr) just below margin. There is no short connective suture but a suture ($r\omega$), which has a course comparable to that of the perrostral suture of olenellids, makes an acute angle with the facial suture and swings outwards in a long sweeping curve to cut the posterior border of the cephalon just inside the genal spine, and immediately below the termination of the facial suture on the dorsal surface. This suture makes a definite angle with the rostral suture (rr), equal to the angle between the rostral suture and the facial suture. Inner margin of doublure (in part, presumably, hypostomal suture) long and curved, following, and lying immediately and closely under inner margin of border furrow. Doublure of free

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EXPLANATION OF PLATE 39

Material from Argentina

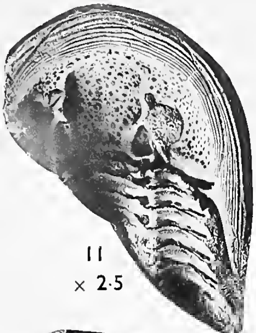
Figs. 1–11. *Australosutura gardneri* (Mitchell 1922). 1–7, Latex cast from external mould of complete specimen (BM In 53675). Province of Chubut, Sierra de Tepuel, about 25 km. south of Tecka. 1, Plan, 2, front view, 3, side view of cephalon, 4, posterior view. 5, Side view of pygidium, ×2. 6, Free cheek, showing puncta in border furrow, and apical openings on cheek tubercles, ×5. 7, Portion showing method of articulation of segments, ×4. 8, 9, Latex casts from external moulds of pygidia, Province of Chubut, La Carlota, about 8 km. south-east of Tecka. 8, ×4 (Coll. Suero 5049, 5051). 9, ×2 (BM In 53676). 10, 11, Latex casts from internal moulds of dorsal surface of cephala showing rostral plate and ventral surface of free cheek, Province of Chubut, Cerro Mina, east of Sierra de Languineo, 75 km. east of Tecka, 10, ×2·5 (Coll. Suero 5029), 11, ×2·5 (Coll. Suero 5023).

EXPLANATION OF PLATE 40

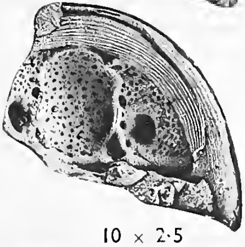
Material from Australia

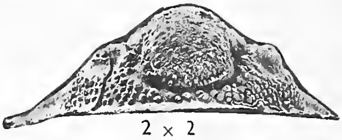
All specimens are from type locality. Catalogue numbers refer to the Australian Museum Collections. Specimens figured as numbers 9, 10, 13, 14, and 15 have been destroyed by fire.

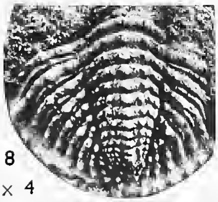
Figs. 1–20. *Australosutura gardneri* (Mitchell 1922). 1, Latex cast from internal mould of F.44640, ×2. 2, 3, Dorsal and lateral views of internal mould of same specimen, ×2. 4, Lectotype, F.26974, ×2 (Mitchell 1922, pl. 54, fig. 1). 5, Latex cast from internal mould of free cheek, part of ventral surface of cephalon, and pygidium, F.26476c–e, ×2. 6, Ventral surface of same cephalon showing position of rostrum, ×3. 7, 8, Lateral and posterior views of same pygidium, ×2. 9, Dorsal view of same pygidium, ×3. 10, Interior view of latex cast from internal mould of cephalon, ×3. 11, Interior view of latex cast from internal mould of pygidium F.26476, ×2. 12, Latex cast from external mould of pygidium, ×3. 13, Posterior view of latex cast from external mould of incomplete pygidium, ×3. 14–16, Latex casts from external moulds of fragmentary cephalons, 14, 15, ×3, 16, F.25593, ×2. 17, Lateral view of latex cast from external mould of part of cephalon, showing facial suture, F.26476a, ×2. 18–20, Dorsal and lateral views of internal mould, F.27949, 18, ×2·2, 19, ×1·8, 20, ×2·2 (Mitchell 1925, pl. 10, fig. 15).


11 × 2·5


6 × 5


10 × 2·5


2 × 2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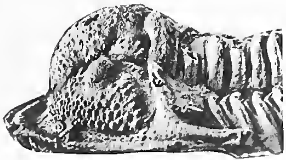
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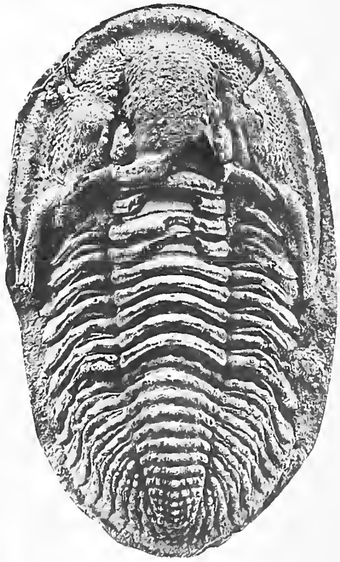
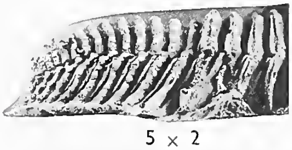
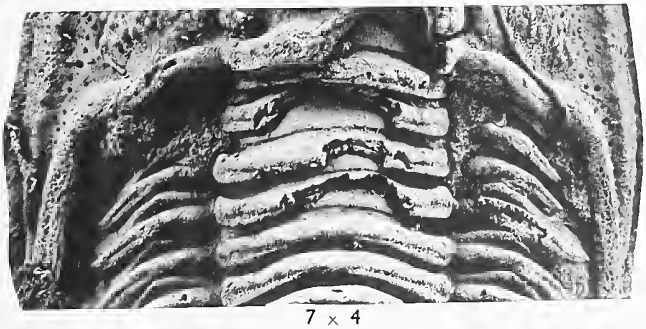

1 × 2


9 × 2

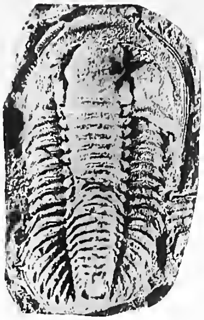

5 × 2

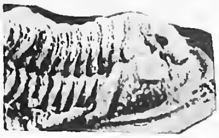

4 × 2


7 × 4

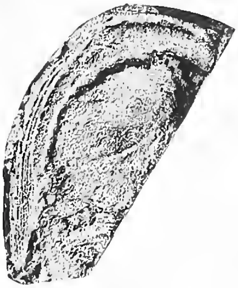
AMOS, CAMPBELL, and GOLDRING, *Australosutura* from Argentina


1 × 2


2 × 2

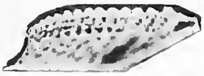

3 × 3

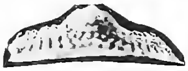

4 × 2

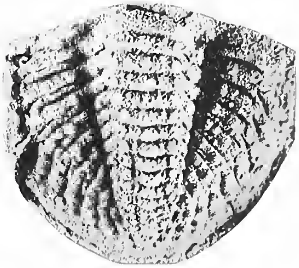

6 × 3


10 × 3


5 × 2

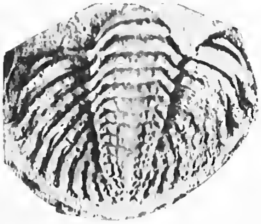

7 × 2

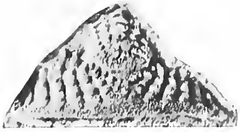

8 × 2

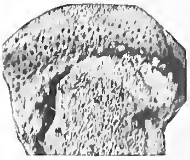

9 × 3

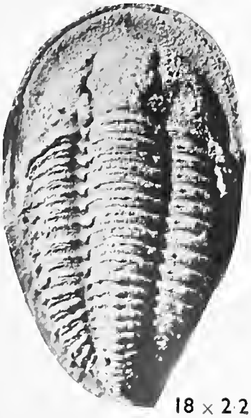

14 × 3

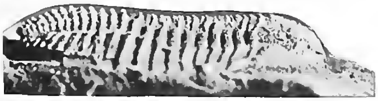

11 × 2

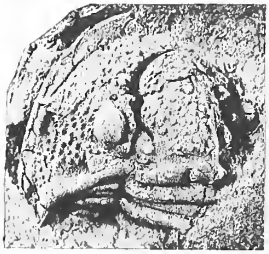

12 × 3

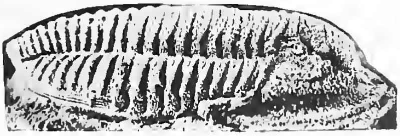

13 × 3


15 × 3


18 × 2·2


19 × 1·8


16 × 2


20 × 2·2

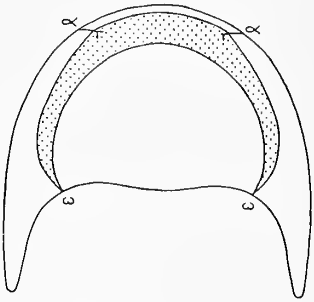

17 × 2

AMOS, CAMPBELL, and GOLDRING, *Australosutura* from Australia

cheeks tapers very rapidly forwards, whilst rostrum broadens complementarily. There is no Panderian notch.

Hypostome. No hypostomes are present in the material from Argentina. One specimen from Australia, since lost, was figured by Mitchell (1922, pl. 54, fig. 4) but was not described.

Thorax of nine segments. Rings with strong bands which arch slightly forwards. Posterior rings slightly narrower (tr.) than those anteriorly, and outline of rings graduates from strongly rounded and close to outline of occipital ring in anterior rings, to outline of pygidial rings in posterior rings. Articulating furrow broad and shallow. Articulating half-ring as long (sag.) as ring. Rings with a weak transverse groove behind which is a very narrow posterior portion. Groove, which is finely pitted, broadens (sag.) towards axial furrow. At posterior margin of ring, at axial furrow, a deep notch. Main portion of ring with tubercles, seven prominent (+1 or 2 more), arranged in rows on successive rings; a median row and three rows on flanks. Distance between median and first lateral tubercle is $1\frac{1}{2}$ times distance between each of the three lateral tubercles. Ring process a strong node. Ventrally of articulating half-ring, front edge of each segment flexed forward to form narrow flange which runs down into ring process.



TEXT-FIG. 2. Outline reconstruction of the ventral surface of the exoskeleton of *Australosutura gardneri* (Mitchell 1922). Rostrum stippled.

Pleurae with convex bend at fulcrum, at about one-third length (tr.). Posterior portions strongly arched (exsag.) (those on posterior pleurae more strongly so than those on anterior pleurae), narrowing at fulcrum, then broadening slightly and curving posteriorly. Posterior portions of pleurae 1–4 with slight anterior swing near margin. Laterally from fulcrum posterior portion is divided by weak furrow into anterior higher and strongly arched part and posterior lower part. At the margin anterior part rises over posterior part so that furrow faces posteriorly. Anterior parts have four to six tubercles, the one at the fulcral angle and the one between the fulcral angle and the axial furrow largest. A deep rounded furrow, which expands slightly at fulcrum, separates posterior portion of pleurae from the anterior portion, which is moderately arched on inner parts and flattens into a broad (exsag.) facet laterally.

Pygidium. Side view. Axis with only gently convex slope to ring 6, thence falling sharply and terminates overhanging postaxial portion. Axial furrow clear, and postaxial portion weakly concave. Height of pleural lobes more than half total height of ring. Rings very prominent with furrows of about equal strength giving a corrugated outline. Anterior rings vertical, those posteriorly becoming increasingly inclined, reaching 60° to horizontal.

Rear view. Outline of axis semioctagonal. Inner parts of pleural lobes almost flat, then curving over strongly and falling very steeply. Border convex with concave curve to pleural lobes.

Plan. Outline subsemicircular, with length of axis rather greater than breadth of axis plus one pleural lobe. Axis with almost straight sides tapering to blunt rounded termination.

Fifteen rings which are even bands not narrowing towards axial furrows. Ring 1 rather narrower than ring 2, and furrow between these two rings longer (sag.) than second furrow. Anterior rings each bear nine to eleven tubercles arranged in somewhat irregular rows. Median row of tubercles, and lateral row of tubercles situated at rather less than half distance from median line to axial furrow larger than the rest giving the semioctagonal outline. A further three to four rows of smaller tubercles; one between median and lateral rows.

Nine ribs, plus three axially arranged rows of tubercles posterior to the axis. Ribs with sharp posterior bend half-way to margin. Anterior portions of ribs twice as strongly arched as posterior portions, and with prominent tubercles, five to eight on ribs 1–8. The tubercles at or near the fulcral angle and the tubercles between the fulcral angle and the axial furrow are more prominent than the others. On rib 5 and posterior ribs the anterior portion does not extend up to the axial furrow and the posterior portion swings diagonally forward across the anterior portion and between it and the axis. Anterior portions of ribs 1–3 join with axial rings so that the junction of the rings and ribs is strongly undulating. The anterior portion of rib 4 scarcely joins the axis and posterior ribs do not do so, so that posterior to rib 4 there is a clear axial furrow which is almost nonundulose. Posterior portions show clearly on ribs 1–6 and narrow to border but do not continue over border except on ribs 1–2. Posterior portions with only one to two tubercles at about half-length (tr.). Border not separated from pleural lobes by any distinct furrow. Border smooth and only slightly undulose but extensions of anterior portions of ribs clear over border and ribs 1–9 with prominent tubercles at margin. Pleural furrows strong and deep, whereas rib furrows clear but weak, deepening at change in slope preceding border. Doublure on pygidium gently convex under border, but inside this it sweeps up steeply. It bears about ten fine raised terrace lines.

Measurements (in mm.)

	Argentina		*Australia*			
	Brit. Mus. In 53675	*Coll. Suero 5049, 5051*				
Length of exoskeleton	36·0	..				
Breadth of exoskeleton between genal spines	20·0	..	14·0	(12·0)	..	(17·0)
Length of cephalon (sag.)	11·5	..	7·5	8·3	..	..
Length of glabella	9·0	..	(5·7)	6·2	4·2	..
Breadth of glabella	8·0	..	..	..	..	..
Breadth of occipital ring (trans.)	7·8	..	5·1	(5·0)	(3·0)	6·2
Length of pygidium	12·5	5·5				
Length of axis	11·0	4·9				
Breadth of pygidium	(16·0)	(8·0)				
Breadth of axis	7·0	3·0				

Comparisons with Australian material. The Australian specimens are all much smaller than those from Argentina, and in general they are not so well preserved. Further, the only external moulds of the thorax yet discovered are very fragmentary, and most of the external moulds of the cephalon are poorly preserved.

Mitchell (1922, p. 536) described the borders of the cephalon as 'abnormally wide, concave between the cheeks and the thickened margins, which concave portions are only finely and sparsely tuberculate; both inner and outer margins are granulate'. On none of the specimens we have examined is there any indication of tuberculation on the concave border, and the region is invariably pitted. Mitchell did not mention the glabellar furrows 2p, but these are evident on all specimens, though much less distinctly impressed on the internal surface than in the Argentine specimens.

In general the topotypes do not have such a strongly inflated cephalon as do the Argentine specimens; the glabella does not form a quadrant in side view, but is much more depressed; the glabella does not approach quite so close to the border furrow; the tuberculation of the anterior and lateral border is much weaker and no tubercles have been observed on the posterior border of the fixed cheeks; the tubercles on the glabella are not weaker than elsewhere on the cephalon in well-preserved specimens; no occipital node or other occipital tuberculation has been observed, though this may be due to poor preservation; the crest of the axis of the pygidium does not drop so rapidly behind the sixth ring, and the concentric ornament of the doublure is coarser.

No specimens have been found showing a rostrum, but the course of the ventral margin of the free cheek suggests that the rostrum was similar to the Argentina form.

Repository of material. From Argentina. Museo la Plate, Buenos Aires, Colleción Suero: (1) La Carlota, 5048–54, (2) Cerro Mina 5018–46. British Museum (Natural History), London: (1) La Carlota In 53676, (2) Sierra de Tepuel In 53675.

From Australia. Australian Museum, Sydney: Lake Boolambayt, lectotype F.26974, F.26476, F.27345, F.27949, F.44640. Specimens from the two other localities, in Campbell's collection, have been involved in a fire.

K. S. W. C. and R. G.

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A CLYMENIID FROM THE *WOCKLUMERIA* ZONE OF NEW SOUTH WALES

by J. W. PICKETT

ABSTRACT. A new species of clymeniid, *Cymaclymenia borahensis*, from the *Wocklumeria* zone of New South Wales, is described, and its stratigraphical significance discussed. This is the first clymeniid described from Eastern Australia.

IN north-eastern New South Wales, Upper Devonian and Lower Carboniferous rocks consist of a series of geosynclinal sediments, chiefly mudstones, which outcrop in a trough along the western edge of the area, and in a few places along the coast, north of Newcastle. On the western side of the western trough marine faunas of Lower Carboniferous age are well known, but to the east of this trough, in a deeper water environment, fossils are rare. Consequently, any fossils which provide bases for accurate correlation, both within the area and with overseas sequences, are extremely valuable. It has never been possible to define the Devono-Carboniferous boundary in this sequence, due chiefly to the lack of Devonian marine faunas.

STRATIGRAPHY

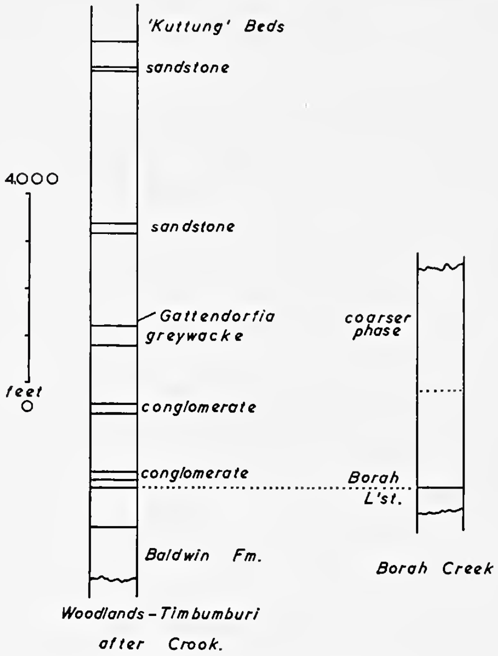
The Borah Limestone, in the type locality, is in an incomplete section, but farther south, where it contains fossils only rarely, it can be located in a complete sequence examined by Dr. K. A. W. Crook. Beneath the limestone at the type locality is little more than 50 feet of banded mudstone, with abundant *Leptophloeum australe*. This is absent from the mudstones which overlie the limestone. These mudstones are 200 feet thick and pass up into a coarser phase, in which fine arenites showing graded bedding are the dominant lithological types. This sequence is then truncated by a fault, so that the only known fossil horizons in the sequence are the limestone itself, and the *Leptophloeum* beds. The nature of the limestone is so distinctive that correlation from this locality farther south is quite positive. It is a fine-grained, blue-grey limestone, weathering whitish, containing recrystallized radiolarian tests, and euhedral crystals of an unknown mineral, which has been replaced by a mosaic of albite and calcite. These pseudomorphs, which occur in bands, and are whitish, in contrast to the blue-grey of the limestone, make it an extremely distinctive rock. The outcrop extends for almost 50 miles south-south-east from the type locality, which is the most northerly known outcrop.

This section includes rocks which would belong to the 'Barraba Series' in the lower part, and 'Burindi Series' (of Browne 1950) in the upper part, but it is impossible to make a division, as the boundary of these two has never been defined in a continuous sequence on the eastern side of the trough. The terminology of this interval is at present under review.

Crook's section, in the south, runs in a conformable sequence from low in the Upper Devonian to the Middle Carboniferous. Above the generally unfossiliferous Baldwin Formation is a thick sequence of marine mudstones, with members of limestone, con-

[Palaeontology, Vol. 3, Part 2, 1960, pp. 237–241, pl. 41.]

glomerate, greywacke, and sandstone. Some 800 feet above the top of the Baldwin Formation is a limestone with which the Borah Limestone has been correlated. Here, as in the type section, *L. australe* occurs below the limestone, and is not known above it. The *Leptophloeum* extends down into the Baldwin Formation, but is most abundant beneath the limestone. A few feet above the greywacke member (see text-fig. 1) Crook reports a specimen of *Gattendorfia*, which has been identified tentatively, by Crook, as *G. minusculum* Miller and Collinson, but as the specimen has since been destroyed by a fire this cannot be checked. In America this species occurs in the Northview Shale, of approximately Middle Tournaisian age. Indirectly, through the Northview Shale, this could be correlated with a fauna containing *Protocanites lyoni* (Meek and Worthen), on the western side of the trough in this area.



TEXT-FIG. 1. Stratigraphical columns.

Above 11,000 feet of these marine mudstones a series of terrestrial, volcanic, and glacial sediments is developed, the 'Kuttung Series' of Browne. It contains plant fossils in places, chiefly *Rhacopteris*. The Tournaisian–Viséan boundary is probably very near this transition from marine to terrestrial sedimentation.

In Catong Gully, north of Somerton, a goniatite which appears to be *Platyclymenia* was collected with specimens of *Leptophloeum australe*. This specimen shows one doubtful suture, and it proved impossible to develop any. The coiling and ornament are quite like that of *Platyclymenia* (see Pl. 41, fig. 7). Unfortunately, the higher part of this section is covered by high-level gravels associated with an earlier stage in the history of the Peel River; as well as this, faulting prevents extrapolation along the strike, so that the relation of this occurrence of *Platyclymenia* to the limestone cannot be determined.

There would be at least 300 feet of sediment between this and the overlying Borah Limestone.

SYSTEMATIC PALAEONTOLOGY

Genus CYMACLYMENIA Hyatt 1884

Cymaclymenia borahensis sp. nov.

Plate 41, figs. 1–6.

Holotype. Specimen No. F4599, University of New England collections. *Paratypes.* Specimens No. F4600, F4602, University of New England collections. All specimens from type locality (L200, U.N.E. catalogue) on south bank of Borah Creek.

Description. The conch is moderately involute, less so in younger whorls, and platyconic. The whorl height increases markedly in later volutions. The maximum number of whorls probably does not exceed six. The largest specimen has a maximum diameter of 5·5 cm., and the smallest does not exceed 1 cm., although four whorls are developed. Decoration consists of growth-lines only, fine lirae parallel to the aperture, with a fairly deep, smooth sinus across the venter, and a pronounced ventro-lateral salient. No radial ribs are present. The whorl profile changes during growth, and at maturity is rather similar to that of *C. striata*. The outer whorl is higher than the inner whorls, with tapering sides, and is much less involute. On a mature test, the height of the last whorl is slightly less than half the total conch height.

TEXT-FIG. 2. Suture of *Cymaclymenia borahensis* sp. nov.

The suture has a very broad ventral lobe, with a broad, shallow, secondary ventral saddle. The first lateral saddle is well developed, rounded, and the lateral lobe is strongly asymmetrical, with an inflected point on the ventral side. The second lateral saddle is flat, gradually receding into the shallow umbilical lobe, divided by the umbilical seam.

Discussion. C. borahensis is more like *C. barbarae* (Loewinson-Lessing) than any of the other species, particularly in regard to the suture. However, Loewinson-Lessing's stratigraphy in the original work is not completely clear. He did not collect the specimens himself, and although he places the fauna in the 'zone of *Sporadoceras münsteri*', it is possible that at least two zones are represented. The only completely reliable report of *C. barbarae* is that of Schindewolf (1952) from Saalfeld, from the *Wocklumeria* zone. The suture of *C. borahensis* is even closer to this than to that of Loewinson-Lessing's specimens.

The two other described species without radial ribs differ from *C. borahensis*, mainly in the degree of development of the first lateral saddle. *C. striata* has a rather similar whorl profile, but the lateral salients are less well developed. *C. camerata* differs in the whorl profile, though the suture is less different. These two species both occur in the *Clymenia* and *Wocklumeria* zones, so that this, together with the similarity to *C. barbarae*, suggests that *C. borahensis* belongs most likely to the *Wocklumeria* zone.

	Platy-clymenia	*Clymenia*	*Wock-lumeria*
C. striata (Münster)		×	×
C. costata (Wedekind)	×	×	
C. evoluta (Phillips)			×
C. ornata (Münster)		×	
C. barbarae (Loewinson-Lessing)	?	×	×
C. cordata Wedekind		×	
C. camerata Schindewolf		×	×
C. ovata Schindewolf		×	
C. borahensis sp. nov.			×
C. dorsocostata (Münster)		?	

Ranges of *Cymaclymenia* species.

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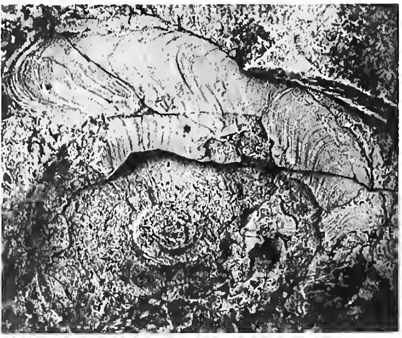
EXPLANATION OF PLATE 41

Figs. 1–6. *Cymaclymenia borahensis* sp. nov., Borah Limestone, Borah Creek. 1, Paratype, F4600, showing aperture and growth lines, ×1. 2, 3, Holotype, F4599, showing sutures; 2, ×1; 3, enlarged. 4, Sutures and part of living chamber, F4601, ×1. 5, Youngest suture and part of living chamber, F4603, ×1. 6, Paratype, F4602, showing umbilicus, growth lines, and part of living chamber, ×1.

Fig. 7. ?*Platyclymenia sp.*, Upper Catong Gully, Attunga; F4618, ×1.

Figs. 8–17. *Dinobolus sp.* cf. *D. conradi* (Hall), Sandpile group, British Columbia. 8–15 are unretouched photographs, ×1; 16, 17 are drawings illustrating the terminology, ×1¼. 8, 11, Internal views of the incomplete pedicle and brachial valves, Geol. Surv. Canada 14487. 9, 10, 12, 13, Internal views of the same valves tilted; 9, 10, pedicle valves, 12, 13, brachial valves. 14, 15, Posterior views of the pedicle and brachial valves. 16, 17, Reconstructions of the complete brachial and pedicle valves (outlines and anterior parts adapted from Davidson and King 1874). *a*, groove; *b*, beak; *c*, cardinal buttress; *d*, pseudodeltidium; *e*, cardinal partition; *i*, cardinal impression; *l*, plate; *m*, median partition; *o*, subcardinal impression; *p*, platform; *s*, cardinal socket; *u*, umbonal chamber; *v*, platform vault; *t*, position of trace of anterior part of crescent.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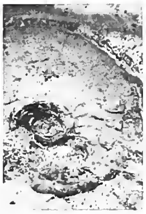
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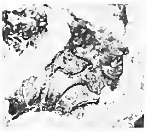
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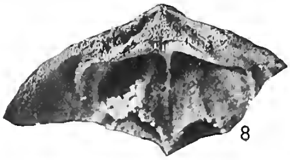
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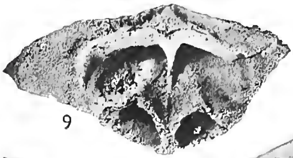
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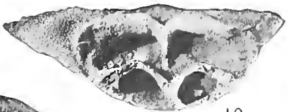
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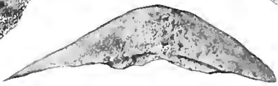
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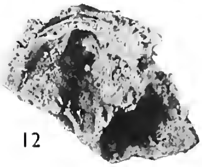
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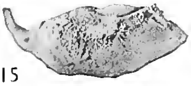
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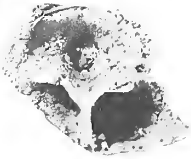
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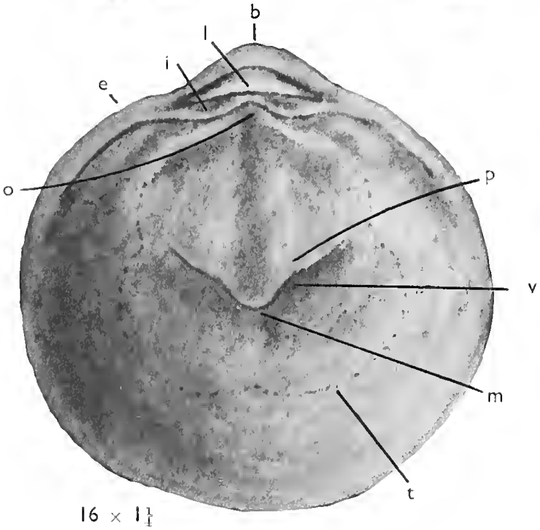
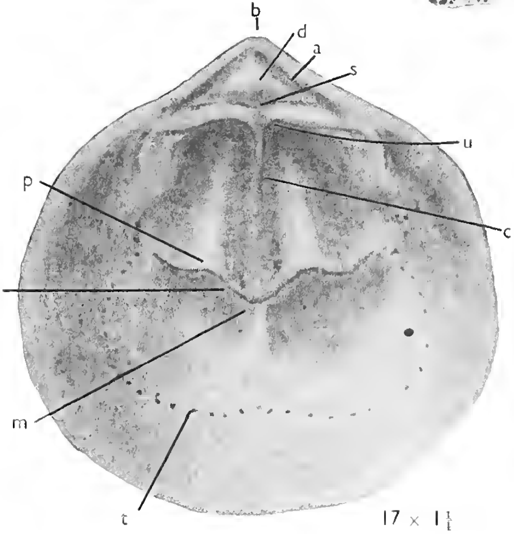


16 × 1¼



17 × 1¼

PICKETT, Clymeniids from Australia
NORFORD, *Dinobolus* from British Columbia

SCHMIDT, H. 1924. Zwei Cephalopodenfaunen an der Devon-Carbongrenze im Sauerland. *Jahrb. Preuss. geol. Landesanstalt* **44,** 98–171, pl. 6–8.

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A WELL-PRESERVED *DINOBOLUS* FROM THE SANDPILE GROUP (MIDDLE SILURIAN) OF NORTHERN BRITISH COLUMBIA

by B. S. NORFORD

ABSTRACT. A silicified individual allows a more detailed description of the posterior portion of *Dinobolus* than was previously available. There is no trace of the existence of a pedicle and a functional pedicle may have been atrophied in the genus.

THE Sandpile group (Middle Silurian) of northern British Columbia contains an extensive silicified coral and brachiopod fauna preserved in fine-grained, slightly cherty, thick-bedded dolostones. A single incomplete specimen of *Dinobolus* was etched free and is thought to represent a mature individual. The two valves were in contact within the rock, but became separated during the etching process.

In the descriptions of the genus and of the family by Hall and Clarke (1892), and by Davidson and King (1874), the internal characters are almost entirely based on naturally forming internal moulds, whereas the Sandpile specimens are silicified valves. The Schuchert Collection at Yale University contains a representative selection of the Trimerellidae including gutta-percha impressions taken from many of the internal moulds from which Hall and Clarke reconstructed drawings of the original valves (Hall and Clarke 1892, pl. 4A–4D). In most of these drawings the beak and hinge regions of the valves have been considerably restored.

The Sandpile material does not amplify knowledge of the interiors of the valves over that presented by Davidson and King, but does allow further description of the structures of the hinge, and of the pseudodeltidium. Most of the terminology is derived from Davidson and King (1874), but the following terms are also used in this discussion for convenience of description: cardinal socket, pseudodeltidium, plate (Pl. 41, figs. 16, 17).

Family TRIMERELLIDAE Davidson and King 1874

Genus DINOBOLUS Hall 1874

Type species *Obolus conradi* Hall 1868

Dinobolus sp. cf. *D. conradi* (Hall)

Plate 41, figs. 8–17

?*Obolus conradi* Hall 1868, pp. 368–9.
?*Dinobolus conradi* (Hall); Davidson and King 1874, pp. 160–1.
?*Dinobolus conradi* (Hall); Hall and Clarke 1892, pp. 38–39.

Description. Test biconvex, thick shelled, with faint concentric growth-lines near the margin. Pedicle valve with a small beak. Pseudodeltidium low, broadly triangular, slightly convex, bounded laterally by two grooves, and with a well-developed anterior slope curving into the cardinal socket at the hinge; without ornament preserved on the surface of the pseudodeltidium and without perforation or median groove (Pl. 41,

Palaeontology, Vol. 3, Part 2, 1960, pp. 241–244.]

figs. 8, 9). Hinge plate bearing a low pedically directed undulation and supported by a well-developed cardinal buttress (*c* of fig. 10). Platform prominently vaulted with a biconvex brachial surface, vaults separated by a median partition (*m*). Cardinal buttress forming a double-chambered umbonal cavity; buttress tapered anteriorly, resting medianly on the platform. Muscle scars present on the platform and on the valve floor outside it.

Brachial valve with an inconspicuous beak. A thin, elevated, saucer-like, transverse plate located in front of the beak and fitting snugly into the cardinal socket of the pedicle valve (fig. 15). Two cardinal impressions on the hinge immediately in front of this plate, moulding the brachial surface of the pedicle valve's hinge plate. Platform vaulted, with a depression above the median partition, surface biconvex but less strongly so than the surface of the platform of the pedicle valve. Umbonal cavity with a deep subcardinal impression (the figured specimen shows a hole in the shell at the centre of this depression).

Distribution. Sandpile group, Geological Survey of Canada collection 35165, from altitude 5,750 feet, 2 miles north-west of the southerly of the two lakes in Sandpile Creek, McDame, British Columbia; 59° 03′ north, 128° 11′ west. Geological Survey of Canada numbers 14487*a* (pedicle valve) and 14487*b* (brachial valve).

Discussion. The paucity of the studied material and the lack of complete valves preclude a complete description and identification, but the individual agrees with *Dinobolus conradi* (Hall) as discussed by Hall and Clarke who allowed a great deal of variation within the species. *D. conradi* has been reported from rocks of Niagaran age.

Davidson and King (1874) described one structure that they thought characterized the Trimerellidae, the sub-marginal crescent, confined to the posterior half of each valve and formed of three portions, the crown, the sides, and the ends. 'This part (p. 130), or merely a portion of it, may present itself in relief, excavated, obscurely, often partially in any of these conditions, or complicated by successive enlargements of its area; so that we feel a difficulty in representing it otherwise than diagrammatically, or in giving a description that is strictly accurate when applied to any single case.'

The crown is described as a line, the sides as pointed ovals, and the ends as obscurely defined areas. Examination of the specimens from British Columbia finds the crown to be situated between the hinge and the pseudodeltidium, i.e. at the site of the cardinal socket, and it appears to have little in common with the sides of the crescent, other than geometric continuity. The sides and ends of the crescent may well be the sites of muscle scars.

The cardinal facet of Davidson and King (p. 128, corresponding to the cardinal socket of this description) 'generally inclines or falls towards the cavity of the shell', and (p. 130) 'there is situated on the cardinal facet an oval-shaped scar or *lozenge* (*g*), having its long axis in the transverse direction of the valve'. This socket houses the plate of the brachial valve when the valves are in contact.

The deltidium of Davidson and King (pseudodeltidium of this description) represents the track on the pedicle valve of the edge of the plate of the brachial valve, and its anterior slope (deltidial slope of Davidson and King) suggests accelerating increase in size of the plate and the cardinal socket during growth.

The grooves bordering the pseudodeltidium are thought to represent the tracks of the cardinal extremities of the brachial valve. No trace was observed of 'deltidial ridges'.

Discussing the brachial valve, Davidson and King state (p. 128): 'The central portion of the hinge in certain species show nothing remarkable, . . . but in others it distinctly displays an excavation or *cardinal scar* . . . the excavation is bicupped in *T. ohioensis*; but the same species also presents it transversely grooved. There is no prominence in these cases. In some other species, however, the cardinal scar, though in general badly seen, appears to be situated on an elevation . . . rounded, or squared, and more or less developed, according to species. Nay, in the same species, as in *T. Lindströmi*, the elevation varies much in size, certain individuals having it very small, others very large and standing out like a great tooth . . . so large that it must have dipped deeply into the umbonal cavity of the pedicle-valve.'

Comparing these statements with the Sandpile specimens, and bearing in mind the nature of the internal moulds from which the authors drew most of their information, their elevation corresponds to the plate, which lies immediately behind the pair of cardinal impressions, referred to by them as the cardinal scar. This explanation suggests that their material revealed these structures so poorly that confusion of such closely adjacent structures was possible.

Investigation of *D. sp.* cf. *D. conradi* reveals no trace of a pedicle opening in the pseudodeltidium, nor of a groove in the hinge region of either valve, such as might be expected had the pedicle passed between the valves. Indeed, the plate of the brachial valve fits into the cardinal socket and would prevent the extrusion of a median pedicle. A functional pedicle may have been completely atrophied in *Dinobolus* and possibly also in the rest of the Trimerellidae.

There is no trace of the hinge teeth and sockets that characterize the class Articulata, but the species certainly does possess articulation as defined by Schuchert and Cooper (1932, p. 6), thus leaving as obscure the position of the Trimerellidae in a scheme of classification.

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