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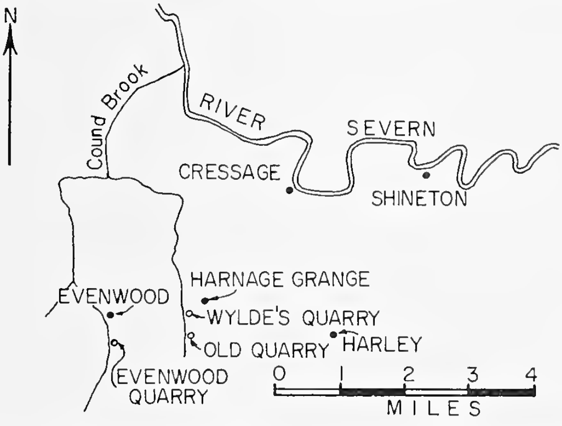
TREPOSTOME BRYOZOA FROM THE CARADOC SERIES, SHROPSHIRE

by JUNE R. P. PHILLIPS ROSS

ABSTRACT. *Mesotrypa bulmani* sp. nov., *Amplexopora thomasi* sp. nov., *Homotrypa* sp. A, and *Homotrypa* sp. B occur in the Hoar Edge Limestone in the lower part of the Caradoc Series, near Evenwood and Harnage. These trepostome species show similarities with species from Cincinnatian strata in Ohio, Indiana, and Anticosti Island.

THE four trepostome species described in this paper were collected from the lower part of the Caradoc Series in the Evenwood and Harnage area in southern Shropshire (text-fig. 1). *Mesotrypa bulmani* sp. nov., *Amplexopora thomasi* sp. nov., and *Homotrypa* sp. A occur in the *Harknessella subquadrata* horizon in the section at Evenwood Quarry (text-fig. 2). *Mesotrypa bulmani* is also found in two quarries in the Hoar Edge Limestone south-west of Harnage Grange, and *M. bulmani* sp. nov., *A. thomasi* sp. nov., and *Homotrypa* sp. B occur in this formation at the Wilderness, Wilstone Farm House. These species are from fossil collections made during the mapping of the Shrewsbury District and locality data and identifications made by Dr. C. J. Stubblefield and Dr. G. Elles are listed in Pocock *et al.* (1938). The cryptostome *Phaenopora stubblefieldi* Ross (1962) from the Hoar Edge Limestone also came from these collections and was located in the upper part of the 15-foot section in Evenwood Quarry in the *Harknessella subquadrata* horizon which overlies lower units containing graptolites of the *Nemagraptus gracilis* Zone. The succeeding sandstone and shale beds above the Hoar Edge Limestone contain graptolites regarded as characterizing the *Diplograptus multidens* Zone.



TEXT-FIG. 1. Index map of Evenwood–Harnage area, Shropshire.

Few bryozoan species have been described from the Caradoc Series and the occurrence of species of *Amplexopora*, *Homotrypa*, and *Mesotrypa* which have been recorded from

[Palaeontology, Vol. 6, Part 1, 1963, pp. 1–11, pl. 1–3.]

Ordovician strata in North America, Greenland, England, Estonia, Russia, and Australia, adds to the knowledge of the distribution of these three genera. *Mesotrypa bulmani* sp. nov. is similar to *M. orbiculata* from the Cincinnatian Arnheim Formation of south-eastern Indiana, *M. patella* from the Whitewater Formation of south-western Ohio (text-fig. 3), and *M. infida* from the *Rhinidictya* beds in Minnesota. It shows little similarity to *M. leus* (M'Coy) (Spjeldnæs 1957) from the Caradocian Horderly Sandstone of eastern Shropshire.

Amplexopora thomasi sp. nov. resembles *A. pustulosa* from the Cincinnatian Waynesville Shale of south-western Ohio, *A. ampla* from the Cincinnatian Leipers Limestone of central Tennessee and the Cincinnatian Fairmount Member of south-western Ohio, and *A. billingsi* from the Cincinnatian English Head and Vaureal Formations of Anticosti Island.

Homotrypa sp. A is similar to a rare species, *H. dumosa*, from the Cincinnatian Fairmount Member of south-western Ohio, and *Homotrypa* sp. B has many morphologic features that resemble *H. obliqua* from the Cincinnatian Fairmount and Corryville Members of south-western Ohio, and *H. wortheni* from the Cincinnatian Whitewater Formation of south-western Ohio and south-eastern Indiana.

Collection numbers with the prefixes WM and RR, and specimen numbers with the prefix GSM refer to material in the Geological Survey Museum, London.

SYSTEMATIC DESCRIPTIONS

Family AMPLEXOPORIDAE Miller 1889

Genus AMPLEXOPORA Ulrich

1882 *Amplexopora* Ulrich, p. 154.
1960 *Amplexopora* Ulrich; Boardman, pp. 16–20.
1920 *Acanthotrypella* Vinassa de Regny, p. 221.

Type species. Amplexopora cingulata Ulrich (1882, pp. 126, 254–6, pl. 11, figs. 5, 5*a*–*c*); designated by Ulrich (1882, p. 255).

Diagnosis. Colonies are ramose, encrusting, massive, or rarely bilaminate. Monticules are commonly present. Zooecial openings are polygonal and are enclosed by generally integrate zooecial walls. Mesopores are generally not abundant. Acanthopores are commonly abundant and occur at the junctions of zooecial walls. In axial regions the zooecial tubes have slender walls. In the peripheral regions the thickened zooecial walls have a laminate microstructure in which the outer parts of adjacent zooecial walls have steeply inclined laminae that intersect at acute angles. Diaphragms are present in the peripheral and subperipheral regions and may be flat, curved, or cystoidal. Some species display cystiphragms.

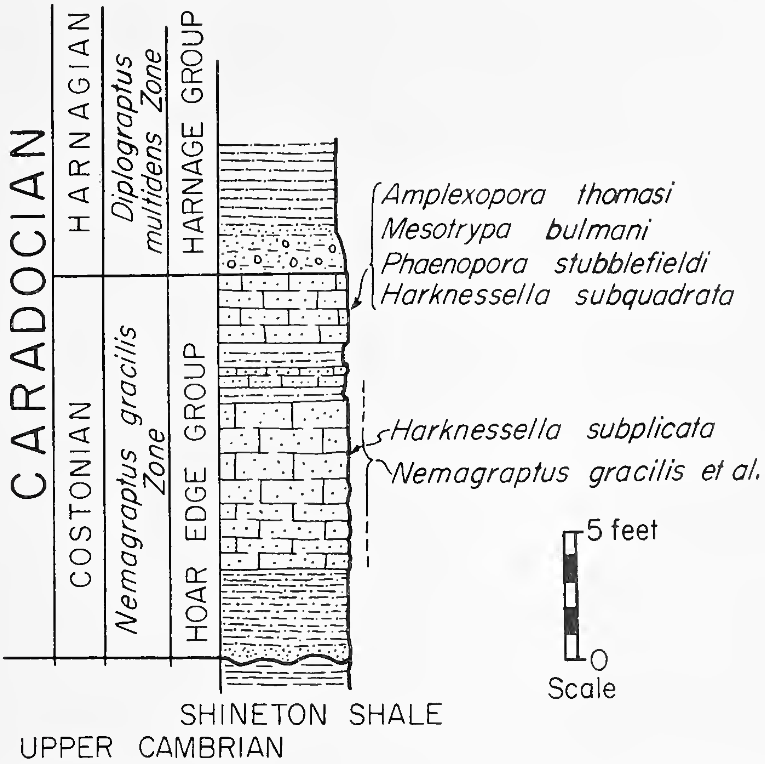
Amplexopora thomasi sp. nov.

Plate 1, figs. 1–10

Material. Collections WM 1265 (including paratype GSM 102009), WM 1267, WM 1273 (including holotype GSM 102004, paratypes GSM 102005, GSM 102006), WM 1274 (including paratype GSM 102007), from the top part of Evenwood Quarry; and collection WM 1279, from the middle part of Evenwood Quarry; Hoar Edge Limestone, Hoar Edge Group; Caradoc Series; Ordovician.

Description. In tangential sections the slender, integrate zooecial walls enclose polygonal or subpolygonal zooecial openings which vary considerably in diameter (Pl. 1, figs. 1, 7, 10). One to two mesopores are generally located at the junctions of the zooecial walls (Pl. 1, figs. 1, 10). Acanthopores are rare and, if present, are small, dense spots in the zooecial walls.

Transverse sections of ramose colonies display axial regions with thin-walled polygonal zooecial tubes and peripheral regions with thickened, integrate zooecial walls and diaphragms crossing the zooecial tubes. Transverse sections of bilaminate colonies display a dark medial line lacking microstructure and with zooecia on both sides of it. The zooecial tubes have thin walls in the medial region and thickened, integrate walls and diaphragms in the peripheral region (Pl. 1, figs. 2, 4).



TEXT-FIG. 2. Measured section of the Hoar Edge Group in Evenwood Quarry (after Pocock *et al.* 1938).

In longitudinal sections of ramose colonies the axial regions display very broadly crenulate zooecial walls that are very slender. For some distance the walls diverge only slightly from the axis of growth of the branch and then bend abruptly into the peripheral region. In this region they thicken and are more closely crenulate and very slightly beaded. The zooecial openings are slightly oblique at the periphery. The zooecial and mesospore walls have an integrate, laminate microstructure as noted in the *Diagnosis* of *Amplexopora* (Pl. 1, fig. 9). The very slender, widely spaced diaphragms crossing the zooecial tubes pass into the steeply inclined wall laminae (Pl. 1, fig. 9). In the mesopores, which develop at the base of the peripheral region, the diaphragms are closely spaced.

In longitudinal sections of bilaminate colonies the zooecial tubes curve gently to the periphery and are crossed by widely spaced diaphragms. The zooecial openings are oblique to the periphery (Pl. 1, fig. 8).

TABLE 1

Measurements of *Amplexopora thomasi* sp. nov. (in millimetres)

Catalogue no.		*GSM 102007*	*GSM 102004 holotype*
Diameter of zoarial stem		6–7	6–7
Diameter of zooecial opening	min.	0·14×0·16	0·15×0·15
	max.	0·31×0·22	0·23×0·21
No. of zooecia per 2 mm.		6–8	6–8
Combined thickness of adjacent zooecial walls in peripheral region		0·04–0·06	0·04–0·06
Diameter of mesopore	min.	0·03×0·03	0·05
	max.	0·10×0·12	0·10
Diameter of acanthopore		0·01–0·04	0·01–0·02
No. of acanthopores per zooecium		0–6	0–5
No. of diaphragms per 1 mm. in zooecium in peripheral region		4–6	3–5
No. of diaphragms per 1 mm. in mesopores		14–20	11–15
Width of peripheral region		1·2	2·0
Ratio: width of peripheral region of zooecium/total width of zooecium		0·4	0·6

Remarks. The species is characterized by slender zoarial stems with wide peripheral regions in which the thickened, crenulate, and slightly beaded zooecial and mesopore walls are distinctly integrate and in which mesopores have closely spaced diaphragms and the zooecial tubes have widely spaced diaphragms. Acanthopores, if present, are not prominent.

Amplexopora thomasi is similar to *A. billingsi* (Bassler 1928) from the Ordovician (Cincinnatian) English Head and Vaureal Formations, Anticosti Island. *A. billingsi* has

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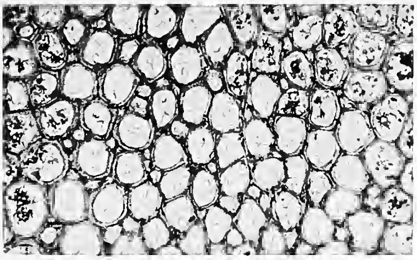
EXPLANATION OF PLATE 1

Figs. 1–10. *Amplexopora thomasi* sp. nov. 1, Tangential section showing integrate walls between zooecial tubes and mesopores, collection WM 1273, holotype GSM 102004, ×20. 2, Transverse section of a bilaminate colony showing narrow peripheral region of thickened walls, collection WM 1273, GSM 102005, ×20. 3, Part of longitudinal section in peripheral region showing thick, laminate zooecial walls and diaphragms in zooecial tubes and mesopores, collection WM 1274, GSM 102007, ×50. 4, Part of transverse section of bilaminate colony showing integrate, laminate zooecial walls in peripheral region, collection WM 1273, GSM 102005, ×50. 5, Part of a longitudinal section in the peripheral part of a ramose colony showing the finely crenulate zooecial walls, collection WM 1273, GSM 102004, ×20. 6, Part of a longitudinal section of a ramose colony showing very slender walls in the axial region and thickened walls in the peripheral region, collection WM 1274, GSM 102007, ×20. 7, Tangential section showing general arrangement of zooecial openings, collection WM 1274, GSM 102007, ×20. 8, Longitudinal section of a bilaminate colony showing diaphragms across zooecial tubes, collection WM 1265, GSM 102009, ×50. 9, Part of a longitudinal section in peripheral part of a colony showing integrate, laminate zooecial walls, and thin diaphragms, collection WM 1274, GSM 102007, ×100. 10, Tangential section showing distinct boundaries between adjacent zooecial walls, collection WM 1273, GSM 102004, ×50.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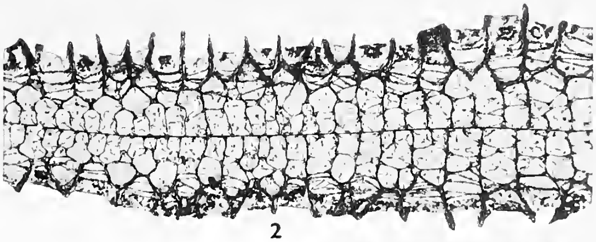
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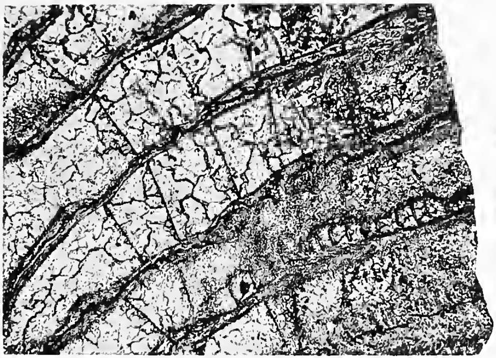
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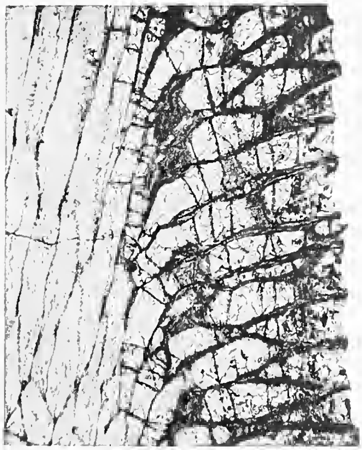
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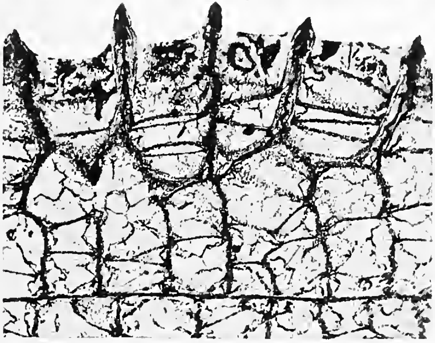
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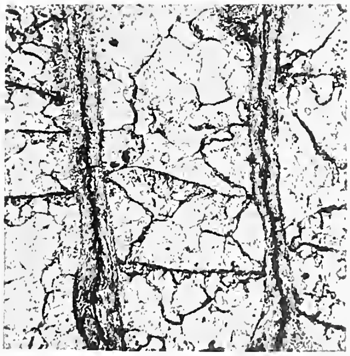
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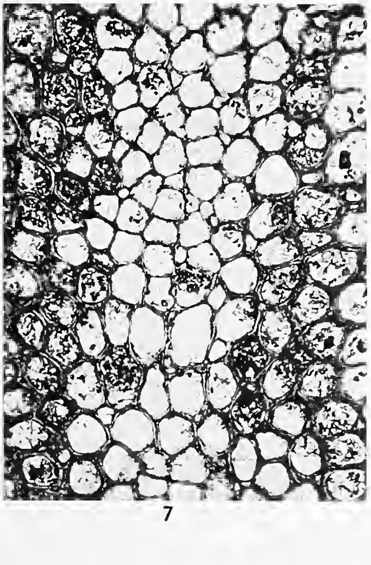
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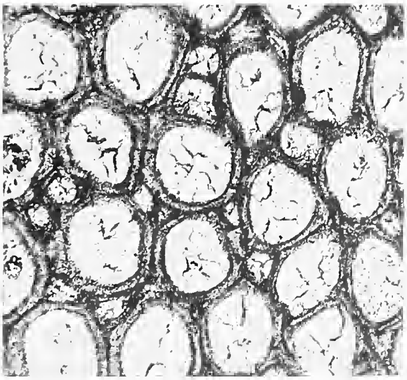
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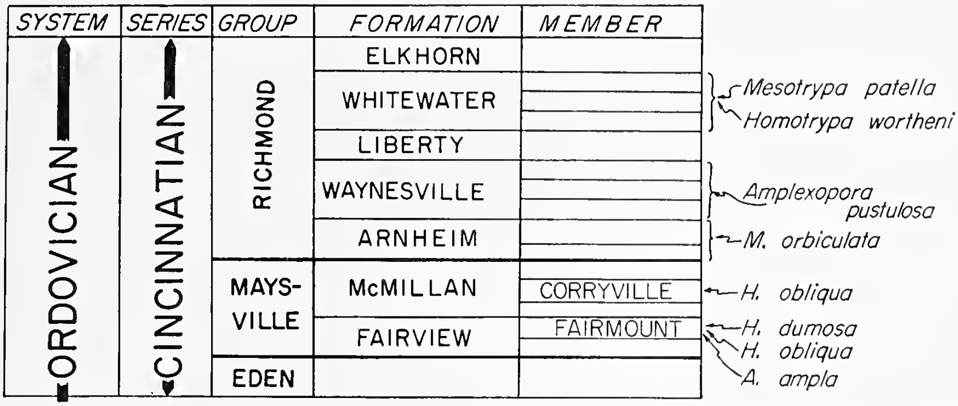
PHILLIPS ROSS, Ordovician Bryozoa

fewer zooecial openings per 2 mm., fewer mesopores, and more numerous diaphragms in the zooecial tubes. Both species have inconspicuous acanthopores, closely spaced diaphragms in the mesopores, and crenulate zooecial walls. *A. thomasi*, *A. pustulosa* Ulrich (1890) from the Ordovician (Cincinnatian) Waynesville Shale, Hanover, Ohio, and *A. ampla* Bassler (1904) from the Ordovician (Cincinnatian) Leipers Limestone, Nashville, Tennessee, are similar in the diameter of their zoarial stems and have about the same number of zooecia per 2 mm. *A. pustulosa* and *A. ampla* differ from *A. thomasi* in having diaphragms in the axial region, and *A. pustulosa* commonly has acanthopores at the junctions of the zooecial walls and has few mesopores in the peripheral region.



TEXT-FIG. 3. General geologic column of formations and members in the Cincinnatian Series in south-western Ohio and south-eastern Indiana from which Bassler (1915) reported the bryozoan species that are here compared with the Caradocian species.

Amplexopora thomasi appears to have some similarity to *A. murchisoni* (Spjeldnæs 1957), the type of which is from 'Horderley', Shropshire, but its exact locality and stratigraphic position is not known. Unfortunately the type material of *A. murchisoni* is partly recrystallized so that recognition of the species is difficult. However, Spjeldnæs (1957, text-figs. 1*a*, *b*) illustrates the typical wall microstructure of species of *Amplexopora* and his text-fig. 1*b* appears to show small mesopores and also acanthopores at the junctions of the zooecial walls.

The species is named in honour of Dr. H. Dighton Thomas, British Museum (Natural History).

Family MONTICULIPORIDAE Nicholson

Genus MESOTRYPA Ulrich 1893

Type species. *Mesotrypa infida* (Ulrich 1886, p. 88).

Diagnosis. Colonies are discoidal, hemispherical, conical, or encrusting expanses. Lower surfaces of discoidal colonies are flat or concave. Polygonal or cylindrical zooecial tubes grow directly upwards from the basal lamina and are crossed by flat and curved diaphragms. Mesopores are present in both the proximal and distal parts of a colony and have closely spaced diaphragms. Zooecial openings are polygonal in some colonies and circular in others. Mesopore openings are rectangular or polygonal and may be very small. Acanthopores are prominent where the zooecial openings are angular and mesopores are small, and they are small and indistinct in colonies where zooecial openings are round and mesopores are large. The zooecial and mesopore walls display a granular microstructure at low magnifications.

Mesotrypa bulmani sp. nov.

Plate 2, figs. 1–9; Plate 3, figs. 2, 4

Material. Collections WM 1262 (including paratype GSM 102003) and WM 1274 (including paratype GSM 102008), from the top part of Evenwood Quarry. Collection WM 1279 (including paratypes GSM 102011–102015), from the middle part of Evenwood Quarry. Collections RR 2635 (including paratype GSM 102016), RR 2636 (including paratype GSM 102019), RR 2637, and RR 2638, from the old quarry in the wood near Coundmoor Brook. Collections RR 2669 and RR 2672 (including holotype GSM 102017), Wylde's Quarry, near Harnage Grange. All collections from Hoar Edge Limestone, Hoar Edge Group; Caradoc Series; Ordovician.

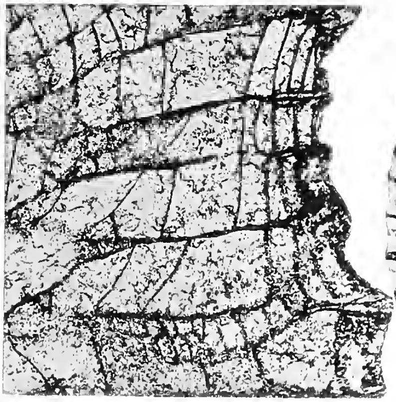
Description. Many of the discoidal colonies, 10 to 13 mm. diameter at their bases, and 1 to 2 mm. high, have flat or concave bases. The encrusting colonies vary from small, cylindrical forms, 1·5 to 2 mm. in diameter, to broad, explanate forms that extend across fragmented shells and other material.

In tangential sections the zooecia are variable in size and shape. In a well-developed discoidal colony, GSM 102017, almost round zooecial openings and polygonal or rectangular mesopores fill the spaces between clusters of large, polygonal zooecial openings and a few mesopores. In these clusters where the mesopores are very few, acanthopores, 0·02 to 0·03 mm. in diameter, are present at the junctions of the zooecial walls (Pl. 2, fig. 7); where the mesopores are distinctly visible between the zooecia, the acanthopores are generally lacking (Pl. 3, fig. 4). In an encrusting form, GSM 102003, and a discoidal form, GSM 102015, the polygonal zooecial openings are separated by a few mesopores, and prominent acanthopores, 0·03 to 0·06 mm. in diameter, lie at the junctions of the zooecial walls (Pl. 2, fig. 8). Deeper tangential sections of colonies display more slender walls enclosing polygonal tubes (Pl. 2, fig. 5). Walls between zooecia and mesopores are slender and amalgamate.

In longitudinal sections the zooecial tubes may be slightly reclined for a short distance along the basal lamina (Pl. 2, fig. 4). Acanthopores and mesopores are commonly present a short distance above the basal lamina and extend to the distal parts of colonies.

EXPLANATION OF PLATE 2

Figs. 1–9. *Mesotrypa bulmani* sp. nov. 1, Part of longitudinal section of subperipheral and peripheral parts of colony showing diaphragms in the zooecial tubes and mesopores, collection WM 1279, GSM 102011, ×50. 2, General aspect of transverse section, collection WM 1279, GSM 102012, ×20. 3, Part of a longitudinal section of a multilaminate colony showing thin, granular walls in the peripheral region, collection RR 2635, GSM 102016, ×50. 4, Longitudinal section of multilaminate colony showing slender zooecial walls and diaphragms in the zooecial tubes and mesopores, collection WM 1279, GSM 102013, ×20. 5, Deep tangential section showing distinct acanthopores at the junctions of very slender zooecial walls, collection WM 1274, GSM 102008, ×50. 6, Tangential section showing polygonal zooecial openings, numerous mesopores, and very fine acanthopores, collection RR 2636, GSM 102019, ×50. 7, 8, Tangential sections showing distinct acanthopores at junctions of zooecial walls; collection RR 2672, holotype GSM 102017, ×50; and collection WM 1262, GSM 102003, ×50, respectively. 9, Oblique longitudinal section showing diaphragms in the mesopores and in the long zooecial tubes, collection WM 1279, GSM 102011, ×20.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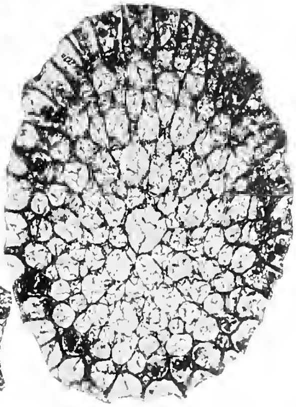
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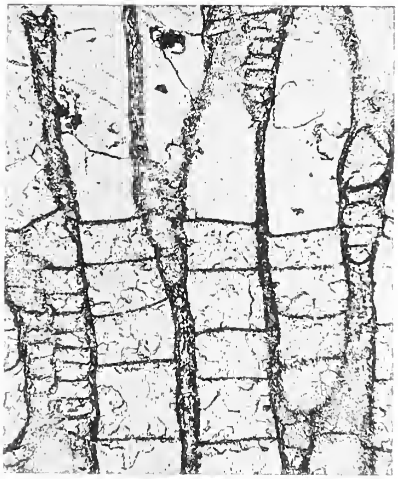
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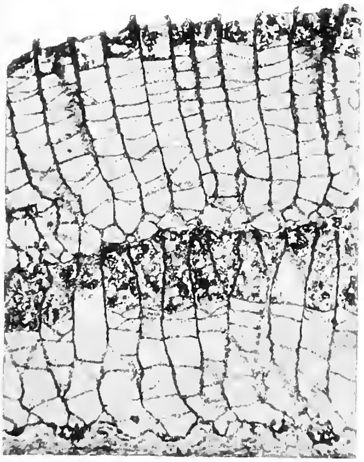
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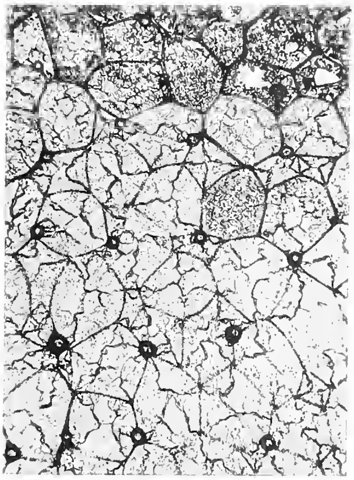
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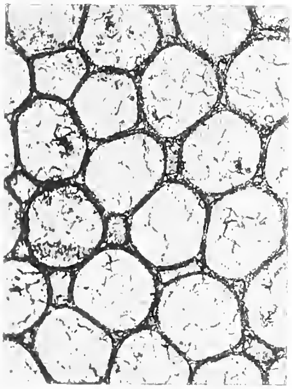
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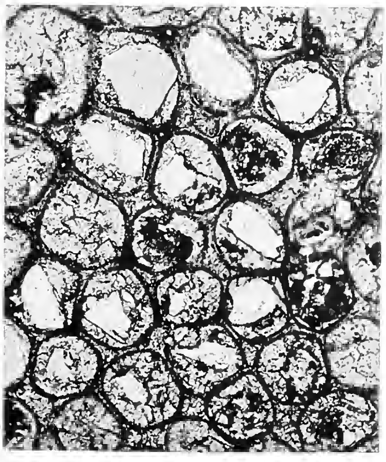
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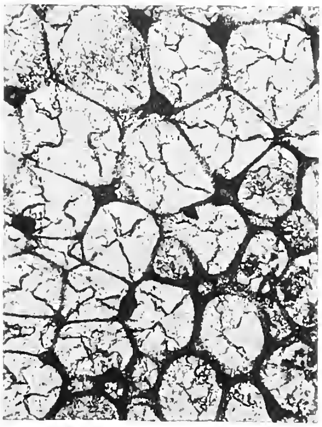
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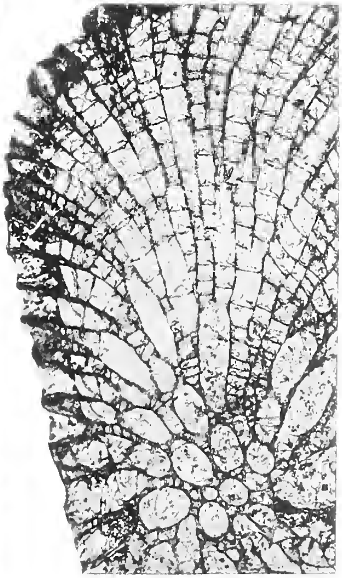
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PHILLIPS ROSS, Ordovician Bryozoa

As the walls, mesopores, zooecial tubes, and acanthopores have some variation in their direction of growth, a longitudinal section may pass across and then back into a mesopore, acanthopore, or even a zooecial tube. The zooecial and mesopore walls thicken slightly as they extend to the periphery (Pl. 2, figs. 4, 9). The very slender zooecial walls have a very fine, laminate microstructure that commonly appears granular at low magnifications. The clear inner parts of the zooecial walls lining the zooecial tubes consist of fine laminae lying at 45 degrees to the inner boundary. The outer parts of adjacent zooecial walls appear as dark bands of intertonguing convexly curved, granular laminae. The thin diaphragms crossing the zooecial tubes and mesopores pass into the wall laminae after bending abruptly at the zooecial wall boundary. Acanthopores have slender, dark walls enclosing clear axial spaces. In encrusting forms the zooecia extend upright to the periphery and in discoidal forms the zooecial tubes curve broadly near the periphery (Pl. 2, figs. 4, 9). Diaphragms are present throughout the length of the zooecial tubes and are commonly flat, or convexly or concavely curved, and in the peripheral region may be more closely spaced and include additional kinds such as compound and cystoidal diaphragms (Pl. 2, fig. 4). The mesopores have closely spaced diaphragms throughout their length (Pl. 2, figs. 3, 4, 9).

TABLE 2

Measurements of *Mesotrypa bulmani* sp. nov. (in millimetres)

Catalogue no.		*GSM 102017*
No. of zooecia per 2 mm.		8–10
Diameter of zooecial opening	max.	0·22×0·22
	min.	0·16×0·16
Diameter of zooecial opening in monticule	max.	0·29×0·29
	min.	0·29×0·26
Combined thickness of adjacent zooecial walls in peripheral region		0·02
Diameter of mesopore	max.	0·10×0·15
	min.	0·06×0·03
Diameter of acanthopore		0·01–0·03
No. of acanthopores per zooecium		2–4 in monticules
No. of diaphragms per 1 mm. in zooecium		6–8
No. of diaphragms per 1 mm. in mesopore		about 25

Remarks. The species is characterized by small, commonly discoidal colonies with round or subpolygonal zooecial openings, sparsely distributed mesopores, abundant diaphragms throughout the length of the mesopores, widely spaced diaphragms in the zooecial tubes, and small acanthopores which are most prominent in the monticules.

Mesotrypa bulmani is similar to *M. infida* (Ulrich 1886, 1893) from 'the middle third of the Trenton Shales at Minneapolis' (= the *Rhinidictya* and *Ctenodonta* beds of Ulrich 1893, p. *l*) in the form of the zoarium and the shape of the zooecial openings. *M. bulmani* has smaller zooecial openings both in and between the monticules, has fewer acanthopores per zooecium, and lacks funnel-shaped diaphragms. *M. bulmani* resembles *M. orbiculata* Cumings and Galloway (1913) from the Ordovician (Cincinnatian) Arnheim Formation near Harmon's Station, Indiana, in the size and form of the colonies, and in the arrangement of the diaphragms in the zooecial tubes and mesopores. *M. bulmani* has a greater number of zooecia per 2 mm., fewer and smaller mesopores between the zooecia, and generally smaller acanthopores. *M. bulmani* resembles *M. patella* (Ulrich 1890) from the Ordovician (Cincinnatian) Whitewater Formation, Oxford, Ohio, in having about the same number of zooecia per 2 mm., small acanthopores of about 0·02 mm. diameter, and in the arrangement of diaphragms in the mesopores and zooecial tubes. *M. bulmani* has fewer mesopores between the zooecial openings in smaller colonies.

The species is named in honour of Professor O. M. B. Bulman, Sedgwick Museum, Cambridge.

Genus HOMOTRYPA Ulrich 1882

Type species (by original designation). *Homotrypa curvata* Ulrich (1882, p. 242, pl. 10, figs. 7, 7*a–d*).

Diagnosis. Colonies are ramose and encrusting. Monticules may be present. In tangential sections, wide integrate zooecial walls enclose polygonal or subpolygonal zooecial openings. Acanthopores with dense, concentrically laminate walls commonly occur at the junctions of zooecial walls. Mesopores are sparse and may be present only in clusters. In longitudinal sections zooecial walls are thin in the axial region and thicken in the peripheral region where they display a laminate microstructure. The thick laminae of the diaphragms and cystiphragms pass into the wall laminae and form part of the zooecial walls. These wall laminae are steeply inclined to the boundary of the zooecial tube and laminae of adjacent walls abut in an irregular dark band or line. Cystiphragms and diaphragms are abundant in the peripheral region.

Homotrypa sp. A

Plate 3, figs. 1, 3, 5, 6

Material. Single fragment of a colony in collection WM 1265, from the top of Evenwood Quarry; Hoar Edge Limestone, Hoar Edge Group; Caradoc Series; Ordovician. Figured specimen GSM 102010.

Description. The specimen is part of a ramose colony. In tangential sections polygonal mesopores are distributed around the polygonal and subpolygonal zooecial openings

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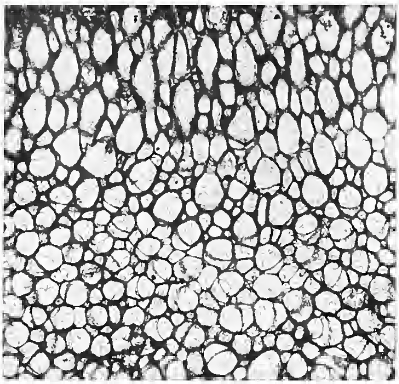
EXPLANATION OF PLATE 3

Figs. 1, 3, 5, 6. *Homotrypa* sp. A. Collection WM 1265, GSM 102010. 1, Tangential section showing general arrangement of zooecial openings and clusters of large zooecia, ×20. 3, Tangential section showing subpolygonal zooecial openings, mesopores, and crescentic lines of cystiphragms curving across zooecia, ×50. 5, Part of an oblique transverse section in the peripheral region showing curved laminate microstructure of zooecial walls, ×50. 6, Part of a longitudinal section in the subperipheral and peripheral regions showing cystiphragms lining the zooecial tubes and diaphragms crossing the zooecial tubes, ×50.

Figs. 2, 4. *Mesotrypa bulmani* sp. nov. 2, Transverse section of a small colony showing the slender zooecial walls and mesopores with closely spaced diaphragms, collection WM 1279, GSM 102014, ×20. 4, Tangential section showing general arrangement of zooecial openings, collection RR 2672, GSM 102017, ×20.

Figs. 7–9. *Homotrypa* sp. B. Collection RR 1481, GSM 102018. 7, Part of an oblique longitudinal section in the peripheral region showing cystiphragms and diaphragms in the zooecial tubes, ×50. 8, General aspect of longitudinal section in peripheral region showing closely spaced diaphragms and cystiphragms in zooecial tubes, ×20. 9, Tangential section showing distinct acanthopores at the junctions of zooecial walls, ×50.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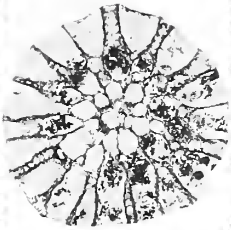
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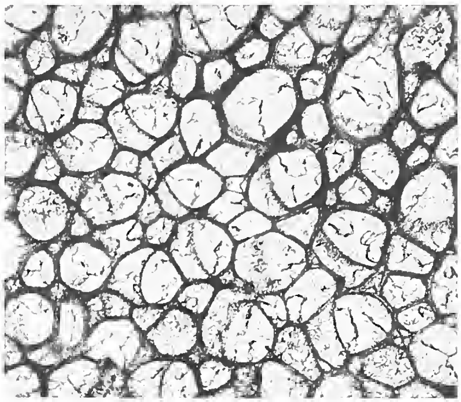
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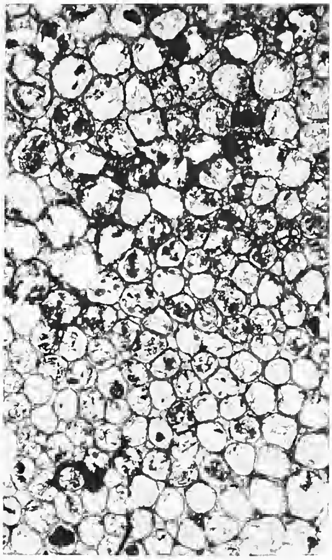
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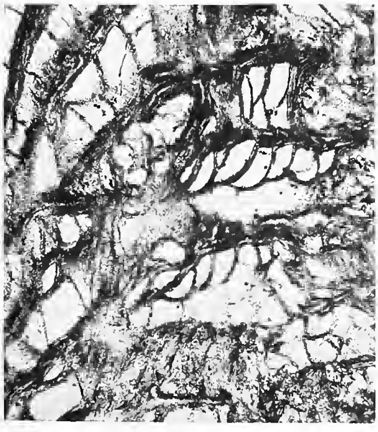
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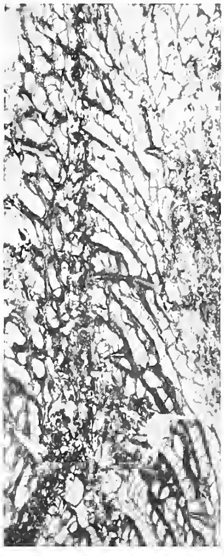
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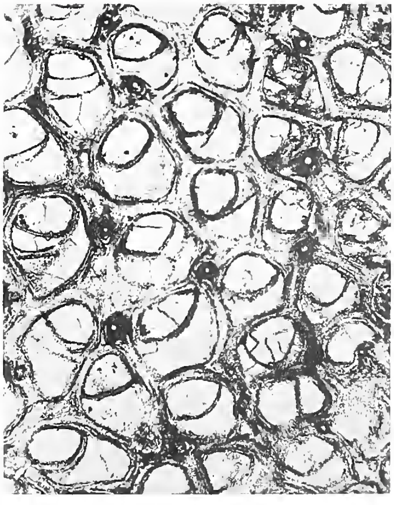
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PHILLIPS ROSS, Ordovician Bryozoa

(Pl. 3, figs. 1, 3). Dense acanthopores are occasionally observed at the junctions of the zooecial walls and they may indent the inner parts of the zooecial walls into the zooecial tubes. Curved cystiphragms cross the zooecial openings (Pl. 3, fig. 3). The zooecial walls are generally integrate but may also appear amalgamate.

In longitudinal sections the zooecial tubes curve in a broad arc and are oblique to the periphery (Pl. 3, fig. 6). In the peripheral region the zooecial walls thicken and display a laminate microstructure. The inner parts of the zooecial and mesopore walls consist of steeply inclined laminae and the laminae of adjacent zooecial walls intertongue and abut in a steeply pitched arc to form a dark, outer band (Pl. 3, fig. 5). Cystiphragms commonly located only on the distal wall in the peripheral region are widely spaced so that adjacent cystiphragms are not always in contact (Pl. 3, fig. 6). Widely spaced, flat diaphragms cross the zooecial tubes in the peripheral region. The mesopores lack diaphragms and acanthopores were not readily observed in longitudinal sections.

TABLE 3

Measurements of *Homotrypa* sp. A (in millimetres)

Catalogue no.		*GSM 102010*
Diameter of zoarial stem		3–5
No. of zooecia per 2 mm.		9–10
Diameter of zooecial opening	max.	0·18×0·16
	min.	0·13×0·13
Combined thickness of adjacent zooecial walls in peripheral region		0·02–0·04
Diameter of mesopore	max.	0·08×0·06
	min.	0·02×0·03
Diameter of acanthopore		0·01
No. of acanthopores per zooecium		0–4
No. of diaphragms per 1 mm. in zooecium in peripheral region		0–2
Width of peripheral region		0·77
Ratio: Width of peripheral region of zooecium/total width of zooecium		0·41

Remarks. The species is characterized by slender, ramose stems in which the peripheral region contains very slender zooecial walls and very few diaphragms and few cystiphragms, the latter generally located on the distal zooecial walls. Acanthopores are sparse, and mesopores are numerous.

Homotrypa sp. A, which is represented by a single specimen in the collections studied, is similar to a rare species, *H. dumosa* Bassler (1903), from the Ordovician (Cincinnatian) Fairmount Member of the Fairview Formation at Covington, Kentucky, and Cincinnati, Ohio. The two species are similar in having slender zooecial walls in the peripheral region and in having few acanthopores, few diaphragms, and few cystiphragms in the peripheral region. Insufficient material does not permit adequate definition of this species from the Hoar Edge Limestone.

Homotrypa sp. B

Plate 3, figs. 7–9

Material. A single fragment of a colony in collection RR 1481, The Wilderness, 18 chains north-west of Wilstone Farm House; Hoar Edge Limestone, Hoar Edge Group; Caradoc Series; Ordovician. Figured specimen GSM 102018.

Description. The specimen is part of a ramose colony with overgrowths. In tangential sections the subpolygonal zooecial openings are crossed by cystiphragms (Pl. 3, fig. 9). Prominent acanthopores with dense, laminate walls and a clear axial region lie at the junctions of the zooecial walls and may project into the zooecial tubes. An occasional acanthopore penetrates the sides of the zooecial walls. Mesopores are rare and, if present, occur as small polygonal structures between the zooecia. The zooecial walls are generally integrate.

In longitudinal sections, which display mainly the peripheral region and only the crushed, delicate walls of the axial region, the zooecial tubes are filled with flat and cystoidal diaphragms and overlapping cystiphragms (Pl. 3, figs. 7, 8). The inner parts of the zooecial walls consist of steeply inclined laminae and laminae of adjacent zooecial walls intertongue in a distally convex arc which extends distally as a dark, rolled band. The thick laminae forming the diaphragms and the cystiphragms pass into the wall laminae. Acanthopores appear as long, clear tubes cutting through the zooecial walls.

TABLE 4

Measurements of *Homotrypa* sp. B (in millimetres)

Catalogue no.		*GSM 102018*
Diameter of zoarial stem		6–9
No. of zooecia per 2 mm.		8–9
Diameter of zooecial opening	max.	0·23×0·22
	min.	0·10×0·10
Combined thickness of adjacent zooecial walls in peripheral region		0·02–0·06
Diameter of mesopore	max.	0·06×0·02
	min.	0·03×0·02
Diameter of acanthopore		0·03–0·05
No. of acanthopores per zooecium		0–2
No. of diaphragms per 1 mm. in zooecium in peripheral region		10–11

Remarks. This species is characterized by a peripheral region which has thick zooecial walls, few but distinct acanthopores, few mesopores, and numerous cystiphragms and diaphragms.

Homotrypa sp. B and *H. obliqua* Ulrich (1882) from the Ordovician (Cincinnatian) Fairmount and Corryville Members at Cincinnati, Ohio, are similar in having about the same number of zooecia per 2 mm., few mesopores, and a similar arrangement of diaphragms and cystiphragms. *Homotrypa* sp. B has larger, more prominent acanthopores. *Homotrypa* sp. B and *H. wortheni* (James 1882; Bassler 1903) from the Whitewater Formation at Oxford, Ohio, and Richmond, Indiana, are similar in having about the same number of zooecia per 2 mm., few mesospores, and thick zooecial walls in the peripheral region. *Homotrypa* sp. B has fewer and more prominent acanthopores.

Insufficient material does not permit adequate definition of this species from the Hoar Edge Limestone.

Acknowledgements. I express my sincere thanks to Dr. C. J. Stubblefield, Director of the Geological Survey of Great Britain, for the loan of the material and for assistance in examining the bryozoan specimens while in London; and to Dr. F. W. Anderson and Mr. J. D. D. Smith, also of the Survey, for generous assistance while examining the collections. I gratefully acknowledge financial support for this study from the National Science Foundation, Washington, D.C., U.S.A.

COLLECTION LOCALITIES

HOAR EDGE LIMESTONE

WM 1262, WM 1265, WM 1267, WM 1273, and WM 1274, from the upper part of Evenwood Quarry at the east end of Black Dick's coppice, 300 yards south of Evenwood, Shropshire: WM 1262 has *Phaenopora stubblefieldi* and *Mesotrypa bulmani*; WM 1274 has *Amplexopora thomasi*, *M. bulmani*, and *P. stubblefieldi*; WM 1267 has *A. thomasi* and *P. stubblefieldi*; WM 1273 has *M. bulmani*, *A. thomasi*, and *P. stubblefieldi*; WM 1265 has *A. thomasi*, *Homotrypa* sp. A, *P. stubblefieldi*, and *Mesotrypa sp.*

WM 1279, from the middle part of Evenwood Quarry at the east end of Black Dick's coppice, 300 yards south of Evenwood, Shropshire: *Amplexopora thomasi* and *Mesotrypa bulmani.*

RR 1481, The Wilderness, 18 chains north-west of Wilstone Farm House, Shropshire: *Homotrypa* sp. B, *Amplexopora? sp.*

RR 2635, RR 2636, RR 2637, and RR 2638, old quarry in the wood near Coundmoor Brook, over ¾ mile south-west of Harnage Grange, Shropshire: *Mesotrypa bulmani.* Locality as indicated by Pocock *et al.* (1938, fig. 28).

RR 2669 and RR 2672, Wylde's Quarry, 30 chains south-west of Harnage Grange, Shropshire: *Mesotrypa bulmani.* Locality as indicated by Pocock *et al.* (1938, fig. 28).

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PLANT MICROFOSSILS FROM THE LOWER TRIASSIC OF WESTERN AUSTRALIA

by B. E. BALME

ABSTRACT. Seventeen species of plant microfossils, made up of nine spores, six pollen grains, and two bodies of uncertain function, are described from the Kockatea Shale, a marine formation of early Triassic age, occurring in the Perth Basin, Western Australia. Nine new species are proposed and a new form genus *Lundbladispora* is instituted to include certain trilete spores of probable lycopodiaceous affinities. Species belonging to the genus *Taeniaesporites* (Leschik) are described for the first time from the southern hemisphere.

Microfloras from the Kockatea Shale differ completely from any known to occur in Australian Permian sediments and are considered to represent a specialized plant community which succeeded the *Glossopteris*-Flora at the end of Permian time. They resemble in some respects Upper Permian and Triassic microfloras from Europe, and Scythian assemblages from the Peace River area in Canada. The palaeofloristic and stratigraphical implications of the palynological data are discussed.

PERMIAN and older rocks in the northern part of the Perth Basin, Western Australia, are, in some places, overlain by the Kockatea Shale, a marine deposit of considerable stratigraphic importance. At two localities it contains ceratitic ammonoids and other marine invertebrate fossils of Lower Triassic (Scythian) age. It is, therefore, the only Triassic sequence in Australia which can so far be dated unequivocally in terms of the Austrian marine standard. The Kockatea Shale consists predominantly of greenish, grey, and red shale with occasional siltstone and sandstone units. It has been known for many years in bores near Geraldton, but its Triassic age was unsuspected until 1957, when Dr. P. E. Playford discovered ammonoids in a core from 1,470 feet in the Geraldton Racecourse Bore. One of these has been identified as an ophiceratid of uppermost Permian or basal Triassic age (Glenister and Furnish 1961). A rich and well-preserved assemblage of spores, pollen grains, and microplankton was recovered from the same core and on the basis of this, a correlation was proposed between the Kockatea Shale and the Blina Shale in the Canning Basin (McWhae, Playford, Lindner, Glenister, and Balme 1957). Refinement of the earlier age determinations became possible in 1959 following the drilling, by the Commonwealth Bureau of Mineral Resources, of a stratigraphic test bore at Beagle Ridge, about 80 miles south of Geraldton. This bore (BMR 10) penetrated over 1,000 feet of Kockatea Shale, and cores from the unit yielded marine faunas at several horizons. Palaeontologists of the Bureau of Mineral Resources, Canberra, are still studying this material, but identifications of some of the key genera have recently been published by Dickins (*in* Dickins, McTavish, and Balme 1961). They include the ophiceratid *Subinyoites* and the pelecypods *Claraia* and cf. *Bakevillia*, and demonstrate the Scythian age of the Kockatea Shale.

Proved exposures of the Kockatea Shale are known only from a small area in the upper reaches of the Greenough River (text-fig. 1) although it may correlate with part of the Chapman Group of Arkell and Playford (1954). It has been recognized in bores at Geraldton, Beagle Ridge, and in the vicinity of Indarra, a small township on the Mullewa road about 45 miles east of Geraldton. In coastal bores the Kockatea Shale has a thickness of up to 1,000 feet, but it thins rapidly to the east of Geraldton and is less

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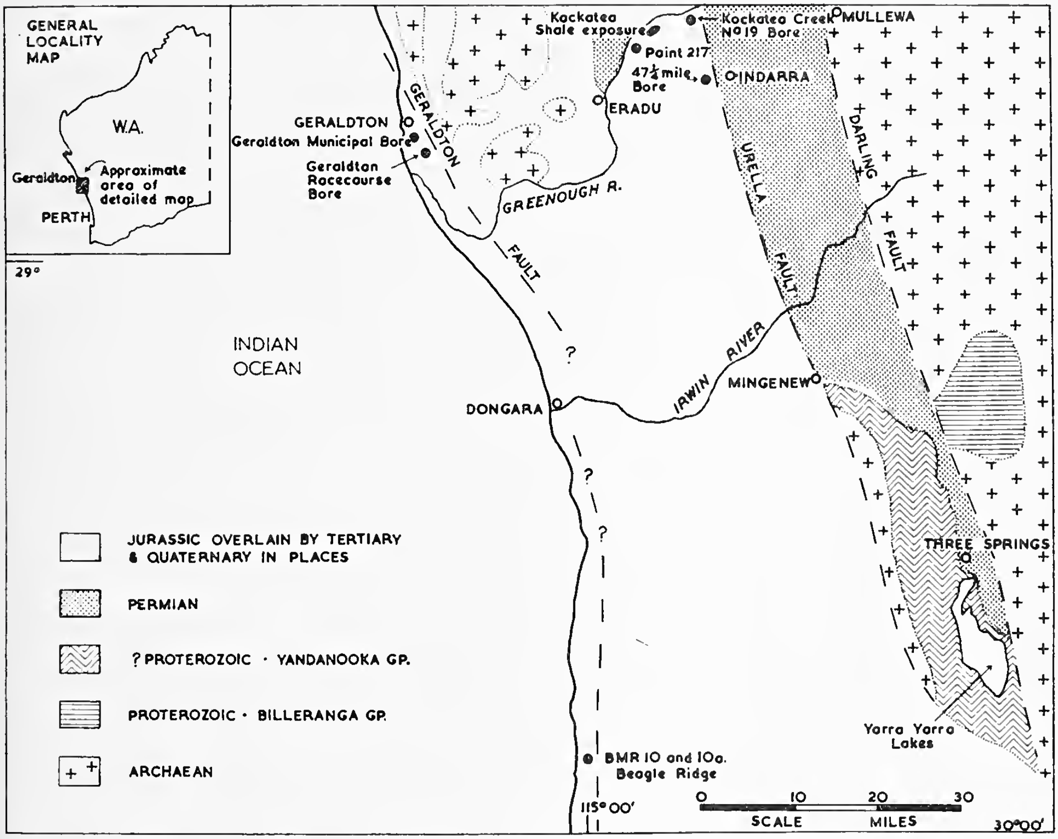
than 300 feet thick in bores close to the Urella Fault. Erosion in the Triassic and Lower Jurassic may partly explain this easterly attenuation but it seems that the Scythian shoreline lay to the west of the present line of the Darling Fault. Spores and pollen grains are most abundant and best preserved in sediments from the Eradu–Indarra district and it is unlikely that these were deposited far from the Lower Triassic coastline.



TEXT-FIG. 1. Generalized geological map of part of the Perth Basin showing localities of the samples examined.

Nevertheless, all samples so far examined from the Kockatea Shale contain hystrichosphaerids, usually in enormous numbers, and there can be little doubt that the unit is marine, even in its easterly occurrences.

Poor exposures and a scarcity of reliable sub-surface data obscure the stratigraphical relationships of the Kockatea Shale. It is clearly transgressive on the Permian, for it overlies Artinskian marine strata in Beagle Ridge Bore and continental Upper Permian sediments at Indarra. Below Geraldton it rests directly on Archaean metasediments.

Triassic beds of probable continental origin overlie the Kockatea Shale in Beagle Ridge Bore; elsewhere it is succeeded by marine or continental Jurassic.

Microfloras from the Kockatea Shale are intrinsically interesting, but their excellent preservation and the precision with which they can be dated, give them an especial stratigraphical and phytogeographical importance. They throw light on the fate of the *Glossopteris*-Flora in Western Australia and can be fairly closely compared with assemblages occurring in Lower Triassic sediments in other parts of the world. The emerging palynological evidence hints, therefore, that plant microfossils may provide a means of placing an upper limit on the Permian System in Australia.

Source and storage of samples. Seventeen samples from the Kockatea Shale provided the material for the present account. They were obtained from five boreholes and a shallow water-well in the northern part of the Perth Basin and their general localities are shown in text-fig. 1. Further details of the samples and their origin are as follows:

Well at Point 217 (28° 34′ 30″ S., 115° 7′ 10″ E.)
  Sample 44070. Pale greenish-grey claystone. Depth 30 ft.
47¼ Mile Peg Bore (28° 39′ 55″ S., 115° 15′ 20″ E.)
  Sample 43813. Greenish-grey shale. Depth 741–749 ft.
  Sample 43815. Pale grey claystone. Depth 808–945 ft.
  Sample 43816. Pale greenish-grey shale. Depth 948–968 ft.
  Sample 43819. Brownish-grey sandy shale. Depth uncertain.
  Sample 43820. Brownish-grey sandy shale. Depth uncertain.
Kockatea Creek No. 19 Bore (28° 33′ 40″ S., 115° 13′ 30″ E.)
  Sample 43305. Pale greenish-grey claystone. Depth 139–190 ft.
Geraldton Racecourse Bore (28° 47′ 36″ S., 114° 39′ 16″ E.)
  Sample 44342. Pale grey claystone. Depth 1,273 ft.
  Sample 44497. Greenish-grey, red-stained, claystone. Depth 1,465 ft.
Geraldton Municipal Bore (28° 46′ 42″ S., 114° 35′ 50″ E.)
  Sample 47563. Pale greenish-grey sandy shale. Depth 1,012–1,096 ft.
  Sample 47564. Yellowish sandy shale. Depth 1,177–1344 ft.
  Sample 47565. Pale greenish-grey calcareous shale. Depth 1,346–1,386 ft.
BMR. 10 (Beagle Ridge) Bore (29° 49′ 38″ S., 114° 58′ 30″ E.)
  Sample 43938. Pale grey sandy siltstone. Depth 2,131–2,141 ft.
  Sample 43939. Grey micaceous shale. Depth 2,223–2,233 ft.
  Sample 43940. Grey micaceous shale with ammonoids. Depth 2,405–2,415 ft.
  Sample 43941. Grey sandy shale. Depth 2,802–2,812 ft.
  Sample 43942. Grey calcareous shale. Depth 3,203–3,213 ft.

Sample numbers in the above list, and throughout the text, refer to the general collection of the Department of Geology, University of Western Australia. Small reference samples of each of the sediments treated are lodged in this repository as are the slides of the type specimens and spore assemblages. The original samples, which provided the source of reference material, are held either by the Commonwealth Bureau of Mineral Resources, Canberra, or by the Geological Survey of Western Australia. Type specimens are mounted singly in glycerine jelly and sealed with bees-wax.

Techniques. Acid insoluble microfossils were extracted by boiling the crushed, carbonate-free sediment in 50 per cent. hydrofluoric acid and treating the residue by the modified Schulze method described by Balme and Hassell (1962). The residues were lightly stained with Safranin 'O' and examined by means of a Leitz 'Ortholux' microscope using a Pl Apo Oel 100/1·32 objective for detailed study of morphography. Photomicrographs were taken on Ilford Pan F film using the same oil immersion objective. They were developed in Kodak D76 and printed on Ilford 'Plastika' paper.

Acknowledgements. The author is indebted to the Director of the Commonwealth Bureau of Mineral Resources, Canberra (Mr. J. M. Rayner), for supplying material from the Beagle Ridge Bore and for permitting publication of the data obtained. The former Government Geologist of Western Australia (Mr. H. A. Ellis) also generously permitted the author access to the collections of the Geological Survey. Thanks are due to the Management of West Australian Petroleum Proprietary Limited, who virtually initiated the investigation and at all times were co-operative and helpful. The author is particularly grateful for the factual information and stimulating discussion provided by two geologists of that Company, Dr. P. E. Playford and Mr. S. P. Willmott. Dr. J. Jansonius, Calgary, Dr. Wilhelm Klaus, Vienna, and Mr. N. F. Hughes, Cambridge, have been patient and helpful correspondents, and the photomicrographs are the work of Mr. K. Bauer.

SYSTEMATIC PALYNOLOGY

With the exception of a short paper by Hennelly (1958) and the recent contribution on megaspores by Dettmann (1961), no formal papers have been published on Australian Triassic palynology. Preliminary descriptions of microfloras from the Leigh Creek and Ipswich coals have been presented by Taylor (1953) and de Jersey (1949) respectively, but neither of these authors attempted to apply a binomial nomenclature to their plant microfossils. In the northern hemisphere, however, palynologists have been increasingly occupied with Upper Permian and Triassic sediments during the past five or six years, and papers from Russia, western Europe, and North America have proved surprisingly relevant to the present account. Malyavkina (1953) was the first to describe a varied assemblage of Triassic spores. These came from the Keuper of the Russian Pre-Urals, but Malyavkina used no photographs and adopted a rather informal taxonomy. Her account is, therefore, less useful as a systematic reference than the subsequent papers of Potonié and Klaus (1954), Leschik (1955, 1956), Klaus (1960), and Jansonius (1962).

Leschik's papers are well illustrated and provide a basis for the classification and comparison of isolated spores and pollen grains of Triassic age. Nevertheless, they contain certain nomenclatural inconsistencies, and some of the new genera and species proposed were poorly defined or based on misinterpretation of morphographic features. Critical revision of Leschik's systematics has been undertaken by Potonié (1958), Klaus (1960), and Jansonius (1962), but no stable taxonomy has yet evolved. This applies particularly to the classification of disaccate pollen grains assignable to the Infraturma Striatiti of Pant. Further discussion of this and other taxonomic problems will be found in subsequent sections of the present paper.

Taxonomic criteria are based on the publication of Potonié and Kremp (1954), and subsequent papers by Potonié. Certain of the suprageneric form taxa proposed by Potonié and Kremp and later authors have also been adopted. However, no attempt has been made to apply the all-embracing scheme of higher form categories favoured by many recent workers. This system has certain advantages in bringing apparent order to the bewildering variety of trilete spores in Upper Devonian and Carboniferous microfloras. Nevertheless, it seems unwise, at this stage of our knowledge of the morphology and affinities of fossil spores, to obscure possible natural relationships by over-rigid codification.

Terminology. With few exceptions morphographic terms have been taken from the glossaries provided by Potonié and Kremp (1955) and Couper (1958). *Amb* was defined by Erdtman as the outline of a spore or pollen grain viewed from the direction of the polar axis, and the term *cavate* is used in the sense of Dettmann (1961), to describe a spore in which the exoexine and intexine have become detached.

Measurements, unless otherwise stated, are taken on specimens preserved in full polar view, and the dimensional nomenclature is based on that of Couper (1958, text-fig. 7, p. 101).

Anteturma SPORITES H. Potonié

Turma TRILETES Reinsch

Genus PUNCTATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. Punctatisporites punctatus Ibrahim, Upper Carboniferous, West Germany.

Punctatisporites fungosus sp. nov.

Plate 4, figs. 10, 11

Holotype. Slide 47544. *Paratype.* Slide 47545.

Diagnosis. Amb circular, periphery smooth, off-polar compressions common and exine frequently ruptured. Trilete, scar distinct, laesurae straight and often of unequal length but seldom extending more than about half-way to the equatorial margin. Groove of commissure visible in some specimens. Exine very thick, with fine irregularly distributed pits visible under oil immersion. Narrow anastomosing pits and channels sometimes developed, particularly in the area of the proximal pole (Pl. 4, fig. 11). These channels are probably due to partial destruction of the exine, either during fossilization or as a result of the maceration process.

Dimensions. Diameter 83–119 μ; 15 specimens.

Locus typicus. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. Latin *fungosus* = 'spongy', from the texture of the exine.

Description. Holotype diameter 114 μ in slightly off-polar view. Exine 6–7 μ thick with irregularly disposed shallow pits less than 1 μ in diameter. The pitting is slightly more pronounced in the vicinity of the proximal pole.

Remarks and comparisons. Punctatisporites fungosus may be distinguished from the Lower Permian species *P. gretensis* Balme and Hennelly by its larger size and relatively thicker, finely pitted exine. It occurred, usually in small numbers, in all the samples examined and has also been found in the Blina Shale (Canning Basin, Western Australia).

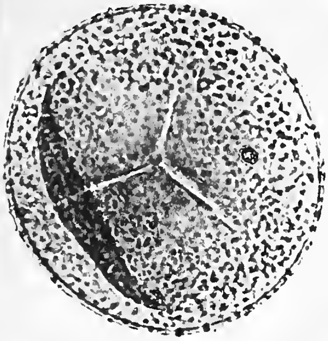
Known stratigraphical range in Australia. Lower Triassic.

Genus OSMUNDACIDITES Couper 1953

Type species. Osmundacidites wellmanii Couper, Upper Jurassic, New Zealand.

EXPLANATION OF PLATE 4

Magnifications ×600
Figs. 1–2. *Osmundacidites senectus.* 1, Holotype. 2, Paratype 47542.
Fig. 3. *Tetraporina sp.* cf. *Azonotetraporina? horologia* Staplin.
Figs. 4–5. cf. *Schizosporis sp.*
Fig. 6. *Lycopodiacidites pelagius,* holotype.
Fig. 7. *Lycopodiacidites sp.*
Figs. 8–9. *Lundbladispora brevicula.* 8, Paratype 47547. 9, Holotype.
Figs. 10–11. *Punctatisporites fungosus.* 10, Holotype. 11, Paratype, showing pitted and channelled exine.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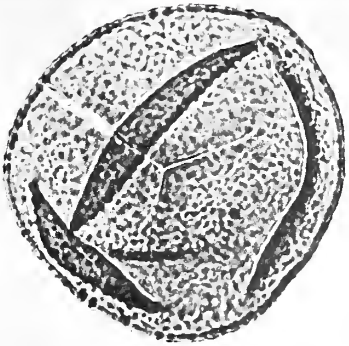
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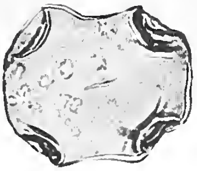
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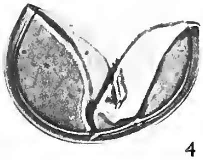
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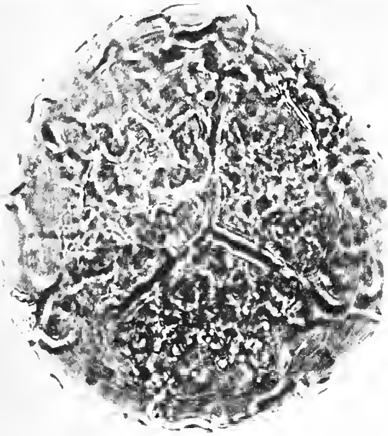
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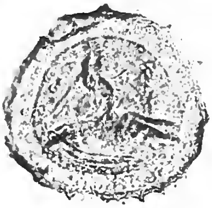
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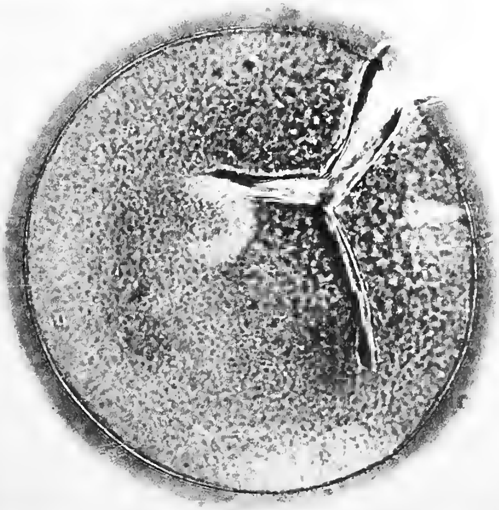
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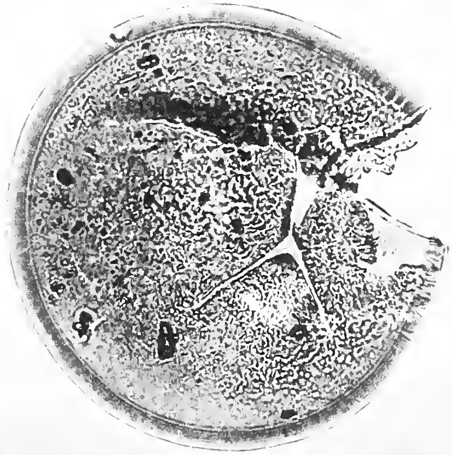
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BALME, Triassic plant microfossils

Osmundacidites senectus sp. nov.

Plate 4, figs. 1, 2

Holotype. Slide 47541. *Paratypes.* Slides 47542 and 47543.

Diagnosis. Amb circular, periphery finely notched. Trilete, scar distinct, laesurae straight and extending about three-quarters of the distance to the distal margin. Exine 1–2 μ thick, sculptural elements small and varied, including cones, grana, and sub-baculate processes. Basal diameter of individual processes 1–3 μ, height 1–2 μ. Off-polar compressions common, suggesting that the spore was originally spherical, and the flattened exine usually has one or more broad, crescentic, folds.

Dimensions. Diameter 58–79 μ; 25 specimens.

Locus typicus. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. Latin *senectus* = 'aged'.

Description. Holotype preserved in full polar view. Diameter 72 μ, exine about 2 μ thick with irregularly distributed but fairly closely spaced sculptural elements. Among these, short cones predominate but grana and sub-baculae also occur; eighty-nine processes were counted around the periphery. In the holotype sculptural elements were less prominent in the region of the proximal pole, but this reduction was not obvious in the paratypes.

Remarks and comparisons. This species is assigned to *Osmundacidites* because of the variability in form of its sculptural elements and its general conformity with Couper's diagnosis. Some hesitation is felt in extending so considerably the stratigraphical range of a 'half-natural' genus, but Klaus (1960) has assigned Carnian spores to *Osmundacidites* and the known antiquity of the family Osmundaceae may be invoked in justification of the use of Couper's genus.

Osmundacidites senectus has finer and more regular sculptural elements than *O. wellmanii* Couper or *O. comaumensis* (Cookson) and is larger than *O. alpina* Klaus. It is fairly common in most samples from the Kockatea Shale and occurs also in the Blina Shale and in the Erskine Sandstone, a continental Triassic formation which overlies the Blina Shale. Occasional specimens have also been found in sediments from the Narrabeen Group in New South Wales.

Known stratigraphic range in Australia. Lower to (?) Middle Triassic.

Genus LYCOPODIACIDITES (Couper) R. Potonié 1956

Type species. Lycopodiacidites bullerensis Couper, Upper Jurassic, New Zealand.

Lycopodiacidites pelagius sp. nov.

Plate 4, fig. 6

Holotype. Slide 47551. *Paratype.* Slide 47550.

Diagnosis. Amb subtriangular to circular, periphery undulate. Trilete, scar clearly defined, laesurae straight and extending about three-quarters of the distance to the equatorial margin. Exine 4–7 μ thick on the distal side, slightly thinner on the proximal. Proximal face smooth or slightly rugulose. Distal face sculptured into low, rounded, irregular and rather indistinct ridges. Ridges 2–7 μ wide and 1–3 μ high, occasionally anastomosing to form a crude reticulum but usually separate from one another, giving the distal surface an irregular rugose pattern.

Dimensions. Diameter 86–100 μ; 10 specimens.

Locus typicus. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. Latin *pelagius* = 'pertaining to the sea', from the wavy appearance of the distal surface.

Description. Holotype diameter 97 μ, exine 6–8 μ thick, measured in optical section along the equatorial margin. Laesurae about 35 μ long and closed along their entire length. Distal ridges 1–3 μ high and 3–6 μ wide, occasionally anastomosing and enclosing rounded lumina.

Remarks and comparisons. Lycopodiacidites kuepperi Klaus, from the Upper Triassic of Austria, is slightly smaller and has more clearly defined distal rugae. *L. pelagius* was not common in the Kockatea Shale, but occasional specimens were recognized in most samples. It has not been found in any other deposit.

Known stratigraphic range in Australia. Lower Triassic.

Lycopodiacidites sp.

Plate 4, fig 7

Figured specimen. Slide 47557.

Description. Amb strongly rounded triangular, periphery undulate. Trilete, scar strongly defined, laesurae extending about half-way to the equatorial margin. Edges of laesurae turned outwards forming a triangular opening at the proximal pole. Exine about 6 μ thick, with an indistinctly rugose distal surface; proximal face perforate. Perforations less than 1 μ in diameter, irregularly distributed, and particularly concentrated around the proximal polar area.

Dimensions. Diameter 79–91 μ; 5 specimens.

Locality of figured specimen. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

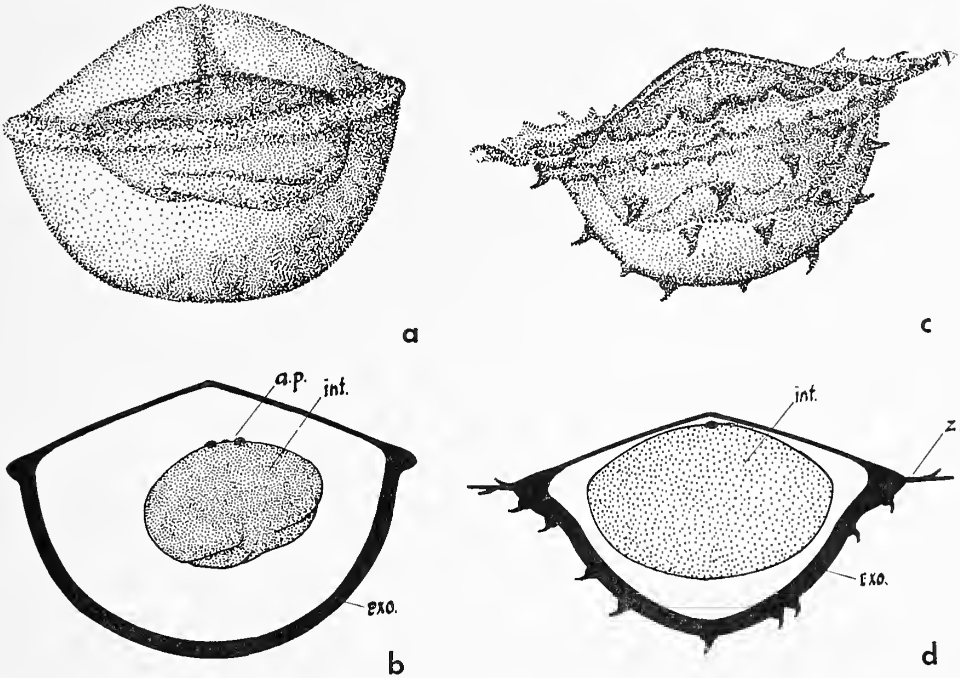
Remarks and comparisons. Lycopodiacidites sp. may represent *L. pelagius* in a corroded condition, but it was too rare adequately to assess this possibility. It has not therefore been named formally, but specimens maintaining the characters described above occurred sporadically in several of the assemblages.

Known stratigraphic range in Australia. Lower Triassic.

Genus KRAEUSELISPORITES (Leschik) Jansonius 1962

Type species. Kraeuselisporites dentatus Leschik, Keuper, Switzerland.

Generic name. The inclusion of *Kraeuselisporites* in the Unterabteilung Zonaletes by Leschik (1955) has led to difficulties in the application of his generic name. It was rejected by Klaus (1960, p. 142), in favour of *Styxisporites* Cookson and Dettmann, on the ground that Leschik's description and interpretation were incorrect. Certainly the original diagnosis of *Kraeuselisporites* was inadequate but the illustrations were fairly clear, and, as Jansonius has noted, a weak trilete scar is visible on some of Leschik's figured specimens. *Styxisporites* and *Kraeuselisporites* have a similar structure, but the form of the flange and lips seems to provide a means of distinguishing between the two genera. In *Styxisporites* the flange is translucent to almost transparent and clearly delimited from the central body, and the prominent laesurae are bordered by fairly strong lips.



TEXT-FIG. 2. *a*, *Lundbladispora playfordi* gen. et sp. nov. lateral view. *b*, *L. playfordi* diagrammatic section parallel to the polar axis. *c*, *Kraeuselisporites cuspidus* sp. nov., lateral view. *d*, *K. cuspidus* diagrammatic section parallel to polar axis. All ×800 approx. *a.p.* apical papillae; *exo.* exoexine; *int.* intexine.

Kraeuselisporites cuspidus sp. nov.

Plate 5, figs. 9, 10, 11; text-figs. 2*c*, *d*

Holotype. Slide 47552. *Paratypes.* Slides 47553 and 47554.

Diagnosis. Amb rounded triangular, periphery dentate. Exine cavate consisting of a zonate exoexine enclosing a thin intexine. Trilete, scar weak but usually clearly visible, laesurae extending to the inner margin of the zona. Distal side hemispherical, proximal flattened pyramidal. Exoexine 2–3 μ thick on distal side and 1 μ or less on the proximal.

Surface of exoexine (including zona) scabrate; distal surface and zona bearing heavy irregularly disposed spines 5–10 μ long, 5–6 μ in basal diameter, and 3–15 μ apart. Intexine thin, smooth, partially or completely detached from the exoexine, and usually folded.

Dimensions. Total diameter 71–112 μ, width of zona 9–25 μ; 25 specimens.

Locus typicus. Kockatea Creek No. 19 Bore, 139–190 ft. (sample 43305), Upper Greenough River area, Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. Latin *cuspis* = 'a point'.

Description. Holotype diameter 91 μ, zona 12–16 μ wide. Distal surface and zona bearing about forty heavy spines. Spines about 8 μ long with a basal diameter ranging from 3 to 5 μ. In the holotype the intexine is detached from the exoexine but unfolded. Paratype 47553 has a zona of irregular width and a shrunken, rather crumpled intexine.

Remarks and comparisons. Kraeuselisporites cuspidus is much larger than any of the forms of *Kraeuselisporites* described by Leschik. *Styxisporites cooksonae* Klaus is of comparable size, but its spines are confined to the distal surface and do not occur on the zona. *K. apiculatus* Jansonius is smaller and has more numerous spines than *K. cuspidus.*

Kraeuselisporites cuspidus was recorded from all the samples examined but was generally most common in material from the Upper Greenough River–Indarra area. It occurs also in the Blina Shale but undoubted specimens have not been recognized in other Triassic deposits. Other species of *Kraeuselisporites* occur in the Australian Permian.

Known stratigraphic range in Australia. Lower Triassic.

Kraeuselisporites saeptatus sp. nov.

Plate 6, figs. 8, 9, 10

Holotype. Slide 47549. *Paratypes.* Slides 47555, 47556, and 47561.

Diagnosis. Amb rounded triangular, periphery slightly ragged. Exine cavate consisting of a zonate exoexine enclosing a thin intexine. Trilete, scar usually distinct, laesurae straight with weak lip development visible on some specimens and extending to the inner margin of the zona. Distal hemisphere strongly inflated, proximal face forming a low pyramid (see Pl. 6, fig. 8). Exoexine 2–3 μ thick on the distal side, less than 1 μ thick on the proximal. Surface of exoexine (including zona) scabrate with a 'scaly' texture,

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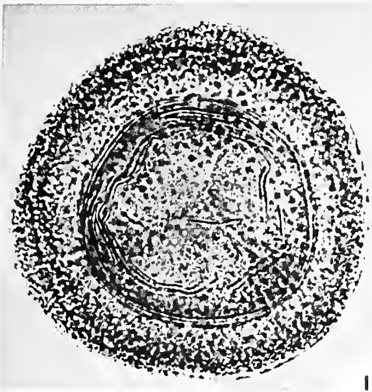
EXPLANATION OF PLATE 5

Magnifications ×600, except fig. 7.

Figs. 1–3. *Lundbladispora willmotti.* 1, Holotype, distal surface showing sculpture. 2, Holotype, proximal surface. 3, Paratype 47533, showing ruptured proximal face and spinose sculpture.

Figs. 4–8. *L. playfordi.* 4, Holotype. 5, Paratype 47838, with indistinct scar and faint apical papillae. 6, Paratype 47536, small specimen with slight lip development. 7, Specimen dissected intexine showing apical papillae. ×700. 8, Adherent tetrad showing free intexine and equatorial thickening, Paratype 47539.

Figs. 9–11. *Kraeuselisporites cuspidus.* 9, Holotype. 10, Paratype 47553, with irregular zona. 11, Paratype 47554.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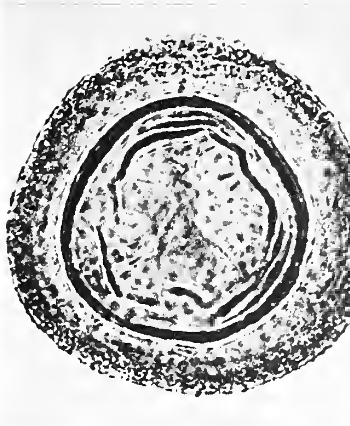
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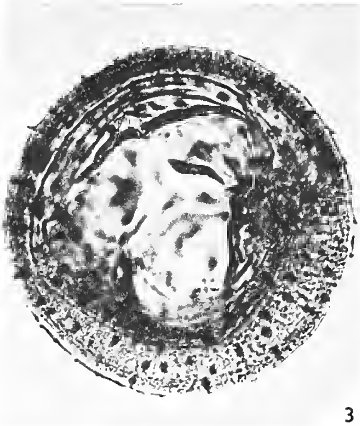
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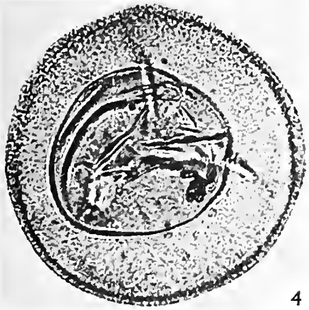
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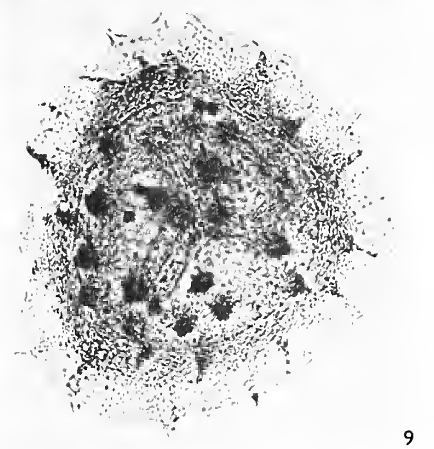
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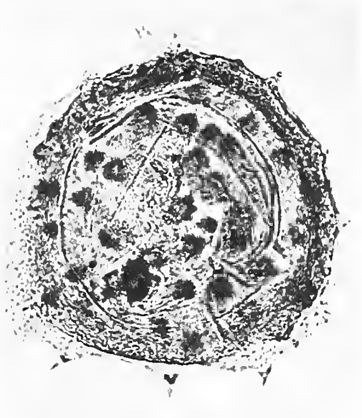
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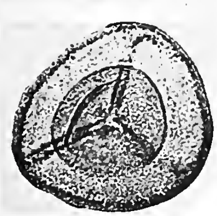
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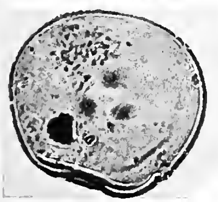
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11

BALME, Triassic plant microfossils

irregularly disposed grana sometimes present on the distal hemisphere. Zona gradually becoming thinner towards its outer periphery. Intexine thin, smooth, with occasional fine marginal folds but rarely crumpled.

Dimensions. Diameter 51–76 μ, width of zona 6–18 μ; 25 specimens.

Locus typicus. Geraldton Racecourse Bore, 1,465 ft. (sample 44497), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. Latin *saeptum* = 'an enclosure'.

Description. Holotype diameter 72 μ, zona 10–13 μ wide, diameter of intexine 42 μ. Intexine weakly folded around its margin and probably still adhering to the exoexine on the proximal side. Paratype 47555 is preserved in lateral view and has a polar diameter of 53 μ.

Remarks and comparisons. Kraeuselisporites saeptatus differs from any species previously assigned to *Kraeuselisporites* in its lack of distinct sculptural elements. However, Jansonius (1962) has included in the genus forms with weakly developed distal grana (cf. *K. punctatus* Jansonius) and the present assignation does not seem an undue extension of his interpretation of *Kraeuselisporites.* Eventually it may become expedient to create a new form genus for unsculptured forms of the *K. saeptatus*-type, but this has been deferred here in order to avoid excessive monotypy.

In lateral compressions *K. saeptatus* is easily distinguished from *Densosporites* by its strongly inflated distal hemisphere and flattened proximal surface. *Simplicisporites laciniatus* Leschik appears, from the original illustration (Leschik 1955, pl. 5, fig. 5), to have a similar structure to *K. saeptatus,* and so do the two forms referred to *Aequitriradites* by Nilsson (1958, p. 47). Rogalska (1956, pl. 31) also has illustrated comparable types from the Liassic of Poland.

Kraeuselisporites saeptatus is one of the most common species in the Kockatea Shale, especially in the sediments from BMR 10 (Beagle Ridge) Bore. It occurs also in the Blina Shale.

Known stratigraphical range in Australia. Lower Triassic.

Genus LUNDBLADISPORA gen. nov.

Type species. Lundbladispora willmotti sp. nov., Lower Triassic, Western Australia.

Diagnosis. Trilete spores with a maximum diameter of less than about 150 μ. Exine cavate with a finely structured exoexine enclosing a thin-walled intexine. Exoexine thinner on the proximal than on the distal side and with a narrow equatorial thickening. Surface of exoexine scabrate with a spongeous appearance. Distal side devoid of sculpture or bearing small cones, spines, or grana. Sculptural elements absent or considerably reduced on the proximal surface. Intexine thin-walled, smooth, with three apical papillae (cf. Bharadwaj 1958) in the area of the proximal pole. Intexine often eccentrically placed with respect to the equatorial margin of the exoexine.

Remarks and comparisons. The distinctive characters of *Lundbladispora* are as follows:

(*a*) The relatively thick finely textured exoexine with an equatorial thickening.

(*b*) The presence of a thin, frequently eccentrically placed, papillate intexine.
(*c*) Virtual restriction of sculptural elements, when they occur, to the distal surface and equatorial region.

Dispersed megaspores of comparable structure to *Lundbladispora* have been described from Palaeozoic and Mesozoic sediments and assigned to a number of form genera. These include *Duosporites* Høeg, Bose, and Manum, *Banksisporites* Dettmann, and *Bacutriletes* (van der Hammen). Few previously described microspores closely resemble *Lundbladispora*, but a possible exception is *Aculeisporites variabilitis* Jansonius, which possesses a papillate intexine and a finely granulose and spinose exoexine. Microspores illustrated by Lundblad (1948) from the Lower Triassic of Greenland appear indistinguishable from *Lundbladispora playfordi*; they were associated with the lycopodiaceous strobilis *Selaginellites polaris* and may be its microspores.

Cavate exines occur frequently in the spores of modern species of *Selaginella* (Knox 1950, Harris 1955) and they are known also in fossil spores obtained from lycopodiaceous strobili (Lundblad 1948, 1950, Bharadwaj 1958). Another lycopodiaceous character of *Lundbladispora* is the restriction of sculptural elements to the distal face (see Couper 1958, p. 105). In so far as one is justified in inferring affinities from spore morphography the evidence favours lycopodiaceous, and possibly selaginellid, affinities for *Lundbladispora*.

The genus is named after Dr. B. Lundblad, Stockholm University, in recognition of her contributions to our knowledge of Triassic floras.

Lundbladispora willmotti sp. nov.

Plate 5, figs. 1, 2, 3

Holotype. Slide 47532. *Paratypes*. Slides 47533, 47534.

Diagnosis. Amb circular or strongly rounded triangular, periphery spinose, exine cavate. Trilete, scar indistinct, laesurae poorly defined, extending about two-thirds of the distance to the equatorial margin. Exoexine 4–6 μ thick on the distal side, about 1 μ thick, and sometimes ruptured, on the proximal. Slightly depressed contact areas sometimes visible on the proximal face. Exoexine scabrate, distal surface and narrow equatorial thickening ornamented with cones or spines. Sculptured elements 1–2 μ in basal diameter, 1–3 μ long and 1–10 μ apart, absent or much reduced in size on the proximal face. Intexine smooth and thin-walled, bearing weak tetrad markings with three apical papillae, one in each inter-radial area.

Dimensions. Total diameter 71–86 μ, diameter of intexine 49–65 μ; 25 specimens.

Locus typicus. Kockatea Creek No. 19 Bore, 139–190 ft., Upper Greenough River area (sample 43305), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. After Mr. S. P. Willmott, geologist of West Australian Petroleum Pty. Ltd.

Description. Holotype diameter 78 μ, diameter of intexine 53 μ. Proximal face extremely thin and translucent, bearing a faint, slightly sinuous tetrad scar. Sculptural elements 2 μ in basal diameter, 1–3 μ high and irregularly disposed. In paratype 47533 the proximal face is ruptured and the spines are fewer and more prominent, ranging up to 6 μ long.

Paratype 47534 is preserved in semi-lateral view and has a total diameter of 86 μ and a polar diameter of about 81 μ.

Remarks and comparisons. Lundbladispora willmotti is distinguished from *L. playfordi* by its spinose sculpture, larger size, and the coarser texture of its exoexine. It was present in all samples from the Kockatea Shale and occurs also in the Blina Shale.

Known stratigraphical range in Australia. Lower Triassic.

Lundbladispora playfordi sp. nov.

Plate 5, figs. 4–8; text-fig. 2*a*, *b*

Holotype. Slide 47537. *Paratypes.* Slides 47538, 47536, and 47839 (tetrad).

Diagnosis. Amb circular or strongly rounded triangular, periphery smooth, exine cavate. Trilete, scar indistinct or clearly defined, lips sometimes present, laesurae straight or slightly curved, length variable but usually extending almost to the equatorial margin. Exoexine scabrate, 2–4 μ thick on the distal face, slightly thinner on the proximal, thickened equatorially in a zone about 3–5 μ wide. Intexine thin, smooth, frequently folded, and bearing three apical papillae in the region of the proximal pole (Pl. 5, fig. 7). In polar compressions the intexine is usually eccentrically placed with respect to the equatorial margin of the exoexine. Exoexine and intexine detached (Pl. 5, fig. 8).

Dimensions. Total diameter 40–71 μ, diameter of intexine 24–48 μ; 25 specimens.

Locus typicus. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. After Dr. P. E. Playford, now of the Geological Survey of Western Australia.

Description. Holotype diameter 66 μ, diameter of intexine 42 μ, equatorial thickening 2–3 μ wide. Laesurae poorly defined, 20–22 μ long, and curved. Paratype 47839 consists of four spores in an adherent tetrad; these show the species to be biconvex with a polar diameter of about 60 μ. In Paratype 47838 the tetrad scar is scarcely visible but the proximal face is ruptured, exposing the papillate intexine.

Remarks and comparisons. Lundbladispora playfordi was abundant in all the samples examined from the Kockatea Shale and has also been found in the Blina Shale and rarely in the Erskine Sandstone. Its resemblance to spores from the Lower Triassic of Greenland has already been noted, but no other obviously similar forms have been previously described. *Endosporites papillatus* Jansonius has a detached, papillate intexine, but the Canadian species is said to have an extremely thin exoexine and is devoid of equatorial thickening.

Known stratigraphical range in Australia. Lower to (?) Middle Triassic.

Lundbladispora brevicula sp. nov.

Plate 4, figs. 8, 9

Holotype. Slide 47546. *Paratypes.* Slides 47547 and 47548.

Diagnosis. Amb rounded triangular, periphery spinose, exine cavate. Trilete, scar distinct, laesurae curved or sinuous, with narrow elevated lips and extending almost to the equatorial margin. Exoexine 2–3 μ thick on distal side, 1 μ or less on the proximal with an equatorial zone of thickening 2–4 μ wide. Surface of the exoexine finely spongeous; ornamented on the distal side and along the equatorial margin, with sparsely distributed cones and spines. Sculptural elements about 2 μ in basal diameter, 1–4 μ high. Intexine thin, smooth and with three faint apical papillae sometimes visible. The intexine is never notably eccentric and is apparently attached proximally to the exoexine.

Dimensions. Total diameter 41–56 μ, diameter of intexine 29–39 μ; 20 specimens.

Locus typicus. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. Latin *breviculus* = 'rather small'.

Description. Holotype diameter 51 μ, diameter of intexine 36 μ. Laesurae sinuous with raised lips about 2 μ wide on either side of the commissure. Sculpture consists of about sixty irregularly disposed cones and spines, 1–3 μ in basal diameter and 2–4 μ high. Except for slight size differences the paratypes show little variation from the holotype.

Remarks and comparisons. Lundbladispora brevicula is distinguished from *L. willmotti* by its smaller size, prominent tetrad scar, and relatively larger spines. It was present in all the samples examined and most common in material from the Upper Greenough River area. The only other Australian sediment in which it is known to occur is the Blina Shale.

Known stratigraphical range in Australia. Lower Triassic.

Anteturma POLLENITES R. Potonié
Turma SACCITES Erdtman
Subturma DISACCITES Cookson

Genus VITREISPORITES Leschik 1955 (= *Caytonipollenites* Couper 1958)

Type species. Vitreisporites signatus Leschik, Keuper, Switzerland.

Vitreisporites pallidus (Reissinger) Nilsson 1958

Plate 6, fig. 7

1938 *Pityopollenites pallidus* Reissinger, *Palaeontographica*, **84B**, 84.
1950 *Pityosporites pallidus* (Reiss.) Reissinger, *Palaeontographica*, **90B**, 109; pl. 15, figs. 1–5.
1958 *Caytonipollenites pallidus* (Reiss.) Couper, p. 150; pl. 26, figs. 7–8.
1958 *Vitreisporites pallidus* (Reiss.) Nilsson, p. 78; pl. 7, figs. 12–14.

Figured specimen. Slide 47529.

Description. Disaccate pollen grain. Central body elongate oval, proximal face infragranulate, distal germinal area smooth and very thin. Sacci microreticulate, slightly inclined distally, and a little longer than the central body.

Dimensions. Length of body 16–25 μ, breadth of body 12–21 μ, total breadth of grain 26–40 μ; 4 specimens.

Locality of figured specimen. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Remarks and comparisons. In form and size these Triassic specimens fall within the range of Couper's diagnosis of *Caytonipollenites pallidus.* Quantitatively the species is unimportant in the Kockatea Shale, but has been recorded because of its possible palaeobotanical interest. *Vitreisporites* was described by Jansonius from the Scythian of Canada, but in Europe the oldest clear record is in Keuper strata (Leschik 1955). Pollens similar to *Vitreisporites pallidus* occur rarely in Upper Permian strata in the Canning Basin, but are not common before the Lower Jurassic.

Known stratigraphical range in Australia. Upper Permian to Lower Cretaceous.

Genus PLATYSACCUS (Naumova) R. Potonié and Klaus 1954

Type species. Platysaccus papilionis R. Potonié and Klaus, Zechstein, Austria.

Platysaccus sp. cf. *P. papilionis* R. Potonié and Klaus 1954

Plate 6, fig. 12

1954 *Platysaccus papilionis* R. Potonié and Klaus, p. 539; pl. 10, figs. 11, 12.
1955 *Lueckisporites fusus* [pars] Balme and Hennelly, p. 92; pl. 1, figs. 6, 9.

Figured specimen. Slide 47527.

Description. Disaccate, strongly diploxinoid pollen grain. Central body subcircular, thick-walled, proximal surface smooth or slightly rugulose. Sacci much larger than the central body, microreticulate, attached distally with their inner bases separated by a narrow germinal area.

Dimensions. Diameter of central body 47–53 μ, length of sacci 71–87 μ, total breadth of grain 104–127 μ; 8 specimens.

Locality of figured specimen. Kockatea Creek No. 19 Bore, 139–190 ft., Upper Greenough River area (sample 43305), Western Australia. Kockatea Shale, Lower Triassic.

Remarks and comparisons. Platysaccus cf. *papilionis* falls within the broad limits proposed for the original species by Potonié and Klaus. It occurred sporadically in the Kockatea Shale and provides one of the few links between Permian and Triassic microfloras in Western Australia.

Platysaccus papilionis has been recorded by Jansonius from the Scythian of Canada and by several authors from the European Zechstein. Pollen grains of apparently similar structure occur also in the Polish Liassic (Rogalska 1956, pl. 21, fig. 1).

Known stratigraphical range in Australia. Lower Permian to (?) Middle Triassic.

Infraturma STRIATITI Pant

Genus STRIATITES (Pant) Pant 1955

Type species (designated by Pant). *Pityosporites sewardi* Virkki, Upper Permian, New South Wales, Australia.

Generic name. Striatites is one of the genera assigned by Potonié (1958) to the Infraturma Striatiti which includes all fossil, disaccate pollen grains bearing transverse bands of exoexinal thickening on their proximal faces. Such pollen grains are particularly characteristic of Permian microfloras from the 'Gondwanaland' countries and are common also in Permian and Triassic sediments from the northern hemisphere. Because of their great variety and abundance it is difficult to establish a satisfactory systematic scheme for the Striatiti and many ill-conceived and inapplicable taxa have appeared in palynological literature. It is obvious that the taxonomy of the whole group needs revision, but this cannot be attempted without considering the great diversity of Permian forms. In the present account the generic name *Striatites* is used to accommodate members of the Striatiti with well-developed sacci and more than about six bands of proximal thickening. It therefore includes forms which Potonié placed in *Striatites*, *Lunatisporites*, and *Striatopodocarpidites*.

Striatites sp. cf. *Taeniaesporites antiquus* Leschik 1956

Plate 6, fig. 13

1956 *Taeniaesporites antiquus* Leschik, p. 134; pl. 22, fig. 4.

Figured specimen. Slide 47526.

Description. Disaccate, sacci joined equatorially in some specimens, haploxinoid pollen grains. Central body oval in polar view. Proximal face of central body bearing about fifteen transverse bands of exoexinal thickening separated by narrow clefts in which the intexine is exposed. Proximal bands scabrate and 5–9 μ wide. Sacci fairly large, attached and inclined distally, separated on the distal side by a thin germinal area consisting of exposed intexine. Sacci microreticulate with clearly defined, slightly radially elongate lumina.

Dimensions. Length of body 76–114 μ, breadth of body 58–88 μ, length of sacci 81–116 μ; breadth of sacci 49–61 μ; 5 specimens.

Locality of figured specimen. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Remarks and comparisons. In its large size and occasional pseudo-monosaccate appearance *Striatites sp.* resembles *Lueckisporites richteri* Klaus from the German Zechstein. However, Klaus's species has heavier and better-defined proximal thickenings. The specimens of *Taeniaesporites antiquus* illustrated by Leschik look similar to some examples of *Striatites sp.*, but Leschik's diagnosis is imprecise and detailed comparisons are not possible.

EXPLANATION OF PLATE 6

Magnifications ×600, except fig. 13.

Figs. 1–3. *Taeniaesporites obex*. 1, Holotype, proximal side. 2, Holotype, distal side. 3, Paratype 47558, showing transverse, proximal scar.

Figs. 4–6. *Taeniaesporites sp.* cf. *T. noviaulensis* Leschik.

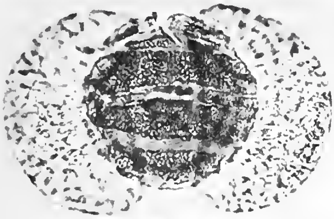
Fig. 7. *Vitreisporites pallidus* (Reissinger).

Figs. 8–10. *Kraeuselisporites saeptatus*. 8, Holotype. 9, Paratype 47555, lateral view. 10, Specimen showing outline of the intexine.

Fig. 11. *Crustaesporites sp.*

Fig. 12. *Platysaccus sp.* cf. *P. papilionis* Potonié and Klaus.

Fig. 13. *Striatites sp.* cf. *Taeniaesporites antiquus* Leschik. ×440.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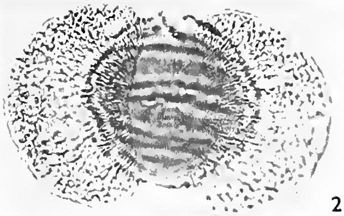
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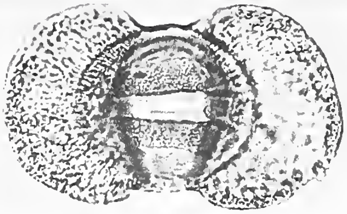
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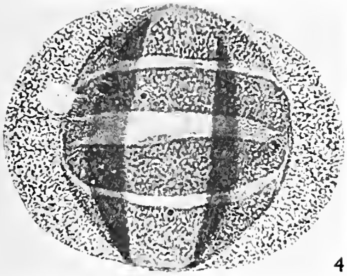
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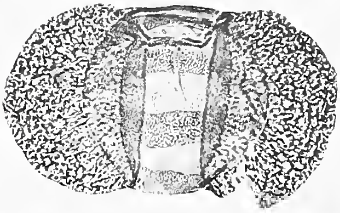
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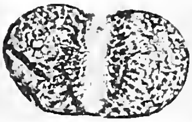
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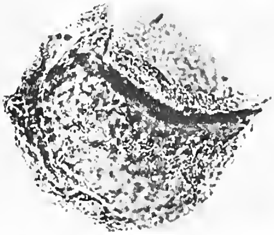
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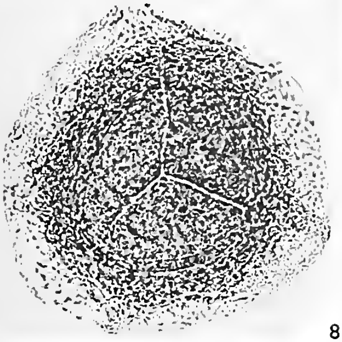
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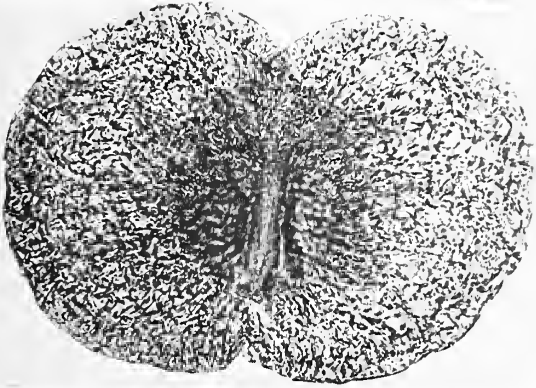
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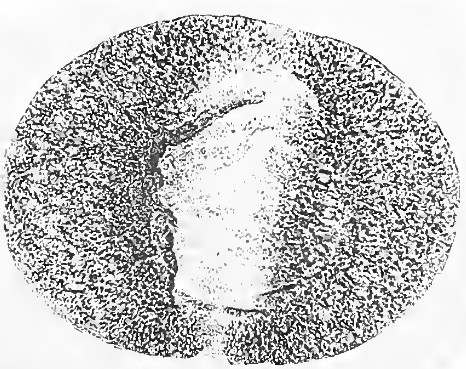
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BALME, Triassic plant microfossils

Striatites sp. is assignable to *Lunatisporites* as that genus was interpreted by Potonié (1958), but recent doubts have been expressed as to the validity of *Lunatisporites* (Klaus 1960, Dr. G. F. Hart, personal communication) and use of the name should be discontinued pending clarification of its status. No form clearly identical with *Striatites sp.* is known from the Australian Permian, but similar types occur rarely in the Blina Shale.

Known stratigraphical range in Australia. Lower Triassic.

Genus TAENIAESPORITES (Leschik) Jansonius 1962

Type species. Taeniaesporites kraeuseli Leschik, Keuper, Switzerland.

Generic name. The genus *Taeniaesporites* was proposed by Leschik (1955, p. 38) on the basis of the following brief diagnosis: 'Mikrosporen mit zwei Luftsäcken. Der sporenkörper ist durch 6 und mehr Streifen zerlegt.' These characters scarcely justified the establishment of a new genus, for they do not distinguish *Taeniaesporites* from several pre-existing form genera. Leschik's subsequent attempt (Leschik 1956) to change the type species of *Taeniaesporites* did nothing to clarify the application of his generic name.

Potonié did not accept *Taeniaesporites* on the ground that Leschik had misconstrued the structure of *T. kraeuseli*, which, Potonié argued, had only three proximal striae and belonged in *Lueckisporites* R. Potonié and Klaus. Leschik's photographs bear out Potonié's interpretation and any attempt to prevent the proliferation of generic names among the Striatiti commands sympathy. Nevertheless, *T. kraeuseli* was adequately illustrated and is a well-characterized and distinctive species. It could certainly have been included in *Lueckisporites* as that genus was originally conceived, but having accepted the restriction of *Lueckisporites* to pollens of the *L. virkkiae* type, it was not altogether consistent for Potonié to reject *Taeniaesporites*.

Leschik's views on the scope of his genus have never been clearly expressed, but he has vigorously defended the separation of *Taeniaesporites* and *Lueckisporites* on morphographic and stratigraphic grounds. His arguments are strongly supported by the evidence from Western Australia. Here forms similar to *Taeniaesporites kraeuseli* and *T. noviaulensis* are common in Lower Triassic sediments, but pollens resembling *Lueckisporites virkkiae* have never been observed.

Jansonius (1962) has recently proposed an emendation of *Taeniaesporites* which restricts and clarifies the genus. In this the generic name *Taeniaesporites* is restricted to striatitid forms with less than six, and most commonly four, bands of transverse proximal thickening. These exoexinal bands are commonly inflated and separated by transverse clefts in which the intexine is exposed. The clefts are wider and more clearly defined than in other genera of the Striatiti. Under the diagnosis proposed by Jansonius both haploxinoid and diploxinoid forms may be assigned to *Taeniaesporites*, for he minimizes the relative size of body and bladder as a criterion in the classification of the Striatiti. One may agree with Jansonius that many Russian authors have over-emphasized this character, without subscribing unreservedly to his view. In the future it may prove convenient to reserve *Taeniaesporites* for haploxinoid forms and create a new genus for thick-walled diploxinoid species such as *Taeniaesporites transversundatus* Jansonius and *T. obex* sp. nov.

Taeniaesporites sp. cf. *T. noviaulensis* Leschik 1956

Plate 6, figs. 4–6

1956 *Taeniaesporites noviaulensis* Leschik, p. 134; pl. 22, figs. 1, 2.
?1962 *Taeniaesporites novimundi* Jansonius, p. 63.

Figured specimens. Slides 47522, 47523, and 47524.

Description. Disaccate pollen grain. Central body subcircular or oval in polar view, intexine thin and translucent, exoexine confined to the proximal side, infrareticulate and slightly thicker than the intexine. Exoexine divided by three, or sometimes four, transverse clefts in which the intexine is exposed; the proximal side, therefore, has four or five bands of transverse exoexinal thickening. A short, transverse, linear, scar is usually visible within the cleft which passes through the proximal pole and from this it is inferred that the species was formed in planar tetrads. Sacci attached, and slightly inclined distally. Structure of sacci microreticulate; mesh lumina fine near the bases of the sacci, becoming coarser towards their peripheries. Distal germinal area fairly broad, consisting of thin, smooth intexine.

Dimensions. Maximum diameter of central body 42–62 μ, breadth of sacci 26–36 μ, length of sacci 43–70 μ, total breadth 72–90 μ; 30 specimens.

Locality of figured specimens. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Remarks and comparisons. Specific discrimination within the genus *Taeniaesporites* is not easy, partly because of the rigidity of the emended diagnosis and partly because the forms encountered have a fairly wide range of apparently continuous variation, both in size and in the arrangement of the proximal thickenings. Jansonius recognized nine species from the Canadian Lower Triassic, but some of these are rather arbitrarily characterized and may prove difficult to maintain. A comparatively wide range of variation has been allowed in the specimens assigned here to *Taeniaesporites* cf. *noviaulensis* and this latitude may be gauged from the three specimens illustrated in Plate 6, figs. 4–6.

The Western Australian form is similar in size to Leschik's species which it also resembles in arrangement and structure of its proximal thickenings and the presence of a short, transverse, tetrad scar. A possible distinction lies in the internal structure of the sacci. In *Taeniaesporites noviaulensis* the lumina are radially elongate. The mesh is variable in the Australian species and appears coarser in poorly preserved specimens. There is some uncertainty, therefore, concerning its reliability as a specific character.

Taeniaesporites cf. *noviaulensis* is a key species in the microflora of the Kockatea Shale. It is easily recognized and occurred in all samples, usually making up between 3 and 10 per cent. of the total spore–pollen assemblage. It occurs commonly in the Blina Shale, less frequently in the Erskine Sandstone and in continental Triassic sediments overlying the Kockatea Shale in BMR 10 (Beagle Ridge) Bore. Rare specimens have been found in Triassic coals from the Springfield Basin, South Australia, but no representatives of *Taeniaesporites* have been recorded from the Leigh Creek Coal Measures. In the Sydney Basin, New South Wales, a few examples have been recognized in assemblages from the Collaroy Claystone (Middle Narrabeen Group), and similar forms occur red fairly commonly in a sample from the base of the Narrabeen Group, collected in the Nattai River area.

The distribution of *Taeniaesporites* is discussed further in a subsequent section of this paper.

Known stratigraphical range in Australia. Lower to (?) Upper Triassic (mainly Lower Triassic).

Taeniaesporites obex sp. nov.

Plate 6, figs. 1–3

Holotype. Slide 47531. *Paratype.* Slide 47558.

Diagnosis. Disaccate, more or less diploxinoid pollen grain. Central body circular in polar view, intexine very thin, translucent and faintly punctate. Proximal face bearing four prominent transverse bands of heavy exoexinal thickening, separated by clefts in which the intexine is exposed. Subsidiary clefts sometimes present in the thickenings giving rise to isolated patches of discontinuous exoexine. Thickenings infragranulate and about 2 μ thick. A short transverse, linear scar passes through the proximal pole. Sacci crescentic in polar compressions, longer than the central body, attached and inclined distally. Sacci microreticulate, mesh clearly defined, lumina radially elongated near the base of the sacci, becoming more equidimensional towards their outer margins.

Dimensions. Diameter of central body 36–43 μ, breadth of sacci 25–37 μ, length of sacci 43–57 μ, total breadth 69–81 μ.

Locus typicus. Well at Point 217, Upper Greenough River area (sample 44070), Western Australia. Kockatea Shale, Lower Triassic.

Derivatio nominis. Latin *obex* = 'a barred gate', from the appearance of the proximal surface.

Description. Holotype dimensions—diameter of central body 38 μ, sacci 30 ×45 μ and and 29 ×46 μ, total breadth 72 μ. The holotype is only slightly compressed and bears four bands of thickened exoexine. An elongated patch of discontinuous thickening occurs between the two major bands and is visible at the right-hand side of the central body in Plate 6, fig. 1. Thickenings 6–8 μ wide, with notched margins, and infragranulate sculpture. The paratype has a wider polar cleft than the holotype and displays a clear transverse scar.

Remarks and comparisons. Taeniaesporites obex is fairly rare in the Kockatea Shale and did not occur in all the samples. It is known from the Blina Shale and similar forms occur in the lower part of the Narrabeen Group in New South Wales. The circular central body and heavier proximal thickenings distinguish it from *T. noviaulensis.*

No species obviously resembling *Taeniaesporites obex* has been described from European sediments, but Jansonius (1962) has recorded forms with heavy discontinuous proximal thickenings from the Scythian of Canada. Of these, *T. transversundatus* is closest to the Australian species but it is smaller than *T. obex* and its proximal thickenings are markedly constricted away from the pole.

Known stratigraphical range in Australia. Lower Triassic.

Genus CRUSTAESPORITES Leschik 1956

Type species. Crustaesporites globosus Leschik, Zechstein, Germany.

Crustaesporites sp.

Plate 6, fig. 11

Figured specimen. Slide 47525.

Description. Trisaccate or irregularly disaccate pollen grain. Central body oval, intexine thin, finely punctate and translucent; proximal side bearing faint, roughly parallel bands of exoexine. Bands infrareticulate, 2–5 μ wide and about 1 μ apart. Sacci attached marginally slightly on the distal side of the equator and inclined distally. Sacci narrow and elongate, occasionally lobed; microreticulate with a clearly defined mesh.

Dimensions. Central body 91 ×78 μ, sacci 73 ×31 μ, 76 ×27 μ, 90 ×27 μ, figured specimen only.

Locality of figured specimen. Kockatea Creek No. 19 Bore, 139–190 ft., Upper Greenough River area (sample 43305), Western Australia. Kockatea Shale, Lower Triassic.

Remarks and comparisons. Crustaesporites sp. is rare in the Kockatea Shale. Representatives of the genus have been found in Australian Upper Permian deposits (cf. Balme and Hennelly 1955, pl. 4, fig. 44) and are known also from the German Zechstein (Leschik 1955, Klaus 1955, Grebe 1957) and the Lower Triassic of Canada (Jansonius 1962).

Jansonius interpreted *Crustaesporites* as a monosaccate form in which the sacci were irregularly constricted to give a multisaccate appearance. In the few specimens seen in microfloras from the Kockatea Shale the sacci were clearly separated, but the species was too rare to judge its range of variation. However, it is certainly possible to envisage a graduation from monosaccate to multisaccate specimens. *Crustaesporites* has clear affinities with the striatitid pollens and not, as Leschik suggested, with the *Podosporites–Microcachryidites* group.

INCERTAE SEDIS

Genus SCHIZOSPORIS Cookson and Dettmann 1958

Type species. Schizosporis reticulatus Cookson and Dettmann, Cretaceous, South Australia.

cf. *Schizosporis sp.*

Plate 4, figs. 4, 5

Figured specimens. Slide 47530.

Description. Spheroidal body of uncertain function. Body wall 2–4 μ thick, two-layered, inner layer very thin and smooth. Outer layer unsculptured, sometimes with occasional scattered pores. Most specimens are split roughly into two halves, along a line of weakness in the body wall. Some, however, are unruptured and in others the incipient split appears as a faint line. The form resists compression and most specimens are strongly three-dimensional.

Dimensions. Diameter 18–41 μ; 60 specimens.

Locality of figured specimens. Geraldton Racecourse Bore, 1,465 ft. (sample 44497), Western Australia. Kockatea Shale, Lower Triassic.

Remarks and comparisons. The generic assignation is tentative as the Triassic form is considerably smaller than any included in *Schizosporis* by Cookson and Dettmann (1958). It is similar in general structure to *Schizosporis spriggi* Cookson and Dettmann, but is smaller and has a relatively thicker body wall. Jansonius (1962) has assigned similar bodies to the genus *Spheripollenites* (Couper) Jansonius, but judging from Couper's original diagnosis and illustrations (Couper 1958, p. 158, pl. 31, fig. 12) the propriety of Jansonius's emendation is dubious. *Spheripollenites scabratus* Couper, the type species, was said by Couper to resemble the pollen grain of *Pagiophyllum connivens*, except in its lack of a thickened equatorial zone. From this comment, and from the original specific diagnosis, *S. scabratus* appears close to the Western Australian Jurassic species *Exesipollenites tumulus* Balme, and is certainly distinct from *Laevigatosporites scissus* Balme and Hennelly, which Jansonius includes in *Spheripollenites*.

From its morphography and its distribution in the Kockatea Shale cf. *Schizosporis sp.* is unlikely to be the spore or pollen grain of a vascular plant. It is usually extremely abundant in samples with a high microplankton content, and is rare or absent elsewhere.

Spheripollenites balmei Jansonius may be identical with *Schizosporis sp.*, but the Canadian species is said to have a faint intrapunctate or interpunctate pattern within the body wall. This feature was not convincingly exhibited by any specimens of cf. *Schizosporis sp.* which have been closely studied.

Known stratigraphical range in Australia. Lower Triassic.

Genus TETRAPORINA Naumova 1950

Type species. Tetraporina antiqua Naumova 1950, Lower Carboniferous, U.S.S.R. (designated Potonié 1960, p. 130).

Tetraporina sp. cf. *Azonotetraporina ? horologia* Staplin 1960

Plate 4, fig. 3

1960 *Azonotetraporina ? horologia* Staplin, p. 6; pl. 1, figs. 4, 6.

Figured specimen. Slide 47528.

Description. Test quadrilateral, two opposite sides concave, others straight or slightly convex. Surface smooth or faintly punctate, thickness of test about 1 μ. Arcuate folds about 10 μ long at each corner of the test.

Dimensions. Maximum length 36–46 μ; 8 specimens.

Locality of figured specimen. Geraldton Racecourse Bore, 1,465 ft. (sample 44497), Western Australia. Kockatea Shale, Lower Triassic.

Remarks and comparisons. Tetraporina sp. belongs to a group of morphographically similar bodies, of obscure origins, which is widely distributed in Carboniferous sediments (Naumova 1950, Teteriuk 1958, Staplin 1960). It is rare in the Kockatea Shale, but its occurrence extends the stratigraphical and geographical range of *Tetraporina*. Churchill (1960) has reported the presence of a form closely resembling *Tetraporina sp.*

in modern lake sediments and considers that it is the aplanospore of a member of the Cyanophyceae.

Known stratigraphical range in Australia. Permian to (?) Recent.

MICROPLANKTON

Except in one core (2,131–2,141 ft.) from BMR 10 (Beagle Ridge) Bore, all samples from the Kockatea Shale were characterized by extraordinarily large numbers of microplankton. Almost invariably they were many times more plentiful than spores or pollen grains, and a single slide from Gerldton Raceourse Bore (sample 44497) was estimated to contain over 25,000 specimens of hystrichosphaerids and leiospheres. Considered individually the various forms present are not particularly distinctive, for they are simple, spinose hystrichosphaerids, not differing obviously from species known to range from the Silurian onwards. On the other hand, both de Jekhowsky (1961) and Jansonius (1962) have noted that microplankton are particularly common in Lower Triassic marine sediments from widely separated parts of the world. Jansonius has already remarked on similarities between the microplankton suites of the Kockatea Shale and the Canadian Toad-Grayling Formation. All the common Western Australian forms are closely similar to species described by Jansonius, although the Canadian suites are more diverse, and in addition to hystrichosphaerids contain dinoflagellate tests. The following list includes all the common microplankton types in the Kockatea Shale, and is presented without taxonomic comment.

Wilsonastrum colonicum Jansonius	abundant
Wilsonastrum spp.	abundant
Micrhystridium setasessitante Jansonius	common
M. breve Jansonius	common
M. sp. cf. *M. inconspicuum* (Deflandre)	common

Colonial unicellular thallophytes similar to *Botryococcus* were common in some samples, particularly those from the Upper Greenough River area.

COMPOSITION OF THE ASSEMBLAGES

Text-fig. 3 shows the quantitative distribution of spore and pollen species in the seventeen samples studied. These figures are based on counts of about 200 specimens, except for three samples in which spores were rare and poorly preserved. In addition, the relative proportions of spores (including pollen grains) to microplankton have been estimated for each assemblage and these are expressed as a fractional ratio in the final column of text-fig. 3.

Except in the uppermost sample from BMR 10 Bore microplankton always outnumber spores, although their relative dominance varies within wide limits. The assemblages from BMR 10 Bore show gradually decreasing microplankton proportions towards the upper part of the section and a similar trend is present in the Geraldton Racecourse and Municipal Bores and in the 47¼ Mile Peg Bore; although these were not sampled in sufficient detail to enable confident interpretations. Frequency of microplankton in a sediment may be influenced by a variety of factors the relative importance

	LOCALITY	Point 217 Bore	Kockatea Creek No. 19 Bore	47¼ Mile Peg Bore					Geraldton Racecourse Bore		Geraldton Municipal Bore			B.M.R. 10 Beagle Ridge Bore				
	SPECIES / DEPTH IN FEET	30	139 — 190	uncertain	uncertain	741 — 749	808 — 945	948 — 968	1273	1465	1012 — 1096	1177 — 1344	1346 — 1386	2131 — 2141	2223 — 2233	2405 — 2415	2802 — 2812	3203 — 3213
SPORES	Punctatisporites fungosus	5	3	X	2	5	1	5	6	12	4	9	7	4	34	5	3	2
	Osmundacidites senectus	26	6	3	6	2	X	3	11	10	4	6	4	4	24	4	3	3
	Lycopadiacidites pelagius	2	2		2	1	X	1	1	1	2	2	1	2	2	1	1	1
	Lycopodiacites sp.	1	1	X	1	1				1	1	1	2	1		X	X	1
	Kraeuselisporites cuspidus	1	10	16	13	10	X	8	3	16	4	4	8	4	10	5	5	1
	K. saeptatus	3	36	20	24	36	9	24	21	58	76	34	39	76	106	104	31	5
	Lundbladispora playfordi	42	98	101	85	129	52	125	127	43	71	98	89	71	91	63	58	15
	L. willmotti	24	13	7	9	7	2	13	24	12	31	13	21	31	11	7	9	5
	L. brevicula	39	16	26	38	6	1	18	5	4	18	2	6	18	8	2	8	2
POLLEN GRAINS	Vitreisporites pallidus	1		1				X			1	2	X	1	1			
	Platysaccus cf. papilionis	1	X	2	1	1			X	1		X	1					
	Striatites sp.	4	1	4	1	X		1	4	3	4	2	5	4	4	X	X	1
	Taeniaesporites cf. naviaulensis	60	22	23	34	7	3	11	16	19	16	20	17	16	11	14	5	7
	T. obex	4	4	6	9	1	1	2	3	1	3	6	5	3	5	4	1	2
	Crustaesporites sp.	4	1	1	X	1		X		X		X		X	X			
TOTAL COUNT		217	215	210	225	207	69	211	221	181	235	199	205	235	307	209	124	45
SPORE / MICROPLANKTON RATIO		1/24	1/15	1/7	1/2	1/2	1/16	1/10	1/16	1/37	1/6	1/35	1/60	3/1	1/2	1/17	1/15	1/65

TEXT-FIG. 3. Distribution of spore and pollen species in samples from the Kockatea Shale.

of which is difficult to assess, particularly when dealing with a group of such divergent origins as the Hystrichosphaeridae. Recent studies (Muller 1959, Staplin 1961) suggest that the most favourable environment for the preservation of large numbers of hystrichosphaerids is a fairly deep, offshore basin in which turbidity is low. The most direct environmental interpretation of the palynological data from BMR 10 Bore is that the depositional basin gradually shallowed during the formation of the Kockatea Shale. Lithological evidence presented by McTavish (1960) favours the same concept, for coarser-grained sediments become more common in the upper part of the section, and the uppermost 100 feet or so are characterized by lingulid brachiopods, worm tubes, wood fragments, and other concomitants of the deltaic environment.

A singular feature of both the microplankton suites and the accompanying spore–pollen assemblages is their remarkable lack of diversity. Almost invariably *Wilsonastrum* was the dominant microplankton genus and in most samples the only other common forms were one or two species of *Micrhystridium*. The microplankton suite, consisting of few species and enormous numbers of individuals, suggests, therefore, a restricting but highly productive environment. High salinity may have been the main cause of this restriction, and could also be invoked to explain the general paucity of invertebrate fossils in the Kockatea Shale. Nevertheless, it would be unwise to imply that salinity was the only possible controlling factor.

Lack of variety in the spore–pollen assemblages is even more marked than a casual glance at text-fig. 3 would suggest, for of the fifteen species described only nine were present in every sample. *Lundbladispora playfordi* was almost always the most abundant species, and spores, especially forms with cavate exines, always outnumber pollen grains. In both paucity of species and relative abundance of pteridophyte spores, microfloras from the Kockatea Shale contrast notably with those from Australian Permian sediments. Assemblages from the Upper Permian in particular, are characterized by their heterogeneity and by a high content of striatitid, disaccate pollen grains (Balme 1962).

It may be argued that impoverishment of the Lower Triassic microfloras is a function of the conditions of deposition of the Kockatea Shale and does not necessarily imply specialization of their parent floras. Almost certainly the plant microfossils have been carried long distances from their sources and selective forces undoubtedly operated during transportation. The abundance of *Kraeuselisporites* and *Lundbladispora*, genera of probable lycopsid origin, suggests, for example, that elements of coastal swamp floras were heavily represented in the plant microfossil assemblages.

Even allowing for the possibility of selective transportation and preservation, however, it seems unlikely that these factors alone can explain the impoverishment in species of these Lower Triassic microfloras. Such impoverishment characterizes assemblages from the Kockatea Shale wherever it has been sampled, even in areas which must have lain close to the shoreline. Qualitatively similar microfloras have, in addition, been recovered from the Blina Shale, the closest outcrop of which lies about 1,000 miles north of Geraldton. Inadequate as the palynological data may be from the phytogeographic point of view, they can most reasonably be interpreted as recording the presence of highly specialized floras in western marginal areas of the Australian continent during early Triassic times.

Phytogeographic changes of the magnitude postulated can only have resulted from major climatic changes at the end of the Permian. It would be rash to attempt a dogmatic inference on the direction of these changes from the palynological evidence alone, although the sudden appearance, in the Western Australian Scythian, of *Taeniaesporites* and other European Zechstein and Triassic forms suggests increasing aridity. The lithology of the Kockatea Shale is compatible with a desertic climate in the adjoining mainland, as it is predominantly fine-grained and contains red layers in Geraldton Racecourse Bore. Clearly this ferric iron cannot have resulted from conditions within the basin of deposition, for even the red shales contain abundant plant microfossils which could not have survived prolonged oxidation. It may be concluded that most of the iron was transported in the ferric state, and partially or completely reduced after deposition in a marine environment.

Nowadays it would be reactionary to invoke a desertic climate to explain the origin of red coloration in sediments. On the other hand, many authorities (Dunham 1953, Dunbar and Rodgers 1958, p. 217) are agreed that arid conditions favour, and may even be essential to, the preservation of ferric oxides during prolonged transportation.

PHYTOGEOGRAPHIC AND STRATIGRAPHIC SIGNIFICANCE OF THE MICROFLORAS

Because of the precision with which the Kockatea Shale can be dated its microfloras have an intrinsic importance to both stratigraphers and palaeobotanists, and when the unusual composition of the assemblages is also taken into account, their significance is further enhanced. In Western Australia at least, it is probable that an upper limit to the Permian System can be established on a palynological basis, and that floral changes of great magnitude were initiated at the beginning of the Triassic Period. These changes involved the extinction of the major elements of the *Glossopteris*-Flora and their replacement by other plant groups, some of which possibly originated in the northern hemisphere during Upper Permian time.

To expand these conclusions on the fate of the *Glossopteris*-Flora a brief consideration of the main characteristics of Australian Permian microfloras is a necessary preliminary. Certain aspects of these microfloras have been discussed by Klaus (1958), Balme (1962) and more cursorily by other authors. Wherever sediments containing the typical *Glossopteris*-association of plant macrofossils have been examined palynologically, they have yielded well-defined and basically similar assemblages of spores and pollen grains. In post-glacial Permian sediments these microfloras are characterized generally by considerable diversity, and particularly by their high content of disaccate pollen grains with striate proximal faces. In Western Australia microfloras of this type make their first appearance in glacial deposits, which form the basal units of the Permian successions in each of the major sedimentary basins. With modifications they persist throughout the Artinskian and attain their maximum variety in Upper Permian times. It is uncertain whether the Upper Permian is completely represented in any Australian state and there is evidence of a break in sedimentation between Permian and basal Triassic sediments in both the Canning and Perth Basins in Western Australia. Nevertheless, the hiatus cannot be a long one, for the Hardman Member of the Liveringa Formation in the Canning Basin contains marine fossils which enable it to be correlated with the Upper Productus Limestone of the Salt Range (Dickins and Thomas 1954), in turn equivalent to the Dzhulfian or uppermost Permian of Russia. If a non-sequence exists in the Upper Permian of the Canning Basin it can, therefore, represent only part of the Dzhulfian Stage.

Typically Permian microfloras occur in the Liveringa Formation wherever it has been examined, and these compare closely with assemblages from the Indarra Beds in the Perth Basin, the Newcastle and Illawarra Coal Measures in New South Wales, the Upper Bowen Group and its equivalents in Queensland and the Cygnet Coal Measures in Tasmania. In other words the palynological evidence strongly implies the existence of a pan-Australian flora in Upper Permian times. This, in classic terms, was the *Glossopteris*-Flora.

Basal Triassic microfloras from Western Australia, represented by assemblages from the Kockatea Shale and Blina Shale, are quite unlike any known from Australian Permian strata. A few Palaeozoic types (e.g. *Platysaccus* cf. *papilionis*) occur rarely in the Mesozoic, but the most prominent Scythian forms, such as *Lundbladispora* and *Taeniaesporites*, have never been observed in Australian Permian sediments. Only one conclusion seems possible from the microfloral evidence, namely that, in Western Australia, Lower Triassic floras were quite distinct from those of the Upper Permian. From this it follows that the *Glossopteris*-Flora did not survive into the Mesozoic, at least in the western part of the present Australian continent.

Virtually nothing is known of the megascopic organs of these Lower Triassic plants which superseded the *Glossopteris*-Flora. No identifiable plant megafossils have so far been recorded from the Kockatea Shale, but plants occur rarely in the upper part of the Blina Shale at Erskine Range in the Canning Basin. These have not been studied in detail, but include equisetalean, and probably lycopodiaceous, stem fragments. *Dicroidium*, the frond genus which particularly characterizes Triassic continental sediments in eastern Australia, has been reported from the Erskine Sandstone, a continental Triassic unit conformably overlying the Blina Shale (Antevs 1913, Brunnschweiler 1954) but is not known to occur in the Perth Basin. On palynological grounds it is unlikely that the pteridospermous group which bore *Dicroidium*-foliage was an important component of the Scythian floras in Western Australia. Neither the Kockatea Shale nor the Blina Shale contains the pollen genus *Pteruchipollenites* (in the sense of Couper 1958), which is always abundant in association with *Dicroidium* in the Triassic of New South Wales, Queensland, and South Australia. *Pteruchipollenites* is present in the Erskine Sandstone, and in the Perth Basin its first known occurrence is in continental Triassic sediments which overlie the Kockatea Shale in BMR 10 (Beagle Ridge) Bore. If, as is implied here, *Pteruchipollenites* can be used as an index for the *Dicroidium*-Flora, it follows that this did not become established in Western Australia until after early Scythian time. Its first appearance cannot be dated unequivocably, but the sediments in which *Pteruchipollenites* occurs in Beagle Ridge Bore conformably overlie the Kockatea Shale, with an apparently transitional contact, and are likely to be late Scythian or early Middle Triassic. From the preceding discussion it is concluded that plant microfossils from the Kockatea Shale record the existence of a specialized and fairly short-lived flora which became established in the late Permian or early Triassic and was replaced by the *Dicroidium*-Flora, probably before the end of the Scythian Age.

Whether this flora existed in eastern Australia is conjectural, in view of the inadequacy of palynological data and the difficulties of correlating Australian Triassic sediments. On *a priori* grounds microfloras similar to those from the Kockatea Shale would be expected to occur in the lower part of the Narrabeen Group in New South Wales. However, from the scanty published evidence, and from the few samples examined by the present author, this is not so. *Taeniaesporites* was present in a shale collected from the base of the Narrabeen Group in the Nattai River district of New South Wales, but in other ways the microflora from this sample resembled those from the Erskine Sandstone rather than the Kockatea Shale. Hennelly (1958) described a rather poorly preserved microflora obtained from the bottom 75 feet of the Narrabeen Group in the Illawarra District of New South Wales. In this, disaccate pollen grains of the *Pteruchipollenites*-type (*Pityosporites reticulatus* Hennelly) were apparently dominant and in general composition the assemblages look younger than those from the Kockatea Shale. Two hypotheses may be advanced to explain the differences between microfloras from the base of the Triassic System in New South Wales and Western Australia. It is possible that a distinct floral province existed in the western part of the Australian continent during Scythian times and that elements of the *Dicroidium*-Flora migrated from eastern Australia late in the Lower Triassic. Alternatively, part of the Lower Triassic may be missing in the Sydney Basin and the conformable contact of the Narrabeen Group with the underlying Illawarra Coal Measures may obscure a sedimentary hiatus representing at least part of the Scythian Stage. Further speculation is unjustified on the published data available, but a convincing answer should follow the assessment of information on the Triassic of eastern Australia at present being accumulated by palynologists of the Bureau of Mineral Resources, Canberra.

The most obviously interesting record from the Kockatea Shale is that of the disaccate pollen genus *Taeniaesporites*, which had not previously been reported from the southern hemisphere. *Taeniaesporites* belongs to the diverse complex of disaccate pollen grains with transverse thickenings on their proximal faces, which have been assigned by Potonié to the Infraturma Striatiti. However, its structural characters set it apart from other genera of the Striatiti, and are so distinctive that it can hardly be doubted that at least the haploxinoid species of *Taeniaesporites* were derived from closely related plants. Such species have been reported from widely separated regions in the northern hemisphere, occurring in Upper Permian and Triassic strata.

In Australia *Taeniaesporites* has never been found in Permian sediments and appears to be confined to the Triassic. Rare specimens have been found in the upper part of the Narrabeen Group and in coals from the Springfield Basin, South Australia. These South Australian coals almost certainly correlate with the Leigh Creek Coal Measures and may be of Upper Triassic or Rhaetic age (Dettmann 1961). Although *Taeniaesporites* probably ranges into the Australian Upper Triassic, it appears to be particularly characteristic of Scythian strata, for it is only known in abundance from the Kockatea Shale and Blina Shale. Records from the northern hemisphere indicate that *Taeniaesporites* has a different stratigraphic distribution in western Europe. One of its oldest documented occurrences is in the Hilton Plant Beds in Westmorland (Jansonius 1962) and it is known also from the German Zechstein (Potonié and Klaus 1954, Leschik 1956). Little published information is available on the palynology of the Buntsandstein or Muschelkalk equivalents, but *Taeniaesporites* (*Lueckisporites*) *kraeuseli* was listed by Klaus from the Carnian of Austria, and similar species are known from the Keuper (Leschik 1955, Pautsch 1958). Post-Keuper records are dubious, but the species *Protosacculina* *glabrescens* Malyavkina from the Rhaetic of Kazakhstan may belong to *Taeniaesporites*, and a single poorly preserved specimen of the genus from the Swedish Liassic was illustrated by Nilsson (1958).

On the available evidence *Taeniaesporites* appeared earlier, and persisted longer, as a prominent microfloral element in Europe, than it did in Australia. Perhaps the apparent differences in the time of first appearance should not be stressed, in view of the possibility that strata homotaxial with the Upper Zechstein are not represented in Australia. The abundance of *Taeniaesporites* throughout the European Triassic, on the other hand, contrasts with its virtual restriction to the Lower Triassic in Australia and these discrepancies in distribution call for some explanation. One interpretation of the evidence is that the parent plants of *Taeniaesporites* were adapted to the more or less desertic environments which characterized the Triassic Period in western Europe. The occurrence of *Pleuromeia*, and other Triassic genera, in the Erskine Sandstone (Brunnschweiler 1954) suggests that desertic plant communities of the European type were stabilized in Western Australia during the early Triassic. These did not survive the extensive climatic changes which were initiated probably in the late Scythian, leading to the establishment of the *Dicroidium*-Flora and the formation of thick coal measures in many parts of the Australian continent.

The only detailed published palynological study of Lower Triassic strata from the northern hemisphere was carried out by Jansonius on sediments from the Scythian section of the Toad–Grayling Formation in Alberta, Canada. Assemblages from the Toad–Grayling Formation are more diverse than those from the Kockatea Shale and contain higher proportions of disaccate pollens, but clear similarities exist between the Western Australian and Canadian microfloras. *Taeniaesporites* is common in both and the Albertan assemblages also contain *Kraeuselisporites*, *Lundbladispora* (cf. *Aculeisporites variabilis* Jansonius), *Vitreisporites*, *Striatites*, *Crustaesporites*, and *Platysaccus*. Close resemblances between the microplankton suites have already been noted by Jansonius, and it seems reasonable to infer that the Australian and Canadian microfloras originated from basically similar communities of parent plants.

Disaccate pollen grains of the *Taeniaesporites*-type are known from the Lower Triassic of Madagascar (de Jekhowsky, personal communication), and the wide distribution of these forms in basal Mesozoic sediments suggests that the postulated late Permian phytogeographic changes were not confined to Western Australia. There is an urgent need for further information on early Mesozoic microfloras, particularly from India and the countries of the southern hemisphere, but the evidence at present available draws attention to the possibility of establishing a palynological basis for the inter-continental correlation of Lower Triassic strata.

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THE MORPHOLOGY AND DEVELOPMENT OF SPECIES OF *MARSSONELLA* AND *PSEUDOTEXTULARIELLA* FROM THE CHALK OF ENGLAND

by TOM BARNARD

ABSTRACT. The morphology and stratigraphical importance of species of *Marssonella* and *Pseudotextulariella* from the Chalk of England are discussed. The type specimens of *Pseudotextulariella* preserved in the Cushman collection have been re-examined. This genus from the Cenomanian has been re-studied particularly in relation to the internal structures, which are re-described. The relationships of several conical arenaceous Foraminifera are discussed.

IN 1953 the author (*in* Barnard and Banner 1953) described species of *Marssonella* and *Pseudotextulariella* from parts of the Chalk succession in England. These species were not dealt with in any detail, but formed part of a general paper on faunas from the Chalk, no emphasis being laid on their relative stratigraphical importance. Abundant new material has become available to the author and a more complete account of the morphology, development, and occurrence of these two genera may now be given. Much new evidence has been found concerning the detailed structure of *Pseudotextulariella cretosa* (Cushman), and its relationships and derivations may be discussed.

The present work was carried out during the tenure of a Leverhulme Fellowship, which enabled the author to visit the U.S.A. and study Cushman's specimens in the Smithsonian Institution, Washington. The author is grateful to Dr. C. A. Cooper for access to these specimens. The author wishes to acknowledge a grant from the Central Research Fund, University of London, which enabled him to collect additional material from a number of localities in southern and eastern England.

Specimen numbers with the prefix P indicate specimens in the British Museum (Natural History) collections.

SYSTEMATIC DESCRIPTIONS

Genus MARSSONELLA Cushman 1933

Genotype. Textularia trochus d'Orbigny.

Gaudryina oxycona Reuss 1860 (designated by Cushman 1933*a*, p. 36; 1933*b*, p. 121) is a synonym of *Textularia trochus* d'Orbigny 1840, p. 45, pl. 4, figs. 25, 26, which predates *Gaudryina oxycona* Reuss 1860 and was redesignated genotype by Barnard and Banner 1953, p. 204.

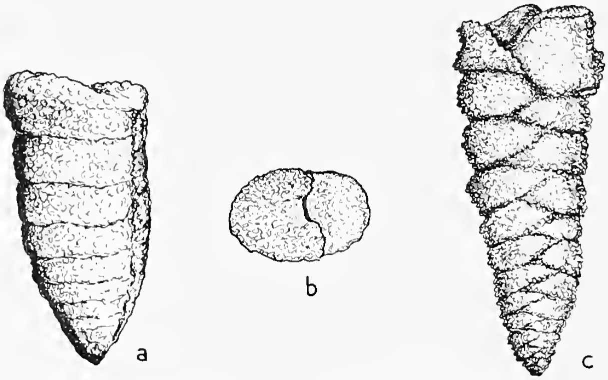
Marssonella ozawai Cushman

Text-figs. 1*a*–*c*

1936 *Marssonella ozawai* Cushman, p. 43, pl. 4, figs. 10*a*, *b*.
1937 *Marssonella ozawai* Cushman, p. 59, pl. 6, fig. 18.
1953 *Marssonella ozawai* Cushman; Barnard (*in* Barnard and Banner), p. 205, pl. 19, figs. 2*a*, *b*.

[Palaeontology, Vol. 6, Part 1, 1963, pp. 41–54, pl. 7.]

Description. Conical test, almost circular in cross-section. The test is coarsely arenaceous, composed of a mosaic of almost equal-sized quartz grains, with little calcareous cement. These grains protrude through the cement so that the surface of the test is rugose. A globular proloculum is followed by one to three whorls of three to five small crescentic or reniform chambers. The test then becomes biserial, the height of the chambers increases slowly, but the diameter increases rapidly, so that initially the edges of the test diverge up to an angle of 60°. After this stage, which sometimes continues up to about half the height of the test, the diameter of the test may remain almost constant giving a cylindrical late portion. Rarely the diameter increases rapidly giving a pseudoflange to the later chambers, or it may increase slowly producing a large conical test.



TEXT-FIG. 1. *Marssonella ozawai* Cushman. All specimens from the Cenomanian. *a*, *b*, From the Portsdown borehole, 1055–1060 feet, P45013. *c*, From the marls 4 feet above 'Chloritic Marl', Arlsey, Bedfordshire, P45014. All specimens ×90.

The septa are almost flat in some varieties, but often become slightly constricted and indented, sometimes near the apertural end or occasionally the whole of the biserial portion. The apertural faces vary from almost flat, in the commonest variety, to either slightly convex or, in rare specimens, concave. Generally the apertural faces are reniform in shape. The basal aperture varies from slit-like to reniform in shape. The test is usually straight, but occasionally may be slightly arcuate or even arranged in several stages. At certain levels, long slender almost cylindrical variants occur.

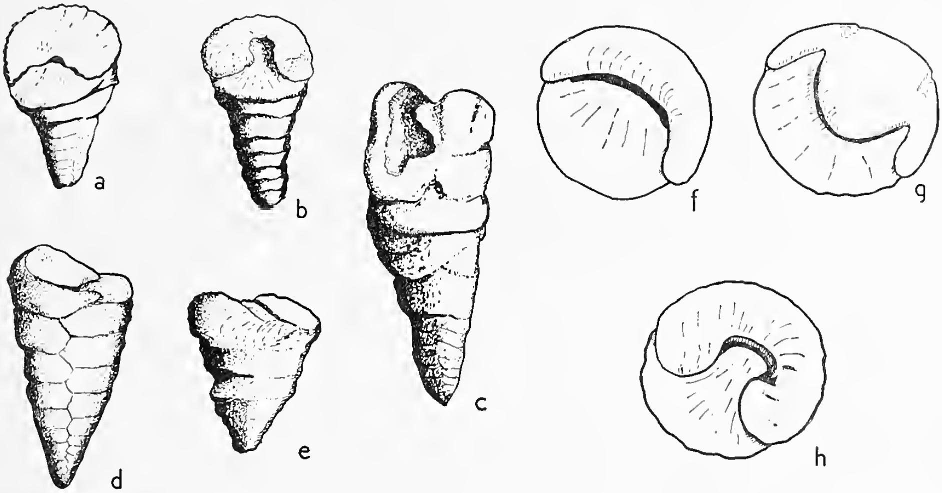
Localities. Numerous.
Horizon. Schloenbachia varians zone.
Dimensions and hypotypes. P45013 (text-figs. 1*a*, *b*). Height 0·99 mm., diameter 0·49 mm. P45014 (text-fig. 1*c*). Height 1·33 mm., diameter 0·57 mm.

Marssonella turris (d'Orbigny)

Text-figs. 2*a–h*

1840 *Textularia turris* d'Orbigny, p. 46, pl. 4, figs. 27, 28.
1890 *Textularia turris* d'Orbigny; Burrows, Sherborn, and Bailey, p. 553, pl. 8, fig. 15.
1928 *Textularia turris* d'Orbigny; Franke, p. 131, pl. 12, fig. 3.
1937 *Textularia turris* d'Orbigny; Cushman, p. 58, pl. 5, fig. 28; pl. 6, figs. 1, 2, (5?).
1957 *Marssonella turris* (d'Orbigny); Hofker, p. 83, text-figs. 84*a–e*, 85*a–e*.

Description. The test is generally a long narrow cone, which can vary to almost cylindrical, or to a cone with an apical angle of about 60°. The size of the test varies considerably, and also the rugosity of the wall. Usually the test is composed of a mosaic of small equi-dimensional quartz grains set in a moderate amount of calcite cement. Occasionally at certain horizons large quartz grains are cemented with little calcite. The quartz grains are usually almost flush with the surface of the test, but when large grains are present they are not deeply set in the cement, but protrude so that the surface is rough. Often in forms with the coarser test, grains of minerals other than quartz are included, such as glauconite, ilmenite, &c.



TEXT-FIG. 2. *Marssonella turris* (d'Orbigny). *a–e*, Showing variation in shape of the test, from the Cenomanian, *Schloenbachia varians* zone, from Sundon, near Dunstable, Bedfordshire, P45016, ×90. *f–h*, Showing the variation in the shape of the apertural face and the position of the aperture.

Variations occur in the shape of the test. Occasionally there are breaks in the normal growth-rate which give the appearance of rejuvenation. Later chambers are often ill-formed or damaged, growth is irregular, and the tests appear to be flanged. Sometimes the tests are slightly arcuate. A globular or hemispherical proloculum is followed by two or three whorls of three to five crescentic chambers which show little or no increase in height. This stage in the growth of the test is difficult to interpret. A biserial stage is soon reached and continues throughout the test. The sutures are straight and scarcely visible except in decorticated specimens, or in the end-chambers of the tests, where they may be constricted, ribbed, or flush with the surface of the test. The apertural face varies from crescentic to reniform in shape, and from highly convex to flat. Occasionally furrows run down the apertural face towards the aperture. The aperture is either slit-like, crescentic, or reniform.

Localities. Numerous.

Horizon. Cenomanian–Lower Senonian.

Dimensions and hypotypes. P45016 (text-figs. 2*a–e*). *a*, Height 0·46 mm., diameter 0·38 mm. *b*, Height 0·49 mm., diameter 0·38 mm. *c*, Height 0·87 mm., diameter 0·46 mm. *d*, Height 0·68 mm., diameter 0·42 mm. *e*, Height 0·46 mm., diameter 0·42 mm.

Marssonella trochus (d'Orbigny)

Text-figs. 3*a–q*

1840 *Textularia trochus* d'Orbigny, p. 45, pl. 4, figs. 25, 26.
1854 *Textularia conulus* Reuss, p. 72, pl. 26, figs. 7*a*, *b*.
1860 *Gaudryina oxycona* Reuss, p. 229, pl. 12, fig. 3.
1891 *Textilaria* cf. *conulus* Reuss; Beissel, p. 68, pl. 13, figs. 23–29.
1899 *Gaudryina oxycona* Reuss; Egger, p. 38, pl. 4, figs. 1–3.
1899 *Haplophragmium petiolus* Egger, p. 143, pl. 2, figs. 37–39.
1925 *Gaudryina oxycona* Reuss; Franke, p. 15, pl. 1, figs. 20*a*, *b*.
1928 *Gaudryina oxycona* Reuss; Franke, p. 143, pl. 13, figs. 8*a*, *b*.
1928 *Textularia trochus* d'Orbigny f. *subconica* Franke, p. 131, pl. 12, fig. 1.
1928 *Textularia trochus* d'Orbigny f. *typica* Franke, p. 131, pl. 12, fig. 3.
1937 *Marssonella oxycona* (Reuss); Cushman, p. 56, pl. 5, figs. 27–29; pl. 6, figs. 1–17.
1946 *Marssonella* cf. *oxycona* (Reuss); Schijfsma, p. 38, pl. 1, figs. 12*a*, *b*.
1953 *Marssonella trochus* (d'Orbigny); Barnard (*in* Barnard and Banner), p. 204, text-figs. 5*o–s*.
1957 *Marssonella oxycona* (Reuss); Hofker, p. 85, text-figs. 86–90.

Description. The conical test varies slightly in shape. During the initial growth-stages the early part of the test is conical with walls diverging at a wide angle as the diameter increases. This is often followed by a period when the diameter does not increase, and a cylindrical growth-stage is produced. Sometimes there is an abrupt increase in the diameter of the test, so that rapid expansion of the end-chambers produces a 'flanged' test. Often there is an abrupt halt in growth, which is then resumed, following a similar pattern as before; this gives the appearance of rejuvenation.

The globular proloculum is followed by whorls of five, four, and three chambers, before the biserial stage is reached. In conical forms the biserial crescentic chambers are overlapped by succeeding chambers.

The septa are usually flat, but can be concave, or convex, often with a slight depression towards the aperture. The face of the end-chamber varies in shape from semicircular, crescentic, to reniform. The aperture varies from its usual position, basal and flush with the surface of the test, to a vertical apertural face. Occasionally this is excavated and the aperture is almost hidden. The aperture is usually slit-like, but can be hemi-elliptical or reniform. The test is smooth with slight constrictions at the septa. The wall is composed of fine quartz grains set in a calcareous cement. Sometimes isolated specimens have up to five radial partitions developed in the last chambers only.

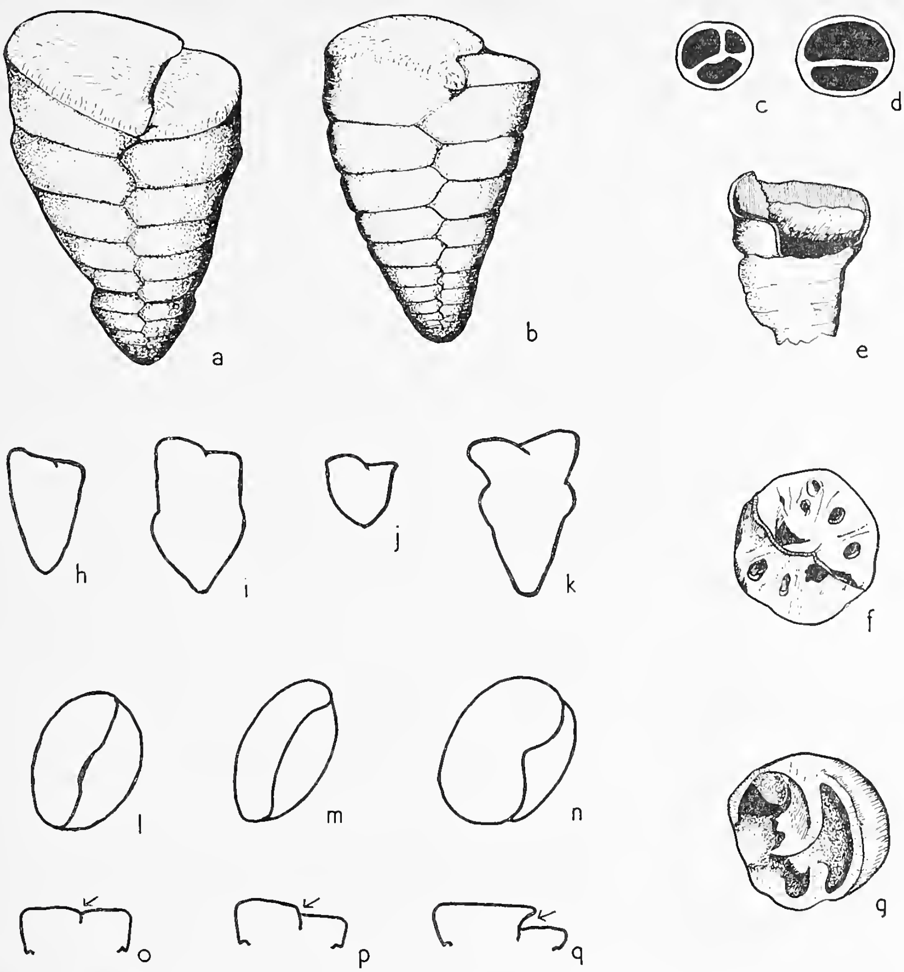
Locality of figured specimens. Whitlingham, near Norwich, Norfolk.
Horizon. Upper Chalk. *Belemnitella mucronata* zone.
Dimensions and hypotypes. P45015 (text-fig. 3*a*). Height 0·95 mm., diameter 0·84 mm. P45015 (text-fig. 3*b*). Height 0·95 mm., diameter 0·72 mm.

Marssonella conoidea (Marie)

Text-figs. 4*a–c*

1941 *Textularia conoidea* Marie, p. 63, pl. 2, fig. 20.

Description. The test is a regular blunt cone, which does not show a great deal of variation in shape. The initial stages are often a curved-sided cone; later the sides of the test become parallel so that it appears bullet-shaped. The cross-section is almost circular. A globular proloculum is followed by whorls of five to three chambers, but rapidly the

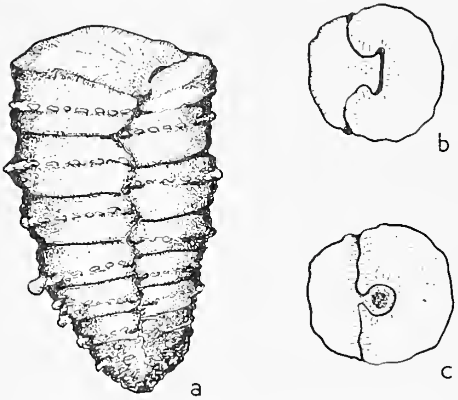


TEXT-FIG. 3. *Marssonella trochus* (d'Orbigny). *a*, *b*, × 90, from the Upper Chalk, *Belemnitella mucronata* zone, from Whitlingham, near Norwich, Norfolk, P45015. *c*, *d*, Showing the triserial and biserial initial stages of the test. *e*, A specimen showing the simple interior to the chambers with no radial partitions. *f*, Showing remnants of radial partitions in the interior of the shell. *g*, Showing chambers with normal simple interiors. *h–k*, Outline lucida drawings showing variation in the shape of the cones. *l–n*, Showing the variation in the shape of the apertural face. *o–q*, Showing the position of the aperture and the slope of the apertural face.

test becomes biserial. This initial part of the test is extremely difficult to interpret due to the rough surface. The wall of the test is rugose. In the initial part, coarse grains of quartz and sponge spicules are set in a thick calcite cement. However, in most of the test the coarse grains protrude above the surface of the cement. Characteristic of this species is that coarse grains appear to be arranged in a rough rib-like pattern, one rib above each suture. The sutures are in deep constrictions, and have flat, concave, or convex surfaces. Often the slit-like aperture is deeply set, almost covered by a lip-like extension of the chamber. In these forms there is a tendency for the chambers of one side of the test to develop, whereas those on the other decrease in size so that the test becomes almost uniserial, especially in forms where the aperture becomes central and deep, appearing to serve both sets of chambers.

Locality. H. Attock's Pit, New Catton, Norwich, Norfolk.
Horizon. Belemnitella mucronata zone.
Dimensions. Height 1·14 mm., diameter 0·76 mm.
Hypotype. P45017.

The development and stratigraphical occurrence of Marssonella. In 1953 the author drew attention (*in* Barnard and Banner 1953, p. 204) to the extreme variation which occurs in the size and shape of the test, as well as the shape of the final chamber and aperture. The species of *Marssonella* from the Chalk were thought (ibid.) to be one group; however, since then numerous specimens have been obtained from widely scattered localities as well as continuous sections, and it has become increasingly apparent that the group consists of a few species which prove to be of stratigraphical value.

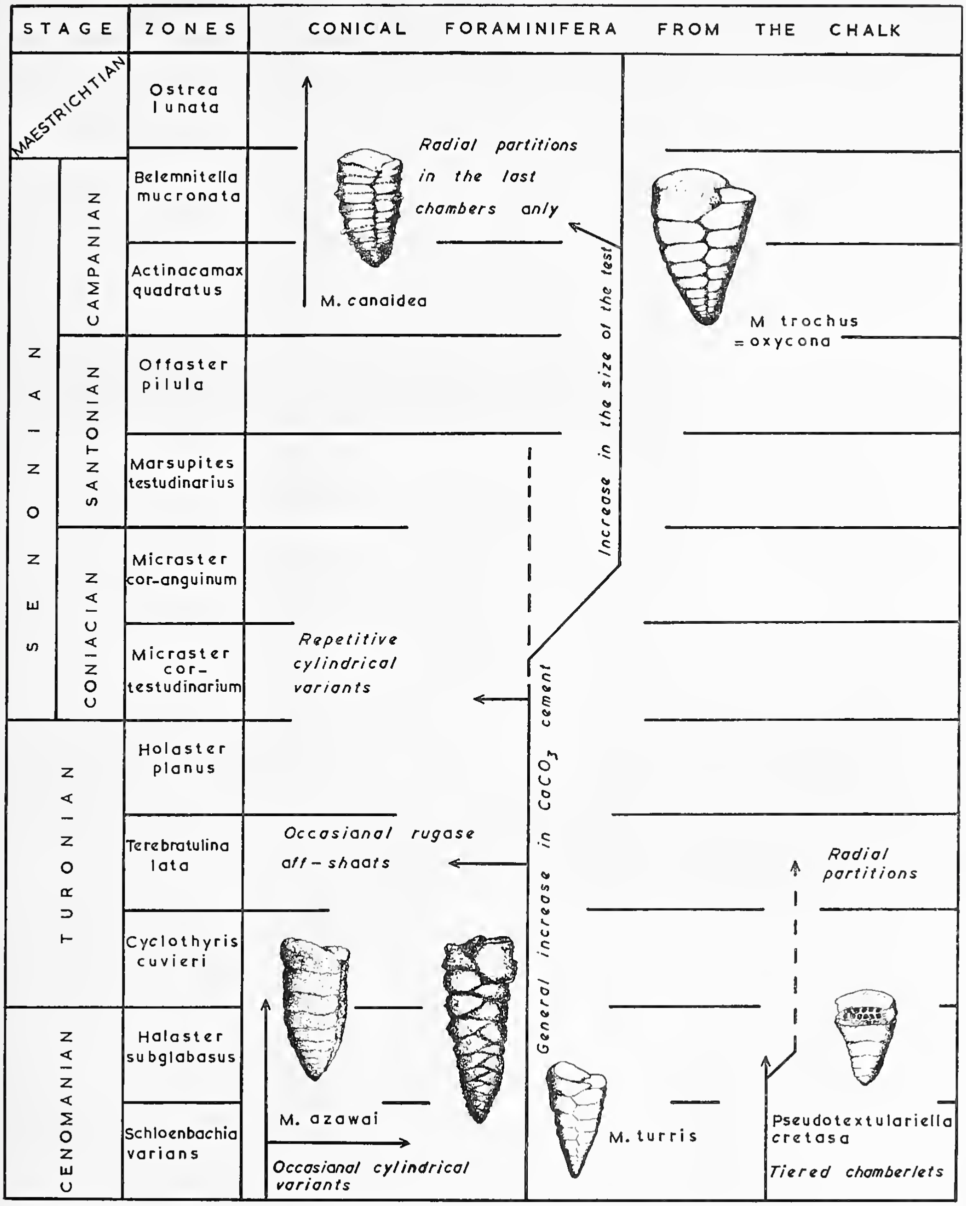


TEXT-FIG. 4. *Marssonella conoidea* (Marie). *a*, ×90, from the Upper Chalk, *Belemnitella mucronata* zone, H. Attock's Pit, New Catton, Norwich, Norfolk, P45017. *b*, *c*, Top view showing the sunken aperture; *b*, lipped and basal; *c*, circular and central.

At some horizons abnormally large forms are produced, at others the general character of the wall changes, so that an abundance of coarsely rugose forms is found. Text-fig. 5 shows in diagrammatic form the general history of the species of *Marssonella* and *Pseudotextulariella* (another conical form, although probably unrelated to *Marssonella*, is often confused with it) throughout the Chalk. Almost confined to the Cenomanian is *M. ozawai* Cushman, a large bullet-shaped species with a rugose wall. This species is easily separated from its contemporaneous, but longer-ranged form *M. turris* d'Orbigny. The latter is the root-stock of the species of *Marssonella* from the Chalk.

Marssonella turris d'Orbigny is usually an acute-angled cone, with a smooth wall. However, at certain horizons there is a tendency for the test to become rugose. Forms with coarser grains in the test generally occur in the Cenomanian, where the coarser silt-grade quartz is found in greater profusion than in higher levels in the Chalk. Generally there is a steady increase in the amount of calcareous cement as the species ranges into higher zones in the Chalk.

However, even here more rugose forms occur at certain levels, which can often be correlated with the size of the quartz grains in the Chalk. Although the test varies considerably in shape, two main trends occur. At some levels in the higher zones of its range there is a tendency for long, narrow, almost cylindrical variants to occur abundantly at sporadic horizons. Also at about the same time (*Micraster cor-testudinarium* zone), broader, blunter cones develop, which may be the forerunners of *Marssonella trochus* d'Orbigny and its synonymous form *M. oxycona* Reuss. In *M. trochus* d'Orbigny there is considerable variation in the shape of the test, as shown in text-figs. 3*h–k* and 3*l–q*. There is, however, a general tendency for the test to increase in size until the



TEXT-FIG. 5. Diagram showing the ranges and development of some conical foraminifera from the Chalk (Upper Cretaceous).

Belemnitella mucronata zone, where large specimens occur, several times the volume of earlier ones. Often in these forms the end-chambers increase abruptly in diameter so that the test appears to be flanged.

At some horizons isolated specimens have irregular radial partitions developed in the end-chambers only. This is rare, but gives a superficial resemblance to *Pseudotextulariella* *cretosa* Cushman, and its Turonian derivatives. However the absence of chamberlets in the later chambers and radial partitions in the early part of the test, separates the two forms.

Marssonella conoidea (Marie) occurs in the *Actinocamax quadratus* and *Belemnitella mucronata* zones, and although it resembles *M. ozawai* Cushman in shape, it is the only species of *Marssonella* from the Chalk which has a rib-like ornament composed of coarse quartz grains arranged in rough lines above the sutures. Also it has a much more regular test than other species.

Summarizing the history of the species of *Marssonella* from the Chalk, it may be stated that one main stock (*M. turris* d'Orbigny) occurs, giving rise, at later horizons, to blunt conical forms, which, when sorted by natural selection, produce such species as *M. trochus* d'Orbigny, and its large, often flanged variety, *M. oxycona* Reuss.

Genus PSEUDOTEXTULARIELLA Barnard 1953

Genotype. Textulariella cretosa Cushman.

In Barnard and Banner 1953, p. 198, the author proposed the genus *Pseudotextulariella* with the holotype *Textulariella cretosa* Cushman, specimens of which had been obtained by Cushman from the Cenomanian, at Barrington near Cambridge. Unfortunately, although the manuscript was sent in during 1952, it was not published until 1953. Since then Thalmann (1955, p. 53) has established that under Art. 25 of the International Rules of Zoological Nomenclature, *Pseudotextulariella* is legitimate.

The author has now had the opportunity of studying Cushman's specimens in the National Museum, Washington, and resulting from this work, certain points can be added to enable a more accurate definition of the genus. More information has also been obtained based on the study of the internal structures.

Pseudotextulariella cretosa (Cushman)

Plate 7, figs. 1–6, 8; text-figs. 6*a–d*, 7*a–f*, 8*a–c*

1932 *Textulariella cretosa* Cushman, p. 97, pl. 11, figs. 17–19.
1937 *Textulariella cretosa* Cushman, p. 61, pl. 6, figs., 26–28.
1948 *Textulariella cretosa* Cushman; Williams-Mitchell, p. 97, pl. 8, fig. 1.
1953 *Pseudotextulariella cretosa* (Cushman); Barnard (*in* Barnard and Banner), p. 198, text-figs. 6*b–i*.

Description. Test conical, broad or narrow, usually straight, but occasionally slightly arcuate, particularly at the initial end. Initial whorl triserial, following a globular or subglobular proloculum. A biserial arrangement of the chambers is soon established and

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EXPLANATION OF PLATE 7

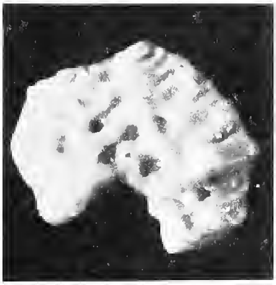
Figs. 1–6, 8. *Pseudotextulariella cretosa* (Cushman). All specimens from the Cenomanian, Barrington, near Cambridge. Fragments of tests to show the distribution and development of the radial and horizontal partitions. 1, ×40. 2–6, ×45. 8, ×60.

Fig. 7. *Textulariella pacifica* Cushman. ×60. Recent, from the H.M.S. *Challenger* Expedition, St. 33, 435 fathoms, Bermuda, to show the development of the radial partitions and the central cavity. The partitions do not reach the centre of the test as in *Pseudotextulariella cretosa* (Cushman). BM No. 1962.3.16 1–2.

1 × 40

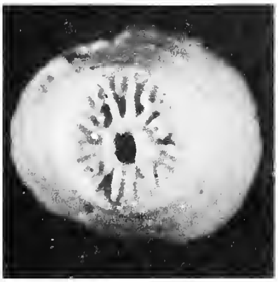
5 × 45

8 × 60



2 × 45

6 × 45



3 × 45

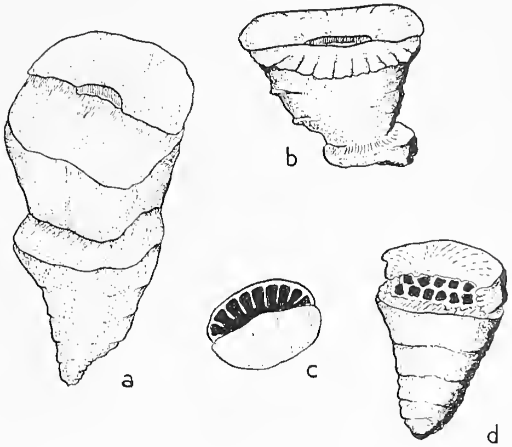
7 × 60

4 × 45

BARNARD, Chalk Foraminifera

remains for the rest of the test. The initial chambers are subglobular, but those in the biserial arrangement become almost semicircular to reniform in transverse section. The height of these chambers varies considerably so that the chambers may have almost parallel faces or sometimes they converge rapidly to become acutely pointed at the medial suture, where the chambers alternate. The height of the chambers varies from an eighth to a quarter of the diameter, and the sides of the test diverge at a constant angle. The walls separating the chambers are often marked at the surface of the test by strong raised ribs; however, on other specimens the sutures are either flush with the surface of the test or even slightly constricted.

In all the numerous specimens examined, the chambers, after the initial stage of the test had been passed through, are divided by an almost regular series of chamberlets. They occur arranged through the biserial portion of the test, and often become multiplied so that two to five tiers of chamberlets are developed. The chamberlets are developed progressively, and usually regularly, appearing at the surface of the test in weathered or decorticated specimens. With the application of water or clove oil to the surface of the test, the pattern of the chamberlets is often seen, and sectioning is not always necessary. The aperture is generally slit-like to reniform in shape, and may be flush with the surface of the apertural face or raised on a surface almost at right angles to the face of the chamber. In some forms irregular depressions occur in the apertural face from the periphery to the aperture.



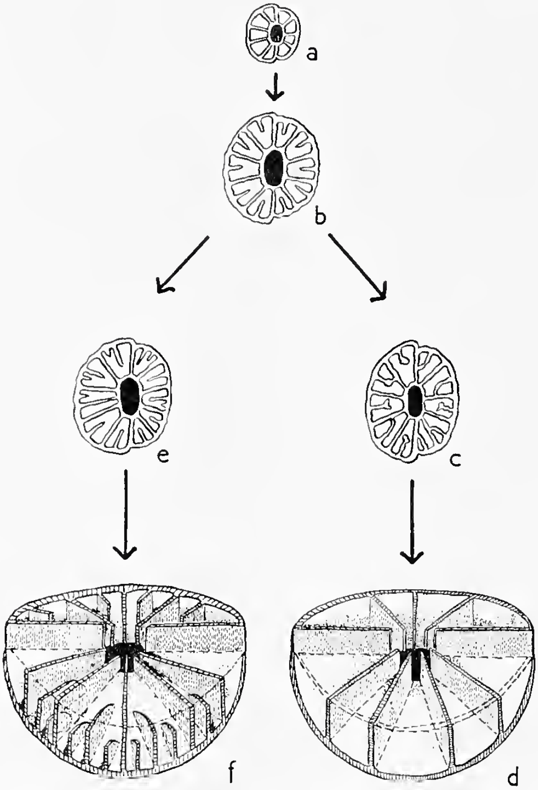
TEXT-FIG. 6. *Pseudotextulariella cretosa* (Cushman). All specimens in the U.S. National Museum, Washington, from the Lower Chalk, *Schloenbachia varians* zone, from Charing, Kent. *a*, 17624, holotype. *b*, 25295, holotype. *c*, *d*, 17625 paratypes.

Specimens. U.S. National Museum, Washington. 17624 (text-fig. 6*a*), holotype. 25295 (text-fig. 6*b*) holotype. 17625 (text-figs. 6*c*, *d*), paratypes.
Locality. Charing, Kent, England.
Horizon. Lower Chalk, *Schloenbachia varians* zone.

Development of the radial septa and chamberlets. Although somewhat irregular and variable, a progressive development of both the radial septa and tiers of chamberlets takes place in both ontogeny and phylogeny. The phylogeny, based on variation in successive populations occurring within the Cenomanian, is beyond the scope of the present paper. However, the general ontogenetic development is described below, and is shown in text-figs. 7 and 8.

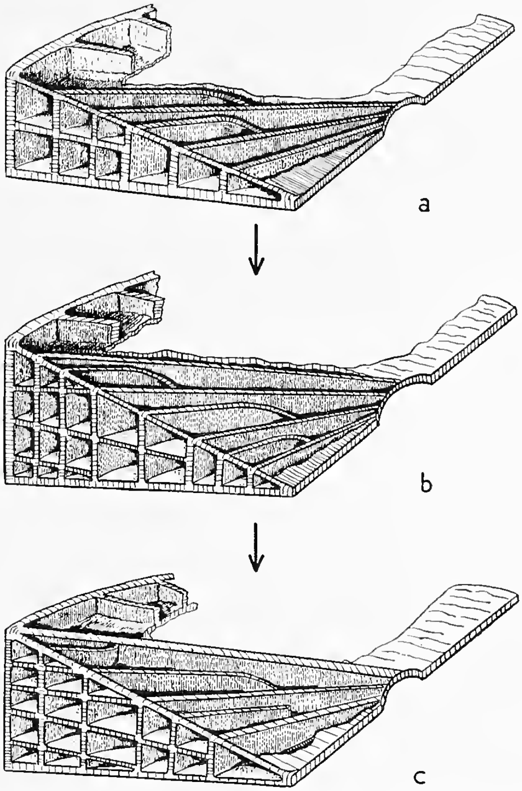
Two main trends in ontogenetic development are shown in text-figs. 7*a*–*f* in forms which only develop radial septa. Text-figs. 7*a*, *b*, *c*, *e* represent transverse sections of the biserial part of the test. Near the initial end (*a*) only a few vertical radial septa are formed, stretching from the periphery to join with a circular wall surrounding the apertural areas. This stage is rapidly followed by one in which the septa alternate in length, apparently forming two generations, one group reaching the circular central wall, whereas the other is shorter and confined to a small peripheral area.

This growth stage is shared by both main variants, but divergence now takes place in later growth stages. In text-fig. 7*c* the septa again are in two main groups, a longer set reaching the centre, and the peripheral group as in earlier growth stages. However, the latter may do one of two things. Usually they elongate until coalescence with the central wall results, or they become bifid or irregular, and sometimes bend, joining the longer sutures about half-way to the centre of the chambers. Text-fig. 7*d* shows the regular development of a few radial vertical septa, when the smaller peripheral septa have reached the centre. In both text-figs. 7*d* and *f* the central circular wall has been omitted for clarity. In the other trend (text-figs. 7*e* and *f*) the primary vertical septa reach the central wall, but secondary and even shorter tertiary septa are formed and confined to the peripheral part of the test. Often the smaller tertiary septa are arranged irregularly and do not usually occur in the gap between every primary and secondary septa. Also these secondary and tertiary septa are not the same height for their whole length, but taper rapidly towards the lower chamber wall. Text-figs. 8*a–c* are block diagrams con-



TEXT-FIG. 7*a–f*. *Pseudotextulariella cretosa* (Cushman). Diagrams to show the development of the radial partitions.

structed to show development of tiers of chamberlets by the growth of not only vertical radial septa, but several generations of horizontal septa parallel to the chamber sutures. Text-fig. 8*a* shows a few primary radial partitions developed, with secondary alternating partitions coalescing. Near the periphery one horizontal secondary septum is formed, confined to the peripheral area and producing two tiers of almost rectangular chamberlets.



TEXT-FIG. 8*a–c*. *Pseudotextulariella cretosa* (Cushman). Block diagrams showing the development of the radial and horizontal partitions.

A further development is shown in text-fig. 8*b*, where further horizontal septa are added, one above and one below the earlier secondary septum. The latter has now grown to extend almost to the centre of the test, whereas the two later septa again are short and confined to the peripheral zone of the test. Text-fig. 8*c* shows an even further development with four secondary septa of varying length, producing five tiers of chamberlets.

THE AFFINITIES OF THE CONICAL FORAMINIFERA

The relationships and development of the conical foraminifera from the Cretaceous to Recent are of considerable interest and importance. In spite of the numerous publications in which mention of these forms is made, little is known concerning their affinities.

As well as the genera dealt with in detail in earlier parts of this paper, suggestions are made below as to the possible derivation of some other Cretaceous forms.

There are two root-stocks from which most of the genera of conical foraminifera may have been derived, namely *Marssonella* and *Arenobulimina*. *Marssonella* consists largely of a biserial arrangement of the chambers which rapidly follows an initial part made up of one or two whorls, composed of three, four, or five chambers. As has already been pointed out, at certain horizons in the Upper Senonian there is a tendency for isolated specimens to produce simple radial partitions dividing the chambers. It is considered that this tendency is repeated to some degree at least three times in the history of the group.

(*a*) In the Cenomanian *Pseudotextulariella* occurs, a genus in which complex internal structures are developed. Radial partitions stretch towards the centre of the test and then are united in a wall surrounding a central circular hole. Later horizontal partitions and further generations of chamberlets are added, resulting in a genus with extremely complex internal structures.

(*b*) In the Upper Senonian, forms develop with a few simple radial partitions only occurring in the end-chambers.

(*c*) A genus found in the late Tertiary to Recent is *Textulariella*, in which a thick zone of radial partitions develops in the wall-zone, and does not reach far towards the centre. This character serves to distinguish this genus from *Pseudotextulariella*.

It is considered that these groups are somewhat similar repetitive forms which converge towards a common plan of development, but which do not produce identical forms. Text-fig. 9 shows the suggested affinities of the various conical genera.

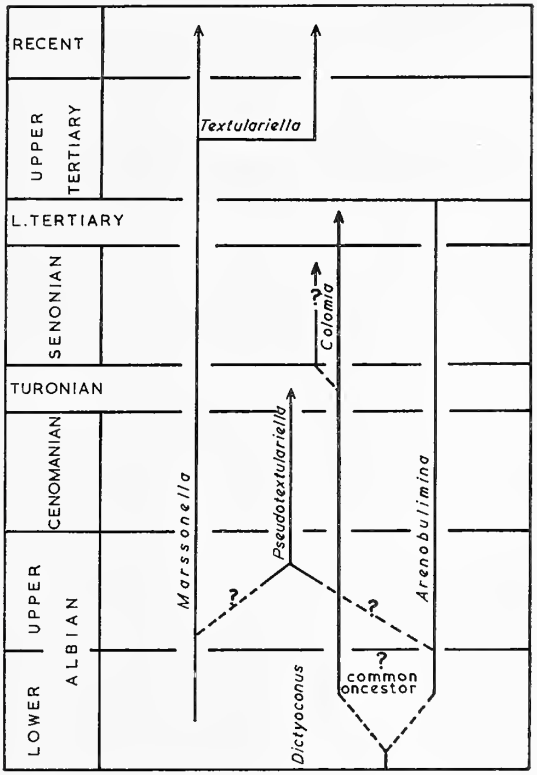
The initial coil in *Pseudotextulariella* suggests that it may have arisen from *Arenobulimina* (Barnard, *in* Barnard and Banner 1953). It is more probable, however, that *Marssonella*, *Pseudotextulariella*, and *Arenobulimina* have arisen at slightly different stratigraphical levels from either a common ancestor or closely similar ancestral stocks. Also the complex internal structures and the progression of these throughout the Cenomanian in *Arenobulimina* are closely parallel to those of *Pseudotextulariella*, and may show the close affinities between the two. It is probable that *Marssonella* is not the root-stock giving rise to *Pseudotextulariella*. *Arenobulimina* occurs first in the Albian in England and the evolution of this genus is the subject of a paper (Barnard and Banner) in preparation. In North America species of *Arenobulimina* appear to be few, and their history apparently terminates in Albian times, whereas in north-west Europe the genus continues and forms an important part of the Chalk faunas.

In the Albian of England there are a few species of *Arenobulimina* and these are associated with the argillaceous environments of the Gault clay and do not develop good internal structures. However, as soon as the Upper Greensand and Cenomanian facies, with their additional limestones, are encountered the internal structures develop in the species.

A form superficially similar to *Pseudotextulariella* is found abundantly in the Walnut Formation (Lower Albian) of Texas. This species, *Dictyoconus walnutensis* (Carsey), possibly related to a later Upper Cretaceous genus, *Colomia*, has recently been studied by Maync (1955).

Somewhat similar developments of chamberlets are shown in various groups of Cretaceous species belonging to the genera *Dictyoconus* and *Coskinolina* and those of

Pseudotextulariella. Although the distribution of these genera has not been studied in detail, it would appear that somewhat similar internal structures develop and evolve in almost the same pattern in different faunal provinces. *Dictyoconus* and *Coskinolina* appear in the Texas–Mexico basins, through Florida, and in the Tethyan areas of Europe, Spain, southern France, sometimes migrating farther north to occur in intermediate areas such as Aquitaine. *Arenobulimina* and *Pseudotextulariella* occur in the north-west European basins. The ranges of the two faunas do not coincide, although there is some overlap. *Dictyoconus* and *Coskinolina* reach their maximum development in the Albian, *Pseudotextulariella* in the Cenomanian, whereas *Arenobulimina* is longer ranged from Albian to Palaeocene, with several periods when development of certain characters reached a maximum.



TEXT-FIG. 9. Diagram showing the affinities of some genera of conical foraminifera.

In parts of the Upper Cretaceous basin of California, the genus *Colomia* has been recorded sporadically. This genus appears closely similar in many aspects to *Dictyoconus walnutensis* (Carsey), except that the development of internal structures may be sporadic, as with later forms of *Marssonella oxycona* Reuss in Europe. Certain authors (Hofker 1958, Cushman and Bermudez 1948) have recorded internal structures, whereas others (notably Bandy 1951) have not. It is possible that *Colomia* may not be closely related to *Dictyoconus*, as it is a calcareous genus.

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WEALDEN MAMMALIAN FOSSILS

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ABSTRACT. Only two of the previous identifications of specimens considered to be teeth of Wealden mammals can be accepted without reservation. A special collecting technique including both chemical and mechanical processes facilitated the discovery of eight more Wealden mammalian fossils. Five were found in the Cliff End Bone Bed, a part of the Ashdown Beds, and the remainder in the Paddockhurst Bone Bed, a part of the Grinstead Clay. These fossils give additional information about the morphology of the multituberculate *Loxaulax valdensis* and demonstrate the presence of a symmetrodont and eupantothere in England in the early (pre-Aptian) Cretaceous.

THE fossil record of Mesozoic mammals is limited. Large collections of mammalian fossils of late Jurassic age have been made in the Purbeck Beds of England and the Morrison Formation of the United States. The Albian mammalian fauna is known from fossils found in the Trinity Sand of Texas. The only record of mammals that certainly lived in the interim between the Purbeckian and Albian consists of the rare specimens discovered in the Wealden of England. Two mammals found in the Husin Series of Manchuria also may be of post-Purbeckian and pre-Albian age, but the correlation of the strata in which they were found is still open to question (see Patterson 1956, pp. 30–31). The first specimen considered to be a mammalian fossil discovered in the Wealden of England was described in 1891; in the two following decades four more specimens were found. After this initial activity almost fifty years elapsed before another Wealden mammalian fossil was discovered. In the autumn of 1960, working under the auspices of a National Science Foundation Postdoctoral Fellowship, I began a survey of British Mesozoic mammals and the localities at which they were found. At the suggestion of Dr. K. A. Kermack, one of the first localities visited was Cliff End, where three of the Wealden mammalian fossils had been found in a bone bed cropping out on the shore. Blocks of the bone bed found scattered along the beach proved to contain mammalian fossils. As word of my interest in Wealden mammals spread, I was told of another promising bone bed in Paddockhurst Park that also proved to contain isolated mammalian teeth. Some of these fossils were exhibited at a meeting of the Geological Society (Clemens 1960). This paper is an interim report on a research project that is being continued under the direction of Dr. K. A. Kermack of the Department of Zoology, University College, London.

All catalogue numbers cited are from the British Museum (Natural History) Catalogue of Fossil Mammalia.

PREVIOUS INVESTIGATIONS

In 1891 A. Smith Woodward announced the discovery of a tooth of a Wealden mammal. Two years later Richard Lydekker described another specimen and in 1911 Woodward reported on three more. Study of these fossils and the circumstances of their discovery has brought to light facts confirming the unpublished suggestions of several palaeontologists that the identification of some of the fossils as teeth of Wealden

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mammals is incorrect. The first fossil thought to be a Wealden mammalian tooth (M13134) was found by Charles Dawson in a bone bed within the Wadhurst Clay exposed in the 'Old Roar Quarry' near Hastings. It was an isolated tooth having both the heavily worn crown and root preserved. Later it was damaged and all that remains is a fragment of the root. Woodward (1891, p. 586) described the crown of the tooth as being '. . . supported by two roots, which are robust, of nearly equal size and depth, incompletely separated in the upper half and terminating obtusely'. Loss of parts of the tooth has revealed that, although deeply grooved on the surface, the root contains a single pulp cavity rather than two as would be expected if this structure were two incompletely separated roots.

After comparing this Wealden tooth (M13134) with haramiyid teeth and the M_2 of *Ctenacodon* (*Plagiaulax*) *minor*, Woodward tentatively identified it as the molar of a multituberculate and allocated it to the genus *Plagiaulax* under the provisional name *P. dawsoni*. The similarities on which this identification was based are neither numerous, detailed, nor fully convincing. Simpson (1928, p. 52) commented that the tooth '. . . is probably Plagiaulacid, although its generic and specific affinities are quite undeterminable'. The presence of a single pulp cavity in the root reduces the probability that the tooth is a plagiaulacid molar, which has two roots, and strongly suggests that it is not the tooth of a mammal.

In 1893 Lydekker identified another fossil (M5691) as an incisor of a Wealden multituberculate. In the discussion following the presentation of Lydekker's paper at the Geological Society, Sir John Evans recounted the history of the discovery of the tooth: 'He [Evans] found it at Hastings, in a block of Tilgate Grit which formed part of a heap by the side of the sea-shore, and almost immediately afterwards gave it to Prof. Prestwich, in whose collection it was mislaid for a period of over thirty years. On again coming across it, Prof. Prestwich placed it at the disposal of the speaker . . .' (Lydekker 1893, p. 283). In the course of the same discussion, Dawson stated: '. . . it was unfortunate that the specimen had been taken from a loose block, because at Hastings stones foreign to the district and miscellaneous drifted stones from the shore were frequently broken up for road-metal. From the limited view permitted him of the specimen that evening he was unable to identify the matrix as from the Hastings district; and he did not recognize the fragmentary specimen before them as a portion of a mammalian tooth.'

Dawson appears to have been alone in questioning the identification of this fossil as a mammalian tooth. Study of the specimen substantiates Lydekker's observation that there is no way of distinguishing it from a rodent incisor. Because it was and still is thought to be unlikely that the Rodentia had evolved as a discrete group in the Early Cretaceous and, because multituberculates possessed somewhat rodent-like incisors, Lydekker and others concluded that this tooth was probably a multituberculate incisor. Excluding the specimen in question, the available fossil record of multituberculates demonstrates that incisors closely resembling those of rodents were evolved only in one Tertiary subfamily, the Eucosmodontinae. The convergence was far from complete and isolated incisors of these and other multituberculates can be distinguished from the incisors of rodents (Jepsen 1937). On the basis of the size, curvature, and cross-section of the crown and the distribution of enamel, the tooth described by Lydekker can be identified as an incisor of a rodent. The only attribute of the fossil that precludes this identification is its supposed stratigraphic provenance. The fossil was preserved in a block of stone picked up on the shore. Its stratigraphic provenance was determined through identification of the enclosing sediment as 'Tilgate Grit', a name once applied to calcareous sandstones now known to be present at various levels within the Hastings Beds. This identification was challenged by Dawson and later Simpson (1928, p. 192) commented: 'The specimen, moreover, is not in such a sandstone [Tilgate Grit] but in a very crumbly clay, so that its exact level must be considered very dubious.'

To the best of my knowledge no teeth closely resembling the fossil described by Lydekker have been found *in situ* in English Wealden strata. The tooth from Hastings is similar in morphology and, superficially at least, in mode of preservation to upper incisors of *Theridomys sp.* found in argillaceous, Tertiary strata cropping out on the Isle of Wight and adjacent parts of the mainland. The nearest outcrops of these strata are over 70 miles away from Hastings. Similar incisors of rodents also have been found in Tertiary strata of the London basin that extend to within approximately 35 miles of Hastings. Dawson was first to suggest that the fossiliferous block might not have come from the Wealden cropping out near Hastings but might have been introduced from some other area. Although well removed from the Hastings district, the Tertiary strata of the Hampshire and London basins are not so distant as to preclude all possibility of the specimen being accidentally introduced from either area.

In summary, if an identification were based on dental morphology alone the tooth in question would be identified as a rodent incisor. The only controverting evidence is the supposed stratigraphic provenance of the fossil. The identification of the enclosing sediment as Tilgate Grit is incorrect, and there is no unequivocal evidence to support the former assignment to the Early Cretaceous. The block containing the fossil possibly was a fragment of a Tertiary stratum drifted on to the beach at Hastings or accidentally introduced during road construction. Although final judgement should be reserved until our knowledge of the morphology of Wealden multituberculates is more complete, the available evidence suggests that the fossil (M5691) probably is the incisor of a Tertiary rodent rather than a Wealden multituberculate.

In 1911 Woodward described three more specimens that had been discovered at Cliff End by P. Teilhard de Chardin and F. Pelletier, who were assisting Dawson. Two of these fossils are multituberculate teeth. One of them (M10480), the type of *Loxaulax valdensis* Simpson, had been described in detail by Woodward (1911, pp. 278–9) and Simpson (1928, pp. 49–50). The second (M10481) is probably a fragment of an M^2 of a member of the same species. Both teeth are still imbedded in sediment that is lithologically similar to the blocks of Cliff End Bone Bed found by our field parties. The third tooth was described by Woodward (1911, p. 278) as follows: '... most of the crown has decayed, but the two divergent roots are well displayed, the one somewhat stouter than the other'. This fossil was not recorded in the British Museum (Natural History) Catalogue of Fossil Mammalia in 1912 when the other two teeth from Cliff End were assigned specimen numbers. Recently a specimen was found in the collection with the following label: 'Mammal tooth, Fairlight, Ashdown Sand, N. Hastings, C. Dawson 15/1/1911.' This fossil, now catalogued as M20241, agrees with Woodward's brief description and probably is one of the fossils discovered by Teilhard de Chardin and Pelletier. The crown is almost completely destroyed; only a small band of enamel or enamel-like substance remains. The coronal dimensions are: length $=$ 3·1 mm., width $>$ 1·2 mm. The root consists of a large, cylindrical, grooved body approximately 1·8 mm.

long that terminates in two divergent branches, the largest of which is approximately 1·1 mm. long. Even though the root is bifid apically it does not resemble the roots of Late Jurassic or Early Cretaceous mammalian teeth. Also the teeth of these mammals are, for the most part, smaller than M20241. The mammalian affinities, if any, of this tooth will have to be regarded as indeterminable.

Thus of the fossils collected in and prior to 1911 only M10480 and M10481 remain as unquestionable Wealden mammalian teeth. The mammalian affinities of two of the other fossils, M13134 and M20241, are doubtful, and the tooth described by Lydekker, M5691, probably was not part of the dentition of a Wealden multituberculate. After 1911 no more Wealden mammalian fossils were discovered until 1960; but interest in the stratigraphy and the fauna of the Wealden did not decline. Of the studies carried on after 1911, the work of P. Allen, especially his reports on the stratigraphy (Allen 1959) and a study of Wealden bone beds (Allen 1949), and Simpson's (1928) review of Wealden mammals, are especially pertinent.

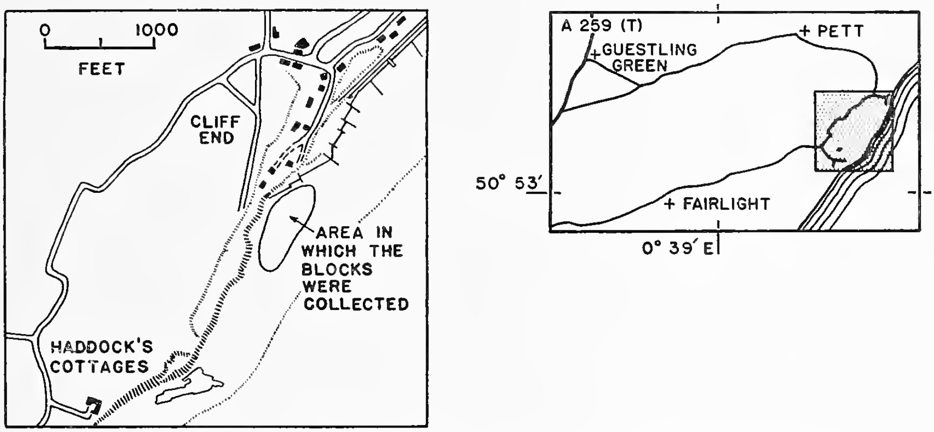
DESCRIPTIONS OF THE LOCALITIES AND THE MAMMALIAN FOSSILS

Grid coordinates given in the locality descriptions are those of the National Grid and lie in the 100-kilometre square 51 (TQ).

(1) CLIFF END BONE BED

Location and collecting technique. The exact locality where Teilhard de Chardin and Pelletier collected was not described in detail by Woodward (1911). Many years later Allen, using a description of the site obtained from Woodward in 1938, relocated the bone bed and published a locality description (Allen 1960*a*, p. 11) in which he stated: '. . . rapid erosion of the cliffs has re-exposed the celebrated bone-bed . . .'. On our collecting trips in the autumn of 1960 and the following spring an outcrop of the bone bed could not be found; apparently the forces of erosion had destroyed or covered what they once revealed. Loose blocks of bone bed containing the new mammalian fossils were, however, collected from the wave-cut platform and the shingle; most were found within 100 yards of the foot of the cliff. These blocks ranged in size from cobbles to a fragment of the stratum nearly 4 feet in diameter and were distributed over an area (text-fig. 1) extending northward from a point approximately 2,000 feet north-east of Haddock's Cottages (88751280) to a point near the northern end of the cliff (88851305). Because no bone beds could be found cropping out in the area, it is assumed that all the loose blocks were derived from the intermittently exposed Cliff End Bone Bed described by Allen.

The Cliff End Bone Bed is a thin stratum composed of the comminuted bones and teeth of fish, amphibians, reptiles, and, very rarely, mammals concentrated in a hard, calcareous, coarse sandstone. The stratum, part of the Ashdown Beds, is never more than 4 or 5 inches thick, and its upper surface is ripple-marked. In order to find the minute mammalian fossils a large quantity of rock, 2 or 3 hundredweights, had to be processed. After some experiment the following technique was found to be most efficient: The calcareous cement was dissolved with dilute formic acid (a 10 to 20 per cent. solution). The material that remained was washed and dried and then passed through a set of graded sieves. The coarser fraction, material caught in 12-mesh and coarser sieves, was sorted without further treatment. The finer fraction was placed in a mixture of bromoform or tetrabromethane and dibromethane to give the density required to separate the quartz from the residue of fossils and heavy minerals. This residue was then washed and sorted. Separating the quartz was of particular importance because it greatly reduced the volume of fine fraction that had to be sorted under a microscope.



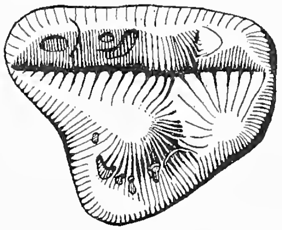
TEXT-FIG. 1. Cliff End Bone Bed, locality map. Area depicted in map on left shaded in the index map on right.

Mammalian fauna. The only fossils in earlier collections that remain as unquestionable teeth of Wealden mammals are the two multituberculate teeth found at Cliff End. One fossil, M10480, is the type specimen of *Loxaulax valdensis*; the other, M10481, is also a fragment of a multituberculate molar identified as '? *Loxaulax* sp.' by Simpson (1928). To date five more mammalian fossils have been discovered in blocks of the Cliff End Bone Bed.

Subclass ALLOTHERIA Marsh 1880
Order MULTITUBERCULATA Cope 1884
Family PLAGIAULACIDAE Gill 1872
Genus LOXAULAX Simpson 1928

Loxaulax valdensis (Woodward 1911)

Specimen M21098 (text-fig. 2). The presence of a small expansion of the crown lateral to the two rows of cusps, the morphology of the cusps, and the morphology and proportions of the crown (length = 2·4 mm., width = 1·9 mm.) indicate that M21098 is probably a right M². The first (anterior) and second lingual cusps are demarcated by a shallow groove, a deeper indentation separates the second and third, and the third and fourth are separated by a deep cleft. The first, second, and third lingual and two labial cusps are of approximately equal height; the fourth lingual cusp is lower. Both the posterior lingual and posterior labial cusps are slightly selenodont with the flatter face anterior. The anterior edge of the crown is concave to allow M² to abut against the posterolingual corner of M¹.



TEXT-FIG. 2. *Loxaulax valdensis* Simpson, right M², M21098, × 15. Occlusal view.

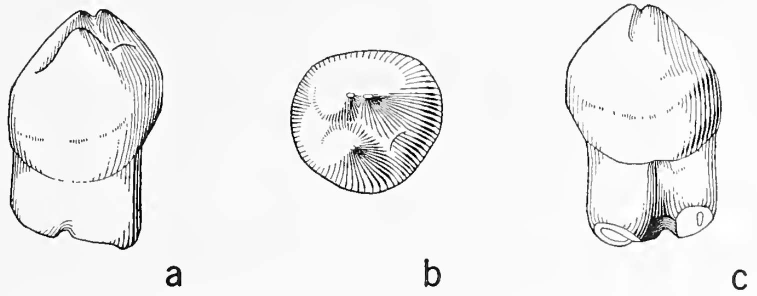
On the labial side of the anterior labial cusp there are several irregular, enamel-lined pits that do not appear to be the result of abrasion during mastication or post-mortem damage. The occlusal surface of the labial expansion of the crown slopes gradually from the anterior labial cusp to the edge of the crown; it is smooth and there is no evidence of a cusp or ridge.

Although the molars of plagiaulacids have only two main rows of cusps, in some species, for example, *Bolodon osborni*, the upper molars also have small expansions of the crown or cuspules in the areas in which a third cusp row is present on ptilodontid or taeniolabidid molars. Another character of the plagiaulacids is that the lengths of the molars of an individual are approximately equal while in members of the other families the first molars tend to be longer than the second. Simpson (1928, p. 49) tentatively identified the type specimen of *Loxaulax valdensis* as a left M_1. M21098 is only 0·4 mm. longer than the type specimen. Although not so pronounced as in the type, its posterior cusps are vaguely selenodont. The labial expansion of the crown appears to be relatively larger than that found on the M^2's of Purbeck multituberculates. In contrast the posterior cusps of the M^2 of *B. osborni*, which is smaller, have a more distinctly selenodont shape than those of M21098. Because M21098 is approximately the same length as the type of *L. valdensis*, because some of the cusps of both teeth are slightly selenodont, and because there is at present no evidence demonstrating the presence of more than one species of multituberculate in the Cliff End fauna, M21098 is provisionally allocated to *L. valdensis*. Future collections will no doubt yield evidence of other multituberculates. However, for the purposes of this preliminary report the best procedure is to refrain from the introduction of species on the probability that they will be validated by subsequent discoveries.

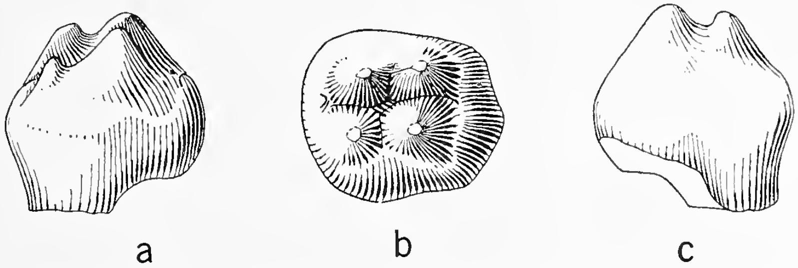
A comparison of M21098 with M10481, a fragment of a molar identified as '? *Loxaulax* sp.' by Simpson (1928, p. 50), suggests that the orientation of the fragment proposed by Simpson is not correct. If M10481 be regarded as a fragment of the posterior end of an M^2, then a number of resemblances to M21098 are apparent. The cusps of M10481 that Simpson thought might correspond to the 'antero-external' cusps of the type specimen are comparable to the posterior lingual cusps of M21098. The labial side of the base of the anterior labial cusp of M10481, using the orientation proposed here, is slightly enlarged, suggesting the presence of a labial expansion similar to that of M21098. The preserved cusps of M10481 differ from their counterparts on M21098 in that the posterior lingual cusp is as high as, but not so well separated from, the penultimate lingual cusp. Differences of this kind have been found in large samples of the molars of ptilodont multituberculates and cannot be accorded great significance.

Specimen M21099 (text-fig. 3). This tooth is a plagiaulacid, anterior upper premolar, that is, P^1, P^2, or P^3. The bulbous crown is surmounted by three main cusps and a small cuspule that is little more than a ridge on the surface of the enamel. Coronal dimensions are: length = 1·4 mm., width = 1·2 mm. There are two distinct but not divergent roots. M21099 closely resembles the P^3 of *Bolodon osborni*, which has three main cusps and an anterolabial cuspule.

Specimen M21106 (text-fig. 4). There are four main cusps on the crown of this anterior upper premolar. Two of them, probably the lingual cusps, are higher than their lateral counterparts. The labial cusps are of different size; judging from the morphology of other multituberculate premolars the smaller cusp can be identified tentatively as the anterolabial cusp. There is a small cuspule anterior to the anterolingual cusp and another cuspule posterior to the posterolabial cusp. The crown is 0·9 mm. long and 0·8 mm. wide and was supported by two roots.



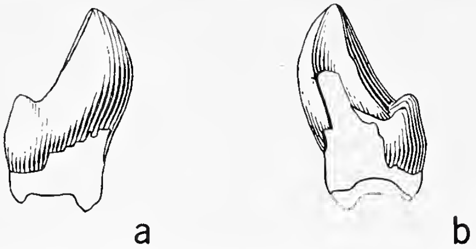
TEXT-FIG. 3. *Loxaulax valdensis* Simpson, anterior upper premolar, probably a left premolar, M21099, ×15. *a*, Labial view; *b*, occlusal view; *c*, lingual view.



TEXT-FIG. 4. *Loxaulax valdensis* Simpson, anterior upper premolar, probably a right premolar, M21106, ×30. *a*, Labial view; *b*, occlusal view; *c*, lingual view.

Most of the anterior upper premolars of Jurassic plagiaulacids have three main cusps. The P^3 of *Bolodon osborni* that has a small fourth cusp or cuspule and the P^3 of *Psalodon potens* could be considered exceptions. The anterior upper premolars of ptilodontids have, in many species, a more complex cuspation. M21106, which has four main cusps, is more closely comparable to anterior upper premolars of certain Late Cretaceous ptilodontids. Probably M21106 is not a P^4 or P^5, because in Jurassic plagiaulacids these teeth are proportionately longer relative to width and have more than four cusps. It can be suggested that M21099, which is the larger and has a simpler crown, is a P^1 or P^2, and M21106 is a P^2 or P^3. Both teeth are of the size that would be expected for premolars of *Loxaulax valdensis* and are provisionally allocated to this species. If these identifications are correct the premolar dentition of *L. valdensis* is slightly more ptilodont-like than those of the Jurassic plagiaulacids.

Specimen M21100 (text-fig. 5). One side of the crown of this single-rooted incisiform tooth is smooth and convex; the other is divided into three concave facets. There are three small cuspules at the base of the medial facet. None of the incisors preserved in English Jurassic mammalian fossils closely resembles this tooth. The lower incisors of *Trioracodon ferox* and *Spalacotherium tricuspidens* are grossly similar but the concave sides of their crowns are not subdivided and basal cuspules are not present. Closer resemblances can be found to the I^2 of the American Jurassic plagiaulacid *Psalodon fortis*, and the upper incisors of some Late Cretaceous and early Tertiary ptilodontids. Therefore M21100 is provisionally identified as an upper incisor of a multituberculate and allocated to *Loxaulax valdensis*.

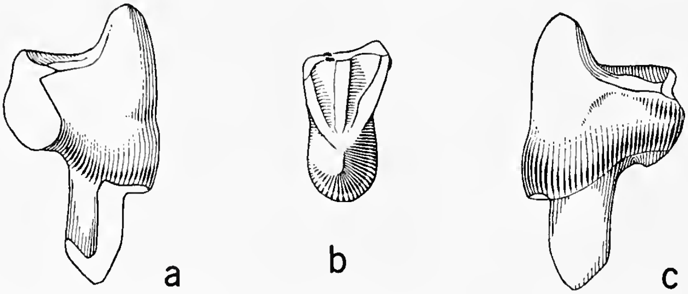


TEXT-FIG. 5. *Loxaulax valdensis* Simpson, probably an upper incisor, M21100, ×7·5. *a* and *b*, Lateral views.

Subclass THERIA Parker and Haswell 1897
Infraclass PANTOTHERIA Simpson 1929
Order EUPANTOTHERIA Kermack and Mussett 1958
Family DRYOLESTIDAE Marsh 1879
Genus cf. MELANODON Simpson 1927

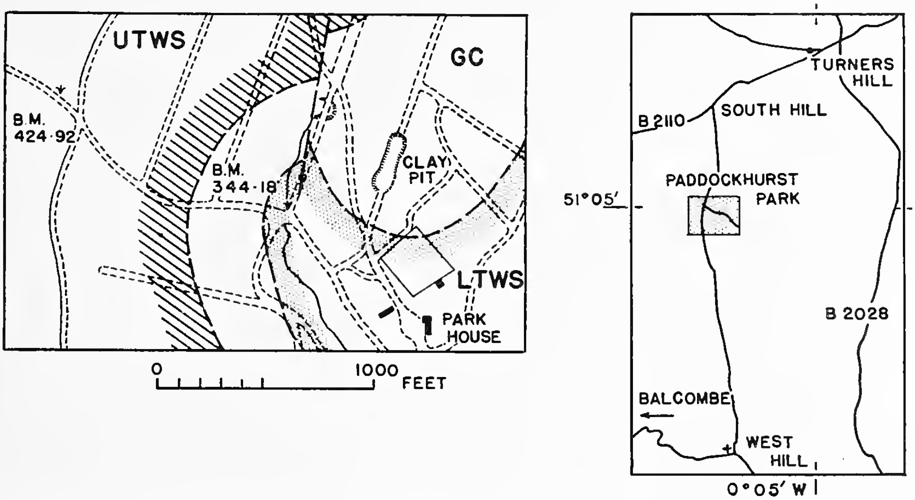
cf. *Melanodon goodrichi* Simpson 1929

Specimen M21101 (text-fig. 6). The fossil consists of the lingual part of the crown and part of the lingual root of an upper molar of a eupantothere. The lingual cusp is high and from its slope three prominent, heavily worn ridges extend labiad. Even though the specimen suffered post-mortem abrasion, the facets on the ridges are so distinct that they must have been well developed prior to the death of the individual. One of the lateral facets is slightly expanded suggesting the presence of a small cusp.



TEXT-FIG. 6. Cf. *Melanodon goodrichi* Simpson, fragment of an upper molar, M21101, ×15. *a*, Mesial view; *b*, occlusal view; *c*, distal view.

The Cliff End fossil differs from the molars of the species of *Amblotherium* in the presence of a large, distinct, median transverse ridge; a structure not present on the molars of *A. pusillum* and small on *A. nanum* molars. The median transverse ridges on molars of *Kurtodon pusillus* are larger and more distinct than those on the molars of *A. nanum*, but not so prominent as their counterpart on M21101. Also neither of the lateral transverse ridges on the molars of *K. pusillus* have an expansion similar to that found on one of the lateral transverse ridges of M21101. As far as can be determined from the illustrations, M21101 is closely comparable to molars of *Melanodon goodrichi* from the American Morrison Formation (Simpson 1929, pl. xv, figs. 1, 2). The molars of the type specimen of *M. goodrichi* have three distinct transverse ridges, there is an expansion of the posterior transverse ridge immediately labial to the lingual cusp, and the transverse ridges appear to have wear facets along their crests. Although not to be construed as a positive or even provisional identification, on the basis of the few available characters the comparison with *M. goodrichi* appears to be close.



TEXT-FIG. 7. Paddockhurst Bone Bed, locality map. Area depicted in map on left shaded on the index map on right. Geologic details taken from a hitherto unpublished map by Professor J. H. Taylor. Abbreviations: UTWS, Upper Tunbridge Wells Sand; GC, Grinstead Clay; LTWS, Lower Tunbridge Wells Sand.

(2) PADDOCKHURST BONE BED

Location and collecting technique. This bone bed was discovered by Professor J. H. Taylor in the course of mapping the geology of Paddockhurst Park. The fossiliferous stratum cropped out in a now abandoned clay pit (53281334) near a park house south-west of Turners Hill (text-fig. 7). The bone bed, which is part of the Grinstead Clay, is a grey, shell-rich limestone. The vertebrate fossils concentrated in it are comminuted but are not so fragmentary or heavily abraded as those found in the Cliff End Bone Bed. During the autumn of 1960 Kermack and I were fortunate to receive several samples of the bone bed. In January 1961 with the help of Professor Taylor, Dr. Cox, and Miss Lees we collected all the fragments of the bone bed that were still visible. Further collecting will involve a large amount of preliminary work for in addition to slumping of the pit walls and the presence of luxuriant undergrowth, a number of trees have blown over and toppled into and across the pit.

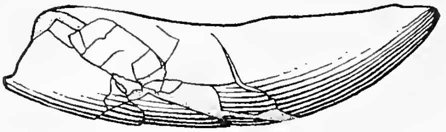
The process used to free the vertebrate fossils from the rock is similar to that applied to the Cliff End Bone Bed. After the rock had been treated with dilute formic acid, usually all that remained with the fossils was a small residue of clay and ferruginous material.

Some of the residual clay could be broken down by thoroughly washing and drying the material left after the acid treatment and then placing it in a hydrogen peroxide solution (30 vol.). On completion of the chemical treatment the fossils and other residual materials were passed through a graded set of sieves. The finer fractions were sorted with the aid of a binocular microscope.

Mammalian fauna. To the best of my knowledge the specimens described below are the only mammalian fossils discovered in the Paddockhurst Bone Bed.

? Subclass ALLOTHERIA Marsh 1880

Specimen M21102 (text-fig. 8). The crushed root is long and appears to have been of approximately the same diameter throughout its length, but it may have been constricted apically. One side of the crown is a shallow, concave basin that is subdivided by a low, longitudinal ridge; the other side (shown in text-fig. 8) is convex and smooth. The tip of the crown has been blunted by wear and the eminence behind the apex may be the base of a cusp. Among the Mesozoic mammals only the multituberculates are known to have had large, long, somewhat gliriform incisors; therefore M21102 is allocated with a query to the Subclass Allotheria.



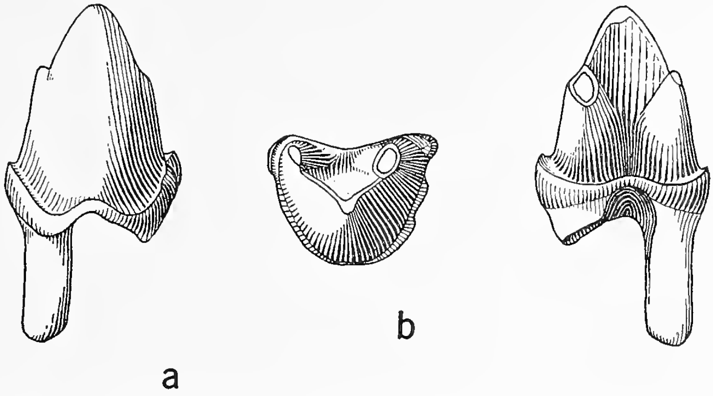
TEXT-FIG. 8. ?Allotherian, incisor, M21102, ×9. Lateral view.

Subclass THERIA Parker and Haswell 1897
Infraclass PANTOTHERIA Simpson 1929
Order SYMMETRODONTA Simpson 1925
Family SPALACOTHERIIDAE Marsh 1887
Genus cf. SPALACOTHERIUM Owen 1854

cf. *Spalacotherium tricuspidens* Owen 1854

Specimen M21103 (text-fig. 9). The paraconid and metaconid of this left lower molar are close to the base of the protoconid, separated from it by shallow grooves. The basal cingulum encircles the crown, and a small anterior and a slightly larger, posterior cingular cusp are present. On the posterolabial side of the crown there are two indentations in the cingulum; probably the lingual indentation received the anterior end of the following molar. The convex lingual side of the crown is higher than the labial; the dimensions of the crown are: length = 0·80 mm., width = 0·55 mm.

The acute angle formed by the trigonid cusps and the presence of a continuous lingual cingulum indicate that M21103 is a molar of a spalacotheriid symmetrodont. Five genera have been allocated to this family: the Late Jurassic *Spalacotherium*, *Tinodon*, *Eurylambda*, and *Peralestes* (based on an upper dentition and probably a synonym of *Spalacotherium*) and the Early Cretaceous *Spalacotheroides*. The molars of *Tinodon* differ from M21103 in their wide-angled trigonid and the absence of a labial cingulum. Among the presently known genera of spalacotheriids, *Eurylambda*, known only from an upper molar, probably is most closely related to *Tinodon*. Allocation of these two genera to the Spalacotheriidae, the family to which M21103 certainly pertains, has been questioned recently by Patterson (1956, p. 87). M21103 is more closely comparable to the molar of *Spalacotheroides*, but it differs in several important characters. The angle formed by the trigonid cusps of the *Spalacotheroides* molar is more acute, the crown is shorter relative to its width, and the basal cingulum is not continuous around the protoconid. M21103 is smaller than any of the molars that have been referred to *Spalacotherium tricuspidens*, but otherwise it resembles any of the anterior molars of this species. The posterior molars of *S. tricuspidens*, particularly M_7, differ from the more anterior molars in the smaller size of the protoconid and greater separation of the cusps of the trigonid. The length of an anterior molar, M_1 to M_5, of *S. tricuspidens* ranges from 1·6 mm. to 1·8 mm. If M21103 is correctly identified as an anterior molar its smaller size (length = 0·80 mm.) indicates that it was part of the dentition of a spalacotheriid distinctly smaller than *S. tricuspidens*. In themselves this difference in size and the temporal separation of the symmetrodonts found in the Paddockhurst Bone Bed and the Purbeck Beds do not warrant the establishment of a new species. Because there is an excellent chance that more material of this Wealden symmetrodont will be discovered, M21103 has not been assigned to a genus or species; only a comparison with *Spalacotherium tricuspidens* is suggested.

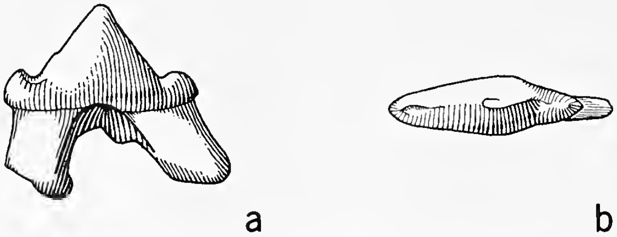


TEXT-FIG. 9. Cf. *Spalacotherium tricuspidens* Owen, left lower molar, M21103, × 30. *a*, Labial view; *b*, occlusal view; *c*, lingual view.

? Subclass THERIA Parker and Haswell 1897

Specimen M21104 (text-fig. 10). The crown of this small, trenchant premolariform tooth (length 0·85 mm., width 0·25 mm.) consists of a large, central cusp and smaller anterior and posterior accessory cusps. On one side of the crown there is a short ridge on the slope of the anterior accessory cusp and a longer but less distinct, cingulum-like expansion of the base of the crown on the posterior half of the central cusp. The two well-separated and divergent roots, which appear to be complete, have narrowly oval cross-sections; their length and disposition suggest that M21104 is a deciduous premolar.

Identification of M21104 poses a number of problems. Considering the roster of mammals that could be expected in an Early Cretaceous fauna only the representatives of one order, Multituberculata, lacked premolars grossly similar to M21104. In spite of the lack of great morphologic differentiation, the premolars of other Late Jurassic and, presumably, Early Cretaceous mammals differ in a few minor characters that might be of taxonomic significance. The premolars of triconodonts have at least a lingual cingulum or a definite expansion of the lingual base of the crown. Anterior and posterior accessory and cingular cusps are common. The roots of the permanent premolars are close together, nearly parallel, and almost twice as long as the crown is high. The DP_4 of *Triconodon mordax*, the only triconodont deciduous premolar discovered so far, is molariform. It appears unlikely that M21104 is a triconodont premolar. Allocation to the Order Docodonta also can be regarded as improbable for the premolars of *Docodon*, a Late Jurassic member of this order, have a distinct lingual cingulum and exhibit other differences in morphology. The premolars of many pantotherian species have a lingual cingulum, but in some species of eupantotheres—for example, note the upper premolars of *Amblotherium pusillum*—basal cingula are indistinct or absent. The Paddockhurst Bone Bed is high in the sequence of Wealden strata and mammals of eutherian–metatherian grade might have been present at the time it was deposited. M21104 is a type of premolar that might be expected in such a mammal. In summary, M21104 is certainly not a multituberculate premolar and probably not a triconodont or docodont premolar. Its allocation to the subclass Theria is based on both a process of elimination and the observation that the premolars of some Mesozoic therians lack a basal cingulum.



TEXT-FIG. 10. ? Therian, premolar, M21104, ×30. *a*, Lateral view; *b*, occlusal view.

STRATIGRAPHY

Although no attempt will be made to describe the stratigraphy of the Cliff End and Paddockhurst Bone Beds in detail, a few comments are necessary in order to interpret the significance of the mammalian fossils.

Derived Upper Kimeridgian and basal Portlandian ammonites and other invertebrates were discovered by Allen (1960*b*) in the Top Lower Tunbridge Wells Pebble Bed. This would suggest that the Wealden mammalian fossils, especially those found in the coarse sands of the Cliff End Bone Bed, might have been derived from older deposits. The Ashdown Beds in which the Cliff End Bone Bed occurs have been interpreted by Allen (1959) as delta-face and shore-face deposits formed during a period of deltaic advance. As would be expected in a unit of this origin, the vertebrate fossils from the Cliff End Bone Bed are comminuted, rolled, and abraded. However, most of the specimens of derived Jurassic ammonites found in the Top Lower Tunbridge Wells Pebble Bed are internal casts of parts of a camera or one or two camerae, the largest being approximately half a whorl (Arkell 1960); and all the derived invertebrates found in this pebble bed give evidence of transport and extended or intensive weathering. It is doubtful if the small mammalian fossils found in the Cliff End Bone Bed could have survived similar weathering and transport in addition to the fragmentation and abrasion involved in their concentration and deposition on the delta face. In contrast to the Ashdown Beds, the Grinstead Clay has been interpreted as a unit deposited during the lacustrine transgression of the Lower Tunbridge Wells delta (Allen 1959). The vertebrate fossils found in the Paddockhurst Bone Bed appear to be less fragmented and abraded than those found in the Cliff End Bone Bed, indicating that they too probably were not derived from older strata.

Additional evidence that the Cliff End mammals were not derived from Jurassic beds comes from a study of the animals themselves. The little that is known of the dentition of *Loxaulax valdensis* suggests that this species had a slightly more ptilodont-like dentition than the Purbeckian plagiaulacids. Assuming that the ptilodont multituberculates evolved from a plagiaulacid ancestor, the stage of evolution of *L. valdensis* suggests that the species is of post-Purbeckian age. The differences between the other Wealden mammals and their Purbeckian counterparts can also be interpreted as being indicative of a post-Purbeckian age. However, knowledge of the phylogeny of Mesozoic mammals is far from complete and any age-determination based on an assessment of the stages of evolution of these mammals can only be regarded as a suggestion. Finally, Allen (1960*b*) has determined that the derived Jurassic fossils found in the Top Lower Tunbridge Wells Pebble Bed were transported into the basin by a river flowing from the north. In contrast he found that the pebbles in the Cliff End Bone Bed were brought in from the north-east. Although the latter sediments contain glauconitic sand apparently derived from Jurassic strata, Upper Kimeridgian and basal Portlandian pebbles from the north-east are absent or rare. None of these lines of evidence conclusively demonstrates that the mammalian fossils found in the Wealden bone beds were not derived from older strata, but in concert they make this improbable.

Neither a precise determination of the stratigraphic position of the Cliff End Bone Bed within the Ashdown Beds nor an exact correlation of its time of deposition with the standard chronology based on the European marine sequence has been accomplished as yet. Currently the bulk of the Wealden of England is regarded as being of post-Tithonian age (Allen 1955, 1959, and Hughes 1958). Certainly the fossil localities are of pre-Aptian age. The differences between members of the Cliff End and Purbeck mammalian faunas suggest, but do not in themselves confirm, that the Cliff End Bone Bed is younger than the mammal-bearing strata of the Purbeck Beds. Hughes (1958), on paleobotanical evidence, allocates the Ashdown Beds to the Valanginian. Allen (1955, 1959) has correlated the period of deposition of the Ashdown Beds with the Berriasian regression. Thus a post-Purbeckian age is indicated for the Cliff End Bone Bed. The Paddockhurst Bone Bed is part of the Grinstead Clay, a unit stratigraphically higher than the Ashdown Beds. Using paleobotanical data, Hughes (1958) allocated the Tunbridge Wells Sandstone, which includes the Grinstead Clay, to the later Hauterivian. Allen (1959) suggested that the Grinstead Clay was deposited during a lacustrine transgression associated with later Valanginian or early Hauterivian changes in the level of the Neocomian sea in the Paris basin.

In summary, it appears that the Wealden mammalian fossils were not derived from older strata. The mammalian fauna of the Cliff End Bone Bed is probably of early Neocomian age, whereas that of the Paddockhurst Bone Bed is distinctly younger. Both faunas are post-Purbeckian and pre-Aptian in age.

CONCLUSION

The discovery of these few Wealden fossils has increased knowledge of the morphology of the plagiaulacid multituberculate *Loxaulax valdensis*; extended the demonstrated range of the Eupantotheria, previously limited to the Middle and Late Jurassic; and established the presence of the Symmetrodonta in England in the Early Cretaceous. The mammalian fauna of the Cliff End Bone Bed, which is part of the Ashdown Beds, consists of *L. valdensis* and a dryolestid eupantothere; the fauna of the younger Paddockhurst Bone Bed includes a spalacotheriid symmetrodont and possibly another therian and a plagiaulacid. These discoveries indicate that with proper collecting techniques more mammalian fossils probably can be obtained from these and other Wealden bone beds.

Acknowledgements. My sincere thanks are extended to Dr. K. A. Kermack for his continuing and extensive help and encouragement. I am indebted also to Professor J. H. Taylor for showing us the Paddockhurst Bone Bed and giving me the opportunity to quote from his unpublished work on the geology of the area, and to Professor P. Allen for specimens and helpful comments. I also gratefully acknowledge the assistance received from Drs. E. I. White and A. Sutcliff, who gave me the privilege of studying material under their care, and Dr. Barry Cox, Mr. H. A. Toombs, and Mr. B. Newman, who allowed me to process their samples of the Paddockhurst Bone Bed. Miss Patricia Lees and Mrs. Francis Mussett have provided valuable assistance in both field and laboratory work. Thanks are due also to Professor P. B. Medawar for making available the necessary laboratory facilities. The field and laboratory work was carried out during the tenure of a National Science Foundation Postdoctoral Fellowship at University College, London, and this report completed at the Museum of Natural History, The University of Kansas.

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LOWER PERMIAN BRYOZOA FROM WESTERN AUSTRALIA

by JUNE R. P. PHILLIPS ROSS

Abstract. Scattered bryozoan localities in the Lyons Group contain three species of *Stenopora*, *S. dickinsi* sp. nov., *S. fisheri* sp. nov., and *S. lyndoni* sp. nov., that show little similarity to previously described species. The fenestellid *Polypora lyndoni* occurring at all the bryozoan localities studied has close affinities with two species from the Lower Permian of eastern Australia and one species from the Asselian of Timor. These species appear to be primitive members of a group of species described from the upper part of the Sakmarian Series of the Urals.

Fossils are generally rare and sporadic in the Lyons Group, which crops out in a belt extending from the Lyndon River to the Wooramel River in the Carnarvon (North-West) Basin, Western Australia (text-fig. 1). The group is about 4,600 feet thick in the Moogooree area and thins southward to 2,640 feet in the Wooramel River area (Condon 1954, pp. 40, 43).

The Lyons Group begins with the Permian? lepidodendroid plant-bearing Harris Sandstone, which rests conformably on the Pre-Cambrian basement, and consists of tillite, greywacke, siltstone, sandstone, and conglomerate. It is conformable with the overlying Permian (Upper Sakmarian or Lower Artinskian) Callytharra Formation (Table 1).

Previous studies of fossils from the Lyons Group include description of brachiopods by Prendergast (1943), Coleman (1957), and Thomas (1958), description of molluscs by Dickins (1956, 1957), description of two species of Foraminiferida by Crespin (1958), and a record of brachiopods, molluscs, Bryozoa, and crinoids by Dickins and Thomas (1959). The Bryozoa occur in thin, local calcareous lenses within the tillite, sandstone, and conglomerate beds.

Age of the fauna of the Lyons Group. From the faunal data in strata overlying the Lyons Group, Teichert (1941, 1947) considered the Lyons Group to be Sakmarian in age. Later studies of the faunas from the Lyons Group, summarized by Dickins and Thomas (1959), and from the overlying strata have supported Teichert's findings.

Relations of bryozoan species in the Lyons Group. The scattered bryozoan collections that were examined from the Lyons Group indicate that the bryozoan species range laterally and vertically throughout the group. At locality ML 6, considered to be in the lower part of the Lyons Group, the bryozoans *Stenopora dickinsi* sp. nov., and *Polypora lyndoni* sp. nov. occur with the following brachiopods and molluscs listed by Dickins and Thomas (1959): *Trigonotreta*? sp. indet., *Neospirifer* sp. indet., *Linoproductus* (*Cancrinella*) *lyoni* Prendergast (1943), Rhynchonellacea gen. indet., Rostrospiracea? gen. indet., *Deltopecten lyonsensis* Dickins (1957). Higher in the succession in the upper part of the Lyons Group in the northern part of the Carnarvon Basin at locality ML 90, the bryozoans *Stenopora dickinsi*, *S. lyndoni*, and *Polypora lyndoni*, are associated with

[Palaeontology, Vol. 6, Part 1, 1963, pp. 70–82, pl. 8–11.]

Stutchburia variabilis Dickins (1957) and *Deltopecten lyonsensis* Dickins (1957); and at localities ML 106, ML 107, and ML 109 in the upper part of the Lyons Group the bryozoans *Stenopora dickinsi* and *Polypora lyndoni* occur with the following fossils listed by Dickins and Thomas (1959): *Trigonotreta* sp. nov., *Linoproductus* (*Cancrinella*) *lyoni* Prendergast (1943), *Neospirifer* sp. nov., *Pseudosyrinx* sp. nov., *Stutchburia variabilis* Dickins (1957), *Astartila condoni* Dickins (1957), *Cleobis sp.*, *Eurydesma* sp. indet., *Schizodus crespinae* Dickins (1957), *Deltopecten lyonsensis* Dickins (1957), *Aviculopecten* sp. indet., *Peruvispira umariensis* (Reed) (1928), *Mourlonia? lyndonensis* Dickins (1957), *Keeneia carnarvonensis* Dickins (1957), Calceolispongidae gen. et sp. nov., *Conularia sp.*, and *Calcitornella stephensi* (Howchin) (1894).

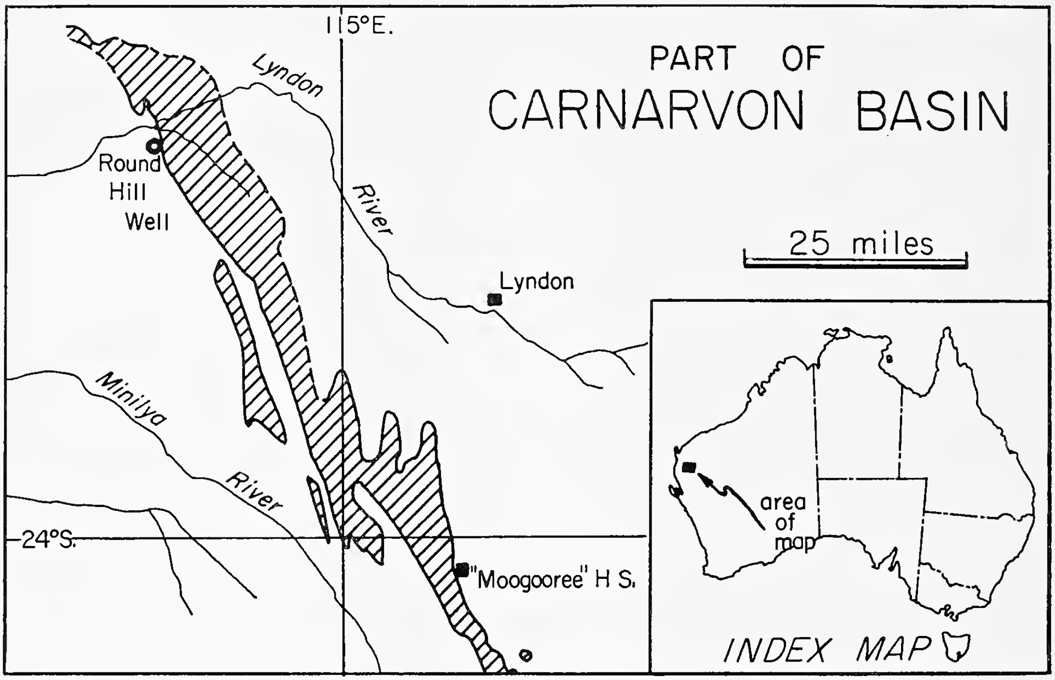
TABLE 1

Suggested correlation of Permian units referred to in text

Ural Mts., U.S.S.R.	*Carnarvon Basin, Western Australia*	*Yarrol Basin, Queensland, Australia*	*Hunter River Valley, N.S.W., Australia*	*South Coast, N.S.W., Australia*	*Eastern Tasmania, Australia*	*Timor*	*Glass Mts., Texas, U.S.A.*	
Kungurian				—?—?— Westley Park Tuffs —?—?—				
Artinskian	—?— Callytharra Formation —?—							
Sakmarian		—?—?—				—?—		
Asselian	Lyons Group —?—	Lake Creek Beds	—?—?— Allandale Formation (*Eurydesma cordatum*) —?—?—		—?—	Bitauni Beds	Lenox Hills Formation	Wolfcampian
			Lochinvar Formation		Berriedale Limestone		Neal Ranch Formation	

The fenestellid *Polypora lyndoni* is closely comparable with two species of *Polypora* occurring in the lower Permian of eastern Australia; one of the species, *Polypora keppelensis* Crockford 1962, is from the Lake Creek Beds, Queensland, and the other, *P. pertinax*, is from the *Eurydesma cordatum* horizon, New South Wales. It also closely resembles *P. tripliseriata* Bassler from the Asselian Bitauni Beds of Timor. All these species appear to be primitive members of a group of species including *P. tuberculifera*, *P. punctata*, *P. subvariicellata*, and *P. nadinae* described from the Sterlitamak Beds (upper part of the Sakmarian Series) of the Urals.

The stenoporids from the Lyons Group show little similarity with previously described species from Australia. However, few species of *Stenopora* have been described from the lower part of the Permian succession in eastern Australia. The four bryozoan species of the Lyons Group show no similarities with those in the overlying Callytharra Formation. The genera occurring in the Callytharra Formation described by Crockford (1951), including *Hexagonella*, *Evactinopora*, *Protoretepora*, *Penniretepora*, *Ramipora*, *Streblotrypa*, *Rhombocladia*, and *Streblocladia*, were not found in the Lyons Group.



TEXT-FIG. 1. Index map to bryozoan collection localities in the Lyons Group, Carnarvon Basin, Western Australia. Hatching indicates outcrop area of Lyons Group. Map after M. A. Condon, J. M. Dickins, and G. A. Thomas.

Acknowledgements. I express my sincere thanks to Drs. J. M. Rayner, Director; N. H. Fisher, Chief Geologist; and J. M. Dickins, Palaeontologist; of the Bureau of Mineral Resources, Australia, for the loan of the specimens examined from the Lyons Group. Dr. J. M. Dickins kindly helped locate the material and compiled information about the collection localities and their stratigraphic position.

Repository. CPC—Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra, A.C.T., Australia.

SYSTEMATIC DESCRIPTIONS

Order TREPOSTOMATA

Family STENOPORIDAE Waagen and Wentzel

Genus STENOPORA Lonsdale

1844 *Stenopora* Lonsdale, p. 178.
1845*a* *Stenopora* Lonsdale, p. 262.
1943 *Stenopora* Lonsdale; Crockford, p. 261.
1962 *Stenopora* Lonsdale; Ross and Ross, pp. 41, 42.
1929 *Ulrichotrypa* Bassler, p. 55.

1844 *Tubuliclidia* Murchison and Verneuil [*nomen nudum*], pp. 497–8.
1845*b* *Tubuliclidia* Murchison, Verneuil, and Keyserling [*nomen nudum*], p. 221.
1949 *Tubuliclidia* Duncan [*nomen nudum*], p. 131.

Type species. Stenopora tasmaniensis Lonsdale, 1844, p. 161, from the Permian, Tasmania, Australia.

Diagnosis (after Crockford 1943). Colonies are ramose, encrusting, laminar, massive, or frondescent. The zooecial tubes have thin walls in the axial region and irregularly thickened, moniliform walls in the peripheral region. Diaphragms are extremely rare or absent. Acanthopores are well developed, are generally large and very numerous, and commonly occur in two series. Mesopores lack diaphragms and are generally fewer in number than the zooecia. Monticules, and less commonly maculae, are generally present except for some ramose species which lack them.

Stenopora dickinsi sp. nov.

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

Type material. Holotype CPC ML 109–2, and paratypes CPC ML 109–1, ML 109–3; from the upper part of the Lyons Group, locality ML 109, 410 feet west of ML 106 in the Lyndon River area. Paratypes CPC ML 106–1 to ML 106–5; from the upper part of the Lyons Group, locality ML 106, approximately 3 miles north-north-east of Round Hill Well, Lyndon River area. Paratypes CPC ML 90–2, ML 90–4; 45 feet below the top of the Lyons Group, approximately 2 miles north-north-east of Round Hill Well, Lyndon River area.

Description. Colonies are slender, branching cylindrical stems, the fragments studied being 1 to 2 cm. in length (Pl. 9, figs. 2, 4). Maculae and monticules were not observed. Some colonies display broad, flat, proximal bases about 8 mm. in diameter (Pl. 9, fig. 8).

In tangential sections the oval zooecial openings are regularly aligned longitudinally (Pl. 8, figs. 6, 7, 8). The zooecial walls are narrower or about the same width as the zooecial openings and are penetrated by prominent acanthopores, generally 0·05 to 0·09 mm. in diameter, but smaller acanthopores with diameters as small as 0·02 mm. are occasionally present. Mesopores are very rare and, if present, are about the same size as the acanthopores (Pl. 8, fig. 6).

In longitudinal sections the zooecial walls are longitudinally laminate in the axial region and may show two or three narrow bands of monilae (Pl. 9, fig. 5). The zooecial walls thicken considerably in the peripheral region and display low, broad monilae that have a laminate microstructure in which steeply inclined laminae line the inner parts of the zooecial walls and pass into the outer part of the zooecial walls as broad, distally convex laminae. The peripheral region is as wide as the axial region (Pl. 8, fig. 2).

In transverse sections the laminate microstructure of the zooecial walls in the peripheral region is well displayed. The laminae curve steeply from the inner part near the zooecial tube and make a broad distally convex arc in the outer part of the zooecial wall. Laminae of adjacent zooecia intertongue inconspicuously in the outer region (Pl. 8, fig. 3). In the peripheral region the steeply inclined laminae of the acanthopores cut through the zooecial walls (Pl. 9, figs. 1, 3). In the axial region where the zooecial walls are slightly moniliform, the polygonal zooecial tubes may have acanthopores at their wall junctions (Pl. 8, fig. 5; Pl. 9, fig. 1).

Remarks. The species is characterized by colonies of small diameter with five to ten distinct acanthopores in slender, moniliform walls. Mesopores and diaphragms are very rare.

Stenopora dickinsi is not closely similar to species described either from the Permian of the Fitzroy Basin (Crockford 1957) or from eastern Australia. It shows certain similarities to *S. gracilis* (Dana) (Crockford 1943) from the Westley Park Tuffs, Permian, New South Wales, Australia, in its broad basal attachment, size of its zoarial stem, number of zooecial openings per 2 mm., remote monilae across the axial region, broad monilae in the peripheral region, and sparse distribution of mesopores. However,

TABLE 2

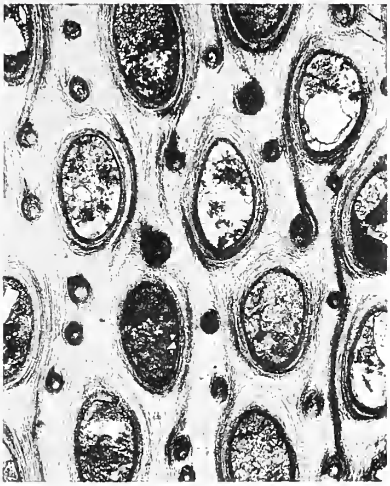
Measurements of *Stenopora dickinsi* sp. nov. (in mm.)

CPC numbers	*ML 109–2*	*ML 90–2*	*ML 90–4*	*ML 106–1*	*ML 106–5*
Diameter of zoarial stem	3·5–4·0	5–6	4·5	4	2·3–2·5
No. of zooecia per 2 mm. longitudinally	3·5–4·5	3–4·5	3–4	3	4
Diameter of zooecial opening max.	0·35×0·21	0·40×0·24	0·31×0·21	0·39×0·17	0·33×0·21
min.	0·24×0·16	0·24×0·15	0·26×0·12	0·26×0·15	0·21×0·12
Diameter of mesopore	——	——	——	——	(0·05–0·08)×0·05
Diameter of acanthopore	0·03–0·09	0·03–0·07, generally 0·05–0·07	0·05–0·09	0·02–0·09	0·04–0·10
Zooecial wall thickness long.	0·11–0·27	0·07–0·26	0·10–0·39	0·15–0·23	0·10–0·19
lat.	0·13–0·29	0·07–0·21	0·07–0·23	0·12–0·28	0·10–0·16
No. of diaphragms in zooecial tube	0–1	——	——	——	——
Width of peripheral region	0·88–0·90	1·26	1·4–1·6	1·54	0·55
Ratio: width of peripheral part of zooecium/total width of zooecium	0·5	0·5	0·64	0·63	0·66
No. of large acanthopores per zooecial opening	3–8	5–8	6–10	5–8	5–8
No. of small acanthopores per zooecial opening	0–1	——	——	0–1	0–1
No. of mesopores per zooecial opening	——	——	——	——	0–2

EXPLANATION OF PLATE 8

Figs. 1–3, 5–8. *Stenopora dickinsi* sp. nov. 1, Tangential section showing oval zooecial openings and zooecial walls pierced by large acanthopores, locality ML 109, CPC ML 109–2, ×50. 2, Longitudinal section showing slender zooecial walls in axial region and greatly thickened, laminate walls in abraded peripheral region, locality ML 106, CPC ML 106–5, ×20. 3, Part of transverse section showing laminate microstructure of zooecial walls in the peripheral region, locality ML 90, CPC ML 90–2, ×50. 5, Transverse section showing thin-walled, polygonal zooecia in axial region and thickened zooecial walls in the peripheral region, locality ML 109, CPC ML 109–3, ×20. 6, Tangential section showing large acanthopores and occasional mesopore around zooecial openings, locality ML 106, CPC ML 106–2, ×50. 7, Tangential section showing longitudinal alignment of zooecial openings, locality ML 109, CPC ML 109–2, ×20. 8, Tangential section showing laminate microstructure in zooecial walls and acanthopore walls, locality ML 109, CPC ML 109–2, ×100.

Fig. 4. *Stenopora fisheri* sp. nov. Part of longitudinal section showing moniliform zooecial walls in peripheral and subperipheral regions, locality ML 107, CPC ML 107–4, ×20.



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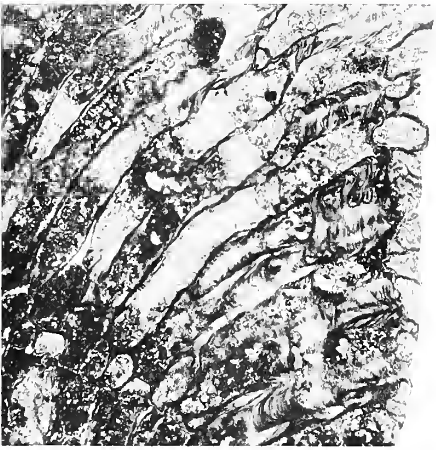

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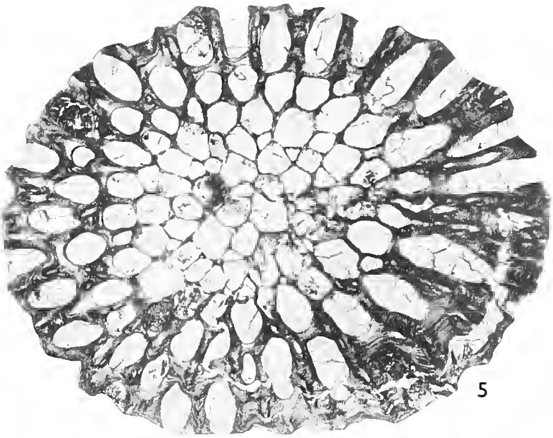

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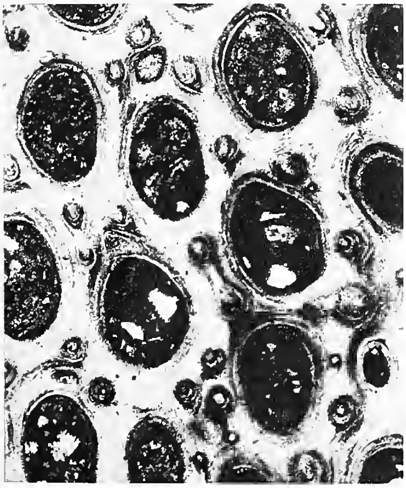

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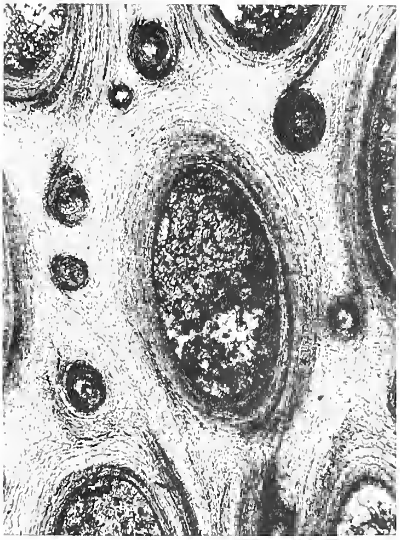

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PHILLIPS ROSS, Lower Permian Bryozoa

S. dickinsi has slightly larger zooecial openings, narrower zooecial walls, fewer acanthopores, and a considerably wider peripheral region. *S. parallela* Crockford (1945) from the Permian, Mt. Wellington, Tasmania, is similar to *S. dickinsi* in the size of its zoarial stem, diameter of the zooecial openings, broad monilae in the peripheral region, and remote monilae in the axial region. It differs from *S. dickinsi* in having fewer acanthopores per zooecium, fewer zooecia per 2 mm., and a narrower peripheral region.

The species is named in honour of Dr. J. M. Dickins, Bureau of Mineral Resources, who has studied extensively the Permian faunas of Western Australia.

Stenopora fisheri sp. nov.

Plate 8, fig. 4; Plate 10, figs. 1–9

Type material. Holotype CPC ML 107–4, paratypes CPC ML 107–2, –5, –8; uppermost part of the Lyons Group, locality ML 107, Lyndon River area. Paratype CPC ML 109–4, upper part of the Lyons Group, locality ML 109, Lyndon River area.

Description. Colonies are slender, cylindrical branching stems (Pl. 10, figs. 2, 3). Monticules and maculae were not observed.

TABLE 3

Measurements of *Stenopora fisheri* sp. nov. (in mm.)

CPC numbers		*ML 107–4*	*ML 107–5*	*ML 109–4*
Diameter of zoarial stem		5–8	5–7	2·5–3·0
No. of zooecia per 2 mm. longitudinally		3–4	3·5–4	4–4·5
Diameter of zooecial opening	max.	0·48×0·36	0·43×0·28	0·46×0·32
	min.	0·26×0·19	0·28×0·17	0·32×0·21
Diameter of mesopore	max.	0·38×0·12	0·16×0·13	0·05×0·05
	min.	0·05×0·05	0·08×0·05	0·26×0·19
Diameter of acanthopore		0·02–0·16	0·02–0·08	0·02–0·13
Zooecial wall thickness	long.	0·05–0·08	0·10–0·21	0·05–0·16
	lat.	0·05–0·17	0·10–0·21	0·04–0·16
No. of diaphragms in zooecial tube		0–1 or 2	0	0
Width of peripheral region		1·76; 2·0	2·2; 2·5	0·88; 0·66
Ratio: width of peripheral part of zooecium/total width of zooecium		0·68; 0·57	0·66–0·70; 0·55	0·66; 0·60
No. of large acanthopores per zooecial opening		5–8	5–6	4–5
No. of small acanthopores per zooecial opening		0–2	1–2	0
No. of mesopores per zooecial opening		1–5	0–3	1–3

In tangential sections the zooecial openings are irregularly spaced and enclosed by slender walls considerably narrower than the zooecial openings (Pl. 10, figs. 1, 4, 6–8). The narrow walls are penetrated by large, dense acanthopores that may protrude into the zooecial openings (Pl. 10, figs. 4, 7). Numerous shallow mesopores also lie in the zooecial walls between adjacent zooecia (Pl. 10, figs. 7, 8).

In longitudinal sections the zooecial walls are slender and longitudinally laminate in the axial region (Pl. 8, fig. 4). The zooecial tubes curve in a broad arch into the peripheral region and are slightly oblique to the zoarial surface. The zooecial walls thicken in the peripheral region and display narrow, elongate monilae (Pl. 10, fig. 5) and have a laminate microstructure in which steeply inclined laminae line the inner parts of the zooecial walls and pass into the outer part of the zooecial walls as broad distally convex laminae (Pl. 10, fig. 9). Laminae of adjacent walls merge inconspicuously in this outer part or are penetrated by the steeply inclined laminae of the acanthopore walls. Diaphragms are generally lacking.

Remarks. *Stenopora fisheri* is characterized by slender, branching, colonies having large zooecia, mesopores, and numerous large acanthopores enclosed in slender zooecial and mesopore walls. It shows little similarity with previously described species, although it resembles *S. dickinsi* in its slender, cylindrical stems and numerous, distinctive acanthopores. It differs from this species in having larger zooecial openings, larger acanthopores, and numerous large mesopores.

The species is named in honour of Dr. N. H. Fisher, Bureau of Mineral Resources, Australia.

Stenopora lyndoni sp. nov.

Plate 11, figs. 1–3, 6–10

Type material. Holotype CPC ML 90–1, paratype CPC ML 90–3; 45 feet below the top of the Lyons Group; locality ML 90, Lyndon River area, approximately 2 miles north-north-east of Round Hill Well; lat. 23° 21′ S., long. 114° 41′ E.

Description. Colonies are slender, cylindrical, branching stems (Pl. 11, figs. 6, 8, 9). Maculae and monticules were not observed.

In tangential sections the oval zooecial openings are irregularly spaced in longitudinal ranges (Pl. 11, figs. 1, 3, 7). The elongate zooecia are separated by walls as thick as the width of the zooecial openings. Numerous large (0·07 to 0·09 mm. diameter), dense acanthopores penetrate the zooecial walls. Small acanthopores, 0·02 mm. in diameter, having less dense walls, are sparse. Mesopores are small and sparsely distributed.

EXPLANATION OF PLATE 9

Figs. 1–5, 7–9. *Stenopora dickinsi* sp. nov. 1, Part of transverse section showing acanthopores at junction of zooecial walls in axial region and thickened zooecial walls in peripheral region, locality ML 106, CPC ML 106–5, ×50. 2, External aspect of fragment of colony, locality ML 106, CPC ML 106–3, ×5. 3, Part of transverse section in peripheral region showing steeply inclined laminae of acanthopore walls cutting through the more gently curved laminae of the zooecial walls, locality ML 106, CPC ML 106–5, ×100. 4, External aspect of fragment of colony, locality ML 106, CPC ML 106–2, ×5. 5, Longitudinal section showing slender walls, partly crushed, in axial region and thickened, slightly moniliform zooecial walls in peripheral region, locality ML 109, CPC ML 109–2, ×20. 7, Part of longitudinal section showing narrow peripheral region of thickened walls, locality ML 106, CPC ML 106–5, ×50. 8, External aspect of zoarial fragment showing broad base of attachment, locality ML 106, CPC ML 106–1, ×5. 9, Part of transverse section showing thin-walled polygonal zooecia in the axial region, and thickened zooecial walls in the peripheral region, locality ML 90, CPC ML 90–2, ×20.

Figs. 6, 10–12. *Polypora lyndoni* sp. nov. 6, External aspect of fenestrate colony showing meshwork pattern and zooecial openings, locality ML 107, CPC ML 107–20, ×5. 10, External aspect of basal part of funnel-shaped zoarium, locality ML 109, CPC ML 109–10, ×2. 11, General aspect of inner surface of funnel-shaped zoarium near its base showing zooecial openings, locality ML 109, CPC ML 109–10, ×2. 12, Inner surface of basal part of colony showing arrangement of zooecia and rudimentary fenestrules, locality ML 107, CPC ML 107–22, ×2.


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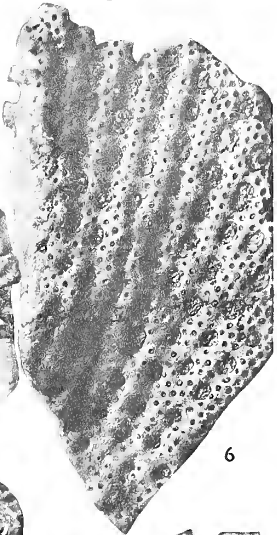
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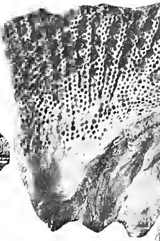
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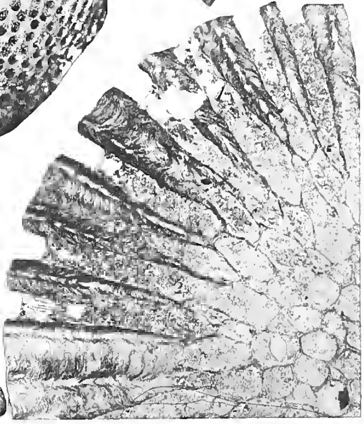
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PHILLIPS ROSS, Lower Permian Bryozoa

In transverse sections the zooecial tubes are polygonal in the axial region. The zooecial walls are greatly thickened in the wide peripheral region but are only slightly moniliform. The zooecia and shallow mesopores have laminate walls in which steeply inclined laminae line the inner parts of zooecial walls and pass into the outer parts of the zooecial walls as broad, distally convex laminae. Laminae of adjacent walls merge inconspicuously or are penetrated by the steeply inclined laminae of the acanthopore walls (Pl. 11, figs. 2, 10).

TABLE 4

Measurements of *Stenopora lyndoni* sp. nov. (in mm.)

CPC numbers	*ML 90–1*	*ML 90–3*
Diameter of zoarial stem	5	4–5
No. of zooecia per 2 mm. longitudinally . .	6	4–5
Diameter of zooecial opening . . . max.	0·26×0·19	0·23×0·13
min.	0·19×0·13	0·09×0·07
Diameter of mesopore	(0·05–0·06)×0·02	(0·04 to 0·06)×(0·04 to 0·05)
Diameter of acanthopore	0·02–0·09	0·02–0·07
Zooecial wall thickness	0·08–0·21	0·13–0·26
Width of peripheral region	1·8	not det.
Ratio: width of peripheral part of zooecium/total width of zooecium	0·68	not det.
No. of large acanthopores per zooecial opening	3–4	3–6
No. of small acanthopores per zooecial opening	1	1–3
No. of mesopores per zooecial opening . .	0–3	0–3

Remarks. Stenopora lyndoni is characterized by slender zoarial stems and small zooecial openings enclosed by wide zooecial walls that are penetrated by prominent acanthopores and small mesopores. It differs from *S. dickinsi* in its smaller zooecial openings and in having small mesopores, 0–3 per zooecial opening.

Order CRYPTOSTOMATA

Family FENESTELLIDAE

Genus POLYPORA M'Coy

1844 *Polypora* M'Coy, p. 206.

Type species. Polypora dendroides M'Coy, 1844, p. 206, pl. 29, fig. 9.

Diagnosis. Infundibuliform or flabellate Fenestellidae having zooecia arranged in three or more rows on the branches, except just after bifurcation, where only two rows may be present.

Polypora lyndoni sp. nov.

Plate 9, figs. 6, 10–12; Plate 11, figs. 4, 5

Type material. Holotype CPC ML 107–20, paratypes CPC ML 107–21 to –28, uppermost part of the Lyons Group, locality ML 107, Lyndon River area. Paratypes CPC ML 109–10 to –16; upper part of the Lyons Group, locality ML 109, Lyndon River area. Paratypes CPC ML 6–5 to –10, locality ML 6 (3½ miles west of north of 'Moogooree' Homestead), considered to be located in the lower part of the Lyons Group and in its lowest known marine beds. Paratypes CPC ML 90–10 to –15, 45 feet below the top of the Lyons Group; locality ML 90, Lyndon River area.

Description. Colonies are funnel-shaped and grow from circular or oval bases 3 to 15 mm. or more in diameter (Pl. 9, figs. 10, 11). The zoarial fragments examined are up to 40 mm. high and above the first 20 mm. the tall, narrow funnels display pronounced flanging of the fenestrate branches. The zoarial bases of solid calcareous material rise 3 to 8 mm. or more in height, lack zooecia, and may have flanges and rootlets.

The zooecial openings lie on the inner surfaces of the fenestrate funnels and the delicate meshwork is poorly defined in the first 2 to 5 mm. (Pl. 9, figs. 11, 12). Above this the slender, smooth, and flat zoarial branches each have three rows of zooecia which extend continuously along the branches (Pl. 9, fig. 6). Four zooecia are generally present just before bifurcation. The obverse surfaces of the branches display fine striae that form irregular polygons and circles around the zooecial openings. The reverse surfaces of the colonies display longitudinally striate branches. The meshwork formula is 8½–13 | 7½–10 || 15–17 | 2–3. The branches are very straight and the meshwork remains regularly developed. The zooecial openings, which are without peristomal rims, do not project into the fenestrules. The lateral rows of zooecia commonly encroach onto the narrow dissepiments. The fenestrules are oval or circular on the obverse surface but commonly appear square, polygonal, or circular on the reverse surface. On the obverse surface the short, narrow dissepiments are commonly depressed below the level of the branches.

In shallow tangential sections the zooecial walls have an amalgamate, laminate microstructure, and the round zooecial openings do not show hemisepta. In very shallow tangential section bands of small capillaries, 0·01 mm. in diameter, fill the zooecial walls, weave around the zooecial openings, and extend across the dissepiments (Pl. 11, fig. 5). Tubules, 0·05 to 0·08 mm. in diameter, occur at the junctions of zooecial walls (Pl. 11, fig. 5). Deep tangential sections show hexagonal, basal zooecial sections (Pl. 11, fig. 4).

Remarks. Polypora lyndoni sp. nov. is characterized by a delicate, fenestrate meshwork of slender branches, three rows of zooecia across a branch, small fenestrules, fine capillaries of 0·01 mm. diameter, and occasional tubules at the junctions of zooecial walls. It closely resembles *P. pertinax* Laseron (Crockford 1941, pp. 412–13) from the *Eurydesma cordatum* horizon, Allandale, N.S.W. The two species are similar in the number of branches and fenestrules per 10 mm., in having about the same number of zooecia per 2 mm., and the occasional small tubules at the junctions of zooecial walls. *P. lyndoni* has

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EXPLANATION OF PLATE 10

Figs. 1–9. *Stenopora fisheri* sp. nov. 1, Tangential section showing arrangement of zooecial openings, slender zooecial walls, mesopores, and acanthopores, locality ML 109, CPC ML 109–4, ×20. 2, 3, External aspect of branching zoarial fragments, locality ML 107, CPC ML 107–7, ML 107–8, respectively, ×5. 4, Part of tangential section showing zooecial opening with slender zooecial walls that are penetrated by larger acanthopores and mesopores, locality ML 109, CPC ML 109–4, ×100. 5, Part of longitudinal section in peripheral region showing moniliform walls, locality ML 107, CPC ML 107–4, ×50. 6, Tangential section showing numerous mesopores and acanthopores around zooecial openings, locality ML 107, CPC ML 107–4, ×20. 7, Tangential section showing large acanthopores and mesopores between large zooecial openings, locality ML 107, CPC ML 107–4, ×50. 8, Tangential section showing zooecial openings, prominent acanthopores, and mesopores, locality ML 109, CPC ML 109–4, ×50. 9, Part of longitudinal section in peripheral region showing laminate, moniliform zooecial walls, locality ML 107, CPC ML 107–4, ×50.

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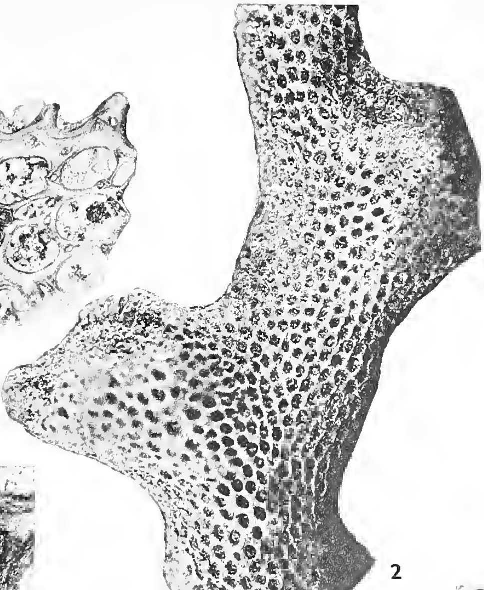

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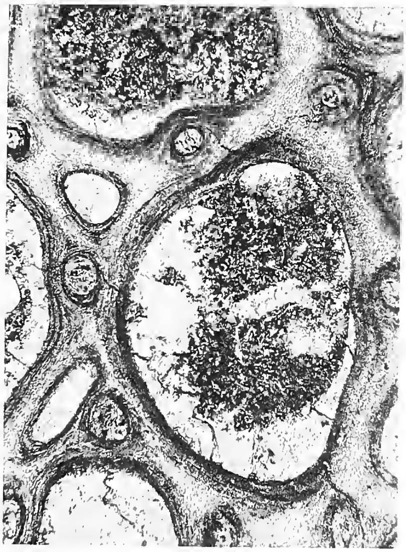

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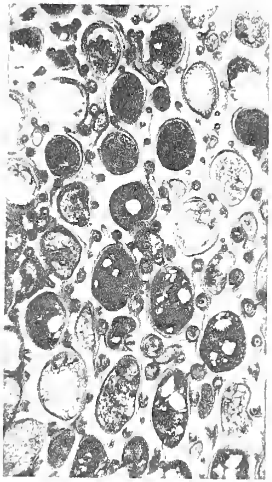

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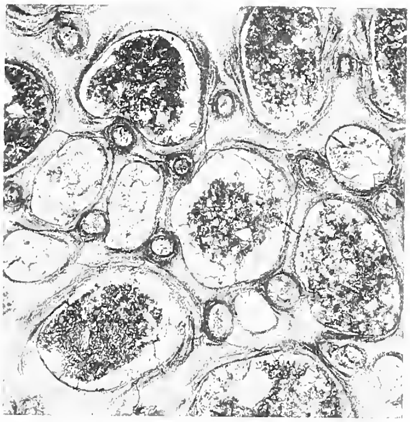

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PHILLIPS ROSS, Lower Permian Bryozoa

TABLE 5

Measurements of *Polypora lyndoni* sp. nov.

No. per 10 mm.		*No. of zooecia*		*Width of*		*Fenestrule*		*Zooecial opening*	
Branches	*Fenestrules*	*Per 5 mm.*	*Per fenestrule*	*branch (mm.)*	*dissepiment (mm.)*	*length (mm.)*	*width (mm.)*	*diameter (mm.)*	*CPC numbers*
8·75–10	7·5–8·75	15	2–3, generally 2	0·60–0·66	0·44–0·66	0·44–0·71	0·22–0·44	max. 0·18×0·13 min. 0·16×0·10	ML 107–20
10–11	8·75–9·5	15–15½	2	0·60–0·68	0·40–0·48	0·56–0·72	0·36–0·56	0·20×0·16	ML 107–21
12·5–13·25	10	17·5	2–3	0·36–0·60	0·32–0·42	0·44–0·60	0·32–0·56	max. 0·20×0·13 min. 0·12×0·12	ML 90–10
10–10·5	8·75–9	15	2	0·36–0·72	0·28–0·44	0·60–0·80	0·32–0·60	max. 0·24×0·16 min. 0·16×0·12	ML 109–10
11·25–12·5 (proximal part of colony)	8·75–10	15–14	2	0·44–0·60	0·36–0·48	0·32–0·60	0·32–0·40	max. 0·20×0·20 min. 0·16×0·12	ML 109–11

a greater number of zooecial openings per fenestrule, and its dissepiments are wider than those in *P. pertinax*.

Polypora lyndoni is similar to *P. keppelensis* Crockford (1962) (new name for homonym *P. minuta* Crockford 1946) from the Lake Creek Beds, Rockhampton, Queensland, in its fine meshwork, in having three rows of zooecia across each branch, and in its obverse surface ornamentation. *P. lyndoni* has wider branches, shorter fenestrules, generally two or three zooecia per fenestrule, wider dissepiments, and lacks high peristomes around the zooecial openings.

Polypora lyndoni is similar to *P. tripliseriata* from the Bitauni Beds of the Permian of Timor, which are probably equivalent in age to the Lenox Hills Formation in the upper part of the standard Wolfcampian Series, Glass Mountains, Texas, and upper part of the Asselian Series, Ural Mountains, Russia (personal communication, C. A. Ross 1962). The two species are similar in the dimensions of their fenestrules, number of branches and fenestrules per 10 mm., number of rows of zooecia across a branch, and presence of capillaries and tubules in the zooecial walls. *P. lyndoni* has wider branches and fewer zooecia along a fenestrule.

In general features *Polypora lyndoni* is similar to a group of species including *P. tuberculifera*, *P. punctata*, *P. subvariicellata*, and *P. nadinae* described by Shulga-Nesterenko (1952) from the Sterlitamak (upper part of the Sakmarian) of the Urals. However, these species display more highly specialized structures in the zooecial walls and around the zooecial openings. *P. sargaensis* and *P. kulivoki*, described by Trizna (1948) from the Permian of the Sulva River, apparently also belong to the same group of species but display more specialized features.

COLLECTION LOCALITIES

ML 90. Approximately 2 miles north-north-east of Round Hill Well, Winning Station, Lyndon River area. Lat. 23° 21′ S., long. 114° 41′ E. 45 feet below the top of the Lyons Group. *Stenopora dickinsi*; *S. lyndoni*; *Polypora lyndoni*.

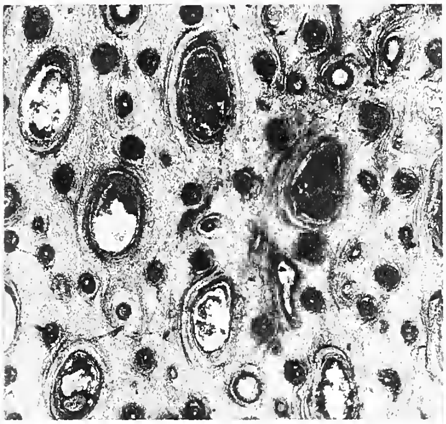
ML 106. Approximately 3 miles north-north-east of Round Hill Well, 1 mile west of Kialawibri Creek road-crossing, Winning Station, Lyndon River area. Lat. 23° 21′ S., long. 114° 42′ E. Upper part of Lyons Group. *Stenopora dickinsi*; *Polypora lyndoni*.

EXPLANATION OF PLATE 11

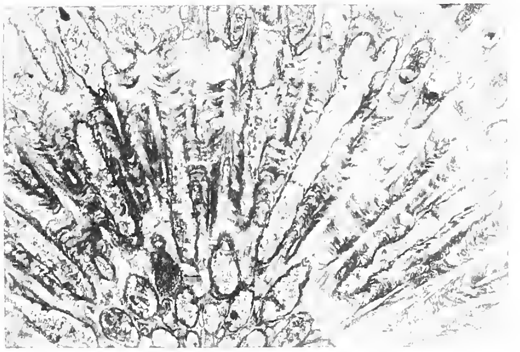
Figs. 1–3, 6–10. *Stenopora lyndoni* sp. nov. 1, Tangential section showing zooecial openings separated by thick zooecial walls that bear numerous large acanthopores and small mesopores, locality ML 90, CPC ML 90–3, ×50. 2, Part of transverse section showing outer edge of axial region and thick, laminate zooecial walls in peripheral region, locality ML 90, CPC ML 90–1, ×20. 3, Tangential section showing regular arrangement of large zooecial openings, distinct acanthopores, and small mesopores, locality ML 90, CPC ML 90–1, ×50. 6, 8, 9, External aspect of branching zoarial fragments, locality ML 90, CPC ML 90–1, ML 90–1, ML 90–3, respectively, ×5. 7, Tangential section showing laminate microstructure of zooecial walls penetrated by acanthopores and mesopores with laminate walls, locality ML 90, CPC ML 90–3, ×100. 10, Part of transverse section showing gently curved laminae of zooecial walls and more steeply inclined laminae of acanthopore walls, locality ML 90, CPC ML 90–1, ×50.

Figs. 4, 5. *Polypora lyndoni* sp. nov. 4, Deep tangential section showing hexagonal form of basal zooecial sections, locality ML 109, CPC ML 109–11, ×20. 5, Tangential section showing round zooecial openings, fine capillaries and an occasional tubule in the zooecial walls, and small fenestrules, locality ML 107, CPC ML 107–20, ×20.

PLATE 11



1



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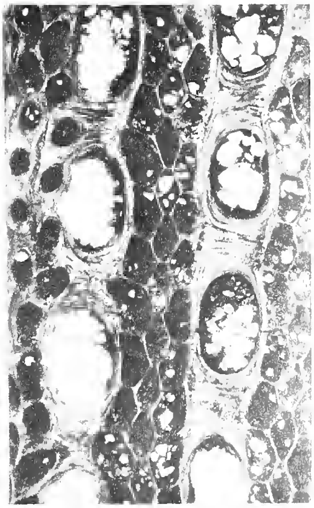

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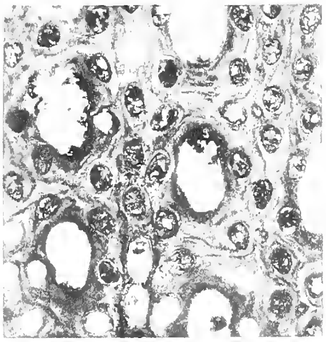

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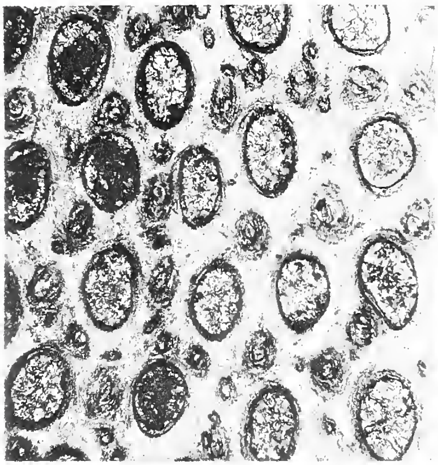

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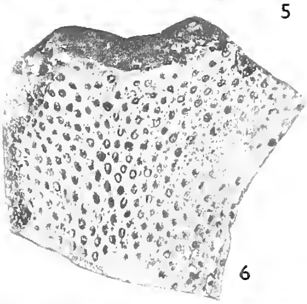
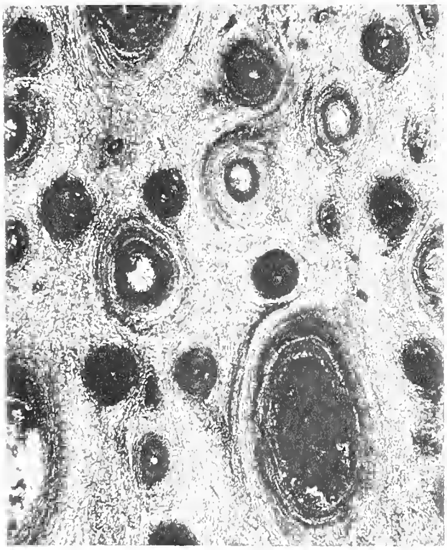


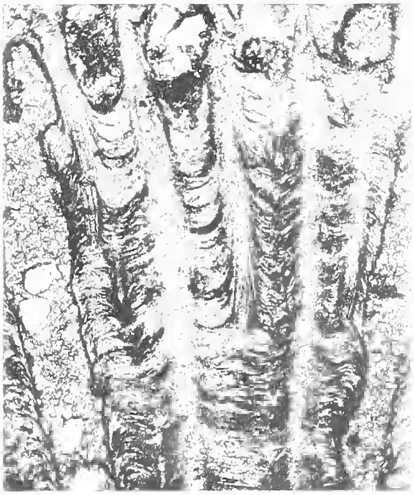
6

8



7

9



10

PHILLIPS ROSS, Lower Permian Bryozoa

ML 107. 100 feet west of ML106, Lyndon River area. Lat. 23° 21′ S., long. 114° 42′ E. Uppermost part of the Lyons Group. *Stenopora fisheri*; *Polypora lyndoni.*

ML 109. 410 feet west of ML 106, Lyndon River area. Lat. 23° 21′ S., long. 114° 42′ E. Upper part of the Lyons Group. *Stenopora dickinsi*; *S. fisheri*; *Polypora lyndoni.*

ML 6. 3½ miles west of north of 'Moogooree' Homestead. Lat. 24° S., long. 115° 17′ E. Considered to be located in the lower part of the Lyons Group and in its lowest known marine beds. *Stenopora dickinsi*; *Polypora lyndoni.*

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ON THE INTERPRETATION AND STATUS OF SOME HYSTRICHOSPHERE GENERA

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ABSTRACT. The taxonomic status of the genera *Micrhystridium*, *Baltisphaeridium*, *Veryhachium*, *Multiplicisphaeridium*, *Leiosphaeridia*, *Leiosphaeridium*, *Protoleiosphaeridium*, and *Archaeohystrichosphaeridium* is examined. The generic names *Multiplicisphaeridium*, *Leiosphaeridium*, and *Protoleiosphaeridium* are rejected: the genera *Micrhystridium*, *Baltisphaeridium*, *Leiosphaeridia*, and *Veryhachium* are redefined: and lists are given of the species now considered to belong to these genera, the generic attribution of 140 species being changed.

IN his recent paper describing assemblages of Devonian microplankton from Alberta, Canada, F. L. Staplin (1961) has made a number of proposals relating to the taxonomy of the hystrichospheres which we consider not acceptable. These proposals have been briefly criticized by Eisenack (1962); they are here discussed fully and the reasons for their rejection are outlined. The status of the genera concerned and of some related genera is examined and the attribution of species to these genera is clarified.

1. *Micrhystridium—Baltisphaeridium*

Deflandre (1937) erected the genus *Micrhystridium* to include all globular hystrichospheres having a shell diameter generally less than 20 μ, regardless of the character of their appendages: he designated as type species *Micrhystridium inconspicuum* (Deflandre 1935), a form having thorn-like processes with closed tips. The distinction between this genus and the genus *Hystrichosphaeridium*, erected in the same paper, lay only in dimensions, *Hystrichosphaeridium* then comprising all forms whose shells were not differentiated into fields by sutures, again regardless of appendage character. In 1958 this latter genus was split by Eisenack, who, retaining the name *Hystrichosphaeridium* for forms which, like the type *H. tubiferum* (Ehrenberg 1838) Deflandre 1937, possess tubular spines open distally, erected a new genus, *Baltisphaeridium*, for forms having spines closed distally, the type species being *B. longispinosum* (Eisenack 1931). No alteration was made to the diagnosis of *Micrhystridium*.

Staplin proposes the abolition of the upper size limit for *Micrhystridium* and a redefinition of the genus on the basis of the spine character of its type species, causing it to correspond exactly with *Baltisphaeridium*. On this basis he proposes abandonment of the latter genus and the reattribution of its species to *Micrhystridium*.

The hystrichospheres having spines closed distally exhibit an overall range in shell diameters from 5 μ to 240 μ. Consideration of the size ranges of individual species reveals two major groupings, two foci of morphology: this has been graphically represented by Downie (1958, p. 334) in an analysis of a Tremadocian hystrichosphere assemblage. The boundary between these two major groupings has been accepted by most workers as being sensibly drawn at 20 μ. While species exist which overlap this boundary from either side, the number of species having a size mode between 20 and 25 μ is very small: of 204 Palaeozoic species and infraspecific groups attributable to the genera

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Micrhystridium and *Baltisphaeridium* (186 species and 18 infraspecies), only 10 overlap the boundary and only 1, *B. ramusculosum* (Deflandre 1942), has a size mode actually on the boundary. Of 164 Mesozoic and Tertiary species and infraspecific groups attributable to the genera *Micrhystridium* and *Baltisphaeridium* (117 species and 46 infraspecies and forms related to named species), only 8 overlap the boundary and only one, *M. piliferum* (Deflandre 1937), apparently has a size mode actually on the boundary: this species is based on a single specimen. (Size ranges are quoted in detail in the accompanying systematic section.) The few forms transgressing the size boundary separating the genera may be regarded as extremes in series surrounding morphological foci: transgressions of the boundary are usually slight and by extremes in the size range of a particular species whose mode is clearly below or above the boundary.

The forms having a shell diameter smaller than 20 μ, the micrhystridia, appear at many horizons in the Upper Palaeozoic and Mesozoic (Carboniferous, Permian, Triassic, and Jurassic) to correspond in their concentration to differences in environment, tending to be either very abundant or extremely few in number in particular assemblages.

Although Staplin's emendation of the genus *Micrhystridium* may be legally valid in terms of the existing Codes of Nomenclature, his proposal to remove from the diagnosis the one distinguishing characteristic specified by its author renders the genus meaningless: to do so would be to make it synonymous with *Hystrichosphaeridium* as defined at the time of publication of the two generic diagnoses. We consider that the genera *Micrhystridium* and *Baltisphaeridium* express two natural size modes, and that the size boundary separating them should be retained at least until more compelling evidence for emendation of the genera is available.

We feel, however, that the genus *Micrhystridium*, as at present defined, is rather heterogeneous, since it comprises not only forms having processes with simple tests, not divided into fields by crests, and with simple spines closed distally, but also forms whose shells are divided into fields and others that have processes open distally. We consider with Staplin that it should be restricted to forms having spines with closed tips: that forms having shells whose surfaces are divided into fields by crests should be transferred to the genus *Cymatiosphaera* and forms having tubular processes to the genus *Hystrichosphaeridium*. If in the future it transpires that within the two latter genera there exists a similar division into natural size modes, new taxa may then be erected to express this difference.

2. *Veryhachium*

The name *Veryhachium* was introduced in 1954, being applied to a species, *V. trisulcum*, which was not at that time validly published. This was subsequently rectified in 1958 and the genus should date from then. The genus was emended by implication by one of us (Downie 1959) when forms with an ellipsoidal test and a single spine were removed to a new genus, *Deunffia*. *Veryhachium* then included hystrichospheres with polygonal tests and a small number of spines. In recent publications (Eisenack 1959, Staplin 1961), markedly contrasted interpretations of the genus have been evident and we consider a clarification of the situation necessary.

It is evident from recent publications (Eisenack 1959, Jekhowsky 1961) that morphological transitions exist between *Veryhachium* and both *Micrhystridium* and *Baltiphaeridium*. Eisenack (p. 207) recognizes these difficulties and prefers to retain in

Baltisphaeridium any polygonal form which, by other morphological criteria, is linked to typically round-bodied forms, e.g. *B. oligospinosum* and *B. visbyense*, which accord in all respects with the diagnosis of *Veryhachium*. He rightly states that the generic boundary would otherwise separate forms that are closely related.

The principle that Eisenack is enunciating, that taxonomic units should express natural relationships, is one with which the authors are in general agreement. However, rigid application of this principle to the hystrichospheres would result in the shrivelling or disappearance of most existing genera, with a resultant vast increase of species within the few remaining (*Micrhystridium* emend. Staplin would, for example, contain about 800 species). It would, moreover, produce a false picture of the real situation where, although overlap and gradation may occur at the fringes, there do exist morphological groupings with intermediates considerably rarer than typical forms. Even Eisenack does not apply his principle rigorously, for he has several times emphasized the existence of continuous gradation between leiospheres and hystrichospheres, and yet separates them into distinct genera.

We consider that the generic name *Veryhachium* should be applied to forms having a low number (generally 3–8) of hollow spines arising from a polygonal or subpolygonal test. The combination of shell shape and spine number is considered to define the genus, and the views of Staplin, that all species having a polygonal test should be placed within this genus, regardless of spine number, are rejected as contrary to the original intention of Deunff.

3. *Diornatosphaera*

The status of this genus and of related genera erected by Timofiev (1959) has been recently reviewed by Deflandre and Deflandre-Rigaud (1961). The decisions of these authors are accepted in their entirety, and their paper is welcomed for its clarification and regularization of a potentially difficult taxonomic situation.

4. *Multiplicisphaeridium*

This proposed new genus (Staplin 1961) is distinguished from *Baltisphaeridium* and *Micrhystridium* in the character of the spine tips: forms having unmodified spine tips are referred to the two latter genera, while forms having multifurcate, expanded, or dissected spine tips are referred to *Multiplicisphaeridium*. The number of species that would be referable to this latter genus in the Palaeozoic is not large (20 species, at present allocated to the genera *Micrhystridium*, *Baltisphaeridium*, and *Archaeohystrichosphaeridium*), but in the Mesozoic and Tertiary it is considerable.

Multiplicisphaeridium is considered morphologically ill-founded for the following reasons:

(*a*) While many species do have entirely simple or entirely complex spine tips, there are a number of species whose representatives consistently have both simple and furcate, or complex, spine tips.

(*b*) In some individual species, the normal range of variation includes specimens with only simple spines, specimens with only furcate, &c., spines, and specimens with spines of mixed types.

(*c*) The species having in common the character of furcate, &c., spine tips show no distinctive combinations of other characters to suggest that they constitute a morphologically separate entity. Examination of assemblages at the same or earlier horizons frequently discloses a higher degree of morphological similarity to species with unbranched spines than to other species of *Multiplicisphaeridium*. There is no evidence for the view that *Multiplicisphaeridium* constitutes an evolutionary chain of species; on the contrary, there is much evidence that the species with furcate or complex spine tips repeatedly arose, by a trend of increasing spine complexity, from forms with simple spines.

(*d*) When combinations of other characters are brought into account, there are seen to be a number of groupings within *Baltisphaeridium* as here defined; species within these groupings may have simple, furcate, or complex spines. Separation of forms having spines of the two latter types into a distinct genus would cut across these groupings and would obscure natural relationships.

In the Palaeozoic, a series of increasing spine complexity is clearly shown in two cases: *Baltisphaeridium polygonale* (Eisenack 1931)→*B. digitatum* (Eisenack 1938); Ordovician. *B. oligofurcatum* (Eisenack 1954)→*B. meson* (Eisenack 1955)→*B. brevifurcatum* (Eisenack 1954); Silurian. Other Palaeozoic species having intermediate characters are listed below.

(*a*) Species having both simple spines and knobbed, bi- or trifurcate spines.

ORDOVICIAN. *Baltisphaeridium longispinosum* (Eisenack 1931) Eisenack 1958; *B. nudatum* (Timofiev 1959) comb. nov; *B. ordovicum* (Timofiev 1959) comb. nov; *B. rjabinini* Timofiev 1959) comb. nov.

SILURIAN. *B. ramusculosum* (Deflandre 1942), Downie 1958.

DEVONIAN. *B.* cf. *digitatum* (Deunff 1954) comb. nov.

(*b*) Species having only briefly furcate spines.

ORDOVICIAN. *B. circumscissum* (Timofiev 1959) comb. nov; *B. setigerfurcatum* (Timofiev 1959) comb. nov.

DEVONIAN. *B. lewisi* (Deunff 1954) comb. nov.; *B. microfurcatum* Deunff 1957.

A large number of Mesozoic and Tertiary species show intermediate characteristics:

(*a*) Species having both simple spines and knobbed, bi- or trifurcate spines.

JURASSIC. *Baltisphaeridium polytrichum* sensu Downie 1957 non Valensi 1947; *B. varispinosum* Sarjeant 1959; *B.* cf. *multifurcatum* (Deflandre 1947), Klement 1960; *B. lumectum* Sarjeant 1960*a*; *B.* cf. *fimbriatum* (White 1842), Sarjeant 1960*a*.

CRETACEOUS. *B. multifurcatum* (Deflandre 1937) Klement 1960; *B. pseudhystrichodinium* (Deflandre 1937) comb. nov.; *B. striolatum* (Deflandre 1937) comb. nov.; *B.* cf. *pseudhystrichodinium* (Deflandre 1937), Lejeune-Carpentier 1941; *B. longifurcatum* (Firtion 1952) comb. nov.; *B.* cf. *striolatum* (Deflandre 1937), W. Wetzel 1952; *B. oligacanthum* (W. Wetzel 1952) comb. nov. and its subspecies.

EOCENE. *Micrhystridium* cf. *stellatum* Deflandre 1942, Deflandre and Cookson 1955; *Baltisphaeridium geometricum* (Pastiels 1948) comb. nov.

OLIGOCENE. *B.* cf. *pseudhystrichodinium* (Deflandre 1937), Gocht 1952.

(*b*) Species having simple spines together with others of complex form.

JURASSIC. *Baltisphaeridium vestitum* (Deflandre 1938) Sarjeant 1960*b*.

CRETACEOUS. *B. flosculus* (Deflandre 1937) comb. nov.; *B. horridum* (Deflandre 1937) comb. nov.; *B. heteracanthum* (Deflandre and Cookson 1955) comb. nov.; *B. tridactylites* (Valensi 1955) comb. nov.

(*c*) Species having capitate (c.), knobbed (k.), or only briefly furcate (f.) spines.

JURASSIC. *Baltisphaeridium* cf. *intermedium* (O. Wetzel 1933), Deflandre 1938 (f.); *Micrhystridium bigoti* Deflandre 1947 (f.); *M. variabile* Valensi 1953 (c. or f.); *B. downiei* Sarjeant 1960*a* (c., k., or f.); *B.* aff. *fimbriatum* (White 1842), Sarjeant 1960*b* (f.); *B. tribuliferum* Sarjeant 1962*b* (f.); *M. rhopalicum* Sarjeant 1962*b* (k. or f.).

CRETACEOUS. *Baltisphaeridium fimbriatum* (White 1842), Sarjeant 1960*b* (f.); *B. intermedium* (O. Wetzel 1933) comb. nov. (f.); *B.* aff. *multifurcatum* (Deflandre 1937), Firtion 1952; *B. rhabdophorum* (Valensi 1955) comb. nov. (f.); *B. huguonioti* (Valensi 1955) comb. nov. (f.).

EOCENE. *B. colligerum* (Deflandre and Cookson 1955) comb. nov. (c. or f.).

OLIGOCENE. *B. longofilum* (Maier 1959) comb. nov. (f).; *B. echinoides* (Maier 1959) comb. nov. (c.).

There are thus a considerable number of species whose spine characters indicate a morphogenetical position between forms having wholly simple spines and forms having multifurcate, expanded, or dissected spines all of one type. The use of the structure of spine tips cannot be considered a satisfactory single criterion for determining generic assignment; the genus *Multiplicisphaeridium* would, if accepted, be an agglomeration of end members of numerous evolutionary trends rather than the focus of a morphological grouping. All, or nearly all, existing genera have been established in the view that they have genetic meaning and express natural groupings: the discovery of overlap with other genera at the extreme limits of their morphological spread does not necessarily invalidate this view. In the case of *Multiplicisphaeridium*, such a view cannot be held even at the inception. We propose therefore that this genus be abandoned and that the present distribution into genera of the species comprising it be retained.

5. *The leiospheres*

The generic name *Leiosphaeridium* Timofiev apparently first appeared in a caption to an illustration (1956) and was not therefore validly published until 1959, when a description was given. (Figures unaccompanied by diagnoses do not constitute valid publication either under the Botanical or Zoological Rules at this date.) It was intended as an alteration of *Leiosphaera* Eisenack (1938) and as such it is invalid. The type species of the genus *Leiosphaera*, *L. solida*, was recognized by Eisenack (1958) as conspecific with *Tasmanites huronensis* (Dawson 1871); he thus abandoned the genus, attributing to *Tasmanites* such species as accord with its diagnosis and setting up a new genus, *Leiosphaeridia*, to accommodate forms not attributable to *Tasmanites*. The name *Leiosphaeridium* was proposed as an amendment of *Leiosphaera* and presumably Timofiev regarded *L. solida* as its type species; *Leiosphaeridium* is thus a junior synonym of *Leiosphaera* and hence of *Tasmanites*. If the single species attributed to *Leiosphaeridium* by Timofiev were considered as its type, its characters are such as to render it attributable to *Leiosphaeridia*, of which the genus then becomes a junior synonym. Whichever viewpoint is taken, the name *Leiosphaeridium* must be abandoned. It is clear that at the time of writing, Timofiev was not aware of the existence of the genus *Leiosphaeridia*.

The genus *Protoleiosphaeridium* Timofiev was likewise not validly published until 1959 and its type species, *P. conglutinatum*, was not so designated until 1960. The size ranges quoted for this genus and for *Leiosphaeridium* are 20–30 μ and 200–300 μ: these size ranges are confusing, since the six species attributed by Timofiev to the former genus have a range 20–50 μ and the single species attributed to the latter genus has a size range of 100–125 μ.

While the name *Leiosphaeridium* cannot be retained, whether in the original meaning of Timofiev or under the amended diagnosis of Staplin (rejected names cannot be re-used under either the Zoological or the Botanical Rules), *Protoleiosphaeridium* might be retained as a subgenus of *Leiosphaeridia* and restricted to thin-walled forms having a diameter less than 50 μ. The type of Eisenack's genus has a size range 80–140 μ: however, the total range size of all species attributed to this genus is 23–150 μ and there is no indication of any division into size modes. We feel that *Protoleiosphaeridium* should be treated as a synonym of *Leiosphaeridia* and rejected, and that its species should be reattributed to the latter genus.

The statement in Eisenack's diagnosis that a pylome exists in *Leiosphaeridia* is to be interpreted as indicating that this is a structure present in some species but not in all. He does not even consider possession of a pylome to be a factor of specific value (Eisenack, *in litt.*).

Timofiev (1959) also established seven other genera in the family Leiosphaeridiaceae. Of these, *Vavososphaeridium* (reticulate ornament), *Orycmatosphaeridium* (pitted surface), *Lophosphaeridium* (tubercular ornament), and *Trachysphaeridium* (shagreen ornament) might be considered subgenera of *Leiosphaeridia* based on different shell ornament. Some of the species listed under *Leiosphaeridia* could probably be attributed to one or other of these subgenera: however, without examination of type material, the authors do not feel competent to make such reallocation. Timofiev's other genera *Zonosphaeridium* (thick walls), *Trematosphaeridium* (perforate test), and *Symplassosphaeridium* (clusters of vesicles) seem either to be the product of accidents of preservation or to be quite different kinds of structure from the typical leiospheres: judgement on them is, for the present, reserved, although the considerable resemblance between *Zonosphaeridium* (thick walls: ? = *Tasmanites*) and the genus *Tasmanites* may be noted.

6. *Archaeohystrichosphaeridium*

Staplin does not consider this genus of Timofiev (1959) in his taxonomic review. The genus was defined as follows: 'Vesicle with diameter 10–35 μ, thin, ornamented with simple, blunt, or pointed spines, sometimes forking on the periphery. Colour pale yellow.'

The range of diameters quoted by Timofiev is in fact 18–70 μ: only ten of seventy-nine species so far attributed to it fail to exceed 35 μ. No type species has yet been designated, so that the genus has not yet been validly published. As at present defined, the genus is indistinguishable from *Baltisphaeridium* Eisenack and may be by intent a synonym of that genus. The thinness of the shell walls might afford a basis for differentiation at subgeneric level. The authors have not reattributed the species of *Archaeohystricho-*

sphaeridium here, since they hope that a validation and redefinition of the genus may be forthcoming.

SYSTEMATIC SECTION

Evitt (1961) has recently drawn together evidence concerning the relationships of the hystrichospheres and has demonstrated the presence in many genera and species, though by no means in all, of structures indicating relationship to the dinoflagellates. In particular he has shown that the genus *Hystrichosphaera*, on which the Order Hystrichosphaeridea is based, is attributable to the Dinophyceae. A reclassification of the hystrichospheres, following this work, is at present in preparation; for the present, classification is made to generic level only. Known range of shell diameters is quoted for the species of *Micrhystridium* and *Baltisphaeridium*: where species are reallocated to these genera, they were previously in *Hystrichosphaeridium* unless otherwise stated.

The authors would like to emphasize that species have been attributed to the various genera on the basis of published descriptions and allocations, and that the inclusion of a species name does not necessarily imply endorsement of its status. Some of the species included differ morphologically only slightly, if at all, from others previously described; others, e.g. those of Sannemann (1955) here attributed to *Baltisphaeridium*, probably constitute distinct genera whose definition is not possible on present knowledge.

Genus BALTISPHAERIDIUM Eisenack 1958, emend.

Emended diagnosis. Hystrichospheres with spherical to oval shells not divided into fields or plates, bearing ± numerous processes, simple, branching or ramifying, hollow to solid, always with closed tips. The processes are not connected together distally and no outer shell, complete or incomplete, is present: the processes are most often of a single basic type, but processes of two or more types may be present. Mean and modal diameter of shell greater than 20 μ.

Discussion. While the spines of species attributed to *Baltisphaeridium* and *Micrhystridium* are most often hollow, some or all spines of particular species may be partly or wholly solid. The hollowness or otherwise of the spines is extremely difficult to determine in many instances, particularly in species of *Micrhystridium*. On a single specimen, spines may be in part hollow, in part solid; Evitt (*in litt.*) notes that this is the case in *B. ferox* and in *B. flosculus*. Species occur whose spines are hollow throughout their length and closed only at the tip; others with spines solid for most of their length, but with a cavity at the base. Sannemann (1955) has described a number of species in which there is a solid central 'spire' within the spine cavity. The importance of distinguishing between these alternatives is doubtful; for the present, no such distinction is made.

Type species. *Baltisphaeridium longispinosum* (Eisenack 1931) Eisenack 1958 (40–75 μ); Cambrian–Ordovician.

Other species (*Palaeozoic*). *Baltisphaeridium aculeatum* (Timofiev 1959) comb. nov. (70–90 μ); *B. alloiteaui* (Deunff 1955) comb. nov. (formerly *Micrhystridium*) (25–30 μ); *B. annulatum* (Timofiev 1959) comb. nov. (93–96 μ); *B. apiculatum* (Timofiev 1959) comb. nov. (50–60 μ); *B. arrectum* (Timofiev 1959) comb. nov. (70–100 μ).

B. bimarginatum (Timofiev 1959) comb. nov. (60–80 μ); *B. bohemicum* (Eisenack 1934) comb. nov. (120 μ); *B. brevifurcatum* (Eis. 1954) comb nov. (60 μ); *B. brevispinosum* (Eis. 1931) Eisenack 1958

(50–70 μ); *B. brevispinosum* (Eis. 1931) subsp. *callosum* Sannemann 1955 (200 μ); *B. brevispinosum* (Eis. 1931) subsp. *castaneioides* Sannemann 1955 (200 μ); *B. brevispinosum* (Eis. 1931) var. *granulifera* Downie 1959 (16–32 μ); *B. brevispinosum* (Eis. 1931) var. *nanum* Deflandre 1942 (25–26 μ); *B. brevispinosum* (Eis. 1931) var. *wenlockensis* Downie 1959 (16–32 μ); *B. breviciliatum* (Staplin 1961) comb. nov. (formerly *Micrhystridium*) (32–37 μ).

B. castaneum (Eisenack 1934) comb. nov. (150–160 μ); *B. circumscissum* (Timofiev 1959) comb. nov. (70–90 μ); *B. cognitum* (Timofiev 1959) comb. nov. (50–100 μ); *B. coniferum* (Sannemann 1955) comb. nov. (340 μ); *B. conspicuum* (Timofiev 1959) comb. nov. (106–109 μ); *B. corallinum* Eisenack 1959 (70–95 μ); *B. corollatum* (Timofiev 1959) comb. nov. (91–99 μ); *B. crassiechinatum* (Staplin 1961) comb. nov. (formerly *Micrhystridium*) (24–33 μ); *B. cristatum* (Downie 1958) Eisenack 1958 (23–30 μ).

B. differtum (Sannemann 1955) comb. nov. (250 μ); *B. digitatum* (Eisenack 1938) Eisenack 1959 (65–75 μ); *B. dignum* (Sannemann 1955) comb. nov. (150 μ); *B. diploporum* (Eis. 1951) comb. nov. (formerly *Micrhystridium*) 35–40 μ).

B. echinosum (Staplin 1961) comb. nov. (formerly *Micrhystridium*) (17–22 μ); *B. eisenackium* (Deunff 1958) comb. nov. (60 μ); *B. eisenackium* (Deunff 1958) var. *crozonensis* Deunff 1958 (25 μ); *B. eisenacki* (Sannemann 1955) comb. nov. (125 μ); *B. eoplanktonicum* (Eisenack 1955) Downie 1959 (20 μ); *B. erraticum* (Eis. 1954) comb. nov. (35–50 μ); *B. franconium* (Sannemann 1955) comb. nov. (200 μ); *B. gotlandicum* (Eis. 1954) comb. nov. (46 μ).

B. hippocrepicum (Timofiev 1959) comb. nov. (69–78 μ); *B. hirsutoides* (Eisenack 1939 emend. Eisenack 1951) Eisenack 1958 (20–50 μ); *B. hirsutoides* (Eis. 1939 emend. Eis. 1951) var. *hamatum* Downie 1958 (18–40 μ); *B. hymenoferum* (Eis. 1938) Eisenack 1958 (65 μ); *B. hystrichoreticulatum* (Eis. 1938) comb. nov. (40–45 μ); *B. inconspicuum* (Timofiev 1959) comb. nov. (45–65 μ); *B. integrum* (Sannemann 1955) comb. nov. (300 μ).

B. lewisi (Deunff 1954) comb. nov. (45 μ); *B. longispinosoides* (Sannemann 1955) comb. nov. (120–200 μ); *B. longispinosum* (Eisenack 1931) forma *filifera* Eisenack 1959 (40–75 μ); *B. longispinosum* (Eis. 1931) forma *latiradiata* Eisenack 1959 (40–75 μ); *B. longispinosum* (Eis. 1931) forma *robusta* Eisenack 1959 (40–75 μ); *B. lophophorum* Eisenack 1959 (30 μ); *B. lucidum* (Deunff 1958) comb. nov. (80–89 μ).

B. macropylum Eisenack 1959 (60–68 μ); *B. meson* (Eis. 1955) comb. nov. (54–62 μ); *B. micracanthum* Eisenack 1959 (68–88 μ); *B. microfurcatum* (Deunff 1957) comb. nov. (22 μ); *B. microspinosum* (Eis. 1954) Downie 1959 (58 μ); *B. multipilosum* (Eis. 1931) Eisenack 1958 (45–60 μ); *B. multipilosum* (Eis. 1931) subsp. *validum* Sannemann 1955 (130–180 μ); *B. mutabile* (Sannemann 1955) comb. nov. (150 μ); *B. nudatum* (Timofiev 1959) comb. nov. (66–69 μ).

B. octospinum (Staplin 1961) comb. nov. (formerly *Micrhystridium*) (24–33 μ); *B. oligofurcatum* (Eisenack 1954) comb. nov. (56 μ); *B. ordovicum* (Timofiev 1959) comb. nov. (80–84 μ); *B. pateum* (Timofiev 1959) comb. nov. (60–100 μ); *B. paucispinum* (Deunff 1954) comb. nov. (formerly *Veryhachium*) (24–28 μ); *B. piriferum* (Eis. 1954) comb. nov. (62 μ); *B. polygonale* (Eis. 1931) Eisenack 1959 (75–230 μ); *B. quadriradiatum* (Timofiev 1959) comb. nov. (93–106 μ).

B. ramispinosum (Staplin 1961) comb. nov. (formerly *Multiplicisphaeridium*) (19–29 μ); *B. ramusculosum* (Deflandre 1942) Downie 1959 (18–23 μ); *B. ramusculosum* (Defl. 1942) var. *macrocladum* Deunff 1955 (30 μ); *B. rigens* (Timofiev 1959) comb. nov. (90–100 μ); *B. rjabinini* (Timofiev 1959) comb. nov. (58–70 μ); *B. robustispinosum* Downie 1959 (30 μ); *B. robustum* (Sannemann 1955) comb. nov. (240 μ); *B. robustum* (Sannemann 1955) subsp. *fissum* Sannemann 1955 (15 μ).

B. sannemanni (Deunff 1958) comb. nov. (formerly *Micrhystridium* (24 μ); *B. sedecimspinosum* (Staplin 1961) comb. nov. (formerly *Veryhachium*) (19–25 μ); *B. sericum* (Deunff 1954) comb. nov. (formerly *Micrhystridium*) (23–26 μ); *B. setigerfurcatum* (Timofiev 1959) comb. nov. (81–84 μ); *B. sexradiatum* (Timofiev 1959) comb. nov. (55–60 μ); *B. spicatum* (Staplin 1959) comb. nov. (formerly *Multiplicisphaeridium*) (63–72 μ); *B. spiciferum* (Deunff 1955) comb. nov. (23–31 μ); *B. spiniscens* (Timofiev 1959) comb. nov. (80–110 μ); *B. spinoglobosum* (Staplin 1961) comb. nov. (formerly *Micrhystridium*) (17–24 μ); *B. sprucegrovensis* (Staplin 1961) comb. nov. (formerly ? *Multiplicisphaeridium*) (35–44 μ); *B. stellaeforme* (Timofiev 1959) comb. nov. (88–99 μ); *B. suecicum* Eisenack 1959 (50–67 μ).

B. timofeevi Deunff 1961 (25–30 μ); *B. trifurcatum* (Eisenack 1931) Eisenack 1958 (50–70 μ); *B. trifurcatum* (Eis. 1931) forma *breviradiata* Eisenack 1959 (70 μ); *B. trifurcatum* (Eis. 1931) forma *longiradiata* Eisenack 1959 (45 μ); *B. trifurcatum* (Eis. 1931) forma *nuda* Eisenack 1959 (52 μ); *B. trifurcatum* (Eis. 1931) forma *paucifurcatum* Eisenack 1959 (37–52 μ); *B. trifurcatum* (Eis. 1931) subsp. *consonum* Sannemann 1955 (150 μ); *B. trifurcatum* subsp. *procerum* Sannemann 1955 (120 μ); *B. triplicativum*

(Timofiev 1959) comb. nov. (62–73 μ); *B. truncatum* (Staplin 1961) comb. nov. (formerly *Multiplicisphaeridium*) (28–38 μ); *B. tuberatum* (Downie 1958) comb. nov. (15–30 μ); *B. tuberosum* (Sannemann 1955) comb. nov. (125 μ).

B. venustum (Sannemann 1955) comb. nov. (150 μ); *B. vigivitispinum* (Staplin 1961) comb. nov. (formerly *Micrhystridium*) (24 μ); *B. zonale* (Timofiev 1959) comb. nov. (93–106 μ).

Remarks. The seventy-nine species attributed to *Archaeohystrichosphaeridium* by Timofiev (1959) have not been reattributed to *Baltisphaeridium* here (although all are capable of such reattribution) in view of the possibility of a redefinition of the genus. Sannemann (1955) refers to a species, *Hystrichosphaeridium saalfieldensis* Eisenack, of which no description could be located: this species is therefore omitted from consideration. The species *Baltisphaeridium lewisi*, *B. paucispinosum*, and *B. sericum* were published as names accompanying figures (Deunff 1956): since no text descriptions have been yet published, their validity is doubtful.

Other species (*Post-Palaeozoic*). *Baltisphaeridium armatum* (Deflandre 1937) comb. nov. (25 × 18–20 μ); *B. asteroideum* (Maslov 1956) comb. nov. (20–28 μ); *B. biformoides* (Eisenack 1954) comb. nov. (50–67 μ); *B. brevispinosum* Pastiels 1948 non Eisenack 1931 (40–55 μ × 22–25 μ).

B. centrocarpum (Deflandre and Cookson 1955) Gerlach 1961 (54–80 μ); *B. claviculorum* (Deflandre 1938) comb. nov. (30 μ); *B. claviferum* (Wilkinson 1849) comb. nov. (*c.* 100 μ); *B. clavigerum* (Deflandre 1937) comb. nov. (*c.* 45 μ); *B. colligerum* (Deflandre and Cookson 1955) comb. nov. (33 μ).

B. danicum (W. Wetzel 1952) comb. nov. (36–72 μ); *B. densicomatum* (Maier 1959) Gerlach 1961 (53–95 × 86–88 μ); *B. dictyophorum* (Cookson and Eisenack 1958) comb. nov. (71 μ); *B. difforme* (Pritchard 1845) comb. nov. (*c.* 30 μ); *B. divergens* (Eisenack 1954) comb. nov. (52–83 μ); *B. downiei* Sarjeant 1960*a* (32–40 × 38–46 μ); *B. echinoides* (Maier 1959) comb. nov. (70–80 μ); *B. ehrenbergi* (Deflandre 1947) Sarjeant 1961 (42–46 μ).

B. ferox (Deflandre 1937) comb. nov. (46–120 μ); *B. fimbriatum* (White 1842) Sarjeant 1959 (31–77 μ); *B.* cf. *fimbriatum* (White 1842), Valensi 1955 (34–35 μ); *B.* cf. *fimbriatum* (White 1842), Sarjeant 1960*b* (dimensions not obtained); *B. flosculus* (Deflandre 1937) comb. nov. (38–45 μ); *B. geometricum* (Pastiels 1948) comb. nov. (44–60 μ); *B. gilsonii* (Kufferath 1950) comb. nov. (formerly *Micrhystridium*) (30 μ); *B. granulosum* (Deflandre 1937) Sarjeant 1962*a* (33–55 × 18–26 μ).

B. heteracanthum (Deflandre and Cookson 1955) comb. nov. (56–107 μ); *B.* cf. *hirsutoides* (Eisenack 1939) Gocht 1952 (*c.* 80 μ); *B. hirsutum* (Ehrenberg 1838) comb. nov. (35–46 μ); *B. hirsutum* (Ehr. 1838) forma *minor* O. Wetzel 1933 (16–28 μ); *B. hirsutum* (Ehr. 1838) forma *varians* O. Wetzel 1933 (35–76 × 25–60 μ); *B. hirsutum* subsp. *amplum* W. Wetzel 1955 (96 μ): *B.* cf. *hirsutum* (Ehr. 1838) Pastiels 1948 (35–40 μ); *B.* cf. *hirsutum* (Ehr. 1838) Cookson, 1953 (26–44 μ); *B.* cf. *hirsutum* (Ehr. 1838), Cookson and Eisenack 1958 (dimensions not stated); *B. horridum* (Deflandre 1937) comb. nov. (55–57 μ); *B. huguonioti* (Valensi 1955) comb. nov. (29–33 × 25–29 μ).

B. iaculigerum Klement 1960 (29–35μ); *B. intermedium* (O. Wetzel 1933) comb. nov. (dimensions not quoted); *B.* cf. *intermedium* (O. Wetzel 1933) Deflandre 1938 (30–35 μ); *B. inusitatum* Klement 1960 (52 μ); *B. lobospinosum* (Gocht in Weiler 1956) comb. nov. (90–95 μ); *B. longifurcatum* (Firtion 1952) comb. nov. (40–46 μ); *B. longofilum* (Maier 1959) comb. nov. (59 μ); *B. lumectum* Sarjeant 1960*a* (45–65 μ).

B. machaerophorum (Deflandre and Cookson 1955) Gerlach 1961 (41–54 μ); *B. malleoferum* (White 1842) comb. nov. (63–85 μ); *B. mariannae* (Philippot 1949) comb. nov. (*c.* 40 μ); *B. mixtispinosum* Klement 1960 (46–60 × 37–52 μ); *B. multifurcatum* (Deflandre 1937) Klement 1960 (45–65 μ); *B.* cf. *multifurcatum* (Defl. 1937), Firtion 1952 (40–60 μ); *B.* cf. *multifurcatum* (Defl. 1937), Klement 1960, (58-63 μ); *B. neptuni* Eisenack 1958 (40–60 μ).

B. oligacanthum (W. Wetzel 1952) comb. nov. (mean 72 μ); *B. oligacanthum* (W. Wet.) var., W. Wetzel 1952 (90 μ); *B. oligacanthum* (W. Wet. 1952) subsp. *complanatum* W. Wetzel 1952 (66–72 μ); *B. oligacanthum* (W. Wet.) subsp. *grandulatum* W. Wetzel 1952 (60 μ); *B. oligacanthum* (W. Wet. 1952) subsp. *stella* W. Wetzel 1952 (36–42 μ); *B. oligacanthum* (W. Wet. 1952) subsp. *velatum* W. Wetzel 1952 (60 μ).

B. palmatum (Deflandre and Courteville 1939) comb. nov. (*c.* 54 μ); *B.* cf. *palmatum* (Defl. and Court.

1939), Valensi 1955 (45 μ); *B. panniforme* Gerlach 1961 (46–68 × 53–105 μ); *B. parvispinum* [Deflandre 1937] (Cookson and Eisenack 1958) Klement 1960 (40–84 × 20–46 μ); *B. pattei* (Valensi 1948) Sarjeant 1960*a* (34–37 μ); *B. pectiniforme* Gerlach 1961 (32–42 μ); *B. pilosum* (Ehrenberg 1843) Sarjeant 1961 (33–60 μ); *B. pilosum* (Ehr. 1843) var. *longispinosum* Sarjeant 1961 (51 × 28 μ); *B. placacanthum* (Deflandre and Cookson 1955) comb. nov. (49–54 μ); *B. plicatum* (Maier 1959) comb. nov. (45 μ); *B. polytrichum* (Valensi 1947) Sarjeant 1960*a* (33–60 μ); *B. polytrichum* Downie 1957 non Valensi 1947 (40 μ); *B. pseudhystrichodinium* (Defl. 1937) comb. nov. (38–45 × 49–54 μ); *B. pseudhystrichodinium* (Defl. 1937) subsp. *magnum* W. Wetzel 1955 (98 μ+); *B.* cf. *pseudhystrichodinium* (Defl. 1937), Lejeune-Carpentier 1941 (dimensions similar to that species); *B.* cf. *pseudhystrichodinium* (Defl. 1937), Gocht 1952 (55 × 72 μ); *B.* cf. *M. pumile* (O. Wetzel 1932), Valensi 1948 (26–30 μ).

B. ramuliferum (Deflandre 1937) comb. nov. (35–45 μ); *B.* cf. *ramuliferum* (Defl. 1937), Gocht 1952 (63 × 50 μ); *B. reginaldi* (Mantell 1846) comb. nov. (?); *B. rehdense* (Maier 1959) comb. nov. (59–66 μ); *B. saturnium* (Maier 1959) comb. nov. (70 μ); *B. seminudum* (W. Wetzel 1952) comb. nov. (30–72 μ); *B. spiculatum* (White 1842) comb. nov. (*c.* 160 μ); *B. spinosum* (White 1842) comb. nov. (40–102 μ); *B. striolatum* (Defl. 1937) comb. nov. (40–58 μ); *B.* cf. *striolatum* (Defl. 1937), W. Wetzel 1952 (72 μ); *B. striatoconus* (Deflandre and Cookson 1955) comb. nov. (52–57μ); *B. stimuliferum* (Defl. 1938) Sarjeant 1960*b* (20–26 μ).

B. tiara (Klumpp 1953) comb. nov. (44–68 μ); *B.* cf. *tiara* (Klumpp 1953), Deflandre and Cookson 1955 (44 × 58 μ); *B. triangulatum* Gerlach 1961 (36–60 × 33–48 μ); *B. tribuliferum* Sarjeant 1962*b* (53–62 × 48–58 μ); *B. tridactylites* (Valensi 1955) comb. nov. (40 × 33 μ); *B. trifurcatum* Pastiels 1948 non Eisenack 1931 (30–50 μ); *B.* cf. *trifurcatum* (Eis. 1931), Gocht 1952 (55 μ).

B. varispinosum Sarjeant 1959 (*c.* 48 μ); *B. vestitum* (Deflandre 1938) Sarjeant 1960*b* (38–70 μ); *B.* cf. *vestitum* (Defl. 1938), Deflandre 1941 (65 μ); *B. whitei* (Deflandre and Courteville 1939) Sarjeant 1959 (56–60 μ); *B. xanthiopyxides* (O. Wetzel 1933) Klement 1960 (28–30 × 10–12 μ).

Remarks. Baltisphaeridium spiralisetum de Wit 1943, of which descriptions have been given only in Dutch, is not treated. *Hystrichosphaeridium mensulum* (O. Wetzel 1933) is, from its description, referred to *Veryhachium. H. pterophorum* Deflandre and Courteville 1939 is transferred to *Cymatiosphaera. H. pumile* (O. Wetzel 1933) and *H.* cf. *pilosum* forma *nana* (O. Wetzel 1933) are transferred to *Micrhystridium.* The latter form, which cannot be considered comparable to *B. pilosum*, is considered probably conspecific with *Micrhystridium inconspicuum* and is therefore renamed *M.* cf. *inconspicuum.*

Genus MICRHYSTRIDIUM Deflandre 1937, emend.

Emended diagnosis. Hystrichospheres with spherical or oval shells not divided into fields or plates, bearing processes with closed tips, most often simple, rarely branching or ramifying, without distal connexions of any kind. The processes are generally of one type only. Mean and modal diameter of shell less than 20 μ.

Type species. Micrhystridium inconspicuum (Deflandre 1935) Deflandre 1937 (7–11 μ); Jurassic–Cretaceous.

Other species (*Palaeozoic*). *Micrhystridium albertensis* Staplin 1961 (18 μ); *M. angustum* Staplin 1961 (14–16 μ); *M. bacilliferum* Deflandre 1946 (8–10 μ); *M. bistchoensis* Staplin 1961 (*c.* 17 μ); *M. duodeciaster* (Staplin 1961) comb. nov. (formerly *Veryhachium*) (18 μ); *M. eatonensis* Downie 1959 (12–22 μ).

M. imitatum Deflandre 1942 (8–10 μ); *M. incertum* Deunff 1958 (6–7 μ); *M. mendax* Deflandre 1945 (11 μ); *M. micropolygonale* Stockmans and Willière 1961 (18 μ); *M. nannacanthum* Deflandre 1942 (10–14 μ); *M. parinconspicuum* Deflandre 1942 (9–13 μ); *M. parvispinum* Deflandre 1946 (9–12 μ); *M. parvispinum* Defl. 1946 forma *major* Deflandre 1946 (15 μ).

M. robustum Downie 1958 (10–12 μ); *M. shinetonensis* Downie 1958 (4–15 μ); *M. stellatum* Deflandre 1942 (11–16 μ); *M. stellatum* Deflandre 1942 var. *inflatum* Downie 1959; *M. tenuissimum* Deflandre

1945 (5 μ); *M. tenuissimum* Deflandre 1945 forma *major* Deflandre 1946 (10 μ); *M. tornacense* Stockmans and Willière (10 μ).

Other species (Post-Palaeozoic). Micrhystridium ambiguum Deflandre 1937 (14–22 μ): *M.* cf. *ambiguum* Deflandre 1937, Cookson 1953 (13–20 μ); *M. arachnoides* Valensi 1953 (5–8 μ); *M.* cf. *arachnoides* Valensi 1953 (7–8 μ); *M. bigoti* Deflandre 1947 (13–25 × 12–22 μ); *M. biornatum* Deflandre 1937 (15–17 μ); *M. castaninum* Valensi 1953 (10 μ); *M. cometes* Valensi 1948 (11–19 μ).

M. deflandrei Valensi 1948 (11–19 μ); *M. densispinum* Valensi 1953 (11–13 μ); *M. echinoides* Valensi 1948 (10–17 μ); *M. echinoides* Valensi 1948 forma *minor* Valensi 1953 (7–10 μ); *M. filigerum* Valensi 1953 (10–13 μ); *M. fragile* Deflandre 1947 (7–20 μ); *M.* cf. *fragile* Deflandre 1947, Valensi 1953 (12–16 μ); *M. heteracanthum* Deflandre 1937 (8 μ).

M. inconspicuum (Defl. 1935) forma *bullosa* Valensi 1953 (7–10 μ); *M. inconspicuum* (Defl. 1935) forma *helios* Valensi 1953 (9–13 μ); *M.* cf. *inconspicuum* Deflandre 1935, O. Wetzel 1933 (= *Hystrichosphaera* cf. *pilosa* forma *nana*) (6–20 μ); *M.* cf. *inconspicuum* (Defl. 1935) Deflandre and Cookson 1955 (dimensions not quoted); *M.* cf. *inconspicuum* (Defl. 1935), Sarjeant 1960*b* (6–9 μ).

M. lagynophorum Valensi 1953 (13–18 μ); *M. leptothrix* Valensi 1953 (17–22 μ); *M. lucasi* Valensi 1953 (14–15 μ); *M. mastigophorum* Valensi 1948 (14 × 16 μ); *M.* cf. *mendax* Deflandre 1945, Sarjeant 1961 (11 μ); *M. multispinosum* Pastiels 1948 (*c.* 15 μ); *M. nannacanthum* Valensi 1953 non Deflandre 1942 (10 μ); *M. operosum* Deflandre 1937 (8·5–11 μ); *M. pachydermum* Deflandre and Cookson 1955; *M. piliferum* Deflandre 1937 (20–22 μ); *M. piveteaui* Valensi 1953 (19 × 18 μ); *M. polyedricum* Valensi 1948 (6 × 8 μ); *M. pumile* (O. Wetzel 1933) comb. nov. (12–20 μ).

M. rarispinum Sarjeant 1960*b* (8–15 μ); *M. recurvatum* Valensi 1953 (10–21 μ); *M. recurvatum* Valensi 1953 forma *brevispinosa* Valensi 1953 (12–14 μ); *M. recurvatum* Valensi 1953 forma *longispinosa* Valensi 1953 (13–14 μ); *M. recurvatum* Valensi 1953 forma *multispinosa* Valensi 1953 (14–15 μ); *M. recurvatum* Valensi 1953 forma *reducta* Valensi 1953 (11 μ); *M.* cf. *recurvatum* Valensi 1953, Valensi 1953 (8 μ); *M.* cf. *recurvatum* forma *multispinosa* Valensi 1953, Sarjeant 1960*b* (22 × 19 μ); *M. rhopalicum* Sarjeant 1962*b* (10–15 μ); *M. roquesi* Valensi 1948 (16 μ).

M. scutospinum Valensi 1953 (14 μ); *M. singulare* Firtion 1953 (14·5 × 18·5 μ); M. cf. *stellatum* Deflandre 1942, Valensi 1953 (up to 18 μ); *M.* cf. *stellatum* Deflandre 1942, Deflandre and Cookson 1955 (14–19 μ); ?*M. stellatum* Deflandre 1942, Sarjeant 1959 (*c.* 25 μ); *M. sydus* Valensi 1953 (5–7 μ); *M. tenuissimum* Valensi 1953 non Deflandre 1945 (5 μ); *M. variabile* Valensi 1953 (15–16 μ).

Remarks. The species of *Micrhystridium* having tubular spines, *M. fucosum* Valensi 1955 and *M. paulinae* Valensi 1953, are transferred to the genus *Hystrichosphaeridium* Deflandre 1937 emend. Eisenack 1958. The species having a shell surface divided by ridges into fields, *M. dictyophorum* Valensi 1953, *M. placophorum* Valensi 1948, *M. reticulatum* Deflandre 1937, and *M.* cf. *reticulatum* Deflandre 1937, Cookson 1953, are transferred to the genus *Cymatiosphaera* O. Wetzel 1933 emend. Deflandre 1954. *M. polyedricum* forma *reducta* Valensi 1953 is transferred to the genus *Veryhachium* and given specific status under the name *Veryhachium valensii* (Valensi 1953) comb. nov.

Genus VERYHACHIUM Deunff (1954) 1958, emend.

Emended diagnosis. A genus of hystrichospheres having polygonal or subpolygonal tests bearing a small number (in general 3–8) of hollow pointed spines with closed tips. Size of tests 10 μ to 40 μ, rarely smaller or greater.

Type species. Veryhachium trisulcum Deunff 1958; Ordovician.

Discussion. Distinction from *Michystridium* and *Baltisphaeridium* is based on the shape of the test and the number of spines. Polygonal and subpolygonal forms with nine or more spines are excluded unless it can be demonstrated that the additional spines are 'accidental' and that the individuals are members of a typical *Veryhachium* group (such forms are known in the Permian). *V. sedecimspinosum* Staplin 1961, with fifteen to sixteen spines, and *V. duodeciaster* Staplin, with twelve spines, are therefore transferred respectively to *Baltisphaeridium* and to *Micrhystridium*. *V. ambiguum* Deunff is stated to have nine processes: unless it can be shown that the extra spines are to be considered 'accidental', this species also should be transferred to *Baltisphaeridium*. Certain species hitherto placed in *Micrhystridium* are transferred to *Veryhachium*: species are also transferred to this genus from *Baltisphaeridium*, *Hystrichosphaeridium*, and *Palaeotetradinium*.

Distinction between *Veryhachium* and *Estiastra* Eisenack depends on the relationship of the processes to the test. In the latter genus the bases of the processes meet at an acute angle and the test cannot be distinguished as a separate structure. In *Veryhachium*, on the other hand, the test is visibly distinct from the processes, although where the latter have wide, flaring bases they curve into the test walls and the point of junction cannot be accurately indicated. Eisenack has placed only one species in *Estiastra*; few others fit the diagnosis accurately. *V. centrigerum* Deunff 1957 accords well with *Estiastra*; the species *V. florigerum* Deunff 1957, *V. libratum* Deunff 1957, and *V. visbyense* (Eisenack 1959) all show transitional features. It is considered for the present best that all four species should be retained in *Veryhachium*, the boundary between the two genera appearing quite arbitrary.

Other species (*Palaeozoic*). *Veryhachium ambiguum* Deunff 1955; *V. asymmetricum* Deunff 1954; *V. bacifer* (Eisenack 1935) Deunff 1954; *V. balticum* (Eis. 1951) Deunff 1954; *V. brevitispinosum* Staplin 1961; *V. bulbiferum* (Deflandre 1944) Deunff 1954; *V. centrigerum* Deunff 1957; *V. ? clava* Deunff 1958; *V. crucistellatum* Deunff 1955.

V. eisenacki Deunff 1954; *V. europaeum* Stockmans and Willière 1961; *V. exasperatum* Deunff 1955; *V. florigerum* Deunff 1957; *V. formosum* Stockmans and Willière 1961; *V. furcillatum* Deunff 1955; *V. geometricum* (Deflandre 1944) Deunff 1954; *V. hebetatum* Deunff 1957; *V. heterogonum* Deunff 1955.

V. irregulare Jekhowsky 1961; *V. irregulare* Jekhowsky 1961 forma *pyrula* Jekhowsky 1961; *V. irregulare* Jekhowsky 1961 forma *subhexahedron* Jekhowsky 1961; *V. irregulare* Jekhowsky 1961 forma *subtetraedron* Jekhowsky 1961; *V. lairdi* (Deflandre 1946) Deunff 1954; *V. ledanoisi* Deunff 1957; *V. libratum* Deunff 1957.

V. ? macroceras Deunff 1958; *V. mamillatum* Deunff 1954; *V. minor* Staplin 1961; *V. minutum* Downie 1958; *V. octoaster* Staplin 1961; *V. oligospinosum* (Eisenack 1934) Deunff 1954; *V. polyaster* Staplin 1961; *V. reductum* (Deunff 1958) Jekhowsky 1961; *V. remotum* Deunff 1955; *V. rhomboidium* Downie 1959; *V. riburgense* Brosius and Bitterli 1961 (pars).

V. staurasteroides (Deflandre 1942) Deunff 1954; *V. stelligerum* Deunff 1957; *V. stelligerum* Deunff var. *robustum* Deunff; *V. tetraedron* Deunff 1954*c*; *V. tetraedron* var. *wenlockium* Downie 1959; *V. trispinosum* (Eisenack 1938) Deunff 1954; *V. trisulcum* Deunff var. *venetum* Deunff 1958; *V. visbyense* (Eisenack 1959).

Remarks. The species *Veryhachium asymmetricum*, *V. eisenacki*, *V. mamillatum*, and *V. tetraedron* were published as names accompanying figures (Deunff 1954); since no text descriptions have yet been published, their validity is doubtful.

Other species. (*Post-Palaeozoic*). *Veryhachium hyalodermum* (Cookson 1956) comb. nov. (formerly *Palaeotetradinium*); *V. mensulum* (O. Wetzel 1933) comb. nov.; *V. tetraxis* (Sarjeant 1960*b*) comb. nov. (formerly *Micrhystridium*); *V. valensii* (Valensi 1953) comb. nov. (= *Micrhystridium polyedricum* forma *reducta* Valensi 1953).

Genus LEIOSPHAERIDIA Eisenack 1958, emend.

Emended diagnosis. Spherical to ellipsoidal bodies without processes, often collapsed or folded, with or without pylomes. Walls granular, punctate or unornamented; thin. Without divisions into fields and without transverse or longitudinal furrows or girdles.

Type species. Leiosphaeridia baltica Eisenack 1958; Ordovician.

Discussion. Eisenack's diagnosis is emended to exclude reference to colour, since this is considered to reflect degree of staining by humic substances rather than any intrinsic difference. Investigations have shown that single species of fossil microplankton can exhibit great variation in colour with provenance, and that colour modification can result from laboratory treatment with oxidizing solutions. The species described under the invalid names *Protoleiosphaeridium* and *Leiosphaeridium* are transferred to this genus.

Other species (Palaeozoic). Leiosphaeridia aurata (Deflandre 1945) Eisenack 1958; *L. cambriense* (Timofiev 1959) comb. nov.; *L. conglutinata* (Timofiev 1959) comb. nov.; *L. cryptogranulosa* (Staplin 1961) comb. nov.; *L. diaphania* (Staplin 1961) comb. nov.; *L. eisenackia* (Timofiev 1959) comb. nov.; *L. fastigatirugosa* (Staplin 1961) comb. nov.; *L. faveolata* (Timofiev 1959) comb. nov.; *L. fragile* Downie 1958.

L. granulata (Eisenack 1938) Eisenack 1958; *L. granulifera* (Staplin 1961) comb. nov.; *L. granulosa* (Staplin 1961) comb. nov.; *L. indefinita* (Timofiev 1959) comb. nov.; *L. major* (Staplin 1961) comb. nov.; *L. megacystis* (Eisenack 1937) Eisenack 1958; *L. microcystis* (Eis. 1937) Eisenack 1958; *L. microgranulifera* (Staplin 1961) comb. nov.; *L. microsaetosa* (Staplin 1961) comb. nov.; *L. minuta* (Staplin 1961) comb. nov.; *L. nervata* (Timofiev 1959) comb. nov.; *L. orbiculata* (Staplin 1961) comb. nov.

L. papillata (Staplin 1961) comb. nov.; *L. reticulata* (Eisenack 1938) Eisenack 1958: *L. parvigranulosa* (Staplin 1961) comb. nov.; *L. retigera* (Deflandre 1945) Eisenack 1958; *L. systematice* ...

Other species (Post-Palaeozoic). Leiosphaeridia aptiana Eisenack 1958; *L. chytroeides* Sarjeant 1962*b*; *L.* cf. *granulata* Eisenack 1938, Gocht 1952; *L. hyalina* (Deflandre 1941) comb. nov.; *L.* cf. *microcystis* (Eis. 1937), Valensi 1953; *L.* cf. *reticulata* Eisenack 1938, Gocht 1952; *L. similis* Cookson and Eisenack 1960; *L. scrobiculata* (Deflandre and Cookson 1955) Eisenack 1958.

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PHYLLOCARID CRUSTACEANS FROM THE SILURIAN AND DEVONIAN OF CZECHOSLOVAKIA

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Abstract. Recent discoveries of phyllocarids in the Silurian and Devonian of the Barrandian area in Bohemia and the Upper Devonian of the Moravian Karst area are described. Nearly complete specimens of *Aristozoe parabolica* Perner and *Pygocaris schuberti* Perner have been found, permitting a more detailed diagnosis of the family Aristozoidae, to which the genus *Heroldina* Broili has also been referred. *Ceratiocaris cornwallisensis damesi* subsp. nov. from the Czech Silurian and *Ceratiocaris* (?) *coherbaria* sp. nov. from the Middle Devonian are described.

Concavicaris desiderata (Barrande) from the Czech Middle Devonian and *C. incola* sp. nov. from the Moravian Upper Devonian are described and assigned to the genus *Concavicaris* Rolfe (formerly *Colpocaris* Meek), previously known only from the American Carboniferous. The systematic position of the genus *Montecaris* Jux is discussed and the description of *M. brunnensis* Chlupáč is amplified.

Phyllocarids from the Silurian and Devonian of Czechoslovakia are known partly from the classical Barrandian area in central Bohemia and partly from the Moravian Karst area in central Moravia. In the Barrandian area phyllocarids have been discovered in beds of Silurian, Lower and Middle Devonian age; in the Moravian older Palaeozoic rocks they have so far been found only in the Upper Devonian.

The fundamental description of the Bohemian Silurian and Devonian phyllocarids was published in J. Barrande's appendix to the first volume of his *Système silurien du centre de la Bohème* (1872). Important facts about Bohemian phyllocarids were added in papers by Novák (1885*a*, *b*; 1886*a*, *b*), but Novák died before his large prepared work was published. In this century Perner (1916, 1919) has studied the Czech phyllocarids and described new forms from the uppermost Silurian, and Gürich (1929) has discussed questions of systematics. Otherwise, with the exception of the author's brief communication (1960*b*), the interesting phyllocarid fauna of the Bohemian Silurian and Devonian has not been studied by modern methods. In the recent literature only sporadic mention can be found of the occurrence of single species, e.g. Bouček (1938), Prantl and Přibyl (1948), and Chlupáč (1953, 1955).

In Moravia the first remains of phyllocarids were only recently discovered in the Upper Devonian of the southern part of the Moravian Karst (Chlupáč 1960*b*).

During new systematic researches in the Silurian and Devonian of central Bohemia as well as in the Devonian of Moravia we have succeeded in finding numerous further specimens. These finds of more completely preserved individuals of formerly known species or of new forms improve our knowledge of the Czechoslovakian phyllocarid fauna. The present paper deals with some finds of systematic and stratigraphical importance.

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Barrandeum of the National Museum of Czechoslovakia. The author wishes to express his thanks to all the above-mentioned scientists for their willingness and understanding as well as his sincere appreciation to Dr. W. D. I. Rolfe, Hunterian Museum, University of Glasgow, for his kind comments and help in the comparative study of phyllocaris.

Repositories. The described material is deposited mainly in the author's collection in the Central Geological Institute in Prague (in the text abbreviated to ICh). Other specimens used in the paper are in the collections of the National Museum in Prague (abbreviated to NM) and Geological-Palaeontological Institute of the Natural Science Faculty of the Charles University (abbreviated to KU). The photographs were made by R. Horný (National Museum, Prague) and H. Váňová (Central Geological Institute, Prague).

SYSTEMATIC DESCRIPTIONS

Order PHYLLOCARIDA Packard 1879
Suborder CERATIOCARINA Clarke 1900
Family ARISTOZOIDAE Gürich 1929

The representatives of this family have been known only on the basis of isolated parts of the carapace. New finds of almost complete specimens of the genus *Aristozoe* Barrande and *Pygocaris* Perner, in which the carapace, abdomen, and telson are preserved connected in their original position, make it possible to improve the diagnosis of the family.

Revised diagnosis. Carapace bivalved, with prominent nodes in the anterior part and distinct marginal rim. Small number (3, in *Heroldina* 5) of abdominal segments preserved outside the carapace, the last of which is strikingly elongated. The caudal part consists of one long spine only—a telson, which is usually dorso-ventrally curved. Furca not found.

Remarks. The bivalved carapace without a dorsal plate and free rostrum of genera of the family Aristozoidae proves that they belong to the suborder Ceratiocarina. The most outstanding feature of the family is that the caudal portion is formed by a single spine, the telson, usually curved, while traces of the furca have not been ascertained even in complete, well-preserved individuals (e.g. even of the genus *Heroldina*). Novák (1886*b*), who first called attention to the absence of furca, had, however, only isolated carapaces at his disposal. In this the representatives of the family Aristozoidae differ not only from other families of the suborder Ceratiocarina, but also from other phyllocarids and archaeostracans in general, to which according to other features they undoubtedly belong. In any case the family Aristozoidae Gürich represents an independent group, markedly differentiated from other families but showing closest relation to the suborder Ceratiocarina Clarke, especially to the family Echinocarididae Clarke. The configuration of the caudal part in the family Aristozoidae is, however, an exceptional phenomenon among the Archaeostraca. The new discoveries indicate that we cannot regard the assignment of the genus *Aristozoe* and other related genera to ostracods given by Barrande (1872) and in the *Treatise on Invertebrate Paleontology*, Part Q (Moore 1961), as correct. The comments of W. D. I. Rolfe (ibid., p. Q429) are, therefore, more than justified.

Genera. The genera *Pygocaris* Perner and *Orozoe* Barrande belong to the family Aristozoidae together with the type genus *Aristozoe* Barrande. The genus *Heroldina* Broili without any doubt belongs here. It agrees with *Aristozoe* and *Pygocaris* in having a greatly elongated last abdominal segment and especially in having the characteristic caudal part represented by the single curved telson (Broili 1929). To this family the author refers the genus *Callizoe* Barrande only with reserve, the nodes of which are situated more antero-ventrally than in other genera and the valves show weak lateral carinae.

Genus *Aristozoe* Barrande 1872

Aristozoe parabolica Perner 1919

Plate 13, figs. 1–3; text-fig. 1

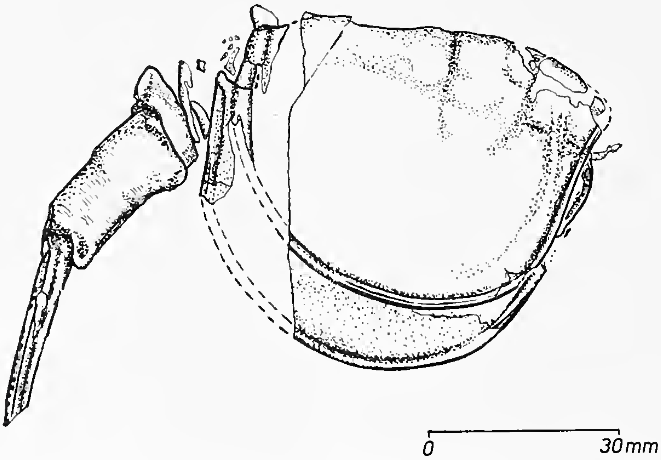
1916 *Aristozoe parabolica* Perner, pp. 5, 6, pl. 1, figs. 9–11 (Czech description).
1919 *Aristozoe parabolica* Perner, p. 228, pl. 1, figs. 9–11 (German description).
1929 *Aristozoe parabolica* Perner; Gürich, p. 62, text-figs. 7–14.
1934 *Aristozoe parabolica* Perner; Straelen and Schmitz, p. 100.

Lectotype. Perner 1919, pl. 1, figs. 9–11, NM Br042.
Type locality. Kosoř, near Praha, Czechoslovakia.
Horizon. Lochkov formation, Radotín-Limestones facies, Lochkovian, Zone of *Monograptus hercynicus*, Silurian.

Emended description. The description of the carapace was given by Perner (1916, 1919). The main features of the carapace are the characteristic and almost parabolic outline of the ventral border of the valves, the closeness of the length to the width of the valves (5:4 to 8:7), an obliquely truncate postero-lateral region, a narrow marginal rim, two nodes in the antero-dorsal region, the posterior one larger and more convex than the anterior one, semi-elliptical, and dorso-ventrally elongated. It is necessary, however, to add to Perner's description and illustrations that the postero-dorsal border is not so broadly rounded as Perner states. The original depicted in Perner's pl. 1, fig. 9 is badly damaged and incompletely preserved in the postero-dorsal part (in the positive entirely broken off), and in this respect the illustration is wrongly reconstructed. From better-preserved specimens (see Pl. 13, figs. 2, 3) it is evident that the marginal rim extends as far as the dorsal border, where the postero-dorsal angle is obtuse.

The recent material (coll. ICh 105) presents a strongly compressed specimen of *A. parabolica*, in which besides the carapace even the abdominal segments and telson in natural position are preserved (see text-fig. 1). The carapace of this individual is ill preserved owing to flattening. The assignment to *A. parabolica* can be proved by the outline preserved in greater part, a narrow marginal rim and smooth surface (the nodes rendered indistinct by deformation). The right and the left valves of the carapace of this individual overlap each other only partially: the left valve was posthumously displaced ventrally relative to the right valve so that a considerable part of the ventral sector of the left valve remains uncovered by the right valve, causing the apparently unusually large dorso-ventral width of the carapace. In the antero-dorsal part two free portions of the carapace are observed which could be interpreted as a broken rostrum. Owing to the strong compression of the valves the possibility that these are secondarily separated fragments of the antero-dorsal part of the carapace cannot be excluded.

Outside the carapace, in addition to the telson, fragments of three abdominal segments have been preserved. The first has been preserved only as three isolated fragments of the posterior part of the segment. The second segment has been preserved more completely, its width considerably exceeding its length (approx. 1:3) while the outline shows that in the dorsal part the segment was longer than in the ventral. The postero-dorsal part is pointed and projects postero-dorsally. The last abdominal segment is considerably elongated, about four times longer than the penultimate one. The proportion between sagittal length and width after lateral compression is 2:1. At the proximal border of the segment in the antero-dorsal part there is a swelling, which in spite of the compression is clearly perceptible. At a distance of 9 mm. from the proximal end of the last segment runs a dorso-ventral transverse furrow which could possibly be considered as a dividing-line between two abdominal segments. The fact that the dividing-line is interrupted in the middle and that the distinct swelling characteristic of the anterior part of the last segment cannot be found near this line is incompatible with this interpretation. The analogy with the closely related genus *Pygocaris* Perner also tends against this explanation. Slight traces of dorso-ventrally running irregular transverse striae are preserved on the last segment.



TEXT-FIG. 1. *Aristozoe parabolica* Perner. ICh 105, laterally compressed specimen with abdomen in natural position, left valve of the carapace displaced ventrally.

The telson, which is articulated with the last abdominal segment and lacks the distal part, shows a slight dorso-ventral curvature. It bears two distinct small longitudinal ridges; at the dorsal border traces of insertions of bristles are partly preserved. Remains of the furca have not been found.

Dimensions. ICh 105 (Pl. 13, fig. 1; text-fig. 1), max. length of the carapace 55 mm, dorso-ventral width of the carapace 42 mm., length of the abdominal part without telson 35 mm. Length of the last abdominal segment 24 mm., width of the last abdominal segment 11 mm. ICh 102 (Pl. 13, figs. 2, 3), max. length of the carapace 47 mm., width 38 mm.

Remarks. *A. parabolica* Perner has hitherto been known only on the basis of isolated valves of the carapace. The described specimen with preserved abdominal part, in spite of its less favourable and somewhat incomplete preservation, is of considerable significance as it constitutes the first specimen of *Aristozoe* in which carapace and abdominal part of the body are preserved in natural position. This confirms to a great extent the correctness of Novák's reconstruction (1885) which was made on the basis of isolated carapaces and segments of *A. regina* Barrande from the Lower Devonian. It is significant that only a small number (3) of abdominal segments was observed, which is analogous with *Pygocaris* Perner and obviously characteristic of the family Aristozoidae.

From the Lochkov Formation of the Kosoř locality Novák (1886*b*, pp. 15, 16) described a minute isolated telson with longitudinal ridges which he designated as *Aristozoe solitaria* Novák. His specimen agrees with the telson of *A. parabolica* described above in having distinct small longitudinal ridges, dorso-lateral insertions of bristles, and a slight curvature. The incomplete preservation of the telson of *A. parabolica* the precludes identification of the species with *A. solitaria*, especially since in the same strata several related phyllocarids occur together.

Occurrence. *A. parabolica* has so far been found only at the classical locality in the Silurian–Devonian boundary beds near Kosoř (quarries at Černá rokle). All known finds come from the blackish-grey thin-bedded fine-grained limestones and dark calcareous shales which alternate with the limestones. The beds belong to the Lochkovian (i.e. to the Lochkov Limestones in the Radotín facies), *Monograptus hercynicus* Zone, uppermost Silurian. The beds are probably younger than the British Upper Ludlovian as mentioned by Boucot (1960). They are assigned to the uppermost Silurian in accordance with the conclusion of the Prague symposium (Svoboda 1958). Specimens are not abundant; about twenty discoveries have so far been made, and except for one whole described specimen consist of valves of the carapace only.

Genus *Pygocaris* Perner 1919

Pygocaris schuberti Perner 1919

Plate 12, fig. 8; Plate 13, figs. 4, 5; text-fig. 2

1916 *Pygocaris schuberti* Perner, pp. 2–5, pl. 1, figs. 1–5 (Czech description).
1919 *Pygocaris schuberti* Perner, pp. 226, 227, pl. 1, figs. 1–5 (German description).
1929 *Pygocaris schuberti* Perner; Gürich, pp. 54, 62; text-pl. 5, fig. 16.
1934 *Pygocaris schuberti* Perner; Straelen and Schmitz, p. 193.
1960 *Pygocaris schuberti* Perner; Krestovnikov, p. 428, fig. 1254.

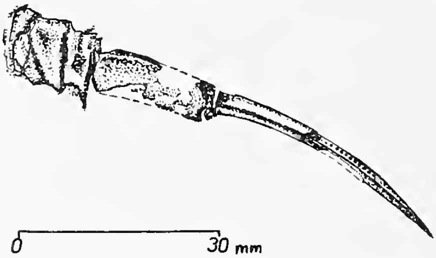
Lectotype. Perner 1916, 1919, pl. 1, figs. 1–4, NM Če1593.
Type locality. Kosoř, near Praha, Czechoslovakia.
Horizon. Lochkov Formation, Radotín-Limestones facies, Lochkovian, Zone of *Monograptus hercynicus*, Silurian.

Emended description. Perner (1916, 1919) described the carapace as possessing the following distinctive features: a prominent tapered-off projection at the anterior border of the valves and a tapering postero-dorsal part of the valves; an outstanding and fairly broad marginal rim separated off by a deep border groove; a greater number (4?) of nodes in the antero-dorsal region; and a characteristic ornamentation formed by prominent longitudinal anastomosing and often bent small ridges of unequal length.

Besides a number of carapaces which confirm the description given by Perner, a young specimen has been found among the new material in which the carapace, abdominal segments, and telson are preserved in the natural position (ICh 100, Pl. 12, fig. 8; Pl. 13, figs. 4, 5), and which allows Perner's specific description to be amplified. The specimen is preserved in a lateral position and is strongly compressed laterally so that the carapace does not show the original convexity. Only the posterior half of the carapace is preserved, and by its characteristic outline, postero-dorsally tapering, broad marginal rim, and traces of striation preserved at the dorsal border of the carapace, clearly belongs to *P. schuberti*.

Outside the carapace traces of three abdominal segments are preserved in addition to the telson. The first, having been evidently partly covered by the carapace, is incompletely preserved; only the posterior, thickened border of the segment, running subparallel to the posterior border of the carapace, is more distinct. Being laterally compressed the second segment has an almost sub-trigonal outline and the dorsal border was evidently longer than the ventral border. The length at the dorsal border approximately equals the dorso-ventral length. As in *A. parabolica* the segment terminates posteriorly in a postero-dorsal projection. The last abdominal segment, unlike the previous ones, is well preserved despite the lateral compression. The length of the segment is conspicuous; it is two and a half times longer than the dorso-ventral width. At the anterior border the segment was evidently more massive, as shown by its convex surface. At the antero-ventral border a laterally situated node is preserved; the swelling of the segment and the elevation of this part are possibly due to muscular insertions. The postero-dorsal border of the segment may have run out in a short caudal projection which partly overlapped the head of the telson.

The head of the telson was articulated with the posterior border of the last segment, which was embayed. On the surface of the last segment an ornament is perceptible formed by dorso-ventrally running, slightly undulating, small ridges. This type of ornament corresponds well with the sculpture of the surface of the carapace in *P. schuberti*. Only the proximal half of the telson is preserved. It is distinctly bent in the dorso-ventral direction and carries two longitudinal ridges. The head is slightly enlarged and the spine tapers gradually backwards. Traces of bristle insertions are not preserved. Furcal rami have not been found, although the articulation between the last abdominal segment and telson is well preserved.



TEXT-FIG. 2. *Pygocaris schuberti* Perner. ICh 110, laterally compressed abdomen.

EXPLANATION OF PLATE 12

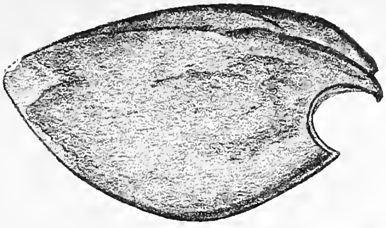
Figs. 1, 2. *Concavicaris incola* sp. nov. Hády, near Brno. 1, Holotype, ICh 176, carapace (left valve), ×2·6. 2, Paratype, ICh 178*a*, carapace (right valve), ×2·3.

Figs. 3–5. *Concavicaris desiderata* (Barrande). Pekárek mill, near Choteč. 3, Paratype D, ICh 193, left valve of the carapace showing the rostral plate, ×2·5. 4, Paratype A, ICh 194, carapace (left valve), ×2·6. 5, Paratype B, ICh 192, carapace (left valve), ×3.

Figs. 6, 7. *Ceratiocaris* (?) *coherbaria* sp. nov. Karlštejn. 6, Restored telson and furca, after holotype, ICh 126*a*, ×2. 7, Detail showing the sculpture of the telson, after ICh 123, ×4·6.

Fig. 8. *Pygocaris schuberti* Perner. Kosoř, near Praha. Paratype A, ICh 100. Incompletely preserved carapace, abdominal segments and telson in natural position, ×1.

Figs. 9, 10. *Ceratiocaris cornwallisensis damesi* subsp. nov. 9, Paratype, ICh 137, detail of the distal portion of telson (lateral view) showing pits marking points of insertion of bristles situated ventrolaterally; Šamor near Liteň; ×4·7. 10, Paratype, ICh 250, detail of compressed telson showing the stripe of pits marking points of insertion of bristles; Kosoř; ×2.



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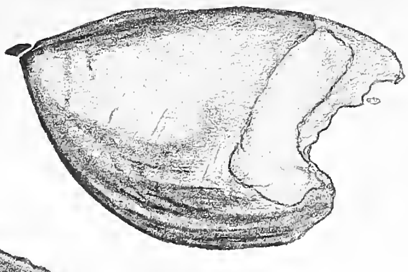

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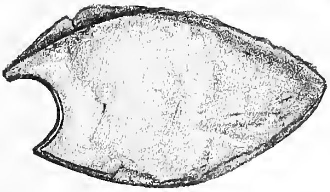

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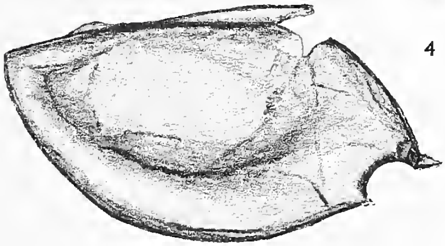

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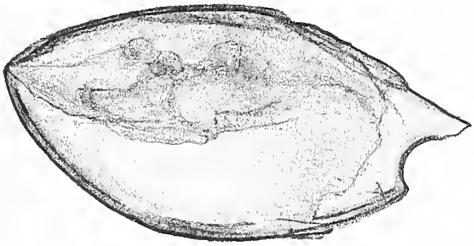

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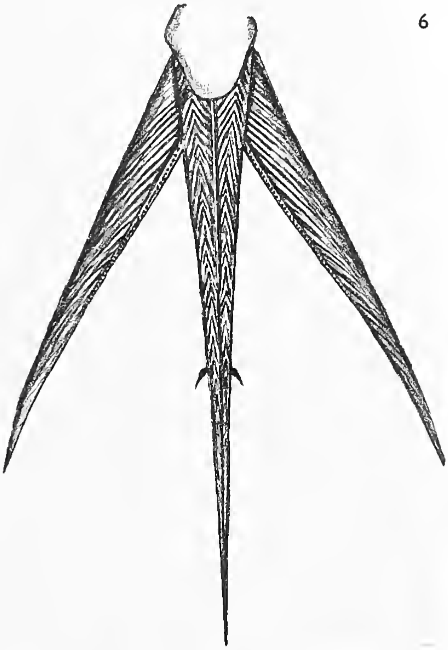

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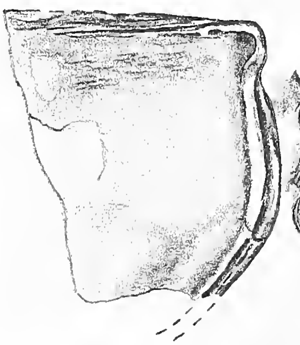

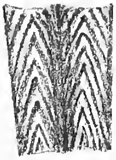

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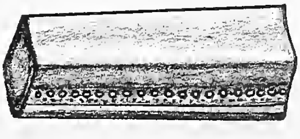

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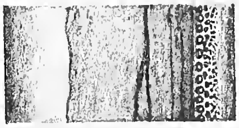

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The shape of the abdominal part of the carapace is also visible in another specimen (ICh 110), which, by analogy with that described above, the author also refers to *P. schuberti*. It is an isolated flattened abdomen with telson, preserved in lateral position (text-fig. 2). In addition to the telson three abdominal segments are clearly visible; the first two are much shorter than the last. The last segment is more than three times longer than it is wide; it is, however, impossible to exclude deformation caused by compression. The telson, characteristically slightly but distinctly dorso-ventrally curved, preserves for part of its length a number of insertions of bristles located dorso-laterally. Traces of furca rami are lacking.

Dimensions (in mm.)	*Holotype (NM Če1593)*	*Paratype A (ICh 100)*	*Paratype B (ICh 110)*
Length of carapace	*c.* 103	*c.* 35	—
Dorso-ventral width of carapace . .	58	*c.* 25	—
Length of last abdominal segment . .	—	16	20
Dorso-ventral width of last abdominal segment	—	6	7
Length of telson	—	*c.* 35–40 (20 mm. preserved)	38

Remarks. New finds of the abdomen of *P. schuberti* show a distinct resemblance to *Aristozoe parabolica*. Their common features are especially the small number of abdominal segments, a considerable elongation of the last segment, and a distinctly curved telson. It is important to note that in neither of these species could traces of furcae be established.

The telson of *P. schuberti* differs by its stronger curvature and shorter head from the isolated telson described by Novák (1886*b*) from the same formation as *Aristozoe solitaria*. On the other hand the possibility that the specimen described by Fritsch (1907) as *Ouchus siluricus* Fritsch is conspecific with *P. schuberti* cannot be excluded. Fritsch's original from the Kotýs-locality, near Kon˘prusy (coll. NM Če 1456), probably from the lower part of the Lochkov formation in the Radotín facies, is doubtless a fragment of an aristozoid phyllocarid. The curved spine bearing longitudinal ridges represents the telson and the fragments interpreted by Fritsch as intraclavicula and scapula are the remains of abdominal segments. The resemblance between Fritsch's original and the telson of *P. schuberti* is striking. As these occur in the older horizon of the Lochkov limestones (*Monograptus uniformis* Zone) where the occurrence of *P. schuberti* has not yet been proved by the discovery of carapaces, and as the telsons of different representatives of the family Aristozoidae resemble each other so closely that it is not yet possible to exclude assignment to another species, the author does not at present consider '*Ouchus*' *siluricus* synonymous with *P. schuberti*.

Occurrence. *P. schuberti* is so far only known with certainty from the classical locality at Kosoř, south-west of Prague, where it occurs in the same beds as *A parabolica*, with a rich marine fauna (Chlupáč 1953). It is found in intercalations of dark fine-grained limestones and in highly calcareous shales, and occurs about as abundantly as *A. parabolica*; twenty-five specimens have so far been found.

Family Ceratiocarididae Salter 1863
Genus *Ceratiocaris* M'Coy 1849

Ceratiocaris cornwallisensis Copeland 1960

1960 *Ceratiocaris cornwallisensis* Copeland, pp. 49, 50; pl. 8, figs. 1, 2; pl. 9, fig. 5.

Ceratiocaris cornwallisensis damesi subsp. nov.

Plate 12, figs. 9, 10; Plate 14, figs. 3–5; Plate 15, figs. 1–4; text-figs. 3–5

1886*b* *Ceratiocaris damesi* Novák, p. 676 (*nomen nudum*).

Derivation of name. After Mr. W. Dames; the original manuscript name suggested by Novák has been used.

Holotype. Two last abdominal segments and telson, NM Br283 (Pl. 15, fig. 1; text-fig. 3).

Type locality. 'Černá rokle', Kosoř, near Praha, Czechoslovakia.

Horizon. Lochkov Formation, Radotín-Limestones facies, Lochkovian, Zone of *Monograptus hercynicus*, Silurian.

Material. Two incomplete carapaces; a great number of caudal appendages partly with abdominal segments; and about thirty mandibles.

Description. Carapace incompletely known, lacking anterior region (text-fig. 5). Outline suboval, the dorsal border much less convex than the ventral one, posterior border truncate, a narrow marginal rim, the border line distinctly marked. Surface sculpture not observed.

The abdominal part has not yet been found with a carapace in natural position, so that the number of abdominal segments is unknown. In several specimens disarticulated

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EXPLANATION OF PLATE 13

The specimens in Figs. 1–3 and 5 were coated with ammonium chloride before being photographed.

Figs. 1–3. *Aristozoe parabolica* Perner. Kosoř, near Praha. 1, Paratype A, ICh 105, laterally compressed specimen showing abdominal portion and telson in natural position (left valve of the carapace displaced ventrally relative to the right valve), ×1·1. 2, 3, Paratype B, ICh 102, left valve of the carapace only slightly compressed showing the vaulting and nodes differently illuminated, ×1·1.

Figs. 4, 5. *Pygocaris schuberti* Perner. Kosoř, near Praha. Paratype A, ICh 100. 4, Incompletely preserved carapace, abdominal segments and telson in natural position, ×1. 5, Detail of the same specimen showing the articulation of the last abdominal segment and telson, ×2.

EXPLANATION OF PLATE 14

The specimens in Figs. 1–3 and 5 were photographed under alcohol, and the specimen in Fig. 4 was coated with ammonium chloride before being photographed.

Figs. 1, 2. *Montecaris brunnensis* Chlupáč. Bedřichovice, near Brno. 1, Paratype C, ICh 200*a*. 2, Counterpart of the same specimen, ICh 200*b*, ×1.

Figs. 3–5. *Ceratiocaris cornwallisensis damesi* subsp. nov. Kosoř, near Praha. 3, Paratype NM 1114, laterally compressed telson showing the backwardly curved posterior projection in the proximal portion, ×1·8. 4, ICh 109, isolated non-compressed mandible of a big specimen. ×1. 5, ICh 115*a*. Compressed mandibles and isolated fragments of the carapace, ×0·9

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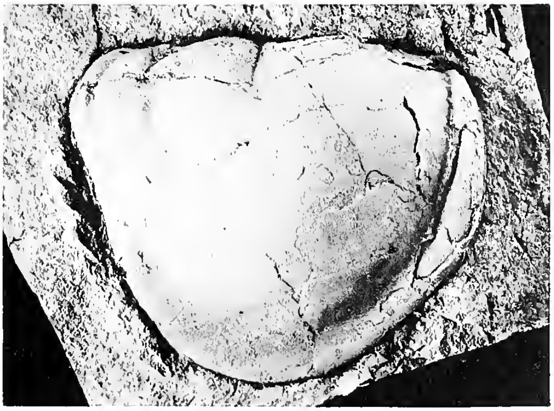

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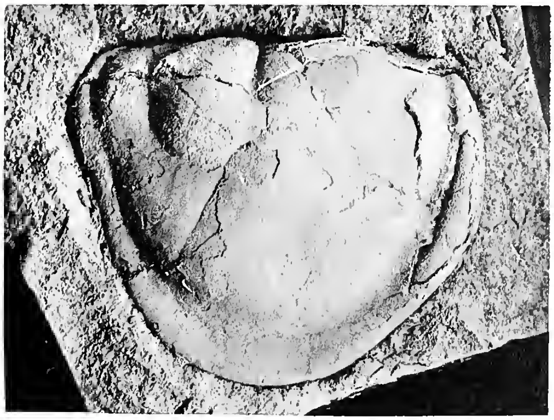

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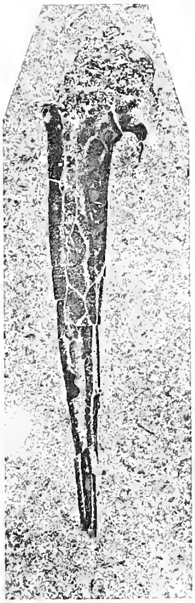
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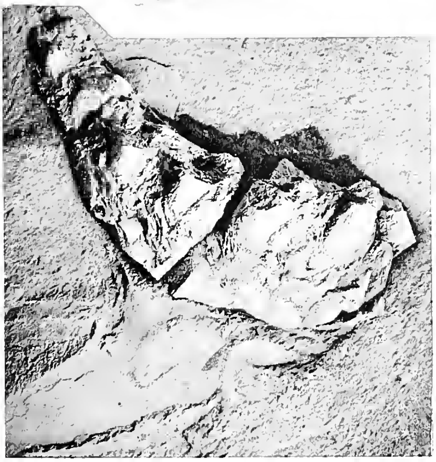
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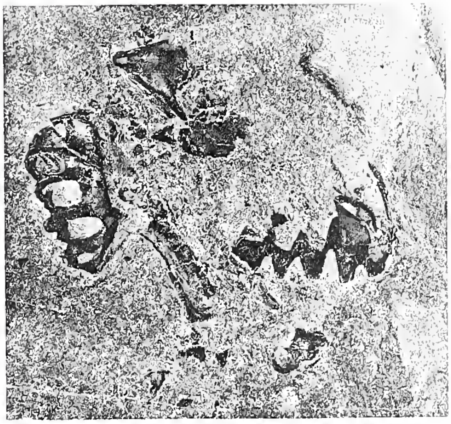
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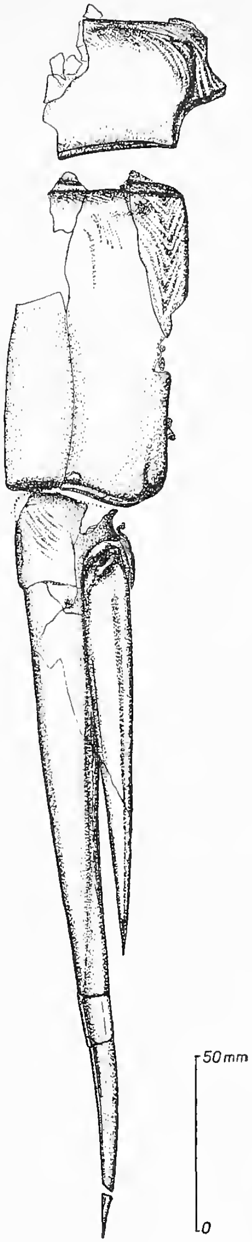
CHLUPÁČ, Phyllocarid crustaceans

abdominal segments and caudal appendages are, however, preserved near the remains of carapaces, so that there is no doubt that they belong to the same subspecies.

It is impossible to decide which abdominal segments the isolated specimens represent, but two last abdominal segments are preserved in natural position. The penultimate segment, e.g. in the holotype (text-fig. 3; Pl. 15, fig. 1), shows a subquadrate outline and is much shorter than the last segment (the ratio of its length to the length of the last segment is 1:2·5). Several pieces show sculpture in the anterior part formed by fine anastomosing small ridges and striae of unequal thickness. In front they run subparallel to the anterior border, but they soon turn obliquely postero-ventrally.

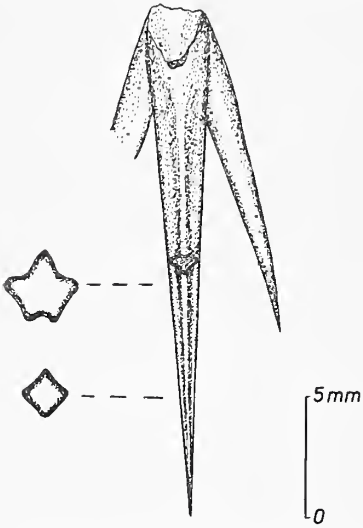
The last abdominal segment is considerably elongated and is about two and a half times longer than the penultimate segment. It is more or less flattened on all specimens so that the original contours are not preserved. It has a subquadrate outline, the length exceeding at least twice the dorso-ventral width. At the anterior border the segment, even in the flattened specimens, is arched and suggests the contours of the original segment. In this position the sculpture is very often preserved and is seen to consist of unequally thick small ridges and striae as on the penultimate segment. Anteriorly the striae are subparallel to the anterior border, but they soon turn away postero-ventrally from the dorsum. On the holotype it can be clearly observed that these small ridges and striae on the ventral side form acute angles with vertices pointing backward. The posterior part of the last segment is unornamented in all the specimens so far known. Near the posterior border the segment was obviously thickened as in the anterior region, although to a lesser extent.

The most frequently found specimens are large caudal appendages, represented by a long telson and shorter lateral spines. The telson is long and dagger-shaped, with a conspicuously broadened strongly vaulted head, and preserves its convexity at least in part, even in the compressed specimens. The telson is almost straight and gradually tapers backwards. In large specimens only was it possible to establish that the distal part of the telson is very moderately dorsally curved. The head of the telson is provided anteriorly with a narrow articulation plate. The head carries on both sides of the ventral surface two strong distinct tooth-like projections, the anterior of which is simply pointed, while the posterior one is produced into a short curved spine (Pl. 14, fig. 3). The head bears traces of sculpture formed as in the abdominal segments by irregular small ridges and striae running postero-ventrally from the anterior border.



TEXT-FIG. 3. *Ceratiocaris cornwallisensis damesi* subsp. nov. Holotype NM Br283, laterally compressed two last abdominal segments and caudal appendages.

A cross-section of the telson cannot be obtained from the large, more or less compressed specimens. When the specimens are laterally compressed only two longitudinal carinae are noticeable, one at the dorsal border, and the other at the ventral. Another lateral longitudinal line, indistinctly marked in relief, runs postero-ventrally from the head. It was possible to study in detail the cross-section and nature of the telson on undeformed young specimens from the locality Šamor, near Liteň. The telson shows five longitudinal ridges. A prominent dorsal ridge running along the median line of the telson has a sharp crest, and two dorso-lateral ridges have rounded crests as do the two ventro-lateral ridges. The ventral concavity of the telson in the proximal part is conspicuous where the section of the spine is star-shaped. This ventral concavity dies out posteriorly and the section of the spine becomes subpentagonal. The ventral concavity disappears completely in the distal part of the telson, and the two ventro-lateral ridges fuse into one so that the section of the telson becomes subquadrate (text-fig. 4).



TEXT-FIG. 4. *Ceratiocaris cornwallisensis damesi* subsp. nov. ICh 139, telson with furcal rami of a young specimen showing the section of the central spine.

The pits marking the insertions of bristles are situated laterally on the telson between the dorso-lateral and ventro-lateral ridges. In the paratype from Kosoř (ICh 250) it is possible to establish that the pits do not form a single row but several longitudinal rows of rounded pits of different sizes (Pl. 12, fig. 10). The largest pits form a row near the dorso-lateral ridge, under which are three to four rows of tiny insertions not quite regularly arranged, the size of the latter decreasing ventrally. Some similarity exists with the specimens described by Barrande (1872) as *Ceratiocaris tardus* from the Devonian of Bohemia.

In the adult specimens the lateral spines of the furca are approximately two-thirds of the length of the telson (in the young specimens the ratio of the length of telson to lateral spines ranges around 5:3). The spines taper posteriorly more rapidly than the telson, and older specimens (text-fig. 3; Pl. 15, fig. 3) show a slight dorsal curvature. Only two longitudinal ridges are visible on the laterally compressed specimens, namely at the dorsal and ventral border. The unflattened specimens from Šamor show a subovate cross-section of the spines, sharp dorsally. The exterior surface of the lateral spines

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EXPLANATION OF PLATE 15

The specimens in Figs. 3 and 4 were coated with ammonium chloride before being photographed.

Figs. 1–4. *Ceratiocaris cornwallisensis damesi* subsp. nov. Kosoř, near Praha. 1, Holotype, NM Br283, two last abdominal segments and caudal appendages laterally compressed, ×0·3. 2, Paratype A, ICh 143, two last abdominal segments and caudal appendages in lateral position, ×0·5. 3, ICh 113*a*, incompletely preserved and laterally compressed caudal appendages showing a slight bending of the spines, ×0·7. 4, ICh 142, isolated abdominal segment showing the sculpture, ×1·8.

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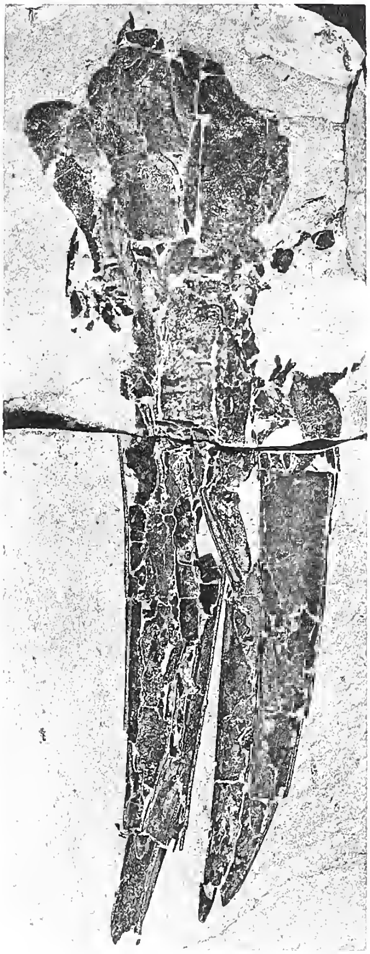

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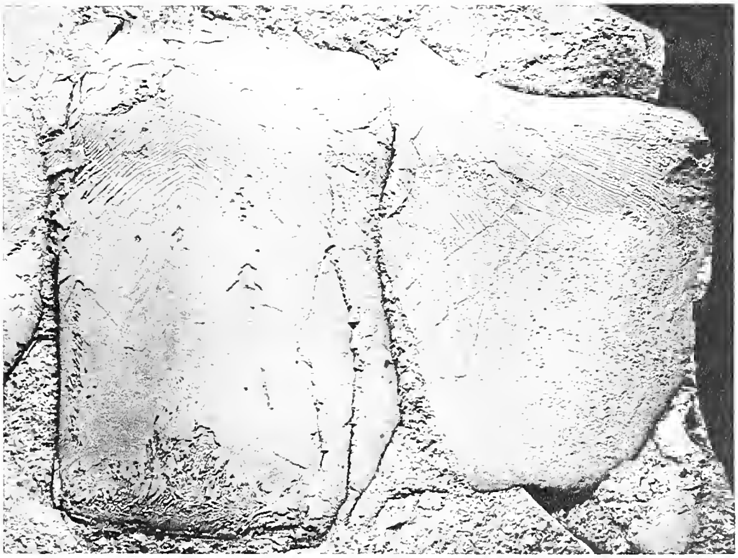

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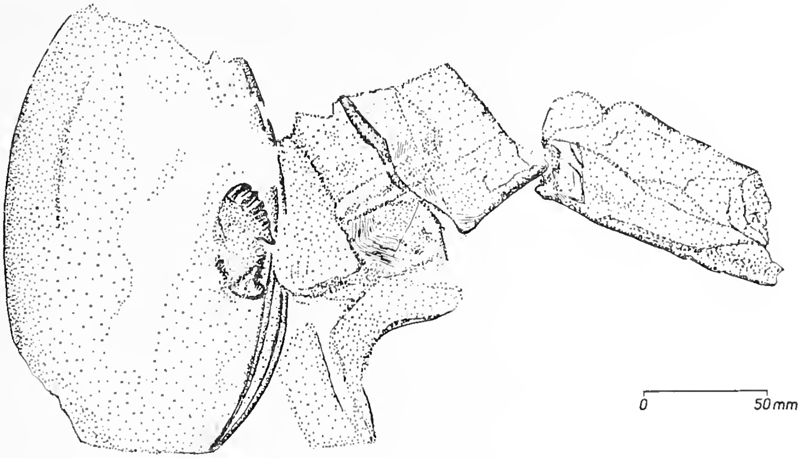
shows no traces of sculpture. Only in the casts from Šamor were irregular, fine, posterodorsally oriented ridges observed which indicate the sculptured interior surface of the integument. Traces of circular insertions of bristles form a longitudinal row on the lateral spines just under the dorsal ridge, but they are rarely preserved.



TEXT-FIG. 5. *Ceratiocaris cornwallisensis damesi* subsp. nov. KU 1208. Displaced carapace, mandibles, and abdominal segments.

In addition to the carapace, abdominal segments, and caudal appendages, mandibles are known, but they are usually isolated from the other parts of the shield. In several cases, however, they were found either directly within the carapace (but not in natural position) or close to the carapace so that the assignment to *C. cornwallisensis damesi* subsp. nov. is certain. The mandibles may be up to 50 mm. long. The corpus mandibulae is produced into a comparatively long sickle-shaped process formed of a much thinner carapace than that over the oral part. The arcuate oral part proper is very massive and carries four to six paired, partly alternating pointed teeth, which have radially running furrows on the surface.

Dimensions. Ceratiocaris cornwallisensis damesi subsp. nov. is probably the largest Bohemian phyllocarid, and of all Bohemian species only *C. bohemica* Barrande attains similar dimensions. The specimens found indicate that the length of the whole body can be estimated as being up to 70–80 cm.

Dimensions (in mm.)	*Holotype (NM Br283)*	*Paratype A (ICh 143)*	*NM 35615*
Length of penultimate abdominal segment .	37	—	—
Length of last abdominal segment . . .	90	70	—
Length of telson	210	*c.* 150	*c.* 300
Length of lateral spine	117	85	210

The carapace (paratype C, KU 1208) is about 200 mm. long, the maximal dorso-ventral width being 110 mm. In ten young specimens from Kosoř and Šamor the length of the telson varies between 17 and 50 mm., the length of the lateral spines being 11–31 mm.

Remarks. The described specimens from the uppermost Silurian of Bohemia were formerly mentioned by a number of authors as *Ceratiocaris damesi* Novák (Novák's manuscript name) but without description and illustration. Copeland (1960) has recently described *C. cornwallisensis* from the Upper Silurian of Cornwallis Island in the Arctic area of Canada, and it is very closely related to *Ceratiocaris damesi* Novák MS. Both forms have the same general structure and agree in the main features of sculpture of caudal appendages and abdominal segments. A more detailed comparison of the specimens figured by Copeland (1960) and the material from Bohemia reveals, however, some differences of lesser importance. The difference between the length of the telson and the lateral spines is in the Bohemian specimens somewhat greater than in the specimens figured by Copeland. In the Canadian form no curvature of the lateral spines has been established. From Copeland's description there seem to be differences in the cross-section of the telson but, considering the compression of the Canadian material, they are probably only secondary. According to Copeland's description the length of the last abdominal segment is much shorter than in the Bohemian specimens; however, according to W. D. I. Rolfe (*in litt.*), the last segment in the holotype of *C. cornwallisensis* is longer (61 mm.); the indication of a shorter length was due to the mistaking of casual cracks for the boundary between segments. The comparison shows that despite close relationship it is not possible to regard the Canadian and the Bohemian forms as completely synonymous. Since a number of features in the Bohemian material could not be established in the described Canadian material, the author considers it appropriate to designate the Bohemian form as a separate subspecies which may be a geographical mutation of the Canadian species.

Occurrence. The occurrence of *C. cornwallisensis damesi* subsp. nov. is restricted in the Barrandian to the uppermost Silurian Lochkov Formation (Lochkov stage) in which it is abundant in some places. Most of the material comes from the Radotín and Kosoř facies of this formation from the Černá rokle quarries near Kosoř (Zone of *Monograptus hercynicus*), where it is accompanied by a rich marine fauna. This subspecies has been found in the same beds at Přídolí near Velká Chuchle, in the former Podolí Cement Works in Praha 14, and in the Švarcava valley near Solopysky, &c. (for more detailed records see Chlupáč 1953). The subspecies was also found in the organo-detritic facies of the same age in the Kotýs Limestones, at Šamor, near Liteň, where it occurs frequently in beds of light grey limestones with a rich trilobite fauna.

Ceratiocaris(?) *coherbaria* sp. nov.

Plate 12, figs. 6, 7; Plate 16, figs. 4–9

1960*a* *Ceratiocaris* sp. nov. Chlupáč, pp. 152, 157, &c.

Derivation of name. From the Latin *co-* and *herbaria* = herbaceous, indicating the common occurrence with plant remains.

Holotype. Telson figured on Plate 16, fig. 7; ICh 126.

Type locality. 'Volfova rokle', Karlštejn, near Beroun, Czechoslovakia.

Horizon. Srbsko Formation, lower part (Kačák Beds), Upper Middle Devonian (Lower Givetian).

Material. Twenty-five telsons, mostly with furca.

Diagnosis. A species referred only with reserve to the genus *Ceratiocaris* M'Coy, characterized by a diagnostic ornament on the telson and furca. The ornament is formed on both sides of the median ridge of the telson by dense fine broken lines, the angles of which point anteriorly, and on the lateral spines by distinct oblique lines. The telson bears a pair of small lateral telson-spines.

Description. The only part of the shield known so far is the telson and paired lateral spines (furca). The telson is produced as a straight central spine of medium length and is slightly longer than the lateral spines. It tapers rapidly posteriorly at an angle of 7–10°, and the telson head is only slightly inflated. A distinct median dorsal keel runs the length of the telson. In well-preserved specimens a pair of lateral spines may be seen just over half-way along the telson; the spines are slightly curved and point obliquely backwards. The characteristic ornament of the telson consists of fine broken lines, which form sharply pointed arches, with vertices pointing anteriorly. When dorsally compressed these arches are arranged symmetrically in relation to the longitudinal keel. Only some specimens show a row of closely spaced circular pits marking points of insertion of lateral bristles. The lateral spines (furcal rami) are almost as long as the central spine. They taper rapidly posteriorly at an angle of about 5–8°, while the dorsally compressed specimens have their distal ends slightly bent inwards towards the central spine. A longitudinal keel runs along the interior margin of the lateral spines, and some specimens show a row of tiny circular pits marking the insertions of setae. The ornament on the lateral spines consists of striae running obliquely from the interior to the exterior margin; it is more distinct than on the telson. The striae become finer towards the exterior margin. The angle formed by the exterior sides of both spines of the furca is fairly constant and varies from 60° to 80°.

Dimensions (*in mm.*)	*Holotype* (*ICh 126*)	*Paratype A* (*ICh 124*)	*Paratype B* (*ICh 133*)
Length of telson along midline . . .	37	21	20
Width of proximal part of telson . . .	6	3·3	3·3
Length of lateral spines along exterior margin	26	15·2	17
Angle between exterior margins of lateral spines	*c.* 65°	60°	70°

Remarks. Since only caudal appendages have so far been found their generic assignment must remain questionable. The author only tentatively refers the specimens described above to *Ceratiocaris* because the characteristic ornament of the telson differs from all other representatives of the genus. Similar ornament may be seen in Bohemian Silurian representatives of the group of *Ceratiocaris stygia* Salter, e.g. *C. scharyi* Barrande, which have an ornament of pointed arches on the last abdominal segment, although this ornament does not usually continue on to the telson. A certain analogy in the ornament can be seen in the specimens described by Novák (1886*a*) as *Phasganocaris pugio*, which according to Gürich (1929) represents the telson and possibly the abdominal segment of *Aristozoe memoranda* Barrande. The shape and spacing of the lines are, however, quite different. On the other hand the ornament of oblique lines on the lateral spines is similar to that of a number of phyllocarids, e.g. of the genus *Mesothyra* Hall from the family Rhinocarididae (especially of *Mesothyra neptuni* Hall) and of the genus *Montecaris* Jux (e.g. *M. antecedens* Chlupáč), &c. The fact that neither the carapace nor other parts of the body except caudal appendages have so far been found suggests that as in many other ceratiocarids only the caudal appendages were suitable for fossilization. It is interesting to note that most of the specimens of caudal appendages are preserved in dorsal or ventral position and only exceptionally in lateral position. The fairly constant angle formed by the lateral spines suggests a close connexion between furca and telson. The weight of the central spine being greater the specimens were necessarily deposited on the sea bottom on the dorsal or ventral side, while the lateral spines remained symmetrically extended on both sides of the telson.

C.(?) *coherbaria* sp. nov. is the youngest known phyllocarid from the Central Bohemian earlier Palaeozoic and comes from beds where no phyllocarids have previously been found.

Distribution. Ceratiocaris(?) *coherbaria* sp. nov. appears rarely in dark calcareous shales of the Kačák division of the Srbsko Beds which form the base of the Givetian in the Barrandian area. Both an abundant marine fauna (tentaculitids, lamellibranchs, brachiopods, &c.) and especially terrestrial plants occur together with this species (see Chlupáč 1960; Obrhel 1961). During recent study *C.*(?) *coherbaria* sp. nov. was found in several localities, e.g. in Karlštejn-Volfova rokle and at the locality 'U dubu' near the forestry, Srbsko, Koda, and the hill Koreňský vrch. For further details of localities and accompanying fauna see the author's stratigraphical paper (1960*a*).

Genus CONCAVICARIS Rolfe 1961

Remarks. The commonly used name *Colpocaris* Meek 1872 has been replaced by *Concavicaris* Rolfe, since the former was a junior homonym of *Colpocaris* von Meyer 1862 (see Rolfe 1961).

Orientation of the carapace. The orientation of the valves of the carapace is disputed in this genus. While Meek (1875) considered the part with a prominent sinus-like incision to be posterior, most of the later authors, e.g. Clarke (1900), Gürich (1929), Cooper (1932), Shimer and Shrock (1944), regarded the sinus as being anterior. By analogy in many other phyllocarids the posterior thorny projections and incisions are more prominent than the anterior ones, and the conspicuous broadening of the carapace towards the sinus in *Concavicaris* suggests that Meek's original orientation is correct. This is

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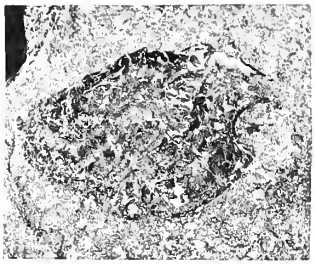
EXPLANATION OF PLATE 16

The specimens in Figs. 2–5 and 9 were photographed under alcohol, and those in Figs. 6–8 were coated with ammonium chloride before being photographed.

Figs. 1, 2. *Concavicaris incola* sp. nov. Hády, near Brno. ICh 176*a*. 1, Carapace (left valve), ×1·7. 2, The same specimen photographed under alcohol, ×1·7.

Fig. 3. *Concavicaris desiderata* (Barrande). Pekárek mill, near Choteč. Paratype A, ICh 194, carapace, ×2·5.

Figs. 4–9. *Ceratiocaris* (?) *coherbaria* sp. nov. Karlštejn, near Beroun. 4, Paratype B, ICh 123*b*, caudal appendages, ×2·4. 5, Paratype A, ICh 124, caudal appendages, ×2·4. 6, Paratype C, ICh 122, the right lateral spine showing the sculpture, ×1·9. 7, Holotype, ICh 126*a*, caudal appendages, ×2·1. 8, ICh 126*b*, counterpart of the same specimen, ×2·1. 9, The same specimen, detail of the telson showing the small lateral telson-spines, ×5·8.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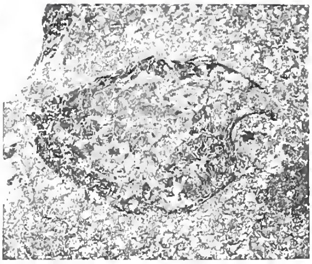
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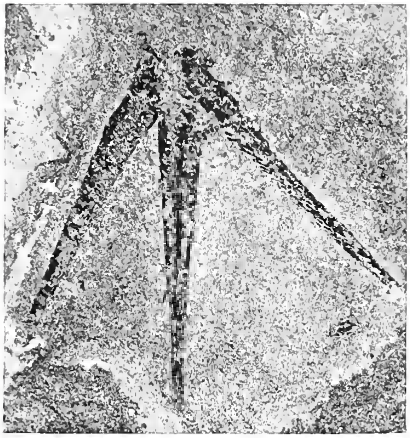
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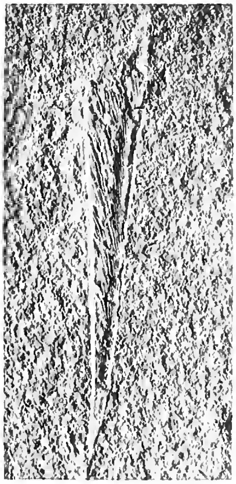
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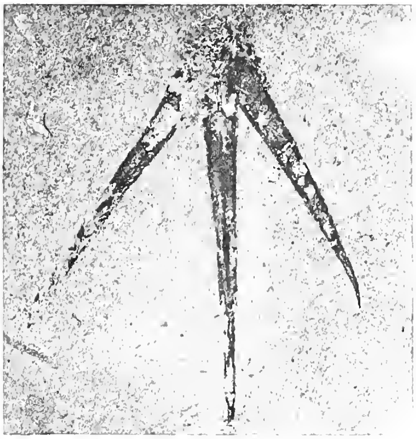
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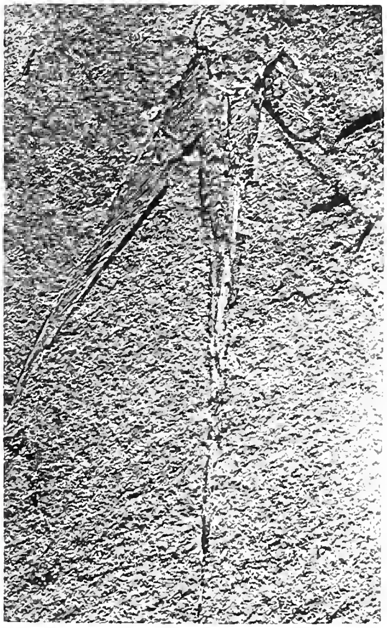
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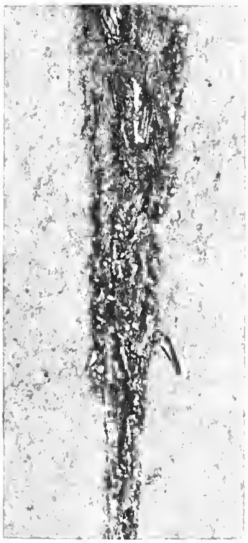
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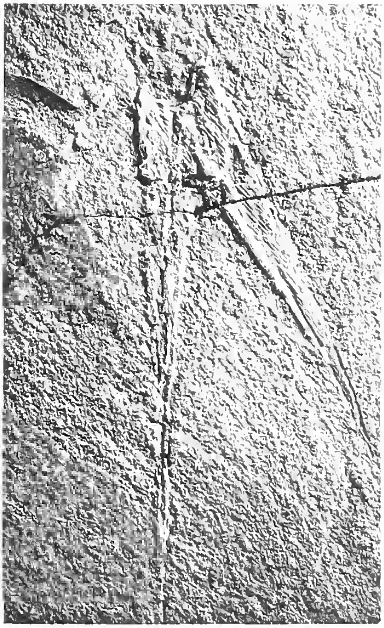
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CHLUPÁČ, Phyllocarid crustaceans

confirmed by the presence in a new American species of a rostral plate at the opposite end to that with the sinus (personal communication, W. D. I. Rolfe).

Distribution. *Concavicaris* has so far been recorded from the North American Lower and Upper Carboniferous only. To this genus the author here refers the species *Concavicaris desiderata* (Barrande) from the Bohemian early Middle Devonian, previously regarded as an ostracod, and *C. incola* sp. nov. from the Upper Devonian of Moravia. Thus the stratigraphic range of the genus is extended to the Middle Devonian and the geographical distribution to Central Europe.

Concavicaris desiderata (Barrande 1872)

Plate 12, figs. 3–5; Plate 16, fig. 3; text-fig. 6

1872 *Leperditia desiderata* Barrande, p. 530, pl. 34, figs. 27, 28.
1938 *Ceratiocaris* sp. nov. Bouček, p. 168.
1959 *Colpocaris*(?) *desiderata* (Barrande); Chlupáč, pp. 460, 491.

Holotype (by monotypy). NM ČF1271. Figured by Barrande 1872, pl. 34, figs. 27, 28; refigured here as text-fig. 6.

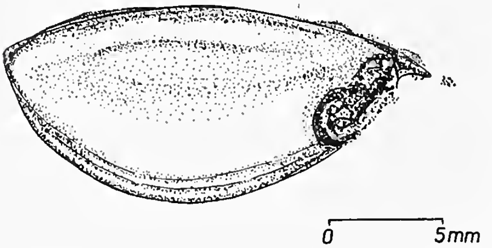
Type locality. Vávra mill at Choteč, Czechoslovakia.

Horizon. Daleje Shales, *Gyroceratites gracilis* Zone, Lower Eifelian, Devonian.

Redescription. Carapace broadly suboval with a distinct sinus, the length being approximately twice the width. Antero-dorsal part of the carapace pointed, with a tapering projection in some specimens which can be interpreted as a rostral plate in natural position. The dorsal border of the carapace is less convex than the ventral and runs in a weak arch to the upper end of the sinus. The ventral border is strongly convex and runs arcuately from the pointed anterior border to the postero-ventral end of the sinus. The ventral marginal rim is indistinct and separated only by a shallow marginal line. The rim reaches its maximum width at the ventral border, and narrows arcuately anteriorly and posteriorly. A conspicuous postero-ventral arcuate sinus incises the posterior of the carapace. The dorsal border forms an acute angle with the dorsal limb of the sinus and forms a tapering postero-dorsal process which exceeds the length of the process enclosed between the ventral border and the lower part of the sinus. The surface of the valves is smooth, but two or three furrows are commonly present in the ventral region, parallel to the border. These are, however, not genuine ornament but the border lines of the opposite valve of the carapace which have been impressed through the surface of the carapace during the natural shifting of the valves under pressure. Numerous irregular longitudinal ridges are the result of compression and of secondary deformations, as their course differs in individual specimens and they are absent in better-preserved specimens.

Dimensions (*in mm.*)	*Holotype* (*NM ČF1271*)	*Paratype A* (*ICh 194*)	*Paratype B* (*ICh 192*)	*Paratype C* (*ICh 211*)
Length of valve . .	19	20	21	25
Maximum width of valve . . .	9	10	10	13

Remarks. Barrande (1872) described and figured this species as an ostracod, *Leperditia desiderata* Barrande, from the locality 'Wawrowitz' (Vávra mill), near Choteč. Later Bouček (1938) mentioned specimens of a phyllocarid which he considered a new species of the genus *Ceratiocaris* M'Coy from the same stratigraphic horizon (Daleje shales) from the Pekárek mill locality, near Solopysky. The author's collections from Pekárek mill proved the identity of the specimens collected by Bouček with Barrande's species *Leperditia desiderata*. Barrande's figure of this species is considerably and inaccurately idealized. Study of the original specimen (NM ČF1271) shows a conspicuous posterior sinus which is filled, however, with broken fragments of the carapace. The shape of the anterior and posterior border is also different from that figured by Barrande, but it corresponds well with the new discovery from Pekárek mill. Otherwise Barrande's original is much damaged by pressure so that it does not show detail of the surface of the valves (text-fig. 6).



TEXT-FIG. 6. *Concavicaris desiderata* (Barrande). Holotype NM ČF1271, laterally compressed carapace (posterior part damaged).

C. desiderata differs from the American Carboniferous representatives of the genus especially in its shorter and broader carapace, and smaller, less incised sinus, placed more postero-ventrally. From the Upper Devonian species *C. incola* sp. nov. it differs in more elongated valves, less curved ventral border, and less incised sinus. *Concavicaris desiderata* is the oldest representative of the genus yet known.

Occurrence. Barrande's original comes from a hard calcareous intercalation in the Daleje shales from Vávra mill, near Choteč, in Bohemia. This species has recently been found in the lowest part of the Daleje shales at the locality near Pekárek mill, near Solopysky (Chlupáč 1959, p. 460). Here it abounds in a thin calcareous intercalation with very abundant tentaculitids, *Nowakia cancellata* (Richter), *Styliolina clavulus* (Barrande), and other fossils. Stratigraphically this horizon is in the lower part of the *Gyroceratites gracilis* Zone, Lower Eifelian, lowest Middle Devonian.

Concavicaris incola sp. nov.

Plate 12, figs. 1, 2; Plate 16, figs. 1, 2

Derivation of name. From Latin *incola*, resident.

Holotype. Carapace figured on Plate 12, fig. 1, and Plate 16, figs. 1, 2. ICh 176*a*.

Type locality. Hády, near Brno, Růžena-quarry, Moravian Karst, Czechoslovakia.

Horizon. Dark platy Hády-Limestones, Famennian, Upper Devonian.

Material. Six carapaces and damaged fragments of body and abdominal spines.

Description. Carapace suboval, deep, with a prominent semicircular sinus in the posterior part, the length being about one and a half times the width. The maximum width is reached in the posterior half. The antero-dorsal part of the carapace slightly pointed.

Dorsal border slightly convex, ventral border strongly convex. Ventral marginal rim narrow, in the anterior part indistinct; ventral border line very fine and narrow. The postero-dorsal projection between the dorsal border and the upper part of the sinus is produced into a ventrally curved, beak-shaped process. It is longer and sharper than the postero-ventral process between the ventral border and the lower part of the sinus. The ventral border line continues to the sinus, rims its margin, and dies out just before the dorsal border. In some specimens an indistinct line parallel to the dorsal border may have been produced by shifting and bending of the dorsal border of the opposite valve. The surface of the carapace is smooth.

Dimensions (in mm.)	*Holotype (ICh 176)*	*Paratype A (ICh 178)*	*Paratype B (ICh 177)*
Length of valve	17·5	16	25
Maximum width of valve . . .	10·5	10	15

Remarks. All the available material is flattened so that the original rotundity is not perceptible. Fragments of abdominal spines found in the same layer are very incompletely preserved, but some show longitudinal ridges.

Concavicaris incola sp. nov. differs from the American Carboniferous species *C. elytroides* (Meek), *C. woodfordi* (Cooper), and *C. bradleyi* (Meek) mainly in the greater dorso-ventral width and lack of sculpture. Its form is more reminiscent of that of the Upper Carboniferous *C. sinuata* (Meek and Worthen), the anterior region of which is, however, even more distinctly pointed and the dorsal border less convex. *C. desiderata* (Barrande) has a different length-to-width ratio, a more gently curved ventral border, and a less incised sinus.

Occurrence. C. incola sp. nov. was found in dark Hády Limestones with calcareous shale intercalations in the north-east wall of the big quarry 'Růžena' at Hády, near Brno, in Moravia. It occurs very abundantly in one thin layer. The accompanying ostracod fauna confirms the Upper Devonian age, namely the lower part of the *Clymenia* Zone (Famennian Vα), i.e. the lower part of the Dasberg substage according to the German division. Further specimens doubtfully referred to this species have been found in the northern part of the Hády plateau in the same formation of thin bedded dark limestones of Famennian age.

Family ECHINOCARIDIDAE Clarke 1900

Genus MONTECARIS Jux 1959

1959 *Montecaris* Jux, pp. 167, 168.
1960*b* *Montecaris* Chlupáč, p. 639.
1960 *Montecaris* Jux, p. 1134.
1961 *Baituganocaris* Krestovnikov, p. 28.

Systematic position. The genus *Montecaris* was initially assigned by Jux (1959) and Chlupáč (1960*b*) to the family Ceratiocaridae of the suborder Ceratiocarina as the anterior region of the carapace was poorly known. After finding more completely preserved specimens Jux (1960) reassigned this genus to the family Rhinocarididae of the suborder Rhinocarina. Krestovnikov (1961) refers the specimens designated by him as *Baituganocaris* to the same family, and these are doubtless congeneric with *Montecaris*. The critical character for classification is the presence or absence of the dorsal median plate which in rhinocaridids separates both valves of the carapace, which come together at one place only. The median plate has not been established in *Montecaris*. In the newly found well-preserved specimen of *M. brunnensis* Chlupáč described below both valves of the carapace touch each other in a simple dorsal line without any trace of median plate. The valves are slightly separated from each other only in the anterior quarter where they leave space for an elongated triangular rostral plate.

The lack of dorsal plate suggests that the assignment to the order Ceratiocarina is correct. The sculpture of the carapace and the shape of caudal appendages would correspond both to rhinocaridids and echinocaridids. The abdominal segments with their distinct postero-lateral spines suggest a relationship with echinocaridids. In spite of this *Montecaris* shows some features reminiscent of rhinocaridids, for example the whole shape of the carapace with the conspicuous mid-posterior spines, especially in the German specimens, suggests a relationship with, for example, the genera *Dithyrocaris* Scouler and *Mesothyra* Hall. The shape of the Moravian specimens, however, is closer to that of *Elymocaris* Beecher. A similar shape of carapace is not, however, unknown in Ceratiocarina, as *Galenocaris* Wells proves.

It would appear that the relationship to the suborder Ceratiocarina is much closer than to the Rhinocarina. From the present study the author thinks it better to refer *Montecaris* to the family Echinocarididae of the suborder Ceratiocarina.

Distribution. The genus *Montecaris* was described originally from the higher Middle or lower Upper Devonian of the Rhineland where it is represented by *M. strunensis* Jux 1959 and *M. lehmanni* Jux 1960. At the same time its representative *M. antecedens* Chl. was found in the uppermost Silurian (Lochkovian) of Bohemia and *M. brunnensis* Chlupáč in the Moravian Upper Devonian (Chlupáč 1960*b*). Caudal appendages undoubtedly belonging to *Montecaris* Jux were described and figured by Copeland (1960) as *Spathiocaris? sp.* from the Upper Devonian of British Columbia, Canada. The genus *Baituganocaris* Krestovnikov from the Upper Devonian of the Transvolga region in the U.S.S.R. is evidently synonymous with *Montecaris*. Of five species described by Krestovnikov (1961) *M. tatarica* (Krestovnikov) seems to be the only species adequately described and thus objectively justified. From the material known to date we may conclude that *Montecaris* had a wide geographical distribution and ranges from the uppermost Silurian to the Upper Devonian.

Palaeoecology. All previously described records of *Montecaris* come from purely marine sediments of similar character. German and Moravian species occur in a facies of thin-bedded platy limestones with many intercalations of dark calcareous shales. The Canadian specimen occurs in dark shales. The specimens from the Chugurovo Beds of the Transvolga region come from beds of alternating shales, limestones, and siltstones. It is obvious that *Montecaris*, like *Ceratiocaris*, found suitable life conditions in the facies of alternating limestones and shales, i.e. in quiet-water conditions with a rich planktonic and nektonic marine fauna (cf. Chlupáč 1960*b*). The shallow-water environment of a reef or organo-detritic facies was evidently inimical to *Montecaris*.

Montecaris brunnensis Chlupáč 1960

Plate 14, figs. 1, 2; text-fig. 7

1960 *Montecaris brunnensis* sp. nov. Chlupáč, pp. 640–2, text-figs. 3, 4; pl. 2, figs. 1, 2; pl. 3, figs. 1, 2.

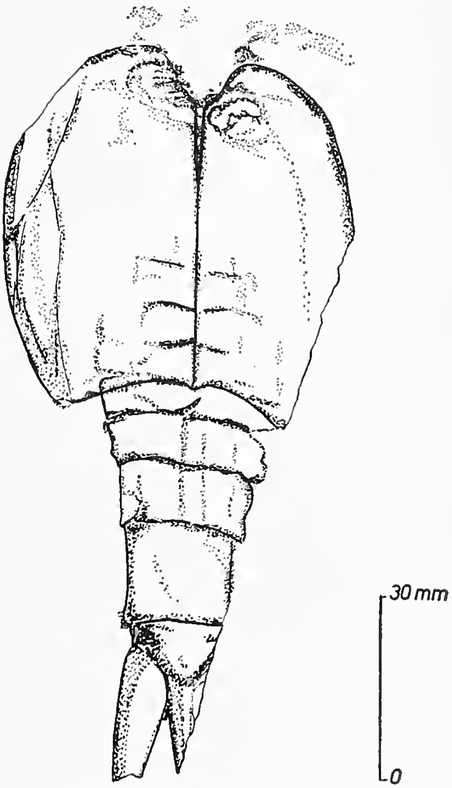
Holotype. Chlupáč 1960, pl. 2, figs. 1, 2. Coll. ICh. 18.

Type locality. Bedřichovice, near Brno, Moravian Karst, Czechoslovakia.

Horizon. Dark platy Hády Limestones, Famennian, Upper Devonian.

Description of new material. The newly found almost complete specimen of *M. brunnensis* from the type-locality makes it possible to augment the author's original description. The new specimen (ICh 200*a*, *b*) is preserved in dorsal view and shows the carapace and abdomen in natural position. The antero-dorsal carapace incision caused by the arcuate truncation of the antero-dorsal part of the valves is very noticeable. The straight median dorsal line in the new specimen is very clear. In the anterior quarter the valves are slightly separated from each other. In this space between the valves are preserved fragments of the test that can be interpreted as a rostral plate, but they do not distinctly project into the antero-dorsal carapace incision. A dorsal median plate has not been found and both valves of the carapace simply meet at the midline.

Distinct nodes are not detectable on the antero-dorsal part of the valves but as in the holotype there are more massive parts of the carapace and irregularities which are probably due to the impression of mandibles through the carapace. The ventral margin of the valves is moderately arcuate but is truncate posteriorly and forms the slightly concave posterior margin. On the surface of the left valve an oblique stripe is preserved in the antero-ventral region as in the holotype, and which runs from the anterior border in a postero-ventral direction. In addition there is another longitudinal stripe not clearly marked in the ventral sector of the left valve produced probably by the dorsal compression of the carapace. Three dorso-ventrally running, equally spaced transverse furrows are discernible in the posterior half of the carapace at the dorsal line on both valves, and probably represent the course of segments covered by the carapace (text-fig. 7).



TEXT-FIG. 7. *Montecaris brunnensis* Chlupáč. Paratype B, ICh 200*a*, specimen dorsally compressed.

In front of the anterior border of the valves of the carapace two disconnected stripes are indistinctly visible formed of the same material as the valves, but finely dispersed.

The stripe in front of the right valve is striking, especially when under alcohol. It runs subparallel to the frontal border of the carapace. By analogy with other rare examples of phyllocarids with appendages preserved the author considers these structures to be the remains of antennae. Articulation or other particulars cannot, however, be established on the specimen.

Four abdominal segments are preserved outside the carapace and increase in length backwards. The ratio of dorsal length to width in the first is 1:4·5, in the second 1:3 to 1:3·5, in the third 1:2·3, and in the last the length equals the width. The outline of all the segments is subquadrate. Short postero-lateral spines, which were well preserved in the previously described holotype and paratype, are not well seen in the new specimen.

The caudal appendages are only partly preserved; only the proximal part of the telson with its broad head and the left lateral spine of the furca are preserved. The latter agrees in shape with the caudal appendages of *M. brunnensis*. The characteristic telson bristles are not preserved.

Dimensions. Paratype B, ICh 200*a*, *b*. Approximate sagittal length of whole exoskeleton 140–150 mm. Maximum length of carapace 60 mm. Maximum width of carapace 58 mm. Length of abdominal part of shield without caudal appendages 41 mm. Length and width respectively of abdominal segments: first segment, 6 mm., 29 mm.; second segment, 8 mm., 26 mm.; third segment, 10 mm., 22 mm.; last segment, 17 mm., 17–18 mm.

Remarks. The new specimen of *M. brunnensis* is important especially because of its good preservation of the anterior region of the carapace. The prominent antero-dorsal incision of the carapace is different from the anterior region of the carapace of the related species *M. lehmanni* Jux, as reconstructed by Jux (1960, text-fig. 3). On the other hand the shape of the frontal part of the carapace corresponds well with the photographs of *M. lehmanni* given by Jux (1960, pls. 142, 143) which in the antero-dorsal part also shows a similar incision, interpreted by Jux as purely secondary. The new specimen of *M. brunnensis* clearly proves the natural existence of the frontal incision of the carapace as in many other phyllocarids.

M. brunnensis agrees with *M. lehmanni* in some features, e.g. in the general shape of the carapace, broad posterior incision, longitudinal stripes in the ventral region of the valves, and the shape of the caudal appendages. *M. brunnensis* differs, however, in having a rounded postero-lateral region without spiny projections; in the greater number (4) of abdominal segments (*M. lehmanni* shows 3); in the much shorter postero-lateral spines on the abdominal segments; and in having fewer bristles on the telson and narrower lateral spines.

On the basis of new knowledge presented by Jux (1960) the comparison with *M. strunensis* Jux may be completed by the fact that in *M. brunnensis* postero-lateral spiny projections on the carapace are not developed while in *M. strunensis* they are distinctly marked. A comparison of the location of nodes in the antero-dorsal part cannot be made owing to the flattening of the Moravian material. The species *M. tatarica* (Krestovnikov) agrees with *M. brunnensis* in the simple midline and probably also in the outline of the posterior part of the carapace, but it has a different telson-length : furcal-length ratio.

The traces interpreted by the author as probable remains of antennae are noteworthy. Similar traces have so far been found only in very rare cases. They are well known and excellently preserved, for example, in *Nahecaris stuertzi* Jaekel from the Rhenish Lower

Devonian (cf. Broili 1928, 1929). The preservation of the specimen of *M. brunnensis* unfortunately does not allow more detailed studies of these organs.

The three transverse lines visible on both sides of the midline in the posterior half of the carapace probably mark the boundaries between the three anterior abdominal segments covered by the carapace valves. As these transverse furrows are shorter than the abdominal segments and die out 7 mm. away from the dorsal line, the possibility that they represent the remains of hinge organs cannot be excluded. The author considers the first explanation, however, to be more probable.

Occurrence. M. brunnensis is so far known only from the Upper Devonian thin-bedded Hády limestones at the type-locality, Bedřichovice, near Brno, in the Moravian Karst.

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THE COMPOSITION OF *PYRITOSPHAERA BARBARIA* LOVE 1957

by LEONARD G. LOVE

ABSTRACT. A bulk sample of *Pyritosphaera barbaria* Love 1957 is shown by microchemical analysis, following other indications, to be dominantly organic in composition.

Pyritosphaera barbaria was isolated (Love 1957) by removal of the pyrite by nitric acid from pyrite microspheres of the Pumpherston Shell Bed and adjacent strata of the Scottish Lower Carboniferous Lower Oil Shale Group. The residual bodies, which average about 8 μ in size and are of much the same diameter as the spheres from which they come, are spherical and microgranular in appearance. They were regarded as being organic on the basis of their pale brown colour, translucency, isotropic character, and chemical inertness except to further oxidation or combustion. Further they were regarded as the remains of micro-organisms on the basis of the regularity of their form, coupled with their great abundance in an environment in which such material might be expected to flourish. The suggestion that they might have had an active significance in the formation of the sulphide is not of immediate concern here. Similar forms were obtained by Love (1962*a*, *b*) from pyrite spheres of Upper Palaeozoic and Mesozoic rocks and much detail of the manner of occurrence was noted. Somewhat similar forms were recorded by Love and Murray from pyrite spheres from Recent sediments.

Direct analysis of the material of *P. barbaria* of Carboniferous age has been made difficult both by problems in adequately concentrating the pyrite spheres from the rock and, of greater importance, in obtaining samples in which the pyrite spheres, and thus the *P. barbaria* bodies, were free from other organic material which often encloses them. A sample recently examined, however, conformed with the latter requirement as far as detailed microscopic examination of the pyrite and of the residues could show, and yielded a good separation of pyrite spheres. It came from Namurian marine shale of R_1 age, from River Noe, Derbyshire, England.

The pyrite was dissolved with brominated concentrated nitric acid acting for one hour at room temperature and the residue consisted dominantly of *P. barbaria*. Preliminary examination of a portion by emission spectrograph between copper electrodes indicated at least 35 per cent. of carbon by the method developed by Dennen (1957), whose observation that a substantial upward correction may be necessary is amply borne out. Electron probe micro-analysis of the spherical bodies in another part of the sample indicated (to a 1 per cent. limit) the absence of iron (which might be expected as insoluble ferric oxide), and of sulphur, silica, calcium, and other metallic elements. Carbon cannot be detected by this method. On a third portion normal microchemical analysis indicated 56 per cent. carbon. Based on bulk analysis of Carboniferous 'kerogen' (Down 1939) this might represent as much as 80 per cent. organic matter but perhaps as low as 70 per cent. if the oxidizing acid had removed any organic material, as indeed is indicated by the C:H ratio being 15·7:1 for the oxidized sample compared with that of 11·3:1 for the

[Palaeontology, Vol. 6, Part 1, 1963, pp. 119–20.]

unoxidized material quoted below. The balancing weight of the sample, proportionately less by volume, was observed to consist of heavy minerals while the *P. barbaria* material was observed to be only a little heavier than water. Infra-red spectroscopy showed the presence of undoubted organic compounds, since C–H bonds, carbonyl groups, and possibly N–H groupings were recognized.

Part of a parallel original unoxidized sample of pyrite spheres was shown by micro-chemical analysis to consist of approximately 85 per cent. pyrite (40·9 per cent. Fe, 45·1 per cent. S) and 3·4 per cent. carbon by weight. The latter perhaps represents 4·25 per cent. of organic material by weight. Heavy minerals and some insoluble residue from the use of hydrofluoric acid were seen to be present (giving 11·2 per cent. ash) but no visible organic matter. A ratio of organic matter to pyrite in the spheres of 1:20 by weight is therefore given.

This demonstration of the organic composition of *P. barbaria* puts the argument that these are remains of micro-organisms occurring *in situ* in the pyrite on a surer basis but is not in itself proof. The data will be of value for comparison with other sediments but this work is not complete and will be discussed elsewhere (Love, in the press).

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SOME UPPER TREMADOCIAN GRAPTOLITES FROM NORWAY

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ABSTRACT. New material of Upper Tremadocian graptolites from the Oslo Region, preserved in full or half relief in pyrite, is described. *Bryograptus ramosus* Brøgger 1882 is shown to have distinct bithecae. '*Didymograptus*' *kiaeri* Monsen 1925 is also shown to have bithecae and is made the type of the new genus *Kiaerograptus*. *Adelograptus bulmani* sp. nov. is a peculiar species, which might have affinities both with the anisograptids and the leptograptids and might be intermediate between them. The presence of bithecae in some graptoloid-like forms in the Upper Tremadoc suggests that the presence of graptoloids in beds older than the Arenig might be questionable. The material present might indicate that a number of graptolite lineages are more complex than previously assumed, and that several lineages in the dichograptids and other graptoloid groups originated directly and independently from the dendroids.

BECAUSE of the bad state of preservation of the material, the details of the structure of most Upper Tremadocian graptolites are virtually unknown. The specimens are generally preserved as mineralized films, and only the number of branches, angle of bifurcation, and the gross outline of the thecae can be observed.

The author recently succeeded in finding some specimens of Upper Tremadocian graptolites from the Oslo Region which are preserved in full or half relief in pyrite. The specimens come from the *Ceratopyge* Shale (Zone 3 aβ) and are found in the upper part of this formation, about 0·4–1·8 m. below the *Ceratopyge* Limestone (Zone 3 aγ), in two road sections at Slemmestad, about 20 km. SW. of Oslo.

The general stratigraphy, and an outline of the geology of the area is given by Størmer (in Holtedahl and Dons 1960, pp. 11–24, 45–47). One locality is about 300 m. ENE. of Størmer's locality 4 (loc. cit., text-fig. 25), and the second is along the same road, about 1½ km. to the SW. The horizon is rich in graptolites, but only a few of them are preserved in full relief.

Parts of the specimens preserved in full relief are sometimes distorted and swollen in a rather peculiar way which is interpreted as a result of the pyritization. The specimens were probably originally filled with, or replaced by, an iron-sulphide gel (possibly hydrotroilite or melnichovite); later the sulphide gel crystallized into pyrite, and the specimens became compressed by the diagenesis of the sediment. In the cases where the quantity of the gel was small, or where it was very rich in water, the specimens were compressed to mineral films. This is the usual preservation of the Tremadocian graptolites from the Oslo Region, and several other areas. In some few specimens, the sulphide content of the gel was sufficient to give an exact replica in massive pyrite of the specimens, or at least one in half relief. In some cases again the gel seems to have swollen, probably due to high osmotic pressure, and the fossils became swollen and distorted. This should be borne in mind when working with pyritized materials, as the process of fossilization may have caused quite considerable changes in the morphology of the specimens, and may make statistical, biometric work on such graptolites rather difficult.

In many specimens the pyrite has been oxidized, and the specimens are preserved as

[Palaeontology, Vol. 6, Part 1, 1963, pp. 121–31, pl. 17, 18.]

casts partly filled with iron oxides. These specimens are studied on, and photographed from latex moulds. The moulds were made from latex emulsion stained with Indian ink and were whitened with ammonium chloride for photography.

The few specimens preserved in full relief reveal a number of details, not previously observed, especially the presence of bithecae in some specimens. In *Bryograptus ramosus* this was expected, even if it had not previously been possible to demonstrate their presence. It was more surprising to find bithecae in '*Didymograptus*' *kiaeri* Monsen, which superficially looks like an extensiform didymograptid. Based on the early stratigraphic occurrence of this species, and some structural features (especially the long nema and the oblique sicula), the author suspected it was not an ordinary didymograptid. Bulman (1941, 1950) had also suggested that this species might be related to the Anisograptids, and this view has gained strong support from the material presented here.

A new genus, *Kiaerograptus*, is made to accommodate the two-branched, extensiform Anisograptids with distinct bithecae.

Acknowledgements. The author is deeply indebted to Professor O. M. B. Bulman, Cambridge, for advice and encouragement in preparation of this paper, and to Dr. Henningsmoen for having read the manuscript critically. The photographs were made by Faculty photographer B. Mauritz and the author.

Bryograptus ramosus Brøgger 1882

Plate 17, figs. 6–9; text-fig. 1

1882 *Bryograptus ramosus* Brøgger, p. 37, pl. 12, fig. 21.
1925 *Bryograptus ramosus* Brøgger; Monsen, pp. 160–2, pl. 1, fig. 9, text-figs. 3*a–c*.
1954 *Bryograptus* cf. *ramosus* Brøgger; Bulman, p. 34, pl. 4, fig. 9.

Description. Some specimens presumably belonging to this species are preserved in full relief, and show distinct bithecae, situated alternately on both sides of the branches. Because of this pattern of budding, the apertures of the autothecae also occur alternately in two rows, instead of in one single row, which is usually the case in Graptoloid rhabdosomes.

The sicula is long, and needle-shaped, and the budding of the proximal part is easily seen in the best specimens (Pl. 17, fig. 8). The rhabdosome is initially rather elongate, and in at least one specimen (Pl. 17, fig. 7) there are definitely three primary branches.

EXPLANATION OF PLATE 17

All specimens belong to Paleontologisk Museum, Oslo, Norway. The specimens shown in figs. 3, 4, 7, 8, 9 are photographed from latex casts coloured with Indian ink and coated with ammonium chloride. The specimens shown in figs. 1 and 2 are coated with ammonium chloride, and the ones shown in figs. 5 and 6 are photographed by the maximum reflection method.

Figs. 1–5 *Kiaerograptus kiaeri* (Monsen). 1, Distal part of a branch showing bithecae, PMO 72833a; ×13. 2, 3, Two proximal parts, PMO 72833b (2) and PMO 72834a; ×10. 4, Specimen showing proximal part in somewhat oblique view, PMO 72834b; ×10. 5, Lectotype, the specimen figured by Monsen (1925, text-fig. 5, pl. 2, fig. 16), PMO 60212a; ×4. Specimens 1–4 from Slemmestad, 20 km. SW. of Oslo; 5 is from Stensberggaten in Oslo; all from Zone 3 aβ.

Figs. 6–9. *Bryograptus ramosus* Brøgger. 6, Lectotype, a large rhabdosome from Zone 3 aβ at Vestfossen, Eiker (70 km. W. of Oslo). Probably the specimen figured by Brøgger (1882), pl. xii, figs. 21, 21a; PMO 72829; ×2. 7, 8, Two proximal parts of young rhabdosomes, Zone 3 aβ, Slemmestad. 7, PMO 72831; ×9. 8, PMO 72832; ×7. 9, Fragments of two branches showing bithecae; Zone 3 aβ Slemmestad; PMO 72830; ×20.

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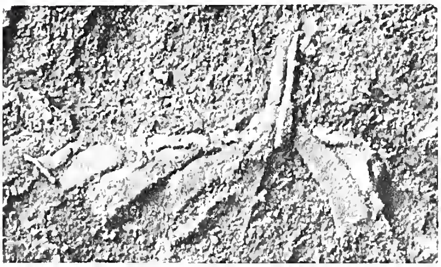

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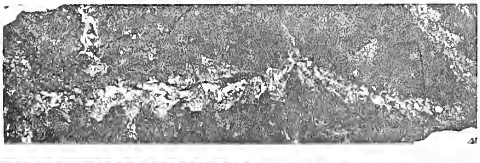

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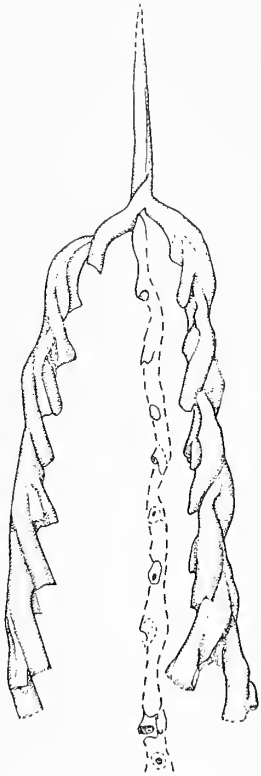
4

SPJELDNÆS, Upper Tremadocian graptolites

There are probably several different Bryograptids in the Upper Tremadocian of the Oslo Region. In the present material there are a number of different types, which vary as to size of the branches, and shape of rhabdosome. Monsen (1925, pp. 162–5, pl. 1, figs. 10–11, text-fig. 4*a–b*) described a new species from this horizon in Oslo, but my studies do not quite agree with the description given. The specimens discussed here as *B. ramosus* agree with the lectotype (Pl. 17, fig. 6) both in the thecal measurements, so far as they can be identified, and in the elongate rhabdosome with infrequent branching in the proximal part. Other specimens, including some of those referred to *B. ramosus* by Monsen (1925) have more frequent branching, and more rapidly expanding rhabdosomes.

It was anticipated by Bulman (1941, p. 106, 1954, p. 34) that this species had three primary branches, and therefore was a true *Bryograptus*. This is quite evident from the present material.

The real number of branches is known only in a few species of *Bryograptus*, and as far as the author knows bithecae have been recorded only in *B. ramosus*. It is possible that a number of the species now referred to *Bryograptus* do not have bithecae, and some might have only two primary branches.



TEXT-FIG. 1. *Bryograptus ramosus* Brogger, from the *Ceratopyge* Shale, Zone 3 aβ, at Slemmestad, Oslo Region, Norway. A young rhabdosome in full relief, showing three primary branches, bithecae, and rather late secondary branching. The specimen is slightly distorted from excessive pyritization. PMO 72831; ×13·5.

KIAEROGRAPTUS gen. nov.

Diagnosis. Dendroid graptolite genus, probably referable to the family Anisograptidae. Sicula of graptoloid type, rhabdosome consisting of two branches of equal width, in one plane (extensiform type of branching). Distinct bithecae placed alternately on both sides of branches. Autothecae resembling the dichograptid type. Initial budding of dendroid type, except that the bithecae related to the early autothecae of each branch appear to be missing.

Type species. *Didymograptus kiaeri* Monsen 1925, from the Upper Tremadoc (Zone 3 aβ) of the Oslo Region.

Remarks. The genus is at present monotypic, and its distribution is therefore identical with that of the type species. For discussion of affinities, see remarks on *K. kiaeri*.

Kiaerograptus kiaeri (Monsen 1925) comb. nov.

Plate 17, figs. 1–5; text-fig. 2

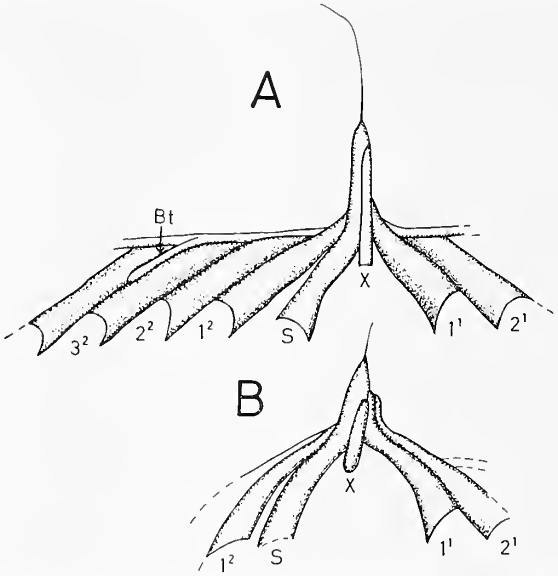
1925 *Didymograptus kiäri* Monsen, pp. 172–5, pl. 2, figs. 9–10, 12–14, 16, pl. 4, figs. 6–8, text-fig. 5*a–c*.

1925 *Didymograptus kiäri* var. *regularis* Monsen, pp. 175–6, pl. 2, figs. 11, 15.

Type data. The lectotype, selected now by Monsen, *in museo*, is PMO 60212a, from Zone 3aβ, subzone b, at Stensberggaten in Oslo. The lectotype of *D. kiaeri regularis* is PMO 60219, from the same horizon and locality.

Material. In the present material there are more than 100 specimens most of which are compressed. About twenty-five specimens and fragments are preserved in relief, and seven of them show the proximal part in relief. The original types of Monsen, and about fifteen topotypes have also been used.

Description. The rhabdosome consists of two horizontal branches, up to more than 2·5 cm. long each. Because most of the specimens are fragmentary or too densely crowded, it is difficult to give exact measurements for the length of the branches. The branches are 1·5 mm. wide. The autothecae are short, straight, and oblique with rather short overlap in the distal parts of the branches, and curved downwards with more overlap in the proximal parts. There are about 11 to 12 autothecae in 10 mm., and they are about 0·65 mm. in longer diameter. The bithecae are placed alternately on each side of the branches. They are somewhat irregularly cylindrical (about 0·3 mm. in diameter) and their apertures are higher up than those of the autothecae.



TEXT-FIG. 2. *Kiaerograptus kiaeri* (Monsen) from the *Ceratopyge* Shale, Zone 3 aβ, at Slemmestad, Oslo Region, Norway. Somewhat diagrammatic drawings. A, Specimen in obverse view; about × 14. B, Proximal part of a distorted specimen showing how both th1^1 and th2^1 (or rather the stolotheca from which th2^1 buds) originates high up on the sicula; based on specimen PMO 72834b, Plate 17, fig. 4; about × 14.

The sicula is long, and inclined, often considerably so. The inclination seems always to be towards the second (th1^2) branch, but since it is difficult to tell which side is the obverse in most of the compressed specimens, and there are few uncompressed ones, this cannot be stated without some reservation. The nema is long (more than 8 mm. in most specimens).

The budding of the initial part of this species differs considerably as could be expected, from that found in *Didymograptus*. Only specimens showing the obverse views of the proximal part are well preserved, and all attempts to prepare the reverse side from them have been in vain. The reverse side is therefore known only from a distorted specimen (Pl. 17, fig. 4), and a fragmentary specimen (Pl. 17, fig. 3), where the left part of the proximal portion is broken away. Owing to this and the sources of error introduced by the preservation, the interpretation given must be regarded as tentative (cf. text-figs. 2*a*, *b*).

Discussion. The type of budding is more related to that found in the Dendroids, as described by Bulman (1936, text-figs. 24*a*, *b*) but it differs in that the first theca gives rise to two other primary thecae very high up on the sicula. One of them (X in text-fig. 2) is interpreted as the first bitheca, and the other as the first theca of the second branch. (In order to conform with Bulman's figure: the term X should be bi 1; first theca (1^1), should be $I^0+I^1+th1^1$, &c. Since the present material does not allow such a delicate anatomic discrimination, the terminology has been somewhat simplified.)

Except for the first (X), bithecae are not found at the first thecae. Normally they do occur at the third or fourth autothecae on each branch. There are no specimens in which the first bithecae can be seen in both branches simultaneously because of the fragmentary nature of the specimens, but in the branches where this feature can be clearly observed, five specimens show the first bitheca after the third autotheca (such as in text-fig. 2*a*), and three specimens after the fourth theca. The number of observations of this kind is higher than the total of well-preserved proximal parts owing to the fact that the proximal part is compressed in a number of specimens where the branches are preserved in relief.

The sicula is long and conical, and where the branches originate it bends slightly towards the second branch. In this feature the distal part of the sicula resembles the distal part of the first thecae in *Didymograptus*, and the usual appearance of the specimen (Pl. 17, fig. 5) is at first glance puzzling, because the sicula resembles the first thecae, and the X resembles the sicula in externally similar Dichograptids. Other specimens (Pl. 17, fig. 4) reveal the three thecae originating from the proximal part of the sicula.

A certain amount of variation is found in this species, but it is difficult to discriminate between real variation, and changes due to different preservation. In some specimens the theca X is almost as long as the sicula, and especially in the small specimens there are distinct slits between the distal parts of the thecae (cf. Monsen 1925, pl. 2, figs. 15–16, text-fig. 5*a*). This is less well developed in old (large) specimens, and in the distal part of the branches.

Remarks. The only species referred to *Kiaerograptus* at present is the type species, but it possibly includes several species now referred to *Didymograptus.* Among the Tremadocian and Lower Arenigian didymograptids which might be suspected to have bithecae, many belong to the *geometricus*-type of branching, with two straight or slightly curved branches meeting at about 120–150° (*D. pritchardi* T. S. Hall, *D. taylori* T. S. Hall, D. *klotschichini* Obut 1961, and *Didymograptus sp.* of Bulman 1954, pl. 5, figs. 7–9). *D. primigenius* Bulman shows the increase in width of branches found in the *D. extensus* group, and might be a real graptoloid. More similar to *K. kiaeri* in rhabdosome shape are *D. abnormis* Hsü, *D. novus* Berry 1960 and *D. latus* T. S. Hall, the latter of which is found in Zone 3 bα (the basal Arenig) in the Oslo District.

D. norvegicus Monsen (1925, pp. 176–7, pl. 2, figs. 6–7; pl. 4. figs. 4–5; text-fig. 6) is another Tremadocian species, from the same horizon as *K. kiaeri.* Like *Tetragraptus kolderupi* Monsen it is found only at the type locality in Oslo (Stensberggaten), which is also the type locality for *Triograptus osloensis* Monsen. All these three species have the same size and shape of the sicula, the same width of the branches, and the same type and size of thecae. The latter are easily identified, being widely conical, and apparently loosely connected. In the type material there are, besides several hundred branch fragments, about ninety-five good specimens of *Triograptus osloensis*, five to six of *D. norvegicus*, and two to three of *T. kolderupi*. It is impossible to separate these three species on branch fragments only, but very easy to discriminate between them and all other graptolites in the same horizon.

This might indicate either that they all belong to one species with a somewhat erratic mode of branching, or that they belonged to a very rapidly developing lineage. The latter was the view held by Monsen (1925, p. 171). The presence of specimens with abnormal budding in *Triograptus osloensis*, such as the specimen figured by Monsen (1925, pl. 3, fig. 7), where the third branch might not be primary, but seems to bud from the second theca in one of the other branches, might suggest the former hypothesis. It is also possible that the peculiar thecal structure made the branches brittle, and *D. norvegicus* may only be specimens of *T. osloensis* from which one branch has been broken off. This problem will, however, have to be studied in more detail on better material, and at present it may only be concluded that the three species in question evidently form a closely related, and possibly isolated, group.

Monsen (1925, pp. 175–6, pl. 2, figs. 11, 15) distinguished a separate variety of *K. kiaeri* (*regularis*). After studying the type material, and the new material described here, the author is inclined to regard the specimens referred to this variety as falling within the normal limits of variation of *K. kiaeri*.

In spite of having only two primary branches, this genus seems to fit conveniently into the family Anisograptidae. This family is somewhat heterogeneous, embracing all few-branched dendroids, even if their number of primary branches is unknown, or less than three. The asymmetrical sicular part of *K. kiaeri* suggests that it might have developed

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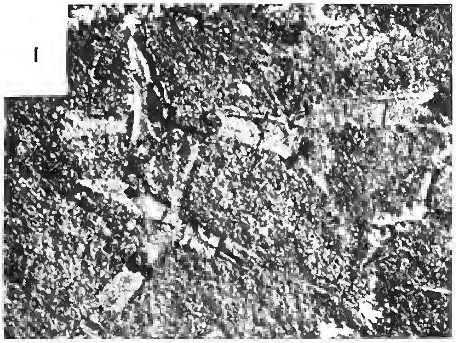
EXPLANATION OF PLATE 18

All specimens belong to Paleontologisk Museum, Oslo, Norway. The specimens shown in figs. 2, 8, and 9 are photographed from latex casts coated with ammonium chloride. The other specimens are photographed directly, without coating.

Figs. 1–10. *Adelograptus? bulmani* sp. nov. 1, Proximal parts of two specimens, the upper one a left-handed specimen in obverse view, and the lower one a right-handed specimen in reverse view (text-fig. 3A is based on the lower specimen); PMO 72835b–c; ×13. 2, Distal branch showing 'Leptograptoid' thecae; PMO 72836c; ×6, 5. 3, Proximal part, 'right' specimen, reverse view; PMO 72835g; ×13. 4, Proximal part, 'left' specimen, reverse view; PMO 72835h; ×13. 5, Proximal part, 'right' specimen, obverse view; PMO 72835i; ×13. 6, Proximal part, 'right' specimen, obverse view, having only the first bitheca and th1^1; PMO 72835e; ×13. 7, Proximal part, 'right' specimen, obverse view showing the small th1^2; PMO 72835d; ×25. 8, Proximal part, 'right' specimen, reverse view, with a constriction of the proximal part of the sicula (prosicula?); PMO 72836a; ×21. 9, Proximal part, 'right' specimen, obverse view, showing sicula, first bitheca and th1^1. The peculiar fringes on the aperture of the sicula might be due to pyritization; PMO 72836b; ×21. 10, Proximal part of two adult specimens; the upper one a 'left', and the lower, the holotype, a 'right'; PMO 72835f and PMO 72835a (holotype); ×25.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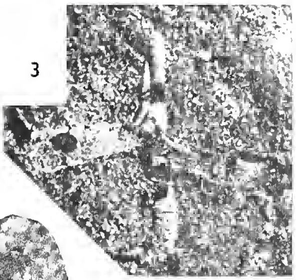
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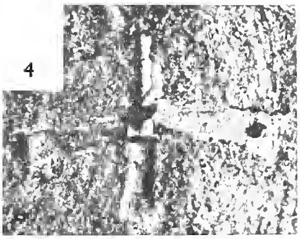
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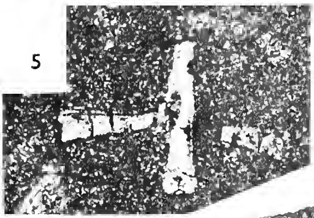
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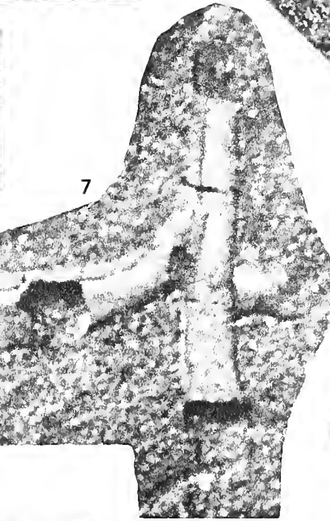
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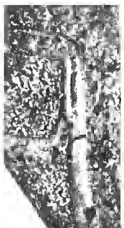
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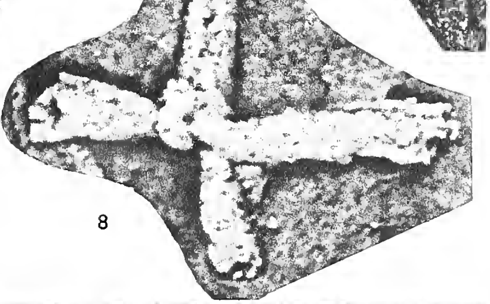
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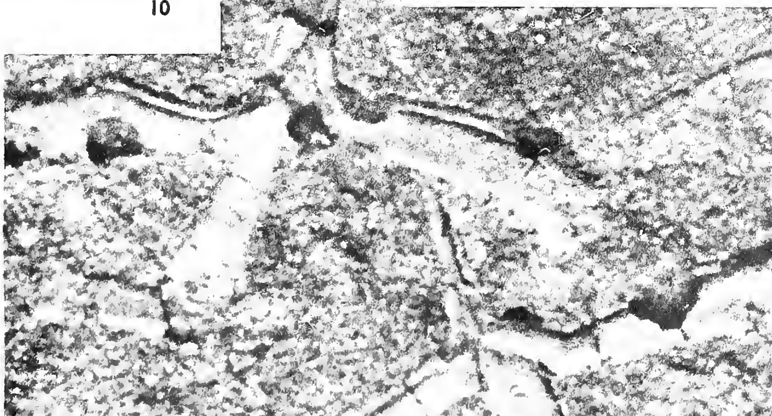
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9

SPJELDNÆS, Upper Tremadocian graptolites

from originally three-branched forms, and the genus is therefore, at least provisionally, referred to the Anisograptidae.

Adelograptus? bulmani sp. nov.

Plate 18, figs. 1–8; text-figs. 3, 4

Type data. The holotype is PMO 72835a, a rhabdosome with five thecae preserved in half relief in pyrite. It is from the upper part of the *Ceratopyge* Shale (Zone 3 aβ) in a road section in Bødalen, about 1·5 km. WSW. of Slemmestad, in the Oslo District, Norway. On the same slab as the holotype there are several other specimens of this species in various stages of development, some of which are figured in this paper. They are preserved in pyrite, in half or full relief.

Material. About fifty specimens, mostly proximal parts, preserved on two small shale slabs from the type locality.

Diagnosis. Species probably referable to *Adelograptus*, having the system of initial budding and general shape of rhabdosome found in that genus. The sicula is very long, and the long, overlapping thecae have almost leptograptoid apertures. Only two branches have been observed; if further branching occurs, it is irregular and in the distal parts of the rhabdosome. No bitheca except the first one has definitely been ascertained. Left- and right-handed forms occur.

Description. The rhabdosome is small, consisting of two horizontal to slightly reclined branches. In most of the specimens in which the sicula is preserved, the branches are short, three or four thecae on each as a maximum. There are a few specimens with longer branches, up to six thecae.

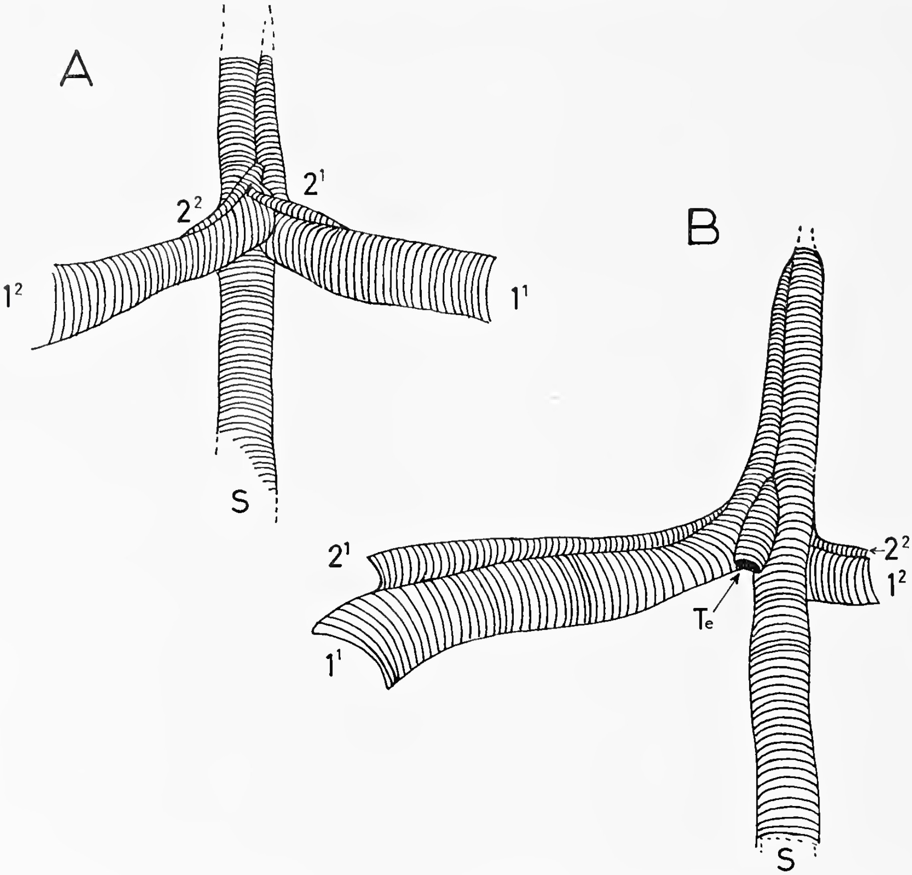
The thecae are long, gradually tapering and with a considerable overlap. Three thecae are observed in a cross-section of a branch. The thecae occur alternately on both sides of the branch, and cross in their initial part, just after budding. The apertures of the first thecae on each branch are curved slightly down, but subsequently are directed distally. In the specimens preserved in half relief, most of the thecae seem to be of the dichograptid type, or intermediate between this and the leptograptoid. Among the specimens preserved in full relief, there are some branch fragments, presumably belonging to this species, which appear to be more like the leptograptoid type of thecae (Pl. 18, fig. 2).

The proximal part is preserved in an astonishing number of the specimens, in fact most of the material seems to consist of immature specimens, showing the sicula, and only some few thecae (text-figs. 3–4). In some specimens (Pl. 18, fig. 8) a well-defined prosicula-like structure is seen. This feature is not consistently found, and might be due to the capricious effects of the pyritization. The sicula is long and narrowly conical, almost cylindrical. The first theca (1^1) buds from the proximal part of the metasicula, follows it until about half-way down, and turns at right angles to the sicula. The proximal part of the first theca is irregularly cylindrical. It is also remarkable in budding alternately from the right (normal) and left side of the sicula. The 'left' specimens are fewer in number than the normal ones, but because of the difficulty in determining this feature with absolute certainty, no exact ratio between the two forms can be given. It appears to be about 1:3 or 1:4.

Subsequent budding seems to be somewhat different in the 'left' and normal specimens, but because of the lack of 'left' material preserved in reverse view (only two specimens) this could not be definitely stated with the present material.

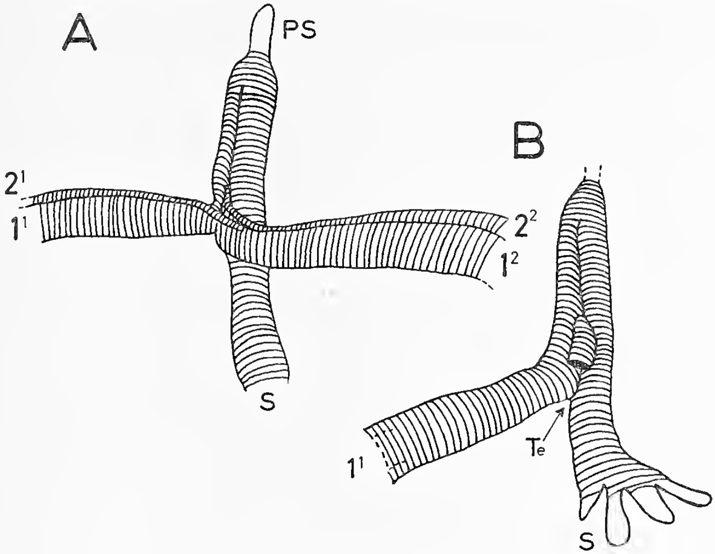
In addition to these thecae there is a special one, which buds from 1^1, before the origin of 2^1, and is interpreted as the first bitheca.

In the branches, bithecae have not been observed. This does not exclude their presence, because a number of the specimens are broken at the critical points (Pl. 18, fig. 7), and in others diffuse swellings of the branches are observed both where bithecae are to be expected, and in other places. These swellings are in most cases probably due to preservation (pyritization), but might in some cases be due to bithecae. Such suspect structures are generally found in the more distal parts of the branches, but have occasionally also been observed in connexion with the early thecae (cf. the extreme left part of the lower specimen in Pl. 18, fig. 7). The first bitheca is always large and distinct, and if other bithecae are present, they must be considerably smaller and less developed.



TEXT-FIG. 3. *Adelograptus*? *bulmani* sp. nov. from the *Ceratopyge* Shale, Zone 3 aβ at Slemmestad, Oslo Region, Norway. A, Proximal part of a 'right' specimen (drawing based on specimen PMO 72835b, Plate 18, fig. 1); about ×30. B, An obverse view (drawing based on specimen PMO 72835d, Plate 18, fig. 7); about ×30. S, sicula; Te, first bitheca.

The branching of the rhabdosome is also difficult to ascertain. In *A. hunnebergensis* the second-order branching generally takes place after the second or third thecae. A great number of specimens of *A.? bulmani* with short branches do not show any second-order branching. This indicates that if second-order branching was present, it took place after the fifth theca, or by lateral budding in branches longer than five theca. None of the longer branch fragments ascribed to this species show branching, but in the same beds there is what is believed to be another species of *Adelograptus* which differs from *bulmani* in having somewhat thinner branches, and shorter, more conical sicula. This species, which is less well preserved than the material of *bulmani*, shows second-order branching rather regularly at the fourth or fifth thecae. Unless the preservation is very good, it might be difficult to discriminate between distal branches of these two species.



TEXT-FIG. 4. *Adelograptus*? *bulmani* sp. nov. from the *Ceratopyge* Shale, Zone 3 aβ, at Slemmestad, Oslo Region, Norway. A, The proximal part of a 'left' specimen in reverse view (drawing based on specimen PMO 72836a, Plate 18, fig. 8); about ×30. B, Proximal part of 'right' specimen in obverse view (drawing based on specimen PMO 72836b, Plate 18, fig. 9); about ×30. PS, prosicula; S, sicula; Te, first bitheca.

Remarks. The affinities of this species are somewhat obscure. It superficially resembles a primitive Leptograptid in the thecal budding in the proximal part, in the direction of the thecae (except the first ones), and in the general shape of the rhabdosome. It differs from the later Leptograptids in the almost cylindrical metasicula, which is regarded as a dendroid feature (Kozlowski 1960), in having the primary branches diverging near the middle of the metasicula instead of near the aperture, in the presence of the first bitheca, and in the existence of 'left' and 'right' forms.

There is a suggestion (text-fig. 4) that $th2^2$ arises from $th1^1$ and, if this should prove to be correct the type of development, differs fundamentally from any of the types described by Bulman (1955, p. V56).

A closer examination of the initial and distal budding suggests that it is closely related to that in *Adelograptus* (cf. Stubblefield 1929, text-figs. 2, 4, 6, and especially Bulman 1941, text-fig. 1) except that the bithecae (other than the first one), are apparently missing.

It is possible to imagine a development of the leptograptoid type of budding directly from that found in this species, but until intermediate forms are found and much more detailed studies are made, this hypothesis could not be seriously considered. If, however, the distal bithecae really are missing in *A.? bulmani*, it might represent a transitional form between the Dendroids and Graptoloids such as *Kiaerograptus*. As mentioned above, it is difficult to show this and other important anatomical features beyond doubt, and the species is therefore, with some doubt, left in *Adelograptus* for the time being. There can be little doubt that it is a descendant of one of the typical representatives of that genus.

GENERAL REMARKS

The presence of bithecae in virtually all upper Tremadocian species which are sufficiently well preserved to show this feature clearly, might indicate that there were few if any graptoloid graptolites before the Arenig. Most Tremadocian graptolites could either be referred to the dendroids, or they are preserved only as mineralized films, and their alleged graptoloid affinities are based only on their astogenic resemblance to various Dichograptids. The discovery of a two-branched, extensiform dendroid indicate that such criteria might not be valid in all cases, and in order to prove that species belong to the graptoloids, more evidence than number of branches and angle of branching is necessary. It is possible that the widening of the stipes characteristic of the didymograptids of the *extensus*-group, which is less prominent in *Kiaerograptus kiaeri*, might be useful in specimens where the presence or absence of bithecae could not be ascertained. It is still possible that there were some graptoloid graptolites in the Tremadoc, but they were certainly fewer than hitherto supposed, and the remaining records must be carefully checked before they can be definitely accepted as graptoloids.

It is also possible that a number of species in the lower Arenig now parading as dichograptids really are few-branched dendroids, only that the bithecae are overlooked because of the state of preservation of the material. Such species might be suspected in the *Bryograptus–Tetragraptus fructicosus–Didymograptus protobifidus* lineage, and in didymograptids of the *geometricus* type, because their constant angle of branching (120–150°) might indicate that they are descendants of three-branched forms. *Didymograptus latus* T. S. Hall, which was shown by Thomas (1961, p. 9) to be as highly developed as the later *D. hirundo*, might also belong to an entirely different group, perhaps that of *Kiaerograptus kiaeri*, or might be one of its descendants. Both have, in contrast to the *extensus*-group, long nemas and branches of uniform width.

The presence of bithecae in *K. kiaeri* has also some phylogenetic significance, showing that the tendency to branch-reduction went as far as two-branched forms in the dendroid graptolites. It also gives support to Bulman's (1954*a*, p. 208; 1958, p. 161) view that the transition between the dendroids and graptoloids was a gradual one, taking part in several lineages independently. This transition was not necessarily contemporaneous in all lineages, but seems to have taken place frequently about the Tremadoc–Arenig boundary.

K. kiaeri is an intermediate species between the Dendroidea and the Graptoloidea. The autothecae, the general shape of the sicula, and the absence of bithecae at the first autothecae are graptoloid features, whereas the initial budding and the bithecae at the distant parts of the branches are dendroid ones.

Urbanek (1960) in a recent paper discussed the evolutionary changes in graptolite colonies. He drew attention to the well-known fact that in Monograptids new thecal types are often introduced in the proximal part of the colonies. This might also be the case with *K. kiaeri*, where the new type of thecae (without bithecae) is found in the proximal part of the branches. If more complete material had been present, it might have been possible to follow the development from a purely dendroid two-branched form through types like *K. kiaeri* to extensiform graptolites without bithecae, such as in the evolutionary lineages referred to by Urbanek, but in this case from one order to another. This might indicate that studies on thecal variation might be of considerable phylogenetic importance in the Dendroids and Dichograptids also.

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ALAIOPHYLLUM MACKENZIENSE SP. NOV., A DEVONIAN TETRACORAL FROM CANADA

by A. E. H. PEDDER

ABSTRACT. The fauna of the Kee Scarp Formation at the type locality near Norman Wells, Northwest Territories, is reviewed, and its only common tetracoral is described as *Alaiophyllum mackenziense* sp. nov. It is concluded that the fauna is either Givetian or early Frasnian in age.

THE age of the Kee Scarp Formation is not clear from a study of published reports. In 1959 the writer visited the type exposure near Norman Wells, Northwest Territories, and collected, among others, the fossils described below. He is indebted to Triad Oil Co. Ltd., for whom the work was carried out, for permission to publish this paper and to present the type specimens to the Geological Survey of Canada (abbreviated to GSC below).

Fauna and age of the type exposure of the Kee Scarp Formation

When first studied and described (Stelck 1944, pp. 15, 16; in Hume 1945, p. 35) the Kee Scarp Formation was considered to be Upper Devonian. Although this opinion has prevailed with some geologists (Warren and Stelck 1956, p. 11; Storey 1961, p. 499), it has been challenged by others (Crickmay 1957, p. 11; Bassett 1961, pp. 492–4), who regard the Kee Scarp Formation as upper Middle Devonian. Galloway (1960, p. 621) considered it to be lower Upper Devonian, but later (in Collinson 1960, p. 1218) abandoned his earlier opinion and regarded it as upper Middle Devonian. Lenz (1961, table 1) considered the lower part as either uppermost Middle, or lowermost Upper Devonian, and the upper part as very low Upper Devonian.

Bassett (1961) extended the use of the term Kee Scarp to include the Ramparts Limestone of the Fort Good Hope area, because Ramparts as a stratigraphical name is preoccupied. Unfortunately this obscures the relationship between the two limestones, which are not physically one and the same, since the Kee Scarp is a discrete reef. Determination of its age must be based on the fauna at the type locality and not on those from other localities in limestones subjectively correlated with it.

Warren and Stelck (1956, pl. 15, figs. 25–27) figured a specimen from the type locality as *Indospirifer sp.* The presence of *Adolfia* [=*Indospirifer*] would strongly suggest a middle Frasnian age, but examination of the Kee Scarp specimen's micro-ornament excludes it from that genus. At the present time the specimen does not help resolve the problem of the formation's age.

Lenz (1961, p. 504, pl. 3, figs. 6, 7) compared a coral from the formation with *Macgeea gallica* Lang and Smith, which is a middle Frasnian species. He stated that the Kee Scarp coral has horseshoe dissepiments, but these cannot be seen in the figure of the longitudinal section and in fact the coral resembles that group of Givetian corals which includes '*Aulophyllum*' *richardsoni* Meek and other undescribed species.

Other forms reported in the literature (Warren and Stelck 1956; Crickmay 1957;

[Palaeontology, Vol. 6, Part 1, 1963, pp. 132–5, pl. 19.]

Galloway 1960; Lenz 1961) from the type locality are: *Stromatoporella dannoniensis* Nicholson, *Stromatopora sp.* cf. *S. planulata* Hall and Whitfield *sensu* Nicholson, *Clathrocoilona aboena* Yavorsky, *Cladopora? sp.*, *Alveolites sp.*, *Aulopora sp.* cf. *A. conferta* Winchell, *Trachypora sp.*, *Schizophoria sp.*, productoid indet., *Atrypa* or *Spinatrypa sp.*, ambocoeliinid, and thick-shelled pelecypods. The following were collected at the type locality by the writer (Triad Oil Co. Ltd. collections D107, 108, 135): calcispheres, *Alaiophyllum mackenziense* sp. nov., *Alveolites sp.*, *Scoliopora sp.*, *Thamnopora sp.*, *Idiostroma sp.*, *Amphipora ramosa* (Phillips), *Stachyodes sp.*, *Hermatostroma sp.*, *Spinatrypa sp.*, *Straparollus* (*Euomphalus*) *sp.* and thick-shelled pelecypod fragments.

None of these forms provides a sure index of their age. *Alaiophyllum*, however, although a rare genus, is significant. It was first described from three widely scattered Givetian deposits in Russia and has subsequently been recognized by the writer in the Maligne equivalent and Swan Hills Member of the Beaverhill Lake Formation of Alberta (these Canadian specimens are being described by the writer for publication by the Geological Survey of Canada). The Maligne Formation contains *Timanites*, indicating that it is early Frasnian, and the Swan Hills Member, as shown by its fauna, is also about the same age. The known range of *Alaiophyllum*, therefore, is Givetian to early Frasnian and it may be concluded that the age of the Kee Scarp reef also falls within these limits.

SYSTEMATIC DESCRIPTION

Family STAURIIDAE Edwards and Haime 1850, *sensu lato*

Genus ALAIOPHYLLUM Goryanov 1961

Type species (*original designation*). *Alaiophyllum jarushevskyi* Goryanov 1961, pp. 71–73, pl. 8, figs. 1*a*–3*d*. Givetian stage, Boord Ridge, southern Ferghana, U.S.S.R.

Remarks. Goryanov referred the genus doubtfully to the Phillipsastraeidae. However, the poorly and variably developed dissepimentarium and thick stereozone appear to relate *Alaiophyllum* more closely to the Stauriidae.

Alaiophyllum mackenziense sp. nov.

Plate 19, figs. 1–6

Name derivation. Mackenzie River, Northwest Territories, Canada.

Types. Holotype and paratypes 1 and 2 are GSC 16850–2 respectively.

Type stratum. Kee Scarp Formation—the lower 140 feet which are exposed.

Type locality. Kee Scarp, 6 miles ENE. of Norman Wells, Northwest Territories, Canada.

Description. Compound tetracoral with loosely fasciculate corallum and gently sinuous subcylindrical corallites. Calice and exterior surface not exposed in the types. All the specimens collected at the type locality were tightly embedded in matrix and corallites were not obviously parts of particular colonies; thus the size of the entire corallum is unknown.

Transverse sections of individual corallites circular, or nearly so, with diameters of up to 14·0 mm., generally about 12·5 mm.; adjacent corallites touching or up to 30·0 mm. apart. Epitheca smooth, commonly enveloped by stromatoporoids, reinforced by a prominent peripheral stereozone, normally about 1·0 mm. thick but as much as 3·0 mm. thick in parts of some corallites. Stereozone composed of dilated septal ends and lamellar tissue. In some sections inner less-prominent sterozones are formed by sclerenchyme deposited on the dissepiments. Septa roughly radially arranged, differentiated in two orders and of such variable length that some minor septa are as long as major ones. Major septa number 20 to 25 in corallites with diameters of 10·0 to 14·0 mm., but not necessarily more numerous in larger corallites. Minor septa very variably developed, some suppressed and discernible only in the microstructure of the stereozone. Dissepiments normal or in 'herringbone' arrangement where the minor septa are suppressed.

Longitudinal sections with subparallel epitheca and up to 50·0 mm. in length. Stereozone broad, surface rough and enveloped by stromatoporoids in places. The dissepimentarium is generally between one-quarter and one-third the total width of the lumen; dissepiments moderately long and gently curved, peripheral ones commonly coated with, or even embedded in, sclerenchyme. Tabulae broad, but mostly incomplete, sinuous, spaced at 1 to 6, typically 3 or 4, per mm. Trabeculae not well displayed in type material, directed upwards and inwards at an angle of about 26° to the walls of the corallite and very slightly divergent distally.

Remarks. The species is similar to another species of *Alaiophyllum* occurring rarely in the Maligne Formation of the central Alberta Rocky Mountains. It is distinguished by its broader dissepimentarium and narrower tabularium with consistently closer-spaced and less complete tabulae. Further, perhaps less diagnostic, distinctions are that the Alberta specimens have sclerenchyme coating on some of the tabulae as well as the dissepiments and have individual corallites of more variable diameters. Both species almost invariably grew with ectoparasitic stromatoporoids. *A. jarushevskyi* Goryanov has shorter septa and a narrower dissepimentarium than *A. mackenziense*. It also has clearer traces of the septa within the stereozones, but this may be due to differences in preservation.

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EXPLANATION OF PLATE 19

All figures are ×4.

Alaiophyllum mackenziense sp. nov., lower 140 feet of the Kee Scarp Formation at Kee Scarp, 6 miles WNW. of Norman Wells, Northwest Territories, Canada.

Figs. 1, 2, 6. Holotype, GSC 16850. 1, 6, Longitudinal sections; 2, transverse section.

Figs. 3, 5. Paratype 1, GSC 16851, longitudinal sections.

Fig. 4. Paratype 2, GSC 16852, transverse section.

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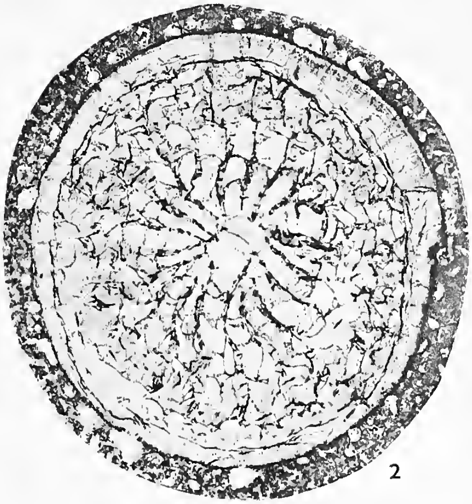

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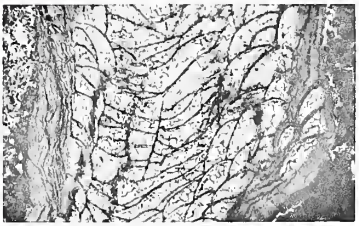

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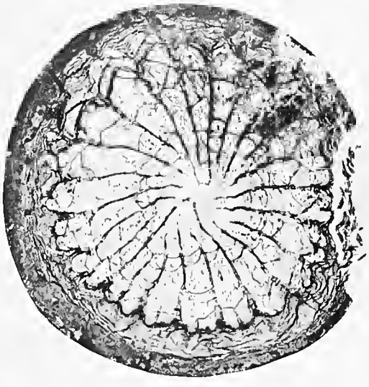

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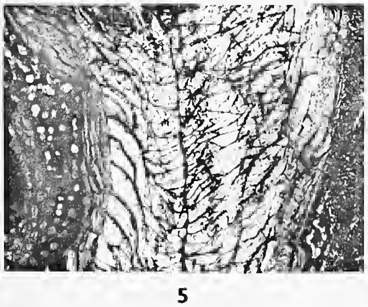

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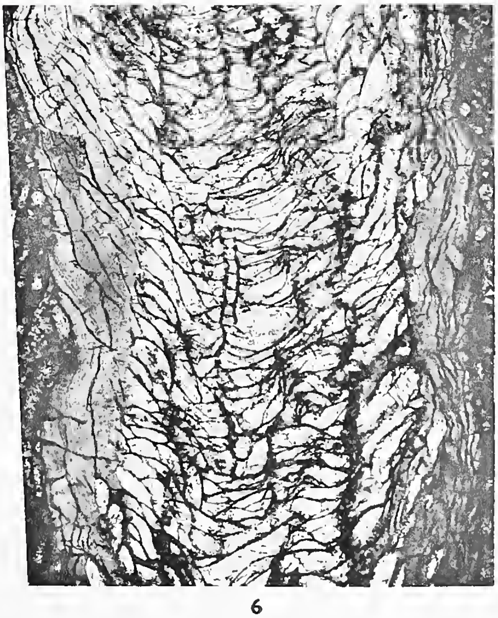

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THE LAMELLIBRANCH GENUS *PROTHYRIS* IN THE UPPER DEVONIAN AND CARBONIFEROUS OF GREAT BRITAIN

by R. B. WILSON

ABSTRACT. The morphology and distribution of the species of the lamellibranch genus *Prothyris* Meek, occurring in the Upper Devonian and Carboniferous of Great Britain, are reviewed. Of the three Upper Devonian species described by Whidborne (1896), *P. scalprata* is regarded as conspecific with *P. contorta*, and it is concluded that *P. recta* should be removed from the genus. A new Upper Devonian species, *P. stubblefieldi*, is described. Four species are recognized in the Carboniferous: *P. breviformis* Wilson, *P. oblonga* Wilson, *P. scotica* sp. nov., and *P. carbonaria* sp. nov. Some general comments are made on the mode of life, environment, and evolution of the genus.

THE lamellibranch genus *Prothyris* Meek 1869, type species *Prothyris elegans* Meek, was first recorded from the Upper Carboniferous of Illinois and Nebraska (Meek and Worthen 1869, p. 172). American authors have since described several species, showing that the genus ranged from the Upper Devonian to the Upper Carboniferous in North America. Whidborne (1896, pp. 86–89) first recognized the genus in Europe when he described three species from the Upper Devonian of Devon. Hind (1906, p. 148) identified a shell as *Prothyris elegans* from the Scottish Namurian, the first record in the British Carboniferous. Since then, various occurrences of *Prothyris* have been cited from several horizons and the present paper attempts to examine the morphology and distribution of the known British species.

For permission to examine specimens in their care, the writer is grateful to the Director of the Geological Survey and Museum, Mr. A. E. Blackwell of the North Devon Athenaeum, Barnstaple, and Mr. A. G. Brighton of the Sedgwick Museum, Cambridge. This paper is published with the permission of the Director of the Geological Survey. Specimens with registration numbers prefixed by GSM are housed in the Geological Survey and Museum, London, and those by GSE are in the Collection of the Geological Survey, Edinburgh.

Genus PROTHYRIS Meek 1869

Meek (in Meek and Worthen 1869, p. 172) proposed the name *Prothyris* for a lamellibranch genus found in the Upper Carboniferous of Nebraska and Illinois, accompanying the announcement with a general description of the genus, but he did not assign any species to it. Later Meek (1871, pp. 8–9) gave a much fuller account, and selected *Prothyris elegans* Meek as the type species. His generic diagnosis is as follows: 'Equivalve, very inequilateral, longitudinally oblong, valves compressed or moderately convex, nearly closed or a little gaping behind and more or less widely gaping in front, where the hiatus is increased in size by a nearly rectangular notch in the margin mainly below the middle; beaks depressed and very near the anterior end with a small ridge usually extending from the anterior side of each to the corner of the anterior marginal notch; dorsal margin without escutcheon or lunule, being erect and sharp behind the beaks. Surface merely marked with striae of growth. Hinge and interior unknown.'

[Palaeontology, Vol. 6, Part 1, 1963, pp. 136–44, pl. 20.]

Only minor additions need be appended to this diagnosis. Immediately posterior and parallel to the ridge running from the umbo to the anterior marginal notch, here called the anterior notch, a shallow groove is present on well-preserved specimens of most species examined. Although the hinge has not been observed, several specimens of Carboniferous species show a structure in the umbonal region which may indicate some degree of dentition. It consists of two subparallel short lines, about 1 mm. long in a valve of 12 mm. length, running postero-ventrally from the umbo, and preserved as faint impressions or ridges. These may indicate poorly developed cardinal teeth; this would support the suggestion made by Meek (1871, p. 8) that the genus has affinities with the Solenidae.

Hind (1908, p. 352) suggested that the ear-shaped process, anterior to the ridge running from the anterior notch to the umbo, here called the anterior lobe, contained the anterior adductor muscle. He also thought that the anterior notch marked a byssal opening. Wilson (1961, p. 102) questioned these suggestions as *P. oblonga* Wilson appears to have the anterior adductor scar posterior to the ridge bounding the anterior lobe, and it seems unlikely that a bivalve gaping at both ends, and probably of burrowing habit, would possess a byssus. Elias (1957, pp. 741–3) recorded radial markings on the valves of *P. soleniformis* and described, but did not figure, a simple hinge apparatus. He, also, regarded *Prothyris* as a subgenus of *Solen* Linnaeus, but the present writer considers that the internal and hinge characters are still not sufficiently well known and that the anterior notch and lobe are of generic significance.

DEVONIAN SPECIES

Whidborne (1896, pp. 86–89, pl. 9, figs. 12–18), in his study of the Devonian faunas of the south of England, described three species from the Upper Devonian of north Devon, which he assigned to *Prothyris*. All the surviving syntypes of these species have been re-examined.

'*Prothyris*' *recta* Whidborne

Plate 20, fig. 3

Discussion. The remaining type material of *Prothyris recta* (Whidborne 1896, pp. 86–87, pl. 9, figs. 12–14) consists of two of the three original figured specimens and several indeterminate cited specimens, all in the Geological Survey Collection, London. The specimen illustrated as fig. 13 cannot be found. Of the figured specimens, GSM 6085 (op. cit., fig. 12) is incomplete anteriorly and posteriorly, and is preserved in a dark-grey limestone. It is too poorly preserved to be used for determining the specific characters. GSM 87343 (op. cit., fig. 14), now refigured (Pl. 20, fig. 3), is an internal mould of a left valve, with the ventral margin missing; it is also preserved in a dark-grey limestone. It is subquadrate in outline, about 19 mm. long, and the height is estimated to be about 14 mm. An angular anterior umbonal ridge runs half-way towards the ventral margin, and a rounded posterior umbonal ridge extends to a point half-way down the posterior border. Between these ridges, the valve is moderately convex and there are several indistinct short ridges radiating from the umbo. The anterior margin has irregularities caused by the granular fracture of the matrix. The largest of these irregularities is about one-third of the way down; Whidborne interpreted it as the anterior notch of *Prothyris*.

There is no ridge extending from this feature to the umbo, and the present writer interprets it as fortuitous and of no morphological significance. Whidborne (1896, p. 87) stated that the species was of variable shape, but the specimen GSM 87343, just described, is the only one of the remaining syntypes which is reasonably well preserved; it is here selected as lectotype of the species '*P.*' *recta*. As it does not possess any of the diagnostic characters of *Prothyris*, the writer excludes it from that genus.

Prothyris contorta Whidborne

Plate 20, figs. 1, 2

Prothyris contorta Whidborne 1896, pp. 87–88, pl. 9, figs. 15–16*a*.
Prothyris scalprata Whidborne 1896, pp. 88–89, pl. 9, figs. 17–18*a*.

Discussion. An examination of the type specimens of *P. contorta* and *P. scalprata* has shown that only one species is involved. As the only factor relevant to determining which specific name is valid is that of page precedence, it is suggested that the name *scalprata* be regarded as a junior synonym of *contorta*.

Lectotype. The specimen figured by Whidborne (1896, pl. 9, fig. 15), marked as such, and housed in the North Devon Athenaeum, Barnstaple, is here selected as lectotype. It is an internal mould of a left valve, preserved in dark-grey limestone from Kingdon's Shirwell, north Devon.

EXPLANATION OF PLATE 20

All the lamellibranch photographs (figs. 1–9) are twice natural size. The accompanying outline drawings are natural size; they were prepared by drawing in waterproof ink the outlines of the shells on ×2 photographs, bleaching the photographs, and then reducing the remaining outlines photographically. Figs. 1–9 were prepared by Mr. W. D. Fisher and the author.

Figs. 1, 2. *Prothyris contorta* Whidborne. 1, GSM 7044, both valves, Upper Devonian, Plaistow Mill Quarry (Sloly Beds), north Devon. Figd. by Whidborne as *P. scalprata* (1896, pl. 9, fig. 17). 2, Specimen in the North Devon Athenaeum, Barnstaple, lectotype, left valve, Upper Devonian, from Kingdon's Shirwell, north Devon. Figd. by Whidborne (1896, pl. 9, fig. 15) as *P. contorta*.

Fig. 3. '*Prothyris*' *recta* Whidborne. GSM 87343, lectotype, left valve, Upper Devonian, South Cave, Baggy, north Devon. Figd. by Whidborne (1896, pl. 9, fig. 14).

Fig. 4. *Prothyris stubblefieldi* sp. nov. GSM 87387, holotype, left valve, Upper Devonian, at 1,458½ feet in Willesden Borehole, north London.

Fig. 5. *Prothyris oblonga* Wilson. GSE 11755, holotype, left valve, Lower Carboniferous, at 3,775½ feet in Archerbeck Borehole, Canonbie, Dumfriesshire.

Fig. 6. *Prothyris breviformis* Wilson. GSE 11758, holotype, right valve, Lower Carboniferous, at 3,393 feet in Archerbeck Borehole.

Figs. 7, 8. *Prothyris scotica* sp. nov. 7, GSE 11719, holotype, right valve, from mudstone under Calmy Limestone, Scottish Upper Limestone Group, Namurian (E_2), shore 135 yards south-east of Hospital, Kirkcaldy. 8, GSE 11827, paratype, both valves, roof of Index Limestone, Namurian (E_2), at 284½ feet in Powis Mains No. 1 Bore, Stirlingshire.

Fig. 9. *Prothyris carbonaria* sp. nov. GSM 87388, holotype, left valve, Mansfield Marine Band, Coal Measures, at 1,724½ feet in Lindholme Borehole, Yorkshire.

Fig. 10. View of serial sectioning machine from side away from the operator showing general layout and position of the coolant drip-feed system. Height of machine to top of coolant tank 20 inches.

Fig. 11. Detail of compound slide rest viewed from operating side. Longitudinal feed handle on the right, cross-feed handle on the left. Magnetic positioner mounted on the tool post block in front of the cupped diamond wheel.

Fig. 12. Detail of magnetic positioner showing specimen attached to steel mounting block held by the positioner.

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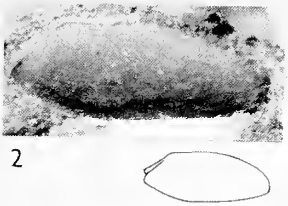

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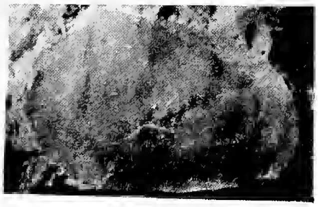

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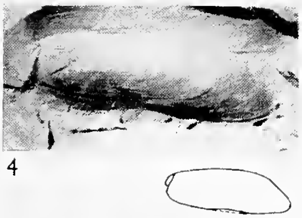

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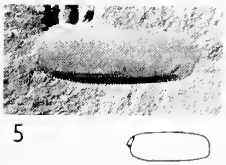

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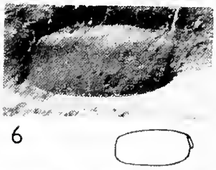

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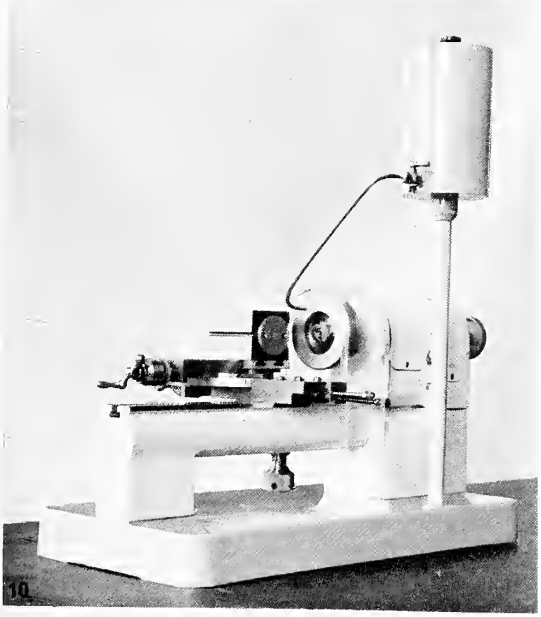

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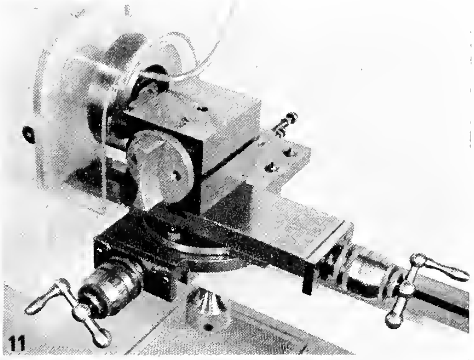

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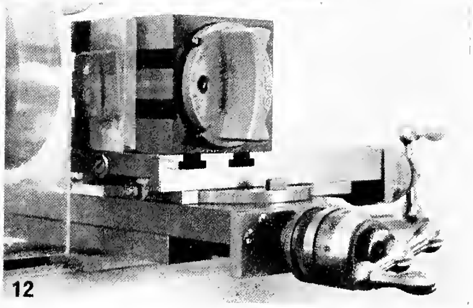

12

WILSON, *Prothyris*

HENDRY, ROWELL, and STANLEY, parallel grinding machine

Description. Small, elongate, subrhomboidal, moderately convex, the maximum convexity occurs along the poorly defined umbonal ridge which fades out half-way to the posterior end of the valve. The umbo is situated at the anterior fifth of the length of the shell; it is prosogyrous and inconspicuous. The anterior end is symmetrically rounded but interrupted by a re-entrant notch from which a narrow, ill-defined ridge runs to the umbo. The dorsal margin is short and straight, passing into the long, gently convex, postero-dorsal border which ends in the acutely rounded postero-ventral extremity of the valve. The ventral margin is very gently convex. Two subparallel linear ridges run from the umbo half-way to the ventral margin. The postero-dorsal region is marked by two broad radiating ribs on the internal mould and by three radiating striae on the exterior of the shell. The musculature and hinge characters are not seen.

Dimensions.

	Length mm.	Height mm.
Lectotype	16	6
GSM 7044 (Whidborne, pl. 9, fig. 17) .	17	6·5

Remarks. Whidborne (1896, p. 87), in his description of *P. contorta*, mentioned that the ventral margin is slightly concave, as shown in his illustration of the specimen now chosen as lectotype (op. cit., pl. 9, fig. 15). This outline was false, caused by some matrix, since removed, which covered part of the margin. The other specimen he figured as *P. contorta* (pl. 9, fig. 16) is very poorly preserved and indeterminate. Of the four specimens he illustrated as *P. scalprata*, GSM 7044 (pl. 9, fig. 17) is now refigured (Pl. 20, fig. 1) and referred to *P. contorta*; Sedgwick Museum specimen H 363 (pl. 9, fig. 18) is poorly preserved, but is probably *P. contorta* as now described, and the two specimens shown on pl. 10, figs. 16, 17, are indeterminate lamellibranch fragments.

Prothyris stubblefieldi sp. nov.

Plate 20, fig. 4

Discussion. Stubblefield (1947, p. 20) reported an occurrence of *Prothyris* from a borehole sunk by the D'Arcy Exploration Company at Willesden, north London. It occurred at a depth of 1,458½ feet in a lilac-stained mudstone of Upper Devonian age. Although only one specimen is known, it is reasonably well preserved and merits description.

Holotype. GSM 87387, a left valve, in the Geological Survey Collection, London.

Description. Small, elongate, dorsal and ventral margins subparallel, diverging very slightly towards the posterior end. Umbo inconspicuous, placed at anterior end of dorsal margin. A rounded, posterior umbonal ridge extends almost to the postero-ventral angle, giving the valve a moderate convexity. The anterior end is incomplete ventrally but a distinct anterior lobe is present, separated from the remainder of the valve by a narrow, rounded ridge, posterior to which a shallow groove occurs. The dorsal and ventral margins are almost straight, the posterior border is obliquely truncate making an angle of about 45 degrees with the ventral margin. The postero-ventral angle is sharply rounded. Dimensions of the holotype are: length 18·5 mm., height 6 mm.

Remarks. P. stubblefieldi differs from the other British Devonian species, *P. contorta*, by having a relatively longer dorsal margin, by the absence of radial striae on the postero-dorsal region, and by the subparallel alignment of its dorsal and ventral margins. It differs from *P. bergica* Drevermann, the German Devonian (Etroeungt) species (Drevermann 1902, pp. 498–9, pl. 14, fig. 15), in that the latter species has convex dorsal and ventral margins. Several species were described in the last century from the Devonian of North America, but the descriptions are meagre. Some of them appear to lack an anterior notch and lobe, suggesting that they may belong to some other genus. Until these species are revised, any comparisons with them must be unsatisfactory but *P. stubblefieldi* shows no marked resemblance to any of the American species so far described.

CARBONIFEROUS SPECIES

The earliest occurring species recorded from the British Carboniferous are *P. oblonga* Wilson and *P. breviformis*, which were found in beds of Lower Visean age in the Archerbeck Borehole, Canonbie, Dumfriesshire (Lumsden and Wilson 1961, p. 11). They have been described already (Wilson 1961, pp. 101–3), but, for the sake of comparison, their salient features are given below.

Prothyris oblonga Wilson

Plate 20, fig. 5

Prothyris oblonga Wilson 1961, pp. 101–2, pl. 3, figs. 5–7.

Description. Relatively small, elongate, the average length/height ratio is 2·75. Dorsal margin slightly arched, the ventral one convex anteriorly and straight posteriorly, while the posterior end of the shell is bluntly rounded. The anterior notch is well developed, almost right-angled, situated about half-way up the anterior end. At this notch the valves gape appreciably. A poorly developed posterior umbonal ridge is present, antero-ventrally to which the shell is marked with fine, regular, concentric striae and obscure radiating striae. On the postero-dorsal area, only faint concentric striae are seen. Dimensions of holotype: length 9·8 mm., height 3·4 mm. The largest specimen seen is about 15 mm. long.

Prothyris breviformis Wilson

Plate 20, fig. 6

Prothyris breviformis Wilson 1961, pp. 102–3, pl. 3, figs. 8–10.

Description. Relatively small, elongate-quadrate, the length/height ratio is approximately 2, which feature distinguishes it from all other known species. The dorsal margin is gently convex, the ventral one convex at the extremities and straight in the middle, while the posterior end of the shell is bluntly rounded and subtruncate. The anterior notch is small and inconspicuous, and the anterior lobe is narrow in the antero-posterior direction. There is no umbonal ridge, the maximum convexity being in the sub-umbonal region. The only markings seen on the shell are fine, concentric striae and obscure radial striae, both confined to the antero-ventral part of the shell. Dimensions of holotype: length 8·9 mm., height 4·2 mm. The largest specimen seen is 10·5 mm. long.

Prothyris scotica sp. nov.

Plate 20, figs. 7, 8

Prothyris elegans, Hind *non* Meek 1908, p. 353, pl. 2, figs. 48–50.
Prothyris sp. nov. Wilson 1962, p. 514, pl. 66, fig. 26.

Holotype. GSE 11719, right valve, internal mould, in silty mudstone under the Calmy Limestone, Scottish Upper Limestone Group (E_2), on shore 185 yards south-east of Hospital, Kirkcaldy, Fife.

Paratype. GSE 11827, both valves, open, attached, in mudstone above the Index Limestone, Scottish Upper Limestone Group, at 284½ feet, in Powis Mains No. 1 Bore 1959 (N.C.B.), Stirlingshire.

Description. Elongate, average length/height ratio (from twenty-three specimens) is 2·9, dorsal and ventral margins parallel. The umbo is situated near the anterior end of the dorsal margin, but not raised above it. The dorsal margin is straight, except for its posterior third which slopes ventrally in a very gentle convex curve to meet the almost vertically truncate posterior border. The ventral margin is almost straight for most of its length, but anteriorly it curves relatively sharply into the anterior notch which is almost rectangular. The anterior lobe is prominent, its height being about twice its length. It is separated from the main part of the valve by a narrow ridge running from the umbo and inclined anteriorly. Posterior to this ridge a shallow groove occurs. A distinct umbonal ridge runs to the postero-ventral angle, angular at its proximal end but becoming less well-defined distally. The anterior lobe and that part of the shell anterior and ventral to the umbonal ridge are marked by fine, regular, concentric striae, but over the umbonal ridge and on the postero-dorsal region the striae tend to coalesce into irregular plications. The valves gape at the anterior notch and at the posterior end. The shell is partly preserved on the paratype and is seen to be very thin. Hinge and interior not seen.

Dimensions.

	Length mm.	Height mm.
Holotype	20	7
Paratype	21·5	*c*. 8

The largest specimen seen is 30 mm. long.

Remarks. The species just described was first recognized as a *Prothyris* by Hind (1908), who identified it as the American species *P. elegans* Meek. This latter species differs from *P. scotica* in being relatively longer, length/height ratio 3·5 (Meek, in Hayden 1872, p. 223), its dorsal margin is arched, and there is no distinct umbonal ridge. *P. scotica* appears to be similar to *P. soleniformis* Elias, a late Mississippian form from Oklahoma, in its general dimensions and by possessing an umbonal ridge, but the illustration of the holotype of the latter species (Elias 1957, pl. 90, fig. 3) shows a shell markedly different in outline from that just described.

P. scotica is found in mudstones, silty mudstones, and, more rarely, in ironstones in the Scottish Midland Valley, ranging from the Hosie limestones up to the lower part of the Passage Group. In terms of the goniatite zonal scheme, this range is from the uppermost part of P_2 to the top of E_2 as it is represented in Scotland.

Wilson (1961, p. 93) named a specimen as *P.* aff. *soleniformis* Elias from the Archerbeck Borehole, Dumfriesshire. The horizon is in the roof of the Linns Limestone, probably near the top of the Visean. A similar form has now been found at the same horizon in Penton Linns, Canonbie. Neither specimen is well preserved but they show a close resemblance to *P. scotica*. This occurrence of *Prothyris* in the Canonbie area, Dumfriesshire, is about the horizon of the Tyne Bottom and Jew limestones of north-east England. From a band between these limestones in the Roddymoor Boring in Co. Durham (Woolacott 1923; Lee 1924), a specimen of *Prothyris* has now been recognized. It is numbered T 3897^{f} in the collections of the Geological Survey, Leeds. Both valves are present, but the shell appears to be a juvenile form, incomplete posteriorly, and it is specifically indeterminate.

Prothyris has recently been recorded from Northern Ireland (Fowler and Robbie 1961, p. 234). It occurred in the Millstone Grit (E) at approximately 150 feet in Palm Lodge No. 1 Borehole. The specimen, NIR 774, at present housed in the Geological Survey Collections, London, is part of a right valve, but both anterior and posterior ends are missing. Sufficient is preserved however, to suggest that it is a specimen of *P. scotica*.

From the Millstone Grit of the north of England, two specimens of *Prothyris* are in the Geological Survey Collections, Leeds. They are HS 4591 and CS 844a and come from Chalk Beck, 2 miles north of Caldbeck, Cumberland, and the Cayton Gill Beds (Dunham and Stubblefield 1945, pp. 241–3) in Watergate Beck at Bay Croft Hill Farm, 3 miles west of Pateley Bridge, Yorkshire, respectively. They are both incomplete, but sufficient is preserved to suggest that they have affinity with *P. scotica*.

Prothyris carbonaria sp. nov.

Plate 20, fig. 9

Holotype. GSM 87388, left valve, internal mould, in mudstone from the Mansfield Marine Band, Coal Measures, at 1,724½ feet in Lindholme Borehole, about 10 miles east-north-east of Doncaster, Yorkshire. It is slightly incomplete on the ventral and posterior margins.

Description. Relatively small, elongate-oval, average length/height ratio (from seven specimens) is about three, dorsal and ventral margins almost parallel. The umbo is inconspicuous, situated almost at the anterior end of the cardinal border. The dorsal margin is very gently convex, with a shallow groove parallel and ventral to it. The anterior lobe is narrow, length about one-third of height, and its height is about one-third of the height of the valve. The lobe is separated from the main part of the valve by a faint linear ridge at right angles to the dorsal margin, with a shallow groove posterior to it. The anterior notch forms an oblique angle passing with a gentle curve into the ventral margin, which is straight for most of its length. The posterior end of the valve is almost vertically truncate, gently convex, its dorsal and ventral extremities symmetrically curved. There is no umbonal ridge, and the valves are only gently convex with slight gapes at the anterior notch and the posterior end. The anterior lobe and antero-ventral part of the valve are marked by fine, regular, concentric striae, whereas the postero-dorsal area has irregular plications apparently formed by the coalescence of groups of striae. Hinge and interior unknown. The approximate dimensions of the holotype are: length 15·5 mm., height 5·5 mm. The largest specimen seen is approximately 24 mm. long.

Remarks. Although *P. carbonaria* is similar in its dimensions to *P. scotica*, it differs from the latter in having an arched dorsal margin and no umbonal ridge; its anterior lobe is relatively smaller, and the ridge dividing the lobe from the valve is normal to the dorsal margin, while in the latter species it is inclined anteriorly when traced from the umbo. *P. carbonaria* resembles *P. elegans* in having a groove parallel to the cardinal edge and in the general shape of the posterior end, but it is distinguished by being relatively shorter than the American species, by having a relatively smaller anterior lobe, and by the ridge posterior to the anterior lobe lying at right angles to the hinge line.

P. carbonaria appears to be a rare species in Britain. Few specimens were available for study, and they all came from the Mansfield Marine Band of the Yorkshire and Nottinghamshire Coalfields and the equivalent horizons in the South Wales and Bristol Coalfields.

GENERAL COMMENTS

Prothyris has been shown to range from the Upper Devonian to the Upper Carboniferous in Britain, as it does in North America. With the exception of *P. contorta*, found in limestone, it normally occurs in mudstones and silty mudstones. The shell matter is very thin, and the normal faunal associates are thin-shelled molluscs, suggesting that the environment was not rich in carbonates. The fact that the valves gape anteriorly and posteriorly, is evidence that the animal was a burrower. The valves are commonly found associated, either open wide or closed, but with one slipped slightly relative to the other. This suggests little disturbance of the bottom deposits, but it is also probably a reflection of the ability of the ligament to withstand decay until the valves were entombed.

From the evidence of the five British species known at present, several changes took place in the valve shape during the evolution of the genus. The Devonian species have the dorsal and ventral margins diverging posteriorly, whereas the Carboniferous forms have these borders more or less parallel. The postero-ventral angle in the Devonian species is acute, but this angle increases to almost a right angle in the later species. The anterior lobe tends to be better defined in the Carboniferous, with the maximum development of this feature being displayed by *P. scotica*. These general trends in the evolution of the valve shape appear to have been paralleled in the North American species.

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A RAPID PARALLEL GRINDING MACHINE FOR SERIAL SECTIONING OF FOSSILS

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FOR many years the internal structures of fossils have been investigated by means of orientated serial sections. There are two essential requirements of any machine used for this purpose: the successive surfaces must be parallel and the interval between them must be known and preferably capable of being controlled. Croft (1950) gave a brief historical account of the development of equipment designed for this purpose. In the same paper he gave details of an instrument that he had designed capable of producing ground surfaces at an interval of 10 μ, a considerable improvement in precision over previous machines. Perhaps the most notable advance in equipment for serial sectioning since 1950 is that described by Jefferies, Adams, and Miller (1962), who have successfully designed and produced a machine capable of automatically grinding and producing a photograph of the surface of the specimen every 100 μ.

Problems currently being investigated in the Department of Geology, University of Nottingham, include studies of the variation of internal structures in species of brachiopods and ontogenetic studies of these forms. With the material used, both these projects require a serial sectioning instrument with an accuracy comparable to that of the Croft grinder. A second requisite is that, as in the Croft grinder, the specimen should be readily removable from the instrument to enable an acetate peel to be made of the ground surface. For our purpose the acetate peels have an advantage over other methods of recording the ground surface of the fossil, since in material that has not recrystallized they record the micro-structure of the shell, which itself may provide some information on the ontogenetic history of the various structures, particularly those associated with the cardinalia. Either 'wet' or 'dry' peel techniques can be used. We employ the former as we find it gives better resolution and freedom from bubbles and with the materials used has a speed comparable with that of the 'dry' method.

The projects were initiated using a hand-operated Croft grinder. Manual methods are, however, extremely time-consuming and laborious if much sectioning has to be done. The machine described below was devised in an endeavour to improve the efficiency and speed with which successive peels could be produced and has proved very successful.

Basically the machine consists of a small lathe unit with several attachments. Grinding of the surface of the specimen is accomplished by passing it across the face of a diamond-impregnated cup wheel. The movement and cutting action are similar to that of the larger machine used by Olsen and Whitmore (1944) in their studies of fossil mammals. Their machine, however, was designed for handling relatively large specimens and its standards of accuracy would be unacceptable when dealing with invertebrates, particularly if they were small.

Among the existing relatively low-priced lathes that are available, the small models initially designed for watch-making are well suited for adaption to a serial sectioning

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machine for use with small- and medium-sized invertebrate fossils. They are compact and designed to work to close limits. The machine used was constructed from basic units of the Pultra lathe, obtainable from Smart and Brown (Machine Tools) Ltd., Biggleswade, Beds. The units employed were a lathe bed, chip tray base plate, high-speed head-stock, compound slide rest, and an arbor for holding the cup wheel. The compound slide rest is screw operated, with precision ground threads of 1 mm. pitch. Micrometer collars, adjacent to the handles, are graduated in $\frac{1}{100}$ths of a revolution, each graduation representing a movement of 10 μ.

The 3-inch diameter electrometallic diamond cup wheel, with 240-grade diamond, is mounted on the arbor held in the headstock spindle of the lathe. The machine is Vee-belt driven by a $\frac{1}{2}$ h.p. electric motor mounted beneath the bench, producing a wheel speed of approximately 5,200 r.p.m. Coolant in the form of a soluble cutting fluid (Sternopal) is supplied by drip feed from a can mounted at the rear of the machine, the waste suds running through the lathe bed, down a plastic tube to a large bottle also beneath the working bench. A ‘Perspex’ guard was formed and mounted round the wheel to reduce spray from the coolant.

The specimen holder consists of a permanent magnet chuck, in this case an ‘Eclipse’ magnetic positioner from which the ‘V’ shape on the face away from the wheel was removed. The positioner is screwed on to the tool post block of the lathe. It has a working face of 63·5 × 51 mm.

The specimens are embedded in polyester resin. ‘Ceemar’ cold-setting resin has been used and found very satisfactory, but extensive tests on other brands have not been carried out and many others may be equally suitable. Small polythene moulds, sold for making ice cubes, make good containers in which to carry out the embedding process, because the resin is adhesive to most common materials except polythene and expands slightly during setting. The embedded specimens are attached by tough wax (obtainable from Cutrock Engineering Co. Ltd.) to mild steel mounting blocks. A number of mounting blocks were made of 6·25 mm. mild steel, both sides being ground to obtain accuracy and maximum holding power. The blocks are all 50 mm. long and of various widths, the actual width of mount used depending on the size of the specimen. The mounting block with specimen fixed can then be readily attached to the magnetic chuck and this switched on. No trouble has been experienced with movement of the specimen on the mounting block or with movement of the block on the magnetic chuck. Care has to be used to keep the working face of the chuck and the back of the mounting block clean if the high precision of the machine is to be utilized.

With the present arrangement of the machine the maximum area it can grind is 50 × 40 mm. and the specimen can be of any length up to 25 mm. It is capable of grinding successive surfaces at a minimum spacing of 10 μ; the grinding time for removal of this increment varies slightly with the size of the specimen and the nature of its matrix, but is in the order of 10–15 seconds. If, as often is the case, larger spacings are required between successive sections, these may be removed in increments of up to 50 μ by successive passes across the diamond wheel.

The cycle for a specimen is as follows. The embedded specimen, attached to its steel block, is fitted to the magnetic chuck while clear of the diamond wheel. Longitudinal and cross feeds are adjusted to bring the specimen block just into contact with the grinding surface of the wheel. The cross feed is wound back and the longitudinal feed advanced not more than 50 μ. Advancing the cross feed now causes the removal of 50 μ from the block surface, this process is repeated until the specimen is exposed. At this stage the block is removed from the chuck and details recorded in the desired manner, the longitudinal feed reading having been noted in readiness for the next grinding operation. After recording the details of the surface of the specimen, it is returned to the chuck, the longitudinal feed then advanced the desired increment between 10 μ and 50 μ over the previous setting and the surface ground as before.

With the 'wet' acetate peel technique used, the longest stage in the preparation is the drying of the acetate solution on the block surface. A solution of 50 per cent. by volume of liquid 'Cerric' DL4013 cellulose acetate and acetone produces a quick-drying film, which with care is free from bubbles. It is necessary to dilute the solution occasionally during use to compensate for the loss of acetone by evaporation. A thin syrupy consistency should be maintained to enable a smooth coat to be brushed on quickly. The drying time can be reduced by using only a very thin layer of acetate solution. The resulting film has little strength, but after its margins have been freed, it may be readily peeled from the block using cellulose adhesive tape ('Scotch' tape or 'Sellotape'). It has been found convenient to process a number of blocks in such a way that the acetate on the earlier ones dries while the following blocks are in turn ground, etched, and coated with acetate solution. Using ten blocks, the acetate on the first may be peeled after the etching and painting of the last is finished, thus a continuous cycle may be maintained by a single operator without having to wait for material to dry. Using the above solution and ten blocks it is possible to produce at least twenty-five peels per hour, which is a very great improvement over any of the hand-operated methods that have been tried. A further advantage is the high degree of cleanliness of the method; it is not necessary after grinding to use more than a paper tissue to dry the block prior to etching.

The total cost of the machine as illustrated (Pl. 20) and described is in the order of £135.

We are indebted to Professor W. D. Evans for his interest and encouragement in the work, to F. Bancroft for modifying the existing lathe, and to J. Eyett for taking the photographs.

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MALAYOMAORICA GEN. NOV. (FAMILY AVICULOPECTINIDAE) FROM THE INDO-PACIFIC UPPER JURASSIC; WITH COMMENTS ON RELATED FORMS

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ABSTRACT. Critical reinvestigation of the aviculopectinid form '*Aucella*' *malayomaorica* Krumbeck from the late Jurassic of the Indo-Pacific region indicates that it does not belong either to the genus *Buchia* (= *Aucella*) or to any other known aviculopectinid genus. A new genus *Malayomaorica* is erected to receive '*Aucella*' *malayomaorica*. This genus is characterized by: (1) presence of a submedian furrow-like excavation in the ligamental pit of the left valve; (2) presence of an irregularly shaped tooth-like bulge in front of the ligamental pit at the anterior margin of the left ligamental plate; (3) presence of a strong ligamental ridge rising above the true dorsal shell margin in the right ligamental plate; and (4) a wide to very wide byssus notch.

Malayomaorica gen. nov. is much more closely allied to *Meleagrinella*, *Aucellina*, and *Arctotis* than to *Buchia*. This genus is, accordingly, placed in subfamily Oxytominae and not in Buchiinae (= Aucellinae). The genus *Aucellina* is also placed in the Oxytominae, as it appears to be an independent offshoot of *Meleagrinella* unrelated to *Buchia*.

The boreal genus *Arctotis* is the closest known ally of *Malayomaorica*. The latter is accordingly interpreted as an offshoot of the *Arctotis* lineage, which immigrated, together with the true *Buchia* species, into the Indo-Pacific region during the early part of the Upper Jurassic.

THE purpose of this paper is to establish a new genus for a peculiar aviculopectinid pelecypod from the Upper Jurassic (Kimeridgian) of Indonesia and New Zealand, as well as to investigate the morphological distinctions and probable phylogenetic ties of this biochronologically important genus.

'*Aucella*' *malayomaorica* Krumbeck 1923 has been the source of a considerable taxonomical and biochronological confusion ever since its original description by Boehm (1911) under the name of *Aucella plicata* Zittel. This species has been assumed to be an 'archaic' member of the genus *Buchia* (better known as *Aucella*) closely allied to the so-called *Buchia radiata–impressae* species group from the Oxfordian stage of Europe (Krumbeck 1923, pp. 70–74). It was, consequently, widely assumed to be of the early Upper Oxfordian age in terms of the international standard stages by the European workers who studied Upper Jurassic rocks and faunas of Indonesia and New Zealand (e.g. Krumbeck 1923, 1934; Wandel 1936; Stolley 1929). At about the same time, however, Crickmay (1932, p. 5) has made an astute but undeservedly neglected observation that: '*Aucella* from the more southerly localities, e.g. India, and New Zealand, are very different, and hardly congeneric.' This conclusion appears to be quite correct, at least so far as '*Buchia*' *malayomaorica* (and possibly '*Buchia*' *misolica*) is concerned.

The Oxfordian dating of '*Aucella*' *malayomaorica* beds has been recently refuted by Fleming (1958, p. 379; 1960, p. 267, table 1), who was able to demonstrate their early to mid-Kimeridgian age. Fleming (1958, p. 380) has, furthermore, concluded that: 'two parallel lineages [of *Buchia*; writer's remark], one represented by *malayomaorica* and

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misolica, the other by the *plicata–subpallasi* group, lived in the south-east Tethyan region during the Kimeridgian–Tithonian.'

Several Upper Jurassic *Buchia* forms of the Canadian Western Cordillera appear to be closely allied to and are possibly conspecific with *Buchia spitiensis* (Holdhaus), *B. leguminosa* (Stoliczka), and *B. blanfordiana* (Stoliczka) of the Indo-Pacific region (Jeletzky 1950, pp. 28–29; 196–). The present paper explains the reasons for the statement (Jeletzky 196–) that ' "*Buchia*" *malayomaorica* is rather different from and probably not congeneric with either the boreal *Buchia* (better known as *Aucella*) or the *Buchia plicata–subpallasi* species group of the Indo-Pacific region.'

The writing of this paper has been facilitated by valuable comments from Dr. C. A. Fleming, Senior Palaeontologist of the New Zealand Geological Survey, who also has kindly provided the writer with several well-preserved specimens of '*Aucella*' *malayomaorica* Krumbeck 1923 from the Kawhia section. It is published by permission of the Director, Geological Survey of Canada.

SYSTEMATIC DESCRIPTION

Family AVICULOPECTINIDAE Etheridge, Jr., 1906 emend. Newell 1938

Subfamily OXYTOMINAE Ichikawa 1958

Genus MALAYOMAORICA gen. nov.

Plate 21, figs. 1–2

Derivation of name. Malayo for the Malay Archipelago; maorica for Maori, the name of the New Zealand native people. Gender feminine.

Type species. Aucella malayomaorica Krumbeck (1923, pp. 65–76, pl. clxxiii, figs. 2–12, 17; pl. clxxvii, figs. 13*a–b*). Early to mid-Kimeridgian beds of Indonesia and New Zealand.

Diagnosis. Ligamental plate of the left valve separated into two parts by a submedian transverse furrow. This transverse furrow is a modification of the spoon-like excavation of the ligamental pit of some other members of the family. This furrow extends all across the ligamental plate from the very tip (underside) of the beak to its lower margin. The lower margin of the ligamental plate is indented at the lower end of the furrow.

The anterior part of the ligamental plate is markedly thickened; it carries an irregularly shaped bulge and an articulation furrow (= 'Gelenkgrube') near the anterior margin.

The byssus notch of the right valve is wide to very wide and broadly triangular in shape. The middle part of the ligamental plate of the right valve has an irregularly swollen, strong ligamental ridge, which rises above the true dorsal shell margin and is directed obliquely upward and forward. This ligamental ridge fits into the transverse furrow of the left ligamental plate.

Type specimen and synonymy. No previous selection of the type specimen of *Malayomaorica malayomaorica* (Krumbeck 1923) is known to the writer. The left valve represented in pl. clxxiii (2), fig. 4 of Krumbeck's (1923) work is, therefore, selected herewith as the lectotype of the type species of the genus *Malayomaorica.* It is from the so-called *Aucella* horizon of Portuguese Timor, and was collected between Bele and Tooi near Kampong Kamlachi, in calcareous marl with *Inoceramus*. According to Dr. Fleming, it is preserved in Geol. Pal. Inst., Bonn.

Fleming (1958, p. 378), Glaessner (1945), and Marwick (1953) have placed *Aucella boehmi* Marwick 1926 into the synonymy of '*A.*' *malayomaorica* Krumbeck 1923. Most other workers concerned (beginning with Krumbeck 1934) have, of course, been aware of the fact that '*Aucella*' *plicata* Boehm non Zittel from Kawhia Point is conspecific with '*Aucella*' *malayomaorica* Krumbeck; they have, however, overlooked the fact that this New Zealand form was formally named by Marwick.

There is little doubt that '*Aucella*' *boehmi* Marwick 1926 is both congeneric and conspecific with *Malayomaorica malayomaorica* (Krumbeck 1923). The characteristic furrow-

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EXPLANATION OF PLATE 21

(Unless otherwise indicated, all specimens are reproduced natural size. To facilitate the comparison of their shapes, the valves of the pelecypods figured are, as a rule, oriented with their hinge margins uppermost.)

Figs. 1A–G. *Malayomaorica malayomaorica* (Krumbeck 1923). New Zealand, North Island, north-east coast of Heteri Promontory, Kawhia Harbour. Heterian stage (early to mid-Kimeridgian). A topotype of *Buchia boehmi* Marwick 1926. GSC Cat. No. 17006.

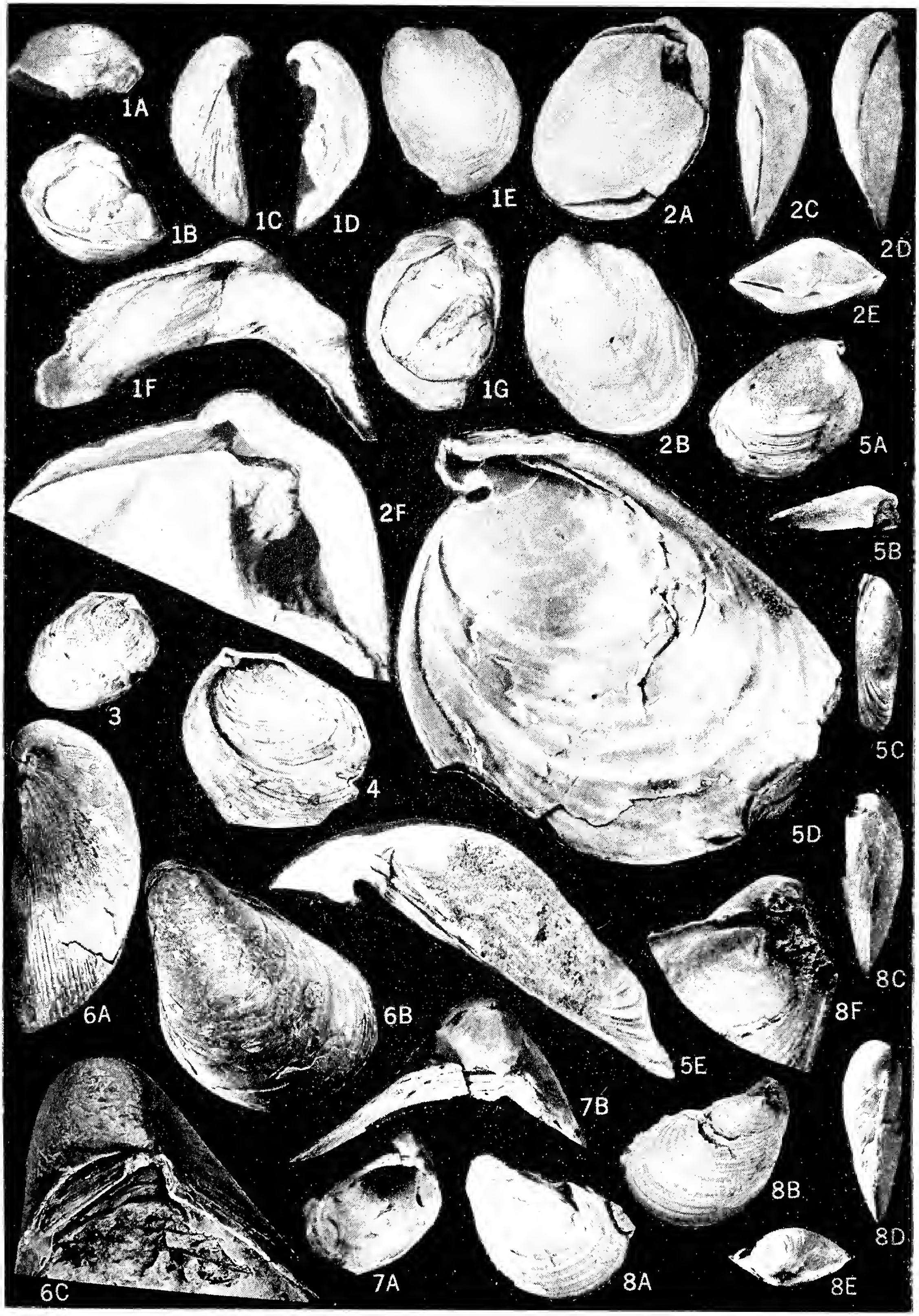
Left valve of a variant with a strongly reduced anterior ear. The semi-smooth appearance of most of the anterior part of the valve (fig. 1E) appears to be due to its abrasion. 1A: Dorsal view of the beak part. 1B: Oblique posterior view of the ligamental plate. Note the furrow-like excavation of the middle part of the ligamental pit. The ligamental plate occupies all of the underside of the beak. 1C: Posterior view. Note the predominance of the concentric, lamellar growth-lines on this part of the valve. 1D: Anterior view. Note the rounded, tooth-like bulge at the anterior rim of the ligamental plate and the pronounced embayment of the valve's margin underneath it. 1E: View from the left. Note the strongly reduced anterior ear and well-developed posterior ear. 1F: The beak part and the ligamental plate, × 3. Oriented exactly as in fig. 1B. 1G: Inside view.

Figs. 2A–F. *Malayomaorica malayomaorica* (Krumbeck 1923). Same locality and age as for the specimen shown in figs. 1A–G. GSC Cat. No. 17007. Complete shell with its valves almost in normal position relative to each other. A variant with typically developed anterior and posterior ears of the left valve and typically developed and well-preserved sculpture of both valves. The flattened, folded appearance of the toothlike bulge at the anterior margin of the ligamental plate of the left valve (figs. 2A and 2F) appears to be an individual feature peculiar to this specimen.

2A: Right valve viewed from the right. The transversally grooved ligamental plate of the left valve and the underside of the left beak are clearly visible. Note that the ligamental plate occupies all of the underside of the left beak up to its very tip. The wide gap between the byssus ear and the anterior ear of the right valve is characteristic of *Malayomaorica*. 2B: Left valve viewed from the left. Note the predominance of radial ribbing over the concentric growth-lines and the nodose to spinose appearance of radial ribs at their intersections with the concentric growth-lines. This ornament contrasts strongly with that of *Buchia erringtoni* (Gabb) shown in figs. 8A, B, F. 2C: Anterior view of both valves. 2D: Posterior view of both valves. 2E: Dorsal view of the beak parts of both valves. 2F: Beak part of the right valve, × 3 viewed from the right. Oriented as in fig. 2A. Note the sculpture of the surface of the byssus ear and the marked bend of the latter toward the left valve.

Fig. 3. *Buchia mosquensis* (Buch non Keyserling non Lahusen). Canada. N.W.T., Mackenzie District. Richardson Mountains. East slope of Aklavik Range, southern side of nameless creek falling into Husky Channel, about $\frac{3}{4}$ mile south of the top of Mount Gifford. Collected on the float of the basal part of lower shale–siltstone division. Middle to late Kimeridgian. GSC Cat. No. 17008. An early form of the species somewhat transitional to *Buchia* ex gr. *concentrica* (Sowerby)–*erringtoni* (Gabb). An internal cast of right valve viewed from the right. The central part of the valve, including its beak part, is strongly abraded.

Fig. 4. *Buchia mosquensis* (Buch non Keyserling non Lahusen). Same locality and age as for the specimen shown in fig. 3. GSC Cat. No. 17009. An early form of the species somewhat transitional to *Buchia* ex gr. *concentrica* (Sowerby)–*erringtoni* (Gabb). Inside view of the right valve with the well-preserved shell layer. The concentric ornament is just as well developed as on the surface of the shell,



JELETZKY, *Malayomaorica*

like excavation of the ligamental pit is neither visible in Krumbeck's (1923) drawings nor clearly described in the text. This feature was, however, excellently figured and described by Wandel (1936, p. 457, pl. xvii, figs. 2–3), who has been able to study Krumbeck's (1923) original material of the species.

Age and correlation. Krumbeck (1923, expl. of pl. clxxii (2), fig. 2) has tentatively dated the *Malayomaorica malayomaorica* beds of Indonesia as of early Upper Oxfordian age. Fleming (1958, p. 379; 1960) has recognized more recently, however, that in New Zealand

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while the radial ornament is subdued compared with its development on the shell's surface. Note the simply grooved, *Meleagrinella*-like appearance and orientation of the inside surface of the byssus ear, which differs from that of the younger *Buchia* species (e.g. *B. piochii* var. *russiensis* shown in figs. 5D, E).

Figs. 5A–E. *Buchia piochii* (Gabb) var. *russiensis* (Pavlow). Canada, N.W.T., Franklin District. Prince Patrick Island, Mould Bay, lat. 76° 16′ 30″ N., long. 119° 27′ 9″ W. Collected on the float of Mould Bay Formation (restricted). Late Portlandian (s. str.) GSC Cat. No. 17010. A well-preserved right valve.

5A: View from the right. Note the pronounced bend of the byssus ear toward the left valve. The byssus ear of *Buchia mosquensis* (Buch) shown in figs. 3–4 is, in contrast, oriented more or less in the plane of contact of the valves. 5B: Anterior view. Note that the anterior surface of the byssus ear is oriented almost perpendicular to the plane of contact of the valves. 5C: Posterior view. 5D: Inside view, × 3. Note the pronouncedly spoonlike appearance of the inside surface of the byssus ear contrasting with the simply grooved appearance of the same in *Buchia mosquensis* (Buch) shown in fig. 4. 5E: Dorsal view of the beak part, × 3, to show structural detail of the right ligamental plate and byssus ear. Note that the byssus ear is oriented almost perpendicularly to the plane of contact of the valves (plane of symmetry of the shell).

Figs. 6A–C. *Buchia keyserlingi* (Lahusen 1888) s. lato. East Greenland, Trail Ø. Locality 92 of Donovan (Medd. om Grønl. Bd. 111, No. 4, 1953, pp. 51–52). Middle or late Lower Valanginian. Property of Min. og Geol. Mus., Copenhagen.

A *Buchia crassicollis*-like variant of the species, possibly identical with *B. crassicollis* var. *gracilis* Sokolov, 1908 non Lahusen 1888. A well-preserved internal cast of the left valve with considerable patches of well-preserved shell layer. Note the pronouncedly lamellar appearance of concentric growth-lines and the absence of any radial ornament.

6A: Anterior view. 6B: Viewed from the left. 6C: Inside view of the beak and hinge areas, × 3.

Figs. 7A–B. *Buchia piochii* (Gabb) var. *russiensis* (Pavlow). Same locality and age as for the specimen shown in figs. 5A–E. GSC Cat. No. 17011. A somewhat distorted and cracked left valve with excellently preserved shell layer.

7A: Inside view of the complete valve. 7B: Inside view of the beak part, × 3, to show structural detail of the beak and ligamental plate. The ligamental plate is broken in the middle of the ligamental pit. The structure of the ligamental plate and the beak is closely similar to that of *Buchia keyserlingi* s. lato shown in figs. 6A–C.

Figs. 8A–F. *Buchia concentrica* (Sowerby) var. *erringtoni* (Gabb). Canada, Western Cordillera of British Columbia. Tyaughton Lake area, north side of a pass 1¾ miles north-west of Peak of Sheba. Lower part of Eldorado Group. Early Kimeridgian? GSC Cat. No. 17012.

A complete internal cast with valves in approximately normal position relative to each other. Small patches of the inner shell layer are preserved around the right beak and near the posterior margin of the right valve. The byssus ear is largely preserved as an internal cast. 8A: Left valve, viewed from the left. 8B: Right valve viewed from the right. The ligamental plate and beak of the left valve are clearly visible above the beak of right valve. 8C: Anterior view; 8D: Posterior view. 8E: Dorsal view of the beak part. 8F: Beak part of the right valve and the inside view of the left valve, × 3. Note the far-reaching similarity of the structure of the byssus ear to that of *Buchia mosquensis* (Buch) shown in fig. 3 and its dissimilarity with that of *B. piochii* var. *russiensis* shown in figs. 5A–E. The left beak is clearly separated from the ligamental plate and protrudes above the latter as is the case in younger *Buchia* species.

this species occurs in early to mid-Kimeridgian rocks. The *M. malayomaorica* beds of Indonesia are, therefore, believed by the writer to be of early to mid-Kimeridgian age.

Morphological and taxonomic remarks. The morphology and infra-specific variability of *M. malayomaorica* have been described in detail by Krumbeck (1923), Marwick (1926), and Wandel (1936). The present discussion of its morphology can, therefore, be limited to description, illustration, and taxonomic analysis of those morphological features that are diagnostic or otherwise significant at the generic and family level.

The generally accepted reference of *M. malayomaorica* to the genus *Buchia* (=*Aucella*) is based exclusively on its morphological similarity to such European forms as '*Aucella*' *impressae* Quenstedt and '*A.*' *radiata* Trautschold. This is stressed in the following statement made by Krumbeck (1923, p. 73) in the original description of *M. malayomaorica*: 'Im ganzen kann es nach meiner Ansicht nicht zweifelhaft sein, dass *Aucella malayomaorica* den älteren Aucellen und zwar vor allem der *Impressae-Radiata*-Gruppe am nächsten steht und in dieser mit *A. impressae* die meisten und engsten Berührungspunkte aufweist. Von den übrigen mir bekannten Aucellen—vielleicht ausgenommen *A. plicata* Zitt, sp.—weicht sie . . . ab.' This conclusion has been accepted by all subsequent workers in its entirety. As we shall see, however, only Krumbeck's claim of the far-reaching similarity of *M. malayomaorica* to '*A.*' *impressa* and '*A.*' *radiata* is apt and valid. His assumption that these two European forms are true representatives of *Buchia* is, on the contrary, erroneous and based on their misinterpretation by Pompeckj (1901).

Malayomaorica malayomaorica typically possesses a fairly well-developed anterior ear in the left valve (Krumbeck 1923, p. 66; Wandel 1936, p. 457; this paper, Pl. 21, figs. 2A, B, F), although this ear can become strongly reduced and barely noticeable in some specimens (Wandel 1936, pl. xvii, figs. 9, 11; this paper, Pl. 21, figs. 1A, E, G).

The taxonomic significance of the presence or absence of the anterior ear in the left valve of *Buchia* has been discussed by Pompeckj (1901) in connexion with his reference of such aberrant forms as '*A.*' *radiata* Trautschold and '*A.*' *impressae* to this genus. The interpretation of these two Oxfordian forms as 'archaic' representatives of *Buchia* connecting this genus with *Pseudomonotis* (*Meleagrinella* of recent usage) led Pompeckj (1901, pp. 327, 339, pl. xv, figs. 12, 16) to the revision of the generally accepted diagnosis of the former genus. Pompeckj concluded that the oldest representatives of *Buchia* possess a distinct, although short, anterior ear in the left valve, which becomes lost in the younger representatives of the genus. This conclusion has been strongly criticized by Sokolov (1908, 1912, and elsewhere).

Sokolov (1908, p. 3) insisted that the possession of an anterior ear in both valves and the peculiar shape of their beaks excludes '*Aucella*' *radiata* and '*A.*' *impressae* from the genus *Buchia*. Only the right valve figured by Pompeckj (1901, pl. xv, figs. 2, 5) under the name of *Aucella impressae* is a representative of *Buchia* according to Sokolov (1908, p. 3, footnote). A new name, *A. pompeckii*, was proposed for this form by Sokolov (1908), only to be passed later (Sokolov 1912, pp. 115–16) into the synonymy of *Buchia lata* (Trautschold).

To strengthen his argument Sokolov (1912, pp. 108–13; pl. 2, figs. 11*a*, *b*, 12*a*–13*b*) has redescribed and refigured the original specimens of '*Aucella*' *radiata* Trautschold and was able to show that this species is in all respects a typical representative of the group of species formerly included in *Pseudomonotis* s. lato but now separated under the name of *Meleagrinella*. Sokolov (1912, pp. 115–16) points out in the same paper that the oldest-known true *Buchia* species, such as *B. lata* (Trautschold), occur already in middle to late Callovian rocks of Russia. They antedate, therefore, the Oxfordian '*A.*' *impressae* and '*A.*' *radiata*, which have been assumed to be the oldest representatives of *Buchia* by Pompeckj (1901, pp. 327, 337). *B. lata* (Trautschold) is, moreover, already a typical representative of the genus in the complete absence of the anterior ear of the left valve and in the sculpture (see below). There is little doubt that Sokolov's (1908, 1912) criticisms of Pompeckj's (1901) treatment of '*A.*' *radiata* and '*A.*' *impressae* are fully valid.

Although published in German, in part at least (Sokolov 1908, pp. 26–27), Sokolov's conclusions have been completely ignored by those European workers who have made the most thorough study of *Malayomaorica malayomaorica* and unreservedly accepted Pompeckj's (1901) interpretation of *Buchia*. Krumbeck (1923, p. 71) actually stated that he did not use Sokolov's works, except for his plates.

As already seen, the presence of the anterior ear in the left valve suffices to exclude *M. malayomaorica* from the genus *Buchia*, as all its true representatives are characterized by the complete absence of the same. Its placement in this genus would probably never have been seriously contemplated except for the authority of Pompeckj's (1901) work and the unfortunate neglect of Sokolov's (1908, 1912) research.

Only Krumbeck (1923, p. 67) describes the ornamentation of *M. malayomaorica* in any detail. He stresses the strong variability of the ornamentation and the common occurrence of the specimens with more or less obsolete sculpture in all population samples available. Specimens characterized by the presence of the concentric ornament alone on parts or all of the shell are also common in his material.

Judging by the New Zealand specimens in the writer's possession (Pl. 21, figs. 1–2), the marked variation in strength and character of ornamentation from one specimen to another (or from one part of the shell's surface to another within a single specimen) is at least partly related to the degree of abrasion of the shells concerned prior to or after their burial. This abrasion (e.g. in specimen shown in Pl. 21, figs. 1A–G) was apparently facilitated by the restriction of ornamentation to the outer layers of the shell. The writer does not deny the strong variability of the ornamentation and the presence of specimens with obsolete sculpture. The sculpture of the specimen of *M. malayomaorica* shown in Plate 21, figs. 2A, B, F is, nevertheless, assumed to be typical of the species. The specimens of *M. malayomaorica* figured by Boehm (1911, pl. 2, figs. 2–4, non 1) and the specimen figured by Marwick (1926, pl. 71, fig. 10) are similarly strongly sculptured. The same is, finally, true of the herewith selected lectotype of the species (see above).

The ornament of the well-preserved specimens studied (Pl. 21, figs. 2A, B, F) consists of closely spaced, fine, sharp, and straight radial ribs intersecting more widely spaced concentric growth-lines (or growth-ridges). In our material the radial ribs are generally speaking stronger developed on the left valve, where they tend to be about as strongly developed as the concentric growth-lines (Pl. 21, fig. 2B). In the right valve the concentric growth-lines or growth-ridges are generally speaking more strongly developed than the radial ribs (Pl. 21, figs. 2A, F). The concentric growth-lines tend to be imbricated and lamellar in appearance in the best-preserved specimens; they also tend to become markedly frilled and to form small, ill-defined tubercles and spines whenever intersected by the radial ribs (Pl. 21, figs. 2A, B, F). The intersection of the radial and concentric elements of sculpture, which are about equally strongly developed, results in the markedly reticulate appearance of some parts of the shell's surface. In the specimens available, I was not able to observe clearly the intercalation of the second-order radial ribs with the first-order radial ribs observed by Krumbeck (1923, p. 67).

The sculpture of *Malayomaorica malayomaorica* described above is quite unlike that of *Buchia*. As it can be seen in Plate 21, figs. 3, 6A, B, 8A, B, F, the ornament of *Buchia* is usually visible on the surface of internal casts as well as on the surface of the shell. Furthermore, as already noted by Sokolov (1912, p. 110), the concentric growth-lines (or growth-ridges) of *Buchia* are always much more pronounced than the radial ribs. The latter are either of a very low relief or almost unnoticeable, even in *Buchia* ex gr. *concentrica* (Sowerby) (= *? B. bronni* Rouillier) (Pl. 21, figs. 8A, B, F), and are mostly completely absent in the majority of younger *Buchia* species (Pl. 21, figs. 6A, B). The imbricated appearance of the concentric growth-lines of *Malayomaorica malayomaorica* and the presence of small tubercles and spines on them is also quite foreign to *Buchia* and characteristic of *Meleagrinella*. The same is true of the intercalation of the second-order radial ribs observed by Krumbeck (1923, p. 67). On the whole the ornamentation of *Malayomaorica malayomaorica* is distinctly more similar to that of *Meleagrinella* than to that of *Buchia*. It differs, however, from that of *Meleagrinella* in much greater strength of the concentric growth-lines (or growth-ridges). In *Meleagrinella* the radial ribs are, indeed, always much stronger developed than the concentric growth-lines, which can be sometimes quite weak (as, for example, in *Meleagrinella radiata* Trautschold, see Sokolov 1912, pl. 2, figs. 11*a*, 12*a*, *c*). The intercalation of the second-order radial ribs with those of the first order is, finally, much better developed in *Meleagrinella* than in *Malayomaorica*.

The sculpture of *Arctotis* (Bodylevsky 1960, p. 44) differs from that of *Malayomaorica* in the same way as that of *Meleagrinella*. It is, furthermore, coarser in the best-known representatives of the genus (Bodylevsky 1960, pl. 7, figs. 1*a*, *b*, 2*a*; Borissiak 1915, pl. 11, figs. 3, 6, 12).

The sculpture of *Aucellina aptiensis* (d'Orbigny) Pompeckj 1901 and other Barremian–Aptian representatives of the genus is essentially similar to that of *Meleagrinella* and *Malayomaorica*. The radial ribs strongly predominate over the concentric growth-lines. The latter are, furthermore, often imbricated, tuberculate and/or spinose whenever they cross the radial ribs (Pompeckj 1901, pp. 353–4, pl. xvi, figs. 1*a*, 5*a*, and the writer's own observations on Canadian specimens). The sculpture of *Aucellina gryphaeoides* (Sowerby), on the contrary, is more like that of *Buchia* than that of older *Aucellina* species. This is, however, probably a secondary phenomenon, reflecting the convergent development of *Aucellina* and *Buchia*.

Pompeckj's (1901, pp. 328–32, 336, expl. of plates) nomenclature of morphological elements of the ligamental plate of Aviculopectinidae is used in the following discussion with some additions (e.g. excavations of the ligamental pit).

The edentulous ligamental plate of the left valve of *Malayomaorica malayomaorica* is wider than that of any other aviculopectinid genus (Pl. 21, figs. 1B, 1F). The ligamental pit of this plate is subdivided into two parts by a deep transverse groove, which is broadly V-like in cross-section (Pl. 21, figs. 1B, F). This groove begins underneath the very tip of the short, blunt, centrally located beak, and extends right across the ligamental plate. Both parts of the ligamental plate slope markedly toward this groove in its proximity. The lower margin of the ligamental plate is more or less clearly indented at the lower end of the transverse groove discussed above (Pl. 21, figs. 1B, F, G). In the specimens available to the writer, as well as in those figured by other workers, the posterior part of the ligamental pit is one and a half to three times longer than its anterior part (Pl. 21, figs. 1F, 2E). It is covered by numerous, more or less sinuous, longitudinal striae (Pl. 21, figs. 1F, 2F). An oblique, more or less sharp rim slanted posteriorly separates the posterior part of the ligamental pit from the still longitudinally striated inner surface of the posterior ear (Pl. 21, figs. 1F, 2F). A curved, low, longitudinal ridge may occur in the middle of the posterior part of the ligamental pit (Pl. 21, figs. 1F, 1G).

The anterior part of the ligamental pit is covered by sinuous, longitudinal striae, similar to those of its posterior part. The shell is markedly strengthened underneath this part of the pit. A more or less pronounced bulge occurs in front of the anterior part of the ligamental pit (Pl. 21, figs. 1B, D, F, G, 2A, E, F). This bulge is often more or less regularly rounded (Pl. 21, figs. 1D, 1F), but it may also be quite irregularly shaped, flat-topped, and folded over (Pl. 21, figs. 2A, C, F). This bulge occupies the inner surface of the anterior ear of *M. malayomaorica*. The inner surface of the bulge described above is also covered by irregularly curved, fine or coarse striae. An irregularly curved groove or depression, corresponding to the articulation pit (= 'Gelenkgrube' of Pompeckj 1901, p. 336) of *Buchia* and other aviculopectinid genera, separates this bulge from the ligamental plate proper. This articulation groove or depression persists right across the ligamental plate, is finely or coarsely striated, and may ramify in some of the specimens studied. The presence of striations on the bulge and articulation groove of *Malayomaorica* described above suggests that these features have also been covered by the ligament.

The anterior margin of the left valve is usually more or less markedly concave just below the above-described bulge (Pl. 21, figs. 1A, B, D, 2C). In some of the specimens studied the anterior margin of this valve forms a broadly rounded, deep embayment at that place. This embayment sharply separates the anterior ear from the rest of the shell (Pl. 21, figs. 1A, B, D).

The above-described structure of the left ligamental plate of *Malayomaorica* differs sharply from that of *Buchia*. In *Buchia* the bottom of the ligamental pit is essentially flat and appears to lack any excavations or furrows similar to the transverse furrow of *M. malayomaorica* (Pl. 21, figs. 6C, 7A, B; Pompeckj 1901, pl. XV, figs. 17, 18, 21; pl. XVI, figs. 4, 6*d*). The left beak of *Buchia* is, at that, situated at the extreme anterior end of the ligamental plate, well forward of the ligamental pit and immediately above the articulation pit (= 'Gelenkgrube'). The articulation pit of *Buchia* differs, furthermore, from that of *Malayomaorica* (and from that of all other Jurassic and Cretaceous aviculopectinid genera) in its regularly hoof-like shape, greater depth, and well-outlined, near vertical rims (Pl. 21, figs. 6C, 7A, B; Pompeckj 1901, pl. XV, figs. 17–18). Finally, no structure homologous to the ligamental bulge of *Malayomaorica* discussed above is present in *Buchia*.

The structure of the left ligamental plate of *Aucellina* is only imperfectly understood. Judging by the description and figures of Pompeckj (1901), and some Canadian specimens available to the writer, *Aucellina* is more similar, in this and other respects, to *Meleagrinella* and *Arctotis* than to *Buchia*. It can, accordingly, hardly be a member of the subfamily Buchiinae Cox (see below).

The structure of the left ligamental plates of *Meleagrinella* and *Arctotis* is much more similar to that of *Malayomaorica* than to that of *Buchia*. To begin with, all better-known representatives of *Meleagrinella* possess an irregularly rounded, more or less transverse excavation of the middle part of the ligamental pit equivalent to the transverse furrow of *Malayomaorica*. The anterior rim of this excavation may, furthermore, become steep and furrow-like in appearance (Pompeckj 1901, pl. xv, fig. 15; Borissiak 1909, pl. ii, fig. 14*a*; Bodylevsky 1960, p. 44). The central excavation of *Meleagrinella* and *Arctotis* differs, nevertheless, from the homologous transverse furrow of *Malayomaorica* in being broad, irregularly rounded in outline, and broadly concave in cross-section. *Malayomaorica* differs, furthermore, from *Meleagrinella* (but apparently not from *Arctotis*) in lacking, completely, the tooth-like bulge separating the ligamental pit from the articulation pit. This tooth-like bulge appears to be present in all better-known species of *Meleagrinella* (Pompeckj 1901, pl. xv, figs. 15–16; Borissiak 1909, pl. i, fig. 12*e*; pl. ii, figs. 14*e*, 15*e*). The ligamental plate of *Malayomaorica* has, instead, an irregular, tooth-like bulge at its anterior rim forward from the furrow-like articulation pit (= 'Gelenkgrube') (Pl. 21, figs. 1A, B, D; 2A, F). This bulge appears to be absent in *Meleagrinella* and *Arctotis*.

The articulation pit of *Meleagrinella*, *Arctotis*, and probably *Aucellina*, differs strongly from that of *Malayomaorica* (and *Buchia*, see above) in being more like a slight sinus than a regular pit or furrow. The articulation pit of *Meleagrinella*, *Arctotis*, and probably *Aucellina*, is an only slightly depressed and ill-defined area of pronouncedly bent and lamellated concentric growth-lines situated on the underside of the anterior ear of the left valve well forward from its beak (Pompeckj 1901, pl. xv, figs. 15–16, 19; pl. xvi, figs, 3*a*, 6*b*, 10*a*; Borissiak 1909, pl. i, fig. 12*e*; pl. ii, figs. 14*e*, 15*e*; 1915, pl. 11, figs. 7–9; Bodylevsky 1960, pl. 7, fig. 1*a*).

The ligamental plate of the left valve of *M. malayomaorica* occupies all of the underside of its short and blunt beak (Pl. 21, figs. 1B, F, 2F). The left beak is, thus, not separated at all from the ligamental plate. In typical representatives of *Buchia* and *Aucellina*, in contrast, left beaks are more or less clearly separated from and protrude above the left ligamental plate (Pl. 21, figs. 6A, C, 7A–B; Pompeckj 1901, pl. xv, fig. 14; pl. xvi, figs. 6*c*, 10*a*). This separation of left beaks from the ligamental plates apparently exists also in the true 'archaic' *Buchia* species (Pl. 21, figs. 8B, C, F), although it is not so well expressed in these forms. The beak structure of Barremian–Aptian *Aucellina* species is unknown.

The structure of the left beak of *Meleagrinella* is much more similar to that of *Malayomaorica* than to that of *Buchia* and *Aucellina*. As pointed out by Borissiak (1909, p. 10, pl. i, fig. 12*e*), the left beak of *M. echinata* var. *donetzensis* protrudes only slightly beyond the upper margin of the ligamental plate. Pompeckj's (1901, p. 325, pl. xv, figs. 15, 16) descriptions and drawings indicate that similar relationships prevail also in *Meleagrinella echinata* and *M. impressae*.

The best-known representatives of *Arctotis* are indistinguishable from *Malayomaorica* in the structure of their left beaks. In *Arctotis lenaensis* (Lahusen), the type species of this genus, the ligamental plate occupies all of the underside of the short, blunt, and centrally located left beak (Borissiak 1915, pl. 11, figs. 7–9), just as in *Malayomaorica malayomaorica*. The same appears to be true also of *A. intermedia* (Bodylevsky 1960, pl. 7, fig. 1*a*).

The ligamental plate of the right valve of *Malayomaorica malayomaorica* possesses a strong ligamental ridge in its middle part. This ridge has been well described and figured by Wandel (1936, p. 458, pl. xvii, figs. 1*a*–*c*, 4*b*–*c*, 11); it rises above the true dorsal shell margin and is directed obliquely forward.

The above-described ligamental ridge of *Malayomaorica* is completely absent in the right valve of *Buchia* to the best of the writer's knowledge (Pl. 21, figs. 3, 4, 5A, D, E, 8B, F; Pompeckj 1901, pl. xv, figs. 2, 5, 6, and 9). A similar ligamental ridge, is however, present at least in some (probably in all) representatives of *Aucellina*, *Meleagrinella*, and *Arctotis* (Pompeckj 1901, pl. xv, fig. 7; pl. xvi, figs. 1*a*, *b*; Bodylevsky 1960, pl. 7, figs. 2*a*, *b*). The ligamental ridge of *Arctotis intermedia* Bodylevsky 1960 is, moreover, particularly similar to the ligamental ridge of *Malayomaorica malayomaorica* in its shape, position on the ligamental plate, &c.

Other characteristic features of the right valve of *Malayomaorica malayomaorica* are: the stoutness and exceptionally large size of the byssus ear (Pl. 21, figs. 2A, F), the large size, the great to very great width and the broadly triangular shape of byssus notch, the marked bend of the byssus ear toward the left valve, and strong ornamentation of the external surface of the byssus ear (Pl. 21, fig. 2F). In some specimens (Pl. 21, figs. 2A, F) the anterior end of the byssus ear is covered by a fold-like flap of the previously described tooth-like bulge of the left valve. If considered in relation to the total shell's dimensions, the byssus ear of *M. malayomaorica* is probably larger and stouter than that of any other Jurassic and Cretaceous aviculopectinid genus, with the possible exception of some small-sized representatives of *Arctotis* (e.g. *A. intermedia* Bodylevsky 1960).

The byssus ear and notch of *Malayomaorica malayomaorica* differ strongly from the homologous features of the true 'archaic' *Buchia* species of the northern hemisphere (*Buchia* of the *B. lata–concentrica–mosquensis* species group); they are at the same time relatively more similar to the byssus ear and notch of the younger *Buchia* species.

The mid-Callovian to Kimeridgian 'archaic' *Buchia* of the *B. lata–concentrica–mosquensis* species group are characterized by the relatively small byssus ear extending forward and upward more or less in the plane of contact of the valves (Pl. 21, figs. 3–4, 8B, F; Pompeckj 1901, pl. xv, fig. 2). The groove occurring on the inner surface of the byssus ear in these *Buchia* species is, unlike that of younger *Buchia* species, open at its anterior end (Pl. 21, figs. 4, 5D). The byssus ear of the presently discussed 'archaic' *Buchia* species is thus rather similar to that of *Meleagrinella* (Pompeckj 1901, pl. xv, figs. 1, 7). This explains the previously discussed erroneous assignment of such *Meleagrinella* species as *M. radiata* and *M. impressae* to *Buchia* (Pompeckj 1901).

In the latest Jurassic and early Lower Cretaceous *Buchia* species, beginning with *B. piochii* (Gabb, s. lato) (= *B. russiensis* Pavlow and *B. unšovnikensis* Pavlow) (Pl. 21, figs. 5A–E), the byssus ear gradually becomes relatively larger and stouter and bends more and more toward the left valve. In the Valanginian *Buchia* forms, such as *B. keyserlingi* s. lato (Pompeckj 1901, pl. xv, figs. 6, 8–10, 21) the external surface of the byssus ear is directed almost perpendicularly to the plane of contact of the valves (plane of symmetry of the shell). At the same time, the anterior margin of the byssus ear begins to extend, ridge-like, across the anterior end of the canal that runs on the inner side of the byssus ear. A distinctly spoon-like shape of byssus ear (when seen from inside; Pl. 21, figs. 5D, E) results; this biochronologically important feature also reaches its maximum development in the Valanginian *Buchia keyserlingi–crassicollis* species group. These morphologically progressive changes of the byssus ear in the course of evolution of

Buchia have already been clearly recognized by Pompeckj (1901, p. 326). They have however, been, completely neglected by later workers.

In spite of its greater similarity to the byssus ear of the younger *Buchia* species, the byssus ear of *Malayomaorica* differs from it in its large and widely gaping byssus notch. As noted by Pompeckj (1901, p. 326, pl. xv, figs. 6, 8–10, 20–21), the byssus notch of the younger *Buchia* species is all but closed. Only a short and extremely narrow fissure remains at the anterior end of the ear in these species. The byssus notch of all Jurassic *Buchia* species, including that of its true 'archaic' representatives (Pl. 21, figs. 3, 4, 8B, F), is also much narrower than that of *Malayomaorica*.

The byssus ear and byssus notch of *Meleagrinella* differ from those of *Malayomaorica* in about the same way as do the byssus ear and notch of the true 'archaic' *Buchia* species (see above). The byssus ear and notch of *Meleagrinella* are, furthermore, proportionally smaller than those of any known *Buchia* species (see Pompeckj 1901, pl. xv, figs. 1, 4, 7).

The byssus ear and notch of *Arctotis* are more similar to those of *Malayomaorica* than are those of any other Jurassic and Cretaceous aviculopectinid genus. As noted in the description, and clearly visible in the figures, of Bodylevsky (1960, p. 45, pl. 7, figs. 1*a*, 2*a–b*), *Arctotis intermedia* possesses a short, stout, and large byssus ear accompanied by a widely gaping byssus notch. The byssus ear of *A. lenaensis* (Borissiak 1915, pl. 11, fig. 10, text-fig. 1) is also similarly large and stout; it is, however, much longer than the byssus ear of *Malayomaorica* and *A. intermedia*. The byssus ears of the *Arctotis* species mentioned above differ from the byssus ear of *Malayomaorica* in the apparently complete absence of the inward bend described above.

Because of the morphological peculiarities of its hinge described above, the articulation of valves of *Malayomaorica* differs markedly from that of *Buchia*. In the latter genus, the byssus ear of the right valve enters the articulation pit of the left valve (Pompeckj 1901, pl. xv, figs. 20–21). In *Malayomaorica*, however (Wandel, 1936, p. 458): 'dient die Gelenkgrube nicht, wie Krumbeck annimmt, zur Aufnahme des Byssusohres, sondern zur Aufnahme des wulstig verdickten und schräg nach oben gerichteten Vorsprung "v" der Bandplatte der rechten Klappe (Taf. XVII, Fig. 1b, c u. 11), der wie ein Zahn in sie eingreift (vgl. Taf. XVII, Fig. 4b). Das Byssusohr schmiegt sich dem präumbonalen Teil der Bandplatte der linken Klappe an (Taf. XVII, Fig. 4a).'

The above description of Wandel (1936) is quite apt, except that his 'Gelenkgrube' corresponds to the furrow-like excavation of the ligamental pit of the writer rather than to the true articulation pit (= 'Gelenkgrube') of Pompeckj (1901).

In *Meleagrinella*, *Arctotis*, and *Aucellina*, the articulation of valves is essentially similar to that of *Malayomaorica*. For *Aucellina* and *Meleagrinella* this is clearly indicated by drawings of Pompeckj (1901, pl. xv, fig. 19; pl. xvi, figs. 4, 6*b*). For *Arctotis* this is clearly indicated by Bodylevsky's (1960, pl. 7, fig. 1*a*) figures of *A. intermedia*. The writer was, furthermore, able to check on the reliability of the above data when studying the still undescribed Canadian representatives of *Aucellina* and *Arctotis*.

Malayomaorica malayomaorica (Krumbeck 1923) itself and *M.* aff. *malayomaorica* (Fleming 1958) are the only species that can be placed with assurance in the genus *Malayomaorica* at the present time.

The generic nature of '*Aucella sp.?* aus der Gruppe der *A. malayomaorica*' (Wandel 1936, pp. 461–2, text-figs. 1*a–c*) from the Demu limestone and Lilinta marly limestone of Misol is uncertain, although the apparent absence of a ligamental ridge in the drawings of its right valve does not favour its assignment to *Malayomaorica*. A detailed study of well-preserved ligamental plates of the left valves of this form is needed for its definite generic assignment.

The generic position of '*Aucella misolica*' of Krumbeck (1934, pp. 454–5, pl. xv, fig. 10*a–b*) is also uncertain, as the type material of this species consists of a unique, poorly preserved right valve. It probably is a representative of *Malayomaorica*, however, as *Buchia* aff. *misolica* (Krumbeck) from the Lower Tithonian of New Zealand has been recognized by Fleming (1958, p. 379; 1960, p. 267, table 1) as a younger representative of *Malayomaorica malayomaorica* lineage. It is to be hoped that *Buchia* aff. *misolica* will be described and figured in the near future.

All other *Buchia* species hitherto described from the Indo-Pacific region seem to be true representatives of the genus, in the present state of our knowledge at least (compare Jeletzky 196–).

CONCLUSIONS

'*Aucella malayomaorica* Krumbeck, 1923' neither belongs to the genus *Buchia* (= *Aucella*), as hitherto assumed, nor is closely allied to this genus. It differs from *Buchia* in all diagnostic morphological features and so cannot even be placed in the subfamily Buchiinae Cox, 1953 (= Aucellinae Fischer, 1887).

'*Aucella malayomaorica*' is much more closely allied to such aviculopectinid genera as *Meleagrinella*, *Aucellina*, and *Arctotis*. It is particularly similar morphologically to the boreal genus *Arctotis*. From this genus it differs, however, in the furrow-like appearance of the excavation of its left ligamental pit, the occurrence of a tooth-like bulge in front of the articulation pit (= 'Gelenkgrube') of the left valve, and in the marked bend of the byssus ear toward the left valve. These morphological distinctions fully warrant the erection of a new genus *Malayomaorica* for '*Aucella malayomaorica*', particularly as it differs even more strongly from *Meleagrinella* and *Aucellina*. *Malayomaorica* is sufficiently close to *Arctotis* and *Meleagrinella* to be included in the subfamily Oxytominae Ichikawa, 1958. *Aucellina* is also a member of the Oxytominae in the writer's opinion. This genus differs strongly from *Buchia* in most of its diagnostic morphological features, while being rather similar to *Meleagrinella* in these same features. It is inferred, therefore, that *Aucellina* is only homoeomorphically similar to *Buchia*, and that it is an independent offshoot of *Meleagrinella*.

Malayomaorica is considered provisionally to be an offshoot of *Arctotis* lineage, which had penetrated the Indo-Pacific region during the early part of the Upper Jurassic together with true *Buchia* species belonging to the *Buchia lata–concentrica–mosquensis* species group. The morphological similarities of *Malayomaorica* to *Meleagrinella* and *Aucellina* are not sufficiently far-reaching to assume its being directly related phylogenetically to either of these two genera.

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CYPRILEPAS HOLMI WILLS 1962, A PEDUNCULATE CIRRIPEDE FROM THE UPPER SILURIAN OF OESEL, ESTHONIA

by LEONARD J. WILLS

ABSTRACT. An account is given of about fifty examples of a pedunculate cirripede, *Cyprilepas holmi* Wills 1962, some still attached to the chitinous skin of *Eurypterus fischeri* Eichw. The bivalve chitinous shell and attachment peduncle of the cirripede are described. Comparison is made with the *Cypris*-larva and early post-larval stages of the present-day *Lepas*.

BIOLOGISTS and ecologists, as well as palaeontologists, may be interested in the discovery of what appears to be a pedunculate cirripede in rocks as ancient as the Silurian; and to find that this sessile animal had a bivalve chitinous shell not unlike that of the *Cypris*-larva invariably present in all cirripedes. Because of this resemblance to the *Cypris*-larva, the fossil has been named *Cyprilepas holmi* (Wills 1962, p. 567), the specific name being in honour of Gerhard Holm, who in his classic paper (1898) on *Eurypterus fischeri* Eichw. figured one on his pl. 4, fig. 22 as 'Kiemenblätter?, zwei zusammenhaftende' of *Eurypterus*, although on p. 39 he rejected this ascription.

Discovery and mode of occurrence. While engaged in etching out the chitinous skins of *E. fischeri* from the silty Upper Silurian limestone of Oesel, Esthonia, I cut one specimen (E10) longitudinally into two parts (R. and L.) before treatment with acid. As etching proceeded I noticed about ten of the small objects which form the subject of this paper waving about in the acid. All were clustered round the first bit of *Eurypterus* to appear (Pl. 22, figs. 1, 2). The majority lay round its edges, but a few were on its flattened surface (Pl. 22, fig. 3). Most of them floated free as the etching proceeded, but in one or two cases I had to prise them off with a fine needle. Ultimately I extracted more than fifty from the two halves of the specimen, and a number can still be observed attached to various appendages now in the final mount, BU 739, and on two leg-joints mounted as BU 748. A few were seen when etching another specimen. As noted above, Holm also isolated one example from the same locality.

As the etching of E10 proceeded it became clear that this specimen of *Eurypterus* was a moulted skin that had lain ventral side up on the sea-bed, and had then been partially covered by calcareous silt. Gentle currents had carried away the metastoma, and displaced and broken up the greater part of the last two appendages, bits of which were found well away from the body. Since all the shells were attached to upward-stretching parts of the appendages or to the drifted bits, it seems certain that these parts were exposed above the layer of silt and were solid objects to which the floating larvae of this sessile organism could anchor themselves.

Morphology. The fossils consist of a chitinous bivalve shell, not unlike a small *Isaura* [*Estheria*] or a *Cypris*, and a cylindrical chitinous attachment-stalk, both now flattened.

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By analogy with modern pedunculate cirripedes these two parts may be regarded as the capitulum and peduncle respectively, joined at the anterior end of the shell. The combined length of shell and stalk varies from about 2·2 mm. to 4·8 mm. (Pl. 22, figs. 4–9).

(*a*) The *shell.* The two valves of the shell are always squashed flat with some distortion and folding. Between the two valves there is usually a small amount of silt, but in no case have I observed any evidence of a cavity such as would be expected if the fossil, *prior to acid etching*, had had calcareous plates comparable to those that reinforce the very tenuous chitin of the bivalve outer-skin of a post-larval present-day *Lepas.* Usually the valves lie fairly symmetrically one above the other, and often it appears as if one is larger than the other, as in ostracods (Pl. 22, figs. 5, 6). In this condition most are roughly oval, approximately two-thirds as wide as long; but the smaller ones have almost circular outlines. The length of the shell, apart from the stalk, varies from 1·4 to 3·0 mm. In a few cases the compression has opened the two valves at the posterior end (Pl. 22, figs. 7, 8). The hinge appears to occupy the full length of the carinal side and to extend part-way across the rather blunt anterior end to the points where the free edges of the two valves merge on either side into the skin of the stalk. The edges of the shells are slightly thickened. The valves have been crushed irregularly, but show no growth-lines at all.

The chitin of a single valve appears structureless at low magnifications, but under a high power it displays a faint meandering mesh-pattern (Pl. 22, fig. 11). On three specimens, however, there is a definite hexagonal patterning visible on the chitin (Pl. 22,

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EXPLANATION OF PLATE 22

Cyprilepas and *Lepas.*

Figs. 1–12. *Cyprilepas holmi* Wills, attached to or associated with *Eurypterus fischeri* Eichw., Upper Silurian, Oesel, Esthonia.

1, 2. Two views of a single specimen attached to an edge of a segment of an appendage of *E. fischeri* (black), moving about in the etching acid which was disturbed between successive exposures, thus altering the posture of the shell.

3. Two segments of an appendage of *E. fischeri* with four specimens of *Cyprilepas* (outlined in ink) held virtually in their original positions by 'Durofix' which is itself blurred by adherent silt-particles. BU 748.

4–6. Young examples, two possibly showing the attachment-disc (*di*). BU 744, 750, 749 (paratypes).

7–9. Larger examples showing the two valves of the shell and variations in the stalk as it is preserved. BU 745, 746 (paratypes), and 743 (holotype).

10. Hexagonal patterning on part of the shell of the holotype (BU 743). Cf. fig. 14.

11. Linear markings on a single valve of the shell. BU 747.

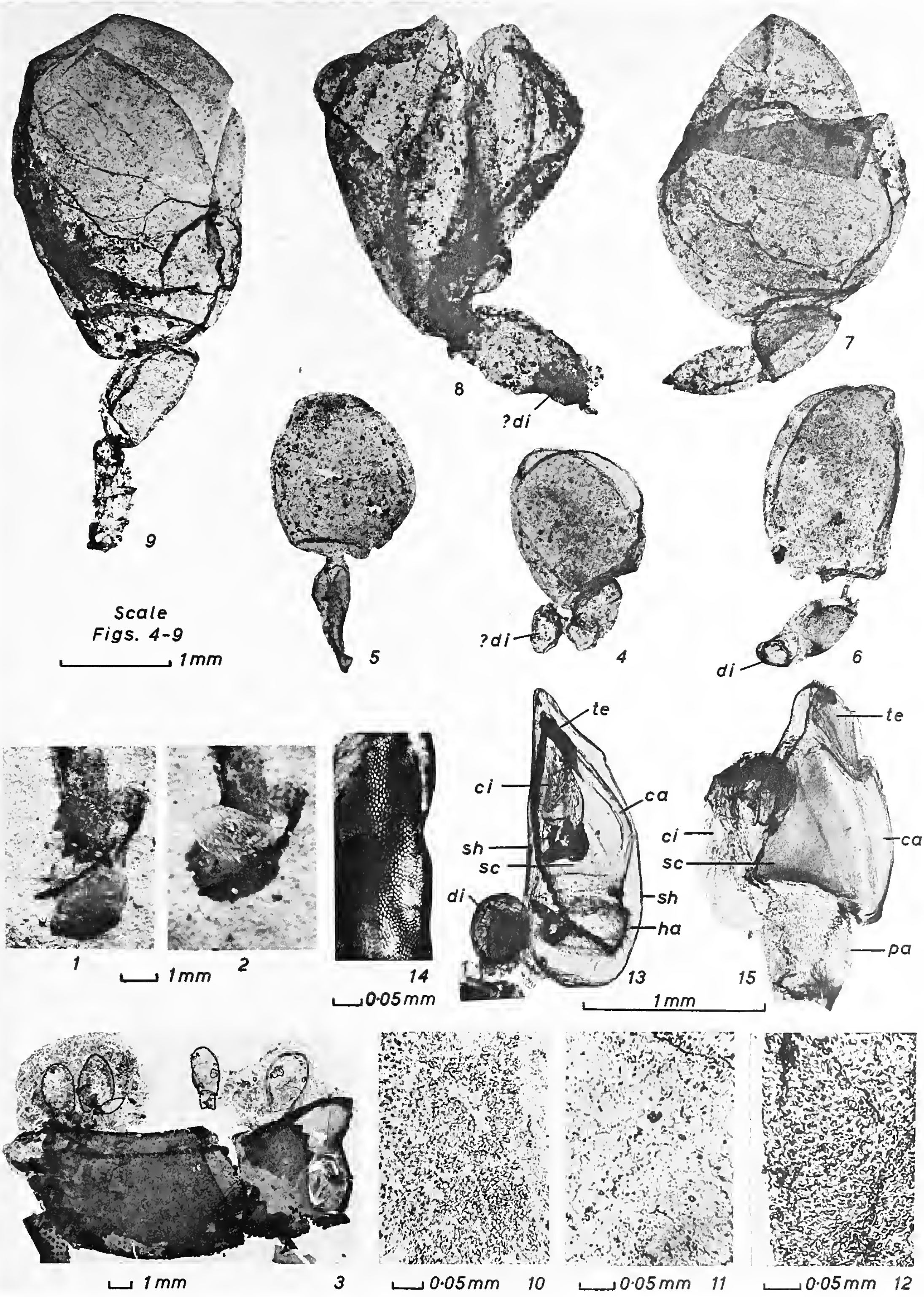
12. ? Papillae seen through the double skin of the stalk (BU 745). Cf. fig. 15.

Figs. 13–15. *Lepas australis* Darwin. Australian and New Zealand waters. Recent.

13. Late *Cypris*-larva showing rudiments of the calcareous plates (*sc*, scutum; *te*, tergum; *ca*, carina) together with the hair-clad stalk (*ha*) of the future post-larval animal, all within the chitinous bivalve shell (*sh*) of the *Cypris*-larva with its attachment-disc (*di*). Cirri (*ci*).

14. Part of the chitinous shell of a *Cypris*-larva at the stage seen in fig. 13, after decalcification, showing the impress of the hexagonal patterning on one of the calcareous plates. Cf. fig. 10.

15. A detached post-larval individual after the first post-attachment moult and the loss of the *Cypris*-like shell; *pa*, papillate stalk (cf. fig. 12); other lettering as in fig. 13.



WILLS, Upper Silurian pedunculate cirripede

fig. 10). The significance of this as evidence for the original existence of calcareous plates within the shell is discussed below.

(*b*) The *peduncle*, now compressed, was a cylindrical structure opening out from the body of the capitulum at the anterior end of the hinge. In some cases it can be seen that its sides are continuations of the two valves. At the distal end where it was attached to the *Eurypterus*, there is either a sucker-like disc (Pl. 22, fig. 6) or a sharp point (Pl. 22, figs. 5, 7). The latter is probably due to fracture, but the disc has only been seen in two or three cases. The stalk may be a simple tapered tube (Pl. 22, figs. 5, 8), but more usually is divided into from two to four parts by transverse bands that appear to be either thickenings or, more probably, folds of the skin. The bands are usually obscured by silt. Their number bears no obvious relationship to the length of the stalk. I incline to the view that they functioned to give flexibility and perhaps muscle attachments in what must have been an organ capable of retraction and of bending.

The texture of the chitin of the stalk is sometimes distinctive. It then appears to be ornamented by transverse rows of drop-like markings which are probably minute papillae on the two superimposed layers of skin (Pl. 22, fig. 12).

The ratio of stalk-length to shell-length lies between 2 and 3, but it varies irregularly —in some cases, no doubt, because the stalk is incomplete.

Affinities. Modern bivalve shells that are sessile belong either to the Mollusca, Brachiopoda, or Crustacea. Only the last (in the pedunculate Cirripedia, such as the Lepadidae) presents any points of similarity to *Cyprilepas*.

For purposes of comparison, I obtained through the kindness of Dr. B. Patel of the Menai Straits Marine Biology Station and of Dr. T. M. Skerman of the New Zealand Oceanographic Institute, both *Cypris*-larvae and young adults of *Lepas*. In these one can recognize the growth stages described by Calman (1909).

Every Cirripede begins as a *Nauplius*-larva and then passes through a *Cypris*-larva stage. In the latter the animal is enclosed within a bivalve chitinous shell. At first the larva is free: later it attaches itself to some object by a disc secreted by its *two* antennules. In the later development of the *Cypris*-larva (Pl. 22, fig. 13) there appears *inside* the chitinous *Cypris*-like shell, a single hair-clad stalk (the pair of antennules is no longer visible) connecting the disc (external to the shell) to the capitulum which displays rudiments of five calcareous plates (*ca*, *sc*, *te*). The plates are milky-white structures exhibiting a conspicuous hexagonal surface-patterning.

After the first moult the *Cypris*-like shell disappears and a miniature adult (Pl. 22, fig. 15) now has its soft parts contained within two valves of tenuous chitin lined by five calcareous plates arranged in two pairs with the fifth or carinal plate along the hinge. The outside of the plates has the same hexagonal patterning as in the larva. The covering of very tenuous chitin thickens somewhat in the sutural strips between the plates. This whole structure is the capitulum. Its chitin is continued into a strong papillate peduncle.

The shells of the *Cypris*-larva of *Lepas* are all about the same size, *c*. 1·6 mm. in length. The youngest post-larval individual that I have seen has a total length of 1·8 mm., of which 1·3 mm. is shell. The smallest known *Cyprilepas* has a total length of 2·2 mm., of which 1·3 mm. is shell. These figures suggest that all the known specimens of *Cyprilepas* were early post-larval individuals.

In order to get a true comparison of the young *Lepas* with the fossils which had been extracted by an acid etch, and consequently must have lost any calcareous plates that may have been present originally, one *Cypris*-larva at the stage represented by Plate 22, fig. 13, and several very small post-larval individuals like the one shown on Plate 22, fig. 15, were treated with acid to remove the calcareous plates; and the soft parts, including as much of the lining of the valves as possible, were dissected away. A very tenuous film of chitin remained, which shows:

(*a*) *in the larva*, a very distinct patterning of hexagons (Pl. 22, fig. 14) representing the impress of the ends of the prismatic columns that formed the rudimentary calcareous plates, but no growth-lines to define the limits of the plates;

(*b*) *in the post-larval individuals*, a similar hexagonal patterning is to be seen, but only on certain small areas of each plate. The outlines of the plates, however, are clearly indicated by narrow growth-lines conspicuous round their edges where the plate adjoined a sutural strip. Earlier growth-lines, where seen, are extremely narrow.

There is a remarkable resemblance between the hexagonal patterning on the inside of the decalcified chitin of *Lepas* and the admittedly less-distinctly hexagonal markings seen on three specimens of *Cyprilepas*, noted above in the description of the shell. It remains a matter of speculation whether the latter can be accepted as valid evidence of the original presence of a calcareous plate or plates within its shell; but the complete absence from the shell of any growth-lines or thickened sutural strips, makes it certain that there were not five plates as in *Lepas*. If there were plates at all, there were two, one lining the inside of each chitinous valve, and perhaps leaving their impress only on certain parts of it, as was noted in the post-larval *Lepas*.

The peduncle seen within the *Cypris*-larva shell of *Lepas* is clad with hairs (Pl. 22, fig. 13*ha*), but after the first moult it is covered with papillae (Pl. 22, fig. 15*pa*). The markings seen on some of the stalks of *Cyprilepas* (Pl. 22, fig. 12) probably represent papillae, but in no case has it been possible to find only a single layer of chitin on which to check this point. All that can be claimed is that the peduncle skin structure in the fossil resembles that of the post-larval rather than that of the larval state in *Lepas*.

The attachment-disc of *Lepas* is conspicuous in the advanced *Cypris*-larva. As growth proceeds it becomes obscured by the stalk, and fully adherent to the supporting object. In line with this is the observation that in the fossils it is on the smaller individuals that the disc can be recognized with some certainty (Pl. 22, figs. 4, 6).

CONCLUSIONS

1. The capitulum of *Cyprilepas* consisted of a bivalve chitinous shell resembling that of a *Cypris*-larva of a cirripede, but equally like that of an adult entomostracan, such as *Isaura* [*Estheria*] or *Cypris*. This chitinous shell may have been reinforced by a lining of calcareous matter possessing a prismatic texture which produced a hexagonal patterning on the chitin that has occasionally been preserved. There is no evidence that such calcareous matter, if it existed, formed five independent plates, like those in Recent pedunculate lepadid cirripedes.

2. The peduncle of *Cyprilepas* resembles that found in early post-larval stages of *Lepas* in having a thick papillate chitinous sheath. The constrictions usually seen in it in the fossils are not matched in any of the small adults of *Lepas* that I have examined.

3. The size of the whole organism and the possession of a papillate peduncle show that *Cyprilepas* was an early post-larval stage of a lepadomorph pedunculate cirripede, differing from young post-larval Lepadidae in the absence of the five calcareous plates forming the capitulum of the latter, and from Scalpellidae in the absence of numerous plates from the capitulum and of calcareous scales from the peduncle.

4. If *Cyprilepas* be accepted as a lepadomorph cirripede, the range of that sub-order is extended from the Middle Carboniferous (*Praelepas jaworskii* Tschernischew) to the Upper Silurian (the Ordovician and Silurian machaeridians are now excluded from the cirripedes). The Lepadidae are not known before the Eocene.

Specimens with the prefix BU are in the collection of types and figured specimens in the Department of Geology, University of Birmingham. Of the figured specimens, BU 743 on Plate 22, fig. 9, is the holotype; the others, BU 744–50, are paratypes.

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THE BRYOZOAN GENUS *POLYPORA* M'COY

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ABSTRACT. The genus *Polypora* M'Coy 1844 is redefined by reference to the type material. M'Coy's four original species of *Polypora* are redescribed, one being only tentatively retained within the genus, and one being assigned to *Fenestella* Lonsdale.

DURING the last 118 years more than 250 species of fenestrate bryozoa have been assigned to the genus *Polypora*. It is probable that imperfect knowledge of the characters of the genus has led to inclusion of species with quite different affinities. Shulga-Nesterenko, Morozova, and Nekhoroshev have attempted to subdivide the genus into species-groups based on the number of rows of zooecial chambers in the branches. In the light of the present re-examination it seems likely that a more valid subdivision of what is certainly an unwieldy genus will be based on the presence or absence of nodes on the obverse of the branches, and the arrangement of these with respect to a central carina, together with consideration of the organization and location of the zooecial chambers in relation to the 'basal plate'.

SYSTEMATIC DESCRIPTIONS

Specimens with the prefix NMI are in the National Museum of Ireland, Dublin.

Order CRYPTOSTOMATA Shrubsole and Vine 1882
Family FENESTELLIDAE King 1850
Genus POLYPORA M'Coy 1844

Type species. Polypora dendroides M'Coy 1844, p. 206; pl. 29, fig. 9; Carboniferous, Tournaisian, Ireland.

M'Coy's diagnosis. 'Expanding, interstices round, branching, having on one side from three to five rows of pores, the margin of which is never raised, interstices connected by thin, transverse, nonporiferous dissepiments.'

Emended diagnosis. Unifoliate fenestrate expansion of straight or slightly sinuous, regularly bifurcating, zooecia-bearing, non-carinate branches joined at regular intervals by transverse non-poriferous dissepiments. Branches circular or elliptical in cross-section, carrying regularly spaced elevated nodes on the central line of the obverse. Zooecia regularly arranged in three or more rows in the branches, the number increased for a short length below a bifurcation and similarly diminished above. In cross-section the zooecial chambers lie side by side on a flat basal plate in the plane of the expansion. In deep transverse section the zooecial base-shape is elongate-hexagonal to irregular polygonal. In shallow transverse section the calcareous investment of the branches is seen to be perforated by small 'tubules' which may be locally clustered, particularly round the margin of the zooecial apertures, and more compactly to form the cores of the branch

[Palaeontology, Vol. 6, Part 1, 1963, pp. 166–71, pl. 23–24.]

nodes. Obverse of zoarium smooth, granular, or striated. Reverse similar to obverse but may also carry more or less regularly spaced node-like projections.

Polypora dendroides M'Coy

Plate 23, figs. 1–3

Polypora dendroides M'Coy 1844, p. 206; pl. 29, fig. 9.

M'Coy's description. 'Flat, fan-shaped, interstices thick, regularly branched, divaricating; dissepiments very thin, frequently oblique, and placed at nearly equal distances; fenestrules large, rhomboidal, poriferous face, with five rows of small impressed pores arranged in quincunx, reverse longitudinally striated.

'This beautiful species is chiefly remarkable for the degree of divergence with which the interstices branch, and the small number of rows of pores. Length one inch, width one and a half inches; the interstices are about one line apart and half a line thick.'

Material. (1) Lectotype NMI XXIX.9*a*, Carboniferous 'Slate', Tournaisian, Hook Head, Fethard, Co. Wexford, Eire. Fragment of zoarium, roughly rectangular (30×25 mm.), showing obverse, on matrix of hard dark grey calcareous mudstone full of crinoidal and bryozoan fragments. (2) Homeotype NMI G.39:1962, Upper Tournaisian, Hook Head, Co. Wexford, Eire. Fragment of zoarium (25×20 mm.), partly obscured, showing obverse, in matrix of hard grey shaly bioclastic limestone.

Micrometric formulae. (1) Lectotype NMI XXIX.9*a*. (2) Homeotype NMI G.39:1962. (3) *Polypora bukhtarmensiformis* Nekhoroshev 1956, p. 210, Lower Carboniferous Ulbinskaya suite, Rudnyi Altai, and Fominskaya zone, Kuznetsk Basin.
(For explanation of column headings see Miller 1962, p. 120; in addition, R/B = number of rows of zooecia in branch, ND = base-diameter of branch nodes.)

	R/B	B/10	D/10	Z/5	N/5	B_W (mm.)	ZD (mm.)	ND (mm.)
1.	*3* 4 6	6–8	4–5½	13–16	5–7	0·5–0·9	0·15×0·2	0·13
2.	4	7–11	5	13½–15½	5–7	0·6–0·8	0·19	0·13
3.	4–6	6–8	4½–5½	14–16	?	0·8–0·85	0·12×0·18	?

Description. Zoarium probably flat, fan-shaped. Branches thick, straight, sub-elliptical in cross-section. Dissepiments short, half the diameter of the branches. Fenestrules long, with rounded ends, occasionally oval, width about equal to the diameter of the branches. Zooecia normally in four rows, but increased to six below a bifurcation, and diminished to three immediately above. Zooecial apertures oval, margins minutely subasteroid due to the presence of fifteen or sixteen short thin internal projections resembling the septa of corals. Branch nodes on obverse circular at base, high conical in profile, with grooved sides and rounded perforate tops. Zooecial bases elongate-hexagonal (eH) to irregular polygonal.

Discussion. The lectotype is considered to be the one used by M'Coy for his lower figure. In the Griffith Collection of the National Museum of Ireland it is labelled '? Type for structure'. Under the same catalogue number (XXIX.9) is a second specimen, hitherto supposed to be a syntype, labelled '? Type for form'. This is a fragment of a zoarium, roughly semicircular, 40×25 mm., showing the reverse, in a matrix of pale grey crystalline limestone, from the Carboniferous 'Upper' Limestone of Blacklion, Co. Cavan, Eire. The rock at this locality is a reef-facies limestone of Upper Viséan (B_2) age. It is clear that this second specimen (now labelled XXIX.9*b*), which, in spite of showing only the reverse of a zoarium, must have been used for M'Coy's *upper* figure, is not conspecific with its companion, and must therefore be discarded from the type material of *Polypora dendroides*. It is probably a specimen of *P.* (?) *verrucosa* (see p. 169), but as the obverse is not visible a precise determination cannot be made.

In shallow transverse section the finely granular (or minutely porous) calcareous tissue of the main zoarial skeleton is seen to be penetrated by small 'tubules'. These appear in the section as clear spots surrounded by a darker zone without a sharp margin. The tubules are 10–12 μ in diameter and are distributed fairly evenly in the skeletal tissue 40–80 μ apart. This wide separation of the tubules is replaced by a closer packing in two situations: (*a*) round the margin of the zooecial apertures, where fifteen or sixteen are placed against the margin, about their own diameter apart, or a little more (12–15 μ); and (*b*) at the site of the branch nodes, where usually eight tubules appear to bend together and coalesce into an asteroid space surrounding a solid central structure. Similar structures were figured (but not discussed) by Ulrich (1890) in *Polypora cesteriensis* Ulrich and *P. halliana* Prout.

This formation of branch nodes by a growing together or bunching of tubules suggests that the carinal nodes in *Fenestella* may have a similar structure. The tentative interpretation by Bassler (1953, p. 120) of these carinal nodes as possibly homologous with the acanthopores of the Trepostomata—an interpretation followed by me (Miller 1961, p. 223)—may have to be revised. It is interesting to note in this connexion that in general appearance and arrangement the tubules in *Polypora* recall the micracanthopores of the Ordovician bifoliate cryptostome genus *Pachydictya* recently described by Phillips (1960, pl. 5, fig. 4).

Polypora marginata M'Coy

Plate 24, fig. 3

Polypora marginata M'Coy 1844, p. 206; pl. 29, fig. 5.

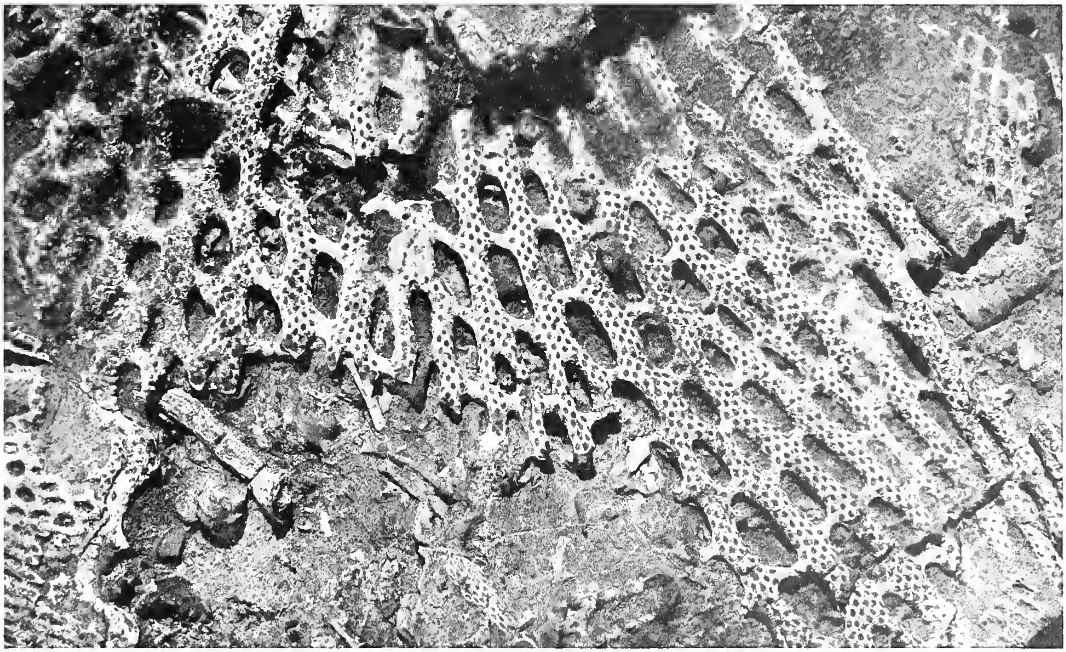
M'Coy's description. 'Interstices thick, irregularly bifurcate; sides margined; dissepiments thin; fenestrules small, elongate, oval, or approaching to a square form; reverse with direct, deep, longitudinal striae; poriferous surface, with five alternating rows of pores, and interjacent, waved striae.

'The broad, flat, margin of the branches distinguishes this rare species at a glance from any of the other corals likely to be confounded with it.'

Material. Holotype NMI XXIX.5, Carboniferous 'Upper' Limestone, Upper Viséan (horizon in Upper *Dibunophyllum* zone ($D_2 = P_1$), *fide* Fowler and Robbie 1961, p. 80), Killymeal, Dungannon, Co. Tyrone, Northern Ireland. Fragment of zoarium, 11 × 25 mm., showing reverse, on matrix of dark grey compact crystalline limestone.

EXPLANATION OF PLATE 23

Figs. 1–3. *Polypora dendroides* M'Coy. 1, Obverse of zoarial fragment, ×4·5. Holotype NMI XXI.X.9*a*. 2, Obverse, showing arrangement of zooecial apertures on branch surface, ×20. Holotype NMI XXIX.9*a*. 3, Shallow transverse section showing arrangement of tubules round apertural margins, and at site of a branch node (irregularly shaped light patch with dark diffuse margin at top right), ×100. Homeotype NMI G.39:1962.



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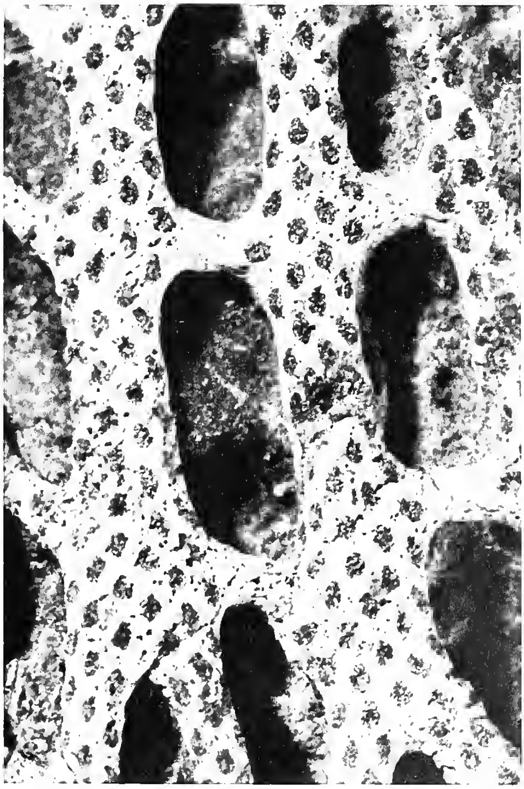

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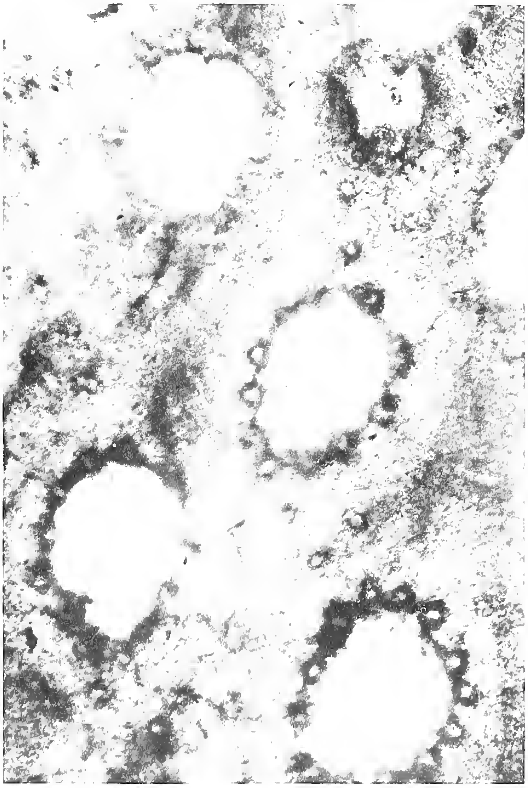

3

MILLER, *Polypora*

Micrometric formula

	R/B			B/10	D/10	Z/5	N/5	B_W (mm.)	ZD (mm.)	ZB
NMI XXIX.5	*4*	5	*8*	5–9	4–5	15½–18	?	0·6–1·1	0·12–0·15	eH

Description. Branches thick, rather sinuous, compressed-elliptical in cross-section. Dissepiments thin. Fenestrules rectangular. Zooecial chambers in five rows, increasing to eight below, and diminishing to four above, a bifurcation. Zooecial apertures small, circular, slightly less than their own diameter apart; the outer rows commonly projecting slightly into the fenestrule so as to produce a sinuous margin. Zooecial bases elongate-hexagonal. Details of branch nodes unknown. Reverse minutely striated parallel to long axes of branches and dissepiments, without auxiliary projections.

Polypora (?) *verrucosa* M'Coy

Plate 24, fig. 2

Polypora verrucosa M'Coy 1844, p. 206; pl. 29, fig. 6.

M'Coy's descripton. 'Interstices rarely bifurcating, regular, equal, rounded; dissepiments thin, distant; fenestrules rectangular, five times as long as wide, about one-third wider than the interstices, equal; obverse with four rows of prominent, wart-like pores, about ten in each row to the length of a fenestrule; between the pores are waving longitudinal striae; reverse nearly smooth.'

Material. Holotype NMI XXIX.6, Carboniferous 'Upper' Limestone, Upper Viséan (horizon in reef-facies, upper *Beyrichoceras* zone ($B_2 = D_1$), *fide* Hodson 1956), Blacklion, Co. Cavan (near Enniskillen, Co. Fermanagh), Eire. Fragment of zoarium, 25 × 10 mm., showing patches of obverse, on matrix of grey crystalline limestone full of fenestellid bryozoan fronds.

Micrometric formula

	R/B			B/10	D/10	Z/5	N/5	B_W (mm.)	ZD (mm.)	ZB
NMI XXIX.6	*3*	4	*5*	5½–7½	2–3	11–12	?	0·48–0·58	0·10–0·13	?

Description. Branches of moderate thickness, straight, subparallel, circular in cross-section, dissepiments thin. Fenestrules long, narrow, rectangular. Zooecial chambers in four rows, increasing to five below, and diminishing to three above, a bifurcation. Zooecial apertures relatively small, circular, with prominent peristomal collars, placed nearly twice their diameter apart along the branches; apertures on the outer rows project slightly into the fenestrules so as to produce a beaded effect. Obverse surface deeply sculptured in ridges and grooves streamlined past and between the zooecial apertures. No nodes on the branches. Reverse with fine longitudinal striations. Shape of zooecial base unknown.

Discussion. The striking feature of this species is the absence of nodal structures from the centre line of the branches on the obverse, combined with the ridged and grooved sculpturing of the calcareous investing tissue. Both these characters recall the condition in the fenestellid genus *Levifenestella* Miller 1961. The question whether M'Coy's *P. verrucosa* should be detached as a member of a genus distinct from *Polypora* must await the recognition of similarly characterized species in other bryozoan faunal assemblages. For the present it is tentatively assigned as *P.* (?) *verrucosa.*

Genus FENESTELLA Lonsdale 1839

Fenestalla papillata (M'Coy)

Plate 24, fig. 1

Polypora papillata M'Coy 1844, p. 206, pl. 29, fig. 10.

M'Coy's description. 'Interstices rarely bifurcating, very narrow, rounded; fenestrules circular or oval; poriferous surface smooth, with three alternating rows of pores; reverse smooth, with a small papillated pore at the origin of most of the dissepiments.

'This species is remarkable for its large and round fenestrules, which are of such a size that the interstices and dissepiments appear disproportionably thin. The prominent pores on the outer side have caused me to doubt the propriety of placing this coral in the same genus with the preceding species [*P. marginata*]. It is very rare.'

Material. Holotype NMI XXIX.10, Carboniferous 'Upper' Limestone, Upper Viséan (horizon in reef-facies, upper *Beyrichoceras* zone ($B_2 = D_1$), *fide* Hodson 1956), Blacklion, Co. Cavan (near Enniskillen, Co. Fermanagh), Eire. Fragment of zoarium, 20×20 mm., showing reverse, on matrix of massive grey calcilutite.

Micrometric formulae

	B/10	D/10	Z/5	N/5	B_w (mm.)	ZD (mm.)	ZB
1. NMI XXIX.10	16	8	15–17	27–30	0·30–0·40	0·10	hH
2. *F. polynodosa* Miller 1961 . . .	12–17	7–9	15–18	32–36	0·30–0·40	0·15	sT

Description. Normal reticulate fenestellid meshwork of carinate zooecia-bearing branches with inter-branch dissepiments. Branches relatively stout, straight, or slightly sinuous. Dissepiments thinner than the branches. Carinae narrow, with a row of small, closely set nodes with elliptical bases. At a few places the line of carinal nodes becomes sinuous, the nodes lying alternately on either side of the central line, thus approaching the condition of the carinal nodes in *Minilya* Crockford 1944. Zooecial apertures large, circular, slightly more than their own diameter apart, with prominent peristomal collars, indenting the fenestrules, four or five to a fenestrule. Zooecial bases of variable shape, from triangular through subtriangular (sT) to hemi-hexagonal (hH). Reverse longitudinally striated, with scattered non-perforate steep-sided elevations, some of which lie opposite the ends of dissepiments.

Discussion. It is difficult to understand M'Coy's attribution of this species to his genus *Polypora*. The holotype, which is undoubtedly the one figured by M'Coy, shows the reverse of a zoarial fragment. By grinding down part of this fragment it has been possible to show the characteristic fenestellid features of the obverse. There is nowhere any trace

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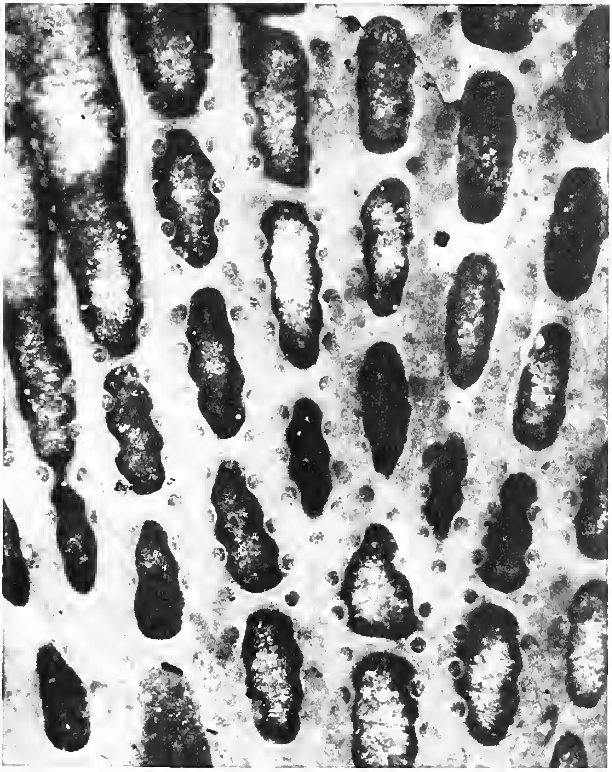
EXPLANATION OF PLATE 24

Fig. 1. *Fenestella papillata* (M'Coy). Holotype NMI XXIX.10, polished surface slightly oblique to plane of zoarial expansion showing at top left the arrangement of carinal nodes, ×17.

Fig. 2. *Polypora* (?) *verrucosa* M'Coy. Holotype NMI XXIX.6, part of obverse, ×16.

Fig. 3. *Polypora marginata* M'Coy. Holotype NMI XXIX.5. Reverse of zoarium with partial transverse section (polished surface) at left, showing arrangement of zooecial apertures, ×14.



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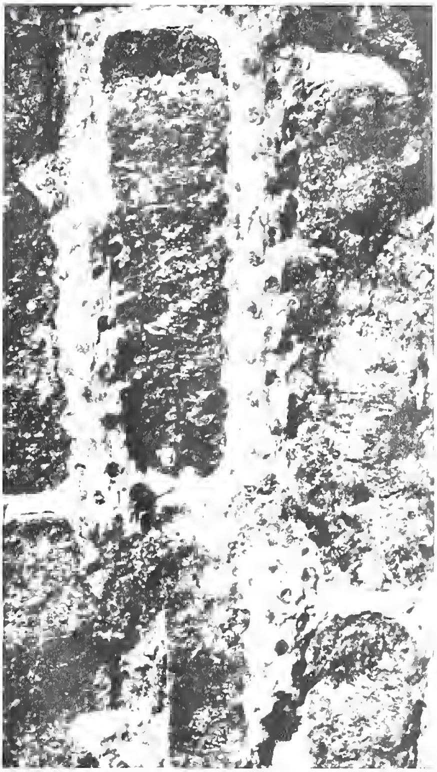

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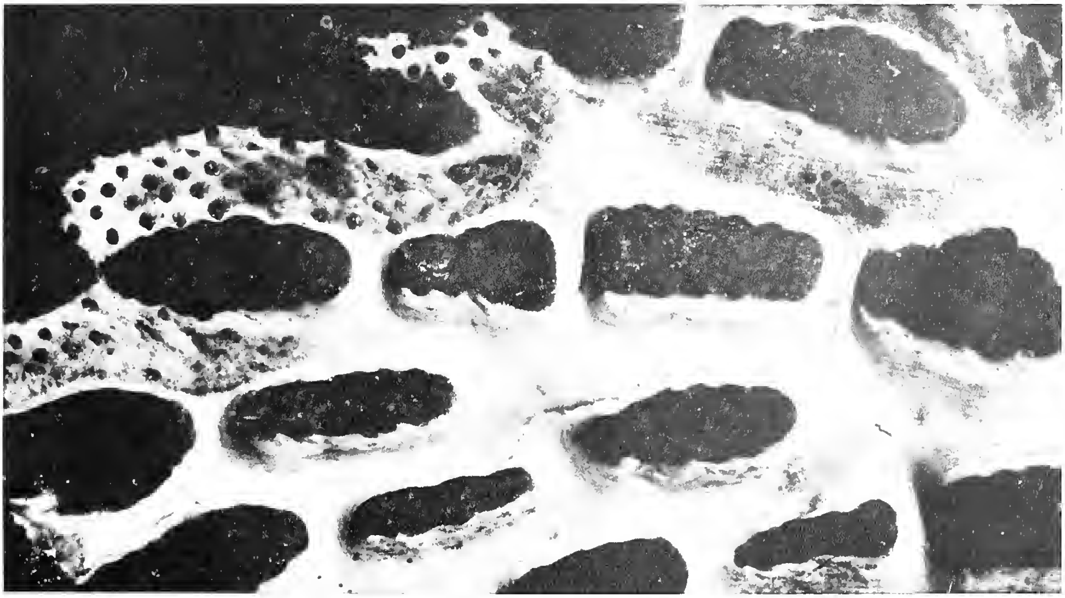

3

MILLER, *Polypora*

of the 'three alternating rows of pores' of M'Coy's description. On the contrary, the typical fenestellid rows of zooecial apertures separated by a noded carina can be clearly distinguished.

F. papillata is close to *F. polynodosa* Miller from the Irish Tournaisian. It differs in having a slightly smaller number of zooecial apertures to a fenestrule, in the smaller zooecial apertures, and in the slightly less closely packed carinal nodes. Also, the zooecial base in *F. papillata* shows a strong tendency to become stabilized as hemi-hexagonal, and is distinguishable from the predominantly subtriangular base in *F. polynodosa*.

Acknowledgements. I am indebted to the Director of the National Museum of Ireland, for allowing me to examine further material from the Griffith Collection; and to Dr. J. S. Jackson, Keeper of the Natural History Division of the same Museum, for information about the stratigraphic position of the various type-localities.

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CUPULADRIA CANARIENSIS (BUSK)—PORTRAIT OF A BRYOZOAN

by R. LAGAAIJ

ABSTRACT. The lunulitiform bryozoan *Cupuladria canariensis* (Busk) is a benthonic marine organism, whose calcareous colonies can easily be recognized with a hand-lens or under the microscope.

This species is eurybenthic (2–> 300 fathoms), eurythermal (12–31° C.), reasonably euryhaline (28–37‰), and requires a stable quartz and/or carbonate sand bottom. It is at present widely distributed over the continental shelves of the Atlantic and East Pacific between the 14° C. surface isocrymes and had an equally wide distribution during the Late Tertiary and Quaternary.

The occurrence of *C. canariensis* in Miocene and Pliocene marine sediments of the southern part of the North Sea basin calls for sea-water surface temperatures at least 9° C. higher than those obtaining at present in this area. Its occurrence in the Miocene, Pliocene, and Early Pleistocene marine sediments of Spain, Italy, and Rhodes suggests that the Mediterranean was somewhat less saline in the geological past than it is at present.

Although lunulitiform Bryozoa range from the Upper Cretaceous to Recent, *C. canariensis* first appears in the Lower Miocene (Aquitanian). Its presence or absence among lunulitiform bryozoan assemblages may serve as a criterion for establishing the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf sediments on both sides of the Atlantic. On this criterion a large part of the 'Caribbean Oligocene' is to be considered as Lower Miocene.

Cupuladria canariensis was named in 1859 by the English bryozoologist George Busk, who discovered it in material collected from the sea bed in the neighbourhood of Madeira and the Canary Islands. Later in the same year he reported its occurrence in the Pliocene Coralline Crag in East Anglia. In the last hundred years the number of records has increased enormously, and the data are widely dispersed in the biological and palaeontological literature. It seemed worth while to try to assemble these widely scattered data so as to give a comprehensive picture of the species in space and time.

Such a synthesis is of considerable geological interest. It will be shown that a study of *Cupuladria canariensis* can not only give an insight into certain ecological, climatological, and hydrological conditions in the geological past, but can also help resolve the problem of determining the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf deposits.

Its interest for the palaeo-ecologist is implied in a variant of Grimsdale's golden rule for systematic palaeontologists: '. . . one detected synonym is worth from ten to one hundred new species' (1951, p. 467). Perhaps this account will help to establish that one ecologically well-known species is worth more than a hundred *tabulae rasae.*

ZOOGEOGRAPHY AND ECOLOGY

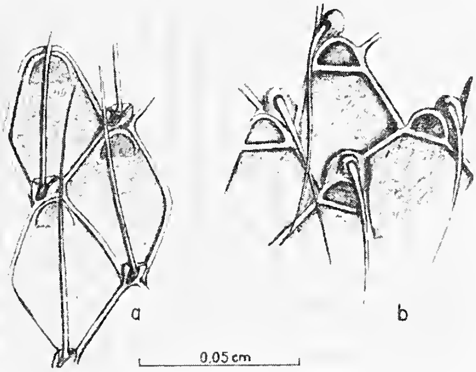
1. *Distribution*

Cupuladria canariensis (Bryozoa: Cheilostomata, Anasca) belongs to the so-called lunulitiform Bryozoa (Pl. 25, fig. 1), all of which possess the same zoarial form as the genus *Lunulites* Lamarck, 1816. The fully grown colony, or zoarium, has the shape of a dome or flattened cone and consists of a single layer of cells, or zooecia, opening on the convex side of the dome. In addition to the normal cells, or autozooecia, in which

[Palaeontology, Vol. 6, Part 1, 1963, pp. 172–217, pl. 25–26.]

the polypides reside, there are other cells, the vibracula, each bearing a long, whip-like vibracular seta. In the genus *Cupuladria* there is, without exception, a vibraculum situated distally to each autozooecium; the tip of each seta is capable of describing a 180° arc in the median plane of its autozooecium (text-fig. 1).

Practically nothing is known with certainty concerning the function of these setae. It has been suggested, notably by Busk (1854, pp. 100, 104, 106; 1859, p. 79), that in certain lunulitiform species the setae might be 'subservient to locomotion'. Alternative views are that they function as defensive or cleansing organs (Busk 1859, p. 79). In my opinion, it is clear that they serve to stir up the water in the colony's immediate vicinity, not so much in order to fan food particles towards the polypides' mouths as to prevent clay particles settling on the colony.



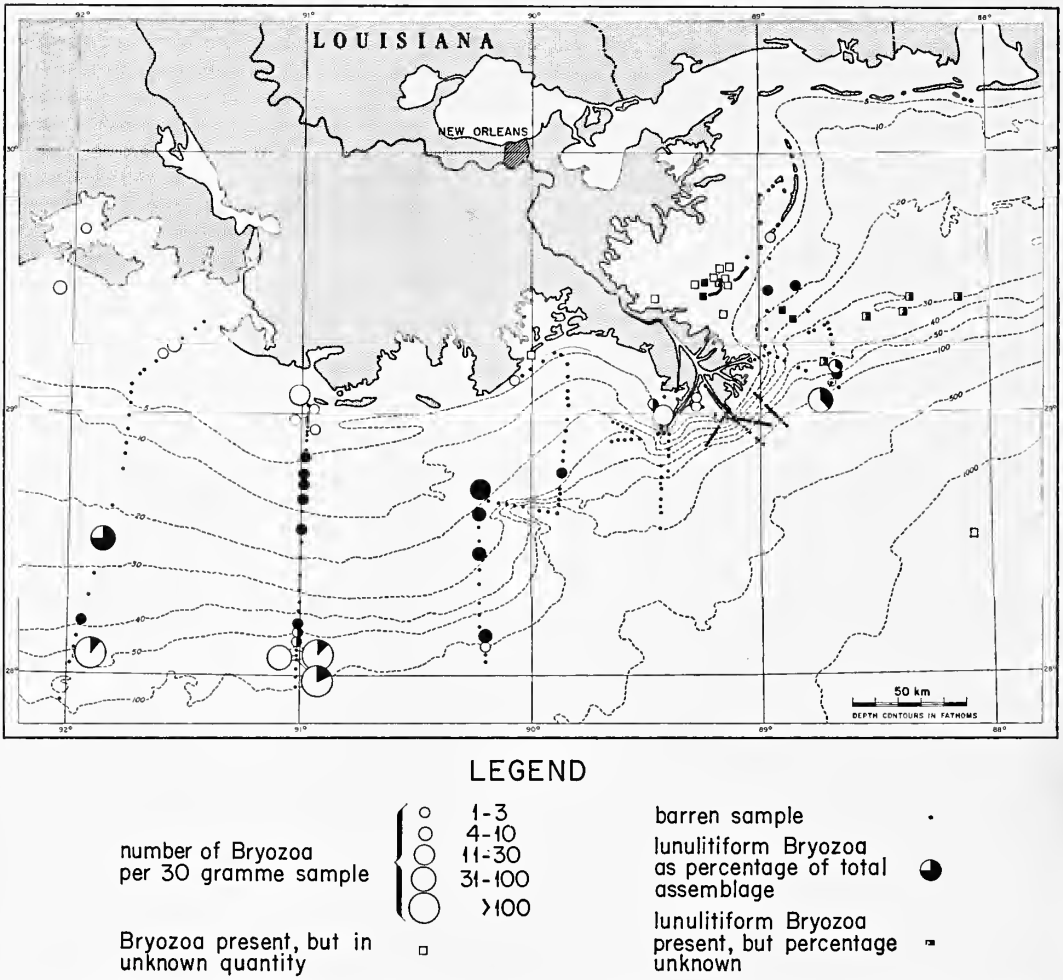
TEXT-FIG. 1. *a*, *Cupuladria canariensis*; *b*, *Discoporella umbellata*. Vibracula with vibracular setae (after Norman 1909).

If this view is correct, then the possession of these setae must be a valuable asset to the lunulitiform Bryozoa, since it would make them some of the least sensitive to clay sedimentation. It is certainly no coincidence that of all the possible zoarial growth-forms it is precisely two lunulitiform genera, *Cupuladria* and *Discoporella*, that venture most closely, on both sides, to the mouths of the Mississippi distributaries (text-fig. 2). On this map the distribution pattern of the Bryozoa can clearly be divided into three zones:

a. An inner zone between the shore and the 5 fathom line, in which swell and breakers begin to disturb the sea bottom. Here, where the water is turbulent, no lunulitiform Bryozoa occur (for reasons given on p. 187) though other types do, such as those that attach themselves to plants or shells.

b. An outer zone between the 50 and 100 fathom lines, having a steep slope and an irregular topography and situated on the outer edge of the continental shelf. Deposition of clay along the outer margin of many continental shelves is notoriously slight to non-existent (Kuenen 1939; Shepard 1948, p. 160), and the Gulf of Mexico is no exception (Phleger 1959, p. 650; 1960, p. 288). The low rate of deposition and the local presence of hard substrata explain why Bryozoa with other growth-forms have been able to settle in this zone.

c. A middle zone, which coincides with the broad plateau lying between the 5 and 50 fathom lines. A large part of the clay brought down to the sea by the Mississippi is deposited on this plateau, and it is in this area that only lunulitiform species of Bryozoa, being equipped with vibracular setae, are able to survive.



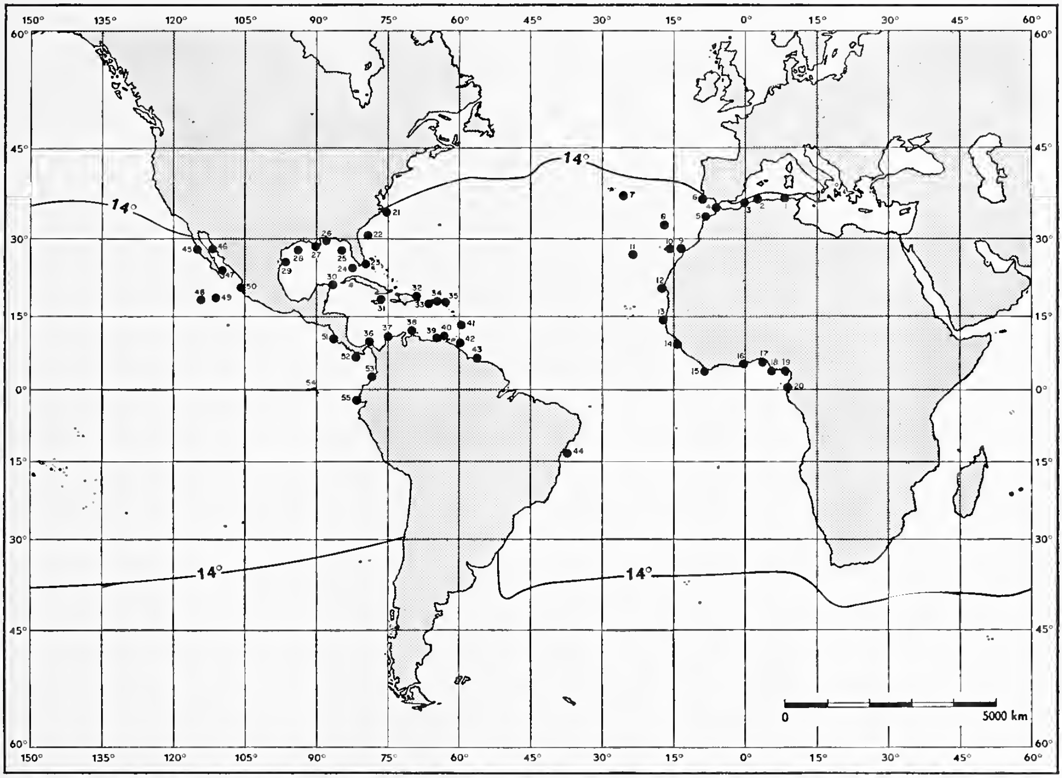
TEXT-FIG. 2. Predominance of lunulitiform Bryozoa in the bottom sediments of the Mississippi Delta area. Sources: (*a*) collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KSEPL, Rijswijk; (*b*) Parker 1956.

There are five characteristics which in combination are responsible for the ability of this type of bryozoan to occupy an exceptionally wide range of environments:

(i) The ability to tolerate a certain amount of clay sedimentation owing to the possession of vibracular setae.

(ii) The ability to exist on almost any kind of bottom as long as the latter consists of small particles.

(iii) The ability to withstand a wide range of temperatures (eurythermal).
(iv) The ability to withstand moderate salinity variations (euryhaline).
(v) An insensitivity to hydrostatic pressure, light penetration, and other factors directly concerned with depth.



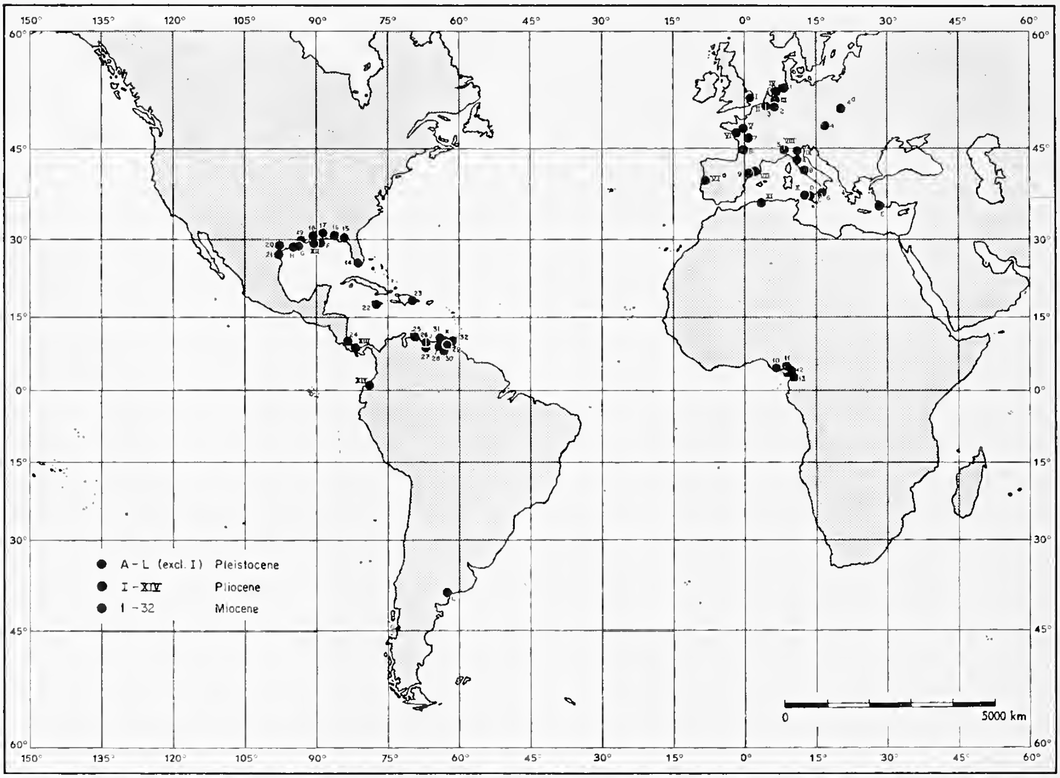
TEXT-FIG. 3. Recent distribution of *Cupuladria canariensis*, showing confinement between 14° C. surface isocrymes (isocrymes after Sverdrup, Johnson and Fleming 1960 and Wust 1960).

This combination of characteristics is the reason for the wide area of distribution of *Cupuladria canariensis*, which includes the tropical and subtropical Atlantic, the eastern Pacific, and the Mediterranean (text-fig. 3), and which has been generally the same throughout the Later Tertiary and Quaternary (text-fig. 4). Yet its distribution is not merely wide on a global scale. Within fairly restricted areas such as the Gulf of Mexico (text-figs. 5, 6) and the Nigerian shelf (text-fig. 7), or in the marine Pliocene of the Low Countries (text-fig. 8) and in the Miocene basin of eastern Venezuela (text-fig. 9), it is also widely distributed on a provincial scale.

2. *Larval stage*

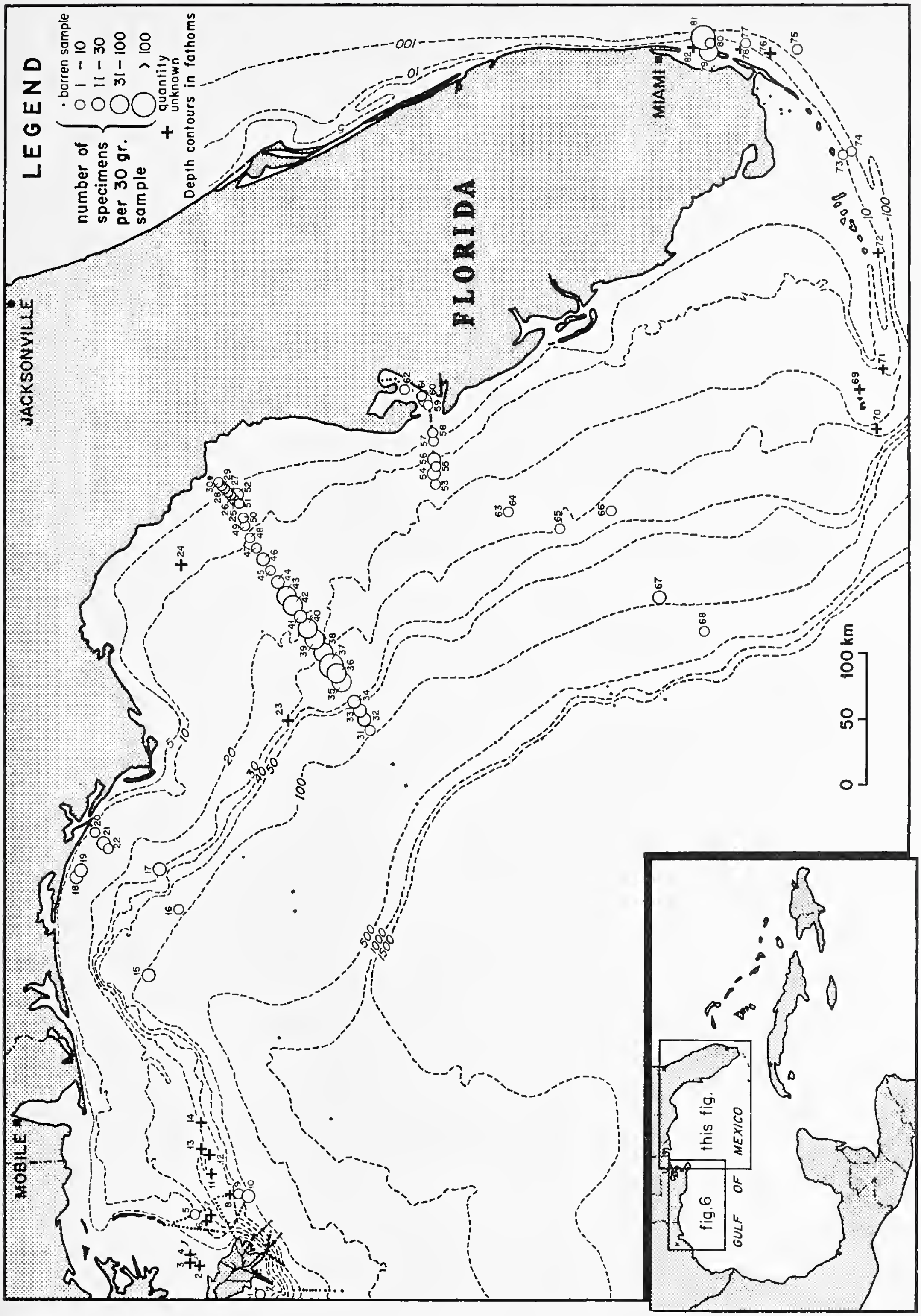
One may wonder whether there is not perhaps a sixth characteristic contributing to this organism's wide distribution: the duration of its larval stage. Like all Bryozoa, the lunulitiforms are sessile, colonial organisms but they possess a free-swimming larval stage. The larvae are able to swim by means of their cilia, and the duration of this free-swimming stage is conceivably one of the factors contributing to the geographical distribution of a benthonic species (Cloud 1959, p. 951).

Unfortunately, the larval stage of *C. canariensis* is still unknown. Within the order Cheilostomata, however, two completely different types of larvae occur. One of these, the so-called *Cyphonautes* larva, which is characterized by the possession of a functional alimentary canal, may spend a period of up to two months in this condition. The large majority of the Cheilostomata, however, have the second type of larva, in which this structure is rudimentary or entirely lacking. According to current views, such larvae are therefore drastically limited in the duration of the free-swimming stage (to no more than 12–24 hours, depending on the supply of yolk), so that they do not become truly pelagic. Nevertheless, there are species of Cheilostomata that have this second type of larva and which, in spite of this, have a very wide, or almost cosmopolitan distribution (e.g. *Microporella ciliata*).



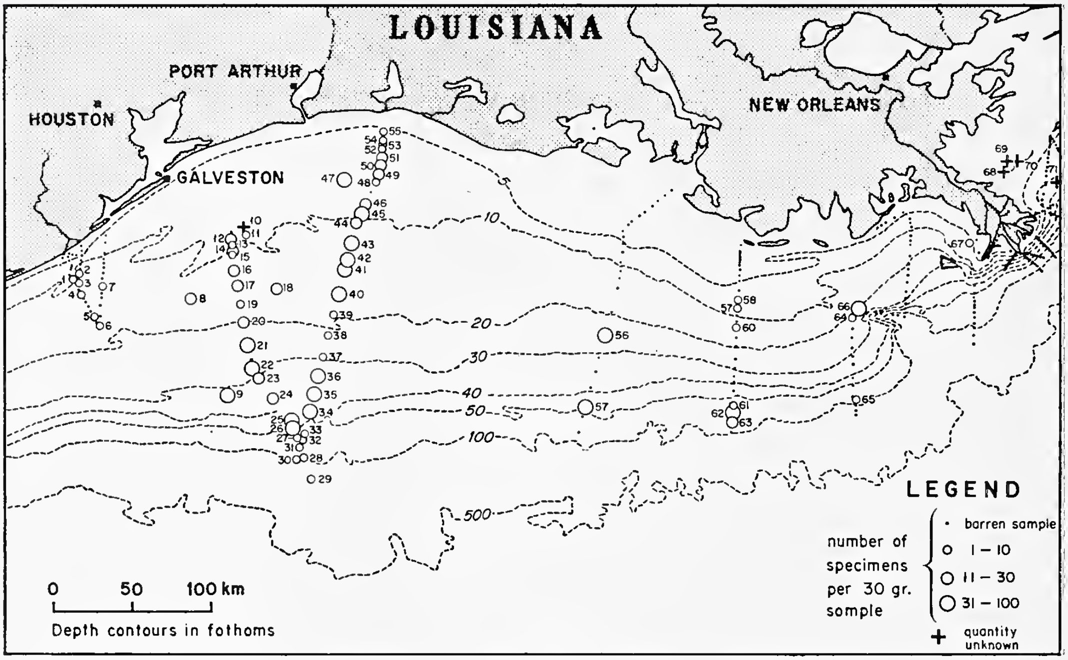
TEXT-FIG. 4. Fossil distribution of *Cupuladria canariensis*.

This is a baffling paradox with which every student of Bryozoa is sooner or later confronted and for which various solutions have been proposed, e.g. continental drift, dispersal via ancient archipelagos or shelf bridges, or trans-oceanic rafting on floating objects by surface currents. Recently Cheetham (1960), in a stimulating paper, discussed



TEXT-FIG. 5. Quantitative distribution of *Cupuladria canariensis* in bottom sediments of the north-eastern Gulf of Mexico.

the merits of each of these three hypotheses in the light of Early Tertiary cheilostome distribution. He clearly favours the third alternative, but did not fully consider the possibility of long-distance dispersal in the larval stage. Yet it is precisely this fourth alternative that most strongly suggests itself in the case of those zoarial form-groups that are most unlikely to become attached to seaweed or other 'rafts'. If the distribution of such species, including *C. canariensis*, is amphi-Atlantic, and if the Wegenerian hypothesis that the surface and bottom configuration of the Miocene Atlantic Ocean were drastically different is rejected, the conclusion is inevitable that their free larval stage must under certain conditions be, and have been, able to last a long time.

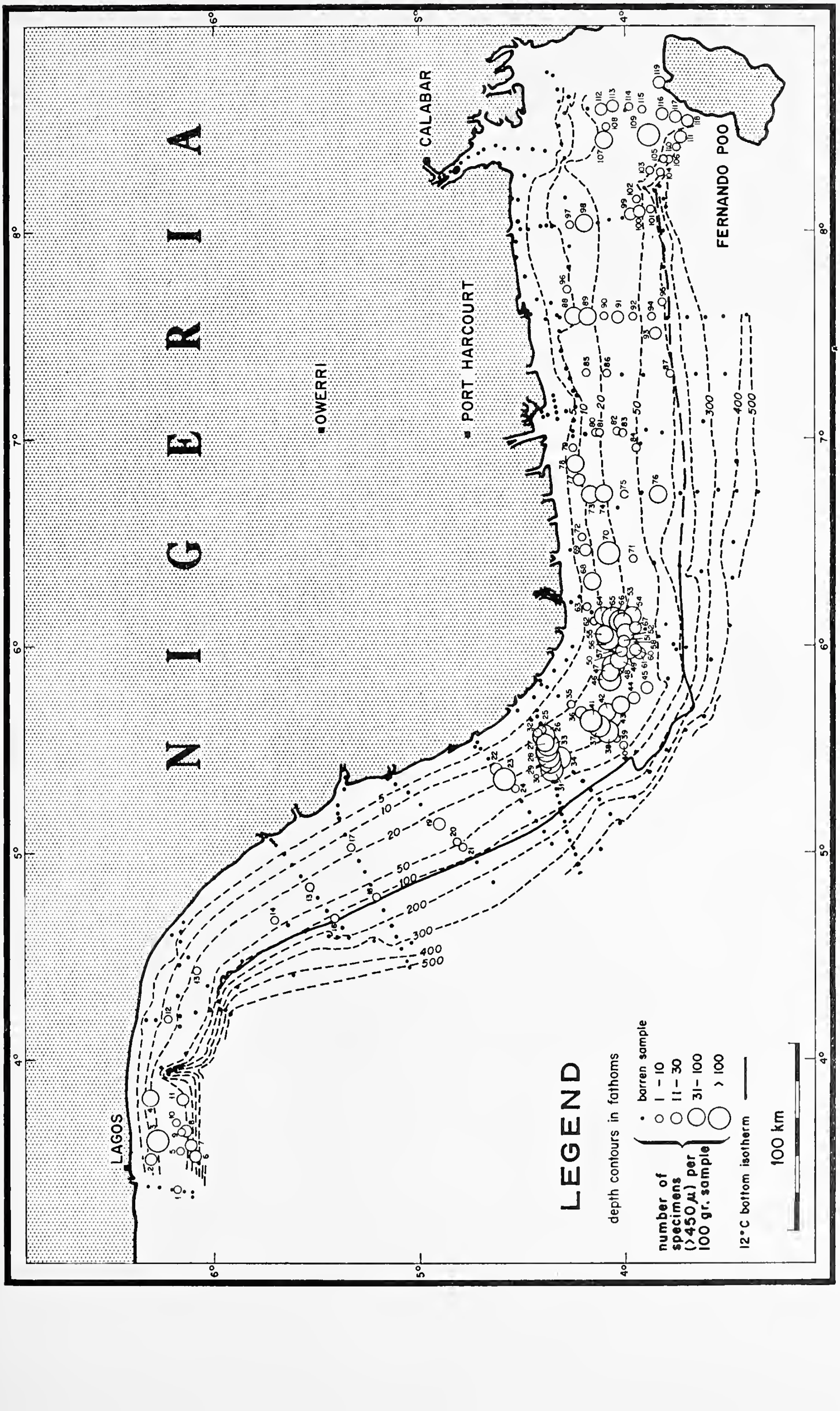


TEXT-FIG. 6. Quantitative distribution of *Cupuladria canariensis* in bottom sediments of the north-western Gulf of Mexico.

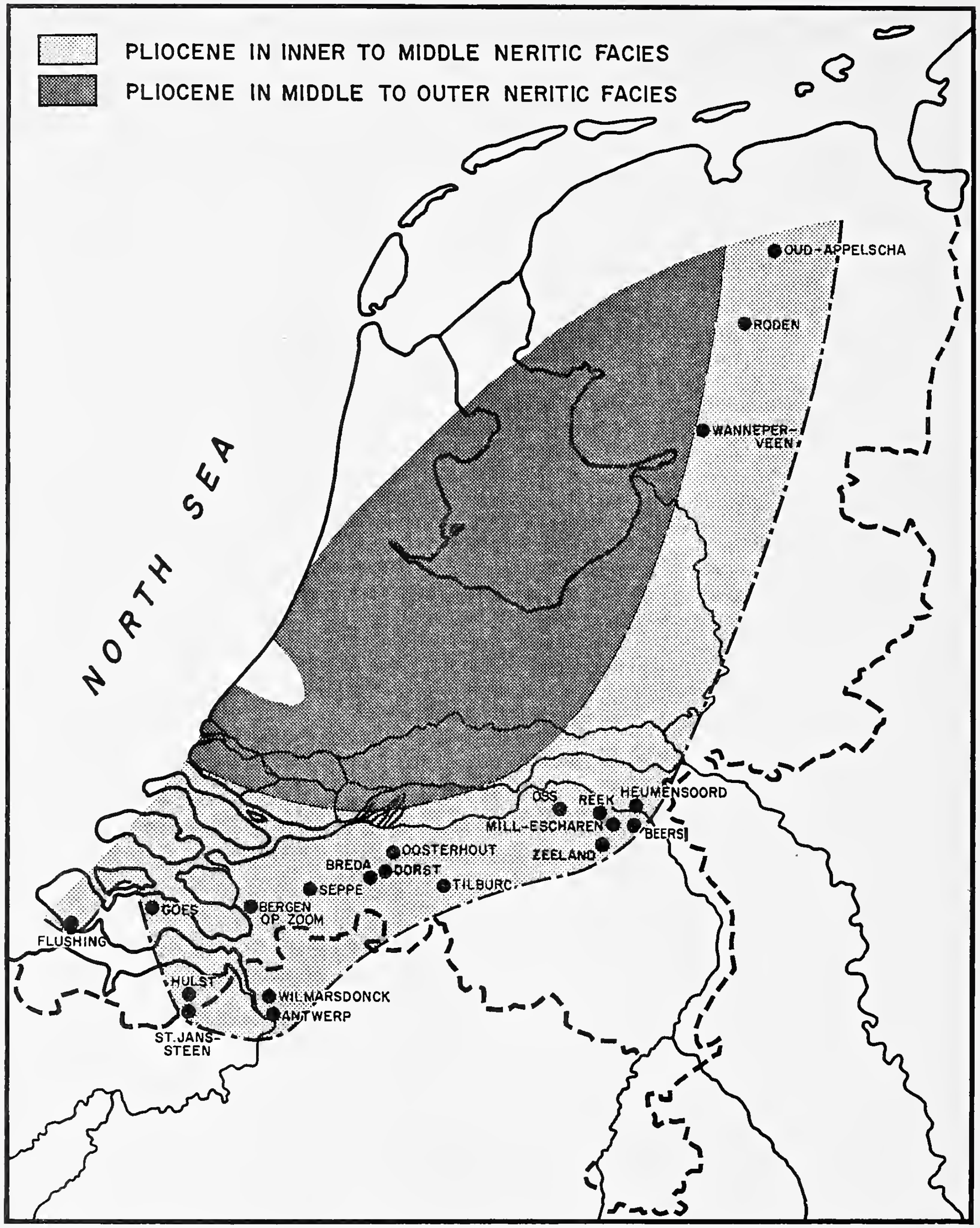
Harmer (1910, p. 520) suggested 'that it does not follow that because we know that a larva may, under favourable conditions, fix itself a few minutes after it becomes free, we should be justified in assuming that that larva would not retain for a long period the power of undergoing a normal metamorphosis should it be drifted away from suitable fixing-grounds'. Silén's (1944, pp. 30, 31) hypothetical concept of external food absorption in larvae which are devoid of an alimentary canal is also interesting in this connexion.

3. *Substratum*

After a brief or protracted period of wandering, the larva settles on a hard substratum. It would seem to make a very careful choice in this matter, as if it knew in advance that the substratum on which it settled would have to be raised above the sea floor and eventually become lodged in the apex of the conical structure which is the adult zoarium.

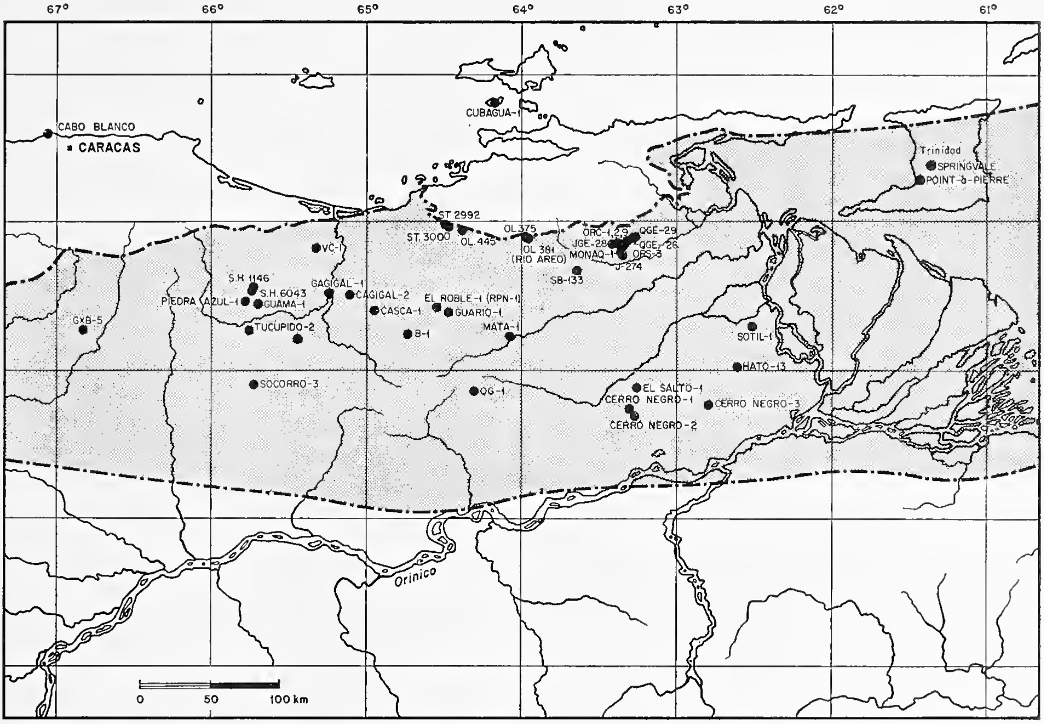


TEXT-FIG. 7. Quantitative distribution of *Cupuladria canariensis* in bottom sediments of the Nigeria shelf (12° C. bottom isotherm from data filed at KSEPL, Rijswijk).



TEXT-FIG. 8. Distribution of *Cupuladria canariensis* in the eastern part of the Pliocene North Sea basin (distribution of marine facies after van Voorthuysen 1956).

Above all, therefore, this substratum must not be too big, and it is for this reason that we usually find coarse quartz grains, glauconite pellets, small shell fragments, broken echinoid spines, even moderately large Foraminiferida such as *Amphistegina gibbosa* and *Globorotalia menardii*, or fragments of other lunulitiform Bryozoa functioning as nuclei for *Cupuladria.* The ideal biotope for the lunulitiform Bryozoa is therefore a small-particle (quartz and/or carbonate sand) bottom. They never occur on a bottom consisting entirely of clay, and are never found encrusting rocks, large pebbles, piles, larger shells, or other such large objects. It is not without reason that lunulitiform colonies are commonly called 'free' (though this is incorrect) as opposed to 'encrusting' forms. So unusual, in fact, is the appearance of an 'encrusting' *C. canariensis* that Silén (1942, p. 14) refers to a juvenile colony on a small stone from Anguilla in the West Indies as only 'possibly belong[ing] to this species'.



TEXT-FIG. 9. Distribution of *Cupuladria canariensis* in the Miocene basin of eastern Venezuela (shaded area).

The question arises whether the larva's power of discrimination is real or apparent. On the one hand one might suppose that the larva settles indiscriminately on all kinds of substrata and that it develops into a colony only on those that are suitable. In that case the selection is the work of external circumstances and not of inherent 'intelligence' in the larvae. On the other hand, selectivity on the part of pelagic larvae has definitely been observed in other groups of marine invertebrates. According to Thorson (1955, p. 390), Wilson (1952 and earlier papers) has shown 'that the larvae of several polychaetes, when ready to metamorphose, will critically examine the bottom substratum to which they are exposed. If they find it attractive, they settle. If they find it less attractive or directly repellent, they will continue their pelagic life for days or even weeks. During such a prolonged larval life these larvae test the substratum at intervals as they are transported by the current directly over the bottom.'

As far as *Cupuladria* is concerned, the following example is pertinent. Plate 25, figs. 2*a*, *b*, show two specimens of *Cupuladria* (not *C. canariensis*, but an allied species, having affinity with *C. pyriformis* Busk) from the subsurface Oficina formation (Miocene) of eastern Venezuela. The larvae of both specimens, and of several others from the same shale samples, originally singled out, and settled upon, specimens of *Planorbulinella trinitatensis* (Nuttall) and persistently neglected several other species of smaller Foraminiferida. This choice seems to have been prompted by the absence of quartz sand; for in a sandy facies with both quartz grains and *Planorbulinella* available in good quantities, such as is found along the southern boundary of the eastern Venezuela basin, settling invariably occurred on the quartz grains only.

4. *Astogeny*

Having attached itself to a suitable substratum, the larva then rapidly undergoes its metamorphosis into the first individual, the 'ancestrula', of the future colony. Further development takes place by a process of budding. It is interesting to follow the juvenile colony through the early stages of this development, especially since Harmer in 1931 (p. 162) was still able to say: 'there is no conclusive evidence with regard to the earliest stages in the discoidal or conical colonies, and a mere count of the number of surrounding zooecia is not enough to settle the matter', and no pertinent observations have been made since then.

By the time the number of zooecia has increased to twenty-six, the zoarium has passed through several separate stages of growth (text-fig. 10):

(*a*) *The single ancestrula.* Despite prolonged searching I have never observed a single ancestrula. Thus it would seem that the process of budding sets in very soon after the metamorphosis is complete.

(*b*) *The three-cell zoarium.* This, the earliest zoarial growth stage observed, invariably consists of three zooecia forming the pattern shown in text-fig. 10*b*. I have recorded several dozens of these three-cell colonies. They display distinct bilateral symmetry. From their mutual relationships it may be inferred that the ancestrula has given rise to two proximo-lateral first-generation zooecia.

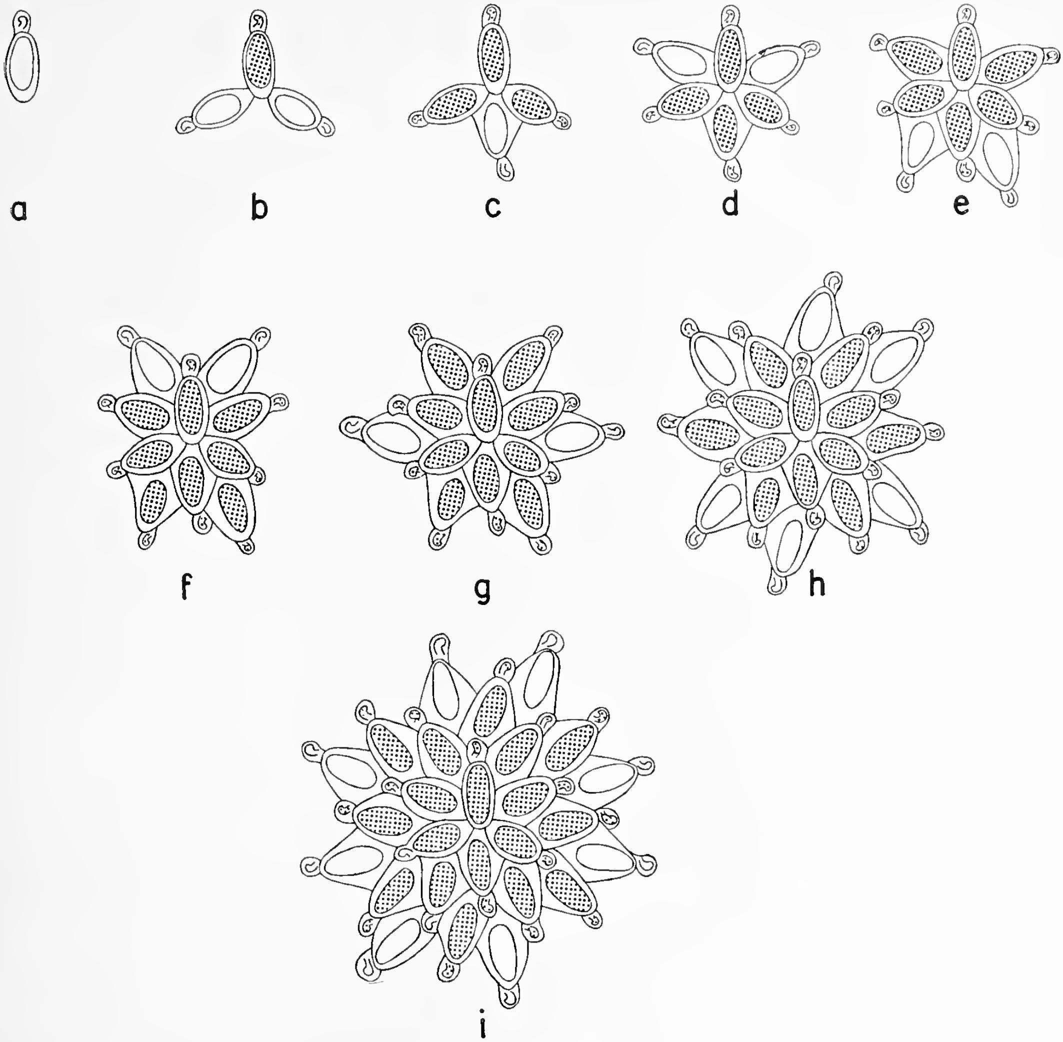
(*c*) *The four-cell zoarium.* A fourth zooecium is added proximally in the plane of symmetry (text-fig. 10*c*). The circle is closed and the colony is ready to start its radial growth.

(*d*) *The six-cell zoarium.* By the addition of two zooecia in the angles between the ancestrula and the two first-generation zooecia, the colony assumes the shape of a six-pointed star (text-fig. 10*d*). The plane of symmetry through the ancestrula is still clearly apparent.

(*e*) *The eight-cell zoarium.* Two new proximo-lateral zooecia appear (text-fig. 10*e*).

(*f*) *The ten-cell zoarium.* Two more zooecia are added distally, one on either side of the ancestrula (text-fig. 10*f*; Pl. 25, fig. 3).

(*g*) *The twelve-cell zoarium.* Two new lateral zooecia appear (text-fig. 10*g*). At this stage the colony is still markedly stelliform; the bilateral symmetry can be seen without



TEXT-FIG. 10. Early stages of zoarial growth in *Cupuladria canariensis* (based on a series of Recent specimens from Nigeria).

difficulty. No zooecia are yet in proximal contact with the vibracula of preceding cells, but this situation changes in the next stage. This earliest, central, part of the colony is therefore relatively less densely covered by vibracular setae than later, peripheral, additions. It is therefore probably no coincidence that preferably (although not exclusively) these central zooecia sometimes regenerate into large vibracula of the type first described by Hastings (1930, p. 714; see also Silén 1942, text-fig. 8), whereas in other lunulitiform species they tend to develop a calcareous closure.

(*h*) *The eighteen-cell zoarium.* Six new zooecia have appeared at the periphery (text-fig. 10*h*), probably via two intermediate stages. The first slight departure from the original plan of symmetry is now apparent, since the proximal and the distal indentations at the periphery in the median line are too large to be filled by a single zooecium and yet too small to accommodate a pair of zooecia. The filling of the gap therefore takes place asymmetrically.

(*i*) *The twenty-six-cell zoarium.* A further departure from bilateral symmetry takes place (text-fig. 10*i*). By now the colony has attained a diameter of 1·9 mm. and is well on its way to adulthood.

Two points emerge from these observations:

i. Waters's (1926, p. 426 and text-fig.) concept of a double ancestrula in *Cupuladria*, the two being turned in opposite directions, and each giving off three distal zooecia, is untenable. Although Waters specifically mentioned *C. canariensis* in connexion with his observations, it is clear from the occurrence of partially closed zooecia and from the provenance of his material (Princess Charlotte Bay, Queensland, Australia), that he was actually dealing with *C. guineensis* (Busk).
ii. Silén's (1942) theory of spiral growth is no longer valid in the case of the genus *Cupuladria*.

I should like to emphasize that the astogeny outlined above only applies to ideal cases, and that deviations from this scheme are common and may appear at an early stage (Pl. 25, fig. 4). Usually such deviations are closely bound up with irregular configurations of the small-particle substratum, or with an excentric position of the ancestrula on the substratum. The eight-cell zoarium figured in Plate 25, fig. 4 deviates in that it has developed a zooecium (on the left) in a position that would normally not be occupied until the twelve-cell stage, while the usual place for the eighth zooecium (on the right-hand side) remains vacant. Occupation of the latter position, which projects beyond the edge of the particle, would have involved building a stronger dorsal wall than the extremely thin one required in the position now preferred, where it is supported by the substratum. Obviously less building energy is required for growth on the substratum than for expansion beyond its edges.

5. *Mode of life of lunulitiform colonies*

The mode of life of the adult colony and, closely connected with that, its orientation with respect to the sea bottom, are controversial matters, and widely differing suggestions

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EXPLANATION OF PLATE 25

Fig. 1. *Cupuladria canariensis* (Busk). Adult colony. *a*, View of the convex surface; *b*, View of the concave surface. G.S. 173, Pliocene of Proefboring 41, Reek, Netherlands, 15·00–20·00 m. × 10. (After Lagaaij 1952.)

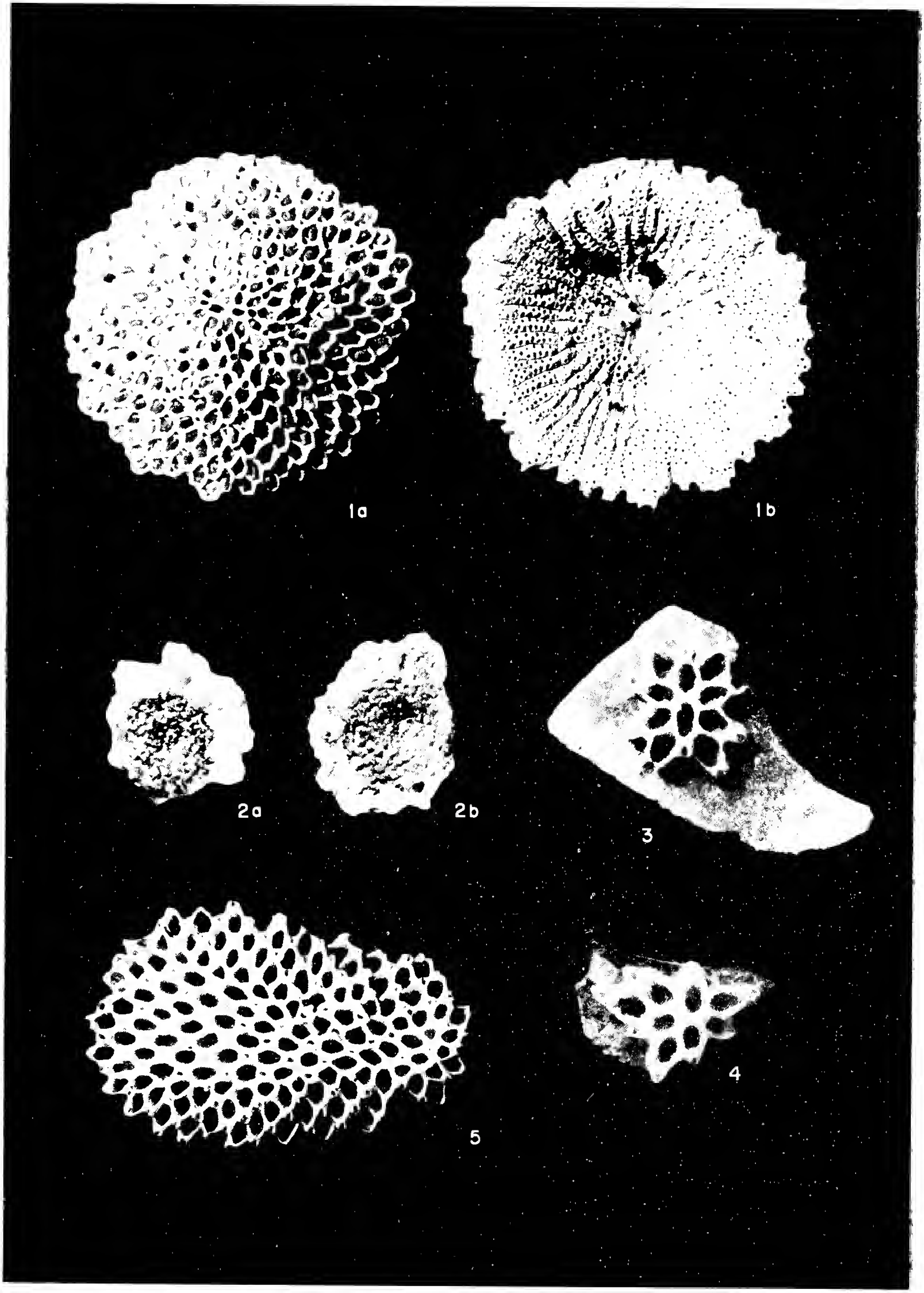
Fig. 2. *Cupuladria sp*. Concave side of juvenile colonies, showing larval predilection for the foraminiferid *Planorbulinella trinitatensis* (Nuttall). Lower Miocene (Oficina formation) of Texas Petroleum Company well Mata-1, Estado Anzoategui, Venezuela; *a*, 8,160–8,170 ft.; *b*, 8,300–8,320 ft. × 20.

Fig. 3. *Cupuladria canariensis* (Busk). Juvenile colony (ten-cell stage) in normal symmetrical development. Recent, Mees Cremer 1959 Sta. 98, Nigeria, 14 fms. × 20.

Fig. 4. *Cupuladria canariensis* (Busk). Juvenile colony (eight-cell stage), showing early departure from bilateral symmetry. Recent, Mees Cremer 1959 Sta. 376, Nigeria, 11 fms. × 20.

Fig. 5. *Cupuladria canariensis* (Busk). Regenerated colony, showing sector of original large flattened conical colony with peripheral outgrowth in radial direction. Recent, Râs-el-Amouch, Mediterranean, 45 fms. × 10. (After Dartevelle 1935.)

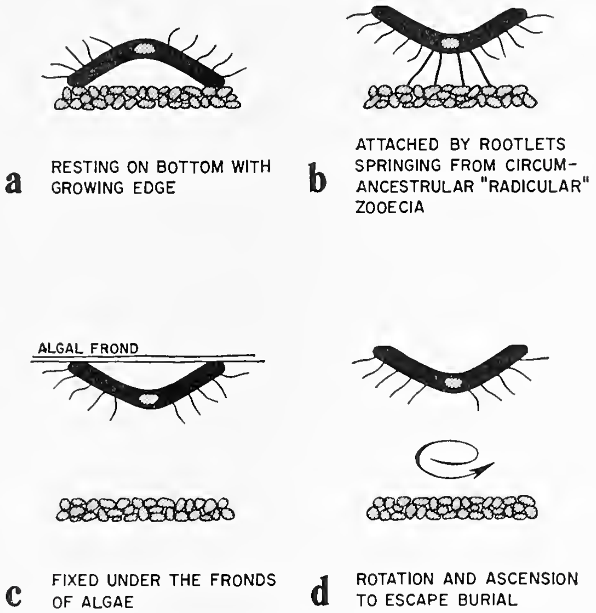
PLATE 25



LAGAAIJ, *Cupuladria canariensis* (Busk)

have been made, none of which, according to Harmer (1931), have been supported by pertinent observations. Four tenable hypotheses have been put forward (text-fig. 11).

As Harmer (1931, pp. 150–1) has shown, the conventional view that the colony rests on its flat 'base' (text-fig. 11*a*) was first disputed by Maplestone (1910, p. 3), who expressed the opinion that 'the conical forms in their living state have the base uppermost'. Although at this time Maplestone was only referring to the conical colonies of the genus *Conescharellina*, later authors have extended his contention to include other genera whose colonies are conical. Moreover, Maplestone was not certain whether the conical colonies (of *Conescharellina*) hang point downwards from some foreign object, or whether they retain this position on the bottom by means of anchoring filaments.



a RESTING ON BOTTOM WITH GROWING EDGE

b ATTACHED BY ROOTLETS SPRINGING FROM CIRCUM-ANCESTRULAR "RADICULAR" ZOOECIA

c FIXED UNDER THE FRONDS OF ALGAE

d ROTATION AND ASCENSION TO ESCAPE BURIAL

TEXT-FIG. 11. Various hypotheses regarding the mode of life of lunulitiform colonies.

Canu (1915, p. 21) adopted and elaborated on both hypotheses. His early reasoning is not generally known (cf. Harmer 1931, p. 151), but later re-statements of his views have profoundly influenced later workers. It is therefore necessary to quote Canu in full on this point: 'Les espèces flottantes comme les *Lunulites* ont le zoarium conique, la pointe en bas. Tantôt il est maintenu sous les Algues [text-fig. 11*c*], tantôt il est attaché à de petits objects par des radicelles [text-fig. 11*b*]. Celles-ci proviennent de *Zoécies radiculaires* (= Zoécies avortées de d'Orbigny) disposées autour de l'ancestrule. . . . Les zoécies radiculaires sont d'abord des zoécies hydrostatiques. La larve, en effet, se fixe sur un grain de sable; l'ancestrule qui se développe émet immédiatement des zoécies radiculaires qui l'enveloppent et permettent à l'animal de commencer son ascension sous une Algue loin du sable dangereux à son développement. . . . Soit attachés par des radicelles, soit retenus sous les Algues, les *Lunulites*, par leur forme turbinée, sont de position très instable: ils chavirent au moindre filet d'eau. L'animal maintient sa position normale à l'aide de longs filaments articulés appelés *vibraculaires*. Ce sont donc des appareils de *stabilisation* un peu analogues au balancier des danseurs de corde.'

The same views, essentially unchanged, are repeated by Faura and Canu (1916), Canu and Bassler (1920, pp. 238 ff.), and Canu and Lecointre (1927, p. 35). Waters (1921) was quick to oppose these views, which have in fact largely been confined to the French school. I refer in particular to his statement (1921, p. 401): '. . . though sometimes the growth is on a much larger stone, as in some specimens of *Cupuladria canariensis* from Petit Tahou, Liberia. It would seem impossible for a colony so heavily weighted to float, nor can we think it could float in a reversed position.' In 1926, however, Waters (1926, p. 425) wrote more cautiously: 'What we have called the upper surface is, in the ancestrular and early stages, at the top, even though there may be a subsequent reversal. . . .'

Finally, Canu and Bassler, realizing how difficult it was to see how a conical colony with its apex downward could 'maintain its equilibrium even in the water, in a position absolutely contrary to the ordinary laws of statics', invoked rotation as a means of conserving its position (text-fig. 11*d*), first for *Conescharellina* (1929, p. 482) and later for *Lunulites* (1931, p. 9): 'Ils vivent donc l'apex en bas au voisinage du fond sableux. Ils s'en dégagent par rotation et ascension pour éviter l'enlissement', and (1931, p. 19) 'Les *Lunulites* sont de petites coupes en perpétuelle rotation pour se dégager du sable et changer de place'.

Dartevelle also attributed a planktonic mode of life to *Lunulites* (1933, p. 69) and to *Cupuladria* (1943, p. 108): 'Leur mode de vie est semblable à celui, bien connu, des *Lunulites*, c'est-à-dire que la colonie flotte entre deux eaux, les zoécies tournées vers le dessous, la face concave vers le haut. . . .' The designation 'face supérieure' for the concave side and 'face inférieure' for the convex, celluliferous side of lunulitiform colonies still persists in recent French literature (Vigneaux 1949; Buge 1957).

Dartevelle (1933, p. 57), moreover, provided a novel explanation of the role played by the small foreign particle at the downward directed apex of the cone: 'La présence de ce substratum constitué par un morceau de coquille, une nummulite, un grain de sable, contribue à maintenir l'équilibre de la colonie et à l'empêcher d'être chavirée par les vagues'; it served, in other words, as ballast, and as such would profoundly influence the shape of the colony. According to Dartevelle (loc. cit., p. 70) the lighter the substratum, the flatter the zoarial cone, and, conversely, the heavier the particle, the higher and more dome-shaped the colony would have to become in order to keep the ballast as low as possible: '. . . ce qui gouverne donc la colonie, c'est la souci d'éviter le renversement et de maintenir le meilleur équilibre possible au sein du fluide.'

Harmer's presidential address to the Linnean Society of London in 1931 made it abundantly clear that Canu and Bassler's reasoning was based entirely on inference and not on direct observation. He added (1931, p. 151): 'I have failed to find any evidence that is really conclusive with regard to the question at issue. Except for Whitelegge's very brief account, I am acquainted with no observations made on living specimens, and in my judgment the matter should for the present be regarded as undecided.' Harmer's statement is still as valid today as it was thirty years ago. Here is clearly a case where laboratory experiment could be of value. It should not be too difficult to collect some living specimens of *Cupuladria* and keep them under observation in a sea-water aquarium.

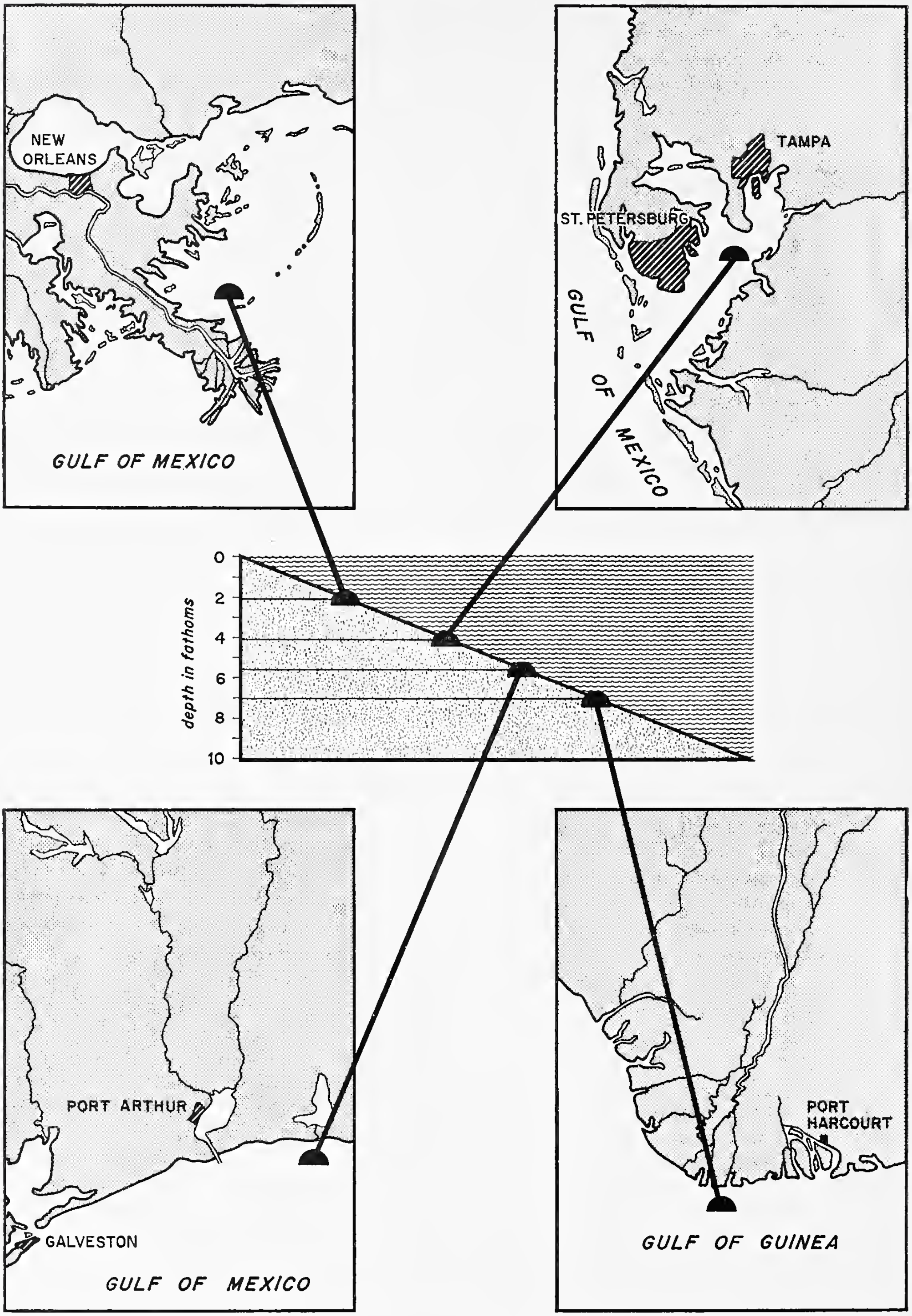
Another example of reasoning by inference, the emphasis in which is laid on the orientation of the ancestrula and of later zooecia with respect to the small-particle substratum, occurs in Silén (1947, pp. 5–6, 8, 15 and text-fig. 8). He concluded (correctly, in my opinion) that the colonies of *Cupuladria* rest freely on the sea bottom with the apex pointing upwards. Silén thereby reverted to the conventional view (see, however, Silén 1942, p. 13).

Two further arguments, both arising from the ecology of *C. canariensis*, support this conventional view, or rather conflict with the hypothesis of a planktonic mode of life postulated by Canu and his school. In the first place, if *C. canariensis* were indeed a planktonic organism, one would expect to find its skeletons distributed over different kinds of bottom and a very wide range of depths. However, its remains are found only on the small-particle bottoms to which it is confined in life by the special requirements of the larvae. Secondly, there is a direct relationship between the maximum depths at which *C. canariensis* has been observed in the various marine areas, and the temperature of the bottom water in those areas (see p. 189). Both these observations suggest that *C. canariensis* is a truly benthonic organism.

6. *Minimum depth*

Cupuladria canariensis occurs mainly on small-particle bottoms and is hence a full member of that rather select level-bottom community described by Petersen (cf. Thorson 1955). A type of small-particle bottom from which it is excluded, however, is one where the sand grains have a tendency to shift under the influence of water movements. The minimum depth at which the larvae of *C. canariensis* and other lunulitiform species, such as *Discoporella umbellata* (Defrance), can settle and develop into adult colonies therefore depends on the intensity of the water turbulence over the bottom, i.e. on the depth of the wave base and on the strength of the bottom currents. Since both these factors are determined by the degree of exposure of the shelf and by oceanographical factors, the minimum depth mentioned above varies from place to place (text-fig. 12).

Cupuladria colonies are therefore unlikely to be washed up on the shore, and there are no records that this has ever occurred, although 'one dead and worn' colony of *D. umbellata* has been found on the shore at Balboa, Panama Canal Zone (Hastings 1930, p. 718). As Stach (1936, p. 63) has put it, 'their free mode of life prohibits their existence in the littoral zone where wave action is strongly felt'. The lunulitiform Bryozoa thus seem to be confined to the *stable* small-particle bottoms below wave base. This conclusion is quite contrary to that of Dartevelle (1933, 1935), who inferred an agitated, current-infested biotope from the common occurrence of broken and regenerated lunulitiform colonies in the Eocene of Belgium. Yet there is no reason why fragmentation should be due solely to mechanical breakage in a highly turbulent environment; the destructive activity of other marine organisms in deeper, quieter water might just as easily be responsible (Ginsburg 1957, p. 83). It is known that holothurians (sea cucumbers) include the lunulitiform Bryozoa in their diet. Silén (1942, p. 13) records eight colonies of *C. canariensis* taken from the stomach of the sea-urchin *Meoma ventricosa*, and I have observed the occurrence of fragments and of several entire colonies of *C. canariensis* among the coarser debris in the stomach of a holothurian in the north-western Gulf of Mexico (Cavalier 1956 Station 227, at a depth of 37·5 fathoms). Dartevelle (1935) gives Recent examples of regenerated zoaria of *C. canariensis* (Pl. 25, fig. 5) taken from the Mediterranean locality Râs-el-Amouch at a depth of 45 fathoms, which is well below that at



TEXT-FIG 12. Minimum depths at which *Cupuladria canariensis* has been found in various areas. Notice shallowest occurrences in sheltered, deepest occurrences in exposed biotopes.

which sand transport could occur, let alone transport and breakage of far larger objects such as bryozoan colonies.

7. *Maximum depth* (*minimum temperature*)

The maximum depth of occurrence of *Cupuladria canariensis* is determined by the temperature of the bottom water. The maximum depths at which *C. canariensis* has been found in three marine provinces is as follows:

	Fathoms	
NW Gulf of Mexico	138	Gulf of Mexico
NE Gulf of Mexico	117	
Straits of Florida	122	
Jamaica	150	W and S confines of Sargasso Sea
E of Jacksonville, Florida	440	
N of St. Thomas, Virgin Islands	300–470	
Sénégal	118	Equatorial West Africa
Nigeria	120	

Since the recent geographical distribution of *C. canariensis* is roughly limited both in the Atlantic and in the eastern Pacific by the 14° C. surface isocrymes (text-fig. 3) (and it must be remembered that the bottom water at shelf depths will be a few degrees colder) it may reasonably be assumed that this approaches the minimum temperature at which *C. canariensis* can survive. The maximum depths of occurrence and the corresponding bottom-water temperatures of approximately 12° C. observed in various marine areas seem to confirm this assumption (text-fig. 13).

The deep occurrences along the western and southern confines of the Sargasso Sea are of particular interest. In all three cases the data refer to living specimens. The hydrography of this region (text-fig. 14) is almost unique in featuring a lenticular body of water of uniform temperature (18° C.) and salinity (approx. 36·5‰) down to a depth of 300–400 metres (Worthington 1959). Below this depth a gradual decrease of temperature takes place down to the main thermocline. Clearly it is only the peculiar temperature conditions prevailing in this area that permit the occurrence of *C. canariensis* at such unusually great depths.

8. *Maximum temperature*

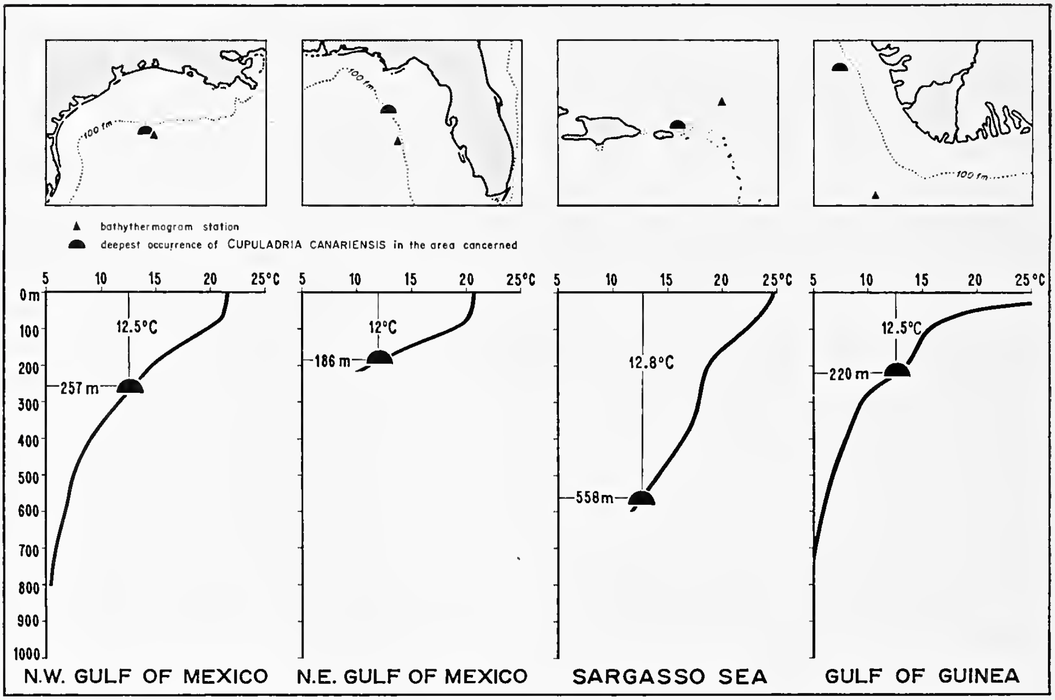
It is at the shallow end of its depth range that one has to seek the maximum temperature which the species will tolerate. This will be in shallow coastal waters, where the effects of atmospheric heat exchange are most strongly felt.

It will be readily understood, however, that the determination of this parameter will be far less precise than that of the minimum temperature, since the absolute maxima vary from year to year. Thus, *C. canariensis* may conceivably form part of the bottom fauna of a shallow bay during the normal summer of a particular year, but the following year an abnormally hot summer may bring its occupation of that bay to a sudden termination. The best approximation will therefore be found by taking the average maximum temperature in the warmest month, recorded over a number of years.

Areas where such shallow occurrences of *C. canariensis* coincide with the necessary amount of regularly recorded temperature data are Tampa Bay, Florida, and Breton

Sound, Louisiana, where *C. canariensis* occurs at minimum depths of 4 and 2 fathoms respectively (text-fig. 12).

According to the records published by the U.S. Coast and Geodetic Survey (1955), the average maximum temperature in the warmest month (July) for the years 1947–54 at St. Petersburg (Tampa Bay) was 31° C. Since this figure is based on surface measurements, the corresponding value for the shallow bottom water is bound to be somewhat less extreme.

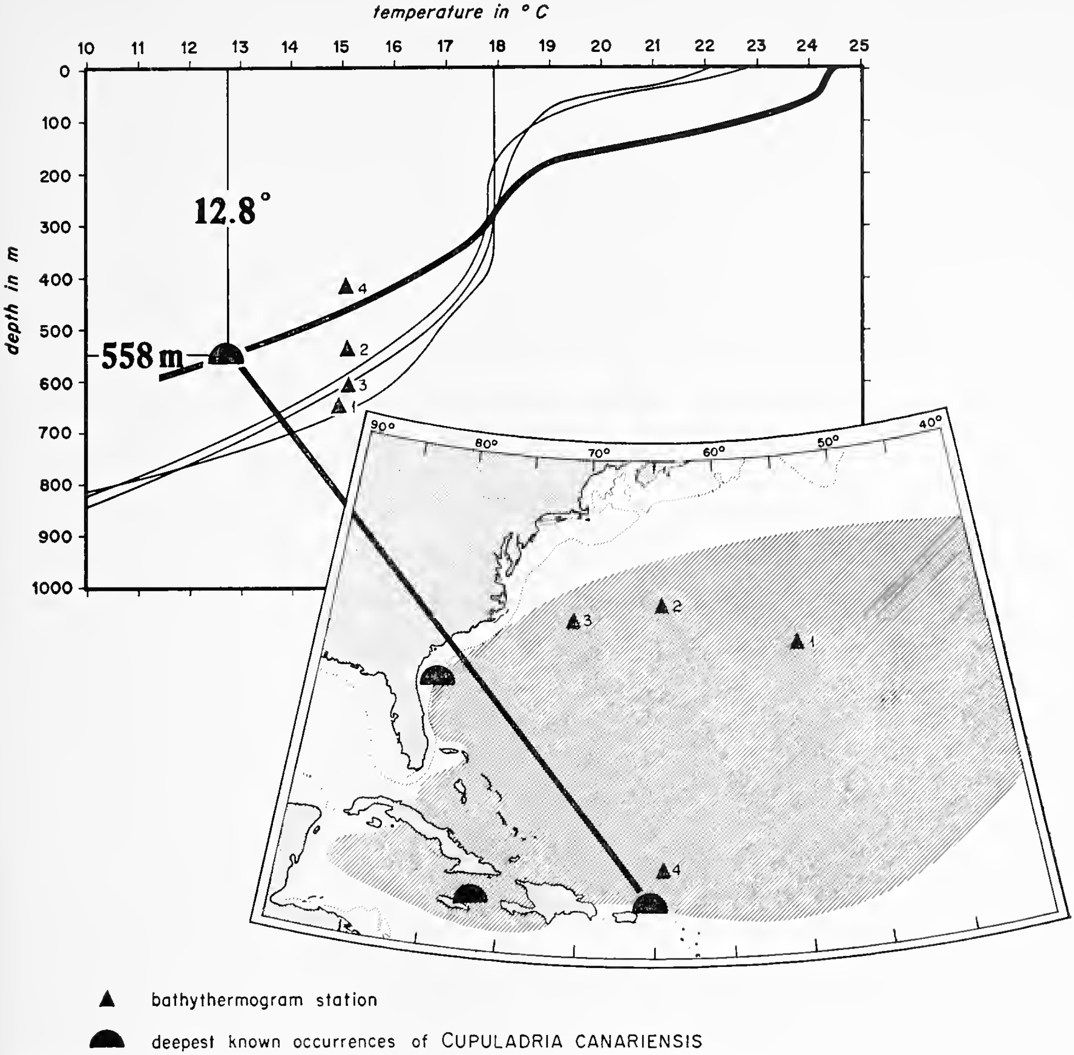


TEXT-FIG. 13. Relation between deepest occurrences of *Cupuladria canariensis* and bottom-water temperature.

In Breton Sound, where *C. canariensis* is known to occur in 2–3 fathoms depth in the lee of Breton Island (Parker 1956), surface-water temperatures during the summer reach an average absolute maximum of about 31–32° C. (Scruton 1956, p. 2937). According to Scruton (loc. cit.), 'vertical stratification is stronger in the summer than at other times, so that bottom temperatures in Breton Sound proper probably seldom reach 32°'.

9. *Maximum salinity*

The clue to the maximum salinity that *C. canariensis* will tolerate lies in the Mediterranean. From its occurrences elsewhere, on the Florida shelf and in the West Indies, one may infer that it still thrives in salinities of approximately 36·5‰. In the Mediterranean, on the other hand, salinities at the surface are everywhere higher than 37‰ (and increase with depth), except where the surface current carries water of Atlantic origin and an original salinity of about 36·25‰ through the Strait of Gibraltar along the



TEXT-FIG. 14. Deepest known occurrences of *Cupuladria canariensis* are found where deeply descending warm water mass of Sargasso Sea intersects with sea bottom. Shading in ocean area indicates the occurrence of water of 18° C. at 300 m. depth (map and graphs after Worthington 1959).

north coast of Africa as far east as Tunisia (Sverdrup, Johnson and Fleming 1960, pp. 643, 646).

The extent of this Atlantic water in the Mediterranean coincides exactly with the Recent Mediterranean distribution of *C. canariensis* (text-fig. 15*d*). The easternmost Mediterranean record of the species is from Cape Rosa, Algeria, 40 km. east of Bône. *C. canariensis*, like all other lunulitiform species, is conspicuously absent among the bryozoan fauna of the eastern Mediterranean, for example in Tunisia (Canu and Bassler 1930), Egypt (O'Donoghue and De Watteville 1939), and Syria (Gautier 1957). Since this entire area lies south of the 14° C. surface isocryme (text-fig. 15*d*) and since bottom temperatures in the Mediterranean, even at great depths, nowhere drop below about 13° C. (Nielsen 1912; Furnestin 1960), it is clear that here the limiting factor is not the water temperature but the >37‰ salinity.

This conclusion has the interesting implication that the Miocene, Pliocene, and early Pleistocene Mediterranean (text-fig. 15*a–c*) was somewhat less saline than it is at present. The difference was most marked in the Sicilian, when *C. canariensis* (and by inference salinities <37‰) extended into the Levantine basin (Rhodes), where present-day salinities constantly remain about 39‰ (Wüst 1960, figs. 2, 5; pl. 7).

10. *Minimum salinity*

Data on the minimum salinity which *C. canariensis* will tolerate must be inferred from its occurrence in the shallow coastal waters, where precipitation and run-off are most effective in lowering the salinity.

Reduced salinities have been observed in the following shallow areas where *C. canariensis* is known to occur:

a. Breton Sound, leeward of Breton Island, Louisiana; depth 2–3 fathoms (Parker 1956); bottom salinity 28·5‰, measured in the autumn of 1951 during flood tide; the ebb tide produces still lower salinities (Scruton 1956, p. 2927).

b. South of Calcasieu Pass, Louisiana; depth 5·5 fathoms (text-fig. 12). Salinities measured at neighbouring stations (Bandy 1954, fig. 8, Sta. 106, Sta. 108) are of the order of 28–28·5‰. To all appearances these figures are based on surface measurements, but in this shallow turbulent part of the Gulf of Mexico vertical stratification is bound to be slight and the corresponding bottom salinities will therefore probably be not very different.

C. canariensis is absent in the Gulf of Mexico off Grand Isle, Louisiana, presumably because here salinities at 10 feet below the surface may drop periodically to as low as 21‰ in June and July, and 14‰ in February (Geyer 1950, p. 103). The lowest monthly average in this area is 22·6‰ (March 1949).

11. *Recognition*

Another, more subjective, factor which affects the boundaries of the known distribution of *C. canariensis* is the ease with which the species can be recognized. Large undamaged colonies may easily attain a diameter of 1·5 cm., and their aesthetically satisfying shape makes them conspicuous among the other members of the macro-fauna. Unfortunately, *C. canariensis* is rather fragile and during rough handling in nature or in

EXPLANATION OF PLATE 26

Fragments of fossil *Cupuladria canariensis* (Busk) from various localities.

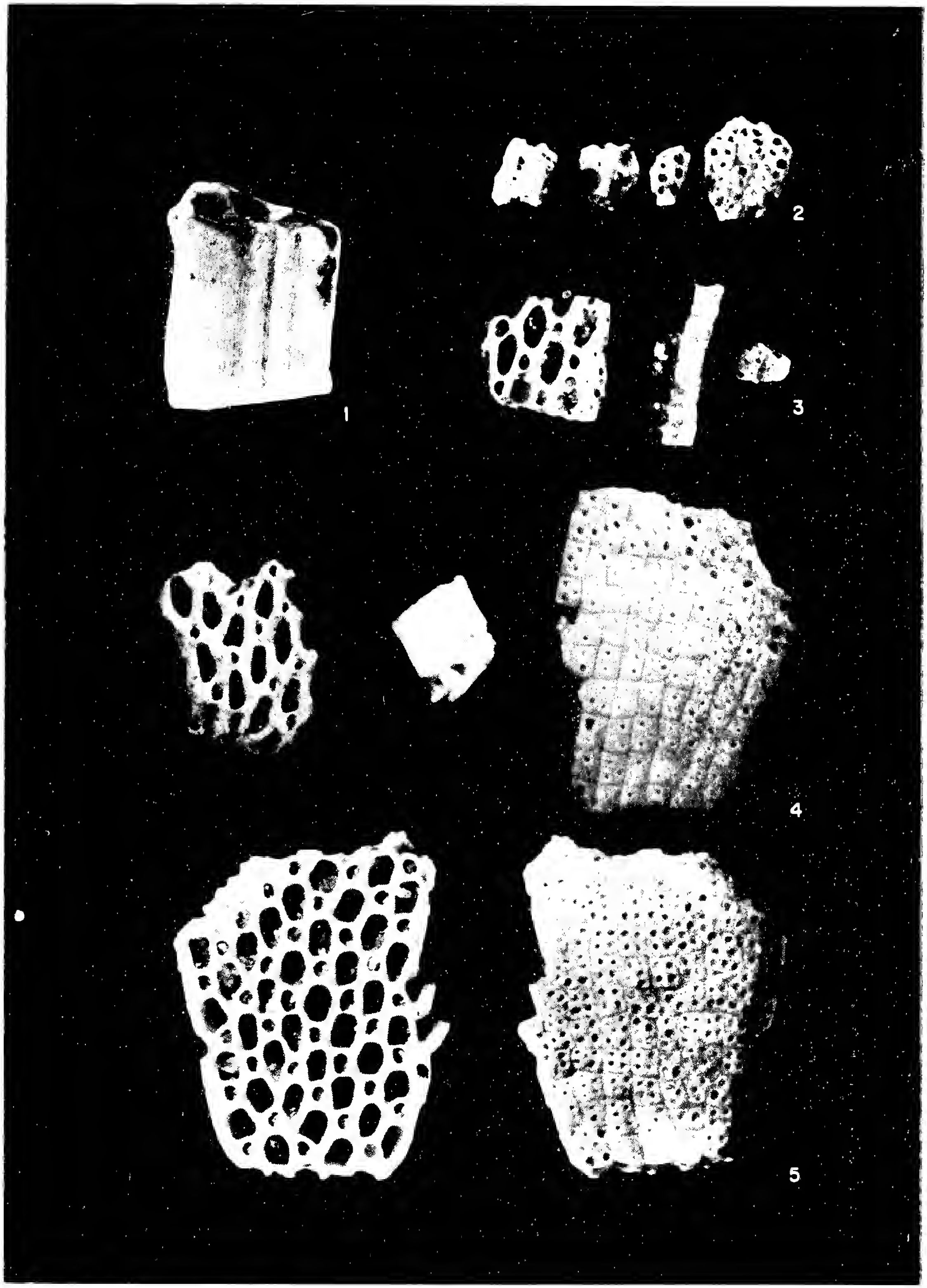
Fig. 1. Detail of the broken surface, showing the characteristic fine, parallel, vertical striation. Lower Miocene (Carapita formation) of Mene Grande Oil Company well SB-133, Estado Monagas, Venezuela, 3,825–3,840 ft. ×40.

Fig. 2. Middle Miocene (Reinbek/Dingdener Stufe) of Twistringen, SSW of Bremen, Germany. ×20.

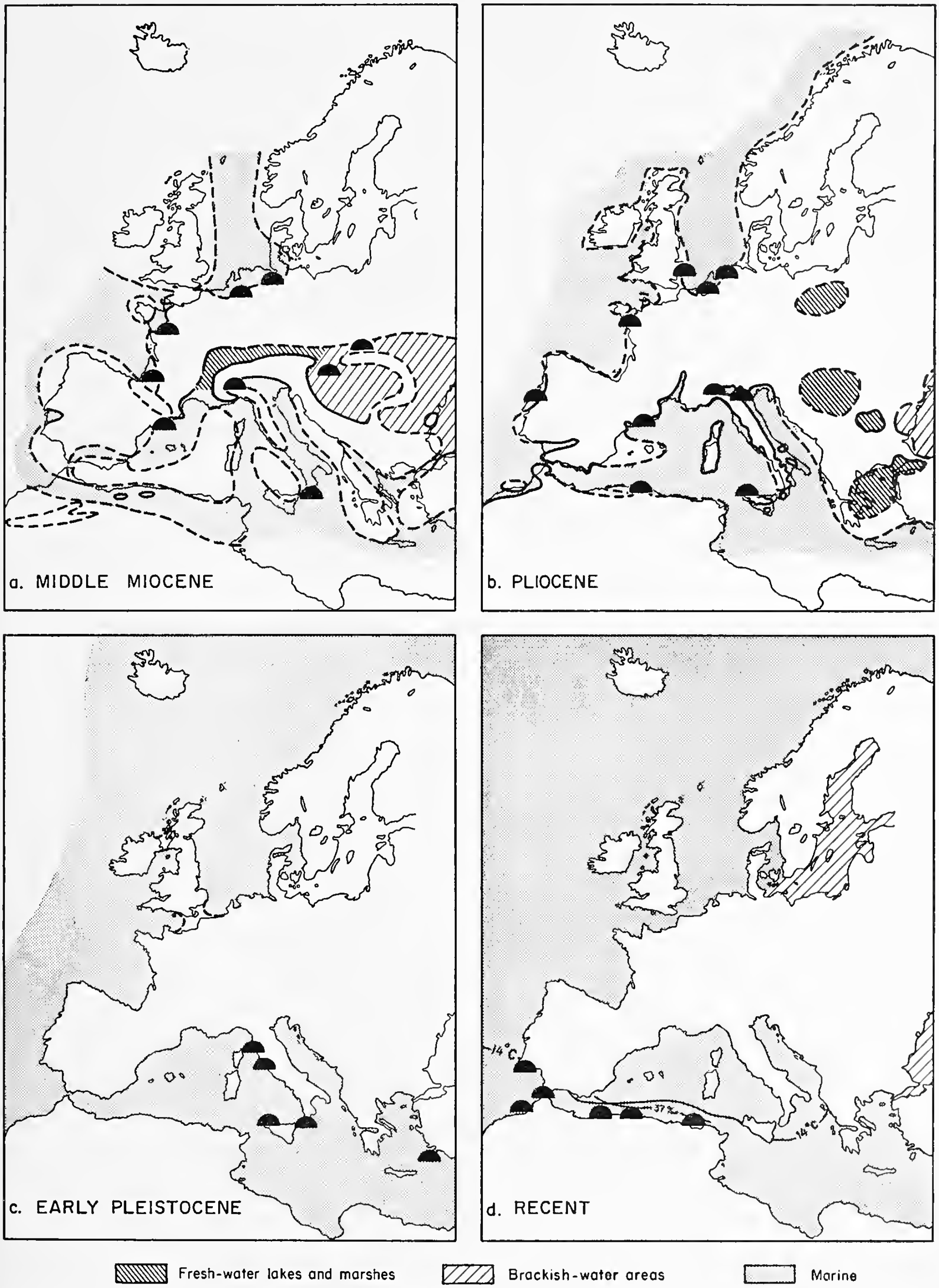
Fig. 3. Lower Miocene of Shell-BP Petroleum Development Company well Ituk-1, Nigeria, 3,320–3,780 ft. ×20.

Fig. 4. Lower Miocene (Chickasawhay formation) of Limestone Creek, Wayne County, Mississippi, U.S.A. ×20.

Fig. 5. Upper Miocene (Cubagua formation) of Socony Mobil Oil Company well Cubagua-1, Cubagua, Venezuela, 218 ft. ×20.



LAGAAIJ, *Cupuladria canariensis* (Busk)



TEXT-FIG. 15. Fossil and recent distribution of *Cupuladria canariensis* in Europe and North Africa (Middle Miocene and Pliocene base maps after Wills 1951).

the laboratory is apt to break, almost always along the radial lines on the concave surface. The smallest recognizable fragments take the form of tiny rectangular prisms (Pl. 26, fig. 1), whose dorsal ends correspond to the rectangular compartments visible on the concave surface (text-fig. 16). These compartments are perforated, and so, consequently, are the dorsal ends of the individual prisms. The vertical faces are flat and show fine, parallel, vertical striation (Pl. 26, fig. 1). Thus even very small fragments can be recognized (Pl. 26, figs. 2–5), and for this reason *C. canariensis* may be regarded as a component of both the macro- and the microfauna.

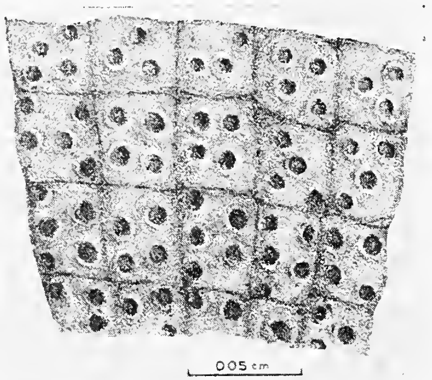
APPLICATIONS

1. *Shifts in sea-water temperature since the Miocene*

Palaeobotany holds the key to the interpretation of Tertiary climates in north-west Europe. It is known that the north-west European climate gradually cooled from tropical (Eocene), through subtropical (Miocene and early Pliocene) to warm temperate (late Pliocene) conditions, after which even more marked and rapid cooling to subarctic conditions introduced the Pleistocene.

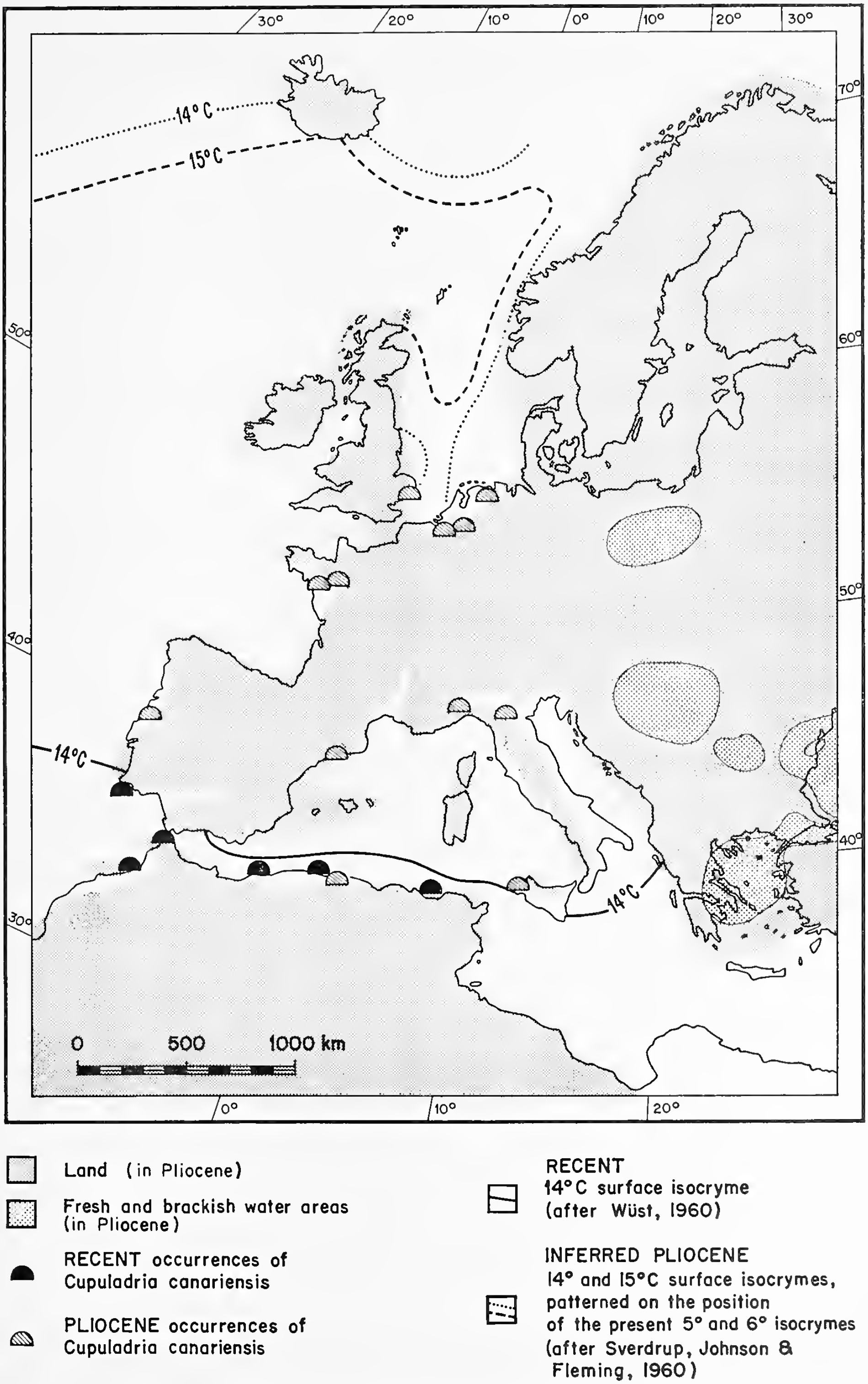
At present both summer and winter air temperatures in north-west Europe are strongly influenced by the temperature of the water in the eastern Atlantic and the North Sea. It is not unreasonable to assume, therefore, that the subtropical and oceanic climates prevailing in north-west Europe during the Miocene and Pliocene periods bore a direct relationship to considerably higher sea-water temperatures in these latitudes.

Such an hypothesis is strongly supported by a comparison of the present-day occurrences of *C. canariensis* with those during Miocene and Pliocene times (text-fig. 17). As has been already mentioned (p. 189), the northern boundary of its present area of distribution in the northern hemisphere coincides with the 14° C. surface isocryme (text-fig. 3). Consequently, Miocene and Pliocene winter surface-water temperatures in the North Sea basin must have been at least 14° C. February surface-water temperatures in this area now average between 5° and 6° C. (*fide* Sverdrup, Johnson, and Fleming 1960, chart II). In the Miocene and even in the Pliocene the water in the southern part of the North Sea must therefore have been at least 8° or 9° C. warmer than it is at present. This conclusion accords well with the figures derived by the Polish palaeobotanist Szafer for the amount by which Pliocene air temperatures in Europe north of the Alps exceeded those now prevailing: January +11°, July +9°, yearly average +9° C. (*fide* Godwin 1956, p. 296).



TEXT-FIG. 16. *Cupuladria canariensis*. Detail of the concave surface (after Busk 1859*a*).

This conclusion is particularly interesting, however, because both in the Middle Miocene (text-fig. 15*a*) and in the Pliocene (text-fig. 15*b*) the land area at present occupied by the British Isles was connected to the continent of Europe. *C. canariensis* (and the entire warm-water fauna associated with it) must therefore have migrated to the North Sea area of those times by a path lying to the north of Scotland. In view of the present-



TEXT-FIG. 17. Shift of sea water temperatures in the Eastern Atlantic and Mediterranean since the Pliocene (Pliocene base map after Wills 1951).

day confinement of the species by the 14° C. surface isocryme, this isotherm must have lain to the north of Scotland in both the Miocene and Pliocene periods and probably resembled in shape the present-day 5° C. isocryme, which under the influence of the Gulf Stream curves around Scotland and penetrates into the North Sea (text-fig. 17). The stranding of a loggerhead turtle, *Caretta caretta* (Linn.), on the Norwegian coast in December 1951 (Willgohs 1953) and the capture of a flying fish, *Cypsilurus heterurus*, in Oslo Fiord in 1848 and in 1937 (Bruun 1938) are indications that even today the Gulf Stream occasionally carries tropical and subtropical marine organisms along this ancient migration route.

During the Pleistocene *C. canariensis* did not have a chance to migrate once more into the North Sea region (text-fig. 15*c*). This sea-water temperature did not rise sufficiently to allow this, even in the interglacial periods, when the climate was somewhat warmer than it is now. From the composition of the molluscan fauna of the Dutch Eemian (the last, late-Pleistocene, interglacial), van Straaten (1956, pp. 224, 225) concluded that the temperature of the sea-water at that time could only have been about 4° C. higher than that of the present North Sea, and might have been no more than 2° or 3° C. higher. It is interesting to note that Spaink (1958, p. 31) concluded that the southern element of this Eemian fauna must also have reached the Dutch coastal area by the route north of Scotland.

2. *The Oligocene–Miocene boundary in the Gulf Coast and Caribbean areas*

During the past decade, several attempts have been made to correlate the Tertiary formations on either side of the Atlantic. The problem of defining the Oligocene–Miocene boundary in the Caribbean area has been closely connected with these attempts and has still not definitely been solved.

A detailed discussion of this problem lies outside the scope of this paper. Those who are interested are referred to the paper by Eames (1953), through whose activity the problem became critical, to the ensuing discussion between Stainforth (1954) and Eames (1954), to the later restatement of the problem by Stainforth (1960*a*; 1960*b*, with extensive bibliography) and to the renewed discussion between Eames *et al.* (1960*a*; 1960*b*) and Stainforth (1960*c*). The arguments put forward by Eames *et al.* have now been stated in full detail in their book on Mid-Tertiary stratigraphical correlation (1962).

Briefly, the Oligocene–Miocene boundary in the Caribbean area has undergone a progressive lowering during the past decade. All concerned agree that this move was justified; there is no agreement, however, about the level in the Caribbean sequence of planktonic foraminiferal zones where this boundary should finally be drawn. Stainforth (1960*b*, p. 226) is undecided 'whether the whole *Globigerina ciperoensis* zone and part of the *Globigerina dissimilis* zone or only part of the *Globigerina ciperoensis* zone represents the whole Oligocene'. Eames (1955, p. 86), on the other hand, implied complete absence of marine Oligocene sediments in Trinidad by his statement that 'probably all the Cipero formation is of Lower Miocene age'. Eames *et al.* (1960*a*, 1960*b*, 1962) have since corroborated this view and have even extended it so that not only the Cipero but also the underlying San Fernando formation is included. If their opinion is correct, a major hiatus occurs in the Trinidad sequence between the Eocene (Navet and equivalents) and the Miocene (San Fernando, Cipero and equivalents) marine deposits.

It is important to discover whether, and to what extent, the lunulitiform Bryozoa, and in particular *Cupuladria canariensis*, throw light on the matter.

Lunulitiform Bryozoa, which range from the Upper Cretaceous to Recent, have long been of interest to palaeontologists. *Lunulites*, the eponymous genus, was introduced by Lamarck in 1816 and since then a considerable number of fossil species have been recorded from Tertiary and Quaternary strata both in Europe and in North America. The accompanying range charts (text-fig. 18) show the time-stratigraphic distribution of these species in the two hemispheres.

Comparison of these two charts reveals several interesting facts:

a. There are no Eocene and Oligocene species of *Lunulites* common to both hemispheres. It is possible that a thorough systematic revision of the group might alter this situation. But whether it would or not, it is significant that there is a similar lack of common species among the contemporaneous larger Foraminiferida of both hemispheres.

b. The disappearance of the genus *Lunulites* clearly did not take place contemporaneously in both hemispheres. In North America it probably no longer occurs *in situ* in the post-Vicksburg formations, whereas in Europe it persists into the Pliocene. It should be borne in mind, however, that several living species of *Lunulites* have been recorded from Australian seas.

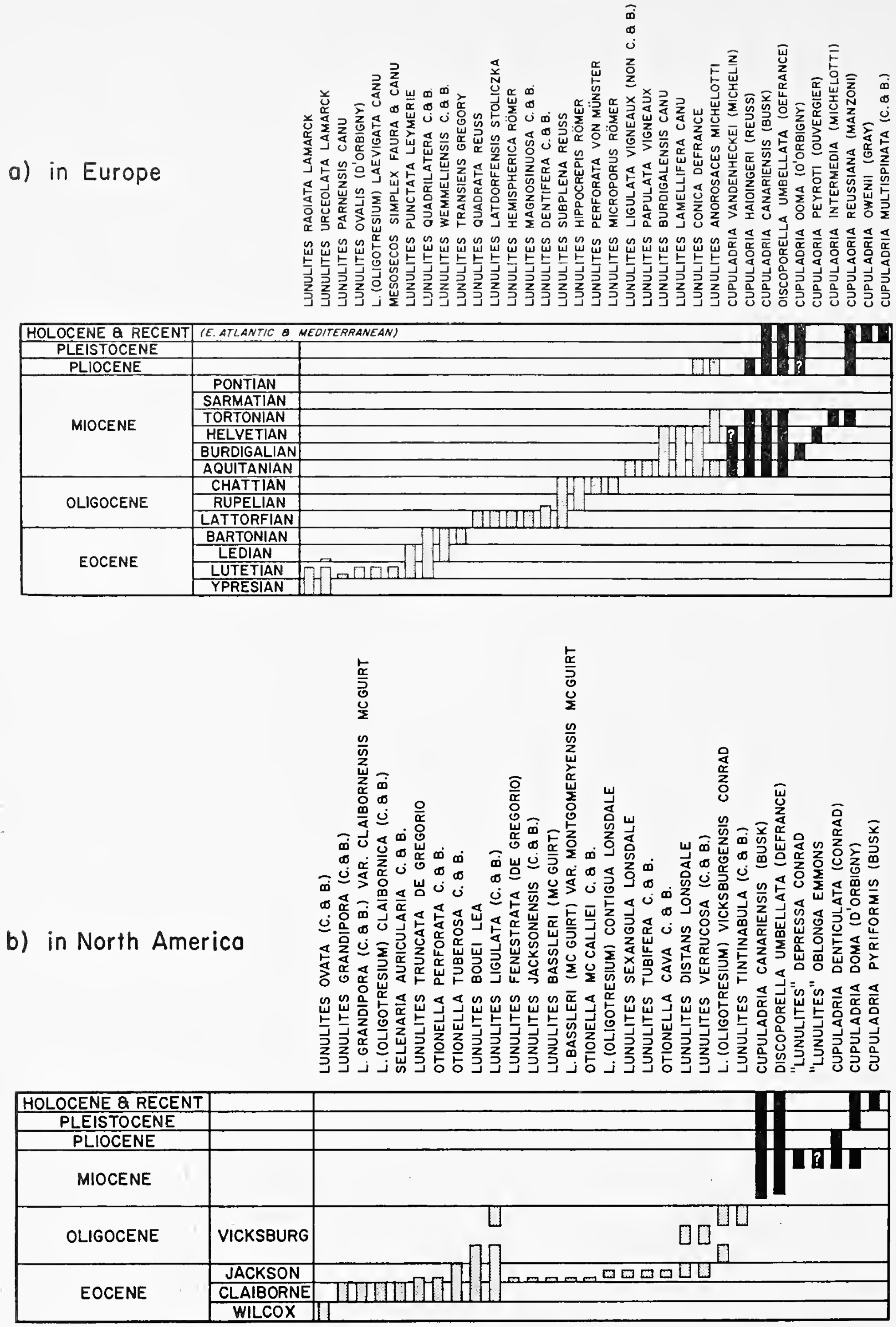
c. Several names common to both charts, of which one is *C. canariensis*, first appear in the Miocene of Europe and in the post-Vicksburg formations of the southern U.S.A. This new appearance of modern lunulitiform genera and species, which, as has been seen in the case of *C. canariensis*, possess exceptional environmental tolerance leading to wide and rapid dispersal, may well serve as a criterion for establishing the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf sediments on both sides of the Atlantic.

By this criterion the Vicksburg group correlates with some part of the European Oligocene (absolute hegemony of *Lunulites*), whereas such post-Vicksburg formations as the Chickasawhay of Mississippi and Alabama and the subsurface Upper Frio of Texas cannot be considered older than Aquitanian (since both contain *C. canariensis*). Although most North American stratigraphers, e.g. Cooke *et al.* (1943), MacNeil (1944), and oil companies do not share this view, it is clear that it was held as long ago as 1934 by others, such as Howe (1934) and McGuirt (1941).

Some of the evidence underlying text-fig. 18*b* is brought out in greater detail on the correlation chart of the Gulf Coast Oligocene and Miocene formations (text-fig. 19), which shows the known occurrences of the genus *Lunulites* and *C. canariensis* according to the published records and my own observations. Conspicuous on this chart is the wide distribution of these lunulitiform Bryozoa throughout the marine Tertiary sediments, even though information on several southern states is still incomplete.

It is interesting to study the Caribbean area in the light of what is known about Europe and the Gulf Coast, where modern lunulitiform species and genera first appear in the Aquitanian and post-Vicksburg formations respectively.

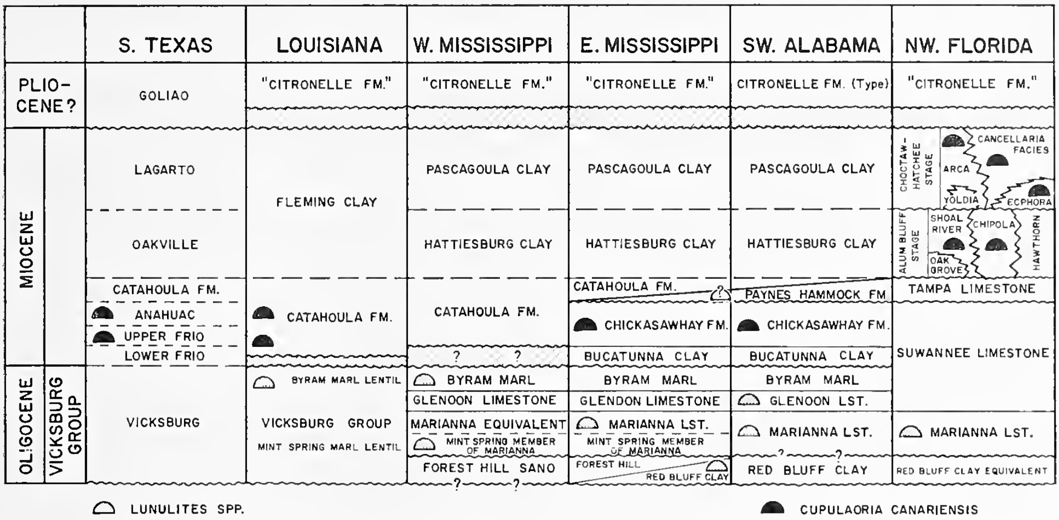
It has already been shown (text-fig. 9) that lunulitiform Bryozoa, in this case *C. canariensis*, are widely distributed throughout the 'Oligocene–Miocene' basin of eastern Venezuela. The vertical distribution of *C. canariensis* in various parts of the basin is



TEXT-FIG. 18. Time-stratigraphic distribution of Tertiary and Quaternary lunulitiform species.

shown in text-fig. 20. As far as the problem of the Oligocene–Miocene boundary is concerned, the oldest occurrences are the most relevant.

In northern Guarico the earliest occurrence is to be found in the upper part of the 'Oligocene' Roblecito formation of well GXB-5. In the Rio Areo of northern Monagas *C. canariensis* occurs at the base of the Areo Shale, directly above its contact with the Los Jabillos formation (text-fig. 21). The Areo Shale is generally considered to be the lateral equivalent of the lower part of the Naricual formation of the Barcelona area, which itself was considered to be of Lower Oligocene, and possibly even Upper Eocene, age (Renz *et al.* 1958, p. 576). This age assessment can no longer be maintained. Since they contain *C. canariensis*, both the upper part of the Roblecito and the Areo Shale (and for that matter the Naricual) cannot be of more than Aquitanian (or post-Vicksburg) age. The correctness of this interpretation is reinforced by the fact that *C. canariensis* is accompanied in both cases by *Discoporella umbellata*, another 'modern' lunulitiform species.

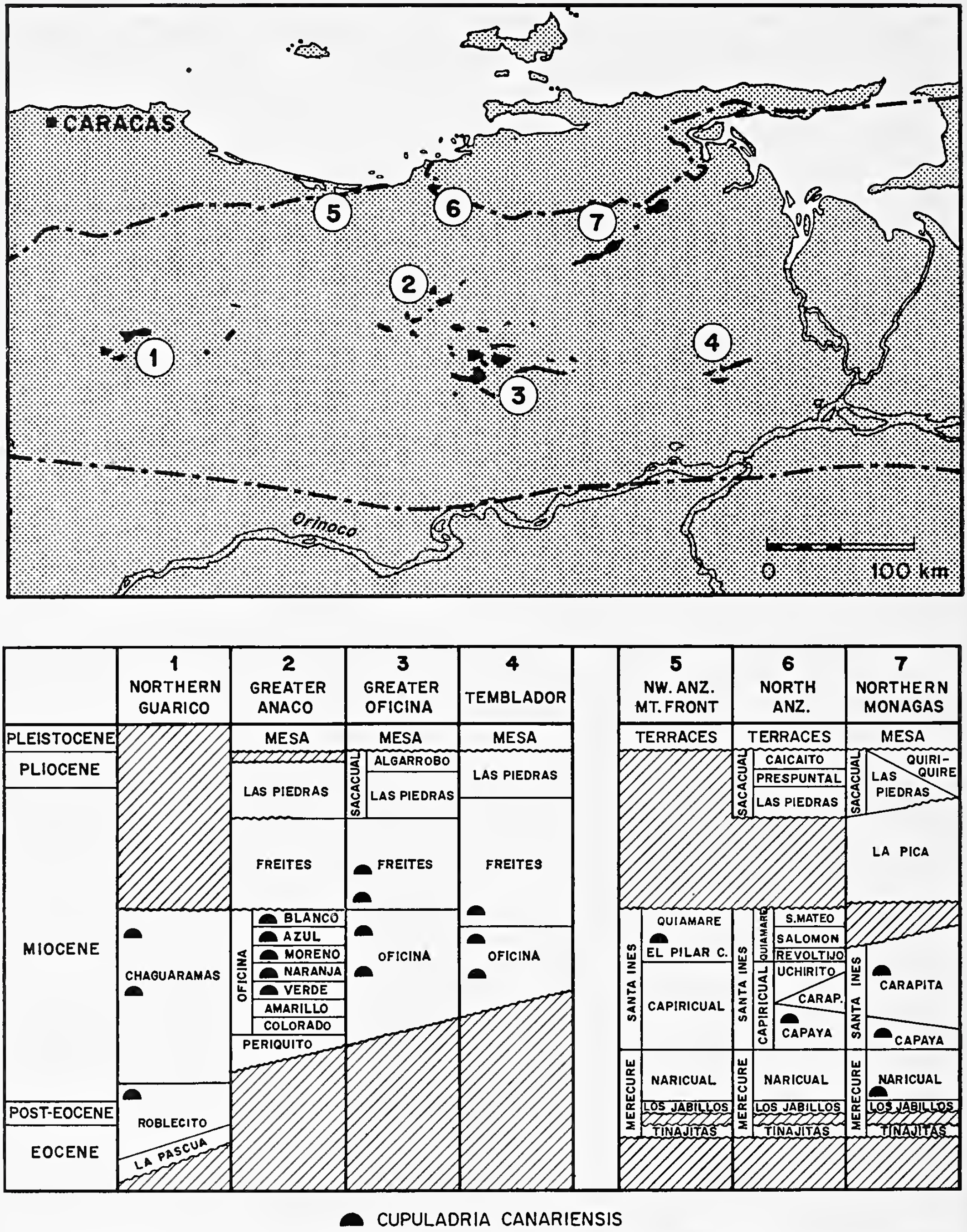


TEXT-FIG. 19. Occurrences of *Lunulites spp.* and of *Cupuladria canariensis* throughout the Oligocene and Miocene formations of the Gulf Coast.

It is interesting to compare these occurrences with the Caribbean planktonic foraminiferal zonation locally established by the Creole Petroleum Corporation.

According to Creole, the Areo Shale represents the upper two-thirds of the *Globorotalia opima opima* zone and the whole of the *Globigerina ciperoensis ciperoensis* zone. The oldest known occurrences of *C. canariensis* at the base of the Areo Shale thus fall in the lower half of the *G. opima opima* zone.

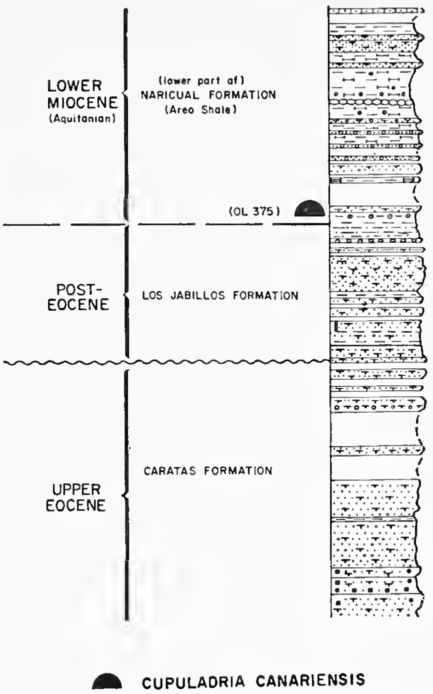
The underlying Los Jabillos formation has hitherto generally been considered as Upper Eocene (*fide* Feo-Codecido 1956, p. 331; Renz *et al.* 1958, p. 576). This age assessment, too, needs revision in the light of newly acquired evidence. According to Creole, the Los Jabillos formation must be post-Eocene, since its stratigraphical position falls slightly above the base of the *G. opima opima* zone.



TEXT-FIG. 20. Occurrences of *Cupuladria canariensis* throughout the Tertiary formations in the eastern Venezuela basin (map and correlation chart after Renz *et al.* 1958, modified).

Again according to Creole, the Los Jabillos formation is in turn underlain by shales with *Globigerina ampliapertura* (not present in the Rio Areo outcrop section shown in text-fig. 21). It is this *G. ampliapertura* zone that on planktonic foraminiferal evidence correlates with the Vicksburg (Bolli 1957, p. 107). Thus one might expect to find a different suite of lunulitiform Bryozoa at this level. Unfortunately, there are no earlier records of this group of Bryozoa from Eastern Venezuela than those mentioned above. All one can say is that the Vicksburg, as it is defined in the southern U.S.A., is characterized, from the point of view of the lunulitiform bryozoan sequences, by the absolute hegemony of the genus *Lunulites* (text-fig. 18*b*) and therefore correlates with some part of the European Oligocene (text-fig. 18*a*). This would imply that the *G. ampliapertura* zone is also Oligocene.

In summary it appears that Eames *et al.* were substantially correct in lowering the Oligocene–Miocene boundary in the Caribbean area farther than any of their critics were prepared to go. From the presence of modern lunulitiform Bryozoa it must be concluded that at least the upper two-thirds of the *Globorotalia opima opima* zone is Miocene (Aquitanian or younger). On the other hand, Eames *et al.* (1960*a*, p. 448; 1962, pp. 48, 49, fig. 5) would definitely seem to be going too far in wishing to submit the Vicksburg to the same rejuvenation course. The Vicksburg lunulitiform bryozoan assemblages have a distinct Oligocene character, and if the planktonic foraminiferal correlation is correct, this would imply that the *Globigerina ampliapertura* zone of the Caribbean sequence of planktonic foraminiferal zones is also Oligocene. The Oligocene–Miocene boundary in the Caribbean, subject of so much discussion in the past decade, would thus be pinpointed in eastern Venezuela somewhere between the top of the *Globigerina ampliapertura* zone and the top of the lower one-third of the *Globorotalia opima opima* zone.



TEXT-FIG. 21. Earliest occurrence of *Cupuladria canariensis* in the Rio Areo outcrop section, northern Monagas, eastern Venezuela (from unpublished Company reports); 1:5,000.

The earliest occurrences of *C. canariensis* in Nigeria of which I am aware have so far been found in the wells Ituk-1 (range 3,320–3,780 feet) (Pl. 26, fig. 3) and Ituk-2 (range 2,770–2,950 feet) in the Calabar flank area, and in Ihuo-1 (range 2,062–2,085 feet).

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The Dutch manuscript was translated by Mr. R. W. Burke; Mr. W. B. Mulder executed the text figures with great care; Messrs. J. Fournier and J. H. H. van Gigch took some of the photographs.

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APPENDIX

1. *Synonymy*

1959*a* *Cupularia canariensis* BUSK, G. On some Madeiran Polyzoa. Collected by J. Yates Johnston, Esq. Zoophytology. *Quart. J. micr. Sci.* **7,** 66, pl. 23, figs. 6–9.

1859*b* *Cupularia canariensis* Busk: BUSK, G. A Monograph of the Fossil Polyzoa of the Crag. *Palaeont. Soc. Monogr.*, p. 87, pl. 13, fig. 2.

1868 *Cupularia canariensis* Busk: MANZONI, A. *Saggio di Conchiologia foss. Subappennina*, p. 71.

1869 *Cupularia canariensis* Busk: MANZONI, A. Bryozoi Pliocenici Italiani. *S.B. Akad. Wiss. Wien,* **59,** p. 26, pl. 2, fig. 17.

1873 *Membranipora canariensis* (Busk): SMITT, F. A. Floridan Bryozoa collected by Count L. F. De Pourtales. II. *Kungl. Svenska Vetensk.-Akad. Handl.* **11,** p. 10, pl. 2, figs. 69–71.

1877*a* *Cupularia canariensis* Busk: MANZONI, A. I briozoi fossili del Miocene d'Austria ed Ungheria. II. *Denkschr. Akad. Wiss. Wien,* **37,** p. 72, pl. 17, fig. 56.

1877*b* *Cupularia canariensis* Busk: MANZONI, A. Bryozoaires du Pliocène supérieur de l'île de Rhodes. *Mém. Soc. géol. Fr.* (3), **1,** p. 67.

1878 *Cupularia canariensis* Busk: BROECK, E. VAN DEN. Esquisse géologique & paléontologique des dépôts pliocènes des environs d'Anvers. *Ann. Soc. Malac. Belg.* **9** (1874), p. 274.

1879 *Cupularia canariensis* Busk: SEGUENZA, G. Le formazioni terziarie nella provincia di Reggio (Calabria). *Mem. Accad. Lincei* (3), **6,** pp. 131, 371.

1881 *Cupularia canariensis* Busk: COPPI, F. *Paleontologia modenese o guida al paleontologo*. Modena, p. 123.

1885 *Lunulites conica* Defrance var. *depressa*: LORIÉ, J. Contributions à la géologie des Pays-Bas. Résultats géologiques et paléontologiques des forages de puits à Utrecht, Goes et Gorkum. *Arch. Mus. Teyler* (2), **2**, p. 133, pl. 3, figs. 15*a*, b.

1887 *Cupularia canariensis* Busk: PERGENS, E. Pliocäne Bryozoën von Rhodos. *Ann. naturh.* (*Mus.*) *Hofmus.* **2**, p. 31.

1889 *Cupularia canariensis* Busk: WATERS, A. W. Supplementary Report on the Polyzoa collected by H.M.S. *Challenger* during the years 1873–1876. *Rep. Sci. Res. Voy. Challenger*, *Zoology*, **31**, pt. 79, p. 36.

1890 *Cupularia canariensis* Busk: NAMIAS, I. Contributo ai briozoi pliocenici delle provincie di Modena e Piacenza. *Boll. Soc. geol. ital.* **9**, p. 506.

1891 *Cupularia canariensis* Busk: NEVIANI, A. Contribuzione alla conoscenza dei briozoi fossili italiani. Briozoi postpliocenici del sottosuolo di Livorno. Ibid. **10**, p. 130.

1894 *Cupularia canariensis* Busk: BROECK, E. VAN DEN. Matériaux pour la connaissance des dépôts pliocènes supérieurs rencontrés dans les derniers travaux de creusement des Bassins Maritimes d'Anvers, Bassin Africa (ou Lefebre) et Bassin America. *Bull. Soc. belge Géol.* **6** (1892), p. 139.

1895*a* *Cupularia canariensis* Busk: NEVIANI, A. Briozoi fossili della Farnesina e Monte Mario presso Roma. *Palaeontogr. ital.* **1**, p. 101.

1895*b* *Cupularia canariensis* Busk: NEVIANI, A. Briozoi neozoici di alcune località d'Italia, I. *Boll. Soc. Romana Studi Zool.* **4**, pp. 238, 243.

1895 *Cupularia canariensis* Busk: DE ANGELIS, J. *Descripción de los Briozoos fósiles pliocénicos de Cataluña.* Barcelona, p. 9, pl. B, figs. 6–9.

1896 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi neozoici di alcune località d'Italia, III. *Boll. Soc. Romana Studi Zool.* **5**, p. 121.

1898 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi neozoici di alcune località d'Italia, V. Ibid. p. 38.

1900 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi terziari e posterziari della Toscana. *Boll. Soc. geol. ital.* **19**, p. 362.

1901 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi neogenici delle Calabrie. *Palaeontogr. ital.* **6** (1900), p. 168.

1905 *Cupularia canariensis* Busk: NEVIANI, A. Briozoi fossili di Carrubare (Calabria). *Boll. Soc. geol. ital.* **23**, p. 522.

1907 *Cupularia canariensis* Busk: CALVET, L. Bryozoaires. *Expéd. sci. 'Travailleur' et 'Talisman' 1880–1883*, **8**, p. 393.

1908 *Cupularia canariensis* Busk: CANU, F. Iconographie des Bryozoaires fossiles de l'Argentine. *An. Mus. nac. B. Aires*, **17**, p. 275, pl. 5, figs. 8–10.

non 1908 *Cupularia canariensis* Busk: ROBERTSON, A. The incrusting chilostomatous Bryozoa of the west coast of North America. *Univ. Calif. Publ. Zool.* **4**, p. 314, pl. 24, figs. 90, 91 = *Discoporella umbellata* (Defrance).

1909 *Cupularia guineensis* Busk: NORMAN, A. M. The Polyzoa of Madeira and neighbouring islands. *J. Linn. Soc.* (*Zool.*), **30**, p. 289, pl. 37, figs. 2–6 (*non Cupularia guineensis:* Busk, G. Catalogue of Marine Polyzoa in the Collection of the British Museum, **2** (1854), p. 98, pl. 114, figs. 1–5).

1913*a* *Cupularia canariensis* Busk: CANU, F. Contributions à l'étude des Bryozoaires fossiles. IV. Pliocène d'Alger. *Bull. Soc. géol. Fr.* (4), **13**, p. 124.

1913*b* *Cupularia canariensis* Busk: CANU, F. Contributions à l'étude des Bryozoaires fossiles. X. Astien de Valle Andona. Ibid., p. 128.

1914 *Cupularia guineensis* Busk: OSBURN, R. C. The Bryozoa of the Tortugas Islands, Florida. *Publ. Carnegie Instn.* **182**, p. 194 (*non Cupularia guineensis*: Busk, G. Catalogue of Marine Polyzoa in the Collection of the British Museum, **2** (1854), p. 98, pl. 114, figs. 1–5).

1914 *Cupularia canariensis* Busk: FAURA, M. Sobre la presencia de un briozoo vivente, la *Cupularia canariensis* descubierto en los terrenos miocénicos de Cataluña. *Bol. Soc. esp. Hist. nat.* **14**, p. 397.

1916 *Cupularia canariensis* Busk: FAURA, M. and CANU, F. Sur les Bryozoaires des terrains tertiaires de la Catalogne. *Treb. Inst. catal. Hist. nat.* p. 77, text-figs. 4*a*, *b*, pl. 3, figs. 7, 8.

1917 *Cupularia canariensis* Busk: CANU, F. Les Bryozoaires fossiles des Terrains du Sud-Ouest de la France. X. Burdigalien. *Bull. Soc. géol. Fr.* (4), **16** (1916), p. 137, pl. 3, figs. 4–6.

1919*a* *Cupularia canariensis* Busk: CANU, F. and BASSLER, R. S. Bryozoa of the Canal Zone and related areas. *Bull. U.S. nat. Mus.* **103** (1918), p. 119, pl. 53, figs. 5–7.

1919*b* *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. Fossil Bryozoa from the West Indies. *Publ. Carnegie Instn.* **291,** p. 78, pl. 1, figs. 8–10.

1920*a* *Cupuladria canariensis* (Busk): CANU, F. Contributions à l'étude des Bryozoaires fossiles. XV. Redonnien du Pigeon-Blanc (Loire-Inférieure). *Bull. Soc. géol. Fr.* (4), **19** (1919), p. 213.

1920*b* *Cupuladria canariensis* (Busk): CANU, F. Contributions à l'étude des Bryozoaires fossiles. XVI. Scaldisien d'Anvers. Ibid., p. 213.

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1921 *Cupuladria canariensis* (Busk): CIPOLLA, F. I briozoi pliocenici di Altavilla presso Palermo. *G. Sci. nat. econ. Palermo*, **32** (1918–20), p. 31, pl. 2, figs. 22–24.

1921 *Cupularia canariensis* Busk: WATERS, A. W. Observations upon the relationships of the (Bryozoa) Selenariadae, Conescharellinidae, &c., fossil and Recent. *J. Linn. Soc.* (*Zool.*), **34,** p. 410 (*partim*), pl. 29, figs. 1–5; pl. 30, figs. 11, 12, 21, 22, 25.

1923 *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. North American Later Tertiary and Quaternary Bryozoa. *Bull. U.S. nat. Mus.* **125,** p. 28, pl. 1, figs. 7–9.

1923 *Cupuladria biporosa* CANU, F. and BASSLER, R. S. North American Later Tertiary and Quaternary Bryozoa. Ibid., p. 29, pl. 47, figs. 1, 2.

1924 *Cupuladria canariensis* (Busk): CIPOLLA, F. I briozoi del Quaternario inferiore dei dintorni di Palermo. Nota preliminare. *Boll. Soc. Sci. nat. econ. Palermo*, **6,** p. 7.

1925*a* *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. Contribution à l'étude des Bryozoaires d'Autriche et de Hongrie. *Bull. Soc. géol. Fr.* (4), **24** (1924), p. 673.

1925*b* *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. Les Bryozoaires du Maroc et de Mauritanie. 1er Mémoire. *Mém. Soc. Sci. nat. Maroc*, **10,** p. 13.

1925 *Cupuladria canariensis* (Busk): CANU, F. and LECOINTRE, G. Les Bryozoaires cheilostomes des Faluns de Touraine et d'Anjou. *Mém. Soc. géol. Fr.* (N.S.), **4,** p. 17, pl. 3, figs. 10, 11.

1925 *Cupuladria canariensis* (Busk): MANSFIELD, W. C. Miocene Gastropods and Scaphopods from Trinidad, British West Indies. *Proc. U.S. nat. Mus.* **66,** pp. 5, 8.

non 1926 *Cupularia canariensis* Busk: WATERS, A. W. Ancestrulae of Cheilostomatous Bryozoa. Part V. *Cupularia*, &c. *Ann. Mag. nat. Hist.* (9), **18,** p. 426, text-fig. on p. 425, pl. 18, figs. 1, 10 = *Cupuladria guineensis* (Busk).

1928*a* *Cupuladria canariensis* (Busk): CANU F. and BASSLER, R. S. Fossil and Recent Bryozoa of the Gulf of Mexico Region. *Proc. U.S. nat. Mus.* **72** (14), p. 15, pl. 1, figs. 7–9.

1928*b* *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. Les Bryozoaires du Maroc et de Mauritanie. 2^{me} Mémoire. *Mém. Soc. Sci. nat. Maroc*, **18,** p. 16.

1929 *Cupuladria canariensis* (Busk): CANU, F. and BASSLER, R. S. Bryozoa of the Philippine Region. *Bull. U.S. nat. Mus.* **100,** p. 73, pl. 3, figs. 1, 2.

1930 *Cupuladria canariensis* (Busk): HASTINGS, A. B. Cheilostomatous Polyzoa from the vicinity of the Panama Canal collected by Dr. C. Crossland on the Cruise of the S.Y. 'St. George'. *Proc. zool. Soc. Lond.* **47,** p. 714, pl. 8, figs. 38, 40.

1934 *Cupulardia* [*sic*] *canariensis* (Busk): HOWE, H. V., HANNA, M. A., and GRAVELL, D. W. Fossil plates with explanations. Fossils present in subsurface formations of Clarke and Wayne Counties, Mississippi, and in wells in South Mississippi. *Shreveport Geol. Soc., Guide Book 11th Ann. Field Trip*, pl. 1, figs. 27, 28.

1935 *Cupuladria canariensis* (Busk): DARTEVELLE, E. Zoarial regeneration of free Polyzoa. *Ann. Mag. nat. Hist.* (10), **15,** p. 559, pl. 19, figs. 1, 2.

1936 *Cupuladria canariensis* (Busk): SCOTTI, P. Briozoi fossili del Miocene della Collina di Torino (Collezione Rovasenda). *Atti Accad. Torino*, **71,** p. 410.

1938 *Cupularia canariensis* Busk: GILLARD, P. A. Sur les Bryozoaires helvétiens des Faluns de la Vienne. *C. R. Soc. géol. Fr.* **9,** p. 155.

1940 *Cupuladria canariensis* (Busk): OSBURN, R. C. Bryozoa of Porto Rico with a résumé of the West Indian bryozoan fauna. *Sci. Surv. P. R.* **16,** p. 354.

1941 *Cupuladria canariensis* (Busk): MCGUIRT, J. H. Louisiana Tertiary Bryozoa. *Bull. Geol. Surv. La.* **21,** p. 46, pl. 1, figs. 1–3, 5–6, 8.

1942 *Cupuladria canariensis* (Busk): SILÉN, L. On spiral growth of the zoaria of certain Bryozoa. *Ark. Zool.* **34**A, p. 13, pl. 4, figs. 15, 16.

1943 *Cupuladria canariensis* (Busk): DARTEVELLE, E. *In* RUTSCH, R. Die Mollusken der Springvale Schichten (Obermiocaen) von Trinidad (British-West-Indien). *Verh. naturf. Ges. Basel*, **54**, p. 107.

1945 *Cupuladria canariensis* (Busk): BUGE, E. Empreintes et moules internes de Bryozoaires de l'Helvétien et du Redonien de Bretagne. *Bull. Soc. géol. Fr.* (5), **15**, p. 590.

1946 *Cupuladria canariensis* (Busk): ROGER, J. and BUGE, E. Les Bryozoaires du Redonien. Ibid. **16**, pp. 218, 226.

1947 *Cupuladria canariensis* (Busk): OSBURN, R. C. Bryozoa of the Allan Hancock Atlantic Expedition, 1939. *Rep. Allan Hancock Atlant. Exped.* **5**, p. 10.

1949 *Cupuladria canariensis* (Busk): VIGNEAUX, M. Révision des Bryozoaires Néogènes du Bassin d'Aquitaine et essai de classification. *Mém. Soc. géol. Fr.* (N.S.), **28**, p. 38, pl. 2, figs. 8, 9.

1950 *Cupuladria canariensis* (Busk): OSBURN, R. C. Bryozoa of the Pacific Coast of America. I. Cheilostomata-Anasca. *Rep. Allan Hancock Pacif. Exped.* **14**, p. 33, pl. 3, figs. 2, 3.

1951 *Cupuladria canariensis* (Busk): MALECKI, J. Contribution à la connaissance des Bryozoaires du Miocène de Benczyn. *Ann. Soc. géol. Pologne*, **19** (1949), p. 488.

1952 *Cupuladria canariensis* (Busk): LAGAAIJ, R. The Pliocene Bryozoa of the Low Countries, &c. *Meded. geol. Sticht.*, serie C-V-5, p. 33, pl. 2, figs. 1*a*, *b*.

1953 *Cupuladria canariensis* (Busk): LAGAAIJ, R. The vertical distribution of the lunulitiform Bryozoa in the Tertiary of the Netherlands. Ibid. (N.S.), **7**, p. 15, pl. 1, figs. 1*a*, *b*.

1955 *Cupuladria canariensis* (Busk): GAUTIER, Y. Bryozoaires de Castiglione. *Bull. Statist. Aquicult. Pêche Castiglione* (N.S.), **7**, p. 231.

1956 *Cupuladria canariensis* (Busk): PARKER, R. H. Macro-invertebrate assemblages as indicators of sedimentary environments in East Mississippi Delta region. *Bull. Amer. Ass. Petrol. Geol.* **40**, pp. 311, 335, pl. 4, fig. 25.

1957 *Cupuladria canariensis* (Busk): BUGE, E. Les Bryozoaires du Néogène de l'ouest de la France, &c. *Mém. Mus. Hist. nat., Paris* (N.S.), **6**, p. 139, pl. 9, fig. 5; pl. 10, fig. 3.

1957 *Cupuladria canariensis* (Busk): GAUTIER, Y. Sur quelques Bryozoaires des Côtes d'Algérie. *Résult. Camp. 'Professeur Lacaze Duthiers'*, **2**, suppl. 6 (*Vie et Milieu*), p. 102.

1959 *Cupuladria canariensis* (Busk): SOULE, J. D. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 6. Anascan Cheilostomata (Bryozoa) of the Gulf of California. *Amer. Mus. Novit.*, No. 1969, p. 8.

1961 *Cupuladria canariensis* (Busk): REGUANT, S. Los briozoos del Neógeno español. *Notas Inst. geol. Esp.* **62**, 227.

1961 *Cupuladria canariensis* (Busk): GALOPIM DE CARVALHO, A. M. Note sur des Bryozoaires du Pliocène de Pombal. *Bol. Soc. geol. Portug.* **14**, 97, pl. 1, figs. 1–3.

1961 *Cupuladria canariensis* (Busk): GHIURCA, V. Contributii la cunoaşterea faunei de Bryozoare din Transilvania (II). Revizuirea taxonomică a Bryozoarelor de la Lăpugiu şi Biuturi publicate de A. Koch. *Studia Univ. Babeş-Bolyai* (2), 1, table.

1962 *Cupuladria canariensis* (Busk): GAUTIER, Y. V. Recherches écologiques sur les Bryozoaires chilostomes en Méditerranée occidentale. Thesis, Aix-en-Provence, 53.

2. *Documentation of maps and figures*

All cited papers are listed in either the References or the Synonymy.

BMNH: British Museum (Natural History).

USNM: United States National Museum.

KSEPL: Koninklijke/Shell Exploratie en Produktie Laboratorium, Volmerlaan 6, Rijswijk Z.H., Netherlands.

TEXT-FIG. 3. The selected localities shown are:

	Reference or repository		*Reference or repository*
1. Cape Rosa, Algeria	BMNH	3. Oran, Algeria	Waters 1921
2. Râs-el-Amouch, Algeria	Dartevelle 1935	4. Tangier Bay	BMNH

	Reference or repository
5. Vanneau Sta. XXIX, Morocco	Canu and Bassler 1925*b*
6. Cape Sagres, Portugal	BMNH
7. Off Punta Delgada, Azores	Silén 1942
8. Madeira	Busk 1859*a*; Norman 1909; Silén 1942
9. 'entrée de la Bocayna', Canary Islands	Calvet 1907
10. Gran Canaria, Canary Islands	Silén 1942
11. Lat. 27° 16′ N, long. 23° 21′ W	Silén 1942
12. Cap Blanc, Mauritania	Calvet 1907
13. Cape Verde, Sénégal	BMNH
14. Conakry, Guinée	BMNH
15. Petit Tahou, Liberia	Waters 1889, 1921
16. Accra, Ghana	BMNH
17. SE of Lagos, Nigeria, 13 fms.	KSEPL
18. Off Fishtown River, Nigeria, 14 fms.	KSEPL
19. N of Fernando Poo, 42 fms.	KSEPL
20. Calypso Sta. 45, W of Libreville, Gabon	BMNH
21. Albatross Sta. 2597, off Cape Hatteras	USNM
22. Albatross Sta. 2415, E of Jacksonville, Fla.	USNM
23. Albatross Sta. 2639, Straits of Florida	Canu and Bassler 1928*a*
24. Tortugas, Florida	Smitt 1873; Osburn 1914; Silén 1942
25. Albatross Sta. 2405, off Cedar Keys, Fla.	Canu and Bassler 1928*a*
26. S of Mobile, Alabama	Parker 1956
27. Lat. 28° 40′ N, long. 90° 14′ W, 19 fms.	KSEPL
28. Lat. 28° 4′ N, long. 93° 44′ W, 40 fms.	KSEPL
29. Lat. 25° 47′ N, long. 96° 27′ W, 50 fms.	KSEPL (ex Mr. R. W. Barker)
30. Albatross Sta. 2361, NE of Cabo Catoche	USNM
31. Port Antonio, Jamaica	USNM
32. Caroline Sta. 55, Samaná Bay, Santo Domingo	USNM
33. Off Guanica Harbor, Puerto Rico	Osburn 1940
34. St. Thomas, West Indies	Silén 1942
35. St. Martin, West Indies	Silén 1942
36. Albatross Sta. 2145, NNW of Aspinwall	Silén 1942
37. Cape la Vela, Colombia	Osburn 1947
38. Aruba, Netherlands Antilles	Osburn 1947
39. Tortuga Island, Venezuela	Osburn 1947
40. Margarita Island, Venezuela	Osburn 1947
41. Barbados, West Indies	BMNH
42. Lat. 9° 28′ N, long. 60° 8′ W, 39 fms.	KSEPL (ex Dr. D. J. Nota)
43. Berbice, British Guiana	BMNH
44. Off Bahía, Brazil	Waters 1889
45. Cedros Island, Lower California	Osburn 1950
46. Albatross Sta. 3012, Gulf of California	USNM
47. Albatross Sta. 2826, Gulf of California	Canu and Bassler, 1929
48. Clarion Island, Mexico	Osburn 1950
49. Socorro Island, Mexico	Osburn 1950
50. West coast of Mexico	Osburn 1950
51. West coast of Costa Rica	Osburn 1950
52. West coast of Panama	Osburn 1950
53. Gorgona, Colombia	Hastings 1930
54. Galapagos Islands	Osburn 1950
55. Ecuador	Osburn 1950

TEXT-FIG. 4. The selected localities shown are:

Miocene

1. Twistringen, SSW of Bremen, Germany	Reinbek/Dingdener Stufe, Middle Miocene (Pl. 26, fig. 2)	ex Dr. C. W. Drooger
2. Beeringen, Netherlands	Diepboring 15, 154–159 m., Middle Miocene	Lagaaij 1953
3. Wyneghem, near Antwerp, Belgium	Lower Diestian (Deurnian), Upper Miocene	Lagaaij 1952
4. Vienna Basin, Austria	Tortonian, Middle Miocene	Manzoni 1877*a*; Canu and Bassler 1925*a*
4*a*. Benczyn, near Wadowice, Poland	Tortonian, Middle Miocene	Malecki 1951
5. Turin, Italy	Miocene	Scotti 1936
6. Reggio, Calabria, Italy	Tortonian, Middle Miocene	Seguenza 1879
7. Ferrière l'Arçon, Indre-et-Loire, France	Pontilevian, Middle Miocene	Canu and Lecointre 1925; Buge 1957
8. Dept. Gironde, France	Aquitanian and Burdigalian, Lower Miocene	Canu 1917; Duvergier 1920; Vigneaux 1949
9. Barcelona province, Spain	Helvetian, Middle Miocene	Faura 1914; Faura and Canu 1916

10. Niger Delta, Nigeria	Exploration well Oloibiri–1, 9,560–9,570′, Miocene	KSEPL
11. Calabar area, Nigeria	Exploration well Ituk–1, 3,320–3,780′, Miocene (Pl. 26, fig. 3)	KSEPL
12. Missellele River, 10 km. N of Tiko, E of Mount Cameroon, Nigeria	Lower Miocene	KSEPL
13. French Cameroons	Middle Miocene	KSEPL
14. Monroe County, Florida	Caloosahatchee formation, Miocene	Canu and Bassler 1919*b*; 1923
15. Jackson's Bluff, Ochlockonee River, Leon County, Florida	Choctawhatchee, Miocene	Canu and Bassler 1919*b*; 1923
16. Shell Bluff, Shoal River, N of Mossyhead, Walton County, Fla.	Shoal River (type locality), Miocene	KSEPL
17. Limestone Creek, Wayne County, Mississippi	Chickasawhay, Miocene (Pl. 26, fig. 4)	KSEPL (ex Mr. R. W. Barker)
18. East Baton Rouge Parish, Louisiana	Superior Oil Prod. Company's Duplantier Community No. 1 well, 7,671–7,687′, *Heterostegina* zone; 8,091–8,101′, *Marginulina* zone, Catahoula formation, Miocene	McGuirt 1941
19. Laguna Atorcosa, Cameron County, Texas	Shell-Continental Fee # 1, 11,810–11,850′, *Marginulina zone*, Miocene	KSEPL (ex Dr. D. D. Bannink)
20. Goliad County, Texas	Housh, Thompson & Crown Central C. G. Wood # 1, 3,163–3,193′, updip limit of Anahuac shale wedge, Miocene	Shell Oil Company, Corpus Christi Division
21. Gulf of Mexico, off Nueces County, Texas	Gulf Oil Corp. and others, Block 889, 3–A, 10,300′, Upper Frio, Miocene	KSEPL (ex Mr. E. M. Wilkins)
22. Bowden, Jamaica	Bowden Beds, upper Middle Miocene	Canu and Bassler 1919*a*; 1919*b*; 1923
23. Cercado de Mao, Santo Domingo	Middle Miocene	Canu and Bassler 1919*b*; 1923
24. Port Limón, Costa Rica	Middle Miocene	Canu and Bassler 1923
25. Rio Coro, at Caujarao, Distr. Miranda, Estado Falcon, Venezuela	Caujarao formation, upper Middle Miocene	KSEPL
26. Cabo Blanco, near Maiquetía Airport, Distr. Federal, Venezuela	Playa Grande formation, Upper Miocene	KSEPL
27. Estado Guarico, Venezuela	Creole Petroleum Corp., GXB–5, Roblecito formation, Miocene	Compañía Shell de Venezuela, Caracas
28. Estado Anzoategui, Venezuela	Mene Grande Oil Company, OG–1, 2,125′; 3,250′, Freites formation; 3,750–4,625′, Oficina formation, Miocene	Compañía Shell de Venezuela, Caracas
29. Estado Monagas, Venezuela	Creole Petroleum Corp., ORC–2, 3,900–4,200′, Carapita formation, Miocene	Compañía Shell de Venezuela, Caracas
30. Estado Monagas, Venezuela	Compañía Shell de Venezuela, Cerro Negro-3, Freites formation; Oficina formation, Miocene	Compañía Shell de Venezuela, Caracas
31. Cubagua Island, Venezuela	Socony Mobil Oil Company, Cubagua–1, 218′, Cubagua formation, Upper Miocene (Pl. 26, fig. 5)	KSEPL
32. Concord quarry, Point à Pierre, Trinidad	Concord marl, Miocene	KSEPL (ex Dr. E. Th. N. Spiker)

Pliocene

I.	Sutton, Suffolk, England	Gedgravian, Pliocene	Busk 1859*b*
II.	Antwerp, Belgium	Scaldisian (prob. Luchtbal horizon), Pliocene	Canu 1920*b*
III.	Heumensoord, Netherlands	Boring 1928, 102·40–109·00 m., 'Scaldisian', Pliocene	Lagaaij 1952
IV.	Roden, Netherlands	Boring 114/23, 184·50–215·00 m., Pliocene	KSEPL (ex Dr. J. H. van Voorthuysen)
V.	Contigné, Maine-et-Loire, France	Redonian, Pliocene	Roger and Buge 1946; Buge 1957
VI.	Pigeon-Blanc (Landreau), near Nantes, France	Redonian, Pliocene	Canu 1920*a*; Roger and Buge 1946; Buge 1957
VI*a*.	Pombal, Portugal	Pliocene	Galopim de Carvalho 1961
VII.	El Ampurdan, near Barcelona, Spain	Pliocene	De Angelis 1895
VIII.	Valle Andona, Asti, Piedmont, Italy	Astian, Pliocene	Manzoni 1869; Canu 1913*b*
IX.	Province of Modena, Italy	Plaisancian, Pliocene	Namias 1890
X.	Altavilla, near Palermo, Sicily, Italy	Pliocene	Cipolla 1921
XI.	Nador, near Algiers, Algeria	Plaisancian, Pliocene	Canu 1913*a*
XII.	Terrebonne Parish, Louisiana	Terrebonne Gas Company Fee #1, 2,300′, Pliocene	McGuirt 1941
XIII.	Minnitimmi Creek, Bocas Island, Almirante Bay, Panama	Pliocene	Canu and Bassler 1928*a*
XIV.	Camarones, 10 km. E of Esmaralda, Ecuador	Pliocene	KSEPL (ex Mr. J. Brouwer)

Pleistocene

A.	Livorno, Italy	Sicilian, Pleistocene	Neviani 1891
B.	Monte Mario and Farnesina, near Rome, Italy	Calabrian	Manzoni 1869; Neviani 1895
C.	Carrubare, Calabria, Italy	Sicilian?	Neviani 1905
D.	Palermo, Sicily, Italy	Sicilian?	Cipolla 1924
E.	Rhodes	Sicilian	Manzoni 1877*b*; Pergens 1887; Silén 1942
F.	Gulf of Mexico, Mississippi River Delta area, Louisiana	South Pass, Block 6 Area, State Lease 2590 1, 500–1,100′, 'Upper Marine', Pleistocene	KSEPL (ex Mr. J. J. Gouty)
G.	Gulf of Mexico, High Island area	Federal Block A–104, Shell-Continental 'Neptune-1', 775–790′; 835–1,000′, Pleistocene	KSEPL
H.	Gulf of Mexico, off Matagorda County, Texas	Ohio Oil Company, State of Texas 403 # 1, 537–599′; 662–754′; 1,935–1,997′, Pleistocene	KSEPL
J.	Cabo Blanco, near Maiquetía Airport, Distr. Federal, Venezuela	Mare formation, Pleistocene?	KSEPL
K.	Estado Monagas, Venezuela	Compañía Shell de Venezuela, Guanipa-1, 640–670′, Paria formation, Pleistocene	Compañía Shell de Venezuela, Caracas
L.	Puerto Militar, Bahia Blanca, Argentine	Pampéan, Pleistocene	Canu 1908

TEXT-FIG. 5. Sources: (*a*) Collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KSEPL, Rijswijk, Netherlands; (*b*) Parker 1956; and (*c*) various other sources (see list):

		Lat. N	*Long. W*	*Depth in fms.*
1.	Cavalier 1956 Sta. 128	29°02′54″	89°28′26″	5·5
2.	Parker 1956 Sta. 410	29°27′	89°15′	2
3.	 321	29°30′30″	89°15′	2
4.	 322	29°30′30″	89°10′	2
5.	G. 2074	29°30′	88°52′	7·5
6.	Parker 1956 Sta. 346	29°24′	88°54′	10
7.	 349	29°22′	88°51′	15
8.	 316	29°12′	88°43′	39
9.	G. 2021	29°09′	88°43′	43
10.	G. 2028, Sandpile Bank	20°04′40″	88°43′	49
11.	Parker 1956 Sta. 311	29°22′	88°32′	32
12.	 309	29°23′	88°22′	30
13.	 308	29°26′	88°20′	30
14.	 244	29°26′	88°08′	29
15.	U.S.S. Hydrographer 1941/2, Sta. 50	29°46′05″	86°58′	103·8
16.	U.S.S. Hydrographer 1941/2, Sta. 23	29°31′	86°26′	77
17.	U.S.S. Hydrographer 1941/2, Sta. 45	29°33′	86°08′	21
18.	U.S.S. Hydrographer 1941/2, Sta. 40	30°15′	86°11′	15
19.	U.S.S. Hydrographer 1941/2, Sta. 39	30°13′	86°08′	12·5
20.	Off Panama City, Florida	30°05′58″	85°45′39″	10
21.	.. ..	30°01′24″	85°51′54″	14·5
22.	.. ..	30°00′45″	85°52′45″	15
23.	Albatross 1885 Sta. 2405 (Canu and Bassler 1928*a*)	28°45′	85°02′	30
24.	Fish Hawk Sta. 7157 (USNM)	29°23′	83°41′45″	9
25.	Off Cedar Keys, Florida	28°58′48″	83°16′42″	5·5
26.	.. ..	29°00′06″	83°15′	5
27.	.. ..	29°01′24″	83°13′20″	4·5
28.	.. ..	29°02′36″	83°11′38″	4
29.	.. ..	29°03′55″	83°09′50″	3·5
30.	.. ..	29°05′16″	83°08′	3·5
31.	Atlantis 1951 Sta. 152	28°09′	85°07′	100
32.	 153	28°11′30″	85°02′	80
33.	 154	28°14′	84°57′	64
34.	 155	28°16′30″	84°52′	43
35.	 156	28°19′	84°46′30″	32
36.	 157	28°22′	84°14′	34
37.	 158	28°24′30″	84°36′	33
38.	 159	28°27′	84°31′	28
39.	 160	28°30′	84°25′30″	25
40.	 161	28°32′	84°20′	22
41.	 162	28°35′	84°14′	20
42.	 163	28°38′	84°08′	20
43.	 164	28°41′	84°02′	17
44.	 165	28°43′30″	83°56′	17
45.	 166	28°46′	83°50′	16
46.	 167	28°49′	83°44′	14
47.	Atlantis 1951 Sta. 168	28°51′30″	83°39′30″	12
48.	 169	28°54′	83°34′30″	11·5
49.	 170	28°55′	83°28′30″	11
50.	 171	28°56′30″	83°22′	8
51.	 172	28°58′	83°16′30″	7?6?
52.	 173	28°59′	83°12′30″	5
53.	Off Egmont Key, Florida	27°36′27″	83°08′57″	11·5
54.	.. ..	27°36′27″	83°04′48″	10·5
55.	.. ..	27°36′27″	83°02′42″	8·5
56.	.. ..	27°36′27″	83°00′30″	8·5
57.	.. ..	27°36′27″	82°53′48″	7
58.	.. ..	27°36′27″	82°51′42″	5·5
59.	Tampa Bay, Florida	27°38′09″	82°37′27″	4·5
60.	.. .. ..	27°39′54″	82°36′06″	5·5
61.	.. .. ..	27°41′14″	82°34′43″	4·5
62.	.. .. ..	27°46′	82°31′36″	4
63.	Vema–3 1954 BT # 18	27°08′	83°30′	23
64.	Albatross 1885 Sta. 2409 (Silén 1942)	27°04′	83°21′15″	26
65.	Vema–3 1954 Dredge # 2	26°50′	83°40′	29
66.	SSW of John's Pass, Florida	26°25′	83°32′	34
67.	Vema–3 1954 BT # 2	26°10′	84°20′	96
68.	Vema–3 1954 Dredge # 1	25°50′	84°30′	117
69.	Tortugas, Florida (Osburn 1914)			10
70.	SW of Tortugas, Florida (Silén 1942)			40 m.
71.	Rebecca Shoal, Florida (Silén 1942)			15 m.
72.	Albatross 1885 Sta. 2315 (Silén 1942)	24°26′	81°48′15″	37
73.	NW of Sombrero Key, Florida	24°39′36″	81°04′12″	6·5
74.	S of Sombrero Key, Florida	24°35′30″	81°06′55″	25
75.	SE of Molasses Reef Light, Fla.	24°54′	80°15′30″	122
76.	Albatross 1886 Sta. 2639 (Canu and Bassler 1928*a*)	25°04′50″	80°15′10″	56
77.	Due E of Carysfort Light, Fla.	25°13′15″	80°07′	78
78.	Off Turtle Harbor, Florida (USNM)			20
79.	Due E of Triumph Reef, Fla.	25°28′30″	80°05′45″	45
80.	Due E of Triumph Reef, Fla.	25°28′30″	80°05′	58
81.	Off Fowey Light, Florida	25°30′48″	80°03′36″	80
82.	Fowey Light, Florida (Canu and Bassler 1928*a*)			40

TEXT-FIG. 6. Sources: (*a*) Collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KSEPL, Rijswijk, Netherlands; (*b*) Parker 1956:

		Lat. N	*Long. W*	*Depth in fms.*
1.	Cavalier 1956 Sta. 12	28°43′18″	95°19′09″	9
2.	 20	28°47′30″	95°15′24″	10
3.	 21	28°45′16″	95°15′24″	10·5
4.	 23	28°42′47″	95°14′30″	12
5.	 28	28°37′03″	95°09′54″	15
6.	 30	28°34′50″	95°08′05″	16
7.	 35	28°44′48″	95°08′05″	11·5
8.	Univ. of Houston, Nos. 1–4	28°40′	94°33′	15
9.	Vema–3 1954 Core ♯ 65 (Top 12″)	28°10′48″	94°15′	30
10.	Heald Bank, N of Heald Bank Light			8·5
11.	Heald Bank	29°04′	94°14′	10·5
12.	Cavalier 1956 Sta. 331	29°03′15″	94°18′45″	6·5
13.	 330	29°01′06″	94°18′45″	8
14.	 329	28°58′45″	94°18′45″	6
15.	 328	28°55′42″	94°18′06″	11·5
16.	 327	28°49′36″	94°16′42″	13·5
17.	 326	28°43′44″	94°14′54″	15
18.	High Island area, Block A–104	28°42′12″	94°01′36″	15·5
19.	Cavalier 1956 Sta. 325	28°37′06″	94°13′14″	18
20.	 324	28°33′	94°12′15″	20
21.	 323	28°26′06″	94°10′30″	23
22.	 321	28°17′30″	94°08′30″	27·5
23.	 320	28°15′24″	94°03′54″	31·5
24.	 319	28°09′06″	94°00′00″	38
25.	 318	28°02′54″	93°51′30″	40
26.	 317	27°58′45″	93°49′45″	50
27.	 316	27°54′15″	93°47′45″	50
28.	 315	27°48′45″	93°45′30″	92
29.	 314	27°44′12″	93°43′48″	138
30.	 312	27°48′	93°47′36″	102
31.	 311	27°51′30″	93°47′	70
32.	 310	27°53′45″	93°46′30″	60
33.	 309	27°56′15″	93°46′	57
34.	 308	28°04′	93°44′20″	40

		Lat. N	*Long. W*	*Depth in fms.*
35.	Cavalier 1956 Sta. 307	28°09′30″	93°43′15″	35·5
36.	 306	28°16′15″	93°42′15″	35
37.	 305	28°22′12″	93°40′30″	30
38.	 304	28°29′06″	93°38′30″	24
39.	 303	28°37′24″	93°36′24″	18·5
40.	 302	28°43′	93°34′45″	15
41.	 301	28°49′	93°33′15″	12·5
42.	 300	28°52′30″	93°32′	11
43.	 299	28°59′15″	93°30′15″	11
44.	 298	29°06′	93°28′12″	11
45.	 297	29°11′30″	93°26″	9
46.	 296	29°15′09″	93°24′08″	8·5
47.	Sabine Bank area, Sta. 2	29°19′20″	93°36′30″	7
48.	Cavalier 1956 Sta. 294	29°21′04″	93°21′18″	8·5
49.	 293	29°23′48″	93°20′04″	6·5
50.	 292	29°24′42″	93°20′	7
51.	 291	29°26′24″	93°19′55″	4
52.	 290	29°27′28″	93°19′50″	6·5
53.	 289	29°30′21″	93°19′38″	6·5
54.	 288	29°33′30″	93°19′26″	6·5
55.	 286	29°40′35″	93°19′40″	5·5
56.	 273	28°31′30″	91°49′15″	24
57.	 278	28°05′15″	91°58′	38
58.	 236	28°42′24″	90°59′38″	7
59.	 235	28°39′50″	90°59′38″	8·5
60.	 217	28°33′12″	90°59′50″	14
61.	 226	28°08′30″	91°01′	56
62.	 227	28°06′30″	91°01′	37·5
63.	 229	28°04′	91°01′	57
64.	 166	28°37′	90°16′12″	21·5
65.	 175	28°10′	90°13′30″	66
66.	 180	28°39′55″	90°13′45″	19
67.	 128	29°02′54″	89°28′26″	5·5
68.	Parker 1956, Sta. 410	29°27′	89°15′	2
69.	 321	29°30′30″	89°15′	2
70.	 322	29°30′30″	89°10′	2
71.	 346	29°24′	88°54′	10

TEXT-FIG. 7. Source: samples kept at KSEPL, Rijswijk, Netherlands; the co-ordinates and depths are listed below:

	Mees Cremer 1959 Stations	*Lat. N*	*Long. E*	*Depth in fms.*
1	158	6°11′20″	3°21′26″	44
2	320	6°20′04″	3°29′14″	13
3	169	6°18′24″	3°34′22″	19
4	168	6°20′31″	3°46′15″	14
5	170	6°11′50″	3°32′04″	42
6	162	6°07′25″	3°30′01″	63
7	163	6°08′45″	3°33′22″	52
8	164	6°10′24″	3°37′26″	44
9	171	6°11′25″	3°37′12″	43
10	165	6°12′00″	3°42′32″	41
11	318	6°11′01″	3°46′21″	47
12	215	6°13′59″	4°11′38″	12
13	147	6°05′40″	4°25′41″	21
14	212	5°42′43″	4°40′30″	37
15	203	5°32′00″	4°49′38″	27

	Mess Cremer 1959 Stations	*Lat. N*	*Long. E*	*Depth in fms.*
16	206	5°24′01″	4°39′51″	120
17	133	5°19′58″	5°01′29″	16
18	137	5°12′46″	4°46′59″	109
19	310	4°54′09″	5°08′26″	25
20	311	4°48′55″	5°02′55″	45
21	312	4°47′34″	5°01′38″	55
22	107	4°37′17″	5°24′22″	12
23	108	4°34′47″	5°21′18″	18
24	109	4°32′19″	5°18′04″	29
25	377	4°24′10″	5°35′49″	10
26	376	4°23′33″	5°33′53″	11
27	375	4°23′01″	5°32′04″	13
28	374	4°22′34″	5°29′53″	14
29	373	4°22′07″	5°27′58″	17
30	372	4°21′41″	5°25′58″	21

	Mees Cremer 1959 Stations	*Lat. N*	*Long. E*	*Depth in fms.*
31	371	4°21′14″	5°23′58″	27
32	299	4°25′07″	5°34′55″	9
33	300	4°21′56″	5°31′46″	13
34	301	4°18′26″	5°27′29″	21
35	96	4°15′39″	5°42′55″	9
36	97	4°12′28″	5°40′38″	12
37	98	4°09′20″	5°38′25″	14
38	99	4°05′44″	5°35′37″	17
39	100	4°02′10″	5°33′06″	26
40	101	3°59′55″	5°31′23″	34
41	220	4°06′56″	5°37′31″	16
42	221	4°04′50″	5°40′50″	17
43	222	4°00′55″	5°43′11″	18
44	223	3°57′06″	5°45′07″	23
45	224	3°52′51″	5°47′47″	31
46	395	4°04′34″	5°50′10″	14
47	396	4°04′09″	5°52′23″	14
48	397	4°02′47″	5°54′24″	14
49	398	4°01′25″	5°56′21″	15
50	399	4°00′37″	5°58′38″	15
51	400	3°59′54″	6°00′59″	16
52	401	3°58′57″	6°03′18″	18
53	402	3°58′17″	6°05′42″	21
54	403	3°57′27″	6°07′50″	23
55	388	4°06′28″	6°02′25″	10
56	389	4°04′40″	6°01′34″	12
57	390	4°02′41″	6°00′52″	13
58	391	4°00′49″	6°00′08″	14
59	392	3°59′01″	5°59′32″	16
60	393	3°57′10″	5°58′58″	22
61	394	3°55′37″	5°58′24″	24
62	83	4°10′39″	6°10′25″	7
63	387	4°08′44″	6°06′38″	8
64	84	4°05′41″	6°07′53″	11
65	85	4°02′49″	6°07′04″	14
66	86	4°00′14″	6°06′26″	17
67	87	3°56′42″	6°05′02″	23
68	81	4°09′13″	6°18′27″	9
69	344	4°11′11″	6°26′59″	8
70	345	4°04′33″	6°26′11″	15
71	346	3°57′37″	6°24′40″	31
72	74	4°12′31″	6°31′22″	8
73	287	4°10′19″	6°43′14″	11
74	288	4°06′16″	6°43′20″	18
75	289	4°00′11″	6°43′24″	32
	Mess Cremer 1959 Stations	*Lat. N.*	*Long. E*	*Depth in fms.*
76	291	3°50′04″	6°43′19″	67
77	77	4°13′41″	6°47′27″	9
78	78	4°14′05″	6°51′59″	9
79	79	4°14′41″	6°56′58″	8
80	11	4°08′46″	7°01′31″	16
81	6	4°06′46″	7°00′54″	20
82	10	4°02′31″	7°02′05″	29
83	7	4°00′31″	7°01′12″	36
84	404	3°56′30″	6°58′42″	48
85	334	4°11′18″	7°18′47″	15
86	335	4°05′35″	7°18′12″	22
87	338	3°46′57″	7°18′17″	91
88	243	4°14′41″	7°35′01″	10
89	244	4°10′18″	7°34′56″	17
90	245	4°05′55″	7°34′59″	25
91	246	4°01′37″	7°34′54″	32
92	247	3°57′16″	7°34′56″	42
93	260	3°50′30″	7°30′10″	76
94	248	3°51′58″	7°35′00″	71
95	259	3°48′34″	7°39′49″	93
96	274	4°16′25″	7°42′38″	9
97	23	4°15′58″	8°01′50″	12
98	24	4°11′50″	8°02′33″	14
99	31	3°57′38″	8°04′39″	36
100	28	3°55′27″	8°05′30″	42
101	29	3°51′43″	8°05′49″	68
102	32	3°56′07″	8°08′35″	40
103	34	3°52′40″	8°18′02″	49
104	36	3°49′19″	8°17′22″	100
105	255	3°47′59″	8°20′19″	62
106	37	3°47′02″	8°20′17″	91
107	73	4°05′38″	8°26′10″	22
108	72	4°05′21″	8°30′16″	26
109	254	3°52′38″	8°28′02″	40
110	38	3°44′50″	8°23′50″	75
111	39	3°43′08″	8°27′22″	56
112	46	4°06′34″	8°34′35″	34
113	45	4°03′36″	8°36′10″	31
114	44	3°58′36″	8°35′43″	36
115	43	3°54′05″	8°35′01″	41
116	42	3°48′53″	8°33′59″	44
117	41	3°44′39″	8°33′01″	44
118	40	3°40′36″	8°32′11″	44
119	70	3°48′10″	8°43′41″	42

TEXT-FIG. 8. Distribution of Pliocene marine facies after van Voorthuysen 1956, fig. 26. Eighteen borings and outcrop localities listed in Lagaaij 1952, p. 33, are shown, to which the following occurrences north of the Rhine have here been added:

Wanneperveen–2	Kernboring NAM	171·50–224·50 m.
Oud-Appelscha		187·25–201·00 m.
Roden	114/23	191·50–213·00 m.

TEXT-FIG. 9. Southern boundary of eastern Venezuela Basin after Mencher *et al.* 1953, fig. 7; northern boundary coincides with 'mountain front'.

The following Miocene occurrences are shown:

Cabo Blanco, near Maiquetía Airport, Distr. Federal	Playa Grande formation
Cubagua Island, Socony Mobil Oil Company, Cubagua–1, 218′	Cubagua formation
Estado Guarico, Creole Petroleum Corp., GXB–5	Roblecito formation
.. .. Socorro–3	Chaguaramas formation
Estado Guarico, Venezuelan Atlantic Refining Company, Tucupido–2	Chaguaramas formation
Estado Guarico, Sinclair Oil & Refining Company, Piedra Azul–1	Chaguaramas formation
Estado Guarico, Venezuelan Atlantic Refining Company, Guama–1	Chaguaramas formation
Estado Guarico, Compañía Shell de Venezuela, Shothole 6043	Upper Santa Inés
.. .. Shothole 1146	Upper Santa Inés
Estado Guarico, Sinclair Oil & Refining Company, Camoruco–1, 2,350–2,790′	Chaguaramas formation
Estado Anzoategui, Compañía Shell de Venezuela, VC–1	Lower Santa Inés
.. .. Cagigal–1, 750–775′	Naranja equivalent
.. .. 4,450–5,025′	Verde equivalent, Oficina formation
.. .. Cagigal–2, 2,200–2,225′	Moreno member
.. .. 6,775–6,800′	Verde member, Oficina formation
Estado Anzoategui, Mene Grande Oil Company, Casca–1, 750–1,225′	Blanco member
.. .. 3,375–3,425′	Moreno member, Oficina formation
Estado Anzoategui, Phillips Oil Company, B–1, 625–1,175′	Blanco member, Oficina formation
Estado Anzoategui, Creole Petroleum Corp., El Roble–1 (RPN–1), 925–950′, 1,300–1,325′	Blanco member, Oficina formation
Estado Anzoategui, Socony Mobil Oil Company, Guario–1, 1,675–1,700′, 2,200–2,225′	Azul member, Oficina formation
Estado Anzoategui, Mene Grande Oil Company, OG–1, 2,125–2,150′, 3,250–3,275′	Freites formation
.. .. 3,750–4,650′	Oficina formation
Estado Anzoategui, Texas Petroleum Company, Mata–1	Oficina formation
Estado Monagas, Creole Petroleum Corp., El Salto–1	Freites formation, Oficina formation
Estado Monagas, Texas Petroleum Company, Sotil–1	Oficina formation
Estado Monagas, Creole Petroleum Corp., Hato–13	Freites formation; Oficina formation
Estado Bolivar, Compañía Shell de Venezuela, Cerro Negro–1	Oficina formation
.. .. Cerro Negro–2	Freites formation; Oficina formation
Estado Monagas, Compañía Shell de Venezuela, Cerro Negro–3	Freites formation; Oficina formation
Estado Anzoategui, Compañía Shell de Venezuela, outcrop sample St. 2992	Capaya formation
.. .. outcrop sample St. 3000	Capaya formation
.. .. outcrop sample Ol. 445	Capaya formation
Estado Monagas, Compañía Shell de Venezuela, outcrop sample Ol. 375, Rio Areo	Areo shale
.. .. outcrop sample Ol. 381, Rio Areo	Areo shale
Estado Monagas, Mene Grande Oil Company, SB–133, 925–6,250′	Carapita and Capaya formations
Estado Monagas, Creole Petroleum Corp., JGE–28	Buena Vista shale (=Areo shale)
.. .. Monaq–1	Carapita formation
.. .. J–274, 5,325–6,700′	Carapita formation
.. .. ORC–1, 2,800–3,800′	Carapita formation
.. .. ORC–2, 3,900–4,200′	Carapita formation
.. .. ORC–9	Carapita formation
Estado Monagas, Compañía Shell de Venezuela, ORS–3	Carapita formation
Estado Monagas, Creole Petroleum Corp., QGE–26, 2,900–4,300′	Carapita formation

Estado Monagas, Creole Petroleum Corp., QGE–29.	Carapita formation
Trinidad, Point-à-Pierre, Shell Trinidad Ltd., outcrop sample Ho. 207, Concord Quarry	Concord marl
Trinidad, Caroni County, Couva Ward, Springvale, near Couva, about ¾ to 1 mile S of Milton, outcrop sample (Mansfield 1925; Dartevelle 1943)	Springvale formation

TEXT-FIG. 12. The four stations shown are:

Parker 1956, Sta. 321, lat. 29° 30′ 30″ N, long. 89° 15′ W
Tampa Bay, Florida, lat. 27° 46′ N, long. 82° 31′ 36″ W
Cavalier 1956 Sta. 286, lat. 29° 40′ 35″ N, long. 93° 19′ 40″ W
Mees Cremer 1959 Sta. 83, lat. 4° 10′ 39″ N, long. 6° 10′ 25″ E

TEXT-FIG. 13. The eight stations shown are:

NW Gulf of Mexico: bathythermogram—Mabel Taylor 1932 Sta. 1106
C. canariensis—Cavalier 1956 Sta. 314, 27° 44′ 12″ N, 93° 43′ 48″ W
NE Gulf of Mexico: bathythermogram—Mabel Taylor 1932 Sta. 903
C. canariensis—Atlantis 1951 Sta. 152, 28° 09′ N, 85° 07′ W
Sargasso Sea: bathythermogram—Atlantis 1933 Sta. 1483, 21° 46′ N, 62° 48′ W
C. canariensis—Caroline 1933 Sta. 94, 18° 39′ N, 65° 03′ 30″ W
Gulf of Guinea: bathythermogram—Meteor 1926 Sta. 235, 3° 33′ 36″ N, 5° 6′ 42″ E
C. canariensis—Mees Cremer 1959 Sta. 206, 5° 24′ 01″ N, 4° 39′ 51″ E

TEXT-FIG. 14. The three occurrences shown are:

Albatross Sta. 2415, lat. 30° 44′ N, long. 79° 26′ W, 440 fms.
Port Antonio, Jamaica, 150 fms.
Caroline 1933 Sta. 94, lat. 18° 39′ N, long. 63° 03′ 30″ W, 300–470 fms.

TEXT-FIG. 15. The Middle Miocene occurrences shown are those listed under text-fig. 4 as Nos. 1, 2, 4, 4*a*, 5, 6, 7, 8, and 9; the Pliocene occurrences shown are those listed under text-fig. 4 as Nos. I, III, IV, VI, VI*a*, VII, VIII, IX, X, and XI; the Early Pleistocene occurrences shown are those listed under text-fig. 4 as Nos. A, B, C, D, and E; the Recent occurrences shown are those listed under text-fig. 3 as Nos. 1, 2, 3, 4, 5, and 6.

TEXT-FIG. 17. The Pliocene occurrences shown are those listed under text-fig. 4 as Nos. I, II, III, IV, V, VI, VI*a*, VII, VIII, IX, X, and XI; the Recent occurrences shown are those listed under text-fig. 3 as Nos. 1, 2, 3, 4, 5, and 6.

TEXT-FIG. 18*a*. Compiled from Canu 1907; Canu and Bassler 1923, 1929, 1931; Dartevelle 1933, 1952; Manzoni 1869; Vigneaux 1948, and others. Not shown on this chart, on the assumption of being junior synonyms, are:

Lunulites rhomboidalis Von Munster [=*Discoporella umbellata* (Defrance); *fide* Canu and Bassler 1929, p. 11]
Lunulites angusticostata Canu and Bassler [=*Lunulites subplena* Reuss; *fide* Dartevelle 1933, p. 57; 1952, p. 183]

TEXT-FIG. 18*b*. Compiled from Canu and Bassler 1920, 1923, 1928*a*; McGuirt 1941; Ulrich and Bassler 1904 and others; and incorporating own observations, e.g. the occurrence of *Lunulites ligulata* (Canu and Bassler) in the Byram marl at Byram, Pearl River, Mississippi, and the occurrences of *Cupuladria canariensis*, *C. doma* (d'Orbigny) and *Discoporella umbellata* (Defrance) in the Pleistocene of the Gulf Coast at the localities listed under text-fig. 4 as Nos. F and G.

TEXT-FIG. 19. Correlation chart largely based on one made by Mr. R. W. Barker, with the south Texas column (1) here added and the NW Florida column (6) adapted to include the latest views of Puri (1953). The following occurrences of *Lunulites spp.* are shown:

Column 2 (Louisiana)	
Rosefield, Catahoula Parish	Vicksburg (McGuirt 1941)
Column 3 (W Mississippi)	
Mint Springs Bayou, near Vicksburg	Mint Springs marl, KSEPL (ex Mr. J. J. Gouty)
Byram	Byram marl (Canu and Bassler 1920)

Column 4 (E Mississippi)	
Red bluff, Wayne County	Red Bluff clay (Canu and Bassler 1920)
Horton's Mill Creek, near Highway 45, Wayne County	Basal Marianna limestone, KSEPL (ex Mr. R. W. Barker)
Locality CX, W bank of Chickasawhay River, Wayne County	Paynes Hammock sand (1 fragment), KSEPL (ex Mr. R. W. Barker)
Column 5 (SW Alabama)	
One mile N of Monroeville	'Chimney Rock' member of Marianna limestone (Canu and Bassler 1920)
St. Stephens Bluff, Tombigbee River	Glendon, KSEPL (ex Mr. E. H. Rainwater)
Column 6 (NW Florida)	
Road cut, U.S. Highway 90, at Chipola River	Marianna limestone, KSEPL

The following occurrences of *Cupuladria canariensis* are shown:

Column 1 (S Texas)	
Gulf of Mexico, off Nueces County, Gulf Oil Corp. and others, Block 889, 3–A, 10,300′	Upper Frio, KSEPL (ex Mr. E. M. Wilkins)
Goliad County, Housh, Thompson & Crown Central C. G. Wood #1, 3,163–3,193′	Updip limit of Anahuac shale wedge, KSEPL
Column 2 (Louisiana)	
East Baton Rouge Parish, Superior Oil Producing Company's Duplantier Community No. 1 well, 7,671–7,687′	*Heterostegina* zone, Catahoula formation (McGuirt 1941)
East Baton Rouge Parish, Superior Oil Producing Company's Duplantier Community No. 1 well, 8,091–8,101′	*Marginulina* zone, Catahoula formation (McGuirt 1941)
Column 4 (E Mississippi)	
Limestone Creek, Wayne County	Chickasawhay, KSEPL (ex Mr. R. W. Barker)
Column 5 (SW Alabama)	
Choctaw Bluff, Alabama River, Clarke County	Chickasawhay, KSEPL (Mr. W. McGlamery Coll.; ex Mr. R. W. Barker)
Column 6 (NW Florida)	
Shell Bluff, Shoal River, N of Mossyhead, Walton County	Shoal River (type locality), KSEPL
One mile below Baileys Ferry, Chipola River	Chipola marl (Canu and Bassler 1923)
Jackson Bluff, Ochlockonee River, ¼ mile above Florida Highway 20 bridge	Choctawhatchee stage, *Ecphora* facies, *Pecten* Bed, KSEPL
Ibid.	Choctawhatchee stage, *Cancellaria* facies, KSEPL
W. D. McDaniel's farm, near Red Bay, Walton County	Choctawhatchee stage, *Arca* facies, marl with *Arca rubisiana*, KSEPL

TEXT-FIG. 20. The following occurrences of *Cupuladria canariensis* are shown:

Column 1 (Northern Guarico)	
Creole Petroleum Corp., GXB–5	Roblecito formation
Sinclair Oil & Refining Company, Piedra Azul–1	Chaguaramas formation
Venezuelan Atlantic Refining Company, Tucupido–2	Chaguaramas formation
Column 2 (Greater Anaco area)	
Compañía Shell de Venezuela, Cagigal–1, 750–775′	Naranja equivalent
.. .. 4,450–5,025	Verde equivalent, Oficina formation
Mene Grande Oil Company, Casca–1, 750–1,225′	Blanco member
.. .. 3,375–3,425′	Moreno member, Oficina formation
Socony Mobil Oil Company, Guario–1, 1,675–1,700′, 2,200–2,225′	Azul member, Oficina formation
Phillips Oil Company, B–1, 625–1,175′	Blanco member, Oficina formation
Column 3 (Greater Oficina area)	
Texas Petroleum Company, Mata–1	Oficina formation
Mene Grande Oil Company, OG–1, 2,125–2,150′, 3,250–3,275′	Freites formation
.. .. 3,750–4,650′	Oficina formation
Column 4 (Temblador area)	
Compañía Shell de Venezuela, Cerro Negro–1	Oficina formation
Compañía Shell de Venezuela, Cerro Negro–3	Freites formation

Column 5 (NW Anzoategui: 'mountain front')	
Compañía Shell de Venezuela, VC–1	Lower Santa Inés
Column 6 (N Anzoategui)	
Compañía Shell de Venezuela, outcrop samples St. 2992, St. 3000	Capaya formation
Column 7 (Northern Monagas)	
Creole Petroleum Corp., JGE–28	Buena Vista shale (=Areo shale)
Mene Grande Oil Company, SB–133, 925–6,250′	Carapita and Capaya formations
Creole Petroleum Corp., J-274, 5,325–6,700′	Carapita formation

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LOWER KIMERIDGIAN AMMONITES FROM THE DRIFT OF LINCOLNSHIRE

by the late W. J. ARKELL and J. H. CALLOMON[1]

ABSTRACT. A collection of ammonites is described from the drift of Lincolnshire; they are of Lower Kimeridgian age, Mutabilis Zone. Almost all of the specimens belong to the genera *Rasenia* and *Aulacostephanus*, and include several new species which are grouped into two new subgenera of *Aulacostephanus*: *Xenostephanus* and *Xenostephanoides*. These new forms have only recently been found *in situ* in England, and are known from the Kimeridge Clay of both east and west Scotland.

THIS paper describes a collection of ammonites made mostly by Dr. R. G. Thurrell while mapping in the Lower Cretaceous of north Lincolnshire, and now deposited in the Sedgwick Museum, Cambridge. The material is all from the drift, and hence does not provide primary stratigraphic evidence; its publication seems of interest, however, for a number of reasons. The various forms were found in such intimate admixture, often in the same block of stone, that there can be little doubt that they give a fairly representative picture of a closely contemporaneous population. Their age is Lower Kimeridgian, Mutabilis Zone. The material is in rock-facies and only slightly crushed, whereas the known exposures in the outcrop of the shales of the Mutabilis Zone in this country yield, mostly, only wholly flattened shells, which have not attracted collectors in the past. Our knowledge of the fauna of the Mutabilis Zone is therefore scanty.

The fauna consists overwhelmingly of forms of the perisphinctid subfamily Aulacostephaninae at the stage where *Rasenia* changes to *Aulacostephanus*, and includes several new and previously little-known forms of great interest. The classification of the genus *Rasenia* is at present still in a state of confusion, but a revision of *Aulacostephanus* has been published by Ziegler (1962). New names will therefore be mostly confined here to the forms being described.

In referring to specimens the following abbreviations will be used:

R, MS, SW: Thurrell collection, material from Ranby, Market Stainton, and South Willingham (Lincolnshire) respectively.
BM: British Museum (Natural History).
SM: Sedgwick Museum, Cambridge.

We wish to thank Dr. R. G. Thurrell for making his material available to us for description; Dr. B. Ziegler for discussions and criticisms, and for very kindly allowing us to see the manuscript of his monograph on *Aulacostephanus*; and Mr. A. G. Brighton (Sedgwick Museum), Dr. M. K. Howarth (British Museum), and Mr. R. B. Wilson (Geological Survey, Edinburgh) for help with material in collections in their custody.

---

[1] This paper is based in part on a provisional manuscript prepared by Dr. Arkell shortly before his illness in 1956. I am grateful to Mr. A. G. Brighton for passing the manuscript on to me for completion after Dr. Arkell's death in 1958. J. H. C.

[Palaeontology, Vol. 6, Part 2, 1963, pp. 219–45, pls. 27–33.]

SYSTEMATIC DESCRIPTIONS

Family PERISPHINCTIDAE Steinmann 1890

Subfamily AULACOSTEPHANINAE Spath 1924 (= RASENIINAE Schindewolf 1925)

This subfamily encompasses a well-defined offshoot of the main perisphinctid tree. It leads back to such typically perisphinctid forms as *Pictonia* in the basal Lower Kimeridgian, with evolute coiling, round whorl-section, and smooth, regular ribbing which passes over the venter without interruption. It terminates in end-forms of *Aulacostephanus* which are of quite different appearance, with compressed, angular whorl-section, smooth tabulate or grooved venter, and strong straight ribbing reminiscent in style of the Cretaceous genus *Hoplites*. Between these extremes, further wide variations in coiling and novel forms of ornamentation occurred, so that the whole subfamily, although in itself closely delimited, covers an unusually wide range of forms. Attempts at classification have usually started from a broad division of the subfamily into two parts: an earlier part grouped around the genus *Rasenia*, leading to the later forms grouped around *Aulacostephanus*. Besides these, there has, however, sprung into existence a large number of other generic names created often on the basis of insufficient material and stratigraphy, inadequate type specimens, and the requirements of phylogenetic theory. The resulting confusion cannot be fully analysed here, but, in order to justify the classification which will be adopted in this paper, a number of points have to be discussed.

(*a*) *Generic classification.* It seems sufficient to divide the subfamily into only two genera: *Rasenia* and *Aulacostephanus*. Further grouping according to sculpture can be conveniently incorporated at subgeneric level.

(*b*) *Dimorphism.* In common with apparently most other perisphinctids, the Aulacostephaninae seem to have been dimorphic, and it is possible to classify most of the shells as macroconchs or microconchs (for full discussion, see Callomon 1957, 1963). As elsewhere, it seems helpful to incorporate this distinction at subgeneric level.

(*c*) *The* Rasenia–Aulacostephanus *boundary.* The transition between these genera is so gradual that, in drawing a dividing-line, many difficulties arise. Development occurred in more than one character of the sculpture, and the breaks in the development of different characters occurred at different times. If the development of a single character were made the sole criterion, an unnatural classification would result. Thus, for example, the presence or absence of a ventral smooth band alone might seem a tempting distinction to use as criterion; but, as is in fact seen in the material being here described, among a collection of shells which in most other respects are clearly conspecific, some have a ventral smooth band, others not. Moreover, many have it at one stage of their ontogeny, but not throughout. The best approach seems to be to group specimens of a contemporaneous population according to species, taking all their characters into account. A particular arrangement of species into genera is then of lesser importance. The arrangement of borderline species used here has been chosen to accord fairly closely with the one used by Dr. Ziegler in his monograph of the genus *Aulacostephanus*, but no claims are made for its uniqueness. It serves also to bring out resemblances between the Lincolnshire material and the fauna of the Mutabilis Zone farther south.

Genus RASENIA Salfeld 1913

Type species. Rasenia involuta (Salfeld MS) Spath 1935, designated by ICZN Opinion 426.

Microconchs. The following subgenera may be recognized, arranged in order of decreasing coarseness of ribbing.

1. PRORASENIA Schindewolf 1925. Type species: *P. quenstedti* Schindewolf, figured 1926, pl. xix, fig. 1. (Synonym *Desmosphinctes* Schindewolf 1925, type species: *Perisphinctes mniovnikensis* Nikitin 1884, p. 30, pl. ii, figs. 11, 12.) Small, strongly ribbed species with lappets. Its special character is the presence of strong triplicate ribbing on the inner whorls, reverting to biplicate perisphinctoid on the final body-chamber. Spath (1935, pl. 14, 15) has figured and named three species from England, and Waterston (1951, pl. 2) records them from Scotland.

2. RASENIA sensu stricto. Salfeld attached the manuscript name *involuta* to a number of specimens in the British Museum, of which Spath selected and figured only one. As, however, Spath is formally the author of the species, this specimen is holotype of *involuta* Spath rather than lectotype of *involuta* Salfeld, and both species and genus have to be interpreted by Spath's figured specimen. This is broken and slightly incomplete, and, in the absence of the last few sutures and peristome, it is impossible to tell conclusively whether the specimen is adult or not. All of the preserved last three-quarters whorl is, however, body-chamber, and it gives the impression near the end of slight contraction indicating maturity. There exist in the collections other specimens (e.g. Geol. Survey Coll. 25550–1) which agree with the holotype closely in all respects including size, and which, although also without peristomes, carry similar amounts of body-chamber. A complete adult from Scotland has been figured by Waterston (1951, pl. ii, fig. 8*a*, *b*). Its final diameter is 40 mm., and the body-chamber is terminated by a final constriction. The peristome shows the stump of a lappet. It seems certain, therefore, that *Rasenia* s.s. was fully grown at *c*. 40 mm. diameter with strong unmodified ribbing maintained to the end, and hence microconch; and it seems probable that it carried at least short lappets. Its special character is the differentiation of strong, sinuous primary and fine, fasciculate secondary ribbing. Inner whorls are always well covered, involute and inflated.

In a recent revision of the genus Geyer (1961, p. 86), rather than re-examine the type specimen of *involuta* Spath himself, quotes Spath's statement describing it as 'small, inner whorls . . .', which, whatever significance one may attach to size in taxonomy, it is not; and interprets *Rasenia* sensu stricto as covering large, typically macroconch forms. *Rasenia* s.s. is now capable of precise interpretation, and it is hoped that the confusion of the past has found an end.

Geyer does point out that, if *Rasenia* sensu lato is taken to include *Involuticeras* Salfeld as a subgenus (see below), *involuta* Spath 1935 is junior homonym of *involuta* (Quenstedt 1849), and proposes *Rasenia anglica* nom. nov. = *involuta* Spath non Quenstedt.

3. RASENIOIDES Schindewolf 1925, p. 335. Type species by original designation: *Nautilus striolaris* Reinecke 1818, which Schindewolf states should be interpreted by *Am. striolaris* Quenstedt pars 1888, pl. 124, fig. 8, non Reinecke. Reinecke's specimen seems to be lost, but his figure represents recognizable characters which seem to differ considerably from

those shown by Quenstedt's figure, notably in whorl-section and coiling. There is nothing in Reinecke's description to indicate a smooth venter, which, in this case, puts Quenstedt's specimen in *Aulacostephanus*; and, as small 'striolarian' Rasenids of the *thermarum* group are common in the Mutabilis Zone (see below), *Rasenioides* fills a useful role, interpreted here as microconch subgenus characterized by very fine, dense fasciculate ribbing. Lappets proper are not known, although some specimens carry a slightly raised sinuous collar on the mouth-border.

(PRORASENIOIDES Schindewolf 1925, p. 338; type species by original designation: *P. transitorius* Schindewolf, which is nom. nov. for *Am. striolaris* Quenstedt pars 1888, pl. 107, figs. 12, 13, non Reinecke, with additional specimens figured by Schindewolf 1926, p. 507, pl. xix, figs. 3–5, resembles *R. striolaris* Reinecke more than *Am. striolaris* Quenstedt 1888, pl. 124, fig. 8. However, as the latter is not strictly the type species of *Rasenioides* whereas, according to the Rules, the former is, *Prorasenioides* and *Rasenioides* are here regarded as synonymous.)

Macroconchs

4. ZONOVIA Sasonov 1960. Type species by original designation: *Amm. uralensis* d'Orbigny 1845. Large, evolute, coarse-ribbed forms with smooth apertures.

5. EURASENIA Geyer 1961, p. 87, 90. Type species: *Amm. Rolandi* Oppel 1863. Large, coarsely ribbed forms intermediate between *Zonovia* and *Involuticeras.*

6. INVOLUTICERAS Salfeld 1913. Type species by monotypy (Salfeld 1914, p. 175) or subsequent designation (Spath 1931): *Amm. involutus* Quenstedt 1849. Large, involute, compressed forms, finely ribbed on inner whorls, becoming smooth.

7. ?SEMIRASENIA Geyer 1961, p. 87, 92. Type species: *Amm. Möschi* Oppel 1863. The holotype of *möschi* is 45 mm. in diameter, and if Oppel's statement in the legend to his figure, that the suture-line shown is the last, is to be believed, it carries three-quarters whorl body-chamber and is hence nearly complete. Geyer states the final size to be 'probably about 70 mm.' without giving reasons based either on Oppel's specimen, which he refigures but does not redescribe, or additional material, of which he cites only one additional, even smaller specimen. The peristome remains unknown, and maximum size and ontogeny of mature examples in doubt.

The only other species included by Geyer in *Semirasenia* is *Amm. thermarum* Oppel. The holotype of this species seems to us to fit equally well into *Rasenioides*, however.

Subgenus RASENIA s.s. Salfeld

1. *Rasenia* (*Rasenia*) sp. ind.

cf. *Rasenia evoluta* (Salfeld MS), Spath 1935, pp. 48–49, pl. 14, fig. 6*a*, *b*.

Material. One (MS 128).

Description. Diameter 17 mm., sutures invisible, but at least half the outer whorl appears to be body-chamber. Coiling moderately evolute; ribbing straight, coarse and strong, modifying on the last quarter-whorl to typically rasenid fasciculate style, passing uninterruptedly over the venter.

Spath assumed that *R. evoluta* was a large species (1935, p. 49, footnote). Like *R. involuta*, however, he figured only a single specimen (BM C.8046 from Market Rasen), which is therefore holotype. It is a wholly septate nucleus, maximum diameter only 24 mm., and on comparing the actual specimen with the type of *R. involuta* (which is broken and shows the inner whorls well) at similar diameters, it is hard to detect even the minutest differences between them. Whatever else Spath may have had in mind, *R. involuta* and *R. evoluta* as defined by the monotypes are the same, and the latter name may be dropped with little regret.

Subgenus RASENIOIDES Schindewolf (= PRORASENIOIDES Schindewolf)

1. *Rasenia* (*Rasenioides*) cf. *transitoria* (Schindewolf)

Plate 33, fig. 2

Ammonites striolaris Quenstedt 1888 pars, pl. 107, figs. 12, 13.
Prorasenioides transitorius Schindewolf 1925, p. 338.

Material. One (MS 80a).

Description. The specimen is crushed, but agrees well with Quenstedt's figures. The ribbing passes uninterruptedly over the venter where visible. Sutures and peristome are missing, but at the maximum diameter of 32 mm. at least some of the outer whorl appears to be body-chamber. The umbilical seam uncoils slightly near the end, indicating maturity.

2. *Rasenia* (*Rasenioides*) cf. and aff. *lepidula* (Oppel)

Plate 32, figs. 19–21

cf. *Ammonites lepidulus* Oppel 1863, p. 242, pl. 67, fig. 4*a*, *b*.

Material. Five, more or less fragmentary (MS 1, 33–35, 53).

Description and comparisons. Oppel's figured type specimen was wholly inadequate to form the basis of a new species, only the final quarter-whorl being recognizable. Fortunately, this shows the specimen to have been a complete adult, and the name is used here for forms of the *R. thermarum* group which are rather larger and more evolute than *R. thermarum*, and in which the secondary ribs cross the round venter with perhaps some weakening but without actual interruption.

Agreement is best between Oppel's figure and the terminal fragment shown in Plate 32, fig. 21. This shows the peristome: the aperture is sinuous, preceded by a broad, shallow constriction and provided with a raised collar, as in *R. thermarum*, with no lappets; whereas Oppel's specimen was armed with lappets.

Oppel's species is very close to *Rasenia eulepida* Schneid (see below). This, however, has a prominent smooth band on the venter (*teste* Dr. Ziegler), but whether this serves to distinguish it from *R. lepidula* it is impossible to say in the absence of more information on the inner whorls of the latter. Schneid also stated that the distinguishing feature of *R. lepidula* was the persistence of the characteristic sheaves of multiple secondaries arising from each primary rib right to the end, whereas in *R. eulepida* near the aperture the ribbing reverts to simple bi- or triplication.

3. *Rasenia* (*Rasenioides*) *thermarum* (Oppel)

Plate 32, figs. 13–18

Ammonites thermarum Oppel 1863, p. 243, pl. 65, fig. 5*a*, *b*.
Rasenia (*Semirasenia*) *thermarum* Geyer 1961, p. 106, pl. 8, fig. 9, (? 10).

Material. Eight, and fragments (MS 9, 14, 31–32, 36, 64, 78, 118; R 20).

Description. All of the specimens seem to carry some body-chamber, and in one (Pl. 32, fig. 14) the peristome is preserved on one side. The impression that they are fully grown and nearly complete is supported by lack of remains of similar shells of larger ammonites. The average size of the eight specimens is 19·5 mm.: Oppel's holotype is 20 mm. in diameter, with nearly complete body-chamber, and he says: 'All the specimens found so far possess a nearly complete body-chamber. The partly visible peristome appears to be straight, without showing the formation of lappets.' The peristome observed here is also without lappet, but is sinuous and bears a slightly raised collar; it is preceded by a broad shallow constriction.

The Lincolnshire material therefore agrees well with Oppel's specimens and differs only in being slightly less inflated than the holotype. On some specimens the secondaries weaken on the venter, which is round, but they are not fully interrupted. Geyer considers *R. thermarum* to be a somewhat larger species, up to 40 mm. in diameter, effectively reinterpreting it on the basis of a specimen previously figured by de Loriol (1878, pl. xiii, fig. 5), which is variocostate like *Aulacostephanus möschi*. The total material available to him was only three specimens, however, including the holotype; and as there is no reason to believe that the holotype is in any way imperfect, incomplete, or untypical, but in fact representative of a readily recognizable group as shown by the Lincolnshire material, we prefer to continue to interpret *R. thermarum* as closely defined by Oppel's type, and retain it in *Rasenioides*.

4. *Rasenia* (*Rasenioides*) cf. *striolaris* (Reinecke)

Plate 31, figs. 6*a*, *b*

Nautilus striolaris Reinecke 1818, p. 77, figs. 52, 53.
cf. *Rasenia* (*Rasenioides*) *striolaris* Geyer 1961, p. 10.

Material. Two (MS 29, figured; MS 141).

Description. The figured specimen is only 16·5 mm. in diameter but carries half a whorl body-chamber. The umbilicus is only some 20 per cent. of the diameter, and inner whorls are almost wholly concealed. The second specimen is crushed, but similar.

Reinecke did not state the magnification of his figure, and his specimen seems to be lost. The present material agrees well with it, if we assume that his figure was about natural size. Geyer has designated and figured a neotype (1961, pl. 21, fig. 3) without, however, an adequate description. Thus, there is no mention of whether it, or supporting material, carries any body-chamber; there is no ventral view; and no indication of the form of the peristome. Moreover, the specimen differs considerably from Reinecke's figure in being much more evolute with very little inclusion of inner whorls, quite unlike both Reinecke's side-view and section.

Subgenus ZONOVIA Sasonov 1960

1. *Rasenia* (*Zonovia*) sp. ind.

Plate 33, fig. 3*a*, *b*

Material. One fragment (R 2).

Description. The specimen consists only of a quarter of two contiguous wholly septate whorls, corresponding to a diameter of about 45 mm. The whorl-section is round, inflated, depressed; the ribbing blunt, subdued, coarse. Short, straight bullate primaries trifurcate into strong secondaries, which cross the venter with sight weakening but no interruption.

Genus AULACOSTEPHANUS Sutner and Pompeckj in Tornquist 1896

Type species. Ammonites mutabilis d'Orbigny non Sowerby = *Ammonites pseudomutabilis* de Loriol 1874, designated by ICZN Opinion 302. A lectotype from the d'Orbigny collection has been figured by Ziegler (1962, pl. 15, fig. 8).

The boundary between *Rasenia* and *Aulacostephanus* is here being drawn such that most forms assigned to the latter have a smooth band on the venter in at least one stage of their ontogeny. Simultaneously, the whorl-section becomes more compressed and quadrate, the venter tending to flatten; and inner whorls are markedly more evolute and serpenticone than in *Rasenia* so that the secondary ribs on them are often partly exposed. The umbilici are in consequence also usually shallow, with often characteristically smooth, gently sloping or even barely perceptible walls. These features together allow a fairly sharp line to be drawn between the two genera.

The material from Lincolnshire falls into four subgenera: two pairs each consisting of a microconch and a macroconch. One of these pairs of subgenera, *Aulacostephanites* and *Aulacostephanoides*, differs but little from *Rasenia* and includes the forms well known from the Mutabilis Zone elsewhere. The other pair of subgenera, *Xenostephanoides* and *Xenostephanus*, is new. A few specimens have been known previously, but the presence of a considerable number in the material under consideration gives it a peculiar stamp of great interest.

Microconchs

1. AULACOSTEPHANITES Ziegler 1962. Type species: *Rasenia eulepida* Schneid 1939, p. 146, pl. v, figs. 13, 13*a*. Small, evolute forms with lappets; ornament similar to that of *Rasenioides*. Smooth band on venter, at least on inner whorls. In crushed material from the typical Mutabilis Zone shales in the south of England *Rasenioides* and *Aulacostephanites* may be indistinguishable.

2. XENOSTEPHANOIDES subgen. nov. Type species: *Aulacostephanus* (*Xenostephanoides*) *thurrelli* sp. nov. (see below). Small species (*c*. 40–50 mm.); coiling evolute, particularly on inner whorls; whorl-section rounded quadrate. Ribbing strong; short bullate primaries with sheaves of strong, straight secondaries often separated from the primaries by a smooth band on the whorl-side. The style of the ribbing is already much more like the 'hoplitid' of the later aulacostephanoids than the sinuous one of the rasenids. On the final body-chamber it may revert to simple biplication, as in *Prorasenia*. The

venter carries a smooth band, sometimes accentuated by a groove. Peristomes with oblique final constrictions and short lateral projections not really long enough to call lappets.

Macroconchs

3. AULACOSTEPHANOIDES Schindewolf 1925. Type species, by original designation: *Amm. desmonotus* Oppel. The type specimen of Oppel's species (1863, p. 241, pl. 67, fig. 1*a*, *b*) seems to have been lost during the war. His figure establishes the style of ribbing, coiling, and umbilicus well, and shows clearly a smooth band on the venter. Oppel stated, however, that no sutures were visible anywhere, and that the peristome was unknown; and it is therefore impossible to say whether the specimen (the only one known to Oppel) was fully grown and complete, or merely the nucleus of a much larger form. This makes the species a highly unsuitable one on which to found a genus, and interpretations have been correspondingly varied. Dr. Ziegler has redescribed the species on the basis of additional material. Among this is one specimen (Ziegler 1962, pl. 2, fig. 14) which resembles the lost holotype extraordinarily closely, with unfortunately the same shortcomings. Others lead from this to more or less complete adults, which are large and nearly smooth with simple peristomes. We follow this interpretation of *A. desmonotus*, which is thus a macroconch.

The subgeneric characters of *Aulacostephanoides* are therefore: macroconch; rasenid ornamentation on the inner whorls which fades, becoming smooth on the final body-chamber; ventral smooth band on at least the inner whorls; simple peristomes. From general experience involuteness of coiling seems of lesser importance, and Dr. Ziegler shows that *Aulacostephanoides* can usefully accommodate a gradation of forms ranging from the discoidal *A. linealis* (Quenstedt) to the true evolute *A. mutabilis* (Sowerby). Several species of the subgenus differ but little from forms still included in *Rasenia*, the dividing-line from which is arbitrary, as discussed above.

4. XENOSTEPHANUS subgen. nov. Type species: *Aulacostephanus* (*Xenostephanus*) *ranbyensis* sp. nov. (see below). Large species (*c.* 120 mm.); coiling stout, depressed, and evolute—particularly on the inner whorls. Primary and secondary ribbing well differentiated on inner and middle whorls, the former tending to extreme bullae or tubercles on the umbilical margin, the latter characteristically strong, triplicate, with intercalatories, fusing into the primaries or sometimes separated from them by a narrow smooth band on the whorl sides. Venter flat on inner whorls, with smooth band, sometimes accentuated by a groove. On the body-chamber the ribbing becomes subdued and degenerates to more perisphinctid form: primary ribs biplicate smoothly or become merely single widely spaced ridges. The whorl-section becomes round, and ribbing passes over the venter without interruption. Peristomes simple.

Inner and intermediate whorls in some species are almost fully homeomorphic with the quite unrelated earlier genus *Reineckeia*; outer whorls are as in *Rasenia* (*Zonovia*), especially *R. uralensis* (d'Orbigny).

Xenostephanus and *Xenostephanoides* form a typical macroconch and microconch pair, and it would be difficult to find a clearer demonstration of the dimorphism among the perisphinctids. The inner whorls are so similar that it would be hard to sort them out in immature, incomplete, or fragmentary material.

Subgenus AULACOSTEPHANITES Ziegler 1962

1. *Aulacostephanus* (*Aulacostephanites*) cf. *eulepidus* (Schneid)

Plate 32, figs. 1–8

Rasenia eulepida Schneid 1939, p. 146, pl. v, figs. 13, 13*a*.
Aulacostephanus (*Aulacostephanites*) *eulepidus* Ziegler 1962, p. 44, pl. 341, figs. 2–7, 8 *partim*, ? 11, 14.

Material. Twenty-five (24 from MS; and R 5), and fragments.

Description and remarks. The Lincolnshire material seems to be consistently somewhat smaller than the type (33 mm.), for the average diameter of seventeen complete adults is 25 mm. (standard deviation 3·9 mm. = 15·5 per cent.). The style of ribbing, however, is the same, including the degeneration of the ribbing near the end, which Schneid cited as diagnostic compared with *Am. lepidulus* Oppel. Peristomes are preserved in several specimens. There is usually a slight terminal constriction and a raised mouth-border. Lateral extensions may be short (Pl. 32, figs. 3, 5), or long enough to qualify as lappets (figs. 2, 10). Smooth bands on the venters are generally present, but narrow and inconspicuous, and they die out on the last half-whorl of body-chamber.

The question of the generic position of the specimens here described raises in its most acute form the difficulty attending attempts to divide *Aulacostephanus* from *Rasenia*. The ventral smooth band is undoubtedly much less prominent here than in the type of *A. eulepidus* and other south German material, and the Lincolnshire forms might, on this account, rest more comfortably in *Rasenia* (*Rasenioides*), with possibly gradations to *R. thermarum* (Oppel). On the other hand, the style of coiling and ribbing resembles *A. eulepidus* much more closely than *R. thermarum* or any other *Rasenioides* so far described (with the possible exception of *R. lepidula* (Oppel), which we exclude from consideration because of the imperfection of the type); and there is gradation to the forms described as *A. ebrayoides* below, which have quite prominent smooth bands on the venter.

It seems therefore that we are here sampling the *Rasenia–Aulacostephanus* boundary at a slightly different stage from that observed in central Europe. There the distinction between *Rasenioides thermarum* and *Aulacostephanus eulepidus* is clear, and the latter grades into more coarsely ribbed forms which nevertheless retain the rasenid (fasciculate) style of secondary ribbing, and which Ziegler designates *A. peregrinus* nov. In contrast, these forms appear to be absent in the Lincolnshire material, which, instead, shows more or less gradation from *A. ebrayoides* (unknown in central Europe), via *A. eulepidus*, to *R. thermarum*. Whether these differences reflect slight differences in ages, or ecological factors (geographic subspeciation), it is at present hard to say.

A. eulepidus is also found in the Mutabilis Zone of Mull (cf. Pl. 33, figs. 4–6).

2. *Aulacostephanus* (*Aulacostephanites*) *ebrayoides* sp. nov.

Plate 30, figs. 14–18

Material. Nine (eight from MS, and R 16), and fragments.

Description. The holotype, MS 5 (Pl. 30, fig. 14) is 26 mm. in diameter, with half-whorl body-chamber preserved. The remaining material is of similar size. Coiling is evolute, the whorl-section quadrate. Ribbing is dense, but strong and sharp, straight, triplicate or biplicate with intercalatories; the furcation point is very low on the whorl-side, so that the primaries (about twenty-two on the outer whorl) are reduced to short ridges on the umbilical margins. There is a distinct smooth band on the venter on inner whorls, fading somewhat on the body-chamber.

Comparisons. The species differs from *A. eulepidus* through the reduced contrast between primary and secondary ribbing, and the straightness and coarseness of the latter. Its name reflects the close homeomorphism with the Bathonian genus *Ebrayiceras* Buckman (Morphoceratidae), e.g. *E. pseudo-anceps* (Ebray) (see Arkell 1955, pl. xvii, figs. 7–11).

There are occasional specimens with more flexuous, but still coarse, secondary ribbing (Pl. 32, figs. 9, 10, with short lappets), which may link *A. ebrayoides* with *A. eulepidus.* These coarse forms of *Aulacostephanites* occur also in Mull (Pl. 33, fig. 7).

Quenstedt's *Amm.* cf. *striolaris* pars, 1888, pl. 107, fig. 18 seems to resemble *A. ebrayoides* closely in its ribbing, but differs in having a much more prominent ventral smooth band, and a deep terminal constriction (which may, however, have only varietal significance.)

3. *Aulacostephanus* (*Aulacostephanites*) sp. aff. *desmonotus* (Oppel)

Plate 32, figs. 11, 12

cf. *Ammonites desmonotus* Oppel 1863, p. 241, pl. 67, figs. 1*a*, *b*.

Material. Three (MS 76, 115; R 17).

Description and comparisons. All three specimens attain between 20 and 23 mm. and appear to carry some body-chamber. They resemble the other specimens described here under *Rasenia thermarum* in ornament, but are distinctly more compressed, have prominent ventral smooth bands and the characteristic shallow umbilicus of Oppel's *Amm. desmonotus.* The latter, however, probably attained a large size (see discussion above).

4. *Aulacostephanus* (*Aulacostephanites*) sp. aff. *möschi* (Oppel)

Plate 32, figs. 22–24

cf. *Ammonites möschi* Oppel 1863, p. 240, pl. 65, fig. 2*a*, *b*.
Ammonites cf. *striolaris* Quenstedt pars 1888, p. 969, pl. 107, fig. 17.

Material. Eleven (MS, ten; R 1), and fragments (MS).

Description and comparisons. These specimens are characterized by the absence of primary ribbing on the inner whorls, which carry only very dense, fine secondary ribbing. The whorl-section is compressed, umbilicus shallow, and there is a ventral smooth band. Agreement with Oppel's figure is fairly close, except that *A. möschi* shows no trace of a ventral smooth band, is bigger, and has the primary ribs, when they appear, lower on the whorl-side. The best agreement is with Quenstedt's specimen.

EXPLANATION OF PLATE 27

Fig. 1*a–c*, *Aulacostephanus* (*Xenostephanus*) *ranbyensis* sp. nov. var. *elshamensis* var. nov. Adult, with half a whorl body-chamber. BM C.47908, T. B. Parks coll., from Elsham, Lincs. All natural size.

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Subgenus AULACOSTEPHANOIDES Schindewolf, emend. Ziegler

1. *Aulacostephanus* (*Aulacostephanoides*) *mutabilis* (J. de C. Sowerby)

Plate 31, fig. 3

Ammonites mutabilis J. de C. Sowerby 1823, **4**, p. 145, pl. 405, fig. 1.
Rasenia mutabilis Salfeld 1913, p. 129.
Pararasenia mutabilis Arkell 1933, p. 612, pl. xxxix, figs. 5, 5*a* (holotype refigured).
Rasenia mutabilis Arkell 1951, p. 188.
Aulacostephanus (*Aulacostephanoides*) *mutabilis* Ziegler 1962, p. 62, figures and plates.

Material. One (MS 80).

Description. The specimen, half an ammonite, is somewhat crushed; maximum diameter 175 mm., wholly septate, the last few septa approximated and degenerate. The complete shell must have attained some 210 mm. Inner whorls are evolute; the whorl-section is at all stages compressed with barely perceptible umbilical walls. Well-differentiated, fine, dense, secondary ribbing is visible to at least 60 mm. with occasional feeble constrictions and flared ribs; primary ribs persist to 90 mm. Thereafter the shell is wholly smooth. Venter on inner whorls not visible.

Remarks. There has been confusion in the past in interpreting this species, largely as a result of Sowerby's poor illustration. The holotype (BM 43934) has a maximum diameter of 71 mm. and is wholly septate, with none of the degeneration and approximation of the last sutures rather typical of adults of this species. Despite the sudden end of primary ribbing at a shallow constriction at 52 mm., it seems certain that the holotype is the inner part of what was a much larger shell. The secondary ribbing on the venter is interrupted by a distinct smooth band. The whorl-section is compressed and angular. All these points are exemplified in another specimen figured here (Pl. 31, fig. 3, from Cambridgeshire) which resembles the holotype very closely, and is also wholly septate to 105 mm. It also shows something of the inner whorls, invisible in the holotype, which are evolute, exposed, and densely ribbed.

As for the generic position of the species, the style of ribbing on middle whorls is that of *Rasenia*; but the compressed whorl-section, evolute inner whorls, shallow umbilical walls, and ventral smooth band place it firmly in *Aulacostephanus*. [This view is contrary to that expressed previously by Dr. Arkell (1951, p. 188); but on re-examining both the holotype and supporting material, and in the light of Dr. Ziegler's study of the whole genus *Aulacostephanus* it seems the only possible one. J. H. C.]

2. *Aulacostephanus* (*Aulacostephanoides*) sp. nov.?, aff. *mutabilis* (Sowerby)

Plate 31, figs. 1, 2

Material. Two, and fragments (MS 37, 102; R 5).

Description. This species resembles *A. mutabilis* in all respects, but seems to be much smaller. Thus the specimen figured in Plate 31, fig. 1 is apparently adult, and complete with peristome at the same size (110 mm.) at which *A. mutabilis* itself (Pl. 31, fig. 3) is still septate. The same specimen is rather more evolute than *A. mutabilis*, and all ribbing has disappeared at 60 mm. The specimen shown in Plate 31, fig. 2 has inner whorls which are evolute and densely ribbed as in *A. mutabilis*; likewise the imprint of the flat venter of the penultimate whorls in the outer (body-chamber) whorls shows the secondary ribbing to be dense, with occasional feeble constrictions and slightly flared ribs, and interrupted by a smooth band.

Similarly, small forms (for macroconchs) are known from the Kimeridge Clay of Cromarty (Scotland). They are to be described by Dr. Ziegler, who proposes the name *R. askepta* for them. They differ from those described here, however, in having oval whorl-section, involute inner whorls, and secondary ribbing uninterrupted on the venter, i.e. belong still to *Rasenia*. Their precise age is not known.

3. *Aulacostephanus* (*Aulacostephanoides*) *circumplicatus* (Quenstedt)

Plate 31, figs. 4, 5; Plate 33, figs. 9–11

Ammonites circumplicatus Quenstedt 1888, p. 978, pl. 107, fig. 19.
Ammonites cf. *trifurcatus* Quenstedt 1888, p. 971, pl. 107, fig. 21.
Tobolia pseudotrifurcata Sasonov 1960, p. 156, pl. v, fig. 4 (= nom. nov. for, and reproduction of original figure of *Amm.* cf. *trifurcatus* Quenstedt, cited above).

Material. One, and two fragments (MS 51, 120; R 19).

Description. The specimen shown in Plate 31, fig. 4 is septate to only 55 mm., and if adult, could not have exceeded 80 mm. complete. The whorl-section is slightly compressed, and in both figured specimens the secondary ribbing is weakened over the venter, but not actually interrupted.

Remarks and comparisons. The present material agrees with *A. circumplicatus* in size and style of ribbing; but the holotype has an exceptionally prominent and broad smooth ventral band. This is, however, in part due to a deformity, and, according to Dr. Ziegler, the ventral smooth band is unusually variable in the species, some specimens being practically without.

There is a considerable resemblance to *Rasenia gemmata* Schneid (1939, p. 147, pl. v (ix), figs. 9, 9*a*), which, however, differs in being inflated, with depressed whorl-section, and is more involute.

The species is common in the Kimeridgian exposure on Mull (Pl. 33, figs. 9–11), and some of the specimens have a clearly defined ventral smooth band.

Subgenus XENOSTEPHANOIDES nov.

1. *Aulacostephanus* (*Xenostephanoides*) *thurrelli* sp. nov.

Plate 30, figs. 1–3

Material. Eight, and fragments (R, five; MS, two; SW, eleven).

Description. The holotype (R 11; Pl. 30, fig. 1) is 44 mm. in diameter; septate to 40 mm.,

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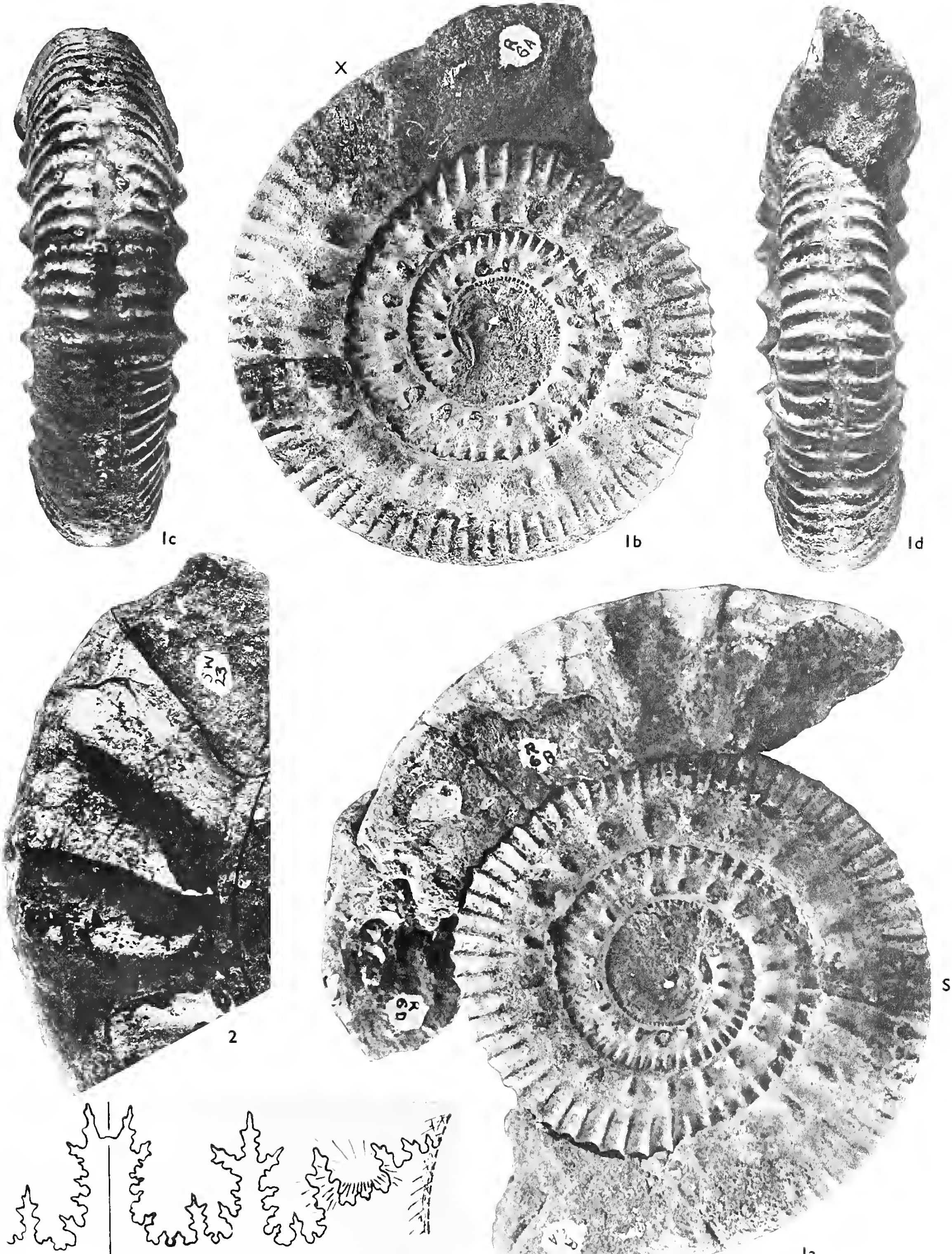
EXPLANATION OF PLATE 28

Fig. 1*a–e*, *Aulacostephanus* (*Xenostephanus*) *ranbyensis* sp. nov. Holotype; adult, with five-eighth whorl body-chamber preserved (1*a*). Suture-line at *s* shown in fig. 1*e*, ×2. Thurrell coll. R 6, from Ranby, Lincs.

Fig. 2, *Aulacostephanus* (*Xenostephanus*) cf. *ranbyensis* sp. nov. Body-chamber fragment, showing the peristome. Thurrell coll. SW 23, from South Willingham, Lincs.

All natural size, except fig. 1*e*.



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with a quarter-whorl body-chamber preserved. The last three septa are approximated, with some degeneration. The coiling is extremely evolute, and the dimensions (between and through ribs or tubercles) at 45 mm. are: 24·5–26·5, 25·5–31, 49. Primary ribs are in the form of tubercles on the umbilical margin (20 per whorl at 45 mm.; 21 at 30 mm.); secondaries are trifid or bifid with frequent intercalatories, separated from the primaries by a nearly smooth lateral spiral band. On the last half-whorl, the secondaries revert to widely spaced, very coarse bifid without intercalatories indicating, together with septal approximation, that the specimen was adult. The secondary ribbing is extremely strong and coarse, resembling that of *A. undorae* (Pavlow) of the Eudoxus Zone, but is quite different on the venter. In *A. thurrelli* it is interrupted by a deep narrow smooth band, accentuated by a groove, with no tendency to form ventro-lateral tubercles.

The paratype R 25 (Pl. 30, fig. 2) resembles the holotype closely. It is septate to only 34 mm., but shows the complete body-chamber of five-eighth whorl with peristome at 50 mm. The ribbing reverts to strictly biplicate on the last quarter whorl; an oblique constriction follows an isolated triplicate rib. The lip of the aperture is flared into a collar on the venter, and has a slight lateral projection too short to be called a lappet proper.

Presumed inner whorls are shown in Plate 30, fig. 3, although no septa are visible.

The species or a close ally seems to be present in the Kimeridgian of Mull (cf. Pl. 33, fig. 8) to judge by inner whorls; but the imprint of the outer whorls is too badly distorted to be certain. There is also a specimen from the Cromarty coast (Royal Scottish Museum, Edinburgh, Hugh Miller coll.).

2. *Aulacostephanus* (*Xenostephanoides*) *lindensis* sp. nov.

Plate 30, figs. 4–13

Derivation. Lindum is the Roman name for Lincoln.

Material. Twenty-seven (SW, twenty-one; R, three; MS, four), and fragments.

Description. The material is plentiful but poorly preserved, and no single specimen is complete. It is with some hesitation, therefore, that we select the specimen MS 13 (Pl. 30, fig. 10) only formally as holotype and designate the other nine figured specimens (Pl. 30, figs. 4–9, 11–13) paratypes, although for purposes of description it would be best to regard all ten as syntypes.

Sutures are rarely visible, but from the difference in preservation between outer and inner whorls (which are usually flattened) it seems probable that most of the specimens carry some body-chamber. The holotype itself definitely does, and was presumably complete at about 30 mm. diameter. Another fragment (SW 59) shows the final peristome with oblique constriction, flared collar, and short incipient lappet (just as in *A. thurrelli*) at a final diameter of *c.* 40 mm. The species is thus small.

The coiling is moderately involute, the whorl-section stouter than in *A. thurrelli*. Ribbing is dense and moderately strong, with three, sometimes four, secondaries per primary, separated, as in *A. thurrelli*, by a lateral smooth band. The venter is flat, broad, with a narrow smooth band but no groove. Inner whorls are shown in Plate 30, fig. 13.

Comparison. The species most closely resembles *Aulacostephanus thurrelli* although the stouter, more involute coiling and finer ribbing appear to be consistently distinct. It stands, like *A. thurrelli*, apart from all other contemporaneous aulacostephanids; but, in its resemblance to some later forms of the *A. eudoxus* group, it heralds the future development of the genus.

A. lindensis has also been found in the drift of Norfolk (SM J48657, one specimen, Baden-Powell coll.).

For completeness it is convenient to mention here another form which belongs to this group.

3. *Aulacostephanus* (*Xenostephanoides*) *scoticus* nom. nov. = *Aulacostephanus* cf. *autissiodorensis* (Cotteau) Spath 1935, p. 49, pl. 13, figs. 8*a*, *b* (BM C13216)

Remarks. The specimen figured by Spath from Culgower, eastern Scotland, seems unique. It carries some body-chamber on which the otherwise trifid ribbing reverts to biplication, indicating maturity, as in *A. thurrelli*; *A. scoticus* is therefore a small species and not a young specimen of giant forms like *Rasenia borealis* Spath, as Spath supposed. Its evoluteness and style of ribbing, particularly on the inner whorls, are typical of *Xenostephanoides*. It differs from *A.* (*X.*) *thurrelli* principally in having rather more inflated inner whorls, about nine more ribs per whorl, and a less-pronounced ventral smooth band, the ventral ribbing on the inner whorls being weakened without actual interruption. The exact horizon is unknown, although there are other Mutabilis Zone faunas from the same area.

Subgenus XENOSTEPHANUS nov.

1. *Aulacostephanus* (*Xenostephanus*) *ranbyensis* sp. nov.

Plate 28, figs. 1*a–e*, 2; Plate 29, fig. 4

Material. Two (R 6; BM C.47909), and fragments (SW).

Description. The holotype (R 6) is a splendidly preserved internal cast of 120 mm. maximum diameter, septate to 81 mm., with the last three sutures approximated and simplified. The body-chamber is broken, but, to judge from the highly degenerate last few visible ribs, represented very nearly up to the peristome and hence occupying five-eighths of a whorl.

Dimensions: at 115 mm.: 23, *c*. 26, 48.
80 mm.: 25–27, 30–33, 54.
55 mm.: 25–27, 29–31, 55.
Ribs: at 40–50 mm.: 19 per whorl; 70–90 mm.: 22; 115 mm.: *c*. 25.

EXPLANATION OF PLATE 29

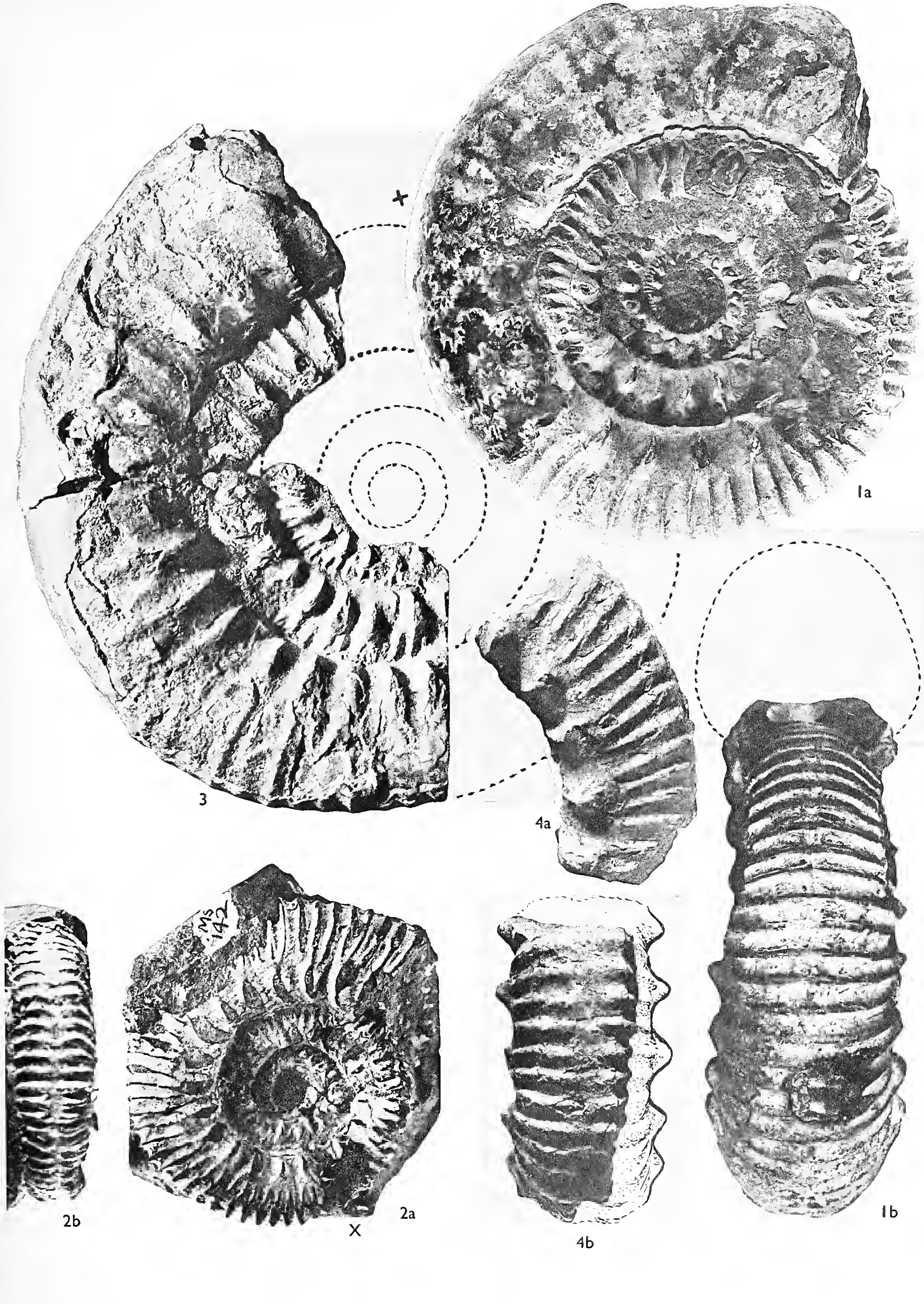
Fig. 1*a*, *b*, *Aulacostephanus* (*Xenostephanus*) *anceps* sp. nov. Holotype; adult, with one-quarter whorl body-chamber preserved, and umbilical suture indicating former extent to five-eighths of a whorl. BM 50761, old collection, no history.

Fig. 2*a*, *b*, *Aulacostephanus* (*Xenostephanus*) *staintonensis* sp. nov. Syntype I; the cross marks what appears to be the last septum. Thurrell coll. MS 142, from Market Stainton, Lincs.

Fig. 3, *Aulacostephanus* (*Xenostephanus*) *staintonensis* sp. nov. Syntype II; wholly septate, last few septa approximated. SW 2/35, from South Willingham, Lincs.

Fig. 4, *Aulacostephanus* (*Xenostephanus*) cf. *ranbyensis* sp. nov. Fragment at commencement of the body-chamber. SW 34.

All natural size.



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In the umbilicus nothing is visible before a diameter of 20 mm. Thereafter the primary ribbing consists of conspicuous dorsolateral tubercles, only slightly bullate, and separated from the strong rectiradiate ribs that spring from them by a lateral smooth band. The ribs are bifid with regular intercalatories, which, on the last septate whorl, tend to join up to form trifid bundles, while fresh intercalatories come in. On the body-chamber the ribbing weakens, the primaries degenerate to bullae and triplicate, finally biplicate, ribs. The last few ribs are single, coarse and irregular, indicating the end of growth. The peristome is not preserved. The venter, where it emerges, has a groove, but no tubercles. The groove fades to a mere smooth band before septation ceases, this coming about as the ribbing loses relief, and persists to the end even when the ventral ribbing is barely perceptible. The whorl-section on inner whorls is quadrate, angular, and becomes rounded towards the end. The suture-line is a typically perisphinctid one, with slender widely spaced lobes on a straight base-line.

The peristome is preserved on another fragment (Pl. 28, fig. 2). It is straight and simple, with slight forward sweep at the umbilical seam.

There is another specimen in the British Museum (C47909, T. B. Parks coll., from Elsham, Lincs., only 72 mm. in diameter, wholly septate, somewhat crushed, which agrees with the holotype in all details, including matrix. The species has also been found in the drift of Norfolk (SM J48657, Baden-Powell coll., one specimen).

Remarks. Inner whorls are practically indistinguishable from *A.* (*X.*) *thurrelli*, and, as remarked previously, it would be hard to find a clearer demonstration of ammonoid dimorphism. Also remarkable is the close homeomorphism between *Xenostephanus* and *Reineckeia* s.s. of the Callovian, yet another instance showing the tendency of ammonites to evolve repeatedly through similar forms.

1a. *A.* (*X.*) *ranbyensis* var. *elshamensis* var. nov.

Plate 27, fig. 1*a–c*

Material. One (BM C.47908, T. B. Parks coll., from Elsham, N. Lincs.).

Description. Size *c.* 130 mm. (slight distortion), septate to 103 mm. with approximation and degeneration, half a whorl of body-chamber preserved with indications of former extent to three-quarters of a whorl, so that the maximum size of the complete shell must have been 150 mm.

Dimensions: at 100 mm.: 25, 29–34, 57.
Ribs: at 130 mm.: 25 per whorl; 120: 23; 100: 22; 80: 20; 60: 19; 40: 19; 30: 20.

The primary ribs are bullate, triplicate with low furcation point up to 80 mm.; they then revert to biplicate, perisphinctid ridges to 120 mm., and single simple ribs thereafter. The secondaries are strong, in regular triplicate sheaves, to about 80 mm., then rapidly weaken and become biplicate at high furcation points, and finally fade altogether. They show some weakening in the middle of the venter where first visible, although there is no fully smooth band, and after about 90 mm. pass over the venter with no interruption.

Comparison. Agreement with the holotype of *A. ranbyensis* is close in proportions and rib-count. The variety differs in becoming bigger, with a more inflated body-chamber, and having less differentiation between primary and secondary ribbing so that a lateral smooth band is present only on the innermost whorls.

2. *Aulacostephanus* (*Xenostephanus*) *staintonensis* sp. nov.

Plate 29, figs. 2, 3

Material. Two (MS 142, SW 2), and fragments (SW).

Description. Neither specimen is really sufficiently complete to serve as sole basis of the species, and the two figured specimens are syntypes.

Syntype I (Pl. 29, fig. 2): maximum diameter 57 mm., apparently septate to only 35 mm. with five-eighths whorl body-chamber. Neither ribbing nor coiling, where last visible, show any signs of modification whatever, and the specimen seems to be genuinely immature.

Dimensions: at 55 mm.: 32, *c.* 33, 45.
Ribs: at 60 mm.: 22 per whorl; 50: 21; 40–20: 20.

Inner whorls evolute, becoming more inflated. Primary ribs moderately bullate, trifid on inner whorls, changing to regular triplicate. Strong secondaries with ventral smooth band, fading at the end.

Syntype II (Pl. 29, fig. 3): maximum diameter 115 mm., wholly septate (details of sutures invisible), flattened through crushing.

Ribs: at 115 mm.: *c.* 30 per whorl; 70: *c.* 27 (counts based on half-whorls).

Ribs on inner whorls triplicate or biplicate with intercalatories; sharp bullate primaries, no lateral smooth band; ventral smooth band. Ribbing has started to modify a 90 mm. to perisphinctid style; and at 115 mm. only straight primaries of low relief remain. The ventral smooth band persists until the entire venter is smooth.

Comparisons. The species differs from *A. ranbyensis* in being markedly more densely ribbed and involute. The primary and secondary ribbing are less well differentiated, so that there is no lateral smooth band even on inner whorls, which are less openly exposed. In this sense the species stands in the same relation to *A. ranbyensis* as *A. lindensis*

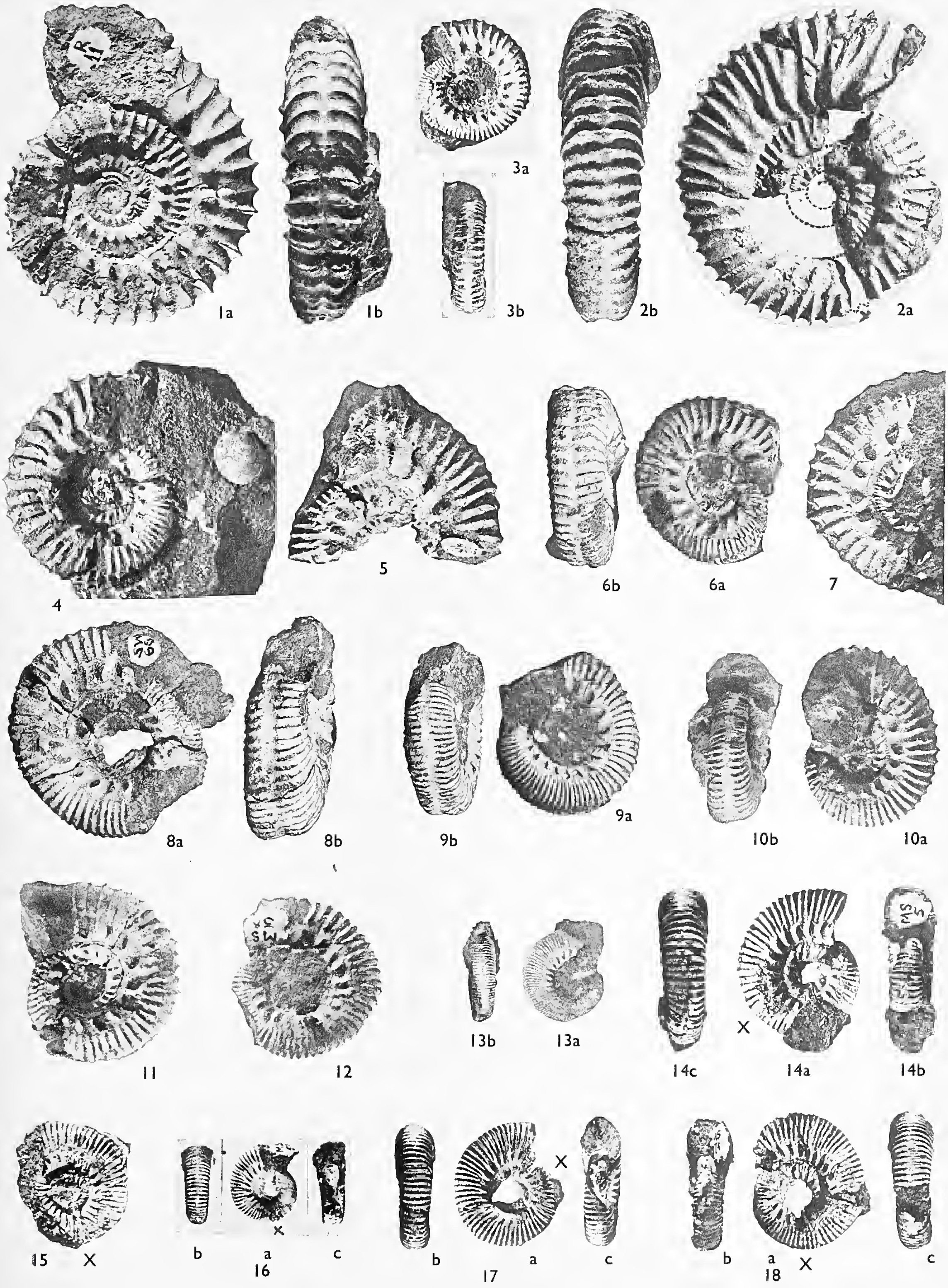
EXPLANATION OF PLATE 30

Figs. 1–3, *Aulacostephanus* (*Xenostephanoides*) *thurrelli* sp. nov. 1*a*, *b*, Holotype; adult, with one-quarter whorl body-chamber preserved. Thurrell coll. R 11, from Ranby, Lincs. 2*a*, *b*, Fragmentary but complete adult, with peristome showing slight lappet. R 19/25. 3*a*, *b*, Inner whorls, no sutures visible. SW 39.

Figs. 4–13, *Aulacostephanus* (*Xenostephanoides*) *lindensis* sp. nov. 4, SW 31, no sutures visible but probably one-half whorl body-chamber. 5, SW 29, last third whorl body-chamber. 6*a*, *b*, SW 33, no sutures visible, but probably at least one-half whorl body-chamber. 7, SW 26, ditto. 8*a*, *b*, SW 60, ditto. 9*a*, *b*, SW 9, ditto. 10*a*, *b*, Holotype, MS 13, seven-tenths whorl body-chamber. 11, SW 53, remarks as 6. 12*a*, *b*, MS 38, ditto. 13*a*, *b*, MS 18, wholly septate. All Thurrell coll.

Figs. 14–18, *Aulacostephanus* (*Aulacostephanites*) *ebrayoides* sp. nov. 14, Holotype; last half whorl body-chamber; MS 5. 15, MS 56, half whorl body-chamber. 16*a*–*c*, MS 57, ditto. 17*a*–*c*, MS 45, eight-tenths whorl body-chamber. 18*a*–*c*, MS 71, six-tenths whorl body-chamber; perhaps transitional to *A.* (*A.*) *eulepidus* (Schneid). All Thurrell coll.

All natural size.



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stands to *A. thurrelli*. An example of this species has also been found in the drift of Norfolk (SM J48658, a double mould, Baden-Powell coll.).

3. *Aulacostephanus* (*Xenostephanus*) *anceps* sp. nov.

Plate 29, fig. 1

Material. One (the holotype, BM no. 50761).

Description. Maximum size 95 mm., septate to 85 mm. with severe approximation and degeneration of the last (and only visible) sutures, and a quarter whorl body-chamber. The umbilical suture indicates a former extent of the final body-chamber to five-eighths whorl, so that the complete shell attained a maximum diameter of *c*. 110 mm.

Dimensions: at 90 mm.: 27, 29–33, 51 (cast).
at 75 mm.: 27, 36–43, 52 (test).
Ribs: at 100–80 mm.: 21 per whorl; 60–50: 20; 40: 19; 30–20: 18.

This is the most inflated of the species described here, with a whorl-section at 75 mm. depressed almost to the point of being coronate. In contrast, the body-chamber contracts and reverts to normal perisphinctid dimensions. Similarly, the ribbing, which is characterized by very high, sharp bullate primaries on the umbilico-lateral margin giving rise to regular sheaves of very coarse triplicate secondaries, modifies to rather widely spaced and in part biplicate ribs of low relief on the body-chamber. The secondaries show only the faintest weakening on the round venter where first visible (at 60 mm.); they smooth out altogether on the body-chamber.

Affinities and remarks. *A. anceps* bears undeniably close resemblance to various species of *Rasenia* from the Cymodoce Zone of Market Rasen, including *R. uralensis* (d'Orb.), and, in the absence of a ventral smooth band, to place it in any but this genus might seem unnatural. Its inner whorls, however, are quite different: evolute, with flat whorl sides and the differentiation, with lateral smooth band, of primary and secondary ribbing characteristic of *Xenostephanus*. The aulacostephanid characters of angular whorl-section and ventral smooth band seem here to make their first appearance in *Xenostephanus* proterogenetically.

The specimen has the test preserved on all but the last half whorl, and it is therefore conceivable that an internal cast might show a ventral smooth band not visible on the outside; and that the difference in this respect between *A.* (*X.*) *anceps* and the other forms of *Xenostephanus* described here, mostly casts, might only be apparent and attributable to differences of preservation. This seems unlikely, however, for a specimen of *A.* (*X.*) *ranbyensis* from Norfolk (SM J48657) shows the same ventral smooth band on both internal cast and external mould of the same part of the body-chamber at 60 mm. diameter.

The holotype was presented to the British Museum by Prof. J. Morris in 1867; there is no other recorded history. Its preservation and matrix are, however, so precisely similar to the other material here described that there can be little doubt that it came from a similar source. It seems to have been one of the specimens which Salfeld included in his MS species *evoluta*; but its inner whorls are quite different from those of the specimen Spath selected as type for his species (see above). Besides oysters, the matrix carries an imprint of *Rasenia* cf. *thermarum* (Oppel).

Xenostephanus seems to occur in the Kimeridgian of Skye. A single specimen of *A.* (*X.*) cf. or aff. *anceps* (Pl. 33, fig. 1) was collected by Mr. W. G. Cordey at Kildorais, Trotternish, in the spring of 1961, and we thank him for presenting it to us. It is crushed, in clay, and encrusted with an oyster on the inner whorls. Neither septa nor venter are discernible, but the ornament is typically that of *Xenostephanus*, and enough is visible of the inner whorls to show that they are evolute just as in *A. anceps*. The Skye specimen differs in having rather fewer ribs on the middle and outer whorls: at 85 mm.: 17 per whorl; 70: 16; 50: 15; 30: *c.* 18. The specimen was unfortunately found without any supporting fauna.

For completeness, we include here:

4. *Aulacostephanus* (*? Xenostephanus*) sp. indet. = *Ammonites* cf. *trifurcatus* Quenstedt 1888, p. 971, pl. 107, fig. 24

Remarks: Quenstedt's figure shows an extremely evolute shell, maximum size *c.* 85 mm., with ornament typical of *Xenostephanus*: well-spaced bullate primary ribs leading to triplicate, strong secondaries with intercalatories. Unfortunately neither venter nor sutures are anywhere visible. At 85 mm. there are 18 ribs per whorl; at 60: 17; at 40: 15. The species differs from *A. ranbyensis* therefore in being less densely ribbed; also, in having the primaries half-way up the whorl-side rather than on the umbilico-lateral margin.

Nautilus trifurcatus Reinecke (1818, p. 75, pl. v, fig. 49) is quite different: inflated, involute, with barely bullate primary ribbing. Spath (1935, p. 49, footnote) thought Quenstedt's specimen belonged to *Rasenia evoluta* Salfeld MS, and in the sense that the specimen described above as *A.* (*X.*) *anceps* appears to have been a syntype of Salfeld's unpublished manuscript species he was probably correct. It is unfortunate that he chose to publish the name on the basis of only a small nucleus (see above).

If the above identification is correct, Quenstedt's specimen seems to be the only representative of these early aulacostephanitids so far known from more southerly regions. It was found in a volcanic erratic at Floriansberg, and ascribed to White Jura δ.

There are a number of other boreal forms intermediate between *Rasenia* and *Aulacostephanus* proper which, when more is known about them, may turn out to be closely related to *Xenostephanus*.

Aulacostephanus groenlandicus Ravn (1912, p. 492, pl. xxxvii, fig. 3*a–c*, from Koldewey Island, 76° N.; Frebold 1930, p. ix, fig. 4, from Spitsbergen) has the evolute coiling and indications of a ventral smooth band, but is densely ribbed and lacks the tuberculate

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EXPLANATION OF PLATE 31

Figs. 1, 2, *Aulacostephanus* (*Aulacostephanoides*) sp. nov. ? aff. *mutabilis* (J. de C. Sowerby). 1, Complete adult, with seven-tenths whorl body-chamber, and peristome transposed unto the figured side (white dotted line) as it is developed on the reverse side. Thurrell coll. MS 37. 2, MS 102; the outer whorl is body-chamber.

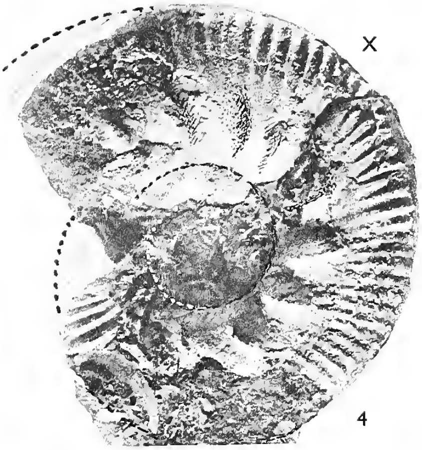
Fig. 3, *Aulacostephanus* (*Aulacostephanoides*) *mutabilis* (J. de C. Sowerby). Wholly septate example, from a nodule-bed in Kimeridge Clay near Haddenham Station, Cambridgeshire. SM J.29157.

Figs. 4, 5, *Aulacostephanus* (*Aulacostephanoides*) *circumplicatus* (Quenstedt). 4, MS 120, with some body-chamber. 5*a*, *b*, MS 51b, outer whorl body-chamber.

Fig. 6*a*, *b*, *Rasenia* (*Rasenioides*) cf. *striolaris* (Reinecke). MS 29, with half whorl body-chamber.

All natural size.

1



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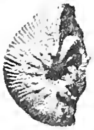
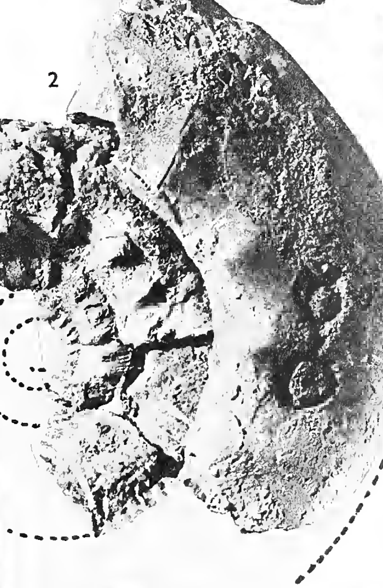


a 6

b



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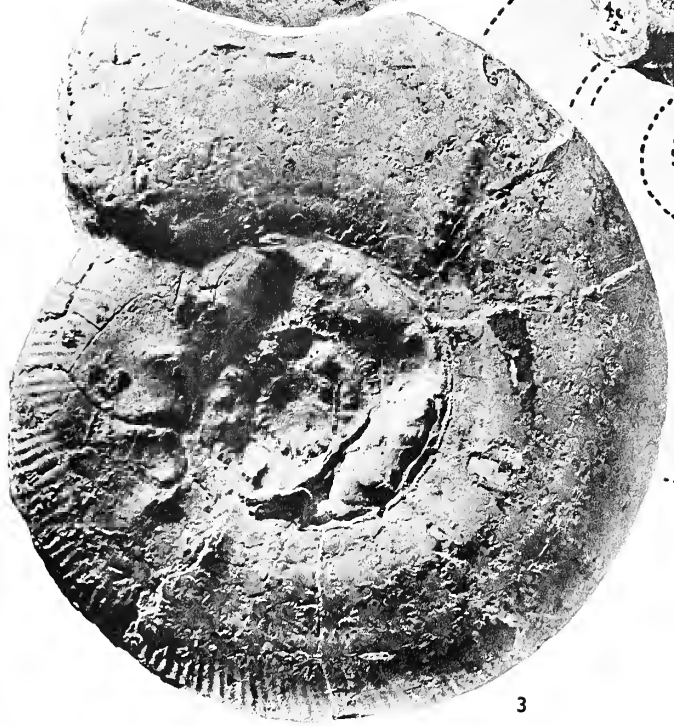
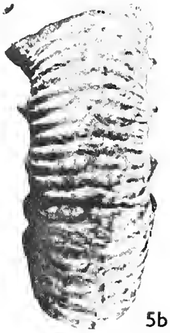


3

5a



5b

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primaries. Precise age unknown, but Kimeridgian of *mutabilis* age is known to be present in east Greenland (J. H. C. 1957).

Aulacostephanus Pischmae Khudyaev 1932 (p. 646, text-fig. 2, pl. 1 fig. 1, from Petchoraland) seems to be very close to *Xenostephanus*, if not actually to belong to it. Khudyaev's text-fig. 2 shows the whorl-section of inner whorls to be depressed with tuberculate or bullate ribbing of high relief, as in *A.* (*X.*) *anceps*. Unfortunately the plate shows only the outer whorl—body-chamber—which has perisphinctid bi- and triplicate ribbing with subtriangular, compressed whorl-section, and, in the absence of better material, affinity with *Xenostephanus* must remain in doubt. *A. pischmae* seems equally close to some of the large, coarsely, but bluntly, ribbed forms like *A. quenstedti* Durand, which Dr. Ziegler places in *Pararasenia* Spath.

A. pischmae is type species by monotypy of the genus *Sarygulia* Khudyaev, proposed in the legend of text-fig. 2 (p. 647) only. The type species comes from the Timan, Petchora, north Russia, whereas Sary-goul (Saragula) is in the southern Urals, where, to judge by Pavlow's plates (1886), the group does not occur. Possibly Khudyaev withdrew the name on account of this but forgot to remove it also from the underline of the text-figure. The original name is invalid, having been proposed after 1931 without diagnosis or citation of a type species. It has been revived by Sasonov (1960, p. 157), who has formally designated *A. pischmae* as type species. He figures no additional material, however, and so *Sarygulia* Sasonov 1960, though valid, will continue to be regarded here as synonymous with *Pararasenia* Spath, emend. Ziegler.

Pomerania ilovaiskyi Sasonov 1960 (p. 162, pl. 3, figs. 1, 1*a*, pl. iv, figs. 2, 2*a*, *b*). This species resembles *Xenostephanus* in having evolute inner whorls; a clear ventral smooth band without tubercles; in its size; and in the extreme degeneration of the ribbing on the body-chamber. It differs in being somewhat more compressed than any of the species here described, and much more densely ribbed: at 50 mm. it has twenty-six ribs per whorl. The primary ribs in consequence never attain the highly differentiated tuberculate character of those in, for example, *ranbyensis*, or even *A.* (*Xenostephanoides*) *scoticus*, which is similarly densely ribbed. There are also prominent constrictions which *Xenostephanoides* does not have. Sasonov's material came from the Sosva basin, on the eastern side of the northern Urals.

Family CARDIOCERATIDAE Siemiradzki 1891

Subfamily CARDIOCERATINAE Siemiradzki 1891

Genus AMOEBOCERAS Hyatt 1900

Type species. Ammonites alternans von Buch 1832.

Subgenus AMOEBITES Buckman 1925

Type species. Amoebites akanthophorus Buckman 1925.

1. *Amoeboceras* (*Amoebites*) cf. *kitchini* (Salfeld)

Plate 32, fig. 26*a*, *b*

Cardioceras Kitchini Salfeld 1913, p. 423.
Cardioceras Kitchini Salfeld 1914, p. 129.
Cardioceras Kitchini Salfeld 1915, p. 189, pl. xix, figs. 8–17; pl. xx, figs. 15, 16.
Amoeboceras (*Amoebites*) *kitchini* Spath 1935, pp. 30–31 (neotype designated); pl. 1, fig. 9*a*, *b*.

Amoeboceras (*Amoebites*) *kitchini* Waterston 1951, p. 42, pl. ii, fig. 4*a*, *b*.
Amoeboceras (*Amoebites*) aff. *rasenense* Waterston 1951, pl. ii, fig. 1.

Material. One (MS 48).

Description. The specimen is 29 mm. in diameter; septate to 20 mm., the last sutures show none of the degeneration or approximation otherwise almost invariably found in adults of the Cardioceratidae, so that the specimen seems to have been immature. It agrees well, as far as it goes, with the neotype (Salfeld 1915, pl. xx, fig. 16), although it does not, and could not at that size, show any of the looped ribbing or ventro-lateral clavi of the adult *A. kitchini*.

Remarks: Salfeld, in his English paper (Oct. 1913), based the species on a drawing in Woodward, 1895, but in his German paper (1914) he compared Woodward's figure with another in de Loriol (1876), which he queried in his monograph (1915). It is possible to interpret the species only as from the 1915 monograph, when photographs were published, including that of the Scottish neotype. Unfortunately, even the latter does not fix the species unambiguously, being itself incomplete and recognizable only up to 27 mm.; and both the neotype of *A. kitchini* and the specimen described here might be hard to distinguish from inner whorls of larger specimens differing in their outer whorls and described under various names, e.g. *A. akanthophorus* Buckman, *A. salfeldi* Spath (nom. nov. for *Card. pinguis* Salfeld pars, 1915 pl. xx, fig. 14), or *A. rasenense* Spath (1935, pl. 1, fig. 6*a*, *b*).

The amoeboceratids of the Lower Kimeridgian are as yet scarcely known. The tuberculate forms of *Amoebites* are of particular interest. Most of those hitherto published are of the *A. kitchini* group, from the Baylei–Cymodoce Zones, and so we take the

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EXPLANATION OF PLATE 32

Figs. 1–8, *Aulacostephanus* (*Aulacostephanites*) cf. *eulepidus* (Schneid). 1*a*, *b*, MS 112, eight-tenths whorl body-chamber with lappet on reverse side. 2*a*, *b*, MS 69, with lappet. 3*a*, *b*, MS 27, with short lappet. 4*a*, *b*, MS 77, nine-tenths whorl body-chamber. 5*a*, *b*, MS 58, no sutures visible, but peristome preserved with lappet and collar. 6*a*, *b*, MS 66, no sutures visible. 7*a*–*c*, R 5, with onset of lappet. 8*a*, *b*, MS 72, outer whorl body-chamber.

Figs. 9, 10, *Aulacostephanus* (*Aulacostephanites*) *ebrayoides* sp. nov., transitional to *A.* (*A.*) cf. *eulepidus* (Schneid). 9*a*–*c*, MS 8, with lappet. 10*a*, *b*, MS 10 with lappet.

Figs. 11, 12, *Aulacostephanus* (*Aulacostephanites*) aff. *desmonotus* (Oppel). 11*a*, *b*, R 17, no sutures visible, but probably part of the outer whorl is body-chamber. 12*a*, *b*, MS 115, ditto.

Figs. 13–18, *Rasenia* (*Rasenioides*) *thermarum* (Oppel). 13*a*, *b*, MS 14, with probably some body-chamber. 14*a*, *b*, MS 118, with eight-tenths whorl body-chamber, peristome, and slight lappet. 15*a*–*c*, MS 9, nine-tenths whorl body-chamber. 16*a*–*c*, MS 32, remarks as 11. 17*a*, *b*, MS 36, ditto. 18*a*, *b*, R 20, ditto.

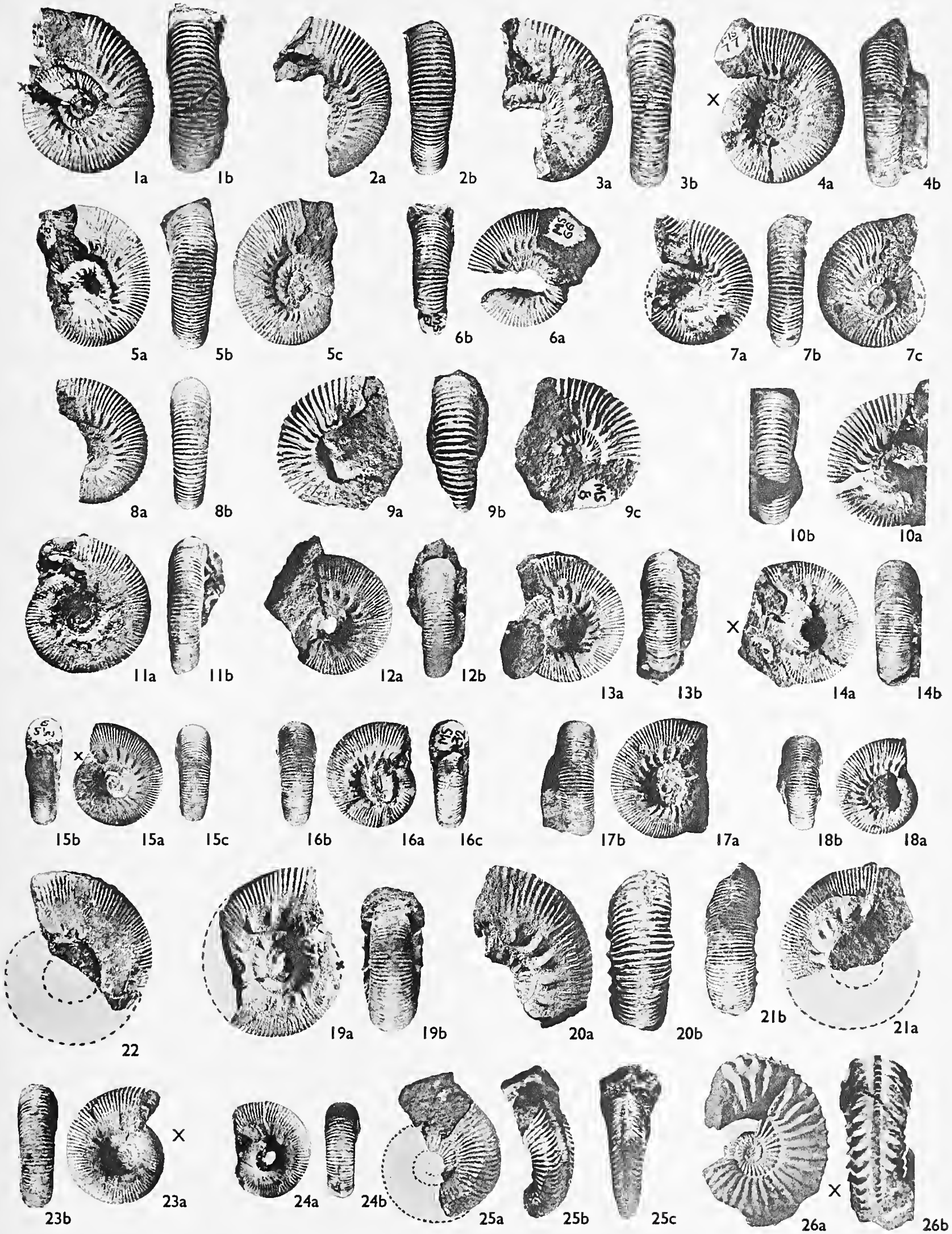
Figs. 19–21, *Rasenia* (*Rasenioides*) cf. *lepidula* (Oppel). 19*a*, *b*, MS 34, eight-tenths of last whorl body-chamber. 20*a*, *b*, MS 53, a fragment with outer whorl body-chamber. 21*a*, *b*, MS 35, body-chamber with peristome.

Figs. 22–24, *Aulacostephanus* (*Aulacostephanites*) sp. aff. *möschi* (Oppel). 22, MS 136, body-chamber fragment. 23*a*, *b*, MS 24, with eight-tenths whorl body-chamber. 24*a*, *b*, MS 19, no sutures visible.

Fig. 25*a*–*c*, *Amoeboceras* (*Amoebites*) *cricki* (Salfeld). MS 111, outer whorl body-chamber with peristome.

Fig. 26*a*, *b*, *Amoeboceras* (*Amoebites*) *kitchini* (Salfeld). MS 48, with half whorl body-chamber.

All natural size.



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opportunity to illustrate two examples of *A.* (*Amoebites*) *salfeldi* Spath from the Mutabilis Zone of Mull (Pl. 33, figs. 12, 13). Development via the ventro-lateral clavi of *A. kitchini* to the fully looped ribs with tubercles of *A. salfeldi* seems systematic and may be of help in dating beds in regions, e.g. east Greenland, in which rasenids are absent.

2. *Amoeboceras* (*Amoebites*) cf. *cricki* (Salfeld)

Plate 32, fig. 25*a–c*

Cardioceras Cricki Salfeld 1914, p. 129.
Cardioceras Cricki Salfeld 1915, p. 191, pl. xix, figs. 2–6.
Cardioceras Kapffi Salfeld pars (non Oppel) 1915, pl. xix, fig. 7*a–c*.

Material. One (MS 111), and two fragments (MS).

Description. The figured specimen is about 22 mm. in diameter. The last half-whorl is body-chamber and the peristome is preserved, with ventral rostrum. The whorl-section is quadrate, compressed, with sharp shoulders and flat venter.

Remarks. The history of the name is similar to that of *kitchini* and interpretation is possible only as from the 1915 monograph. Salfeld's best figured specimen (pl. xix, fig. 2) attains 25 mm., and is slightly more densely ribbed than the one described here. The species seems to stay small and not to develop the modified ribbing characteristic of the *A. kitchini* group.

ORIGIN AND AGE OF THE FAUNA

The Lincolnshire material has been collected at four localities (from north to south): Elsham, 9 miles east of Scunthorpe and 15 miles north-north-west of Market Rasen; South Willingham, 6½ miles south-east of Market Rasen; Market Stainton, 9½ miles south-east of Market Rasen; and Ranby, ½ mile south of Market Stainton.

Elsham. The material in the British Museum (T. B. Parks coll.) came from 'huge boulders in sand' found in a small pit on the Chalk Wolds ¼ mile from Elsham chalk-pit. The ammonites were briefly mentioned by Spath (1954), who described them as 'probably new and undescribed species of *Rasenia*'.

South Willingham. The following are extracts from notes kindly supplied by Dr. Thurrell.

'Specimens labelled SW were collected from the village at a point 250 yards east of the church where a water-main trench intercepted the boulders within the Chalky Boulder Clay.'

Market Stainton. 'Specimens labelled MS were collected from two massive boulders (each about 3 feet across) in the corner of a large field 500 yards south-east of the church.'

Ranby. 'Specimens labelled R were collected on the roadside 600 yards east of Ranby church.

'The MS and R specimens are from blocks which are only 725 yards apart, but it is quite obvious that the blocks have been dumped. Enquiries failed to locate their exact origin, except that the MS blocks came from the centre of the field in the corner of which they lie.

'It seems certain that all the blocks come from—or are likely to occur in—the lowest levels in the Boulder Clay spread and one might presume also that they are of fairly local origin. Mapping of the boulder-clay suggests ice-movement from north to south over the existing Jurassic clay vale, the stream being confined by the Chalk Wolds escarpment not a mile to the east of Market Stainton. Evidence of possible derivation from the North Sea basin is lacking.'

The matrix and preservation of all the material is very similar: fine grey siltstone, some pieces crowded with fossils including, besides the ammonites, small gastropoda, pectens, oysters, and *Astarte*. There is no known outcrop of Lower Kimeridgian in such facies in England, nor has any been found in borings. The origin of the material must remain conjectural. Some of it has found its way to Norfolk, although for boulders of the size of those found in Lincolnshire transport over such distances seems improbable. The Kimeridgian is known to thin rapidly towards the Market Weighton axis, only some 30 miles north of Market Rasen, which influenced sedimentation in Jurassic times; and a more sandy development in its immediate vicinity, perhaps under chalk cover or even some way out to sea, would not be unexpected.

The question arises: do all these boulders contain identical faunas and hence are they, geologically speaking, all of the same age? The distribution of the material among the various localities is shown in Table 1, counting only identifiable specimens (some unnumbered fragments are indicated '+'). The species of Aulacostephaninae can be divided into two groups: those known elsewhere from the Mutabilis Zone—group (A); and species of the subgenera *Xenostephanus* and *Xenostephanoides* peculiar to the present collection (B). Whereas species of the second group (B) were found at all the localities, those of the first (A) occurred only at Ranby and Market Stainton, and not at South Willingham. There exist boulders, therefore, which contain exclusively the *Xenostephanus–Xenostephanoides* fauna. This leads to two possibilities for the age of the latter.

Firstly, if segregation is not general, and there also exist boulders containing both groups of species, then these have the same age which is Mutabilis Zone *sensu stricto*. The segregation of species in some parts of a 'contemporaneous' deposit would require explanation, but cases of this have been observed in other deposits of dogger facies.

EXPLANATION OF PLATE 33

Fig. 1, *Aulacostephanus* (*Xenostephanus*) aff. *anceps* sp. nov. Kildorais, Trotternish, Skye. W. G. Cordey coll.

Fig. 2, *Rasenia* (*Rasenioides*) cf. *transitoria* (Schindewolf). MS 80a, Thurrell coll., with probably some body-chamber.

Fig. 3*a*, *b*, *Rasenia* (*Zonovia*) sp. ind. R 2, wholly septate.

Figs. 4–6, *Aulacostephanus* (*Aulacostephanites*) *eulepidus* (Schneid). Latex casts of crushed impressions from Kimeridgian shales of Mull (Geol. Surv. Scotland, nos. M4512i, T4734c, T1981d).

Fig. 7, *Aulacostephanus* (*Aulacostephanites*) *spp*. aff. *eulepidus* (Schneid) or *ebrayoides* sp. nov. As above, from Mull (T1970d).

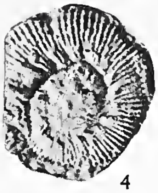
Fig. 8, *Aulacostephanus* (*Xenostephanoides*) aff. *thurrelli* sp. nov. or *scoticus* sp. nov. Mull (M4525i).

Figs. 9–11, *Aulacostephanus* (*Aulacostephanoides*) *circumplicatus* (Quenstedt). 9, Imprint of smooth band on the venter shown at 'v'. 10, Imprint of venter of *Amoeboceras* in the umbilicus. Mull (M4516i, T4732c, T4733c).

Figs. 12–13, *Amoeboceras* (*Amoebites*) *salfeldi* Spath. Mull (T1991d, T4721c).

All natural size. Figs. 4–13 are photographs under oblique lighting of latex moulds coated with magnesium oxide.


1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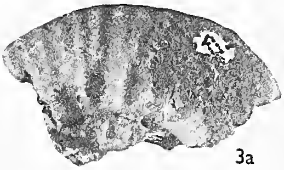
5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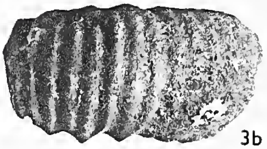
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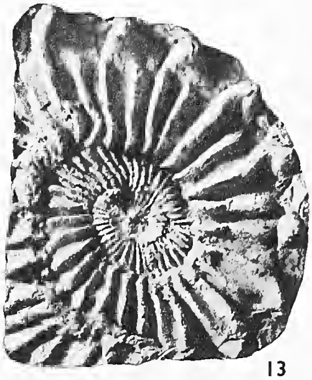
13

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The fossils occur notably in isolated pockets, the chance remains of accumulations through wave-action at different moments over considerable periods of time in shifting, unconsolidated sandbanks whose relics we must consider to be geologically of uniform age. Segregation in such pockets might then be a reflection of ecology, particularly if the remains are those of organisms that were gregareous.

TABLE 1. Summary of distribution of species in the Lincolnshire Drift

	R	MS	SW	E
A. *Rasenia* (*Rasenia*) *sp.*		1		
(*Rasenioides*) *transitoria*		1		
cf. & aff. *lepidula*		5		
thermarum	1	8		
cf. *striolaris*		2		
(*Zonovia*) *sp.*	1			
Aulacostephanus				
(*Aulacostephanites*) *eulepidus*	1	24		
ebrayoides	1	8		
aff. *desmonotus*	1	2		
aff. *möschi*	1	10		
(*Aulacostephanoides*) *mutabilis*		1		
aff. *mutabilis*	1	2		
circumplicatus	1	2		
B. (*Xenostephanoides*) *thurrelli*	5	2	11	
lindensis	3	4	21	
(*Xenostephanus*) *ranbyensis*	1		1+	1
—var. *elshamensis*				1
staintonensis		1	1+	
anceps				
Amoeboceras				
(*Amoebites*) cf. *kitchini*		1		
cf. *cricki*		3		
Totals	17	77	34+	2

E = Elsham.

Alternatively, if the segregation of species is rigorous, we must deduce differences of age. This could not have been large, for on zoological grounds *Xenostephanus* and *Xenostephanoides* would fit into the faunal succession best as descendants of at least the earliest of the well-known rasenids of the Cymodoce Zone, and certainly as precursors of the aulacostephanids of the Eudoxus Zone (the lower part of the former Pseudo-mutabilis Zone *sensu lato*—for revision, see Ziegler 1961). On geological grounds it would also seem unlikely to have a selection of faunas of two zones, 1 and 3, with no trace of the intermediate zone 2. At most, therefore, it seems possible that *Xenostephanus* and *Xenostephanoides* mark a separate subdivision or subzone of the Mutabilis Zone.

The two alternatives above can only be resolved by further collecting, and careful attention should be paid to analysis of new material boulder by boulder.

Note added in proof (*1 February 1963*). The pit at Elsham which yielded *Xenostephanus* has been recently re-examined by P. E. Kent and R. Casey (*Proc. Geol. Soc., London,*

1605, 1963). They report that the sands and doggers exposed there are in fact *in situ*, showing the presence of a local sandy development of Lower Kimeridgian immediately under the Chalk. This had previously been mapped as Spilsby Sandstone (Neocomian).

The *Xenostephanus* fauna has also been found in drift at Miningsby, 4 miles west of Spilsby, at the southernmost end of the Wolds. Two specimens are figured by Ziegler (1962, pl. 22, figs. 5–6, 13–14; University of Nottingham Collection).

COMPARISON WITH OTHER AREAS

East Scotland. Lower Kimeridgian is exposed at two places: Eathie, on the Moray Firth, south of Cromarty; and the Brora–Helmsdale strip in Sutherlandshire.

The Eathie exposure seems to lie mainly in the Baylei–Cymodoce Zones (Waterston 1951), although nodules washed up on the beach indicate some higher beds offshore. The Lincolnshire fauna does not appear to be represented among them.

A more complete section is to be found in Sutherlandshire. The collections contain material from all the zones of the Lower Kimeridgian, but there seems to be no systematically collected succession (for summary, see Bailey and Weir 1932). The specimens that have found their way into the museums have tended to be the well-preserved ones out of mudstone nodules, often found loose on the shore; among them is *A.* (*Xenostephanoides*) *scoticus* sp. nov. (see above). Of the crushed ammonites from the rest of the great thickness of shales making up most of the succession there is little record.

Some of the lower of these shales—the Loth River Shales—are highly fossiliferous. The following section was recorded during a brief visit (J. H. C. 1956), in the river gorge south of Loth station, just east of the railway bridge on the north bank of the river. From above:

Loth River Shales	ft.	in.
6. Black paper shales with sandy intercalations and seams; to below rail-level at the north end of the bridge.	seen *c.* 15	0
5. Soft yellow sandstone or sand, cross-bedded, with large doggers; variable	*c.* 6	0
4. Black varved paper shales with sandy white layers; many crushed ammonites, especially 2 ft. from the top: *Amoeboceras* (*Amoebites*) *beaugrandi* (? Sauvage) Spath (1935, pl. 5, fig. 4). *A.* (*A.*) *sp.* aff. *kitchini* (Salfeld). *Rasenia*? cf. *möschi* (Oppel). *Aulacostephanus* (*Xenostephanoides?*) cf. *lindensis* sp. nov. also profuse plant remains, and *Aucella sp.*	6	0
3. Sandstone, doggery, cross-bedded, barren	2 to 8	0
2. Black paper shales, as above, with sandy layers	10 to 15	0
Allt na Cuile Sandstone		
1. Sandstone, white, massive, weathering black	seen 15	0

This section was not recorded in connexion with the present work, and only a few specimens from bed 4 were brought back. There seems little doubt about the *Aulacostephanus*, however, and more careful collecting from this section might settle the precise age of the Lincolnshire material.

West Scotland. There are indications of the Lincolnshire fauna from two localities: Kildorais, northern Skye, and Duart Bay, eastern Mull (see Arkell 1933, p. 114, fig. 19).

The only description of the Skye section so far published is by MacGregor (1934, p. 400), although it seems to be one of the most complete and fossiliferous successions from Lower Oxfordian to Lower Kimeridgian in Britain (J. H. C. 1961). The Pseudocordata Zone (uppermost Oxfordian), with profuse *Ringsteadia*, and Baylei Zone (Lower Kimeridgian) with typical *Pictonia* are thick and easily recognizable. Higher beds are present, but much less fossiliferous and badly covered by beach material: from one of these Mr. W. G. Cordey obtained the *Xenostephanus* shown in Plate 33, fig. 1. MacGregor submitted his material to Spath for identification, and in a more detailed account in a thesis (1931) mentions '*Pararasenia pseudomutabilis*' in text. Illustrations show nothing identifiable of post-*baylei* age, and search has failed to find the material. Thus there is so far no unconfirmed material which could throw light on the age of the single *Xenostephanus* mentioned above.

The occurrence in Mull is in a tiny faulted patch of baked blue shale on the right bank of the stream flowing into Duart Bay (Lee and Bailey 1925). The identification of the ammonites has had a varied history. They were first reported by Buckman to be Callovian *Kosmoceras* and *Reineckeia*. This was corrected by Spath (1932, p. 149) and Arkell (1933, p. 371), who identified them as *Amoeboceras* and *Rasenia*; but their precise age was not mentioned and none of them has so far been described. They are in fact from the Mutabilis Zone and the following species can be recognized in the collections of the Scottish Geological Survey:

Aulacostephanus (*Aulacostephanites*) *eulepidus* (Schneid) (Pl. 33, figs. 4–6).
— — cf. *ebrayoides* sp. nov.
— — aff. *möschi* (Oppel).
— (*Aulacostephanoides*) *mutabilis* (Sow.).
— — *circumplicatus* (Quen.) (Pl. 33, figs. 9–11).
— — *linealis* (Quenstedt).
— (*Xenostephanoides*) cf. *thurrelli* sp. nov. (Pl. 33, fig. 7).
— (*Xenostephanus*) aff. *raubyensis* sp. nov.
Amoeboceras (*Amoebites*) *beaugrandi* (Sauvage).
— — *beaugrandi* Spath (non Sauvage).
— — *cricki* (Salfeld).
— — *kitchini* (Salfeld).
— — *salfeldi* Spath (Pl. 33, figs. 12, 13).
— (*Euprionoceras*) cf. *sokolovi* Sokolov and Bodylevsky.

Thus there is considerable similarity with the Lincolnshire fauna. The *Xenostephanus* resembles the one from Skye, but is too poorly preserved to be worth figuring. *Amoeboceras* predominates (this seems to apply to most Scottish Lower Kimeridgian), and the small fine-ribbed rasenids seem to be rare or absent. This further suggests that the Mutabilis Zone may be capable of subdivision.

England. Nowhere between Yorkshire and Dorset does the Mutabilis Zone appear to exceed a few feet in thickness, and very little is known about it in detail. Locally it is condensed or absent. Once again the museum material is largely that from nodules, found in many of the small brick-pits which have now all vanished. Such material from Lincolnshire is fairly abundant, but contains no *Xenostephanus*. This, too, may indicate that these forms occur at a somewhat different level from the rest of the Mutabilis fauna. Otherwise, if the Lincolnshire drift boulders are of relatively local origin, there would have to be a very sharp ecological boundary in the neighbourhood of the Humber.

South Germany. Due largely to the work of recent years the faunal successions are now known in considerable detail. The fauna of the Mutabilis Zone seems to be confined to the White Jura δ 1–2 (Ziegler 1962) (Tenuilobatum Zone *partim*, Badener Schichten of Switzerland), but constitutes only a minor part of the whole fauna. It seems unlikely therefore to become the type area for subdivisions of the Mutabilis Zone. Only one specimen of *? Xenostephanus* has so far been found (see above) and that not in place. This confirms the impression that this group is primarily characteristic of the boreal faunal realm.

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A NEW SPECIES OF *KOMIA* KORDE AND THE SYSTEMATIC POSITION OF THE GENUS

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ABSTRACT. Study of *Komia eganensis* sp. nov. from the Middle Pennsylvanian (Atokan) rocks of eastern Nevada suggests that the genus be assigned to the Stromatoporoidea (Kingdom Animalia) rather than the Rhodophyceae (Kingdom Plantae). *Komia* has been reported from rocks of Middle Carboniferous, Early Pennsylvanian, and Middle Pennsylvanian (Atokan and Desmoinesian) ages. *K. eganensis* and *Fusulinella acuminata* define a restricted biostratigraphic zone within the Middle Pennsylvanian (Atokan) rocks of eastern Nevada.

THE Palaeozoic fossil *Komia* Korde (1951, p. 181) has been reported from eastern Europe, central Japan, and western North America (Johnson 1960, p. 51; 1961, p. 86). The following historical résumé presents previous investigations concerning *Komia* and is intended to serve as background for consideration of the genus.

This study is one in the series on the stratigraphy and palaeontology of the Ely No. 3 Quadrangle, White Pine County, Nevada. A list of previous papers in this series may be found in Wilson and Langenheim (1962, p. 495).

Historical résumé. Korde (1951, p. 181) described the genus *Komia* with *Komia abundans* as the type species (loc. cit., text-figs. 4, 5; pl. 2, figs. 3, 4) and considered it to be a rhodophytean alga.

Maslov (1956, p. 21), in questioning the validity, in part, of Korde's (1951, pp. 175–82) study, suggested that *Komia* might be referable to the Echinodermata.

Johnson (1957, pp. 13, 80) cited *Komia* as a fossil alga. Later (1960, p. 45; 1961, p. 85) he placed *Komia* among several genera of calcareous red algae of uncertain affinity. He remarked (1960, p. 51; 1961, p. 86) that *Komia* has long been called '*Desmoinesia*' [*nomen nudum*] by certain North American geologists and that it occurs in the 'Middle Carboniferous of Russia, Lower Pennsylvanian of central Japan, Des Moines group (Pennsylvanian) of west Texas and New Mexico'. He also figured *Komia sp.* ? from the Pennsylvanian of southern New Mexico (1960, pl. 19; 1961, pl. 25).

Kordeophyton Rezak, apparently listed as a junior synonym of *Komia* Korde in Johnson (1961, p. 286), appears to be a *nomen nudum*. We have been unable to verify that it has ever been published elsewhere.

Illustrations (reconstructions?) labelled *Komia abundans* Korde appeared in Drushchits and Yakubovskaya (1961, pl. 2, fig. 10). They considered it (ibid., p. 44) to be a Middle Carboniferous rhodophytean alga.

Komia sp. was recorded, without description or figures, from the Pennsylvanian of Utah by Mollazal (1961, p. 26) and Wright (1961, p. 154). We have found no other reports of the genus.

SYSTEMATIC DESCRIPTION

The morphological terminology used is largely that of Galloway (1957, pp. 350–60). Type specimen and locality numbers refer to the collections of the Museum of Paleontology, University of California, Berkeley (abbreviated to UCMP).

[Palaeontology, Vol. 6, Part 2, 1963, pp. 246–53, pl. 34–35.]

Phylum COELENTERATA Frey and Leuckart 1847
Class HYDROZOA Owen 1843
Order STROMATOPOROIDEA Nicholson and Murie 1878
Family *Incertae sedis*
Genus KOMIA Korde 1951

Type species. Komia abundans Korde (1951, p. 181, text-figs. 4, 5; pl. 2, figs. 3, 4).

Diagnosis. Coenosteum small, cylindrical, ramose, composed of a broad outer region and a narrow axial cylinder; outer region formed of superposed, truncated cones of perforate laminae and interlaminar to continuous pillars with minutely trabeculate, *en jet d'eau* (Steiner 1932, pp. 24–28, text-figs. 3, 5) microstructure; axial cylinder composed of elongate grooves curving upwards and outwards from axis and partially enclosed abaxially by incomplete, perforate, distally thickening walls.

Remarks. In this study we have chosen to consider the Order Stromatoporoidea in the broad concept presented by Lecompte (1956, p. F127). The combined features of *Komia* appear so singular that it has been impossible to compare the genus closely with other stromatoporoid genera except on the basis of individual characters. For this reason we have not placed *Komia* in a family. Furthermore, we do not wish to erect a new family on the basis of one genus and two species.

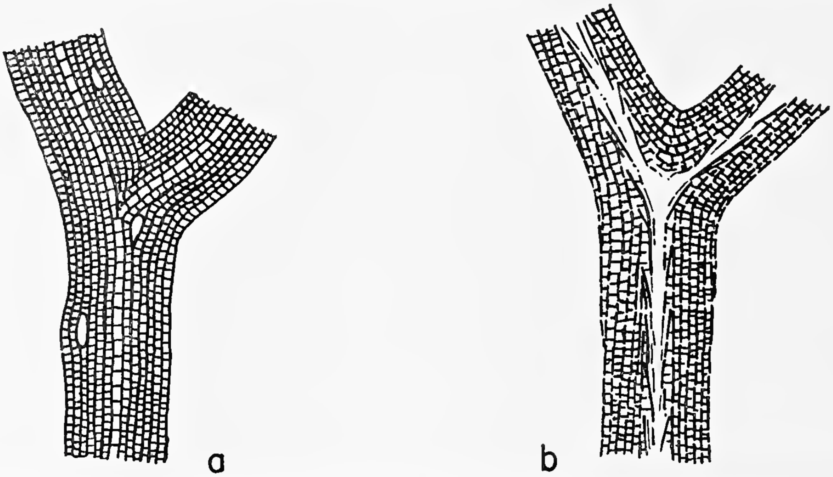
In its cylindrical and ramose form, in its possession of a differentiated axial region, and in its possession of regular laminae and pillars, *Komia* most closely resembles two Middle Devonian stromatoporoids, *Idiostroma* and *Dendrostroma* (see Galloway 1957, pp. 443–4, pl. 34, figs. 8, 9). *Komia* differs significantly from these two genera in the nature of the pillar microstructure, the relatively small size of the coenosteum, the comparatively close spacing of the skeletal elements, the structure of the axial region, and the coarsely porous nature of the laminae. Although differing in most characters, *Komia* resembles the Permo-Triassic stromatoporoid *Disjectopora* (see Lecompte 1956, p. F138, text-figs. 111, 112) in the presence of a rectilinear perforate network of laminae and pillars. The microstructure of the pillars of *Komia* most closely approaches that of Mesozoic stromatoporoids such as *Steinerella* (see Lecompte 1956, p. F138, text-fig. 2*c*) and *Dehornella* and *Astroporina* (see Hudson 1960, pl. 26).

In summary, *Komia* closely resembles the Middle Palaeozoic stromatoporoids mentioned above in its ramose and cylindrical form and in the relative regularity of its pillars and laminae. It more closely resembles the Mesozoic and Late Palaeozoic stromatoporoids in the more open and porous nature of the laminae, in the microstructure of the pillars, and, to a lesser degree, in the relatively minute dimensions of the skeletal framework.

Korde (1951, p. 181) interpreted *Komia* as an alga with a decidedly branched cylindrical thallus formed of a hypothallus of a small bundle of elongate, cellular filaments and a thick perithallus of dichotomously branching, cellular filaments. Our study demonstrates that *Komia* is a stromatoporoid with a non-cellular coenosteum formed of (1) an outer region (= perithallus of Korde) composed of trabeculate pillars and perforate, conical laminae, and (2) an axial cylinder (= hypothallus of Korde) composed of elongate, abaxially walled grooves. To our knowledge, this combination of structures is not known to occur in undoubted algae (Paul C. Silva, oral communication to Wilson and

Waines, July 1962, agrees). Calcareous algal skeletons are composed of cells or fine tubules, or are gross as in some of the Cyanophyta, or are uniquely specialized as in the Dasycladaceae and Charophyta. *Komia* is like none of these. On the other hand, the presence of coarsely perforate laminae and trabeculate pillars strongly suggests affinities with some of the Late Palaeozoic and Mesozoic stromatoporoids.

Our differences with Korde (1951, text-fig. 5) in the interpretation of the axial section of *Komia* are illustrated, very diagrammatically, in text-fig. 1. The conceptacle (?) chambers in Korde's reconstruction (see text-fig. 1*a*) were neither mentioned nor otherwise illustrated by her (Korde 1951) and were not observed by us in our material. Since Korde (*in litt.*, May 1962), after examination of a thin section of *K. eganensis*, found our fossils closely similar to her *K. abundans*, we discount the possibility that our widely differing interpretations are both correct and founded on non-related fossils.



TEXT-FIG. 1. Diagrammatic representations of axial sections of *Komia* Korde showing differing structural interpretations. *a*, after Korde; *b*, present paper.

Maslov's (1956, p. 21) passing suggestion of similarities between *Komia* and some echinoderms seems invalid since the discrete skeletal units do not behave as single calcite crystals in polarized light, but are composed of microcrystalline fibres.

The two undescribed illustrations labelled *Komia abundans* by Drushchits and Yakubovskaya (1961, pl. 2, fig. 10) appear, possibly in agreement with our observations, to be less cellular than the reconstruction of Korde (1951, p. 181, text-fig. 5). However, the inclination of the laminae is totally different from that described in Korde (loc. cit.) and in this study. Furthermore, the transverse section lacks the characteristic concentric

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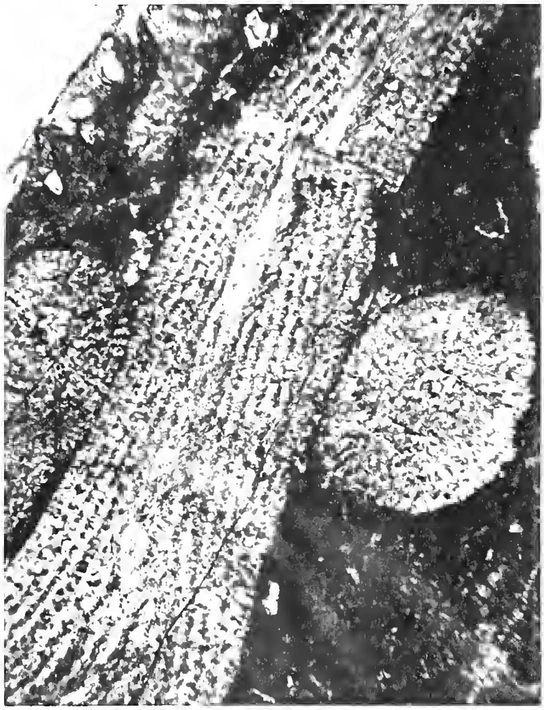
EXPLANATION OF PLATE 34

Photographs not retouched; figs. 1 and 5 photographed by transmitted light, figs. 2, 3, and 4 by reflected light.

Figs. 1–5. *Komia eganensis* sp. nov. 1, 2, Axial section of holotype UCMP 30781 and transverse sections of two other specimens, ×28. 3, 4, Transverse section of paratype UCMP 30782; 3, ×88; 4, ×28. 5, Transverse section of paratype UCMP 30783, ×30. Twin central zones in figs. 4 and 5 indicate sections were cut just below a dichotomous branch.



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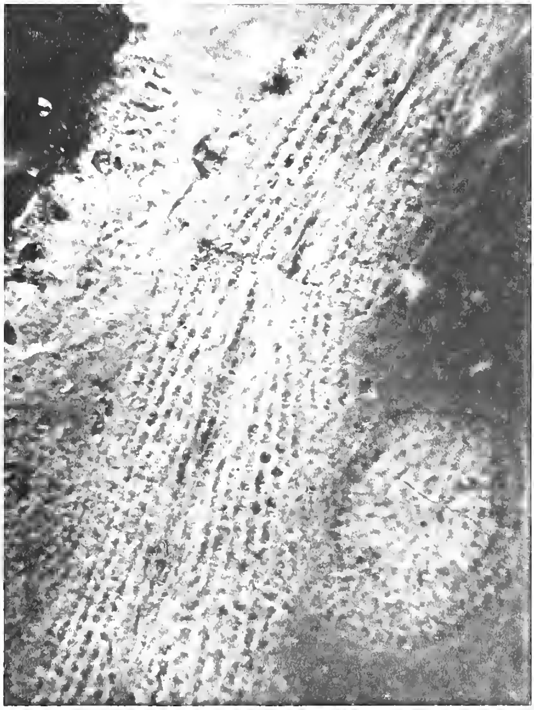

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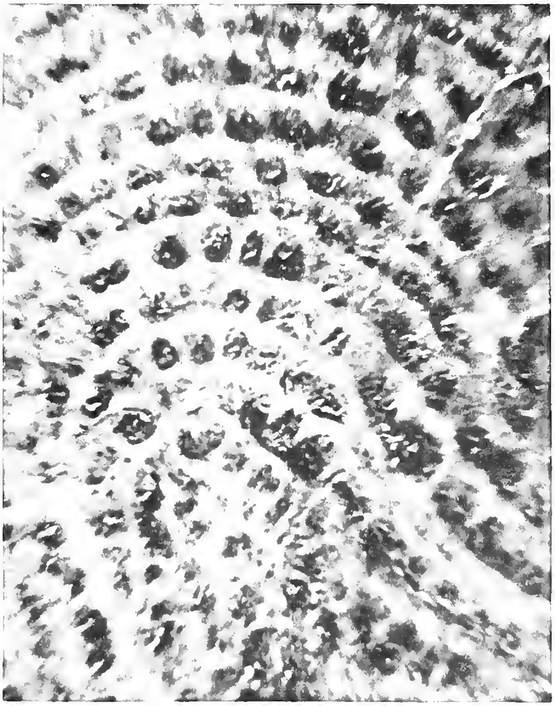

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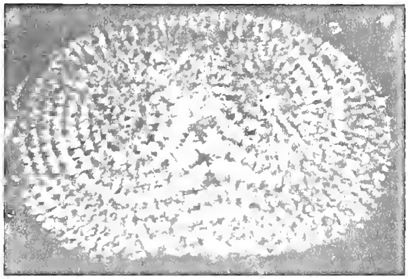

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4

WILSON, WAINES and COOGAN, *Komia*

nature of the laminae of *Komia* and the structure of the inner zone is very obscure. Because these important inconsistencies were not justified by Drushchits and Yakubovskaya (1961) we feel that their figures either may represent fossils which are not referable to *Komia* or else may be erroneously executed reconstructions. We therefore have elected to disregard them as accurate representations of *Komia*.

Komia eganensis sp. nov.

[by Wilson and Waines]

Plate 34, figs. 1–5; Plate 35, figs. 1–4

External features (Pl. 35, fig. 3). Coenosteum ramose, uniformly cylindrical in mature portions, tapering distally to blunt conical tips, exceeding 5·2 mm. in length, up to 1·7 mm. in diameter; surface very minutely granulate; basal region of growth not observed.

Transverse section (Pl. 34, figs. 1, 2 in part, 3–5; Pl. 35, fig. 1). Coenosteum circular, varying from 0·2 to 1·7 mm. in diameter, formed of an outer zone of concentrically arranged laminae and radially arranged pillars and a central zone of irregular construction.

Outer zone. Laminae concentric, usually complete but in places incomplete and merging with subjacent laminae, regularly spaced, numbering 6 to 7 in 0·33 mm., varying respectively from 1 to 13 with coenosteal diameters of 0·2 to 1·7 mm., irregular in thickness, varying from 0·015 mm. between pillars to 0·035 mm. in vicinity of pillars, in many places uniperforate between pillars with pores varying from 0·005 to 0·03 mm. or more in width (best observed in tangential section); pillars generally spool-shaped between laminae, less frequently expanding abaxially and tapering axially, occasionally irregular or incomplete, confined to one interlamina or continuous or superposed through 2 to 5 or more interlaminae, generally from 0·01 to 0·035 mm. in width, numbering from 5 to 7 in 0·33 mm.; galleries generally circular, less frequently semicircular or horizontally rectangular with vertical constrictions, generally 0·01 to 0·035 mm. in height, varying from 0·01 to 0·165 mm. in width though averaging from 0·015 to 0·035 mm.; filaments (possibly representing incompletely developed pillars) occasional, irregular, generally vertically disposed, confined to interlaminae, generally less than 0·005 mm. in width; microstructure of pillars fibrous with fibres curving upwards and outwards from central portions of pillars (Pl. 35, fig. 2).

Central zone. Generally circular, averaging 0·15 to 0·25 mm. in diameter, bounded by innermost lamina of outer zone, generally composed of three intergrading portions: innermost portion composed of an amoebiform complex of frequently interconnected galleries; galleries measuring up to 0·05 mm. in width, frequently intersected by pillar-like and filament-like structures with dimensions similar to those of comparable structures in outer zone; middle portion interfingering with gallery complex within and grading to more regularly constructed outer portion, composed of an irregular perforate network of galleries and pillar-like, lamina-like, and filament-like structures with dimensions similar to those of comparable structures in outer zone; outer portion generally interlamina-like with normal pillars and galleries as in outer zone.

Axial section (Pl. 34, figs. 1, 2). Coenosteum elongate, ramose, of uniform width in mature portions, tapering distally to blunt tips, greatly exceeding 5·0 mm. in length, up to 1·1 mm. in width, formed of an outer zone of regular laminae and pillars and a central zone of less regular construction.

Outer zone. Laminae generally inclined downwards and outwards about 15 degrees from the axis in inner portion of outer zone, becoming subparallel to parallel to surface of coenosteum in outer portion, successively emerging at surface in a recessively overlapping manner, terminating axially by merging indistinctly with elements of central zone and terminating unobtrusively on surface; complementary laminae on either side of central zone generally terminating in apposition axially, rarely terminating in apposition surficially; dimensions and mutual disposition of laminae, laminar pores, pillars, filaments, and galleries similar to comparable elements in outer zone of transverse section; microstructure of pillars similar to that of pillars in transverse section.

Central zone. Slender, elongate, continuous, averaging 0·2 mm. in width, generally composed of two intergrading portions: inner portion composed of a complex of irregular, perforate, indistinct filament-like structures gently curving upwards and outwards from axis and irregular, elongate, generally indistinct galleries frequently intersected by irregular filament-like structures and very rarely intersected by thin transverse structures; heights of galleries and widths of filament-like structures similar to those of comparable elements in transverse section; outer portion merging indistinctly with inner margin of outer zone, composed of a complex of thickening distal extremities of the curved filament-like structures of the inner portion, pillar-like and filament-like structures and round irregular galleries; dimensions of galleries and structural elements similar to those of comparable elements in outer zone.

Tangential section (Pl. 35, fig. 4). Pillars round to irregular, generally separate, occasionally coalescent; usually 0·015 to 0·030 mm. in diameter, numbering about 20 to 25 in 0·28 of a square mm., galleries coalescent about pillars; laminae appearing as irregular perforate areas; laminar pores generally round, usually 0·015 to 0·035 mm. in diameter, numbering about 15 in 0·28 of a square mm.

Documentation. Holotype 30781 and paratypes 30782 to 30790 are from locality B.4854. Approximately fifteen polished sections and eighteen thin sections, exhibiting a total of several hundred specimens of *K. eganensis*, were prepared and studied. In addition, serial photographs of successive transverse sections of one coenosteum served to reveal more fully the nature of the skeletal framework.

Name. The species is named after the Egan Range in eastern Nevada, from which many of the specimens of *K. eganensis* used in this study were obtained.

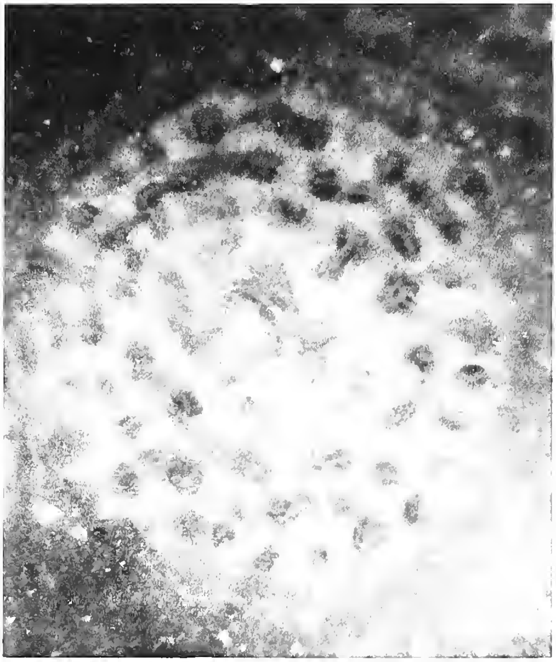
Occurrence. K. eganensis was collected from six localities in eastern Nevada, which are listed below.

Discussion. K. eganensis is similar to *K. abundans* in the overall form and size of the coenosteum and in the general spacing of the laminae. In the former species, less closely spaced pillars (5 to 7 in 0·33 mm. *vs.* 8 or more in the latter) and a larger diameter (0·2 *vs.* 0·08 mm.) of the axial cylinder are considered characteristic.

EXPLANATION OF PLATE 35

Photographs not retouched; figs. 1, 3, and 4 photographed by reflected light; fig. 2 by polarized light.

Figs. 1–4. *Komia eganensis* sp. nov. 1, Transverse section near distal extremity of coenosteum, × 105. 2, Microstructure of pillars, × 250. 3, Fragments of silicified coenostea, × 5·4. 4, Tangential section showing perforate lamina, paratype UCMP 30784, × 75.



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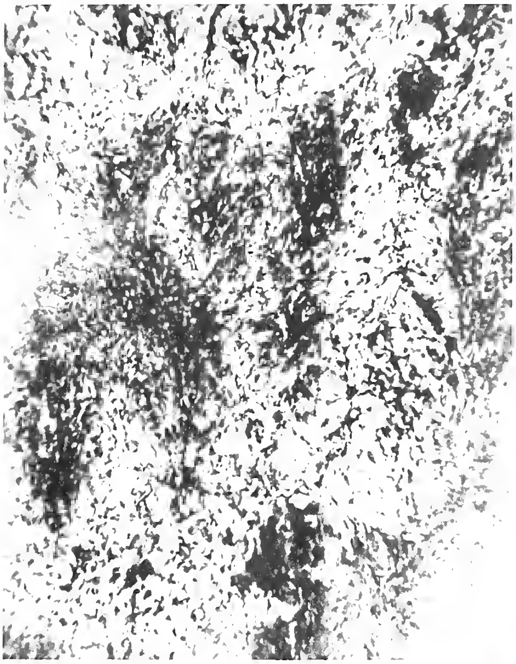

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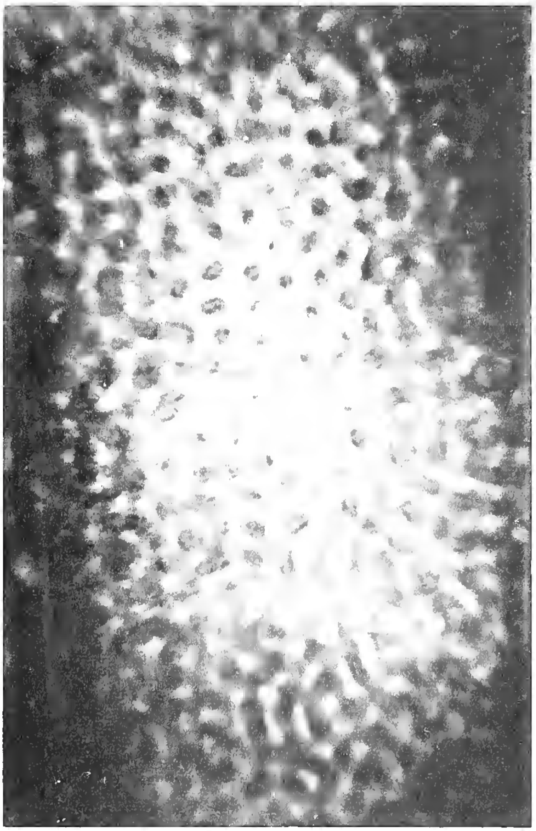

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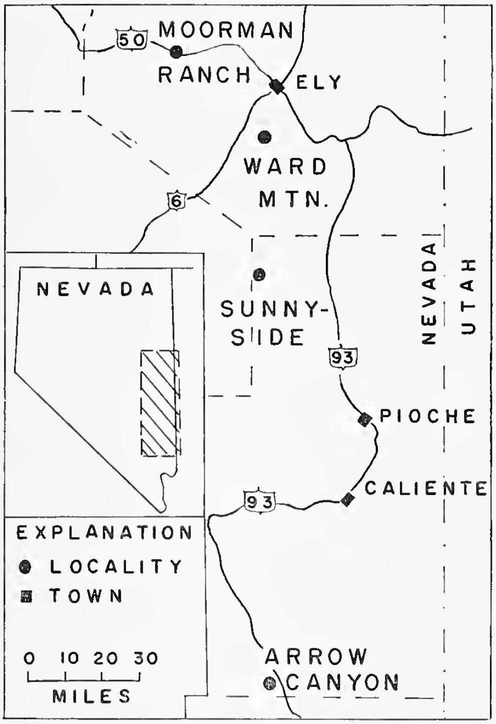
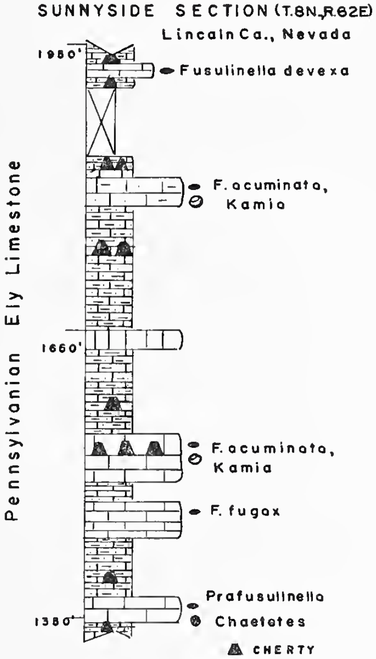
WILSON, WAINES and COOGAN, *Komia*

Komia sp. ?, figured by Johnson (1960, pl. 19; 1961, pl. 25), is not described and is insufficiently well illustrated for specific comparison.

The material upon which the present study is based occurs as abundant, fragmentary, partially silicified coenostea in a medium grey-brown, fine-grained, biofragmental limestone. Due to some as yet unidentified character inherent in the structure of the unaltered skeletal elements, much more morphological detail was revealed by the study of polished and slightly acid-etched surfaces under oblique reflected light (e.g. Pl. 34, figs. 2–4; Pl. 35, figs. 1, 4) than was revealed by thin sections under transmitted light (e.g. Pl. 34, figs. 1, 5). The nature of the microstructure of the pillars, however, was best observed by means of the latter method. We recommend use of both methods in studying *Komia*. It is felt that observations limited only to transmitted light (e.g. Korde 1951, pl. 2, figs. 3, 4, text-fig. 4; and Johnson 1960, pl. 19; 1961, pl. 25) may have restricted some investigators' interpretations of the structure of *Komia*.



TEXT-FIG. 2. Map of part of eastern Nevada showing localities from which *Komia eganensis* sp. nov. was collected.



TEXT-FIG. 3. Generalized columnar section of part of the Ely Limestone near Sunnyside, Nevada, showing stratigraphic distribution of *Komia eganensis* in relation to some other fossils.

STRATIGRAPHIC DISTRIBUTION

Komia is widespread in the Pennsylvanian rocks of the western United States. Johnson (1960, p. 51) reported its presence in west Texas and New Mexico in rocks of Desmoinesian age. Mollazal (1961, p. 26) and Wright (1961, p. 154) reported it in rocks of Derryan

(= Atokan) age in the Ely Limestone of Millard County, Utah, and the Oquirrh Formation of Tooele County, Utah, respectively. Mollazal (1961, p. 26) further commented that he had observed *Komia* elsewhere 'in eastern Great Basin in Derryan to Desmoinesian limestones'. In the Ely Limestone of east-central Nevada and in the Bird Springs Formation of southern Nevada, *K. eganensis* occurs with *Fusulinella spp*. of Atokan age. Fragmentary remains with associated fusulinids and other bioclastic debris form coquinoid limestones. Korde (1951, p. 181) reported similarly that *Komia* together with foraminifera substantially make up many limestone beds along the Un'ya River in the northern Ural Mountains of Russia. Johnson (1960, p. 51) reported *Komia* in the Lower Pennsylvanian of central Japan, but did not further discuss its occurrence there.

In a characteristic section near Sunnyside, Nye County, Nevada (text-fig. 3), *Komia eganensis* is associated with *Fusulinella acuminata* Thompson in the Ely Limestone from about 1,500 to 1,820 feet above the base. Its lowest occurrence is 150 feet above the *Chaetetes–Profusulinella* faunizone. *Komia* is not known to occur with *Profusulinella*, *Fusulinella devexa* Thompson, or younger faunas in this area.

In the Ely Limestone at Moorman Ranch, White Pine County, Nevada, *K. eganensis* occurs 375 feet above *Caninia torquia* (Owen) and 150 feet above the *Chaetetes–Profusulinella* faunizone. In the Arrow Canyon Mountains, Clark County, Nevada, *K. eganensis* and *Fusulinella acuminata* are present 1,375 feet above the base of the Bird Spring Formation and 40 feet above the *Chaetetes–Profusulinella* faunizone. The association of *K. eganensis* and *F. acuminata* Thompson apparently characterizes a restricted biostratigraphic zone in eastern Nevada.

LOCALITIES

The abbreviations T. 00 N., R. 00 E. appearing below represent Township 00 North, Range 00 East, Mt. Diablo Base and Meridian.

B.4851. Bird Spring Formation, Arrow Canyon Quadrangle, Clark County, Nevada. Two- to three-foot resistant limestone ledge 1,285 feet above base of formation near red painted number 26 and yellow painted 'C'. The outcrop is in Arrow Canyon, accessible from U.S. Highway 93 by turning west past a ranch house 12 miles north of Glendale Junction on to a dirt road which passes through a dump and into the canyon. Collected by Coogan.

B.4853. Ely Limestone, Illipah Quadrangle, White Pine County, Nevada. 'Moorman Ranch' locality. *Komia* occurs with fusulinids 1,360 feet above base of Ely Limestone exposed on a spur overlooking U.S. Highway 50 (north side). The line of traverse is marked with many wooden stakes. *Komia* can be collected at the stake with a brass ring numbered 485, approximately 150 feet above a well-defined bed with silicified *Chaetetes*. Collected by Coogan.

B.4852. Ely Limestone, T. 8 N., R. 62 E., Lincoln County, Nevada, near Sunnyside. Locality is 1,490 feet above base of Ely Limestone in section due east of Silver Spring, which lies a short distance north of Shingle Pass road at the base of the west side of the Egan Range. Collected by Coogan.

B.7873. Same section as B.4852, 20 feet higher.

B.7874. Same section as B.4852, about 310 feet higher and 10 feet below a red number 7 painted on the rocks.

B.4854. Ely Limestone, Ely No. 3 Quadrangle, White Pine County, Nevada. Locality lies in T. 14 N., R. 62 E. just south of crest of ridge bordering north side of south fork of Willow Creek near 9040-foot contour line as shown on USGS Advance Sheet for the SE. quarter of the Ely No. 3 Quadrangle, 1958 Edition. Grey limestone unit with *K. eganensis*, *Chaetetes favosus*, *Multithecopora hypatiae*, and Atokan fusulinids. Collected by R. L. Langenheim, Jr.

Acknowledgements. J. Harlan Johnson (of the Colorado School of Mines), Wayne L. Fry, and Paul C. Silva (paleobotanist and botanist, respectively, of the University of California, Berkeley), kindly examined some of our specimens and discussed possible algal affinities. Drs. Fry and Silva also read the manuscript and suggested apposite changes. K. B. Korde, of the Paleontological Institute, U.S.S.R. Academy of Sciences (Moscow), graciously examined one of our thin sections of *Komia eganensis* and agreed that it was properly placed in her genus. Thanks are due to J. Wyatt Durham of the University of California (Berkeley) for criticisms and suggestions made during this study and for reading the manuscript. R. L. Langenheim, Jr., of the University of Illinois, supplied the fossils which instigated this study and contributed locality and stratigraphic data for his material.

Coogan contributed specimens from and information regarding localities B.4851–3 and B.7873–4, text-figs. 1 and 3, and the section entitled Stratigraphic Distribution. In addition, he assisted with translations. Wilson and Waines are responsible for the remainder of the paper, including the description of *K. eganensis* sp. nov.

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SOME SILICIFIED ORDOVICIAN FOSSILS FROM SOUTH WALES

by NILS SPJELDNÆS

ABSTRACT. A preliminary description is given of a silicified fauna from the Upper Llanvirn or Lower Llandeilo of South Wales. The material consists mostly of trilobites, ostracods, and bryozoans. One new genus and two new species of ostracods are named, and the ontogeny of *Tallinnella complicata* (Salter) is described. Because of the silicified and fragmentary nature of the material, most of the numerous bryozoan species have not been named formally.

DURING the author's studies on some Ordovician brachiopods (Spjeldnæs 1959), it was discovered that a slab of limestone, stated to come from the Llandeilo of Llan Mill, near Narberth, Carmarthenshire, was rich in silicified fossils. The specimen, which belongs to the Geological Survey and Museum, London (no. 85415), is part of an old collection, and further details concerning the horizon and locality are not known. A description of the localities near Llan Mill is given by Strahan *et al.* (1914, pp. 31–33). The age of the fauna is discussed below.

The unsilicified fossils found on the slab are: *Macrocoelia* (*?*) *llandeiloensis* (Dav.), *Sowerbyella antiqua Jones*, *Horderleyella* cf. *subcarinata* MacGregor, *Dalmanella* cf. *parva* Williams, and other brachiopods (for the brachiopod fauna, see MacGregor 1961), indeterminate gastropods and cystid fragments.

The brachiopods, molluscs, echinoderms, and some of the trilobites are not silicified, and are preserved as moulds in the shale partings only. In spite of the small size of the slab (about 20×8×2 cm.), it yielded, after solution in hydrochloric acid, several hundred silicified fossils, mainly ostracods, bryozoans, and trilobites. The silicified fossils are described below.

Except for the fragmentation, which might be a local feature only, the silicified specimens are excellently preserved, almost equal to the famous material from the Edinburgh Formation in Virginia, U.S.A. (cf. Whittington and Evitt 1956).

The author is deeply indebted to Dr. Stubblefield, Geological Survey and Museum, London, for the loan of the specimens, Dr. Gunnar Henningsmoen and Dr. A. L. Guber for inspiring discussions about the ostracods, and to Miss B. Mauritz and Mr. O. Brynhildsrud for photographing the specimens.

SYSTEMATIC DESCRIPTIONS

Class TRILOBITA

Marrolithus inflatus incipiens Williams 1948

Plate 36, fig. 1*a–b*

1948 *Marrolithus inflatus incipiens*—Williams, *Geol. Mag.* **85**, p. 77, text-fig. 6, pl. vi, fig. 2.

Material. Very plentiful (about 120 fragments), but fragmentary. In most specimens, only one-half of the fringe is preserved, and this prevents a statistical study of the material.

[Palaeontology, Vol. 6, Part 2, 1963, pp. 254–63, pl. 36–37.]

The wide range in size of the specimens allows a study of the variation of the fringe. In the largest specimens, the raised pits are more numerous, and they approach *M. inflatus inflatus*. In the smaller specimens the number of raised pits gradually decreases with size, and in the smallest specimens they are absent.

The preservation of the material shows that the pits are continuous, and hyperbolic in cross-section. The raised pits are steeper (more cylindrical) than the ordinary ones.

In *Tretaspis*, from studies made by Störmer (1930), it is known that the pits are hourglass-shaped, parted by a suture in the middle. In *M. inflatus incipiens* no suture is observed, and the curvature of the walls of the pits is the reverse of that found in *Tretaspis*.

Other trilobites. The other silicified trilobites are *Flexicalymene cambrensis*, indeterminable asaphid fragments, and a small cephalon of an *Ampyx sp.*, which was broken during preparation.

Class CRUSTACEA
Subclass OSTRACODA
Tallinnella complicata (Salter)

Plate 36, figs. 9–13, text-fig. 1

1947 *Tetradella complicata* (Salter)—Harper, *Geol. Mag*. **84**, pp. 345–53 (for further references, see this paper).

Material. Four hundred valves which were sufficiently complete for measurement, and a large number of fragmentary valves. As mentioned above, it is possible that this is topotype material of Salter's species.

Description. The markedly preplete valves are rather flat in profile in adult specimens, whereas in the larval instars they are more regularly swollen. In all stages the surface is smooth, except for the four distinct lobes, two of which (L1 and L3) protrude over the hinge-line.

The smaller larval valves also have a marginal row of short, thin spines which are not found in the adults.

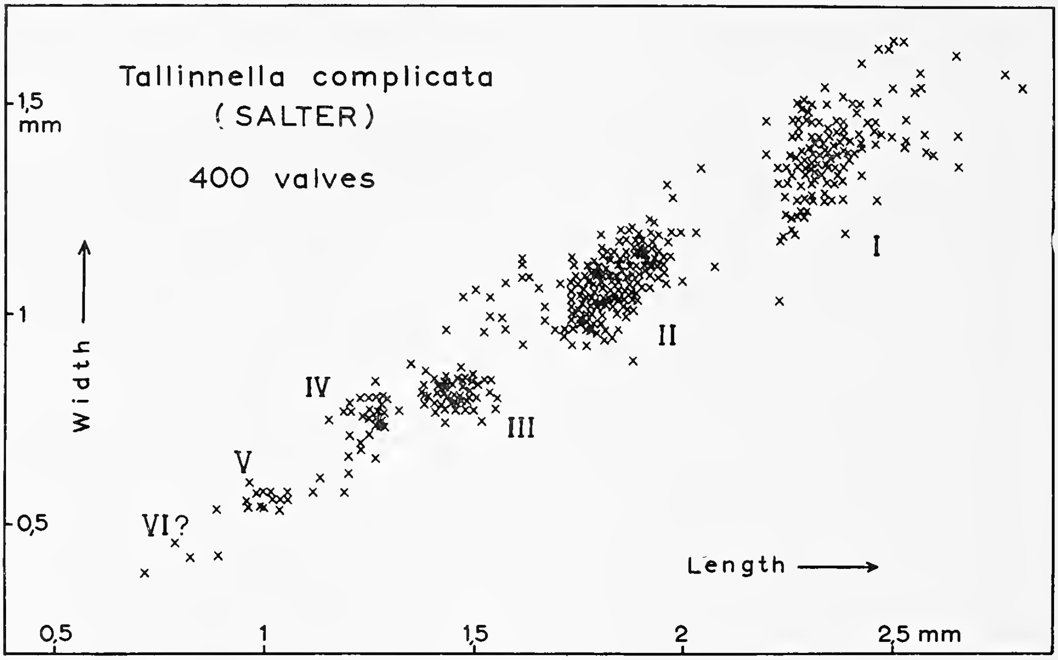
The hinge itself is generally smooth in both valves; some teeth-like structures were observed, but, as usual in silicified specimens, it is very difficult to determine if such delicate structures are original or due to somewhat capricious silicification. It is, anyhow, not a constant feature in the present material.

Some slight variation was observed in the material present, especially in the size of the swollen ends of L1 and L3, and in the outline of the domicilium.

Text-fig. 1 records measurements of 400 valves. Several growth stages are discernible (I–VI). Some of them have the size theoretically expected (growth factor about 1·26, cf. Spjeldnæs 1951), but between the third and fourth larval stage the difference in size is much smaller than expected, especially the width, which is almost the same in both.

If the growth series demonstrated by the stages VI–V–IV is extrapolated according to Brooke's law, the theoretical stage III should be about 1 mm. wide and 1·5–1·6 mm. long. Some few specimens of this size are found, in addition to the normal stage III. If, similarly, the growth series of the larger stages I–II–III are extrapolated, the theoretical stage IV will fit with some few scattered specimens, and not with the majority observed in stage IV. This peculiar disconformity in the growth series might be due either to a mixing of two populations, or an unknown feature in the ontogenetic development of *T. complicata*.

Öpik (1937) suggested that *Tallinnella* showed sexual dimorphism, and this is confirmed by the present material. About 30 per cent of the adult specimens show a prominent velar flange in the anterior part (Pl. 36, fig. 12), and about 40 per cent are without this flange (Pl. 36, fig. 13). In the rest, this feature could not be observed clearly. Variation in size of the flange was observable but small, and all specimens in which the inside was well preserved could be referred to one of the two dimorphs without doubt.



TEXT-FIG. 1. *Tallinnella complicata* (Salter) from Llan Mill, near Narberth, Geol. Surv. Mus. No. 85415. Measurements of 400 valves, showing instars.

Remarks. This species resembles in most features *T.* (?) *bohemica* (Barr.) as described by Jaanusson (1957, pp. 342–3, pl. x, fig. 3). The lobes are stronger, and the extralobal area is not visible in lateral view in *T. complicata*. The limitation of the genus *Tallinnella* is not considered here, the term is used in the wide sense of Henningsmoen (1953, pp. 213–14), and not in the more restricted sense of Jaanusson (1957). *T. complicata* differs considerably from the type species, *T. dimorpha*, especially in the development of the extralobal area.

Genus GUNNAROPSIS gen. nov.

Diagnosis. Four-lobed ostracods with L1, L2, and L3 each developed as a sharp crest, and L4 as a gentle swelling. A histial (?) flange starts at the upper anterior end of the domicilium, turns almost horizontal below L1–3, and stops abruptly in the lower part of L4. A velar (?) flange starts just in front of the middle of the valve, and runs parallel to the histial flange almost to the upper posterior corner, where it stops abruptly. Dimorphism not observed.

Type species. Gunnaropsis cristata sp. nov.

Remarks. This genus resembles some from the Lower Ordovician, such as *Rigidella* Öpik, *Protallinnella* Jaanusson, and *Tallinnellina* Jaanusson. It differs from them, and, as far as the author knows, from most other Palaeozoic ostracods in that the velar and histial flanges are not parallel to the margin of the valves. *Gunnaropsis* also differs from the three mentioned genera in that its four lobes are not distinctly united, and that L4 is developed as a rounded ridge, contrasting with the sharp edges of the other lobes. In the other three genera, the differences between the lobes in this respect are much less strong.

The family relationship of *Gunnaropsis* is at present obscure, especially since the presence or absence of dimorphism, and the possible type of dimorphism, cannot be ascertained because of the small amount of material present. The three other genera mentioned, as well as *Tallinnella,* have been referred to the Quardijugatorinae by Jaanusson (1957, pp. 338–40), but it is rather doubtful if *Gunnaropsis* can be accommodated to this subfamily.

Gunnaropsis cristata sp. nov.

Plate 36, fig. 6

Diagnosis. Same as diagnosis for genus.

Description. Outline of valves slightly preplete, with long, straight hinge-line. L1, L2, and L3 have sharp crests, and L1 and L2 are connected ventrally, forming a sharp V. L4 is well developed, but lacks a crest in its dorsal part. L3 protrudes over the hinge-line, and this is generally the case also with L1 and L4, but to a lesser extent.

There are two flanges; one, which is interpreted as the velar, starts below L1–2, at the margin of the valve, and ends abruptly beside L4, just before reaching the hinge-line. The distance from the margin of the valves increases gradually. Below L1–2, it is found at the margin of the valve; at the end, it is in close contact with L4, some distance from the margin.

The other flange, which is interpreted as a histial one, starts at the upper anterior end of the valve, near the margin, and the distance from it gradually increases. Below L1–2, it joins the connecting lobe and turns horizontally. It ends abruptly in the ventral part of L4.

Fifteen specimens of this species were found, the larger ones being about 1·5 mm. long and 0·9 mm. wide. Some smaller specimens, about 1·0 mm. long and 0·55 mm. wide, probably represent a larval stage. No dimorphism is observed, and it is possible, also, that the larger specimens are not adults.

Ceratopsis britannica sp. nov.

Plate 36, fig. 7

Diagnosis. A long and low *Ceratopsis* species with a prominent carina-like bulge connecting L1 and L4.

Description. The holotype is 1·3 mm. long and 0·7 mm. wide. L4 is faintly developed, L3 is prominent and rounded, L2 is shorter, but still prominent, and L4 continues into the rounded triangular 'horn' with strong horizontal striation, which is characteristic for this genus. A histial (?) bulge unites L4 and possibly L1. It is blunt-edged, and directed outwards. A velar flange is developed, and is widest in the anterior part of the valve. No sexual demorphism was observed among the about 20 specimens studied.

Some of them are rather small (1·0–1·1 mm. long and 0·55 mm. wide), representing larval stages, and as usual the lobes are bulbous and diffuse. The horn on L4 is also proportionally much longer in the smaller specimens. This species differs from the other members of the genus in the proportions, and in the strong development, of the carinal bulge.

Lomatobolbina sp.

Plate 36, fig. 8

Seven specimens of this species are present, both tecnomorphs and heteromorphs. An average specimen is 1·2 mm. long. Because of the development of a histial dolon, the sigmoidal sulcus S2, and the strongly developed posteroventral lobe, it probably belongs to *Lomatobolbina* Jaanusson (1957, pp. 395–9). It resembles *L. mammillata* (Thorslund) cf. Jaanusson (1957, pl. 12, figs. 6–8) in the absence of a distinct node on the posteroventral lobe, but differs from it in outline, and in the more anterior position of S2.

Other ostracods. In addition to the species described above, there are also some smooth specimens in the material present. One species represented probably belongs to *Conchoprimitia*, but the number of undamaged valves is too small (4–5 specimens) for a detailed description. The other smooth valves are very small, and of different shapes. Some of them might be young larval valves.

Phylum BRYOZOA

Bryozoans are very abundant in the material, but they are generally fragmentary. In order to give a modern description of Ordovician bryozoans, thin sections are absolutely necessary, especially for the Trepostome bryozoans, and also for Cryptostomes. As it is

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EXPLANATION OF PLATE 36

All specimens belong to the Geological Survey and Museum, London. The specimens have not been whitened and the photographs are not retouched. All the specimens come from the Upper Llanvirn or Lower Llandeilo at Llan Mill, near Narberth, Carmarthenshire.

Fig. 1. *Marrolithus inflatus incipiens* Williams. Upper (fig. 1*a*) and lower (fig. 1*b*) sides of a fragment of the fringe, ×about 6.

Figs. 2, 4. *Mesotrypa* aff. *lens* (M'Coy). 2, Lower surface of a zoarium, showing numerous mesospores surrounding the zooecia. 4, Upper surface of another zoarium, showing only very few and small mesospores, ×about 8.

Fig. 3. *Orbignyella favulosa* (?) (Phillips). Upper surface of a fragmentary zoarium, ×about 8.

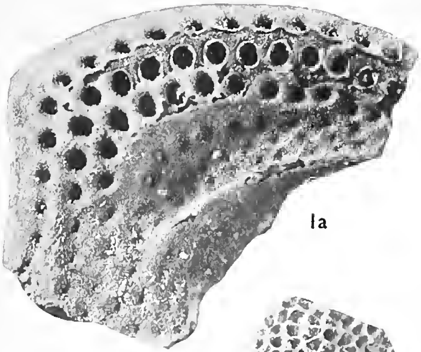
Fig. 5. Indeterminate trepostome bryozoan D, showing central tube in a fragmentary zoarium, ×18.

Fig. 6. *Gunnaropsis cristata* gen. and sp. nov. Holotype. Large, complete valve, ×27.

Fig. 7. *Ceratopsis britannica* sp. nov. Holotype, × 27.

Fig. 8. *Lomatobolbina sp.*, ×27.

Figs. 9–13. *Tallinnella complicata* (Salter). 9, 10, Young instars of the two last larval stages, ×27. 11, Exterior of an adult valve with histial dolon (female ?), ×27. 12, Interior of an adult valve with histial dolon (female ?), ×27. 13, Interior of an adult valve without histial dolon, ×27.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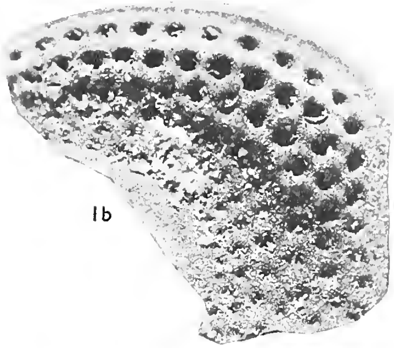
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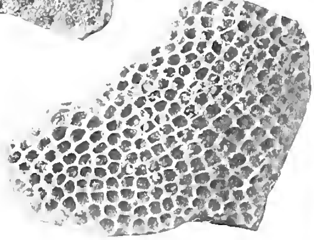
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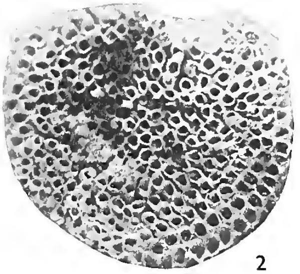
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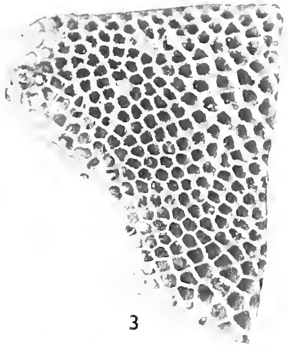
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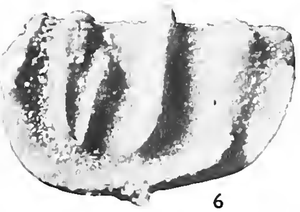
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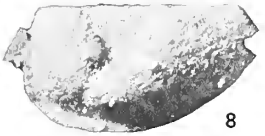
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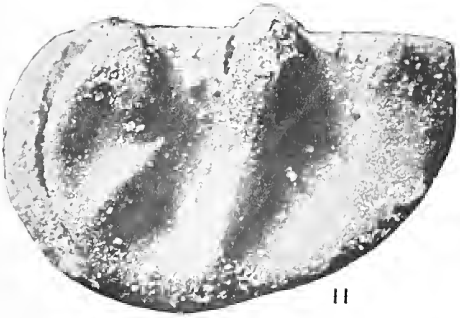
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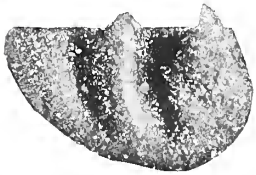
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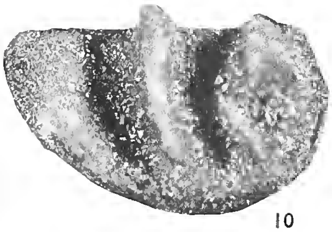
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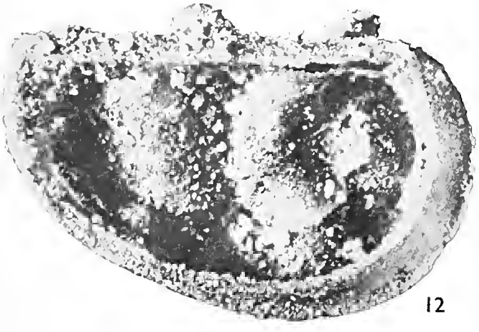
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SPJELDNÆS, Silicified Ordovician fossils

difficult to get good thin sections from silicified material, description of the species from the present material must remain incomplete at present. Therefore no new species have been named even though the whole fauna is new. The external features, as usual in silicified material, are very well preserved, and this, combined with the few features of the interior which were observed, gives some indication of the type of fauna found.

Order TREPOSTOMATA

Orbignyella favulosa? (Phillips)

Plate 36, fig. 3; Plate 37, figs. 12*a–b*

(?) 1957 *Orbignyella favulosa* (Phillips 1848)—Spjeldnæs, pp. 367–8, pl. 12, figs. 3, 7. (For further references, see this paper.)

Thin encrusting zoaria probably referable to this species are common. They differ from the type in being thinner, and smaller in diameter. The typical curved diaphragms are observed only in the larger specimens, but the maculae can be seen clearly, and acanthopores and mesopores are absent, both at the base and surface of the zoaria.

The type of this species (GSM 56404, cf. Spjeldnæs 1957, p. 367) comes from the Llandeilo Limestone of Llan Mill, and the present material might therefore be topotypes. The detailed locality and horizon is, however, not known either for the type or for the present material.

Mesotrypa aff. *lens* (M'Coy)

Plate 36, figs. 2, 4

Externally this species resembles *O. favulosa*, but it has smaller zooecia, less-developed maculae, and shows the characteristic development of the mesopores. They are clearly visible at the base of the specimens (Pl. 36, fig. 2), but very few are seen at the upper surface (Pl. 36, fig. 4).

The present material differs from the types (cf. Spjeldnæs 1957, pp. 368–70, pl. 13, figs. 5, 7, text-fig. 1C–E) in its smaller size and less-developed maculae. There are also fewer tabulae in the zooecia.

Species of this kind, usually referred to as '*Nebulipora lens*' in the older literature, are common in the British Middle Ordovician, and seem to replace the *Diplotrypa petropolitana*, which is the most common trepostome bryozoan in the Scandinavian–Baltic Province, and rather rare in Britain.

Indet. Trepostome A

Plate 37, fig. 7

Ramose zoaria, with branches about 2·5 mm. thick. Bifurcation unknown. The elongate-rounded zooecia have thick walls, and are almost completely surrounded by the numerous, rounded polygonal mesopores. There are numerous small acanthopores. No tabulae have been observed in the zooecia (only the outer part of the exozone is preserved), but the mesopores appear to be tabulated.

This species is the most common ramose trepostome bryozoan in the material.

Indet. Trepostome B

Plate 37, fig. 6

Thin ramose zoaria (branches approximately 0·5 mm. in diameter) without branching in the fragments at hand. Zooecia rather large (approximately 0·06 mm. in diameter), polygonal, and with few mesopores. Walls thin, and no acanthopores observed. Only few diaphragms have been observed in the zooecia and in the mesopores. A considerable variation is found as to number and arrangement of the mesopores, but maculae are not developed.

This species recalls thin-branched species of *Hallopora*, but generic identification cannot be confirmed without thin sections.

Indet. Trepostome C

Plate 37, fig. 8*a–b*

A small zoarium forming a hollow cone about 2 mm. in diameter, and 1 mm. high. Large, polygonal zooecia with thick walls. No mesopores and acanthopores observed. No diaphragms.

The conical shape might either be due to incrustation of a conical object, or it might be the normal shape of the zoarium. The material is insufficient for a final decision.

Indet. Trepostome D

Plate 36, fig. 5

Externally the zoaria appear to be normal ramose ones, with 1–1·2 mm. diameter, but cross-sections show that the colony was formed around a hollow tube with 0·3 mm.

EXPLANATION OF PLATE 37

All specimens belong to the Geological Survey and Museum, London. They come from the Upper Llanvirn or Lower Llandeilo of Llan Mill, near Narberth, Carmarthenshire. The specimens have been whitened with ammonium chloride, but the photographs have not been retouched.

Figs. 1–5. Arthrostylid cryptostome bryozoans. Six fragments of zoaria, three of which (figs. 1, 2, and 5) have the articulated base preserved. They illustrate the wide range of variation found in this material, ×30.

Fig. 6. Indeterminate trepostome bryozoan B. Fragment of a zoarium with unusually many mesopores, ×18.

Fig. 7. Indeterminate trepostome bryozoan A. Fragment of the surface of a zoarium, ×18.

Fig. 8. Indeterminate trepostome bryozoan C. The only complete zoarium seen from above (fig. 8*a*) and below (fig. 8*b*), ×18.

Figs. 9, 10. Indeterminate bifoliate cryptostome bryozoan A. 9, A fragment of an old zoarium, showing rounded zooecial apertures, and zooecia covered with surface sculpture, ×18. 10, A fragment of a young zoarium, ×18.

Fig. 11. Indeterminate bifoliate cryptostome bryozoan B. Fragmentary zoarium, ×18.

Fig. 12. *Orbignyella favulosa ?* (Phillips). Half of a zoarium seen from above (fig. 12*b*) and below (fig. 12*a*), ×18.


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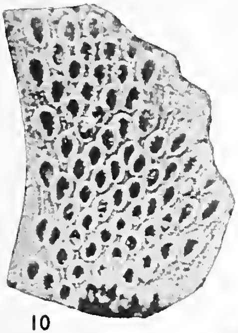
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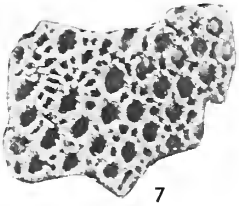
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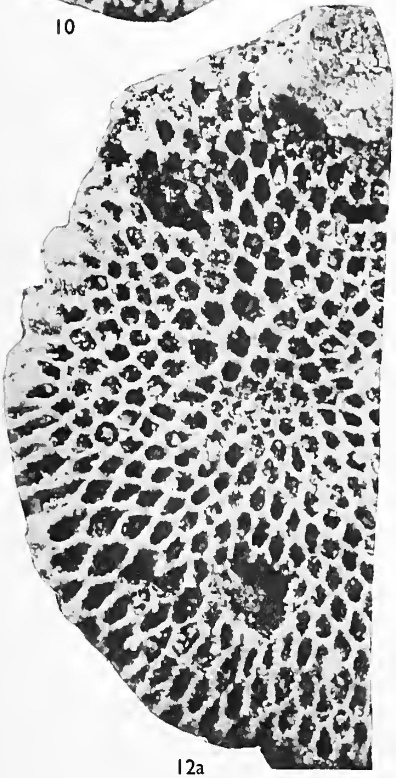
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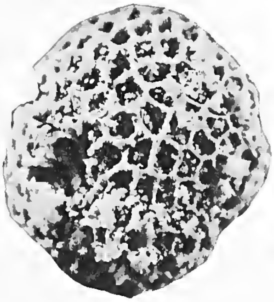
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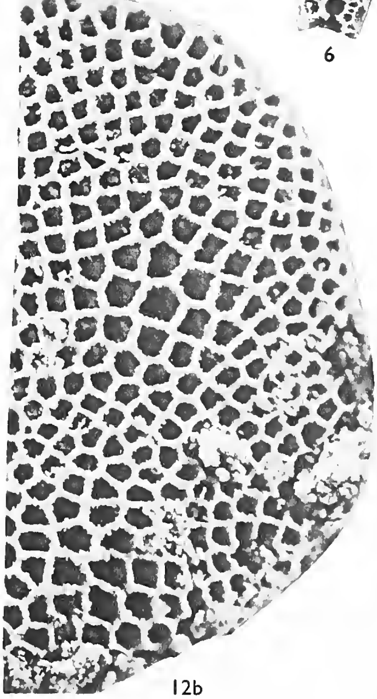
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SPJELDNÆS, Silicified Ordovician fossils

diameter. The zooecia are similar to species B in shape, they are generally slightly larger, and have more mesopores.

The hollow tube might either be a part of the zoarium, formed by the bryozoan, or it might be the tube filled by an organism encrusted by the bryozoan. Both cases are well known in Ordovician bryozoans.

Order CRYPTOSTOMATA

Indet. Bifoliate Cryptostome A

Plate 37, figs. 9–10

Nine fragments are known of this species. Young parts of the zoaria are sharp-edged, the older ones blunt-edged, about 1·5 mm. wide. The thickness also increased with age. There are five to seven rows of zooecial apertures, which are arranged diagonally. They are elongate, drop-shaped in the young, and more regularly circular in the old ones. Along the margin of the branches and between the zooecia there are longitudinal ridges. In some older specimens (Pl. 37, fig. 9) this sculpture covers some of the zooecia.

The considerable variation found in this species can be attributed to the different age of the fragments, such variation is known within a single zoarium both of fossil and recent bryozoans. The marked sculpture recalls *Arthropora* (= *Graptodichtya*), but this cannot be confirmed without thin sections of better-preserved material.

Indet. Bifoliate Cryptostome B

Plate 37, fig. 11

This species, which is found only in two small fragments, differs considerably from species A. The zooecial apertures are larger and more regularly arranged in diagonal rows, there are no peristomes, and no sculptured edge of the branches, and no sculpture between the zooecial apertures. The species recalls certain species of *Escharopora*, but also in this case it is not wise to refer it to a genus without thin sections.

Arthrostylid cryptostomes

Plate 37, figs. 1–5

The arthrostylid bryozoans are second in number only to the flat, discoid trepostomes. They occur in a variety of types having 3, 4, 5, or even 6 rows of zooecia, and a number of different sculptures, and sizes of zooecial apertures.

A number of new genera and species have been founded on such fragmentary silicified material (cf. Bassler 1953, pp. G128–G130), but the author has no wish to follow this procedure. Studies, on both fossils and recent species with fine-branched jointed zoaria, show that considerable variation is found in numbers of zooecial rows and in sculpture in different parts of the same zoarium (cf. Marcus 1940, text-figs. 97, 113). Some of these species also have primary, secondary, and tertiary branches which are rather different, especially in number of zooecial rows, and in length of segments.

Nevertheless, the present material shows such a variation in sculpture and size of zooecia that it must be assumed that more than one species is present. For the reasons stated above, these species remain unnamed because of the scanty and incomplete material at hand.

Other bryozoans. Besides those mentioned here, there are a number of others in the material, chiefly very fragmentary trepostomes. One of them has very oblique zooecial apertures, and resembles *Bythopora.*

THE AGE OF THE FAUNA

Judging from the presence of *Marrolithus inflatus incipiens,* and the trilobite and brachiopod fauna which accompany this subspecies, the age of the fauna would be either Upper Llanvirn (*D. murchisoni* Zone) or Lower Llandeilo. The stratigraphy of these forms are well known from the type Llandeilo district through the papers of Williams (1948, 1950) and earlier authors.

The ostracod and bryozoan fauna described here resemble faunas generally found in Caradoc beds. *Lomatobolbina* is not recorded below the Crassicauda Limestone (uppermost Llandeilo), and has its main distribution in the Caradoc. *Tallinnella* has been reported from Lower Ordovician onwards, but the Bohemian section of the genus, to which *T. complicata* belongs, is not elsewhere reported from beds older than the Caradoc. *Conchoprimitia,* on the other hand, is mainly a Lower Ordovician genus. The ostracod faunas known from the Scandinavian Llanvirn and Lower Llandeilo are strikingly different from that described here (Henningsmoen 1953*b*, Jaanusson 1957).

The bryozoan fauna, although it cannot be identified as to species and genus, resembles in general pattern those found in the Caradoc beds of Scandinavia, Estonia, and eastern U.S.A. (especially the Edinburgh Formation of Virginia). The resemblance with the latter might partly be due to facies and preservation since the arthrostylids, which are so prominent in many silicified bryozoan faunas of this age, are easily overlooked in other preservations. The few known bryozoan faunas of this age (Oil Creek Formation in Oklahoma, and Kanosh Shale in Utah) have a quite different set of species, which are considerably more primitive-looking and resemble the Lower Ordovician fauna.

The apparent difference from other early Ordovician faunas is perhaps because very few bryozoan and ostracod faunas of Llanvirn–Llandeilo age are well known, and it is quite possible that the picture of faunal distribution will have to be changed when material from other facies and areas are studied.

A check of the exact correlation between the type Llandeilo and the standard graptolite succession might, however, be advisable in light of the new material presented here.

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THE BRITISH CARBONIFEROUS SPECIES OF *GIRVANELLA* (CALCAREOUS ALGAE)

by ALAN WOOD

ABSTRACT. The type specimens, or topotypes, of the known species of *Girvanella* from the Lower Carboniferous rocks of Britain are redescribed. The two species found in the Girvanella Band in northern England are identical with those described by Wethered from the Avon Gorge, which occur at a very similar horizon. It is shown that the type of preservation and the amount of decay before burial affects appearances of the specimen in thin section, blurring specific characters. Various growth-forms of a species may be recognized, but such forms do not seem to be of value for stratigraphic work.

THE best-known occurrence of *Girvanella* is in the Carboniferous Limestone of northern England, where Garwood (1912, 1924) found algal nodules to be useful as horizon markers at a level which he took as the base of the D_2 zone. Though this Girvanella Band has been recorded over hundreds of square miles of north-western England, and bands have been found at a similar horizon in Derbyshire and in Northumberland, no specific names have been given by British authors to the forms occurring there, nor have their ranges in time or space been ascertained. This is due in part to the inherent difficulties of identification of such a featureless fossil, but even more to uncertainty as to the exact characters of the already named species. Garwood himself (1931) when describing a new species, *G. staminea*, from C_1 beds at Bewcastle, could only refer to the types found in the typical Girvanella Band as 'showing two sizes of threads', with a reference to his two figures of '*Girvanella sp.*' (1924). The position will be made easier in the future by the discovery of the type specimens of the species described by Wethered (1890) from the Avon Gorge, which were contained in a large collection of thin sections given by the late Judge Wethered to the University of Bristol. These were kindly put at my disposal by Professor W. F. Whittard. Though the original drawings did not show all the features which might be useful for specific identification, they were very accurate representations, and it has proved possible to pick out all the figured specimens of both species.

Perusal of Wethered's paper will show that he was chiefly concerned with the origin of oolitic granules. Already (1889) he had demonstrated that the pisoliths of the Pea Grit in the Inferior Oolite of Gloucestershire were of organic origin, and in 1890 he was concerned with both Jurassic and Carboniferous rocks, *Girvanella* being considered to be the main agent in the formation of ooliths. It seemed possible, he thought, to trace a series from clear examples of *Girvanella*, through those ooliths in which the *Girvanella* structure was in process of being destroyed, to ooliths with only a trace of organic structure, the end-member being perhaps those with a regular radial crystalline arrangement. This preoccupation with the origin of ooliths has introduced peculiar difficulties in the choice of a type specimen for *G. ducii*.

In these delicate species of *Girvanella* accurate comparisons can only be made on enlarged photographs, repeatedly checked under the microscope. A uniform enlargement of 450 diameters has been used. When whole-plate photographs are held side by

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side, comparison is rendered easy. It becomes clear that there are a number of different growth habits among species whose internal and external diameters appear to be the same. When the eye can hardly observe these in thin section and the memory cannot retain the details while one slide is changed for another on the microscope stage, the practical value of these subtle differences almost vanishes. If more species were erected, based on those features which have become familiar to the writer through a long period of observation they would be unidentifiable by other workers, except when a full range of species was available for study. Consequently the present observations are limited to named species or figured specimens.

SYSTEMATIC DESCRIPTIONS

Girvanella wetheredii Chapman 1908 (= *G. incrustans* Wethered *non* Bornemann)

Plate 38, fig. 1; Plate 39, fig. 1

Diagnosis. Flexuous, winding, interlaced tubes, not observed to taper, wrapping around a central foreign body, perhaps also free. External diameter, measured on circular cross-sections, 0·013 mm. to 0·015 mm., internal diameter ranging between 0·006 and 0·009 mm. Closeness of packing variable; wall dark, fine-grained, thickness generally about 0·003 mm.; septa not observed. Branching occurring at a rather wide angle; sometimes the branches come off close together from the same side of the parent thread. In one case the branch bends round rapidly to grow subparallel with the others, in a manner reminiscent of *Garwoodia.*

Observations. Bornemann (1886) described the genus *Siphonema*, type species (here chosen) *S. incrustans*, from a pebble of Silurian limestone found in Pleistocene glacial drift and presumed to be from the Baltic area. This genus, as pointed out by Hinde (1887), was a synonym of *Girvanella*, so that *G. incrustans* of Wethered (1890) was invalid. Chapman (1908) noticed this and proposed the name *G. wetheredii* to replace it.

The original figures of this species were of the same specimen at different magnifications, one (1a) being reversed in reproduction. The slide in which the type specimen is contained has the locality 'B below New Rd.' engraved on the glass, and the labels read 'Carboniferous M. L. Clifton' and 'No. 1. B. Below New Rd. Dolomite'. The rock is a fragmental foraminiferal limestone, the matrix being of granular interlocking crystals of calcite whose grain size ranges between 0·01 and 0·05 mm. Scattered in the granular matrix are organic fragments ranging in size from 0·02 mm. to foraminifera 0·6 mm. across, and even larger fragments of brachiopods and gastropods. The algal growths occur around circular or slightly elliptical bodies about a millimetre in diameter, which are probably sections of Productid spines. These are hollow, with transparent fibrous walls which show a black cross under crossed nicols, and their centres are filled with matrix. A considerable amount of finely disseminated pyrite occurs in the algal growth, particularly near the nucleus, and this has invaded the material of the spine itself. Owing to the thickness of the section, the tubuli of *G. wetheredii* are difficult to make out, but they seem to have been continuous all round the nucleus, though dense structureless calcite intervenes between the nucleus and the visible threads. Similarly, tubes are difficult to discern in the outer layers. The whole gives an impression of a nodule formed by growth of various creatures around a common centre, some of which left no trace of their presence beyond a dense precipitate. Around the nodule a narrow discontinuous zone of clear calcite occurs, in continuity with a vein penetrating it, as if the nodule had shrunk slightly away from the surrounding matrix and the gap had been filled with material from solution.

One small portion of this algal nodule was figured at a higher magnification by Wethered, and is the portion in which the threads can be most clearly seen. It is figured in Plate 38, fig. 1, and is here chosen as the type specimen. The tubuli are more closely packed than in the other examples described later, and are confusedly interwoven. Probably they are cut parallel to the surface on which they grew, and they are seen to branch as they spread over it. Direct measurement on circular cross-sections of threads gives internal diameters varying from 0·006 mm. to 0·009 mm., with the average nearer the latter figure. The outer limits of the walls are extraordinarily difficult to determine owing to the slice not having been ground thin enough, but the two largest cross-sections approach 0·015 mm. in diameter while some are smaller, down to perhaps 0·012 mm. The photograph, which has not been touched up, but whose contrast has been increased by every possible means, gives an impression of clear definition not borne out when the specimen is observed by eye under the microscope.

Two other slides, both engraved with the words 'New Rd. Oolite', are almost certainly from the same bed, since they match the type slide in grain size, foraminiferal content, and especially in the algal growths being around identical nuclei. Since the slides are thinner the tubuli are more clearly seen, and an enlarged figure (Pl. 39, fig. 1) is given here. All the measurements discussed below have been taken from these two slides. In one case *G. wetheredii* occurs in contact with the nucleus, and in another it reaches the outer surface of the nodule. In all cases it seems to have had a general encrusting habit and to have taken a real part in the growth of the nodule. Layers of dense calcite devoid of tubuli are constantly present, as in the type specimen. The nucleus of one nodule is a piece of fragmental limestone with a clear crystalline matrix different from that of the rest of the section.

When enlarged photographs were studied it was found that cross-sections showing truly circular interiors were more rare than had been anticipated, most sections showing irregularities due probably to partial collapse of the external mould after death. Circular cross-sections showing the thickness of the wall were even rarer, usually one side or another being in contact with and blending into the dense matrix. It was interesting to note that measurements of internal tube diameter on longitudinal sections were on the average slightly over 0·001 mm. less than those measured on circular cross-sections, while measurements of the external diameter measured in the same way were in error by nearly 0·002 mm. Presumably Wethered made his measurements on longitudinal

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EXPLANATION OF PLATE 38

Fig. 1. *Girvanella wetheredii* Chapman. Type specimen (here chosen). Branching can be seen in three places. Upper D_1, Avon section, Bristol. Geological Survey Collection, GSM. PF1923.

Fig. 2. *G. staminea* Garwood. Type specimen. Tubuli indistinct for reasons discussed in text. C_1, White Beck, Bewcastle, Cumberland. British Museum (N.H.) Collection, V43735.

Fig. 3. *G. ottonosia* Pia. Topotype. Branching visible near the centre of the photograph. Km, Avon section. Geological Survey Collection, GSM. PF2047.

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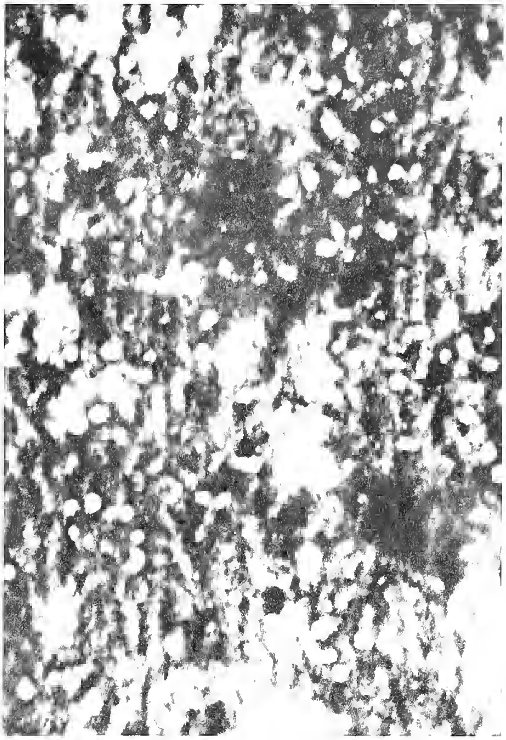

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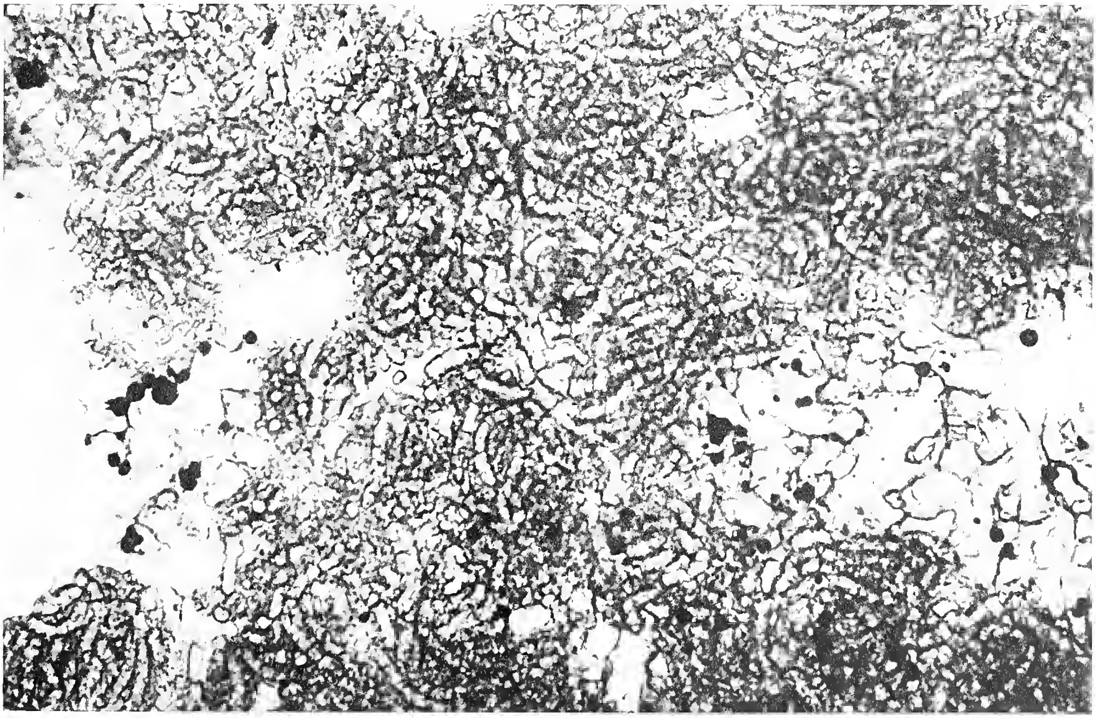

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sections, since he stated that the diameter was 0·01 mm. The thickness of the wall varied from rather over 0·0015 mm. to 0·003 mm., the latter being nearer the average figure.

The two slides from the Wethered collection show slightly different growth habits or types of preservation. In one the tubes remain for relatively long distances in the plane of the section. In the other, cross-sections of the walls are more obvious, and the impression of free and rapid growth parallel to the surface of the nodule is less strong. The tubes also appear to be more contorted. There is no doubt that both specimens are from the same level, perhaps from the same hand specimen, for the reasons given above. A similar range of variation in appearance can be seen in specimens from the Girvanella Band at Hull Pot, Yorkshire, in the Garwood collection in the British Museum, Natural History (Slides V43730 and 157B). The difference in appearance probably depends in part on a small variation in thickness of the thin section, but also is likely to depend on an original slight difference in the position of the threads with respect to the angle at which light fell on the algal nodule and also, perhaps, to the influence of competing organisms. In other cases, the threads are well separated and even more contorted. This is well seen in the specimen figured by Garwood in 1924 from Hull Pot in which the tubes are rendered conspicuous by a dark coating, and their contortion and the degree of separation are noteworthy. It seems likely that this specimen is conspecific with Wethered's specimens, since similar variations in degree of contortion have been described in *Girvanella problematica* itself (Wood 1957).

As stated in the introduction, *G. wetheredii* has not been positively identified since Wethered's time, though in 1932 Pia, who had made collections from the Carboniferous Limestone of England, stated that in his opinion *G. staminea* Garwood was identical with '*G. incrustans*'.

Type specimen. Figured on Plate 38, fig. 1, deposited in the Geological Survey Museum, South Kensington, GSM. PF1923.

Locality. A bed of dark nodular limestone, with argillaceous material, 9 inches thick, immediately below an oolitic bed 10 feet thick, a short distance below the junction of the road from Clifton with that along the banks of the River Avon. Upper D1 (Reynolds 1921, pp. 233–4). National Grid Reference 31/563734.

Girvanella ottonosia Pia 1937

Plate 38, fig. 3

Diagnosis. Highly contorted flexuous tubes, circular in section, forming a pellicle around a foreign body with a digitate *Ottonosia*-like outer surface. External diameter of tubes usually about 0·007 mm., internal diameter 0·004–0·005 mm., wall thickness 0·001–0·002 mm. Occasionally one tube may be as much as 0·007 mm. in internal diameter, but in general the threads are remarkably uniform in size. Branching apparently dichotomous, but contorted, usually at an angle of less than 40°.

Observations. The specimens are preserved in a fragmental limestone, consisting of crinoid ossicles and plates, broken gasteropods, polyzoa and lamellibranch shells, enclosed in a granular calcite matrix. Brachiopods are apparently absent. The matrix is of two types, one yellowish in transmitted light, probably nearly in its original state except as modified by grain growth, average grain size 0·02–0·03 mm., and a clearer more translucent portion irregularly dispersed around and among the organic fragments.

This is slightly coarser and probably represents a cavity infilling. The range of size of the organic fragments is from 0·2 mm. upwards to 7 mm., the size of the largest algal nodule. The rock was probably rapidly deposited as a mass of transported fragments in a cloud of fine silty calcite which partially filled the interstices between the fragments.

The algae are preserved as thin coatings on polyzoa and around recrystallized lamellibranch (?) shells. The coating ranges in general from 0·3 to 0·5 mm. in thickness (maximum 1·4 mm.), and displays the digitate outer margin described by Pia. Sections parallel to the surface of the alga show that the projections are irregularly peg-like, rather than parallel-sided wrinkles. The spaces between the outgrowths were certainly present before burial; they are filled generally by the yellowish original matrix described above and occasionally by the later clear drusy grains. The algal growth must have been quite stiff and crisp to withstand transport and to retain this surface appearance. There is not sufficient evidence that the algal threads originally grew parallel to the present outer margins of the projections, though occasional portions of a section suggest this. On the other hand the interstices do not have the form of later burrows which had destroyed part of a once continuous coating. The absence of growth parallel to the margins may be due to the former presence of a living, uncalcified layer, which decayed before fossilization; certainly the whole series of outgrowths gives the impression of being an original feature.

Locality. Lower Limestone Shales, Km, Avon Gorge (Clifton Side), Bristol.

Material. Four slides from the Wethered Collection, labelled 'Lower Limestone Shales, Clifton, Bristol', or some variant of this. Figured specimen in the Geological Survey Museum, GSM. PF2047.

Girvanella staminea Garwood 1931

Plate 38, fig. 2; Plate 39, fig. 2

Diagnosis. Flexuous winding interlaced tubes, not observed to taper, wrapping around a central foreign body. External diameter, measured on circular cross-sections, 0·011–0·013 mm. internal diameter 0·006–0·008 mm. Closeness of packing variable, wall dark, fine-grained, thickness about 0·003 mm., septa not observed. Branching occurring at a wide angle.

Observations. The type specimen forms part of a single composite algal nodule, without matrix, showing a well-preserved specimen of *Garwoodia gregaria* (Nich.) enveloped by a thin layer of *Girvanella* threads. These extend in varying states of preservation nearly around the central spherical alga, being separated at intervals by thin layers and irregular blebs of clear calcite, often showing traces of organic structure. This *Girvanella* layer is in turn surrounded by another organically deposited portion which forms the outer part of the nodule. In this there are a variety of encrusting organisms, worm tubes,

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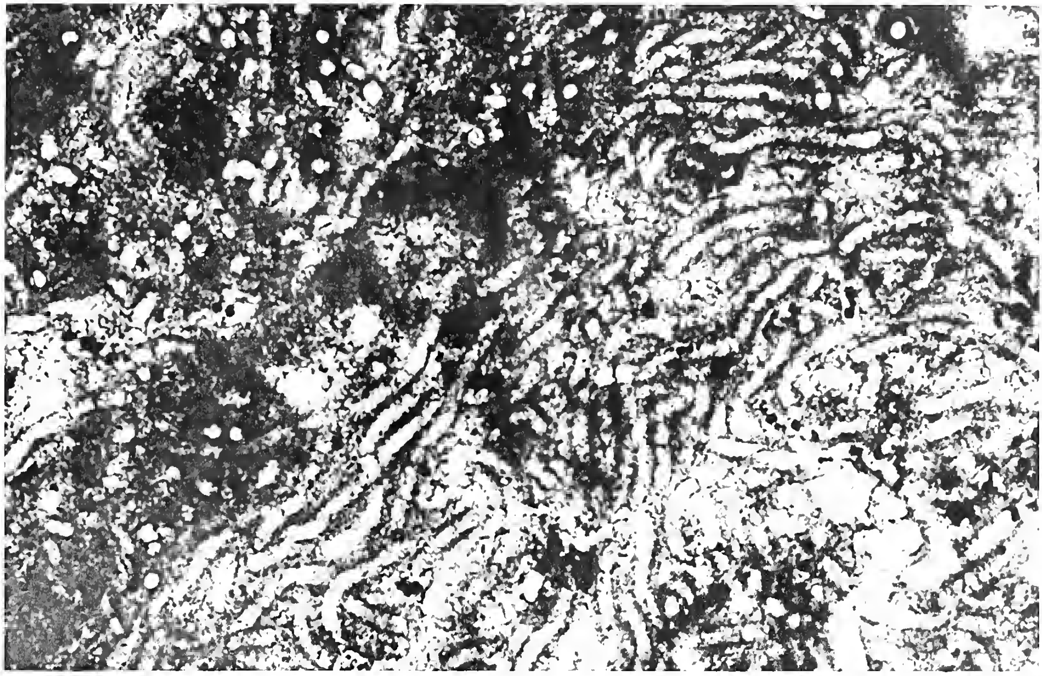
EXPLANATION OF PLATE 39

Fig. 1. *Girvanella wetheredii* Chapman. Topotype. To show growth habit. Compare tube-diameter and growth habit with *G. staminea* (below). Upper D_1, Avon section, Bristol. Geological Survey Collection, GSM. PF1925.

Fig. 2. *G. staminea* Garwood. To show tube size, branching, and general growth-habit. Compare with *G. wetheredii* (above). ? C_2, Cambeck, Spadeadam, Cumberland. British Museum (N.H.) Collection, V43734.



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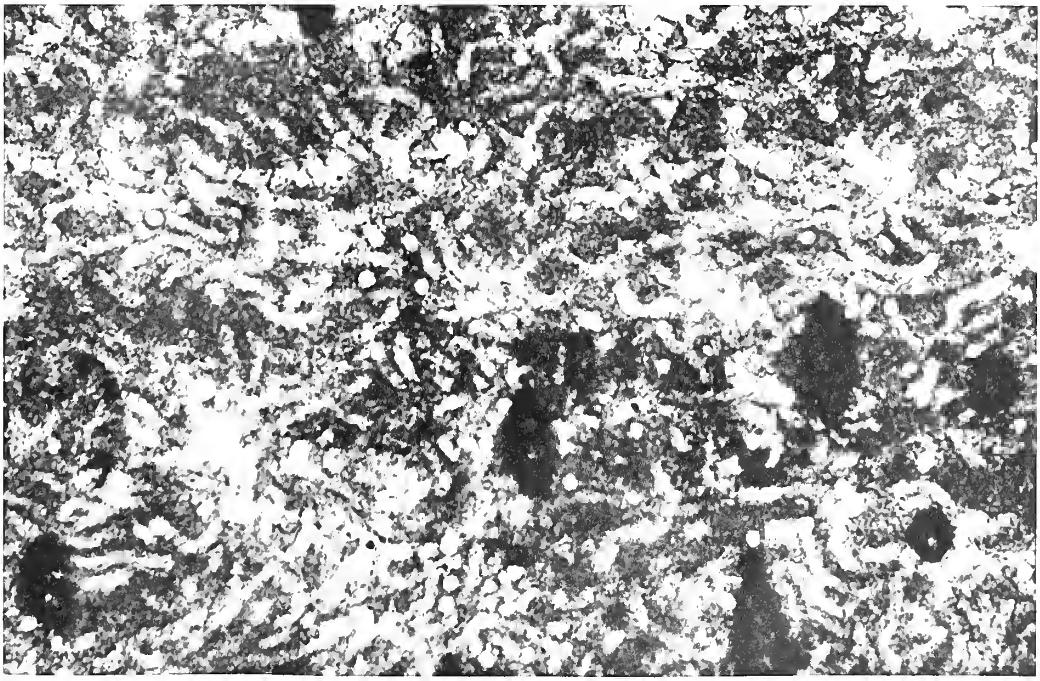

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'bean-shaped organisms', and a few small, nearly stifled layers of *Garwoodia*. The nodule was thus formed in a period to be measured in months rather than weeks. Growth of the *Girvanella* layer, itself only an insignificant portion of the whole, was interrupted by colonization of other organisms or by boring creatures or both, which gave rise to the clear patches described above.

Though the slide is labelled 'too thick' in Garwood's handwriting, the polarization colours of the clear calcite infilling of the *Girvanella* tubes are bright, and the indefinite appearance and lack of character of the algal tubes must be ascribed to partial decay before lithifaction. The nodule must have lain on the sea floor for some time, and colonization by other creatures would affect the preservation of this specimen if only by the penetration of their basal cells. Much, if not all, of the indefinably different impression this specimen gives is to be explained in this manner.

The original diagnosis is: 'This species is distinguished from other Carboniferous species previously described by the minute size of its tubes, which measure 0·006 mm. in diameter.' It is certain that Garwood made his measurements on the bright circles which represent infilled cross-sections of the tubes, and thus give the internal diameter of the threads. All previous measurements of species of *Girvanella* had been made on the threads as seen in longitudinal sections, including the thickness of the wall. Because of the close packing of the threads in this specimen, and because of subsequent changes, longitudinal sections are always indefinite. A few cross-sections of the whole thread can be distinguished; and the measurements cited above fall into the range of variation of *G. wetheredii*, as do the measurements of internal diameter.

Nevertheless, other better-preserved material from north Cumberland contained in the Garwood collection seems to show that a species with slightly slimmer threads than *G. wetheredii* is characteristic of this horizon in Cumberland. The specimen figured on Plate 39, fig. 2 is from Cambeck, Spadeadam, north Cumberland, and is said by Garwood to come from a horizon in C_2. Reference to Garwood's map (1931) will show that this locality is only just above the Main Algal Series, from which the type specimen of *G. staminea* was obtained. In the Cambeck specimen well-preserved *Girvanella* threads closely envelop a *Garwoodia* nodule, and are enclosed in a fine-grained bioclastic limestone containing occasional tiny rounded quartz grains. They closely resemble the type specimen in appearance, growth, habit, and even in the ecological niche they have chosen to inhabit. The preservation is good, the threads are clear, and branching can be seen.

Comparison with the figures of *G. wetheredii* shows that the average diameter of the threads is slightly less, though the growth-habit is similar. Such a difference may be due to a differing environment, but it seems more probable that there was a real, though by now almost inappreciable, distinction between the C_1 and C_2 species and that characteristic of the upper part of the D_1 and base of the D_2 zones.

Type specimen. Figured on Plate 38, fig. 2, deposited in the British Museum (N.H.), V43735.

Locality and horizon. 'Main Reef', Main Algal Series; White Beck, Bewcastle, Cumberland; C_1.

Girvanella ducii Wethered 1890

Plate 40, figs. 1–2

Diagnosis. Gently flexuous tubes, generally loosely interwoven or not in contact, sometimes closely wrapped around a foreign body. External diameter, measured on circular cross-sections, ranging from 0·026 to 0·033 mm., average 0·029 mm., internal diameter ranging from 0·015 to 0·020 mm., average 0·018 mm. Wall dark, fine-grained, thickness generally about 0·006 mm., branching irregularly dichotomous, at a varying angle. No cell-walls observed.

Observations. The original figures of *G. ducii* were from three different thin sections and two localities. I here choose the original of Wethered's figure 2*a* as the type; this specimen is figured on Plate 40, fig. 1. It occurs in a fragmental limestone, in which the majority of organic fragments have a pellicle of algal or inorganic radial fibrous coating up to 0·1 mm. thick. The fragments are often rounded and range in size from 0·05 mm. to nearly 1 mm. in diameter, the latter being rare. The average grain size is about 0·4 mm. Some foraminifera, in particular, have no precipitated layer around them. The fragments are closely packed, but rarely in contact, and the matrix is transparent and granular, with an average grain size of about 0·01 mm. The minute nodule containing *G. ducii* is the largest fragment in the slide, measuring 2·8 mm. in longest diameter. The margins are dark and composed of fine-grained 'algal dust' in which threads of *G. ducii* occur, while the centre is occupied by clear calcite similar to the matrix and containing similar murky ooliths and organic fragments. In the clear calcite near the centre, tubuli of *G. ducii* are common, and are not so closely packed as in the less transparent margins. There is no suggestion of a concentric arrangement of the threads, but this may be due to the nodule being irregular in shape and excentrically cut. This suggestion is supported by the presence of ooliths in the apparent centre of the nodule. Branching is not seen in this specimen.

Wethered stated that the diameter of the tubuli was 0·02 mm. Measurement on his figure 2*a* gives a diameter of 0·03 mm. for the external diameter of the larger cross-sections, a figure which is substantiated by the present measurements (see above). It is, however, particularly noticeable that the threads seem to be of greater external diameter when they are not touching, and are surrounded by clear calcite. This fact has not affected the measurements given in the diagnosis above, since it happens that only one cross-section occurs in this region, but it is very noticeable when measurements are made on longitudinal sections of threads. These measurements in the dense closely packed regions average 0·027 mm. for external diameters, while in the clear area with loosely packed threads, the average is slightly above 0·030 mm., with a maximum of 0·035 mm. In each case the threads were measured at the point of greatest diameter and greatest interior brightness, this being presumed to indicate nearness to a median section. The difference is probably due in the main to the outermost boundaries of the walls being easily visible in the areas of clear calcite, while they are taken to be part of the matrix in the more crowded regions.

The second specimen figured by Wethered (fig. 2*b*) shows rather indistinct tubuli

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EXPLANATION OF PLATE 40

Figs. 1–2. *Girvanella ducii.* Wethered. 1, Type specimen (here chosen). Tubes winding loosely in a fine-grained limestone with cavity infillings. Upper D_1, Avon section, Bristol. Geological Survey Collection, GSM. PF1924. 2, Specimen from Girvanella Band, Yorkshire, to show growth-habit and tube diameter identical with the Bristol specimen. Base of D_2, Hull Pot, Pen-y-Ghent, Yorkshire. British Museum (N.H.) Collection, V44935.

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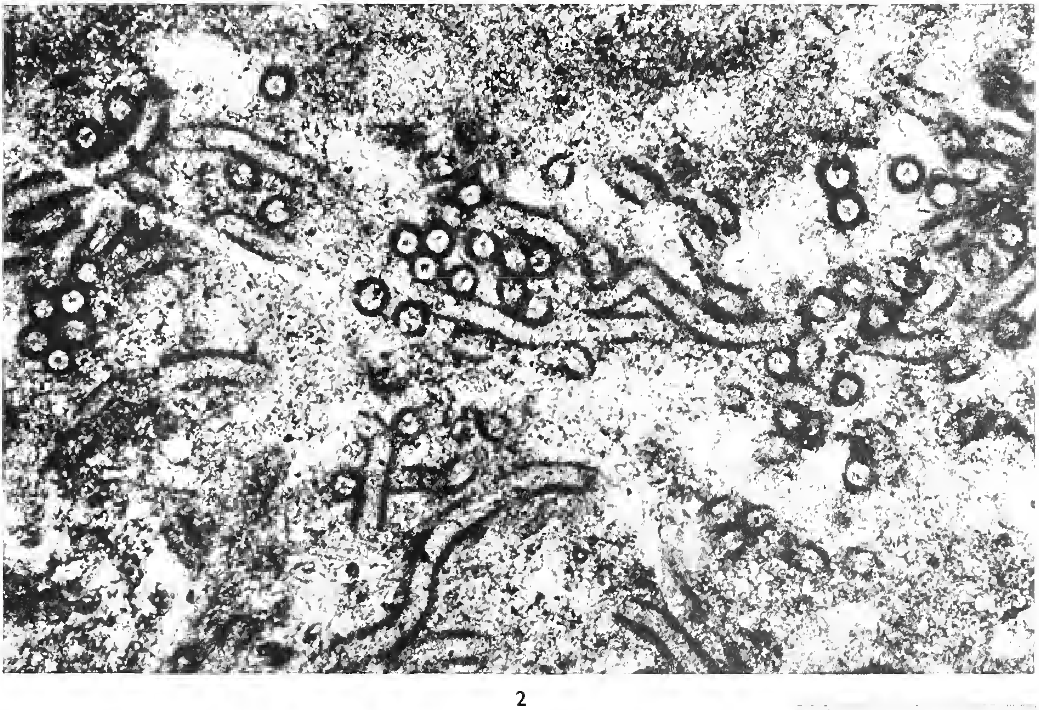

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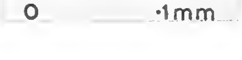

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partly enveloping a compound nucleus. The internal diameter of the tubuli is between 0·017 mm. and 0·020 mm., and they are surrounded by a dense structureless 'algal dust'. The largest diameter of the whole granule is 0·7 mm. The chief interest of this specimen is that it shows that *G. ducii* could grow concentrically around a nucleus and envelop it, as do other species of *Girvanella*. The tubes are markedly less flexuous than in *G. wetheredii*, and they lie at one side of the nodule only. This may well be due to attrition before fossilization.

The original of Wethered's figure 2*c* came from Tortworth Park, Gloucestershire, and is an algal aggregate enclosed in radially disposed calcite crystals. It occurs in an oolitic limestone in which every organic fragment is covered with a thin layer of radiating crystals; the matrix is entirely recrystallized. It is clear that the fragment of *Girvanella* is detrital and had been rounded before being incorporated into the sediment. Unfortunately no circular cross-section of the threads is visible. However, there is no doubt that the tubuli are markedly thinner than in the type specimen, measuring only 0·016 mm. in external diameter on longitudinal sections, and they must belong to another species. The internal diameter measured in the same way varies from 0·008 to 0·010 mm.

The choice of a type specimen is not entirely straightforward. On p. 272 of Wethered's paper a measured section of the New Road Oolite is given, six beds being listed. Concerning the topmost bed, he stated 'a form of *Girvanella* was here discovered to which I propose to give the name of *Girvanella Ducii*, for reasons to be presently explained. It consists of an aggregation of tubules similar to those represented in Pl. XI, figs. 2*a* and *b*; but in this instance the outlines are to a large extent obliterated by mineral changes. . . .' On page 273 he wrote, when describing bed 3, 'In this bed we again meet with the organism I propose to call *Girvanella Ducii*, occurring in loose aggregations as represented in fig. 2*a*.' At first sight it seems difficult to come to any other conclusion than that the type specimen must be that first mentioned by Wethered, unfigured and undescribed. However, when one considers his interest in the origin of ooliths, and the fact that the measured section was described in logical order from above downwards, it becomes apparent that *Girvanella ducii* was here referred to as an agent in oolith formation, without any intention of making a type specimen from among the tubules of Bed 1.

The specimen figured by Garwood (1924, pl. xix, fig. 2) from the Girvanella Band at Hull Pot, Penyghent, is undoubtedly *G. ducii*. A similar specimen from the same locality (B.M.N.H. slide V44935) is identical with the type specimen in dimensions, growth habit, and branching. It is made up of a lax aggregation of tubes forming a small part of a typical 'algal' nodule, 15 mm. long, which shows a series of irregular concentric layers around a fragment of a brachiopod shell. The whole is contained within a fragmental foraminiferal and crinoidal limestone.

The fact that Wethered gave an incorrect diameter for the tubuli of *G. ducii* might well have led to confusion, but fortunately no other species has been named from Carboniferous rocks with a tube diameter of 29 μ. Indeed most authors, including Maslov (1956), quote diameters of around 20 μ for the specimens they ascribe to *G. ducii*. The growth-habit of the specimens from the Urals, and those figured by Dangeard (1948) from Belgium is closely similar to that of typical *G. ducii*, and the difference in external diameters requires explanation. Part of the difference may be explained by other workers measuring tube diameter on longitudinal sections, rather than on cross-sections and a part may be due to grain growth in the matrix of the limestone, whereby the outer part of the calcareous envelope has been taken over and incorporated in the crystals around.

G. liebusi Paul is stated to have a tube diameter of 20 μ. It is interesting to note, in view of the remarks given above concerning the preservation of *G. ducii*, that Paul (1938) stated that his species with elongated weakly curved threads did not build nodules, and thus is separated from other forms of *Girvanella*, though the threads were individually identical with those of *Girvanella* so that a generic distinction was not possible. Later in 1938 he added that this alga was found in a coarsely crystalline limestone with foraminifera, a habitat that algae usually avoid. In this respect too it is similar to *G. ducii* and the limestone figured does not look any coarser than the beds in which *G. ducii* usually occurs. In view of these facts, and the incorrect magnification given by Paul for the type figure (the true magnification is around 25 diameters) it is possible that *G. liebusi* is synonomous with *G. ducii*.

Both Dangeard (1948) and Maslov (1935) mention the occurrence of cell walls transverse to the tubes, in specimens they consider to belong to this species and Dangeard gives a fine photograph of these. Similar features are occasionally seen in specimens from Britain, but observation is very difficult at the magnifications that have to be employed, and the present author has not been able to feel certain that they are not simply the boundaries of the relatively more clear crystals filling the interior of the tubes.

Though this form has frequently been referred to by other authors, for example Pia (1932, 1937) and Johnson (1945), the original incorrect statement concerning the tube diameter necessitates a re-examination of the evidence in each case.

Type specimen. Figured on Plate 40, fig. 1, deposited in the Geological Survey Museum, GSM. PF1924.

Locality. A bed of blue limestone with some oolitic spherules, 2·5 feet thick, lying immediately below the thin dark limestone with *G. wetheredii*. Upper D_1.

Girvanella nicholsoni (Wethered) 1886

This appears to be a rare species, and there is nothing new to add to the description given by Wood (1941).

NOTE ON THE 'GENUS' *GIRVANELLA*

Johnson (1946) considered the present author's use of the generic name *Girvanella* for so coarse a species as *G. nicholsoni* 'unfortunate'. There can be no doubt that the various species included above in one genus are not congeneric. *G. ottonosia* Pia, for instance, with strongly contorted minute tubuli and peculiar growth habit is very different from *G. ducii* Wethered. The latter does, however, have many characters in common with *G. problematica* Nich. and Eth., the type species. At some time in the future it will be necessary to split off the forms with highly contorted minute threads as a separate genus, and at that time the form with very wide tubuli now called *G. nicholsoni* could conveniently and logically resume the name *Mitcheldeania*, at present suppressed as a synonym.

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THE OSTRACOD GENUS *NEOCYTHERE* IN THE SPEETON CLAY

by P. KAYE

ABSTRACT. Six species of the genus *Neocythere* Mertens are described from the Barremian and Albian beds in east Yorkshire. Three species are new, one of which is the earliest known occurrence of the genus. The genus *Centrocythere* is regarded as a subgenus of *Neocythere* s.l.

THE material which forms the basis for this paper is part of a large fauna from the upper part of the Speeton Clay studied as the topic for a thesis at the University of Hull.

The bulk of the material is of Albian age and in some cases has been obtained from inland exposures. The upper Red Chalk at Speeton is extremely hard, but the equivalent strata inland is found to be softer and easier to break down. The species have, however, all been recorded from Speeton, but are generally poorly preserved. Away from the coast exposures are very rare and samples have only been obtained from South Cave near Market Weighton (Grid Ref. 925326) and West Heslerton near Malton (Grid Ref. 913769).

The Albian strata at Speeton falls into two divisions: a thin series of grey-green marly clays comparable to the Gault Clay of the south of England and a thick sequence of Red Chalk. There is a gradual transition in colour and lime content between the two divisions, and an exact boundary is hard to draw. At the base of the Gault Clay there is a 6-inch seam of glauconitic clay and phosphatic nodules known as 'The Greensand Streak'. This seam is underlain by dark clays of Aptian age, and it has yielded fragments of ammonites indicative of the *regularis* Subzone. Apart from belemnites, the Gault and Red Chalk are almost barren of macrofossils, and consequently detailed zoning has been impossible. The author, in his observations over the last five years, has found the lithological section, published by C. W. Wright in Swinnerton's *Monograph of Lower Cretaceous Belemnites*, to be extremely sound.

All of the specimens are catalogued and deposited in the collection of the Department of Geology at Hull (HU).

SYSTEMATIC DESCRIPTIONS

Family PROGONOCYTHERIDAE Sylvester-Bradley 1948
Genus NEOCYTHERE Mertens 1956

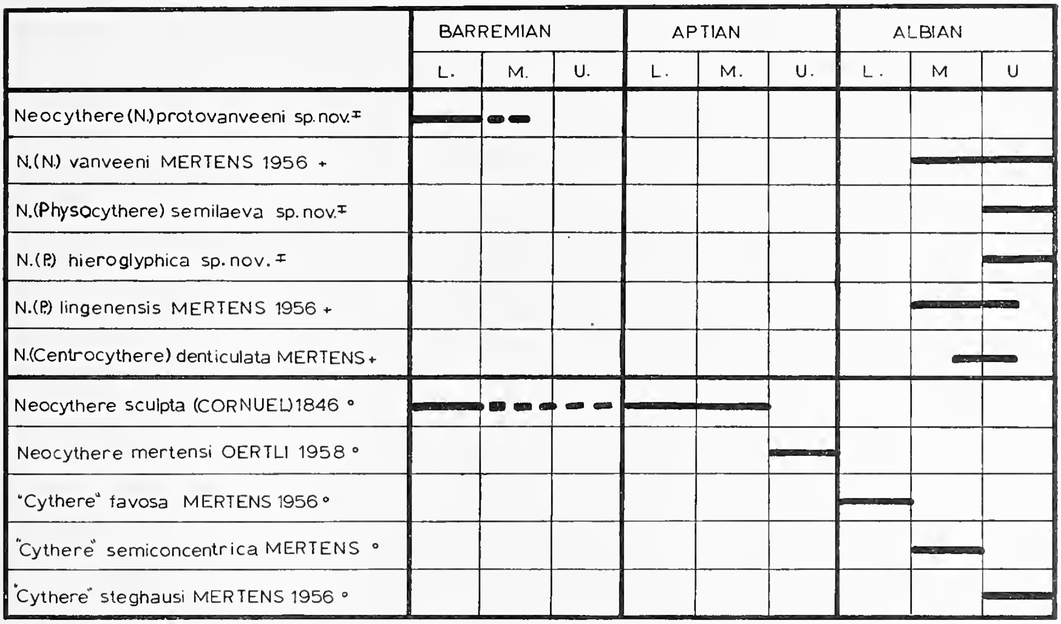
Type species. Neocythere vanveeni Mertens 1956.

This genus was erected by Mertens (1956) for forms similar to *Cythere concentrica* Reuss, but having an amphidont hinge and an accommodation groove in the left valve. There is a great deal of uncertainty about the interpretation of the forms related to this group, and, until quite recently, all Cretaceous ostracoda having concentric ornament and slight ventral tuminity were referred to *Cythere concentrica* Reuss. Mertens

[Palaeontology, Vol. 6, Part 2, 1963, pp. 274–81, pl. 41.]

has done extensive work on these forms and has redescribed Reuss's types. Unfortunately, the material was not well enough preserved, particularly the hinge structure, to allow correct generic assignment, and the species, together with related forms named for the first time, were left tentatively in the genus '*Cythere*'. Mertens did, however, distinguish two new genera, *Neocythere* and *Centrocythere*, on the basis of the hinge structure.

On examination of the hinge of species referred to the genus '*Cythere*', it is found that they differ from *Neocythere* in being symmetrical merodont and in having no accommodation groove. Though these differences do occur, it is not, in the author's opinion, sufficient to warrant generic separation. It has been shown on many occasions that the hinge in ostracods is unreliable as a basis for higher taxonomic division, and therefore to split this group of very similar ostracoda on that basis is considered unwise. It is proposed, therefore, to include all these forms under the genus *Neocythere* s.l. and to create new subgenera for the different hinge varieties. *Neocythere* s.s. is used for forms having an amphidont hinge, whilst the new subgenus *Physocythere* is erected for the forms grouped by Mertens under '*Cythere*' and having a merodont hinge. On the same basis, the genus *Centrocythere*, which differs from *Neocythere* s.s. only in the nature of the anterior tooth in the right valve, is therefore included as a subgenus of *Neocythere* s.l.



Species of Progonocytheridae from the Speeton Clay and equivalent beds in N.W. Europe.
+ = Speeton & N.W. Europe; ° = N.W. Europe only; ‡ = Speeton only.

TEXT-FIG. 1

The ranges of the species of *Neocythere* found at Speeton together with related forms are given in text-fig. 1.

Subgenus NEOCYTHERE Mertens 1956

Type species. Neocythere vanveeni Mertens 1956.

Diagnosis. A subgenus of *Neocythere* s.l. including forms similar to the genotype having an inflated, ventrally tumid carapace. The hinge in the right valve consists of two terminal crenulate teeth, between which is a locellate furrow deepened at its anterior end to form a smooth circular socket. The left valve is complementary, and possesses a distinct accommodation groove above the median element.

Neocythere (*Neocythere*) *vanveeni* Mertens 1956

Plate 41, figs. 23, 25

Cythere concentrica Dupper 1952, p. 106, pl. 4, fig. 14.
Neocythere vanveeni Mertens 1956, p. 205, pl. 12, figs. 72–78; pl. 14, figs. 100–2.

Material. Mounted specimens HU 17.C.10.1–10, from 1 foot above the Greensand streak, Middle Albian at Speeton.

Measurements	*Length*	*Height*	*Total width*
Male carapace	0·65 mm.	0·35 mm.	0·42 mm.
Female carapace	0·65 mm.	0·38 mm.	0·42 mm.

Description. Carapace rounded, inflated, ventrally tumid. Greatest height at one-third length, greatest width at mid-length. Dorsal margin strongly arched in the left valve, but straight with marked cardinal angles in the right valve. Ventral margin straight or slightly convex, being obscured in lateral view by the prominent ventral tumidity. Anterior margin rounded, slightly asymmetrical ventrally; posterior margin forming a blunt point at mid-height.

The surface is ornamented with concentric ribs, which parallel the anterior, ventral, and posterior margins. These ribs are rounded and prominent ventrally, but elsewhere are rather indistinct. There are three major concentric ribs, but many other subsidiary ribs are enclosed within them. The ventral surface is crossed by several strong longitudinal ribs. A low, rounded muscle node occurs just in front of the centre of the lateral surface.

A narrow duplicature occurs with a steep drop into the inflated interior of the valve. Inner margin and line of concrescence coincide. Radial pore canals short, straight, and few in number. Normal pore canals numerous, concentrated along the crests of the concentric ribs.

The hinge of the right valve consists of two bar-like terminal teeth divided into four or five distinct lobes. These teeth are separated by a long, straight furrow, which is coarsely crenulate and deepened at its anterior end, to form a smooth oval socket. In the left valve there are two long, shallow, crenulate sockets, partially open to the interior of the valve, and separated by a long, high, prominent median bar. This bar is denticulate and often enlarged at its anterior end into a boss-like tooth. Above the median bar lies a broad, shallow accommodation groove.

Sexual dimorphism is well marked, with the females being higher than the males.

Juveniles are common, and differ from the adult principally in the fact that the hinge is symmetrical, merodont in all the instars, and also in the fact that the ornament is much less strongly developed. Certain of the earliest moults appear smooth. A constant feature of the hinge in all the instars is the presence of an accommodation groove in the left valve. The muscle node is also more prominent in many of the moult stages.

Remarks. Neocythere vanveeni is easily recognized by the smoothly arched dorsal margin in the left valve, and by its hinge. The amphidont nature of the hinge is not always apparent in the left valve, but can always be seen in the right. The presence of the accommodation groove is diagnostic.

The specimens found here are seen to be rather smaller than those found by Mertens in Germany. It is therefore possible that no adult specimens have been found. The largest forms are rare, and the bulk of the material found belongs to the early instars. This fact is borne out by the poor sexual dimorphism shown, and the less strongly developed hinge than the German forms.

Neocythere (*Neocythere*) *protovanveeni* sp. nov.

Plate 41, figs. 1–3, 5, 6

Holotype. A female right valve from 14 feet above the base of 'Lower B' (Lower Barremian) at Speeton, no. HU 17.C.11.1.

Other material. Three paratypes mounted as HU 17.C.12.1–3.

Diagnosis. A species of *Neocythere* s.s. basically similar to *N. vanveeni* but having the dorsal margin of the left valve less arched, and the posterior margin more bluntly pointed.

Measurements	*Length*	*Height*	*Total width*
Holotype female right valve, HU 17.C.11.1.	0·65 mm.	0·37 mm.	0·20 mm.
Paratype male left valve, HU 17.C.12.1.	0·67 mm.	0·41 mm.	0·20 mm.

Description. Carapace rounded, inflated, ventrally tumid. Greatest height at one-third length, greatest width at mid-length. Dorsal margin of the left valve slightly arched, but with a flattened central portion. Dorsal margin of the right valve straight, with marked cardinal angles. Ventral margin convex, but obscured in its central portion by the ventral tumidity. Anterior margin rounded ventrally asymmetrical; posterior margin forming a blunt point at mid-height. Muscle node not well defined. Surface ornamented with concentric ribs, which are most prominent ventrally and arranged as in *N. vanveeni.* The dorsal third of the valve is, however, noticeably smooth. Internal features are identical to *N. vanveeni.* Radial pore canals are short, straight, and number ten anteriorly and four posteriorly. Normal pore canals are numerous and arranged along the crests of the concentric ribs. Hinge identical to *N. vanveeni*, having the median element noticeably subdivided, but with a deeper and narrower accommodation groove in the left valve.

Remarks. This species is very similar to *N. vanveeni*, to which it is almost certainly related. It differs in the nature of the dorsal margin, in the width and depth of the accommodation groove in the left valve, and also in the shape of the posterior margin.

Subgenus PHYSOCYTHERE subgen. nov.

Type species. '*Cythere*' *lingenensis* Mertens 1956.

Diagnosis. A subgenus of *Neocythere* s.l., showing the characteristic inflated ventrally tumid shape of the genus, but differing from *Neocythere* s.s. in the structure of the hinge.

The hinge is symmetrical, consisting in the right valve of two strong, terminal, crenulate cusps separated by a long, straight locellate groove. In the left valve there is no accommodation groove, but a wide shelf occurs above the median element sloping down to the dorsal margin. The hinge elements as a whole are much stronger than in *Neocythere* s.s.

Neocythere (*Physocythere*) *lingenensis* Mertens 1956

Plate 41, figs. 15–22, 24

'*Cythere*' *costata* Mertens 1956, p. 190, pl. 9, figs. 27–30; pl. 10, figs. 31–32.
non *Cythere costata* M'Coy 1844, p. 165, pl. 23, fig. 11.
'*Cythere*' *lingenensis* Mertens 1958, p. 359.

Material. Mounted specimens HU 17.C.13.1–7 from the Middle Albian at Speeton.

Measurements	*Length*	*Height*	*Total width*
Female carapace	0·69 mm.	0·39 mm.	0·41 mm.
Male carapace	0·73 mm.	0·39 mm.	0·41 mm.

Description. Carapace egg-shaped, inflated, ventrally tumid. Greatest height at one-quarter length, greatest width at mid-length. Dorsal margin straight or slightly concave; ventral margin convex. The tumidity is not strong enough to obscure the ventral margin. Anterior margin broadly rounded, slightly asymmetrical ventrally; posterior margin triangular, forming a blunt point at mid-height. A muscle node is not developed.

Ornament consists of a reticulate honeycomb-like network of ridges covering the lateral surfaces. This network is bordered by three major concentric ribs paralleling the anterior, ventral, and posterior margins. These are most strongly developed ventrally, and often have the uppermost rib accentuated into a keel-like prolongation which forms an ear-like projection when the valve is viewed dorsally. A series of longitudinal ribs

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EXPLANATION OF PLATE 41

All figures ×50

Figs. 1–3, 5, 6. *Neocythere* (*Neocythere*) *protovanveeni* sp. nov., Barremian. All figured specimens from 14 feet above the base of Lower 'B' at Speeton. 1, Right valve female (holotype) lateral view HU. 17.C.11.1. 2, Right valve female (holotype) internal view HU. 17.C.11.1. 3, Left valve male (paratype) lateral view HU. 17.C.12.1. 5, Carapace (paratype) dorsal view HU. 17.C.12.2. 6, Carapace (paratype) ventral view HU. 17.C.12.2.

Figs. 4, 7. *Neocythere* (*Physocythere*) *semilaeva* sp. nov., Upper Albian, South Cave. 4, Left valve (holotype) lateral view HU. 17.C.16.1. 7, Carapace (paratype) from right HU. 17.C.17.1.

Figs. 8–12, 14. *Neocythere* (*Physocythere*) *hieroglyphica* sp. nov. 8, Left valve (holotype) dorsal view HU. 17.C.14.1. 9, Right valve lateral view HU. 17.C.15.1. 10. Left valve (holotype) lateral view HU. 17.C.14.1. 11. Right valve dorsal view HU. 17.C.15.1. 12. Right valve internal view HU. 17.C.15.1. 14. Left valve (holotype) internal view HU. 17.C.14.1.

Fig. 13. *Neocythere ?* (*Centrocythere*) *denticulata* Mertens, Upper Albian. Carapace from left HU. 17.C.18.1.

Figs. 15–22, 24. *Neocythere* (*Physocythere*) *lingenensis* Mertens, Middle Albian. 15, Left valve female dorsal view HU. 17.C.13.1. 16, Right valve male lateral view HU. 17.C.13.3. 17, Left valve female lateral view HU. 17.C.13.1. 18, Right valve male dorsal view HU. 17.C.13.3. 19, Right valve female internal view HU. 17.C.13.2. 20, Female carapace ventral view HU. 17.C.13.4. 21, Female carapace dorsal view HU. 17.C.13.4. 22, Right valve female lateral view HU. 17.C.13.2. 24, Left valve female internal view HU. 17.C.13.1.

Figs. 23, 25. *Neocythere* (*Neocythere*) *vanveeni* Mertens, Middle Albian. 23, Right valve female lateral view. HU. 17.C.10.1. 25, Left valve female lateral view HU. 17.C.10.2.


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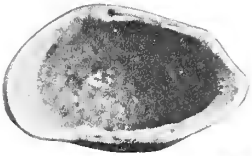
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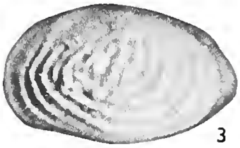
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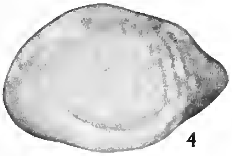
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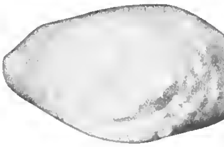
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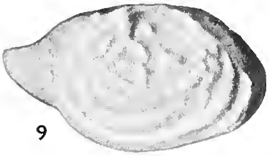
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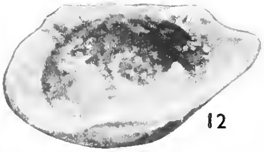
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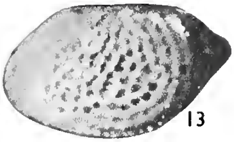
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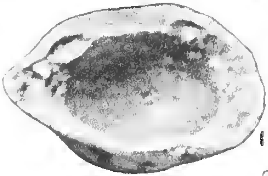
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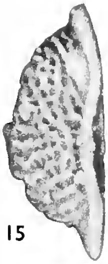
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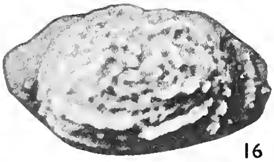
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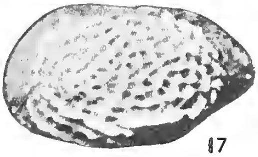
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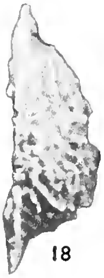
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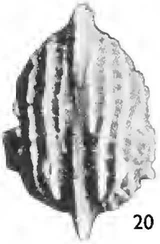
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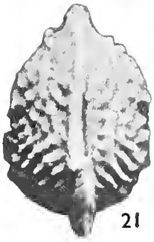
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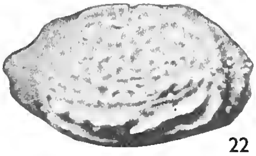
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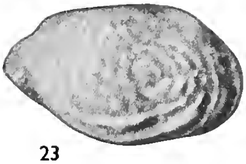
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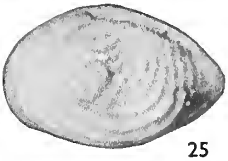
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KAYE, *Neocythere*

crosses the ventral surface. Duplicature narrow, dropping steeply into the inflated interior of the valve. Inner margin and line of concrescence coincide.

The hinge of the right valve consists of two bar-like teeth divided into four or five lobes. These teeth are separated by a long, straight locellate furrow. In the left valve there are two elongated divided sockets separated by a long straight denticulate bar. Above the bar, there is a broad flat shelf sloping to the dorsal margin but no accommodation groove.

Remarks. This species can be differentiated from other members of the group by the shape of the dorsal margin and by the ornament.

Neocythere (*Physocythere*) *hieroglyphica* sp. nov.

Plate 41, figs. 8–12, 14

Holotype. A left valve from the Red Chalk, bed N4 at West Heslerton, no. HU 17.C.14.1.

Other material. Specimens no. HU 17.C.15.1–6, from the uppermost Red Chalk at South Cave.

Diagnosis. A species of the subgenus *Physocythere* having a straight to concave dorsal margin, and an ornament of ridges arranged in a hieroglyphic pattern.

Measurements	*Length*	*Height*	*Total width*
Holotype left valve, HU 17.C.14.1	0·69 mm.	0·46 mm.	0·26 mm.
Right valve, HU 17.C.15.1.	0·73 mm.	0·39 mm.	0·24 mm.

Description. Carapace strongly inflated, ventrally tumid. Greatest height at one-quarter length, greatest width at mid-length. Dorsal margin straight or slightly concave with rounded cardinal angles. Ventral margin convex, and obscured in its central portion by the ventral tumidity. Anterior margin rounded, ventrally asymmetrical; posterior margin triangular, forming an acute upturned point at mid-height. There is usually a flattened rim along the dorsal margin, particularly in the left valves.

Lateral surfaces strongly ornamented with a pattern of concentric ribs enclosing an irregular, hieroglyphic-like pattern of ridges. These concentric ribs radiate from the centre of the dorsal margin, and parallel the other three margins, being most prominent ventrally. Several sinuous ridges run from the centre of the dorsal margin, across the lateral surface, branching and forming the hieroglyphic-like pattern with the concentric ribs. The marginal areas are smooth. Inner margin and line of concrescence coincide. Radial pore canals short and straight, numbering eight anteriorly and three posteriorly. Normal pore canals large, but rather rare; situated along the crests of the concentric ribs.

Hinge very strongly built. In the right valve there are two large, elongated terminal cusps, each divided into five lobes. They are separated by a long, straight locellate furrow open ventrally, but bordered dorsally by a smooth bar. In the left valve there are two large, strongly divided sockets separated by a long, straight denticulate bar. Above the median element there is a broad, flat shelf sloping down to the dorsal margin.

Remarks. N. (*P.*) *hieroglyphica* appears to be restricted to the Red Chalk. It differs from the other members of the group in the ornament, the greater inflation, and the strong hinge.

Neocythere (*Physocythere*) *semilaeva* sp. nov.

Plate 41, figs. 4, 7

Holotype. A left valve from the uppermost Red Chalk at South Cave; no. HU 17.C.16.1.

Other material. Five paratypes mounted as HU 17.C.17.1–5.

Measurements	*Length*	*Height*	*Total width*
Left valve holotype, HU 17.C.16.1.	0·60 mm.	0·39 mm.	0·26 mm.

Description. Only left valves and one complete carapace of this species are known, and therefore internal details of the right valves are lacking.

Carapace rounded, strongly tumid ventrally. Greatest height and width at mid-length. Dorsal margin of the left valve strongly arched, forming a broad obtuse angle at about the centre of the valve. Ventral margin convex, but obscured in lateral view by the tumidity. Anterior margin broadly rounded, posterior margin subtriangular, forming a rounded point at mid-height. The lateral surfaces are largely smooth, but show traces of concentric ribbing. A large inflated rib follows the ventral margin and can be vaguely traced around the edge of the lateral surface. This ridge is swollen ventro-laterally almost forming alaeform expansions. The ventral surface is smooth.

The hinge of the left valve consists of two strong divided terminal sockets separated by a long, straight denticulate bar. Above the median element there is a broad, flat shelf.

Occurrence. This species is only known from the Red Chalk (Upper Albian).

Remarks. N. (*P.*) *semilaeva* differs from the other species of the genus in the shape of the dorsal margin, the prominent ventral rib, and the smooth dorso-lateral surface.

Subgenus CENTROCYTHERE Mertens 1956

Subgenotype. Centrocythere denticulata Mertens 1956.

Diagnosis. A subgenus of *Neocythere* s.l. showing the usual inflated shape and ventral tumidity, but having a characteristic hinge arrangement. In the right valve the anterior tooth is step-like, the back portion being twice as high as the front. The posterior tooth is crenulate, and the median element consists of a locellate furrow, deepened at its anterior end to form a smooth socket. There is an accommodation groove above the median element in the left valve.

Neocythere ? (*Centrocythere*) *denticulata* Mertens 1956

Plate 41, fig. 13

? Cythere punctatula Jones 1849, p. 11, pl. 1, fig. 2*a–n*.
Centrocythere denticulata Mertens 1956, p. 204, pl. 11, figs. 66–71; pl. 14, figs. 97–99.
Brachycythere concentrica (Reuss); Deroo 1956, p. 1512, pl. 3, figs. 35, 36.

Material. Five carapaces, from the Red Chalk at Speeton.

Diagnosis. As only complete carapaces have been found, details of the hinge are unknown and the material is therefore only tentatively referred to this subgenus. It is placed here on a basis of the shape of the dorsal margin and posterior end, and also on the ornamentation.

Measurements	*Length*	*Height*	*Total width*
Carapace, HU 17.C.18.1.	0·60 mm.	0·39 mm.	0·35 mm.

CONCLUSIONS

The genus *Neocythere* has been subdivided into three subgenera on a basis of hinge structure. The subgenera are all represented in the Speeton Clay, and are of similar shape and ornamentation. Five of the six species are of Albian age. Of these, three are restricted to the Upper Albian, but the other two are also found in the Middle Albian. *Neocythere* (*Neocythere*) *Protovanveeni* sp. nov. occurs in the Lower Barremian and is the lowest form of the genus in the Cretaceous yet described, though the author has in his possession specimens of this, or a closely related form, from the Hauterivian Tealby Clay of Lincolnshire. It is possibly ancestral to the other forms, but, as the genus is absent or very rare from the Middle and Upper Barremian, Aptian, and Lower Albian, this cannot be proved with certainty. Of the six species, three are new, two belong to known German species, and one is tentatively compared to a known species.

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REVISION OF SOME LOWER CRETACEOUS MICROSPORES FROM BELGIUM

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ABSTRACT. Most of the new Wealden spore species described in 1955 by Delcourt and Sprumont are refigured; some have been placed in different genera. Two infra-specific taxa in the genus *Concavissimisporites* have been raised to specific rank. The diagnoses of the genera *Biretisporites*, *Concavissimisporites*, and *Aequitriradites* have been emended.

MANY of the spore species described by Delcourt and Sprumont (1955) in their pioneer work on the Belgian Wealden have subsequently been widely reported from Lower Cretaceous strata. Some of them are type species of important Mesozoic form-genera of wide distribution, and a clearer understanding of them is obviously of great importance. We have therefore re-examined the type specimens of those species instituted in 1955 and in 1959 (French Wealden) which need clarification. As a result of our investigation several species are transferred to different genera and some genera are emended; two infra-specific taxa are raised to specific rank, as we consider that subdivisions of form species of virtually unknown affinities are inappropriate. All the spores are now discussed in the order in which the various groups are treated by Potonié (1956, 1958, 1960).

We have faced considerable nomenclatural difficulty over the current Russian policy (Bolkhovitina 1961, Samoilovitch *et al.* 1961, and others) of placing large numbers of fossil dispersed spore species in Recent (extant) genera. The tangle of names in microfossil nomenclature is unfortunately unavoidable in a subject developing so quickly in several different continents, but this particular (Russian) solution seems to be totally undesirable. Knowledge of Mesozoic plants can only be obtained by studying *all* the fossils patiently; no advantage accrues from implying on very slender evidence that such genera as *Lygodium* Swartz and *Anemia* Swartz were present in the Lower Cretaceous. Search is being made continuously for the ancestors of these genera, but the circumscription of *Lygodium* Swartz cannot be blindly and indefinitely extended into the past on the basis of dispersed spores alone, without making the Recent taxon meaningless. We therefore intend to continue using and improving the generally recognized fossil spore taxa. We also notice that there has recently been conflict within the U.S.S.R. on this subject, in the two contrasted papers in the same volume by Zauer *et al.* (1960) and Zaklinskaya *et al.* (1960).

Some of the new photographs are oriented in the same way as the originals, but this is not always possible because some of the originals are 'mirror images' due to reversal in photographic printing. Some slight technical faults in a few of the new photographs are noted in the plate legends. A few of the type slides have deteriorated badly and this is noted in the worst cases. All the preparations remain in the collection of M. Delcourt at Ath, Belgium.

Acknowledgements. We are grateful to Dr. W. Mullenders, of Louvain, for providing facilities for one of us (M. E. D.) to study some of the type material mentioned, while Delcourt was away abroad.

Palaeontology, Vol. 6, Part 2, 1963, pp. 282–92, pls. 42–45.]

SYSTEMATIC SECTION

Anteturma SPORITES H. Potonié 1893
Turma TRILETES Reinsch 1881, emend. Potonié and Kremp 1954
Subturma AZONOTRILETES Luber 1935
Infraturma LAEVIGATI Bennie and Kidston, emend. Potonié 1956
Genus CYATHIDITES Couper 1953

Type species. Cyathidites australis Couper 1953.

Discussion. The slight extension of the genus by inclusion of further species makes it a more purely morphographic unit, and less dependent on the affinities implied by Couper (1953, 1958). Following the emendation of Delcourt and Sprumont (1955) *Concavisporites* Pflug is retained for smooth spores having a concave amb and proximal 'kyrtomes'. In uncompressed spores the kyrtomes constitute an abruptly convex exine area surrounding the laesurae; in compressed spores it is reduced to arcuate folds in the proximal inter-radial regions (Potonié and Kremp 1955, p. 13; Klaus 1960, p. 122). Few Lower Cretaceous spores attributed to *Concavisporites* exhibit kyrtomes around the laesurae.

Comparison. Deltoidospora has straight sides (Potonié 1956). From the Palaeozoic, *Leiotriletes* (convexly triangular amb) was validated in 1954 (Potonié and Kremp).

Cyathidites punctatus (Delcourt and Sprumont) comb. nov.

Plate 42, figs. 1–4

1955 *Concavisporites punctatus* Del. and Spr., p. 25, pl. 1, fig. 8; pl. 2, fig. 2.
1955 *Concavisporites baldurnensis* Del. and Spr., p. 24, pl. 1, figs. 7 *a*, *b*.
1955 *Cingulatisporites cavus* Del. and Spr. p. 38, fig. 8.
1961 *Lygodium asper* (Bolk.) Bolkhovitina (pars), p. 86.

Description. The equatorially tapering 'laesurate lips' are narrow oblique exposures of the slightly thickened exine adjoining the laesurae; undehisced (or uncompressed) spores do not show this 'feature', which is elucidated by Van Campo (1961, figs. 3–8). As mentioned by Couper (1958), the wall 'has a rather undulose appearance and is not punctate'; the species (holotype—Pl. 42, fig. 3) can therefore be included in *Cyathidites*, which is described as psilate.

Discussion. The species *baldurnensis* included uncompressed (or inflated) specimens (Pl. 42, figs. 1–2) of *punctatus*, the latter being the name selected by us for retention (Art. 57 of Code of Botanical Nomenclature, 1961—Montreal). The holotype of the species *cavus* is a specimen of *punctatus* with much adherent mineral matter (Pl. 42, fig. 4). The Canadian spore figured by Pocock (1962) as *C. punctatus* may be distinct in possessing a sculpture of 'distinct granules'.

Genus BIRETISPORITES Delcourt and Sprumont 1955, emend.

1955 *Biretisporites* Del. and Spr., p. 40.
1955 *Punctatisporites* Ibrahim, emend. Del. and Spr. (pars), p. 29.
1957 *Hymenophyllumsporites* Rouse, p. 363.

Emended diagnosis. Microspores trilete with a triangular to subtriangular amb. Laesurae enclosed within elevated lips which are upturned extensions of the proximal exine. Exine smooth or almost smooth.

Type species. B. potoniaei Del. and Spr. 1955.

Comparison. The type species was originally considered to have equatorial thickenings (Del. and Spr. 1955, Potonié 1956). The holotype, however, has no more than a smooth, uniformly thick exine and a trilete aperture enclosed within elevated lips. *Biretisporites* is therefore synonymous with *Hymenophyllumsporites*, which was instituted and clearly defined by Rouse (1957). It is distinct from *Dictyophyllidites* Couper, the exine of which is thickened about the laesurate margins ('margo' of Couper 1958). The type species of *Psilatriletes* van der Hammen ex Potonié resembles *Biretisporites*, but its diagnosis does not mention elevated laesurate lips.

Biretisporites potoniaei Delcourt and Sprumont 1955

Plate 42, figs. 12–14; Plate 44, fig. 11

1955 *Biretisporites potoniaei* Del. and Spr., p. 40, fig. 10.
1955 *Punctatisporites pileolus* Del. and Spr., p. 30, pl. 2, fig. 5.
1955 *Punctatisporites nidosus* Del. and Spr., p. 31, fig. 4 (cf. Kremp, W. 1958, *Catalogue of fossil spores and pollen*, **4**, 17).
1956 *Psilatriletes pileolus* (Del. and Spr.) Potonié, p. 15.

Holotype. Delcourt and Sprumont 1955, p. 40, fig. 10; here refigured on Plate 42, figs. 12, 13. Distal oblique aspect.

Description. Microspore trilete, biconvex; amb convexly subtriangular, diameter 48μ. Laesurae 23μ long; lips narrow (1–2μ wide), elevated (2–3μ high) extensions of the promimal exine. Exine smooth, 2·5μ thick. The specimen has a median fold in the distal exine, as does another specimen shown on Plate 44, fig. 11.

Discussion. The further specimens of *Psilatriletes* (al. *Punctatisporites*) *pileolus* (Del. and Spr. 1959, pl. 5, fig. 15) are here refigured on Plate 42, fig. 14; they conform to the above description of *potoniaei* as does the designated holotype of *pileolus* on which the apparent granules are mineral grains.

Infraturma APICULATI Bennie and Kidston, emend. Potonié 1956

Genus CONCAVISSIMISPORITES Delcourt and Sprumont, emend.

1955 *Concavissimisporites* Del. and Spr., p. 25.
1961 *Lygodium* Swartz; Bolkhovitina (pars), p. 100.
1961 *Lygodium* Swartz; Ivanova (pars) in Samoilovitch *et al.*, p. 90.
1962 *Concavisporites* Pflug; Pocock (pars), p. 46.

Emended diagnosis. Microspores trilete; amb triangular with concave to almost straight sides. Exine of uniform thickness (inclusive of sculpture), verrucate; verrucae more or less uniformly developed and evenly distributed over entire spore surface.

Type species. C. verrucosus Del. and Spr., emend.

Discussion. The genus was originally instituted to include trilete, azonate microspores characterized by a 'concavissime' amb. Potonié (1956) suggested, but did not formally propose, that the genus should be restricted to contain only such spores with verrucate sculpture. The genus is here formally restricted to include verrucate spores which have concave, but not necessarily strongly concave, ambs; it is distinct from *Trilobosporites* Pant ex Potonié, which has a differentially thickened exine and/or larger sculptural elements about the radial regions at the equator.

Concavissimisporites verrucosus Delcourt and Sprumont 1955, emend.

Plate 42, figs. 5–7

1955 *C. verrucosus* forma *verrucosus* Del. and Spr., p. 25, pl. 2, fig. 1*a*.
1961 *Lygodium verrucosus* (Del. and Spr.) Bolkhovitina, p. 100, pl. 37, figs. 2*a*, *b*.
non 1955 *C. verrucosus* f. *crassatus* Del. and Spr., p. 26.
non 1962 *Concavisporites verrucosus* (Del. and Spr.) Pocock, p. 46.
non 1962 *Concavisporites verrucosus* var. *minor* Pocock, p. 47.

Holotype. Delcourt and Sprumont 1955, p. 25, pl. 2, fig. 1*a*, here refigured on Plate 42, figs. 5–7. Proximal aspect.

Description. Amb 90μ in diameter (60μ in maximum radial length), triangular with concave sides and broadly rounded angles. Laesurae 43μ long (2/3 spore radius), straight, and with linearly arranged verrucae along margins. Exine 3·5μ thick (inclusive of sculpture); verrucae closely spaced, 1–2μ high, semicircular in optical section, and with circular to polygonal bases 2–4μ in diameter.

Comparison. This specimen is considered specifically distinct from the holotypes of the two validly designated infra-specific taxa, f. *crassatus* and var. *minor*, which are (below) elevated to specific rank.

Discussion. *C. verrucosus* is distinct from spores assigned to *Concavisporites variverrucatus* by Couper (1958, p. 142, pl. 2, figs. 4–5); it is considerably larger, more strongly concave, and has more regular verrucae.

Concavissimisporites crassatus (Del. and Spr.) sp. nov.

Plate 42, figs. 9–11

1955 *C. verrucosus* f. *crassatus* Del. and Spr., p. 26, pl. 2, fig. 1*b*.
non 1962 *Concavisporites verrucosus* (Del. and Spr.) Pocock, p. 46.

Holotype. Delcourt and Sprumont 1955, pl. 2, fig. 1*b*, here refigured on Plate 42, figs. 9–11. Proximal aspect.

Description. Amb triangular with rounded angles and concave sides, 78μ in diameter (50μ in maximum radial length). Laesurae 43μ long (4/5 spore radius), straight; margins obliquely exposed and with linearly arranged verrucae. Exine 3μ thick (including sculpture); with low, dome-shaped verrucae which are 1–3μ in basal diameter and spaced 1–3μ apart.

Comparison. The species differs from *C. verrucosus* in having smaller and more widely spaced verrucae and longer laesurae.

Concavissimisporites minor (Pocock) sp. nov., comb. nov.

1962 *Concavisporites verrucosus* var. *minor* Pocock, p. 47, pl. 5, fig. 75.

Discussion. The imperfectly preserved holotype is distinct from *C. verrucosus* and *C. crassatus* in having smaller verrucae which are more widely spaced.

Genus PILOSISPORITES Delcourt and Sprumont 1955

Pilosisporites verus Delcourt and Sprumont 1955

Text-fig. 1

Comparison. Text-fig. 1 shows the broad-based form of the sculptural elements of the holotype. The other difference from *P. trichopapillosus* is in the close spacing of sculptural elements in the equatorial radial regions.

TEXT-FIG. 1. Detail of sculpture of *Pilosisporites verus*, holotype (Del. and Spr. 1955, pl. 4, fig. 1). × 1000.

Infraturma MURORNATI Potonié and Kremp 1954

Genus LYCOPODIUMSPORITES Thiergart ex Delcourt and Sprumont 1955

Discussion. The genus was only validated in 1955 by selection of a 'lectogenotype', *L. agathoecus* (Potonié). Nilsson (1958, p. 45) used this genus but Krutzsch (1959, pp. 159, 164, 165) suggested that the genus should be abandoned; although we sympathize with his reasons we do not find his argument convincing. The two species mentioned below could be placed in *Klukisporites* Couper 1958, if this genus should fall.

EXPLANATION OF PLATE 42

All figures × 500, unless otherwise stated.

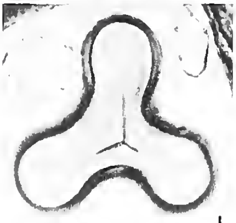
Figs. 1–4. *Cyathidites punctatus* (Del. and Spr.) comb. nov. 1–2, Distal aspect, specimen of *Concavisporites baldurnensis* D. and S. 1955, prep. ϵ; 1, Low focus; 2, Mid focus. 3, Holotype, *Cyathidites punctatus*, optical section; aspect distal. 4, Proximal aspect of holotype of *Cingulatisporites cavus* D. and S. 1955, p. 38; optical section, air bubble subcentral.

Figs. 5–7. *Concavissimisporites verrucosus* D. and S. emend., Holotype. 5, Mid focus. 6, Detail, × 1000, mid focus. 7, × 1000, high focus.

Figs. 8–11. *Concavissimisporites crassatus* (D. and S.) sp. nov., holotype, proximal aspect (D. and S. 1955, pl. 2, fig. 1*a*). 8, High focus. 9, Mid focus. 10, Detail, × 1000, mid focus. 11, × 1000, high focus.

Figs. 12–14. *Biretisporites potoniaei* D. and S. 1955. 12, Holotype, oblique distal aspect; mid focus. 13, Low focus. 14, Spores illustrated as *Psilatriletes pileolus* (D. and S.) D. and S. 1959, pl. 5, fig. 15.

Note. Two extraneous hairs are present in figs. 6, 7, 10, 11.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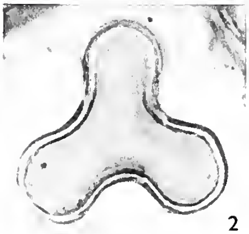
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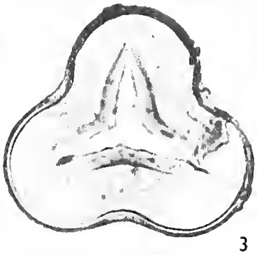
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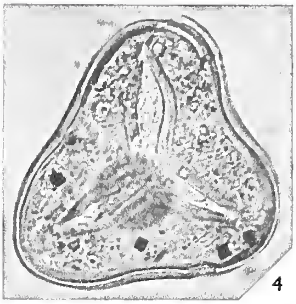
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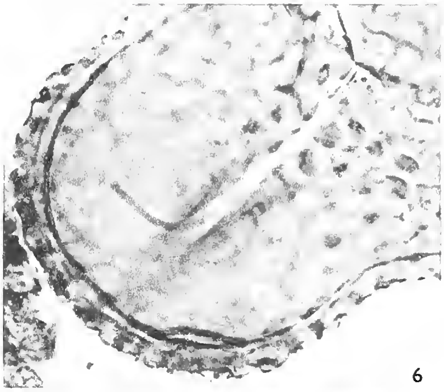
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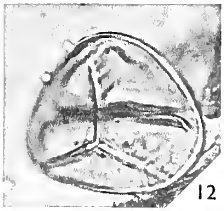
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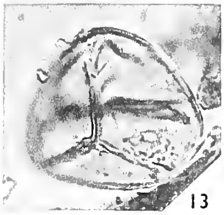
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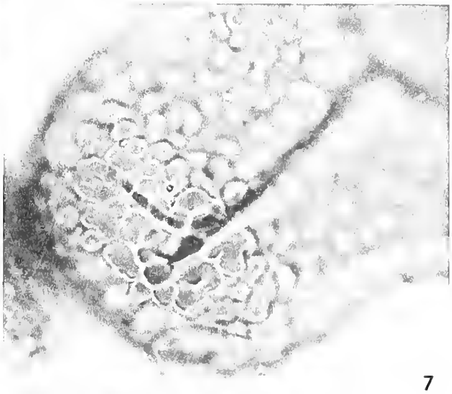
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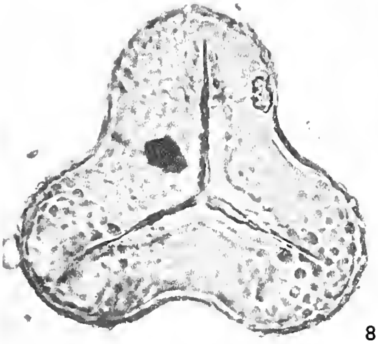
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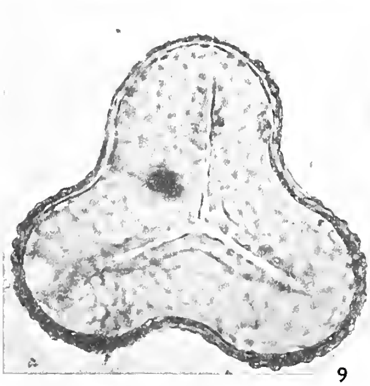
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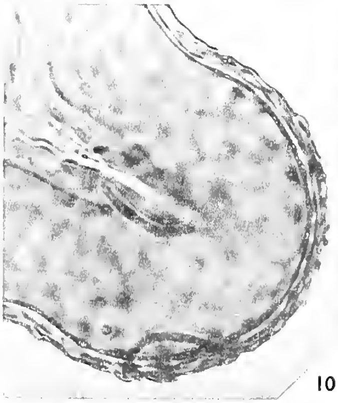
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11

DELCOURT, DETTMANN and HUGHES, Lower Cretaceous Spores

Lycopodiumsporites triarcuatus Delcourt and Sprumont 1955

Plate 43, figs. 1, 2, 5

Description. The damaged holotype is refigured (Pl. 43, fig. 1) and supported by two other specimens from the same material (Pl. 43, figs. 2, 5). The proximal face is smooth, unsculptured; other features as previously described. The two *formae* mentioned (1955) are not validly published.

Lycopodiumsporites elongatus Delcourt and Sprumont 1955

Plate 43, figs. 3, 4

Description. The holotype is refigured. Again the proximal face is smooth, unsculptured.

Genus CICATRICOSISPORITES Potonié and Gelletich 1933

Type species. C. dorogensis Pot. and Gell.; Eocene, Hungary.

Discussion. Kedves (1961, p. 124) selected neotypes (*sic*) for *C. dorogensis*, and rediagnosed the species to exclude, among other things, the many Mesozoic references (Couper 1958, and others); he did not entirely succeed in this, but the purpose is clear and we agree that none of the illustrated Lower Cretaceous specimens conforms with the species. We therefore follow and amplify the policy of Delcourt and Sprumont (1955).

Cicatricosisporites hallei Delcourt and Sprumont 1955

Plate 43, figs. 6, 7

Description. The holotype is refigured. The muri are regular with sharply defined edges, and are flat-topped; they are twice as wide as the intervening canals (lumina). The spacing of four canals and muri in 11μ, is as previously illustrated (1955, text-fig. 1).

Comparison. C. hallei differs from *C. dorogensis* in possessing flat-topped muri with sharp edges.

Cicatricosisporites sewardi Delcourt and Sprumont 1955

Plate 43, fig. 8

Description. The holotype is refigured as a photograph; diameter 55μ, not as previously stated. The spacing (four canals and muri) is about 12μ only and thus differs little from *C. hallei*; the canals are, however, relatively wider, and the muri more round-topped with less sharp edges.

Cicatricosisporites mohrioides Delcourt and Sprumont 1955

Discussion. It was not possible to improve on the original figure of this species because the holotype is now orientated in a lateral aspect, and does not appear to be well preserved.

Turma ZONALES Bennie and Kidston, emend. Potonié 1956
Subturma AURITOTRILETES Potonié and Kremp 1954
Infraturma AURICULATI Schopf, emend. Potonié and Kremp 1954
Genus TRILOBOSPORITES Pant ex Potonié 1956

1956 *Trilobosporites* Pant ex Potonié, p. 55.
1961 *Lygodium* Swartz; Ivanova (pars) in Samoilovitch *et al.*, p. 90.

Type species. T. hannonicus (Del. and Spr.) Potonié 1956.

Restated diagnosis. Microspores trilete; amb triangular. Exine differentially thickened in equatorial radial regions where sculptured valvae are developed. Sculptural elevations (grana, verrucae) larger and sometimes coalescent on valvae.

Discussion. Trilobosporites is distinct from *Concavissimisporites* on distribution of sculptural elements and presence of valvae. *Matonisporites* Couper has a smooth exine and *Cibotiumidites* Maljavkina is defined by Potonié (1960, p. 62) as cingulate.

Trilosbosporites hannonicus (Del. and Spr.) Potonié 1956

Plate 43, figs. 9, 10

Holotype. Delcourt and Sprumont 1955, p. 24, pl. 2, fig. 3. Refigured here on Plate 43, figs. 9, 10; distal aspect.

Description. Amb concavely triangular with truncated angles, diameter 58μ. Laesurae 25μ long; margins weakly thickened and obliquely exposed. Exine 2·5μ thick, 4μ in equatorial radial regions where verrucate valvae are developed; verrucae low (*c.* 1μ high), closely spaced, and with circular to polygonal bases 3–4μ in diameter. Remainder of exine with smaller, verrucae and granules, which are polygonal to circular in outline and 1–3μ in basal diameter.

Remarks. Potonié (1956, p. 55) described the exine wrongly as microreticulate. It is now shown to be verrucate.

Trilobosporites bernissartensis (Del. and Spr.) Potonié 1956

Plate 43, figs. 11–14

Holotype. Here figured as a photograph, Plate 43, figs. 11, 12; distal aspect.

EXPLANATION OF PLATE 43

All figures ×500 unless otherwise stated.

Figs. 1, 2, 5. *Lycopodiumsporites triarcuatus* D. and S. 1955. 1, Holotype, proximal aspect; mid focus. 2, Prep. B301, proximal aspect, high focus. 5, Prep. B103, distal aspect, high focus.

Figs. 3, 4. *L. elongatus* D. and S. 1955. Holotype, distal aspect. 3, Mid focus. 4, High focus.

Figs. 6, 7. *Cicatricosisporites hallei* D. and S. 1955. Holotype, oblique distal aspect. 6, ×1000, high focus. 7, Mid focus.

Fig. 8. *C. sewardi* D. and S. 1955. Holotype, proximal aspect, high focus.

Figs. 9, 10. *Trilobosporites hannonicus* (D. and S. 1955). Holotype, distal aspect. 9, Low focus. 10, ×1000, mid focus.

Figs. 11–14. *Trilobosporites bernissartensis* (D. and S. 1955). 11, Holotype, distal aspect, optical section. 12, High focus, proximal surface. 13, Single mount X3, Loc. Baudour Bed 1, proximal aspect, optical section. 14, Single mount X14, Loc. Baudour Bed 1, proximal aspect, mid focus.


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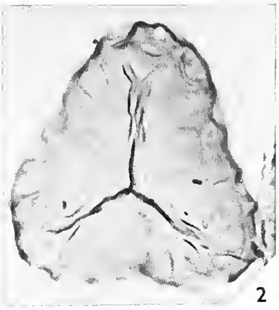
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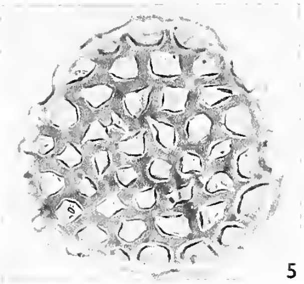
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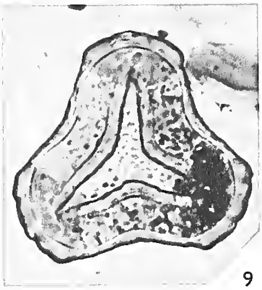
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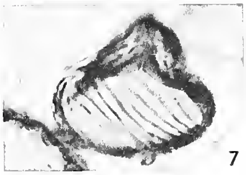
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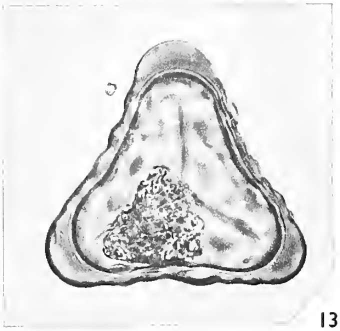
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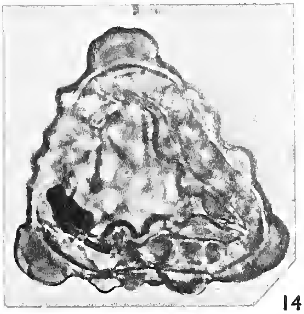
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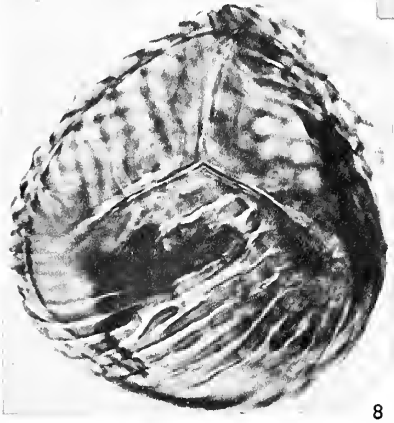
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12

DELCOURT, DETTMANN and HUGHES, Lower Cretaceous spores

Description. The holotype is not well preserved and the isotype could not be located; two other specimens from the same material are shown in Plate 43, figs. 13–14. As stated by Couper (1958, p. 141), the proximal face is sculptured.

Genus APPENDICISPORITES Weyland and Krieger 1953

Appendicisporites ethmos Delcourt and Sprumont 1959

Plate 44, figs. 12, 13

Description. The holotype is here refigured. Distal aspect, diameter 60μ, not as previously stated. Sculpture as in *Cicatricosisporites,* with four canals and muri in about 12μ; muri pitted throughout, pits up to 1μ diameter; the pitting is very constant.

Remarks. This species may have to be placed in *Plicatella* Maljavkina ex Potonié 1960; this should be determined, however, by the origin of the 'appendices' (Dettmann 1963, in press), rather than by their length (Potonié 1960, p. 50). The holotype of *A. ethmos* does not illustrate this clearly.

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI Potonié and Klaus 1954

Genus DENSOISPORITES Weyland and Krieger 1953

Densoisporites triradiatus Delcourt and Sprumont 1955

Plate 45, figs. 7–9

Holotype. Delcourt and Sprumont 1955, text-fig. 11; here refigured on Plate 45, fig. 7. Proximal aspect, corroded; diameter 125μ, not as previously stated.

Description. Laesurae straight, extending to the periphery, and with elevated (3μ high) lips. Tapering cingulum, 25μ wide. The second specimen (Pl. 45, figs. 8, 9) is smaller (96μ) and shows the surface detail more clearly.

Genus BALDURNISPORITES Delcourt and Sprumont 1955

Discussion. Potonié (1956, p. 60) regarded the genus as insufficiently defined, but placed it in the Cingulati; he removed the megaspore species *Minerisporites marginatus* (Dijkstra) from *Baldurnisporites,* with which we agree. The specimens of the two remaining species are refigured below, but further specimens seem to be rare in the preparations; there is a slight suspicion that these spores may be perinate specimens of *Cyathidites* (al. *Concavisporites) punctatus* (Del. and Spr.) comb. nov.

Type species. B. cernuus.

Baldurnisporites cernuus Delcourt and Sprumont 1955

Plate 44, figs. 7, 8

Type specimens. The holotype (Del. and Spr. 1955; pl. 3, fig. 5) has been accidentally destroyed. The isotype (Del. and Spr. 1955, p. 44) is now figured on Plate 44, figs. 7, 8.

Baldurnisporites papillosus Delcourt and Sprumont 1955

Plate 44, figs. 9, 10

Description. The holotype, distal aspect, diameter 100μ, is refigured. The laesurae do not appear to reach the flange as originally described; the 'baton' supporting the flange is clearly seen near one radius.

Infraturma ZONATI Potonié and Kremp 1954

Genus AEQUITRIRADITES Delcourt and Sprumont, emend. Cookson and Dettmann 1961

1955 *Aequitriradites* Delcourt and Sprumont, p. 44.
1961 *Selaginellidites* Krasnova in Samoilovitch *et al.*, p. 38.
1961 *Aequitriradites* D. and S. emend. Cookson and Dettmann, p. 426.

Restated diagnosis. Microspores tetrahedral, with a membraneous zona. Exine inaperturate or hilate; with structural and/or sculptural modifications at and about the distal pole, where a 'hilum' may be formed as the result of a natural exinous breakdown. Proximal tetrad mark distinct, or only faintly represented, especially towards the pole.

Type species. A. dubius.

Aequitriradites dubius Delcourt and Sprumont 1955

Plate 45, figs. 1–4

1955 *A. inconspicuus* Delcourt and Sprumont, p. 45, pl. 2, fig. 6.

Holotype. Delcourt and Sprumont 1955, pl. 3, fig. 7*a* only (not fig. 7*b*—see below); here refigured on Plate 45, figs. 1–3.

Description. Proximal aspect, diameter 85μ; exine $2\cdot5\mu$ thick, coarsely granulate except in a circular area (25μ in diameter) about the distal pole, where it is composed of discrete, low, polygonal-based (2–3μ diameter) irregular verrucae. Zona 20μ wide, scabrate, with four short (5–6μ long), radially oriented ridges which emanate outwards from its interradial inner margin. Proximal tetrad mark comprises two, long (30μ), sinuous ridges (2μ wide) which extend from pole to zone.

EXPLANATION OF PLATE 44

All figures ×500 unless otherwise stated.

Figs. 1–6. *Rouseisporites granospeciosus* (D. and S.) comb. nov. 1, Holotype, distal aspect, high focus. 2, Mid focus. 3, Single mount X7, Baudour Bed 1, distal aspect, mid focus. 4, High focus. 5, Single mount X21, Baudour Bed 1, distal aspect, high focus. 6, Mid focus.

Figs. 7, 8. *Baldurnisporites cernuus* D. and S. 1955, Isotype, proximal aspect. 7, High focus. 8, Mid focus.

Figs. 9, 10. *B. papillosus* D. and S. 1955. 9, Holotype, distal aspect, mid focus. 10, Detail, ×1000.

Fig. 11. *Biretisporites potoniaei* D. and S. 1955; prep. θ, proximal aspect.

Figs. 12, 13. *Appendicisporites ethmos* D. and S. 1959. 12, Holotype, distal aspect, high focus. 13, Mid focus.

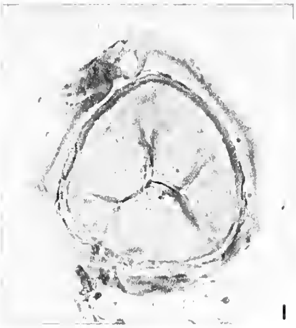
EXPLANATION OF PLATE 45

All figures ×500.

Figs. 1–4. *Aequitriradites dubius* D. and S. 1955. 1–3, Holotype, proximal aspect. 1, Low focus. 2, Mid focus. 3, High focus. 4, Distal aspect, holotype of *A. inconspicuus* D. and S. 1955, pl. 2, fig. 6; high focus.

Figs. 5, 6. *Schizaeoisporites phaseolus* D. and S. 1955; holotype, lateral aspect. 5, High focus. 6, Low focus.

Figs. 7–9. *Densoisporites triradiatus* D. and S. 1955. 7, Holotype, proximal aspect, mid focus. 8, Prep. θ, proximal aspect, high focus. 9, Mid focus.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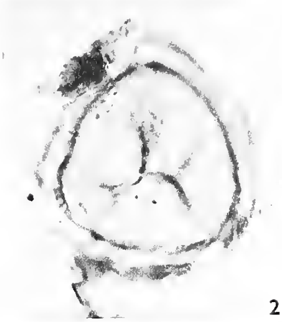
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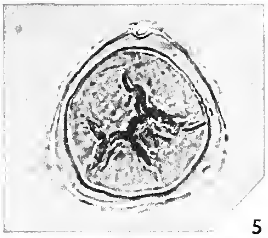
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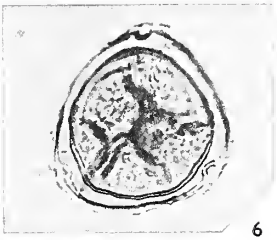
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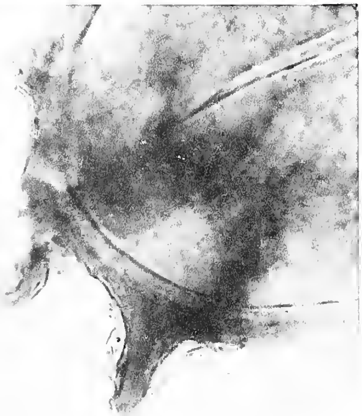
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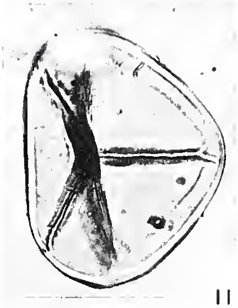
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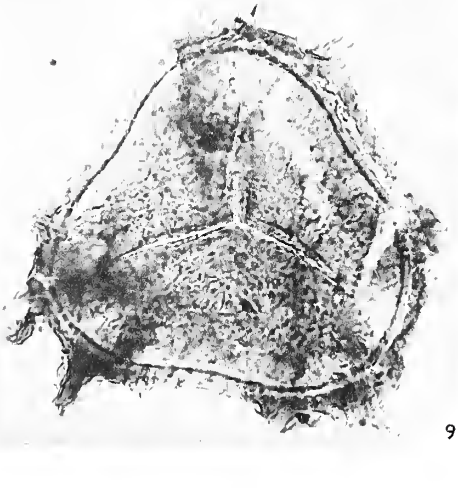
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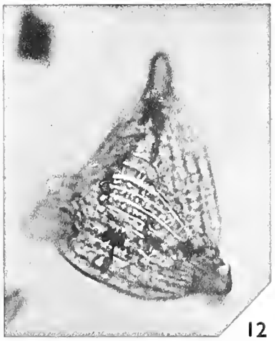
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DELCOURT, DETTMANN and HUGHES, Lower Cretaceous spores


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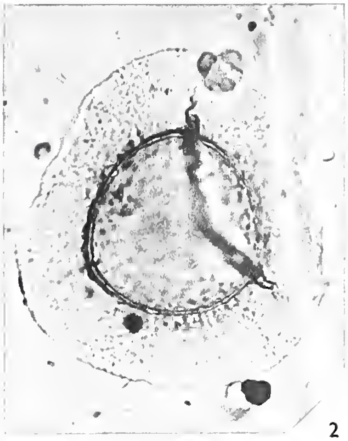
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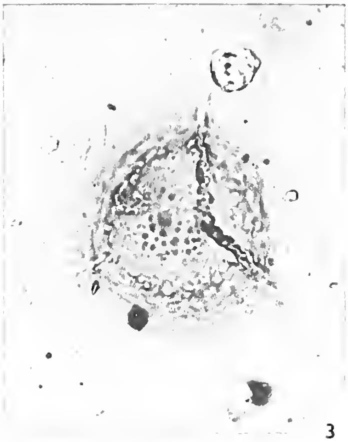
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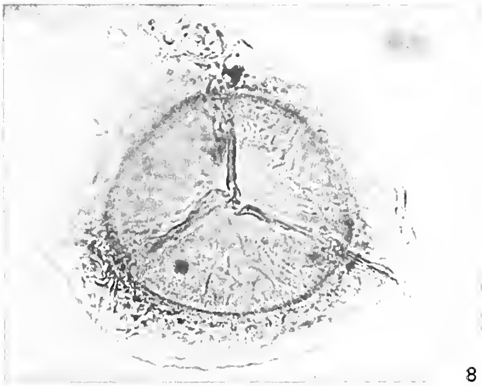
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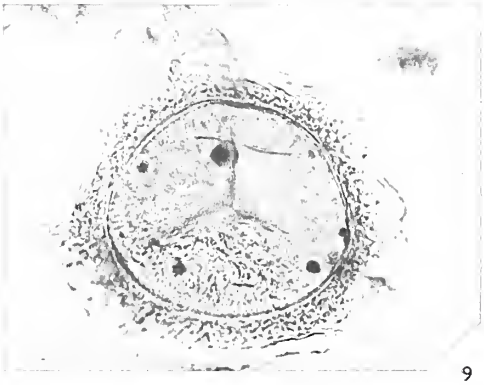
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DELCOURT, DETTMANN and HUGHES, Lower Cretaceous spores

Discussion. Delcourt and Sprumont's holotype of *A. inconspicuus* (pl. 2, fig. 6), which is here refigured on Plate 45, fig. 4, has a coarsely granulate exine and is conspecific with *A. dubius.* Delcourt and Sprumont's specimen in pl. 3, fig. 7*b* has a rugulo-reticulate sculpture, and belongs to a separate undescribed species.

Genus ROUSEISPORITES Pocock 1962

Type species. R. reticulatus Pocock 1962.

Discussion. This genus appears to be distinct from *Zlivisporis* Pacltova 1961, and *Seductisporites* Chlonova 1961, on the presence of zonal invaginations in each radial, equatorial region.

Rouseisporites granospeciosus (Del. and Spr.) comb. nov.

1955 *Cingulatisporites granospeciosus* Del. and Spr., p. 39, pl. 4, fig. 2.

Holotype. Delcourt and Sprumont 1955, p. 39, pl. 4, fig. 2. Here refigured on Plate 44, figs. 1–2. Distal aspect. Diameter 65μ.

Description. Microspore zonate, biconvex; amb subcircular. Sclerine two-layered consisting of a granulate inner layer (2μ thick) and an enveloping membraneous, zonate outer layer. Zona smooth (8μ wide) with a flask-shaped invagination (5μ diam.) in each region at the equator. Proximal surface smooth except for a faint tetrad mark. Distal surface with radially orientated, bifurcating, muroid ridges (2–3μ high).

Discussion. Two other specimens are figured on Plate 44, figs. 3–6. The species has been removed from *Cingulatisporites* on the basis of its clearly special characters of the zona. *C. euskirchensoides* Delcourt and Sprumont 1955, p. 38, might have required similar treatment, but we were unable to illustrate the holotype further.

Turma MONOLETES Ibrahim 1933
Subturma AZONOMONOLETES Luber 1935
Infraturma SCULPTATOMONOLETI Dybova and Jachowicz 1957
Genus SCHIZAEOISPORITES Potonié 1951
Schizaeoisporites phaseolus Delcourt and Sprumont 1955

Plate 45, figs. 5, 6

Description. The holotype is refigured as a photograph; lateral view, length 68μ. Specimen dense, as originally implied.

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PROBLEMATICAL MICROFOSSILS FROM THE CRETACEOUS AND PALAEOCENE OF THE MIDDLE EAST

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ABSTRACT. During studies of the non-foraminiferal microfossils, especially the algae, of the Middle East over the last decade a considerable number of problematical organisms have been noted. These include some whose allocation is doubtful, at varying taxonomic levels, or whose position has only recently been established, as well as new or unusual examples of known families and genera. A selection of these, Cretaceous and Palaeocene in age, is now placed on record as a further contribution to Tethyan micropalaeontology.

1. *Calcareous Algae*

Pseudolithothamnium was described by Pfender (1937) as an organism apparently similar in growth-form and appearance in reflected light to the melobesioid algae (of which *Lithothamnium* and *Lithophyllum* are common examples), but differing in the transparent appearance of the tissues in thin section, in which condition the melobesioids appear more or less uniformly dark. This distinction was ascribed to differences in the calcification during life. Pfender saw no close resemblance in the cell-structures of *Pseudolithothamnium* to those of the melobesioids, and although she described apparent sporangial structures she did not regard the fossil as close to this algal family, and only doubtfully referred it to the Rhodophyta (red algae). She recorded it from rocks ranging from Lower Cretaceous to Oligocene in age, over a very wide area of central and southern Europe, the Mediterranean Basin, the Middle East, and Madagascar.

Pseudolithothamnium was figured from the Upper Cretaceous of the Carpathians by Andrusov (1939), and recorded from both Upper Cretaceous and Palaeocene of northern Iraq by Elliott (1955, 1960). These records, following Pfender, were all referred to the single described species *P. album*.

More recently a convincing case has been put forward by Massieux and Denizot (1962) for the identity of the fossil *Pseudolithothamnium* with the Recent *Ethelia*. This is an encrusting lamellar red alga (family Squamariaceae), with a central mesothallus margined by upper and lower perithalli; the reproductive structures are temporary deciduous outgrowths from the upper surface. The internal structures are not normally easy to prepare in orientated section owing to the contorted and twisted nature of the thallus. Fossil records of *Pseudolithothamnium* are all based on random cuts in thin-section or fractured surfaces, and it is not surprising that the detailed structure of *Ethelia* has not been seen in them before. The somewhat doubtful alleged reproductive structures in the fossils are discounted and ascribed to mineralization and fracture.

Ethelia is a calcified warm-water genus; the calcium carbonate is in the form of aragonite, unlike the melobesioids, which are calcitic. This initial difference is considered the probable cause of the different appearance of the fossils in thin-section. It may be added that similar exceptions are known in largely aragonitic groups, e.g. *Pseudovermiporella* (calcitic) in the Dasycladaceae (largely aragonitic).

[Palaeontology, Vol. 6, Part 2, 1963, pp. 293–300, pl. 46–47.]

Massieux and Denizot show similar structure in Recent Atlantic *Ethelia fosliei* and French Eocene *Pseudolithothamnium album* Pfender, but wisely do not attempt to equate the long-range fossil *Pseudolithothamnium album* with any of the modern botanical species of *Ethelia*, and therefore propose the combination *Ethelia alba* (Pfender 1937).

The Iraqi material now figured from the Palaeocene of Kurdistan, a richly algal level, comes from the Kolosh Formation at Rowanduz and the Sinjar Limestone at Sarmord. The Rowanduz slide (Pl. 47, fig. 1) shows a tangle of thalles of *Ethelia* intergrown with those of the melobesioid *Archaeolithothamnium* (and also with other algae, not shown). *Ethelia* is transparent, *Archaeolithothamnium* dark, except for the chains of sporangial cavities. Although the section shows a considerable area of *Ethelia*, only at one spot (Pl. 47, fig. 2) was it possible to discern a vertical cut of the thin thallus showing the central mesothallus and upper and lower perithalli. The thickness of this thallus-section (0·26 mm.) is comparable with that of the Recent *Ethelia* (0·23 mm.) given by Massieux and Denizot (1962, fig. 2). Much of the section shows as highly oblique cuts through successive laminae about 0·10–0·12 mm. thick; this is even better shown on the Sarmord specimen (Pl. 47, fig. 3), where the varying laminae range up to 0·24 mm. in thickness as seen, traversed by a curved-radial cell arrangement, and the section is presumably very highly oblique through a gently curved flat growth. This may not be the same species, but Pfender (1937, fig. 2) shows a somewhat similar section of Turkish Palaeocene material, with similar transparent tissues, and she refers to the curved-radial 'jet d'eau' cell-arrangement. In the Recent *Ethelia* the species *biradiata* and *fosliei* show considerable differences in section (Weber-Van Bosse 1921).

Ethelia alba is easily distinguished from the associated solenoporoid *Parachaetetes asvapatii*, a much more massive species in which the curved-radial structure is much coarser, and which is normally yellowish or buff in thin-section appearance. It is also different from those melobesioids in which diagenesis has altered the dark calcite to a translucent appearance with partial obliteration of cell-structure, a condition seen not uncommonly in various Tertiary limestones.

2. Bačinella

Bačinella was diagnosed by Radoičić (1959), from the Lower Cretaceous of Jugoslavia, as nodular and encrusting algae whose interior is constructed of irregular cells of different size and form, filled with crystalline calcite, whereas the intercellular mass is cryptocrystalline; the dermal structure is differentiated. In her description she states that, when exceptionally preserved, *B. irregularis* may show a subdermal structure like that of *Lithocodium aggregatum* Elliott.

Elliott (1956) described *L. aggregatum*, also Lower Cretaceous in age, as irregular nodular growths largely formed of thin superimposed thalles: within the outer zone of definite *Lithocodium* structure there occurs in some, but not all, cases a very coarse irregular inner mesh or spongy mass, described originally as 'a larger mass of irregular tubules, never radial and presumably of *Lithocodium* itself'. This inner structure is the same as in *Bačinella*.

There is thus often a close association between these two doubtfully algal growths; in spite of frequent recrystallization, they have been seen to occur both separately and together in favourable thin-sections of Middle Eastern material. Moreover, *Lithocodium* is itself often intimately intergrown with the lamellar stromatoporoid *Burgundia*.

It seems likely that *Lithocodium* and *Bačinella* may be constructed by the same organism, but, pending a full investigation on favourable material, it seems best to use both names, for the appropriate structures. Both are typically Lower Cretaceous, but Radoičić (1959) states that she has seen structures like *Bačinella* in both the Upper Jurassic and Upper Cretaceous. Upper Jurassic species of *Lithocodium* have been described by Endo (1961) from Japan. The example now figured (Pl. 48, fig. 3) is from the Qamchuqa Limestone, Albian level, of Zewiya, Pir-i-Mugrun, Sulaimania, north-east Iraq.

3. Microcalamoides

As described by Bonet (1956) from the Lower Cretaceous (Barremian to Lower Albian) of Mexico, this is a problematic microfossil in the form of a thin-walled cylinder, fluted or grooved with about thirty longitudinal sulci, and ranging from about 0·2 to nearly 1·0 mm. in diameter; the fossils are all fragmentary or incomplete. Bonet discusses the pelagic associations, filamental and perhaps ramifying structure, and possible algal nature of this organism, which he describes as *M. diversus*, with varieties A, B, and C.

It is now recorded from the Lower Cretaceous Yamama Formation (Valanginian–Hauterivian) of Iraq (Pl. 47, fig. 4). The example shown is larger (diameter 1·69 mm.) and approximates most closely to Bonet's type C; fragments of type B have been seen also. It is associated with debris of *Permocalculus*, dasyclads, and *Bačinella*; all are shallow-water algae, but fragmented and washed out to a deeper zone, and it could be a pelagic addition to this debris from the littoral zone.

As well as the Mexican and Iraqi records, *Microcalamoides* has been seen by the writer from the Lower Cretaceous of Borneo, and so it has a very wide distribution.

4. Calymenospongia

Studies of calcareous algae from the Middle East (bibliography in Elliott 1960; 1961) were largely carried out on thin-sections, owing to the nature of the material collected, though weathered or loose specimens were examined whenever available. A sample from the Palaeocene of Bekhme, Erbil Liwa, northern Iraq, consisted of a loose detrital serpentine sand rich in dissociated calcareous algae. Some of these, such as *Cymopolia* and *Halimeda*, were instantly recognizable; some, e.g. *Pagodaporella* (Elliott 1956), proved on dissection to be already well known in thin-section, and the solid fossil permitted description of the genus. The earlier reconstruction from sections of the external appearance of *Dissocladella* by Pia (Rama Rao and Pia 1936) was proved correct from specimens in this sample. Among these little algae was a fossil which, similar in size-range and general appearance to the others, was revealed on sectioning to be, not an alga, but a small calcisponge.

Genus CALYMENOSPONGIA gen. nov.

Small calcisponge of uniserial consecutive near-spherical hollow growths, fused at junctions, and communicating internally by large, single apertures; a few scattered, irregularly placed pores penetrating outer surface of growths. Palaeocene, Iraq.

Type species. C. kurdistanensis sp. nov.

Calymenospongia kurdistanensis sp. nov.

Plate 46, figs. 1, 2, 3

Description. This sponge is about 2·3 mm. long (incomplete), with a maximum diameter of 0·72 mm. It consists of a simple, straight or gently curved, single series of consecutive swellings delimited by constrictions, like a row of fused spheres. These are circular in transverse section: in the measured example quoted above there are six (one incomplete), the others having a height of 0·42 mm. A few scattered coarse pores are to be seen on each swollen surface. Internally, a longitudinal section reveals that each swelling or unit is hollow and thin-walled, with a wall-thickness of 0·03 mm. measured at the maximum diameter of the unit. Top and bottom, inside from the external constrictions, the walls continue inwards to fuse with those of the next unit in a swollen thickening; this is perforated in the centre by a large intercommunicatory pore. The vertical thickness of the swollen fused internal walls, and the horizontal diameter of the intercommunicatory pores which they encircle, are about the same, 0·15 mm. The scattered pores of the external surfaces are filled with calcite, but are believed to have originally perforated the wall: the diameter of one seen in section is 0·026 mm. The wall-structure throughout shows as mottled grey calcite interpreted as fused spicules; thin-sections of material from the famous Lower Cretaceous calcisponge locality of Faringdon, England, show a similar appearance.

Holotype. BM S8335 (Pl. 46, fig. 1), Kolosh Formation (Palaeocene), Bekhme, Erbil Liwa, northern Iraq.

Paratypes. BM S8336, S8337 (Pl. 46, figs. 2, 3), same locality and horizon.

Remarks. This sponge is closest to *Sollasia* (Steinmann 1882) from the Carboniferous of Spain, resembling it in size and general simplicity of structure, but differing in having a wall showing one layer only, unlike the two of *Sollasia*, and in showing a more complete fusion internally at the junctions of the walls of the consecutive units. This latter feature is probably only a consequence of the different wall-structure. The group of sponges to which *Sollasia* belongs has recently been carefully revised in great detail by Seilacher (1962), on the occasion of the description of new and exceptionally well-preserved material. He places *Sollasia* in the family Celyphiidae de Laubenfels, superfamily Aporata Seilacher, suborder Sphinctozoa Steinmann, order Pharetronida Zittel. Like *Sollasia*, *Calymenospongia* is catenulate and cryptosiphonate. Seilacher interprets the wall-structure

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EXPLANATION OF PLATE 46

Fig. 1. *Calymenospongia kurdistanensis* gen. et sp. nov. Holotype, BM S8335, ×50. Kolosh Formation, Palaeocene; Bekhme, Erbil Liwa, northern Iraq.

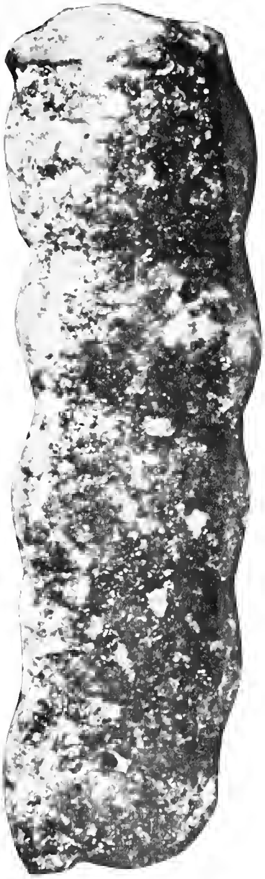
Figs. 2, 3. *C. kurdistanensis*, paratypes, BM S8336, S8337, vertical and transverse thin-sections, ×50; same locality and horizon.

Fig. 4. *Coptocampylodon lineolatus* gen. et sp. nov. Holotype, BM Z988, ×56. Sarmord Formation, Hauterivian, Lower Cretaceous; Surdash, Sulaimania Liwa, north-east Iraq.

Figs. 5, 6. *C. lineolatus*, lateral and terminal views of two examples, same locality and horizon, ×56.

Fig. 7. *Favreina prusensis* Paréjas. BM Z996, thin-section, ×56. Chia Gara Formation, bottom Cretaceous (Berriasian); Ser Amadia, Mosul Liwa, northern Iraq.

Fig. 8. *Coptocampylodon lineolatus*. Paratype, BM Z993, thin-section, ×56; Garagu Formation, subsurface Lower Cretaceous, Fallujah Well, Dulaim Liwa, Iraq.



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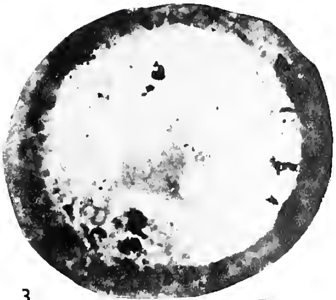

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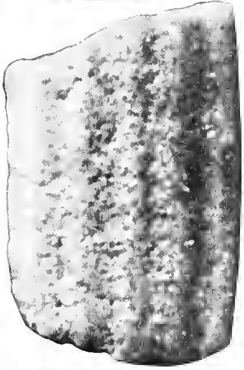

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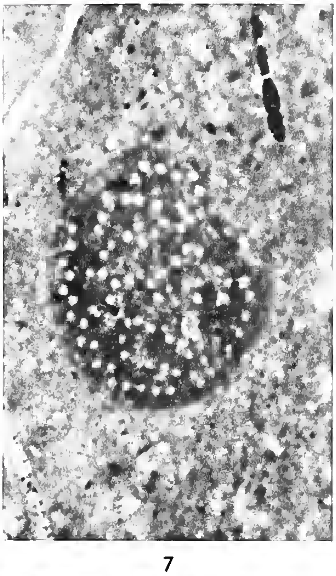

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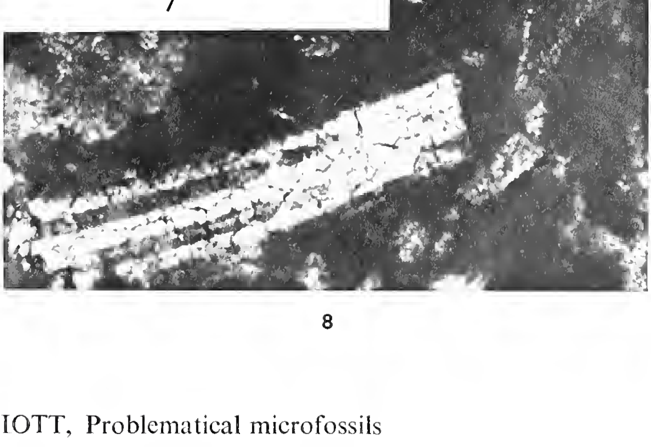

8

ELLIOTT, Problematical microfossils

of the Palaeozoic genus as spicules embedded in an original calcareous sclerosome, giving a rigid wall in life and hence occasioning intermittent segment growth. The hollow segments seen in this fossil are considered to have contained soft sponge tissue originally. These interpretations are applicable to *Calymenospongia* also.

Calymenospongia is the first member of the Sphinctozoa to be described from post-Cretaceous strata. It is easily distinguished from the somewhat similar *Sphaerocoelia* (Upper Jurassic–Cretaceous), which has a markedly perforate wall.

Simple sponges of this kind, of microfossil dimensions, may be of much more common occurrence than has been realized hitherto.

5. Coptocampylodon

Grooved spicules of Lower Cretaceous age have been familiar to micropalaeontologists handling Middle Eastern material for many years, and have usually been referred to as *Acicularia sp. Acicularia* s.s. (Tertiary and Recent) is a genus of dasyclad algae with a terminal calcified sporangial disc which eventually falls apart into radial petal-like calcareous spicules each containing numerous, tiny, spherical, sporangial cavities. More or less similar algal structures of varying form occur from the Jurassic onwards, usually as small dissociated bodies, and have been described as species of *Acicularia* s.l. At least three are known from the Lower Cretaceous: a small, spherical, sporangial body '*Terquemella*' *sp.*, the ovoid *A. antiqua* Pia, and the long, irregular *A. elongata* Carozzi. Transverse cuts of the Middle East spicule referred to above are not unlike similar sections of worn examples of the acicularians, but numerous longitudinal and oblique cuts reveal that it is different. It is now described and its possible biological nature discussed.

Genus COPTOCAMPYLODON gen. nov.

Small solid cylindrical calcareous bodies, longer axis gently curved or irregular, circular in cross-section but deeply incised by longitudinal grooves, ends irregularly rounded. Lower Cretaceous; Middle East and Borneo.

Type species. C. lineolatus sp. nov.

Coptocampylodon lineolatus sp. nov.

Plate 46, figs. 4, 5, 6, 8; Plate 48, fig. 2

Description. Solid short cylindrical calcareous bodies (units), up to 3·0 mm. in length (incomplete) and varying from about 0·25 to 1·0 mm. in diameter. The longer axis of the unit is gently curved or slightly irregular: the ends, when not obviously broken, are irregularly rounded. The outer surface, itself usually smooth, but in some examples showing a feeble transverse lamination, is deeply incised by parallel equidistant longitudinal grooves, from five to eight in number. In transverse section these grooves are seen to widen inwards and often to be near-circular in cross-section, with an internal diameter of 0·04–0·05 mm. The circular transverse section of the whole unit is notched by the grooves and has the appearance of a coarse sparsely spoked cog-wheel or of a stellate structure with truncated rays. Longitudinal sections show the parallel, matrix-filled grooves, either curved or passing out of the plane of the section owing to their irregularity.

Holotype. BM Z988 (Pl. 46, fig. 4); Sarmord Formation (Hauterivian level), Lower Cretaceous; Surdash, Sulaimania Liwa, north-east Iraq. *Paratypes.* BM Z993) (Pl. 46, fig. 8), subsurface Garagu Formation, Lower Cretaceous; Fallujah Well, Dulaim Liwa, Iraq.

Other material. Numerous examples, solid and thin-section, from the Lower Cretaceous of Iraq. Seen in thin-section from the Lower Cretaceous of Borneo.

Remarks. As stated above, transverse sections of *Coptocampylodon* have previously been interpreted as acicularian, but the longitudinal sections disprove this, since all known acicularian spicules, long or short, have near-spherical sporangial cavities giving circular cross-sections at all angles of cut.

Nothing similar to the units of *Coptocampylodon* is known amongst the algae or the spicular elements of calcareous sponges. The mineral structure is not that of echinoderm skeletal elements, and the form is quite different from that of 'alcyonarian spicules'. These latter are the minute embedded calcareous elements of the horny corals or subclass Octocorallia. In the octocoral family Isididae Lamouroux there occur genera showing an alternation of horny nodes and calcareous internodes; the latter are known fossil, notably in the genus *Moltkia* (Upper Cretaceous). Typically these isolated calcareous bodies are larger than those of *Coptocampylodon*, and show conspicuous calicular pits; they are also associated with the larger, dichotomously branching structures characteristic of the genus. However, comparison of the varied series of skeletal remains of *Moltkia* figured by Voigt (1958) shows that some of the smaller dissociated elements are very similar to the Iraqi fossil (cf. Voigt 1958, pl. 3, figs. 9, 10; *Moltkia isis* Steenstrup). A comparison may also be made with the elements of the decorticated axis of *Isis* (Recent). It is therefore suggested that *Coptocampylodon* comprises the skeletal remains of a small octocoral in which horny and calcareous joints alternated. *Coptocampylodon* is earlier (Lower Cretaceous) than these genera; most pre-Upper Cretaceous records of fossils referred to the octocorals seem doubtful (Bayer 1956; Voigt 1958; Häntzschel 1958), but this allocation seems the most likely.

EXPLANATION OF PLATE 47

Fig. 1. Transparent *Ethelia* (*Pseudolithothamnium*), contrasted with dark *Archaeolithothamnium* showing chains of conceptacles. BM V44845, thin-section, ×40. Kolosh Formation, Palaeocene; Rowanduz, Erbil Liwa, northern Iraq.

Fig. 2. *Ethelia alba* (Pfender). BM V44845, thin-section, ×100. Vertical cut of single growth showing central mesothallus with upper and lower perithalli. Kolosh Formation, Palaeocene; Rowanduz, Erbil Liwa, northern Iraq.

Fig. 3. *Ethelia alba* (Pfender). BM V44844, thin-section, ×30. Sinjar Limestone, Palaeocene; Sarmord, Sulaimania Liwa, north-east Iraq.

Fig. 4. *Microcalamoides diversus* Bonet, cf. type C. BM Z992, thin-section, ×28. Subsurface Yamama Formation, Valanginian–Hauterivian; Makhul no. 1 well, Mosul Liwa, northern Iraq.

EXPLANATION OF PLATE 48

Fig. 1. *Favreina montana* sp. nov. Syntypes, BM Z997, thin-section, ×56. Qamchuqa Formation, Cretaceous (Albian); Gund-i-Shikavt, Erbil Liwa, northern Iraq.

Fig. 2. *Coptocampylodon lineolatus* gen. et sp. nov. BM Z994, random cuts in thin-section, ×56. Yamama Formation, subsurface Lower Cretaceous (Valanginian–Hauterivian); Makhul no. 1 well, Mosul Liwa, northern Iraq.

Fig. 3. *Bačinella irregularis* Radoičić. BM Z995, thin-section, ×28. Qamchuqa Formation, Cretaceous (Albian); Zewiya, Pir-i-Mugrun, Sulaimania Liwa, north-east Iraq.

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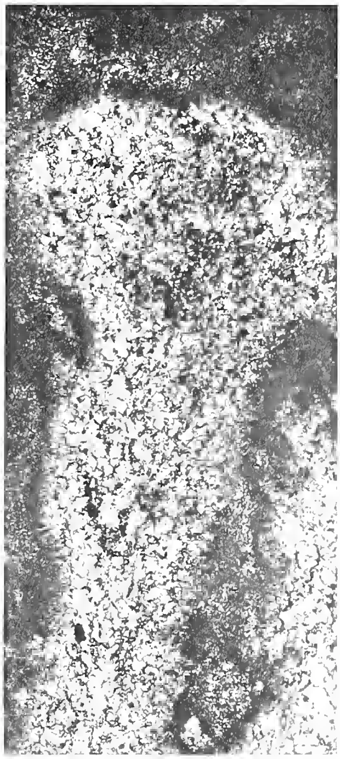

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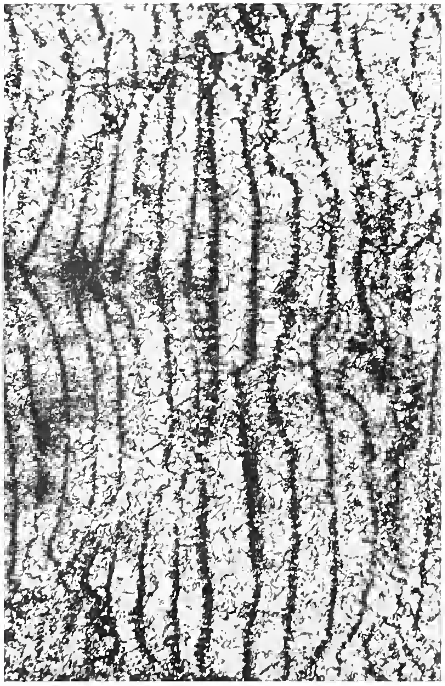

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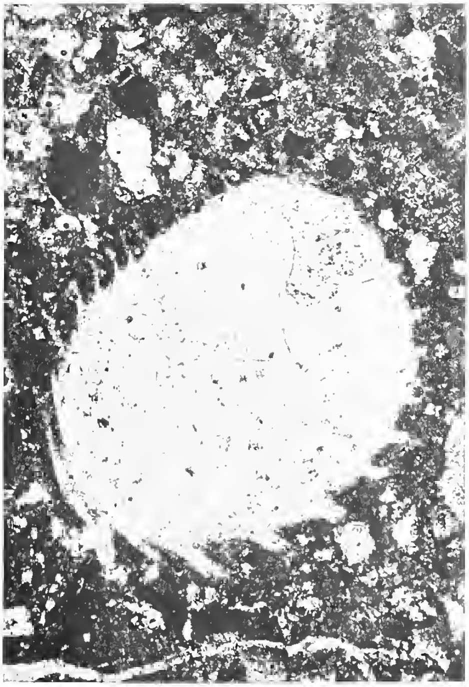

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ELLIOTT, Problematical microfossils

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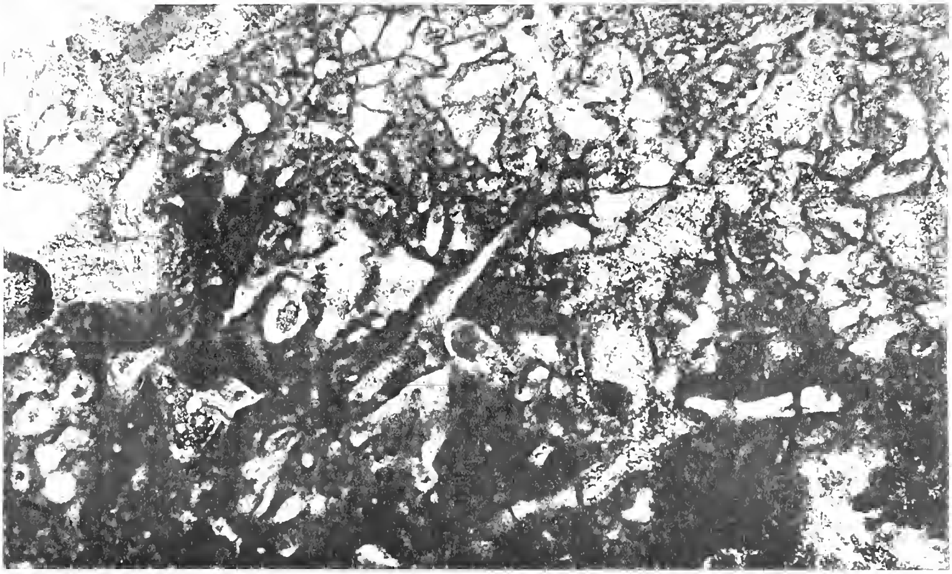

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ELLIOTT, Problematical microfossils

6. Favreina

The peculiar microfossils named *Favreina* by Bronnimann (1955) are short, solid, cylindrical pellets perforated by varying numbers of fine longitudinal canals in arrangements showing as characteristic patterns in cross-section. They were first figured from the Swiss Jurassic (Joukowsky and Favre 1913), but we owe to Paréjas (1935, 1948) the recognition of these as the faecal pellets of certain crustaceans, the Anomura, in which the fleshy structure of the stomach initiates perforations in the gut-content of largely inorganic ingested material. Since different genera and species of living Anomura show distinctively different pellet-patterns (Moore 1932), numerous species of *Favreina* have been described on the morphology of the fossils; two recent review studies are those of Bronnimann and Norton (1961) and Elliott (1962). Two new records can now be added to the Middle East species listed and described in the latter study.

Favreina prusensis Paréjas

Plate 46, fig. 7

Remarks. This distinctive species (Paréjas 1948) from the Upper Jurassic (Portlandian) of Turkey, shows from 66 to 136 canals, set in a complicated pattern of zigzag lines as seen in transverse section. No doubt this pattern increased in complexity with the growth of the individual originating the pellets. Listed for comparison by Elliott (1962) on the strength of Paréjas's described material, it is now recorded from the Upper Chia Gara Formation, Berriasian, of Ser Amadia, Mosul Liwa, northern Iraq. This example, 0·57 mm. in diameter, shows over 100 canals: the arrangement may be interpreted as similar to that in the type material.

Favreina montana sp. nov.

Plate 48, fig. 1

Description. Pellet of up to 1·3 mm. in length and 0·6 mm. diameter, cylindrical, with circular or near-circular cross-section. Canals very fine, circular to comma-shaped in section, about sixty in number, seen in some examples to be paired by very fine lines. Pattern of canals in transverse-section not definite, but obscurely spiral.

Syntypes. BM Z997 (Pl. 48, fig. 1); Qamchuqa Formation (Albian level), Cretaceous; Gund-i-Shikavt, Erbil Liwa, northern Iraq.
Other material. Numerous random cuts in thin-section, same locality and horizon.

Remarks. F. montana resembles the Lower Cretaceous *F. cuvillieri* Bronnimann in size and arrangement of paired canals, but possesses double the number of canals. It is easily distinguished from the third Cretaceous species occurring in the Middle East, *F. kurdistanensis* Elliott, which shows eight large canals thinly crescentic in section.

Specimens in the Department of Palaeontology, British Museum (Natural History), which are referred to in the text, have the prefix BM.

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ON THE STRUCTURE OF LEAVES OF *RHABDOTAENIA* PANT FROM THE RANIGANJ COALFIELD, INDIA

by D. D. PANT and B. K. VERMA

ABSTRACT. A new species of *Rhabdotaenia* Pant (*R. fibrosa*) and additional details of epidermal structure of *Rhabdotaenia danaeoides* (Royle) Pant, based on a number of leaf fragments, collected from the Raniganj coalfield, India, are described. It is pointed out that these two species and *R. harkinii* Pant, are all structurally distinct.

TONGUE-SHAPED leaves found in the Glossopteris flora include, besides *Glossopteris* and *Gangamopteris*, the three other forms, *Noeggerathiopsis*, *Palaeovittaria*, and *Taeniopteris*. Pant (1958) has assigned some of these *Taeniopteris* leaves to a new genus *Rhabdotaenia*, in which he distinguishes two species, *R. danaeoides*, based on three incomplete leaves from the Raniganj coalfield, India, and *R. harkinii*, based on a single leaf fragment from East Africa. A third species, *R. fibrosa*, which shows interstitial fibres, is described here from the Raniganj coalfield. Besides these, additional characters of *R. danaeoides* are also described from numerous compressions of leaves of the species from the same locality.

Genus RHABDOTAENIA Pant

Rhabdotaenia fibrosa sp. nov.

Plate 49, figs. 1–7; text-figs. 1, 2B–E

Diagnosis. Leaf large, elongated oval, length unknown, 3·5–9·5 cm. wide, lamina widest in middle region, tapering towards apex. Apex acute, margins entire, midrib up to 3 mm. wide in middle region, narrower towards apex, showing many longitudinal strands towards base, fewer above. Lateral veins parallel, arising at an acute angle from midrib and almost immediately arching outwards and running at about 90° to midrib. Vein ends near margin sometimes slightly curved towards apex, but marginal veins or loops not seen. About one-fifth of total number of lateral veins forked once, forking either at point of origin from midrib or elsewhere in lamina. Forked veins less frequent towards apex. Concentration of veins 15–27 per cm. near midrib and 19–31 per cm. towards margin. Veins normally up to 167 μ thick. Areas between lateral veins often showing interstitial fibres, fibres up to 45 μ thick.

Upper epidermis of lamina nonstomatiferous. Cells between veins sinuous-walled, amplitude of sinuosities of cell walls averaging at 5 μ, average lateral distance between two antinodes 9 μ. Cells rectangular, arranged in longitudinal rows parallel to veins, typically averaging at 93 μ long × 36 μ wide. Average thickness of walls 5 μ in middle region and 8 μ near midrib. Cells over veins narrower and longer with less sinuous sides. Surface of cells vaguely mottled, papillae not seen.

Lower epidermis of lamina stomatiferous. Cells between veins usually averaging at 79 μ long × 60 μ wide, cell walls slightly more sinuous than in upper, amplitude of

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sinuosities of cell walls 7 μ, lateral distance between two antinodes 15 μ. Cells less regularly arranged than those of upper epidermis and elongated in various directions. Cells over veins narrower, elongated in direction of veins, sides of cells over veins less sinuous. Surface of cells clearly mottled, occasionally showing median hollow papillae. Trichomes absent. Stomata haplocheilic, unevenly distributed in areas between veins and normally absent in vein courses. Guard cells irregularly orientated, exposed, generally 51 μ long × 19 μ wide, stomatal opening 6 μ wide. Subsidiary cells 3–5, irregularly shaped like ordinary epidermal cells; polar subsidiary cells unspecialized and like laterals.

Upper and lower epidermis of midrib showing rectangular or polygonal cells tending to be arranged in longitudinal rows; cell rows forming bands of narrow almost straight-walled cells (above longitudinal strands of midrib), alternating with bands of somewhat wider slightly sinuous-walled cells (in areas between midrib strands). Surface of epidermal cells above and near midrib often showing longitudinal surface striations.

Upper and lower cuticles of lamina like respective epidermal layers, surface mottled, cell outlines usually well defined over veins but often obscure between them.

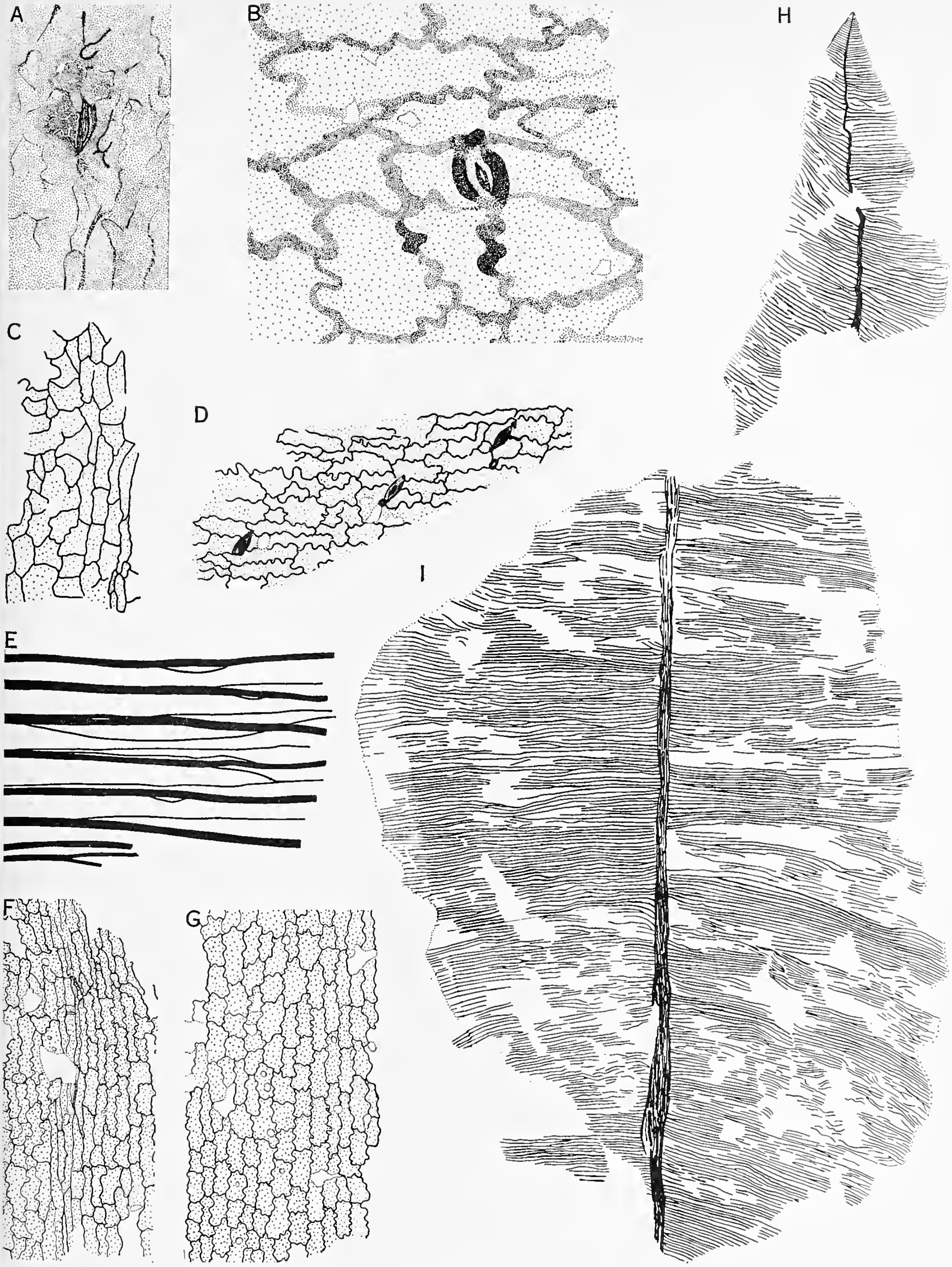
Holotype. Specimen No. 229 of Divya Darshan Pant Collection at present located in Botany Department, University of Allahabad, Allahabad, India.

Locality and horizon. Raniganj coalfield, India. Lower Gondwana.

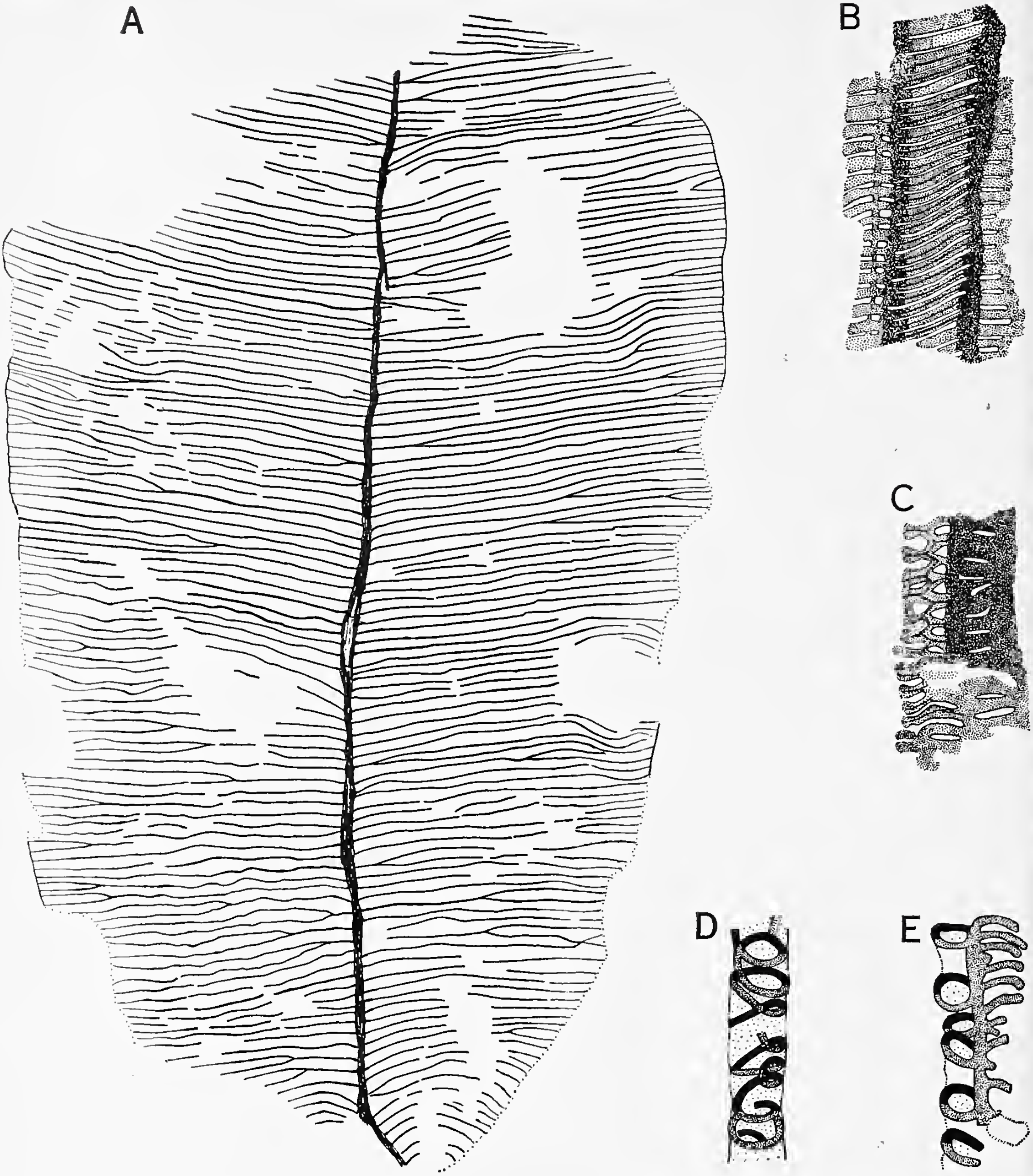
Description. The species is based on nine fragments of leaves, including one apex and eight pieces representing middle portions. None of our specimens shows the basal part of the leaves. The single apex is acute but its concentration of veins and epidermal structure are like those found in other fragments assigned to this species although interstitial fibres are seen only at a few places in the apical fragment. The width of various fragments from middle region of leaves varies from 3·5 to 9·5 cm. Lateral veins, which run almost straight up to the margin, are 62–167 μ thick. Displaced lateral veins, like those of *R. danaeoides* and *R. harkinii*, sometimes appear sinuous (Pl. 49, figs. 1, 7; text-fig. 1H, I). In an incident-light examination, small compressed creases and folds in the lamina may sometimes appear like anastomoses between lateral veins, but such apparent anastomoses can be clearly made out in transmitted-light examination of celloidin pulls, as the cells above vein courses run straight without anastomoses. Actual connexions between veins were never seen.

Interstitial fibres, which are 22–45 μ thick, come out of the lateral veins, usually in the middle part of the lamina. For some distance the fibres run between two veins and

TEXT-FIG. 1. *Rhabdotaenia fibrosa* sp. nov. A, Lower cuticle of lamina showing obscure epidermal cell outlines. 231d; ×267. B, Lower epidermis of lamina showing an enlarged stoma with lignified lateral and polar lamellae (the lamella at the lower pole is broken (see also Pl. 49, fig. 3). 232a; ×267. C, Lower epidermis of midrib showing elongated cells above vein and longitudinal rows of slightly sinuous-walled rectangular cells between them. 232a; ×83. D, Lower epidermis of lamina with irregularly arranged sinuous-walled cells and stomata. 232a; ×83. E, Side veins of lamina (thicker lines) showing interstitial fibres (thinner lines) between them (see also Pl. 49, fig. 4). 232; ×10. F, Upper epidermis of lamina showing longitudinal rows of almost straight-walled narrow cells above a vein and wider cells with more sinuous sides on its two flanks. 232b; ×83. G, Broader upper epidermal cells in area between two veins. 229; ×83. H, Apical portion of lamina showing venation (see also Pl. 49, fig. 1). 233; ×1. I, Middle portion of lamina showing furcate or simple parallel lateral veins diverging at a wide angle from longitudinally striped midrib (see also Pl. 49, fig. 7). 229; ×1.



TEXT-FIG. 1



TEXT-FIG. 2. A, *Rhabdotaenia danaeoides*, B–E, *Rhabdotaenia fibrosa* sp. nov. A, Middle portion of lamina showing venation (see also Pl. 50, fig. 1). 251; ×3/2. B, Xylem element from midrib showing scalariform thickenings. 231a; ×800. C, Xylem element from midrib showing alternate biseriate pits (see also Pl. 49, fig. 5). 231a; ×800. D, Xylem element from midrib showing spiral thickenings (see also Pl. 49, fig. 6). 231a; ×800. E, Xylem element from a vein showing annular thickenings (see also Pl. 49, fig. 2). 234; ×800.

they may then take an oblique course to re-enter the same or another vein and subsequently they may emerge once again on the same or the opposite side. Sometimes they meet or cross other fibres running between two veins (Pl. 49, fig. 4; text-fig. 1E). Marginal fibres could not be seen clearly at any point.

Amplitude of sinuosities of cell walls in upper epidermal cells varies from 3 to 14 μ and the lateral distance between two antinodes from 5 to 12 μ. Cells between veins are rectangular and 62–128 μ long and 26–48 μ wide. The thickness of their lateral walls varies, these being generally thicker over and near midrib. The cell walls are 4–7 μ thick in areas between veins and 6–11 μ near and over midrib.

Cells between two veins in the lower epidermis are 48–112 μ long and 40–80 μ wide. Surface of cells is clearly mottled and shows well-marked lighter oval or rounded areas, like those of *R. harkinii*. Surface striations are generally present in the cells over and near the midrib. These run parallel to the longitudinal axis of cells but never radiate from their centre. The guard cells are 37–63 μ long and 15–26 μ wide and the stomatal opening is 4–7 μ. The stomata are generally exposed and not protected by subsidiary cells as in *R. danaeoides*, or their papillae as in *R. harkinii*. The guard cells show clear lignified lateral and polar lamellae of gymnosperm type, which are dissolved after maceration with concentrated nitric acid and potassium chlorate, followed by ammonia.

The side veins and midrib in various leaf fragments show tracheids in abundance. Some of them showing clear spiral (Pl. 49, fig. 6; text-fig. 2D) and annular (Pl. 49, fig. 2; text-fig. 2E) thickenings, but most of them being scalariform (Pl. 49, fig. 5; text-fig. 2B). Some tracheids of the midrib also show alternate biseriate pits (Pl. 49, fig. 5; text-fig. 2C). The fibrovascular elements of midrib and veins sometimes show rounded or oval pinhole-like pits as in *R. danaeoides*.

Comparison and discussion. Rhabdotaenia fibrosa agrees with *Macrotaeniopteris feddeni* Feistmantel in shape, size, midrib characters, and above all in having about the same concentration of veins per centimetre. Therefore, perhaps it would have simplified matters if the present leaves were also included under the old species *M. feddeni*, but epidermal structure of that species is unknown. Six specimens of *M. feddeni* in the Museum of the Geological Survey of India, Calcutta (Nos. 5200, 5203, 5204, 5205, 5206, and 5498, figured by Feistmantel 1881, pl. xxi A, fig. 3; pl. xxii A, figs. 1–4; and 1886, pl. 1 A, fig. 1 respectively), were examined to see if they could yield any epidermal and cuticular preparations, but none of them shows any carbon. All are fragments of the middle regions of leaves impressed on ferruginous stone and even in specimens where veins are otherwise clear, no thinner lines representing impressions of interstitial fibres are seen (cf. *Glossopteris fibrosa* Pant, 1958). Accordingly, for the present we presume that our specimens of *R. fibrosa* are distinct from *M. feddeni*. In fact we consider it possible that two specimens (Nos. 5200 and 5498) of taeniopterid leaves, which Feistmantel assigned to *M. feddeni*, may not belong to it because they are bigger than others and show clear impressions of side veins running at an acute angle to the midrib (cf. *Palaeovittaria*), instead of running at right angles to it as is typical of *Rhabdotaenia*.

Among comparable Lower Gondwana forms whose epidermal structure is known, *Rhabdotaenia fibrosa* differs from other species of the genus in having characteristic interstitial fibres. In addition, *R. fibrosa* differs from *R. danaeoides* in having an acute apex (the apex in *R. danaeoides* is obtusely pointed). It differs from both *R. danaeoides* and *R. harkinii* in having a higher concentration of veins per centimetre (*R. fibrosa* has 15–27 veins per cm. near midrib and 19–31 veins towards margin; *R. harkinii* has 15–18 veins per cm. near midrib and 24–28 veins near margin and *R. danaeoides* has 7–16 veins per cm. near midrib and 8–20 veins towards margin). In *R. harkinii* about half of the total number of veins are forked, but in *R. fibrosa* only one-fifth are forked as in *R. danaeoides*. The epidermal structure of the three species is also quite distinct. The upper epidermal cells in *R. fibrosa* are rectangular and arranged in rows parallel to the lateral veins. Their anticlinal walls are sinuous and generally unevenly thickened, their thickness is generally 4–7 μ in areas between veins over the lamina and 6–11 μ in the region of the midrib. The upper epidermal cells in *R. danaeoides* and *R. harkinii* are polygonal and irregularly arranged. Their sides are straight. The surface of upper epidermal cells in *R. danaeoides* sometimes shows obscure marks of hollow papillae, but these have not been seen in *R. fibrosa* (or even in *R. harkinii*). The sides of lower epidermal cells in all the three species are sinuous, but the walls in *R. fibrosa* and *R. danaeoides* show many more smaller undulations, while the waves in walls of lower epidermal cells in *R. harkinii* are fewer and larger. The figures depicting the amplitude of sinuosities and the lateral distance between two antinodes in the lower epidermis of the three species are:

	Amplitude of sinuosities		*Lateral distance between two antinodes*	
Name of species	*Range*	*Average*	*Range*	*Average*
R. fibrosa	3–13 μ	7 μ	11–21 μ	15 μ
R. danaeoides	5–16 μ	11 μ	8–24 μ	13 μ
R. harkinii	13–28 μ	19 μ	20–43 μ	31 μ

Surface striations are present almost in every cell of the lower epidermis in *R. harkinii*. In *R. fibrosa* and *R. danaeoides* these are present usually in the lower epidermal cells of the midrib region. In *R. harkinii* the surface papillae are very prominent and generally present in most cells of the lower epidermis, but in *R. fibrosa* and *R. danaeoides* they occur only occasionally in the cells of the lower epidermis of the lamina. The guard cells of stomata in *R. fibrosa* are always exposed and never protected by papillae of surrounding cells as in some stomata of *R. harkinii*. The tracheids in the side veins of *R. fibrosa* show annular and spiral thickenings besides scalariform elements like those described by Pant (1958) in *R. danaeoides* and *R. harkinii*. Some tracheids of the midrib in *R. fibrosa* also show alternate biseriate pits.

R. fibrosa may also be compared with *Glossopteris fibrosa* Pant on account of the occurrence of interstitial fibres. However, it clearly differs from *G. fibrosa* in having side

EXPLANATION OF PLATE 49

Figs. 1–7. *Rhabdotaenia fibrosa* sp. nov. 1, Apex of a leaf. 233; ×1. 2, Xylem element from a lateral vein showing annular thickenings. 234; ×552. 3, Lower epidermis showing an enlarged stoma with polar and lateral lignin lamellae and epidermal cells with sinuous anticlinal walls. 232a; ×447. 4, A portion of lamina showing lateral veins running parallel to each other (thicker lines) and a few interstitial fibres (thinner lines) between them. 232; ×15. 5, Xylem elements from midrib showing alternate biseriate pits on the lower, left side and also scalariform thickenings elsewhere. 231a; ×552. 6, Xylem elements from midrib showing spiral thickenings. 231a; ×1220. 7, Fragment of middle region of a leaf. 229, ×1.

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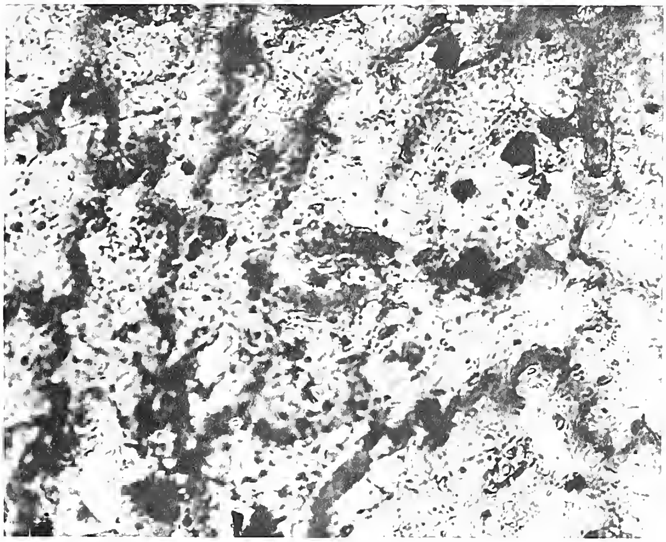

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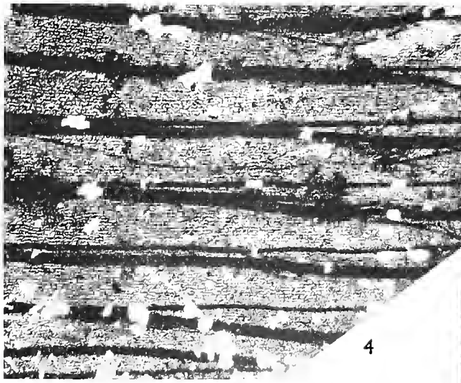

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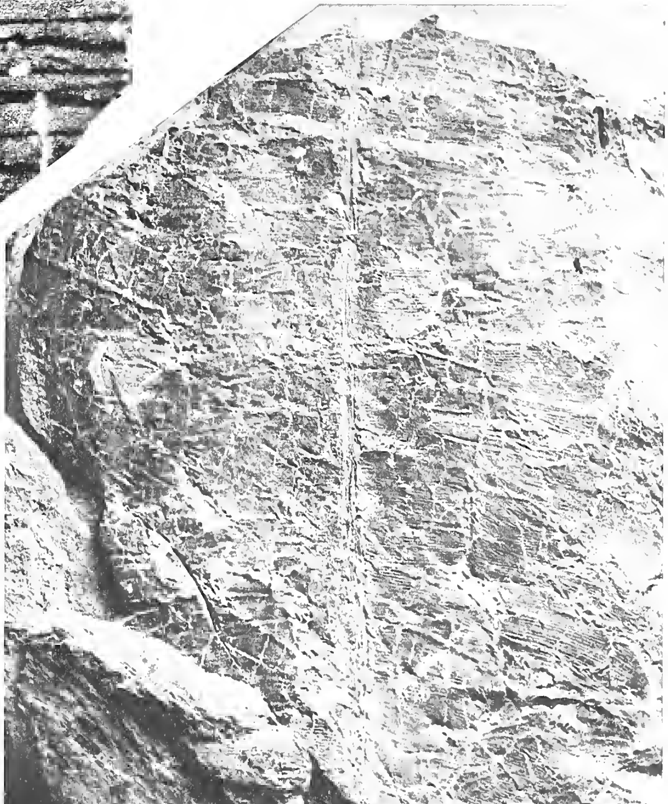

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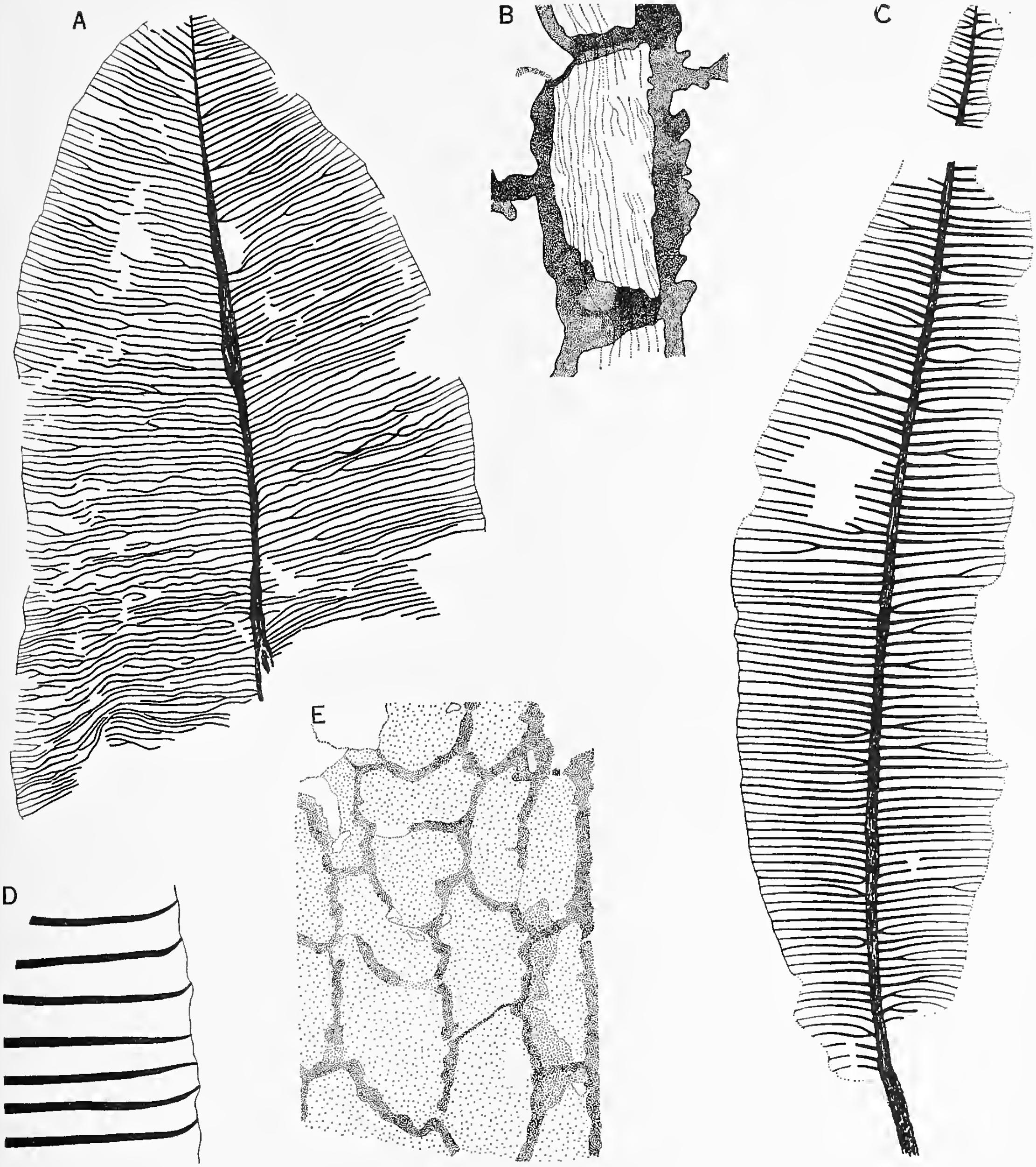
PANT and VERMA, Leaves of *Rhabdotaenia*



TEXT-FIG. 3. *Rhabdotaenia danaeoides.* A, Apical portion of leaf showing arrangement of veins (see also Pl. 50, fig. 1). 240; ×4/3. B, An epidermal cell of midrib showing surface striations. 241e; ×533. C, Middle and basal portions of a leaf showing venation. 245; ×4/3. D, Margin of leaf with veins slightly curved towards the apex. 248d; ×*c*. 5. E, A few cells between the veins in text-fig. 5E, more magnified. 238p; ×267.

veins running at right angles to the midrib and in the absence of anastomoses between them. Moreover, the epidermal structure of the two forms is quite distinct.

Rhabdotaenia danaeoides (Royle) Pant

Plate 50, figs. 1–2; text-figs. 2A, 3–6

Synonymy. See Pant (1958).

Emended diagnosis. Leaves oval, oblong, petiolate, 3–9·4 cm. wide and up to 15·9 cm. long, widest in middle region, apex obtusely pointed, base more or less abruptly contracted, margins entire, sometimes slightly undulate. Midrib up to 6·5 mm. wide below, narrower towards apex, showing numerous longitudinal strands in basal part, fewer above. Lateral veins parallel, arising at an acute angle from midrib and almost immediately arching outwards and running at about 90° to midrib, vein ends near margin often slightly curved towards apex. At an average about one-fifth of lateral veins forked once, forking either at points of origin from midrib or elsewhere in lamina, but mostly in middle region; twice forked veins very rare; other veins remain unforked. Cross connexions between veins present but extremely rare. Concentration of veins 7–16 per cm. near midrib (near points of origin) and 8–20 per cm. towards margin.

Upper epidermis of lamina without stomata. Cells between veins straight-walled, polygonal, sometimes showing obscure marks of papillae. Marginal epidermal cells longitudinally elongated, almost straight-walled, leaf substance at margin showing elongated thick-walled cells.

Lower epidermis of lamina stomatiferous. Cells between veins irregularly shaped, 64·0–132·8 μ (93·3 μ) long and 35·2–92·8 μ (60·8 μ) wide, walls sinuous sometimes showing rounded marks of median hollow papillae, becoming gradually straight near midrib. Cells over veins narrower, elongated in direction of veins, walls almost straight. Stomata usually confined to areas between veins, rarely over veins, somewhat unevenly distributed, frequency about 66 stomata per sq. mm., orientation irregular. Stomata haplocheilic. Guard cells 16–28 μ wide and 32–64 μ long, stomatal opening 1·6–8 μ wide. Stomata exposed or more or less covered by subsidiary cells but never overarched by subsidiary cell papillae. Subsidiary cells 3–5, irregular, not forming a ring, polar subsidiary cells like laterals, size and shape of subsidiary cells similar to ordinary epidermal cells.

Upper and lower epidermis of midrib showing straight-walled cells above veins and slightly sinuous-walled cells between them, cells tending to be arranged in longitudinal rows. Cells of lower epidermis showing fine longitudinal surface striations.

Upper cuticle of lamina showing cells with somewhat obscure outlines, cell walls thin. Lower cuticle of lamina stomatiferous like lower epidermis. Cells between veins with

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EXPLANATION OF PLATE 50

Figs. 1, 2. *Rhabdotaenia danaeoides.* 1, Apical and middle portion of a leaf showing venation. The lighter patches are caused by the removal of carbon in pulls. 240; ×1. 2, Lower epidermis showing an exposed stoma. 245b; ×471.

Figs. 3, 4. *Rhabdotaenia harkinii*; V34454. 3, Lower epidermis showing sinuous-walled cells and irregularly placed protected stomata, ×193. 4, Lower epidermis with papillate epidermal cells and an exposed stoma, ×400.

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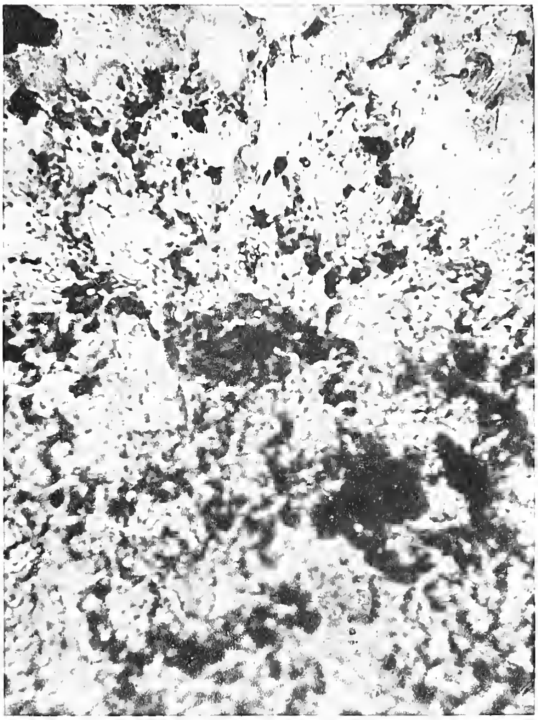

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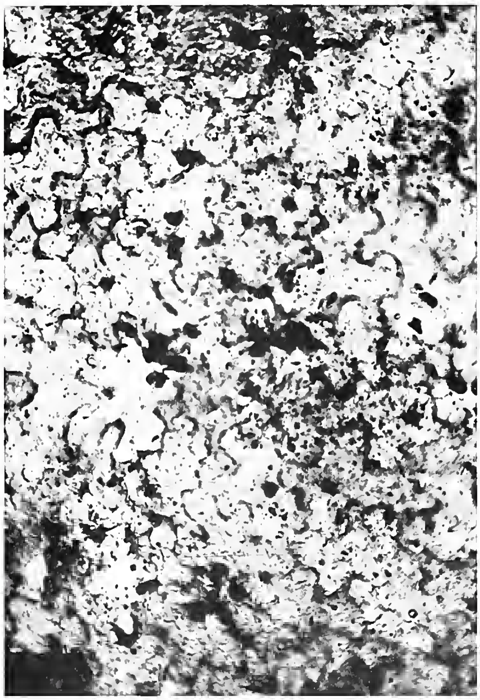

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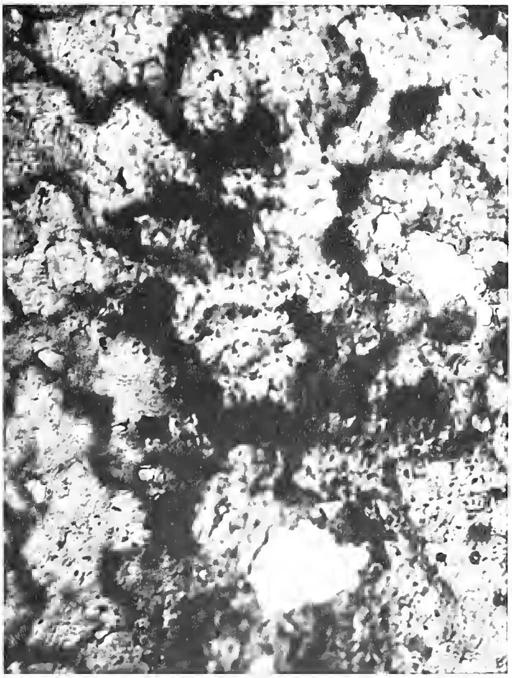

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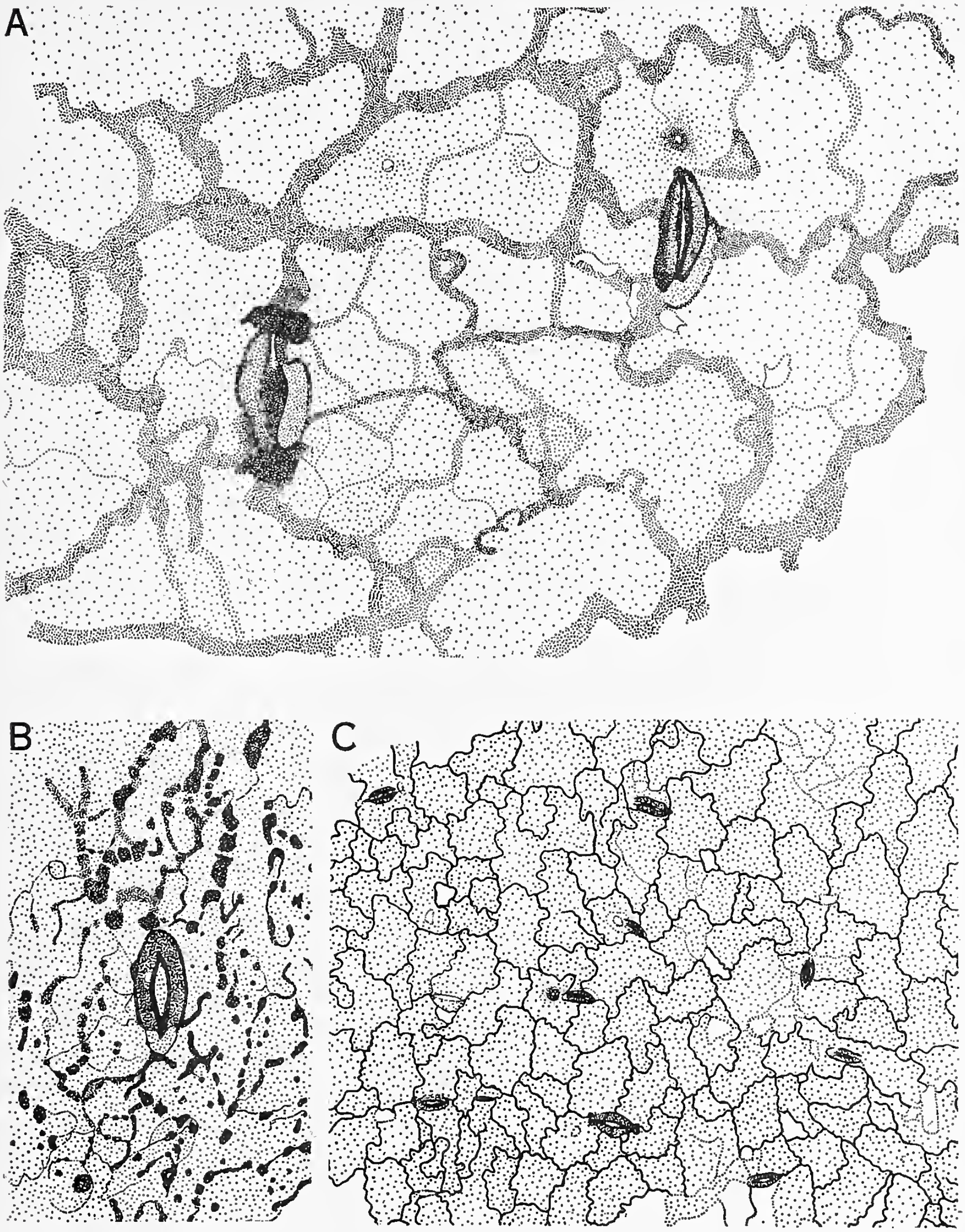
PANT and VERMA, Leaves of *Rhabdotaenia*



TEXT-FIG. 4. *Rhabdotaenia danaeoides.* A, Lower epidermis with two stomata, one (left) showing lignified polar lamellae on the two poles and the other (right) showing a hollow mark of papilla in one of its subsidiary cells. 238a; ×400. B, Lower cuticle showing a stoma and obscure sinuous-walled cells (under phase-contrast microscope). 308n; ×301. C, Lower epidermis showing sinuous-walled cells. The stomata are irregularly placed in between the veins. 238a; ×125.

obscure cell walls usually appearing broken, but sometimes showing sinuous waves; cell walls below veins less obscure, straight.

Neotype. Brit. Mus. (N.H.) Palaeont. Dept. No. V4191. Figured Royle (1833, pl. 2, fig. 9) and Arber (1905, pl. 5, fig. 1).

Isotypes. Specimen Nos. 237–330 deposited in the Divya Darshan Pant Collection, at present located in Botany Department, University of Allahabad.

Locality and horizon, Raniganj coalfield, India, Lower Gondwana.

Description. The emended diagnosis is based on ninety-five leaf fragments from the Raniganj coalfield, India (including five apices, one base, and eighty-nine pieces from the middle region of leaf laminae). Some of the leaves appear to have been quite narrow, about 3 cm., but others were up to 9·4 cm. wide. The midrib was up to 6·5 mm. wide in the basal part. Lateral veins, which run almost straight up to the margin, are sometimes slightly curved upwards towards the apical region (text-fig. 3D). In places the veins appear sinuous (Pl. 50, fig. 1; text-figs. 2A, 3A), but, as already pointed out by Pant (1958), such sinuosities are obviously due to a displacement of the veins inside the epidermal and cuticular coat of the leaf, when its more delicate mesophyll tissue has partially or wholly dissolved.

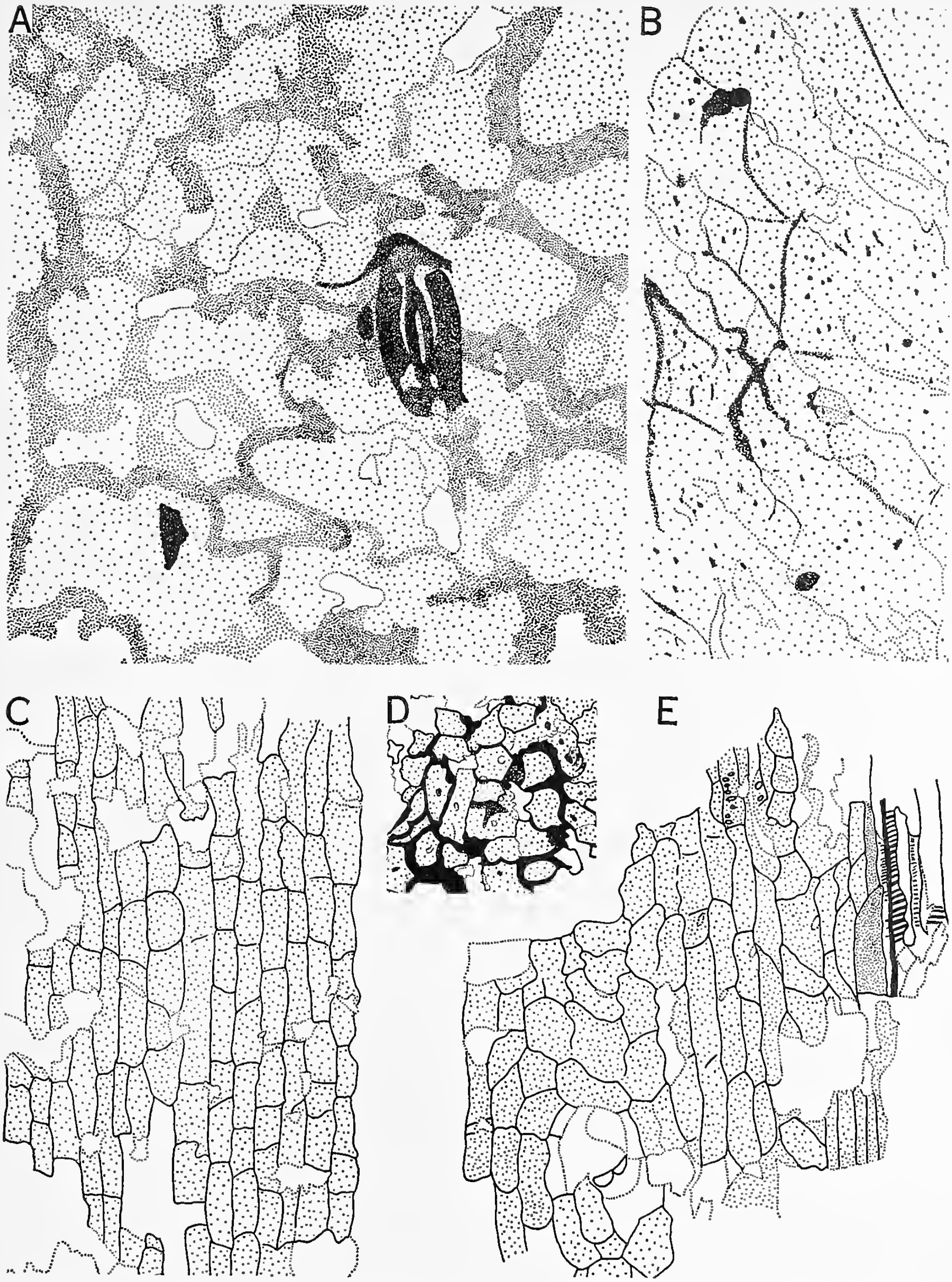
The margins of simple spathulate leaves are seldom torn. In the absence of regular anastomoses between the side veins, like those found in *Glossopteris* and *Gangamopteris*, it was difficult to understand how such large laminae remained intact, but a specimen with a well-preserved margin reveals that this was possibly due to the presence of longitudinal strands of thick-walled cells running parallel to the margin (text-fig. 6B, C). The thick-walled marginal cells appear to be fibrous, but at one point (text-fig. 6C) their walls show pits like those of xylem, suggesting that there could even be some marginal tracheids present among them.

The number of bifurcated veins is usually higher in the middle region. The concentration of veins per cm. is higher in the apical and basal portions (at the point of their origin from the midrib). In different leaf fragments the ratio of once-forked lateral veins and those remaining unforked ranges from one-third to one-fifteenth.

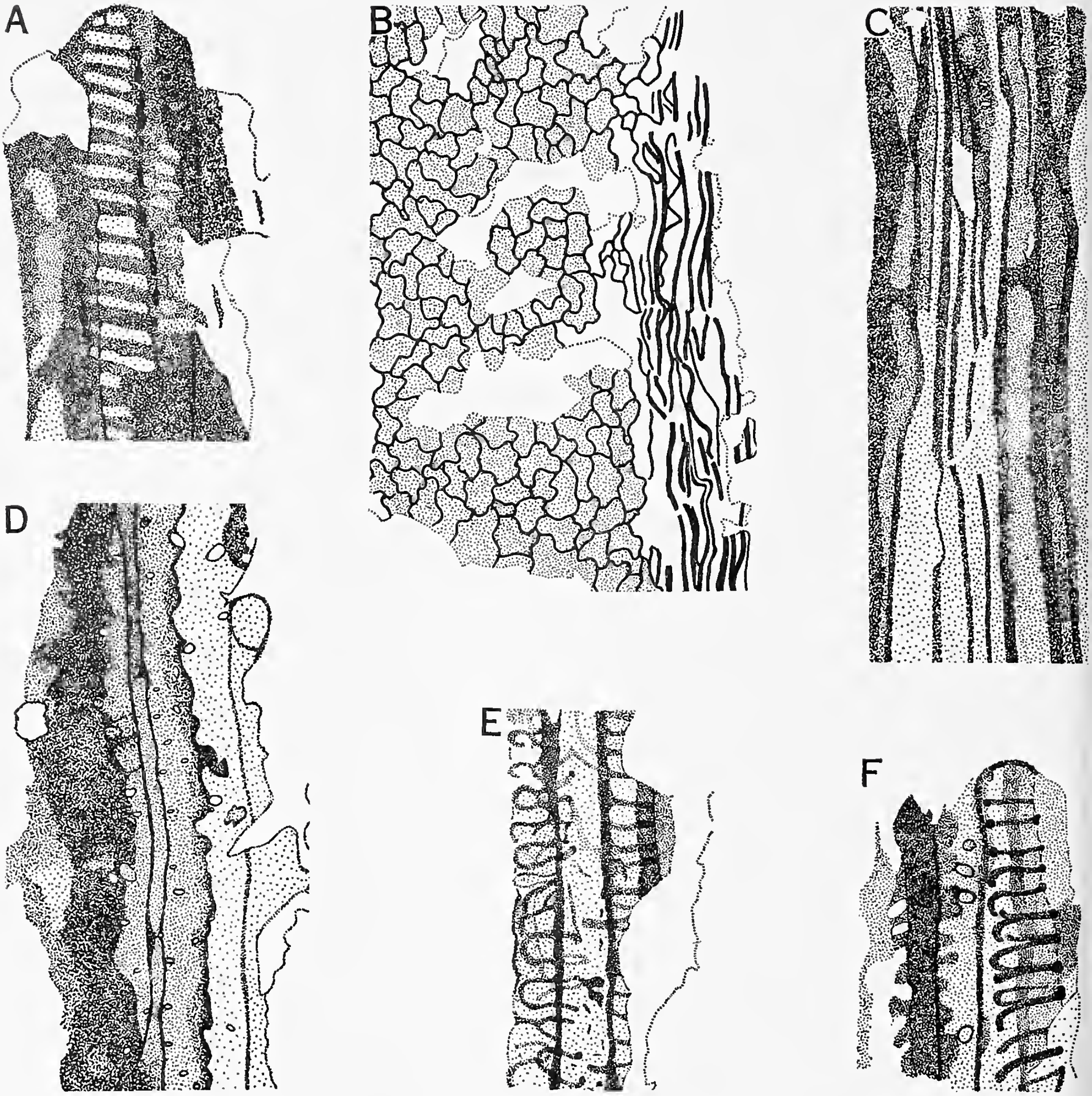
The typical sinuous-walled cells of the lower epidermis are clearly seen in most of the specimens, but fragments of the upper epidermis are seen only in one specimen. The cells of upper epidermis seem to be relatively less sinuous-walled or with almost straight walls like the cells over the meshes of the veins in the midrib (text-fig. 3E).

The lateral veins and midrib show abundant tracheids. Some of them have spiral (text-fig. 6F) and reticulate thickenings (text-fig. 6E), but most of them are scalariform (text-fig. 6A). Along with the typical xylem cells of the veins and the midrib are seen some thick-walled elongated elements with oval or rounded pinhole-like pits. They may represent fibres or tracheids (text-fig. 6D, and also Pant 1958).

Comparison and discussion. Pant (1958) has already discussed the differences between *Rhabdotaenia* and other leaves of *Taeniopteris* type which possess haplocheilic stomata, such as *Doratophyllum* (Harris 1932) and *Bjuvea* (Florin 1933). The Jurassic leaves of *Nipaniophyllum raoi* (Sahni 1948) also have haplocheilic stomata. Like *Rhabdotaenia*, their midribs contain a number of parallel veins. However, they belong to a different age and their size, form, and epidermal structure are clearly different. Moreover, they occur



TEXT-FIG. 5. *Rhabdotaenia danaeoides.* A, Lower epidermis with a single enlarged stoma showing two lateral lignin lamellae. 241a; ×400. B, Upper cuticle showing obscure outlines of cells (under phase-contrast microscope). 308j; ×144. C, Epidermis of midrib showing straight-walled cells arranged in longitudinal rows. 238e; ×125. D, Upper epidermis showing straight-walled cells some of which show median papillae. 238a; ×125. E, Epidermis of midrib showing straight-walled cells, above its parallel veins and slightly sinuous-walled cells between them. All cells tend to be arranged in longitudinal rows. A few cells of the fibrovascular midrib bundles are also seen. Note the simple pits and scalariform thickenings in some of these. 238p; ×125.



TEXT-FIG. 6. *Rhabdotaenia danaeoides.* A, Xylem of midrib showing scalariform elements. 238p; ×800. B, Portion of a lamina showing thick-walled marginal cells arranged parallel to the margin of leaf. 261a; ×125. C, A portion of B, more magnified. 261a; ×400. D, Fibrovascular elements from midrib showing pinhole-like pits. 275; ×800. E, Xylem elements from a vein showing reticulate and scalariform elements. 264; ×800. F, Xylem elements of a vein showing spiral elements. 275; ×800.

associated with their characteristic fructifications, the like of which have never been reported associated with *Rhabdotaenia*. The mode of preservation of the two leaves is not comparable and we therefore assume that they are clearly different. Pant (1958) has also compared *Rhabdotaenia* with other Lower Gondwana leaves, but their cuticular structure is unknown.

The general form and epidermal structure of *Rhabdotaenia* are nevertheless comparable with those of *Glossopteris*, *Gangamopteris*, and *Palaeovittaria*, and it is quite likely that *Rhabdotaenia* too will ultimately prove to belong to a plant of the same general alliance.

Pant (1958) distinguished the two species *Rhabdotaenia danaeoides* and *R. harkinii*, on the basis of concentration of veins per centimetre, the relative frequency of forking veins and certain epidermal characters. The epidermal structure of *R. danaeoides* was, however, described by Pant from very small bits of epidermis, and the range in the concentration of veins and other characters was also unknown in both the species. Our study of ample material of *R. danaeoides* has shown that the concentration of veins in this species is never so high as in *R. harkinii*. *R. danaeoides* has on an average about one-fifth of the lateral veins which fork once and only a single vein in one specimen is twice-forked, but in *R. harkinii* about half of the total number of veins are once-forked and a number of them twice. Among other differences between the two species is the usual occurrence of a median prominent papilla and surface striations in the cells of *R. harkinii*. Striations and surface papillae are present in *R. danaeoides* as well, but in this species papillae occur relatively rarely in the lower epidermal cells and surface striations are usually restricted to the lower epidermal cells of the midrib. The anticlinal walls of the epidermal cells show numerous small waves in *R. danaeoides*. The waves of the walls in *R. harkinii* are fewer and larger. The amplitude of sinuousities in the cell walls of lower epidermal cells and the distance between two antinodes of sinuous-walled cells are also different in both the species (see above). The stomata of *R. harkinii* are usually protected by papillae of the surrounding subsidiary cells (Pl. 50, fig. 3) which may be drawn apart and expose the underlying guard cells (Pl. 50, fig. 4) or they may partially or wholly cover the stoma (Pant 1958, pl. 20, fig. 5). The stomata in *R. danaeoides* are never so well protected. The surface of epidermal cells in *R. harkinii* shows well-marked lighter oval or rounded areas which may be surface pits like those present in the Cycadales (Pant and Nautiyal 1963). In *R. danaeoides* such areas are seemingly present but less marked.

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A PALAEOCENE TEREDINID (MOLLUSCA) FROM IRAQ

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ABSTRACT. The teredinid mollusc *Bankia* (*Bankiella*) *kurdistanensis* sp. nov. is described from an association of tubes, valves, and pallets in the Palaeocene of Iraq.

WOOD bored by *Teredo* and allied genera is a common Tertiary fossil at various levels and localities, as in the London Clay of England. Current zoological classification of these highly modified molluscs is based neither on the valves nor on the conspicuous tubular shell-lined borings, but on the morphology of the little calcareous structures known as pallets, which in life are associated with the fleshy siphons. Such pallets are not commonly recorded as fossils. Although the Iraqi material described below was in solid preservation not permitting the isolation of pallets, numerous thin-sections show these and other structures excellently preserved.

The specimens, of petrified dicotyledonous wood showing well-preserved structure and riddled with calcite-filled teredinid burrows, were collected from the Kolosh Formation (van Bellen 1959). This is composed of sands and sandstones of detrital serpentine, chert, and radiolarite, with subordinate shales and limestones, and outcrops extensively in northern Iraq. It has yielded foraminiferal faunas and an algal microflora of Palaeocene–Lower Eocene age, as well as some molluscs and other macrofossils. The present material comes from three separate localities, but all the pallets seen in sections are of one distinctive type, suggesting that one species only is present.

In a revision and classification of the Teredinidae, Bartsch (1922) subdivided the genus *Bankia* Gray 1842, which comprises those forms whose pallets show cone-in-cone structure. Such pallets consist of a proximal rod-like portion or stem, from which a series of laterally flattened cones, opening distally, arise one within the other, together forming a blade-like structure. In the subgenus *Nausitora* the cones are fused on one flattened side and backed by a calcareous deposit ('thick periostracum' of Bartsch). In the three subgenera *Bankia* s.s., *Bankiella*, and *Neobankia* the cones are free and covered by a thin investing membrane; distally this membrane is fimbriated in *Bankia* s.s., entire in *Bankiella*, and denticulated in *Neobankia*.

Nausitora-pallets showing calcareous fusion might be expected to occur as fossils and have in fact been recorded from the Lower Eocene London Clay (Wrigley 1930). The Iraqi fossils now discussed show pallets with free cone-in-cone structure and entire margins. It would at first sight seem doubtful that the membrane permitting subgeneric differentiation would be preserved, and hence that *Bankia* s.l. would be the best allocation that could be made. However, Stinton (1957) described denticulated-margin pallets recognizable as *Neobankia* from the Upper Eocene Barton Clay. This preservation is probably inferior in fine detail to that of the material now examined. It seems likely, therefore, that the entire margins seen are original, and for this reason the fossil is referred to *Bankiella*.

[Palaeontology, Vol. 6, Part 2, 1963, pp. 315–17, pl. 51–52.]

Genus BANKIA Gray 1842
Subgenus *Bankiella* Bartsch 1921
Bankia (*Bankiella*) *kurdistanensis* sp. nov.

Plates 51, 52

Diagnosis. *Bankia* with pallets of 4·3 mm. length or more, maximum diameter about 2·5 mm., of flattened cone-in-cone type, about fifteen cones with distal margins entire, free stem presumed relatively short. Valves incompletely known; tubes typically variable in length and diameter, incipiently septate in large examples.

Holotype. BM LL30332 (Pl. 51, fig. 1), Kolosh Formation (Palaeocene), Dohuk, Mosul Liwa, northern Iraq. *Paratypes*. BM LL30333–5 incl. (Pl. 51, figs. 2, 3; and Pl. 52, figs. 1, 2), Kolosh Formation (Palaeocene), Dohuk, Mosul Liwa, and Koi Sanjak, Erbil Liwa, northern Iraq.

Other material. Specimens from the Kolosh Formation (Palaeocene), of Shaqlawah and Koi Sanjak, Erbil Liwa, and Dohuk, Mosul Liwa, northern Iraq.

Description. (*a*) *Tubes*. The calcite- or matrix-filled shelly tubes show great variety both in size and degree of crowding. In diameter they vary from 1·5 to 12·0 mm. The larger examples may have reached a length of 20 cm. or more, though this cannot be proved from the pieces of bored wood collected. These specimens show all the usual varieties of wood penetrated by straight parallel tubes, small, crowded, and twisted tubes, &c. Some larger tubes show a regular, narrowly annular internal septation (Pl. 52, fig. 2); in an example of 5 mm. tube-diameter the septa are 2 mm. apart. This feature is developed in individuals of some Recent teredinid species. In one fossil tube the section shows two smaller, conjoined but complete tubes, associated with matrix. This is presumably the broken apertural end, out of position: such a constricted double apertural siphonal tube has been described from the London Clay by Sowerby (1815), Davis (1936), and Wrigley (1940); the last, by analogy with Recent species, did not regard it as of specific value. Only two examples have been seen in the Iraqi material (BM LL30331).

(*b*) *Valves*. The valves are known only from cross-sections of two paired examples (Pl. 51, fig. 2; Pl. 52, fig. 1). Presumably they were of the specialized pattern common to the family (Bartsch 1922, Stinton 1957), functioning as excavating tools. The distinctive

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EXPLANATION OF PLATE 51

Bankia (*Bankiella*) *kurdistanensis* sp. nov., thin-sections, ×15. Kolosh Formation, Palaeocene; Dohuk, Mosul Liwa (fig. 1); and Koi Sanjak, Erbil Liwa, northern Iraq (figs. 2, 3).

Fig. 1. Vertical section of pallet (in two pieces) at right angles to maximum width of the pallet blade. In calcite-filled burrow, in dicotyledonous wood. Holotype, BM LL30332.

Fig. 2. Oblique section through blade of pallet, showing stem, cones, and concave pallet-face; also the two valves. Post-mortem association in burrow. Paratype, BM LL30334.

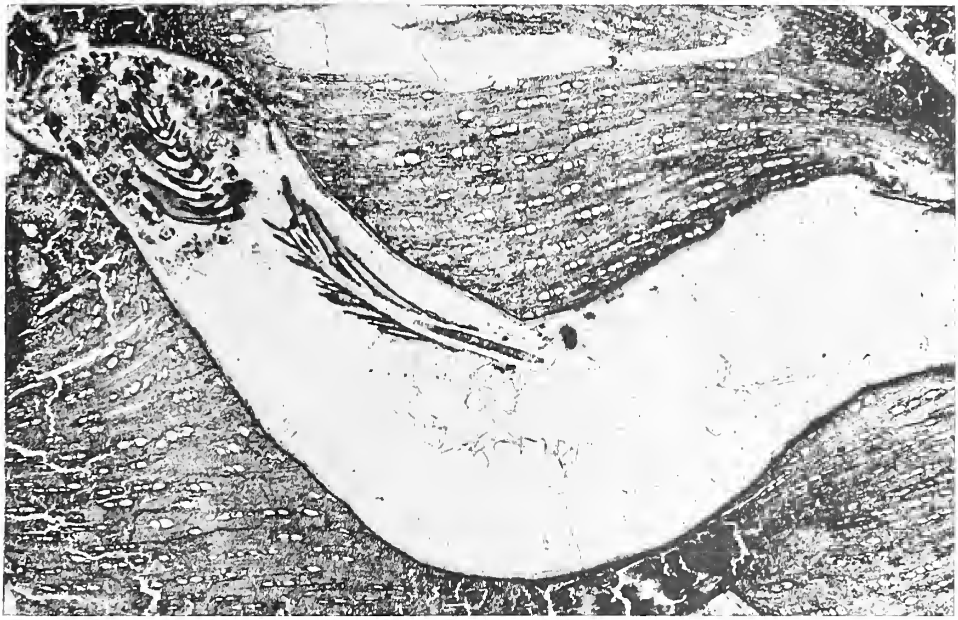
Fig. 3. Oblique and transverse sections of two adjacent pallets in burrow. Not in position held during life. Paratype, BM LL30334.

EXPLANATION OF PLATE 52

Bankia (*Bankiella*) *kurdistanensis* sp. nov., thin-sections, ×15. Kolosh Formation, Palaeocene; Dohuk, Mosul (fig. 1); and Koi Sanjak, Erbil Liwa, northern Iraq (fig. 2).

Fig. 1. Approximately vertical section of two associated valves, one showing well the external ridges used for mechanical excavation. In burrow, in wood. Paratype, BM LL30333.

Fig. 2. Portion of longitudinal section of large burrow, showing spaced annular septa on inside of shelly lining to burrow (conspicuous calcite parting on one side). Paratype, BM LL30335.



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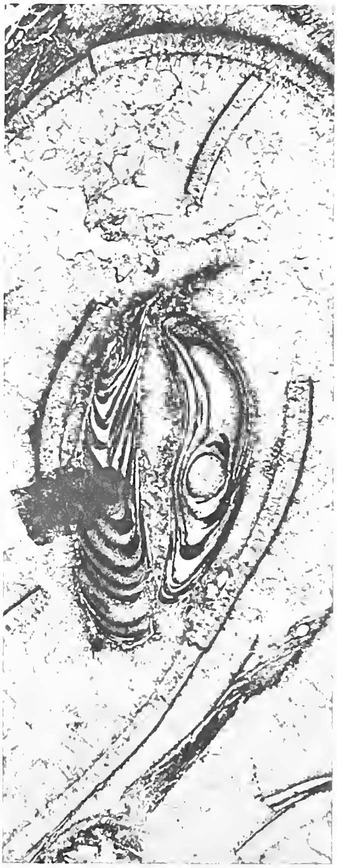

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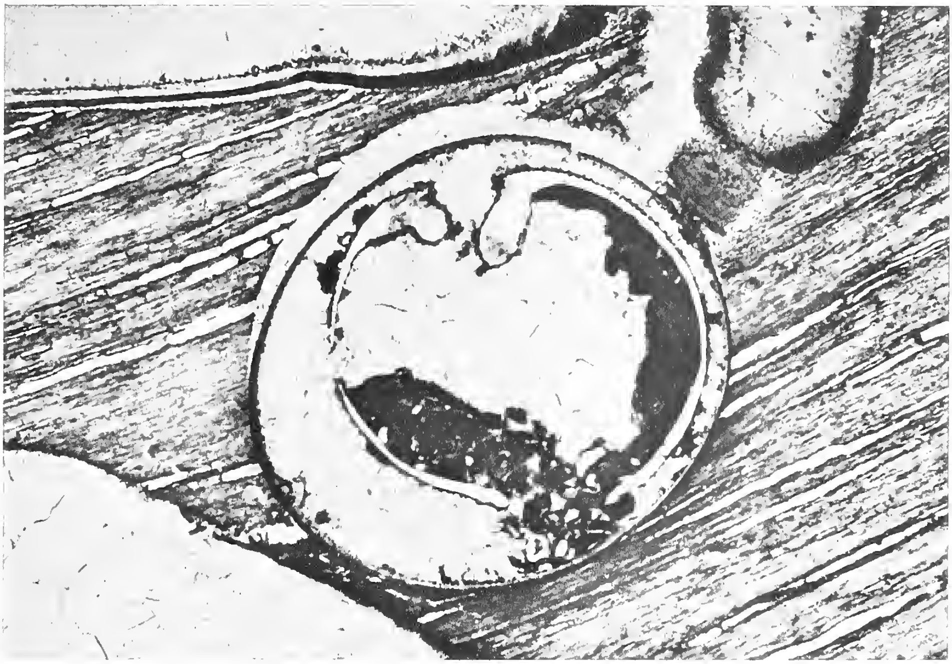
ELLIOTT, Palaeocene teredinid



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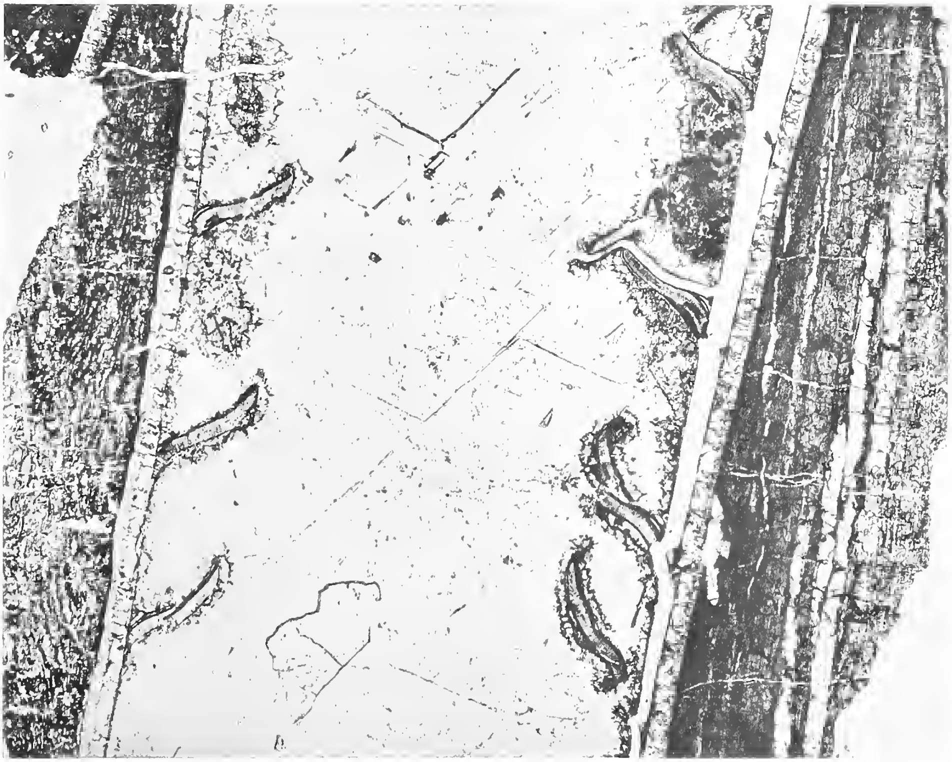

2

ELLIOTT, Palaeocene teredinid

fine concentric ridges ('dental ridges' of part of the outer valve surface) are seen in Plate 52, fig. 1.

(*c*) *Pallets.* Thin-sections reveal numerous pallets, single or paired, occurring usually at the inner, closed end of the burrows. This is not the position in life, when the pallets are adjacent to the siphons at the mouth of the burrow, but presumably most such fossil pallets did in fact belong to the individual inhabiting the burrow in which they now occur. In each of four random cuts the count of component cones is about fifteen; these structures are seen to be closely set, laterally flattened, with one face convex and the other slightly concave with median convexity over the stem. The only possible trace of accessory detail on the oblique cuts through the margins, which were entire, is seen at the lateral margins, which may have been produced into spines as in Recent species. The length of the free stem, proximal to the cones or blade of the pallet, is not known, but as it is infrequently seen in random cuts of different burrows, as compared with the blades, it is suggested that it was relatively short. There is great variation in the lengths of free stem to blade in the pallets of different Recent teredinid species.

A Recent *Bankiella* species with pallets of about the same size is *Bankia* (*Bankiella*) *edmondsi* (Balakrishnan Nair 1956), from the Madras coast, India. This agrees in the close-set cones (eleven in the type specimen) with entire margins except for lateral spines, but possesses a proportionally longer stem and a narrower blade.

Pallets of *Nausitora*, *Neobankia*, and *Bankia* s.l. are all known from the English Eocene, as well as those of *Teredo* (*Psiloteredo*) and remains of the pallet-less *Teredina* (Wrigley 1930, Stinton 1957; see also Davis 1936, Moll 1942), so the present occurrence of *Bankiella* in the Iraqi Palaeocene is in keeping with an early Tertiary differentiation of the group.

Specimens in the collections of the Department of Palaeontology, British Museum (Natural History), which are referred to in the text have the prefix BM.

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THE RECOGNITION OF SALINITY-CONTROLLED MOLLUSC ASSEMBLAGES IN THE GREAT ESTUARINE SERIES (MIDDLE JURASSIC) OF THE INNER HEBRIDES

by J. D. HUDSON

ABSTRACT. The Great Estuarine Series was deposited in large, shallow lagoons. Its abundant molluscan faunas are restricted to very few genera and species, several of which are similar to modern fresh- and brackish-water forms. Consideration of the nature and history of the brackish-water fauna, together with direct comparison with the modern brackish-water environments of the Texas coast, results in an interpretation of the faunas as being controlled very largely by salinity variations in time. The salinities ranged from freshwater to fully marine, but were usually intermediate.

THE purpose of this paper is to show that the molluscan faunas of the Great Estuarine Series lived in brackish waters in a lagoonal environment, and that it is possible to recognize a series of overlapping faunal assemblages whose composition and distribution were controlled largely by salinity variations in time. The detailed evidence on which this thesis is based, the stratigraphical distribution of the faunas, and the ecology of the fossils concerned, is described in a second paper (this journal, p. 327).

THE GREAT ESTUARINE SERIES

The stratigraphy of the Great Estuarine Series (Upper Bajocian–Bathonian) has been described elsewhere (Hudson 1962); the Staffin Bay Beds (Upper Bathonian?–Lower Callovian) of Trotternish are not now included in the Great Estuarine Series. The 'Series' has long been recognized as of unusual facies, 'estuarine' in the wide sense of nineteenth-century geologists (Judd 1873, 1878), since it bears unmistakable signs of deposition in very shallow water, and has a fauna which is impoverished in numbers of species but very abundant in numbers of individuals.

Depositional environment. The conditions of deposition of the Great Estuarine Series naturally varied from one formation to another, but some generalizations can be made. The characteristic feature of all the shale and limestone formations is that lithologies and faunas may vary very rapidly from bed to bed up the succession, but are laterally persistent; some beds can be traced for several miles. There is abundant evidence of very shallow-water conditions throughout, with frequent mudcracked surfaces, but the area never became a land surface. These features, together with the brackish-water nature of the fauna, are best explained if deposition was in extensive shallow lagoons, probably partially separated by a bar from the open sea. The sandy formations represent the subaqueous portions of deltas built into these lagoons, which persisted throughout the deposition of the 'Series'. Such lagoons are very favourable to the establishment of more or less stable brackish-water conditions; the best modern examples—the bays of the Texas coast—are discussed below.

[Palaeontology, Vol. 6, Part 2, 1963, pp. 318–26.]

Nature of the fossil assemblages. Most of the fossils of the Great Estuarine Series are not in position of life. They occur as accumulations of dead shells, probably winnowed by wave action, with the valves of lamellibranchs disarticulated. However, the shell beds are enclosed in fine-grained shales, and there is seldom any evidence of strong currents or of long distance derivation. So that, although the shell beds are death assemblages, they are indigenous death assemblages in the sense of Hallam (1960), and represent the general environment in which they are found, though small-scale patchiness of distribution may have become blurred. The uniformity of composition of many of the shell beds, especially some of the more obviously drifted ones, supports this interpretation; and adjacent shell beds, separated by only a few inches of shale, may have different compositions. There is much less need to invoke faunal mixing to explain assemblages than might be expected.

SOME ASPECTS OF BRACKISH WATER FAUNAS

The chemical and biological classification of brackish waters has been reviewed by Hiltermann (1949); and Table 1 is slightly modified from his paper. The biological classification is based mainly on the work of Remane at Kiel (see below); it assumes, of course, reasonable constancy of other environmental conditions. When used of conditions (e.g. brackish lagoon), the word 'brackish' usually implies a fairly stable intermediate salinity, contrasted with the tidally fluctuating salinity of an estuary, but never as stable as that of the sea. The following discussion on modern brackish-water faunas is based mainly on review articles on the fauna in general (Gunter 1947, Hiltermann 1949, Schmidt 1951, Pearse and Gunter 1957, Hedgpeth 1957) and on special areas (Segerstråle 1957, Sorgenfrei 1958 on the Baltic, Ladd *et al.* 1957, Parker 1959, Shepard *et al.* 1960 on Texas coast bays).

TABLE 1. *Classification of brackish water. Mainly after Hiltermann (1949)*

Biological classification (mainly after Remane)	*Descriptive term*	*Total salinity (parts per thousand)*
Freshwater	Freshwater	0–0·5
Freshwater province with reduced number of species	Oligohaline brackish water	0·5–3
Brackish freshwater	Miohaline brackish water	3–5
Typical brackish water	Mesohaline brackish water	5–9
Brackish-marine	Pliohaline brackish water	9–16·5
Marine province with reduced number of species	Brachyhaline sea water	16·5–30
Marine	Sea water	30–40
(Not considered by Remane)	Hypersaline water	greater than 40

The most obvious and well-known characteristic of brackish-water faunas, whether stable-brackish or estuarine, is their paucity in numbers of species, contrasted frequently with great abundance of individuals. Temperature effects, oxygen deficiency, and extreme exposure to waves can cause a similar restriction, but can frequently be eliminated as an important cause by regional studies (Sorgenfrei 1958). The explanation of this effect is that, while brackish waters are often rich feeding grounds, few animals are able to use them because of physiological difficulties, mainly of osmoregulation, so that those few which have overcome the difficulties multiply greatly.

Two other points from the literature are relevant:

1. Even at quite low salinities the brackish-water fauna is predominantly reduced-marine; hence the minimum number of species is found, not midway between marine salinity and freshwater, but at a salinity of around 5–9‰. This was first established by Remane at Kiel, and the general result seems to be accepted (Hedgpeth 1957, pp. 702–3).

2. The brackish-water fauna is recruited from a small part only of the marine fauna. Whole phyla or other major taxa are stenohaline (corals, echinoderms, cephalopods, articulate brachiopods). Even among the molluscs and the crustaceans, which are the most important groups in brackish waters today, only a few relatively small groups produce brackish-water forms in any numbers.

Rapid fluctuations in salinity are more deadly to marine animals than slow ones; hence, for a given gradient of average salinities, estuaries will show a sharper faunal reduction than stable brackish waters. Stable brackish waters are also more liable to invasion, at low salinities, by freshwater forms (e.g. *Unio* at salinities of up to 3–4‰ in the Baltic area). Many animals of brackish lagoons also live in near-by hypersaline ones. 'This suggests that once an organism is capable of adjusting itself to salinity changes its range of tolerance may exceed the usual changes in its immediate environment, so that salinity is not the governing factor and the organism is able to meet unusual conditions, and colonise extreme environments' (Pearse and Gunter 1957, p. 147).

This may also help to explain the second observation, that the brackish-water fauna comes from only a few invertebrate taxa. Few organisms seem actually to require the fluctuating conditions always associated with low salinity, but once an organism can withstand them it has a permanent advantage in an evolutionary sense (Hedgpeth 1957, p. 695). Since brackish-water animals can by definition withstand large short-period oscillations, usually of temperature and depth as well as of salinity, they are better equipped to withstand small secular changes than animals adapted to a narrower range of conditions. These less-adaptable animals must either evolve distinct features to encounter the changed environment, or become extinct. Therefore estuarine (and brackish-water) species are often conservative forms with a long history (Hedgpeth 1957, p. 696). Hedgpeth quotes the oysters as a typical case, and concludes that 'euryhalinity runs in families'.

Hutchinson (1960) makes the further point that freshwater faunas, too, are very long-ranging. He estimates that only 20–30 separate invasions from the sea are required to account for all the flourishing molluscan faunas of modern lakes and rivers. Their inability to re-enter any but the most dilute of brackish waters makes these freshwater forms extremely valuable environmental indicators.

The recognition of fossil brackish-water faunas. An admirable review of this problem has been given by Schmidt (1951). This has the encouraging result of reaffirming most of the traditional criteria for brackish water; Schmidt concludes that the following four criteria should be diagnostic of fossil brackish-water faunas, and hence deposits.

1. Paucity of species, often forming monotypic shell beds.
2. Absence of stenohaline groups.
3. Presence of euryhaline animals, including special brackish-water forms, notably lamellibranchs (and also some gastropods) among the macrofauna, and, among the hard-shelled microfauna, particularly ostracods.

4. Association of marine and freshwater (not hypersaline) deposits. This means considering the palaeogeography, e.g. hypersaline deposits should be associated with evaporites, true brackish deposits with deltaic sands and drifted plant remains.

Among general conditions mentioned by Schmidt as favourable for the production of brackish-water areas are a wet climate in the source area, leading to high run-off; and in the depositional area, leading to small evaporation. The absence of strong sea currents near the river mouths is favourable; hence lagoons and restricted gulfs are often brackish. If brackish water is deduced from other considerations, those conditions are correspondingly indicated, a fact which is obviously useful in palaeogeography. Schmidt gives a review of brackish-water faunas and sediments in the stratigraphical column, and remarks that their recognition back, as he claims, to the Lower Palaeozoic suggests that the salt sea is very ancient. As a result of their review, Pearse and Gunter (1957, pp. 131–3) also conclude that the salinity of the open ocean has been fairly constant. For the following discussion, which is mainly concerned with relative salinity, it will therefore be assumed that the Jurassic ocean, like the modern one, had a salinity of 35‰.

THE GREAT ESTUARINE SERIES AS A BRACKISH-WATER DEPOSIT

The Great Estuarine Series, taken as a whole, admirably fits Schmidt's criteria for a brackish-water deposit.

1. The total number of macro-invertebrate species recorded is less than 50, compared with over 200 species each of gastropods and lamellibranchs as well as numerous brachiopods, echinoderms, &c., from the English Great Oolite (Cox and Arkell 1948–50). This result is too extreme to be explained entirely by deficient collecting. Monotypic shell beds are extremely characteristic.

2. A few feet of strata in the Lower Ostrea Beds are responsible for nearly all records of stenohaline forms from the Series—one echinoid plate and spine, one polyzoan, one species of articulate brachiopod, a few records of foraminifera. Corals and cephalopods are completely unknown.

3. Lamellibranchs, less often gastropods, ostracods, and *Euestheria* (*Estheria* auct.), or some combination of these groups, dominate the fauna at all horizons. They include several well-known brackish-water forms.

4. Marine beds occur above and below the Series; one or two freshwater beds occur within it. Drifted plant remains are common in the sandstones. Evaporites are absent throughout the British Middle Jurassic, and plant remains and deltaic deposits are common.

The conclusion that the Great Estuarine Series is a brackish-water deposit is not new; Hugh Miller (1858, especially p. 55) has a very well-argued passage on the subject. It has been deduced without subdividing the Series, and without considering the fauna except in the most general terms of phyla and classes.

The appropriate taxonomic level at which to discuss the fauna in more detail is that of rather broad genera. It is immediately striking that, of the small total number of genera in the Great Estuarine Series, several are still living in brackish or fresh waters; they are plausibly regarded as members of those conservative euryhaline or freshwater groups discussed above. *Liostrea* (*Ostrea* s.l.), *Mytilus*, *Unio*, *Viviparus*, and *Euestheria* are the best known. Not only do all these occur in the same group of rocks, which in itself strengthens the 'conservative' hypothesis, but when separate formations are considered, and still more when the rocks are examined bed by bed, it is found that they do not occur indiscriminately mixed. *Liostrea hebridica* and *Mytilus strathairdensis*, which are members of marine-euryhaline genera, both occur most typically in monotypic shell beds, recalling modern oyster and mussel beds. *Liostrea* also occurs in the marine horizon mentioned above, with genera usually regarded as fully marine (*Rhynchonella*, *Myopholas*, *Anisocardia*) in assemblages very similar to those of the fully marine Great Oolite. *Unio* and *Viviparus*, on the other hand, which are freshwater at the present day, do not occur with the marine genera, nor with *Liostrea* or *Mytilus*, but they do occur together. Their other main associate is the extinct lamellibranch *Neomiodon*, which forms with *Unio* and *Viviparus* the well-known Hastings Beds assemblage of the Wealden, which has always been regarded as freshwater. *Neomiodon*, however, also occurs with the more marine genera mentioned above. It seems to have been euryhaline, though as usual with such forms it is most abundant numerically in low-salinity assemblages, often forming monotypic shell beds. A frequent associate of *Neomiodon* and *Viviparus* is *Euestheria*, which inhabits fresh or rarely brackish water today. Ostracods are also most abundant in the beds with *Euestheria* and *Neomiodon*.

It is therefore possible to divide the Great Estuarine Series assemblages at least into more and less saline, as briefly indicated by Anderson (1948) and others, and perhaps to arrange them in a salinity series. On the whole the Estheria Shales, the Concretionary Sandstone Series, and the Ostracod Limestones have a low-salinity fauna, and the Lower Ostrea Beds and the Staffin Bay Beds (= Upper Ostrea Beds and Belemnite Sands, of Anderson and Cox 1948) a high-salinity one. The Mytilus Shales, and parts of the Estheria Shales and Lower Ostrea Beds, show rapid alternations within a few feet (or sometimes a few inches) from one type of fauna to the other, within a fairly constant gross lithology. These reversed and repeated changes rule out evolution or long-range immigration as explanations of the faunal changes, and render large changes of depth most improbable. Salinity changes seem much the most reasonable explanation. Salinity-controlled assemblages of similar type are known in the Baltic and in the Texas Bays, where conditions more closely approach those envisaged for the Great Estuarine Series.

THE TEXAS COAST BAYS AND THEIR MOLLUSCAN FAUNA

These bays have been intensively studied in the last few years, and the results have now been collected and summarized in Shepard *et al.* (1960). The earlier reports most relevant to the present topic are by Ladd *et al.* (1957) and Parker (1959). The situation is intermediate between that in large masses of stable brackish water, such as the Baltic, and that in a typical estuary.

The bays form a complex series of estuaries and lagoons behind a string of sandy barrier islands, through which are narrow connexions to the Gulf of Mexico. The climate in the area varies from humid in the north-east, near the Mississippi delta, to semi-arid in the south-west. The whole system is extremely shallow, less than 9 ft., but the bays rarely dry up. Tides are negligible. The total salinity variation is large, from virtually fresh to hypersaline, but in any one part of the system may be constant for several years. A typical pattern is a slow build-up to high salinities in a spell of dry years, leading to an invasion of marine forms, followed by sudden freshwater floods. These have been recorded as reducing salinities from 40‰ to 2–4‰ in a few weeks, causing mass-mortalities of the marine forms. The sediment is mainly mud, stratified in the bay heads where the fauna is sparse, structureless in the lower bays. The sediment of the barrier islands and passes is more sandy and contains echinoid remains.

The distribution of both micro- and macrofaunas is controlled very largely by salinity, or at least parallels the salinity contours. Minor variations due to the nature of the bottom, &c., are superimposed on this salinity-controlled pattern. The fauna of the waters of very low salinity is very poor in numbers of species, and the change from this to the 'mid-estuarine' fauna inhabiting waters of about half the salinity of sea water is much sharper than the change from the mid-estuarine to the marine fauna. This accords with Remane's observations in the very different environment of the Baltic.

The macro-invertebrate assemblages (especially of the molluscs), as described by Parker (1959), are of great interest. The bay-head facies, with strong influence from rivers and salinity at normal times less than 6‰, has a very sparse fauna with only five macro-invertebrate species. In this environment ostracods dominate foraminifera (Ladd *et al.* 1957).

In enclosed bays of low to variable salinity (12–25‰) the characteristic feature is the occurrence of 'reefs' of *Crassostrea virginica*, the American estuarine oyster. The only other common lamellibranch on the reefs is the Mytilid *Brachidontes*. This association strongly recalls the *Liostrea hebridica–Modiolus* association which occurs both in the Hebrides and in the Upper Estuarine Series of the Midlands. *L. hebridica* is thought to be related to the modern *Crassostrea*. On the muddy bottoms between the reefs there are seven macro-invertebrates, including especially the small triangular lamellibranch *Mulinia lateralis*. This occurs in all environments, including some hypersaline ones and the open Gulf coast, but is most common in low salinities. Its behaviour is considered a good analogy for that of *Neomiodon*, which it somewhat resembles in morphology. In times of stable high salinities (> 25‰) these bays are invaded by the fauna normally characteristic of the more open bays nearer the inlets. This has far more species (34 according to Parker 1959), most of which also inhabit the open Gulf. Lamellibranchs and gastropods are still dominant. The assemblage at the algal bed horizon of the Lower Ostrea Beds is thought to be of this kind—a somewhat restricted selection of shallow water, open-sea forms typical of the Great Oolite limestones.

In his conclusion Parker reaffirms the classical account of the response of animals to adverse salinities, high or low. In unusual salinities there are few species, but many individuals. 'As salinity decreases or increases to normal values (along with relative stability), the number of species increases and the number of individuals per species decreases' (Parker 1959, p. 2158).

SALINITY-CONTROLLED ASSEMBLAGES IN THE GREAT ESTUARINE SERIES

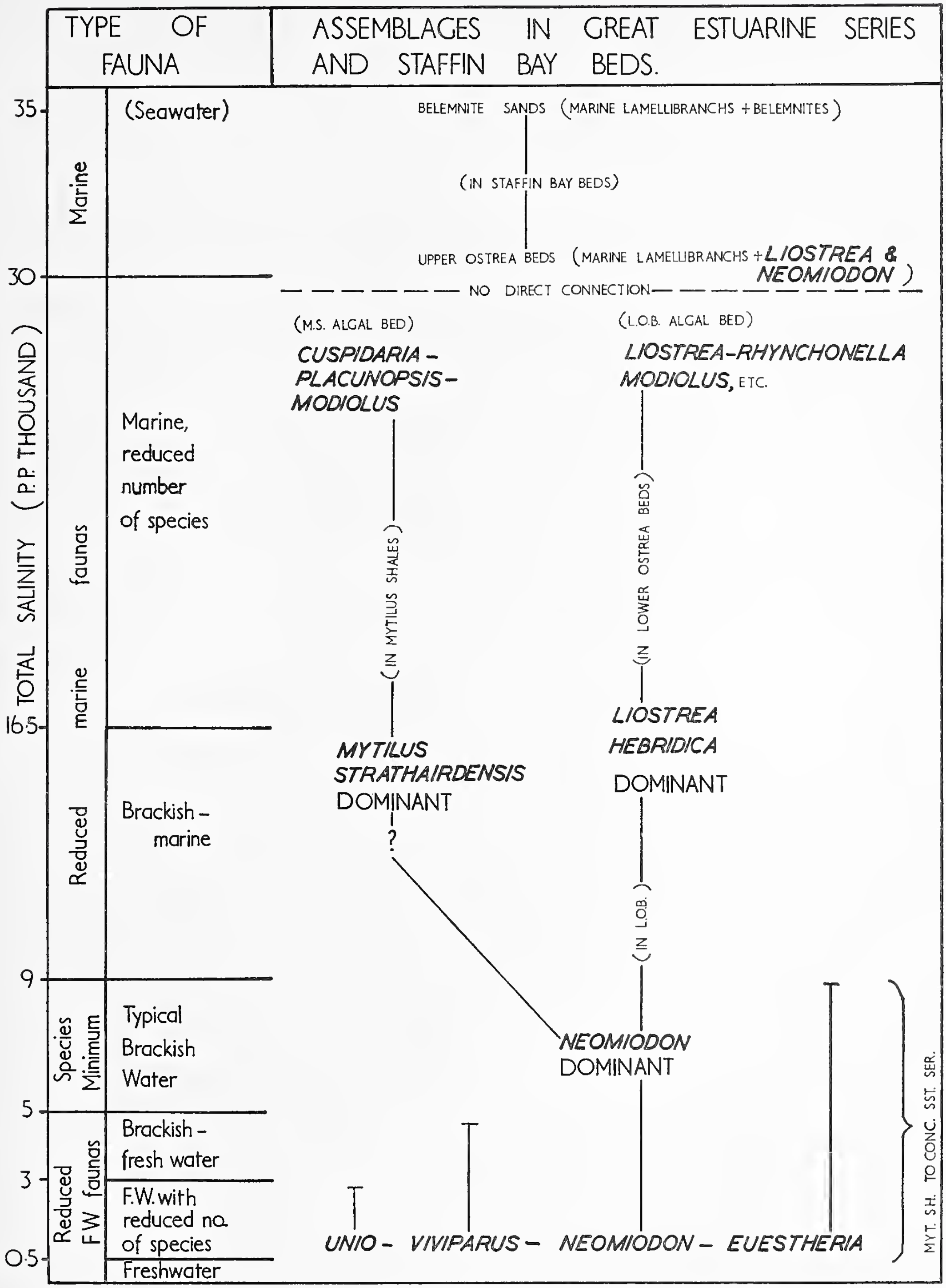
Rather a striking analogy can be drawn between the well-documented macro-faunal assemblages of the Texas Bays and those of the Great Estuarine Series. If such a system of bays and estuaries had existed in the Jurassic—and there is evidence independent of the fauna to show that it did in the Great Estuarine Series—it is reasonable to suppose that it would have been inhabited by assemblages of animals adapted to different salinity conditions, as in Texas today. I have argued that the general response of the fauna to salinity changes (relative numbers of species and individuals) should be similar, and that the estuarine genera concerned are likely to have been conservative ones. These are the general predictions, and direct comparison as outlined above shows that they are fulfilled.

Assuming actual mean salinity values for the habitats of the Jurassic assemblages having the best analogies with Recent ones, and using 'overlapping' of faunas for the others, I have constructed a 'salinity series' or spectrum for the Great Estuarine Series and Staffin Bay Beds (text-fig. 1). The principal values assumed are: *Unio–Viviparus–Neomiodon* = fresh water or less than 3‰; *Neomiodon* as only mollusc = the species minimum, 5–9‰; *Liostrea* dominant = *Crassostrea* reefs of Texas, 12–20‰; marine assemblage in Lower Ostrea Beds = open bays of Texas, more than 25‰; belemnites = marine, 35‰. The order which emerges does not involve reversing the salinity preferences of any of the surviving genera.

Several points must be made in qualification. (1) The order of the assemblages is obviously more certain than the actual salinity values assigned, which depend upon several assumptions (e.g. the salinity of the Jurassic ocean). (2) The values assigned are supposed to represent mean salinities; the salinity doubtless varied widely from time to time, as happens in Texas, but short-period oscillations have not usually been recorded in the fossil fauna. (3) The Jurassic assemblages are seen in vertical succession, and it is not possible as yet to prove lateral passage from one into another. However, except for the apparent extinction of *Mytilus strathairdensis*, there is little evidence of evolutionary change in the succession.

The salinity series presented is based entirely on the macrofauna, and especially on molluscs. Among the microfauna, ostracods are very abundant in what I regard as the low salinity (*Neomiodon–Viviparus–Euestheria*) assemblages of the Estheria Shales and Ostracod Limestones. I have not studied these, but Dr. F. W. Anderson informs me that they are mostly Metacyprids, which would not conflict with the interpretation given. Foraminifera are apparently absent from most of the Series, but have been seen in thin-sections and, as chitinous, decalcified shells, in microplankton separations, from the marine horizon of the Lower Ostrea Beds. A group of samples was examined for spores and microplankton by Mr. N. F. Hughes and Mr. R. N. Shrivastava. Most of the samples yielded spores and pollen, but only those from the Garantiana Clay (the bed immediately below the Great Estuarine Series), the Basal Oil Shale (a transition bed at the base of the Series), the two algal bed horizons, and the Staffin Bay Beds, yielded microplankton (dinoflagellates and hystrichospheres). Such microplankton is usually regarded as marine, and each of the samples yielding it had a marine or brackish-marine mollusc fauna.

Very few such salinity series have been constructed for fossil assemblages, and very few indeed from rocks as old as Jurassic. Schmidt (1951) quotes one, with some similarities to mine, prepared for Senonian rocks by Mertin (1939, unpublished thesis). Hiltermann (1949) has assigned salinity values to microfossil assemblages; some of these were criticized by Schmidt (1951). Less precise statements have often been made—marine-brackish, quasi-marine, &c.—not usually referred to any definition of the terms. Considerable scattered information of this sort exists on the Middle and Upper Purbeck Beds, which are in many respects similar to the Great Estuarine Series, but no synthesis has been published. By far the best-known non-marine rocks and faunas are those of the Coal Measures (Eagar 1960). Large salinity changes can be recognized both



TEXT-FIG. 1. Salinity-controlled assemblages in Middle Jurassic faunas. For explanation see text. Continuous lines show 'overlapping' of faunas in the formations indicated.

palaeontologically and geochemically, with consistent results (Ernst, Michelau, and Tasch 1960), but the effects of minor fluctuations in salinity are difficult to differentiate from the large effects of organic content, water turbulence, &c. (Eagar 1960, 1962). It would be surprising if further work did not extend, and in some respects complicate, the picture from the Great Estuarine Series, from which very little collecting has been done compared with the Coal Measures. But I am confident that the main thesis—that the faunas are brackish-water ones controlled mainly by salinity variations—is correct.

Acknowledgements. I wish to thank Dr. G. Larwood for reading the manuscript and suggesting improvements, and Mr. N. F. Hughes and Dr. F. W. Anderson for discussions and information.

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THE ECOLOGY AND STRATIGRAPHICAL DISTRIBUTION OF THE INVERTEBRATE FAUNA OF THE GREAT ESTUARINE SERIES

by J. D. HUDSON

ABSTRACT. The invertebrate macrofauna of the Great Estuarine Series is reviewed, with special reference to the ecological inferences which can be drawn from it. Evidence from modern relatives, and from association with other fossils, is used to deduce the probable ecological preferences, especially of salinity, of each of the common species. The stratigraphical distribution of the fauna among the formations of the Series is comprehensively described for the first time. *Unio andersoni* sp. nov. is described and figured.

THIS paper records the stratigraphical distribution of the more important faunas of the Great Estuarine Series (Middle Jurassic) of north-west Scotland, and reviews the evidence for the ecology of the fossils concerned. The stratigraphy of the Series has been described elsewhere (Hudson 1962), and is summarized in text-fig. 1.

The fauna is dominated by the Mollusca. As systematic descriptions of most species have recently been published or are readily available, I have only included morphological descriptions and taxonomic discussions where my own work has added materially to existing knowledge. Ecological information, on the other hand, is very scattered in the literature; part of it comes from modern representatives of fossil groups, and part from association with other fossils. This information is brought together here, attention being concentrated on the commonest species or those giving a clear ecological indication, especially of palaeo-salinity (Hudson, this journal, p. 318).

In the stratigraphical section, all the important invertebrate macro-fossils are listed (Table 1); this is the first such survey for the whole Great Estuarine Series.

THE INVERTEBRATE FAUNA

The restricted nature of the invertebrate fauna of the Great Estuarine Series as compared with that of the equivalent marine beds of the English Great Oolite Series is immediately apparent even when allowance is made for deficient collecting.

The common mollusc species of the Great Estuarine Series were mostly described by Forbes (1851) and Tate (1873). They also identified some fossils with already described English species. Anderson and Cox (1948) redescribed Forbes's and Tate's species, and assigned them to their correct stratigraphical horizons. They also described some new species, and reviewed the fauna of the Great Estuarine Series as then defined. In fact most of this discussion refers to the Staffin Bay Beds of my classification (Hudson 1962), the faunas of which are more marine than those of the Great Estuarine Series *sensu stricto*, and which are not dealt with in detail here. Some of the lamellibranchs were further revised by Casey (1952, 1955), and British Great Oolite mollusca generally have been revised by Cox and Arkell (1948–50). Yen (1948) redescribed some gastropods, but his conclusions have been disputed. Forsyth (1960) records a few fossils new to the 'Series'.

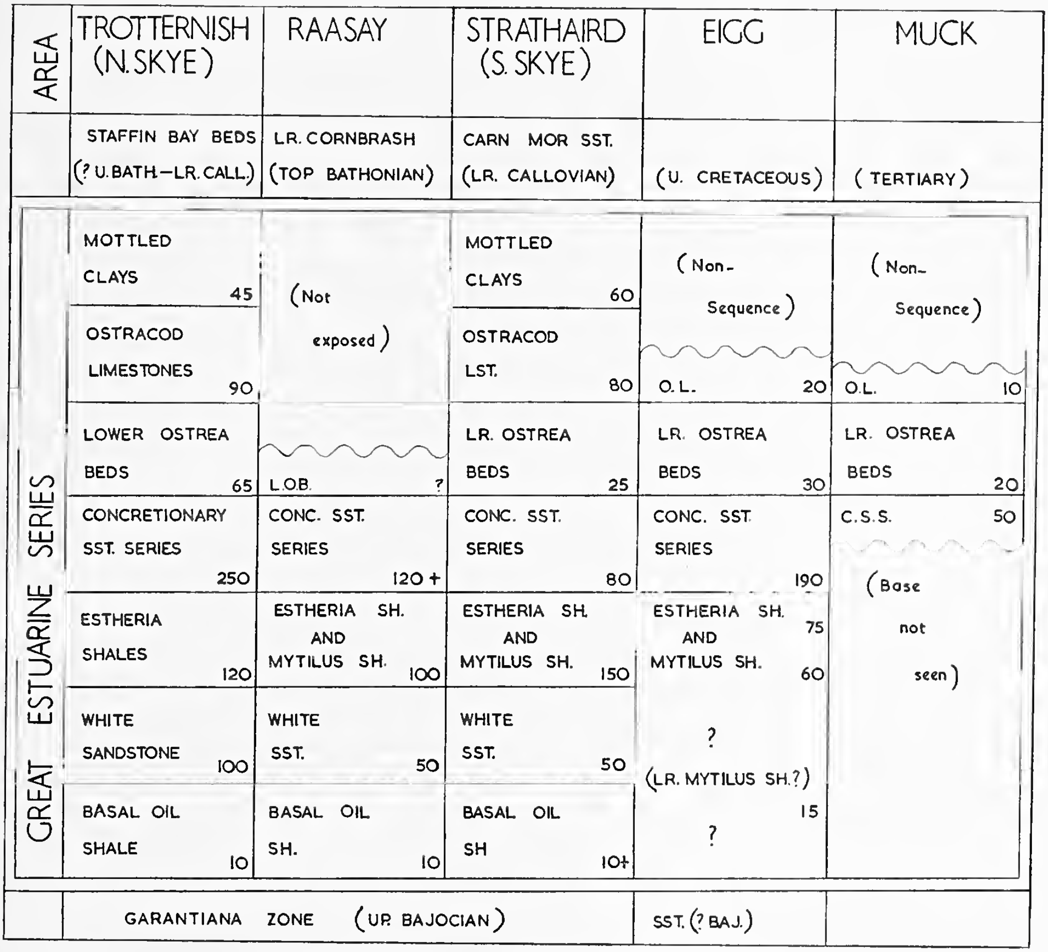
[Palaeontology, Vol. 6, Part 2, 1963, pp. 327–48, pl. 53.]

TABLE 1. _List of invertebrate fossils from the Great Estuarine Series_

Formation abbreviations from text-fig. 1. * = _new record for Great Estuarine Series;_
† = _single occurrence only._

	Formation
Foraminifera: Miliolids, and family indet.*	L.O.B.
Echinoderma: Regular echinoid, plate and spines*	L.O.B.
Isocrinus?†	B.O.S.
Annelida: ‘_Serpula_’ _sp._*†	L.O.B.
Brachiopoda: _Discinisca sp._*†	L.O.B.
‘_Rhynchonella_’ cf. _concinna_ (J. Sow.)	L.O.B.
Polyzoa: Cyclostome indet.*†	L.O.B.
Lamellibranchia:	
Modiolus cf. _imbricatus_ J. Sow.	M.S., E.S., L.O.B.
Mytilus (_Praemytilus_) _strathairdensis_ Anderson and Cox	M.S.
_Meleagrinella sp._*†	B.O.S.
_Pteroperna sp._*	M.S.
Placunopsis socialis Morris and Lycett*	M.S., E.S., L.O.B.
Placunopsis aesturina (Tate)	M.S., E.S.
Liostrea hebridica (Forbes)	E.S., L.O.B.
Lopha sp.†	M.S.
Unio andersoni sp. nov.	M.S., L.O.B.
Neomiodon brycei (Tate) and _N. spp._	M.S., L.O.B. incl.
Anisocardia (_Antiquicyprina_) _cucullata_ (Tate)	L.O.B.
Quenstedtia cf. _bathonica_ (Morris and Lycett)	B.O.S.
Quenstedtia? staffinensis (Forbes)	O.L.
‘_Quenstedtia_’ _forbesi_ Anderson and Cox*	L.O.B.
Pleuromya robusta (Tate)	L.O.B.
Corbula hebridica Tate	L.O.B.
Myopholas acuticostata (J. de C. Sowerby)	L.O.B.
Cuspidaria ibbetsoni (Morris)*	M.S., E.S., L.O.B.
Gastropoda:	
Neridomus arata (Tate)	L.O.B.
Hydrobia praecursor Sandberger†	O.L.
Zebina caledonica (Tate)	L.O.B.
Tornus praecursor (Tate)	M.S., E.S.
Assiminea skyensis Anderson and Cox†	O.L.
Procerithium cf. _pisoliticum_ (Hudleston)†	O.L.
Procerithium (_Rhabdocolpus_) cf. _vetustum_ (Phillips)†	O.L.
Globularia formosa? (Morris and Lycett)*†	L.O.B.
Globularia hebridica Anderson and Cox	M.S., E.S.
Viviparus scoticus (Tate)	M.S.–O.L. incl.
Viviparus bithnyoides (Yen)†	O.L.
Cylindrobullina inermis (Tate)	M.S., E.S., C.S.S.
Arthropoda:	
Phyllopoda: _Euestheria murchisoniae_ (Jones)	B.O.S.–O.L. incl.
Ostracoda: Ostracods including Metacyprids	B.O.S.–O.L. incl.
Bairdia sp.†	B.O.S.
Trace fossils: _Pelecypodichnus amygdaloides_ Seilacher*	C.S.S.

My own collection (in the Sedgwick Museum, Cambridge) contains specimens of all the important species and some additions to the fauna. I have also examined the collections in the Geological Survey Museum, Edinburgh (through the kindness of Mr. R. B. Wilson), and have redetermined some of the fossils. I have also been able to correct the stratigraphical assignment of a few groups of specimens.



AREA	TROTTERNISH (N.SKYE)	RAASAY	STRATHAIRD (S.SKYE)	EIGG	MUCK
	STAFFIN BAY BEDS (? U.BATH.–LR.CALL.)	LR. CORNBRASH (TOP BATHONIAN)	CARN MOR SST. (LR. CALLOVIAN)	(U. CRETACEOUS)	(TERTIARY)
GREAT ESTUARINE SERIES	MOTTLED CLAYS 45	(Not exposed)	MOTTLED CLAYS 60	(Non-Sequence)	(Non-Sequence)
	OSTRACOD LIMESTONES 90		OSTRACOD LST. 80	O.L. 20	O.L. 10
	LOWER OSTREA BEDS 65	L.O.B. ?	LR. OSTREA BEDS 25	LR. OSTREA BEDS 30	LR. OSTREA BEDS 20
	CONCRETIONARY SST. SERIES 250	CONC. SST. SERIES 120+	CONC. SST. SERIES 80	CONC. SST SERIES 190	C.S.S. 50
	ESTHERIA SHALES 120	ESTHERIA SH. AND MYTILUS SH. 100	ESTHERIA SH. AND MYTILUS SH. 150	ESTHERIA SH. 75 AND MYTILUS SH. 60	(Base not seen)
	WHITE SANDSTONE 100	WHITE SST. 50	WHITE SST. 50	? (LR. MYTILUS SH.?) 15 ?	
	BASAL OIL SHALE 10	BASAL OIL SH. 10	BASAL OIL SH 10+		
	GARANTIANA ZONE (UP. BAJOCIAN)			SST. (? BAJ.)	

TEXT-FIG. 1. Stratigraphy of Great Estuarine Series. Thicknesses in feet.

THE ECOLOGY OF THE INVERTEBRATE FAUNA

The fauna listed in Table 1 may be readily divided into ecological groups.

(*a*) The typical fossils of the Great Estuarine Series. Certain species may be considered with more abundant species of the same genus, so that the ecological interpretation of the 'Series' turns very largely on the interpretation of only twelve species or groups: *Modiolus* cf. *imbricatus*, *Mytilus* (*Praemytilus*) *strathairdensis*, *Placunopsis socialis*, *Liostrea hebridica*, *Unio andersoni* sp. nov., *Neomiodon brycei*, *Cuspidaria* *ibbetsoni*; *Viviparus scoticus*; *Tornus praecursor*, *Globularia hebridica*, and *Cylindrobullina inermis*; *Euestheria murchisoniae*.

These species are discussed in detail below. Taxonomic discussion is included where necessary.

(*b*) Six records of marine stenohaline major taxa and eight species of marine mollusca, confined to the marine horizon of the Lower Ostrea Beds. These are listed and discussed under Lower Ostrea Beds on p. 340. They were normal shallow-water marine animals.

(*c*) Three species of marine genera confined to the Basal Oil Shale, a transition bed at the base of the Series.

(*d*) The remaining seven species are single records or of very restricted occurrence (Table 1), so that extended discussion is not possible.

LAMELLIBRANCHS

Modiolus cf. *imbricatus* J. Sowerby

Occurrence. A *Modiolus* comparable to this species, but generally smaller, has been recorded from several localities and horizons (e.g. Lee 1920, p. 54). I have collected it from three horizons: from just below the Mytilus Shales algal bed with *Placunopsis* and *Cuspidaria*, from the algal bed horizon of the Lower Ostrea Beds with *Rhynchonella* and marine mollusca, and from the Estheria Shales in Raasay alone.

Ecology. *Modiolus* belongs to a very ancient group, which has always been shallow-water marine, or even littoral (Newell 1942). Data on modern *Modiolus* are not so abundant as on *Mytilus*, but at least in Britain it apparently lives in somewhat deeper water, below the littoral zone proper (Yonge 1949), and in the Baltic it does not extend into water of such low salinity as *Mytilus edulis* (Sorgenfrei 1958). The genus is thus marine, shallow-water but not littoral, and able to tolerate limited reduction in salinity. Its occurrence in the Great Estuarine Series is consistent with this, since it occurs principally in the more marine beds.

Mytilus (*Praemytilus*) *strathairdensis* Anderson and Cox

Preservation. This species (Pl. 53, fig. 6) was described by Anderson and Cox (1948) from near the base of the Estheria Shales of Strathaird. Their material consisted of internal and external moulds in hard black shale. No further occurrences were known, and none has since been described. The species is, however, abundant on the same horizon in Eigg, where it characterizes the Mytilus Shales (Hudson 1962). In Eigg the shell is preserved; except for a very thin outer layer, which may be calcitic, it is composed of nacreous aragonite (checked by X-ray powder photograph by Dr. P. Gay). The *Myoconcha* n.sp. of Kitchin (in Barrow 1908, pp. 21–23) and Lee (1920, p. 54) belongs to this species (Geological Survey Museum, Edinburgh, T 2963A–T 2968A, from Eigg, and T 215E, from Raasay).

Occurrence. Except for one doubtful record from the Upper Estheria Shales of north Eigg, this species is confined to the Mytilus Shales of Eigg, Skye, and Raasay. In these it is extremely abundant, and except for a few thin beds it dominates the fauna. It usually occurs in monotypic shell beds, never with *Unio* or *Viviparus*, and doubtfully with *Neomiodon*.

Ecology. M. strathairdensis is one of the earliest representatives of its genus, although subgenerically distinct from *Mytilus* s.s. At the present day *Mytilus* is one of the best examples of a euryhaline marine mollusc. In the Baltic area *M. edulis* inhabits the Gulf of Finland, one of only four lamellibranchs, out of ninety-two inhabiting the Kattegat, to do so. The mean salinity at the limit of its range is 6–10‰; there is no doubt that salinity is the limiting factor (Segestråle 1957, Sorgenfrei 1958). *M. edulis* is also a common littoral species in waters of normal salinity. It is extremely gregarious (Newell 1942). There is every reason to suppose that *M. strathairdensis*, like *Midiolus*, shared the general preferences of the Mytilacea, and it almost certainly resembled *Mytilus* s.s. in tolerating extreme conditions of salinity and in being gregarious. Its exclusion from the more certainly marine beds with *Placunopsis*, *Cuspidaria*, and *Modiolus* supports this. On the other hand, *Mytilus* has always been a marine-euryhaline, rather than a fresh or true brackish-water genus, and this is supported by the absence of *M. strathairdensis* from beds with *Unio* and *Viviparus*. The species does not overlap in stratigraphical range with *Liostrea hebridica*, which may have had similar ecological requirements.

Placunopsis socialis Morris and Lycett

Placunopsis aesturina Tate

Previous records. Placunopsis socialis (Pl. 53, figs. 3, 4) is a well-known species in the Great Oolite, especially in the Upper Estuarine Series of the Midlands. It has not been recorded from the Hebrides before. *P. aesturina* was described by Tate (1873, p. 349, pl. 12, fig. 12) from the Estheria Shales, and has been recorded from various horizons and localities in the Great Estuarine Series.

Tate's description of *P. aesturina* mentions central umbones, whereas his figure shows an inequilateral shell. The holotype is in fact inequilateral, like the figure (Geological Survey Museum, London, 8621). Most of the records from the Great Estuarine Series are of specimens with central umbones, better referred to *P. socialis*, or are not specifically determinable. *P. socialis* is a very variable species. An inflated form, very common in the Mytilus Shales, is rather distinct, but also occurs in the Upper Estuarine Series of the Midlands.

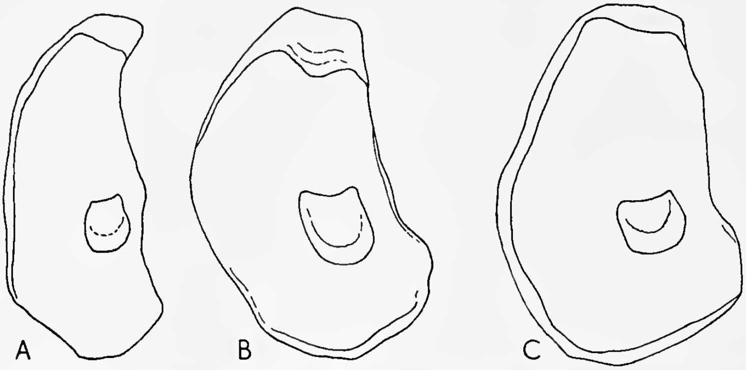
Occurrence. Placunopsis occurs at various horizons in the Mytilus and Estheria Shales, and in the Lower Ostrea Beds. In the limestones just below the Mytilus Shales algal bed *P. socialis* is almost a rock-former, especially the inflated form. It is associated with *Cuspidaria ibbetsoni*, *Modiolus*, *Lopha*, and rare *Neomiodon*.

Ecology. Placunopsis is undoubtedly a marine genus. It is gregarious and common in restricted assemblages, and may have been tolerant of very shallow water and variable salinity.

Liostrea hebridica (Forbes)

Discussion. This is one of the most important fossils (text-fig. 2) of the Great Estuarine Series, where it dominates the fauna of the Lower Ostrea Beds. A discussion of the species, with synonymy and excellent figures, is given by Arkell (1934). In the Great Oolite Series it was long known as *Ostrea sowerbyi*. The variety *rugosa* is not known in the Hebrides. Most specimens are moderately elongated, but the extreme variety *elongata*, which is the commonest form in the Fuller's Earth at Langton Herring in Dorset, is uncommon.

The genus *Liostrea* Douvillé may conveniently be used for smooth and not strongly curved Mesozoic oysters, but it is probably only a form genus, as are other 'genera' of oysters based on shell form and sculpture. As is becoming well known, living oysters can be distributed among three genera—*Pycnodonte*, deep-water and non-gregarious; *Ostrea* s.s., with type species *O. edulis*; and *Crassostrea*, type species the American oyster, *C. virginica* (Yonge 1960). The biological differences are considerable, and are correlated with ecological station: *Ostrea* is smaller, rounded, larviparous, and marine, while *Crassostrea* is larger, elongated, oviparous, and estuarine. It possesses a structure, the promyal chamber, for removing suspended mud from its system. Correlated with this is the position of the muscle-scar well back from the hinge-line, as opposed to its central position in *Ostrea*. Ranson (1939, 1942) showed that the larval shells, or prodissoconchs, afforded a clear distinction between the oyster genera, and demonstrated by this criterion that some fossil genera could be assigned to either *Ostrea* or *Crassostrea* (*Gryphaea* of Ranson).



TEXT-FIG. 2. Interiors of right valves of *Liostrea hebridica* (A, B) and *Crassostrea virginica* (C), to show similarity of shell form and position of muscle-scar. A, Langton Herring (tracing of Arkell 1934, pl. iv, fig. 6; *L. hebridica* var. *elongata*, × 1. B, Ketton, Upper Estuarine Series, original, × 1. C, After Orton, × $\frac{1}{2}$.

In general shape and position of muscle-scar *L. hebridica* closely resembles *Crassostrea virginica*, though it is only about half as large (text-fig. 2). The muscle-scar is regarded as significant in fossils by Gunter (1950) and Yonge (1960). Hallam (1959) relates *L. irregularis* to *Ostrea* by this criterion. Preliminary work has been done on separating prodissoconchs from the matrix of *L. hebridica* shell-beds, especially that of Langton Herring in the Fuller's Earth of Dorset. A few have been found which are strongly inequilateral, like those of *Crassostrea* and unlike *Ostrea* (Yonge 1960). It is hoped to continue this work, but at present both lines of evidence suggest that *L. hebridica* was more closely related to *Crassostrea* than to *Ostrea*.

Occurrence. The chief occurrence of *L. hebridica* is in monotypic shell-beds in the Lower Ostrea Beds. Less often, the shell beds also contain *Neomiodon*, and this lamellibranch is perhaps more common in the associated shales. At the marine Algal Bed horizon *L. hebridica* occurs with a much greater variety of lamellibranchs (listed in next section) and with *Rhynchonella*. Very similar assemblages occur in the Upper Estuarine Series of the Midlands. In the Staffin Bay Beds *L. hebridica* is common, but less completely dominant.

Ecology. Summaries of the vast literature on oyster ecology are given by Korringa (1952) and Yonge (1960). *Crassostrea*, to which *L. hebridica* is thought to have been related, has a narrower temperature range than *Ostrea*, but is much more tolerant of low and fluctuating salinities; *Ostrea* extends to salinities of 23‰, *Crassostrea* to 12‰ (Yonge 1960). *Crassostrea* in fact does not normally form reefs except in reduced salinities. In the enclosed bays of Texas the pure *C. virginica* reefs which flourish in salinities of 12–20‰ are invaded at higher salinities by marine forms, including *Ostrea*.

The morphological and ecological analogies between *L. hebridica* and *C. virginica*, further discussed in the accompanying paper (p. 323), are so close that it seems reasonable to infer that *L. hebridica*, in the form of pure oyster reefs, inhabited shallow, partially enclosed bays with salinity about half that of sea water.

Unio andersoni sp. nov.

This species (Pl. 53, figs. 1, 2) is described at the end of the paper.

Previous records. There has been some doubt about the occurrence of *Unio* in the Great Estuarine Series; as Anderson and Cox (1948) show, most of the early records were erroneous. *Unio* was, however, correctly identified from Eigg by Kitchin (in Barrow 1908), but was not described. Jackson (1911*a*, p. 120) records *Unio*, compared to *U. distortus* Bean, from Eigg. I have examined the specimen (Manchester Museum, L.10504), and do not accept the pseudocardinal tooth mentioned by Jackson. There is no proof that the shell is a *Unio*.

Occurrence. Reptile Bed and Unio Bed, Mytilus Shales, Eigg; Lower Ostrea Beds (?), Trotternish.

Ecology. *Unio* is perhaps the best known of all freshwater lamellibranchs, and the Unionidae have been exclusively freshwater at least as far back as the Jurassic. The typical occurrence of present-day Unionidae is in freshwater lakes and rivers. However, *U. andersoni* certainly did not live in inland waters, since both the Reptile Bed and the Unio Bed are followed without a break by beds with marine-brackish fossils. It is therefore interesting to note that *Unio* occurs at the present day in the shallow coastal waters of the Gulf of Finland, with salinities up to a maximum of 3–4‰ (Segerstråle 1957). Therefore, if modern *Unio* is taken as a guide, *U. andersoni* could have inhabited coastal lagoons like those envisaged for the deposition of the Great Estuarine Series, but these must have become temporarily almost freshwater.

The Reptile Bed occurrence, with gastropods usually regarded as marine (see under *Tornus praecursor*, below), may be an ecologically mixed one in a condensed deposit, and in any case I prefer to regard the gastropods, rather than *Unio*, as euryhaline.

Neomiodon brycei (Tate) and *Neomiodon spp.*

Discussion. The genus *Neomiodon*, the *Cyrena* of earlier authors, may be considered as a whole. It is the commonest mollusc of the Series; it dominates the faunas of the Estheria Shales and Concretionary Sandstone Series, where it forms monotypic shell-beds and is a rock-former in the limestones. It also occurs in the Mytilus Shales and the Lower Ostrea Beds. In the Staffin Bay Beds it forms part of a more varied and more marine fauna.

The taxonomic history of the Great Estuarine Series *Neomiodons* is complicated. Forbes and Tate described several species of '*Cyrena*', mostly from the Staffin Bay Beds. These were redescribed by Anderson and Cox (1948), who referred some to marine genera, and erected a new genus *Protomiodon*, for *Cyrena brycei* Tate and species considered congeneric with it. Casey (1955), in a comprehensive paper on the Neomiodontidae, showed that *Protomiodon* was a synonym of *Neomiodon*. Casey (1952) has also demonstrated extensive external homeomorphy among such smooth, trigonal-ovate lamellibranchs as *Neomiodon* and *Staffinella* [*Protomiodon*] *staffinensis*. Fortunately this problem concerns mainly the Staffin Bay Beds; the forms which dominate the fauna of the middle part of the Great Estuarine Series are undoubtedly *Neomiodon*. Most can be referred to *N. brycei* (Tate) and its variety *quadrata* on shell outline (Anderson and Cox 1948), but other species, including *N. cunninghamii* (Forbes), are probably present.

Occurrence and ecology. Since the Neomiodontidae are extinct, it is not possible to draw ecological conclusions from close modern relatives, and arguments must be based on associations with other fossils. Casey (1955) considers the family to be the ecological forerunners, but not the direct ancestors, of the fresh- and brackish-water Corbiculidae, of the Tertiary and the present day, which they so closely resemble. He sums up the ecology of *Neomiodon* itself as 'fresh or brackish water, gregarious, sometimes associated with members of marine genera'. He cites evidence from the Purbeck and Wealden of frequent association with *Unio* and *Viviparus*, and much less frequent occurrence with *Modiolus*, *Corbula*, and *Pecten*. Despite association with marine genera in the Staffin Bay Beds, Casey considers Middle Jurassic *Neomiodon* to have had the same ecological preferences. It is now possible to cite evidence, similar to Casey's from the Purbeck, from the Great Estuarine Series itself. *Neomiodon* occurs with *Viviparus*, *Euestheria*, and metacyprid ostracods at many horizons, and with *Unio* at two, as well as with *Liostrea*. As in the Purbeck, however, it is not usually abundant in precisely the same bed as marine-brackish genera. The analogy with the Middle Purbeck is the more striking as the facies is so similar. I therefore support Casey's conclusions on the ecology of *Neomiodon*. The extensive beds with *Neomiodon* alone may have been deposited in water just saline enough to exclude *Unio* and *Viviparus*, but still too dilute to admit marine genera; this is the 'species minimum' of the Great Estuarine Series.

The trace fossil *Pelecypodichnus amygdaloides* Seilacher is extremely common in the thin-bedded sandstones and shales of the Concretionary Sandstone Series. It is formed as the 'resting trace' of a lamellibranch inhabiting shallow, temporary burrows in a thin layer of sand over mud (Seilacher 1953). In this case *Neomiodon* was undoubtedly the lamellibranch responsible, and the occurrence confirms the mode of life of *Neomiodon* which could also be predicted from its typically 'active lamellibranch' morphology (cf. Yonge 1949, pp. 228–9).

Cuspidaria ibbetsoni (Morris)

This species (Pl. 53, fig. 5) has not previously been positively identified from the Series, though Anderson and Cox (1948, p. 120) record a probable fragment.

Occurrence. *C. ibbetsoni* is abundant at several horizons in the Mytilus and Estheria Shales, especially just below the algal bed, and also occurs in the Lower Ostrea Beds. It is associated especially with *Placunopsis socialis*, an association also characteristic of the Upper Estuarine Series of the Midlands.

Ecology. Modern *Cuspidaria* is deep-water marine, and Cox (1960) has questioned whether the Jurassic species, which are all shallow-water forms, were related to it, or were septibranchs at all. *C. ibbetsoni* occurs widely in the Great Oolite Series in England, and is especially abundant in the Upper Estuarine Series of the Midlands. The forms in the clays there have long rostra, like my specimens and unlike those from the Great Oolite limestones (Cox and Arkell 1948)—a fact which may be ecologically significant. The occurrence and associations of *C. ibbetsoni* suggest a shallow marine habitat, and tolerance of muddy and perhaps brackish conditions.

GASTROPODS

Viviparus scoticus (Tate)

Previous records. This is by far the most important gastropod in the Great Estuarine Series, occurring in all formations from Mytilus Shales to Ostracod Limestones, and it has given rise to much controversy. It was described as a *Paludina* (= *Viviparus*) by Tate (1873), and considered as freshwater until Yen (1948) proposed a new genus *Bathonella* for it, and claimed that it was marine. The ecological and taxonomic arguments are linked, since many palaeontologists are unwilling to admit that a marine shell was a *Viviparus*, or vice versa. The purely morphological differences between *Bathonella* and *Viviparus* have been very differently assessed by different authors. Yen (1948) placed it in a different family from *Viviparus*; this was accepted by Anderson and Cox (1948). Arkell (1948) doubted the generic separation, and Watson (1950) firmly rejected it. Cox (1950) admitted that the distinction could be specific only, but held that since *Bathonella* was marine the generic distinction was desirable. Since I do not consider that the ecology of *Bathonella* differed materially from that of other *Viviparus*, I propose to reject the name, regarding the slight morphological differences listed by Yen as of specific rank only (Watson 1950). *Bathonella bithnyoides* Yen 1948 is assumed to be congeneric with *V. scoticus*.

Occurrence. Yen (1948), who was originally responsible for the view that *V. scoticus* was marine, did not in fact record marine fossils from the same bed, but only from an adjacent one (see Stratigraphical section). In view of the repeated oscillations of conditions known in the Great Estuarine Series this cannot count as a true association. Cox (1950) drew up a list of occurrences of *V. scoticus* in the Great Estuarine Series, mainly from Anderson's unpublished records, but including two of Tate's (1873) lists, which alone contain undoubtedly marine genera. Cox admits that these may have been compiled from more than one bed, and from field experience of the localities concerned I should regard this as certain. This reduces Cox's list of associates to *Neomiodon*, *Euestheria* and ostracods, all at many localities, and *Hydrobia praecursor* and *Quenstedtia? staffinensis* at one each. The only marine genus here is *Questedtia*, and the generic attribution of the species is quite uncertain (Anderson and Cox 1948). To this list I can add, from my own collecting, *Unio* in two localities, both with *Neomiodon* also. I can also add several more occurrences of *V. scoticus* alone or with *Neomiodon*, *Euestheria*, and ostracods, and a great deal of negative evidence, on the non-occurrence of *V. scoticus* with marine or marine-brackish genera.

The other well-known occurrences of *V. scoticus* (or species regarded by Anderson and Cox (1948) as synonymous with it) are in Oxfordshire (Watson 1950) and Indre, France (Fischer 1961). Neither yields acceptable evidence of marine associates. Fischer shows clearly that *Viviparus* occurs immediately above a lignite bed which rests on an erosion surface, that it is associated with '*Valvata*' and '*Planorbis*', and that none of these gastropods is found in the marine beds above and below.

Ecology. Present-day *Viviparus* is one of the best known of all freshwater gastropods. There is therefore a presumption that beds containing shells which appear to be fossil *Viviparus* are also freshwater, especially if they contain other freshwater fossils. This conclusion has always been accepted, for instance, in the Wealden Beds. On the basis of the above review, there seems no reason to depart from it in the case of the Great Estuarine Series. There only remains, as with *Unio*, the possibility that *Viviparus*, since its habitat in this case was certainly coastal, could tolerate a slight degree of brackishness in the water. This is quite possible; but the total exclusion of marine genera shows that salinity stayed on the freshwater side of the 'species minimum'.

Tornus praecursor (Tate)
Globularia hebridica Anderson and Cox
Cylindrobullina inermis (Tate)

These three small gastropods may be considered together. The type localities are all in the Estheria Shales of the Portree district, Skye, where the species occur together and with *Modiolus* (Tate 1873, Anderson and Cox 1948). Tate referred the species to *Valvata*, *Neritina* (*G. hebridica* = *N. staffinensis* Tate non Forbes), and *Melania* respectively. In referring them to marine genera, Anderson and Cox comment on the difficulty of generic assignment of imperfectly preserved small gastropods, and in the case of *T. praecursor* they were influenced by association with other marine fossils.

Occurrence. Most small gastropods in my collection do not show apertural characters, and are therefore difficult to determine. However, all three species mentioned above probably occur in the Reptile Bed of the Mytilus Shales. *G. hebridica* is the abundant small naticoid shell of Kitchin (in Barrow 1908, p. 22). Here they are associated with *Unio*, as well as with numerous fish scales and teeth and disaggregated reptilian bones, so the assemblage is an ecologically mixed one if the gastropods were truly marine. I have also found *Cylindrobullina sp.* with young *Mytilus strathairdensis* and with *Neomiodon brycei*. Small, low-spired gastropods, possibly referable to *T. praecursor*, occur associated with *Neomiodon* and *Euestheria* at several localities in the Estheria Shales of Skye.

It is possible that these small gastropods were euryhaline, as many small gastropods are today, but until more taxonomic work has been done on better-preserved material they are unsafe environmental indicators.

PHYLLOPODA

Euestheria murchisoniae (Jones)

Previous records. In 1862 Jones described this species of '*Estheria*' from material collected by Murchison in 1826. His type material appears to be lost. Subsequently the species, or the genus '*Estheria*', has been recorded several times from the Great Estuarine Series, but no further descriptions or figures have been published. The classification of fossil '*Estheria*' (itself a preoccupied name) is in a confused state; the genus accepted here for *E. murchisoniae* is *Euestheria* Déperet and Mazeran, of which the type species is *Eu. minuta* of the Triassic (Kobayashi 1954).

Occurrence. *Euestheria* is most abundant in the Estheria Shales, where bedding planes may be covered by its carapaces. It is associated with *Neomiodon*, ostracods, fish fragments, and oogonia of *Chara*. In the Ostracod Limestones it is again very common, but less universally present, accompanied by ostracods and fish fragments. It occurs more locally in the Basal Oil Shale, the Mytilus Shales, and the Concretionary Sandstone Series.

I have collected twelve samples with abundant *Euestheria* from the Estheria Shales and the Ostracod Limestones, and studied the variation within and between them (210 specimens were examined). Carapace outline, position of umbo, number of growth-rings, and interspace ornament are among rather few features of fossil '*Estheria* 'which can be used in classification, but there has been no agreement as to which of them is most important (compare Raymond 1946, Bock 1953, Kobayashi 1954, Tasch 1956). My study showed that each sample was reasonably homogeneous within itself, but that there was considerable variation between samples, especially in interspace ornament and also in size. This suggests that several taxa are present—these range from varieties or subspecies to genera or even families, depending on the classification employed. In general the specimens were smaller and less elongated than those figured by Jones, but their general outline and number of growth-rings were similar. At present I propose to retain all the specimens in *Eu. murchisoniae*. The variations did not have any obvious stratigraphical significance, but the largest specimens were from the Ostracod Limestones.

Ecology. Modern '*Estheria*' species are most common in very shallow ponds, including temporary 'playas', in inland basins in warm temperate areas. They mostly inhabit fresh waters, occasionally brackish lagoons, but never live in the sea (Kobayashi 1954, Jones 1862, pp. 5–7). The vast majority of fossil '*Estherias*' come from continental formations. It is certainly significant that they are completely absent from the marine Jurassic and Cretaceous of north-west Europe, but occur in the Triassic (including the Rhaetic), the Great Estuarine Series, the Purbeck, and the Wealden. In the Great Estuarine Series the associates listed above are all freshwater or freshwater-brackish.

THE STRATIGRAPHICAL DISTRIBUTION OF THE FAUNA

The faunas of the formations of the Great Estuarine Series are here described in stratigraphical order. All macro-invertebrate species are listed (apart from a few early records which have not been confirmed); vertebrates and microfossils are only mentioned in passing. Measured sections are given of a few important localities; much fuller stratigraphical information, including many more measured sections, is in my thesis (University of Cambridge, Ph.D. 1962). Figures in brackets after locality names refer to the National Grid.

a. Basal Oil Shale

The Garantiana Clay, the last marine formation below the Great Estuarine Series, passes gradually up into the Basal Oil Shale. The lithology changes from blue, blocky clay to black fissile shale, and the fauna changes from one of ammonites to a peculiar and restricted assemblage in which fish scales are the commonest fossils.

The gradual passage is best seen in the cliffs above Prince Charles's Cave, north of Portree, Skye (513477 to 515490). The Oil Shale here contains *? Quenstedtia* cf. *bathonica* (Morris and Lycett), with valves attached (cf. Forsyth 1960), *Meleagrinella* sp. indet., indeterminate tiny gastropods and ostracods, in addition to numerous cycloid and ctenoid fish scales and one almost complete leptolepid fish (identified by Mr. H. A. Toombs; Sedgwick Museum J.29055). In Raasay the Quenstedtia Shale of Forsyth (1960), the equivalent of the Basal Oil Shale, contains *Isocrinus* in its lower part and *Quenstedtia* alone in its upper part; just below the White Sandstone *Euestheria* occurs. At Port na Cullaidh, Elgol, Strathaird, the Basal Oil Shale is intermittently exposed; it is very similar to the Trotternish development and yields abundant fish scales, *Euestheria*, ostracods, gastropods, and ? *Mytilus*. The abundance of fish material contrasted with the paucity of mollusca, together with the high carbon content, suggest that the bottom water may have become stagnant at this time. There was probably also a gradual decline in salinity.

b. The *White Sandstone* is unfossiliferous.

c. Mytilus Shales

These form the lower part of the Estheria Shales of Eigg, Strathaird, and Raasay (Hudson 1962). The type section in Eigg, north of Kildonnan (495870), gives the best record of rapid vertical variations in lithology and fauna in the Great Estuarine Series. A detailed account will be published elsewhere; the following is a summary of the faunas, from top to bottom.

9. *Algal Bed*, 1 ft. 4 in. An 'algal-dome' bed partly composed of faecal pellets (Hudson 1962). *Placunopsis socialis* near the base.

8. *Placunopsis Limestones*, 6 ft. Hard blue limestones separated by shales. *P. socialis*, *P. aesturina?*, *Cuspidaria ibbetsoni*, *Modiolus sp.*, *Lopha sp.*, *Neomiodon sp.* (rare). Following the interpretations of Section III, this is a high-salinity fauna.

7. *Unio Bed*, 8 in. Sandy argillaceous limestone. *Unio andersoni*, common; *Neomiodon*, *Viviparus*. A freshwater fauna.

6. Limestones and shales, 5 ft. *Cuspidaria ibbetsoni* near base, *Neomiodon brycei* near top. First occurrence of these two species. Last occurrence of *Mytilus strathairdensis*.

5. Silty shale with thin limestones, 30 ft. The main mass of the Mytilus shales; fauna dominated by *M. strathairdensis*, forming 'mussel beds'.

4. Complex Bed, 3 ft. Coarse sandstone with common fish remains. First occurrence of fully grown *M. strathairdensis*.

3. Shale, 8 ft. Very abundant *M. strathairdensis*, but nearly all young individuals. Near the base a 1-in. bed with *Viviparus* but no *Mytilus*.

2. Reptile Bed, 4 in. Hard sideritic limestone. Abundant small gastropods (*Globularia hebridica*, *Tornus praecursor*, *Cuspidaria ibbetsoni*), common *Unio andersoni*.

Abundant fish teeth, scales and fin-spines, reptile vertebrae, and limb bones. Possibly a condensed deposit.

1. Shale, 8 ft. Sparsely fossiliferous. Near base, *Euestheria murchisoniae* (therefore low salinity) and fish scales like those from the Basal Oil Shale. Base not seen.

These rapid changes of fauna within a fairly constant gross lithology are regarded as characteristic of lagoonal conditions, and due to salinity changes (see accompanying paper). The above succession records a gradual (and fluctuating) increase in salinity from bed 1 to bed 5, to perhaps half the salinity of sea water; a decline in beds 6–7 to almost fresh water, and a more sudden increase in beds 8–9 to definite marine-brackish salinities, as judged by the ecology of the fossils deduced in the previous section of this paper.

In Strathaird *M. strathairdensis* is common, and the Placunopsis limestone below the algal bed is well developed. It is exposed north of Elgol (Anderson 1948, Hudson 1962), where it yields *Placunopsis socialis*, *Cuspidaria ibbetsoni*, *Pteroperna sp.*

In Raasay the Mytilus Shales are not well known, but *M. strathairdensis* occurs and loose blocks of the Algal Bed and of the Placunopsis limestones have been found (Lee 1920).

d. Estheria Shales

The typical Estheria Shales have an abundant and highly characteristic fauna of *Euestheria*, *Neomiodon*, ostracods, and scattered fish fragments; in certain beds these are accompanied by *Viviparus* and small gastropods.

At the Lealt River in Trotternish, the type locality (Anderson 1948, pp. 125–6, with map), the typical lithology is well seen. The black shale immediately overlying Anderson's algal limestone, on the south bank of the river just above the road-bridge, yields *Euestheria murchisoniae*, a form with radial-linear interspace ornament (in great abundance and well preserved), *Neomiodon*, ostracods, and fish scales. Similar shale a few feet higher in the succession, on the north bank, yields *Eu. murchisoniae*, form with punctate ornament, *Neomiodon*, *Viviparus*, and very abundant ostracods.

The burn north of Rigg Burn (crosses road at 518571) gives a good section, which affords an excellent example of the characteristic rapid variation of fauna. The following section is about 100 yards west of the road, and 30 ft. above the base of the Estheria Shales:

	ft.	*in.*
3. Shale with *Cuspidaria ibbetsoni*, *Placunopsis socialis*, cf. *Quenstedtia*, *Procerithium spp.*	1	0
2. Shell limestone, *Cuspidaria*, with shale partings	1	0
1. Shale with *Euestheria murchisoniae*, ostracods, fish fragments, *? Mytilus*	2	0

A similar shale to bed 1, about 10 ft. lower in the succession, yielded *Eu. murchisoniae*, ostracods, *Neomiodon sp.*, *Viviparus scoticus*, *? Tornus praecursor*. This is a complete low-salinity assemblage; it is notable that bed 1 above contains *Euestheria* and Mytilid shells, but not *Viviparus*, and may thus represent somewhat higher salinity. Bed 3 is definitely brackish-marine, with no freshwater-brackish indicators.

In Raasay the shales are identical to those of Trotternish, with abundant *Euestheria*. Oolitic limestones are well represented; one of these yielded *Modiolus* cf. *imbricatus*.

In Strathaird the beds are baked by intrusions, and less amenable to search for fossils. The most notable feature is the occurrence of *Liostrea hebridica* just above the algal bed (Anderson 1948, p. 127). Higher up, some *Viviparus* beds occur. In Eigg the shales yield *Euestheria*, *Neomiodon*, ostracods, and *Viviparus*, with no additions to the Trotternish fauna. *Cuspidaria ibbetsoni* and *Placunopsis sp.* occur a short way above the algal bed on the north coast (474907), and I have a queried record of *Mytilus* from here. Immediately above is a *Viviparus* bed.

e. Concretionary Sandstone Series

This is the thickest formation in the Great Estuarine Series, and it is very variable. Its deposition is an involved study in sedimentary petrology and sedimentation. Its fauna, however, is monotonous. *Neomiodon* is the only macrofossil in many beds; *Viviparus* is the only other common mollusc. A few beds contain ostracods; *Euestheria* is rare. There are isolated records of *Placunopsis* (from Strathaird, T 4311, T 4318; Wedd 1910, p. 124), and *Cylindrobullina?* (from Eigg, T 719A, T 720A, two forms; Kitchin in Barrow 1908, p. 24); these are in the Survey Museum, Edinburgh.

My collection includes well-preserved *Neomiodon brycei* and *Neomiodon sp.* from the Lealt River, Trotternish (with brown on white colour banding), from the Valtos shore section, Trotternish, from Eist, Duirinish (associated with small *Cylindrobullina sp.*), and from Raasay. The best-preserved *Viviparus scoticus* are from Eist and from Strathaird, where they occur near the top of the formation on the shore at Cladach a' Ghlinne (Wedd 1910, p. 124). The trace fossil *Pelecypodichnus amygdaloides* is abundant, especially in Trotternish.

f. Lower Ostrea Beds

These beds, with their extraordinary abundance of oysters, have attracted attention and comment from the earliest investigators onwards. Everywhere limestones composed of *Liostrea hebridica*, alternating with shales, are the dominant lithology. The beds are exposed over a wider area than any other formation of the Series, and are fairly constant, though thicker and sandier in Trotternish than elsewhere (Hudson 1962). Exposures yielding *L. hebridica* are far too numerous to list here. This account concentrates on the more extensive fauna of the marine horizon which is constantly associated with Anderson's (1948) Algal Bed. The important exposures are described below. Since knowledge of the distribution of this fauna at present depends more on the vagaries of collecting than on true geographical variation, it is convenient first to review the fauna as a whole.

The greatest thickness of the marine beds is not more than 10 ft., in Trotternish and Waternish, and these beds are always underlain and overlain by ordinary *Liostrea* beds. The Algal Bed usually occurs towards the top of the marine beds.

The following members of marine stenohaline groups are confined to this horizon: foraminifera (several records, mostly of miliolids), echinoids (regular, plates and spines, 2 records), '*Serpula*' (1 record), *Discinisca* (1 record), *Rhynchonella* cf. *concinna* (common in north Skye), polyzoan (cyclostome, 1 record).

Of the mollusca, *Liostrea hebridica, Modiolus imbricatus, Cuspidaria ibbetsoni*, and *Placunopsis socialis* were dealt with above, and the following are confined to this horizon: *Anisocardia* (*Antiquicyprina*) *cucullata* (Tate), '*Quenstedtia*' *forbesi* Anderson and Cox, *Pleuromya robusta* (Tate), *Corbula hebridica* Tate, *Myopholas acuticostata* (J. de C. Sowerby); *Neridomus arata* (Tate), *Zebina caledonica* (Tate), *Globularia* *formosa?* (Morris and Lycett). These are discussed below. In addition there are fragments of *Mytilus* (*Falcimytilus*) sp. in my collection (see also Tate 1873, p. 346), and indeterminate lamellibranchs and gastropods. It is doubtful if *Neomiodon* occurs. The smooth, trigonal ovate lamellibranchs ('*Cyrenas*' of the old authors) in these beds are usually larger than typical *Neomiodon*, and in the absence of preserved dentition are very difficult to determine. Most are probably members of marine genera, like *Anisocardia cucullata*, which was itself one of Tate's '*Cyrenas*' (cf. Cox 1947, Anderson and Cox 1948, Casey 1952, 1955).

Anisocardia (*Antiquicyprina*) *cucullata* (Tate). The specimens recorded here do not show dentition, but may be referred to this species on shell outline. Some are not distinguishable from small specimens of *A.* (*A.*) *loweana* (Morris and Lycett) from the Great Oolite.

'*Quenstedtia*' *forbesi* Anderson and Cox. One specimen from Duntulm agrees with Anderson and Cox's figure (1948, pl. 2, fig. 9). The dentition is unknown and the shell may not be a *Quenstedtia* (Casey, personal communication).

Pleuromya robusta (Tate). Several specimens from Lovaig Bay, of which the best is figured (Pl. 53, fig. 8), appear to confirm Anderson and Cox's tentative conclusion that this species is distinct from *P. uniformis* (J. Sow.), being shorter and relatively higher.

Corbula hebridica Tate. This small species is quite common at this horizon.

Myopholas acuticostata (J. de C. Sowerby). This distinctive lamellibranch (Pl. 53, fig. 7) was recorded by Tate (1873, p. 346), but not mentioned by Anderson and Cox. It is quite common at Duntulm and at Loch Bay. It is widespread in the Great Oolite Series, including the Upper Estuarine Series of Northants.

Neridomus arata (Tate) and *Zebina caledonica* (Tate). Two of Tate's species, revised by Anderson and Cox (1948). I have no further records.

Globularia formosa? (Morris and Lycett). Two specimens from Loch Bay are doubtfully referable to this common Great Oolite species.

These are all normal, shallow-water, marine fossils, either identical with or closely related to species of the English Great Oolite Series. The marine incursion was short-lived, however, and it seems likely that the lagoons reached almost marine salinity for a while, rather than that truly open-sea conditions were established. A closely analogous case is the invasion of the Texas *Crassostrea* reefs by a more saline fauna, of species which also inhabit the open Gulf, when salinity rises above 25‰ (see Hudson, this journal, p. 318).

Trotternish succession

The best exposure of the marine horizon is the shore section at Cairidh Ghlumaig, Duntulm (410737), where Macgregor first discovered *Rhynchonella* in the Great Estuarine Series (Macgregor 1934, Anderson 1948). The section shows, in summary:

	ft.	*in.*
3. Shale and limestone, alternating, with *Liostrea*	10	0
2. Shale, sandstone, and limestone with *Liostrea* and *Rhynchonella*, algal bed 3 in. below top	7	7
1. Sandstone with plant remains and *Liostrea*	11	0

The marine beds, as defined by the range of *Rhynchonella* (*R.* cf. *concinna*, Macgregor 1934), are no. 2 of the above succession. A bed of sandy shale, 2 ft. above the base of bed 2, yielded, in addition to *L. hebridica*, *Myopholas acuticostata*, *Anisocardia cucullata*, *Quenstedtia forbesi*, and indeterminate heterodonts. From bed 2 generally come *Discinisca sp.*, *Serpula sp.* and, according to Macgregor (1934), *Modiolus sp.*

A stream section ½ mile SSW. of the above locality (406728), above the road-bridge, is in beds probably entirely above those just described. It shows 7 ft. of green silty shales, with *Neomiodon*, overlain by 5 ft. of *Liostrea* beds, which also contain *Placunopsis*. This section is important as showing *Neomiodon* shales within the Lower Ostrea Beds. Loose blocks of sideritic mudstone, apparently nodules, yielded a well-preserved fauna of *Neomiodon brycei* and *N. sp.*, *Unio andersoni*, and *Viviparus scoticus*. All three genera occur in one hand specimen. This is one of the best freshwater faunas from the Great Estuarine Series. The loose blocks almost certainly came from the green *Neomiodon* shales within the Lower Ostrea Beds, and thus imply a very marked oscillation in salinity. It is notable that *L. hebridica* does not occur with the freshwater fossils. It is just possible, but unlikely, that the blocks came from the Ostracod Limestones higher up the stream.

Waternish succession

The small inlier at Loch Bay gives excellent exposures of the marine horizon. There are three sections showing algal beds in the Bay River and its tributaries. They differ in details but agree in showing two algal beds, separated by 1 to 2½ ft. of shale and oyster limestone, and probably are all on the same horizon. Anderson (1948, pp. 133–4) gives a map of the exposures, but only records one algal bed.

The following section is seen in the tributary to the Bay River at grid reference 271537; beds 1–3 in the right bank at a bend in the stream, beds 4–7 in the stream itself a little farther downstream:

	ft.	*in.*
7. Shale and limestone with *Liostrea*	3	9
6. Algal bed, brecciated	0	9
5. Shale with *Liostrea*	1	0
4. Algal bed, laminated, with *Rhynchonella* and foraminifera	0	9
3. Shale and limestone with well-preserved *Liostrea*	6	3
2. Sandstone, grey, fine-grained, uncemented	3	6
1. Clay, grey, sandy, base not seen	3	0

The top of bed 2 is somewhat hardened and yields abundant but fragile *Placunopsis socialis*, *Cuspidaria ibbetsoni*, and numerous ostracods.

Near the mouth of the Bay River a richly fossiliferous white limestone outcrops, overlain by the algal beds and *Liostrea* beds. It probably yielded many of the fossils listed by Tate (1873, pp. 346–7) from Loch Bay. My collection includes *L. hebridica*, *Myopholas acuticostata*, *Modiolus* cf. *imbricatus*, *Anisocardia cucullata*, *Corbula hebridica*, heterodont lamellibranchs, *Globularia formosa?* The top of this bed yielded the only polyzoan from the Great Estuarine Series, a cyclostomatous form revealed by a thin section.

At Lovaig Bay, about 2 miles WNW. of Loch Bay, there is a small outcrop of Lower Ostrea Beds below basalt, and richly fossiliferous blocks of limestone are strewn on the beach. One of these yielded *L. hebridica*, *Pleuromya robusta* (abundant), *Corbula hebridica*, *Anisocardia cucullata*, *Mytilus* (*Falcimytilus*) *sp.* Blocks of the algal bed also occur.

Duirinish succession

Only loose blocks of the Lower Ostrea Beds occur at Eist, in the stream draining Loch Mor and on the shore. They include the algal bed. One block of limestone yielded *Corbula hebridica*, *Pleuromya robusta*, and echinoid spines (in thin-section).

Raasay, Strathaird, and Eigg make no additions to the faunas from north Skye. *A. cucullata* is recorded from Raasay (Lee 1920). A thin-section from Eigg showed a regular echinoid plate and spine. This occurrence of regular echinoids in the oyster beds recalls the well-known association of *Hemicidaris* with the Cinder Bed in the Purbeck.

Muck succession

The typical oyster beds are better exposed in Camas Mor, Isle of Muck, than anywhere else (Hudson 1962). The transition from Concretionary Sandstone Series shales, with *Neomiodon*, is also well seen. Harker (1908) included these shales in the Ostrea Beds, and said that the oysters increased in size up the succession. According to my observations, *L. hebridica* comes in sharply, and is its normal size at the base. The algal bed occurs near the top of the exposed succession. A limestone about 5 ft. below this reveals numerous foraminifera in thin-section, mostly Miliolids.

Some of the fossils collected by the Geological Survey are wrongly listed in the Memoir (Harker 1908, p. 33). Lithologies and catalogue entries show that the following groups of specimens are truly from the Lower Ostrea Beds. I have revised the identifications. All are in the Survey Museum, Edinburgh.

1. T 3238A–T 3247A. Base of Ostrea Beds.
   Modiolus sp., *Placunopsis socialis*, fish scales.
2. T 3227A–T 3237A. Probably about 5 ft. below the algal bed.
   Liostrea hebridica, *Placunopsis sp.* or *spp.*, small lamellibranchs and gastropods; *Pholidophorus sp.* (ident. by Kitchin).
3. T 3221A–T 3226A. Ostrea Beds isolated among dolerite intrusions, i.e. near top of formation.
   Liostrea hebridica, including some very large specimens.

g. Ostracod Limestones

The fauna of this formation is extremely restricted. The typical lithology is alternating shale and argillaceous limestone, but the limestones are more muddy and the shales usually more calcareous than in the Estheria Shales. Mudcracks are very common. Many of the limestones are crowded with ostracods, and *Euestheria* is common; *Viviparus scoticus* is common in certain beds but other molluscs (notably *Neomiodon*) are rare. Scattered fish remains are frequent.

The most important exposure in Trotternish is at Kilmaluag Bay (437751, map in Anderson 1948, p. 129). Near the base of the formation, grey sandy shales with plant remains (5 ft.) are overlain by white calcareous shales with pyrite nodules and mudcracks

(2 ft.). Both these beds yield ostracods, *Euestheria murchisoniae* (unusually large in the calcareous shale) and lamellibranchs comparable to *Quenstedtia? staffinensis*, but generically uncertain. Higher up a limestone with *Viviparus* is interbedded with ripple-marked sandstone; the exact succession is difficult to determine because of discontinuous exposures. Yen (1948) collected fossils from here, but I have been unable to locate the beds in my succession. They were said to be 9 ft. above the Lower Ostrea Beds. Yen's succession, written out from his description (1948, p. 167), is:

	ft.	*in.*
4. Sandy limestone	1	0
3. Black shale	0	1½
2. Fine-grained cementstone	0	4
1. Sandy limestone	1	0

Bed 2 yielded two species of *Procerithium*, 'the sandy limestone' (it is not stated which) yielded *Viviparus scoticus*, *V. bithnyoides* (*Bathonella* of Yen), and *Neomiodon sp.* (*Cyrena jamesoni* Forbes). These *Procerithiums* are the only marine fossils from the Ostracod Limestones. I have not found a rock like that containing them elsewhere in the Great Estuarine Series, but similar small gastropods occur in the Estheria Shales with *Cuspidaria* and *Placunopsis*. They do not occur in the same bed as *Viviparus*. Anderson and Cox (1948) record *Assiminea skyensis* from 5 ft. above the base of the Ostracod Limestones here, and Cox (1950) records *Hydrobia praecursor* from the Ostracod Limestones of Skye, locality unspecified but probably from Trotternish. Both these genera of small gastropods inhabit brackish water today (Anderson and Cox 1948).

In Strathaird, Eigg, and Muck the Ostracod Limestones yield only ostracods, *Euestheria*, *Viviparus scoticus*, and fish fragments *V. scoticus* ('Paludina') gives its name to the Paludina Limestones of Wedd (1910). The Geological Survey's specimens from Muck are wrongly listed in the Memoir (Harker 1908, p. 33) as from the Ostrea Beds. Their true source is easily established from lithology. The fossils (T 3199A–T 3220A) comprise ostracods, fish fragments, *Euestheria murchisoniae*, and *Viviparus scoticus*.

Thus, except for one thin bed at Kilmaluag, the Ostracod Limestones contain a low-salinity assemblage throughout. The water must have been almost continuously muddy, and mudcracks show that it very frequently dried up. These facts may account for the

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EXPLANATION OF PLATE 53

Figures natural size except 3, 4; figs. 1, 4, 5, 6 coated with ammonium chloride. Sedgwick Museum registered numbers.

Figs. 1, 2. *Unio andersoni* sp. nov. 1*a*, *b*, Holotype, Lower Ostrea Beds?, near Duntulm, Skye; J.48684. Reversed stereo-pair, separation 6·5 cm. The specimen is an internal mould. 2, Mytilus Shales, near Kildonan, Eigg; J.48685. Left valve with nacreous shell preserved.

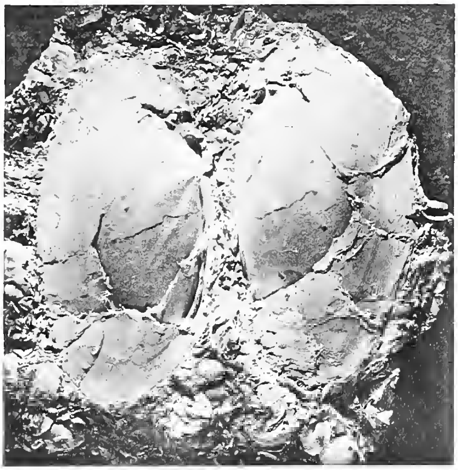
Figs. 3, 4. *Placunopsis socialis* Morris and Lycett. Mytilus Shales, near Kildonan, Eigg. 3, J.48686, left valve. 4, J.48687, left valve of large specimen of inflated form. Both ×2.

Fig. 5. *Cuspidaria ibbetsoni* (Morris). Mytilus Shales, near Kildonan, Eigg; J.48688. Left valve.

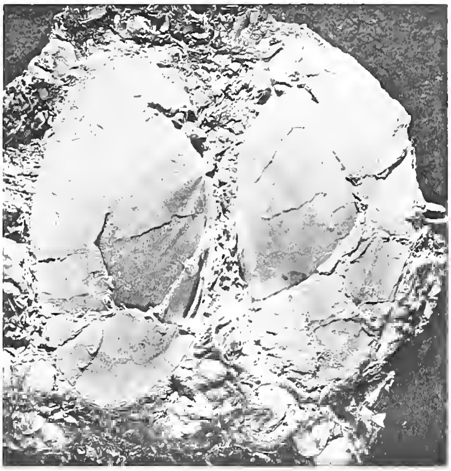
Fig. 6. *Mytilus* (*Praemytilus*) *strathairdensis* Anderson and Cox. Mytilus Shales, near Kildonan, Eigg; J.48689. Left valve with nacreous shell preserved.

Fig. 7. *Myopholas acuticostata* (J. de C. Sowerby). Lower Ostrea Beds, Duntulm, Skye; J.48690. Right valve.

Fig. 8. *Pleuromya robusta* (Tate). Lower Ostrea Beds, Lovaig Bay, Waternish, Skye; J.48691. *a*, Right valve. *b*, Anterior view. *c*, Dorsal view.



1a



1b

2

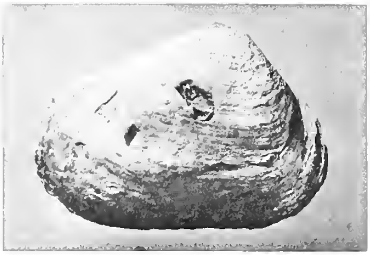
3 ×2

4 ×2

5

6

7



8a

8b

8c

HUDSON, Middle Jurassic Mollusca

absence of most of the usual mollusca, especially *Neomiodon*. It is also possible that the lagoons at this time were almost isolated from the open sea, so that even if salinity did increase (for instance during evaporation) marine forms could not enter the area.

h. Mottled Clays

These red beds are almost completely unfossiliferous, and were probably deposited largely above average water-level.

i. The Great Estuarine Series as now defined (Hudson 1962) ends with the Mottled Clays. In Trotternish it is overlain by the Upper Ostrea Beds, with a somewhat reduced marine fauna, and the Belemnite Sands, with a fully marine fauna. These faunas have been listed by Anderson and Cox (1948). They both include *Liostrea hebridica* and *Neomiodon brycei*.

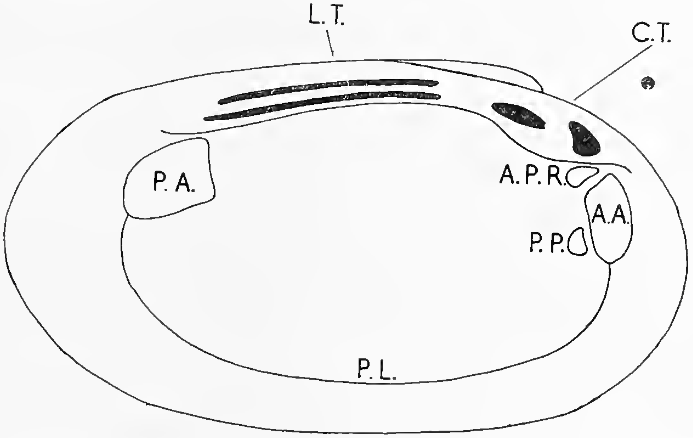
SYSTEMATIC DESCRIPTION

Genus UNIO Retzius, 1788

Unio andersoni sp. nov.

Plate 53, figs. 1, 2; text-fig. 3

Diagnosis. Species of *Unio* with the following generic characters: transversely elongate lamellibranch, with nacreous shell composed of aragonite. In the left valve, two large cardinal teeth anterior to the umbo, with a socket between them; two long lateral teeth, posterior to the umbo. In the right valve, one large cardinal tooth, sometimes (at least) divided; lateral teeth not seen, but probably one only. Anterior adductor muscle impression deep, anterior to and below the cardinal teeth. Anterior pedal retractor between anterior adductor and cardinal teeth; pedal protractor immediately posterior to anterior adductor. Posterior adductor large, high, shallow. Pallial line simple. External ligament long, posterior to umbo.



TEXT-FIG. 3. *Unio andersoni* sp. nov. Interior of left valve, ×2. Somewhat idealized reconstruction to show Unionid musculature and dentition. L.T., lateral teeth; C.T., cardinal teeth; A.A., anterior adductor muscle impression; A.P.R., anterior pedal retractor; P.P., pedal protractor; P.A., posterior adductor; P.L., pallial line.

Specific characters: shell small for a *Unio*, ovoid, length nearly twice the height, compressed. Umbones depressed, scarcely projecting above hinge-line, situated at the anterior third of the length. Outline smoothly ovate, the ventral margin very gently convex. Inflation smooth, at maximum below the umbo; posterior ridge feebly developed or absent. Shell rather thin for a *Unio*, unornamented except for faint growth-rugae.

Holotype. Sedgwick Museum no. J48684; Lower Ostrea Beds?, Great Estuarine Series (Bathonian), stream 1 mile south of Duntulm Castle, Isle of Skye, Scotland.

Dimensions. Holotype: length 4·5 cm., height 2·5 cm., thickness through both valves (approximate) 1·5 cm. These dimensions are approximately constant for well-preserved, apparently adult, individuals, in the many specimens examined. The maximum length seen was 5·5 cm.

Name after Dr. F. W. Anderson in recognition of his researches on the Great Estuarine Series.

Material. All from the Great Estuarine Series, Middle Jurassic, of the Inner Hebrides.

Locality 1. As for holotype; loose blocks, probably from the Lower Ostrea Beds. The holotype and four other specimens. The holotype is the most complete specimen known. It originally had some shell attached, but was developed as an internal mould to show dentition and musculature. Reversed stereo photographs, used at the suggestion of Dr. C. L. Forbes, enable the mould to be seen as a three-dimensional shell, and greatly help in interpreting the structures.

Locality 2. Reptile Bed, Mytilus Shales, Eigg. My collection, several specimens mostly fragmentary. Geological Survey, Edinburgh: T 2843A, T 2862A, T 2878A (cf. Jackson 1911*a*, pl. 10, fig. 2, neanic form of *U. distortus*), T 2902A, T 2928A–T 2930A.

Locality 3. Unio Bed, Mytilus Shales, Eigg. My collection, fifteen specimens, some with nacreous shell. Geological Survey, Edinburgh: T 2944A–T 2947A. Almost certainly from this bed, from the matrix. T 2944A has part of the ligament preserved.

In the Geological Survey, Edinburgh, are some small *Unios* from the Brora Estuarine Series which may be conspecific with *U. andersoni* (R and S 3564–7). None of them shows musculature or dentition. A small *Unio* from Brora was referred to *U. distortus* by Jackson (1911*a*, p. 120).

Discussion. The shell characters are undoubtedly those of a Unionid (text-fig. 3) and compare closely with those of modern *Unio* (e.g. Cox 1961, p. 329). The species appears to be more closely related to *Unio* than to *Margaritifera*, from the list of shell characters given by Mongin (1961, p. 341).

The only described Middle Jurassic *Unios* from Britain are from the Yorkshire 'Estuarine' Series. In internal characters my species agrees with *U. kendalli* Jackson (1911*b*) from the Lower Estuarine Series (Bajocian), but in shape of shell and lack of ornament it more closely resembles *U. distortus* Bean (Jackson 1911*a*) from the Upper Estuarine Series (Bathonian?). The internal characters of *U. distortus* are unfortunately not accurately known, and it is also about twice as large as my species. Jackson (1911*a*) referred it tentatively to *Margaritana* (= *Margaritifera*).

Various genera, or subgenera, of *Unio*, have been proposed for Mesozoic Unionids from North America and Japan; Dr. L. R. Cox kindly sent me a list of these. The only one which at all resembles my specimens is *Rhabdotophorus* Russell 1935, from the Cretaceous of Alberta. The internal structures, size, and outline are similar, but it has costae on the post-umbonal slope which my species lacks. The geological horizon and locality are also very different. Until a comprehensive review of Mesozoic Unionacea is undertaken it seems best to leave the species in *Unio sensu lato*.

Acknowledgements. I wish to thank Dr. F. W. Anderson, Dr. L. R. Cox, and Dr. R. Casey for discussions on the mollusca, and Dr. Anderson, Mr. R. B. Wilson, and Dr. R. M. C. Eagar for access

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MICROBIOLOGICAL COLONIZATION AND ATTACK ON SOME CARBONIFEROUS MIOSPORES

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ABSTRACT. The paper describes *Palynomorphites diversiformis* gen. et sp. nov., a saprophytic organism thought to be related to the Fungi, and which is responsible for some part of the microbiological attack on Carboniferous miospores. The different organization of this attack on several groups of miospores of widely varied structural characteristics is described. The miospores were preserved in a chert band within the Upper Oil Shale Group of the Calciferous Sandstone Series of Scotland at a horizon considered on the evidence of goniatites to be of Upper Viséan age.

DURING studies of the micropalaeontology and constitution of the Scottish Carboniferous Oil Shales, problems of the recognition and possible interrelationships of the organic contents of the Oil Shale were encountered. The presence of a relatively opaque organic groundmass in close association with inorganic material led to difficulties in the resolution of the finer organic material as seen in normally prepared thin-sections. This was also true of larger organic entities such as wood cells, spores, or algae embedded in the groundmass. To some extent these difficulties were overcome by the production of microtomed sections and by the application of peel techniques to polished and etched surfaces. On the other hand, the improved techniques indicated the presence of a considerable content of fine cellular material within the groundmass and upon the surface of many larger remains such as fragments of wood and spores. The application of maceration techniques resulted in the isolation of some ingredients e.g. spores and algae, and provided substantiation of the presence of microbiological remains upon their surface or within their body. These studies also indicated the possibility of selective, partial, or complete destruction of the various organic constituents during the varied maceration processes. However, in favourable preparations considerable quantities of fine thread-like filaments, or small rounded cells often in groups or chains, were present within the groundmass and upon subjects embedded within it. This material, present to some extent in all the oil shales studied, appeared to play a significant part in the constitution of certain types of oil shales.

In order to investigate what appeared to be evidence of microbiological attack, possibly of a saprophytic character, upon the organic material, other rocks within the Oil Shale succession were studied. These included calcareous shales, limestones, ironstone nodules, and chert nodules and bands. This account describes the evidence provided by one chert band, and from the sum total of the microbiological attack on a wide variety of organic remains presents that evidence concerned with the attack on miospores. Subsequent papers will be concerned with the attack on other plant remains by a variety of microbiological agents.

Brief summary of previous work. There is considerable literature concerned with the presence of microbiological remains of a type resembling in morphological details those

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herein described. The occurrences relate to most geological systems from the Precambrian (Tyler and Barghoorn 1954) to the present day, with particular abundance within the Tertiary (Meschinelli 1902). The remains have been recorded from a wide diversity of rock types in association with fossil plant and animal remains, or as isolated entities. The ubiquitous distribution is striking and references to either Fungi, Algae, or Bacteria are equally varied and controversial. In many cases the association of microbiological remains with recognizable fossil plants or animals led to a direct comparison with existing organisms and their known methods of attack, and resulted in identification of genera and species which imply genetic affinity with members of these three main classes.

Bacteria have long been regarded as the main instruments of organic decay and an early record of their fossil occurrence was due to Van Tieghem (1879), who recorded *Bacillus amylobacter* from silicified Coal Measures rocks of St. Etienne. This work was followed by Renault (1896, 1900), who described and named a great variety of bacteria, both micrococci and bacilli. On the basis of their morphology and association with particular organic material, a number of genera and species were erected principally for Carboniferous and Permian forms.

A further group of organisms consisting of fine filaments from $0{\cdot}7\mu$ to $2{\cdot}0\mu$ in diameter have received consistent reference in literature. Thus Wedl (1858) described remains from animal shells of various geological ages as due to the 'alga' *Saprolegnia ferox* (Kützing), while other authors, e.g. Kolliker (1859), referred similar organisms to the Fungi. Renault (1900) referred to fine aseptate filaments of the saprophytic fungus *Phellomyces* in the bark cells of Carboniferous plants; similar remains from carbonaceous shales, oil shales, and cannel coals were referred to the saprophyte *Anthracomyces cannellensis*.

Kidston and Lang (1921) described forms of somewhat greater geological age consisting of a felt of aseptate unbranched tubular filaments 2μ in diameter from the Rhynie chert. The organisms, designated Schizophyta No. 2 and No. 3, were compared with *Archaeothrix contexta* and *A. oscillatoriformis*, and, while they were regarded as possible fungal hyphae, they were believed to be suggestive of the Trichobacteria, *Beggiatoa* or *Oscillatoria*.

In recent years organisms with affinities between Fungi and Bacteria have received considerable attention as the Actinomycetes. Although some indecision is evident regarding the systematic position of these organisms from the works of Drechsler (1919), Henrici (1947), Waksman (1950), and Bergey (1948), there is a clear understanding of their morphological characteristics. Thus according to Waksman, the Actinomycetes are organisms forming elongated, usually filamentous, cells; the filaments are usually 1μ or less and do not exceed $1{\cdot}5\mu$ in diameter. They multiply by special spores (oidiospores) or by conidia; the oidiospores are formed by segmentation or simple division of the filaments, whilst conidia are formed singly at the ends of simple conidiophores. The genus *Actinoplanes*, a fungus allied to the Actinomycetes, was responsible for the attack on certain modern pollen described by Goldstein (1960).

There have been few references to the attack of micro-organisms on fossil spores; this is particularly true for those of Carboniferous age. Reinsch (1884) figured and described what he believed to be fungi on spore coats, and Renault (1900, p. 204) described the presence of the saprophytic fungus *Anthracomyces cannellensis* on the surfaces of micro- and megaspores, and from within the latter.

The attack of modern aquatic and soil-inhabiting fungi on pollen has long been known to botanists. Goldstein (1960) gave a summary account of some of this work and described the attack by Phycomycetes, both filamentous forms and Chytrids. He draws attention to the importance and interest of the degradation and destruction of pollen grains in pollen analysis studies, and amongst other conclusions refers to the different modes of attack of the various fungi on pollen, and to the greater susceptibility to attack of some types of pollen grains.

Sangster and Dale (1961) carried out controlled experiments on three genera of pollen, *Populus*, *Pinus*, and *Typha*, placed in four different habitats: pond, lake, swamp, and bog. Their work indicated considerable variability in preservation and fossilization of these genera under identical conditions. They concluded also that the decomposition of a given pollen is dependent on the environment which affects not only the rate of decomposition, but the nature of the processes involved. The processes were in part microbiological, and, particularly in the cases of *Populus* and *Typha*, were due to bacteria, although these organisms were not described nor the nature of the decomposition discussed. Other experimental evidence indicated oxidation to be an important factor in disintegration for certain environments and suggested that the resistance of the exine to an oxidizing agent favours fossilization. The *Pinus* pollen was very resistant to disintegration and was well preserved in all four sites; *Typha* pollen was preserved only in the bog; *Populus* disintegrated at all four sites. The authors concluded that the exines possess in varying proportions the material 'sporopollenin', a substance of extraordinary chemical resistance; they drew attention to differences in the percentage frequency of species in the pollen rain spectrum and the fossil spectrum. These differences follow from the differential preservation of the exine, and also from the fact that bog environments or stagnant water will not necessarily 'fossilize' pollen grains.

Studies on the degradation of modern and near-recent plant tissues have focused attention upon the importance of the microbiological action of fungi and bacteria as the most effective agents of degradation. Many authors, including Barghoorn (1952), Siu and Reese (1953), Savory (1954), and Reese (1959), have described these processes and the factors which affect susceptibility to microbial attack. Of considerable relevance to the present study is the readiness with which cellulose is attacked and the effect of the amount and nature of the non-cellulosic components. Where the latter are resistant, e.g. lignin and waxes, the more resistant is the structure to microbiological decomposition. Barghoorn (1952) drew attention to the pronounced differences in the rates of degradation of various cellulosic layers of a single cell wall. This differential degradation of cellulosic lamellae is stated to be a consistent feature of anaerobic decomposition. It is thought to be due to chemical differences in the more resistant lamellae of the cellulosic framework and to the presence of substances, notably lignin, which retard the hydrolysis of cellulose. Lignin is stated to be a primary factor in retarding the action of many fungi and most bacteria.

The mechanism of microbiological attack upon cellulose described by Siu and Reese (1953) and Reese (1955, 1959) is dependent upon physico-chemical action. The active hyphal tip of the fungus produces hydrolytic enzymes which diffuse into the substrate and digest it, the hypha growing into the digested region and maintaining contact with the substrate. The growing fungus appears to follow the cellulose distribution and in certain cases seems to have followed the orientation of the cellulose fibrils (Bailey and Vestal 1937, Savory 1954, Reese 1959).

The possibility of an interrelationship between the presence and activity of the attacking organism and the distribution of materials of varied constitution over the spore body cannot be overlooked. This may be brought about by distribution of material resulting from major differences in the structure of the spore, or may be due to differential changes in composition in a given layer or in different layers of the exine. For this reason the microbiological attack on miospores is presented in a systematic manner in the following pages.

THE CHERT BAND

Locality and horizon. The chert band occurs within the Midhope Burn of Midlothian, where it outcrops on the south bank of the stream at the locality described by Kennedy (1943, p. 12) and within the following section:

	ft.	*in.*	
Dark shales with ironstones bands and nodules	30	0	
Hard, bedded ashy limestone	4	0	
Dark shale with plant remains (*Lepidostrobus*)		6	
Dark shale with entomostraca and fish remains		6	
Grey micaceous shale	1	6	
Entomostracan limestone		2	
Shale with plant detritus		6	
Black coaly shale, irregular distribution in small pockets		0–2	Horizon of Two Foot Coal
Chert brown or grey in nodules, mammillated upper surface—plant remains		0–3	
Calcareous and ferruginous siltstone, containing chert nodules and banded black chert		0–1	
Thin coaly shale		1	
Impure ferruginous sandstone		2–6	
Black, sulphurous carbonaceous shale with entomostraca		6	
Oil shale of inferior quality		6	

This section occurs within the Upper Oil Shale Group of the Calciferous Sandstone Series, and towards the top of that Group. Kennedy (1943, p. 12) observed the chert band to contain petrified plant remains and considered that it replaced the normal position of the Two Foot Coal. The band occurs below the Raeburn Shell Bed which is exposed within the Midhope Burn and nearer Dovecotes Farm. Stratigraphically the horizon appears to lie within the Bollandian Stage of the Lower Carboniferous and possibly within the lower part of that stage, namely P_1. Such a reading of horizon follows Currie (1954, p. 531) and depends upon the correlation of the goniatite-rich Fordell Marine Band of Fife, with a horizon near to that of the Raeburn Shell Bed. Currie (1954, p. 533) also pointed out that corroboration of such correlation follows from the occurrence and range of *Posidonia becheri*, which reaches a maximum in the higher Basket Shell Bed. The latter horizon by analogy with the local maximum in the north of England would indicate Zone P_{1b}. The chert band probably occurs within P_1, possibly near the base of that zone, and is thus of Upper Viséan age.

Mode of occurrence of the chert. The upper layer of the chert has a nodular or mamillated surface, the hollows of which are filled by a black laminated coaly shale of very irregular distribution. The higher or brown chert is remarkably pure and contains well-preserved macroscopic plant remains; it is principally from this part of the chert that the organic remains have been obtained. The lower black and banded chert is organic rich but impure, and evidence of replacement of the original sediment by chert is seen in thin-section and will be described elsewhere. The combined evidence supports Kennedy's opinion (p. 12) that the horizon marks the position of the Two Foot Coal Seam. It points to penecontemporaneous inundation of a peat or soil by siliceous waters prior to diagenesis of the underlying sediment. Whether the upper band of the chert contains precisely autochthonous plant material, or whether that material was introduced by the invading solutions cannot be ascertained. However, much of the plant material could not have been transported far in view of the delicate structures preserved. The material represents the decayed remnants of a terrestrial flora in which the processes of decay were arrested by saturation in the siliceous water and subsequently preserved in the chert. The methods of disintegration, the various stages reached, and the selective action of parasitic or saprophytic attack upon a variety of organic ingredients provides important evidence of the microbiological agents concerned with the eventual disintegration of organic material. At the same time, some appreciation of the intermediate and final products of decay is of inestimable value in a consideration of the organic detritus which would be swept from a soil or peat into the depositional areas of the oil shale accumulation.

The mode of occurrence of the chert and state of preservation of the organic material is reminiscent of the remarkable Rhynie chert of Aberdeenshire described by Kidston and Lang (1921); there is, however, no detailed evidence of peat succession and inundation such as occurred at Rhynie. The wide range of microfossils, including spores and pollen, wood cells, algae, fungi, and presumed bacteria, together with fragments of insect remains and possible protozoa, suggests the presence of a very shallow water cover such as a pool or pond at the time of inundation.

Preservation of plant material. The organic material is preserved within the chert with no sign of appreciable chemical alteration of the spore coat substances. Such a conclusion is suggested by examination of thin-sections, and demonstrated by the ease with which the organic matter can be chemically released by hydrofluoric acid. There is little or no subsequent alteration of the material by bituminization or coalification processes, such as would lead to darkening of colour or disruption of structures. Consequently it has been unnecessary to subject the material to maceration techniques other than that involving hydrofluoric acid digestion; therefore the difficulties of partial or selective destruction of some material in attempts to clear the remainder have been avoided.

Chert provides the best possible medium for the preservation and study of microbiological remains. It is homogeneous and its hardness prevents compression. The relative insolubility, and the unjointed and non-porous character of the rock, preclude the introduction of a microbiological population by groundwater or surface solutions. Likewise, it is resistant to weathering and erosion and prevents the subsequent introduction of those microbiological remains associated with rock weathering and disintegration.

Techniques of study. The upper brown or grey chert was cut into a rectangular block and thus freed from the possibility of surface contamination. Smaller slices from this block were placed in polythene containers to which 40 per cent Analar hydrofluoric acid was added. A light-brown sludge settled on to the base of the container from which the hydrofluoric acid was removed by repeated dilution with distilled water. This was carried out manually at high acid concentration, and later by means of a suction pump using an inverted micro-porcelain filter until acid reaction was negligible. The filter was attached to a suitable cover and set at a constant level within the container, thereby causing a minimum amount of mechanical movement in the organic material and preserving detailed structures. The organic material, taken direct from the polythene container, was mounted in glycerine jelly while still moist. Since the difference of refractive indices between the material and mounting medium was sufficient to provide good resolution of detail at high magnifications, the majority of the slides were thus prepared. Some of the organic material was stained with safranin or Cotton Blue with the original objective of improving resolution of detail. However, the material proved to be selective in its absorption of stain and particularly so with safranin, and this selectivity provided an initial basis for the recognition of related but scattered organic components; some remains in the slides were avid in their absorption of Cotton Blue. Concurrently with examination of these mounts, the study of thin-sections served to demonstrate the presence of similar material within the chert, but the mounted isolated organic material possessed considerable advantages for study of detail. The mounts have been prepared for a number of years and in some instances a series of photographs taken of the same object. In no single case have there been any changes in the nature or distribution of the microbiological remains associated with the spores and pollen described in this paper. Under these circumstances the author is confident that an indigenous microflora was responsible for the saprophytic attack, and that such studies can be conducted with advantage, particularly when chert is the parent rock.

THE MICROBIOLOGICAL ATTACK

The various forms described are all characterized by a prominent, dark, and relatively thick cell wall which encloses colourless or pale-yellow contents of high refractivity. The commonest forms are spherical cells of the coccoid type which range in size from $0{\cdot}75\mu$ to $1{\cdot}5\mu$, but a frequent modification provides larger ovoid cells which reach 1–2μ on the longer axis.

The cells may occur singly or in pairs of either rounded or ovoid forms, and this arrangement is usually in the 'end-on' position when the appearance resembles the diplococcoid organization. Occasionally a T-shaped grouping of three cells is observed, but more commonly an irregular grouping of the cells results. Increase in the number of spherical individuals in the 'end-on' position forms a chain which resembles the streptococcal organization. The presence of predominantly ovoid or elongate cells in a linear arrangement forms a beaded filament. The latter may be short (2–3μ) or much longer (10–20μ) and occasionally show lateral bifurcation; the termination of such a filament is marked by a highly refractive and larger spherical cell, but there is no clear evidence of septation. Rod-shaped forms (2–3μ) resembling bacilli in appearance are present; these do not show a beaded structure and may possess either bluntly rounded ends or swollen terminations. While straight forms are more common, simply curved examples have been observed.

Filaments with well-defined parallel walls and resembling hyphae in appearance vary from $0{\cdot}75\mu$ to $1{\cdot}5\mu$ in thickness and may be straight, flexuous, or with polygonal, curved, or concentric arrangement, and vary considerably in length. Branching of the filaments is a common feature and the angle of bifurcation most variable from acute to right-angled and obtuse. At the point of bifurcation there is usually some swelling and the point is generally marked by the appearance of a spherical cell. Occasionally single swollen vesicles may occur along the length of a filament, and many filaments end in a beaded structure or are represented by a beaded filament at certain points. No evidence of septation has been observed in any of the filaments examined.

Organization of attack. The small spherical cells are commonly randomly distributed, but they may show some orientation which follows the structure of the host material. When this occurs their form becomes ovoid and the long axis of the cell lies in the orientated direction. Under these circumstances pairs of cells in the 'end-on' position result, and the eventual linear arrangement of elongate cells gives rise to a beaded filament which possesses a prominent orientation. The filaments commonly show a similar orientated relationship, particularly when they are in part beaded or are in close association with beaded filaments. However, when the filaments are particularly well developed they may indicate an independence of structural orientation.

The considerable diversity of elements may suggest more than one kind of organism to be concerned with the attack. However, the similarity in size and appearance, and the continued association of all these elements, point to a single organism exhibiting various stages of vegetative development and which may be observed on the several regions of the same spore. Modification of the host material following upon changes in the degree of attack may lead to changes in the vegetative form of the attacking organism at a given point. In this manner the incidence of attack by coccoid or ovoid cells may lead to the presence of beaded filaments and finally give rise to filaments. The latter in turn may produce beaded filaments or fragment into cocci when absorption is completed. Some supporting evidence occurs in cases where well-defined filaments cross areas of totally destroyed exine, they become beaded in part and possess large terminal spherical cells.

The biological affinity of the attacking organism is in doubt; morphologically it might be similar to certain bacteria, actinomycetales, or fungi. The filaments respond only faintly to staining and are merely tinted with Cotton Blue. From the evidence presented in this paper it is impossible to decide on the parasitic or saprophytic nature of the attack. Nevertheless, the presence of this or a similar organism on a wide variety of organic material, such as could only be brought together as a result of continued processes of decomposition, suggests the action to have been saprophytic.

This saprophytic attack upon various groups of miospores is described below. In some instances it has been possible to follow the attack from its incidence to its completion by selecting spores (of the same genus) which clearly show a progression of events. In this manner some degree of selectivity of the saprophyte upon the host is demonstrated, and the structural features of the various spores are shown to exert considerable control over the distribution and manner of attack; the organism follows these features to a great extent. In spores where there is no marked structural differentiation the ornament of the exine, particularly in thick-walled forms such as *Convulutispora* (p.364), plays an important part in controlling the distribution of the attack and the manner in which it is carried out.

SYSTEMATIC DESCRIPTIONS

Fungi incertae sedis

The organism in some of its characteristics bears resemblances to the small saprophytic fungus referred to by Renault (1900, p. 334) as *Anthracomyces cannellensis* and recorded from a variety of Carboniferous and Permian rocks. Renault considered this fungus to be closely related to the groundmass of the carbonaceous rocks and to be generated within this medium, spreading on to the other recognizable organic fragments contained within it. His insistence upon the rôle of this fungus as a means of producing organic detritus under certain conditions is reflected in the specific name *A. cannellensis*. The fungus was described as forming a small plant 5–6μ in height, with straight sinuous or branching filaments 2–2·9μ long and 0·85μ wide. Short branches were noted to end in a spherical conidium. The propagation of individual plants was believed to form a felt which spread over the organism attacked.

Renault did not provide a systematic diagnosis of generic characters or give a specific definition, and no reference was made to the method or organization of the attack by the fungus. Considerable difficulties are involved in interpreting the very general and much-restricted account of the organism as given by Renault, especially since the present work has shown a very much wider range of variation on both sides of what might be considered the mean characteristics referred to by Renault. As a result it is proposed, at a later stage in these studies, to emend the genus *Anthracomyces* and to restrict its use for the reference of similar saprophytic fungi present in the disorganized organic matter of carbonaceous rocks. The present organism, in view of its considerable morphological variation and the close relationship of its organization with the structural features of the spores, is referred to a new genus *Palynomorphites*. There may well be overlap between the new genus *Palynomorphites* and the forms to be included in the emended genus *Anthracomyces*, but at the present stage of the investigations it is necessary to refer to form genera.

Genus PALYNOMORPHYTES gen. nov.

Type species. P. diversiformis sp. nov.

Diagnosis. Single coccoid, ovoid, or bacilli-like cells, or aggregates of such cells; beaded or non-beaded filaments, aseptate. 0·75μ to 1·5μ in cross-section and occurring on or within fossil spores.

Palynomorphites diversiformis sp. nov.

Holotype. Plate 54, fig. 13; fungal elements investing a specimen of *Densosporites*.

Type locality. Slide Mb/Ch/3/4/907260. Chert Band, Midhope Burn, Upper Oil Shale Group of Calciferous Sandstone Series (Scotland), Upper Viséan, P_1 subzone.

Diagnosis. Coccoid or ovoid cells 0·75μ to 1·5μ arranged in a linear 'end-on' position, and associated aseptate filaments 0·75μ to 1·5μ in width.

Description. Cell walls dark and well defined; cell contents highly refractive, colourless or pale yellow. The filaments may be straight, flexuous, or curved, or exhibit simple bifurcation to produce a rounded or reticulate pattern. At the point of bifurcation a rounded cell is present and filaments may terminate in a swollen rounded cell.

Coccoid cells may occur alone as on *Punctatisporites*, Plate 55, fig. 10, or be associated with beaded filaments only as on *Punctatisporites*, Plate 56, fig. 2*c*. Filaments both beaded and non-beaded may occur in close association and of very variable length. They may occur together or singly without the normal association of coccoid cells. These features are exemplified by *Lycospora*, Plate 54, fig. 11.

Comparison. P. diversiformis sp. nov. in certain characteristics bears resemblance to *A. cannellensis* Renault (1900, pl. 22, figs. 4–10; text-fig. 24) but *A. cannellensis* Renault (1900, p. 334) was defined as 'a plant 5–6μ high, with straight branching or sinuous filaments 2–2·9μ long and 0·85μ wide'.

DESCRIPTION OF MICROBIOLOGICAL ATTACK ON VARIOUS MIOSPORES

Schulzospora (Pl. 54, figs. 1, 2, 3).

The grain of *Schulzospora* consists of a circular central body, with an enveloping saccus which may be attached to the proximal polar region of the central area.

The three grains illustrated represent the varying degrees of saprophytic investment observed for this genus. Thus Plate 54, fig. 1 indicates incipient attack by isolated irregularly distributed coccoid cells, while in Plate 54, fig. 2, with a greater intensity of action, some pattern of distribution becomes apparent. With the heavier concentrations near the equatorial margins of the saccus, and in a region near the junction of the saccus with the central area, there is a tendency to the formation of chains of cells and beaded filaments. On the saccus alone there is little definite arrangement but many filaments cross on to the region underlain by the central area where a distinct radial arrangement is followed. Many of the filaments branch or coalesce to enclose irregularly shaped polygonal or rectangular areas of pitted or thin exine. In some cases the proximal exine has been removed from the polar region of the central area as at Plate 54, fig. 2. A high concentration of saprophytic material around the junction of the saccus and central area and over the surface of the latter is demonstrated by Plate 54, fig. 3. The concentric organization of the disturbed wall substance appears to have resulted from attack in depth which has totally disorganized the saccus covering and the exine of the central area. Some part of the disorganized infected exine was partly moved from the body of the spore during mounting and is seen (Pl. 54, fig. 3) to consist of coccoid cells and beaded filaments.

Other examples of this type of spore were noted in which the central area was either partly destroyed or even absent. These may indicate the ultimate effects of the form of attack upon the saccus and central area, or alternatively the partial destruction of the enveloping saccus may lead to release of the central body. There appears to be some relationship between the form of the spore and the resulting organization of attack. Thus the polygonal or rectangular habit of the filaments enclosing the pits on the flatter polar region of the central area gives place to a radial orientation of elongate cells and beaded filaments on the sloping sides of that area. The fringes of the saccus show a less definite arrangement over their flattened surface, but the concentric orientation of elongate cells followed in Plate 54, fig. 3 appears to be directly related to the presence and influence of the central body. The dark region on the central area of Plate 54, fig. 1

consists of a dense mass of very thick-walled dark-brown cells of a type differing from those under present description.

Lycospora (Pl. 54, figs. 4–12)

The illustrated spores represent common forms in the preparations and they have been selected to show the varying degree of saprophytic attack and its manifestations on the various structural units of the spore. There is a close correlation between areas of microbiological action, the nature and orientation of the attacking cells, and the structure of the spore. Demonstration of this relationship follows from a study of proximal and distal surfaces, and as a result of separate consideration of the central area and cingulum. The latter is further subdivided into the thickened inner region (crassitudo) and the outer equatorial flange.

Plate 54, fig. 4 depicts in proximal view a typical *Lycospora* with granular ornament and carrying incipient attack over its surface by isolated or small groups of coccoid cells. A concentration of elongate cells and beaded filaments with a linear orientation occurs along the dehiscence slits of the central area. The crassitudo carries a similar concentration of cells orientated in a concentric manner.

The central area. On the proximal surface along the margins of the triradiate marks, the concentration of linearly orientated cells, and the subsequent development of beaded filaments are characteristic but variable features. Plate 54, fig. 4 depicts the earlier stages of this development, which is continued in Plate 54, figs. 5 and 6. The spores of Plate 54, fig. 10, and particularly Plate 54, fig. 11, illustrate the eventual production of relatively thick-walled filaments. Each proximal intertectal segment carries independently orientated elongate cells or beaded filaments traversing the exine between the triradiate marks in broken or continuous lines, as illustrated by Plate 54, figs. 5, 6, 8. Some of the filaments either branch or coalesce to enclose rounded, rectangular, or polygonal areas of altered exine, as shown by the circular pale areas of Plate 54, fig. 5*a*.

The absence of haptotypic features on the distal surface of the spore leads to a different organization of attack. In the initial stages this consists of rounded coccoid cells which

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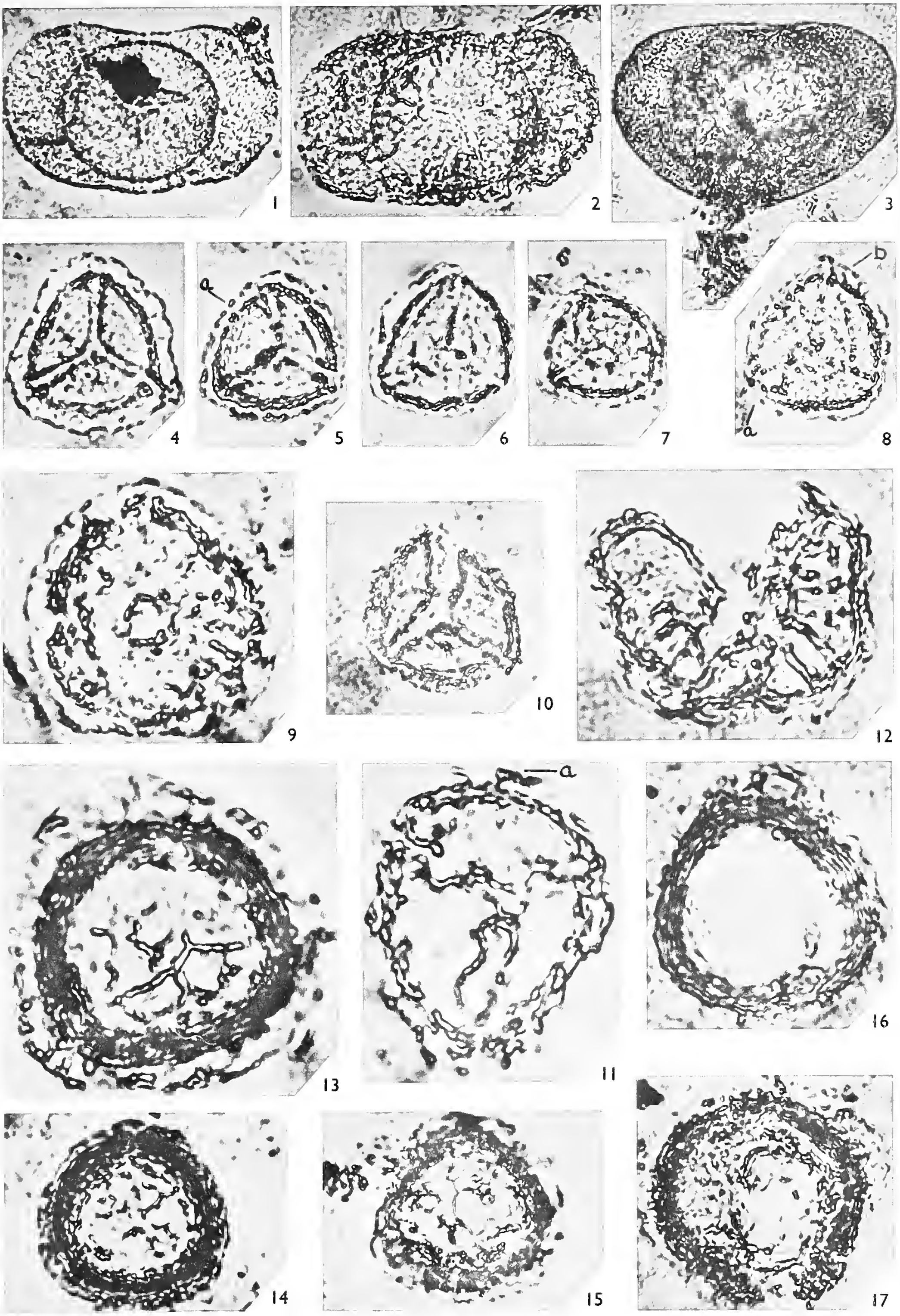
EXPLANATION OF PLATE 54

All figures are of specimens from the Chert Band, Midhope Burn, Upper Oil Shale Group of the Calciferous Sandstone Series (Scotland). Upper Viséan, P_1 subzone. Magnification ×750 unless otherwise stated. Slides all labelled M.B.Ch.

Figs. 1–3. *Schulzospora sp.* 1, 3/5/726.334, proximal surface. 2, 3/7/793.200, proximal surface. 3, 3/3/776.341, distal surface.

Figs. 4–12. *Lycospora sp.* 4, 3/7/712.260, proximal surface. 5, 3/6/779.403, proximal surface; *a*, rounded and polygonal areas of altered exine on central body. 6, 3/6/803.360, proximal surface. 7, 3/6/810.247, distal surface with reticulum of filaments. 8, 3/6/776.295, distal surface; *a*, single large lumen; *b*, concentrically orientated elongate cells and radial filaments on the equatorial flange. 9, 3/6/730.256, distal surface, ×1500. 10, 3/6/766.290, proximal surface. 11, 3/6/811.230, proximal view of '*Palynomorphites* pseudomorph', ×1500; *a*, fragments of the equatorial flange with filaments spreading from the annular zone. 12, 3/7/690.322, distal view, ×1500.

Figs. 13–17. *Densosporites sp.* 13, 3/4/907.260, distal surface. Type of *Palynomorphites diversiformis* gen. et sp. nov. investing distal surface of *Densosporites sp.*, ×1500. 14, 3/8/805.188, distal surface, ×1000. 15, 1/4/798.140, distal surface. 16, 3/5/750.197, presumed distal view, concentric arrangements of filaments within annular region, ×1500. 17, 3/5/782.166, presumed proximal view.



MOORE, Microbiological attack on Carboniferous miospores

are either randomly distributed or show a very general concentric organization, e.g. Plate 54, fig. 8. The development of elongate cells, beaded filaments, and short true filaments (Pl. 54, fig. 9) results in the formation of irregular areas from which the exine has been destroyed; a single lumen is shown in Plate 54, figs. 8*a* and 9. The eventual pattern of attack for the distal surface is represented by Plate 54, fig. 7, in which the surface of the central area is represented by a reticulum of filaments.

The Cingulum, thickened inner zone (*crassitudo*). One of the most remarkable areas of investment is the thickened annular ring of exine concentric to and bordering the central area of the spore. Incipient action on this region (Pl. 54, fig. 4) is represented by rounded or elongate coccoid cells orientated longitudinally in a concentric manner. With more severe attack prominent filaments lie within the structure, and their strong concentric orientation is particularly well illustrated by Plate 54, figs. 5, 7, 11. Prominent vesicle-like swellings give rise to filaments which branch on to or into the central area of the spore, particularly with respect to the distal surface (Pl. 54, figs. 7, 12), but also at some points on the proximal surface (Pl. 54, fig. 11). Other filaments radiate from this region into the flange area towards the equatorial margin of the spore, and are seen in Plate 54, figs. 11*a*, 8*b*.

The Cingulum, equatorial flange. This region extends from the outer area of the thickened zone to the equatorial margin of the spore and consists of a double layer of thin colourless exine. The radiating filaments referred to above cross the flange and either end in a spherical vesicle at the equator of the spore or are connected with beaded filaments developed there. The equatorial margin is often markedly indented and carries concentrically orientated elongate cells and filaments, e.g. Plate 54, figs. 4, 8*b* and the lower equatorial margins of Plate 54, figs. 5, 6, 7. The flange is often much reduced in width and may be absent.

Plate 54, fig. 4 illustrates incipient attack on the equatorial flange by isolated coccoid cells with some radial and concentric filaments. The area of the flange is often reduced by increased microbiological activity upon its equatorial margin, e.g. Plate 54, figs. 5, 7, 8, but equally severe action also takes place from the inner margin of the flange at a stage when the attack on the thickened inner zone (crassitudo) is well defined. Thus Plate 54, figs. 5–8 show a colourless and irregularly patterned area from which the exine of the inner margin of the flange has been removed, due either to the concentration of radial filaments or, more likely, to the absorptive effect of the concentric filaments in the neighbouring annular zone. This destruction of the inner flange exine is due to microbiological action, and not to mechanical effects since the remaining flange exine is entirely isolated from the central body of the spore, except at those points where the radial filaments which cross this area act as connecting links. In Plate 54, figs. 5, 6, 8 the filaments alone hold the remainder of the flange to the body of the spore. Such a fragile connexion serves to emphasize the importance of microbiological destruction of the external border of the flange, for it is most unlikely that the apparently eroded configuration of the external margin would result from mechanical disintegration without disrupting the entire flange structure. The absence of a flange from parts of Plate 54, fig. 6, its almost total absence from Plate 54, figs. 10–12, the presence of delicate filaments at the present flange margins of Plate 54, figs. 6, 10, 11, indicate disintegration of the flange to be principally due to microbiological action, and not to mechanical deformation.

The remarkable specimen illustrated by Plate 54, fig. 11 indicates the essential unity of the microbiological attack in its later organization, to produce a '*Palynomorphites* pseudomorph' of *Lycospora*, represented by the filaments developed in the thickened inner cingulum region and along the triradiate marks. The exine from the central area has been almost completely removed, while mere fragments of the equatorial flange remain (Pl. 54, fig. 11*a*). The severity of this attack is remarkable, and the preservation of such a delicate structure indicates the action to have taken place after settlement and with little or no subsequent mechanical transport. The most frequently occurring forms exhibiting advanced stages of attack are shown (Pl. 54, figs. 10, 12); where the equatorial flange has been removed and a well-defined triradiate attack has developed, the remainder of the spore breaks up into three triangular segments. These isolated segments, bounded on one side by concentric filaments and with linear filaments along two other tapering margins, are common ingredients of the preparations; they may contain remnants of partially altered original exine.

The attack on *Lycospora* is very clearly controlled by the structural features of the spore. The order of this attack is less clearly defined; it is somewhat variable in the relative time of onset and in the degree of severity on or within the various areas of the spore. The effect of the microbiological action is to reduce partially or completely the equatorial flange, to destroy the exine of the central body, and to cause break-up of the spore into segments. Where the development of filaments has been particularly strong a 'pseudomorph' of the spore results.

Densosporites (Pl. 54, figs. 13–17)

The illustrated spores represent common forms of this genus in the preparations and are selected to indicate both the methods of microbiological attack and its organization and relationship to the structure of the spore. The method of attack is very similar to that described for *Lycospora*, and since the structure of the two spores is essentially similar this is to be expected. The weaker development of haptotypic features in *Densosporites* as compared with *Lycospora* does not lead to such well-differentiated features of attack on the proximal surface of the former. In many cases the action was so severe that recognition of the two surfaces of the spore was a matter of considerable difficulty. For descriptive purposes the following regions of the spore are considered: central area and cingulum, (*a*) inner thickened zone, (*b*) outer equatorial flange.

Central area. Plate 54, fig. 13 indicates the elements which constitute the basis of the investment. They consist of coccoid cells and elongate bacilli-like fragments in association with beaded filaments and short thick-walled branching filaments often carrying spherical terminal vesicles. The filaments may be straight or curved and towards the margin of the central area are somewhat radially directed from the inner thickened zone of the cingulum; they appear to originate from dense filaments within this zone. The result is a loose reticulum of filaments which produces an overall concentric pattern of pentagonal to polygonal lumena. Within each lumen the exine has been either partially or totally absorbed or destroyed. Plate 54, fig. 14 indicates a completely reticulate distal surface with partially absorbed exine, while in Plate 54, fig. 15 fragments of exine are only present around the margins. Some filaments still retain the elements of reticulate patterning and preserve filamentous connexions across the destroyed middle portion of the central area. The eventual result of microbiological action on the central area is to destroy it completely, as shown by Plate 54, fig. 16.

Cingulum, inner thickened zone. The dense brown region which represents an inner thickened and annular zone of the cingulum is the most heavily invested part of *Densosporites.* Upon and within this structure the elements of microbiological attack form an anastomosing and interweaving bundle of concentric cellular 'tissue' which completely fills this annulus. This organization is particularly well seen in the spores (Pl. 54, figs. 13, 14, 16). At certain points, beaded filaments proliferate into thicker masses from whence arise other filaments which either pass into and over the central area of the spore or extend into the equatorial flange as far as the present equatorial margin.

Many spores which show an advanced stage of attack upon this feature (Pl. 54, figs. 15, 17) exhibit some degree of disorganization within the concentric structure at certain points. There is a tendency for the filaments to be replaced by swollen masses of coccoid or elongate cells, which occur in dense groups without any particular orientation. The break in outline shown by Plate 54, fig. 17 coincides with such an area and is likely to coincide with the position of a trilete ray affecting the structure of the inner zone. The eventual result of the attack is to break the thickened annular zone into fragments which, by the concentric organization of filaments, can still be recognized in the preparation as fragments of *Densosporites.*

Cingulum, outer equatorial flange. Where the flange is reasonably complete there is little significant orientation of the attacking cells. Thus Plate 54, fig. 13 carries coccoid cells and occasional beaded filaments occur at various points upon the flange. With a greater degree of investment filaments spread from the annulus in a general radial direction towards the equator of the flange; these are well seen in Plate 54, figs. 13, 15–17. The fretted nature of the equatorial margins (Pl. 54, 15–17) is governed in part by the position of filaments emanating from the inner thickened zone. At the same time the existing margin of the spore is marked by elongate cells and beaded filaments which are not continuous, but which show a concentric orientation (Pl. 54, fig. 13). Thus in part, the attack on the equatorial flange also takes place from its outer margin; its absence at some points and partial representation at other points in Plate 54, figs. 15–17 is principally the result of biological absorption rather than mechanical disintegration.

While the attack on *Densosporites* is mainly controlled by the structural features of the spore body, the order of this attack on the various features is less clearly known. The inner thickened zone of the cingulum may be preferentially selected and rapidly invested with either concomitant or subsequent spreading of filaments into neighbouring regions of the spore. Alternatively, the attack may be more widespread initially, but, due to the rapidity of growth within the annulus, the organization there outstrips that at other places on the spore. The central area is severely affected at an early stage and its entire removal may be brought about before major changes are effected in the equatorial flange. The latter may be partly or entirely removed, and when this coincides with the removal of the central area a '*Palynomorphites* pseudomorph' of *Densosporites* remains, which consists of a brown mass of concentric filaments representing the inner thickened zone or annulus of the cingulum as shown in Plate 54, fig. 16. A comparison of the 'pseudomorphs' of *Densosporites* and *Lycospora* emphasizes the difference in structure between the two spores, and illustrates the part played in structural control by the trilete rays. The eventual break up of the 'pseudomorph' after *Densosporites* into fragments completes the biological disintegration of this type of spore.

Leiotriletes (Pl. 55, fig. 1)

Plate 55, fig. 1 illustrates the proximal surface of a thick-walled yellow resinous spore with broadly rounded apices and slightly concave sides. While the exine on the proximal surface is present and reasonably complete, that of the distal surface has been partially destroyed. The microbiological attack on this spore appears to be located in two main regions, (*a*) near the equatorial margin, (*b*) along the triradiate structure.

Near the equatorial margin. The body cavity near the equatorial margin carries beaded filaments which anastomose but in general follow the spore outline; their beaded character is visible at several points near the right-hand margin of Plate 55, fig. 1. That this feature is not to be confused with an optical effect is demonstrated at Plate 55, fig. 2, where, after following the equatorial outline, a prominent filament curves into the centre of the spore. There, in conjunction with a filament which has followed a triradiate ray, it encloses an elliptical area of pale-yellow partially absorbed exine.

Along the triradiate structure. The broken wall of exine following this structure is accompanied along part of its course by isolated coccoid and elongate cells, and beaded and non-beaded filaments. Occasionally, beaded filaments with swollen terminal vesicles branch on to the triradiate segments and enclose the elliptical areas of pale partially absorbed exine referred to above. The characteristic form of the beaded filament and terminal vesicle is well seen at Plate 55, fig. 1*b*.

Leiotriletes (Pl. 55, figs. 2–5)

The illustrations (Pl. 55, figs. 2–4) represent an advanced stage of investment upon a thick-walled resinous triangular spore possessing blunt or flattened apices and concave

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EXPLANATION OF PLATE 55

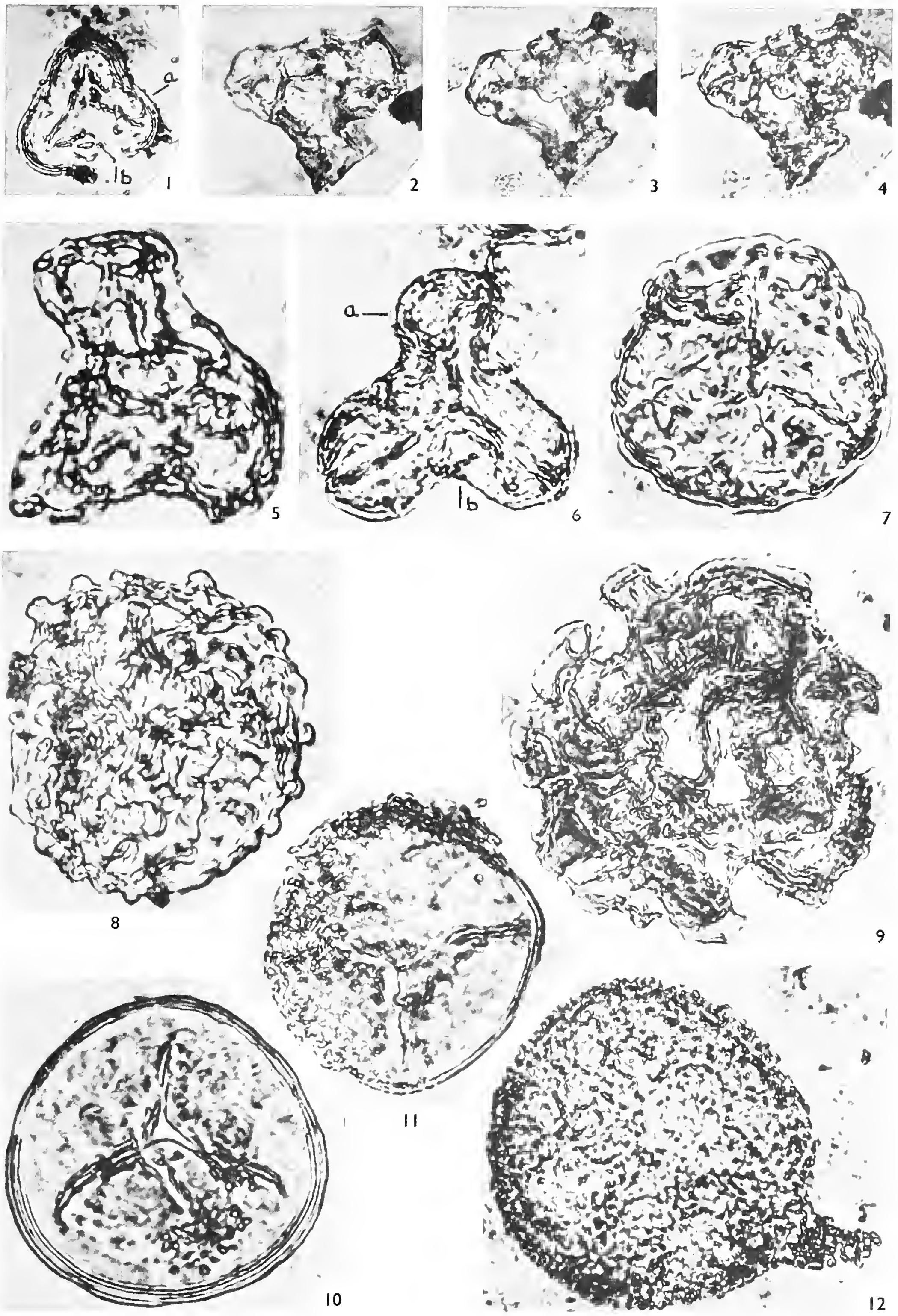
All figures are of specimens from the Chert Band, Midhope Burn, Upper Oil Shale Group of the Calciferous Sandstone Series (Scotland). Upper Viséan, P_1 subzone. Magnification ×750 unless otherwise stated. Slides all labelled M.B.Ch.

Figs. 1–5. *Leiotriletes sp.* 1, 3/6/731.245, proximal surface; *a*, curved filament partly enclosing elliptical area of partially absorbed exine; *b*, beaded filament with swollen terminal vesicle. 2, 3/7/665.289, distal surface taken with ground-glass filter. 3, Same spore, proximal surface taken with ground-glass filter. 4, Same spore, distal surface in ordinary light illustrating details of attack. 5, 3/6/728.245, distal surface, ×1500.

Fig. 6. *Granulatisporites sp.*, 3/7/677.312, distal surface with view of underlying triradiate mark, ×1500; *a*, beaded filaments surrounding an area from which the exine has been partially removed; *b*, curved filaments enclosing areas of thin or totally absorbed exine.

Figs. 7–9. *Convolutispora sp.* 7, 3/6/765.248, proximal surface, ×1500. 8, 3/5/826.250, presumed distal surface, focal plane slightly below equator of spore to show surface detail, ×1500. 9, 3/10/731.170, surface unknown, advanced stage of attack with well-defined and branching filaments.

Figs. 10–12. *Punctatisporites sp.* 10, 3/11/790.179, proximal surface, ×1500. 11, 3/7/784.169, proximal surface, partial investment of the surface of the spore by coccoid cells and marginal filaments, ×1500. 12, 3/10/768.192, distal surface, coccoid, paired cells, chains of cells, beaded filaments on the surface.



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inter-radial margins. The distal and proximal surfaces, taken with a ground-glass filter in order to illustrate major features, are represented by Plate 55, figs. 2, 3 respectively; Plate 55, fig. 4 represents the distal surface of the same spore in ordinary light.

Distal surface. The surface is marked by coccoid and orientated elongate cells, beaded and non-beaded filaments, all arranged in a general concentric manner around areas where the exine is absent. These areas are illustrated by Plate 55, figs. 2, 4 and although the distal exine has been entirely removed from most of them, thin fragments remain nearer the margins of the spores. The attack appears to result from the establishment of isolated centres and to spread outwards, eventually producing a reticulate pattern. The margins of the lumena in Plate 55, figs. 2, 4 are formed partly by filaments, but also in part by ridges of incompletely destroyed or unattacked exine. The remaining exine may represent a thicker part of the spore wall such as would be the case if the original spore exine was differentially ornamented; strong features at the equatorial margin of the spore suggest this possibility. It is evident that the microbiological action has destroyed well-defined areas of exine so that either an original structure has been emphasized by partial destruction of the exine, or a reticulate pattern has been created by the attack and is now represented on the distal surface.

Proximal surface. The method of degradation on this surface is essentially similar but for the presence of haptotypic features. Between the thickened exine associated with a triradiate mark and lip and the equatorial margin along the left-hand side of the spore the exine has been removed from one continuous vacuity; a similar feature also marks the right-hand side of the spore. However, in the upper segment the exine between the triradiate structure and the equatorial margin is more complete and contains smaller well-defined vacuities which produce a reticulate pattern. The indented marginal form of the larger vacuoles indicates a more advanced stage of destruction, whereby the intervening exine which formed the margins of the smaller lumena has been destroyed, leading to coalescence into one larger vacuity.

The evidence provided by this thick-walled resinous spore is of particular interest since microbiological action on both surfaces of the same specimen is represented. It is principally superficial with independent action on the two surfaces and which initially leads to destruction of exine from circular or polygonal areas, with the eventual formation of large, elongate vacuoles. The thickened exine along the triradiate mark is effective in restricting the organization of the attack on the proximal surface, but that on the distal surface is not so restricted. It may to some extent be controlled by other factors such as an original thickness differentiation or material differentiation of the exine. A further and similar spore (Pl. 55, fig. 5) emphasizes the features of the attack described, and depicts clearly the nature of the organism responsible. Very little of the original exine remains on the body of this spore. The spores described represent to a great extent 'skeletons' of microbiological decay, and differ in important respects from the 'pseudomorphs' of *Lycospora* and *Densosporites*. Principally they differ in the facts that no major structural elements of the spore are missing, and that some part of the skeleton consists of original exine which preserves the spore form. The 'skeleton' may break down further into fragmentary remains; the thick rounded radial extremities of these spores are preserved in the preparations.

Granulatisporites (Pl. 55, fig. 6)

The distal surface is represented in the focal plane of the illustration, and the triradiate mark of the proximal surface is visible beneath it. The spore is much compressed, has broadly rounded extremities with deeply concave sides, and a thin yellow exine ornamented with granules. There is little structural differentiation of the spore body, and consequently a less well-defined distribution and organization of microbiological attack. The latter is carried out by elongate orientated cells and beaded filaments, but thick-walled filaments are present and these in particular occur within the spore body. The equatorial outline is followed, along most of its length, by prominent filaments which are particularly well developed and proliferate in the neighbourhood of the radial extremities. The upper extremity is most severely affected; there, beaded filaments arising from a marginal filament enclose a region from which the exine has been partially removed. This lighter-coloured area and its surrounding filaments are shown in Plate 55, fig. 6*a*. At the concave lateral margin, beaded and non-beaded filaments follow a modified course. They swing in towards the centre of the spore by means of prominent curved but irregular loops and thereby enclose areas of thin or totally absorbed exine (Pl. 55, fig. 6*b*) so inaugurating a coarse reticulate pattern.

Convolutispora (Pl. 55, figs. 7–9)

The spores illustrated are characterized by a very thick resinous exine, and rugulate ornament. The rugulae may either consist of irregular ridges with a rounded cross-section and protruberances (Pl. 55, fig. 8) or of flattened ridges (Pl. 55, fig. 7), and are separated by lower-lying areas. The three spores illustrated indicate the method of microbiological attack. In Plate 55, figs. 7, 8 this organization is well seen upon spores which retain sufficient original structure to warrant recognition of the genus. The spore in Plate 55, fig. 9 represents a much more advanced stage of destruction, and although the thicker irregularly distributed exine is still partially visible, reference to the spore genus is more doubtful.

The proximal surface of a spore with incipient attack is represented by Plate 55, fig. 7, where elongate cells and beaded filaments predominate but occasional thick-walled filaments occur. The distribution is very localized and follows a linear organization in the neighbourhood of two rays of the triradiate mark and a concentric direction at several points near the equator of the spore. In places the exine has been destroyed and circular or irregular perforations are surrounded by elongate cells flanking the thicker exine of the marginal wall.

Plate 55, fig. 8 represents the distal surface of a spore upon which the attack is very diversified and locally intense. The lower part of the spore is reasonably unaffected; the prominent rugulae are devoid of attached cells, but the inter-spaces between the rugulae carry coccoid cells and short beaded filaments. The right-hand margin of the spore illustrates a progressively greater intensity of investment in which beaded filaments, occurring in the hollows of the surface, produce a concentric pattern. At the upper margin of the spore, coalescence of the beaded filaments surrounding the rugulae has resulted in a linear organization of beaded filaments. The region of greatest investment is the dark area along the left-hand side of the spore, where the entire surface is covered by a fine cellular mat of elongate cells and beaded filaments which fan out in a 'ray-like' manner from darker centres. The most severe attack is located on the upper central portion of the spore, where a red highly refractive spherical body is seen as a sphere on the plate. This appears to be a reproductive body caused by fusion of the filaments, or it is the focal point from which filaments radiate in several directions. Around this body the exine has been totally destroyed, for the light-coloured areas hereabouts are circular or polygonal vacuities, many of which have coalesced. The method of destruction of the exine is further emphasized by Plate 55, fig. 9, in which severe action has culminated in the complete removal of exine from areas in the central regions of the spore and from deep embayments into its equatorial margin. These areas are surrounded by the thicker remaining exine which carries filaments, some of which extend into and across the vacuities. With this more advanced stage significant changes are notable in the nature of the attacking organism. Thus beaded filaments give way to well-defined thick-walled and larger filaments which are straight or curved and commonly branched. Several branches may arise from or fuse in a common centre which then carries one or more small spherical vesicles or radiating groups of beaded filaments. The action is also in depth, for the bundles of filaments cross one another at lower focal planes. The overall organization produces a reticulate pattern, and at this more advanced stage of destruction the investing organism may be less seriously controlled by the structure of the remaining exine. Thus a broadly concentric organization develops in which filaments follow the spore contour and are interconnected by other radial filaments.

In thick-walled ornamented spores of the *Convolutispora* type there are no outstanding differential structural units of the spore body, and the haptotypic features are of minor importance in controlling the attack. However, the strong ornamentation produces hollows of relative protection from which centres of microbiological action could be generated; the same regions contain thinner and possibly more favourable exine for organic assimilation. The exine is therefore more rapidly absorbed with the formation of vacuities, and the rugulae isolated by this means. The resulting configuration passes from one in which the exine has been removed from smaller circular polygonal or irregular vacuities, to one of larger irregular but rounded vacuities. A 'skeleton' spore results in which both the remaining exine and the attacking organism play a part. The breakdown of the spore into a number of isolated, irregularly shaped, and thickened fragments is envisaged as the final stages in its destruction.

Punctatisporites (Pl. 55, figs. 10–12; Pl. 56, figs. 1–3)

The spores included in this genus are characterized by a circular outline, with little structural differentiation of the body except in the presence of a frequently well-marked triradiate feature. They are characterized by an infra-punctate or infra-granular exine. There is consequently little selectivity of this uniform surface for microbiological activity and a degree of uniformity pertains in distribution and organization of attack. Thus Plate 55, fig. 10 illustrates a spore generally free of saprophytic cells and which therefore exhibits the typical infra-granular exine structure over most of its surface. At one point a colony of saprophytic cells is clearly visible, which at a higher focal plane consists of orientated beaded filaments and elongate cells with a radial symmetry. The only other attack on this spore is associated with the triradiate mark, where the dark areas consist of linear chains of cells and beaded filaments. A greater concentration of saprophytic material is illustrated for the proximal surface of the spore (Pl. 55, fig. 11), where half of the surface is covered by coccoid cells often paired in the streptococcal manner. They possess little definite or regular orientation, for while some occur as radial clusters, others towards the margin show a general orientation following the spore contour. The dark marginal area on the upper border represents a region of concentrically orientated filaments.

The complete investment of a distal surface is illustrated in Plate 55, fig. 12, where the principal elements are coccoid cells. Groups of cells with radial arrangements are found in association with cells containing two or more individuals in streptococcal arrangement, or with short beaded filaments 2–3μ in length. Over the greater part of the spore the distribution presents an impression of minute reticulation. The dense marginal distribution produces a concentric pattern which eventually results in a curvilinear distribution of beaded filaments. The spore exine is severely attacked and the isolated mass of cells lying off the margin of the spore (Pl. 55, fig. 13) illustrates the elements responsible for the investment. A possible further stage of this attack is represented by Plate 56, fig. 1, in which a change in the form of the saprophytic elements is notable. While the streptococcal-like cells are still common there is a preponderance of beaded filaments and of short branching filaments 2–5μ long. This development has resulted in an irregular but distinct reticulate appearance particularly evident in the central regions of the spore. This figure (Pl. 56, fig. 1) is taken at a slightly higher than median focus to accentuate the affected and partially destroyed exine, which therefore appears as white lines or areas. An overall concentric reticulate pattern for most of the spore suggests a contour control, but this is lost towards the margins. There a distinct radial distribution may indicate a change in the underlying spore exine or merely a region of originally modified spore contour.

The four spores described illustrate the increased areal degradation upon a surface which shows little differentiation. It is questionable whether the infra-granular structure of the exine exercises much control upon the organization of attack, and yet it is significant that the earliest stages of investment are by minute coccoid cells and beaded filaments only. The spores also indicate the degrees of intensity or stages of the attack, for, as the microbiological action becomes well established and the exine is made viable, there are significant changes. These result in the development of branching filaments with the establishment of a reticulate pattern and the final breakdown of the spore wall.

The spore in Plate 56, fig. 2 is referred to the genus *Punctatisporites* with some doubt, in view of the general lack of original exine visible. The investment is predominantly by elongate cells, beaded and non-beaded filaments. The latter are 0·75–1·5μ wide and may be short branched forms of 2–3μ, or long unbranched forms 10–15μ long. There is a very general concentric orientation of the saprophytic remains, particularly near the margin of the spore, where the darker regions consist of both types of filaments. Several of the filaments curve inwards towards the centre and are seen in connexion with other concentrations of filaments near the centre of the spore. There is a secondary concentric arrangement illustrated by the pale patches of Plate 56, fig. 2, and which exhibits some diversity and may represent progressive stages in the attack. Thus Plate 56, fig. 2*a* represents some areas of thin and altered exine upon which occasional coccoid cells and filaments remain; they are surrounded by a diffuse boundary along which occurs a concentration of orientated cells and filaments which form an incomplete concentric boundary. At Plate 56, fig. 2*b* the structure is larger and the exine from the upper surface of the spore has been removed. The boundary is formed by concentrically-arranged beaded filaments and by filaments which are in connexion with well-defined thick-walled filaments traversing other areas of the spore. The structure at Plate 56, fig. 2*c* is surrounded for the most part by a concentric bundle of beaded filaments, the left-hand margin has suffered mechanically, and the exine is folded upon itself. The exine from the upper surface of the spore has been removed, but a part of that of the lower surface is still represented.

This organization appears to be significantly different from that described for other members of this group and appears to commence with an original cover of saprophytic material distributed in a broadly concentric pattern. Within this general pattern, localized areas have been affected more seriously than others, and the spread of the attack outwards results in a concentration of filaments around the margins. Similar features are shown around the marginal region of the spore (Pl. 56, fig. 3).

Microreticulatisporites (Pl. 56, fig. 4)

The surface of this spore carries a great number of coccoid- and streptococcal-type cells of two or three units, dispersed over the surface in irregular groups. There are, however, two regions of the spore where some organization is noticeable. Firstly, the equatorial margin is densely covered and the cells are orientated in a concentric manner and may pass into beaded filaments as near the lower border: the broken left-hand margin indicates the cellular nature hereabouts and gives little evidence of the presence of exine. Secondly, the most remarkable organization is that based on the irregularly shaped reddish-brown and resinous mass in the centre of the spore. Leading to it or from it, according to its function, is a complicated irregular system of anastomosing lines of saprophytic cells which are organized, and orientated in the direction of the main structure. The resulting pattern is the encirclement either completely or partially of areas of the surface; nearer the centre of the structure the enclosed areas are irregular but they tend to become hexagonal or polygonal in shape at some distance away. It is significant that many of the pale areas from which the exine of the upper surface has been removed are bounded by cells and filaments marking the furthermost extensions of the structure.

The 'focus' of the system appears to be a vesicle or vegetative reproductive centre from which the attack commenced. The organization of the ensuing attack possibly bears some resemblance to that already described (Pl. 56, fig. 2), but comparison is not obvious. The meandering nature and quasi-reticulate pattern of this particular organization is symptomatic of microbiological action upon a uniform structure lacking surface ornamentation.

Knoxisporites (Pl. 56, figs. 5, 6)

The spores included in this genus and represented by the above figures have a very different appearance. The spore in Plate 56, fig. 5 is red-brown with a thick resinous exine, while Plate 56, fig. 6 represents a pale-yellow central region with a thin colourless outer zone, the exine being considerably thinner for the spore as a whole. Despite these differences, there is a similarity of structure, in that both spores consist of a central body bearing haptotypic features and surrounded by a cingulum. The latter structure is subdivided into an inner thickened annulus concentric with the central body and a thinner outer flange. This differentiation is most marked in Plate 56, fig. 6.

The attack on the heavier spore (Pl. 56, fig. 5) is restricted and simple, consisting of coccoid cells and beaded filaments irregularly scattered over the outer flange, but with a tendency to overall concentric distribution. Locally, the coccoid cells occur in small concentric groups enclosing small circular areas from which the exine has been partially removed to provide a pitted surface, illustrated at Plate 56, fig. 5*a*. Filaments follow a discontinuous but concentric path nearer the margin of the flange and are best seen where the exine has been partially destroyed, as at Plate 56, fig. 5*b*. A much greater degree of attack is shown by the thinner-walled spore (Pl. 56, fig. 6, distal surface), and the organization follows closely upon the structural elements of the spore in a manner previously described for spores of a similar structural type, e.g. *Lycospora* and *Densosporites*.

Central body. A dense infestation of coccoid cells and filaments characterize this region; the filaments are curved or branched and, while they produce no distinctive pattern, they tend to surround circular regions from which the exine is either partially destroyed or absent as in the light areas (Pl. 56, fig. 6).

Cingulum, inner thickened zone. The darker-brown thickened zone forming an annulus around the central body is heavily attacked and both types of filaments are present as bundles with an entirely concentric orientation which follows this structural feature of the spore. At various points branching filaments spread both on to the central body and outwards over the outer flange. At two points on the lower part of the structure (shown as dark areas on Pl. 56, fig. 6) a dense mass of filaments containing swollen vesicles results in unusual expansion of the concentric structure, and a similar but smaller aggregate occurs in the opposed segment of the annulus. These masses represent a concentration of saprophytic activity at points along the prolongation of the triradiate rays and where these cross the annulus.

Cingulum, outer equatorial flange. Very little of the original exine remains and even where the equatorial margin is complete the exine is much altered. The presumed outer margin is marked by highly refractive beaded filaments (Pl. 56, fig. 6) which are often present

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EXPLANATION OF PLATE 56

All figures are of specimens from the Chert Band, Midhope Burn, Upper Oil Shale Group of the Calciferous Sandstone Series (Scotland). Upper Viséan P_1 subzone. Magnification ×750 unless otherwise stated. Slides all labelled M.B.Ch.

Figs. 1–3. *Punctatisporites sp.* 1, 3/11/820.315, presumed distal surface, figure at slightly higher than median focus to illustrate reticula. 2, 3/11/782.177, presumed distal surface; *a*, areas of thin and altered exine with coccoid cells and filaments; *b*, area bounded by concentric filaments, exine removed from the upper surface of the spore; *c*, area bounded by concentric filaments, exine removed from upper surface over whole area and from lower surface over part of the area (white), ×1500. 3, 3/5/796.186, proximal surface.

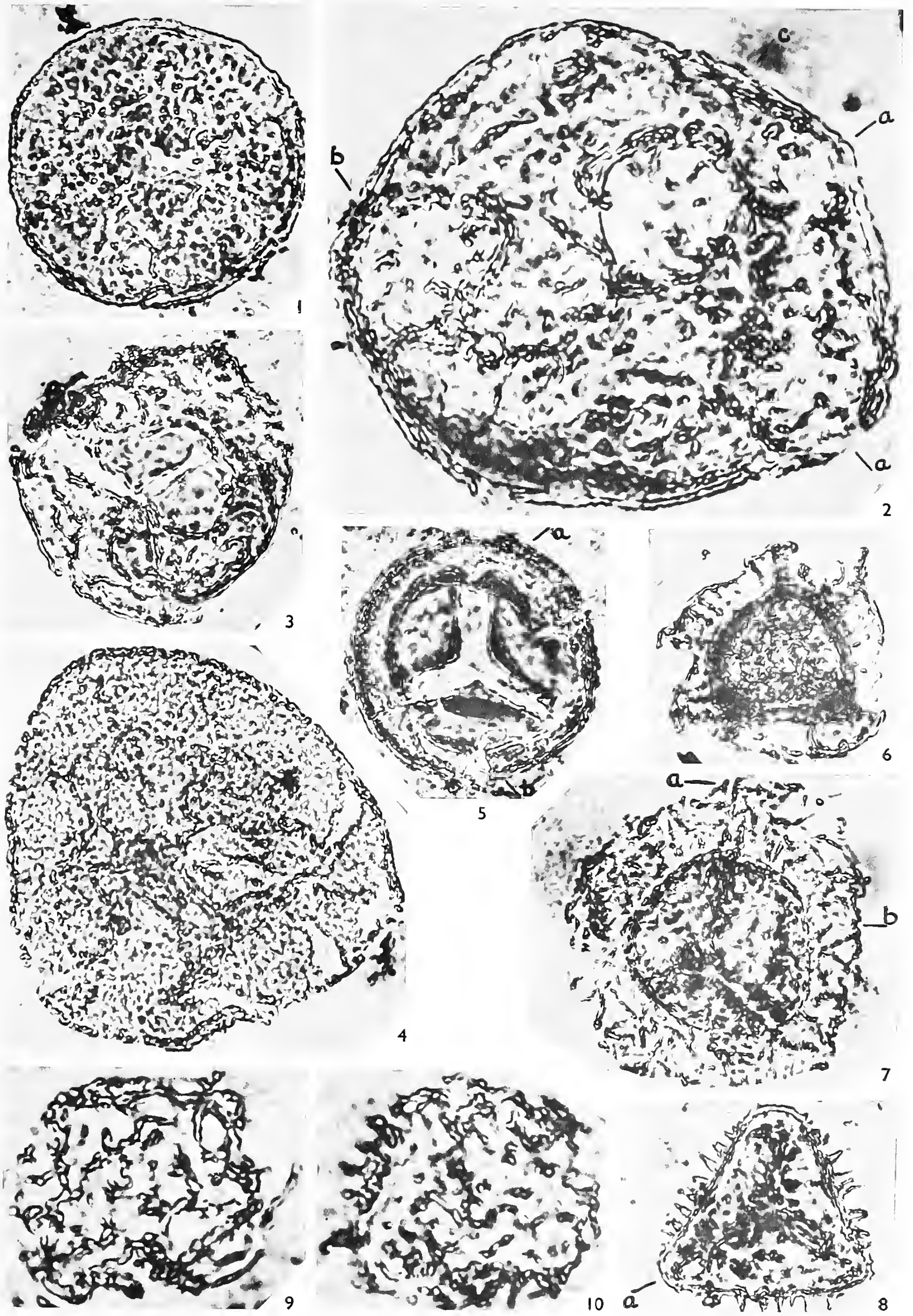
Fig. 4. *Microreticulatisporites sp.*, 3/6/710.213, presumed proximal surface.

Figs. 5–6. *Knoxisporites sp.* 5, 3/13/802.334, proximal surface; *a*, small circular pits in the exine; *b*, filaments with concentric organization. 6, 1/1/784.190, distal surface.

Fig. 7. *Auroraspora sp.*, 1/4/680.161, proximal surface; *a*, alignment of attacking cells on the saccus and near the position of the triradiate mark; *b*, dark line marking present line of saccus margin.

Fig. 8. *Diatomozonotriletes sp.*, 4/6/737.142, proximal surface; *a*, circular area surrounded by a filament, exine destroyed.

Figs. 9–10. *Incertae sedis*, presumed '*Palynomorphites* pseudomorph', 9, 3/4/850.183, ×1500. 10, 3/4/850.184, ×1500.



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even where the remainder of the flange has been destroyed. Other filaments arise from the region of the annulus, cross the equatorial flange radially, and are connected or fused with the equatorial filaments. A 'ghost' framework is thereby produced within which the exine may either be totally destroyed are partly preserved between the filaments. The equatorial margin has suffered from some degree of mechanical effects, but this is slight since the margins of the prominent embayments are lined with coccoid cells and beaded filaments. Along the lower border the equatorial flange and part of the annulus have been destroyed, yet the line of the equatorial margin is preserved by a beaded filament in continuity with a well-preserved portion of the flange.

There is a remarkable similarity in the distribution and organization of this attack with that described for certain stages of attack on *Lycospora* and *Densosporites*, based as it is upon a similarity of spore structure. No other specimens indicated a more advanced stage of investment on this type of spore, and it was impossible to complete the comparison for all stages.

Auroraspora (Pl. 56, fig. 7)

The illustration represents the proximal surface of a large spore of this genus in which the focal plane is coincident with the equatorial margin of the spore. The characteristic features include a pale-yellow resinous central body carrying prominent trilete sutures. This body is enclosed by a thin-walled colourless saccus which extends beyond its periphery as a double layer of tissue uniting in the equatorial margin of the spore. The saprophytic action is directed upon the saccus and also upon the central body.

Saccus. This thin colourless membrane shows evidence of original ornamentation in the form of closely spaced granules, and the attack upon it is best seen in the outer zone consisting of the proximal and distal layers of the saccus alone. Coccoid cells, beaded filaments, and branching filaments are common, the latter two form an irregular network of straight or curved, branching remains. The complexity suggested by Plate 56, fig. 7 is in part due to the superimposition of elements occurring on both surfaces of the saccus. There is a general radial direction in the filament distribution, and many are continuous from the marginal saccus on to its continuation over the surface of the central body. This is generally evident but particularly so where the influence of the haptotypic structures has affected the saccus (Pl. 56, fig. 7*a*). Over portions of the proximal surface the saccus has been removed from the central body by microbiological activity. Thus the greater part of the right-hand segment is free (paler coloured); the present margin of the saccus is represented by the dark line crossing the lower portion of this segment, which consists of a concentration of linearly arranged coccoid cells and beaded filaments marking its edge (Pl. 56, fig. 7*b*).

The central body. The most prominent regions of attack are along the two margins of the triradiate ridges. The investment is principally concerned with the saccus, which is destroyed along such lines, and it extends into the exterior wing as seen along the north-east triradiate mark. The fact that this trilete mark on the central body is not accompanied by a double row of filaments follows from the destruction of the saccus along one side of this line and the retreat of its margin to the further dark line in the right-hand segment (Pl. 56, fig. 7*b*). The central body is only exposed in the right-hand segment; here its surface carries isolated cells and filaments, but no obvious pattern of distribution has been established. While the margin of the central body carries a somewhat denser concentric distribution of elements, these are predominantly in the saccus and no unusual development is present.

The attack on this saccate spore appears to be relatively simple, and at the stage represented consists largely of the destruction or modification of the saccus. The prominent radial organization on this part of the spore may follow an original structure of the integument, either of ornamentation or radial folding. When compared with spores such as *Tensosporites*, which possess an inner thickened cingulum which is followed by annular concentric filaments, the contrast in the organization of attack on this saccate spore is well marked.

Diatomozonotriletes (Pl. 56, fig. 8)

The figure illustrates the proximal view of a typical spore of this genus characterized by a thick-walled trilete form with sharply rounded extremities and straight sides, the latter adorned by strong, pointed, spine-like processes. Attack on the proximal surface is very restricted and generally limited to the region of the trilete mark. The rays are attended by thick-walled filaments, with prominent swollen cells, which diverge from the margins of the ray on to the surrounding exine. The left-hand ray is followed by a filament which branches and recurves to enclose a small circular area at the radial extremity of the spore, from which the exine has been removed (Pl. 56, fig. 8*a*). Isolated clusters of cells are scattered over the surface.

Incertae sedis (Pl. 56, figs. 9, 10)

The remains represented by the above figures are common ingredients of the preparations and further illustrate the nature and association of the elements here described as *Palynomorphites*. They consist of that organism preserved in a skeletal network, and may be other examples of '*Palynomorphites* pseudomorphs' but with no indisputable indication of an original organism which may have been replaced; Plate 56, fig. 10 may possibly bear some resemblance to the 'pseudomorph after *Lycospora*'. These remains serve to illustrate the advanced degree to which microbiological action may progress under certain conditions without destruction of the evidence. The figures are of value in providing a comparative basis upon which the selection of material used in the other illustrations, indicating stages of attack, may be judged.

CONCLUSIONS

Spores of very divergent characters are invested by the organism *Palynomorphites diversiformis* gen. et sp. nov. under suitable environmental conditions. There is an organization in the nature and distribution of the elements which form the basis of the colonization or attack; this organization is not uniform but dependent either upon the major structural features or upon the ornamentation of the spore: the organism is therefore often selective in its distribution upon a given spore. The major structural features are important in controlling or modifying the organization of the attack, but in certain cases serious modification of a structural feature may result, culminating in its partial destruction or complete removal. The loss of a central body or flange, or the removal of both structural features, exemplifies this modification as in *Densosporites* and *Lycospora*. One effect of the attack on the structural features results in the production of a '*Palynomorphites* pseudomorph' of the spore in which the form of certain structural features is represented by the organism which has destroyed the original spore.

In the case of spores with few structural features and strong ornamentation, particularly that of rugulae on thick-walled spores such as *Convolutispora*, the attack is controlled by the surface ornament. The destruction of irregular or reticulate areas of the exine may follow and eventually result in the formation of a '*Palynomorphites* skeleton' of the spore as in *Convolutispora* and *Leiotriletes*.

Where the spore has no marked structural features, and little or no well-defined surface ornamentation, as in the case of some forms of *Punctatisporites* described in this paper, there is little selectivity and a greater degree of uniformity in distribution results. The organization is more diverse, but tends to follow a reticulate or concentric pattern. The eventual degradation of the spore is followed by its disintegration into segments often controlled, but not necessarily so, by the haptotypic features (e.g. *Lycospora*).

A spore may be modified by the addition of *Palynomorphites* cells or filaments, and confusion with normal ornament may arise with the varied elements and organization of attack which *Palynomorphites* assumes. Thus the formation of radial, reticulate, or concentric patterns by filaments, and the absorption and pitting of the exine may severely affect the appearance of the spore.

While the attack on miospores by the agent, *Palynomorphites diversiformis*, has been established, it is not possible to provide reliable evidence as to whether this attack was preferential on certain groups of spores. All spores present show some degree of attack, and even within the same group there is wide diversity in the intensity of attack. The most commonly attacked spores are *Lycospora*, *Densosporites*, and *Schulzospora* in this order, the first two groups being most regularly and most seriously affected. Some substantiation for this statement follows from the larger number of recognizable fragments of these spores in the preparations. It is of interest to record that microbiological attack has largely destroyed wood cells; only algae of the *Botryococcus* type are less affected than the miospores.

The severity of attack on the miospores described may be regarded as unusual and possibly due to special circumstances of the environment. As described, the environment was abnormal, but similar attack by the same organism on spores isolated from other oil shales and organically rich sediments, has been noted by the writer. This has been particularly well seen where isolation by hydrofluoric acid alone has been used, or where calcareous sediments have been digested with hydrochloric acid and the organic material separated.

In conclusion, *Palynomorphites diversiformis* is not the only organism which attacks fossil spores; reference to Plate 54, fig. 1 indicates a further organism investing *Schulzospora*, and other presumed saprophytic organisms of a type similar to *Polymorphyces* (Moore 1963).

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LATE JURASSIC MAMMALIAN FOSSILS IN THE SEDGWICK MUSEUM, CAMBRIDGE

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ABSTRACT. The collection of the Sedgwick Museum contains three mammalian fossils found in the Late Jurassic Purbeck Beds: dentaries of *Trioracodon ferox* and *Spalacotherium tricuspidens* and a fragment of a skull of *Peralestes longirostris*. The dentary of *Trioracodon* was discovered in 1933. The other two fossils, part of the Brodie collection, demonstrate that the postcanine dentitions of *Spalacotherium* and *Peralestes* consist of three premolars and seven molars. *Phascolestes dubius* is shown to be a junior synonym of *Peralestes longirostris*.

THE collection of the Sedgwick Museum contains three mammalian fossils from the Purbeck Beds of Durlston Bay, Dorset, that have escaped notice in recent studies of Mesozoic mammals. The whereabouts of two of these fossils, which were discovered in the Mammal bed by W. R. Brodie and first described by Richard Owen (1854), was unknown to Simpson when he prepared his monograph of British Mesozoic mammals and they were listed as lost (Simpson 1928, pp. 100 and 143). Dr. F. R. Parrington began a report on these fossils, but the pressure of other commitments has prevented him from completing it. In the course of my study of British Mesozoic mammals, I had the opportunity to see these fossils, and Dr. Parrington graciously suggested that I should publish this note communicating their whereabouts and describing certain aspects of their morphology pertinent to other research problems.

Fossils identified by catalogue numbers prefixed with the letter 'J' are part of the collection of the Sedgwick Museum, Cambridge. Catalogue numbers lacking this prefix pertain to fossils in the collection of the Palaeontology Department, British Museum (Natural History).

Order TRICONODONTA Osborn 1888
Family TRICONODONTIDAE Marsh 1887
Subfamily TRICONODONTINAE Hay 1902
Genus TRIORACODON Simpson 1928
Trioracodon ferox (Owen 1871)

Description. Sedgwick Museum No. J13141 is a fragment of a right dentary containing the canine and all the postcanine dentition. Most of the dentary anterior to P_1 has been broken away and the bulk of the large, curved canine root is exposed. The root extends beneath P_1, and there is a shallow, longitudinal groove along its lingual side. Unfortunately the premolars and molars were broken and the fragments displaced during fossilization. In the initial preparation of the fossil the crown of P_3 came free. It was replaced in a reversed position, thus exposing the labial surface of the crown, which has a narrow basal cingulum. Specimens of *Trioracodon* in the collection of the British Museum (Natural History), in which the labial side of the lower dentition is exposed, demonstrate that small but distinct labial cingula are present on at least the P_3 and P_4; these cingula have been overlooked by some students of the triconodonts. The teeth preserved in J13141 resemble those found in other mandibles of *Trioracodon ferox* and do not warrant

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additional comment. Ventral to M_3 and the anterior end of the coronoid process there is a short, internal groove. Although of approximately the same length, the groove is more dorsal and posterior in position than the internal groove on the dentary of the type specimen of *Trioracodon ferox*, No. 47775.

Comments. This fossil was found in 1933 by D. A. Curry. The following locality data were obtained from him by Dr. C. L. Forbes. The fossil was discovered in Purbeck beds cropping out in Durlston Bay approximately half-way between Peveril Point and Durlston Head. It came from a band of blue-grey marl between 3 and 6 inches thick, and softer than the adjacent strata.

Order SYMMETRODONTA Simpson 1925
Family SPALACOTHERIIDAE Marsh 1887
Genus SPALACOTHERIUM Owen 1854
Spalacotherium tricuspidens Owen 1854

Description. Sedgwick Museum No. J11378 is a fragment of a right dentary containing an incisor, the alveoli of the ultimate incisor and the canine, and the postcanine dentition.

TEXT-FIG. 1. *Spalacotherium tricuspidens* Owen, reconstruction of part of the lower dentition based on a fragment of a right dentary containing the penultimate incisor, alveolus of the ultimate incisor, alveoli and part of the anterior root of the canine, and the postcanine dentition; J11378; ×6·2. Lingual view, broken surfaces blackened.

Since 1854, when this fossil was described and illustrated by Owen (1854, fig. 10), it has suffered considerable damage especially to its molars. The preserved incisor is a small, single-rooted tooth. The posterolingual side of its crown is concave. The penultimate incisor, P_1, and P_2, as well as the alveoli for the ultimate incisor and the two-rooted canine, are preserved in a fragment of the dentary that does not appear to be distorted. Posterior to P_2 the dentary has been broken and the adjacent part displaced. The crown of P_3 was also broken and rotated out of position. In the reconstruction (text-fig. 1), P_3 has been returned to its proper orientation, but gaps have been left between P_2, P_3, and M_1 to indicate that the fossil is broken and distorted in this region. Other fossils show that in their natural position these teeth were more closely approximated. The dental arcade of J11378 also may have been distorted by a fracture of the dentary beneath M_6. The morphology of the postcanine dentition of *Spalacotherium tricuspidens* has been fully described by Simpson (1928, pp. 100–1).

Dimensions. Measurements in millimetres of the teeth preserved in No. J11378.

	P_1	P_2	P_3	M_1	M_2	M_3	M_4	M_5	M_6	M_7
Length	1·5	1·7	1·7*	1·6	1·7	1·8	1·8	1·7	1·6*	1·4*
Width	0·6	0·8	0·9*	1·0	1·3*	1·4*	1·5*	1·5*	1·5	1·2

* Estimated minimal value

Comments. This fossil is the only specimen of *Spalacotherium tricuspidens* containing a complete incisor and the entire, albeit fragmentary, postcanine dentition. With the exception of the number of incisors, it gives final confirmation to the dental formula adopted by Simpson (1928, p. 100), I_{3+}–C_1–P_3–M_7.

Peralestes longirostris Owen

1871 *Peralestes longirostris*; Owen, p. 33.
1871 *Phascolestes dubius*; Owen, legend plate I, fig. 40.

Description. Sedgwick Museum No. J11379 is a heavily damaged fragment of a skull containing an incisor, the canine, and the postcanine dentition. Most of the alveolar region of the maxilla and probably part of the premaxilla are preserved. The bone (text-fig. 2*a*) has been severely crushed and distorted and the suture delimiting the premaxilla and maxilla obliterated. The preserved incisor, now lacking the apex of its crown, has small anterior and posterior accessory cusps. Its root is long and has a longitudinal

TEXT-FIG. 2. *Peralestes longirostris* Owen, fragment of the left side of a skull containing an incisor, the canine and the postcanine dentition; J11379. *a*, Outline of the skull fragment, × 3·3. *b*, Occlusal view of M^5–M^7, × 20. *c*, Labial view of the incisor, canine, and P^1–P^3, reconstruction of alveolar margin shown by a dashed line, × 10. In figs. 2*b* and 2*c* the broken surfaces of the teeth are stippled.

groove near the middle of the labial surface. Because of damage to the specimen it cannot be determined if a diastema separated the canine and the ultimate incisor. Most of the canine has been lost, but an indistinct impression in the matrix and Owen's illustrations show that the canine was long and lanceolate. P^1 (text-fig. 2*c*), which is directly behind the canine, is separated from P^2 by a diastema approximately 1 millimetre long. The alveolar edge of the maxilla between these premolars does not appear to be distorted. A smaller gap now separates P^2 and P^3, but the intervening bone is broken and these premolars have been displaced. Probably they were more closely approximated prior to the fragmentation of the specimen. P^1 has a simple, trenchant crown and lacks accessory cusps and a labial cingulum. The larger P^2 has small anterior and posterior accessory cusps and a short labial, basal cingulum on the posterior end of the crown. P^3 has a large posterior accessory cusp and a distinct, crenulated labial cingulum. The lengths of the premolars are as follows: $P^1 = 1{\cdot}0$ mm., $P^2 = 1{\cdot}4$ mm., and $P^3 = 1{\cdot}6$ mm.

The molars are heavily damaged. Not only were they broken and distorted during fossilization, but many fragments were lost, apparently in the first attempts to prepare the fossil. The crowns of the molars are dominated by the large paracone (nomenclature following Patterson 1956). Ridges along the margins of the crown connect the paracone with the stylar region. Cusps were present on these ridges, but have been damaged or destroyed on most of the teeth. Enough remains to indicate that at least one cusp was present on the anterior, and another on the posterior, side of the crown of most molars. These cusps appear to have been as distinct as, but possibly smaller than, those found on the type of *Peralestes longirostris*. The ridges along the anterior and labial edges of the crown terminate at a large stylar cusp. Although of different sizes and somewhat variable in position the other stylar cusps are smaller than the anterior cusp. A small but prominent posterior stylar cusp is present on the labial ridge of most molars. As far as can be determined, the molars preserved in J11379 are of approximately the same size and closely resemble the molars preserved in the type specimen of *P. longirostris*, no. 47740. Recently the type specimen was more fully prepared and cleaned, revealing the alveoli of M^7 containing fragments of the tooth. Thus the only emendation to Simpson's (1928, pp. 105–6) description of the molars of *Peralestes* required by J11379 is the addition of a description of the seventh molar. M^7 (text-fig. 2*b*), like the preceding molars, is heavily damaged. Its crown appears to have resembled that of M^6, differing in its smaller size, the shallower medial notch on the labial edge of the crown, and, possibly, in the relatively smaller size or absence of cusps along the anterior and posterior edges of the crown.

Comments. Simpson (1928, pp. 102–4) has reviewed the evidence for the allocation of *Peralestes* to the Spalacotheriidae. He seconded the suggestion that the genus *Peralestes* might be based on the upper dentition of *Spalacotherium tricuspidens*. But Simpson commented (ibid., pp. 103–4): 'It is not to be definitely considered as a synonym of *Spalacotherium*, however, until their association can be considered proven beyond any question.' Since publication of Simpson's monograph the upper and lower molars of an Albian symmetrodont, *Spalacotheroides bridwelli*, have been described by Patterson (1955, 1956). Information obtained from these fossils supports the allocation of *Peralestes* to the Spalacotheriidae, but does not bear directly on the problem of the synonymy of the Purbeck genera. Now it can be demonstrated that the postcanine dental formulae of *Peralestes* and *Spalacotherium* are equivalent and that the posterior molars of both, M$^7_7$, are distinctly smaller than the penultimate molars. This adds support to the suggestion that *Peralestes longirostris* is a junior synonym of *Spalacotherium tricuspidens*, but it does not prove their association beyond any question.

Recognition of the whereabouts of J11379 requires one minor change in the currently accepted classification. This fossil appears to be the specimen originally identified by Owen (1854, p. 430) as a fragment of the right dentary of *Spalacotherium tricuspidens.* The illustration of the specimen (ibid., fig. 12) is not detailed, but the identification can be based on the gross similarities between J11379 and the illustration. Also, of the fossils listed by Owen (ibid., p. 431) as associated with the mammalian fossil, only the '. . . jaw with a few teeth . . .' and '. . . the impression of the dentary bone . . .' of *Macellodus* are missing from the block in which J11379 is preserved. In the text of his monograph on Mesozoic mammals Owen (1871, pp. 36–37) identified the mammalian fossil as '*Incertae sedis, Peralestes* sp.?', but in the legend of Plate I he allocated it to a new species of *Phascolestes, P. dubius.* Because Owen's description and illustrations were inadequate, the whereabouts of the type specimen was unknown, and the referred specimen was indeterminate, Simpson (1928, p. 143) deemed the species *Phascolestes dubius* to be a *nomen nudum.* Now that the type specimen has been found, *P. dubius* can be demonstrated to be a junior synonym of *Peralestes longirostris.*

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CATALOGUE OF DESCRIBED AND FIGURED SPECIMENS IN THE BEGG COLLECTION IN THE HUNTERIAN MUSEUM OF THE UNIVERSITY OF GLASGOW

by ETHEL D. CURRIE and T. NEVILLE GEORGE

JOHN L. BEGG (1874–1958) of Glasgow was a distinguished amateur palaeontologist who for many years collected fossils notably from the Ordovician and Silurian rocks of southern Scotland. His specimens, many of them exceptionally well preserved, have been used by Begg himself and by others in palaeontological and stratigraphical studies that have enriched Lower Palaeozoic geology. Most of them were presented to, or bought by, the Hunterian Museum of the University of Glasgow, where they form the Begg Collection.

The collection is especially rich in fossils of the Bala and Valentian series of the Girvan district, represented by several hundred trilobites and as many protrematous brachiopods, about 100 asteroids, 70 gastropods, 60 lamellibranchs, 60 cystids, and smaller numbers of inarticulate brachiopods, nautiloids, and crinoids. The local fossils are supplemented by about 200 other specimens, most of which Begg got by exchange, from comparable horizons in Scandinavia, Canada, and the U.S.A.; and by about 60 extra-British Cambrian trilobites. A group of Carboniferous fossils includes about 100 lamellibranchs (mainly Scottish), about 80 crinoids, about 70 gastropods (many from the Isle of Man), and 30 nautiloids; but Carboniferous corals, brachiopods, goniatites, and polyzoans are very poorly represented. Mesozoic and Tertiary fossils are mostly lacking, but there is a heterogeneous group of about 50 ammonites, and a few gastropods from the Pleistocene clays of the Clyde estuary.

This catalogue lists all the described and figured specimens in the Begg Collection. References are given to the original figure or description of each specimen, and to any subsequent renaming or redescription. Where possible, references are also given to the use of several specimens or of supplementary specimens in description, and comment is made on the manner of preservation of the specimens.

Specimens 'lost' or unidentifiable are omitted from reference; a number of type-specimens that should have come to the Museum, and that may be recorded elsewhere as being in the Museum collections, were never received from Mr. Begg, and, although it is likely that he gave or lent them to other workers or deposited them in other institutions, no record of them is now to be found in Glasgow.

Specimens are listed under Hunterian Museum numbers, but Mr. Begg's private numbers (prefaced by BG) are also included in round brackets where the specimens carry them. An explanation of Mr. Begg's Starfish Bed horizons may be found in Begg 1947, p. 29.

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TRILOBITA

Ordovician

Acidaspis (*Ceratocephala*) *discreta* Reed
Internal mould, A1030*a* (BG2102), and external mould, A1030*b* (BG2103), of an almost complete specimen.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1935*a*, p. 38, pl. 1, figs. 22, 22*a*, *b* (A1030*a*), pl. 4, fig. 10 (A1030*b*). Whittington 1956, p. 515, pl. 59, fig. 13; pl. 60, fig. 10 (A1030*b*). Whittington placed the species in synonymy with *Proceratocephala terribilis* (Reed), to which he referred Begg's specimen.

Acidaspis (*Miraspis*) *solitaria* Reed
Holotype, a small cranidium, A939 (BG3142).
Caradoc, Stinchar Limestone Group, *Didymograptus superstes* Shales; Aldons, near Girvan.
Reed 1935*a*, p. 37. pl. 3, fig. 21.

Ampyx (*Ampyxina*) *aldonensis* Reed
Syntypes, 'a few head-shields', only two of which are specified by number, A919 (BG2124) and A920 (BG3101). There is also a pygidium, A1126 (BG2141), which according to Reed may be associated with them.
Caradoc, Stinchar Limestone Group, *Didymograptus superstes* Shales; Aldons, near Girvan.
Reed 1935*a*, p. 7, pl. 1, fig. 23 (A919). Whittington 1959, p. 487, pl. 28, fig. 10 (A1126), figs. 11, 13 (A919).

Ampyx carrickensis Begg
Holotype, A3690, a small cephalon.
Caradoc, Balclatchie Group; Dow Hill, near Girvan.
Begg 1947, p. 42, pl. 3, figs. 7, 8.

Asaphus (*Parabasilicus*) cf. *powisi* Murchison
Part of a thorax comprising axial lobe and pleura of seven segments, A934 (BG2261).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1935*a*, p. 12, pl. 2, fig. 13.

Astroproetus reedi Begg
Holotype, A1082 (BG6451), a complete specimen.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Begg 1939, p. 375, pl. 6, fig. 2.

Astroproetus whittardi Begg
Holotype, A1083 (BG7707), a complete specimen.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1939, p. 376, pl. 6, fig. 3.

Calymene (*Colpocoryphe?*) *aldonensis* Reed
Syntypes, two imperfect cranidia, A1037 (BG2111) and A1038 (BG2110).
Caradoc, Stinchar Limestone Group, *Didymograptus superstes* Shales; Aldons, near Girvan.
Reed 1935*a*, p. 48, pl. 1, fig. 14 (A1037), fig. 15 (A1038). Shirley 1936, p. 418.

Calymene (*Diacalymene*) *bigener* Reed
The description is based on one nearly perfect cephalon with attached thorax, A1098 (BG929).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1935*a*, p. 47, pl. 1, fig. 3. Shirley 1936, p. 418.

Clypoproetus asteroideus Begg
Holotype, A1080 (BG7713), a complete specimen.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1939, p. 374, pl. 6, fig. 1.

Cryptolithus nicholsoni Reed

The specimen, A3623 (BG142), shows the lower lamella of the fringe.

Ashgill, Pusgill Beck, Westmorland.

Begg 1944, pl. 5, fig. 1.

Cybele (Cybeloides) loveni Linnarsson var. *girvanensis* Reed

A specimen split to separate the glabella with hypostome attached beneath, A737, A737*a*, and A737*b* (BG8217).

Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.

Begg 1943*a*, p. 61, pl. 2, figs. 2, 2*a* (A737).

Cybele (Cybeloides) loveni Linnarsson var. *radiata* Reed

Holotype of the variety, a specimen consisting of a pair of free cheeks displaced from their correct relative position, together with some broken fragments of the thorax, A1054 (BG259).

Ashgill, Upper Drummuck Group, Ladyburn mudstone, Zone of *Dicellograptus anceps*; South Threave, near Girvan.

Reed 1930, p. 195, pl. 9, figs. 2, 2*a–b*.

Cybele (Cybelina) monoceros Reed

The description of this species is based on a cranidium, A1067 (BG252). Two small pygidia, A1068 (BG254) and A1069 (BG253), are said to be probably referable to the same species.

Caradoc, Balclatchie Group; Balclatchie, near Girvan.

Reed 1931*a*, p. 101, pl. 5, fig. 1 (A1067), fig. 2 (A1068), fig. 3 (A1069). Reed 1931*b*, p. 26.

Cybele (Cybele) nicholsoni Reed

This species is apparently based on a cranidium, A1042 (BG2260).

Caradoc, Balclatchie Group; Dow Hill, near Girvan.

Reed 1935*a*, p. 52, pl. 4, fig. 4.

An isolated right free cheek, A1043 (BG2273), from the same locality, probably belongs to the same species (Reed 1935*a*, p. 53, pl. 2, fig. 14).

Cybele nicholsoni Reed

A hypostome, counterpart moulds, A4127*a* (BG11903) and A4127*b* (BG11904), is referred tentatively to this species.

Caradoc, Balclatchie Group; Dow Hill, near Girvan.

Begg 1951, p. 367, pl. 1, fig. 14 (A4127*a*).

Cybele (Cybele?) perversa Reed

Holotype, a small incomplete cranidium, A1100 (BG1052).

Caradoc, Balclatchie Group; Balclatchie, near Girvan.

Reed 1935*a*, p. 53, pl. 4, fig. 5.

A specimen referred doubtfully to this species (ibid., p. 54) cannot be found in the Begg Collection.

Encrinurus multisegmentatus (Portlock) var. *girvanensis* Reed

This variety 'is represented by one perfect individual [A1040 (BG963)] and by several incomplete specimens, thoraces, pygidia and head-shields one of which [A1136 (BG960)] shows the hypostome in position'. Specimens A1040 and A1136 are labelled, but the others, for which numbers are not given, cannot be positively identified.

Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.

Reed 1935*a*, p. 50, pl. 4, fig. 9 (A1040).

A hypostome, A733 (BG7573).

Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.

Begg 1943*a*, p. 58, pl. 2, fig. 4.

A hypostome, A4128 (BG11905).

Same horizon and locality.

Begg 1950*b*, p. 367, pl. 1, fig. 15.

Encrinurus sublanceolatus Reed
Holotype, a pygidium, A1093 (BG2265).
Caradoc, Stinchar Limestone Group; Glenlochrie, near Girvan.
Reed 1935*a*, p. 49, pl. 4, fig. 8.

Encrinurus aff. *trispinosus* Reed
A large cranidium, A4099 (BG3368).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; east brow of Quarrel Hill, New Dailly, near Girvan.
Tripp 1957, p. 68, pl. 11, fig. 14.

Flexicalymene cf. *meeki* (Foerste)
A cranidium, A1096 (BG1011).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; east brow of Quarrel Hill, New Dailly, near Girvan.
Shirley 1936, p. 404, pl. 29, fig. 8.

Illaenus balclatchiensis Reed var. *cristata* Reed
Holotype of the variety, a cranidium, A935 (BG25).
Caradoc, Balclatchie Group; Dow Hill, near Girvan.
Reed 1935*a*, p. 24, pl. 3, fig. 2.

Illaenus drummuckensis Reed
Holotype, A3687 (BG6454), a complete pygidium; paratype, A3688 (BG7740), the posterior half of another.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed *in* Begg and Reed 1945, p. 260, pl. 1, fig. 3 (A3687), fig. 4 (A3688).

Illaenus longicapitatus Reed
A cephalon with the epistome in place, split to expose the hypostome *in situ*, counterparts, A734 (BG7669*a*) and A734*a* (BG7669).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Begg 1943*a*, p. 59, pl. 2, figs. 1, 1*a* (A734).

Illaenus oblongatus (Angelin) var. *exstans* Reed
Holotype of the variety, a small pygidium, A1108 (BG9478).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1941, p. 270, pl. 5, fig. 7.

Illaenus roemeri Volborth var. *transversalis* Reed
Holotype of the variety, a pygidium, A1053 (BG290).
Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.
Reed 1930, p. 194, pl. 9, figs. 1, 1*a*, *b*.

Illaenus superstes Reed
Syntypes, a cephalon and pygidium of the same individual with the thorax crushed between them, A3630 (BG9685); a cephalon lacking the right free cheek, A3631 (BG9686); a pygidium with thorax attached, A3632 (BG9653); a pygidium, A3633 (BG9687); and a cephalon, A3646 (BG9680), which is not figured (p. 60).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1944*a*, p. 59, pl. 2, figs. 3, 3*a* (A3630), figs. 4, 4*a* (A3631), fig. 5 (A3632), fig. 6 (A3633).

Lichas (*Metopolichas?*) *congruens* Reed
Holotype, a well-preserved cranidium, A937 (BG2084).
Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.
Reed 1935*a*, p. 34, pl. 3, fig. 10.

Lichas (*Platylichas*) *crescenticus* Reed

The fragments (BG2080 and BG2082) on which Reed based his description are counterparts; the holotype thus consists of part of a cranidium with hypostome in place, A915 (BG2082), an external mould of the complete cephalon, A915*a* (BG2082), and an external mould of the ventral surface and hypostome, A915*b* (BG2080).

Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.

Reed 1935*a*, p. 29, pl. 3, figs. 13 and 15 (A915), fig. 14 (A915*b*), fig. 16 (A915*a*). Phleger 1937, p. 254 (BG2080*a* misquoted for BG2082). Begg 1943*b*, p. 160.

Lichas (*Hemiarges*) *maccullochi* Reed

A hypostome *in situ*, exposed in dorsal view beneath the cephalon which has been partly removed, A730 (BG5404).

Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.

Begg 1943*a*, p. 56, pl. 2, fig. 6.

Reference is made (p. 56) to four specimens in which ornament is well shown, A743 (BG3305), A744*a* (BG3307*a*), A745 (BG3219), A746 (BG7561).

Lichas (*Acrolichas*) *tenuilobatus* Reed

A small cranidium, A3647 (BG9783).

Caradoc, Balclatchie Group; Balclatchie, near Girvan.

Reed 1944*a*, p. 61, pl. 2, fig. 8. Tripp 1958, p. 580, pl. 85, fig. 12.

Lichas (*Platylichas*) *thraivensis* Reed

Holotype, a pygidium, A916 (BG2087), and its external mould, A916*a* (BG2081).

Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.

Reed 1935*a*, p. 32, pl. 3, fig. 17 (A916), fig. 18 (A916*a*).

A hypostome, A917 (BG2090), is referred to as possibly belonging to this species (Reed 1935*a*, p. 33, pl. 3, fig. 19).

Lichas (*Platylichas*) *vicinus* Reed

Holotype, a crushed pygidium with parts of a few thoracic segments attached, A918 (BG2083).

Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.

Reed 1935*a*, p. 33, pl. 3, fig. 12.

Otarion elongatus Begg

Holotype, A1089 (BG9325), a nearly complete specimen; paratype, A1090 (BG6453), an external mould of a small, almost complete specimen.

Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.

Begg 1939, p. 380, pl. 6, fig. 8 (A1089), fig. 7 (A1090).

Otarion (= *Cyphaspis*) cf. *minima* (Cooper)

A small, incomplete cranidium, A1034 (BG1017).

Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.

Reed 1935*a*, p. 44, pl. 1, fig. 17.

Paraharpes hornei (Reed)

An almost complete specimen, E4472 (BG759) and E4473 (BG760), counterparts; and part of a cephalon with fringe, A4475 (BG2362).

Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.

Whittington 1950, p. 39, pl. 4, fig. 4 (A4473), fig. 6 (A4475). The specimen (BG803) of figs. 1 and 3 cannot be found in the Begg Collection.

Phacops (*Monorakos*) *asteroideus* Reed

A complete specimen with pygidium displaced, A1058 (BG594), and a cephalon with part of the thorax attached, A1059 (BG595).

Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.
Reed 1930, p. 198, pl. 10, figs. 1, 1*a*, *b* (A1058), figs. 2, 2*a* (A1059). Reed 1931*b*, p. 24.

Phacops (*Calliops*) *jukesi* Salter var. *vicina* Reed
Holotype, A5370 (BG11768), a nearly complete cephalon.
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1945, p. 314, pl. 1, fig. 6.

Phacops (*Pterygometopus?*) *quarrelensis* Reed
Syntypes, two pygidia, A1056 (BG603), A1057 (BG602).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.
Reed 1930, p. 197, pl. 10, figs. 3, 3*a* (A1056). Reed 1931*b*, p. 24.

Phacops (*Pterygometopus*) *retardatus* Reed
An almost complete specimen, A736 (BG8208*a*), with part of the cephalon missing so that it presents an external mould of the hypostome.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1943*a*, p. 60, pl. 2, fig. 10.

Phillipsinella parabola Barrande
A hypostome in place behind the glabella, in ventral aspect, counterparts, A735 (BG8211) and A735*a* (BG8211*a*).
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1943*a*, p. 60, pl. 2, fig. 8 (A735).

Platylichas congruens (Reed)
A large individual in which the cephalon and pygidium are crushed and incomplete, (A3967).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Tripp 1958, p. 579, pl. 85, figs. 7, 8.

Pliomera (*Pliomerops*) *girvanensis* Reed
Holotype, part of a cephalon, A1079 (BG445).
Caradoc, Stinchar Limestone Group; Aldons Quarry, near Girvan.
Reed 1930, p. 196, pl. 9, figs. 3, 3*a*.

Pliomerella serotina Reed
Holotype, part of a cranidium, A1107 (BG9480), and a fragment of its impression, A1107*a* (BG9481).
Caradoc, Balclatchie Group; Dow Hill, near Girvan.
Reed 1941, p. 268, pl. 5, fig. 1 (A1107), fig. 2 (A1107*a*).

Proceratocephala terribilis (Reed)
Internal and external moulds, A1030*a* (BG2102) and A1030*b* (BG2103), of an almost complete specimen. The specimen is the holotype of *Acidaspis* (*Ceratocephala*) *discreta* (Reed) (q.v.).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Whittington 1956, p. 515, pl. 59, fig. 13, pl. 60, fig. 10 (A1030*b*).

Proetus ardmillanensis Begg
Holotype, A3692, part of a small cranidium.
Caradoc, Balclatchie Group; Dow Hill, near Girvan.
Begg 1947, p. 42, pl. 3, fig. 3.

Proetus balclatchiensis Begg
Holotype, A4122 (BG11898), an incomplete cephalon and part of the enrolled thorax.
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Begg 1951, p. 362, pl. 1, fig. 1.

Proetus fardenensis Begg
Holotype, A3821 (BG11894), a cephalon with part of the thorax.

Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1950, p. 285, pl. 14, figs. 1, 2.

Proetus girvanensis Nicholson and Etheridge
Part of a cephalon with hypostome in place beneath the glabella, A731 (BG8341).
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1943*a*, p. 57, pl. 2, figs. 7, 7*a*.

Proetus mactaggarti Begg
Holotype, A3691 (BG11871), a complete specimen.
Ashgill, Upper Drummuck Group, Starfish Bed a few feet above No. 3; Ladyburn, near Girvan.
Begg 1947, p. 40, pl. 3, figs. 1, 2.

Proetus scobiei Begg
Holotype, A3689 (BG11017), a cephalon.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg, *in* Begg and Reed 1945, p. 261, pl. 1, figs. 1, 2.

Proetus trefoileum Begg
Holotype, A4123 (BG11899), external mould of an almost complete cephalon.
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Begg 1951, p. 364, pl. 1, fig. 2.

Proetus sp.
A small, incomplete cranidium, counterparts, A4124*a* (BG11900) and A4124*b* (BG11900*a*).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Begg 1951, p. 365, pl. 1, fig. 3 (A4124*a*).

Pseudosphaerexochus granulatus (Angelin)
Reed referred to two cranidia (BG2075 and BG2335), but only one of them, A1050 (BG2075), is in the Hunterian Museum. The other was sent by Begg to the Senckenberg Museum, Frankfurt-on-Main, there numbered SMF X 929*a*.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1935*a*, p. 56, pl. 4, fig. 2 (A1050).

Pseudosphaerexochus subquadratus Reed
Part of a cranidium, A1048 (BG748).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1935*a*, p. 56, pl. 4, fig. 3.

Remopleurides asteroideus Reed
Three glabellae, A933 (BG2066), A1127 (BG785), A1128 (BG2341).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1935*a*, p. 11, pl. 4, fig. 6 (A933), fig. 7 (A1127).

Remopleurides hedströmi Reed
Holotype, a cranidium, A3629 (BG9502).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Threave Glen (Ladyburn), near Girvan.
Reed 1944*a*, p. 58, pl. 2, figs. 2, 2*a*.

Selenoharpes youngi (Reed)
Cephala with fringe, A4468 (BG206) and A4469 (BG205).
Caradoc, Balclatchie Beds; Balclatchie, near Girvan.
Whittington 1950, p. 30, pl. 3, fig. 4 (A4469), fig. 5 (A4468).

Sphaerocoryphe hastata Begg
Holotype, A1095 (BG2151) and A1095*a* (BG2512), counterparts, part of a cephalon.
Caradoc, Stinchar Limestone Group, *Didymograptus superstes* Shales; Aldons Quarry, near Girvan.
Begg 1940*a*, p. 302, pl. 4, fig. 8 (A1095).

Sphaerocoryphe thomsoni Reed

Of six specimens referred to, BG7729–31, BG955, BG7727, and BG7728, the first three cannot be found. The specimens in the Hunterian Museum are a cranidium, A1110 (BG955), and two specimens on a single slab, A838 (BG7727 and BG7728), in each of which the glabella is removed and the hypostome exposed.

Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.

Begg 1940*a*, p. 300, pl. 4, fig. 3 (A1110), fig. 6 (A838).

Stygina latifrons (Portlock)

A specimen in which the glabella is removed, exposing an external mould of the hypostome, A732 (BG3308).

Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.

Begg 1943*a*, p. 58, pl. 2, fig. 5.

Telephus girvanensis Reed

Reed implied that the Begg Collection includes more than one example of this species, but only one specimen, a cranidium, A921 (BG3140), is quoted by number.

Caradoc, Stinchar Limestone Group, *Didymograptus superstes* Shales; Aldons, near Girvan.

Reed 1935*a*, p. 9, pl. 1, figs. 2, 2*a* (A921).

Teratorhynchus sp.

A cephalon and a few thoracic segments, A3823 (BG229).

Caradoc, Balclatchie Group; Dow Hill, near Girvan.

Begg 1950, p. 290, pl. 14, fig. 3.

Tretaspis cerioides (Angelin) var. *sortita* Reed

Three almost complete specimens, A3625 (BG2251), A3626 (BG24), A3628 (BG23), and two cephala, A3624 (BG3049), A3627 (BG9515).

Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.

Begg 1944, p. 113, pl. 5, fig. 2 (A3624), figs. 3 and 6 (A3625), fig. 4 (A3626), fig. 5 (A3627), fig. 7 (A3628).

Trinucleus (*Cryptolithus*) *gibbifrons* M'Coy var. *praeterita* Reed

Reed referred the following specimens to this variety: A930 (BG1000), A924 (BG1002), A925 (BG2263), A926 (BG1003), A927 (BG2264), A928 (BG1013), A929 (BG1014), and BG1004. Of these, BG1004 is missing. The specimens are cephala or parts of cephala, except A928 and A929, which are pygidia.

Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.

Reed 1935*a*, p. 1, pl. 4, fig. 11 (A924), fig. 12 (A925), fig. 13 (A926), fig. 14 (A927), fig. 15(A928).

Trinucleus (*Tretaspis*) *persulcatus* Reed

The species appears to be based on one specimen in the John Smith Collection and on several specimens in the Begg Collection, of which three (BG951, BG964, and BG967) are missing. The specimens remaining are A1116 (BG968), A1117 (BG974), A1118 (BG975), A1119 (BG980), A1120 (BG981), and A932 (BG982).

Ashgill, Upper Drummuck, Starfish Bed No. 1; Ladyburn, near Girvan.

Reed 1935*a*, p. 6, pl. 4, fig. 16 (A932).

Warburgella rotundata Begg

Holotype, A1084 (BG9323), and paratype, A1085 (BG6458), both almost complete specimens.

Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.

Begg 1939, p. 378, pl. 6, figs. 5 and 6 (A1084), fig. 4 (A1085).

Silurian

Acidaspis (*Globulaspis*) *prominens* Reed

Holotype, an incomplete cranidium, A1066 (BG735).

Middle Valentian, Saugh Hill Group; Newlands, near Girvan.

Reed 1931*a*, p. 100, pl. 5, figs. 5, 5*a*, *b*.

Acidaspis (*Miraspis*) *ultima* Reed
Holotype, a small incomplete cranidium, A1065 (BG738).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1931*a*, p. 99, pl. 5, figs. 6, 6*a*.

Cheirurus conjunctus Reed
Holotype, a well-preserved cranidium, A1045 (BG1198), and its external mould, A1045*a* (BG1199).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1935*a*, p. 55, pl. 4, fig. 1 (A1045).

Cheirurus elongatus Reed
The species is based on four syntypes—two incomplete cranidia, A1072 (BG421) and A1073 (BG420), an external mould of a pygidium, A1074 (BG422), and a hypostome, A1075 (BG419).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1931*a*, p. 103, pl. 4, figs. 5, 5*a* (A1072), fig. 6 (A1073), fig. 7 (A1074); pl. 5, fig. 4 (A1075).
Begg 1943*a*, p. 62 (A1075).

Cyphoproetus newlandensis Begg
Holotype, A3824 (BG11895), a small cranidium.
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Begg 1950, p. 287, pl. 14, fig. 7.

Illaenus aemulus Salter
A pygidium, A936 (BG1028).
Middle Valentian, Saugh Hill Group, Upper Pentamerus Bed; Penwhapple Glen, near Girvan.
Reed 1935*a*, p. 25, pl. 2, fig. 9.
A head-shield (BG1036), referred to as probably belonging to this species, cannot be found in the Begg Collection.

Phacops elliptifrons Sars and Boeck
An incomplete hypostome, A742 (BG8715).
? Saugh Hill Group; north of Mulloch Hill, near Girvan.
Begg 1943*a*, p. 61, pl. 2, fig. 9.
Specimens that show some detail of the ventral 'interlocking' furrow of the cephalon, A4141 (BG586), A4142–5.
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Begg 1950, p. 367, pl. 1, figs. 6 and 7 (A4141), fig. 8 (A4142), fig. 9 (A4143), fig. 10 (A4144), fig. 11 (A4145).

Proetus sp.
External moulds of two pygidia, A4125 (BG11901), and A4126 (BG11902).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Begg 1950, p. 366, pl. 1, fig. 4 (A4125), fig. 5 (A4126).

Proetus (*Cyphoproetus*) *externus* Reed
Holotype, a cranidium, A1032 (BG911).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1935*a*, p. 42, pl. 2, fig. 15.

Proetus interjectus Reed
Holotype, a small cranidium, A1031 (BG2057).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1935*a*, p. 40, pl. 3, fig. 23.

Proetus scoticus Reed
Holotype, a cranidium, A1109 (BG9483).
Lower Llandovery, Mulloch Hill Group; Craigens, near Girvan.
Reed 1941, p. 271, pl. 5, fig. 3.

Proetus subtriangularis Begg
Holotype, A3822 (BG11896), a cranidium.
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Begg 1950, p. 287, pl. 14, fig. 6.

Scutellum (*Bronteus*) *cunctatum* Reed
According to Reed there are three nearly perfect cranidia and two pygidia in the Begg Collection, which are presumably the syntypes of the species. One of these specimens cannot be found, but the four figured specimens are available. These are two cranidia, A1061 (BG501) and A1062 (BG503), and two pygidia, A1063 (BG499) and A1064 (BG495).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1931*a*, p. 97, pl. 4, fig. 1 (A1061), fig. 2 (A1062), fig. 3 (A1063), fig. 4 (A1064).

Carboniferous

Cummingella balladoolensis Reed
The species is represented by three syntypes—two cephala, A3704 (BG8601) and A3705 (BG8601*a*), and a glabella, the latter on the same rock-fragment as a pygidium, A3706 (BG8601*x*).
Carboniferous Limestone, Upper Limestone; Balladoole, Isle of Man.
Reed 1942, p. 668, pl. 10, fig. 1 (A3704), fig. 2 (A3705), figs. 3, 3*a* (A3706).

Cyphinioides ashfellensis Reed
Holotype, a complete individual enrolled so that the cephalon is pressed against the pygidium, A3700 (BG7853).
Lower Carboniferous, Ashfell Limestone; near Kirkby Stephen, Yorkshire.
Reed 1942, p. 654, pl. 8, figs. 1, 1*a*, 2.

Eocyphinium clitheroense Reed
Holotype, a cephalon, A3701 (BG8602).
Lower Carboniferous; Clitheroe, Lancashire.
Reed 1942, p. 656, pl. 9, figs. 1, 1*a*.

Eocyphinium? bivium Reed
Holotype, a pygidium in interior view, A3702*a* (BG9082), and its internal mould, A3702 (BG9089).
Upper Limestone Group, Calmy Limestone; Linn Spout, Dalry, Ayrshire.
Reed 1942, p. 659, pl. 9, figs. 2, 2*a*, *b* (A3702).

Griffithides? ambiguus Reed
Holotype, a pygidium, A3714 (BG7579).
Carboniferous Limestone, Upper Limestone; Balladoole, Isle of Man.
Reed 1942, p. 667, pl. 11, figs. 6, 6*a*, *b*.

Weberides dalriensis Reed
Holotype, a pygidium, A3707 (BG9080)
Upper Limestone Group, Calmy Limestone; Linn Spout, Dalry, Ayrshire.
Reed 1942, p. 666, pl. 10, figs. 4, 4*a*,*b*.

Weberides mucronatus M'Coy var. *lata* Reed
Holotype of the variety, a pygidium, A3713 (BG7851).
Lower Limestone Group; Leslie, Fife.
Reed 1942, p. 663, pl. 11, figs. 5, 5*a*.

Weberides mucronatus M'Coy var. *traquairi* Reed
Syntypes of the variety appear to be a cephalon, A3709 (BM104), and two pygidia, A3710 (BM103) and A3711 (BM102).
Carboniferous Limestone Series; Garple Burn, Muirkirk, Ayrshire.
Reed 1942, p. 660, pl. 11, fig. 1 (A3709), figs. 2, 2*a* (A3710) and fig. 3 (A3711).
A pygidium, A3712 (BG7852).

Lower Limestone Group; Leslie, Fife.
Reed 1942, pl. 11, fig. 4.

Weberides parilis Reed
Holotype, a pygidium, A3708 (BG9094).
Upper Limestone Group, Calmy Limestone; Linn Spout, Dalry.
Reed 1942, p. 664, pl. 10, figs. 5, 5*a*, *b*.

BRACHIOPODA

Ordovician

Aegiria? balclatchiensis (Reed)
An internal mould of a ventral valve, L2795 (BG9477).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1941, p. 273, pl. 5, fig. 6.

Bimuria perrugata Reed
Holotype, L3191 (BG11754), an external mould of a dorsal valve with the hinge-area of the ventral valve; paratypes, two external moulds of dorsal valves, L3192 (BG11874) and L3193 (BG11729).
Caradoc, Balclatchie Group; Balclatchie Bridge, near Girvan.
Reed 1945, pp. 313–14, pl. 1, fig. 1 (L3191), fig. 2 (L3192), fig. 3 (L3193).

Chonetes (*Eodevonaria*) *celtica* Reed
Holotype, L3315 (BG9748), a dorsal valve with the hinge-areas of both valves.
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed, 1944*c*, p. 217, pl. 3, figs. 2, 2*a*.

Coelospira? insoleta Reed
Holotype, an internal mould of a complete shell, L2805 (BGS75).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Threave Glen (Ladyburn), near Girvan.
Reed 1935*b*, p. 8, pl. 1, figs. 2, 2*a*–*d*.

Lingula girvanensis Begg
Holotype, L2992, a ventral valve.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1947, p. 32, pl. 2, fig. 2.

Lingula? isosceles Begg
Holotype, L2990.
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Begg 1947, p. 36, pl. 2, figs. 7, 7*a*.
In a letter (27 June 1949), Begg stated: 'I have now become convinced that this is a peculiarly preserved example of the *Hyolithes* present in the Balclatchie Beds.'

Lingula pustulosa Begg
Holotype, L2994, a ventral valve.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1947, p. 31, pl. 2, fig. 1.

Lingulasma? concatenata Begg
Holotype, L2991, a ventral valve; paratype, L2993, an internal mould of a ventral valve with part of the shell in place.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1947, p. 35, pl. 2, figs. 5, 5*a* (L2991), fig. 6 (L2993).

Lingulasma? fardenensis Begg
Holotype, L2996, a ventral valve; paratype, L2997, an internal mould of a ventral valve with part of the shell attached.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1947, p. 33, pl. 2, fig. 4 (L2996).

Lingulasma cf. *penultimum* Reed
A ventral valve, L2998.
Ashgill, Upper Drummuck Group, Starfish Bed No. 2; Ladyburn, near Girvan.
Begg 1947, p. 33, pl. 2, figs. 3, 3*a*.

Orthis (*Glyptorthis*) *biornata* Reed
Holotype, L3194 (BG11716), external mould of a brachial valve.
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1945, p. 309, pl. 1, fig. 5.

Orthis (*Barbarorthis*) cf. *foraminifera* Opik
External mould of a dorsal valve, L2799 (BGS37).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Threave Glen (Ladyburn), near Girvan.
Reed 1935*b*, p. 4, pl. 1, fig. 10.

Orthis (*Platystrophia*) *praecursor* Foerste var. *molaris* Reed
Holotype of the variety, a ventral valve, L2800 (BG110).
Whitehouse Group; Shalloch Mill, near Girvan.
Reed 1935*b*, p. 4, pl. 1, fig. 4.

Orthis (*Barbarorthis*) *quarrelensis* Reed
Holotype, an internal mould of a ventral valve, L2798 (BG126).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.
Reed 1935*b*, p. 3, pl. 1, figs. 6, 6*a*.

Plectambonites praeteritus Reed
Holotype, L3195 (BG11726), external mould of a dorsal valve.
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1945, p. 312, pl. 1, fig. 4.

Plectodonta thraivensis (Reed) var. *divergens* Reed
Holotype of the variety, an internal mould of a ventral valve, L3314 (BG9558).
Caradoc, Craighead Mudstones (not Craighead Limestone, as stated); Craighead Quarry, near Girvan.
Reed 1944*c*, p. 216, pl. 3, figs. 3, 3*a*.

Ptychoglyptus shallochensis Reed
Holotype, half of a dorsal valve showing the hinge-area, L2803 (BG144).
Whitehouse Group; Shalloch Mill, near Girvan.
Reed 1935*b*, p. 7, pl. 1, fig. 5.

Ptychoglyptus virginiensis Willard var. *irregularis* Reed
Holotype of the variety is based on one valve showing ornament, L2794 (BG9482).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1941, p. 274, pl. 5, fig. 8.

Rafinesquina cf. *hadelandica* Holtedahl
A small ventral valve, L2796 (BG9479).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1941, p. 274, pl. 5, fig. 9.

Siphonotreta lagganensis Begg
Holotype, L3371, a small ventral valve.
Caradoc, Balclatchie Group; Laggan Gill, near Girvan.
Begg 1947, p. 44, pl. 3, fig. 9.

Sowerbyella cf. *undosa* Öpik
Internal mould of a small ventral valve, L2804 (BG1124).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Threave Glen (Ladyburn), near Girvan.
Reed 1935*b*, p. 7, pl. 1, fig. 8.

Strophomena planumbona (Hall) var. *girvanensis* Reed
Holotype of the variety, a ventral valve in interior view, L3316 (BG9741).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1944*c*, p. 218, pl. 3, fig. 5.

Triplecia asteroidea Reed
Syntypes, three internal moulds, one of a complete shell, L2801 (BGS49), which is figured. Of the other two, only one, L2802 (BG5228), is in the Hunterian Museum.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Threave Glen (Ladyburn), near Girvan.
Reed 1935*b*, p. 5, pl. 1, figs. 1, 1*a–c* (L2801).

Silurian

Meristina mullochensis Reed
Syntypes, an internal mould of a ventral valve, L2807 (BG2015), and an internal mould of a complete shell, L2808 (BG1154).
Lower or Middle Valentian, Mulloch Hill Group; Rough Neuk (L2807) and Mulloch Hill (L2808), near Girvan.
Reed 1935*b*, p. 10, pl. 1, figs. 9, 9*a* (L2807).

Orthis (*Orthostrophia*) *camreganensis* Reed
Holotype, an internal mould of a ventral valve, L2797 (BG108).
Upper Llandovery, Camregan Group; Penwhapple, near Girvan.
Reed 1935*b*, p. 2, pl. 1, fig. 7.

Rhynchospirina dispar Reed
Holotype, a small ventral valve, L2806 (BG2030).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1935*b*, p. 9, pl. 1, fig. 3.

Carboniferous

Fluctaria undata (Defrance)
A ventral valve, L1536.
Viséan; Poolvash, Isle of Man.
Muir-Wood and Cooper 1960, pl. 115, figs. 15–19.

LAMELLIBRANCHIA

Ordovician

Ambonychinia balclatchiensis Reed
Holotype, a nearly complete shell, S7639 (BG9722).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1944*b*, p. 213, pl. 2, fig. 2.

Byssonychia quarrelensis Reed
Holotype, an internal mould of a right valve, S7644 (BG11885).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.
Reed 1946, p. 203, pl. 14, figs. 3, 4.

Ctenodonta collina Reed
Holotype, internal mould of a left valve, S7641 (BG11880).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.
Reed 1946, p. 202, pl. 14, fig. 1.

Cyrtodonta reposita Reed
Holotype, an internal mould of a left valve, S7637 (BG9765).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1944*b*, p. 210, pl. 2, fig. 5.

Goniophorina sp.
A left valve, S7648 (BG11889).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.
Reed 1946, p. 204, pl. 14, fig. 6.

Orthodesma cf. *approximatum* Foerste
An internal mould of a right valve, S7647 (BG11888).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.
Reed 1946, p. 204, pl. 14, fig. 5.

Plethocardia propinqua Reed
Holotype, a nearly complete shell, S7638 (BG9762).
Caradoc, Balclatchie Group; Balclatchie, near Girvan.
Reed 1944*b*, p. 211, pl. 2, figs. 3, 3*a–c*.

Vanuxemia? girvanensis Reed
Holotype, a small shell, S7564 (BG9484), both valves, side by side but not in contact.
Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.
Reed 1941, p. 276, pl. 5, fig. 4.

Vanuxemia aff. *sardesoni* Ulrich
Internal mould of a left valve, S7645 (BG11886).
Ashgill, Lower Drummuck Group, Quarrel Hill mudstones; Quarrel Hill, near Girvan.
Reed 1946, p. 203, pl. 14, fig. 2.

Silurian

Nuculites seductus Reed
Holotype, an internal mould of a right valve, S7563 (BG9485).
Middle Valentian, Saugh Hill Group; Newlands, near Girvan.
Reed 1941, p. 276, pl. 5, fig. 10.

GASTROPODA

Ordovician

Archinacella unica Reed
Holotype, S9659 (BG6742).
Ashgill, Upper Drummuck Group, Ladyburn mudstones, Zone of *Dicellograptus anceps*; South Threave, near Girvan.
Reed 1941, p. 275, pl. 5, figs. 5, 5*a*.

Carboniferous

Bucaniopsis decussatus (Fleming)
An almost complete specimen, S9679 (BG6988).
Carboniferous, Lower Limestone Group, 'Chiton Bed'; Woodmill, Dunfermline.
Weir 1931, p. 821, pl. 8, fig. 12.

Eoptychia sulcata (de Koninck)
Two almost complete specimens, S9493 and S9494. A young specimen also figured (fig. 3) cannot be found in the Begg Collection.
Carboniferous, Viséan; Balladoole, Isle of Man.
Longstaff 1933, p. 113, pl. 10, fig. 1 (S9493), fig. 2 (S9494).

Euphemus urei (Fleming) var.
A specimen with incomplete apertural margin, S9674 (BG7013).
Carboniferous, Lower Limestone Group, 'Chiton Bed'; Woodmill, Dunfermline.
Weir 1931, p. 845, pl. 9, fig. 8.

Glabrocingulum atomarium (Phillips)
A complete specimen, S9070 (BG9326).
Lower Limestone Group, Charlestown Main Limestone; Woodmill, Dunfermline.
Thomas 1940, p. 40, pl. 2, figs. 2*a*, *b*.

Mourlonia monensis Weir
This species is founded on two specimens in neither of which is the aperture preserved, S9076 (BG7121), S9077 (BG7122).
Carboniferous, Poolvash Limestone; Balladoole, Isle of Man.
Weir 1925, p. 434, pl. 19, figs. 1, 2 (S9076).

Polytremaria beggi Weir
Syntypes, three specimens, none with complete aperture, S9078 (BG7123), S9079 (BG7125), S9080.
Carboniferous, Poolvash Limestone; Balladoole, Isle of Man.
Weir 1925, p. 435, pl. 19, figs. 3, 4.

Portlockia cf. *blanda* (de Koninck)
Two well-preserved specimens, S9082, S9083. In S9082 the outer lip is slightly fractured, and in S9083 it is absent.
Carboniferous, Poolvash Limestone; Balladoole, Isle of Man.
Weir 1925, p. 436, pl. 19, figs. 5, 6 (S9082). Knight 1933, p. 38.

Scalites ambiguus Weir
Holotype, a well-preserved specimen, S9081 (BG7110).
Carboniferous, Poolvash Limestone; Balladoole, Isle of Man.
Weir 1925, p. 437, pl. 19, figs. 8, 9.

Tychonia near *Tychonia omaliana* (de Koninck)
One specimen, S9075 (BG7126).
Carboniferous, Poolvash Limestone; Balladoole, Isle of Man.
Weir 1925, p. 433, pl. 19, fig. 7.

ECHINOIDEA

Ordovician

Aulechinus grayae Bather and Spencer
An external mould of part of a test, E1225 (JLB19), one of the specimens used in description of the species.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
MacBride and Spencer 1938, p. 98, pl. 12, fig. 2.

Ectinechinus lamonti MacBride and Spencer
An external mould of part of a test, E1226 (JLB21), and internal moulds of parts of tests, E1127 (JLB22) and E1232 (JLB26), are part of the material used in the description of this species.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
MacBride and Spencer 1938, p. 99, pl. 12, fig. 4 (E1226), pl. 12, fig. 6 (E1127), pl. 11, fig. 4 (E1232).

Eothuria beggi MacBride and Spencer
Holotype, E1224 (JLB31), internal mould of part of a test, and a portion of its external mould, E1224*a* (JLB30).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
MacBride and Spencer, 1938, pp. 95, 126, pl. 16, figs. 1, 2 (E1224).

CRINOIDEA

Ordovician

Anulocrinus drummuckensis Ramsbottom
Holotype, E3508*a* and E3508*b* (BG9300*b*), counterparts, external moulds of cup and arms.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 9, pl. 2, fig. 9 (E3508*b*), fig. 10 (E3508*a*).

Anulocrinus thraivensis Ramsbottom
Paratypes, E3524 (BG3386) and E3496 (BG3389), both external moulds of cup and arms. The holotype and other paratypes are in the British Museum, and there is also a paratype in the Lamont Collection (Hunterian Museum).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 8, pl. 2, fig. 8 (E3524).

Archaeocrinus elevatus Ramsbottom
Holotype, E3488*a*; paratypes, E3487*a*, E3488*e*, E3513, E3529, E3615; all cups or parts of cups.
Caradoc, Stinchar Limestone Group, *Orthis confinis* Beds; Minuntion, near Girvan.
Ramsbottom 1961, p. 23, pl. 8, fig. 4 (E3488*a*), fig. 2 (E3487*a*), fig. 1 (E3488*e*), fig. 3 (E3615), text-fig. 11, p. 24 (based on E3487*a*, E3488*a*, E3488*e*, E3513, E3529).

Cupulocrinus heterobrachialis Ramsbottom
Holotype, E3614 and E3614*a* (counterparts); paratypes, E3484 and E3484*a* (BG3377 and BG3377*a*) (counterparts), and E3485 (BG3378*a*); all external moulds of stem, cup, and arms.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 12, pl. 5, figs. 1, 2 (E3614*a*), fig. 3 (E3484), fig. 5 (E3485).

Dendocrinus granditubus Ramsbottom
Paratypes, E3509 (BG7948), E3516 (BG3396), E3518 (BG7950), E3603, E3605, all external moulds of the anal tube and parts of the stem, cup, and arms. The holotype is in the British Museum (Natural History).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 15, pl. 4, fig. 1 (E3603), fig. 4 (E3509), fig. 5 (E3518), fig. 6 (E3605), fig. 7 (E3516). (Ramsbottom's fig. 1 and fig. 2 should be interchanged: fig. 1 is the Hunterian paratype, not, as stated by Ramsbottom, the holotype, which is fig. 2.)

Diabolocrinus sp.
Internal and external moulds of part of a large cup, E3504*a* (BG7841*a*) and E3504*b* (BG7841*b*).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 29, pl. 4, fig. 10 (E3504*b*).

Macrostylocrinus cirrifer Ramsbottom
An external mould of stem with cirri, E3492 (BG9451). The holotype and paratypes are in the Lamont Collection (Hunterian Museum).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 20, pl. 6, fig. 11 (E3492).

Protaxocrinus girvanensis Ramsbottom
An external mould of stem, cup, and arms, E3606 (BG9475). The holotype is in the British Museum (Natural History).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 19, pl. 6, fig. 15 (E3606).

Undetermined heterocrinid
An external mould of stem, cup, and arms (E3613).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Thraive Glen (Ladyburn), near Girvan.
Ramsbottom 1961, p. 10, pl. 6, fig. 5.

Carboniferous

Dialutocrinus aculeatus (T. and T. Austin)
A young specimen in side view, E3459.
Tournaisian; Hook Head, Co. Wexford, Eire.
Wright 1955, p. 247, pl. 59, fig. 4.

Dialutocrinus cataphractus (T. and T. Austin)
A young specimen in side view, E3472*a* (BG7349); calyx and arms somewhat crushed, E3473 (BG9467); calyx and arms in side view, E3450 (BG7330).

Tournaisian; Hook Head, Co. Wexford, Eire.
Wright 1955, p. 248, pl. 59, fig. 1 (E3473), pl. 59, fig. 5 (E3472*a*), pl. 64, fig. 3 (E3450).

Holcocrinus smythi (Wright)
Calyx and arms in side view, E3464 (BG9446).
Tournaisian, Supra-Dolomite Beds; Hook Head, Co. Wexford, Eire.
Wright 1952, p. 105, pl. 36, fig. 14.

Onychocrinus hibernicus Wright
Paratypes, E3466 (BG9447), calyx and arms in dorsal view, and E3478 (BG7359), part of calyx and arms in side view.
Tournaisian, Supra-Dolomite Beds; Hook Head, Co. Wexford, Eire.
Wright 1934, p. 261, pl. 15, fig. 1, text-fig. 29 (E3466); 1954, p. 174, pl. 45, fig. 16, text-fig. 93 (E3466).

Ophiurocrinus dactyloides (T. and T. Austin)
Part of calyx and arms in side view, E3467.
Tournaisian; Hook Head, Co. Wexford, Eire.
Wright 1950, p. 21, pl. 6, fig. 3.

Scytalocrinus beggi Wright
Holotype, E3354 (BG8556), calyx and arms in side view.
Viséan, Upper Caninia zone; Cass-ny-hawin, Isle of Man.
Wright 1938*a*, p. 285, pl. 11, fig. 12; 1938*b*, p. 343, pl. 13, fig. 2; 1950, p. 22, pl. 6, fig. 6.

Ulocrinus unciformis (M'Coy)
A cup with two columnals, E3436 (BG7544).
Lower Limestone Group; Corrieburn, Campsie.
Bather 1920, p. 207, text-figs. 1 and 2. Wright 1939, p. 28.

Ureocrinus bockschii (Geinitz)
A calyx and one arm in side view, E3435.
Lower Carboniferous; Penton Linns, Liddesdale.
Wright and Strimple 1945, p. 225, pl. 9, fig. 10.

INCERTAE SEDIS—CYCLOCYSTOIDES

Ordovician

Cyclocystoides decussatum Begg
Syntypes, an almost complete lower plate, E5071 (BG2004), a fragment of its counterpart upper plate, E5071*a* (BG2005), together with two specimens in the Lamont Collection.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Begg 1934, p. 220, pl. 11, fig. 2 (E5071*a*), fig. 3 (E5071).
Part of a lower plate and marginal ring, E5074 (BG9038).
Same horizon and locality.
Begg 1940*b*, p. 24, pl. 1, fig. 3.

Cyclocystoides wrighti Begg
Holotype, E5073 (BG8213) and E5073*a* (BG8213*a*), counterparts, complete upper and lower plates with marginal ring.
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Begg 1940*b*, p. 23, pl. 1, fig. 1 (E5073), fig. 2 (E5073*a*).

CONULARIIDS

Ordovician

Conularia asteroidea Reed
Holotype, a crushed fragment, S9715 (BG2002).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1933, p. 357, pl. 19, figs. 4, 4*a*.

Conularia cunctata Reed
Holotype, a nearly complete specimen, S9714 (BG2310).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1933, p. 357, pl. 19, figs. 3, 3*a–b*.

Conularia mirifica Reed
Holotype, S9711 (BG238).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1933, p. 356, pl. 19, figs. 1, 1*a–b*.

Conularia slateri Reed
Holotype, a crushed specimen, S9710 (BG237).
Ashgill, Upper Drummuck Group, Starfish Bed No. 1; Ladyburn, near Girvan.
Reed 1933, p. 355, pl. 19, figs. 2, 2*a–c*.

Conularia truemani Begg
Holotype, C5980, an almost complete specimen.
Ashgill, Upper Drummuck Group, Starfish Bed a few feet above No. 3; Ladyburn, near Girvan.
Begg 1947, p. 37, pl. 3, figs. 4, 5.

Pseudoconularia currieae Begg
Holotype, C5981 and its counterpart C5981*a*, a large specimen.
Ashgill, Upper Drummuck Group, Starfish Bed a few feet above No. 3; Ladyburn, near Girvan.
Begg 1947, p. 39, pl. 3, fig. 6 (C5981).

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